

20 AND 40 C/SEC POWER FUNCTIONS IN THE VISUAL, MOTOR, AND
AUDITORY CORTICES OF THE CAT DURING THREE LEVELS
OF PERFORMANCE IN A SUCCESSIVE VISUAL
DISCRIMINATION TASK

A Thesis

Presented to

the Faculty of the Department of Psychology

University of Houston

In Partial Fulfillment
of the Requirements for the Degree
Master of Arts

By

Lyllian B. Hix

January, 1969

463856

ACKNOWLEDGMENTS

I want to express my gratitude to several people who assisted in the research of this thesis: Dr. Daniel E. Sheer for his continual guidance throughout the project, Dr. Netta Grandstaff who implanted the electrodes, Mr. Richard Miller who recorded the magnetic tapes analyzed, Mrs. Carol Deaton and Mr. Ron Hoffman for their assistance in the computer analysis of the data, and Mr. Henry Pekar for his many ingenious innovations in the computer hardware which materially lessened the labor and increased the accuracy of the computer analysis.

The author wishes to acknowledge support by NASA Grant NsG(T)-52 Sup. 3.

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ABSTRACT

The electrical activity in 5 frequency bands in the arousal spectrum was studied in the primary visual cortex, motor cortex, and primary auditory cortex of one cat during prestimulus (PS) and stimulus periods at 3 levels of performance in a successive visual discrimination task. The task involved pressing a bar to obtain milk only in the presence of a 10 c/sec flashing light as the S_D and inhibiting during an S_Δ period of a 3 c/sec light.

EEG records representing the poorest, an intermediate, and the best behavioral performance, based on S_D/S_Δ ratios, in the visual discrimination task were computer analyzed to give average continuous power functions at 1/3 octave frequency bands with center frequencies of 20, 25, 31.5, 40, and 50 c/sec. The trials in the task on each tape were divided into as many as six behavioral categories, depending on the availability of trials within each category, as follows: PS, S_D , and S_Δ concomitant with a response (PS_R , S_{D_R} , S_{Δ_R} , respectively) and PS, S_D , and S_Δ in which no response occurred (PS_{NR} , $S_{D_{NR}}$, $S_{\Delta_{NR}}$, respectively). Initiation of computation was contingent upon a response, either behavioral or artificial and either with or without a delay, so that the averaged band powers in a period of time prior and subsequent to the response could be accurately ascertained. The analysis epoch was divided

into two periods of time, one in which the electrical activity was assumed to be response related, the other assumed to be sufficiently removed in time from the response that the electrical activity was little affected by the response. The results were:

1. At all three levels of performance the 40 c/sec activity in visual I and motor cortex, but not in auditory I, was consistently higher during S_{D_R} than during the other behavioral conditions studied.

2. The 40 c/sec electrical activity in visual I coincident with a reinforced response increased as performance improved, although the 40 c/sec activity with intermediate performance appeared to be more similar to that occurring with superior performance than to that concomitant with poor performance. The 40 c/sec electrical activity in the motor cortex with a reinforced response varied little with performance level.

3. A marked peaking of the 40 c/sec activity and a marked decrease in 20 c/sec activity occurred coincident with a reinforced response in both visual I and motor cortex, but not in auditory I. These phenomena were particularly evident with intermediate and superior performance in visual I.

4. Graphic data indicated an inverse relationship between the 20 c/sec and 40 c/sec activity in the visual and motor cortices during S_{D_R} and $S_{A_{NR}}$. The 20 c/sec activity

was higher during $S_{A_{NR}}$ than during S_{D_R} and the 40 c/sec was higher during S_{D_R} than during $S_{A_{NR}}$. Statistical analysis was not possible because of the small N (N=3).

5. A marked peaking of the 20 c/sec activity in auditory I occurred approximately 2 to $2\frac{1}{2}$ sec following a reinforced response during "lapping" behavior. At the same time, significant but very small decreases in the 40 and 50 c/sec bands occurred. The 20 c/sec activity was consistently higher during lapping than it was following a response that was not reinforced or during a prestimulus period.

6. Since 40 c/sec activity was observed in association with facilitatory or arousal behavior and the 20 c/sec with behavioral inhibition, a tentative hypothesis was advanced that the 40 c/sec activity is an electrical correlate of the orienting response and that the 20 c/sec activity is an electrical correlate of the inhibition of the orienting response.

TABLE OF CONTENTS

CHAPTER	PAGE
I. STATEMENT OF THE PROBLEM	1
II. REVIEW OF THE LITERATURE	6
Anatomical and Physiological Mechanisms of the	
Arousal Response	7
Activation Pattern and the Role of Arousal	
Systems in Learning	19
Anatomical Considerations of Visual and Motor	
Systems	30
Fine-Grained Analyses of Fast Frequency	
Spectrum	45
III. METHODS AND PROCEDURES	79
Subjects	79
Electrodes	80
Surgery	80
Experimental Apparatus	89
Experimental Procedure	91
Data Analysis	92
IV. RESULTS	106
Descriptive Statistics	103
Frequency x Condition Interaction for each	
Tape	110

CHAPTER	PAGE
Response x Frequency and Stimulus x Frequency	
Interactions across Tapes	125
Between Tapes Analyses	123
Between Periods Analyses across Tapes	135
V. DISCUSSION	145
Evidence for 40-20 Inverse Relationship in	
Visual and Motor Cortices	148
VI. SUMMARY AND CONCLUSIONS	160
BIBLIOGRAPHY	163
APPENDIX A. Visual I: Three Dimensional Plots of	
Frequency x Time x Power	178
APPENDIX B. Motor Cortex: Three Dimensional Plots of	
Frequency x Time x Power	190
APPENDIX C. Auditory I (3-1/2 Sec): Three Dimensional	
Plots of Frequency x Time x Power	202
APPENDIX D. Auditory I (5 Sec): Three Dimensional	
Plots of Frequency x Time x Power	212
APPENDIX E. Mean Proportional Powers: Visual I,	
Motor Cortex, Auditory I (3-1/2 Sec), and Auditory I	
(5 Sec)	219
APPENDIX F. Mean Absolute Powers: Visual I, Motor	
Cortex, Auditory I (3-1/2 Sec), and Auditory I	
(5 Sec)	228

CHAPTER	PAGE
APPENDIX G. Spectrograms Based upon Algebraic Variations from Prestimulus Level: Visual I, Motor Cortex, Auditory I (3-1/2 Sec), and Auditory I (5 Sec)	237
APPENDIX H. Spectrograms Based upon Ratio of Stimulus to Prestimulus Level: Visual I, Motor Cortex, Auditory I (3-1/2 Sec), and Auditory I (5 Sec)	246

LIST OF TABLES

TABLE	PAGE
1. Number of Trials Averaged	105
2. Frequency x Condition Interaction for Tapes 19A(1), 18A, and 10A--Visual I, Motor Cortex, and Auditory I (3-1/2 Sec)	120
3. Frequency x Condition Interaction for Tapes 19A(1), 18A, and 10A--Auditory I (5 Sec)	121
4. Frequency x Response and Frequency x Stimulus Interactions across Tapes	126
5. Between Tapes--Visual I, Motor Cortex, and Auditory I (3-1/2 Sec)	130
6. Between Tapes--Auditory I (5 Sec)	134
7. Between Periods Analyses across Tapes--Visual I, Motor Cortex, and Auditory I (3-1/2 Sec)	136
8. Between Periods Analyses across Tapes--Auditory I (5 Sec)	141

LIST OF FIGURES

FIGURE	PAGE
1. Continuous Unnormalized 40 c/sec Power Functions for S_D Trial: Visual I and Motor Cortex	4
2. Continuous Unnormalized 20 c/sec Power Function for S_D Trial: Auditory Cortex	5
3. Unfiltered EEG--Tape 18A: S_{DR}	81
4. Unfiltered EEG--Tape 18A: S_{DR}	82
5. Unfiltered EEG--Tape 18A: S_{DNR}	83
6. Unfiltered EEG--Tape 18A: S_{DNR}	84
7. Unfiltered EEG--Tape 18A: $S_{\Delta R}$	85
8. Unfiltered EEG--Tape 18A: $S_{\Delta R}$	86
9. Unfiltered EEG--Tape 18A: $S_{\Delta NR}$	87
10. Unfiltered EEG--Tape 18A: $S_{\Delta NR}$	88
11. Program 5, Flow Diagram	98
12. Event Contingencies and Timing for 3-1/2 Sec Analysis of EEG of Motor, Visual, and Auditory Cortices with Program 5	101
13. Event Contingencies and Timing for 5 Sec Analysis of EEG of Auditory Cortex with Program 5	102
14. Brush Recorder Output of Program 5	104
15. 126 and 345 Periods and abf and cde Periods	107
16. Average Continuous 40 CPS/BB and 20 CPS/BB Power Functions: Visual I-- S_{DR} , $S_{\Delta NR}$, $PSNR$	111

FIGURE	PAGE
17. Average Continuous 25 CPS/BB, 31.5 CPS/BB, and 50 CPS/BB Power Functions: Visual I--SD _R , S _{ΔNR} , PS _{NR}	112
18. Average Continuous 40 CPS/BB and 20 CPS/BB Power Functions: Visual I--SD _{NR} , S _{ΔR} , PS _{NR}	113
19. Average Continuous 40 CPS/BB Power Functions: Visual I--SD _R , S _{ΔR} , PS _{NR} , PS _R	114
20. Average Continuous 40 CPS/BB and 20 CPS/BB Power Functions: Motor Cortex--SD _R , S _{ΔNR} , PS _{NR}	115
21. Average Continuous 40 CPS/BB Power Functions: Motor Cortex--SD _R , S _{ΔR} , PS _{NR} , PS _R	116
22. Average Continuous 40 CPS/BB and 20 CPS/BB Power Functions: Auditory I (3-1/2 Sec)-- SD _R , S _{ΔNR} , PS _{NR}	117
23. Average Continuous 20 CPS/BB and Broad Band Power Functions: Auditory I (5 Sec)--SD _R , S _{ΔR} , PS _{NR}	118
24. Spectrograms for Visual, Motor, and Auditory Cortices Plotted from Mean Proportional Powers (Appendix E) for 345 Period: SD _R , S _{ΔNR} , PS _{NR}	123

FIGURE	PAGE
25. Spectrograms for Auditory Cortex Plotted from Mean Proportional Powers (Appendix E) for 345 (3-1/2 Sec) and cde (5 Sec) Periods	124
26. Average Continuous 40 CPS/BB Power Functions: Visual, Motor, and Auditory Cortices-- SD_R and Prestimulus	131
27. Average Continuous 40 CPS/BB Power Functions: Visual, Motor, and Auditory Cortices-- SD_R Adjusted to PS_{NR} Baseline ($SD_R - PS_{NR}$)	132
28. Spectrograms for Visual, Motor, and Auditory Cortices Plotted from Mean Proportional Powers (Appendix E): SD_R - Periods 345 and 126, and PS_{NR}	137
29. Average Continuous BB/TP Power Functions: Visual I - SD_R	139
30. Average Continuous, 20 CPS/BB Power Functions: Motor Cortex - PS_R	140
31. Average Continuous 20 CPS/BB, 40 CPS/BB, and 50 CPS/BB Power Functions: Auditory I - SD_R . . .	143

CHAPTER I

STATEMENT OF THE PROBLEM

The general trend of the literature has been to conceptualize such behaviors as learning and memory in terms of two types of processes, one a reversible, unstable short-term process, the other a more stable long-term process (Grossman, 1967; Sheer, Benignus, & Grandstaff, 1966a; John, 1967). The oscillatory short-term process has been assumed in most hypotheses to come about through a temporal facilitation of synaptic transmission between the central representation of the conditioned and unconditioned stimuli. This short-term process has been assumed to represent a functional modification which decays rapidly and leaves no permanent trace in the central nervous system. It is apparently very susceptible to electrical effects, drug effects, trauma, and other kinds of external interference. The more stable long-term process seems to require some time for fixation in order for it to occur, e.g., through the repeated presentation of a particular combination of stimuli in such a fashion that the same central pathways are subjected to recurrent or continual facilitation. In other words, this long-term process has been assumed to represent some kind of structural modification of the central nervous system, either biochemical or anatomical in nature.

Early theories with regard to the second process tended

to point to anatomical measurements as the most suitable measurement operations, however more recent theories, e.g., Hyden (1959), have suggested that perhaps chemical measurement operations are preferable. Sheer, Grandstaff, & Benignus (1966b) have suggested that the flexible, dynamic brain organizations required for the short-term process may be in the form of 40 c/sec electrical activity. Their designation of "40 c/sec electrical activity" refers to highly dynamic changes within the fast frequency spectrum usually designated as "EEG arousal" and undoubtedly may be expected to vary from species to species. There is evidence both from microelectrode work (Ricci, Doane, & Jasper, 1957; Kogan, 1960) and from studies of intrinsic electrical activity (Yoshii, Matsumoto, Ogura, Shimokochi, Yamaguchi, & Yamasaki, 1960) that the so-called cortical arousal or activation pattern may be associated with a complex organization of neural activity which may represent inhibitory as well as excitatory processes.

The purpose of this thesis is to make a correlation between a measurement of behavior and a measurement of brain function. Pilot analyses of the EEG data to be reported in this thesis had shown what appeared to be significant response-related changes taking place in the electrical activity of the visual and motor cortices and perhaps a reinforcement-related change in the electrical activity of the auditory cortex several seconds after the response. Continuous write-

outs of the 40 c/sec power function for individual trials (Figure 1) showed simultaneous peaks in the functions of the visual and motor cortices with a reinforced response. In the auditory cortex approximately 1-3/4 to 2-1/2 sec following a reinforced response, but not following an unreinforced response, there appeared to be a large peak in the 20 c/sec power function, as shown in Figure 2. The results of these pilot analyses suggested that a more sophisticated analysis of these data might be profitable. A program was designed in which the continuous band power was averaged and the averaging process was triggered by the appropriate stimulus and response contingencies.

The data of this investigation are (1) behavioral performance measures in a successive visual discrimination task which show fluctuations above and below criterion over a period of 6 weeks and (2) the intrinsic electrical activity of the visual, motor, and auditory cortices of the brain. Recordings of the intrinsic electrical activity of a quality required for computer analysis were carried out for 8 experimental sessions. Three recordings, representing three levels of performance in the discrimination task, were analyzed with a hybrid computer specially designed for the analysis of frequency and power changes in the arousal spectrum, i.e., 20-50 c/sec (Benignus, 1967). The performance of the animal was compared to the power spectral functions.

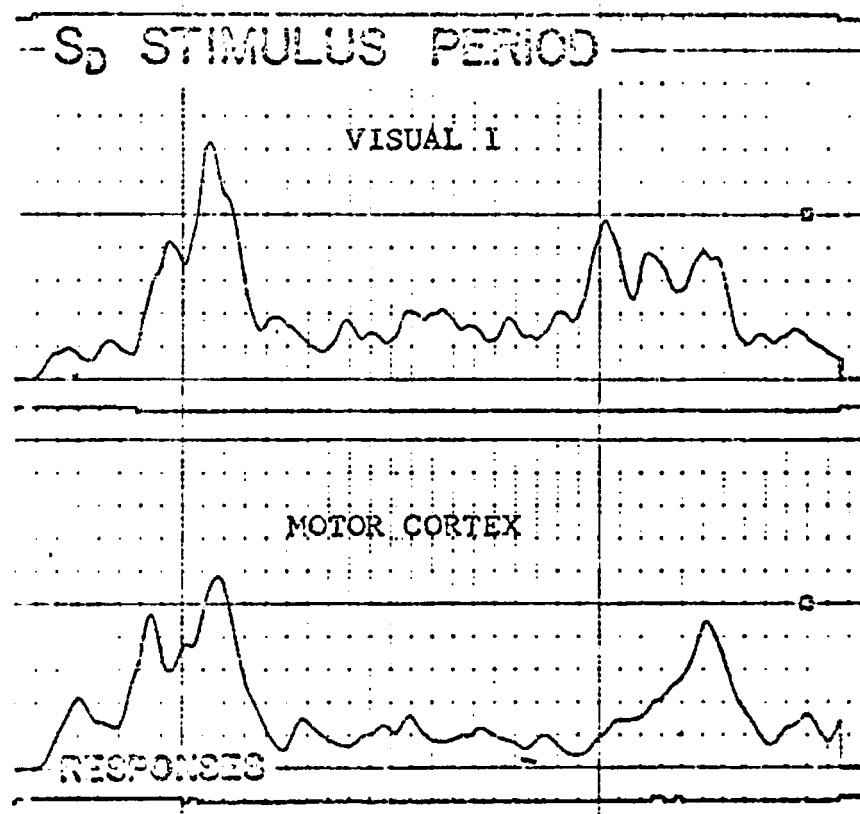


FIGURE 1
CONTINUOUS UNNORMALIZED 40 C/SEC POWER FUNCTIONS FOR S_D TRIAL
VISUAL I AND MOTOR CORTEX

Note the increases in power coincident with the two bursts of responses. EEG signals were passed through 40% band-pass filters with a center frequency of 40 c/sec. Amplification of the motor power function is twice that of the visual power function.

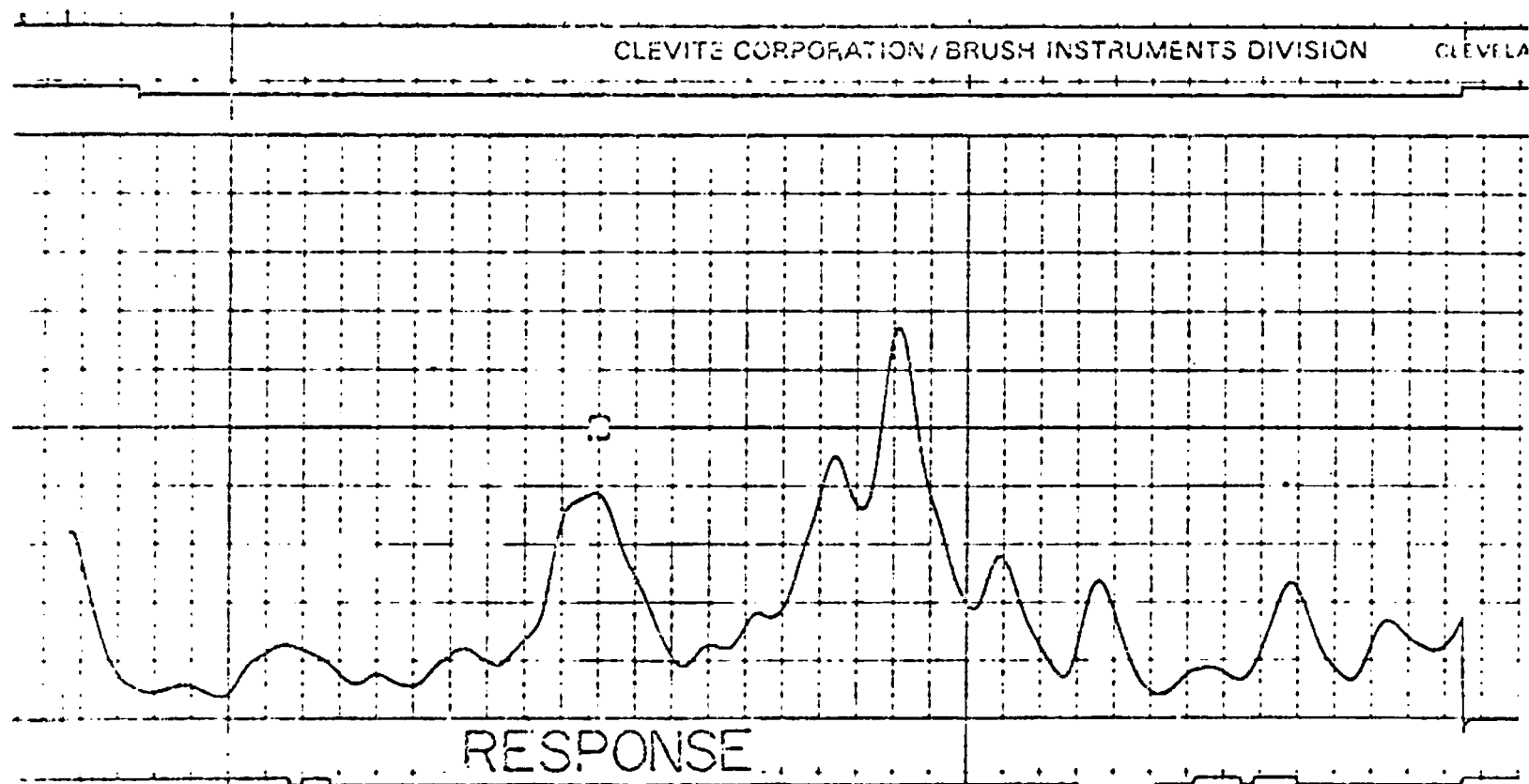


FIGURE 2

CONTINUOUS UNNORMALIZED 20 C/SEC POWER FUNCTION FOR S_D TRIAL
AUDITORY CORTEX

Note the increase in power approximately 2 to 2-1/2 sec following the response. EEG signal was passed through 23% filter with center frequency of 20 c/sec.

CHAPTER II

REVIEW OF THE LITERATURE

Numerous studies (Morrell & Jasper, 1956; Sakhiulina, 1960) have shown similar manifestations in conditioning in several animal species: A previously habituated cortical desynchronization response to the conditioned stimulus is disinhibited as soon as the stimulus is paired with a noxious or appetitive unconditioned stimulus. Conditioned cortical desynchronization usually appears before the overt conditioned response can be observed. In the initial stages of conditioning this desynchronization is diffuse, occurring in all areas of the cortex. Repetition of the combined stimuli leads to a gradual narrowing of the zone of desynchronization and it becomes localized in the motor cortex as conditioning proceeds and as overt conditioned responses begin to appear. Fine-grained analyses of this desynchronization have indicated that certain dynamic changes occurring within this broad spectrum may be correlates of the learning process (Lesse, 1960; Sheer et al, 1966a, 1966b).

This review will be restricted primarily to: (1) anatomical and physiological mechanisms responsible for the arousal response, (2) studies with reference to the activation pattern and the role that the arousal systems play in learning, except those which are based upon fine-grained analyses of

the fast frequency spectrum which will be dealt with separately, (3) anatomical considerations of the visual and motor systems with reference to their function in conditioning or learning, and (4) fine-grained analyses of the fast frequency spectrum usually designated as "EEG arousal," particularly as related to conditioning or learning.

Anatomical and Physiological Mechanisms of the Arousal Response

Brainstem and Thalamic Reticular Systems

Many of the anatomical characteristics of the reticular formation have been known for some time. The reticular formation is a core of neural tissue running centrally through the entire brainstem and extending from the spinal cord anteriorly into the hypothalamus and thalamus. Thin cross sections of the reticular formation under a microscope reveal an interlacing of nerve fibers making a weblike network or "reticulum" of fibers in which the cell bodies of neurons are diffusely embedded. The reticular formation is surrounded on both sides by the pathways and nuclei of the specific sensory projections and the pyramidal and extrapyramidal motor systems. At the level of the upper mesencephalon, the reticular core branches into two divisions. The dorsal limb enters the thalamus in the centre median nucleus and the ventral limb extends into

the sub- and hypothalamus forward toward the septal area. Jasper (1961) distinguishes the thalamic reticular system as the dorsal limb of the cephalic end of the brainstem reticular formation.

Nuclei. Ninety-eight nuclear masses have been classified in the brainstem reticular formation, of which the most conspicuous nuclei are: (1) the lateral reticular nucleus, lying dorsolateral to the olive; (2) the reticular nucleus of the pontine tegmentum lying dorsal to the pontine nuclei; (3) the paramedian reticular nucleus, which lies near the midline dorsal to the olive; (4) the large-celled reticular nucleus (gigantocellularis), extending from the middle of the olive to the level of the facial nucleus occupying the medial two-thirds of the reticular formation; (5) the caudal reticular nucleus of the pons extending cranialward from the large-celled nucleus; and (6) the oral reticular nucleus of the pons extending up to the mesencephalon. Other less conspicuous nuclei include the small-celled reticular nucleus medial to the spinal nucleus of the 5th nerve and the ventral reticular nucleus extending caudalward from the large-celled nucleus. (Ranson & Clark, 1959)

The thalamic reticular system is made up of a closely interconnective network of nerve cells and fibers, which are situated between and around the specific thalamic nuclei. Jasper (1961) determined the distribution of the thalamic

reticular system in terms of those regions which produced recruiting responses upon repetitive stimulation. He found that the fibers from the ventral portion of the ventral anterior nucleus passed forward into the anterior limb of the internal capsule bordering upon and even extending somewhat into the head of the caudate nucleus. The thalamic reticular system appeared to extend further than the classical intralaminar system of the thalamus. It included all of the rostral pole of the reticular nucleus, as well as the border zones of the medial group of nuclei and of the lateral posterior nucleus, and extended posteriorly into the suprageniculate region, but did not include the posterior pole of the centre median nucleus.

Inputs. Connections to the brainstem reticular formation are widespread. The reticular formation of the brainstem receives collaterals from all ascending pathways. Additional spinoreticular pathways synapse on cells scattered throughout the lateral extent of the brainstem reticular formation. Collaterals from cranial nerve nuclei also feed into it. Microscopic examination of the brainstem reveals that the central core of the reticular formation is characterized by cells which have diffusely branching dendritic fields and short axons. This is a structure which is ideally suited to the convergence of afferents from many different sources on a single reticular neuron, thereby permitting the integrative activity ascribed to the system as a whole (Grossman, 1967).

Reticular neurons are subject to influence from the cerebral cortex. Corticifugal influences on the reticular formation have been shown to originate in the sensorimotor cortex, particularly in the motor region, the orbitofrontal cortex, the cingulate gyrus, the temporal lobe, the parietal, the lateral temporal, and the paraoccipital areas (French, 1960; Grossman, 1967). The corticifugal potentials appear in the same general brainstem regions which are influenced by ascending sensory collaterals. In this respect, Worden and Livingston (1961) view the reticular formation as advantageously situated as a site of interaction between activities induced by cortical and by peripheral sources of stimulation.

Important connections from rhinencephalic structures, principally the hippocampus and entorhinal region, have been demonstrated (French, 1960).

Brookhart (1960) has assigned to the cerebellum an important role in "modulating the excitability of key neurons in transmission pathways [of the brainstem] which receive their principal activation from sensory sources or sources higher in the brain." The cerebellum is believed to exercise facilitatory as well as inhibitory influences on the reticular system. French (1960) cited evidence that the nature of the influence induced is a function of cerebellar discharge rate. Both facilitatory and inhibitory responses have been elicited by excitation of the same cerebellar site with different stimulus

frequencies.

The brainstem reticular formation also receives important extrapyramidal motor inputs from the basal ganglia, indirectly via the thalamic nuclei and directly from the fastigial nuclei of the cerebellum (Grossman, 1967). Jung and Hassler (1960) regard the reticular formation as the main lower center for extrapyramidal motor functions. They remind the reader that "the reticular formation is mainly a motor coordinating center, the lower part for respiration, the higher parts for eye movements and body posture" and that "the psychological effects of attention and conscious acts are only secondary specializations, derived from the basic reticular functions controlling motor behavior."

In addition to its intimate connection with the brainstem reticular formation, corticofugal projections into the thalamic reticular formation have been demonstrated by Jasper (1961). There is a considerable overlapping of corticofugal projections from many areas of the cortex to the same general region in the thalamic reticular system, suggesting to Jasper a confluence of projections which might provide the basis for the considerable integrative function arising from cortical influences.

Outputs. The brainstem reticular formation projects both downward and upward within the neuraxis. The brainstem reticular formation of the lower brainstem projects to the cortex either directly via diffuse extrathalamic projections through

the ventrolateral diencephalon or indirectly via reticulo-thalamic connections. A reticulostriatal connection is established via the midline and intralaminar nuclei of the thalamus. Cells in the bulbar portion of the reticular formation project extensively to the cerebellum. (Grossman, 1967)

Jasper (1961) has determined the cortical projections of the thalamic reticular system on the basis of the distribution of those regions from which recruiting responses can be elicited with repetitive stimulation. He found that with complete exploration it is possible to demonstrate recruiting responses in all cortical areas, but not from a single site within the thalamic reticular system. The most medial portions of the system were found to project forward to the frontal regions, while the lateral portions in the central lateral nucleus were found to project posteriorly into the parietal and occipital areas. In addition, he found a rostrocaudal organization whereby the posterior limits of the system in the centre median nucleus project forward, while the projections to the more posterior cortical areas are obtained only in the more rostral portions of the thalamic reticular system.

The extrathalamic division of the reticular formation projects ventrally into the hypothalamus by way of the medial forebrain bundle. Many of its fibers continue on through the hypothalamus to enter nearby structures at the base of the cerebral hemispheres in the rhinencephalon. Many of the hypo-

thalamic cells that receive axons from the reticular formation also send their axons into the rhinencephalon. (McCleary & Moore, 1965)

Reticular influences on sensory and motor systems and the cerebral cortex. Worden and Livingston (1961) have identified two activating systems in the reticular formation, one working upward and the other downward within the neuraxis. The descending reticular system is capable of modifying the electrical activity in nerve cells throughout the lower brainstem and spinal cord and can facilitate and inhibit the transmission of nerve impulses in both sensory and motor systems, accounting for such phenomena as attention, habituation, and adaptation (Hernández-Peón, Guzman-Flores, Alcaraz, & Fernández-Guardiola, 1956; Hernández-Peón & Scherrer, 1955; Hernández-Peón, Scherrer, & Jouvet, 1956). Grossman (1967) offered much evidence to support his interpretation of reticular influences on sensory mechanisms at the receptor level and in central relay stations, with a central control over sensory reception, conduction, and perception being exercised by a system which originates in the cortex of the cerebrum (and perhaps the cerebellum) which essentially parallels the entire course of the primary sensory pathways, picking up additional influences from integrative centers along the way.

The reticular formation also influences tonic and phasic motor functions. Excitation of the reticular formation may

produce sufficient spinal facilitation to elicit movements, but more typically, reticular influences act primarily to facilitate or inhibit spinal motor mechanisms and thus modify rather than elicit postural and phasic movements (Grossman, 1967). Worden and Livingston (1961) have found in general that stimulation of the lowermost portion of the reticular network yields a widespread inhibitory influence downstream, affecting reflexes and cortically induced movement at spinal levels, and that similar stimulation in more anterior portions of the brainstem and in the midline thalamic nuclei yields an essentially facilitatory downstream effect. Although this is true in a general way, Grossman (1967) cited studies in which inhibitory effects were obtained from all portions of the brainstem reticular formation and from related nuclei in the thalamus and septal area.

Perhaps one of the most significant influences of the reticular formation with regard to this thesis is its influence on cortical functions. Moruzzi and Magoun (1949) demonstrated that EEG changes seemingly identical with those in the physiological arousal reactions can be produced by direct stimulation of the reticular formation of the brainstem, without exciting classical sensory paths. The arousal response could be elicited by stimulating the medial bulbar reticular formation, pontine and midbrain tegmentum, and dorsal hypothalamus and subthalamus. The EEG response to reticular excitation

was best obtained with low voltage, high frequency stimulation. Stimulus frequencies of 50/sec were the lowest at which definite alterations could be elicited, and the response was considerably improved by increasing frequencies up to 300/sec. According to Worden and Livingston (1951), reticular, peripheral, and cerebellar activation all induce a similar kind of behavioral arousal. Also behavioral arousal can be brought about by stimulation of the cortical zones which project to the reticular formation.

Most studies have shown that the arousal system cannot function in the absence of sensory input directly to the reticular formation itself. Large lesions of the reticular formation seriously impair consciousness and if extensive enough result in a comatose animal (Lindsley, Schreiner, Knowles, & Magoun, 1950; Lindsley, Bowden, & Magoun, 1949). However, Adametz (1959) found that equally large lesions inflicted in multiple stages failed to abolish behavioral and EEG arousal.

A second arousal system--the limbic system. Attention has been focussed on the reticular system as an arousal system--to be more exact, perhaps, as the arousal system--for the past twenty years since it was originally described by Moruzzi and Magoun (1949). It has been employed to account for attention (Hernández-Peón et al, 1956a; Hernández-Peón et al, 1956b), and "habituation" or "adaptation" (Hernández-Peón & Scherrer, 1955), and learning, about which more will be said later.

More recently a two-arousal hypothesis has been advanced by Routtenberg (1968) in which Arousal System I is the reticular formation and Arousal System II is the limbic system. It is Routtenberg's thesis that the reticular formation alone as an arousal system is unable to account for all the data; e.g., lesions destroying the reticular formation alone in multiple-stage operations do not render animals comatose (Adametz, 1959), animals with reticular lesions are able to perform complex behavioral conditioning tasks (Doty, Beck, & Kooi, 1959). Other data contrary to the hypothesis of a single arousal system include Feldman and Waller's (1962) investigations in which they found that lesions in the midbrain reticular formation of cats which cause EEG synchronization do not cause somnolence, but that lesions restricted to the posterior hypothalamic medial forebrain bundle region produce a sleeping or comatose animal capable of demonstrating low voltage fast EEG activity. In addition, there is the problem of REM (rapid eye movement) sleep, which is characterized by a desynchronized EEG pattern (Dement & Kleitman, 1957) and which still appears following lesions of the reticular formation (Jouvet, 1961; Hobson, 1965). Jouvet (1961) reported that certain limbic lesions eliminated the low voltage fast activity seen during REM sleep.

On the basis of such evidence as the above, Routtenberg concluded that other structures must be involved in EEG arousal and that "neither the reticular formation alone nor the limbic

system alone is critical for LVF (low voltage fast activity), but that either one may be capable of bringing about LVF." Routtenberg has suggested that the medial forebrain bundle (MFB) system running through the hypothalamus and telencephalon also mediates the low voltage fast activity. Routtenberg (1968) cited the following as evidence for his hypothesis of MFB mediation of LVF:

. . . stimulation of MFB at the level of posterior hypothalamus produced neocortical desynchronization and hippocampal theta. It should be recalled that theta activity has often been referred to as a "hippocampal arousal response." If a cerveau isolé transection was performed neocortical desynchronization disappeared but theta remained. Thus, the transection reduced neocortical "arousal" by virtue of cutting off midbrain RF; the same section, however, left hippocampal "arousal" intact . . . If a sufficient time for recovery of function is allowed . . . then this system might be able to produce neocortical desynchronization, perhaps via a septal-cingulate pathway (p. 54) . . .

According to Routtenberg's theory then Arousal System I is the primary system in producing neocortical desynchronization, although Arousal System II can produce neocortical desynchronization when Arousal System I is damaged. It would be expected that elimination of Arousal System I would eliminate or reduce neocortical desynchronization; however in Routtenberg's theory Arousal System II would be sufficient to maintain the wakefulness of the organism. With elimination of Arousal System II somnolence or severe disruption of primary vegetative activities would be likely, but LVF might still persist. Arousal System I

is ascribed a more sustaining, or tonic, influence with respect to neocortical desynchronization, and Arousal System II, on the other hand, is assumed to be more critical than Arousal System I for the maintenance of basic "vegetative" activities. Arousal System I is assumed to be active where stimulation-produced neocortical desynchronization is obtained and Arousal System II where stimulation-produced reward effects are obtained. However, it is postulated that each may contribute, in the other's absence, to the function of the other.

Although Routtenberg does not feel that complete anatomical specification of the two systems is yet possible, in his current formulation (1968) he identifies Arousal System I with the reticular formation and Arousal System II with the limbic-midbrain system, with the major ascending component of Arousal System I being Forel's tractus fasciculorum tegmenti and the major component of Arousal System II being the MFB, which contains both ascending and descending components.

Activation Pattern and the Role of Arousal Systems in Learning

Study of the EEG response to light led accidentally to the discovery that the alpha blocking response could be conditioned. Durup and Fessard (1935) noted that the click of the camera shutter used in photographing the alpha blocking elicited by light soon induced the same electrographic response even when the light was withheld. The click had not previously produced an electrocortical response and had apparently acquired the property of altering the occipital alpha rhythm specifically as a result of its association in time with the visual stimulation. Gastaut, A. Jus, C. Jus, Morrell, Storm Van Leeuwen, Dongier, Nacquet, Regis, Roger, Bekkering, Kamp, and Werre (1957) found in humans that the rolandic rhythm (rhythme en arceau), which is preferentially blocked or desynchronized by movement of the limb but is unaffected by visual stimulation, could be conditioned to a tone. The CS was a pure tone which produced no alteration of EEG rhythms before conditioning. The UCS was a continuous or intermittent light. The subjects had been instructed previously to clench the fist (recorded electromyographically) the instant the light appeared. Combination of somatomotor and visual unconditioned signals produced desynchronization of both the alpha and rolandic rhythms. After paired trials in which visual stimulus and fist clench

were preceded by the previously ineffective acoustic signal, a bilateral desynchronization of alpha and rolandic rhythms occurred in response to the sound and before appearance of the light. This phase of widespread responsiveness was brief and was soon replaced by an isolated blocking of the contralateral rolandic activity upon presentation of the tone.

A number of theoretical formulations have used the brain-stem reticular formation as a nodal point. Several investigators (Gastaut, 1958; Yoshii, Pruvot, & Gastaut, 1957; Yoshii et al, 1960) have suggested that the activity of the brainstem reticular activating system is first conditioned and, subsequently the activity of the amygdaloid-hippocampal system and the thalamic reticular system, which suppresses the activity of the midbrain reticular system. Gastaut (1958) explained the mechanism of "closure" in terms of synaptic convergence of heterogeneous sensations on the neurones of the reticular formation:

Whatever sensory modalities are utilized in the elaboration of a conditioned reflex, one of the signals (the unconditioned) is capable of causing the neurones of the brain-stem reticular formation to discharge. The latter are efficaciously bombarded by the reticulopetal collaterals of the ascending pathways in which the signal circulates; some of the peripheral manifestations of the unconditioned reflex depend on this discharge. On the other hand, the other signal (the conditioned) is not able to make these same neurones of the reticular formation discharge; the reticulopetal collaterals converge on these same neurones but the bombardment is ineffective. Finally, the succession at brief intervals of the conditioned and the unconditioned stimuli

and the repetition at more widely spaced intervals of these combinations of stimuli create, at the neurones which have been converged upon, phenomena of spatial and temporal summation. The functional "traces" of these phenomena (which are phenomena of facilitation and of potentiation) and the plastic traces (structural modification of protein molecules) finally make the conditioned stimulus capable of causing these neurones to discharge on their own account (p. 265).

Yoshii et al's (1957) evidence for the early participation and later inhibition of the mesencephalic reticular formation is the appearance in the early stages of conditioning of desynchronization during the presentation of the conditioned stimulus, a continuous tone, and the replacement of this desynchronization in a later stage by hypersynchronous repetitive discharges which progressively tend to follow the frequency of the unconditioned stimulus, an intermittent photic stimulus. Gastaut (1958) concluded that the reticular neurones which participate in the conditioned closure are chiefly found at the thalamic level (the thalamic reticular system), because the closure is expressed on the cortex by local and not by generalized desynchronization, i.e., there is a contraction of the cortical response to the region of the unconditioned analyzer.

Grastyán (Grastyán, Lissák, Madarász, & Donhoffer, 1959; Grastyán, 1961) has proposed that one role of the hippocampus may be to produce reticular inhibition. In earlier studies Grastyán et al (1959) had found that stimulation of the retic-

ular system elicits an orientation reflex very similar to a natural one and at the same time high amplitude slow waves (4 to 6 c/sec), theta waves, in the hippocampus (Green & Arduini, 1954), while stimulation of the hippocampus effectively inhibits the orientation reflex and conditioned reflexes and is accompanied in the contralateral hippocampus by a clearcut desynchronization in the hippocampus and rhythmic slow potentials only appeared after a sufficient number of associations of the stimuli, i.e., at an early stage of development of the temporary connection. At the stabilization of the conditioned reflex, the slow waves ceased and desynchronization reappeared. However the rhythmic slow waves were found to reappear in association with the orientative reflex, whenever the conditioned reflex became labile, or regressed (e.g., at the beginning of development of differential inhibition, or at extinction). Considering desynchronization in the hippocampus, as at the neocortex, an expression of enhanced activity and the rhythmic slow waves that of an inhibitory state, Grastyán et al (1959) concluded that the normal function of the hippocampus may be to prevent the occurrence of orienting responses to insignificant sensory stimulation, and that this inhibitory function may be suppressed during the initial phase of learning. In this formulation the rhythmic slow response of the hippocampus is taken as an early sign of the appearance of a temporary connection. The release phenomena such as hypermotility and increased orientation

following hippocampal ablation (Karmos & Grastyán, 1962) support Grastyán's proposal that the reticular formation can be inhibited by the hippocampus.

Galambos (Galambos, 1958, 1961; Galambos & Morgan, 1960) has suggested that changes associated with learning are to be found in many places within the central nervous system and that a much broader formulation--if indeed we are ready for formulation of hypotheses at all at this stage--is necessary. He has proposed that learning involves four main systems: (1) the classical afferent pathway to specific thalamic nuclei and to corresponding cortical projection areas; (2) the descending efferent sensory systems arising from cortical and subcortical regions and making synaptic contact with ascending pathways at all levels including the first sensory relay; (3) the reticular or non-specific ascending pathways receiving collaterals from specific sensory tracts and passing to the cortex by way of the intralaminar and mid-line nuclei of the thalamus; and (4) limbic-midbrain circuit in which activity arising in the midbrain passes to the hippocampus, amygdala, hypothalamus, septal nuclei and then back to the midbrain reticular formation. The classical afferent systems (specific sensory pathways), modulated by efferent control systems are ascribed the function of disseminating information about current environmental events to the cortex and to the reticular formation. Galambos suggested that the reticular formation

suberves arousal and alerting functions and that motivational factors depend upon activity in the limbic system circuit. For Galambos (1961) "the neural change of learning is not a single event occurring at a single point in time but rather a sequence of events occurring over a more or less prolonged interval in widespread brain locations." He sees the neural change of learning as a "dynamic course of events during acquisition according to which responses grow and fade in one structure after another until at last a stable pattern of brain activity associated with the fully elaborated CR becomes established."

The theoretical formulations involving arousal systems presented thus far have been of a type which might be called "connectionistic." Other have developed formulations which might be termed "pattern coincident," i.e., they involve in general a matching by the brain of a pattern established by learning with the current signal coming in. The typical experiment involves the presentation of a repetitive stimulus. The initial idea of such studies was the identification of anatomical structures that respond to conditioned stimuli during different phases of the learning process.

One of the earliest studies involving the frequency-specific responses to repetitive stimuli upon which such formulations are based is that of Livanov and Poliakov (1945). The

UCS was repetitive electrical stimulation of the skin; the CS, a light flickering at the same rate (3/sec) as the electrical stimulation. They observed that 3 c/sec driving of the cortical EEG appeared after only a few CS-UCS pairings during the CS presentation as well as during the intertrial intervals. When the behavioral CR (leg flexion) became well established, the spontaneous repetitive rhythms disappeared from the intertrial periods, but occurred reliably when the CS was presented. It was noted that frequency-specific activity was most pronounced in the visual cortex during the early stages of conditioning but later became localized primarily in the motor cortex which had shown little or no photic driving during the initial CS-UCS presentation.

McCrrell and Jasper (1956) achieved similar results using a flickering light as the UCS and a tone, touch, or change in background illumination as CS. However, they noted that the repetitive response is not always uniform nor frequency-specific and that these repetitive responses can be conditioned only within the narrow range of frequencies which appear spontaneously in the background rhythm of the animal. Although it was possible in a given animal to condition several different repetitive rates by using different frequencies, the conditioned response was usually not precisely at the flicker frequency but merely tended to approach that frequency with repetitive trials.

McAdam, Snodgrass, Knott, and Ingram (1961), with a 20/sec flash for the CS and a delayed shock as the UCS in cats, recorded the electrical response of the reticular formation, hippocampus, thalamus, and several cortical regions. They observed good frequency-specific responses at 20 c/sec in the hippocampus and in the reticular formation during the early stages of conditioning. As in Livanov and Poliakov's (1945) and Morrell and Jasper's (1956) experiments, as the conditioned reflex became more regular, the frequency-specific responses disappeared.

Yoshii et al (1957) were among the first to advance the hypothesis that there is a relationship between the frequency-specific discharges and the physical expression of a mnemonic trace. They found that the frequency-characteristic waves predominated in the reticular formation and were less clear in the centre-median. When the authors became aware of the hippocampal arousal pattern in the same frequency band appearing during classical conditioning, they studied the frequency-specific waves with higher stimulus frequencies. Yoshii et al (1960) found that frequency-characteristic waves appeared sporadically from a wide area of the cortex and amygdala, hippocampus and reticular formation, but the rate of occurrence of the response was smaller than when the UCS was of a frequency of 4 or 5 per second. At the same time the hippocampal arousal pattern of subcortical 5 c/sec waves was also seen arising from the amygdaloid nuclei, hippocampus, reticular

formation, septal region, fornix, and nucleus commissurae posterioris. However, they noted that the frequency-characteristic waves occurred in the cortex after the hippocampal pattern disappeared. Yoshii et al (1960) concluded that a distinction should be made between nonfrequency-specific slow waves of hippocampal origin which appear during the early phase of conditioning in subcortical as well as cortical leads and the frequency-characteristic waves which are seen only in cortical leads and persist after the hippocampal arousal pattern has habituated. They consider the two phenomena as basically different and merely superficially similar due to the use of a UCS incidentally of the same frequency of the hippocampal arousal pattern.

John (1961, 1967) has advanced a "pattern coincident" or "coincidence detection" hypothesis on the basis of similar observations of responses to repetitive stimuli and studies of the characteristics of electrographic data obtained for appropriate and erroneous behavioral responses during differential conditioning. When behavioral responses in the frequency-discrimination task were appropriate for the particular stimulus which was presented, potentials recorded from the specific sensory system and from nonmodality specific structures agreed with the frequency of the CS. When inappropriate responses occurred, the frequency of potentials in the specific sensory structures still agreed with the CS. However, the potentials

observed in nonspecific structures deviated from the presented CS frequency and tended to correspond with that of the stimulus appropriate to the behavioral response which was performed. John concluded that:

. . . in certain brain regions the electrical activity elicited by a stimulus was largely stimulus-bound, and primarily reflected the peripheral input, while in other structures the mode of electrical activity reflected the release of temporal patterns which were related to previous experience [and that] the behavioral outcome in discrimination situations seemed to involve interaction between these two systems (p. 252).

John (1967) postulated that two representational systems are established during conditioning: (1) a general representational system built as a consequence of repeated experiences, which might be called the "memory trace" or "engram" of that experience. John has suggested that nonspecific structures, e.g., regions of the reticular formation, the intralaminar and association nuclei of the thalamus, the hypothalamus, and the rhinencephalon, which are in a sustained nonrandom state of activity during the stimulus or which are activated by the stimulus, become associated in the general representational system. (2) A specific representational system established between structures in the specific sensory system which are activated by the stimulus. John's coincidence-detection hypothesis demands a mechanism for the comparison of the pattern of activity in the general and specific representational systems. John has proposed that, as these two representational

systems are elaborated, a set of associated links is established whereby phase-locked activity in the two systems interacts. According to his hypothesis, the dominant temporal pattern activated by a stimulus in the reticular formation and other associated nonspecific regions, reflecting the tonic influences of the moment from structures reporting the state and "set" of the organism, is propagated upward to the intralaminar nuclei of the thalamus, then to the association nuclei, and then to the association areas of the cortex. From the association areas, John has suggested that this pattern might project to the specific sensory areas of the cortex via axodendritic synapses, with information arriving along the classical sensory pathways activating axosomatic synapses. In this fashion, the probability of consequent efferent discharge from the cortex might be altered by proper phasing of patterns of axosomatic and axodendritic impulses, impinging on cortical neurons.

Anatomical Considerations of Visual and Motor Systems

Since it was not the intent of this thesis to study either the visual or motor systems per se, only a brief description of the general anatomy of each is presented, followed by studies concerning the changes in the electrical activity of those systems with arousal or with learning.

Visual System

The visual system consists of (1) the retina which contains the primary photoreceptors as well as the first (bipolar) and second (ganglion cell) relays of the system; (2) the optic nerve which partially decussates at the optic chiasma in such a way that each postchiasmatic optic tract carries information from the nasal half of the contralateral retina and the temporal half of the ipsilateral retina; (3) relay nuclei in the brainstem, including the lateral geniculate body, superior colliculi, and pretectal area; (4) the optic radiations from the geniculate body to the visual cortex; and (5) the primary visual projection area (area 17) and the visual association areas (areas 18 and 19) of the occipital cortex.

Area 17, the striate cortex, projects to the visual association areas. The parastriate cortex, which surrounds area 17 and extends anteriorly to area 19 and the border of

the occipital lobe, does not receive direct fibers from the visual system. The major afferent input to area 18 arises from the primary visual projection area of the striate cortex. The parastriate cortex is reciprocally connected through the long association bundles of the hemispheres to the somatosensory, auditory, and frontal association areas as well as the primary somatosensory and motor areas which surround the central fissure. It projects corticotectal and corticomesencephalic fibers to the superior colliculi and pretectal nuclei for the control of eye movements.

Hubel and Wiesel (1965) have worked out in cats the retinotopic organization of the three visual areas using microelectrode recording of single cell activity and have, in addition, analyzed the histological appearance of the cortex in the three areas. Hubel and Wiesel have found an exact correspondence between physiologically defined area I and histologically defined area 17, between area II and area 18, and between area III and area 19. Also, on the basis of fiber degeneration, they have confirmed the existence of a previously described fourth visual area Vss in the medial suprasylvian sulcus.

The visual system apparently projects to the reticular formation (French, Verzeano, & Magoun, 1953). Anatomical data (Brodal, 1957) suggest that this might be via a pathway from the superior colliculus to the reticular formation.

There are apparently also projections from the brainstem reticular formation to the visual system. The resting activity of geniculate neurons has been found to vary as a function of general "arousal" with some cells showing an increased rate of firing during EEG and behavioral activation, others a decrement. Ogawa (1963) has shown that electrical stimulation of the brainstem reticular formation increases the rate of spontaneous discharge of some geniculate neurons. Arden and Söderberg (1961) found that sudden auditory stimuli (whistling, hand-clapping, and other noises) increased the geniculate response to light as well as the resting level of spontaneous discharge. Maintained or frequently repeated presentations of visual stimuli tended to reduce the response of geniculate neurons. Arden and Söderberg found that electrical stimulation of the brainstem reticular formation caused the same effect as natural "arousing" stimuli.

Using the height of response recorded from the pyramidal tract as an index of excitability, Wall, Remond, and Dobson (1953) found increased excitability of the motor cortex with visual stimulation. They concluded from the results of lesions placed at various levels in the visual system that neither the visual receiving area nor the visual association area were responsible for the facilitatory effect of visual afferent volleys on the motor cortex. Only lesions placed in the pretectal region abolished the facilitatory effect of stimulation.

Kuypers, Szwarcbart, Mishkin, and Rosvold (1965) have shown that cortical mechanisms in vision undoubtedly extend into the temporal area. The temporal area in question is located on the inferior convexity of the temporal lobe and comprises parts of the inferior and middle temporal gyri. They suggested that perhaps the visual function of this temporal area depends primarily on corticocortical connections which link it to visual cortical areas. The effects of crosshatching and undercutting on original learning and postoperative retention in visual pattern discrimination tasks have been inconsistent. Fribram, Blehert, and Spinelli (1966) found crosshatching produced no impairment in learning or retention, whereas undercutting resulted in impairments in both situations. Chow (1961), on the other hand, found impairment when the temporal cortex was crosshatched.

Morrell's (1960) microelectrode study of behavior of single units in the visual cortex, reticular formation, dorsal hippocampus, and nucleus ventralis anterior of the thalamus (nonspecific thalamic nucleus) during sensory-sensory conditioning indicated cortical participation at all stages of conditioning with predominance of excitatory effects (with reference to single unit discharge) at some stages and inhibitory at others.

Motor System

Two types of motor systems are commonly distinguished: the pyramidal and the extrapyramidal. The pyramidal system is usually characterized as controlling the rapid and precise movements of the extremities of the type often called skilled movements. The influences of the extrapyramidal system seem more concerned with alterations in response tendency ranging in complexity from gross postural adjustments to subtle and as yet poorly understood control of movement.

Pyramidal motor system. The pyramidal system, as defined by Grossman (1967), includes all cortical cells which project axons through the pyramids of the ventral medulla descending into the spinal cord. The primary motor area (Brodmann area 4) occupies most of the precentral gyrus. Anteriorly, it is bounded by a "suppressor" area (area 4s). Layer V of the motor area contains many giant pyramidal cells of Betz which give rise to many of the long, myelinated fibers of the corticobulbar and corticospinal tracts. Other fibers of the pyramidal motor system arise from smaller pyramidal cells located in the primary motor area as well as areas 6 and 8 of the frontal lobe and the sensory-motor areas of the postcentral gyrus (areas 3, 2, and 1 of Brodmann). The posterior portion of area 6 contributes to the pyramidal and extrapyramidal fiber system. Stimulation of this area typically gives rise to gross limb movements.

Extrapyramidal motor system. The extrapyramidal motor system consists of several interacting components which are to some extent anatomically and functionally distinct. The extrapyramidal system, as described by Grossman (1967), contains (1) cortical neurons from most if not all sections of the cerebral hemispheres; (2) the striatum and pallidum of the telencephalic basal ganglia; (3) certain diencephalic nuclei (the subthalamic nucleus and the nuclei ventralis anterior, ventralis lateralis, and medialis of the thalamus); (4) mesencephalic structures (the red nucleus and substantia nigra); (5) certain reticular and cranial nerve nuclei of the lower brainstem; and (6) the cerebellum.

Some pathways forming part of the extrapyramidal motor system and arising from the primary motor area of the frontal lobe project to motor centers of the brainstem and spinal cord. The axons of these tracts arise primarily in the fifth and sixth layers of the precentral gyrus and pass to the caudate nucleus, putamen, globus pallidus, thalamus, red nucleus, substantia nigra, and subthalamus.

The precentral gyrus receives afferents from areas 3, 2, 1, 5, and 21 and 22 of the temporal lobe and areas 6, 8, 9, and 10 of the frontal lobe. Area 4 projects association fibers to areas 1, 5, and 7 of the parietal lobe, to the secondary motor area at the foot of the central fissure, and to areas 4 and 6 of the frontal lobe.

Stimulation of the anterior portion of the precentral gyrus (area 4s) produces a general relaxation of muscular tension and terminates spontaneous activity. This "suppressor" effect is independent of direct connections between areas 4 and 4s. It seems to be mediated by subcortical projections which connect area 4s with the caudate nucleus, globus pallidus, nucleus ventralis anterior of the thalamus, and primary motor cortex.

A secondary sensory-motor area has been demonstrated at the base of the precentral and postcentral gyri.

The more anterior portion of area 6 and the adjacent area 8 project largely to the basal ganglia and bulbar motor nuclei. Corticobulbar efferents also arise from area 44 located ventrally to area 3. The premotor areas 6 and 8 are reciprocally connected to the primary motor area of the precentral gyrus as well as to portions of the cingulate gyrus and the parietal lobe. These areas project afferents to the putamen, globus pallidus, red nucleus, and midbrain via corticostriate and corticorubral pathways and fibers which join the ansa lenticularis.

Creation of a Dominant Focus by Anodal Stimulation

A "dominant focus of excitation" can be created by the application of a constant current low level anodal stimulus to the cerebral cortex. An anodal current applied to the

motor region of the cerebral cortex does not itself produce movement, but when a sensory stimulus such as tone or light is administered during the current flow, a discrete movement corresponding to the polarized region is noted. On cessation of the polarizing current, presentation of the sensory stimulus continues to elicit the motor response for periods of about half an hour, the effectiveness gradually diminishing during this interval.

Rusinov and Rabinovich (1958) have reported the results of a number of Russian researches in which temporary connections have been formed in the presence of a dominant focus established by surface anodal polarization. Naumova (1956) studied in rabbits the nature of the changes in electrical activity of the cortical dominant focus under the influence of motor reflexes to sound. She showed that the appearance of a dominant focus in the polarized part of the motor cortex is accompanied by a moderate rise in the frequency of electrical oscillations which increases during the movement. Sokolova and Hon Sek-Bu (1957) likewise observed an acceleration of the rhythm of electrical oscillations in the EEG under the action of continuous current, which acceleration they regarded as an increase in the lability of the polarized area. In cases when a motor reaction accompanied the acceleration of rhythm it was preserved after the switching off of the current. In cases when a dominant focus could not be created the rise in rhythm was unstable and the

faster rhythm disappeared in the EEG immediately after the switching off of the continuous current.

Novikova and Farber (1956) studied in rabbits the properties of the dominant focus created in the occipital cortex and showed that the focus of stable excitation created in the occipital area by frequent photic stimuli, as well as the focus of excitation created by the anode of continuous current, possess the properties of a dominant.

Rabinovich and Trofimov (1957) demonstrated that during the formation of a conditioned reflex an excitation focus appears in the cortex which possesses certain properties of a dominant. According to Rabinovich and Trofimov:

This dominant focus expands to the cortical areas between which a temporary connection is formed arising whenever the conditioned stimulus exerts its action and inhibits the areas of the cortex which have no direct relation to the given reflex. This excitation focus in its electrographical expression may arise in response to impulses from other sources and then it inhibits the capacity of other parts of the cortex to respond to stimulation addressed directly to them. Finally, this excitation focus possesses certain inertia (p. 27).

Rusinov and Rabinovich (1958) concluded from their review of the Russian researches that the dominant focus of excitation plays an important role in the formation of temporary connections.

