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An Introduction to Neural Information Processing

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Preface

The human brain might be the most complicated system in the universe. Neuroscience, the aim of which is to elucidate the mechanisms underlying brain functions, is one of the scientific frontiers in the twenty-first century. To understand how brains work, neuroscience researches involve various approaches.

It has long been understood that anatomical architecture of the brain, morphological structure of cells, and even chemical structure of membrane proteins are essential for brain functions, and knowledge about how brain functions are realized has been accumulated via traditional approaches of neuroscience including neuroanatomy, neurophysiology, neurochemistry, cellular and molecular neuroscience, etc. However, brain functions mostly involve neural information processing, which relies on dynamic processes at various levels; computational approaches are therefore indispensable for understanding the process and mechanism underlying neural information processing.

Although a brain should have somewhat stable anatomical connectivity among its different areas, the functional connectivity among relevant brain areas is dynamically changing corresponding to the brain function it is undertaking; at the meantime, the activation of a certain brain area is characterized by the firing activity of the neurons in the area, while the temporal pattern of neuronal firing sequence and the concerted activity of neuronal population are crucial for neural signal transmission and neural coding; furthermore, biophysical properties of ion channels located on the plasma membrane and their dynamic modulation under various physiological and functional conditions determine the activity of a neuron and also influence the synaptic connectivity between neurons which is responsible for signal transmission. To understand these aspects, experimental observations made by approaches such as neuroimaging and neuroelectrophysiology are doubtlessly necessary, but quantitative analyses or even theoretical analyses via modeling and simulation using mathematical tools contribute significantly for getting more insight into such processes in detail. Such demands in neuroscience research give rise to the branch of computational neuroscience, which is developed based on the interactions between neuroscience and other disciplines such as mathematics, physics, as well as cybernetics and information science and makes it a growing field during the past decades.

However, to solve biological problems by approaches from mathematical and/or relevant disciplines is not simply for biologists to pass their data to mathematicians for computation. To make such interdisciplinary collaboration efficient and productive, it is necessary for researchers with different backgrounds to understand the language of his/her collaborators. It should be good for people conducting computation to understand relevant background of the biological problems they are dealing with, so that they can have an insight into their biological significance. At the meantime, it would also be helpful for his/her partner-biologist to understand the philosophy underlying the mathematical tools adopted, so as to make the communication effective.

On the other hand, given that the human brain is the most complicated and delicate system for information processing, people have long been exploring to develop brain-like machine or system to mimic brain functions. Actually, artificial intelligence has persistently been inspired by the functions of biological neural systems. Therefore, to acquire some basic knowledge about biological neural systems should also be beneficial for those who are working in the field of neural engineering, neuromorphic engineering, neural robotics, and so on and so forth.

Having backgrounds in relevant fields such as mathematics, physics, and biomedical engineering and having been working in this multidisciplinary area of computational neuroscience for decades, the authors of this book are well experienced in combining knowledge from these different disciplines into the field of computational neuroscience. They well understand the difficulties that may be encountered by those with background other than biology but are practicing in or preparing themselves for neuroscience research. The authors wish that this book can provide some basic knowledge about neurobiology at a proper level, neither too detailed nor too simple.

The potential readers for this book are mainly supposed to be those with mathematics, physics, or informatics background, who are willing to join neuroscience research and apply their knowledge in these fields to solve neurobiological problems. For those with neurobiology background who are interested in employing mathematical tools in neuroscience studies, this book may also provide some guidance by introducing some pioneer works as well as some recent advances in the field. Some of the authors' own works are also introduced.

The main parts of this book are organized as follows:

Chapter 1 is an introduction about the interdisciplinary essence of computational neuroscience. An overview of this particular branch of neuroscience is presented by giving a historical review on the development of this field together with a number of pioneers' contribution to this field.

In Chap. 2, the necessary neuroscience background is introduced in more depth than is generally the case in monographs with similar topics. In addition, the materials presented there were selected from a point of view of neural information processing, so that the readers would have enough knowledge to read monographs and original papers without too much difficulties.

In Chap. 3, models of single neurons—typical examples of neural information processing studies—are elucidated in detail. This is not only for the reason that neurons are considered as both anatomical and functional elements of nervous systems, understanding neurons is essential for further reading, but also the classical studies on neuron modeling give readers good examples how to develop neural models based on questions raised by neuroscientists and how to solve such problems using mathematics and informatics approaches verified by biological experiments. This chapter gives readers many classical examples to show how to build models firmly grounded on experimental results and in turn guide further experiments. Both reductionist and dynamic approaches are used. The topics discussed in this chapter are simple enough to be understood without too much background knowledge and detailed enough to make readers realize the essence of interdisciplinary studies. Some arguments unsolved until now are also mentioned for reader's own consideration and judgment.

In Chap. 4, neural coding theories are introduced. Given that the main task of the nervous system is to process and transmit the information of the environment stimulations, as well as conduct the action of motor system, one of the essential issues of neuroscience research is to understand the "code" that the nervous system applies for information processing and transmission. During the past decades, neuroscientist investigated the relationships between the environmental stimulation/motor actions and the properties of neuronal activities, such as firing rate, the temporal structure of the firing sequence, as well as the coordination of neuronal activities in neuronal assembly, which are termed as rate coding, precise time coding (temporal coding), and population coding, respectively. These aspects will be introduced together with Bayesian inference.

In Chap. 5, a number of advanced fields in sensory information processing are introduced, including some aspects in visual information processing and olfactory information processing. Among the sensory systems, the visual system is the most complex and at the meantime the best understood one. Visual information processing occurs in the retina which is the peripheral part of the system, as well as in the central visual regions. Neurons in different parts of the visual pathway have different response properties, which can be measured using well-designed laboratory stimulations together with proper computational tools. Besides, adaptation to the environment is one of the important features of visual neurons; such property allows the visual neurons to well encode the visual stimulations which changes among a wide range via their limited range of activity. Coding during visual adaptation forms another topic of this chapter. The olfactory system is another sensory system which is important for animals to survive in the natural environment. Olfactory information processing is a hot topic that has been intensively studied in recent years.

