Colloquium

Linear and nonlinear pathways of spectral information transmission in the cochlear nucleus

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At the level of the cochlear nucleus (CN), the auditory pathway divides into several parallel circuits, each of which provides a different representation of the acoustic signal. Here, the representation of the power spectrum of an acoustic signal is analyzed for two CN principal cells-chopper neurons of the ventral CN and type IV neurons of the dorsal CN. The analysis is based on a weighting function model that relates the discharge rate of a neuron to first- and second-order transformations of the power spectrum. In chopper neurons, the transformation of spectral level into rate is a linear (i.e., first-order) or nearly linear function. This transformation is a predominantly excitatory process involving multiple frequency components, centered in a narrow frequency range about best frequency, that usually are processed independently of each other. In contrast, type IV neurons encode spectral information linearly only near threshold. At higher stimulus levels, these neurons are strongly inhibited by spectral notches, a behavior that cannot be explained by level transformations of first- or second-order. Type IV weighting functions reveal complex excitatory and inhibitory interactions that involve frequency components spanning a wider range than that seen in choppers. These findings suggest that chopper and type IV neurons form parallel pathways of spectral information transmission that are governed by two different mechanisms. Although choppers use a predominantly linear mechanism to transmit tonotopic representations of spectra, type IV neurons use highly nonlinear processes to signal the presence of wide-band spectral features.

As sensory systems are studied more completely, it is apparent that they are composed of multiple parallel subsystems (for example, see refs. 1–4). The physiological characteristics of these segregated pathways are often quite different, leading to the assumption that each subsystem plays a specialized role in the processing of sensory information. The cochlear nucleus (CN), the termination zone of auditory nerve fibers, is an ideal structure in which to investigate the parallel processing of information within a sensory system. Not only does the CN contain at least seven different principal cell types—each with distinct morphological and physiological properties—but these distinct neuron classes project to auditory nuclei in anatomically segregated pathways (5, 6). These findings suggest that the CN is the origin of multiple functionally distinct subsystems of auditory information processing.

The parallel organization of sensory systems suggests that different neural populations may be responsible for processing different aspects of a sensory stimulus. Distinct neuron classes of the CN likely exist to decompose complex natural sounds into more simple information-bearing elements—forms that are necessary for subsequent processing in other auditory nuclei. What acoustic information is contained within each of these elements and by what mechanism do the auditory neurons compute this information? In this paper we address these questions by considering only information that is present in the power spectra of sounds. Sound spectra, distribution plots of the energy content in a stimulus across frequency, have been shown to convey information necessary for the identification and localization of behaviorally important acoustic stimuli. For example, the identity of a speech vowel appears to be determined by its formant frequencies, the frequencies at which there are peaks of energy in the power spectrum (7). We limit our discussion in this paper to the behavior of chopper and type IV neurons in the ventral CN (VCN) and dorsal CN (DCN), respectively. Both neuron types have been implicated in aspects of the representation of the frequency spectra of stimuli (8, 9). We will show that these two principal neurons of the CN compute spectral information about the acoustic environment by using different mechanisms.

Importance of Spectral Shape in Sound Localization

Spectral shapes of acoustic stimuli provide cues that are necessary for accurate sound localization in cats and humans (10, 11). Spectral sound localization cues are produced by the directiondependence of sound propagation through the external ear. This dependence is captured by the head-related transfer function (HRTF), a measure of the ratio of the sound pressure near the eardrum to the sound pressure in free field (12, 13). Two examples are shown in Fig. 1 (14). Flat spectrum broadband noise presented in free field at two different spatial locations will be modified by two different HRTFs, like those shown in Fig. 1. As a result, spectra at the eardrum are different and can be used to identify the sound source directions. In the midfrequency region between 8 and 18 kHz, HRTFs commonly exhibit broad spectral notches (at 13.6 kHz for EO and just below 10 kHz for E2) with center frequency positions that vary systematically with source position in the frontal field. The variation of first notch position with azimuth and elevation suggests that notch positions occurring at each ear are in principle sufficient to provide a unique determinant of sound location (14). The complex spectral patterns seen at high frequencies (above 18 kHz) also change rapidly as the sound source is moved. These high-frequency cues have been shown to provide cats with the ability to discriminate between two source locations (15); however, in cats, the midfrequency notch appears to be necessary for localizing a single sound source (11).

