PROCESSING OF PITCH INFORMATION IN COMPLEX STIMULI BY A MODEL OF OCTOPUS CELLS IN THE COCHLEAR NUCLEUS

Yidao Cai, JoAnn McGee, Edward J. Walsh

Developmental Auditory Physiology Laboratory
Boys Town National Research Hospital
555 North 30th Street, Omaha, NE 68131, USA

1.   Introduction

It is widely accepted that pitch is an important attribute of speech. However, how pitch information is processed in the central auditory system is largely unknown. Various models of pitch perception have been proposed on the basis of psychophysical studies [7][9] [17][19], but the physiological mechanisms underlying the process are poorly understood. For example, although responses of neurons in the cochlear nucleus complex (CN) to complex stimuli have been studied [12], their role in processing pitch information remains unclear.

One of the principle neuronal classes in the posteroventral cochlear nucleus is the octopus cell. Cells in this category respond to tonal stimulation mainly at the time of stimulus onset and are thus commonly referred to as "onset" responders. Octopus cells are thought to play an important role in pitch perception [6][10][12]. They carry precise temporal information in the timing of action potentials comprising spike trains resulting from acoustic stimulation. This property is determined, at least in part, by a low input impedance and a low-threshold potassium (K^+) channel [2][6][7].

In this study, we used a computer model of octopus cells to examine the processing of pitch information contained in complex stimuli. Inputs to the model were auditory-nerve fiber spike trains recorded from anesthetized cats. Harmonic or "inharmonic" stimuli, similar to those used in psychophysical studies, were used to record data from the cat auditory nerve as well from the cochlear nucleus of the gerbil. Our simulation results demonstrate that octopus cells take advantage of converging inputs from an array of auditory-nerve fibers spanning a wide frequency range to process pitch information. This finding is consistent with experimental studies of CN neurons *in vivo* and support the hypothesis that interspike interval information is a correlate of pitch.

2.   Methods

2.1 The Model

The model used in this investigation was developed explicitly to study the mechanism(s) whereby onset responses are generated by octopus cells [3]. As shown in Figure 1, the model consists of a soma, an axon, and four identical dendrites. The axon and soma are each represented by a single compartment and each dendrite is represented by 20 compartments. The axon and soma compartments contain Hodgkin–Huxley-like sodium (Na^+) and K^+ channels. The soma compartment contains two additional active mechanisms: a low-threshold K^+
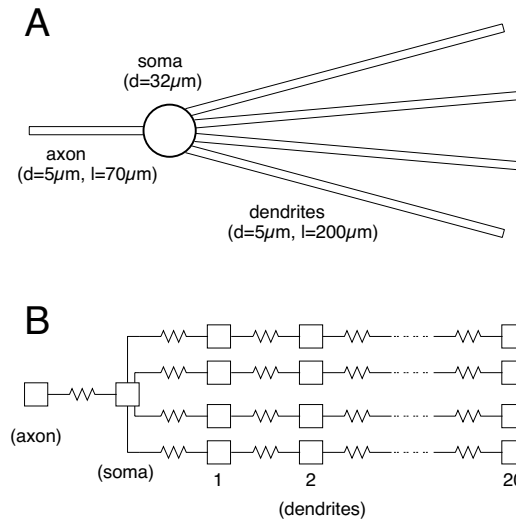
Figure 1 A. The octopus cell model. B. Compartmental representation of the model.

channel, K_{LT}, and a Cs^+-sensitive, hyperpolarization-activated inward rectifier, I_h. The dendrites are passive and have a space constant of 354 μm. The resting membrane potential is -62 mV.

