An Application of Abstract Algebra to the Neural Code for Sound Localization in the Barn Owl

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Abstract

Patterns of neural firing can be viewed as a binary code with each neuron as a bit, with neurons which actively fire in response to a stimulus associated to a 1 and those which do not fire associated to a 0. In previous work, Curto et al. demonstrate that by studying the neural code as a ring, information can be recovered about the ways the regions over which the different neurons fire intersect as well as the convexity of these regions.

In this work, these ideas are applied to the system of sound localization in the owl. One of the properties of the sound used to determine its location is the interaural time difference, which is represented in the nucleus laminaris when a neuron fires in response to being stimulated by signals coming from both ears at the same time. Though the signals arrive at the same time at the neuron, it is still ambiguous by how many periods the two sound waves differ, resulting in periodic firing in the columns of the nucleus laminaris and behavioral errors in the owl's response in locating the sound. Using the concepts from neural coding theory, it is demonstrated that neural codes with a perfectly patterned periodic form do not correspond to a set of convex sets, reflecting this ambiguity. It is further shown that by introducing stochasticity into these patterns, hence introducing new codewords, the new code may have a convex realization. This suggests that the stochastic nature of neural firing may be necessary for disambiguating stimuli.

Contents

Acknowledgments

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1   Introduction

The brain is one of the most complex human organs, consisting of 100 billion neurons and 1,000 trillion synaptic connections in the human. Working in the 1950s on the giant squid axon, Hodgkin and Huxley developed a model to describe the action potential of a neuron, allowing for a strong understanding of the biophysics of the action potential. Thus, while the dynamics of neuronal firing are well understood, the ways in which these patterns of firing control our behavior and the information that these patterns convey is still not well understood.

In Shannon's development of information theory and mathematical coding theory in 1948, he introduced new ways to study the way information is stored and represented, two questions of direct relevance to the operation of the brain. Each neuron is associated with a single bit of the code, and it is the different combinations of the firing of neurons that different patterns of bits are created, forming a set of codewords, with each codeword representing a different stimulus. Information theory seeks to explain how these stimuli are represented as well as how errors are corrected, which is particularly important in a highly stochastic biological system.

The relationship between the firing of neurons and which stimuli are represented has been highly explored in the visual system. In 1959, Hubel and Wiesel demonstrated that neurons in the primary visual cortex fire at different levels depending on the angle at which a stimulus is presented, resulting in bell-shaped tuning curves as their response functions. Different neurons have different preferred angles, so the angle of a presented light bar can be inferred by which neurons are firing. In 1971, O'Keefe discovered place cells in the hippocampus. Each place cell is a neuron that fires when an animal is in a particular region in space, the cell's place field, but does not fire in other regions. Again, by analyzing which neurons are firing, the location of the animal in space can be inferred. The discoveries of both tuning curves and place cells were recognized with Nobel Prizes, highlighting the importance the scientific community places on the ability to understand how patterns of neural firing correspond to stimuli in the environment.

Another biological system in which these information theory questions of how information is presented are particularly relevant is the system of sound localization. The location of a sound course is determined by two cues, interaural time difference and interaural intensity difference. Different models have been proposed as to how each of these cues is represented in the brain with an understanding of which structures represent the information but open questions about how the information is represented and transmitted to higher level brain structures. In humans, the lateral superior olive measures interaural intensity difference. In owls, the nucleus laminaris measures interaural time difference. In this work, both of these systems are explored as neural codes using the concepts stemming from information theory to better understand how the information about the sound signal is represented and what can be learned from this representation.

2   Neural Coding Theory

The brain encodes different stimuli as patterns of neural firing, creating the neural code. Each neuron, x_i, fires over some subset, U_i of the stimulus space, the neuron's receptive field. When two neurons fire at the same time, they must be responding to a stimulus that lies in the intersection of the receptive fields of each of the neurons. In this way, different patterns of activity code for different subsets of the stimulus space based on the intersections of the neurons' receptive fields. In this way, information about the stimulus is stored in a

receptive field code. By giving the neural code the same structure as the codes studied by information theory, the mathematical concepts used to study codes can be applied to this complex biological system.

2.1 Neural Firing as a Combinatorial Code

One way to analyze neural firing patterns is by viewing them as a combinatorial code. In general, a code is a set of sequences of bits from a field, where each sequence is a codeword in the code. In the neural code, each neuron acts as a binary bit and the patterns of neural firing create the set of codewords. In response to a stimulus, neurons respond by firing at some rate. Neurons which fire above a certain firing rate are determined to be "on" and correspond to a 1 in the code. In contrast, neurons firing below this threshold are determined to be "off" and correspond to a 0 in the code. In this way, neural activity forms a binary combinatorial code.

Combinatorial codes are parameterized by their size, length, sparsity, and redundancy. The size, $|C|$, is the number of codewords. The length, n, is the number of bits in a codeword. In a binary code, each code has a Hamming weight, the number of 1's which occur in the codeword. The sparsity, s, is the average Hamming Weight over the length of the code across all codewords, and is given by $\frac{1}{|C|}\sum_{c \in C}\frac{w_h(c)}{n}$. The redundancy, ρ, is given by $1 - \frac{log_2(|C|)}{n}$ as a comparison of the number of bits in the code to the minimum number of bits that would be needed to store all of the information. Codes viewed in this framework have traditionally been the subject of information coding theory.

These parameters can be applied to the neural code. In the neural code, the length of the code is the number of neurons in a codeword, and the redundancy is a measure of the number of excess neurons compared to those needed to encode the number of stimuli. In this way, neural activity can be viewed as an abstract algebraic object.

2.2 The Neural Code as a Simplicial Complex

This neural code may also be viewed as a simplicial complex. To associate the neural code to a simplicial complex, each neuron is viewed as a point, and the subsets of neurons which give the support for each of the different codewords correspond to higher dimensional simplices. Given a code, C, define the simplicial complex associated with that code, $\Delta(C) = \{\sigma | \sigma \subset c$ for some c$\in C\}$. For example, whenever two neurons fire at the same time, an edge is drawn between them. Similarly, whenever k neurons fire together, a (k-1)-dimensional face is added to the simplicial complex. It should be observed that all of the simplices in the complex do not correspond to a codeword in C but to a subset of the support of some codeword in C.

A simplicial complex is a set of finite sets that is closed under the operation of taking non empty subsets. The homology groups, $H_q(K)$ where K is a simplicial complex, are defined by the structure of K and correspond to (q+1)-dimensional holes in K. To calculate this homology group, first consider a q-dimensional chain. The qth chain group, $C_q(K)$ is generated by the oriented q-simplexes of K. Also consider the boundary homomorphism, $\partial : C_q(K) \rightarrow C_{q-1}(K)$, where the boundary of an oriented q-simplex is determined by the sum of its (q-1)-dimensional faces. So we have, $\partial(v_0, ...v_q) = \sum_{i=0}^{\infty}(-1)^k(v_0, ..., \hat{v_k}, ...v_q)$, where $\hat{v_k}$ denotes that the vertex v_k has been deleted. Define $Z_q(K)$ to be the kernel of $\partial : C_q(K) \rightarrow C_{q-1}(K)$, the group of q-cycles. Define $B_q(K)$ to be the image of $\partial : C_{q+1}(K) \rightarrow C_q(K)$, the group of bounding q-cycles. Then the qth homology group is given by, $H_q(K) = Z_q(K) \backslash B_q(K)$. In this way, viewing the code as a simplicial complex allows topological properties of the neural code to be explored.

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2.3   The Neural Code as a Ring

The code may also be viewed from an algebraic perspective as a ring. The binary code, C, is a subset of $\{0,1\}^n$. Let each of the neurons be an indeterminant over a binary field. The neural ideal is defined by the set of functions, $I = \{f \in \mathbf{F}_2[x_1,...,x_n]|f(c) = 0$ for all $c \in C\}$. Then the neural ring corresponding to the code is defined by, $R = \mathbf{F}_2[x_1,...,x_n]/I$. The generators of this neural ideal give combinatorial information about the structure of the ring, which corresponds to combinatorial information about the receptive field structure of the neurons as explained in chapter 3.

2.4   Questions Arising from the Neural Code

Viewing the neural code in these two different ways gives rise to several questions about the structure of the neural code, including the error correction capabilities and the information that can be conveyed by the code.

2.4.1   Error Correction Capabilities

For a code to be useful in transmitting information, it must be able to detect and possibly correct errors that occur during the process of transmission. This is especially true in the case of the neural code since the firing rate of any individual neuron is subject to large variability even in response to the same stimulus. It is of interest to determine how well the code corresponding to a neural system is able to correct errors and the impact that this decoding process has on the system's perception of the stimuli.

2.4.2   Information Stored by the Neural Code

While the codewords are patterns of firing that result from the presentation of a single stimulus, the entire code is a collection of patterns that can result from any stimulus in the stimulus space. This observation raises the question of what information can be learned from the structure of the code itself. In particular, it has been shown that the structure of the receptive fields of the neurons can be recovered from knowledge of the code (Curto et al., 2013).

Two well studied instances of receptive fields are tuning curves and place fields. Tuning curves refer to the fact that neurons have a maximum firing rate when a light bar is presented at a preferred angle. This results in a bell shaped response curve when the neuron is presented with a light bar at varying angles. For a specific angle, the set of neurons which fire in response to that angle form the codeword for that angle. This results in a 1D RF code, since the code represents the single dimension of the angle of the stimulus. Place fields refer to the fact that neurons fire in response to the animal being in a specific region in space. For a point in space, the set of neurons which fire in response to that location form the codeword for that point. This results in a 2D RF code, since the information represented is the animal's position in a 2-dimensional plane. In both cases, the structure of the receptive field space refers to the structure of intersections of the various receptive fields of the neurons. It is the information about these intersections that is needed to interpret what stimuli are represented by different patterns of neural firing.

3   Error Correction and Maximum Likelihood Decoding

Previous work based on information theory has argued that the neural code should try to maximize the stored information, but this contradicts biological findings which show neu-

ral activity to be highly redundant. It has been hypothesized that this redundancy allows for greater error correcting capabilities. In their work, Curto et al. (2013) demonstrate that in comparison to random codes, receptive field (RF) codes have poor error correcting capabilities. However, the error correcting capabilities of the RF codes are similar to the optimal random codes when a tolerance to error is introduced. This reflects the fact that the redundancy within neural codes allows the code to better represent relationships between stimuli.

Curto et al. compared the performance of randomly generated codes to RF codes. Shannon's work suggests that random codes will have optimal error correcting capabilities. To understand the error correcting capability of RF codes, their performance is compared to randomly generated codes of the same size, length, and sparsity. These random codes were generated in two different ways. The first method is to create shuffled codes, where each codeword from the RF code is reordered using a different randomly generated permutation. The second method is to use constant weight codes. These codes are constructed by first calculating the average weight of the RF code and then generating random subsets of that weight until the code matches the RF code in size.

Curto et al. then carried out simulations of the encoding and decoding process to test the error correction capabilities of the three codes. In the encoding and decoding process, as shown in Figure 1, a point in the stimulus space is first encoded according to an encoding map. This encoding then passes through the noisy binary asymmetric channel (BAC), resulting in a received pattern. Next, through decoding, the brain interprets this pattern as one of the codewords in the neural code. Finally, applying the inverse of the encoding map, an estimate of the stimulus is produced.

In this model, the noise introduced by the BAC reflects the biological noise in the encoding process in addition to the noise in the transmission of the encoded word in the brain. The binary asymmetric channel is governed by two parameters, p, which is the probability that a 0 is flipped to a 1, and q, which is the probability that a 1 is flipped to a 0. The parameterization of the channel makes several assumptions. First, it is assumed that $p, q < \frac{1}{2}$ because faithful transmission should be more likely than errors. Second, it is assumed $p \leq q$ because it is more likely for a neuron not to fire than to misfire. Third, it is assumed that $p < s$ and $s < \frac{1}{2}$ because the code is sparse and this ensures an appropriate firing level. Finally, it is assumed that the BAC acts on each bit of the encoded stimulus independently. The series of independent bit flips then forms the output of the BAC, the received word, which must then be decoded.

There are two possible schemes for the decoder. The first is the maximum a posteriori (MAP) decoder. The MAP decoder is always the optimal decoder and returns, $c' = argmax_{c \in C}\mathbf{P}(sent = c | rec = r)$. However, this requires knowledge of the probability distribution of the stimuli, making it difficult to implement. For this reason, this study used the maximum likelihood (ML) decoder. The ML decoder is used instead of the MAP decoder because the most likely codeword is determined by maximizing the expression, $c' = argmax_{c \in C}\mathbf{P}(rec = r | sent = c) = argmax_c(c \cdot r) \ln \frac{(1-p)(1-q)}{pq} - w_H(c) \ln \frac{(1-p)}{q}$ This is equivalent to maximizing the dot product of r and c with a penalty term for adding additional 1's.

