
SYLLABI-BOOK MAPPING TABLE

Advanced Biopsychology

Syllabi

Mapping in Book

Unit-I Biological Foundations of Behaviour

Meaning of biological psychology, biological psychology and other disciplines of neuroscience, branches of biological psychology of viewpoints to explore biology of behaviour, research methods in biological psychology.

Unit 1: Biological Foundations of Behaviour
(Pages: 3-17)

Unit-II Evolution, Genetics and Experience

Biology of Behaviour: Problems and models of the biology of the behaviour.

Human Evolution: Evolution and behaviour, course of human evolution, evolution of human brain, evolutionary psychology.

Fundamental Genetics: Mendelian genetics, chromosomes, reproduction and linkage, sex chromosomes and sex-linked traits, genetic code and gene expression, human genome project, the genetics of human psychological differences.

Genetic Engineering: Gene knockout techniques, gene replacement techniques.

Unit 2: Evolution, Genetics and Experience
(Pages: 19-43)

Unit-III

Functional Neuroanatomy: Divisions of the nervous system, cells of the nervous system.

Neuroanatomical Techniques: Golgi stain, Nissl stain, electron microscopy, neuroanatomical tracing techniques.

Major Divisions of the Brain: Functional descriptions of brain structures, blood supply to the brain, newer imaging techniques, cell specialization.

Neurophysiology: Electrical signals, transmission processes, circuits, gross electrical activity, chemical bases of behaviour, neurotransmitters, hormones and the brain, ways by which hormones act, endocrine glands and their hormones, impact of hormones on behaviour.

Unit 3: Functional Neuroanatomy
(Pages: 45-104)

Unit IV

The Sensory Motor System: Three principles of sensory motor association cortex, secondary motor cortex, primary motor cortex, cerebellum and basal ganglia, descending motor pathways, sensory-motor spinal circuits, central sensory motor programs.

Motor Control and Plasticity: The behavioural view, the control systems view, the neuroscience view, movement control, extra-pyramidal systems, disruption of movement, tracing a choice response.

Unit 4: Sensory Motor System
(Pages: 105-146)

Unit V: Regulation and Behaviour

Sexual Behaviour: Stages of reproductive behaviour, regulation of reproductive behaviour, role of pheromones, diversity of human sexual behaviour.

The Two Sexes: Fetal hormones and the development of reproductive organs, beneficial mutations of sexual reproduction, reproductive strategies of male and females, basic types of mating systems, sexual selection.

Sexual Differentiation: Determination of sex, sex differences, defining gender, role of gonadal hormones, social influences on sexual differentiation.

Hormones and Sex: Neuro-endocrine system, glands, hormones, gonads, sex steroids, hormones of the pituitary glands, female gonadal hormone levels are cyclic, male gonadal hormone levels are steady, neural control of the pituitary gland, control of the anterior and posterior pituitary by the hypothalamus, discovery of hypothalamic releasing hormones, regulation of hormone levels.

Neural Mechanism of Sexual Behaviour: Structural differences between the male hypothalamus and female hypothalamus, hypothalamus and male sexual behaviour, hypothalamus and female sexual behaviour, hormonal control of maternal behaviour, neural control of maternal behaviour, neural control of paternal behaviour.

Unit 5: Regulation and Behaviour
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INTRODUCTION

Advanced biopsychology is a sophisticated course which is based on the biological aspects of behaviour. It covers the most important features of neurophysiology and neuroanatomy, from a functional perspective. This book emphasizes on the anatomy of the human nervous system. It analyses and discusses the physiological basis of behaviours by an examination of contemporary researches in areas like reproduction, aggression, ingestion, learning and memory, motivation and mental disorders.

Advanced biopsychology is a dynamic and absorbing introduction to brain and its influence on behaviour. Considering that the reader has limited knowledge about biology or psychology, this book will update him about the developments and studies in this dynamic and modern branch of science. Its contemporary appearance and user-friendly text offers information which is academically valuable. The information that is presented pertains to all major areas of the discipline in a simple way that is easy to understand. Supported by data which is related to human beings and various species of animals, this book conveniently leads the reader through some details of important concepts and cutting edge research in biopsychology.

The book presents a simple demonstration of important topics that engage students by imparting knowledge of even complicated topics and processes, in a clear way. It presents a wide viewpoint which governs well-structured explanations of behaviour, history of evolution, progress, adjoining procedures and applications.

Each unit begins with an Introduction to the main topic, followed by an outline of Unit Objectives. Each topic is then explained in detail, in a easy to understand manner. The units comprise of 'Check Your Progress' questions to test the understanding of the reader. Each unit has a Summary, a glossary of Key Terms, Answers to 'Check Your Progress' and Questions and Exercises. At the end of each unit, Further Reading lists the names of other books which the students can use for research on the topics covered.

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UNIT 1 BIOLOGICAL FOUNDATIONS OF BEHAVIOUR

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Structure

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1.0 INTRODUCTION

The biological foundations of behaviour are controlled by the brain, which is a network of versatile, complex and flexible systems. The nervous system is divided into the central nervous system and peripheral nervous system. The central nervous system coordinates the activities of all parts of the body. It comprises of the brain and the spinal cord. The peripheral nervous system connects the central nervous system to the limbs and other parts of the body. It comprises of the somatic nervous system and the autonomous nervous system. The somatic nervous system controls various movements of the body through skeletal muscles and also associates the body with the external environment. The autonomous nervous system controls functions related to the viscera.

1.1 UNIT OBJECTIVES

After going through this unit, you will be able to:

- Understand the meaning of biological psychology
- Relate biological psychology with other disciplines of neuroscience
- Explain the viewpoints of biological psychologists
- List and describe various research methods in biological psychology

1.2 BIOLOGICAL PSYCHOLOGY

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Biological psychology is a branch of science, which pertains to behavioral, cognitive, and clinical neuroscience.

1.2.1 Meaning

The word biological psychology makes one think that it is the study of psychology from a biological perspective. In other words, it can be stated as the scientific study of biological mechanisms underlying the observable aspects of behaviour and covert behaviour (i.e., the non-observable aspects of behaviour such as learning, memory, thinking, motivation, perception and emotion). It is also popularly known as psychobiology, behavioral biology or behavioural neuroscience. Biological psychologists use their psychological knowledge and behavioural research methods to gain deeper understanding of the biological aspects related to psychological concepts.

Biological psychology tries to study biological the basis of behaviour by attempting to describe behaviour, study its evolution and observe its development and biological characteristics, over its span of life. It focuses on the biological mechanisms that are fundamental to behaviour and studies the applications of biological psychology. Although the discipline has a long history, but it is extremely difficult to give any date so as to specify its origin. However, D.O. Hebb's work has certainly played a key role in the emergence of this field. He was the first one to develop a comprehensive theory of complex psychological phenomena, such as perceptions, emotions, thoughts and memories. He held that these phenomena might be produced by the activities of the brain. He postulated that psychological functioning has its roots in the physiological and biochemical functioning of the brain. His method was largely based on clinical case studies, on experiments involving both humans and laboratory animals and on his insightful observations. Even today, these methods are frequently followed by biological psychologists.

1.2.2 Relation with Other Disciplines of Neuroscience

Biological psychology is closely related to neuroscience and its various disciplines. It is an integrative discipline which draws its knowledge from the following disciplines:

- (i) Biology
- (ii) Psychology
- (iii) Neurology
- (iv) Physiological psychology
- (v) Psychopharmacology
- (vi) Neuropsychology
- (vii) Psychophysiology

- (viii) Cognitive neuroscience
- (ix) Comparative psychology

All these disciplines have a lot in common and they tend to overlap each other. We study some of them in detail as follows:

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- (i) Physiological psychology:** It studies the neural basis of behaviour by directly manipulating the brain. It does so by surgically and electrically manipulating the brain (almost always) of laboratory animals, because of ethical reasons in controlled experiments. It also focuses on developing theories of the neural control of behaviour. Such kind of research is largely theoretical in nature and it lays little emphasis on immediate practical benefits.
- (ii) Psychopharmacology:** In contrast to physiological psychology, psychopharmacology is largely concerned with conducting researches that have practical implications. The practical implications may range from development of therapeutic drugs to reduction of drug abuse. Sometimes, they also make use of drugs to study the basic principles of the brain's behaviour and interaction. Keeping ethical considerations in mind, psychopharmacologists study the effects of drugs on laboratory animals and human beings.
- (iii) Neuropsychology:** It is the study of psychological effects of brain damage in human patients. It conducts its research by studying human beings who have damaged their brains in accidents, during surgeries, or due to some diseases. In the brain, they focus more on the study of the cerebral hemisphere (primarily the cerebral cortex), as this area of the brain is most likely to be damaged by an accident or surgery. This discipline is also concerned with conducting neuropsychological assessment of these individuals. It facilitates diagnosis, helps in devising an effective line of treatment, helps in counseling the patient and his family members and also helps in the rehabilitation of the individual.
- (iv) Psychophysiology:** It is the division of biopsychology that studies the relation between various psychological processes that individuals engage in and the corresponding physiological activity. It largely conducts its research on human beings, mostly by the use of using noninvasive recording procedures. In psychophysiology, the physiological activity is recorded from the surface of the body. The most commonly used recording procedure is EEG (Electroencephalography), which studies the electrical activity of the brain by using electrodes attached to the scalp of a person. Some of the other recording procedures are muscle tension, eye movement and several indicators of autonomic nervous system activities such as, heart rate, blood pressure, pupil dilation, etc. It also uses electrical conductance of the nervous system that regulates the body's inner environment. The research in this field is largely concerned with gaining an in-depth understanding of the physiology of psychological processes, such as attention, emotion, perception, thinking, decision-making and processing of information.

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(v) **Cognitive neuroscience:** It is the youngest, the most active and exciting division of biopsychology. The term cognition refers to higher mental processes such as thought, memory, attention and complex perceptual processes. On the other hand, the term neuroscience refers to neural bases. Thus, the field of cognitive neuroscience is largely concerned with the study of the neurological bases of cognition. This field is based on the following two assumptions:

- a. Simple cognitive processes combine together to form complex cognitive processes.
- b. The simple processes are mediated by neural activity in various parts of the brain.

Cognitive neuroscientists try to find the parts of the brain that mediate various cognitive processes. Cognitive neuroscientists largely conduct their researches on human beings by using noninvasive methods rather than direct manipulation of the brain. The most frequently used noninvasive recording method by them is functional brain imaging, which refers to recording images of the living human brain, when it is involved in some activity. Often cognitive neuroscientists ask individuals to engage in various cognitive tasks such as memorizing a list of words, solving a set of given problems, etc. They record the activity of their brains while the individuals are performing these cognitive tasks. The field of cognitive neuroscience is quite interesting and yet complex, hence research in this area often involves an interdisciplinary collaboration between individuals with different types of training. For instance, individuals with training in the fields of biopsychology, cognitive psychology, computing and mathematics and various types of neuroscientists commonly work together while conducting a research in the area of cognitive neuroscience. Sometimes, the boundaries between cognitive neuroscience, psychophysiology and neuropsychology, get blurred. Research is conducted on individuals with brain pathology by the use of noninvasive electrophysiological recording methods.

(vi) **Comparative psychology:** It is concerned with the study of the biology of behaviour, rather than focusing only on the neural mechanisms of behaviour. Comparative psychologists compare the behaviour of different species in order to gain deeper insights into the processes of evolution, genetics and adaptability of behaviour. They are largely concerned with the study of behaviour, from an evolutionary perspective.

It engages in experimental investigation of animal behaviour in both, controlled laboratory environment and their natural environment. Advancements in the field of genetics of behaviour and other psychological processes have also contributed significantly to the field of comparative psychology.

All these disciplines focus on different aspects of behaviour of the brain. These are quite complex in nature and have their respective strengths and weaknesses. Thus, in order to gain maximum understanding about a specific problem or an issue, these various disciplines work together in collaboration.

1.2.3 Viewpoints of Biological Psychologists

Biological psychologists largely adopt three viewpoints to explore the biology of behaviour, namely *somatic intervention*, *behavioural intervention* and *correlation*. Somatic intervention tries to study the relationship between brain and its behaviour. It does this by altering a structure or function of the brain or body, to see its effects on behaviour. For example, a biological psychologist may stimulate a part of the brain of an individual and see how the individual eventually reacts. Somatic interventions involve electrical stimulation of a part of the brain by administering a hormone, cutting the connection between two parts of the nervous system, etc.

In contrast to somatic intervention, in behavioural intervention, the biological psychologist manipulates the behaviour of the organism and studies its effects in the bodily structure or function. Behavioural intervention may involve exposing a person or an animal to a visual or an auditory stimulus and observing the resultant changes in the electrical activity and blood flow in certain parts of the brain, etc.

However, correlation tries to study the degree to which a given bodily measure varies with a given behavioural measure. This approach tries to investigate whether people with larger brains are more intelligent than those with smaller brains. It also tries to study the relationship between the severity of schizophrenia and structural changes in the brain. The correlation approach gives us no information about the cause and effect of relationship between the variables that it attempts to study. The variables can have a linear or a curvilinear relationship and they can be directly or inversely correlated to each other.

Biological psychologists deal with various levels of biological analysis, in order to find explanations that inspire behaviour. They try to divide the brain into successive less complex and simpler units like nerve cells, etc. This process is termed as *reductionism*. The method of reductionism tries to gain an understanding of a complex whole by breaking it into its simpler molecular and atomic components.

CHECK YOUR PROGRESS

1. Define biological psychology.
2. What is biological psychology popularly known as?
3. What is comparative psychology?

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1.3 RESEARCH METHODS IN BIOLOGICAL PSYCHOLOGY

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The objectives of biological psychologist are directed at studying various biological processes that give rise to psychological phenomena. Biological psychologists conduct their research using various methods; for example, they conduct research either on human or non-human subjects, they conduct formal experiments or non-experimental studies and their research may be either pure or applied in nature.

The research is conducted on human beings in order to understand the functioning of the brain in a better way. This research also regulates the behaviour of the brain. When conducting research on human beings, biological psychologists largely use non-invasive methods. This is done due to ethical reasons. At times, the subjective experiences of human beings can also provide information which can be quite insightful at times.

Research is also conducted on animals in order to understand the evolutionary process better. Such researches help one see how the brain has undergone several changes in its size and development, across various species over the years. Another advantage of conducting researches on animals is that, the differences in the brain of humans and other species are more quantitative than qualitative. Thus, the generalization of the information obtained from the study of animals and human beings is easy and meaningful.

Another advantage of research on non-human subjects over humans is that their brain and behaviour are relatively simpler. This makes it more likely to reveal the fundamental behaviour and interactions of the brain. The information obtained from the comparative study of humans and non-humans can be quite revealing and informative. This makes it possible to conduct even those researches which cannot be conducted on human beings because of ethical reasons.

As mentioned earlier, biological scientists make use of both experimental methods and non-experimental studies, such as quasi-experimental studies and case studies. Experimental studies are usually conducted to understand the cause and effect of relationships. This method involves arranging two or more conditions under which a subject will be tested. Two most commonly used experimental designs are between subject designs (involves testing different groups of subjects under each condition) and within subject designs (involves testing the same group of subjects under each condition).

The different conditions are referred to as *independent variables*. These are manipulated and the effect of these conditions on a specific behaviour (known as dependent variable) is measured. This method involves controlling all extraneous factors, as far as possible to ensure that the changes in the dependent variable are purely the result of the manipulations of independent variable. Often, it is quite difficult to eliminate all extraneous or confounding variables.

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In practice, it is not possible to use experimental methods to study all problems that are of interest to biological psychologists. This is due to ethical and practical reasons. In such cases, they make use of 'quasi-experimental studies'. These studies are conducted on individuals who have been naturally exposed to the conditions of interest, in the real world. Though these methods provide a large amount of valuable information, but their major drawback is that in these studies the potential confounding variables cannot be fully controlled.

Biological psychologists conduct both pure and applied researches. Pure researches are conducted primarily with the purpose of acquiring knowledge without laying much emphasis on the practical application of the results so obtained. On the other hand, applied researches focus primarily on utility and practical applicability and are intended to bring about some immediate direct benefit to mankind. Biological psychologists who conduct pure researches believe that the better one understands the basic principles, the more readily can they be applied. It is not necessary for a research to be completely pure or applied in nature. In fact, a research project can have both elements of pure and applied research.

In addition, biological psychologists try to study unobserved working of the brain by the use of scientific inferences. Scientific inferences are based on careful measurement of key events that can be observed (such as observable behaviour and neural activity of the brain). They come up with logical inferences about the nature of the events, that cannot be observed (such as the nature of the neural processes that regulate behaviour), based on these measures.

Biological psychologists also make use of psycho-physiological recording methods (like scalp electroencephalography, muscle tension, eye movement, skin conductance and cardiovascular activity) to record physiological activity from the surface of the human body.

Scalp electroencephalography, commonly known as EEG is used to measure electrical activity of the brain. This is done through large disc-shaped electrodes which are taped to the scalp, by using a device known as electroencephalograph (EEG machine). The EEG signal gives information about action potentials, postsynaptic potentials and electrical signals from the skin, muscles, blood and eyes. EEG is used both as a research and also as a diagnostic tool, as EEG wave forms are associated with particular pathologies (such as epilepsy) and states of consciousness (for example, alpha waves are associated with relaxed wakefulness). EEG activity is often recorded simultaneously from many sites because EEG signals decrease in amplitude, as they spread from their origin. Therefore, a comparison of signals which are recorded from various sites on the scalp can give information about the origin of particular waves.

Biological psychologists are more concerned in studying event related potentials (ERPS), which give information about EEG waves that are associated with specific psychological events. When a sensory stimulus is momentarily presented, it brings about a change in the cortical EEG signal. This change is

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known as *sensory evoked potential*. The cortical EEG consists of both the signal (the response to the stimulus) and the noise (ongoing background EEG activity). The noise is often so loud that it tends to mask the signal, hence the method of signal averaging is used to reduce the noise of the background EEG

The method of signal averaging is also used in PET (Positron Emission Tomography) and fMRI (functional Magnetic Resonance Imaging), to significantly reduce the noise which is produced by irrelevant events. These irrelevant events may be, looking at a fly on the screen, thinking about something else when engaging in a specific cognitive task assigned to them, etc. It involves averaging the different images obtained by asking the subjects to repeat the same test several times. This would increase the signal-to-noise ratio. Although this method is very useful, but it has one serious problem associated with it. This problem is that if two subjects have specific but different patterns of cortical activity, then the averaged image will give us little information about specific parts of the brain, which are involved in the cognitive process under study.

Electromyography is used to measure muscle tension by placing two electrodes taped to the surface of the skin, over the muscle of interest. Electromyography represents an increase in the muscle contraction by an increase in the amplitude of the raw EMG signal. This reflects the number of muscle fibers that contract together. It is seen that anxious individuals display high resting levels of tension in their muscle.

Electrooculography is the process of recording eye movements by placing electrodes around the eye. It measures horizontal movements by placing electrodes on each side of the eye and measures vertical movements by placing electrodes above and below the eye.

Electrodermal activity is used to measure the background level of skin conductance. This in turn, is associated with a particular situation (skin conductance level) and transient changes which are associated with discrete experiences (skin conductance response). The ability of the skin to conduct electricity increases with emotions, thoughts and experiences.

Heart rate, arterial blood pressure and local blood volume are commonly used by biological psychologists to measure cardiovascular activity. An electrocardiograph records electrical signals which are associated with each heartbeat. This is done by placing electrodes on the chest of a human being. A sphygmomanometer is used to measure blood pressure. Various psychological events can result during changes in the volume of blood in particular parts of the body. Plethysmography is the process of measuring changes in the volume of the blood, for example by wrapping a strain gauge.

Stereotaxic surgery involves using a stereotaxic atlas to locate various brain structures and the stereotaxic instruments. These instruments consist of the head holder to hold the brain firmly in a specific position and orientation and an electrode holder. The electrode holder holds the device to be inserted. The electrode holder

can be moved in three dimensions: anterior-posterior, dorsal-ventral and lateral-medial.

The lesion method involves removing, damaging and destroying some part of the brain and studying its effects on the behaviour. The objective of this is to determine the functions of the lesion structure. The four common types of lesions are:

- (i) Aspiration lesions: involve removal of the cortical tissue by suction through a finely tipped hand-held glass pipette.
- (ii) Radio-frequency lesions: involve passing a high-frequency current through the target tissue, by using a stereotaxically positioned electrode.
- (iii) Knife cuts: involve cutting a section of the brain.
- (iv) Cryogenic blockade: involves pumping a coolant, till the tips of the neurons are cooled to a point at which they stop firing. This is done by using an implanted cryoprobe.

The lesions can be unilateral (involving only one half of the brain) or bilateral (involving both sides of the brain) in nature.

Electrical stimulation is used to study the functions of various parts of the brain by stimulating them electrically. This is done by using bipolar electrodes. This method has often been used by biological psychologists to study the effects of such stimulations on eating, drinking, attacking, copulating and sleeping. The behavioural response thus produced depends on the location of the tip of the electrode, the parameters of the current and the test environment in which the stimulation is administered.

Intracellular unit recording gives a momentary record of graded fluctuations in a neuron's membrane. Extra cellular unit recording involves recording the action potentials of a neuron. This is done by placing a microelectrode with its tip positioned in the extra cellular fluid next to it. It provides information about the firing of the neuron but provides no information about the neuron's membrane potential. The action potential of several neurons is measured through multiple-unit recording. It is done by using electrodes with larger tips. These electrodes are fed into an integrating circuit that adds them together into a graph that depicts the total number of recorded action potentials, per unit of time. Invasive EEG recording is a process that involves the recording of EEG signals through large implanted electrodes, rather than through scalp electrodes. Cortical EEG signals are frequently recorded through stainless steel skull screws, whereas sub cortical EEG signals are recorded through wire electrodes that are implanted stereotaxically.

The biological basis of behaviour can also be studied by administering drugs that either increase, or decrease the effects of particular neurotransmitters. These drugs can be fed to the subject or can be injected through a tube into the stomach. They can also be injected hypodermically into the peritoneal cavity of the abdomen, into a large muscle, or the fatty tissue beneath the skin, or into a large surface vein. To ensure that the drugs pass through the blood-brain barrier, a cannula is used to

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administer them in small amounts. This cannula is stereotaxically implanted in the brain. Precise lesions can be made by injecting neurotoxins such as kainic acid or ibotenic acid, by using microinjection. This microinjection destroys specific neurons, leaving other neurons undamaged.

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The chemical activity of the brain can be measured using 2-deoxyglucose technique and cerebral dialysis. The 2-deoxyglucose technique involves injecting an animal with radioactive 2-DG, which is readily absorbed by neurons but is not metabolized by it. After the animal engages in an activity, it is killed and its brain is removed and sliced. The slices are coated with a photographic emulsion, stored in the dark for a few days and then developed like a film. The black spots on the slides represent those areas of the brain that absorbed high levels of the radioactive 2-DG. Cerebral dialysis is the activity of measuring the extracellular concentration of specific neurochemicals in an animal that engages in different behaviours. This is done by implanting a fine tube with a short semipermeable section in a specific part of the brain, so that the extracellular chemicals from that part will diffuse into the tube. These neurochemicals are then frozen, stored and later analysed.

Immunocytochemistry and in situ hybridization are used to locate particular neurotransmitters in the brain. Immunocytochemistry is a procedure for locating particular neuroproteins in the brain. They are located by labelling their antibodies with a dye or a radioactive element and then exposing slices of the brain tissue to the labeled antibodies. The locations of the target neuroprotein are indicated by accumulation of the dye or radioactivity in the brain slices. Since all enzymes are proteins, only those neurons that release a particular neurotransmitter are likely to contain all the enzymes that are needed for its synthesis. By binding to the enzymes that are needed to produce a neurotransmitter, this method is used to locate neurotransmitters. This is done by exposing brain slices to labeled antibodies that bind to enzymes. These enzymes are located in only those neurons that contain the neurotransmitter of interest.

In situ hybridization is a process that involves binding of hybrid RNA strands that have been labelled with a dye or a radioactive element, to the complementary mRNA strands. They mark the location of neurons that release the target neuroprotein. By locating such neurons, information about the location of a particular neurotransmitter can be obtained.

Neuropsychological testing serves several purposes like helping the diagnosis, providing a base for counseling and evaluating the effectiveness of the treatment and its side effects, etc. Initially, single specific tests were devised to detect the presence of brain damage. However, this single test approach was less useful as it is nearly impossible to devise any single test that is sensitive to all the varied and complex psychological symptoms. These systems could potentially occur in any patient whose brain is damaged. As a result, the use of standardize batteries for tests began. This standardized test battery approach proved marginally successful as they were able to distinguish between patients having neurological problems

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and healthy patients, but were not able to discriminate well between patients who were suffering from neurological and psychiatric problems. As further improvization, customized-test-battery approach is now widely used. This not only identifies patients with brain damage, but also categorizes the nature of psychological deficits of each brain-damaged patient. This approach requires administering a common battery of test to identify neuropsychological symptoms. This is followed by a series of tests which are customized for each patient. These tests characterize the general symptoms which are revealed by the common battery, in more detail. The customized test-battery approach makes use of newer test that are specifically designed to measure aspects of psychological function, which are based on modern theories and data. This approach not only focuses on the results of the performance, but also takes into account the cognitive strategy which is adopted by the patients in solving the test. It also involves a more skillful choice and examination of the tests that are to be used with each patient.

Some of the tests that are commonly used as a part of the neuropsychological test battery are intelligence tests (such as Wechsler Adult Intelligence Scale). This intelligence test depends on knowledge of the patient's IQ, which can help in interpreting the results of other tests. The pattern of scores on all the subtests of the WAIS can help in drawing inferences about a patient's neuropsychological dysfunctions. For instance, low scores on the tests of verbal ability tend to be associated with left hemisphere damage, whereas low scores on tests of performance ability are associated with right hemisphere damage. Tests of memory functions help to identify whether impairment is of short-term memory, long-term memory, anterograde memory, retrograde memory, semantic memory, episodic memory, explicit memory or implicit memory. Tests of language-related deficits such as token test help in identifying whether there are problems of phonology, syntax or semantics. The tests of language lateralization, such as the sodium amytal test and the dichotic listening test are used to determine the hemisphere which is dominant for language. This test is helpful in interpreting the results of other tests. Frontal lobe functions can also be assessed by using tests such as the Wisconsin Card Sorting Test.

Paired-image subtraction technique is commonly used by cognitive neuroscientists to identify the parts of the brain that mediate various cognitive processes. This technique involves the use of both PET and fMRI images, during a pair of cognitive tasks. While the subjects are doing the task, their brain activity is recorded in the form of respective images which are obtained on PET or fMRI. The neuroscientist removes the activity from the images that they recorded during the two tasks. This is done to obtain a difference image, which illustrates the areas of the brain that were specifically obtained in the constituent cognitive process.

The open field test is used to study the common behaviour of species (behaviour that is displayed by nearly all members of a species, of the same age and sex). These activities of behaviour may be grooming, swimming, eating, fighting, drinking, nest-building and copulating. It involves placing subjects in large chambers

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to record their activities. The activity level (recorded by counting the number of times the subject crossed the line during the test) and the numbers of pieces of excrement by the subject are recorded as an indicator of fearfulness. For instance, low activity and greater number of excrements are associated with fearfulness.

The colony-intruder paradigm aims to study the patterns of aggressive and defensive behaviours that animals engage in, by observing and measuring a combative encounter between the dominant animal of an established colony and an intruder. For instance, the dominant rat is often seen to attack an intruder by pushing it away and biting it, whereas, the intruder rat exhibits defensive behaviours by pushing the attacker away and rolling on its back. Similarly, the elevated plus maze is used to study the effects of reduced anxiety in rats. This maze has four arms, two of which has sides and the other two do not have sides. Anxiety is measured by observing the amount of time spent by a rat in the protected closed arms as compared to the time spent by it on the open exposed arms.

Learning paradigms such as the Pavlovian conditioning paradigm, operant conditioning paradigm and self-stimulation paradigm, are often used by biological psychologists. This is because learning principals have been found to be effective in producing and controlling animal behaviour and are helpful in gaining information about the sensory, motor, motivational and cognitive state of an animal, from its ability to learn and perform various responses. The self-stimulation paradigm requires an animal to press a lever to deliver electrical stimulation to certain sites in his own brain. The parts of the brain that support self-stimulation are known as pleasure centers. In a semi-natural animal learning paradigm, animals are placed in situations that closely simulate the situations they may encounter in their natural environments. This paradigm believes that behaviours that help in survival process are more highly developed and tend to be directly related to innate neural mechanisms. It is seen that animals like rats tend to consume a new food in small doses. They may not consume it again if it made them fall ill; this behaviour helps in their survival process. This finding and other findings so obtained from the experiments on conditioned taste aversion have broadened the understanding of biological scientists. For instance, it is now believed that conditioning to certain stimuli can also take place in a single trial. This conditioning does not necessarily have to be a gradual step-by-step process. Further, temporal continuity is not necessary for conditioning to take place. Since rats can acquire an aversion to a food item even when they fall ill several hours after the consumption of that food item. Conditioning to certain stimuli can occur faster than conditioning to other stimuli. This suggests that we may be biologically primed for certain conditioning responses over others. Similarly, a radial arm maze consists of an array or more arms. These are used to study the spatial abilities of animals like rats. These abilities help them to learn about the locations where they are likely to find food and water. In short, biological psychologists make use of the various methods mentioned above to study the complex biological mechanisms underlying psychological processes. The reason for this is that no single method is efficient alone to provide

answer to all questions, which pertain to such complex phenomenon that biological psychologists try to study.

CHECK YOUR PROGRESS

4. How do comparative psychologists function?
5. List the basic viewpoints that are adopted by biological psychologist to explore the biology of behaviour.
6. What does behavioural intervention involve?

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1.4 SUMMARY

- Biological psychology is another term for behavioural neuroscience and psychobiology. It involves the learning of physiological processes and their influence on human behaviour.
- This concept believes that behaviour is inseparably linked to somatic or physiological experiences, which emerge as a result of the brain's interpretation of sensory impingement.
- Thus, biological psychology works on the assumption that the mind and body are independent and behaviour is caused by sensory perceptions which are based on physiology.
- Though human beings may serve as experimental subjects in biological psychology experiments, most of the experiments related to biological psychology are performed on animals such as rats, monkeys or mice.
- Biological psychology involves the analysis of the effects behaviour on the nervous system, by internal and external stimulation.

1.5 KEY TERMS

- **Biological psychology:** The application of the principles of biology (in particular neurobiology), to the study of mental processes and behaviour in human beings and animals
- **Psychopharmacology:** The study of drugs that affect the mind
- **Neuropsychology:** A branch of psychology that deals with the relationship between the nervous system, especially the brain and cerebral or mental functions such as language, memory and perception
- **Psychophysiology:** A branch of physiology dealing with the relationship between physiological processes and thoughts, emotions and behaviour
- **Electroencephalography:** The recording of electrical activity along the scalp, produced by the firing of neurons within the brain

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- **Stereotaxic surgery:** Brain surgery which is done through a small opening in the skull and is guided by X-rays or computer-aided imaging techniques
- **Cryoprobe:** An instrument used to apply extreme cold to a tissue as part of cryosurgery
- **Cerebral dialysis:** The activity of measuring the extracellular concentration of specific neurochemicals in an animal that engages in different behaviours
- **Immunocytochemistry:** A procedure for locating particular neuroproteins in the brain

1.6 ANSWERS TO 'CHECK YOUR PROGRESS'

1. Biological psychology is the scientific study of the biological mechanisms, underlying psychological overt (the observable aspects of behaviour) and covert behaviour (the nonobservable aspects of behaviour such as learning, memory, thinking, motivation, perception, and emotion).
2. It is also popularly known as psychobiology, behavioural biology or behavioural neuroscience.
3. Comparative psychology is concerned with the study of the biology of behaviour, rather than focusing only on the neural mechanisms of behaviour.
4. Comparative psychologists compare the behaviour of different species in order to gain deeper insights into the process of evolution, genetics and adaptability of behaviour. They are largely concerned with the study of behaviour from an evolutionary perspective. Comparative psychologists engage in both, experimental investigation of animal behaviour in controlled laboratory environment and in their natural environment.
5. Biological psychologists basically adopt three viewpoints to explore biology of behaviour, these are: somatic intervention, behavioural intervention and correlation.
6. Behavioural intervention involves manipulation of the behaviour of an organism and the analysis of its effects in the bodily structure or function. Behavioural intervention may involve interventions like exposing a person or an animal to a visual or an auditory stimulus and observing the resultant changes in the electrical activity and blood flow, in certain parts of the brain, etc.

1.7 QUESTIONS AND EXERCISES

Short-Answer Questions

1. Name a few other disciplines related to biological psychology.
2. What does physiological psychology mean?
3. How do biological psychologists conduct pure researches?

4. Why is the method of signal averaging used in PET and fMRI?
5. List the four common types of lesions.

Long-Answer Questions

1. Explain cognitive neuroscience.
2. Write a note on the various research methods in biological psychology.
3. Discuss the importance of the Wechsler Adult Intelligence Scale.

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1.8 FURTHER READING

Pinel, John. 2003. *Biopsychology*, Fifth edition. New Jersey: Allyn and Bacon.

UNIT 2 EVOLUTION, GENETICS AND EXPERIENCE

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Structure

- 2.0 Introduction
- 2.1 Unit Objectives
- 2.2 Biology of Behaviour
- 2.3 Human Evolution
- 2.4 Fundamental Genetics
- 2.5 Genetic Engineering
- 2.6 Summary
- 2.7 Key Terms
- 2.8 Answers to 'Check Your Progress'
- 2.9 Questions and Exercises
- 2.10 Further Reading

2.0 INTRODUCTION

Evolution is a collection of changes which are transmitted from the past generations to future generations of living beings. It is also a result of the natural processes in the environment, with the passage of time. Charles Darwin collated different types of factors that provided evidence in favour of the theory of evolution. This emerged after many years of thinking and personal researches. Evolution plays a vital role in helping us to understand the living world around us, from a modern perspective. Primarily, a sound foundation is important for the ecological understanding of the natural world. Every individual is unique. All living creatures around us, including ourselves, have a form that we perceive. Scientists have researched that these forms are a result of the activity of genes, as explained in detail in this unit. This unit also explains the fundamentals of genetics and the working methodology of genes.