2.2 The Stimuli

The inputs to the model were auditory-nerve (AN) fiber spike trains, collected from adult cats. In addition to tone bursts of different frequencies, responses to harmonic and "inharmonic" complex stimuli, similar to those used in psychophysical studies [11][15-20], were recorded. As shown in Figure 2, two groups of stimuli were employed: in one group (A-E) the stimuli contained three components centered at 1000 Hz, and in the other group (F-H), the stimuli contained 6 components between 1000 and 2000 Hz with 200-Hz spacing. Except for the "inharmonic" complex shown in Figure 2E, which is a frequency-shifted version of B, all stimuli produce the same pitch of 200 Hz (equivalent to the fundamental frequency), although the fundamental component is present in only two stimuli (A and F). Psychophysical studies have shown that the fundamental component is not essential for pitch perception (the so-called phenomenon of the "missing fundamental"). The frequency-shifted stimulus (E) was chosen because this stimulus, with a frequency spacing of 200 Hz, yields a pitch slightly higher than 200 Hz. The amplitude-modulated (AM) stimuli (C and D) have the same frequency components but their temporal waveforms are inverted versions of each other. Due to the rectifying characteristic of the inner-hair-cell transfer function, only the positive portion of the waveform is utilized when generating the spike events on the AN fibers. Psychophysically both stimuli sound the same despite the difference in temporal waveforms. The stimulus shown in Figure 2H was generated using the same six frequency components as those in Figure 2G, except that the phase of each component was randomized between 0 and 360 degrees, while their counterparts in Figure 2F and G all have a starting phase of zero degrees. Compared to the zero-phase versions, the random-phase version lacks temporal periodicity in its waveform. Psychophysical studies suggest that phase has no effect on the perception of pitch [11]. Except for the AM stimuli, all individual components have the same amplitude and the sound pressure level (SPL) pertains to the entire waveform.
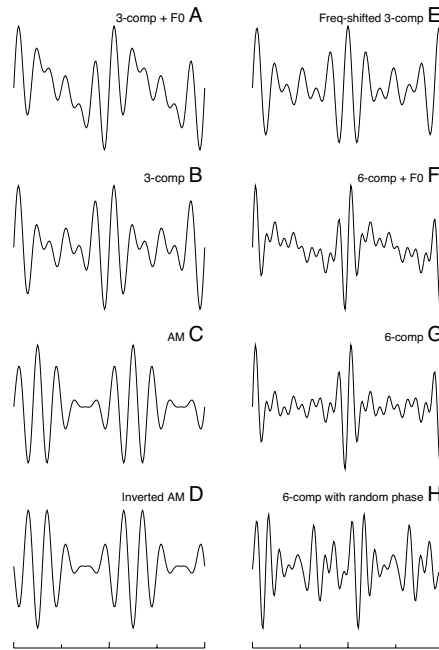
Figure 2 Temporal waveforms of stimuli used in the collection of auditory-nerve spike trains. The "3-comp" refers to a three-component complex of 800, 1000 and 1200 Hz, while the "6-comp" refers to a six-component complex of 1000–2000 Hz with 200-Hz spacing between the harmonics. Except for the frequency-shifted, three-component complex (E, 850, 1050, 1250 Hz), all stimuli have a fundamental period of 5 ms. Waveforms are normalized according to their respective peak magnitude and are shown for a 10-ms time window. Except for the AM stimuli (C and D), all frequency components in each complex have the same magnitude. F_0 refers to the fundamental frequency (200 Hz).

2.3 Auditory Nerve and Cochlear Nucleus Neuron Spike Train Data

Standard experimental procedures were used to collect data from the auditory nerve of cats and the cochlear nucleus of gerbils. Adult cats were deeply anesthetized using sodium pentobarbital (40 mg/kg, i.p.), the pinna was removed, and a craniotomy was performed to gain access to the posterior fossa. Cerebellar tissue was aspirated to expose the root of the auditory nerve. A glass microelectrode filled with 2 M KCl, and with an impedance of 15–20 MΩ, was inserted into the auditory nerve. Before recording, a routine calibration curve was obtained. Stimuli were generated using both the amplitude and phase characteristics of the calibration. The stimuli were 50 ms in duration, had a repetition interval of 120 ms, and were presented 50 times. The same stimulus conditions were used to collect data from each AN fiber encountered.

