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Cambridge University Press
978-0-521-87303-1 - Information Processing by Neuronal Populations
Edited by Christian Holscher and Matthias Munk
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Part I INTRODUCTION

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1

How could populations of neurons encode information?

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Information representation in neuronal populations: what is the "machine language" of the brain?

Research in the area of neuroscience and brain functions has made extraordinary progress in the last 50 years, in particular with the advent of novel methods that enables us to look at the properties of neuroanatomy and neurophysiology in much finer detail, and even at the activity of living brains during the performance of tasks. However, the question of how information is actually represented and encoded by neurons is still one of the "final frontiers" of neuroscience, and surprisingly little progress has been made here. How information is encoded in the brain has captivated medics, scientists, and philosophers for centuries. Scholars such as Leonardo da Vinci or René Descartes had already an astonishingly detailed knowledge of the anatomy of the brain, and had made suggestions that it is the brain that processes information and even harbors the seat of the personality or of the soul. However, whenever suggestions are brought forward how information might be processed and represented in the brain, these often turn out to be simplistic and idealistic. These rarely add up to more than a kind of "homunculus" that somehow receives information that is received via the eyes or the ears. This model only transfers the problem of information representation from the brain to the homunculus.

One problem with the research of information encoding is that it is completely counter-intuitive. Often it is very helpful to explain complex anatomical and functional processes with mental images or sketches that compare

Information Processing by Neuronal Populations, ed. Christian Hölscher and Matthias Munk.
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a difficult, unknown process with objects and machines of everyday use that people can easily picture. Unfortunately, it is impossible to do so with the topic of information encoding without ending up with comparisons that convey a completely wrong message. In the past, the brain had been compared to machines that were in use at the time, e.g. Descartes compared the nervous system to water pipeline networks that convey information via liquid-filled tubes to the brain ventricles, where the information is gathered and presented to the pineal gland, the proposed seat of the soul. Later, the brain had been compared to a telephone exchange, with information arriving from the outside at the "central switchboard" where it is processed, and leaving the brain through outgoing lines. More recently, the brain has been compared to a computer.

However, none of these images actually really explains how the brain processes information, since the architecture and the actual algorithms that govern information processing in neuronal populations are completely different from a computer that runs a piece of software on a silicon chip. The reason for this is based in the very counter-intuitive process of translating information about the real world (e.g. the color of a plant) into abstract symbols or codes that have nothing in common with the original information. It is difficult to explain to the lay person that a digital camera translates an image into rows of zeroes and ones. These rows encode the information "somehow" and can be translated again by a monitor or a printer into a two-dimensional picture that we can "understand." It is impossible to grasp intuitively where the information of the picture is located in the string of zeroes and ones. In a similar fashion, it will not be possible to provide an intuitive model of how information about the real world is encoded in neuronal activity. Neuronal activity consists of discrete "digital" states such as action potentials, but also encompasses analogue states of membrane potentials on dendrites and cell bodies. Any model that wants to explain neuronal encoding of information will have to work within these parameters.

In the 1930s, techniques became available that permitted to record the activity of single neurons, and of large brain areas (electroencephalograms, EEGs). This very much formed and influenced the models and concepts developed in those times. The main concepts that were emphasized then were the models of information coding in neurons by rate coding. Even though several other mathematical concepts and network models did exist back then, the available techniques did not provide any data that could be used to underpin such models.

With the development of single-cell recording in freely moving animals it became possible to actually observe neurons during the process of information processing and storage. The data of single-cell recording had been mainly interpreted in the traditional view that neurons code information by modulating firing rates. In parallel, large-scale activity of brain areas became observable

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with the development of PET scan technology. However, the resolution of these techniques did not allow for any analysis of neuronal population activities and network properties, and the available data very much biased the views and models greatly towards a single-cell information encoding theory, even though it was understood at the time that information was most likely represented in a distributed form in networks.