Curto et al. compared the accuracy of the decoding produced by the ML decoder when using the RF codes to each of the randomly generated codes. When correct decoding was defined as returning the originally sent codeword, the random codes corrected errors optimally. However, the RF codes consistently performed below this level. This can be explained because the high redundancy and low sparsity allows for codewords to be spaced far apart as
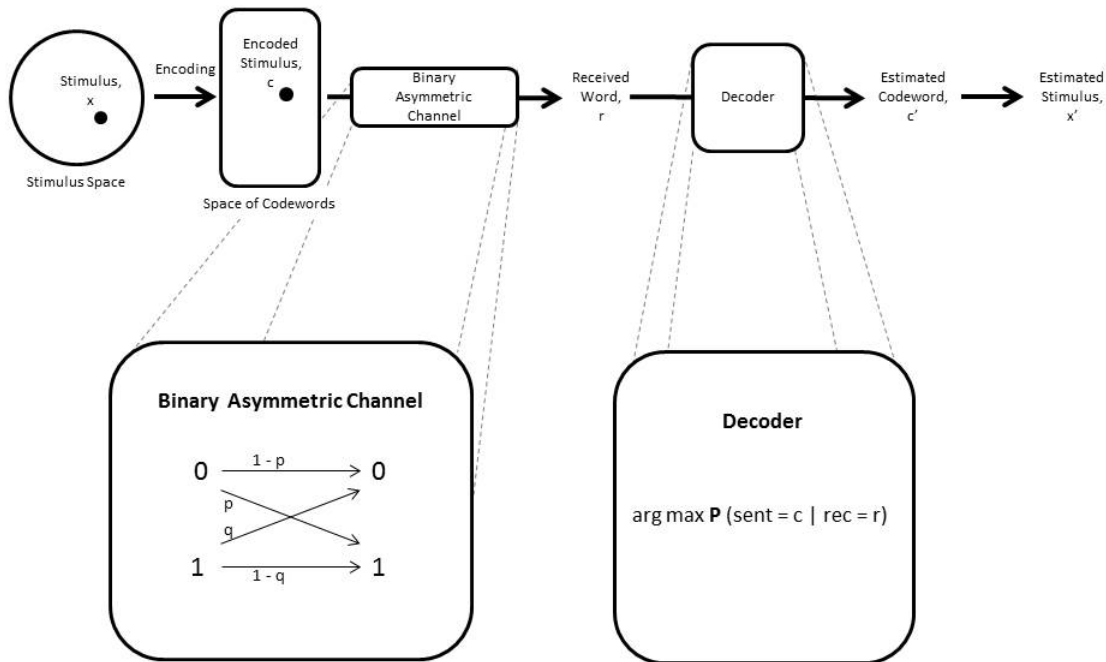
Figure 1: The Encoding and Decoding Process

occurs in the randomized codes, but in the case of the RF codes, the codewords are still close together, often with Hamming distance of 1, resulting in poor error correction. When correct decoding was defined as returning a codeword corresponding to a stimulus within some error tolerance, the performance of the RF codes became similar to the randomized codes. This result can be explained by the fact that Hamming distance and stimulus distance are correlated for the RF codes but not for the randomized codes. For the RF codes, Hamming distance is also correlated to d_{ML}, a measure of the similarity between two codewords from the perspective of the ML decoder. The error tolerance at which RF codes perform about the same as the randomized codes is similar to the level of stimulus discrimination that has been observed biologically.

3.1 A General Example of Maximum Likelihood Decoding

We now present an example of the process of maximum likelihood decoding in the case of a receptive field code. Consider a collection of five neurons with receptive fields arranged as in Figure 2. Each of the neurons (denoted 1-5) has a circular region in which it actively fires. Each region (denoted A-M) in the space has a different codeword which corresponds to it.

This corresponds to the following codewords:
C = {A:(10000), B:(11000), C:(01000), D:(10001), E:(11001), F:(01001), G:(00001), H:(00011), I:(01011), J:(01010), K:(00010), L:(00110), M:(00100)} The code has the following parame-
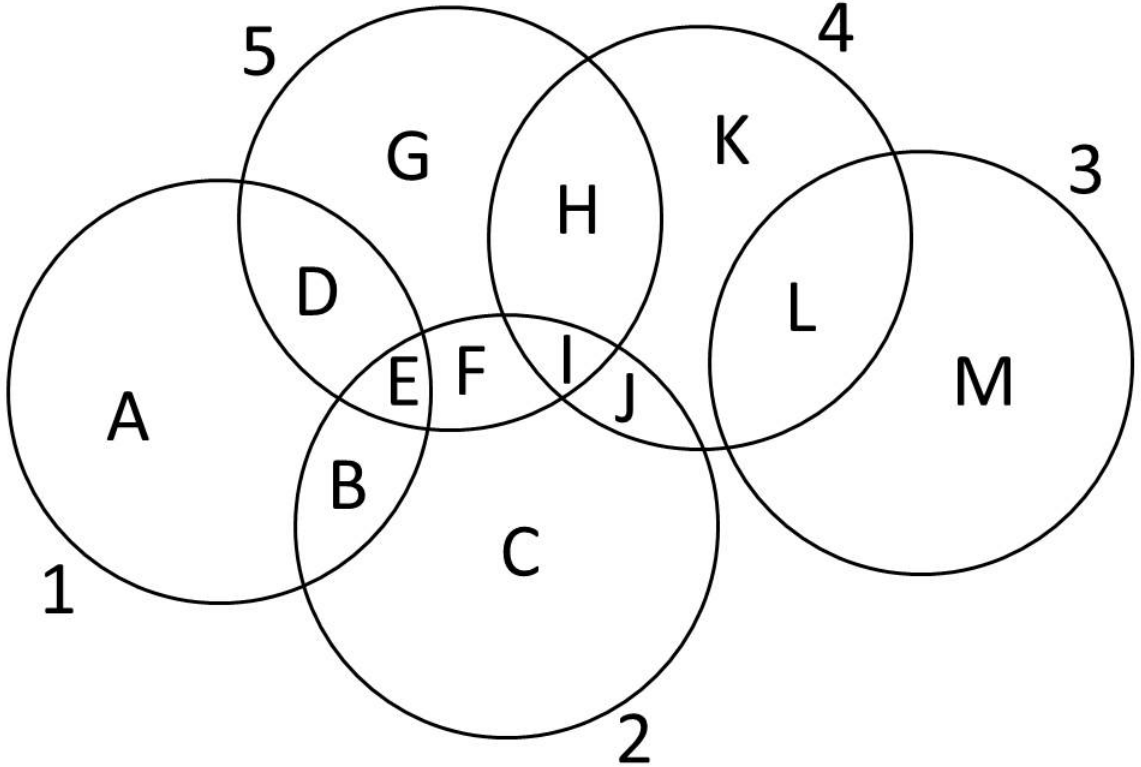
Figure 2: The receptive field layout in the example of ML decoding

ters:

- size $= 13$, there are 13 different regions

- length $= 5$, there are 5 different neurons

- sparsity $= \frac{1}{|C|} \sum_{c \in C} \frac{w_h(c)}{n} = \frac{1}{13} * \frac{24}{5} = 0.369$

- redundancy $= 1 - \frac{log_2(|C|)}{n} = .2599$

Recall that ML decoding seeks the codeword which maximizes,

c' $= \arg \max_{c \in C} \mathbf{P}(rec = r | sent = c) = argmax_c(c \cdot r) \ln \frac{(1-p)(1-q)}{pq} - w_H(c) \ln \frac{(1-p)}{q}$

Call this equation ML(c).

By assumption, $p \leq q$ and $p < s$. For this example, consider the case where $q = \frac{1}{3}$ and $p = \frac{1}{6}$. So we want the codeword which maximizes, $argmax_c(c \cdot r) \ln 10 - w_H(c) \ln 2.5$.

First, we consider an example of accurate error correction. Consider a stimulus from region L. The encoding map gives c $= (00110)$. Assume due to the noise of the encoding process, one of the neurons misfires and the received codeword is r $= (10110)$. We calculate

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ML(c) for each $c \in C$.

$\{$ML(A) $= \ln 10 - \ln 2.5$, ML(B) $= \ln 10 - 2 * \ln 2.5$, ML(C) $= 0 - \ln 2.5$, ML(D) $= \ln 10 - 2 * \ln 2.5$, ML(E) $= \ln 10 - 3 * \ln 2.5$, ML(F) $= 0 - 2 * \ln 2.5$, ML(G) $= 0 - \ln 2.5$, ML(H) $= \ln 10 - 2 * \ln 2.5$, ML(I) $= \ln 10 - 3 * \ln 2.5$, ML(J)$= \ln 10 - 2 * \ln 2.5$, ML(K) $= \ln 10 - \ln 2.5$, **ML(L)** $= 2 * \ln 10 - 2 * \ln 2.5$, ML(M) $= \ln 10 - \ln 2.5\}$

This correctly results in the estimate of the stimulus as region L.

Now, we consider an example of inaccurate error correction. Again, consider a stimulus from region L. The encoding map gives c $=$ (00110). Assume due to the noise of the encoding process, one of the neurons fails to fire and the received codeword is r $=$ (00100). We calculate ML(c) for each $c \in C$.

$\{$ML(A) $= 0 - \ln 2.5$, ML(B) $= 0 - 2 * \ln 2.5$, ML(C) $= 0 - \ln 2.5$, ML(D) $= 0 - 2 * \ln 2.5$, ML(E) $= 0 - 3 * \ln 2.5$, ML(F) $= 0 - 2 * \ln 2.5$, ML(G) $= 0 - \ln 2.5$, ML(H) $= 0 - 2 * \ln 2.5$, ML(I) $= \ln 10 - 3 * \ln 2.5$, ML(J)$= 0 - 2 * \ln 2.5$, ML(K) $= 0 - \ln 2.5$, ML(L) $= \ln 10 - 2 * \ln 2.5$, **ML(M)** $= \ln 10 - \ln 2.5\}$

This results in the estimate of the stimulus as region M as opposed to region L. Note that while not exact error correction, the estimated stimulus, M, is still close to the original stimulus, L, in terms of distance. Additionally, note that the Hamming distance between the codewords, the number of bits where the two codewords differ, for L and M is 1, making them likely to be confused in the decoding process.

4   Receptive Field Structure

When the neural code is viewed as a ring, there is an associated neural ideal, given by $\{0,1\}^n \backslash C$. In their work, Curto et al. develop an algorithm which allows the neural ideal to be expressed in a canonical form. From this canonical form, a description of the receptive field structure can be extracted. The activity of neural populations has previously been studied as a stimulus-response function. This approach ignores the fact that the brain does not necessarily know the encoding map but, instead, needs to be able to infer properties of the stimulus space from firing patterns. Through their work, Curto et al. address this by analyzing what information can be extracted from the knowledge of the code itself.

The structure of the receptive field space is one of the properties that can be extracted from knowledge only of the code and the assumption that the receptive field of each neuron is convex. Viewing the ideal as giving relationships among the receptive fields, the ideal can also be described by $I_U = < \{x_\sigma \prod_{I \in} (1 - x_i) | U_\sigma \subset \bigcup_{i \in} U_i >$. There are four different types of relations that can appear as generators for the ideal:

1. Boolean relations: $x_i(1 - x_i)$, which are necessary in $\mathbf{F}_2$ so does not provide information about the RF structure. It corresponds to $U_i \subset U_i$

2. Type 1 Relations: x_σ, which corresponds to $U_\sigma = \emptyset$

3. Type 2 Relations: $x_\sigma \prod_{i \in \tau} (1 - x_i)$ where $\sigma, \tau \neq \emptyset$, $\sigma \cap \tau = \emptyset$, $U_\sigma \neq \emptyset$, $\bigcup_{i \in \tau} U_i \neq X$ gives $U_\sigma \subset \bigcup_{i \in \tau} U_i$

4. Type 3 Relations: $\prod_{i \in \tau} (1 - x_i)$ corresponds to $X \subset \bigcup_{i \in \tau} U_i$

Curto et al. develop an algorithm which shows it is possible to express the generators of the ideal in a canonical form as one of these types of relations, allowing the RF structure to be read directly from the generators of the neural ideal.