2.1 UNIT OBJECTIVES

After going through this unit, you will be able to:

- Explain the biology of behaviour
- Discuss human evolution
- Give a detailed account of fundamental genetics
- Define and describe the concept of genetic engineering

2.2 BIOLOGY OF BEHAVIOUR

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The field of biological psychology is very complex and it has several inherent problems. The study of biology of behaviour not only has its specific problems but the methods or techniques used to study this phenomenon are also faced with several problems. Some of the problems in the field of biological psychology are listed below:

- (i) Pertaining to the choice of method, it is not known when to use the appropriate technique, how to use it and how to interpret the results which are obtained with it.
- (ii) The field is quite variable in nature. For instance, many children with no apparent damage to the brain have incapacitating learning disorders. Yet, there are other children with brain damage who are bright and intelligent and show little impairment in learning.
- (iii) The brains of different animals and individuals within a species show high anatomical similarities.
- (iv) Significant variation is seen in the size, topography and structure of brains of an individual.
- (v) Some functions do not seem to be fixed to rigid anatomical boundaries, e.g., in some people speech is localized in the right, rather than in the left hemisphere.
- (vi) There is lack of clarity in the relationship between brain mass and function.
- (vii) To further complicate the matter, it is seen that when some part of the brain is removed, the other parts take over the functions of the removed part.
- (viii) Even today, the functions of some parts of the brain are not well understood, for example, the function of a large brainstem nucleus, called the babenua, is unknown. Some people think that the hippocampus plays a role in olfaction, emotion or in internal inhibition. They believe that it influences long-term and short-term memory, configured associations or spatial navigation.
- (ix) There are some visible gaps in understanding the relation of biochemical organization with behaviour. For example, increase in nor-epinephrine cause mania, whereas decrease in nor-epinephrine cause depression. Also, decrease in the amount of dopamine is seen to be related to a motor disease known as Parkinson's disease. But, the symptoms of the disease do not appear until more than 97 per cent of the central concentrations of dopamine are depleted.
- (x) In order to understand the functioning of the brain, direct manipulation of biochemistry can be informative. But unfortunately, such studies cannot be done on human beings.

- (xi) Most individuals who are part of such studies are often on drugs which may modify both their brain function and their behaviour. This also confounds the results which are thus obtained.
- (xii) Brain lesion studies cannot be conducted on human beings due to ethical reasons. They are often conducted on animals and the results are generalized to understand the functioning of the human brain. Brain lesions can have three different effects on behaviour, namely, loss of function, release of function (i.e., a new behaviour appears or there is an increase in the frequency of a particular behaviour) and disorganization of function (i.e., bits or pieces of behaviour occur either in an incorrect order, or at the wrong time and place). The following problems are inherent in the interpretation of the effects of brain lesion:
- a. More than the extent of damage, it is sometimes the location of damage that causes severe impairment. For example, damage in the brainstem can have more devastating effects on behaviour in general, than a similar extent of damage in the neocortex.
 - b. Sometimes, the impairment caused by brain damage appears transient and gradually disappears as if it has been recovered.
 - c. The time of the injury also plays a critical role. For instance, a brain injury sustained in infancy has far less severe effects on behaviour, than a similar damage inflicted in adulthood.
 - d. Brain damage can have both direct and indirect effect on one's behaviour, for instance, in epilepsy, the cells in the region of lesion are not destroyed. However, they act in an abnormal way.
 - e. Sometimes, changes in the behaviour are not a direct result of the part of the brain that is damaged. They may result from disturbances in regions which are not directly affected by the lesion. For example, lesions in the neo-cortex cause the cells of the thalamus to get damaged. This is due to the axons of thalamic cells, which project the neo-cortex and get damaged by the cortical lesion.
 - f. In certain circumstances, brain lesions can have unexpected effects. For example, when brain injury takes place in very young children, then some parts of the brain take over the functions of the damaged part and starting performing the activities that they would ordinarily not perform.
 - g. Usually the same effects are seen on the behaviour, when lesion occurs naturally or are surgically induced. However, tumor patients frequently show different behavioural effects as tumors may produce pressure on widespread parts of the brain. These would result in symptoms that are not related to the region where the tumor actually resides.
 - h. The method of brain stimulation, much like the method of brain lesions, has its own share of problems. Brain stimulation is seen to evoke three general types of effects. It produces relatively discrete actions;

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or may produce an overall energizing effect on behaviour; or may elicit abnormal electrographic effects on the brain tissue. These could lead to convulsions or other behaviours. It is not always easy to find the type of effect which is related to a particular behaviour, nor are results always wisely interpreted. Stimulation is seen to evoke the above-mentioned effects in some patients. Nearly 50 per cent of the patients show that stimulation concomitantly produces an activity which is known as after discharge. There is also an absence of a clear relationship between the location of stimulation and the category of the experience. Also, the same stimulation often evokes different effects. Further, it is seen that only patients with certain types of personality appear to display this phenomena. This phenomenon often appears to be related to events of the moment and can be changed by altering the mood of the patient.

- i. Interpreting the electrical activity which is recorded from the brain has its own special problems. The major problem is differentiating the real electrical activity from the background noise. For example, the pattern of EEGs which are recorded from the neo-cortex is similar to the pattern which is obtained from a wide range of cortical areas. This is despite the fact that these different areas perform different functions.
- j. The activated state which is obtained in an EEG recording also looks very similar in different species of animals.
- k. The activated pattern can occur during sleep, when people or animals are under certain kinds of anesthetics and when they are in a state of coma.
- l. Similarly the slow wave EEG can be obtained by closing one's eyes or taking them out of focus.

The models that are widely followed to study the biology of behaviour are, the hypothetico-deductive method and the empirico-inductive method. The hypothetico-deductive method requires the biological psychologists to state a theory that is composed of a set of postulates. This set has all its terms defined operationally. It then draws logical deductions or predictions about behavioural outcomes and compares these predictions with the results of carefully controlled experiments. These comparisons confirm the theory.

In contrast to this method, the empirico-inductive method requires the biological psychologist to make careful observations and experience, without regarding systems and theories. Then they may draw meaningful generalization or regularities from the results of the observations. In practice, both the methods can be used together. For instance, the empirico-inductive method can be used to obtain new phenomena and new insights into behaviour. The hypothetico-deductive method can be used to test these new insights against the carefully controlled experiments.

However, both these methods tend to face certain problems regarding the method of gathering information, the number of subjects required to make observations, the behaviour to be studied and the problems which are associated with measurement of the behaviour.

- The most common error which associated with the gathering of information results from the bias that the researcher faces at times. He ends up by exclusively gathering information, which is in favour of a particular position. It is usually believed that larger the sample size, the more valid are the generalizations that can be drawn from it. When the differences between particular behaviour are larger, then fewer subjects are required. But the biggest question one faces here is the definition of a larger difference. At times, even interesting phenomena do not require the support of many subjects.
- Often neuropsychological research is conducted on a single subject. However, care should be taken while drawing generalizations, since the behaviour and brain structure of individuals varies enormously. It is also seen that even when there is no gross variation between the structures of two brains, two normal people can significantly vary on neuropsychological tests.
- Another debate is the subject of study for biological psychologists. Some believe that they should study only observable discrete behaviours, while others recommend the study of mental constructs like emotion, motivation, thought, memory, etc. It is usually believed that the more observable an event is, the lesser are the chances of making an error.
- To measure psychological phenomenon, several measures are available. These measures differ from one another to such a great extent, that almost any result can be obtained. Hence, it becomes important to choose a measure that is likely to reveal the most meaningful information.

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2.3 HUMAN EVOLUTION

The study of human evolution aims to focus on how human beings have evolved over the past several years. With reference to this, Charles Darwin's work on origin of species provided a large body of supporting evidence. This evidence suggested that new species evolve as a result of gradual orderly changes that occur in the pre-existing species. Charles Darwin was also the first person to suggest how evolution occurs, by documenting the evolution of fossil records through progressively more recent geological layers. He described several structural similarities among living species. These similarities suggested that they had evolved from common ancestors. He also pointed out that plants and animals undergo major changes through the process of selective breeding.

Darwin postulated that evolution occurs through the process of *natural selection*. This process is responsible for passing only specific heritable traits

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from one generation the other. These traits help in survival of the species and in the higher rates of their reproduction. This process of natural selection keeps on repeating generation after generation, thus leading to the evolution of species that is better adapted for survival and for reproducing its young ones in its particular environmental niche. He came up with the concept of 'survival of the fittest'. This concept stated that it is through the process of natural selection that nature automatically selects species that are better fitted for survival and reproduction. The theory of human evolution initially met with lot of resistance, but later it came to be seen as an empirical law which governed different disciplines of biology like genetics and biochemistry.

Evolution and behaviour

Different behaviours are seen to play a varying degree of role in the process of evolution. For instance, behaviours like the ability to find food, protect oneself from one's predators, etc., are seen to play a direct role in the process of evolution by ensuring that the genes will be passed onto the future generations. However, there are some other behaviours like social dominance and courtship display, which may not play a direct role but are important in the evolutionary process.

Social dominance

Social dominance refers to the presence of stable hierarchy of power, which is established through combative encounters between males of the same species. These males are seen to show their power by engaging in physical fights, threats and displaying aggressive posture towards other males of the same species. In these combative encounters, the male who wins against all the other males is regarded as the dominant male in that particular group. At the second level is the male who wins against all other males except the dominant one and so on. In this manner, a hierarchy of social dominance gets established. Once the hierarchy is established, the hostility seems to diminish as the males who are lower in the hierarchy learn to avoid or submit to the dominant males.

Social dominance seems to play an important role in the evolutionary process as the dominant males tend to copulate more than the non-dominant males. This increases the probability that their genes will be passed on to the future generations. In some species, the dominant females are more likely to produce more and more healthy offsprings, which are more likely to survive and reach the stage of sexual maturity.

Courtship display

In several species, copulation is seen to be preceded by an intricate series of courtship displays. Males show their interest in the female by sending olfactory, visual, auditory or tactual signals to her. The female may send certain signals back to the male. This process of sending signals back and forth continues for a while between the male and the female, until copulation occurs. But if one partner fails to react appropriately to the signals that are sent by the other partner, then copulation does not take place.

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Courtship displays can promote the evolution of new species by bringing the male of a specific species to send courtship signals to a female of the same species. This may have been separated by a reproduction barrier, which may either be geographic or behavioural in nature. By this we mean that the two may be living in different parts of the world. The male bird of the same species may fly down to an island where the female bird of the same species may have been living with other members its group, for several years. The two may send courtship signals to each other and might eventually copulate, which can give rise to a new species. The reproductive barrier can be behavioural in nature. The members of the same species that have been living in different parts of the world, may develop different courtship displays, over a period of time. This difference in courtship display may act as a barrier in the reproduction between them.

Course of human evolution

While we look at the course of human evolution, a few points should always be kept in mind, for instance, evolution does not take place in a linear fashion and may not always proceed slowly and gradually. Sudden changes in the environment can trigger rapid evolutionary changes in at least a few generations, by bringing about adaptive mutations in the genes of the organism. Although human beings seem to be most recently evolved and the last species left of the hominids, but it is still not clear whether their evolution was sudden or gradual in nature. Environmental changes, in terms of sudden cooling of the earth that took place over the last few years, may have accelerated human evolution. This process of evolution is continuous in nature and several species have evolved from it and several have become extinct too. Only a few of these species are still alive. The evolutionary process is never always perfect. This means that the changes which take place are not always the most effective to deal with the new demands of the time. Also, behaviour or structures that were once adaptive, might become non-adaptive or even maladaptive to new changes in the environment. They may also end up performing some other functions, than the ones for which they initially appeared. All structures that seem similar may not always have the common evolutionary origin.

The study of fossil records and their comparisons with the current species has suggested that the human species is a result of the evolution process, which has occurred in our pre-existing species. It is believed that about 600 million years ago, complex multicellular organism appeared and dwelled in water. From them, about 150 million years later, the first chordates evolved. These chordates had a dorsal nerve cord that ran along the center of the back or dorsum. About 25 million years later, the dorsal nerve cord was seen to be protected by the spinal bone in these chordates. These chordates were named as vertebrates, which were the primitive bony fishes. At present seven classes of vertebrates are seen to exist, namely, three classes of fishes, amphibians, reptiles, birds and mammals.

Nearly about 410 million years ago, it is believed that the first bony fishes came out of the water. Of those, the ones that were able to survive were able to escape the drying pools and gain access to terrestrial food. Through the process

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of natural selection, over the years, the fins and gills got transformed into legs and lungs respectively. This resulted in arrival of the first amphibians about 400 million years ago. Amphibians in their young form tend to grow in water and as adults, can grow on land.

As a result of the process of evolution, about 300 million years ago from amphibians, reptiles such as, lizards, snakes and turtles evolved. These were the first beings to lay eggs and were covered by dry scales. Before hatching, reptiles lived in a watery environment, but after hatching could live comfortably on land far from water.

Some reptiles evolved to give rise to dinosaurs, about 180 million years ago. The female dinosaurs developed mammary glands. Secretions from these glands fed their babies and hence a new species evolved. This species was termed as mammals. In a watery environment, these mammals would grow their young ones within their body, before they gave birth to them.

At present, about 14 different orders of mammals exist. Human beings were seen to develop from primates. In fact there are five families of primates, namely, prosimians, new-world monkeys, old-world monkeys, apes and hominids. It is believed that apes (gibbons, orangutans, gorillas, and chimpanzees) evolved from old-world monkeys and looked much like them. They had long arms, grasping hind feet and opposable thumbs, but unlike them, they did not have tails and could walk upright, at least for short distances. Of these apes, chimpanzees are believed to be the closest to human beings.

The study of fossil and genetic evidence suggests that around 6 million years ago, after apes, australopithecines evolved. The australopithecines existed for nearly 5 million years before becoming extinct. They resembled humans in having an upright posture, but unlike human beings they had a small brain and were about 4 feet tall.

Later, homo sapiens evolved from australopithecines, nearly 2 million years ago. Homo sapiens had large brains and used fire and tools. They seemed to coexist with australopithecines for nearly half a million years in Africa, but later they were believed to move into Europe and Asia, about 1.7 million years ago. About 40,000 years ago, carvings and wall paintings appeared. Farming and writing were established about 10,000 years and 3,500 years ago respectively. These inventions seemed to result from the developments that took place in the human brain. Initially, it was believed that the greater the brain size the better is the intellectual functioning. However, problems related to this assumption soon surfaced. One was that, human beings were regarded as the most intelligent creatures on earth, but their brain size was found to be much less than that of whales and elephants. It was later realized that there is no clear relationship between brain size and intelligence as larger animals tend to have larger brains, simply because bodies require more brain tissue to control and regulate them. As a result, brain weight expressed as a percentage of total body weight was thought to be a better indicator of one's intellectual capacity. However, this approach also did not lead to much success.

Eventually, researchers began to study the evolution of brain and the evolution of different regions of the brain, across different species. In this regard, the study of the evolution of the brain stem and the cerebrum or the cerebral hemispheres, separately turned out to be more informative in nature. Brain stem is responsible for the regulation of reflex activities (such as heart rate, respiration, blood glucose level, etc.) that are critical for one's survival. The cerebrum is involved in more complex adaptive processes such as learning, perception and motivation.

When the sizes of the brain stems and cerebrums of several species are compared, it becomes evident that the human brain has certainly increased in size and there has been an increase in the number of convolutions or folds on the cerebral cortex. Further, the maximum increase in the size has occurred in the cerebrum. In addition to these differences, certain remarkable similarities were seen among the brains of several related species. For instance, the brains of related species (such as humans, monkeys, rats, and mice) were made of neurons and were composed of similar neural structures, which were connected in the same way.

Evolutionary psychology

The process of evolution appeared so interesting and magnetic in its nature that it drew a couple of psychologists. These psychologists keenly studied several factors that led to evolution, in order to gain a better understanding of human behaviour. This eventually led to the emergence of a field termed as evolutionary psychology. The evolutionary psychologists have focused on studying some interesting and controversial issues like mate bonding.

In most species it is seen that both males and the females tend to indiscriminately copulate with many different partners during each mating period (known as promiscuous mating). However, in some species such as mammals, it is seen that males and females form enduring mating relationships with members of the other sex (known as mating bonds). When seen from an evolutionary point of view, such bonds are seen as a result of the fact that in mammals the female gives birth to relatively smaller number of offspring, as compared to other species. These offspring develop slowly and need support for a longer period. For a male mammal to be able to successfully pass his gene to future generations, it is adaptive if he stays with the female and contributes to successful development of the offspring. It is through this process of natural selection, that male and female mammals tend to form mating bonds. Similarly, for the female mammals to be able to successfully pass their genes to future generations, it is essential that they induce the male to bond with them. As a result, in mammals, mating bonds are seen to last a lifetime.

Polygyny is another pattern of mating, which is seen in mammals. In polygyny, one male mammal forms mating bonds with more than one female. The evolutionary process might have led to polygyny, as female mammals are seen to contribute much more than male mammals in the rearing of young ones. Female mammals tend to carry them for several months before their birth and get more involved in their development and growth, for few months following their birth. In contrast,

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the male mammal contribution to reproduction is not more than providing their sperm. Unlike females, males have a capacity to give rise to several offspring.

Since female mammals can give rise to only a few offspring, so to ensure that their genes pass onto future generations, they must take good care of the offspring. They should choose to mate with the fittest male in their community, which in turn increases the likelihood that her offspring will be fit. It will pass on her genes, along with those of her mate, to the next generation and will survive well.

Since the male can give rise to several offspring and females can produce only a few offspring, hence females are likely to face greater evolutionary pressure in contrast to males. Therefore females tend to form bonds with only fit males, whereas males of most mammalian species form mating bonds with as many females as possible. This gives rise to polygyny in mammals.

Unlike mammals, there are other species like seahorses in which the male's contribution to reproduction is greater than that of females. They engage in a mating pattern known as polyandry. In polyandry, it is the female who forms mating bonds with more than one male. For instance, in the case of seahorses, it is the female who deposits her eggs in the male's pouch, who fertilizes them and carries them until they are mature enough to hatch and give birth to young ones. The female's tendency to selectively bond with only a few males may have contributed to a fierce competition in males for reproduction. It is through this competition, that the fittest male in the community emerges easily and the female has no difficulty in finding reproductive partners.

Although most mammals are polygynous, but about 3 per cent of mammalian species, including humans, are primarily monogamous. In these species, the mating bonds are enduring and are formed between one male and one female. Monogamy is thought to have evolved in those mammalian species, in which each female could raise more young ones, or more fit young ones. If she had undivided help as in such species, exclusive bonding of a female with the male would increase the chances of her heritable characteristics being passed on to future generations. Each female tends to keep other females of reproductive age away from her mate and copulates with the male only if he has stayed with her for a certain period of time. This makes it difficult for the male to bond with other females. In such a circumstance, both partners are able to successfully pass their genes onto their future generations. Both, the male and the female need to choose fit partners (where the female is fit and the male is strong enough to take protect her and her offspring) and direct all their reproductive efforts towards the birth and development of the offspring.

The evolutionary theory of selection of mates has led to many predictions about the current aspects of selection of human mates. Most of them have even been confirmed through further research in this area. For instance, it is seen that men look for young and attractive females for mating in many cultures. On the other hand, women in look for powerful men with good earning capacity. Hence, females then to display their physical attractiveness and men prefer to display their

power and resources. It has also been seen that across many cultures, men are more likely to engage in adultery than women.

Evolutionary psychology certainly illustrates that the analysis of evolution across different species can bring greater insights into even the most complex psychological processes. This suggests that humans are a result of the evolutionary processes of adaptation and natural selection. It also states that humans are closely related to other animal species. The theories of evolutionary psychology are by no means the only ways in which the above mentioned behaviours have developed over these years. They are just hypothesis which have been framed to gain a better understanding of human behaviour from an evolutionary perspective.

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CHECK YOUR PROGRESS

1. What can be informative in understanding the functioning of the brain?
2. Which is the most common error that is associated with the gathering of information?
3. How does social dominance play an important role in the evolutionary process?

2.4 FUNDAMENTAL GENETICS

Although Darwin gave his theory of evolution, but he was unable to understand how and why members of the same species differ from one another in their characteristics. He was also not able to find out how anatomical, physiological and behavioural characteristics are passed from parent to its offspring. However, it was Gregor Mendel who had answers to these questions. However, the importance of his work was recognized much after his death, in the early 20th century.

Mendelian genetics

Mendel began to study the process of inheritance in pea plants by crossing the offspring of true breeding lines (i.e., the breeding lines in which interbred members always produce offspring with the same trait, generation after generation). In his study he focused on dichotomous traits (i.e., the traits that never occur in combination but occur in one form or the other). For instance, the seeds of the pea plant are either brown or white in colour and are never a mixture of these two colours.

In one of his experiments, he began to study the inheritance of colour in seeds by cross-breeding the offspring of a line of pea plants. These pea plants had bred true for brown seeds, with the offspring of a line of pea plants that had bred true for white seeds. He cross-bred all offspring of the first generation among themselves. It was found that about three quarters of the resulting second generation offspring had brown seeds and about one quarter had white seeds. Following this, he repeated this experiment several times with various pairs of dichotomous pea plant traits. Every time the result was the same. The trait that appeared in all first

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generation offspring was termed by him as the *dominant trait*. And the trait that appeared in one-fourth of the second generation offspring was termed by him as the recessive trait. Mendel also termed the observable traits of an organism as the *phenotype*. The traits which the organisms could pass on to its offspring through its genetic material were referred as the *genotype*, by him.

The results of his experiments challenged the basic premise that offspring inherit the traits of its parents. The earlier ideas about inheritance were based on this premise. He explained the results of his experiments by postulating that there are two kinds of inherited factors (genes) for each dichotomous trait and each organism possesses two genes for each of its dichotomous traits. The two genes that control the same trait are called alleles. A particular portion or region of the chromosome, which represents a single gene is called gene locus. The alleles of a gene occupy the same gene locus on two homologous chromosomes. More than two alternate forms of a gene which are present on the same locus are called multiple alleles. These multiple alleles result from repeated mutations of the same gene in different directions. Mendel further stated that homozygous organisms are the ones that have identical genes for a trait. Similarly, heterozygous organisms are the ones that have two different genes for a trait. In heterozygous organisms, one of the two kinds of genes for each dichotomous trait dominates the other. In addition, the offspring inherit one factor (gene) from the father and one from the mother, for each trait randomly.

Chromosomes, reproduction and linkage

The human body is made of cells. Each human cell has a nucleus which is surrounded by cytoplasm and intracellular bodies. The nucleus of the cell contains thread like structures known as chromosomes. Chromosomes occur in matched pairs and each species has a characteristic number of pairs in each of its body cells. For example, humans have 23 pairs of chromosomes. Genes are located on chromosomes. As mentioned above, for each trait there are two genes known as *alleles*. These two genes alleles, that control each trait, are situated at the same locus, one on each chromosome of a particular pair.

Chromosomes carry hereditary material and every chromosome or the chromosome pair has a definite role in the development of an individual. Hence, loss of a complete or part of the chromosome produces structural and functional deficiency in the organism. Chromosomes perform several functions such as transmitting heredity information from one generation to the other; controlling the synthesis of structural proteins and helping in cell division and cell growth. The control cellular differentiation and cell metabolism lead to variations in members of the same species.

The cells can divide by the process of mitosis or meiosis. In mitosis, just before the cell divide, the number of chromosomes in their nuclei becomes double, so that after division both the daughter cells have the full complement of the chromosomes. Through *meiosis*, *gametes* (egg cells and sperm cells) are produced. In meiosis, the chromosome divides and one chromosomes of each

pair goes to each of the two gametes that results from the division. This results in the gametes having only half of the usual number of chromosomes.

During fertilization, the sperm cell and the egg cell combine together to form a zygote. The zygote has the full complement of chromosomes. In this manner, the genetic diversity within each species results from meiosis. In humans, two gametes are formed as a result of a meiotic division. Each gamete contains one chromosome, from each of the 23 pairs of chromosomes which are contained in each body cell. Since each of the 23 pairs is randomly sorted into the two gametes, each human can produce gametes with 8,38,8,6,08 different combinations of chromosomes. Chromosomes are DNA protein complexes which store, replicate and transcribe coded hereditary information. The DNA is present in both, the nucleus of the cell and in the mitochondria. The DNA in the mitochondria is known as mitochondrial DNA. Mitochondria are known as power houses of the cell as they are involved in the production of energy which is needed for the cell to function adequately. All mitochondrial genes are inherited from the mother. Mutations in mitochondrial DNA can provide insight into the process of evolution and are known to play a role in causing several disorders.

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DNA (Deoxyribonucleic acid) is a helically twisted, double-stranded molecule. It constitutes the genetic material of all organisms with the exception of riboviruses. A DNA molecule has two complementary strands that are spirally coiled and are collectively known as DNA duplex. Each strand of DNA contains sequences of nucleotide bases. These bases are attached to a chain of phosphate and deoxyribose. The four nucleotide bases of DNA are adenine, thymine, guanine and cytosine. These bases belong to two groups, namely, purines (Adenine and guanine) and pyrimidines (cytosine and thymine). The alternate deoxyribose and phosphoric acid group forms the back bone of a DNA chain. The sequence of these bases on each chromosome constitutes the genetic code of an organism.

The two strands that compose each chromosome are coiled around a common axis. They are bonded together by the attraction of adenine for thymine and guanine for cytosine. These two strands are complementary in nature, i.e., the sequence of adenine, guanine thymine, cytosine and guanine on one strand is always attached to the complimentary sequence of thymine cytosine adenine, guanine and cytosine on the other strand. The two DNA strands run parallel to each other, but in opposite directions. One strand runs in the 5'-3' direction and the other runs in the 3'-5' direction. These two chains are held together by hydrogen bonds between their bases.

Only one of the strands of DNA possesses correct hereditary information and is known as the *sense strand*, whereas the complimentary strand is known as the *antisense strand*. Part of the sense strand which specifies a polypeptide or corresponds to a gene is called *cistron*. Adjacent cistrons are separated by non coding regions. Each cistron has a number of codons which consists of three adjacent nitrogen bases.

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The replication of DNA is semi-conservative in nature, as DNA forms its own template. It usually occurs during the S-phase of cell cycle. In this phase, chromosomes are in highly extended form. Replication of DNA requires the strands to separate and act as templates. The new strand then builds over the template of the old strand, having complementary base pairs. DNA replication is considered to be semi-conservative in nature as in it, one strand of the daughter duplex is derived from the parent while the other strand is formed new.

Replication of chromosomes does not always follow the sequence which is mentioned above. Sometimes certain errors take place such as, the presence of an extra chromosome or depletion of a part of the chromosome, etc. These errors are known as *mutations*, which give rise to several disorders. Since the organisms in which mutations occur are often unfit and die, therefore in most cases, mutations disappear from the genetic pool within a few generations. It is not necessary for mutations to always be maladaptive. Sometimes they may increase an organism's fitness and may lead to rapid evolution.

In order to understand several genes on the chromosomes, linkage studies were conducted. The term linkage refers to the phenomenon of certain genes staying together during inheritance, over generations, without any change or separation. This is because these genes are present on the same chromosomes. Sutton and Boveri were the first ones to suggest the phenomenon of linkage when they propounded the chromosomal theory of inheritance.

In the early 20th century, Morgan and his colleagues clearly proved and defined linkage on the basis of breeding experiments with fruit flies. They found that there are four different clusters of fruit fly genes. If the gene for one trait in a cluster was inherited from one parent, that fruit fly would have a probability greater than 0.5 of inheriting genes for other traits in the cluster, from the same parent. Based on this observation, they concluded that linkage occurs between traits that are encoded on the same chromosome. Linked genes lie in a linear sequence in the chromosome. There is a tendency to maintain the parental combination of genes, except for occasional cross over. The strength of the linkage between two genes is inversely proportional to the distance between the two. Their conclusion was supported by the observation that in every species in which linkage has been assessed, the number of cluster of linked traits has been found to equal the number of pairs of chromosomes.

To explain why the genes on the same chromosome are not always inherited together, Morgan and his colleagues proposed the concept of cross over. Cross over takes place during meiosis. They stated that in meiosis, the chromosomes line up in their pairs after replicating themselves. Then, they usually cross over one another at random points. They are further seen to break apart at the point of contact and end up exchanging their sections. Sometimes, two or more cross overs may occur simultaneously in the same non-sister chromatids of the homologous chromosomes, without altering the frequency of recombinations. Therefore, the frequency of cross-over may be higher than the frequency of

observed recombinations. As a result, the offspring rarely receive the intact cluster of genes from their parents. Hence, each gamete contains chromosomes that are a result of the cross over between the chromosomes that are inherited from their parents.

In this way, the process of cross over increases the diversity of the species. The study of cross over also contributed to the construction of gene maps or linkage maps. A linkage map is a linear graphic representation of the sequence and relative distances of various genes, which are present in a chromosome. Because each cross over occurs at a random point along the length of a chromosome, the degree of linkage between two genes indicates how close they are together on the chromosome. Cross over is frequently seen to occur between genes at opposite ends of a chromosome and it rarely occurs between adjacent genes.

Cross over can be single, double, multiple or somatic in nature. A single cross over occurs at one point between two non-sister chromatids. A double cross over takes place at two points in the same tetrad. It can be reciprocal (the cross over takes place at two points between the same two sister chromatids, so that two parental and two double recombinant chromatids are produced) or complementary (three or all the four chromatids are involved in a double cross over) in nature. In multiple cross over, there are three, four or many points at which cross over is found in the same tetrad. A somatic cross over takes place between homologous chromosomes, even without meiosis. It is rare and produces chromosomes with unequal chromatids.

Several factors are known to influence cross overs. Increase in physical distance between the two genes and increased exposure to X-rays, increases the frequency of cross over. Increase in age, the presence of centromere and heterochromatic areas, decreases the frequency of cross overs. Factors like variations in temperature, number of chemicals present in food, are associated with greater frequency of cross over. In some heterogametic organism, one sex shows an increase in the frequency of cross-over. Also, one cross over reduces the occurrence of another cross over in its vicinity.

Cross over and mutations are responsible for genetic variations. Mutations are new, sudden inheritable and discontinuous variations which appear in the organisms due to permanent change in their genotypes. Mutations can be of three types:

- (i) Genomic (refers to changes in the number of chromosomes)
- (ii) Chromosomal (refers to changes in the number and arrangement of genes in the chromosomes, which may occur either due to loss of a terminal, intercalary segment of chromosome or due to inversion of chromosome segments or due to representation of genes twice in the same chromosome, etc.)
- (iii) Gene mutations (refers to changes in the form and expression of genes).

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Several factors that are known to increase the frequency of mutations in organisms. These are: variations in temperature, increased exposure to high energy radiations, presence of chemicals like nitrous acid, alkalizing agents, base analogues and acridness.

Sex chromosomes and sex-linked traits

All chromosomes occur in matched pairs, except the sex chromosomes. Sex chromosomes determine the sex of an individual. There are two types of sex chromosomes, X and Y. Both of these chromosomes carry different genes. The Y chromosome is slightly smaller than the X chromosome. The female mammals have two X chromosomes and male mammals have an X and a Y chromosome.

Sex linkage or sex-linked inheritance refers to the transmission of characters and their determining genes, along with sex determining genes. These are present on the sex chromosomes and therefore, are inherited together from one generation to the next. Sex-linked inheritance is criss-cross in its nature. In cross over inheritance, the parent passes the traits to the grand child of the same sex through offspring of the opposite sex, i.e., the mother transfers the traits to her granddaughter through her son and the father passes the traits to grandson through his daughter.

Any trait that shows criss-cross inheritance is located on the sex chromosome. The knowledge of criss-cross inheritance is useful in knowing the past, present and future transmission of sex-linked disorders. The father does not pass the sex-linked allele of a trait to his son, but the same is passed to the daughter as the males have only one X chromosome. Since the mother has two X chromosomes, therefore, it passes the alleles of sex-linked traits to both sons and daughters. In addition, because of this, males suffer from sex-linked disorders more often than females and the majority of the sex-linked traits are recessive. Females function as carriers of sex-linked disorders and these disorders rarely manifest themselves in females, as recessive genes can express themselves in females only in the homozygous state.

Traits governed by sex-linked, recessive genes produce disorders in males more often than in females. They express themselves in males even when represented by a single allele. This is because the Y chromosomes do not carry any corresponding alleles and seldom appear in both father and son. It fails to appear in females, unless their father also possesses the same recessive genes and the mother is a carrier of female heterozygous. A female which is homologous for the recessive trait transfers the trait to all the sons. The traits governed by sex-linked dominant genes produce disorders in females more often than in males; all female offspring will exhibit them if the father possesses the same. They do not get transmitted to the offspring if the mother does not exhibit them.

The genes on the sex chromosome influence certain traits, which are known as sex-linked traits. The X chromosome is larger and contains genes that virtually control all sex-linked traits. The Y chromosome is comparatively smaller and contains fewer genes. It is the Y chromosome that causes an individual to develop

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into a male. Traits that are controlled by genes on the X chromosome occur more frequently in one sex than in the other. If the trait is dominant, it occurs more frequently in females. Since females have two X chromosomes, they have twice the chance of inheriting the dominant gene. Recessive sex-linked traits are manifested only in females who possess two of the recessive genes, one on each of their X chromosomes. On the other hand, traits are manifested in all males who possess the gene because they have only one X chromosome. Therefore, recessive sex-linked traits occur more frequently in males. For example, colour blindness is a recessive sex linked trait and is frequently seen in males than in females.

Genetic code and gene expression

The term gene was given by Johanssen in 1909. Gene refers to a unit of genetic material which is able to replicate itself. This material can undergo cross over and mutations and is connected with a somatic structure or function that leads to a phenotypic expression. This is a linear segment of DNA known as cistron. DNA is the genetic material of the chromosome. Genes serve the following functions:

- They are the units of inheritance
- They control the morphology or phenotype of individuals
- They play an important role in cell division
- They transmit genetic information from one generation to the other
- They control the structure and metabolism of the body
- They are responsible for producing variations by means of cross over and mutations
- They control the differentiation or formation of different types of cells, tissues and organs in various parts of the body
- They control the development and production of different stages in the life history of an organism.

The different types of genes are as follows:

- **Constitutive genes:** are those genes that are constantly expressing themselves in a cell. Their products are required for normal cellular activities, for example, genes for glycolysis, etc.
- **Non-constitutive genes:** are those genes which do not always express themselves in a cell and are switched on and off according to the requirement of cellular activities. There are two types of non-constitutive genes, inducible and repressible.
- **Inducible genes:** are switched on in response to the presence of chemical substance or inducer, which is required for the functioning of the product of gene activity, e.g., nitrate for the nitrate reeducates.

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- **Repressible genes:** are those genes which continue to express themselves till a chemical (often an end product) inhibits or represses their activity. Inhibition, by an end product, is known as feedback repression.
- **Multi genes:** refer to a group of similar or nearly similar genes for meeting the requirement of time and tissue-specific products, e.g., globin gene family.
- **Repeated genes:** are those genes that occur in multiple copies, e.g., histones.
- **Single copy genes:** are genes that are present in single copies and they form 60–70 per cent of the functional genes.
- **Pseudogenes:** are genes which have homology to functional genes but are unable to produce functional products due to intervening non-sense codons, insertions, deletions and inactivation of promoter regions, for instance, snRNA genes.
- **Processed genes:** are eukaryotic genes which lack introns and have been formed probably due to reverse transcription or retroviruses. They are usually non-functional as they lack promoters.
- **Split genes:** are those genes which possess extra or nonessential regions (known as introns), interspersed with essential (known as exons) or coding parts.
- **Transposons or jumping genes:** are segments of DNA that can jump or move from one place in the genome to another.
- **Overlapping genes:** are genes that tend to overlap one another.
- **Structural genes:** are those genes which have encoded information for the synthesis of chemical substances. These are required for cellular machinery. They contain information which is necessary for the synthesis of a single protein. Proteins are long chains of amino acids which form important components of the structure of the cell and control the physiological activities of cells.
- **Regulatory genes:** are genes that control the functions of structural genes.
- **Operator genes:** determine the probability and rate of expression of structural genes. They control the expression of the gene which determines how a cell will function, once it reaches maturity. These genes can be regulated in two ways. Some operator genes are normally off and are turned on by DNA binding proteins. Whereas, others are normally on and can be turned up, down and off by DNA binding proteins. The DNA binding proteins are influenced by signals that are received by the cell from its environment. In this way the environmental factors influence the development and expression of genes.