With the advent of modern technology that allows the recording of groups of single-cell activity of large populations of neurons, as well as the recording of local field potentials with electrode arrays in several brain areas simultaneously, it has become possible to observe how large networks behave during the performance of memory or recognition tasks. We now can ask specific questions of how exactly networks are coordinated and how neurons are associated or dissociated in their activity during information processing. We can test network models and adapt them or discard them. The gap between single neuron activity and large-scale cortical activity can now be filled, and the experimental results allow us to make specific statements on how information is processed and stored in the brain.

We are now at a threshold where the novel observations and experimental data need to be integrated into new concepts and models of how the brain processes information. While the technology has made extraordinary advances, the concepts in people's minds still lag behind. We can still find books, reviews, papers that reiterate single neuron encoding concepts and do not mention network properties that have been observed and described in neuronal networks in the living brain. The time has come to get people from different backgrounds together to synthesize the available results and information that have accumulated in the last 10 years.

This book will try to do exactly that. The different authors that have contributed chapters in this book present their research findings and formulate a set of theories and concepts that will encompass the latest findings. The authors present data at single-cell level in vitro and in vivo, and at neuronal population level in vivo comparing field potentials (EEGs) in different brain areas, and also data from spike recordings from identified neuronal populations during the performance of different tasks.

The results obtained over the last decade cast new light on how the brain acts as a system, bringing together separate areas of research that could not have been seen in functional context before. For example, neuronal firing is affected by activating projections from the basal brain, e.g. the nuclei that use acetylcholine as their main neurotransmitter. The neurophysiology and pharmacology of acetylcholine receptors have been known for many decades. However, the functional context of their activity could only have been guessed at. We now know how the state of cortical activation is modulated by these projections that

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basically activate inhibitory feedback oscillation loops. These oscillations impose temporal patterns on neuronal activity that are crucial for information processing and memory formation. This controls how neuronal functional assemblies are brought together or are kept separate and how synaptic weights are changed through synchronous excitatory input, and they dynamically switch associations of different cortical areas and of different information. This concept then can be applied to states of cognitive dysfunctions or disorders, such as schizophrenia. Here, the disturbance of the dynamic network association control could well be responsible for the inability to separate disconnected events in time and space or to bring together segments of events that belong together.

This book strives to cover the range of single-cell activity analysis through to observation of network activity and finally to brain area activity and cognitive processes of the brain, discussing and proposing mechanisms that are of importance for the system to function.

Questions that will be addressed in the book are:

How do different brain areas interact when processing information? As recent research has shown, brain areas such as the hippocampus are not isolated units that can be studied independently of other brain areas that relay already highly processed information to the hippocampus where it is associated with higher-level representations.

How do neuronal populations encode information? More and more neurophysiologists employ multi-electrode recording techniques to study how information is encoded in networks. It has become increasingly clear that single-cell recording and analysis is limited and is insufficient in the assessment of what information is encoded in the particular neuronal populations of interest. We know information is distributed in networks that are best analyzed *in toto* and in behaving animals. Modern techniques make it possible to use electrode arrays, and the computing power and software available today makes it feasible to analyze large sets of data.

It is now possible to investigate how information is distributed over networks, and that this distribution does follow "holistic" network and parallel processing rules rather than linear data relay and analysis. Convincing evidence for this are the error correction properties, pattern completion properties, and distributed information properties of specific brain areas.

How are networks formed and separated from or associated with other networks? The observation that neurons fire in temporal patterns, and that

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EEG field potential oscillations have powerful influences on the firing probability of neurons, seems to have been accepted in the last 10 years, with some initial reluctance. While there are still schools of thought that completely ignore these findings and do not incorporate them into their models, the large increase of available data from different laboratories and from different species, brain areas, and task performances in this area clearly emphasizes the need to do so. We will incorporate these findings into our models, and they will allow us to develop specific models of information processing and representation in the brain.

A brief overview of current ideas how information might be encoded in the brain

To help interested readers who have only a limited background in this topic to understand the very specific reports in the following chapters, we provide a brief overview of theories and concepts of how information might be encoded in neuronal activity.

Frequency coding

The first and main theory of how information is translated from input systems such as temperature receptors in the skin to neuronal activity is that of frequency coding. Recordings of neurons in the skin have shown that temperature or pressure is represented in the firing rate of the neuron that gets the input from the sensors in the skin. A low-temperature stimulus causes the relay neuron to fire slowly, and increasing temperature will increase the firing rate of that neuron. There is a direct relation between sensory quality (temperature) and neuronal activity (see Fig. 1.1).

