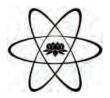


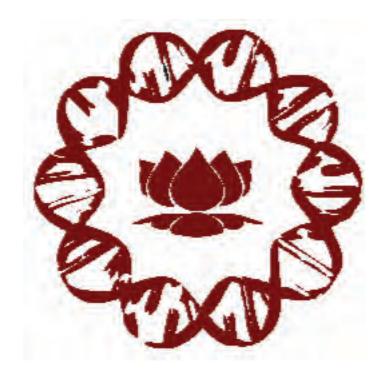
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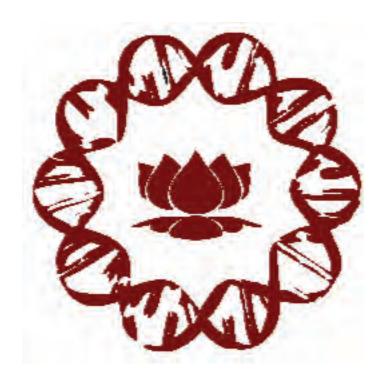


ETSI Neuroscience Primer II

Neurons & Neuronal Activities

Written and organized by **Arri Eisen, Wendy Hasenkamp, Jennifer Mascaro, and Carol M. Worthman**Translated by **Geshe Dadul Namgyal**

Emory - Tibet Science Initiative SCIENCE PRIMERS



अ'र्अ'रे'न्न'ने'र्थे'अंन'रेन। ਫ਼न'रेग'गे'र्थेन'दर्शेंदि'र्स्चन'रेन।

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A joint project of the Library of Tibetan Works and Archives, Dharamsala, India and Emory University, Atlanta, Georgia.

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क्रुन'र्सेग'न्न'हुस'तर्मेन। नश्चन'तहें ब'श्रेग'न्स्रम्।

Written by: Arri Eisen, Wendy Hasenkamp, Jennifer Mascaro, and Carol Worthman

Translated by: Geshe Dadul Namgyal

Translation Reviewed by: Geshe Lhakdor and Tsondue Samphel

Layout and design by: Tenzin Migmar

र्चेन'मेर'रर'लेगस'गर्सेला

Foreword and acknowledgements



FOREWORD

Despite their obvious differences, science and Buddhism share several key features in common. Both are committed to empirical observation, the testing of hypotheses, avoiding blind adherence to dogma, and cultivating a spirit of openness and exploration. Most importantly, Buddhism and science share as a fundamental aim the contribution they can make to humanity's well-being. While science has developed a deep and sophisticated understanding of the material world, the Buddhist tradition has evolved a profound understanding of the inner world of the mind and emotions and ways to transform them. I have no doubt that improving collaboration, dialogue and shared research between these two traditions will help to foster a more enlightened, compassionate, and peaceful world.

I have long supported the introduction of a comprehensive science education into the curriculum of the traditional Tibetan monastic educational system. When I first heard that Emory University proposed to develop and implement such a science education program for Tibetan monks and nuns in collaboration with the Library of Tibetan Works and Archives, I thought it would take many years. When I visited Emory University in October 2007, I was genuinely surprised to be presented with the first edition of a science textbook for Tibetan monks and nuns, the result of more than a year's work by a team of dedicated scientists and translators at Emory.

By extending the opportunities for genuine dialogue between science and spirituality, and by training individuals well versed in both scientific and Buddhist traditions, the Emory-Tibet Science Initiative has the potential to be of great meaning and significance to the world at large. Once more, the creation of this primer series, presented in both Tibetan and English, is a clear tribute to the commitment and dedication of all those involved in this project. With the preparation having been done with such care, I am confident that the long-term prospects for this project are bright.

I congratulate my friend Dr. James Wagner, President of Emory University, the science faculty and translators of the Emory-Tibet Science Initiative, and everyone who has lent their support to this project for achieving so much in such a short time and offer you all my sincere thanks.



THE DALAI LAMA

ब्र्न से न्।

प्रमित्राचित्राच्यात्रक्रिक्क्षण्ठात्त्रच्यात्रक्षण्यात्रकष्णात्रक्षण्यात्रकष्णवात्रकष्णवात्रकष्णवात्रकष्यात्रक्षण्यात्रकष्यात्रकष्णात्रकष्णवात्रकष्णवात्रकष्णवात्रकष्णवात्रकष्यात्रकष्णवात्रकष्णवात्रकष्णवात्रकष्णवात्रकष्णवात्रकष्णवात्रकष्णवात्रकष्णवात्रकष्णवात्रकष्णवात्रकष्णवात्रकष्णवात्रकष्णवात्रकष्णवात्रकष्णवात्रकष्यात्रकष्णवात्रकष्यवात्रकष्यात्रकष्णवात्रकष्णवात्रकष्णवात्रकष्णवात्रकष्णवात्रक



Office of the President

Education is one of the most potent tools we have for ensuring a better world for ourselves and for generations to come. To be truly effective, however, education must be used responsibly and in service to others. This ideal of an education that molds character as well as intellect is the vision on which Emory University was founded, and the challenges of our time show that the need for such education is as great as ever.

This vision is one that His Holiness the Dalai Lama shares deeply, and it is the reason for the close relationship that has emerged between His Holiness and Emory over the past two decades. On October 22, 2007, it was my pleasure and privilege to welcome His Holiness to Emory to be installed as Presidential Distinguished Professor and to join our community as a most distinguished member of our faculty.

The interdisciplinary and international nature of the Emory-Tibet Science Initiative, the most recent and ambitious project of the Emory-Tibet Partnership, is an example of Emory University's commitment to courageous leadership for positive transformation in the world. This far-reaching initiative seeks to effect a quiet revolution in education. By introducing comprehensive science instruction into the Tibetan monastic curriculum, it will lay a solid foundation for integrating insights of the Tibetan tradition with modern science and modern teaching, through genuine collaboration and mutual respect. The result, we trust, will be a more robust education of both heart and mind and a better life for coming generations.

The Emory-Tibet Partnership was established at Emory in 1998 to bring together the western and Tibetan traditions of knowledge for their cross-fertilization and the discovery of new knowledge for the benefit of humanity. This primer and its three companion primers are splendid examples of what can be accomplished by the interface of these two rich traditions. We at Emory University remain deeply committed to the Emory-Tibet Science Initiative and to our collaboration with His Holiness and Tibetan institutions of higher learning.

To the monastic students who will benefit from these books, I wish you great success in your studies and future endeavors.

James W. Wagner

President

Emory University Atlanta, Georgia 30322

An equal opportunity, affirmative action university



Office of the President

ર્વત્રું રે. ત્રિધીયાત્ર કર્યા ત્રી લે શેવ ત્રી તે ત્રી તર્યો હો. શેં સેન્દ્ર ન્યૂર્ય સે થયા ત્રી હો. શેવ ત્રી કુવે. ત્રુદ્ધ માત્ર જ્યા ત્રુદ્ધ હિને ત્રવયો માત્રો શેવા ત્રા કુવે. જુવે જૂને પ્રત્યો મુખ્ય ત્રી હો. જુવે. જુવ કુવે. ત્રુદ્ધ માત્ર જુવે ત્રિક ત્રવયો માત્રો શેવા ત્રા કવા જુવે જુવે જૂને પ્રત્યા મુખ્ય ત્રુદ્ધ હો. જુવે જુવે ત્રુદ્ધ ત્રુદ્ધ માત્ર જુવે ત્રુદ્ધ કુવે હોય ત્રવે ત્રા ત્રુદ્ધ ત્રા હો ત્રા કુવે ત્રુદ્ધ ત્રા ત્રુદ્ધ ત્રા ત્રુદ્ધ ત

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हेअ'से'सेग्'क्र्या ग्रह्म

Emory University
Atlanta, Georgia 30322
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ACKNOWLEDGEMENTS

The Robert A. Paul Emory-Tibet Science Initiative (ETSI) grew out of the longstanding vision of His Holiness the Dalai Lama and is sustained by His Holiness's continued guidance and support at every step of the way. Not only has His Holiness provided annual operational funds, but he has also provided \$1 million towards the ETSI endowment fund thereby ensuring the long-term sustainability of the program. The ETSI also owes its existence to the patronage of Dr. James W. Wagner, President of Emory University, who has allocated considerable funding on behalf of Emory University and from his personal discretionary fund.

The Emory-Tibet Partnership (ETP) was established in 1998 in the presence of His Holiness the Dalai Lama through the collaborative vision and work of Dr. Robert Paul and Geshe Lobsang Tenzin Negi. ETSI is the most ambitious project to grow out of the Emory-Tibet Partnership, and in 2010 ETSI was renamed the Robert A. Paul Emory-Tibet Science Initiative in honor of Dr. Paul's visionary leadership and guidance. We express our heartfelt thanks to both these individuals for helping to establish the many programs of the Emory-Tibet Partnership, including ETSI.

We gratefully acknowledge Geshe Lhakdor, Director of the Library of Tibetan Works and Archives, Dharamsala, India, whose leadership has been invaluable to the establishment and development of this initiative.

The project would also not have been possible without the support of Dr. Gary Hauk, Vice President and Deputy to the President at Emory University, who has guided ETP from the beginning and continues to be one of ETSI's strongest supporters. Additionally, ETSI is greatly indebted to Dr. Robin Forman, Dean of Emory College of Arts and Sciences, for providing critical resources and faculty from Emory College, which houses this initiative, to assist the ongoing development and implementation of the ETSI.

We thank also the ETSI science faculty, who have worked tirelessly to develop the science textbooks and who have traveled to India each summer to teach the science intensives, and the ETSI science translators who have given of their skills and time to contribute an entirely new scientific vocabulary to the Tibetan literary tradition and lexicon. In particular, Drs. Carol Worthman, Arri Eisen, John Malko, and Mark Risjord, team leaders for neuroscience, biology, physics, and philosophy of science respectively, oversee all of the curricular aspects of the ETSI and have been integral to any success experienced by the ETSI. Additionally, the principal ETSI translators, Tsondue Samphel and Geshe Dadul Namgyal oversee the entire translation of all ETSI materials, and with the assistance of ETSI staff members Michael Romano and Carol Beck, manage logistics for the production of the video lectures and textbooks. Without this dedicated team of exceptional faculty members and translators, the ETSI would not be where it is today.

Along with the hard-working staff of the Emory-Tibet Partnership, everyone has labored far beyond the call of duty, showing time and again that their efforts are not only work, but also an act of love.

येग्रायार्थेया

र्षण्यस्त्र्वाच्छणस्यात्रस्य प्रमानस्य स्त्रित् स्त्रित् प्रमानस्य स्त्रम्य स्त्रम

We thank all those who have contributed the financial support needed to operate ETSI and ensure its long-term sustainability. We are particularly indebted to Joni Winston for her long-term generous support to ETSI and for her unwavering conviction in the worth of this endeavor. Funding for ETSI has also come from Emory University and Emory College, including the Office of Global Strategy and Initiatives.

Generous support has also come from:

- The Dalai Lama Trust
- The Joni Winston Fund
- The John Templeton Foundation
- Judith McBean Foundation
- Lostand Foundation
- Jaynn Kushner
- · Drepung Loseling Monastery, Inc., Atlanta, Georgia

We would also thank these individuals for their guidance and advice:

- Dr. Gary Hauk, Vice President and Deputy to the President, Emory University
- Geshe Thupten Jinpa, Principal English Language Translator for H.H. the Dalai Lama and President, Institute
 of Tibetan Classics
- Geshe Lhakdor, Director, Library of Tibetan Works and Archives
- Dr. Alan Wallace, President, Santa Barbara Institute
- Dr. Preetha Ram, former Associate Dean for Pre-Health and Science Education, Emory University
- Dr. Arthur Zajonc, former President, Mind and Life Institute
- Dr. Richard Davidson, Director, Center for Investigating Healthy Minds, University of Wisconsin, Madison
- Dr. Robert A. Paul, Charles Howard Candler Professor of Anthropology and Interdisciplinary, Emory University
- Geshe Lobsang Tenzin Negi, Director of Emory-Tibet Partnership, Emory University

We would like to thank the venerable abbots and the administration of the Tibetan monastic institutions for embracing the ETSI curriculum and incorporating this material into the Tibetan monastic core curriculum. Lastly, we thank the highly dedicated monastic students of the Emory-Tibet Science Initiative, who are not only beneficiaries, but also essential collaborators in the success of this program. May the knowledge that they gain through this program and these materials benefit them greatly, and through them, all of humankind.

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चण्ठा।

चण्ठाण्यात्र स्वाप्त स्वाप्त

SUPPORT AND INSPIRATION

This primer was written by Wendy Hasenkamp, Arri Eisen, Jennifer Mascaro, and Carol Worthman, based on curricular materials developed by a group of Emory faculty along with graduate students and post-doctoral fellows at Emory University and Georgia Institute of Technology. Carol Worthman led this group, which also included Gaelle Desbordes, Dieter Jaeger, Michael Iuvone, Michael Kuhar, Todd Preuss, Lena Ting, Leah Roesch, and Nicole Taylor. These thoughtful, generous scientists and educators are responsible for many of the ideas and much of the substance as they are elaborated in this primer. Concepts, evidence, and graphics also were drawn widely from the literatures of neuroscience, a global, diverse, multi-disciplinary field whose findings continually expand our understanding of brain, mind, experience, behavior, and the nature of sentience in living beings.

Geshe Dadul Namgyal translated this primer, and Tsondue Samphel led the translation of all Year 2 course materials. They, along with translators at the Library of Tibetan Works and Archives (LTWA), are creating a new science lexicon in Tibetan, a historic undertaking whose fruits are evident in this text. LTWA translators include Karma Thupten, Tenzin Paldon, and Nyima Gyaltsen. These skilled scholars (along with Tenzin Sonam and Sangey Tashi Gomar) also participated in the pilot teaching program that led to this primer. In the process, they have not simply translated our words, but have managed to convey complex systems of thinking and knowing from one culture to another. Such a dual act of translation-first of words and second of meaning is utterly essential to our project. Reciprocally, the authors and other participating scientists have been educated and humbled by the wealth of ideas and insights gleaned from the translators and the monastic students themselves, whose questions and drive for clarity and understanding motivate the approach and content of this primer.

The spiritual leaders and guiding lights of the Emory-Tibet Science Initiative are Geshe Lhakdor and Geshe Lobsang Negi. The seed and inspiration is His Holiness the 14th Dalai Lama of Tibet.

The Emory-Tibet Science Initiative Neuroscience Team Emory University 2015

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Neuroscience Primer II

Neurons & Neuronal Activities

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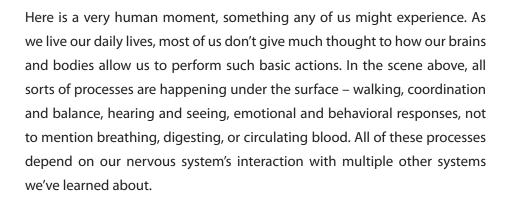
Neurons & Neuronal Activities

Basic Processes of Transmission, Integration, and Response

INTRODUCTION

Imagine you are walking through the woods on a beautiful day—the cloudless sky is a clear sharp blue. Suddenly, you trip on a tree root and nearly fall, but you catch yourself at the last minute and keep walking with only a slightly sore toe to remind you of the incident. As you walk, you listen to the wind in the trees and enjoy the auiet.

But then, you hear something; it sounds like a child crying, and as you turn the corner on the path, there is indeed a young boy sitting by the path, and he is sobbing. The boy looks to be about four years old and so upset he is unable to respond to your questions: is he lost? What is his name? Your heart goes out to him, and carefully you pick him up and carry him to the nearest village, hoping to find his parents.



You already know that our nervous systems control things like movement and sensory processes. But how does this work, on a cellular level? In our first primer, we have mentioned that neuroscientists measure 'brain activity,' and that neurons 'are activated.' Decades of research have focused on determining how neurons become activated. We've referred to this in varying detail throughout the Life Sciences and Neuroscience primers you have read previously; however, here you now have enough knowledge and background to explore neuronal activity in some detail.

As we have seen in previous primers, it is a central tenet of biology that anything a human (or any other organism) does must have a biological substrate. This is because we are limited by our cells and molecules, organs and organ systems, their capacities and their emergent properties. This principle holds true for phenomena as relatively simple as digesting food



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or circulating blood, but also for more complex phenomena like vision and social behaviors. In this primer, we will use the scenario described above as a way of gaining a deeper understanding of how the nervous system works. Along the way, we will continue to synthesize the knowledge and concepts we have learned in past primers.

BACKGROUND

To help us more easily integrate the ideas in this primer, let's examine some of the background information that is presented in other primers in this series. If you haven't covered these other primers yet, it may be useful to review these sections before diving into *Neurosciences II*.

Life Sciences Primer (LSP)-I: Evolution sets the stage for all else we learn in the biological sciences by outlining Charles Darwin's great and transformative idea of evolution. We learn how, through a few basic laws of selection operating from the interactions between biology and the environment, all of life evolved and continues to do so. We learn how mechanisms for transmitting biological information between generations, particularly DNA (and the RNA and proteins it encodes), form the universal substrate for evolution, and how random changes in the DNA code that result in biologic advantage in a particular environment are selected and passed on. We also learn how different environments affect when, if and to what extent genes are expressed. Over millions of years, this process of evolution has resulted in all of the diversity and abundance of life forms that exist or ever have existed on earth.

In LSP-II: Genes and Cells, using the example of what happens when we touch a cup of very hot chai, it becomes clear that a few chemicals, most notably carbon, nitrogen, hydrogen and oxygen, are the basic constituents of all life molecules: proteins and nucleic acids (RNA and DNA), as well as carbohydrates and fats. We learn how the dynamic principle of structure/function—that structure predicts function and vice versa—applies at all levels of life, from molecules to cells and tissues, on to organs, organ systems, and organisms. We examine the basic chemistry of life and how it is deeply related to change, structure and function.

In *LSP-II:* Genes and Cells and Neurosciences I we also learn that the core molecules of life combine to form cells and their parts and allow different cells to interact. We learn that the same basic elements build a vast diversity of

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In *Neurosciences I* and *LSP-III: Development and Physiology,* we expand from molecules and cells to organs and organ systems, the next step up the biological staircase of life. Remembering the consistent underlying principle of structure and function as we move up the staircase, we learn constituents of and interactions among the many organ systems that make up our bodies—the nervous system as well as our reproductive, digestive, skeletal, muscle, immune, cardiovascular, respiratory, endocrine, integumentary, and urinary systems.

Finally, in LSP-III: Development and Physiology, we discuss development, again from an evolutionary prospective, starting with the relatively simple slime mold and then showing how its basic cellular and molecular strategies—chemotactic signaling based on chemical gradients and resulting in cellular movement—are the same as those used in development in all organisms. We learn how an organism starts with one cell and one set of DNA and then divides over and over, each cell having the same DNA. Nonetheless, during development each cell gradually takes on a different personality. All of this eventually results in the development of new organs, organ systems, and organisms, some of which (like humans) have trillions of cells!

WHAT EXACTLY IS NEURONAL ACTIVITY?

So how do neurons really work? Thorough comprehension of neural activity requires synthesizing many of the biology facts and concepts we've learned previously. Let's think about the underlying biology—from organisms to molecules—of the scenario described above.

Two **organisms** of the same species interacted. Doing so involved many of your physiological systems (discussed in *LSP-III: Development and Physiology)*, such as your muscle-skeleton system (you walked, tripped, caught yourself, and picked up the boy), your respiratory system (you breathed), and your nervous system, including both your peripheral and central nervous systems.

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Your nervous system was particularly important for many aspects of this scene: your reflex reaction (you tripped and didn't fall), your sensory systems (you sensed the boy through vision and hearing), your limbic and emotional system (you determined the boy was sad by his motions, sounds, and facial movements, and you felt emotion in response), your movement, balance, and posture, and your speech to communicate with the boy. Organs that were used included your eyes, ears, brain, lungs, muscles, and nerves. Throughout this experience, your nervous system kept track of all these systems and their interactions with each other.

And, of course, all these organs are composed of their own particular cell types. As we learn in *LSP-II*: *Genes and Cells*, within one organism all cells share basic characteristics and the same genes; the cells of different organs within that organism express different sets of genes to produce different proteins and other molecules that enable their particular functions.

Recall that the primary cells of your nervous system are called neurons (Figure 1). As you walked through the woods, your neurons were working at many levels—all involved in gathering, processing and sending information. Your sensory neurons gathered information about the environment and sent it to your central nervous system (spinal cord and brain). Other neurons connecting your central nervous system and muscles allowed you to walk, catch yourself, and pick up the boy. Neurons in your central nervous system integrate and synthesize information from the peripheral neurons, and send information back out to the periphery through more neurons; the result is that you respond to the information your neurons received and processed. The function of the neurons is reflected in their structures; neurons that do different things look and act differently.

Even within a single neuron, the different structures of the cell reflect different functions (Figure 2). Look at the interesting shape of a typical neuron. Neurons have dendrites at one end where they receive information from the environment, usually in the form of signals from other neurons. Neurons have a cell body where the nucleus and other cellular machinery reside, an extended axon down which the neuronal message is sent, and a terminal where the message is passed to other cells. Depending on which part of the cell you look at, you'll find different types of molecules carrying out the functions of that part of the cell. For example, as we'll see, the parts of the neuron involved in receiving external information have special protein receptors in their cell membranes for binding information molecules.

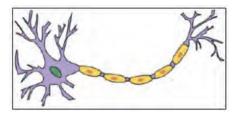
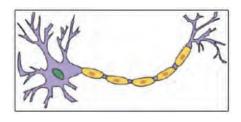


Figure 1: A neuron is a specialized type of cell found in the nervous system.

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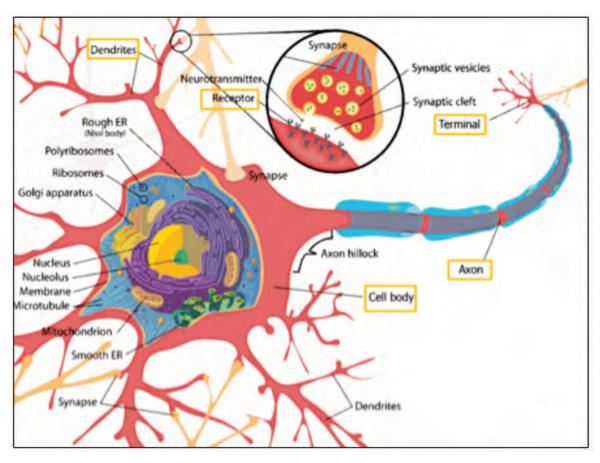


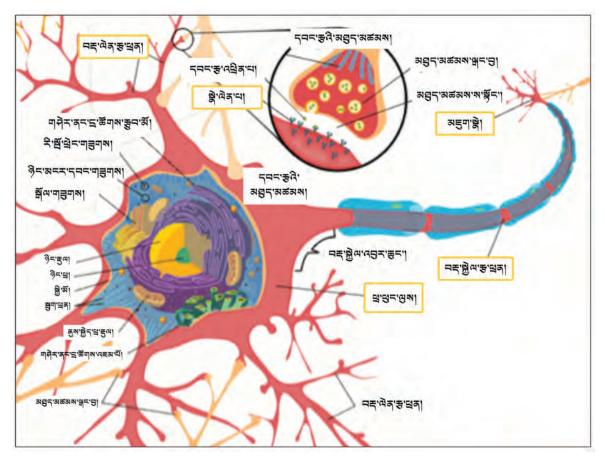
Figure 2: Detailed view of a neuron. Key structures from text outlined in orange. Other structures found in the cell body are discussed in LSP 2

THE NATURE OF THE INFORMATION

How are the neurons involved in your walk along the path, and in finding and helping the boy? How do they receive and send all that information? Neurons send information in two different ways: (1) electrical transmission due to forces caused by the flow of electrically charged particles; and (2) chemical transmission due to forces caused by movement of ions. The overall process is called neurotransmission. Within neurons, the information is sent using electrical charge; between neurons, information is almost always sent chemically (in rare cases information is sent between neurons electrically). First, let's look more closely at electrical charge

ELECTRICAL CHARGE

The fact that the building blocks of all chemicals, atoms, may have a "charge" is fundamental to electricity and to how neurons work. To fully appreciate electrical charge, we first must briefly move pretty far away from your walk in the woods. As we do, remember that a full biological understanding



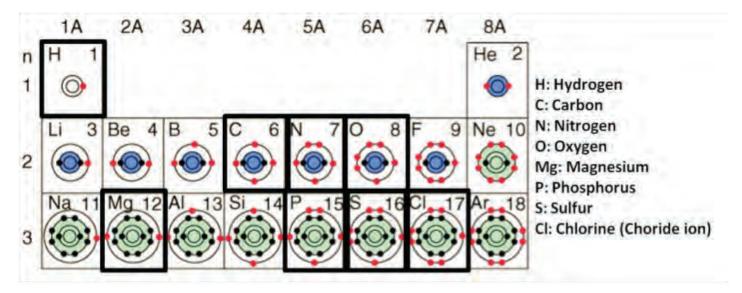
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of such complex behaviors as walking or helping a child must include an understanding of the physics and chemistry of the biological molecules underlying all our complex behaviors.



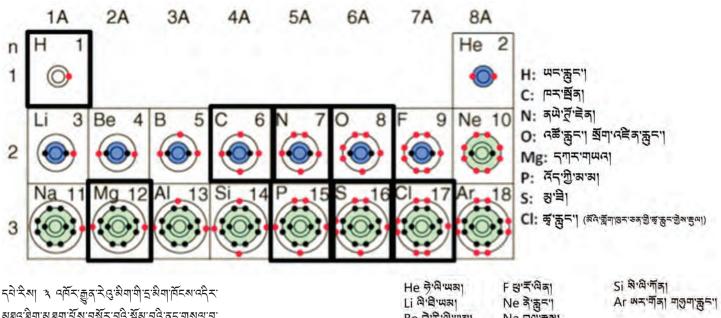
To begin thinking about charge, it is useful to review our discussion of atoms and basic chemistry from *LSP-II*: Genes and Cells. Recall that all living things are made up of different molecules, and all those molecules are composed of atoms or elements (Figure 3). The most common elements in biological organisms carbon, oxygen, nitrogen, and hydrogen, but many others are vital, including phosphorous, calcium, sulfur, iron, magnesium, zinc, and copper. Three elements are particularly important for neurotransmission: potassium, sodium, and chlorine. To explore this further, the discussion below is reprinted here from *LSP-II*: Genes and Cells:

How and why do atoms interact to form molecules like water? Just like cells and organisms interact with their environments based on their traits, atoms also interact with their environments (which include many other atoms). Atoms interact with each other based on their chemical and physical traits. In this case the important trait is the electrical charge of the particles that make up atoms.

Notice the central ball and surrounding circles shown for each atom in the periodic table. The ball in the middle of each element represents the nucleus of the atom (this nucleus is, of course, very different than the nucleus of a cell). The atomic nucleus is made of positively charged particles called

Figure 3: The elements most vital for brain function shown (with bold box) within a subset of the periodic table. Elements in the same column are said to be in the same "group" and share similar properties in that they have the same number of electrons in their outer shell. Notice that all of the biologically relevant atoms have space in their outer shell, while the elements in the rightmost column have a full outer shell and are not important for brain function.

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*₹*अशक्ते'यान्'रावे'त्रेन्'यश्यान्दायत्रेयानवे'स्स्यानावन्के' र्नेश:इस्रश:रेट्रा धट:रे.वु:सेग:देवे:दट:वी:द्र:सेग:स्रेट: द्या.बर्.सूर.जेवूर्.सदु.झ.इस.अस....२.क्ट्र्यास...याड्या. यसःवर्ष्टिवाश्यःयः द्वाःधिदःबिदः। देःगुदःस्टःवीःधिदेःर्श्लेवाश्यः रेशार्वेन्'न् र्क्क्षेन् ह्याची चारशामिकेना सर्ह् रशार्थेन् संदे स्क वसाह्यनःक्रें सामकुं दसानाधीता वदीनः में सूरानीन व्येतामा दी श्रुं स्वर श्रॅमा कम् भार्य र वहीया के नदे हिया स्वर हमा रे.वु:सेनानी नापर्यासम्स्तिन् सदे नुःसेना दर्मी हारूरा इस्रस्यर्भान्द्राती द्वीते भूजिया सेस्यावेद्रस्य द्वर्सा सेन्य કુ<u>ો.સ.વનું.નવા.ૹૈન.તવું.કુ</u>ોન.તજાતાનું.શ્જાતાતા.છું.જુવાના নতম'ঐবা

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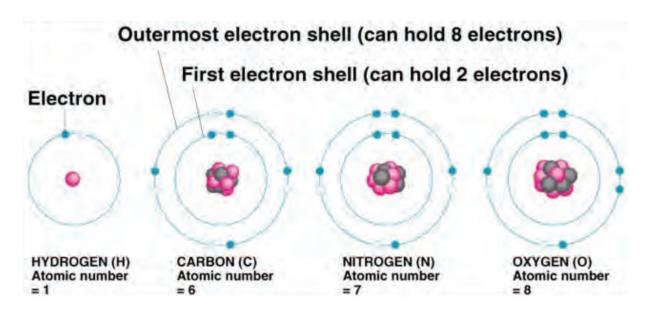
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"ૡૢૼૡॱĘે੶ૡૢਸ਼੶ઽૢਜ਼੶ਜ਼ૄૢ੶ਸ਼ਜ਼ਫ਼੶૱૾ૹ੶૬ૣૡ੶ਖ਼ਫ਼੶ਫ਼ਸ਼ਖ਼੶ਖ਼ਫ਼ੑ੶ਫ਼ੑਫ਼ੑਫ਼੶ૡઽ૽૱੶ਖ਼ૢૄ૾ૼૠ૽૱ઌ૽૽ૺ੶ૡૢ੶ૡૢ੶ૡૢૡ૽૽૱ૡ૽૽૱૱૽૽૱૱૱૱ हे भूराद्या सुराप्तर हो भूर देश का स्टास्ट की हिन्या ने का विषय हो की की की की की <u></u> ڄ؆:ڄڋٷૣૺૹ:ૹૄ૾ૢૼ*ૠ*૽ૢ૾ૢ૾ૢૢૢૢૢૢૢૢૢૢ૽૾ૹ૽૽૾૽૱૽૽ૺૢ૾૾ૢૢૢૼૡૹ૱ૢઌ૽ૹ૽૽૾ૹ૽ૼૹ૽૽ૹ૽૽ૹ૽૽ૹ૽૽ૡ૽૽૱ૹૢઌ૽ૹ૱ૹ૽૽ૹ૽૽ૹ૽૽ૹ૽૽ૹ૽૽ૹ૽૽ૹ૽૽ૹ૽૽ૹ૽૽ૹ૽ लूरी)रेट. ब्रैज. ब्रैं.र. ग्रेर.जो देज. संबर सम्मा. क्रि.र.र.र. र. मी. इमा. प्रचीर. रेट. जेमा प्रचीर विदायी क्रिया चीता है। युनामदे द्रवाह्र अद्गर्य वार्षे न प्रदे क्षेत्र वार्षे न प्रदे के वार्षे न प्रदे के वार्षे न प्रदेश के वार्षे न

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protons and non-charged particles called neutrons. The circles represent the paths, or shells, of the negatively charged particles called electrons. Each element is defined by the number of these particles—protons, neutrons, and electrons— it has. For example, you can see in the chart that a single atom of hydrogen has one electron and one proton.