Kalinin and Sokolova (1961) investigated the effects of indifferent stimuli during the simultaneous polarization of both the sensorimotor cortex and the midbrain reticular forma-

tion of rabbits. Following anodal stimulation of the motor cortex alone they observed, after only a few applications of an "unextinguished" (novel) stimulus, a motor reaction set in that was characteristic for the reinforcement of a dominant focus in a polarized area. On the other hand, with the application of an "extinguished" (habituated) stimulus, they found it was only very rarely possible to obtain a motor reaction. The following modifications appeared in the EEG with the application of the direct current: Against the background of the DC action, the unextinguished stimulus evoked a distinctly prolonged reaction of blocking, which did not become extinguished with repetition of the stimulus. The extinguished stimulus against the background of the DC action elicited, at best, a relatively weak blocking reaction. With simultaneous polarization of the cortex and the midbrain reticular formation, both the extinguished and the unextinguished stimuli elicited a movement, although that to the unextinguished stimulus was more powerful. The EEG of the sensorimotor cortex showed a distinct reaction of desynchronization in response to both stimuli. The authors concluded that a dominant focus is reinforced by an indifferent stimulus only when this stimulus evokes in the EEG a distinct reaction of activation and that a stimulus to which the reaction of activation has been previously extinguished either evokes no movement at all or a weak and unsteady one. They suggested that the reinforcement of a dominant focus is

closely bound up with influences exerted by the reticular formation of the midbrain.

Summation in the dominant focus is explained by Kalinin and Sokolova (1961) in terms of an interaction of local excitation in that focus with the diffuse reaction in the nervous system in response to a stimulus appearing on the EEG in the form of the so-called arousal or activation reaction, which they assume to be a reflection of the activity of the midbrain reticular formation. In other words, Kalinin and Sokolova postulate that the reinforcement of a dominant focus in the cerebral cortex is closely connected with the influences emanating from the midbrain reticular formation, which are reflected in the form of the diffuse changes in the EEG in response to the stimulus.

John (1961) cited a study of Sokolova (1958) in which motor movements to visual and auditory stimuli were elicited during anodal polarization of the motor cortex. Sokolova found that when a motor response is obtained to a sound, the sound elicits first a suppression of activity in the visual cortex, then slow waves followed by a desynchronization of motor cortex as the movement occurs.

Rusinov and Rabinovich (1953) cited a study of Sakhiulina (1955) in which changes in electrical activity of the motor and auditory areas of the cortex of dogs were studied during the development of a defensive motor conditioned reflex to

sound. The formation of the conditioned connection was accompanied by an increment in frequencies and amplitudes of electrical activity in both areas. As the conditioned reflex became stronger, high-amplitude electrical activity rhythms became concentrated in the motor area of the cortex in a focus which corresponded to the projection of the animal's limb stimulated by electrical current.

Morrell (1961), in confirmation of the Russian studies, found that during the period of current flow, the polarized region appeared to be sensitized in a nonspecific manner so that any transitory event such as a handclap, extraneous noise, a puff of air to the animal's face, entrance of the experimenter into the recording cage or tone or light stimulus would trigger the appropriate behavioral response. However, in the postpolarization interval, behavioral responses appeared only upon presentation of those stimuli which had been administered during the actual current flow and were absent during the administration of signals of the same or other modalities having no prior association with the anodal current.

Morrell (1961) also studied the activity of single units within the polarized field. He found that the low level anodal current did not itself produce any significant change in the unit discharge frequency, but the superimposition of a peripheral stimulus, which prior to polarization failed to alter the rate of unit firing, produced a clearcut change in unit

discharge frequency. In the immediate postpolarization interval unit discharge patterns showed a selectivity similar to that in the behavioral response when "differential" signals were presented.

Morrell (1961) concluded that such findings indicate that the selective sensitivity is a function of the past history of a signal rather than an incident characteristic at the moment of presentation. On the basis of the selectivity of the polarized neuronal population, Morrell has tentatively proposed that the imposed potential gradient has conferred upon these cells a property analogous to some attributes of short-term memory. Particularly in support of his hypothesis are the results of certain single unit studies. During the passage of nodal current, a "conditioning" train of 3/sec flicker causing 3/sec unit driving was delivered. A single test flash presented 30 seconds to several minutes after cessation of the conditioning train elicited a repetitive unit discharge at a 3/sec frequency, from which he assumed that the polarizing current had conferred upon the sampled cells the property of retaining some representation of the temporal pattern of a prior experience.

Laminar Analyses in Cerebral Cortex during CR Formation

Rabinovich (1961) has conducted several laminar analyses of the motor and visual, auditory, and cutaneous analyzers

during establishment of a conditioned defensive reflex to the stimulus specific to the analyzer under investigation. Prior to pairing the CS and UCS, he found that when the stimulus (sound, light, or electrical skin shock) was applied, there was an increase in the amplitude and frequency of the potentials in all layers of the analyzer specific for the stimulus. However, this increase was most pronounced in layers II and IV of the appropriate CS analyzer. Electrocutaneous stimulation of the paw sometimes induced a very weak reaction in layers III and V of the motor analyzer, but less frequently than in the cutaneous analyzer. Rabinovich felt that the relative weakness and infrequency of the motor reaction effectively eliminated the possibility that these changes might be due to the act of paw flexion itself.

After a few pairings of the CS with electrical stimulation of the paw, the light or sound began to induce responses in the somatic sensory and motor cortex that were similar in nature and localization to those previously induced by stimulation of the paw, while stimulation of the paw elicited the potential changes specific for such stimulation in the visual or acoustic cortex. Although initially there was a generalized elevation of activity in response to the application of the CS and UCS, as a stable CR began to appear, the elevation was found only in layers II and IV of the appropriate CS analyzer and the somatic sensory cortex and layers III and V of the

motor cortex. A selective activity increase of lesser magnitude was also seen occasionally in the background records between trials, especially in layers II and IV of the CS analyzer and somatic sensory cortex, and somewhat less regularly in layers III and V of the motor cortex.

Rabinovich (1961) has also demonstrated that internal inhibition, irrespective of the conditions of its emergence (differentiation, extinction), develops simultaneously in all analyzers participating in the closure of the given CR. As inhibition became stabilized, the frequency and amplitude of the potentials in all cortical layers decreased. However, in many cases the application of an inhibitory CS resulted in a reduction in activity primarily in layer IV, and more rarely in layer II, of the analyzer to which the CS was addressed, and in layer V of the motor cortex, simultaneously with a greater reduction in layer IV of the cutaneous analyzer. Rabinovich regarded these findings with regard to inhibition as particularly significant since it suggested to him that structures of layer IV may participate not only in CR closure, but also in CR inhibition at the cortical level.

On the basis of these laminar analyses, Rabinovich (1961) suggested that afferent input to the CS analyzer causes an outflow from layers III and IV via association fibers of pyramidal neurons. Contact with the motor region is assumed to be made through cells in layer II of motor cortex. These in turn are

assumed to send short axons to synapse with pyramidal cells in layer V where the final efferent discharge originates.

Fine-Grained Analyses of Fast Frequency Spectrum

Structures from which 40 c/Sec Activity Has Been Recorded

There have been many studies reporting generalized cortical desynchronization during conditioning, particularly during the earlier phases and often continuing into later phases of conditioning (John, 1961). Also a number of researchers have observed the appearance of specific frequencies, particularly "40 c/sec activity," within the fast frequency "arousal" spectrum at various stages in the development of conditioned responses; however in such studies the observation of such fast activity has frequently been merely incidental to the investigation of other phenomena. Further, 40 c/sec electrical activity has been elicited by electrical stimulation of certain structures. A few studies involving fine-grained analyses of the entire fast frequency spectrum (20-50 c/sec) have indicated the presence of synchronous 40 c/sec activity within the diffuse, "desynchronized" EEG activation response. The discussion of studies relating 40 c/sec activity to learning, or stages of learning, will, for the most part, be deferred pending description of the loci within the nervous system where 40

c/sec activity has been observed. In a few instances a study involving a learning task will be discussed in the earlier section when its close connection with the material under discussion would render its exclusion at that point unnatural.

Olfactory bulb and other rhinencephalic structures. Adrian (1942), studying olfactory reactions in the hedgehog, found that when air is blown or sucked forcibly through the nose 35-45 c/sec electrical activity occurs in the pyriform lobe. Similarly, series of volleys with a frequency of 30-40 c/sec were evident in the olfactory bulb when air was blown into the nostril or sucked through it by post-nasal cannula. The intense stimulation produced by such odors as tobacco smoke also provoked volleys at a frequency of about 40/sec, although respiratory movements were completely inhibited.

Since Adrian's early observation of these rhythmic bursts of approximately 40 c/sec in the olfactory bulb and pyriform lobe, numerous investigators have recorded such activity from various rhinencephalic structures, including the olfactory bulb, olfactory tubercle, lateral olfactory stria, prepyriform cortex, pyriform cortex, and the amygdaloid complex. This activity has been observed in rhinencephalic structures in many species, although the exact frequency has varied somewhat from species to species. However it is usually approximately 40 c/sec. It has been observed in the catfish (Adrian & Ludwig, 1938); toad (Takagi & Shibuya, 1961); frog (Gerard &

Young, 1937); turtle (Boudreau & Freeman, 1962); rabbit (Adrian, 1955; Yamamoto & Iwama, 1961; Stumpf, 1965); rat (Woolley, Barron, & Timiras, 1966; Woolley & Timiras, 1965); hedgehog (Adrian, 1942); dog (Domino & Ueki, 1960; Ueki & Domino, 1961); cat (Lavin, Alcocer-Cuarón, & Hernández-Peón, 1959; Lesse, 1957a, 1960; Hernández-Peón, Lavin, Alcocer-Cuarón, & Marcelin, 1960; Freeman, 1962a, 1962c; Boudreau & Freeman, 1963; Gault & Leaton, 1963; Eidelsberg & Neer, 1964; Pagano & Gault, 1964; Gault & Coustan, 1965; Pagano, 1966; Sheer et al, 1966a, 1966b; Peña-loza-Rojas & Alcocer-Cuarón, 1967); monkey (MacLean & Delgado, 1953; Domino & Ueki, 1960; Ueki & Domino, 1961; Hughes & Mazurowski, 1962a, 1962b); chimpanzee (Adey, 1963); and man (Brazier, 1961; Gedevanishvili, 1959; Sem-Jacobsen, Peterson, Dodge, Jacks, Lazarte, & Holman, 1956).

The 40 c/sec rhythmic activity in the olfactory bulb has been attributed both to activation of mechanical receptors by airflow (Ueki & Domino, 1961; Gault & Coustan, 1965; Gault & Leaton, 1963; Pagano, 1966) and to a centrifugal influence which is assumed to originate from some region of sensory convergence related to arousal, e.g., the mesencephalic reticular formation (Lavin et al, 1959; Hernandez-Peon et al, 1960).

The evidence at this time seems to indicate that the 40 c/sec activity in the olfactory bulb is a function of both nasal airflow and centrifugal input, but nasal airflow must be present for the occurrence of this rhythmic activity in the

olfactory bulb. Pagano (1966) appears to have performed the crucial experiment to resolve the conflict concerning the importance of nasal air flow versus direct reticular influences upon olfactory bulb activity. He investigated the effects of nasal air flow and brainstem stimulation in the medullary reticular formation (Med RF), mesencephalic reticular formation (Mes RF), and mesencephalic central gray (Mes CG) on induced activity recorded from olfactory structures in acute, artificially respired, curarized cats. In this way, it was possible to observe the influence of this stimulation upon olfactory bulb induced activity without the confounding by air flow changes normally elicited by the effect of such stimulation on brainstem respiratory centers. Nasal air flow was manipulated independently by pumping air in puffs through a cannula placed in one naris.

With nasal air flow held constant from puff to puff, stimulation in the Mes RF, Med RF, and Mes CG produced a strong augmentation of olfactory bulb induced activity. Stimulation in the absence of nasal air flow, however, produced no observable increase in pre-existing olfactory bulb activity. This augmentation was completely eliminated by severing the olfactory peduncle showing that the augmentation was effected via centrifugal fibers running in the olfactory peduncle to the olfactory bulb. Increases in nasal air flow in the absence of brainstem stimulation caused augmentation of the olfactory

bulb induced activity without significant changes in neocortical arousal. From these results Pagano concluded that olfactory bulb induced activity varies in amplitude and duration as a function of nasal air flow and centrifugal input and that the effect of brainstem stimulation is one of modulation of a response elicited by nasal air flow. The variations associated with changes in nasal air flow alone were assumed to reflect recruitment of different numbers of olfactory receptors.

As early as 1953, Arduini and Moruzzi (1953a, 1953b), with less evidence, suggested that the pons and the medulla facilitate in some way the olfactory arousal reactions. Arduini and Moruzzi had found that the electrical activity of the olfactory bulb is synchronized by stimulating recruiting areas of the thalamus and that bulbo-reticular stimulations, eliciting generalized arousal reactions, are able to disorganize the thalamically induced but not the peripheral synchronization of the olfactory bulb. Also, burst activity of the cerebral cortex was observed to be blocked in the cerveau isolé cat by olfactory but not by visual impulses. On the basis of their findings, they advanced the hypothesis that the olfactory and the reticular ascending impulses converge on the cephalic areas of the activating system.

Freeman and his associates (Biedentach & Freeman, 1965; Boudreau & Freeman, 1963; Freeman, 1960a, 1960b, 1962a, 1962b, 1962c, 1964) have made extensive researches into the electrical

activity of the prepyriform cortex of the cat. Freeman has found that the prepyriform cortex exhibits a spontaneous sinusoidal waveform of approximately 40 c/sec, which appears in high amplitude bursts, synchronous with respiration. Freeman (1962b) has devised a four-parameter system for describing evoked potentials: amplitude, frequency-spectrum, phase of onset, and degree of resonance, or Q. Q gives an indication of the number of cycles of oscillation in the evoked response and is estimated by the equation

$$Q = \frac{\pi}{\ln (V_n/V_{n+1})}$$

where V_n is the amplitude of a chosen peak in the time response and V_{n+1} is the amplitude of the peak of the following cycle. Biedenbach and Freeman (1965) regard these four parameters as indices of cortical excitability, with the highest Q value being associated with "optimal" cortical excitability.

Biedenbach and Freeman (1965) stimulated the lateral olfactory tract and recorded the evoked potentials from the prepyriform cortex of cats. The evoked potential was isolated from the background of spontaneous activity by averaging many responses with a Mnemotron CAT 400. A set of averaged potentials was obtained at five intensities of stimulation for each

of 12 cats. The first stimulus intensity was near threshold, the last was that intensity at which the form of the potential no longer significantly changed, usually between 2.5 and 3.5 times threshold intensity. This intensity range was divided by four to obtain five stimulus intensities.

The Q parameter of the evoked potentials was plotted as a function of increasing stimulus intensity and it was found that Q became maximum; i.e., the evoked potential became most oscillatory, between 1.1 and 1.8 times threshold intensity. The peak value occurred at 1.4 times threshold intensity. At the highest intensities Q decreased.

Fourier transforms from a set of averaged evoked potentials were obtained at four stimulus intensity levels--threshold, $\times 1.3$, $\times 1.7$, and $\times 2.5$. At threshold there was a broad distribution of frequency components, all with low amplitudes. At 1.3 times threshold intensity (almost corresponding to the maximum value for Q), a marked peaking occurred at 40 c/sec. At 1.7 times threshold a low frequency component increased in amplitude, and at 2.5 times threshold intensity the dominant waveform shifted to a low frequency band and the high frequency component, which was dominant at the lower intensities, became subsidiary.

Freeman (1962c) measured amplitudes of evoked potentials in the prepyriform cortex as a function of frequency of stimulation to the lateral olfactory tract of cats during bar pressing for milk. Frequency-response curves plotted from these

data revealed that at one week after criterion there was a dominant peak at approximately 44 (41-46) c/sec. As over-training progressed the frequency-response curve underwent a gradual change consisting of a flattening and increased irregularity, with the appearance of one or more additional peaks at low frequencies, particularly the enlargement of an amplitude peak at one-half the initial peak frequency (18-24 c/sec). Within 4 to 7 weeks the original peak near 44/sec was absent or greatly reduced, and the new amplitude peak had become dominant.

Eoudreau and Freeman (1963) performed power spectral analyses on the spontaneous activity from the prepyriform cortex of cats in a standardized food response, consisting of orientation to a light signifying imminent arrival of milk and, following presentation of the milk 4 sec later, lapping of the milk for approximately 10 sec. They found that the dominant component in the spectrum is a sinusoidal waveform of about 40 c/sec, which appears in large amplitude bursts synchronous with respiration. In a number of records large changes occurred in the lower frequency end of the spectrum coincidental with "lapping." In some records a definite peak at 24 c/sec appeared and in others there was an increase in the amplitude of the 6 c/sec band.

Although air flow is both a necessary and sufficient condition for the occurrence of rhythmic 40 c/sec electrical ac-

tivity in the olfactory bulb, in certain other rhinencephalic structures, e.g., amygdala, air flow appears to be a necessary, but not a sufficient condition for the occurrence of the characteristic electrical activity. Apparently there must be air flow and some level of arousal for this rhythm to occur.

MacLean and Delgado (1953) described rhythmic burst activity synchronous with respiration in the amygdala of monkeys that disappeared when the nasal passages were occluded or when a tracheal cannula was inserted.

Sheer et al (1966a) also observed that air flow through the nasal passage is essential for the occurrence of the 40 c/sec activity not only in the olfactory bulb, but also in the prepyriform cortex and the basolateral amygdala. Bilateral ablation of the olfactory bulb abolished the 40 c/sec activity; ipsilateral nasal occlusion abolished it ipsilaterally with an increase contralaterally. Autocorrelograms and frequency analyses were computed with and without nasal occlusion. Both loss of periodicity and a flat frequency spectrum were demonstrated with nasal occlusion.

Observations of Domino and Ueki (1960) indicated that behavioral arousal is necessary for the appearance of the 40 c/sec activity in the amygdala in monkeys. When aroused, bursts of 40 c/sec activity every few seconds were evident in the amygdala and related olfactory areas. Spontaneous arousal from sleep was sufficient to produce the 40 c/sec activity;

however loud noises, stimulation of the tooth pulp at slightly above threshold, and pain induced by increasing the pressure in a balloon inserted into the rectum were more effective. Neocortical desynchronization accompanied all four conditions of arousal, but was less evident in the case of rectal distension. When the animal began to sleep again, the bursts in the amygdala subsided.

On the other hand, Lesse (1957a) found that the rhythmic amygdaloid pattern in the cat was not merely a stereotyped concomitant of the neocortical arousal pattern and was not associated with spontaneous changes from sleep to wakefulness. Stimuli, such as a buzzer, which resulted only in waking or in brief attentiveness did not induce the rhythmic 40 c/sec activity but did elicit desynchronization in the neocortex. Certain stimuli, e.g., noxious stimuli, very loud noises, visual, olfactory, or auditory stimuli associated with food or water after periods of deprivation, proximity of a mouse or dog, for a cat, tended to elicit the characteristic 40 c/sec activity from the basolateral portion of the amygdala and the adjacent pyriform cortex. The modality of the stimulus was found to be unimportant in eliciting the electrical response--visual, auditory, olfactory, and noxious stimuli all proved effective. Food or water stimuli were found to be effective when the animals were hungry or thirsty but not after they were satiated. From this evidence Lesse concluded that "this type of electrophysiologic

activity, unlike neocortical 'desynchronization' may be associated with behavioral responses encompassing 'vigilance' or 'excited attentiveness' as distinct from mere arousal from sleep or alerting to brief attentiveness."

Subsequent to these early observations of the necessity for air flow and arousal for the occurrence of rhythmic 40 c/sec bursts in the amygdala, there have been numerous demonstrations of a dissociation between amygdaloid and olfactory activity (Gault & Leaton, 1963; Gault & Coustan, 1965; Grandstaff, 1965; Sheer et al, 1966a). Gault and Leaton (1963) noted that it is possible for bursting to occur in the bulb without activation of the amygdala and that amygdala bursting and activity in the olfactory bulb are most closely associated when the animal is in an excited state.

Grandstaff (1965) observed that during the behavioral resting state 40 c/sec bursting occurred clearly only in the olfactory bulb and pyriform cortex, but during behavioral arousal 40 c/sec electrical bursting occurred also in the basolateral amygdala. Sheer et al (1966b) have shown that the occurrence of 40 c/sec rhythmic activity in the amygdala is not directly related to the amount of airflow but to the novelty and/or "meaningfulness" of the odor associated with the airflow, e.g., sardine odor as compared with anise. Orienting behavior, characterized by a high level of alertness, cortical EEG arousal pattern, and sniffing responses, appeared to be a

necessary condition for the occurrence of 40 c/sec rhythmic activity in the amygdala.

Since a dissociation between the 40 c/sec activity in the olfactory bulb and the amygdala can be clearly demonstrated, Pagano and Gault (1964) have suggested that there must be two inputs into the amygdala, one from the olfactory bulb, and the other from central origins. The latter is assumed to gate the 40 c/sec activity from the bulb while at the same time regulating cortical activity.

A dissociation also has been observed between the prepyriform cortex and the olfactory bulb. Pagano (1966) noted that in the absence of nasal air flow changes, the prepyriform activity induced by brainstem stimulation is not a mere reflection of olfactory bulb activity. From this evidence he concluded that different mechanisms apparently are operating in the two areas.

Forty c/sec activity has also been recorded from the hippocampus by Torii (1961) with stimulation of the medial septum, the lateral hypothalamus, and the medio-ventral part of the tegmentum of the midbrain of the rabbit and by Stumpf (1965) in the rabbit with reticular or septal stimulation. Torii (1961) found that direct stimulation of the medial preoptic area, medial hypothalamic region, central gray matter and dorso-lateral part of the tegmentum of the midbrain produced the slow wave pattern of the hippocampus, characterized by regular slow waves at 5 to 7 c/sec. Torii suggested that two separate

systems within the brain, occupying separate pathways, influence the hippocampal activity, one producing a slow wave pattern, the other a fast wave pattern, each system being activated by stimulation of separate brain areas. One system is assumed to run from the ventro-medial part of the tegmentum of the mid-brain through the lateral part of the hypothalamus to the medial septal region and fimbria, and the other from the dorso-lateral part of the tegmentum through the central gray matter to the medial part of hypothalamic and preoptic area. He suggested that the slow and fast wave induced systems may correspond to Schutz's system, composed mainly of fibers which ascend from the periaqueductal gray midbrain substance to the caudal region of the periventricular zone of the hypothalamus, and the medial forebrain bundle, respectively. The fast wave induced system passing through the medial forebrain bundle of the lateral hypothalamus is assumed by Torii to be concerned with the parasympathetic activity and the slow wave induced system including Schutz's system with sympathetic activity.

Stumpf (1965) has found that several separate patterns of hippocampal activity can exist under various experimental conditions: the hippocampal slow activity may be irregular, regularized (theta rhythm), or depressed and each of these slow wave patterns may be associated either with an inconspicuous, irregular and low voltage fast activity or with fairly regular, relatively high voltage fast activity. On

the basis of this evidence, he postulated that three separate mechanisms must influence hippocampal activity: one inducing the hippocampal theta rhythm, a second the regular fast activity, and the third the depression of hippocampal slow waves.

Cerebellum. Three patterns of spontaneous electrical activity have been reported from the cerebellum: (1) low voltage fast waves at 150-250 c/sec; (2) extremely fast potential oscillations (1,000-2,000 c/sec) superimposed on the low voltage fast waves, and (3) much slower regular rhythmic waves of a frequency ranging from 20-40 c/sec and, according to Irger, Koreisha, and Tolmasskaya (1949), a slower frequency of 6-8 c/sec. The latter slow wave pattern, which has been described variously as 30-50, 30-40, and 20-40 c/sec activity, has been observed by a number of investigators (Matsumoto, 1961; Irger et al, 1949).

Rusinov and Rabinovich (1958) cited the research of Irger et al (1949) in which they studied the electrical potentials on the human cerebellum, the results of which studies they confirmed from the recording of electrical activity of the cerebellum from the exposed brain during an operation. They recorded three types of potentials of the electrical activity of the cerebellum through an electrode inserted through the hollow of an injection needle to the cranium at the site of the projection of the cerebellum: oscillations of 170-220 c/sec; oscillations of 30-50 c/sec; and oscillations of 6-8

c/sec. In experiments on animals the authors established that oscillations with a 6-8 c/sec frequency are recorded chiefly from the cerebellar hemispheres and oscillations of 30-40 c/sec frequency are registered from the vermis area. The rapid oscillations (200-300 c/sec) were observed in all parts of the cerebellum both in man and in animals.

Matsumoto (1961), recording primarily from the vermal parts of the cerebellum and occasionally on the lobulus ansiformis, studied the morphology, conditions of occurrence, and possible mechanisms involved in the production of what he called CRA ("cerebellar rhythmic activity") in 43 cats. He found that CRA is induced by (1) sensory stimulation, e.g., a pinch of the hindleg; (2) electrical stimulation of the ascending activating system, including the bulbar and mesencephalic reticular formation, the thalamic nuclei (e.g., n. centralis lateralis), but not the specific thalamic nuclei, and the posterior hypothalamus, and (3) electrical stimulation of the frontal cortex. CRA could not be induced by stimulation of the cerebellar cortex, nucleus lateralis of the cerebellum and brachium pontis. The optimal frequency to elicit a train of cerebellar responses by repetitive reticular stimulation was approximately 30 c/sec, a frequency identical to that of CRA.

The tetanus waves induced by topical application of strychnine to the reticular formation as well as by systemic strychninization closely resembled the CRA induced by arousal stimu-

lation and a laminar analysis revealed that the same component of the cell layers of the cerebellar cortex was responsible for both CRA and strychnine tetanus waves. Both strychnine tetanus and the rhythmic activity produced by high frequency reticular stimulation were found to be abolished by barbiturates and by the surgical isolation of the cerebellum from the brainstem.

The CRA was observed to closely parallel the electrical events in the neocortex and the hippocampus: the appearance of the CRA always accompanied arousal or activated patterns in the cerebrum (low voltage fast waves in the neocortex and regular large slow waves in the hippocampus), irregardless of whether the CRA was produced by sensory stimulation or by electrical stimulation of the reticular formation. The injection of nembutal prevented the production of CRA with arousal stimulation and irregular slow and spindle-like waves similar to those of the cerebrum occurred in the cerebellar cortex.

From the foregoing evidence, Matsumoto concluded that the CRA appears to be related to the whole ascending activating system, including lower brainstem, thalamic and hypothalamic structures. Matsumoto has suggested that direct reticulo-cerebellar connections may form the substrate of a circuit in producing and maintaining a train of rhythmic waves in the cerebellar cortex which reflect the occurrence of certain rhythmic alterations of the reticular activity with arousal. The fact that

the CRA occurs most prominently in the vermis adds credence to his hypothesis since the vermis is abundantly supplied with fiber connections from the reticular formation.

Neocortex. Gedevanishvilli (1959) has reported rhythmic bursts of sinusoidal potential oscillations 55/sec in the frontal pole of the brain during any orienting reactions (alertness, attention) in rabbits, cats, dogs, and man. Gedevanishvilli has interpreted this rhythmic activity as an electrical expression of the orienting reflex. He suggested that it indicates a change in the condition of the cortex such that the most adequate reaction to external stimuli is secured. The spread of this activity from the frontal pole to other regions of the cortex during the formation of conditioned reflexes is interpreted by Gedevanishvilli as an electrical expression of the "temporary connection."

Structures from which 20 c/Sec Activity Has Been Recorded

Although the dominant frequency in the rhinencephalic structures appears to be 40 c/sec, there are persistent references to a second frequency, usually approximately 20 c/sec, e.g., Freeman's (1962c) observation of a shift to a dominant frequency of 18-24 c/sec with overtraining previously described and MacLean and Delgado's (1953) observation of electrical bursts of 26 c/sec in the amygdala of monkeys under amobarbital anesthesia. These 26 c/sec bursts disappeared when the

nasal passages were blocked or when a tracheal cannula was inserted. Feindel and Gloor (1954) have similarly noted 20 c/sec activity in the amygdala of cats with stimulation of either the reticular formation or the opposite amygdala. Presentation of a strong olfactory stimulus like lysol solution also was found to result in a similar activation of the amygdaloid region.

Domino and Ueki (1960) observed that, although the frequency of the bursts in the olfactory bulb of the dog were approximately 40 c/sec (40-46 c/sec), every second spike seemed somewhat enhanced and that the basic frequency of the bursts in the medial amygdala and posterior hypothalamus were precisely half (20-23 c/sec) the frequency of the bursts in the olfactory bulb.

A 20-25 c/sec activity with nasal air insufflation was noted by Gault and Coustan (1965) in the amygdala of cats also. The administration of light doses of cocaine enhanced the 20-25 c/sec activity in the amygdala and the 40 c/sec activity in the bulb. Frequently, the 20-25 c/sec response appeared in the amygdala in animals in which there had been no prior indication of amygdaloid activity elicited by nasal air flow.

Woolley et al (1966) used the technique of spectral analysis, based on Fourier transforms, to investigate the electrical activity of the prepyriform cortex in rats with chronically implanted electrodes. Using this technique, he was

able to evaluate the relative contributions of waves with different frequencies to the total energy present in the prepriiform spontaneous (SEA) and evoked (AEP) electrical potentials. For evoked potentials the lateral olfactory tract (LOT) was stimulated electrically. Three principal components in SEA spectra, in order of frequency of occurrence, appeared in the 35-55, 1-5, and 15-20 c/sec frequency ranges. At low intensity stimulation of the LOT, the major peak in spectra of the AEP also occurred in the 35-55 c/sec frequency range; however, with increasing intensity of stimulation, the principal component of AEP spectra increased in amplitude and shifted to 15-20 c/sec. Exposure to simulated 18,000 ft altitude for 2 hrs markedly decreased the amplitude and frequency of the fastest waves, while exposure to 12,500 ft decreased the frequency, but not the amplitude, of the same component. Woolley et al (1966) interpreted their results in terms of an interaction of excitatory impulses arriving continuously via the LOT and inhibition occurring periodically as the result of cortical loop activity. They suggested that several built-in-cortical circuits, each with a different number of cells and synapses, may explain the presence of several frequencies and the similarity of the frequencies in both SEA and AEP spectra. The fast component is assumed to dominate the AEP spectra at low stimulus intensities because circuits for that frequency have relatively low threshold, whereas circuits for the intermediate

frequency appear to have higher thresholds but are capable of attaining greater amplitude. They further suggest that the decreased frequency with increasing stimulus intensity to the LCT may be related either to a prolonged inhibition of mitral cells or to a prolongation of the inhibitory phase in the pyriform cortex.

A 20 c/sec activity has been observed by several investigators in the hippocampus. Boudreau (1966) analyzed the fast wave spontaneous activity recorded from the hippocampus of awake cats with computers and found a dominant rhythm of about 15 to 20 c/sec, which could be detected in the presence of theta. Most of the spectral energy was concentrated within the 10-30 c/sec range. Boudreau's results indicate that there may be two high energy periodicities within the 10 to 30 c/sec range, one at 14 and another at 20 c/sec, although the 20 c/sec component appeared predominant.

Brooks (1962) reported dominant spectral components of both 15-25 c/sec and 35-40 c/sec in the hippocampus of lightly anesthetized cats. Tokizane, Kawakami, and Gellhorn (1959), using multiple narrow band pass filtering, reported that the spectral energy of fast activity recorded from cats with chronically implanted electrodes is concentrated in the 10-14 c/sec and 20-25 c/sec bands with a 40 c/sec component appearing occasionally.

Recording from the hippocampus of cats; Green and Shimamoto

(1953) observed with the puncture of the hippocampus by the recording electrode a 30-45 c/sec activity which within a few seconds spread to adjacent regions on the same side or to the opposite hippocampus. With a weak stimulus, the magnitude of the discharges waxed and waned and gradually died out. However, with a stimulus of greater intensity, the rate of the discharge frequently changed suddenly to 18 to 22 a second and the discharge spread to adjacent regions, often even to the rest of the brain.

The investigations of Starzl, Taylor, and Magoun (1951) have shown that the spontaneous activity of the red nucleus of cats under B-erythroidine is characterized by 20-30 c/sec waves. Low frequency (3 to 10 c/sec) stimulation of the sciatic nerve produced 20 c/sec waves in the red nucleus. An afterdischarge of these waves continued upon cessation of stimulation. With high frequency stimulation, the activity of the area was desynchronized, but the afterdischarge remained the same. The red nucleus receives cerebello-rubral afferents from the dentate, globose, and emboliform nuclei of the cerebellum (Grossman, 1967). Starzl et al (1951) found that bilateral extirpation of the somatic cortex and complete removal of the cerebellum abolished the 20 c/sec wave afterdischarge.

40 c/Sec Activity during Learning

The presence of electrical activity of approximately 40 c/sec has been reported by numerous investigators at certain stages of learning, although usually such reports have been incidental to the problem under investigation. The studies reporting 40 c/sec activity in subcortical loci will be discussed first, followed by a discussion of those reporting such activity in the neocortex.

Rhinencephalic structures. Gedevanishvilli (1959) has reported intensification of sinusoidal potential oscillations 55/sec in the olfactory bulb during the formation of conditioned reflexes to external signals.

Adey, Dunlop, and Hendrix (1960) reported 40 c/sec rhythmic bursting in the amygdala in approach training, however, they found no clear correlation between the onset or duration of these bursts with either the animal's behavioral pattern or the slow-wave pattern in the entorhinal cortex. There appeared to be a slight diminution in amplitude and duration of the bursts as each motor performance was completed.

Lesse (1957a, 1957b, 1960) recorded 40 c/sec synchronous activity from the basolateral amygdala and pyriform cortex of cats during the formation of a delayed conditioned response in a shuttle box. Recordings were also made of the electrical activity from the caudate nucleus, the hippocampus, hypothalamus, medial geniculate body, mesencephalic reticular formation,

septal area, and neocortex, but the rhythmic activity was not observed in any of these structures. At first, the synchronous activity appeared only in response to the shock, but as the animal began to make avoidance responses, the 40 c/sec rhythmic activity appeared also in response to the CS, a buzzer. During extinction the electrical bursting ceased to occur to the CS shortly after the animal stopped making the behavioral response.

John and Killiam (1959) observed 40/sec bursts in the amygdala of cats during a conditioned avoidance task. The conditioned signal for the avoidance response was a 10/sec flickering light. As behavioral responses gradually appeared the electrical activity at the flash frequency was reduced in the hippocampus, reticular formation, superior colliculus, fornix and septum, and was increased in lateral geniculate and nucleus ventralis anterior of the thalamus. When criterion was reached (100% CAR), bursts of 40 c/sec activity occurred in the amygdala and the nucleus ventralis anterior of the thalamus showed a marked frequency-specific response to the tracer conditioned stimulus. At this time, the cortical response was observed to be a superior harmonic (20-30 c/sec). Following training to 100% CAR with 10/sec flickering light, two animals were transferred to an auditory CS (10/sec clicks). Initially presentation of 10/sec clicks did not evoke frequency-specific potentials in the electrical records nor the

CAR. However, with full establishment of the CAR to 10/sec clicks, the electrical activity evoked at central sites by 10/sec clicks then became almost identical to that evoked by 10/sec flicker, particularly with respect to the incidence of 20 and 30/sec activity in visual cortex, the high voltage slow waves in the superior colliculus, and the 40/sec bursts in the amygdala.

Sheer et al (1966b) have shown a phase lock-in of 40 c/sec activity between the amygdala and the auditory cortex (auditory area I) during CS arousal and the CS-UCS acquisition phase of learning in an appetitive classical conditioning situation with tone as the CS, milk as the UCS, and licking as the CR. With CS habituation and CS-UCS overtraining, on the other hand, there was no phase lock-in between amygdala and auditory cortex, although 40 c/sec was still present in the amygdala. It is of interest that Sheer et al (1966a) in a successive discrimination task failed to show such a relationship between the amygdala and visual cortex and that the visual 40 occurred just as markedly in animals with both olfactory bulbs removed.

Other subcortical structures. Kogan (1949) systematically studied the changes in electrical activity of a number of subcortical structures in the cerebrum of the cat (pons Varolii, optic thalami, quadrigeminal bodies, the striopallidal system, the hypothalamus) during the formation of food-taking and defensive reflex acts. He demonstrated that the electrical

activity of subcortical formations consists of slow waves of a duration of up to one second and even longer with superimposed oscillations of a 30-40/sec frequency.

Galambos (1959) reported 38 to 42 c/sec activity in both the caudate nucleus and the globus pallidus of the cat concomitant with the learning that the last click of a series of 11 clicks was a signal for an unavoidable shock across the chest. Although the evoked responses were substantially reduced in size with extinction, the 38 to 42 c/sec activity tended to remain.

In a similar experiment, Rowland (1958) demonstrated the appearance of 40 c/sec activity in both cortical (right ectosylvian gyrus and right lateral gyrus) and subcortical (medial geniculate, reticular formation, centre median, and hippocampus) placements. A 5 sec CS consisting of two clicks per second was gradually lengthened over the course of 20 days to 120 sec duration. Shock (UCS) was applied to the skin at the end of the auditory stimulus. By the 8th trial the presence of 40 c/sec bursts after the UCS was noted; by the 10th trial, these 40 c/sec bursts were appearing during the CS and were present in all placements.

Neocortex. Welch (1964) recorded epidurally the evoked potentials from the posterior lateral gyrus (visual primary receiving area) in cats to light flashes of 1/sec. Response averaging with a Mnemotron CAT 400 computer was performed on

successive groups of ten evoked potentials for seventy consecutive flashes. Fourier transforms performed with a digital computer on the first two and last three sets of evoked potentials revealed a marked peaking at the 40 c/sec band of the spectra of the evoked potential in the first two sets, i.e., in response to a novel visual stimulus. Frequencies below 20 were predominant in the last three sets of habituated potentials and there was little or no peaking at the 40 c/sec band.

During a successive visual discrimination task, Sheer et al (1966a) studied the power spectra functions of visual area I of the cat on 1/3 octave bands with center frequencies at 31.5, 40, and 50 c/sec, normalized by total band power. The cats were first trained to press a bar for milk only during a 10 sec S_D period when a 7/sec flickering light was presented on a 20 sec variable interval schedule. Later they were taught to press only during the 7/sec S_D period and to inhibit during a 10 sec S_A period when a 3/sec light was presented. A significant shift in proportional power from 31.5 to 40 c/sec occurred during the S_D , as compared with the S_A , after learning had occurred. The electrical bursting in visual area I was not invariably correlated with the 40 c/sec activity in the amygdala. In fact, the visual 40 occurred just as strongly in animals with both olfactory bulbs removed.

Sheer et al (1966a) made a fine-grained analysis of the relationship between the 40 c/sec activity in the visual area

I and the behavioral response, utilizing an analog computer technique providing continuously moving normalized power functions at 1/3 octave frequency bands with center frequencies of 31.5, 40, 50, and 7 c/sec. Comparisons were made between successive 10-sec periods of prestimulus, S_D and S_{Δ} , and poststimulus. A characteristic pattern of electrical activity in visual area I which occurred only during the S_D trials after the S_D discrimination had been learned was demonstrated by Sheer et al (1966a). Both the 31.5 and the 40 c/sec bands rose sharply with each behavioral response and, although both dropped after the response, only the 31.5 remained down for the rest of trial. The 40 dropped only momentarily and then increased and remained up for the rest of the trial, although not at the same level as during the response. Although the 50 c/sec activity was higher during S_D trials than during S_{Δ} trials, it showed no increase with the behavioral response.

Power functions were computed at the 7 c/sec frequency band in an effort to obtain an index of the relative degree to which the evoked potentials occurred during S_D and S_{Δ} trials and during the prestimulus, stimulus, and poststimulus periods. The 7 c/sec activity was found to increase in the S_D following the behavioral responses and in the 10 sec poststimulus period after S_D trials. No such increase was noted in S_{Δ} trials or prior to the response in S_D trials.

From simultaneous examination of both unfiltered EEG

records and those high-pass filtered at a 10/sec 3db cut-off, at a high resolution 200 mm/sec paper speed, Sheer et al (1966a) suggested that congruent with the behavioral response on an S_D trial, the primary positive component and oscillation train of the evoked potential lock in with the intrinsic EEG activity at 40 c/sec. While the primary positive component with a pulse duration of 25 msec (40/sec) and the 40/sec EEG seemed to be most prominent at the time the response was made, the primary negative and secondary negative components appeared to be more prominent after the response when the cat was drinking milk.

McAdam and his associates (McAdam, 1962; McAdam, Knott, & Ingrax, 1962) have studied the electroencephalographic changes during classical aversive conditioning in two subcortical locations (n. ventralis anterior thalamus and dorsal hippocampus) and two cortical locations (the posterior sigmoid gyri and the posterior lateral gyri) of cats. The CS was a light flashing at 20/sec, the UCS a shock to the pads of the animal's paw. The purpose of these experiments was to provide information with respect to Gastaut's (1958) suggestion that the nonspecific thalamic projection system mediates the conditioned stimulus. The research is of interest here because McAdam (1962) used as his index of driving a complex combination of the output from two resonators through which he fed his EEG data--one set to respond to the fundamental (20 c/sec) and the second

set to respond to the second harmonic (40 c/sec). His purpose in choosing 20 c/sec as the flash frequency was to choose a frequency somewhere between one which might produce fusion and one which could be construed to be producing quasi-trace conditioning; however it seems likely that his choice was a poor one since his results may represent a confounding of an actual driving effect and the intrinsic 40 c/sec activity reported by numerous investigators to be associated with various stages of learning. For this reason, his results are not cited here. However, an illustration accompanying the study which shows the output of the two resonators for the posterior lateral gyrus for the 102nd trial (out of 150) is of interest. In this illustration, although the fundamental was 20 c/sec, the output of the 40 c/sec resonator was almost as high as that of the 20 c/sec resonator.

In a very difficult visual discrimination task, Pribram, Spinelli, and Kambach (1967) have demonstrated that marked bursts of activity approximately 40 c/sec in the visual striate cortex of monkeys occurs just after differential response if the choice is incorrect; i.e., with nonreinforcement. The task involved the activation of a stimulus display for 0.01 msec by the monkey and then the pressing of the right half of a panel with the display of a circle and the left half with the display of vertical stripes. One monkey failed to learn the task at all, and the other two monkeys reached a criterion of

85% correct in 200 consecutive trials only after 1800 and 2800 trials.

Dumenko (1961) studied the electrographic changes in the projection zones of the forelimb and hindlimb of the motor cortex and in the cutaneous, auditory, and visual cortical analyzers. The dogs were first trained for defense CRs from the hindpaw; then they were switched to a defense CR from the forepaw in the same room and with the same CS stereotype. Certain changes were seen to occur in both the hindlimb and the forepaw zones. Potentials in the area corresponding to the hindlimb began to appear which were independent of the synchronized potentials still seen in the auditory and cutaneous analyzers. At the same time and prior to the development of the correct forepaw response, the slow waves (20-25/sec) which had characterized the forepaw zone prior to the switch gave way to faster waves (approximately 40/sec). With the appearance of the correct responses from the forepaw a distinct synchrony of the potentials in the auditory and cutaneous analyzers and cortical forelimb representation first appeared.

Sakhiulina (1960) reviewed some of her previous research in connection with conditioned-reflex activity, from which the following material with reference to high frequency oscillations (30-40 c/sec) in the sensorimotor area is quoted:

When separate conditioned reflexes or the stereotype elaborated from them became well established (after hundreds of combinations), the electrical activity

in the intervals between the applications of the stimuli was distinguished by a very low voltage, while the positive stimuli during their action sometimes evoked considerable volleys of high-frequency oscillations (30 to 40 per second) in the sensorimotor region of the hemisphere contralateral to the leg, the lifting of which conditioned reflexes were being elaborated. In all other points of the cortex considerable and slow oscillations were recorded which we are inclined to regard as an indication of the phenomenon of induction inhibition developing within them.

During their action the negative conditioned stimuli evoked modifications in the EEG contrary to those observed during the action of the positive conditioned stimuli. If by the moment of the application of the differentiating stimulus high-frequency oscillations took place in the EEG they underwent complete depression, and slower oscillations appeared in their place. In all other points of the cortex the recorded frequencies were also undergoing certain changes, lower frequencies being predominant (p. 212).

Sakhiulina (1960, 1961) also studied the changes occurring in the EEG of the dog in more complex forms of CR activity: shifting the site of application of the US, CR switching, and reversal of the signal significance of the CSs. One common observation emerged from all three types of experiments: elevated high-frequency electrical activity appeared in one or another area of the cerebral cortex and was maintained during the phase of solution of the problem posed and disappeared once the problem was solved and stable performance under the new condition was achieved. Characteristically this high frequency activity was 25-30, sometimes 40-45, c/sec. This activity was observed primarily in two

lobes: in the frontal lobe at the junction of the anterior portion of the coronal and anterior ectosylvian gyri, and in the parietal lobe, at the junction of the transitional fields of the visual, auditory, and somatosensory analyzers. With respect to the primary focus in the frontal lobe, it appeared that the frequencies of 25-30 c/sec are dominant in the more medial portion of the area (in the anterior portion of the coronal gyrus), while higher frequencies predominate in the more lateral portion (the region of the ectosylvian gyrus). Sakhiulina suggested that this activity may be due to the influences of the reticular formation since the areas in which the elevated high-frequency activity was observed coincide with the cortical points that have the densest representation of the brainstem and thalamic reticular formations, or to the cortical points that, when stimulated, induce an arousal effect via the reticular formation.

Rowland (1958) referred briefly to an experiment in which cats were trained under partial reinforcement to expect shock following 30 sec of silence interspersed within a background of clicks at the rate of 1/sec throughout the day. At a middle point between full reaction and full extinction bursts of 40 c/sec were occurring in the second half of the CS, predominantly in the sensory motor cortex and the association cortex. With full extinction, the 40 c/sec bursts were replaced by the characteristic synchronized background of the

sleeping animal.

20 c/Sec Activity during Learning

Slow rhythms of approximately 20 c/sec have occasionally been reported in connection with internal inhibition. Yoshii et al (1960) reported waves of about 20 (18-23) c/sec appearing from the cortex and subcortical structures "when alternate presentation of positive and negative CS is stopped and the negative one alone is repeatedly presented, or when the negative CS is given in the course of experimental extinction of the positive CS, that is, when a change in the sequence of the stimulation occurred." They have suggested that the appearance of such 20 c/sec waves may be related to hippocampal activity, since similar electrical activity is elicited by stimulation of the hippocampus. Green and Shimamoto (1953) found 20 c/sec activity is propagated from the hippocampus into the temporal lobe.

During the learning of a problem involving both delay of response and delay of reinforcement, Roth, Sterman, and Clemente (1967) observed a 12-20 c/sec synchronized activity over the coronal gyrus and adjacent sensorimotor cortex during inhibitory behavior. This synchronous rhythm, which he called SMR (sensori-motor rhythm), was observed during the portion of the trial in which the cat had learned to inhibit bar-pressing and, even in the highly overtrained cat, if the behavioral

inhibition was not observed, SMR did not occur.

During a CR switching experiment previously discussed, Dumenko (1961) noted 20-25 c/sec waves in the projection zone of the forepaw of the motor cortex when the correct CR was flexion of the hindlimb.

CHAPTER III

METHODS AND PROCEDURES

Subjects

The subject was one male mature cat, OB-2, which was one of an OB series who had bilateral removal of their olfactory bulbs for a previous study (Grandstaff, 1965). The animal was a healthy alley cat secured from the city pound. The cat was housed in the air-conditioned animal colony of the psychology laboratory of the University of Houston both during the interim period prior to and during his use in this study. OB-2 was administered the standard dosage of Feline Distemper Vaccine. The normal diet consisted of one cup per day of c/d prescription solid food, especially designed to meet feline nutritional requirements, or an alternate equivalent diet of dry pellet food, in addition to a milk supplement, which consisted of equal parts of evaporated milk and water. Food and water were available to the animal on an ad-lib basis except during the period of discrimination testing when the animal was adapted to a diet of dry pellet food and no liquid except for the milk reinforcer he received during the performance of the task.

Electrodes

Concentric electrodes were used in both subcortical and cortical loci. Construction of the concentric electrodes and the connector by which chronic implantation was accomplished are described elsewhere (Grandstaff, 1965).

Surgery

Although OB-2 was one of the animals from which the olfactory bulbs were removed, electroencephalographic records (Figures 3-10) from the basolateral amygdala indicate that there must have been at least some regrowth of the bulbs between the completion of the previous study (June, 1965) and initiation of this study (June-August, 1966). The rhythmic bursting of 40 c/sec activity so characteristic of the amygdala with air flow is clearly evident in all recordings.

Bilateral, concentric depth electrodes were implanted in the anterior basolateral amygdala, corticomедial amygdala, posterior hypothalamus, septal region, and hippocampus. Bilateral cortical electrodes were in the following areas: visual I (striate gyri), visual II (posterior suprasylvian gyri), auditory I (middle ectosylvian gyri), anterior suprasylvian gyri, insular gyri, and temporal gyri.

The ablation of the olfactory bulbs and the implantation

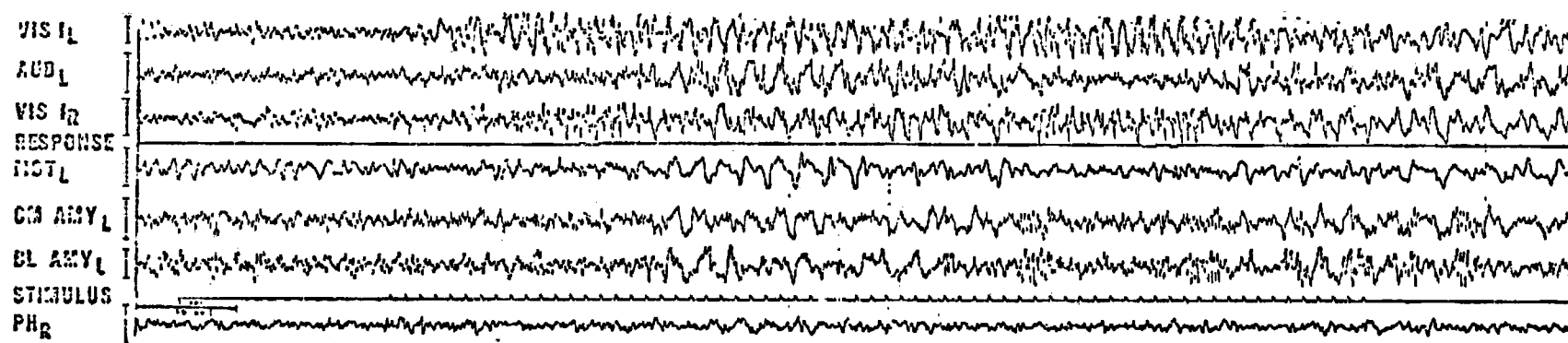


FIGURE 3

UNFILTERED EEG - TAPE 18A: S_{DR}

Illustrative of the electrical activity associated with a reinforced response. Note the 40 c/sec activity in right visual I coincident with the reinforced response. The 20 c/sec activity in left auditory cortex during lapping coincides with the large voltage slow waves in left motor cortex, left auditory cortex, and sometimes left corticomedial amygdala and left basolateral amygdala. Abbreviations: VIS IL, left visual I; AUD L, left auditory cortex; VIS IR, right visual I; MOT L, left motor cortex; CM AMY L, left corticomedial amygdala; BL AMY L, left basolateral amygdala; PH R, right posterior hypothalamus.

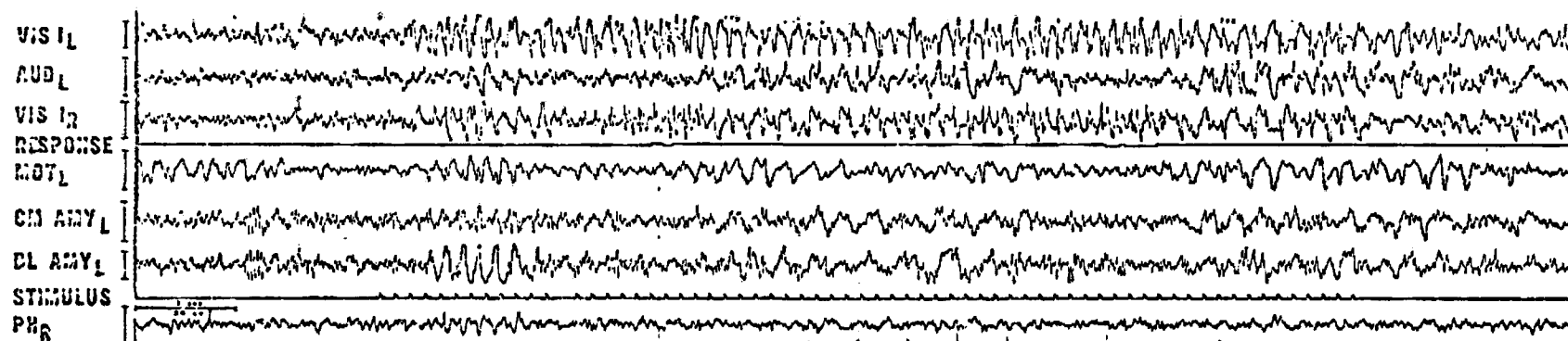


FIGURE 4

UNFILTERED EEG - TAPE 18A: SDR

Abbreviations: VIS I_L, left visual I; AUD_L, left auditory cortex; VIS I_R, right visual I; MOT_L, left motor cortex; CM AMY_L, left corticomedial amygdala; BL AMY_L, left basolateral amygdala; PH_R, right posterior hypothalamus.

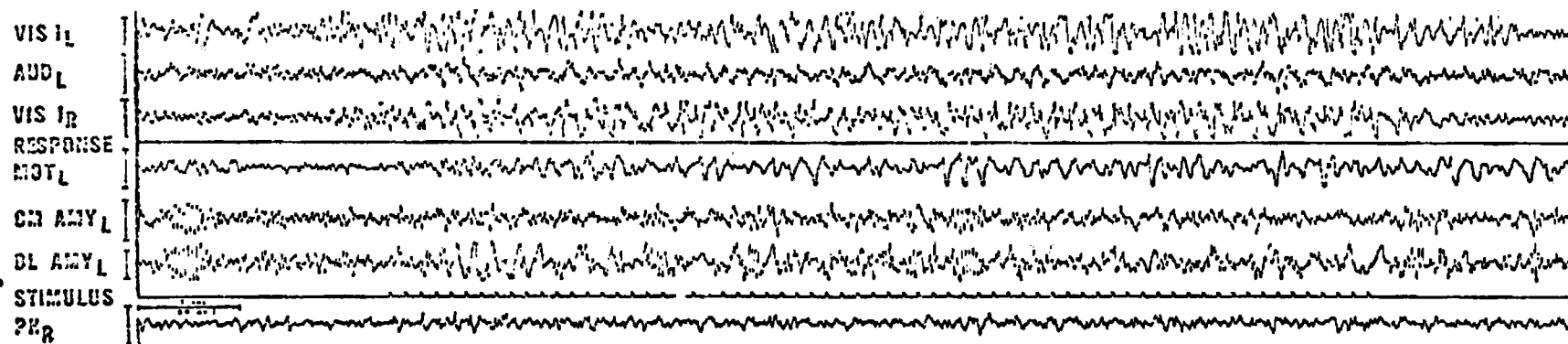


FIGURE 5

UNFILTERED EEG - TAPE 18A: S_{DNR}

Note that, in the absence of a response during S_D , the marked 40 c/sec activity seen in Figures 3 and 4 coincident with a response does not occur. Abbreviations: VIS IL, left visual I; AUD L, left auditory cortex; VIS IR, right visual I; MOT L, left motor cortex; CM AMY L, left corticomedial amygdala; BL AMY L, left basolateral amygdala; PHR, right posterior hypothalamus.

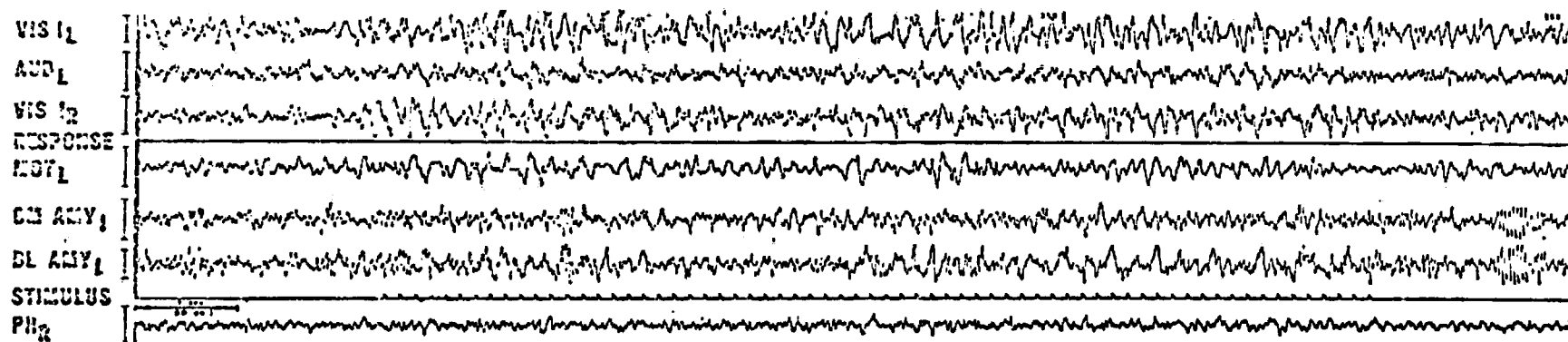


FIGURE 6

UNFILTERED EEG - TAPE 18A: S_{DNR}

Abbreviations: VIS I_L, left visual I; AUD_L, left auditory cortex; VIS I_R, right visual I; MOT_L, left motor cortex; CM AMY_L, left corticomedial amygdala; BL AMY_L, left basolateral amygdala; PH_R, right posterior hypothalamus.

