CONTENTS OF VOLUME 45

NO. 1, JANUARY 1981

Electrotonic Structure and Specific Membrane Properties of Mouse Dorsal Root Ganglion Neurons
T. H. Brown D. H. Perkel J. C. Norris J. H. Peacock 1

Characteristics of Neurons in Auditory Cortex of Monkeys Performing a Simple Auditory Task
B. E. Pfingst T. A. O'Connor 16

Comparison of Response Properties of Inferior Colliculus Neurons of Two Inbred Mouse Strains Differing in Susceptibility to Audiogenic Seizures *J. F. Willott* 35

Responses of Single Neurons in Physiologically Defined Primary Auditory Cortex (AI) of the Cat: Frequency Tuning and Responses to Intensity *D. P. Phillips D. R. F. Irvine* 48

Thalamic Input to Areas 3a and 2 in Monkeys
D. P. Friedman E. G. Jones 59

Afterpotential Generation in Hippocampal Pyramidal Cells
R. K. S. Wong D. A. Prince 86

Comparative Aspects of Neural Circuits for Inking Behavior and Gill Withdrawal in *Aplysia californica* *J. H. Byrne* 98

Spatial Tuning of Cells In and Around Lateral Geniculate Nucleus of the Cat: X and Y Relay Cells and Perigeniculate Interneurons
Y. T. So R. Shapley 107

Inhibition of Nociceptive and Nonnociceptive Responses of Primate Spinothalamic Cells by Stimulation in Medial Brain Stem
K. D. Gerhart T. K. Wilcox J. M. Chung W. D. Willis 121

Somatotopic Organization of Hindlimb Cutaneous Dorsal Root Projections to Cat Dorsal Horn
P. B. Brown J. L. Culberson 137

Taste Sensitivity of Hamster Parabrachial Pontine Neurons
R. L. Van Buskirk D. V. Smith 144

NO. 2, FEBRUARY 1981

Functional Properties of Neurons in Cat Trigeminal Subnucleus Caudalis (Medullary Dorsal Horn). I. Responses to Oral-Facial Noxious and Nonnoxious Stimuli and Projections to Thalamus and Subnucleus Oralis
J. W. Hu J. O. Dostrovsky B. J. Sessle 173

Functional Properties of Neurons in Cat Trigeminal Subnucleus Caudalis (Medullary Dorsal Horn). II. Modulation of Responses to Noxious and Nonnoxious Stimuli by Periaqueductal Gray, Nucleus Raphe Magnus, Cerebral Cortex, and Afferent Influences, and Effect of Naloxone
B. J. Sessle J. W. Hu R. Dubner G. E. Lucier 193

Tonotopic Organization and Encoding Features of Single Units in Inferior Colliculus of Horseshoe Bats: Functional Implications for Prey Identification *G. D. Pollak G. Schuller* 208

Single Quickly Adapting Mechanoreceptive Afferents Innervating Monkey Glabrous Skin: Response to Two Vibrating Probes
A. W. Goodwin B. D. Youl N. P. Zimmerman 227

Population of Quickly Adapting Mechanoreceptive Afferents Innervating Monkey Glabrous Skin: Representation of Two Vibrating Probes *A. W. Goodwin M. E. Pierce* 243

Cortical Recovery From Effects of Monocular Deprivation: Acceleration With Norepinephrine and Suppression With 6-Hydroxydopamine
T. Kasamatsu J. D. Pettigrew M. Ary 254

Regulation of Soleus Muscle Stiffness in Premammillary Cats: Intrinsic and Reflex Components
J. A. Hoffer S. Andreassen 267

Neuronal Activity in Cerebellar Cortex Related to Control of Prehensile Force *A. M. Smith D. Bourbonnais* 286

Interneurons Involved in Mediation and Modulation of Gill-Withdrawal Reflex in *Aplysia*. I. Identification and Characterization
R. D. Hawkins V. F. Castellucci E. R. Kandel 304

Interneurons Involved in Mediation and Modulation of Gill-Withdrawal Reflex in *Aplysia*. II. Identified Neurons Produce Heterosynaptic Facilitation Contributing to Behavioral Sensitization
R. D. Hawkins V. F. Castellucci E. R. Kandel 315

Interneurons Involved in Mediation and Modulation of Gill-Withdrawal Reflex in *Aplysia*. III. Identified Facilitating Neurons Increase Ca^{2+} Current in Sensory Neurons
R. D. Hawkins 327

Interneurons Involved in Mediation and Modulation of Gill-Withdrawal Reflex in *Aplysia*. IV. Morphological Basis of Presynaptic Facilitation *C. H. Bailey R. D. Hawkins M. C. Chen E. R. Kandel* 340

Announcements 361

NO. 3, MARCH 1981

Center-Surround Antagonistic Organization in Small-Field Luminosity Horizontal Cells of Turtle Retina
M. Piccolino J. Neyton H. Gerschenfeld 363

Response Dynamics of Horizontal Canal Afferents in Barbiturate-Anesthetized Cats *D. L. Tomko R. J. Peterka R. H. Schor D. P. O'Leary* 376

Visual Response Properties of Neurons in Four Extrastriate Visual Areas of the Owl Monkey (*Aotus trivirgatus*): a Quantitative Comparison of Medial, Dorsomedial, Dorsolateral, and Middle Temporal Areas *J. F. Baker S. E. Petersen W. T. Newsome J. M. Allman* 397

A Quantitative Analysis of Generation of Saccadic Eye Movements by Burst Neurons *J. A. M. Van Gisbergen D. A. Robinson S. Gielen* 417

Spinal and Medullary Lamina I Projection to Nucleus Submedius in Medial Thalamus: a Possible Pain Center *A. D. Craig, Jr. H. Burton* 443

Submodality Distribution in Sensorimotor Cortex of the Unanesthetized Monkey *J. Tanji S. P. Wise* 467

Neuronal Responses in Sensorimotor Cortex to Ramp Displacements and Maintained Positions Imposed on Hindlimb of the Unanesthetized Monkey *S. P. Wise J. Tanji* 482

Presynaptic Inhibition of Transmission From Identified Interneurons in Locust Central Nervous System *K. G. Pearson C. S. Goodman* 501

Neurogenesis in Olfactory Epithelium: Loss and Recovery of Transepithelial Voltage Transients Following Olfactory Nerve Section *P. A. Simmons T. V. Getchell* 516

Physiological Activity of Newly Differentiated Olfactory Receptor Neurons Correlated With Morphological Recovery From Olfactory Nerve Section in the Salamander *P. A. Simmons T. V. Getchell* 529

Interneurons Between Giant Axons and Motoneurons in Crayfish Escape Circuitry *A. P. Kramer F. B. Krasne J. J. Wine* 550

Stochastic Properties of Gustatory Impulse Discharges in Rat Chorda Tympani Fibers *T. Nagai K. Ueda* 574

Announcements 593

NO. 4, APRIL 1981

Efferent Activity During Fictitious Scratch Reflex in the Cat *T. G. Deliagina G. N. Orlovsky C. Perret* 595

GABA Conductance of Chick Spinal Cord and Dorsal Root Ganglion Neurons in Cell Culture *D. W. Choi G. D. Fischbach* 605

Chlordiazepoxide Selectively Potentiates GABA Conductance of Spinal Cord and Sensory Neurons in Cell Culture *D. W. Choi D. H. Farb G. D. Fischbach* 621

GABA-Mediated Synaptic Potentials in Chick Spinal Cord and Sensory Neurons
D. W. Choi D. H. Farb G. D. Fischbach 632

Effect of Vertical Linear Acceleration on H-Reflex in Decerebrate Cat. I. Transient Stimuli *D. G. D. Watt* 644

Effect of Vertical Linear Acceleration on H-Reflex in Decerebrate Cat. II. Sinusoidal Stimuli *D. G. D. Watt* 656

Organization of Cat Anterior Parietal Cortex: Relations Among Cytoarchitecture, Single Neuron Functional Properties, and Interhemispheric Connectivity
T. M. McKenna B. L. Whitsel D. A. Dreyer C. B. Metz 667

Neuronal Basis of Leech Swimming: Separation of Swim Initiation, Pattern Generation, and Intersegmental Coordination by Selective Lesions *J. C. Weeks* 698

Regeneration of Earthworm Giant Axons Following Transection or Ablation *S. C. Birse G. D. Bittner* 724

Physiological and Pharmacological Basis of GABA and Glycine Action on Neurons of Mudpuppy Retina. I. Receptors, Horizontal Cells, Bipolars, and G-Cells *R. F. Miller T. E. Frumkes M. Slaughter R. F. Dacheux* 743

Physiological and Pharmacological Basis of GABA and Glycine Action on Neurons of Mudpuppy Retina. II. Amacrine and Ganglion Cells *R. F. Miller T. E. Frumkes M. Slaughter R. F. Dacheux* 764

Physiological and Pharmacological Basis of GABA and Glycine Action on Neurons of Mudpuppy Retina. III. Amacrine-Mediated Inhibitory Influences on Ganglion Cell Receptive-Field Organization: a Model *T. E. Frumkes R. F. Miller M. Slaughter R. F. Dacheux* 783

Announcements 805

NO. 5, MAY 1981

Phase of Responses to Moving Sinusoidal Gratings in Cells of Cat Retina and Lateral Geniculate Nucleus
B. B. Lee A. Elepfandt V. Virsu 807

Phase of Responses to Sinusoidal Gratings of Simple Cells in Cat Striate Cortex *B. B. Lee A. Elepfandt V. Virsu* 818

Simultaneous Optical Monitoring of Activity of Many Neurons in Invertebrate Ganglia Using a 124-Element Photodiode Array
A. Grinvald L. B. Cohen S. Lesher M. B. Boyle 829

Processing of Somatosensory Information in Striatum of Behaving Cats *J. S. Schneider T. I. Lidsky* 841

Convergence and Interaction of Neck and Macular Vestibular Inputs on Vestibulospinal Neurons *R. Boyle O. Pompeiano* 852

Optokinetic Response in Monkey: Underlying Mechanisms and Their Sensitivity to Long-Term Adaptive Changes in Vestibuloocular Reflex *S. G. Lisberger F. A. Miles L. M. Optican B. B. Eighmy* 869

Spectral-Response Properties of Optic-Nerve Fibers in the Ground Squirrel *G. H. Jacobs R. B. H. Tootell* 891

Color-Discrimination Tests on Fibers in Ground Squirrel Optic Nerve *G. H. Jacobs B. Blakeslee R. B. H. Tootell* 903

Laminar Organization of Superior Colliculus in the Rabbit: a Study of Receptive-Field Properties of Single Units *J. Graham H. E. Pearson N. Berman E. H. Murphy* 915

Temporal Patterning in Simple Spike Discharge of Purkinje Cells and Its Relationship to Climbing Fiber Activity *T. J. Ebner J. R. Bloedel* 933

Correlation Between Activity of Purkinje Cells and Its Modification by Natural Peripheral Stimuli *T. J. Ebner J. R. Bloedel* 948

Role of Climbing Fiber Afferent Input in Determining Responsiveness of Purkinje Cells to Mossy Fiber Inputs *T. J. Ebner J. R. Bloedel* 962

NO. 6, JUNE 1981

Two Types of Muscle Spindles in Cat Neck Muscles: a Histochemical Study of Intrafusal Fiber Composition *G. J. Bakker F. J. R. Richmond* 973

Dependence of Auditory Cortex Evoked Unit Activity on Interstimulus Interval in the Cat *S. Hocherman E. Gilat* 987

