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## 1 Applications of Coding Theory in Neuronal Systems

I have started working on this topic a few weeks ago. Since I am not very familiar with the neuronal systems of the living species, my first job was to study the principles of these systems. I started by reading two good books on these topics [1] and [2], which Prof. Gerstner had introduced to me.

These books are very interesting in the sense that they describe mathematical approaches to model the neuronal system. In what follows, I briefly explain the principles of how these systems work and their similarities to our information transmission/processing units.

### 1.1 Neuronal Systems Anatomy

Neuronal systems are made out of small cells called neurons. Each neuron is composed of four main parts, as shown in figure 1: Somma, which is the main cell body, axon, which carries action potential towards the neighboring neurons, axon terminal (or synapses), where electrical signal is transformed

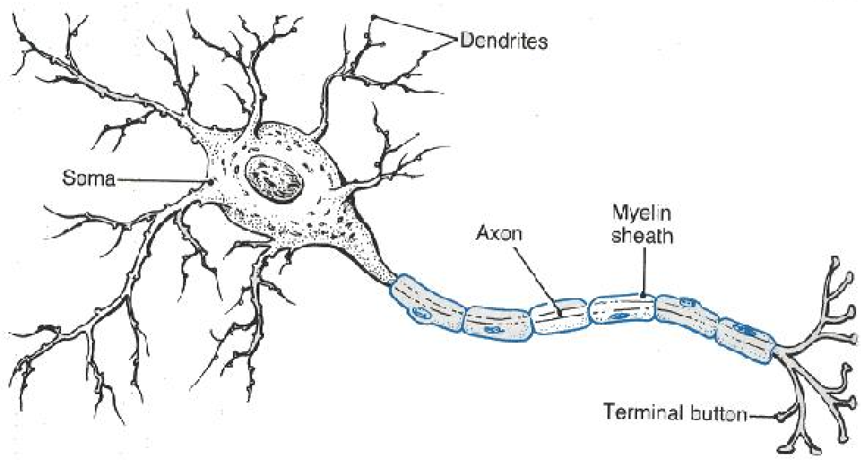


Figure 1: Anatomy of a neuron

into chemical form and dendrites, which re-transform chemical signals back into electrical format and transmit them to the somma.

The cell body or soma of a typical cortical neurons ranges in diameter from about 10 to 50 $\mu m$ [2]. The somma receives signals from dendrites and send them along the axon. The structure of the dendrites which have many branches allows a neuron to receive inputs from many other neurons via synapses. Length of dendrites vary from a few microns up to 100 microns. In contrast, axons are much longer and a single axon could even traverse the whole body. The axon makes an average of 180 synaptic connections with other neurons per $mm$ of length while the dendritic tree receives, on average, 2 synaptic inputs per $\mu m$ [2].

However, the most important feature of neurons is their specialty in transmitting electrical pulses. This specialty is a result of many ion channels that allow ions, predominantly sodium ($Na^+$), potassium ($K^+$), calcium ($Ca^{2+}$), and chloride ($Cl^-$), to move into and out of the cell. The concentration of ions are not the same inside and outside of the cell. For instance, sodium ion is much more concentrated outside a neuron, while the concentration of potassium ion is significantly higher inside. Ion channels control the flow of ions across the cell membrane by opening and closing in response to voltage changes and both internal and external signals [2].

## 1.2 Action Potential

In neuronal systems, information is carried on via short electrical pulses called action potential or simply spikes. Each neuron sends action potentials along its axon toward the synapses where the electrical pulses are transformed into chemical signals. These chemical materials (called neurotransmitters) stimulates the neighboring neuron(s) and make them generate action potentials again.

Under resting conditions, the potential inside the cell membrane of a neuron is about -70 $mV$ relative to that of the surrounding medium. In this case, the cell is said to be *polarized*. When positively charged ions flow out of the cell (or negative ions flow inward), a current is created which makes the membrane potential more negative. This is called *hyperpolarization*. The reverse process, in which positive ions move inward, makes the membrane potential less negative (or even positive), a process called *depolarization*. If a neuron is depolarized sufficiently to raise the membrane potential above a threshold level, the neuron generates an action potential [2].

The shape of an action potential is depicted in figure 2. It is an electrical pulse with amplitude of almost $100mV$ and approximate width of $1ms$.