4.1 A General Example

Consider a collection of 5 neurons, labeled 1 to 5, arranged in a ring as in Figure 3. This creates 10 different regions with unique codewords corresponding to each. As an example, we pose the question of whether the hole in the center of the ring can be detected from the neural code.
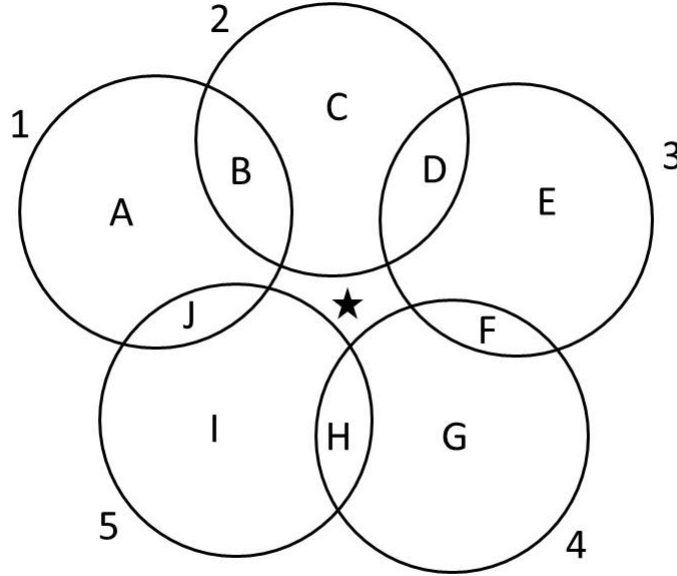
Figure 3: The layout of the receptive fields in the example of detecting the layout of receptive field space

First, we associate each region in the receptive field space with a codeword, based on which neurons are actively firing over this region, creating an encoding map. This corresponds to the following set of codewords: {A=(10000), B=(11000), C=(01000), D=(01100), E=(00100), F=(00110), G=(00010), H=(00011), I=(00001), J=(10001)}.

Knowing the code, we are able to reconstruct the receptive field space. From the codeword corresponding to region A, (10000), we know that there is some part of the receptive field of neuron 1 which does not intersect with any other neuron. Similarly, from C, (01000), we know that there is some part of the receptive field of neuron 2 which does not intersect with any other neuron. From B, (11000), we know that there is some part of the receptive field of neuron 1 which intersects the receptive field of neuron 2. Using just these three codewords, we now know the following about the receptive field structure:
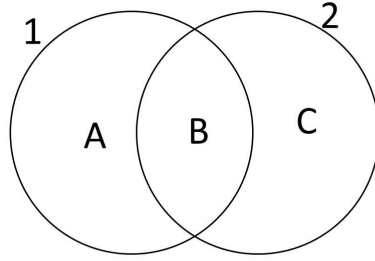
Continuing to use the codewords to extract more information about the structure, D, (01100), reveals that there is some part of the receptive field of neuron 3 that intersects with neuron 2. From E, (00100), there is some part of the receptive field of neuron 3 which does not intersect with any other neuron. The pattern, (10100), is not a codeword, so the receptive fields of neurons 1 and 3 do not intersect. We now know the following:
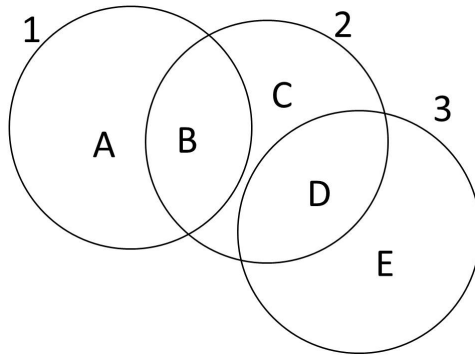
Continuing in this manner, we are able to reconstruct the entire structure of the receptive field space. Curto et al. demonstrate that this could have been done algorithmically using the neural ideal. They show that, from the canonical form of the neural ideal, the structure of the receptive field space can be determined, including not only the intersection of receptive fields but also which receptive fields are subsets of other receptive fields.

4.2 Algorithm for Finding the Canonical Form of the Neural Ideal

Curto et al. present the following algorithm for finding the canoncial form of the neural ideal starting from the neural code. The resulting canonical form is generated entirely by pseudo-monomials, where a pseudo-monomial is a function of the form $\prod_{i\in\sigma} x_i \prod_{j\in\tau} (1-x_j)$ where $\sigma \cap \tau = \emptyset$. A pseudo-monomial f is minimal if there is no g in the ideal such that f=hg for some h in the field. The canonical form of the neural ideal J is given by $J =< f_1, ..., f_m >$, where $CF(J) = \{f_1, ..., f_m\}$ is the set of all minimal pseudomonomials in J. Curto et al. observe that CF(J) is unique for any J and CF(J) may not be a minimal set of generators for J. Writing J in the canonical form such that all the generators are pseudo-monomial ideals allows the different RF relationships to be read directly from the canonical form. Additionally, this canonical form imposes minimal relationships, so there are no lower order intersections than the ones read from the canonical form.

Beginning with just the code, the algorithm for finding the canonical form that allows the RF structure to be determined is as follows:

1. Use the code to compute $J_C =< \{p_v | v \notin C\} >$, where p_v is a pseudo-monomial.

2. Find the primary decomposition of $J_C = \bigcap_{a \in A} p_a$ where $p_a =< \{x_i - a_i | a_i \neq *\} >=< \{x_i | a_i = 0\}, \{1 - x_j | a_j = 1\} >$

3. Any pseudo-monomial f in J_C must be a multiple of one of the linear generators of p_a. Compute $M(J_C) = \{\prod_{a \in A} g_a | g_a = x_i - a_i \, for \, some \, a_i \neq *\}$. This is a set of polynomials, one from each of the ideals in the primary decomposition.

4. Reduce the elements which are not pseudo-monomials by imposing the binomial relations.

5. Remove any elements that are multiples of lower degree polynomials.

This process results in the canonical form of the ideal. From this canonical form, the RF structure can be read off.

In order for this process to be successful, there must also be a method for determining the primary decomposition of J_C. In their work, Curto et al. also develop an algorithm for this process, which begins with a set of generators for the neural ideal and outputs the primary decomposition of the ideal. The steps of the algorithm are as follows:

1. Initialization: Remove any generators of J which are multiples of other generators. Initialize $D = J$ and $P = \emptyset$.

2. Splitting: For each $I \in D$, choose $z_i \in \{x_i, 1 - x_i\}$. Define $D_I = \{< I, z_{i_1} >, ... < I, z_{i_m} >\}$, so $I = \bigcap_{K \in D_I} K$.

3. Reduction: Reduce each D_I by setting each generator of I, z_i, equal to zero. Eliminate 0 terms and multiples of other generators. If there is a 1 generator, eliminate $< I, z_i >$ since this implies I is not proper.

4. Remove any D_I which are the same, and set $D = \bigcup D_I$. If $I \in D_I$ has only linear generators, it is prime, so should be moved to the set of ideals to be included in the primary decomposition.

5. Repeat until $D = \emptyset$.

6. Output: Remove any ideals in P which have the same generators as or are contained in another ideal in P.

Through these two algorithms, the neural ideal can be represented in a canonical form which allows for the receptive field structure to be obtained from the generators of the ideal using the three possible types of relations.

5   Receptive Field Structure and Convexity

A receptive field code is convex if each of the receptive fields, U_i is a convex set. Without the restriction that the RF code be convex, any code can be realized as an RF code by defining U_i as the union of the neighborhoods of each point where the neuron fires. However, not every code can be realized as a convex RF code because of the geometric and topological constraints imposed by convexity.

Recall that the nerve of a finite collection of convex open sets $\{U_i\}$ contains a subset of $[n]$ if and only if the intersection of the corresponding U_i is nonempty. This definition allows us to apply the Nerve Theorem, which states that the homotopy type of a union of a finite number of convex sets is the same as the homotopy type of the nerve of the cover, which implies the sets have the same homology groups. In relation to the neural code, each neuron's receptive field is associated with an open set and a simplicial complex is formed from the subsets of neurons which give the support for the different codewords. The nerve of the cover of the receptive fields is the simplicial complex associated with the code. In this way, each neuron corresponds to a vertex and edges are drawn between neurons when their receptive fields intersect. The Nerve Theorem then puts constraints on the spatial layout of the convex receptive fields. The Nerve Theorem can be applied to convex receptive fields because the intersections of convex receptive fields are contractible. In the case of nonconvex fields, the Nerve Theorem no longer applies.

The results of Curto et al. (2015) give a condition for when a code does not have a convex realization based on the results of the Nerve Theorem. Given a code, C, define the simplicial complex associated with that code, $\Delta(C) = \{\sigma | \sigma \subset c \text{ for some } c \in C\}$. Recall the definition of the link of a simplex in the simplicial complex, $Lk_\sigma(\Delta) = \{\omega \in \Delta | \sigma \cap \omega = \emptyset \text{ and } \sigma \cup \omega \in \Delta\}$. Each of the neurons in the code is associated with a receptive field, U_i, and these receptive fields give a covering of the space. A good cover is a cover such that the intersection of any collection of these open sets U_i is contractible. The Nerve Lemma gives the result that if the collection of open sets forms a good cover, then the covered space and the nerve of the open sets are homotopy equivalent. Now define a local obstruction as a case where the combinatorial data stored in the code results in a violation of the Nerve Lemma if the sets were to be realized convexly. If a code has no local obstructions, then it is locally good. Using these definitions, Curto et al. prove that for a code to be convex it must also be locally good.

Curto et al. also derive conditions that are equivalent to a local obstruction. They prove that a code is locally good if and only if for every simplex in $\Delta(C)$ that has a non-contractible link that simplex is included in the code. Thus, there is a set of mandatory codewords that must be included in the code for it to be convex, $M(\Delta) = \{\sigma \in \Delta | Lk_\sigma(\Delta) \text{ is non-contractible}\}$. By the relationship between the link of a simplex and the nerve of a cover, this condition is equivalent to $U_\sigma \subset \cup_{i \in \tau} U_i$ with $\sigma \cap \tau = \emptyset$ and the nerve of the cover $\{U_i\}_{i \in \tau}$ is non-contractible. They use these results to further derive more conditions for codes on four or fewer neurons, including a complete analysis of all possible simplicial complexes on four neurons and the corresponding mandatory codewords for these complexes. Thus, Curto et al. derive a set of necessary conditions for a code to be convex, but they have yet to prove that these conditions are sufficient and instead pose the question of what non-local obstructions can arise to convexity.

5.1 Consideration of Nonconvex Receptive Fields

One of the key assumptions by Curto et al. is that the receptive fields of each neuron be convex. As explained previously, without this restriction, any code can be realized as an RF code. The problems resulting from nonconvex neural codes are not limited to the fact that any code can be realized as an RF code, but also create the potential for nontrivial second homology groups arising from a planar configuration of receptive fields.

We consider several cases where where a configuration of nonconvex receptive fields results in the failure of the Nerve Theorem. Consider the case where one receptive field is an anulus and the other is a disc, intersecting as shown in Figure 4. The nerve of the

complex is an edge, so the first homology group of the nerve is 0. In contrast, the first homology group of the union is $\mathbb{Z}$ because the anulus contains a two dimensional hole.
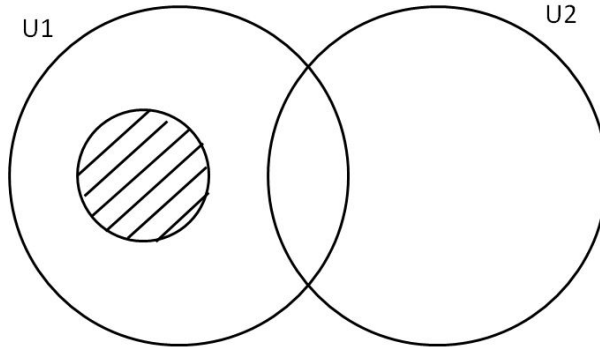
Figure 4: U_1 is an anulus, so nonconvex

Now consider the case where one of the receptive fields is disconnected as shown in Figure 5. The union has nontrivial H_0 because it is not connected. In contrast, the nerve again is just an edge so is connected and has trivial H_0.
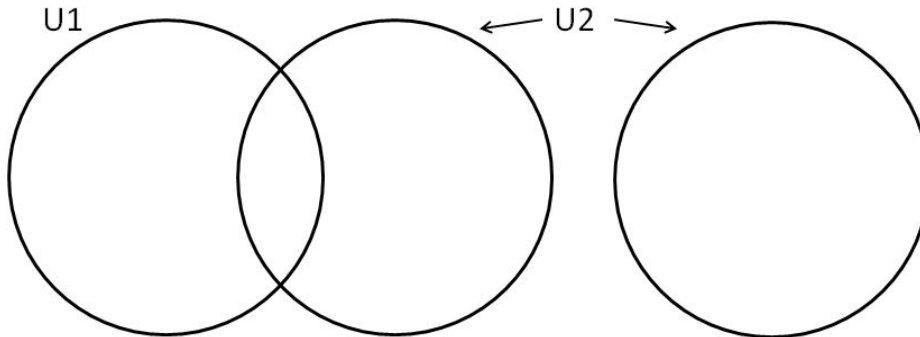
Figure 5: U_2 is a disconnected set, so nonconvex

Another potential problem that can arise from the case of nonconvex receptive fields is that nontrivial H_2 can arise from a planar configuration of receptive fields. A nontrivial H_2 group results from closed, hollow tetrahedra. The faces of the tetrahedron correspond to intersections of three receptive fields. So we want to find a configuration of four receptive fields such that every subset of 3 receptive fields intersects but the intersection of the four receptive fields is empty.