Potassium Ion Homeostasis in Amphibian Brain: Contribution of Active Transport and Oxidative Metabolism *T. J. Sick N. R. Kreisman* 998

Auditory Representation Within Principal Division of Cat Medial Geniculate Body: an Electrophysiological Study *M. B. Calford W. R. Webster* 1013

Descending Inhibition From Medial and Lateral Midbrain of Spinal Dorsal Horn Neuronal Responses to Noxious and Nonnoxious Cutaneous Stimuli in the Cat
E. Carstens H. Bihl D. R. F. Irvine M. Zimmerman 1029

Response to Movement of Neurons in Areas 17 and 18 of the Cat: Velocity Sensitivity *G. A. Orban H. Kennedy H. Maes* 1043

Response to Movement of Neurons in Areas 17 and 18 of the Cat: Direction Selectivity *G. A. Orban H. Kennedy H. Maes* 1059

Responsivity of Normal Kitten Striate Cortex Deteriorates After Brief Binocular Deprivation
R. D. Freeman R. Mallach S. Hartley 1074

Static Characteristics of Muscle Afferents From Gluteus Medius Muscle: Comparison With Joint Afferents of Hip in Cats
G. Carli G. Fontani M. Meucci 1085

Interaction of Activity in Frog Skin Touch Afferent Units
M. D. Goldfinger Y. Fukami 1096

Rhythmical Synaptic Control of Axonal Conduction in a Lobster Motor Neuron *F. Nagy P. S. Dickinson M. Moulins* 1109

Interganglionic Communication by Spiking and Nonspiking Fibers in Same Neuron *P. S. Dickinson F. Nagy M. Moulins* 1125

Focal Activtions of Human Cerebral Cortex During Auditory Discrimination
P. E. Roland E. Skinhøj N. A. Lassen 1139

Indexes 1152

JOURNAL OF NEUROPHYSIOLOGY
Vol. 45, No. 2, February 1981. *Printed in U.S.A.*

Tonotopic Organization and Encoding Features of Single Units in Inferior Colliculus of Horseshoe Bats: Functional Implications for Prey Identification

GEORGE D. POLLAK AND GERD SCHULLER

Arbeitsgruppe Neuro- und Rezeptorphysiologie Fachbereich Biologie, Universitat Frankfurt, D-6000 Frankfurt, West Germany

SUMMARY AND CONCLUSION

1. Current ideas hold that the specializations in the auditory systems of horseshoe bats are important for the detection and recognition of prey. To evaluate this hypothesis more thoroughly, the response patterns of neurons in the inferior colliculus of horseshoe bats were investigated with tone bursts and sinusoidally frequency-modulated (SFM) signals. The SFM signals represent approximations to the frequency-modulation patterns in the constant-frequency (CF) component of the echoes that are created when the long CF component first strikes and is then reflected from the beating wings of a small insect.

2. The best frequencies (BF) of collicular neurons were divided into three frequency bands: *a*) the filter frequencies, which correspond to the frequencies of the CF component of the emitted cries and echoes (i.e., 78–88 kHz); *b*) the frequencies of the final FM portion of the biosonar cries (i.e., 65–77 kHz); and *c*) the nonecholocation frequencies (i.e., frequencies below 65 kHz). The probability that a neuron would fire in registry with the modulation waveform of an SFM signal was highly correlated with the unit's BF. Eighty-one percent of the neurons tuned to the filter frequencies (i.e., 78–88 kHz) showed time-locked responses to SFM signals, whereas only 35% of the neurons tuned to the final FM portion of the cries and 34% of neurons having BFs below 65 kHz exhibited time-locked discharges.

3. The tonotopic organization of neurons tuned to the filter frequencies is different from that of the rest of the inferior colliculus (IC). The tonotopy in the central, filter region is highly unusual and is characterized by a quasi-cortical appearance where almost all neurons along a particular vertical axis have the same BFs.

4. The influence of signal intensity on the discharge registration evoked by SFM signals was examined in 42 units. Two general types of neurons were found. The first type had discharge registrations that were about equally secure at all intensities above threshold and had firing rates that increased monotonically or slightly nonmonotonically with intensity. The second type of neuron exhibited the most vigorous responding and sharpest locking only at low or moderately low intensities and had a significant decline or complete absence of locking at higher intensities.

5. Many collicular neurons also exhibited preferences for certain ranges of modulation rates but other neurons would respond with discharges synchronized to the modulation waveform over a very wide range of modulation rates. Similar characteristics were observed for neurons when the depth of modulation was systematically varied. The lowest modulation depths that would evoke time-locked discharges were $\pm$10–40 Hz.

6. The locking behavior of 34 units was investigated when the carrier frequency was systematically moved in and around the unit's tuning curve. In about a third of the

units, there were sharp changes in discharges that were symmetric around the BF and agreed closely with the extent to which the SFM signal encroached on the tuning curve; the greater the encroachment, the more vigorous the response. In the remainder of the neurons the vigor with which the neurons would discharge to the SFM signal was asymmetrically related to the BF. In these units the amplitudes of the peaks in the histograms were superior for carrier frequencies below or, in other units, for carrier frequencies above the BF of the neuron.

7. The tonotopic organization and the SFM excitatory properties suggest that the spatial extent of neural activity evoked by an echo reflected from an insect should be sharply confined within the anterior-posterior axis of neural space. Within the active region, the frequency-modulation pattern in the echo CF component is coded by the temporal sequence of discharges. Moreover, due to changes in position, orientation, and speed of either the bat or its target, each echo will differ more or less in carrier frequency, modulation pattern, and intensity from the previous echoes. The preferences of many filter neurons for selective ranges of intensity as well as modulation depth and rate seem important in this regard. These features should endow the system with the ability to encode the perturbations imposed on the echo CF component with the sum total of spatiotemporal activity being a dynamic pattern, which differs from echo to echo.

INTRODUCTION

Several species of bats emit echolocation cries where the most prominent feature is a long constant-frequency (CF) component followed by a less conspicuous brief, downward sweeping, terminal frequency-modulated (FM) portion. The greater horseshoe bat, *Rhinolophus ferrumequinum*, is one of these so called long CF-FM bats and emits an 80- to 84-kHz CF component having a duration of 10–100 ms (11, 15, 16, 22).

Each horseshoe bat has its own private emission frequency, which is regulated with remarkable precision (15, 18, 22). When no echoes are heard or when the echo has the same frequency as the cry, these bats emit successive CF components that vary by only ±100 Hz from pulse to pulse. However, under most conditions echoes reflected from an object will be Doppler shifted upward due to the approach of the bat toward its target. In response to the upward shift in echo frequency the horseshoe bats lower the frequency of their emitted CF signals by an amount almost equal to the Doppler shift in the echo. This maneuver, called Doppler-shift compensation (15, 22, 24), allows the bat to hold the frequencies of the subsequent echoes to within a narrow frequency band only 50–100 Hz wide.

The auditory system of the horseshoe bat has a number of impressive specializations for processing the CF component. In the cochlea, the portion of the basilar membrane devoted to the frequencies of the CF portion of the emitted cries and Doppler-shifted echoes is greatly elongated (2–4, 9). Furthermore, the elongated region is demarcated from the more apical regions of the basilar membrane by a number of pronounced structural adaptations. The structural features create a highly resonant hydromechanical system, which is responsible for producing the high degree of frequency selectivity seen in many auditory neurons (2, 3, 8, 9, 19, 29).

The population of auditory neurons can be divided into two categories on the basis of tuning. Neurons in the first category have best frequencies (BF) between 78 and 88 kHz and are referred to as "filter neurons" (8, 10, 30) because of their sharp tuning curves. The degree of tuning is indicated by the $Q_{10\,dB}$ value, which is defined as the unit's BF divided by the bandwidth of the tuning curve at 10 dB above the minimum threshold (i.e., threshold above the BF). The $Q_{10\,dB}$ values of filter neurons are typically 50–200, with some as high as 300–400, and are the most sharply tuned neurons observed in the auditory systems of any animal studied so far. Neurons in the second category have BFs below 78 kHz and have much broader tuning curves. The $Q_{10\,dB}$ values of these nonfilter neurons rarely exceed 20 and in this respect they are similar to the tuning curves seen in auditory neurons of other animals.

The specialized features of both the emitter and receiver of horseshoe bats have considerable functional significance. The system is exquisitely sensitive to motion that is

thought to be important for the detection and recognition of prey (5, 17, 18, 20, 21, 23). The emission of a long CF component together with neurons having high Q values are both seemingly well suited for these purposes. Even very small Doppler shifts in the echo CF component are easily detected by the sharply tuned filter neurons and the perception of a Doppler shift alerts the bat to a target in its acoustic environment. If the target is a flying insect the echo CF component will also have amplitude and frequency modulations (AM and FM), which are produced as the long CF component first strikes and is then reflected from wings having a more or less high rate of periodic motion. Furthermore, since insects differ in size, wingspread, and wingbeat frequency, the profile of modulations in the echo CF component contains considerable information about the target. If the auditory system can encode the profile of modulations in the echo CF component, the bat should be able to resolve a number of target features and utilize that information for target identification.

Preliminary information concerned with response features of peripheral auditory neurons in the long CF-FM bats, reported by Suga and his co-workers (28, 30), suggests that both AM and FM are encoded with precision. A more recent and comprehensive study by Schuller (21), of single neurons in the inferior colliculus (IC) of the horseshoe bat, confirmed and greatly extended Suga's original observations. Schuller simulated the variety of frequency-modulation patterns that occur in echoes reflected from insects. He accomplished this by utilizing acoustic signals that had sinusoidal frequency modulation (SFM) patterns and he found that many neurons respond with firings tightly locked to the modulating waveform. Here we present data that compliment Schuller's earlier study. In this report particular attention is directed toward an analysis of the differences existing among the population of filter neurons with regard to their response features when the depth or the rate of the frequency-modulation patterns was varied. We also examined the influence of stimulus intensity and variations in carrier frequency on the coding security for these signals. Finally, we obtained data concerning the tonotopic organization of the horseshoe bat's IC. The tonotopy proved to be considerably different from that of other mammals and has an important bearing on the functional organization of the horseshoe bat's IC.

METHODS

Surgical Procedures

Eleven greater horseshoe bats, *Rhinolophus ferrumequinum*, were prepared under Metofane anesthesia (Pitman-Moore, Washington Crossing, N.J.). In each animal, a long incision was made along the midline of the skull and the underlying musculature was reflected. The skull was dried and dental cement applied to the anterior and posterior portions of the cranium. Small wisps of cotton soaked in procaine were placed on all open wounds. An indifferent tungsten electrode was placed in the skull overlaying the cerebellum or cortex and cemented in place. A small screw was mounted on the anterior portion of the cranium with dental cement. Each animal was then placed in a Plexiglas holder that restricted gross movements and the screw was locked onto a rigid metal bar above the head. This procedure immobilized the bat's head and allowed a clear sound field to the animal's ear. Small holes, approximately 200–300 μm in diameter, were drilled over the inferior colliculus with a Narishige stereotaxic drill (model SD-101). Holes were systematically placed to permit us to sample much of the rostrocaudal extent as well as the mediolateral extent of the colliculus. The Metofane was then removed and the animals were allowed to recover. The animals appeared to be comfortable in that they remained calm and quiet throughout the experiment sessions. As a precautionary measure, the local anesthetic was reapplied to the wound margins once every 3–4 h. Under these conditions the bats occasionally exhibited spontaneous movements of the shoulders, wings, or feet but rarely was there any intense struggling indicative of pain. In such cases, refreshing the cotton wisps with additional procaine resulted in a cessation of struggling movements.