Due to structure of the neuron and ion channels, it is impossible to generate an action potential right after another. One must wait a certain amount of time before the neuron is able to generate the next action potential. This period is called the *absolute refractory period*. Moreover, for a longer interval after generation of an action potential, producing another action potential is more difficult. This longer interval is called *relative refractory period*.

Action potentials traverse along the axon in an active process, meaning that the ion currents are generated continuously along the way through the axon membrane. This prevents an action potential to become severely attenuated (and vanished finally). Nevertheless, in a particular class of neurons, where there is *myelin* sheath around the axon, spikes could travel along the axon without being regenerated in distances up to $1mm$. Then, action potentials are regenerated in openings in the myelin sheath called *Ranvier nodes*. This process is known as *saltatory transmission* which is much faster and resembles the transmission of electrical signals along power transmission lines.

Axons terminate at synapses where the electrical pulse opens ion channels

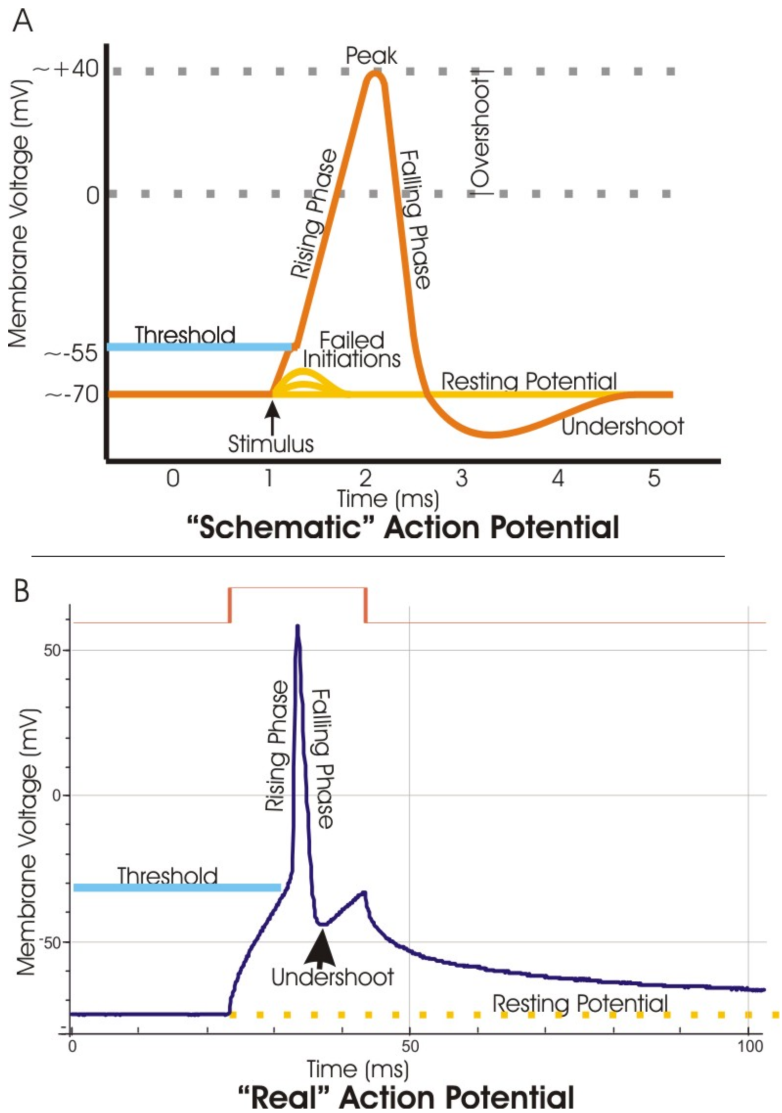


Figure 2: An action potential (from Wikipedia)

producing an influx of $Ca^{2+}$ which leads to the release of a neurotransmitter. The neurotransmitter binds to the dendrites of the neighboring neuron(s) causing ion-conducting channels to open [2]. Depending on the nature of the ion flow, the synapses can have either an excitatory, depolarizing, or an inhibitory, typically hyperpolarizing, effect on the postsynaptic neuron.