The mechanism by which a gene is able to express itself in the phenotype of an organism is known as *gene expression*. This expression consists of the synthesis of specific RNAs, polypeptides, structural proteins and proteinaceous bio-

chemicals or enzymes which control the structure or functioning of specific traits. The process of gene expression involves two phases. One being the transcription of the DNA based sequence code, to an RNA based sequence code and the other phase involves the translation of the RNA base-sequence code into a sequence of amino acids, to form a protein.

It begins with the unraveling of a segment of DNA molecule. The unraveled section of one of the DNA strand serves as a template for the transcription of a short stand of RNA (ribonucleic acid). The process of formation of RNAs from genes is known as transcription. RNA is like DNA, except that it contains a nucleotide-based uracil instead of thymine and has a phosphate and ribose backbone, instead of a phosphate and deoxyribose backbone. The strand of transcribed RNA is called messenger RNA, because it carries the genetic code from the nucleus of the cell. On leaving the nucleus, the messenger RNA attaches itself to one of the many ribosomes in the cytoplasm of the cell. The ribosome then moves along the strand of mRNA, translating the genetic code as it proceeds.

Each group of three consecutive nucleotide bases, along the messenger RNA strand, is called a codon. Each codon instructs the ribosome to add 1 of the 20 different kinds of amino acids to the protein that it is constructing. The molecules of transfer RNA carry each kind of amino acid to the ribosome. As the ribosome reads a codon, it attracts a tRNA molecule that is attached to the appropriate amino acid. In this manner, the ribosome continues to add amino acids one after the other, as it goes along reading one codon after the other, until the synthesis of protein is complete. Then, the completed protein is released into the cytoplasm.

Human genome project

The human genome project was undertaken in 1990 to determine the base sequence of each human gene. This is based on the belief that deciphering the human genome will significantly contribute to the understanding of human development. A few years earlier, this project appeared more like fiction rather than a reality. However, research in genetics has realized the dream of several biological psychologists.

Although it can be seen as a major step in enhancing our understanding of human development, it still leaves several questions unanswered. One still has to identifying millions of variations that occur among human genes and how these variations interact with other genes and the environment. This influences the development of human structures and functions.

It is believed that deciphering the entire human genome will not only enhance our understanding of human and its psychological processes, it but will also help us in developing preventive and therapeutic drugs for certain diseases by identify the genes that are involved in that disease. It will also help us to determine, the genetic differences among various human populations, thereby enhancing our understanding of the evolutionary process.

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CHECK YOUR PROGRESS

4. What did Mendel focus on, in his study of inheritance?
5. State the two processes of cell division.
6. How is the strength of the linkage between two genes related to the distance between them?

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2.5 GENETIC ENGINEERING

The field of genetic engineering aims at studying the functions of genes. It involves the manipulation of DNA from different sources so as to recombine the desired DNA portions for repair, improvement, perfection and matching of a genotype. The beginning of the field of genetic engineering is marked by the discovery of restriction genes in the late 1960s. Restriction genes could cut DNA with great precision at a specific base sequences. They make use of recombinant DNA techniques to form new combinations of heritable genetic material. This is done by introducing heritable material which is prepared outside the organism, either directly into the host, or into a cell that is then fused or hybridized with the host. This fusion takes place either indirectly through the vector system, or directly through micro-injection, macro-injection and micro-encapsulation techniques. It involves removing genes from an organism, making multiple copies of them (cloning) and then implanting them into other organisms. An organism in which a genetic material of some other species has been added is known as a *transgenic organism*, whereas an organism in which the genetic material of the same species, or a species that can naturally breed with the host is used, is known as a *cisgenic organism*.

Various techniques that are used in genetic engineering are as follows:

- **Isolation of genes:** DNA is broken by endonucleii and is fractioned by gel electrophoresis. The segments are transferred on nitrocellulose filters for hybridization with known cDNA or RNA. Thus, the genes are identified, separated and purified.
- **Artificial or synthetic genes:** This process involves the synthesis of genes artificially. This is done by using gene machines which can automatically link nucleotides in a specific sequence. These machines are operated by a microprocessor.
- **Reverse transcription:** It involves isolation of a purified mRNA and its treatment with reverse transcriptase and necessary nucleotides. A single stranded copy DNA (cDNA) is thus produced. mRNA is then hydrolysed through treatment with alkali. Complementary DNA strands are then synthesized over the template of cDNA. cDNA is formed through reverse transcription and it does not contain introns and other non-coding regions. Thus, it is shorter than the actual gene.

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- **cDNA library:** In this library, all mRNAs of the cell are separated and made to transcribe cDNAs by means of reverse transcriptase. They are then cloned with plasmids, by breaking plasmids with restriction endonuclease followed by treatment with terminal transferase and complementary nucleotides. Terminal transferase is also used to treat cDNA to make its ends sticky. Following which, plasmids and cDNA are allowed to fuse with the help of enzyme ligase. Plasmid free bacterial and other suitable cells are then made to pick up recombinant DNA by treatment with dilute calcium chloride. The transformed cells are then multiplied and provided with raw materials to form the desired biochemicals. By this technique, insulin became the first product of genetically transformed bacteria that was marketed for human use.
- **Gene library:** It refers to an assemblage of clones having different segments of the whole genome or gene complement of an organism. Gene library gives information of introns.
- **Gene amplification:** in it selected DNA sequence is mixed with nucleotides, polymerase and other bio-chemicals required for DNA synthesis. The mixture is alternatively heated and cooled. The cycle takes about 30 minutes. It is repeated several times to obtain a number of copies of the same genes.
- **Gene knock out techniques**

Gene knock out techniques are procedures used for creating organisms that do not possess a particular gene that is of interest to the researcher in order to look for any observable neural or behavioural anomalies these creatures may possess. Though informative, but these techniques have certain major drawbacks. For instance, most behaviours are a result of a complex interaction between various genes and removal of a gene and experience can both influence the expression of other genes. Hence any observed change in the behaviour may not be a direct result of that specific gene which has been eliminated and the experiences the created organisms may undergo can also affect his behaviour. Then in that case these techniques can only provide us information about the small genetic contribution of that specific gene to the behaviour of the created organism.
- **Gene replacement techniques**

Gene replacement techniques involve replacing a gene with some other gene and seeing its effects on the behaviour of the animal. These techniques are largely used for the purpose of developmental research and therapy. For instance a pathological gene from a human cell and be removed and inserted in mice to see the effects of that gene. These techniques involve replacing a gene with another nearly identical gene except for the addition of a few bases that can act as a switch, turning the gene off or on in response to particular chemicals. These chemicals help in the activation or suppression of a gene at certain points in one's development or in certain brain structures.

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Genetics of human psychological differences

Human beings are a result of complex interaction between genes and environmental influences, which in turn affects their expression. Research on the complex interactions between genes and the environment has revealed that enriched early environments can overcome the negative effects of disadvantaged genes. This is possible by facilitating the development of thicker cerebral cortexes. Several genes are involved in the development of a normal behavioural trait but a defect in a single gene is enough to disrupt the normal development of a behavioural trait. Genes are also known to prepare an individual to acquire certain behaviour, adequately during the sensitive period.

In order to understand specific contributions of genetics and environment in making us the way we are, biological psychologists carry out twin studies by comparing identical (twins that develop from the same zygote and are thus genetically identical) and fraternal twins (twins who develop from two zygotes and are genetically no more similar than any pair of siblings), who have been separated at infancy by adoption and reared in different environments.

For a better understanding of the contribution of genetics and environment in determining psychological differences in human beings, a classical study was done at the University of Minnesota. In this study, 59 pairs of identical twins and 47 pairs of fraternal twins, who had been reared apart, as well as many pairs of identical and fraternal twins who had been reared together were subjected to 50 hours of testing. This testing primarily focused on the assessment of intelligence and personality. The results of the study revealed that in general, adult identical twins were substantially more similar to one another on all psychological dimensions than were adult fraternal twins, irrespective of the fact whether they were raised in the same family environment or not.

It is seen that genetic differences can promote psychological differences by influencing experience. Research has indicated that individuals of similar genetic endowment tend to seek out similar environments and experiences. For example, individuals whose genetic endowment promotes aggression are likely to get involved in aggressive activities, e.g., football or competitive fighting and these experiences further contribute to the development of aggressive tendencies in these individuals.

In short, it is impossible to clearly delineate how much and to what extent, the genetic and environmental factors independently contribute to the development of psychological differences in humans. But it is certain that both, the genes and the environment make significant contributions and interact in multiple ways, thereby affecting the development of human beings.

Genetic engineering techniques have been applied to fields like biotechnology and medicine. Human growth hormones and insulin are now being produced in bacteria or mice by using the techniques of genetic engineering. These techniques have also been used to produce insect resistant or herbicide tolerant crops and for producing biotechnology drugs, at a low cost. It is also useful in knowing defective genes in the fetuses and for gaining an understanding of gene structure and mechanisms of gene expression. They can also be used to repair and replace defective genes. The field of genetic engineering carries immense potential to teach biological psychologists more about the functioning of the brain and its effects on the behaviour. It can also provide treatments for several brain disorders.

Certain problems are also associated with the field of genetic engineering. For instance, it can lead to accidental synthesis of powerful microbes like the HIV AIDS virus and can lead to biological wars. Hence, the knowledge of genetics should be wisely used for the benefit of mankind.

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2.6 SUMMARY

- Biology has caused a chain of events that are related to behaviour. Each of these events is related to the other.
- Biological psychologists seek and identify areas on the complete set of genes, in a cell or living thing, which affects behaviour.
- The fact that genes play a role in determining a person's mental state is very significant for psychologists.
- Studying how genes can affect a person's mental being can lead to a better understanding of the biological influences on behaviour.
- This unit has focused on the process of human evolution in the context of humans as animals. Simultaneously, it also shows the physical context of human evolution, including climate change and impact of extinctions.
- This unit has introduced several basic genetic concepts. The origin of life and the evolution of the domains of life are described briefly.
- Genetic engineering is the artificial alteration of genetic code and therefore; it is different from traditional selective breeding.

2.7 KEY TERMS

- **Topography:** A study of the physical features of an area of land, especially the position of its rivers, mountains, etc.
- **Brain lesion:** An area of tissue within the brain that has been damaged through injury or disease
- **Neo-cortex:** Part of the brain in mammals

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- **Hypothetico-deductive method:** A method that requires the biological psychologists to state a theory that is composed of a set of postulates
- **Empirico-inductive method:** A method that requires the biological psychologist to make careful observations without regard to systems and theories
- **Social dominance:** Superiority of relationship and rank of an individual in relation to his associates
- **Cerebrum:** The portion of the brain (frontal lobes) where thought and higher function reside
- **Polygyny:** The practice of a man having several wives at once
- **Dichotomous:** The presence of two equal branches resulting from division of the growing point
- **Heterozygous:** The existence of two different alleles of the same gene
- **Mitosis:** A method of indirect division of a cell
- **Meiosis:** A method of direct cell division

2.8 ANSWERS TO 'CHECK YOUR PROGRESS'

1. Direct manipulation of biochemistry can be informative in understanding the functioning of the brain.
2. The most common error which is associated with the gathering of information is the bias that a researcher faces at times.
3. Social dominance seems to play an important role in the evolutionary process as the dominant males tend to copulate more than the non-dominant males.
4. In his study of inheritance, Mendel focused on dichotomous traits (i.e., the traits that never occur in combination but occur in one form or the other).
5. There are two processes of cell division, they are mitosis and meiosis.
6. The strength of the linkage between two genes is inversely proportional to the distance between the two.

2.9 QUESTIONS AND EXERCISES

Short-Answer Questions

1. What is the hypothetico-deductive method?
2. Define the empirico-inductive method.
3. Why is a neuropsychological research conducted?
4. What behaviours should biological psychologist study?
5. Mention the various factors that can influence a cross over.

Long-Answer Questions

1. List and explain some of the problems in the field of biological psychology.
2. What problems are inherent in the interpretation of the effects of brain lesion?
3. Write a note on human evolution, from Darwin's perspective.
4. Explain Mendelian genetics and the reproduction and linkage of chromosomes.

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2.10 FURTHER READING

Pinel, John. 2003. *Biopsychology*, Fifth edition. New Jersey: Allyn and Bacon.

UNIT 3 FUNCTIONAL NEUROANATOMY

NOTES**Structure**

- 3.0 Introduction
- 3.1 Unit Objectives
- 3.2 Divisions of the Nervous System
 - 3.2.1 Cells of the Nervous System
- 3.3 Neuroanatomical Techniques
- 3.4 Major Divisions of the Brain
 - 3.4.1 Functional Description of the Brain
 - 3.4.2 Blood Supply to the Brain
 - 3.4.3 Neuroimaging Techniques
 - 3.4.4 Cell Specialization
- 3.5 Neurophysiology
 - 3.5.1 Electrical Signals
 - 3.5.2 Transmission Process
 - 3.5.3 Circuits
 - 3.5.4 Gross Electrical Activity
 - 3.5.5 Hormones and the Brain
- 3.6 Summary
- 3.7 Key Terms
- 3.8 Answers to 'Check Your Progress'
- 3.9 Questions and Exercises
- 3.10 Further Reading

3.0 INTRODUCTION

The human behaviour is enabled by the brain. Hence, it is not possible to study human behaviour without studying the physical structure of the brain. While a sense of the molar (general or large-scale) structure is essential for a basic recognition of the master organ of the body, an appreciation of the molecular (denser, inner-intricacies) provides foundation and insight to the complex nuances of human behaviour.

Functional neuroanatomy is the field that concerns itself with the linking function of the brain, this is sometimes referred to as behavioural neuroanatomy. Functional anatomy is important in understanding the symptoms of damage to the nervous system and associated areas. Many problems related to the nervous system can be attributed to specific brain structures, or areas of associated functional systems. Therefore, the knowledge about functional anatomy and associated domains enables one to locate the point of damage in a nervous system. Functional neuroanatomy includes a cross-sectional view of the brain, the brain stem, MRI images in three planes and identification of key concepts. Functional neuroanatomy

also enables one to understand the function of the central nervous system in a thorough manner.

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3.1 UNIT OBJECTIVES

After going through this unit, you will be able to:

- Explain the divisions of the nervous system
- Discuss various neuroanatomical techniques
- Define and explain the major divisions of the brain
- Analyse the concept of neurophysiology

3.2 DIVISIONS OF THE NERVOUS SYSTEM

The nervous system can be divided into the Central Nervous System (CNS) and the Peripheral Nervous System (PNS). The central nervous system is divided into the brain and the spinal cord. The brain has been structurally divided into the forebrain, midbrain and hindbrain. The forebrain is further divided into the telencephalon and the diencephalon. The telencephalon consists of the cerebrum, basal ganglia and the limbic system. The cerebrum is divided into the right and the left hemisphere. Each hemisphere is further divided into four lobes, namely, frontal, temporal, parietal and occipital lobes. The limbic system consists of amygdala, septum and the hippocampus. The diencephalon consists of the thalamus and the hypothalamus.

The midbrain is divided into tegmentum and tectum. The tectum consists of the superior and the inferior colliculus. The hindbrain consists of the medulla, the pons and the cerebellum. The spinal cord consists of three nerve pathways, namely, the ascending, the descending and the transverse pathways. The ascending pathways are further divided into the cuneate gracile (lemniscal system) and the spinothalamic system, whereas, the descending pathways are divided into the pyramidal motor system and the extrapyramidal motor system.

The peripheral nervous system consists of cranial nerves and spinal nerves. Each cranial and spinal nerve has sensory and motor fibres. These motor fibres are somatic and autonomic in nature. The autonomic nervous system further consists of the sympathetic nervous system and the parasympathetic nervous system. After this brief review of the major divisions of the nervous system, we now read about them in further detail.

The PNS (peripheral nervous system) consists of nerves which originate from the CNS and connect either receptors or efferent organs. The nerves which arise from brain are called cranial nerves, while the nerves which originate from the spinal cord are termed as spinal nerves. The PNS has both sensory and motor fibres which are spread over the entire body. Mixed nerves are nerves that contain both sensory and motor nerve fibres and thus perform sensory and motor functions.

The parasympathetic nervous system consists of one set of motor fibres. These nerve fibres originate from the brain and the spinal cord. They are seen to exert inhibitory and excitatory control. The parasympathetic nervous system is further controlled by the central nervous system. Its motor fibres directly reach the target organ. In humans, cranial nerves are present in twelve pairs. These are as follows:

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- **Olfactory nerve:** It is connected to the brain and different parts of the body, through the olfactory epithelium of the nasal chamber. It is sensory in nature and its main function is to regulate the sense of smell.
- **Optic nerve:** It is connected to the side of the diencephalon. The optic nerve is connected to the retina of the eye. It is sensory in nature and its main function is to regulate the sense of sight.
- **Oculomotor nerve:** It is connected to the floor of the midbrain and also to the inferior oblique, superior and inferior rectus and medial and rectus eye muscles. It is motor in nature and its main function is to control the movement of the eye ball.
- **Pathetic nerve:** It is connected to the floor of the midbrain and the superior oblique eye muscles. It is motor in nature and its main function is to control the movement of the eye ball.
- **Trigeminal nerve:** It is connected to the ventral side of the pons varolli. It is a mixed nerve and regulates the sensation of taste, touch and jaw movements (that are largely involved in chewing).
- **Abducen nerve:** It is connected to the ventral side of the medulla oblongata and the lateral rectus eye muscle. It is a motor nerve and is involved in the regulation of the sensation of taste, touch and jaw movements.
- **Facial nerve:** It is connected to the lateral side of the pons varolli and also to the taste buds of the tongue, muscles of the face and salivary glands. It is a mixed nerve and is involved in the regulation of the sensation of taste, facial expressions and salivary secretions.
- **Auditory nerve:** It is connected to the lateral side of the medulla oblongata and the internal ear. It is a sensory nerve which regulates the sense of hearing and balance.
- **Glucce-pharyngeal nerve:** It is connected to the lateral side of the medulla oblongata and to the tongue, pharyngeal mixed muscles and the parotid salivary glands. It is a mixed nerve and is involved in the regulation of taste, movement of pharynx and salivary secretions.
- **Vagus nerve:** It is connected to the lateral side of the medulla oblongata and to the larynx, pharynx, oesophagus, lungs, heart, intestine and stomach. It is a mixed nerve and is involved in the regulation of speech, swallowing, decrease of heart rate, stimulus for peristalsis and respiratory movement.

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- **Spinal accessory nerve:** it is connected to the lateral side of the medulla oblongata and to the larynx, pharynx, neck and the shoulder. It is a motor nerve and it regulates the movement of the larynx, pharynx, neck and shoulders.
- **Hypoglossal nerve:** it is connected to the ventral side of the medulla oblongata and to the muscles of the tongue. It is a motor nerve and it regulates the movement of the tongue.

In contrast to the cranial nerves, the spinal nerves originate from the spinal cord. These nerves are bilaterally symmetrical and hence occur in pairs. There are 31 pairs of spinal nerves and they are numbered and named according to the vertebrae with which they are associated. These consist of 8 pairs of cervical nerves, 12 pairs of thoracic nerves, 5 pairs of lumbar nerves, 5 pairs of sacral nerves and 1 pair of coccygeal nerve. Spinal nerves are formed by the union of the dorsal and ventral roots shortly after they leave the spinal cord. Each spinal nerve has afferent (sensory) and efferent (motor) fibres. Motor fibres come from the ventral root and the sensory fibres go into the dorsal root. Thus all spinal nerves are mixed nerves because they carry both, sensory and motor impulses. Some of the spinal nerves are connected to the autonomic nervous system. Motor nerves of this system stimulate the skeletal muscles whereas ANS stimulates the cardiac muscles.

Certain spinal nerves combine to form the following plexuses.

- **Cervical plexus:** innervates the neck and diaphragm
- **Brachial plexus:** connects the chest and the arm
- **Lumbar plexus:** innervates the legs
- **Sacral plexus:** connects the pelvic region
- **Coccygeal plexus:** also innervates the pelvic region

After getting an understanding of cranial and spinal nerves, we look at the various functions performed by the PNS. The parasympathetic nervous system carries sensory information from receptors to CNS, through the cranial and spinal segments. It also carries information from the CNS. PNS forms the core for stimulus response associations.

The autonomic nervous system (ANS) is called so because it controls and coordinates the involuntary activities of various organs. It is also known as the visceral motor system because it consists of motor fibre of PNS, which in turn, stimulate the smooth muscles and glands. ANS consists of the sympathetic nervous system and the parasympathetic nervous system.

In contrast to the parasympathetic nervous system, the autonomic nervous system has two sets of motor fibres, namely sympathetic and parasympathetic. Its nerve fibres originate from the spinal cord. Both, the sympathetic and the parasympathetic fibres are seen to have opposite effects on the smooth muscles and fibres. For instance, if the sympathetic nerve excites a particular muscle then the parasympathetic nerve inhibits the same muscle and vice versa. The motor

pathways consist of preganglionic and postganglionic fibres. Preganglionic fibres originate from the spinal cord, whereas postganglionic fibres connect preganglionic fibres with smooth muscles and glands.

Sympathetic and the parasympathetic fibres have certain similarities and certain differences. The similarities are that both are parts of ANS; both are motor fibres and both contain preganglionic and postganglionic fibres. But the two are structurally and chemically different. The preganglionic fibres of the sympathetic nervous system originate from the thoracic and the lumbar region of spinal cord, whereas, the preganglionic fibres of the parasympathetic nervous system originate from the brain stem and the sacral region of spinal cord. The preganglionic fibres and the postganglionic fibres of the sympathetic nervous system are short and long respectively. The preganglionic fibres enter into the ganglia, which lies outside the spinal cord and from there postganglionic fibres originate. These reach the target organ. The preganglionic fibres and the postganglionic fibres of the parasympathetic nervous system are long and short respectively.

The sympathetic nervous system prepares the body during emergencies like states of stress and arousal, whereas, the parasympathetic nervous system orients the body towards internal maintenance. The sympathetic nervous system dominates during muscle activity and helps in spending energy. The parasympathetic nervous system, in contrast, acts during conservation of energy. In addition, both sympathetic and parasympathetic nervous systems have opposing effects on several parts of the body. For example, the sympathetic nervous system dilates the pupil, inhibits salivary flow, increase heart rate; dilates bronchi, inactivates the intestines, constricts blood vessels, has no effect on the tear glands and causes the adrenal medulla to release hormones. On the other hand, the parasympathetic nervous system constricts the pupils, stimulates the tear glands, stimulates salivary flow, decrease heart rate, constrict bronchi, activates intestines, dilate blood vessels and has no reaction of the adrenal medulla.

The autonomic nervous system performs several functions. It shifts the flow of blood from one part of the body to another, so as to control its supply according to the needs. It also regulates the internal environment whenever the homeostasis is upset, in order to restore the balance and facilitate normal functioning.

Both sympathetic and the parasympathetic nervous system are influenced largely by the hypothalamus, which is often known as the 'head ganglion' of the autonomic nervous system. Earlier, it was thought that the peripheral nervous system controls and coordinates voluntary activities of the body and the autonomic nervous system controls and coordinates involuntary activities of our body. However, a research by Miller (1969) showed that lower animals and humans can be trained to control some ANS responses. Since blood pressure can be controlled voluntarily, so this functional difference is questionable.

The central nervous system (CNS) is a hollow, dorsally placed structure, lying along the middorsal axis of the body. It comprises of the brain and the spinal cord. The brain is lodged in the skull while spinal cord is enclosed by the vertebral

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column. The spinal cord is a posterior part of the CNS. It is a conical structure which is surrounded by three protective membranes, namely, the pia mater, the arachnoid mater and the dura mater. The pia mater consists largely of grey matter. It is a thin innermost layer. It is surrounded by the arachnoid membrane, which forms the middle layer. The outermost tough membrane is the dura mater, which largely consists of white matter. Certain spaces are present in between these membranes. The subarachnoid and subdural spaces are filled with cerebrospinal fluid. The epidural space above the dura mater contains fatty and connective tissues and veins.

The spinal cord runs mid-dorsally within the vertebral column and lies in its neural canal. It is protected by the vertebral column and passes through a hole in each vertebra. The vertebral column is composed of 24 individual vertebrae. It consists of 7 cervical vertebrae; 12 thoracic vertebrae and 5 lumbar vertebrae. The 7 cervical vertebrae are present in the neck, the 12 thoracic vertebrae are present in the chest and the 5 lumbar vertebrae are present in the lower back region. The fused vertebrae that make the sacral and coccygeal portion of the column are located in the pelvic region. The 5 sacral vertebrae are fused in the adult. These form one structure known as the sacrum and the 4 coccygeal vertebrae are fused to form a curved triangular bone known as the coccyx.

The diameter of the spinal cord is less than 3/4th of an inch. It is only about 2/3 times as long as the vertebral column, the rest of the space is filled by a mass of spinal roots. These compose of the *cauda equina*. A root is bundle of axons running in and out of the spinal cord, surrounded by connective tissues. The spinal roots consist of the ventral and the dorsal roots. The dorsal root of the spinal cord consists of incoming afferent or sensory fibres and the ventral root contains the outgoing efferent or motor fibres. They join together, outside the spinal cord and merge to form the spinal nerves. The sensory fibres, with their cell bodies outside the cord, form a bundle which constitutes the dorsal root ganglion. No such ganglion formation is seen in the ventral root.

The spinal cord consists of a central pia mater which is also known as the grey matter. The surrounding white matter is the dura mater. The dura mater has a myelin sheath covering it. Because of the presence of the myelin sheath, the white matter becomes tough. The grey or pia mater has no myelin sheath and it is hence fragile. The white matter consists of ascending and the descending myelinated nerve axons. On the contrary, the grey matter consists of nerve endings, neural cell bodies and non-myelinated axons which form the synapse.

The structure of the spinal cord also consists of nerve pathways connecting the brain on one hand and PNS on the other. The spinal cord acts as a relay station between the brain and the PNS, through these ascending and descending pathways. It is involved in all behaviours below the neck, that is, behaviours relating to skeletal autonomic sections and voluntary behaviours with brain involvement. It helps in coordinating behaviours with environmental stimuli as it connects information

from receptors and responding muscles. The spinal cord is also acts as a centre for reflex actions.

A reflex is a rapid automatic response made to a particular stimulus. There are two types of reflexes namely, *skeletal reflex* (for example, the knee jerk) and the *autonomic reflex* (for example, salivation, eyelid movement, sneezing, etc). A reflex behaviour is rooted in simple neural circuits called reflex arcs. One such arc is a two neuron circuit known as the monosynaptic reflexes. It is so called as it involves only one synapse between a sensory and a motor neuron. The knee jerk reflex is controlled by monosynaptic reflexes.

All behaviours are not simple. Some behaviours are complex, which involve other sides of the body and other organs. These behaviours are executed through polysynaptic reflexes. These reflexes involve more than one synapse between a sensory and a motor neuron. For example, when reflex involves both sides of the body requiring balance, the neural activity passes in two directions once it reaches the spinal cord. The two directions involve the ipsilateral reflex and the contralateral reflex. The ipsilateral reflex activates the same side of the body. The contralateral reflex activates the other side of the body. These are done by crossing through the grey matter.

All reflex actions are triggered purely by the spinal cord. Some reflexes also take place with the involvement of the brain. For example, we can consciously stop knee jerks that occur as the circuits of the spinal reflex are lined to nerve pathways. These nerve pathways ascend and descend from the brain. Hence, it is possible for the brain to control the autonomy of the spinal nerves.

Ascending pathways are sensory and they carry the sensory information from the body to the brain. Most of the information entering at the spinal level of CNS originates from the body's skin. This information is known as *somatosensory*. Ascending pathways consist of the lemniscal and the spinothalamic pathways.

The lemniscal pathway is situated in the dorsal and medial section of the spinal cord. It consists of the gracile tract, which covers the lower torso and lower limbs and the cuneate tract, which covers the upper torso and upper limbs. In these portions of the spinal cord, the cuneate and gracile tracts lie adjacent to each other, with each on both sides of the spinal cord. These tracts carry information arising from the sensations of light touch on the skin, kinesthetic movement cues, and limb position. Most of this sort of information crosses through the brain to the contralateral side and eventually reaches the right side of the neo cortex.

In contrast to the lemniscal pathway, the spinothalamic pathway is situated in the ventral and lateral portion of the spinal cord. It carries information arising from the sensations on the skin related to deep pressure, temperature changes and pain. These tracts are divided into about 50 per cent contralateral (opposite sided) and 50 per cent ipsilateral (same sided) systems. It means that half of the ascending spinothalamic fibres cross the midline of the CNS while the other half do not cross the midline, but rather stay on the same side of the midline of the CNS.

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The descending pathways are motor nerves carrying information from the brain to the PNS, for motor responses of the body. They consist of pyramidal and extra pyramidal pathways. Both these pathways are seen to differ functionally and structurally in primates and humans. For example, the pyramidal pathways control the capacity to perform discrete movements, whereas, the extra pyramidal pathways control the capacity to execute smooth and integrated movements. Pyramidal fibres originate from specific sites on the neocortex, whereas, extra pyramidal fibres originate in widespread sites on the neocortex as well as in several areas of the brain, underneath the neocortex. These areas are known as sub-cortical areas.

Around 80 per cent of the descending pyramidal fibres form the neocortex. They cross over the middle of the CNS at the base of the brain and continue along the lateral corticospinal tract in the spinal cord; the remaining 20 per cent continue without crossing through the ventral corticospinal tract. Extra pyramidal fibres either cross or do not cross the midline as they descend from cortical and sub-cortical areas.

3.2.1 Cells of the Nervous System

The central nervous system consists of neurons and supporting cells. Neurons constitute only about half the volume of the central nervous system. The rest consists of a variety of supporting cells. Neurons are essential for transmitting and processing all information that reaches and moves out of the central nervous system. Since neurons have a very high rate of metabolism and do not have any means of storing nutrients, hence they have to be constantly supplied with nutrients and oxygen. If the nutrients and the oxygen do not reach neurons, they die. Unlike most other cells of our body, neurons cannot be replaced when they die. The cells that protect and support neurons are known as supporting cells.

The nervous system is made of cells. A single nerve cell is known as a neuron. It is the information processing and the information transmitting element of the nervous system. The nervous system brings information in from the outside environment, interprets that information and remembers some of it. In turn, it controls the body by making it respond to that environment, in a particular way. Depending on the circumstances, it can alter the body's response. In short, neurons do everything that is needed to survive. All these tasks are carried by the nervous system, with the help of highly specialized and mutually communicative cells known as neurons.

Neurons differ in terms of their shapes and the kind of specialized jobs they perform. Neurons usually have the following 4 structures or regions, in one form or another:

- (i) Cell body/ soma
- (ii) Dendrites
- (iii) Axon
- (iv) Terminal buttons

- (i) **Soma:** The soma or the cell body contains the nucleus and several other cell bodies that are needed to perform life processes of the cell. Its shape varies considerably in different kinds of neurons. The nucleus contains the genetic material of the neurons which becomes actively engaged during the process of cell reproduction and the manufacture of protein. The soma contains most of the cytoplasm (cell fluid) of the neuron. It also contains the neuroplasm, spherical nucleus, mitochondria, golgi bodies, endoplasmic reticulum, ribosome, lysosome, fat globules, Nissl's granules and neurofibrils. Nissl's granules are comparatively large and have irregular ribosomes and the rough endoplasmic reticulum. Nissil granules are believed to be involved in the synthesis of proteins in the cell.
- (ii) **Dendrites:** The term dendrite comes from a Greek word, *dendron*, which means tree. It is through dendrites that different neurons are able to communicate with each other. Dendrites serve as important recipients of these messages. The messages that pass from one neuron to another are transmitted across the synapse. Synapse refers to a junction between the terminal button of the sending cell and a portion of the somatic cell. In special instances, the branching can be extraordinary complex, such as, in the case of the Purkinje cells of the cerebellum. Small bumps present on the dendrites are known as dendritic spines. Both the membranes surrounding the soma and the dendritic spines have the capability to receive information from other cells. A neuron may have either one or many dendrites.
- (iii) **Axon:** Every neuron has only one axon. It emerges from the soma as a single fibre, usually much longer than any dendrite. The axon is a long and slender tube, which is covered by a myelin sheath in some neurons. The axon carries information from the cell body to the terminal buttons. The basic message that it carries is called an *action potential*. When it reaches a point where the axon branches, it splits but does not diminish in size. Each branch receives a full-strength action potential.

About 80 per cent of all neurons have axons covered with the myelin sheath. The myelin sheath is a fat and proteinaceous substance which is whitish in appearance. This covering is arranged in segments, each separated at discrete intervals, along the length of the axon. These segments begin at a point just beyond the axon hillock. This point serves as an electrical insulation. Between each segment of myelin sheath, at interval of 1 mm to 2 mm, there are spaces known as the Nodes of Ranvier. At the Nodes of Ranvier, the axon is not insulated. The presence of a myelin sheath is an important feature of neurons with axons. This sheet carries information over a considerable distance. Myelinated axons carry information faster than unmyelinated ones, over a given distance. Without myelinated axons, efficient processing of information over such long distance is not possible.

The point on the axon which is nearest to the soma is called the *axon hillock*. This is a part of cyton from where the axon rises. Far away from the

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soma, the axon branches into axon collaterals, which later split into smaller branches called telodendria. The telodendria eventually branch into smaller structures at the tips. These are called terminal buttons. The axon is often very long and forms the base of each nerve fibre. The axon contains neuroplasm and neurofibrils of the neuron, but they lack Nissl bodies. The central core of the axon, which takes part in the formation of nerve fibres, is called axis-cylinder or neuroaxis.

The axons and their branches come in different shapes. Neurons can be classified (according to the way in which their axons and dendrites leave the soma) as follows:

- a. **Multipolar neurons:** are neurons in which the somatic membrane gives rise to one axon and several dendritic trees. Multipolar neurons occur in the nervous system of adults.
- b. **Bipolar neurons:** are neurons that give rise to one axon and one dendritic tree, at opposite ends of the soma. These neurons are usually sensory in nature; that is, their dendrites detect events occurring in the environment and communicate all the sensory information to the central nervous system. Bipolar neurons occur in the retina of the eye.
- c. **Unipolar neurons:** are neurons which have only one axon. They do not have any dendritic branches. A unipolar neuron has only one stalk, which leaves the soma and divides into two branches, a short distance away. Unipolar neurons, like bipolar neurons, transmit sensory information from the environment to the cells. Most of the unipolar neurons detect touch, temperature changes and other sensory events that affect the skin. Other unipolar neurons detect events in our joints, muscles and internal organs. They occur in nervous system of the embryo.