Prior to being placed in the holder, three bats were given injections of a neuroleptic agent (4 mg/kg droperidol). The other eight bats were not given any drugs other than the Metofane and topically applied local anesthetic. All animals were fully awake during the experiment and no differences in response properties could be detected between the bats given neuroleptic agents and those given no drugs.

Stimulation

Acoustic stimuli were presented under free-field conditions by a condenser loudspeaker lo-

cated 10 cm from the ear contralateral to the colliculus from which we monitored activity. The loudspeaker was calibrated with a 0.25-inch Bruel and Kjaer microphone that had a flat free-field response (±2 dB) from 50 to 100 kHz.

The acoustic signals consisted of tone bursts and sinusoidally frequency-modulated (SFM) signals having durations of 60–100 ms and rise-fall times of 2.0 ms. Tone bursts were produced by shaping the output of a Wavetek oscillator (model 136), hereafter called the tone-burst oscillator. The SFM signal that was presented to the bat was generated in the following way. An SFM waveform was obtained from a phase-locked Wavetek oscillator (model 112), which was triggered by the same sync pulse that initiated tone bursts. Consequently, the SFM waveform was phase-locked to the beginning of each stimulus and always started with a precise phase angle relative to the envelope of the tone burst. The SFM waveform was then sent to a set of calibrated attenuators, which determined the amplitude of the waveform. The waveform was then fed to the VCG input of the tone burst oscillator. When an SFM waveform was at the input of the tone burst oscillator, the output was an SFM signal. Three parameters of the SFM signal were of interest and were under our control: *1*) the carrier or center frequency, *2*) the modulation frequency or the frequency at which the FM pattern was repeated within each signal, and *3*) the modulation depth or the amount by which the frequency of the signal oscillated around the carrier frequency (Fig. 1). The carrier or center frequency of the SFM signal was set by the Wavetek 136 tone-burst oscillator, whereas the modulation frequency was controlled by the frequency setting of the phase-locked oscillator. All frequencies were measured with an electronic frequency counter (Eldorado 325B). The modulation depth was determined by the calibrated attenuators. We used modulation frequencies that varied from 30 to 500 Hz and modulation depths that ranged from ±10 Hz to ±5 kHz.

The spectrum of a frequency-modulated signal contains an infinite series of side frequencies ($f_o \pm kf_m$; $k = 1, 2, 3, \ldots$), where f_o is the carrier frequency and f_m is the modulating frequency. The distribution of energy to the side frequencies depends on the modulation index, which is defined as the ratio of the maximum instantaneous frequency deviation, df, of the signal to the modulating frequency, f_m. If the frequency modulation depth is small compared to the modulating frequency, f_m (i.e., the modulation index is much smaller than 1), only the first two side frequencies contain considerable energy. Whenever the modulation index is greater than 1, p spectral components ($f_o \pm kf_m$; $k = 1, 2, 3, \ldots$) contribute significant energy to the frequency-modulated signal, where $p = 1 + df/dm$. For example, a frequency modulation of ±200 Hz at a modulation frequency of 100 Hz yields 13 spectral components on each side of the carrier frequency whose relative amplitudes are above 0.1 of the amplitude of the unmodulated carrier frequency. Most energy, however, is distributed to the frequencies around $f_o \pm df$.

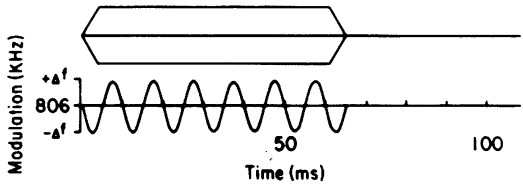

FIG. 1. Relation of the signal envelope to the SFM waveform. The carrier frequency in this case would be 80.6 kHz and would be frequency modulated by $\pm\Delta f$ at the rate of 100 Hz. The value of Δf is determined by the amplitude of the SFM waveform that is fed to the VCG input of the tone-burst oscillator. The SFM waveform always has the same phase relationship to the signal envelope.

Recording and histological procedures

Single units were recorded with micropipettes filled with 3 M KCl and 3% alcian blue dye (8–20 MΩ), which allowed electrophoretic marking in each penetration (6). Prior to recording, the tips of the electrodes were positioned within about ±200 μm of the collicular surface with the aid of a Zeiss operating microscope. The electrodes were attached to a Wells microdrive unit having a stepping motor and digital display. The micropipettes were advanced in steps of 1 μm and when a unit was encountered, the depth was recorded. In general, the electrodes were driven to a depth of 2,000–2,500 μm, which corresponds to the ventral extent of the horseshoe bats' IC. On completing a penetration we deposited a small amount of alcian blue dye by passing 1 μA of current for 3 min at one or two electrode locations along the electrode tract. The depths of the dye depositions were recorded and carefully chosen to facilitate tract identification and to avoid any confusion with penetrations made earlier or subsequently in different parts of the bat's IC. At the end of each experiment the animals were killed with an overdose of anesthesia and the brains fixed in Formalin. Frozen sections, 40–60 μm thick, were then prepared and stained with cresyl violet. Each electrode tract was identified and the appropriate position of each unit along the tract was determined.

Data analysis

Spikes were amplified and processed with conventional methods and fed on-line to a PDP 11/40 laboratory computer that generated poststimulus time (PST) histograms. The spikes were

timed relative to the stimulus onset, and all histograms had a bin width of 0.1 ms. The computer programs for acquisition and processing spike information were written by H. Zöller. In addition, the tone-burst frequency for which the lowest sound pressure was needed to evoke a just noticeable change in firing rate from the background activity was determined audio-visually. We shall refer to this frequency as the unit's best frequency (BF). Since the majority of units had very low rates of spontaneous activity, or no spontaneous activity at all, we were able to determine the BFs with considerable accuracy. We routinely evaluated the BFs of filter units to an accuracy of ±50 Hz and, when necessary, we increased the accuracy to ±10 Hz. Tuning curves of 87 units were determined audio-visually by raising the signal level in steps of 10 dB above threshold at the BF and carefully assessing the upper and lower frequency limits to which the neuron would respond. In experiments where we needed to relate the SFM carrier frequency to the limits of the tuning curve (see RESULTS), PST histograms generated by tone bursts at a particular frequency and SFM signals having the same carrier frequency and intensity were obtained and compared.

RESULTS

General response features evoked by tone bursts and SFM stimulation

In this section we first describe the response patterns elicited by tone bursts. We then consider whether any relation exists between the firing pattern evoked by a tone burst and the ability of a unit to follow SFM signals with spike trains in registry with the phase of the modulation waveform (i.e., locked or synchronized firings). Unless otherwise stated, the tone-burst frequency and the carrier or center frequency of the SFM stimulus were set at the unit's BF.

Activity evoked by tone bursts was evaluated in 444 neurons. In 378 of the units tone bursts evoked one of three types of firing patterns (Fig. 2): *1*) a phasic response pattern where the neuron fired only to the onset, only to the offset, or to both the onset and offset of the signal (154 units, 35%); *2*) a tonic or sustained pattern where firings occurred throughout the duration of the signal presentation (160 units, 36%); *3*) an inhibitory pattern where the response was a prominent inhibition of the spontaneous activity, which lasted for the duration of the signal (64 neurons, 14%). The remaining 66 neurons (14%) failed to respond to tone bursts at any frequency-intensity combination.

Of the 444 neurons encountered, 282 units were tested with both tone bursts and SFM signals having modulation depths of from ±500 Hz to ±2,000 Hz at intensities ranging from 40 to 70 dB SPL. About half of the neurons tested with SFM stimulation responded with discharges tightly locked to the modulation waveform. In general, there was a relationship between a unit's discharge pattern evoked by tone bursts and its ability to fire in registry with the SFM envelope. Neurons having a tonic pattern to tone bursts were more likely to lock to the SFM waveform than were phasic units. Inhibitory neurons and neurons that were unresponsive to tone bursts were least likely to fire in synchrony with SFM envelope; 73% of the tonic units, 50% of the phasic units, and 25% of the inhibitory neurons had locked firing patterns to the SFM signals. Examples of each type are shown in Fig. 2. In addition, only 23% of the neurons that were unresponsive to tone bursts responded with brisk, synchronized firings to SFM stimulation.

Filter neurons compared to nonfilter neurons

RESPONSE PROPERTIES. The probability that a neuron would fire in registry with the modulation waveform of an SFM signal was highly correlated with the unit's BF. The collicular neurons were grouped into neurons with BFs equal to: *1*) the filter frequencies (i.e., 78–88 kHz), *2*) the frequencies of the final FM portion of the biosonar cries (i.e., 65–77 kHz), and *3*) the nonecholocation frequencies (i.e., frequencies below 65 kHz). A much larger percentage (81%) of neurons tuned to the filter frequencies showed time-locked responses to SFM signals than did neurons tuned to the frequencies of the FM portion of the cries (35%) or to frequencies below 65 kHz (34%).

The tendency for a much higher proportion of filter neurons to lock to SFM was also found within the populations of phasic units, tonic units, as well as units that were unresponsive to tone bursts but that responded to SFM. Of the 50 phasic units that had firings in registration with the SFM

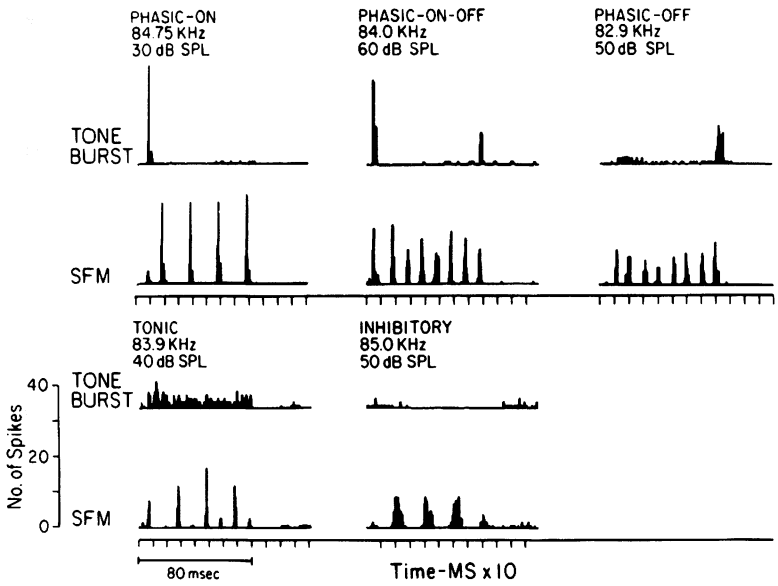

FIG. 2 Firing patterns elicited by SFM signals in three types of phasic neurons (top), a tonic neuron, and an inhibitory neuron. The BF of each neuron is shown above each of the histograms generated by tone bursts. The tone bursts and SFM carrier frequencies were always set at the BF for each neuron. The signal duration was 80 ms, as indicated by the bar in the lower left.

waveform, 41 were filter units, 7 were FM units, and 2 were tuned to nonecholocation frequencies (Fig. 3), a finding in agreement with Schuller's (21) earlier report. A similar distribution was found for tonic neurons although a larger number of nonfilter neurons locked to SFM in this population than were found for the population of phasic neurons (Fig. 3). Another striking result was obtained for the neurons that were unresponsive to tone bursts but that locked to SFM. Of the 15 neurons in this category, 12 had their best SFM frequencies between 78–86 kHz (the best SFM is the carrier evoking the highest number of discharges per SFM cycle at 10–20 dB above threshold). The three other neurons had best SFMs of from 76.0 to 76.5 kHz while none of the cells had best SFMs in the nonecholocating frequency range (Fig. 3).