Representation of Spectral Shape Across Neural Populations

At threshold, auditory neurons respond most strongly to a single frequency called the best frequency (BF). At higher sound levels,

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Abbreviations: BF, best frequency; CN, cochlear nucleus; DCN, dorsal CN; VCN, ventral CN; RSS, random spectral shape; HRTF, head-related transfer function.

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Fig. 1. Examples of HRTFs for the external ear of the cat. Plot shows gain versus frequency for sound propagation from free field to a point near a cat's eardrum (14) for two directions in space. Gains were computed as the ratio of the sound pressure measured near the eardrum divided by the sound pressure in free field, i.e., with the cat removed. E0 was 15° to the right of midline (the recording microphone was in the right ear) and 30° above the horizon. E2 was also 15° to the right, but was 15° below the horizon. Test stimuli in later figures were generated by filtering broadband noise with these and similar gain functions, thereby producing stimuli whose spectra had the shape of these gain functions (for details, see ref. 18). Earphone delivery of these stimuli simulates presentation of a broadband noise from the corresponding directions in free field.

they respond primarily to frequency regions surrounding BF. Auditory nuclei are tonotopically organized, meaning that BF values of neurons at sequential anatomical positions differ in a systematic, sequential manner (16). For example, more ventral areas of the DCN house neurons with progressively lower BF values than those in more dorsal areas (17). Tonotopic organization can be viewed as a physiological correlate in the brain to the frequency axis of the sound power spectrum.

The BF tuning of auditory neurons is the basis for two different mechanisms by which sound spectra can be represented across a neural population. In response to an auditory stimulus, an array of neurons may produce a tonotopically organized distribution of average rates that are proportional to spectral shape (e.g., ref. 18). This tonotopic representation must involve narrowly tuned neurons that produce discharge rates that are monotonically related to the spectral energy near BF. Alternatively, auditory neurons may provide a tonotopic representation of stimulus features. In this case, the responses of neurons strongly depend on the presence of wide-band spectral shapes within their receptive fields. Previous studies have shown that VCN chopper neurons possess the physiological characteristics to provide a tonotopic representation of a sound spectrum (8). In contrast, DCN type IV neurons are likely to be feature detectors, exhibiting strong rate sensitivity to the presence of wide-band spectral notches at BF (9, 19). The current study corroborates these earlier findings by applying techniques of system identification to explore the two mechanisms for the rate-encoding of spectral information.

A System Identification Approach to Understanding Spectral Processing in Auditory Neurons

Neurons producing the spectral shape representations described above are assumed here to pass spectral information to other areas of the brain in the form of average discharge rate. The transformation of spectral information into rate is assumed to be given by the following stimulus-response function:

$$r = R_0 + \sum_{j=j1}^{j2} w_j S(f_j) + \sum_{j=j1}^{j2} \sum_{k=j}^{j2} w_{jk} S(f_j) S(f_k), \quad [1]$$

where discharge rate r is a weighted sum of energy at different frequency components of the stimulus. The frequency axis is divided into bins of 1/8-octave width with values $S(f_j)$ equal to the energy in one such bin. The spectrum S is expressed as dB

