**Chapter 1**

**第一章**

**Neural Encoding I: Firing Rates and Spike Statistics**

**神经编码 I：神经冲动发射频率及其动作电势的统计学**

**1.1 Introduction**

**1.1 简介**

Neurons are remarkable among the cells of the body in their ability to propagate signals rapidly over large distances.

神经元在众多体细胞中以他们能在很长的距离内快速传递信号引人注目。

They do this by generating characteristic electrical pulses called action potentials, or more simply spikes, that can travel down nerve fibers.

他们通过产生能够在神经纤维上传导的被称为动作电势的特征性电脉冲（更简单的叫法是脉冲）来实现这样的特性。

Neurons represent and transmit information by firing sequences of spikes in various temporal patterns.

神经元以各种时间模式发射电脉冲序列来表示并传递信息。

The study of neural coding, which is the subject of the first four chapters of this book, involves measuring and characterizing how stimulus attributes, such as light or sound intensity, or motor actions, such as the direction of an arm movement, are represented by action potentials.

本书的前四章是关于神经编码的研究。其中涉及到检测和描述各种刺激的属性是如何用动作电势来表示，例如光或声音的强度以及运动动作（例如手臂运动的方向）。

The link between stimulus and response can be studied from two opposite points of view.

刺激和反应之间的关系可以从两个相反的观点来研究。

Neural encoding, the subject of chapters 1 and 2, refers to the map from stimulus to response.

第一至第二章的主题神经编码，指的是从刺激到反应的映射。

For example, we can catalogue how neurons respond to a wide variety of stimuli, and then construct models that attempt to predict responses to other stimuli.

例如，我们可以就神经元如何对多种刺激做出应答进行进行归类，然后建立模型来尝试预测其对其他刺激的反应。

Neural decoding refers to the reverse map, from response to stimulus, and the challenge is to reconstruct a stimulus, or certain aspects of that stimulus, from the spike sequences it evokes.

神经解码指的是从应答到刺激的映射，这其中的挑战是从该刺激中引起的动作电势中重新生成一个或部分刺激。

Neural decoding is discussed in chapter 3. In chapter 4, we consider how the amount of information encoded by sequences of action potentials can be quantified and maximized.

神经解码在本书中的第三章。第四章中我们考虑通过动作电势编码的信息如何能被量化和最大化。

Before embarking on this tour of neural coding, we briefly review how neurons generate their responses and discuss how neural activity is recorded. The biophysical mechanisms underlying neural responses and action potential generation are treated in greater detail in chapters 5 and 6.

在我们开始神经编码的旅程之前，我们先简要的回顾一下神经元是如何产生应答并讨论神经活动是如何被记录下来的。神经应答和动作电势的产生所依赖的生物物理学原理会在第五章和第六章中以涉及更多细节的方式来讨论。

**Properties of Neurons**

**神经元的性质**

Neurons are highly specialized for generating electrical signals in response to chemical and other inputs and transmitting them to other cells.

神经元是高度分化的细胞，它们对化学和其他输入产生电信号并将其传输至其他细胞。

Some important morphological specializations, seen in the drawings of figure 1.1, are the dendrites that receive inputs from other neurons and the axon that carries the neuronal output to other cells.

图例1.1是一些神经元重要的形态学特化，树突从其他神经元接受信息，轴突输出信息至其他神经元。

The elaborate branching structure of the dendritic tree allows a neuron to receive inputs from many other neurons through synaptic connections.

树突详尽的分支结构允许一个神经元通过突触连接从其他众多的神经元来接受输入。

The cortical pyramidal neuron of figure 1.1A and the cortical interneuron of figure 1.1C each receives thousands of synaptic inputs, and for the cerebellar Purkinje cell of figure *axons and* 1.1B the number is over 100,000.

图1.1A的皮质锥体神经元和图1.1C的皮质中间神经元各自接收数千个突触输入，对于图形轴突的小脑浦肯野细胞和1.1B，突触的数量超过100,000。

Figure 1.1 does not show the full extent of *dendrites* the axons of these neurons.

图1.1没有显示这些神经元轴突的树突的全部范围。

Axons from single neurons can traverse large fractions of the brain or, in some cases, of the entire body.