Another good example for frequency coding is found in the auditory system. Sound waves activate the eardrum which in turn transmits these waves to the cochlear system. The basilar membrane is a resonant structure and is deflected in response to these sound waves. Each location along the basilar membrane responds best to a small range of sound frequencies and acts as a filter. When sound waves activate the basilar membrane of the inner ear, these vibrations are transmitted to the hair cells. This triggers the release of neurotransmitter at the base of the hair cell and the excitation of primary afferent neurons. The neurons encode the information for transmission to the CNS. The firing frequency of these neurons is a direct related to the sound frequency up to 1 kHz. This means a 500-Hz sound will activate a 500-Hz neuronal firing, a direct frequency encoding of the sound waves into neuronal firing activity. However,

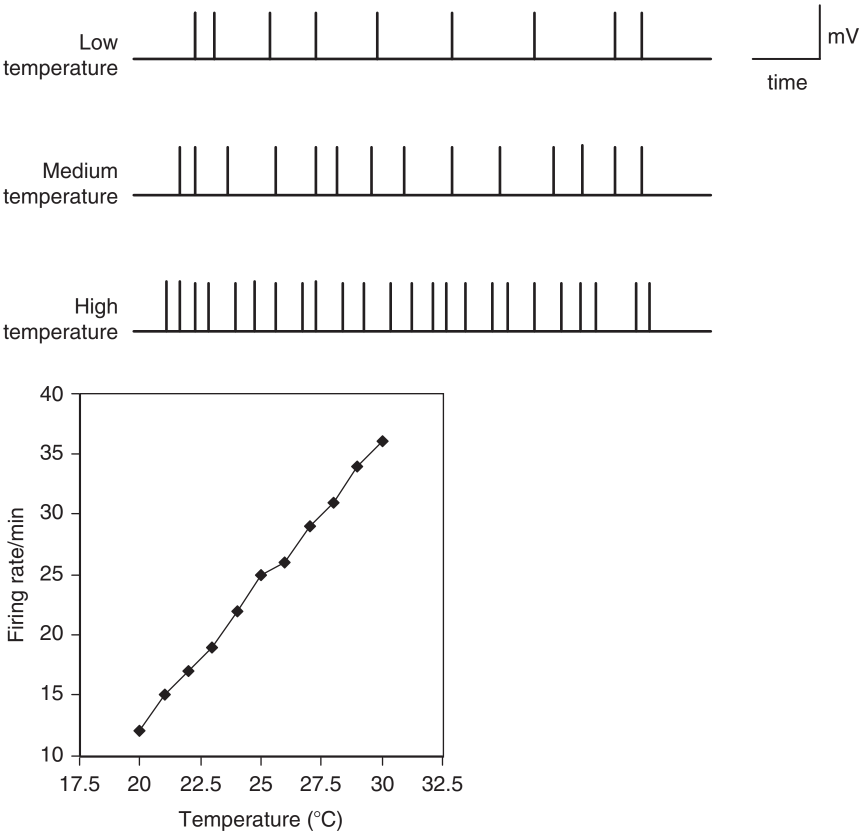

Figure 1.1 (Top) Schematic representation of frequency coding of a temperature-sensitive peripheral neuron in the skin. Recordings of neuronal activity are made while heating the skin to higher temperatures. The change in temperature is directly correlated with the firing rate of the neuron (tonic type of response). (Bottom) Linear correlation between stimulation of skin with a temperature probe and the firing rate of a neuron in the skin.

the maximal firing frequency is limited to about 1 kHz. Above this threshold, different encoding strategies must be chosen.

Frequency coding is seen by a majority of researchers as the main (if not only) type of information encoding.

Topological coding (labeled line)

It is important to note that the firing activity of a neuron that conveys temperature is in no way different to the firing activity of a neuron that relays touch or pain information. The rate coding and the action potential is similar. The reason why a sensory sensation is identified as touch or pain is that it is defined from which type of sensory input system the information comes.