If one of the receptive fields is allowed to be disconnected, this can be accomplished by the following configuration:
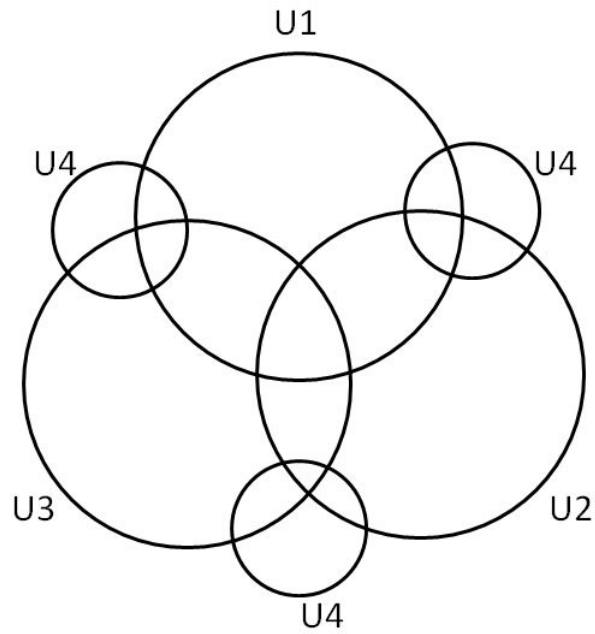
This disconnected field could be connected so that U_4 is homeomorphic to an anulus in the following configuration. In addition to nontrivial H_2, this configuration also has nontrivial H_1.
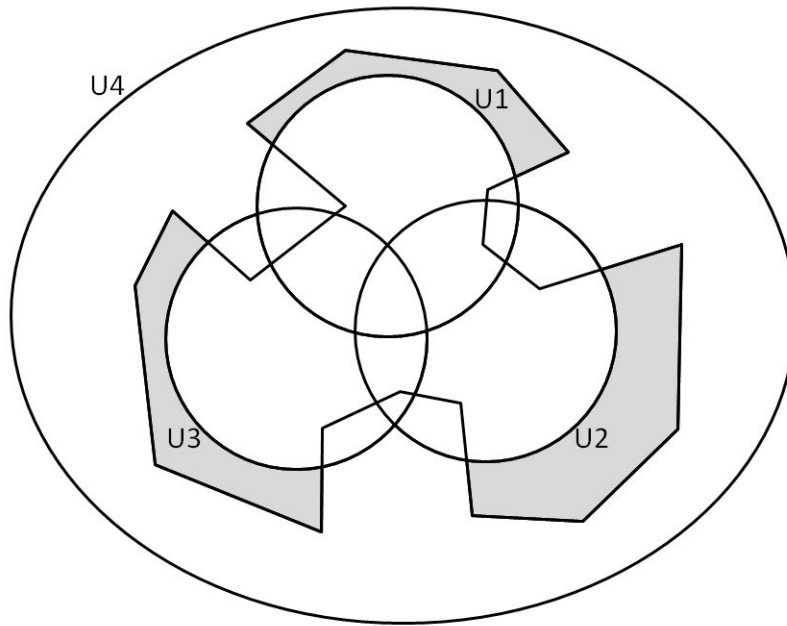
It is also possible to have a nontrivial H_2 with trivial H_1. Consider the following configuration:
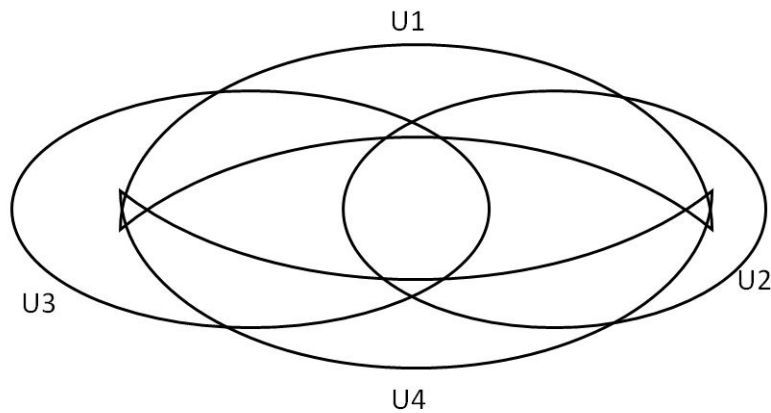
These cases illustrate the importance of the assumption that receptive fields be convex and the question of when a code can be realized convexly.

6   Neural Coding Theory and The Lateral Superior Olive

Viewing the code as a combinatorial code, with an associated simplicial complex, or with an associated ideal gives information about the neural system creating the code, both its error correction capability and information about the receptive fields of its neurons. This raises the question of what biological information may is reflected by applying these mathematical concepts to biological systems. The first system we consider is the lateral superior olive, the brain structure which represents interaural intensity differences of sound stimuli.

6.1 The Biology of the Lateral Superior Olive

Biologists have observed that animals are able to calculate the azimuthal position of an object based on the difference in intensity and time delay in sound waves to each ear. The Jeffress Model explains the calculation of interaural time differences, which is performed by the medial superior olive using delay lines. Studies have shown that the lateral superior olive, which receives excitatory input from the ipsilateral anteroventral cochlear nucleus (AVCN) and inhibitory input from the contralateral medial temporal nucleus of the trapezoid body (MNTB), codes for interaural intensity differences.

Studies of the LSO demonstrate several properties of the response of the LSO to different auditory stimuli. Regarding structural organization, the neurons of the auditory system are generally organized spatially by preferred frequency, so it is possible to consider a single column of isofrequency cells. In mammals, including cats, gerbils, and bats, the cells of a column of the LSO fire in a burst followed by a steady output. More importantly, the steady firing of the LSO corresponds to interaural intensity differences, where the response is independent of the overall sound intensity. Reed and Blum (1990) developed a model of an LSO column which captures this behavior.

6.2 A Model of the Lateral Superior Olive Operation

The model of Reed and Blum captures the reponse of the LSO as a result of the excitatory input from the AVCN and inhibitory input from the MNTB. In their model, it is assumed that the output of each cochlear nucleus is dependent on the intensity of the sound, where firing rate increases to saturation with increasing intensity. The output of a neuron in the cochlear nucleus is given by, $S = B + V[\frac{I-T_i}{K_i+I-T_i}]$ for $I > T_i$, where B is the base firing rate, I is the sound intensity, T_i is the threshold, and K_i is the intensity level at half saturation. It is further assumed that each neuron projects onto the LSO on the basis of its intensity threshold. Lower threshold neurons send excitatory connections to the bottom of the LSO column, and the threshold of the neurons increases moving up the column. The same organization but with opposite orientation is assumed for the inhibitory connections for the MNTB. The output firing of a cell in the LSO has the same form as the output of the neurons in the cochlear nucleus and is given by $S = B + V[\frac{D_i-T_i}{K_i+D_i-T_i}]$, where D_i is the difference between the excitatory and inhibitory inputs to the ith neuron.

It was first assumed that each neuron in the cochlear nucleus makes the same number of connections to the LSO, centered around a target cell. This organization results in a model where the excitation to the cells in the LSO decreases moving up in the column corresponding to the increased threshold of the neurons in the cochlear nucleus while the inhibition to the cells in the LSO increases corresponding to the decreased threshold of the neurons in the MNTB. The LSO cells fire only when the excitatory input is greater than the inhibitory input. At some point along the column, the excitatory and inhibitory input curves intersect, resulting in a break in the firing of the LSO. When the intensity to the contralateral ear is increased, this position moves down the column, and the opposite is true when intensity is increased. The position in the LSO where the break in firing occurs varies linearly with the interaural intensity difference, but independently of the absolute sound intensity.

The model was further refined to account for the varied structure which naturally arise in biological systems by developing a scheme of stochastic connections as opposed to a model with a fixed pattern of connections. In one scheme, each neuron in the cochlear nucleus and MNTB makes a fixed number of connections to the LSO. The location of the connection is pulled from a Gaussian distribution with mean at the target cell. This scheme results in very

irregular curves for the levels of excitation and inhibition to the cells of the LSO, resulting in high variability for the location where the LSO ceases to fire, regardless of the value chosen for the standard deviation. The high variability results because the number of connections to an area of the column varies along the column. In a second trophic scheme, each cell in the LSO has a fixed number of synapses to it. Each synapse is chosen by selecting a point in the Gaussian distribution centered at the target cell and making a connection with the neuron whose target is closest to the point. This results in regular curves for the levels of excitation and inhibition.

In summary, the model uses three key assumptions concerning neuroanatomy to explain how the lateral superior olive is able to code for azimuthal location on the basis of interaural intensity differences. First, it is assumed that the information is processed in a column of the LSO, which receives excitatory input from the AVCN and inhibitory input from the MNTB. Second, it is assumed that the synapses between the LSO and the AVCN as well as between the LSO and MNTB are distributed based on threshold. Third, it is assumed that the AVCN column is organized based on increasing threshold from the bottom to the top of the column, while the MNTB is organized with increasing threshold from the top to the bottom of the column. Based on these assumptions, the results of the model demonstrate a linear relationship between the point where the LSO ceases firing and the interaural intensity difference, despite the fact that the neurons are modelled with nonlinear response curves. Furthermore, the point where the LSO ceases firing is independent of the absolute sound intensity. Consequently, these results suggest that the number of cells in the LSO column directly relates to the degree of precision in calculating azimuthal position. Additionally, the model is robust to parameter variation but also demonstrates the importance of the trophic principle in which synaptic connections are guided by the LSO in order for this robustness to be possible.

6.3   The Neural Code in the Lateral Superior Olive

The model by Reed and Blum demonstrates that the neurons in the LSO column fire up to a certain crossover point where the inhibition exceeds the excitation. In this way, all the neurons below this point actively fire and all the neurons above this point do not fire. Thus, we are able to associate the firing response of the LSO with a neural code.

Consider an LSO column consisting of n neurons. So the firing patterns of the LSO are of the form $(1...1_j 0_{j+1}...0_n)$ for $0 \leq j \leq n$. This set of firing patterns forms a set of codewords. Viewing this from the perspective of neural coding theory, we are able to identify the parameters of the code. The size of the code is given by, $|C| = n + 1$. The length of the code is n. The sparsity is given by, $s = \frac{1}{|C|} \sum_{c \in C} \frac{w_h(c)}{n} = \frac{1}{(n+1)n} \sum_{c \in C} w_h(c) = \frac{1}{(n+1)n} \sum_{k=0}^{n} k = \frac{1}{n(n+1)} \frac{n(n+1)}{2} = \frac{1}{2}$. The redundancy is given by, $p = 1 - \frac{log_2(|C|)}{n} = 1 - \frac{log_2(n+1)}{n}$.

6.4   Maximum Likelihood Decoding in the Lateral Superior Olive

We now consider how the principles of error correction apply to the LSO. Assume that the correct codeword is given by $(1...1_j 0_{j+1}...0_n)$. We want to consider the decoding of the possible received words, where decoding is accomplished by the maximum likelihood method proposed by Curto et al. The decoding, c', of a received word, r, is given by $c' = argmax_c(c \cdot r)ln\frac{(1-p)(1-q)}{pq} - w_h(c)ln\frac{(1-p)}{q}$. Since $p \leq q \leq \frac{1}{2}$, let $ln\frac{(1-p)(1-q)}{pq} \geq ln\frac{(1-p)}{q}$. Let $x = ln\frac{(1-p)(1-q)}{pq}$ and $y = ln\frac{(1-p)}{q}$. Let $f(c) = (c \cdot r)x - w_h(c)y$. We want to find c' to maximize f. Let c_m denote the codeword $(1...1_m 0_{m+1}...0_n)$. Consider the following cases:

Case 1: $r = (1...1_j0_{j+1}....0_n)$
The received word is the correct codeword. For $m < j$, we have $f(c_m) = mx - my < jx - jy = f(c_j)$. For $m > j$, we have $f(c_m) = jx - my < jx - jy = f(c_j)$. Therefore, maximum likelihood decoding returns c_j. Thus, the decoding is correct.