来自单个神经元的轴突可以穿过大脑的大部分，在某些情况下甚至能穿过整个身体。

In the mouse brain, it has been estimated that cortical neurons typically send out a total of about 40 mm of axon and have approximately 4 mm of total dendritic cable in their branched dendritic trees.

根据估计，在小鼠脑中每个皮质神经元有约40mm的轴突以及总长度约为4mm的树突。

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 μm.

轴突平均每毫米与其他神经元形成180个突触连接，而树突树平均每微米接收2个突触输入。

The cell body or soma of a typical cortical neurons ranges in diameter from about 10 to 50μm.

典型皮质神经元的细胞体或体细胞的直径范围为约10-50μm。

Along with these morphological features, neurons have physiological specializations.

伴随着这些形态特征，神经元具有生理学特征。

Most prominent among these are a wide variety of membrane-spanning *ion channels* ion channels that allow ions, predominantly sodium (Na+), potassium (K+), calcium (Ca2+), and chloride (Cl−), to move into and out of the cell.

其中最突出的是各种各样的跨膜离子通道，这些通道允许离子（主要是钠离子、钾离子、钙离子和氯离子）进出细胞。

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.

离子通道能对电压变化以及内外信息做出反应，通过开启或闭合控制离子的跨膜流动。

The electrical signal of relevance to the nervous system is the difference in electrical potential between the interior of a neuron and the surrounding extracellular medium.

与神经系统相关的电信号是神经元内部和周围细胞液之间的电势差。

Under resting conditions, the potential inside the cell membrane of a neuron is about -70 mV relative to that of the surrounding bath (which is conventionally defined to be 0 mV), and the cell *membrane* is said to be polarized.

在静息状态下，细胞膜内部的电势约为-70mV（相较于细胞液的电势，通常定义为0mV），这时我们成细胞膜是极化的。

Ion pumps located in the cell membrane maintain *potential* concentration gradients that support this membrane potential difference.

位于细胞膜上的离子泵通过维持电势浓度梯度来保证这样的细胞电势差。

For example, Na+ is much more concentrated outside a neuron than inside it, and the concentration of K+ is significantly higher inside the neuron than in the extracellular medium.

比如，钠离子的浓度在细胞外远高于细胞内，而钾离子则相反。

Ions thus flow into and out of a cell due to both voltage and concentration gradients.

离子的流入和流出细胞同时受电压和浓度梯度的影响。

Current, in the form of positively charged ions flowing out of the cell (or negatively charged ions flowing into the cell) through open channels makes the membrane potential more negative, a process called hyperpolarization.

通过打开离子通道使带正电的离子流出细胞（或带负电的离子流入细胞）形成的电流，使细胞内的电势更负，这个过程称为超静息。

Current flowing into the cell changes the membrane potential to less negative or even positive values. This is called depolarization.

相反，正电的离子流入细胞（或带负电的离子流出细胞）形成的电流，使细胞内的电势更正或甚至称为正值，这个过程称为去极化。

If a neuron is depolarized sufficiently to raise the membrane potential above a threshold level, a positive feedback process is initiated, and the neuron generates an action potential.

如果一个神经元去极化使细胞膜电势升高至一个临界值，一个正反馈的过程就此激活并产生了一个动作电势。

An action potential is a roughly 100mV fluctuation in the electrical potential across the cell membrane that lasts for about 1ms (figure 1.2A).

一个动作电势是一个持续时间约为1ms，电势差约为100mV的跨膜电势波动（见图1.2A）。

Action potential generation also depends on the recent history of cell firing.

动作电势的产生还依赖于细胞最近的产生冲动的历史。

For a few milliseconds just after an action potential has been fired, it may be virtually impossible to initiate another spike.

在一个动作电势发射之后的几毫秒内，可能根本不可能再产生另外一个动作电势。

This is called the absolute refractory period.

这个时间段被称为绝对抑制期。

For a longer interval known as the relative refractory period, lasting up to tens of milliseconds after a spike, it is more difficult to evoke an action potential.

在一个动作电势数十毫秒之后，相较于平常状态更难产生一个动作电势。这段时间被称为相对抑制期。

Action potentials are of great importance because they are the only form of membrane potential fluctuation that can propagate over large distances.