(iv) **Terminal buttons:** Most axons divide and branch many times. At the ends of these branches, there are little knobs known as terminal buttons. Terminal buttons have a very special function to perform. When an action potential travels down the axon, they secrete a chemical called neurotransmitter. The neurotransmitter either excites or inhibits the receiving cell. This helps in determining whether an action potential occurs in its axons or not. An individual neuron receives information from the terminal buttons of axons of other neuron. The terminal buttons of the axons of that neuron form synapses with other neurons. A neuron may receive information from dozens or even hundreds of other neurons, each of which can form a large number of synaptic connections with it.

Since the supporting cells protect and support neurons, by doing so they help us to survive and function effectively. The various supporting cells are, glial and schwann cells.

a. **Glia or glial cells:** (derived from the Greek word for glue) the most important supporting cells of the CNS are the neuroglia. They buffer neurons physically and chemically from the rest of the body. They also help in holding neurons to their respective place. They tend to control the supply of some of the

chemicals that are needed by the neurons to exchange messages with other neurons. They are seen to insulate neurons from one another so that the neural messages do not get scrambled. They even act as housekeepers by destroying and removing the carcasses of neuron that are killed by injury, or die as a result of old age.

There are several types of glial cells, each of which plays a special role in the CNS. The most important types of glial cells are astrocytes, oligodendrocytes and microglia.

- **Astrocytes:** They are star-shaped cells which provide physical support to neurons and clean up debris. Within the brain, they produce some chemicals that neurons need to fulfill their functions. They help to control the chemical composition of the fluid surrounding neurons. This is done by actively taking up or releasing substances the chemical concentration of which must be kept within critical levels. They are involved in providing nourishment to neurons from blood capillaries. In cases of neuronal death, astrocytes proliferate to fill the formerly occupied and now vacant spaces. They also provide the basis for a type of protective shield against certain substances, thus attempting to enter the brain from the blood stream. This selective mechanism is known as the *blood-brain barrier*.
- **Oligodendrocytes:** are present in the CNS and their principal function is to provide support to axons and to produce the myelin sheath. This sheet insulates most axons from one another. Oligodendrocytes are found in the brain and in the spinal cord.
- **Microglia:** is the smallest of the glial cells. They act as phagocytes, engulfing and breaking down dead and dying neurons. They also protect the brain from invading microorganisms and are responsible for the inflammatory reaction, in response to brain damage. They are found both, in the grey and in the white matter.

b. Schwann cells: In peripheral nervous system (PNS), schwann cells perform the functions of supporting axons and producing myelin (as performed by the oligodendrocytes). In the PNS, schwann cells provide myelin sheath for axons. In response to any damage, these cells aid in the digestion of the dead and dying axons.

Based on their functions, the neurons can be divided into sensory, motor and interneurons.

- **Sensory or afferent neurons:** are neurons that detect changes in the external or internal environment and send information about these changes to the CNS. They gather information in the form of light, sound waves, odor, taste or contact with objects.
- **Motor or efferent neurons:** are neurons that are located within the CNS which controls the contraction of a muscle or the secretion of a gland. It is responsible for movement.

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- **Interneurons/adjustor neurons:** In between the sensory and the motor neurons, lie the interneurons. They are seen to lie entirely within the CNS. Circuits of interneurons are responsible for perceiving, learning, remembering, deciding and controlling complex behaviour for distant transmission of impulses.

Nerve fibres transmit messages through nerves, from a sense organ to the brain or from the brain to a muscle or gland. When dendrites are stimulated by a noxious stimulus, such as contact with a hot object, it sends messages through the axon to the terminal buttons, which are located in the spinal cord. The terminal buttons of sensory neurons release a transmitter substance that excites the interneuron, causing it to send messages down its axon. Terminal buttons of the interneuron release a transmitter substance that excites the motor neuron, which in turn, sends messages down its axon. The axon of the motor neuron joins a nerve and travels to a muscle. When terminal buttons of the motor neuron release their transmitter substance, the muscle cells contract and cause the hand to move away from the hot object.

In the above -mentioned example, the synapse had an excitatory effect. They can also have inhibitory effects. Suppose a hot casserole has been removed from an oven. As one holds it, the heat begins to penetrate through the thin potholders. The pain caused by the hot casserole triggers a withdrawal reflex that tends to make one drop it. The pain from the hot casserole increases the activity of excitatory synapses on the motor neurons. This tends to cause the hand to pull away from the casserole. However, this excitation is counteracted by the inhibition which is supplied by another source, the brain. An axon from a neuron in the brain reaches in the spinal cord, where its terminal buttons form synapses with an inhibitory interneuron. When the neuron in the brain becomes active, it excites this inhibitory interneuron. The interneuron releases an inhibitory transmitter substance, which decreases the activity of the motor neuron, blocking the withdrawal reflex. These neural circuits send information to the spinal cord that prevents the withdrawal reflex, from making one drop the dish.

The axon forms the basis of the nerve fibre. Based on the structure, nerve fibres are of two types, namely, myelinated and unmyelinated nerve fibres.

Myelinated nerve fibres: are also known as the medulated nerve fibres. In these nerve fibres, around the neuraxis, a sheath of fatty substance is formed. This is termed as medullary or myelin sheath. The myelin sheath is not continuous. It is absent at certain intervals, due to which nodes are produced. These are called the Nodes of Ranvier. The part between adjacent nodes is called internode. The medullary sheath and the Nodes of Ranvier are surrounded by a transparent cellular outer covering, known as neurolemma. A thin layer of cytoplasm lies just beneath the neurolemma. This layer contains nuclei to form schwann cells at regular intervals. These nuclei are known as the nuclei of Schwann cells. The modulated nerve fibres are found in the brain, spinal cord, cranial and spinal nerves. In the CNS, medulated nerve fibres form the white matter.

Unmyelinated nerve fibres: lack myelin sheath. In these fibres the neuraxis is surrounded by neurolemma. Just below the neurolemma, a layer of cytoplasm containing nuclei is present. The Nodes of Ranvier and the internodes are absent in these nerve fibres. Unmyelinated nerve fibres are found in the autonomic nervous system. In the CNS, unmyelinated nerve fibres form the grey matter.

On the basis of their function, nerve fibres are of two types, namely, sensory and motor. The afferent or sensory fibres carry sensory impulses from receptor organs to the CNS (brain and spinal cord), whereas, the efferent or motor fibres carry impulses from the CNS to the various effectors organs or muscles and glands.

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CHECK YOUR PROGRESS

1. Which are the two main divisions of the nervous system?
2. What is the main function of the optic nerve?
3. Why is the autonomic nervous system also known as the visceral motor system?

3.3 NEUROANATOMICAL TECHNIQUES

Neuroanatomical techniques are required to study the neuron but there are some problems in undertaking this study. The main problem in the study of neuron has little to do with their size but more to do with the fact that several neurons are quite tightly packed and their axons and dendrites are intricately intertwined. As a result, an unprepared neural tissue under the microscope hardly reveals any valuable information.

In order to enhance one's understanding about neurons, several neuroanatomical techniques are used. These techniques enable the researchers to get a clear view of the different aspects of a neuronal structure. The knowledge so obtained from each of these preparations is combined together to get a better understanding of the structure of the neuron.

(i) Golgi Stain

It is a technique which was discovered by the Italian physician, Camillo Golgi, in the early 1870s. This technique was accidentally discovered when Golgi was trying to stain the meninges by exposing a block of neural tissues to potassium dichromate and silver nitrate. He noticed that the silver chromate which was created by the chemical reactions of potassium dichromate and silver nitrate, invaded in a few neurons in each slice of the tissue. Each invaded neuron was stained entirely black. As a result of this, individual neurons became visible for the first time. This technique was thus known as the Golgi Stain technique. One major drawback of this technique was that it blackened all neurons on a slide. It provided no information

about the structure of the neurons, as they were tightly packed together. Although the Golgi stain method was able to make the neuron clearly visible, but it failed to provide any information about the number of neurons and the nature of their inner structure.

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(ii) Nissl stain

In order to deal with the shortcomings of the Golgi stain method, the technique of Nissl stain was developed. This technique was developed by the German psychiatrist, Franz Nissl. In this technique, the most commonly used dye is cresyl violet. The cresyl violet and other Nissl dyes penetrate all cells on a slide, but they bind effectively only to the structures in neuron cell bodies. This enables one to count the number of neurons by counting the number of Nissl-stained dots.

(iii) Electron microscopy

Electron microscopy is the method which enables us to understand and gain information about the details of neuronal structure. These details cannot be obtained using a light microscope as its level of magnification is only about 1500 times. This level of magnification is insufficient to know the details of the internal structure of the neurons. In this regard, the technique of electron microscopy appears quite useful. In this method, a slice of neural tissue is taken and is coated with a substance that absorbs electrons. This substance is taken up by different parts of the neuron, in different degrees. Then, a beam of electrons is passed through the tissue onto a photograph film. This results in the formation of an electron micrograph. The electron micrograph captures exquisite details of the neuronal structure. A scanning electron microscope provides spectacular electron micrographs in three dimensions. When compared to conventional electron microscopes, the scanning electron microscope is able to provide better magnification.

(iv) Myelin stains

Myelin stains is a technique which is used to study and visualize myelinated axons which are usually seen in the white matter of the brain. Myelin stains tend to selectively dye the myelin sheaths of axons but they are not useful in tracing the pathways of neurons. Some reasons behind this are given below:

- They fail to tell us much about the pathways of neurons as they do not stain the unmyelinated axon, thus making it impossible to track unmyelinated axons.
- They provide no information about the termination and origin of myelinated axons, as the terminal branches of myelinated axons are unmyelinated.
- Since this technique stains all myelinated axons indiscriminately, hence it becomes impossible to trace it through a series of slices, once a myelinated axon mingles with others.

(v) Neuroanatomical tracing techniques

Neuroanatomical tracing techniques are of two types, anterograde and retrograde. The anterograde tracing technique is used when one wants to study the path of axons which are projecting away from the cell bodies and are located in a particular area. In this technique, a specific chemical is injected in the area and is taken up by the cell body. It is transported forward to the terminal buttons along the axon. After few days, the brain is removed and sliced to see the location of the injected chemical. In contrast to the anterograde tracing method, the retrograde tracing method is used when one wishes to trace the path of axons that are projected within a particular area. This technique requires the researcher to inject a particular chemical in a specific area. The chemical so injected is then taken up by the terminal buttons and is transported backwards along their axons, to their cell bodies. After a few days the brain is removed and sliced to see the location of the injected chemical.

3.4 MAJOR DIVISIONS OF THE BRAIN

The brain has four major divisions:

- (i) Brainstem (including the medulla oblongata, pons and midbrain)
- (ii) Cerebellum
- (iii) Cerebrum
- (iv) Diencephalon

The diencephalon is further divided into thalamus, hypothalamus, epithalamus and ventral thalamus or subthalamus.

3.4.1 Functional Description of the Brain

Brain is the anterior most part of the CNS which is lodged in the cranial cavity (cranium) of the skull. The brain is covered by 3 membranes, namely the pia mater, arachnoid matter and the dura mater.

Pia mater: is the innermost, thin and very delicate vascular membrane that closely invests the brain.

Arachnoid matter: is a thin, 'spider webby' structure, from which it gets its name.

Dura mater: is the outermost, tough fibrous membrane which adheres closely to the inside of the skull.

The space between the arachnoid membrane and pia mater is known as subarachnoid space, whereas, the space between the arachnoid membrane and dura mater is known as subdural space. Both these spaces are filled with cerebrospinal fluid. This fluid serves as a pad to cushion the CNS from shocks. It also provides a medium for exchange of food, waste, respiratory gases and other materials.

The brain is functionally divided into:

- (i) **Rhombencephalon (hindbrain):** This consists of pons varolii, medulla oblongata and cerebellum.
- (ii) **Mesencephalon (midbrain):** This comprises of brain stem, superior and inferior colliculi, reticular formation, red nucleus, and substantia nigra.
- (iii) **Prosencephalon (forebrain):** This consists of two cerebral hemispheres (i.e., right and left hemisphere), corpus callosum, cerebral cortex with 4 lobes, limbic system, basal ganglia, thalamus and hypothalamus.

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(i) Hindbrain

Hindbrain is the link between the spinal cord and the brain. It surrounds the fourth ventricle and contains the following two major divisions:

- a. The metencephalon: which consist of the Pons Varolii and the cerebellum
- b. The myelencephalon: which consist of the medulla
 - i. **Cerebellum:** it is the second largest part of the brain. It is dorsal to the medulla and the pons. It represents about one eighth of the weight of the entire brain and lies underneath the skull, approximately at the nape of the neck. It consists of two lateral cerebellar hemispheres and a central worm-shaped part, known as the vermis. A cross section of the hemisphere shows a branching tree like arrangement of grey and white matter. This is known as *arbor vitae* (the tree of life). It resembles a miniature version of the cerebrum. It is covered by the cerebellar cortex and has a set of deep cerebellar nuclei. These nuclei receive projections from the cerebellar cortex and send projections to other parts of the brain. Each hemisphere of the cerebellum is attached to the dorsal surface of the pons, through bundles of axons (the superior, middle and inferior cerebellar peduncles).

The primary function of the cerebellum is motor coordination and transmitting positional information from the inner ear and individual muscles. Serious problems of motor control range from disturbances in balances to flaccid muscles or tremors. These result from lesion in the cerebellum. Any damage to cerebellum impairs standing, walking or performance of coordinated movements.

The cerebellum receives visual, auditory, vestibular and somatosensory information and it also receives information about individual muscle movement, being directed by the brain. The cerebellum integrates this information and modifies the motor outflow by exerting a coordinated and smoothing effect on the movement. Cerebellar damage results in jerky, poorly coordinated and exaggerated movements.

- ii. **Pons Varolii:** It was named by Varolius, a 16th century anatomist. It is situated in front of the cerebellum below the midbrain and above the

medulla oblongata. The pons contains a portion of the reticular formation in its core. This formation includes some nuclei that are important for sleep and arousal. It also contains a large nucleus that relays information from the cerebral cortex to the cerebellum.

- iii. **Medulla oblongata:** It extends from the pons varolii above and is continuous with the spinal cord below. Its shape is like a pyramid. The medulla oblongata has a very thin, nonvascular, folded structure on its lower side. This is known as the posterior choroid plexus.

It is largely a continuation of the spinal cord. The major ascending and descending pathways of the spinal cord pass through the medulla. The medulla oblongata plays a crucial role in regulating the basic life support systems of the body. It controls blood pressure, the rhythm of breathing, heart rate, digestion and vomiting. It also regulates the cardiovascular system, respiration and skeletal muscle tone.

(ii) Midbrain

Midbrain defines the region between the hindbrain and forebrain. It is generally divided into tectum and tegmentum.

- a. **Tegmentum:** includes the rostral end of the reticular formation, several nuclei controlling eye movements, the periaqueductal grey matter, the red nucleus, the substantia nigra and the ventral tegmental area.

- i. **Reticular formation:** is a large structure consisting of many nuclei. It is also characterized by a diffused, interconnected network of neurons with complex dendrites and axonal process. The reticular formation occupies the core of the brain stem, from the lower border of the medulla to the upper border of the midbrain. The reticular formation receives sensory information by means of various pathways and projects axons to the cerebral cortex, thalamus and spinal cord. It plays a role in sleep and arousal, attention, muscles tone, movement and various vital reflexes. That is why it is also known as reticular activating system (RAS).
- ii. **Periaqueductal grey matter:** is so called because it mostly consists of cell bodies of neurons that surround the cerebral aqueduct, as it travels from the third to the fourth ventricles. It contains neural circuits that control sequences of movements that constitute species-typical behaviour such as fighting and mating.
- iii. **Red nucleus:** A bundle of axons that arise from the red nucleus constitutes one of the two major fibre systems, which bring motor information from the cerebral cortex and cerebellum to the spinal cord. Rubrospinal tract, which is a very important nerve, starts from the red nucleus and takes information from the brain to the spinal cord.

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iv. **Substantia nigra:** is so called because it is very dark in colour and is connected to the basal ganglia of the Forebrain. It is black because of melanin (a hormone) and is involved in dopamine (neurotransmitter) synapses. It contains a neuron whose axons project to the caudate nucleus and putamen (parts of the basal ganglia). It is also responsible for balance and movement, i.e., starting and stopping of movements. People with Parkinson's disease exhibit degeneration of this area.

b. **Tectum:** It lies just above the pons varolii. It contains two pair of nuclei, namely the superior colliculi (which receives information for the visual system and also controls the eye movement) and inferior colliculi (which receives information for the auditory system and controls the movement related to sound). In mammals, both, the superior and inferior colliculi are primarily involved in visual reflexes and reactions to moving stimuli.

(iii) Forebrain

The forebrain surrounds the rostral end of the neural tube. It consists of diencephalon and telencephalon.

a. **Diencephalon:** surrounds the third ventricle. It consists of the thalamus and hypothalamus.

i. **Thalamus:** has two lobes, connected by a bridge of gray matter known as the mass intermedia.

ii. **Hypothalamus:** lies at the base of the brain, under the thalamus. It is situated on both sides of the inferior portion of the third ventricle. It is a complex structure which contains many nuclei and fibre tracts. The pituitary gland is attached to its base, via the pituitary stalk. This is called infundibulum. Hypothalamus regulates activities like, eating, drinking and sexual behaviour. It controls the endocrine behaviour and maintains homeostatis. Electrical stimulations of the hypothalamic nuclei produce feelings of pleasure, pain, etc.

b. **Telencephalon:** consists of the basal ganglia, limbic system and the cerebrum.

i. **Basal ganglia:** it is an important component of the motor system. According to Snell (1987), basal ganglia consists of the corpus straitum, amygdoid nucleus and the claustrum. The **corpus straitum** lies lateral to the thalamus and further, consists of caudate nuclei and lentiform nuclei (lens shaped nuclei). The corpus straitum plays an important role in the control of posture. Caudate nucleus is a large nucleus that adheres close to the thalamus on one side and to putamen on the other. Caudate nucleus is believed to be important in personality development. The lentiform nuclei consist of putamen and globus pallidus. The putamen lies adjacent to the caudate and its functions are associated with caudate nuclei. The caudate is separated from the putamen by means of the internal capsule. The globus pallidus is

involved in the initiation of the movement. The amygdaloid nucleus lies at the end of the tail of the caudate nucleus, in the temporal lobe. It is part of the limbic system. Claustrum is a thin sheet of grey matter with uncertain functions.

- ii. **Limbic system:** near the midline of the brain, there is a circuit of interconnected structures that form a ring around a central part of the brain. This ring is called the limbic system. It consists of the cingulate gyrus, parahippocampal gyrus, subcallosal gyrus, hippocampus, hypothalamus, anterior nucleus of the thalamus, amygdaloid nucleus and septal area. The limbic system largely deals with emotions. It also plays a role in perception, memory and certain types of behaviour. It provides bridges that link brain, mind and behaviour in a functional continuum. It is involved in mediating intellectual reflection; in decoding and transmission of affective signals; in the recognition of threat; elaboration of aspects of aggressive behaviour and in dreaming. Hippocampus is believed to play an important role in long-term memory.
- iii. **Cerebrum:** is the largest and the most complex part of the human brain. It consists of the right and the left hemispheres, which are connected by a large bundle of myelinated fibres called the corpus callosum and other small fibre bundles. The corpus callosum is folded back to form the genu in the anterior section. In the posterior section, it curves ventrally to form a rounded splenium which joins a fibrous strip called fornix. The fornix is a paired structure, with each of the pair being present in each hemisphere.

The outer layer of the cerebrum has many folds. The cerebral cortex forms the grey matter of the cerebrum. The upward folds are called gyri and the downward grooves are called sulci. A very deep fissure, known as the central fissure, separates the two hemispheres. Each hemisphere of the cerebrum is divided into four lobes: the frontal lobe, the parietal lobe, the temporal lobe and the occipital lobe.

- **Frontal lobe:** is the most developed part of the brain and makes up about one-third of the mass of the cerebral hemisphere. It is divided into the motor area, premotor area and the prefrontal area. The area of the frontal lobe which is closest to the central sulcus is known as the motor area. Near the forehead, in the frontal region is the premotor cortex. At the front of the brain, is the large prefrontal cortex. In humans, it accounts for almost one-third of the entire weight of the cerebral cortex. Its two specialized areas: the frontal eye field and the Broca's area. The frontal eye field is situated in the middle zone of the dorsolateral surface, taking prefrontal and the premotor area. The Broca's area is situated in the front of the motor cortical area and in the prefrontal cortex.

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The frontal regions have well developed systems of efferent nerve cells that lead from the cortex to the lower brain centres and the peripheral parts of the nervous system. Efferent projections from the frontal area pass to the entral and dorsal nuclei of the thalamus, as well as the numerous other structures. The afferent fibres reach the frontal cortex through thalamo-frontal radiation. According to Luria, there is hierarchical arrangement in the frontal lobe. The region of primary association is the motor cortex, the secondary association is the pre-motor cortex and the tertiary association is the pre-frontal cortex.

The main connections in the frontal lobe are the projections from the pre-frontal cortex to the pre-motor and motor area. There are corticocortical connections from the posterior part of the temporal auditory and visual association regions and the medial temporal lobe. These connections are reciprocal in nature. There are also reciprocal corticocortical connections from the medial temporal lobe and anterior temporal lobe. There are thalamic connections from three thalamic areas, including the anterior nuclei, dorsomedial nuclei and the pulvinar region. The frontal lobe also has reciprocal connections with the amygdala. Nonreciprocal connections are also present from the frontal cortex to the caudate nuclei. Projections extend from the frontal lobe to other sub-cortical structures, especially to the superior colliculus and hypothalamus. Projections from various areas of the brain stem to the frontal lobe are also present.

The frontal lobe has several functions. The motor area of the frontal lobe is responsible for controlling movement in different parts of the body. The specialized subsections of the motor cortex correspond to specific body parts. That is why, damage to the motor area results in paralysis. The premotor area controls fine motor movements like passing a threading through a needle. The primary motor cortex is also known as the precentral gyrus. This motor region is specialized to control and coordinate fine and gross movements on the contralateral side of the body. The prefrontal area is involved in an individual's ability to make judgments, plan, attend, reason, perseverance, solving problems, critical thinking, forward thinking, organize, control impulse and engage in self-monitoring. It integrates our personality with emotions and is involved in working of the memory. Frontal eye field is believed to mediate voluntary and involuntary eye movement. The Broca's area controls the movements of our mouth and tongue and is involved in speech production. Lesions to the Broca's area result in a language disorder known as *aphasia*. However, the Wernicke's area is more involved in comprehension of speech.

Damage to the frontal lobe

Due to their location at the front of the cranium, frontal lobes are extremely vulnerable to injury. Damage to motor cortex results in disintegration of motor activities; inability to plan and coordinate a sequence of complex movements that are needed to complete multi-stepped tasks like making coffee, etc. Damage to speech areas results in disorganization of the speech activity. Damage of the Broca's area leads to expressive aphasia and damage to the Wernicke's area leads to inability of

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comprehending language or speech. Lesions anterior to the Broca's area result in other speech disturbances like inability to make spontaneous discursive statements, difficulty in expressing thought in discursive speech, frontal dynamic aphasia, etc. Damage of prefrontal cortex leads to the frontal lobe syndrome. Bilateral frontal damage results in personality changes (like diminished anxiety, concern for future, lack of initiative and spontaneity, mild euphoria, mania, lack of initiative and spontaneity) and intellectual changes (such as impaired integration of behaviour over a period of time, loss of abstract thinking, impairment in recent memory and inability to plan). Confabulation often accompanies amnesia. Berlyne (1972) distinguished between two forms of confabulation, namely, momentary confabulation (involves production of autobiographical material, often of habitual nature, where the responses are brief but not stereotyped) and fantastic confabulation (is less common and often arises spontaneously). Such individuals are seen give an instrumentally appropriate but exaggerate response to objects that were introduced to them. They are seen to perform poorly on tasks of abstraction. They tend to have difficulty in carrying out everyday tasks that have multiple sub-goals. These sub goals are necessary for successful completion. The extent of difficulty depends on the location of the lesion. They are usually affected by posterior and superior lesions.

Posterior lesions cause loss of spatial organization which leads to constructional difficulties. These are termed as *constructional apraxia*. This is a failure to organize and integrate the components into a whole. There is an apparent lack of full awareness of deficits, which may result from a general loss of some feedback mechanism, disturbance in signals of error and inadequate evaluation of patients own actions. A lack of flexibility in their approach to many situations is seen in such individuals. A reduction in their ability to shift from one concept to another takes place. The behaviour of these individuals is characterized by inflexibility, rigidity and perseveration or stereotyped behaviour. These individuals exhibit memory impairment for recent memories and difficulty in voluntary hearing or memorization.

- **Temporal lobe:** lies below the lateral cerebral fissure of the Sylvius. It resides between the frontal and occipital lobe, approximately at the midline of the skull. It is richly connected to other lobes, sensory system, limbic system and basal ganglia. It contains the primary olfactory, auditory and peripheral projection areas.

The temporal lobe helps in the integration of visual perception with information from other sensory system. It also helps in integration of sensory information, keeping a record of conscious experiences and perception and recognition of auditory stimulation. It provides olfactory information, controls emotions and stability of mood, helps in acquisition of memory, comprehension of language and in the understanding of social cues.

The dominant side of the temporal lobe (usually left) is involved in an individual's ability to receive and understand speech and written words. Problems in this region lead to miscommunication and reaching disabilities. Memories are

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integrated and stored in the temporal lobe. The hippocampus is associated with long term memory. It enables the retrieval of language or words. Optimal activity in temporal lobe enhances the stability of mood. Increase and decrease in temporal activity leads to fluctuation of moods. It also plays a role in visual and auditory processing. The nondominant side of the temporal lobe (usually right) is involved in the reading of facial expression, processing of verbal tone and motivation, hearing rhythm and appreciation of music, visual learning and understanding of social cues.

Damage to the temporal lobe results in certain disturbances. For instance, damage to the acoustic nerve leads to deafness on the side of damage. Damage to principal auditory pathway in the brainstem leads to partial deafness, as both crossed and uncrossed pathways are present in this tract. Lesions in the auditory association cortex of the left side, produces sensory or receptive aphasia. Acoustic agnosia is association with right hemisphere lesions.

Disorders of phonemic hearing are produced by lesions in superior temporal gyres. Disorders of phonemic hearing refer to difficulty to learn new language, as the individual cannot distinguish between phonemes like [P],[b]; difficulty in understanding spoken; lack of awareness of one's own defective speech leading to a word salad; difficulty in writing when the material is dictated but are able to readily copy written material.

Auditory amnesic aphasia is produced by lesions in the middle temporal gyrus. Auditory amnesic aphasia refers to inability to repeat a series of words that have been presented acoustically. With a series of words, the patient may show primacy effect (repeating the first word) recency effect (repeating the last word) and loss of other members of the series.

Nominal aphasia is produced by lesions in the posterior temporal lobe. In it, the person is able to perceive an object but cannot name it. But circumlocution can describe its use or function. Damage to the temporal lobe leads to inability to integrate visual perceptual information with the information from other sensory receptors, effectively. Damage to olfactory pathways leads to anosmia. Lesions in the olfactory receptive area lead to olfactory hallucination. These are known as uncinatate fits. Two phenomena known as Déjà vu (seen before) and Jamais vu (never seen, never heard) are frequently experienced by patients with temporal lobe seizures.

Unilateral lesions in the dominant temporal hemisphere lead to poor performance and memory on verbal tasks, whereas, unilateral lesions in the nondominant hemisphere, leads to poor performance and memory in non-verbal tasks.

Bilateral lesions are associated with general amnesia syndrome (in which the memory loses are profound, pervasive and generally lasting). But all memory functions are not lost. In transient global amnesia (in which defects occur for four to eight hours, during which memory for several functions is lost), both anterograde

and retrograde amnesia are found. Recovery is usually rapid and automatic. Vestibular and cerebellar disturbances are associated with bilateral lesions.

- **Parietal lobe:** the term parietal means side. It is another term for the parietal bone on the side of the head. It lies behind the frontal lobe and the center fissure, above the temporal lobe and in front of the occipital lobe. It is closely related in function to each of the other lobes of the brain. Parietal lobe has two main surfaces, namely, the lateral aspect and the medial aspect. The anterior border of the lateral aspect is formed by the central sulcus and its posterior border is formed by the parietal occipital sulcus. The lower border separates the inferior part of the parietal lobe from superior part of the temporal lobe. The intraparietal sulcus divides it into superior parietal lobe and inferior parietal lobe. The anterior border of the medial aspect is formed by the central sulcus, which extends about the midway through the para-central lobule, to the top of corpus collasum. The posterior border is formed by the parieto occipital sulcus, the region anterior to which is known as the precuneus. It is difficult to precisely draw its boundaries.

The parietal zone is divided into the anterior parietal cortex (containing the central gyre, known as the somatosensory cortex) and the posterior parietal cortex. The posterior parietal cortex is further divided into the superior parietal lobule and the inferior parietal lobule. The parietal lobe is connected to other parts of the brain. The main afferents to the posterior parietal cortex project from the pulvinar in the posterior thalamus and other cortical regions. The parietal lobe in turn, sends its major projections to the frontal and temporal association cortex as well as sub cortical structures. These include the pulvinar and the posterior region of the straitum, midbrain and spinal cord. The corticocortical projections to the frontal lobe provide sensory input to the frontal lobe because there are no direct sensory projections in this region. The descending projections to the straitum and the spinal cord in particular, probably function as a guidance system in the control of movements in space.

The anterior parietal cortex integrates and coordinates the following sensory streams:

- o Touch or tactile stream: may be superficial on the surface of the skin or may be deep.
- o Pain stream: gathers information all over the surface of the body in the skin and perhaps to some extent in the walls of some of the viscera. These are bare nerve endings, which immediately report any contact that is likely to be injurious. It is a subjective phenomenon.
- o Temperature stream: provides information about different degrees of heat and cold.
- o Position sense: provides awareness of the extent and direction of movement.

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- o The two point sensibility refers to the ability of an individual to accurately localize the two points that have been stimulated simultaneously, on the surface of the body.
- o Topognosis: tells us where certain stimuli are being applied, on the surface of the body or within the body.

The anterior parietal cortex is also involved in certain other functions like integrating information from multiple sensory modalities like visual, auditory, etc. It also integrates information about spatial location with visual and tactile information. Because of anterior parietal cortex, we are able to recognize the same object from different visual angles and are able to draw or use maps to guide movement. It also has the discriminative capacity that enables finer control of the body in expressive behaviour.

The main function of the superior parietal lobule of the posterior parietal cortex is the construction of spatial representation of the world. It is also regarded as the association cortex, part of which may be concerned with motor functions. However, the main function of the inferior parietal lobule is to recognize and produce abstract stimuli. It has two components, namely the sensory component (which is involved in perceiving objects and symbols) and the motor component (which is involved in covert manipulation of symbols, for example, mental rotation of objects). It is also implicated in language functions (for example, it contains the Wernicke's area).

Damage to the parietal lobe results in several disturbances. For instance, it leads to sensory and perceptual disturbances like impaired somatosensory discrimination, difficulty with complex sensorimotor task (such as using scissor, dressing and transient or permanent loss of somesthetic sensation). It also results in disorders of tactile perception in which an individual's judgment of stimulus orientation is impaired.

Damage to the parietal lobe is also associated with an individual's inability to recognize objects with touch (tactile agnosia), failure to synthesize separate tactile sensation into the perception of form (amorphosynthesis), impaired performance on cross modal matching task like reading and writing (disorders of inter-sensory association), acalculia (the person may remember and understand the problem and the rules, but may be unable to carry out the necessary operation), difficulty in carrying out abstract logical relations of syntax. Damage to parietal lobe also impairs an individual's spatial orientation. It results in impaired judgment of the location or orientation of stimuli, both, with respect to each other and to the person. Impairment in the memory for location is seen (disorder of location and orientation). The individual may be unable to recall the spatial arrangement of familiar surroundings and may be unable to recall and describe well-known geographical relationship, with which the patient was formerly familiar (topographical disorientation and loss of topographical memory). He may be unable to find his way in long and familiar surrounding, or in a frequently encountered location, in the recent past (difficulties of finding route). Such patients may be able

to give adequate verbal description of familiar routes but are unable to execute them. It may result from an inability to recognize objects that serve as landmarks (topographical amnesia).

Constructional apraxia may also occur due to disruption between the visual and kinesthetic processes. The right hemisphere lesions produce more consistent disturbance than the left, while posterior lesions of either hemisphere produce more consistent disturbances than anterior ones. Sometimes such patients can recognize letters and words but are unable to read them (spatial dyslexia). This may be due to difficulty with continuous scanning movements that are necessary for reading. Unilateral spatial neglect (USN) is caused by lesions in the posterior region. It refers to an individual's tendency to neglect one half of tasks like drawing and reading. This neglect can affect both, visual and tactile modality.

The disorders of body schema are more prominent with right parietal lesions than with left parietal lesions. These refer to an individual's failure to perceive illness (anosognosia). These individual's may show denial of unilateral paralysis with damage to the right hemisphere. They tend to rationalize their failure to use the paralyzed limbs.

Occipital lobe: forms the posterior part of the cerebral hemisphere. It is divided into the medial side and the lateral side. On the medial side, the parieto-occipital fissure is seen, whereas on the lateral side, it merges with parietal lobe and the temporal lobe. Cytoarchitectural studies have shown that cortical cellular compositions of various layers of the occipital lobes vary from place to place. This difference in structure may suggest difference in functions.

Broadman (1909) proposed three areas of the occipital lobe, namely, the striate region, the parastriate region and the peristriate region. In the striate region, fibres carrying information from visual receptors from the retina reach their termination. It is known as the visual cortex. The parastriate region surrounds the striate region and is known as the secondary sensory area. It is concerned with elaboration and synthesis of visual information. It has several inter-hemispheric connections with corresponding areas in the other hemisphere. The peristriate region is concerned with the unity of visual information with speech and other executive functions and is concerned with the visual memory.

The occipital lobe has numerous inter-hemispheric or commissural fibre connections with corresponding areas in other hemispheres. This area is surrounded by the peristriate region, which borders the parietal and the temporal lobe. It appears to be chiefly involved in the integration of visual information with the information gathered by auditory and other sensory systems. It also unites visual information with the brain systems subserving speech and other executive functions. The occipital lobe is primarily concerned with vision. Each eye lens focuses the stimulation arising in the outer part of the each visual field onto the inner half of each retina and vice versa. Fibres from the outer half of the retina enter the lens on the same side, but fibres from inner half of retina cross the midline and enter the contralateral hemisphere. Thus each eye projects visual information to each

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hemisphere. From the optic chiasm, visual pathways move backward into lateral geniculate bodies. These bodies convey neural information to the visual cortex. The final part of optic pathways is known as optic radiation. The geniculocalcarine tract passes through an area known as temporal isthmus. From here, the fibres reach the calcarine cortex.