The trend for neurons responding with an inhibitory pattern to tone bursts was different from the trend of the other neuronal types described above. The feature to note is the lack of any pronounced tendency for the inhibitory filter neurons to lock to SFM stimulation (Fig. 3), although some units of this type did show locking (Fig. 2). Furthermore, there seemed to be a paucity of neurons tuned to the filter frequencies within this population. Although the sample size was small (e.g., 26 inhibitory neurons were tested with SFM signals), only 23% (six units) were tuned to the filter frequencies.

TONOTOPIC ORGANIZATION. The finding that filter neurons have characteristics that distinguish them from nonfilter neurons is also reflected in the tonotopic organization of the IC. The tonotopy reveals that the filter neurons are both segregated from and are arranged in a manner different from the neurons tuned to the FM portion of the orientation sounds and neurons tuned to the lower, nonecholocation frequencies. These features are especially evident in the middle or central portion of the IC. This region of the colliculus is functionally divided into a dorsal region, where the BFs of neurons range from 9 to 76–77 kHz, and a ventral region, where the filter frequencies are represented (Fig. 4).

The tonotopic arrangement in the dorsal, nonfilter region is, in principle, similar to the tonotopy found in all other mammals that have been studied (1). Proceeding from the dorsal aspect of the IC to a depth of approximately 800–1,200 μm, the BFs of the neurons encountered increased progressively

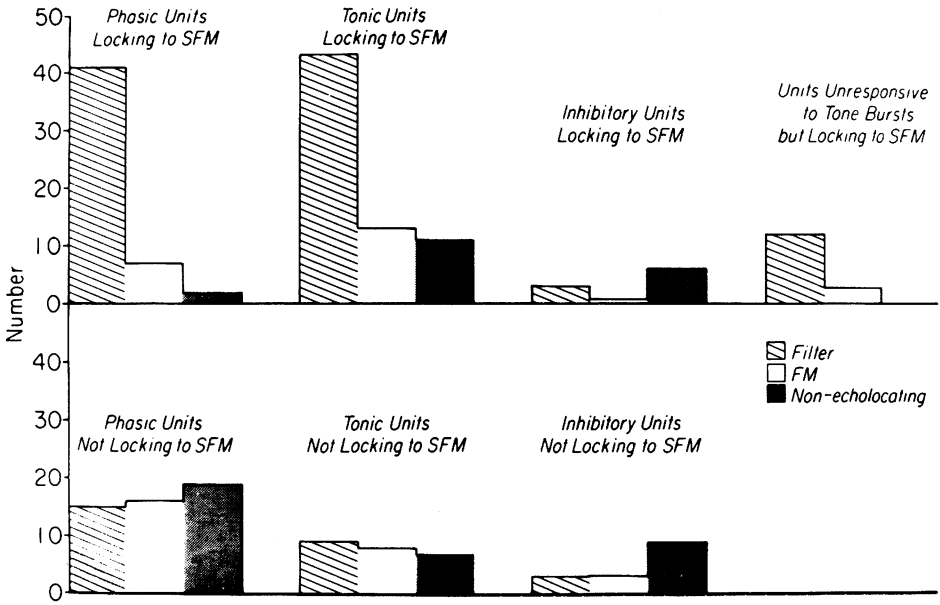

FIG. 3. Bar histograms showing the number of neurons that had time-locked discharges to SFM signals (above) and the number of units that would not lock to SFM signals (below). Each set of histograms is divided up according to the response pattern evoked by tone bursts (e.g., phasic, tonic, or inhibitory) and further subdivided into filter units (crosshatched), FM neurons (white), and nonecholocation neurons (stippled). Notice the large number of filter units that locked to SFM in both the phasic and tonic categories. See text for further explanation.

from about 10 kHz or below to the mid to upper 70-kHz range (Figs. 4 and 5). At that point there was an abrupt change in the topographic mapping of the cochlea on the IC. For the final 1,000–1,200 μm of depth the tonotopy assumed a quasi-cortical appearance where almost all neurons along a particular vertical axis had the same or nearly the same BFs (Figs. 4 and 5).

It is important to note that only the filter frequencies are represented in the ventral region of the IC. We, therefore, refer to this area as the filter region of the IC. Furthermore, the tonotopic organization of the filter region is in the anterior-posterior axis. In this part of the IC, vertical arrays of neurons tuned to the low filter frequencies (i.e., 77–80 kHz) are represented in the anterior portion while arrays of neurons having progressively higher BFs (i.e., 81–86 or 87 kHz) are represented in the more posterior regions (Fig. 4).

The tonotopic arrangement described above holds true only for the central portion of the IC. A very different organization is found in both the medial and lateral margins of the IC. The tonotopy in the most medial edge of the colliculus is somewhat of a compromise between the dorsal and filter regions. The BFs of neurons in this region proceed from low to high with increasing depth but, with few exceptions, only the filter frequencies are represented. Here the range of BFs extends only from 78 to 91 kHz and the lower, nonfilter, frequencies are noticeably absent (Fig. 6).

The most lateral region of the IC has yet a different organization. In this margin there is also a systematic progression of BFs with depth, from low to high, but the filter frequencies are only sparsely represented (Fig. 6). Typically, the neurons in the most dosal portion have BFs around 20 kHz, or lower, and the BFs systematically increase with depth to a maximum of about 77 kHz, the highest BF we have recorded in this part of the colliculus. However, the distinguishing feature of the lateral margin is the large number of inhibitory neurons, which are by far the most prevalent variety.

Responses to SFM stimuli

In the above analyses neurons were treated in a categorical manner in that they were

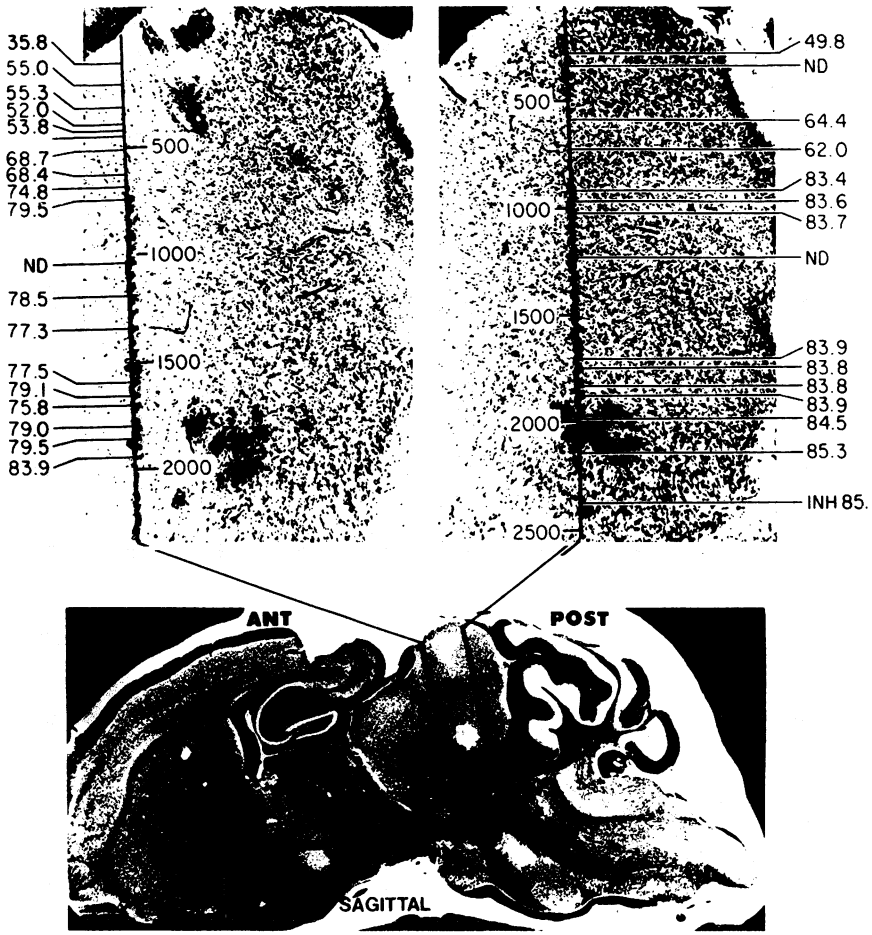

FIG. 4. Sagittal sections through the inferior colliculus of a horseshoe bat showing BFs of neurons encountered in two electrode penetrations. The position of each neuron encountered and its BF are shown. The depth in micrometers within the colliculus is also shown next to each penetration. Regions in the anterior-posterior axis from which these sections were obtained can be seen in the lower sagittal section from one entire brain. Note the progressive increase in BFs from the dorsal surface to a depth of 700–900 μm and the relatively constant BFs for neurons at lower depths. Also note that BFs in the filter region were all 77–79.5 kHz in the anterior electrode tract, whereas in the posterior tract BFs were 83.4–83.9 kHz. All electrode tracts were retraced from alcian blue dye marks deposited from the electrode. Neurons that could not be driven with any acoustic stimulation are labeled ND.

classified either as filter, FM, or nonecholocation neurons, which either locked or did not lock to SFM stimulation. Such analyses showed that the probability of having neuron respond with locked firings to SFM signals is much greater if the neuron is tuned to the filter frequencies than if it is tuned to other frequencies. Moreover, the filter neurons are spatially segregated from other neurons and occupy a disproportionate amount of neural space. The filter neurons are of particular interest because they constitute the neuronal population that processes the modulation patterns in the CF portion of the echo. However, a categorical assessment tells little about how filter neurons process these signals; specifically, how discharge synchrony and vigor are affected by variations in signal intensity or by variations in modulation depth and rate. These features are important because during echolocation bats receive echoes reflected from targets having a variety of shapes and sizes situated at various distances and at various angles with respect to the bat. Each of these factors has an important influence on the echo intensity as

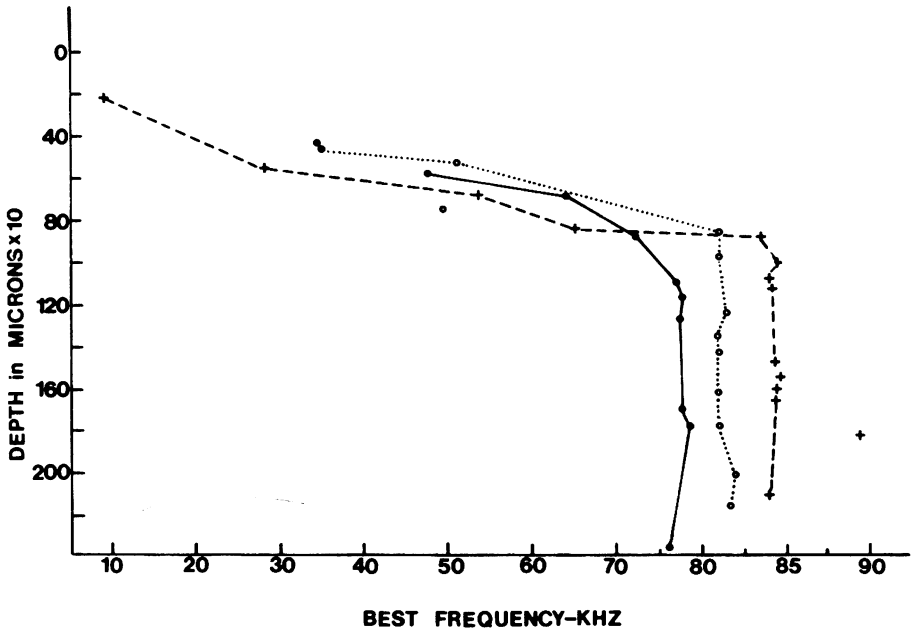

FIG. 5. Change in best frequencies with depth for three penetrations made in the inferior colliculi of two horseshoe bats. The three curves represent penetrations made in the anterior (filled circles) and progressively more posterior portions (open circles and crosses) of the colliculus. Note how similar the best frequencies in the filter region are within a given electrode tract.

well as on the modulation profile. Below we present data that provide some insights into how neurons respond to variations of SFM parameters. We shall first consider the influence of signal intensity on discharge registration and then present data pertaining to the effects of modulation rate and depth, with special attention devoted to filter neurons.