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Another example is the projection of a touch receptor in the thumb that will relay information to the primary somatosensory cortex that represents the thumb. No special encoding of location in the firing activity of neurons is required here, since the anatomical projections are fixed. This is sometimes called the “labeled line” type of coding. Proof for this concept is that these projections can be wrong in some instances, and phantom pain can be observed. An example is the typical pain in the arm that patients with angina pectoris (blood supply problems to the heart) experience. The pain receptors that originate in the heart also appear to project to somatosensory areas that represent the arm, and cause pain sensation in the wrong body part.

Another good example of topological coding comes from the auditory system. As described above, each location along the basilar membrane responds best to a small range of sound frequencies and acts as a filter. Therefore, it is sufficient for a neuron that innervates an area of a defined frequency to fire when it is activated in order to transmit the information that this defined frequency had arrived. No further information is required, since these sensory neurons can only be activated if the particular frequency has been received. The firing frequency of the neuron is of secondary importance, since due to the physical properties of the cochlea the neuron can only be activated by this defined frequency. Instead, the firing frequency of neurons can be used to indicate the intensity of sound. A low-frequency activity of a 5-kHz neuron will indicate that the received sound intensity is low, while high-frequency firing activity will indicate a loud 5-kHz sound. Here, topological and frequency coding are combined.

Phase coding

Phase coding is a different type of information coding that is independent from firing rate. Here, the timing of the neuronal action potential is of importance. A simple example is given in Fig. 1.2, where pressure changes in

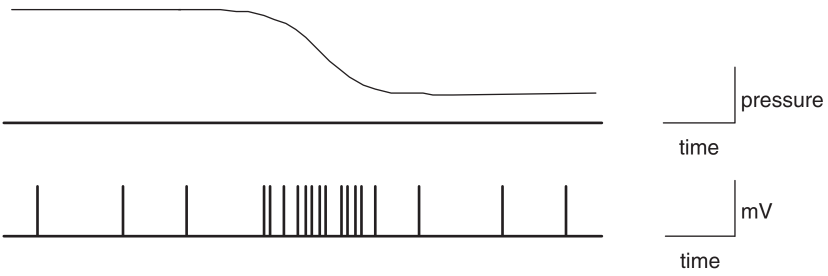

Figure 1.2 Schematic representation of a neuronal response to touch. The top trace shows the change of pressure applied to skin. Only the changes of pressure on the skin are coded by this type of neuron, not the absolute values of pressure (phasic type of response).