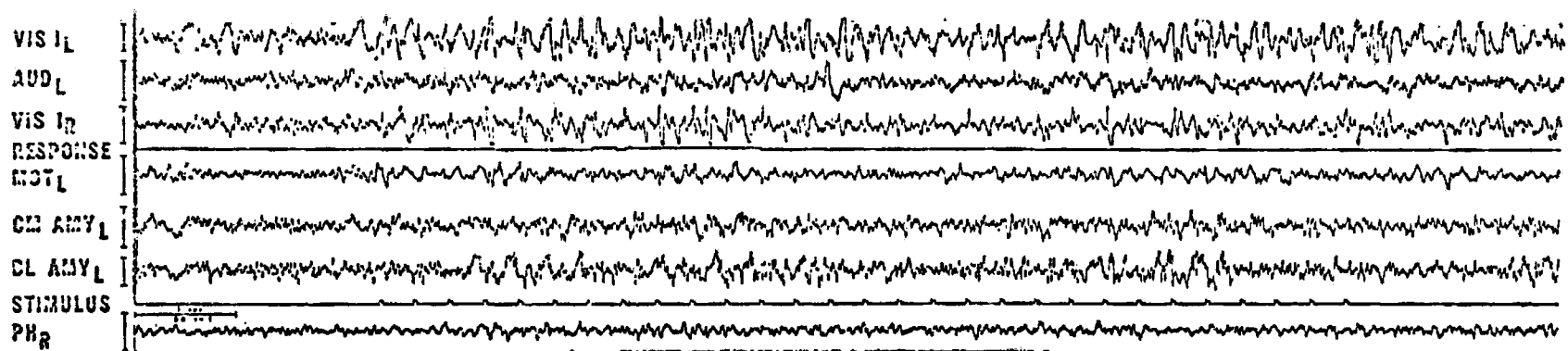


FIGURE 7

UNFILTERED EEG - TAPE 18A: $S_{\Delta} R$

The marked 40 c/sec activity clearly visible in Figures 3 and 4 is barely detectable when a response occurs during S_{Δ} . Note also that the large voltage slow waves associated with reinforcement (Figures 3 and 4) do not occur with an unreinforced response. Abbreviations: VIS I_L, left visual I; AUD_L, left auditory cortex; VIS I_R, right visual I; MOT_L, left motor cortex; CM AMY_L, left corticomedial amygdala; BL AMY_L, left basolateral amygdala; PH_R, right posterior hypothalamus.

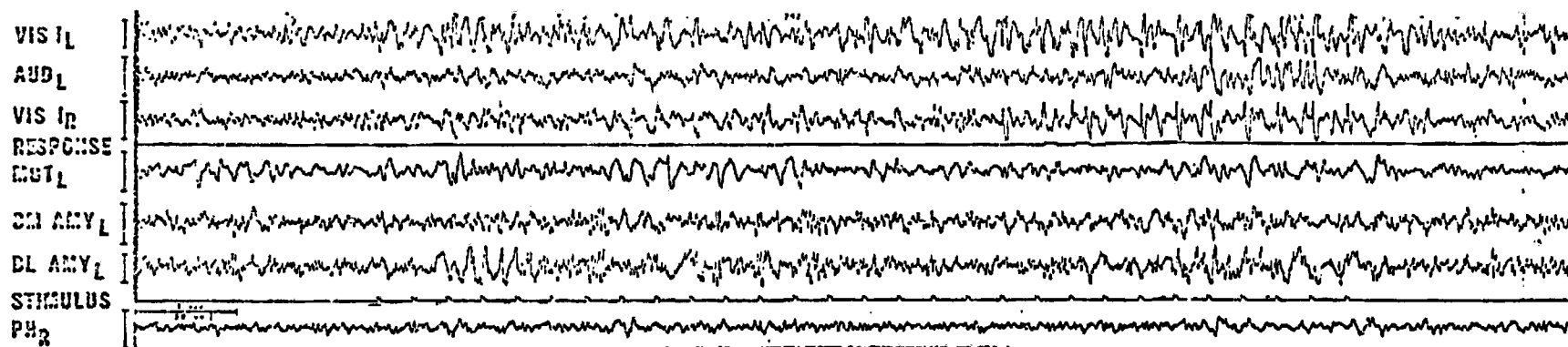


FIGURE 8

UNFILTERED EEG - TAPE 18A: S Δ R

Abbreviations: VIS I_L, left visual I; AUD_L, left auditory cortex; VIS I_R, right visual I; MOT_L, left motor cortex; CM AMY_L, left corticonedial amygdala; BL AMY_L, left basolateral amygdala; PH_R, right posterior hypothalamus.

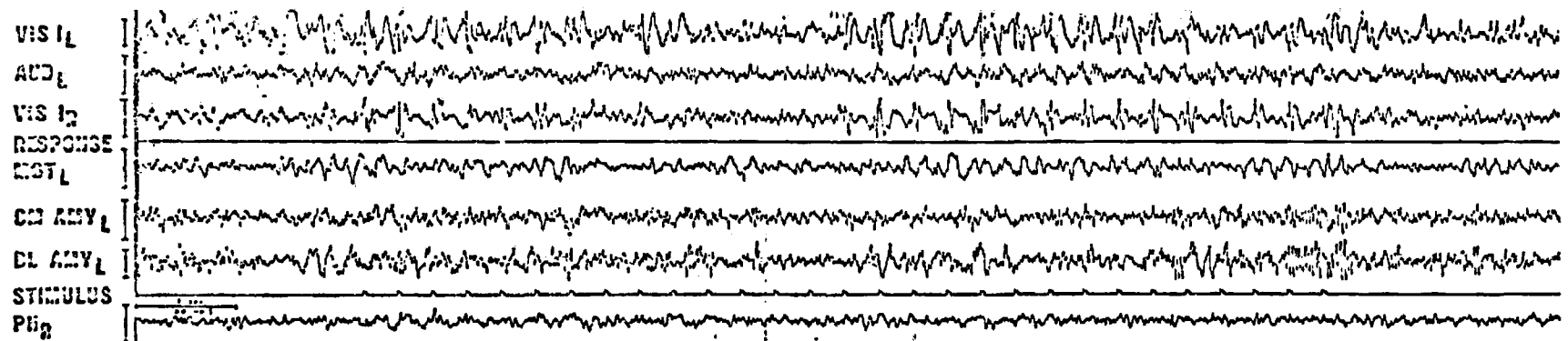


FIGURE 9

UNFILTERED EEG - TAPE 18A: S_{ANR}

Abbreviations: VIS I_L, left visual I; AUD_L, left auditory cortex; VIS I_R, right visual I; MOT_L, left motor cortex; CM AMY_L, left corticomedial amygdala; BL AMY_L, left basolateral amygdala; PH_R, right posterior hypothalamus.

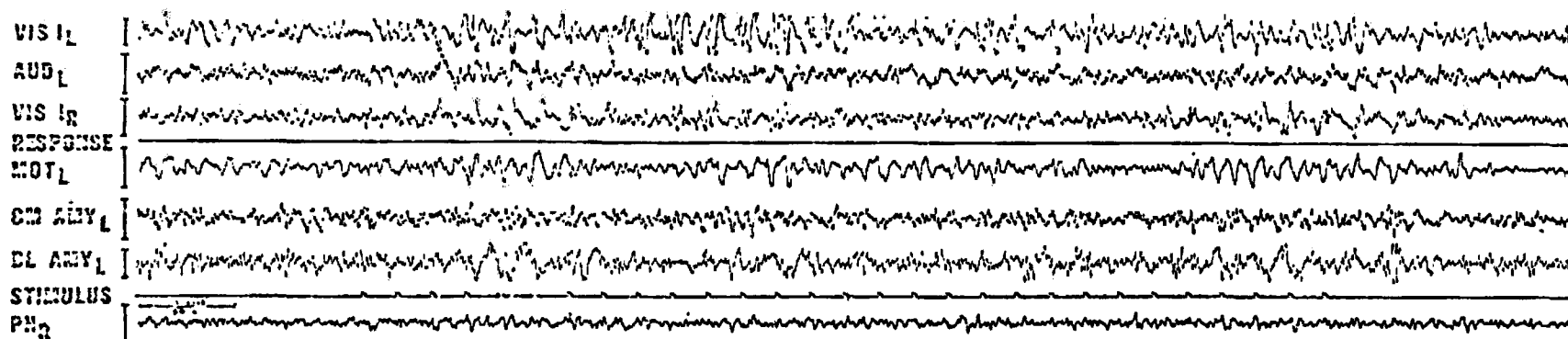


FIGURE 10

UNFILTERED EEG - TAPE 18A: $S_{\Delta NR}$

Abbreviations: VIS IL, left visual I; AUD L, left auditory cortex; VIS IR, right visual I; MOT L, left motor cortex; CM AMY L, left corticomedial amygdala; BL AMY L, left basolateral amygdala; PH R, right posterior hypothalamus.

of both the depth and cortical electrodes were described by Grandstaff (1965).

Experimental Apparatus

The testing chamber, liquid feeder system, photic stimulator, control and timing apparatus, and electroencephalographic and magnetic tape recorder systems were described in detail by Grandstaff (1965); therefore only a brief description will be given.

The experimental chamber, constructed of formica and plexiglas, was positioned in a sound resistant room before a one way vision glass, which enabled the experimenter to observe the animal from an adjacent room during the experimental session. The chamber could be divided into two smaller compartments with a clear plexiglas partition, the operant chamber of which was approximately 18" x 23" x 24". Dim or bright illumination was provided by two DC lights located in the ceiling. A Grass model PS 2 stimulator activated a neon photic light which was mounted externally at one end of the experimental chamber to produce a 7 c/sec flashing light for the S_D and a 3 c/sec flashing light for the S_A , for a period of 1.0 sec each. The flashes were seen through a port 4" above the bar and feeding cup. For both these events the intensity setting was 2.0. Seven inches above the photic port was a sound port, behind

which was an audio speaker connected to an auditory oscillator. The sound port was used to deliver a masking click to the chamber (65 db). The milk reinforcer was delivered to the liquid feeder inside the chamber through polyethylene tubing by triggering a solenoid valve. When the bar was pressed during the S_D 0.3 cc of milk was delivered to the feeder cup. The solenoid valve could also be controlled externally by the experimenter.

Foringer and Grayson-Stadler automatic control and timing equipment were used in conjunction with an eight channel Rheem Tape Reader to program the desired stimulus events into the experimental chamber.

A seven-analog and two-event channel Grass, Model III D, electroencephalograph was the basic recording unit. The seven analog channels recorded electrographic responses. One event pen was used to record the onset and duration of the photic stimulus events and the second to record the behavioral responses. The EEG was at the same time recorded on magnetic tape using a seven-analog and eight-event channel magnetic tape recorder, more fully described elsewhere (Grandstaff, 1965). The magnetic tape was started automatically 10 sec before each trial for the Prestimulus Period (PS) and remained on for the 10 sec Stimulus Period (S_D or S_{Δ}) and 10 sec Post-stimulus Period. Seven different EEG channels were recorded: left visual I, left auditory I, right visual I, left motor,

left corticomедial amygdala, left basolateral amygdala, and right posterior hypothalamus. Stimulus onset and duration and behavioral responses were recorded on the event channels of the tape recorder. Samples of EEG records are shown in Figures 3 through 10.

Experimental Procedure

The results reported in this thesis are based upon a re-testing approximately one year later in the successive visual discrimination task which was the final phase (Phase II) in the experiment reported by Grandstaff (1965). The following is a brief description of the behavioral testing prior to the animal's use in the experiment from which the results reported in this thesis were derived: Grandstaff (1965) first shaped the animals to bar press for milk and then carried them through a series of successive days on continuous reinforcement, fixed ratio 3, and fixed ratio 5, after which Phase I was initiated in which fifty daily trials were presented on a 30 sec variable interval schedule. Each trial consisted of a 10 sec S_D period of a light flashing at the rate of 7 c/sec, during which the cat would be reinforced with milk for each bar press. If the animal made more than 3 bar presses in a 10 sec period preceding the S_D period, the timer would reset the 10 sec interval until responses did not ex-

ceed 3 in the 10 sec interval preceding the S_D trial. The daily sessions were continued until the animal met a learning criterion of twice as many S_D responses as intertrial responses for three consecutive days. The animal was then run for three additional sessions before going to Phase II.

In Phase II, sixty daily trials were presented, thirty of S_D and thirty of S_Δ , in which a 3/sec flicker was on for 10 sec and the animal did not receive milk when he pressed the bar. The reset was not used in this phase of testing. A "blackout" occurred for the duration of the S_Δ periods on 50% of the S_Δ trials if a response was made. This testing procedure was continued until the animal met a learning criterion of three times as many responses during the S_D trials as during the S_Δ trials for three consecutive days. The experimental procedure for this experiment is essentially that described for Phase II by Grandstaff (1965).

Data Analysis

Data Selection

Magnetic tape recordings of EEG data were carried out over a period of approximately six weeks for one cat, OB-2, in a visual discrimination task, which the animal had learned to criterion one year previously. Eight recordings were of a quality suitable for computer analysis, i.e., all analog and

event channels were functioning, noise level was low, gains were stable throughout any single recording session. S_D/S_Δ response ratios were calculated for each of these tapes. Three tapes, 19A(1), 18A, and 10A, with S_D/S_Δ ratios of 1.32, 1.97, and 7.75, respectively, were selected to represent the lowest, an intermediate, and the highest levels of performance.

Behavioral Conditions

The power functions were analyzed under as many as six different behavioral conditions, depending on the availability of data in the various conditions, as follows:

	Pre-Stimulus	S_D	S_Δ
Response	PS_R	S_{D_R}	S_{Δ_R}
No response	PS_{NR}	$S_{D_{NR}}$	$S_{\Delta_{NR}}$

The effect of a response may have entered into one or two trials of the 19 to 24 PS_{NR} trials averaged.

Computer Analysis

The analyses of the EEG were performed on a hybrid computer system developed in the University of Houston laboratory. The design and theory of the various prewired computer programs are discussed elsewhere (Benignus, 1967).

The input to the computer is from a seven analog-channel Ampex SP-300 with additional mod-demod equipment for eight event channels, on which are recorded prestimulus, stimulus, or poststimulus period, S_D or S_{Δ} , and behavioral responses.

The output of the computer is in two forms: (1) a Brush recorder model Mark 280, with two analog channels and three event pen markers, for indicating the onset and termination of analysis periods, stimuli (S_D or S_{Δ}), and behavioral responses concurrent with the EEG analyses on the analog channels; (2) a Hewlett-Packard digital voltmeter and associated equipment for analog to digital conversion and digital print-out to an interface for control of an IEM card punch, where the cards are automatically punched for further processing digitally.

The main body of the computer consists of (1) control components, which include an Amp program board, digital timers, sealed multipole dry circuit relays, the event channels on the tape recorder, a 5 x 11 matrix of banana jacks for selection of options, and a 29-variable buffer memory with simultaneous

read-in and sequential read-out; and (2) analog computing components, which include ten channels of selectable band-pass filters and two channels of broad-band filters, twenty-eight variable time constant integrators, eight low-pass filters with variable time constants from .105 to 1.75 sec, eight high-pass filters, four quarter-square multipliers, nine two-variable magnetic multipliers, five pulse type two-variable multipliers, two two-variable dividers, six sign changers, six differential 90 degree phase shifters, two sin/arcsin generators, and associated high stability operational amplifiers, RC circuits, etc.

The band-pass filters are 23% $1/3$ octave filters with center frequencies at 20, 25, 31.5, 40, and 50 c/sec. The center frequencies were selected so that bands overlap at the half power points. The two broad-band filters have a center frequency of 31.5 c/sec and their lower half power point is 18 c/sec with their upper half power point at 53 c/sec. The area between 20 and 50 c/sec is flat $\pm 2.5\%$. The bandpass of these two filters encompasses the five $1/3$ octave filters between 20 and 50 c/sec. The broad-band filters were specially designed such that their output could be used to compute percent power in the $1/3$ octave bands, i.e., normalized band power. Total power, high pass filtered with the filter set at a low frequency half power point of 12 c/sec, was used as a second normalization quantity.

Normalized power was used, first, because the absolute value of voltage from a given site is not stable across animals or across electrodes. Secondly, absolute value as computed by the hybrid computer is meaningless, except within a single EEG recording session, because the operation of the computer requires the adjustment of the input signal to a standard level for the highest amplitudes in the EEG data. Normalization of the power functions by broad-band or total power makes possible spectrum comparisons across different sites of measurement, across recording sessions for the same animal, and across animals. Power functions normalized by both broad-band and total power were computed on this data; however only the functions normalized by broad-band power were statistically analyzed and all the figures were plotted either on the broad-band normalization data or, in one instance, on the absolute values. Normalization by broad-band was chosen because the primary interest here was in the changes in the distribution of power within the broad-band, i.e., 18-53 c/sec. Since normalization by broad-band power excludes effects from outside the range of the broad-band filter, a normalization of broad-band power by total power was computed by hand. Examination of this quantity permits the detection of extraspectral events.

Program 5, an average continuous band power computation program was used for the analysis of data in this study. With

this program an epoch of continuous computation is broken down into seven parts and the mean power is computed for each of the seven parts over trials.

Figure 11 is a flow diagram for Program 5. Each of two input signals may be fed into a five-band power computer and into a normalizing power computer, yielding analyses of one frequency for two input channels with normalization by either broad-band or total power for each input, but not by both. Alternatively, as was done in the analysis of the data in this study, one input may be fed into each of two five-band power computers and normalizing power computers, yielding analyses of two frequencies for one input channel with normalization for those two frequencies by both broad-band and total power. The five-band power computers consist of band-pass filters with squaring operators on their outputs. The normalizing power computer computes the broad-band power and the total power. To compute an approximation to a continuous band-power writeout, one of the band-power outputs is fed into one of the four sequential sampling averagers. Each of the four sequential averagers begins at $t=0$ and averages up to $T/7$ secs, then takes another sample for $T/7$ secs until seven sequential samples have been taken. This process is repeated automatically for each trial until the preselected number of trials has been read in. Once all trials have been read in, the outputs of the sequential averagers and the dividers (for

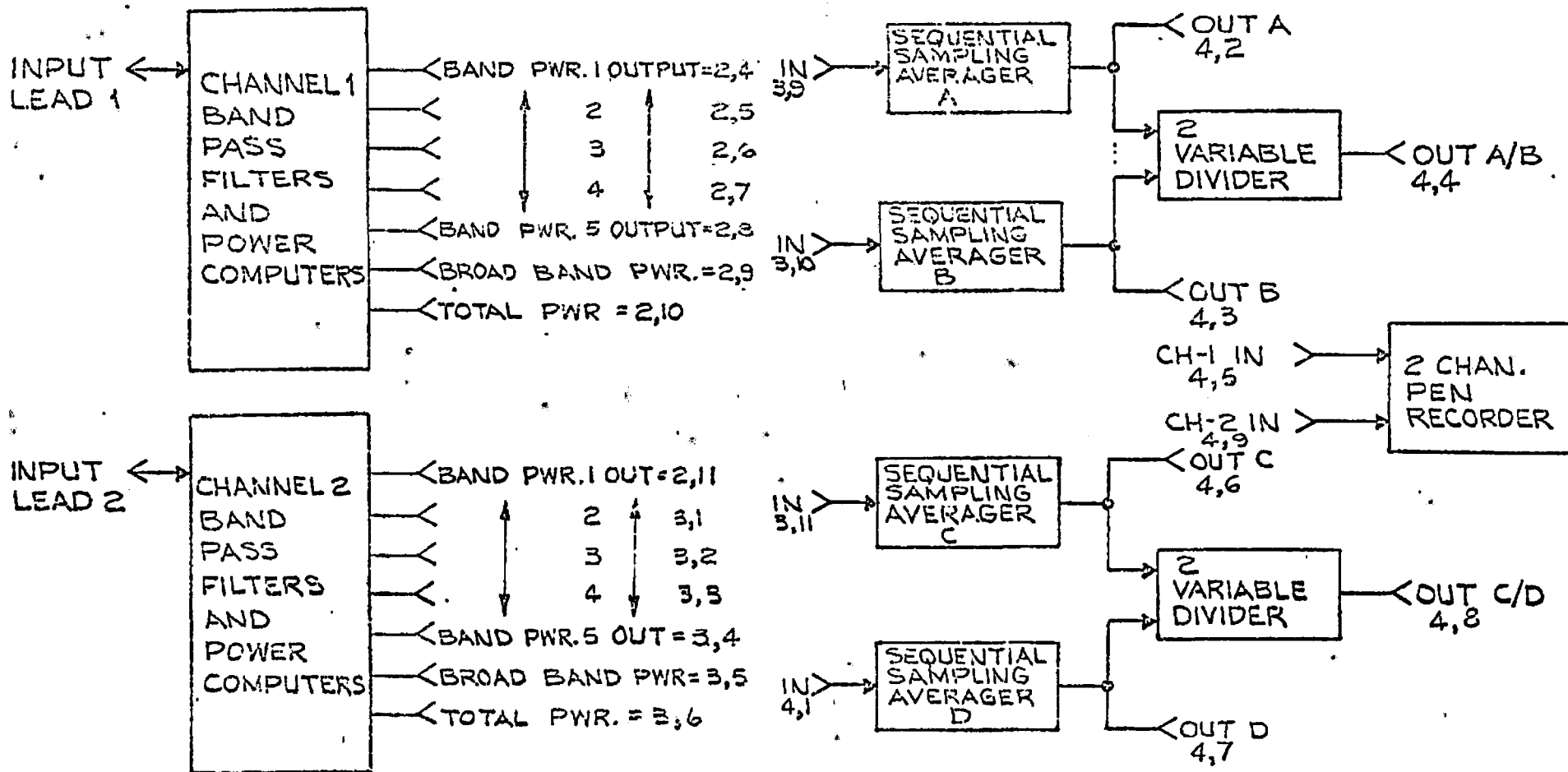


FIGURE 11

REVISIONS			UNIVERSITY OF HOUSTON PSYCHOLOGY DEPT.
NO.	DATE	BY	
1			PROGRAM 5, FLOW DIAGRAM
2			
3			
4			
5			
			DRAWN BY <i>James E. Guebert</i>
			CHK'D <i>VAB</i>
			TRACED

the normalized band powers) are read out.

The program is designed so that averaging may be made contingent on a single event, or some logical combination of up to three events at a time. A tape loop may be used as an option to delay the input wave which is being averaged so that the averaging may be begun before the event upon which the start is contingent occurs. The length of both the delay and the analysis epoch are variable, depending, respectively, upon the length of the tape loop and an oscillator which is connected to a chain of countdown binaries on the program board.

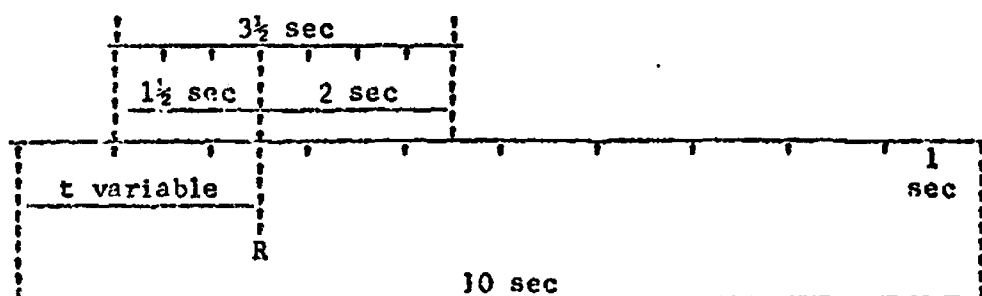
The epoch length and delay were chosen so as to include the phenomenon under investigation plus some unrelated activity. Pilot studies had indicated that 3-1/2 sec with a delay of 1-1/2 sec for visual I and the motor cortex would be necessary to achieve this result. It appeared that the peak in the 40 c/sec band occurred either at, or perhaps slightly before, the response. Auditory I was analyzed with the same epoch length and delay as an anatomical control for the visual and motor areas. The peaking in the 20 c/sec band in auditory I seemed to occur at approximately 1-3/4 to 2-1/2 sec following a reinforced response; therefore a second analysis was computed on auditory I with a 5 sec epoch length and, of course, with no delay.

Several combinations of contingencies determined the initiation of the averaging process in the analysis of the data

in this study. In all cases, the averaging was contingent upon the simultaneous occurrence of a "response" and either (1) S_D , (2) S_{Δ} , or (3) PS. However, the "response" in some cases was a behavioral response of the animal and in others an artificial response signal fed into the response event input to the computer to initiate analysis. In the case of the 3-1/2 sec analysis epoch and a behavioral response, a tape loop constructed to yield a 1-1/2 sec delay was used. Thus 1-1/2 sec of the analysis represented events occurring prior to the response and 2 sec, events occurring after the response. In the case of the 5 sec analysis epoch with a behavioral response (auditory I only), the tape loop was not used. Here the full 5 sec of the analysis represented events occurring in the 5 sec after the response. In the case of both the 3-1/2 and 5 sec analysis epochs with the nonoccurrence of a behavioral response, the tape loop was not used and a timer was set to introduce an artificial response 1 sec after the beginning of the 10 sec period. With the 3-1/2 sec analysis epoch, this resulted in the analysis of 3-1/2 sec from $t=1$ sec to $t=4-1/2$ sec during S_D , S_{Δ} , and PS. In the analysis of auditory I where the 5 sec analysis epoch with an artificial response was used, the 5 sec from $t=1$ sec to $t=6$ sec was analyzed during PS only. Figures 12 and 13 illustrate the initiation and termination of the analysis periods with respect to stimulus onset, pre-stimulus onset, and the response for the 3-1/2 sec analysis

MOTOR, VISUAL I, AUDITORY I
3½ SEC ANALYSIS EPOCH

With Behavioral Response for Analysis of S_{D_R} , S_{Δ_R} , PS_R



With Artificial Response for Analysis of $S_{D_{NR}}$, $S_{\Delta_{NR}}$, and PS_{NR}

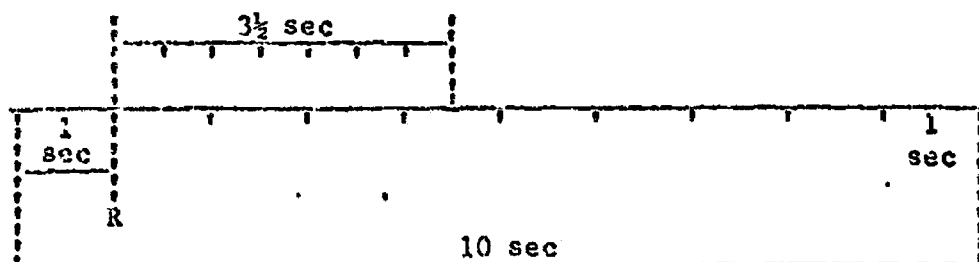
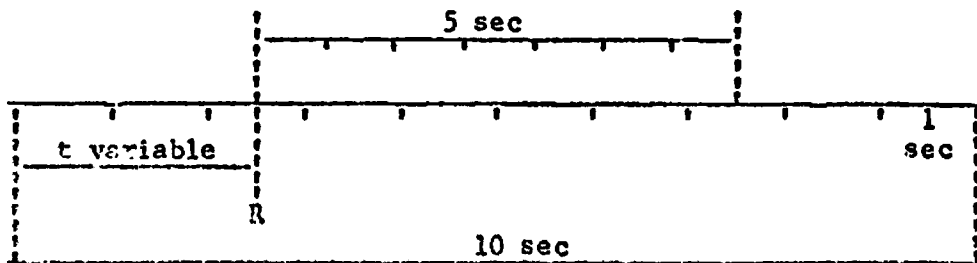


FIGURE 12

EVENT CONTINGENCIES AND TIMING FOR 3½ SEC
 ANALYSIS OF EEG OF MOTOR, VISUAL, AND AUDITORY
 CORTICES WITH PROGRAM 5
 (AN AVERAGE CONTINUOUS BAND POWER COMPUTATION PROGRAM)
 UNIVERSITY OF HOUSTON HYBRID COMPUTER

AUDITORY I
5 SEC ANALYSIS EPOCH

With Behavioral Response for Analysis of S_{D_R} and S_{Δ_R}



With Artificial Response for Analysis of FS_{NR}

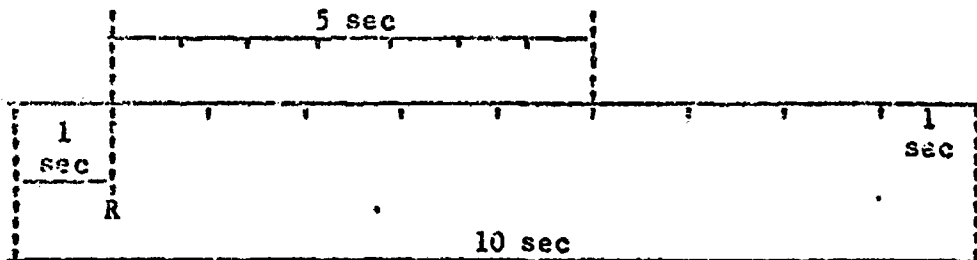


FIGURE 13

EVENT CONTINGENCIES AND TIMING FOR 5 SEC
 ANALYSIS OF EEG OF AUDITORY CORTEX WITH PROGRAM 5
 (AN AVERAGE CONTINUOUS BAND POWER COMPUTATION PROGRAM)
 UNIVERSITY OF HOUSTON HYBRID COMPUTER

epoch and 5 sec analysis epoch, respectively.

Figure 14 shows the output of one pen recorder channel-- in this case, 20 c/sec in auditory I with a 5 sec analysis epoch and no delay. The first bar graph shows the output of the sequential sampling averager of the band power for each of the seven time periods, each of which is $5/7$ sec in length; the second, the output of the sequential sampling averager of the broad band power, again in $5/7$ sec increments; and the third, the output of the two-variable divider; i.e., the band power normalized by broad band power for each of the $5/7$ sec intervals.

The number of trials averaged for each behavioral condition is shown in Table 1.

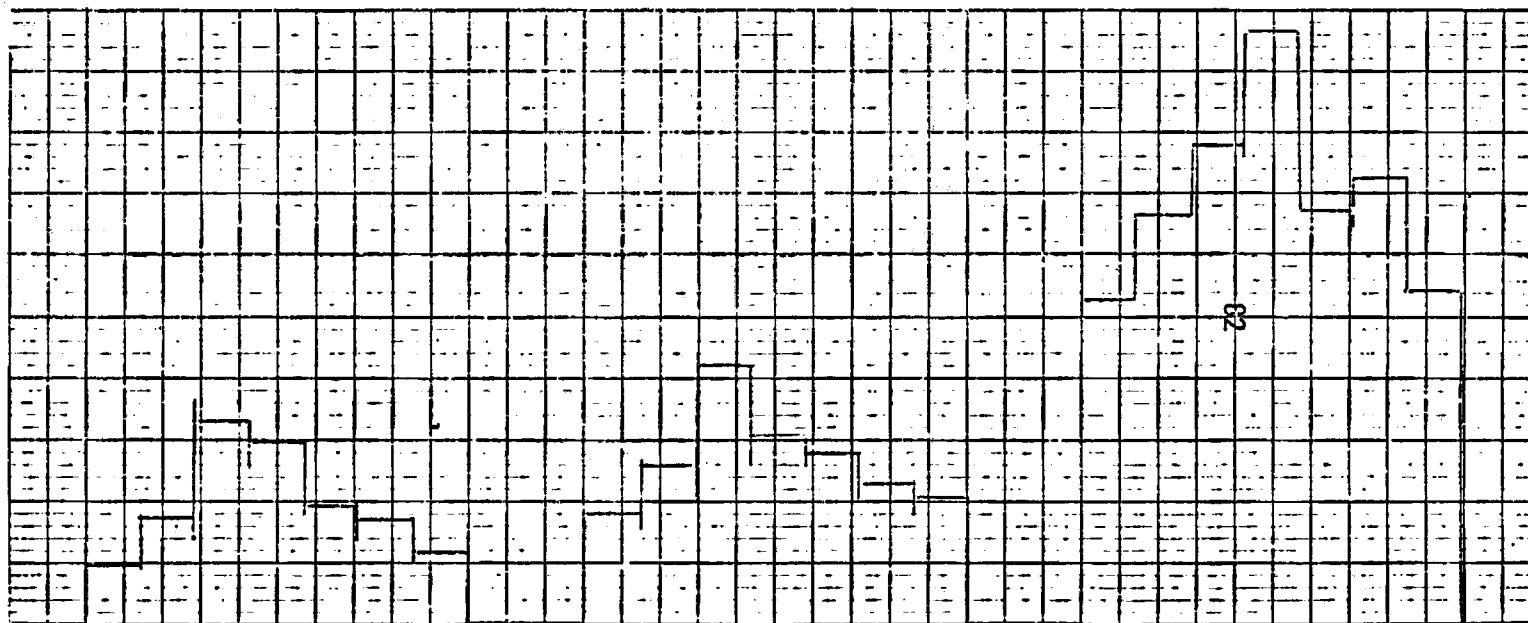


FIGURE 14

BRUSH RECORDER OUTPUT OF PROGRAM 5,
AN AVERAGE CONTINUOUS BAND POWER COMPUTATION PROGRAM

The first set of bars shows absolute band power; the second, absolute broad band power; the third, band power normalized by broad band power. The magnification factor of the first set is twice that of the second. Each small division in the writeout of the normalized band power is 1%; e.g., the highest bar in the normalized writeout is read 48.3% and means that the frequency band analyzed contains 48.3% of the power in the broad band.

TABLE 1

NUMBER OF TRIALS AVERAGED

Tape	Condition					
	PSNR	PSR ^a	S _{ΔNR} ^b	S _{ΔR}	S _{DNR} ^b	S _{DR}
19A(1)	19	3	7	8	6	11
18A	24	4	4	11	3	11
10A	19	0	13	2	4	14

^aNot computer analyzed for auditory I.

^bNot computer analyzed for auditory I (5 sec).

CHAPTER IV

RESULTS

Statistical analysis, primarily Friedman two-way analysis of variance or Friedman with interactions, was performed on the data presented in this thesis. The statistical analysis is supplemented by the more customary graphic presentation of the EEG data.

Two EEG records each of S_{DR} , S_{DNR} , $S_{\Delta R}$, $S_{\Delta NR}$, respectively are presented in Figures 3 through 10.

Pilot analyses indicated that the 3rd, 4th, and 5th time intervals (hereafter referred to as the "345 Period") in the bar graph output of the computer, representing the time from $t=1$ to $t=2-1/2$ sec of the analysis epoch, encompassed the response related event in the motor cortex and visual I. Intervals 1, 2, and 6 are referred to as the "126 Period." One bar was eliminated from all analyses in order to equalize the N_s for the two groups; the 7th bar was eliminated, since, by two seconds after the response, the 20 c/sec band in auditory I following a reinforced response was beginning to show indications of the previously described auditory event. Figure 15A, showing the bar graphs for normalized 40 c/sec frequency band for visual I, tape 10A, illustrates the 345 and 126 periods. The crosshatched portion represents 345 Period. Auditory I 5 sec epoch data was similarly divided into two groups, the

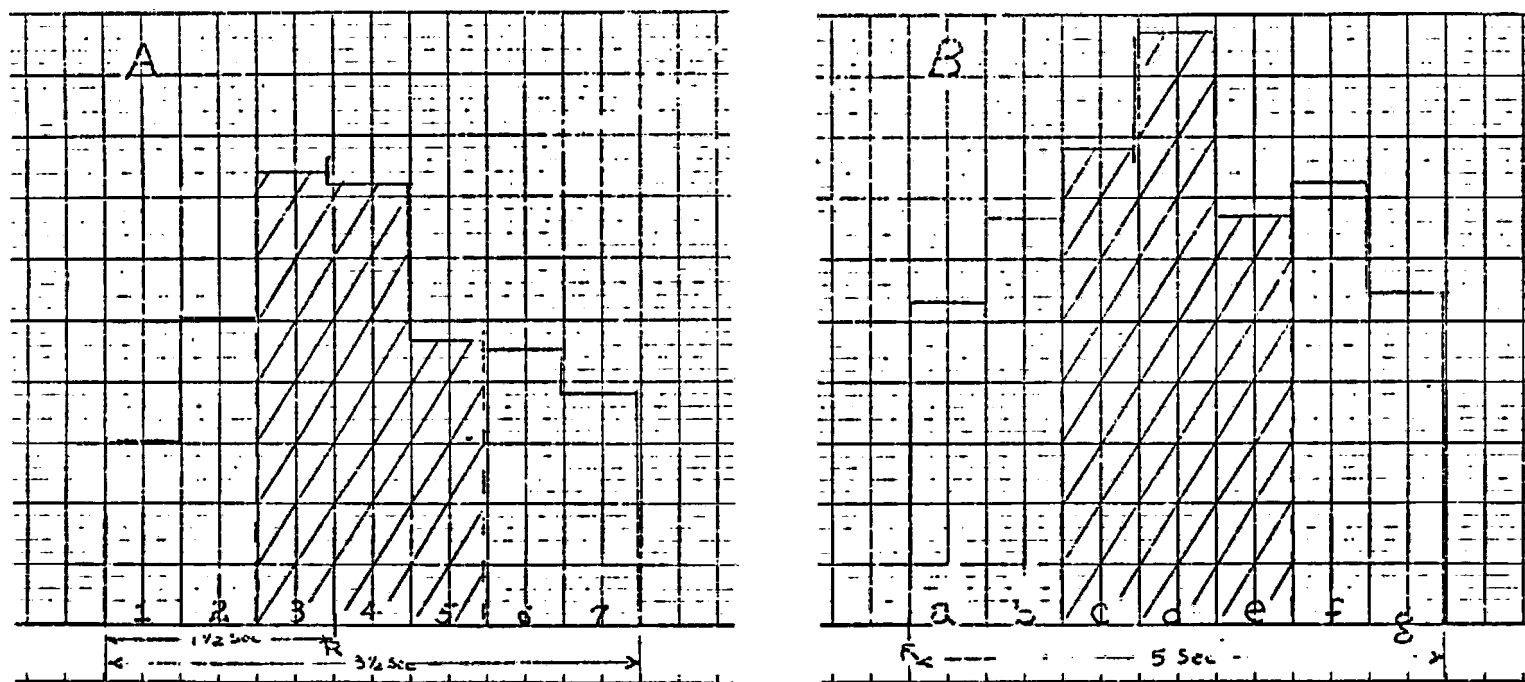


FIGURE 15

- A. 126 AND 345 PERIODS: The analysis epoch was divided into two periods such that 345 Period represented the period just prior to and subsequent to the response. The 345 Period was selected to coincide with the maximal development of the 40 c/sec activity observed in pilot analyses of visual I and motor cortex coincident with a reinforced response.
- B. abf AND cde PERIODS: The analysis epoch was divided into two parts such that cde Period coincided with maximal development of the 20 c/sec activity observed in pilot analyses of auditory I approximately 2 to 2-1/2 seconds after a reinforced response.

3rd, 4th, and 5th intervals in this case representing the time period from $t=10/7$ sec to $t=25/7$ sec, hereafter referred to as "cde Period." The 1st, 2nd, and 6th time intervals are hereafter referred to as "abf Period." Figure 15B, showing the bar graphs for normalized 20 c/sec frequency band for auditory I, tape 18A, illustrates the cde and abf periods. The cross-hatched portion represents cde Period.

Appendices A, B, C, and D are three dimensional plots of proportional power (band power normalized by broad band power) vs. time vs. frequency for each condition for each tape for visual I, motor cortex, and auditory I (3-1/2 sec) and auditory I (5 sec), respectively. These plots present diagrammatically the basic data for this thesis--the proportional powers obtained directly from the computer. Midpoints were drawn both between the time intervals and between the frequency intervals in order to give the surface stability. The dashed line is the 40 c/sec band. The lightly shaded center area represents the 345 and cde periods for the 3-1/2 and 5 sec epochs, respectively.

Descriptive Statistics

For analysis purposes, the band powers and the broad band powers for a given period, e.g., 345 or cde, were summed and the summed band powers were divided by the summed broad band

powers for that period, yielding in effect a mean normalized band power for the period:

$$\text{Mean Normalized Band Power} = \frac{\sum_{i=1}^3 \text{Band Power}}{\sum_{i=1}^3 \text{Broad Band Power}}$$

Broad band power was normalized similarly by total power.

Appendix E contains tables of these descriptive measures of mean proportional power, which are in effect weighted means, categorized according to tape, period, frequency, and behavioral condition for visual I, motor cortex, auditory I (3-1/2 sec) and auditory I (5 sec).

Mean band powers, broad band power, and total power for visual I, motor cortex, auditory I (3-1/2 sec), and auditory I (5 sec) are tabulated in Appendix F. These mean absolute powers shown in Appendix F are presented separately for each tape since absolute values are comparable only within, not across, tapes. The absolute values are adjusted values. The operation of the hybrid computer requires that values at each stage of computation, e.g., input, band pass filtering, squaring, integrating, dividing, etc., be adjusted to a maximum within a 10V. limit. Therefore different scale factors are frequently required depending on the behavioral condition and upon the number of trials averaged. In order to compare absolute values

within tapes, the output of the computer was adjusted to a common magnification factor of 32 and a constant N of 15 trials with the following formula:

$$\text{Adjusted Value} = \frac{15}{N} \cdot \frac{32}{X} \cdot \text{OP}$$

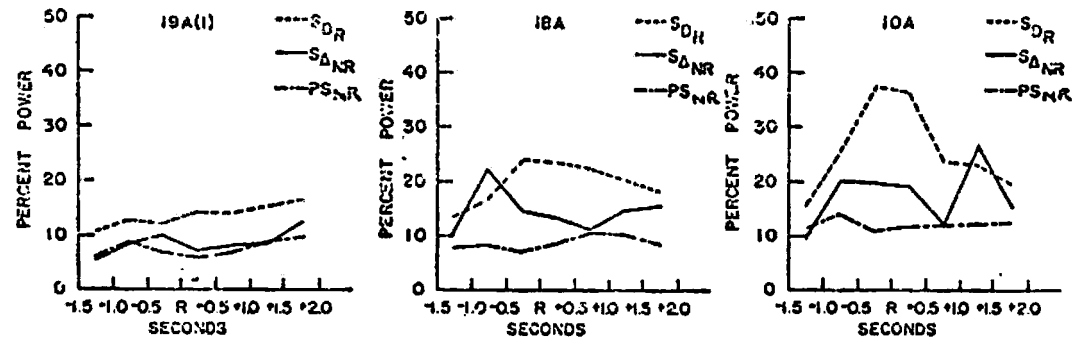
where N is the number of trials averaged, X is the composite computer scale factor based on magnifications at each computational stage, and OP is the absolute value output by the computer.

Figures 16 through 19 are two dimensional plots of proportional power across seven time intervals for each tape for visual I; Figures 20 and 21, for motor cortex; Figure 22 for auditory I (3-1/2 sec). Two dimensional plots of the proportional power in the 20 c/sec frequency band and of the absolute power in the broad band across seven time intervals during SD_R , $\text{S}\Delta_R$, and PS_{NR} for auditory I (5 sec) are shown in Figure 23.

Frequency x Condition Interaction for Each Tape

The significance of the Frequency x Condition interaction for each tape for both the 126 and 345 periods was tested with the Friedman nonparametric analysis of variance with interactions (Wilcoxon, 1949) for visual I, motor cortex, and auditory I

VISUAL AREA
40 CPS/BB



20 CPS/BB

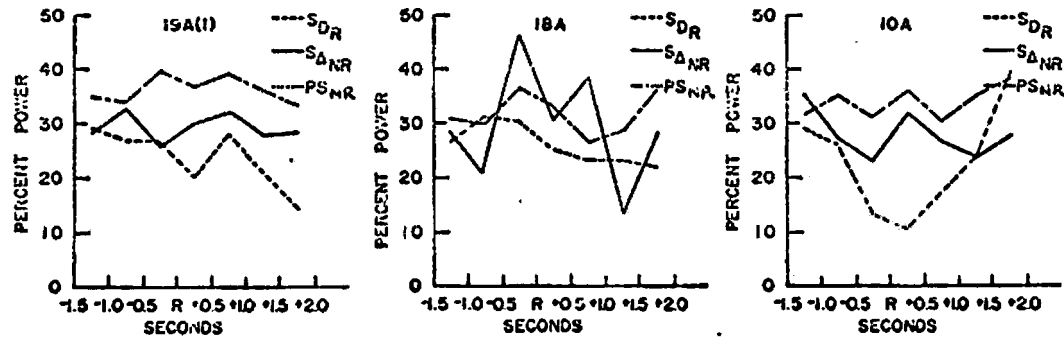


FIGURE 16

AVERAGE CONTINUOUS 40 CPS/BB AND 20 CPS/BB POWER FUNCTIONS

VISUAL I - S_{DR} , $S_{\Delta NR}$, PS_{NR}

VISUAL AREA
25 CPS/BB

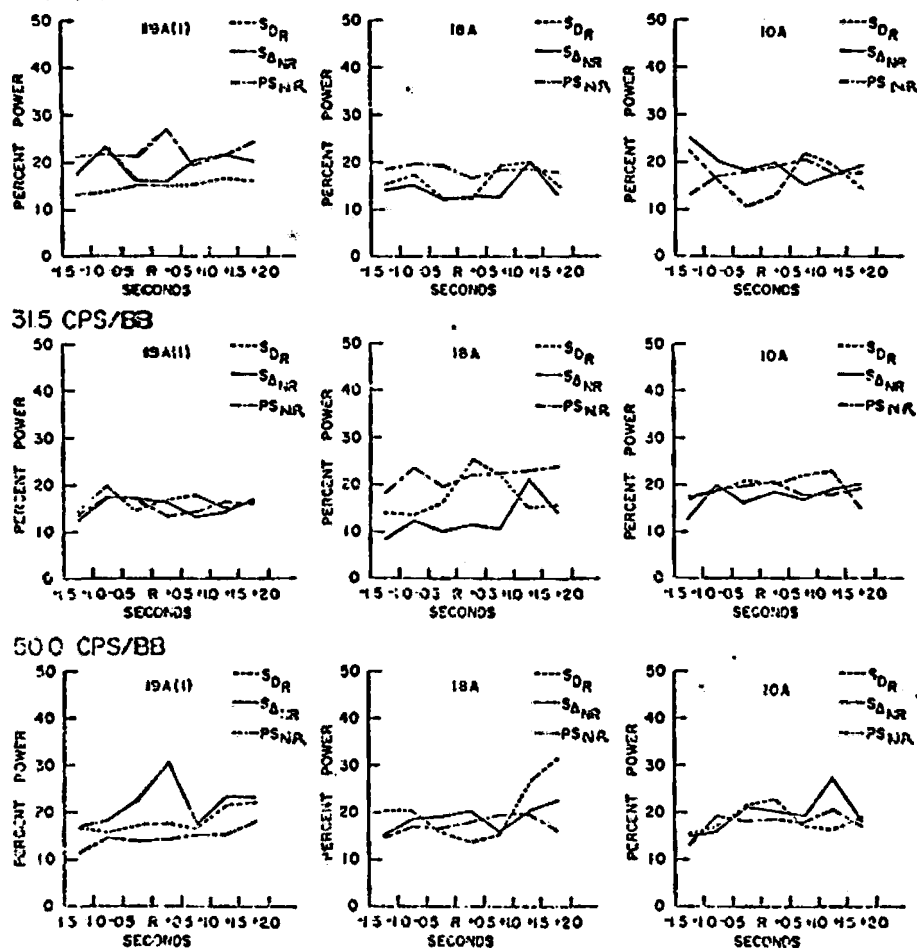


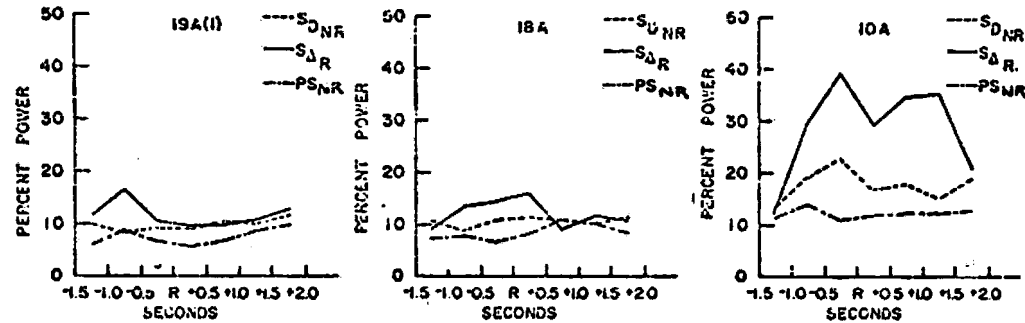
FIGURE 17

AVERAGE CONTINUOUS 25 CPS/BB, 31.5 CPS/BB, AND 50 CPS/BB
POWER FUNCTIONS

VISUAL I - S_{DR}, S _{Δ NR}, PS_{NR}

VISUAL AREA

40 CPS/BB



20 CPS/BB

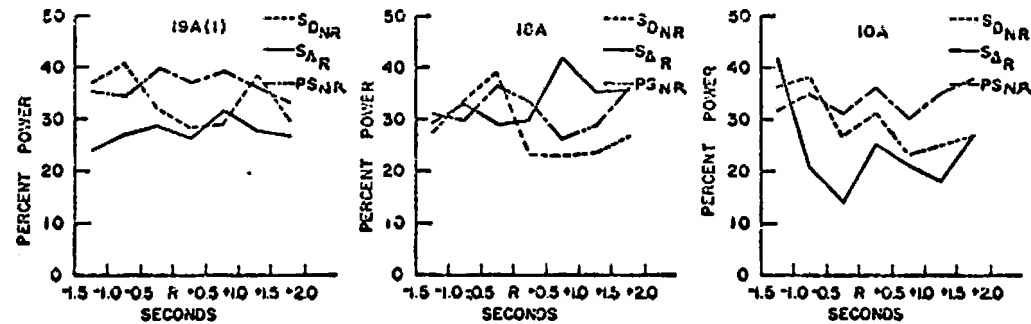


FIGURE 18

AVERAGE CONTINUOUS 40 CPS/BB AND 20 CPS/BB POWER FUNCTIONS

VISUAL I - S_{DNR} , $S_{\Delta R}$, $PSNR$

VISUAL AREA

40 CPS/BB

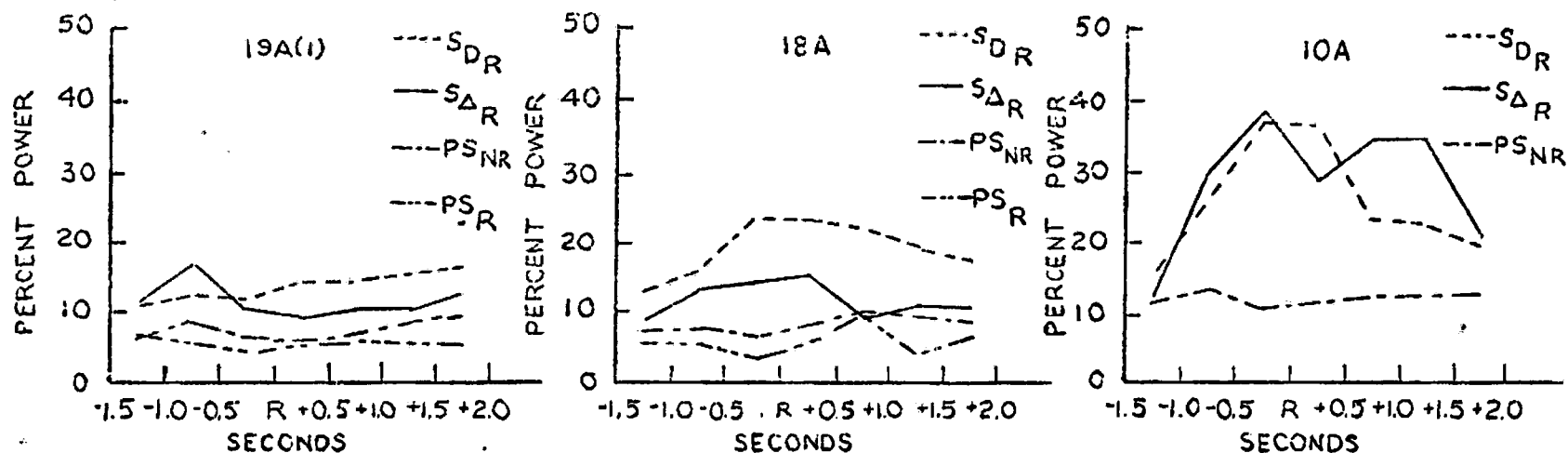


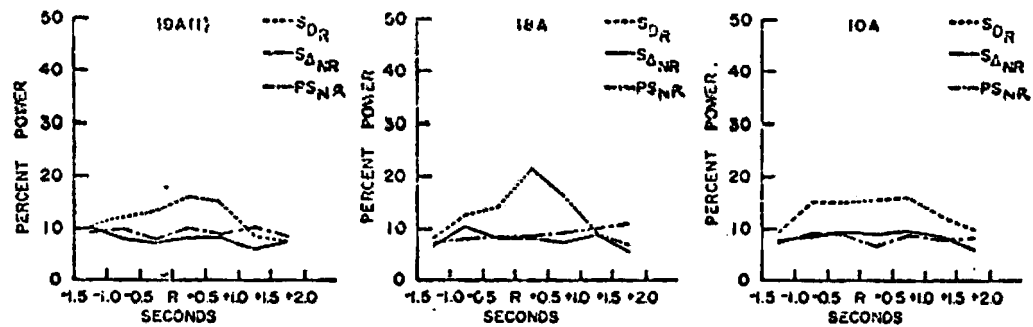
FIGURE 19

AVERAGE CONTINUOUS 40 CPS/BB POWER FUNCTIONS

VISUAL I - S_{DR} , $S_{\Delta R}$, PS_{NR} , PS_R

MOTOR AREA

40 CPS/BB



20 CPS/BB

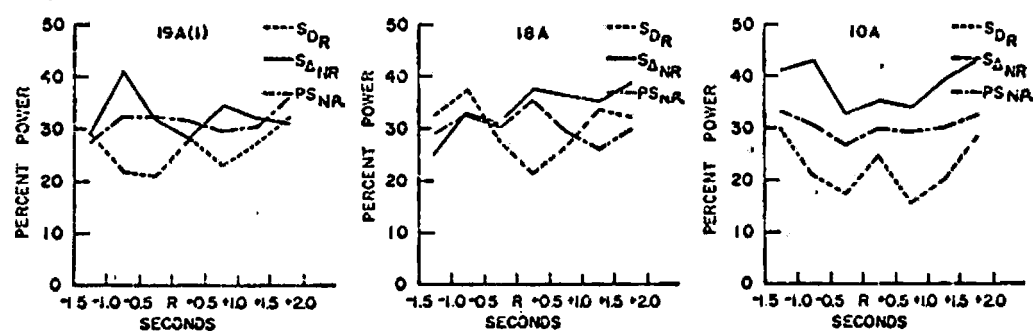


FIGURE 20

AVERAGE CONTINUOUS 40 CPS/BB AND 20 CPS/BB POWER FUNCTIONS

MOTOR CORTEX - S_{DR} , S_{ANR} , PS_{NR}

MOTOR AREA

40 CPS/BB

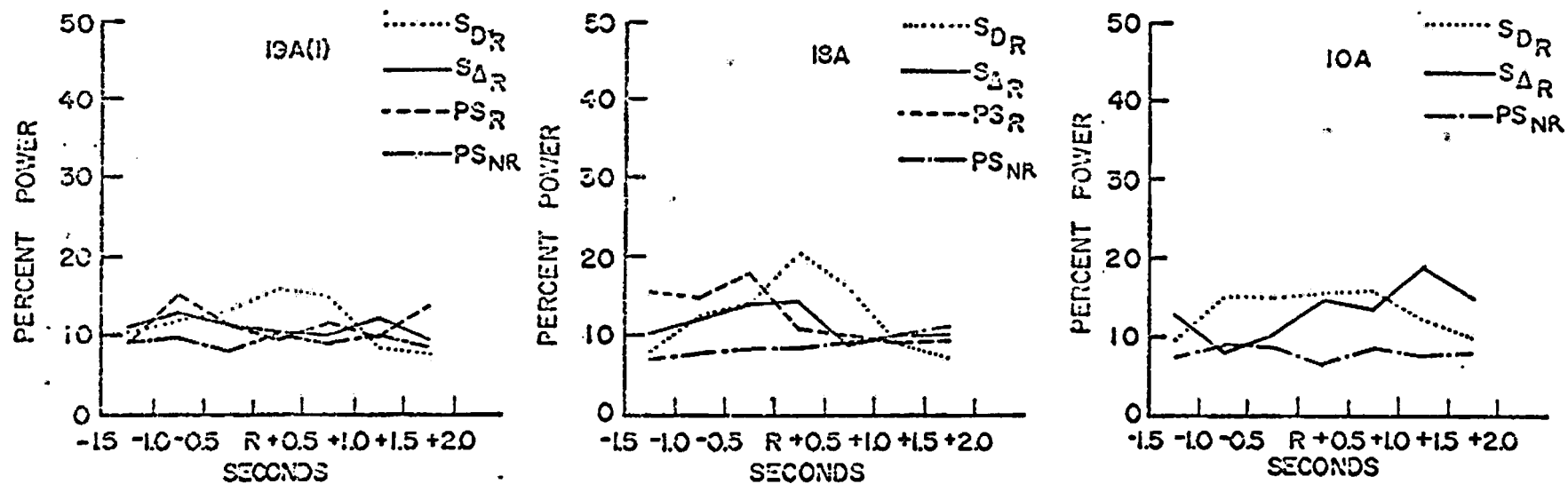


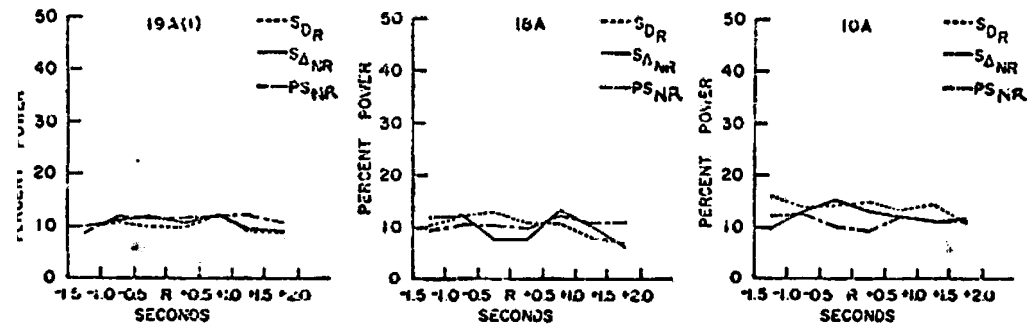
FIGURE 21

AVERAGE CONTINUOUS 40 CPS/BB POWER FUNCTIONS

MOTOR CORTEX - S_{DR} , S_{AR} , PS_{NR} , PS_R

AUDITORY AREA

40 CPS/BB



20 CPS/BB

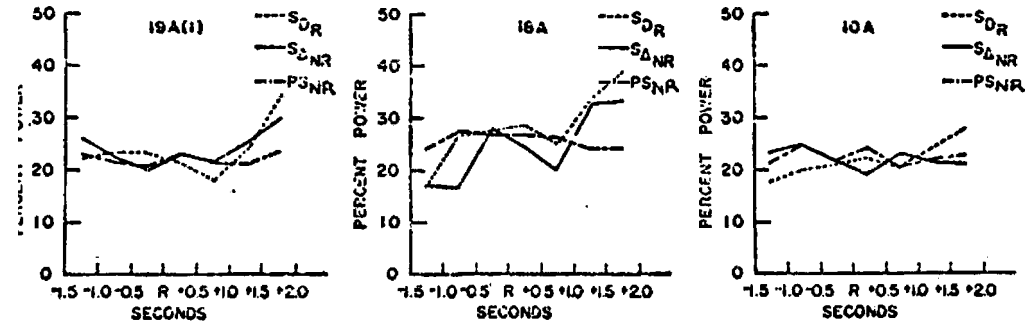


FIGURE 22

AVERAGE CONTINUOUS 40 CPS/BB AND 20 CPS/BB POWER FUNCTIONS

AUDITORY I (3-1/2 SEC) - S_{DR}, S _{Δ NR}, PSNR

AUDITORY AREA - 5 SEC EPOCH

20 CPS/BB

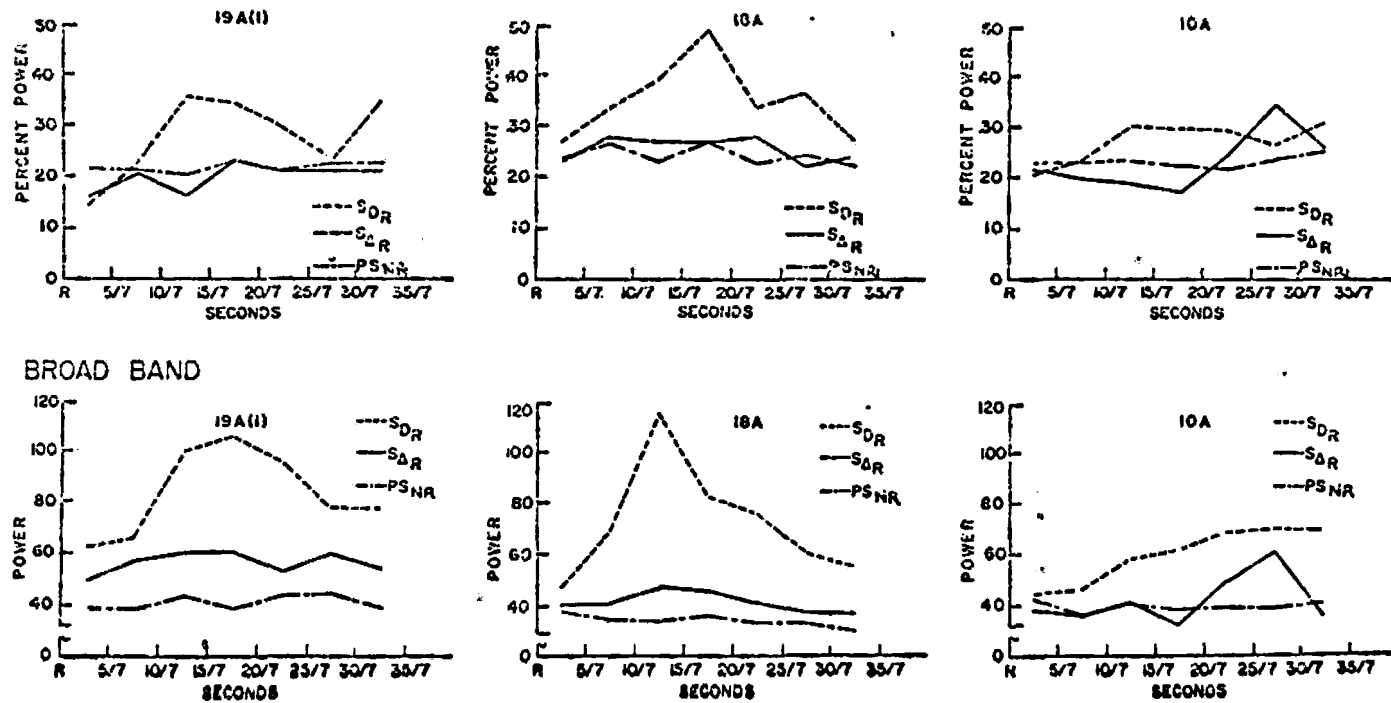


FIGURE 23

AVERAGE CONTINUOUS 20 CPS/BB AND BROAD BAND POWER FUNCTIONS

AUDITORY I (5 SEC) - SDR, SAR, PSNR

for the 3-1/2 sec epoch data. Frequency bands were 20, 25, 31.5, 40, and 50 c/sec; conditions were PS_{NR} , $S_{\Delta NR}$, $S_{\Delta R}$, S_{DNR} , S_{DR} . The results of these analyses are presented in Table 2. There was a significant Frequency x Condition interaction at at least .05 level during 345 Period for all tapes for visual I and motor cortex, and during 126 Period for tapes 18A and 19A(1), visual I, and for tapes 18A and 10A, motor cortex. No significant Frequency x Condition interaction was found in auditory I for either 345 Period or for 126 Period.