INFLUENCE OF INTENSITY ON FIRING PATTERNS EVOKED BY SFM SIGNALS. The signal intensity was varied systematically in 42 units. Two general types of neurons were found based on the way in which intensity influenced the discharges synchronized to the SFM waveform. The first type of neuron had discharge registrations that were about equally secure at all intensities above threshold. Furthermore, the height of the histogram peaks evoked by SFM signals increased monotonically or slightly nonmonotonically with intensity. The neuron shown in Fig. 7 and one of the neurons shown in Fig. 8 (unit *17-4-17* on the far right) illustrate locking behavior of the first type.

For the second type of neuron the peaks of the PST histograms were highest only at low or moderately low intensities and there was a significant decline or complete absence of locked discharges at higher intensities. Curiously, we never observed any unit that locked only at high intensities and not at lower intensities. If a neuron exhibited synchronized firings to SFM, that synchronization was always apparent within 20 dB of the unit's threshold.

The preference for a small intensity range is illustrated by three neurons in Fig. 8. As an example of such behavior consider unit *15-5-16* (Fig. 8). This neuron responded to 10-dB SPL signals with a firing registration that was, at best, poorly locked to the modulation waveform but at 20 and 30 dB SPL the peaks were well synchronized. Locking was still present at 40 and 50 dB SPL, although it was much reduced, and it almost disappeared completely at higher intensities (60 dB SPL). Of particular importance, two of the other cells shown in Fig. 8 also displayed a deterioration of locked responses at higher intensities but the preferred intensity range differed slightly from cell to cell. This was due in part to the differences in threshold to the SFM signals. The popula-

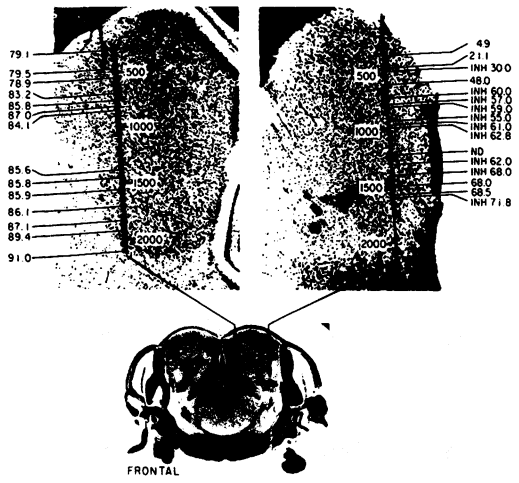

FIG. 6. Frontal sections through the inferior colliculus of a horseshoe bat showing the arrangement of BFs in the lateral and medial margins of the colliculus. In the two top sections, the BF of each neuron and the neuron's depth are shown. Note the orderly increase in filter frequencies, from 79.1 to 91.0 kHz, for the penetration made in the medial margin of the colliculus. This tonotopy contrasts with that seen in the lateral margin where BFs increased from 4.9 kHz to only 71.8 kHz. INH indicates that the neuron had an inhibitory firing pattern and neurons labeled ND could not be driven with any of the acoustic signals at our disposal.

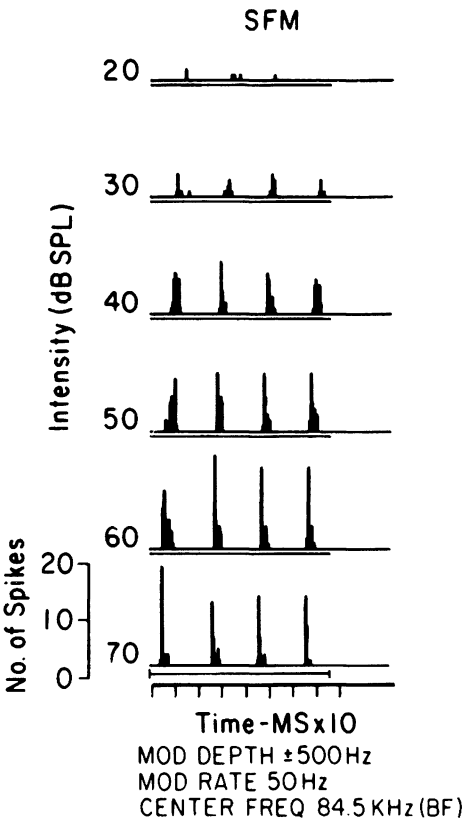

FIG. 7. An example of the effect of intensity on the response patterns of neurons of the first type. Notice that the discharges were well synchronized to the modulation waveform at all intensities. Signal duration is indicated by bars under each histogram. Unit *15-5-17*.

tion of locking neurons, then, apparently forms a continuum where some cells are selective and encode the modulation pattern "best" when the signal falls within a narrow-intensity slot (neurons of the second type) whereas other neurons are less selective and encode the modulation pattern about equally well over a wide range of intensities (neurons of the first type).

An important feature of many, but not all, units having a preferred intensity range for locked firings is that their spike-count functions to tone bursts at the BF were monotonic. This is shown in Fig. 9 where the responses to tone bursts and SFM signals that had various intensities are displayed, side by side, for unit *43-5-18* (the histograms for this unit are also shown in Fig. 8). Notice that the discharges evoked by SFM signals were well locked to the modulating waveform at signal intensities of from 10 to 40 dB SPL but that the locking, as well as the number of discharges per stimulus, deteriorated markedly at 50 dB SPL. The responses to tone bursts at the BF shows, however, that the spike-count function was monotonic and did not decrease with intensity.

EFFECTS OF MODULATION RATE. As was the case for intensity, many units exhibited preferences for certain ranges of modulation rates while other neurons responded with discharges synchronized to the modulation waveform over a wide range of modulation rates. Figure 10 illustrates the differences in the ability to encode progressively higher modulation rates in four neurons. One neuron (unit *36-5-16*) could accurately encode modulation rates up to, and probably beyond, 500 Hz. However, most other neurons reached their limitations at lower modulation rates. For example, each of the three other neurons in Fig. 10 had an upper rate limit that it could follow; unit *13-3-13* could follow rates up to 400–450 Hz, while unit

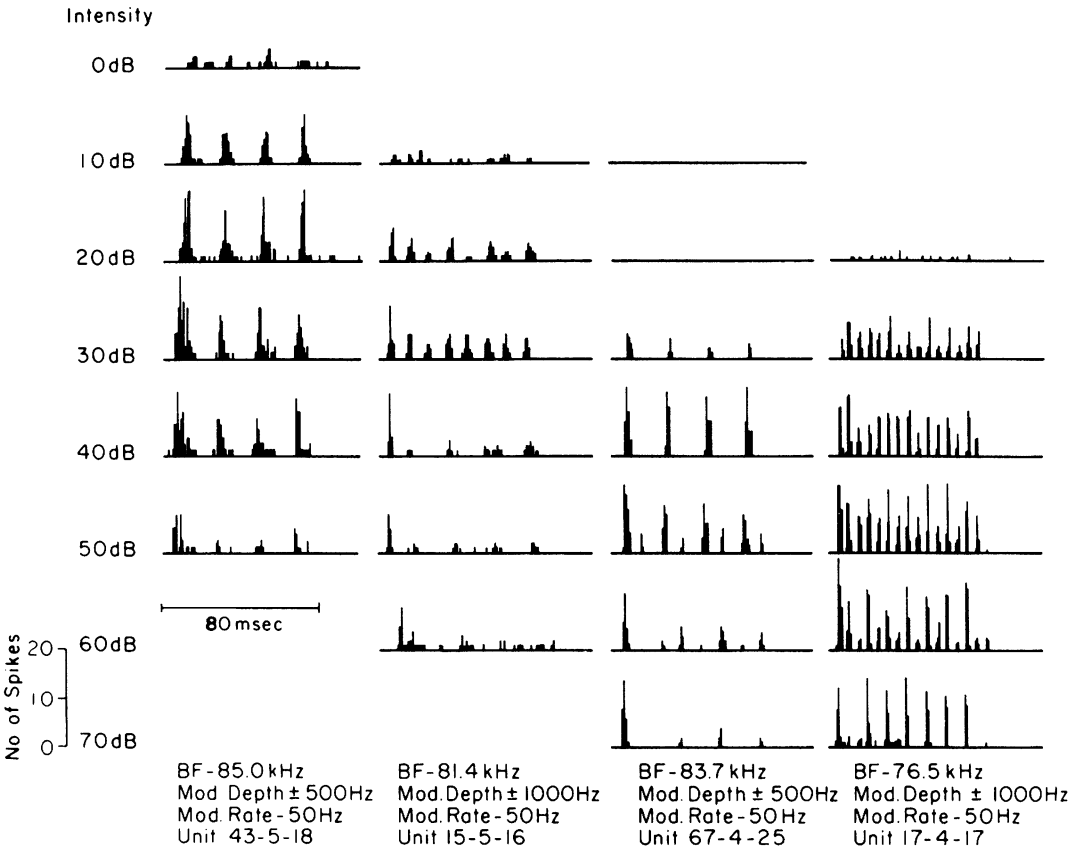

FIG. 8. Effect of stimulus intensity on the locked discharges to SFM signals in four collicular units. The neuron on the right (unit *17-4-17*) had tightly locked firings at all intensities above threshold while the three other units each locked best to only a small range of intensities. All signals were 80 ms long, as indicated by the bar at lower left.

15-5-17 could only follow rates up to about 250 Hz or slightly lower. The limiting rate for unit *28-3-22* was less than 100 Hz.

EFFECTS OF MODULATION DEPTH. The majority of units responding with locked firings to SFM signals exhibited reasonably good synchronization to at least some modulation depth between ±500 to ±2,000 Hz. A few filter neurons locked to depths as low as ±20 or ±40 Hz. These depths approach the lowest modulation depths of ±6 and ±10 Hz capable of evoking locked discharges in filter neurons that have been recorded from the mustache bat (30) and from the horseshoe bat (21), respectively. We should point out that modulation depth was not a parameter in which we were primarily interested and, as a consequence, the response patterns evoked by a wide range of modulation depths were studied in only 10 neurons. However, in each of these cells a particular range of modulation depths was effective for generating locked discharges. As was the case for both intensity and rate, the range of effective depths seemed to span a continuum where some units locked best only to high and intermediate depths while others locked to intermediate and low depths.

