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RICE UNIVERSITY

**Optimal Binaural Processing Based on
Point Process Models of Preprocessed Cues**

by

Lin Yue

A THESIS SUBMITTED
IN PARTIAL FULFILLMENT OF THE
REQUIREMENTS FOR THE DEGREE

Master of Science

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May, 1995

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Optimal Binaural Processing Based on Point Process Models of Preprocessed Cues

Lin Yue

Abstract

In localizing high-frequency tonal signals in the horizontal plane, the lateral superior olive (LSO) encodes the interaural level differences (ILD), the crucial cue for azimuthal angle extraction at some nuclei more central than LSO in the binaural pathway. The current work focuses on optimal processing at higher center(s), with inputs from LSO and anteroventral cochlear nucleus (AVCN). Besides Poisson processes, non-Poisson point processes are developed to model these cell responses more accurately. The LSO projection (if available), is shown to be the only input used in maximum likelihood angle estimation, and it is processed similarly under different models of LSO responses. However, localization performance depends strongly on the model's regularity. A more regular process, consistent with LSO chopping responses, improves localization accuracy and precision. Temporal integration in lower nuclei and neuron ensemble processing are both helpful to binaural localization at this stage.

Acknowledgments

My special thanks to my thesis advisor, Dr. Don Johnson, for his invaluable guidance and encouragement during this research work in the past year. Dr. Johnson inspired my interest in auditory information processing and patiently taught me the basics that made later work much easier. I am influenced by Dr. Johnson's sharp insight, academic enthusiasm, and friendly personality in more ways than I could describe here. I also would like to thank Dr. Chiyeko Tsuchitani for sharing her knowledge on the auditory system and providing the empirical data.

I am grateful to Dr. Behnaam Aazhang, Dr. David Scott, and Dr. Tsuchitani for serving on my thesis committee. I also thank my colleagues interested in my poster on part of this work at the 1995 ARO midwinter meeting, especially Dr. Laurel Carney of Boston University.

I benefit from the discussions during our weekly auditory group meeting, and would like to thank everyone associated with it. Also, I thank my fellow graduate students and my friends here at Rice for all their help.

To my parents and all my family, I am deeply indebted; their consistent moral support, as well as their unalterable confidence in me, has always urged me to excel. I really appreciate the love and support of my companion, Haitao Guo, who has been exploring life with me and shares my interest in academic endeavor.

The funding of this research was provided by NSF grant IBN-9309263.

To my parents

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Chapter 1

Introduction

Binaural hearing is superior to monaural hearing in sound localization because differences between the stimuli at the two ears provide crucial cues that supplement those available in the monaural case. The superior olivary complex (SOC), which consists of the lateral superior olive (LSO), medial superior olive (MSO) and medial nucleus of the trapezoid body (MNTB), is believed to be the first stage in the auditory pathway where binaural processing takes place [7]. Neurophysiological studies have shown that most LSO units are high-frequency sensitive ($CF \geq 3\text{kHz}$), and they receive ascending projections bilaterally. These LSO cells are excited by ipsilateral input from anteroventral cochlear nucleus (AVCN) and inhibited by contralateral input from MNTB, and they are presumed to be involved in the localization of high frequency tonal stimuli using binaural cues [3, 18]. The potential role of LSO in encoding interaural level differences (ILD) between ipsilateral and contralateral stimuli is suggested by the sensitivity of its unit's discharge rate to ILD [42]. Theoretical studies [13, 24] describe the role of LSO in localization as an optimal processor that provides the sufficient statistic related to ILD to some higher auditory center.

AVCN discharges as well as LSO discharges are conveyed more centrally, and a higher center must extract lateral angle from these discharges. The inferior colliculus (IC) is believed to be one such center. Among the numerous pathways that converge at the contralateral IC, the ipsilateral LSO and ipsilateral AVCN provide major ascending projections [2, 19].

We are interested in studying how a higher center localizes a sound source using LSO and AVCN discharges:

- Which information is crucial in localization at this stage? Does the LSO provide the sufficient statistic as predicted by previous studies? If so, what happens when both LSOs are totally inhibited at midline?
- What is the optimal way of using the input(s)?

We approach the localization problem from an estimation theoretic point of view, and consider the higher center as an optimal processor that produces an angle estimate by processing inputs from LSO and AVCN (Figure 1.1). Our work is mainly concerned with three aspects of the optimal processor: What information it uses in localization, how the form of the information impacts its processing, and how well it performs.

Figure 1.1 Block diagram of the localization problem setup. Inputs to the processor are LSO and AVCN discharges averaged over a fixed time interval of length T . Outputs are the lateral angle estimate and the sound amplitude estimate.

To derive the optimal angle estimator, we first study point process models of its inputs, the AVCN discharges and LSO discharges. Based on previous data analysis, most AVCN units have been categorized as primary-like and choppers [31]. Rostral

AVCN spherical cells projecting to LSO are primary-like units, and the discharges of a single neuron are modeled as sample functions of a Poisson process whose intensity is determined by the neuron's discharge rate [5]. AVCN stellate cells and small cells projecting to IC are choppers, and their discharges are more regular [2, 31]. Discharge regularity of LSO responses has also been demonstrated in experiments [4, 39]. The regularity in unit discharge patterns suggests that these responses are not well described by Poisson processes. So, in addition to the Poisson model, we define models that accommodate the non-Poisson nature of the responses of AVCN stellate cells and LSO cells, analyze these models, and compare the statistical characteristics of the models with those of empirical data wherever appropriate.

Because the lateral angle is a deterministic unknown parameter, maximum likelihood estimation is exploited to derive the angle estimator under various Poisson and non-Poisson models of inputs from AVCN and LSO. The localization performance of the angle estimator is evaluated by its bias and standard deviation of angle estimate, corresponding to localization accuracy and precision respectively. The comparison of the optimal estimator under Poisson and non-Poisson models allows us to investigate the effect of neuron discharge regularity on localization at higher neural centers. Several other properties of the optimal angle estimator, such as the effect of spatial summation within neuron population, are studied.

The organization of the thesis is as follows.

- Chapter 2 describes relevant background information, including binaural acoustics and the anatomy and physiology of the nuclei of interest;
- Chapter 3 focuses on the Poisson and non-Poisson point process models, and presents the point process modeling of AVCN and LSO unit responses;

- Chapter 4 derives the optimal angle estimator based on the input models developed in Chapter 3, evaluates the localization performance, and discusses the characteristics of the optimal processor in several aspects;
- Chapter 5 contains conclusions and discussions.

Chapter 2

Background Information

2.1 Physical acoustics

2.1.1 Geometry of binaural acoustics

Binaural acoustics is greatly complicated by the complex geometry of the torso, head, and pinna. For analysis, a simplified geometry of incident plane wave relative to the head is depicted in Figure 2.1.

Figure 2.1 Simplified geometry of incident plane wave relative to the head (adapted from [28]). The lateral angle θ is defined as the direction of the sound source with respect to the midline, τ is interaural time delay of the shadowed ear with respect to the center of the head, r is the radius of the sphere equivalent as the head, and c is the speed of sound traveling in air.

The actual complex geometry produces direction-dependent information of sound waves in terms of both amplitude and time-of-arrival discrepancies at the two ears. Incident plane waves are reflected by the head on the side facing the incident wave (known as head-baffle effect) and diffracted to the shadowed ear (known as head-shadow effect) before entering the ear canal. These reflections and diffractions of sound waves give rise to interaural level differences (ILD) and interaural time differences (ITD), which are major cues for sound localization.

2.1.2 Localization cues and directivity function

As will be discussed later, most LSO cells are high-frequency sensitive. With the sound frequency above 2kHz, the ITD is given by [28]

$$\text{ITD} = 2\tau \approx \frac{2r}{c} \sin \theta, \quad (2.1)$$

where θ is the lateral angle (Figure 2.1), τ is interaural time delay of the shadowed ear with respect to the center of the head, r is the radius of the sphere equivalent as the head, and c is the speed of sound traveling in air.

ILD is defined as the ratio between sound pressure at the left ear and sound pressure at the right ear, and is usually expressed in dB. Three primary mechanisms contribute to the ILD [28]: The scattering of the sound by the head, the directivity produced by the pinna, and the backscattering of the sound to the ears from the shoulders or torso. Through comparison of the theoretical results and experimental data, Kuhn concluded [28] that

- for sound with frequency below 2.5 kHz, the horizontal directivity is determined primarily by the head;
- for sound with frequency above 2.5 kHz, the directivity is determined by the directly irradiated pinna and the shadowed region of the head.

ILD is a reliable localization cue only at high frequencies when significant level differences are present at the two ears because of the head-shadow effect and pinna directivity. We focus our attention on ILD instead of ITD since it is well known that high-frequency sound signals incident in the horizontal plane are not generally localized on the basis of ITD [28]. At high frequencies, ILD is the binaural cue crucial in sound localization [17].

Taking into account both the amplitudes of the sound reaching each ear and the ILD relative to lateral angle, we define the directivity function $D[\cdot]$ as

$$D(\theta) = e^{k \sin \theta}. \quad (2.2)$$

Equation (2.2) approximates the actual directivity function, which can be very complex [28] due to the geometry of the torso, head and pinna. Figure 2.2 depicts the directivity function defined in (2.2) when $k = 1$.

Figure 2.2 Directivity function when $k = 1$: $e^{\sin \theta}$ for the right ear, $e^{-\sin \theta}$ for the left ear.

For a high-frequency tonal signal, the simplified model of binaural acoustics is defined by

$$S_l(t) = AD(-\theta) \sin(w(t - \tau)), \quad S_r(t) = AD(\theta) \sin(w(t + \tau)), \quad (2.3)$$

where A is the amplitude of the sound, and $S_l(t), S_r(t)$ denote the signals at the left ear and the right ear respectively.

Obvious from formula (2.3), ignoring the interaural time delay τ , the ILD under high-frequency stimulus is given by the ratio of the directivity functions,

$$\text{ILD} = \frac{D(-\theta)}{D(\theta)}. \quad (2.4)$$

Using the directivity function in formula (2.2), ILD is depicted in Figure 2.3 as a function of lateral angle.

Figure 2.3 ILD decreases monotonically as a function of lateral angle (with directivity functions when $k = 1$).

Figure 2.3 shows that ILD decreases monotonically as the lateral angle increases from -90° to 0° . The maximum ILD occurs at $\theta = -90^\circ$, when the sound source faces the left ear directly. At the other extreme, we have the situation when the sound source is located directly in front of the subject, and no ILD is available. We choose $k = 1$ in the directivity function so that the maximum ILD is approximately 20dB. Like the ideal directivity function, the ILD defined in formula (2.4) is a simplification of the ILD measured from cell responses. The actual ILD-azimuth relationship in the cat is highly frequency-dependent and may be non-monotonic [20].

2.2 Auditory anatomy and physiology

2.2.1 Binaural pathway divisions

The binaural pathway from the auditory nerve to the inferior colliculus (IC) has a complicated structure with a highly divergent and convergent nature [21]. The auditory nerve projections diverge at the cochlear nucleus (CN) and take various routes, and lots of ascending projections converge at the IC. The following describes the ascending pathway in detail.

Sound signals travel through external ear and middle ear to the inner ear (cochlea). Hair cells sense the motion of the basilar membrane in cochlea, and, in turn, stimulate the auditory-nerve fibers that innervate them. Auditory-nerve fibers project to three major divisions of the CN: Dorsal cochlear nucleus (DCN), posteroventral cochlear nucleus (PVCN), and anteroventral cochlear nucleus (AVCN). The next stage of the auditory pathway is the superior olivary complex (SOC), which contains the lateral superior olive (LSO), medial superior olive (MSO), and medial nucleus of trapezoid body (MNTB). The AVCN sends afferent discharges to the ipsilateral LSO and the contralateral MNTB. The AVCN input excites the LSO neurons. The LSO also receives inhibitory input from the homolateral MNTB. The IC is an auditory mid-brain nucleus, and almost all the major divisions of the brainstem auditory system

send ascending projections to the IC. The central nucleus of the IC (ICC) receives a highly convergent projection from more than 20 identified neuron types in approximately 10 major brainstem nuclei. Focusing on those projections of interest here, the AVCN projects bilaterally to the ICs (described in section 2.2.2), and the LSO projects bilaterally according to its tonotopic organization to the ICs [15] (described in section 2.2.3). The major nuclear divisions of the brainstem auditory pathway that concern us here are shown schematically in Figure 2.4.

