Encoding Schemes in Rat Primary Auditory Cortex

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Introduction

Since the 1940s, researchers have used information theory to create models that describe neural physiology (MacKay and McCulloch, 1952). Claude Shannon, in his work for Bell Laboratories, developed a mathematical framework for information theory (Shannon, 1948) and introduced a powerful new tool for analyzing neural communication. Researchers have attempted multiple applications of Shannon's model to neural coding (Butts, 2003). The main motivation behind the development of these models was to quantify the information contained in unique sets of responses. The limitations of the computations involved (such as the need for a large data set to be collected or generated) have meant that many of the most interesting phenomena predicted by information theory based models go untested in live experiments.

One commonly used characterization of neuronal responses is the tuning curve. Originally, researchers believed that the characteristic stimuli of tuning curves were also the most informative responses because they correspond to the largest response of the neuron. With further investigation researchers found that more relevant responses could come from lower firing areas. These lower firing areas would then represent a

better encoding of stimuli other than the characteristic stimulus (Butts and Goldman, 2006). Such high information, non-characteristic stimuli could be predicted using models developed with different decompositions of Shannon's original equations. By integrating the entropy of the stimulus with a decomposition of Shannon's mutual information called specific information, Dan Butts (2003) developed Stimulus Specific Information (SSI). Because it calculates the information transmitted by a single neuronal response, SSI is a single response model. Single response models of information have the interesting property of showing distinct information curves for different scenarios (Butts and Goldman, 2006). In high noise situations, the most obvious response encodes the most information, much like traditional interpretations suggest. In low noise scenarios, however, high information responses shift to lower firing regions of the tuning curve. We refer to the separate high and low noise scenarios as encoding schemes because they represent different patterns of information encoding in the neuron.

The encoding scheme was found to shift depending on the level of "neuronal variability" (Butts and Goldman, 2006). Neuronal variability measures noise from various sources. The source of neuronal variability can be within the neural circuitry, the response, or the stimuli, and SSI shows a transition no matter the type of variance used to manipulate noise level. Another useful aspect of single response models is that they can be applied to both linear and nonlinear neurons. The rise in complexity in transitioning from a model to a biological system requires powerful tools to obtain comprehensible results. Therefore, we chose SSI to explore experimentally the existence of multiple encoding schemes in neurons. Our test focused on the B-G shift, the transition between the traditional and alternate encoding scheme. Knowing that neuronal variability can be varied based on properties of the stimulus we carried out *in vivo* experiments to

attempt to observe the B-G shift. By increasing the intensity of tones we expected to raise the signal to noise ratio of the neuronal response, and shift the area of highest SSI from the peak (low intensity, high noise) to the slopes (high intensity, low noise).

Methods

Activity was recorded from the primary auditory cortex (A1) using tungsten electrodes. Stimulus tones were 25 ms pure tones at twenty-two frequencies ranging from 1 kHz to 32 kHz and four intensities from 20 to 80 dB. By establishing a tonotopic gradient we ensured that recordings came from A1. The tuning curves used for calculating stimulus specific information came from sites that produced well tuned results. Spikes were extracted to produce a spike rate response field that gave the necessary data for calculating SSI. A spiking window of 100 ms, post-stimulus, was used to identify auditory evoked responses. The stimulus specific information content was calculated using the method described by Dan Butts and Mark Goldman (2006). The resulting curve of the information content was overlaid on the turning curve. This information represents the informational entropy of the response as it relates to sound frequency. To ensure that the observed B-G shift was not due to noise, the relevant data was split in half and replotted to check that both halves of the data showed the effect. To create error bounds on information curves we used a bootstrapping process. All calculations were done using Matlab.

Results

After calculating the SSI for the collected tuning curves, the B-G shift appeared to be observed in 27.8% (35 of 126) of sites in rat primary auditory cortex (Figure 1). The relative information content in low firing areas varied from site to site. Most of the sites with high information at lower firing areas showed the effect only with very high (80 dB) intensity

stimuli. Cross validation failed to uphold the observation of the B-G shift in any of the recordings (Figure 2). For this reason we conclude from these results that the B-G shift does not occur in the rat primary auditory cortex.

Discussion

In this experiment we sought to explore the possible existence of an alternative encoding scheme in neurons of the rat auditory cortex. Butts and Goldman (2006) demonstrated the existence of such an alternative encoding scheme in the cricket cercal system and the macaque visual system. They generated their data using model neurons, a process that invites questions about the applicability of their findings to biological systems. Our findings show that, for information about sound frequency, the highest information is encoded consistently by the highest firing response. Because the shift to high information at the high slope areas of a tuning curve was shown to depend on the existence of low neuronal variability (Butts and Goldman, 2006) for some set of stimuli, our findings are evidence that when encoding information about sound frequency there is a large neuronal variability to responses in the rat auditory cortex.

