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A Neurophysiological Study of the Auditory Midbrain of the Goldbish

Zhong-min Lu
Loyola University Chicago

LOYOLA UNIVERSITY OF CHICAGO

A NEUROPHYSIOLOGICAL STUDY OF THE AUDITORY MIDBRAIN OF THE GOLDFISH

A THESIS SUBMITTED TO
THE FACULTY OF THE GRADUATE SCHOOL
IN CANDIDACY FOR THE DEGREE OF
MASTER OF ARTS

BY

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CHICAGO, ILLINOIS

MAY 1993

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Single units of the goldfish torus semicircularis (TS) were recorded in response to pure tones. Response areas (RA) were obtained by recording the number of spikes evoked by tones in a range of frequencies and levels within the units' dynamic range. RAs gave estimates of best sensitivity (BS), characteristic frequency (CF), most excitatory frequency at each level (BF), and Q_{10dB}. Peri-stimulus-time histograms (PSTH), inter-spike interval histograms (ISIH), and period histograms were obtained at various frequencies and levels to describe the units' temporal response patterns.

The distribution of CF is nonuniform with modes at 155, 455, and 855 Hz. The distribution of the coefficient of synchronization to standard tones is also nonuniform, revealing a dichotomy between units with little or no phase-locking and those that phase-lock strongly. PSTHs for units without significant phase-locking vary widely and include patterns resembling those of the mammalian auditory brainstem. Compared with saccular afferents, torus units tend to have lower spontaneous rates, greater sensitivity, and sharper tuning. Unlike saccular afferents, BF is independent of level for most torus units. Some

torus units are similar to saccular afferents while others reveal significant transformations of information between the periphery and the midbrain.

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Special thanks to Fengmei for all I owe to her, and for her love and patience. She has put up with me for these years.

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Vita

The author, Zhong-min Lu, is the son of Jia-zhen Wang and Ying-jie Lu. He was born on September 28, 1963, in Beijing, PRC.

In September, 1981, Mr. Lu entered Beijing Teachers' College, Beijing, PRC, receiving the degree of Bachelor of Science in Biology in July, 1985.

In September, 1985, Mr Lu, with outstanding academic credits and ranked among the top 3%, was recommended to enter the graduate school of Beijing Teachers' College. He received the degree of Master of Science in Neurophysiology jointly from Beijing Teachers' College and Yunnan University.

In September, 1989, Mr. Lu was granted a graduate assistantship in psychology at Loyola University of Chicago, enabling him to complete the Master of Arts in 1993. He is currently a member of the Acoustical Society of America and the Society for Neuroscience.

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CHAPTER I

INTRODUCTION

Behavioral experiments on sound detection and discrimination in several fish species have revealed a sense of hearing essentially like that of other vertebrates (see Fay 1988, for a review of the behavioral data). Among fishes, the frequency range of hearing, sensitivity, and sound discrimination abilities are particularly well developed in the goldfish (Carassius auratus). Neurophysiological studies on saccular nerve fibers (e.g., Furukawa and Ishii 1967; Fay and Ream 1986) have demonstrated many functional similarities between the goldfish and other vertebrates, including amphibians (e.g., Narins 1987), reptiles (e.g., Köppl and Manley 1990), birds (e.g., Manley and Gleich 1992), and mammals (e.g., Ruggero 1992).

In a series of studies aimed at revealing the neural codes underlying sensory behaviors in the goldfish, Fay and his colleagues have investigated the representation of acoustic information with respect to frequency discrimination (Fay 1978b), level discrimination (e.g. Fay 1985), masking and temporal summation (Fay and Coombs 1983; Coombs and Fay 1989, Fay 1991), directional hearing (Fay 1984), temporal envelope processing (Fay 1980; 1982a), and the analysis of complex spectra (Fay et al. 1983). These and other studies on primary afferents have led to hypotheses regarding the

dimensions of neural activity used in the brain for the detection, discrimination, and perception of sound (e.g., Fay 1992; Fay and Coombs 1992). For example, goldfish are able to detect and discriminate differences between frequency components presented both successively (e.g., Fay 1970) and simultaneously (e.g., Fay and Coombs 1983; Fay 1992). The peripheral neural codes underlying frequency analysis have been hypothesized to be temporal rather than spatial patterns, in part because phase-locking error in primary saccular afferents predicts frequency discrimination thresholds (Fay 1978), and because peripheral tuning is rather broad with "grouped" rather than continuously distributed characteristic frequencies (Fay and Ream 1986).

In order to understand the fate of peripheral tuning and phase-locking patterns in the brain, and as a step toward evaluating hypotheses about the mechanisms underlying behavioral frequency analysis, this paper describes the response properties of units of the torus semicircularis (TS), the major auditory nucleus of the midbrain in fishes. The TS is analogous and possibly homologous to the mammalian inferior colliculus, receiving ascending information from medullary nuclei (portions of the anterior, descending, medial, and superior olivary nuclei) (Striedter 1991; Fritzsch et al. 1990; McCormick et al. 1992), and descending information from the diencephalon (Striedter 1991). Although there have been several neurophysiological studies of the response of units or unit clusters in the auditory brainstem of fishes (e.g., Enger 1967; Page 1970; Piddington 1971a, b; Horner et al. 1980; Sawa 1976; Fay

1982b; Plassmann 1985; Echteler 1985a, b; Nederstigt and Schellart 1986; Crawford 1993), there are no data on the transformations of peripherally coded information that occur in the brain. The present study was carried out to describe some of these transformations evident at the level of the TS, and to help guide the development of hypotheses and further experiments on the brain mechanisms of sound perception in fishes.

CHAPTER II

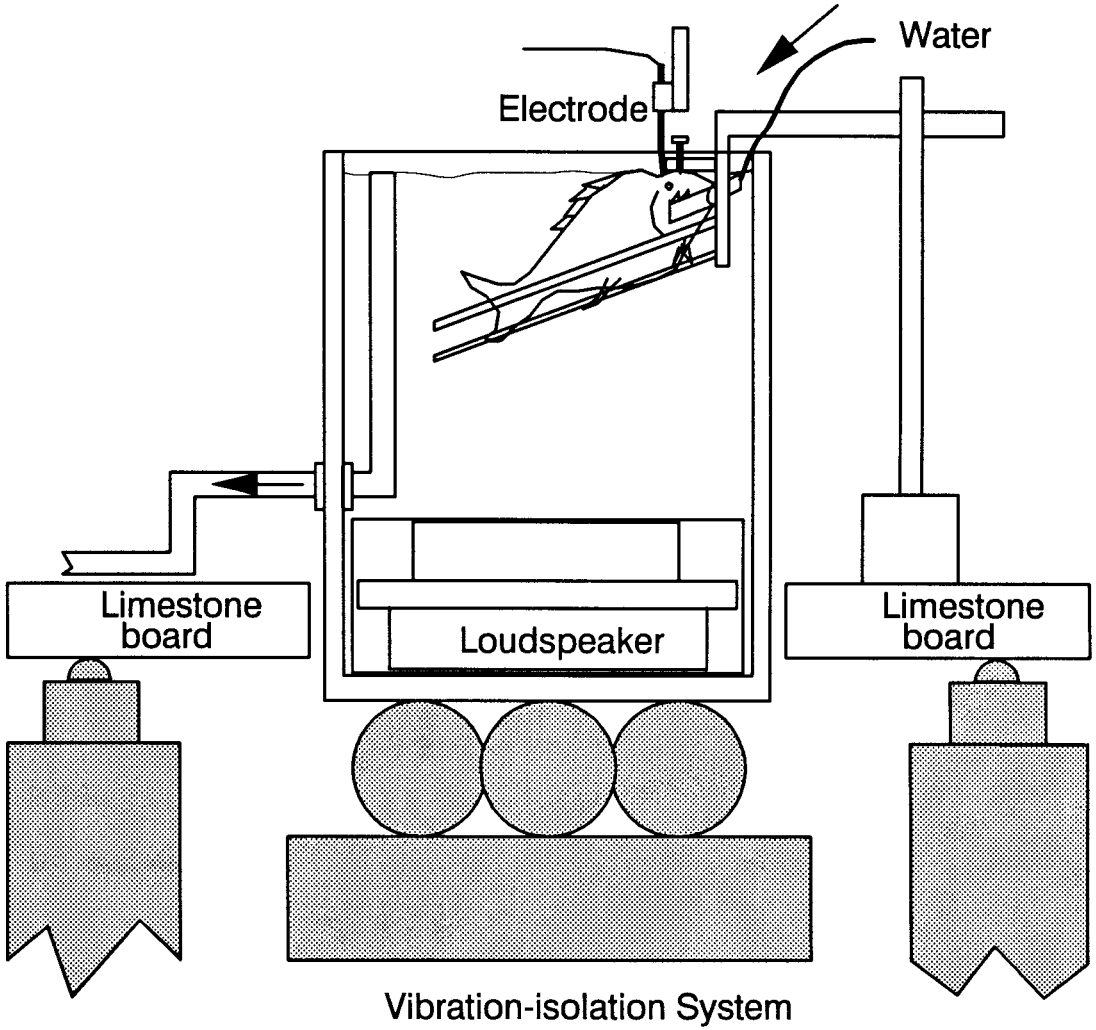
MATERIALS and METHODS

Animal preparation

Goldfish (Carassius auratus), weighing from 20 to 40 g and a body length of approximately 12 to 15 cm measured from tail to snout, were obtained from Chicago local suppliers and maintained in the lab for up to one year in large communal tanks. Nineteen goldfish were used.

Before recording, an animal was anesthetized in a bath of 1:2000 MS-222 and immobilized with a 1 μg/g body weight intramuscular injection of Flaxedil. The anesthetized animal was placed in an experimental water tank, and its head clamped to a rigid tube through which water flowed for respiration, as shown in Figure 1 (see Fay 1978a for more detail). The animal was positioned in the center of the tank with its head tipped up at about 30° with the dorsal surface of the skull just above the water surface. The skull over the optic tectum was removed, the fatty substance overlying the optic tectum carefully removed, and the optic tectum exposed. The fish was kept in the respirator for about two hours before the first electrode penetration.

Figure 1. Schematic diagram of the acoustic tank setup. A fish is secured in a respirator by clamping the frontal bone of the skull. The arrows show the direction of flowing water. The distance between the surface of the loudspeaker and the center of the fish's body is 6.5 cm. The tank is supported by a vibration-isolation system (shaded) through the central hole of the limestone table suspended by four Barry Stable-Level shock absorbers (SLM-1). The tank is supported independently of the limestone table.



Vibration-isolation System

Acoustic tank setup

As illustrated in Figure 1, the experimental tank was a plexiglas cylinder (20 X 23 cm) filled with Lake Michigan water at room temperature (about 20°C). The loudspeaker was enclosed in a grounded copper mesh cage and was placed at the bottom of the water tank covered with coarse, water-saturated sand (see Fay 1978a; Crawford 1993 for details). The experimental tank rested on a multi-stage vibration-absorbing system inside an Industrial Acoustics, 400 series room.

Sound stimulation and calibration

Sinusoidal tone bursts of 192-ms duration were digitally synthesized with 32 ms raised-cosine rise and fall times, read out of a 12-bit D-to-A converter at a conversion rate of 20 kHz, and low-pass filtered at 2000 Hz. These signals were then attenuated (Charybdis programmable attenuator) and led to a Crown power amplifier. The output of the power amplifier was attenuated by 20 dB using a resistor network and led to a University UW-30 underwater loudspeaker. A diagram of the equipment is shown in Figure 2. Sound-pressure levels were measured at the beginning of experiments using a Gould CH-17 calibrated hydrophone suspended in the tank in the position normally occupied by the fish. Calibration was done automatically by sequentially presenting all tone bursts used, and digitally recording the amplified hydrophone output. Figure 3 shows the frequency-response function of the

Figure 2. A diagram of the equipment used in the experiments.