Figure 2.4 Auditory pathway from periphery to IC. LSO receives excitatory inputs from ipsilateral AVCN bushy cells and inhibitory inputs from contralateral AVCN bushy cells via homolateral MNTB. High-CF LSO cells project contralaterally to IC. AVCN stellate cells send major projections contralaterally and minor projections ipsilaterally to IC.

2.2.2 AVCN units: Anatomy and physiology

According to anatomical studies [5, 6], there are two types of large neurons, bushy cells and stellate cells, located in the AVCN. In the anterior division, the bushy and stellate cells correspond to the spherical and ovoid cells respectively; in the posterior division, they have been identified as globular and multipolar cells respectively [37]. Firm correspondence between physiological response and cellular morphology in the CN has been observed [1, 33]. According to Pfeiffer's classification, bushy cells are primary-like units, and stellate cells are choppers [31].

Figure 2.5 Typical samples of AVCN bushy cells of young kittens [6].

Figure 2.5 illustrates typical AVCN bushy cells of the young kitten. The spherical bushy cells are heavily concentrated in the rostral part of the AVCN, and they send excitatory projections to the ipsilateral LSO. These spherical cells are called primary-like units because their temporal response patterns and interspike interval statistics are remarkably similar to those of primary afferents, the auditory-nerve fibers [31].

Another type of bushy cells, the globular ones, are found in the interstitial nucleus and the posterior part of the AVCN. These globular bushy cells provide inhibitory inputs to the contralateral LSO via the contralateral MNTB. They are categorized as primary-like-with-notch units because their responses are primary-like, except that the initial peak is more prominent and is followed by a sharp notch [5, 16, 31].

Because of their primary-like property, the responses of AVCN bushy cells (spherical and globular) to continuous tone stimuli are Poisson-like [5], and we model them as sample functions of Poisson processes.

Figure 2.6 Typical samples of AVCN stellate cells of young kittens [6].

In contrast to primary-like bushy cells, the stellate units (illustrated in Figure 2.6) in AVCN are classified as choppers because their responses exhibit chopping patterns. The PST histograms (defined in section 3.1) of tone burst responses of these units are characterized by distinct, regularly spaced peaks sometimes remaining distinct for the entire duration of the tone burst [31]. Both the spontaneous and the driven activity

of chopper units are more regular (defined in section 3.2.4) than those of primary-like units. The interspike interval distributions (defined in section 3.1) from the tone burst responses of these cells are either asymmetric with slower-than-exponential decays or are relatively symmetric. The symmetric interval distributions reflect the more regular discharges of those units in which the chopping pattern is sustained for the duration of the tone burst stimulus [19, 31, 44].

Two distinct stellate morphologies have been identified: The sustained choppers (C_S) have tapering dendrites that branch little, and the transient choppers (C_T) have greater branching and dendritic appendages [33]. The first type of dendritic pattern is associated with physiological chopping responses that are more regular than those of the second type. These two types of stellate units, along with some small chopper neurons, provide major ascending projections to the contralateral IC and minor projections to the ipsilateral IC. Compared with the AVCN input delivered to the LSO, the AVCN input to the IC is more regular, and Poisson processes are inadequate in modeling these regular projections.

2.2.3 LSO units: Anatomy and physiology

The LSO is one of the three major components in the SOC, and the LSO and MSO are believed to be the first centers that receive binaural projections in the auditory pathway. LSO cells receive ipsilateral inputs from the spherical bushy cells in the rostral AVCN [8, 46]. The contralateral inputs to LSO cells are from the homolateral MNTB's principal cells, which receive ascending projections from globular bushy cells of the posterior contralateral AVCN [47]. The projections from AVCN and MNTB both have primary-like discharge patterns [18, 33].

Figure 2.7 illustrates a Golgi stained LSO. Most LSO units have high characteristic frequency (CF), and they are excited by ipsilateral inputs and inhibited by contralateral inputs (E/I characteristic) [3, 18]. It has been observed that the discharge rates of these LSO units are related to ILD [3, 24]. The initial discharges of

LSO cells to tone bursts are of the chopper-type, time-locked to stimulus onset and producing peaks in the PST histogram. Two types of LSO units have been defined according to the width and spacing of initial peaks in the PST histogram [38]: Fast choppers have relatively narrow and closely spaced peaks, and slow choppers exhibit relatively broad peaks that are widely spaced. Interestingly, fast choppers and slow choppers manifest different discharge rate characteristics in their sustained responses, with the discharge rates of fast choppers usually higher than those of slow choppers. The statistical properties of LSO discharges from empirical data and previous LSO modeling work [48] suggest that LSO responses are non-Poisson.

Figure 2.7 Ramon y Cajal's classical illustration of the LSO.
A : central fusiform cells; *B, C* : marginal cells.

Figure 2.8 depicts the LSO ascending projections to the IC nuclei. The tonotopic organization of LSO indicates that LSO neurons projecting to IC ipsilaterally and contralaterally are partially segregated, and that only a small percentage of LSO units send collaterals to both sides. The majority of the high-CF LSO units project

to the contralateral IC.

Figure 2.8 Schematic drawing: Tonotopy organization of LSO determines ascending projections from LSO to IC [15]. High-CF LSO cells project to IC contralaterally, while low-CF cells ipsilaterally.

Chapter 3

Point Process Modeling of Neuron Discharge Patterns

3.1 Neuronal data statistics and point process modeling

Typical of neuron responses, the responses of AVCN cells and LSO cells consist of trains of action potentials or spikes, each of which has approximately the same waveform. Thus, the information conveyed by the spike train is carried in the times of occurrences rather than in the waveforms of these spikes. These responses are well described as point processes [11]. The signal conveyed by neuronal discharges is encoded in the intensity function, which determines the corresponding point process completely. For example, if a Poisson process is used to model the neuronal discharges, then the discharge rate of the cell determines the intensity of its corresponding Poisson process.

In modeling neuron responses, the point process should capture the statistical properties of the empirical data. Such properties are usually characterized by the post stimulus time (PST) histogram and several interspike interval (ISI) statistics. The PST histogram represents the times of occurrences of discharges relative to the stimulus-onset time over repeated presentations of the same stimulus [22],

$$\text{PST}(m) = \frac{1}{K\delta} \sum_{k=0}^{K-1} c(m + kM), \quad (3.1)$$

where K denotes the number of stimulus presentations, M is the total number of bins of width δ , and $c(m)$ denotes the count of events in the m^{th} bin $[m\delta, (m+1)\delta)$.

The PST histogram is usually used to select the more stationary, sustained portion of the tone burst response, from which interval statistics are computed. One of the informative interval statistics of neuronal discharges is the interval histogram, which estimates the probability density of interspike interval durations $p_\tau(\tau)$. The hazard function is defined analytically as a function of the interval distribution,

$$h(\tau) = \frac{p_\tau(\tau)}{\int_\tau^\infty p_\tau(\alpha) d\alpha}. \quad (3.2)$$

It describes the probability of an immediate spike occurrence given that no spike has occurred in the elapsed interval [43]. In turn, the interval distribution is determined by the hazard function,

$$p_\tau(\tau) = h(\tau)e^{-\int_0^\tau h(x)dx}. \quad (3.3)$$

In practice, the interval histogram is first calculated from the interspike intervals of the empirical data, and then the hazard function is obtained from interval histogram by calculating the number of intervals with a given duration relative to the number of intervals having longer durations.

The conditional mean, $E[\tau_i|\tau_{i-1}]$, estimates the mean interspike interval as a function of the previous interval's duration. It can be used to study correlation between successive interspike intervals. For a renewal process, the expected conditional mean is a constant because there is no dependence among interspike intervals.

For a stationary renewal process, the intensity is equivalent to the hazard function. Since the interval distribution and the hazard function of the point process completely determine one another, the intensity, and thus the point process underlying the neuron's responses, can be specified by either of these two interval statistics. For a stationary non-renewal process with first-order correlation between interevent intervals, the intensity is given by the first-order conditional hazard function $h(\tau_i|\tau_{i-1})$, which is specified by the conditional interval distribution in a similar way as in formula (3.2). Thus, the interevent interval distribution (if renewal) and the dependence among intervals (if non-renewal) determine the stationary point process completely.

Several previous studies on point process modeling of the sustained portion of an LSO neuron's tone burst responses [25, 48] took the approach of estimating and modeling the intensity first, and then generating simulated sequences of events characterized by that intensity to fit other data statistics. It is possible to approach the problem of point process modeling from another viewpoint. We can specify the interval distribution of the point process (if renewal) and the dependence structure among the intervals (if non-renewal) according to the statistics of empirical data being modeled. Although the intensity of the point process may be hard or even impossible to define analytically in some cases, it is nonetheless implicitly determined by the interval statistics characterizing the point process. The latter framework is exploited in this study.

No matter which approach is used in point process modeling of neuron discharges, the statistics of the model should agree with the data. Figure 3.1 illustrates several LSO data statistics that are important in developing point process models for LSO responses. For instance, the PST histograms of LSO data exhibit chopping response patterns, the hazard functions of LSO data increase with interspike interval length, and the negative slope in the conditional mean function suggests that successive interspike intervals are negatively correlated. With the knowledge of the data statistics, we propose point process models based on interval statistics that model the data. In the next section, we will discuss several point processes, each of which captures the characteristics of the data to some extent.

Figure 3.1 Examples of PST histogram and interval statistics of LSO data (t108-1c.r1). a. PST histogram; b. ISI distribution; c. Hazard function; d. Conditional mean function.

3.2 Point process models and regularity

In this section, we describe several point processes studied to model AVCN and LSO responses, and define the quantity that reflects the randomness of a point process — regularity. The actual modeling of neuron discharges using these point processes is described in section 3.3.

3.2.1 Poisson process

Poisson processes have been used successfully, ignoring the refractory properties of neuron discharges, to model the responses of auditory-nerve fibers and primary-like units in nuclei such as the AVCN [5, 26]. For the homogeneous Poisson process with intensity λ , the interevent intervals are independent, and identically distributed, (i.i.d.) as the exponential random variable with $p_\tau(\tau) = \lambda e^{-\lambda\tau}$. The time constant of the exponential decay in interval distribution is determined by the process's intensity. The probability of obtaining N spikes in the time interval of length T is given by [35]

$$\Pr\{N_T = N\} = \frac{e^{-\lambda T}(\lambda T)^N}{N!}, \quad N = 0, 1, \dots \quad (3.4)$$

In using a Poisson process to model neuron responses, the intensity λ is the only parameter that needs to be specified in the model. The average discharge rate of the neuron being modeled determines the intensity of the corresponding Poisson process.

3.2.2 Renewal Erlang process and Gaussian ISI process

The interspike intervals can be distributed as random variables other than exponential ones, and result in point processes that are non-Poisson. Within the non-Poisson point process family, we are particularly interested in Erlang and Gaussian ISI processes because of their capability of modeling regular discharge patterns. For neurons in complex neuronal systems, a previous study revealed the variability in interspike intervals when external stimuli are held constant, and Gamma density was employed in the study to provide excellent fit to the interspike interval distribution of some neuronal data [36]. We justify the Erlangian (Gamma density with an integer n) and Gaussian interspike interval distributions theoretically by a neuron discharge's temporal integration mechanism, which is found compatible with neurophysiological recordings of regular discharge patterns [44].

The theory of integrate-and-fire describes the temporal integration process by assuming that an integrating neuron gives one output spike for every n input spikes. Consequently, for an integrating neuron, the interspike interval length of its output is the sum of those input interspike intervals between the neuron's previous spike and the final input spike that triggered the cell's response. Hence, the interval distribution of the output is determined by the statistical properties of the input to the neuron. If the input process is Poisson, the interevent intervals of the point process corresponding to the discharges of an integrating neuron is given by the sum of n i.i.d. exponential random variables,

$$\tau = \sum_{i=1}^n \tau_i, \quad (3.5)$$

where $\tau_i, i = 1, \dots, n$, are distributed as $\lambda e^{-\lambda\tau}$. The interval distribution of the neuron's discharges is the convolution of the densities of n i.i.d. exponential random variables, and is given by

$$p_\tau(\tau) = \frac{\lambda(\lambda\tau)^{n-1} e^{-\lambda\tau}}{(n-1)!}. \quad (3.6)$$

The density in formula (3.6) is called Erlangian, or Gamma if n is not restricted to be an integer. The point process characterized by i.i.d. Erlangian intervals is called an Erlang process or a generalized Poisson process. The mean value of the interevent interval duration is n/λ , and the variance is n/λ^2 . Figure 3.2 shows several Erlangian densities with different parameter n but with identical mean of 1 (i.e. $\lambda = n$). In this case, the variance of an Erlangian density is $1/n$. From the plot, it is clear that the variance of Erlangian density decreases as n increases, and the density becomes more symmetric around its mean. For large enough n , the Erlangian density is approximately Gaussian because of the central limit theorem.