Defects in the visual field lead to several disorders. For instance, cerebral blindness involves both white matter and the cortex. It is caused by cerebral ischemia that is produced by narrowing or occlusion of the posterior cerebral artery. It is characterized by the loss of vision in half of the contralateral field. When occipital fibres on both sides are affected, then complete blindness occurs. It is followed by a period of unconsciousness or confusion known as the vascular confusion. It is also accompanied by the amnesic syndrome of marked severity. Damage to optic radiation leads to complete blindness in relative area of the visual field (blind sight). Some subjects may show colour discrimination.

Some individual's shows indifferences and lack of awareness for their defect (denial of blindness or Anton's syndrome). The degree of denial is associated with the location of the lesion. Some patient's may show reverse of Anton's syndrome, where they may deny perception. Some subjects may see complete objects even when some part is covered by card (known as adaption of visual deficits). This depends upon their past experiences and expectations. Some individuals may show hysterical blindness.

Bilateral occipital and parieto-occipital lesions lead to disorders in depth perception. A few of the patients may be unable to recognize objects with visual sense (visual agnosia). They may be unable to recognize, name or use an object but can recognize the object through other sense modalities like touch (visual object agnosia). Some patients may be unable to recognize faces (prosopagnosia). These individuals can recognize a face as a face, can identify its feature but cannot identify familiar faces like those of friends, family members, etc. Some individuals are unable to associate colour with its concept (colour agnosia), some are unable to recognize words or copy written material or read a sentence. In spelling alexia, patients can identify specific letters and can spell words without understanding them.

Elementary hallucinations result from focal epileptic seizures in the occipital lobes.

Functions of brain

In order to understand the functions of brain, it is essential to study both, structural and the functional relationships. Broadly speaking, the brain performs the following three functions:

- Controlling vital body functions, i.e., regulating body functions like blood flow, B.P., respiration, etc., in relation to energy demands. It is influenced by events in the hypothalamic region of the forebrain.

- Maintaining contact with the environment by means of gathering sensory information and in turn producing appropriate motor response. This involves all three structural divisions of the brain.
- Selection of appropriate response on the basis of present needs which are derived from past experiences. These include, memory, learning, etc. It is controlled by the cortical part of the forebrain.

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3.4.2 Blood Supply to the Brain

For the brain to function effectively, it is essential that it receives proper supply of blood. Interestingly, our brain is only about 2 per cent of our overall body weight, but it takes nearly 15–20 per cent of the blood supply. The blood supply to the brain is also important as the brain cells are seen to die even when the blood supply is stopped for a moment. Blood also carries oxygen, carbohydrates, amino acid, fats, hormones and vitamins to the brain. These substances are essential for the brain to function properly. Blood also removes harmful substances like carbon dioxide, ammonia, lactate and hormones.

There are two pairs of arteries which supply the blood to the brain. These are known as the internal carotid arteries and vertebral arteries. The entire body, except the lungs, gets supply from the artery which is known as aorta. The aorta is further divided into two subclavian arteries. Each subclavian artery has two main branches, namely, the carotid and the vertebral. Both, the carotid and the vertebral, carry blood to the brain. Each carotid is divided into two parts, external and internal carotid. External carotid supplies the blood to the face and internal carotid supplies the blood to the brain. This is shown in Figure 3.1.

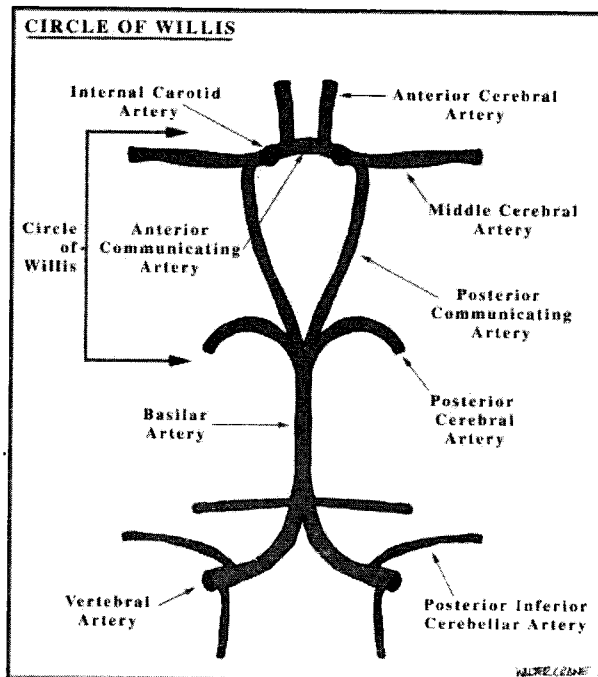


Fig. 3.1 Cerebral Arterial Circle

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The internal carotid ascends along one side of neck and passes through the temporal lobe. There, it enters the subarchonoid space. From there, they run posterior to the medial end and the fissure of Sylvius. Thereafter, they bifurcate into the anterior and the middle cerebral artery.

The anterior cerebral artery supplies blood to the medial cortex, including the motor and sensory strip. Damage to this artery can cause motor and sensory loss in the lower body. It also provides blood to some parts of frontal lobe and the corpus striatum. Damage to this area may result in cognitive and motor problems.

The middle cerebral artery and its branches supply the blood to each lateral hemisphere, including cortical areas like Broca's area, Wernicke's area, Heschl's gyrus, angular gyrus and most parts of the corpus striatum. Damage to this part can cause aphasia, impaired cognition, corticohyposthesia, numbness, or problems with hearing and sense of smell.

Two other arteries known as the anterior communicating artery and the posterior communicating artery, arise from the internal carotid arteries. The anterior communicating artery joins the anterior cerebral arteries of each hemisphere together. The posterior communicating arteries join the middle cerebral arteries to the posterior cerebral arteries, which are parts of the basilar artery system. Through the magnum foramen, both the vertebral arteries enter the brain. Once in the brain, they continue to ascend, travelling beside the brain stem. The two vertebral arteries join together to form the basilar artery or the vertebro-basilar artery. The posterior inferior cerebellar artery not only supplies blood to the cerebellum, but also takes blood to the lateral medulla. The anterior and posterior spinal arteries supply blood to the ventral and dorsal medulla respectively (Fitzgerald 1996).

The posterior cerebral arteries supply blood to the posterior fossa of the skull, medial area of the occipital lobes and inferior aspects of the temporal lobes. They also supply blood to the midbrain and deliver blood to the thalamus and some other sub cortical structures. Blockages in this artery can affect the sense of smell and cause cranial nerve damage, as well as visual problems, including visual agnosia, hemianopsia and alexia.

The vertebral arteries join together at the base of the brain and form a single basilar artery. The basilar artery joins the blood supply which is given by the internal carotid arteries, in a ring at the base of the brain. This ring of arteries is called the Circle of Willis. The Circle of Willis provides a kind of safety mechanism. Suppose, if one of the arteries gets blocked, this circle will still provide blood to the brain.

The blood-brain barrier (BBB) is important for the functioning of the brain as it protects our brain from the unwanted substances like bacteria, red blood cell toxins, etc. The blood-brain barrier is a cellular and metabolic barrier which is located in the capillaries within the brain, alters permeability. On one hand, it restricts the passage of some chemical substances and microscopic objects from the blood stream and on the other, it allows the passage of some substances to the brain like

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oxygen, glucose, amino, acids and white blood cells. It also works to control the volume in the vertebrate brain (its hard brain case) by maintaining constant levels of ions and peptides and limiting the movement of water and salts. In this way it helps in maintaining a constant environment for the brain. The blood-brain barrier also protects the brain from hormones and neurotransmitters that keep circulating with the blood stream, throughout the rest of the body. In several diseases like multiple sclerosis and meningitis epilepsy, the blood-brain barrier is seen to be broken.

3.4.3 Neuroimaging Techniques

Neuroimaging techniques are used to provide images of various organs of interest to the researcher. For example, it helps one to obtain images of a living brain. Now let us know more about various neuro-imaging techniques, as given below:

X-rays: For an X-ray photograph to be taken, one is required to pass a beam of X-rays through the object and then onto the photographic plate. Each molecule of the object from which the X-rays pass, absorbs some of the radiation. As a result, only unabsorbed portion of the beam reaches the photographic plate. This technique is essential for the study of the objects which differ with respect to the degree to which they absorb X-rays. Since, several brain structures hardly differ in their ability to absorb the X-rays, therefore, when this technique is used to study the brain, it provides little information.

Contrast X-rays: unlike conventional X-rays, contrast X-rays are useful for the study of the brain. A contrast X-ray involves a substance to be injected into one part of the body that absorbs X-rays, either more or less than the surrounding tissue. Because of this differential ability to absorb X-rays, the contrast between the compartment and the surrounding tissue gets heightened during X-ray photography.

In cerebral angiography (a contrast X-ray technique), a radio-translucent dye is infused into a cerebral artery to visualize the cerebral circulatory system during the X-ray photography. Vascular damage gets easily localized using cerebral angiograms. The location of tumor can be indicated by the displacement of blood vessels from their normal position.

X-ray computed tomography: X-ray computed tomography (CT), was introduced into clinical practice in 1972. It is a computer assisted X-ray procedure that can be used to visualize the brain and internal structures of the body. This technique makes the X-ray measurements of all the possible orientations around the patient. This procedure consists of an X-ray tube that projects an X-ray beam through the head to an X-ray detector, which is mounted on the other side. The X-ray tube and the detector automatically rotate around the head of the patient at one level of the brain, thus taking several individual X-ray photographs as they rotate.

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When all measurements are complete, information is processed by a nearby computer, and X-ray pictures are reconstructed for any section of the head, as long as the plane of view is perpendicular to the midline axis of the body. Normally, ten to fifteen images are examined during a CT- scan of the brain, a procedure that takes 15 to 30 minutes. Other than injecting of a contrast dye (delivered into a vein in the arm), the CT- scan technique is 'noninvasive', in the sense that no physical procedure is performed on the brain itself. The level of exposure of radiation is kept within safe limits for diagnostic work.

Magnetic Resonance Imaging (MRI): this technique is based upon the combined use of a magnetic field, radio waves and a particular characteristic of hydrogen atoms in the brain (as well as in all body tissue). Ordinarily, the nuclei of these atoms spin like tops, in random directions. When the MRI patient is positioned in a magnetic field, then all spins are in a single direction. The scanner then delivers pulses of radio waves at these nuclei, temporarily jarring them out of alignment. Several milliseconds later, when the nuclei rebound, they emit faint radio frequency signals that can be interpreted by a computer. The tissues that vary in their density emit varying amounts of energy. This is used by the computer to construct an image.

In several ways, MRI offers advantages over CT scan, such that, in this technique there is no need for a contrast dye or exposure to radiation. The spatial details in MRI exceed that of CT scan, thus, making MRI an ideal procedure for screening possible neurological disorders. In addition, an MRI scan, unlike the CT scan can construct an image in any desired plane on view, without repositioning the patient.

MRI also has certain drawbacks when compared to the CT scan, for instance, it takes a longer period to scan. This makes CT scan as the method of choice, when required. In addition, MRI cannot be used in patients with cardiac pacemakers or metallic material that may be present in their body.

Positron emission tomography (PET): permits investigators to assess the amount of metabolic activity in various parts of the brain. This technique provides the images of the brain activity, rather than the structure of the brain. In this technique, the patient first receives an injection of radioactive 2-DG (2 – deoxyglucose) in the carotid artery. Since, 2-DG is quite similar to glucose, hence it is readily taken up by active neurons. 2-DG cannot be metabolized, hence it gets accumulated in the cells. The person's head is placed in a machine similar to a CT scan. When a beam of X-ray passes, the damage is confirmed by sectioning and staining the brain, after the experiment is over. The tissues are then studied with a microscope. A PET scan measures important functions of the body, such as, blood flow, use of oxygen and sugar (glucose) metabolism. This helps to evaluate the functioning of organs and tissues.

Functional magnetic resonance imaging: Functional magnetic resonance imaging or fMRI, is a technique for measuring brain activity. It works by detecting changes in the oxygenation blood flow that occur in response to neural activity.

When a brain area is more active, it consumes more oxygen and to meet this increased demand, blood flow increases to the active area. fMRI can be used to produce activation maps. These maps show which parts of the brain are involved in a particular mental process.

The fMRI has certain advantages over PET. Unlike PET, in this technique, nothing is injected into the subject and the same image provides both, structural and functional information. Its spatial resolution is better than PET and it can be used to produce three-dimensional images of the activity, across the entire brain. This technique has certain disadvantages too, for instance, its temporal resolution is poor and it takes several seconds to collect enough information to form a single image. This is important as various neuronal events occur in milliseconds.

Magnetoencephalography (MEG): It measures small electrical currents emerging within the neurons of the brain. These currents produce small magnetic fields. MEG generates a remarkably accurate representation of magnetic fields which are produced by neurons. It measures changes in the magnetic fields on the surface of the scalp that are produced by changes in underlying patterns of neural activity. When it is combined with structural imaging, it is known as *magnetic source imaging* (MSI). This technique has been found to be useful in the study of different brain functions and epilepsy.

3.4.4 Cell Specialization

Cell specialization is also known as cell differentiation. It is a process by which generic cells change into the specific cells. These specific cells perform specific functions in the body. Cell specialization is important for the development of embryos. In an adult person cell specialization is done by the stem cells, which tend to replace cells that are worn out in the bone marrow, brain, heart and blood.

The actual mechanism behind cell specialization is not yet known. But scientist are trying find out the mechanisms underlying cell specialization. At present, it is known that for cell specialization to take place, some genes in the cell's DNA have to be activated or deactivated in order to produce a particular type of cell. Strokovskyy Yaroslav, a scientist has hypothesized that cell differentiation occurs when neighboring cells introduce an agent into the cell, which causes the cell to differentiate. Bone marrow cells have been proven to specialize when the white blood cell count in the body gets too low.

The zygote consists of only one cell at the time of conception, but later it develops to form an embryo. The embryo consists of a multicellular organism. Development of the embryo cannot take place without cell specialization, since it is only through the process of cell specialization that a single celled zygote gives rise to other cells. These cells are eventually needed to form vital organs like brain, heart, hands, legs, etc., of the organism.

An adult body consists of somatic cells and stem cells. Somatic cells do not change, whereas, the stem cells can be specialized to replace cells that are worn out in different parts of the body. The stem cells are found in different areas of the

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body of an adult person like the brain, bones, bone marrow, blood, etc. The stem cells that form the blood are known as the hematopoietic cells and the ones that form the bone or the tissues of the body are known as stromal cells.

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Quite opposite to the process of differentiation, is the process of dedifferentiation. In this process specialized cells revert to generic cells or basic cells. Unlike human beings, some animals contain cells that are capable of dedifferentiation. This process of dedifferentiation is used in the regeneration of injured limbs.

Nowadays, researches on stem cells are being carried out with a hope that some day it will open the possibility of treating several diseases like diabetes, heart diseases, etc. The researchers in this area have proposed that stem cells can be triggered to replace the diseased cells in affected areas of the body. In cases of leukemia and certain types of breast and ovarian cancers, this technique has already been used to generate more white cells.

CHECK YOUR PROGRESS

4. How was the technique of Golgi stain discovered?
5. Why was the technique of Nissl stain developed?
6. List the two types of neuroanatomical tracing techniques.
7. List the four major divisions of the brain.
8. What does the tectum consist of?

3.5 NEUROPHYSIOLOGY

3.5.1 Electrical Signals

The following electrical signals are transmitted by nervous tissues:

Excitability: It is the ability of the nerve cells and fibres to enter into an active state known as the state of excitation, in response to a stimulus. The excitation arises at receptors on account of various stimuli such as light, temperature, pressure, chemical or electrical stimuli. These stimuli constantly act on the organism.

Conductivity: The transmission of excitation : along nerve fibres in a particular direction is called conductivity. The nervous tissue is involved in sending information across the central nervous system and the different parts of the body, by conducting nerve impulses. In psychological terms, a nerve impulse is a general physiological effect (physical, chemical and electrical) that is exhibited by a nerve fibre, on its stimulation. It causes depolarization of the membrane of the nerve cell. The nerve impulse travels along a neuron or across a synapse, between neurons, or between a neuron and an effector such as a muscle or gland. It carries messages from the sensory area to the brain and from the brain to the motor region. It is responsible for establishing connection between sensory stimuli and the appropriate

motor response. The neural signals are believed to underlie the whole range of thought and action. The three kinds of electrical events which are seen in the nervous system are as follows:

- (i) **Resting potential:** The separation of the electrically charged ions across the nerve membrane results in a small electrical difference between inner and outer surfaces of the membrane. Changes in the resting potential of the nerve cells are seen as signals that can be transmitted and integrated in complex ways.
- (ii) **Action potential:** These are brief and propagated changes that travel rapidly along the axons of the neurons. These changes are conducted in the form of chain reactions. They maintain a uniform size as they advance. They enable axons to serve as channels for rapid communication.
- (iii) **Graded potential:** They are also known as local potentials. They vary in their size and duration and are initiated at postsynaptic sites. They are known as postsynaptic potentials. The amplitude of such potentials decreases gradually as they move away from the site of origin. The information is processed by the nervous system through the mechanism of interaction between graded postsynaptic potentials.

3.5.2 Transmission Process

In the transmission process, nerve impulses are transmitted along nerve fibres. A particular nerve fibre goes through the process of polarization, depolarization and repolarization, in order to transmit the nerve impulse. Following are the details of each of these processes:

Polarization/resting potential: A nerve fibre that is dormant and is not involved in the activity of conducting an impulse is known as a resting nerve fibre. In a resting nerve fibre, sodium and chlorine ions predominate in the extracellular fluid, in an approximate ratio of 9:1 and 14:1, whereas, the potassium ions predominate the intracellular fluid (i.e., the cellular fluids that is present within the fibre) in an approximate ratio of 40:1. Intracellular fluid also has many negatively charged protein molecules. These protein molecules, carrying a double negative charge and are restricted, due to their large molecular size. Thus they are unable to pass through the membrane.

Sodium ions are 10 times more outside the neuron and potassium ions are 25 times more inside the cell. There is a large degree of variation between concentration of ions external and those internal to the plasma membrane. This variation gives rise to different electrical charges on both sides of the plasma membrane. The membrane is positively charged on the outside and negatively charged towards the inside. This difference is called the potential difference. Another term for this difference is resting potential.

Three basic factors are responsible for causing this electrical difference, they are:

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- (i) The special character of the membrane forms the 'skin' of the neuron.
- (ii) The presence of electrically charged particles known as ions, exist near the internal and external surfaces of the membrane.
- (iii) In addition to this, the movements of ions across the membrane also cause this electrical difference. The movement of the ions is governed by the two principles of diffusion and electrostatic pressure. Diffusion refers to the movement of molecules from the region of high ions to that of low concentration. The electrostatic pressure refers to the force of attraction that exists between the atomic particles that are charged with opposite signs, or the force of repulsion that exists between the atomic particles charged similarly. It moves ions from place to place, i.e., cations are pushed away from the region with an excess of cations and anions are pushed away from regions with an excess of anions.

Due to different concentration of ions on either sides of the plasma membrane, sodium ions are inclined to disperse into the nerve fibre and potassium ions are inclined to disperse outside the nerve fibre. The membrane of a resting nerve fibre allows more potassium ions to pass through it, than sodium ions. As a result, potassium ions leave the nerve fibre faster than the sodium ions can enter it. This phenomenon is known as the polarized state. In this state, the inner area is electronegative to the outer area.

Depolarization/Action potential: As soon as a nerve fibre is stimulated mechanically, electrically, thermally or chemically, the area of stimulation is affected. This results in a local excitatory state. Consequently, the membrane becomes permeable to sodium ions. This causes sodium ions to suddenly rush into the nerve fibre and the potassium ions to diffuse out of the axon membrane. Because of the changes within the membrane potential, the sodium and potassium ion channels are opened. Hence these channels are known as the voltage-dependent ion channels. The influx of positively charged sodium ions produce a rapid change in the membrane potential from -70 mV to $+40$ mV.

Since the ions are diffused, increased number of sodium ions enters the axon. This number is much higher than the potassium ions which are in the process of leaving it. As a result, the positive and the negative charges, which are internal and external to the axon membrane, are reversed. This causes the membrane to be negatively charged, externally and positively charged, internally. This state of the membrane is known as the depolarized state. This wave of depolarization flows across the nerve fibre. This depolarization is in the form of an impulse of reversed polarity. This wave of depolarization, traveling down a nerve fibre, is called action potential. The action potential is also known as spike potential, as the shift occurs rapidly. This impulse functions as the fundamental mode of communication within the nervous system.

The action potential is governed by two laws, namely, the all-or-none law and the rate law. According to the all-or-none law, once a neuron has received a stimulus above the threshold level, it conducts an impulse of constant maximum

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size, throughout the length of the neuron. Thus, the all or none principle states that a neuron either conducts or does not conduct an impulse. It operates only at the axonic level. In contrast to the all-or-none law, the rate law states that the variation in the intensity of a stimulus, or other information being transmitted in an axon, is represented by variations in the rate at which that axon fires. A high rate of firing causes a strong muscular contraction and a strong stimulus causes a high rate of firing in axons. Thus the rate law supplements the all or none law.

Repolarization: As the number of sodium ions grow within the nerve cell, the permeability of the membrane decreases for sodium ions. On the other hand, the permeability increases for potassium ions. Thus, sodium ions are pumped out of the cell and the potassium ions are pumped into the cell. This activity goes on until the original resting state of ionic concentration is achieved. Thus, this makes the membrane internally negative and externally positive. This process is known as repolarization.

Once the nerve impulse is fired, it must return to the resting stage so that it can be fired again. The nerve undergoes the following stages of repolarization:

- **Absolute refractory period:** refers to a period during which the neurons cannot be excited any further because of the all or none law.
- **Relative refractory period:** refers to a period in which the neuron is capable of getting excited again but only with a stimulus that is stronger than its threshold level.
- **Supernormal period:** refers to a period in which the neuron can be excited with a stimulus which is weaker than the threshold level.
- **Subnormal period:** refers to a period in which the neuron becomes insensitive again and can be excited only with intense stimulation. This cycle is again followed by a resting potential.

It is believed that the last movement of ions takes place by means of an active transport mechanism. This mechanism is known as Na-K pump (sodium-potassium exchange pump or sodium pump). This active transport mechanism involves the expulsion of sodium ions outside the membrane and drawing of potassium ions inside the membrane, against the concentration and the electrochemical gradient. The Na-K pump consists of a large number of individual protein molecules which are located in the membrane. These molecules are driven by the energy which is provided by the mitochondria, as they metabolize the cell's nutrients. These molecules are known as Na-K transporters. They exchange sodium ions for potassium ions by, pushing three sodium ions outside the membrane for every two potassium ions that are pushed inside the membrane. Most cells of the body, like the neurons, muscle cells, glial, etc., have the Na-K transporters in their membranes.

It was Pafferfish (1944) in Japan, who showed that ATP (adenosine triphosphate) is responsible for the working of the Na-K pump. When formation of the ATP was prevented by introducing toxic substances like TTX (tetrodotoxin), STX (sanutotoxin) or when oxygen was deprived, the cells lost the capacity to

expel sodium out and draw potassium in. The entire process of repolarization requires some time, during which the nerve cannot be stimulated again. This period is called refractory period. During repolarization, as the cell return to original state of rest, the neuron is prepared for stimulation.

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Several factors affect the initiation and conduction of a nerve impulse. These are as given below:

The strength of stimulus: For an impulse to be initialized, the stimulus must be strong enough to depolarize the neuron beyond the threshold level of depolarization for that neuron. This threshold determines the minimum strength of a stimulus to which a neuron will respond, with an action potential. It varies among neurons and the different conditions that affect a particular neuron.

Summation: A sub-threshold stimulus is a stimulus that is too weak to initiate an impulse. If a series of these stimuli reach a neuron in rapid succession, their accumulated effect may succeed in initiating an impulse. This additive effect of several sub-threshold stimuli is called summation.

All-or-none principle: Once a neuron has received a stimulus above the threshold level, it conducts an impulse (of a fixed maximum magnitude) throughout the length of the neuron. Thus, the all-or-none principle states that a neuron either conducts, or does not conduct an impulse.

Saltatory conduction: The properties of impulse conduction described above so far, apply to unmyelinated neuron. However, the myelins of many axons in the body insulate those axons, except at the Nodes of Ranvier. When an impulse travels along a myelinated neuron, depolarization occurs only at the nodes. The process of depolarization, leaps over the myelinated sheath from one node to the next. This process is known as saltatory conduction. The word saltatory originates from the word, 'salter', which means to leap.

Saltatory conduction has several advantages, as mentioned below:

Speed of impulse: an impulse travels faster along a myelinated neuron, than along a nonmyelinated one.

Less energy: Saltatory conduction requires less energy, as compared to the energy needed to conduct an impulse along an unmyelinated neuron. This is because smaller amounts of ATP are used to operate the Na-K pump.

Conduction velocity: The speed of an impulse is also affected by the diameter of the axon. The impulse travels slower in a thinner fibre, than in a thicker one. Invertebrates like squids (molluscs) have unmyelinated fibres only. Therefore, they must possess thick nerve fibres for conducting impulses. Therefore, giant squids have thick nerve fibres.

3.5.3 Circuits

The neurons and the synapses combine together to form circuits, thereby helping in conveying messages and processing information. In this case, a circuit here refers to an assemblage of neurons and their synaptic interconnections. The neurons

represent singles in the form of graded potentials and the all-or-none action potentials. Various aspects of behaviour and experience, such as, cognition, emotion and action are accomplished by different types of neural circuits that are present in the nervous system. Of the several circuits present, following are the three basic types of neural circuits seen in our nervous system:

- **Neural chain:** refers to the linking of the neurons in a chain, for example, the knee jerk reflex. This reflex consists of a sensory neuron, a motor neuron and a single synapse, at the site where the sensory neurons joins the motor neuron. It is believed that hundreds of such circuits work in parallel, to enable the stretch reflex. The knee jerk reflex occurs in about 40 milliseconds and several factors account for this rapid speed. For instance, the large diameter of the sensory and the motor neuron and the direct synapse of the sensory cells on the motor neurons, makes the conduction rapid. Also, both the central synapse and the neuromuscular junctions are fast synapses.

The afferent parts of the visual system can also be seen as a neural chain. In many parts of the nervous system, the axons from the large number of neurons, converge on certain cells. These convey information from certain parts of the body to the brain. This process is known as convergence. In contrast to the process of convergence, divergence is seen to occur more in the visual system. For instance, one million axons of the optic nerve communicate to billions of neurons in several different specialized regions of the cerebral cortex. Both, convergence and divergence are two important features of the several neural circuits.

- **Feedback circuit:** is believed to act as a regulator. It was first discovered in the 1940s and its relevance to psychological and neuroscience theory was pointed out by the psychologist Donald O. Hebb. In these circuits, a part of the output acts as a feedback to the input. There are two types of feedback circuits: the positive feedback circuit and the negative feedback circuit. In positive feedback circuits, the output sustains or increases the activity of the initial input, whereas, in the negative feedback circuit, the output inhibits the activity of the initial input. The feedback circuit acts in two ways: one, in where a branch of the axon of a neuron loops back to the same neuron and the other, where one or more intermediate neurons form the feedback loop.

In order to maintain a motivational state, a positive feedback circuit can be used to sustain neural activity. Whereas, a negative feedback circuit can be used to maintain a relatively constant condition of several bodily functions, for example, a thermostat. Similarly, the stretch reflex serves as part of the negative feedback system, thus helping in maintaining posture, as we stand.

- **Oscillator circuit:** is involved in the control of rhythmic behaviour like breathing, heartbeat, walking, sleeping, etc. Largely in vertebrates, some

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neurons show inherent spontaneous rhythm of activity. The frequency of neural impulses in such cells are seen to wax and wane in regular alterations. In both vertebrates and invertebrates, the oscillatory activity usually depends on the circuits of neurons.

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3.5.4 Gross Electrical Activity

In brain, the electrical activity of thousands of cells, working together, adds to the potentials which can be recorded at the surface of the skull. This electrical activity can be recorded by placing large electrodes on the scalp or within the brain. These recordings provide relevant information about the simultaneous workings of the population of neurons. The various brain potentials can be divided into the following broad categories: potentials that appear spontaneously without any specific stimulation and potentials that are evoked by particular stimuli.

- **Spontaneous brain potentials:** The recording of spontaneous brain potentials is known as electroencephalogram (EEG). EEG recordings of a sleeping person, helps one to distinguish between different kinds and stages of sleep. EEG also provides relevant diagnostic information that helps in the diagnosis of seizures. Such recordings also provide the investigators with prognostic data that helps to make predictions of the functional effects of brain injury. EEG recordings also help us to know whether an individual is alive or dead. A more detailed analysis and display of the brain potentials have been made possible by newer techniques like, the brain electrical activity mapping (BEAM), etc.
- **Event related potentials:** Gross potential changes which are evoked in the brain by discrete stimuli are known as event-related potentials (ERPs). In order to obtain a reliable estimate of stimulus-elicited brain activity, ERPs in series are averaged. Sensory-evoked potentials have distinctive characteristics of wave shape and latency that reflects the type of stimulus, the state of the subject and the site of recording. Some characteristics of evoked potential can get altered by subtler psychological processes like expectancy, etc.

Computerized techniques are also used to record brain potentials, some distance away from sites at which they are generated. An example of such brain potentials is the auditory-evoked brain stem potential. Hearing impairments in very young children have been detected on the basis of a decrease in the amplitude of certain waves or increase in their latency. The brain-stem-evoked potentials have also been found to be useful in the assessment of brain stem injury or damage produced by stroke or tumor. The impact of variables that process information like attention, decision-making, etc., are reflected by long-latency components of the scalp-recorded ERPs. In contrast to long-latency components, exogenous factors like stimulus intensity, etc., are better reflected by the short-latency components of the scalp-recorded ERPs. Techniques like functional MRI clearly help in indicating which brain region is active, while performing a certain activity.

Chemical basis of behaviour

The chemical basis of transmission of the signals from one neuron to the other takes place across the synapse. This process is known as synaptic transmission. The term 'synapse' was first used by Sir Charles Sherrington (1861–1954). This term was derived from a Greek word meaning 'clasp'. Synapse refers to an area of functional contact between one neuron and the other, for the purpose of transferring information. Synapses are usually found between the fine terminal branches of the axons of one neuron and the dendrites or cell body of another. This type of neuron is called axo-dendritic synapse. Synapse can occur in three places—on the dendrite, on the soma and on other axons. These synapses are referred to as axodendritic, axosomatic and axoaxonic synapses.

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A typical generalized synapse consists of a bulbous expansion of a nerve terminal called a pre-synaptic knob. This lies close to the membrane of a dendrite. The cytoplasm of the synaptic knob contains cisternae, smooth endoplasmic reticulum, microfilaments, microtubules (responsible for transporting material between the soma and terminal buttons), mitochondria (provides the energy required for by terminal button to perform its functions) and numerous synaptic vesicles (small, rounded objects in the shape of spheres). Many terminal buttons contain two types of synaptic vesicles, large and small. Small synaptic vesicles are found in all terminal buttons and contain neurotransmitters. These vesicles are found in greatest numbers around the part of the presynaptic membrane that faces the synaptic cleft. Small synaptic vesicles are produced in the Golgi apparatus, which is located in the soma and are carried by fast axoplasmic transport to the terminal buttons. They are produced by the cisternae from recycled material in the terminal button. Large synaptic vesicles contain a number of different neuropeptides. Large synaptic vesicles are produced in the soma and are transported through the axoplasm, to the terminal buttons.

The membrane of the synaptic knob nearest the synapse is thickened and forms the presynaptic membrane. The membrane of the dendrite is also thickened and is called the post synaptic membrane. These membranes are separated by a gap known as the synaptic cleft. The synaptic cleft is usually around 200 Å wide. It contains extracellular fluid, through which the transmitter substances diffuse. The post synaptic membrane contains large protein molecules which act as receptor sites for neurotransmitter and numerous channels and pores.

Chemical transmission across synapse was discovered by Henry Dale (1936). The physiological importance of synapse for the transmission of nerve impulses was established by Mc Lennan in 1963. The transmission of the impulse across the synapse takes place in the following manner:

When an impulse arrives at a pre synaptic knob, calcium ions from the synaptic cleft enter the cytoplasm of the pre synaptic knob. This activity of the calcium ions is controlled by a chemical substance known as calmodulin. Increase in the calcium ions increases the release of neurotransmitters. Calcium ions cause the synaptic vesicles to move to the surface of the knob. The synaptic vesicles

burst when they are fused with the pre synaptic membrane (this process is called exocytosis). Their contents are discharged (largely neurotransmitters) into the synaptic cleft.

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According to Almers (1990), calcium ions that enter the terminal buttons bind with the clusters of protein molecules. These molecules join membranes of the synaptic vesicles with the pre synaptic membrane. Henser and Reese (1973) proposed that as the synaptic vesicles fuse with the pre synaptic membrane and burst open, their membrane becomes incorporated into that of the terminal button, which consequently becomes larger. In order to maintain the proper size of terminal buttons, little buds of membrane squeeze into the cytoplasm. This process is known as pinocytosis. The buds of membrane migrate to the cisternae and fuse with them. Beads of membrane break off from the cisternae and form new synaptic vesicles. These vesicles are then filled with molecules of transmitter substance, the appropriate proteins are inserted into the membrane and they are then transported towards the pre synaptic membrane. The vesicles go back into the cytoplasm of the synaptic knob. There, they are refilled with a neurotransmitter.

The release of neurotransmitters is regulated by enzymes. Neurotransmitters can fit into one or several receptor molecules in the postsynaptic membrane. The neurotransmitters of the synaptic cleft get linked to the protein receptor molecules on the post synaptic membrane. This linking activity alters the potential of the post synaptic membrane, by opening channels in it. This allows sodium ions to enter the cell. It causes the depolarization and generation of action potential in the post synaptic membrane. As a result, the impulse gets transmitted to the next neuron.

This change in the permeability of the post synaptic membrane, leads to the loss of several neurotransmitters immediately from the synaptic cleft. In the case of cholinergic synapses, acetylcholine (ACH) is hydrolyzed by acetylcholinesterase (AChE). This enzyme is present in high concentration at the synapse. The products of the hydrolysis are acetate and choline, which are reabsorbed into the synaptic knob where they are re-synthesized into acetylcholine. This activity uses the energy from ATP.

A particular neuron may receive thousands of synapses from a network of other neurons. Some neurons release neurotransmitters that are excitatory while others release neurotransmitters that are inhibitory. Depending on the arrival of action potential, different neurons release neurotransmitters at different times. At a particular moment, at a particular place on the membrane, if excitatory effects dominate inhibitory effects, then depolarization will take place and axons will fire. This depolarization is known as the excitatory postsynaptic influence (EPSP).

The depolarization of the post synaptic membrane (from -70 mV to say -68 mV) to a slightly negative value is called EPSP because EPSP must summate (add up in intensity) to reach a threshold. Summation occurs in two ways, namely spatial summation and temporal summation.