动作电势十分重要，因为它是唯一一种能够远距离传输的细胞膜电势波动。

Subthreshold potential fluctuations are severely attenuated over distances of 1 mm or less.

未能达到临界值的电势波动在传递了一毫米甚至更短的距离时就已经严重地衰减了。

Action potentials, on the other hand, are regenerated actively along axon processes and can travel rapidly over large distances without attenuation.

相反地，动作电势在沿着树突传递的过程中主动地再生，可以无衰减地在很长的距离上进行传递。

Axons terminate at synapses where the voltage transient of the action potential opens ion channels producing an influx of Ca2+ that leads to the release of a neurotransmitter (figure 1.2B).

树突在突触处终止，在突触处瞬时的动作电势打开离子通道，使钙离子内流并导致神经递质的释放。（图1.2B）

The neurotransmitter binds to receptors at the signal receiving or postsynaptic side of the synapse causing ion-conducting channels to open.

神经递质在信号接受一侧或突触后部一侧和受体相结合，导致离子通道的打开。

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.

根据不同性质的离子流动，突触对突触后部的神经元的作用既可以是使其兴奋的（去极化的）或者是使其抑制的（通常是超静息的）。

**Recording Neuronal Responses**

**记录神经反应**

Figure 1.3 illustrates intracellular and extracellular methods for recording neuronal responses electrically (they can also be recorded optically).

图1.3中展示了如何通过电学记录细胞内外的神经元反应（也可以通过光学来记录）。

Membrane potentials are measured intracellularly by connecting to a neuron a hollow glass electrode filled with a conducting electrolyte and comparing the potential it records to that of a reference electrode placed in the extracellular medium.

细胞膜内的电势通过一个和神经元相连并充满了电解质的中空玻璃电极测得，并以细胞膜外介质的作为参照来确定。

Intracellular recordings are made either with sharp electrodes inserted through the membrane into the cell, or patch electrodesthat have broader tips and are sealed tightly to the surface of the membrane.

细胞内电势的记录可以用尖的电极穿过细胞膜进入细胞或用有较大前端的片状电极紧贴细胞膜。

After the patch electrode seals, the membrane beneath its tip is either broken or perforated providing electrical contact with the interior of the cell.

在片状电极贴紧细胞膜后，其下的细胞膜破裂或穿孔从而为其提供与细胞内部的电交流。

The top trace in figure 1.3 is a schematic of an intracellular recording from the soma of a neuron firing a sequence of action potentials.

图1.3中最上部分，是来自激发了一系列动作电势的细胞体的细胞内记录示意图。

The recording shows rapid spikes riding on top of a more slowly varying subthreshold potential.

这个记录展示了变化相对较慢的亚阈值电势之上的快速动作电势。

The bottom trace in figure 1.3 is a schematic of an intracellular recording made some distance out on the axon of the neuron.

图1.3中底部的图线是一个距离一个神经元轴突一段距离的细胞内记录示意图。

These traces are drawings, not real recordings, and such intracellular axon recordings, although possible in some types of cells, are difficult and rare.

这些图线是为了展示而绘制而非实际的记录。这种细胞内的轴突记录虽然在少数几种细胞中是可行的，但操作起来还是很困难。

Intracellular recordings from the soma are the norm, but intracellular dendritic recordings are increasingly being made as well.

来自细胞体的细胞内记录较为常见，不过来自树突的细胞内记录也越来越常见。

The subthreshold membrane potential waveform, apparent in the soma recording, is completely absent on the axon due to attenuation, but the action potential sequence in the two recordings is the same.

在细胞体记录中的亚阈值膜电势波形因为在轴突上的衰减而完全消失了，但是动作电势在这两个记录上是相同的。

This illustrates the important point that spikes, but not subthreshold potentials, propagate regeneratively down axons.

这表明了重要的一点：动作电势而非亚阈值电势沿着轴突再生地传递。

The middle trace in figure 1.3 illustrates an idealized, noise-free extracellular recording.

中间的图线展示了一个理想化的没有噪音干扰的细胞外记录。

Here an electrode is placed near a neuron but it does not penetrate the cell membrane.

这里电极被放置在靠近神经元但却没有穿透细胞膜的位置。

Such recordings can reveal the action potentials fired by a neuron, but not its subthreshold membrane potentials.