The procedure for collecting responses from CN neurons was similar, but adult gerbils were used. Sodium pentobarbital (50 mg/kg, i.p.) was used in conjunction with ketamine HCl (30 mg/kg, i.m.) to anesthetize the animals. The cochlear nucleus was exposed using standard surgical procedures, and recordings made from the posteroventral division. The stimuli used to collect data from the AN were also used in recording from the CN. The care and use of the animals were approved by the Boys Town IACUC.
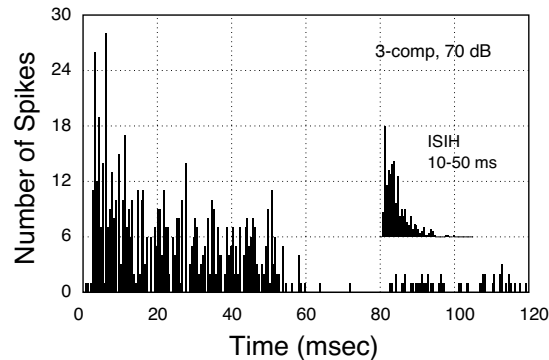
Figure 3   Responses of an auditory-nerve fiber (CF = 1050 Hz, SR = 63 spikes/s, threshold = 13 dB SPL) to a three-component complex (cf. Figure 2B) at 70 dB SPL. The ISIH for spikes falling between 10 and 50 ms from stimulus onset is shown in the insert. The histogram bin width is 0.5 ms. The maximum bin height in the ISIH corresponds to 60 occurrences and the abscissa ranges between 0 and 40 ms.

2.4 Application of Auditory Nerve Inputs to the Model

Figure 3 shows the responses of a typical AN fiber to a three-component harmonic complex (cf. Figure 2B) presented at 70 dB SPL. Although synchronization to the fundamental frequency (200 Hz) can be seen, the temporal response is "noisy" because of synchronization to individual harmonic components. Spike trains from six AN fibers were chosen as inputs to the model in order to mimic the natural input to octopus cells (incorporating a broad range of characteristic frequencies [CFs] and high spontaneous rates [SRs]). The fibers selected have CFs between 1050 Hz and 3250 Hz and they all have high SRs. To increase the number and temporal variability of inputs, we distributed each spike train over multiple locations. By varying the number of the starting trial and applying the trials in a circular manner (e.g., trials 7, 8,..., 50, 1,..., 6), we ensured that no two inputs were identical at a given moment in time. A total of 120 inputs were distributed across different locations of the model: 40 at the soma, and the remainder at different dendritic compartments.

Only excitatory inputs were used because there is little evidence suggesting the existence of inhibitory inputs onto octopus cells. In addition, a previous study showed that inhibitory inputs are not needed to generate the basic onset response pattern observed in octopus cells [3]. The dynamics of the synaptic conductance were modeled by an alpha function. The maximum synaptic conductance, adjusted to produce little or no spontaneous firing, had a value of 3.68 nS.

2.5 Simulation

Simulations were performed on a PC running Linux (a PC-based version of UNIX), with a program developed in our laboratory [2]. Simulation of 50 trials (120 ms per trial) requires about 13 minutes to complete when running on a Pentium-133 computer. The parameters used in this study were almost identical to those used in our previous current injection simulations [3], except for the implementation of faster K_{LT} kinetics, an adjustment that resulted from knowledge gained from simulations using spike trains collected with tone bursts of different frequencies. Octopus cells are typically associated with both O_I (a response peak at stimulus onset with little or no steady-state response) and O_L response patterns (with steady-state responses, usually > 10 spikes/s.). We adjusted the model parameters such that the model neuron produced phase-locked responses (entrainment) at lower frequencies (< 500 Hz). This
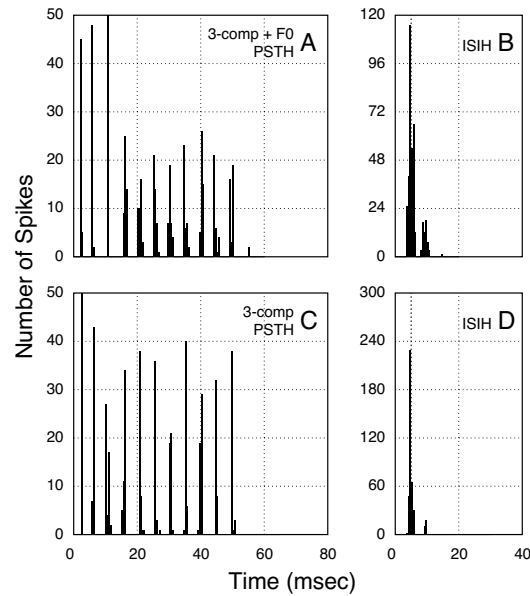
Figure 4 Responses of the model to three-component complexes with (upper panels) and without (lower panels) the fundamental component f_0. The repetition interval was 120 ms, but only the initial 80 ms of the PSTHs is shown for clarity. The stimulus level used to collect the spike trains was 70 dB SPL. The bin width of the histograms is 0.5 ms. For ISIHs a window of 4.5–60 ms was used to exclude the initial peak in the PSTHs from analysis and a vertical dotted line is drawn at 5 ms (corresponding to the fundamental frequency of 200 Hz). This convention applies to all subsequent figures.

pattern is typical of responses to low-frequency stimuli. The model neuron mainly responded at stimulus onset when high-frequency stimuli were used. At 3 kHz the model produced an O_I pattern at 70 dB SPL (35 dB above rate threshold), with a steady-state rate of 4.5 spikes/s. After the parameter set was established, simulations were performed with spike trains collected using complex stimuli.