The same analysis was applied to the auditory I 5 sec epoch data. Frequency bands were as above; conditions were PS_{NR} , $S_{\Delta R}$, and S_{DR} . The results of these analyses are presented in Table 3. A significant Frequency x Condition interaction at at least the .05 level was found during cde Period for tapes 18A and 19A(1), but not for 10A ($p=.083$). No significant interaction was found for the abf Period except for tape 18A ($p=.011$). During the computation of these analyses it was noted that prior to the inclusion of S_{DR} , when the analysis involved only conditions PS_{NR} and $S_{\Delta R}$, none of the χ^2 ($df=4$) were significant.

The size of N ($N=3$) precluded the use of the appropriate analysis for detecting exactly where significance within the Frequency x Condition interactions lay; however the graphic data were of value here.

Figure 16 shows that in the visual area during 345 Period, 40 c/sec proportional power was consistently higher during S_{DR}

TABLE 2

FREQUENCY X CONDITION INTERACTION FOR TAPES 19A(1), 18A, AND 10A--VISUAL I, MOTOR CORTEX, AND AUDITORY I (3-1/2 SEC):
Friedman nonparametric analysis of variance with interactions

Interactions:

Frequency: 20, 25, 31.5, 40, 50 c/sec
Condition: PS_{NR}, S_{ΔNR}, S_{ΔR}, S_{DNR}, S_{DR}

N = 3
K = 5
df = 16

	125 Period		345 Period	
	χ^2	p	χ^2	p
Visual I				
Tape 19A(1)	41.33	.001	34.14	.006
Tape 18A	32.80	.008	34.40	.005
Tape 10A	23.73	.094	37.07	.002
Motor Cortex				
Tape 19A(1)	23.73	.094	29.27	.022
Tape 18A	30.67	.015	28.47	.028
Tape 10A	26.41	.048	33.60	.006
Auditory I				
Tape 19A(1)	20.73	.19	17.34	.36
Tape 18A	18.94	.27	18.40	.30
Tape 10A	21.39	.17	18.26	.31

TABLE 3

FREQUENCY X CONDITION INTERACTION FOR TAPES 19A(1), 18A, AND 10A--AUDITORY I (5 SEC): Friedman nonparametric analysis of variance with interactions

Interactions:

Frequency: 20, 25, 31.5, 40, 50 c/sec

Condition: PS_{NR} , $S_{\Delta R}$, SD_R

N = 3

K = 5

df = 8

Tapes	abf Period		cde Period	
	χ^2	P	χ^2	P
19A(1)	9.06	.34	16.80	.032
18A	19.93	.011	19.80	.011
10A	8.54	.38	13.87	.083

than during either $S_{\Delta NR}$ or PS_{NR} , whereas 20 c/sec proportional power tended to be higher during PS_{NR} and $S_{\Delta NR}$ than during SD_R . From Figure 17 it may be seen that no consistent trends across tapes were apparent in the other frequency bands. In the motor area, as shown in Figure 20, during 345 Period the proportional power in the 40 c/sec frequency band during SD_R again was observed to exceed that present during $S_{\Delta NR}$ or PS_{NR} . Similarly, the proportional power in the 20 c/sec frequency band tended to be higher during PS_{NR} and $S_{\Delta NR}$ than during SD_R during 345 Period. The 20 c/sec results seem to be less clear-cut than the 40 c/sec results, but certainly there was a trend toward lower proportional power in the 20 band during SD_R .

Shown in Figure 24 are composite spectrogram plots for SD_R , $S_{\Delta NR}$, and PS_{NR} for visual I, motor cortex, and auditory I based on the mean proportional powers presented in Appendix E. These plots indicate that in all three tapes in visual I and motor cortex the mean proportional power in the 40 c/sec band was higher and that in the 20 c/sec band was lower during SD_R than during $S_{\Delta NR}$ or PS_{NR} and that this "40 high-20 low" pattern was not present in auditory I. Figure 25 shows spectrograms plotted from mean proportional powers shown in Appendix E for 345 and cde periods for auditory I: SD_R - 5 sec, $S_{\Delta R}$ - 5 sec, PS_{NR} - 5 sec, SD_R - 3-1/2 sec, and $S_{\Delta R}$ - 3-1/2 sec. It is clear from these plots that the only consistent changes between conditions across tapes were the increases in 20 c/sec

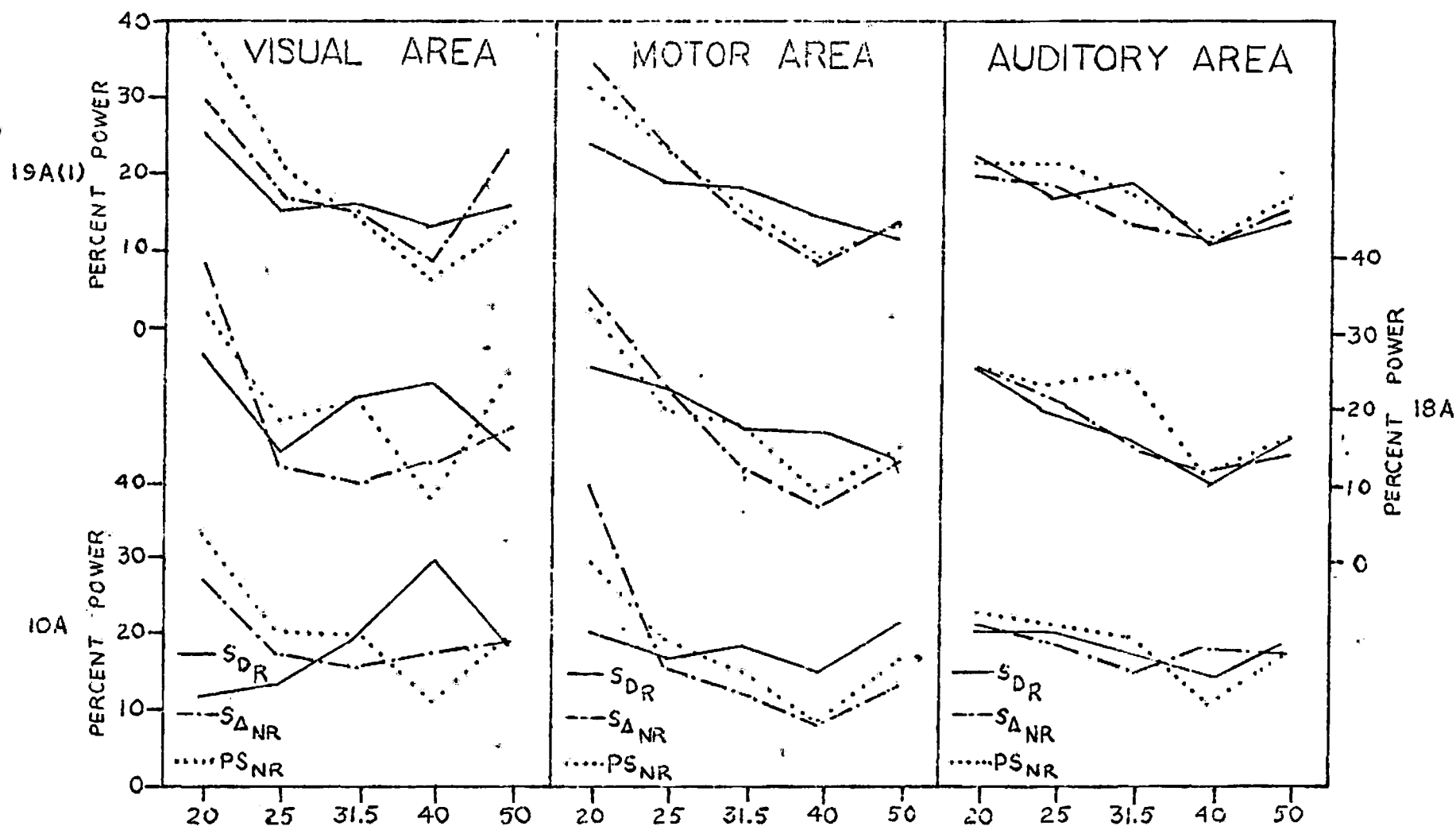


FIGURE 24

SPECTROGRAMS FOR VISUAL, MOTOR, AND AUDITORY CORTICES PLOTTED FROM MEAN PROPORTIONAL POWERS (APPENDIX E) FOR 345 PERIOD: SDR, S Δ NR, PSNR

Note in the visual and motor areas 40 c/sec activity is higher in SDR than in S Δ NR and 20 c/sec is higher in S Δ NR than in SDR.

AUDITORY AREA

345 AND cde PERIODS

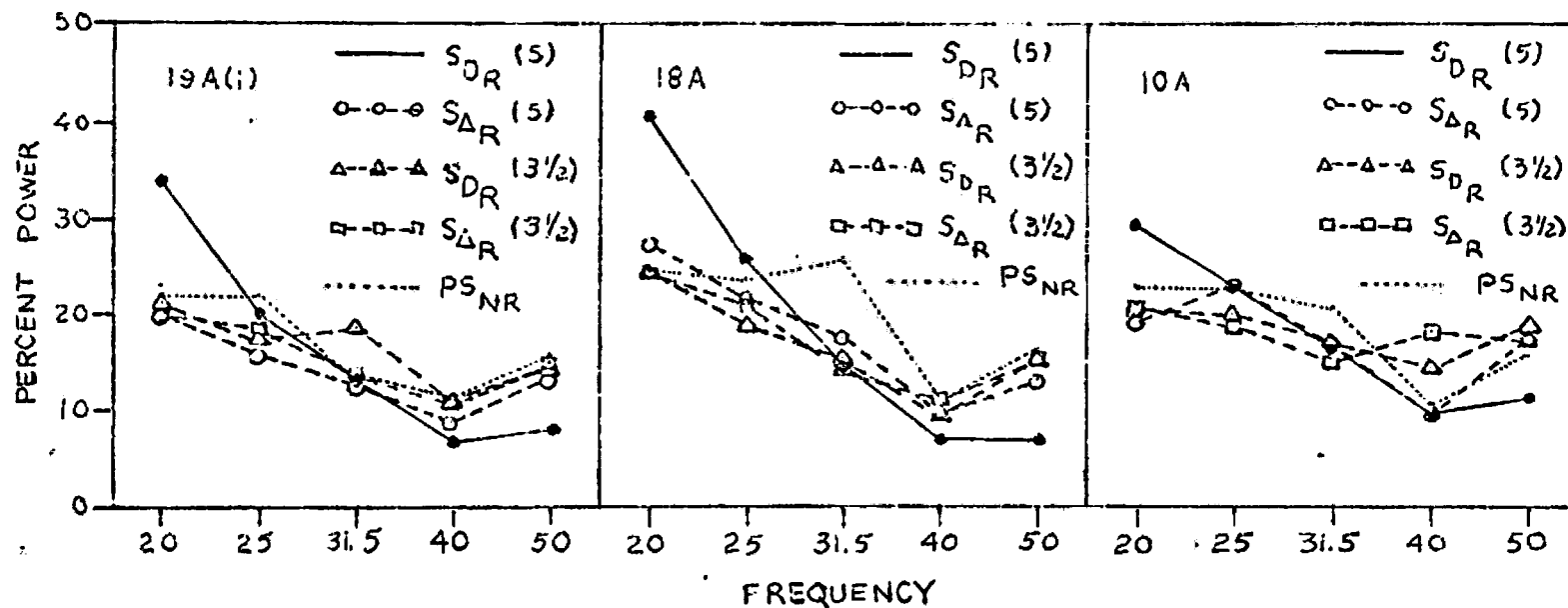


FIGURE 25

SPECTROGRAMS FOR AUDITORY CORTEX PLOTTED FROM MEAN PROPORTIONAL POWERS (APPENDIX E) FOR 345 ($3\frac{1}{2}$ SEC) AND cde (5 SEC) PERIODS

Note the increase in 20 c/sec and decreases in 40 and 50 c/sec activity in the auditory cortex during $S_{DR} = 5$ sec, i.e., Auditory 5 sec cde Period.

and the decreases in the 40 and 50 c/sec frequency bands during S_{DR} - 5 sec cde Period.

Response x Frequency and Stimulus x Frequency Interactions across Tapes

Since each tape showed a significant Frequency x Condition interaction during 345 Period for both visual I and motor cortex and since the 40 c/sec activity during S_{DR} Period was higher than that during $S_{\Delta NR}$ 345 Period in both the visual and motor areas in each tape, it seemed appropriate to test the significance across tapes of the Response (R and NR) x Frequency and Stimulus (S_D and S_{Δ}) x Frequency interactions by using the mean proportional powers presented in Appendix E for S_{DR} , $S_{\Delta R}$, S_{DNR} , and $S_{\Delta NR}$ during 345 Period. Again the analysis used was the Friedman analysis of variance with interactions. The results are shown in Table 4. Examination of the rank sums, where rank "1" was assigned to the smallest number, revealed that in the visual and motor analyses of the Frequency x Response interaction the 40 c/sec frequency band had the largest sum of ranks and the 20 c/sec frequency band had the smallest sum of ranks. In the analyses of the Frequency x Stimulus interactions in the visual and motor cortices the high frequency bands had the larger sums of ranks and the lower frequency bands the smaller sums of ranks;

TABLE 4

FREQUENCY X RESPONSE AND FREQUENCY X STIMULUS INTERACTIONS
ACROSS TAPES: Friedman nonparametric analysis of variance
with interactions for visual I, motor cortex, and auditory I
during 345 Period for 3-1/2 sec epoch data

Interactions:

Frequency: 20, 25, 31.5, 40, and 50 c/sec

Response: R (S_{DR} and $S_{\Delta R}$) and NR (S_{DNR} and $S_{\Delta NR}$)

Stimulus: S_D (S_{DR} and S_{DNR}) and S ($S_{\Delta R}$ and $S_{\Delta NR}$)

Cortical Area	<u>Frequency x Response</u>		<u>Frequency x Stimulus</u>	
	<u>χ^2</u>	<u>p</u>	<u>χ^2</u>	<u>p</u>
Visual I	13.73	.008	9.20	.054
Motor cortex	17.73	.001	6.67	.15
Auditory I	2.93	.54	3.37	.50

however, there was no clearcut 20-40 relationship as in the Frequency x Response analyses in those same areas. A critical constant was calculated according to the method presented by Miller (1966):

$$|\bar{R}_i - \bar{R}_{i'}| \leq (\chi^2_r)^{\frac{1}{2}} \left[\frac{k(k+1)}{6n} \right]^{\frac{1}{2}} \quad i, i' = 1, 2, \dots, k$$

with probability greater than $1 - \alpha$. Any difference which exceeds the critical value is taken to be indicative of a population difference $\theta - \theta_{i'} \neq 0$. The critical constant for $k=5$, $n=6$, $\alpha=.05$ is 2.79. The only differences which met this critical value were between the 20 c/sec and 40 c/sec bands in visual I (3.0) and motor cortex (3.5) for the Frequency x Response interaction.

Figure 18 indicates that tape 10A may have unduly influenced the results obtained in the previous analysis since $S_{\Delta R}$ power functions for tape 10A were based upon two trials only and the results from these two trials were unlike those for tapes 18A and 19A(1) and, in fact, were almost indistinguishable from those for S_{DR} in both visual I and motor cortex. In view of this possibility, the analyses for the visual and motor areas were recomputed, omitting tape 10A and reducing N from 6 to 4. The significant interaction between frequency and response remained in the motor cortex ($p=.005$); however the previously significant Frequency x Response interaction

in the visual cortex disappeared ($p=.09$).

The plots in Figures 19 and 21 provide additional information concerning the Frequency x Response interaction in visual I and motor cortex, respectively, this time in the absence of a stimulus. These figures show that there is little or no increase in the proportional power in the 40 c/sec band during PS_R 345 Period in either visual I or motor cortex; i.e., during a response in the absence of a stimulus, S_D or S_{Δ} . In the visual area this is very clear; in the motor cortex, the result is less clear, there being a slight increase in the proportional power in the 40 c/sec band during a period of time prior to the response, but not at the time of the response.

Between Tapes Analyses

Although all tapes showed significant Frequency x Condition interactions in 345 Period and most of the tapes showed significant Frequency x Condition interactions in 126 Period for both the visual and motor cortices, it was still possible that there might be significant differences between the tapes. Friedman two-way analyses of variance were calculated between tapes for the 40 c/sec frequency band for PS_{NR}, S_{D_R} , and $S_{D_R} - PS_{NR}$, i.e., variations of S_{D_R} above or below PS_{NR} as a baseline and for the 20 c/sec frequency band for PS_{NR}, $S_{\Delta_{NR}}$, and $S_{\Delta_{NR}} - PS_{NR}$. These analyses were computed for visual I,

motor cortex, and auditory I based upon all seven time intervals for the 3-1/2 sec epoch data. Due to the presence of the 20 c/sec event which pilot analyses had indicated in auditory I at approximately 1-3/4 to 2-1/2 sec following a reinforced response, the analyses for auditory I were recomputed based upon the first six time intervals only with essentially the same results as those obtained for all seven time intervals. The results of these analyses for the 40 c/sec frequency band are presented in Table 5. Auditory PS_{NR} showed the only significant difference between tapes in the 20 c/sec band ($p=.027$). In the order of highest 20 c/sec activity during PS_{NR} the tapes were arranged $18A > 10A > 19A(1)$. Motor ($S_{\Delta NR} - PS_{NR}$) 20 c/sec activity showed near significance ($p=.052$) with the tapes arranged $10A > 18A > 19A(1)$. In the visual cortex, there were significant differences in the 40 c/sec band between the three tapes in all three conditions, i.e., SD_R , PS_{NR} , and $SD_R - PS_{NR}$. Figure 26 indicates that the tapes arranged in order of the relative amounts of proportional power in the 40 c/sec band during SD_R were: $10A > 18A > 19A(1)$. The analyses for the motor cortex showed no significant difference for either PS_{NR} or SD_R ; but when SD_R was adjusted for PS_{NR} as a baseline, the tapes arranged in order of the sum of the ranks were: $10A > 18A > 19A(1)$. However, Figure 27 indicates that tape 10A's superiority in the statistical analysis was due to a small sustained increase above baseline PS_{NR} over the major portion of the analysis epoch,

TABLE 5

BETWEEN TAPES--VISUAL I, MOTOR CORTEX, AND AUDITORY I (3-1/2 SEC): Friedman two-way analysis of variance for 40 c/sec frequency band

Cortical Area	PSNR		S _{DR}		S _{DR} - PSNR	
	χ^2		χ^2		χ^2	
		p		p		p
Visual I	10.79	.003	14.00	.000021	6.50	.037
Motor cortex	3.07	.24	3.07	.24	8.86	.009
Auditory I	0.64	.77	10.57	.003	8.00	.016

$S_{DR} - 40 \text{ CPS/BB}$

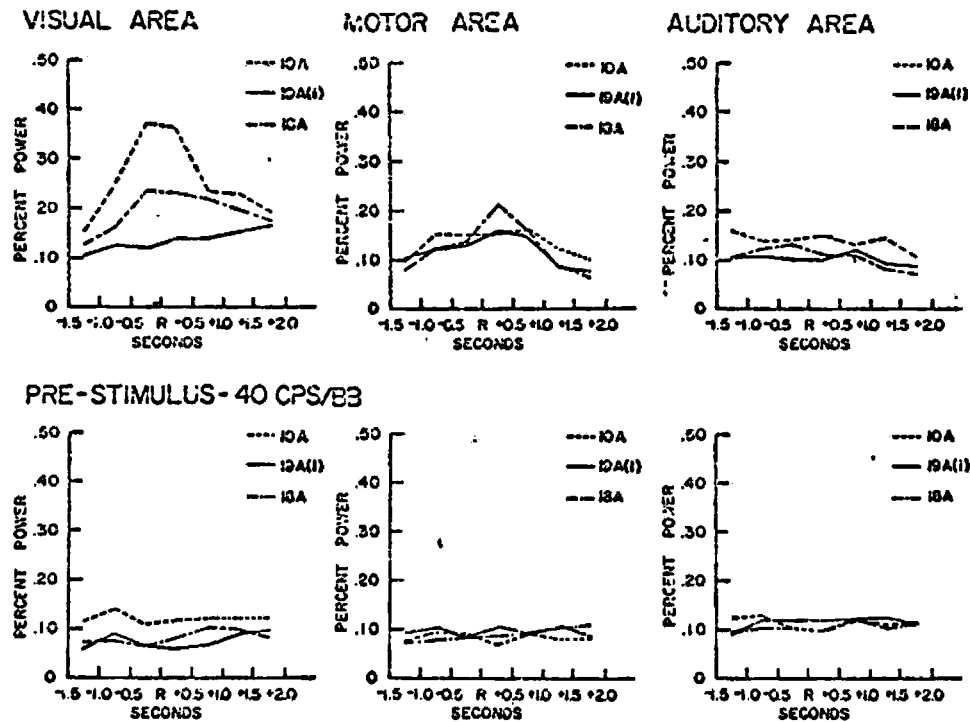


FIGURE 26

AVERAGE CONTINUOUS 40 CPS/BB POWER FUNCTIONS

VISUAL, MOTOR, AND AUDITORY CORTICES - S_{DR} AND PRE-STIMULUS

$S_{DR} - PS_{NR} - 40 \text{ CPS/BB}$

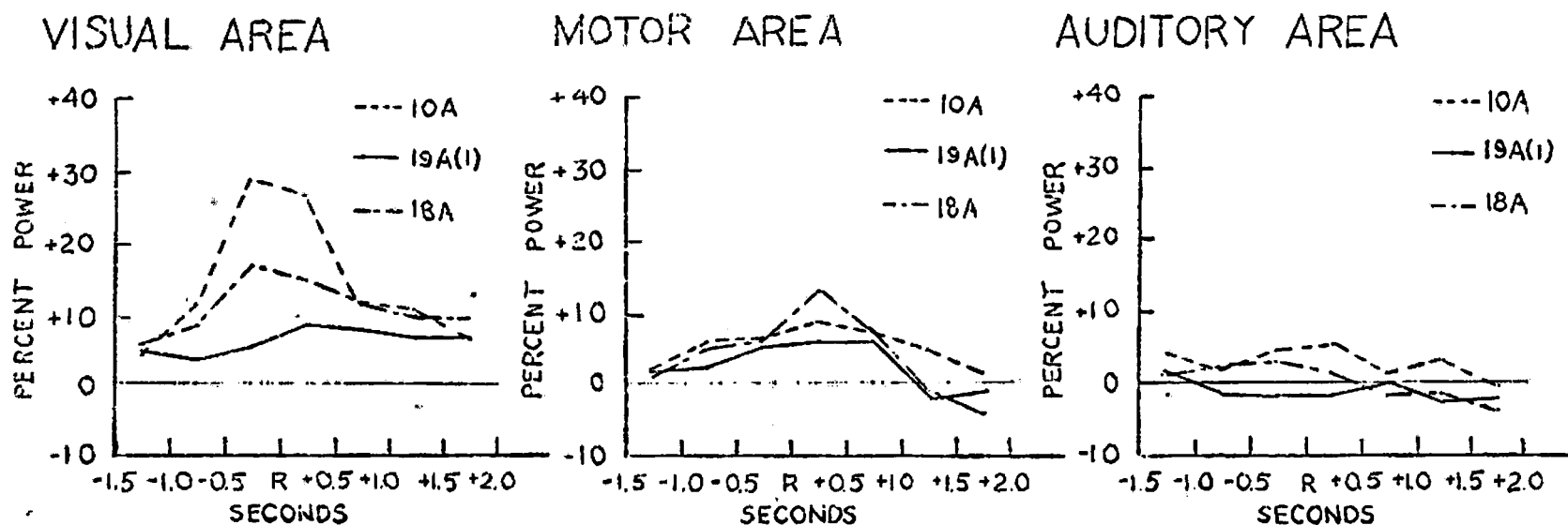


FIGURE 27

AVERAGE CONTINUOUS 40 CPS/BB POWER FUNCTIONS
VISUAL, MOTOR, AND AUDITORY CORTICES

S_{DR} ADJUSTED TO PS_{NR} BASELINE ($S_{DR} - PS_{NR}$)

rather than to a large increase restricted to 345 Period. In auditory I, although the tapes did not differ significantly during PS_{NR} , they did differ significantly ($\alpha = .05$) during S_{DR} and $S_{DR} - PS_{NR}$. In auditory I the sum of ranks was much larger for 10A than for either 18A or 19A(1) during S_{DR} and $S_{DR} - PS_{NR}$, i.e., proportional power for 40 c/sec frequency was higher throughout the 3-1/2 sec epoch in tape 10A than in either 18A or 19A(1). The latter result with respect to S_{DR} is quite clearly seen in Figure 26. —

The auditory I 20-40 c/sec 5 sec epoch data was similarly handled for PS_{NR} , S_{DR} , and $S_{DR} - PS_{NR}$. The results of these analyses are presented in Table 6. There was no significant difference at the .05 level between the three tapes for S_{DR} in the 20 c/sec frequency band. However, a significant difference between tapes was noted in PS_{NR} and when S_{DR} was adjusted for PS_{NR} baseline $S_{DR} - PS_{NR}$ approached significance ($p=.052$). Examination of the sum of ranks indicated that this difference lay primarily with tape 18A: $18A > 19A(1) = 10A$. Note in Figure 23 the considerable increase in 20 c/sec proportional power during S_{DR} over that during PS_{NR} in tape 18A as compared to 19A(1) and especially as compared to 10A. In the 40 c/sec frequency band, there was no significant difference between tapes during PS_{NR} , however significant differences were found for S_{DR} and for adjusted S_{DR} , i.e., $S_{DR} - PS_{NR}$. Here the tapes arranged in order of the sum of their ranks were:

TABLE 6

BETWEEN TAPES--AUDITORY I (5 SEC): Friedman two-way analysis of variance for 20 and 40 c/sec frequency bands

N=7, K=3, df=2				
Condition	20 c/sec band		40 c/sec band	
	χ^2	p	χ^2	p
PSNR	7.14	.027	1.14	.520
SDR	5.43	.035	11.64	.001
SDR - PSNR	6.00	.052	10.29	.004

10A > 18A > 19A(1).

Between Periods Analyses across Tapes

A test described by Wilcoxon (1949) was used to test whether there was a significant difference between time periods 126 and 345 across tapes. The test involves the ranking from 1 to 6 of the six scores for time intervals "1" through "6" for each tape and a summing of the ranks across tapes, first for the 126 scores and then for the 345 scores. A specially prepared table is available for determining significance at .01, .02, and .05 levels only. The results of this analysis are presented in Table 7. The arrows indicate the direction of difference. Upward arrow indicate that mean proportional power was greater in 345 Period than in 126 Period for the specified condition and frequency, i.e., at the time of the response mean proportional power for the band analyzed was greater than it was somewhat prior and subsequent to the response. Downward arrows, of course, indicate the reverse. The mean proportional power in the 20 c/sec frequency band for S_{DR} , visual I, barely missed significance at the .05 level. Recomputation with a baseline adjustment ($S_{DR} - PS_{NR}$) resulted in a significant difference between periods at the .02 level. Figure 28 is a composite plot for visual I, motor cortex, and auditory I of spectrograms based on the mean proportional powers

TABLE 7

BETWEEN PERIODS ANALYSES ACROSS TAPES--VISUAL I, MOTOR CORTEX, AND AUDITORY I (3-1/2 SEC): Wilcoxon's test for groups of unpaired replicates for mean proportional power for 125 Period vs. 345 Period in 20, 25, 31.5, 40, and 50 c/sec and BB bands during S_{DR} , $S_{\Delta R}$, and PS_R

Freq c/sec	P							
	Visual I			Motor Cortex			Auditory I ^a	
	S_{DR}	$S_{\Delta R}$	PS_R	S_{DR}	$S_{\Delta R}$	PS_R	S_{DR}	$S_{\Delta R}$
20	b	-	-	<.05↓	-	<.01↓	-	-
25	-	-	-	-	-	-	-	-
31.5	-	-	.05↑	.02↑	-	-	-	-
40	<.05↑	-	-	<.01↑	-	-	-	-
50	-	-	-	-	-	-	-	-
BE	<.01↑	-	-	-	-	-	-	-

Note.--There were 3 replicates in each of 3 groups, except for PS_R , where there were 3 replicates in each of 2 groups. Significance levels are shown for all significant differences. A dash indicates that the difference was not significant at at least the .05 level. Upward arrows indicate that mean proportional power was greater in 345 Period than in 125 Period for the specified condition and frequency; downward arrows, the reverse.

^a PS_R of auditory I was not computer analyzed.

^bBarely misses significance at .05↓. Significant at .02↓ level if S_{DR} is adjusted for variations from baseline.

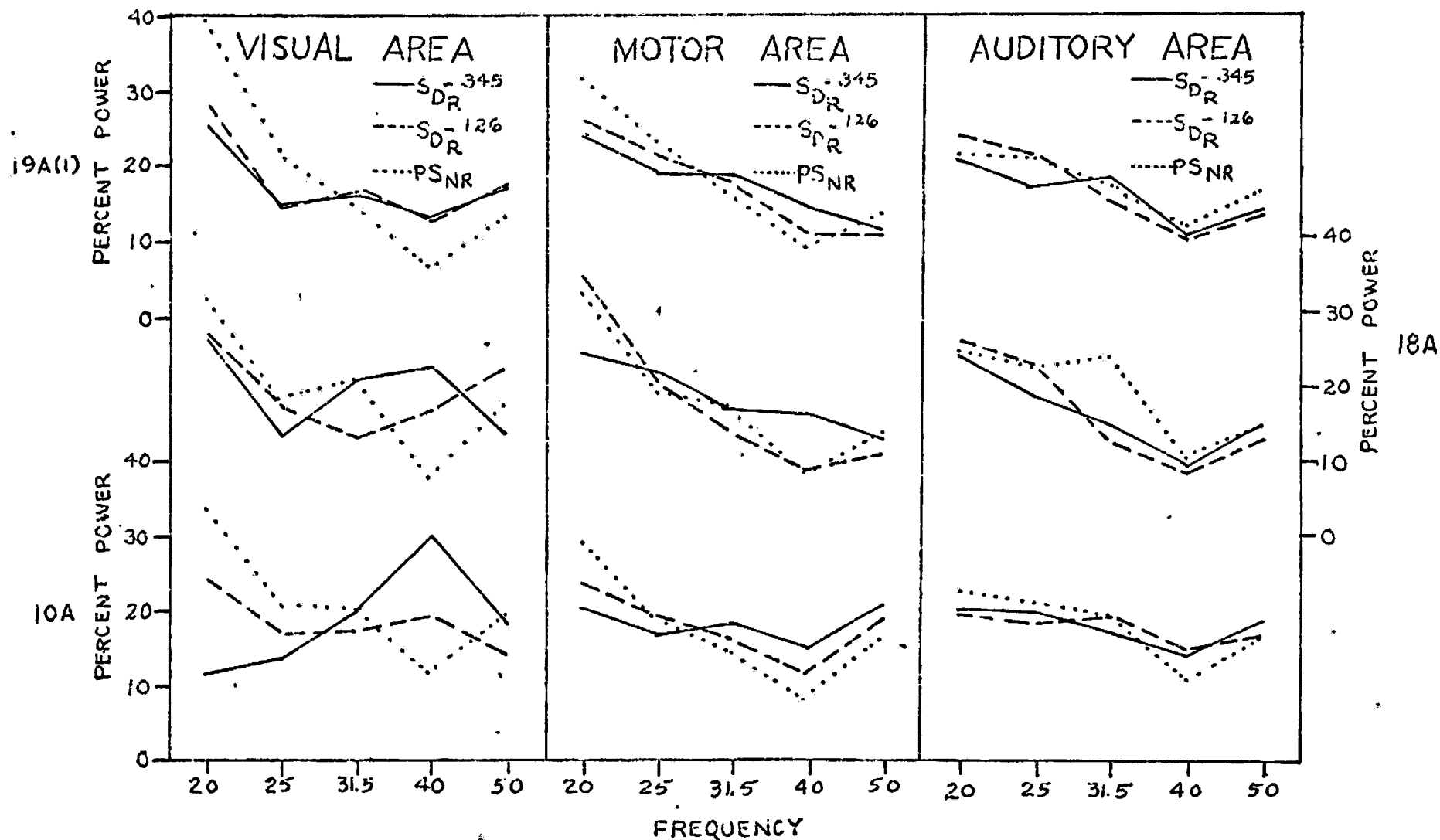


FIGURE 23

SPECTROGRAMS FOR VISUAL, MOTOR, AND AUDITORY CORTICES PLOTTED FROM MEAN PROPORTIONAL POWERS (APPENDIX E): S_{DR} -- PERIODS 345 AND 126, AND PSNR

Note that in the visual and motor areas 40 c/sec activity is higher during S_{DR}^{345} Period than during S_{DR}^{126} Period.

shown in Appendix E for S_{DR} 126 Period, S_{DR} 345 Period, and PS_{NR} . Comparing the results shown in Table 7 with the graphic data in Figure 16, in the visual cortex the increase in 40 c/sec proportional power during S_{DR} 345 Period over that during S_{DR} 126 Period is very clear in tapes 18A and 10A. In fact, as shown in Figures 3 and 4 taken from Tape 18A, the 40 c/sec activity centered around the response is clearly visible even prior to computer analysis in the unfiltered EEG record. Figure 29 shows the peaking in the broad band power normalized by total power (BB/TP) during S_{DR} 345 Period in visual I in tapes 10A and 13A. Tape 19A(1) BB/TP power function shows only a slight peaking with the response. Figure 20 shows that the peaking in the 40 c/sec power functions in the motor cortex during S_{DR} 345 Period, although not large, is very clear and consistent across tapes. The generalized decrease in the 20 c/sec proportional power during S_{DR} 345 Period is very evident, however in tapes 19A(1) and 10A there is a slight rise in the middle of the rather large drop. Figure 30 shows the decrease in 20 c/sec proportional power in the motor cortex during PS_R 345 Period in tapes 18A and 19A(1). There were no responses during PS in tape 10A, hence no such analysis was possible for tape 10A.

Analyses similar to those used for the 3-1/2 sec epoch data were performed on the auditory I 5 sec epoch data for S_{DR} and $S_{\Delta R}$, the results of which are presented in Table 8.

VISUAL AREA

S_{DR} - BB/TP

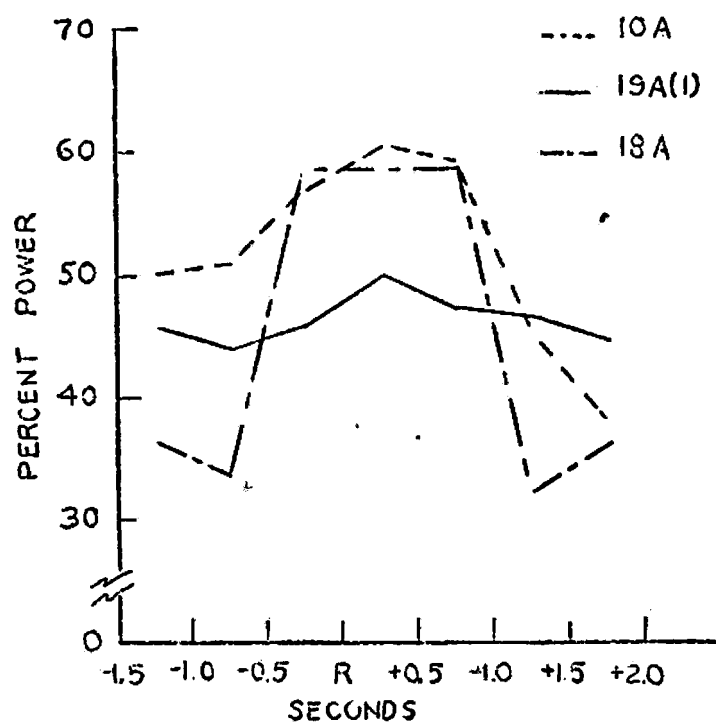


FIGURE 29

AVERAGE CONTINUOUS BB/TP POWER FUNCTIONS

VISUAL I: S_{DR}

MOTOR AREA

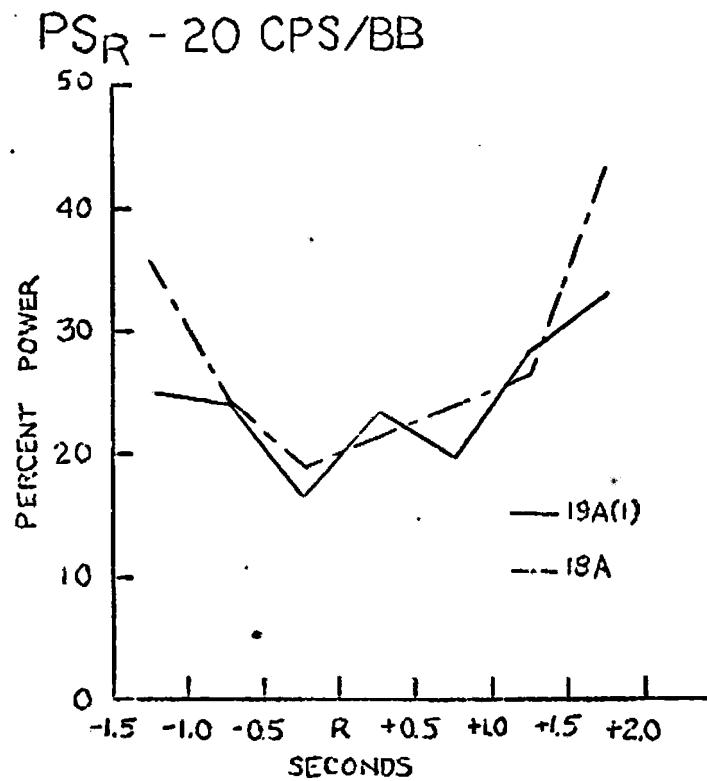


FIGURE 30

AVERAGE CONTINUOUS 20 CPS/BB POWER FUNCTIONS

MOTOR CORTEX: PS_R

TABLE 8

BETWEEN PERIODS ANALYSES ACROSS TAPES--AUDITORY I (5 SEC):
 Wilcoxon's test for groups of unpaired replicates for proportional power for periods cde vs. abf in 20, 25, 31.5, 40, and 50 c/sec and BB bands during S_{DR} and $S_{\Delta R}$

Frequency c/sec	p	
	S_{DR}	$S_{\Delta R}$
20	.01↑	-
25	-	-
31.5	-	-
40	.01↓	-
50	.01↓	-
BB	-	-

Note.--There were 3 replicates in each of 3 groups. Significance levels are shown for all significant differences. A dash indicates that the difference was not significant at at least the .05 level. Upward arrows indicate that mean proportional power was greater in 345 Period than in 126 Period for the specified condition and frequency; downward arrows, the reverse.

The results indicated a significant increase in the 20 c/sec frequency band and significant decreases in the 40 and 50 c/sec bands during SD_R cde Period as compared to SD_R abf Period. The center of cde Period is approximately 2-1/2 sec after the response. No significant differences between $S\Delta_R$ cde and $S\Delta_R$ abf periods were found. Figure 31 shows the peaking in the 20 c/sec proportional power and the small but consistent decreases in 40 and 50 c/sec proportional power in auditory I during SD_R cde Period. It is clear both from Figure 23 and from Figure 31 that the 20--40 and 50 c/sec auditory I phenomenon was much stronger in tapes 18A and 19A(1) than in tape 10A.

Two sets of spectrograms were prepared in order to facilitate comparisons between conditions across frequency bands. One set, presented in Appendix G, depicts the changes with condition in mean proportional powers (Appendix E) across the five frequency bands in terms of algebraic differences from baseline, PS_{NR} . A second set, shown in Appendix H, was prepared in an attempt to better compensate for the different baseline values of the five frequencies by plotting the ratio of the mean proportional power in a given frequency for a given condition to the PS_{NR} mean proportional power for the given frequency. In the first set "0" represents no change; in the second set "1" of course represents no change. These plots have been made for all conditions for all three areas for both

S_{DR} - AUDITORY AREA 5 SEC EPOCH

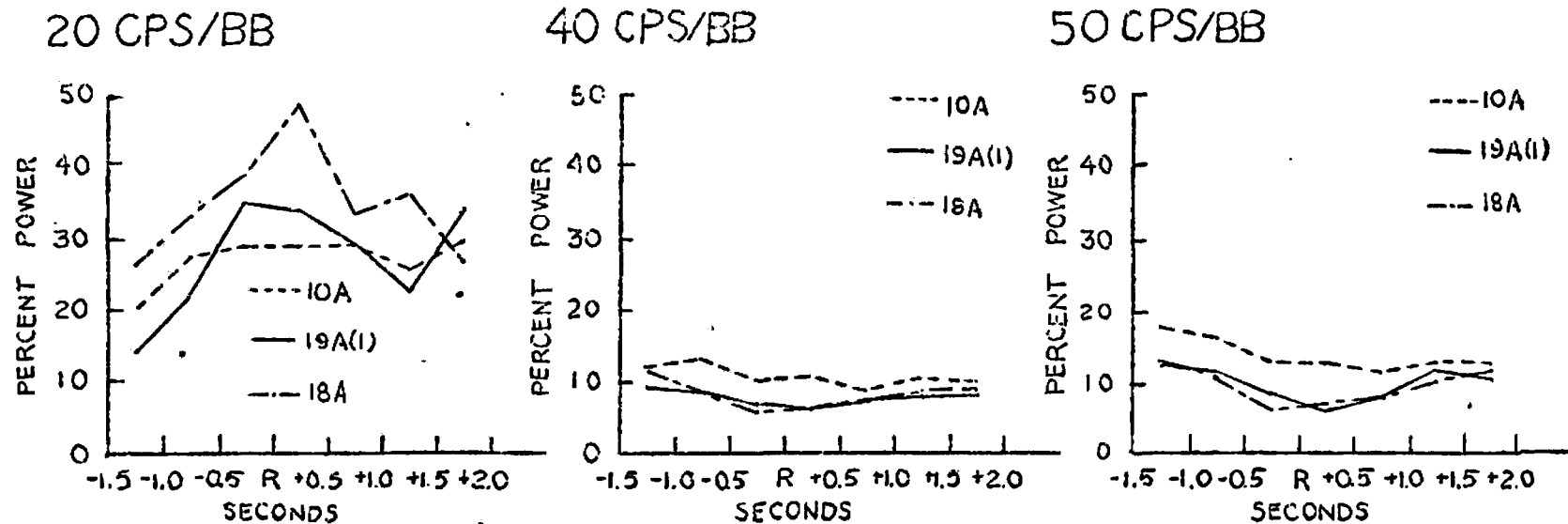


FIGURE 31

AVERAGE CONTINUOUS 20 CPS/BB, 40 CPS/BB, AND 50 CPS/BB POWER FUNCTIONS

AUDITORY I: S_{DR}

periods 345 and 126, and in the case of auditory I - 5 sec,
for cde and abf periods.

CHAPTER V

DISCUSSION

Two principal findings emerged from the data. One of these indicates that significant changes coincident with the response occur in the proportional power functions within each of two frequency bands within the LVF "arousal" spectrum -- 20 and 40 c/sec -- in visual I and motor cortex, but not in auditory I, of one cat tested during the performance of a successive visual discrimination task. There appears to be an inverse relationship between the two frequency bands, with an increase in 40 and a decrease in 20 c/sec proportional power appearing to be associated with a situation in which facilitation or behavioral arousal is required and the reverse (a decrease in 40 and an increase in 20) when the behavioral situation demands inhibition of the response. The second finding is an increase in 20 c/sec activity in auditory I approximately 2 to 2-1/2 sec after a reinforced response during "lapping" behavior in the same visual discrimination task.

The first question here is: Could not the computation of proportional power of itself produce a result in which, if one frequency increases, another must decrease? The model, of course, does demand that if one frequency rises, one or more others must fall. However, if the change in the second frequency band is simply an artifact of the change in the first

frequency band, then the three remaining frequency bands should be similarly affected. Both the statistical data and the graphic data bearing upon this question indicate that in both visual I and motor cortex the significant changes occurring at the time of a reinforced response (S_{D_R} , 345 Period as compared to 126 Period) occurred in the 20 and 40 bands and only in these two bands, with one exception--the 31.5 band in the motor cortex. This rise in the 31.5 band may be a part of the blockage of the so-called "Rolandic wicket rhythm" which Chatrjian, Petersen, and Lazarte (1959) have demonstrated in the motor cortex with any movement, active or passive.

The second problem is the possibility that the increased 40 c/sec power in the motor cortex with a reinforced response was simply an artifact of movement. The analyses of the 345 Period compared to the 126 Period indicated that neither an increase nor a decrease in either the 20 or the 40 c/sec frequency band, or, for that matter, any other frequency band, was associated with a response to the 3/sec light (S_{Δ}) in either the visual or the motor cortex. Furthermore, during the very few responses in the prestimulus period in tapes 18A and 19A(1), no significant changes occurred in the proportional power in visual I in either the 20 or 40 bands, although a significant rise occurred in the 31.5 band. A similar rise in the 31.5 activity in the continuous normalized power functions which were part of the data for another experiment in the University

of Houston Laboratory (Miller, 1968) was observed in the visual cortex of another cat during the response in the prestimulus period. With a nonreinforced response during the prestimulus period, the motor cortex did not show the 40 high-20 low pattern characteristic of a reinforced response, although there was a significant decrease in the 20 c/sec activity. From the motor area spectrograms for the 345 Period in Appendix G it is clear that the decrease in the 20 band in the motor cortex during a response in the prestimulus period was accompanied by essentially equal increases in the other four frequency bands. In other words, there apparently is a significant decrease in the power in the 20 band with the unreinforced bar press in the prestimulus period, but such a response is not accompanied by the 40 c/sec increase characteristic of a reinforced response.

Although numerous studies have found blocking of the rolandic rhythm (wicket rhythm, or "rythme en arceau"--EAR) with movement, the general trend of the results reported in the literature is toward greater changes with meaningful, alerting movements, involving adjustment of the animal to its environment. Studying the activity of single pyramidal fibers in cats and monkeys, Hardin (1967) found that a general increase of background activity accompanied all movements, but particularly quick movements and patterns of alertness. Calvet, Calvet, and Langlois (1965) found that movements which enabled the animal to adjust to its environment were accompanied by so-

called cortical activation waves (CAW); whereas movements of the head or even the whole body to adjust posture only were not accompanied by CAW. Automatic movements, e.g., scratching, licking, ear jerks, yawning and passive movements of a leg or of the head did not produce CAW. Chatrian et al (1959), studying the blocking of the wicket rhythm in man, noted the occurrence of contralateral blocking of the wicket rhythm preceding spontaneous movement. He suggested that the blocking of the rolandic rhythm has the effect of preparing the precentral area for action, probably by increasing its susceptibility to complex integrations of the plan of the movement in the form of spatially and temporally varied patterns of movement. Kornhuber and Deecke (1967) recorded a large negative potential of the contralateral motor area with voluntary movements in humans. It was not present when the movements were purely passive. The potential was reduced when the subject was "mentally indifferent." Laursen (1967) suggested that this large negative potential is related to attention.

Evidence for 40-20 Inverse Relationship in Visual and Motor Cortices

Two of the most compelling pieces of evidence for the 20-40 inverse relationship in visual I and motor cortex are the graphic data presented in Figures 16 and 20, respectively, and

the statistical analyses between 126 and 345 periods presented in Table 7. Figures 16 and 20, in which plots of S_{DR} and $S_{\Delta NR}$ are superimposed for both 40 and 20 c/sec proportional power, indicate that during the critical 345 Period, in both visual I and motor cortex, the 40 c/sec proportional power was higher during S_{DR} than during $S_{\Delta NR}$ and the 20 c/sec proportional power was higher during $S_{\Delta NR}$ than during S_{DR} . The diagrams also show a peaking in the 40 c/sec band and a simultaneous drop in the 20 c/sec band during the 345 Period with a reinforced response. A similar peaking in the 40 band and drop in the 20 band was not anticipated and was not seen in $S_{\Delta NR}$ in the absence of a behavioral response.

The statistical analysis between periods across tapes, the results of which are shown in Table 7, confirmed the relative increase in 40 and decrease in 20 c/sec activity in visual I and motor cortex with a reinforced response. The same analyses indicate that similar changes did not occur in the 20 and 40 activity in the visual or motor areas with a nonreinforced response in S_{Δ} period and that they did not occur in auditory I. Interpretation of the Frequency x Response and Frequency x Stimulus interactions in terms of arousal with a reinforced response is possible with the elimination of tape 10A from the analysis. The results of the $S_{\Delta R}$ analysis for tape 10A were unlike those for tapes 18A and 19A(1) and represented averages based on only two trials. The only significant

interaction that remained with the removal of tape 10A from the analysis was the Frequency x Response interaction in the motor cortex. Therefore it would appear that neither the occurrence of a response nor the presentation of the S_D alone is sufficient to produce the 40 high-20 low electrical pattern and that the pattern occurs only with a response to S_D . Figure 28 graphically illustrates the tendency during S_{D_R} toward higher proportional power in the 40 band and lower proportional power in the 20 band at the time of the response (345 Period) as compared to a time somewhat prior to and subsequent to the response (126 Period).

The visual and motor area spectrograms for the 345 Period, based both upon algebraic variations from prestimulus level (Appendix G) and upon the ratio of a given stimulus value to the prestimulus value (Appendix H), indicate that in every case the relative 40 c/sec activity was highest during S_{D_R} and lowest during $S_{\Delta_{NR}}$, or in one instance $S_{D_{NR}}$, when compared to all other stimulus conditions. The 20 c/sec activity, in many cases was lower during S_{D_R} and higher during $S_{\Delta_{NR}}$ and $S_{D_{NR}}$. Assuming that the 20 c/sec activity represents an inhibitory process, the absence of a large rise in 20 c/sec activity during $S_{\Delta_{NR}}$ and $S_{D_{NR}}$, when compared to PS_{NR} , is not surprising in view of the considerable penalty imposed upon bar presses during the intertrial interval, i.e., extension by 10 sec of the time until stimulus presentation. Baseline

recordings prior to the introduction to the bar pressing task would have afforded a more adequate control for the 20 c/sec activity.

As stated above, it seems reasonable to the experimenter to interpret these data in terms of "facilitation" or arousal for the 40 c/sec activity and perhaps "inhibition" for the 20 c/sec activity. The spectrograms for S_{DR} and $S_{\Delta NR}$ in Figure 24 support this interpretation, especially for the 40 c/sec activity. The 20 c/sec frequency was dominant even with a reinforced response in tape 19A(1) in the visual area; however, even in this tape recorded when performance was poorest ($S_D/S_{\Delta} = 1.32$, criterion=3), 20 c/sec activity was lower during S_{DR} than during $S_{\Delta NR}$. With an intermediate level of performance (tape 18A: $S_D/S_{\Delta} = 1.97$) the 40 c/sec activity was again higher during S_{DR} than during $S_{\Delta NR}$ and 20 was higher during $S_{\Delta NR}$ than during S_{DR} , but here 40 was much higher during S_{DR} than in tape 19A(1), although the 20 c/sec frequency band remained dominant during S_{DR} . With the almost perfect performance during the recording of tape 10A ($S_D/S_{\Delta} = 7.75$), the electrical picture changed considerably. During S_{DR} the 40 c/sec frequency band became dominant and the power in the 20 c/sec band dropped to a very low level.

Figure 24 shows that in the motor cortex a rise in 40 c/sec activity above base level PS_{NR} during a reinforced response (S_{DR}) occurred in each tape, i.e., at all three levels of performance,

although the increase was greater in tapes 18A and 10A. A statistical analysis of the difference between tapes indicated that the tapes were arranged $10A > 18A > 19A(1)$. However, Figure 20 indicates that tape 10A's superiority in this ranking was a result of a sustained rise in the 40 c/sec activity over a longer period of time than in either of the other two tapes rather than a larger increase restricted to the 1-1/2 sec 345 Period.

The results in Figures 24 and 20 appear to support the hypothesis of an association between 20 c/sec electrical activity and behavioral inhibition. Comparing the 20 c/sec activity in the motor cortex in Figures 24 and 20, it appears that the spread between the 20 c/sec activity during S_{DR} and that during $S_{\Delta NR}$ was much greater in tape 10A than in tapes 13A and 19A(1). Apparently, the major part of this increase in spread between 20 in S_{DR} and in $S_{\Delta NR}$ was attributable to the greater rise of 20 above PS_{NR} during $S_{\Delta NR}$ in tape 10A, where the animal's inhibition of the bar press during S_{Δ} was almost perfect, than in either 18A or 19A(1), where inhibition of incorrect responses was poor. S_{DR} , of course, represents a situation in which inhibition should be minimal and $S_{\Delta NR}$ a condition in which inhibition should be maximal. This result is congruent with Roth et al's (1967) finding of 12-20 c/sec synchronous activity in the coronal gyrus and sensorimotor cortex during the development of inhibitory behavior.