To fully explore the possible existence of alternative encoding schemes in the auditory cortex, it will be important to move from multiunit recordings to single unit recordings. Butts and Goldman (2006) found that populations of neurons seem to mitigate noise effects on encoding by individual neurons. Therefore, it is possible that moving to single unit recordings could give the same result, but this cannot be assumed. Also, varying stimulus properties other than frequency and intensity could show that information concerning other attributes of sound do show the B-G shift.

References

Butts DA (2003) How much information is associated with a particular stimulus? *Network Computation Neural Systems* 14: 177-187.

Butts DA, Goldman MS (2006) Tuning curves, neuronal variability, and sensory coding. *PLoS Biology* 4(4): e92.

MacKay DM, McCulloch WS (1952) The Limiting Information Capacity of a Neuronal Link. *Bulletin of Mathematical Biophysics* 14: 127-135.

Shannon CE (1948) A Mathematical Theory of Communication. *Bell System Technical Journal* 27: 379-423.

Figures

Figure 1 - Example of a site showing the B-G shift

Figure 1a - 75 dB

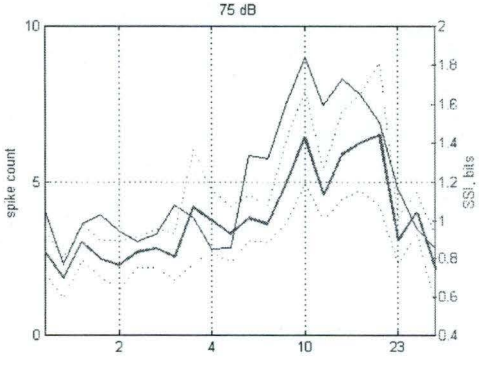


Figure 1b - 57 dB

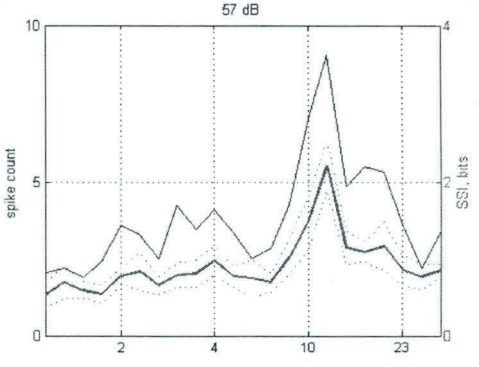


Figure 1c - 38 dB

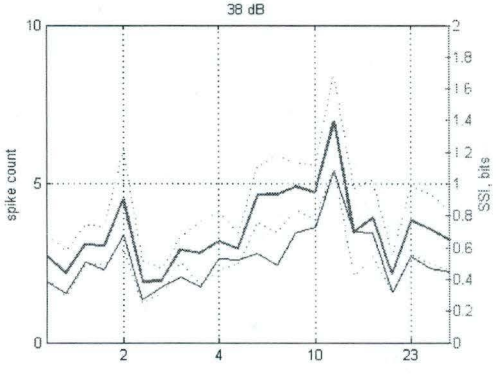
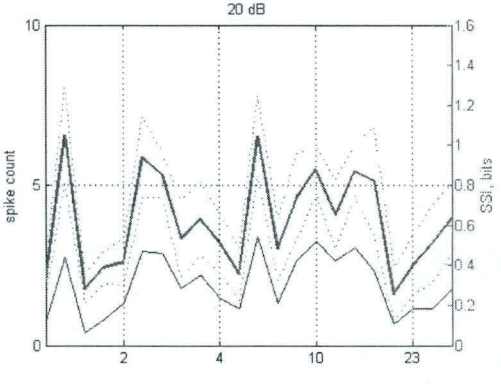


Figure 1d - 20 dB



The high information area on the slope of the 75 dB tuning curve can be seen to be roughly equal to the peak at the highest firing rate. As the intensity of the stimulus drops, and the signal to noise ratio (SNR) drops, the information shifts to be highest at the highest firing rate. The dashed lines are error bounds on SSI calculation (plus and minus one standard deviation).

Figure 2 - Example of a Cross Validation Result

For each decibel level, a and b are halves of the data replotted.

