RELATIONSHIPS BETWEEN HIPPOCAMPAL EEG AND BEHAVIOR IN THE RAT

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SCOPE AND CONTENTS: Relationships between dorsal hippocampal EEG and behavior were studied in the rat. Walking etc. and lever pressing were associated with significantly more hippocampal RSA than operant licking, normal drinking, polydipsic drinking, grooming, saliva spreading and holding still. The results suggested that hippocampal EEG is related to the form of response, rather than to perceptual or sensory processes or to central integrative processes. Furthermore, the results suggested that hippocampal EEG is not related to the operant role of response or to relative intensities of response.

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CHAPTER I

Introduction

The main purpose of the experiments described in this thesis is to study the relationships between the electroencephalographic (EEG) activity of the dorsal hippocampus and behavior in the rat. In research of this type, one is attempting to relate two complex types of phenomena to each other. There are problems in the analysis of each of these phenomena. For example, in the case of EEG, the relationships between the neural events that underlie EEG and different patterns of EEG are not well understood. In the case of complex behavioral processes such as attention, motivation, and learning, it is often difficult to establish clear operational definitions that do not confound one of these processes with any others.

This type of research, therefore, is necessarily beset by many pitfalls. At the same time, certain relationships between EEG and behavior have been established which are theoretically and practically useful. One obvious example is the relationship between cortical EEG patterns and stages of sleep (Milner, 1970). It is hoped that the data that are described in this thesis will help to establish similarly useful relationships between dorsal hippocampal EEG and behavior.

Although the hippocampal formation is a relatively large structure in many mammalian species, its function is not well known. At the same time there is no lack of hypotheses and theories concerning the functional significance of the hippocampus; indeed, there are perhaps too many hypotheses and theories. One possible cause for the proliferation of hypotheses and theories has been the failure to carefully analyze behavioral processes that are correlated with different patterns of hippocampal electrical activity. Suppose, for example, that one observes the development of a particular EEG pattern during the conditioning of an operant response such as lever pressing. One might be tempted to suggest that this EEG pattern reflects the learning process. This may be true; but it may not. Many physiological and behavioral processes change during the course of learning. Examples include the amplitude and topography of the conditioned response, attention to any discriminative stimuli, and the intensity of conditioned anticipatory goal responses. The EEG pattern could be related to any one or all of these processes just as easily as to the learning process. It requires careful analytical experimental procedures to distinguish among these alternatives.

The experiments described in this thesis have been designed in an effort to avoid confounding various physiological and behavioral processes that might be related to specific EEG patterns in the hippocampus. An attempt was made to keep the variables controlling attentional, motivational and associational processes constant while varying the type of response that is reinforced. If the pattern of EEG activity varies as the type of operant response is changed, one

could conclude that these patterns of EEG activity reflect processes associated with the different types of response. If the pattern of EEG activity remains unchanged during the performance of different responses, one could conclude that this pattern of electrical activity is correlated with processes in the conditioning situation other than the type of response.

Hippocampal Anatomy

The hippocampus is a bilaterally symmetrical forebrain structure that lies below the neocortex and is a major component of the oldest and most primitive cortex, the allocortex or archipallium (Grossman, 1967) The left and right hippocampi are joined at their anterio-dorsal regions. From this junction the two separate and extend in a posterior and lateral direction, while at the same time curving downward around the lateral surface of the thalamus. The ventral portions of the hippocampus then curve in an anterior direction and terminate deeply within the temporal lobe.

Organization of neurons within the hippocampus

A coronal section of the dorsal hippocampus reveals an organization that continues through most of the posterior and ventral parts (see Figure 1). The hippocampal formation consists mainly of the hippocampus proper (Cornu Ammonis) and the dentate gyrus. Lorente de No (1934) divided the hippocampal formation into four anatomical regions, CA-1 (Cornu Ammonis 1), CA-2, CA-3, and CA-4. There are two prominent cell layers in the hippocampal formation: the granule cell layer in the dentate gyrus, and pyramidal cell layer which extends through the CA-4, CA-3, CA-2, and CA-1 fields of the hippocampus proper. The axons (mossy fibers) of the dentate granule cells intersect the dendrites of the pyramidal cell layer in the CA-3 and CA-4 fields. Shaeffer collaterals from pyramidal cells in the CA-3 and CA-4 fields intersect the dendrites of pyramidal cells in the CA-1 and CA-2 fields.

Afferent connections to the hippocampus

There are two main afferent pathways to the hippocampus (see Green, 1960; Green, 1964; Raisman, Cowan and Powell, 1965 for reviews). One proceeds from the hypothalamus via the septal area and the dorsal fornix to the hippocampal fimbria. The afferent fibers in the fimbria project primarily to the CA-3 and CA-4 fields of the hippocampus. The second afferent pathway is the perforant tempero-ammonic tract whose fibers originate in the entorhinal cortex and terminate in the CA-3 field of the hippocampus and in the dentate gyrus.

Efferent connections from the hippocampus

Three efferent tracts project from the hippocampus. One efferent pathway passes via the dorsal fornix, while another projects via the hippocampal fimbria. Fibers of these two pathways terminate in a number of areas, including the septum, thalamus, and mamillary nuclei (see Green, 1960; Green, 1964; Raisman, Cowan and Powell, 1966 for reviews). Recently Hjorth-Simonsen (1971) has provided evidence for an efferent pathway originating in the CA-3 field of the hippocampus and terminating in the medial portion of the entorhinal cortex.

Hippocampal EEG-behavior Relationships

A number of hypotheses have been proposed which attempt to relate EEG activities in the hippocampus to psychological and neural processes. One of the EEG patterns that has been studied extensively is a regular, nearly sinusoidal slow wave form, originally designated as a "theta wave" pattern by Jung and Kornmuller (1938), that depends upon the integrated electrical activity of single neurons in or near the pyramidal cell layer in the hippocampus (Von Euler and Green, 1960; Andersen, Eccles, and Loyning, 1964a; Andersen, Eccles, and Loyning 1964b; Fujita and Sato, 1964; Yokato and Fujimori, 1964). The frequency range of this theta wave pattern varies from species to species; for example, in the dog and cat the range is from 4 to 7 Hertz (Hz.) and in the rat 5 to 11 Hz. Stumpf (1965) has suggested that the low frequency EEG patterns derived from the dorsal hippocampal pyramidal cell layer be classified into three main types: (1) the theta wave pattern described above which Stumpf labeled rhythmic slow activity (RSA), (2) large irregular activity (LIA) consisting of irregular high amplitude low frequency waves, (3) small irregular activity (SIA) consisting of irregular low amplitude high frequency waves.

Rather than leading to a consensus, the numerous publications attempting to relate hippocampal EEG to psychological and neural processes have generated a wide variety of hypotheses concerning the functional significance of hippocampal EEG patterns. For the sake of convenience and clarity the hypotheses will be roughly divided into three categories: (1) those which relate hippocampal electrical

activity to perceptual and sensory processes, (2) those which relate it to central integrative processes (cognition, motivation, learning, etc.), (3) those which relate it to output or motor behavior. It is fully realized that these three categories are not precise since each of these categories is not necessarily independent of the others.

I. Hypotheses relating hippocampal electrical activity to sensory and perceptual processing

There are three relevant hypotheses in this category: the arousal hypothesis of Green and Arduini (1954); the orienting response hypothesis of Grastyan, Lissak, Madarasz, and Donhoffer (1959) and Lissak and Grastyan (1960); and the attention hypothesis of Bennett (1970, 1971) and Bennett and Gottfried (1970). Each of these three hypotheses will be discussed separately; a general discussion will conclude this section.

1. Arousal hypothesis of Green and Arduini (1954)

Green and Arduini (1954) proposed that hippocampal RSA was related to arousal produced by electrical stimulation of the brainstem reticular formation, medial thalamus or medial hypothalamus. Electrical stimulation was interpreted as producing effects similar to those produced by normal sensory input. The hypothesis was based on the findings that electrical stimulation of these brain sites produced RSA in the hippocampus and cortical desynchronization in sensory and motor areas. Since cortical desynchronization is thought to be an indicator of arousal, the correlation of hippocampal RSA with cortical

desynchronization was purported to be an indicator of a related arousal process in the paleocortex. Others have also observed that electrical stimulation in the subcortical regions used by Green and Arduini produce hippocampal RSA (Eidelberg, White, and Brazier, 1959; Torii, 1961; Kawamura, Nakamura, and Tokizane, 1961; Petsche, Stumpf, and Gogolak, 1962; Corrazza and Parmeggiani, 1963; Yokota and Fujimori, 1964; Anchel and Lindsley, 1972).

Green and Arduini propose that desynchronization of the cortex and synchronization of the hippocampus represent processes which occur when a normal animal is aroused by some external stimulus. According to this hypothesis, one would always expect cortical desynchronization to be accompanied by hippocampal synchronization during the presentation of an arousing stimulus. Data by Black and Young (1972a), however, indicate that in dogs, either hippocampal synchronization or desynchronization can occur during cortical desynchronization in response to an arousing stimulus. The data of Black and Young seem to indicate that hippocampal synchrony occurs when the animal moves in response to the arousing stimulus and desynchrony occurs when the animal is not moving. This suggests that the hypothesis of Green and Arduini is incorrect.

2. Orienting response hypothesis of Grastyan, Lissak, Madarasz, and Donhoffer (1959) and Lissak and Grastyan (1960)

Grastyan, Lissak, Madarasz, and Donhoffer (1959) and Lissak and Grastyan (1960) proposed that hippocampal RSA was associated with orienting responses during the early stages of learning. Grastyan et al. defined the orienting response in the following manner. Orienting

responses occur during the early stages of conditioning when an animal is learning to associate a stimulus with a reinforcer, or a stimulus with the response that produces reinforcement.[1]

Grastyan et al. reported that in the process of associating an auditory stimulus with either the presentation of food or electric shocks, the first few presentations of the auditory stimulus neither evoked an orienting response toward the source of the sound nor were accompanied by hippocampal RSA. According to Grastyan et al., after a few stimulus presentations the cats began non-specific orienting responses which developed into specific orienting movements toward the source of the stimulus. These orienting responses were correlated with hippocampal RSA. Finally, as the conditioned responses became well-established and the orienting responses gradually diminished, hippocampal RSA gradually diminished and finally disappeared. Thus, it was proposed that hippocampal RSA was associated with a temporary learning process during which the animals were orienting toward the external enviroment and attempting to determine the functional significance of the auditory stimuli. This led the authors to postulate that desynchronized electrical activity in the hippocampus plays a part in the inhibition of orienting responses and that hippocampal RSA reflects a lack of such inhibition.

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[1] Note that this definition of orienting responses is different from that proposed by many other psychologists, such as Pavlov (1927). For Pavlov, orienting responses were responses to any stimuli, particularly novel stimuli. There was no limination to the early stages of learning. The hypothesis that orienting responses of this type are correlated with hippocampal RSA is discussed in Section 3.

Since the orienting response as defined by Grastyan et al. is not necessarily behaviorally observable, the hypothesis that RSA is correlated with orienting responses is difficult to test directly. The hypothesis would be supported indirectly, however, by demonstrating that orienting responses and consequently the occurrence of hippocampal RSA decrease as a function of learning. Evidence against the orienting response hypothesis of Grastyan et al. includes the report that hippocampal RSA did not disappear during repeated performances of a well-established approach response by cats in an alley runway to obtain food rewards (Adey, 1966; Adey, Dunlop, and Hendrix, 1960); and the report that well-established approach responses in the runway situation were accompanied by higher frequency RSA than approach responses early in training (Elazar and Adey, 1967).

3. Attention hypothesis of Bennett (1970,1971) and Bennett and Gottfried (1970)

Bennett (1970, 1971) and Bennett and Gottfried (1970) suggested that hippocampal RSA reflects an alert or attentive state of an animal. It was reported that hippocampal RSA accompanied orienting responses (Bennett, 1970; Bennett and Gottfried, 1970); was elicited by the onset of a buzzer which immediately preceded an S^D in the presence of which cats could lever press for milk rewards (Bennett, 1970); and followed non-rewarded responses during non-S^D periods in a discrimination procedure (Bennett, 1970). Bennett et al. seem to be defining orienting responses in a manner similar to that used by Pavlov (1927).[1] It is also apparent that Bennett et al. are employing orienting responses as an index of attention.

The attention hypothesis predicts that alert or attentive states and, therefore, hippocampal RSA may occur when animals are motionless. The already mentioned data of Black and Young (1972a) do not confirm this prediction. Furthermore, orienting responses are usually detected by observing correlated skeletal movements towards a sudden change in environmental stimuli such as the buzzer used by Bennett (1970). Such signals may elicit preparatory behaviors in anticipation of subsequent S^D presentations; thus, the occurrence of hippocampal RSA reported by Bennett et al. may be associated with either orienting responses or preparatory behaviors.

4. General Discussion

In summary, the hypotheses relating hippocampal electrical activity to sensory or perceptual processes do not seem to be viable for two reasons. First, there are many data that are inconsistent with the predictions. For example, the arousal hypothesis of Green and Arduini (1954) predicts a correlation between hippocampal RSA and cortical desynchronization; the orienting response hypothesis of Grastyan et al. (1959) predicts that the occurrence of hippocampal RSA should diminish after the establishment of a well-conditioned response; and the attention hypothesis of Bennett (1970) predicts that attentive animals should produce hippocampal RSA while motionless. None of these predictions was supported by the data. Second, the sensory and perceptual processes to which the hippocampal RSA is believed to be related are confounded with movement because orienting

responses are usually defined in terms of overt movement. Therefore, whenever RSA is correlated with sensory and perceptual processes it is also correlated with movement, and one cannot conclude that the causal relationship is with one, or the other, or both, or neither.

II. Hypotheses relating hippocampal electrical activity to central integrative processes

There seem to be two appropriate subdivisions in this category: hypotheses relating hippocampal EEG to motivation, and hypotheses relating hippocampal EEG to learning and information processing. Each subdivision will be discussed separately, followed by a general discussion.

1. Hypotheses relating hippocampal electrical activity to motivation

Three hypotheses will be discussed in this section: a revised orienting response hypothesis by Grastyan, Karmos, Vereczkey, and Kellenyi (1966); the motivation hypothesis of Konorski, Santibanez-h and Beck (1968); and the frustration hypothesis of Gray (1970).

(1.) Revised orienting response hypothesis of Grastyan, Karmos, Vereczkey, and Kellenyi (1966)

The original orienting response hypothesis of Grastyan, Lissak, Madarasz, and Donhoffer (1959) was later modified (Grastyan, Karmos, Vereczkey, and Kellenyi, 1966) by associating hippocampal RSA with orienting responses linked to what Grastyan et al. called low intensity nonspecific motivational processes. In their paper Grastyan et al. (1966) reported an experiment in which cats had the opportunity to terminate electrical stimulation of the hypothalamus by depressing

a metal plate in the experimental chamber. Relatively low intensity stimulation values at many brain sites produced hippocampal RSA below 6 Hz. and orienting-like approach ("pull") behaviors to the metal plate. If the cats terminated the low intensity stimulation, a rebound EEG desynchronization occurred along with an avoidance or "push" response from the metal plate. Under this condition, according to Grastyan et al., cats developed a pronounced avoidance of the metal plate during stimulation as indicated by the development of longer latencies from the onset of stimulation to the depression of the metal plate. In many cases, relatively higher intensity stimulation at the same brain sites produced a desynchronized hippocampal EEG pattern and a decrease in latencies from the onset of the stimulation to the depression of the metal plate. In this case, the offset of stimulation produced a rebound RSA pattern and cats remained on the plate. Thus, according to Grastyan et al., a desynchronized EEG pattern was accompanied by avoidance of or a "push" away from the metal plate, and an RSA pattern was accompanied by a "pull" to the plate.

In the interpretation of their results Grastyan et al. (1966) noted that Sohnierla (1959) had proposed in his revised "biphasic" theory of motivation that weak stimuli elicit approach behaviors and that strong stimuli elicit withdrawal behaviors. and that Olds and Olds (1963) had discovered that self-stimulation sites, including those in the hypothalamus, can be either positively or negatively reinforcing. Taking everything into consideration, Grastyan et al. proposed that the hypothalamus might be the site of two basic non-

specific and mutually opposed motivational mechanisms, and that the hippocampus might be part of a negative feedback system regulating this hypothalamic system. Thus, a mild "non-specific motivational" state induces an inhibition of the hippocampus that is correlated with hippocampal RSA, the release of orientation responses, and "pull" behaviors. A more intense "non-specific motivation" in the hypothalamic system induces hippocampal desynchronization and "push" behaviors.

The definitions of "push" and "pull" behaviors as employed by Grastyan et al. (1966) are not particularly clear; this lack of clarity makes it difficult to test the hypothesis. The revised hypothesis of Grastyan et al. (1966) does seem to predict, however, that escape and avoidance behaviors should be accompanied by a desynchronized hippocampal EEG pattern, while approaches toward pleasant situations should be accompanied by hippocampal RSA. Routtenberg and Kramis (1968) reported that hippocampal RSA produced by aversive electrical brain stimulation in unrestrained rats was correlated with avoidance and escape behaviors. Pond and Schwartzbaum (1970) have reported similar results. Therefore, the hypothesis of Grastyan et al. (1966) was not supported, at least in these two experimental situations.

(2.) Motivation hypothesis of Konorski, Santibanez-h, and Beck (1968)

Konorski, Santibanez-h, and Beck (1968) proposed that increases in hippocampal RSA frequency, not the mere occurrence of RSA, were correlated with arousal produced by drive states. Konorski et al. required dogs to pedal press fourteen times in the presence of an S^D

in order to produce a second stimulus of fixed duration that terminated with the delivery of food. The highest frequency of hippocampal RSA occurred during the pedal press S^D. If the dogs did not move during the stimulus associated with food deliveries, the RSA frequency decreased from that during the pedal press S^D. The experimenters explained that the pedal press S^D was associated with an arousal state produced by a hunger drive. The pedal pressing and high frequency RSA were considered to be an expression of that arousal. In contrast, it was proposed that the consummatory act of eating activated anti-drive brain centers related to states of satisfaction which, in turn, were reciprocally related to the hunger drive state. Since the stimulus associated with food deliveries was also associated with a state of satisfaction, the hunger drive would be reduced in its presence and the frequency of any correlated hippocampal RSA would decrease.

Another explanation of the data might be that the higher frequency RSA was related to the motor act of pedal pressing and the lower frequency RSA with the absence of movement. The data of Black and Young (1972a) is relevant at this point. In their study, dogs that were required to pedal press during an S^D to avoid shocks displayed hippocampal RSA. When the same dogs were required to hold still during a second S^D to avoid shocks, they displayed hippocampal LIA or SIA. If one accepts the view that the dogs were motivated to respond correctly in the presence of both S^D's, it could be concluded that the hippocampal EEG varied with the type of response rather than with the relative degree of motivation.

(3.) Frustration hypothesis of Gray (1970)

Gray (1970) and Gray and Ball (1970) observed that in rats 7.5 to 8.5 Hz. hippocampal RSA accompanied exploration of a new enviroment, 8.5 to 10.0 Hz. RSA was associated with running down an alley toward a known reward, 6.0 to 7.5 Hz. RSA along with superimposed high frequency activity occurred during the consumption of these rewards, and 7.5 to 8.5 Hz. RSA was correlated with behaviors produced by frustrative non-reward. Gray (1970) postulated that 7.5 to 8.5 Hz. RSA is associated with exploration or with the behavioral process produced by frustrative non-reward during extinction. Thus, according to Gray, 7.5 to 8.5 Hz. RSA should interact with this behavioral process. For example, the occurrence of relatively more 7.5 to 8.5 Hz. RSA during a specified unit of time should enhance this behavioral process, while the absence of 7.5 to 8.5 Hz. RSA should interfere with this behavioral process.

Gray presented three main types of support for his hypothesis. First, the production of 7.7 Hz. hippocampal RSA by electrical stimulation of the septal area during the extinction of a conditioned response enhanced the rate of extinction, while septal driving of 7.7 Hz. hippocampal RSA during the acquisition of a conditioned response on a crf schedule of reinforcement enhanced responding during extinction. Gray called this enhancement of responding a "pseudo partial reinforcement effect." Second, the prevention of the possible occurrence of 7.7 Hz. hippocampal RSA by either medial septal lesions or by high frequency electrical stimulation of the medial septal area blocked the establishment of any partial reinforcement effect. Third, low doses of sodium amobarbital which attenuated the frustration re-

actions to the extinction of a conditioned response also increased the frequency of septal stimulation necessary to produce 7.7 Hz. hippocampal RSA.

Since Gray employs skeletal movement as an indicator of frustration during extinction, it seem possible that he has confounded the inferred frustration process with increases in general motor activity that commonly accompany extinction. A crucial test of Gray's hypothesis would be to produce frustration in an animal that is motionless. If such frustration were accompanied by hippocampal RSA, one could argue that RSA accompanied that frustration. If such frustration were not accompanied by hippocampal RSA, one could argue that RSA is related to general motor activity. This proposed test of Gray's hypothesis has not been done.

2. Hypotheses relating hippocampal electrical activity to learning and information processing

Three hypotheses will be discussed in this section: the sensory processing hypothesis of Pickenhain and Klingberg (1967), the information processing hypothesis of Elazar and Adey (1967), and the central processing hypothesis of Routtenberg (1968a, 1971).

(1.) Sensory processing hypothesis of Pickenhain and Klingberg (1967).

Pickenhain and Klingberg (1967) proposed that hippocampal

RSA appears in situations in which current sensory information is being compared with formerly stored sensory information. It was reported that hippocampal RSA accompanied "motivated" behaviors such as "non-automatized motor acts" which include orienting responses and freezing before the initiation of a conditioned avoidance response. These situations were purported to require information processing of sensory data. Hippocampal RSA did not accompany "automatized" behaviors such as drinking and scratching. These behaviors presumably do not require any processing of sensory information since they are instinctive or prewired behaviors and are presumed by many to be unlearned responses and not dependent on learning processes.

It would seem that the hypothesis of Pickenhain and Klingberg would predict the occurrence of hippocampal RSA when current sensory information is being compared with formerly stored sensory information independent of the presence or absence of movement. However, dogs that were required to hold still during an S^D to avoid shocks displayed non-RSA hippocampal patterns (Black and Young, 1972a). A more parsimonious explanation for the observations of Pickenhain and Klingberg might be that hippocampal RSA accompanies "non-automatized" motor acts and other hippocampal EEG patterns accompany "automatized" behaviors.

(2.) Information processing hypothesis of Elazar and Adey (1967)

Elazar and Adey (1967) proposed that the hippocampus is involved in information processing, decision making, and memory consolidation during the learning of a conditioned behavior. In their experiment, cats were trained to run down an alley in the presence

of an S^D to obtain food rewards. Spectral analyses of the hippocampal EEG indicated a predominance of 4 Hz. activity during pre-S^D periods, a concentration of 5 Hz. activity during the initial portion of the S^D presentations, a 6 Hz. predominance during the approach response to the goal area, and a concentration of 4 to 5 Hz. activity during eating. These differences in EEG associated with different aspects of the experimental paradigm became more distinct as learning proceeded. This was interpreted as an indicator of information processing, decision making, and memory consolidation.

Charles Hatfield (personal communication) replicated the study of Elazar and Adey using the same alley length and conditioning procedure. Elazar and Adey collected their EEG samples for spectral analyses in 1.5 second epochs, one immediately preceding the S^D, one during the first 1.5 seconds of each S^D presentation, and others during subsequent 1.5 second periods. Hatfield found that early in training the cats spent from 2 to 3 seconds running down the alley. The EEG during the first 1.5 seconds of each S^D was, therefore, associated with running, while the EEG associated with the following 1.5 seconds was associated with not only running, but also with stopping at the end of the alley and eating. Later in training, the cats spent around 1.5 seconds running down the alley. The EEG samples dur- the first 1.5 seconds of the S^D were, therefore, associated with running (at a faster speed than earlier in training), while the EEG associated with the following 1.5 seconds was associated with stopping and eating. If the faster frequency hippocampal RSA were associated with faster running, the differences in the behaviors occurring during the 1.5 second epochs at the beginning and ending of training could

account for the shifts in the power spectral peaks, rather than information processing, decision making, and memory consolidation.

(3.) Central processing hypothesis of Routtenberg (1968a, 1971)

A series of studies by Routtenberg and colleagues (Routtenberg, 1968a; Routtenberg and Kramis, 1968; Kramis and Routtenberg, 1969; Routtenberg, 1970) resulted in the formulation of the hypothesis that hippocampal RSA was associated with assessment of the rewarding or aversive qualities of reinforcements. At the same time, it was proposed that non-RSA patterns were associated with the modulation of organized motor acts. In these studies both positively and negatively reinforcing subcortical electrical stimulation produced hippocampal RSA patterns in rats and gerbils. At the same time, the positivity or negativity of the reinforcing stimulus was behaviorally defined. In the Routtenberg and Kramis (1968) study the aversiveness of the electrical brain stimulation was determined by avoidance and escape behaviors as was the case in the Pond and Schwartzbaum (1970) study. Furthermore, rewarding stimulation in the gerbils (Kramis and Routtenberg, 1969) was self-administered as a consequence of operant lever pressing. Thus, the hippocampal activity believed to be associated with assessing the reinforcing qualities of stimuli may have, in fact, been associated with the overt behaviors used to define these qualities. In support of this view, data by Paxinos and Bindra (1970) can be cited which show that no RSA occurs when the subject is required to hold still during positively reinforcing brain stimulation.

Routtenberg (1968b, 1971) extended his hypothesis by suggesting that the hippocampus modulates two subcortical arousal systems, one being linked to the reticular formation, the other to the limbic system. It was suggested that the reticular formation system is involved in the response organization and execution of "automatic" behaviors such as grooming and drinking, and that hippocampal EEG desynchronization indicates an active functional role of the hippocampus in this system. It was also proposed that the limbic system is involved in the processing of stimulus information and the presence of hippocampal RSA indicates an active functional role of the hippocampus in this system.

The hypothesis of Routtenberg predicts that hippocampal RSA should occur when an animal is motionless, if that animal were processing stimulus information. The data of Paxinos and Bindra (1970) and Black and Young (1972a), again, do not support such a hypothesis.

3. General Discussion

In summary, the hypotheses relating hippocampal electrical activity to central integrative processes seem to have two major faults. First, there are data that do not support the predictions. For example, the revised orienting response hypothesis of Grastyan et al. (1966) predicts that "push" or avoidance behaviors should be correlated with hippocampal non-RSA patterns; the motivation hypothesis of Konorski et al. (1968) predicts that hippocampal RSA should accompany states of high levels of arousal, even if subjects are motionless; the frustration hypothesis of Gray (1970) predicts that frustrative non-reward situations should be accompanied by hippocampal RSA, even if

the subjects are motionless; and the sensory processing hypothesis of Pickenhain and Klingberg (1967) or the central processing hypothesis of Routtenberg (1968a, 1971) predict that any processing of sensory information should be correlated with hippocampal RSA, even if the subjects are motionless. Data, contrary to these predictions, have been cited. Second, the suggested associations of hippocampal RSA with central integrative processes are confounded with movement. Examples include the pedal pressing or skeletal activity of the dogs in the Konorski et al. (1968) study; the possibility that skeletal behaviors accompanied frustration (Gray, 1970); the avoidance and escape behaviors of the rats in the Routtenberg and Kramis report (1968); the behavioral correlates of hippocampal EEG observed by Pickenhain and Klingberg (1967); and the goal oriented running of cats (Elazar and Adey, 1967). In these examples, with the exception of Gray (1970), overt movement was used as an index of the activation of the inferred central integrative processes.

III. Hypotheses relating hippocampal electrical activity to output or motor functions

Four hypotheses will be discussed in detail in this section: the goal-oriented hypothesis of Adey, Dunlop, and Hendrix (1960), the triggering of voluntary movement hypothesis of Vanderwolf (1967, 1968, 1969, 1971), the brainstem reticular formation (BSRF)activation hypothesis of Klemm (1970, 1971, 1972a, 1972b), and the rhythmic driving hypothesis of Komisaruk (1970). Other output hypotheses will be briefly discussed.

1. Goal-oriented hypothesis of Adey, Dunlop, and Hendrix (1960)

Adey, Dunlop, and Hendrix (1960) proposed that, in the cat, 5 to 6 Hz. dorsal hippocampal RSA was a correlate of the execution of a planned or goal-oriented motor act. Ventral hippocampal RSA accompanied initial searching and investigating behaviors in the experimental chamber, but the RSA eventually disappeared and no clear relationship existed between ventral hippocampal EEG and overt behavior. Dorsal hippocampal RSA accompanied initial searching and investigating behaviors, and also accompanied the running of the cats down an alley to obtain food rewards. Similar differences between dorsal and ventral hippocampal EEG patterns and behavioral correlates have been reported by Black and Young (1972a) with dogs.

This hypothesis seems too restrictive since behaviors that are not part of a well-planned or goal-oriented sequence of responding have been reported to be associated with hippocampal RSA (for example, Vanderwolf, 1971).

2. Triggering of voluntary movement hypothesis of Vanderwolf (1967, 1968, 1969, 1971)

Vanderwolf (1967, 1968, 1969, 1971) observed that in normal awake rats dorsal hippocampal RSA accompanies "voluntary phasic skeletal" activities such as walking, running, or lever pressing; dorsal hippocampal LIA accompanies consummatory behaviors involving considerable skeletal activity such as eating, drinking, and grooming, and accompanies sustained intervals of immobility, even though this

immobility may involve considerable isometric muscle tension such as clinging to the edge of a table by the forepaws; dorsal hippocampal SIA accompanies the abrupt cessation of movement. Similar observations have been reported for the rat by Pickenhain and Klingberg (1967), Routtenberg (1968b), Routtenberg and Kramis (1968), Irmis, Madlafousek and Hlinak (1970), Paxinos and Bindra (1970), Routtenberg (1970), Bland (1971), Whishaw and Vanderwolf (1971), Bland and Vanderwolf (1972a), Bland and Vanderwolf (1972b), and Whishaw, Bland, and Vanderwolf (1972); for the gerbil by Kramis and Routtenberg (1969) and Whishaw (1972); for the guinea pig by Sainsbury (1970); and for the dog by Black, Young, and Batenchuk (1970), and Black and Young (1972a). Vanderwolf also observed that gross movements were accompanied by higher mean frequencies and higher amplitudes of RSA than slight movements.

On the basis of such data, Vanderwolf (1967, 1968, 1969, 1971) proposed that the hippocampus is part of a triggering mechanism that is involved in the initiation of voluntary movement. Furthermore, Vanderwolf suggested that an increase in the frequency of dorsal hippocampal RSA precedes the initiation of voluntary movements.

Other studies have described a high correlation between relatively higher frequency hippocampal RSA and voluntary phasic skeletal behavior in rats (Bremner, 1964; Vanderwolf and Heron, 1964; Gray, 1970; Gray and Ball, 1970; Teitlebaum and McFarland, 1971), in dogs (Yoshii, Shimokochi, Miyamoto, and Ito, 1966; Ellison, Humphrey, and Feeney, 1968; Dalton and Black, 1968; Lopes da Silva and Kamp, 1969; Kamp, Lopes da Silva and Storm van Leeuwen, 1971), in cats (Holmes and Beckman,

(1969), and in rabbits (Drewczybski and Traczyk, 1968; Harper, 1971). The hypothesis of Vanderwolf predicts that voluntary phasic skeletal movement should always be accompanied by hippocampal RSA. However, several investigators have reported the occurrence of voluntary phasic skeletal movement without a correlated hippocampal RSA pattern, for example, Brown (1968).

3. BSRF activation hypothesis of Klemm (1970, 1971, 1972a, 1972b)

Klemm (1970, 1971, 1972a, 1972b) has proposed that dorsal hippocampal RSA in rabbits and rats is related to BSRF activation and non-specific muscle tone increases produced by such activation, and, in some instances, to the enhancement of spinal reflexes.

One problem with this hypothesis is that consummatory behaviors are associated with BSRF activation and muscle tone increases; consummatory behaviors have been reported to be correlated with non-RSA hippocampal patterns (for example, Pickenhain and Klingberg, 1967; Routtenberg, 1968; Vanderwolf, 1971). Furthermore, as already mentioned, Konorski et al. (1968) reported that dogs displayed relatively lower frequency RSA when immobile than when lever pressing. Ellison et al. (1968) demonstrated in another study, that with the same paradigm used by Konorski et al., dogs displayed muscle tone increases during the immobility.

4. Rhythmic driving hypothesis of Komisaruk (1970)

Komisaruk (1970) postulated that hippocampal RSA is related to a limbic-hypothalamic system involved in the rhythmic driving of

motor neurons. This hypothesis was based on the observation in rats of a high correlation between the frequency of hippocampal RSA and the rhythm or rate of vibrassae movements during exploration. However, Whishaw and Vanderwolf (1971) and Whishaw, Bland, and Vanderwolf (1972) have reported that phasic relationships between hippocampal RSA frequencies and rhythmic behaviors such as licking, sniffing, shivering, face washing or heart rate are not consistent. Thus, the hypothesis of Komisaruk does not have any generality.

5. Other output hypotheses

Other motor or output hypotheses have been proposed for the functional significance of the hippocampus which do not attempt to deal with the various EEG patterns of the pyramidal cell layer. For example, Olds (1969) has postulated that the CA-1 field of the hippocampus is concerned with motor functions, and Kilmer and McLardy (1970) have suggested that the CA-3 field of the hippocampus is involved in the "selection of species typical acts," while Douglas (1967) and Kimble (1968) have proposed an inhibitory role for the hippocampus based upon the extensive hippocampal lesion literature. In regard to the latter hypothesis, hippocampectomized animals perform poorly on tasks requiring the absence of movement, delayed responding, and alternation of responding. In addition, hippocampectomized animals show a perseverance of behavior in reversal paradigms, extinction procedures, and reactions to novel stimuli. This inhibition theory seems compatible with other output or motor hypotheses if one assumes that a hippocampal SIA or LIA pattern reflects active

inhibition and a RSA pattern reflects the absence of such inhibition. (The lesioning data will not be extensively reviewed in this thesis because the emphasis of this thesis is on the EEG correlates of behavior.)

6. General Discussion

In summary, the goal-directed hypothesis of Adey, Dunlop, and Hendrix (1960) seems too restrictive. For example, behaviors that are not a part of a well-planned or goal-oriented sequence of responding have been reported to be associated with hippocampal RSA. In contrast, those hypotheses proposed by Klemm (1970, 1971, 1972a, 1972b) and Komisaruk (1970) are based on relationships between EEG and specific behaviors and lack general support. In the case of Klemm's proposal, increases in muscle activity can occur during periods of relative immobility and during behaviors such as drinking; these conditions are associated with non-RSA patterns. With respect to Komisaruk's hypothesis, rhythmic licking, sniffing, shivering, face washing, and heart rate can occur without being in phase with hippocampal RSA. In turn, Vanderwolf's hypothesis does not predict that voluntary phasic skeletal movements should occur without correlated high frequency RSA.

One might expect that the correlation between RSA and various types of behavior would show the same sorts of "confounding" that were described earlier in this Chapter. That is because sensory processes, central integrating processes, and observable behavior usually occur together; when RSA is correlated with one it is also correlated with the others. This problem is found for many of the

experiments that had been referred to in the previous sections. There are two experiments, however, which have avoided the problem, at least in part. In one experiment, Black and Young (1972a) trained dogs to pedal press or hold still in order to avoid electric shocks. In a second experiment, Paxinos and Bindra (1970) required rats to remain immobile in order to receive positive brain stimulation. In both cases RSA was correlated with form of response rather than some some other process.

This conclusion is consistent with two types of hypotheses. The first is that RSA represents some process in the hippocampus which is part of the motor control system. Vanderwolf, for example, as noted earlier, has suggested that RSA represents the activation of a triggering system for certain responses. Second, the results are consistent with the hypothesis that RSA represents some non-motor process, such as attention or motivational arousal, which is only activated during the occurrence of certain types of movement.

IX. General Conclusions

For all of the hypotheses that have been described in preceding sections of this Chapter, data can be cited which seem to contradict predictions derived from the hypotheses. In some cases, of course, reasonable explanations could be suggested to account for the discrepancies. For example, on the basis of histological data the failures to observe RSA during the occurrence of voluntary movement may have been observed because the recording electrodes were not placed across or near the pyramidal cell layer of the dorsal hippocampus (Green, Maxwell, Schindler and Stumpf, 1960). In other cases, such explanations are more difficult to suggest.

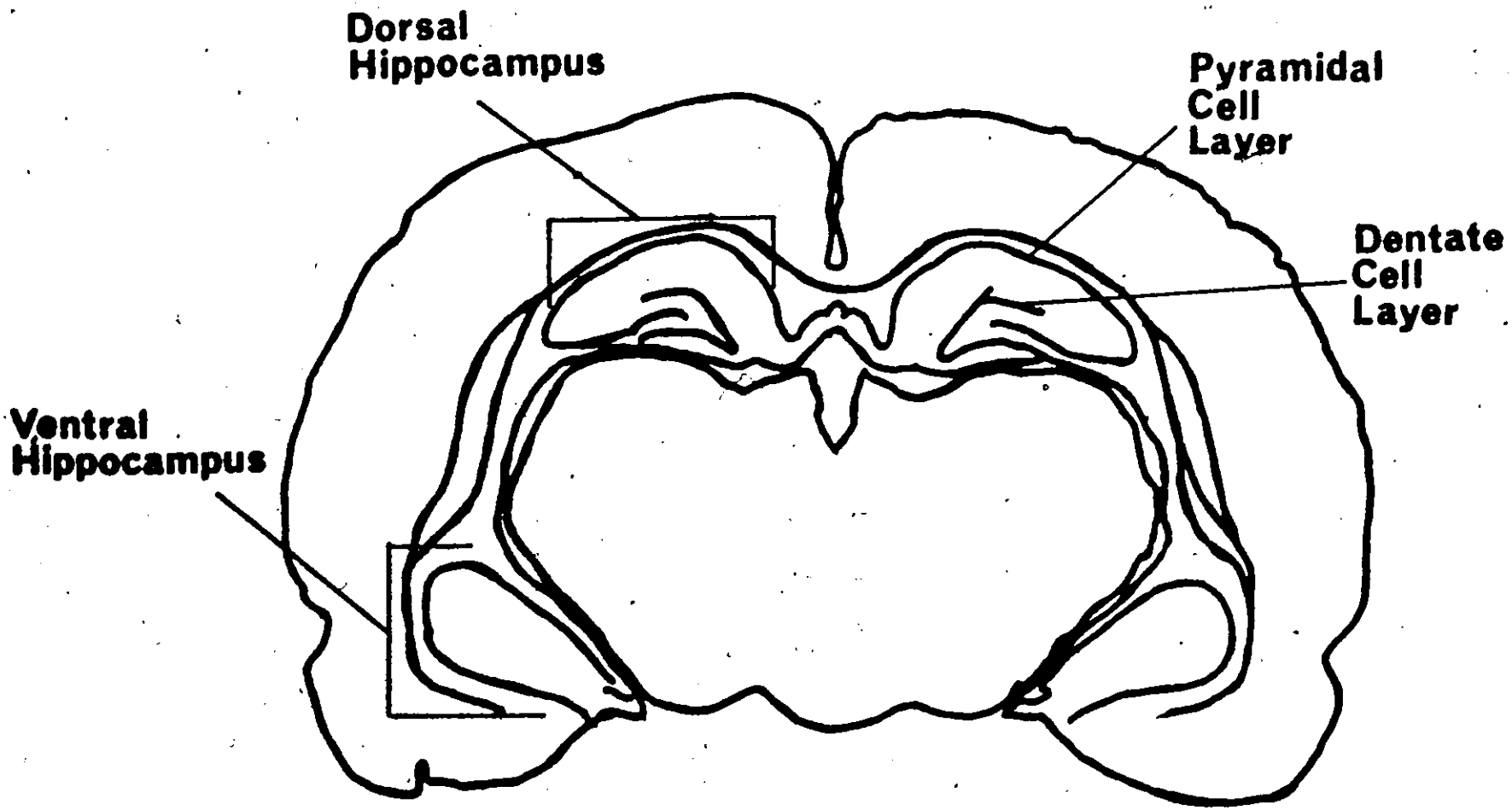
The main problem, however, in attempting to distinguish among these hypotheses arises from the confounding between the types of processes to which the hippocampal RSA is supposed to be related. In most experiments, sensory processes, central integrative processes and movement processes occur at the same time. Therefore, one could argue that RSA was related to any or all of them. In one previous experiment, Black and Young attempted to compare conditions in which motivational and sensory processes were held constant and the response was allowed to vary (Black and Young, 1972a). Dogs were trained to press a pedal to avoid shock in the presence of one S^D, and to refrain from movement to avoid shock in the presence of another S^D. Paxinos and Bindra (1970) employed a similar paradigm to study the relationship of brain stimulation to hippocampal EEG. The results of these experiments indicated that the hippocampal RSA was related to the type of

response rather than to these other processes.