In Chap. 6, a number of neural network models aiming for modeling brain functions are introduced. The Hopfield model is such a classical one which played a very important role in the early time of applying network models to mimic brain functions. It assumes very simple and abstract forms of neurons and synapses, but nevertheless captures some fundamental features of neural information retrieving. Continuous attractor neural network is a one-step advance of the Hopfield model. It incorporates more biological elements and describes the encoding of continuous variables in neural system successfully. Reservoir networks, including liquid state machine and echo state machine, emphasize on the fact that a neural system typically contains a huge number of neurons. It exploits the enormous variations of network states and simplifies the effort of information decoding significantly. Special network models are also proposed to implement decision-making in the brain. Recent studies have explored how the short-term plasticity of synapses enriches the dynamics and computational capacities of a neural network.

Among these, Fan-Ji Gu drafted Chaps. 1 and 3; Chap. 2 was drafted by Fanji Gu and Peiji Liang; Chaps. 4 and 5 were coauthored by Pei-Ji Liang and Si Wu, and Chap. 6 was by Si Wu.

Although numerous textbooks on neurobiology and neuroscience are available, textbooks dedicated to computational neuroscience are comparatively scarce. By providing knowledge on both biological and computational sides, as well as the combination of these knowledge in the field of computational neuroscience, we wish this book provides a good guidance for those researchers and students who are preparing themselves for this interdisciplinary field. Of course, it is unrealistic to pack all aspects of computational neuroscience in one book; further readings are encouraged. Reading materials including more detailed textbook on neurobiology and relevant references about computational neuroscience are recommended in the last sections of related chapters.

Last but not least, we would like to express our heartiest gratitude to Prof. Walter J. Freeman for his kind permission to quote his words in our personal communication and the figures published in *Scientific American*, which he owes the copyright. We are also indebted to Profs. Tiande Shou, Hongbo Yu, Hans Liljenstöm, and Hans Braum for discussing some ideas published in this book. We acknowledge Drs. Danke Zhang, Yuanyuan Mi, Mrs. Wenhao Zhang, Luozheng Li, Liutao Yu, Xiaolong Zhou, Gang Wang, Tao Wang, and Miss Yan Xia for their hardworking in preparing the documents for the book. We also wish to thank Dr. Peter Butler and Dr. Peng Zhang for encouraging us to publish this book in Springer and helping us with many things.

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Contents

Chapter 1
Introduction

Abstract In its essence, the brain is an information processing system, which is the most complicated system people have ever known. Mathematical modeling and computer simulation may play a vital role in integrating data from different levels of the brain and thus to elucidate the underlying mechanisms of the brain function. Many interdisciplinary fields have been developed for different aspects of this topic. However, the core of these different branches is the same—neural information processing, which is the main topic of this book.

A brief history of the study of neural information processing is given. Close combining theoretical analysis, modeling and simulation, and biological experiments is emphasized. This book is mainly for those readers who want to know the necessary knowledge about the brain with adequate depth, learn how to use mathematical modeling and computer simulation to solve neurobiological problems, and learn some latest progress in this field.

Keywords Neural information processing • Mathematical modeling • Computer simulation • Interdisciplinary study

People are used to using the most advanced machine at their time as a metaphor of the brain, such as a water-powered mill, a steam engine, a telephone switchboard, a digital computer, and the Internet. However, the brain is the most complicated system in the universe we have ever known; no machine mentioned above is a precise metaphor of the brain, which contains 10^{11} neurons, a number that can be compared with the one of all the stars in our known universe. In addition, there are 10^{15} connections called synapses between neurons. Thus, to study the brain and mind is the biggest challenge scientists have ever met; the task is a little like imaging an elephant by a group of blind men where each man can only touch a part of the animal. The man who touches its nose may say that it is like a tube and the one touching the foot may say that it is a column, while the one touching its trunk announces that it is just like a wall. Only summarizing all the impressions together may give a quite realistic picture. So does brain research. What makes the thing more complicated is the fact that the brain is a multilevel hierarchical system, where each level has its own emergent properties which its composing elements do not have. No single technology can solve all the problems; a variety of different technologies are needed to study the brain and mind from different aspects and at

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different levels, and only synthesizing all the results together may give an approximately realistic view of the brain and its function, for which mathematical modeling and computer simulation may play a vital role.

One thing now we definitely know is that brains are information processing systems. Of course, energy and substances are important for normal functions of the brain; however, these are so-called enabling factors of the brain function. The essential role which the brain plays for the survival of the animal is to receive, transfer, process, store, and retrieve information, based on which the animal can decide its action, e.g., fight or flight.

A quantitative approach should be used for such studies. This idea can be traced back to the 1940s. American neurophysiologist Warren McCulloch and mathematical biologist and logician Walter Harry Pitts, Jr. (1943), are among the first to describe neuronal function with mathematics. They are the founders of neural network theories. Their 1943 paper is the first important one to inspire others to study neural information processing quantitatively, although some mathematical models of neurons had been developed even long ago before them (Lapicque 1907).

In 1948, American mathematician Norbert Wiener, who had been interested in biology since his childhood, published his classical book *Cybernetics: Or Control and Communication in the Animal and Machine* (Wiener 1948), in which he used the word "communication" to denote information coding, processing, storage, and retrieving; he emphasized the key role of the concept "information" in understanding an animal's behavior. He is also a pioneer in encouraging mathematicians, physicists, electrical engineers, and experts from other fields to study nervous systems. In the introduction of his book, he emphasized:

> It is these boundary regions of science which offer the richest opportunities to the qualified investigator. They are at the same time the most refractory to the accepted techniques of mass attack and the division of labor. If the difficulty of a physiological problem is mathematical in essence, ten physiologists ignorant of mathematics will get precisely as far as one physiologist ignorant of mathematics, and no further. If a physiologist, who knows no mathematics, works together with a mathematician who knows no physiology, the one will be unable to state his problem in terms that the other can manipulate, and the second will be unable to put the answers in any form the first can understand. Dr. Rosenblueth has always insisted that a proper exploration of these blank spaces on the map of science could only be made by a team of scientists, each a specialist in his own field, but each pocessing a thoroughly sound and trained acquaintance with the fields of his neighbors; all in the habit of working together, of knowing one another's intellectual suggestion before it has taken on a full formal expression. The mathematician need not have the skill to conduct a physiological experiment, but he must have the skill to understand one, to criticize one, and to suggest one. The physiologist need not be able to prove a certain mathematical theorem, but he must be able to grasp its physiological significance and to tell the mathematician for what he should look.