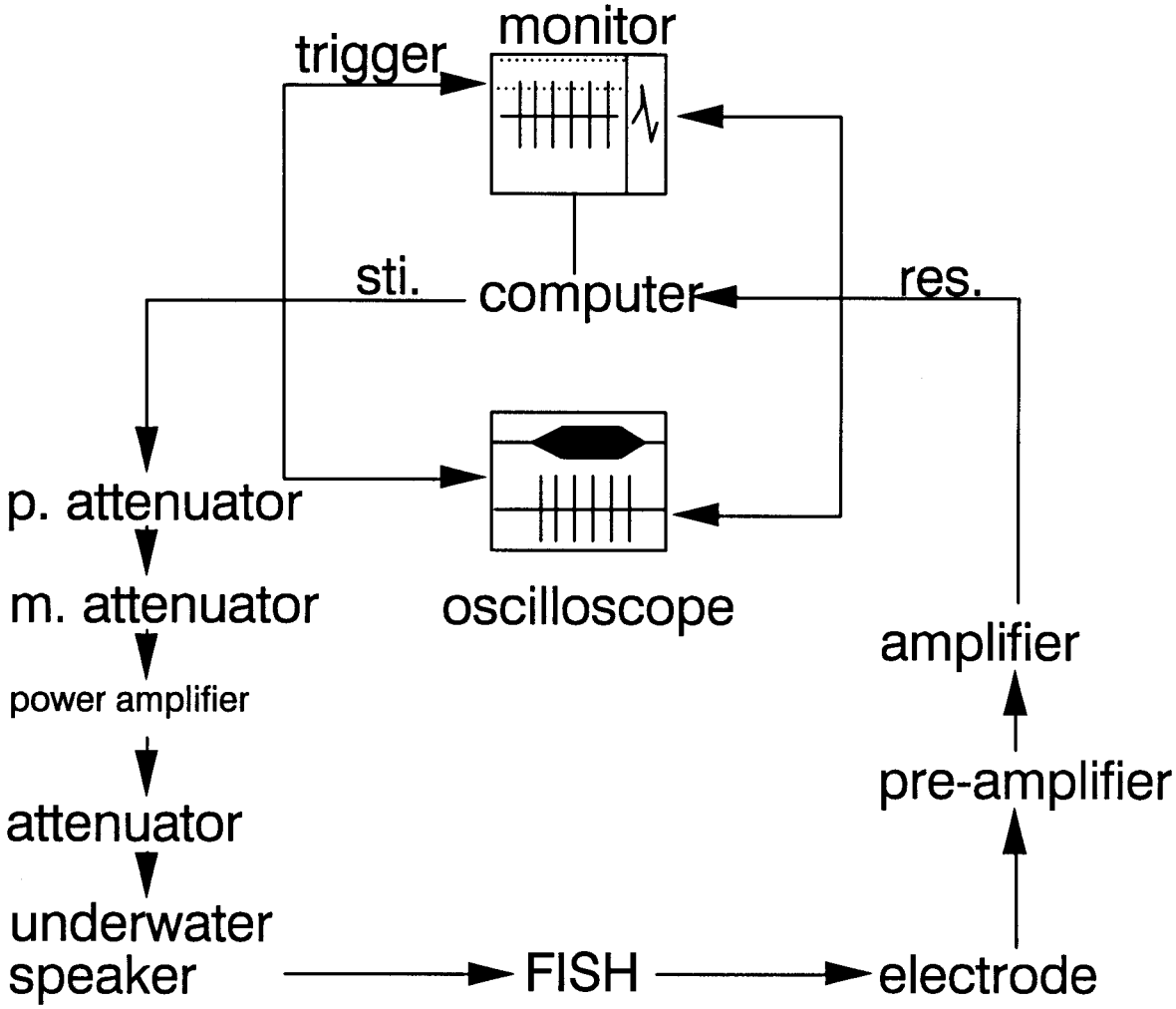
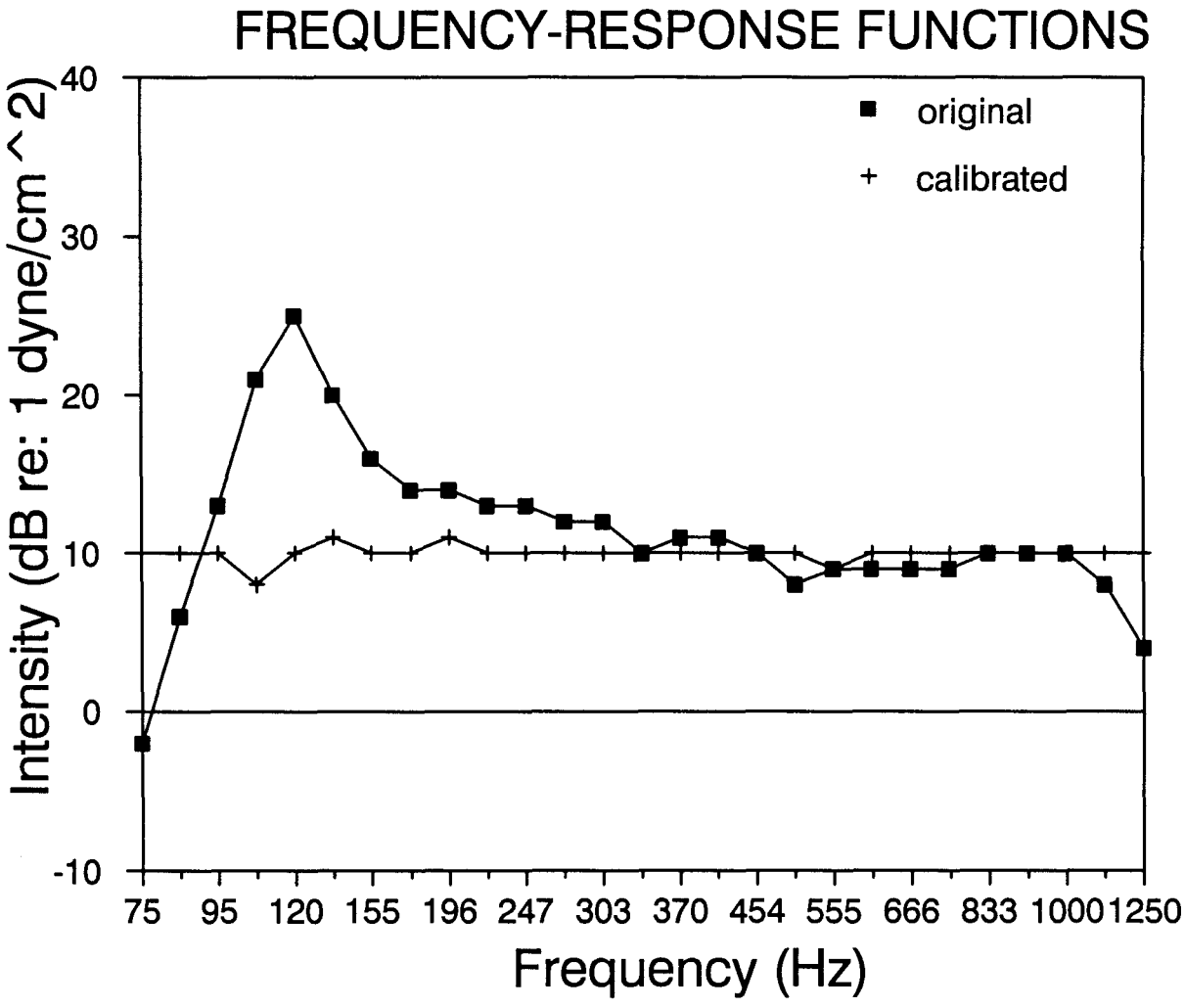

trigger
monitor
sti.
computer
res.
p. attenuator
m. attenuator
power amplifier
attenuator
underwater
speaker
oscilloscope
FISH
electrode
amplifier
pre-amplifier

Figure 3. The frequency-response characteristics of the acoustic tank. The square-labelled curve represents the frequency-response function of the tank at 40 dB attenuation; the cursor-labelled curve shows the calibrated frequency-response characteristics at the same attenuation level.


FREQUENCY-RESPONSE FUNCTIONS
original
calibrated
Intensity (dB re: 1 dyne/cm ^ 2)
40
30
20
10
0
-10
75
95
120
155
196
247
303
370
454
555
666
833
1000
1250
Frequency (Hz)

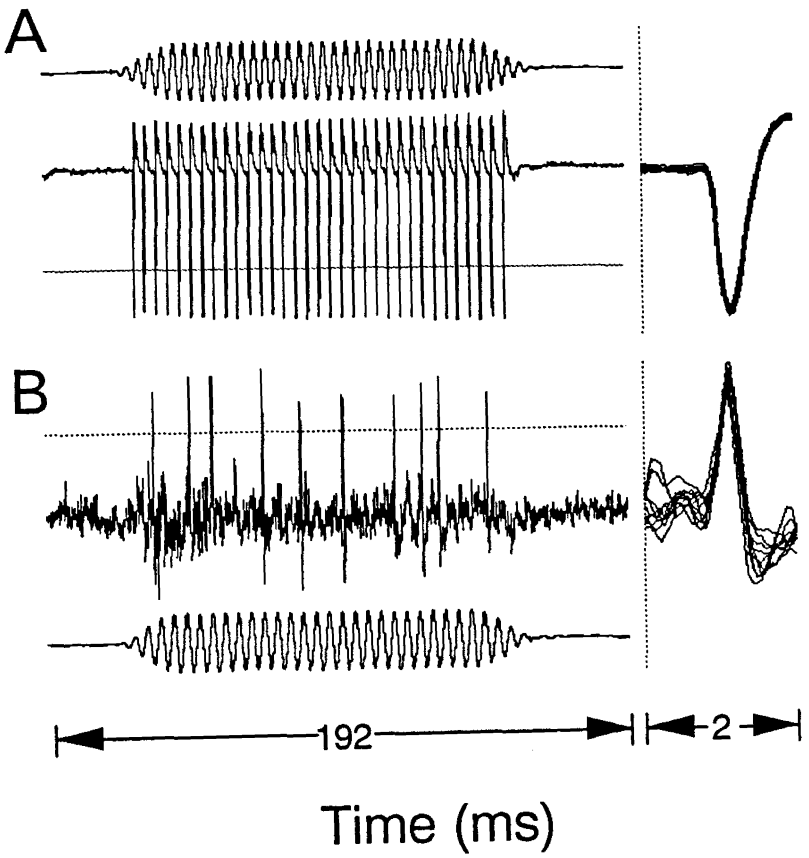
acoustic tank. The RMS voltage was calculated from the digital records. All sound levels are given in dB with respect to 1 dyne/cm^2 RMS (1 Pa = 10 dyne/cm^2, the intensity (dB) re 1 dyne/cm^2 can be converted into the intensity (dB) re Pa by subtracting 20 dB).

Search stimuli were tone bursts of 196, 417, and 833 Hz presented sequentially about once per sec at 12 dB.

Recording

Responses from single torus semicircularis units were recorded using fluid-filled micropipettes (20-50 MΩ) or indium electrodes with 4-10 μ tip diameter (Dowben and Rose 1953) vertically advanced by a remote hydraulic drive through the optic tectum and into the TS. Micropipettes were filled with 3 M KCl or 0.5 M sodium acetate with 2% Chicago Sky Blue 6B. Indium electrodes were glass pipettes filled with indium alloy. The tip was plated with gold and then platinum. The electrode's output was amplified using a Grass P-511, filtered between 300 and 3000 Hz, amplified again, and digitally recorded at 20 kHz sampling rate. Spike times were determined with 50 μsec accuracy using a voltage threshold in software. A sweep of action potentials as well as the discriminator level selected was displayed on the left side of the monitor screen, and each discriminated spike waveform was displayed on an expanded time scale on the right side of the screen during data acquisition. These spike waveforms were visually inspected to discriminate single unit recordings from

Figure 4. Neural response recorded by a glass micropipette (A) and an indium electrode (B). The horizontal lines in A and B show the voltage criterion for spike discrimination. Right column in A and B shows superimposed spike waveforms. Spikes recorded by an indium electrode usually have a large positive peak (right column in B) and those recorded by a glass pipette show a large negative peak (right column in A). Averaged stimulus waveforms (196 Hz and 12 dB; 175 Hz and 12 dB) recorded by the hydrophone are shown.


A
B
192
2
Time (ms)

multi-unit clusters (see Figure 4). Some of the recordings from indium electrodes were determined to be unit clusters, but all recordings using fluid-filled pipette electrodes were of single units. This report focuses on the recordings from single units.

When a single unit was isolated, the mean and standard deviation of its spontaneous rate were determined for 50, 192 ms periods of time. A response area (RA) was determined as iso-level, spike count functions of frequency by presenting tone bursts at 27 frequencies, logarithmically spaced between 75 and 1250 Hz, at eight to 10 levels in 5 dB steps spanning the unit's dynamic range. Stimuli were repeated once per 1.5 sec. The times of all spikes were stored for later analysis. If time permitted, RAs for a given unit were repeated one or more times, and were later averaged. From these data, tuning curves were determined with thresholds defined as levels producing spike rates that equalled or just exceeded the mean spontaneous rate plus two standard deviations. Tuning curves gave estimates of the frequency at which threshold was lowest (characteristic frequency, or CF), the threshold at CF (best sensitivity, or BS), and the ratio of CF to tuning curve bandwidth 10 dB above BS (Q_{10dB}). Best frequencies (BF) were defined as the frequencies producing the maximum number of spikes for different levels above BS.

When time permitted, stimuli were presented 50 times at selected frequencies (near CF and at other frequencies) and levels, and all spike times stored for later construction of peri-stimulus time histograms (PSTH), inter-spike

interval histograms (ISIH) (plotted for 25 ms), period histograms, and other analyses.

Histology

At the end of each experiment, the location of the electrode tip was marked. For pipettes containing Chicago Sky Blue 6B, a 5 μA DC current was passed (Stoelting CS-4) for 1 minute. For indium electrodes, high-frequency AC current was passed (Birtcher Hyfracator model 733) for one second. The anesthetized animal was perfused through the conus by Hickman's ringer (pH = 6.8-7.2) for about 10 min, until both gills turned white, and then perfused with 10% phosphate buffered formalin for 5 min. The fish's head was removed and immersed in 10% buffered formalin for about one week. The brain was removed and immersed in 10% formalin with 30% phosphate buffered sucrose for four days, embedded in 10% gelatin with 30% buffered sucrose, and then kept in 30% buffered sucrose for four days. The brain was frozen by dry ice, and sequentially sectioned at 50 μ using a sliding microtome (AO 708), and then stained with either cresyl-violet (to visualize the indium electrode mark) or safranin (to visualize the blue dye from the pipette electrode).

CHAPTER III

RESULTS

Anatomy

Fifteen marks showing electrode tip locations near physiologically characterized units were made in 15 goldfish. All fifteen marks were identified: 10 were marked using indium-filled electrodes and five using glass pipettes. The indium-electrode mark was a lesion with metal deposits, about 100 μ in diameter. The glass-pipette mark was visualized as a blue spot, about 10 μ in diameter. Figure 5 shows representative sections at the level of the midbrain, and higher-magnification photos of the two types of electrode marks. The general topology of a goldfish brain and estimates of electrode tip location are illustrated in Figure 6. All marks are located in the dorso-medial part of TS (see shaded area in Figure 6A) and about 1.5 to 2.5 mm from the surface of the optic tectum. These locations are similar to those found in a previous study on TS units (Page 1970). No marks in this study appear within the lateral lemniscus (LL). Not all recording locations were marked. However, based on the correspondence between manipulator coordinates for the marked and unmarked recording sites, the probability is high that the electrode tip was located in the TS for all unit responses presented in this report.

Figure 5. Two representative transverse sections through the auditory midbrain, and types of electrode marks (cresyl-violet (A1) and safranin (B1)). High-magnification pictures of regions indicated by boxes in A1 and B1 are shown in A2 and B2, and the locations of an indium-electrode and a glass micropipette mark are indicated by the white arrows. OT = optic tectum; CER = cerebellum; TS = torus semicircularis; LL = lateral lemniscus; IL = inferior lobe of hypothalamus.