3. Results

3.1 Harmonic Complexes With and Without the Fundamental

In Figure 4 are illustrated the responses produced by the model when inputs were spike trains collected using the three-component harmonic complexes. The responses are presented as post-stimulus time histograms (PSTHs) and interspike interval histograms (ISIHs). At low sound pressure levels, the model typically responds with a single peak in the PSTH (at a threshold of 30-35 dB SPL). At higher sound pressure levels, the model neuron also produced spikes during the steady-state portion of the stimulus (Figure 4A and C). We only present results obtained at 70 dB SPL in this and all subsequent figures, since it is unlikely that temporal responses containing an onset spike alone convey pitch information.

The responses of the model to the three-component harmonic stimuli, with or without the fundamental component, are very similar: strong responses (high, driven discharge rates) were evoked by both stimuli during the steady-state portion of the stimulus (Figure 4A and C), and ISIHs exhibited a prominent peak (Figure 4B and D). Average interspike intervals in both cases were about 5 ms, which corresponds to the fundamental frequency (200 Hz) of
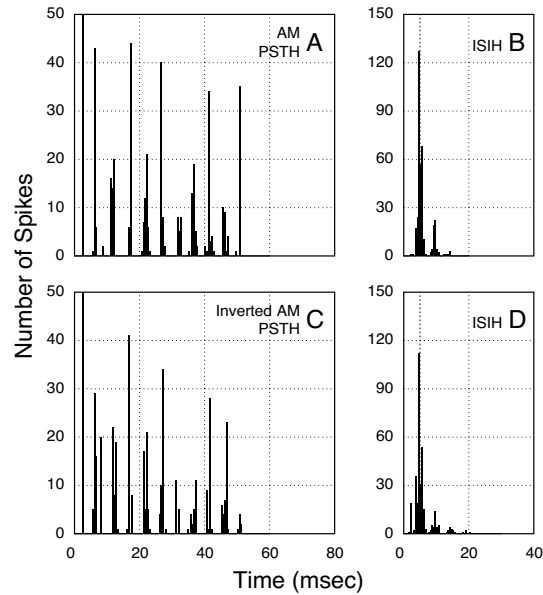
Figure 5 Responses of the model to an amplitude-modulated stimulus (upper panel) and its inverted version (lower panel). The stimulus level was 70 dB SPL.

the stimuli. Compared to the inputs (i.e., the AN spike trains; cf. Figure 3), responses produced by the model showed greatly increased synchrony to the fundamental component.

When the fundamental component was not present in the stimulus, response peaks during the steady-state portion (Figure 4C) were relatively higher than those observed when the fundamental component was present (Figure 4A), although the overall response (i.e., number of spikes) was about the same. This is reflected in the form of a sharper peak at ca. 5 ms in the ISIH (Figure 4D).

3.2 AM and Inverted AM Stimuli

With AM stimuli, the model responses were synchronized to 200 Hz, the modulation frequency of the signals (Figure 5A). The inverted AM stimulus has exactly the same frequency components, but its temporal waveform is different: it has two major peaks instead of one in the positive direction. However, the model neuron seems to more or less ignore the difference: the peak in the ISIH becomes only slightly wider for the inverted AM stimulus (Figure 5D), and there is little difference in the PSTHs.