Although these words were written more than 65 years ago, they are still as instructive today as at that time. Wiener pointed out that the concept of energy, which people had paid much attention to before, was not the key to understand control and communication. Energy is only an enabling factor for information coding and processing. The core concept is information! He and Hungarian–American mathematician John von Neumann, who is also one of the founders of digital computers and wrote a book titled *The Computer and the Brain* (von Neumann 1958) to compare these two systems just before his death in 1957, organized a series of symposiums on control and communication since 1943. At his later years, Wiener had paid more attention to a branch of cybernetics, biological cybernetics, especially to neural information processing (Wiener and Schade 1964).

Although McCulloch and Pitts proposed a mathematical model of neurons and elucidated that their neural network could do any job a Turing machine could do, their network lacks the ability to learn. However, brains can learn. Canadian psychologist Donald Hebb is the first to denote that synaptic plasticity may underlie learning. He wrote in his famous book *The Organization of Behavior: A Neuropsychological Theory* (Hebb 1949) the following hypothesis: "When an axon of cell A is near enough to excite a cell B and repeatedly or persistently takes part in firing it, some growth process or metabolic change takes place in one or both cells such that A's efficiency, as one of the cells firing B, is increased." This hypothesis is usually summarized as "Cells that fire together, wire together." And it is used to being named as the Hebbian learning rule. His idea was later used by neural network modelers to build networks which can learn. Although the idea was only a hypothesis without experimental evidence when Hebb proposed it, now it has been strongly supported by physiological experiments (Paulsen and Sejnowski 2000).

American psychologist Frank Rosenblatt's perceptron is the first neural network, which can learn with try-and-error approach (Rosenblatt 1962). After many times of training, the network can learn to classify some inputs, such as handwriting digits, into categories defined by regular printed types, with slight modification of connection weights based on its output if it is the one expected by the trainer or not; Rosenblatt thought brains would work in a similar way.

The success of the perceptron absorbed many artificial intelligence (AI) students to shift their researches to neural networks, and part of the financial support to AI flowed to neural network studies. This annoyed AI researchers. AI was the mainstream in technologies trying to duplicate human intelligence at that time. They insisted that machine intelligence could be realized only by the way of finding some formal representation of knowledge, reasoning, and programming. It seemed to them that any idea that a machine could create its own knowledge representation and logic with changing its own connection weights would only lead to a dead end. In 1969, American cognitive scientist and mathematician Marvin Minsky, one of AI pioneers, and mathematician Seymour Papert published their famous book *Perceptrons: An Introduction to Computational Geometry*, in which they proved rigorously that a one-layer perceptron cannot even classify some very simple inputs. This was a heavy blow on the neural network movement, which was in an awkward predicament in the 1970s. There were only a few scientists who still insisted on neural network studies. However, Minsky's proof is only true for a neural network with one layer. For neural networks with multilayers, they only said: "We consider it to be an important research problem to elucidate (or reject) our intuitive judgment that the extension is sterile" (Minsky and Papert 1969). No detailed explanation was given, but they were wrong this time. Neural networks with multilayers can solve problems which Minsky and Papert thought they could not. Although Rosenblatt himself had thought about such possibilities, he could not find a way to train the intermediate layers.

In 1982, American biophysicist John Hopfield developed a recurrent neural network rather than a feedforward network such as a perceptron; he proved that, under certain conditions, the state of his network would converge to certain local minimum, depending on its connection weights, which could be considered as stored memory in wildly distributed synaptic strengths, and the stored memory (local minimum) could be retrieved by partial information (the initial state), a phenomenon similar to associative memory of the brain (Hopfield 1982). Hopfield's paper is one of the landmarks of the rejuvenation of the neural network movement. For details, please see Sect. 5.1 of this book. Others also found that a network with multilayers could do jobs that Minsky thought it could not. However, the progress of artificial neural network studies just as traditional AI studies met its bottleneck around the turn of this century. These techniques have been found very difficult or even failed to carry out many important functions of brains such as cognition or acting in a new environment; the key problem is that they just try to mimic human behavior without understanding the underlying mechanism of the brain. For artificial neural networks, although its elements are similar to biological neurons in some way, they usually are oversimplified, and the networks are not organized in similar ways that biological neural circuits do. Now neural network modelers are paying more attention to the underlying mechanism of their biological prototypes and their works become one important part of the field of neural information processing. We will give some important examples in Chap. 5.

The rise and fall of traditional AI and artificial neural network studies has given people an important lesson: To understand human intelligence, create an intelligent machine, and treat mental disorders, the behaviorist approach is far from enough; digging deeply into the underlying mechanism of brains is necessary. It is essential to understand how brains process information, using all available techniques, including mathematical modeling and computer simulation. Developing new technologies is also important for this purpose, as what the US BRAIN Initiative suggested.

As a matter of fact, exploring the biological mechanism of nervous systems using mathematical model and simulation can be traced back to British physiologists Alan Hodgkin and Andrew Huxley's seminar papers (Hodgkin and Huxley 1952) on the generation and propagation of action potentials in the 1950s (for details, see Sect. 2.1 of this book). By the way, although Hodgkin took physiology as his main major in the university when he was a college student, he also took mathematics and physics as elective courses, as suggested by his zoology professor, and Huxley was a physics student in his college days, taking physiology as an elective course.

In the 1950s and 1960s, there were several other important works in this field.

American biophysicist Haldan Keffer Hartline found that there was mutual inhibition between neighboring eccentric cells (a kind of bipolar neurons; their axons form optical nerves to its brain) in the retina of *Limulus* compound eyes, which could enhance the spatial contrast of the edge and details in a scene (Hartline 1974). He and his colleagues established a nonlinear algebra equation—Hartline–Ratliff equation—to model such a lateral inhibitory network and used it to elucidate the mechanism underlying the Mach band, an optical illusion discovered by Austrian scientist Ernst Mach in the nineteenth century. Now lateral inhibition has been proven to be one of the universal principles in sensory information processing. Hartline is also the one who firstly proposed the concept of a visual receptive field of a given neuron—an area in the retina, on which a proper optical stimulus could change the pattern of this neuron's activities.