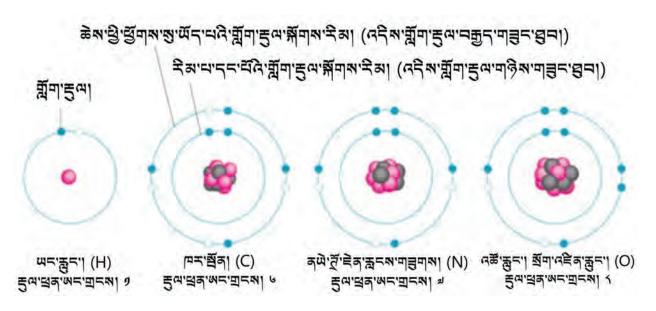
An established principle of physics, chemistry and biology is that negative and positive charges attract, while equal charges repel each other. This is important in many areas. In terms of the atom, the positively charged protons of the nucleus attract the negatively charged electrons of the outer shells, holding the atom together. The degree to which the atom 'holds' its electrons becomes important for determining how each atom interacts with other atoms in its environment.



Electrons move around the atomic nucleus in complicated paths, but we use a circle to simplify the story. Electron shells fill up with electrons beginning from the inside, nearest the nucleus, and moving to the outside. Notice the shell closest to the nucleus can only hold two electrons, while the shells farther from the nucleus can hold up to eight electrons (Figure 4). In each of the elements highlighted with the periodic table in Figure 3 - the ones most commonly found in living organisms (hydrogen, carbon, nitrogen, oxygen, sodium, magnesium, phosphorous, sulfur, and chlorine) - the outside electron shell is not full. This outside shell is called the valence shell, and it is no coincidence that valence shells are unfilled in these elements of life.

Figure 4: Four biologically relevant elements are pictured here and represented by the nucleus (made of protons and neutrons) and negatively charged electrons within the electron shells

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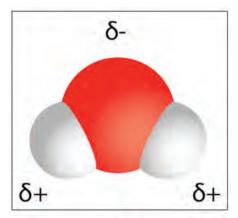
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Some atoms are more susceptible than others to losing or gaining electrons in their valence shells. Look at the table of elements in Figure 3. Which atoms do you think are most likely to lose electrons? Which atoms are most likely to gain them? To get started, look carefully at two atoms that have important roles in neurotransmision, sodium (Na) and chlorine (Cl). How do you think their valence electrons are most likely to interact with other atoms in their environment? Sodium only has one electron in a valence shell that is most stable if it has eight electrons, thus, it will easily give up that electron. When sodium loses an electron, it loses a negative charge and, therefore, becomes more positive; it is now known as a sodium ion (Na+). Note that "losing" an electron means that the electron moves: recall that electricity is defined as the movement of charged particles, such as electrons. Potassium (K), like sodium, often exists as a positive ion (K+). Now look carefully at chlorine; chlorine already has seven electrons in its valence shell, so it only needs one more to be stable. So, each chlorine atom tends to add an electron, making it more negative. It becomes a chloride ion (Cl-). It is perhaps hard to comprehend that all of our behaviors – in the scenario above, a pleasant walk and helping a little boy find his parents - are associated with ions and charges and atoms. However, as we shall see, without the action of ionically charged particles, none of the rest is possible!

Electrically charged atoms (ions) like Na+, K+, and Cl- create charge in biological systems. We measure charge in terms of voltage. The number of volts measures the difference in charge between two locations. When this charge moves in a system, it is called an electrical current, and the structures within which the current flows (neurons, in this case) are called conductors.

The medium in which current flows in neurons and all biological systems is primarily made up of water. And so, another piece of the chemical story of electrical charge we should understand is the unique chemical structure of water. We also discuss this in *LSP II: Genes and Cells*. Recall from that primer that each molecule of water is composed of two hydrogen atoms and one oxygen atom and that, due to the extreme electronegativity (attraction for electrons) of oxygen, each molecule of water has two 'partial' positive charges and one partial negative charge (Figure 5). These partial charges give water many unique properties. In terms of our discussion of electrical charge, water being both negative and positive allows ions (and their charges) to dissolve in it, so that we now have a medium for moving charge and creating current.



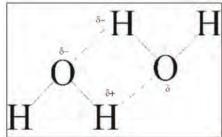
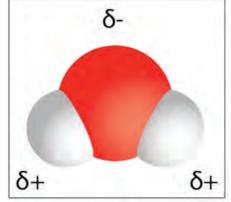
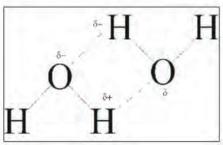


Figure 5: A molecule of water is composed of two hydrogen atoms and one oxygen atom (H2O). Water molecules exhibit interesting properties due to their chemical structure.

क्षे अद्धरमःभेरा ह्या बदायवादारे वाबदायार्थ्वे भाने वें सर्वे दार्थी क्षेत्रायर वार्येन द्वे रेग ३ दरावी विवेर क्रुव-देख-भ्रेन-वा-क्रिंश-वा ब्रिंन-क्ष्र-वा-मुख-बाद-ने-नना-वा-विना-नी-क्रिन-मुख-क्रिक-क्रेन-क्र-न-न-। नान-विना ૡૠૣ૽ૼૼૼૼૼૼૼૼૼૼૡૡ૽૽ૼૼ૱૽૽ૼ૽ૹ૽૽ૡ૽૽ઌ૾ૢ૽ૡૢૻઌૣ૽૾૽૾૽ૢૼૡ૽૽ૡ૽૽ૡૡ૱ૡૢઌ૽ઌ૽૽૽૽ૼઌ૽૽૱૽૽ૢ૽ૺઌ૾ઌ૽૽ઌ૽૽૱૽૽ૡ૽૽૱ઌ૽૽૱ઌ૽૽૱ઌ૽૽૱ઌ૽૽૱ઌ૽૽ૺઌ श्रे। ननरः इत्य्वेदः नहिंदः ने होन् देशः दरः शुन्यशः होदः के नवेः हुत्यः बदः नहिशः वेदः देनः विनः स्रुः विना हिंदः ૡૢૻૣૣૣૻૻૡૻૻૡૻૡૻૡ૽ૻૡ૽૽ૼઌ૽ૻૡ૽ૺૼૡૼ૽૽ઌ૽૽ૡ૽૽ૼૡ૽૽ઌ૽ૺઌ૽ૺઌ૽ૺઌ૽ૺઌ૽ૺઌ૽૽૱ૡૡ૽ૺૡ૽૽ૢૼઌ૽૽ૡઌૡ૱૱ઌૡ૽ૡૡૡૡ૽ૺૡ૽ૺ૱ૡ૽ૺ૱ૡ૽ૺ૱ ^{ख़ॢ}ॸॱॿॖॆॸॱॿॾॕॱढ़ॸॖॖॖॖॺॱॺऻॴ॒ॖॹॖख़ॱॾॺॱख़ॱॸॸॱॺॏॱॿॆढ़ॱॺ॔ढ़ॱऄॣॕॺऻॺॱॸऀॴऻॕॿ॔ॸॱॺॣॕॺॱड़॒ख़ॱॺऻढ़॓ॺॱख़ॺॱऄॸॱॻॖॸॱऻ॒ॸॆॸॱॺॣॕॺॱ ह्यानक्कृत्रळ्टानिविश्वरास्टानी प्रताद्धयाळेशानह्रवाचरानुशासाधीवाचशा देशस्टानी र्ह्मिनाह्यानिवेनासुने ॱढ़ॆऀॸॱॸ॒ॻऻॺॱख़॓ॺऻॺॱऄॸॖॱॺॸॱॺॕॸॱॸॖॱॺॾॖॺऻॸ॓ॺॱॺऀॺऻॱ॔ॹॺॱॾॺॱॻॖऀॱॺॣॕॺऻॱहुॺॱॺऻॖढ़ॆॺऻॱख़ॱॸ॓॔ॺऀॱक़ॕढ़॓ॸॆॣढ़॓ॱख़ॕढ़ऀॱॿॣॕॺऻॿॎॸॱ ૾ૡૺવા^{ૹૢ}ૼૻૡૹૼ૽ૼ૱ૹૻૻ૽૽ૺ૾ૢ૽૱૾ૺૹૼૡ૿૽ૹૣૼૼૼૼૼૼૼૼૼૼૡૢૻ૱ૻ૱ૢૻ૽ૡૣ૿૱૽ૡૺ૱૽૽૱ૺ૱૱૱૱૽૽ૺૡૡૺૺૺૺૺૺૺૺૺૺૺૺૺૡઌ हराक्रीरान्या(Na+)विनानुप्रकुरानानेन। यनेराधिनायानेरान्वीरानावेनाने। र्क्षेनान्यावेनानेरान्त्रार्वेना नदे में दें दें दें कें मून ह्या हे कें केंद्र हो हारा हे प्येदाया में मानी हे शक्त मान भदारा है मान श्री वहा केंद्र होते. खिरः ठवः ग्रीः हुवः ह्वाः श्रीः श्रीं द्रां ग्रीः क्षां द्रवाः वर्षा प्रवाः प्रवाः वर्षाः वर ঽ৾৾৽(K)ড়ৼয়ৢয়য়৽য়য়ড়ড়ড়৾৽য়ৼড়৾য়৾য়ৢয়য়ৢঀঢ়ৼড়য়ড়ৣ৾৽ৼৢয়৽য়ড়৽ৼৢয়ৼয়৾য়ড়ৢয়৽ৼৢড়৽(K+)ড়ৣ৾৽ৼ৾৽য়ৼয়ৢয়য়৽ यानेत्। न्याक्ष्याकृत्तुन्यालेनाकृतिनानु। कृत्तुन्यान्यानेन्यानेन्यानेन्यानेन्यानेन्यानेन्यानेन्यानेन्यानेन्या ननुत्रात्वरानम् ने ने ने नित्रान्त्र से संस्थान स्वार्मिया न महिना हमा स्वित्र स्वार्मिया न स्वर रे'रेअ'र्ज्ञुन्।'हुब'र्क्चव'नरे'नबूद'हे'र्र्राक्षेद्र'क्षेद्र'र्ज्ञेन्'र्ज्ञ्चन'व्याक्षेत्र'क्षेद्र'र्वेद'र्ज्ञेन'क्षेद्र'र्ज्ञेन'र्जेद'र्ज्जेन'र्ज्ञेन'र्जेद'र्ज्जेन'र्ज्ञेन'र्जेद'र्ज्जेन'र्ज्ञेन'र्जेद'र्ज्जेन'र्ज्ञेन'र्जेद'र्ज्जेन'र्ज्ञेन'र्ज्ञेन'र्जेद'र्ज्ञेन'र्ज्ञेन'र्ज्ञेन'र्ज्ञेन'र्जेद'र्ज्ञेन'र्ज्ञेन'र्ज्ञेन'र्जेद'र्ज्ञेन हिरः ठवः ग्रीः कृं हुरः ग्रीशः हुतः (CI-) देवा हुः ग्रुवः सरः ग्रीता वीरः वीरः वीरः हिरः अळस्य शः श्रीरः ग्रुवः यदेशः विरः विराधिः स्त्रीयः विरः ૮ઃૹ૾ૺૼૼ૽૾ૺ૽૽૽૽ઌ૾ૺૹૺૹ૾ૢૣૼૢૼ૽ૺૢૺ૽ૹ૽૽ૼૹઌૹ૾ૢ૽ૢ૽ૺ૾૽ૹ૽ૺ૽૽ૺ૱ૡઌ૽૽ૹઌઌૹ૽૽ૹઌઌૹ૽૽ૼઌઌ૱ઌ૽૽ૹઌઌ૽૽૱ઌ૽૽ૡ૽૽ઌ૽૽૱ઌ૽૽૱ઌ૽૽ ૡૢઃ૱ૡઽૄૢૺ૾૽૽૽ૢ૽૱૾ૡૼૡૻૹ૽ૣૺઌ૽ૡ૽૽ઽ૽ૹૣૼૼઌૼૢૡ૱ઌ૽૽ૢ૽ૺ૾ૡૢઌ૽૽૱ઌ૽૽ૢ૽૾૽૱ઌ૽૽૱ઌ૽૽૱ઌ૽૱૱ઌ૽૽૱ઌ૽૽૱ઌ૽૽૱૱ૡ૽ૺ૱૱ૡ૽ૺ૱૱ૡૺૡ धररःक्षेत्राम्वयःद्यक्षेत्रःकुःरेत्





स्रैर.त्यीयोत्पृत्विर्याचुम्रार्ट्रेत्यात्त्री चीयःसियोभाजाः सम्बेद्धावभाजरिभा देवानु रियोजारः स्कूत्र हु. चीयःसः सूरी कृतु तर्रिभा देवान्यायाः इभावची राय्यूर्यात् स्वयः योष्ट्रेभा र कृतु तर्रिभा देवाः सब्धायावृत्यां यत्राय्यूर्याः राष्ट्रेशा र कृतु तर्रिभा देवाः सब्धायावृत्यां वृत्याः स्वरः सी देवाः

Neurons have evolved as cells that serve as information carriers for the nervous system, and current is a big part of the way they communicate. Information is passed through neurons because of changes in the amount and location of charge. On the one hand, two different biochemical states are possible: current and no current. On the other hand, the quantity of current enriches the complexity of the information being sent.

Neurons and their surrounding environments are full of dissolved ions. How do you think neurons might be able to control the location of these ions and thus use them to create and send information? The answer to this question has two main parts.

First, from our discussion of the function of cell membranes in *LSP II: Genes and Cells*, we learn about the importance of the membrane that surrounds the whole cell and the many membranes surrounding organelles within the cells. These membranes provide a separation of the cell or its organelles from the surrounding environment, which allows for careful regulation of what enters and leaves the cells or organelles.

Second, remember that chemicals move in and out of cells in diverse ways: small uncharged molecules diffuse through membranes, but most molecules—larger or charged ones—only move through membranes via specific protein receptors, channels, or pumps (Figure 6). The structure of these proteins has evolved exquisitely to fit their function.

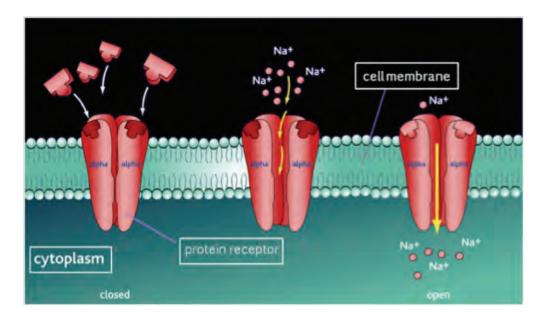


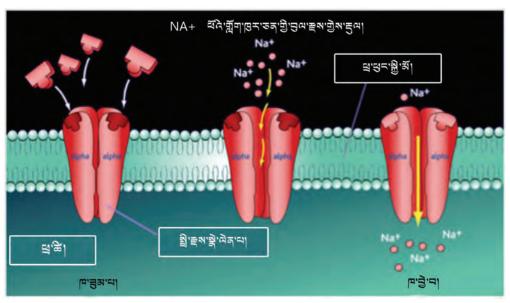
Figure 6: Specific molicules in the environment bind to the protein receptor in the cell membrane and change the shape of the receptor, allowing sodium ions to pass into the cell.

याब्य दि. यु. तर्ह यं वाष्ट्र र. यो स्क्री वा क्षेत्र क्षेत्र प्रति स्वाय का स्वय स्वाय क्षेत्र क्

दर्शनायदेन्यान्त्रम् कुंदेःवाद्याक्ष्म्भान्त्रम् व्याक्ष्म्भान्त्रम् व्याक्ष्म्यान्त्रम् व्याक्ष्म्यान्त्रम् व द्याः द्वाः स्वान्त्रम् वित्तः क्ष्म्यः द्वाः वित्यः व्याक्ष्म्यः व्याक्ष्मः वित्यः वित्यः वित्यः वित्यः वित्य वित्यः क्ष्मः वित्यः वित्य वित्यः वित्य

यह्न्यःग्रीःस्ट्री

प्राप्तः विवास्त्रभावादः विवास्त्रव्यः प्राप्तः विवास्त्रव्यः प्राप्तः विवास्त्रभावादः विवासः विवासः

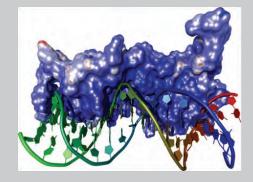


૬વેઃઋેઆ ૯ ફિન્સ્યુનાત્રદઃવોઃવદુઅઃફુવઃ૬સેનાઅઃનાન્સ્વવેઃઋેનાઅઃગ્રેઅઃક્ષ:ક્ષુદઃક્ષુ:ક્ષેટ્ર ફિન્સઃગ્રેઃવેઠઃવરાવઢેદઃશ્ર્યા નુઅઃનુઃશ્રેઃ વોતઃવઃફેવેઃનર્નેદઃ૬ગ્રેનઅઃવઃવશુઃર-વઃનાર્ફેદઃવા દેઅઃક્ષઅઃગ્રેઃગ્રેઅઃક્ષ્ય:કાર્યક્ષ:ક્ષેટ્ર ક્ષેટ્ર ક્ષેટ્ર ક્ષેય વોતઃવઃફેવેઃનર્નેદઃફોનઅઃવઃવશુઃર-વઃનાર્ફેદઃવા દેઅઃક્ષ્ય:ગ્રેઃગ્રેઅઃક્ષ્ય:કાર્યક્ષ:ક્ષેટ્ર ક્ષેય:કાર્યક્ષ:વેઠાનો

Like all proteins, these receptors, channels and pumps are encoded by genes in the nuclei of cells. The genes (made of DNA) are transcribed into RNA, and then translated into proteins that are woven into the specific membrane in guestion. Once in the membrane, these proteins respond to different environmental cues to pass messages or prevent the passing of messages into or out of the cell. The proteins' interaction with the environmental cues changes the shape of the proteins, which in turn alters their function. This change in shape and function is usually transitory—it is reversed guickly but not before the message has been sent across the membrane. As we learned in LSP II: Genes and Cells, environmental cues and the function and shape of proteins vary depending on the kind of message being sent. For example, photons (light) interact with membrane proteins in the eye, hormones or other molecules bind to membranes in many organ systems' cells (including during the chemical part of neurotransmission, as we'll see below), temperature or pressure influence membrane proteins, and electrical charge (ions) affect the membrane proteins' shape so that they regulate specific ion transport across neuron membranes.

Box 1. IN-DEPTH: THE EVOLUTION OF PROTEIN RECEPTORS

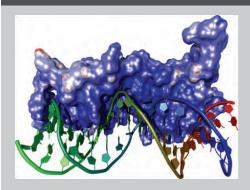
Hormones bind to a specific receptor with the specificity and affinity that could only arise through natural selection. Importantly, it is becoming clear that slight modifications – even individual mutations – can result in meaningful changes in the protein structure of a given receptor. And these changes in protein structure can have profound effects on the function of the cell and thus, on the organism. Take, for example, the glucocorticoid receptor (GR), which is activated by cortisol, a hormone important for the stress response that we will discuss more in primers 3 and 4. There is a related protein receptor called the mineralocorticoid receptor (MR), which is primarily activated by the hormone aldosterone, but is also weakly activated by cortisol. Both GR and MR act as transcriptional factors by binding to DNA and either increasing or decreasing expression of proteins. Scientists have recently traced the lineage of these two related receptors and found that a



Visualization of a glucocorticoid receptor binding to DNA. In this way, it modifies the activity of the DNA and influences the amount of protein that is made.

total of 7 mutations, in combination, give GR its specific affinity to cortisol. By following related genes through a "gene family tree", scientists identified the point approximately 400 million years ago that these two receptors diverged from a single receptor gene. They have also been able to recreate the protein structure for each successive evolutionary change. By doing this, they have determined that two of the mutations had a major effect in switching the receptor's preference from aldosterone to cortisol simply by changing the physical shape of the receptor. Three of the other seven mutations during the same period shifted the affinity of the receptor for cortisol.

खेदे दें चॅरप्यन येद नुसप्तर प्रमुराया देवसारे ह्वा ही हुस ही दें चॅरप्यन हुर हेनसारे क्राया ही ही ही से स्वर् नम्भारे अपन्न बुद रहत द्वा पुरन्त नम्भारे दिवस्य अभाग्य प्रमुख्य स्वा स्वी स्वी स्वा स्वी अपने स्वी स्वा स्वी स नन्त्राशः उंदःश्वेः इशः दरेः द्वाः वीशः विंदः धुवाः दशः वेंचः पदेः नदः श्वेंदः शेः दर्ः नः यः विवाशः नेः श्वः सुदः यः नदः दश्चेदः गर्हेर-वर-श्वन-ब्रेंग्रथ-ग्री-ल-वर-श्वेंर-वरमा लर-वा सन्तर-ने-विंग्।वर-र्-वर-दर्शव-व्याय-वर-रमा लर-व श्चे इसप्तनानी त्वर्राञ्चे वर्ष्ट्वे र व्यावादा वर्दे सर्श्वे इसर्ग्ये वर्गे तत्त्वी वसर्वा व्यावस्था वर्षे तत्त्वा वे सर्वे प्रवासी होत यसप्यादक्यूर-वन्तर्हिन्दारेत्। <u>भ</u>्नेर-दन्तर्गोन्दन्तिसस्य-दन्तिन्यसप्य-भ्रेतस्य-दिव्यूर-वन्दि-वह्द-क्वासप्य-<u>५,'५वो</u>सस'निहेंटस'नुस'र्नेट'<u>५</u> 'हुस'र्सेन'से'नेुन्। ट'ळेंस''देनस'ह्स'द्दानुद''सेट'नुह'ठद'नी'ळें'सेंन'ळद रेया'ची 'र्श्व 'वर्चेदि 'र्श्वेच 'हेन 'चाहे अ'रादे 'वह 'सूर 'सुर अ'रा'राबेदा। वहेव 'चाहें हि 'चु कुंदे 'चह 'वर्धेव 'ची 'रह रावेद 'ख' ऀढ़ॕॴॱॸॖ॓ॱॺॕॎॸॱॶॖॴॱॺॏॱॺड़ॱढ़ॕॕॺॱॸ॔ॸॱऄॗॖॱॾॖ॓ॴॱॻॖऀॱऄॖॸॱ॔ॺॴॱॸ॔ॸॱक़ॴॴॸऒ॔ॸ॔ॱॺढ़ॴॴॱॠऀॺ॓ॴऒ॔ॱऄ॔ॸॱऄऀॱॺ॔ड़ॱॺॱढ़ॻॗड़ॱॺॱ नेत्। ते'य्यर'त्येर'त्। वॅत्'त्व्य'(वॅत्')त्वाचीय'येवात्रर'वी'भ्री'यवाय'धी'ह्य'त्रर'धेव'र्धीर'वेत्'यत्रा क्रेत'ह्य' <u>અમા ભરાષી હર્ય, રંતા. ત્રાવેષ દ્વીતા ધુ. (૨.૦૦, ૪.૧) તેમારે ત્રાફ્રા કર્યા તરવા ૧૮૪૧ કેમાં ત્રાફેટ કરી તરફા ક</u> वर्षु र-तृ सन्देशः स्नेनसः सूरः) न्नदः सेवै:सः यना सदः सेवै:सः सुदः स्टः नीः स्ने :पन्य सः वर्षेदः सूर्यः होनः य। कः हेन् न्सः વર્વેઠ બુવાય છેય સું તવાય સું ક્યા સેન્ડ, રોડ લુય વર્નેઠ વન્ડા ખન્ડ (છેય ક્યા ક્યા વર્ષ) ર્સેવા લુસ છેય સું पनाशःश्चे <u>इश्चारनानी पर्नोत् प्रवित्रश्चार्य</u>नुनशः कुतानविश्वासायानहेत्र दशः देशः प्रवार क्रेटे श्ची प्रवारा वितर् ह्यानुः त्र्या प्रते प्रतेर पद्देव न्तुः चाया सूर या पद्देव न्तु हाया सूर नुष्येवा



यम्.स.स्मा याद्या, याद्याम् कृते, श्री इत्यामी याद्या, याद्या सबर क्रिय क्रिया मा स्वाप्त क्रिया क

So, if we have channels and pumps specifically to regulate transport of particular ions (the most important ones in this case are K+, Na+, and Cl-) in or out of the cell depending on information in the cell's environment, we begin to see how the presence or absence of charge dictates the transport of messages.

Box 2. IN-DEPTH: THE ELECTRICAL NATURE OF NEUROTRANSMISSION

Neural interactions, and thus all thoughts and movement, require neurotransmission, which is both electrical and chemical. It is odd to think of our bodies as being full of electricity—the same force that drives our mobile phones and lights—but it's true. The electrical nature of neurotransmission is made strikingly evident by the technology of prostheses, or artificial body parts that alleviate severe deficits. For example, soldiers who lose arms or legs in war, can have 'new' artificial



prostheses attached to their bodies to replace those missing limbs. The most modern of these prostheses have electrodes that electrically link them to the person. Over time people 'electrically train', that is learn, to move their prosthesis by thinking to move it just like they do with their natural limbs. Their thoughts are translated into electrical activity that moves the prosthesis, just as thoughts are translated into the electrical activity that moves a natural limb.

Brain implants are especially amazing. Working with people who are paralyzed, scientists have hooked electrodes either directly to the paralyzed person's brains or to their skull. Scientists then ask the person to think certain thoughts, for example, 'up' or 'down'. The general pattern of brain electrical output for each type of thought is determined by a computer, and after much effort, the computer software that results allows the paralyzed person to electrically control a computer mouse so that the person can move a cursor to point to or spell out their thoughts on a computer! The paralyzed person can communicate by having their thoughts—electrical neural activity - electrically transferred to a computer. These scientists are also discovering possible additional benefits of this work. Sometimes an electrode implanted in the brain seems to replace electrical activity from neurons that have died. The result is that the paralyzed person is now able to make certain movements that were not possible before receiving the electrode implant. Such research is very preliminary, but clearly has exciting potential. And for our purposes here, these examples illustrate how the nervous system uses the same kind of electricity that can run through wires and control machines.

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RESTING MEMBRANE POTENTIAL

Scientists discovered another crucial aspect of electrical charge's role in neurotransmission once technological advances enabled them to measure the voltage difference (also known as membrane potential) between the inside and outside environments of typical neurons (Figure 7). They discovered that when a neuron is not active, its so-called resting potential is negative—specifically around -70 mV (mV stands for millivolt or one-thousandth of a volt, and measures the difference in electropotential). This means that the outside of the neuron has a voltage 70 mV more positive than the inside.

In general, ions flow through membranes based on two principles: concentration gradients and electrical gradients. Let's first consider the concentration gradient. Ions naturally move toward equilibrium, from higher to lower concentration (Figure 8). So, if a membrane allows ions to move across it by opening a specific channel for a particular type of ion, say Na+, these ions would, without

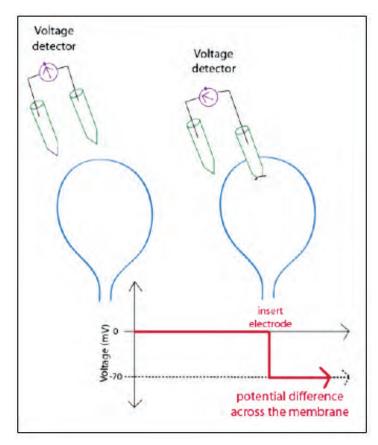
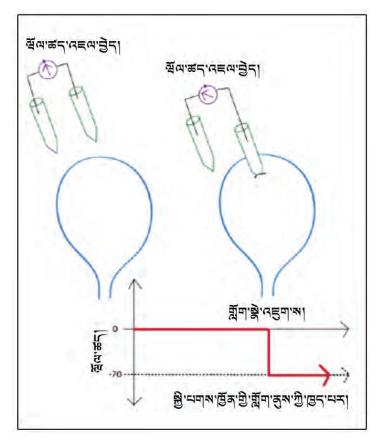


Figure 7: A voltage clamp measures the voltage difference between the inside and outside of a cell.

the addition of extra energy, move from the side of its higher concentration to the side of its lower concentration, until the concentration of sodium ion was the same on both sides. However, as the Na+ ions move through the sodium channels down their concentration gradient from the outside to the inside of the neuron, they also take their charge with them. Because Na+ ions carry a positive charge, opening of sodium channels in the memrane will lead to the flow of positive current into the neuron, and therefore this neuron will become depolarized (i.e. become less negative on the inside). Why then does the neuron show a negative charge inside during resting? Well, this is because normally the membrane has many more open K+ channels than Na+ channels in its membrane. Because K+ is more concentrated on the inside it will flow to the outside down its own concentration gradient and make the outside more positive. In effect, negative charges from other ions that cannot move through the membrane are left behind and result in the negative charge seen inside.

So why does the membrane then not become even more negative on the inside than -70 mV, which is the normal resting potential in many neurons? What keeps the ions from continuing their movement indefinitely? Again,



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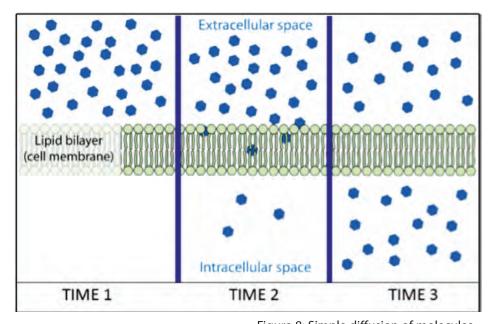


Figure 8: Simple diffusion of molecules through a permeable membrane. Over time, there will be equal concentration of molecules on both sides of the membrane.

the positive K+ ions and makes them less likely to move outside (Figure 9). In fact, when this electrical force is equal but opposite to the force provided by the concentration gradient, K+ ions stop moving through the membrane altogether, even if K+ channels are open. The membrane potential that exactly counteracts the concentration gradient of an ion is called the equilibrium potential of this ion.

Now we still have an important question: How, if ions always flow down their concentration gradient, can there be a higher concentration on one side of the membrane in the first place? The answer to this question lies in another type of membrane protein, called an ion pump. Ion pumps move ions against their natural concentration gradient, but this process requires spending energy. For instance, the Na+/K+ exchange pump (Figure 10) uses one molecule of ATP for each 3 Na+ ions pumped to the outside, while 2 K+ ions are also transported to the inside. Because for each 3 Na+ ions leaving only 2 K+ ions enter in this process, the Na+/K+ exchange pump also helps the inside of the membrane to stay negative. The Na+/K+ pump is essential for maintaining the resting membrane potential of neurons.

ACTION POTENTIALS

So, now we have most of the key elements of an information-sending system: a specialized cell (the neuron) with specialized parts (some for receiving, some for sending information), including proteins that regulate the amount

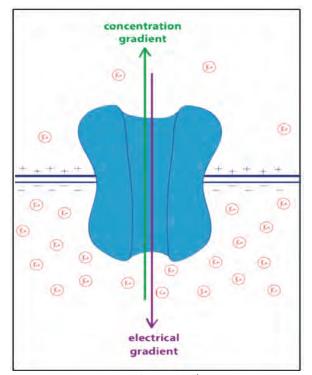
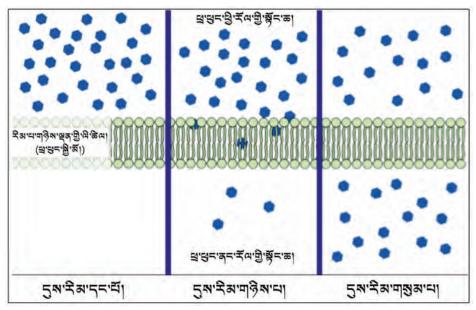
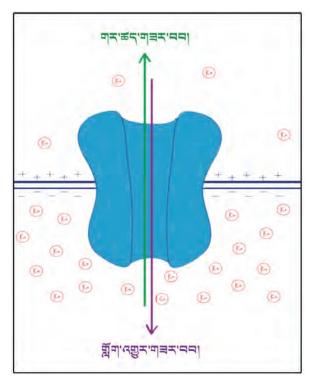


Figure 9: Because there is more K+ inside the cell, the concentration gradient pushes it out. As K+ leaves the cell, a net charge begins to build along the membrane, creating an opposing electrical gradient.