Spatial summation: a single telodendria produces small amount of neurotransmitters and hence produces small amount of EPSP. When several

telodendria coincide they produce a large number of neurotransmitters and hence several EPSP combine together to exceed the threshold level. This process is known as spatial summation. In spatial summation two or more adjacent locations on the presynaptic membrane can overlap in the middle of the post synaptic membrane.

In contrast to spatial summation, temporal summation is the repeated impulse on the same telodendria. It may add to the previous impulse, thereby exerting an excitatory post-synaptic influence. It is based on the fact that a neurotransmitter remains active for a period of time. Thus, temporal summation is a successive summation of several impulses and is dependent on the timing of successive impulses. Neurotransmitters, like the Acetylcholine (ACH), Epinephrine (E), Non-epinephrine (NE), Dopamine, etc., are examples of excitatory neurotransmitters.

Some neurotransmitters that are released by neurons neither excite nor depolarize adjacent neurons, rather they hyperpolarize them. This is referred to as inhibitory postsynaptic influence (IPSP). The summation process seems to underlie IPSP, but the cumulative effect makes it difficult to excite. An example of an inhibitory neurotransmitter is GABA. IPSP is hyperpolarizing in nature and is marked by a shift in the potential, i.e., say from -20 mV to -72 mV. The shift is away from the threshold. Inhibitory postsynaptic influences are localized.

Neurotransmitters

Neurotransmitters are the chemicals that are released at a synapse. Each neuron synthesizes its neurotransmitters from materials in the blood. There are some types of neurotransmitters that produce either excitation, or inhibition. There are certain other neurotransmitters which produce excitations, when they are bound to some of their receptor subtypes. They produce inhibition, when they are bound to others.

Each neuron synthesizes its neurotransmitters from precursor molecules that reach the cell, through the blood. They are derived originally from food that an individual eats. Many neurotransmitters can be synthesized both in the cell body and in the terminal close to their point to release. The peptide neurotransmitters are synthesized only in the cell body. Some neurons synthesize dopamine. Other neurons have additional enzymes that convert dopamine to norepinephrine and norepinephrine to epinephrine. Acetylcholine is synthesized from choline, which is abundant in cauliflower and milk. The body can also make choline from lecithin a compound of egg yolks lever, soya beans butter, peanuts and several other foods. Following are the details about some of the neurotransmitter:

- **Amino acid neurotransmitters:** are present in large numbers in the fast acting, directed synapses of the central nervous system. The four most commonly known amino acid neurotransmitters are, glutamate, aspartate, glycine and gamma-aminobutyric acid (GABA). The first three are commonly present in proteins, whereas GABA is synthesized by a simple modification of the structure of glutamate. Glutamate is an excitatory neurotransmitter which is present in the mammalian central nervous system, whereas, GABA is an inhibitory neurotransmitter.

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- **Monoamine neurotransmitter:** are small molecule neurotransmitters, which are synthesized from a single amino acid. These neurotransmitters are slightly larger than amino acid neurotransmitters and their effects tend to be more diffuse. They are usually present in the neurons of the brain stem. The four most commonly known monoamine neurotransmitters are dopamine, norepinephrine, epinephrine and serotonin. On the basis of structure, they are subdivided into catecholamines and indolamines. Dopamine, nor-epinephrine and epinephrine are catecholamines and are synthesized from the amino acid, tyrosine. Tyrosine is converted to L-dopa, which in turn is converted to dopamine. Neurons that release norepinephrine (known as noradrenergic) have an extra enzyme, which converts the dopamine in them to norepinephrine. Similarly, neurons that release epinephrine (known as adrenergic) have enzymes that convert nor-epinephrine to epinephrine. Serotonin is an indolamine and is synthesized from the amino acid, tryptophan.
- **Soluble gas neurotransmitters:** consists of gases like nitric oxide and carbon monoxide. They are produced in the neural cytoplasm and once produced, they immediately diffuse through the cell membrane into the extracellular fluid and then into nearby cells. Since they are soluble in lipids, therefore they are able to easily pass through cell membranes. On reaching other cells, they stimulate the production of a second messenger and are immediately broken down. They are difficult to study because they exit for only a few seconds.
- **Acetylcholine:** are created by adding an acetyl group to the choline molecule. It acts as a neurotransmitter at neuromuscular junctions, for many of the synapses in the autonomic nervous system and for synapses in several parts of the central nervous system. In the synapse, acetylcholine is broken down by an enzyme known as acetylcholinesterase. Neurons that release acetylcholine are said to be cholinergic.
- **Neuropeptides:** are peptides that play a role in neurotransmission. The most commonly known neuropeptides are endorphins. They are endogenous opiates. In our brain, several different endorphins and subtypes of the endorphin receptors are present. Endorphins activate neural systems that produce analgesia and that mediate the experience of pleasure.

3.5.5 Hormones and the Brain

Hormones are specific chemical substances secreted by endocrine glands. They were first discovered by the English physiologists, William M. Bayliss and Ernest H. Starling, in 1903. The term hormone was introduced by Starling in 1905 and was first used with reference to secretin and gastrin.

Based on their chemical nature, hormones can be divided into the following five types:

- (i) **Steroid hormones:** are hormones that are composed of steroids, for example, the adrenal cortex, testes, ovaries and placenta.
- (ii) **Proteinous hormones:** are hormones that are made up of proteins, for example, the somatotrophic, thyrotropic and gonadotrophic hormones. These are secreted by the anterior lobe of the pituitary gland and insulin hormone is secreted by the pancreas.
- (iii) **Peptide hormones:** are hormones that are composed of peptides, for example, calcitonin hormone secreted by the thyroid gland and parathormone is secreted by the parathyroid glands.
- (iv) **Amino acid derivative hormones:** are hormones that are derived from amino acids. The hormones, adrenaline and nor-adrenaline are secreted by the adrenal medulla and the thyroxine hormone is secreted by the thyroid gland. These are examples of amino acid derivative hormones.
- (v) **Biogenic amines:** are non-protein compounds which contain the amino group. An example of biogenic amines is thymosin, which is secreted by the thymus.

Hormones are marked by certain characteristics as follows:

- Hormones neither initiate biological process like sleeping, respiratory, etc., nor do they stop it. They exert influences which are governed by regularity mechanism, either by speeding or slowing down a process.
- Hormones have catalytic quality.
- They do not get used up as a result of their influence in a particular process.
- They are effective in low concentration.
- They have low molecular weight.
- Many hormones are produced in an inactive form known as prohormones. For example, insulin is secreted as proinsulin.
- They have variability in the rate of secretions. Some hormones are secreted as a regular function of a rhythm that follows a diurnal (24 hours period cycle, for example, adrenal hormones or the pineal body's melatonin), or a lunar (28 days) period (for example, the female sex hormones). The secretion of growth hormones is measured in terms of years. There are several other hormonal secretions which rise or fall according to internal situational demands, (for example, a rise in insulin is seen after food intake) or due to some environmental stimulation (for example, a rise in ACTH is seen when one is faced with danger).

It is possible to measure the infinitesimal quantities in which hormones are required, through a technique known as radio immunological assay (RAI). This technique was developed in 1959 by an endocrinologist, Jay Tepperman. This

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technique of RIA, helps to measure levels of a large number of hormones and others substances, which can be monitored every minute.

Ways in which hormones act

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Hormones act in a variety of ways both throughout the body and on a wide variety of cellular mechanisms. Hormones usually act according to the following general principles:

- It is not frequent for hormones to act gradually, long after their concentration in the blood has fallen. They act by activating behavioural and physiological responses.
- Hormones neither initiate nor stop a behaviour. They either speed up or slow down some regularity process, regardless of the context.
- All these behavioural processes are mediated by enzymes. They act as catalysts.
- Both environmental and endogenous factors influence the quantities and types of hormones that are released. A reciprocal relationship exists between behaviour and hormones, where hormones change behaviour and behaviour changes hormone levels or responses. For example, aggression is related to high levels of testosterone. In some species, males who lose on aggressive encounters show a reduction in testosterone levels.
- Each hormone can have multiple effects on different tissues, organs and behaviours. Similarly, a single kind of behaviour or physiological change can be affected by many different hormones.
- Hormones are produced in small amounts and are often secreted in bursts. This secretion pattern is sometimes crucial for a small amount of hormone to be effective.
- The levels of many hormones vary rhythmically throughout the day and many hormonal systems are controlled by circadian 'clocks' in the brain.
- Metabolic processes are affected by hormones. For instance, hormones tend to facilitate both the buildup and breakdown of carbohydrates, lipids and proteins.
- Hormones are seen to interact among themselves, that is, the effect of one hormone can be changed by the actions of another.
- The chemical structure of a given hormone is similar in all vertebrates, but the functions served by that hormone can vary across species.
- Hormones can affect only cells that possess a receptors protein that recognizes the hormone and alters the functioning of the cell. The same brain region often possesses the same hormone receptors, among different vertebrate species.

Organisms tend to communicate using different categories of chemical signals in the body. Following are some types of communication:

- **Synaptic communication:** occurs by the release of neurotransmitters across the synaptic cleft. This causes a change in the polarization of the postsynaptic membrane. The change in the polarization of the membrane helps in the transmission of neural signals.
- **Autocrine communication:** in it, a released or secreted hormone acts on the releasing cell itself and thus affects its own activity; for example, nerve cells that have auto-receptors are seen to get affected by the release of synaptic transmitter molecules which also help in monitoring their own activity. In this case, a signal molecule serves as both an autocrine and a synaptic transmitter's function.
- **Paracrine communication:** In such a communication, the released chemical signal diffuses to nearby target cells, through the intermediate extracellular space. The strongest impact is experienced by the nearest cells.
- **Endocrine communication:** In it, hormones (the chemical signals) are released into the bloodstream and are taken up selectively by target organs.
- **Pheromone communication:** Pheromones are hormones produced by an individual that are released outside the body. They help an individual to communicate with other individuals of the same species. For example, ants produce a wide variety of pheromones that help in communicating about the presence of intruders in the nest.
- **Allomone communication:** such a communication system involves the use of chemical signals that help members of one species and affects the behaviour of individuals of other species. These chemical signals or hormones are called allomones. Allomones can carry messages between different animal species or from plants to animals. For example, flowers produce scents to attract insects and birds in order to facilitate the process of pollination.

The neural and hormonal communication differs in the following four ways:

- In neural communication, messages travel over fixed channels to precise locations. Information from one cell to the other is transmitted through anatomical connections between neurons. In contrast to neural communication, hormones are secreted directly into the blood stream and from there they are selectively taken up by various target organs.
- Neural communication is quite fast and takes place in milliseconds, whereas hormonal communication is relatively slower and is measured in seconds and minutes.
- Most neural messages follow the all-or-none principle but most hormonal messages are graded in strength.

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- Most of the hormonal communication is not under voluntary control. However, most of the neural communication seems to be under voluntary control. However, this distinction between the hormonal and neural communication is not absolute.

Despite the differences mentioned above, the following similarities are seen between neural and hormonal communication:

- Both neurons and endocrine glands tend to store their secretions (neurotransmitters and hormones respectively) and release them later, when needed.
- Both neurons and endocrine glands are stimulated by either other neurons (in case of neural communication), or other glands in response to neural or chemical messages (in case of hormonal communication).
- Several types of neurotransmitters and hormones are present in the body of an organism. Also, sometimes the same substance is seen to act as a neurotransmitter at one time and as a hormone at some other time.
- Both neurotransmitters and hormones react with specific receptor molecules, which are present on the surface of the post-synaptic membrane (in case of neural communication) and on the surface or in the interior of target cells (in case of hormonal communication).
- Often when hormones act on receptor molecules on the cell surface, a second messenger is released in the target cells. This brings about changes within the cell. Similar to endocrine glands, certain neurons also involve the release of second-messengers in the post-synaptic neuron. In addition to this, the same chemicals have been seen to act as second messengers in both, the nervous and the endocrine system.

Hormones act on a wide variety of cellular mechanisms in the following three ways:

(i) Hormones tend to affect cells by influencing their growth and activity: Hormones promote the proliferation, growth and differentiation of cells. They are also seen to modulate cell activity. For example, the thyroid hormone tends to promote early developmental processes. Lack of sufficient number of thyroid hormones results in mental retardation. Hormones also cause certain cells in some organs to divide and grow at later stages in life. For example, during adolescence the male and the female hormones cause secondary sexual characteristics to appear in both the sexes. In already differentiated cells, hormones can modulate their rate of functioning. For example, insulin and thyroid hormones promote the metabolic activities of most of the cells in our body. However, there are certain other hormones that modulate activities in certain types of cells, for example, the luteinizing hormone promotes the secretion of sex hormones by the testes and ovaries.

(ii) Hormones tend to initiate action by binding to receptor molecules: Three classes of hormones (namely, the protein hormones, amine hormones and

steroid hormones) exert their influence on target organs in the following two different ways:

- Protein hormones bind to specific receptors, which are usually found on the surface of target cell membranes. When the hormones bind with the extracellular portion of the receptor, then the receptor molecules change their overall shape. This in turn, changes the internal chemistry of the cell by activating a second messenger. These receptors tend to release a second messenger when they are stimulated by appropriate hormones. For instance, the cyclic adenosine mono-phosphate (cAMP) acts as a second messenger and carries the messages of many peptide and amine hormones. This mechanism is used by protein hormones to alter the existing proteins, within the cell. Most amine hormones are also seen to act via the surface receptors and the second messengers. The protein hormones usually act rapidly (within seconds to minutes). However, some proteins can have prolonged effects; for example, ACTH promotes the proliferation and growth of adrenal cortical cells, thereby increasing the long-term capacity to sustain production of their hormones.
- Unlike protein hormones, the steroid hormones act by passing through the membrane and binding to specific receptor proteins, inside the cell. The steroid-receptor complex then binds to DNA in the nucleus of the cell and tends to alter the transcription of specific genes. This further increases the production of certain proteins and decreases the production of certain other proteins. Steroid hormones typically act more slowly than protein hormones. They take several hours to show an effect. Steroids may be able to affect cells in several other ways too. For example, estrogen can have a rapid, but brief effect on some neurons by means of a separate class of steroid receptors in the membranes of these neurons. This may modulate the excitability of neurons in reproductive behaviours.

(iii) Hormone secretion may be regulated by feedback control mechanisms: Some hormones act by following a feedback loop system, by detecting and evaluating the effects of the hormone. This helps in monitoring and regulating the rate of hormones, so that their level in the blood is appropriate to ongoing activities and needs of the body. The hormones follow an autocrine response (the hormones both act on the target cells and also provide feedback to inhibit the gland that releases it).

Sometimes the biological response which is elicited by the hormone, from the target cells, acts as a feedback loop. The responses of these hormones are monitored by some cells in the circuit. Additional hormones are released if the initial effects are too small. For example, the hormone, insulin, controls the level of glucose circulating in the blood in the following way: After a meal, glucose from the food enters the bloodstream and the extracellular fluids, thus causing the pancreas to release insulin. The insulin so released, causes the extracellular glucose to enter

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muscle and fat cells. These muscle and fat cells are thus stimulated to use the glucose. When the glucose level falls in the blood, it causes the pancreas to secrete less insulin. This helps in maintaining the balance of insulin in the blood.

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To illustrate this mechanism of feedback let us take another example of the thyroid gland. The thyroid gland, under normal circumstances, maintains an optimal level of thyroxin secretion through a feedback relationship with the anterior pituitary gland and the hypothalamus. If the thyroxin levels in the bloodstream become too low, the hypothalamus appears to sense the deficiency and produce thyroxin. This is done by releasing the hormone (TRH), which causes the anterior pituitary to secrete the hormone thyrotropin, into the blood. The increased levels of thyrotropin then cause the thyroid gland to increase its production of thyroxin, until the proper level is restored. Too much thyroxin in the blood has opposite effects on the hypothalamus and anterior pituitary, causing thyroxin levels to decline. Thus, this kind of a feedback system regulates the release of or inhibition of a hormone, depending on its level in the blood.

Endocrine glands and their hormones

On the basis of secretion, glands are of two types: endocrine and exocrine. Endocrine glands are known as ductless glands because their products are secreted directly into the circulatory system (blood), without intermediate 'passageways'. Examples of endocrine glands are thyroid, adrenalin, etc. Exocrine glands secrete their products through specific ducts. Examples of exocrine glands are salivary glands, tear glands, sweat glands, etc.

The endocrine glands which secrete only hormones are known as holocrine glands. Examples of holocrine glands are thyroid gland, parathyroid gland, adrenal gland and pituitary gland. However, endocrine glands that perform the dual function of secreting both hormones and performing some other function are known as heterocrine glands. Examples of holocrine glands are pancreas, testes and ovaries. The study of endocrine glands and hormones secreted by them is known as *endocrinology*.

Endocrine glands are characterized by the following features:

- Endocrine glands contain chemicals which are known as hormones. These control behaviours.
- Some glands (for example, parathyroid), secrete only one hormone while others (like anterior pituitary), secrete several hormones.
- Glands are under neural control. For example, hypothalamus is responsible for hormonal secretion.
- Each hormone modulates the functioning of a target tissue or target organ, which is located somewhere in the body. The effects of the hormones may be specific to a localized region. Whereas, many of the anterior pituitary hormones act on the target organ, which itself can be a gland.
- The endocrine glands have balanced secretion that depends on the need of the body, thereby maintaining homeostasis. This implies that these

behaviours are associated with stress, growth and development in general and reproduction.

Now, let us learn about some of the endocrine glands and the hormones secreted by them in detail.

Thyroid gland

The thyroid gland develops from the endoderm of the embryo. It is the largest endocrine gland, which is located anterior to the thyroid cartilage of the larynx, in the neck above the trachea. It secretes three hormones, namely, Thyroxine /Tetra-iodothyronine (T4); Tri-iodothyronine (T3) and Calcitonin (CT).

Both T4 and T3, help in increasing the metabolic rate of the body and help in maintaining the basal metabolic rate (BMR). BMR refers to the rate at which cells utilize energy. They promote growth of body tissues and development of mental faculties. They stimulate tissue differentiation. Thyroxine also affects the physiology of excretion as its deficiency causes decrease in the urine output. However, Calcitonin regulates the balance of calcium in the body and helps in lowering blood calcium.

Both, excess and deficiency of thyroxine hormone leads to certain disorders. These are given below:

Hyperthyroidism/ Graves disease/ exophthalmic goitre: It is thyroid enlargement in which the thyroid secretes excessive amount of thyroid hormones. This condition is characterized by over-excitability, reduced attention, chronic insomnia, reduced capacity to focus upon a particular task, loss of weight, rapid heartbeat, nervousness and restlessness. The individuals suffering from this disorder tend to have protruding eyes and often have a starring appearance known as exophthalmia. This disorder can be corrected by the surgical removal of a portion of the gland, in order to reduce the amount of thyroxine secretion.

Hypothyroidism: results from less secretion of thyroxine. It results in three disorders, namely, goitre, cretinism and myxoedema.

- **Goitre:** It refers to an enlargement of the thyroid gland, along with a swelling in the neck. It results from inadequate amount of iodine in the diet. Iodine is necessary for the adequate production of thyroxine. In this condition, the thyroid cells multiply to compensate for each cell's lowered level of thyroxine production, leading to enlargement of the gland. It may lead to cretinism/myxoedema. This disease is common in hilly areas. Addition of iodine to the table salt prevents this disease.
- **Cretinism:** is caused by deficiency of thyroid hormones in infants. It is characterized by failure of CNS or other systems of the body to develop normally leading to mental retardation; protruding tongue; puffy eyes; poor muscle tone (which causes the stomach and shoulders to sag); sluggish body movements; pot-belly; pigeon chest; slow heart beat and low blood pressure. Due to inadequate skeletal and muscular development, the bodies of these individuals become dwarfed and grossly

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misshapen. This condition is corrected by early administration of thyroid hormones.

- **Myxoedema:** is caused by deficiency of thyroid hormones in adults. It is characterized by puffy appearance due to accumulation of fat in the subcutaneous tissue, because of low metabolic rate. These patients tend to lack alertness, intelligence and initiative.

Parathyroid gland

It develops from the endoderm of the embryo. It consists of four separate glands which are located on the posterior surface of the lobes of the thyroid gland. They do not have colloidal substance but contain acidophilic cells. Internally, the gland consists of densely packed cords of epithelial cells. These are adequately supplied with blood vessels. It secretes a hormone known as parathormone. Parathormone is also known as Collip's hormones as it was discovered by a person named Collip. This hormone is not regulated by the pituitary gland.

Parathormone helps in the regulation of the metabolism of calcium and phosphate, for proper functioning of the neural, skeletal and muscle tissues. It decreases the level of phosphate in the blood by stimulating the kidneys to eliminate phosphate in urine. It also helps in the reabsorption of water from kidneys, thereby maintaining a water balance in the body. It increases the absorption of both phosphate and magnesium from intestinal tracts. It also stimulates the osteoclasts to break down bone and release calcium and phosphate. Thus, parathormone regulates the metabolism of calcium and phosphate.

The parathyroid hormone is under the feedback control of blood level of calcium. A fall in the level of calcium in the blood stimulates the parathyroid gland to secrete parathormone. Similarly, a rise in the blood level of calcium inhibits the secretion of parathormone by the parathyroid gland.

Parathormone increases the level of calcium in blood in the following two ways:

- It increases the reabsorption of calcium as it is being processed by kidneys, so that it is not lost through the excretion of urine. This is a faster way of increasing the level of calcium in blood.
- It acts on the bone tissue, by converting the calcium into a form that the body can use. This is a relatively slower way of increasing the level of calcium in blood.

The combined effect of parathormone and calcitonin normally maintains the level of calcium in blood. Both, an excess and deficiency of parathormone results in the following disorders:

- **Hypoparathyroidism:** It results due to the deficiency of parathormone. It lowers the level of calcium in blood, which in turn increases the excitability of nerves and muscles. It also results in sustained contractions (tetany) of the muscles of the larynx, face, hands and feet. This disease is known as Parathyroid Tetany.

- **Hyperparathyroidism:** It results due to an excess of parathormone. It leads to osteoporosis, in which the bones become soft and some of the bone substance is replaced by fibrous connective tissue. It causes the calcium to get deposited in the kidneys and leads to kidney stones.

Pancreas

The pancreas are derived from the endoderm of the embryo. They lie inferior to the stomach in a bend of duodenum. They are both exocrine and endocrine glands. The tissues of pancreas have acinar cells and groups of cells called the islets of Langerhans. Following are the four kinds of cells which have been identified in the islets:

- **Alpha cells or A cells:** they constitute about 60 to 70 per cent of the islets of Langerhans and produce glucagon
- **Beta cells or B cells:** they constitute about 32 to 38 per cent of the islets of Langerhans and produce insulin
- **Delta cells or D cells:** produce somatostatin (SS)
- **F-cells:** produce pancreatic polypeptide (PP)

Both delta cells and F-cells constitute about 2 to 8 per cent of the islets of Langerhans. The hormones produced by the pancreas are glucagon, insulin, somatostatin and pancreatic polypeptide.

- **Glucagon:** stimulates the liver to convert stored glycogen into glucose. It is controlled by the feedback mechanism in accordance with the level of glucose in the blood, that is, when the blood sugar rises, the secretion of glucagon is suppressed and when it drops, the secretion of glucagon is stimulated.
- **Insulin:** decreases the blood glucose level by the increasing the rate at which glucose is transported out of the blood and into the cells and by stimulating muscle cells to take sugar from the blood and convert it into glycogen. It is primarily regulated by feedback from the blood glucose concentration. It promotes protein synthesis in tissues from amino acid; reduces catabolism of protein, increases the synthesis of fat in the adipose tissues from fatty acids and reduces the breakdown and oxidation of fat. It is through the action of insulin that the cells in the body receive the necessary nourishment from blood glucose. It allows the transport of glucose from the blood stream through the cell membrane and into the cells itself. In fact when a meal is eaten, the breakdown of the food to glucose stimulates the pancreas to increase the secretion of insulin. The amount of glucose entering the cell is directly related to the level of insulin secretion.
- **Somatostatic (SS):** It suppresses the release of other hormones from the pancreas and digestive tract.

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Pancreatic Polypeptide (PP): inhibits the release of digestive secretion of the pancreas. Certain disorders associated with these hormones are mentioned as follows:

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- **Diabetes mellitus (Hyperglycemia):** It is of two types, namely, insulin dependent form or type-I (caused by a failure of beta-cells to produce adequate amount of insulin) and non-insulin-dependent form or type-II (caused due to the failure of insulin to facilitate the movement of glucose into cells. It appears to be inherited as an autosomal recessive characteristic.)

Diabetes mellitus is characterized by an increase in the level of blood glucose, above the normal range. Some of the glucose is excreted in the urine and leads to excessive urination and dehydration of body tissues. This results in excessive thirst (Polydipsia). In diabetes mellitus, the cells are unable to utilize glucose and other carbohydrates for energy production. These cells utilize their proteins for it. Consequently, the person becomes very weak and the degradation of fats increases, producing Ketone bodies (Ketosis) which are acidic and poisonous in nature. The blood cholesterol level also rises and the body's healing power gets impaired. A progressive deterioration in the peripheral nerves, eyes and kidneys is also seen.

- **Hypoglycemia:** It occurs when the blood glucose level falls below normal. It may be caused by an excess of insulin, or by the deficiency of glucagon or by the failure of the secretion of these two hormones to completely regulate blood sugar. Some individuals have few or no alpha cells and are thus deficient in glucagon, whereas others produce excessive quantities of insulin because of the presence of tumors in the beta cells.

Hypoglycemia is characterized by weakness, unconsciousness, convulsions, profuse sweating, irritability and confusion. This condition can be rectified by an urgent intake of sugar or glucose.

Adrenal/ suprarenal glands/glands of emergency: These are paired structures which are located superior to the kidney. Each adrenal gland consists of an outer cortex and an inner medulla.

Adrenal cortex: consists of three distinct layers of cells—glomerulosa, fasciculata and reticular cells. It is surrounded by a fibrous capsule. It contains fat and acids with a remarkable power of regeneration. Adrenal cortex is glandular and consists of the urinogenital tract. Externally, it is surrounded by the medulla, which is neural

Adrenal Medulla: is neural in nature and arises out of the sympathetic nervous system (SNS). It consists of chromaffin cells, which are surrounded by venous sinuses. The hormones travel quietly into these sinuses, through the blood, to target organs.

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- **Epinephrine or adrenaline:** is secreted at the time of emergency and is therefore also known as the *emergency hormone*. It has almost same effects as nor-epinephrine, but it differs from nor-epinephrine in the sense that it has greater effect on the cardiovascular activity and causes weak constriction of blood vessel as compared to nor-epinephrine. Both epinephrine and nor-epinephrine differ in their effects on tissue metabolism.

Hypothalamus lies below the thalamus. It provides anatomical connection between the nervous and the endocrine systems. This connection is through pituitary gland. It is connected to the anterior pituitary by special blood vessels and to the posterior pituitary by nerve fibres. The neurosecretory cells of hypothalamus secrete hormones known as neurohormones (or releasing factors). These are:

- **Adrenocorticotrophic releasing hormones (ARH):** stimulates the anterior pituitary to secrete adrenocorticotrophic hormones (ACTH).
- **Thyrotrophic releasing hormones (TRH):** stimulates the anterior pituitary to secrete thyroid stimulating hormones (TSH).
- **Somatotrophic releasing hormones (SRH):** stimulates the anterior pituitary to release growth hormones (GH).
- **Growth inhibiting hormones (GIH):** stimulates the anterior pituitary to inhibit the secretion of growth hormones.
- **Gonadotrophic releasing hormones (GRH):** stimulates the anterior pituitary to secrete its follicle stimulating hormone (FSH), or luteinizing hormone (LH) in ovaries and to secrete its intestinal cells stimulating hormones (ICSH) in the testes.
- **Prolactin releasing hormones (PRH):** stimulates the anterior pituitary to secrete prolactin.
- **Prolactin inhibiting hormones (PIH):** stimulates the anterior pituitary to inhibit the secretion of prolactin.
- **Melanocyte releasing hormones (MRH):** stimulates the intermediate lobe of the pituitary to secrete its melanocyte stimulating hormones (MSH).
- **Melanocyte inhibiting hormones (MIH):** stimulates the intermediate lobe of the pituitary to inhibit the secretion of melanocyte stimulating hormones (MSH).

Pituitary gland (hypophysis)

This is known as the *master gland*. It is the smallest endocrine gland and is located just below the hypothalamus. It is attached to the brain by a stalk which is continuous with the hypothalamus. The pituitary gland can be divided into three parts, namely, the anterior pituitary, the intermediate pituitary and the posterior pituitary. Each of these secrete their own respective hormones.

Hormones of the Anterior Lobe (pars distalis or adeno hypophysis)

- **Somatotrophic hormones:** It is not a tropic hormone. Its secretion occurs episodically, with 6–7 bursts each day in adolescence and a smaller number of bursts in adulthood. The secretion of growth hormone is accomplished by the growth releasing and growth inhibiting hormones. Growth hormones promote protein metabolism, absorption of calcium from the bowel and conversion of glycogen to glucose. They act directly on the body, stimulating the growth process in these cells. It also promotes gradual enlargement of the large bones of the arm and leg. It influences the functions of the thyroid, parathyroid and several glands during critical times in an individual's life. It is seen to play a role in the metabolism of food. Its secretion is triggered by the hypoglycemia and even by the decrease of glucose from an elevated level, following a meal that is rich in glucose (Brown *et al.* 1978). It is highly sensitive to the glucose level in the blood and thus is associated with fasting (Woods, Decke and Vasselli 1974).

NOTES**Hormone secreted by the intermediate lobe (middle lobe or pars intermedium)**

- **Melanocyte stimulating hormone:** It causes dispersal of pigment granules in the pigment cells, thereby darkening the colour in certain animals like fishes and amphibians. It is believed that it is associated with the growth and development of melanocytes in man which gives colour to the skin.

Hormones of the posterior lobe (pars nervosa or neurohypophysis)

The secretion of the posterior lobe is known as pituitarin and it contains two hormones, namely oxytocin and vasopressin.

- **Oxytocin or pitocin:** It promotes contraction of the uterine muscle and contraction of the myoepithelial cells of the lactating breasts. This results in the activity of squeezing milk into the large ducts situated behind the nipple. In late pregnancy, the uterus becomes very sensitive to oxytocin. The amount secreted is increased just before and during labour and at time of sucking by the baby.
- **Antidiuretic hormones (ADH) /vasopressin or pitressin:** This hormone produces two effects; namely, the antidiuretic effect and the pressor effect. The antidiuretic effect refers to increased re-absorption of water in the distal convoluted tubule, collecting tubule and collecting ducts of the nephrons of the kidneys. As a result, the re-absorption of water from the glomerular filtrate is increased. The pressor effect refers to the contraction of the involuntary muscle in the walls of the intestine, gall bladder, urinary bladder and blood vessels. Contraction of the walls of the blood vessels raises the blood pressure.

Certain disorders that are associated with the secretion of the pituitary gland are given below:

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- **Pituitary dwarfism:** It is caused by the deficiency of the growth hormone. It is characterized by a small but well proportioned body and sexual immaturity.
- **Gigantism:** It is caused by an excess of growth hormones since an early age. It is characterized by a large and well proportioned body.
- **Acromegaly:** It is caused by an excess of growth hormone in adulthood. It is characterized by disproportionate increase in the size of bones of face, hands and feet.
- **Diabetes insipidus:** It is caused by the deficiency of antidiuretic hormone. It is characterized by excessive excretion of dilute urine.
- **An excessive secretion of antidiuretic hormone:** results in excessively dilute blood and low plasma sodium.

The Pineal body

It is also known as a regulator of regulators. It is a small structure that lies posterior to the thalamus, in the diencephalon. It is situated exactly along the midline axis of the brain. It is a small rounded body which consists of pineal cells and supporting glial cells. The hormones secreted by the pineal body are given below:

- **Serotonin:** plays a role in the regulation of mood and sleep. It is a neurotransmitter, which is found in other locations in the brain too.
- **Melatonin:** lightens the skin colour and regulates the working of gonads (testes and ovaries). It also provides a link between the endocrine system and the cycles of light and dark in the environment. Its secretion follows a cyclical pattern over a 24-hour period. The night time release of melatonin into the blood stream and into the cerebrospinal fluid is nearly 10 times more than its release during the day time. Since the secretion of melatonin is suppressed by the light of the day time, therefore it is also known as the Dracula hormone.

Sex hormones

In females the ovary releases the following hormones:

- **Estrogen:** It is responsible for the development of the primary and secondary sexual characteristics in females. Increase in the secretion of estrogen initiates the development of an egg cell/ovum from the ovary, in a sexually mature adult.
- **Progesterone:** It is secreted by the corpus luteum of the ovary and stimulates further development of the uterine epithelium and mammary glands. It is required for the formation of the placenta and for the maintenance of pregnancy.

Impact of hormones on behaviour

Hormones are seen to exert a significant influence on one's behaviour. Some of their influences are:

- **Hormones and growth:** Growth is stimulated by hormones which are secreted by the anterior pituitary. At times, a tumor in the anterior pituitary results in certain abnormalities, by altering the release of hormones. Curtis (1977) showed that poverty, malnutrition and stress can cause a reduction in the secretion of growth hormones. He called this *psychosocial dwarfism*. Because of genetic and hereditary reasons or because of severe malnutrition in childhood, the tissues of the target organs may not respond to growth hormones, as is seen in the case of African pigmies. Nearly excessive secretions of androgens and estrogen can end growth processes early in childhood. This is due to precocious puberty development.
- **Homeostasis and hormones:** Hormones tend to maintain homeostasis by regulating the distribution of ions and maintaining ionic balance. They also control the concentration of glucose in the blood and the brain. Under the condition of stress, hormones play an important role in maintaining the body's homeostatic level.
- **Hormones, learning and memory:** In experiments conducted by Davenport on rats in 1986, it was seen that the thyroid gland was responsible for early development of the nervous system. Hypothyroidism was seen to cause insufficient neural synaptic connection which tend to inhibit learning and memory. Dunn, in 1989, postulated that the removal of pituitary impairs learning and this impairment can be overcome by synthetically administering ACTH. He concluded that hormones are important for learning.
- **Hormones and emotions:** According to Levi (1985), Brown (1990) and Mason (1994), assignment of epinephrine level shows various capacities for emotional status. During stress they studied professional sports people, soldiers in wars and ordinary people in a state of anxiety. They found that the nor-epinephrine levels were high in states of aggression and anxiety, as compared to passive state. They studied monkeys in fear and avoidance behaviour and found higher levels of epinephrine, cortisol, thyroxine and growth hormone. They also found a decrease in insulin and testosterone levels in these monkeys. In depressive patients, they found a decrease in hormonal levels of thyroid and adrenal glands.
- **Hormones and Aggression:** Mckinney, in 1992, studied levels of androgen and sex hormones in relation to emotion and aggression. They found sexual cycles and seasonal rhythm changes can produce aggressive behaviour. They found that castration (removal of male penis) was seen to be associated with reduction in aggression and fighting behaviour.

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CHECK YOUR PROGRESS

9. Define the transmission process.
10. What is a resting nerve fibre?
11. What is the Na-K pump mechanism?
12. How do techniques like functional MRI help?