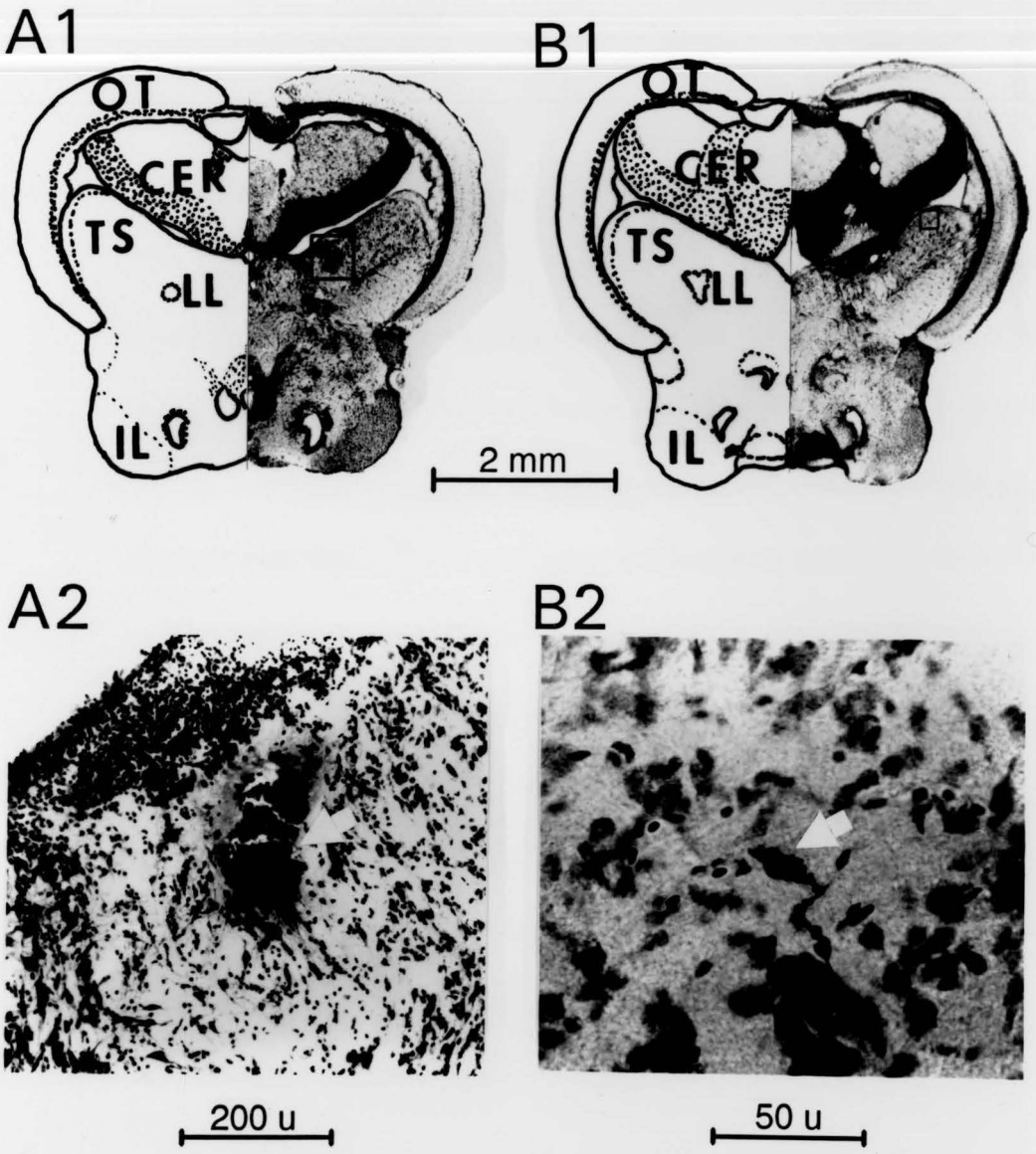
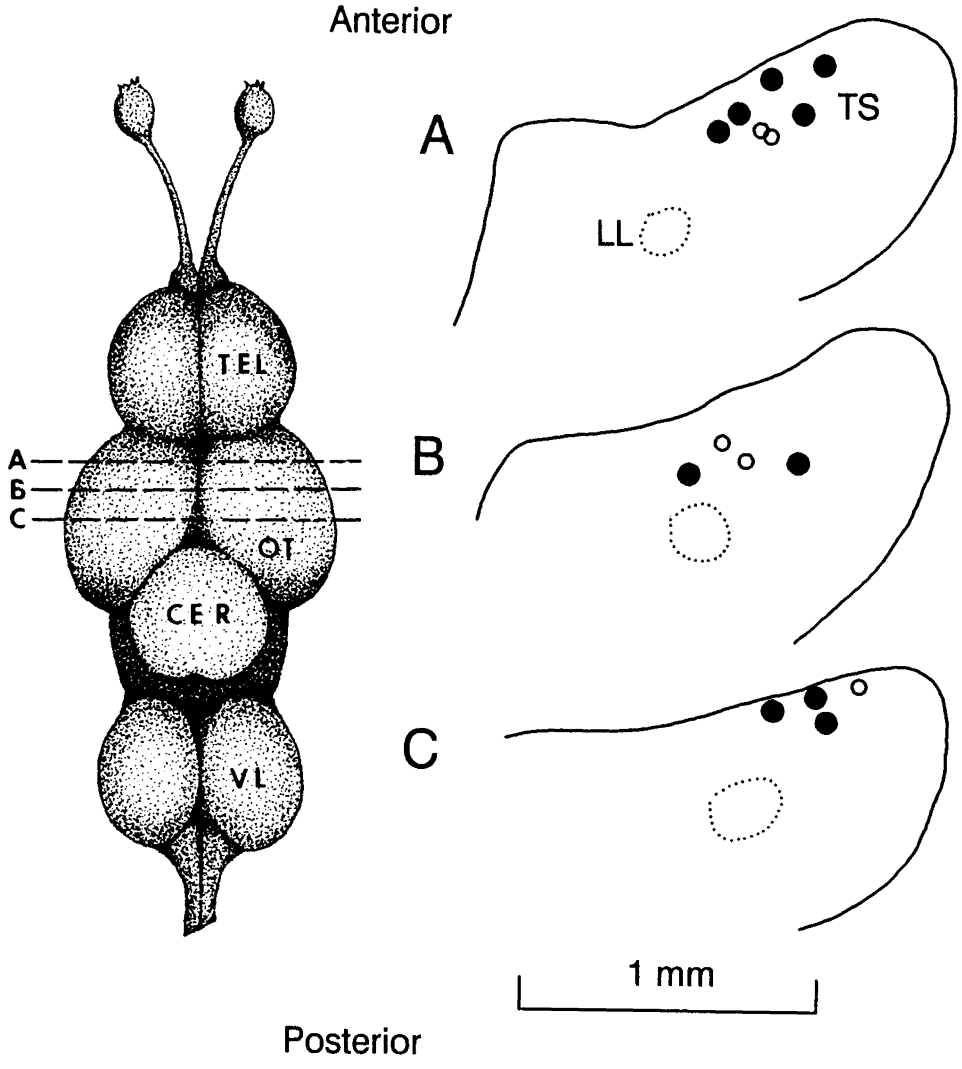

A1
OT
CER
TS
LL
IL
2 mm
B1
OT
CER
TS
LL
IL
A2
200 u
B2
50 u

Figure 6. Left panel: a dorsal view of goldfish's brain. TEL = telencephalon; OT = optic tectum; CER = cerebellum; VL = vagal lobe. The dashed lines shows the approximate locations of three transverse sections (A, B, and C) through the auditory midbrain. Right panel: profiles of the right auditory midbrain (A, B, and C) and the confirmed locations of electrode tips. Filled and open circles represent the locations of indium electrode and glass-pipette marks respectively. The dashed circles represent the lateral lemniscus (LL). The auditory zone (shaded area in A) and the mechanosensory zone (diagonal lines in A) described by McCormick (1990) are located in the dorso-medial and dorso-lateral parts of the torus respectively.


Anterior
TEL
A
Б
C
OT
CER
VL
A
TS
LL
B
C
1 mm
Posterior

Physiology

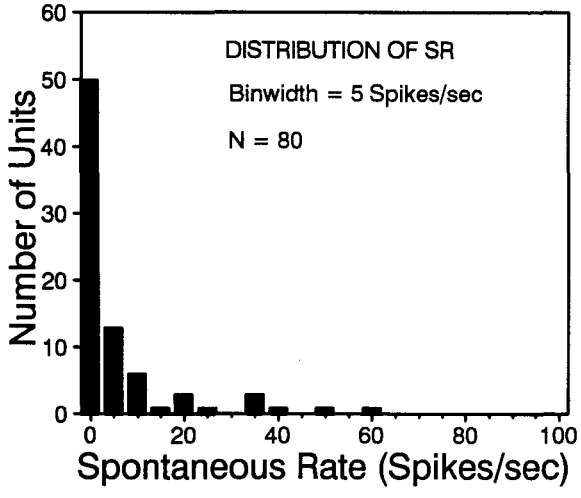
One hundred and thirty-one single-unit recordings were made from the TS of goldfish. Of these, 54 were obtained using indium electrodes, and 77 using glass pipettes. Complete data (including RA and spike-time histograms) were obtained for 55 units (28 using glass pipettes and 27 using indium electrodes). RA or spike time data were obtained for an additional 39 and 37 units, respectively (see Table 1). Distributions of spontaneous rate, CF, BS, and Q_{10dB} were based on RA data from 80 units. Descriptions of temporal response patterns were based on both RA and spike-time histogram data from 55 units. In addition to single units, several multiunit recordings using indium electrodes are also presented in this paper.

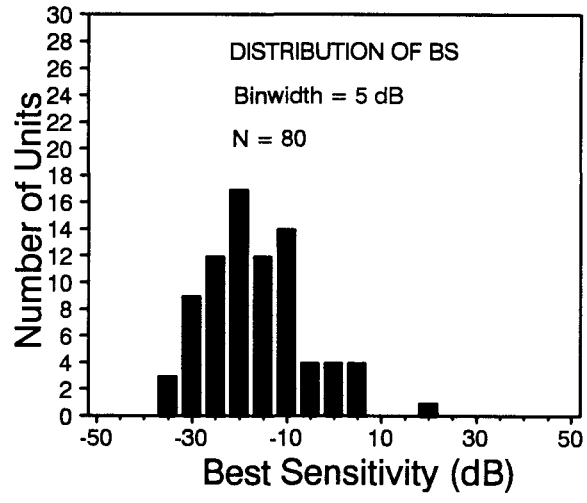
Distributions of spontaneous rate, BS, and Q_{10dB}. The distributions of spontaneous rate, BS, Q_{10dB}, and CF are shown in Figure 7. The maximum spontaneous rate was less than 60 spikes/sec, and about 63% of units (50/80) had no spontaneous activity. The mean spontaneous rate for all units was about 5 spikes/sec ± 0.56 SE. The BS of units ranged from -38 to 17 dB, with 80% (64/80) having best threshold below 0 dB. The average BS of units was about -19 dB ± 2.12 SE. Torus units varied widely in sharpness of tuning. The mean Q_{10dB} was 1.46 ± 0.16 SE. Sixteen percent of units (13/80) had Q_{10dB} values greater than 2.

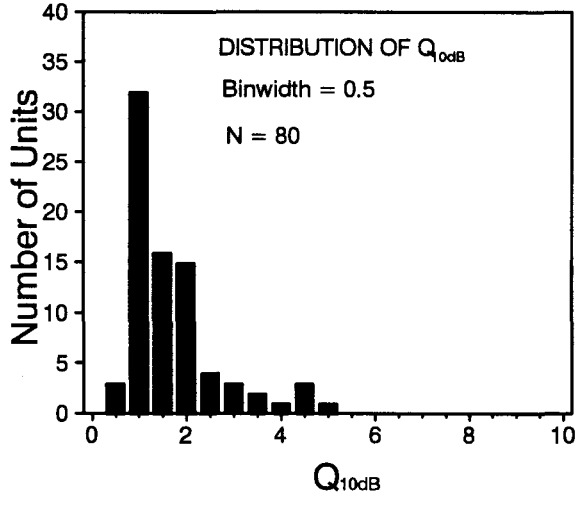
Table 1. Disposition of 131 torus units from 19 goldfish. NPL = not phase-locked; WPL = weakly phase-locked; SPL = strongly phase-locked

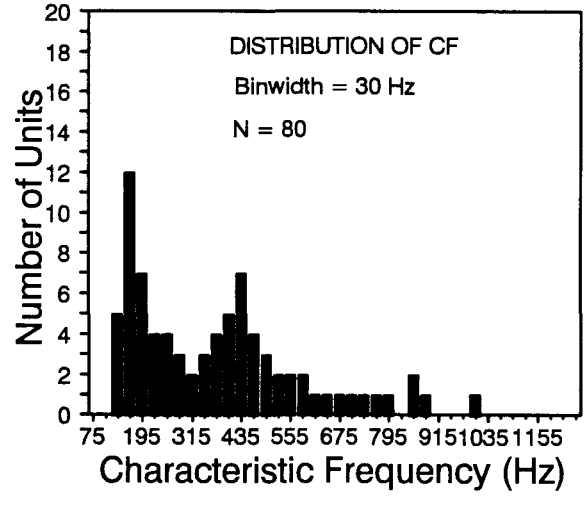
A. Units recorded							N = 131		
B. Units with RA data							N = 94 (72% of A)		
C. Units with RA data and Q_{10dB} estimates							N = 80 (85% of B)		
	CF < 300 Hz			300 Hz < CF < 650 Hz			CF > 650 Hz		
	N = 36 (45%)			N = 35 (44%)			N = 9 (11%)		
D. Units with RA data and spike time data							N = 55 (42% of B)		
	CF < 300 Hz			300 Hz < CF < 650 Hz			CF > 650 Hz		
	N = 28 (51%)			N = 20 (36%)			N = 7 (13%)		
	NPL	WPL	SPL	NPL	WPL	SPL	NPL	WPL	SPL
	11	14	3	11	5	4	4	2	1

Figure 7. Distributions of spontaneous rate, best sensitivity (BS), Q_{10dB}, and characteristic frequency (CF) for 80 torus units.


DISTRIBUTION OF SR
Binwidth = 5 Spikes/sec
N = 80
Number of Units
Spontaneous Rate (Spikes/sec)


DISTRIBUTION OF BS
Binwidth = 5 dB
N = 80
Number of Units
Best Sensitivity (dB)


DISTRIBUTION OF Q10dB
Binwidth = 0.5
N = 80
Number of Units
Q10dB


DISTRIBUTION OF CF
Binwidth = 30 Hz
N = 80
Number of Units
Characteristic Frequency (Hz)

Distribution of CF. The frequency distribution of CF for torus units (Figure 7) is nonuniform, having modes at 155, 455, and a distribution tail reaching to about 1 kHz. For descriptive purposes only, TS units were placed into three groups based on the distribution of CF: low frequency (CF < 300 Hz), mid frequency (CF: 300-650 Hz), and high frequency (CF > 650 Hz). This grouping is somewhat arbitrary, but was made here because of the correspondence between the shapes of the CF distributions for torus units and for saccular afferents (Fay and Ream 1986), and the previous classification of saccular afferents into three CF groups (see Discussion). A summary of spontaneous rate, BS, and Q_{10dB} of these three groups is shown in Table 2. About 45% of the units (36/80) fall into the low frequency group, 44% (35/80) in the mid-frequency group, 11% (9/80) in the high-frequency group. Units in the low-frequency group have the highest spontaneous rate (8 spikes/sec), the greatest BS (-21 dB), the sharpest tuning (Q_{10dB} = 1.95). The mid-frequency units are similarly sensitive (-19 dB), have the lowest averaged spontaneous rate (2 spikes/sec), and are the least sharply tuned (Q_{10dB} = 0.95). The high-frequency units are the least sensitive (-11 dB), and have an intermediate spontaneous rate (4 spikes/sec) and sharpness of tuning (Q_{10} = 1.62).

RAs typical of each CF group are shown in Figures 8 and 9. Some units were broadly tuned (Figure 9A), and some were sharply tuned (Figure 7B). Most units had "V" shaped tuning curves, but a few units showed a "⊔" shaped tuning curve with steep upper- and lower-frequency slopes (up to 200

Table 2. The summary of spontaneous rate (SR), BS, and Q_{10dB} of 80 torus semicircularis units (C in Table 1) placed into three groups based on characteristic frequency (CF) (Note SE = standard error, which is defined as standard deviation over the sample size).

		CF (Hz)			
		< 300 Hz	300-650 Hz	> 650 Hz	MEAN
SR (Spikes/sec)	Max.	57	30	31	
	Mean	8	2	4	5 ± 0.56SE
	Min.	0	0	0	
BS (dB)	Max.	-38	-33	-28	
	Mean	-21	-20	-11	-19 ± 2.12SE
	Min.	-2	17	2	
Q_{10dB}	Max.	4.70	2.48	2.73	
	Mean	1.95	0.95	1.62	1.46 ± 0.16SE
	Min.	0.48	0.45	0.74	
%		45%	44%	11%	

Figure 8. Typical response areas (RA) of low-CF (A1 and A2), mid-CF (B1 and B2), and high-CF (C1 and C2) units. Left panel: sound level versus frequency functions with tuning curves (solid lines). The size of filled boxes represents the number of spikes. Right panel: the smoothed spike count versus frequency functions for 8 levels. For smoothing, each spike-count weighted by 2 was averaged with the eight spike counts at eight adjacent levels and frequencies weighted by 1.