Figure 3.2 Erlangian pdfs with average 1 and parameter $n = 1, 2, 8, 16$. As n increases, the variance of the density decreases, and the density becomes more Gaussian-like.

While the exponential and Erlangian densities as interval distributions are non-zero only for positive intervals, the Gaussian density gives rise to the possibility of negative intervals. For a renewal Gaussian ISI point process with $\mu/\sigma = a$ (equivalent to $CV = 1/a$, CV is defined in section 3.2.4), the probability of getting negative intervals is given by

$$\Pr\{\tau < 0\} = \Pr\left\{\frac{\tau - \mu}{\sigma} \leq \frac{-\mu}{\sigma}\right\} = 1 - Q\left[\frac{-\mu}{\sigma}\right] = Q\left[\frac{\mu}{\sigma}\right] = Q[a]. \quad (3.7)$$

Fortunately, the probability of negative intervals is negligibly small if the value of a is chosen properly. For example, with $a = 5$, the probability of getting negative intervals is approximately 2.8×10^{-7} . For reasonable values of a , $5 \leq a \leq 10$, the probability of negative intervals lies between 10^{-6} and 10^{-23} . With this constraint on a , negative intervals almost never occur, and Gaussian density can be used to describe interval distributions.

The point process characterized by Gaussian interevent intervals is called a Gaussian ISI process. It approximates an Erlang process when Erlangian density is Gaussian-like, and thus, it can also be justified by the temporal integration mechanism.

Hazard functions resulting from Erlang processes are plotted in Figure 3.3. As can be seen, the hazard function when $n = 1$, which corresponds to the exponential interval distribution characterizing a Poisson process, is constant. Another interesting observation is that for suitably large n , these hazard functions approximate that of LSO slow chopper (Figure 3.1), and they saturate at long interval lengths. Hence, besides its consistency with the temporal integration explanation of the chopping responses, the Erlang process model also has statistical properties consistent with empirical data.

Figure 3.3 Hazard functions of Erlang processes with interval distributions depicted in Figure 3.2. The integral in hazard function computation (formula (3.2)) is approximated by summation with the distribution tail cutoff at probability 98%.

Supposing that the interspike intervals of the Gaussian ISI point process are identically distributed as $\mathcal{N}(\mu, \sigma^2)$, the hazard function is readily obtained as

$$h(\tau) = \frac{e^{-\frac{(\tau-\mu)^2}{2\sigma^2}}}{\sqrt{2\pi}\sigma Q\left(\frac{\tau-\mu}{\sigma}\right)}, \quad (3.8)$$

where $Q(x)$ is the probability that a zero-mean, unit-variance, Gaussian random variable exceeds x .

Figure 3.4 illustrates a typical hazard function for a Gaussian ISI process model used in our study imposed on a hazard function for discharges of a cat's typical LSO slow chopper. The hazard functions of the Gaussian ISI process and the data agree well.

Figure 3.4 The hazard function of the Gaussian ISI model matches with that of LSO data (t108-1c.r3).

For any point process, the probability of N events occurring in time interval of length T is given by the general result [10],

$$\Pr\{N_T = N\} = \Pr\left\{\sum_{i=1}^{N+1} \tau_i > T\right\} - \Pr\left\{\sum_{i=1}^N \tau_i > T\right\}, \quad N = 0, 1, \dots, \quad (3.9)$$

where τ_i , $i = 1, \dots, N+1$, are the interevent intervals. Formula (3.9) is based on the universal fact that the following two events are equivalent: N events have occurred in the time interval $(0, T]$, and time T occurs between the N^{th} and the $(N+1)^{\text{th}}$ events. This general formula allows calculation of the probability mass function (pmf) of a non-Poisson point process. If the distribution function of the summation of interevent intervals is obtainable, which happens in the Gaussian ISI case, the pmf of the point process can be readily determined.

For the renewal Gaussian ISI point process with interevent interval distribution $p_\tau(\tau) \sim \mathcal{N}(\mu, \sigma^2)$, we have $\sum_{i=1}^N \tau_i \sim \mathcal{N}(N\mu, N\sigma^2)$. Thus,

$$\Pr\{N_T = N\} = Q\left[\frac{T - (N+1)\mu}{\sqrt{N+1}\sigma}\right] - Q\left[\frac{T - N\mu}{\sqrt{N}\sigma}\right]. \quad (3.10)$$

The pmf of an Erlang process with interval distribution in formula (3.6) can be similarly derived,

$$\Pr\{N_T = N\} = e^{-\lambda T} \sum_{k=0}^{n-1} \frac{(\lambda T)^{(Nn+k)}}{(Nn+k)!}, \quad (3.11)$$

but it is too complicated to be further studied analytically in our localization problem because of the sum. The Gaussian ISI process is relatively simple, and we use it instead of the Erlang process to model regular neuron discharge patterns. The parameters μ and σ , determined by the statistics of the neuron responses under the constraint of small CV, specify the intensity of the corresponding point process as in formula (3.8). Thus, in developing the Gaussian ISI model for neuron responses, we need to specify only the Gaussian parameters μ and σ .

3.2.3 Non-renewal Gaussian ISI process

To represent the first-order correlation found between successive interevent intervals in LSO data, a non-renewal Gaussian ISI process is considered. Suppose the interspike interval between spike $i - 1$ and spike i is distributed as $\mathcal{N}(\mu_i, \sigma_i^2)$, $i = 1, 2, \dots$, distributions of adjacent intervals are jointly Gaussian, and the correlation coefficient between adjacent interevent intervals is ρ . Then,

$$p_{\tau_i|\tau_{i-1}}(\tau_i|\tau_{i-1}) \sim \mathcal{N}\left(\mu_i + \frac{cov}{\sigma_{i-1}^2}(\tau_{i-1} - \mu_{i-1}), \sigma_i^2 - \frac{cov^2}{\sigma_{i-1}^2}\right), \quad i = 2, 3, \dots, \quad (3.12)$$

where $cov = \rho\sigma_{i-1}\sigma_i$, and $p_{\tau_1}(\tau_1) \sim \mathcal{N}(\mu_1, \sigma_1^2)$. If we further assume that the intervals are identically distributed as $\mathcal{N}(\mu, \sigma^2)$, then formula (3.12) reduces to

$$p_{\tau_i|\tau_{i-1}}(\tau_i|\tau_{i-1}) \sim \mathcal{N}(\mu + \rho(\tau_{i-1} - \mu), (1 - \rho^2)\sigma^2). \quad (3.13)$$

The probability of negative intervals,

$$\Pr\{\tau_i < 0|\tau_{i-1}\} = Q\left[\frac{\mu + \rho(\tau_{i-1} - \mu)}{\sqrt{1 - \rho^2}\sigma}\right], \quad (3.14)$$

so, if $\mu \gg \sigma$, negative intervals can be avoided as in the renewal case.

If an interevent interval is negatively correlated with its previous interval, then the mean interspike interval varies inversely with the duration of the previous interval. In other words, the conditional mean function, which estimates the mean interspike interval as a function of the previous interval's duration, is a decreasing function. In particular, the conditional mean of interspike interval in our non-renewal Gaussian model is given by

$$E[\tau_i|\tau_{i-1}] = \mu + \rho(\tau_{i-1} - \mu) = \rho\tau_{i-1} + (1 - \rho)\mu. \quad (3.15)$$

So, if the correlation coefficient ρ is negative as in LSO data, the conditional mean function in formula (3.15) as a function of the previous interval's duration has negative slope.

Figure 3.5 depicts a typical conditional mean function of the non-renewal Gaussian model along with that of the LSO data.

Figure 3.5 The conditional mean function of the non-renewal Gaussian ISI model matches with that of LSO data (t108-1c.r3). The negative correlation coefficient in the model is -0.3 , approximating that measured from the data.

The conditional hazard function $h(\tau_i|\tau_{i-1})$ is given by

$$h(\tau_i|\tau_{i-1}) = \frac{e^{-\frac{(\tau_i - (\rho\tau_{i-1} + (1-\rho)\mu))^2}{2(1-\rho^2)\sigma^2}}}{\sqrt{2\pi(1-\rho^2)}\sigma Q\left(\frac{\tau_i - (\rho\tau_{i-1} + (1-\rho)\mu)}{\sqrt{(1-\rho^2)}\sigma}\right)}. \quad (3.16)$$

Clearly, the change of conditioning interval duration τ_{i-1} shifts the conditional hazard function horizontally. This is the direct result of the effect of the negative correlation on the conditional mean. Specifically, larger τ_{i-1} shifts the conditional hazard function toward smaller interval durations. This shifting property has been found in LSO slow chopper data [25].

Assuming interevent intervals $p_\tau(\tau) \sim \mathcal{N}(\mu, \sigma^2)$ with first-order correlation coefficient ρ , we have $\sum_{i=1}^N \tau_i \sim \mathcal{N}(N\mu, (N + 2\rho(N-1))\sigma^2)$. By formula (3.9), the probability of getting N events in time interval of length T is given by

$$\Pr\{N_T = N\} = Q\left[\frac{T - (N+1)\mu}{\sqrt{N+1+2\rho N}\sigma}\right] - Q\left[\frac{T - N\mu}{\sqrt{N+2\rho(N-1)}\sigma}\right]. \quad (3.17)$$

In spike count generation of the non-renewal Gaussian ISI process, the very first interval τ_1 is generated by a Gaussian $\mathcal{N}(\mu, \sigma^2)$, and the subsequent intervals are generated successively by iteration according to the distribution in formula (3.13). The number of intervals generated is accumulated and the last interval contributing to the total spike count is the interval whose next interval makes the total length of all the interval durations exceed T .

3.2.4 Regularity

The regularity of a stationary renewal point process is quantified by the interevent interval's coefficient of variation (CV) $\mathcal{C}[\tau]$ defined as

$$\mathcal{C}[\tau] = \frac{\sigma[\tau]}{\varepsilon[\tau]}, \quad (3.18)$$

where $\varepsilon[\tau]$ and $\sigma[\tau]$ denotes the mean and the standard deviation of the interevent interval distribution respectively [23]. For a renewal point process, the larger the CV, the more irregular the process. A Poisson process is considered a very irregular point process with $\mathcal{C}[\tau] = 1$ ($\sigma[\tau] = \varepsilon[\tau] = 1/\lambda$). In contrast, Erlang and Gaussian ISI processes are much more regular with smaller CVs. For example, the CV of the interval distribution is 0.2 for the Gaussian ISI point process that produces a hazard function similar to that plotted in Figure 3.4, and 0.027 in Figure 3.1. As pointed out in section 3.2.2, an Erlang process is consistent with the temporal integration mechanism, which suggests that the neuron is capable of producing discharges more regular than its input process. Specifically, if the integration involves n input intervals in the

production of one output, the CV of the output process is reduced to $1/\sqrt{n}$ times of the input process's CV. In the Erlang process case, the CV is $1/\sqrt{n}$ because the input process is Poisson by definition, with a CV of 1.

Figure 3.6 Pmfs of Poisson process and Gaussian ISI process. In either plot, the average rates of the two processes are the same. (a) low rate. (b) high rate. These two rates are the minimum and maximum average rates we use for AVCN discharges in our simulations.

Figures 3.6 depicts the pmfs for Poisson processes (formula (3.4)) and Gaussian ISI processes (formula (3.10)) at low average rate and high average rate respectively. Comparing the two pmfs of the same process with different rates in the two plots, we can see that a bigger discharge rate results in wider mode in the pmf. This is due to the fact that the CV characterizes the point process and remains the same regardless of the difference in average rate. So, a higher rate corresponds to larger standard deviation of the interval distribution for a specific point process with a

certain CV value. In each of the two plots, the average rates of the two processes are the same. As expected, the pmf of the Poisson process spreads more widely than that of the Gaussian ISI process with the same average rate, indicating that a Gaussian ISI process is more regular than a Poisson process. The pmf of an Erlang process (not shown in the figure), fits between those of the Gaussian ISI and the Poisson processes with the same mean rate.