relative to the average bin power across frequency. In the first sum of Eq. 1, the first-order weight, w_i , quantifies the contribution of the bin with center frequency, f_i , to the overall rate response. In the second sum, the second-order weight, w_{ik} , captures either quadratic dependence of rate on stimulus energy at a single frequency, f_j , or interactions between energy at frequency pairs f_j and f_k . R_0 is the rate response to a sound with constant spectral level of 0 dB re: the average value. The form of this model is motivated by the fact that, in response to small fluctuations in level of a fixed broadband stimulus, auditory nerve fibers and VCN neurons exhibit discharge rates that are approximately linearly related to spectral level at BF (20-22). Eq. 1 is a small-signal linearization of a nonlinear system that is valid over a restricted range of spectral levels S(f). Although the range of the approximation has not been investigated, it seems to be large enough to encompass the range of spectral levels seen in HRTFs, where levels $S(f_i)$ vary by less than 10–20 dB from an average value. Similar models have been used previously (e.g., refs. 23–25).

The system parameters R_0 , w_j , and w_{jk} can be deduced by presenting stimuli with predetermined spectral shapes and recording observed discharge rates. Responses to spectra with a constant level of 0 dB are averaged to obtain an estimate of R_o . First- and second-order weights then are estimated by recording responses to stimuli with random spectral shapes (RSS) and solving Eq. 1 by using least squares (normal equations, ref. 26). Spectra of three of the RSS stimuli are shown in the bottom three plots of Fig. 2B. The amplitudes of the spectra in each frequency bin are pseudorandom with mean 0 dB and standard deviation 12 dB. The waveforms of the stimulus set are generated by first discretizing spectra into tones that are logarithmically spaced at frequency steps of 1/64 octave. Each of the frequency bins are 1/8-octave wide and contain eight of these tones, each with identical amplitude. Sinusoidal tones with random phase are summed for each spectrum to generate the RSS stimuli. Because the model is valid only over a limited level range, model parameters are computed for different overall stimulus levels at 10-dB intervals.

The first-order weights shown in Fig. 2C were obtained from the rate responses to 192 RSS stimuli. First-order weights for two different neurons, a VCN chopper (Fig. 2C Left) and DCN type IV (Fig. 2C Right), are plotted as a function of frequency in terms of octaves relative to BF. The mean and standard deviation of the weights are determined by using a bootstrap procedure (27) in which weights are computed repeatedly by sampling with replacement from the set of 192 stimulus-rate pairs. As many as 192 weights (total number of first- and second-order weights) can be computed by using the least-squares fitting method; however, only a subset of these are useful in characterizing a neuron. Three criteria are used to estimate a useful range of first-order weights ([j1, j2] in Eq. 1). First, a weight is considered significant if it is at least one standard deviation (determined from the bootstrap calculations) away from zero. Second, weighting functions are assumed to be continuous. That is, weights near zero that are located between two significant weights are included in the range. Third, weights considered significant must improve the accuracy with which Eq. 1 can predict responses to novel stimuli (described below). The filled circles in Fig. 2C indicate weights that are considered significant under these criteria. The range of weights [j1, j2] defines the bandwidth of the neuron. Second-order weights are computed over the same or wider bandwidth to ensure that the higher-order model includes all contributing frequency bins.

If Eq. 1 truly describes the transformation of spectral level into rate, then estimated parameters should accurately predict responses to novel stimuli. A set of broadband noise stimuli filtered by HRTFs is used to test the model and study the representation of behaviorally relevant spectral cues. The 100



Fig. 2. (A) The acoustic calibration from one experiment. This represents the sound pressure level near the eardrum across a range of frequencies, given fixed electrical signal amplitude (0-dB attenuation) at the input of the earphone. Broadband noise with a flat spectrum at the input to the earphone will have this spectrum. All stimuli presented during an experiment are modified by the shape of this calibration. (B) The spectral envelopes of four of a set of 200 stimuli (each 5.875 octaves wide) that were used to compute the unknown system parameters of Eq. 1. The first (flat) spectrum is used to estimate R₀. The remaining three spectra are examples of RSS stimuli. Although spectra are periodic along the frequency axis, a single period is wide enough to encompass the receptive field of the neurons studied. Ordinate values of these spectra are given in dB re: the average sound level in the stimulus. As explained in the text, overall sound levels were varied systematically during the experiment. (C) Examples of first-order weighting functions for two neurons whose response maps are shown in Fig. 3. Mean weights (bold lines) and \pm 1 standard deviation (gray shaded region) are computed by using a bootstrap procedure. The weights indicated by • are significantly different from zero (see text). Weights were computed from RSS stimuli presented at the average spectral levels given in the legends.