The present thesis was carried out in order to provide further data using a paradigm identical to that employed in the previous Black and Young experiment. In this case, an attempt was made to extend the range of responses that were studied. In the previous experiment, lever pressing and holding still were compared. In this thesis, lever pressing and operant licking are compared. The purpose of the various experiments in the thesis are described in more detail at the beginning of each Chapter.

Figure 1

Coronal section of the rat brain, 3.4 mm. anterior to the interaural line.


Dorsal
Hippocampus
Pyramidal
Cell
Layer
Dentate
Cell
Layer
Ventral
Hippocampus

CHAPTER II

Experiment 1

The purpose of Experiment 1 was to determine whether dorsal hippocampal RSA is related to the type of response or to some other factor in the conditioning situation. This was accomplished by varying the type of operantly conditioned response (lever pressing versus licking) and attempting to hold constant those variables that might affect sensory and perceptual processes and central integrative processes (variables such as type of discriminative stimulus, number and type of reinforcements, parameters of conditioning). Licking and lever pressing were chosen as the operant responses because previous studies have indicated that dorsal hippocampal RSA accompanies operant lever pressing (Bremmer, 1964) and that dorsal hippocampal LIA accompanies normal drinking for water regulation (Vanderwolf, 1971).

If one found that hippocampal RSA occurred during operant lever pressing but not during operant licking, one could conclude that the RSA was related to the type of response. If this were the case, the next step would be to attempt to determine the property or properties which distinguish RSA correlated responses from non-RSA correlated responses. For example, the distinguishing property might be, as Vanderwolf (1971) has suggested, that RSA is related

to "voluntary phasic skeletal" movements and that non-RSA is related to "automatic" responses.

If one found that hippocampal RSA occurred during both operant lever pressing and operant licking, there are at least two possible conclusions. First, RSA could be related to some process in the conditioning situation other than type of response. It might for example, be related to attentional or motivational processes regardless of what the operantly conditioned response happened to be. Second, RSA could be related to the role of a response. In this case the responses would be classified according to their role in operant conditioning situations. That is, RSA might accompany operant responses, but not non-operant responses. Further research would be required in order to choose among these alternatives.

Method

Subjects

The subjects were seven experimentally naive male hooded rats (SA-1, SA-2, SA-4, F-1, F-2, F-3, and F-5) from the Quebec Breeding Farms and one experimentally naive male Sprague-Dawley rat (SA-3), each weighing approximately 275 grams at the beginning of the experiment. Each rat was individually housed and Purina rat chow and water were available at all times in the home cages, except during deprivation schedules that will be described later in this section.

Apparatus

The experimental chamber consisted of a modified Gerbrands Model C Skinner box. The inside dimensions measured 7 1/2 inches long, 8 inches wide, and 7 3/8 inches deep. The grid floor consisted of 3/16 inch diameter stainless steel bars, 1/2 inches apart. The Skinner box was situated on a table, 3 feet in height, located in the rear of a sound attenuated and electrically shielded room that was 9 feet wide, 12 feet long, and 8 feet high. The room was illuminated with eight 100 watt incandesent bulbs, electrically shielded with metal screening.

A retractable lever was located in the center of the right hand wall of the Skinner box, 3 inches from the grid floor. Twenty to 25 grams of force were required to operate the lever and during shock avoidance sessions each operation of the lever resulted in a

0.5 second retraction of the lever. A drinking tube attached by a rubber stopper to a 250 ml. glass bottle was placed 1/4 of an inch behind the inner surface of the right hand wall and in the middle of a 1 inch diameter circular hole that was 1 3/8 inches from the front of the Skinner box and 4 inches from the grid floor. The drinking tube was made from 3/8 inch inter diameter glass tubing drawn to a 1/4 inch aperture at the tip. A fine tungsten wire in the center of the tubing was part of a BRS-Foringer drinkometer circuit that employed the grid floor of the Skinner box as an electrical ground. A contact of the rat's tongue with a liquid in the glass tube completed the drinkometer circuit. Feedback from each lick was provided by a brief closure of a C.P. Clare 24VDC 300 ohm relay.

During avoidance sessions 150 msec. shocks were delivered by a modified Grason-Stadler E7110A recording attenuator which delivered shocks on a linear scale from zero to 1.0 ma. Before shocks were delivered an Ashman Electronic (Greenville, Ontario) custom-made 18 point relay switched the ground of the drinkometer out of the circuit and the output of the shock generator into the circuit. This prevented interactions between the shock and drinkometer circuits.

During the food reinforcement sessions the feeder, which was a part of the original Gerbrands Model C Skinner box, was removed from its original location and placed inside the Skinner box in the left lower corner of the right hand panel. The top and sides of the original feeder were removed; the feeder was secured to the grid floor. This was done so that the rats could easily pick up

food rewards while they were connected to the EEG recording system. During water reinforcement sessions a Lehigh-Valley 1527 liquid reinforcement feeder was mounted on the Skinner box in the right corner of the back wall so that the delivery spout was located 3 inches from the right hand corner and 1/2 of an inch from the grid floor.

Discriminative stimuli were provided by a 75 decibel (db; re: 0.0002 dynes/cm^2) click generator operating at a frequency of 5 Hz. (BRS-Foringer) and an audio oscillator pulsing at 1800 Hz. (BRS-Foringer), both operating through a 3 1/2 inch diameter, 4 ohm speaker located 1 1/2 inches in back of the right hand wall of the Skinner box. A third S^D was a flashing 12VDC lamp (Canadian Tire Corporation # 1072) located over the center of the top of the Skinner box which was on for 1 second and off 1 second.

Recording was carried out with a Gerbrands six pen event recorder and a Grason-Stadler printout counter (E12505A). Sessions were monitored with a Sony Video Camera (DXC-2000) and Sony 110 monitor; terminal performance sessions were videotaped with a Sony EV-210 videocorder.

EEG activity of hippocampal sites was recorded on a Grass Model 5 polygraph with Grass Model 5P5 preamplifiers. EEG was also recorded with the use of Model R5DC Reverters on an Ampex SP-300 Recorder/Reproducer and subjected to spectral analyses on a Digital Equipment Corporation PDP-8i computer equipped with an extended memory. The EEG was filtered between 1.5 Hz. and 15 Hz.

Surgical procedure

The rats were anesthetized with 4 mg./kg. of sodium pentobarbital (Nembutal, 60 mg./ml.) supplemented with 22 mg./kg. of chloral hydrate (400 mg./ml. of distilled water). Both were injected intraperitoneally. Supplementary doses of 0.05 ml. of each were given whenever necessary. In addition, 0.05 ml. of atropine sulfate in isotonic saline solution were administered intramuscularly (0.004 mg./ml.) and 2% xylocaine hydrochloride (Astra) was injected subcutaneously over the entire surface of the skull.

After placing each rat in a Krieg Model 51200 sterotaxic instrument, the dorsal surface of the skull was exposed, and holes were drilled with a #11 dental burr to receive the electrodes. At least four stainless steel jeweler's screws (#P52-10 from the Lomat Watch Material Co., Montreal, P.Q.) were inserted in the skull. One was employed as a ground and a second as a reference for monopolar electrodes.

Seven rats (SA-1, SA-2, SA-3, SA-4, F-1, F-3, and F-5) were implanted with monopolar electrodes -- stainless steel insect pins (Size 00 from Peder-Pedersen Ltd., Guelph, Ontario) covered with Insul-x except for a 0.5 mm. section at the tip. One rat (F-2) was implanted with bipolar electrodes. The tips of the electrodes were 1.0 mm. apart horizontally and 1.0 mm. apart vertically. Each electrode was connected via 0.010 inch diameter nichrome wire (Driver Harris Co., Harrison, N.J.) into an Amphenol 220-801 female pin. The electrodes were lowered sterotaxically into both sides of the dorsal

hippocampus (3.0 mm. posterior to bregma, 2.0 to 2.5 mm. lateral, 3.5 mm. vertical from the surface of the skull) with the aid of the atlas by de Groot (1959). The Amphenol 220-S01 pins were inserted into a proper length of Amphenol 221-2253 connector strip and the strip along with the jeweler's screws were imbedded in dental cement. Immediately after surgery, each animal was injected intramuscularly with 0.2 cc. of Strepenalean suspension (MTC Pharmaceuticals Ltd.).

Histological procedure

After the completion of data collection, each rat was sacrificed with an overdose of sodium pentobarbital (Nembutal) and immediately perfused intracardically with isotonic saline, followed by 10% Formalin. Serial coronal sections, 100 u thick, were mounted on microscopic slides, and stained with thionin. The electrode tip locations were microscopically verified from the slides.

Training procedure

The eight rats were divided into two groups. One group (SA-1, SA-2, SA-3, and SA-4) was operantly conditioned to lever press at one time and to lick at another time in order to avoid electric shocks. A second group (F-1, F-2, F-3, and F-5) was operantly conditioned to lever press and to lick in order to receive positive reinforcements (food and water). One rat in each group was trained in a discrimination procedure, and three rats in each group were trained in a sequential procedure.

1. Discrimination procedure: avoidance

SA-1 was initially trained, employing a shaping procedure, to avoid shocks on a Sidman schedule by drinking 10% sucrose (weight/volume) in the presence of an S^D (see Table 1). The response lever was kept fully retracted during this portion of the experiment. The response-shock interval was 10 seconds and the shock-shock interval was 1.35 seconds. The first shock in each S^D presentation was scheduled to occur 10 seconds after the S^D onset. During shaping and training SA-1 was 22 hours water deprived and was allowed access to water in the home cage for 1 hour immediately after each experimental session. During each session, three to eight separate S^D's were presented. Interstimulus intervals (ISI's) were five minutes. During each S^D period, the shock level began at an intensity of zero and increased linearly during 108 seconds of cumulative shock-shock time to a maximum of 1.0 ma. Shock durations were 150 msec.

After stable levels of licking to avoid shocks were established, SA-1 was then trained to avoid shocks in the presence of a second S^D by pressing the retractable lever. The parameters of the Sidman schedule were the same as those used for the licking response. The drinking tube was removed during this portion of the training.

After stable levels of lever pressing were established, a final phase of training was begun. SA-1 was presented with the S^D's for lever pressing and licking in a random order during each session; thus, the response lever and drinking tube were available at all times and the procedure required a discrimination between the two S^D's and

Table 1

Experimental Histories of Sidman Avoidance Group

Lever Pressing Sessions

Rat	Total Sess.	S^D	Total S^D's	Total Shocks
SA-1	17*	Flashing Light	89	2326
SA-2	6	Flashing Light	47	1472
SA-3	6	Tone	48	2842
SA-4	4	Flashing Light	32	4029

Operant Licking Sessions

Rat	Total Sess.	S^D	Total S^D's	Total Shocks
SA-1	19*	Clicker	80	1839
SA-2	3	Clicker	18	533
SA-3	6	Clicker	48	4097
SA-4	2	Clicker	14	911

*A discrimination procedure was employed in the last ten sessions; both lever press S^D's and lick S^D's were presented randomly.

the two responses. (See Tables 1 and 2 for the description of each S^D for all rats in this Experiment.)

After stable levels of discriminated responding were established, SA-1 was tested in a single recording session. In this session two S^D's of each type were presented with the same response requirements and schedule parameters as those in the preceding training sessions. This was followed by three presentations of each type of S^D in extinction during which scheduled shocks were not delivered. During this recording session hippocampal EEG was recorded and overt behavior was videotaped.

2. Discrimination procedure: positive reinforcement

F-1 was initially trained, employing a shaping procedure, to obtain 50 mg. Noyes pellets by licking deionised water in the presence of an S^D (see Table 2). F-1 was maintained at 80% of its normal body weight; appropriate amounts of Purina rat chow required to maintain this level were dispensed in the home cage immediately after each training session. A variable ratio schedule of reinforcement with an average requirement of 16 responses was employed. 128 second S^D presentations alternated with 128 second ISI's. An average of 10 S^D's were presented during each session. The response lever was completely retracted at all times during the training of licking.

After operant licking had stabilised, a second S^D was introduced. During this second S^D the rat was trained to lever press on a variable ratio schedule of reinforcement with an average requirement of 16 responses to obtain 50 mg. Noyes pellets. The drinking tube

Table 2

Experimental Histories of Positive Reinforcement Group

Lever Pressing Sessions

Rat	Total Sess.	S^D	Total S^D's	Total Food S^R's	Total Water S^R's
F-1	6*	Clicker	58	730	
F-2	11	Clicker	60	379	
F-3	8	(Free operant procedure)			434
F-5	7	(Free operant procedure)			353

Operant Licking Sessions

Rat	Total Sess.	S^D	Total S^D's	Total Food S^R's
F-1	11*	Flashing Light	52	1023
F-2	7	Tone	75	364
F-3	11	Tone	110	1017
F-5	8	Tone	80	713

*A discrimination procedure was employed in the last three sessions; both lever pressing S^D's and licking S^D's were presented randomly.

was removed during the training of lever pressing. The lever did not retract during this or any positive reinforcement situation.

In the final stages of training, F-1 was presented with both S^D's in a random order during each session; thus, the response lever and drinking tube were available at all times and the procedure required a discrimination between the two S^D's and the two responses.

After stable levels of discriminated responding were established, F-1 was run in a single recording session during which hippocampal EEG was recorded and overt behavior videotaped. The experimental parameters employed during the recording session were the same as those used in the training sessions.

3. Sequential procedure: avoidance

SA-3 was trained to lick 10% sucrose in the presence of one S^D in order to avoid electric shocks, and, then to lever press in the presence of a second S^D in order to avoid electric shocks (see Table 1). The Sidman avoidance schedule parameters were the same as those employed for SA-1, except that the ISI's were 128 seconds. Furthermore, SA-3 was trained with one S^D and one response and then switched to another S^D and response in a sequential manner; a discrimination procedure was not employed. After stable levels of responding were established, SA-3 was tested in two recording sessions during extinction; one after stabilized licking and another after stabilized lever pressing.

SA-2 and SA-4 were trained in the reverse order; that is, lever pressing was trained first as an avoidance response and licking was

trained second.

4. Sequential procedure: positive reinforcement

F-2 was trained first to lever press in the presence of one S^D in order to obtain food reinforcements, then, to lick deionized water in the presence of a second S^D in order to obtain food reinforcements (see Table 2). The schedule of reinforcement parameters were the same as those employed for F-1, except that F-2 was trained with one S^D and one response and then switched to another S^D and response in a sequential manner; a discrimination procedure was not employed. After stable levels of responding were established, F-2 was tested in two recording sessions; one after stabilized licking and another after stabilized lever pressing.

F-3 and F-5 were initially trained, employing a shaping procedure, to obtain 0.1 ml. water reinforcements in a free operant procedure (no S^D's) by lever pressing on a variable ratio schedule of reinforcement requiring an average of 16 responses. The rats were run after 22 hours of water deprivation and were allowed one hour of free access to water in their home cages immediately after each training session. Each training session was terminated after approximately 50 reinforcements had been obtained. F-3 and F-5 were then trained to lick for food in the same manner as that employed for F-2; recording sessions were conducted for F-3 and F-5 in a similar manner as those for F-2.

Results

The operant responses

There are two questions which must be asked about the behavioral data. First, were the probabilities of lever pressing and licking modified by the reinforcement contingencies? That is, were the two responses under operant control? Second, were the two responses under S^D control at the end of training?

1. Discrimination procedures

Acquisition: The percentage of the total possible programmed shocks that were actually received during the first and last training sessions for SA-1 are shown in Table 3. If a rat did not respond at all during a single S^D presentation, the rat could receive a total of 215 shocks. An analysis of variance was carried out with all four avoidance rats in order to compare the per cent of shocks received. The main factors were the responses and the training sessions. The difference between the first and last training sessions was significant at the 0.001 level. The difference between the responses and the interaction factor were not significant.

The average number of reinforcements that were received per S^D presentation during the first and last training sessions for F-1

Table 3

Percent of Shocks Received $\left(\frac{\text{Shocks Received}}{\text{Total Possible Shocks}}\right) \times 100$ During Training Sessions

Rat	Lever Pressing		Operant Licking	
	First	Last	First	Last
SA-1	75.6	10.2	98.2	3.6
SA-2	93.5	9.8	63.1	8.8
SA-3	80.8	25.5	95.4	35.4
SA-4	91.3	16.4	86.4	23.9
Means	85.3	15.5	85.8	17.9

$F_{response} = 0.06$, df = 1, 3, $p > 0.20$

$F_{session} = 7.63$, df = 1, 3, $p < 0.001$

$F_{response \times session} = 0.02$, df = 1, 3, $p > 0.20$

are shown in Table 4. (Analyses of variance were not carried out with the positive reinforcement group since two animals had no S^D's associated with the lever pressing.) These data indicate that learning occurred since the number of reinforcements that were received increased from the first training session to the last. Licking apparently had an advantage over lever pressing in producing more reinforcements per unit time.

S^D control: The terminal response rates of SA-1 and F-1 during the acquisition sessions, which immediately preceded the recording sessions, are shown in the top sections of Tables 5 and 6. Lever pressing and licking rates during S^D presentations and ISI's are shown. Discriminative stimulus control was assessed by computing the response rate during each S^D presentation and during an equivalent period of time in each ISI. Analyses of variance were carried out by comparing these lever pressing rates during the lever pressing S^D's with lever pressing rates during licking S^D's and ISI's; licking rates were similarly analyzed. If the homogeneity of variance hypothesis was not rejected at the 0.05 significance level, the data were analyzed with t^2 statistical tests; if the homogeneity of variance hypothesis was rejected at the 0.05 level, the data were analyzed with a variation of the student's t statistical test (t' test) in which the critical values were approximated as suggested by Winer (1962).

For F-1, lever pressing rates during lever pressing S^D's were significantly greater than rates during licking S^D's ($p < 0.005$) and

Table 4

Average Reinforcements Per S^D During Training Sessions

	Lever Pressing		Operant Licking	
Rat	First	Last	First	Last
F-1	0.3	12.6	2.2	19.7
F-2	1.1	3.7	1.5	18.8
F-3	---*	---*	1.2	6.3
F-5	---*	---*	0.7	6.6
Means	0.7	8.2	1.4	12.9

*The lever pressing of F-3 and F-5 was during free operant situations; there were no S^D's.

Table 5

Average Operant Response Rates of Sidman Avoidance Group (Responses/Minute)

Discrimination Procedure (SA-1)			Statistical Tests
Lever Presses			
S^DLP	S^DLick	ISI	S^DLP vs. ISI ($t^2 = 34.24$, df = 10, $p < 0.01$)
9.1	3.3	1.2	S^DLP vs. S^DLick ($t^2 = 3.28$, df = 6, $p > 0.05$)
Operant Licks			
S^DLick	S^DLP	ISI	S^DLick vs. ISI ($t' = 5.02$, df = 11, $p < 0.005$)
70.0	12.4	18.2	S^DLick vs. S^DLP ($t^2 = 11.88$, df = 6, $p < 0.05$)

Sequential Procedure (SA-2, SA-3, SA-4)					Statistical Tests
	Lever Presses		**Operant Licks**		
Rat	S^DLP	ISI	S^DLick	ISI	
SA-2	13.7	6.0	61.9	37.0	S^DLP vs. ISI ($t' = 2.65$, df = 9, $p < 0.025$)
					S^DLick vs. ISI ($t^2 = 41.73$, df = 10, $p < 0.01$)
SA-3	5.5	0.4	41.5	3.6	S^DLP vs. ISI ($t' = 12.95$, df = 9, $p < 0.005$)
					S^DLick vs. ISI ($t' = 2.83$, df = 8, $p < 0.025$)
SA-4	18.0	10.2	78.9	31.6	S^DLP vs. ISI ($t^2 = 58.56$, df = 14, $p < 0.01$)
					S^DLick vs. ISI ($t^2 = 396.04$, df = 10, $p < 0.01$)

Table 6

Average Operant Response Rates of Positive Reinforcement Group (Responses/Minute)

Discrimination Procedure (F-1)			Statistical Tests
Lever Presses			
S^DLP	S^DLick	ISI	S^DLP vs. ISI ($t' = 10.32$, $df = 7$, $p < 0.005$)
95.6	20.4	3.8	S^DLP vs. S^DLick ($t^2 = 42.05$, $df = 6$, $p < 0.005$)
Operant Licks			
S^DLick	S^DLP	ISI	S^DLick vs. ISI ($t^2 = 50.00$, $df = 10$, $p < 0.005$)
138.2	1.2	27.9	S^DLick vs. S^DLP ($t' = 11.91$, $df = 3$, $p < 0.005$)

Sequential Procedure (F-2, F-3, F-5)					Statistical Tests
	Lever Presses		Operant Licks		
Rat	S^DLP	ISI	S^DLick	ISI	S^DLP vs. ISI ($t^2 = 3.54$, $df = 16$, $p < 0.05$)
F-2	27.0	19.5	142.2	120.4	S^DLick vs. ISI ($t^2 = 1.51$, $df = 16$, $p > 0.125$)
F-3	23.2*		47.7	17.6	S^DLick vs. ISI ($t' = 2.34$, $df = 12$, $p < 0.025$)
F-5	28.2*		50.6	30.1	S^DLick vs. ISI ($t^2 = 6.36$, $df = 18$, $p < 0.025$)

*Free Operant Rates

the rates during ISI's ($p < 0.005$). For SA-1, lever pressing rates were significantly greater during lever pressing S^D's than the lever pressing rates during ISI's ($p < 0.01$), but not during licking S^D's. For both rats, licking rates were significantly greater during licking S^D's than the rates during liver pressing S^D's ($p < 0.05$ or better) and during ISI's ($p < 0.005$).

These results indicate that there was discriminative stimulus control in all cases in which S^D rates were compared with ISI rates, and in all but one case in which S^D rates for one response were compared with rates during the other S^D.

One could argue that the responses were under the discriminative control of reinforcement presentations rather than under the control of S^D's. That is, when an S^D was presented, the rat may have attempted both responses and continued with the response that was reinforced. Analysis of the avoidance responding does not support this suggestion. SA-1 displayed the appropriate response to the S^D before any shocks occurred in seven out of eight S^D presentations (three lever pressing S^D's and four of four licking S^D's). F-1, however, displayed the appropriate response first in only five of eight S^D presentations (three of four lever pressing S^D's and two of four licking S^D's).

2. Sequential procedures

Acquisition: The percentage of the total possible shocks that were actually received during the first and last training session

are shown in Table 3. Previously described analyses of variance indicated that learning occurred since the number of shocks that were received was significantly reduced from the first sessions to the last. Also, there appeared to be no advantage of one response over the other in efficiency of avoiding shocks.

The average number of reinforcements that were received per S^D presentation during the first and last training sessions are shown in Table 4. These data indicate that learning occurred since the number of reinforcements received per S^D increased from the first training sessions to the last. Also, the data of all four positive reinforcement animals indicated that there was no advantage of one response over the other in producing a particular number of reinforcements per S^D.

S^D control: The terminal response rates of the subjects during the acquisition sessions that immediately preceded the recording sessions, are shown at the bottom of Tables 5 and 6. The response rates were analyzed by comparing lever pressing rates during lever pressing S^D's with lever pressing rates during ISI's; licking rates were similarly analyzed.

For four of four rats, lever pressing rates during lever pressing S^D's were significantly greater than rates during ISI's ($p < 0.05$ or better). For five of six rats, licking rates were significantly greater during licking S^D's than the rates during ISI's ($p < 0.025$ or better).

These results indicate that there was discriminative stimulus control in nine of ten cases in which S^D rates were compared with ISI

rates.

Electrical activities of the hippocampus

1. EEG samples and the histology

EEG samples of 25 seconds in duration were selected according to criteria which are described later in the section on spectral analyses. Representative samples of approximately 12 seconds in duration were chosen from these 25 second samples. Two representative samples are shown for each rat in Figures 2 through 16; one for each of the two bilaterally implanted electrodes.[1]

Visual inspection of these sample records, of videotapes of concurrent behavior, and of the histology[2] indicates the following for 13 cases in which all three types of data were available:

(1) When the rats displayed overt behaviors such as walking and rearing, dorsal hippocampal RSA was recorded from nine electrode placements, while relatively less RSA was recorded from four electrode placements during similar behaviors.

(2) When the rats were lever pressing, dorsal hippocampal RSA was recorded from the same nine electrode placements. The correlation of lever pressing RSA was not as high

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[1]The EEG of the left hippocampus of F-2 is not shown. The recording from this electrode contained high frequency artifact. This was probably due to a broken connection.

[2]The histology of SA-2 was not available because this animal was accidently discarded. The electrode placements were determinated with the aid of the atlas of Pellegrino and Cushman (1967).

Figure 2

Left dorsal hippocampal EEG samples of SA-1 from the discriminated Sidman avoidance session.

RAT SA-1

LEFT HIPP.

DISC. SESS.

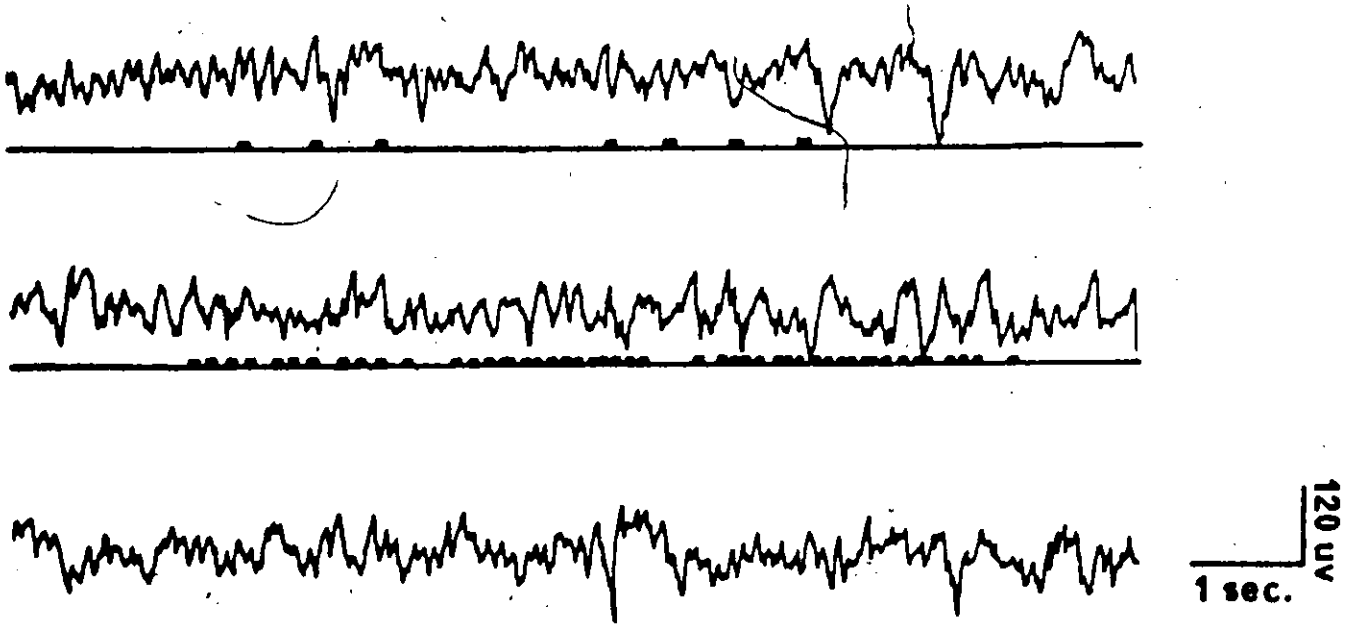


Figure 3

Right dorsal hippocampal EEG samples of SA-1 from the discriminated Sidman avoidance session.

RAT SA-1

RIGHT HIPP.

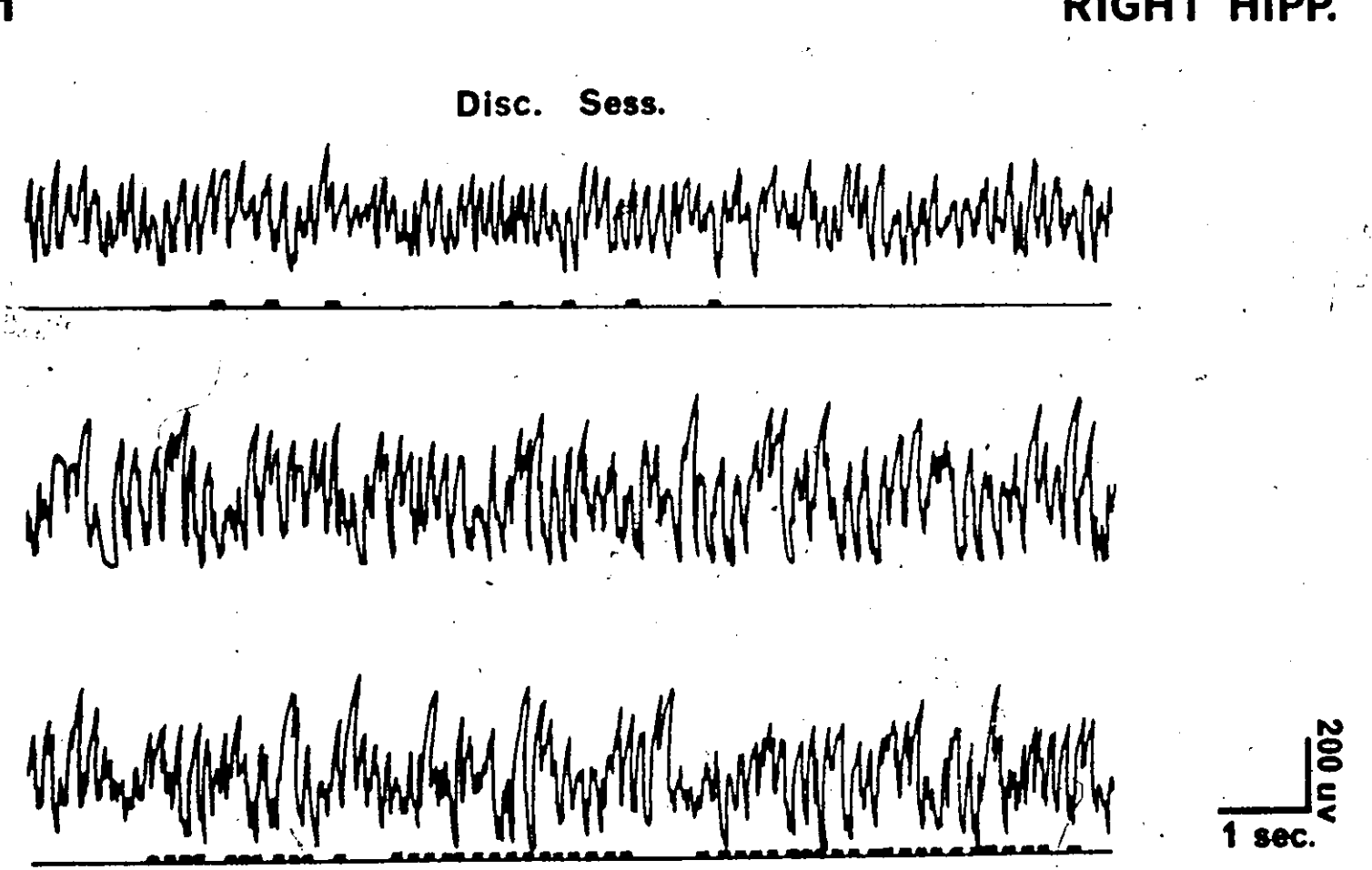


Figure 4

Left dorsal hippocampal EEG samples of SA-2 during Sidman avoidance sessions.

RAT SA-2

LEFT HIPP.

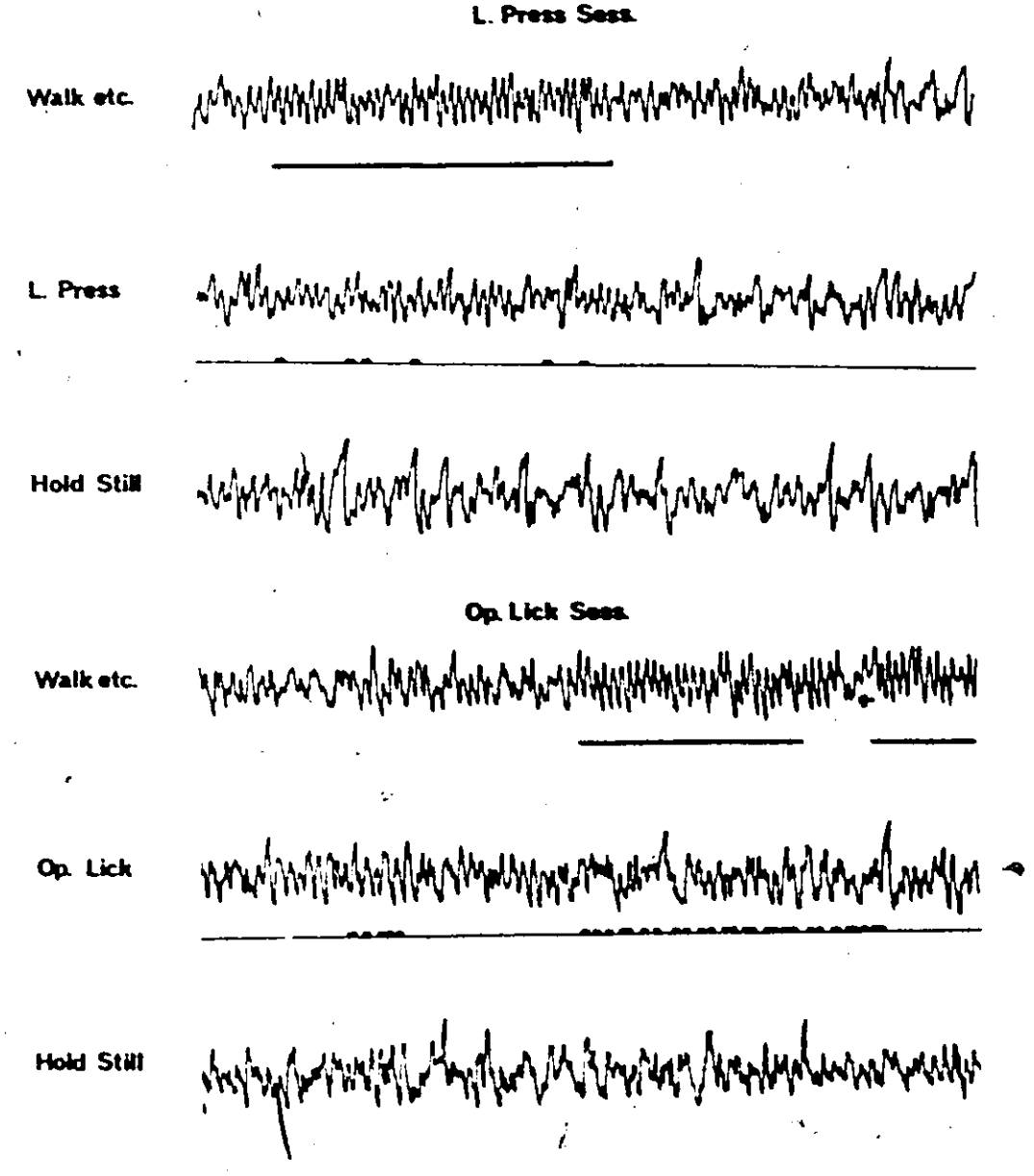


Figure 5

Right dorsal hippocampal EEG samples of SA-2 during Sidman avoidance sessions.

RAT SA-2

RIGHT HIPP.