A non-renewal point process is more regular than the corresponding renewal point process with the same interval distribution, even though they have the same CV. Consider the non-renewal Gaussian ISI process with first-order correlation. Because the correlation between intervals means that the next interval's duration can be partially predicted from the current interval's duration, the interval duration is less random and the process is more regular than a renewal Gaussian ISI process with the same CV.

3.3 AVCN and LSO modeling

The Poisson process model is investigated as the first model for both AVCN and LSO neuron discharges. The advantage of using a Poisson model follows directly from the fact that it is the simplest point process: We can usually obtain analytic solutions to problems related to Poisson processes. Furthermore, the characteristics of the optimal processor under a Poisson model provide a reference for comparing the predictions of more complicated and more accurate point process models.

Although its simplicity is very desirable for analysis, the Poisson process does not accurately model the discharges of either LSO cells or AVCN cells projecting to IC. The first non-Poisson model we use is the renewal Gaussian ISI process. We determine the Gaussian parameters according to several criteria, one of which is that the probability of negative intervals is negligibly small. In addition to its good agreement with certain LSO data statistics (e.g. Figure 3.4), the Gaussian ISI model with properly defined parameters is consistent with certain stimulus-dependent character-

istics of LSO responses found in [40, 48]. Moreover, the Gaussian ISI point process model allows us to study the impact of discharge regularity on localization through the comparison of the optimal processor with that under the Poisson assumption.

The major weakness of the renewal models for LSO discharges lies in their inability to capture the serial dependence between successive interspike intervals found in LSO responses [25]. The non-renewal Gaussian ISI model with negative correlation is studied as a more accurate model for LSO responses. Table 3.1 summarizes the point processes studied as models of the responses of several neuron types in this research work.

	AVCN bushy cells	AVCN stellate cells	LSO cells
Poisson	✓	*	*
Renewal Gaussian ISI		✓	*
Non-renewal Gaussian ISI			✓

Table 3.1 The point processes and the neuron types of interest in this study. The entry marked by either * or ✓ relates the point process studied to the neuron type whose responses it models; ✓ indicates that the point process models well the responses of the corresponding neuron type. Discharges of AVCN bushy cells are well modeled by Poisson processes. AVCN stellate cells and LSO cells have chopping responses, and Erlang processes model the regular discharge patterns well. Renewal Gaussian ISI processes are inferred from Erlang processes and model the chopping responses. LSO discharge patterns are more accurately modeled by Gaussian ISI processes with first-order negative correlation.

To model neuron responses by certain point process, we need to define the parameters that determine the process's intensity according to neuron response characteristics. For a Poisson process, the parameter is the intensity itself; for a renewal Gaussian ISI process, the parameters are μ and σ of interval distribution.

In sections 3.3.1 and 3.3.2, the modeling of AVCN and LSO responses is discussed in detail, with a focus on defining these parameters.

3.3.1 AVCN modeling

Discharge patterns of AVCN cells projecting to LSO (bushy cells)

The statistical properties of AVCN bushy cells are primary-like, so the model of AVCN discharge patterns is based on the studies of the responses of auditory-nerve fibers. Simple homogeneous Poisson processes model well responses of these units, so we use the Poisson process as the only model for AVCN bushy cell responses. Because the responses of MNTB units are also primary-like, they are modeled by Poisson processes as well.

We focus our study on the effect of interaural levels on localization, and assume that no interaural timing information is conveyed to the optimal processor. In addition, throughout our study, we assume that the stimulus amplitude A at the midline is an unknown constant. Under these assumptions, the discharge rates of AVCN cells under a high-frequency stimulus are monotonically related to the signal amplitudes present at the ears,

$$\lambda_{lp}(t, \theta) = R[AD(-\theta)], \quad \lambda_{rp}(t, \theta) = R[AD(\theta)], \quad (3.19)$$

where $\lambda_{lp}(t, \theta)$ and $\lambda_{rp}(t, \theta)$ denote the intensities of the Poisson processes characterizing discharges of a single primary-like bushy cell in the left AVCN and the right AVCN respectively. The rate-level function $R[\cdot]$ describes the transformation from stimulus amplitude to a bushy cell's discharge rate. The average discharge rate of most auditory-nerve fibers increases roughly in proportion to the logarithm of sound pressure over a limited level range, and reaches a rate plateau eventually. The discharge rate of a single AVCN cell has similar property as a function of the sound level at the ear [26, 34].

Figure 3.7 illustrates the rate-level transformation $R[\cdot]$.

Figure 3.7 Transformation from level to AVCN discharge rate. The discharge rate of a single AVCN cell increases monotonically with sound level at the ear before saturation.

Discharge patterns of AVCN cells projecting to IC (stellate cells)

Unlike the AVCN primary-like units, the AVCN stellate neurons and small neurons that project to IC exhibit chopping discharge patterns in their initial responses to tonal stimuli. For simplicity, we first model the discharge patterns of AVCN stellate cells as sample functions of Poisson processes. Although the actual unit responses are more regular than Poisson sample paths, the Poisson model casts a relatively simple localization problem and allows us to investigate the effect of discharge regularity when compared with other point process models for AVCN stellate cell responses. Given the Poisson assumption, formula (3.19) describes the intensities of the processes.

To model more accurately the chopping responses of AVCN stellate cells, we employ the temporal integration idea and assume that stellate cells are integrating neurons. Since AVCN cells receive ascending projections from auditory-nerve fibers, whose responses are well modeled by Poisson processes, the input process to these

integrating neurons has exponential intervals. By the result in section 3.2.2, if CV is small, the Gaussian ISI process approximates the output process and models the regularity underlying these stellate cells' chopping responses.

Supposing that the interspike intervals of the point process are identically distributed as Gaussian random variables, $p_\tau(\tau) \sim \mathcal{N}(\mu, \sigma^2)$, the discharge rate of a single AVCN chopper modeled by this point process is implicitly determined by the Gaussian parameters μ and σ , and the average discharge rate is approximately $1/\mu$. Relating to AVCN discharge rate defined in formula (3.19), we define the Gaussian parameters μ and σ corresponding to the responses of a single left AVCN stellate cell by

$$\mu = \frac{1}{R[AD(-\theta)]}, \quad \sigma = \frac{\mu}{a}, \quad (3.20)$$

where a is determined by the CV of the interval distribution ($CV = 1/a$), and it determines the shape of the Gaussian interval distribution.

3.3.2 LSO modeling

Our first model for discharge patterns of LSO cells is the Poisson process. Previous studies have suggested the representation of ILD in the sustained discharges of LSO neurons [4, 9, 24]. Based on the result that the responses of high-CF LSO cells exhibit E/I characteristics, we relate the sustained discharge rates of LSO cells to ILD, and model the intensities of the Poisson processes as

$$\lambda_{lso}(t, \theta) = f\left[\frac{D(-\theta)}{D(\theta)}\right], \quad \lambda_{rso}(t, \theta) = f\left[\frac{D(\theta)}{D(-\theta)}\right], \quad (3.21)$$

where $\lambda_{lso}(t, \theta)$ and $\lambda_{rso}(t, \theta)$ denote the intensities of the Poisson processes characterizing responses of a single cell in the left LSO and the right LSO respectively. The function $f[\cdot]$ describes the transformation from ILD to a LSO cell's discharge rate. By simplifying the relationship between the discharge rate of a single LSO cell and the ILD [3], we assume that the discharge rate increases monotonically until it

saturates at the highest discharge rate possible for the neuron when a large ILD is reached. For the ILD range in our study, $[0, 20)$ dB, the saturation point is not reached for almost all LSO cells according to experimental data. Because our simplified directivity function ensures that ILD is monotone in lateral angle θ (Figure 2.3), the discharge rate is monotone in lateral angle also. Figure 3.8 depicts the monotone property of ILD with respect to lateral angle. Specifically, as the sound source moves from the side ($\theta = -90^\circ$) toward the midline ($\theta = 0^\circ$), the discharge rate decreases monotonically as a function of lateral angle, going to zero at midline. This one-to-one mapping between LSO discharge rate and lateral angle avoids any ambiguity in angle estimation using LSO responses.

Figure 3.8 Transformation from lateral angle to LSO discharge rate. The discharge rate of a single LSO cell decreases monotonically with lateral angle, and goes to zero at midline.

We investigated several possibilities for the transformation $f[\cdot]$ from ILD to discharge rate:

- linear: $\lambda_{lso}(t, \theta) = b_1 \left(\frac{D(-\theta)}{D(\theta)} - 1 \right),$
- logarithmic: $\lambda_{lso}(t, \theta) = b_2 \left(20 \lg \frac{D(-\theta)}{D(\theta)} \right),$
- square-root: $\lambda_{lso}(t, \theta) = b_3 \sqrt{\frac{D(-\theta)}{D(\theta)} - 1}.$

Here, $b_i, i = 1, 2, 3$ are constants selected to make the maximum discharge rate a predefined value. These transformations of discharge rates as functions of lateral angle θ are depicted in Figure 3.8. The linear model and the logarithmic model for $f[\cdot]$ are studied because of their simplicity. The few data we have of LSO sustained discharge rates for cats suggest that the discharge rate is linear with ILD on a log-log scale, and the slope of the line is measured to be approximately 1/2 [24]. The square-root model describes this relationship quantitatively.

It should be pointed out that, due to the lack of LSO data relative to ILD, there are many other possible functional forms of $f[\cdot]$ that can approximate the transformation from ILD to LSO discharge rate. However, as will be discussed in section 4.3.2, these various forms for $f[\cdot]$ are not a crucial factor in the performance of the optimal angle estimator. Hence, we choose the simplest linear model for the sustained discharge rate of a single left LSO cell,

$$\lambda_{lso}(t, \theta) = f \left[\frac{D(-\theta)}{D(\theta)} \right] = b \left(\frac{D(-\theta)}{D(\theta)} - 1 \right), \quad (3.22)$$

where b is a constant directly related to the maximum discharge rate of the neuron, and it may vary from cell to cell.

Like AVCN choppers, LSO cells exhibit chopping responses, which are inconsistent with Poisson processes. The inconsistency is manifest in the discrepancy of interval statistics of the model and the data. For example, the hazard function for a Poisson process is constant, but LSO data consistently have increasing hazard functions. In

contrast, Figure 3.4 indicates that the Gaussian ISI process can model LSO data better. Like the ascending projections to the AVCN choppers from auditory nerves, the inputs to LSO choppers from AVCN and MNTB are well modeled by Poisson processes (sections 2.2.2 and 2.2.3). So, if LSO choppers are in fact integrating neurons, we can use the point process characterized by Gaussian interspike intervals as a more precise, yet analytically tractable, model for their responses. The Gaussian parameters are selected under several major criteria:

- The average rate of the point process model is a function of ILD, which is determined by lateral angle as in formula (2.4);
- The probability of negative intervals occurring under the model is negligibly small ($\leq 10^{-6}$);
- The resulting hazard function of the model agrees with the shifting and scaling characteristics described in [40, 48] with LSO binaural stimuli responses:
 - Stronger contralateral stimuli tend to scale down the hazard function;
 - Stronger ipsilateral stimuli shift the hazard function toward shorter intervals and scale the hazard function up to a higher slope.

We now define the parameters μ and σ as functions of lateral angle, then verify that the above criteria are obeyed by the Gaussian ISI model with this set of parameters.

In binaural localization, the contralateral and ipsilateral stimuli levels at LSO are related to lateral angle, and LSO discharge rate is related to ILD. Suppose the sound source is located in the left half plane in front of the subject ($-90^\circ \leq \theta < 0^\circ$), then by formula (2.3), $D(-\theta)$ is proportional to the ipsilateral stimulus level, and $D(\theta)$ to the contralateral level. We choose

$$\mu \triangleq \frac{1}{f\left[\frac{D(-\theta)}{D(\theta)}\right]} = \frac{1}{b\left(\frac{D(-\theta)}{D(\theta)} - 1\right)}, \quad \sigma = \frac{\mu}{a}, \quad (3.23)$$

where a and b are constants, θ is the lateral angle, $f[\cdot]$ is the linear rate-ILD function plotted in Figure 3.8. As discussed in section 3.2.2, the probability of negative intervals can be ignored by selecting a properly.