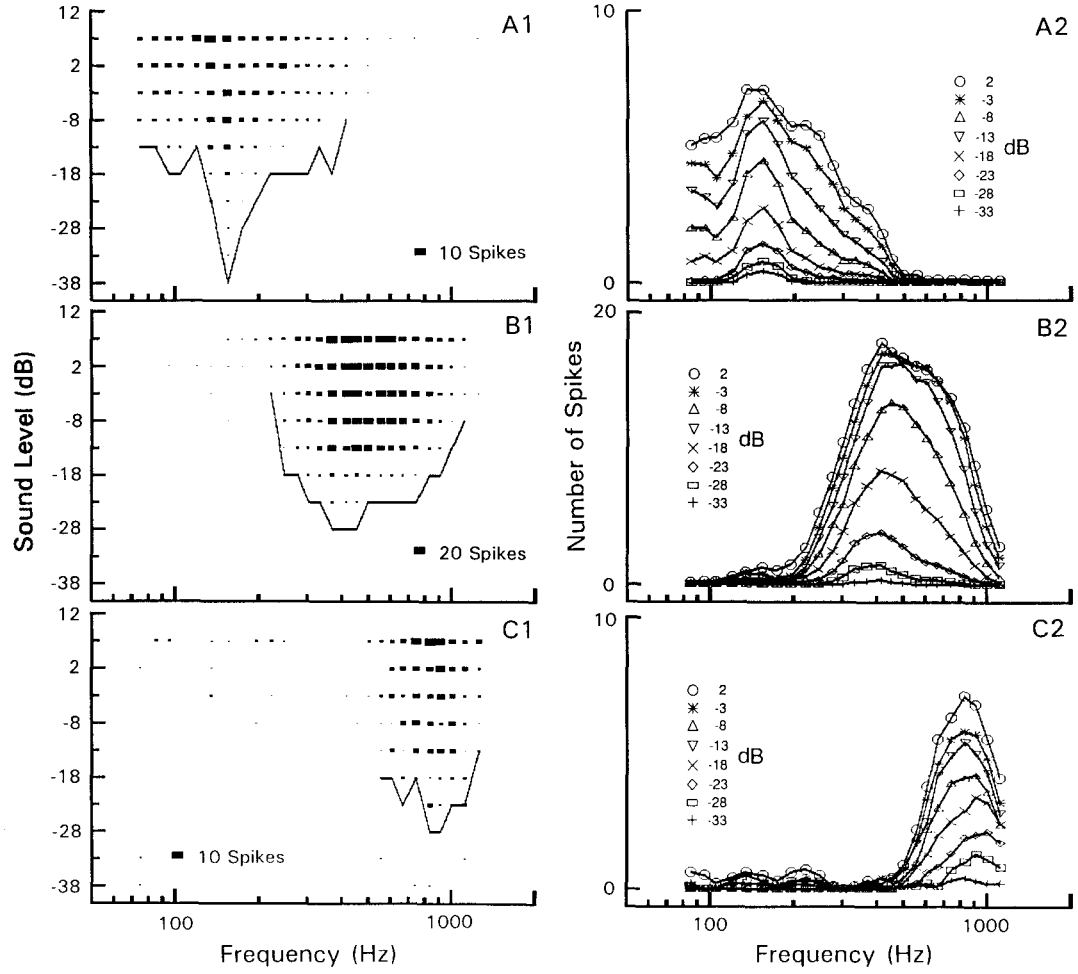
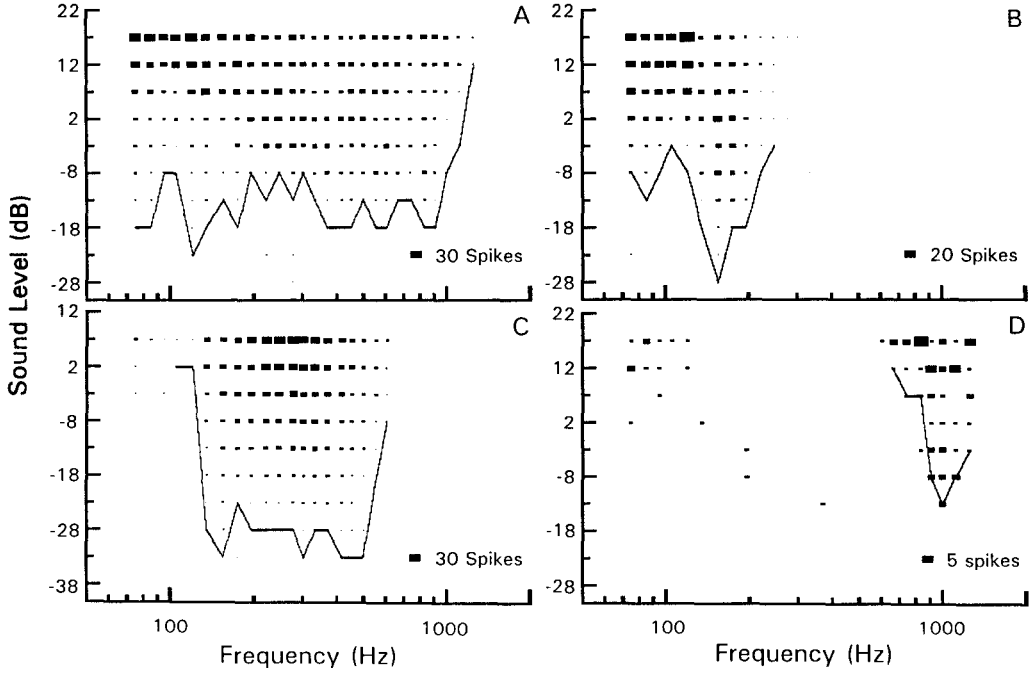

A1
B1
C1
A2
B2
C2
10 Spikes
20 Spikes
10 Spikes
dB
2
-3
-8
-13
-18
-23
-28
-33
Sound Level (dB)
Number of Spikes
Frequency (Hz)
Frequency (Hz)
100
1000

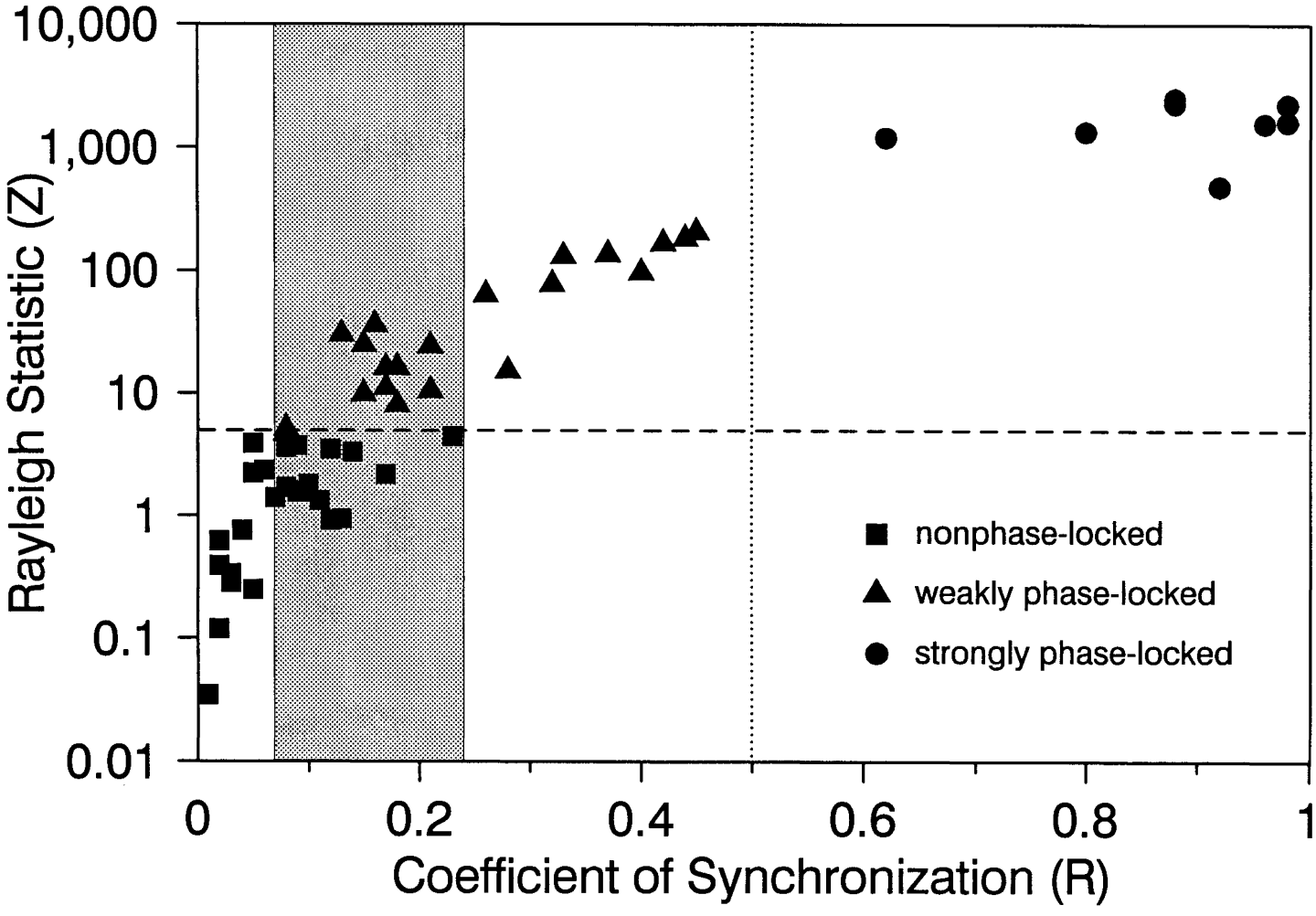
Figure 9. Four types of response areas (RAs): broadly tuned (A), sharply tuned (B), unusual or "⊔" shaped (C), discontinuous (D).


A
B
C
D
22
12
2
-8
-18
-28
-38
30 Spikes
20 Spikes
30 Spikes
5 spikes
Sound Level (dB)
100
1000
Frequency (Hz)

dB/octave) (Figure 7C). Several high-CF units had discontinuous RAs with responses to low-frequency pure tones at levels well above BS (Figure 7D).

Diversity of temporal response patterns. Torus units were categorized into three general groups with respect to their degree of phase-locking to pure tones (the coefficient of synchronization, R, Anderson 1973) using a stimulus frequency at or near CF, at about 12 dB. Some units were strongly phase-locked, having an R value equal to or greater than 0.5. An R value in this range generally means that spike rate is modulated more than 100% during a stimulus tone cycle. Other units were weakly phase-locked, having an R value less than 0.5 but with a period histogram that differed significantly from a uniform distribution ($p < 0.01$, Rayleigh test: $Z = N*R^2$, where Z is Rayleigh statistic and N is the number of spikes; Batschelet 1981). For some units, the Rayleigh test failed to reach significance ($p >= 0.01$). Figure 10 shows the Rayleigh statistic (Z) versus the coefficient of synchronization (R). Strongly phase-locked units (8/55) are circles at the upper right. Weakly phase-locked units (21/55) are shown as triangles, and units without significant phase-locking (26//55) are shown as squares. The shaded region shows a range of R values within which some units phase-locked weakly, and others were not significantly phase-locked. This overlap is due to the fact that both the sample size (N) and the coefficient of synchronization (R) determines statistical significance. For all symbols below the horizontal dashed line, the hypothesis that the period

Figure 10. A scatter plot of Rayleigh statistic (Z) versus coefficient of synchronization (R). The horizontal dashed line indicates the critical value of the Rayleigh statistic (4.5), dividing units into those without significant phase-locking (below) and those with significant phase-locking (above). The vertical dotted line at R = 0.5 divides the phase-locked units into weakly phase-locked (upper left) and strongly phase-locked groups (upper right). See text for more detail.


10,000
1,000
100
10
1
0.1
0.01
Rayleigh Statistic (Z)
0
0.2
0.4
0.6
0.8
1
Coefficient of Synchronization (R)
nonphase-locked
weakly phase-locked
strongly phase-locked

histogram is uniform cannot be rejected. A summary of the relationship between CF and phase-locking patterns is shown in Table 1, illustrating that torus semicircularis units of all CF ranges shared all phase-locking patterns.

Examples of period histograms, PSTHs, and ISIHs of two phase-locked units are shown in Figure 11. Units strongly synchronized to pure tones (left panel) showed a period histogram with a narrow peak (R = 0.98 in this example). Most strongly phase-locked units (7/8) produced tonic responses with little or no adaptation (the range of R was from 0.62 to 0.98, and the mean was 0.88). ISIHs of these units have one or more preferred peaks corresponding to the stimulus period and its multiples. Most strongly phase-locked units discharge one spike per cycle for stimulus frequencies up to about 600 Hz. An example of RAs, PSTHs, ISIHs and period histograms for a strongly phase-locked unit is shown in Figure 12.

Thirty-eight percent of units studied (21/55) were weakly phase-locked to pure tones, and showed a tonic, adapting PSTH profile (right panel in Figure 11). Units of this type often exhibited transient robust phase-locking during the first 50 to 100 msec of the stimulus, and a relative loss of phase-locking for the remainder of the 192 msec tone burst. Thus, period histograms for these units appear to have a synchronization peak superimposed on a pedestal of unsynchronized responses (uniform portions of the period histogram in Figure 11, B3). The ISIHs for these units do not show obvious peaks at the stimulus period or its multiples.

Figure 11. Two phase-locked units. Left panel: a dot-raster and PSTH (A1), ISIH (A2) and period histogram (A3) of a single, strongly phase-locked unit (R = 0.98 at 417 Hz, 10 dB). Right panel: a single, weakly phase-locked unit (R = 0.37 at 417 Hz, 12 dB). The longer tick marks on the horizontal axes in A2 and B2 indicate the stimulus periods. 50 stimulus repetitions.