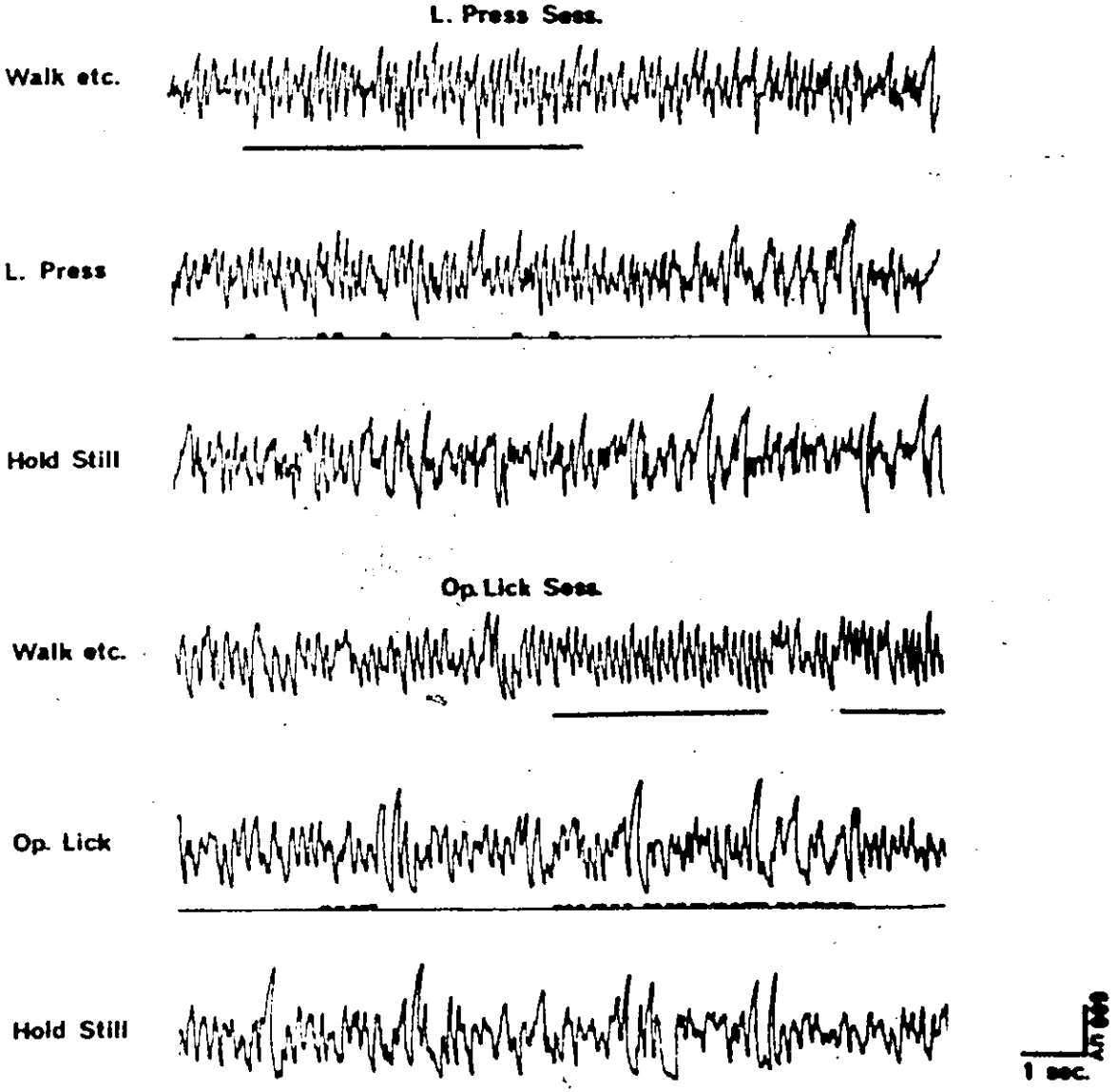


Figure 6

Left dorsal hippocampal EEG samples of SA-3 during Sidman avoidance sessions.

RAT SA-3

LEFT HIPP.

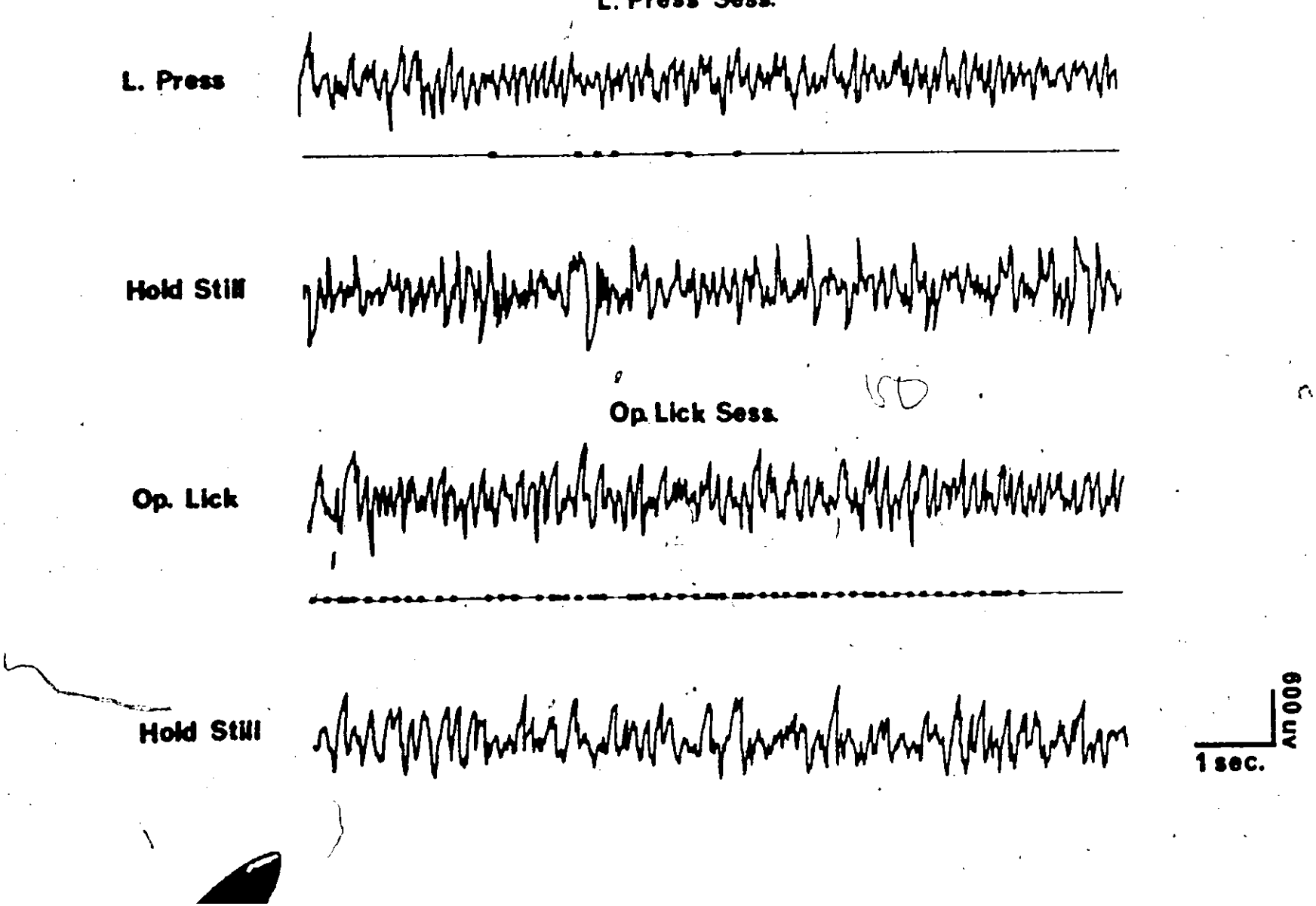
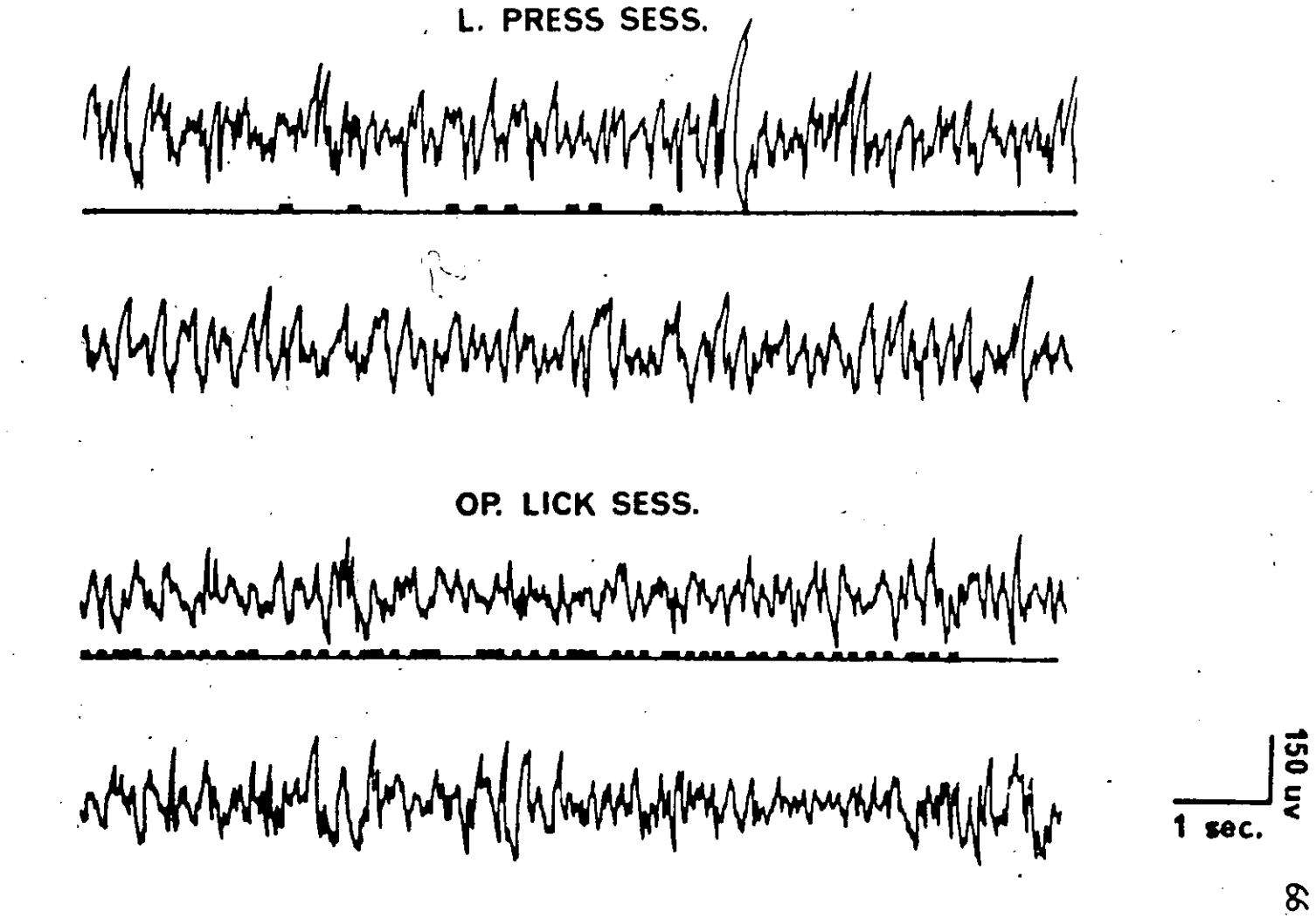


Figure 7

Right dorsal hippocampal EEG samples of SA-3 during Sidman avoidance sessions.

RAT SA-3

RIGHT HIPP.



66

Figure 8

Left dorsal hippocampal EEG samples of SA-4 during Sidman avoidance sessions.

RAT SA-4 LEFT HIPP.

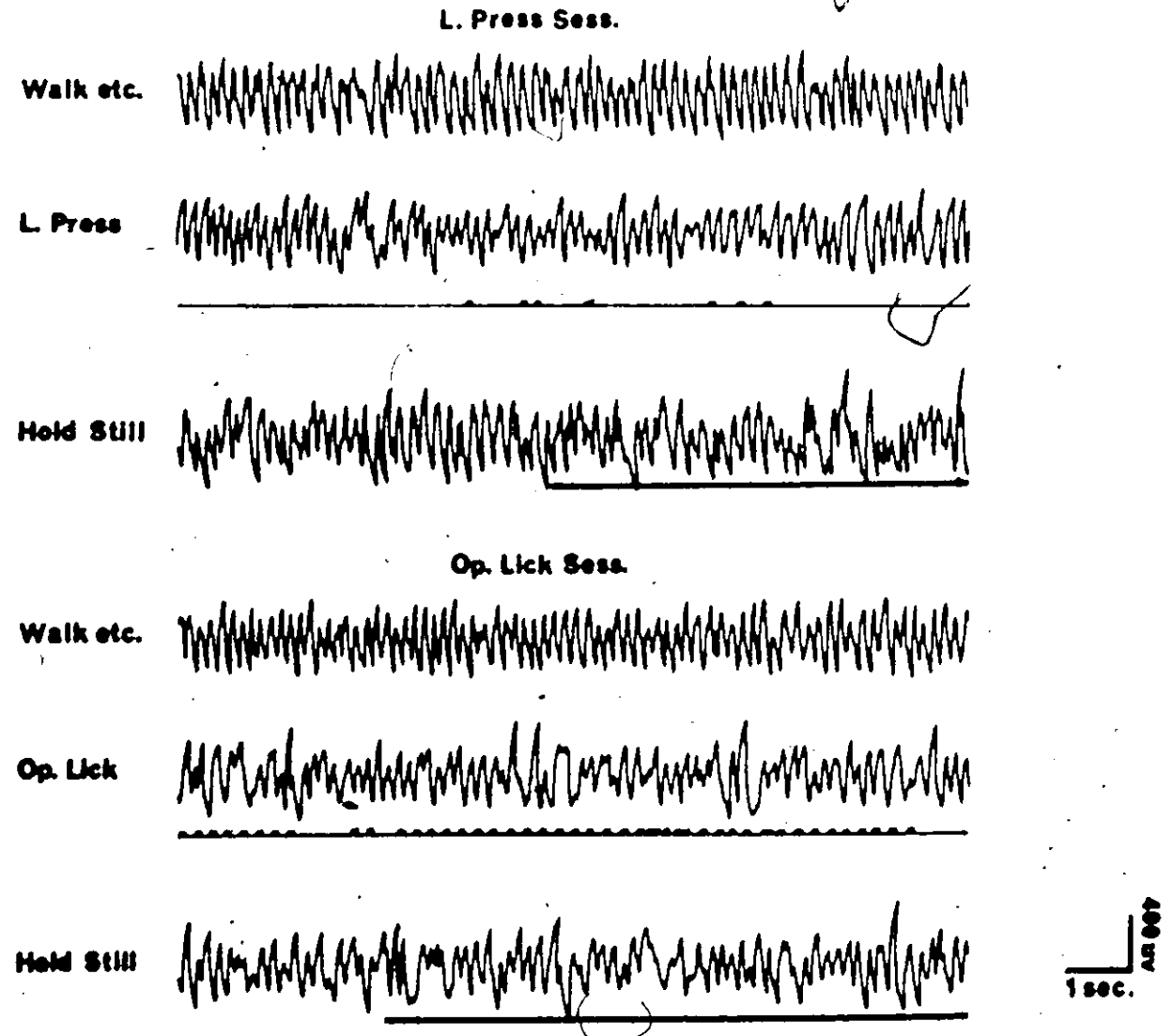


Figure 9

Right dorsal hippocampal EEG samples of SA-4 during Sidman avoidance sessions.

RAT SA–4

RIGHT HIPP.

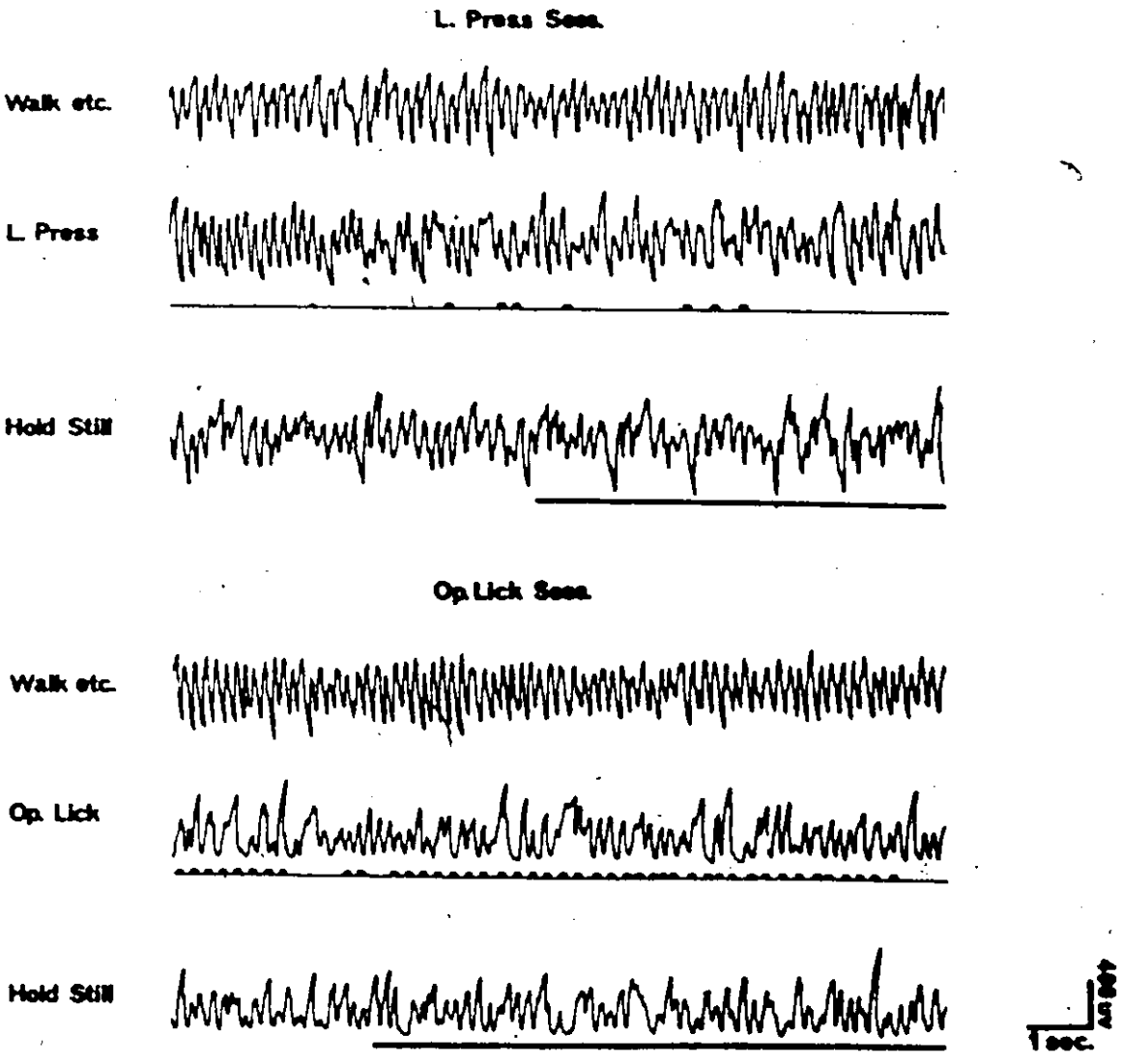


Figure 10

Left dorsal hippocampal EEG samples of F-1 during the discriminated positive reinforcement session.

RAT F-1

LEFT HIPP.

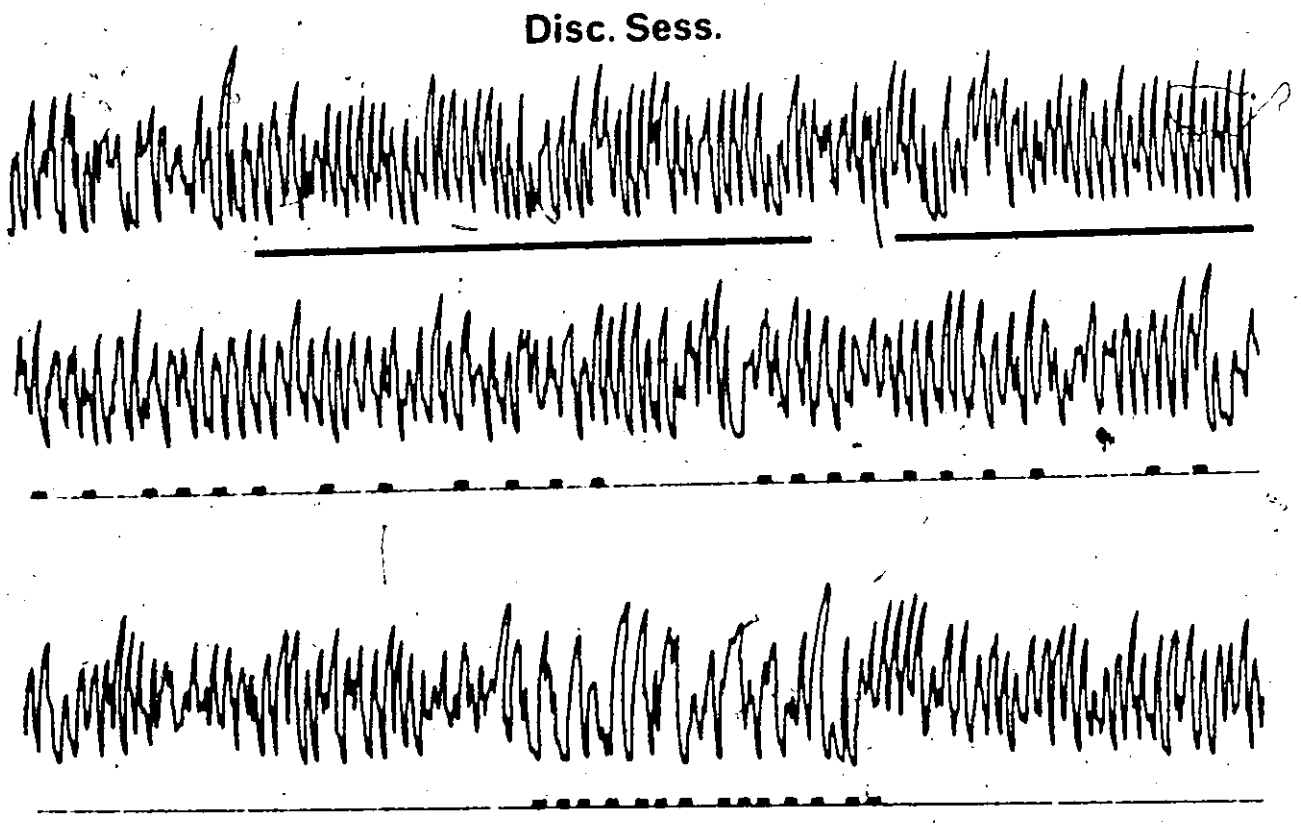


Figure 11

Right dorsal hippocampal EEG samples of F-1 during the discriminated positive reinforcement session.

RAT F-1

RIGHT HIPP.

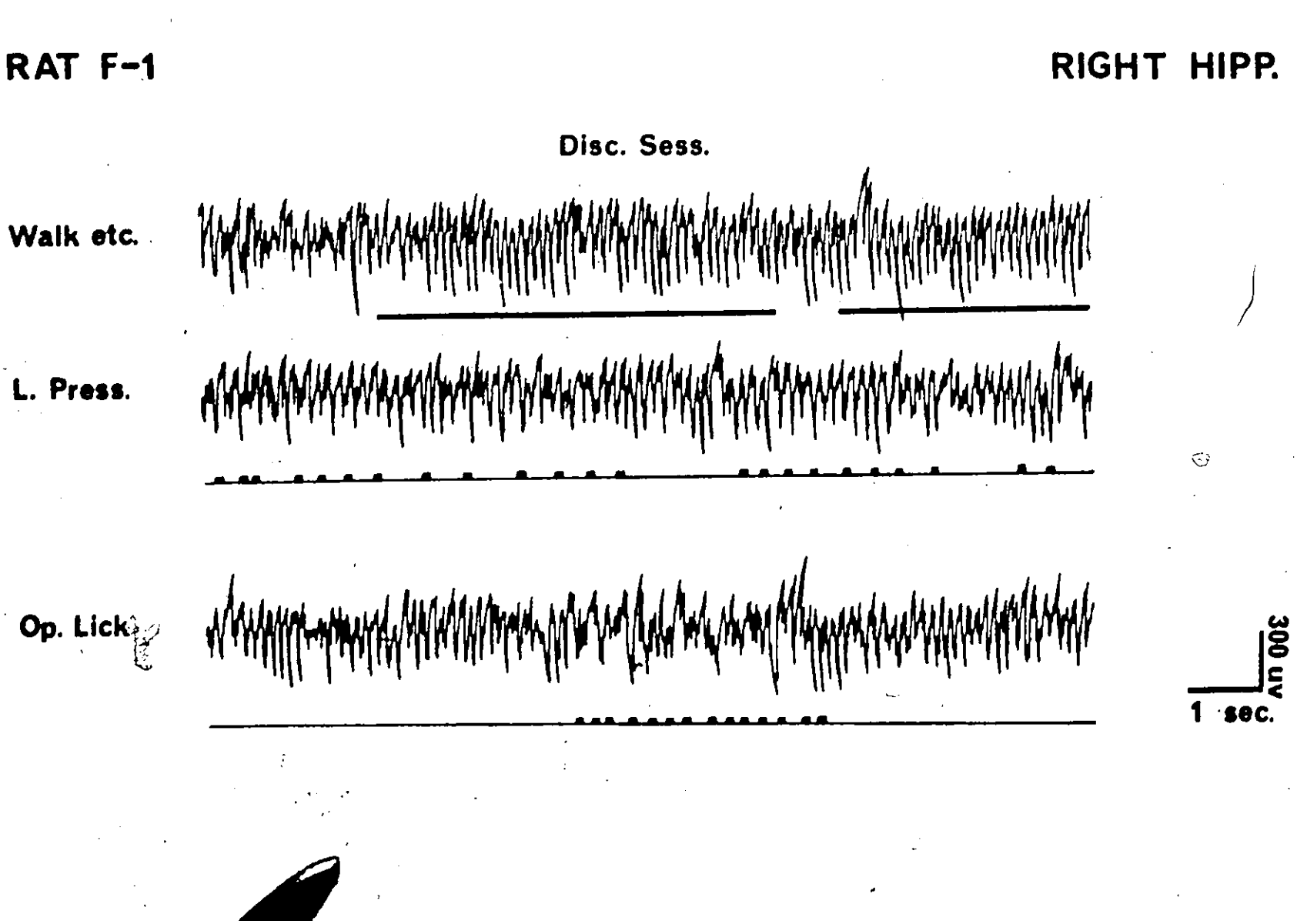


Figure 12

Right dorsal hippocampal EEG samples of F-2 during positive reinforcement sessions.

RAT F-2

RIGHT HIPP.

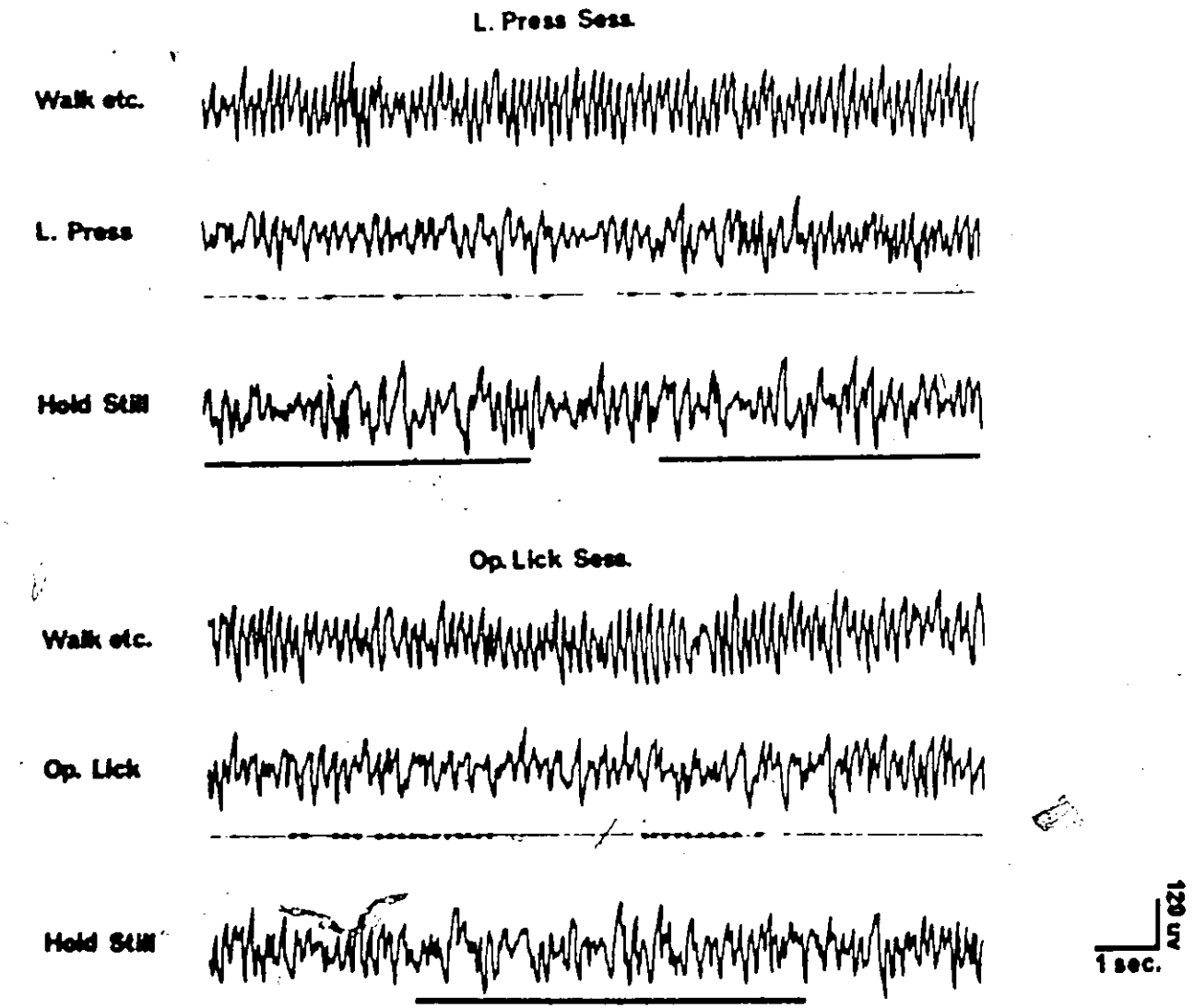


Figure 13

Left dorsal hippocampal EEG samples of F-3 during positive reinforcement sessions.

RAT F-3

LEFT HIPP.

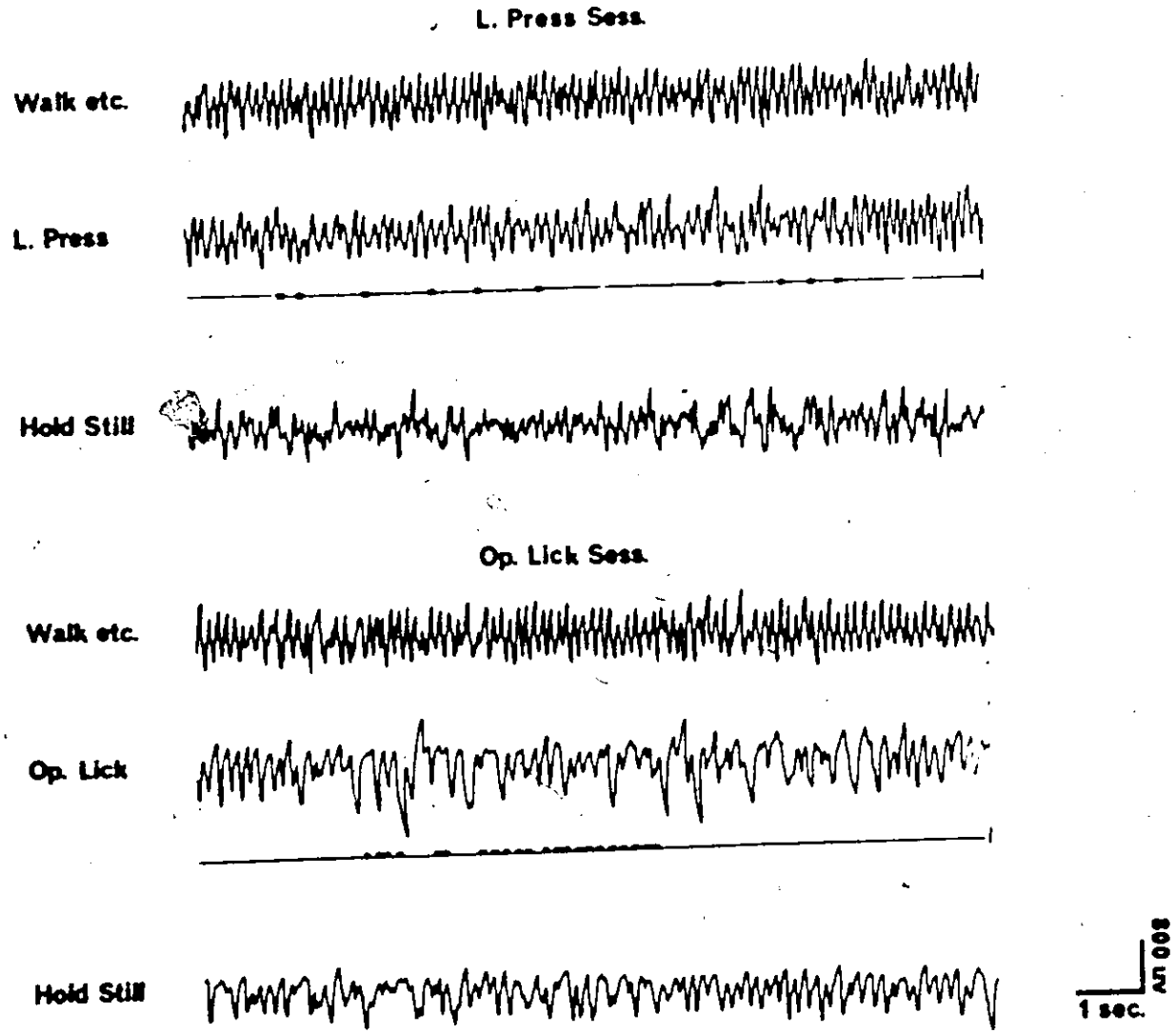


Figure 14

Right dorsal hippocampal EEG samples of F-3 during positive reinforcement sessions.

RAT F-3

RIGHT HIPP.

L. PRESS SESS.

Walk etc.

L. Press

Hold Still

OP. LICK SESS.

Walk etc.

Op. Lick

Hold Still

120 uv

1 sec.

Figure 15

Left dorsal hippocampal EEG samples of F-5 during positive reinforcement sessions.

RAT F-5

LEFT HIPP.

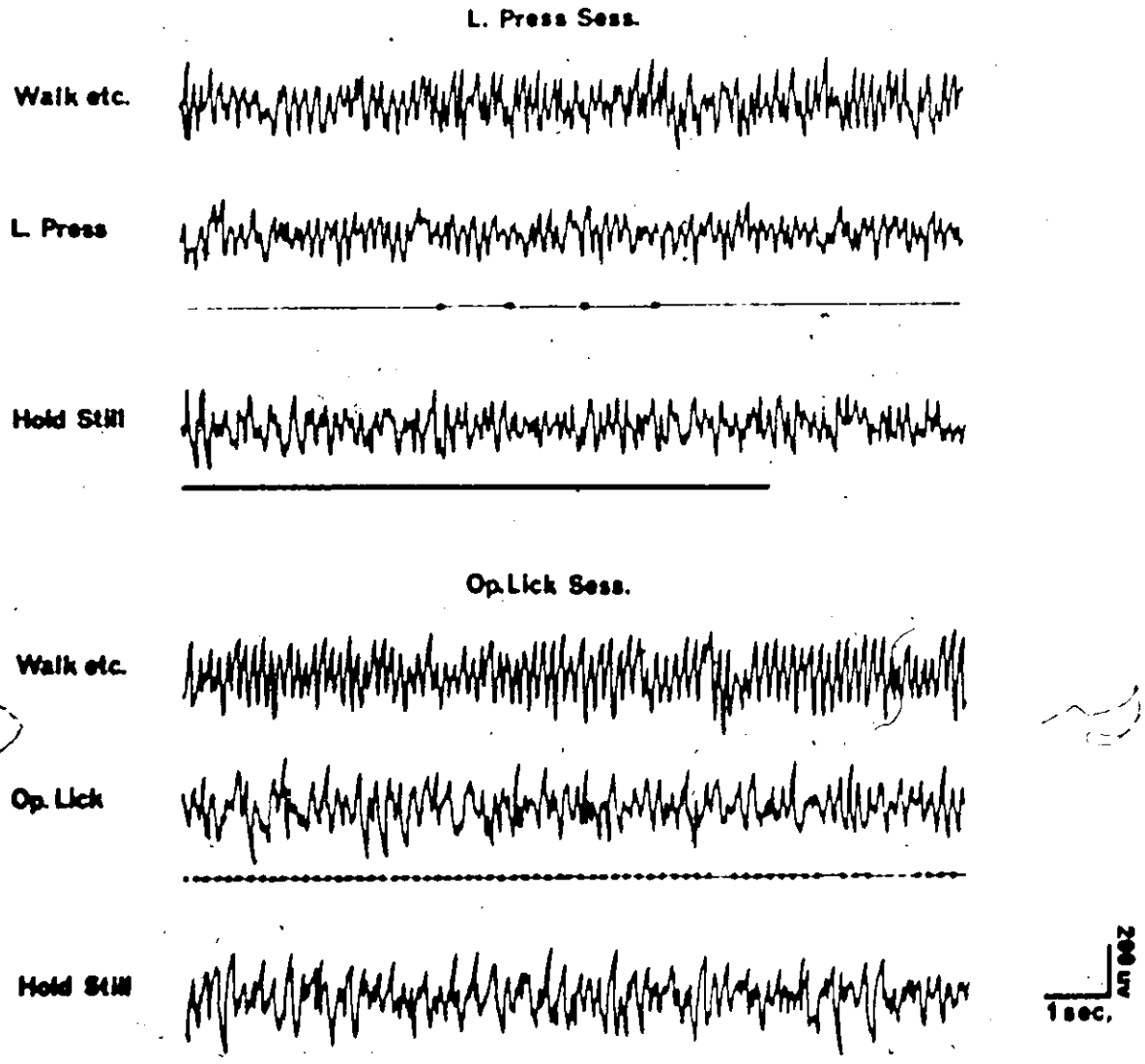


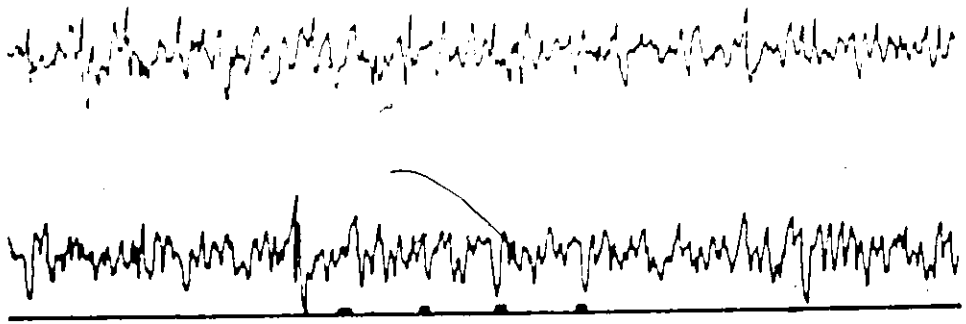
Figure 16

Right dorsal hippocampal EEG samples of F-5 during positive reinforcement sessions.