Case 2: $r = (1...1_{k-1}0_k1_{k+1}...1_j0_{j+1}...0_n)$
This pattern of firing would occur if extra inhibition was sent from the MNTB to the kth neuron or if insufficient excitation was sent from the CN to the kth neuron, preventing it from firing. Consider the possible choices for c'. For $m < k$, $f(c_m) = mx - my = m(x-y) < (k-1)(x-y) < f(c_{k-1})$. For m=k, $f(c_k) = (k-1)x - ky < (k-1)(x-y) < f(c_{k-1})$ and $f(c_k) = (k-1)x - ky < kx - (k+1)y = f(c_{k+1})$. For $k < m < j$, we have $(m-1)x - my < (j-1)x - jy = f(c_j)$. For $m > j$, we have $(j-1)x - my < (j-1)x - jy = f(c_j)$. So there are two possible choices for c', c_{k-1} and c_j. To determine c', we compare $(k-1)x - (k-1)y$ and $(j-1)x - jy$. We have $(j-1)x - jy - ((k-1)x - (k-1)y) = (j-k)x - (j-k+1)y$. So if $(j-k)x - (j-k+1)y > 0$, the method returns c_j and if $(j-k)x - (j-k+1)y < 0$, the method returns c_{k-1}.

Case 3: $r = (1....1_j0_{j+1}...0_{k-1}1_k0_{k=1}....0_n)$
This pattern of firing would occur if extra excitation was sent from the CN to the kth neuron or if insufficient inhibition from the MNTB was sent to the kth neuron, allowing it to fire. Consider the possible choices for c'. For $m < j$, $f(c_m) = mx - my = m(x-y) < j(x-y) < f(c_j)$. For $j < m < k$, $f(c_m) = jx - my < jx - jy = f(c_j)$. For $m > k$, we have $f(c_m) = kx - my < kx - ky = f(c_k)$. So there are two possible choices for c', c_j and c_k. $c_1 \cdot r = j$ and $c_2 \cdot r = j + 1$. $w_h(c_j) = j$ and $w_h(c_k) = k$. To determine c', we compare (jx - jy) and ((j+1)x - k(y)). We have ((j+1)x - k(y)) - (jx - jy) = x + (j-k)y. So if $x + (j-k)y > 0$, the method returns c_k, and if $x + (j-k)y < 0$, the method returns c_j.

We now consider the implications of the resulting error corrections in the perception of the interaural difference by the LSO. In each case where there is an error in transmission, the parameters of the binary asymmetric channel create bounds on the number of neurons that a codeword will differ from the correct codeword. It has been shown that firing position of the LSO is linearly related to the interaural intensity difference. This means that each neuron that differs from the correct codeword proportionally contributes to the difference in perceived interaural intensity difference. The azimuthal angle is related linearly to the interaural difference. This implies that the error in the perceived angle is proportional to the number of neurons which misfire in the case of an error in the firing of the LSO.

6.5 The Receptive Field Structure of the Neurons in the Lateral Superior Olive

We now apply the work of Curto et al. to analyze the receptive fields of the neurons in the LSO. We associate neuron 1 with the bottommost neuron in the column. It is expected that the receptive field structure is given by $U_n \subset U_{n-1} \subset ... \subset U_1$ since neurons in the upper part of the column fire only when the neurons below them in the column fire.

For simplicity, begin by considering the case of two neurons, where neuron 1 is the bottom most neuron. We have the code given by $C = \{00, 10, 11\}$. The corresponding ideal is given by $\{0,1\}^4 \backslash C = \{01\}$. This ideal, J_C has generator $< (1 - x_1)x_2 >$. This ideal is already in canonical form. This generator gives a Type 2 relation, and so it implies $U_2 \subset U_1$ as expected.

Now consider the case of three neurons. We have the code given by $C = \{000, 100, 110, 111\}$. The corresponding ideal is given by $\{0,1\}^3 \backslash C = \{010, 001, 101, 011\}$. This ideal, J_C has generators $< (1 - x_1)x_2(1 - x_3), (1 - x_1)(1 - x_2)x_3, x_1(1 - x_2)x_3, (1 - x_1)x_2x_3 >$. We apply Curto's algorithm for finding the primary decomposition of a pseudomonomial ideal.

1. Initialization: Set $P = \emptyset$ and $D = \{J\}$.

2. Splitting: We compute D_I for each element of D. $D_I = \{< (1 - x_1)x_2(1 - x_3), (1 - x_1)(1 - x_2)x_3, x_1(1 - x_2)x_3, (1 - x_1)x_2x_3, (1 - x_1) >, < (1 - x_1)x_2(1 - x_3), (1 - x_1)(1 - x_2)x_3, x_1(1 - x_2)x_3, (1 - x_1)x_2x_3, x_2 >, < (1 - x_1)x_2(1 - x_3), (1 - x_1)(1 - x_2)x_3, x_1(1 - x_2)x_3, (1 - x_1)x_2x_3, (1 - x_3) >\}$.

3. Reduction: In $< (1 - x_1)x_2(1 - x_3), (1 - x_1)(1 - x_2)x_3, x_1(1 - x_2)x_3, (1 - x_1)x_2x_3, (1 - x_1) >$ we set $(1 - x_1) = 0$, so we have $< 0, 0, (1 - x_2)x_3, (1 - x_1) >=< (1 - x_2)x_3, (1 - x_1) >$. In $< (1 - x_1)x_2(1 - x_3), (1 - x_1)(1 - x_2)x_3, x_1(1 - x_2)x_3, (1 - x_1)x_2x_3, x_2 >$, set $x_2 = 0$, so we have $< 0, (1 - x_1)x_3, x_1x_3, 0, x_2 >=< (1 - x_1)x_3, x_1x_3, x_2 >$. In $< (1 - x_1)x_2(1 - x_3), (1 - x_1)(1 - x_2)x_3, x_1(1 - x_2)x_3, (1 - x_1)x_2x_3, (1 - x_3) >$, we set $(1 - x_3) = 0$, so we have $< 0, (1 - x_1)(1 - x_2), x_1(1 - x_2), (1 - x_1)x_2, x_3 >=< (1 - x_1)(1 - x_2), x_1(1 - x_2), (1 - x_1)x_2, x_3 >$.

4. Update: $D = \{< (1 - x_2)x_3, (1 - x_1) >, < (1 - x_1)x_3, x_1x_3, x_2 >, < (1 - x_1)(1 - x_2), x_1(1 - x_2), (1 - x_1)x_2, (1 - x_3) >\}$. There are no ideals with only linear generators.

5. Repeat Reduction: $D_{I1} = \{< (1 - x_2)x_3, (1 - x_1), (1 - x_2) >, < (1 - x_2)x_3, (1 - x_1), x_3 >\}$. In $< (1 - x_2)x_3, (1 - x_1), (1 - x_2) >$, we set $(1 - x_2) = 0$, so we have $< (1 - x_1), (1 - x_2) >$. In $< (1 - x_2)x_3, (1 - x_1), x_3 >$, we set $x_3 = 0$, so we have $< (1 - x_1), x_3 >$. $D_{I2} = \{< (1 - x_1)x_3, x_1x_3, x_2, (1 - x_1) >, < (1 - x_1)x_3, x_1x_3, x_2, x_3 >\}$. In $< (1 - x_1)x_3, x_1x_3, x_2, (1 - x_1) >$, we set $(1 - x_1) = 0$, so we have $< x_3, x_2, (1 - x_1) >$. In $< (1 - x_1)x_3, x_1x_3, x_2, x_3 >$, we set $x_3 = 0$, so we have $< x_2, x_3 >$. $D_{I3} = \{< (1 - x_1)(1 - x_2), (1 - x_1)x_2, x_1(1 - x_2), (1 - x_3), (1 - x_1) >, < (1 - x_1)(1 - x_2), (1 - x_1)x_2, x_1(1 - x_2), (1 - x_3), (1 - x_2) >\}$. In $< (1 - x_1)(1 - x_2), (1 - x_1)x_2, x_1(1 - x_2), (1 - x_3), (1 - x_1) >$, we set $(1 - x_1) = 0$ so we have $< (1 - x_2), (1 - x_3), (1 - x_1) >$. In $< (1 - x_1)(1 - x_2), (1 - x_1)x_2, x_1(1 - x_2), (1 - x_3), (1 - x_2) >$, we set $(1 - x_2) = 0$ so we have $< (1 - x_1), (1 - x_3), (1 - x_2) >$.

6. Repeat Update: $D = \cup D_I = \{< (1 - x_1), (1 - x_2) >, < (1 - x_1), x_3 >, < x_3, x_2, (1 - x_1) >, < x_2, x_3 >, < (1 - x_1), (1 - x_2), (1 - x_3) >, < (1 - x_1), (1 - x_2), (1 - x_3) >\}$. All the ideals have only linear generators so P = D.

7. Output: We remove from P, the ideals which are contained in other ideals, so we have $J =< (1 - x_1), (1 - x_2) > \cap < (1 - x_1), x_3 > \cap < x_2, x_3 >$.

We now take all possible products among these ideals. Recalling that the Boolean relations give $x_i^2 = x_i$, $(1 - x_i)^2 = (1 - x_i)$, and $x_i(1 - x_i) = 0$, we get the set $M(J) = \{(1 - x_1)x_2, (1 - x_1)x_2x_3, (1 - x_1)x_3, (1 - x_2)(1 - x_1)x_3, (1 - x_2)x_3\}$. Removing all elements that are multiples of lower degree elements, we get the canonical form, $CF(J) =< (1 - x_1)x_2, (1 - x_1)x_3, (1 - x_2)x_3 >$. These type 2 relations specify, respectively, $U_2 \subset U_1$, $U_3 \subset U_1$ and $U_3 \subset U_2$ as was expected.

7 An Overview of Sound Localization in the Barn Owl

We also explore these concepts in the context of the system of sound localization in the barn owl.

7.1 System Overview

Owls use two cues to localize sounds in space, based on the differences in the properties of the sound coming to each ear. Owls use interaural intensity differences to determine the elevation of the sound source and interaural time differences to determine its azimuth. The interaural time difference pathway begins in the nucleus magnocellularis, which responds in a phase locked fashion to the incoming sound waves. This nucleus projects onto the nucleus laminaris, the first place of binaural convergence in the time difference pathway. Neurons in this nucleus are arranged tonotopically, meaning neurons fire in response to different frequencies, and fire based on the phase difference of the waves arriving at both ears. However, because sound waves are periodic, these neurons also fire at different multiples of the period of the frequency to which they correspond (Konishi et al., 1988). Thus, the response at these different periods is a result of the periodic nature of the sound rather than the actual time difference of the sound in space, and experiments have shown that owls may respond to these phantom targets as the result of the ambiguity of the code.

The nucleus laminaris then projects to the central nucleus of the inferior colliculus, which in turn projects to the external nucleus of the inferior colliculus. It is in this nucleus that the first space mapped cells exist; these cells fire over a narrow region in space and no other areas.
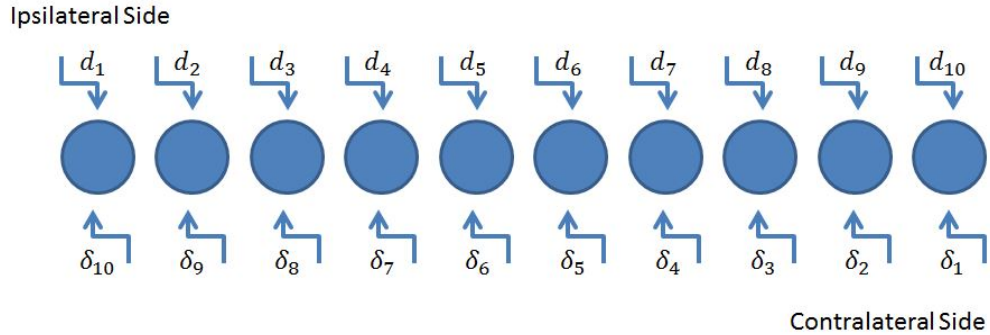
These behavioral patterns suggest that the neural code in the nucleus laminaris does not have a convex realization because the owl makes behavioral errors which suggest it is unable to determine which of the possible targets is the source of the sound. However, higher in the brain stem, this ambiguity is resolved in the external nucleus of the inferior colliculus, suggesting that the code corresponding to this structure has a convex realization of receptive fields.