They found that the amplitude of this synchronization which they called sensori-motor rhythm (SMR) increased only slightly as training proceeded, but its occurrence was strictly related to the development of inhibitory behavior in a task involving both delay of response and delay of reinforcement. Even in the highly overtrained cat, if behavioral inhibition did not occur, SMR did not occur.

The increase in 40 c/sec activity during S_{DR} in visual cortex in the better performance tapes 18A and 10A was so strong that it is easily identified in Figures 3 and 4 in the unfiltered EEG prior to computer analysis. The 40 c/sec activity was barely discernible in the EEG records of the poor performance tape, 19A(1), prior to computer analysis. Note that in Figures 7 and 8, showing $S_{\Delta R}$ EEG records, the 40 c/sec activity cannot be detected. Computer analysis was required to identify the 40 c/sec activity coincident with the response in the motor cortex in all tapes, i.e., at all three performance levels. Figures 3 and 4 show only a general desynchronization in the motor cortex coincident with a reinforced response.

Comparable changes in the 20 and 40 bands during S_{DR} and $S_{\Delta NR}$ were not present in auditory I. Figure 24 indicates that there was little or no difference between the spectrograms for S_{DR} and $S_{\Delta NR}$ and the change, if any, was in the opposite direction, i.e., 40 lower in S_{DR} than in $S_{\Delta NR}$. However, a

striking electrical phenomenon, which was maximal approximately 2 sec after a reinforced response, was observed in auditory I. A significant and large increase in the relative power in the 20 c/sec band and significant, although very small, decreases in the relative power in the 40 and 50 c/sec bands characterized the electrical activity of auditory I during a several second period of time following reinforcement. The investigator is hesitant, however, to attach much significance to the small decreases in the 40 and 50 c/sec bands since such small changes in the two high frequencies may be merely artifacts of the very large rise in 20 c/sec activity.

Figures 3 and 4 show that the large increase in 20 c/sec activity was coincident with the occurrence of large voltage synchronous slow waves (3-6 c/sec) in auditory I and motor cortex and sometimes in visual I, although generally the electrical activity in visual I tended toward clearly identifiable 7 c/sec activity at this time. A similar slow activity during "lapping" behavior has been observed both by Roth et al (1967) and Boudreau and Freeman (1963).

Although this study was not designed to answer the question either of the origin or of the functional significance of the strong 20 c/sec activity in auditory I following a reinforced response during "lapping" behavior, the occurrence of this electrical phenomenon poses interesting questions. The investigator has attempted earlier to link the occurrence

of 20 c/sec activity in the visual and motor cortices with inhibitory processes, and here again in auditory I 20 c/sec activity has been observed at a time when inhibition of bar pressing is the most adaptive behavior for the animal pending the consumption of the milk from the previous bar press. The large increase in 20 c/sec activity observed may represent some event specific to the temporal lobe, or on the other hand it may represent some sort of inhibitory process acting on all sense modalities other than the visual. Recordings from the somatosensory area, had they been available, would have shown whether another nonrelevant sense modality was similarly affected. The 5 sec epoch analysis was not performed on the visual and motor systems and therefore the writer can make no definite statements with respect to the presence or absence of this activity in those areas as late as 2 to 2-1/2 sec after the response, but comparing the 20 c/sec activity shown in Figures 16 and 20 with that in Figure 22, the large rise characteristic of the final 1/2 sec of the analysis period in the auditory 3-1/2 sec epoch data was absent from the visual and motor cortices. Although there were some rises in the 20 band during the final 1/2 sec of the analysis epoch, they rarely exceeded the baseline prestimulus level.

Since this investigation was limited to one cat, generalization to other animals is hardly justified.* However with the replication of such results in other animals with respect to

20 and 40 c/sec activity, the increases in 40 c/sec activity during S_{DR} might reasonably be related to the orienting response (Sheer et al, 1966a) and the increases in 20 c/sec activity, both in visual I and motor cortex during $S_{\Delta NR}$ and in auditory I following reinforcement to inhibitory processes--perhaps to the inhibition of the orienting response.

It is tempting to relate the results with respect to the 40 c/sec activity in this experiment to Calvet et al's (1965) cortical activation waves (CAW) which he found concomitant with the so-called desynchronized EEG pattern. He has described CAW as slow-surface positive waves with the following specific properties: (1) they are associated with an increase in the number of neuronal discharges, (2) they are diffuse, and (3) they occur during the course of low-voltage EEG activity. Calvet et al (1965) have suggested that they may be considered a manifestation of an extensive activation of the cortex. They have found that a cortical phenomenon very similar to the spontaneous CAW occurs with stimulation of the mesencephalic reticular formation with stimulation parameters almost identical to those usually employed to provoke an EEG arousal. Calvet et al's (1965) investigation of the relationship of CAW to movement revealed that only those movements which involve a relatively complex and nonautomatic activity of the higher nervous centers were accompanied by CAW. Neither passive movements of a limb nor flexion of a limb provoked by reflexogenic

stimulation produced activation waves. Automatic movements, such as scratching, also failed to give rise to CAW. It appeared to Calvet et al (1965) that any movements that led to a modification of the relationships of the animal with his environment produced CAW.

A 40 c/sec activity has been shown to be present throughout the performance of an instrumental learning task of considerable difficulty (Sheer et al, 1966a). They found that the 40 c/sec in the visual cortex was always present with the behavioral response and suggested that perhaps the explanation lay in the complex nature of the successive discrimination task which penalized errors in the intertrial interval with a 10-sec extension of the time until stimulus presentation and penalized errors in S_{Δ} with blackout. The nature of the task made it necessary for the animal to be constantly alert and attentive; consequently some orienting behavior occurred on every trial. This is a very different result from that obtained in those studies employing a classical conditioning paradigm which have shown a narrowing of the zone of desynchronization with localization finally in the motor cortex, once the critical stage of learning has been completed. Sheer et al (1966a) reported that in a simple auditory classical conditioning situation, the crosscorrelation of the 40 c/sec activity between auditory cortex and amygdala occurred only at the initial stage of learning and was no longer present with the establishment of

a well-conditioned response. In the experiment reported herein, using the same successive visual discrimination task as that of Sheer et al (1966a), the 40 c/sec activity with a reinforced response was strongest in the visual cortex in tape 10A, where the behavioral response was unquestionably well-established.

The observation of hyperactive orientation reflexes during conditioning of an alimentary reflex following ablation of the hippocampus suggested to Karmos and Grastyán (1962) that the hippocampus plays an essential role in the formation of temporary connections by inhibiting or controlling the orientation reflex. Perhaps the 20 c/sec phenomenon described in this thesis is an electrical correlate of this sort of inhibitory process.

Several investigators have reported 20 c/sec activity in hippocampal and other rhinencephalic structures. Boudreau and Freeman (1963) found increases in amplitude in the 24 c/sec and 6 c/sec bands in the prepyriform cortex of the cat during "lapping" behavior in a simple learned food response. Green and Shimamoto (1953) in a study of the propagation of hippocampal discharges of from 18 to 22 a second suggested that the projection of the after-discharges produced by hippocampal stimulation must be into the pyriform cortex or temporal lobe after ablations in various cats of all other possible routes. Based on the observation of a considerable difference in the

activity of monopolar and bipolar leads, Green and Shimamoto (1953) proposed that volume conduction plays a part in the conduction of these hippocampal discharges, although comparisons of the activities in the cerebellum and hippocampus led them to believe that some degree of localization is also possible. Fangel and Kaada (1960) have suggested that an orbito-insulo-temporal polar and a temporal zone should be included in the cortical fields for inhibition of movements and have suggested that "the functional significance of the inhibition of spontaneous movements as induced from cortical fields, including the much discussed 'suppressor' areas, is probably related to the attention response."

Perhaps the presence or absence of orienting behavior is the key factor in the 20-40 relationship described herein. Pending replication of these results in other animals, a tentative hypothesis for the inverse relationship between the 20 and 40 c/sec activity observed in this investigation is suggested: The occurrence of 40 c/sec activity is associated with orienting behavior and 20 c/sec activity is associated with inhibition of the orienting response.

CHAPTER VI

SUMMARY AND CONCLUSIONS

The electrical activity in 5 frequency bands in the arousal spectrum was studied in the primary visual cortex, motor cortex, and primary auditory cortex of one cat during prestimulus (PS) and stimulus periods at 3 levels of performance in a successive visual discrimination task. The task involved pressing a bar to obtain milk only in the presence of a 10 c/sec flashing light as the S_D and inhibiting during an S_{Δ} period of a 3 c/sec light.

EEG records representing the poorest, an intermediate, and the best behavioral performance, based on S_D / S_{Δ} ratios, in the visual discrimination task were computer analyzed to give average continuous power functions at 1/3 octave frequency bands with center frequencies of 20, 25, 31.5, 40, and 50 c/sec. The trials in the task on each tape were divided into as many as six behavioral categories, depending on the availability of trials within each category, as follows: PS, S_D , and S_{Δ} concomitant with a response (PS_R , S_{D_R} , S_{Δ_R} , respectively) and PS, S_D , and S_{Δ} in which no response occurred (PS_{NR} , $S_{D_{NR}}$, and $S_{\Delta_{NR}}$, respectively). Initiation of computation was contingent upon a response, either behavioral or artificial and either with or without a delay, so that the averaged band powers in a period of time prior and subsequent

to the response could be accurately ascertained. The analysis epoch was divided into two periods of time, one in which the electrical activity was assumed to be response related, the other assumed to be sufficiently removed in time from the response that the electrical activity was little affected by the response. The results were:

1. At all three levels of performance the 40 c/sec activity in visual I and motor cortex, but not in auditory I, was consistently higher during S_{DR} than during the other behavioral conditions studied.

2. The 40 c/sec electrical activity in visual I coincident with a reinforced response increased as performance improved, although the 40 c/sec activity with intermediate performance appeared to be more similar to that occurring with superior performance than to that concomitant with poor performance. The 40 c/sec electrical activity in the motor cortex with a reinforced response varied little with performance level.

3. A marked peaking of the 40 c/sec activity and a marked decrease in 20 c/sec activity occurred coincident with a reinforced response in both visual I and motor cortex, but not in auditory I. These phenomena were particularly evident with intermediate and superior performance in visual I.

4. Graphic data indicated an inverse relationship between the 20 c/sec and 40 c/sec activity in the visual and

motor cortices during S_{DR} and $S_{\Delta NR}$. The 20 c/sec activity was higher during $S_{\Delta NR}$ than during S_{DR} and the 40 c/sec was higher during S_{DR} than during $S_{\Delta NR}$. Statistical analysis was not possible because of the small N (N=3).

5. A marked peaking of the 20 c/sec activity in auditory I occurred approximately 2 to 2-1/2 sec following a reinforced response during "lapping" behavior. At the same time, significant but very small decreases in the 40 and 50 c/sec bands occurred. The 20 c/sec activity was consistently higher during lapping than it was following a response that was not reinforced or during a prestimulus period.

6. Since 40 c/sec activity was observed in association with facilitatory or arousal behavior and the 20 c/sec with behavioral inhibition, a tentative hypothesis was advanced that the 40 c/sec activity is an electrical correlate of the orienting response and that the 20 c/sec activity is an electrical correlate of the inhibition of the orienting response.

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APPENDIX A

VISUAL I

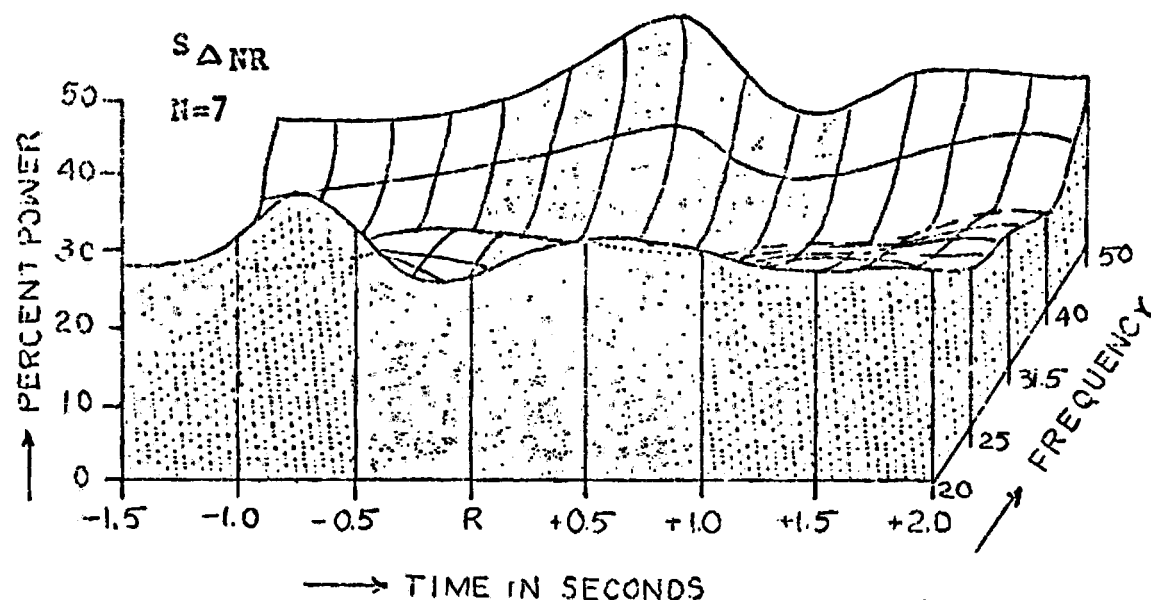
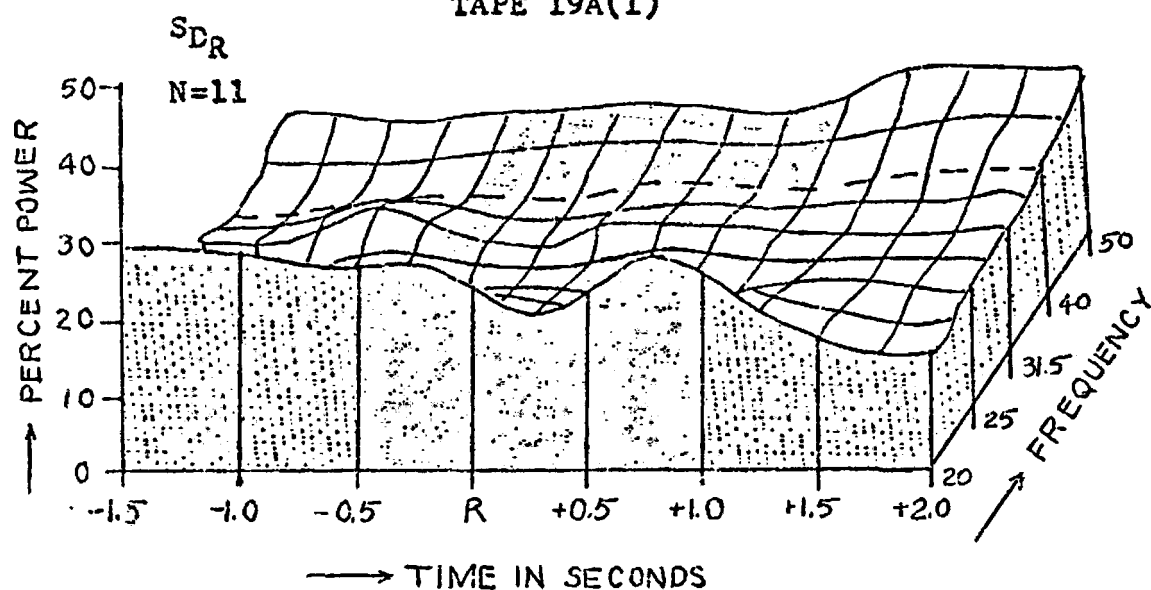
THREE DIMENSIONAL PLOTS

?

OF

FREQUENCY x TIME x POWER

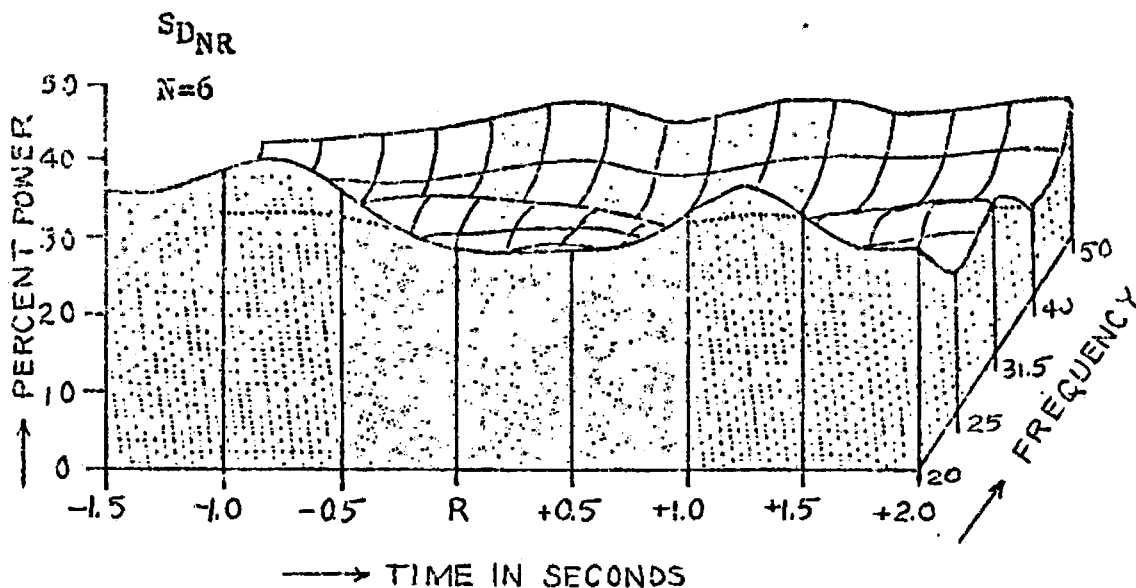
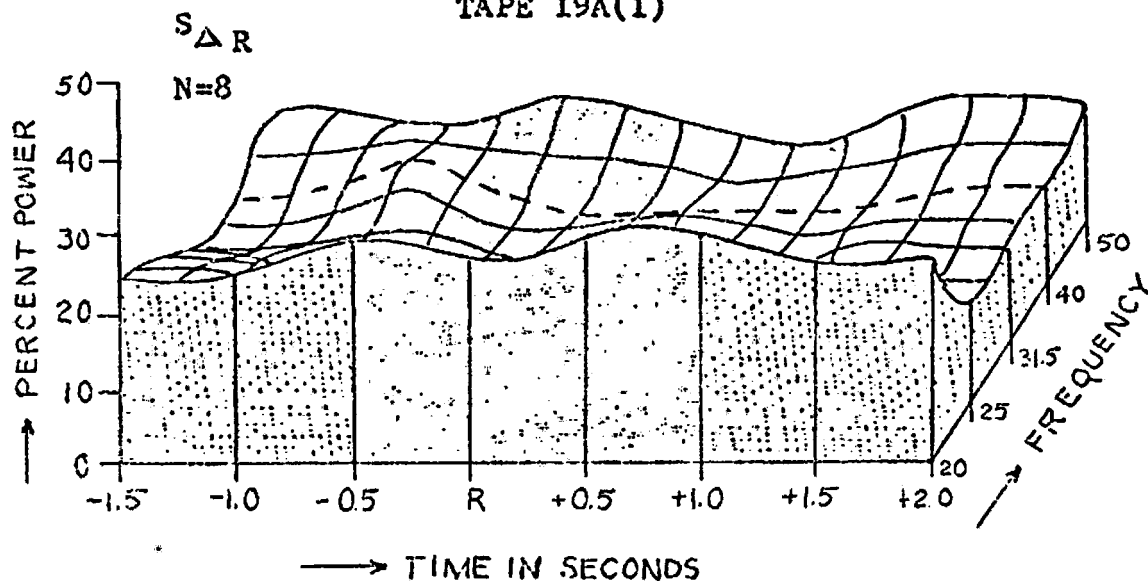
VISUAL I
TAPE 19A(1)



Both response and nonresponse conditions are plotted on a response-based time scale in order to facilitate comparisons. The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The 345 Period is lightly shaded.

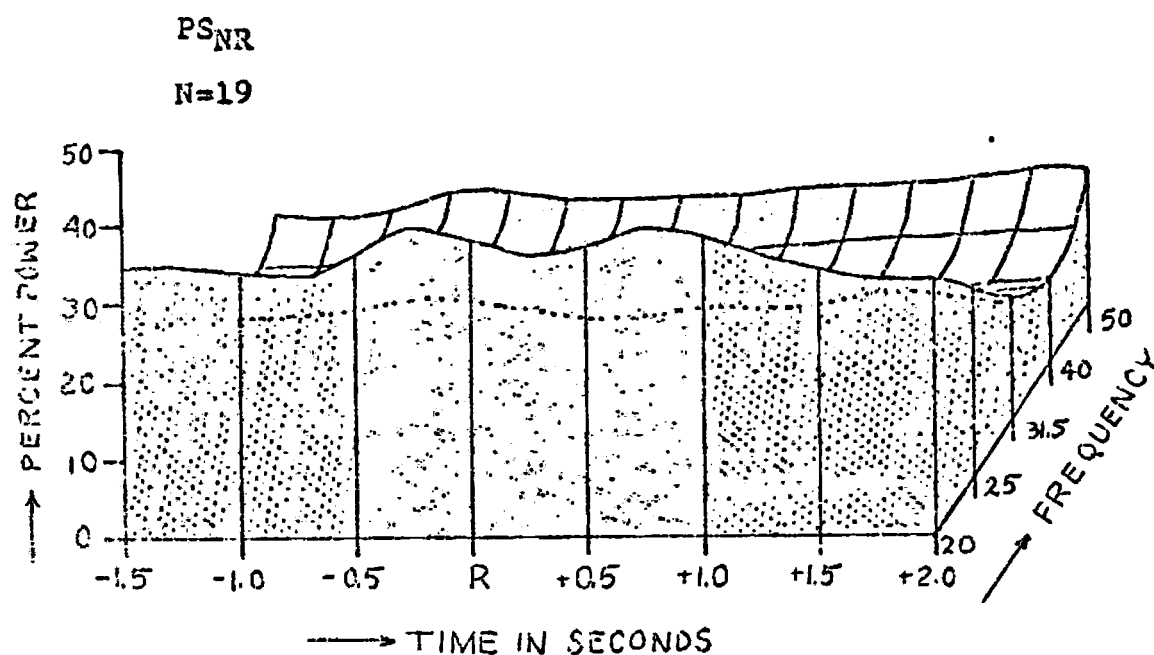
VISUAL I

TAPE 19A(1)



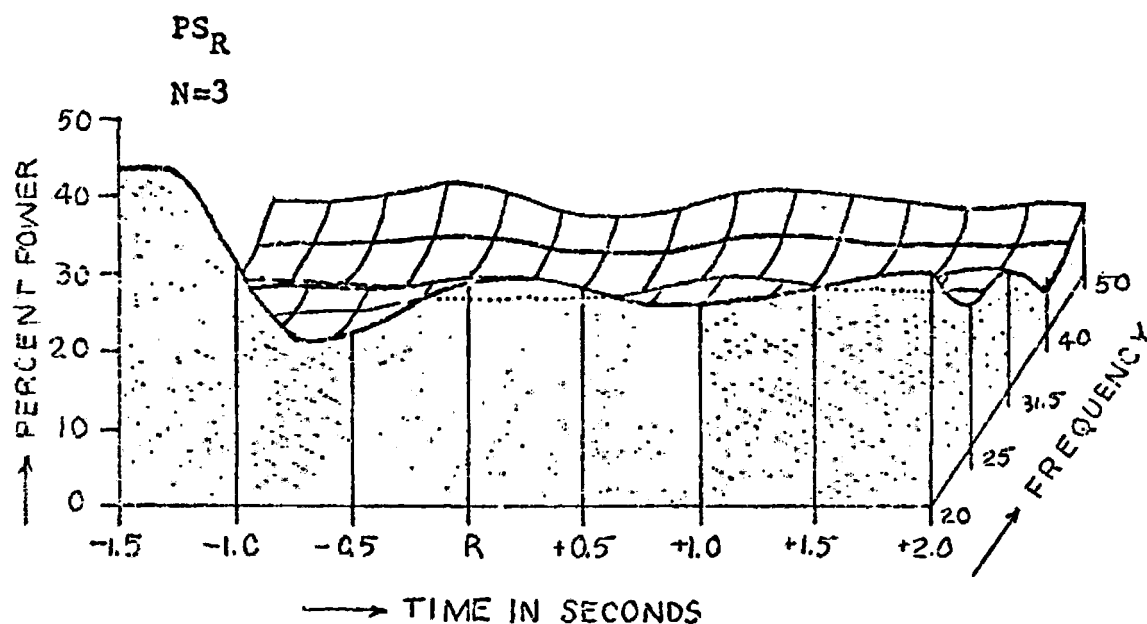
Both response and nonresponse conditions are plotted on a response-based time scale in order to facilitate comparisons. The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The 345 Period is lightly shaded.

VISUAL I
TAPE 19A(1)



Both response and nonresponse conditions are plotted on a response-based time scale in order to facilitate comparisons. The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The 345 Period is lightly shaded.

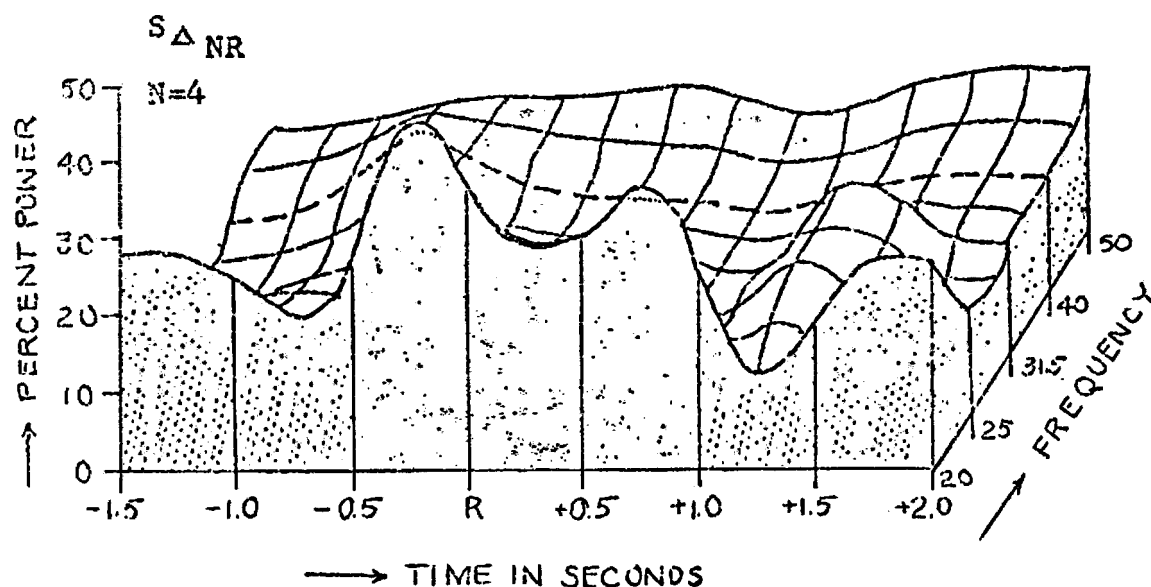
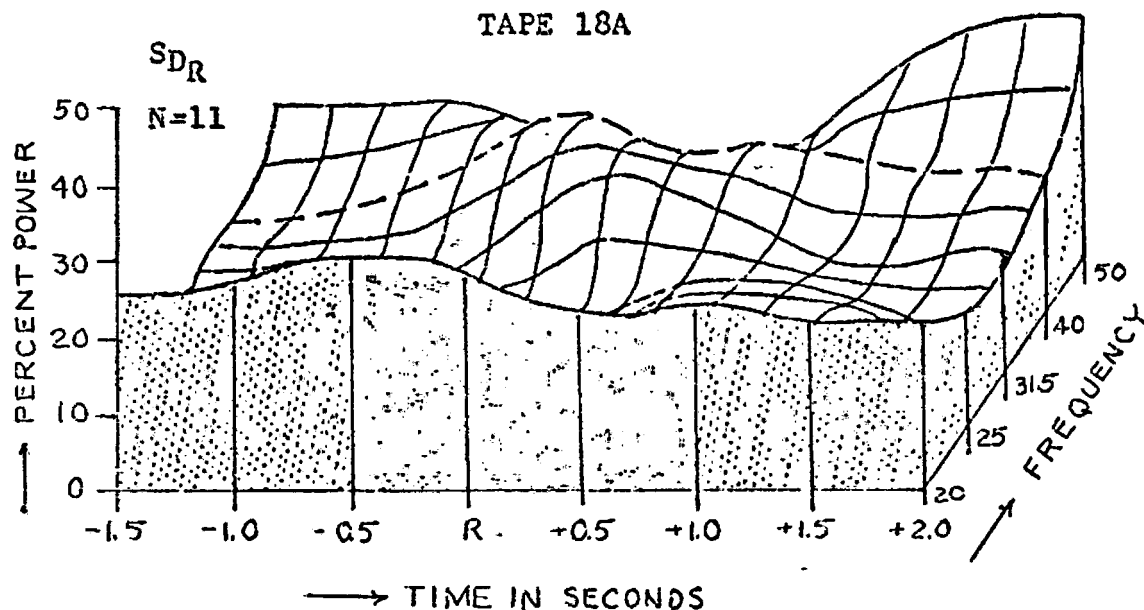
VISUAL I
TAPE 19A(1)



Both response and nonresponse conditions are plotted on a response-based time scale in order to facilitate comparisons. The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The 345 Period is lightly shaded.

VISUAL I

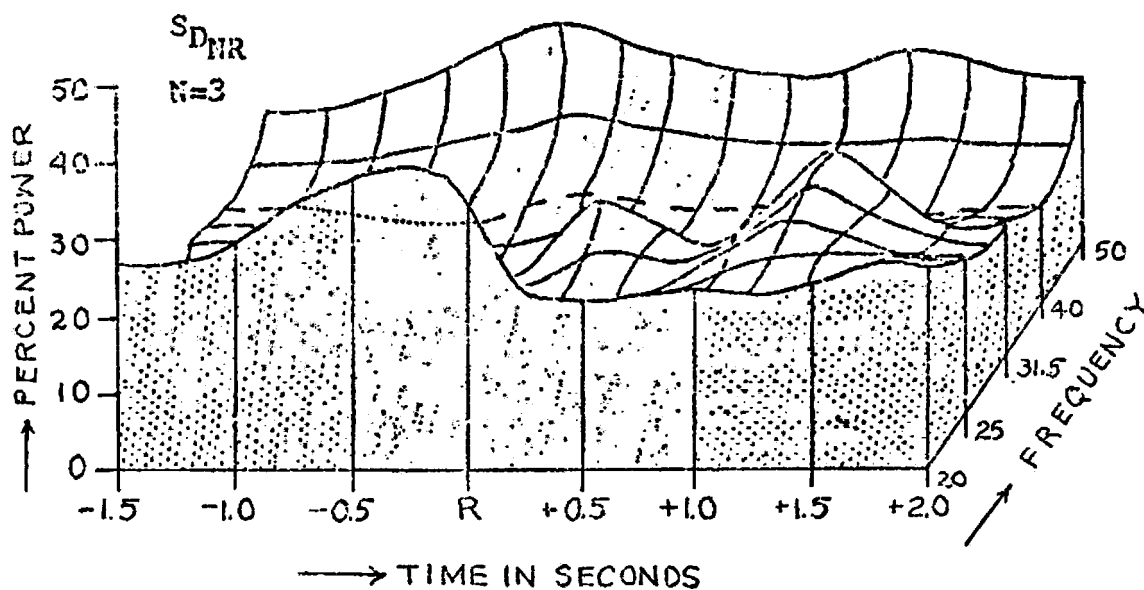
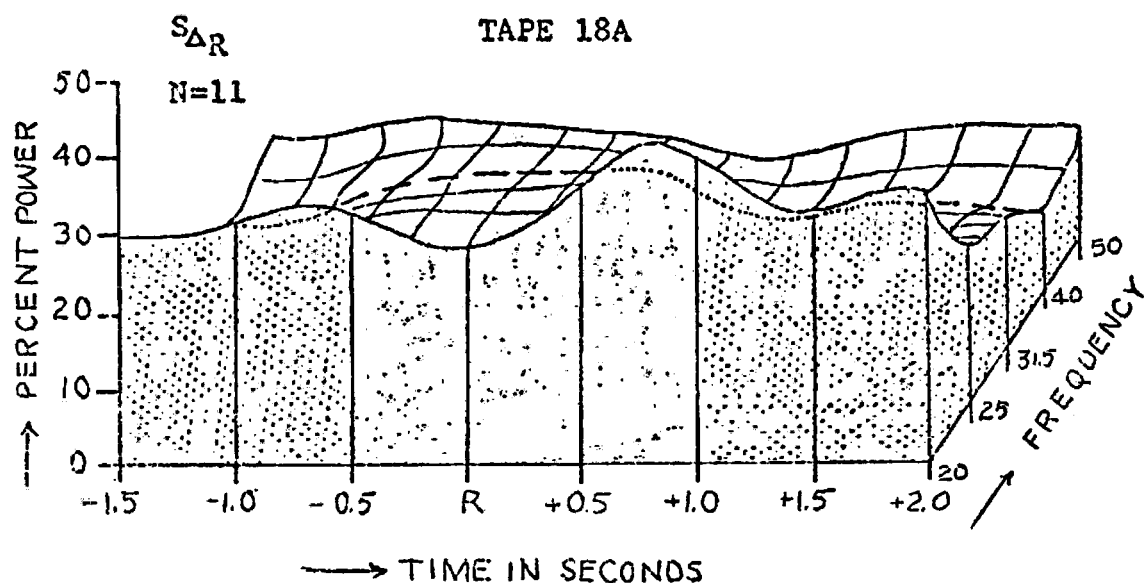
TAPE 18A



Both response and nonresponse conditions are plotted on a response-based time scale in order to facilitate comparisons. The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The 345 Period is lightly shaded.

VISUAL I

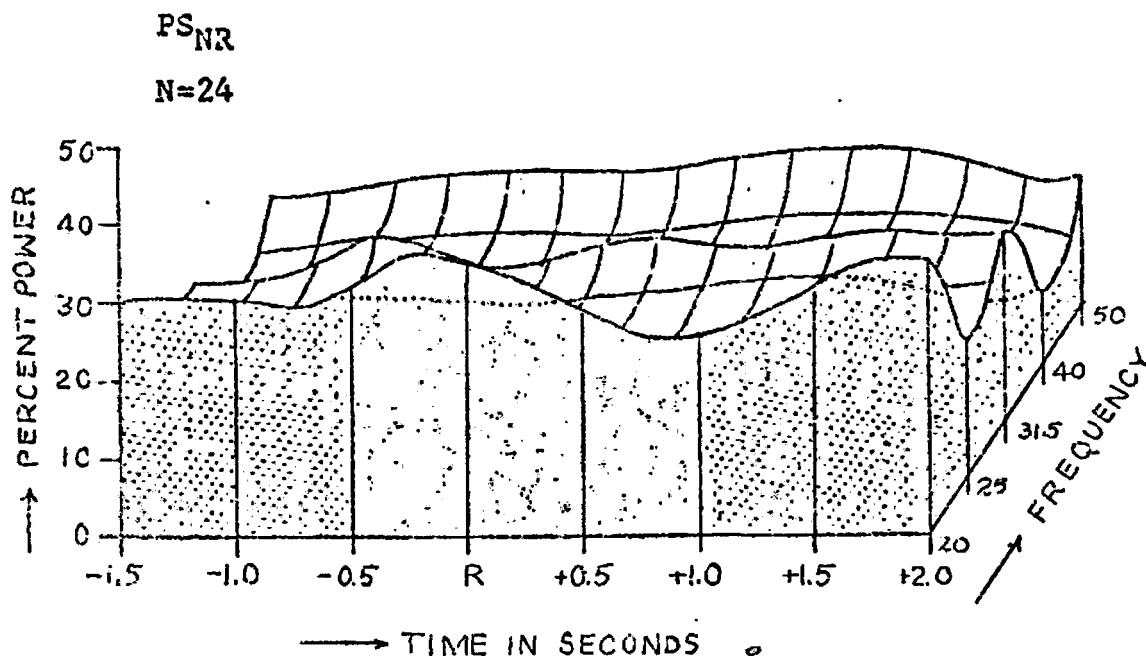
TAPE 18A



Both response and nonresponse conditions are plotted on a response-based time scale in order to facilitate comparisons. The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The 345 Period is lightly shaded.

VISUAL I

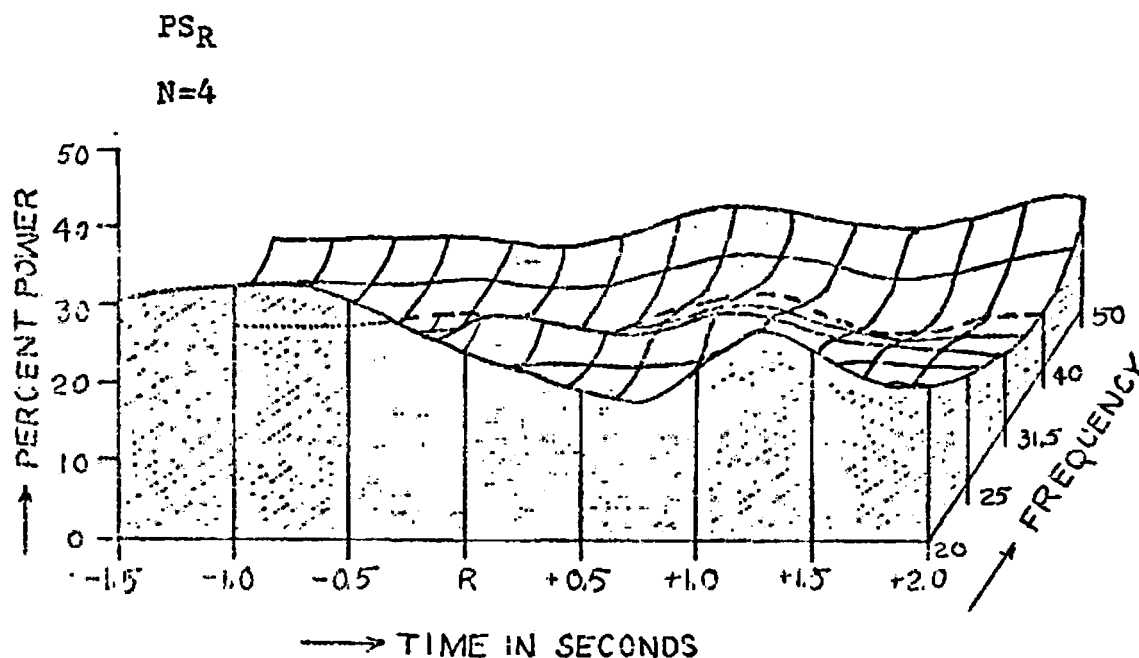
TAPE 18A



Both response and nonresponse conditions are plotted on a response-based time scale in order to facilitate comparisons. The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The 345 Period is lightly shaded.

VISUAL I

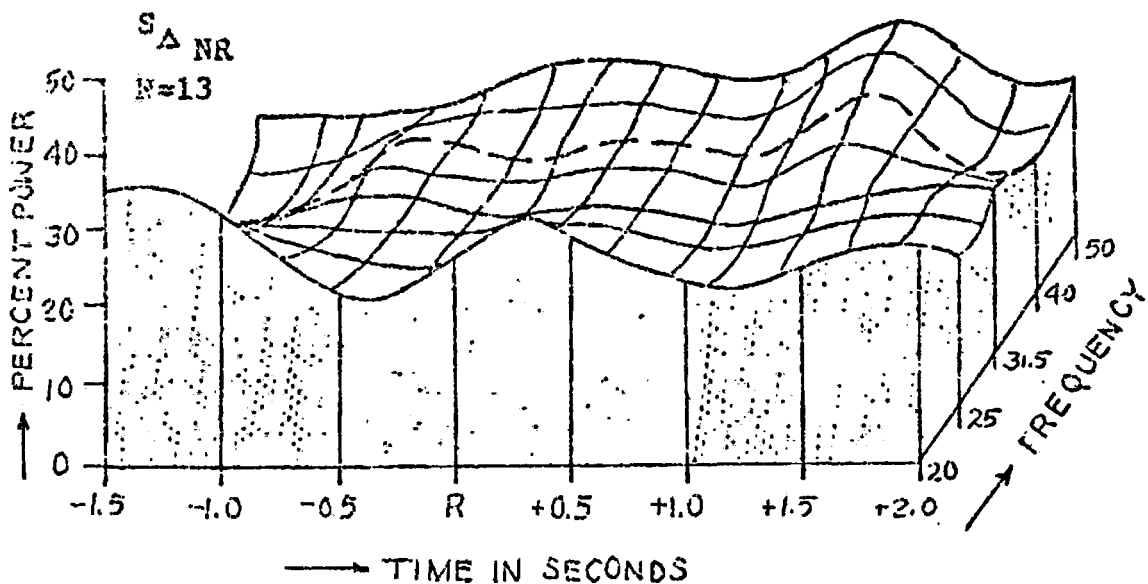
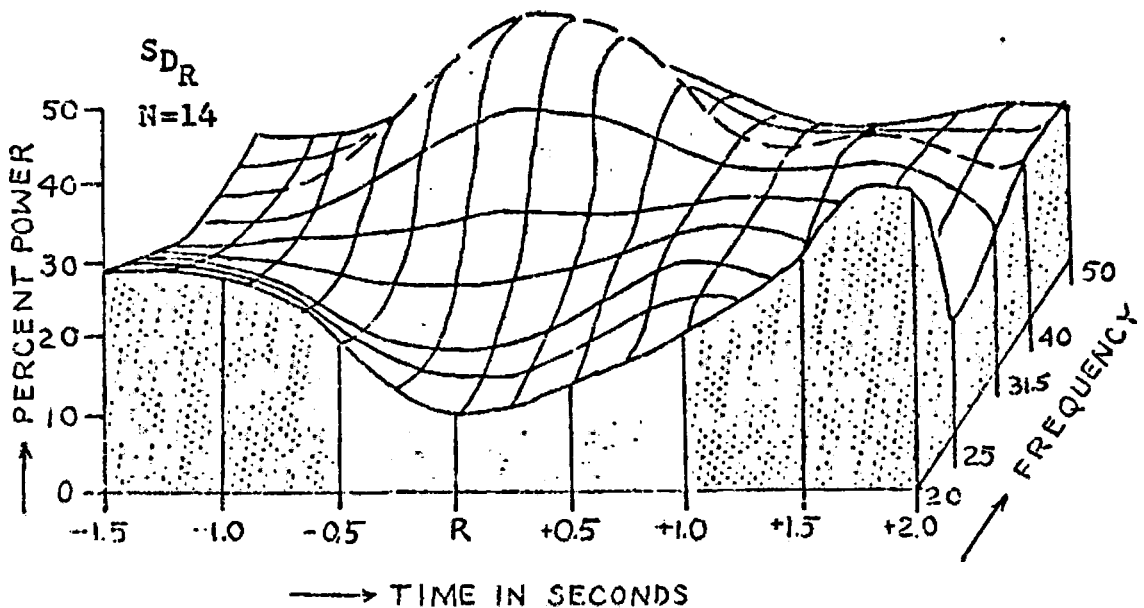
TAPE 18A



Both response and nonresponse conditions are plotted on a response-based time scale in order to facilitate comparisons. The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The 345 Period is lightly shaded.

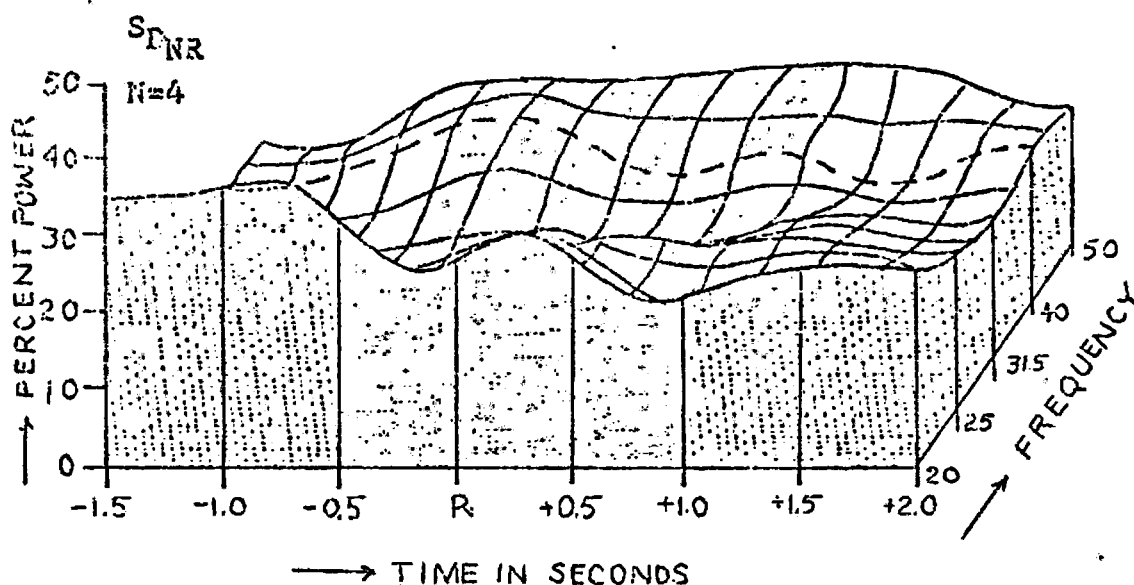
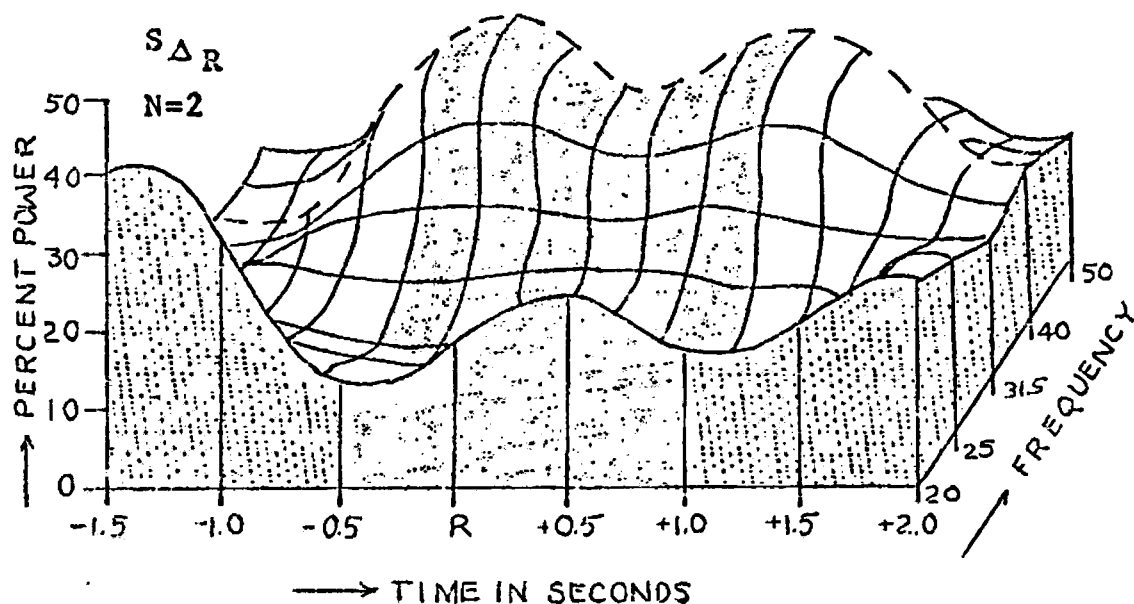
VISUAL I
TAPE 10A

187



Both response and nonresponse conditions are plotted on a response-based time scale in order to facilitate comparisons. The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The 345 Period is lightly shaded.

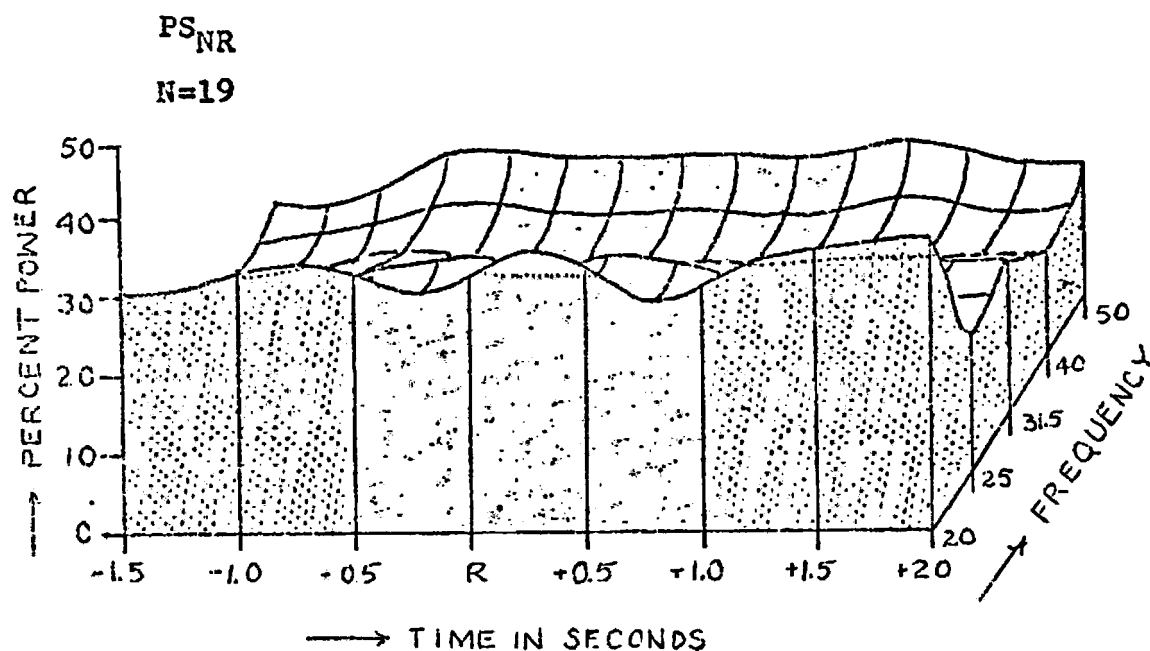
VISUAL I
TAPE 10A



Both response and nonresponse conditions are plotted on a response-based time scale in order to facilitate comparisons. The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The 345 Period is lightly shaded.

VISUAL I

TAPE 10A



Both response and nonresponse conditions are plotted on a response-based time scale in order to facilitate comparisons. The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The 345 Period is lightly shaded.

APPENDIX B

MOTOR CORTEX

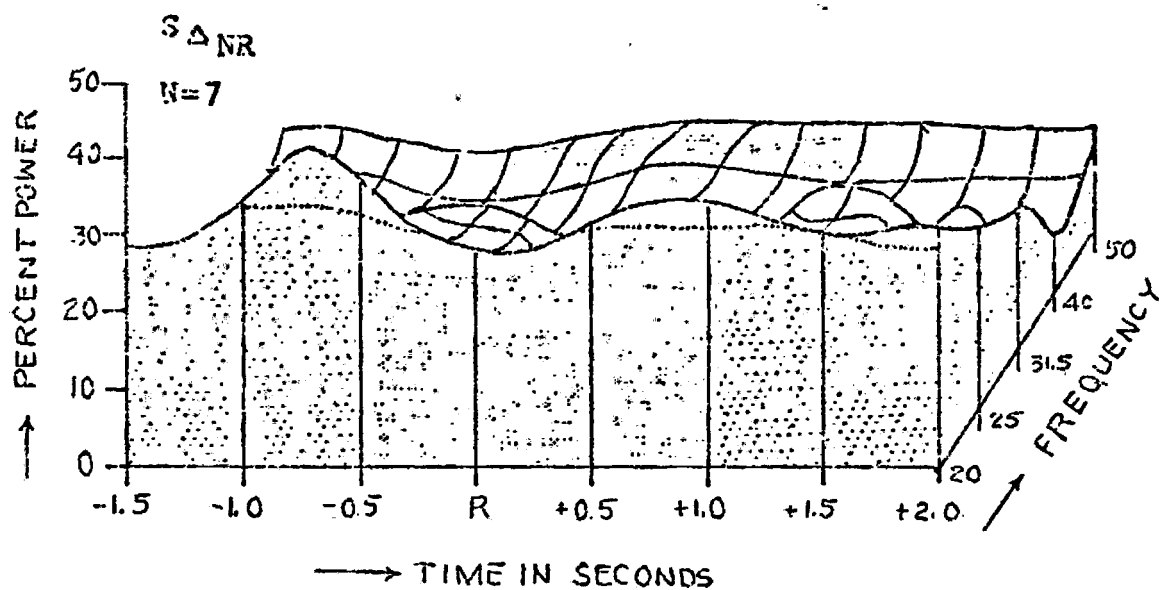
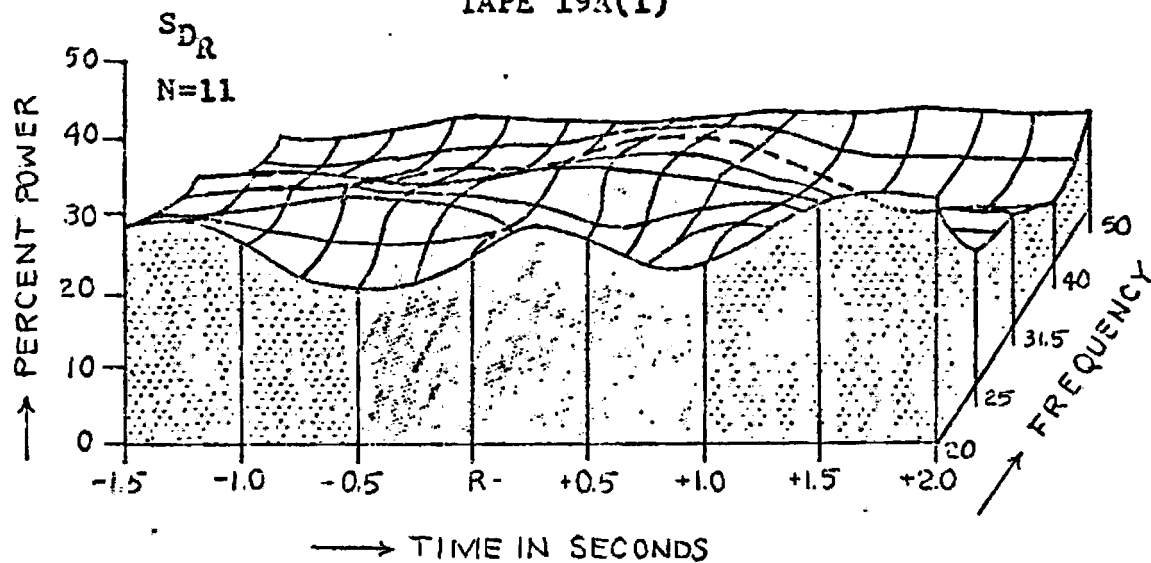
THREE DIMENSIONAL PLOTS

OF

FREQUENCY x TIME x POWER

MOTOR CORTEX

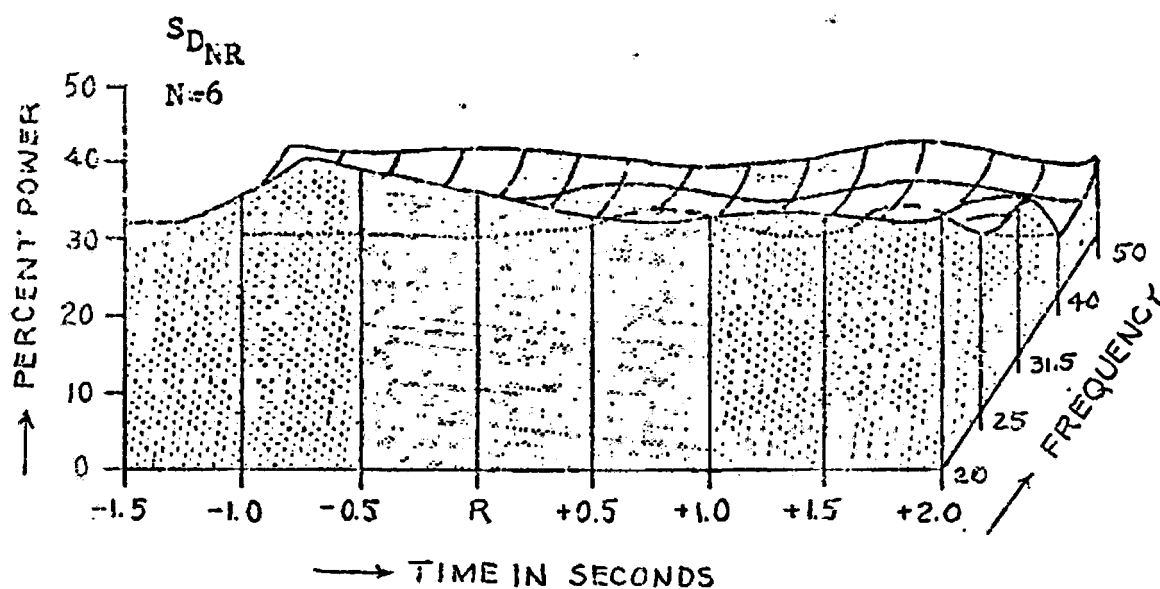
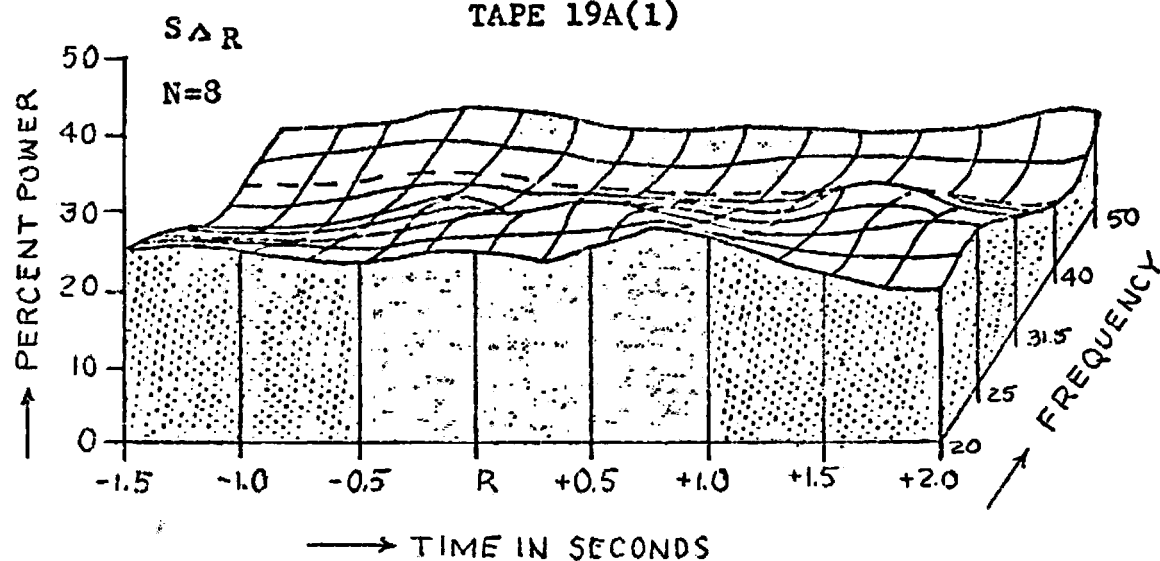
TAPE 19A(1)



Both response and nonresponse conditions are plotted on a response-based time scale in order to facilitate comparisons. The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The 345 Period is lightly shaded.