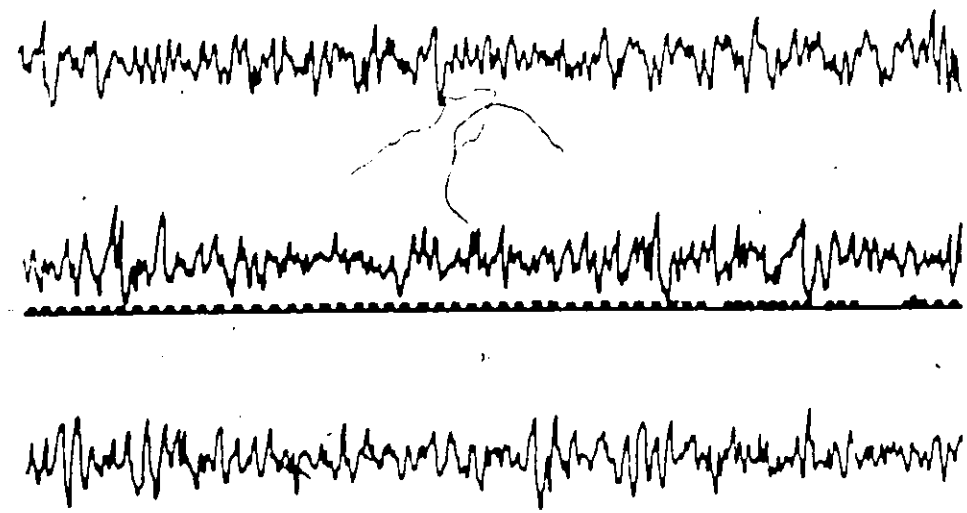
RAT F-5

RIGHT HIPP.

L. PRESS SESS.



OP. LICK SESS.



as that which was observed during walking, etc., because some lever presses did not seem to be accompanied by RSA. The EEG that was recorded from the remaining four electrode placements during lever pressing showed little RSA.

(3) During operant licking, the EEG from all thirteen electrode placements consisted of non-RSA patterns; primarily dorsal hippocampal LIA.

(4) During periods of immobility, the EEG from all thirteen electrode placements consisted of non-RSA patterns, with some low frequency RSA occurring at times.

An inspection of the relationships between EEG-behavior correlations and electrode placements (see Table 7 and Figures 17 through 25) indicates the following:

(1) The nine electrodes for which a relationship between dorsal hippocampal RSA and walking and lever pressing was observed, were in or near the pyramidal cell layer.

(2) The four remaining electrodes were in or near the dentate gyrus.

Based upon these observations, analyses were carried out only on EEG-behavior relationships for electrode placements in or near the pyramidal cell layer. One location was chosen for each rat. If both electrode placements of an individual rat were in or near the pyramidal cell layer, the placement with the most prominent RSA was selected for further analysis.

Table 7[3]

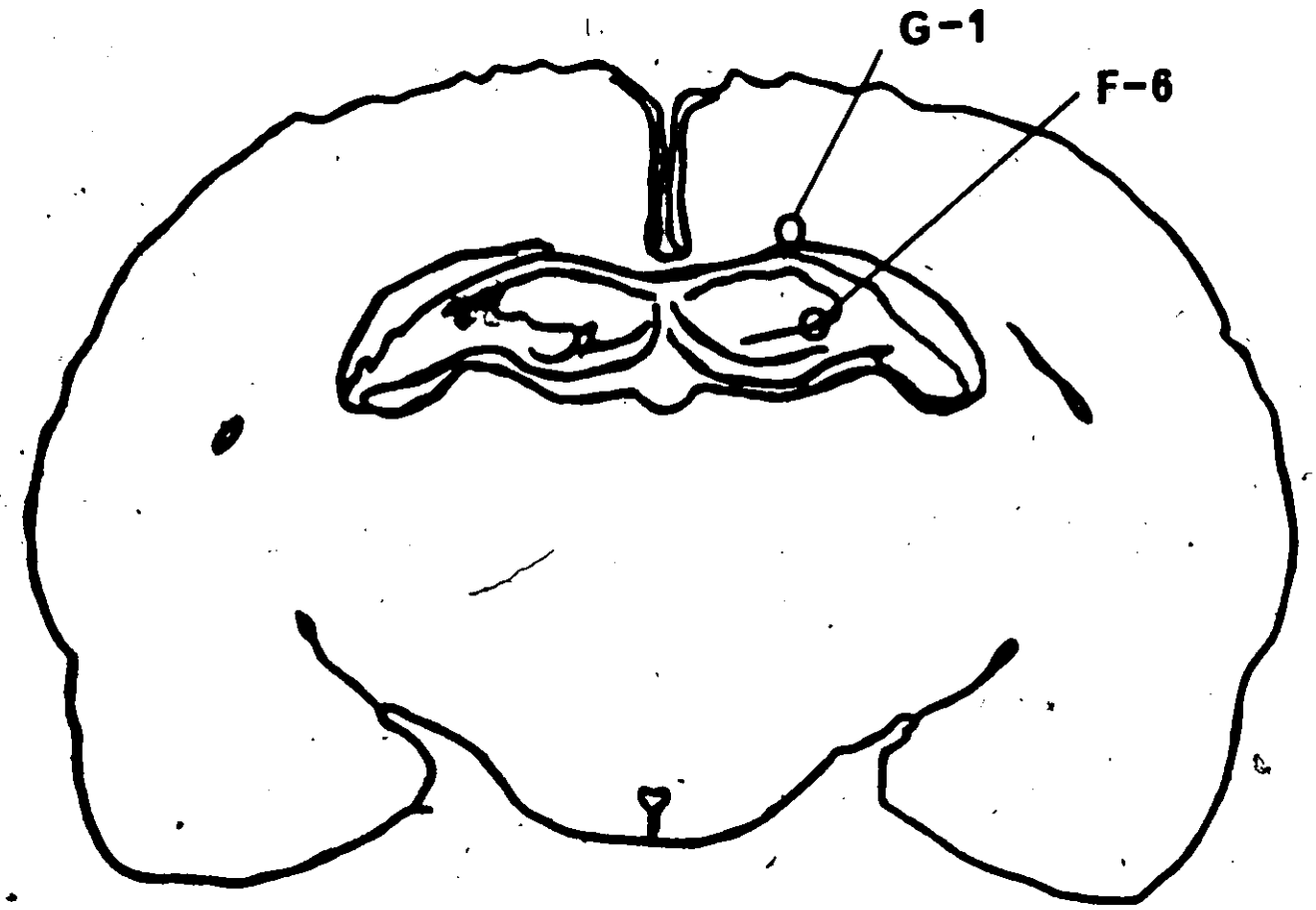
Relationships of Hippocampal EEG, Types of Behavior and Histologies

Rat		On or Near Pyramidal Cell Layer	Between Pyramidal Cell Layer and Granule Cell Layer	On or Near Granule Cell Layer
SA-1	L. Hipp.			X
	R. Hipp.	X RSA*		
SA-3	L. Hipp.		X RSA*	
	R. Hipp.			X
SA-4	L. Hipp.	X RSA*		
	R. Hipp.	X RSA		
F-1	L. Hipp.		X RSA*	
	R. Hipp.	X RSA		
F-2	L. Hipp.	---	---	---
	R. Hipp.	X (Bipolar) RSA*	X (Bipolar) RSA*	
F-3	L. Hipp.	X RSA*		
	R. Hipp.			X
F-5	L. Hipp.		X RSA*	
	R. Hipp.			X

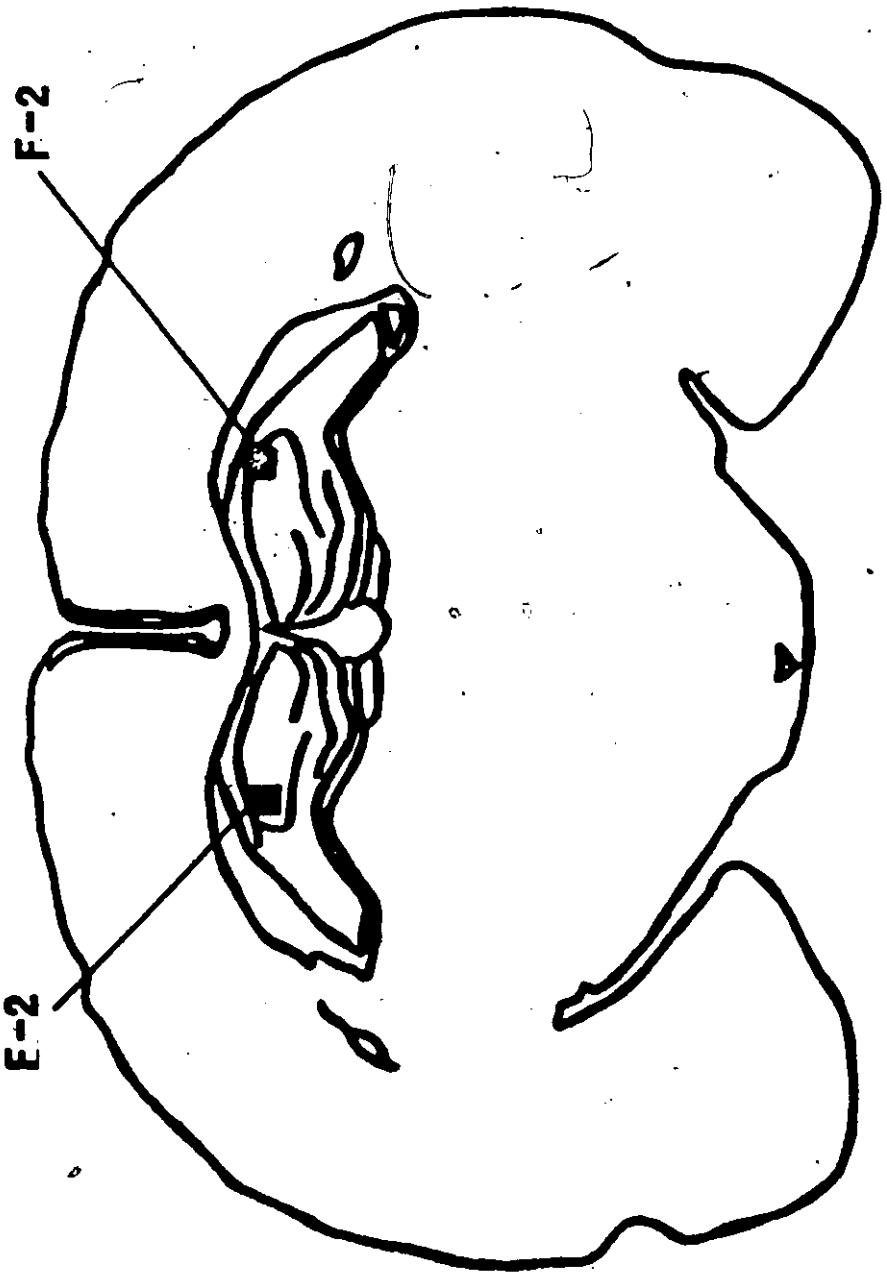
[3]Electrode tip placements are indicated by an "X". Placements associated with RSA during walking and lever pressing are indicated by "RSA". Placements used in further analysis are indicated by an asterisk, (*).

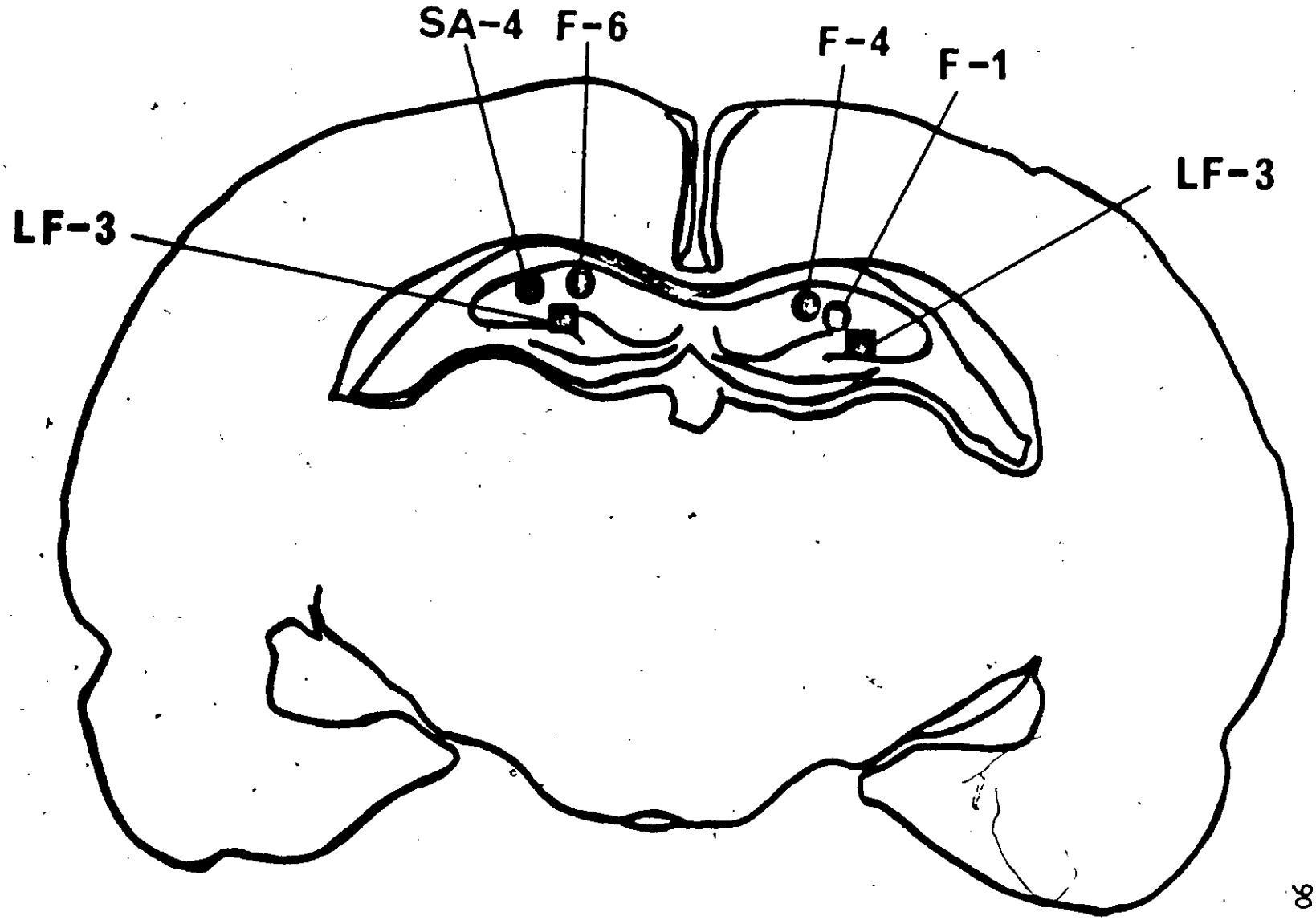
Figures 17 through 25

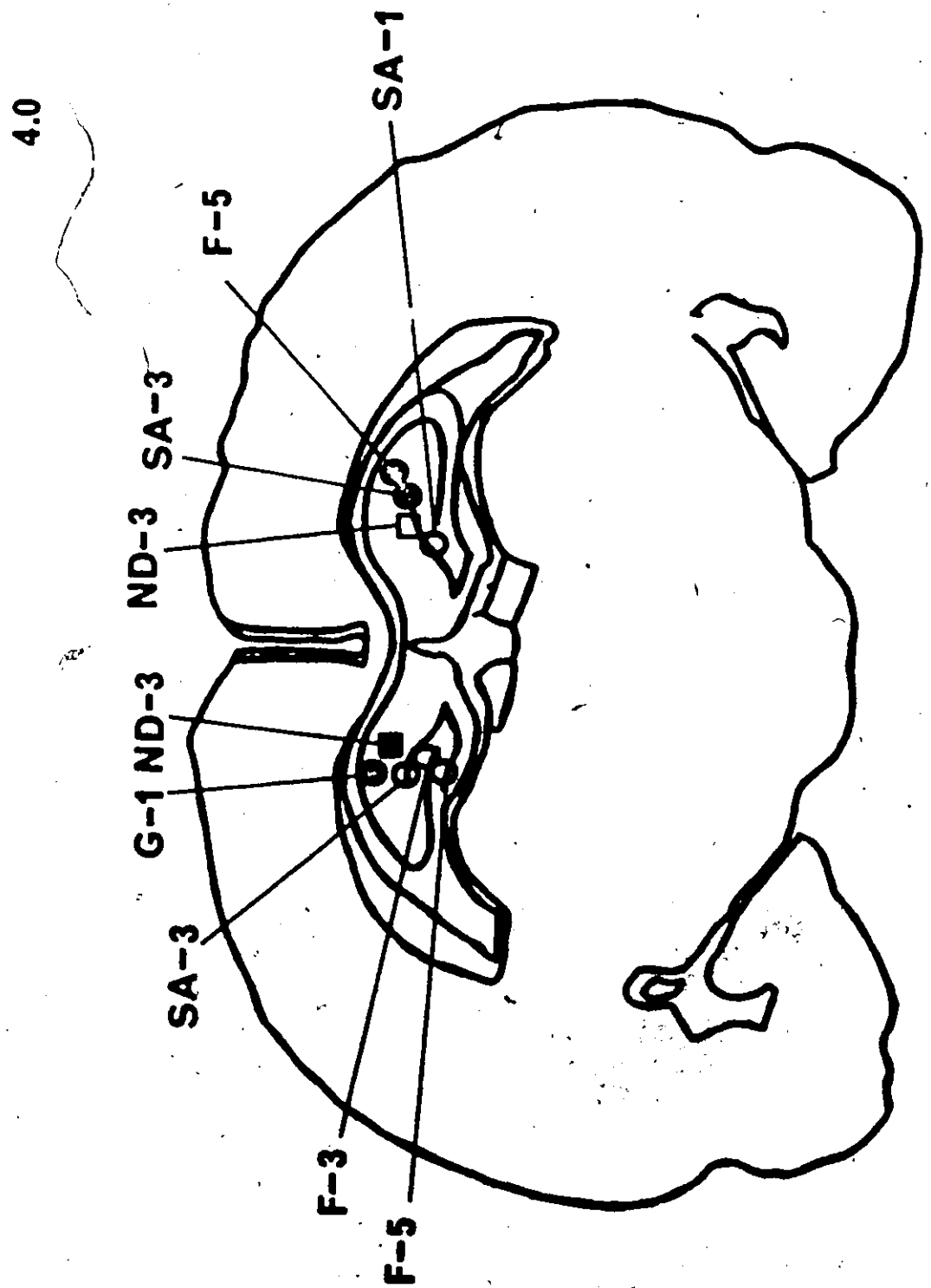
Coronal sections of the rat brain. Numbers in the upper right hand corner of each figure denote the anterior-posterior position of that section (mm.) in respect to the interaural line. The filled circles represent electrode tip locations of monopolar electrodes from which dorsal hippocampal RSA was correlated with walking, etc. and lever pressing and from which LIA was correlated with operant licking, normal drinking, polydipsic drinking, and holding still. The open circles represent electrode tip locations of monopolar electrodes from which there were no apparent relationships between hippocampal EEG and behavior. In a similar manner, the filled and open squares represent electrode tip locations of bipolar electrodes.

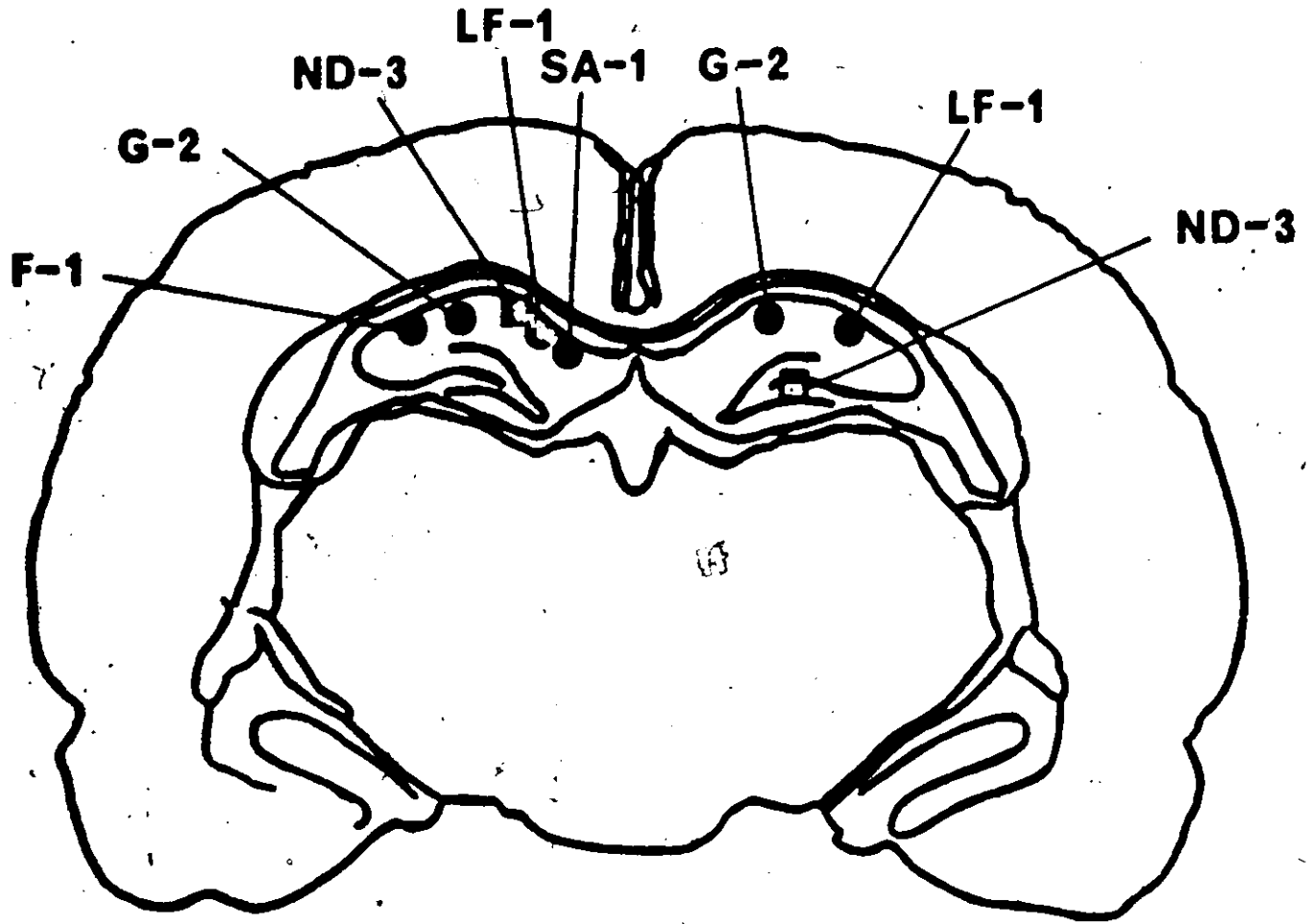

G-1
F-6

4A

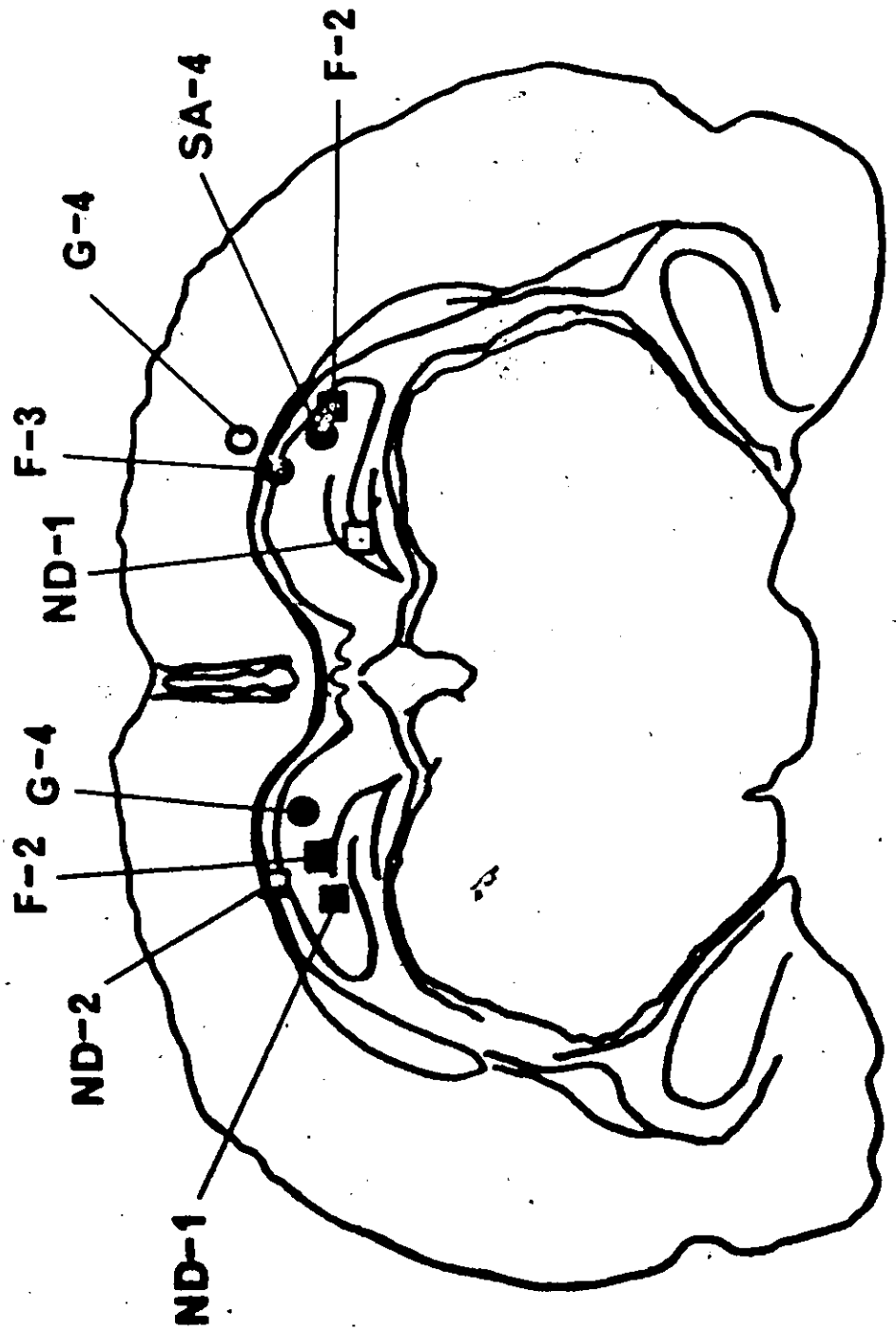


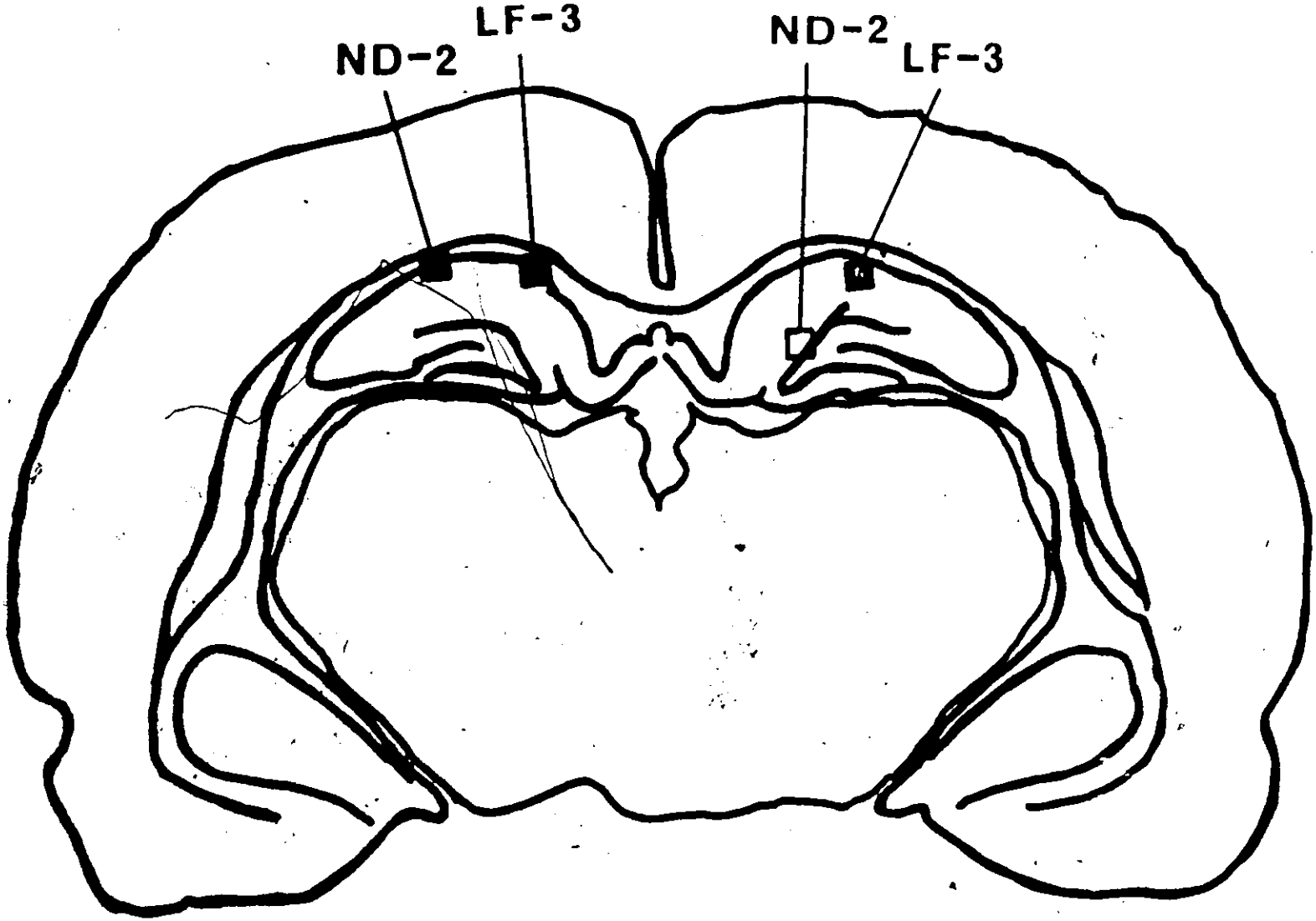

SA-4
F-6
F-4
F-1
LF-3
LF-3

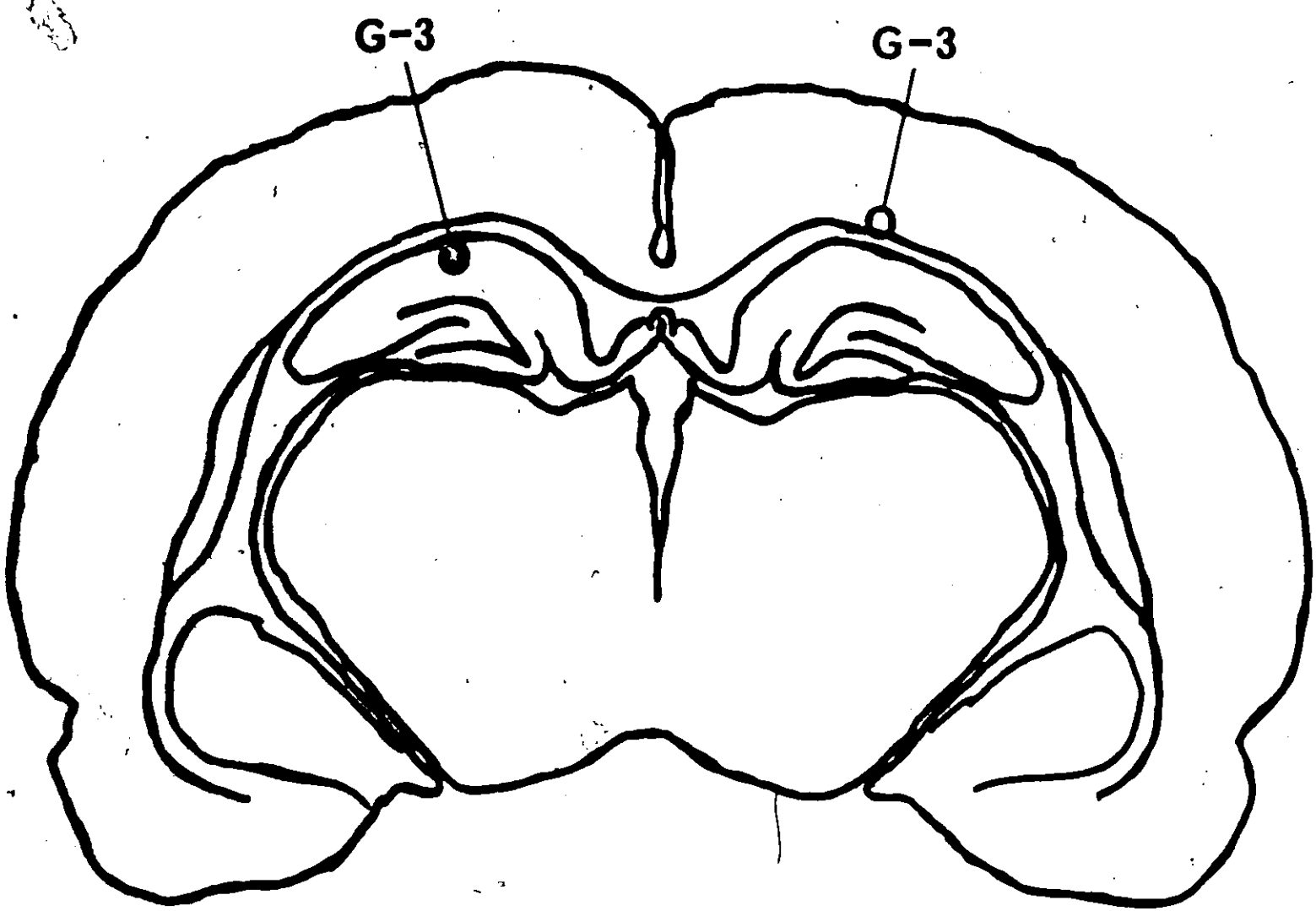

4.0
SA-1
F-5
SA-3
ND-3
G-1
ND-3
SA-3
F-3
F-5


LF-1
ND-3
SA-1
G-2
LF-1
G-2
ND-3
F-1

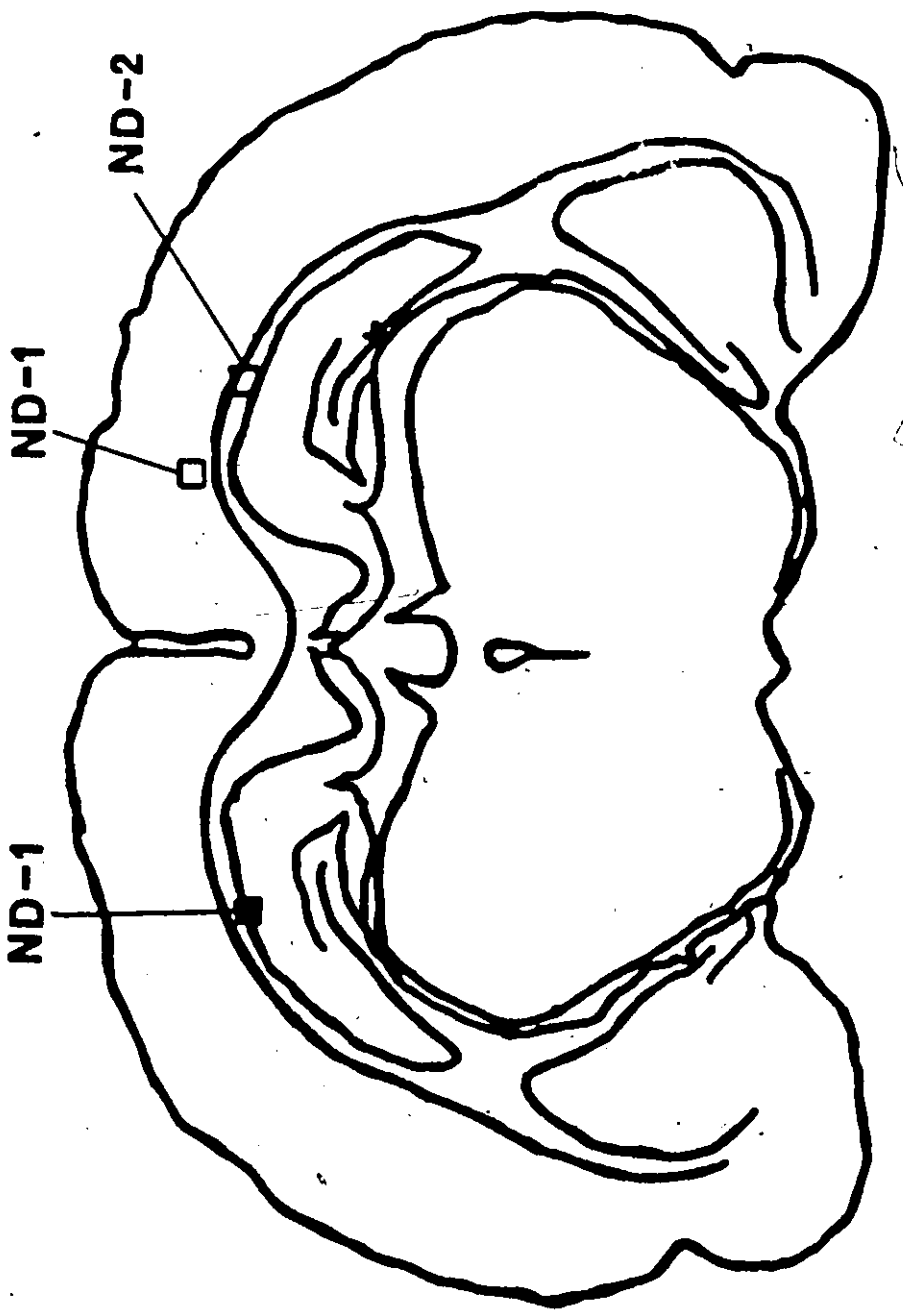
3.6




ND-2
LF-3
ND-2
LF-3


G-3
G-3

2.8



2. Analyses of EEG correlates of single responses

In order to make more precise comparisons of hippocampal EEG associated with lever pressing and licking, the following analyses were carried out. High rate lever pressing and licking, and low rate lever pressing and licking were analyzed separately.

(1) High rate responding: During the recording sessions, the first ten lever presses that occurred in sequences of four or more with a rate of at least one per second were selected. Similarly, during the recording session, the first ten licks that occurred in sequences of four or more with a rate of at least one per 0.5 seconds were selected.[4] The waveform that occurred during each separate lever press or lick was determined. The period of each single wave was measured with an optical reticle. If the frequency of each waveform was 5 to 10 Hz., it was defined as RSA; if the frequency of each waveform was less than 5 Hz., or greater than 10 Hz., it was defined as non-RSA.

The results are shown in Table 8. An analysis of variance (treatments by subjects design) indicates

---

[4] A 0.5 second criterion was used for licking, in contrast to a 1.0 second criterion for lever pressing, because the maximum rate of licking that was physiologically possible seemed greater than that for lever pressing. In addition, the licking sequences that were sampled involved only movements of the tongue and jaws; if any licking was associated with other movements such as postural readjustments or limb movements, that particular sample was not collected for analysis. This was accomplished by carefully reviewing the videotapes.