7.2 A Model of the Nucleus Laminaris

The nucleus laminaris is tonotopically organized in isofrequency laminae as the result of the tonotopic projections from the nucleus magnocelluaris. The ipsilateral signal enters through the dorsal surface and the contralateral signal enters through the ventral surface of the nucleus. Since the signals enter on opposite sides, this creates a system of delay lines resulting in a system of coincidence detection, where neurons fire when they receive simultaneous stimulation from both sides, and periodic firing due to the periodic nature of the sound waves (Carr & Konishi, 1988). Each neuron has a characteristic delay, the interaural time difference at which the neuron responds best regardless of frequency, corresponding to the actual time difference. However, neurons may also fire corresponding to virtual disparities, time disparities that are integer multiples of the period away from the characteristic delay. This results in two axes to describe the firing of each neuron. Along one axis is frequency and along the perpendicular axis is time disparity. This arrangement projects directly to the central nucleus of the inferior colliculus. Biological tracers show that the neurons in the external nucleus of the inferior colliculus then receive inputs from multiple isofrequency laminae in a column of cells from the central nucleus perpendicular to the isofrequency axis. However, it is unclear what the purpose of the additional synapse is between the central nucleus and the external nucleus because it is not understood why the nucleus laminaris

does not project directly to the external nucleus since the firing is replicated in the central nucleus. All of the neurons in this perpendicular column in the central have the same characteristic delay, which is also the same characteristic delay as the neuron to which they project in the external nucleus (Wagner, Takahashi, & Konishi, 1987).

Based on this information we are able to build a model of the firing in the nucleus laminaris to demonstrate its properties. We consider a single isofrequency column of the nucleus laminaris. Along this column, each neuron receives a different delayed signal from each side.

Ipsilateral Side

| d_1 | d_2 | d_3 | d_4 | d_5 | d_6 | d_7 | d_8 | d_9 | d_{10} |

○ ○ ○ ○ ○ ○ ○ ○ ○ ○

| δ_{10} | δ_9 | δ_8 | δ_7 | δ_6 | δ_5 | δ_4 | δ_3 | δ_2 | δ_1 |

Contralateral Side

Experiments have shown that the conduction delay varies linearly with depth, suggesting that $d_x = xD$ and $\delta_x = x\Delta$ for D and Δ the rate of linear change in the conduction time with firing depth.

Ipsilateral Side

| $1D$ | $2D$ | $3D$ | $4D$ | $5D$ | $6D$ | $7D$ | $8D$ | $9D$ | $10D$ |

○ ○ ○ ○ ○ ○ ○ ○ ○ ○

| 10Δ | 9Δ | 8Δ | 7Δ | 6Δ | 5Δ | 4Δ | 3Δ | 2Δ | 1Δ |

Contralateral Side
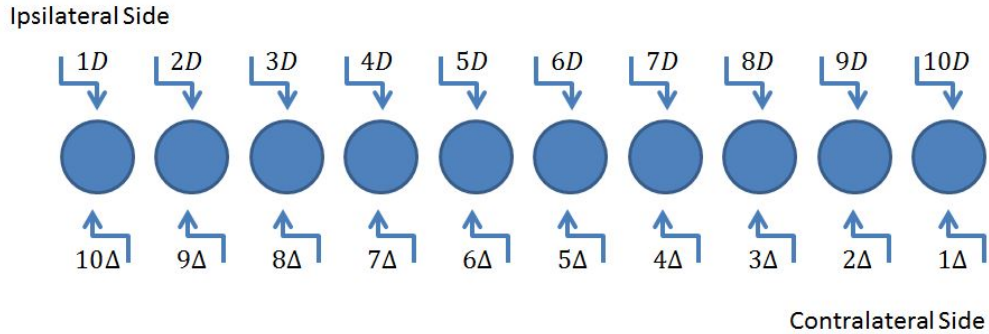
However, experiments also show that the rates of change of the conduction time differ slightly for each side. The ipsilateral side changes at approximately .46 degrees per micrometer, and the contralateral side changes at approximately .68 degrees per micrometer. Thus, Δ can be expressed as some multiple of D, cD. This allows the time differences coming from each of the two sides to be compared.

Ipsilateral Side

| 1D | 2D | 3D | 4D | 5D | 6D | 7D | 8D | 9D | 10D |

$(1-10c)D$ $(3-8c)D$ $(5-6c)D$ $(7-4c)D$ $(9-2c)D$

$(2-9c)D$ $(4-7c)D$ $(6-5c)D$ $(8-3c)D$ $(10-1c)D$

$10cD$ $9cD$ $8cD$ $7cD$ $6cD$ $5cD$ $4cD$ $3cD$ $2cD$ $1cD$

Contralateral Side
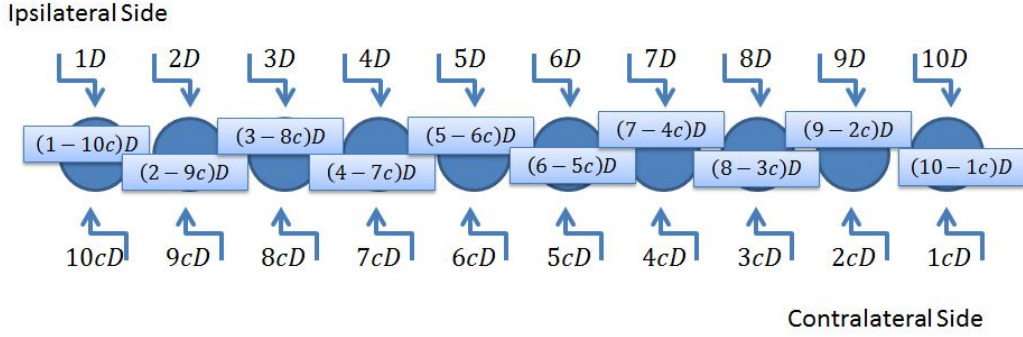
From this analysis, it can be seen that the difference in the relative delay changes at a constant rate, (1+c)D, per neuron despite the fact that the delays coming from each side change at different constant rates.

7.3 The Neural Code in the Nucleus Laminaris

Each neuron in the column of the nucleus laminaris acts as a coincidence detector. Because the change in time difference between the two waves arriving at a neuron varies linearly along the isofrequency column, firing in the column will be periodic depending on the period of the column. Let the period of the column be P and the true time difference be t. The signals will coincide at a time difference of t in the column, but because the signals are phase locked, they will also coincide at $t + nP$ for $n \in \mathbb{Z}$. This implies that a neuron in the column fires every $\frac{P}{1+cD}$ neurons. Thus the code contains periodic bands of firing, and the exact neurons which are firing is determined by t.

We now consider the firing of multiple columns. The firing of the columns occurs at $\frac{P_1}{1+cD}, \frac{P_2}{1+cD}, ..., \frac{P_k}{1+cD}$ neurons. Every column will fire at a difference of t, which the data suggests occurs at the same depth in each column. This implies that all of the columns fire simultaneously every $lcm(\frac{P_1}{1+cD}, \frac{P_2}{1+cD}, ..., \frac{P_k}{1+cD})$ neurons. The rest of this paper explores the ambiguity that results from the periodic nature of these codes.

8 Periodic Codes

Inspired by the periodic structure of the neural code in the nucleus laminaris of the barn owl, we explore whether codes of this form have a convex realization. The ambiguity of the stimulus and the confusion in the behavioral response of the barn owl suggest that such codes should not be able to be realized convexly.

8.1 Definitions

- nonintersecting code: A code is nonintersecting if whenever a neuron is on in a codeword, it is on in no other codewords.

- periodic code: All codewords are strings of the same number of actively firing neurons separated by the same number of inactive neurons with no other sized breaks in firing.

  - All codewords have the same patterned form.

– k-m periodic code: Codewords are all strings of k 1's, followed by strings of m 0's, followed by strings of k 1's, and so on. The only exception is the first and last bits of the code which can be less than or equal to k or m depending on if these are firing bits.

- complete k-m periodic code: All possible codewords with the k-m pattern are included in the code.

8.2   Examples Exploring the Convexity of Periodic Codes

Curto et al. derive an alogorithm to compute the canonical form of a code from the generators of the ideal associated with the code by using primary decomposition. This algorithm has been implemented in MATLAB and made publicly available. This code is used to analyze the following cases (Youngs, 2015).

8.2.1   Complete Periodic Codes on Three Neurons

A 1-x complete periodic code has a convex realization by associating each neuron to a convex set, where the collection of convex sets is pairwise disjoint.

Consider the complete 2-1 periodic code on three neurons:

$C = \{(110), (101), (011)\}$

The canonical form of the ideal is $\{(1-x_1)(1-x_2), (1-x_3)(1-x_2), (1-x_3)(1-x_1), x_1x_2x_3\}$, which correspond to the minimal relationships, $\{X \subset U_1 \cup U_2, X \subset U_3 \cup U_2, X \subset U_3 \cup U_1, U_1 \cap U_2 \cap U_3 = \emptyset\}$. Since $X \subset U_2 \cup U_3$, this implies that $U_1 \subset U_2 \cup U_3$. Since $U_1 \cap U_2 \cap U_3 = \emptyset$, we have $U_1 \subset U_2$ or $U_1 \subset U_3$. Without loss of generality, assume $U_1 \subset U_3$, so $U_1 \cap U_2 = \emptyset$. We also have $X \subset U_1 \cup U_2$, which implies $U_3 \subset U_1 \cup U_2$. This implies that $U_3 \subset U_1$ because otherwise the triple intersection would be nonempty. So we have $U_1 = U_3$. But we also have $X \subset U_3 \cup U_1$ which implies $X \subset U_1$. But this would imply $U_2 \subset U_1$, which is a contradiction. This suggests there is no convex realization for the code.

In the case of $k \geq 3$, the all ones codeword is in the code, which implies that the code has a convex realization with minimum embedding dimension less than or equal to 2 as proven by Curto et al.

8.2.2   Complete Periodic Codes on Four Neurons

By the same argument as above, a 1-x complete periodic code has a convex realization since it is nonintersecting.

Consider the complete 2-2 periodic code, $C = \{1100, 0110, 0011, 1001\}$. The neural ideal of this code has generators, $(1 - x_1)(1 - x_3), x_1x_3, (1 - x_2)(1 - x_4), x_2x_4$. This covering of open sets contains a local obstruction. Since $(1 - x_1)(1 - x_3)$ is a generator, the entire stimulus space is covered by $U_1 \cup U_3$, but x_1x_3 is also a generator, implying that $U_1 \cap U_3 = \emptyset$. Since the sets are disjoint, the covering is non-contractible, giving rise to a local obstruction. Note that this can also be seen by associating this code with L19 and noting that the patterns corresponding to the vertices which are mandatory codewords for the code to be convex are not included in the code (Curto et al.).

Consider the complete 3-1 periodic code, $C = \{1110, 0111, 1101, 1011\}$. The neural ideal of this code has generators $(1 - x_1)(1 - x_4), (1 - x_1)(1 - x_3), (1 - x_3)(1 - x_4), (1 - x_1)(1 - x_2), (1 - x_2)(1 - x_3), (1 - x_2)(1 - x_4), x_1x_2x_3x_4$.

Consider the complete 3-2 periodic code, $C = \{1110, 1100, 1001, 0011, 0111\}$. The neural ideal of this code has generators $(1 - x_2)(1 - x_4), (1 - x_1)(1 - x_3), (1 - x_1)(1 - x_4), x_1x_3(1 - x_2), x_1x_3x_4, x_1x_2x_4, x_3x_4(1 - x_3)$.

Consider the complete 2-1 periodic code, $C = \{1101, 1011, 0110\}$. The neural ideal of this code has generators $(1-x_2)(1-x_3), (1-x_1)(1-x_2), (1-x_1)(1-x_3), x_4(1-x_1), x_1(1-x_4), (1-x_2)(1-x_4), (1-x_3)(1-x_4), x_1x_2x_3, x_2x_3x_4$. The generators $x_4(1-x_1)$ and $x_1(1-x_4)$ imply $U_4 \subset U_1$ and $U_1 \subset U_4$ respectively, implying $U_1 = U_4$. With this simplification, $x_1 = x_4$, we see that the generators for the code are the same as those for the 2-1 complete periodic code on 3 neurons.

We also observe that for the 3-1, 3-2, 2-2, and 2-1 patterns, the code is not max intersection complete. Curto et al. prove that for $n \leq 4$, being max intersection complete is a necessary and sufficient condition for convexity.

As in the case of three neurons, for $k \geq 4$, the all ones codeword is in the code, so by the results of Curto et al., the code is convex.

8.3 Results on The Convexity of Periodic Codes

Any complete k-m periodic code with $k \geq n$ is convex.

Proof. If $k \geq n$ and C is a complete k-m periodic code, then C contains the all ones codeword. By the results of Curto et al., any code containing the all ones codeword is convex. □

The size of a complete k-m periodic code is k+m.