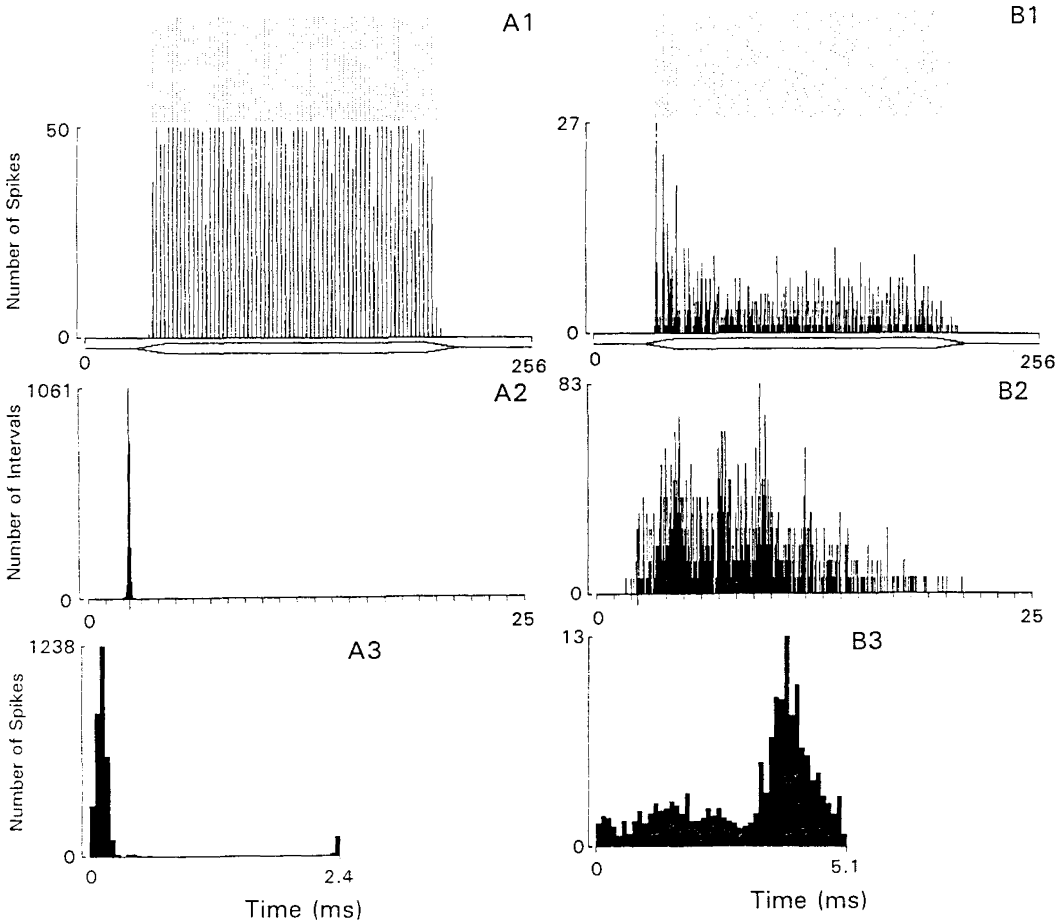
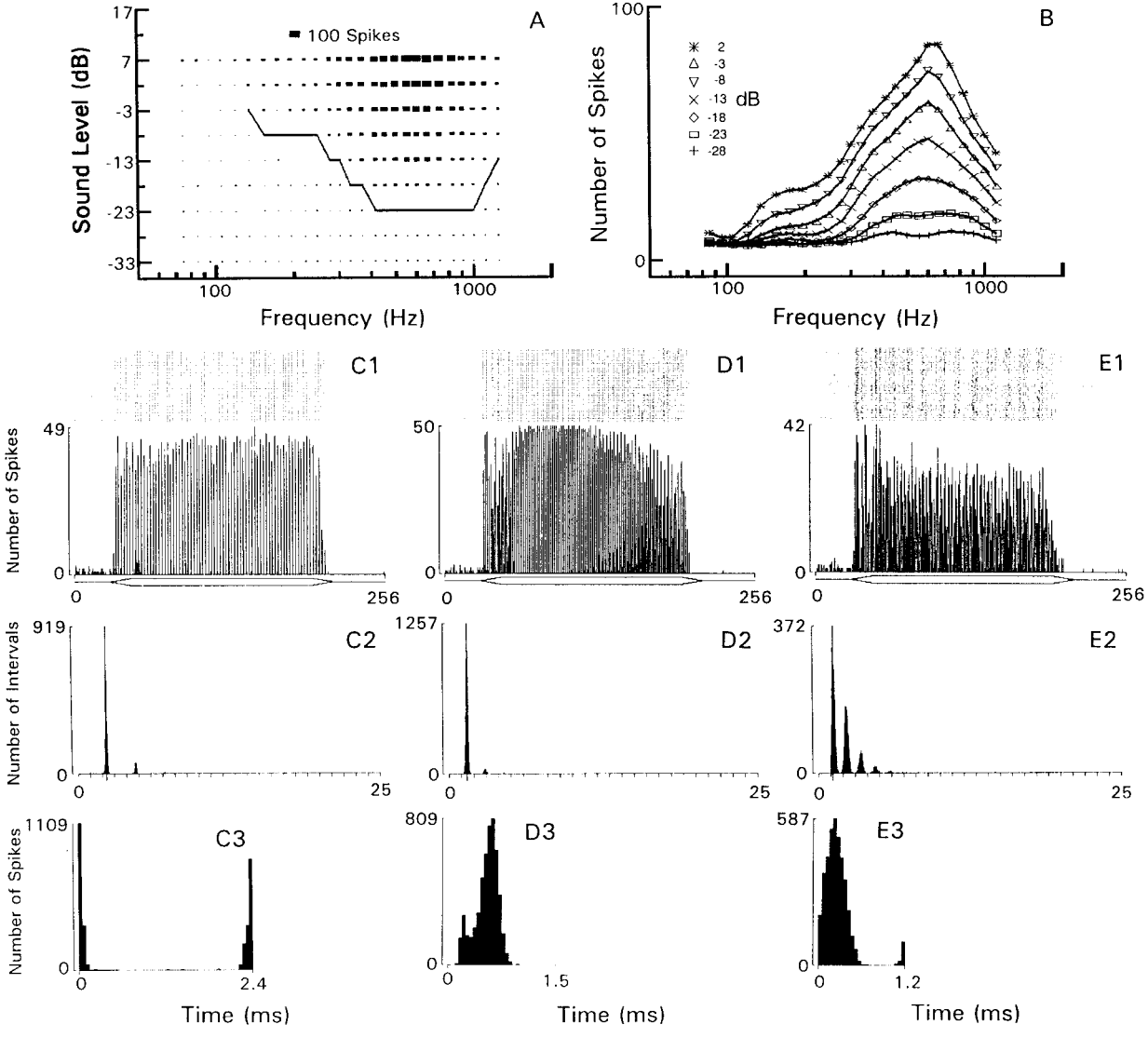

A1
B1
50
27
Number of Spikes
0
0
256
0
256
A2
B2
1061
83
Number of Intervals
0
0
0
25
0
25
A3
B3
1238
13
Number of Spikes
0
0
0
2.4
0
5.1
Time (ms)
Time (ms)

Figure 12. A strongly phase-locked single unit. Upper panel A and B: response areas. Lower panel: dot-raster patterns and PSTHs (C1, D1, and E1), ISIHs (C2, D2, and E2; stimulus periods indicated by the longer tick marks on the horizontal axes), and period histograms (C3, D3, and E3) at 417 Hz (C, left), 667 Hz (D, middle), and 833 Hz (E, right). The intensity of stimuli was 12 dB. 50 stimulus repetitions.


A
100 Spikes
Sound Level (dB)
17
7
-3
-13
-23
-33
100
1000
Frequency (Hz)
B
Number of Spikes
100
0
2
-3
-8
-13
-18
-23
-28
dB
100
1000
Frequency (Hz)
C1
D1
E1
Number of Spikes
49
50
42
0
256
C2
D2
E2
Number of Intervals
919
1257
372
0
25
C3
D3
E3
Number of Spikes
1109
809
587
0
2.4
1.5
1.2
Time (ms)
Time (ms)
Time (ms)

Some phase-locked units exhibited period histograms with two major peaks, usually separated by about one-half the stimulus period, or 180° in phase. The double-peaked period histogram patterns were observed both during recording with indium electrodes (Figure 13, right panel), sampling a unit cluster, and during clear, single unit recording with KCl-filled pipettes (Figure 13, left panel). Sixteen percent of single units (9/55) discharged at two preferred phases in their period histograms. For these single units, the average difference in phase of the two peaks was 178° with a standard deviation of 19°. All of these units had CFs below 320 Hz. The multi-unit data suggest, in addition, the existence of pairs of adjacent units approximately 180° out-of-phase with one-another. Eight recordings from five animals using indium electrodes showed two peaks in their response areas and two clear modes in their period histograms, as illustrated in Figure 14. The average phase distance between the modes in the period histogram was 185°, with a standard deviation of 9°. For all eight recordings, the dominant peak in the RA ranged from 370 to 450 Hz, with a smaller peak averaging 0.6 octaves higher.

The PSTHs for six types of units that did not phase-lock significantly are shown in Figure 15. Twenty-seven percent of these units (7/26) discharged 1 to 3 spikes/sweep at the beginning of stimulation (Figure 15A). This "onset" response occurred for all stimulus frequencies within the units' response areas. Twenty-three percent of unsynchronized units (6/26) produced spikes with preferred ISIHs (1.2 to 3 msec) that were independent of the stimulus periods

Figure 13. Left panel: single unit recorded using a KCl-filled glass micropipette. Right panel: a unit cluster recorded using an indium electrode. Dot-raster patterns and PSTHs (A1 and B1), ISIHs (A2 and B2, the longer tick marks on the horizontal axes show stimulus periods), and period histograms (A3 and B3) for two recordings. Both A3 and B3 show two obvious peaks, about 180° apart (the longer tick marks on the horizontal axes show the phase of the peaks: 142° and 305° in A3, and 97° and 285° in B3). 50 stimulus repetitions.

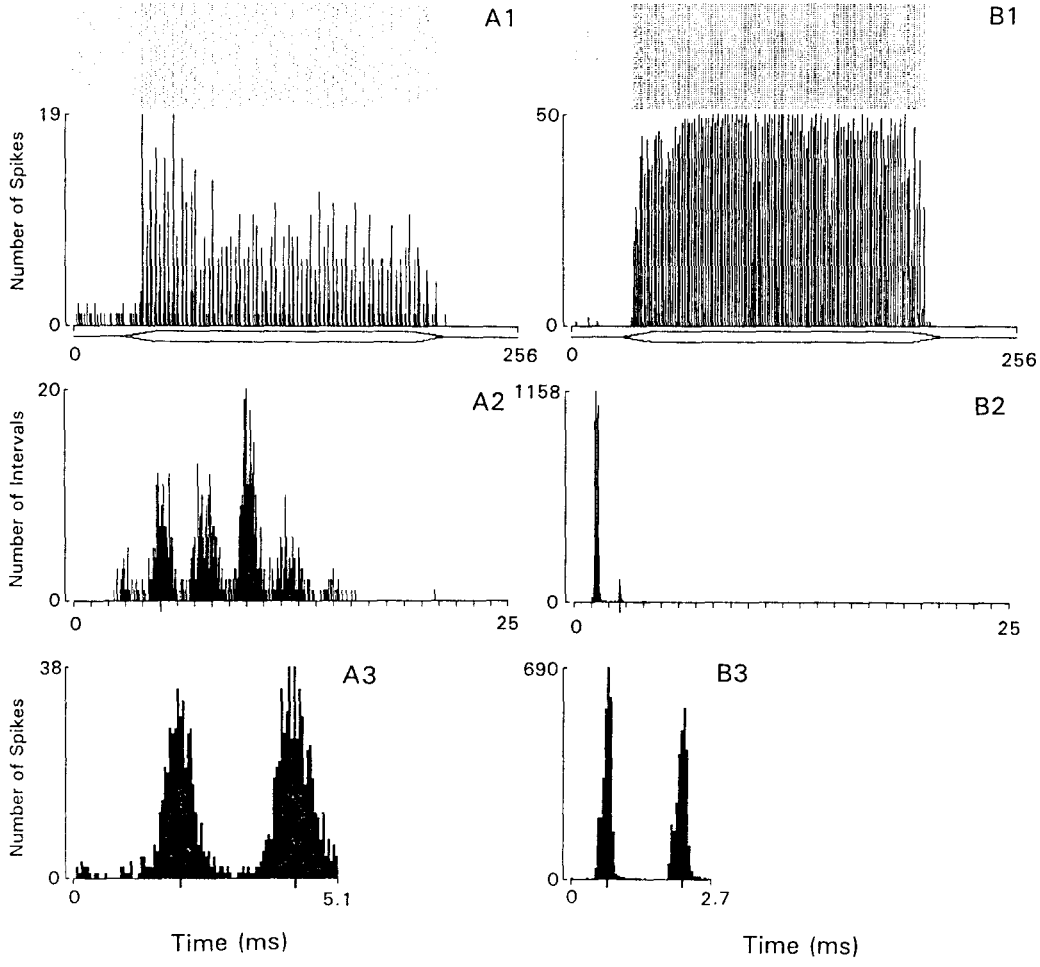

A1
B1
19
50
Number of Spikes
0
256
A2
B2
20
1158
Number of Intervals
25
A3
B3
38
690
5.1
2.7
Time (ms)

Figure 14. RAs, dot-raster patterns, PSTHs, and period histograms for a multiunit recording. Upper panel A and B: response areas.Lower panel: dot-raster patterns and PSTHs (C1 and D1), and period histogram (C2 and D2) in response to 556 Hz (12 dB) and 303 Hz (0 dB) tones. Both period histograms show two peaks separated approximately 180° in phase (The longer tick marks on the horizontal axes show the phase of the peaks: 141° and 326° in C2, and 128o° and 304° in D2).