In 1959, American neuroscientist Jerome Lettvin and his colleagues including McCulloch and Pitts published a paper titled "What the frog's eye tells the frog's brain" (Lettvin et al. 1959), in which four different types of ganglion cells in frog's retina were reported that could detect different features in visual stimuli. A feature detection theory was proposed for visual information processing.

In the same year, Canadian–American and Swedish neuroscientists David Hubel and Torsten Wiesel found that, in the primary cortex, there were neurons sensitive to special orientations of bars in their receptive fields. Such function may be the basis of form perception (Hubel 1981).

After these findings, a lot of papers on receptive field modeling were published. Recent progresses in this direction are given in Chap. 4 in detail.

American neuroscientist Wilfrid Rall, who was a physics student, treated every branch of dendrites as a kind of cable (Rall 1959, 1960, 1962, 1964); he analyzed electrical conduction in branched dendrites by the cable theory, which was developed by engineers to study the similar problems of undersea cables across oceans. Although anatomists had already found complicatedly arborescent structures of dendrites, neuron modelers used to neglect such complexity and treat them just as a node. Rall is the first to describe the dendrite tree with a mathematical approach to explain how synaptic inputs are integrated to control spiking. In his model, he even predicted that there might be dendrodendritic synapses (Rall et al. 1966), which were verified experimentally a few months later by his colleagues. In the following years, he not only considered passive properties of dendrites but also active properties and suggested that the latter may contribute to local amplification of the input signals.

During the Second World War, Bernhard Hassenstein, a biology student, and Werner Reichardt, a high school graduate, were sent to the field. They agreed that they would organize an institute combining biology and physics if they could survive. Fortunately, both survived. After the war, Hassenstein got his Ph.D. degree in biology with a thesis on beetle optomotor responses, and Reichardt got a Ph.D. degree in physics and they met together again; the latter found that he could model the former's results, and a model was developed (Hassenstein and Reichardt 1956; Reichardt 1961), which can not only mimic Hassenstein's biological experiment results but also predict that the response would not increase monotonically with the stimulus speed forever; instead, it would reach a peak at certain speed and then decline, and the optimal speed depended on stimulus spatial frequency. These predictions were verified by further biological experiments. Their researches promoted the trend to study nervous system activities quantitatively with mathematical modeling. Intuition is not always true; mathematical analysis may uncover the truth, as what was said that "a pen might be wiser than the person who holds it."

They established a biological cybernetics group in the Max Planck Institute of Biology in Tübingen, which has been developed into an independent institute—the Max-Planck-Institut für biologische Kybernetik in Tübingen. Reichardt's model started studies on movement detectors and he launched a journal *Kybernetik* (now *Biological Cybernetics*), which is the first international journal devoting itself to topics about biological cybernetics. Although having graduated in physics, Reichardt advised every young person that joined in his institute that theories must always combine with experiments closely, and he did not believe that any brain theory without biological foundation would have any chance to be successful.

About the same period, British neuroscientist David Marr, who obtained his BA in mathematics and Ph.D. in physiology, developed a model of the cerebellum based on Australian neurophysiologist John Eccles' anatomical and physiological data in his Ph.D. thesis. He shifted his focus on visual information processing after that. His classical book *Vision: A Computational Investigation into the Human Representation and Processing of Visual Information* (Marr 1982) summarizing his studies was completed by his colleagues after his passing away, in which he proposed that there are three analysis levels in visual information processing: theory, algorithm, and hardware levels. He emphasized the independence between these levels; however, later studies showed that such independence was not as strong as what he thought. In fact, brain function is heavily constrained by its structure. And ironically he himself paid much attention to visual physiology and psychology in his book. His works inspired studies on computer vision and became a classical example for visual information processing research using mathematical tools.

Although feature detection and receptive field theories tell us how visual systems analyze different features in a scene, they have not answered how visual systems synthesize these features into a unified object or combine different local features into different objects in a scene—the so-called binding problem. In the 1980s, German computer scientist Christoph von der Malsburg proposed a synchronization theory to answer it—neurons giving response to the same object fire synchronously (von der Malsburg 1981, 1985)—and his theory were supported by German neuroscientists Wolf Singer and his colleagues (Singer 1993); their results were confirmed by another German group headed by Reinhard Eckhorn (1988).

American neuroscientist Walter J. Freeman, who also graduated in physics and mathematics, is one of the pioneers who proposed a mesoscopic dynamic approach to model the olfactory system; he is also one of the pioneers to study chaotic dynamics in nervous systems (Freeman 2000). German physicist Hermann Haken used a synergetic approach developed by him to study brain activity and its dynamics (Haken 1996, 2002).

The above has only given an uncompleted list of pioneering works on neural information processing, which promote researchers to study nervous systems with mathematical modeling and computer simulation. In 1985, Eric L. Schwartz, a cognitive neuroscientist and computer scientist, coined the term “computational neuroscience” and organized the first international conference on this topic (Schwartz 1990). In 1994, the first international journal titled *Journal of Computational Neuroscience* devoting to this topic was published. In the editorial of its first issue, it is emphasized that the goal of computational neuroscience is to study “how the nervous system processes information to produce meaningful behavior in animals and humans,” i.e., to understand the rules how the nervous system encodes, processes, or “computes” the information, and how neural machinery implements the corresponding computational algorithms (Rinzel et al. 1994).

Computational neuroscience has been one of the frontiers in twenty-first century’s sciences. In a supplement to *Nature Neuroscience* focused on computational approaches to brain function organized by the NIH, it is said that “Clearly, computational neuroscience is, and will continue to be a growing field” (NIH 2000).

In the recent years, more related disciplines such as neuroinformatics, neuroengineering, neurodynamics, computational neuroethology (computational neuroecology), neurorobotics, neuromorphic engineering, etc., have emerged and grown quickly. Although their emphasized aspects are different in some way, they share a core concept—neural information processing—and they are all interdisciplinary fields between neuroscience and informatics/IT. For such researches, theoretical analysis, modeling and simulation, and biological experiments must go hand in hand; now a lot of mathematicians, physicists, computer scientists, and IT engineers are rushing into these golden mine areas. Just as what Norbert Wiener said more than half a century ago: “For many years, Dr. Rosenblueth and I had shared the conviction that the most fruitful areas for the growth of the sciences were those which had been neglected as a no-man’s land between various established fields” (Wiener 1948). British molecular biologist and neuroscientist Francis Crick, who also graduated in physics and called as the greatest biologist in the twentieth century by Nobel laureate Eric Kandel, also pointed out that: “In nature hybrid species are usually sterile, but in science the reverse is often true. Hybrid subjects are often astonishingly fertile, whereas if a scientific discipline remains too pure it usually wilts” (Crick 1988).