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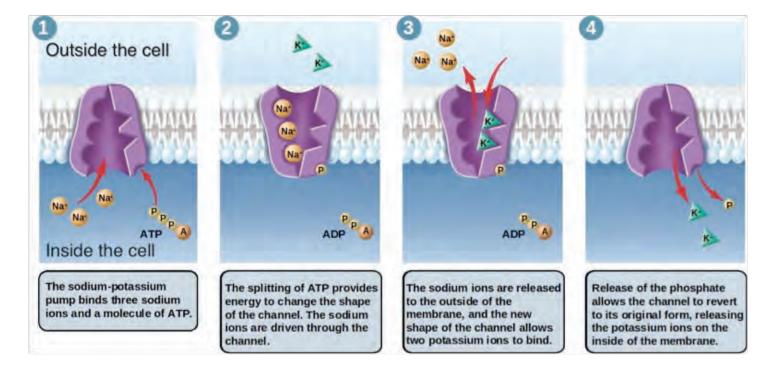
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८:क्टॅर-५-५८:३:न'माय'ळेद'वेना'र्थे५'स'दे। माय'हे:ग्रीश' ह्य'द्वश्रशहना',हु:ग्रर'ळंद'माबर'नन'ग्री' सर्वे अ'बेन'वर्षास्त्राचनन्त्रम्यत्त्रम्यत्त्रम्य भीति भीति स्त्रम्य स्त्रम्य स्त्रम्य स्त्रम्य स्त्रम्य स्त्रम् दर्गेशःसः दे विवासरः वायदः ग्रुसः हे ग्रुदः वः धोदः द्वसः विरुपः सः यदे : धोदा देः वः यदे रः वादवः कुवेः यदः ऍट्। ॼॖॆॴॱहुख़ॱय़ॹॖॸॱॻऀऄॴॼॖऒॱहुख़ॱइॺऒॱॸॸॱॹॗ॓ॸॱॸऻॗढ़ॱॹऻॸॱख़॔ॸॖॱॹॿॸॱय़ॸॱॸॗॸॱऄॗ॔ॹऻॷॕॹऻऒॱ शुन्तभुव्यन्तरेन्। वेद्याग्रद्यनेन्द्रभावदेन्यत्यस्यामुर्जेद्यन्तेन्द्रनेव्याग्रेर्वेद्यान्तेन्द्रभावत्याम् <u>ॼ</u>ॆॴॱड़ॕॖॴॱॸॣॸॱॸॖज़ॱऄॴॸॖॴॸॱऄ॔ऄॱॼॖॆॴॱड़ॖॴॱॺक़ॱढ़ॗ॔क़ॱॸऻॾ॓ॱॷॗॣॸॱज़ऻॸॕॸॱॸऄॱफ़ॹॖॸॱग़ॴॱ(ॸऄॱॸॆॴ ૧૦)તુવા ૄર્યા શું : શું આ ત્વાવાશુયા છું : ર્વા તુઃવહ્યા સુવા વાર્તે દાવા નાર્વા સાથા સામા સામા સાથા માના માના वॅदि'क्येश'हुवाम्बिक्ष'त्रम्'र्सेव'तु'वदेत'महिंद'क्येद्विस्थानेराखे'ते'चे'(ATP) वतुक्ष'हुवाम्बिन्। नेन-ब्र्ॅन-वर्निन्ने प्पेन्। नुवाह्रा क्रीका हुवा नुवाना सुसादी न वित्र केन्याने वा निवास कराती है । શ્રેશ-દ્વાનફિશ-હંશ-દ્વ-વદેવ-શેન-શુન-શુન-શે-બેન્ નેવે-ક્રુ-શ્રહ્ય-શ્રેશ-લુવ-દ્વાનાનું સ્થાન-દ્વાનન એવઃ૬૧૧૨⁻દેવિ:ॻૢ૽ૺ૱ઃ૬્વઃવद:&ৢৱ:વहे:ૹૄૢ૱:વૢ૽૽૽ૼઽ:વવે;વવુ૬:&૱:ઌ૽૾ૢ૱:ૹ૾ૢૢૺ:વવા૱:ઌ૽૾ૢ:૱ઽ:&:दे:ૹ૽ૺ૱: ર્જ્સેનાલિમ હવાને ક્ષાંત્ર શ્રુપ્ત શ્રુપ્ત કુમાના મામામામામાં મામામામાં મામામામાં મુખ્યત્વે છે. ત્યારા મામામામા इशः ग्रेशः ह्वः प्रः विदेश्चित्। तुरः उदः ग्रीः पुता सेवः प्राप्तः विदेशे स्वः पदः विदेशः विदेशः नदे प्रतृत्याने निनम् सामा त्रामा निमानी क्षेत्रे से मुक्षा प्रते महिष्या महिष्य प्रति स्त्री सामा स्त्री सामा सर्वि के न धीता

यस'तह्म'कुस'म।



of charge moving across its membrane (enabling the cell to use charge as a medium for sending information). The next question is: what constitutes a signal? And how exactly is that signal received, translated and sent?

Figure 10: The Na+/K+ exchange pump moves 3 Na+ molecules out of the cell for every 2 K+ molecules it moves into the cell. This helps maintain the resting membrane potential.

The signal that a neuron sends is called an action potential, because it represents a charge difference (potential) that leads to action. This signal is initiated at a part of the neuron called the axon hillock, which contains a

particularly high density of sodium channels (Figure 11); we will soon see why this is important. An action potential is generated when stimuli sent from other neurons and systems and received by the dendrites lead to the opening of enough ion channels at the axon hillock that the inside of the cell reaches the threshold potential, which is usually around -55 mV. (Recall the concept of thresholds from other primers: a threshold is the tipping point at which a system responds; just below the threshold, nothing happens, but at or beyond it, there is a response. Thresholds occur in all systems, biologic or not.)

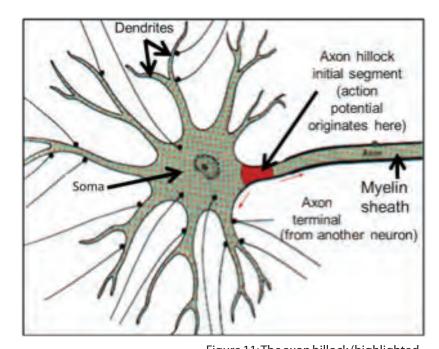
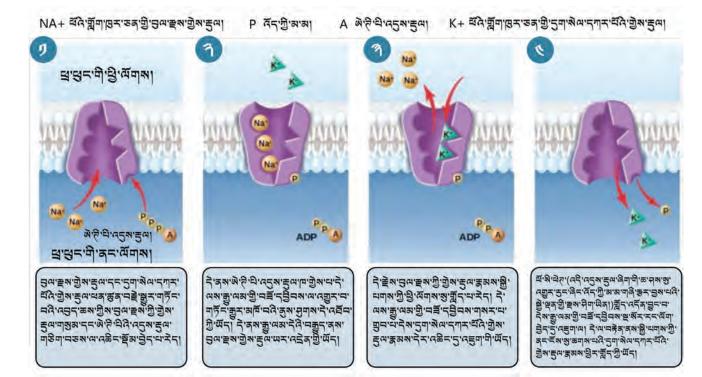


Figure 11: The axon hillock (highlighted in red), located where the axon arises from the cell body, is where an action potential originates.

Once the membrane potential depolarizes (that

is, becomes less negative) to the threshold potential, an action potential is triggered (Figure 12). Very quickly, within 1/1000 of a second, an action



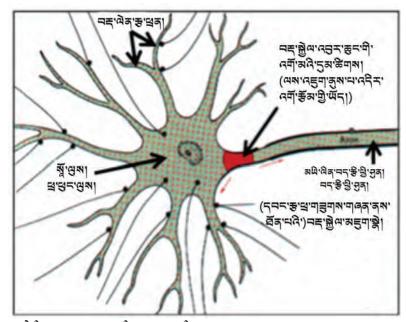
सुत्र चे.सुर्-चेश्वरत्व्यवश्वर्याच्याक्षेष्वरत्त्रच्यं स्वयः स्वयं स्वयं साम्रीने क्षेत्रः चेत्रः स्वरं स्वयं साम्रीने व्यत्त्रः स्वरं स्वयं साम्रीने व्यत्त्रः स्वरं स्वयं स्ययं स्वयं स

देश ११) वदे हे वह वे नाव केंद्र पोद पाद केंद्र पोद पाद केंद्र केंद्र पोद पोद के पाद के पाद केंद्र पाद केंद्र प

नाते परि सुर्भे। नह पर्से देते नार विनानी यायमुना माणी तत्राया नह पर्से दास्य स्थान है स्थूर प्रोत विरा

हे : क्षुर : सन: क्षुर : बेनक: य: प्राप्त | हे : क्षुर : वाहित : यर : वेठ : प्राप्त | वेक: य: यदे : प्राप्त |

स्वाह्मास्य स्वाह



दह्यात्रुषायाः विवानी में मार्थायाः विद्यात्र्याः स्ट्रेस्या विवान्याः में स्ट्रेस्य स्ट्रेस्य

द्दश १४)। देवशक्षः इट्टन्स् श्लेस्टल्यः श्लेस्टल्यः विवानी वटः द्वेद देवायः वट्टियाः वेशः सः विवानी श द्वरः देवियः) हे मेश्रासक्स्रश्च श्लेश्यः स्टल्यः श्लेसः स्वी व्यश्यः द्वियः त्वेशः सः विवाश्वरः स्वाधः स्वाधः व्यः विवाश्चिः स्वाधः स्वाधः स्वाधः स्वरः स्वाधः स्वरः स्वीयः स्वरः स्वीयः स्वरः स्वीयः स्वरः स्वीयः स्वरः स्व potential produces a sharp rise in membrane potential to as high as +50 mV, which is a value determined by the sodium concentration gradient, which will be explained below. This spike is followed immediately by a sudden decrease in potential down to below the original resting potential, and in fact to a level even a little more negative than the resting potential (hyperpolarization). For a given neuron, the shape (form and extent) of its action potential is always the same. Neurons, then, may receive signals and depolarize slightly, but only if they depolarize enough and reach the threshold potential will they 'fire' an action potential.

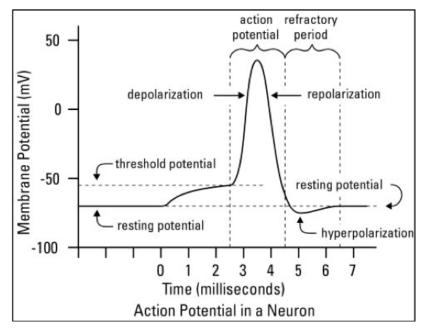
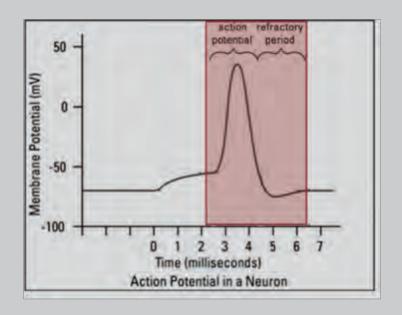


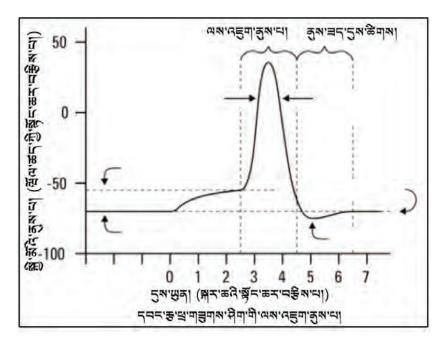
Figure 12: An action potential, shown as membrane voltage over time.

Box 3. IN DEPTH: THE IMPORTANCE OF A FAST RETURN TO REST

Let us think more about the dynamic process illustrated in figure 12. Notice the amount of time it takes the neuron to go from the onset of the action potential to the point when the resting potential is reached again, shown in the image to the left in the red box. Why is it important that this process be fast? As will be discussed in more detail later in this primer, the rate at which a neuron creates an action potential encodes crucial information about the stimulus that triggered the action potential, such as the intensity (e.g. temperature, pressure) or speed. The faster a neuron is capable of firing, the more

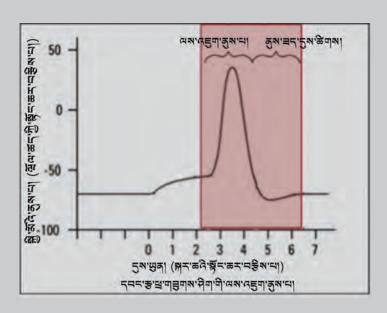


potential the neuron has for encoding this type of information, and the more sensitive the information can be. To understand this, imagine how the ability to encode information would be compromised if, rather than the approximate 5 msec (5/1000 of a second), it took 500 msec (1/2 a second) to produce an action potential and return to the resting potential. Instead of a maximum rate of firing of 200 action potentials per second (1000ms/5ms), the neuron would only be able to generate 2 action potentials per second. To appreciate the effect of this difference, look at the scenario below and pay close attention to the variable rate of firing that is evident over the 2 second period of time plotted here. Now, imagine how the function of this neuron would be changed if it was only capable of firing twice each second.



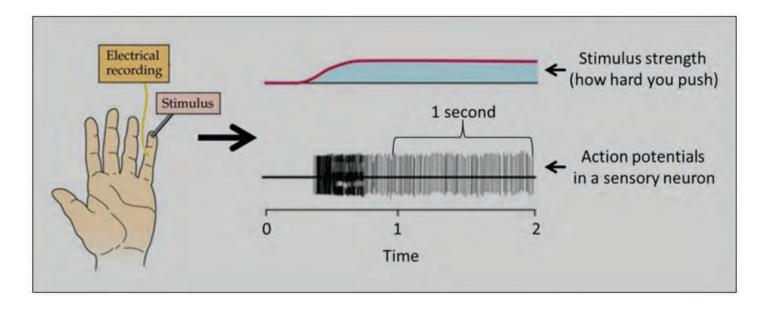
वृद्धः स्वयः मुक्तः स्वयः स्ययः स्वयः स्यः स्वयः स्वय

मुँ अ'चु'गुरुअ'च। गुढेर'ङ्क्षणस'चते 'स्रु'दिन। चु'ऄर'ग्री'गुरुष'चन'स'तद्यस'नु'ड्डेर'सँग'चेर'चदि'गस'गुरु।



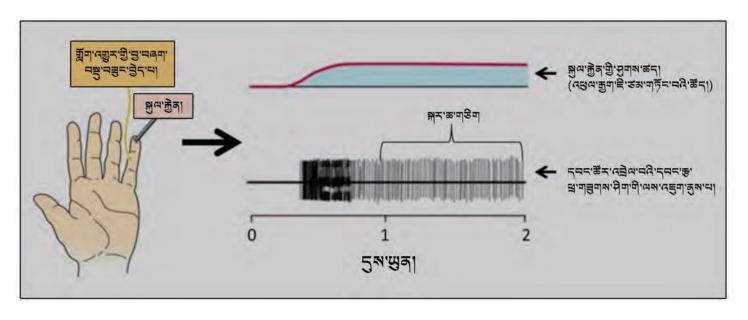
प्रविश्वास्त्रीक्षर्वास्त्रम् स्वत्त्रीत् स्वत्त्रम् स्वत्त्यस्यत्त्रम् स्वत्त्रम् स्वत्त्यस्यत्त्रम् स्वत्त्रम् स्वत्त्यस्यत्त्रम् स्वत्त्रम्यत्त्रम् स्वत्त्यस्यत्त्रम्यत्त्यस्यत्त्रम् स्वत्त्यस्यत्त्रम् स्वत्त्यस्यत्य

इस्थान्त्रिश्चः अस्यायश्वास्त्राच्यां सुर् देने त्यश्वात्वाची सूर्या है वर्षा विद्यास्त्रा स्थान्त्री स्थान्त्र स्थान्त्री स्थान्त्र स्थान्त्य स्थान्त्र स्थान्त्र स्थान्य स्थान्त्र स्था



Before we consider how an action potential has its effects and propagates its signal, let's walk carefully through the molecular details of what happens during an action potential. Together the many complex steps below all occur in just a few milliseconds! Follow each point below corresponding to Figures 12 and 13.

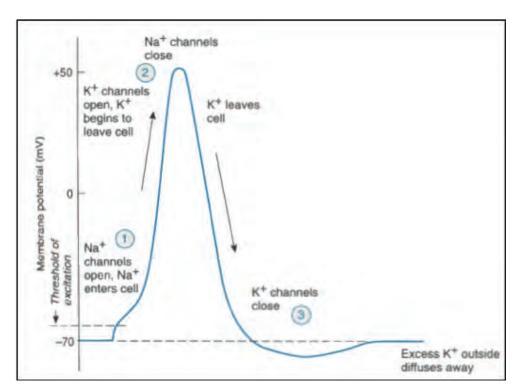
- First, remember the charge across the membrane rests at a negative potential (about -70 mV, see Figure 12) of inside versus outside the cell.
- The key ions to consider for generating an action potential are K+ and Na+. At rest, more Na+ is outside than inside the neuron, and more K+ inside than outside the neuron.
- Two types of voltage-gated channels—one for each of these ions—are
 in the membranes of the cell body and axon hillock of the neuron. These
 channels are called 'voltage-gated' because their shape changes so
 that they are 'open' or 'closed' based on the voltage (charge) across the
 membrane in their immediate environment.
- For an action potential to occur, the membrane potential must depolarize (become more positive) due to signals sent from other neurons; we will talk more about these signals later. As the inside of the neuron begins to depolarize because of these signals, voltage-gated sodium ion channels in the membrane open in response to the voltage change.
- At rest, more sodium is outside the cell than inside (creating a concentration gradient), and the inside of the cell is negative while sodium ions are positive (creating an electrical gradient). Thus, when sodium channels open, sodium rushes into the cell, due to the force of both its concentration and electrical gradients. Because sodium is a positive ion, the inside of the neuron becomes more positively charged as more sodium enters (Figure 13,#1).



क्रिश्चूब् चिः क्र्या विवास्त्रा त्रिः स्था १४ ८८. १४ योष्ट्रेशः स्थाः यद्यः योष्यः याश्वाः क्र्यः विवास्त्राः स्थाः स्थाः विवास्त्राः स्थाः विवास्त्राः स्थाः स्

- न्दःस्य अस्दःश्चेश्वेदःश्चितःश्चे (श्चित्रःश्चे) स्वरःश्चे क्ष्यःश्चरःश्चे श्चे स्वरःश्चरःश्चे श्चे स्वरःश्चे स्व
- त्याप्तह्त्वा तुमानाम् अति । स्वत्या के निवास के निवास का मुन्या निवास के निवा
- न्वरः इ.स.च बीच्यायः क्री. यर्स् क्षीयः त्वरः क्षिरः स्टर्स स्वरः स्वरं स्वरः स्वरः

At this point, sometimes change in charge the from inside to outside is not enough to reach the threshold potential, and the cell returns to resting potential. But other times, the change in charge is sufficient to reach the threshold potential (Figure 12). The opening of sodium channels results in further depolarization, which results in even more sodium channels opening, and an action potential occurs.

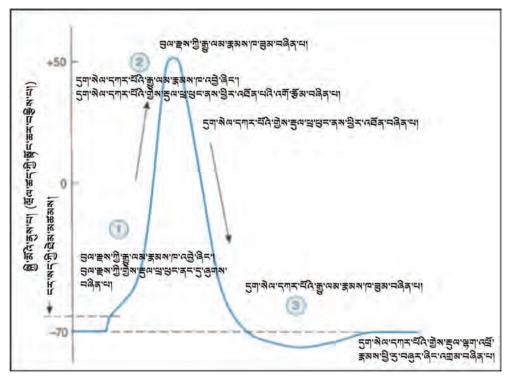


• The increased potential that causes the sodium channels to open in the first place also causes them to close, but more slowly than they open. This is a special mechanism of closing called inactivation. If you think of the opening of a channel as removing a plug in the channel, inactivation is a special kind of plug that is pulled into the channel by the positive membrane potential. After the sodium channels inactivate due to this process, no more ions can flow through the channel, and thus no further depolarization occurs (Figure 13, #2).

At the same time, the depolarized potential also causes voltage-gated potassium channels to open. These channels, like the sodium channels, are sensitive to depolarization, but they are slower to react to voltage changes than are sodium channels. Remember that K+ is more concentrated inside the cell (concentration gradient) and now the membrane potential is quite positive (around +50 mV; electrical gradient). Thus, when K+ channels open at this point, K+ rushes out of the cell, following both its concentration and electrical gradients. As K+ leaves the cell (and with Na+ no longer moving into the cell), the membrane potential becomes more negative due to the loss of the positive ions.

 Because more potassium channels than usual are open after the action potential peak, the membrane potential drops, for a brief time, even below the resting potential (Figure 13, #3). This is called hyperpolarization (Figure 12).

Figure 13: Several important stages of an action potential, shown by membrane voltage over time. See the points in the text for a description of each stage.



यतुः रूप्तः योषटः यक्षेट्रः यक्षेत्र्या अस्त्राक्षाः क्ष्यां अस्त्रः यक्षेत्रः यक्षेत्रः यक्षेत्रः यक्षेत्रः य इतः श्रुः श्रुषः युः रूप्तः यक्षितः यक्षेत्रः यक्षेत्रः श्रुपः यक्ष्यः यक्षयः यक्ष्यः यक्षयः यक्ष्यः यक्षयः यव्यवः यव्यवः यव्यवः यव्यवः यव्यवः यव

- तहै बी बेश ता बुची च भेंदे र ता देती प्रतिस्तर देति ता व के प्रत्य के प्रतिस्ति के प्रत्य का स्ति के प्रतिस्ति के प्रति के प्रतिस्ति के प्रतिस्ति

द्री(द्रिन्द्रश्रा ७ ४ वट्याश्रेश ४)

स्टाविद्यास्य १ वियानहेव वश्यान्य विद्यास्य विश्वास्य विश्वास्य विद्यास्य विद

- द्रान्त्रम्भःक्रेन्तर्व्याद्रम्भः विराद्यकर्त्वरं क्रेम्रान्त्रम्भःक्रेन्यर्व्यम्भःभ्रे स्वाद्रम्भः विराद्यम्भः विराद्यमः विराद
- तर्भ त्यस्त्र प्रमुख श्चे त्यस्य ने स्तर्भ हो स्तर्भ १८)

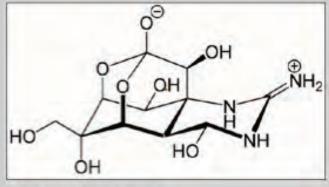
 त्र त्यस्त्र स्त्र स्तु त्यस्य स्तर्भ स

- Finally, there is a refractory period (Figure 12) for the portion of the neuron's membrane that has just fired an action potential—a period when the voltage-gated sodium channels cannot react to depolarization again. Indeed, they need a period of hyperpolarization to become ready to open again.
- Once the action potential is complete, the membrane slowly returns to the resting membrane potential, due to the passive diffusion of K+ back into the cell. Remember that the Na+/K+ pump serves to maintain the proper concentration of Na+ and K+ ions inside the cell, so the concentration gradients remain stable.

Box 4. IN-DEPTH: NEUROTOXINS AND NEUROTRANSMISSION

As we've seen many times in our science studies, one important way to understand how things work normally is to study them when they don't work normally. Many molecules that poison the nervous system, called neurotoxins, have in fact been very useful for studying neurotransmission. One neurotoxin comes from a fish called fugu, shown here, that can puff up with air to increase its size and scare off predators. Even though the fish is extremely toxic to humans—as it contains in its liver and ovaries the neurotoxin tetrodotoxin, whose structure is shown here—it is a very expensive delicacy at fancy restaurants throughout Japan. Special chefs require years of training to be able to effectively and safely prepare the fish by removing the organs containing the toxin.





PUFFERFISH AND TOXIN

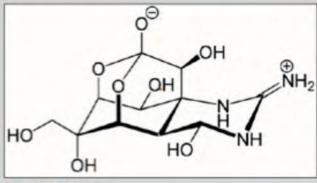
Why is tetrodotoxin poisonous? The toxin binds to sodium channels on neural membranes, causing

them permanently to close. Knowing what you now know about how action potentials work, what would this toxin do to neural signaling? In fact, tetrodotoxin stops all neural signal transmission, easily causing paralysis and eventual death in humans. Scientists have used this neurotoxin and others to help elucidate the electrical aspects of neurotransmission. Neurotoxins also have been useful in studying the chemical part of nerve signaling that occurs both between neurons and between neurons and muscle cells. Another illustrative example is the toxin from cobra venom, which is also fatal to humans. This toxin blocks the signaling between neurons and muscle cells, and thus paralyzes the heart and other muscles.

- ढ़ेचा.केर.बीट.चीट.खीट.ला ट्रे.का.चहेष.वंश.चाट.क्ट्रंचाचट.चच.इश्श.चहंष्ट्च.स्ट्चाष्ट्रश्च.स्ट्रंचि छिट.ठथ.की.चीला.इश.कीश.देल.चंट.सुंदु.क्यूंचा.खिट.ठथ.की.टीचा.शुंचा.चेचा.सा.सुंदु.कीश.देल.चंट.सुंदु.क्यूंचा. खूचा.चीट.च.दुंची. क्ट्रंटरंट्चूंचा.स्थ.चंचा.स्वी.खी.खी.खंट.ठथ.की.ची.सुंदु.ची.सा.सुंदु.कीश.देल.चंट.सुंदु.क्यूंचा. संसी.चंट.देत.दुंची.खेश.सचे.सुंदु.कीश.संखुचा.सी. सुंदु.क्यूंचा.खिट.ठथ.की.ची.संदु.कीश.संदु.ची.सूंचा.संट.दे.सुंदु.क्यूंचा. संसी.चंट.देत.दुंची.चेश.सचे.सुंदु.चीश.स.खेचा.खी.खी.स्वी.ची.सुंदु.ची.संदु.ची.संदु.ची.श्चर.चंचा.खी.स्वी.स्वी.स्वी.स्वी.स्वी.संदु.ची.संदु.ची.श्चर.स्वी.सुंदु.ची.संदु.ची

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न्ध्यान्द्राच्यान्य

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Let's go back to the imaginary scene that began this primer. Is it possible that complex behaviors such as walking or empathizing with a child are made possible by emergent properties of these invisible ions and channels, proteins and genes, obscure and complex biophysical mechanisms? At first, it seems ridiculous, even impossible. But you, as scientists, who have studied evolution, development, physiology, genes and cells, should think carefully about this.

We have learned some ways to think about such big questions. What organ systems and organs are involved in these behaviors? (Surely, at least the nervous system—the brain, spinal cord and nerves.) What cells in these systems might be functionally responsible for the actions in the story? More generally, what, biologically speaking, is sensation, movement and even emotion? (Apparently it's a collection of signals from a set of neurons in response to an environmental signal.) What molecules in these neurons send the signals and how are they sent? (Here is where electricity and ions and proteins and milliseconds come in!) And so, it seems, there is a deep connection among ions, proteins and behavior. And, as you're learning, all these ideas can be tested experimentally. We design experiments in different organisms to see if our hypotheses and ideas are consistent with what we observe happening.

Now, do ions and neurons and electricity explain everything? Do they, on their own, fully account for complex behaviors like we see in our imaginary scene? The answer is probably not. At each level of the story, as we discussed in *LSP-I: Evolution*, there is the potential for new and emergent properties, characteristics that molecules or cells or systems manifest only when acting in combination with each other. For example, in this primer, we are not going to discuss the higher cognitive functions involved in our story, like emotion and motivation – these topics will be covered in later primers.

ACTION POTENTIAL PROPAGATION

Based on what we have learned thus far, we have a sense of how signals are initiated in the neurons of your body as you walked through the woods, tripped, heard and saw the boy, felt compassion for him, picked him up and carried him home. To better understand how neurons work, we need to understand two more crucial parts of the story, beyond what action potentials are and how they are formed. We should understand signaling on either side, so to speak, of the action potential. What exactly happens

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to lead to an action potential and how does the action potential, which happens in one small part of the neuron's membrane, get passed on to other neurons? The two questions are related. Let's start with the latter one first: how does the action potential pass on its information? That is, how does the initial action potential 'translate' into a signal that moves down the axon—a process known as propagation—and then get passed to the next cell?

Two concepts are important in comprehending the mechanism of nerve electrical signal propagation:

- (1) Propagation is unidirectional: during the refractory period, the part of the axon that just underwent an action potential can't depolarize again until the sodium channels are ready to activate again (Figure 12). Because action potentials are generated at the axon hillock, the 'charge signal' provided by the action potential cannot go in both directions, but only in one direction—away from the neuron soma and down the axon.
- (2) The individual action potential is always the same for a particular neuron. That is, the nature of the activation potential depends on the neuron, its membrane and its membrane proteins, not on the strength of the signal the neuron receives. This is known as the all-or-none principle—a neuron either fires (depolarizes) or it doesn't. When it fires, it always does so to the same extent.

Once an initial action potential occurs, the resulting charge spreads out in both directions from the starting point. But, as noted, only the neighboring membrane on one side of the axon hillock can respond because the other side is in a refractory period. The action potential now has moved to this neighboring patch of axon membrane and the signal continues in this way, as a wave, all the way to the end of the axon. Importantly, the axon is surrounded by a sheath of lipid (fat) called myelin, which insulates the axon, keeping the electrical current of the action potential from dissipating. Because of the all-or-

none principle, the signal does not diminish as it moves, but is just as strong at the end of the axon as when it was initiated at the axon hillock (Figure 14).

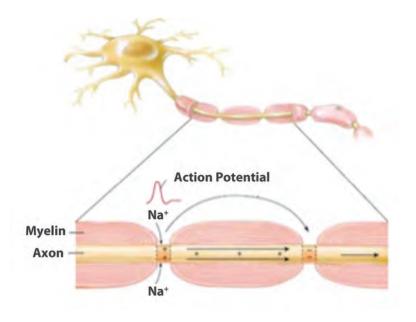
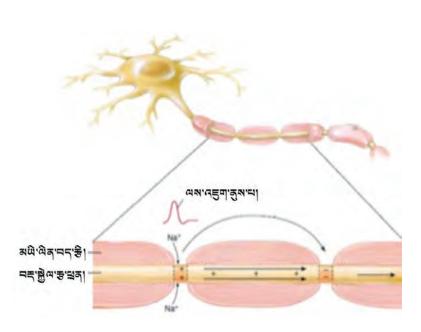


Figure 14: An action potential does not diminish as it moves down the axon – it is renewed at each new patch of membrane.

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Imagine a line of 25 monks holding hands, standing in a row. Monk #1 on the far left end of the line receives a signal from his friend. His friend tells him this message: 'Send a signal, pass the word. It's time for prayers!' Monk #1 hears his friend, but he is busy studying and doesn't do much until three of his other friends also start yelling, 'Wake up! It's time for prayers!' At this point, Monk #1 becomes aware of his friends' yelling (his 'threshold potential' is reached) and he squeezes hard the hand of Monk #2, the second monk in line. This causes Monk #2 to squeeze the hand of Monk #3 just as hard; he squeezes the hand of Monk #4 just as hard, all the way to Monk #25. Each squeeze is like the movement of the action potential, each squeeze sends the initial message and sends it at the same squeeze intensity, so the signal is just as strong when Monk #1 squeezes Monk #2's hand as it is when Monk #24 squeezes Monk #25's hand. This is propagation—with all the monks together representing one action potential moving down one neuron.