Effects of carrier frequency

Although horseshoe bats stabilize echo frequencies by compensating for Doppler shifts, the continuous changes in flight speed and orientation between the bat and its target result in the reception of a variety of echo frequencies. For any given echo carrier frequency, some units will be stimulated at their BFs whereas others will be excited by

frequencies falling either below or above their BFs. The prior discussion was concerned with response features to SFM signals when the carrier frequency of the SFM signal was set at the unit's BF. In this section we consider the locking behavior of 34 cells when the carrier frequency was systematically moved in and around the unit's tuning curve at a particular intensity. We shall refer to the frequency range of tone bursts capable of evoking responses at a given intensity as the unit's excitatory area (EA) and the range of carrier frequencies capable of eliciting locked responses at a particular signal intensity as the SFM excitatory area.

The most striking feature of the SFM excitatory areas of filter units is the very sharp boundaries on both the high- and low-frequency sides. This was especially evident in units that locked in a symmetrical manner around a carrier set at the unit's BF. In Fig. 11 is an example of a symmetrical cell exhibiting dramatic changes in responsiveness for shifts of only 70–100 Hz in carrier frequency. The sharp changes in locked discharges can apparently be explained on the basis of the extent to which the SFM signals encroached on the EA. In this unit, the EA was only 370 Hz wide with an excitatory frequency range of from 83.58 to 83.95 kHz. The BF was 83.75 kHz. Tone bursts at the BF evoked brisk phasic on-responses at 60 dB SPL, the intensity of the SFM signals. When the modulation depth was ±500 Hz and the carrier frequency was set at 83.0 kHz, the SFM signal failed to enter the EA and no firings were evoked. When the carrier was 83.10 kHz, the SFM signal just clipped the lower limit of the EA and some locked firings were elicited. The locked firings became increasingly vigorous as the carrier frequency progressively entered more of the EA. As the carrier rose above the BF, the histogram peaks decreased in amplitude and an upper limit for eliciting responses was reached when the carrier was 84.43 kHz. The unit failed to respond when the SFM carrier was 84.5 kHz, i.e., when the signal just failed to enter the upper part of the EA.

Other units had asymmetric SFM excitatory areas where the locking, as judged by the amplitudes of the peaks in the histograms, was superior either on the low- or on the high-frequency side of the BF. Enhanced

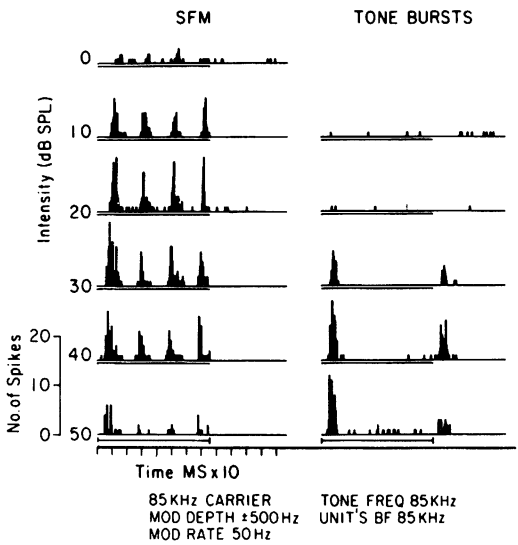

FIG. 9. Differential behavior to SFM and tone-burst stimulation. Notice that the neuron responded monotonically with intensity to tone bursts but was clearly nonmonotopic to SFM. The threshold for SFM was also approximately 25 dB lower than it was for tone bursts at the unit's BF. Signal duration is indicated by bars below each histogram.

locking when the carrier was on the high-frequency side of the EA has also been reported by Schuller (Fig. 3 of Ref. 21). Unit *15-5-17* (Fig. 12) is an example of a unit that locked much better to carrier frequencies at or below the BF than it did when the carrier frequency was higher than the BF. Besides the very narrow (600 Hz) EA and the sharp boundaries of the SFM excitatory area, especially on the low-frequency side, two additional features of this unit are noteworthy. First is the superiority of carrier frequencies of 85.0 kHz and below for evoking high-amplitude peaks in the histograms as compared to carrier frequencies above 85.0 kHz. For example, when the carrier was set at 85.3 kHz, with a modulation depth of ±500 Hz, locked responding was quite weak even though the SFM signal clearly swept through the 84.9-kHz BF as well as most of the excitatory area. On the other hand, when the carrier was set at 84.4 kHz, brisk, well-synchronized firings were evoked and produced the high-amplitude peaks in the histograms. The second noteworthy feature is the marked contrast between the relatively poor responsiveness to tone bursts at the BF and the high-amplitude peaks evoked by

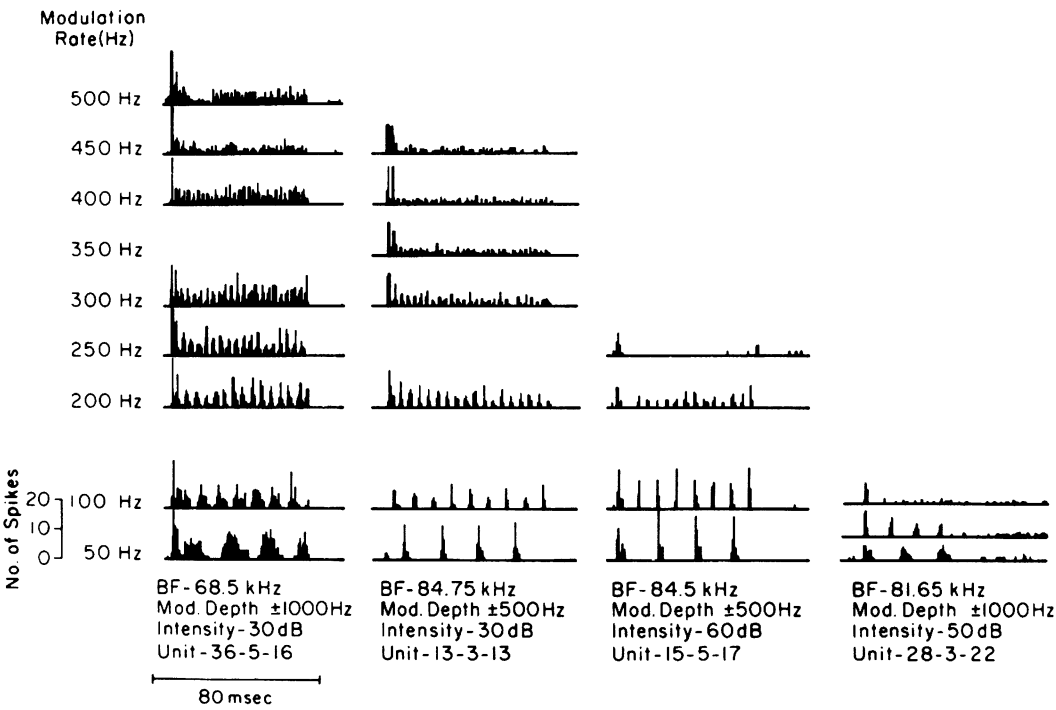

FIG. 10. Effect of different modulation rates on the locked discharges evoked by SFM signals in four collicular units. Unit *36-5-16* (left) followed rates as high as 500 Hz with well-synchronized firings while unit *28-3-22* (right) could only follow rates below 100 Hz. The two other units could follow rates up to 200 Hz (unit *15-5-17*) and 300–400 Hz (unit *13-3-13*). All signals were 80 ms in duration, as indicated by the bar at lower left.

SFM signals having carrier frequencies of 85 kHz and below. This unit illustrates, once again, the large discrepency that can exist between the encoding features for tone bursts and more complex stimuli.

Effects of intensity on SFM excitatory area

SFM excitatory areas were obtained at two or more intensities above the BF threshold in 10 units. Although the sample size is small, some of the results are quite interesting and are worth recounting. In general, the SFM excitatory areas become wider with intensity and the increase in width followed directly from the changes in the unit's EA. If the unit were very sharply tuned, as was the case for most of the filter units, there was little broadening of the SFM excitatory area whereas the broadening was considerably greater in most nonfilter units due to the widening of the EA at higher intensities.

The interaction of intensity and carrier frequency often led to complex changes in the SFM tuning properties. The complexity was evident in gaps in the SFM excitatory area, where certain carriers that evoked little or no locked firings were sandwiched between carriers that evoked brisk, well-synchronized responses. This feature is illustrated by unit *16-3-13* (Fig. 13), which had a typical asymmetric SFM excitatory area at an intensity of 30 dB SPL. When the intensity was increased to 40 dB SPL, the first notable gap appeared for the 85.0-kHz carrier. When the intensity was 70 dB SPL, the gap widened to include carriers ranging from 84.0 to 85.0 kHz that were surrounded by well-developed discharge peaks at carriers of 83.5 and 85.5 kHz. The appearance of this SFM excitatory area is due to the fact that both monotonic (82.5 and 85.5 kHz) as well as strongly nonmonotonic input-output functions were generated by SFM signals having different carrier frequencies.

DISCUSSION

The CF portion of the biosonar signals is clearly of considerable importance to the

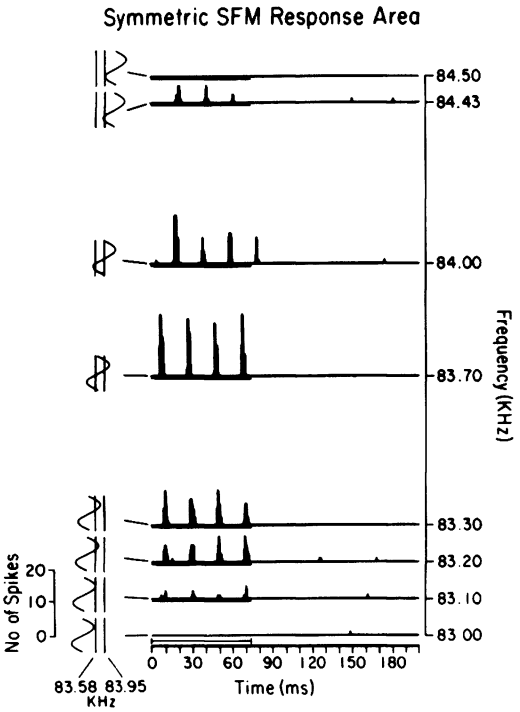

FIG. 11. Symmetric SFM excitatory area. The two parallel lines on the left represent the low- and high-frequency sides of the unit's tuning curve at 40 dB SPL (i.e., the unit's excitatory area). The BF was 83.75 kHz. The position of the modulation waveform within the excitatory area is shown for different carrier frequencies. The modulation depth was ±500 Hz and the modulation rate was 50 Hz. The signal duration is indicated by the bar below each histogram. Unit *67-4-25*. See text for further explanation.