From the above brief review of the history of this field, it is easy to notice that all the pioneers are people like what Wiener demanded. Although they focused their studies on neuroscience, they had sound foundation of mathematics, physics, or informatics. However, as what is stated in the quotation we cited from Wiener, it is not easy to master all these different disciplines. Every discipline has its own approach and its own thinking habit. Pure mathematicians are good at logical reasoning based on some axioms; they don’t care what concrete object they are treating, so that a joke says that a pure mathematician is the person who does not know what he or she is talking about. Traditional biologists emphasized observation and experiment while physicists are used to idealizing an object into a model, deducing results from the model, and comparing them with experimental ones. Every approach has its own merit and deficit. People working with neural information processing should combine all these approaches into one and be accustomed to discussing with colleagues from other fields. For doing this, one must have background knowledge with some depth in his neighboring fields and understand others' thinking habit.

This book is for readers who are interested in brain research with backgrounds other than neuroscience, just like the authors themselves of this book. At the very beginning, when they try to work in this field, they often find that they lack enough knowledge about nervous systems. Neuroscience textbooks are often too detailed for them to quickly grasp the essence of the neuroscience background for studying, just as what American neuroscientist John Dowling (2001) said: "Textbooks in neuroscience (and most other branches of biology) have become more and more encyclopedic and, in my view, less and less useful for the beginning student or for others interested in the principles of a field." On the other hand, monographs on computational neuroscience usually do not give enough pages to introduce the neuroscience background, which makes the beginners have difficulty to really understand. Even worse, some popular science books on these topics just give a cartoon-like description of the brain, and this may mislead readers to think that their descriptions are the realistic view of the nervous systems, thus underestimating the complexity of the living brain. Some readers may develop their "brain models" which almost share nothing common to a living brain, just like the model proposed by a scientist visiting Francis Crick, who thought that his model was pretty and worked well. However, the comment given by Crick is "My dear chap, that's a criterion you would use for selling a vacuum cleaner – I don't see what it has to do with the brain" (Ramachandran 2004). Thus, the authors have to make some trade-off in introducing the neuroscience background neither too detailed nor too simplified.

Of course, this book may also be useful for neuroscience students, who have some mathematical background and are interested in using mathematics, physics, and informatics approaches for their own studies. This book will give those readers a review of basic neuroscience background related to information processing and give them classical examples on how to use mathematical and physical ideas and approaches to solve biological problems and some recent important advances in this field so that they may learn some lessons to solve their own problems. For those who don't have enough mathematical background, reading some concise mathematics textbook, especially those for neuroscience students, is necessary (Gabbiani and Cox 2010).

As an introductory book, of course, it is impossible to cover all achievements in neural information processing, which are so broad, that the first edition of a handbook on this topic published in 1995 which has 1,118 pages and a weight over 3 kg (Arbib 1995); however, the main criticism about the handbook in a book review is that many important achievements hadn't been included in that book (Aleksander 1995)! Further reading is necessary and lists of them are recommended in the last sections of the related chapters.

From the authors' view, studies on neural information processing are still in its infant period; the mysteries of the brain and mind could not be solved in the near future. Just as what Walter J. Freeman said (Personal communication 2006):

> Fifty years ago, enthused by successes in creating digital computers and the DNA model of heredity, scientists were confident that solutions to the problems of understanding biological intelligence and creating machine intelligence were within their grasp. Progress at first seemed rapid. Giant 'brains' that filled air-conditioned rooms were shrunk into briefcases. The speed of computation doubled every 2 years.
>
> What these advances revealed is not the solutions but the difficulties of the problems. We are like the geographers who 'discovered' America, not as a collection of islands but as continents seen only at shores and demanding exploration. We are astounded less by the magnitude of our discoveries about how brains cogitate than by the enormity of the tasks we have undertaken, to explain and replicate the higher functions of brains.

There is still a long way to explore these mysteries; it seems unlikely that the goal could be reached by one or two giant projects in the next decade or even a little longer (Gu 2013). However, as what Francis Crick pointed out more than 20 years ago (Crick 1988): "The present state of the brain sciences reminds me of the state of molecular biology and embryology in, say, 1920s and 1930s. Many interesting things have been discovered, each year steady progress is made on many fronts, but the major questions are still largely unanswered and are unlikely to be without new techniques and new ideas . . .. . . The brain sciences have still a long way to go, but the fascination of the subject and the importance of the answers will inevitably carry it forward. It is essential to understand our brain in some detail, if we are access correctly our place in this vast and complicated universe we see all around us."

The future to understand the brain is bright; the way ahead is still long. For young readers, we will present them Shakespeare's verse with all respect:

> There is a tide in the affairs of men,
> Which taken at the flood leads on to fortune;
> Omitted, all the voyage of their life
> Is bound in shallows and in miseries.
> (William Shakespeare: Julius Caesar, Act IV, Scene 3, Line 217)

Enjoy reading.

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Chapter 2
Neurobiological Basis Underlying Neural Information Processing

Abstract Although modeling and calculation from a perspective of neural information processing are sometimes based on some necessary assumptions to make the nervous system a simplified one, which enables the computation feasible, the nervous system is itself a very complicated one. Besides, different parts of the nervous system have their own characteristics. Therefore, it should be very helpful for those people who are naïve of neuroscience but wish to work on topics related to neural information processing to start with some fundamental ideas about neuroscience. This chapter provides the necessary biological background of the brain with adequate details. Gross anatomy of nervous systems, structural and functional properties of nerve cells, functional organization of various sensory systems and somatomotor system, as well as structure and function of cerebellum and hippocampus are introduced from a point of view of information processing.