MOTOR CORTEX

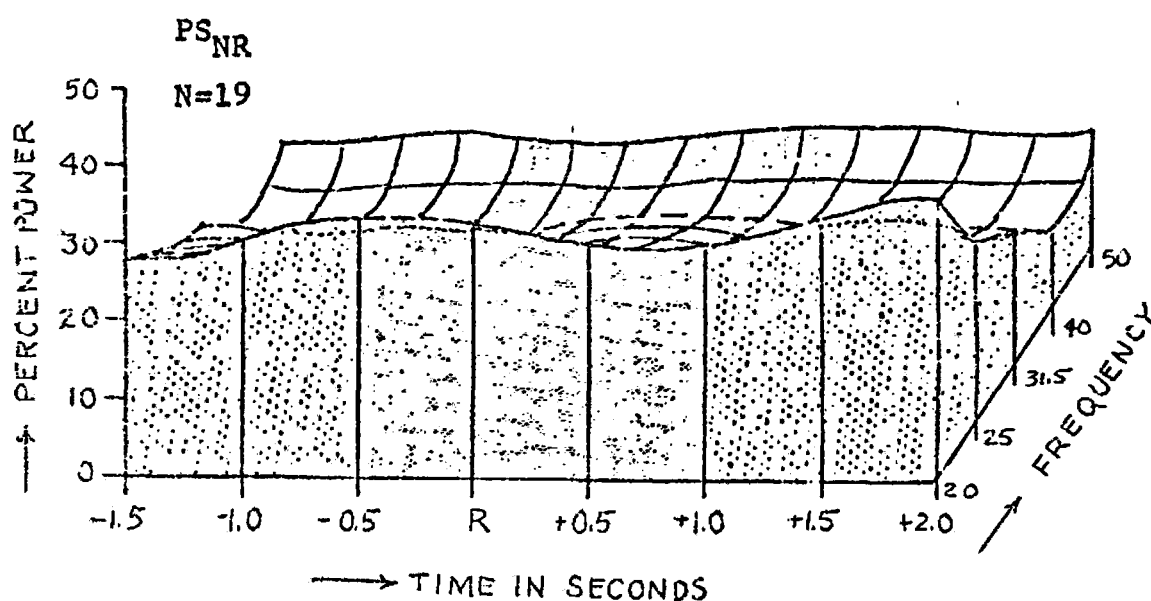
TAPE 19A(1)



Both response and nonresponse conditions are plotted on a response-based time scale in order to facilitate comparisons. The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The 345 Period is lightly shaded.

MOTOR CORTEX

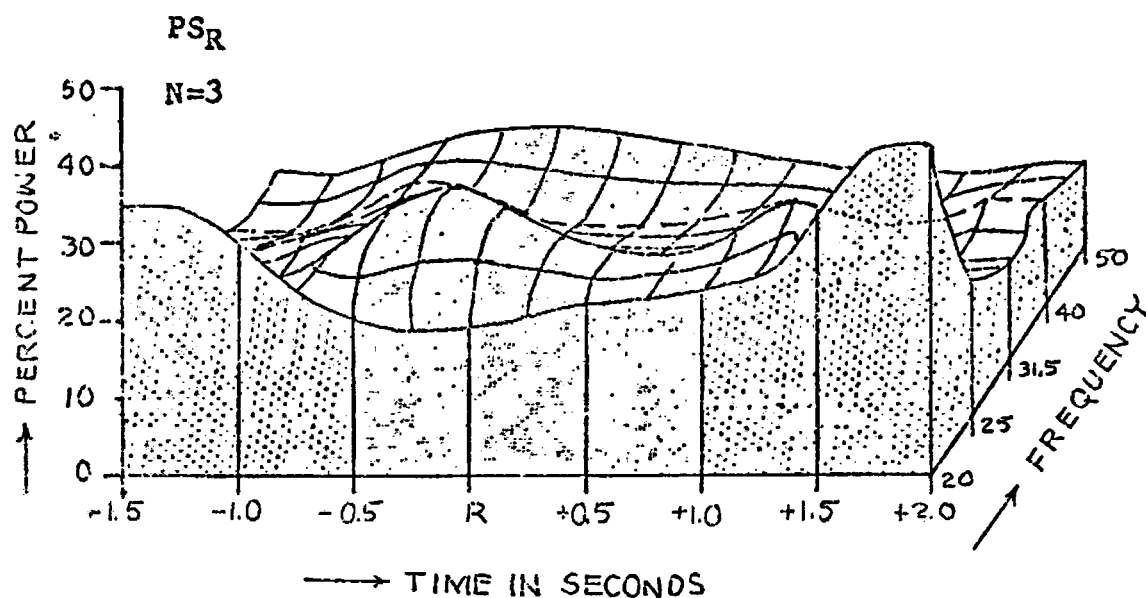
TAPE 19A(1)



Both response and nonresponse conditions are plotted on a response-based time scale in order to facilitate comparisons. The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The 345 Period is lightly shaded.

MOTOR CORTEX

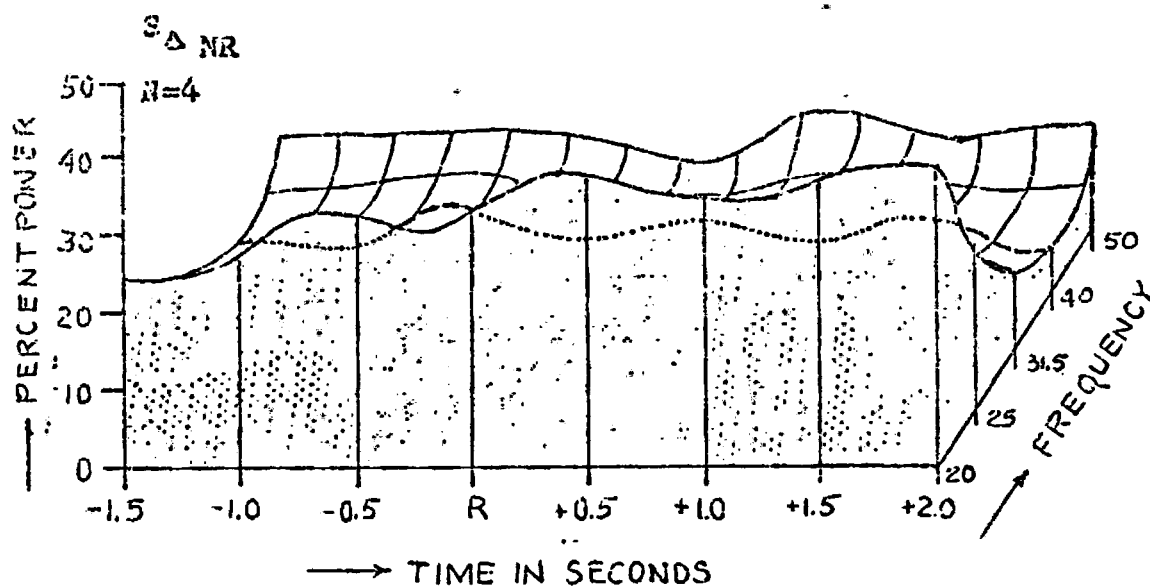
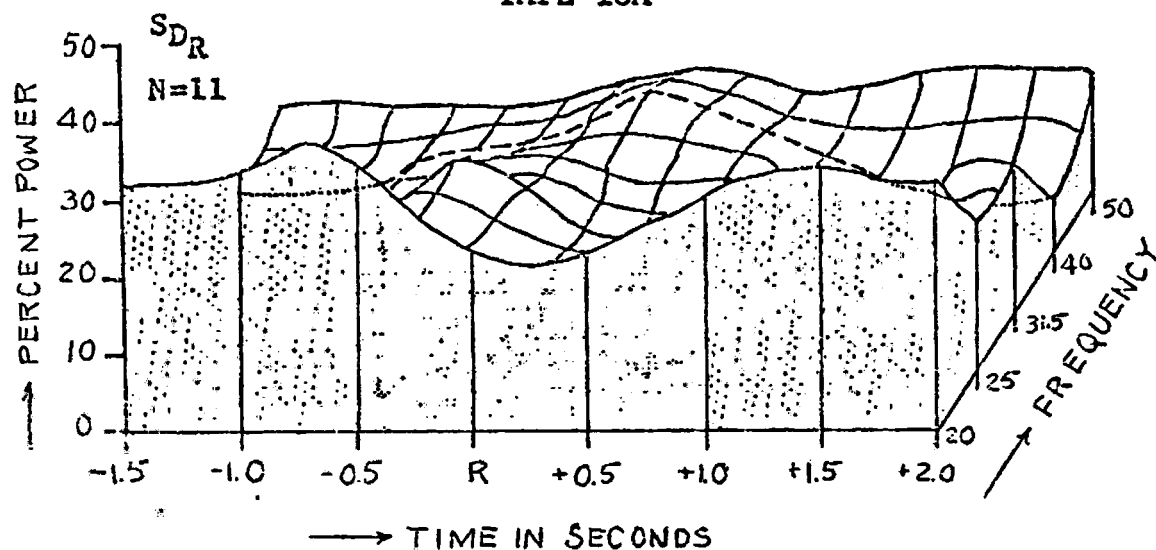
TAPE 19A(1)



Both response and nonresponse conditions are plotted on a response-based time scale in order to facilitate comparisons. The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The 345 Period is lightly shaded.

MOTOR CORTEX

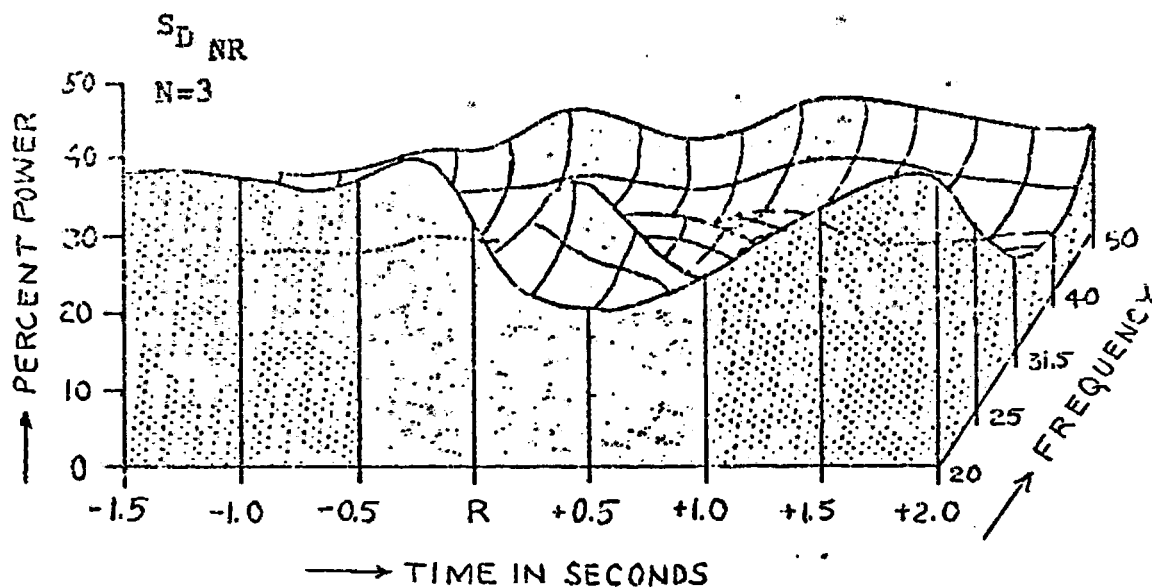
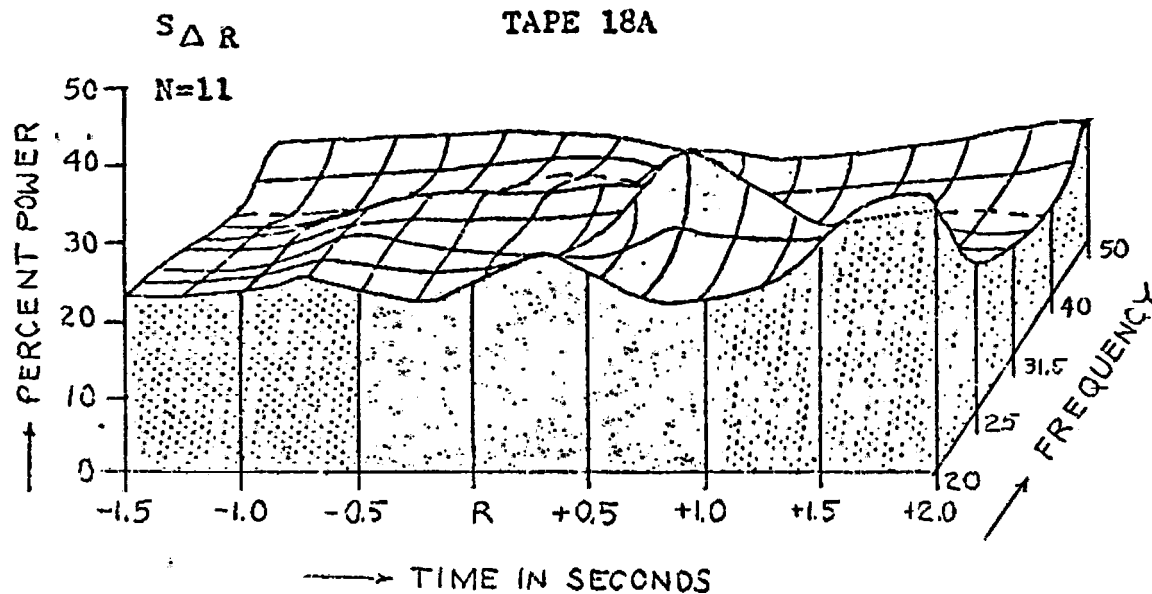
TAPE 18A



Both response and nonresponse conditions are plotted on a response-based time scale in order to facilitate comparisons. The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The 345 Period is lightly shaded.

MOTOR CORTEX

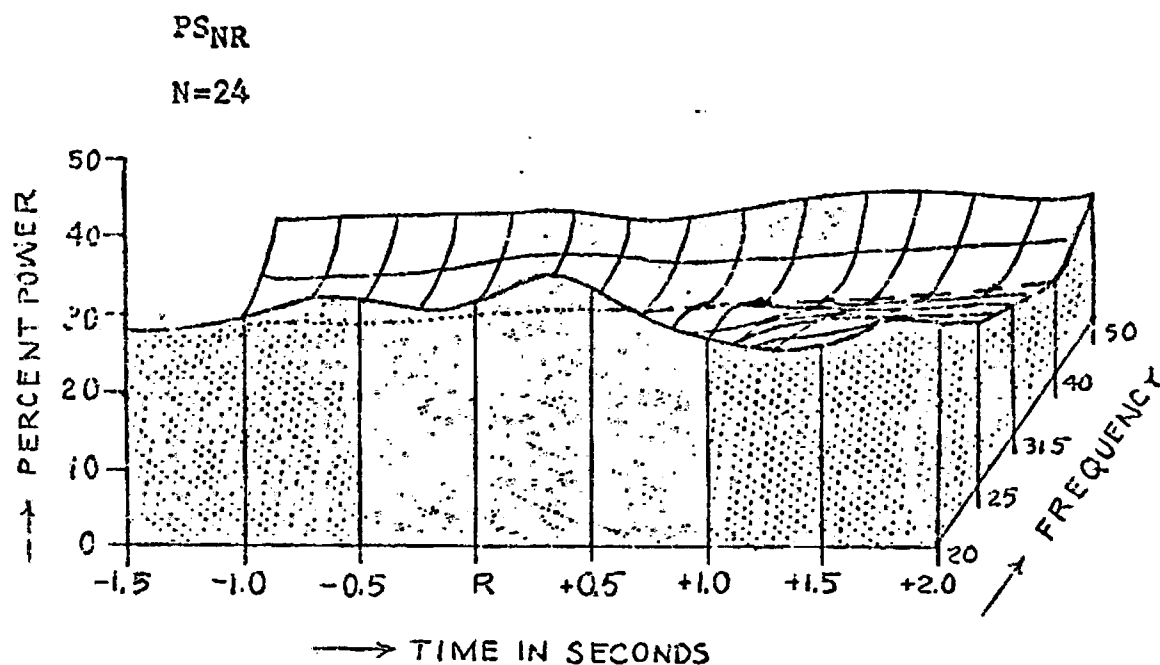
TAPE 18A



Both response and nonresponse conditions are plotted on a response-based time scale in order to facilitate comparisons. The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The 345 Period is lightly shaded.

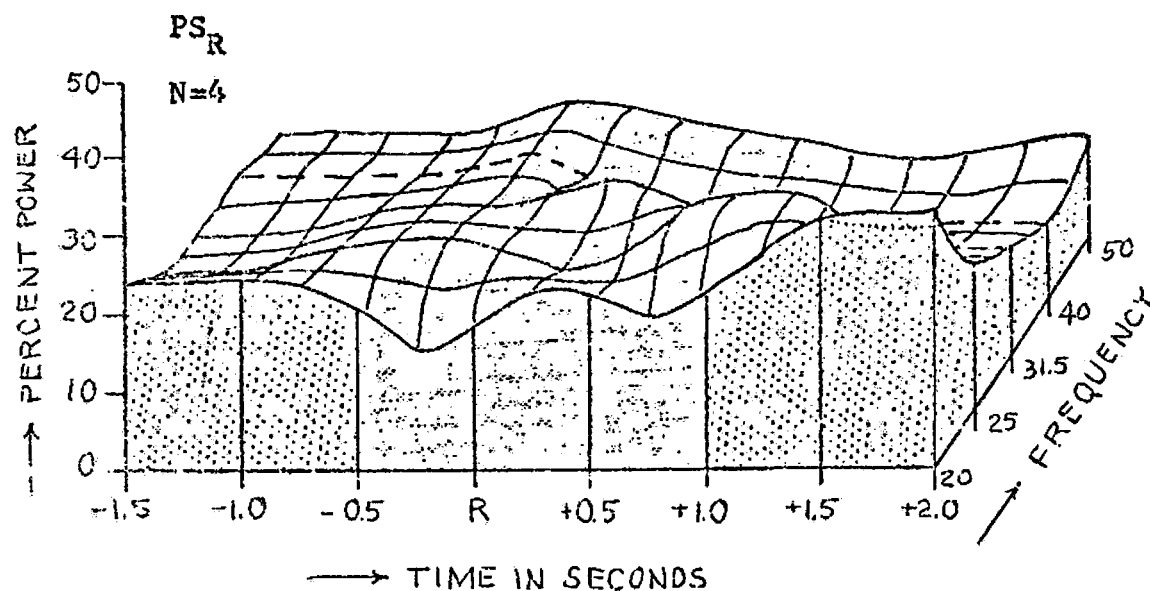
MOTOR CORTEX

TAPE 18A



Both response and nonresponse conditions are plotted on a response-based time scale in order to facilitate comparisons. The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The 345 Period is lightly shaded.

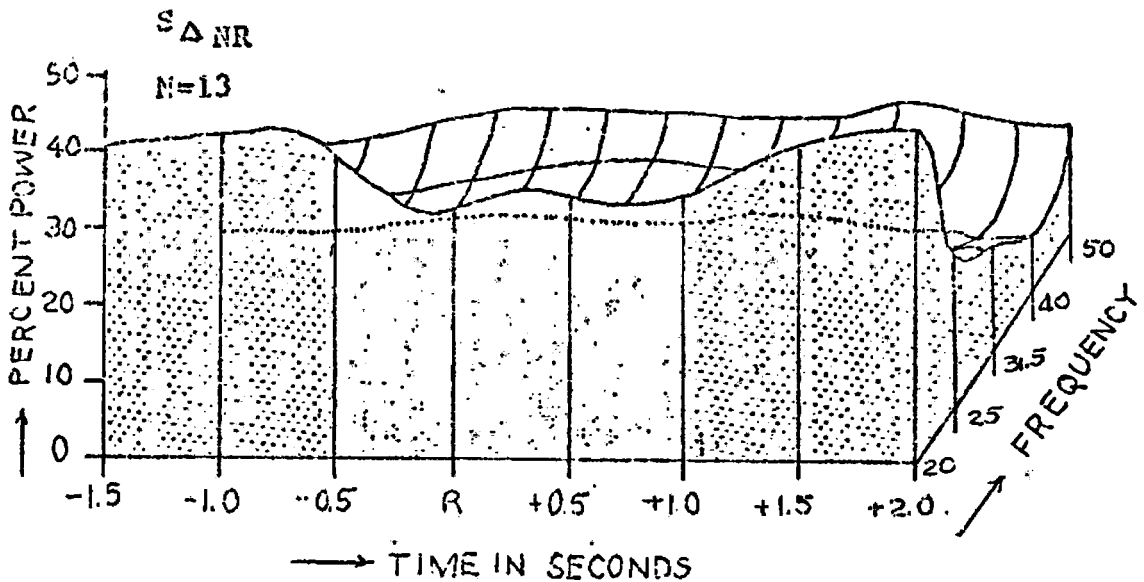
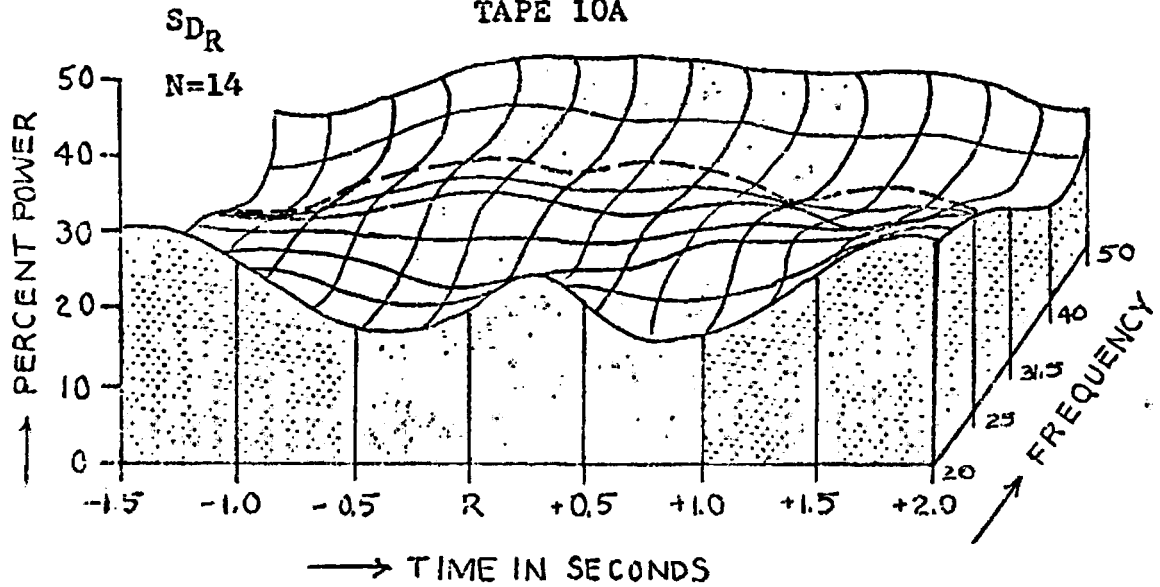
MOTOR CORTEX
TAPE 18A



Both response and nonresponse conditions are plotted on a response-based time scale in order to facilitate comparisons. The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The 345 Period is lightly shaded.

MOTOR CORTEX

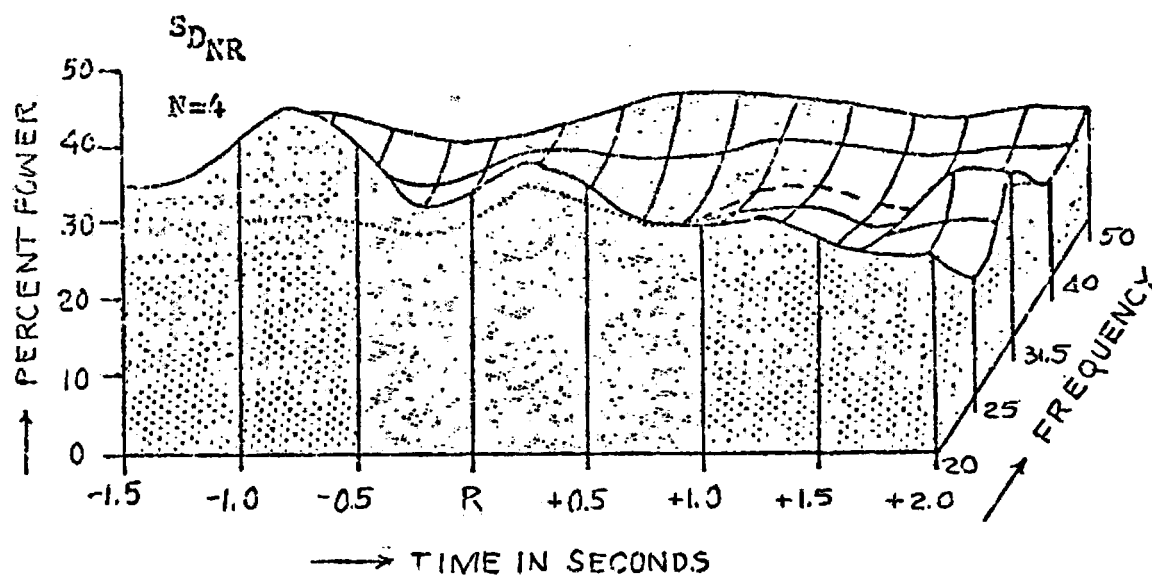
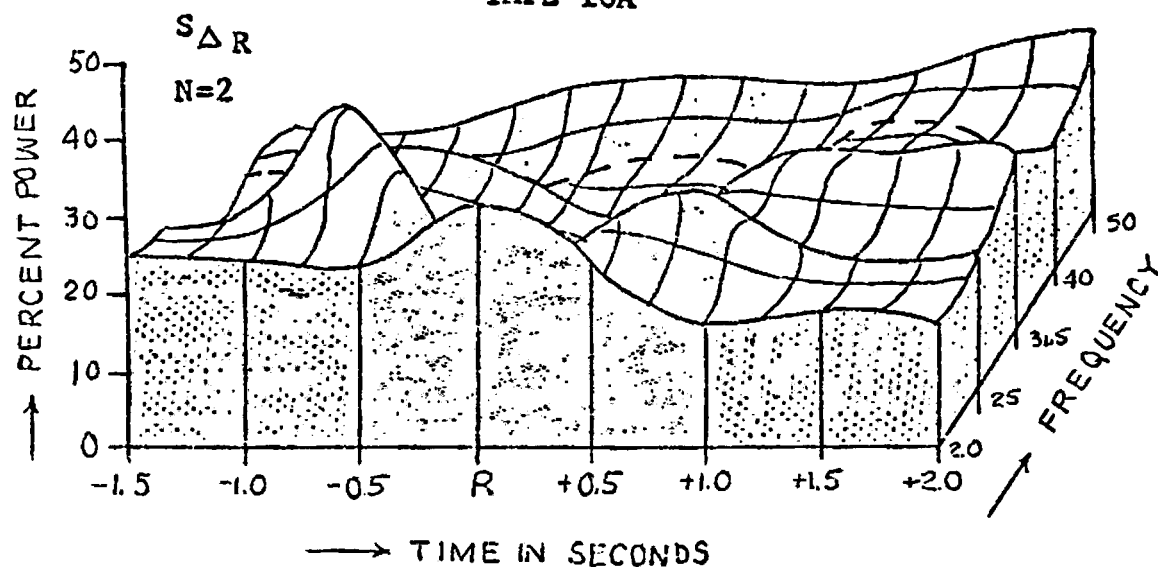
TAPE 10A



Both response and nonresponse conditions are plotted on a response-based time scale in order to facilitate comparisons. The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The 345 Period is lightly shaded.

MOTOR CORTEX

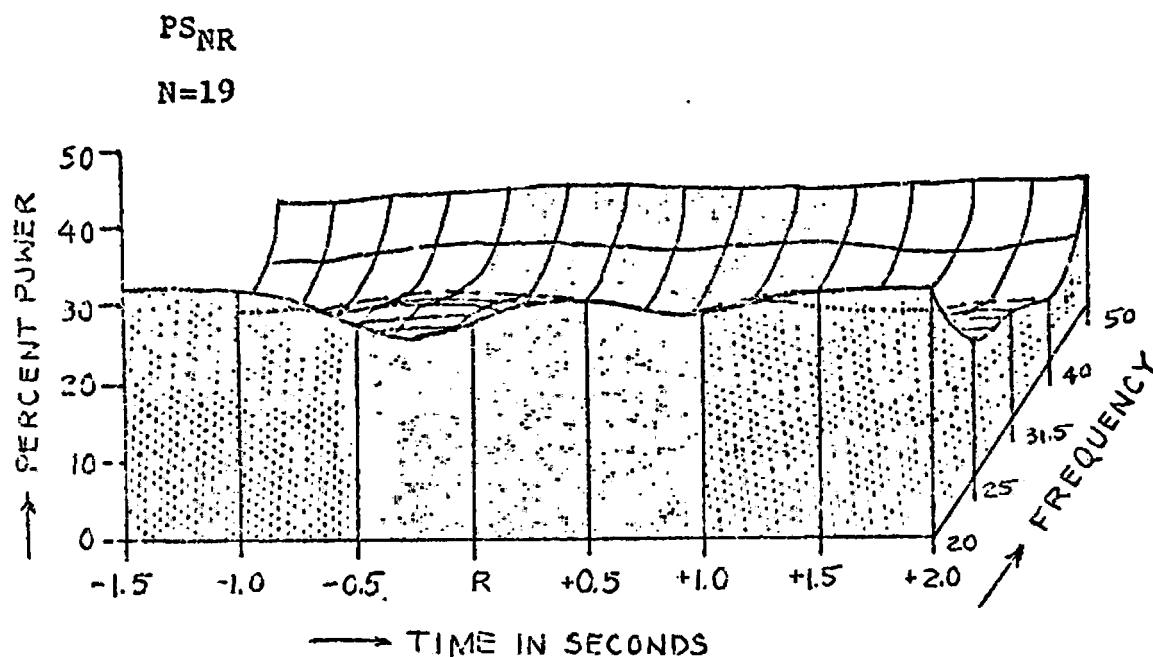
TAPE 10A



Both response and nonresponse conditions are plotted on a response-based time scale in order to facilitate comparisons. The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The 345 Peroid is lightly shaded.

MOTOR CORTEX

TAPE 10A



Both response and nonresponse conditions are plotted on a response-based time scale in order to facilitate comparisons. The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The 345 Period is lightly shaded.

APPENDIX C

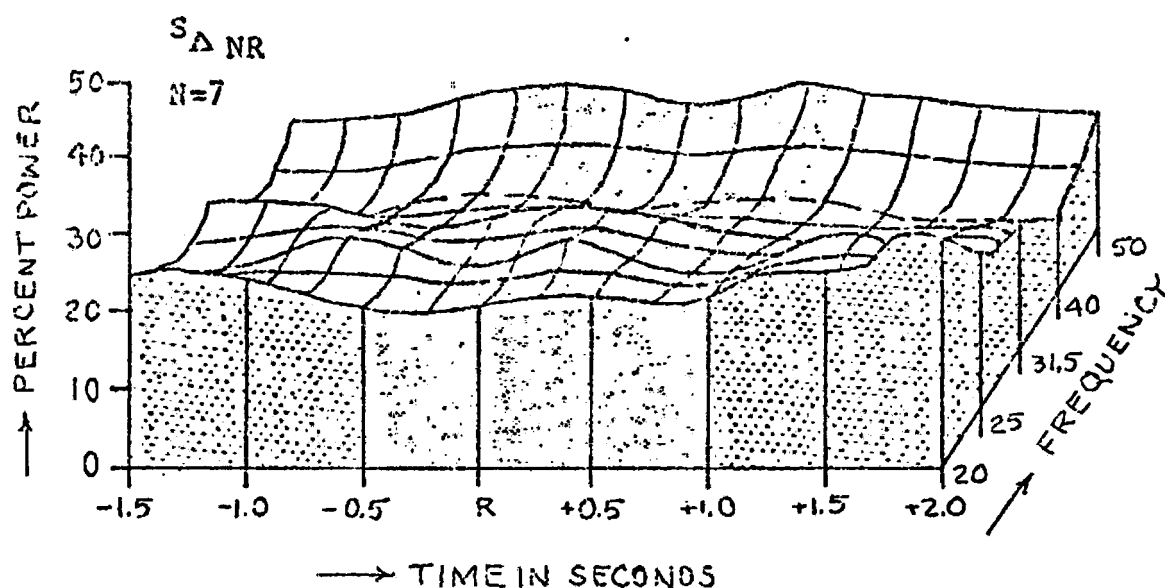
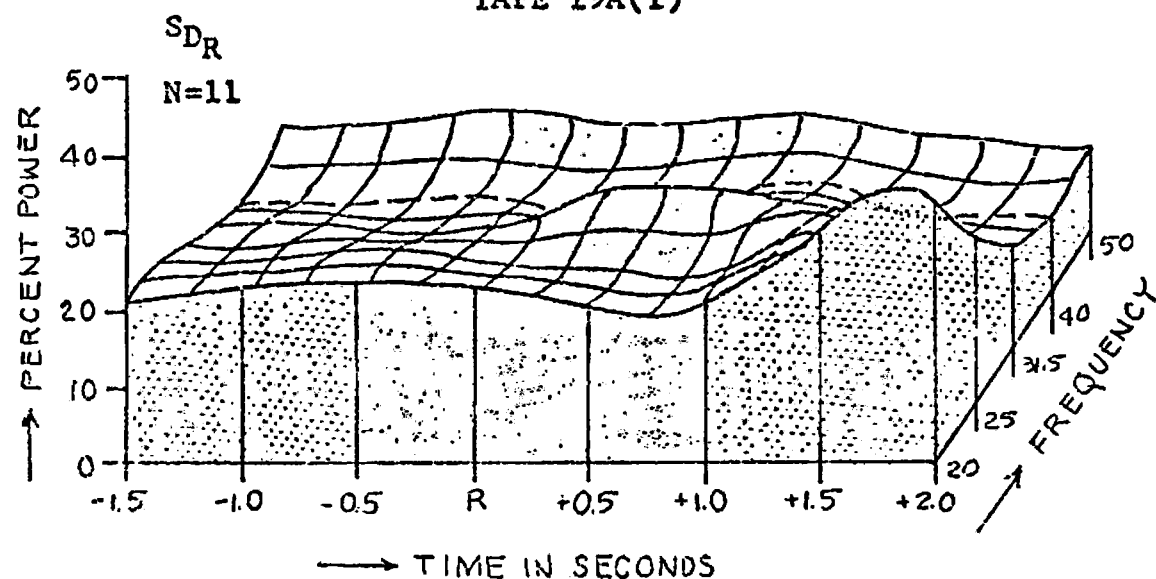
AUDITORY I ($3\frac{1}{2}$ SEC)

THREE DIMENSIONAL PLOTS

OF

FREQUENCY x TIME x POWER

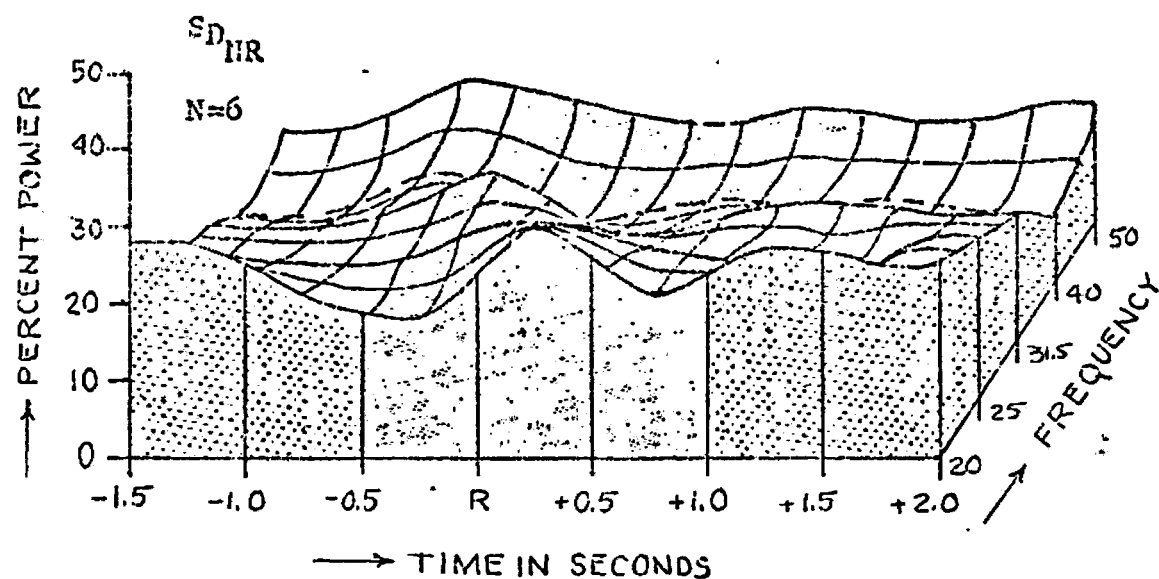
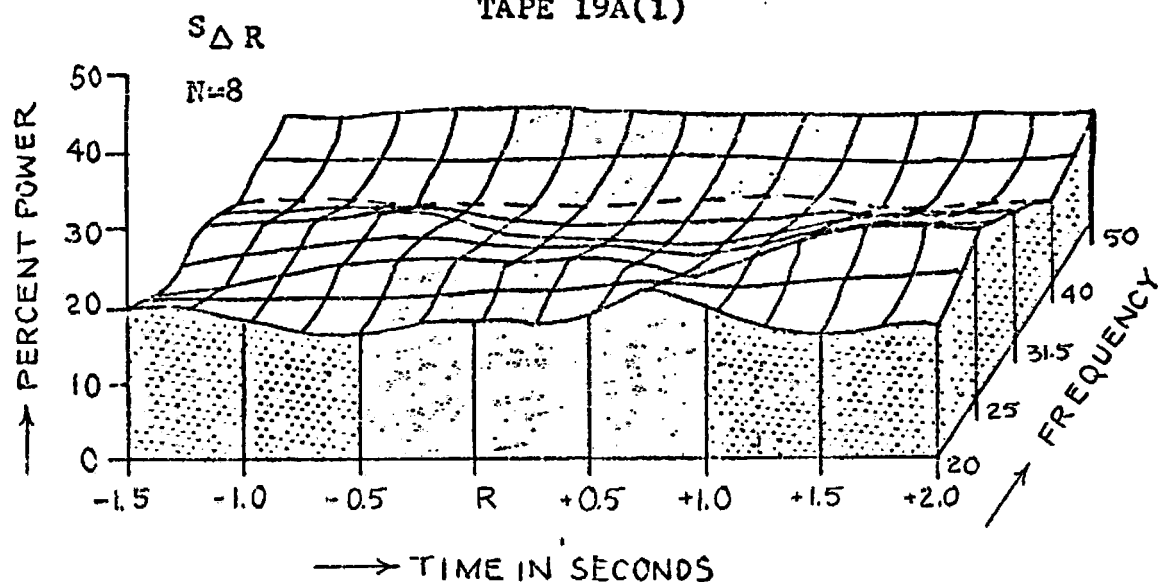
AUDITORY CORTEX (3-1/2 SEC)
TAPE 19A(1)



Both response and nonresponse conditions are plotted on a response-based time scale in order to facilitate comparisons. The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The 345 Period is lightly shaded.

AUDITORY CORTEX (3-1/2 SEC)

TAPE 19A(1)



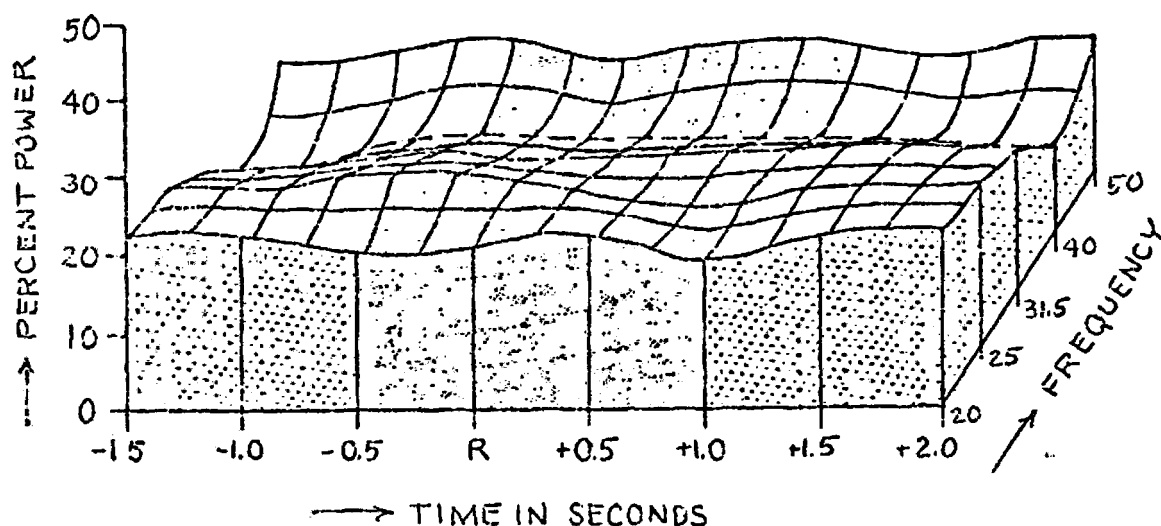
Both response and nonresponse conditions are plotted on a response-based time scale in order to facilitate comparisons. The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The 345 Period is lightly shaded.

AUDITORY CORTEX (3-1/2 SEC)

TAPE 19A(1)

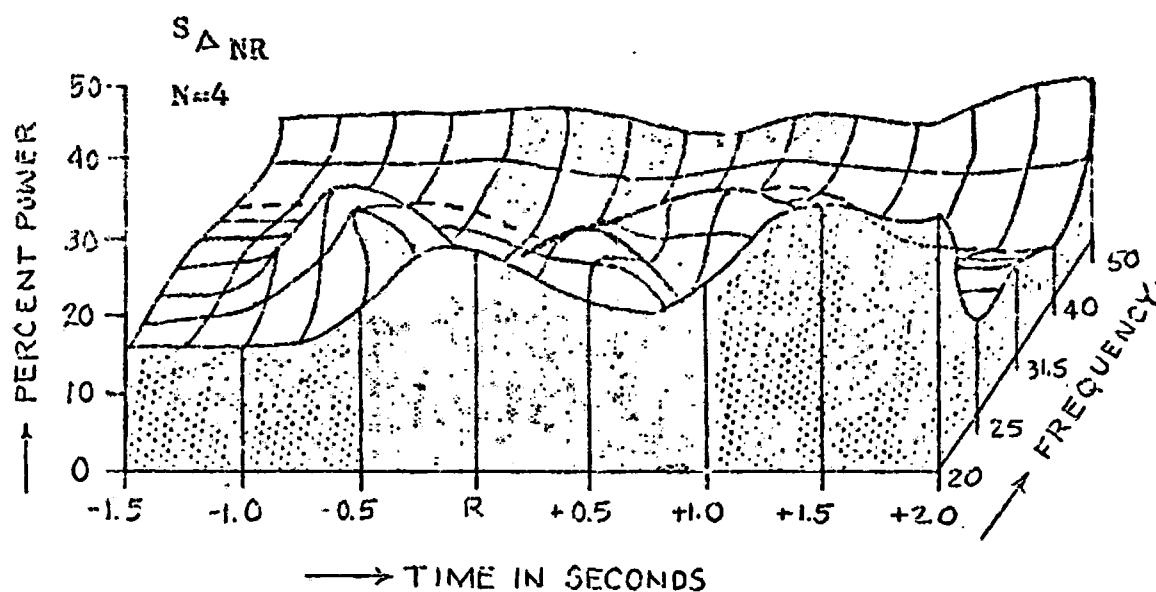
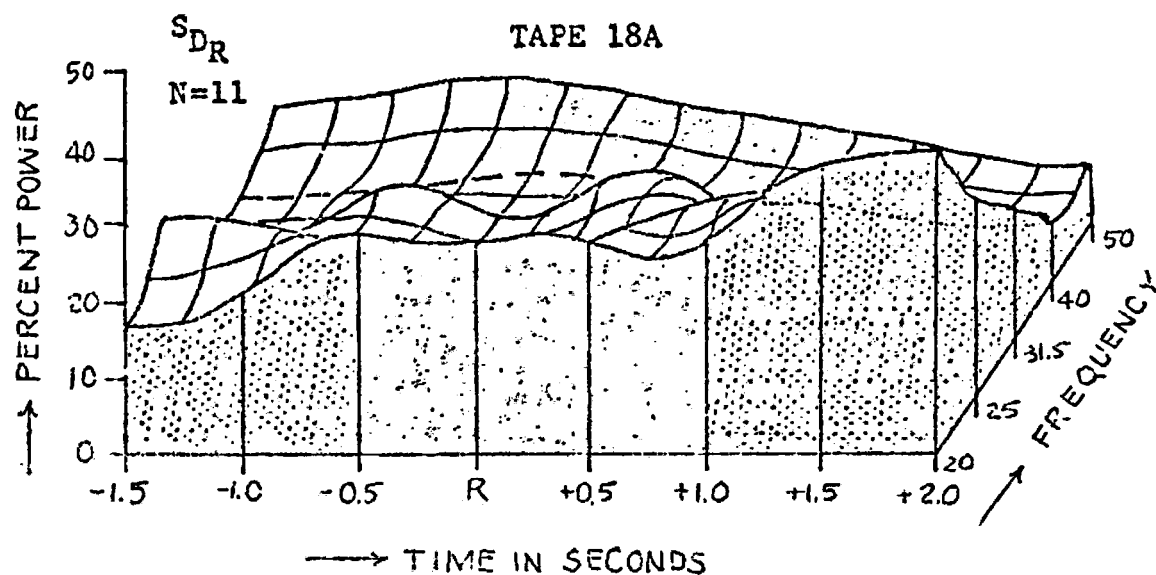
 PS_{NR}

N=19



Both response and nonresponse conditions are plotted on a response-based time scale in order to facilitate comparisons. The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The 345 Period is lightly shaded.

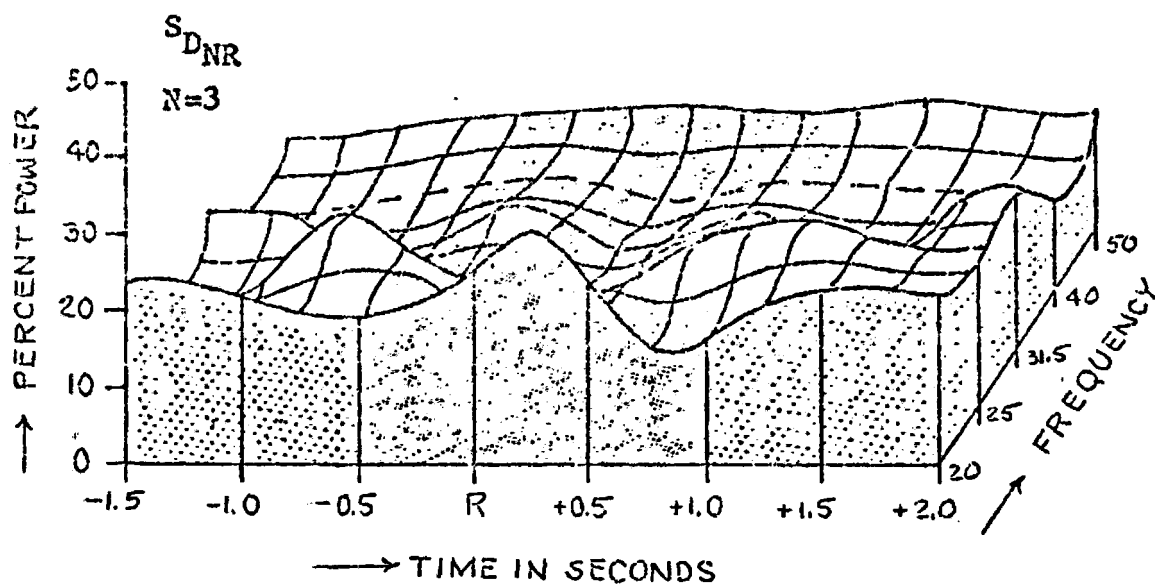
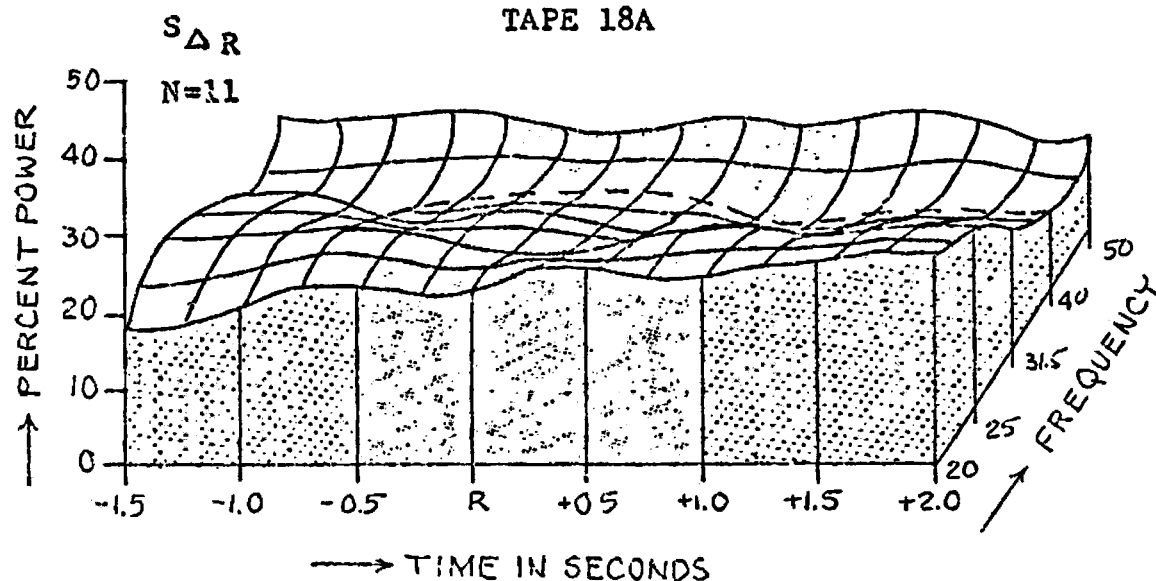
AUDITORY CORTEX (3-1/2 SEC)



Both response and nonresponse conditions are plotted on a response-based time scale in order to facilitate comparisons. The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The 345 Period is lightly shaded.

AUDITORY CORTEX (3-1/2 SEC)

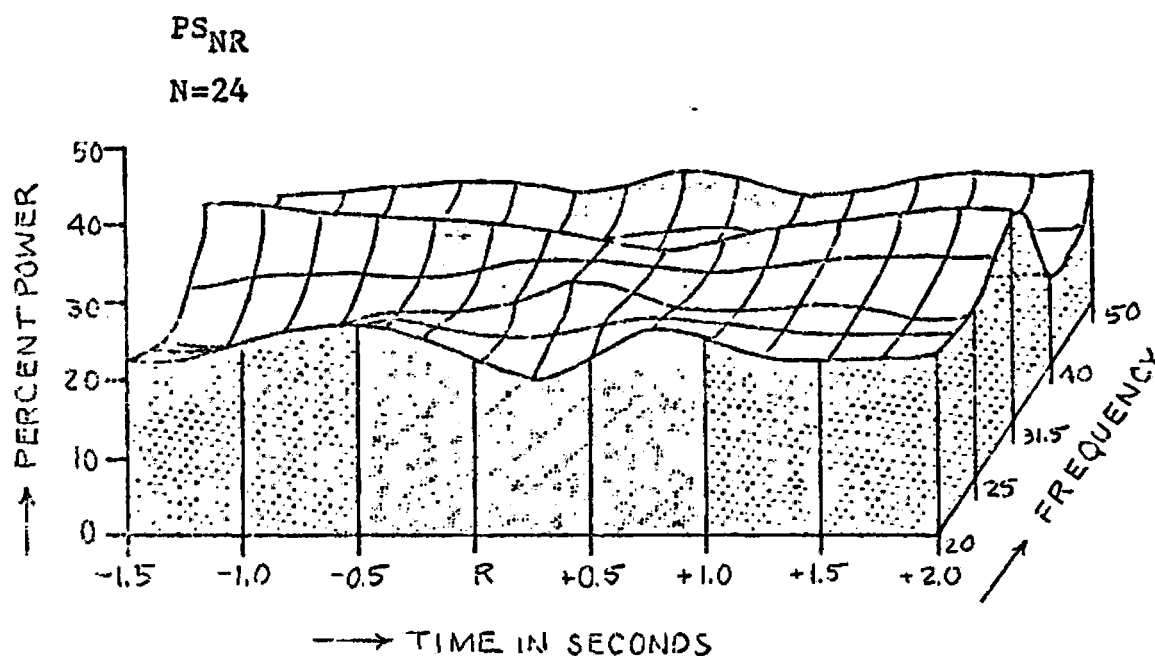
TAPE 18A



Both response and nonresponse conditions are plotted on a response-based time scale in order to facilitate comparisons. The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The 345 Period is lightly shaded.

AUDITORY CORTEX (3-1/2 SEC)

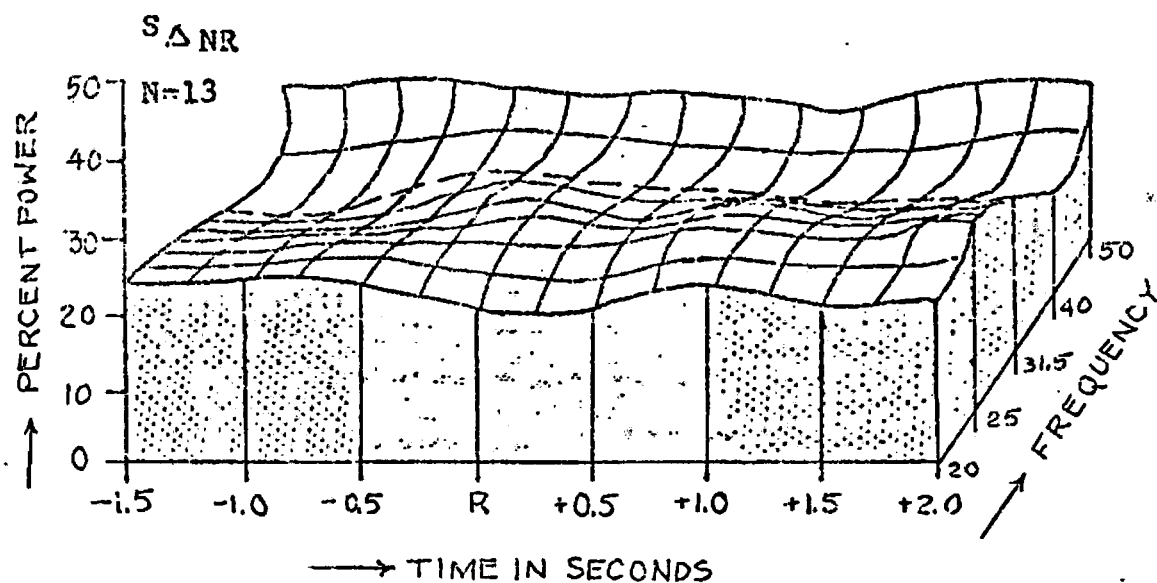
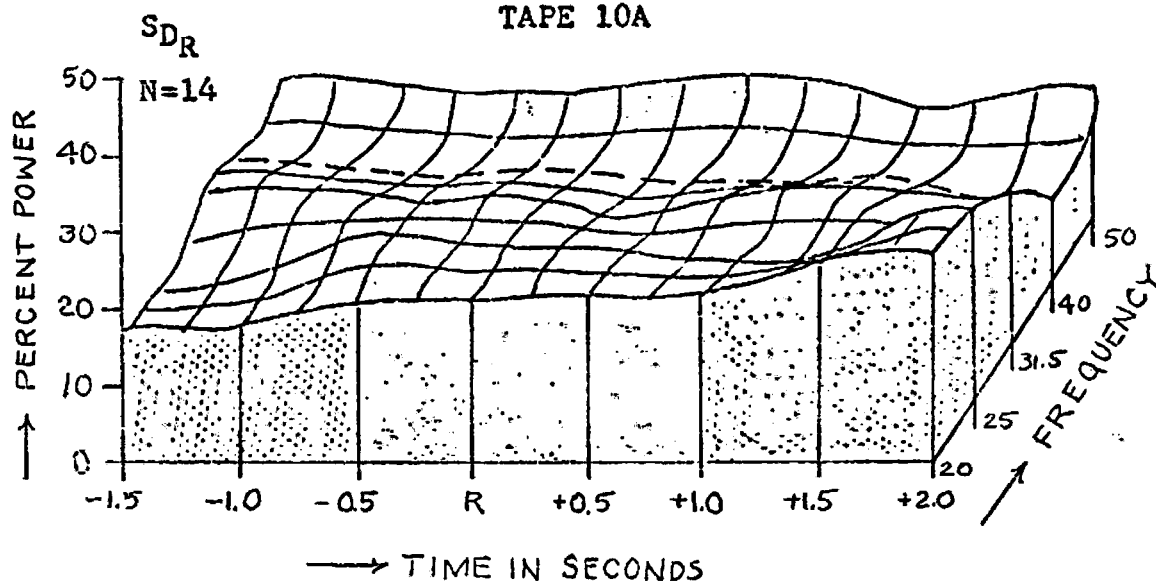
TAPE 18A



Both response and nonresponse conditions are plotted on a response-based time scale in order to facilitate comparisons. The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The 345 Period is lightly shaded.