The discharge rate of the LSO cell modeled by this point process is implicitly determined by the Gaussian parameters μ and σ . The average discharge rate is related to ILD and is approximately $1/\mu$ *. To verify that the scaling and shifting characteristics of hazard functions for LSO discharges are satisfied by the Gaussian ISI process with parameters μ and σ defined in formula (3.23), first consider the effect of μ on the hazard function. By formula (3.8), it is obvious that the hazard function is shifted toward longer intervals if μ increases and vice versa. The parameter σ determines the steepness of the slope of the hazard function because

$$\lim_{\tau \rightarrow \infty} \frac{d}{d\tau} h(\tau) = \frac{1}{\sigma^2}, \quad (3.24)$$

and thus,

$$\text{slope} \propto \frac{1}{\sigma^2} = \left(ab \left(\frac{D(-\theta)}{D(\theta)} - 1 \right) \right)^2. \quad (3.25)$$

Clearly, stronger ipsilateral stimulus (larger $D(-\theta)$) increases the slope, while stronger contralateral stimulus (larger $D(\theta)$) reduces it. Also, at stronger ipsilateral stimulus, μ decreases, shifting the hazard function to shorter intervals.

Therefore, if the interspike intervals of LSO responses are independent, the Gaussian ISI model with parameters defined in formula (3.23) can model well the discharge patterns.

*The mean of the pmf of a Gaussian ISI point process can't be derived analytically. The numerical mean of spike count in time interval of length T is T/μ if the number of spikes is large. In our simulations, the difference between T/μ and the mean spike count of simulated data is always less than 0.5 spike on average. Moreover, the optimal processor we study later doesn't rely on the mean spike count of the process directly, thus the analytic form of the optimal estimator is exact.

Analyses of experimental data of LSO responses suggest that there exists negative correlation between successive interspike intervals [25], an effect presumably due to accumulation of refractoriness when two action potentials occur closely together. In LSO data, a longer than average interval tends to follow a shorter than average interval. Therefore, a more accurate LSO model encompasses not only regularity, but also serial dependence of interspike intervals. Because the renewal point process models are unable to describe any dependence structure among the intervals, we study the non-renewal point process model by introducing first-order negative correlation into the Gaussian ISI model to account for the serial dependence.

The Gaussian parameters μ and σ are defined in formula (3.23), and the correlation coefficient between successive intervals is -0.3 , as measured from the slope of the conditional mean function of LSO data.

Chapter 4

Optimal Localization with LSO and AVCN Responses

4.1 Maximum likelihood estimator of lateral angle

For the binaural localization problem, we assume that the sound source is located at the front ($-90^\circ \leq \theta \leq 90^\circ$). We further divide the front into left half plane ($-90^\circ \leq \theta \leq 0^\circ$) and right half plane ($0^\circ \leq \theta \leq 90^\circ$). Because of the symmetry of the localization problem, sounds coming from the left and right half planes are processed the same way. Without loss of generality, we assume that the sound source is located in the left half plane at the subject's front ($-90^\circ \leq \theta \leq 0^\circ$), and this fact is known by the optimal estimator. In addition, we assume that the right LSO cells are completely inhibited by our sound signal, except in section 4.4.2 where the discharges of different threshold LSO cells are studied. According to the discussion of ascending projections to IC (section 2.2.1), left AVCN choppers and left LSO cells project to the right IC. Although the right AVCN cells might send minor projections to the right IC, we do not take this possibility into account until later in section 4.4.1. To avoid midline complications (described in section 4.4), we assume that $-90^\circ \leq \theta < 0^\circ$ and the inputs to the optimal estimator are the spike counts from the left AVCN and the left LSO only. Obviously, the optimal estimator models the right IC according to the anatomy of the binaural pathway (Figure 2.4).

4.1.1 Maximum likelihood estimation

In our localization problem, the angle is a deterministic unknown parameter, of which we have no *a priori* knowledge. We use maximum likelihood estimation not only because it suits the situation, but also because it is the only systematic estimation method known in non-random parameter estimation. The maximum likelihood estimate has the following desirable properties [45]:

- Asymptotically unbiased
- Consistent
- Asymptotically efficient.

These properties ensure that as the duration T of the observation interval increases, the mean of angle estimate approaches the actual lateral angle, and that the variance of the angle estimate approaches zero. In other words, asymptotically, the maximum likelihood estimate is optimal.

Suppose the point processes representing two different cells' outputs are independent; the joint pmf of the number of events occurring in each of the two processes can be separated as the product of the marginals

$$p_{N_1, N_2 | (\theta, A)}(N_1, N_2 | (\theta, A)) = p_{N_1 | (\theta, A)}(N_1 | (\theta, A)) \cdot p_{N_2 | (\theta, A)}(N_2 | (\theta, A)), \quad (4.1)$$

where N_1 and N_2 are the total number of discharges of the two cells respectively within observation interval of length T for specific values of θ and A . The maximum likelihood estimates of the lateral angle and sound amplitude are those at which this joint pmf reaches its maximum value. The result of the joint pmf in formula (4.1) can be extended to more than two inputs situations as long as the input processes are independent.

As discussed in Appendix A, the angle estimate is solely determined by LSO discharges (if non-zero) regardless of AVCN discharges. Because the model for AVCN discharges doesn't affect the optimal processor of lateral angle when LSO discharges are available, we always assume for simplicity a Poisson model for AVCN discharges and focus on different models of LSO discharge patterns. The impact of AVCN discharges regularity on angle estimation is discussed in section 4.4.1 when both LSOs are totally inhibited. Under the assumption of non-zero input from LSO, the maximum likelihood angle estimate occurs when the joint pmf associated with only LSO cell(s) is maximized.

4.1.2 LSO Poisson model

Under the Poisson model for LSO discharges with the intensity given in formula (3.21), the maximum likelihood estimator of lateral angle based on AVCN and LSO discharges is given by

$$\hat{\theta} = -\sin^{-1} \left[\frac{1}{2k} \ln \left(f^{-1} \left[\frac{N_{lso}}{T} \right] \right) \right], \quad (4.2)$$

where N_{lso} is the total number of discharges observed in the left LSO cell's output during the time interval of length T , and $f^{-1}[\cdot]$ is the inverse of the rate-ILD function. Letting $\lambda_{lso}(t, \theta) = b \left(\frac{D(-\theta)}{D(\theta)} - 1 \right)$, a linear relation between the discharge rate and ILD (Figure 3.8), we have

$$f^{-1}[x] = 1 + \frac{x}{b},$$

and thus

$$\hat{\theta} = -\sin^{-1} \left[\frac{1}{2k} \ln \left(1 + \frac{N_{lso}}{bT} \right) \right]. \quad (4.3)$$

Unexpectedly, the angle estimator given in formula (4.2) doesn't have the primary-like component from AVCN. The spike count of LSO outputs, N_{lso} , provides the sufficient statistic for angle estimation. Considering the fact that LSO discharges are directly related to ILD, we conclude that ILD plays a crucial role in localization.

Closer observation of the estimator shows that, as long as it is not saturated [†], the AVCN discharge rate-level function $R[\cdot]$ doesn't influence the lateral angle estimate. Therefore, in this range, the absolute signal amplitudes at each ear do not matter in sound direction estimation. However, if we are interested in the signal amplitude estimation as well as the angle estimation, we need both the rate-level function $R[\cdot]$ and N_{lp} , the total number of discharges provided by the left AVCN cell during the same interval of length T , because

$$\hat{A} = \frac{R^{-1}[\frac{N_{lp}}{T}]}{\sqrt{f^{-1}[\frac{N_{lra}}{T}]}}. \quad (4.4)$$

While a single LSO cell is theoretically capable of providing the information sufficient for the higher center to localize the sound source, it is quite unlikely that only one LSO cell is involved in processing binaural information. In fact, a population of neurons should be responding to our binaural stimulus. The tuning curves (the minimum stimulus level required to excite a cell as a function of the stimulus frequency) of LSO units have been described to be similar to those of auditory-nerve fibers and AVCN units [27]. The shape (bandwidth) of the tuning curves suggests two facts:

- For a single neuron, there is a range of stimulus frequencies when the neuron is excited.
- At a specific stimulus frequency, a population of neurons whose threshold levels of activation are crossed are excited.

Hence, the number of LSO neurons simultaneously activated by the sound signal is presumably large, and it is very probable that the higher neural center processes the responses of a neuron population in extracting the angle. To study how populations of neurons, as opposed to a single neuron, would be processed, we start by assuming

[†]If either the rate-level function $R[\cdot]$ or the rate-ILD function $f[\cdot]$ is saturated, we have a degenerate localization problem, and the optimal processor can't localize the sound source without ambiguity.

that the population consists of two identical (i.e. same CF, same threshold) neurons. Although the actual convergence among units is probably much more complicated, this assumption allows us to study the situation beyond a single LSO cell and gain some insight into the impact of ensemble processing on localization.

Suppose that we have two identical LSO units projecting to the optimal angle estimator, and that the intensities of the two corresponding independent Poisson processes are given by

$$\lambda_{lso1}(t, \theta) = \lambda_{lso2}(t, \theta) = f \left[\frac{D(-\theta)}{D(\theta)} \right]. \quad (4.5)$$

Along with the input from AVCN, the maximum likelihood estimator of lateral angle is

$$\hat{\theta} = -\sin^{-1} \left[\frac{1}{2k} \ln \left(f^{-1} \left[\frac{N_{lso1} + N_{lso2}}{2T} \right] \right) \right], \quad (4.6)$$

which ignores the primary input from AVCN as the one-input case. Generalizing this result to M identical LSO units, we have

$$\hat{\theta} = -\sin^{-1} \left[\frac{1}{2k} \ln \left(f^{-1} \left[\frac{\sum_{i=1}^M N_{lsoi}}{MT} \right] \right) \right]. \quad (4.7)$$

Now consider another situation when we have only one LSO cell projecting to the optimal processor, but with a discharge rate M times as big as that described in equation (4.5),

$$\lambda_{lso}(t, \theta) = M f \left[\frac{D(-\theta)}{D(\theta)} \right]. \quad (4.8)$$

Then, the maximum likelihood angle estimator is given by

$$\hat{\theta} = -\sin^{-1} \left[\frac{1}{2k} \ln \left(f^{-1} \left[\frac{N_{lso}}{MT} \right] \right) \right]. \quad (4.9)$$

Figure 4.1 The negative of the angle estimate relative to inputs (spike counts) from the two LSO cells modeled by Poisson processes.

Figure 4.2 Iso-angle-estimate contours of Figure 4.1. The angle estimate remains constant when the sum of the spike counts from the two cells is constant.

Comparing the estimators given in formulae (4.7) and (4.9), it is clear that having a large number of identical convergent LSO cells is equivalent to having one cell with a correspondingly high discharge rate. Hence, superposition holds under the Poisson model. In other words, if LSO discharges were nicely modeled by Poisson processes, the optimal processor would superimpose (add) its LSO inputs and produce the angle estimate based on the sum. Figures 4.1 and 4.2 demonstrate the superposition result for two LSO cells. The iso-angle contours coincide with constant $N_{lso1} + N_{lso2}$ lines, indicating that the optimal processing is operated on the sum of the spike counts from the two cells.

4.1.3 LSO renewal Gaussian ISI model

In comparison with the Poisson model, we now assume that a LSO cell's discharges have interevent intervals distributed as independent Gaussian random variables with parameters μ and σ determined in formula (3.23). Assuming the linear model for $f[\cdot]$, the maximum likelihood angle estimator with AVCN and LSO inputs is (shown in Appendix A)

$$\hat{\theta} = -\sin^{-1} \left[\frac{1}{2k} \ln \left(1 + \frac{\sqrt{N_{lso}(N_{lso} + 1) \left(a^2 - \ln \left(\frac{N_{lso}}{N_{lso} + 1} \right) \right)}}{abT} \right) \right]. \quad (4.10)$$

In general, we can assume the total spike count $N_{lso} \gg 1$ except when the average discharge rate is too low or the observation interval of length T is too short. From the estimation viewpoint, a smaller value of the input to the angle estimator incurs a larger localization error. Hence, if the input from LSO is small, it is very probable that the higher center incorporates responses from some other lower neural centers for more reliable localization. The average discharge rate of a typical LSO cell is low only when the sound source is located near the midline, the situation studied in section 4.4.

The assumption $N_{lso} \gg 1$ allows us to simplify the angle estimator to

$$\hat{\theta} = -\sin^{-1} \left[\frac{1}{2k} \ln \left(1 + \frac{N_{lso}}{bT} \right) \right]. \quad (4.11)$$

As in the Poisson case, the ILD, which determines the spike count of the input from LSO, is the only important factor in estimating the lateral angle (formula (4.10)). More interestingly, the optimal estimator in formula (4.11) having the Gaussian ISI input has the same form as that under the Poisson input (formula (4.3)). In other words, under certain conditions, not only is the information used by the optimal processor for angle estimate the same, but also how this information is used.