Keywords Nervous system • Nerve cells • Sensory and somatomotor systems • Cerebellum • Hippocampus

Pioneers of traditional AI thought that machine intelligence, which might be compared with human intelligence or even surpass, could be realized by sophisticated programming and symbolic processing. In 1967, Marvin Minsky, one of the AI founders, concluded optimistically that the task could essentially be solved within one generation. However, his prediction failed. In 1982, he had to acknowledge that the problem of artificial intelligence was one of the most difficult one which science had ever met. The traditional AI approach met its bottleneck. For creating intelligent machines or treating mental disorders, in addition to understanding human beings ourselves, we must know mechanisms underlying neural information processing in the living brain. Thus, at the very beginning of this book, the necessary and essential background about neuroanatomy and neurophysiology for understanding neural information processing should be given.

As what we have mentioned in the introduction, brain functions are constrained by their "hardware." Marr's three levels for analyzing brain function, computational theory, representation algorithm, and hardware implementation (Marr 1982), are not absolutely independent to each other as what he declared in his book. In biology, functions always depend on structures. "If you want to understand function, seek to understand structure." (Koch 2004) American neurophilosopher

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Patricia S. Churchland and computational neuroscientist Terrence J. Sejnowski indicated (Churchland and Sejnowski 1992): "In contrast to the doctrine of independence......Knowledge of brain architecture, far from being irrelevant to the project, can be the essential basis and invaluable catalyst for devising likely and powerful algorithms—algorithms that have a reasonable shot at explaining how in fact the neurons do the job."

Therefore, before discussing neural information processing, it is necessary to give fundamental facts about neural anatomy and physiology in this chapter. We will first describe gross structures of nervous systems, introduce its functional and structural units—neurons, and its most important composing elements for information processing—synapses, and ionic channels. Its electrical properties will also be explained, as the electrical signal is one of the essential carriers of neural information the readers must understand. As what we have mentioned in the introduction, nervous systems are hierarchical systems; there are many levels[1] in them: from ionic channels or even below (say, biological macromolecules), synapses, neurons, neural circuits, maps, specific systems such as the visual system, the auditory system, etc. until the whole brain or the whole nervous system. For brevity, only some of such specific systems which are most important to neural information processing and their subsystems are introduced in the next sections. In addition to the organization of the cerebral cortex which is the organ for the higher brain functions, the anatomical structure and physiological function of sensory systems including visual systems, auditory systems, olfactory systems, and somatosensory systems are introduced in details. The functional organization of the somatomotor system is also described. Besides, cerebellums and the hippocampus are introduced, respectively—not only for their own functions involved in motor control and in learning and memory but also that these two systems provide nice models for studying synaptic plasticity. Of course, in a short chapter as this one, it is impossible to cover all the fields in neurobiology; further readings are recommended in the last section for those readers who wish to learn more.

2.1 Gross Anatomy of Nervous Systems

Nervous systems have inhomogeneous 3D structures. To determine the location and shape of some structure within it, one way is to view its projection on some section plan with special orientation. The following three special section plans are generally accepted to be the reference ones: The sagittal plane is the plane which divides the head (or body) into right and left parts (Fig. 2.1d); the coronal plane is the one which divides the head into front and back parts (Fig. 2.1c), usually people view it from behind; and the horizontal plane is the one which divides the head into upper and lower parts (Fig. 2.1b), usually people look down to it. Generally speaking, a central sagittal section, which is the sagittal section dividing the body into equal

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[1] Here the term "level" means organization level, which is different from Marr's analysis level.

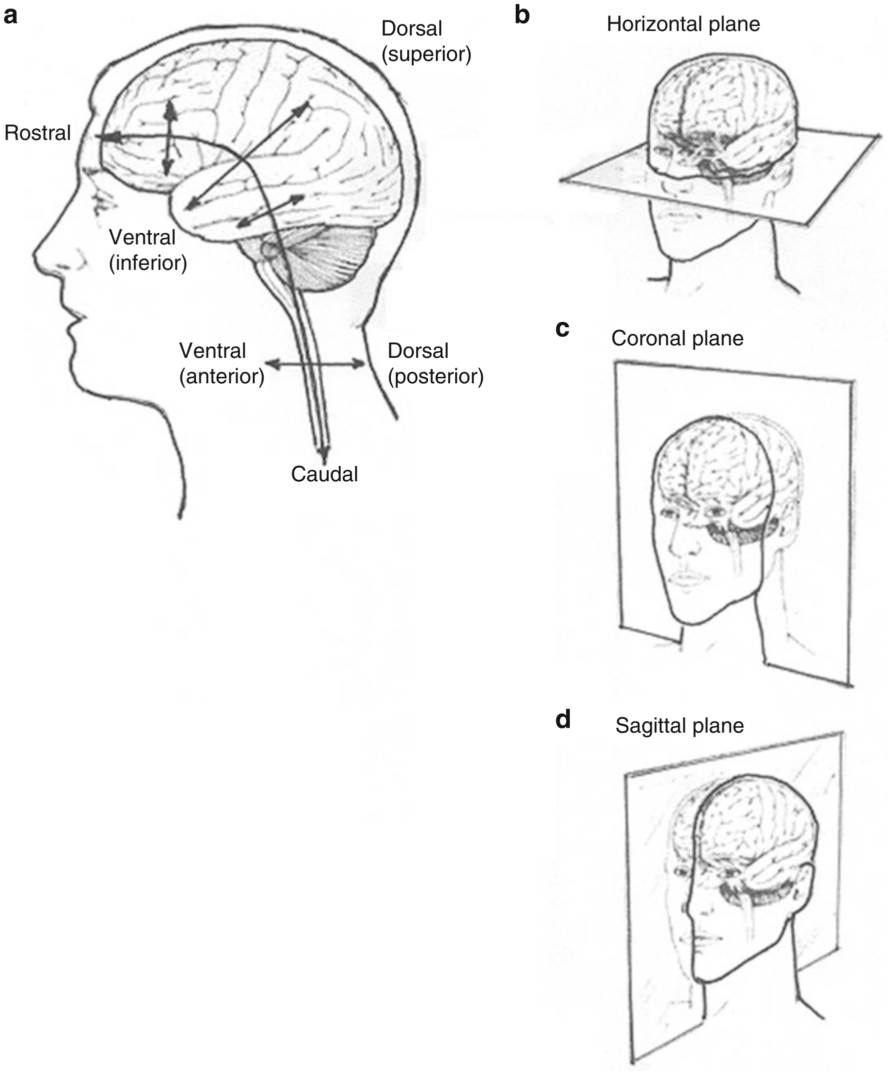

Fig. 2.1 Terms of reference. (**a**) Direction terms along the body axes and cerebrum axis, (**b**) horizontal plane, (**c**) coronal plane, (**d**) sagittal plane (Adapted with permission from Steward O (2000) *Functional Neuroscience,* Springer, Fig. 1.1, from Martin JH (1989) Neuroanatomy Text and Atlas, Elsevier, and Kandel ER Schwartz JH (1985) Principles of Neural Science, Elsevier)

halves, is taken first to locate where the structure is along the body axis; then a coronal section is taken to show the projection of location and shape of that structure on the plane.