HRTFs chosen for the stimulus set were recorded from locations in the frontal field of a cat at 15° intervals in azimuth and 7.5° intervals in elevation (14). Parameters estimated by using RSS stimuli and found to be significant are used to predict responses to HRTF stimuli of matched average level. The quality of the model fit is quantified by a measure Q given by

$$Q = \frac{1}{1 + \sum_{i=1}^{n} (r_i - \hat{r}_i)^2 \left| \sum_{i=1}^{n} (\hat{r}_i - \bar{\hat{r}})^2 \right|},$$
 [2]

where r_i are the experimental rates, \hat{r}_i are the rates predicted by the model, and \bar{r} is the mean of the \hat{r}_i . Q varies from 0 to 1 where 0 indicates a poor fit and 1 is obtained for a perfect fit.

Responses of Chopper and Type IV Neurons to Spectral Notches

The results shown in this paper were obtained in the CN of unanesthetized, decerebrate cats by using standard extracellular recording techniques. Stimuli were applied through a calibrated closed acoustic system. An example of an acoustic calibration is shown in the top plot of Fig. 2.4. Details of the animal preparation can be found in recent publications (28–30). All procedures were approved by the Johns Hopkins Animal Care and Use Committee.

Fig. 3 illustrates how chopper and type IV neurons differ in their physiological response properties. Fig. 3 *A1* and *B1* are response maps that show excitatory and inhibitory frequency regions in the receptive fields of a chopper and a type IV neuron at multiple sound levels. Each subplot within a response map is constructed from average rate responses to a set of 100 tone bursts whose frequencies are logarithmically interpolated across



Fig. 3. (A1) Response map of a VCN chopper neuron. The V-shaped excitatory area is centered on BF (25.5 kHz: dark grav vertical line) and flanked by inhibitory areas at higher and lower frequencies. Each subplot shows average rate responses to a 200-ms tone sweep over a range of frequencies at fixed attenuation. Attenuation values are given to the right of the plots. Zerodecibel attenuation corresponds roughly to 90- to 100-dB re: 20 μ Pa; however, the actual sound pressure level varies slightly across frequency because of the acoustic calibration (see the example in Fig. 2A). The rate scale shown at the lower left applies to the 80-dB attenuation subplot. Subsequent plots are shifted vertically but use the same scale factor. Horizontal lines indicate the spontaneous rate (same at all levels). (A2) Discharge rate of the same chopper in response to HRTF-filtered noise stimuli (400-ms duration, ~40 dB re: threshold) containing salient midfrequency spectral notches. Each observed rate (gray filled circle) is plotted against the frequency at which the notch occurs relative to BF. The solid black curve is a 1/8-octave smooth of the points. The horizontal gray bar indicates the spontaneous rate. This chopper encodes notch position by producing a rate minimum when the notch is centered on BF. (B1) Response map of a DCN type IV neuron (BF = 15.9 kHz) characterized by a mixture of excitatory and inhibitory areas (see text). (B2) Notch responses for the same type IV neuron at \approx 30 dB re: threshold. Although the response is qualitatively similar in shape to that in A2, this neuron is inhibited when the notch is centered on BF. Note that the logarithmic frequency axes in parts 1 and 2 are the same for both A and B.