Table 8

Number of RSA Waves Associated with Individual Operant Responses that Occurred in Sequences (10 samples)

Sidman Avoidance Group			Positive Reinforcement Group		
Rat	Lever Presses	Licks	Rat	Lever Presses	Licks
SA-1	9	2	F-1	10	2
SA-2	9	7	F-2	7	4
SA-3	6	5	F-3	10	3
SA-4	10	6	F-5	8	3
Means	8.5	5.0		8.8	3.0

$F_{group} = 1.30$, df = 1, 3, $p > 0.20$

$F_{response} = 28.50$, df = 1, 3, $p < 0.025$

$F_{group \times response} = 1.73$, df = 1, 3, $p > 0.20$

that the number of RSA's associated with lever pressing and the number associated with licking is significant at the 0.025 level. The differences in RSA between avoidance and positive reinforcement groups and the interaction factor are not significant.

(2) Low frequency responding: The comparisons were repeated with one change in criterion. Lever presses and licks with rates less than one per second were selected.

The results are shown in Table 9. An analysis of variance indicates that the difference between the number of RSA's associated with lever presses and the number associated with licks is significant at the 0.01 level. The differences between avoidance and positive reinforcement groups and the interaction factor are not significant.

3. Spectral analyses

The EEG samples were also subjected to spectral analyses. Twenty-five second samples that were correlated with each type of response were analyzed. Power densities for the EEG frequencies from zero to 25 Hz. were determined. The sampling rate was 50 per second and there were 100 lags. There were 21 degrees of freedom (Blackman and Tukey, 1958).

For walking etc. and holding, the EEG was sampled only when the behavior occurred continuously for five or more seconds. Periods of walking and holding still were selected by reviewing the videotapes. For lever pressing, the EEG was sampled only when four

Table 9

Number of RSA Waves Associated with Individual Operant Responses that Occurred in Isolation from One Another (10 samples)

Sidman Avoidance Group			Positive Reinforcement Group		
Rat	Lever Presses	Licks	Rat	Lever Presses	Licks
SA-1	9	5	F-1	8	3
SA-2	10	6	F-2	9	4
SA-3	10	6	F-3	8	4
SA-4	9	5	F-5	9	3
Means	9.5	5.5		8.5	3.5

$F_{group} = 1.25$, df = 1, 3, $p > 0.20$

$F_{response} = 38.25$, df = 1, 3, $p < 0.01$

$F_{group \times response} = 0.85$, df = 1, 3, $p > 0.20$

or more responses made sequentially with a rate of at least one per second. For licking, the EEG was sampled only when four or more responses were made sequentially with a rate of at least one per 0.5 seconds. (See footnote 4.) In addition, sequences of licking that were sampled involved only movements of the tongue and jaw; if any licking was associated with other movements such as postural readjustments or limb movements, that particular sample was not collected for spectral analysis.

The following statistical analyses (treatments by subjects design) were carried out on the power spectral data (the power spectra can be found in the Appendix section, Figures 1 through 8). First, the spectral power in the zero to 5 Hz. range was compared (see Table 10). Second, the spectral power in the 5 to 10 Hz. range was compared (see Table 11). Third, the ratios of the spectral power in the 5 to 10 Hz. range divided by the spectral power in the zero to 10 Hz. range were compared (see Table 12). The ratio measurement is sensitive to relative distributions of power in the zero to 5 and 5 to 10 Hz. ranges. For example, if more power exists in the 5 to 10 Hz. range than in the zero to 5 Hz. range, the ratio will be larger than if the power were equal in the two ranges. Furthermore, the ratio measurement normalized differences in absolute power values between subjects. Fourth, the modal frequencies (0.25 Hz. intervals) were compared (see Table 13).

Licking was associated with significantly more spectral power in the zero to 5 Hz. range than lever pressing. No significant differences were found in the 5 to 10 Hz. range. The ratios of spectral power were significantly greater with lever pressing than with licking.

Table 10

Spectral Power During Operant Lever Pressing and Licking
(zero to 5 Hz.)

Sidman Avoidance Group			Positive Reinforcement Group		
Rat	Lever Presses	Licks	Rat	Lever Presses	Licks
SA-1	3.967	8.133	F-1	1.599	3.551
SA-2	1.321	1.930	F-2	2.551	7.589
SA-3	2.095	4.244	F-3	0.791	7.558
SA-4	6.020	4.136	F-5	4.793	8.401
Means	3.351	4.611		2.434	6.775

$F_{group} = 0.23$, df = 1, 3, $p < 0.20$

$F_{response} = 11.67$, df = 1, 3, $p < 0.05$

$F_{group \times response} = 3.51$, df = 1, 3, $p > 0.10$

Table 11

Spectral Power During Operant Lever Pressing and Licking (5 to 10 Hz.)

Sidman Avoidance Group			Positive Reinforcement Group		
Rat	Lever Presses	Licks	Rat	Lever Presses	Licks
SA-1	7.050	6.240	F-1	2.553	1.756
SA-2	3.671	3.174	F-2	7.071	5.757
SA-3	3.191	3.387	F-3	5.351	3.386
SA-4	9.187	5.272	F-5	11.055	11.616
Means	5.775	4.518		6.508	5.629

$F_{group} = 0.18$, df = 1, 3, $p > 0.20$

$F_{response} = 4.09$, df = 1, 3, $p > 0.10$

$F_{group \times response} = 0.13$, df = 1, 3, $p > 0.20$

Table 12

Spectral Power Ratios During Operant Lever Pressing and Licking
(5 to 10 Hz.)
(zero to 10 Hz.)

Sidman Avoidance Group			Positive Reinforcement Group		
Rat	Lever Presses	Licks	Rat	Lever Presses	Licks
SA-1	0.64	0.44	F-1	0.73	0.43
SA-2	0.73	0.62	F-2	0.52	0.42
SA-3	0.60	0.44	F-3	0.81	0.41
SA-4	0.60	0.56	F-5	0.70	0.58
Means	0.64	0.52		0.69	0.46

$F_{group} = 0.01$, df = 1, 3, $p > 0.20$

$F_{response} = 19.98$, df = 1, 3, $p < 0.025$

$F_{group \times response} = 1.63$, df = 1, 3, $p > 0.20$

Table 13

Modal Frequencies During Operant Lever Pressing and Licking
(Upper Limit of 0.25 Hz. Interval)

Sidman Avoidance Group			Positive Reinforcement Group		
Rat	Lever Presses	Licks	Rat	Lever Presses	Licks
SA-1	6.00	2.75	F-1	6.25	4.50
SA-2	6.25	5.75	F-2	6.50	2.25
SA-3	6.50	6.50	F-3	6.75	5.50
SA-4	6.00	6.00	F-5	6.75	6.00
Means	6.19	5.25		6.56	4.56

$F_{group} = 0.05$, df = 1, 3, $p > 0.20$

$F_{response} = 6.60$, df = 1, 3, $p > 0.05$

$F_{group \times response} = 1.48$, df = 1, 3, $p > 0.20$

These combined results indicate that the power spectra associated with lever pressing and licking had different distributions; that is, lever pressing was associated with relatively more spectral power in the 5 to 10 Hz. range than in the zero to 5 Hz. range, while licking was associated with spectral power throughout the zero to 10 Hz. range. Finally, there was no significant difference between the modal frequencies during lever pressing and licking.

Further analyses of variance (treatments by subjects design) were carried out on the power spectral data by comparing ratios and modal frequencies associated with the lever pressing, licking, walking, and holding still of SA-4, F-2, F-3, and F-5, the only rats on which all these measures were available. (See Tables 14 and 15.)

Both tests indicated significant differences at the 0.001 level. For the ratios, multiple t tests (0.05 level) indicated that the ratios associated with walking were significantly different from those associated with lever pressing, licking, and holding still. In turn, the ratio associated with lever pressing was significantly different from those associated with licking and holding still.

For the modal frequencies, multiple t tests (0.05 level) indicated that the modal frequencies associated with walking, lever pressing, and licking were significantly different from those associated with holding still.[5]

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[5]Additional EEG records and power spectra for two rats (F-4 and F-6) that were trained to lever press for water reinforcements can be found in Figures 9 through 12 in the Appendix section.

Table 14

Spectral Power Ratios
$\frac{(5 \text{ to } 10 \text{ Hz.})}{(\text{Zero to } 10 \text{ Hz.})}$

Rat	Lever Presses	Licks	$Walk_{LP}$	$Walk_{Lick}$	$Still_{LP}$	$Still_{Lick}$
SA-4	0.61	0.56	0.74	0.82	0.41	0.51
F-2	0.52	0.42	0.87	0.83	0.37	0.31
F-3	0.81	0.41	0.91	0.87	0.51	0.54
F-5	0.70	0.58	0.69	0.75	0.46	0.42
Means	0.66	0.49	0.80	0.82	0.44	0.45

$F_{responses} = 16.78$, df = 5, 15, $p < 0.001$

Multiple t Tests

$Walk_{Lick}$	$Walk_{LP}$	Lever Press	Lick	$Still_{Lick}$	$Still_{LP}$
	—	*	*	*	*
	/	*	*	*	*
			*	*	*
				—	—
					—

*significant at 0.05 level.

Table 15

Modal Frequencies
(Upper Limit of 0.25 Hz. Intervals)

Rat	Lever Presses	Licks	$Walk_{LP}$	$Walk_{Lick}$	$Still_{LP}$	$Still_{Lick}$
SA-4	6.00	6.00	5.75	6.00	5.75	5.25
F-2	6.25	4.50	6.75	6.75	1.50	2.50
F-3	6.75	5.50	7.75	7.25	2.00	6.00
F-5	6.75	6.00	8.00	7.00	2.75	3.50
Means	6.44	5.50	7.06	6.75	3.00	4.31

$F_{responses} = 8.15$, df = 5, 15, $p < 0.001$

Multiple t Tests

$Walk_{LP}$	$Walk_{Lick}$	Lever Press	Lick	$Still_{LP}$	$Still_{Lick}$
	—	—	—	*	*
		—	—	*	*
			—	*	*
				—	*
					—

*significant at 0.05 level

Discussion

The main results of Experiment I indicated that lever pressing was more highly correlated with dorsal hippocampal RSA than licking. In addition, the data indicated a difference between the hippocampal EEG for walking and lever pressing, and between the hippocampal EEG for walking and lever pressing compared with that for operant licking and holding still.

These results suggest that hippocampal RSA is correlated with the form of response. One could, of course, suggest that there were differences in sensation, perception, and central integrating processes between the operant lever pressing and operant licking situations and that this difference accounts for the differences in EEG. This suggestion seems unlikely to the extent that such differences in sensation, etc. were produced by the type of S^D, type of reinforcer, or by the relationships between these variables. There were no apparent differences in EEG that were related to the different types of S^D or to the free operant situation. There were no apparent differences in the EEG that were related to the different reinforcers; there were no systematic differences between the procedural variables that were employed for operant lever pressing and operant licking.

The question that one should deal with next is what property or properties of the response might account for the differences. The possibility that RSA is related to operants and other EEG patterns to non-operants can be ruled out on the basis of the present results. This, of course, holds true only if one accepts the position that both

responses were operants as seems to be indicated by the results in the behavioral section.

Several features of the responses can be suggested as candidates for the distinguishing property; for example, relative intensities, relative topographies, and different associated neural control circuits. The one that will be examined in Experiment 2 is the relative intensities of responses.

CHAPTER III

Experiment 2

Although the differences in dorsal hippocampal EEG during lever pressing and operant licking might be attributed to the form or topography of response, one might also attribute the difference to intensity of response. That is, lever pressing might be a more intense response than licking. One rough definition of intensity is provided by the amount of gross movement that is involved in the performance of a response. For example, in this sense running is more intense than turning the head, and grooming the body is more intense than licking at a tube. This definition was employed in the present Chapter, where intense saliva spreading and licking of the body were induced by increasing the temperature of the rat (Hainsworth, 1967; Hainsworth, Stricker, and Epstein, 1968). If these responses are accompanied by dorsal hippocampal LIA, it would be difficult to maintain that hippocampal RSA is related to the intensity of a response, in the sense that intensity is used above.

Method

Subjects

The subjects were four male naive hooded rats (G-1, G-2, G-3, and G-4) from the Quebec Breeding Farms, each weighing approximately 275 grams at the beginning of the experiment. Each rat was individually housed, and Purina rat chow was available in the home cages at all times. Water was also available in the home cages except during periods that will be described later in this section.

Apparatus

The experiment was conducted in a well insulated incubation chamber that allowed precise temperature control. The modified Skinner box used in the previous experiments was placed in this chamber. EEG recordings and videotapes of behavior were obtained with the same equipment employed previously, except that EEG was not recorded on an Ampex magnetic tape recorder.

Surgical procedure

The surgical procedure was the same as that employed previously. All four rats were implanted with monopolar electrodes.

Recording procedure

Each rat was placed in the incubation chamber and allowed to adapt to the novel surroundings for 30 minutes at room temperature. Hippocampal EEG recordings and videotapes of behavior were then obtained

during the next hour; videotapes were obtained form a side view through the glass pane in the door of the incubation chamber. In the first ten minutes of this hour the rats were kept at room temperature. Then the temperature was slowly raised to 40° C., and was maintained at this level for approximately 30 minutes. Finally, the chamber was allowed to cool back to room temperature. Each rat was then returned to its home cage and allowed free access to water for one hour. On the following day after 23 hours of water deprivation, each rat was allowed one hour of access to water in the incubation chamber. EEG recordings and videotapes were obtained during any normal drinking.

Results

Electrical Activities of the Hippocampus

EEG samples for each rat are shown in Figures 26, 27, 28, and 29. (Additional data can be found in Figure 13 of the Appendix section.) EEG samples correlated with grooming and saliva spreading were carefully selected during periods in which no other skeletal behaviors occurred other than grooming or saliva spreading; for example, foot movements, postural shifts, etc.

Visual inspection of the EEG samples indicates that all cases of walking, rearing, etc. were associated with dorsal hippocampal RSA. All cases of grooming at room temperature, holding still , grooming and saliva spreading at 40° C., and drinking to regulate water balance were associated with hippocampal LIA.

In order to make more precise comparisons between the EEG patterns associated with the different behaviors, the following analyses of variance (treatments by subjects design) were carried out. The first ten seconds of each type of behavior were selected with the aid of the videotapes; the criteria for selection were either ten seconds of continuous behavior or two separate samples of five seconds of continuous behavior. The number of individual RSA waves in the EEG samples associated with these ten second samples of behavior were determined with an opticle reticle in the same manner as described in Experiment 1. The length of RSA sequences was also determined; that is, the number of RSA waves in a row without the interjection of a wave less than 5 Hz. or greater than 10 Hz. Both statistical tests were

Figures 26 through 29

Dorsal hippocampal EEG samples of G-1, G-2, G-3, and G-4 during sessions conducted at room temperature and 40° C., and during normal drinking sessions.

RAT G-1

RIGHT HIPP.

Room Temp.

Walk etc.

Grooming

Hold Still

40° C.

Grooming

Norm. Drink Sess.

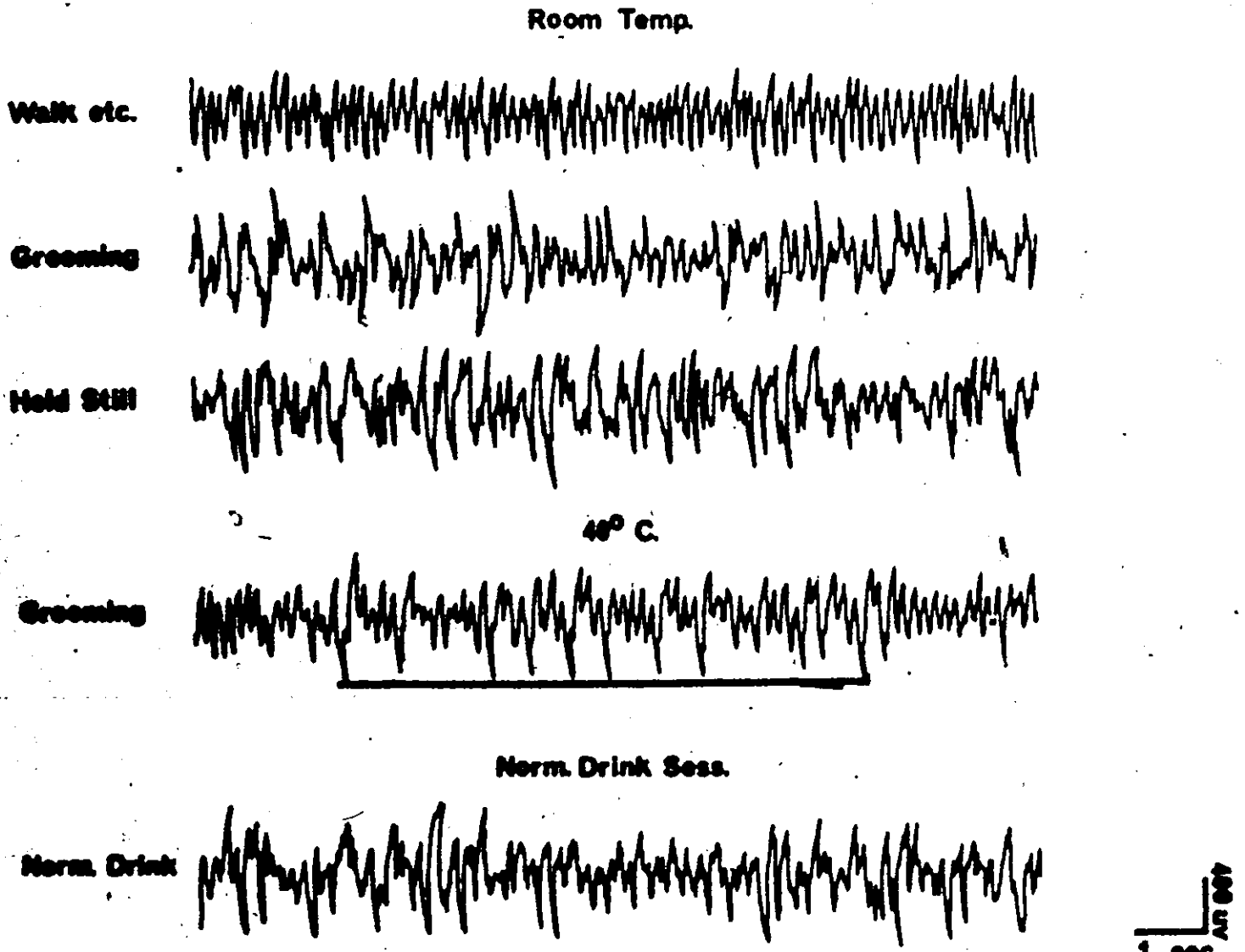
Norm. Drink

200 uV

1 sec

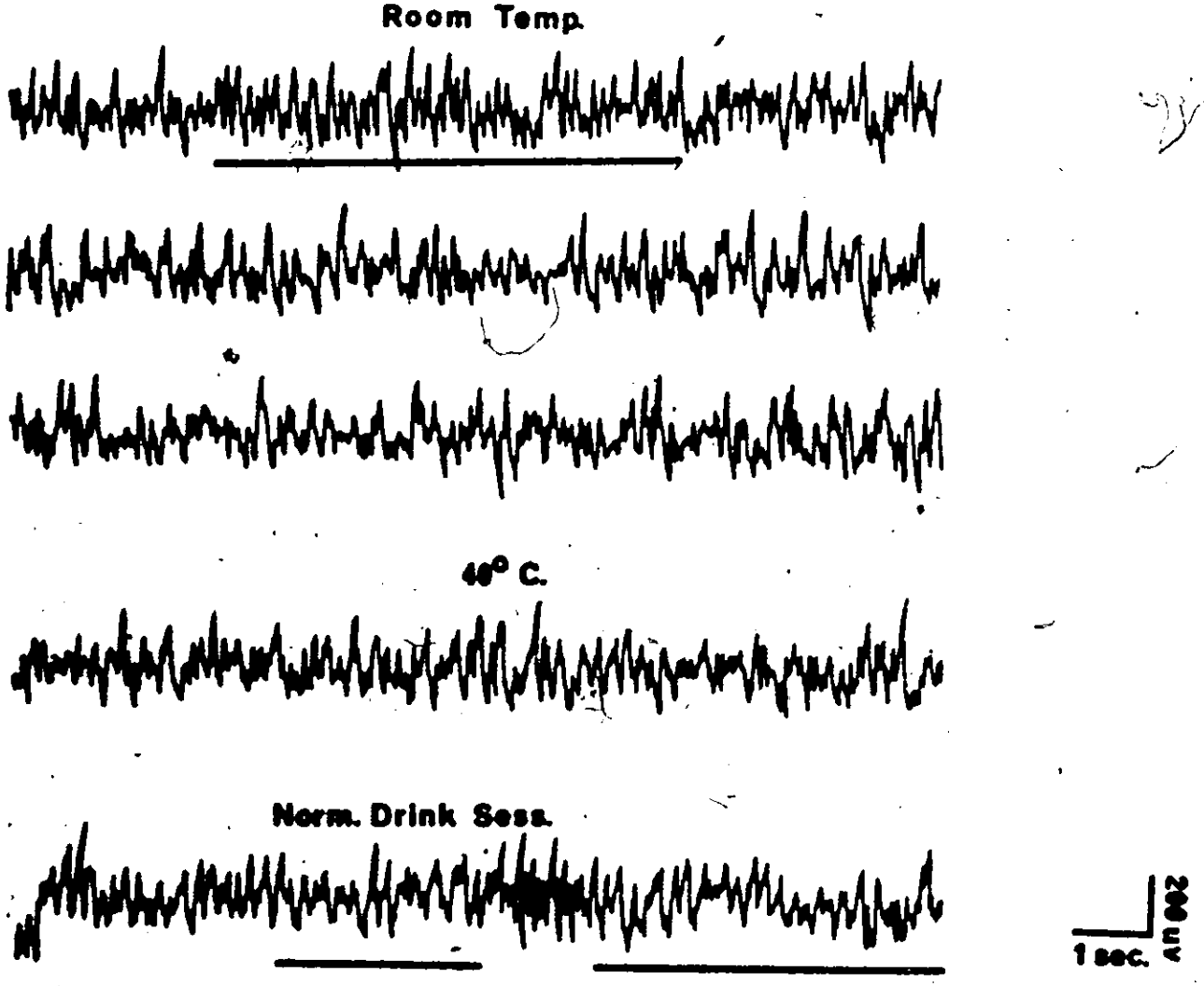
Rat G-2

Right Hipp.



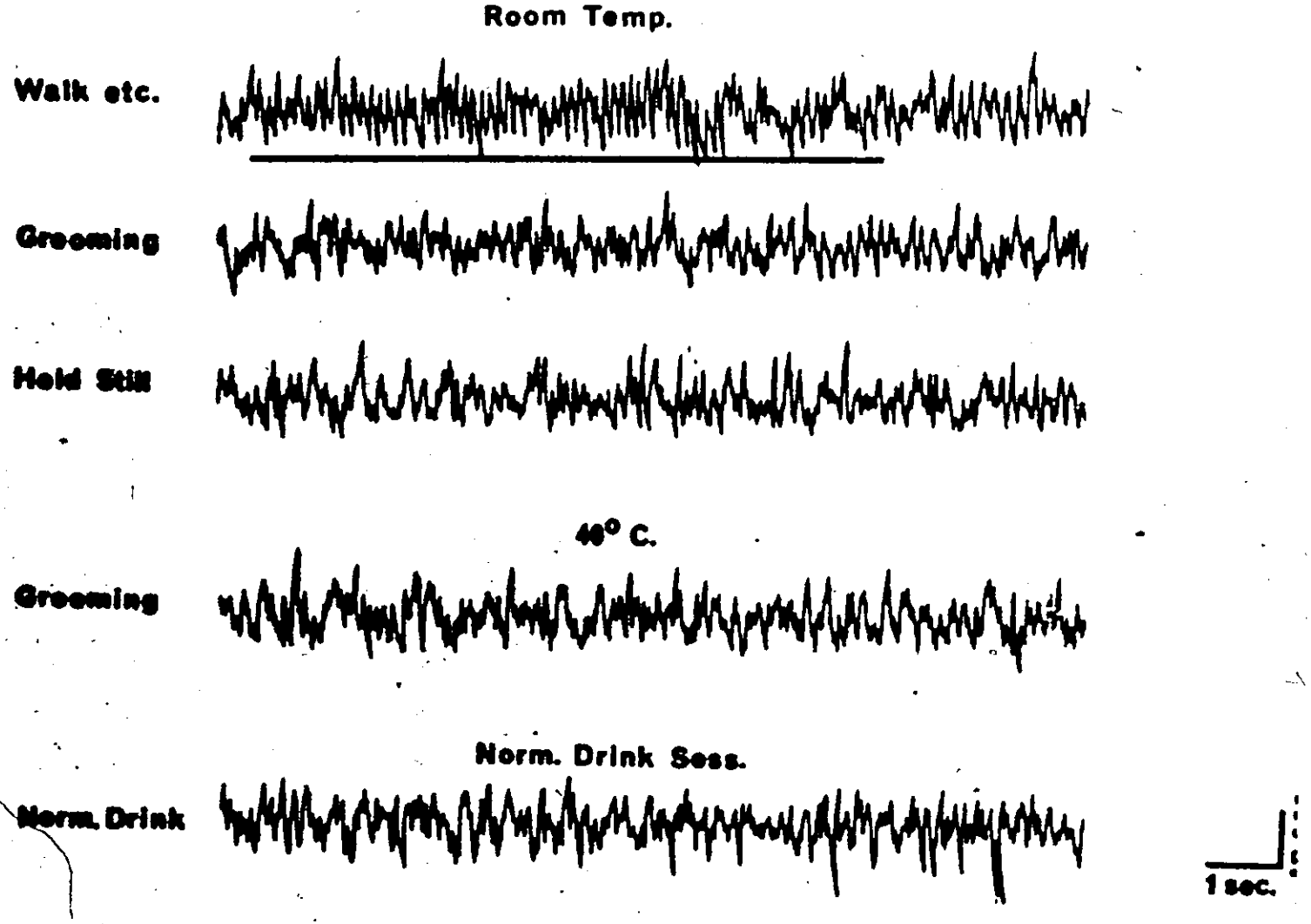
RAT G–3

RIGHT HIPP.



RAT G-4

RIGHT HIPP.



significant at the 0.01 level or better; visual inspection of the data (Tables 16 and 17) indicates that the significant differences were due to the measures associated with walking, etc. being different from those associated with the other behaviors, while the measures associated with these other behaviors were not different from each other.

Histological results

The electrode tip locations can be found in Figures 17 through 25 in Chapter II. Of the placements from which hippocampal RSA was associated with walking, etc. and LIA with grooming, saliva spreading and holding still, four (G-1, G-2, G-3, and G-4) were directly below the pyramidal cell layer in the CA-1 and CA-2 fields. Of the placements from which relatively less hippocampal RSA was associated with walking, etc. three (G-1, G-3, and G-4) were in the cortex.

Table 16

Number of RSA Waves (Ten Second Samples)

Rat	Walking Etc.	Grooming RT	Grooming and Saliva Spreading 40° C.	Drinking	Holding Still
G-1	74	13	12	17	14
G-2	73	10	25	11	15
G-3	74	10	16	18	22
G-4	64	18	11	11	16
Means	71	13	16	14	17

$F_{responses} = 11.73$, df = 4, 12, $p < 0.001$

Table 17

Average RSA Wave Sequences

Rat	Walking Etc.	Grooming RT	Grooming and Saliva Spreading 40° C.	Drinking	Holding Still
C-1	14.80	1.30	1.50	1.70	1.55
C-2	18.25	2.00	2.50	1.38	2.18
C-3	6.17	1.67	1.60	1.38	1.83
C-4	7.11	1.29	1.11	1.10	1.77
Means	11.58	1.57	1.68	1.39	1.83

$F_{responses} = 12.16$, df = 4, 12, $p < 0.01$

Discussion

The results of this experiment indicate that grooming at room temperature and saliva spreading and licking of the body at 40° C. were associated with dorsal hippocampal LIA. These results confirm those of Vanderwolf (1969, 1971). Grooming and saliva spreading and licking of the body are at least as vigorous and probably more vigorous than the lever pressing and operant licking which were observed in Experiment 1. These findings suggest that the differences in hippocampal EEG while lever pressing or operantly licking cannot be attributed to gross differences in the intensity of the two responses.

CHAPTER IV

In this Chapter, three experiments are described in which licking and the associated hippocampal EEG are examined in different behavioral situations. In the experiment described in Chapter II, two different responses were employed, and an attempt was made to hold physiological and other behavioral processes constant. In the experiments described in this Chapter, the opposite approach was taken. One response was employed (the licking response) and an attempt was made to vary the physiological and behavioral processes which controlled that response. Presumably, if RSA and non-RSA are related to the form or topography of response, then non-RSA should accompany licking no matter what processes control the response.

Experiment 3a

The purpose of this experiment was simply to attempt to replicate the findings of Vanderwolf (1971) that normal licking for water regulation is accompanied by dorsal hippocampal LIA.

Method

Subjects

The subjects (ND-1, ND-2, and ND-3) were three experimentally naive male hooded rats from the Quebec Breeding Farms, each weighing approximately 275 grams at the beginning of the experiment.

Apparatus

The experiment was conducted in an open top box with wooden sides and a grid floor; the lower half of one side consisted of clear plexiglas. The box was 12 inches wide, 12 inches long, and 10 3/4 inches deep. The grid floor consisted of 3/16 inch diameter stainless steel bars, 1/2 of an inch apart. A drinking tube was extended into the box from the middle of one wall, 1 1/2 inches from the grid floor. Data was collected on the fourth day of the normal drinking schedules.

Surgical procedure

The surgical procedure was the same as that employed previously. All three rats were implanted with bipolar electrodes.

Experimental procedure

Each rat was water deprived for 23 hours and then placed in the experimental box. Each rat was allowed one hour of free access to the water; no water was provided in the home cages. Each rat was kept on this schedule for four days. On the last day hippocampal EEG recordings and videotapes of overt behavior were obtained.

Results

Electrical activities of the hippocampus

Hippocampal EEG samples are shown for each rat in Figures 30, 31, and 32. These samples were a part of those selected for spectral analyses; the criteria for selecting EEG samples for spectral analyses were the same as those employed in Experiment 1.

Visual inspection of the EEG samples indicates that all cases of walking, rearing, etc. were accompanied by dorsal hippocampal RSA.

All cases of normal drinking without extraneous movements were accompanied by dorsal hippocampal LIA. One case of normal drinking that was accompanied by slight vertical head movements (ND-1) was associated with RSA.

All cases of holding still were accompanied by dorsal hippocampal LIA.

The power spectral data were analyzed (treatments by subjects design) by comparing the power spectral ratios and the modal frequencies during walking, etc., normal drinking without extraneous movements, and holding still (see Table 18). (The power spectra can be found in Figures 14, 15, and 16 in the Appendix Section.) The differences between power spectral ratios were significant at the 0.025 level; the differences between modal frequencies were not significant. In the case of the power spectral ratios, those associated with walking, etc. were significantly larger than those associated with normal drinking and holding still.

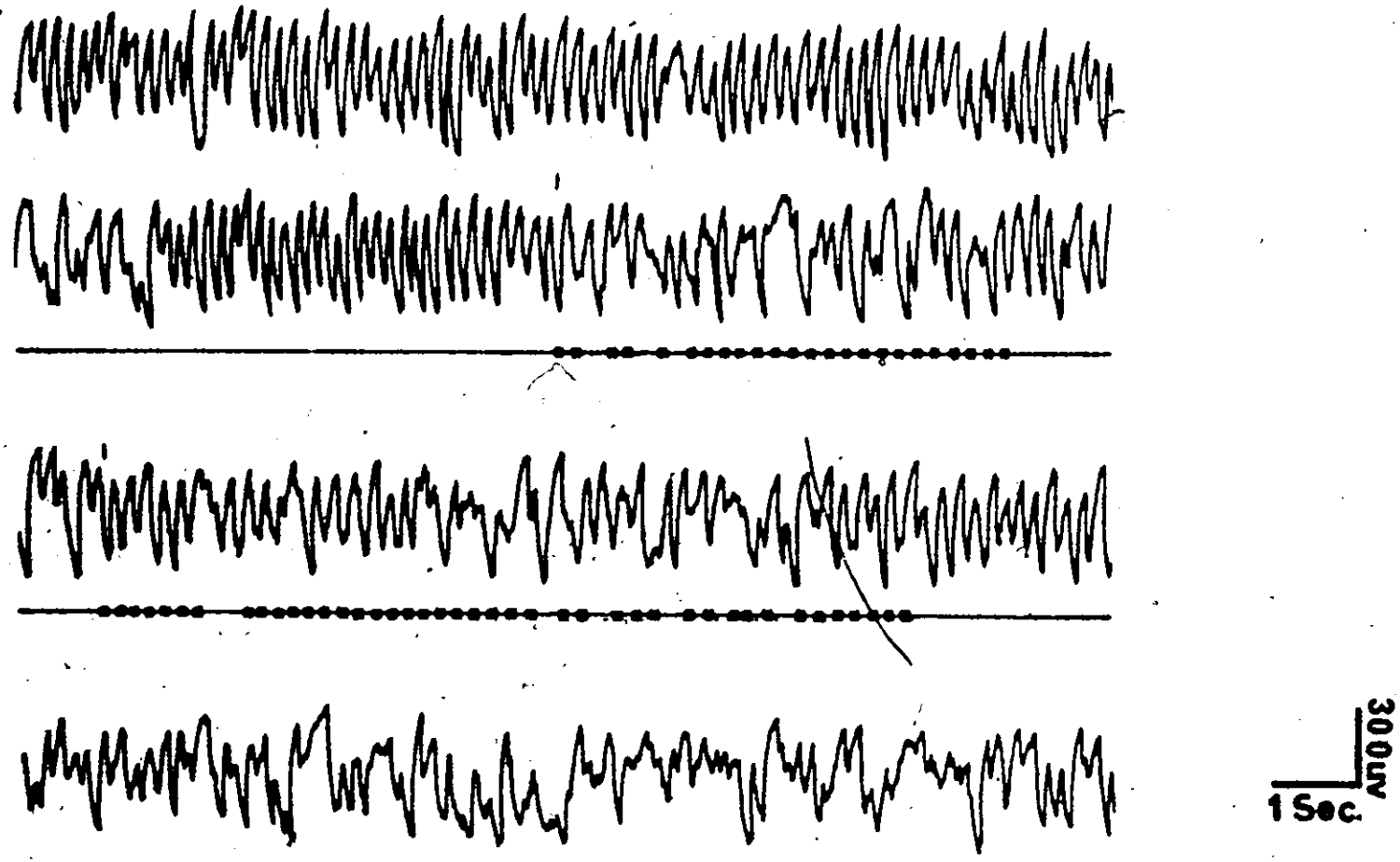
Figures 30, 31, and 32

Dorsal hippocampal EEG samples of ND-1, ND-2, and ND-3 during normal drinking sessions.

RAT N D- 1

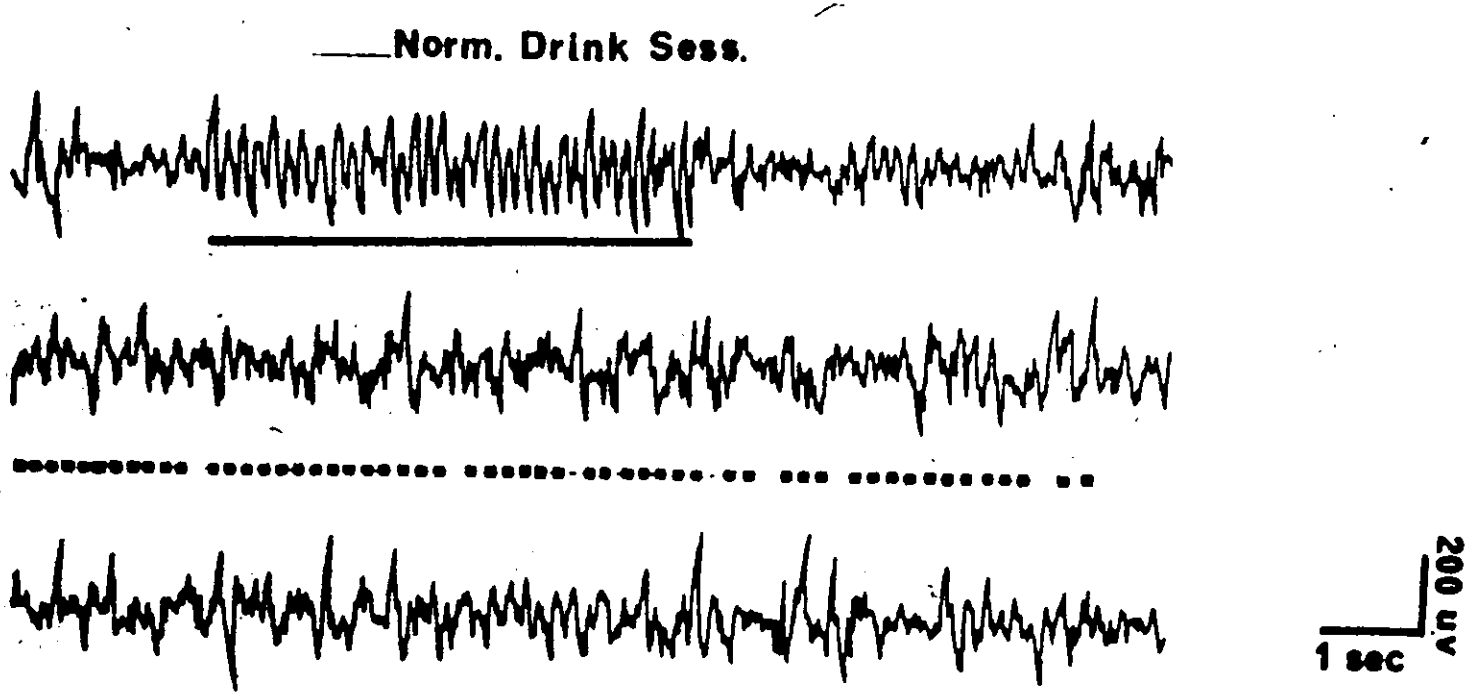
RIGHT HIPP.

Norm. Drink Sess.



RAT ND–2

RIGHT HIPP.



RAT ND – 3

RIGHT HIPP.