3.3 Frequency-Shifted Three-Component Complex

When the frequency-shifted, three-component complex was used as the stimulus, the model produced a less synchronized steady-state response, as shown in the PSTH and in the broader ISIH peak (Figure 6) as compared to responses to the harmonic three-component stimuli (cf. Figure 4C and D). Such responses are expected, since the stimulus is "not harmonic" with regard to 200 Hz. Psychophysical studies have shown that this stimulus has a slightly higher pitch than the harmonic three-component complex. Computation of the average interspike intervals in the first peak in the ISIHs (Figs. 4D and 6B) indeed yields a smaller interval (corresponding to 211 Hz) for the frequency-shifted version.
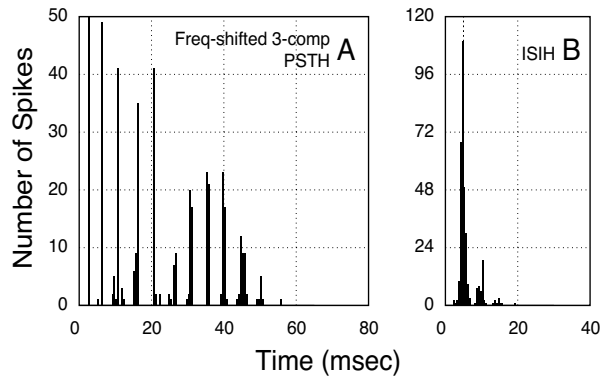
Figure 6   Responses of the model to a frequency-shifted, three-component complex at 70 dB SPL.

3.4 Six-component Complexes

The responses of the model to six-component complexes, with and without the fundamental component, are very similar to those for the three-component complexes (i.e., the one without the fundamental produced sharper peaks in the PSTH and a narrower peak in the ISIH). In Figure 7, we compare responses of the model to two, six-component stimuli, one in which all the components have a starting phase of zero (Figure 7A and B), and one in which component phases are randomized (Figure 7C and D). As can be seen, the model produced fewer discharges and poor synchronization during the steady-state portion when the random-phase stimulus was used, although psychophysical studies suggest that the two stimuli are almost identical perceptually.
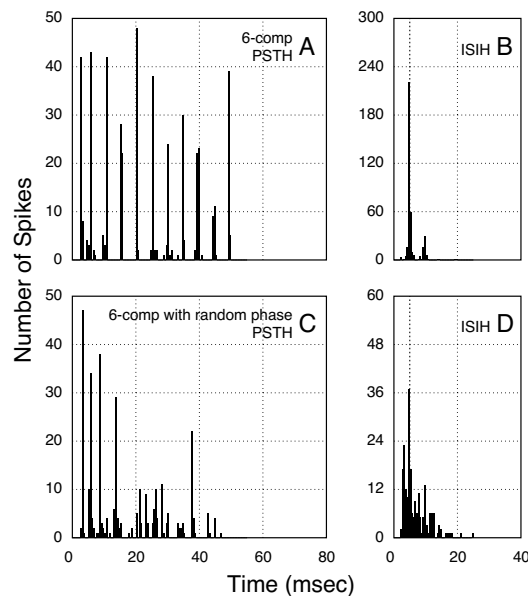
Figure 7   Responses of the model to six-component complexes with (lower panel) and without (upper panel) random phase. The stimulus level was 70 dB SPL.
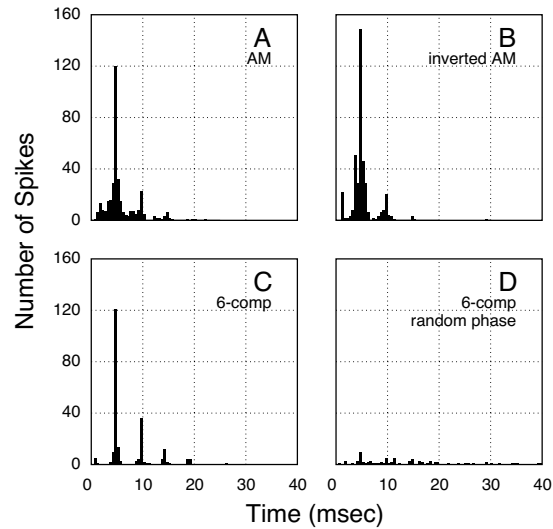
Figure 8 Responses of a gerbil cochlear nucleus neuron (CF = 750 Hz, SR = 0.5 spikes/s, threshold = 26 dB SPL). ISIHs are shown. A and B. AM and inverted AM stimuli, respectively (compare to Figure 5). C and D. six-component complexes with and without random phase (compare to Figure 7). The stimuli were presented at 73 dB SPL.