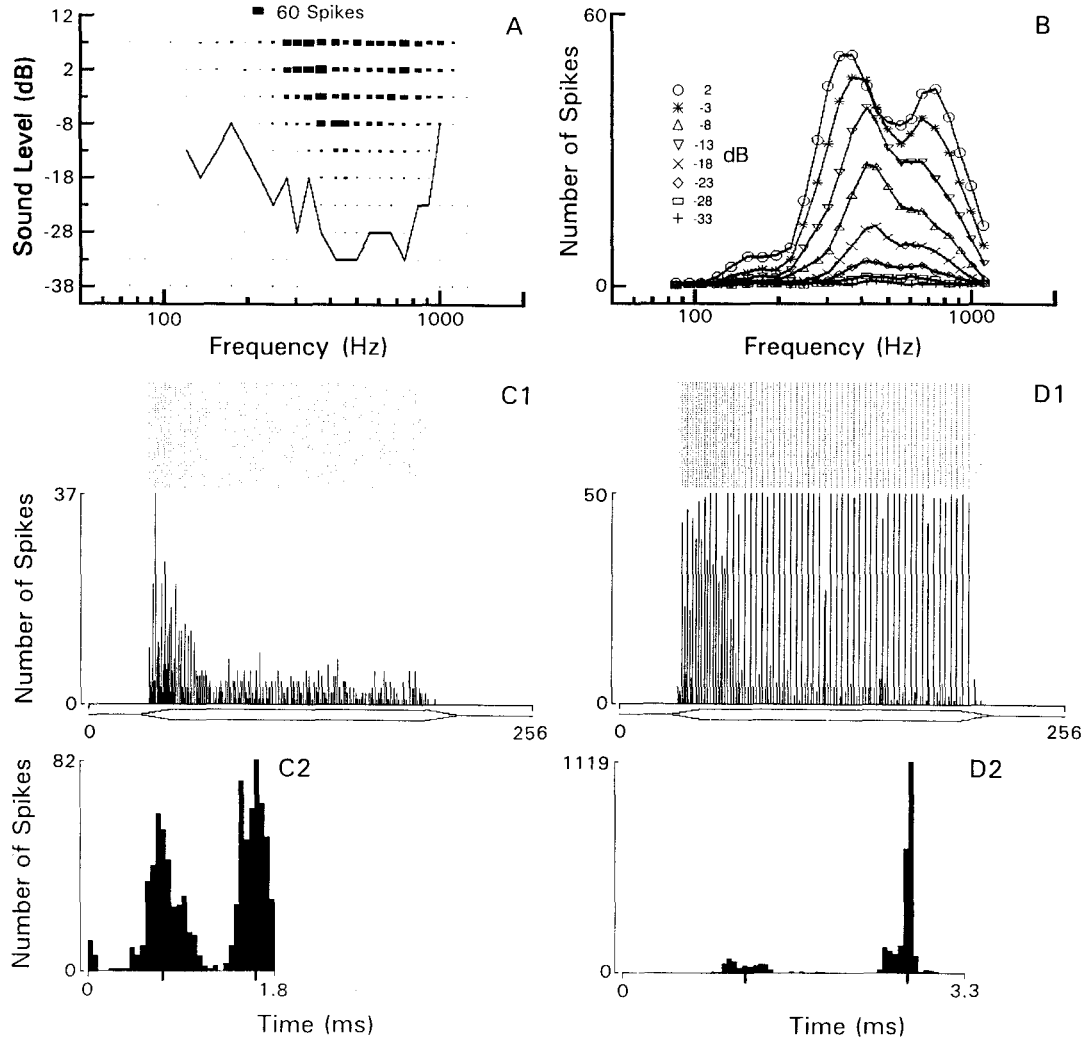
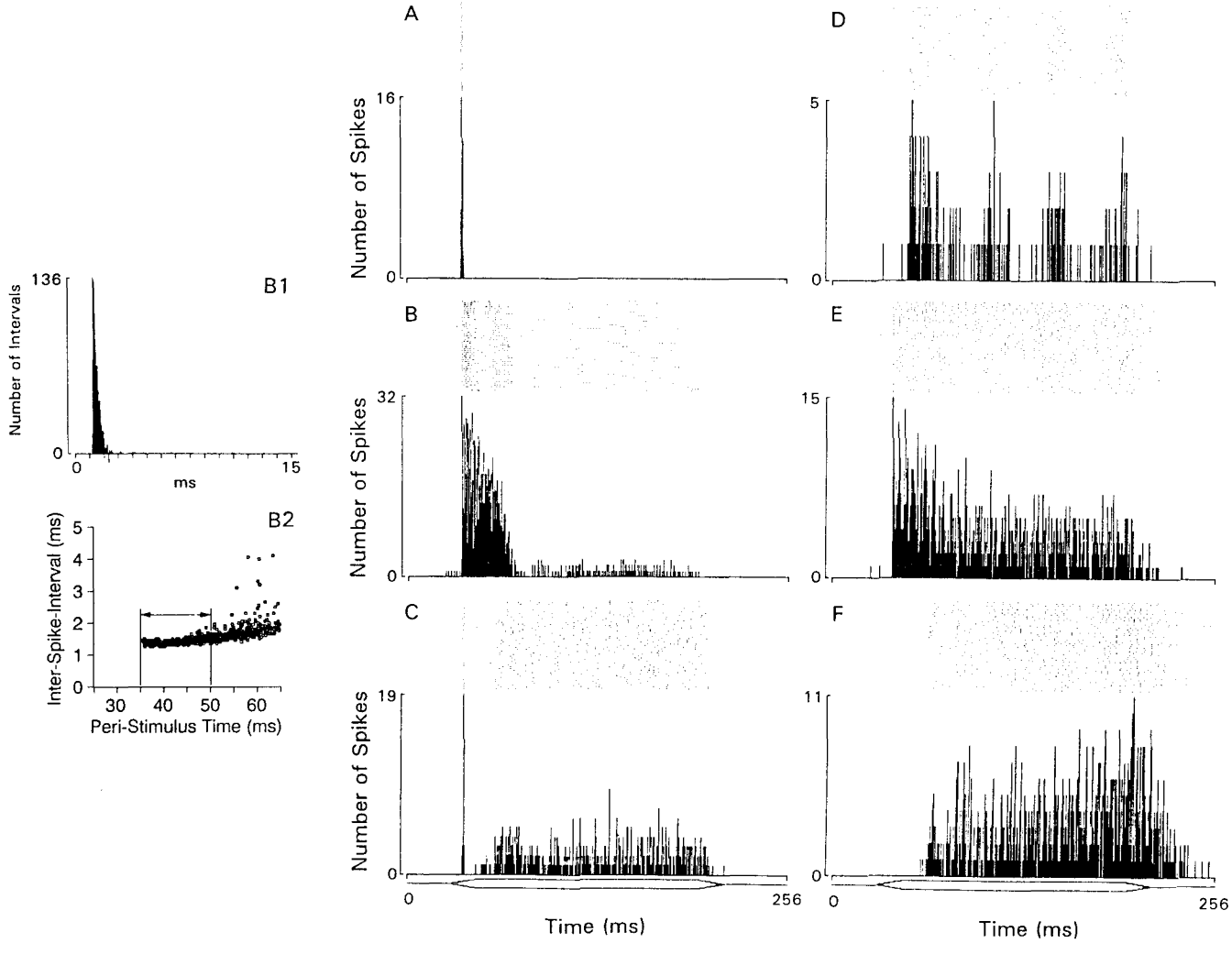

60 Spikes
A
12
2
-8
-18
-28
-38
Sound Level (dB)
100
1000
Frequency (Hz)
B
60
0
Number of Spikes
2
-3
-8
-13
-18
-23
-28
-33
dB
100
1000
Frequency (Hz)
C1
37
0
Number of Spikes
0
256
D1
50
0
0
256
C2
82
0
Number of Spikes
0
1.8
Time (ms)
D2
1119
0
0
3.3
Time (ms)

Figure 15. A-F: dot-raster patterns and PSTHs for six distinctive temporal response patterns for torus units without significant phase-locking. B1 and B2 show the ISIH and a regularity analysis, respectively, for the PSTH data shown in B (see text for details). The stimulus period (2.4 ms) is indicated by the longer tick mark on the abscissa in B1. The regularity analysis (B2) is plotted for the first 15 msec of the response.


A
D
B
E
C
F
Number of Spikes
16
5
32
15
19
11
0
256
Time (ms)
B1
136
Number of Intervals
0
15
ms
B2
Inter-Spike-Interval (ms)
5
4
3
2
1
0
30
40
50
60
Peri-Stimulus Time (ms)

tested (Figure 15B). These units showed oscillatory response patterns resembling those of the mammalian cochlear nucleus classified as "choppers" (e.g., Young et al. 1988). The ISIHs for these units show a single peak at inter-spike times not equal to the stimulus period or its multiples (see Figure 15B1). These oscillatory response patterns were analyzed using a "regularity analysis" (Young et al 1988), as shown in Figure 15B2. In this analysis, inter-spike times are plotted as a function of the time the interval occurred during the stimulus. The regularity of the oscillatory response can be described using the coefficient of variation (inter-spike time standard deviation divided by the mean inter-spike time over the 15 ms of the response). For this unit, the mean inter-spike interval was 1.39 ms, the standard deviation was 0.08 ms, and the coefficient of variation was 0.05. In general, the six units showing such oscillatory responses had minimum coefficient of variations ranging between 0.05 and about 0.15.

Fifteen percent of unsynchronized units (4/26) showed a periodic bursting pattern, as illustrated in Figure 15D. Peaks in the PSTH occurred with inter-peak-intervals usually longer than 30 ms.

Nineteen percent of unsynchronized units (5/26) showed tonic, adapting PSTH patterns characteristic of primary afferents (Figure 15E).

Twelve percent of unsynchronized units (3/26) had long latencies and spike probabilities that grew over 100 msec or more during the stimulus. These resemble cochlear nucleus units termed "buildup" (Rhode and Greenberg 1992)

(Figure 15F). Note that this unit also shows oscillatory behavior in the dot-raster display (regular inter-spike-intervals), particularly during the latter portions of the stimulus burst.

One of the unsynchronized units showed a PSTH profile with an initial peak, a 15-20 msec period of reduced response, and a following period of tonic excitation (Figure 15C). This PSTH resembles those of the mammalian cochlear nucleus termed "pauser" (e.g., Rhode and Greenberg 1992).

Evidence of inhibition in the torus semicircularis. Evidence of inhibition was found in some units both with and without spontaneous activity. The RA of the non-spontaneous unit shown in Figure 16A and B shows that the BFs are shifted to lower frequencies as sound pressure increases, and the rate-level functions for some frequencies are non-monotonic at levels greater than 20 dB above threshold (Figure 17C). Tone-evoked reduction of spontaneous activity was also observed in some units. This phenomenon was usually observed for strongly phase-locked units stimulated at frequencies above CF. Figure 17 shows the RAs, rate-level functions, and PSTHs for one of the three units encountered showing this type of spontaneous rate reduction. The frequency region at which response rate falls below spontaneous rate tends to shift upward as sound pressure is increased (Figure 17A and B). The rate-level functions are non-monotonic at frequencies above 222 Hz (Figure 17C).

Figure 16. An example of inhibition in a single torus unit with little spontaneous activity. A and B: response areas. C: rate-level functions at some frequencies are non-monotonic as sound level is raised 20 dB above threshold.

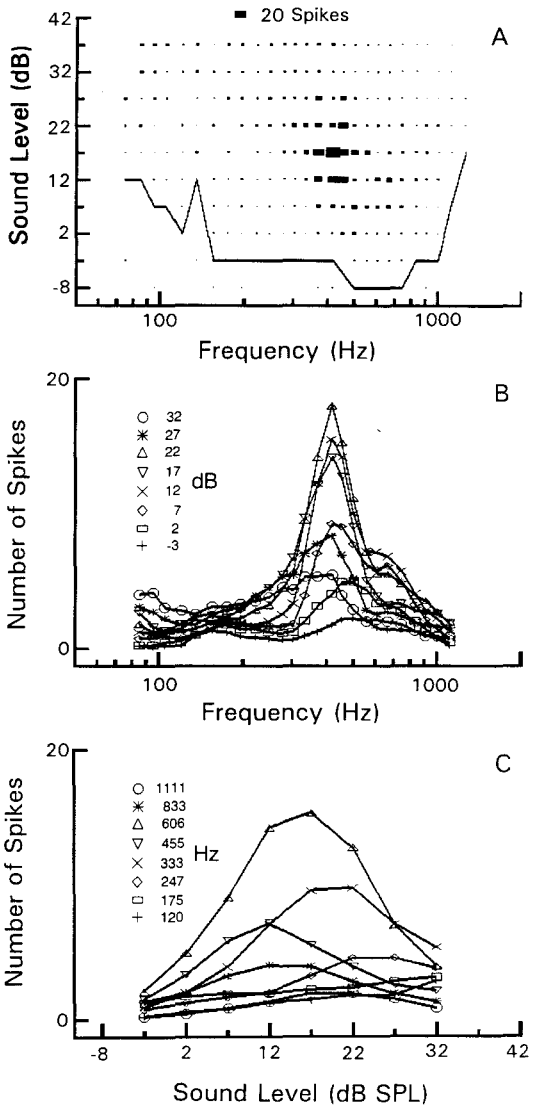
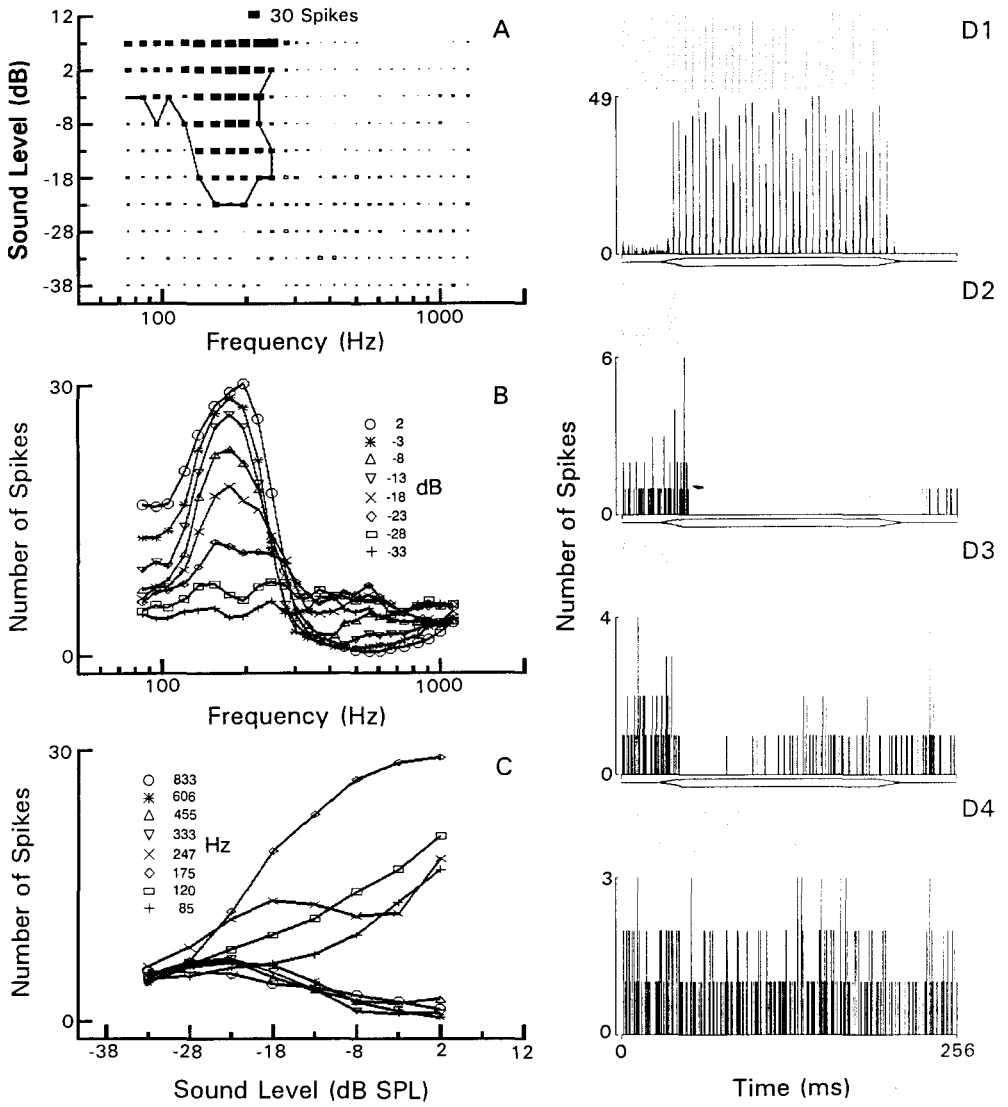

20 Spikes
A
Sound Level (dB)
42
32
22
12
2
-8
100
1000
Frequency (Hz)
B
Number of Spikes
20
0
32
27
22
17
12
7
2
-3
dB
100
1000
Frequency (Hz)
C
Number of Spikes
20
0
1111
833
606
455
333
247
175
120
Hz
-8
2
12
22
32
42
Sound Level (dB SPL)

Figure 17. Sound-evoked reduction of spontaneous activity for a torus unit. A and B: response areas show an area of reduced spontaneous activity above CF and that discharge rate falls below the spontaneous rate at mid and high frequencies for high sound levels. C: rate-level functions at some frequencies are non-monotonic at sound levels well above threshold. Right panel: dot-raster patterns and PSTHs for 196 Hz, 10 dB (D1); 417 Hz, 10 dB (D2); 833 Hz, 10 dB (D3); and spontaneous activity (D4).