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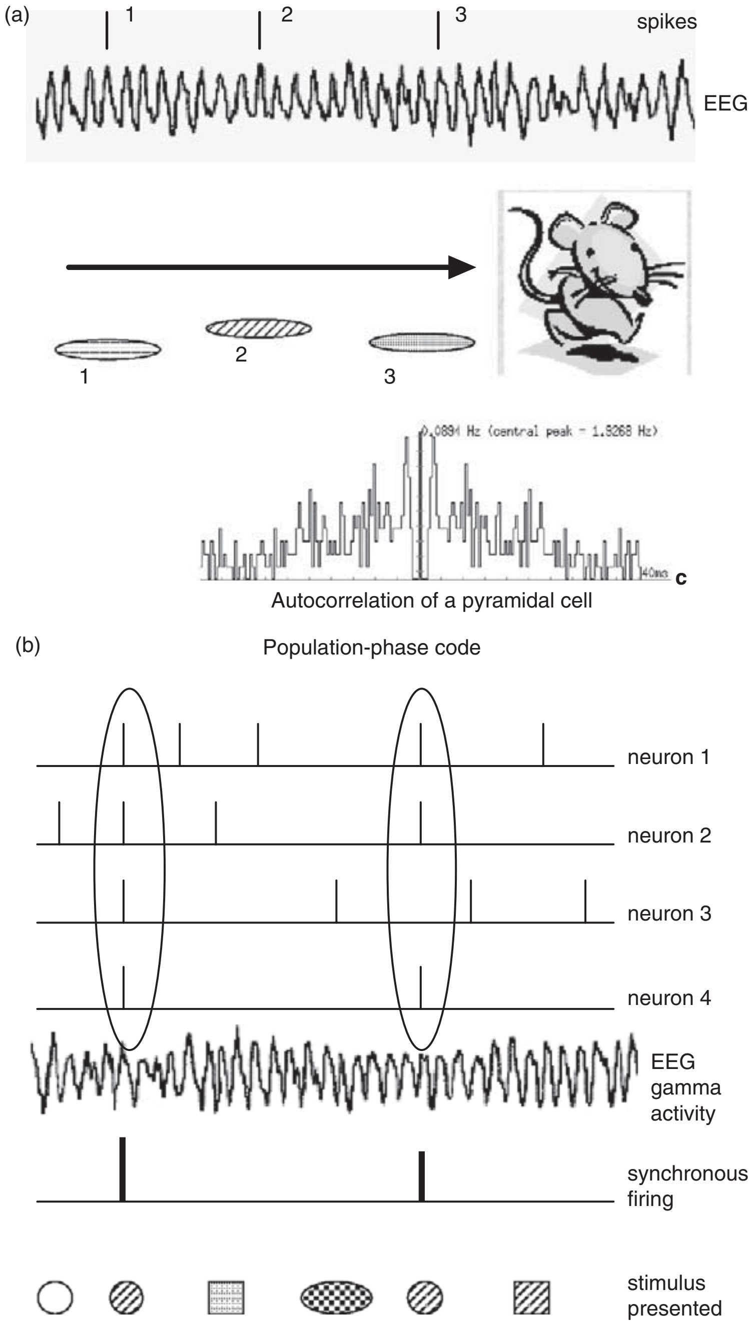

Figure 1.3 (a) Phase coding in the hippocampus. Pyramidal neurons in the hippocampus often fire in a burst mode, with one to five spikes followed by inactivity. The firing activity is tightly coordinated in time in relation to theta activity in the EEG. A neuron recorded from a rat that travels through space will fire in a particular

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skin receptors are coded by neurons that only respond to changes in pressure (phasic response), and not to the absolute amount of pressure. A single spike would be sufficient to relay the information “pressure change,” since the spike will only fire under those conditions. Other examples are given in Chapters 7 and 16, where the timing of neurons signify a particular information content, e.g. the location of an animal in space. Figure. 1.3 (below) shows an example of how hippocampal neurons appear to encode space. The firing activity of these neurons rarely exceeds 10 Hz, suggesting that frequency encoding is not of importance in this system. In fact, most hippocampal neurons only fire bursts of about five spikes and then remain silent for some time until the next burst appears. Such a firing mode would not be suitable for frequency coding. It is ideal for phase coding, and the highly controlled temporal relationship of firing activity of these neurons with the theta EEG rhythm strongly points into the direction of phase coding. The advantage of this coding principle that it is very fast and can relay information with only one spike. The disadvantage is that it is a digital type of information coding and cannot differentiate between various states of pressure, which would require an analogue type of encoding as seen in the frequency modulation technique. An overlay of frequency with phase coding therefore allows a combination of digital and analogue information encoding.

Population coding

Single neurons can only convey a very limited amount of information. In addition, single neurons are noisy and unreliable and therefore cannot be depended on in absolute terms. Therefore, information is often encoded in populations that code similar information. Instead of relying on one noisy neuron,

Caption for Figure 1.3 (cont.)
area in space (the place field), and the spikes will be highly coordinated in relation to the phase of the theta wave. Spikes of three neurons are shown that fire at different place fields while the rat is moving through space. This is reproducible, and the neurons will (almost) always fire in this confined way. An autocorrelation of the spike activity will also show a temporal order. Shown is the time between spikes in the firing activity of this neuron. The firing in time is not random, but follows a temporal ordered in the theta frequency (see also Chapter 7 for details). (b) Phase coding of neuronal activity. Neurons of a population are brought together by firing synchronously. The synchronous activity is controlled and induced by EEG field potentials (in this case in the gamma frequency). The EEG field potential oscillations control the firing probability of excitatory neurons and confine neuronal spikes to defined time windows. Populations of neurons can be assembled or separated by this method.

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