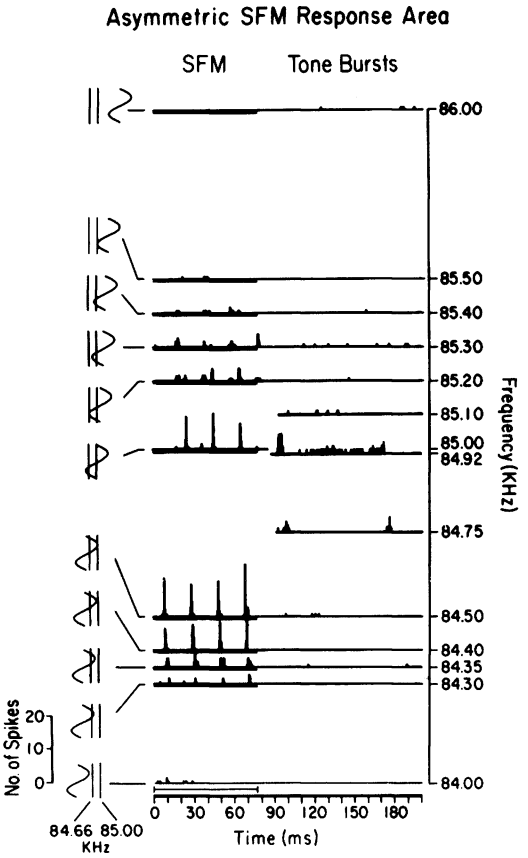

FIG. 12. Asymmetric SFM excitatory area. The position of the modulation waveform within the excitatory area is shown to the left of each histogram. The SFM histograms were generated with signals that had modulation depths of ±500 Hz and modulation rates of 50 Hz. Histograms on the right side of the figure were generated with tone bursts. The BF was 84.92 kHz and the EA was very narrow. Notice that SFM signals having carriers below 85 kHz were much more effective than were carriers above 85 kHz. All signals were 50 dB SPL. The signal duration is indicated by the bar below each histogram. Unit *15-5-17*. See text for further explanation.

long CF-FM bats. This is reflected in the remarkable specializations that have evolved in these bats for processing the CF component. For convenience, the specializations can be divided into architectural and physiological adaptations.

The two best-known architectural specializations in the central nervous system are the novel tonotopic organization of neurons tuned to the filter frequencies and the overrepresentation of these frequencies at all levels of the auditory pathway (2, 8, 12, 23, 27, 29, 30). The unique tonotopy was first observed by Suga and Jen (27) in the cortex of the long CF-FM mustache bat and a similar organization has recently been found by Ostwald (12) in the auditory cortex of the horseshoe bat. One of the points emerging from this study is that a segregated filter region having an unusual tonotopic organization is also found in the IC.

The novel feature of the tonotopic arrangement in the horseshoe bat's IC can be appreciated by comparison with the auditory tectum of other mammals. In cats, for example, the isofrequency contours, which presumably reflect the orientation of the incoming lateral lemiscal fibers, are arranged in an onionskin-like series of curved shells. Those shells receiving input from the basal cochlea, representing high frequencies, are

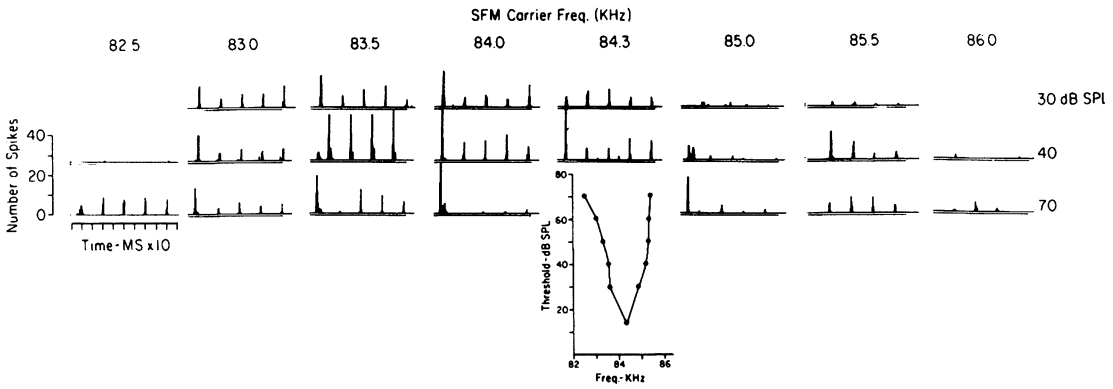

FIG. 13. SFM excitatory areas at three intensities. The BF was 84.3 kHz. The modulation depth was ±1,000 Hz and the modulation rate was 50 Hz. Notice the asymmetry in the SFM excitatory area at 30 dB SPL where the carrier frequencies at or below the BF were clearly superior to carriers above the BF for evoking vigorous, locked discharges. Gaps in the SFM excitatory area are first seen for the 85-kHz carrier when the signal intensity was 40 dB SPL. The gaps became wider at 70 dB SPL and encompassed carriers from 84 to 85 kHz. Unit *16-3-13*.

located ventrally; stacked above them are the shells whose inputs derive from progressively more apical portions of the cochlea (7, 25). Such a laminar arrangement of isofrequency contours is also found in the IC of several species of mollossid bats (31; unpublished observations) and it appears to be the general arrangement of the incoming lemniscal fibers in the dorsal, nonfilter region of the horseshoe bat's IC.

However, the tonotopic organization in the ventral, filter region of the IC is clearly different from the arrangement presented above. In the ventral region, the insofrequency contours of the filter frequencies are orthogonal to those of the dorsal region, suggesting that the lateral lemniscal fibers project perpendicularly to the collicular surface. If this proves to be the case, then the innervation pattern in the ventral portion of the IC would more closely resemble the thalamic input to the cerebral cortex than it would the concentric innervation pattern of the vertebrate acoustic tectum.

The other striking architectural feature is the overrepresentation of the filter frequencies (2, 23, 29). The functional significance of the overrepresentation is considered below and has been discussed in detail in recent reports (13, 23).

A physiological feature that is closely associated with filter units is the ability to respond to SFM signals with discharges tightly locked to the modulation waveform. In previous reports Suga and Jen (28) suggested and Schuller (21) found that it is largely the filter neurons that can encode the SFM patterns. The results of the present study support, in part, this suggestion, since they demonstrate a dramatic difference in the absolute numbers and proportions of filter cells locking to SFM when compared to neurons tuned to the FM or nonecholocation frequencies. However, the results also show that 35% of the FM and 34% of the nonecholocation neurons locked to SFM waveforms. Furthermore, the nonfilter neurons that locked to SFM exhibited the same preferences for certain signal intensities, modulation rates and, with one important exception, modulation depths as did the filter neurons. Consequently, neurons tuned to the horseshoe bat's entire audible range are able to encode frequency-modulation patterns although the proportional representation of filter units that lock to SFM is greater than the proportion, as well as the absolute number, of locking neurons tuned to other frequencies.

The one response property that is only observed in some filter neurons, and never in nonfilter units, is the ability to fire in registration with SFM waveforms having modulation depths as low as ±10–40 Hz (21). This finding, coupled with previous reports showing that large proportions of filter neurons discharge in synchrony with SFM waveforms, has led to the hypothesis that the

locked discharge patterns are a direct result of the very sharp tuning of filter neurons (21, 30). The rationale is that a modulated signal sweeping in and out of a very narrow EA would evoke firings only when the signal was within the EA, thereby producing a response pattern having the same periodicity as the SFM waveform. However, it should be pointed out that discharges synchronized to small modulation depths can also be evoked when the spectrum of the signal is confined entirely to, and sweeps back and forth within, the EA (21). Furthermore, if tuning were the predominant factor, then one would expect there to be a strong correlation between $Q_{10\,dB}$ values and the lowest modulation depth capable of evoking discharges locked to the SFM waveform. Such a correlation has not been found. Rather, neurons that lock to very low modulation depths always have $Q_{10\,dB}$ values of at least 40 but neurons having even sharper tuning curves, with $Q_{10\,dB}$ values of 100–300, seem not to derive any additional advantage in this regard. In other words, it is not possible to predict the lowest modulation depth that a filter unit will synchronize with by knowing its $Q_{10\,dB}$ value. The conclusion from all of this seems to be that while tuning may contribute to the locking evoked by low modulation depths, the sequence and potency of the synaptic events evoked by the temporal and spectral features of the signals are at least as important, if not more so.

Functional implications of Doppler-shift compensation system and filter units

The filter system evolved in conjunction with a specialized emitting system (11, 14, 18, 22, 24). Under laboratory conditions, the system works in the following way: when echoes returning to the bat are not Doppler shifted and have the same frequencies as the emitted cry, the horseshoe bat emits pulses having a CF component of 81.0–84.0 kHz, regulated to an accuracy of ±100 Hz in an individual bat. Schuller et al. (22) refer to this frequency as the bat's resting frequency. If the bat received an echo that is Doppler shifted upward, the subsequent emitted pulses are lowered such that the echoes are held within a narrow band of frequencies ±50–100 Hz wide. The frequency at which the bat holds the echo is called the reference frequency and is typically 100–300 Hz higher than the resting frequency; e.g., the reference frequency would be 83.1–83.3 kHz if the resting frequency were 83.0 kHz.

One cannot help but be impressed with the precision of the Doppler compensation system. However, the constant-frequency echoes heard by the bats in experimental studies rarely, if ever, occur outside of the laboratory. In this regard, it is important to remember that echolocation evolved as a mechanism to enable bats to hunt insects in the night sky. The echoes reflected from a small insect are not constant in frequency but are rich in frequency and amplitude modulations, which are created as the echo CF is reflected from the insect's beating wings. These considerations led to the hypothesis that the filter system is important for encoding the profile of modulations in the echo CF, which provides the information for prey recognition (5, 9, 13, 18, 20, 23, 28). The results of the present study provide strong support for this hypothesis and it is worthwhile to develop the arguments in favor of prey recognition in greater detail.

It seems reasonable to suppose that on detecting a target, the bat first needs to determine if the target is animate or is inanimate, i.e., a falling leaf or background objects. A basis for such a discrimination resides in the temporal patterns of the responding elements. Flying insects can, presumably, be recognized as such by the synchronized discharges locked to the modulation pattern of the echo, whereas the echo from an inanimate object will be encoded in a manner more like that of a tone burst.

After ascertaining the nature of the target, it may well be that the horseshoe bat seeks to determine whether or not the insect is one that is palatable and worthy of pursuit and capture. In this context, the two manipulations the bat performs on the emitted CF component during the goal-directed portion of echolocation seem to be important. The first type of manipulation is the systematic lengthening of the emitted CF component that occurs after target detection and continues for a considerable time as the bat tracks its target (11, 15). One effect of the pulse lengthening is to increase the number

of modulation cycles present in each echo. It appears, then, that horseshoe bats actively create a signal that is designed to ensure that an echo having a sufficient number of modulation cycles will be received.

The second manipulation concerns Doppler-shift compensation, where the bat stabilizes the echoes to a narrow frequency band around its reference frequency. Since the echoes from a small insect will have modulations, the bandwidth of the echoes are considerably broader than the bandwidth of the emitted CF component. While hunting insects, the bat presumedly attempts to match more or less roughly the echo carrier frequency to its reference frequency. The significance of this behavior is that a disproportionately large number of filter neurons are tuned to frequencies ± 1.5 kHz around the bat's reference frequency (23). In other words, by manipulating the frequency of the emitted CF component, each echo is confined to a very narrow frequency band and this behavior ensures the bat that each echo will be processed by a large population of sharply tuned filter neurons, most of which are well suited for encoding some component of the modulation pattern. In this regard, Doppler-shift compensation can be thought of as a mechanism for "foveation," a point developed in considerable detail in other reports (4, 13, 23).

Insights into the spatial extent of activity evoked by a modulated echo can be obtained from consideration of the features of the SFM excitatory areas. There is, however, a caveat in such an analysis. The downward (or upward) movement of an insect's wing will reflect sound from each position along its length. Since each place moves with a different velocity, an echo will, in reality, not contain a modulation of one frequency, as occurs in SFM signals, but rather a modulation of a frequency band (18). In this regard, the very sharp tuning of most filter units should reduce the differential effects of a modulation of a narrow frequency band compared to the modulation of a single frequency. But there is another difference between natural and artifical echoes. In natural echoes, a simultaneous amplitude modulation will also be present due to the changes in the effective reflecting area of the moving wing. The SFM signals used in the present experiments, on the other hand, represent an approximation to the natural frequency modulation without the confounding influence of amplitude modulation. The discharge patterns evoked by SFM signals, then, can be thought of as reasonable approximations to the responses that would evoked by a component of the more complex natural signal.