## 1.3 Neural Encoding

[1] Neurons encode information about the stimuli by firing sequence of spikes. Sensory neurons often respond most strongly to rapid changes in stimulus properties and are relatively insensitive to steady-state levels. In other words, they adapt to the stimulus [1]. Another important fact about the response of a neuron to a stimulus is that it is stochastic in nature. More precisely, if a fixed stimulus is applied to a neuron, the resulting spike train is not always the same and the relative timing of different spikes vary from trial to trial.

A hot topic in neuroscience is the way neurons encode information. There are two main candidates: rate codes and temporal codes. In rate codes, all the information about the stimulus is stored in the average number of spikes in a given time window. Therefore, the relative timing of individual spikes in that time window does not matter, i.e. it does not convey much information. In contrast, temporal codes are those in which the relative timing of each spike is important.

There are pieces of evidence suggesting that much of information about certain stimuli is conveyed by rate codes. Moreover, it is found out that [2]. However, it is shown in [1] that the relative timing of spikes plays a crucial role in behaviorial decisions of different species. This becomes even more important when one notes that certain decisions are made by only observing one or two spikes, which is clearly insufficient for *averaging* and determining the average rate since the output of the neuron to a fixed stimuli contains certain uncertainty itself, as discussed before. Moreover, it is show that neurons are not only sensitive to first order properties of the spike train (like mean), but also their second order such as variance and correlation [1].

Another concept in neural coding is the population coding. Neurons are often not stimulated individually but a stimulus causes many neurons to fire. This results in several interesting issues one of which is to investigate

[1] In this report, the words coding and decoding is different from what we mean in communication sciences for error correction purposes. Here, coding is equivalent to mapping between different set of symbols (stimulus on one side and spike trains on the other).

the way a population of neurons encode stimulus: do individual neurons act independently or they perform collective coding of the stimulus? If it is the latter case, how do they perform the task of coding and decoding? For instance, synchronous firing of two or more neurons is one mechanism for conveying information in a population code.

In [2], the authors have investigated encoding problem in a mathematical way. They have addressed the issue of estimating the firing rate of neurons. They have explained different models for neuron and statistical approaches to approximate the rate. Apparently, the firing rate is a function of the stimulus and much effort has been made to estimate this function. A very widely used model relates the stimulus $s(t)$ to the firing rate $r(t)$ according to the following equations:

$$r(t) = r_0 + F(L(t)) \tag{1}$$

where $r_0$ is the background firing rate and

$$L(t) = D(t) \star s(t) \tag{2}$$

in which $D(t)$ is a filter depending on neuron's characteristics. An example of function $F(.)$ is given by:

$$F(x) = r_{max}[tanh(\alpha(x - x_0))]_+, \tag{3}$$

where $x_0$ and $\alpha$ are two parameters determining the shape of $F(x)$, $r_{max}$ is the maximum firing rate and $[.]_+$ is $\max([.], 0)$.

## 1.4 Neural Decoding

The goal of neural decoding is to play the role of the brain, i.e. decode the spike train to understand what the neuron has tried to send about the outside world. Almost all of the approaches that investigate neural decoding use MAP decoding. The only issue here is to obtain the table which gives us the conditional probability of observing spike train $t_i$ when stimulus $s_j$ is applied to the neuron.

The result of different experiments show that one can distinguish between two different values of a stimulus by just observing the resulted spike train [2]. Even more, one can approximate a continuous stimulus by recoding spike trains of the corresponding neuron and employing appropriate filters [1].

# 2 Information Theory and Neural Encoding/Decoding

Information theory will help us understand how much information a neuron can transmit. In other words, it tells us how much information we gain about the stimulus by observing the response of a neuron to that stimulus. Here, we only focus on rate codes. If we denote the stimulus by $s$ and the firing rate by $r$, then we are interested in calculating $I(r;s) = H(r) - H(r|s)$.

An interesting question about neural code is if it is capacity achieving. By capacity achieving we mean that the firing rate distributions that maximize $H(r)$. For discrete rate functions, the probability distribution that maximizes $H(r)$ is a uniform distribution, i.e. $U(0, r_{max})$, where $r_{max}$ is the maximum firing rate.