a range spanning the response area of the neuron. Regions of rate increase above spontaneous activity are excitatory areas, whereas regions of decrease are inhibitory areas. The VCN chopper response map in Fig. 3A1 is typical of auditory neurons in that it has a V-shaped excitatory area centered on BF (16). This particular chopper neuron also exhibits inhibitory side bands. In contrast, the DCN type IV response map in Fig. 3B1 exhibits more complex patterns of inhibition. At low levels there is a small excitatory area that represents the tip of the tuning curve of the cell's excitatory inputs. At higher levels, a substantial inhibitory area appears that is centered on or just below BF. This central inhibitory area is likely to be the result of glycinergic input from DCN interneurons (vertical cells; ref. 31). At frequencies away from BF, type IV response maps vary from neuron to neuron. In general, type IV neurons exhibit a wideband inhibitory area that extends both above and below BF (30). This inhibitory area is likely to be derived from two inputs: the first being a glycinergic D-multipolar or radiate neuron in VCN, and the second being a GABAergic input whose source has not been identified. Detailed features of type IV response maps have been described elsewhere (19, 28).

Chopper and type IV neurons also differ in the way that they respond to spectral notches. Fig. 3A2 shows responses of the same chopper neuron to HRTF stimuli with spectral notches located at different frequency positions relative to the neuron's BF. Each point indicates the average discharge rate of the chopper in response to an HRTF stimulus, plotted as a function of the stimulus notch frequency relative to BF. The result shows a single-neuron analog of a tonotopic population representation in that the rate response is at a minimum when the notch is centered on BF and increases as the notch moves away from BF. In this chopper, as in auditory nerve fibers (32), the rate minimum occurs because of the reduction in sound power within the excitatory area when the notch is centered on BF. The response of the DCN type IV neuron to a spectral notch (Fig. 3B2) is qualitatively similar to that of the chopper neuron in that there is a minimum discharge rate when the notch is centered on BF. However, there are two important differences. First, the notch response goes below spontaneous rate in the type IV neuron when the notch is centered on BF. This inhibitory response does not occur in the chopper neuron. Second, notch responses are qualitatively consistent with the chopper response map in that centering the notch on BF removes energy from an excitatory response area. This should produce a reduction in discharge rate, although not necessarily an inhibitory response. In contrast, the type IV neuron gives predominantly inhibitory responses to tone energy near BF at most sound levels. Centering a notch on BF therefore should produce an excitatory response instead of the inhibitory one actually observed. The explanation for this contradiction is the dual inhibitory nature of the DCN circuit (28, 30). Type IV neurons are inhibited by vertical cells in response to tones and by D-multipolar and perhaps also GABAergic neurons in response to noise-notch stimuli.

For Chopper and Near-Threshold Type IV Neurons, the Model Accurately Predicts Responses to HRTF Stimuli

Near threshold, chopper and type IV neurons respond to noise spectra in a similar manner. Weighting functions determined within 20 dB of threshold for a chopper (Fig. 4*A1*) and a type IV (Fig. 4*B1*) neuron both are triangular with peak excitatory (positive) weights that occur within 1/8 octave of BF. Negative values in the chopper function indicate that this neuron is also weakly inhibited at frequencies below BF. First-order weights that were found to be significant were used to predict responses to notch stimuli. The quality of first-order predictions for the chopper ($Q_1 = 0.46$; Fig. 4*A3*) and type IV ($Q_1 = 0.42$; Fig. 4*B3*) neurons are moderate, suggesting that both behave reasonably linearly in the regime near threshold (see also ref. 29). However,