Now, how does this signal progress from the end of the axon to another neuron? Or, another way to ask this question is: how did the initial action potential at the axon hillock get started in the first place? How did it receive information from other neurons that induced an action potential? That is, in neurotransmission, what is it that is analogous to the yelling of the Monk #1's friends that gets the process going?

CHEMICAL NEUROTRANSMISSION: FROM ONE NEURON TO THE NEXT

Consideragain your walk through the woods and the crying child. Experiments suggest that the cells in your brain, when you hear that child, integrate a number of signals, thoughts and potential actions that result in your response to the child: your ears hear—receive sensory information that is passed to your auditory nerves and then to the neurons of your brain. Then, you turn the corner on the path through the woods and your eyes see the child. Why do you notice the child rather than the flower by the side of the path? This is an important question that we discuss later. For now, consider what happens when you look at the child. We learn about vision in neurobiological terms in the *Neurosciences I*; many connections and associations exist between the neurons in the visual part of the brain and other regions involving emotion and action. You see the facial expression caused by the muscles on the child's face and process the emotion of that child. This is amazing! Without any words, just from seeing, you can "read" the mind of another person. Furthermore, the interconnected brain systems involved in seeing

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and responding to the child are able to communicate with your peripheral nervous system—in your legs and arms—to signal the muscles in those arms and legs to move, pick up and comfort the child (see detailed discussion of movement below).

For this entire scene to occur, clearly neurons must not only send signals down their axons, but they also must send signals to other neurons and to the muscles. Let's investigate how neurons do this. First, how do neurons send signals to other neurons? Second, how do neurons send signals to muscles? Then, finally, how do neuron-neuron and neuron-muscle interactions translate into whole-body movement?

Look at Figure 15; it shows the terminal of one neuron on the

upper right interacting with the dendrites and cell body of another neuron on the upper left. The tiny space between the axon terminal sending a signal and a neuron receiving the signal is called a synapse. The electrical signal of the action potential that has moved all the way down the pre-synaptic neuron is now converted into a chemical signal when it reaches the axon terminal.

The conversion from an electrical to a chemical signal happens as follows.

- Once the action potential reaches the end of the pre-synaptic neuron, the depolarization of the action potential alters the shape of voltage-gated calcium channels, causing them to open.
- Because calcium normally is at a greater concentration outside than inside the cell, calcium rushes into the end of the axon, following its concentration gradient.

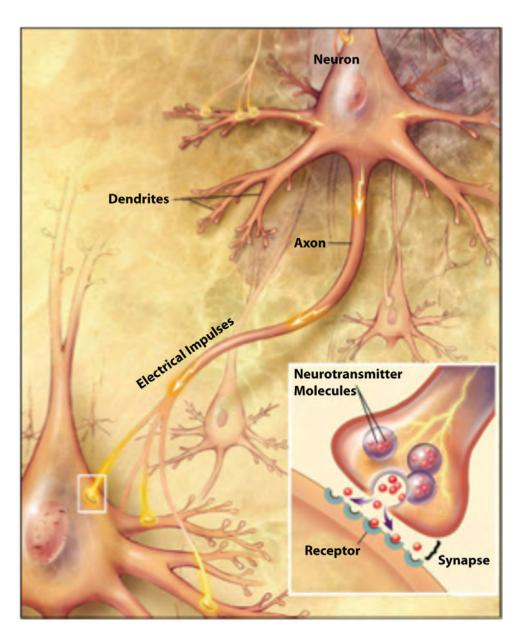
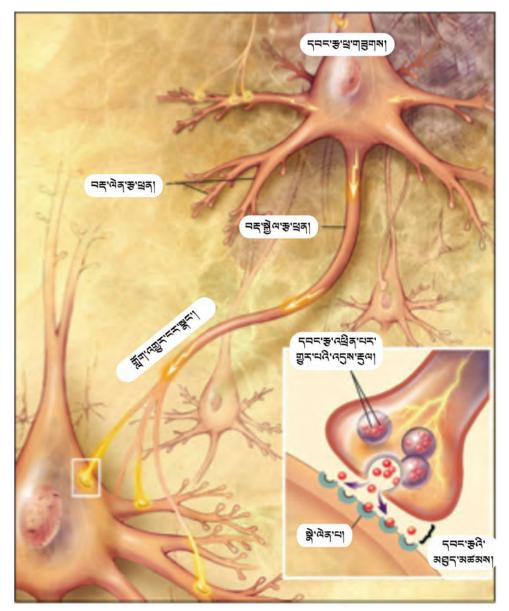


Figure 15: The synapse is the space where the terminal of one neuron interacts with the dendrites or cell body of another neuron.



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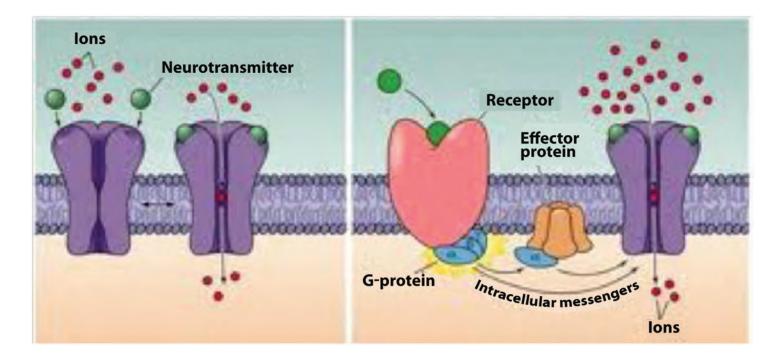
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. कः प्रशः ने 'गुदा: कंट' चित्र 'याद्र शः सूर्यः 'दर्वे 'दर्दः 'वेवा' बुन'सर'दे' 'हद' हद' दनर' इ' झ'म बुग्र अ'दग' में अ' श्.श्रृषुःचरःश्चेताः इत्रचः क्टिंटः टी.चरः तह्येषः दशासरः यर्षेट्र-ट्यू अ.स.अ.स.चरी ट्यट.क्.स.यां चीयां अ. मालव र्रा प्रमान प्रमालव राज्या व्यापन विश्व वि देश'सर'गर्हेर'दर्गेश देश'द'दनर'इ'ख'ग्राबुग्रश न्नानी अर्जो र ना अवायअर्जे द्वारदे हे सूर व्युना कुंत्र बद्दार क्रें भावह्या या देवा वसूत्र वर वर्देन दे **षट विवासम् । इतट इ.व.व विवास क्रीस र्यट इ.** स्या विष्यान्याविष्यायायम् तस्री वाहे त्रुम्या विष्या <u> २८। पर्हिशस्त्र २२८:इ.स.पर्श्वेशस्त्र</u> यात्र द्या त्य यह त्ये व हे त्यू र या हैं द खें या अवस् न्नरः इः सः माञ्जारा जनरः स्वतः रहेवः नृहः। नृन्दः इः सः ग्राह्म अर्म् इस्रमासुमासुमार्थेम्यान्ते । द्यायाः र्सेन् । इस्रमासमार् য়ৢয়য়য়য়ৣয়য়য়য়৻ড়ৢয়য়য়য়য়য়য়য়য়ঢ়ঢ়ৢয়ৢয়

न्दे देश १५ व्याचिवा हूँ शन्दा ने स्क्रेट ची.

टक्ची-स्यम् तम्रेत् क्रीत् क्री में स्वान्त स

- લયાવદ્વાલુયાનાને દ્વારક્ષેય ક્રેત્ર ક્રેંત્ર અકરાષ્ટ્રી ક્રાપ્ત સ્થાન ક્ષેત્ર અધ્યાન ક્ષેત્ર સ્થાન ક્યાન ક્ષેત્ર સ્થાન ક્ષેત્ર સ્થાન ક્ષેત્ર સ્થાન ક્ષેત્ર સ્થાન ક્ ક્ષેત્ર સ્થાન ક્યાન ક્ષેત્ર સ્થાન ક્ષેત્ર સ્થાન
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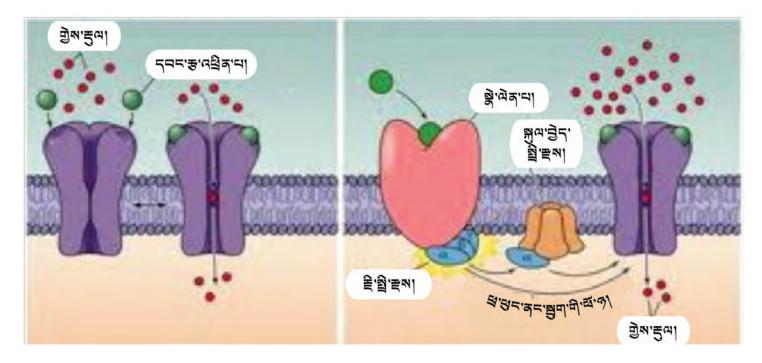


- The calcium induces vesicles (small membrane-bound sacs) carrying chemicals called neurotransmitters (Figure 15, inset) in the terminal to fuse with the membrane, emptying the neurotransmitters into the synapse. There are many different neurotransmitters, including glutamate, GABA, acetylcholine, dopamine, serotonin, epinephrine and norepinephrine. In addition, there are many short protein neurotransmitters, also called neuropeptides. In all, there are more than 100 chemicals that are currently known to act as neurotransmitters at synapses in the brain!
- When the chemical messagers are released into the synapse, the neurotransmitters interact with membrane protein receptors on the post-synaptic neuron. This interaction passes the neural signal along from the pre-synaptic neuron into the receiving post-synaptic neuron.
- In the post-synaptic neuron, the chemical signal from the neurotransmitters is re-converted into an electrical signal in ways we will explore below.

Depending on the type of neurotransmitter and the receptor it binds to, different effects will result in the post-synaptic cell. Each receptor has binding sites for a specific neurotransmitter. You can think of how for every lock, there is only one kind of key that fits. In the same way, only the correct neurotransmitter can bind to a given receptor. There are two main types of receptors for neurotransmitters, known as ionotropic receptors and G-protein coupled receptors

Figure 16: Two main types of neurotransmitter receptors.

- (a.) lonotropic receptors, on the left, allow ions to quickly pass through under specific conditions.
- (b.) G-protein coupled receptors, on the right, use a slower, second-messenger system.



सर्गुचित्राधूरः स्त्रीयः चर्जुद्द्रितः वा क्षेट्र अ. ट्रेश्चेच अ. श्रे च्या चर्जु अ. द्व्या स्त्र अ. क्षेट्र अ. ट्रेश्चेच अ. श्रे च्या चर्जु च्या चर्जु अ. स्त्र च्या चर्ज्यः क्षेत्र अ. ट्रेश्चेच अ. श्रे च्या चर्जु च्या चर्जु च्या चर्ज्यः सर्वे) श्रे च्ये चर्ज्य चर्ज्य चर्जु चर्ज्य चर्ज्यः चर्जु चर्ज्यः चर्ण्यः चर्ज्यः चर्ज्यः चर्ण्यः चर्ज्यः चर्यः चर्यः चर्यः चर्ज्यः चर्यः चर्ज्यः चर्यः चर्ज्यः चर्यः चर्ज्यः चर्यः चर्यः चर्यः चर्यः चर्यः चर्यः चर्यः चर्यः चर्ज्यः चर्यः चर

- त्वीर्म्भः स्ट्रिस्स् स्ट्रिस्य स्ट
- इस्याद्युक्त्याचे त्येवेद्याने निवाद्य द्वेद्याय इत्याय स्वाद्य व्याद्य विवाद द्वेद्य विवाद वि
- नियम् इ.स.च्याप्त्र अ.सूचा चिन्याची क्षित्र विकास स्थाप क्षित्र प्रमाणका क्षित्र प्रमाणका क्षित्र क्षित्

त्वी स्टर्मी स्वीत्विभागम् द्वी स्ट्वी स्वार् होस् निह्म स्वार में अस्त स्वी स्वार हो से स्वार स्वी स्वार हो से स्वार स

(Figure 16). Ionotropic receptors are similar to the voltage-gated channels we learned about above in as much as both proteins form a channel that allows a certain ion to pass through when the channel is open. However, the mechanism by which voltage-gated channels and ionotropic receptor proteins open are different. Voltage-gated channels open when there are changes in membrane potential, whereas ionotropic receptors open when the right neurotransmitter binds to them. Ionotropic receptors are also said to mediate "fast" neurotransmission, because when the neurotransmitter binds and the channel opens, ions immediately pass through, changing the membrane potential within milliseconds (Figure 16a). Depending on the ion that flows through the channel, as well as the direction it flows (based on its concentration and electrical gradients), the inside of the cell can become more positive or more negative. When the cell becomes more positive, or depolarizes, this is called an excitatory response, because it pushes the neuron closer to reaching the threshold potential. Conversely, when the cell becomes more negative, this is called an inhibitory response, because it makes it more difficult for the neuron to reach threshold potential and fire an action potential. Can you think of which ions would make the cell more excited (positive) versus inhibited (negative)?

In contrast to ionotropic receptors, G-protein coupled receptors act more slowly and do not allow ions to pass through when neurotransmitter binds to them. Instead, these receptors bind neurotransmitter, and activate attached proteins (G-proteins), which send signals to other molecules known as second messengers (because they are the second ones to carry the signal after the primary receptor at the cell surface; see Figure 16b) inside the cell. Second messengers (of which there are also a great variety, including cyclic adenosine monophosphate, or cAMP, which we discuss extensively in the *LSP-III: Development and Physiology*) then activate enzymes or other molecules. These molecules might be proteins that turn on genes, or they might be other ion channels or pumps, or neurotransmitter receptors themselves. All these reactions take time (hundreds of milliseconds to minutes), which is why action at G-protein coupled receptors is slower than ionotropic receptors. However, in both cases, the responses can end up being excitatory or inhibitory, depending on the resulting changes in membrane potential.

A single neuron can have thousands of synapses communicating with it; these synapses can occur on the dendrites as well as the cell body of the neuron. Each neuron constantly 'adds up' the many signals it receives at all its synapses (Figure 17), an information-integrating process known as

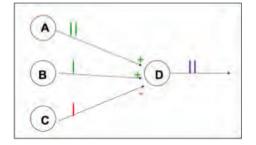
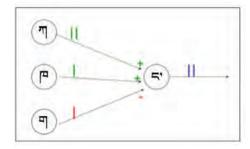


Figure 17: A single neuron (D) receives input from many synapses (A-C), the sum of which determines whether the threshold potential is reached.

र्सेयः हेत्र क्चें पठन् ग्री क्चु यस पाहेश सें द्धंया है यूर-पि पत्ती पति वत्र सप्तापत्त्रीय ती पाहेत्या से स् नवे श्वे चेत्र न इसमा है निम्म स्थान स्यान स्थान देरः अः बद्याः क्री अः ह्वाय्यवेदः प्रदेश्वे योदः प्राप्ताः वीशः देः प्रवाः उद्ये यदीदः पर्हितः क्रायः अर्कीवाशः परः प्रभूतः र्द्धयानम्दारम्द्री देवे हु अळ्दादी नन्दा हायद्वेदायाविना नेशायळेटा र्श्वेसा हुशाहे । हु यसा दे हिनायही नवा देवे नकुन्नु के सम्बन्धिया द्वारा द्वारा स्थाप स्याप स्थाप स्याप स्थाप स्याप स्थाप स्य ब्रॅंदि:तुषायायायमुद्रायायभूवायषायेत्(त्रोप्येषा १६ म्)। क्रुप्ययात्रेप्रयायत्रायदेन्त्रेषात्र्याः ररायबेद्राहरा दे केराव र्श्वेमशामार रा. (ररायी याराळ राया बराया राज्ये या व्यापा विकास चुरुष्वर))नत्रः नदेः नद्वराष्ट्रस्य नरुषायाः द्वेशाद्याः सुरः नरः नेदे दरः विवायः ने स्रूरः नरा से प्रा यम् यत्रम् वर्षे वरमे वर्षे वर निवत्रह्मायन्त्र्यायम् क्षुमार्के देश्याममार्थायम् प्रायवान् प्रायविक्तान्त्रम् देशे कुष्यक्रविदेशे साम्यवस्य याञ्चवायाने किन्द्रोत्रायळ्याय तुषायाने खुँवाया सुरहे चन्द्राया नयाने न वे त्याया के वायाने खुँवाया सुरहार देॱख़ॕॱ॔ॺॱक़॓ॱज़ॸॱॹॗॸॱक़॓ऻॗढ़॓ॱख़ॱढ़क़ॕज़ॱॷॕक़ॱख़ॱख़ढ़ॱढ़ॏॺॱढ़ऄ॔ॸ॔ॱॸ॓ऻॗढ़॓ॴॱॸज़ॾॱॹॱज़ॿॖज़ॴॱॸ॓ॱऄऀॸॱॿ॓ॴ रेता रेंशवरग्रीशर्वाणीःरेवाशवारावीशायासुरावीर्द्यायुराहे केरा(विभाग)र्थेरावराग्रीर्वासार्वा

मुक्तान्त्रवाद्येत्रप्रते श्रुप्तेत्रपान्दार्थे पद्मानावा हे श्रुप्तान्य समुद्रश्री राउतामु श्री स्वित्रपान्य ननर इत्वेद रामा पकेर मूँ माने रामे के हैं भी हमाया समुद मी राम पने प्राप्त माने प्राप्त सम् ॱइटॱबट्'यह्वा'क्कु'तुत्य'वर'क्कुर'य'द्रदा' यदे 'दवा'वीथ'क्केश'ह्या'क्क्यथ'वक्कुद्'वर्वेद'क्केद'त्रे 'क्रेर'व'दे धोत् । दे प्यश्च व्यासे । क्षेप्योत प्राप्तदे प्रमाणी शप्तवर इत्यत्रेत प्रमाणम् प्रमाणी स्वाप्त । दे प्रायन्त नवे हे हें हराना बदा हरा या बदा हरा हो है । हे न्यू र अदार वे हें हरा है हमा है । हमा हो हिना विदा वी प्रस्तेत मानाहे अप्तर (स् सुर हिन र्टे अप्तु क्वा अप्तरे र्वेन स्तरे प्रसेत मान्स्य अप्ते अपनर प्रसेत प्रहर नवे हे अ शुःदने 'न्नाची अ 'वसुर न ने 'ने अ 'स 'चित्रे अ स 'धी त 'सवे 'कु 'अळत 'ची अ 'ने 'कूर 'नु 'वर्चे न देश १६ व वार्क्षेश) ज्ञाना याये वर्षे या द्वा नावदा द्वा या नावदा द्वा वर्षे वार्षे राव हे वार्षे वार्ये वार्षे वार्ये वार्षे वा देवा वी र्बेट्ट पर्वेदि र्ब्सेट देव वाशुक्ष यर क्रुक यर र्वेट युक्त यह पर्वेट पर्वेट क्रुट के क्षेत्र ये पर्देक શ્રે ત્રવે ત્રદ નાયો યા દેવાયા શ્રું જેવાયા ખેતી) ક્ષ્યયા ગ્રીય શ્રેત દયા યથા વિદ્વારા ત્રામાં સાથે ત્રામાં સ્ लरःश्चॅरःब्रेन्'सःनेन वर्षःस्यावदे'न्यादेयायःस्यायन्।ब्रेन्'खेःश्चेस्याने वर्षःस्रेन्'या सरः ब तदे द्वा को शाह्म का स्वा का स्व तद्वा लुब्र.बुट्टी ब्रैजा.बुट्ट.जुब्दा.जुब्दा.(स्रम.कुट्ट.बुट्ट.क.नुक्ट.बुवा.टे.स.ब्या.सम्प्रांचन्या.वुट्टी.)र्या.लीब वर्षो र न प्रें न वा े ने वा नहें देश हैं हैं। हरा वा सहन हैं रें र उठ ही हैं वो द रावा वर्ष र हा वा विवा ने योष्ट्रेशःम्रःक्षुःद्वेद्वेद्वेशःसःयःद्वयायदेद्देशःयन्त्रशःग्रीःवशुरःमःहःवशुरःयःयविषयशहःररःशनःयरःद

यर्जूश्वभः चे.य.चुर.य.पुरी मूर. र्रेश्चिशः सायषुषी यद्दः पद्चीयः पद्दीयः स्वायाः स्वायः प्राप्ति वा किरः श्वरः वा कृताः विद्वारः स्वायः स्वयः स्वायः स्वयः स



र् भुँजाश्च भुँजाजी, योध्यातवृज्याचीरास्त्रास्त्री तस्र भी यर्ष्ट्रश्चरा योच्याचे साम्रक्षश्चरा वे यास्य छूर यरः)ये याक्ष्यत्रचे स्मित्य प्रत्ये साम्रक्षश्चरा वे यास्य छूर्यः यान्य सम्बद्धः श्वरीत् शक्षश्चरा यास्य प्रत्ये स्मित्य हिस्सा विवास्य स्मित्य स्मित्य स्मित्य स्मित्य स्मित्य summation. As we mentioned, some of these signals will be inhibitory (decreasing charge), while some will be excitatory (increasing charge). The many simultaneous signals may or may not sum up to a voltage that reaches the threshold potential at the axon hillock. If the threshold level of excitation is reached, an action potential fires and the signal is passed down the neuron to other parts of the nervous system.

A rare, but even faster way that a few neurons interact is by skipping the

neurotransmitter-chemical step of neurotransmission altogether (Figure 18). Via these purely electrical synapses, two neurons are directly connected through a gap junction. Gap junctions are composed of exactly aligned pairs of channels at the membranes of the pre- and post-synaptic neurons. The space through the membranes created by gap junctions is much bigger than that of ionotropic channels. Thus, relatively larger molecules can move from one neuron to the other. lons, which are very small, can move easily through the gap junctions at electrical synapses. The result is that action potentials can move from one neuron to the next, as if they the two neurons were one, taking even less than a millisecond. What do you think would be advantages and disadvantages of such neurotransmission? Why do you think this mechanism is so rare in us?

One hint to help you answer these questions is that gap junctions are found not only in the brain but in muscles all over the body, and they play a very important role in cardiac functioning. Because the physical proximity allows two cells to act as if they are one, gap junctions are thought to cause synchrony in an assemblage of cells, which allows the muscles of the heart to contract concurrently. In the brain, gap junctions may be important for the development of the nervous system and are thought to facilitate complex neural processes such as learning and memory. However, it is very likely that neural synchrony is not always a good thing – it is thought that pathological activity in gap junctions may contribute to, and in some cases even initiate seizures, a condition in which a grouping of neurons exhibits abnormally rapid and synchronous firing.

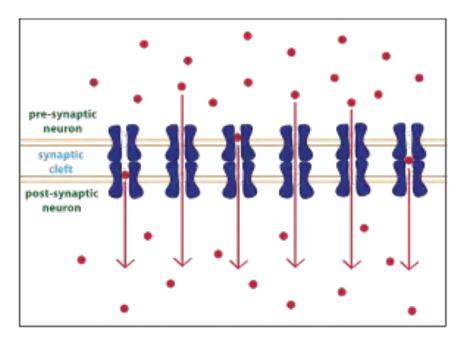
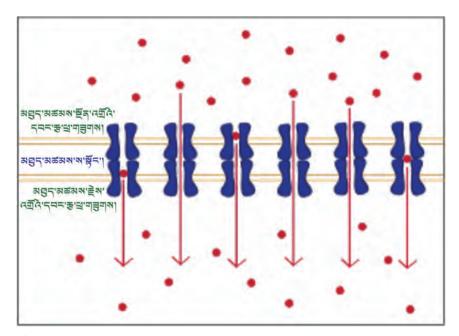


Figure 18: Gap junctions form when channels on the pre- and post-synaptic neuron are perfectly aligned with one another.



द्वःदेश। १४ द्वरः इते समुद्रः सक्यायः की वाची इंदः द्वरः हे अः ग्रीः द्वरः इतः वा त्ववायः के कि विद्यायः इस्रायः स्वरः इतः स्वरः स्वरः वा त्ववायः के कि विद्यायः वरः क्षेत्रं व्याप्तः स्वरः स्वरः सम्बद्धः सम्बदः सम्बद्धः सम्बद्धः सम्बद्धः सम्बद्धः सम्बद्धः सम्बद्धः सम्बद्धः सम्बद्धः सम्बद्धः सम्बदः सम्बदः सम्बद्धः सम्बदः सम्वदः सम्बदः स

ल्ट्-द्रश्च चिंट्-रिक्ट-र्यः वचका त्येला त्ट्रे-ट्रिक्ट्-प्रक्षेत्र प्राचित्र स्ट्रिक्ट-प्राचित्र स्ट्र-प्राचित्र स्ट

HOW DO THESE BASIC NEURAL PROCESSES LEAD TO VARYING OUTCOMES?

You can see that evolution has built much diversity into neural signaling. Let's take the senses as an example. Think about all the steps that are involved—from the initial signal to the sending of the signal to the response to that signal. We will look more closely at each step to appreciate the diversity.

First, there is the initial signal received from the environment; we examine many of these receptors in other primers. Sense receptors allow us to see, hear, smell, taste and touch (Figure 19). Somatosensory receptors in skin allow sensing of touch, pain, and temperature change. Proprioceptors in muscles interpret force, length, and velocity of muscles, all necessary information for the coordination of movement. Sensors in our inner ear tell us about the angle of our heads and our body balance and movement. As you can see in Figure 19, although these receptors are somewhat different in their location in the body and in their molecular structure, they all are also very similar in that they all have one axon and multiple dendrites. Another similarity is that they involve protein channels on the membrane that alter upon stimulation to allow a change in membrane potential.

Another way to diversify the system is to evolve different types of neurons with different shapes and properties, as well as different types and numbers of connections. There is also incredible diversity in the kinds of neurotransmitters that neurons use (Figure 20), as well as the receptors that bind to them and send signals on to other neurons. Moreover, one neuron may receive and send more than one neurotransmitter. Interactions between neurotransmitter and receptor can have a wide range of effects on membrane potential, and over variable time spans. This extensive diversity allows for tremendous flexibility in neural signaling – a good thing when you consider all the important functions your nervous system serves! Indeed, all of these variables are at play as you walk through the woods and respond to the upset boy.

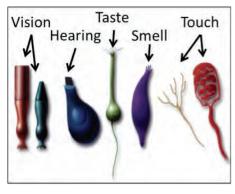
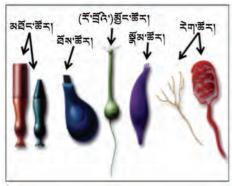


Figure 19: Types of sensory receptors.

Figure 20: Diversity of neurotransmitters. Structures for some of them are shown here: (from left to right) GABA, glutamate, acetylcholine, serotonin, dopamine and norepinephrine.

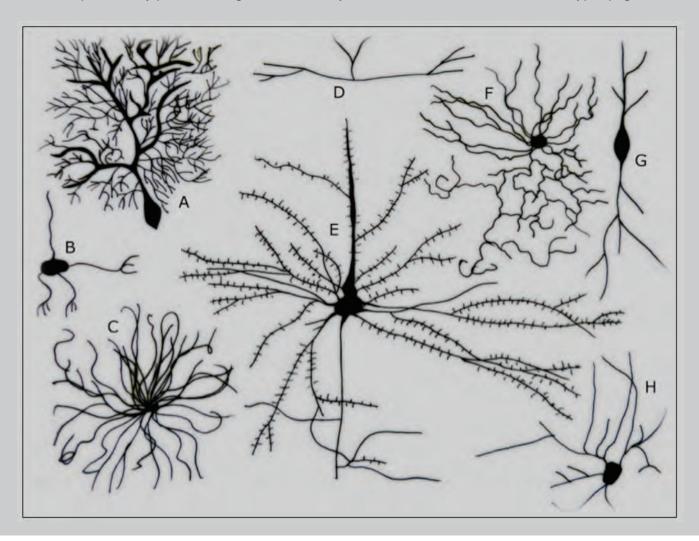
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-इसे देश १६ इनदः क्टें दःश्चे खेद सदे देगाया

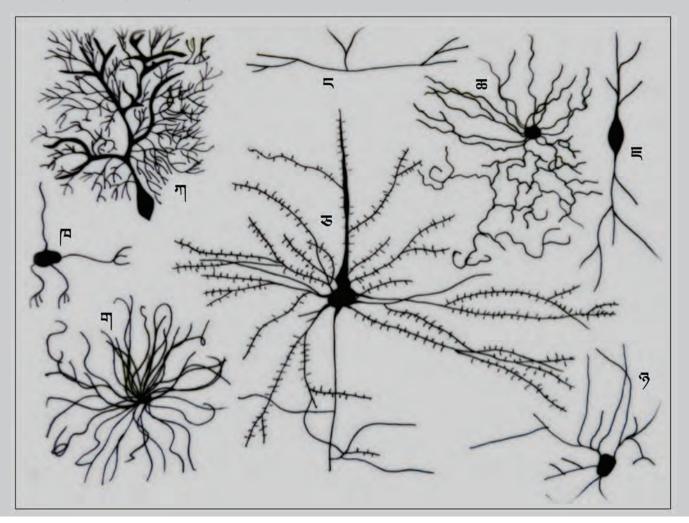
Box 5. IN DEPTH: DIVERSITY OF FORM AND FUNCTION THROUGHOUT THE NERVOUS SYSTEM

Here are some of the different neuron types in the brain. Think about what you know about structure and function, and consider what the structural differences in these cells might mean for function. A. Purkinje cell B. Granule cell C. Motor neuron D. Tripolar neuron E. Pyramidal Cell F. Chandelier cell G. Spindle neuron H. Stellate cell (Credit: Ferris Jabr; based on reconstructions and drawings by Cajal). See http://neuromorpho.org/neuroMorpho/index.jsp for a catalogue of neurons by neuroscientists, and Browse the Cell Types page



WHERE NERVES MEET MUSCLE: THE NEUROMUSCULAR JUNCTION

Another example of the extreme variation found in the different types of neural connections is a specific type of neuron called the motorneurons. Rather than communicating with other neurons, these neurons, whose cell body lies in the brain, interact directly with muscle cells. As we've seen, the story about you walking through the woods and helping the young boy



न्दःतुःन्दःक्षःक्षस्यःभःन्वन्दःन्दःत्यःन्दःन्वस्यः न्दःकःन्दःभ्नःन्वन्धेलःस्रस्यस्य

श्चर्यत्योषर्द्रितः स्वीतः श्चर्याः क्षेत्रः स्वीत्रः स्वीतः स्व

involves neurons communicating with muscles at many levels, and thus inducing movement. At the most basic level: you are walking, one foot in front of the other, keeping your balance, as in the case when you trip and catch yourself before you fall. But even at the more complex, emotional level, movement is essential: your face muscles and the boy's face muscles form expressions, you move your lips as you talk with the boy, you pick up the boy, your eye muscles move your eyes, etc. Some say that movement is the most vital of our physiological functions, because without movement we would not be able to interact with the world. Thus, we will examine movement very carefully here.

In LSP-III: Development and Physiology, we discuss how muscles work together to contract at the organ level within the musculoskeletal system. Here, we will move down to the cellular level.