To see if neural transmission is capacity achieving, consider a neuron which in response to a stimulus $s$ fires at rate $f(s)$. Denote the probability distribution of $s$ is shown by $p[s]$. Then the probability of having the stimulus falling between $s$ and $s + \Delta s$ is $\delta s p[s]$. On the other hand, the probability of having the response falling within this range for a capacity achieving neuron (the one with uniform probability distribution) is $|f(s+\delta s) - f(s)|/r_{max}$. By equating these two quantities we obtain [2]:

$$f(s) = r_{max} \int_{s_{min}}^{s} p[u] du, \tag{4}$$

where $s_{min}$ is the minimum amount of stimulus which leads to a response.

Equation (4) gives a testable criterion to see if the neural code is capacity achieving. All we need to do is to measure $f(s)$ for a given neuron and see if it satisfies equation (4). If it does, it shows that information transmission achieves capacity for that neuron. Laughlin has performed this experiment on the large monopolar cell (LMC) in the visual system of the fly and verified that the its firing pattern satisfies equation (4) [3].

The above analysis concerns a single neuron. Nevertheless, it could be extended to a population of neurons as well. In this case, the firing rate becomes a vector and we are now interested in maximizing $H(\mathbf{r})$, where $\mathbf{r}$ is the firing rate vector. Obviously, $H(\mathbf{r})$ is maximized when different neurons respond independently and have response probabilities that are optimal according to whatever constraint imposed (i.e. limited maximum firing rate). In this way, neurons remove inherent redundancy of natural stimuli to encode data efficiently. In other words, neurons act as whitening filters.

Similar tot the approach for a single neuron, information maximization criterion will result in a firing rate function for a group of neurons in population coding. We can verify the information maximization criterion by measuring actual firing rate pattern and compare to one predicted by theory. In fact, this is exactly what done in [4] for cat's visual system and the results indicate a good match between theory ad reality.

Note that maximizing other measures of performance, different from the mutual information, may give similar results. Nevertheless, the principal of information maximization is quite successful at accounting for properties of receptive fields early in the visual pathway [2].

The above approach only addresses sensory neurons as transducers where stimuli is translated into spike trains in a way that maximum information is carried on during this process. However, another interesting issue would be the rate of information transmission *inside* a neuron, i.e. along the axon. Experimental results show that typical information transmission rates of a single neurons is of the orders of a few hundred bits/s. For instance, in a particular case, information rates of $300 bits/s$ or $3 bits/spike$ was observed [1].

# 3 Reliability of the Neural System

In [1] authors have investigated the reliability of the neural system. They have considered neurons as noisy transmitters and have addressed the issue of how much reliable is the neural system. Here, reliability is equivalent to the preciseness of the neural system: noise and other physical phenomena imposes a limit on the accuracy according to which stimuli can be encoded and processed.

Now the main question is if the neural system is able to achieve these limits. If that is the case, then we can say that the neural system is reliable in a sense that it can reliably encode and process information up to the limits allowed by nature. According to the numerous experiments, it is apparent that we have a reliable neural system which means that not only neurons efficiently encode stimuli, but also that brain processes the data without adding much more noise to it.

# 4 Future Activities

So far, I have become only slightly familiar with how neuronal systems work and some issues regarding their mathematical modeling. From now on, I will start to read corresponding papers on topics related to coding theory and information processing in neuronal systems. I would also discuss our thoughts with Prof. Gerstenr to see if he has any ideas on this topic.

Currently, there are three main issues that I would like to study more:

- Error correction in neuronal systems: whether or not error correction is used in the neural system is not yet known to me. However, I would like to see if there are works on this topic. In particular, I think there could be error correction at two levels in the neuronal systems: neuron's level and brain's level. In neuron's level it is important to see if a neuron transmits information robustly. To check this hypothesis, we could represent spike trains by zero and ones. Then we check the dimension of this space to see if it is less than the number of spikes. Lower dimensions could suggest redundancy and error correction in neuron's level.

  At the brain's level, what I would like to study is to see how is brain able to tackle error in, for example, written language: if I write "problm" instead of "problem" you could easily understand what I meant. How brain implements such error correction in a fast and practical manner is what I like to investigate in more details.

- Fast decoding versus optimal decoding tradeoff: Living species are usually faced with a dilemma: they have to be fast in making a decisions based on the response of their neurons. However, fast decisions are more susceptible to error because of noise (when you have more time, you average the signal for longer times which suppresses noise to greater extents). Apparently, living things are capable of making appropriate decisions in very short amount of time and based on receiving one or two spikes. How they do that is another topic that I would like to consider in more details.

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