AUDITORY CORTEX (3-1/2 SEC)

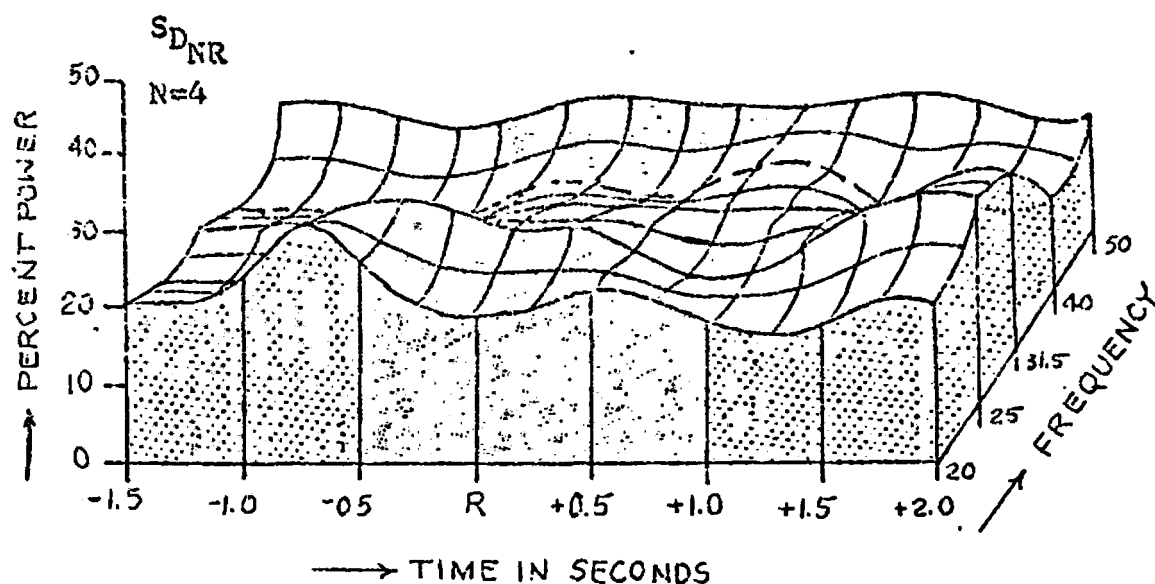
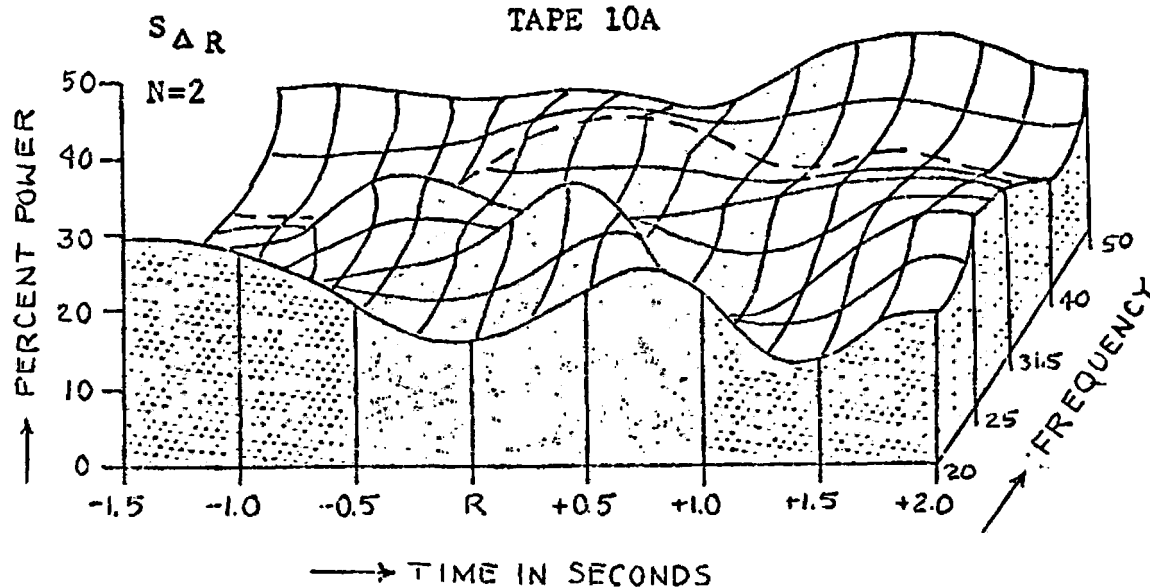
TAPE 10A



Both response and nonresponse conditions are plotted on a response-based time scale in order to facilitate comparisons. The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The 345 Period is lightly shaded.

AUDITORY CORTEX (3-1/2 SEC)

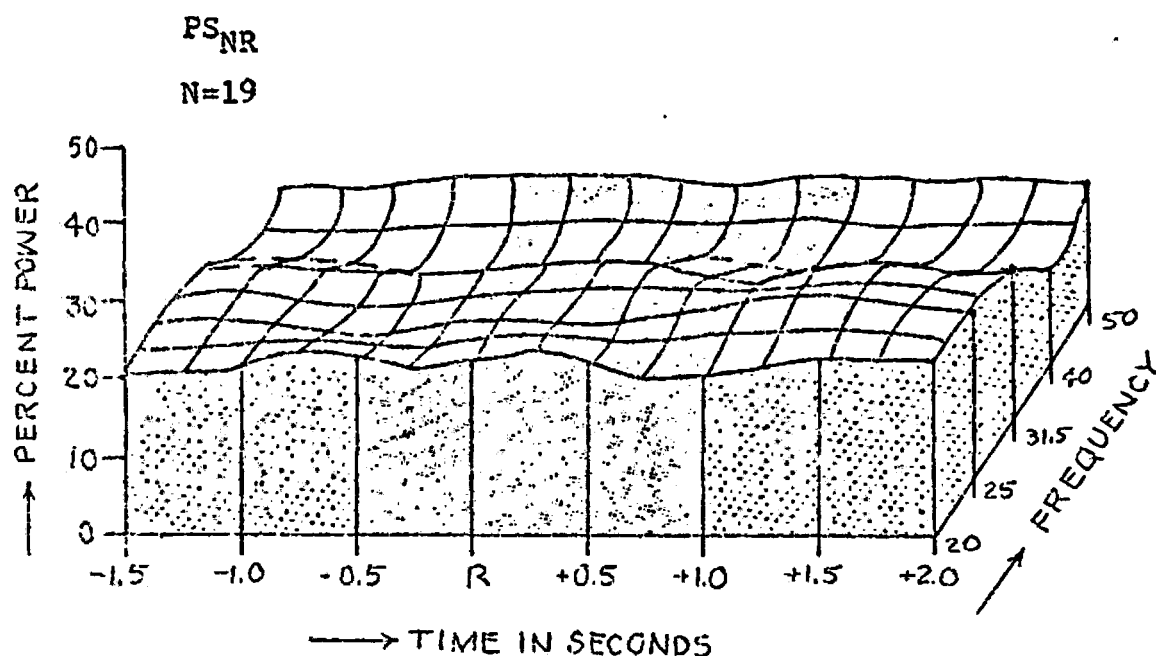
TAPE 10A



Both response and nonresponse conditions are plotted on a response-based time scale in order to facilitate comparisons. The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The 345 Period is lightly shaded.

AUDITORY CORTEX (3-1/2 SEC)

TAPE 10A



Both response and nonresponse conditions are plotted on a response-based time scale in order to facilitate comparisons. The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The 345 Period is lightly shaded.

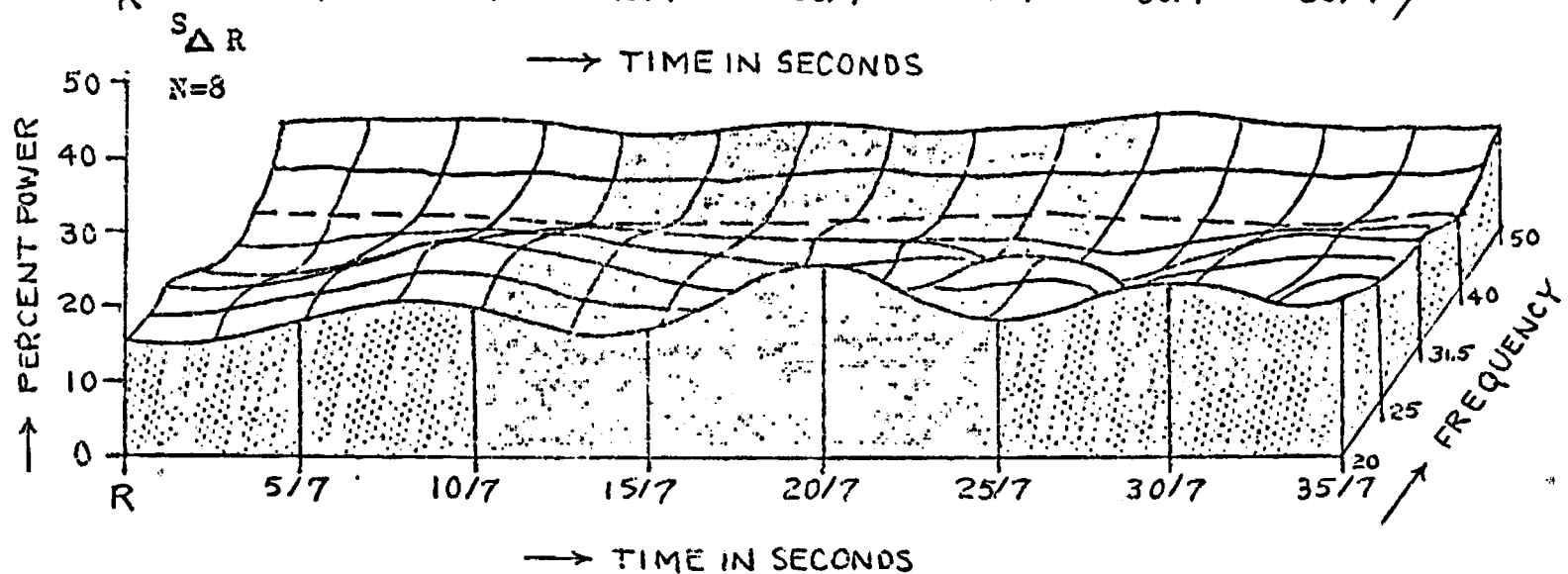
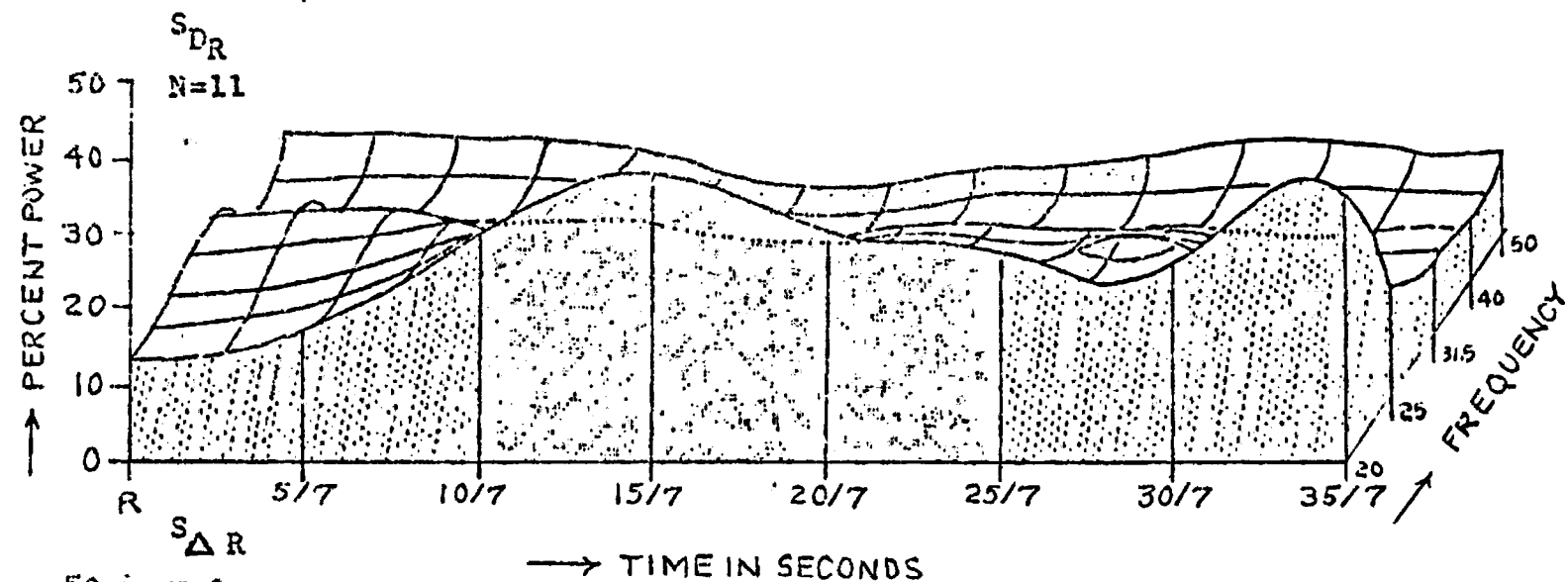
APPENDIX D

AUDITORY I (5 SEC)

THREE DIMENSIONAL PLOTS

OF

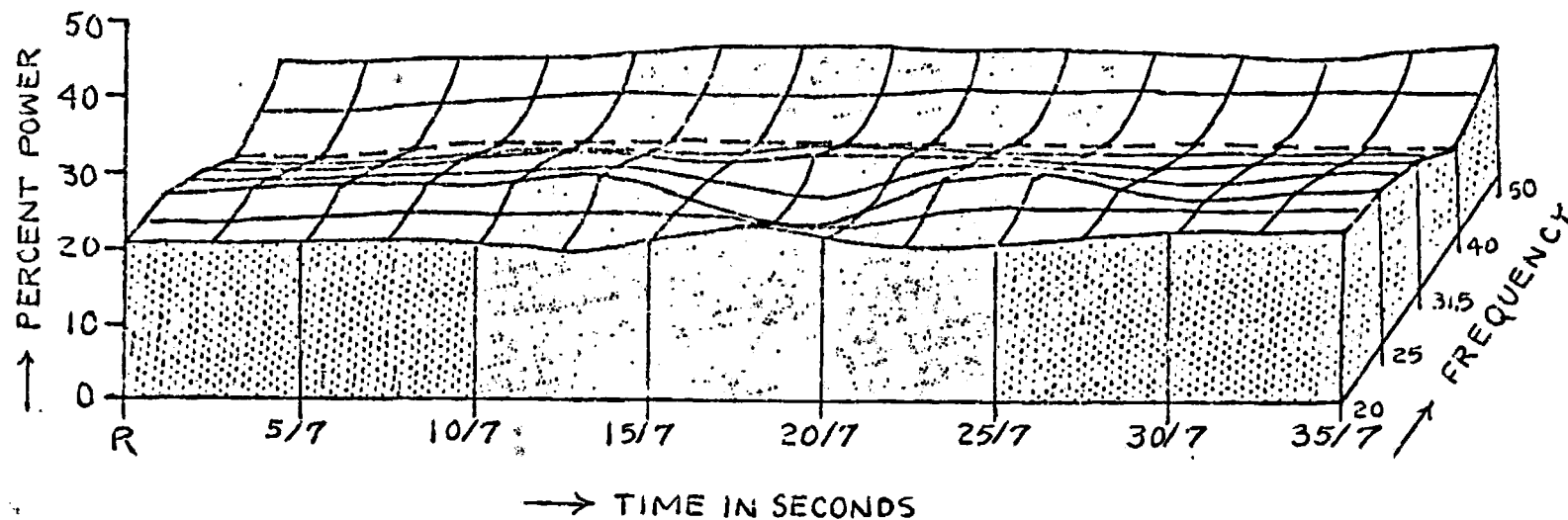
FREQUENCY x TIME x POWER



AUDITORY CORTEX (5 SEC)
TAPE 19A(1)

The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The cde Period is lightly shaded.

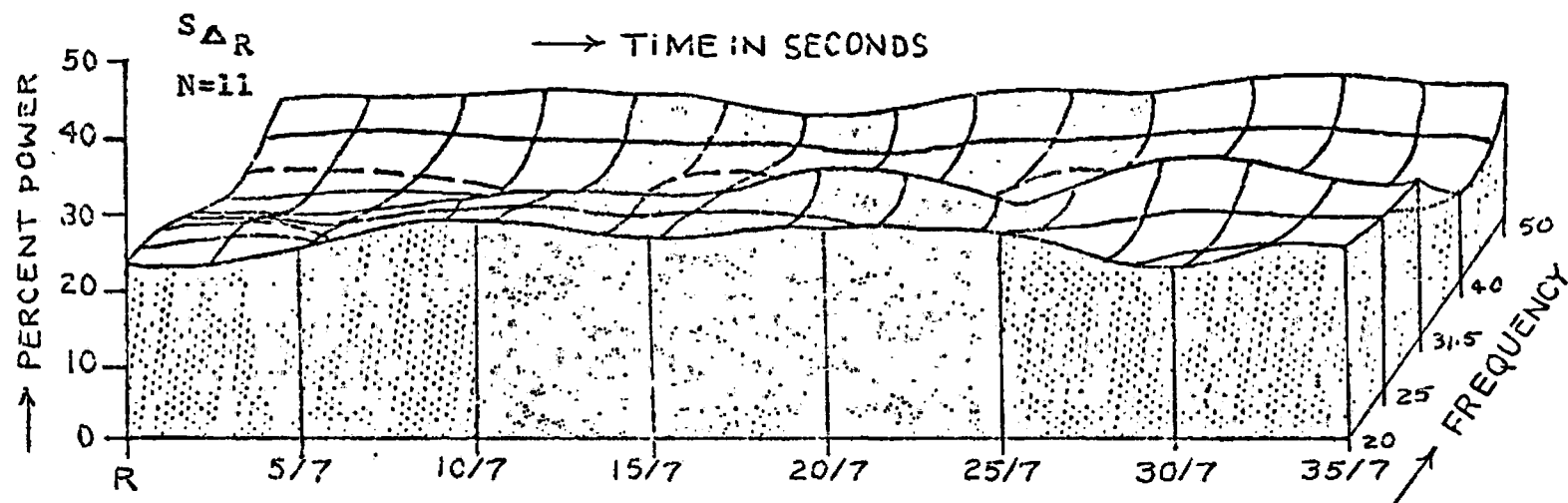
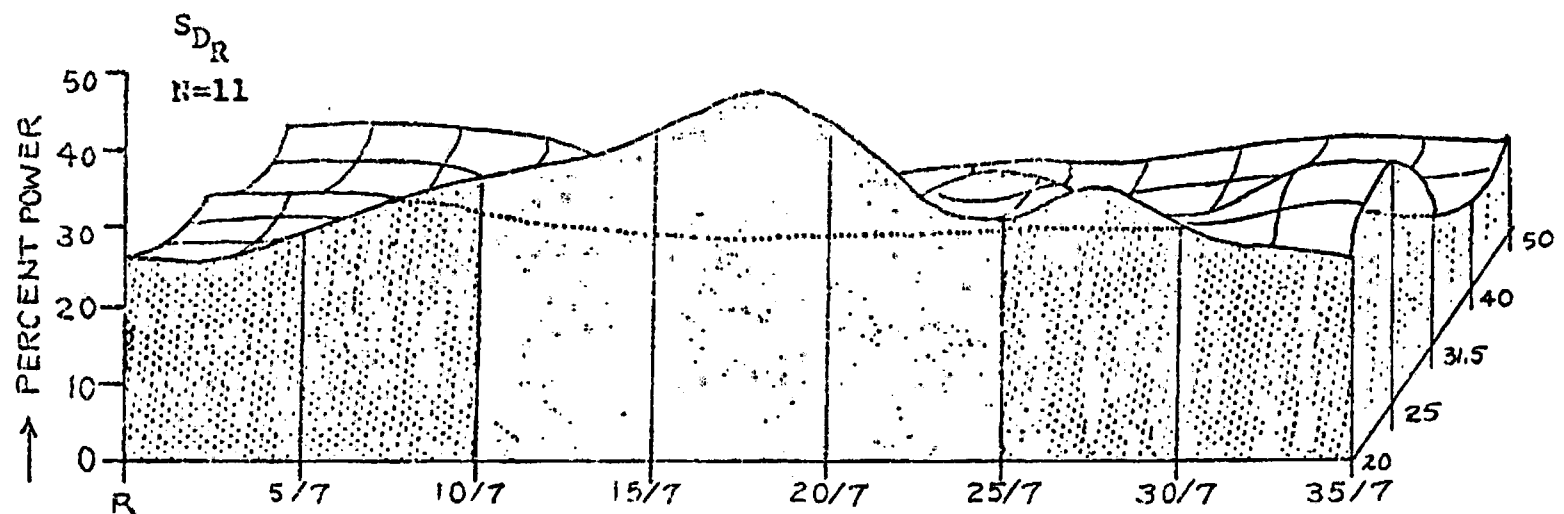
PS_{NR}
N=19



AUDITORY CORTEX (5 SEC)

TAPE 19A(1)

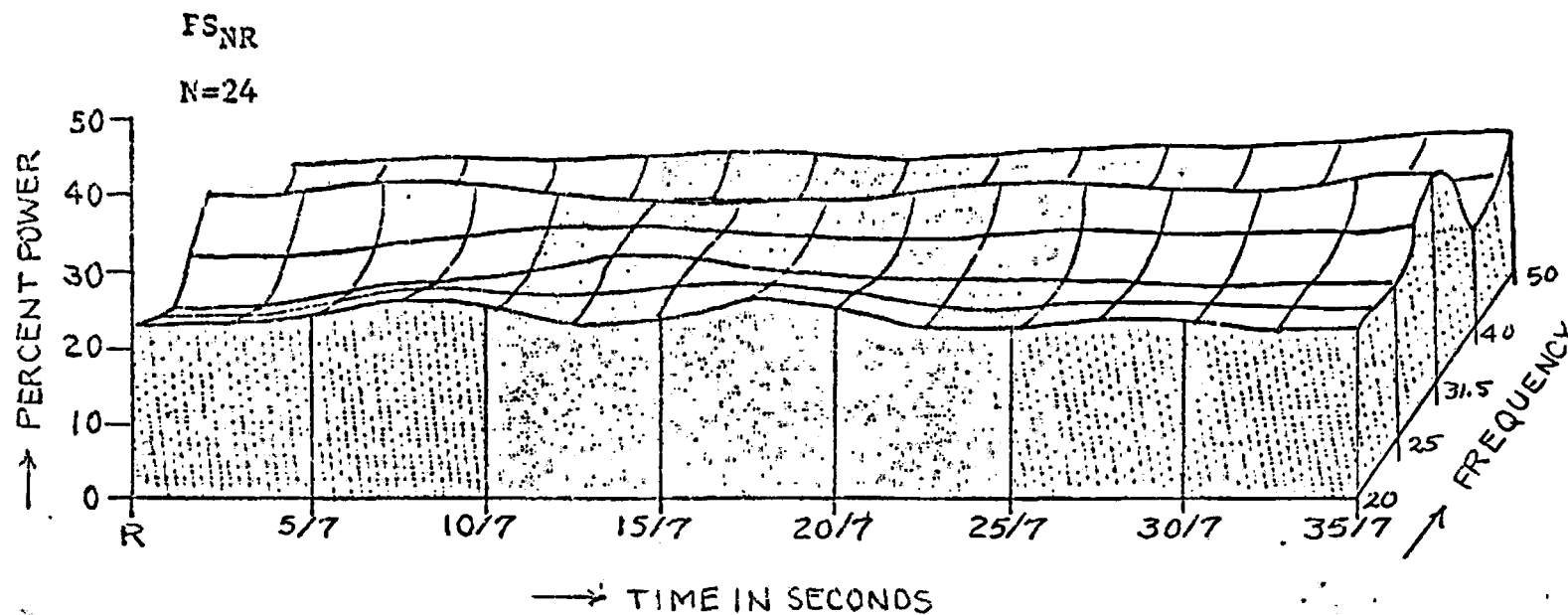
The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The cde Period is lightly shaded.



TIME IN SECONDS
AUDITORY CORTEX (5 SEC)

TAPE 18A

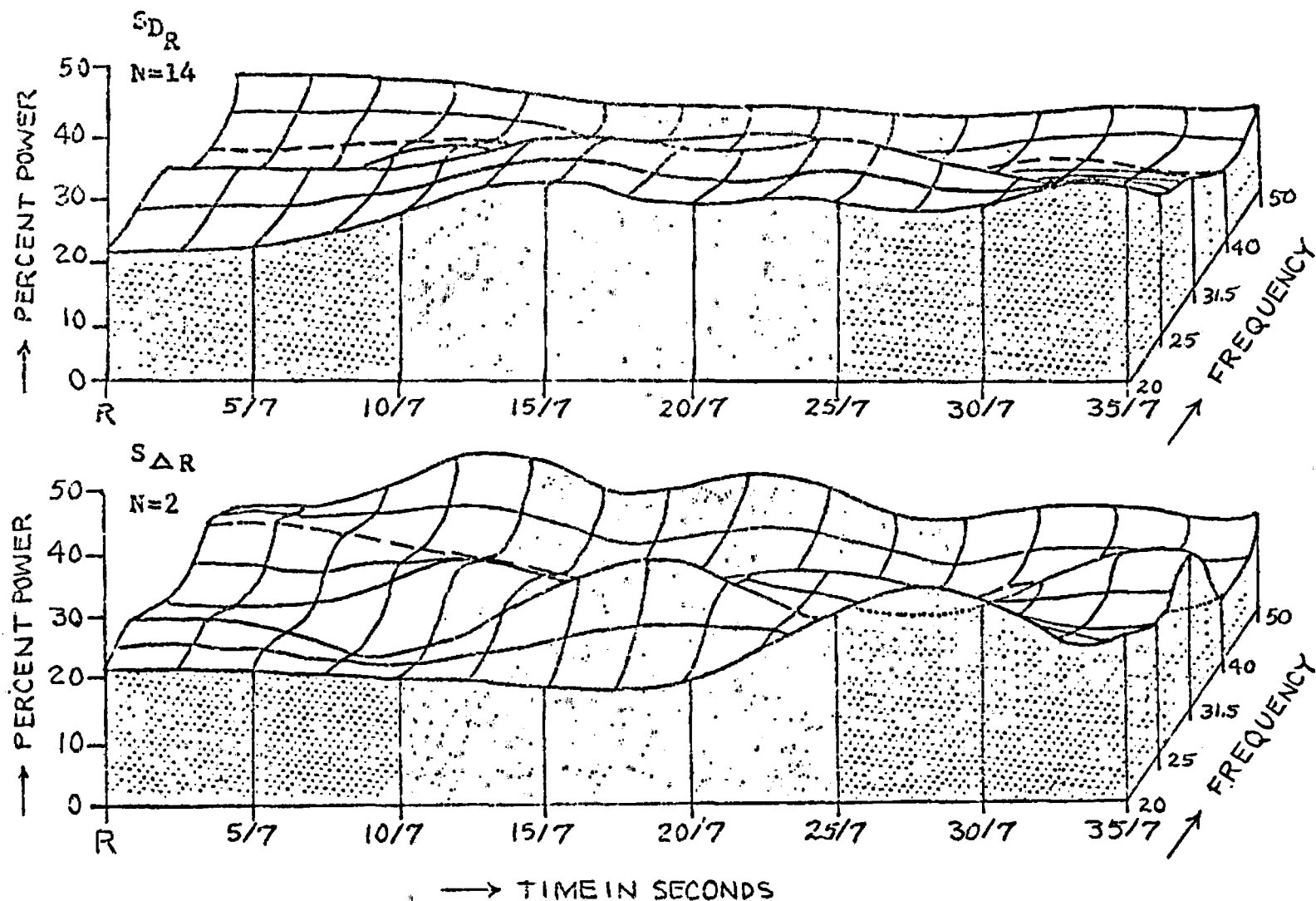
The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The cde Ferid is lightly shaded.



AUDITORY CORTEX (5 SEC)

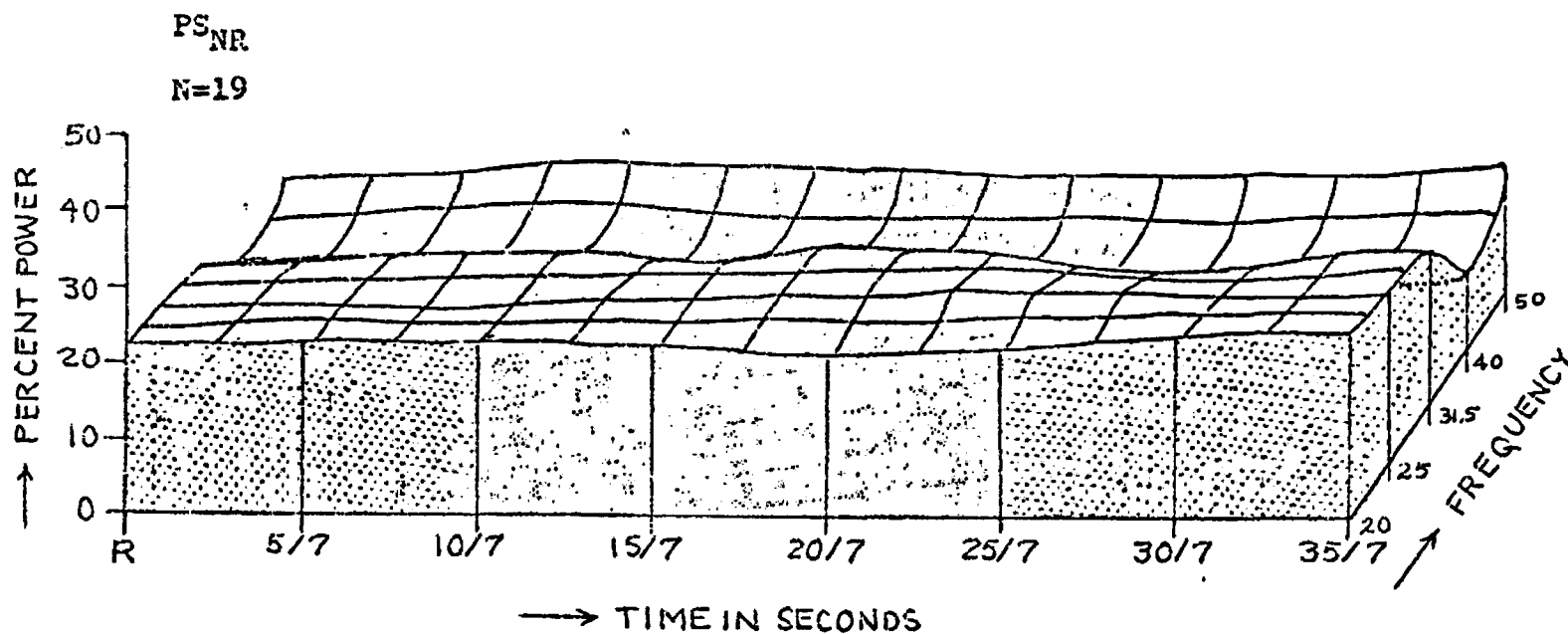
TAPE 18A

The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The cde Period is lightly shaded.



→ TIME IN SECONDS
 AUDITORY CORTEX (5 SEC)
 TAPE 10A

The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The cde Period is lightly shaded.



AUDITORY CORTEX (5 SEC)

TAPE 10A

The 40 c/sec contour is shown as a dashed line when visible in the projection, as a dotted line when obscured by the 20 c/sec contour. The cde Period is lightly shaded.

APPENDIX E

MEAN PROPORTIONAL POWERS

VISUAL I, MOTOR CORTEX, AUDITORY I ($3\frac{1}{2}$ SEC)

AND

AUDITORY I (5 SEC)

MEAN PROPORTIONAL POWERS: VISUAL I

Tape and Period	Condition					
	PSNR	PSR ^a	S _Δ NR	S _Δ R	S _D NR	S _D R
20/BB						
Tape 19A(1)						
126	35.4	32.8	29.6	26.4	39.3	28.0
345	38.5	26.3	29.7	28.7	30.8	25.5
Tape 18A						
126	29.7	32.7	19.8	31.5	32.2	27.5
345	32.2	25.3	38.7	32.9	30.3	26.5
Tape 10A						
126	35.8	-	30.6	21.4	33.9	24.0
345	33.6	-	27.0	14.3	27.6	11.6
25/BB						
Tape 19A(1)						
126	21.2	13.1	20.7	16.4	16.2	14.3
345	22.1	13.4	17.3	17.7	19.1	15.2
Tape 18A						
126	19.1	14.4	16.2	20.1	15.6	17.4
345	18.4	10.2	12.1	17.7	14.8	14.0
Tape 10A						
126	16.6	-	20.4	7.0	19.9	16.8
345	20.4	-	17.6	6.7	18.8	13.6
31.5/BB						
Tape 19A(1)						
126	15.1	13.1	14.2	13.9	18.0	16.2
345	14.8	14.4	15.3	12.1	18.6	16.1
Tape 18A						
126	21.9	9.5	14.1	14.4	18.4	13.5
345	21.2	13.7	9.9	17.1	15.9	20.8
Tape 10A						
126	18.0	-	16.0	12.1	14.8	13.5
345	20.1	-	15.5	14.9	14.3	19.6

MEAN PROPORTIONAL POWERS: VISUAL I
(Continued)

Tape and Period	Condition					
	PS _{NR}	PS _R ^a	S _{ΔNR}	S _{ΔR}	S _{DNR}	S _{DR}
40/BB						
Tape 19A(1)						
126	7.7	6.2	7.3	13.4	10.0	12.6
345	6.5	5.0	8.3	9.8	9.7	13.3
Tape 18A						
126	3.6	5.1	17.5	10.1	11.1	16.7
345	8.2	6.0	12.1	11.7	12.3	22.9
Tape 10A						
126	12.4	-	17.2	18.1	16.6	19.3
345	11.9	-	17.2	26.5	18.8	30.0
50/BB						
Tape 19A(1)						
126	13.6	9.8	19.1	14.5	14.0	17.3
345	13.4	8.3	23.2	13.2	17.3	17.1
Tape 18A						
126	16.3	9.1	18.4	11.9	23.0	22.7
345	17.6	10.1	16.7	9.9	26.0	14.2
Tape 10A						
126	17.5	-	17.7	9.8	16.8	14.1
345	19.5	-	18.6	10.0	19.9	18.4
BB/TP						
Tape 19A(1)						
126	36.2	51.0	37.3	56.7	34.4	45.2
345	38.5	55.0	33.7	48.5	33.8	47.5
Tape 18A						
126	42.0	58.8	46.5	41.6	33.0	33.9
345	40.7	70.8	35.4	46.0	28.3	58.6
Tape 10A						
126	52.8	-	46.0	43.4	35.6	48.6
345	50.6	-	46.0	64.0	35.3	58.9

Note.--All entries in this table are percentage figures; e.g., read 35.4 as 35.4%.

^aNo responses during PS in tape 10A.

MEAN PROPORTIONAL POWERS: MOTOR CORTEX

Tape and Period	Condition					
	PS_{NR}	PS_R^a	$S_{\Delta NR}$	$S_{\Delta R}$	S_{DNR}	S_{DR}
20/BB						
Tape 19A(1)						
126	30.1	29.2	34.2	25.0	36.5	26.0
345	31.5	21.3	31.9	25.9	36.6	24.0
Tape 18A						
126	30.0	25.2	31.8	27.0	36.7	34.8
345	32.9	19.8	35.0	23.1	29.5	24.8
Tape 10A						
126	33.4	-	40.0	23.4	38.7	23.8
345	29.8	-	34.1	27.9	33.4	20.2
25/BB						
Tape 19A(1)						
126	20.7	22.3	23.8	19.7	21.7	21.8
345	23.4	24.3	22.3	23.2	23.9	19.1
Tape 18A						
126	20.8	22.5	21.6	22.3	26.3	20.3
345	19.8	22.9	22.2	25.6	24.5	22.2
Tape 10A						
126	18.1	-	15.6	26.3	19.6	19.7
345	19.2	-	18.0	21.8	16.8	16.6
31.5/BB						
Tape 19A(1)						
126	17.3	16.3	14.1	16.2	15.6	17.7
345	16.0	14.8	14.5	15.5	16.9	19.0
Tape 18A						
126	15.3	15.5	10.7	15.1	13.2	14.1
345	17.5	20.4	11.9	18.4	15.3	17.2
Tape 10A						
126	14.6	-	12.2	18.6	12.5	16.1
345	15.0	-	14.4	16.3	12.8	18.3

MEAN PROPORTIONAL POWERS: MOTOR CORTEX
(Continued)

Tape and Period	Condition					
	PS _{NR}	PS _R ^a	S _{ΔNR}	S _{ΔR}	S _{DNR}	S _{DR}
40/BB						
Tape 19A(1)						
126	10.1	10.1	8.0	11.8	9.6	10.6
345	9.4	9.0	7.6	10.5	9.7	14.5
Tape 18A						
126	8.3	11.3	8.5	11.0	6.3	9.1
345	8.7	11.2	7.6	12.2	6.7	16.6
Tape 10A						
126	8.3	-	8.0	12.6	7.1	11.9
345	8.4	-	9.1	14.5	10.8	15.5
50/BB						
Tape 19A(1)						
126	14.3	9.0	12.9	11.5	12.0	10.6
345	13.6	11.8	13.6	10.9	10.8	11.7
Tape 18A						
126	14.3	11.5	12.6	11.8	11.0	11.0
345	14.2	13.7	12.0	10.9	15.5	13.1
Tape 10A						
126	15.5	-	13.2	12.2	12.0	18.6
345	16.0	-	15.3	16.5	15.2	21.1
BB/TP						
Tape 19A(1)						
126	31.5	53.1	30.0	50.3	32.2	49.0
345	33.8	45.0	32.6	48.1	33.2	50.5
Tape 18A						
126	27.4	50.0	31.8	42.0	29.4	39.5
345	27.9	53.4	29.6	45.6	21.7	42.1
Tape 10A						
126	28.0	-	35.9	44.6	28.8	39.7
345	29.0	-	28.5	42.7	27.8	43.9

Note.--All entries in this table are percentage figures; e.g., read 30.1 as 30.1%.

^aNo responses during PS in tape 10A.

MEAN PROPORTIONAL POWERS: AUDITORY I (3-1/2 SEC)

Tape and Period	Condition				
	PSNR	S _{ΔNR}	S _{ΔR}	S _{ΔNR}	S _{ΔR}
20/BB					
Tape 19A(1)					
126	21.9	24.7	18.0	27.2	24.1
345	21.7	21.8	19.8	24.2	20.7
Tape 18A					
126	24.8	22.5	22.4	24.6	26.2
345	24.8	24.6	24.4	25.7	24.5
Tape 10A					
126	23.1	22.8	23.6	24.9	19.7
345	22.6	21.0	20.7	21.5	20.5
25/BB					
Tape 19A(1)					
126	21.7	20.6	18.4	18.5	21.7
345	21.3	19.2	18.2	21.8	17.3
Tape 18A					
126	20.0	19.8	21.3	23.4	23.5
345	22.7	19.4	20.9	19.4	18.9
Tape 10A					
126	22.0	21.4	14.5	22.0	18.4
345	21.3	22.3	18.8	21.7	20.0
31.5/BB					
Tape 19A(1)					
126	17.1	17.6	16.4	18.1	15.9
345	17.6	17.5	13.8	18.0	18.5
Tape 18A					
126	27.7	16.5	12.0	17.0	13.2
345	24.4	17.2	14.2	18.8	15.5
Tape 10A					
126	20.1	16.3	15.9	15.6	18.9
345	19.7	17.8	15.2	18.2	17.3

MEAN PROPORTIONAL POWERS: AUDITORY I (3-1/2 SEC)
(Continued)

Tape and Period	Condition				
	PS _{NR}	S _{ΔNR}	S _{ΔR}	S _{DNR}	S _{DR}
40/BB					
Tape 19A(1)					
126	11.0	10.9	10.1	12.2	10.3
345	12.0	11.9	10.9	9.9	10.8
Tape 18A					
126	10.4	11.1	9.9	13.2	9.1
345	10.9	9.8	11.0	14.7	9.9
Tape 10A					
126	11.9	11.2	12.1	9.0	14.8
345	10.7	12.7	18.0	14.2	14.3
50/BB					
Tape 19A(1)					
126	15.6	16.6	14.1	15.5	13.5
345	16.6	18.7	15.0	15.3	14.2
Tape 18A					
126	15.4	15.2	14.1	16.2	13.2
345	15.1	15.4	13.5	18.9	15.3
Tape 10A					
126	15.3	19.1	19.6	15.5	17.2
345	16.5	16.6	17.0	17.1	18.6
BB/TP					
Tape 19A(1)					
126	50.4	46.8	55.1	46.6	56.6
345	49.0	43.7	53.8	40.2	52.5
Tape 18A					
126	54.2	50.6	43.0	41.9	40.6
345	53.9	41.1	46.4	46.6	48.3
Tape 10A					
126	59.7	49.0	46.0	39.1	54.3
345	55.7	48.0	55.3	39.9	52.4

Note.--All entries in this table are percentage figures;
e.g., read 21.9 as 21.9%.

MEAN PROPORTIONAL POWERS: AUDITORY I (5 SEC)

Tape and Period	Condition		
	PSNR	S _{AR}	S _{DR}
20/BB			
Tape 19A(1)			
abf	21.9	18.6	19.8
cde	21.8	19.7	33.9
Tape 18A			
abf	25.0	25.8	32.2
cde	24.6	27.5	40.2
Tape 10A			
abf	23.2	24.3	23.0
cde	22.6	19.1	29.1
25/BB			
Tape 19A(1)			
abf	22.0	16.8	19.0
cde	21.9	15.8	19.9
Tape 18A			
abf	19.8	23.4	23.7
cde	23.6	21.8	25.8
Tape 10A			
abf	21.3	17.6	21.7
cde	22.5	23.0	23.0
31.5/BB			
Tape 19A(1)			
abf	12.1	12.1	16.1
cde	13.0	12.4	13.4
Tape 18A			
abf	26.5	17.5	15.7
cde	25.9	17.6	14.7
Tape 10A			
abf	19.3	13.9	16.9
cde	20.4	16.9	16.4

MEAN PROPORTIONAL POWERS: AUDITORY I (5 SEC)
(Continued)

Tape and Period	Condition		
	PS_{NR}	$S_{\Delta R}$	S_{DR}
40/BB			
Tape 19A(1)			
abf	11.3	10.4	8.3
cde	11.7	8.8	6.9
Tape 18A			
abf	11.0	10.3	9.3
cde	11.1	9.9	7.2
Tape 10A			
abf	11.3	13.3	11.9
cde	10.9	9.3	9.9
50/BB			
Tape 19A(1)			
abf	17.0	14.7	12.0
cde	16.8	13.2	8.0
Tape 18A			
abf	15.7	15.3	11.6
cde	16.2	13.1	7.2
Tape 10A			
abf	15.8	15.6	14.2
cde	15.7	17.6	11.1
BE/TP			
Tape 19A(1)			
abf	49.5	52.2	50.1
cde	50.2	51.6	47.0
Tape 18A			
abf	54.0	45.8	43.0
cde	54.0	39.1	44.1
Tape 10A			
abf	58.7	57.3	49.7
cde	56.6	54.9	47.3

Note.--All entries in this table are percentage figures;
e.g., read 21.9 as 21.9%.

APPENDIX F .

MEAN ABSOLUTE POWERS

VISUAL I, MOTOR CORTEX, AUDITORY I ($3\frac{1}{2}$ SEC)

AND

AUDITORY I (5 SEC)

MEAN ABSOLUTE POWERS: VISUAL I

Frequency and Period	Condition					
	PS _{NR}	PS _R ^a	S _{ΔNR}	S _{ΔR}	S _{DNR}	S _{DR}
Tape 19A(1) ^b						
20 c/sec						
126	17.4	22.0	16.3	30.4	30.8	32.0
345	19.0	16.9	13.2	31.4	23.2	34.2
25 c/sec						
126	10.4	8.8	11.4	18.9	12.7	16.4
345	10.9	8.6	7.7	19.4	14.4	20.4
31.5 c/sec						
126	7.4	8.9	7.8	16.0	14.1	18.5
345	7.3	9.6	6.8	13.2	14.0	21.6
40 c/sec						
126	3.8	4.3	4.0	15.4	7.8	14.4
345	3.2	3.3	3.7	10.7	7.3	17.8
50 c/sec						
126	6.7	6.7	10.5	16.7	11.0	19.8
345	6.6	5.5	10.3	14.5	13.0	22.9
Broad Band						
126	49.1	67.8	55.1	115.1	78.3	114.3
345	49.3	65.5	44.4	109.5	75.3	134.2
Total						
126	135.6	132.8	147.6	202.8	227.4	252.8
345	128.1	119.2	131.6	225.7	222.9	282.5
Tape 18A						
20 c/sec						
126	13.8	25.1	14.3	34.0	24.6	23.7
345	13.7	18.6	23.4	38.4	21.7	57.3
25 c/sec						
126	8.9	11.1	11.7	21.7	11.9	15.0
345	7.8	7.5	7.3	20.7	10.6	30.4
31.5 c/sec						
126	10.2	7.1	10.2	15.6	14.1	11.6
345	9.0	10.1	6.0	20.0	11.4	45.1
40 c/sec						
126	4.0	3.8	12.6	10.9	8.5	14.4
345	3.5	4.4	7.3	13.6	8.8	49.5
50 c/sec						
126	7.6	6.8	13.3	12.9	17.6	19.6
345	7.5	7.5	10.1	11.6	18.6	30.8

MEAN ABSOLUTE POWERS: VISUAL I
(Continued)

Frequency and Period	Condition					
	PS _{NR}	PS _R ^a	S _{ΔNR}	S _{ΔR}	S _{DNR}	S _{DR}
Broad Band						
126	46.5	75.5	72.1	108.0	76.5	86.2
345	42.5	73.8	60.4	116.7	71.5	216.5
Total						
126	110.7	128.5	155.1	259.4	232.0	254.1
345	104.5	104.3	170.5	253.6	252.5	359.6
Tape 10A						
20 c/sec						
126	12.1	-	23.1	17.3	34.9	27.5
345	10.7	-	22.6	16.6	25.3	15.1
25 c/sec						
126	5.6	-	15.4	5.7	20.5	19.3
345	6.5	-	14.7	7.8	17.2	17.7
31.5 c/sec						
126	6.1	-	12.1	9.8	15.2	20.0
345	6.4	-	13.0	17.3	13.1	25.4
40 c/sec						
126	4.2	-	13.0	14.7	17.1	22.1
345	3.8	-	14.4	30.8	17.2	39.0
50 c/sec						
126	5.9	-	13.4	7.9	17.3	16.2
345	6.2	-	15.6	11.6	18.2	23.9
Broad Band						
126	33.8	-	75.5	81.0	102.8	114.7
345	31.8	-	83.7	116.3	91.5	129.9
Total						
126	64.0	-	164.0	186.8	288.4	236.2
345	62.9	-	181.8	181.6	259.1	220.7

^aNo responses during PS in tape 10A.

^bComputer analysis of PS_R was run several months after the other conditions and input gains were adjusted to a maximum value in order to achieve the most accurate analysis possible with the small values occasioned both by the small number of trials averaged and by the low values characteristic of PS.

MEAN ABSOLUTE POWERS: MOTOR CORTEX

Frequency and Period	Condition					
	PS _{NR}	PS _R ^a	S _{ΔNR}	S _{ΔR}	S _{DNR}	S _{DR}
Tape 19A(1)						
20 c/sec						
126	21.4	39.0	26.0	33.6	33.3	36.9
345	24.1	21.3	22.2	37.0	39.8	39.2
25 c/sec						
126	14.7	29.8	18.1	26.4	19.8	31.0
345	17.9	24.3	15.5	33.1	26.0	31.2
31.5 c/sec						
126	12.3	21.8	10.7	21.7	14.2	25.2
345	12.2	14.8	10.1	22.2	18.4	31.0
40 c/sec						
126	7.2	13.5	6.1	15.9	8.8	15.1
345	7.2	9.0	5.3	15.0	10.6	23.8
50 c/sec						
126	10.2	12.0	9.8	15.4	11.0	15.1
345	10.4	11.8	9.5	15.6	11.8	19.1
Broad Band						
126	71.1	133.5	76.0	134.3	91.3	142.1
345	76.4	100.0	69.6	142.9	108.8	163.6
Total						
126	225.8	251.5	253.3	267.0	283.9	289.9
345	225.8	222.0	213.4	297.0	327.5	323.7

Tape 18A

20 c/sec						
126	20.6	24.8	26.2	29.2	33.4	38.4
345	22.0	18.9	31.9	28.6	17.1	27.0
25 c/sec						
126	14.3	22.1	17.8	24.1	23.9	22.4
345	13.2	21.9	20.3	31.7	14.2	24.1
31.5 c/sec						
126	10.5	15.2	8.8	16.4	12.0	15.6
345	11.7	19.5	10.8	22.8	8.9	18.7
40 c/sec						
126	5.7	11.1	7.0	11.9	5.7	10.0
345	5.8	10.7	6.9	15.1	3.9	18.1
50 c/sec						
126	9.8	11.3	10.4	12.8	10.0	12.2
345	9.5	13.1	10.9	13.5	9.0	14.3

MEAN ABSOLUTE POWERS: MOTOR CORTEX
(Continued)

Frequency and Period	Condition					
	PS _{NR}	PS _R ^a	S _{ΔNR}	S _{ΔR}	S _{DNR}	S _{DR}
Broad Band						
126	68.6	98.3	82.5	108.3	91.0	110.4
345	66.8	95.6	91.1	123.9	58.0	103.8
Total						
126	250.5	196.5	259.2	258.0	309.0	279.5
345	239.3	178.9	307.9	272.0	267.0	258.3
Tape 10A						
20 c/sec						
126	22.0	-	35.4	23.7	34.9	38.9
345	19.9	-	27.5	21.8	29.0	35.2
25 c/sec						
126	11.9	-	13.8	26.6	17.7	32.3
345	12.8	-	14.5	17.0	14.6	28.9
31.5 c/sec						
126	9.6	-	10.8	18.8	11.3	26.4
345	10.0	-	11.6	12.7	11.1	31.9
40 c/sec						
126	5.5	-	7.1	12.8	6.4	19.5
345	5.6	-	7.3	11.3	9.4	26.9
50 c/sec						
126	10.2	-	11.7	12.4	10.8	30.5
345	10.7	-	12.3	12.9	13.2	36.8
Broad Band						
126	65.9	-	88.6	101.3	90.1	163.7
345	66.7	-	80.6	78.1	86.7	174.0
Total						
126	235.0	-	246.8	227.3	313.2	412.3
345	229.9	-	282.5	183.0	312.1	396.1

^aNo responses during PS in tape 10A.