30 Spikes
A
Sound Level (dB)
12
2
-8
-18
-28
-38
100
1000
Frequency (Hz)
B
Number of Spikes
30
0
2
-3
-8
-13
-18
-23
-28
-33
dB
100
1000
Frequency (Hz)
C
Number of Spikes
30
0
833
606
455
333
247
175
120
85
Hz
-38
-28
-18
-8
2
12
Sound Level (dB SPL)
D1
49
0
D2
6
0
D3
4
0
D4
3
0
0
256
Time (ms)
Number of Spikes

Comparisons between 80 torus semicircularis units and 340 saccular nerve fibers. Figure 18 compares spontaneous rate, BS, and Q_{10dB} versus CF for 80 torus units and 340 saccular nerve fibers (Fay and Ream 1986). The mean spontaneous rate of torus units (5 spikes/sec ± 0.56 SE) is much less than that of saccular nerve fibers (19 spikes/sec ± 2.82 SE). The maximum spontaneous rate of torus units is about 60 spikes/sec, whereas that of saccular nerve fibers is about 260 spikes/sec. BS ranges from -38 to +17 dB for torus units, but from -25 to 42 dB for saccular nerve fibers. The mean BS of torus units (-19 dB ± 2.12 SE) is greater than for the saccular nerve fibers (4 dB ± 0.75 SE). The lowest BS of torus units as a function of CF corresponds closely to the behavioral audiogram (e.g., Fay 1969). Only a few torus units, but more than half of saccular nerve fibers, have a BS higher than 0 dB. Torus units have sharper tuning than saccular nerve fibers (Q_{10dB} averages 1.46 ± 0.16 SE and 0.62 ± 0.02 SE, respectively). No saccular nerve fiber has a Q_{10dB} greater than 2, but 16% of torus units do.

One of the most interesting differences I observed between the auditory torus semicircularis and the saccular nerve was that the frequency eliciting the most excitation in torus units seemed to be level-independent; as level was increased, the unit tended to continue giving a maximal response at the CF. This is an important finding because unpublished data from the saccular nerve (Fay 1990, 1991) showed that there was a marked level-dependence, or BF-shift, in primary afferents. BF was defined as the frequency eliciting the most

Figure 18. Comparisons of spontaneous rate (left), BS (middle), and Q_{10} (right) versus CF for torus semicircularis units (top) and saccular nerve fibers (bottom; from Fay and Ream (1986)).

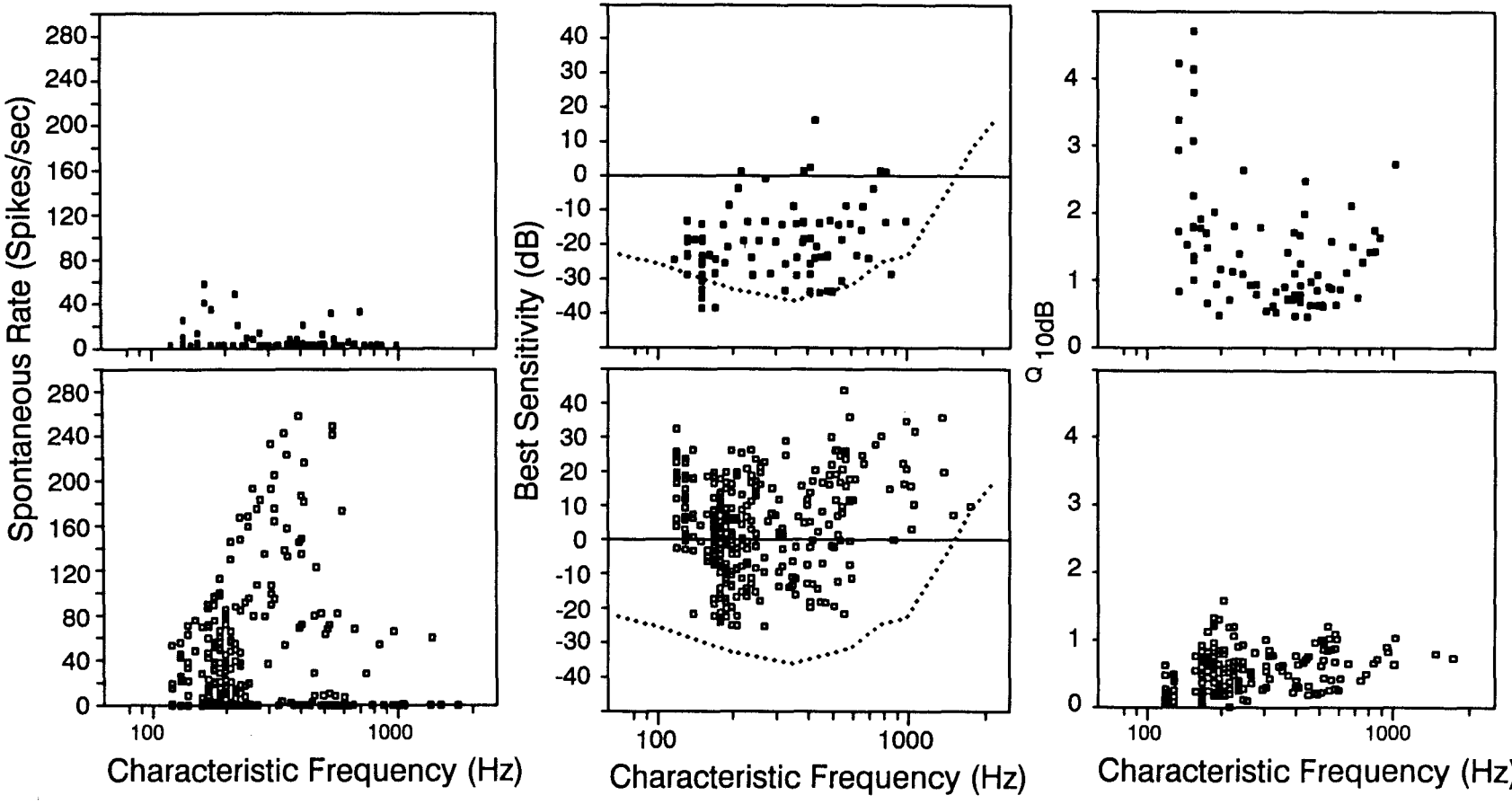
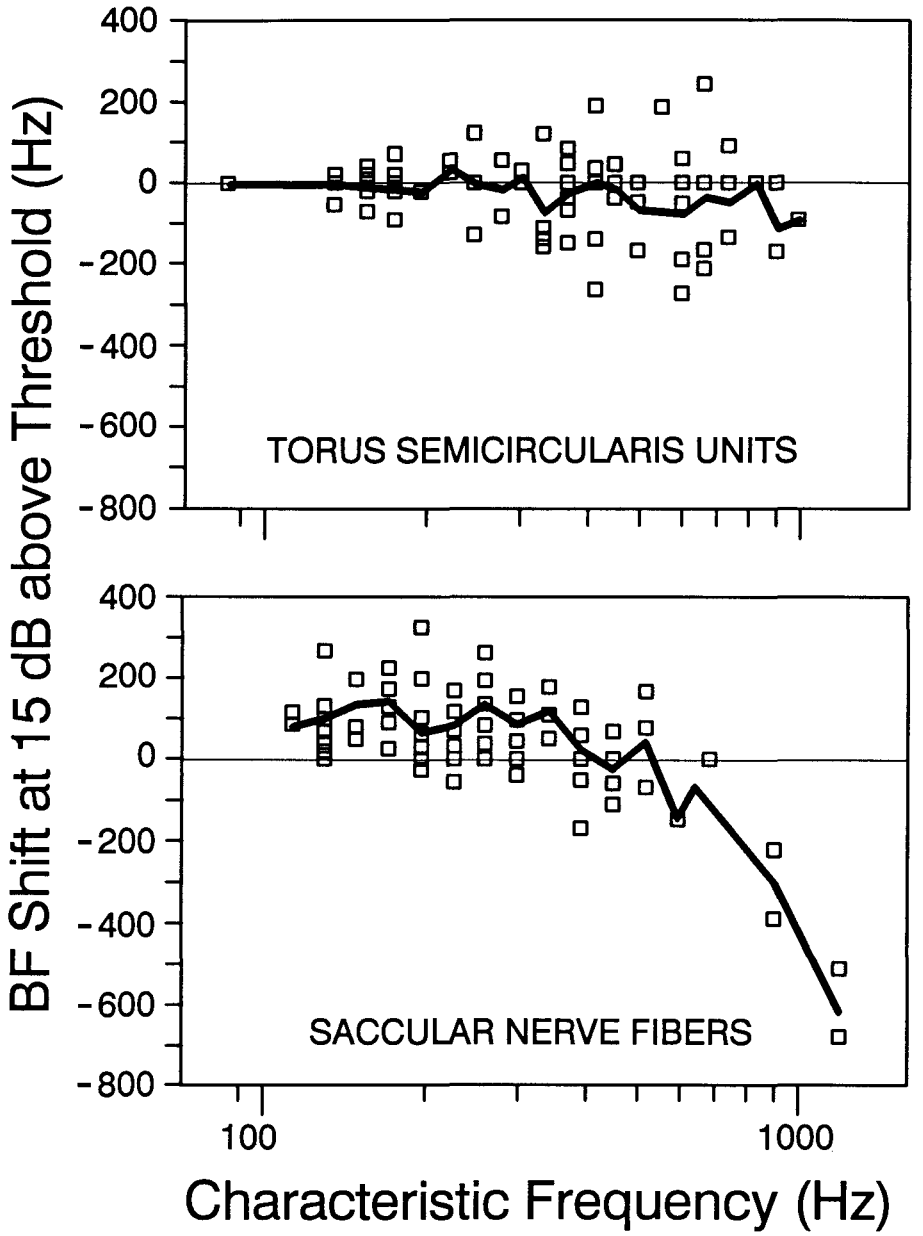

Spontaneous Rate (Spikes/sec)
280
240
200
160
120
80
40
0
100
1000
Characteristic Frequency (Hz)
Best Sensitivity (dB)
40
30
20
10
0
-10
-20
-30
-40
100
1000
Characteristic Frequency (Hz)
Q 10dB
4
3
2
1
0
100
1000
Characteristic Frequency (Hz)

Figure 19. A comparison of BF-shift at 15 dB above BS versus CF for torus units (top) and saccular nerve fibers (bottom; unpublished from Fay (1990; 1991)). BF-shift for saccular nerve fibers is dependent on CF, while BF-shift for torus units tend to be zero.


400
200
0
-200
-400
-600
-800
TORUS SEMICIRCULARIS UNITS
400
200
0
-200
-400
-600
-800
SACCULAR NERVE FIBERS
100
1000
BF Shift at 15 dB above Threshold (Hz)
Characteristic Frequency (Hz)

spikes when the level was about 15 dB above BS, and the BF shift was defined as the difference between CF and BF (BF - CF). The mean BF-shift was only -22 Hz (±9.35 SE) for torus units, whereas it was +55.84 Hz (±12.53 SE) for the saccular nerve. This difference in BF-Shift was highly significant ($P = 0.0001$; $t = 4.67$; $df = 219$; unpaired t-test). A plot of BF-shift is shown in Fig. 19 for both torus units and saccular nerve fibers. The BF-shift for torus units is small and appears to be independent of CF. We term this phenomenon "BF constancy." This pattern is different for saccular nerve fibers. The BFs for saccular nerve fibers tend to be higher than the CF at CFs below 500 Hz, and tend to be lower than the CF at CFs above 500 Hz. The BF-shift of primary afferents occurs because the saturated spike rate tends to be equal to the stimulus frequency up to 400 to 500 Hz (entrainment). Clearly, the BF-shift occurring in peripheral channels is not simply mirrored in the response of torus semicircularis units.

CHAPTER IV

DISCUSSION

Frequency selectivity, tuning and tonotopic organization

Several previous studies on saccular nerve fibers of goldfish and other species have demonstrated frequency selectivity. Furukawa and Ishii (1967) defined 2 types of saccular fibers based on CF and other criteria: 250-400 Hz tuned ("S2") and 700-800 Hz tuned ("S1"). Fay and Ream (1986) grouped saccular afferents into four types: untuned or flat (± 10 dB), low frequency (CF: 120-290 Hz), mid-frequency (CF: 300-670 Hz), and high frequency (CF: 790-1770 Hz). Sawa (1976) studied auditory responses from units recorded in the goldfish medulla, and classified them into two groups based on their CF: 200-300 Hz and 600-700 Hz. Differences of acoustic setup, criteria for defining CF, and methodology may have led to these different classifications. Our acoustic tank setup and the criteria selected were similar to those of Fay and Ream (1986). Almost all torus units show some degree of frequency selectivity with CFs ranging from about 100 Hz to about 1 kHz. There are two clear modes in the CF distribution (Figure 5) corresponding to the low and mid-frequency saccular afferents that Fay and Ream (1986) have described (see Figure 16). As is the case for saccular fibers, however, the existence of a

separate group of units with CFs above 650 Hz in the torus is difficult to clearly demonstrate due to the small number of units encountered with high CFs. In general, the distribution of torus unit CFs (Figures 5 and 16) is similar in shape to that for saccular afferents (Fay and Ream 1985).

Page (1970) suggested that auditory units at higher levels of the teleost CNS tend to have progressively sharper tuning. Our results are consistent with this hypothesis. Torus units, especially those with low-CF, tend to be more sharply tuned than primary afferents.

RAs (the number of spikes versus frequency functions) of goldfish torus units usually show a single BF peak. RAs having more than one major peak were usually observed from multiunit recordings (see Figure 14). However, we did observe two-peaked RAs for two kinds of single units. First, some low-CF units with one RA peak at about 155 Hz had another small peak at or below 100 Hz. The origin of the lower-frequency peak is not clear, but may reflect additional input from the lateral line system or from otolith organs other than the saccule (i.e., the lagena or utricle). In studies on the torus semicircularis of the trout, Salmo gairdneri, three types of acousticolateral units have been defined: H (auditory), L (lateral line), and B (both auditory and lateral line) (Schellart et al. 1989). The B units were hypothesized to receive inputs from both the auditory and lateral line systems. Auditory and mechanosensory lateral line regions have been described in TS of goldfish (McCormick 1990; McCormick et al. 1992). The auditory zone is located medially and the

mechanosensory lateral line zone is located more laterally in the torus (see Figure 6A). The low-CF units having two-peaked RAs could possibly receive inputs from both the auditory and lateral line systems. It is not yet clear whether and to what extent the torus receives inputs from the lagena or utricle.