Fig. 4. Notch response predictions at sound levels near threshold. (A1) First-order weighting function for a chopper neuron (BF = 25.5 kHz; same neuron in Fig. 3A), plotted as in Fig. 2. Data were taken \approx 20 dB above threshold. (A2) Second-order weighting functions for the same chopper. Color scale bar is shown at right. Note that the plot is symmetric about the diagonal, i.e., $w_{jk}S(f_j)S(f_k)$ is the same as $w_{kj}S(f_k)S(f_j)$ and each such pair of terms is included in Eq. 1 only once. The largest weight corresponds to a quadratic term involving the frequency bin at BF (white square). (A3) Rate versus notch frequency for actual data (crosses; dashed line), first-order model predictions (unfilled circles; light solid line), and second-order model predictions (filled circles; bold solid line). Q1 and Q2 (first- and second-order Q-values, respectively) are shown in the legend. Horizontal shaded bar indicates spontaneous discharge rate. (B1) First-order weighting function for a type IV neuron (BF = 15.9 kHz; same neuron as in Fig. 3*B*). Data were taken \approx 10 dB above threshold. (B2) Second-order weighting function for the same type IV neuron. Largest weight values are located off-BF and off-diagonal. (B3) Response rate predictions for the same type IV neuron, plotted as in A3.

in both cases, when the notch is located above BF, predicted rates undershoot actual rates.

Second-order weights for the same chopper and type IV neurons are plotted in Fig. 4 A2 and B2, respectively. In these checkerboard plots, on-diagonal values indicate the degree to which a simple quadratic term $S(f_i)^2$ at a single frequency f_i contributes to the overall rate response. Off-diagonal values describe more complex interactions between the indicated frequency pairs. Although the chopper neuron has a single large second-order weight at BF (Fig. 4A2), the type IV neuron has a more variable second-order weight pattern with substantial components off-BF (Fig. 4B2). In both cases, inclusion of these second-order terms in the model (Eq. 1) improves the predicted responses to HRTF stimuli with notches above BF. The overall Q-value rises from 0.46 to 0.76 in the second-order chopper prediction (Fig. 4A3) and from 0.42 to 0.54 in the type IV prediction (Fig. 4B3). These improvements in the model suggest that both systems have significant second-order nonlinearities that are accurately depicted by the weight patterns shown. In the



Fig. 5. Weighting functions and notch response predictions for two chopper neurons studied at approximately 40 dB above threshold. The chopper in *A* is the same neuron shown in Figs. 3*A* and 4*A*. The chopper in *B* has a BF of 10.2 kHz. Plot layout is the same as Fig. 4. Note the good match of the predictions to actual data.

chopper, the BF component is the most significant and is relatively independent of all other frequency components. The second-order term is simply required to better describe the sigmoidal shape of the input-output function near threshold. In contrast, responses of type IV neurons appear to depend on more complex interactions between frequency components away from BF. For example, the largest second-order weights for this type IV neuron suggest that the response depends on an inhibitory process involving frequency components located 0.25 and 0.75 octaves below BF and an excitatory process at an adjacent frequency. However, the second-order weight estimates somewhat depend on the frequency range over which they are computed, and it is not yet clear how they are to be interpreted.

In chopper neurons, the noise response properties at levels above threshold are similar to those at levels near threshold. Fig. 5 shows the weighting functions and response predictions for two chopper neurons at ≈ 40 dB above threshold. At this higher level, both neurons exhibit triangular first-order weighting functions that peak at BF. Weaker inhibitory side bands are also present (Fig. 5 A1 and B1). Note the large magnitude of the peak weights in the first-order functions. In choppers, peak weights often range between 5 and 10 spikes/s per dB at high levels. Weight values observed in auditory nerve fibers at these levels are substantially smaller (1–2 spikes/s per dB, ref. 33), suggesting that chopper neurons are receiving converging input from multiple auditory nerve fibers. Note also that first-order peak weight values are level-dependent. The neuron shown in Fig. 5Ais the same as that depicted near threshold in Fig. 4A. In general, peak weights are small at low sound levels but monotonically increase in amplitude to a maximum in the middle of the neuron's dynamic range. Saturation effects eventually cause a decrease in peak weight values at higher stimulus levels (not shown).