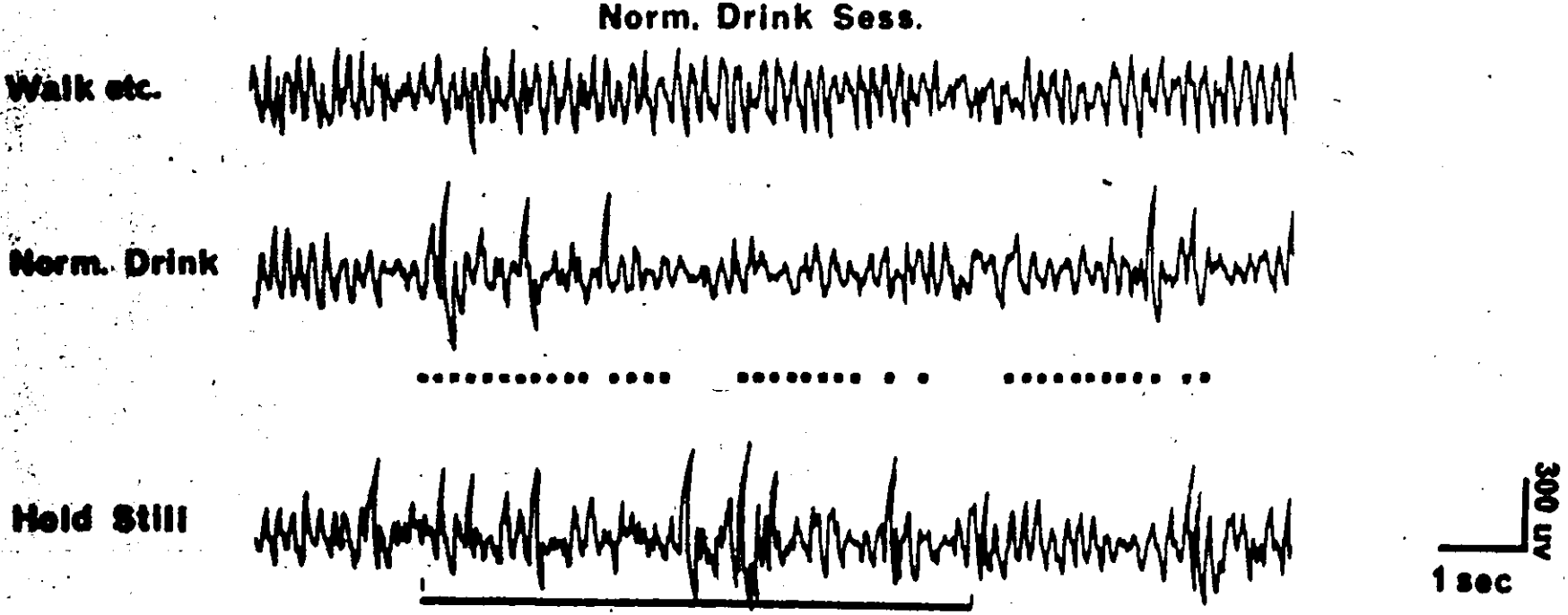


Table 18a

Spectral Ratio

Rat	Walking, etc.	Drinking	Drinking & Move	Holding still
ND-1	0.80	0.38	0.53	0.48
ND-2	0.74	0.41	——	0.39
ND-3	0.79	0.62	——	0.62
Means	0.78	0.47	0.53	0.50

$F_{responses} = 17.67$, df = 2, 4, $p < 0.025$

Table 18b

Modal Frequency

Rat	Walking, etc.	Drinking	Drinking & Move	Holding still
ND-1	6.25	3.75	5.25	5.75
ND-2	6.50	3.50	——	5.75
ND-3	6.25	5.50	——	5.75
Means	6.33	4.25	5.25	4.67

$F_{responses} = 2.82$, df = 2, 4, $p > 0.10$

Histological results

The electrode tip locations can be found in Figures 17 through 25 in Chapter II. Of the placements in which dorsal hippocampal RSA was associated with walking, etc. and LIA was associated with normal drinking and holding still, two subjects (ND-1 and ND-3) had one tip of a bipolar pair directly on the pyramidal cell layer and the other tip between the pyramidal cell layer and the granule cell layer, while ND-2 had both tips of a bipolar pair directly on the pyramidal cell layer. Of the placements that displayed relatively little RSA during walking, etc., ND-1 had one tip of a bipolar pair in the dentate gyrus and the other in the cortex, ND-2 had one immediately below the pyramidal cell layer and the other immediately above the pyramidal cell layer, and ND-3 had both tips in the granule cell layer.

Discussion

The results of Experiment 3a indicate that normal drinking, not associated with extraneous movements, was correlated with dorsal hippocampal LIA, while normal drinking associated with small vertical head movements was correlated with a mixture of dorsal hippocampal LIA and RSA, thus, replicating the findings of Vanderwolf (1971).

In a similar vein, Vanderwolf (1971) reported that small amplitude hippocampal RSA accompanied head scratching in rats, if the rats assumed an unstable posture in which the neck and trunk were curved laterally. Vanderwolf suggested that such an unstable posture required small, but continual, voluntary phasic skeletal adjustments. Scratching in rats without postural readjustments, according to Vanderwolf, is associated with dorsal hippocampal LIA.

Experiment 3b

When food deprived rats are trained to lever press for food pellets on intermittent schedules of reinforcement and when drinking water is continuously available in the experimental chambers, most rats will, after a few sessions, develop a highly repetitive post-pellet drinking bout that results in abnormally large intakes of water during the experimental sessions. This phenomenon was first reported by Falk (1961) and is known as schedule induced polydipsia (SIP). SIP does not appear to be under the control of normal thirst stimuli (Stricker and Adair, 1966). Furthermore, when subjects are not water deprived, SIP is non-regulatory, especially after considerable water has already been ingested in an experimental session. If SIP were associated with RSA, one would have to redefine the behavioral correlates of RSA. If SIP were associated with non-RSA, one could still maintain that hippocampal EEG is related to the form or topography of response.

The purpose of Experiment 3b was, therefore, to determine whether dorsal hippocampal EEG during SIP differs from that during operant licking or normal drinking.

Method

Subjects

The subjects were F-2 that had been previously employed in Experiment 1, and LF-1, an experimentally naive male hooded rat from the Quebec Breeding Farms.

Apparatus

The equipment that was employed was the same as that previously used in Experiment 1.

Training procedure

The rats were trained to lever press on a fixed interval of 30 seconds schedule of reinforcement for 50 mg. Noyes rat pellets. A drinking tube, providing a source of deionized water, was continuously available during each experimental session; the sessions were terminated after approximately 100 food pellets had been delivered. F-2 was run for three training sessions and LF-1 for five training sessions. After the training sessions, recording sessions were conducted in which EEG records and videotapes of behavior were obtained.

Results

Acquisition of lever pressing and polydipsic drinking

Event record samples of lever pressing and polydipsic drinking in the last training sessions before the recording sessions for each rat are shown in Figure 33. Lever pressing predominated in the latter part of each fixed interval and polydipsic drinking predominated after the delivery and consumption of each food pellet. During the last training session, F-2 produced 1215 lever presses and 7146 licks, while receiving 125 food rewards. (Previous behavioral data had indicated that an average of 125 licks was necessary to consume 1.0 ml. of liquid with the drinkometer used in this experiment; thus, F-2 consumed approximately 57.2 ml. of water in approximately 62.5 minutes.) During the last training session, LF-1 produced 1013 lever presses and 5361 licks, while receiving 100 food pellets. (A consumption of approximately 42.9 ml. of water in 50 minutes.)

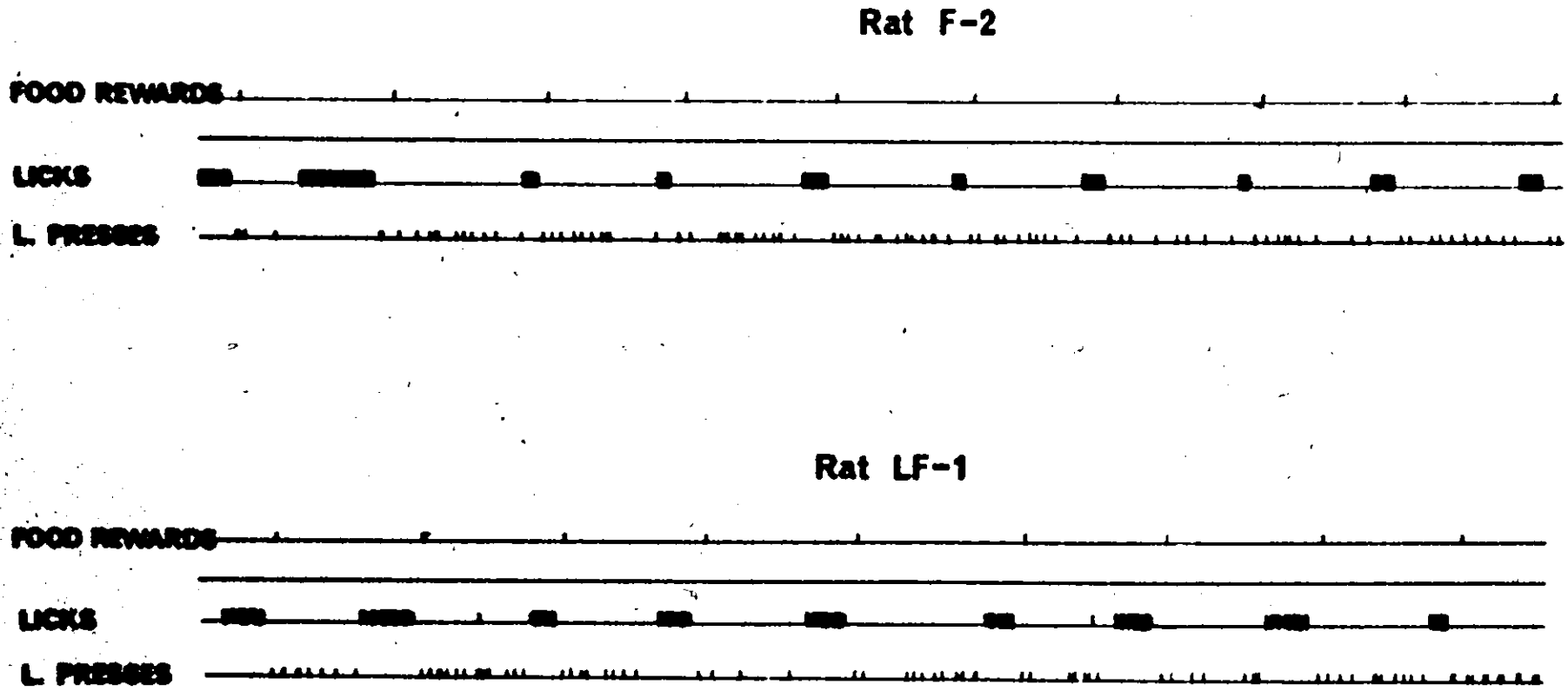
Electrical activity of the hippocampus

EEG samples are shown for F-2 and LF-1 from the recording sessions in Figures 34 and 35. The EEG sample of LF-1 during walking, rearing etc. was selected near the beginning of the recording session. The samples associated with lever pressing and polydipsic drinking for both rats were selected after approximately 50 Noyes pellets had been delivered in the recording sessions.

Visual inspection of the EEG samples indicates that the walking, rearing etc. of LF-1 were accompanied by dorsal hippocampal RSA. The

Figure 33

Event records of food reward deliveries, polydipsic licks, and operant lever presses for F-2 and LF-1.

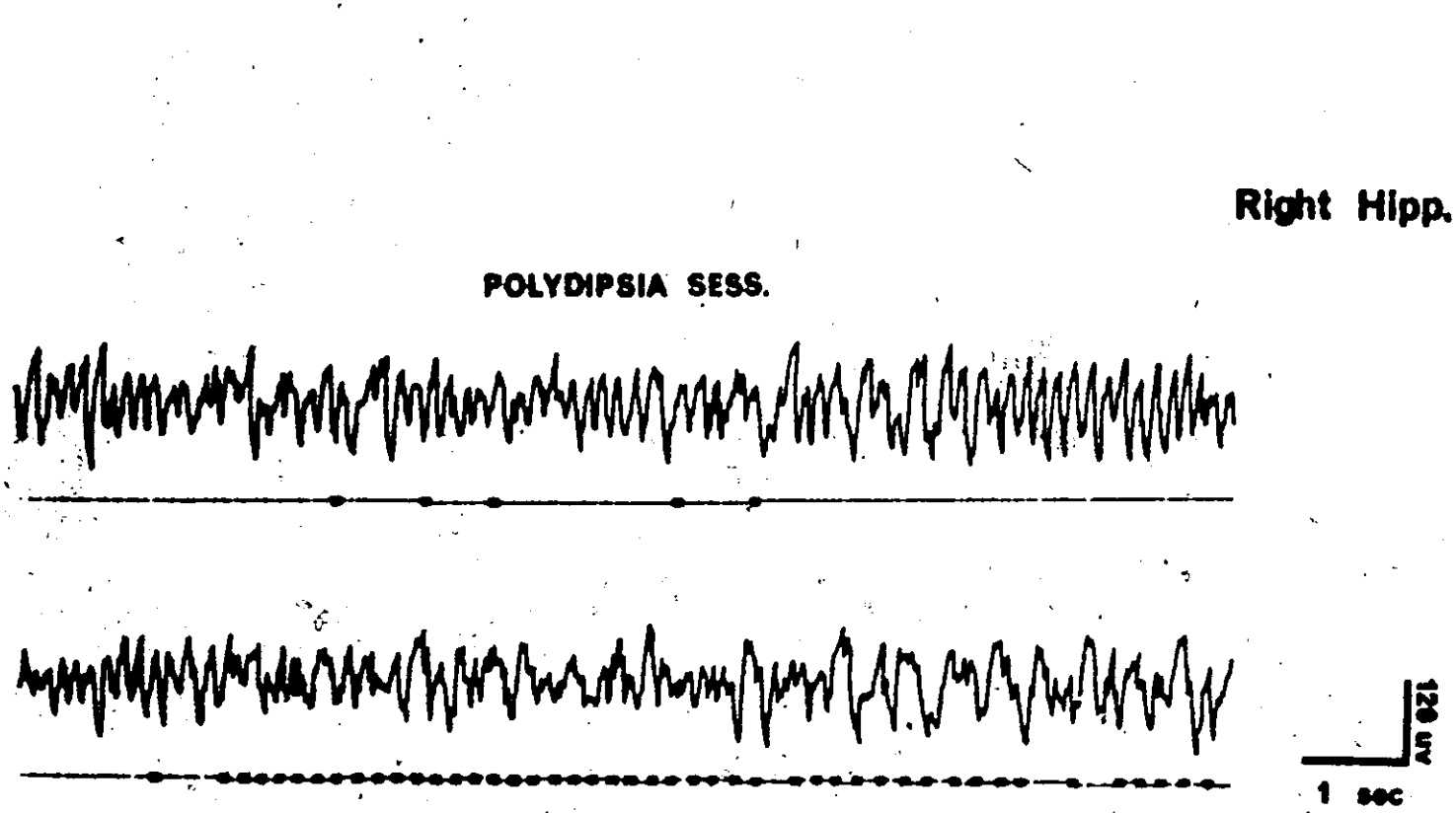

Rat F-2
FOOD REWARDS
LICKS
L. PRESSES
Rat LF-1
FOOD REWARDS
LICKS
L. PRESSES

Figures 34 and 35

Dorsal hippocampal EEG sample of F-2 and LF-1 during polydipsia sessions.

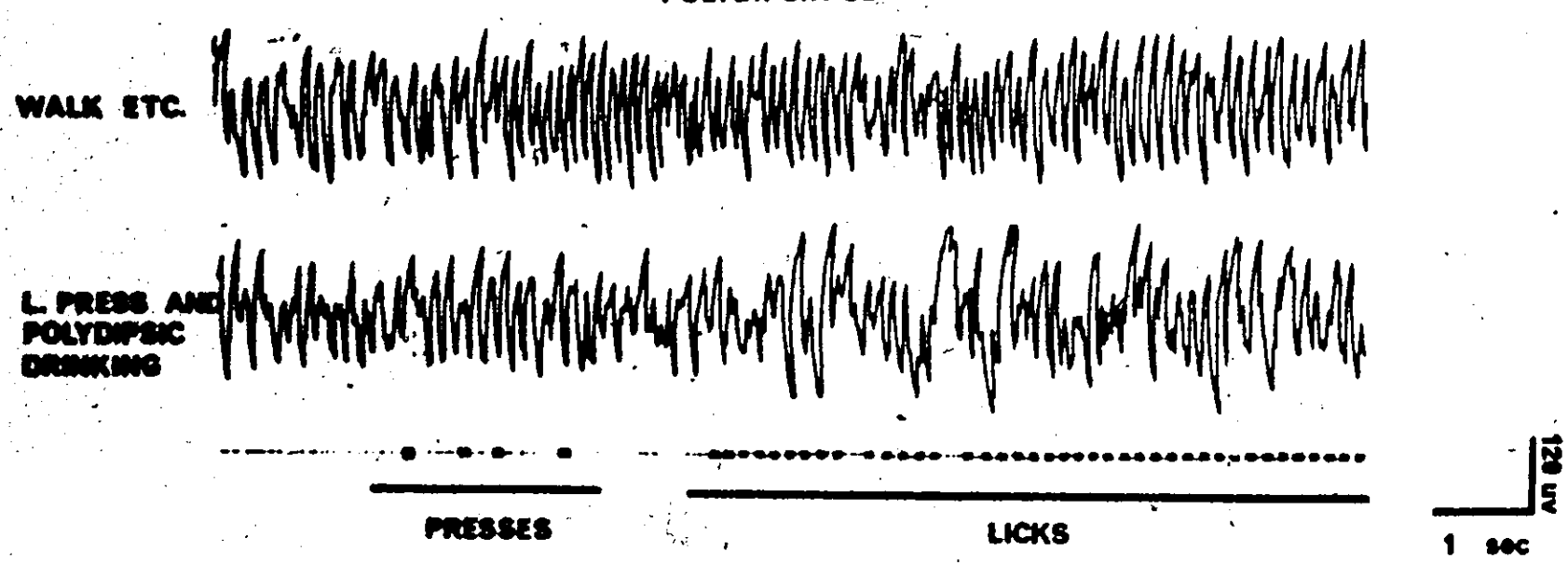
Rat F-2

Right Hipp.



Rat LF-1

Left Hipp.



lever pressing of both rats was associated with dorsal hippocampal RSA, while the polydipsic drinking of F-2 was associated with dorsal hippocampal LIA, and that of LF-1 with a mixture of LIA and relatively smaller amplitude RSA.

Power spectral data derived from the EEG samples are shown in Table 19. (The power spectra can be found in Figures 17 and 18 of the Appendix section.) Samples were collected for spectral analyses according to criteria previously described. The power spectral ratios were the same during lever pressing and polydipsic drinking with F-2, and, in the case of LF-1, the ratio associated with lever pressing was greater than that associated with polydipsic drinking. The modal frequencies associated with lever pressing were greater than those with licking in both cases.

Table 19a

Spectral Ratio

Rat	Walking, etc.	Lever pressing	Polydipsic drinking
F-2	....	0.58	0.58
LF-1	0.70	0.70	0.47
Means	0.70	0.64	0.53

Table 19b

Modal Frequency

Rat	Walking, etc.	Lever pressing	Polydipsic drinking
F-2	....	6.25	6.00
LF-1	7.25	7.00	2.50
Means	7.25	6.63	4.25

Discussion

The results of Experiment 3b indicate that the SIP of LF-1 was correlated with relatively less dorsal hippocampal RSA than that with lever pressing; F-2 showed similar though much weaker differences. Since SIP does not appear to be under the control of normal physiological thirst stimuli (Stricker and Adair, 1966), one could suggest that there is no difference between SIP and normal drinking, as far as the hippocampal correlates of such drinking responses are concerned.

Experiment 3c

The purpose of Experiment 3c was to determine whether the dorsal hippocampal EEG that is associated with the operant licking of a tungsten rod in order to obtain food rewards differs from that associated with licking in other behavioral situations.

The subjects were not water deprived and did not ingest water when licking the tungsten rod. Therefore, such licking is clearly non-regulatory. If the operant licking of the tungsten rod were associated with RSA, it is possible to conclude that RSA is related to certain instances of non-regulatory licking. If the operant licking of the tungsten rod were associated with non-RSA, one could still maintain that hippocampal EEG is related to form of response.

Method

Subjects

The subjects were two male hooded rats from the Quebec Breeding Farms. One (LF-3) was naive and one (LF-1) had been previously employed in Experiment 3b. Each rat was individually housed and maintained at 80% of its normal body weight; water was available at all times in the home cages.

Apparatus

The equipment that was employed was the same as that used in previous experiments with the modification that a lickometer was substituted for the drinking tube. The lickometer (Wall, Walters, and England, 1972) consisted of an 1/8 inch diameter tungsten rod coated with an insulating layer of glass, except for a small exposed area on the underside of the tip. Each contact of the rat's tongue with the exposed area of the tungsten rod completed the drinkometer circuit.

Surgical procedure

The surgical procedure was the same as that used previously. LF-1 was implanted with monopolar electrodes and LF-3 with bipolar electrodes.

Normal drinking sessions

EEG recordings and videotapes of behavior were obtained during normal drinking sessions before any operant training was started. The

apparatus and schedule parameters that were employed were the same as those used in Ecperiment 3a. The data were obtained during the fourth normal drinking session for each rat.

Training procedure

The two rats were trained, employing a shaping procedure, to lick the lickometer on a variable ratio schedule of reinforcement with an average requirement of 16 responses in order to obtain 50 mg. Noyes food pellets; sessions were terminated after approximately 50 pellets had been delivered. After licking rates had stabilized, recording sessions were conducted during which hippocampal EEG and videotapes of behavior were obtained. LF-1 was then trained, employing a shaping procedure, to lever press on a variable ratio schedule of reinforcement with an average requirement of 16 responses in order to obtain 50 mg. Noyes food pellets; LF-1 had two lever pressing training sessions. Again, a recording session was conducted after stabilized responding.

Results

Terminal performances of operant responses

LF-1 operantly licked at an average rate of 62.7 responses/minute during the last training session prior to the recording session; LF-3 at a rate of 9.1 responses/minute. LF-1 pressed at a rate of 10.1 responses/minute during the last training session prior to the recording session.

Electrical activity of the hippocampus

Hippocampal EEG samples are shown for LF-1 and LF-3 in Figures 36 and 37. The EEG samples were a part of those selected for spectral analyses; the criteria for selecting EEG samples for spectral analyses were the same as those previously employed. (Additional data can be found in Figures 19 and 20 of the Appendix section.)

Visual inspection of the EEG samples indicates that all cases of walking, rearing etc. were associated with dorsal hippocampal RSA. The lever pressing of LF-1 was associated with dorsal hippocampal RSA, while the operant licking of both rats was associated with dorsal hippocampal LIA. The normal drinking of both rats was associated with LIA. Finally, the holding still of LF-3 was associated with LIA.

Power spectral data derived from the EEG samples can be found in Tables 20 and 21. (Power spectra can be found in the Appendix section, Figures 21 through 24.) The lever pressing of LF-1 was associated with a power spectral ratio of 0.68, and the operant licking of the tungsten rod with a ratio of 0.53. The operant licking of

Figures 36 and 37

Dorsal hippocampal EEG samples of LF-1 and LF-3 during operant lever pressing session, operant licking sessions (tungsten rod), and normal drinking sessions.

RAT LF-1 RIGHT HIPP.

L. Press Sess.

Walk etc.

L. Press

Op. Lick Sess.

Walk etc.

Op. Lick

Norm. Drink Sess.

Walk etc.

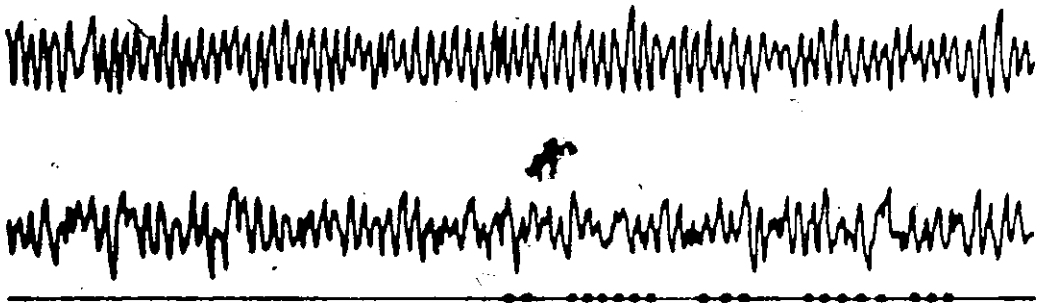
Norm. Drink

1 sec

RAT LF-3

RIGHT HIPP.

Op. Lick Sess.



Norm. Drink Sess.

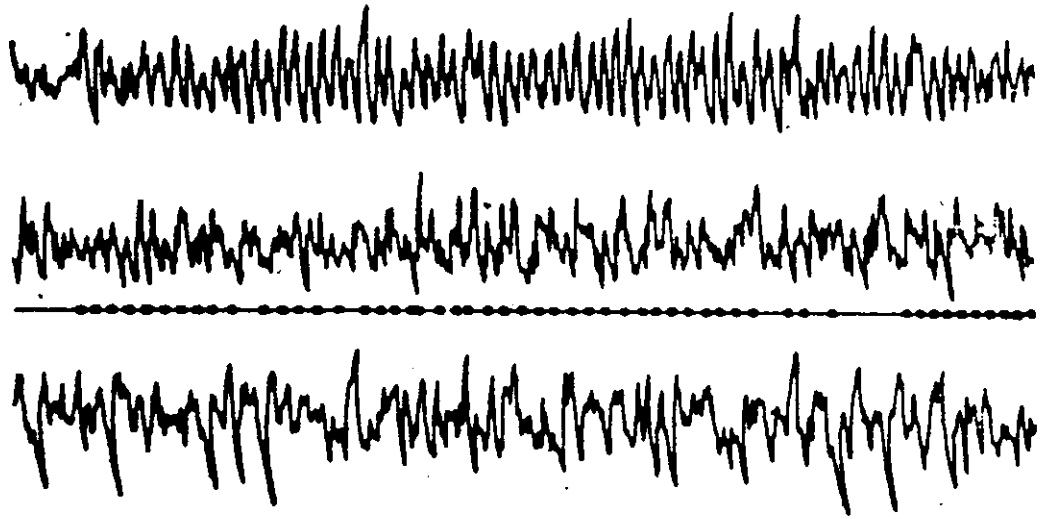


Table 20

Spectral Power Ratios $\frac{(\ 5 \text{ to } 10 \text{ Hz.}\ )}{(\text{zero to } 10 \text{ Hz.})}$

	Normal Drinking Sess.			Positive Reinforcement Sess.			
Rat	Drinking	Walk	Still	Lever Press	Operant Lick	Walk_{LP}	Walk_{Lick}
LF-1	0.45	---	---	0.68	0.53	0.78	0.84
LF-3	0.53	0.87	0.42	---	0.46	---	0.87

Table 21

Modal Frequencies (Upper Limit of 0.25 Hz. Intervals)

	Normal Drinking Sess.			Positive Reinforcement Sess.			
Rat	Drinking	Walk	Still	Lever Press	Operant Lick	$Walk_{LP}$	$Walk_{Lick}$
LF-1	6.25	---	---	6.75	6.50	6.50	6.75
LF-3	5.25	6.50	3.00	---	3.75	---	6.00

LF-3 was associated with a power spectral ratio of 0.46. The lever pressing of LF-1 was associated with a modal frequency of 6.75 Hz., and the operant licking with a modal frequency of 6.50. The operant licking of LF-3 was associated with a modal frequency of 3.75.

Histological results

The electrode tip locations can be found in Figures 17 through 25 in Chapter II. Of the placements from which dorsal hippocampal RSA was associated with walking etc. and lever pressing and LIA was associated with normal drinking, operant licking of the tungsten rod and holding still, LF-1 had one monopolar tip immediately below the pyramidal cell layer in the CA-2 field, while LF-3 had one tip of a bipolar pair directly on the pyramidal cell layer and the other immediately below the pyramidal cell layer.

Discussion

The results of Experiment 3c indicate that lever pressing was associated with dorsal hippocampal RSA, while operant licking of a tungsten rod was associated with LIA. These findings suggest that hippocampal EEG is not related to differences between normal drinking and licking of a tungsten rod.

General Discussion

The results of the three experiments in this Chapter, along with those described in earlier experiments, indicate that licking in several behavioral situations was aasociated with relatively less hippocampal RSA than that associated with lever pressing. Normal regulatory drinking and polydipsic drinking, which can be conceived of as a form of non-regulatory drinking were associated with hippocampal LIA. Finally, the operant licking of a tungsten rod, during which no water was ingested, was associated with hippocampal LIA. It would seem, then, that the hippocampal EEG associated with licking is related to the form of response rather than to the type of physiological and behavioral processes that elicit the response, at least in the situations that were explored in this Chapter.

CHAPTER V

Discussion

The main finding of the research reported in this thesis is that operant lever pressing was associated with significantly more dorsal hippocampal RSA than was operant licking. This result suggests that dorsal hippocampal EEG is related to the form of response. Furthermore, results with other responses (walking and holding still) also support this conclusion. That is, walking was accompanied by dorsal hippocampal RSA and holding still by dorsal hippocampal LIA. The results also suggested that the correlation of RSA and walking was better than the correlation of RSA and lever pressing. This conclusion is compelling only if sensory and perceptual processes and central integrative processes were identical in the situations in which the operant response was lever pressing and in the situations in which the operant response was licking. To the extent that such processes were affected by the type of S^D, the type of reinforcer and the conditioning situation, it seems that these requirements were met. There were no apparent differences in EEG that were related to the type of S^D, type of reinforcer, or parameters of the experimental situation. It is, of course, possible that other untried values of these variables might have led to differences in EEG, but this seems unlikely.

Similarly, manipulations in the types of variables that affect licking produced no apparent differences in EEG. That is, it did not seem to make any difference whether the subjects were water deprived or

satiated when they licked , whether drinking was produced by variables that lead to polydipsic drinking rather than by water deprivation, nor whether licking was associated with the ingestion of water or not. All of these types of licking were associated with dorsal hippocampal LIA.

The data of this thesis support the position, therefore, that patterns of dorsal hippocampal EEG are related to the form of response; that is, RSA to responses such as lever pressing and walking, and LIA to responses such as licking and grooming (Vanderwolf, 1969, 1971). The relevant features that distinguish these two groups of responses will be discussed later.

There is evidence that does not agree with this conclusion. For example, there are reported occurrences of hippocampal RSA during periods of immobility (Pickenhain and Klingberg, 1967; Brown, 1968; Bennett, 1970; Harper, 1971), during paradoxical sleep (Jouvet, 1967), and during hypnosis (Klemm, 1966, 1969; McBride and Klemm, 1969). It may have been, however, that in the cases of reported immobility that actual small movements may have occurred without detection. In the cases in which paradoxical sleep and animal hypnosis were correlated with hippocampal RSA, instructions that would normally lead to movement may have been sent out from the central nervous system, but may have been inhibited at some lower level (Vanderwolf, 1969).

It has also been reported that movements such as walking were not accompanied by RSA (Bennett and Gottfried, 1970; Black and Young, 1972a). In such cases, it is possible that electrode sites may have been influenced by electrical activity originating from sources other than the pyramidal cell layer of the dorsal hippocampus. For example, Adey, Dunlop, and Hendrix (1960) and Black and Young (1972a) have

demonstrated that the electrical activity of the ventral and dorsal portions of the hippocampus differ during similar behaviors. In addition, Vanderwolf (1969) has shown that with certain electrode placements that the relatively higher frequency EEG originating from the granule cell layer interacts with the EEG from the pyramidal cell layer. In such cases, the RSA associated with movements such as walking and lever pressing is "mixed" with the relatively higher frequency EEG from the granule cell layer. Furthermore, it is possible that the electrodes were not able to pick up the electrical activity originating from the pyramidal cell layer because of the orientation of the electrodes in respect to the pyramidal cell layer (Green, Maxwell, Schindler, and Stumpf, 1960).

In any event, whether these exceptions are related to differences in the function of different parts of the hippocampus, poor electrode placements in respect to the distance from and orientation to the pyramidal cell layer, problems in detecting certain types of responses, species differences (Winson, 1972), or are actual exceptions to the findings of this thesis is not clear.

Specification of response features that might be related to different hippocampal EEG patterns

If one accepts that RSA in the dorsal hippocampus is related to movements such as lever pressing and walking, and that LIA patterns are related to consummatory responses such as licking and eating and to sustained periods of immobility, a further question naturally arises as to how one can specify common features of responses to which these patterns of hippocampal EEG are related.

The results of this thesis indicate that hippocampal EEG patterns are not related to two features of the responses. One feature of these responses is intensity. Lever pressing might be a more intense response than licking, when intensity is roughly defined by the amount of movement that is involved in the performance of a response.. It was found in this thesis that the intense saliva spreading and licking of the body that is induced by increasing temperatures (Hainsworth, 1967; Hainsworth, Stricker, and Epstein, 1968) was accompanied by dorsal hippocampal LIA. Therefore, it is difficult to maintain that RSA is related to the gross intensity of a response.

A second feature is whether the response is an operant or not. One might have argued that RSA accompanies operant responses, and that other hippocampal EEG patterns accompany non-operant responses. That is, RSA might accompany operant lever pressing and operant licking, and LIA might accompany normal drinking. The data force one to reject this suggestion. This rejection, of course, depends on the assumption that both lever pressing and licking for reinforcements are actually operants. In the case of lever pressing, this assumption seems valid and straightforward. However, in the case of licking, it could be argued, as suggested by Vanderwolf (1971), that approaching the water spout or the tungsten rod is an operant response, but that the licking is reflexive. That is, contact of the tongue upon the water or rod elicits a series of licks. Behavioral observations of the operant licking described in this thesis, however, do not support this suggestion. During many inter-trial intervals in the avoidance situation when the rats were not licking, they maintained a position near the tube, almost touching it. In such cases, when the S^D was presented, they often began licking without any

noticeable approach responses.

If one assumes, however, that "voluntary" and "operant" are not identical terms, then one could still maintain, as Vanderwolf (1971) has, that RSA accompanies more voluntary responses and LIA accompanies more reflexive responses. That is, although licking was made an operant response, it still may have retained properties of a more reflexive response. Vanderwolf (1971) has suggested that more reflexive responses such as licking have the following two properties. First, they are more fixed in topography than less reflexive responses. Second, they are primarily affected by the relative state of one motivational system, while less reflexive responses may be affected by the relative states of several motivational systems. According to Vanderwolf, such responses would not be accompanied by hippocampal RSA.

Black and Young (1972b) have made a similar proposal based upon data obtained during a behavioral study of licking. They found that the efficiency of licking as an avoidance response was affected by the relative deprivation state of the physiological thirst system, while lever pressing was not. Black and Young also found that the efficiency of licking as an operant response for food rewards was not affected by the relative state of the physiological thirst system. These findings led Black and Young to propose that hippocampal RSA accompanies responses such as lever pressing and running that can be defined as being relatively free from "constraint" with respect to their "amenability to operant conditioning", while hippocampal LIA accompanies a response such as licking that seems to be "constrained" in respect to its "amenability to operant conditioning."

One problem with the suggestions of Vanderwolf (1971) and

Black and Young (1972b) is that they require holding still to be less voluntary and more constrained than walking or lever pressing. This assumption can be questioned.

A number of other possibilities have been proposed to explain the response features related to different hippocampal EEG patterns. For example, Adey, Dunlop, and Hendrix (1960) proposed that hippocampal RSA is a correlate of the execution of a well-planned or goal-directed behavior. The data of this thesis support this hypothesis only if one assumes that lever pressing was a well-planned or goal-directed behavior and operant licking was not.

In another proposal, Komisaruk (1970) suggested that hippocampal RSA was related to a limbic-hypothalamic system involved in the rhythmic driving of motor neurons. The data of this thesis do not support this proposal if one assumes that licking is rhythmic.

As another possibility, Klemm (1970, 1971, 1972a, 1972b) suggested that increases in brainstem reticular formation activity and muscle tone are correlated with occurrences of hippocampal RSA. The data of this thesis are consistent with this hypothesis provided that brainstem reticular formation activity and muscle tone are greater during lever pressing, walking, and rearing than during operant licking, grooming, saliva spreading, licking of the body and sustained periods of immobility. In the cases of grooming, saliva spreading and licking of the body, this seems unlikely. These behaviors were as intense as lever pressing. However, these behaviors were accompanied by hippocampal LIA, while lever pressing was accompanied by hippocampal RSA.

In summary, the data of this thesis support the hypothesis

Vanderwolf (1969, 1971) that RSA accompanies the initiation and maintenance of voluntary responses, if one assumes that operant lever pressing is more voluntary in nature than operant licking. The data of this thesis also support the proposal of Black and Young (1972b) that RSA accompanies "unconstrained" responses, if one assumes that lever pressing is less constrained in respect to its amenability to operant conditioning than is licking.

The data of this thesis do not support the suggestions that dorsal hippocampal EEG is related to the relative intensity of a response, the operant function of a response, to the execution of a well-planned or goal-oriented behavior (Adey, Dunlop, and Hendrix, 1960), to the rhythmic driving of motor neurons (Komisaruk, 1970), nor to increases in brainstem reticular formation activity and muscle tone (Klemm, 1970, 1971, 1972a, 1972b).

Relationship between hippocampal electrical activity and skeletal movement

A final question concerns the nature of the relationship between hippocampal EEG and the response that it accompanies. What is the role of the neural processes that are reflected by hippocampal EEG in circuits that control different responses? One possibility is that the pattern of EEG in the hippocampus is produced by feedback from the occurrence of overt skeletal responses. This suggestion, however, is not supported by data obtained with curarized subjects. Curare-like drugs block biochemical activity at neuromuscular junctions and, therefore, block skeletal movements, while leaving other physiological processes nearly normal. Therefore, if curarized subjects can pro-

duce RSA, then RSA obviously cannot be related to feedback from the occurrence of overt skeletal movement. Regarding this point, Dalton (1970) and Black, Young and Batenchuk (1970) have shown that different patterns of hippocampal EEG were operantly conditionable in curarized dogs. Furthermore, Black and Young (1972a) found that S^D's continued to elicit patterns of hippocampal EEG in paralyzed dogs that were similar to those produced in the normal state. This, of course, does not rule out the possibility that hippocampal EEG patterns are involved in central components of neural circuits affecting responses, since curare-like drugs leave these intact.

Although a number of hypotheses have been proposed about the neural circuits relating the hippocampus and behavior (see Bennett, 1971; Douglas, 1967; Kimble, 1968; Vanderwolf, 1971 for recent reviews), the structure of such circuits is still not clear. The results of this thesis and of other experiments suggest that the circuits could be one of two types. First, the hippocampal EEG could reflect the activity of neural circuits directly involved in the control of different behaviors. For example, hippocampal RSA could reflect the activity of neural circuits directly involved in the control of voluntary responses (Vanderwolf, 1969, 1971) or in the control of unconstrained responses Black and Young, 1972b) and hippocampal LIA could reflect the activity of neural circuits directly involved in the control of automatic behaviors (Vanderwolf, 1969, 1971) or in the control of constrained responses (Black and Young, 1972b). Second, the hippocampal EEG could be related to processes other than output or motor processes that are activated only during certain types of behavior. For example, RSA could be

related to sensory processes that occur only during walking, etc. Further research will be necessary to choose between these alternatives.

SUMMARY AND CONCLUSIONS

1. Operant lever pressing was associated with significantly more dorsal hippocampal RSA than was operant licking. Furthermore, walking was accompanied by hippocampal RSA and holding still by hippocampal LIA. These results suggest that dorsal hippocampal EEG is related to the form of response rather than to sensory and perceptual processes or to central integrative processes.