Figure 2a - 75 dB

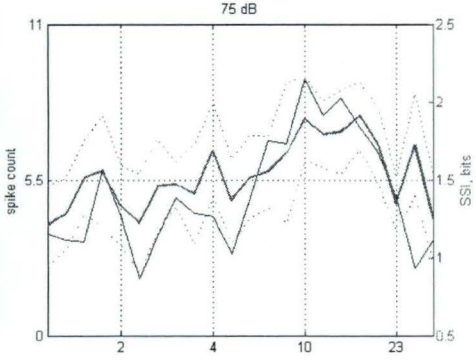


Figure 2b - 75 dB

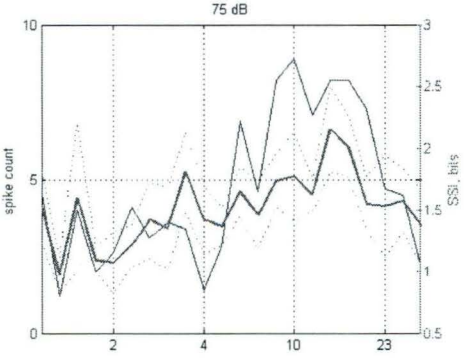


Figure 2a -57 dB

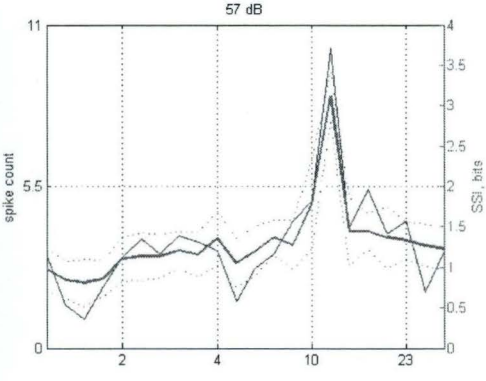


Figure 2b -57 dB

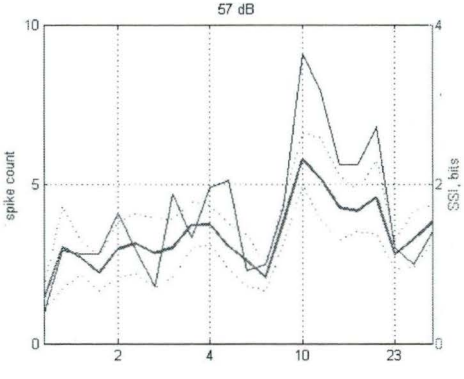


Figure 2a - 38 dB

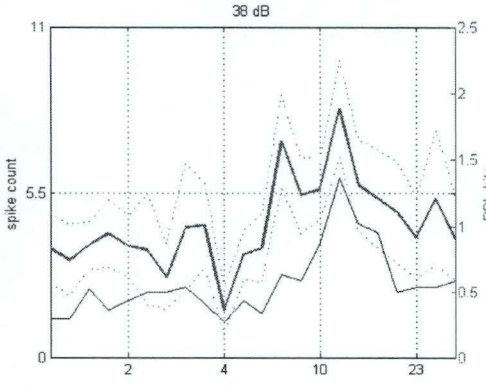


Figure 2b - 38 dB

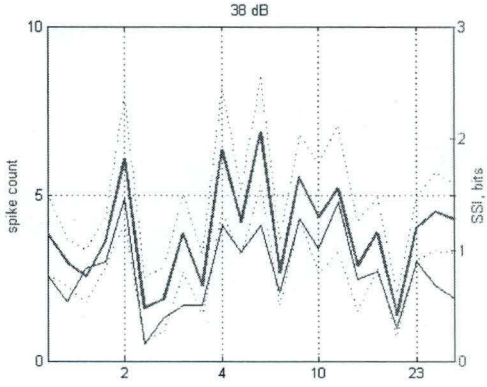


Figure 2a - 20 dB

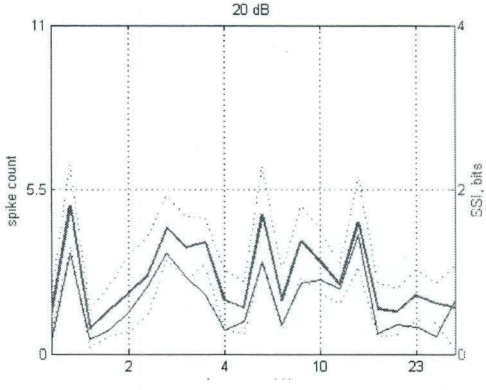
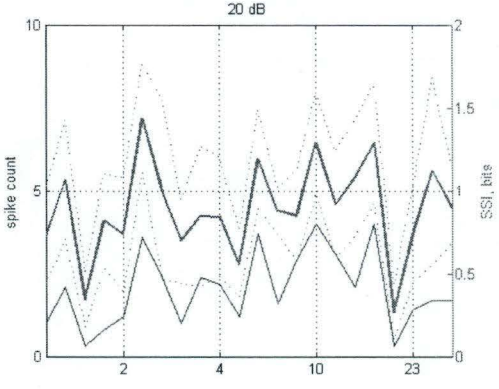


Figure 2b - 20 dB



Each a-b pair represents two halves of a single data set that had appeared to show the B-G shift. The areas of highest information do not appear at areas of high slope on either set of tuning curves. Dashed lines are error bounds (plus and minus one standard deviation)