Two-peaked, discontinuous tuning curves were also sometimes observed for high-CF units. In these cases, responses were observed at low frequencies at levels well above BS (Figure 9D). This discontinuous RA may be the result of inhibition by units tuned at mid frequencies.

Several torus units had unusual tuning curves. For example, "⊔" shaped tuning curves (Fig. 7C), not found in saccular primary afferents, show a broad region of equal sensitivity with sharp cut-off slopes up to 200 dB/octave. Low-CF units with steep high-frequency slopes and high-CF units with steep low-frequency slopes were also observed. Although suppression can produce steep low-pass slopes in some saccular fibers with CFs in the 250 Hz range (Fay 1990), steep low- and high-pass slopes have not been observed for primary afferents tuned to mid and high frequencies (Fay and Ream, 1986).

Several studies have provided evidence of tonotopic organization in the auditory periphery (saccule) using different methods and fish species (Anderson and Enger 1968; Sand and Michelsen 1978; Sugihara and Furukawa 1989). In general, some evidence suggests an anteroposterior distribution of high to low frequencies in the saccule. Echteler (1985b) demonstrated a crude tonotopic organization of latero-medial and postero-anterior distributions of low

to high frequency in TS of the carp (Cyprinus carpio) using a multiunit recording method. A similar tonotopic organization was demonstrated in rainbow trout, Salmo gairdneri (Schellart et al 1987). Although the present study was not designed to map the TS in goldfish, we observed examples of small unit clusters for which the BFs of different units differed by up to one octave. Thus, we believe that tonotopic organization of the goldfish TS is somewhat diffuse, at best.

Phase-locking

Almost all peripheral nerve fibers of the goldfish phase-lock robustly to tones (Furukawa and Ishii 1967; Fay 1978). Page (1970) studied the auditory response characteristics of single units in the medulla and torus semicircularis of goldfish, and found that half of the medullary units and none of the torus units were significantly phase-locked. In this study, the Rayleigh test was used to quantitatively determine whether or not a unit's period histogram was significantly synchronized to tones. Fifty-three percent (28/55) of torus units were found to significantly synchronize to tones ($p < 0.01$), and about 15% (8/55) were strongly phase-locked (coefficient of synchronization, R greater than or equal to 0.5), some with phase-locking accuracy exceeding that of primary afferents. It is possible that Page (1970) missed the strongly phase-locked units due to the difficulty of isolating them using indium electrodes. We had difficulty isolating this type of unit using indium electrodes, and all of the

strongly phase-locked units we observed were recorded using glass micropipettes. Strongly phase-locked units have been recently observed in the auditory midbrain of mormyrids (Crawford 1993). It is possible that these units are inputs to the TS that originate at lower levels (e.g., medulla), but it is clear that this kind of entrained unit does exist at the level of the auditory midbrain.

Some phase-locked units recorded using both indium and pipette electrodes had two peaks in the period histogram separated by about 180° (Figures 13 and 14). In the case of the pipette recordings, we are certain that the responses originated from a single cell. In some of the cases using indium electrodes, we believe that the electrode sampled from at least two units that were about 180° out of phase. For multi-unit recording, the evidence for this is that the spikes locked to one phase were of lower amplitude than the spikes locked to the other phase, and that the RAs for these mid-frequency units showed two peaks located several hundred Hz apart (see Figure 14B). Thus, we believe that some units recorded in the torus represent the combined influence of at least two oppositely oriented saccular hair cells, and that in other cases, pairs of neurons exist close to one another that have different CFs, but have phase-locked responses 180° out of phase. The functional significance of these out-of-phase pairs is not clear.

There are two groups of hair cells of the goldfish saccule having opposite morphological polarizations (Platt 1977). Furukawa and Ishii (1967) have recorded single saccular afferents which phase-lock to both the compression

and rarefaction phases of a sinusoidal stimulus, indicating that some afferents innervate hair cells of both orientations. Our observation of double-peaked period histograms in the goldfish torus indicate either that afferent inputs from the two hair-cell populations converge on single neurons in the torus, or that the afferents innervating both types of hair cells relay information faithfully to the torus. In any case, some neurons at the level of the midbrain represent the combined influence of both hair-cell groups.

Comparisons of acoustic response features of the TS between goldfish and mormyrids

Recently, Crawford (1991a, 1993) has surveyed the acoustic response properties of auditory midbrain units in two species of african mormyrids (Pollimyrus isidori and Brienomyrus niger). One species studied (Pollimyrus isidori) uses vocal communication during courtship (Crawford 1991b). Both the goldfish and mormyrids have specialized accessory structures to enhance sound pressure sensitivity (swimbladder and Weberian ossicles for goldfish; air-filled bladder within the ear for mormyrids). Our experimental design and acoustic setup were similar to Crawford's, so it is possible to compare Crawford's results with the present results for the goldfish. The sample of mormyrid and goldfish midbrain units studied have a similar range of characteristic frequencies (about 100 Hz to about 1000 Hz). However, most units of the mormyrid auditory midbrain are tuned near 200 Hz, while the distribution of CFs for the

goldfish show major modes at 155 and 455 Hz. The most sensitive units from both species have BSs in the -35 to -40 dB range for frequencies between 100 and 200 Hz.

Midbrain units of both the goldfish and mormyrids are similar in that Q_{10dB} can be as high as about 5.0, the most sharply tuned units have Cfs at low frequencies, spontaneous rates are similarly low, some units are strongly phase-locked, and non-monotonic rate-level functions have been observed. In addition, units that phase-locked to the stimulus waveform at two phase angles, about 180° apart, were observed in both the goldfish (Figure 13A) and mormyrid (Crawford's Figure 9B) midbrain. This type of response has not been previously reported in the CNS of other fishes. On the other hand, Crawford did not report entrained, strongly phase-locked responses of the type illustrated in Figures 4, 11, and 12. Crawford did not use glass pipette electrodes, so it is possible that this difference may reflect electrode sampling characteristics. In general, however, there are more similarities than differences between goldfish and mormyrids in the response properties of auditory midbrain units.

Inhibition

Two hypothetical inhibitory mechanisms have been advanced to explain non-monotonic rate-level functions observed in the cochlear nucleus of mammals (Voigt and Young 1980; Shofner and Young 1985). One postulates that inhibition arises from interneurons having a similar CF but a higher

threshold than the unit recorded. The other postulates inhibitory inputs from units with different Cfs.

In the goldfish TS, we observed non-monotonic rate-level functions and a reduction of spontaneous activity in several units as illustrated in Figure 17A, B and C. This response pattern is similar to that observed in some low-CF saccular afferents showing "single-tone suppression," an effect probably arising peripherally (Fay, 1990, 1991). Thus, the similar behavior of some of the torus units could represent a faithful relaying of peripheral, single-tone suppression to the midbrain. However, non-monotonic rate-level functions shown in Figure 14C for a unit without spontaneous activity were not observed in peripheral saccular fibers of the goldfish, suggesting that this phenomenon is probably due to inhibitory neuronal interaction within the auditory CNS. Further experiments using more complex stimuli are underway to determine the extent to which tone-evoked reductions in spontaneous activity and non-monotonic rate-level functions observed in the torus are the result of neural inhibition or peripheral suppression.

CHAPTER V

CONCLUSIONS

In general, this survey of acoustic response properties of the midbrain units of the goldfish reveals response patterns similar to those observed in many other vertebrate auditory systems, including those of mammals. The limited frequency selectivity of primary afferents has apparently been sharpened prior to or at the midbrain level. While the mechanisms for this sharpening have not yet been investigated in fishes, it is possible that they result from inhibitory interactions (Fay and Lu 1992) of the types demonstrated in the mammalian cochlear nucleus (reviewed by Rhode and Greenberg, 1992). The relatively sharp frequency tuning of torus units is an indication that frequency-domain spectral processing may be of more importance for hearing in the goldfish than was previously suspected (e.g., Fay 1978b). This suggests that spectral filtering and its enhancement are important elements of auditory processing in all vertebrates investigated, and that these processes may have evolved quite early in the history of vertebrate auditory systems. The observation of temporal response patterns resembling those of mammalian auditory systems (e.g., chopper-like behavior) further reinforces our view that many fundamental features and information-processing strategies of mammalian

auditory systems represent general, primitive characters that may have originated early in vertebrate evolution. Further comparative investigations may help us to determine what characteristics of auditory systems are special or derived among more recently evolved species.

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APPENDIX

A

The summary of data of the types of electrodes used, characteristic frequency (CF), best sensitivity (BS), Q_{10dB}, and spontaneous rate (SR) for 80 torus units.

ID	ELECTRODE	CF(Hz)	BS(dB)	Q_{10dB}	SR(S/s)
A8	Indium	155	-38	3.79	1.32
B7	Indium	459	-23	0.97	0.52
B8	Indium	417	-28	0.68	0
B10	Indium	579	-8	0.63	0
B11	Indium	145	-18	1.52	0
B13	Indium	176	-38	0.66	0
B14	Indium	488	-33	0.85	0
B15	Indium	417	-33	1.67	0.10
C1	Indium	394	-13	0.47	5.21
C2	Indium	676	-8	1.5	1.04
C3	Indium	135	-18	4.22	0
C4	Indium	389	-18	0.71	1.30
C7	Indium	436	17	2.48	0
C9	Indium	244	-23	1.09	0
C10	Indium	488	-23	1.08	1.04
C11	Indium	455	-13	0.62	0
C13	Indium	555	-18	0.87	0
D3	Indium	442	-20	0.45	0
E4	Indium	278	0	0.93	11.67
E5	Indium	417	-25	0.79	18.65

E6	Indium	155	-25	2.25	11.56
F3	Indium	155	-35	1	2.81
G6	Indium	871	-28	1.64	0
G8	Indium	506	-33	0.63	1.67
G9	Indium	512	-33	0.61	0
H3	Glass	370	-23	0.71	5.42
H4	Glass	370	-28	1.41	0.10
H7	Indium	290	-28	1.78	0
I1	Indium	667	-15	2.11	0
I2	Indium	556	-30	1.58	5.73
I4	Indium	196	-20	0.48	
I5	Indium	191	-25	0.94	0.10
J3	Glass	155	-30	1.8	0
J6	Indium	333	-25	0.52	0
K3	Glass	833	-13	1.43	0
K7	Glass	333	-33	0.83	0.10
L2	Glass	602	-13	0.86	0
L4	Glass	135	-28	0.83	7.5
L6	Glass	135	-23	3.38	23.33
L7	Glass	217	-3	0.71	0
L8	Glass	222	2	1.12	47.71
L9	Glass	394	2	1.71	0
L10	Glass	417	-3	0.92	0.20
L12	Glass	741	-3	1.27	0
L13	Glass	155	-23	4.14	0.10
L14	Glass	262	-18	0.92	5.63
L15	Glass	155	-23	1.35	0.2
M1	Glass	394	-13	0.79	0.10
M3	Glass	417	-33	0.79	1.56

M4	Glass	394	-18	1.1	0
M5	Glass	227	-18	1.8	18.65
M7	Glass	435	-23	1.99	0
M8	Glass	166	-23	1.77	39.27
M9	Glass	709	-23	0.74	31.04
M11	Glass	155	-13	1.78	0.15
M12	Indium	417	-18	1.25	0
M13	Glass	237	-13	1.39	0
N3	Glass	637	-23	1.11	3.13
N4	Glass	370	-13	0.73	0
N5	Glass	278	-13	0.79	01.0
N8	Indium	155	-33	1.29	0.25
N9	Indium	324	-13	0.61	0
N12	Indium	155	-23	4.13	0
N14	Indium	487	-23	0.62	1.15
O1	Indium	1000	-13	2.73	0
O3	Glass	176	-23	1.48	33.33
O6	Indium	833	2	1.75	0.31
P3	Glass	541	-13	0.9	30.10
P4	Glass	135	-13	1.72	0.10
P7	Glass	175	-28	1.7	0
P9	Glass	155	-28	4.7	0
P11	Glass	155	-18	3.07	0
R3	Indium	199	-8	1.16	0
R4	Glass	135	-18	2.93	0.20
R5	Glass	189	-13	2.01	0
R6	Glass	166	-23	1.91	56.88
R7	Glass	360	-8	0.9	1.15
R8	Glass	247	-28	2.63	7.29

R10	Glass	305	-18	0.54	0
S1	Glass	787	2	1.42	0

The list of complete data of coefficient of synchronization (R), the number of spikes, the values of Rayleigh statistic (Z), and phase-locking significance for 55 torus units (The critical value of Rayleigh statistic is 4.5).

ID	R	SPIKES	Z	PHASE-LOCKING
G9	0.01	350	0.04	
J6	0.02	298	0.12	
C5	0.05	100	0.25	
C9	0.03	316	0.28	
D3	0.03	374	0.34	
L15	0.02	982	0.39	
J3	0.02	1561	0.62	
G1	0.04	476	0.76	
O1	0.12	64	0.92	
G5	0.13	56	0.95	
R3	0.11	110	1.33	
F1	0.15	67	1.51	
H8	0.10	156	1.56	no
N9	0.09	193	1.56	($p > 0.01$)
G2	0.08	267	1.71	
O6	0.10	181	1.81	
B14	0.17	76	2.20	
N8	0.05	894	2.24	
R10	0.06	658	2.37	
M1	0.14	170	3.33	
M13	0.12	244	3.51	
N4	0.08	568	3.64	
P9	0.08	573	3.67	
B8	0.09	461	3.73	

N14	0.05	1568	3.92	
L10	0.23	85	4.50	
A8	0.08	737	4.72	
P7	0.08	811	5.19	
F3	0.18	250	8.10	
N10	0.15	441	9.92	
C7	0.21	241	10.63	
P4	0.17	386	11.16	
C11	0.28	196	15.37	
P11	0.17	565	16.33	
S1	0.18	505	16.36	
N12	0.21	553	24.39	weak
R4	0.15	1115	25.09	($p < 0.01$)
B13	0.13	1800	30.42	($R < 0.5$)
G10	0.16	1415	36.22	
L8	0.26	945	63.88	
M11	0.32	763	78.13	
K3	0.40	604	96.64	
M5	0.33	1209	131.66	
K7	0.37	997	136.49	
M3	0.42	951	167.76	
B12	0.44	949	183.73	
H3	0.45	1023	207.16	
M2	0.92	576	487.53	
C13	0.62	3144	1208.55	
M9	0.80	2114	1352.96	strong
O3	0.96	1715	1580.54	($p < 0.01$)
R8	0.98	1694	1626.92	($R > 0.5$)
N5	0.98	2360	2266.54	

M12	0.88	2957	2289.90
P3	0.88	3267	2529.96

APPROVAL SHEET

The thesis submitted by Zhong-min Lu has been read and approved by the following committee:

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The final copies have been examined by the director of the thesis and the signature which appears below verifies the fact that any necessary changes have been incorporated and that the thesis is now given final approval by the Committee with reference to content and form.

The thesis is therefore accepted in partial fulfillment of the requirements for the degree of Master of Arts.

Apr 14 '93
Date

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Director's Signature