3.5 Responses of Cochlear Nucleus Onset Neurons

Responses of cochlear nucleus neurons from adult gerbils were compared with simulation results, using an identical set of complex stimuli as were used in the computer simulation. An example of a response from a cochlear nucleus neuron is shown in Figure 8. Spike trains of this low-CF (750 Hz) neuron entrained to tones below 500 Hz. For tone bursts at or above CF the neuron produces an O_I pattern (the steady-state rate was 0.9 spikes/s). The responses of this cell were similar to model outputs (Figs. 5 and 7); both exhibit similar ISIHs in response to the AM and inverted stimuli (Figure 8A and B, cf. Figure 5B and D) and different response patterns when the six-component complexes (with either fixed starting phase or with randomized starting phase) were used as stimuli (Figure 8C and D, cf. Figure 7B and D). When the six-component complex with randomized phases was used, the neuron generated a poor steady-state response (not shown) and exhibited poor synchrony to the fundamental component (200 Hz).

Although more data are required to validate the utility of the model, we are encouraged by the similarities between the model's output and the actual neuronal responses shown here.

4. Discussion

Overall, the model neuron studied here produces sharply defined PSTH peaks that correspond with peaks in the stimuli. Additionally, synchrony to the fundamental component is greatly enhanced in model responses when compared with responses of AN fibers. Using interspike interval estimates, responses of the model to the frequency-shifted three-component complex (Figure 6) correspond to a pitch of 211 Hz, a value very close to that obtained from psychophysical studies. Estimates for other stimuli yield values ranging from 202.5 to 208.9 Hz. Thus, the reciprocal of the average interspike interval in the model responses roughly corresponds to the pitch of the stimuli. These results are consistent with results from

experimental studies of CN neurons using complex stimuli [12][13], and suggest that octopus cells are able to process pitch information in complex stimuli.

4.1 Responses to AM Stimuli

Interestingly, the model produced similar responses to the AM and inverted AM stimuli (Figure 5). Such model behavior corresponds well with responses observed in onset cells *in vivo* (Figure 8). The results are also consistent with the psychophysical observation that the two stimuli are perceptually similar. According to Brugge et al. [1], auditory-nerve fibers respond to the envelope of multiple component stimuli. Consistent with that observation, AN fiber responses (inputs to the model neuron) to AM stimuli appear to "follow" the envelope waveform. Envelope following was not observed in responses of the model neuron, suggesting that octopus cells extract critical information about the fundamental periodicity of multiple component signals despite a difference in the temporal waveforms (Figure 2C and D) (i.e., octopus cells do not simply function as a "peak picker" as a simple stimulus "fine, structure" theory suggests [18]).

4.2 Responses to Harmonic Complexes With and Without Random Phase

The model exhibited less robust responses to six-component complex stimuli with randomized starting phases during the steady-state than it did to stimuli in which all components had a starting phase of zero (Figure 7, cf. Figure 2 for waveforms). This was true regardless of the fact that in psychophysical studies these stimuli produce the same pitch. The neuronal responses recorded from the gerbil are similar to the results produced by the model (Figure 8). Although similar results have been reported by Evans and Zhao [4] for high-frequency onset neurons, our results demonstrate that this response property holds for lower frequency neurons which, presumably, play a more important role in the perception of pitch in complex stimuli [15].

Since AN fiber responses are known to "follow the stimulus waveform" faithfully in the frequency range of interest, these differences in responses can be explained by

(1) differences in inputs to the model,
(2) the relatively broad tuning, and
(3) the onset response characteristics of octopus cells.

Broad tuning ensures that octopus cells receive inputs from all harmonic components of the complex stimuli studied here. Consequently, the overall input to the octopus cell would be less synchronized for the random-phase condition than for the zero-starting-phase condition. The onset response character of octopus cells ensures that the cell will respond better to stimuli that are more synchronized (zero starting phases) than to those that are less well synchronized (random-phase version).

4.3 Cellular Basis for Octopus Cell's Processing of Pitch Information

The ability of octopus cells to process pitch information from complex stimuli appears to be derived from its basic onset response characteristics. At low frequencies onset responding neurons entrain to the stimulus. Such onset characteristics are mainly due to a low membrane impedance [3][6][8] and a low threshold K^+ channel of the octopus cell [3]. It would be interesting to study how changes in channel kinetics affect response characteristics of the model to complex stimuli, especially the seemingly contradictory behavior observed when the random-phase and AM stimuli are considered (Figs. 5 and 7). For example, a direct rela-

tionship between the kinetics of K_{LT} channels and spike frequency during the steady-state has been observed [3]. If the kinetic characteristics of the K_{LT} channel are faster than in our model, would the response pattern to the inverted AM stimulus change (Figure 2D), and would average interspike intervals decrease? Our preliminary results suggest that the model's response to complex stimuli is less sensitive to changes of model parameters than are its responses to tone bursts.