At levels above threshold, second-order chopper response functions often show significant positive (excitatory) quadratic terms that involve one or a few frequency bins near BF. This typical second-order weight pattern, similar to that observed near threshold, is illustrated in Fig. 5 A2 and B2. Note that in both plots, negative second-order weights exist off-BF, which suggests that these particular choppers are weakly inhibited by joint activity of the BF component and an adjacent component above BF.

At levels within the dynamic range of chopper neurons, the transformation of the stimulus spectrum into rate is predominantly a first-order (or linear) transformation of spectral level. Rate minima are produced when the HRTF notch, a bin of minimum spectral energy, is centered at the excitatory peak of the first-order weighting function. Fig. 5 A3 and B3 shows chopper rate predictions to notch stimuli at moderate levels. Qualitatively, the shape of the rate versus notch frequency relationship is captured by the linear model. Q-values for first-order predictions ($Q_1 = 0.70$ and 0.68) are high. In both neurons, the linear model does overestimate the actual rate when the notch is located above BF. This discrepancy can be corrected by adding second-order terms to the model; however, the addition of this nonlinearity does not improve the model by much ($Q_2 = 0.79$ and 0.70).

Spectral Notch Encoding Is a Nonlinear Process in Most Type IV Neurons at Suprathreshold Levels

Unlike chopper response functions at suprathreshold levels, type IV weighting functions are variable in form. In some of the first-order weighting functions, the excitatory (positive) peaks at BF that are observed near threshold are retained with increasing level. In others, these peaks are replaced by wide areas of inhibition. Second-order weighting functions are similarly variable and often exhibit significant off-BF terms. The variability of type IV response functions is apparent in Fig. 6, which shows the weights estimated for two different type IV neurons at 30-40 dB above threshold. Unlike chopper neurons, type IV neurons at suprathreshold levels have first-order functions with large inhibitory regions, relatively small positive peaks, and relatively low overall gains. A wide band of negative (inhibitory) weights below BF, as in Fig. 6A1, is a common finding in the weighting functions of type IV neurons. Alternatively, type IV weighting functions may resemble the example in Fig. 6B1. This weighting function reveals an excitatory drive at BF and strong inhibition extending above and below BF. Note that the amplitude of first-order weights rarely exceeds a value of 2 in type IV neurons.

The responses of type IV neurons with large inhibitory values in their first-order weighting functions are poorly described by the model in Eq. 1. Actual responses of two type IV neurons to HRTF stimuli are compared with model predictions in Fig. 6 A3 and B3. The inhibitory notch responses in the two examples are clear; in both neurons, actual rates fall below spontaneous rate as the notch approaches BF. The first-order model qualitatively fails to predict the depth of notch responses and does not show inhibition. It also yields a positive DC rate offset across all notch frequencies. The second-order model corrects for the DC offset to some extent, but overall predictions remain poor.

Q-values for a first-order model (Q_I) were computed for 19 chopper and 23 type IV neurons across a range of seven levels. Results are compiled in Fig. 7, showing the level dependence of Q_I for each neuron. The trend in level dependence across each of the two neural populations is summarized by computing the median Q_I within a 10-dB range centered at the indicated level. At low levels, both chopper and type IV neurons exhibit roughly



Fig. 6. Weighting functions and notch response predictions for two type IV neurons studied at approximately 30 (*A*) and 40 (*B*) dB above threshold. The type IV in A is the same neuron shown in Figs. 3*B* and 4*B*. The type IV in *B* has a BF of 9.9 kHz. Plot layout is the same as Fig. 4. Note the poor match of the predictions to the data.

equivalent linearity. However, as stimulus level rises, the Q_1 continues to rise in choppers but begins to fall in type IV neurons. Choppers often maintain Q_1 values above 0.6 across a 30-dB range of high stimulus levels. In contrast, across these same stimulus levels, the Q_1 of type IV neurons declines toward 0. This summary corroborates previous studies that have shown that the behavior of type IV neurons is driven by a nonlinear process that emerges 10–20 dB above threshold (24, 29). The results shown in Fig. 6 indicate that this nonlinearity can be described only by a response function of order greater than 2.