3.6 SUMMARY

- Functional neuroanatomy gives a clear overview about the functions of the central nervous system.
- Neuroanatomical procedures give a deeper understanding of the structural organization of neural systems.
- The adult brain can be divided into four major divisions: the cerebrum, diencephalons, cerebellum and brainstem.
- The brain controls the flow of information throughout the body, through the spinal cord and network of nerves. This information comprises of voluntary actions such as walking, reading and talking and involuntary reactions like breathing and digestion.
- Blood transports oxygen and other nutrients which are vital for the health of the neurons. Therefore, an uninterrupted flow of blood to the brain must be maintained.
- Neuroimaging is a combination of various techniques, to either directly or indirectly image the structure and function/pharmacology of the brain.
- Cell specialization is a process wherein a group of cells work together to perform single functions for large organs and tissues.
- Neurophysiology has a wide and interdisciplinary scope which covers original studies on molecular, cellular and systemic neurophysiology, functional neuromorphology, neuropharmacology and neurochemistry.

3.7 KEY TERMS

- **Neuroanatomy:** Anatomy of the nervous system
- **MRI:** The use of nuclear magnetic resonance of protons to produce proton density images
- **Neurophysiology:** The branch of neuroscience that studies the physiology of the nervous system
- **Autonomic nervous system:** Part of the nervous system of vertebrates that controls involuntary actions of the smooth muscles, heart and glands

- **Dendrites:** Branched projections of a neuron that act to conduct the electrochemical stimulation received from other neural cells to the cell body, or soma, of the neuron from which the dendrites project
- **Axon:** Long nerve fibre that conducts away from the cell body of the neuron
- **Nodes of Ranvier:** Small gaps in the myelin sheath of myelinated axons
- **Telodendria:** The terminal branching of an axon
- **Astrocytes:** Characteristic star-shaped glial cells in the brain and spinal cord
- **Schwann cells:** Type of cells which coat the peripheral segment of nerves and produce a substance called myelin
- **Golgi stain:** A nervous tissue staining technique which was discovered by the Italian physician and scientist, Camillo Golgi
- **Pons Varolii:** A band of nerve fibres linking the medulla oblongata and the cerebellum with the midbrain

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3.8 ANSWERS TO 'CHECK YOUR PROGRESS'

1. The two main divisions of the nervous system are: the Central Nervous System (CNS) and the Peripheral Nervous System (PNS).
2. The main function of the optic nerve is to regulate the sense of sight.
3. The autonomic nervous system is also known as the visceral motor system, because it consists of motor fibre of PNS, which in turn stimulate the smooth muscles and glands.
4. The technique of Golgi stain was accidentally discovered when Golgi was trying to stain the meninges by exposing a block of neural tissues to potassium dichromate and silver nitrate.
5. The technique of Nissl stain was developed in order to deal with the shortcomings of the Golgi stain method.
6. The two types of neuroanatomical tracing techniques are: anterograde and retrograde.
7. The four major divisions of the brain are:
 - (i) Brainstem
 - (ii) Cerebellum
 - (iii) Cerebrum
 - (iv) Diencephalon
8. The tectum consists of two pair of nuclei, namely, the superior and the inferior colliculi.

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9. In the transmission process, nerve impulses are transmitted along nerve fibres. A particular nerve fibre goes through the process of polarization, depolarization and repolarization, in order to transmit the nerve impulse.
10. A nerve fibre that is dormant and is not involved in the activity of conducting an impulse is known as a resting nerve fibre.
11. The Na-K pump mechanism involves the expulsion of sodium ions outside the membrane and drawing of potassium ions inside the membrane, against the concentration and the electro-chemical gradient.
12. Techniques like functional MRI help in indicating which region of the brain is active, while performing a certain activity.

3.9 QUESTIONS AND EXERCISES

Short-Answer Questions

1. What is the main function of the peripheral nervous system?
2. What are the plexuses that are formed by the combination of certain spinal nerves?
3. On the basis of their functions, how can neurons be divided?
4. How is the brain divided functionally?
5. Which sensory streams does the anterior parietal cortex integrate and coordinate?
6. What are the three major functions of the brain?
7. Which three kinds of electrical events are seen in the nervous system?
8. How can various brain potentials be divided?

Long-Answer Questions

1. Write in detail about the various neuroanatomical techniques.
2. What do you understand by the term, cell specialization?
3. What are neurotransmitters? Describe the various types of neurotransmitters.
4. How do hormones act on different cellular mechanisms?
5. Do hormones affect behaviour? Illustrate with examples.

3.10 FURTHER READING

Pinel, John. 2003. *Biopsychology*, Fifth edition. New Jersey: Allyn and Bacon.

UNIT 4 SENSORY MOTOR SYSTEM

Structure

- 4.0 Introduction
- 4.1 Unit Objectives
- 4.2 Three Principles of Sensory Motor Association
- 4.3 Secondary Motor Cortex
- 4.4 Primary Motor Cortex
- 4.5 Cerebellum and Basal Ganglia
- 4.6 Descending Motor Pathways
- 4.7 Sensory Motor Spinal Circuits
- 4.8 Central Sensory Motor Programs
- 4.9 Motor Control and Plasticity
 - 4.9.1 Behavioural View
 - 4.9.2 Control System View
 - 4.9.3 Neuroscience View
- 4.10 Movement Control
- 4.11 Extrapyrmidal Systems
- 4.12 Disruption of Movement
- 4.13 Tracing Responses
- 4.14 Summary
- 4.15 Key Terms
- 4.16 Answers to 'Check Your Progress'
- 4.17 Questions and Exercises
- 4.18 Further Reading

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4.0 INTRODUCTION

Human sensors (receptors) measure the physical state of the human body and relate it to the external environment. Nerves from the spinal cord and those from the sensory organs carry sensory information to the brain. The process by which knowledge and understanding is developed in the human mind is needed to understand the perceived information and initiate a motor reaction. Knowledge about the sensory motor system is important for understanding the basic concepts. The sensory motor system is very important in learning the difficulties that are associated with the most fundamental problems of basic impulses. The key highlight of the sensory motor system is that it is able to represent the most prominent features of the external environment. The sensory motor system organizes abstract matter. It also analyses and differentiates the semantic concepts that correspond to our way of functioning with the external environment. The sensory motor system of the brain is multimodal rather than modular.

4.1 UNIT OBJECTIVES

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After going through this unit, you will be able to:

- Explain the principles of sensory motor association
- Discuss concepts like: secondary and primary motor cortex
- Describe the importance and functions of the cerebellum and basal ganglia
- Define and elaborate on descending motor pathways
- Identify sensory motor spinal circuits
- Analyse central sensory motor programs
- Discuss motor control and plasticity
- Explain extrapyramidal systems
- List the reasons for disruption of movement

4.2 THREE PRINCIPLES OF SENSORY MOTOR ASSOCIATION

The three principles of sensory motor association are:

- (i) It is hierarchically organized
- (ii) The motor output is guided by sensory input
- (iii) Based on learning, the nature and locus of sensory motor control can be modified

We now look at these three principles in detail. The sensory motor system is arranged in the form of a hierarchy: the association cortex lies at the top of the hierarchy. The association cortex which often sends commands that are quite general in nature, rather than specific plans of action. It exerts direct control, only when an individual has to perform complex functions. The signals seem to flow between various levels of the hierarchy, over multiple paths. With this flow of signal, the association cortex can control the levels that are below it in different ways. Information mainly flows down from the top level to the lower levels in the hierarchy. These different levels of the hierarchy perform different functions. Hence it can be said that the sensory motor system is a parallel and functionally segregated hierarchical system.

In sensory motor system, the motor output is guided by the sensory input. The response depends on the information which is received from various sense organs, like, the eyes, ear and receptors in the skin, muscles and joints. This sensory information is fed into sensory motor circuits, which monitor the progress of our response. In most instances, except those involving ballistic movements (such as swatting of a fly, etc.), this sensory feedback plays an important role in directing the continuation of the responses, that produce it.

The lower levels of the sensory motor hierarchy unconsciously control several adjustments in motor output that occur in response to the sensory feedback. The higher levels of the sensory motor system play no role in controlling these adjustments, in the motor response. As a result, the sensory motor system is able to function effectively.

During a sensory motor task, individual motor responses are initially performed under conscious control. However, soon, with repeated practice and learning, the same response gets organized into continuous and integrated sequence of actions. These actions flow smoothly and are adjusted by sensory feedback, without conscious regulation.

The association cortex is at the top of the sensory motor hierarchy. The sensory motor association cortex has two major areas, namely, the posterior parietal association cortex and the dorsolateral prefrontal association cortex. Both these association cortexes are composed of several areas, each of which has a different function.

The main function of the posterior parietal association cortex is to integrate the information about the original positions of the parts of the body. These parts are to be moved with the information about the positions of any external objects with which the body is going to interact. Since it receives inputs from more than one sensory system, therefore it is classified as an association cortex. It receives information from three sensory systems that play roles in the localization of the body and external objects, in space. The three sensory systems are: the visual system, the auditory system and the somatosensory system. Much of the output of the posterior parietal cortex goes to those areas of the motor cortex, which are located in the frontal cortex, the dorsolateral prefrontal association cortex, various areas of the secondary motor cortex and the frontal eye field. The frontal eye field is a small area of prefrontal cortex that controls the movement of the eyes. Much of the output from the posterior parietal cortex goes to, the areas of the motor cortex (these are located in the frontal cortex), the dorsolateral prefrontal association cortex, the various areas of secondary motor cortex and to the frontal eye field (a small area of prefrontal cortex that controls eye movements).

Sensory motor deficits (like deficits in the perception and memory of spatial relationship, in accurate reaching and grasping, control of eye movement, apraxia, contralateral neglect and attention) result from damage to the posterior parietal cortex. Unilateral damage to the left posterior parietal lobe or its connections results in apraxia. Apraxia is a disorder of voluntary movement. The affected patients experience significant difficulty in certain movements. However, they are able to engage in the same movement, easily, when they engage in those movements as part of their normal routine. For example, a carpenter may be able to hammer a nail well, while doing his routine work, but he may fail to do so when specifically asked to demonstrate the hammering of a nail.

Large lesions of the right posterior parietal lobe often result in contralateral neglect. An individual with contralateral neglect is unable to react to any stimulus,

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which occurs on the side of the body that is opposite to the side of a brain lesion, in the absence of simple sensory or motor deficits. Although patients with contralateral neglect tend to neglect visual stimuli to the left, as defined by gravitational coordinates. This is not always the case as their contralateral neglect can sometimes be manifested in terms of external object based coordinates. For instance, in one experiment, in which a vertically positioned wheel was rotated anticlockwise and then clockwise, the patient had more difficulty reacting to movements of the experimenter's right hand than to those of the left. In another case, the experimenter rotated the wheel clockwise. Similarly, in another somatosensory study, patients suffering from contralateral neglect were found to be more responsive than to touches on their left hand, if their arms were crossed.

Dorsolateral prefrontal association cortex performs important sensory motor functions. Its key function is to assess external stimuli and initiate appropriate reactions in response to them. Projections are sent to it by the posterior parietal cortex. Similarly, the dorsolateral prefrontal association transmits projections to the secondary motor cortex, primary motor cortex and the frontal eye field. In several studies that have been conducted on monkeys, it has been seen that the neurons of the monkey's dorsolateral prefrontal association cortex show activity when the monkey identifies and responds to objects. The location of the object, its characteristics and in some cases both, determine the activity of different neurons in the dorsolateral prefrontal association cortex. The activity of certain other neurons in this area are determined by the response that is produced, rather than the object per se. These neurons usually begin to fire before the response and continue to fire until the response is complete. Certain neurons in all cortical motor areas are seen to fire before a response occurs, in its anticipation. However, since neurons in the dorsolateral prefrontal association cortex fire first, therefore it is believed that area may be responsible for making decisions about the initiation of voluntary actions.

4.3 SECONDARY MOTOR CORTEX

A majority of inputs are received by the secondary motor cortex from the association cortex and a majority of its output goes to the primary motor cortex. The secondary motor cortex is broadly divided into the supplementary motor area, the premotor cortex and two cingulate motor areas. The supplementary motor area and the premotor cortex are clearly visible on the lateral surface of the frontal lobe, just anterior to the primary motor cortex. On the other hand, the two cingulate motor areas lie within the cortex of the cingulate gyrus of each hemisphere, just ventral to the supplementary motor area. The supplementary motor area wraps over the top of the frontal lobe and extends its medial surface to the longitudinal fissure. The premotor cortex runs in a strip from the supplementary motor area to the lateral fissure.

All areas of the secondary motor cortex send most of its axons to the primary motor cortex and receive axons back from the primary motor cortex. They are reciprocally connected to other parts of the secondary motor cortex and send axons directly into the motor circuits of the brain stem. In this way, all areas are anatomically similar to one another. All these areas also seem functionally similar to one another in the following three respects:

- (i) The electrical stimulation to particular sites within each of these areas results in complex movements of the body.
- (ii) The neurons in each of these areas, fire prior to and during voluntary motor responses.
- (iii) The movements of one side of the body are often associated with activation of each of these areas in both hemispheres.

In general it is believed that areas of the secondary motor cortex play a role in programming precise patterns of movement. Evidence of such a function comes from several brain-imaging studies, in which the patterns of activity in the brain have been measured, while the subject is either imaging his or her own performance of a particular series of movements, or planning the performance of the same movements. However, depending on the kind of instruction given and the kind of target movements employed, specific results of these studies have varied. Yet, a bilateral increase of activity in various areas of the secondary motor cortex has often been observed. For example, in a study done by Parsons and his colleagues in 1995, they asked the subjects to imagine grasping and picking up of an object. They found an increase in the PET (Positron Emission Tomography) activity in the supplementary motor area, premotor cortex and cingulate motor areas.

Several other PET studies, where subjects were asked to engage in the repetition of simple responses, extensive activation in the various areas of secondary motor cortex has been found. As it has been proposed earlier, the main function of the secondary motor cortex is to programme various movements into complex sequences of behaviour. When the subjects were asked to engage in the repetition of simple responses, there is little or no activation in these areas. The reason behind this observation is still not clear. However, complex sequences of movements do not activate additional regions of the secondary motor cortex, but they do produce more activity in the same areas compared to simple movements.

Different areas of the sensory motor cortex are similar functionally and anatomically, but they are seen to play different roles in planning, programming and generation of movement. Although several theories have been proposed to explain the functional differences between the various areas of secondary motor cortex, none has received consistent support.

Research has also been conducted extensively to understand how the premotor cortex encodes spatial relations. The research has shown that many premotor neurons respond to touch and each of these has a somatosensory receptive field, on a particular part of the body. Many of these neurons are referred

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to as bimodal neurons, as they respond to both, visual inputs and inputs received from touch. The visual receptive field of a bimodal neuron is always adjacent to its somatosensory receptive field. By this we mean, that if the somatosensory receptive field of a bimodal neuron is on the left hand, then its visual receptive field will be usually in the space adjacent to the left hand.

4.4 PRIMARY MOTOR CORTEX

The primary motor cortex is present within the gyrus of the frontal lobe. The cortical sensory motor signals are seen to converge here. The sensory motor signals from the cerebral cortex tend to depart from the primary motor cortex.

In 1937, Penfield and Boldrey mapped the primary motor cortex. They did this by applying electrical stimulation to various points on the cortical surface of conscious human patients. This was done during neurosurgery and parts of the body which moved in response to each stimulation were noted. They found that the primary motor cortex is somatotopically organized. The somatotopic structure of the human primary motor cortex is commonly referred to as the motor homunculus. Major part of the primary motor cortex is involved in the control of parts of the body which perform complicated movements, such as the hands and mouth.

The somatotopic structure of the human primary motor cortex, as given by Penfield and Boldrey, accurately describes different parts of the body. These parts were controlled by the primary motor cortex. However, researches in the recent years have necessitated an important revision of the original somatotopic layout, with respect to the hand areas. Researches that were conducted on monkeys, in which they were asked to perform individual finger movements, it was found that the control of any individual finger movement depended on the activity of a network of neurons. These neurons were widely distributed throughout the primary motor hand area, rather than being located in one somatotopically segregated finger area. Using fMRI, a similar pattern in the hand area of the human primary motor cortex was also seen. A further support for this observation came from the fact that small lesions in the hand area of the primary motor cortex of humans and monkeys did not cause any selective disruption in the activity of a single finger. Thus, it is now clear that the movement of even a single finger is regulated by a much larger area of the primary motor cortex that overlaps with areas controlling the movement of other fingers.

Usually, each general area in the primary motor cortex controls the movement of a particular group of muscles, which receives somatosensory feedback, via somatosensory cortex from receptors in these muscles and in the joints that they influence. However, an exception to this general pattern of feedback is seen in monkeys. For instance, monkeys have two different hand areas in the primary motor cortex of each hemisphere. One of the hand areas receives input from receptors in the skin rather than from receptors in the muscles and joints. It is quite

possible that such an arrangement facilitates the identification of objects by touch. This process is known as stereognosis. The process of stereognosis requires a complex interplay between motor responses and the somatosensory stimulation produced by them.

It is believed that each neuron in the arm area of the primary motor cortex has a different preferred direction, as they tend to fire maximally when the arm reaches in a particular direction. In 1995, Georgopoulos dissociated the direction of movement by applying external forces to monkeys' arms, while they reached in different directions. He found that the firing of the primary motor cortex neurons was correlated with the direction of the force that was generated to produce the movement. Each neuron was seen to fire maximally, before and at the time of the movement, in a preferred direction. The neurons also fired movements in different directions. The closer the movement was to the preferred direction, the more the neuron tended to fire.

Extensive damage to the human primary motor cortex has less effect than one would expect, keeping in mind the fact that most of the motor fibres from the cerebral cortex depart from this region. However, large lesions to the primary motor cortex are likely to hinder a patient's movement of one part of the body, independent of the rest. This may result in disruption of speed and accuracy of a patient's movements. Voluntary movements do not get disrupted in response to large lesions in this area as there are certain pathways that descend directly from secondary motor areas to subcortical motor circuits, without passing through primary motor cortex.

CHECK YOUR PROGRESS

1. What are the three principles of sensory motor association?
2. What is the key function of the dorsolateral prefrontal association cortex?
3. Where is the primary motor cortex present?

4.5 CEREBELLUM AND BASAL GANGLIA

The cerebellum and the basal ganglia act as two very important sensory motor structures, but do not form a part of the sensory motor hierarchy. They rather work together with different levels of the sensory motor hierarchy and assist in the coordination and modulation of its activities. Despite damage to the cortical connections between the visual cortex and the frontal motor areas, the visually guided responses do not get abolished, because the sensory and motor areas are interconnected via the cerebellum and basal ganglia. Now let us look at the role played by these areas, separately, in the sensory motor functioning of an organism:

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Cerebellum

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The cerebellum is quite a complex structure which is organized systematically in lobes, columns and layers. It constitutes only about 10 per cent of the mass of the brain, yet contains more than 50 per cent of the neurons of the brain. The cerebellum receives information from a variety of sources; for instance, it receives information from the primary and secondary motor cortex, descending motor signals from the brain stem motor nuclei and receives feedback from motor responses via the somatosensory and vestibular system. The cerebellum is primarily involved in the comparison of the information which is received from these different sources. In modulating the ongoing movement, it deviates from its intended course. Hence, by performing this function, cerebellum is believed to play a major role in motor learning.

Damage to the cerebellum results in inability of the patient to precisely control the direction, force, velocity and amplitude of movements. It also makes it difficult for these patients to adapt to the pattern of motor output, with respect to changing conditions. These patients also experience difficulty in maintaining steady postures. Attempts by them to do so frequently lead to tremors. In addition, severe disturbance in balance, gait, speech and control of eye movement is seen. Learning of new pattern is also greatly impaired.

Theories about the function of the cerebellum are still evolving. For instance, it was earlier believed that the function of the cerebellum is limited to the fine tuning and learning of motor responses. But the observation of activity in the cerebellum by functional brain imaging, during the performance of a variety of non-motor cognitive tasks by healthy human subjects, has proposed an alternative view. This view states that the cerebellum is involved in the fine tuning and learning of cognitive responses, in the same way, as it is involved in the fine tuning and learning of motor responses. Support for this view also comes from the documentation of cognitive deficits in patients with cerebellar damage.

Basal ganglia

The basal ganglia is a complex heterogeneous collection of interconnected nuclei. Much like the cerebellum, it is believed to perform a modulatory function. The basal ganglia forms a part of neural loops. These loops receive cortical input from various cortical areas and transmit them back, via the thalamus, to various areas of the motor cortex.

Theories about the function of the basal ganglia have also been changing in the light of newer research in this area. For instance, it was earlier believed that much like the cerebellum, basal ganglia also plays a role in the sequencing of movement. However, studies have proposed that the basal ganglia is also involved in a variety of cognitive functions, in addition to its role in the modulation of neural output.

Several experiments conducted on rats, have shown that the basal ganglia play an important role in associative learning. Some patients with basal ganglia

damage have often been seen to display difficulties in solving complex puzzles that require only a single key press.

4.6 DESCENDING MOTOR PATHWAYS

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Neural signals are conducted from the primary motor cortex to the motor neurons of the spinal cord via four different pathways. Two pathways descend in the dorso-lateral region of the spinal cord and two descend in the ventro-medial region of the spinal cord. These pathways act together in the control of voluntary movement.

The two pathways that descend in the dorsolateral region of the spinal cord are the dorsolateral corticospinal tract and dorsolateral corticorubrospinal tract. One group of axons that descends from the primary motor cortex to the contralateral dorsolateral spinal white matter, through the medullary pyramids, constitutes the dorsolateral corticospinal tract. The dorsolateral corticospinal tract is the direct division of the dorsolateral motor pathways. The dorsolateral corticospinal tract contains neurons which are known as the Betz cells. Betz cells are extremely large pyramidal neurons of the primary motor cortex. Their axons terminate in lower regions of the spinal cord, on motor neurons that project to the muscles of the legs. Thus, they help in regulating a rapid and powerful voluntary control on the legs. Most axons of the dorsolateral corticospinal pathway synapse on small interneurons of the spinal gray matter, which synapse on the motor neurons of distal muscles of the wrist, hands, fingers and toes. Primates and few other mammals that are capable of moving their digits independently, have dorsolateral corticospinal tract neurons that synapse directly on digit motor neurons.

A second group of axons that descends from the primary motor cortex synapses in the red nucleus of the midbrain. The axons of neurons in the red nucleus then decussate and descend through the medulla. Some of these axons terminate in the nuclei of the cranial nerves (that control the muscles of the face), while the others continue to descend in the dorsolateral portion of the spinal cord. This pathway is called the dorsolateral corticorubrospinal tract. This tract is an indirect division of the dorsolateral motor pathway. The axons of the dorsolateral corticorubrospinal tract synapse on interneurons. These, in turn, synapse on motor neurons that project to the distal muscles of the arms and legs.

Similar to the dorsolateral motor pathway, the ventromedial motor pathway is divided into the ventromedial corticospinal tract and the ventromedial cortico-brainstem-spinal tract. The long axons of the ventromedial corticospinal tract descend ipsilaterally from the primary motor cortex, directly into the ventromedial areas of the spinal white matter. The ventromedial corticospinal tract is a direct division of the ventromedial pathway. As each axon of the ventromedial corticospinal tract descends, it branches diffusely and innervates the interneuron circuits in several different spinal segments, on both sides of the spinal gray matter.

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In contrast to the ventromedial corticospinal tract, the ventromedial cortico-brainstem-spinal tract is an indirect division of the ventromedial pathway. The ventromedial cortico-brainstem-spinal tract comprises of motor cortex axons. These axons feed into a complex network of brain stem structures. The axons of some of the neurons in this complex brain stem motor network then descend bilaterally in the ventromedial portion of the spinal cord. Each side carries signals from both hemispheres and each neuron synapses on the interneurons of several different spinal cord segments that control the proximal muscles of the trunk and limbs.

The following four structures of the brain stem tend to interact with the ventromedial cortico-brainstem-spinal tract:

- (i) **Tectum:** receives auditory and visual information about spatial location
- (ii) **Vestibular nucleus:** receives information about balance from receptors in the semicircular canals of the inner ear
- (iii) **Reticular formation:** among other things, contains motor programs for movements such as walking, swimming and jumping
- (iv) **Motor nuclei of the cranial nerves:** controls the muscles of the face

Both the dorsolateral and the ventromedial motor pathways are similar to each other in the sense that both have one direct division and one indirect division. The direct division descends directly to the spinal cord and the indirect division descends to the spinal cord. However, the two dorsolateral tracts differ from the two ventromedial tracts in the following two respects:

- (i) The two ventromedial tracts are much more diffuse. Many of their axons innervate interneurons on both sides of the spinal gray matter, in several different segments. On the other hand, the axons of the two dorsolateral tracts terminate in the contralateral half of one spinal cord segment, sometimes directly on a motor neuron.
- (ii) The motor neurons that are activated by the two ventromedial tracts, project to proximal muscles of the trunk and limbs, whereas the motor neurons that are activated by the two dorsolateral tracts project to distal muscles.

Since all four descending motor tracts originate in the cerebral cortex, therefore they are believed to mediate voluntary movements. However, they differ in their functions, based on major differences in their routes and destinations.

This difference was first demonstrated in two experiments that were reported by Lawrence and Kuypers in 1968. In their first experiment, Lawrence and Kuypers transected the left and right dorsolateral corticospinal tracts of their monkey subjects, in the medullary pyramids, just above the decussation of the tracts. They found that these monkeys could stand, walk and climb quite normally; but their ability to use their limbs for other activities was impaired. For instance,

their reaching movements were weak and poorly directed, particularly in the first few days following the surgery. Although after few weeks a substantial improvement in the reaching ability of monkeys' was seen, but two other deficits continued to exist. The first deficit was that the monkeys never regained the ability to move their fingers independent of one another. That is, they tended to use all their fingers while picking up food, as if they were glued together. And the second deficit was that, they never regained the ability to release objects from their grasp. However, it was quite interesting to see that they had no difficulty releasing their grasp on the bars of their cage when they were climbing. This observation made the researchers to postulate that the same response performed in different contexts can be controlled by different parts of the central nervous system.

In their second experiment, Lawrence and Kuypers took one group of monkeys whose dorsolateral corticospinal tracts had already been transacted in the first experiment. They transacted the dorsolateral corticorubrospinal tract. They saw that these monkeys were still able to stand, walk and climb, but when they were sitting, their arms hung limply by their sides. In order to draw small objects of interest back along the floor, the monkeys were seen to throw their arms out from the shoulder, using it like a rubber handled rake.

In the other group of monkeys in the second experiment, both the researchers transacted the ventromedial tracts of these monkeys. Unlike the first group, these subjects had severe postural abnormalities. They were seen to display significant difficulty in walking or sitting. If they did manage to sit or stand without clinging to the bars of their cages, the slightest disturbance, such as a loud noise, frequently made them fall. They were also unable to control the movement of the shoulders. When they fed, they did so with elbow and whole hand movements while their upper arms hung limply by their sides.

These two experiments suggested that the two ventromedial tracts are involved in the control of posture and movements of the whole body. They can exert control over the limb movements which are involved in such activities. In contrast, both dorsolateral tracts are involved in the control of reaching movements of the limbs. Only the corticospinal division of the dorsolateral system is capable of mediating independent movements of the digits.

4.7 SENSORY MOTOR SPINAL CIRCUITS

Muscles

Motor units are the smallest units of motor activity. Each motor unit comprises of a single motor neuron and all of the individual skeletal muscle fibres that it innervates. All the muscles fibres of the motor unit are seen to contract together, when the motor neuron fires. The motor units differ with respect to the number of muscle fibres that they contain. Selective motor control is seen in those units that contain the fewest fibres. For example, motor units of the fingers and face have few fibres and they permit the highest degree of selective motor control.

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A skeletal muscle consists of hundreds of thousands of threadlike muscle fibres. All these muscle fibres are bound together in a tough membrane and are attached to a bone, by a tendon. The motor neurons at neuromuscular junctions, release Acetylcholine, which activates the motor end plate on each muscle fibre and causes the fibre to contract. All of the motor neurons that innervate the fibres of a single muscle are called its motor pool.

Broadly speaking, skeletal muscle fibres can be divided into fast muscle fibres and the slow muscle fibres. The fast muscle fibres contract and relax quickly. They are capable of generating a strong force, but they tend to fatigue quickly because they are poorly vascular. In contrast to fast muscle fibres, the slow muscle fibres contract and relax slowly. They are relatively weak and are more capable of sustained contraction, because they are highly vascular. Depending on their function, muscles have different proportions of fast and slow muscle fibres.

Most skeletal muscles belong either to the category of flexors or extensors. Flexors act to bend or flex a joint and extensors act to straighten or extend it. The biceps and triceps are the flexor and extensor of the elbow joint, respectively. The synergistic muscles are any two muscles whose contraction produces the same movement, be it flexion or extension, whereas, antagonistic muscles are those muscles whose contraction produces the opposite movement. Biceps and triceps of the elbow joint are examples of antagonistic muscles.

Muscles have elastic properties and they engage in two types of contractions, namely *isometric contractions* and *dynamic contractions*. Isometric contractions occur when activation of a muscle increases the tension that it exerts on two bones, without shortening and pulling them together. Dynamic contraction occurs when activation of a muscle increases the tension that it exerts on two bones by shortening and pulling them together. The tension in a muscle can be increased by increasing the number of neurons in its motor pool.

The activity of the skeletal muscles is monitored by two kinds of receptors, namely the golgi tendon organs and muscles spindles. Golgi tendon organs connect each skeletal muscle to the bone and are embedded in the tendons, whereas, muscle spindles are embedded in the muscle tissue itself. Because of their different locations, golgi tendon organs and muscle spindles respond to different aspects of muscle contraction. Golgi tendon organs respond to increase in muscle tension, but do not respond to changes in the muscle length. In contrast to Golgi tendon organs, the muscle spindles respond to change in muscle length, but do not respond to changes in muscle tension.

Golgi tendon organs are usually responsible for providing the central nervous system with information about muscles tension. However, when the contraction of a muscle is extreme enough that it can cause damage, then the golgi tendons organs excite inhibitory interneurons in the spinal cord. This causes the muscle to relax. In this way they serve a protective function.

Each muscle spindle has its own threadlike intrafusal muscle, which is innervated by its own intrafusal motor neuron. The muscle spindle will not be able

to respond to slight changes in the extrafusal muscle length, if it does not have its own intrafusal motor neuron. This happens because, without intrafusal motor input, a muscle spindle would fall slack whenever its skeletal muscle contracts.

The stretch reflex refers to a reflex that is elicited by a sudden external stretching force on a muscle. An example of a stretch reflex is the patellar tendon reflex. Some of us must have seen or experienced the patellar tendon reflex, though at that time, we may not be aware of its name. When our knee is tapped with a little rubber-headed hammer, resulting in a sudden leg extension, then this reflex is known as the patellar tendon reflex. Let us look at how exactly a stretch reflex takes place.

When the doctor strikes the tendon of the knee, the extensor muscle running along the thigh is stretched. This sudden stretch of the thigh muscle stretches its spindle stretch receptors. These stretch receptors initiate action potentials that are carried into the spinal cord, by spindle afferent neurons, via the dorsal root. On reaching the spinal cord, the action potentials excite motor neurons in the ventral horn of the spinal cord. This in turn, sends the action potential back to the muscle whose stretch originally excited them. The arrival of these impulses at the starting point, results in compensatory muscle contraction and a sudden leg extension.

The main function of the stretch reflex is to keep external forces from altering the intended position of the body. Let us understand the function of the stretch reflex with the help of the following example: Suppose one is holding a cup of coffee and his arm is pushed accidentally. This sudden push (an external force), causes unanticipated extrafusal muscle stretch. Following this, the muscle spindle feedback circuit produces an immediate compensatory contraction of the muscle that counteracts the force and keeps one from spilling the coffee. Thus, the stretch reflex helps in maintaining the limb stability. The stretch reflex is monosynaptic in nature.

The withdrawal reflex is opposite to the stretch reflex. This is not monosynaptic in nature. An example of withdrawal reflex is when one suddenly pulls back one's hand, on touching a hot object. Let us see how a withdrawal reflex exactly takes place. When a painful stimulus is applied to the hand, the first response is recorded in the motor neurons of the arm flexor muscles, about 1.6 milliseconds later. This is the time taken for neural signals to cross two synapses. Thus, the shortest route in the withdrawal reflex circuit involves one interneuron. Other responses are recorded in the motor neurons of the arm flexor muscles, after the initial volley. These responses are triggered by signals that have travelled over multisynaptic pathways, some involving the cortex.

An important principle of spinal cord circuitry is reciprocal innervations, which refer to the fact that during an antagonistic muscle contraction, when one muscle contracts, the other muscles relax. Reciprocal innervations play a role in the withdrawal reflex. Information about sudden painful stimuli in the hand, on reaching the dorsal horn of the spinal cord excites both, the excitatory and inhibitory interneurons. The excitatory interneurons excite the motor neurons of the elbow

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flexor and the inhibitory interneurons inhibit the motor neurons of the elbow extensor. In this manner, a single sensory input produces a coordinated pattern of motor output. The internal circuitry of the spinal cord automatically coordinates the activities of the agonists and antagonists.

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When there is simultaneous excitation of all agonists and complete inhibition of all antagonists, then the movement occurs very quickly. Voluntary movements are not produced normally in this manner. In the normal position, most muscles always contract to some degree. As a result, movements are produced by adjustment in the level of relative contractions between the antagonists. Such movements so produced by cocontraction are smooth and can be stopped with precision, by a slight increase in the contraction of the antagonistic muscles. Also, cocontraction insulates us from the effects of unexpected external forces.

Muscle fibres and the motor neurons cannot continue to work indefinitely. For them to function adequately, the inhibitory neurons in the spinal cord ensure that they get occasional breaks during which they do not continue to work. This process takes place in the following manner; just before leaving the spinal cord, each motor neuron branches. The branch synapses on a small inhibitory interneurons, which inhibit the very motor neuron from which it receives its input. The inhibition produced by these local feedback circuits is called recurrent collateral inhibition. The small inhibitory interneurons that facilitate this process are known as Renshaw cells. As a consequence of recurrent collateral inhibition, each time a motor neuron fires, it momentarily inhibits itself and shifts the responsibility for the contraction of a particular muscle to other members of the muscle's motor pool.

The stretch and the withdrawal reflexes are relatively simple reflexes. Let us now look at more complex sensory motor reflexes. Walking is a complex sensory motor reflex, as it requires one to integrate visual information from the eyes; somatosensory information from the feet, knees, hips, arms and so on; with information about balance from the semicircular canals of the inner ears. Based on this information, it must produce an integrated series of movements that involve the muscles of the trunk, legs, feet and upper arms. In addition to it, it should be able to adjust its movements immediately, in response to new information from outside, like presence of obstacles in the path of walking, etc.

Grillner (1985) showed that walking is controlled largely by circuits in the spinal cord, by conducting his experiments on cats. In his experiments, he separated the spinal cord of a cat from the brain. On suspending the cat in a sling over a treadmill, he saw that when the treadmill started, it began to walk.