4.4 Limitations of the Octopus Cell's Pitch Processing Ability

Although octopus cells are able to process pitch information contained in complex stimuli, the results presented in this chapter suggest that such an ability might be limited. First, only moderate and high-SPL stimuli produce substantial steady-state responses in octopus cells, at least in the current model. At low levels the model only responds at stimulus onset, and it is thought that pure onset spikes convey little information other than the onset of the stimulus. Second, as demonstrated by both model output and experimental data (Figs. 7 and 8), octopus cells respond poorly to harmonic complex stimuli with randomized starting phases for each of their components. Third, octopus cells primarily receive inputs from AN fibers with high-SRs. However, AN fibers with lower SRs also carry pitch-related information. These limitations suggest important roles for other neurons within the cochlear nucleus as well as those located at later stages of the central auditory pathway in processing pitch information.

Based on the simulations in this study, neurons with onset-like response characteristics have an advantage over other types of neurons in processing pitch-related information. This is because onset neurons respond well to synchronized inputs. Low-threshold K^+ channels, which are the main cellular component contributing to the onset responses of octopus cells, have been found in both the CN and other nuclei of the central auditory pathway. Those found in higher centers also respond with onset-like discharge behavior and may contribute to pitch perception.

Responses to harmonic complex stimuli with randomized starting phases were as poorly synchronized in the model as in the onset neuronal model. In all likelihood, this reflects the broad tuning of octopus cells and is not characteristic of neurons with relatively narrow tuning characteristics. Fewer inputs converge onto sharply tuned neurons and as a result, inputs are more synchronized, increasing the probability that spikes will occur. Almost all neurons in the cochlear nucleus are more sharply tuned than the octopus cells (the exception being the multipolar stellate cells, a.k.a. onset choppers) and are thus more likely to respond in a more synchronized fashion than octopus cells to harmonic signals with random phase. Generally, these neurons have lower response thresholds than octopus cells and presumably play an important role in the processing of pitch information at low intensities.

Among the different response types associated with octopus cells and large multipolar stellate cells (both have relatively broad tuning characteristics), O_L and O_C types are probably more important in pitch perception than the O_I type, due to their higher discharge rates during the steady-state portion of the response. Psychophysical studies have shown that the lower frequency region plays a dominant role in the perception of pitch [15]. Although all O_I, O_L and O_C units show entrainment at low frequencies (some up to 2 kHz [5][14]), the O_{LF} (low-frequency onset) units should have an advantage due to lower thresholds in this frequency region.

5. Summary and Conclusions

An octopus-cell model neuron was used to study how neurons with broad tuning and transient temporal response properties extract pitch information from complex stimuli. Harmonic and inharmonic complex stimuli, similar to those used in psychophysical studies, were used to collect auditory-nerve data from anesthetized cats, and the resulting spike trains served as input to the neuronal model. The model produced sharply defined peaks in PSTHs at every cycle of the fundamental component in response to three- or six-component harmonic complex stimuli, regardless of the presence or absence of the fundamental component. In response to a frequency-shifted three-component complex, average interspike intervals decreased slightly, corresponding to an upward pitch shift. The model produced very similar responses to an AM stimulus and its inverted version, in conformity with psychophysical data and responses from *in vivo*. In all cases, synchrony to the fundamental frequency of the stimulus was enhanced in the model neuron when compared to the responses of auditory-nerve fibers. These results, consistent with experimental studies of cochlear nucleus neurons, demonstrate that octopus cells are capable of processing pitch information in stimuli through the action of converging inputs from auditory-nerve fibers that originate over a wide frequency range. This result supports the hypothesis that interspike interval information is a correlate of pitch. However, the poor responses of the model and CN neurons to six-component, random-phase stimuli do not agree with the psychophysical finding that phase is unimportant in pitch perception. This suggests that other neurons in the auditory system play an important role in pitch perception as well.

Acknowledgments

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