Proof. A complete k-m periodic code contains all possible codewords with the k-m firing pattern. Once the position of the first switch in firing is set, the bits for all of the other neurons are fixed. There are k different switch positions between firing and not firing if the first neuron in the code is firing, one codeword corresponding to the initial lengths of firing being between 1 and k neurons long. Similarly, there are m different switch positions between not firing and firing if the first neuron in the code is not firing, one codeword corresponding to the initial length of not firing being between 1 and m neurons. This gives a total of k+m possible codewords. Since all the patterns are included in a complete k-m periodic code, the size of the code is k+m. □

Nonintersecting codewords always have a convex realization.

Proof. We give a proof by a construction of the convex sets. Associate each codeword to a convex set, where the collection of these sets is mutually disjoint. For all the neurons which are firing in a codeword, assign their receptive field to the convex set associated with the codeword. Thus, the receptive field for all of the neurons firing in the same codeword is the same convex set. This gives a convex realization of the code since there are no other intersections between the neurons in the code. □

Note that this realization has minimum embedding dimension 1.

A complete k-m periodic code is nonintersecting if and only if k=1.

Proof. Assume C is a a complete k-m periodic code and is nonintersecting. Since C is complete it contains both $(1, ..., 1_k, 0, ..., 0_m, 1, ...)$ and $(0, 1, ..., 1_k, 0, ..., 0_k, 1, ...)$. If k is greater than 1, then neuron 2 is active for both codewords, so it is not nonintersecting. Therefore, k=1. Now assume C is a complete 1-m periodic code. Each of the codewords in C are shifts of $(1, 0, ..., 0_m, 1, ...)$. Assume that neuron j fires in one of the codewords. Because C is periodic, neurons j+m+1 and j-m-1 also fire. Thus, whenever neuron j fires, there is only one possible codeword that can occur because of the periodic structure of the code. Therefore, C is nonintersecting. □

This suggests that if there was no noise in the biological system and a single neuron fired at every multiple of the period then there would be no phantom targets in the localization of sounds.

The convexity of a complete k-m periodic code depends only on whether the code can be realized convexly on the first k+m neurons.

Proof. Since every codeword in the code must have a k-m firing pattern, if the position of two neurons differs by k+m, then the neurons will have the same state in every codeword. This corresponds to the two neurons firing over the same open set, so they can be associated to the same receptive field. As noted previously, there are k+m possible firing patterns within the first k+m neurons and the firing of each of these neurons is not always the same as the firing of another one of these first k+m neurons, implying a changing pattern of intersections. However, there are no additional relationships reflected in the next k+m neurons, which are not already captured by the first k+m neurons. Therefore, the convexity of a complete k-m periodic code depends only on whether the complete k-m periodic code on k+m neurons has a convex realization. □

A complete k-m periodic code with $k > 1$ does not have a convex realization.

Proof. We define $M_H(C)$ to be the set of simplices for which the link of the simplex in the simplicial complex associated to the code is not contractible. It has been shown that for a code to have a convex realization, the codewords corresponding to the simplices in $M_H(C)$ must be in C itself.
Consider a complete k-m periodic code, C. In a previous result, we showed that the convexity of a periodic code depends only on the first k+m neurons, so it suffices to let C be a code on n=k+m neurons. The maximal facets of the code are the (k-1)-dimensional simplices. The union of these maximal facets gives the simplicial complex corresponding to C. Since the code is periodic, these maximal facets are also the only simplices in the complex with corresponding codewords in C.
Label the bits of C from 1 to n. The facets of the code are the (k-1)-dimensional simplices of all the sets of k adjacent vertices. Note that since the code is on k+m neurons, we also consider the nth bit and the first bit to be adjacent since the k neurons which are firing may be split among each end of the codeword.
Define $\sigma_{j,l}$ to be the simplex containing the jth to lth adjacent vertices. Note that this simplex must be in the simplicial complex associated to C if it contains less than or equal to k vertices. We want to consider the link of $\sigma_{j,j+k-2}$ which contains k-1 adjacent vertices, a (k-2)-dimensional simplex. The link of this simplex is the j-1th vertex and the j+k-1th vertex. This set is not contractible. This implies that if C has a convex realization, then $\sigma_{j,j+k-2} \in M_H(C)$. Since the code only contains codewords with k actively firing bits, $\sigma_{j,j+k-2}$ is not in C. Therefore, C does not have a convex realization.

□

9 Stochasticity and Convex Completions of Periodic Codes

9.1 Definitions

- perfect code: code that conforms perfectly to the patterns set by the parameters of the periodic code

- convexly completed periodic code: a k-m periodic code completed by adding the codewords corresponding to taking any subset of the neurons firing in the k-m periodic code

- convexly completed k-m periodic code: a convexly completed periodic code such that the largest j value for which a j-(m+k-j) complete periodic code is contained in the code is k

- edges of firing bands: the two neurons that correspond to a switch in the firing activity of the string of neurons in a perfect code; for example, if 0001111100 is a codeword, then neurons 3 and 4 and neurons 8 and 9 are the edges of the firing band

9.2   Results on Convex Completions of Periodic Codes

A convexly completed periodic code is convex up to local obstructions.

Proof. The code is closed under taking subsets. This implies that the codeword corresponding to any simplex in the simplicial complex is included in the code. There can be no local obstructions because any possible mandatory codeword is already included in the code.   □

10   Minimum Convex Completions of Periodic Codes

10.1   Definitions

- convex completion of C: a set of additional codewords, A, such that $C \cap A = \emptyset$, C does not have a convex realization, and $C \cup A$ has a convex realization up to local obstructions

- minimum convex completion: a convex completion, A, such that $|A|$ is minimized

- convex subcompletion: a convex completion, A, where if $a \in A$, $a \subset c$ for some $c \in C$

- subcodeword: s is a subcodeword of t if $s \subset t$

- minimum convex subcompletion: a convex subcompletion, A, such that $|A|$ is minimized

10.2   Results on Convex Completions

The all 1's codeword is the minimum convex completion of any code.

Proof. By adding the all 1's codeword to a code on n neurons. The simplicial complex associated with the code is the n-1 dimensional simplex on n points and simplices on all possible subsets of these n neurons. Since the n-1 dimensional simplex is connected, the link of any of the simplices consists of the union of all the other points in the simplicial complex. Since the complex is fully connected, this link is contractible. Thus, there are no mandatory codewords, which correspond to simplices that have noncontractible links. Therefore, the code is locally convex.   □

The set A = $\{a | a \notin C$ and $a \subset c$ for some $c \in C\}$ is a convex subcompletion.

Proof. Let Δ be the simplicial complex corresponding to C. Let $W = \{\omega \subset \Delta | \omega$ has non-contractible link$\}$. Let w be the codeword corresponding to ω. Since $\omega \subset \Delta$, either $w \in C$ or $w \in A$. Therefore, $W \subset A \cup C$. Therefore, $A \cup C$ is locally convex. Observe that this also proves that every code has a subcompletion. $\square$

The minimum convex subcompletion does not always contain all possible subsets of the codewords in C.

Proof. Consider the code, C = $\{11100, 01110, 00111, 10011, 11001\}$ with corresponding simplicial complex Δ. The codeword w = $10100 \subset 11100$. This codeword corresponds to the simplex, 13. We have $Lk_{13}(\Delta) = \{2\}$. Since the link is a single point, it is contractible and w is not a mandatory codeword. Thus, w is not included in the minimum convex subcompletion of C. $\square$

Let A be a set of subcodewords of C. The simplicial complex corresponding to C is the same as the simplicial complex corresponding to $A \cup C$.

Proof. Let Δ be the simplicial complex corresponding to C. Let $w \in A \cup C$ and let ω be the simplex corresponding to w. Since $A \cap C = \emptyset$, either $w \in C$ or $w \in A$. Suppose $w \in C$, then $\omega \in \Delta$ by the construction of the simplicial complex. Suppose $w \in A$. We have $w \subset p$ for some $p \in C$. Let ρ be the simplex corresponding to p. By construction of the simplicial complex, $\rho \in \Delta$. Since $w \subset p$, $\omega \subset \rho$. Since Δ is a simplicial complex, it is closed under taking subsets. This implies $\omega \in \Delta$. Therefore, C and $A \cup C$ have the same corresponding simplicial complex. $\square$

Let A be a set of subcodewords of C. The set of mandatory codewords for C is the same as the set of mandatory codewords for $A \cup C$.

Proof. Since A is a set of subcodewords of C, C and $A \cup C$ correspond to the same simplicial complex. The set of simplices with noncontractible links is the same for the simplicial complex corresponding to C and the simplicial complex corresponding to $A \cup C$ since the simplicial complexes are the same. Observe that this implies the addition of any subcodewords to a code does not change the minimum convex subcompletion. $\square$

10.3   The Minimum Subcompletion of k-m Complete Periodic Codes on k+m Neurons

We have proven previously that any k-m periodic code with $k > 1$ and $m > 0$ does not have a convex realization. The proof of this followed from the fact that the (k-1) contiguous firing bands had a disconnected, and so noncontractible, link.

10.3.1   Examples

We consider several examples of periodic codes. We examine the link of representatives of the possible patterns of representatives for subcodewords for contractibility. This analysis determines which subcodewords are mandatory for the code to be free from local obstructions, so these codewords must be included in a convex subcompletion of the code. 2-x Periodic Codes The only possible subcodewords are the codewords of the 1-(x+1) complete periodic code. These codewords correspond to the (k-1) contiguous firing bands with disconnected links. Thus, the minimum subcompletion of any 2-x periodic code is the 1-(x+1) complete periodic code. 3-1 Periodic Code This code is the set $\{1110, 0111, 1011, 1101\}$. The corresponding simplicial complex is the hollow tetrhedron. We have $Lk_{12}(\Delta) = \{3, 4\}$

which is disconnected and noncontractible, so the set of codewords containing the pattern 11 with all other positions 0 is needed in the minimum subcompletion; this is the 2-2 complete periodic code. We also have $Lk_{13}(\Delta) = \{2, 4\}$ which is disconnected and noncontractible, so the set of codewords containing the pattern 101 with all other positions 0 is needed in the minimum subcompletion. We also have $Lk_1(\Delta) = \{23, 34, 24\}$ which is homotopy equivalent to a circle and noncontractible. Thus, the set of codewords in the 1-3 complete periodic code must are also needed in the minimum subcompletion. Thus, the minimum subcompletion of this code contains all subcodewords of the code.

3-2 Periodic Code This code is the set $\{11100, 01110, 00111, 10011, 11001\}$. We have $Lk_{12}(\Delta) = \{3, 5\}$ which is disconnected and noncontractible, so this code requires the 2-3 complete periodic code in this minimum convex subcompletion. $Lk_{13}(\Delta) = \{2\}$, which is a single vertex and hence contractible, so the subcodewords containing the pattern 101 with zeroes elsewhere are not required in the minimum subcompletion. $Lk_1(\Delta) = \{23, 45, 25\}$ which is contractible. Thus, the minimum subcompletion for the 3-2 complete periodic code is the 2-3 complete periodic code.

We continue to explore several other examples of periodic codes in this way.

4-1 Periodic Code C $= \{11110, 01111, 10111, 11011, 11101\}$
$Lk_{12} = \{34, 45, 35\}$ noncontractible with nontrivial homology
$Lk_{13} = \{24, 45, 25\}$ noncontractible with nontrivial homology
$Lk_{123} = \{4, 5\}$ noncontractible because disconnected
$Lk_{124} = \{3, 5\}$ noncontractible because disconnected

4-2 Periodic Code C $= \{111100, 011110, 001111, 100111, 110011, 111001\}$
$Lk_{134} = \{2\}$ contractible
$Lk_{123} = \{4, 6\}$ noncontractible
$Lk_{12} = \{34, 56, 36\}$ contractible
$Lk_1 = \{234, 456, 256, 236\}$ noncontractible

4-3 Periodic Code C $= \{1111000, 0111100, 0011110, 0001111, 1000111, 1100011, 1110001\}$
$Lk_{123} = \{4, 6\}$ noncontractible because disconnected
$Lk_{134} = \{2\}$ contractible
$Lk_{12} = \{34, 67, 37\}$ contractible
$Lk_{13} = \{24, 25\}$ contractible
$Lk_1 = \{234, 567, 267, 237\}$ contractible

10.4   Convex Subcompletions

Let C be a k-m complete periodic code on k+m neurons with $m \geq k - 1$. The minimum convex subcompletion is the (k-1)-(m+1) complete periodic code.