Fig. 7. A summary of Q_1 -values obtained in rate predictions of 19 chopper (*Left*) and 23 type IV (*Right*) neurons. Q_1 -values obtained at multiple levels for a single neuron are connected by a thin gray line. The level dependence is summarized (bold black line) by computing the median Q_1 -value within a 10-dB range centered at the indicated level (i.e., abscissa position of the filled square).

Tonotopic Representation Versus Feature Detection

Although responses of chopper and type IV neurons to notches are qualitatively similar, the data in Figs. 5 and 6 show that the mechanisms that govern these responses are quite different. In chopper neurons, the transformation of spectral level into average discharge rate is predominantly a linear (first-order) process that involves a narrow band of frequencies centered on BF. This property suggests that axonal projections from a tonotopic array of chopper neurons transmit, to other auditory areas, a set of rate responses that are homomorphic with spectral shape. In fact, chopper neurons have been shown to produce stable tonotopic representations of vowel spectral shape (8).

Unlike choppers, type IV neurons do not encode spectral information through a homomorphic spectral representation. This is apparent from (i) the complexity and wide bandwidth of their first-order weighting functions, and (ii) the strong nonlinearity in the stimulus-response function. The nature of these nonlinearities has been discussed elsewhere (24, 29) and will not be further elaborated here. It is sufficient to point out that, as Fig. 3 illustrates, type IV neurons give inhibitory responses to both a narrow peak of energy (tone) and a narrow notch of energy located at BF. The rate dependence of type IV neurons to spectral notch position (Figs. 3 and 6), in addition to their wide bandwidth and nonlinear behavior, suggests that these neurons are not simply detectors of spectral level. Type IV neurons provide a second pathway of spectral information transmission—a nonlinear one that signals the presence of a specific complex spectral feature.

The Significance of the System Identification Method

A mathematical representation of a neural system can be a powerful tool for exploring the functional roles of component neurons in a complex acoustic environment. The system identification approach described in this work is a straightforward method for determining the receptive field of an auditory neuron that is responding to noise stimuli. It clarifies the excitatory and inhibitory nature of converging inputs to CN neurons and their location on a tonotopic frequency axis. Moreover, it can be used to study the nature of the information-bearing elements that are processed within the specialized parallel pathways of the auditory system.

The strength of the method lies in the fact that response functions that describe neural receptive fields can be computed simply. The validity of the model weighting functions can be tested by predicting responses to novel stimuli in a manner that is easy and direct. In principle, this method can be modified to study higher-order nonlinearities. Admittedly, however, the latter endeavor would be difficult because it would require the collection of large amounts of stationary data over lengthy time periods.

This method has been shown to work well for VCN chopper neurons. The failure of the system identification model to predict type IV responses is somewhat surprising because the model is essentially a linearization method that should be expected to work over some range of sound level variation. The fact that the model fails at suprathreshold levels suggests that the behavior of type IV neurons is governed by a nonlinear process of high order that cannot be linearized. Although it is possible that such a strong nonlinearity could be linearized by using smaller sound level deviations, such a result would not be particularly interesting because fluctuations of 10–12 dB are typical of the spectral level variations in natural stimuli.

The weighting function method discussed in this paper can serve as a guide to the methods that must be applied in delineating the nature of stimulus representations in a particular neuron. If the behavior of a neuron is found to be linear or nearly linear by using the model in Eq. 1, tonotopic representations sufficiently describe the neuron's spectral information encoding mechanism. If the behavior cannot be linearized, then receptive fields derived by any single method are unlikely to be informative about the manner in which a neuron encodes arbitrary stimuli. Such neurons must be studied carefully with a variety of stimuli. Considerations of

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biological function will be important in extracting the important response properties of such neurons.

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