The synapses where nerves meet muscle are called neuromuscular junctions. As you can see in Figure 21, this specialized synapse looks and acts very much like a neuron-neuron synapse. The pre-synaptic cell is a motoneuron projecting all the way from the spinal cord. The defining feature of motoneurons is that the post-synaptic cell is a muscle cell, and the muscle cells use the changes in membrane potential induced by neurotransmitter released from the motoneurons to activate muscle contraction. The neurotransmitter used by these motoneurons is acetylcholine, and the acetylcholine receptors are ionotropic (recall we discussed ionotropic receptors above, in the section on Chemical Neurotransmission). Binding of acetylcholine to the receptor opens a channel in the middle of the receptor (see Figure 21), which leads to an inflow of sodium into the muscle cell, and therefore depolarization. The depolarization leads to the opening of voltage-gated calcium channels. When these channels open and calcium rushes into

the cell, a complex series of reactions then leads to muscle fiber contraction. When your brain sends a signal to bend your arm, this is how the muscles in your arm can make it happen.

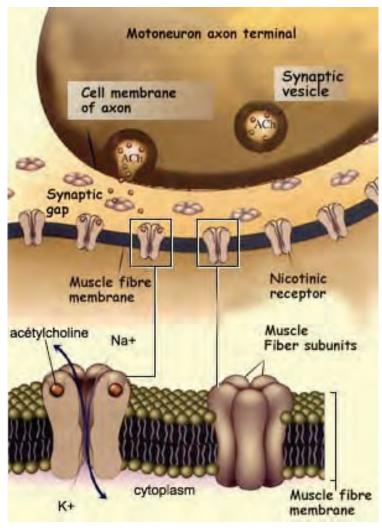


Figure 21: The synapse of a motoneuron at the muscle. Acetylcholine neurotransmitters released by the motoneuron bind to and open receptors on the muscle cell.

क्ष्रात्यीयाः श्रीरायाः विचाल्यायाः क्षेत्राः ह्यापाल्यायाः विचान्त्रां विचान्त्रां विचान्त्रायाः विचान्त्रायः विचान्त्रायः विचान्त्रायः विचान्त्रायः विचान्त्रायः विचान्त्रयः विचान्त्यः विचान्त्यः विचान्त्यः विचान्त्यः विचान्त्रयः विचान्त्रयः विचान्त्रयः विचान्त्रयः

NA+ হ্রমের্ল্লিন্রেন্ডের্ট্রেন্ড্রেন্ট্রেন্ড্রেন্ট্রন্ডর্ন্ডর্ন্তর্ভিন্তন্তর্ভিন্তন্তর্ভিন্তন্তর্ভিন্তন্তর্ভিন্তন্তর্ভিন্তন্তর্ভিন্তন্তর্ভিন্তন্তর্ভিন্তন্তর্ভিন্তন্তর্ভিন্তন্তর্ভিন্তন্তর্ভিন্তন্তর্ভিন্তন্তর্ভিন্তন্তর্ভিন্তন্তর্ভিন্তন্তর্ভিন্তন্তর্ভিন্তন্ত্রন্ত্তন্তর্ভিন্তন্তন্তন্তল্ভিন্তন্তর্ভিন্তন্তন্তর্ভিন্তন্তন্তন্তন্তন্তল্ভিন্তন্তন্তন্তল্ভিন্তন্তন্তন্তল্ভিন্তন্তন্তল্ভিন্তন্তন্তন্তল্ভিন্তন্তন্তল্ভিন্তন্তন্তল্ভিন্তন্তন্তল্ভিন্তন্তল্ভিন্তন্তল্ভিন্তন্তন্তল্ভিন্

> क्ष्याः संस्टान्त्रेयाः सम्यान्त्रम् स्वयाः देवान्त्रेयाः स्वयाः स्वयाः स्वयाः स्वयाः स्वयाः स्वयाः स्वयाः स्व च स्वयाः सम्प्राचित्राः स्वयाः स

> ननरः इते अशुन् अळ्अशः नारः नुः ननरः इत्युश्यः भागवनः नरः वस्रनः शः नेरः ननरः इन्दर्भवावद्रभ्रेषायळ्यशस्य सर्वेद्रन्य सेन्। हिन् ग्रेशन्ये सेश ४१ वदः सर्वेदः न'नबिद'सबुद'सळंसस'दसेनस'नसय'उद'ददे'देद'दनद'ऋ'झ'नबुनस'दद' नवः र्ह्नवः चीः समुनः सर्वस्य स्वेताः नृतः स्वृतः रहेवः नृतः त्यसः रहेवः त्विक्षः मृतेः कः वृत्रः नृतः नबेद'र्'दोव्र्ट्र'संद्र'त्वीताःश्चेर्'र्नर्यः इ.स.च बचायःश्चेताः रूपायःश्चेर्र्रान्यः इ.स.चर्चियश्चियाःस.क्टर.चन्नु.रंभुयोश्चर्यम्.स्क्री.विटर.क्र्यश्चियाःस.ट्रेनुःस.बीर. सक्समः हे भः दर्शेदेः संस्टाने ने भागस्य भागत्र न संस्टाने वा प्रीतः ने में व्दवे भागवन सास्टरने अन्ते व्यायाः र्सेन् न्नर इसाग त्रम् अभी गाव अस्ति । वर्षेत्र बुदःनवे द्वरः इ विदेव प्रभावभ्रयः नवे भ्रु केंदि त्यापाना देन केंना पवे प्रशूनः नःइसस्यभ्यानवर्।सुस्रानधूते:ग्रु:नःर्सूरःकेर्-तु-नेर्न्सूर्-ग्रे-ग्री:पॅर्ना दन्तुत्यःर्सूर्-न्नरः इः श्रामाञ्चम् अप्यने प्नमानी अः श्रुप्तः प्रवेषः नन्नरः इः व्यवेषः पाने 'खे' की हो वा विरायेषः धोदःबिदः। खोःसोःतेवाविंग्योदःसेन्यस्यस्यस्य देःश्रीसःहवावमेदःसदेःसेन्यस्य देग्रयःभेत्रा (र्वेदःर्ः"इर्यःदशुरःश्चीः द्वदः इत्देव पर्वेदःश्चेदः देशः" देशः यदेः स्वेः ळद ने राटाळे अ ची अ ह्वा विवेदायते खें खेद पति क्रें राचे अ खूर ची अ या ने विदेर इत्दर्भेश। श्रे खेत्र राज्य स्विता या खेर शे ते या विर खेत प्रकेट श्रें सामेन सामे सा श्चे प्येत माने दे प्रेमे नमार्थेन प्रदे क्रुप्य अविषा विषय हो साम हो साम विषय है। तार्क्षेत्रा) नेसम्पानवराद्यास्टर्नेदेवनर-नुस्ताह्रसातुनास्यास्यान्त्रात्रह्नाःहेरा नेत्या नहेव वसाब्रे वत्या द्वेन देशा र्बेन परेन ब्रे वत्या द्वार न ने सार्से वाहेव हो जिल्हा ૹ૽૾ૢ૽:ૻૻઌ૽ૻ૱ઌૹ૽૽૽૾ૺૺૼૼૼૼૹૹ૽૽૽ૢ૾ઌ૱ઌ૽૽ૢૺ૾ૺ૱ૡ૽ૺઌ૽૽ૢ૽ઌૢ૽૽ૺૺૺ૾૽ૺૢઌૢ૽ઌૺૺૺ૾૽૽ૢૡૹ૽૽૽ૢ૾ૺઌૺઌ૽૽૽ૢૺઌ *न्*रा अ:स्रत्वरानगरःत्रयाञ्चेषाञ्चेनाञ्चेनायाः क्षेत्रायः स्राप्ताः स्वाप्ताः स्वाप्ताः स्वापाः

REGULATION OF THE SIGNAL

One final example of the diversity in neurotransmission that we will consider arises with respect to how the nerve signal is regulated. We've already talked about one built-in type of neuron regulation. Recall that neurons only fire if they reach their threshold potential. So, each neuron will only fire if its many excitatory and inhibitory signals add up to at least that threshold potential.

Two other types of regulation occur at synapses to control the impact of each presynaptic depolarization event on the receiving cell. Reuptake is prominent in nearly all synapses (Figure 22). Proteins called transporters on the presynaptic neuron cell membrane move neurotransmitters back into the pre-synaptic cell so the neurotransmitters can no longer activate the post-synaptic cell (muscle or other neuron). These neurotransmitters are recycled into vesicles and used later for further neurotransmission.

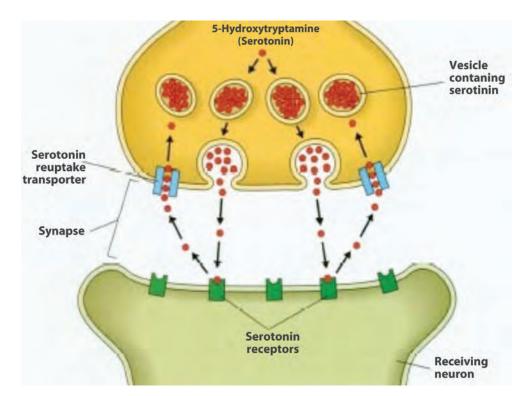


Figure 22: Reuptake transporters move neurotransmitter from the synapse back into the pre-synaptic cell.

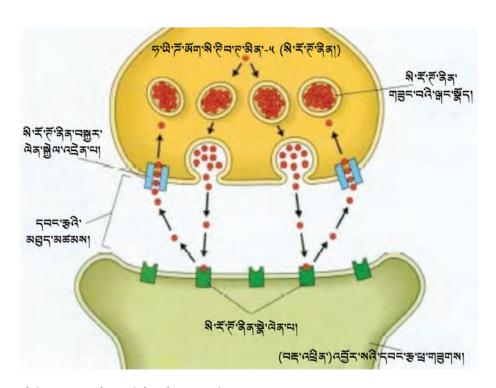
The second type of regulation is degradation. This happens when a specific enzyme digests neurotransmitter in the synaptic cleft or space, so the neurotransmitter can no longer activate the post-synaptic cell. For example, in the neuromuscular junction, acetylcholinesterase degrades acetylcholine to stop the signal. Imagine what would happen if reuptake and degradation did not take place. This type of regulation is very important; otherwise the signals of neurons would continue to be sent non-stop.

SOMATOSENSORY AND MOTOR SYSTEMS

So, how do a bunch of neurons, muscles and the many synapses among them result in movements and behaviors like those you exhibit walking in

नम्'वधेन'য়्रम्भ'वम्मेन'हेन'स्वा

सक्सम्भवितान्ते, स्वर्मान्त्रम् स्वरम् स्वर्मान्त्रम् स्वर्मान्त्रम्यः स्वर्मान्त्रम् स्वरम्यस्वरम् स्वरम्यस्वरम् स्वरम्यस्वरम् स्वरम्यस्वरम् स्वरम्यस्वरम् स्वरम्यस्वरम् स्वरम्यस्वरम् स्वरम्यस्वरम्यस्वरम्यस्वरम्यस्वरम्यस्वरम्यस्वरम्यस्वरम्यस्वरम्यस्वरम्यस्यस्वरम्यस्यस्वरम्यस्वरम्यस्वरम्यस्वरम्यस्वरम्यस्वरम्यस्वरम्यस्वरम्यस्वरम्यस्वरम्यस्वरम्यस्वरम्य



र्वयाश्राक्त्रीय तस्या श्रदे : श्रद्धा श्रेटः न् स्वा स्वतः स्वा श्र क्रेन'नेर'क्टेन'वहेंद'शुकेन'ननर'क्ते'सश्चन'सळसमार्थे' र्शेन् सूर्य पहें दानु निर्देश्य मान्द्र महिषा प्रमुन छी। र्षित्। दे त्यस्य नहिना है "नस्नूर स्वेद" वेर न स्वे। दे है स्वयः केरस्म बुद्रसळ्सभागुन्, तृत्वायायदे स्टूर्भ वहेन गुन न् उदः अर्देव अळव उदा दे पीव (द्वी देश ११) अ शुर सक्सरार्स्व पर्सेद निर्म सास्तर मी भी निर्माण मेरित्र कवार्यान्त्रेन्द्राचेद्राचार्या भ्रीतायद्वेत्राचर वर्षेत्राचित्र भ्री ह्रा श्रीताय गैर्भाद्यदः इत्वेदायः इस्यश्यश्रुदः सळ्सर्थः श्रृदः दर्वेदेः अअर्जनमा विवायर दे कि स्ट्रिंग के स्वाय के स्वाय के स्वाय के स वसान्नरः इत्वेवत्राने न्याः वीसासम्बद्धाः सक्तस्य स्रोहेसः र्ज्युष्टुः सःसिरः (अ.चोबरः रेशा लरः वी रेयरः इ.सं.चो श्वेचार्यः नाबद्र:रनाः)द्रस्रसःसर् र्सूर:होर्-स्रे:बुन:सर:दशुर:नः रेना नगरा इपदी दाया परि । इस सामा मिना मी जिला न् नश्चरः श्वेंना ग्रुभः हे भः नः नार्वेन ननमः इते व्यवे नार्नेनः ब्रेन देश भ्रमास इसमा सुनर्गे वार्सेन ब्रेन परेना

सर्वि- सक्समार्ज्य त्यूंद्र में त्री साची यावया मू मूह

सतुःस्थान। सबी-(अक्ट्रमशःकूर्यत्त्युतुःसं सिम्तानुमः पद्मेर पद्मेर प्रमेर पद्मेर पद्म

त्त्रुयम्बर्गात्रक्षात्राक्ष्यात्रक्षात्रम् स्वान्त्रम् स्वान्त्यम् स्वान्त्रम् स्वान्त्यम् स्वान्त्रम् स्वान्त्यम् स्वान्त्यम्यान्त्रम्यान्त्रम् स्वान्त्रम् स्व

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 the woods? This is a huge question neuroscientists don't entirely understand the answer to, but we do know a lot about it. We know that we have to integrate information about our environment (somatosensory information) with the planning and execution of movements. As thought through by James Knierim of Neuroscience Online (http://neuroscience.uth.tmc.edu), a good interaction of sensory and movement (motor) systems should:

- generate movements that allow us to accomplish our goals.
- coordinate signals to many muscle groups and determine the necessary forces to produce smooth movement.
- know the starting position of the body in space, the length of muscles and the forces being applied to them.
- constantly produce postural adjustments in order to compensate for changes in the body's center of mass as we move our limbs, head, and torso.
- compare desired activity with actual activity, and use sensory feedback for corrections in movements as they take place, and allow modifications to motor programs so that future movements are performed more accurately.
- compensate and account for the physical characteristics of the body and muscles themselves.
- perform many procedures in an automatic fashion, without the need for high-order control.
- adapt to changing circumstances over the short term as well as over developmental time, aging, etc.

In fact, the Emory Tibet Science Initiative primers extensively discuss many of these characteristics, which our motor systems do have, and consider how, together with our nervous systems, they respond to our environment. In LSP-II: Genes and Cells, we discuss the simplest such collection of nerves, muscles, and synapses—known as reflexes (Box 6). These reactions—like when you draw your hand back from a scalding cup of chai or when you catch yourself after tripping over a root in the woods—are automatic and unconscious. They don't even involve the brain, only neurons that sense the stimulus, an intermediate neuron in the spinal cord, and the motor neuron that synapses on the muscle to stimulate its contraction. Such reflexes often involve a chain of only one, two or three synapses, although many receptors and motor neurons may act in parallel.

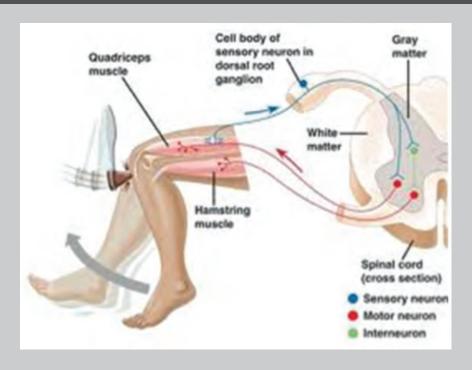
द्युद्धः सेन्याश्यक्षः तेत्व विद्यास्त्र क्षात्र क्

- दळें अन्दरनी द्रश्चेन अर्दे द्रन्यून यर यह यह प्रवे प्रमुख क्रें द्रन्थ हें द्रम्
- वित्यक्षास्त्रे वेश्वभ्वाकाः अवस्य अवह्रवा वेत् वित्रवा
 वित्यवित् क्ष्यां अवस्य अवस्य अवस्य अवह्रवा वेत् वित्रवा
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 वित्यवित् क्ष्यां अवस्य अवस्य
- सुत्यः च्चीः वीं स्थरः त्वेर्वेन् स्वतेः नृदेशः वा त्वावा स्वावा वी विवासिः वा व्यवः वा वा स्वतः विवासिः विवासिः वा विवासिः वा
- स्यामानाहेर् स्थान भारत्या स्थानान्ते प्रश्चा सम्माना स्थाना स्थान स्य
- रे. श्रॅंब. क्री. ची.चीलची. स्थाया. खीचीया. अर्थे थे. त्यचीया. त्यचीया. त्यचीया. खेचीया. व्यचिता. क्रिंच क्रिंच ची. ची.ची. व्यचिता. व्यचता. व्य
- सुर्यादेवे क्षेत्रे हिन् के यान्य प्राप्त प्राप्त प्राप्त प्राप्त स्वाप्त प्राप्त स्वाप्त प्राप्त स्वाप्त स्व
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- रीयालीय-बीट-टी-टी- लट्डी क्रीय-क्

दरः स्टाची त्यश्चात्य ह्या स्वर्धः श्रीत् । वत्य स्वर्धः स्वरं स्वरं

Box 6. IN-DEPTH: REFLEX IN ACTION

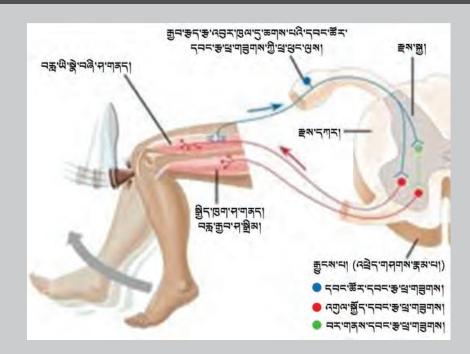
Here is a short exercise you can do to get a sense of how reflexes work. Have a friend sit with his or her legs dangling over the edge of a table. With the side of your hand firmly strike your friend's leg just below the kneecap. When you hit the right place, the lower leg will kick out immediately exhibiting the knee-jerk reflex. Try it again with one hand on your friend's quadriceps muscle, the muscle on the front of the thigh. When the knee jerks, you will feel the quadriceps contract.



This knee-jerk reaction happens in less than 50 milliseconds and involves just two neurons. One neuron reaches from the kneecap to the spinal cord, and the second reaches back to the muscle, as shown at the right. How might this reflex be useful?

In order to move, to stroll through the woods, to pick up a crying little boy, we need to know both where things are in our environment, and where our bodies are in relation to those things. This sense is called proprioception. The receptors that give us information about our environment are known as somatosensory receptors; 'somato' refers to our bodies and 'sensory' to sensing the environment. As we have seen, generally speaking, all sensing is similar, although each type of sensing has its own particular type of receptor (see Figure 19 above). As we've discussed, any sensory event begins with a receptor on afferent neurons. Once stimulated, membrane ion channels open to cause an action potential. In LSP-II: Genes and Cells, we look extensively at some of these: vision receptors, touch, pain, and temperature receptors. Vision receptors are an example of receptors that give us information about the external world; the touch, pain, and temperature receptors in our skin are also examples of such receptors. Here, in terms of movement, we will discuss 2 additional somatosensors that sense the forces and motions of our bodies: (1) proprioceptors in muscle that tell us about the force, length, and velocity of muscle contraction and (2) vestibular sensors in the inner ear that tell us about the angle of our head and how fast it is moving.

म्रियान्त्राच्याचा वित्रास्य वित्रास्य वित्रास्य वित्रास्य वित्रास्य वित्रास्य वित्रास्य वित्रास्य वित्रास्य वि



> श्चेर-वहर-वज्ञुवावतुर-ग्रेर-वर्गन्। वन्यश्चावक्रयावक्रयावार्श्चेर-वर्गन्। यरावर-हर्न्याः ग्रेर-वित्याः युत्राः ञ्चानवना यः ब्निस्यान्य दः स्टिं यः वित्रः स्प्राना हिंदा न् रूप ने स्थयः नादः न् र्यवित् स्थेदः नदः। उत्तरियः ने रन्ना यः वेद्रियः ने रन्ना यः वित्रियः वित्रि रम् १९८ मी खिराने नाम १९ वर्षित सेन नरसाया मुसार्थित मेन प्रति । वर्षे १९६ भी सार्के माम्रान्यसाय मुसार्थिय सेन नन्दा धरारास्त्रीते विराधाना नरायम् वात्रास्त्रीया नरी स्वाप्तीया विराधीन विराधीन विराधित हो निर्माधीन विराधित यदेवे सेर में क प्रशामिक प्रशामिक प्रशास के साम के सम्मान प्रमान प्रशास के सम्मान प्रभास के सम्मान प्रभास के स र्के के स्पर्य स्पर्य के स्पर्य स्पर्य स्पर्य स्थापन स्यापन स्थापन स्यापन स्थापन स्थाप नर्वोभा रार्क्षभावेरिनु वेश्वभाष्ट्रमञ्जभाषानविद्या ननरार्क्षमान्यते स्वरापनि स्वराप इ.स.चंचिका के स्वाप्त के स्वप्त के स्वाप्त के स्व वर्वेदैः श्वें नःनेनः नहेशः नवेद्वानः वदेवेदे नेनाशः वनावः विनायः नः स्वें शः श्वेंशः नविनः नुशः विना ने निनावे निनावः निनावः विनावः विनावः निनावः विनावः व योदायान्या नेपार्केन्स्रोयोदाया तुपार्केन्स्रोयोदाया इनिकेन्स्रोयोदायायवारीया नेप्यास्त्रीम्स्रोयोदायान्यादीया कॅर द्वेदे पहेना हेन क्रें र ची क पहेन स्रोर पर्देन चीर पदे र चीर पदे र चीर पदे र ने सर्केन निमाणिन पा रे पतिन है। र केंदि पमान पदे बद्दानी देना क्रिंदान्दा हुना हुन हेंद्र क्रिंदा श्रेषोव पाइसमा ग्राह्म देखे श्रेषोव प्रवेष देशे सक्रिंद भी वा वर्ग वा श्रेर्त प्रदेश प्रवेष प्रवेश यात्र शर्देत : बद्देन : दर्देन : दर्स अ: खुअ: खुर : वी: श्वाय : दर्दा वा विद्या विदः श्वेय : विदः : विदः श्वेय : विदः : विदः : विदः : व क्रॅ-क्रॅंश:धू-र:बुर्हें। ने:नवादी १ ने भःगहन:बर:वी:ननशःदशुर:ब्रे:वोद:स:नवा:ब्रे) भःगहन:शुरःनध्ये:सुवाश:नन। नुशः . धुद्रा अर्चुन्य अर्चन्य चर्च प्रकार के प्रमान के स्वापन के स्वापन के सम्बद्ध स्वापन के सम्बद्ध स्वापन के सम्बद्ध स्वापन द्याःश्रे। यदःद्याःवीशःस्टःवीःशर्वे वेदिः।वःश्चेंयशःश्चीः बुस्।व्याःश्चेंस्र्यः। स्टःवीःशर्वे वेद्येंयशः वुत्यःश्चीः क्वेंद्यः विवासः र्भू द्राचेद्रायत्वेद्रायत्रे भू राटा केंद्रायाद्र शास्त्रीया या विद्राया विद्राय विद्रा

Our muscles have two kinds of proprioceptors: (1) muscle spindles inside muscles sense stretching (Box 3) and (2) Golgi tendon organs, at the junction of muscles and tendons, sense the force generated when our muscles contract (Figure 23). Muscle spindles have a sensory neuron wrapped around them; they are like strings lying in parallel to muscle. When muscles stretch, the spindle also stretches, causing action potentials to fire. The spindle neuron synapses directly onto the motoneuron of the muscle, as well as onto other neurons in the spinal cord and brain. Interestingly, the muscle spindle also synapses onto

inhibitory neurons that suppress the firing of motor neurons and therefore block the contraction of muscles that perform the opposite function. This inhibition is useful in suppressing the simultaneous firing of motor neurons that lead to flexion and extension movements of the same joint, say the elbow, which allows the joint to either flex or extend.

Sensors in our heads help us keep track of where our heads are. These vestibular organs (Figure 24) are made up of vestibular canals and otoliths (utricle and saccule) filled with fluid. When your head moves down with the rest of your body to pick up the boy, fluid shifts in your vestibular organs, which leads to bending of hairs in receptors that open sodium ion channels. Therefore these mechanical receptors activated by the flow of fluid in our inner ear also lead to the firing of action potentials (Figure 25). See Box 4 for the description of a reflex that helps us keep our balance.

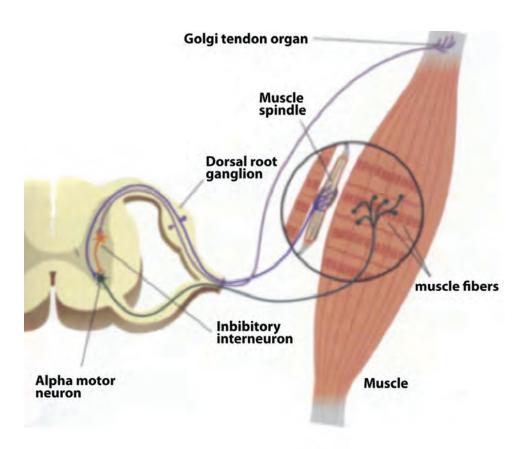


Figure 23: Golgi tendon organs are proprioceptors that relay information about the force of muscle contraction.

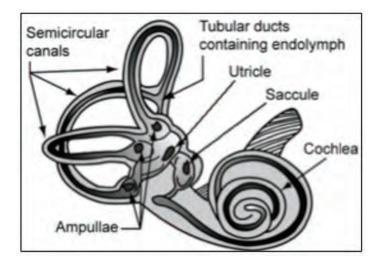
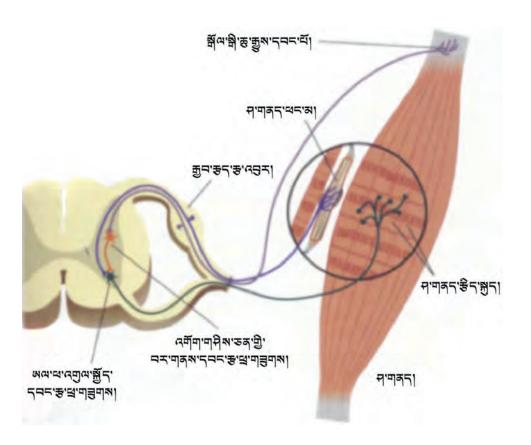


Figure 24: The vestibular system helps with balance



યણ ત્વન શત્વી માર્કે . હવુ ના મું તર્મ મું મારી હવુ ન સુધ . હવુ .

र्नः देश। ४० श्रुवाः ध्वाः वावाः वीशः राक्षेत्रः सुरः वीः द्रां स्वकृत्रः श्रुदः विहेत् वः रास्यः वरेवाशः चेता

८.क्ट्रुंदु-भ्-श्रुव्य-५वा-व-नन्न-वन्नु-र-ब्रे-व्येद-पदे-देवायामहेयार्थेदायादी १ न् नाञ्चेयाददानी र्जेट *ॱ*लेन्ॱळॅन्रन्दे भ्लाग्वन् स्याः स्यान्त्रान्ता (र्झेस्यानुः यशियायो) ४ ने निःश्चेयार्टाः क्रिःश्चेयायदः मक्त्रमा श्रीतिर्दिन हिना नि श्रीयातिश्वास्तिन ही भीन ब्रु.क्ट्र्र-चट्ट.ब्रु.वा.ब्री.क्ट्रिश-ट्यट.त्.चठशायाहेश. धोबा(द्रमे:देश १३) भःगवदःवस्यः सम्वादेः सबदःश्लॅर-५-५नट-१४-४-१न्दर्भ-४-१ लूर्यान्दा अञ्जूषान्दायम् विवान् कृता हेटा वर्डे न्हे वसः सुन्यः वदः वः विवार्षेत्। न्यावर द्रम्य वर कुराया वर्षा स्थान स्थान त्यायद्यान्यः व्याक्रीत्राचीनाया ने त्यानहेत त्रश यसप्तह्या त्रारा ह्रस्य रायमेत्रा रारेत्। र्यर.इ.स.चार्चयाश्वरम्बन्धःक्रीश्वर्त्वाचरःक्रीःप्यीकाः र्क्केट्र-५न८:इ:झ.बाबुबाश:५बा:५८:घ५:बार:सबु५: सक्तर्भाश्चेताया दे नित्तित्तु दे दस्य राष्ट्री साम् प:र्रः ऋर्ष्यातुः प्रेःर्वरः इःश्रःग्राञ्चग्रःग्वत्रः न्ना वर्ट वर् मार समुन् सर्म सम्मित्र में र्दे अळ्र- न विवाला वर्वे वा वा विश्व उदा ही न न र श्रम्बन्यस्त्रे यहार्म्यस्यायाः स्त्रीतः स्त्रीतः स्त्र

यर्ष्य ग्रेट्र-प्रम्म्यक्ष्म्याशास्त्री त्यीकःश्च्रीट्र-प्रम्म्यक्ष्म्याश्चर्या स्त्र-य्येक्षःश्चर्याश्चर्याश्चर्याश्चर्याश्चरः त्येष्याश्चरः त्येष्याश्चरः त्येष्याश्चरः त्येष्याश्चरः त्येप्याश्चरः त्येष्याश्चरः त्येष्यः त्यः त्येष्यः त्ये

यन्तरः छुट् सूट्याश्वरः श्रीयः यद्वे स्वरः सूश्वा राष्ट्र र खिशः कुट् स्वरः श्रीयः यद्वे स्वरः सूश्वा राष्ट्र र खिशः कुट् स्वरः श्रीयः यद्वे स्वरः स्वरः यद्वे स्वरः सुवरः स्वरः स्वरः

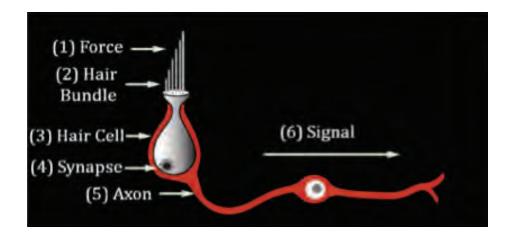


Figure 25: Head movements create forces in the inner ear that move hair bundles, which sit on top of vestibular hair cells. This deflection opens sodium channels, thus creating an action potential that then moves from the vestibular system to the central nervous system (CNS)

Box 7. IN-DEPTH: THE VESTIBULO-OCULAR REFLEX

This reflex allows the important coordination between head movement and vision. Measurements of this and other reflexes allow physicians to identify deficits in people's nervous systems. For example, in this series of pictures, a physician moves the patient's head 45 degrees to the side, and then quickly moves her head down so that the center of her head is lower than her inner ear. In this case, a vestibular pathology is indicated by involuntary and abnormal eye movements.



TO GAIN AN APPRECIATION FOR THE VESTIBULE-OCULAR REFLEX:

Hold a piece of paper with words on it in front of you.

Rotate your head from side to the side.

Can you read the paper?

Hold the paper in front of you and move the paper without moving your head.

Can you still read it? Why or why not? Do you or do you not receive sensory input from both your head and your hands? What are the possible pathways involved?

Ask a friend to stare straight ahead, either in a rotating chair, or standing up.