Proof. The (k-1)-(m+1) complete periodic code is the set of all (k-1) contiguous firing bands. We have shown that the link of the simplices corresponding to these codewords is the disconnected set of two vertices so these codewords must be contained in the minimum subcompletion. We want to show that no other subcodewords are needed in the convex subcompletion by showing that no other codewords have noncontractible link. Consider the other subcodewords containing (k-1) firing neurons. These codewords consists of discontiguous firing bands. They are subsets of the k contiguous firing bands, which fire on nuerons j to j+k-1. So the subcodewords containing k-1 firing neurons that are discontiguous must contain j and j+k-1 with the ith neuron not firing for some i with $j < i < j+k-1$. However,

in the code, neurons j and j+k-1 only cofire in the codeword consisting of the k contiguous firing band that fires on neurons j to j+k-1 because $m \geq k - 1$. Thus, the link of this discontiguous subcodeword is only the ith neuron, which corresponds to a link containing a single vertex. Thus the discontiguous subcodewords with k-1 neurons firing are not needed in the subcompletion. The same argument holds for any subcodeword containing the jth and j+k-1th neuron, as since they only cofire in one codeword, the link is only one simplex so is contractible. We want to show that any subcodeword containing less than (k-1) firing neurons has connected link. Suppose the subcodeword, p, contains nuerons j and j+l. Note that l must be less than k-1. Suppose the subcodeword does not have contiguous firing on j to j+1. Let Y the set of neurons which are not firing. The set Y is contained in any ω such that $\omega \cup \rho \subset \Delta$. The set of ω satisfying this condition is the link of ρ. Thus, the link is connected since all ω contain the vertices in Y. Now suppose p has contiguous firing from j to j+l. Since this band contains less than k-1 firing neurons. The simplices of the link of this subcodeword must contain either the j-1th or j+l+1th vertex. The j-1th vertex is contained for the codewords which have contiguous firing on k to k+m-1 with $j - k < k < j$. The j+l+1th vertex is contained for codewords with $k \geq j$. Furthermore, there is at least one simplex in the link which contains both j-1 and j+l+1 corresponding to the codewords where $k < j$ and $j - k < l$. Thus, every simplex in the link is connected to either the j-1th or j+l+1th vertex and there are simplices where the j-1th and j+l+1th vertex are connected. This implies that the link is connected. Thus, the link will not be non-contractible as a result of being disconnected. In the following lemma, we prove that codewords of this form also cannot have links with nontrivial homology. This shows that the link of these codewords is contractible, so they are not mandatory codewords and are not needed for a minimal convex subcompletion. Thus, we have shown that the only codewords needed for the minimal convex subcompletion are exactly the codewords corresponding to the complete (k-1)-(m+1) periodic code. □

The subcodewords which contain the jth and j+l+1th neuron cannot have links with nontrivial homology.

Proof. Suppose that the link has nontrivial homology. This implies the neuron of greatest index which cofires with the j to j+l+1 pattern and the neuron of least index which cofires with the j to $j + l + 1$ pattern must fire at the same time in some codeword. The difference between the neurons of greatest and smallest index that cofire with these two neurons is $2k - l > k$. These neurons cannot fire at the time since this distance is greater than k, so they do not occur as part of the same firing band. □

11 The Effects of Stochasticity on Convexity

For these results, we make the assumption that errors in firing will only occur at the edges of the contiguous bands of neurons that fire in the perfect code. We also assume that the brain records all patterns of firing that occur and incorporates them into the code. Finally, we assume that at most one error occurs in firing at a time.

Additional firing on the edges of firing bands in convexly completed periodic codes preserves convexity for m sufficiently large. This corresponds to neurons on the edges firing when they should not.

Proof. Let the code be a convexly completed k-m periodic code. Assume a neuron on the edge of a band fires. This increases the dimension of the greatest dimensional simplex in

the simplicial complex to k. This new simplex has trivial link because there are no simplices of greater dimension in the complex. The addition of these firing neurons creates a new simplicial complex where the k-1 dimensional simplices associated with the original bands of k neurons firing now have non-contractible links. However, the codewords corresponding to these simplices are already included in the code as part of the perfect code. As argued previously, for m sufficiently large, these original bands of k firing neurons are the only (k-1)-dimensional simplices with non-contractible links. □

The introducton of stochasticity can make nonconvex codes convex.

Proof. Consider a 2-2 code on four neurons. The code is not max intersection complete, so the code is not convex. Introduce stochasticity so that sometimes the neurons fail to fire. This adds the additional codewords, {1000, 0100, 0010, 0001}. The code is now max intersection complete, resulting in convexity. Thus, stochasticity can make a nonconvex code convex by the failure of neurons to fire. □

12 Convex Completions of Hamming Distance 1

12.1 Definitions

We assume that $m >> k - 1$ to avoid the potential for the link of a k-1 subband to be noncontractible as the result of homology rather than nonconnectedness.

Hamming distance 1 convex completion: a set, S, of codewords of Hamming distance 1 from one of the codewords in the complete k-m periodic code, C, such that $S \cup C$ has a convex realization

12.2 Results

Adding a codeword of Hamming distance 1 changes whether the link is contractible for at most one simplex in the simplicial complex.

Proof. We have noted previously that adding any subcodeword of a codeword in the code does not change the simplicial complex and hence does not change whether the link of any of the simplices in the simplicial complex are contractible. So we only consider the effects of adding codewords with k+1 neurons firing. Observe that adding these codewords adds new edges to the simplicial complex. We have shown previously that the k-1 subband starting at j has a noncontractible link because neuron j-1 and j+k are not connected. This is the only simplex where whether the link is contractible is dependent on the connection between these two nuerons. Thus, adding a codeword of Hamming distance 1 which contains both the j-1th and j+kth neuron only changes whether the link is contractible for the subband starting at j.

□

The minimum convex completion of Hamming distance 1 of a complete k-m periodic code is k+m codewords.

Proof. We have already shown that the minimum subcompletion of a k-m periodic code is k+m codewords, the complete (k-1)-(m+1) periodic code, consisting of k-1 subbands. All of these subbands are at Hamming distance 1 from one of the codewords in the code. All of these subbands also must be included because they have a noncontractible link. We have

proven previously that for $m \geq k - 1$, the fact that the link is noncontractible for the (k-1) subband starting at j results from the fact that neuron j-1 and neuron j+k are not connected. In the previous result, we showed that adding a codeword can change whether the link is contractible for at most one simplex, which corresponds to a subband. Therefore, if we add a codeword of Hamming distance 1 with k+1 neurons firing, at most one of the subbands no longer needs to be included in the code because the link has been made contractible. Thus, the total number of codewords needed to convexly complete the code remains the same. Therefore, the minimum convex completion of Hamming distance 1 of a complete k-m periodic code contains k+m codewords. $\qquad \square$

13 Stochasticity and Convexity

We have shown that for a k-m periodic code with $m \geq k - 1$, k+m codewords of Hamming distance 1 must be added to the code. We consider the probability that stochasticity in firing will form a convex code.

13.1 Biologically Based Assumptions

- We assume the probability of a neuron firing correctly is p, so the probability of a 1 being switched to a 0 is 1-p, and the probability of a neuron remaining inactive correctly is q, so the probability of a 0 being switched to a 1 is 1-q.

- It is also assumed that q is greater than p because it is more likely for a neuron to fail to fire rather than to misfire.

- It is assumed that only the 4 edge bits have this possibility for error and that all other neurons will fire correctly. Note that this would require 2 or more errors.

13.2 Probability of Codewords

Based on these assumptions, we determine the probability of receiving the following patterns.

- P(correct codeword) $= p^2 q^2$

- P(k-1 subband) $= 2q^2 p(1-p) - q^2(1-p)^2$

- P(k-2 subband) $= q^2(1-p)^2$

- P(k+1 superband) $= 2(1-q)qp^2 - (1-q)^2 p^2$

- P(k+2 superband) $= (1-q)^2 p^2$

- P(gap) $= 2(1-q)(1-p)$

We need to see a specific combination of 2(k+m) different codewords, the correct set and k+m needed for the completion, for the code to be convex with many of the combinations having different probabilities. We also consider how many of the patterns the brain will remember. In n codewords, we want to know the probability that there is the correct combination of codewords for convexity.

This combinatorial question remains open.

14 Biological Implications

The fact that complete periodic codes are nonconvex suggests that the neurons in a single isofrequency column of the nucleus laminaris do not have convex receptive fields. This may correspond to the owl's response to phantom targets when hearing only a pure tone. This suggests that multiple frequencies are needed in order to successfully locate a sound in space.

However, it is unlikely that a biologically based system will exhibit perfectly regular patterned behavior as required by the definition of a complete k-m periodic code. Instead, what is more likely is that the size of the bands fluctuates slightly as the neurons on the edges of the band are least likely to fire. It should be explored in future work whether codes that are periodic but with fluctuations in k between the different codewords correspond to a convex realization of receptive fields. Furthermore, this raises the question of how the later structures, which combine the information from multiple columns so still have a periodic pattern but with firing occuring at a lower frequency, are able to resolve the ambiguity that arises from the periodic codes lower in the brainstem.

15 Directions for Future Research

15.1 Stochastic Codes

In order to more accurately model the firing of neurons in the code, future work should explore the impacts of creating a stochastic code by assigning each neuron a probability of misfire and a probability of failure to fire. This stochastic nature will result in a code with patterns that do not conform strictly to that of a k-m periodic code as k and m will vary, and the string of k neurons may even be broken by a neuron that fails to fire. It will be interesting to explore the implications that these additional codewords have for convexity.

15.2 The Relationship Between Stochasticity and Convexity for k-m Periodic Codes on n Neurons

In the analysis of periodic codes, the highly structured pattern made it so that questions of convexity could be explored by limiting the consideration to k+m neurons. However, when stochasticity is introduced, the assumption that when one neuron fires the neurons which are k+m neurons away also fire is no longer valid. This means that each neuron has a different receptive field so it becomes important to consider all n neurons. It should be explored how errors in a single one of the firing bands relate to the convexity of the entire code.

15.3 Questions of Near Convexity

The above results on periodic codes suggest a class of codes that cannot have a convex realization. However, consider the situation where the receptive fields of the neuron correspond to open intervals. Consider the example of a 2-x periodic code. Based on the code, for any point, there should be exactly two neurons firing. Suppose each neuron fires over a unit interval with the firing of each consecutive neuron beginning half a unit away from the start of the first neuron. Consider what occurs at this boundary point. It is not contained in the interval, so only one neuron is firing, which is inconsistent with the code. However, at all other points on the line, there are exactly two neurons firing. It is unclear what the

implications are for this situation where the code can be represented by a set of convex sets at all but the boundaries of the receptive fields.

15.4 Minimum Embedding Dimension

More theoretic algebraic work also remains to be done in determining the minimum embedding dimension in which a code can be realized. The work of Curto et al. has derived upper bounds on the dimension but work remains to be done in determining a tight bound. Furthermore, the fact that the owl uses a system of interaural time differences to determine the azimuth of sounds suggests that this code should have a minimum embedding dimension of 1. Similarly, the code for the interaural intensity differences used to determine the elevation should also have a minimum embedding dimension of 1, corresponding to the angle of the sound. However, these two codes are combined to locate the exact direction of a sound, suggesting that the combination of these two 1-dimensional codes forms a code with a minimal embedding dimension of 2. More work should explore how these codes combine and how combining codes of different minimal embedding dimension changes the minimum embedding dimension of the resulting code.

15.5 Biological Questions

The results of behavioral experiments in owls make it clear that a single tone is insufficient to accurately locate a sound because the owl also responds to phantom targets corresponding to locations that differ by periods of the corresponding frequency. However, in general, owls have been shown to have very precise sound localization abilities. This raises the question of how many different frequencies must be present in the bandwidth of the sound in order for the owl to locate the sound accurately. The results on the periodic nature of the firing suggest that this question can be related to combinatorics and number theory since the resultant firing pattern depends on the least common multiple of the periods of the frequencies present in the sound.

16 Conclusion

In conclusion, viewing the firing patterns of neurons as a combinatorial algebraic object, the neural code, allows brain systems to be analyzed from an algebraic perspective. This work applied the results of Curto et al. to two specific neural systems, the lateral superior olive which codes for interaural intensity differences in humans and the nucleus laminaris which codes for interaural time differences in the barn owl. Further work can continue to apply these techniques to the other structures involved in the system of sound localization in the owl. Moreover, neurobiologists have noted differences in the biology of birds and mammals. One of the primary differences is that mammals require both time and intensity differences to localize sounds only along the horizon in a single dimension. Using the concepts of neural coding theory may provide insight into the differences between the aviary and mammalian systems of sound localization. Furthermore, viewing patterns of neural firing in this way may explain other observations in sensory patterns as an area of further research. Dr. Jennifer Groh, a neurobiologist, conducts psychophysical experiments on the interaction between the auditory and visual system. For example, she found that seeing a flash of light before hearing a sound impacts the estimated location of the sound on the horizon. An understanding of how the receptive fields associated with the auditory and visual systems

combine and the role that stochasticity plays may lead to a better understanding of this and other similar phenomena.

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