2. Intense saliva spreading and licking of the body that is induced by increasing temperatures (Hainsworth, 1967; Hainsworth, Stricker, and Epstein, 1968) were accompanied by dorsal hippocampal LIA. These results suggest that hippocampal EEG is not related to the gross intensity of response.

3. Since dorsal hippocampal RSA accompanied operant lever pressing, but not operant licking, the data suggest that hippocampal EEG is not related to the operant role of response.

4. Operant licking, normal drinking, polydipsic drinking, and the operant licking of a tungsten rod were all accompanied by dorsal hippocampal LIA. Therefore, manipulations in the types of variables that produce licking did not result in any apparent differences in hippocampal EEG.

5. The hippocampal EEG-behavior relationships in this thesis were dependent on the electrical activity of the pyramidal cell layer. This verifies the observations of others, including Vanderwolf (1969, 1971).

6. The data of this thesis support the hypothesis of Vanderwolf (1969, 1971) that hippocampal RSA accompanies the initiation and

maintenance of voluntary phasic skeletal responses and hippocampal LIA accompanies more "automatic" responses such as licking, if one assumes that operant lever pressing was more voluntary in nature than was operant licking.

7. The data of this thesis support the proposal of Black and Young (1972b) that hippocampal RSA accompanies "unconstrained" responses in respect to their "amenability to operant conditioning" and hippocampal LIA accompanies "constrained" responses, if one assumes that lever pressing was less constrained than operant licking.

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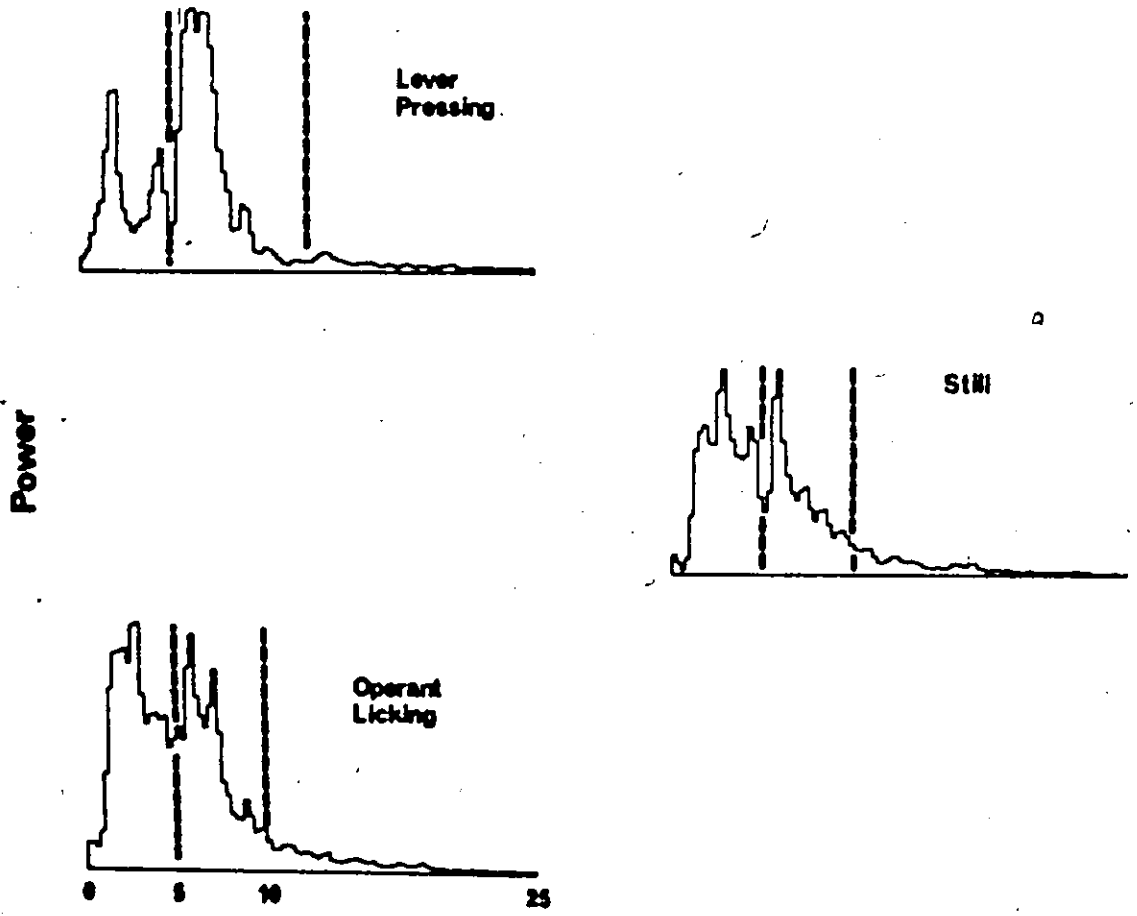
APPENDIX

RAT SA-1

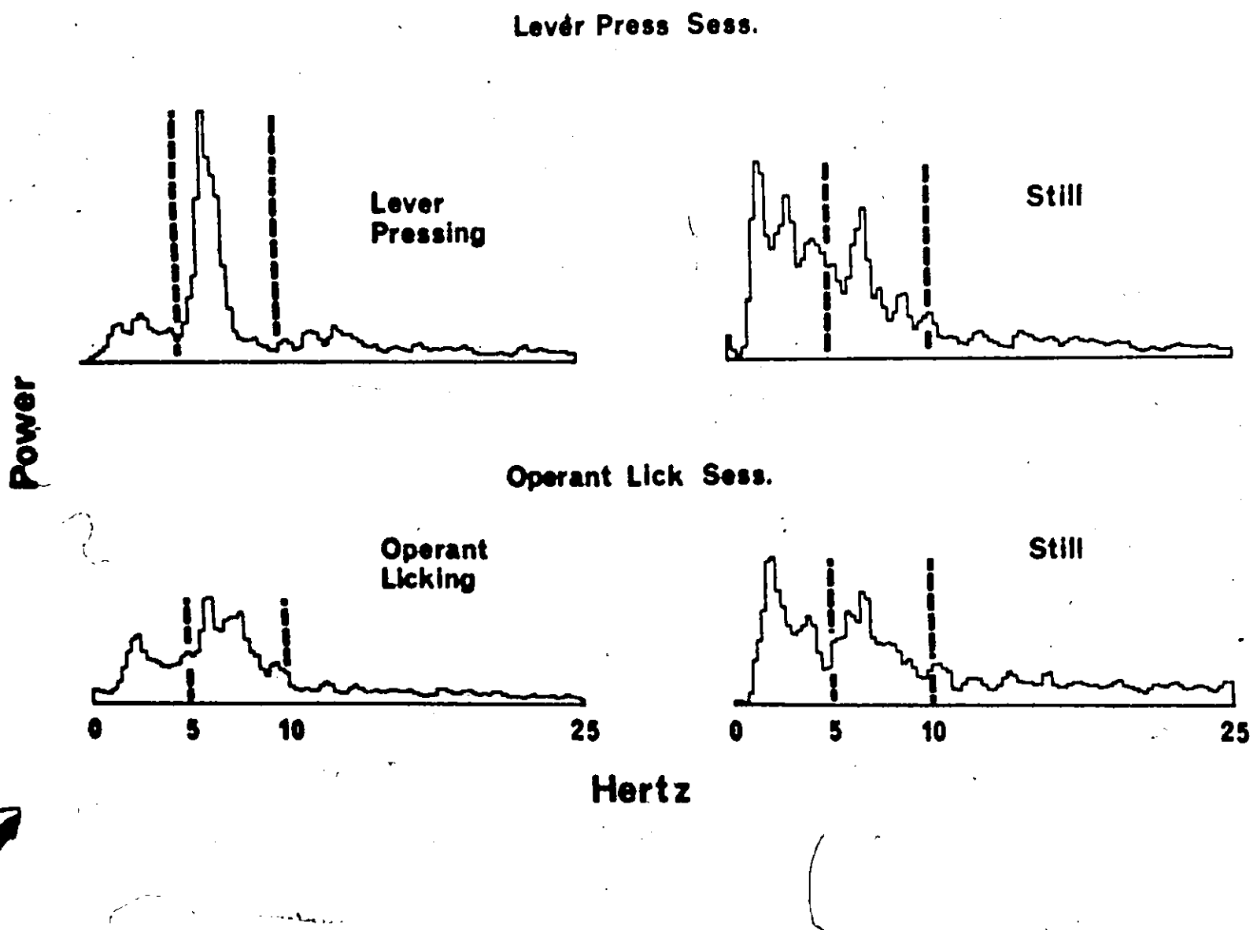
RIGHT HIPP.

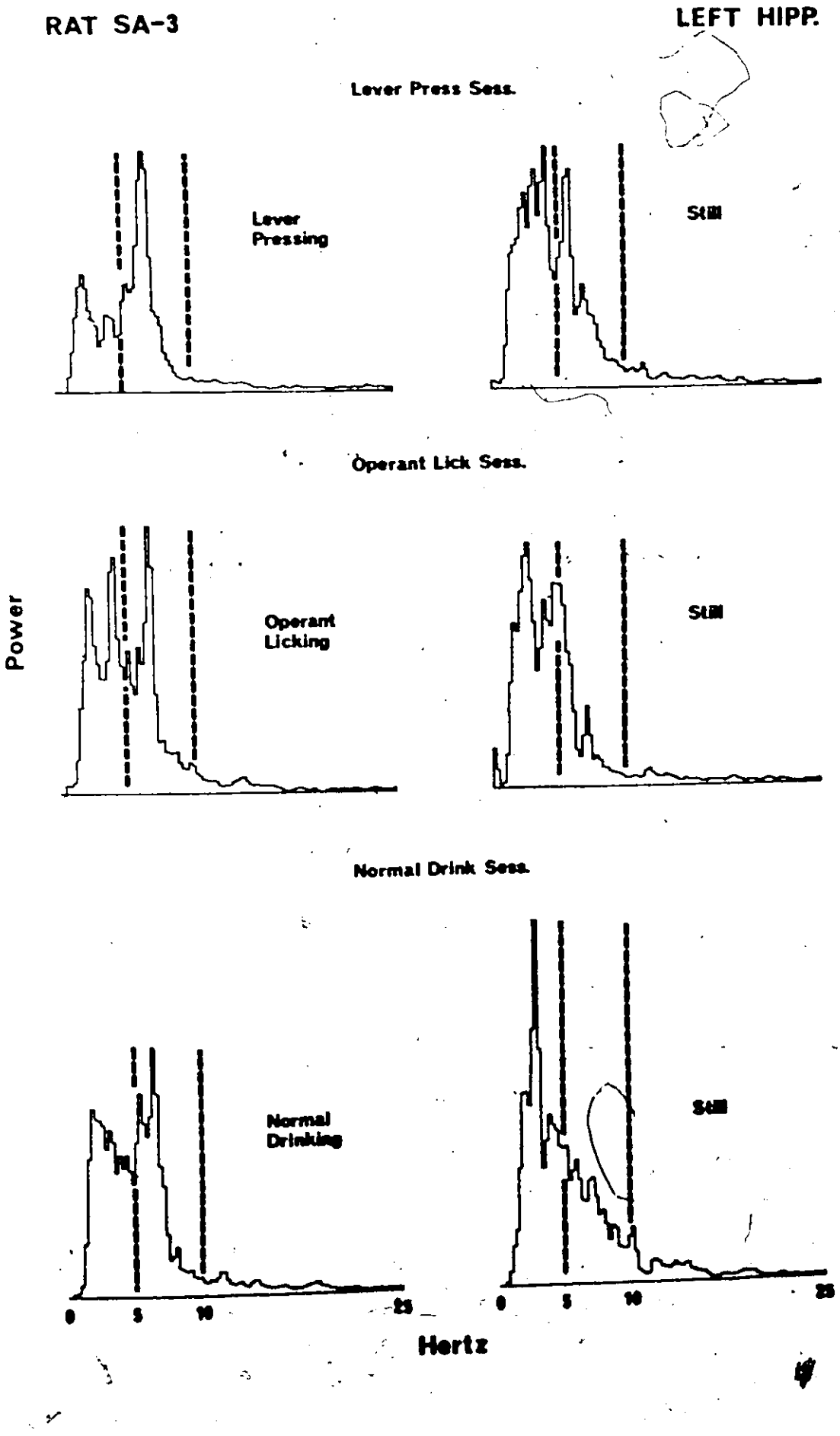
Discrimination Sess.



RAT SA-2

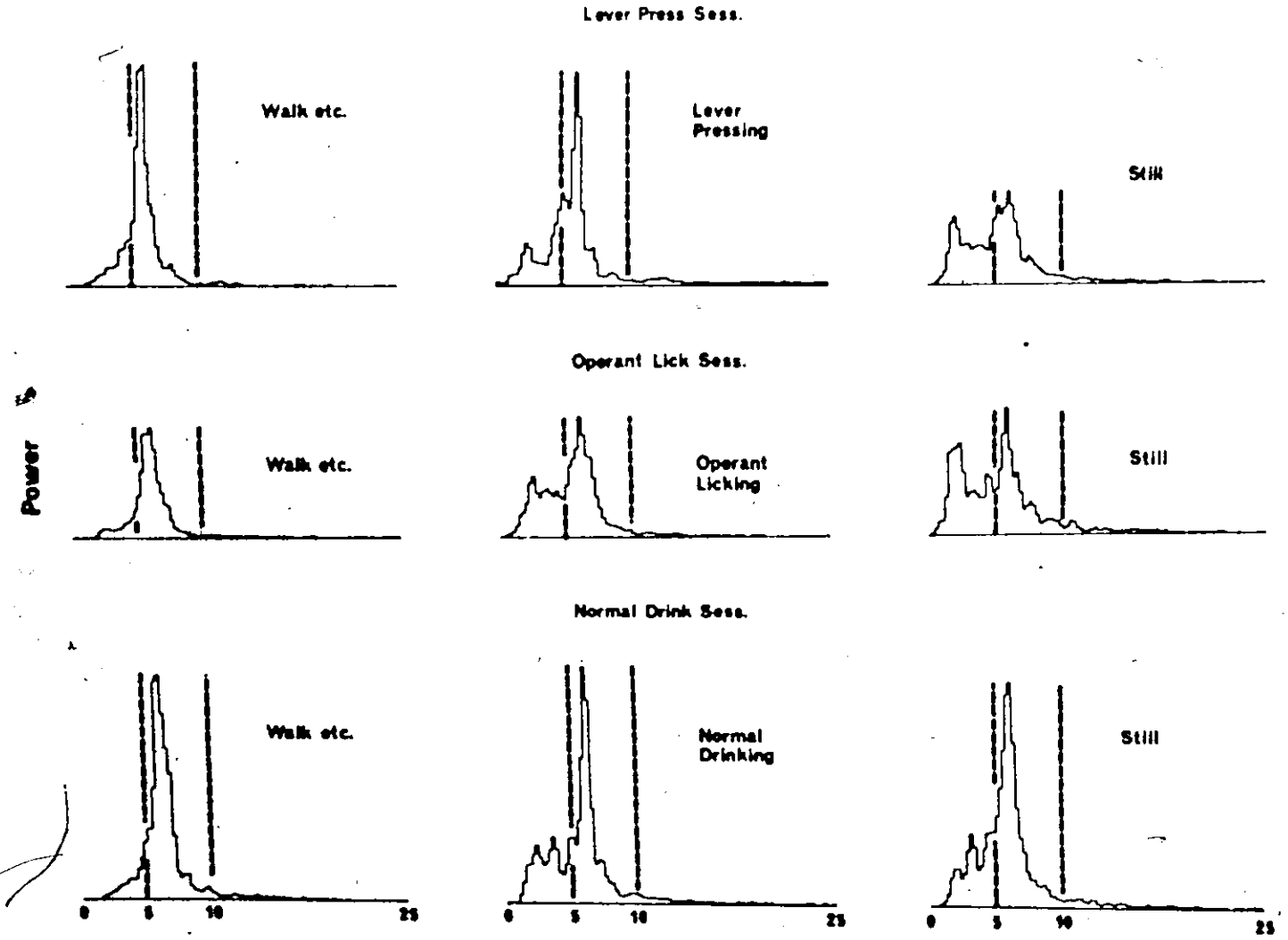
LEFT HIPP.

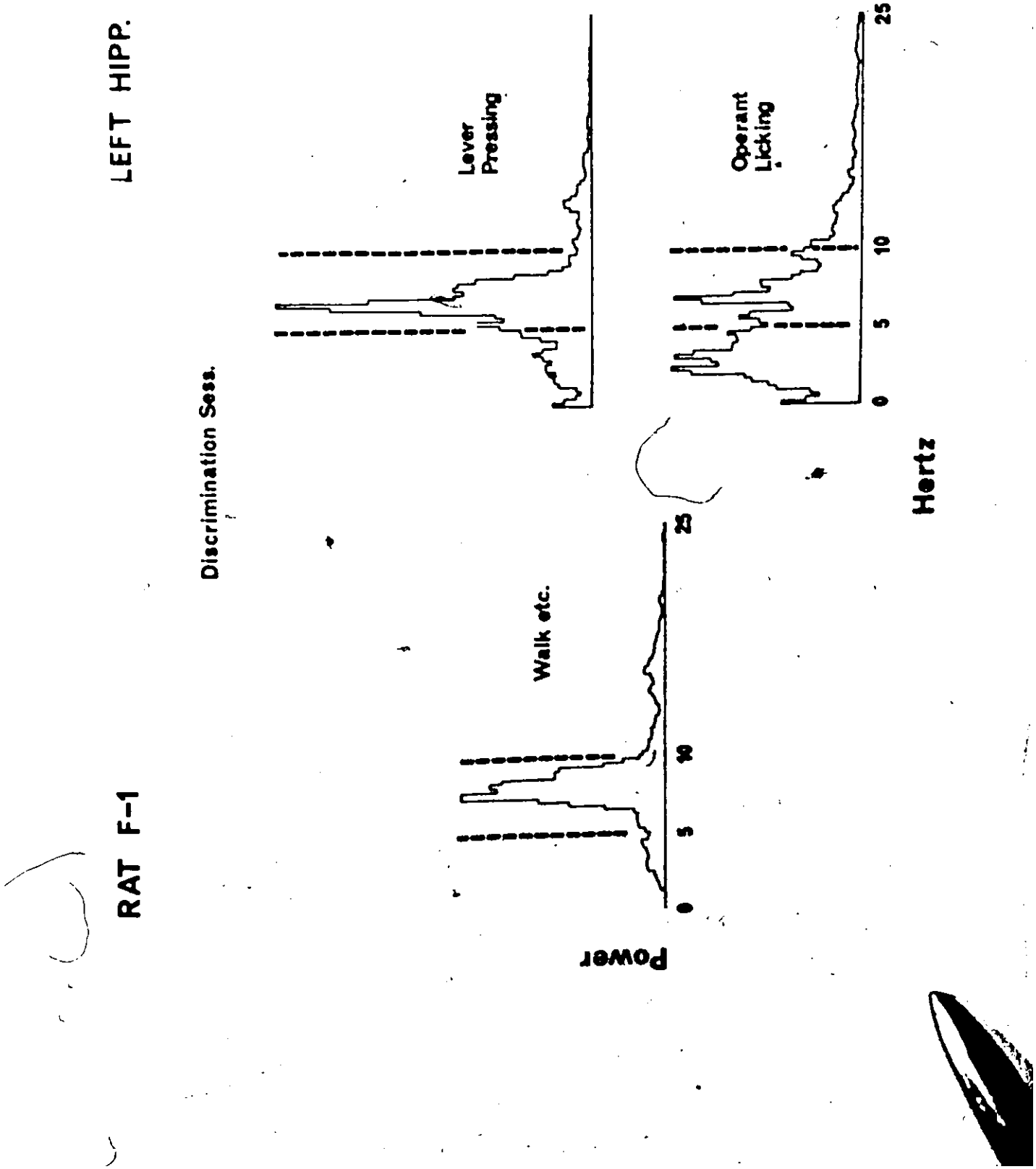



RAT SA-3
LEFT HIPP.
Lever Press Sess.
Lever Pressing
Still
Operant Lick Sess.
Power
Operant Licking
Still
Normal Drink Sess.
Normal Drinking
Still
0
5
10
25
Hertz

RAT SA-4

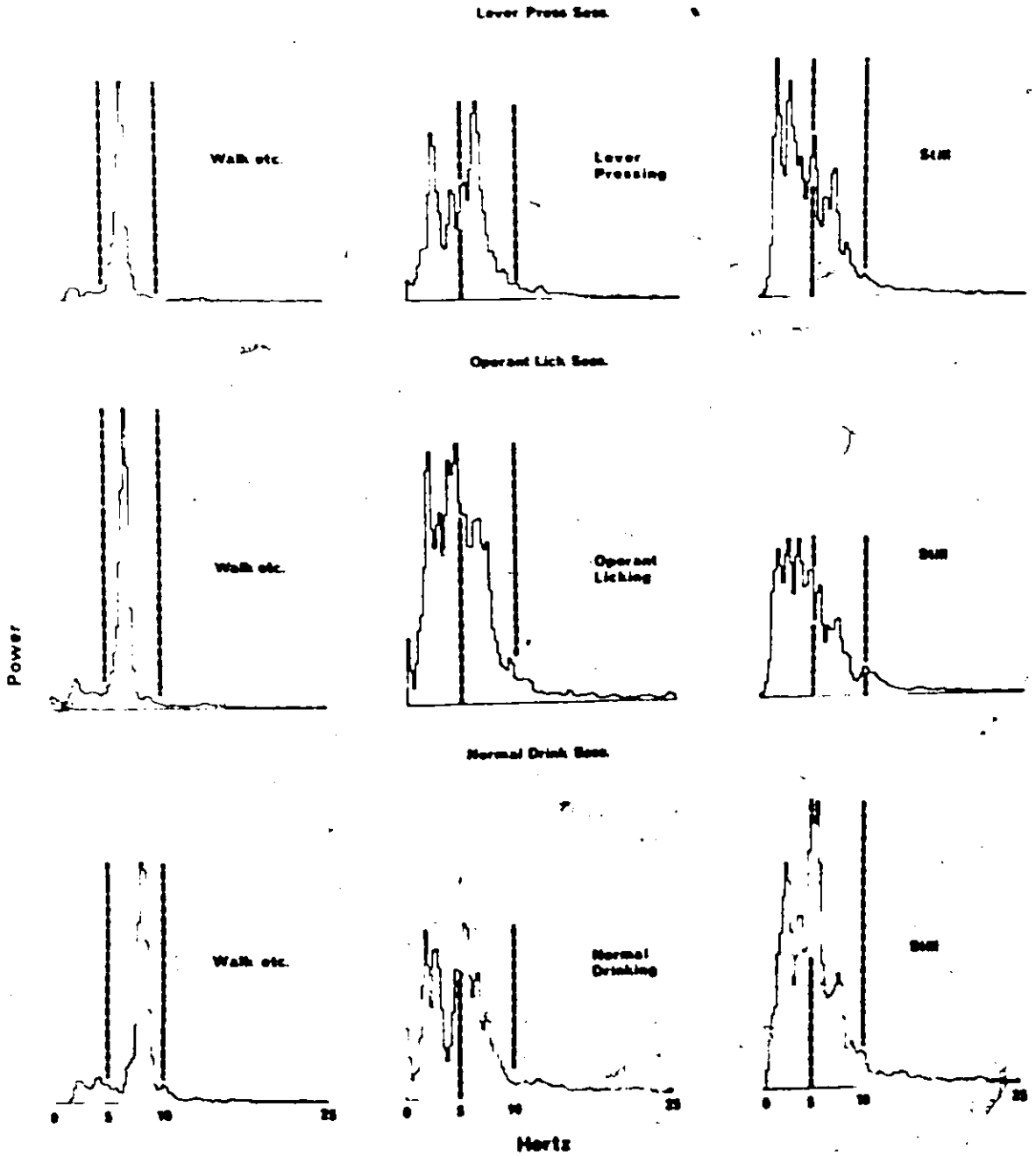
LEFT HIPP.

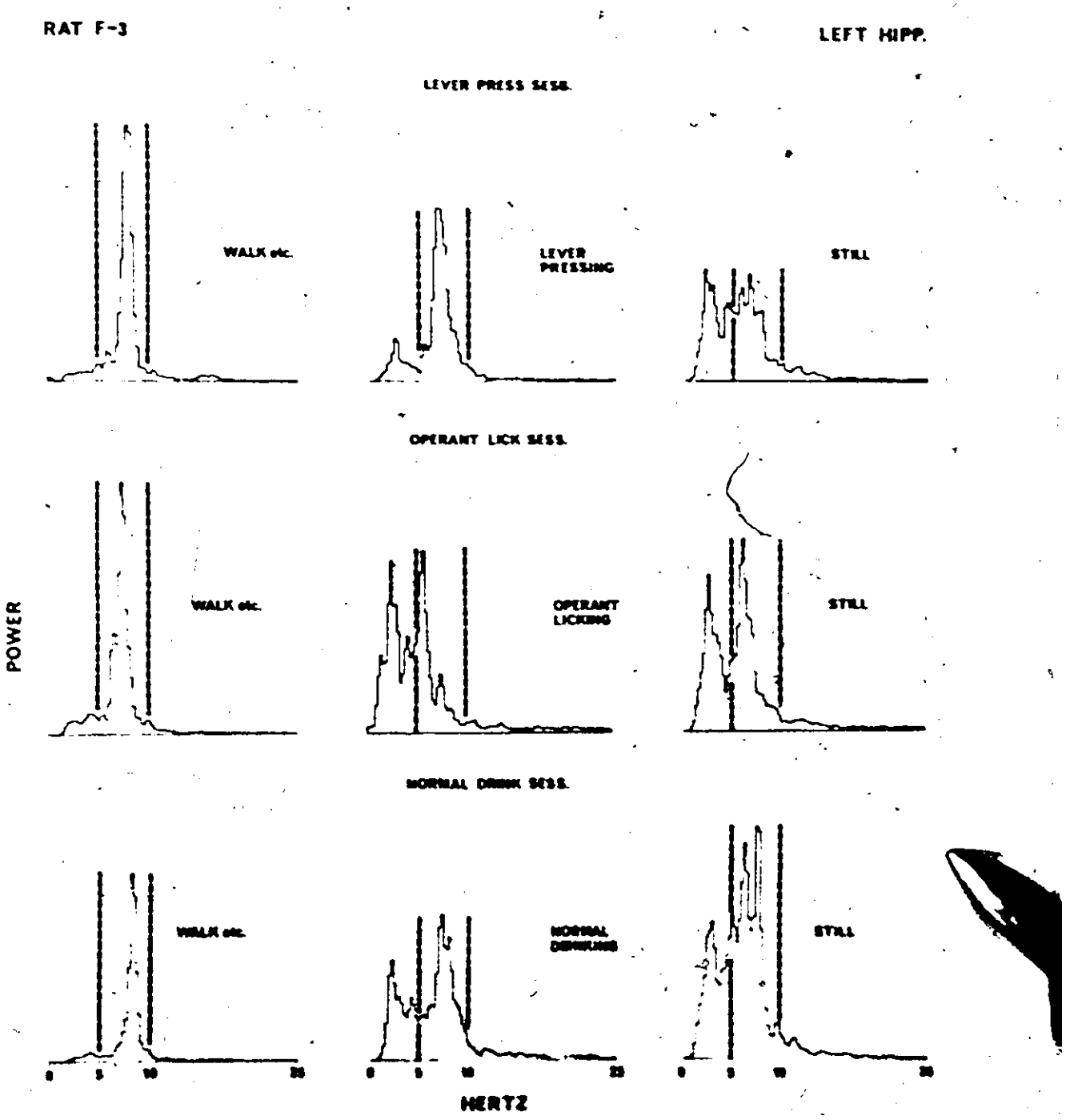



LEFT HIPP.
RAT F-1
Discrimination Sess.
Lever Pressing
Operant Licking
Walk etc.
Power
Hertz
0
5
10
25

RAT F-2

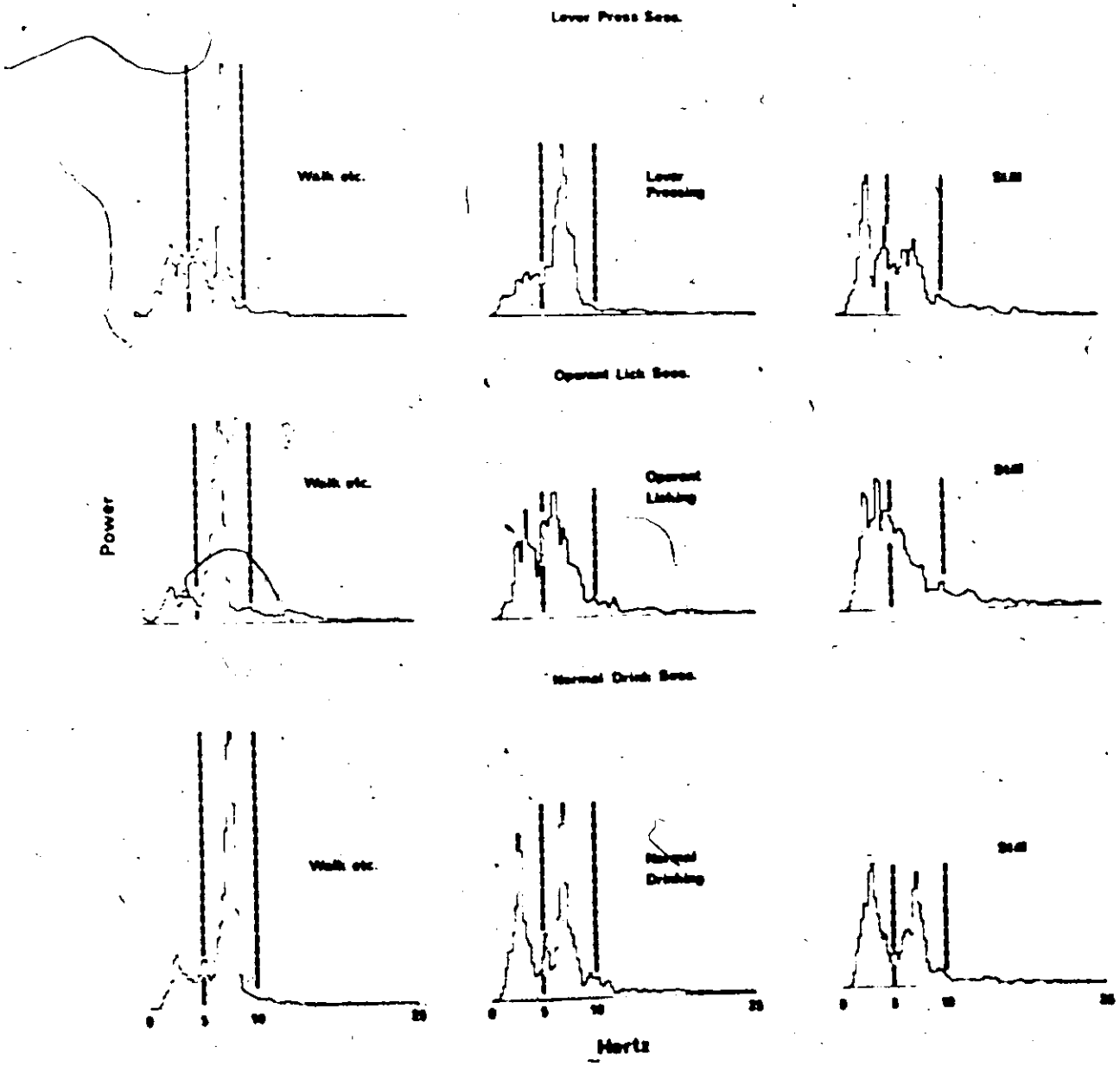
RIGHT HIPP.




RAT F-3
LEFT HIPP.
LEVER PRESS SESS.
WALK etc.
LEVER PRESSING
STILL
OPERANT LICK SESS.
POWER
WALK etc.
OPERANT LICKING
STILL
NORMAL DRINK SESS.
WALK etc.
NORMAL DRINKING
STILL
HERTZ

RAT F-5

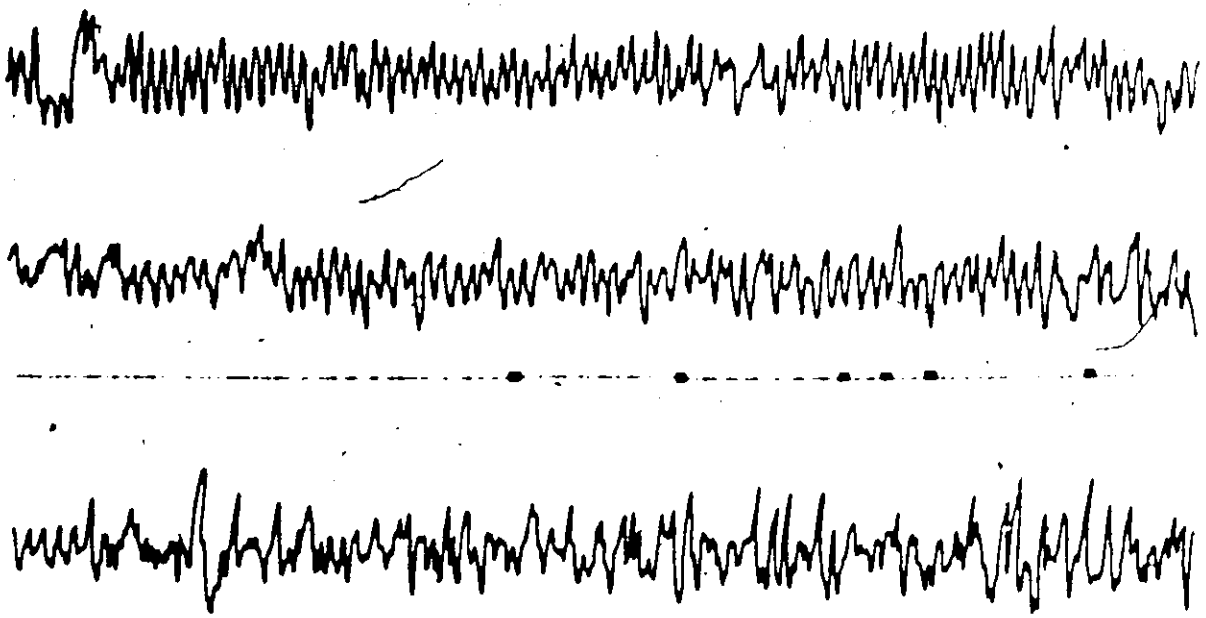
LEFT HIPP.



RAT F-4

LEFT HIPP.

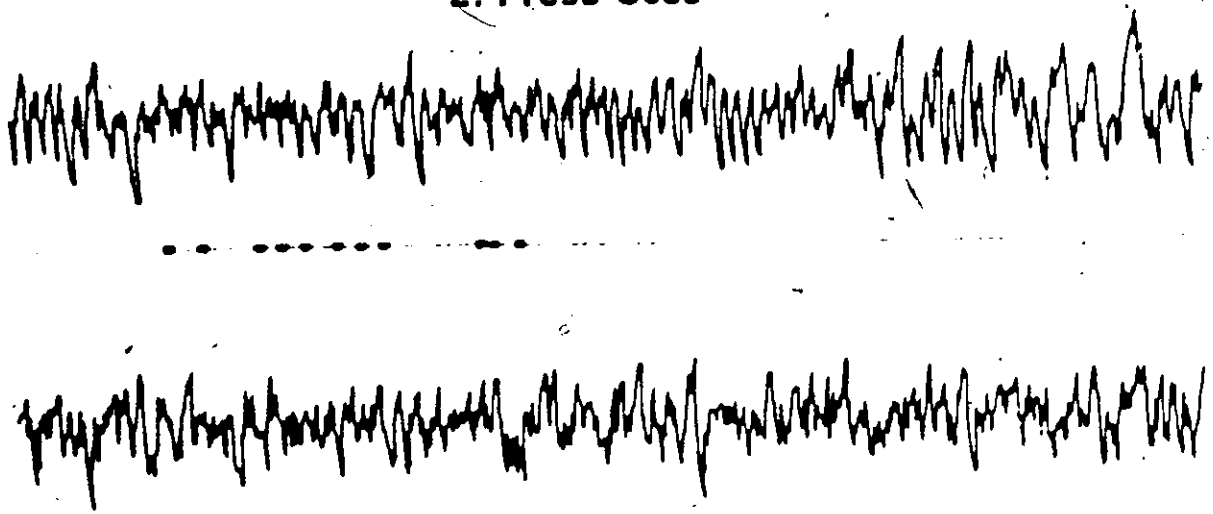
L Press Sess.



RAT F-6

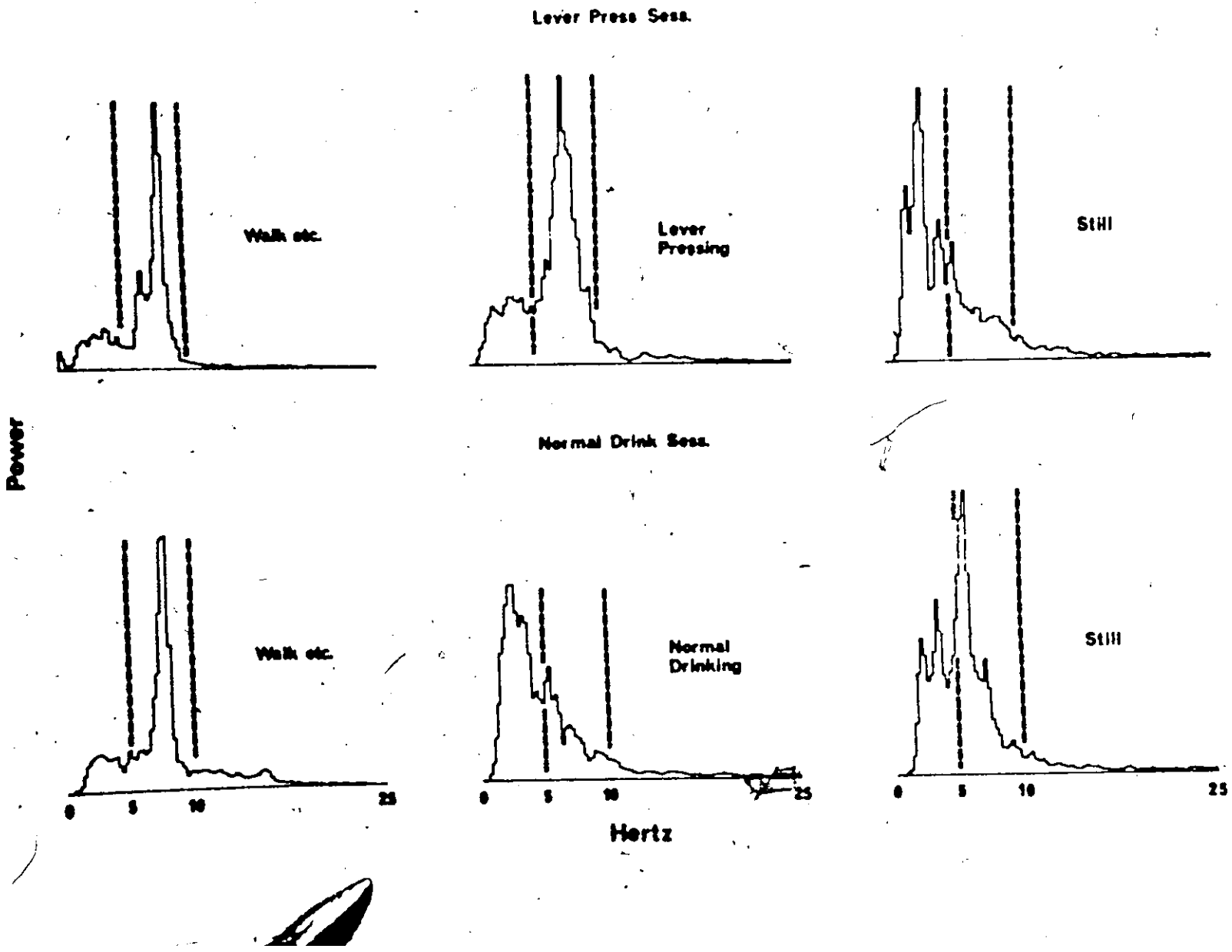
RIGHT HIPP.