Again, we study localization by the neuron family instead of a single LSO cell by considering the two-input case. Since it is impossible to solve for the maximum likelihood estimator analytically in this case, we obtained the angle estimate numerically. In our simulations, the numerical approach converges well, and the maximum found is global because of the unimodal property of the likelihood joint pmf function (see Appendix B).

To investigate the optimal processing of the two inputs, we plot angle estimate $\hat{\theta}$ relative to LSO discharges N_{lso1} and N_{lso2} in Figures 4.3 and 4.4. From these two plots, it is obvious that the angle estimate doesn't remain constant when the total spike count $N_{lso1} + N_{lso2}$ is constant. Thus, unlike the Poisson case, the inputs of the two LSO units are not simply superimposed together. In general, superposition doesn't hold under the LSO Gaussian ISI model.

However, if the two LSO neurons are identical, we expect the spike counts N_{lso1} and N_{lso2} to be similar despite of the randomness of the underlying process. In the region near the diagonal line ($N_{lso1} = N_{lso2}$) in Figure 4.4, the curvature of the iso-angle contours is relatively flat. Hence, in this case, the suboptimal superposition rule may give similar localization performance as the optimal processing.

Figure 4.3 The negative of the angle estimate relative to discharges of two identical LSO cells modeled by Gaussian ISI processes. The angle estimate is obtained numerically at the maximum of the corresponding joint pmf function. Angle estimates at some values of N_{lso1} and N_{lso2} are not possible because of the precision limitation of Q-functions.

Figure 4.4 Iso-angle-estimate contours of Figure 4.3. The angle estimate is not constant when the sum of discharges of the two cells is constant.

4.1.4 LSO non-renewal Gaussian ISI model

Under the non-renewal Gaussian ISI model, the pmf of LSO input is given in formula (3.17). Similar derivation as that in Appendix A results in the single-input maximum likelihood estimator of lateral angle

$$\hat{\theta} = -\sin^{-1} \left[\frac{1}{2k} \ln \left(1 + \frac{N_{lso}}{bT} + \frac{c}{abT} \right) \right], \quad (4.12)$$

where c is a root of the quadratic equation

$$(2\rho + 1)c^2 + 2aBc + \left(C \ln \left(\frac{B}{C} \right) - a^2 \right) B = 0$$

with $B = (1 + 2\rho)N_{lso} - 2\rho$ and $C = (1 + 2\rho)N_{lso} + 1$.

In our simulations, we use $\rho = -0.3$ and $a = 5$ for the Gaussian interval distribution to have CV= 0.2. By choosing these parameters, we have $aN_{lso} \gg c$ except when N_{lso} is small (Figure 4.5).

Figure 4.5 In our simulations, $aN_{lso} \gg c$ in general. This condition allows us to simplify the angle estimator in formula (4.12).

So the angle estimator, in general, reduces to

$$\hat{\theta} = -\sin^{-1} \left[\frac{1}{2k} \ln \left(1 + \frac{N_{lso}}{bT} \right) \right]. \quad (4.13)$$

Assuming that the total spike count available to the optimal angle estimator is not too small, we compare the form of the optimal estimator under the non-renewal Gaussian ISI model (formula (4.13)) with that under the Poisson model (formula (4.3)) or that under the renewal Gaussian ISI model (formula (4.11)). In all cases, the input from LSO, and thus the ILD, is the crucial information in localization. Interestingly, this information is processed in the same straightforward way to produce the angle estimate. Striking similarity exists in the form of the optimal angle estimator under different LSO models even without the assumption of large N_{lso} (formulae (4.3), (4.10), and (4.12)). It would be misleading to suggest that the choice of LSO model may be unimportant in angle estimation. As will be discussed in the next section, LSO modeling does have great impact on localization performance of the optimal angle estimator.

4.2 Performance of the optimal angle estimator

Although the resulting optimal angle estimator has similar form under different single-input LSO models, the localization performance is quite different. The performance of an optimal estimator is evaluated by its bias and standard deviation of angle estimates. These criteria correspond to localization accuracy and precision respectively. For a specific azimuthal angle, the simulation results of mean and standard deviation of the angle estimate are based on the statistics of only 50 trials.

4.2.1 Bias of the lateral angle estimate

In Figure 4.6, the mean of angle estimate under each LSO model is shown. The bias towards the side ($\theta = -90^\circ$) is an artifact due to the assumption that the sound comes from the front instead of the back of the subject. The other extreme situation occurs when the sound source is located near the midline ($\theta = 0^\circ$). If the LSO cell's discharge rate is too low and the cell produces no input to the processor because of strong inhibition, the angle estimator can't distinguish between the situations of

midline source and no sound source. Except for these artifacts, the optimal estimator under each LSO model is approximately unbiased, and the Gaussian ISI models give rise to less biased angle estimates than the Poisson model.

Figure 4.6 The mean of angle estimate under different LSO models. The significant bias near -90° is an artifact of the estimator assumption about the sound direction. The Gaussian ISI models result in much smaller bias than the Poisson model, while the non-renewal factor doesn't contribute as much. All the performance figures in chapter 4 are based on the statistics of 50 trials per angle point.

4.2.2 Standard deviation and Cramér-Rao bound

The optimal estimator under the LSO Gaussian ISI model gives much smaller variance than under the Poisson model, and the non-renewal Gaussian ISI model results in slightly smaller variance in angle estimate than the renewal Gaussian ISI model. Figure 4.7 demonstrates these results by comparing the standard deviation of angle estimates. Only the approximately unbiased angle estimate portion is included for

reasonable comparison.

Figure 4.7 The standard deviation of angle estimate under different LSO models is quite different. Similar to the comparison of bias results, Gaussian ISI models result in much smaller standard deviation than the Poisson model, while the non-renewal factor doesn't contribute as much.

Cramér-Rao bound is a lower bound of the estimation variance [12]. For the localization problem under the Poisson model, the Fisher information F is given by

$$F = \begin{bmatrix} \left(\frac{\partial \ln p}{\partial \theta}\right)^2 & \frac{\partial \ln p}{\partial \theta} \cdot \frac{\partial \ln p}{\partial A} \\ \frac{\partial \ln p}{\partial A} \cdot \frac{\partial \ln p}{\partial \theta} & \left(\frac{\partial \ln p}{\partial A}\right)^2 \end{bmatrix}, \quad (4.14)$$

where p is the joint pmf

$$\begin{aligned} & p_{N_{lp}, N_{lso}}(\theta, A)(N_{lp}, N_{lso} | (\theta, A)) \\ &= \frac{e^{-R[AD(-\theta)]T} (R[AD(-\theta)]T)^{N_{lp}}}{N_{lp}!} \cdot \frac{e^{-f\left[\frac{D(-\theta)}{D(\theta)}\right]T} \left(f\left[\frac{D(-\theta)}{D(\theta)}\right]T\right)^{N_{lso}}}{N_{lso}!}. \end{aligned} \quad (4.15)$$

Assuming linear $R[\cdot]$ and linear $f[\cdot]$ in formula (3.22), we have

$$F = \begin{bmatrix} k^2 \cos^2 \theta T D(-\theta) \left(A + \frac{4b}{D(\theta) \left(1 - \frac{D(\theta)}{D(-\theta)} \right)} \right) & -k \cos \theta T D(-\theta) \\ -k \cos \theta T D(-\theta) & \frac{T D(-\theta)}{A} \end{bmatrix}. \quad (4.16)$$

For any unbiased angle estimator, the Cramér-Rao bound on the angle estimator's mean-squared error is $(F^{-1})_{11}$, where F^{-1} is the inverse of the Fisher information matrix. The bound is plotted in Figure 4.8 imposed on the variance of the maximum likelihood angle estimator under the LSO Poisson model. The biased angle estimate portion is left out. The variance of the unbiased angle estimate matches with the theoretical bound.

Figure 4.8 Cramér-Rao bound for any unbiased angle estimator under the Poisson model. The standard deviation of the maximum likelihood angle estimate matches with Cramér-Rao bound. Only the unbiased angle estimate portion is compared.

4.2.3 Regularity and localization performance

While the optimal estimator retains similar form under each LSO model, localization performance does vary with the model. The major difference among the models is the degree of randomness in the data they represent. Relating the performance of the optimal estimator to the randomness of its input data, we set up Table 4.1 to describe the point process models, the regularity, and the angle estimator performance in terms of estimation bias and standard deviation.

Estimator	Poisson	Renewal Gaussian	Non-renewal Gaussian
Input regularity	irregular	more regular	the most regular
Estimation bias	biggest	smaller	smaller
Estimation variance	biggest	smaller	smallest

Table 4.1 The inputs under the Gaussian ISI process models are much more regular than that under the Poisson model. The serial dependence in the non-renewal model makes the data even more regular. More regular process models give rise to less biased angle estimation and smaller estimation variance.

Because regularity is the only prominent factor that varies from model to model, we attribute the performance improvements in localization to more regular discharge patterns of LSO units.

To further demonstrate our point, we used non-renewal simulated data as the input to the optimal estimator obtained under either the renewal Gaussian ISI model or the non-renewal Gaussian ISI model. The localization performance of optimal estimator under both models is quite similar in this case. The apparent reason for this interesting result is that the optimal estimator under different models approximates each other in forms, and the randomness of the input data determines the localization performance.

4.3 Further analyses of the optimal angle estimator characteristics

4.3.1 Neuron population processing

Under both the Poisson and the renewal Gaussian ISI LSO models, the effect of neuron ensemble processing is studied by making the discharges of identical neurons available to the processor. For the Poisson model, superposition holds for convergent cells: More than one convergent cell providing inputs to the processor is equivalent to a single LSO neuron with a higher discharge rate. The bigger the number of convergent cells M , the better the localization performance. For the Gaussian ISI models, there is no simple superposition rule among convergent cells even if they are identical. However, the performance of the optimal estimator with two convergent LSO cells as inputs exhibits a significant reduction in the variances of angle estimates over only one LSO cell case. Under either LSO model, neuron ensemble processing tends to result in an optimal angle estimator with better performance than a single LSO cell.

Figure 4.9 demonstrates these results by comparing the standard deviation of angle estimates produced by processor having inputs either from a single LSO cell or from two identical LSO cells under each model. The angle estimator with inputs from two identical LSO cells has less variance in angle estimation under either the Poisson or the Gaussian ISI model. The variance is reduced to approximately half of the corresponding single LSO cell case. Based on this result, we predict that the estimation variance would decrease by the factor of M , the total number of convergent cells. Consequently, spatial summation of LSO neurons improves the localization capability of the higher center.

Figure 4.9 LSO neuron population improves localization capability of the higher neural center. Besides the result that the Gaussian ISI model results in smaller standard deviation than the Poisson model, localization with inputs from two LSO cells gives rise to smaller standard deviation than one LSO cell under either point process model.

4.3.2 LSO rate-ILD functional form

For all our analysis, we assumed that the transformation from ILD to LSO discharge rate is linear. Here, we investigate some other functional forms to probe the angle estimator's sensitivity to that assumption. With the functions described in section 3.3.2, we derive the corresponding maximum likelihood angle estimator under the LSO Poisson model. For the logarithmic $f[\cdot]$,

$$\hat{\theta} = -\sin^{-1} \left[\frac{1}{2k} \left(\frac{\ln 10}{20} \frac{N_{lso}}{b_2 T} \right) \right]. \quad (4.17)$$

For the square-root $f[\cdot]$,

$$\hat{\theta} = -\sin^{-1} \left[\frac{1}{2k} \ln \left(1 + \left(\frac{N_{lso}}{b_3 T} \right)^2 \right) \right]. \quad (4.18)$$

Figure 4.10 Mean of angle estimate under different rate-ILD functional forms. The bias under each model is similar.

Figure 4.11 Standard deviation of angle estimate under different $f[\cdot]$. Along with the bias result in Figure 4.10, we conclude that the exact form of $f[\cdot]$ is unimportant to our localization problem.

Figures 4.10 and 4.11 depict the performance of the optimal estimator under different assumptions of $f[\cdot]$. Although the optimal estimator processes the input from LSO differently (formulae (4.3), (4.17), and (4.18)) under different rate-ILD transformation, the localization performance in each case is similar. Hence, as long as the discharge rate has a proper monotone relationship with ILD, the exact form of $f[\cdot]$ has little effect on the performance.