这样的记录可以记录神经元发射的动作电势，但是不能记录亚阈值膜电势。

Extracellular recordings are typically used for *in vivo* experiments, especially those involving behaving animals.

细胞外记录通常用于体内实验，特别是那些涉及行为的动物实验。

Intracellular recordings are sometimes made *in vivo* but are more commonly used for *in vitro* preparations such as experiments on slices of neural tissue.

细胞内记录有时会用于体内实验，不过更多的用于体外实验的准备工作中，例如神经组织的切片。

The responses studied in this chapter are action potential sequences that can be recorded either intra- or extra-cellularly.

本章中所研究的是动作电势序列，可以通过细胞内或细胞外记录来获取。

**From Stimulus to Response**

**从刺激到应答**

Characterizing the relationship between stimulus and response is difficult because neuronal responses are complex and variable.

确定刺激和应答之间的关系面临的主要困难是神经应答的复杂性和多变性。

Neurons typically respond by producing complex spike sequences that reflect both the intrinsic dynamics of the neuron and the temporal characteristics of the stimulus.

神经元通常通过产生复杂的动作电势序列，同时反映了细胞内在的动力学以及当前刺激的特性。

Isolating features of the response that encode changes in the stimulus can be difficult, especially if the time scale for these changes is of the same order as the average interval between spikes.

分离编码了刺激变化的应答的特性很困难，当刺激变化的时间间隔和动作电势之间的平均时间间隔是同阶时尤为困难。

Neural responses can vary from trial to trial even when the same stimulus is presented repeatedly.

另外，即使重复施加完全相同的刺激，神经反应可能每次实验都不相同。

There are many potential sources of this variability including variable levels of arousal and attention, randomness associated with various biophysical processes that affect neuronal firing, and the effects of other cognitive processes taking place during a trial.

有很多潜在的因素会造成这种不确定性，比如不同程度的性唤醒和注意力，影响神经发射的各种生物物理学过程相关的随机性，以及实验期间发生的其他认知过程。

The complexity and trial-to-trial variability of action potential sequences make it unlikely that we can describe and predict the timing of each spike deterministically. Instead, we seek a model that can account for the probabilities that different spike sequences are evoked by a specific stimulus.

动作电势序列的复杂性和多变性使我们几乎不可能决定论式地描述和预测每个动作电势。所以，我们寻求一个可以表示一个特定刺激所引发的不同动作电势序列的概率。

Typically, many neurons respond to a given stimulus, and stimulus features are therefore encoded by the activities of large neural populations.

通常，很多神经元会对同一个刺激做出反应，因此刺激的特性是由大量神经元集群的活动所编码的。

In studying population coding, we must examine not only the firing patterns of individual neurons, but also the relationships of these firing patterns to each other across the population of responding cells.

在研究集群编码时，我们不仅需要考虑单个神经元细胞的发射模式，还需要考虑应答状态下细胞群不同发射模式之间的关系。

In this chapter, we introduce the firing rate and spike-train correlation functions, which are basic measures of spiking probability and statistics.

本章中，我们介绍发射频率以及动作电势序列的相关性方程，他们是动作电势的概率与统计学的基础。

We also discuss spike-triggered averaging, a method for relating action potentials to the stimulus that evoked them.

我们也会讨论动作电势触发平均法，以此来将动作电势和引起他们的刺激联系起来。

Finally, we present basic stochastic descriptions of spike generation, the homogeneous and inhomogeneous Poisson models, and discuss a simple model of neural responses to which they lead.

最后，我们讨论动作电势生成的基本随机描述——均匀和非均匀泊松分布，以及一种由此得到的神经反应的简单模型。

In chapter 2, we continue our discussion of neural encoding by showing how reverse-correlation methods are used to construct estimates of firing rates in response to time-varying stimuli.

在第二章中，我们通过展示如何用逆相关性方法生成对时间变化做出反应的刺激引起的神经发射速率的估计来继续讨论神经编码。

These methods have been applied extensively to neural responses in the retina, lateral geniculate nucleus (LGN) of the thalamus, and primary visual cortex, and we review the resulting models.

这些方法已经大规模地应用在视网膜，丘脑外侧膝状核（LGN）以及初级视觉皮层等部位的神经反应中，我们会回顾这些模型。

本小节术语表