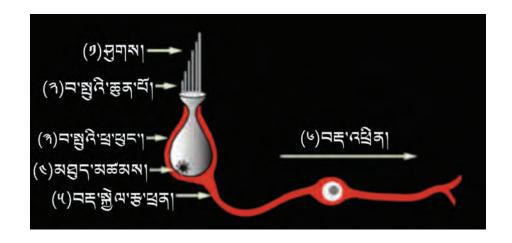
Spin the person around.

As the person is spinning, watch the motion of his or her eyes.

Is the person aware of the eye motion?

Why is it occurring? What sensory and motor pathways are involved? What might this reflex be useful for?

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सत् श्री मान् तिर्माल श्री मान्य स्त्री स्थान स्त्री स्थान स्त्री मान्य स्त्री स्थान स्त्री स्यान स्त्री स्थान स्त्री स्थान स्त्री स्थान स्त्री स्थान स्त्री स्त्री स्थान स्त्री स्यान स्त्री स्थान स्त्री स्थान स्त्री स्थान स्त्री स्थान स्त्री स्त्री स्थान स्त्री स्त्री स्त्री स्त्री स्थान स्त्री स्थान स्त्री स्त्री स्थान स्त्री स्त्री स्त्री स्त्री स्थान स्त्री स

८. च्रि.ट. ग्रीया च्रीया के प्राप्त के प्रा

श्चेमः र्सेन् भेनमः नतिदः नते र्सेन्य भारते देवे सेनानी नार्ये वन्तायः वर्षेमा

(ઋનઅ'ને'नार') मैंना अ'सें' ने अ'र्र्स मी' से ना मी'ना वें' प्रत्ता वा इसका रह हिन मी अ'र्कें र मी वें प्रांत निया

ઋવાત્રા ત્રી ત્રવાતા કું કું કું ત્રાન ત્રી ત્રાવિદ ત્રાણે કાર્યા વાય ત્રામાં ત્રામા ત્રામાં ત્રામ

In general, somatosensory information moves in hierarchical fashion from the afferent neurons of our somatosensors to our spinal cord to the thalamus and then to the somatosensory cortex of our brains. Recall from our discussion of vision in Neurosciences I that somatosensory information encodes four fundamental types of information: modality, location, intensity, and duration.

Let's consider these four types of information in terms of the modality of touch and our skin receptors as we touch the boy to pick him up in the forest. As you can see in Figure 26, we have four different types of skin touch-receptor cells, each with 'receptive fields' (analogous to visual receptive fields we discussed in *Neurosciences I*) in which they can sense stimuli. Different sensations occur when different types of receptors are stimulated. Pacinian corpuscles detect rapid vibrations (about 200–300 Hz), Meissner's corpuscles detect changes in texture (vibrations around 50 Hz) and adapt rapidly, Ruffini endings detect tension deep in the skin, and Merkel's receptors detect sustained touch and pressure.

When you feel your hands touch the boy, all four types of touch receptors fire. Activation of only Merkel and Ruffini receptors gives the sensation of steady pressure; activation of only Meissner's and Pacinian corpuscles gives the tingling sensation of vibration.

Location is sensed because receptors only activate when the stimulus occurs near them, in their particular receptive field. Merkel cells and Meissner's corpuscles encode the most precise localization information since they have the smallest receptive fields that are the most sensitive to pressure. They are also located closest to the surface of the skin.

Intensity of the sensation is encoded by the firing rate of the receptor neurons. The more action potentials are fired per second, the stronger the sensation (Figure 27). Receptors closest to the stimulus have higher firing rates

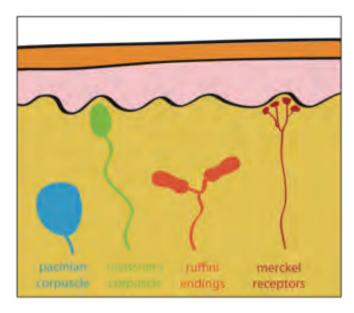


Figure 26: Four different types of mechanoreceptors or skin touch-receptors, each of which has a characteristic response to a different sensations.

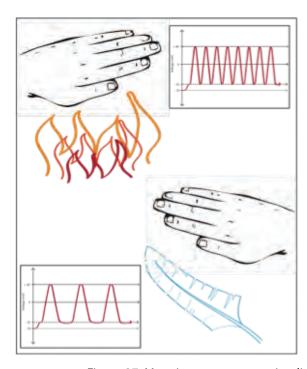
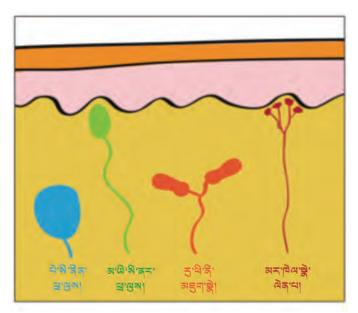
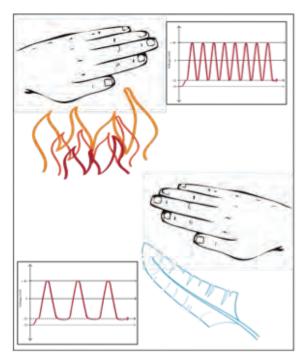


Figure 27: More intense sensory stimuli (for example, holding your hand close to a fire) results in a more rapid rate of neuronal firing than less intense stimuli (touching a feather)



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than distant receptors. Different somatosensory neurons adapt differently to stimuli. Slowly-adapting sensors respond during the entire time the stimulus occurs so we can sense duration. These sensors increase frequency of firing when pressure increases. Rapidly adapting sensors fire only when the stimulus starts and finishes, allowing us to sense change in skin pressure.

Like with all somatosensation, the interpretation or processing of touch is hierarchical (Figure 28). Stimulation of a population of skin receptors sends signals through a series of relay nuclei in the spinal cord to higher brain centers. As the signal moves through the nervous system hierarchy it is integrated with more complex sensory information. For example, the signal of 'touching the boy to pick him up' is integrated with emotional information, perhaps about 'feeling compassion for the boy' and with information about your past experiences and how to respond to sensations like contact warmth or the weight and trembling of the child.

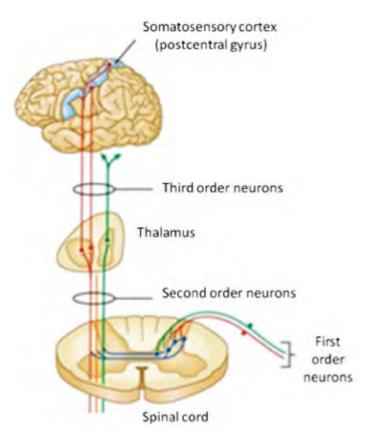


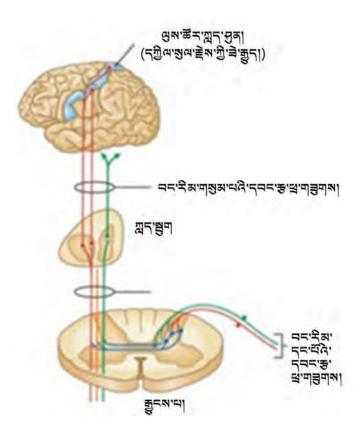
Figure 28: Hierarchical relay of sensory information through the spinal cord and thalamus and synapsing final in the somatosensory cortex

Box 8. IN-DEPTH: THE SENSE OF TOUCH: TWO-POINT DISCRIMINATION ACTIVITY

How does the skin let the brain know what it is touching? When we want to find out if something is smooth or rough, we run our fingertips over it, rather than the palm of our hands or our elbows. We can feel a tiny fragment of a bone in our mouths when we're eating, but we don't notice one at all if we step on it barefoot. How is it that part of your body is "better" at getting touch information?

Information from our skin allows us to identify distinct types of sensations, such as tapping, vibration, pressure, pain, heat, and cold. As we see in Figure 26, human skin contains different kinds of sensory receptor-cells that respond preferentially to various mechanical, thermal, or chemical stimuli. Next, these receptors convey the information to the central nervous system (CNS), to areas where we perceive the stimuli. To accomplish this, the nerve endings of the sensory receptors transduce, or convert, mechanical, thermal, or chemical energy into electrical signals.

To sense two separate points of touch contact, we must be able to discriminate one point from another. When a stimulus is presented within the receptive field of a single sensory afferent, the location within that receptive field cannot be determined by information from that single sensory neuron alone. Two-point discrimination therefore depends on both the size of the receptive field as well as the distance between receptors in the skin. Some regions of the skin have a large number of receptors, while other regions have fewer. Neurologists, physicians



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who specialize in diseases of the nervous system, sometimes test patients for two-point discrimination. They may do this if they suspect a problem with sensory information entry to the skin, the pathways to the brain, or the interpretation of sensory information.

Try these activities investigating two-point discrimination in groups of at least three people: a respondent, an experimenter, and a recorder:

- 1. Choose at least two different areas of the skin to test. Respondents must sit with eyes closed.
- 2. Experimenters take two toothpicks and prick subjects' skin about 1 cm apart with both toothpicks at the same time
- 3. Respondents report if they feel one or two pricks. If respondents feel two pricks at different times, then the trial should be repeated with the toothpicks touching the skin simultaneously. Experimenters then gradually reduce the distance between the toothpicks. The tester may also want to alternate between one and two toothpicks in order to keep the volunteer from guessing.
- 4. For each respondent and each skin location, record the smallest distance found between the two pricks where the volunteer can feel two rather than one prick. This is the discrimination sensitivity. Repeat each test at least 3 times for each skin location.
- 5. Each group should test all members in a few different areas of the body (hands, fingers, arm, leg, back, etc.)

QUESTIONS

- 1. How different is the two-point discrimination sensitivity across different body regions? Why do you think the differences exist? Are they the same across different individuals? Illustrate these differences by plotting the responses on a graph.
- 2. Which areas of your skin have the highest receptor density? Do you think it is the areas with the largest two-point discrimination distances or the smallest distances?
- 3. Draw a diagram of how the information from the skin receptors reaches the brain. Which brain area do you think is larger, the one receiving information from skin with lots of receptors or with few receptors?

Each sensory receptor connects through a series of relay neurons with a central nervous system neuron. A given central neuron responds to all information from its input area (the skin area that is the gathering field for only that cell) as if it were coming from one point. This skin area is called the receptive field of the central neuron. On the arm, each sensory receptor gathers information from a much larger skin area than a receptor on the fingertip, and this receptor is also connected to a defined central neuron. This central neuron, like the central "finger neuron", interprets all input as coming from one point, even though the skin area in this case is much larger. In order for a person to feel two points, two separate central neuronal populations must be activated by stimulation of their respective receptive fields. When this happens, two points are reported.

In sum, two-point discrimination depends on activating two separate populations of neurons, and in order to discriminate two closely placed points, the receptive fields of the neurons must be small. This in turn means that the receptors must be densely packed in a sensitive area, so that two points very close together activate different receptors.

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After it has left the spinal cord and passed through the brainstem, most of the incoming motor control and somatosensory information moves through a part of the brain called the thalamus (Figure 28). The thalamus serves as the gateway for all of the incoming sensory information and for the outgoing motor information; the thalamus monitors and modulates sensory information on its way to the rest of the brain. The thalamus is particularly important because it can increase or decrease the intensity of the signal on its way to the cortex. The more intense the signal sent on by the thalamus, the more attention we give to the stimuli. Importantly, there is heavy communication feeding back to the thalamus from the higher levels of the brain that helps determine how the thalamus modulates the information coming through it. It is thought that this back and forth communication between the brain cortex and the thalamus is central to what we call attention.

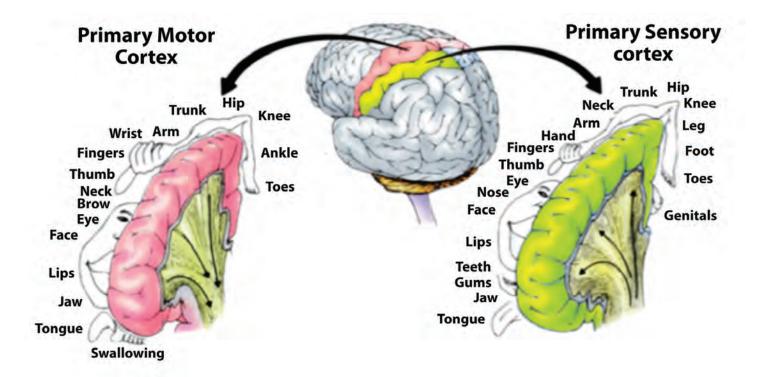
To appreciate how important sensory gating is to our minute-to-minute functioning, let us think back to your walk in the woods. Your attention was drawn to your sore toe after you tripped on the root; although your brain was receiving sensory information from all of your toes prior to the injury, it simply did not reach the level of your awareness. Similarly, as you sit and read, your brain is receiving information from all parts of your body and your environment, from the sensation of your legs touching the surface of the chair to the background sounds you notice once you willfully pay attention. Imagine what our realities would be if we were aware of all of this sensory information that descends upon our brains! The sensory gating that goes on in the thalamus is crucial for enabling us to pay attention to the most pressing sensory information, as ultimately demonstrated by your ability to completely forget your injured toe as soon as you heard the urgent cries of a child.

Clearly—through the thalamus and other cortical areas—sensing and movement are tightly coordinated and regulated. Thus, it is probably no coincidence that somatosensory and motor cortex control centers are so close to each other in the brain. Remember from Neurosciences I that the motor and somatosensory cortices are organized as detailed maps that correspond to all the parts of the body (Figure 29). In the somatosensory cortex, more sensitive body parts have more of the cortex devoted to it. Likewise in the primary motor cortex, muscle groups that make the most skilled movements have the most cortical neurons. Therefore, thinking back to the third question in Box 6, we can expect that the more sensitive areas that have more receptors will have greater representation in the somatosensory cortex.

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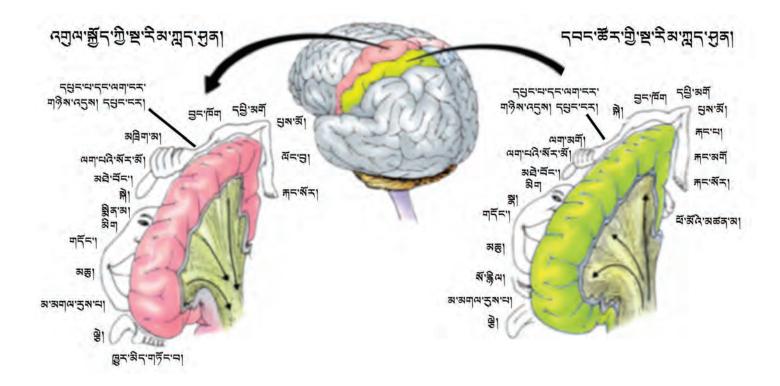
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There is a strong temporal association between behavior and cortical activity. Much like the direct correspondence between visual cortex activation and what we see, motor cortex activity corresponds to very specific aspects of movement. Specific patterns of neural activity correspond to the direction of movement, the force required to maintain the movement, and even the particular task in which the movement is involved. Figure 30 summarizes the neural pathways involved in conscious, directed movement. Trace through this pathway in your mind, from motor cortex to muscle fiber. Recall that earlier in the lesson we introduced motor neurons as a unique and specialized type of neuron that synapses directly onto a muscle cell. Here we see that pathway in more detail as neurons in the primary motor cortex fire action potentials that move down very long axons that synapse onto motor neurons on the spinal cord. Those motoneurons then synapse directly onto muscle cells to activate muscle contraction.

Your motor system has evolved to carry out very different types of movement; these can be broadly classified into two types that we already have discussed: (1) reflex movements that are automatic, have predictable neural patterns, and graded responses (the more stimulus, the greater the movement); (2) directed movements in response to somatosensory information about the environment that are voluntary and complex and not generally predictable; and a third type we have yet to discuss (3) centrally-programmed, patterned, rhythmic movements, which have predictable and complex neural activation patterns and are not voluntarily controlled.

Figure 29: A representation of the connections between the body and primary motor (left) and sensory (right) cortices. The relative size of the body part drawn next to the cortex represents the number of cortical neurons that are devoted to innervating that particular body part.



As we have said, what happens when you are in the woods and trip and catch yourself is called a reflex movement (type 1 above). When you hear the boy cry and move to help him, that's directed somatosensory integration and response (type 2). On the other hand, your walking and breathing, swallowing and heartbeat are regular, automatic rhythmic patterns controlled by what are called central pattern generators (type 3).

Unlike all the other neurons and neuron systems we've discussed, central pattern generators are neural networks that produce regular rhythmic neural outputs on their own, without the requirement for input from any external source. Central pattern generators can even create their pattern of neural outputs when they are entirely isolated from the rest of the brain!

Central pattern generators consist of sets of neurons that are connected to each other such that they can create regular rhythmic firing patterns (see Figure 31). In fact, in some cases only 2 neurons are sufficient to create such a pattern. These neurons inhibit each other so that only one can fire at a given time. After a period of activity one of the neurons 'tires' and the other one takes over the rhythm. Importantly, many of these regular rhythmic activities are

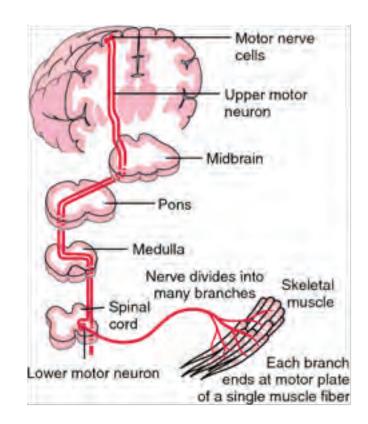


Figure 30: The pathway of a motor neuron: the axon extends from the primary motor cortex, through the midbrain and spinal cord, and then synapses directly onto a skeletal muscle.

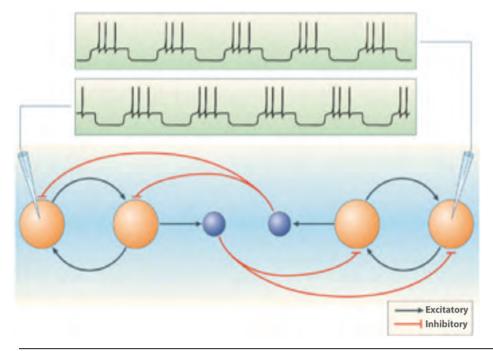
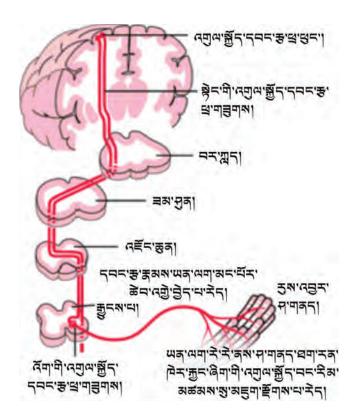


Figure 31: Rhythmic neural activity (above) recorded from neurons that are part of a central pattern generator



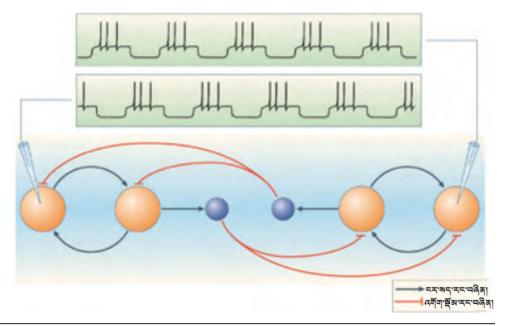
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MOTOR PLANNING

Prior to action, you actually—unconsciously and very quickly—think about what you're going to do and plan out your movements before you do them. This can be thought of as feedforward regulation, because you are projecting what you'll do next. We know that many cortical association areas (recall the definition of these areas from our vision discussion in *Neurosciences I*) send signals to the primary motor cortex — many are from premotor and supplementary motor areas involved in motor planning. These regions are located just in front of the primary motor cortex (Figure 32). Motor

association areas also receive information from higher cortical areas like those associated with language. As you might imagine, the motor planning areas like the primary motor cortex are organized similarly to the somatosensory cortex in that it also has a somatotopic representation of limb and muscle groups (see NS primer I).

Directed movements like those you make in deciding to walk through the woods in the first place, or those you decide to do upon hearing the crying boy—leaning over and picking him up-involve many levels of control beyond simply carrying out the action. Given the fact that movement is absolutely crucial to all our behaviors and actions—from walking to breathing to loving—you should not be the least surprised that the amount of regulation, modulation, and control put into our movements is complex, vast, and diverse.

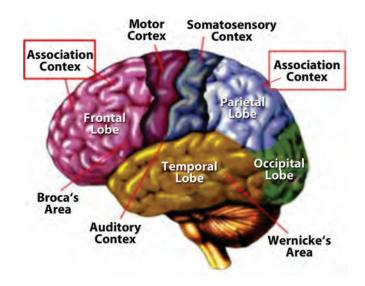
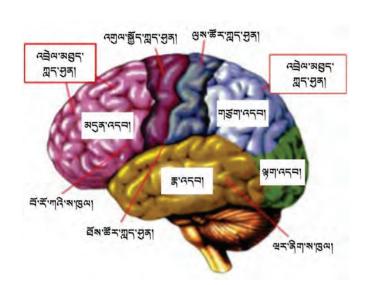


Figure 32: Association cortex located anterior to motor and sensory cortex is the site for premotor and supplementary motor areas important for motor planning

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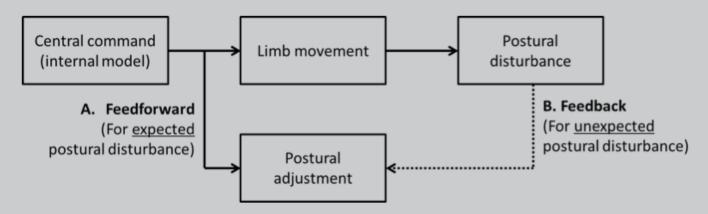
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Box 9. IN DEPTH: FEEDFORWARD SYSTEMS



In a feedforward system (A.), action occurs without the online use of output from the action itself. Because the system does not rely on output from the action (i.e. feedback), it is thought to require an internal model for accuracy. As you will soon see, the cerebellum is a region of the brain that is crucial for feedforward control. Contrast this with a feedback system (B.), which involves modifications based on information that loops back to guide future actions. The benefit of a feedforward system is speed, since there is no delay for feedback of information. However, it likely does not allow for the correction of errors, and thus, accuracy, that can occur with a feedback system. As you might imagine, the optimal situation is one in which feedforward and feedback occurs in concert.



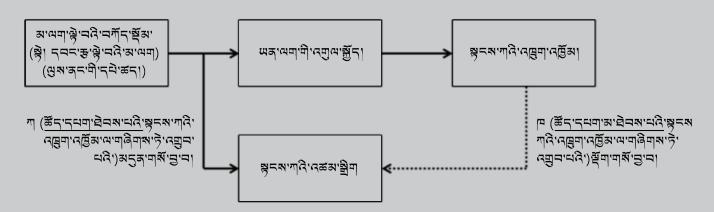
One example of this is the way your body moves during exercise. It uses a feedforward system in preparation for a dynamic action, changing the activity of postural muscles in order to ready the body for the movement when it occurs. For example, in preparation for a lateral arm movement that will shift your center-of-gravity, your postural musculature makes compensations to allow you to maintain your balance. It does this quickly, without incorporating any feedback somatosensory information. However, if your foot strikes on uneven ground, sensory information feeds back into the system to allow your muscles to adapt to this unexpected change.



ब्विं अ'तु'न्गु'म। महिन'ह्यम्य'मदि'ङ्ग'दिम। अनुव'मर्से'अ'यम



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As we have studied more and more science, you have seen the evolutionary theme exemplified at all levels of the living staircase, from molecules to populations: all biological systems are regulated and, the more important a biologic phenomenon is for survival of the organism and its offspring, the more refined and complex its regulation. A key mechanism of regulation—feedback control—is used in many situations (box 9). We have seen this in several lessons thus far including feedback at the global level during the nitrogen cycle (discussed in *LSP I: Evolution*), feedback between slime mold cells and their external environment, and (discussed in *LSP III: Development and Physiology*) feedback in humans among different hormones and organs affecting behavior, and feedback among many of the molecules regulating energy production in cells. We'll investigate another kind of regulation—feedforward control—in our discussions below.

As we've discussed, the downside of complex, refined regulation, is that the more complex the regulation, the more things can go wrong. But the upside is that the regulated phenomenon in question can be adjusted slightly or significantly up or down in response to many different environmental parameters. Thus, instead of the process simply being on or off, it can be adjusted to be on a little or a lot depending on time of development, time of day, type of cell, temperature, amount of energy available, or other environmental demands.

Since movement is the manifestation of our thoughts, feelings, and actions, perhaps nothing is more important in our biologic lives —other than those thoughts, feelings, and actions themselves—than movement. Think about it: we could have the most compassionate and deep feelings in the world, but if we can't or don't act on those feelings, their value is greatly diminished. We might hear the boy crying, but without the ability to move, we could not even walk toward the sound of crying to make the effort to find him. As movement is so important, it is highly regulated in many ways in humans, who have one of the most, if not the most complex brain on earth. Here we will examine two important regulatory parts of the brain—the basal ganglia and the cerebellum.

BASAL GANGLIA AND CEREBELLUM

In addition to the motor and premotor cortex, at least two other important brain regions are involved in movement planning and execution: the basal ganglia and the cerebellum.

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Recall the basic anatomy of the brain from *Neurosciences I*. The basal ganglia include the caudate nucleus, putamen, nucleus accumbens and globus pallidus. Together, the caudate and putamen are called the striatum. The basal ganglia also include the subthalamic nucleus and the substantia nigra.

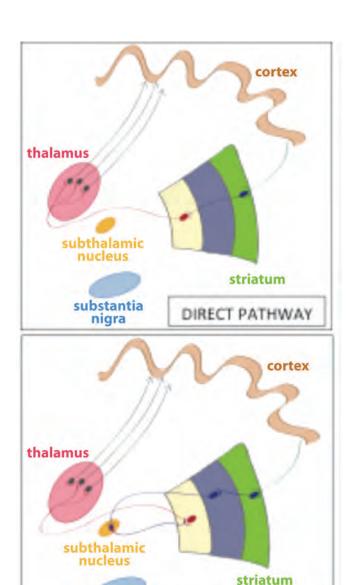
As we know, one important way toward understanding the functions of a particular brain region is to identify the other parts of the brain to which this region connects. Let's think carefully through Figure 33 that shows a simplified outline of the connections within the basal ganglia and between the basal ganglia and other areas of the brain.

Most neural connections that send signals into the basal ganglia project into the striatum. These neurons are excitatory; they originate from the thalamus and from wide ranging areas of the cortex (including motor and somatosensory regions). Remember that the thalamus is the gateway for modulating information going to the cortex, and that the thalami themselves receive information back from the cortex. In addition to this bidirectional communication with the cortex, the thalamus is covered by a sheet of inhibitory neurons called the reticular nucleus. These inhibitory neurons terminate on nuclei within the thalamus and in this way modulate the information that travels between the thalamus and the cortex. The fact that there are so many connections between

the basal ganglia and the cortex, the basal ganglia and the thalamus, and the thalamus and the cortex again emphasizes the complex integration of diverse kinds of information in the brain.

Within the region of the basal ganglia that receives excitatory neural connections from motor regions of the cortex, neuroscientists have again discovered a motor map or homunculus just as we see in the primary motor cortex.

The basal ganglia process motor cortex and somatosensory information and send inhibitory neural signals out, back to the thalamus (and other brain regions) in a kind of loop. These signals come from the globus pallidus and the substantia nigra. There are also many internal neural communications among different parts of the basal ganglia.



substantia

nigra

Figure 33: The basal ganglia, including the caudate nucleus and putamen (also called the striatum) and the nucleus accumbens, globus pallidus, subthalamic nucleus and the substantia nigra.

INDIRECT PATHWAY





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य्यन् । वनशासः यनु शार्हेव नुः नदः यद्येव निर्हेनः नवे नवनः स्वते : स्रवनः र्वे न्यायः के नवे । स्रवन् शुवनः । षियान् वर्में राम्यावर्षात्रां नियान् नियान् स्वाम्यम् वर्षात्रम् स्वाम्यम् स्वाम्यम् स्वाम्यम् स्वाम्यम् स्वाम्यम् ड्यालुयान्त्रा हे.स्वा.यान्त्रीयान्त्रा(त्वीयार्श्वेन्त्रान्त्राक्ष्याञ्चान्त्रे)यान्त्रीत् प्रकार क्षेत्र नार्के दाये हो दाया उत् की कार बोद दो इस सामी साम हो हो दाया है है दाया प्रकार के साम हो है है ळावडीबाइसमायानासुनाने ननाकेनायावर्डीं स्त्री प्रेन्सायहरू सम्बन्धायने साध्याप्त स्वापन श्चन'यरे 'हेर' सन् 'ल्र' र्राय्वर र्'नर्केर हिंग्य पहिशानर कें अपार के वार् ज्यार कि वार प्राप्त के वार्य त्रुन्'र्भुना'यने'हेन'यर्नेना'र्थेअ'रमः'निनेश'ठद'त्री'न्नमः'ह' झ'ना बुनाश'अमः'र्थे अ'तुन'मये'येन धुना डेना नी शनार्षे न शन्ये द शन्ये द हिन्ता है स्वाह स्वे हैं है स्वाह स्वे न स्वे न स्वे न स्वे न स्वे न स्व <u>क्ती:त्वर:इ:स:मञ्जूबाय:दर्ने:त्वा:क्षत:धूवा:दर:वी:क्षे:क्षेत:ह्वय:तु:स्टरस्ट:वी:स्ट्वा:क्षे:क्षूत्रया</u> क्ष्याने १८१८ म् नामी अयान सुनापर यान श्रुवापर सामा स्वाप स्वर्ध स्वर्य स्वर्य स्वर्य स्वर्य स्वर्य स्वर्य स्वर्ध स्वर्य स्वर्य स्वर्य स्वर्य स्वर्य स्वर्य स्वर्य होन्यन्तेन नेत्यामन्वयम् इत्रमन्त्रम् १९४५न्य न्यर्न्त्। यरम्मन्वयम् इत्रमन्त यान भ्रमानम् ने निवेत न् यान भ्रमानन यान भ्रमानम ने भ्रमान भ्रमानम निवास निवास निवास निवास निवास निवास निवास न चते प्रदेश र्देव प्रदेश सून प्रते वर प्रतः है क प्रदेश रे नाया श्रुप्य प्रतः प्रवर क्रिक श्रुप्त श्रेव हैं ना वहैंद उद विवायम्ब द ख्या दद मुक्ष वार्य में द में दे हो द में कि व

Asyoucansee in Figure 33, these many excitatory and inhibitory connections of the basal ganglia add up to two distinct pathways for information processing, the direct pathway and the indirect pathway. In normal individuals, when the direct pathway is excited, it activates the thalamic neurons, and they in turn excite cortical neurons. The net effect of this excitement of cortical neurons is muscle contraction, and thus, movement. When the indirect pathway is excited, the opposite happens: thalamic neurons are inhibited, and they in turn inhibit cortical neurons and thus, inhibit movement. The direct pathway may help us carry out the behavior that best fits the situation, while the indirect pathway prevents other alternative behaviors from occurring. The two pathways are maintained in a fine equilibrium, balancing each other out.

So, in terms of movement, the basal ganglia are involved in facilitating particular actions, probably sorting through potential actions that are stored and initiated in the motor cortex, and then helping to determine which action actually is performed. Because a person can only do one movement at a time, the basal ganglia might be involved in allowing, or at least not inhibiting, one particular action, while inhibiting others. The basal ganglia also perform a similar balancing and gating of emotional and cognitive information coming from the other cortical areas.