4.3.3 Non-constant rate input

The PST histograms computed from experimental data show that the discharge rates of LSO cells are not constant. In fact, LSO cells are known for the initial chopping transient in their responses. We investigate the effect of LSO non-stationary discharge rate on the performance of the optimal angle estimator by localization with LSO step rate inputs. The step rate assumption is essentially equivalent to assuming that the actual observation window doesn't lie entirely within the sustained rate portion of the response, and that the discharge rate is zero outside the sustained region.

The direct result of a step rate input compared with a constant rate input in the same time interval of length T is that the spike count N_{lso} is smaller. Because the estimator assumes a constant discharge rate input from the LSO, the fewer spikes it receives, the smaller the estimated discharge rate. This reduction affects the lateral angle estimate considerably since smaller estimated rate corresponds to a lateral angle closer to midline. Hence, if the inputs to the estimator are actually generated with step rate, the lateral angle estimate is biased toward the midline. In general, the angle estimator under constant LSO discharge rate assumption can't adapt itself to transient inputs.

4.4 Localization at midline

From previous studies [13, 24] and the analysis in section 4.1, LSO is believed to provide the sufficient statistic for the higher neural center to localize the sound source. However, responses recorded from LSO cells suggest that contralateral cells are usually totally inhibited, and cells in both ipsilateral LSO and contralateral LSO may be totally inhibited if the ILD is small [4]. Because small ILD corresponds to the situation when the sound source is located near the direct front of the subject, a midline problem arises when both LSOs are totally inhibited: How does the optimal processor localize the sound source when LSO provides no input to the higher center at all?

For all the previous discussions, the information available to the contralateral (right) optimal estimator is from only the ipsilateral (left) LSO and ipsilateral (left) AVCN, and only identical LSO neurons contribute to the inputs to the higher center. In the following, we first address what happens if the contralateral AVCN input is also used, and then consider LSO cells with different thresholds to help solve the midline problem.

4.4.1 Ipsilateral LSO and both AVCNs

The anatomy of IC suggests that both AVCNs might provide inputs to the optimal processor. In our localization problem with the $-90^\circ \leq \theta < 0^\circ$ assumption, the discharge rates of left AVCN cells are larger than right ones. Hence, our acoustic model agrees with the anatomical result that the left AVCN sends major projection and the right AVCN minor projection to the right IC. Given inputs from the ipsilateral LSO and both AVCNs, the maximum likelihood angle estimator was derived to be the same as one AVCN case if LSO input is non-zero. So, if LSO discharges are available to the higher center, the direct projection to the IC from neither AVCN contributes to localization. However, if LSO is totally inhibited or damaged so that no LSO input is available to the higher center, then localization is possible by processing the inputs from AVCNs.

Suppose the optimal processor receives inputs from both AVCNs, but no LSO input is available. If the AVCN inputs are Poisson, then the optimal processor acts just like a replica of LSO in that it computes the ILD and gives out the angle estimate as studied in [13, 24]. However, the inconsistency between the Poisson model and AVCN projections to the IC indicates the possibility that the localization capability of the higher center is different from that of the LSO. If the AVCN discharges are modeled by the more regular Gaussian ISI point process, the functional form of the optimal estimator could not be derived. Despite of this disadvantage, the numerical results do show that the performance of the optimal processor for the higher center is greatly improved over that for the LSO.

Figures 4.12 and 4.13 demonstrate the localization improvements by AVCN regular inputs.

Figure 4.12 The AVCN Gaussian ISI model results in almost unbiased angle estimate, while the AVCN Poisson model performs much worse.

The optimal estimator with regular inputs from AVCN produces almost unbiased angle estimates, while the Poisson model results in angle estimates that are very biased (Figure 4.12). Therefore, the higher center is capable of extracting the angle more accurately than LSO by processing inputs from both AVCNs. In addition, the localization precision (Figure 4.13) of the higher center with solely AVCN discharges is similar to that with solely LSO discharges; both are much better than the localization precision at LSO. Hence, localization performance is preserved when LSO discharges are not available to the higher center in situations such as the midline source.

Figure 4.13 The standard deviation of angle estimate under the AVCN Gaussian ISI model is much smaller than under the Poisson model. Along with the results in Figure 4.12, the localization capability of the higher center with solely AVCN discharges is better than that of the LSO.

4.4.2 Ipsilateral AVCN and different ipsilateral LSO cells

Experimental data indicate that LSO cells are not identical, even when they have the same characteristic frequency (determined by tuning curves). In particular, the threshold level at which the cell is excited may be different from cell to cell [27, 41]. Hence, it is reasonable to assume that, within the neuron population that project to the higher center, some LSO cells with certain thresholds don't get totally inhibited when ILD is small.

We model this possibility by supplying discharges of two LSO cells with different thresholds (still same CF) to the optimal estimator along with the input from the ipsilateral AVCN. If at least one of the LSO cells is not totally inhibited at midline, localization is always possible, and the midline problem is solved. Whenever LSO responses are available, the input from AVCN is ignored by the optimal angle estimator. If the threshold levels of the two cells have the same non-zero value, then we have two convergent cells projecting to the optimal processor. From the discussion in section 4.3.1, we know that some performance improvement can be achieved over a single LSO cell input case. If the threshold levels are different but both non-zero, our simulations show similar performance improvement for the optimal estimator over the one LSO case. Because the threshold levels of different cells don't have significant effect on the performance of the optimal processor, we study only identical threshold cells except at the midline.

4.4.3 Ipsilateral AVCN and both LSOs

In section 4.4.2, we modeled the possibility of incomplete inhibition of some ipsilateral LSO cells at the midline. Given the assumption that the non-zero discharge rate crosses the midline, it is reasonable to assume that some contralateral LSO cells provide discharges to the higher center in localization of sound signal located near midline. However, the projections from contralateral LSO cells are minor because of

their relatively low discharge rates compared with those of ipsilateral LSO cells, and our simulations show no observable effect on localization performance.

Chapter 5

Conclusions

The main goal of this research is to understand what information is used, and how this information is used, by nuclei more central than LSO in localizing high-frequency tonal signal sources in the horizontal plane. Previous studies have shown that, as an optimal processor, LSO provides the sufficient statistic based on the ILD cue to some higher neural center [13, 24]. According to the anatomy and physiology of the auditory pathway, the IC receives major ascending projections from many nuclei including LSO, and could be a higher center responsible for lateral angle extraction based on monaural and binaural cues preprocessed by nuclei along the lower auditory pathway. Although the nucleus of lateral lemniscus (LL), located along the pathway between LSO and IC, receives major ascending projections from LSO, the available physiological and anatomical data unfortunately shed little light on the functional importance of LL. All of the nuclei that project to LL also project to IC. Hence, we considered the IC as the higher center responsible for the extraction of the lateral angle. We simplified the ascending projections to the IC by assuming that it receives inputs unilaterally from LSO and either unilaterally or bilaterally from AVCN(s). An optimal processor having these inputs was derived in an attempt to investigate the optimal localization processing at this auditory level. Specifically, the higher center is considered as a maximum likelihood estimator that extracts a sound source's lateral angle and sound amplitude.

Since the LSO and AVCN provide inputs to the optimal processor, we developed accurate point process models of their unit discharge patterns. Both Poisson and non-Poisson point process models for AVCN and LSO discharges were investigated.

The point process models are defined based on interval distributions and conditional mean functions: The Poisson process is characterized by the exponential intervals and describes irregular responses; the renewal Gaussian ISI model describes a more regular process that agrees with the chopping discharge patterns of AVCN stellate cells and LSO cells; the non-renewal Gaussian ISI model approximates LSO responses even more accurately. The utility of Gaussian ISI point process in neuron discharge modeling can be justified by the mechanism of temporal integration, which is a possible, but not necessarily the unique, reason for regular neuronal responses. For example, early studies exploring the effect of afferent convergence on postsynaptic response properties demonstrated that several fibers synapsing on a postsynaptic element could result in the typical regular discharges of choppers [30].

The regularity of a renewal point process is measured by the CV of its interval distribution. A Poisson process specified by exponential intervals ($CV = 1$) can model well the input to LSO from either AVCN or MNTB; by the argument of temporal integration, the Gaussian ISI model for chopper responses has a CV of approximately $1/\sqrt{n}$ (exact for the Erlang model), where n is the number of intervals of the Poisson process accumulated to elicit an output discharge. Modeling chopper responses by a Gaussian ISI point process with $CV = 0.2$, we expect that the LSO cell produces an output given about 25 input spikes. While the ISI histogram of AVCN sustained choppers (C_S) is well modeled by Gaussian distribution with such a small CV (some data can be found in [33]), that of AVCN transient choppers (C_T) is asymmetric and has a broader mode. A CV value of 0.34 was used to separate these two response patterns of AVCN stellate cells [5]. Diversity in cell responses is also found in LSO data. The CV values reported in measurements of LSO slow chopper data [43] seldom exceed 0.4 for monaural stimulation (for example, $CV = 0.3$ in Figure 3.1), but they can be greater than 0.4 for binaural stimulation, and the interval histograms are not perfectly symmetric. We have argued that the Gaussian ISI process is capable of describing chopping data with small CVs (section 3.2.2). However, for a point

process with a CV as big as 0.4, which corresponds to integration of about 6 interspike intervals, the utility of the Gaussian ISI model is questioned by both the possibility of negative interval ($6 * 10^{-3}$) and its poor approximation to the Erlangian density. In this case, the skew of the Erlangian interval distribution with small parameter n is ignored by the Gaussian density. It should be noted that the hazard functions of LSO fast choppers may be better modeled by a Rayleigh interval distribution. Although these densities approximate the interval statistics of the data better than the Gaussian, they are too complicated to be studied analytically as models of input processes to the optimal processor. We use the Gaussian ISI model because of its simplicity and its better approximation of the data statistics than the Poisson model. Negative correlation between successive interevent intervals is considered in the non-renewal point process, which models LSO discharges more accurately. The correlation factor can be easily taken into account by simple modification of the renewal Gaussian ISI model. The first-order correlation coefficient used in our simulations, according to the measurement of the slope in the conditional mean function of LSO data, is about -0.3 .

The discharges of LSO and AVCN cells are assumed to be observed over a time interval of length T , and the total spike counts are the sole information available to the optimal processor. Empirical data of LSO tone burst responses suggest that the initial transient response of a LSO cell can last about 20 – 30ms. In our continuous tone signal localization problem, we specify the observation interval length T and the maximum discharge rate of a single LSO cell (at the azimuth angle -90° when the ILD is the maximum), so that the maximum number of LSO discharges to the optimal processor is about 32 spikes. Although localization within a shorter period of time is possible, it requires a higher LSO discharge rate for the optimal angle estimator to produce small localization error. For example, the mean spike count of a Poisson process with intensity λ over interval T is λT , and the standard deviation of the spike count is $\sqrt{\lambda T}$. Any decrease in the product of the rate and the interval

length results in a bigger CV of the spike distribution ($1/\sqrt{\lambda T}$), a more random spike count to the optimal processor, and thus a larger localization error. The existence of cell spontaneous activity, which is ignored in our study, offers another reason for using a relatively long observation window: If both the discharge rate and the observation window length are small, it becomes difficult for the higher center to distinguish between driven activity and spontaneous activity of its inputs, leading to large localization errors.

Similar arguments apply to the midline problem when LSO discharge rate is too small or zero because of contralateral inhibition. Even if the window length is large, the total number of LSO discharges available to the optimal processor is not large enough for reliable localization. Therefore, the higher center must incorporate information from some other nuclei to compensate for the lack of LSO responses. We suggested several possibilities in solving the midline problem, but there is no anatomically detailed data available to confirm or refute any of the conjectures.