For convenience of talking about the location of some structure related to others, it may be necessary to define some terms to denote the location relationship between them. It is shown in Fig. 2.1a that the structures of the nervous system are almost placed in a straight line along the body axis below the cerebrum; however, the line turns off for 120° approximately in the cerebrum, as shown in this figure. It is clear for the meaning of "superior," "inferior," "anterior," and "posterior" for all structures, as shown in the figure. However, the meaning of "rostal," "caudal," "dorsal," or "ventral" is a little bit different for different cases. In the case of subcerebral structures, "dorsal" means the direction to the back, "ventral" to the belly, "rostal" to the top of the head, and "caudal" to the opposite direction, while in the case of cerebrum, "dorsal" means the direction to the top of the head, "ventral" to the opposite direction, "rostal" to the face, and "caudal" to its opposite direction. In addition, "medial" is used to denote the direction toward the middle line of the body, while "lateral" away from it.

Laymen are apt to confuse brains with nervous systems. As a matter of fact, the brain is only a part of the nervous system. The nervous system is composed of the central nervous system and the peripheral nervous system, while the central nervous system is composed of the brain and the spinal cord (Fig. 2.2).

The brain is the organ which is responsible for all the higher functions, such as perception, initiation of movements, learning, memory, emotion, and consciousness, and other basic functions for survival such as breathing, regulating heart rate, blood pressure, and so on and so forth. The spinal cord is responsible for reflex activities and rhythmic actions and is the pathway both for transmitting peripheral sensory information from sensory receptors to the brain and action instructions from the brain to muscles and glands.

A more detailed division of nervous systems could be listed as follows:

- Nervous system
  - Central nervous system
    - Brain
      - Forebrain
        - Cerebral hemisphere
          - Neocortex
          - Basal ganglia
          - Limbic system
      - Diencephalon
        - Thalamus
        - Hypothalamus
      - Midbrain (mesencephalon)
      - Hindbrain
        - Metencephalon
          - Cerebellum
          - Pons
        - Medulla oblongata

    - Spinal cord
- Peripheral nervous system
    - Somatic nervous system
    - Autonomic nervous system
        - Sympathetic division
        - Parasympathetic division

The above jargons may make beginners feel dizzy. However, it would be much clearer if one looks for the structures corresponding to these terms in Figs. 2.2 and 2.3, while reads the above list.

Central Nervous Systems Mainly, the information processing in central nervous systems is discussed in this book, while only a very brief introduction to peripheral nervous system is given. The locations of a variety of structures in the central nervous systems in sagittal section are shown in Fig. 2.3a. The terms forebrain, midbrain, and hindbrain are named from their locations in the early stage of the development of the brain.

Cerebrum The cerebrum is composed of two hemispheres: the left hemisphere and the right hemisphere, separated by a longitudinal fissure (Fig. 2.4). Sensation and movement of the trunk and limbs are controlled by the contralateral hemisphere, while sensation and movement of the head and face are controlled by the ipsilateral hemisphere.

There is a giant bundle of nerve fibers—corpus callosum—interconnecting the two hemispheres at the bottom of the longitudinal fissure (the section of this bundle is shown in Fig. 2.3a). Besides corpus callosum, another bundle of nerve fibers—fornix (its fimbria is shown in Fig. 2.4c)—interconnects bilateral hippocampus and hypothalamus between the two hemispheres. It is these fibers that make information be exchanged between the two hemispheres and make it possible to coordinate their functions.

The surface of cerebrum is separated by many sulci (only very deep sulcus was named as fissure) into many gyri. The main sulci and gyri on the cerebrum surface and their names are shown in Fig. 2.4b. According to its location and function, the surface of cerebral hemisphere can be separated by some sulci or fissures into four main lobes—frontal lobe, parietal lobe, temporal lobe, and occipital lobe (Fig. 2.4b); sometimes, a part of the medial cerebral surface encircling the upper brain stem is called limbic lobe as the fifth lobe (Fig. 2.5). Lateral sulcus (Sylvian fissure) separates temporal lobe from the other areas (Fig. 2.6). There is also an area called insula at the bottom of this fissure, which is related to tasting. Central sulcus (Rolandic fissure) separates front lobe from parietal lobe. Parietooccipital sulcus is the border between parietal lobe and occipital lobe.