Why would the cortex-basal ganglia-thalamic loops decide on one action and movement versus another? Why do you stop and help the crying boy in the woods rather than ignore him? Why do you notice the boy and not the trees? Here we once again turn to that central principle of biology—understanding how things work normally by studying them when they don't work. Much about the answer to action decisions has been garnered from studying people with missing or defective basal ganglia neurons. Model systems—especially monkeys—have also been very useful in understanding basal ganglia and their modulation and selection of action.

The neurotransmitter dopamine appears to be central to this story. As you might imagine, if the equilibrium between the direct and indirect pathways breaks down or is compromised, serious diseases can occur. Parkinson's disease and Huntington's disease are two of the best studied movement disorders. People with Parkinson's move slowly if at all and at rest they suffer from hand tremors. Those with Huntington's suffer nearly opposite symptoms: uncontrolled, continuous movements of their bodies. Determining which neurons are affected in each disease was very important in understanding the mechanisms of the direct and indirect pathways.

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In Parkinson's disease, dopamine-producing neurons in the substantia nigra degenerate over time (Figure 34). Thus, the neurons in the striatum are lacking an important source of neural input usually provided by these dopamine neurons. Recall from our discussion above that dopamine is a neurotransmitter that modulates the properties of target neurons. Also above, we discussed ways that the same neurotransmitter could result in different neural effects if it bound to different receptors. This is the case with dopamine in the basal ganglia of healthy individuals: different neurons in the striatum have different kinds of responses to dopamine because they have different receptors. The lack of dopamine neurons (and the subsequent

reduction in dopamine) results in neurons in the basal ganglia firing action potentials at abnormal rates and in unusual spurts, which causes movement abnormalities.

Interestingly, research suggests that in addition to modulating movement, dopamine is the key neurotransmitter for two related processes: reward processing and learning, although in the case of reward and learning the dopamine arises from an area neighboring the substantia nigra called the ventral tegmental area (VTA). Intuitively, reward processing and learning are linked - it makes sense that you would more likely do something and in fact remember it if you received some kind of reward for doing it.

Evidence for this comes from studies where the action potentials of basal ganglia dopamine neurons in monkeys were recorded during different types of behavior. Dopamine neurons show increased activity at the time the monkey receives a novel reward, which implies that dopamine may be involved in signaling salience or novelty of stimuli. In addition, when a monkey learns that a specific stimulus always predicts a reward, its dopamine neurons fire strongly after this stimulus, but not as much after the reward itself. This phenomenon suggests that dopamine neurons are involved in reward prediction, and in motivating the animal to carry out actions that will lead to rewards. We will discuss dopamine, reward, and motivation more in the next NS primer.

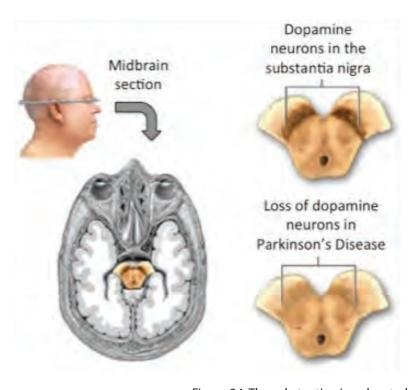
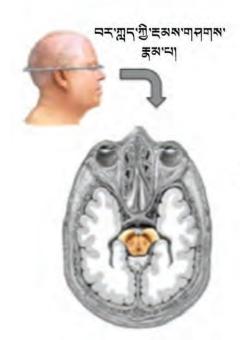
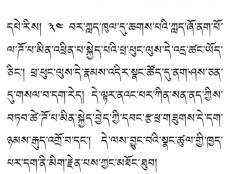


Figure 34: The substantia nigra, located in the midbrain, contains cell bodies that produce dopamine. The cell bodies appear dark; however, in the case of Parkinson's Disease the dopamine producing neurons degenerate. The difference in color is often evident to the naked eye.









न् अः र्केंन प्रक्रों मे अप्तिवेद सम् गीव अव वन सम् ना प्यासन विवासिय षिता.की.पूर.सा.साय.सी.र.सीय.वी.र.साय.र्य.सा.याचीयाया.स्याया.ध्याया क्तु-पर्वो निवेद र्षेन्। (निवे नेशा २०) नेर निहेद भ्रव पुतालिय की निवन इ.स.च बेचे ४.टचे.ल.झपूर्यपुर्य स्थान १ चेचा के विष्य के स्थान विषय की विषय हो थ *ॸ्ॱॸॕॱ*य़ॱऄढ़ॱॸॖॺॸॱॹॱॿॱॺऻॿॖॺऻॴढ़ॸऀॱॸऀॺऻॴॱॻॖऀॴढ़ॎॸऀढ़ॱऄॗॴॱढ़ॖ॓ॸॱय़ॱॸ॓ढ़॓ॱ <u> ५ वृद्दासुरअ'नाय'ळेठ,'वेन'र्रञ्ज मुज्ज भुन्न'यर'ययुर्द्र</u>'रार्द्रा र्बेअःसूनःग्रुअःसःनविदःर्तेःसःस्रेदःदेःन्दःनीःन्स्रेग्रयःदवेदःन्:ग्रुनःसदेः व्ह्रीत्र प्रवे सेवास नेवा प्रेत प्रवे स्ट्रिस ह्या प्रवेश हे प्रवेत स्ट्रा स्ट्रिस हा स्ट्री स्ट्रिस हिंदी स्ट्री स्ट्रिस है स्ट्री स्ट्रिस होते हैं स्ट्रिस है स्ट् दब्रेब्र-मःम्हिन्-स्रेन्।क्रेन्-स्रेन्थेन्येव्यक्तःसःस्रेन्द्र-न्न-प्रस्त्र-स्रेन्द्र-न्न-नुः त्रीरः व्यन् वात्र अधूर अप्यन्ते हो स्वरं वि स्वरं वि स्वरं स्वरं स्वरं स्वरं स्वरं स्वरं स्वरं स्वरं स्वरं त्र्भात्त्वाः क्रीः तें नासेदायाय क्रुटानदेदायायेदाने। <u>भूदा</u>श्वादायो प्रनार महिमानाधीताया देवि श्वे त्ये त्ये त्या से त्य नार्धिन नार्थे नार्ये नाय्ये नार्ये नार्ये नार्ये नार्ये नार्ये नाय्ये नार्ये नार्ये नाये नाय्ये नार्ये नार्ये नाय्ये नाय्ये नाय्ये नाय्ये नाय्ये नाय्ये प्राप्तेत्रप्तप्तः सः अवात्र्वायाः श्रुदः दुः सः श्रुदः प्तः । (५८: देशः श्रुवः भः नें प्राप्तेतः ने । नश्राहे :कुर:५: ख्रीवरपः) देवे व्यवश्रानु राग्नु रावनश्राहाय है । यह श्राह्म विवश्

समायहैयाचे समायहैयाची सम्बद्धियाचे स्थापन स्यापन स्थापन स्यापन स्थापन स्थापन स्थापन स्थापन स्थापन स्थापन स्थापन स्थापन स्

स्यान्त्रियान्त्रियाः वित्तान्त्राः वित्तान्त्राः वित्तान्त्राः वित्तान्त्राः वित्तान्त्राः वित्तान्त्राः वित् स्वः स्वायान्त्राः वित्तान्त्राः वित्राः वित्तान्त्राः वित्तान्त

Neuroscientists can look specifically at the activity of dopamine-responsive neurons in the striatum when they receive cortical input. Results of such experiments show that the size of the synaptic potential of these neurons is plastic (that is, it changes depending on the experience). When the same cortical input is repeatedly present briefly before the neuron fires, the neuron learns to make bigger responses over time. This is a basic mechanism for learning, or forming memories, which we also will discuss in NS primer 3. In other words,

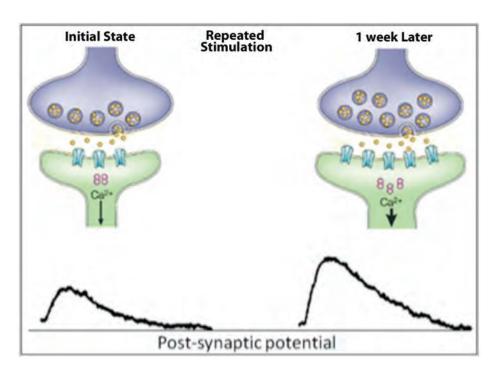


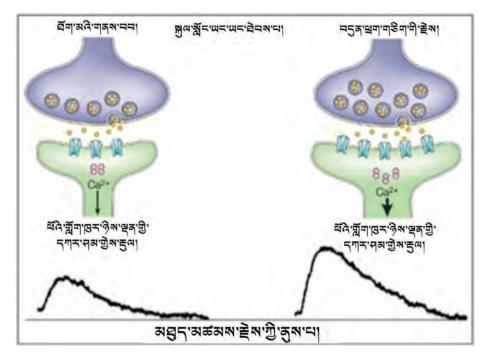
Figure 35: With repeated exposure to a stimulus the neuron produces a larger response.

the more times you have experienced the same thing, the more response your brain has to it (Figure 35). In contrast, if one of these striatal neurons repeatedly receives cortical input after it already has fired, it will show smaller and smaller responses to such cortical input. This type of change in synaptic responses is a kind of neural plasticity and it appears to underlie certain kinds of learning. Strikingly, this plasticity of response of striatal neurons to cortical input depends on dopamine. When dopamine receptors are blocked, this kind of plasticity no longer occurs, and the organism can no longer learn.

Thus, reward, learning, and action all come together in the basal ganglia to allow 'neural decision making.' Dopamine neurons in the striatum evaluate several inputs from cortex in each situation, and based on previous learning the striatum chooses one of these cortical patterns, one of these movements and actions. The basal ganglia tell the cortex what to do. Dopamine activity and synaptic plasticity are keenly tuned to rewards; the striatum performs reward learning and tells the animal which action will most likely result in a reward. Think about why reward should be important for learning and motivation.

CEREBELLUM

We have talked in depth about movement and its regulation. We started our discussion with the big picture: how, biologically, do we stop and help the boy? This led us all the way down to the cellular and molecular level of neurons: how does a neuron work? Then we began to build back up toward



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र्टे.स.भ्रुय.स.क्ष्र्य.स्रुट.स्रुव.सदे.८्यट.ऋ.स.म.बुनाश. न--दनाः भ्रदः शुद्राहितः दुः दिवे दः सः देः दनाः ऋदः शुद्राहितः **ग्री:**बर:पदेव:क:पद्मेव:इसम्भ:दर:ब्रद:स:व:ग्रु:पर्गुत्य: द्यी:इस्रामानाद्वियापर्वेदामान्याच्येदानेयापाद्वस्रा ग्रीभान्सीमाभानद्वमाभाने विनासु होन् मुना नहमानहान *े*वितःबहुनाःवरेःननाःनेःसहुनाःबङ्गःननाःनेसःन्वरः इ.स.च बेचाशावरे स्चाशाकी सरीर अक्सरा वेशायहर ळन् पादी ने प्रयूप्त पिशा उदा (हे ह्यू मान से से माही सा यविष्यान्, भेर.क्रीया (जनायदिया वेनाया) भाषत्रस्या मवे मॅिन्देर माया हे सार श्वर हिया ही वर वहेव का वहेव गडेगार्रावेगार्भुरादशायरातुः खुराडसाखुराडसा *दैर:*दवर:इ:ब्र'ग्*बुग्*थ:दे:दर:दब्द:ळें:तृश:धुद:ग्रर: सक्समार्थराहे मान्यराहाषात्राचा सुवासाने सार्खराष्ट्रराहे केर श्वेत कुर वें नशायों भे भें भी वर्द है वें वें न निश র্বন্য-মূদ্র-মান্যা

लस्भुभः खूचः इंचभः क्रिंच्यं विचान्त्रः विद्यान्त्रः विचान्त्रः विचान्तः विचान्त्रः विचान्त्रः विचान्त्रः विचान्त्रः विचान्त्रः विचान्तः विचान्तः विचान्तः विचान्त्रः विचान्त्रः विचान्त्रः विचान्तः विचान्तः विचान्तः विचान्तः विचान्तः विचान्तः विचान्तः विचान्त

शक्ष्यं त्र्य्यं त्रम्यां स्यां स्यां स्यां स्यां स्यां त्रां व्यां त्रां स्यां स्य

य्चन'क्षेन्।

चैट्-द्रश्च-द्रेट-भेंद्रे-ट्रश्च-विकासी सुवास्त्र विकास का त्योवास कर्ने स्थाने स्थान

the actions and thoughts of a whole human again: how do neurons work together? How can many neurons working together result in different activities and behaviors? Then, because movement is vital to any action, we focused on how the neuromuscular junctions are vital, at the cellular level, to movement. We learned about the three different types of movement in which our neuromuscular junctions are involved: reflex, voluntary or directed, and central-pattern generated. Finally, we've been asking questions about directed movement: how are movements controlled and regulated in the brain? First, how do we select movements? Then, why do we select one movement over the other? Finally, here we ask: how do the actions and movements that we do perform happen so smoothly? How do the muscles necessary for action work together and other muscles not needed stay out of the process? How does the body keep track of its posture and balance so that we can carry out the same movement irrespective of the position of the rest of our body?

The cerebellum is a large structure located at the back of the brain (Figure 36) and is deeply involved in addressing the above questions concerning balance, muscle coordination, and posture maintenance. Although it is easy to overlook the cerebellum when we see pictures of the brain, it contains more than half of all the neurons in the brain (despite making up only 10% of brain size). The more is learned about it, the more complex and diverse its functions appear: we can expect to learn much more in the near future. Much about the function of the cerebellum was determined by studying people who have movement disorders, and matching the particular area of neural damage to the particular symptom of the disease (see Box 10).

The cerebellum contains more than half of all the neurons in the brain (despite making up only 10% of brain size), and like the basal ganglia, it receives information from the cortex about movement and then helps organize and carry out particular movements. The cerebellum also receives input from the vestibular organs and proprioceptors we discussed above to help us make adjustments to our posture so that we keep our balance. In addition, the cerebellum coordinates the timing and force of the many muscles required to effectively perform any movement. Not surprisingly then, the cerebellum probably plays a role in language and other processes that require movement and the sequencing of actions. The cerebellum is also crucial for trial-and-error motor learning so we can make smooth and effective movements. This is the kind of learning we experience in say,

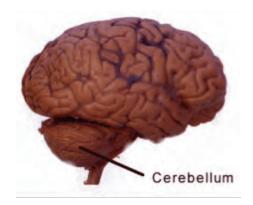


Figure 36: The cerebellum is a large structure located in the back of the brain. It contains more neurons than any other single subdivision of the brain.



स्यात्तर्यास्त्री लय.जयो.वर्ट्र-रेयट. झ.स.चीचीयाः की.चेट्यावस्ट्र-स्यट. की.ट्याक्ष्य. की. संया-याव्याकु.वट्: बुची.टेट. यर्बेट्र-स्यट. संप्र-टिक्ट्रीययान्यसूट कु.व्यावृत्तालुयी सटे-सप्ट्र-बट्टायोश्या टेव्र-ट्रम्या ४० सट्-ब्रीट्-ब्र-सिट्-सप्ट-क्चिय. ब्रीचायाः श्रीत्यूट्ट-

वी ।वः र्स्चे वा या ने : न तनः इः सः वा त्रु वा या ननः विदेशः या स्वः निष्यः ने या निष्यः वा वा या विदः विदः व तुःनादःसॅॱबिनानी नर्भसःर्ह्वे दृदः तुःर्श्वेद्र व्हंत्यःवरः द्वेद्रःलॅना तुरुः तः श्ले दिनदः सः नातुनाशः वदः यह व्हंदः त्वेः અજ્ઞાયમાં ગ્રેનઃસ્થાનદા <u>નિવદ ઋચાવી વીત્રામાં ને સામજ</u>્ઞાયમાં ગ્રેન્યાનામાં ગ્રેન્યાનામાં ત્રાપ્યાના સાથે સાથે ત્ર *ने न्ना प*र्देत रहेवा नरुषाया क्षेत्र पृत्व अपर्येत्। ने त्र यान क्रें या सासुन मी ने या परान्त राम्या प्राप्त सक्तम्यः क्षेत्रायः क्ष्मयः त्रत्युः वः र्र्भुट् । चुः नः नृत्याः यावायः यावनः है । या बुदः यो गावसः हे देवः वः ઽઃૐ૽૾ઽ૽૱ઽઃફઃઽઽઃબઃૹૢૢૢૢૢૢઽૢૡ૽ૹૹૹૹ૽ૹ૱ઽઌૢ૽૽૱૱ૡ૽૽૱ૡઌૢૹૹૢ૽ૼઽ૽૱ઌૹઌૹૢ૽ૹૢ૽૱૱ૹ૽૽ૹ૽ૢૺૹ૽ૢૼૼ૱૱ૹ૽ૹ૱૱ૺ नेशनान्ते र्ह्मेनावनुवान्दा केदाक्ष्याव्यस्त्रम्भवात्रम्भवात्रम्भवात्रम्भवात्रम्भवात्रम्भवात्रम्भवात्रम्भवात्रम् नक्षरअःचतेःवन्।वःक्रुँदःचठअःधोर्ता अवतःअह्नाःहःच्छैंअःद्रश्चेनअःवह्नायःवन्।वःक्रुँदःक्रूँदःदूँन्।अःदेः द्युअःवा ळॅंअप्यज्ञायाः र्क्केन् ग्री:रेजाअप्यन्यायअप्यादे व्हार होन न्या ने त्रअप्यज्ञायाः र्क्केन् जान लेजायने आहेन जान लेजाः से वनेअन्तरे हेते हो र वहुर र आ क्षुनु धेना अवर वरेर क्षुर धर र केंग्यरे कृतरे क्षुर र वहे क्षेत्र र केंग्यर वही ॼॱऄॕॗ॔॔॔5ॱॸ॔ॸॱढ़ज़ॖॺॱऄॕॗ॔॔5ॱढ़ऺॴढ़ॾ॔ॸॱढ़ॾॴक़ॴॱॵॱॸॸॱढ़ॼॖॸॱॳढ़ॏ॒ॸॱढ़ॹॗॸॱढ़ॹॗॸॱढ़ॴ॒<u>ॗॹऀॕ</u>ॸॱढ़ॏॴॱॺॱॸ॓ॴॱॼ स्रोतिन्दिः भागवर इससायसाया सङ्गार् , (वृनासायेरा) विरासी स्रोतिन्दिः भागवर इससा हो राजेस है राजे । वृनासा स'ने'हे'धूर'वज्ञुर'रम। वन्।व'र्भून'ग्रे'रेन्थ'न्नेन्य'महेन्।रर'दोन'वज्ञुन'सर'सर्वि'नवे'सुर्थ'ग्रे'सूर्थ'ग्।'न्र'रें'स्थस्य' नावर्याननः इसर्यास्य स्वातः ही द्यारी विदेश स्वातः विदेश स्वातः स

त्यसंद्रभागिथ्यचे चेशाल्स् (क्रिंश्चियचेश्चर्यंश्वर्या)

विवाचे चेयां तार्युः सूर्यं त्यस्त्राचे त्यस्त्रयस्त्राचे त्यस्त्रचे त्यस्त्यस्त्रचे त्यस्त्रचे त्यस्त्यस्त्रचे त्यस्त्रचे त्यस्त्रचे त्यस्त्य

यद्यः ग्री-सवृद्धात्राच्यात्राच्याः श्री-स्वृद्धात्यः भ्री-स्वृद्धात्यः स्वात्यः स्

figuring out how to hit a cricket ball, or to play ping-pong or basketball. Figure 37 shows an example of one of the many cerebellar connections that communicate with the cortex, spinal cord, thalamus, and vestibular organs.

In addition to movement, the cerebellum is becoming more widely appreciated for its role in cognitive and emotional processing. For example, the cerebellum is important for emotion regulation, and people suffering from disorders of emotion such as depression have

abnormal cerebellar function and structure. Furthermore, the cerebellum is critical for processing of language, above and beyond its use in the motor aspects of language production. Evidence for this comes from neuroimaging studies showing activation of the cerebellum during tasks that require language processing, as well as studies showing that individuals who have suffered damage to their cerebellum have impaired language processing. This makes sense given what we have said about the role of the cerebellum in timing and in error detection, since both of these processes are critical for comprehending a sentence, the meaning of which is conveyed by the specific orientation of words in relation to one another.

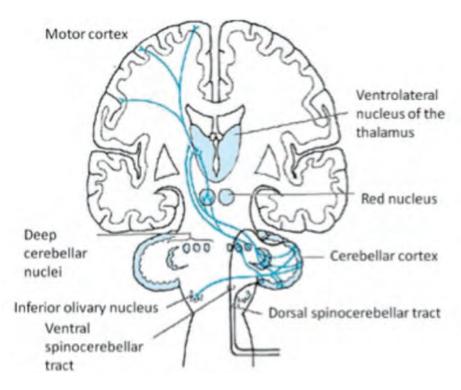


Figure 37: In this cross-section of the brain, we see connections (in blue) between the cerebellum, the spinal cord, the thalamus, and the vestibular organs. Connections from the cerebellum relay in the thalamus and descend on the motor cortex.

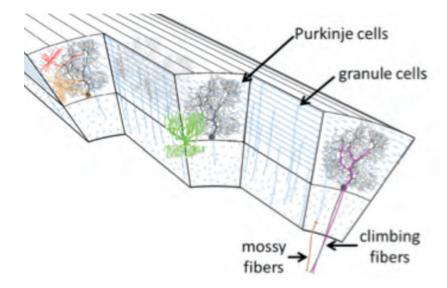
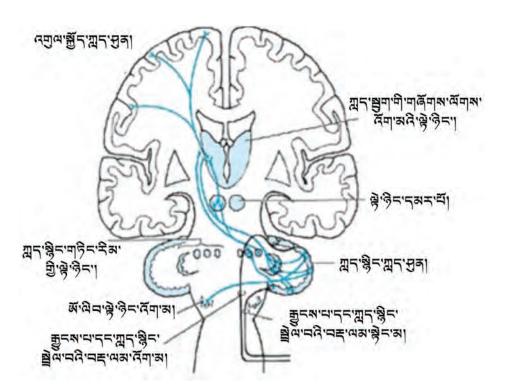


Figure 38: Cross-section of the cerebellar cortex showing some of the diverse cell types. The inner (lower) layer contains mostly granule cells, the middle layer is comprised of Purkinje cell bodies, and the outer (upper) layer contains their dendritic trees and other cells. Purkinje neurons have a long axon that stretches through other layers and out of the cerebellar cortex, while axons of the granule cells ascend to the outer layer and bifurcate to form the parallel fiber system (blue lines). Rokni et al. 2008. Frontiers in Neuroscience. doi: 10.3389



य्यीयः श्रृट्रिस्ति स्थित्। स्वयायः स्ट्री श्रीत्वश्च्यः हे स्मत्स्य स्थायः स्थितः स्यातः स्थितः स्यातः स्थितः स् ल्य में में स्वाप्त स्वाप्त में में स्वाप्त में में स्वाप्त में स्वाप्त में स्वाप्त में स्वाप्त में स्वाप्त स

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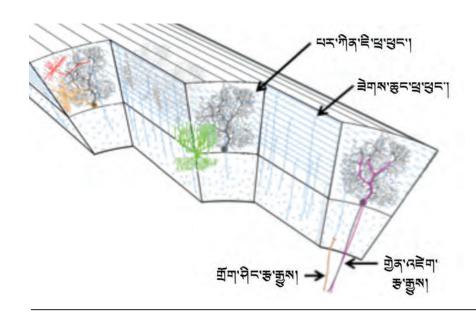


Figure 38 shows examples of the unique types of neurons in the cortex of the cerebellum and how they interconnect through the layers of the cerebellar cortex. Note the different structures of these neurons and consider how these structures might help you predict their functions. The very small granule cells make up nearly half of all neurons in the brain. Their long axons form a system of fibers in the outer layer. Purkinje cells' flat tree-like structures are particularly striking, as is their arrangement in the cerebellar cortex—they are all lined up in parallel to each other and are the only neurons that supply neural output from the cerebellar cortex, while the mossy and climbing fibers carry input.

Box 10. IN DEPTH: CEREBELLAR DEFICITS

What happens when there are problems with the cerebellum? Many different symptoms can occur, some of which are described below. What do these symptoms tell you about the normal function of the cerebellum?

Decomposition of movement

Patients with cerebellar defects can't perform smooth movements; they break movement down into separate parts. Leaning down to pick up the sad boy in the woods requires your hips, arms, shoulders, elbows and hands to work together. Patients with cerebellar damage first move the hips, then the shoulders, elbows, etc., rather than move all in one smooth motion.

Intention tremor

When performing that movement with a purpose, say to pick up the boy, cerebellar patients often reach out, but then their hands start to shake and move back and forth as they get closer to the target.

Dysdiadochokinesia

Patients have difficulty performing rapidly alternating movements, such as hitting a surface rapidly and repeatedly with the palm and back of the hand

Deficits in motor learning

When you lean over to pick up the boy, you shift your head position in relation to the rest of your body. Cerebellar patients often have trouble sensing this shift and adjusting their body movements appropriately, resulting in loss of balance or inability to carry out the task. Not only are they unable to perform previously long-practiced actions fluently, but they also have difficulty learning new ones.

Based on the phenotypes of the cerebellar disorders described in Box 10, it is clear that the cerebellum synthesizes information from cortex,

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न्याचीश्वारक्षराचने बराक्षराक्षेत्राकष्ठेते

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proprioceptors, and other parts of the nervous system to allow fine muscle coordination and maintain posture and balance. As with the basal ganglia, the cerebellum also seems to help in learning and decision-making (although with different types of learning in different types of situations than the basal ganglia), deciding which action to take and bases much of this decision on comparing the current situation to past experiences of similar situations. It is in this latter step of comparision that a special process called feedforward regulation occurs. Indeed, feedforward principles are particularly prominent in how the cerebellum works.

Almost all the biological systems we've discussed to this point involve feedback regulation. Here, as you recall, information from the process in question and its environment feeds back to fine-tune and adjust the process as it occurs. In feedforward control, information that leads to a resultant action is set (based on matching with past environmental cues) and does not change once it's activated (see box 9). Such feedforward processes also must be flexible, but instead of changing as they happen like in feedback regulation, what changes in feedforward regulation is the pre-settings. The settings are readjusted based on trial and error. This shifting of feedforward settings can be viewed as a disadvantage. On the other hand, feedforward-regulated processes do not have to continually readjust during the action, as they do in feedback-regulated processes.

Let's look at a couple of examples of action that probably involve a combination of feedforward and feedback regulation in the cerebellum. When you are walking through the woods and lean over to talk to the crying boy, as your head moves down toward the boy, your eye must move in a way that allows you to keep looking at the boy. The cerebellum permits the movement of the eyes to just counterbalance the movement of your head to happen by using information it receives from both vestibular organs in your head, and other sensors interpreting the environment of the woods and boy. If the cerebellum made an error, you would lose your view of the boy for a second. This error information would be fed back to the cerebellum, so that the next time this situation occurred, the feedforward control would work in a fashion so that your eye would move just right in relation to your head, and you would not lose sight of the boy.

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Box 11. IN DEPTH: BALANCE ACTIVITY

Sensory systems and movements are integrated. How is balance maintained when our sensory systems are needed for performing different kinds of tasks?

- Have a friend stand on one leg with the head tilted slightly upward.
- Now have him or her look at a strip of paper with words on it as you move the paper smoothly from right to left or left to right as they try to read it. What happens?
- How does the subject's balance change if the head is not tilted or if your friend stands on two feet? Why?
- Repeat this activity with your friend standing on some foam or other very soft, giving surface.

Sensory deficits can be evaluated using balance control tasks like these. Sensory signalling shows another important biological principle, which is redundancy, or the ability of differing structures or processes to perform similar functions under certain conditions even though they may usually do different things. We discussed a prominent example of redundancy in *LSP I*, the genetic code, where several different nucleotide sequences on the DNA code for the same amino acid. Such redundancy is important for robustness and flexibility of complex systems, such as the nervous system. The redundancy in sensory signals means that deficits in one sensory system can be compensated for by another. For example, individuals with vestibular loss can compensate with visual information. However, if proprioceptive information is impaired by standing on foam and visual information is removed by closing the eyes, a person with vestibular loss can no longer maintain postural orientation.

Similarly, all the muscles required for you to then pick up the boy must be coordinated in time and space. The muscles that must contract and those that stop the contraction need to be coordinated so that they contract and relax at precisely the right time and in the right location. This gets even more complicated when you realize two things: this coordination changes as you get older and heavier and must be adjusted depending on the weight of the boy (or whatever you are picking up). The cerebellum may already have a preset regulation plan for a motor action that has been learned and stored from past experience of leaning over and picking up something like the boy. It recognizes the situation in the woods as you lean over to pick up the boy, based on information from all the internal and external receptors matched to previous experience. Then it feeds forward that stored regulated action and allows you to smoothly pick up the boy and maintain your balance the whole time.

Perhaps you can begin to see that voluntary, directed movement is highly dynamic and multisensory. Even seemingly simple actions involve an evaluation of the emotional, physical and environmental context of each

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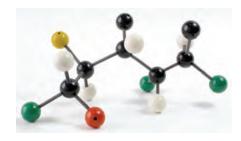
specific situation, integration of many inputs, and matching them with past experiences and learning. All of this is carried out in various areas of your brain, and results in finely executed motion and behaviors.

LESSONS LEARNED

Our mission to understand a walk in the woods in neuroscientific terms has taken us through many details and layers of complexity, from the physics and chemistry of how neurons work, through how they communicate, to how their combined action gathers and processes information, and produces and regulates movement and behavior. Along the way, we also have encountered big ideas, including insights about organic design—how living beings develop, survive, and evolve. Let's step back a moment to reflect on some of those insights. What fundamental principles have you discovered along the way? If none come to mind, go back through the text and see what you find. A few are mentioned below, but you can discover more yourself.

Few elements, great diversity: The nervous system follows a principle in the evolution of life forms that was discussed in earlier *LS* and *NS primers*: variations on a limited number of basic elements can be combined to create a wide array of forms and a related diversity of functions. Thus, neurons rely on a few elements—ions, receptors, neurotransmitters—for their activity and functions, but the diversity in these few elements allows for the enormous variety of form and function that allows us to see, think, and act. Imagine that the different colored balls in Figure 39 are different types of neurons: even in this simple example, you can see how many different arrangements can be made, with corresponding differences in activity.

Selection: You already have learned about the evolutionary power of selection working through interactions of organisms and their environments. Selection results in differential transmission of genetic information through reproduction. It therefore acts as a mechanism for sifting existing biological diversity by keeping what works better under real-world conditions. Selection is a powerful factor within organisms as well. Such functional selection is vividly exemplified by the immune system, as is discussed in *LSP IV*. The nervous system also must solve problems of functional selection, gathering the information and directing our attention to what is important at that moment and backgrounding what is not. Thus, in our imagined walk in the woods, you immediately noticed the crying child and not the flower by the path. This lesson about neurons has included several mechanisms for



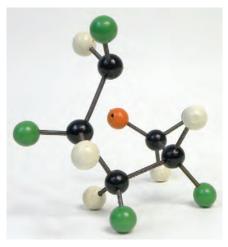


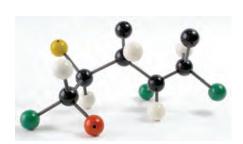
Figure 39

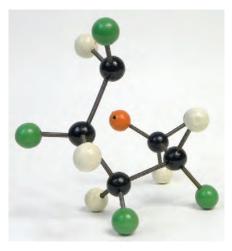


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selection, such as summation, thresholds, and receptive fields. Keep this principle in mind, as we will see the power of functional selection in later primers as well.