Under the non-saturation assumptions on the AVCN-rate-level function $R[\cdot]$ and the LSO-rate-ILD function $f[\cdot]$, the discharge rate of an AVCN cell is a function of both sound amplitude and lateral angle, while the LSO discharge rate is modeled as a function of ILD regardless of sound amplitude. With inputs from LSO and AVCN averaged over the time period T , maximum likelihood angle estimator is derived under each LSO model. Surprisingly, AVCN discharges don't affect the angle estimate as long as the input from LSO is available to the processor, and the optimal processor retains a similar form under each LSO model. Moreover, the non-linear processing of LSO responses to extract lateral angle under each model is the same if the spike count from the LSO is not too small. Despite of the similarity in estimator form, we found that the localization performance depends strongly on the point process model of LSO responses. Specifically, the regularity of the point process has significant impact on the localization performance of the corresponding angle estimator. The more regular the point process, the smaller the bias and the standard deviation of the angle estimate. In

other words, localization accuracy and precision can be improved greatly with more regular input from LSO. Take CV as a measurement of regularity; compared with the estimation standard deviation under the Poisson model, the reduction under the renewal Gaussian ISI model at a specific azimuthal angle is by a factor approximately equal to the CV. For example, the reduction is about 0.2 in Figure 4.7, where the CV of the Gaussian is 0.2 as compared with 1 for the Poisson. By considering the correlation between successive intervals, localization performance is improved even more. However, because the correlation is not significant, we don't gain as much in localization performance as the regularity factor. These results suggest that regular discharge patterns (manifest in chopping responses) of LSO cells can give rise to improved stimulus processing by later stages in the binaural pathway.

The significance of discharge regularity in localization is demonstrated again by the result of one of our solutions to the midline problem. When both LSOs are totally inhibited and provide no input to the optimal processor, localization is still possible if the processor receives inputs from both AVCNs. Simulations show that localization accuracy and precision at the higher center using AVCN regular inputs are much better than at the LSO using AVCN irregular discharges with the same mean discharge rates. Because of the impact of the regularity difference of AVCN responses, it is clear that the higher center is not simply a replica of LSO, even if AVCNs were the only nuclei providing ascending projections.

The optimal estimator doesn't specify M , the number of convergent LSO cells with identical threshold and identical average discharge rate. We have shown that, under the LSO Poisson model, simple superposition rule exists among LSO cells, i.e. the optimal angle estimator processes the inputs from M cells (each with the same discharge rate) as if the input was from a single LSO cell with a discharge rate M times as big as that of any convergent cell. For a given observation window within the sustained portion of the responses, localization performance is closely related to the value of M : The larger M , the better the accuracy and precision of angle estimate.

According to general statistical rules of thumb, the reduction in standard deviation of angle estimate at a given azimuthal angle is predicated to be $1/\sqrt{M}$ times, which agrees with the CV reduction from one-input to M -input models. In the two-input situation, the reduction of $1/\sqrt{2}$ times is confirmed by our simulations (see the two curves under the Poisson model in Figure 4.9).

The optimal processing of neuron ensembles was also studied under the LSO Gaussian ISI model. Because the exact form of the optimal angle estimator combining the inputs from multiple LSO cells couldn't be derived, we studied the two-input processing problem numerically. The simulation results (Figures 4.3 and 4.4) implies that the optimal processing of the two inputs is not to simply superimpose them. The curvature of the iso-angle contours can not be easily fitted by any simple function (e.g. linear, multiplicative, etc.) because the curvature depends on the values of the two inputs in some non-trivial manner. This dependence suggests that the optimal processing of the convergent inputs at high discharge rate may be different from that at low discharge rate. If this dependence is true, it implies that the higher neural center should have the ability of adjusting its two-input processing strategy according to the characteristics of its inputs. Although the optimal rule of ensemble processing under the Gaussian ISI model is different from the superposition rule under the Poisson model, similar performance improvement can be obtained through processing two neuron discharges. Under the Gaussian ISI model (see the two Gaussian curves in Figure 4.9), the reduction of standard deviation due to one extra input from LSO is again approximately $1/\sqrt{2}$.

The assumption that convergence only occurs among identical neurons is not realistic because neurons with different threshold and/or different CF may be excited simultaneously. The sensitivity of the binaural auditory system to ILDs remains relatively constant across a large range of stimulus frequencies [29]; this fact suggests that the number of convergent cells may remain relatively stable across frequency. We studied the effect of convergence of two LSO cells with different thresholds, and the

localization performance results are similar to those of two same-threshold LSO cells, with great improvement over one LSO cell case. It is reasonable to expect that a larger neuron population can improve the localization performance even more significantly. However, we do expect a limit in the number of convergent cells because the higher center might be saturated by the total LSO responses at certain high discharge rate. The reduction in localization error by multi-neuron inputs processing suggests that spatial integration among input cells improves the localization capability of the higher center.

The duplex theory argues that ILD is primarily responsible for localization of high-frequency signals, and that ITD is used in localization of low-frequency ones [32]. The theoretical study of optimal localization of high-frequency signals at LSO implies that the level cue should be processed separately from the phase cue, and that level-based processing is more effective than phase-based processing [14]. Although it is reasonable to consider ILD as the most important cue in high-frequency localization at the higher center, we leave out other possible localization information conveyed in LSO responses by using only the sustained portion of cell responses. One of the prominent cues possibly used by the higher center is the highly structured chopping responses obvious in PST histograms of LSO data. A recent study [49] points out that the chopping discharge pattern can be produced by the joint effect of the deadtime and the driven process with an exponentially decaying intensity. Another important cue in LSO responses is the tightly distributed time-of-occurrence of the first spike, which accurately represents the ipsilateral stimulus onset. In contrast, we have derived the optimal angle estimator based on the simple mechanism of counting the number of spikes generated by LSO unit(s) in observation interval of length T under the sustained discharge rate condition. It is not very surprising that the optimal processor can't be adapted to non-constant discharge rate input, and that the angle estimate is biased if the stationary LSO discharge rate assumption is violated. Hence, how the

chopping information is represented and what effect the timing of initial discharges has on localization are interesting and unexplored research topics.

In summary, we have investigated, in certain aspects, the role of a higher center after LSO in binaural localization with LSO and AVCN discharges. Non-Poisson point processes were developed to model cell responses more accurately. The theoretical result that LSO encodes sufficient statistics (ILD cue) in its discharges for localization is confirmed in this study, and the non-linearity of processing LSO discharges optimally is obtained under both LSO Poisson and non-Poisson models. Our study suggests that regularity helps higher centers in localization, and that temporal and spatial integration are two mechanisms that can improve localization performance.

Appendix A

Derivation of the Optimal Angle Estimator

Take an example to show that AVCN discharges modeling doesn't affect the optimal angle estimate. Assume LSO discharges are modeled by the renewal Gaussian ISI point process and the input from AVCN is Poisson.

Assuming a linear $R[\cdot]$, the joint pmf of the two point processes is given by

$$p_{N_{lso}, N_{lp}}(\theta, A)(N_{lso}, N_{lp} | (\theta, A)) \quad (A.1)$$

$$= \left(\frac{e^{-AD(-\theta)T} (AD(-\theta)T)^{N_{lp}}}{N_{lp}!} \right) \cdot \left(Q \left[\frac{T - (N_{lso} + 1)\mu}{\sqrt{N_{lso} + 1}\sigma} \right] - Q \left[\frac{T - N_{lso}\mu}{\sqrt{N_{lso}}\sigma} \right] \right),$$

where μ and σ are defined in formula (3.23).

First, take a log of formula (A.1), we have

$$\ln p_{N_{lso}, N_{lp}}(\theta, A)(N_{lso}, N_{lp} | (\theta, A)) \quad (A.2)$$

$$= -AD(-\theta)T + N_{lp} \ln(AD(-\theta)T) - \ln N_{lp}! + \ln(Q[t_1] - Q[t_2]),$$

where

$$t_1 = \frac{T - (N_{lso} + 1)\mu}{\sqrt{N_{lso} + 1}\sigma} = \frac{abT(\frac{D(-\theta)}{D(\theta)} - 1)}{\sqrt{N_{lso} + 1}} - a\sqrt{N_{lso} + 1},$$

$$t_2 = \frac{T - N_{lso}\mu}{\sqrt{N_{lso}}\sigma} = \frac{abT(\frac{D(-\theta)}{D(\theta)} - 1)}{\sqrt{N_{lso}}} - a\sqrt{N_{lso}}.$$

Then, take the partial derivative of the log-likelihood function with respect to A , we have

$$\frac{\partial \ln p}{\partial A} = -TD(-\theta) + \frac{N_{lp}}{A}. \quad (A.3)$$

So, the maximum likelihood estimates of A and θ must satisfy

$$\hat{A}D(-\hat{\theta}) = \frac{N_{lp}}{T}. \quad (A.4)$$

Now take the partial derivative of the likelihood function in formula (A.1) with respect to θ directly, we have

$$\begin{aligned} \frac{\partial \ln p}{\partial \theta} = & \left(\frac{e^{-AD(-\theta)T} (AD(-\theta)T)^{N_{lp}}}{N_{lp}!} \right) \cdot \left(\frac{d}{d\theta} (Q[t_1] - Q[t_2]) \right) \\ & + (Q[t_1] - Q[t_2]) \cdot \left(\frac{\partial}{\partial \theta} \frac{e^{-AD(-\theta)T} (AD(-\theta)T)^{N_{lp}}}{N_{lp}!} \right). \end{aligned} \quad (\text{A.5})$$

The partial derivative in the second term of formula (A.5)

$$\begin{aligned} & \frac{\partial}{\partial \theta} \frac{e^{-AD(-\theta)T} (AD(-\theta)T)^{N_{lp}}}{N_{lp}!} \\ & = \frac{e^{-AD(-\theta)T} (AD(-\theta)T)^{N_{lp}-1}}{N_{lp}!} \frac{dD(-\theta)}{d\theta} \cdot A(N_{lp} - ATD(-\theta)). \end{aligned} \quad (\text{A.6})$$

Note that $N_{lp} - ATD(-\theta)$ explicitly appears as a product term. Because the maximum likelihood solution must satisfy formula (A.4), this term must be zero for the maximum likelihood estimates of θ and A . Combining with formula (A.5), we have

$$\frac{d}{d\theta} \left(Q \left[\frac{abT(\frac{D(-\theta)}{D(\theta)} - 1)}{\sqrt{N_{liso}} + 1} - a\sqrt{N_{liso} + 1} \right] - Q \left[\frac{abT(\frac{D(-\theta)}{D(\theta)} - 1)}{\sqrt{N_{liso}}} - a\sqrt{N_{liso}} \right] \right) \Big|_{\hat{\theta}} = 0. \quad (\text{A.7})$$

Solving equation (A.7) for $\hat{\theta}$, we have the result in formula (4.10).

For other models of inputs to the higher center from AVCN and LSO, similar structures occur in solving for maximum likelihood estimates of θ and A , and the AVCN input is always discarded in angle estimation.

Appendix B

Unimodal Two-Input Likelihood Function

In the two-input from LSO situation, we can show easily that the angle estimate depends only on the LSO inputs. The independence of the angle estimate with respect to the AVCN input is, as in the one-input case, the direct result of the special structure discussed in Appendix A. Taking advantage of this structure, the joint pmf needed to be maximized can be simplified into a function of LSO inputs only,

$$\begin{aligned}
 & p_{N_{lso1}, N_{lso2}}(\theta, A)(N_{lso1}, N_{lso2} | (\theta, A)) \\
 &= \left(Q \left[\frac{T - (N_{lso1} + 1)\mu}{\sqrt{N_{lso1} + 1}\sigma} \right] - Q \left[\frac{T - N_{lso1}\mu}{\sqrt{N_{lso1}}\sigma} \right] \right) \\
 & \quad \cdot \left(Q \left[\frac{T - (N_{lso2} + 1)\mu}{\sqrt{N_{lso2} + 1}\sigma} \right] - Q \left[\frac{T - N_{lso2}\mu}{\sqrt{N_{lso2}}\sigma} \right] \right),
 \end{aligned} \tag{B.1}$$

where μ and σ are defined in formula (3.23).

The mesh plot of the likelihood function in formula (B.1) relative to θ and $\hat{\theta}$ is shown in Figure B.1. In our simulations, LSO discharges N_{lso1} and N_{lso2} are generated by Gaussian ISI processes given a specific lateral angle θ . In seeking the numerical solution to the maximum likelihood angle estimate, we vary the value of the estimated angle within the range $[-90^\circ, 0^\circ]$ and find the angle that gives rise to the maximum value of the pmf (product of two differences of Q-functions). From Figure B.1, we find that the function being maximized has a nice single mode in $\hat{\theta}$ once the actual angle θ is fixed. This property makes it easy for simple optimization algorithms to find the global maximum of the pmf, and thus the corresponding estimated angle.

Figure B.1 The likelihood function under two-input Gaussian ISI model. For a specific sound direction θ , the function is nicely unimodal in $\hat{\theta}$.

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