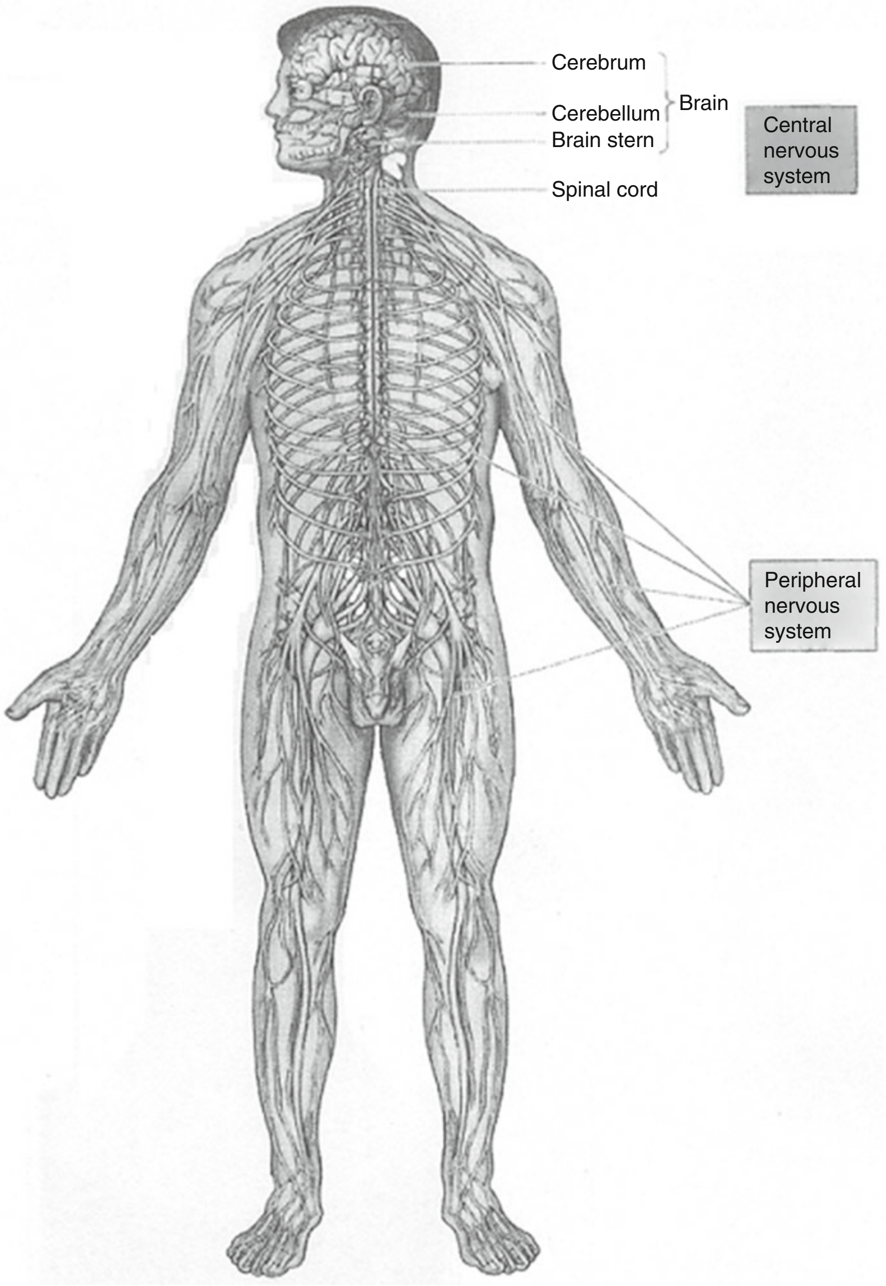

Fig. 2.2 The nervous system. The nervous system is composed of central nervous system (CNS) and peripheral nervous system (PNS), while the former consists of the brain and the spinal cord, and the latter consists of the nerves and nerve cells outside CNS (Reproduced with permission from Bear MF, Connors BW, Paradiso MA (2007) Neuroscience: Exploring the Brain (3rd Edition). Lippincott Williams & Wilkins. Fig. 1.7)

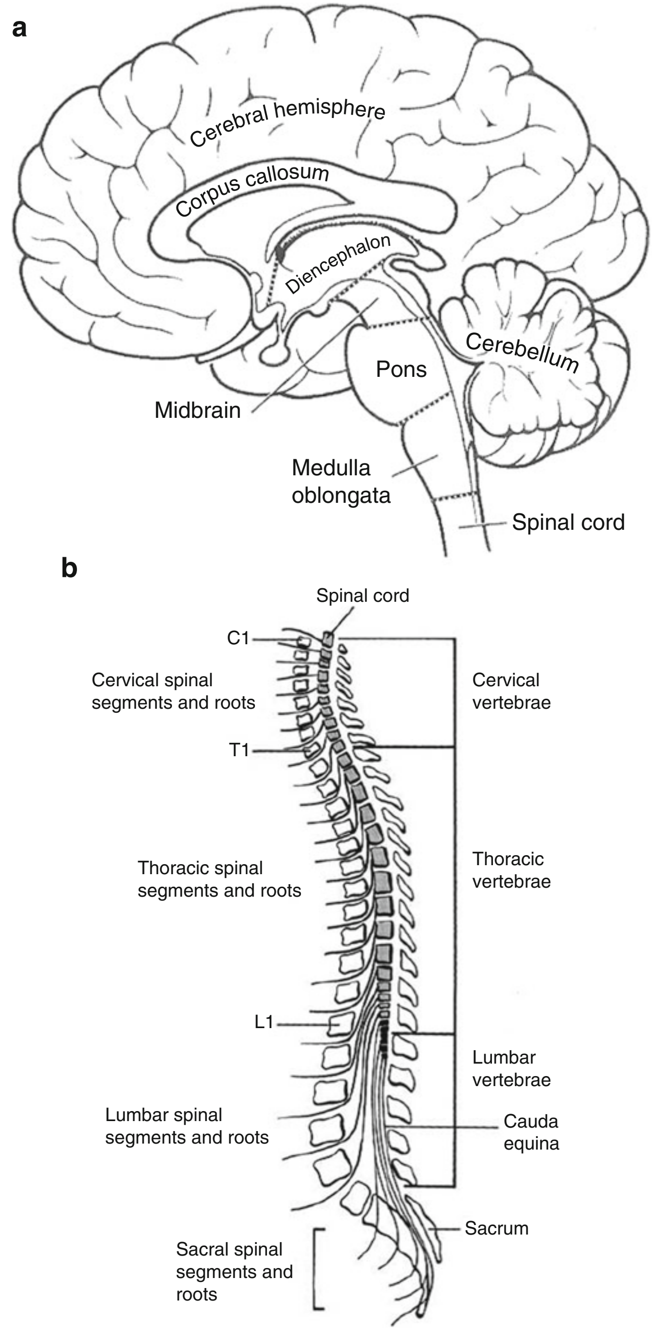

Fig. 2.3 The sagittal section of the central nervous system. (**a**) A sagittal section of the brain, which consists of cerebral hemispheres, diencephalon, midbrain, pons, medulla oblongata, and cerebellum (Reproduced with permission from Strominger NL, Demarest RJ, Laemle LB (2012) *Noback's Human Nervous System Seventh Edition: Structure Function*. Humana Press. Fig. 1.1). (**b**) A sagittal section of the spinal cord, which consists of cervical, thoracic, lumbar, and sacral segments (Reproduced with permission from Conn PM (Ed) (2008) *Neuroscience in Medicine (3rd Edition)* Humana Press (Murray M. Organization of the spinal cord. Fig. 1))