MEAN ABSOLUTE POWERS: AUDITORY I (3-1/2 SEC)

Frequency and Period	Condition				
	$P_{S_{NR}}$	$S_{\Delta NR}$	$S_{\Delta R}$	$S_{D_{NR}}$	S_{D_R}
Tape 19A(1)					
20 c/sec					
126	19.1	22.7	20.2	24.3	28.6
345	18.5	16.9	22.1	21.3	24.8
25 c/sec					
126	18.9	18.9	20.7	16.6	25.8
345	18.1	14.9	20.3	19.2	20.7
31.5 c/sec					
126	14.9	16.2	18.4	16.2	18.9
345	15.0	13.6	15.4	15.8	22.2
40 c/sec					
126	9.6	10.0	11.4	10.9	12.3
345	10.2	9.2	12.2	8.7	12.9
50 c/sec					
126	13.6	15.2	15.9	13.9	16.1
345	14.1	14.5	16.7	13.5	17.0
Broad Band					
126	87.1	91.8	112.4	89.5	118.9
345	85.1	77.5	111.7	88.0	120.0
Total					
126	172.8	196.0	203.9	192.0	210.0
345	173.6	177.4	207.7	218.8	228.6

Tape 18A

20 c/sec					
126	18.2	17.5	18.3	18.6	29.7
345	19.3	18.0	21.7	16.6	23.5
25 c/sec					
126	14.7	15.4	17.4	17.7	26.7
345	17.7	14.2	18.6	12.5	18.1
31.5 c/sec					
126	20.3	12.8	9.8	12.8	15.0
345	19.0	12.6	12.6	12.1	14.9
40 c/sec					
126	7.6	8.6	8.1	10.0	10.3
345	8.5	7.2	9.8	9.5	9.5
50 c/sec					
126	11.3	11.8	11.5	12.2	15.0
345	11.8	11.3	12.0	12.2	14.7

MEAN ABSOLUTE POWERS: AUDITORY I (3-1/2 SEC)
(Continued)

Frequency and Period	Condition				
	PS_{NR}	$S_{\Delta NR}$	$S_{\Delta R}$	S_{DNR}	S_{DR}
Broad Band					
126	73.4	77.8	81.6	75.5	113.5
345	77.9	73.3	88.9	64.5	96.0
Total					
126	135.4	153.7	189.8	180.0	279.4
345	144.4	178.3	191.7	138.5	198.6

Tape 10A

20 c/sec					
126	19.0	16.5	18.4	19.6	18.5
345	17.5	15.7	16.9	16.6	18.7
25 c/sec					
126	18.1	15.5	11.3	17.3	17.3
345	16.5	16.7	15.4	16.8	18.2
31.5 c/sec					
126	16.5	11.8	12.4	12.3	17.8
345	15.3	13.3	12.4	14.1	15.8
40 c/sec					
126	9.8	8.1	9.4	7.1	14.0
345	8.3	9.5	14.7	11.0	13.0
50 c/sec					
126	12.6	13.8	15.3	12.2	16.2
345	12.8	12.4	13.9	13.2	17.0
Broad Band					
126	82.1	72.3	78.0	78.8	94.1
345	77.5	74.9	81.8	77.3	91.2
Total					
126	137.5	147.5	169.6	201.5	173.4
345	139.1	156.1	147.8	193.9	174.2

MEAN ABSOLUTE POWERS: AUDITORY I (5 SEC)

Frequency and Period	Condition		
	PSNR	$S_{\Delta R}$	S_{D_R}
Tape 19A(1)			
20 c/sec			
abf	26.1	28.5	40.0
cde	26.8	33.6	100.7
25 c/sec			
abf	26.2	25.8	33.4
cde	26.9	27.0	59.2
31.5 c/sec			
abf	14.4	18.5	32.5
cde	16.0	21.2	39.9
40 c/sec			
abf	13.4	15.9	16.7
cde	14.4	15.0	20.4
50 c/sec			
abf	20.2	22.5	24.3
cde	20.6	22.5	23.7
Broad Band			
abf	119.1	153.4	202.4
cde	122.8	170.9	296.8
Total			
abf	240.6	294.0	404.2
cde	244.5	331.5	631.1
Tape 18A			
20 c/sec			
abf	26.2	30.5	57.3
cde	25.5	36.4	109.1
25 c/sec			
abf	20.8	27.6	42.0
cde	24.5	28.9	70.1
31.5 c/sec			
abf	27.8	20.6	27.9
cde	26.9	23.4	39.9
40 c/sec			
abf	11.5	12.2	16.5
cde	11.5	13.1	19.5
50 c/sec			
abf	16.5	18.0	20.6
cde	16.8	17.4	19.7

MEAN ABSOLUTE POWERS: AUDITORY I (5 SEC)
(Continued)

Frequency and Period	Condition		
	PS_{NR}	$S_{\Delta R}$	S_{DR}
Broad Band			
abf	104.8	118.0	177.2
cde	103.8	132.6	271.6
Total			
abf	194.1	257.7	412.4
cde	192.1	338.7	616.3

Tape 10A

20 c/sec			
abf	26.3	31.5	35.8
cde	25.8	22.5	53.1
25 c/sec			
abf	24.1	22.9	33.8
cde	25.7	27.1	41.9
31.5 c/sec			
abf	21.8	18.0	26.3
cde	23.3	19.9	29.9
40 c/sec			
abf	12.8	17.3	18.5
cde	12.4	11.0	18.0
50 c/sec			
abf	17.9	20.3	22.1
cde	17.9	20.7	20.2
Broad Band			
abf	113.2	129.8	155.6
cde	114.0	117.9	182.5
Total			
abf	193.0	226.5	312.8
cde	201.4	214.6	385.7

APPENDIX G

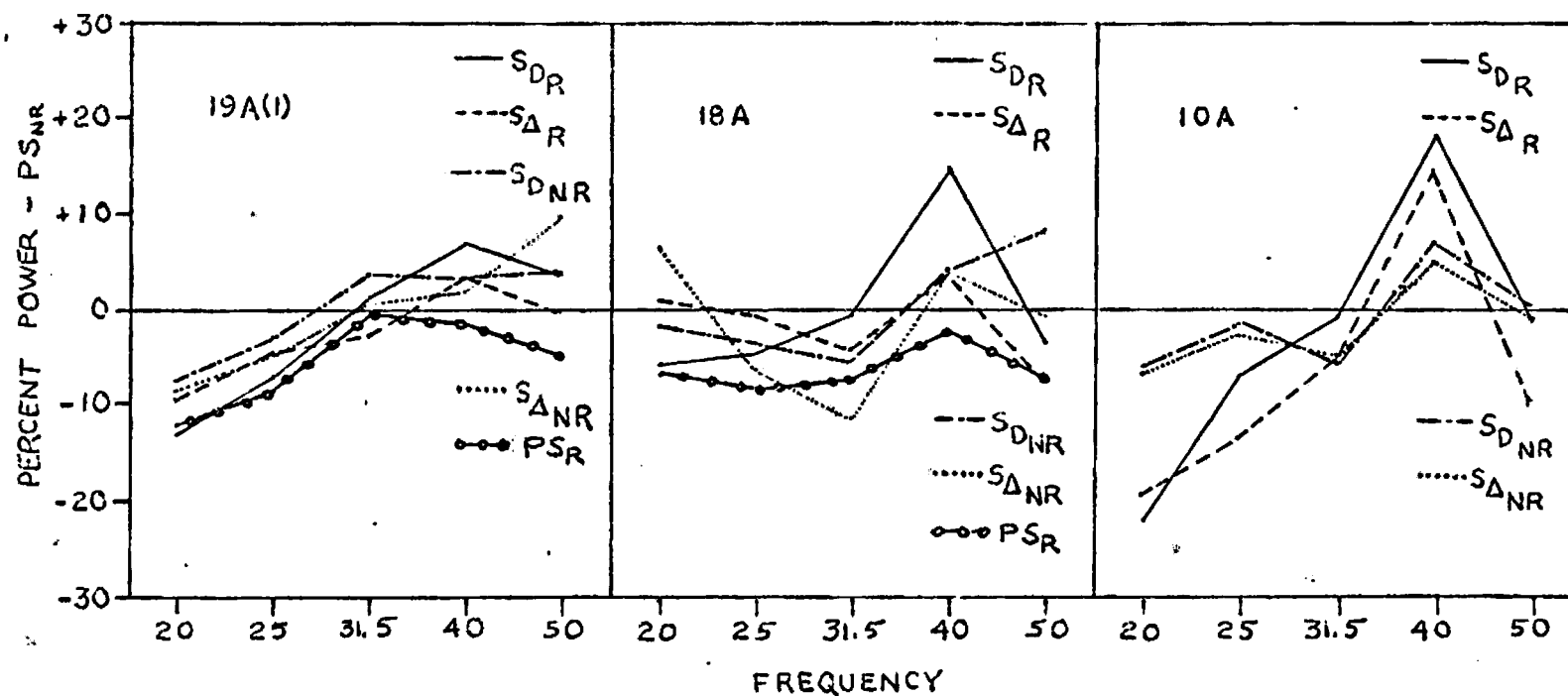
SPECTROGRAMS BASED UPON ALGEBRAIC VARIATIONS
FROM PRESTIMULUS LEVEL

VISUAL I, MOTOR CORTEX, AUDITORY I ($3\frac{1}{2}$ SEC)

AND

AUDITORY I (5 SEC)

VISUAL AREA - 345 PERIOD

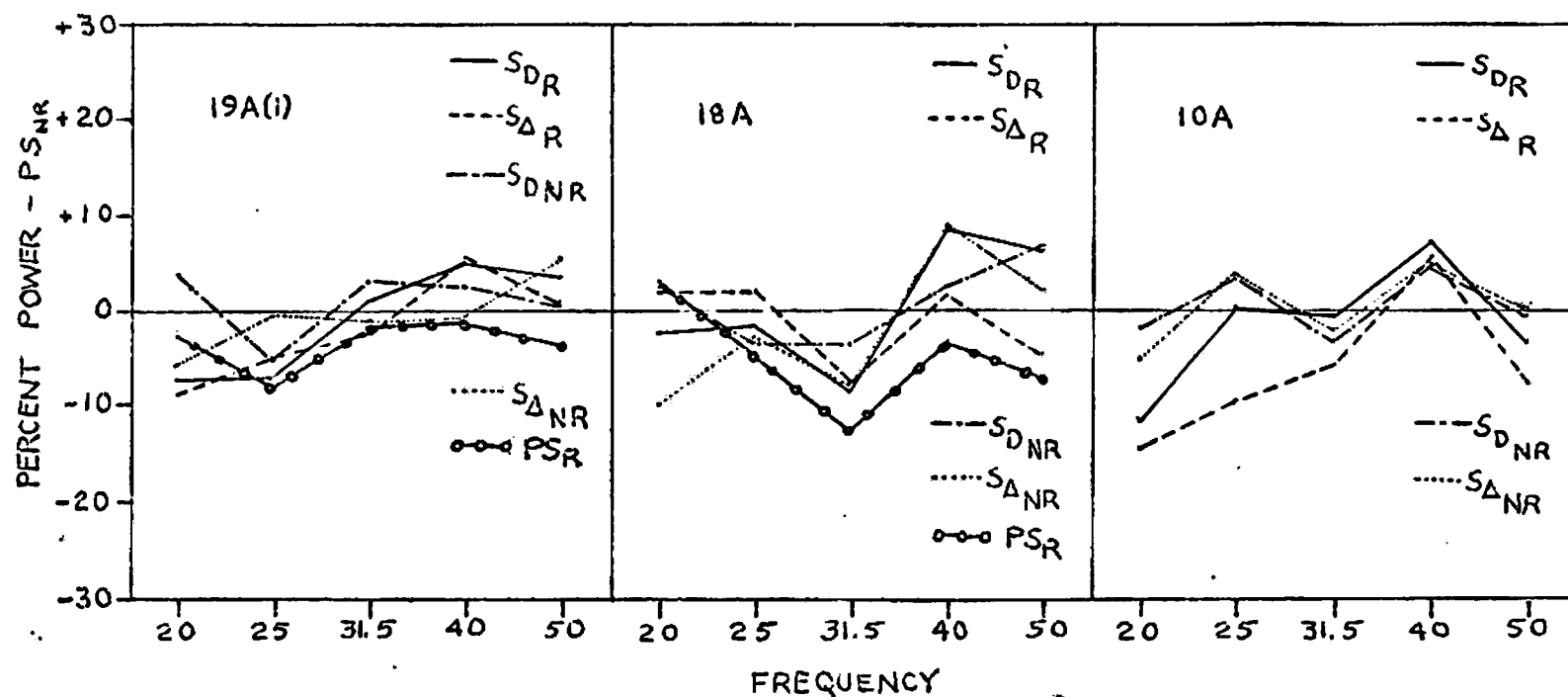


SPECTROGRAMS

BASED UPON ALGEBRAIC VARIATIONS FROM PRESTIMULUS LEVEL

Values plotted were computed from mean proportional powers shown in Appendix E. Normalization was by broad band power.

VISUAL AREA - 126 PERIOD

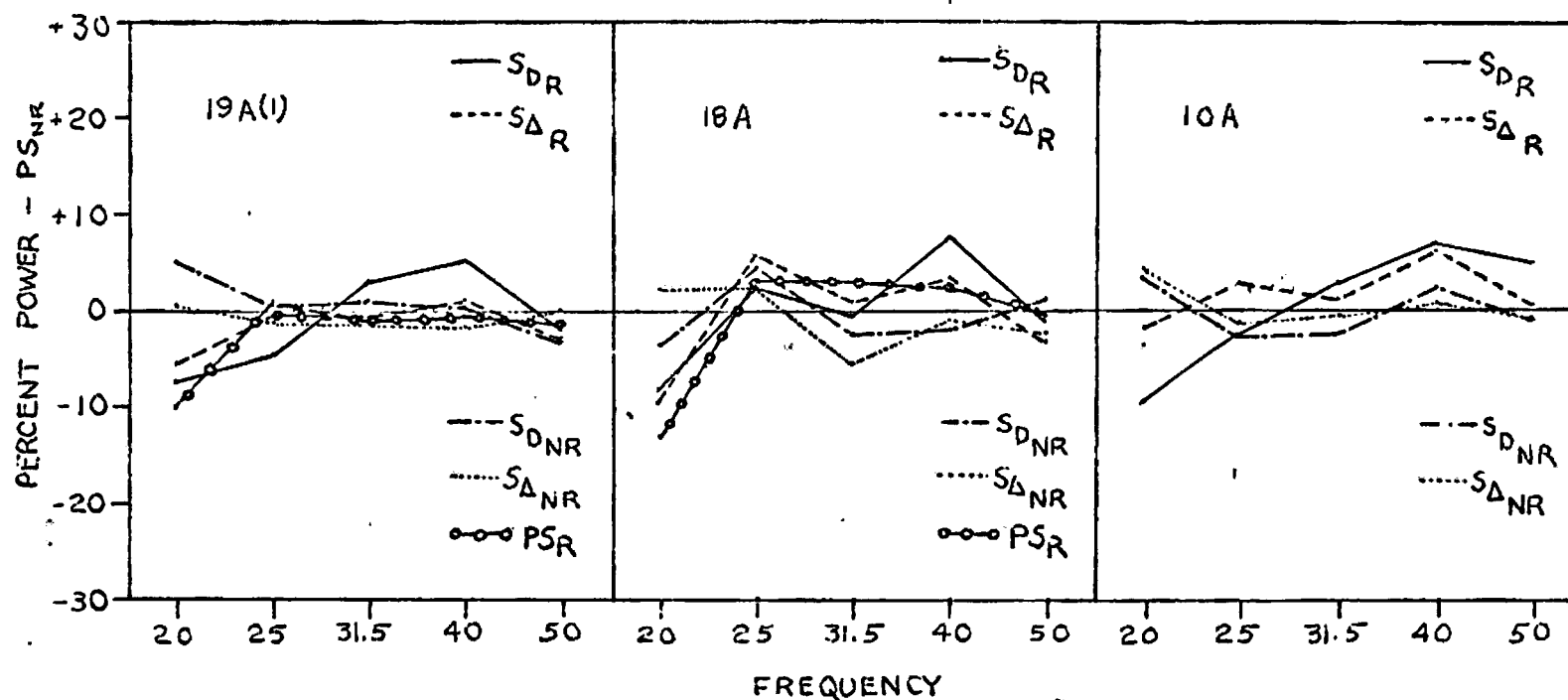


SPECTROGRAMS

BASED UPON ALGEBRAIC VARIATIONS FROM PRESTIMULUS LEVEL

Values plotted were computed from mean proportional powers shown in Appendix E. Normalization was by broad band power.

MOTOR AREA - 345 PERIOD

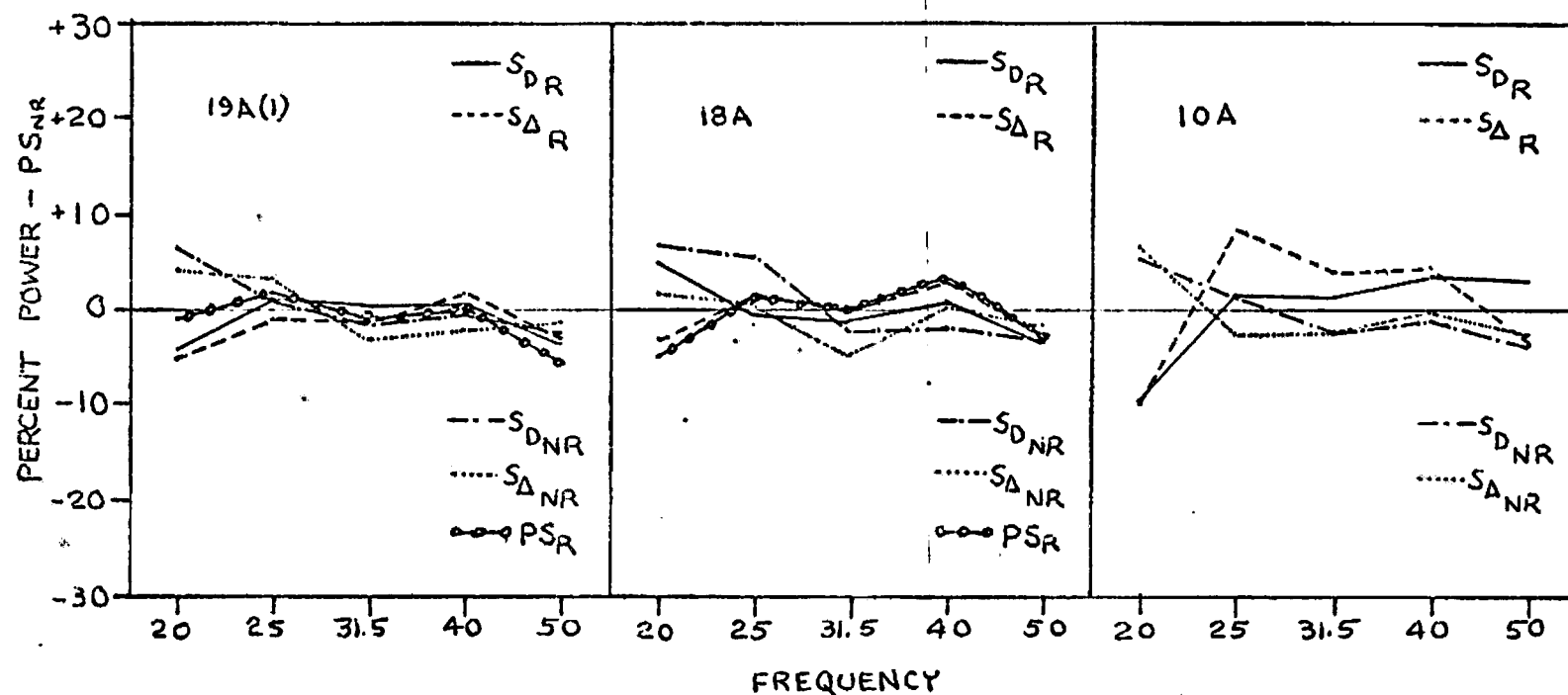


SPECTROGRAMS

BASED UPON ALGEBRAIC VARIATIONS FROM PRESTIMULUS LEVEL

Values plotted were computed from mean proportional powers shown in Appendix E. Normalization was by broad band.

MOTOR AREA - 126 PERIOD



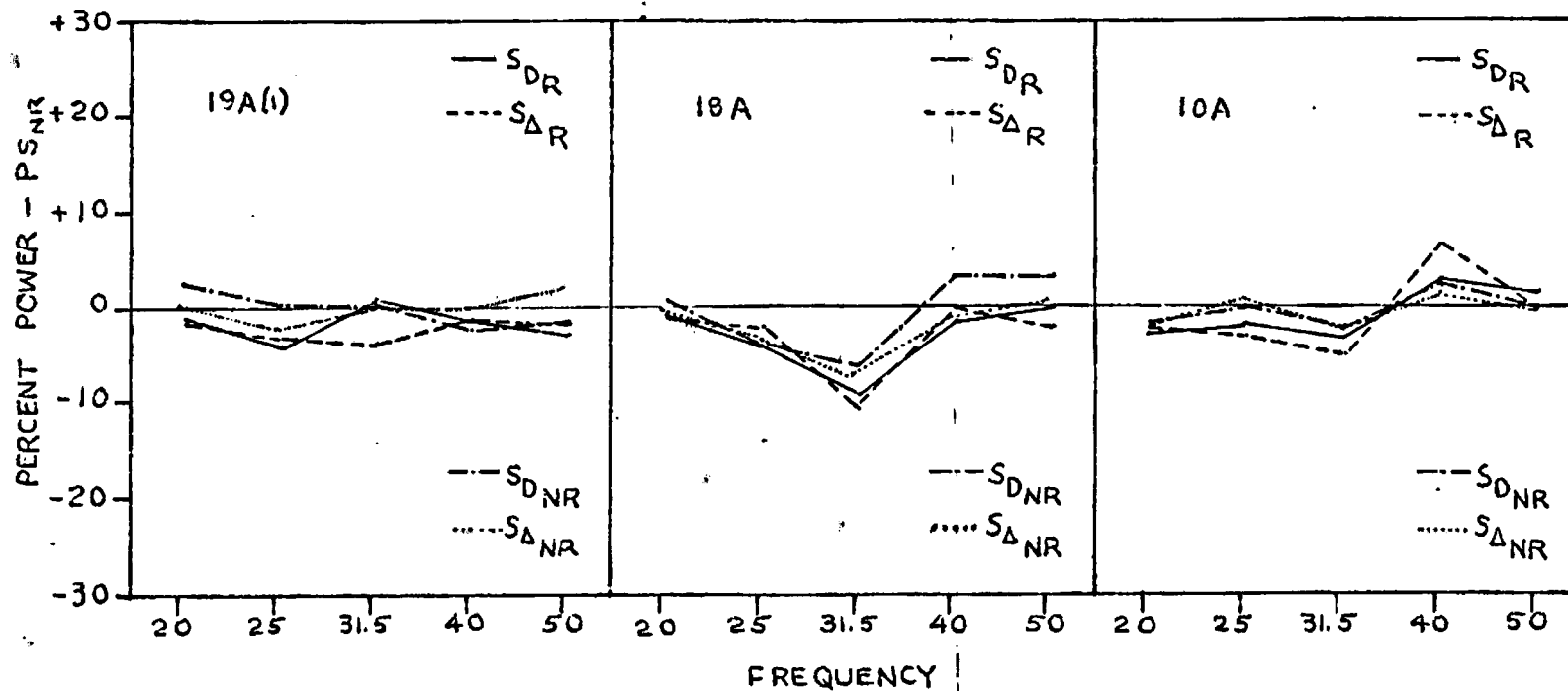
SPECTROGRAMS

BASED UPON ALGEBRAIC VARIATIONS FROM PRESTIMULUS LEVEL

Values plotted were computed from mean proportional powers shown in Appendix E. Normalization was by broad band power.

AUDITORY AREA - 345 PERIOD

3 1/2 SEC



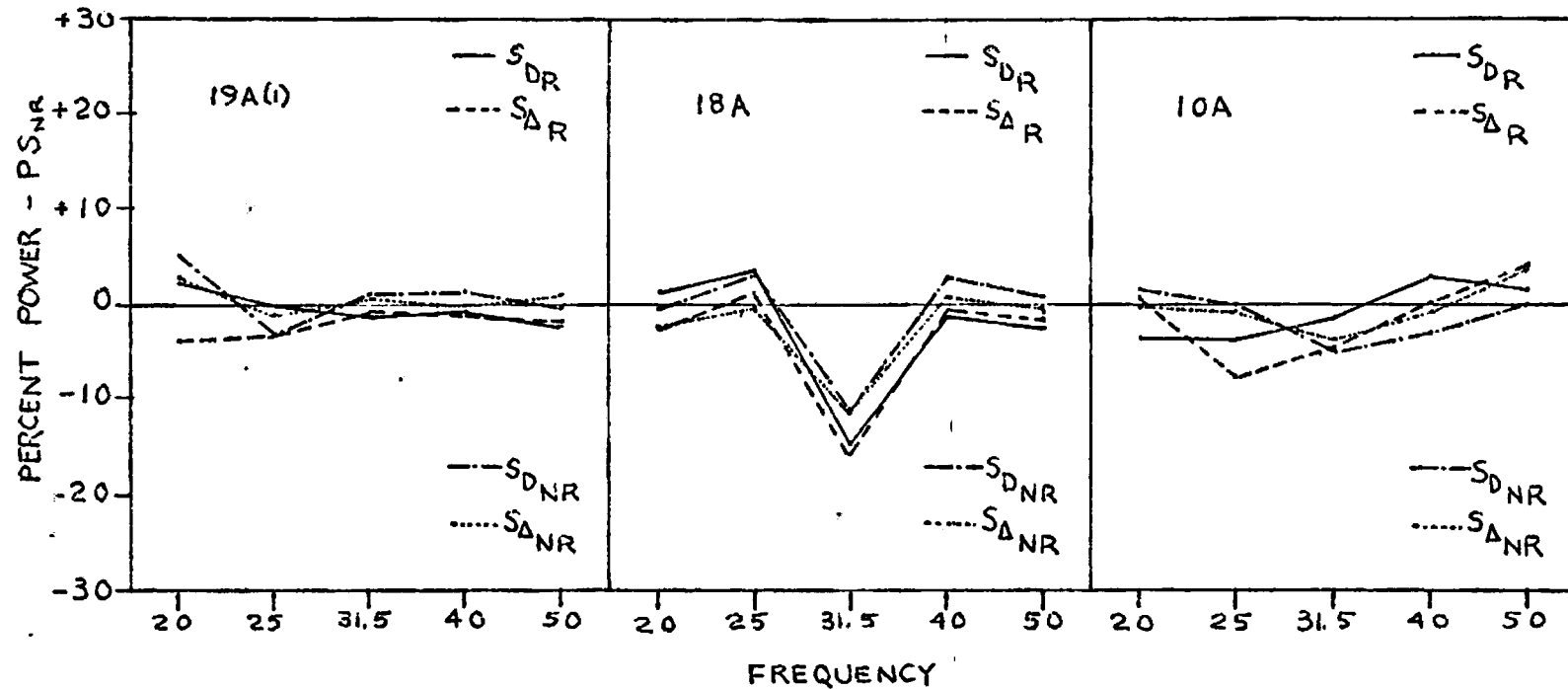
SPECTROGRAMS

BASED UPON ALGEBRAIC VARIATIONS FROM PRESTIMULUS LEVEL

Values plotted were computed from mean proportional powers shown in Appendix E. Normalization was by broad band power.

AUDITORY AREA - 126 PERIOD

3 1/2 SEC



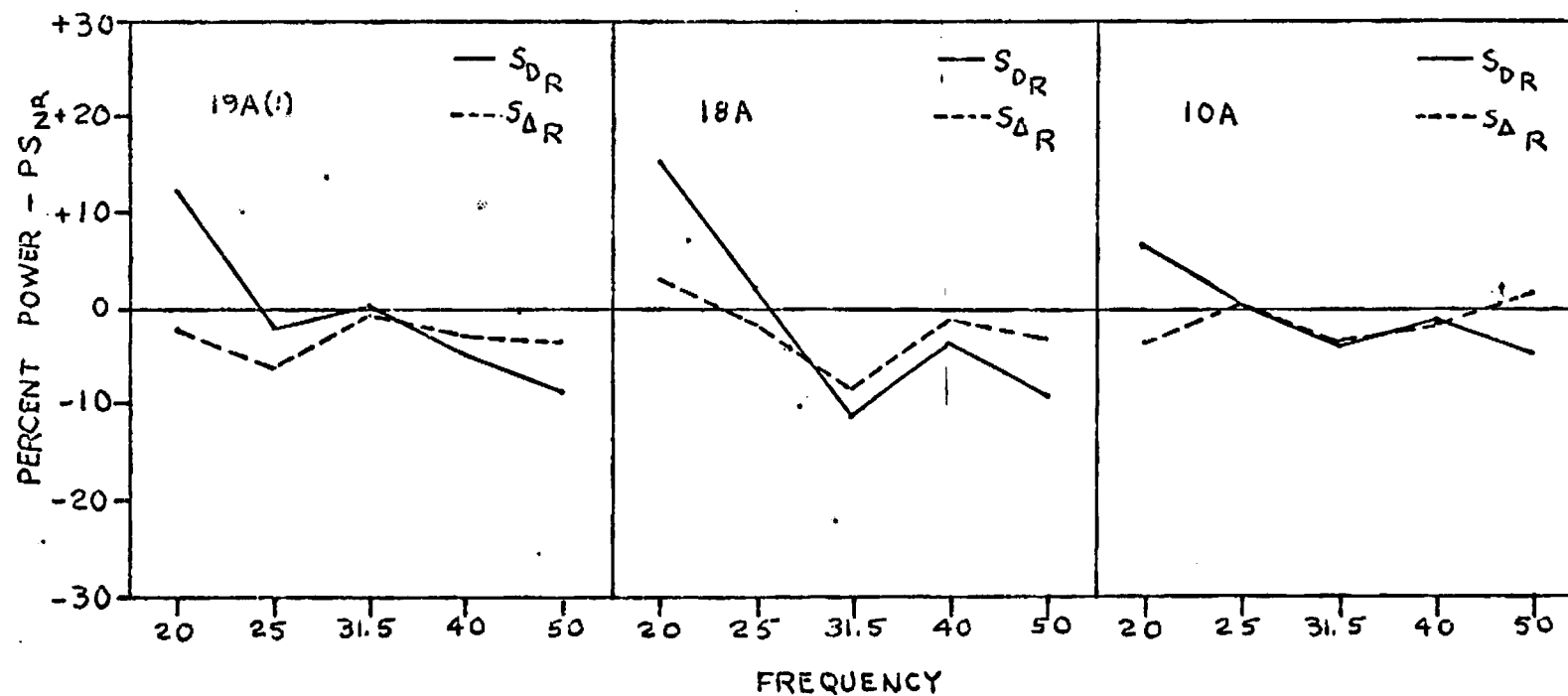
SPECTROGRAMS

BASED UPON ALGEBRAIC VARIATIONS FROM PRESTIMULUS LEVEL

Values plotted were computed from mean proportional powers shown in Appendix E. Normalization was by broad band power.

AUDITORY AREA - cde PERIOD

5 SEC



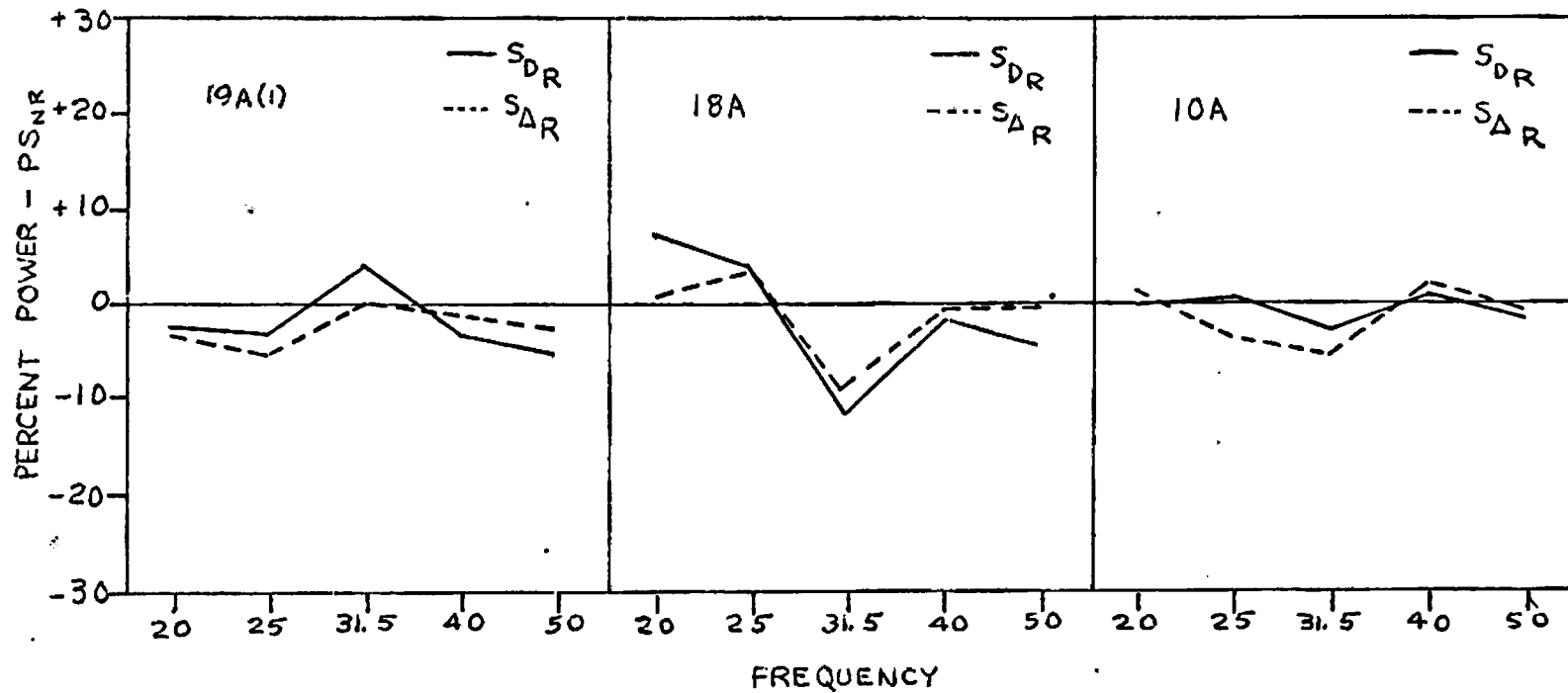
SPECTROGRAMS

BASED UPON ALGEBRAIC VARIATIONS FROM PRESTIMULUS LEVEL

Values plotted were computed from mean proportional powers shown in Appendix E. Normalization was by broad band power.

AUDITORY AREA - abf PERIOD

5 SEC



SPECTROGRAMS

BASED UPON ALGEBRAIC VARIATIONS FROM PRESTIMULUS LEVEL

Values plotted were computed from mean proportional powers shown in Appendix E. Normalization was by broad band power.

APPENDIX H

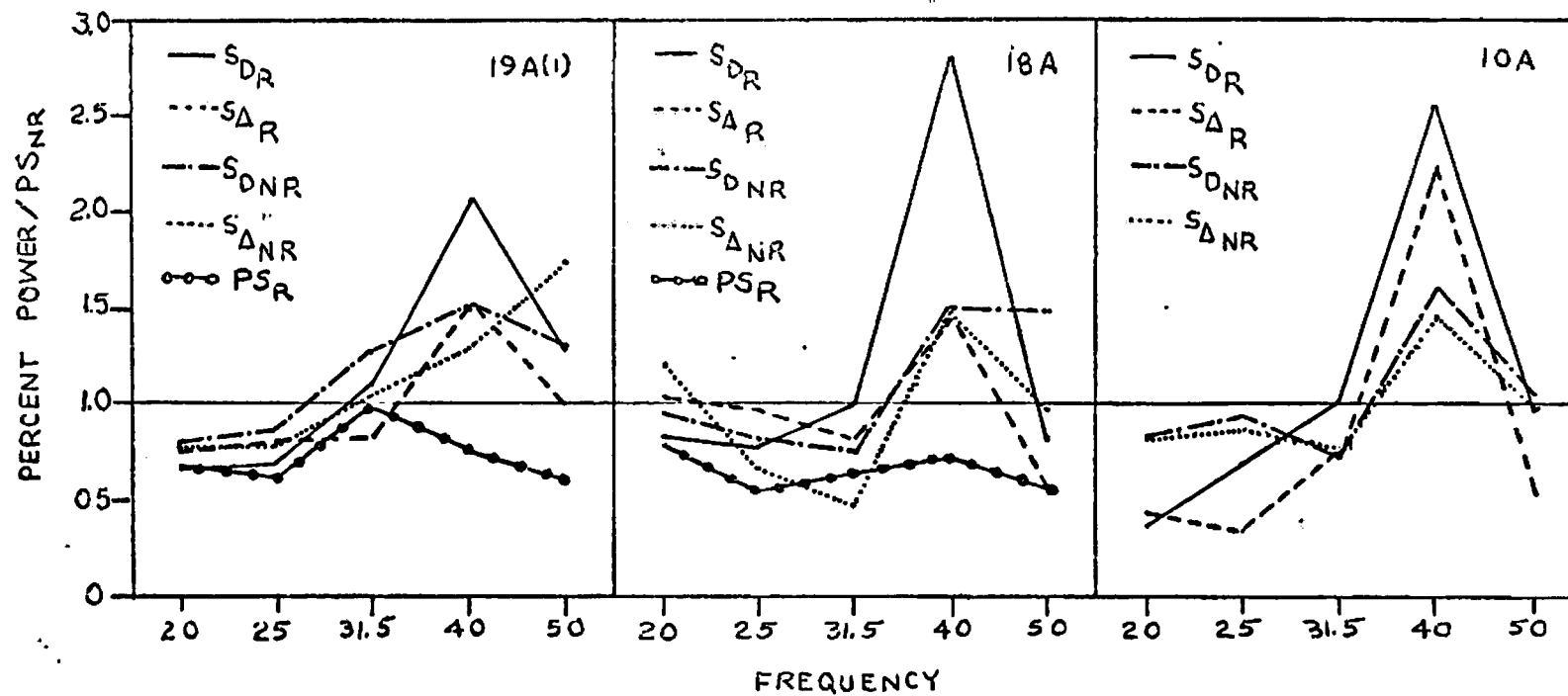
SPECTROGRAMS BASED UPON RATIO OF STIMULUS
TO PRESTIMULUS LEVEL

VISUAL I, MOTOR CORTEX, AUDITORY I ($3\frac{1}{2}$ SEC)

AND

AUDITORY I (5 SEC)

VISUAL AREA - 345 PERIOD

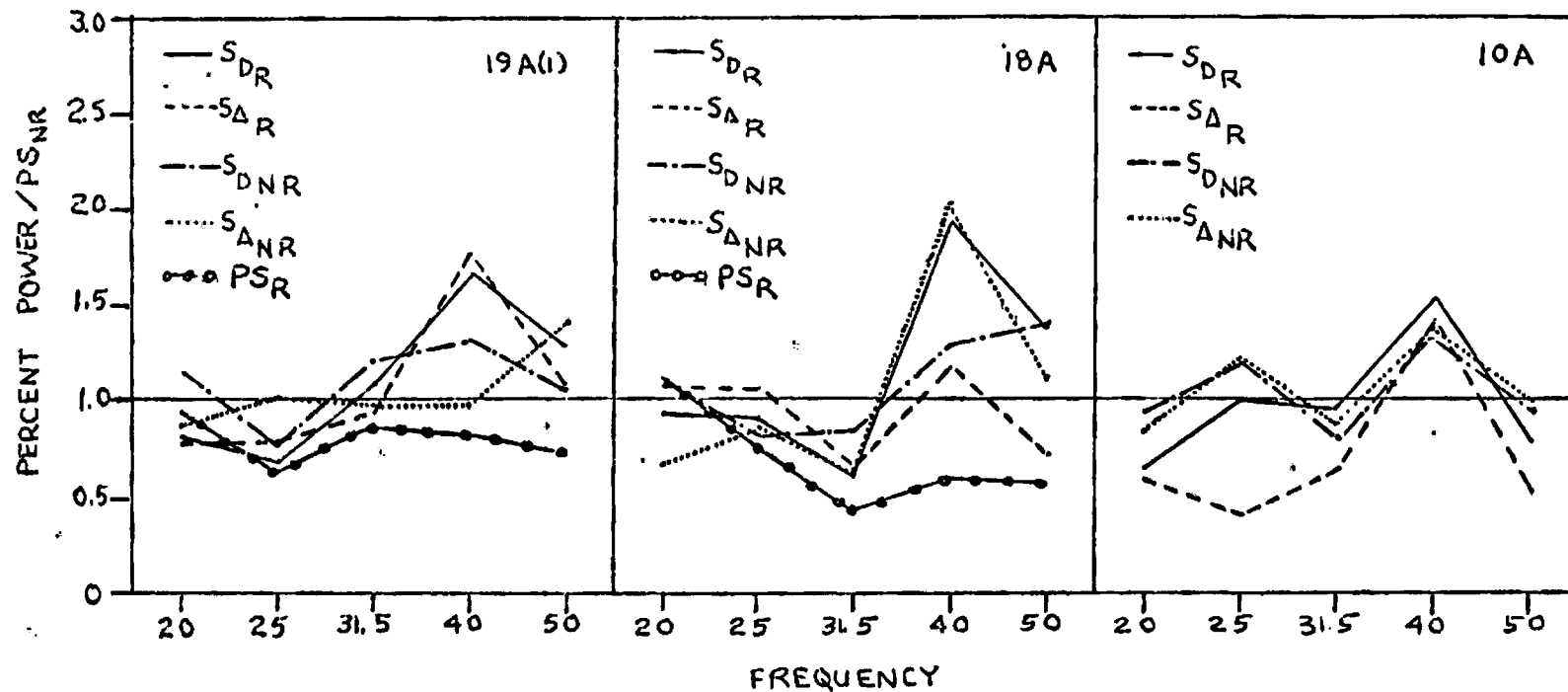


SPECTROGRAMS

BASED UPON RATIO OF STIMULUS TO PRESTIMULUS LEVEL

Values plotted were computed from mean proportional powers shown in Appendix E. Normalization was by broad band power.

VISUAL AREA - 126 PERIOD

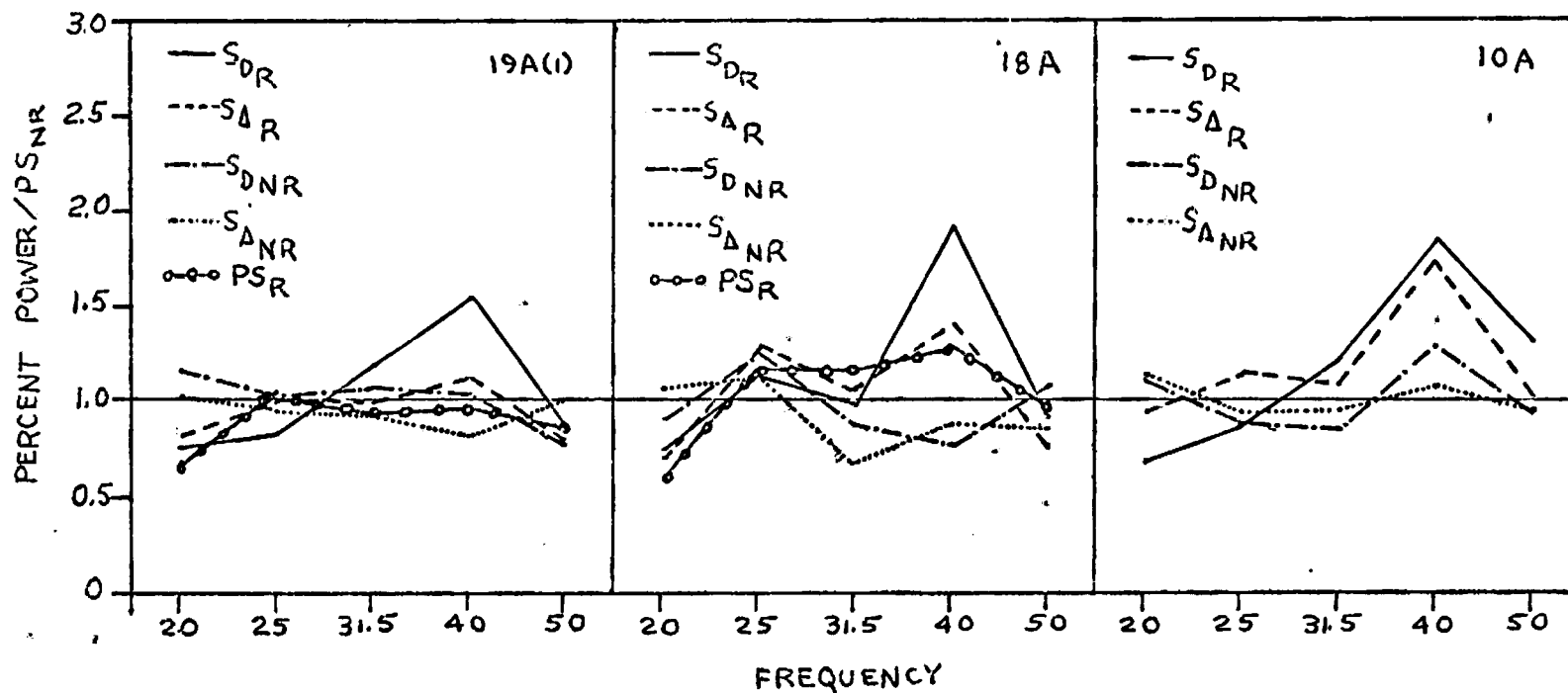


SPECTROGRAMS

BASED UPON RATIO OF STIMULUS TO PRESTIMULUS LEVEL

Values plotted were computed from mean proportional powers shown in Appendix E. Normalization was by broad band power.

MOTOR AREA - 345 PERIOD

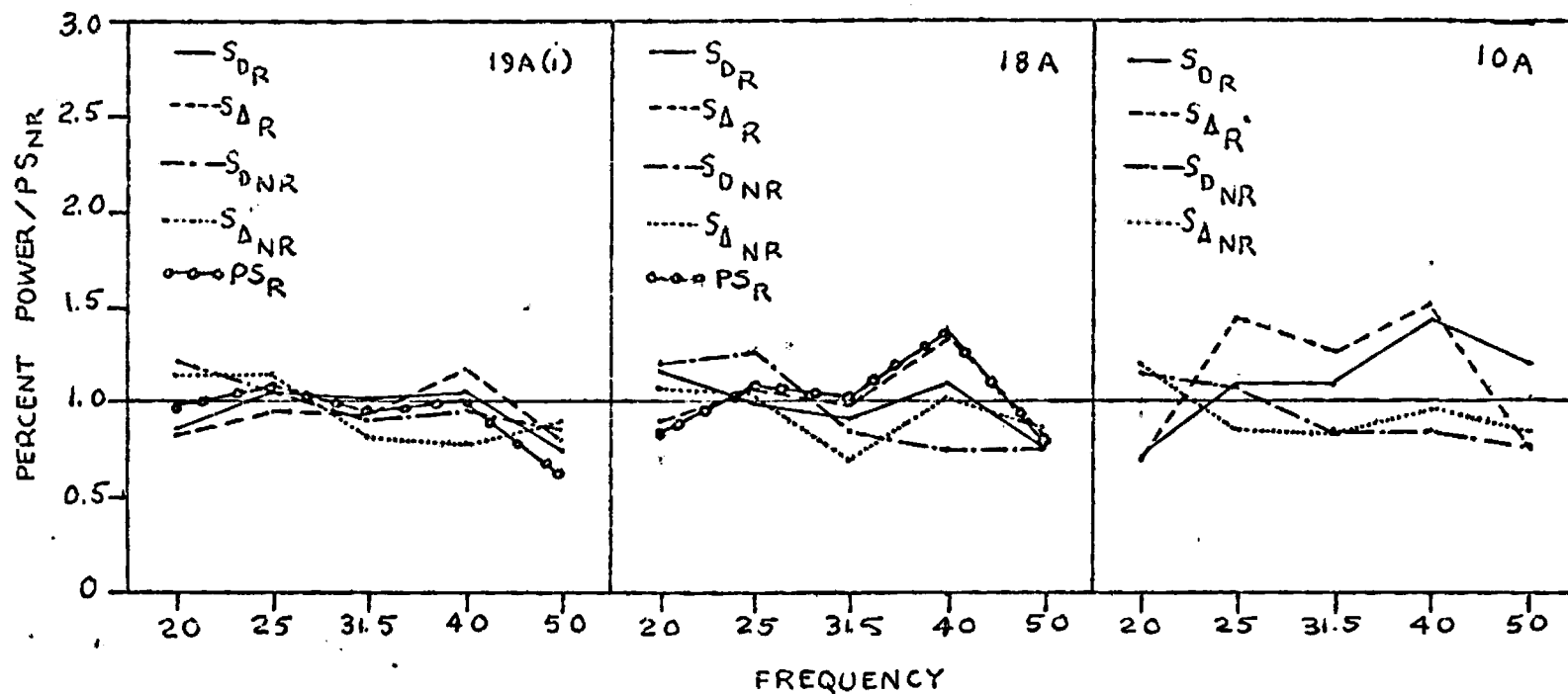


SPECTROGRAMS

BASED UPON RATIO OF STIMULUS TO PRESTIMULUS LEVEL

Values plotted were computed from mean proportional powers shown in Appendix E. Normalization was by broad band power.

MOTOR AREA - 126 PERIOD



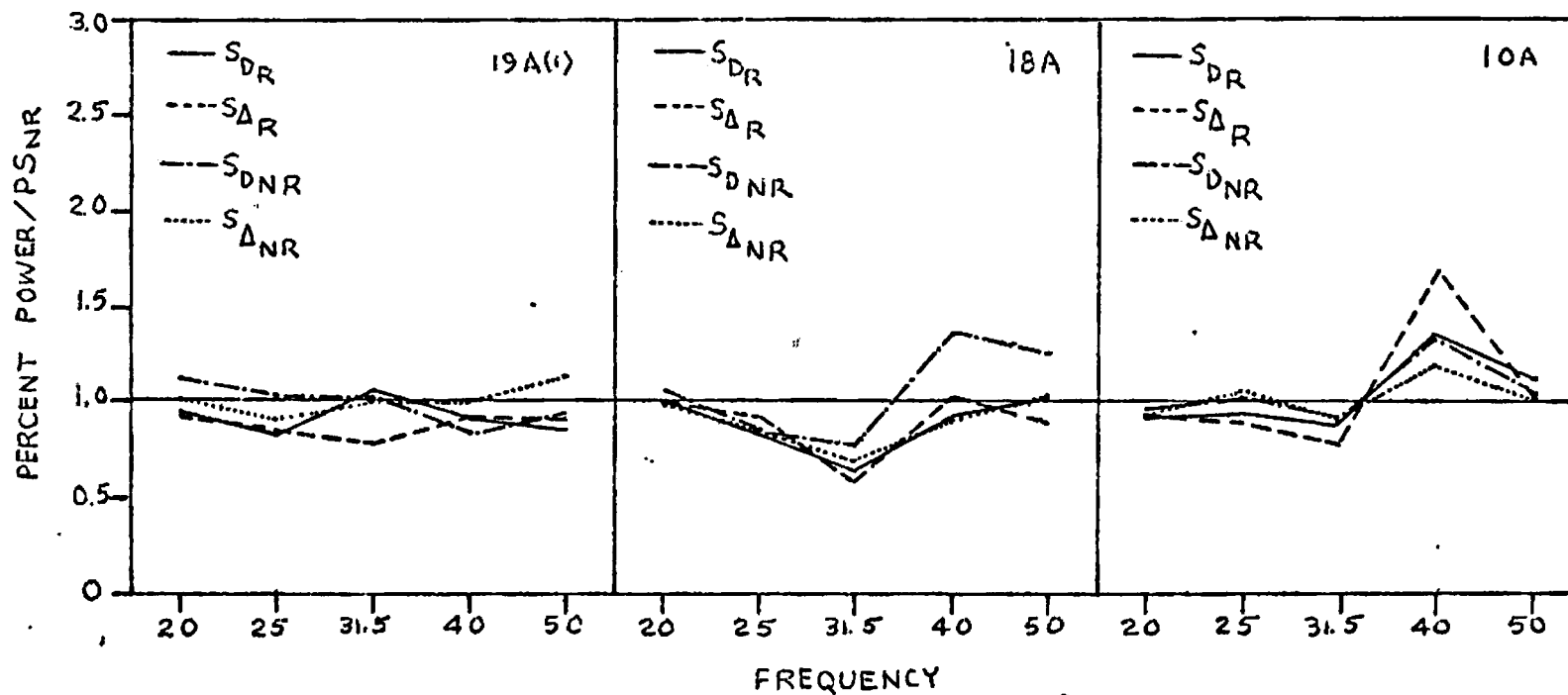
SPECTROGRAMS

BASED UPON RATIO OF STIMULUS TO PRESTIMULUS LEVEL

Values plotted were computed from mean proportional powers shown in Appendix E. Normalization was by broad band power.

AUDITORY AREA - .345 PERIOD

3 1/2 SEC



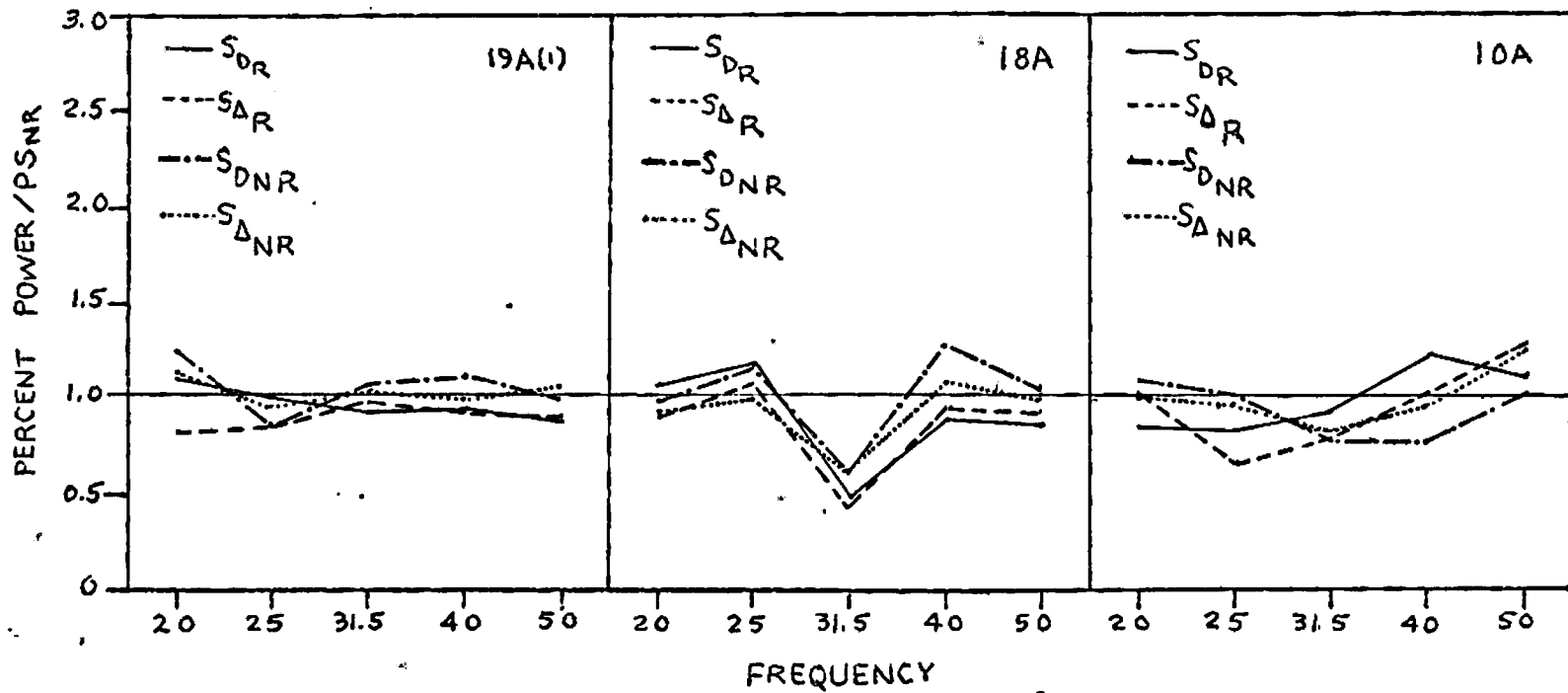
SPECTROGRAMS

BASED UPON RATIO OF STIMULUS TO PRESTIMULUS LEVEL

Values plotted were computed from mean proportional powers shown in Appendix E. Normalization was by broad band power.

AUDITORY AREA - 126 PERIOD

3 1/2 SEC



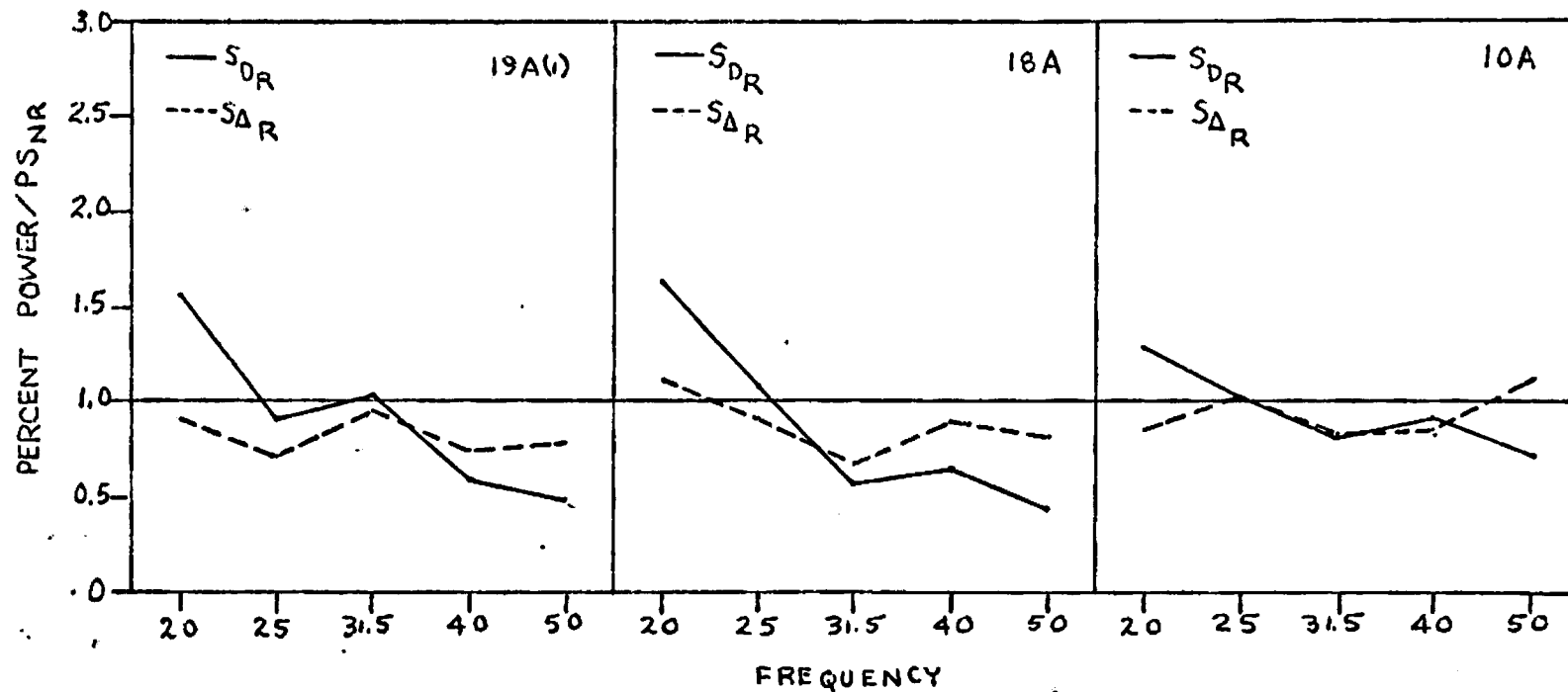
SPECTROGRAMS

BASED UPON RATIO OF STIMULUS TO PRESTIMULUS LEVEL

Values plotted were computed from mean proportional powers shown in Appendix E. Normalization was by broad band power.

AUDITORY AREA - cde PERIOD

5 SEC



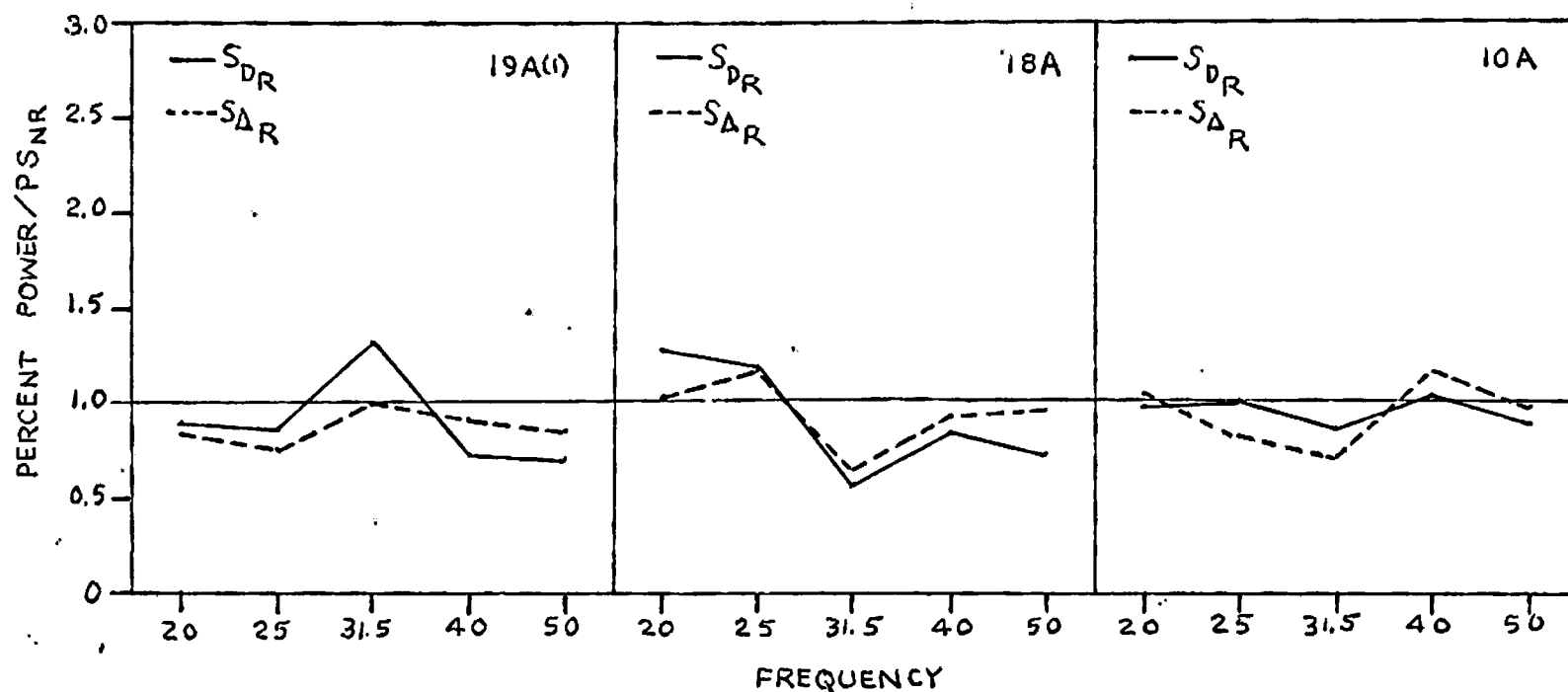
SPECTROGRAMS

BASED UPON RATIO OF STIMULUS TO PRESTIMULUS LEVEL

Values plotted were computed from mean proportional powers shown in Appendix E. Normalization was by broad band power.

AUDITORY AREA - a b f PERIOD.

5 SEC



SPECTROGRAMS

BASED UPON RATIO OF STIMULUS TO PRESTIMULUS LEVEL

Values plotted were computed from mean proportional powers shown in Appendix E. Normalization was by broad band power.