If one assumes that filter units respond to frequencies in a natural echo as they do to SFM signals, then the characteristics of SFM excitatory areas suggest that a modulated echo should produce more or less equally vigorous activity over a large expanse of neural tissue. That is, the discharge rate and synchrony should be maximal in units tuned to the echo-center frequency and having symmetric SFM excitatory areas. However, the activity should also be maximal in other units having BFs above and yet in other units having BFs below the center frequency of the echo because these neurons have asymmetric SFM excitatory areas. Furthermore, the tuning properties of the filter neurons indicate that the active region will have sharply confined boundaries in neural space, whereas the tonotopy suggests the geometric arrangement of the elements within that region.

Within the active region, the echo will evoke discharges synchronized to the modulation waveform. Moreover, the frequency changes occurring in the echo will, by virtue of their variations with time, also cause a corresponding shifting, back and forth, of the locus of activity as the spectrum enters and leaves the sharp excitatory areas of elements tuned to different frequencies. Thus, the frequency-modulation pattern is coded both by the temporal sequence of discharges in a sharply bounded subpopulation of filter neurons and in the spatial shifting of activity within that subpopulation over time.

Due to changes in position, orientation, and speed of either the bat or its target, subsequent echoes will differ more or less in carrier frequency, modulation pattern, and intensity from the previous echo(es) (18). In principle, each echo will be encoded in a similar manner. However, the preferences of many filter units for selective ranges of intensity as well as modulation rate and depth suggest that the changes in echo parameters

will cause some neural elements to drop out and new elements to be recruited, while others will simply change response vigor and/or firing registration to reflect the changes in echo characteristics. In short, the properties of filter neurons endow the system with the ability to encode the perturbations imposed on the echo CF component with the sum total of spatiotemporal activity being a dynamic pattern that differs from echo to echo.

Given the capacity to encode target features, the question arises as to whether the information derived from one echo is sufficient for target recognition or whether several echoes are required. In this regard, it should be pointed out that there is considerable variation of both wing length and wingbeat frequency among insect species. Both of these features have profound effects on the frequency and amplitude modulations in the echo CF components and must result in substantial differences among the spatiotemporal patterns of activity generated by echoes reflected from different insects. Schuller (21) has discussed this issue in considerable detail and from a number of considerations has concluded that the possibility for recognition from one echo, while not impossible, is unlikely. On the other hand, the system encodes modulation patterns with great precision and diversity. It therefore seems reasonable to suppose that a horseshoe bat can associate the acoustic image derived from the profile of activity integrated over several echoes with a particular population of insect.

Whether the bat chooses to act on this information or under what conditions it uses the information is, at the present time, not entirely clear. Little is known about the hunting strategy of the horseshoe bat but recent studies of the long CF-FM mustache bat (5) as well as the horseshoe bat (18) are highly suggestive. Both studies have shown that long CF-FM bats pursue and capture free-flying and tethered insects when the wings are moving rapidly but they are not attracted to insects or mechanical models when the wing beats are slow. Furthermore, Goldman and Henson (5) showed that the mustache bat, *Pteronotus parnellii*, is selective in its choice of which insects, among a population having fast wingbeat frequencies, it will track and capture. Several species of beetles and moths are ignored by the mustache bat, whereas other species of moths and beetles are vigorously pursed and eaten. If the hunting strategy of the horseshoe bat proves to be as selective as that of the mustache bat, then the encoding properties of the filter system would clearly be important for prey identification.

ACKNOWLEDGMENTS

The encouragement and suggestions of Gerhard Neuweiler and Albert Feng are gratefully acknowledged.

This study was supported by grants from the Alexander von Humboldt Foundation and the University Research Institute at the University of Texas to G. D. Pollak and by Stiftung Volkswagenwerk, AZ: 111858 and by the Deutsche Forschungsgemeinschaft Grants Schu 390/12 and Br 59312.

Present address of G. D. Pollak: Dept. of Zoology, University of Texas, Austin, TX 78712.

Received 28 March 1980; accepted in final form 17 September 1980.

REFERENCES

1. AITKIN, L. M. Tonotopic organization at higher levels of the auditory pathway. In: *International Review of Physiology. Neurophysiology II*, edited by R. Porter. London: University Park, 1976, vol. 10, p. 249–280.
2. BRUNS, V. Peripheral auditory tuning for fine frequency analysis by the CF-FM bat, *Rhinolophus ferrumequinum*. I. Mechanical specialization of the cochlea. *J. Comp. Physiol.* 106: 77–86, 1976.
3. BRUNS, V. Peripheral auditory tuning for fine frequency analysis by the CF-FM bat, *Rhinolophus ferrumequinum*. II. Frequency mapping of the cochlea. *J. Comp. Physiol.* 106: 87–97, 1976.
4. BRUNS, V. AND SCHMIESZEK, E. Regional variation in the innervation pattern in the cochlea of the greater horseshoe bat. *Hearing Res.* 3: 27–43, 1980.
5. GOLDMAN, L. J. AND HENSON, O. W., JR. Prey recognition and selection by the constant frequency bat, *Pteronotus p. parnellii*. *Behav. Ecol. Sociobiol.* 2: 411–419, 1977.
6. HARNISCHFEGER, G. An improved method for extracellular marking of electrode tip positions in nervous tissue. *J. Neurosci. Methods* 1: 195–200, 1979.
7. MERZENICH, M. M. AND REED, M. D. Representation of the cochlea within the inferior colliculus of the cat. *Brain Res.* 77: 397–315, 1974.

8. MÖLLER, J., NEUWEILER, G., AND ZÖLLER, H. Response characteristics of inferior colliculus neurons of the awake CF-FM bat, *Rhinolophus ferrumequinum*. I. Single tone stimulation. *J. Comp. Physiol.* 125: 217–225, 1978.
9. NEUWEILER, G. Auditory processing of echoes: peripheral processing. In: *Animal Sonar Systems*, edited by R. G. Busnel and J. F. Fish. New York: Plenum, 1980, p. 519–548.
10. NEUWEILER, G. AND VATER, M. Response patterns to pure tones of cochlear nucleus units in the CF-FM bat, *Rhinolophus ferrumequinum*. *J. Comp. Physiol.* 115: 119–133, 1977.
11. NOVICK, A. Echolocation in bats: some aspects of pulse design. *Am. Sci.* 59: 198–209, 1971.
12. OSTWALD, J. The functional organization of the primary auditory cortex in the CF-FM bat, *Rhinolophus ferrumequinum* In: *Animal Sonar Systems*, edited by R. G. Busnel and J. F. Fish. New York: Plenum, 1980, p. 953–956.
13. POLLAK, G. Organization and encoding features of neurons in the inferior colliculus of bats. In: *Animal Sonar Systems*, edited by R. G. Busnel and J. F. Fish. New York: Plenum, 1980, p. 549–588.
14. RUBSAMEN, R. AND SCHULLER, G. Activity of laryngeal nerves due to the production of ultrasonic echolocation sounds in the CF-FM bat, *Rhinolophus ferrumequinum*. In: *Animal Sonar Systems*, edited by R. G. Busnel and J. F. Fish. New York: Plenum, 1980, p. 969–972.
15. SCHNITZLER, H.-U. Discrimination of thin wires by flying horseshoe bats (Rhinolophidae). In: *Animal Sonar Systems*, edited by R. G. Busnel. Jouyen.Josas: Laboratorie de Physiologie Acoustique, 1967, vol. 1, p. 69–87.
16. SCHNITZLER, H.-U. Die Ultraschall-Ortungslaute der Hufeisen-Fledermause (*Chiroptera, Rhinolophidae*) in verschiedenen. Orientier-ungesituationen. *Z. Vergl. Physiol.* 57: 376–408, 1968.
17. SCHNITZLER, H.-U. Control of Doppler-shift compensation in the greater horseshoe bat, *Rhinolophus ferrumequinum, J. Comp. Physiol.* 82: 79–92, 1973.
18. SCHNITZLER, H.-U. AND HENSON, O. W., JR. Performance of airborne anonal sonar systems: echolocation in microchoropteran bats. In: *Animal Sonar Systems*, edited by R. G. Busnel and J. F. Fish. New York: Plenum, 1980, p. 109–182.
19. SCHNITZLER, H.-U., SUGA, N., AND SIMMONS, J. A. Peripheral auditory tuning for fine frequency analysis by the CF-FM bat, *Rhinolophus ferrumequinum*. *J. Comp. Physiol.* 106: 99–110, 1976.
20. SCHULLER, G. Echoortung bei *Rhinolophus ferrumequinum* mit frequenz-modulierten Lauten. Evoked potentials in colliculus inferior. *J. Comp. Physiol.* 77: 306–331, 1972.
21. SCHULLER, G. Coding of small sinusoidal frequency and amplitude modulations in the inferior colliculus of the CF-FM bat, *Rhinolophus ferrumequinum*. *Exp. Brain Res.* 34: 117–132, 1979.
22. SCHULLER, G., BEUTER, K., AND SCHNITZLER, H.-U. Response to frequency shifted arificial echoes in the bat, *Rhinolophus ferrumequinum*. *J. Comp. Physiol.* 89: 275–286, 1974.
23. SCHULLER, G. AND POLLAK, G. D. Disproportionate frequency representation in the inferior colliculus of horseshoe bats: evidence for an "acoustic fovea." *J. Comp. Physiol.* 132: 47–54, 1979.
24. SCHULLER, G. AND SUGA, N. Laryngeal mechanisms for the emission of CF-FM sounds in the Doppler-shift compensating bat, *Rhinolophus ferrumequinum*. *J. Comp. Physiol.* 107: 253–262, 1976.
25. SEMPLE, M. N. AND AITKIN, L. M. Representation of sound frequency and laterality by units in the central nucleus of cat inferior colliculus. *J. Neurophysiol.* 42: 1626–1639, 1979.
26. SIMMONS, J. A. Response of the Doppler echolocation system in the bat, *Rhinolophus ferrumequinum*. *J. Acoust. Soc. Am.* 56: 672–682, 1974.
27. SUGA, N. AND JEN, P. H.-S. Disproportionate tonotopic representation for processing CF-FM sonar signals in the mustache bat's auditory cortex. *Science* 194: 542–544, 1976.
28. SUGA, N. AND JEN, P. H.-S. Further studies on the peripheral auditory system of the CF-FM bats specialized for fine frequency analysis of Doppler-shifted echoes. *J. Exp. Biol.* 69: 207–232, 1977.
29. SUGA, N., NEUWEILER, G., AND MÖLLER, J. Peripheral auditory tuning for fine frequency analysis by the CF-FM bat, *Rhinolophus ferrumequinum*. IV. Properties of peripheral auditory neurons. *J. Comp. Physiol.* 106: 111–125, 1976.
30. SUGA, N., SIMMONS, J. A., AND JEN, P. H.-S. Peripheral control of acoustic signals in the auditory system of echolocating bats. *J. Exp. Biol.* 62: 277–311, 1975.
31. VATER, M., SCHLEGEL, P., AND ZÖLLER, H. Comparative auditory neurophysiology of the inferior colliculus of two molossid bats, *Molossus ater* and *Molossus molossus*. *J. Comp. Physiol.* 131: 137–145, 1979.