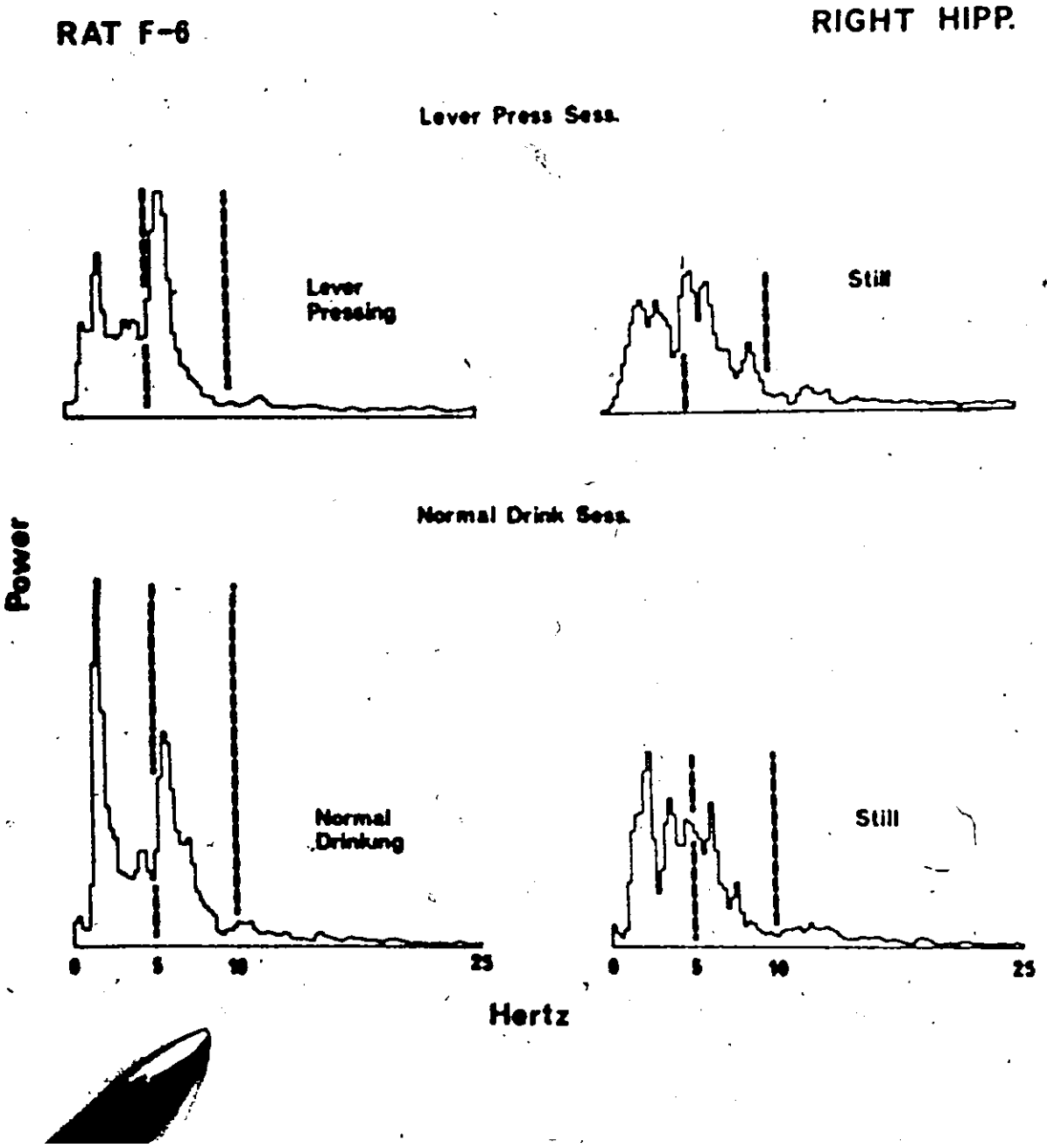
L. Press Sess



RAT F-4

LEFT HIPP.




RAT F-6
RIGHT HIPP.
Lever Press Sess.
Lever Pressing
Still
Normal Drink Sess.
Power
Normal Drinking
Still
0
5
10
25
Hertz

Left Hipp.

Rat G-2

Room Temp.

Walk etc.

Grooming

Hold Still

40° C.

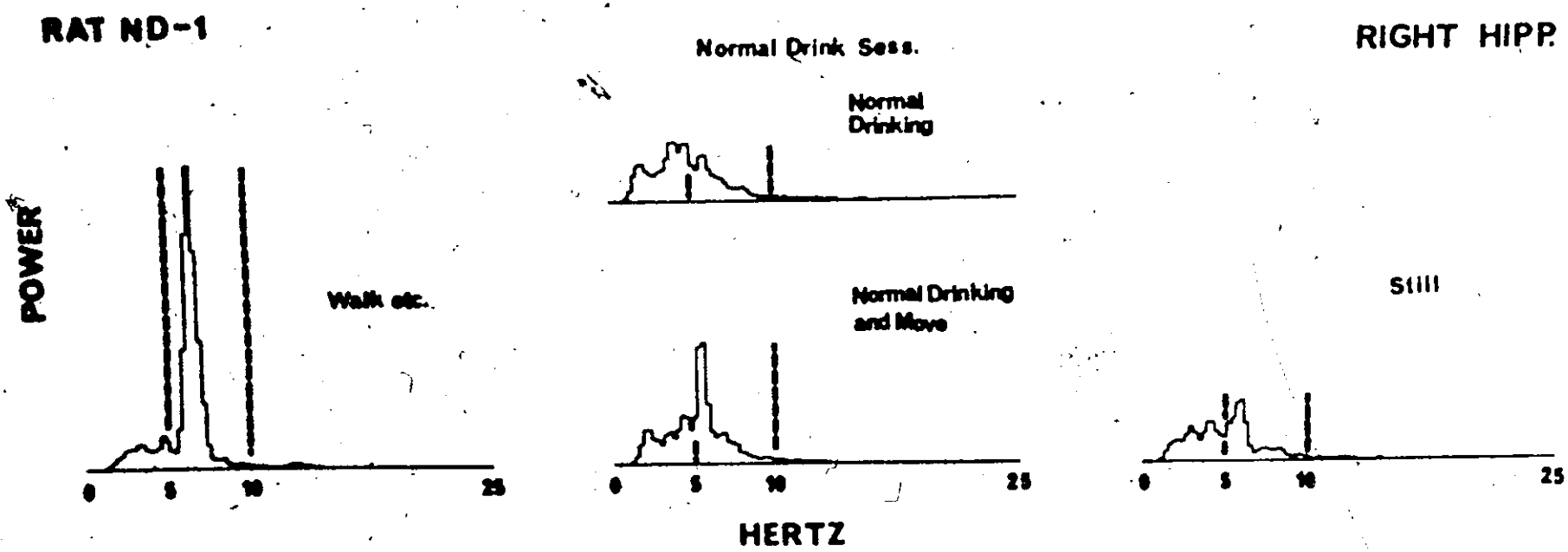
Grooming

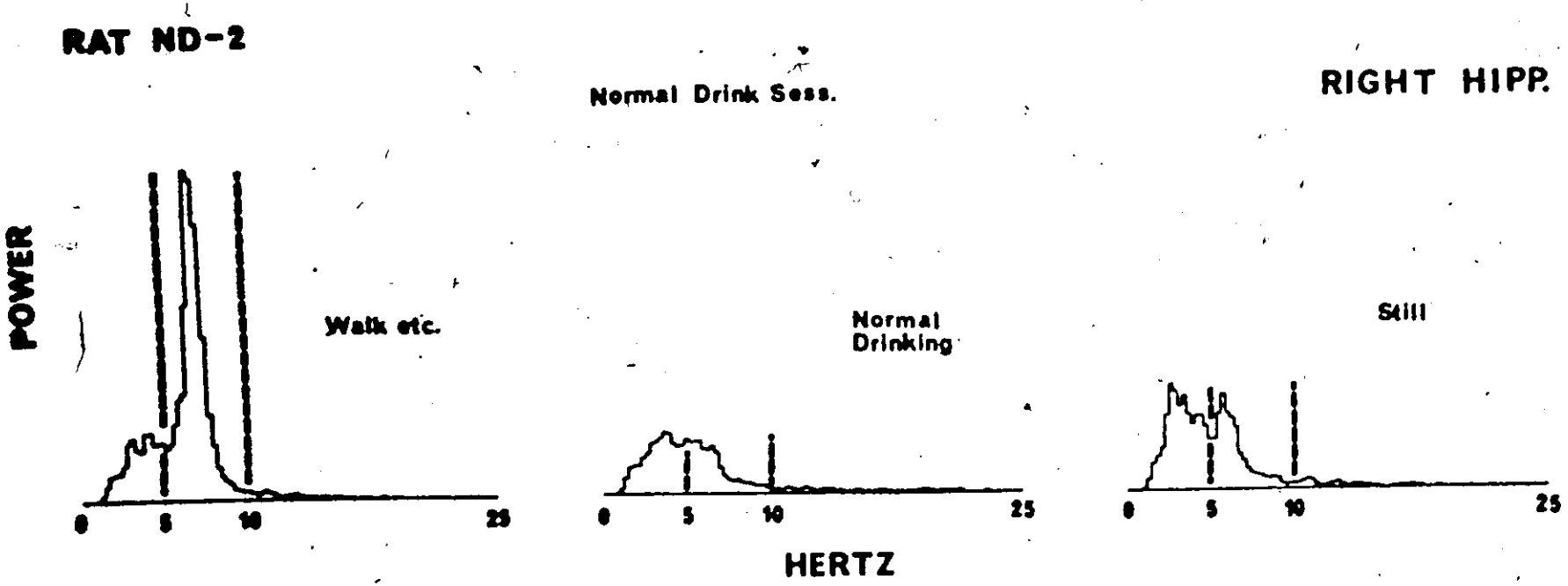
Norm. Drink Sess.

Norm. Drink

600 uv

1 sec

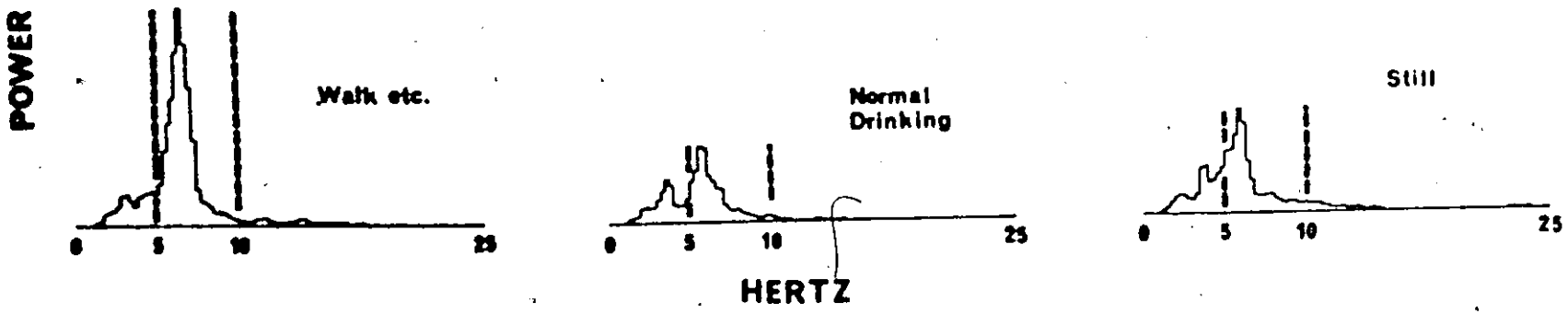

RAT ND-1
Normal Drink Sess.
RIGHT HIPP.
Normal Drinking
POWER
Walk etc.
Normal Drinking and Move
Still
0
5
10
25
HERTZ

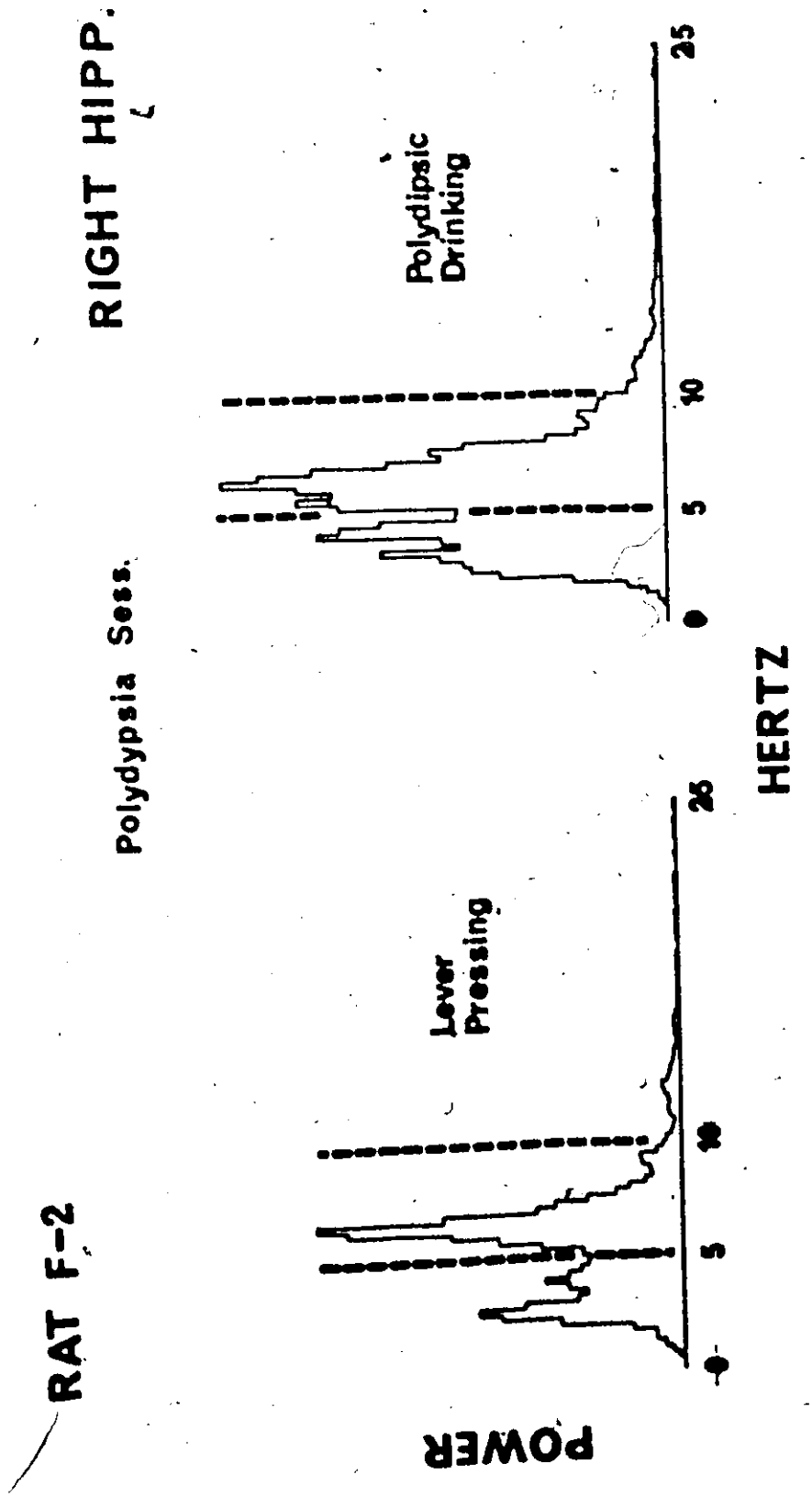

RAT ND-2
Normal Drink Sess.
RIGHT HIPP.
POWER
Walk etc.
Normal Drinking
Still
0
5
10
25
HERTZ

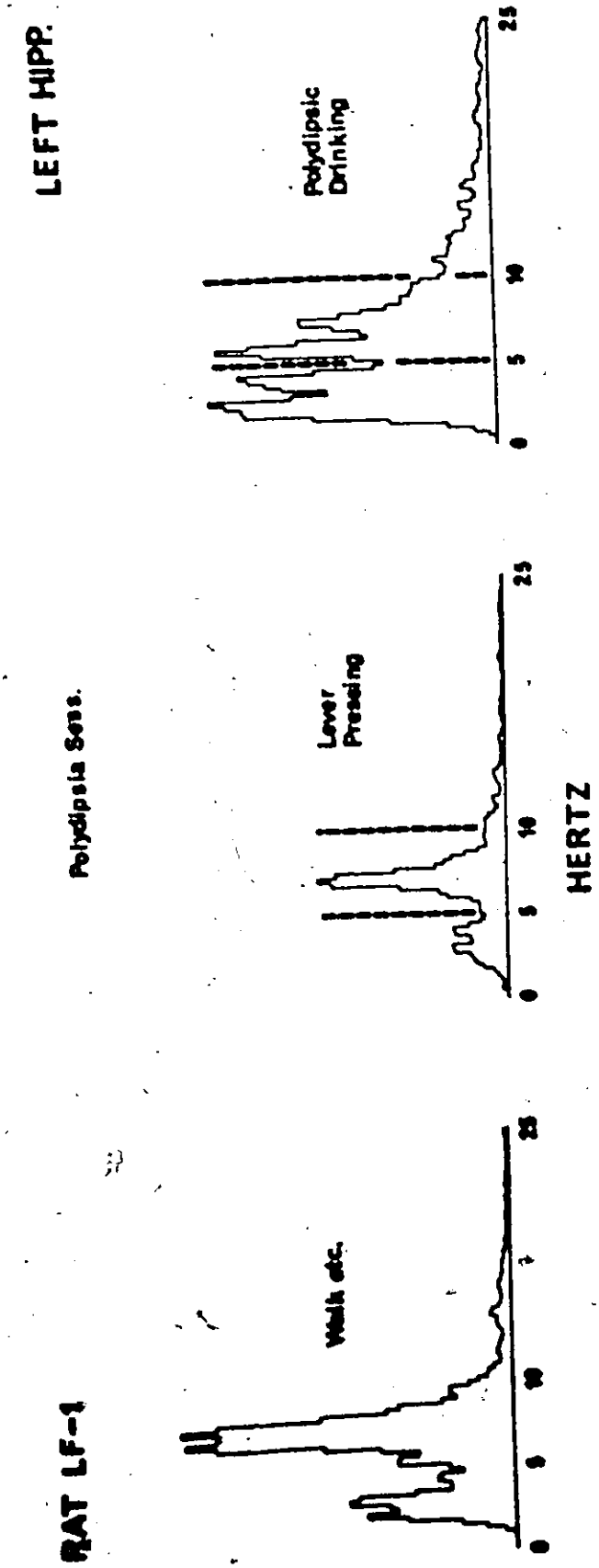
RAT ND-3

Normal Drink Sess.

RIGHT HIPP.

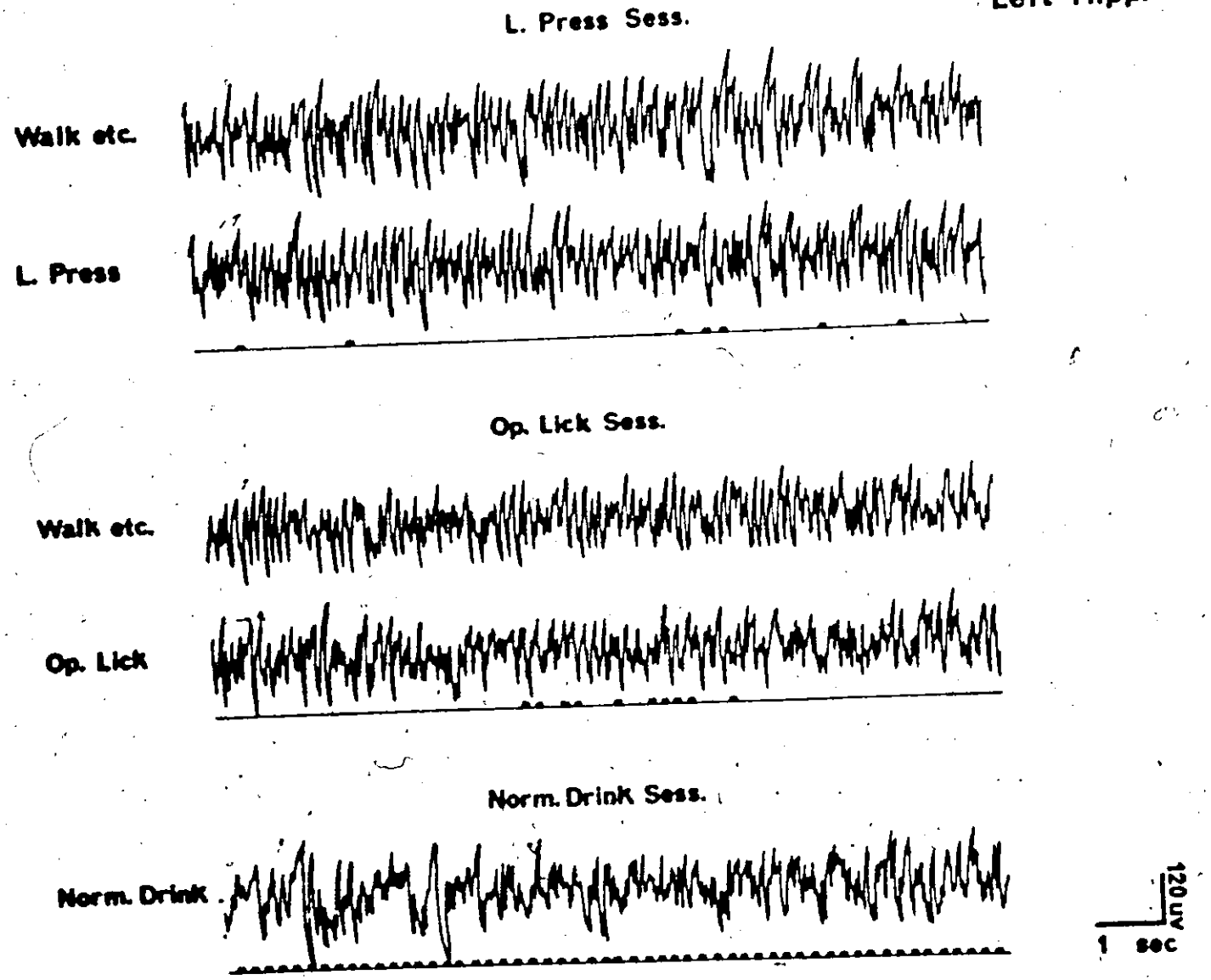



RAT F-2
RIGHT HIPP.
Polydypsia Sess.
Lever Pressing
Polydipsic Drinking
POWER
HERTZ
0
5
10
20
25


RAT LF-1
Walk etc.
Polydipsia Sess.
Lever Pressing
Polydipsic Drinking
LEFT HIPP.
POWER
HERTZ
0
5
10
25

Rat LF-1

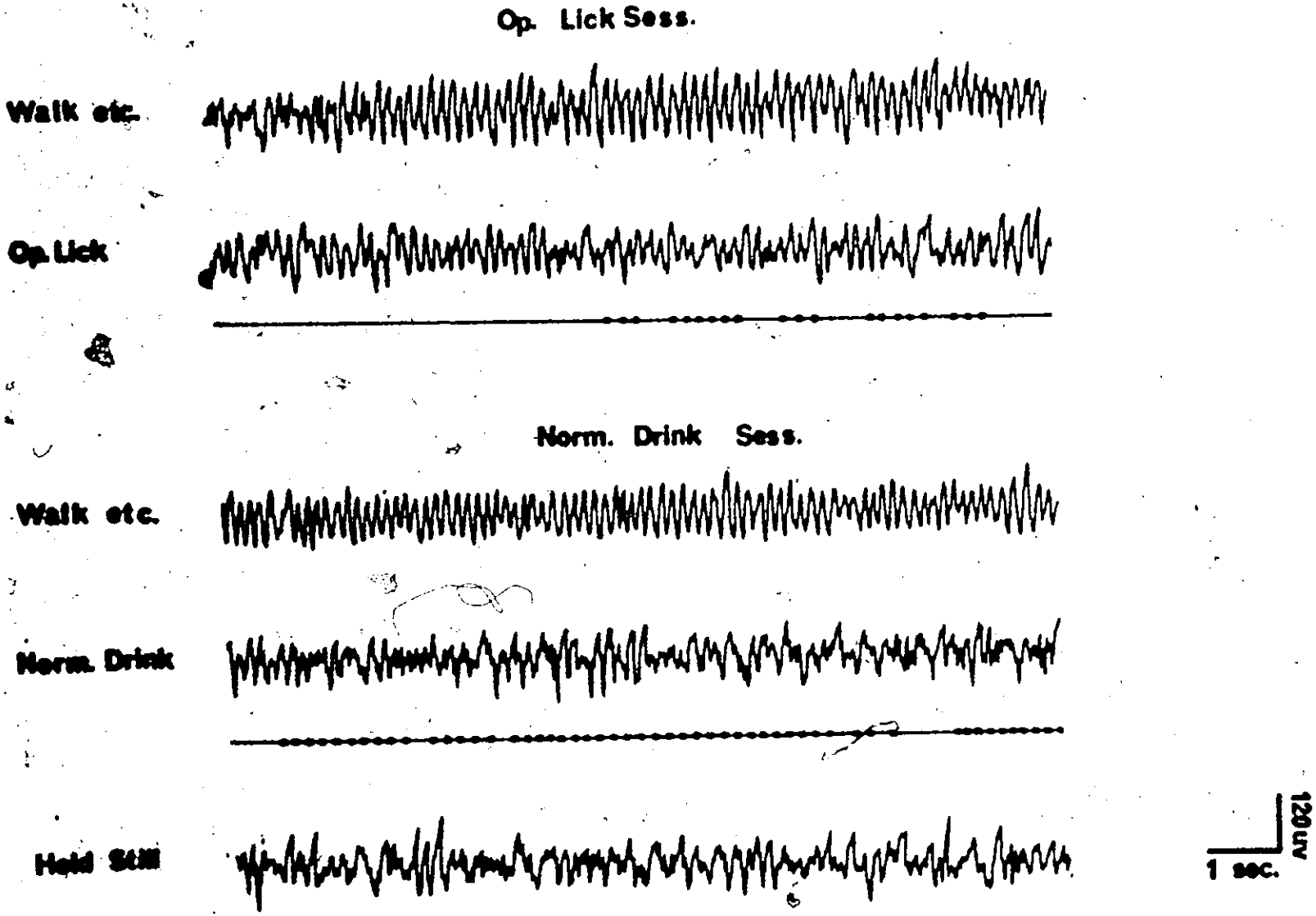
Left Hipp.



195

RAT LF-3

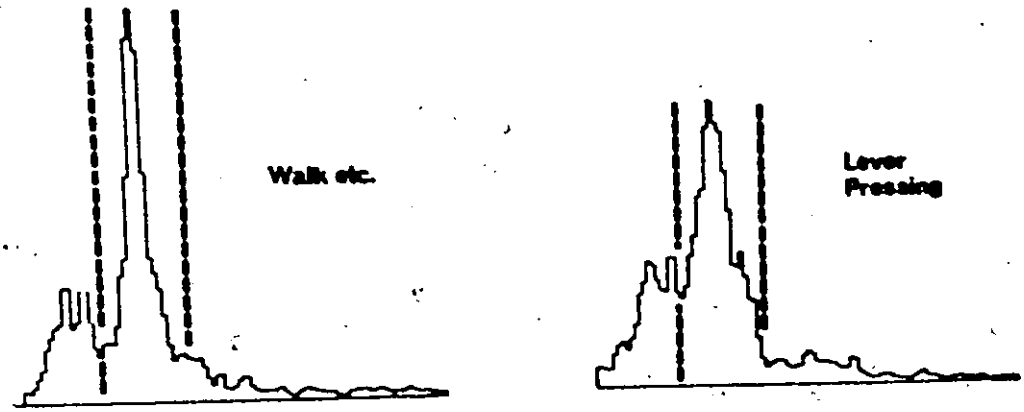
LEFT HIPP.



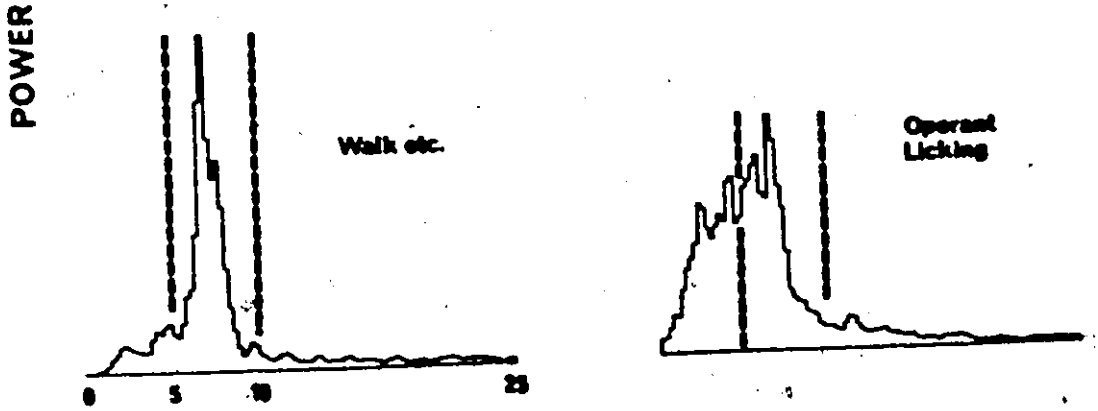
RAT LF-1

Lever Press Sess.

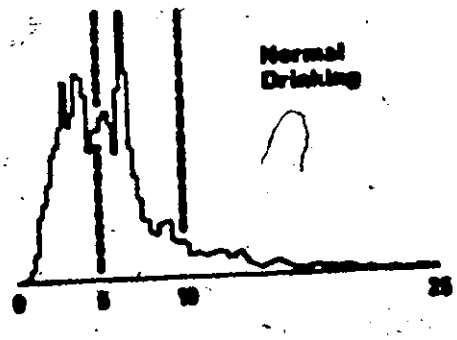
RIGHT HIPP.



Operant Lick Sess.



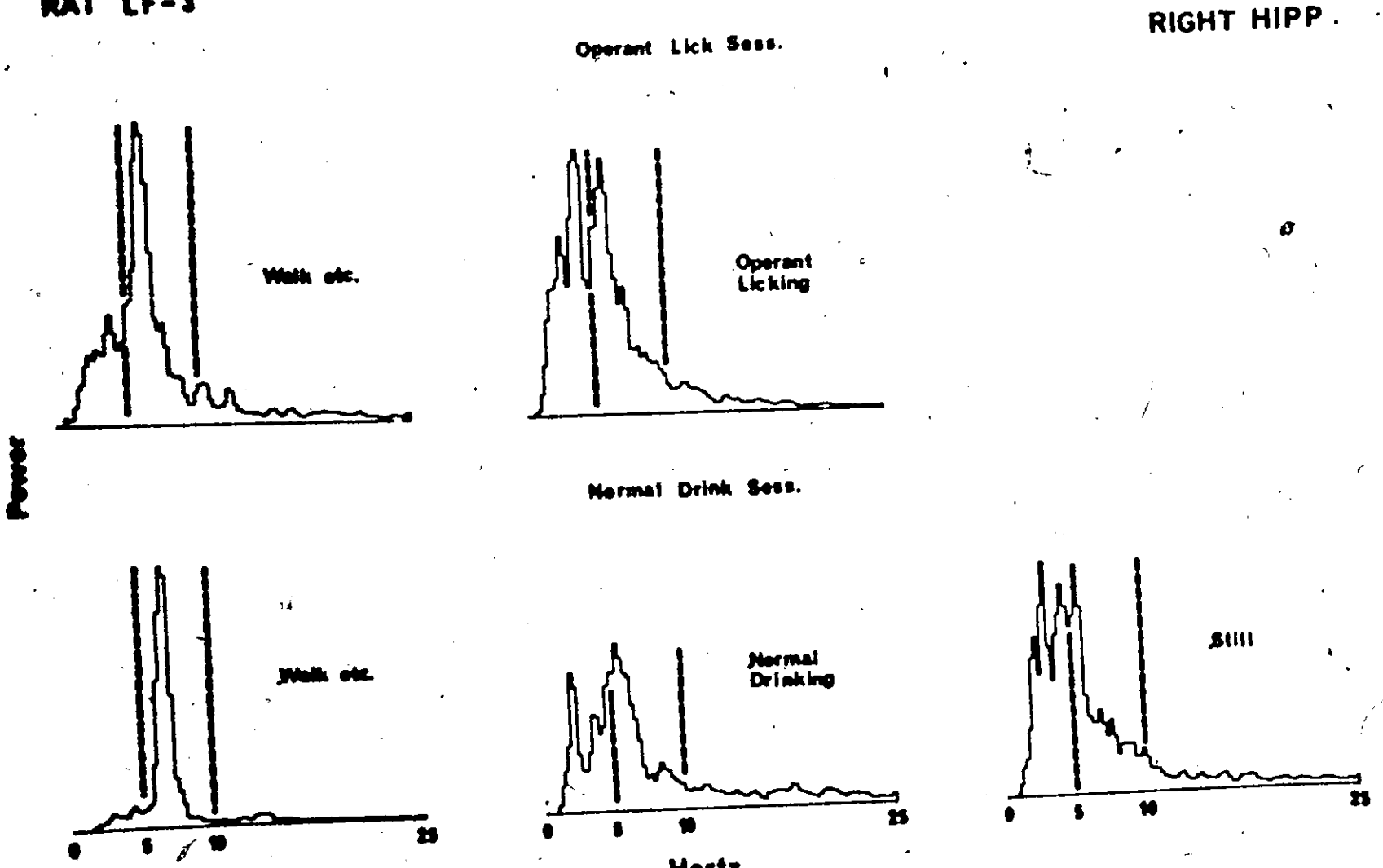
Normal Drink Sess.



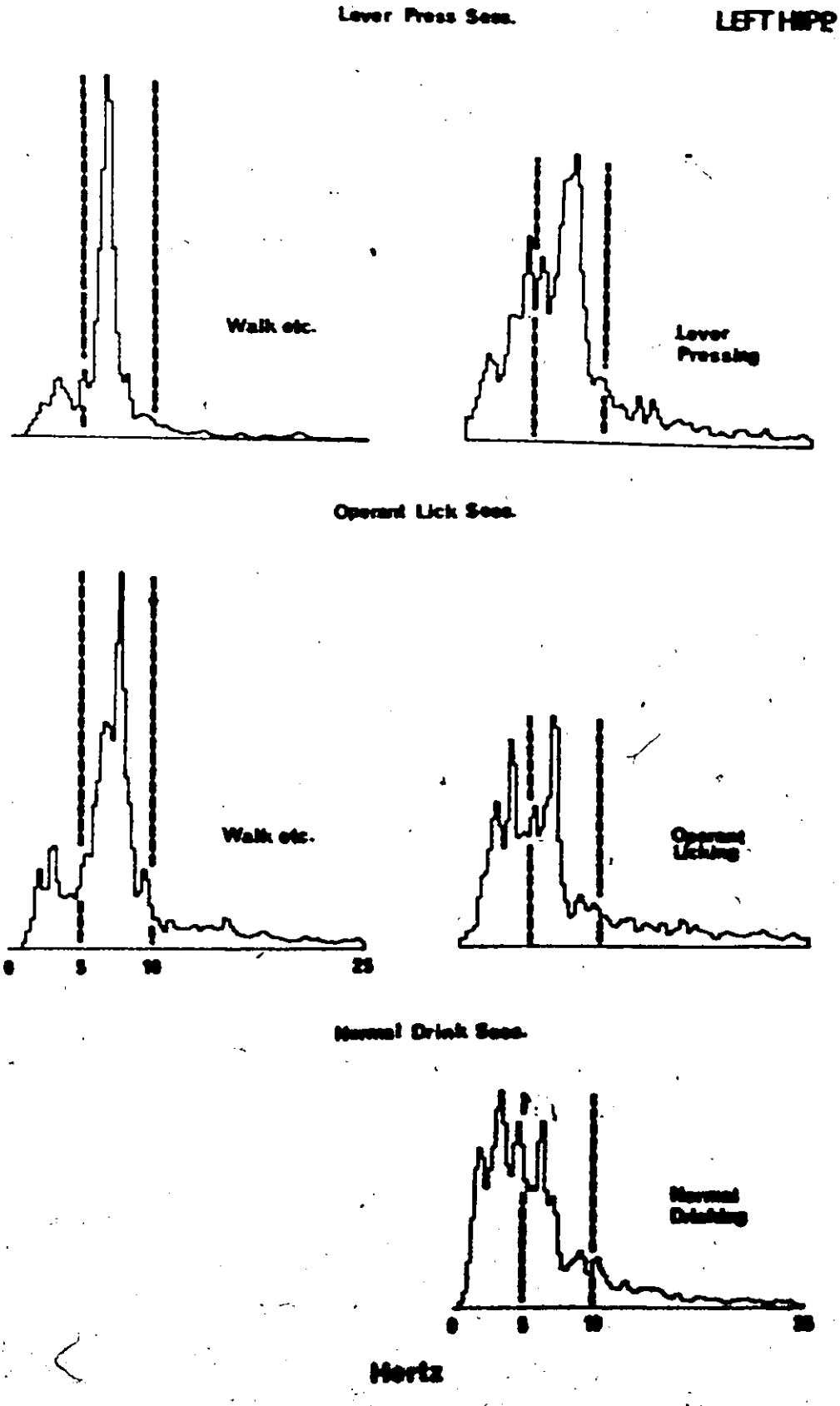
HERTZ

RAT LF-3

RIGHT HIPP.



RAT LF-1


Lever Press Sess.
LEFT HIPP
Walk etc.
Lever Pressing
Operant Lick Sess.
Power
Walk etc.
Operant Licking
0
5
10
25
Normal Drink Sess.
Normal Drinking
0
5
10
25
Hertz

RAT LF-3

LEFT HIPP.