Transduction: How can we know something about the world and respond appropriately to it? A key is to convert external signals into biological signals, or transduction. In NSP I you learned that organisms have evolved elaborate methods for transduction, and in this lesson you learned how they do it. Figure 40 summarizes the transduction process from light waves entering the eye to perception of a face in the brain. In the nervous system, sensory cells turn physical stimuli (light waves, pressure) into electrical signals (action potentials). Then, these neurons convert electrical signals to chemical signals that communicate with other neurons by releasing neurotransmitters, at the nerve terminal. The receiving neuron converts chemical signals back to electrical signals through shifts in its membrane potential.

These basic physical processes allow us to sense and respond, to see a crying child and rush to it.

Regulation: Survival of living organisms requires continual work to maintain the conditions necessary for staying alive. Your body must regulate temperature, water balance, and nutrients, and motivate behaviors such as putting on a sweater, drinking water, or getting food. Living systems therefore must build in layers of regulation such as feedback and feedforward interactions. Paying attention to these regulatory pathways can reveal important clues to how a system works—what it is designed to do—and what may cause it to have problems or break down. This lesson covers two important forms of regulation, feedback and feedforward. What do the

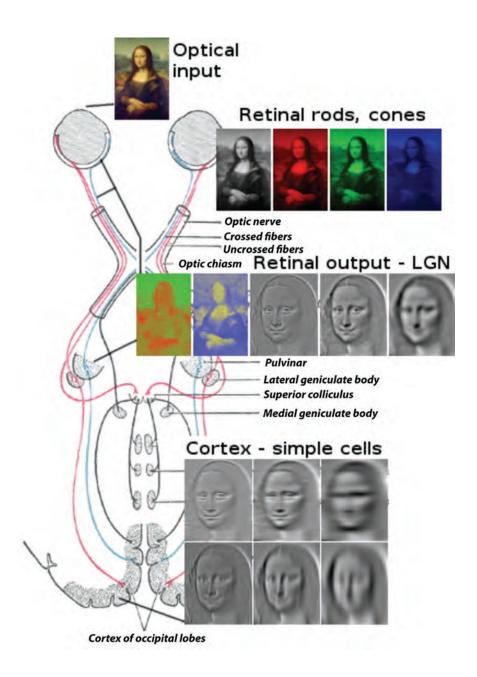
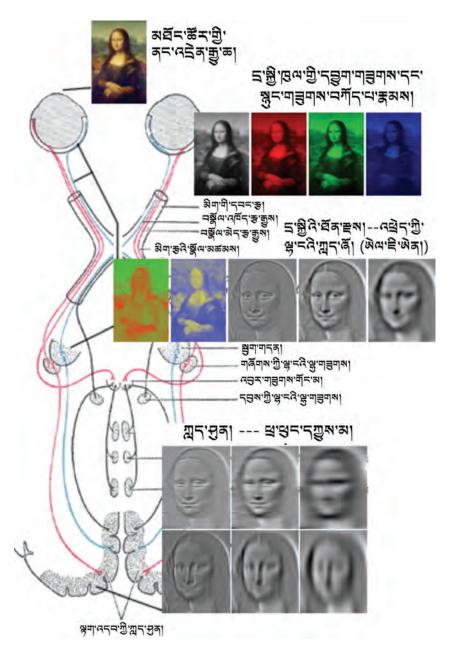


Figure 40: From outside to inside: steps in visual processing.



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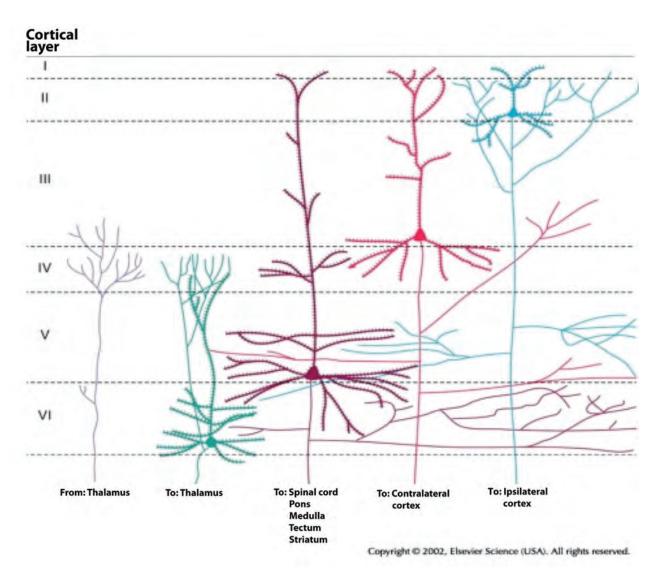
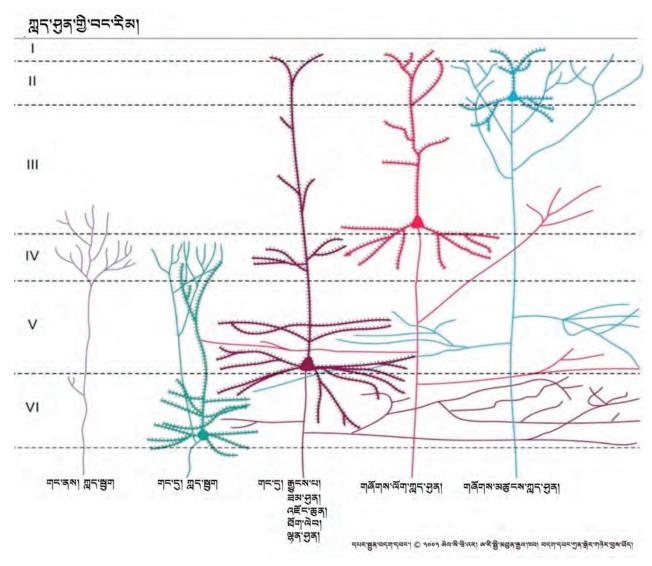


Figure 41: Cell types in the cerebral cortex.

differences in the two forms of feedback tell us about the kinds of survival problems that regulation aims to solve? How does feedback regulation help? What might be the advantages of feedforward regulation?

Form and function: Neurons are the basic units of the nervous system. But the differences in structure among types of neurons determines their function to a large degree. Figure 41 shows different types of neurons in the brain's surface layers, or cortex. More subtly, the fine structure of an individual neuron—the number and placement of synapses from other neurons, and the number and placement of its connections with receiving neurons—also determines its function. We have seen that neuronal plasticity in connectivity with other cells, particularly among neurons, is a distinctive feature of the nervous system. We will learn more about the importance of neuronal plasticity in *NSP III*.



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क्र्यत्यूष्टःश्च्र्यन्त्राचीश्चरायद्वराटःक्ष्यान्त्रान्त्राचीश्चराय्वयः स्वान्त्राचीश्चराय्वयः स्वान्त्राचीः स्वान्त्राच्याचीः स्वान्त्राचीः स्वान्तः स्वान्त्राचीः स्वान्तः स्वान्त

FULL CIRCLE

So much about what it means to be human is implicit, embedded in our capacity to be aware, perceive, learn, feel and move. These basic capacities are essential for us to be able to perform more complex functions, such as acts of compassion. In this text we have explored one of the biological substrates that allow us to have these capacities—our nervous systems—from the actions of single neurons to the coordinated communication of the whole brain, from ions to movement and complex behavior.



Do we need to know all this biology to truly experience the richness of our lives? Certainly not. But understanding our biology, our brains, and our thinking gives us both more hope of helping those who have deficits in their neural abilities, as well as a deeper appreciation of what it means to be human.

In the next primer we will build on the lessons we learned here. In particular, the focus will be on emotions, with an attempt to characterize what emotions are and how they are manifested in the brain and body. With this discussion we will look more closely at the systems at work when you found the lost child, for such a situation both prompted an emotional response from you and involved reading the emotions of the child. As we will see, the two processes – feeling emotions and understanding the emotions of others - are integrally related. Consistent with previous lessons, understanding the basic systems involved in emotion and emotion understanding will to a large extent involve an understanding of what happens when these systems go awry, in this case, in afflictions of emotion such as depression, anxiety, and addiction. Your understanding of neurotransmitters will be crucial for this discussion.

In later lessons we will return to the basic processes involved in action potentials and in neuronal synchrony, as we will begin to think about how the brain regulates arousal. We will ask how the brain is functionally and structurally connected on a large scale in ways that allow the entire brain to work in concert, and we will again visit the microscopic level of neurotransmitters to understand sleep, stress, and pain. Again and again we will return to the basic mechanisms learned here that fundamentally govern the thoughts, emotions, and behaviors that make us human.



র্মুন'নদ্ব'শ্টী'মদ্ভৃদ'র্শ্বর'মা

चित्राल्ल्र्ड्ट्रा देड्राट्क्कुद्रट्यट्ड्राल्याचे लेवा चित्राल्ल्र्ड्र्ड्राच्कुद्रट्यट्ड्राल्याचे लेवा चित्राल्ल्र्ड्र्ड्राय्ड्र्ड्र्याचे च्याचे त्याचे त्य

बीक्षा होत्या के स्वत्य स्वत्य

<u>੨ਫ਼ੵਫ਼੶ਜ਼ੑ੨੶ਖ਼ਫ਼੶ਫ਼ੵ੨੶ਫ਼ੵ੶ਫ਼੶ਖ਼ਜ਼ੑੑ</u>

Acetylcholine के से ते व्यक्ति के ते व्यक्ति के ते के

Action potential propagation অশন্ত্ৰাৰ্শন্ত্ৰাৰ্

Action potential

Aldosterone hormone

All-or-none principle

Alpha motor neuron

অব্যাহর্ণ কুল হাল কুল বিশ্ব ক্রিল ক্রাল ক্রাল কুল বিশ্ব ক্রাল ক্রাল

Aluminum (Al) সূত্র্মন্

Auditory cortex

Ampulla/ampullae নুমনী নুমনী নুমনী নুমনী নুমনী নুমনী বুমনী বুমনী

Axon hillock Terminal नहः भ्रेल वर्त स्टूर ने यह्ना भ्रे

Axon hillock नहः क्षेत्राव्युरः ह्रह्म Axon नहः क्षेत्राः हः बद्दा Basal ganglia व्युरः व्युका

Beryllium (Be) ने दे ते प्याया

Biochemical states ষ্ক্রী শ্বর হ্ মার্ক্সী নার্ম ননা

Biological molecules श्ले भुः स्वाप्तु अः हुण

Biological organism वर्के विस्पार्थे सुभु प्रस्थि। Biological substrate सुभाष्यभाग्री हेद्रापादी

Boron (B) ক্র'ব্যব্দার্থী Broca's area র্মার্কার্থা Carbon (C) দুম্'র্মুরা

Caudate nucleus धुन् रुर्गे (सूर्वरम् इत्रूम् क्रेक्ष्मे)

Cell इस्

Central finger neuron क्षेत्रवेत्रसह्नाङेवेत्रन्वराङ्ग सामानुगान्। सामानुगान्

गर्नेन्यश्रासंदे न्यर इ.स.च बियाश्रामर वियास है य है , न्या देवा या ।

Central neuron क्षेत्रविष्ट्रचराज्ञ अण्या अण्या क्षेत्रविष्ट्रचराज्ञ अण्या (द्वराज्ञ क्षेत्रविष्ठा विष्ट्रचराज्ञ अण्या क्षेत्रविष्ट्रचराज्ञ क्षेत्रविष्ट्रचराज्ञ अण्या क्षेत्रविष्ट्रचराज्ञ क्षेत्रविष्ट्रचराज्ञ क्षेत्रविष्ट्रचराज्ञ क्षेत्रविष्ट्रचराज्ञ क्षेत्रविष्ट्रचराज्ञ क्षेत्रविष्ट्रचराज्ञ क्षेत्रविष्ट्रचराज्ञ क्षेत्रचराज्ञ क्षेत्रविष्ट्रचरचराज्ञ क्षेत्रविष्ट्रचराज्ञ क्षेत्रविष्ट्रचराज्ञ क्षेत्रविष्ट्रचराज्ञ क्षेत्रविष्ट्रचराज्ञ क्षेत्रविष्ट्रचराज्ञ क्षेत्रविष्ट्रचरचराज्ञ क्षेत्रविष्ट्रचराज्ञ क्षेत्रविष्ट्रचरचराज्ञ क्षेत्रविष्ट्रचरचराज्ञ क्षेत्रविष्ट्रचरचरचरचरचरचरचरचरचन्त्रचरचरचरचया विष्ट्रचरचरचरचरचरचरच्या विष्यविष्य विष्यविष्यविष्

নাৰ্নাশা)

Central pattern generators क्षेत्रवेष्वर्शिक्षः देशः क्षेत्रवेष्वर्शिकः विद्यालया विषय विद्यालया विद्यालय

रेयःश्चॅरःग्रेन्।

Cerebellar cortex ন্নন্ধুন্য্রন্ত্র্ Cerebellum ন্নন্ধুন্

Charge [5x.5]

<u>੨ਫ਼ੵਫ਼੶ਜ਼ੑ੨੶ਖ਼ਫ਼੶ਫ਼ੵ੨੶ਫ਼ੵ੶ਫ਼੶ਖ਼ਜ਼ੑੑ</u>

Chemical stimuli हरा श्वें र र र वित की भूषा के ता हरा विकास की ता कि का कि का विकास की ता कि का विकास की ता कि का विकास की ता कि का विका

Chemical transmission इसप्यूरप्रीक्षार्मित

Chloride क्.ब्रुट्स्क्रेश्-ईत्य

Chlorine (CI)

Climbing fibers শ্রীর্নেইল্,স্বা Cochlea শ্রীর্ন্সান্দ্রন্ন্ Concentration gradients শ্রম্ভ্রেন্স্রন্

Conductor पदेव कथा (र्म्मे पायी पदेव कथा)

Contralateral cortex पर्विग्रशःर्भेगःग्रुन्:भुन्। Cortex of occipital lobes क्ष्णःयन्तरःग्रीःग्रुन्:भुन्।

Cortex শ্লন্থনা

Cortex—simple cells ग्रान्श्वा --- इ:सुर:न्युरु:बा Cortisol विराहित ग्रीका (क्षेत्राह्म अ:सी क्षेत्राह्म अ:सी क्षेत्र हो क्षेत्र क्षेत्र सी क्षेत्र हो क्

Crossed fibers নর্মুন্ম নর্মির প্রধ্ন ন্মির ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রান্থ ক্রিন ক্রান্থ ক্রিন ক্রান্থ ক্রান্থ

Degradation क्तुः पशुन् (भूरुषः पहें तः गुःनदेः ने गुषः भेग)

Dendrite न्हासेन् इस्

Depolarization श्रे'वर्स । श्

Direct pathway प्रतामिक्स प्रमाने प्र

Directed movements ५ इंश्रेग्रायह्न्य्रायः र्भेट्र

Dorsal root ganglion ক্লুবাস্তব্য

Dorsal spinocerebellar tract क्रुट्यान् ख्रुट्यान् ख्रुट्यान्य क्रुट्यान् ख्रुट्या

Effector protein 됐어. 형수 활목째 Electrical charge 표한 명시 Electrical current 표한 명시

Electrodes र्क्षणः श्रे। Electron र्क्षणः स्था

Environmental cues विन्यस्थित

Epinephrine अभे तेन देत्र (त्यर ह यहेत् परे देव्य अभेग)

र्के्यायार्श्यः स्ट्रिन्।

Equilibrium potential জ'মঙ্ম'র্ম'শ্

Exchange pump नहें श्रु र प्यु र किश नहें श्रु र प्यु र किश नहें श्रु र प्यु र र प्यु

Feedback control

<u>ॸॖॖॖऀ॓॓क़ॱॸॕॸॱॺक़ॱॾॗॸॱॻॖऀॱॿॱॹॢॸॱॺਞॕॸऻ</u>

Flexion and extension movements টুন্পুমণ্ট্র ব্ব্ৰাপ্ত্রিন্

(flex or extend)

Flourine (F) ধ্রন্থ ইবা Force ধ্রন্থ Frontal lobe মন্ত্র্বের্

GABA श्रुश्च (५न८ इ.प.चे.व. ५न० १५)

Gap junction ন্ম:স্টেশ্ব্

Golgi apparatus র্থি শ্বান্থ্য রূপ্য Golgi tendon organs র্মিশেস্ট্রান্থ্য রূপ্য

G-protein coupled receptor है क्वे ह्र भारतास बुद क्वें दरहत की क्वे प्रोत पा

Granule cell àेग्रथः अञ्चासुरा Gray matter ह्रथः भ्रु| Hair bundle नःशुक्षेः क्रुवः व्या Hair cell नःशुक्षेः अञ्चासुरा

Hamstring muscle শ্বী বৃদ্ধিশ প্ৰাপ্ত শ্বী মা

Helium (He) ने जे जे ज्या प्याप्त Huntington's disease नृज् ते न् ज्या प्याप्त Hydrogen (H) प्यास्त्र

Hyperpolarization क्ष्म् प्रस्था क्ष्म् प्रस्था प्राप्त क्ष्म् प्रस्था स्थाप स्थाप

Inhibition বর্নীবা-ই্রা Inhibitory বর্নীবা-ই্রা

Inhibitory interneuron वर्गेन्यान्वेश उद्या । वर्गेन्यान्वेश उपया । वर्गेन्यान्वेश उद्या । वर्गेन्यान्वेश उपया । वर्गेन्यान्वेश उद्या । वर्गेन्यान्वेश उपया । वर्गेन्यान्वेश उपय । वर्गेन्यान्वेश उपया । वर्गेन्यान्वेश वर्ये । वर्येन्यान्वेश वर्येन्यान्यान्वेश वर्येष वर्ये । वर्येष वर्येष

Inhibitory response दर्भेन्यास्थ्य प्रमान

Interneuron नरः न्यात्र अप्तरः इत्या महामार्थाः Intracellular messenger इत्या स्थार्थः स्यार्थः स्थार्थः स्थार्यः स्थार्यः स्थार्यः स्थार्यः स्थार्यः स्थार्यः स्थार्यः स्थार्थः स्थार्यः स्यार्यः स्थार्यः स्थार्यः स्थार्यः स्थार्यः स्थार्यः स्थार्यः स्थाः स्थार्यः स्थार्यः स्थार्यः स्थार्यः स्थार्यः स्थार्यः स्थार्यः

Ion pumpग्रीशाह्तवायतुन्द्वाग्रीशाह्तवायतुन्द्वाग्रीशाह्तवायतुन्द्वाIonically charged particlesग्रीशाह्तवायतुन्द्वाग्रीशाह्तवायतुन्द्वा

स्रस्राज्य स्थानी स्रीत्रा

Ionotropic receptorग्रीश हुँ या प्रश्नेत प्रांते श्रुं 'यो तृ पाIpsilateral cortexपार्ति पाश्रा सही प्रांति श्रुं पा प्रांति प्रा

Intracellular space

Lateral geniculate body पविंगुरा कुरिये सुपा बुगाया

Lipid bilayer (cell membrane) ইম্বেশ্বরিক্রিক্রির্ (প্রস্তের্ম্নির্মা)

Lithium (Li) নি স্থিত

Lower motor neuron देनाने त्स्त्य क्षेत्र प्राप्त स्वाप्त स्व

Magnesium (Mg) স্থান শ্ৰমণ

Mechanical stimuli व्युव्यःभुवाशःस्ट मबीद छी सुव्यः क्रेत्रा

Medulla দুইন:দ্ভবা Meissner's corpuscles ই:মী:ব্রম্মা Membrane potential শ্লী:মাই:বুঝ্মা

Membrane श्रुं श्रें

Merkel's receptors अर्प्से के त्रिक्ष

Microtubule भुगः अर्ग

Midbrain section সম্স্লেন্ট্রংমম্প্রাপ্রাম্পর্মান্

Midbrain न्यः यून्

Millivolt शे.बे.क्व्यत् क्व.क्ट्र.क्व.क्व.क्व.

Mineralocorticoid receptor (MR) अःवेः र विं विं र हैं विं के हैं श्वें के वा (बेर न सूर्य ख्रें खेर खर से र् वे प्रें के वा प्रें के वा प्रकार के र वे प्रें के वा प्रकार के र वे प्रें के वा प्रकार के प्रें के वा प्रकार के प्र

Mitochondrion वुश् क्षेत्र झ हु श्र Mossy fibers वेंग्भिन्द कुश

Motoneuron द्र्यायः र्र्भेन् 'न्ननः स्ट अ'या हुण्या

Muscle भृज्ञाहरू

Muscle fiber subunits প्रावि प्रावि प्रावि

Muscle fibers প্ৰাৰ্থ স্থান্

Muscle Fiber membrane व्यव्हर है न्सू र छे हैं।

Muscle spindle वृत्रवृत्रदाया

Musculoskeletal system १ न्यूबर् न्द्र-सुन्य स्थ्ये अधि स्थित स्थत स्थित स्थि

Neon (Ne) वे द्धूरा

Nerve divides into many branches र्नर्ज्ञ्च स्थापन स्यापन स्थापन स्यापन स्थापन स्थापन

Nervous system স্মন্ত্র্

Neurons ব্নহ:স্ক:প্রান্থ্য

Neuropeptides ५७८ इतः क्षेत्रे की (५७८ इतः क्षेत्र प्रते देग्य भीग)

Neurotoxins ५न= इते है श रून

Neurotransmission ५नर इते पदीव पहिंद गुना ५नर इते पदीव पहिंद गुना

Neurotransmitter molecule ५न८ इ.५ व्होब स्वरं क्ष्य स्वरं व्हार स

Neurotransmitter ५नः इते प्रश्चेत्रम्

<u>੨ਫ਼ੵਫ਼੶ਜ਼ੑ੶ਖ਼ਫ਼ਫ਼ਸ਼੶ਫ਼ੵ੶ਫ਼੶ਖ਼ੑ੨੶ਖ਼ਫ਼ੑੑ੶</u>

Nicotine receptor के 'गें (है कर के प्या

Nitrogen (N) क्ये. तृं हेत् (क्रूर्या ज्ञुनाया)

Norepinephrine र्द्भ स्थित क्षेत्र क्

Nucleolus 35-31

Nucleus accumbens য়ৢ৾ৼ৾ঀ৻৻য়ৢঢ়৻ঀঀয়৻য়৻৻য়ৢঢ়৻য়ঀয়৻ঀঀ৻ঀ

Nucleus ঈ্ন'্র্ন্ Occipital lobe দ্ব্না'ন্ন্ন্ Optic nerve ঈন্'ন্ন্

Optical input अर्बेन् रहेन रहेन सुः ह्य

Organ与本語Organism親子系列

Otoliths (utricle and saccule) क्रिंदु। (क्रिक्य के निर्देश्वर क्रिंप)
Oxygen (O) वर्के क्रिंप व्यक्ति क्रिंप व्यक्ति क्रिंप

Phosphorus (P)

Pacinian corpuscles

Parietal lobe

Parkinson's disease

Polarization

Polyribosomes

মন্দ্রীর্শ্নর্শ্র্মা

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মন্দ্রীর্শ্নর্শ্র্মা

Pons इसः भुत्

Postcentral gyrus ५ च्रैल सुला हे सामी चे चुन्

Post-synaptic neuron अञ्जू (अळ्थका हे का प्रत्ये के प्

Potassium त्वार्भेवाद्यार्स्

Premotor area व्युवःर्भुदःश्वानश्चि

Primary motor cortex व्युवार्श्केन्ध्राचेन्ध्रा

Proprioception वनसन्तुर-भेसः र्हेर् वनसन्तुर-भेसः रहेर्न

Proprioceptors नन्यायमुनः श्रुं त्येत् या

Prosthesis ক্রন্ডমা Protein receptor খ্রী হ্ম খ্রী থৌর বা Pulvinar খ্রনা নাম্বা Purkinje cell ব্যামীর ই শ্রাপ্তমা

Putamen यून्:इशःकें:न्:या (यून्:बनशःइ:दन्शःग्री:कःपृश्यंपेन्)

Pyramidal cell गाँहें र ग् त्वा श्रास्ता Quadriceps muscle (नङ्का भी) श्रे न् वे भागवा

Receiving neuron (বহু'বহীর')৭রীর'ব্বহ'স্ক'র্বার্ক্স্থা

Receptive field श्रें 'यो ब 'राज श्रे

Receptor क्षेप्रेच स्वा Red nucleus क्षेप्रेच स्वा

Reflex movements र्ष्ट्रेन्य्तुत्यः इस्यादशुन्यः र्ष्ट्रेन्यान्त्रीयः र्स्ट्रेन्

Reflex

<u>੨ਫ਼ੵਫ਼੶ਜ਼ੑ੨੶ਖ਼ਫ਼੶ਫ਼ੑ੨੶ਫ਼ੵ੶ਫ਼੶ਖ਼ਫ਼ੑ੨</u>

Refractory period ব্ৰান্ত্ৰন্'ন্ৰ্ৰান্তিদামা

Relay neuron नकु<u>र</u> गहेँद द्वर इस म्बुग्रा

Relay nuclei নক্রুদ্রবের্নপ্লে র্ট্রন্য

Repolarization ब्रे.ध्र.चब्रेंच्रत्वला ब्रे.ध्र.चब्रेंच्रत्वल.घे.च

Response बुःसेदःत्रुशःश Resting potential 5'सर्रे। Reticular nucleus

इंश्लेदे र्झेद र्झ्या—वर्झेद ग्री खूर्दि ग्लार हिं। (अवरहे अंदा) Retinal output—LGN ५:श्चे:वियःक्चे:नव्युनायात्वन्यःनरःश्वरःगत्वन्यःनर्गेन्।सःहस्या Retinal rods, cones

নষ্ণুস:ঐরা Reuptake

र्वेन मन्त्री मार्चेन प्रम्थेन स्थित स्थित स्थित स्थित स्था Reward processing and learning

क्षेट्र अट्ट्र प्रवट या बुवाया Ribosomes यानेरवर:इ.क्ट्रियाश:इतःश्री

Rough Endoplasmic Reticulum

(Rough ER)

र् से दे सह्या है। Ruffini endings रु से दी से खेतरा Ruffini receptor প্য:ইা S: Sulfur(S)

Saccule इ.भेज.क्ट.या ব্স্থ্রব্রম্যবার্ট্টশ্রমা Second messenger Semicircular canals वेरः स्ट्रेंनः सः श

*द्*यर:र्क्टें:र्न्यर:ह:झ:वाबुवाशा Sensory neuron शे:र्रे:हें हेत श्रे:बेत:या Serotonin receptors

शे में हिं देव न सम् लेव से वा पदेव ना Serotonin reuptake transporter

शे. र्रे. हें देवा (५ न म् उसे व्येव मिन से निया) Serotonin

নহ'ব্য্বীরা Signal থ-নি-প্র Silicon (Si)

Skeletal muscle रुषायग्रहाराभागवरा

ग्रानेर:दर:इ:क्वेंग्रश:वह्रस:र्ये। Smooth Endoplasmic Reticulum

(Smooth ER)

Sodium (Na) র্অ:₹ঝা

র্বঅ.ছ×া.মু.ফু.লমা Sodium channels Soma (cell body) র্মু'রেখা (র'র্ম'রেখা) Somatosensation থ্ৰুমার্ক্টহান্ত্রুনা

सुर्यार्कें राष्ट्रे त्ये ता सुर्यार्कें रार्कें रार्चे दा Somatosensor

ন্তুৰ্ ক্ৰিন্সুন্-পূব্য Somatosensory cortex લુશ્ર ર્સેં મસ્ટ્રે વ્યેત યા Somatosensory receptor

(ग्लून्प्रते स्ट्रेन्प्री) १ वर्षे अध्यव्यवस्त्र द्वारा के द्वारा स्वारा के स्वर्धा स्वराप्त के स्वर्ध स्वर्य स्वर्ध स्वर्य स्वर्ध स्वर्ध स्वर्ध स्वर्ध स्वर्ध स्वर्ध स्वर्ध स्वर्ध स्वर्य स्वर्ध स्वर्य स्वर्ध स्वर्ध स्वर्य स्वर्य स्वर्य स्वर्य स्वर्य स्वर Somatotopic representation

यर सून परे श्रेर न पर्वेन परे नन कें र सकें व हम

क्रीटश्रासी (तस्रुट्रायीलयोशः ईश्रासी) Spinal cord (cross section)

Spinal cord ক্রুদ্রুম্যা

Spindle neuron सर.श.र्यर.श्र.सं.याञ्चयाश

<u>੨ਫ਼ੵਫ਼੶ਜ਼ੑ੨੶ਖ਼ਖ਼ਫ਼ੵਸ਼੶ਫ਼ੵ੶ਸ਼ਖ਼ੑੑੑ੶ਖ਼</u>

Stellate cell শ্লম্মান্ত্রন্থাপ্রত্য

Striatum झुनःशुना Substantia nigra यूनःर्वे न्रमार्थे।

Subthalamic nucleus ধ্রুণা ৰ্নম শূর্ম বা ক্রাম বা ক্রাম

Superior colliculus বর্ম'বার্বাঝ'র্বাম'র্মা

Supplementary motor areas व्यायः र्क्केट्रान्सः वरेनाशः स्वाहाया Synapse रनरः क्षेत्रः सहरासस्या

Synaptic cleft (synaptic gap) सञ्जद्भरा ची सञ्जद्भर ची सञ्जद्भर ची सञ्जद्भरा ची सञ्जद्भर ची सञ्जद्भरा ची सञ्जद्भरा ची सञ्जद्भर ची स्वाप ची सञ्जद्भर ची सञ्जद्भर ची सञ्जद्भर ची सञ्जद्भर ची स्वाप चित्र ची सञ्जद्भर ची स्वाप ची सञ्जद्भर ची स्वाप ची सञ्जद्भर ची स्वाप ची स्वाप ची सञ्जद्भर ची स्वा

Synaptic vesicle अनुन्यळंबर्थाञ्चनः

Tectum ইন্'ঐন্ Temporal lobe ক্'ব্ন্' Tetrodotoxin ন্'ক্'ক্'জ্'্ন্

Thermal stimuli कं र्हेन् रह निवेद ग्री सुन्य के वा Threshold potential वेद्यायह्यस्था नुस्या Transduction नह सुन्य नह सुन्य नह सुन्य नह

Transmission चक्कर पहिल्ला के प्रश्निम के प्रश्निम प्रिम प्रश्निम प्रश्निम प्रश्निम प्रश्निम प्रश्निम प्रस्निम प्रस्निम प्रस्म प्रस्निम प्रस्निम प्रस्निम प्रस्निम प्रस्निम प्रस्निम प

Tripolar neuron খ্রু'লাগ্রুম'ব্নন'স্ক'র'বারুল্মা

Tubular ducts containing endolymph বৃদ্যবৃদ্ধ কুমৌন্সাৰুদ্যবিষ্ণু স্থাত বৃদ্ধি বৃদ্ধি

Two-point discrimination activity শ্বীশান্ত্রী ব্যাধান

Upper motor neuron ब्रेट्सी प्रमुख क्रिंद्र क

Utricle इ.म्ब.क्.च

Vesicle
Vestibular canals

মূল্ম মূ

Vestibular organ धुनाभून नगरास्त्री Vestibular sensors धुनाभून नगरास्त्री

Vestibule-ocular reflex अँग'न्न' श्रुवा'ख्व, सः यग श्रुवा 'यती व्यापिता'

Voltage detector र्स्याः हेन्।

Voltage र्षेत्रळंत्

Voltage-gated channels र्स्ताहेन र्झी पठन क्वाहिता Wernicke's area स्माहिता