4.8 CENTRAL SENSORY MOTOR PROGRAMS

To explain sensory motor functions, several theories have been put forward. According to one theory, the sensory motor system comprises of a hierarchy of central sensory motor programs. It states that in this hierarchy, the highest levels have certain patterns of activity programmed into them. Activation of the appropriate

combinations of these programs produces complex movements. For example, if a person's association cortex decides to switch on the television, then it will activate high level cortical programs. These high level cortical programs will, in turn, activate lower level programs in the brain stem for walking, switching on the television switch, picking up the remote, etc. These programs will further activate specific spinal programs that control various elements of the sequences. They will cause the muscles to complete the objective of watching television. Once activated, each level of the sensory motor system is capable of operating, on the basis of current sensory feedback, without the direct control of higher levels. At the same time the higher levels of the sensory motor system can still directly control these various activities

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A particular task is not always accomplished by the sensory motor system in exactly the same way. In fact, the same basic movement can be carried out in different ways, by involving different muscles. This phenomenon is known as motor equivalence. For example, most of us sign with our fingers and hands. However, if one is asked to sign with his foot, some basic similarities may still be found in both these signatures. This suggests that the central sensory motor programs for signing one's names are not stored in the neural circuits that directly control one's preferred hand. These are stored higher in the sensory motor hierarchy (most likely in the areas of secondary motor cortex that control the preferred hand).

Several studies done on the neuropsychological patients, showed an interesting phenomenon. It was seen that the neuropsychological patients could respond to visual stimuli for which they had no conscious awareness and some patients could not effectively interact with objects they had consciously perceived. Such observations led to a theory which states that the sensory information that controls the central sensory motor programs is not necessarily conscious.

In another study, Haffenden and Goodale (1998) showed healthy subjects a three-dimensional version of the visual illusion (Ebbinghaus illusion). The subjects tended to report that the disc that was surrounded by smaller discs was larger than the disc that was surrounded by larger discs, using their right thumb and the pointing finger. Despite this, when the subjects reached to pick up the disc, the gap between their thumb and the pointing finger accurately reflected the real size of the disc, rather than its consciously perceived size. This experiment thus demonstrated that there is evidence for the separation of conscious perception and sensory control of behaviour in intact subjects

The central sensory motor programmes for behaviours can be established by both, practicing the behaviour and without explicit practice of the behaviours. In fact, specific behaviours of many species are established without explicit practice of these behaviours. The classic study of Fentress (1973), provided support for the same. In his classic study, Fentress showed that adult mice which were without forelimbs since their birth, still made the patterns of shoulder movements, typical of grooming in their species. These movements were well coordinated with normal tongue, head, and eye movements. Fentress's study also demonstrated the importance of sensory feedback in the operation of central sensory motor programs.

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Learning or practice has also been seen to generate or modify the central sensory motor programs. The two kinds of processes that influence the learning of central sensory motor programs are response chunking and shifting control to lower levels of the sensory motor system. According to the response chunking hypothesis, practice combines the central sensory motor programs. These control individual response into programs that control sequences of behaviour. An important principle of chunking is that chunks can themselves be combined into higher-order chunks.

During the development of a central sensory motor program, control is shifted from higher level to lower level of the sensory motor hierarchy. During training, this kind of shifting has two advantages, firstly, it increases the efficiency by speeding up the process and secondly, it frees higher levels to focus on more complex aspects of performance.

The functional brain imaging techniques have now enabled researchers to look for the neural correlates of sensory motor learning. These techniques involve recording of the activity of the brain, of human subjects, as they learn to perform new motor sequences. This helps researchers to develop hypothesis about the roles of various structures in sensory motor learning. The PET study conducted by Jenkin and his colleagues (1994), highlighted the following findings:

- During the performance of both, the newly learned sequence and the well-practiced sequence, activation in the posterior parietal cortex was seen. But the activation was more when the organism engaged in the newly learned sequence. This finding is consistent with the hypothesis that the posterior parietal cortex integrates sensory stimuli that are used to guide motor sequences. Also, a higher activity in the posterior parietal cortex is seen when the subjects attend to the stimuli. During the early stages of motor learning, the organism usually attends more to the stimuli.
- Activation in the dorsolateral prefrontal cortex was seen, when the organism engaged in the newly learned sequence. However, no activity in this region was seen, while the organism engaged in a well-practiced sequence. This suggests that the dorsolateral prefrontal cortex plays a particularly important role when motor sequences are being performed, largely under conscious control. This is more likely to happen during the early stages of motor learning.
- A higher activity in the contralateral premotor cortex was seen when the organism engaged in the performance of the newly learned sequence. On the other hand, the supplementary motor area was more active bilaterally, during the well-practiced sequence. This finding is consistent with the hypothesis that the premotor cortex plays a more prominent role when performance is being guided largely by sensory stimuli, which is more likely to be seen in the early stages of motor learning. The supplementary motor area plays a more prominent role when performance is largely independent of sensory stimuli, as is often the

case for well-practiced motor sequences. These sequences can be run off automatically with little sensory feedback.

- During the performance of both the newly-learned and well-practiced motor sequences, both the contralateral primary motor and somatosensory cortexes were almost equally activated. This finding is consistent with the fact that the motor elements were the same, during both sequences.
- An equal activation was seen in the contralateral basal ganglia, during the performance of the newly learned sequence and the well-practiced sequence. Jenkins and his colleagues speculated that different subpopulations of basal ganglia neurons may have been active during the two conditions, but this could not be detected because of the poor spatial resolution of PET.
- A bilateral activation was seen in the cerebellum during the performance of both, the newly learned and the well-practiced sequences. However, a greater activation was seen during the performance of newly learned sequence. This is consistent with the idea that the cerebellum plays a prominent role in motor learning.

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CHECK YOUR PROGRESS

4. Which two important sensory motor structures do not form a part of the sensory motor hierarchy?
5. In how many ways are neural signals conducted from the primary cortex to the motor neurons?
6. What is the responsibility of the golgi tendon organs?

4.9 MOTOR CONTROL AND PLASTICITY

Movement and action of human being seems very effortless and easy, but it is not so. Actually complex amount of coordination between several muscles is needed to carry out even the simplest task of, for example, saying a single word. To understand this better, let us take an example of climbing the staircase. On the surface it seems such a simple task, but if we carefully think, we will realize that this requires massive and precise coordination between our leg muscles, spatial perception, hand movements and maintaining the balance of the body. In this process we are also required to estimate the height of the staircase and accordingly pull the leg up. Without adequate coordination and precision, we are bound to fall.

Each and every motor behaviour has underlying neural mechanism by which it decides which muscles should act and how. This mechanism requires motor

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neurons to be activated in the proper order, on the basis of the information which is gathered by sense organs and various signals that are received from the CNS. Voluntary behaviour, in addition to this, requires a motor plan. This helps in showing, how the initial idea for a movement or action is to be translated into the selection of muscles.

Let us try and look at movements and their coordination from different points of view, namely the behavioural view, the control system view and the neuroscience view.

4.9.1 Behavioural View

If we observe different animals, we will find that each and every animal has different underlying mechanism which is responsible for its movement from one place to another. For example, in insect and birds, the regular beating of their wings suggests that the nervous systems of these animals have some kind of a rhythm generator, or oscillator. The different gaits of four-legged animals suggest that different oscillators are coupled in precise, but flexible ways to produce coordinated movement. Similarly, in humans, a greater versatility in their learnt movements is seen. This indicates that in humans, the motor system is likely to engage in a wide range of complex adjustments. This makes all these movements possible.

Broadly speaking, various movements can be classified as mechanical actions which are seen in animals and the voluntary behaviour of humans. In the seventeenth century, Rene Descartes, a philosopher, was the one who emphasized the distinction between these two movements. In the 18th and the 19th centuries, it was discovered that dorsal roots of the spinal cord serve sensory functions while the ventral roots serve as motor functions. It is the connection between the dorsal and ventral roots of the spinal cord that forms the basis for simple movements.

British physiologist, Charles Sherrington, has carried out many studies on spinal animals in the 19th and early 20th century. He found that skin stimulation provokes simple acts, like withdrawal. Based on such observations, he argued that the basic unit of the movement and action are reflexes. He defined a reflex as a simple, highly stereotyped and unlearned response to external stimuli. He also proposed that the intensity of reflex is directly proportional to the stimulus intensity. Based on his extensive studies, Sherrington stated that some reflexes only involve the dorsal and ventral roots of the spinal cords. However, there are other reflexes that involve longer loops, connecting spinal cord segments to each other, or to brain regions. His work also inspired intensive attempts to identify different reflexes and their pathways in the nervous system, particularly in the spinal cord.

According to this view, the more complex movements and acts are a combination of simple reflexes. These reflexes are carried out in a particular temporal order. This simpler way of reducing all complex behaviours into simple reflexes was criticized heavily, as it failed to explain several complex movements and acts. Suppose, we look at speech from the perspective of reflexes, then the

speech should be a series of stimulus response units which are chained together. Each response triggers the next. According to this perspective, reflexes are based on the claim that movements and sounds are associated with each element of speech. These provide the stimuli that instigate the next element.

On the contrary, it is seen that individuals, while speaking, sometimes engage in errors called spoonerism. They tend to mix up the order of sounds in a sentence. In such errors, often, the units are misplaced but the pattern seems to be preserved. An example of such an error is when an individual says 'you hissed all my mystery lectures' instead of saying 'you missed my all history lectures'. Such errors suggest that the speaker must be having a plan in which he is anticipating a later sound, but tends to execute it too soon. If the complex behaviour of speech was a result of a combination of simple reflexes, carried out in a particular temporal order, then such errors would not have occurred.

More advanced research in this field has added more clarity to the notion of motor plan, which is now seen as complex movements. It is controlled and produced by a set of commands, which are completely established before an act occurs. The motor plan works according to the feedback system. This governs and shapes the way the action is executed. A motor plan seems to exist for both skilled movements like playing a guitar and simpler movements like escape behaviours, shown by animals such as the crayfish.

Movements and acts can be analyzed and measured in a variety of ways. In the present scenario, hi-tech photography and use of computers makes it easy to analyze the movement of the body, more precisely. With these techniques, we can see the precise movement of the different body parts. Sensors that are placed on the joints and on different parts of the body also provide relevant information about the movement of the body. This movement can be analysed. Methods of simplification or numerical analysis are used to deal with the large amounts of data that are obtained through high speed photography. Computer programs process digitized photos to help quantify the performance, thereby enabling detailed measurement of the positions of different body parts, in successive instants. This information, gathered through a different method is useful in the process of analysing the movement and in creating the simulation program which further helps in the research program.

Contraction of muscles involves electrical potentials, which are generated by the muscles fibres. These electrical potentials are measured by putting fine, needle-like electrodes, on the skin over the muscles. The electrodes so placed provide the electrical portrait of the contraction of the muscles involved in a distinct act, including the progressive buildup and decay of their activity. This technique is used in the diagnosis of neuromuscular disorders. This technique is called electromyography (EMG). Thus, EMG helps in engaging in fine analysis of movements by recording the electrical activity of muscles.

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4.9.2 Control System View

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Movements are regulated and controlled by means of two types of mechanisms, namely, the closed-loop and the open loop control mechanisms. Both these mechanisms ensure accurate and fast movement. This ensures quick and efficient execution of movements. This further helps in optimizing the performance of an organism.

Closed-loop mechanisms are those in which the information flows from whatever is being controlled, back to the device that controls it. An example of closed-loop mechanism is the endocrine secretion. Endocrine secretion is a closed-loop mechanism, as in this system, information goes back to the particular endocrine gland and then that gland restricts or secretes hormones. In this mechanism of endocrine system, information flows back to the source of control. This is known as closed-loop mechanism. The basic feature of this closed-loop mechanism is that it is guided continuously by feedback.

The other example of close-loop mechanism is that when we drive a car, we need constant feedback to put the car on the track. Suppose if we do not receive any feedback, then another way of putting the car on the road is to get access to accurate details of all turns and bends in the road. This type of memory system is called the open-loop type mechanism. In this kind of a mechanism, the car will not be able to deal with any new piece of information, for instance, that which is obtained from other cars running on the same road. Hence, the open-loop control mechanism does not involve external forms of feedback. In them, output is measured by a sensor and the activity is preprogrammed.

In open-loop control mechanism, the system must anticipate potential error in advance, as it does not follow a feedback mechanism. In such a system, prior learning may be the basis for accurate anticipation. Open-loop controls are needed in systems that must respond rapidly. This is so because these mechanisms are quick to respond as they do not need to analyse the feedback. Such open-loop movements are called ballistic movements.

The combination of open and closed-loop characteristics control eye movement, by controlling the extra ocular muscles, which move our eyes. Visual feedback plays an important role in controlling the extra ocular muscles.

The quick, accurate movement of eyes, which transfers the gaze from one fixed point to another are called *saccades* or *saccadic movements*. Such movements are also required to direct the attention to a stimulus that appears suddenly in the periphery of our visual field. The superior colliculi plays a significant role in controlling saccades.

The normal, slow, involuntary to and fro and oscillatory movement of eyes, in a situation when our eyes are focusing on an object or a thing for a certain period of time, are called physiological nystagmus. This physiological nystagmus has an important role as we all know that our eyes adapt quickly to constant stimulation. It means, if we gaze steadily at anything, without blinking our eyes,

then the image begins to fade out in a minute. This is because the visual system adapts rapidly to constant stimulation. But this physiological nystagmus moves the eyes enough to prevent adaptation, thus enabling us to see the image adequately. However, in case of dizziness or some diseases, the eye may show large oscillatory movements. Such a condition is known as nystagmus.

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Pursuit movements are movements that occur when one tries to gaze smoothly and tries to continuously follow a moving object. Such movements require a feedback to keep the gaze close to the target. This smooth pursuit is made possible by the visual feedback which guides extraocular muscles. The basal ganglia are thought to provide signals that allow the ramp movements in underlying smooth pursuit. However, there are some people that are unable to perform smooth, accurate pursuit movements. Their gaze tends to go under and then go over, the moving position of the target.

4.9.3 Neuroscience View

Neuroscience view describes how the brain and the spinal cord process and pass instructions to turn on and cause neural activity in the motor neuron, connected to muscles. Neuroscientists have distinguished several different levels of hierarchically organized motor control systems, as given below:

- Possibility of occurrence of a movement is decided by the skeletal system and the muscle attached to it.
- Spinal cord controls the reflex action (the response of these muscles) of the person, in response to the sensory information and also implements the motor command of the brain.
- Brain stem is known as a relay system of the brain as it integrate motor commands from higher level of the brain and transmit them to the spinal cord. It also relays sensory information about the body, from the spinal cord to the forebrain.
- Primary motor cortex is the place where some of the main commands, for the action are initiated
- Other areas adjoining the primary motor cortex, initiate another level of cortical processing.
- The activity of these hierarchically organized control systems are modulated by the other brain structures, mainly the cerebellum and basal ganglia.

Now we look at each of these levels of control, in detail:

The skeletal system enables particular movements and precludes others. The structure of our body, specifically the bone structure, determines certain aspects of behaviour. For instance, our skeletal system is made up of several separate bones, which vary in their shape, size and length. It is this length, form and weight of the limb that determines the animal's stride. In response to sustained unusual use or weight, the bones do not bend but their shape may change. The bending movement takes place at joints, which are the primary sites where bones meet.

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Muscles control the actions of the skeletal system. The skeletal system is covered by muscles. The distribution of muscles, their size, the site at which they act and the manner in which they act, determines the kind of movements that a body makes. For instance, some muscles produce forces that sustain the body weight, by contracting and some muscles produce movement near joints. There are other muscles like, muscles of eyes, lips, tongue, etc., which do not act on the skeleton at all. Muscles have spring like properties that influence the timing of behaviour and the forces that can be generated. The responses of a body are limited by the rate and force of muscular contractions.

Thousand of muscle fibres make a muscle. Muscles are attached to the bone by tendons. The manner in which a muscle is mechanically attached to a bone or bones, generates the movement or maintains the position by contracting its muscle fibres. The muscles are either synergistic in nature or antagonistic in nature. At joints, we find antagonistic muscles, where the contraction of one muscle leads to the extension of the other. Coordinated action around a joint may require one set of motoneurons to be excited, while the antagonistic set of motoneurons is inhibited. The muscles which act together are called *synergistic muscles*. Cocontraction of the opposed muscles helps to lock a muscle in a certain position.

Many thick and thin filaments, arranged in an alternate manner comprise a muscle fibre. Such an arrangement gives a stripped appearance to a muscle fibre. These thick and thin filaments tend to always overlap and the contraction of the muscle further increases the overlap. On contraction, the filaments slide past each other, shortening the overall length of the muscle fibre.

There are two types of muscles, namely the *smooth muscles* and the *striated muscles*. The smooth muscles are those muscles that are not under our direct control and are controlled by the autonomic nervous system. For example, the muscles of the heart are smooth muscles. In contrast to smooth muscles, striated muscles are under our voluntary control.

Muscles perform a wide variety of tasks. To function effectively muscles need speed, precision, strength and endurance. Striated muscles are further divided into two types of muscle fibres, namely the fast and the slow muscle fibres. Fast muscles are quick and accurate but they can not maintain the tension for long and tend to get easily fatigued like the muscles of the eye and the extraocular muscles. Eye movements need to be quick and accurate, so that we can follow moving objects and shift the gaze from one target to another. For this purpose, they are made of fast muscle fibres. Ocular muscles are not required to maintain the posture for long periods of time, as some of its fibres relax while others contract. Hence, they too consist of fast muscle fibres. In activities like running and walking, the muscle tension changes rapidly and fast and accurate movements are needed, therefore, the leg muscle are also be composed of fast muscle fibres.

In contrast to fast muscle fibres, slow muscle fibres are able to maintain the tension for long and do not get fatigued easily. These muscles are used in activities like maintaining posture where greater resistance to fatigue is required. In short,

depending on the kind of activity muscle fibres need to perform, they consist of fast or slow muscle fibres.

The neural messages reach muscle fibres at the neuromuscular junction. On integrating all the information received by thousands of synapses, a motoneuron produces an action potential. This action potential is carried by all branches of the split axon near the target muscle. This action potential, further causes the release of acetylcholine at its terminals. As a result, all muscle fibres which are innervated by that motoneuron, respond to Acetylcholine by producing action potentials of their own. The action potential travels along each muscle fibre, permitting sodium (Na^+) and calcium (Ca^{2+}) ions. In this manner, it triggers the molecular changes that produce contraction.

Neuromuscular junction is the place where the motoneuron terminal and the adjoining muscle fibres meet and produce distinctive structures for communication. In this neuromuscular junction, almost every action potential that reaches the axon terminal, releases enough Acetylcholine to cause a large enough depolarization in the muscle fibre. This produces an action potential. This results in contraction of the postsynaptic fibre. In vertebrates, muscles can only be excited, so the only way to prevent a muscle from contracting is to inhibit its motoneuron and prevent it from sending an action potential to the neuromuscular junction. The neuromuscular junctions are quite and effective.

The properties of neuromuscular junction can change with use. Extended use causes the muscle to fatigue, thus reducing its responsiveness by diminishing the effectiveness of the neuromuscular junction. When a rapid series of action potentials is induced in a motor nerve, the neuromuscular junctions are altered for a period so that subsequent single action potential causes a stronger end plate potential in the muscle. This potential is caused by a buildup of calcium ions in the pre-synaptic terminal. This results in the release of more Acetylcholine. This aspect of neural plasticity is known as *posttetanic potentiation*.

Since acetylcholine receptors are present along the entire length of muscle fibres, therefore, the application of acetylcholine anywhere along the muscle fibre, during early embryogenesis, causes a response. But as the growing axon tip from a motoneuron contacts the fibre, acetylcholine receptors migrate from other parts of the muscle fibre to clusters that are opposite to the axon tip. From this point, muscle fibre tends to insert more acetylcholine receptors beneath the motoneuron terminal, at the newly formed neuromuscular junction. In vertebrates, the terminals of motoneurons are seen to release other substances like peptides. A commonly released peptide is calcitonin (a gene-related peptide), which tells the muscle fibres where to insert Acetylcholine receptors.

In adults, a phenomenon known as *denervative super-sensitivity* is seen. In this phenomenon a contraction can be produced anywhere along the muscle fibre, by the application of acetylcholine. If the muscle fibres are denervated, then they are seen to produce Acetylcholine receptors again, along their entire length.

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But once, the regenerating motoneuron axons reach the muscle fibre, the fibre again provides acetylcholine receptors only at the point of contact.

Early in life, every muscle fibre is contacted by several motoneurons, but later, during the postnatal period of neuromuscular synapse elimination, every muscle fibre is innervated by only a single motoneuron. This is because all motoneurons are seen to withdraw some of their terminal branches. The mechanism through which the motoneurons and the muscle fibres eliminate the right number of synapses is still not fully understood. But, as a result of this elimination, each motoneuron has exclusive control of a pool of muscle fibres, which further enables finely graded contractions of the muscles.

The precise control of a movement depends on the ratio of motor axons, to muscle groups. For instance, when each axon connects only to a few muscle fibres, a fine neural control takes place. A better understanding of this phenomenon can be developed, when one looks at the motor unit. As studied earlier, the motor unit consists of a single motor axon and all muscle fibres, that it innervates. The innervations ratio is the ratio of motor axons to muscle fibres. The muscles which are involved in fine movements like that of the eye, have high innervations ratio, whereas, muscles that act on large body masses, have a low innervations ratio. In case of low innervations ratio, a signal from a neuron goes to several hundred muscle fibres at the same time.

Motoneurons are the largest cells in the spinal cord. These have a widespread dendritic field as they receive information from many sources. After integrating the information from the brain and spinal cord, the motoneuron initiates the neural activity that travels along motor axons, to the muscles. In this way, motoneurons act as the final common pathway that links the activity of the rest of the spinal cord and brain, to different muscles of the body. In addition, motoneurons must respond to a tremendous variety of both, excitatory and inhibitory synaptic transmitters.

The size or electrophysiological properties of the motor cells of the spinal cord are not uniform. For instance, the large motoneurons conduct impulses faster, as their axons have a wide diameter. They innervate fast muscles and because of their large size, they are less readily excited by synaptic currents and hence tend to respond after small motoneurons. In contrast, small motoneurons innervate slow muscles and are more easily excited by synaptic currents. Because of this, small motoneurons are usually activated before large motoneurons. Their discharge characteristics are more phasic or abrupt. Both, large and small motoneurons are present in all spinal levels.

In addition to the integrative mechanisms of the brain and spinal cord, which monitor movements, the movements also get monitored by the sensory feedback from muscles, tendons and joints. This feedback about the state of the muscles, the positions of the limbs and the instructions being issued by the motor centers, facilitates the production of rapid and coordinated movements of the body. This kind of information about body movement and positions is called *proprioceptive neuromuscular facilitation*.

The sensory receptors, which provide information about the state of muscles and joints, to circuits that initiate and guide movements, monitor the sequence and intensity of muscle activation. This information about the state of muscle length or contraction can be provided by several kinds of sensory receptors. The two major kinds of receptors are muscle spindles, which lie in parallel with the muscle fibres and Golgi tendon organs, which lie in series with muscles, one end attached to tendon, the other to the muscle.

Both the muscle spindles and Golgi tendons tend to differ in their mechanical sensitiveness. For instance, the stretching of a muscle activates the spindles and the tendon organs. On the other hand, the shortening of a muscle during contraction activates the tendon organs because they lie in series with the muscle. Both the muscle spindles and the golgi tendons, tend to transmit a wide range of information about the muscle activities to the central nervous system.

In a study, two deafferented patients were found to rely heavily on visual feedback to allow them to walk and pick up objects. This suggested that people, who lose their proprioceptive sense, can sometimes compensate by using other sensory modalities for feedback. This observation led researchers to speculate that it is possible that there may be certain channels of visual information to the motor system, of which we are presently unaware. Support for this speculation comes from observing that a patient with damage to the visual cortex was not able to report whether a slot was vertical or horizontal. However, when he was asked to insert a card in the slot, the patient consistently rotated the hand to put the card in smoothly. Similar experiments suggest that even neurologically intact people, sometimes use visual cues of which they are unaware to guide their movements.

In vertebrates, the muscle spindle consists of both afferent and efferent elements. The small muscle fibres, within each spindle are called intrafusal fibres and the ordinary muscle fibres, that lie outside the spindles are referred to as extrafusal fibres. The muscle spindle also contains two kinds of receptors: primary sensory endings and secondary sensory ending, which are related to different parts of the spindle. The primary ending wraps in a spiral fashion, around a region. This region is called the nuclear bag. The secondary endings terminate towards the thin ends of the spindle.

When one tries to hold his arm straight outwards, then an additional load is felt on the biceps. This results in the stretching of muscles of the bicep, thus causing the arm to move down transiently. This will also cause the muscle spindles to stretch. Such a stretch deforms the ends of a stretch and sets up nerve impulses in the afferent fibres. These impulses inform the spinal cord. From the spinal cord, the information about the muscle stretch goes to the brain. In this manner, these elements of the muscle spindle get excited.

The muscle stretch depends on mainly two factors—the rate of change of muscle length and the force continuously exerted by the muscle, in order to prevent the load from falling. Both the primary sensory ending and the secondary sensory ending are differently sensitive to these two features of muscle stretch. The primary

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endings show a maximum discharge, early in stretch and then adapt to a lower discharge rate. In contrast, the secondary endings are maximally sensitive to maintained length and are slow to change their rate during the early phase of stretch. Because of this differential sensitivity, the primary endings are called *dynamic* and the secondary endings are called *static* indicators of muscle length.

Muscle spindles not only help in maintaining posture, but also help in coordinating movements. Innervations by special motoneurons, known as Gamma efferents, inform the spindles about the planned and ongoing actions and movements in the body. This information alters the tension within the spindle and thus controls the sensitivity of its receptors. The cell bodies of gamma efferents are found in the ventral horns of the spinal cord.

The gamma efferent axon fibres connect to a contractile region of the spindle. The activity in the gamma fibres causes a change in the length and tension of the spindle, which modifies its sensitivity to changes in the length of adjacent extrafusal muscle fibres. Hence, the muscle stretch and the resting tension in the muscle spindle determine the number of impulses elicited in the spindle afferents.

By altering the tension in the extrafusal and intrafusal fibres, the gamma efferents help in coordinating movements. To understand this better, let us take an example of the up and down movement of a human forearm. As the forearm moves up, the extrafusal and intrafusal fibres shorten. Following which, the gamma efferents correspondingly increase the tension on the intrafusal fibres to maintain their sensitivity.

The muscle spindles are responsive primarily to stretch and it is the golgi tendon organs that are especially sensitive to muscle contraction. Golgi tendon organs also detect overloads that threaten to tear muscles and tendons. Stimulation of these receptors inhibits the motoneurons supplying the muscle that pull on the tendon. Thus, by relaxing the tension, this prevents mechanical damage.

4.10 MOVEMENT CONTROL

Movements are also controlled at several levels of the nervous system. Motoneurons are directly responsible for the excitation of muscle in the ventral region of the spinal cord and in the brain stem nuclei of several cranial nerves. This is the simplest level in the neural control of motoneurons. The onset, coordination and termination of muscle activity are determined by the firing patterns of these cells. Motor neurons receive information from different sources, for example, in the spinal area, they receive information from muscle afferents and intrinsic circuitry of the spinal cord. They also receive information from several brain pathways.

Automatic movements are mediated by spinal reflexes. When connection between the spinal cord and the brain is cut, then an interval of decreased synaptic excitability in spinal cord neurons is seen. This condition is known as *spinal shock*. The spinal shock may last for few hours in species like cats and dogs, but in humans it may even last for few months. During this period, no reflexes mediated

by the spinal cord can be elicited by either skin stimulation or excitation of muscle afferents.

As spinal shock fades, various kinds of reflexes can be elicited. The spinal animal can show various stretch reflexes. For instance, stimulation of the skin of a spinal animal can also elicit reflex effects, which may result in abrupt withdrawal of the stimulated limb. This response is known as the flexion reflex, which is controlled by a multisynaptic pathway within the spinal cord. Emptying of the bladder and penile erection are other reflexive behaviours which are evident in the spinal animal. Thus, there are certain behaviours that are exhibited without any involvement of the brain.

Studies of behaviours of the spinal animal have revealed the presence of pattern generator circuits in the spinal cord. For example, mechanical stimulation of the feet or electrical stimulation of the spinal cord can elicit rhythmic movements of the legs. If the cut is high on the spinal cord, the alternating movements of the limbs are coordinated, as in walking. This coordination indicates that the pattern generators for the different limbs are linked within the spinal cord. Usually spinal reflexes are integrated and modulated by the activity of brain circuits and do not function in isolation. The activity of the brain circuits enhance and inhibit the activity of certain spinal circuits.

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4.11 EXTRAPYRAMIDAL SYSTEMS

Different aspects of movements are controlled by pathways from the brain. The pathways from the brain to the cranial and spinal motoneuron are many and complex. Complex movements are regulated and controlled by the brain. Some pathways, for example, the vestibulospinal tract, deliver discrete information such as information about the position of the head, which influences postural muscles to adjust the body.

Studies conducted on individuals with brain damage have provided useful anatomical and functional distinctions between two major divisions of the motor system, namely, the pyramidal and extrapyramidal motor systems. Studies of the brain and observation of changes in posture and locomotion so produced, has added to our knowledge about the different roles played by different pathways of the brain. The pyramidal system consists of neuron cell bodies, within the cerebral cortex and their axons, which pass through the brain stem. These form the pyramidal tract to the spinal cord. Many of these cell bodies are located in the primary motor cortex.

One can clearly see the pyramidal tract, when it passes through the anterior aspect of the medulla. The pyramidal tract is a relatively recent development in evolution and consists of large-diameter axons. Movement of individual joints and limbs are controlled by the pyramidal system and lesions in the pyramidal system deprive the patient of the ability to move individual joints and limbs.

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From the forebrain to the brain stem and spinal cord, several motor tracts run, in addition to the corticospinal outflow, through the pyramidal tract. Since these motor tracts and their connections lie outside the pyramids of the medulla, hence they are called the extrapyramidal system. Lesions in the extrapyramidal system result in the interference with spinal reflexes.

The flow of information to the spinal cord from the extrapyramidal system, is via two principal pathways, namely, the reticulospinal and rubrospinal tracts. Various aspects of movements are regulated and modulated by reticular formation. The reticular formation either facilitates or inhibits certain movements. Reticulospinal tracts are descending tracts that arise from the reticular formation and produce either inhibitory or facilitatory effects on movements. The reticulospinal tract connects to spinal interneurons, where they influence the excitability of spinal motor circuitry. Some neurons of the reticular formation also help in regulating the activation of muscles. These muscles are responsible for breathing. The second motor pathway of the extrapyramidal system originates from the midbrain's red nucleus. It is called the rubrospinal tract. In the brain stem, cranial motor nuclei are also present, which innervate muscle of the head and neck.

The primary motor cortex is regarded as the executive motor control mechanism. Injury to the primary motor cortex produces partial paralysis on the side of the body which is opposite to the brain lesion. This disturbance is greatest in distal muscles, such as those of the hand or the leg. And individuals with lesions in this area are less likely to use the affected limb.

An accidental injury or disease is not just limited to any single neural system. As a result, the observed changes are quite complex. A part of this complexity stems from loss of adjacent motor control systems, in the corticospinal injury. Experimental lesions which are restricted to the pyramidal tracts are also seen to show similar changes, but the symptoms are less severe. For instance, when bilateral interruption of the pyramidal tracts were made in monkeys, then after about six weeks they were able to run, climb and reach accurately for food. Only deficits in the ability to engage in individual finger movements were persistent.

Examination of certain anatomical relations between motor cortex and other levels of movement control system showed that electrical stimulation of some regions of the cerebral cortex could elicit body movements, particularly flexion of the limbs. Such studies further showed that the more elaborate or the more complex movements are needed to be made, the larger portion of motor regions are involved. For instance, humans and other primates have extremely large cortical fields. These are concerned with the movement of hands. In the cortex, vertical columns of colonies of cells are seen to exist. These relate to particular muscle groups.

From the motor area of the cortex, about one-third of human pyramidal tract fibres originate. Nearly one-fifth of human pyramidal tracts originate from the post-central gyrus. The rest of the pyramidal tract fibres arise from many other cortical regions. Thus, the motor control is regulated by areas that are dispersed among cortical areas. Voluntary movements are controlled and regulated by the

motor cortex – pyramidal tract system. According to this view, particular kinds of movement, especially fine movements of the limbs, etc., are regulated by the motor cortex. Activation of cells in the motor cortex causes excitation in relevant spinal and cranial motoneurons. Some monosynaptic connections with the spinal motoneurons are present in the pyramidal tract, in primates. However, largely polysynaptic connections with the spinal motoneurons are present in most of the pyramidal tract fibres. These motor cells are further controlled by other descending influences.

To understand the function of motor cortex neurons, the activity in these neurons is monitored and analysed while an organism is performing certain movements. Certain experiments have been conducted on monkeys, where they were trained to make particular movements such as reaching or pressing levers and the activity from single motor cortex cells was monitored. It is comparatively much easier to see the relationship between the firing pattern of a single cell and the different measures of movement, while examining the fine movements of a hand, than when examining gross movements of a limb.

Certain experiments were conducted by Apostolos Georgopoulos, in which he recorded the activity in the motor cortex neurons of monkeys. These monkeys were trained to make free arm movements in eight possible target directions. He found a change in the firing rate of many cells, according to the directions of the movement. For any one cell, the discharge rates were found to be the highest, in a particular direction. He also found that each cell carried only partial information about the direction of reaching and that different cells prefer different directions. When the activity of several hundred neurons is combined, their overall vector shows a good relation to the actual direction of the reaching arm.

Non-primary motor cortex is believed to aid motor sequencing. In studies on monkeys, in which the activity of the single non-primary motor cortex was recorded, it was seen that many nerve cells in nonprimary motor cortex change their discharge rate just before the onset of conditional movements. In these regions some nerve cells were also seen to respond to a sensory stimulus, without any evidence of elicited movement. This suggested that these regions are involved in the sensory guidance of movements, or that they represent higher level intentions for movement. During the preparation of skilled movements and particularly during sequential movements, a greater activity is seen in non-primary motor cortical areas.

The non-primary motor cortex consists of two main regions, namely the supplementary motor cortex (which lies mainly on the medial aspect of the hemisphere) and the premotor cortex (which is anterior to the primary motor cortex). Unilateral lesions of premotor cortex lead to impairment in maintaining stance and gait and problems in the coordination of the two hands, but the fine motor control of the fingers remains intact. However, bilateral damage to the supplementary motor cortex results in inability to move or speak voluntarily, although some automatic and reflex movements remain. These long lasting effects suggest

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that this region is involved in the conception and initiation of movement and movement sequence.

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Studies of localized cerebral blood flow and metabolism have revealed that in simple tasks, blood flow increases markedly in the hand area of the opposite primary motor cortex. But as the complexity of the motor task increases or the individual is required to engage in sequential movement, then an increase in the area of blood flow is seen in the supplementary motor cortex. An increased blood flow is also seen in the supplementary motor cortex, when the individual is asked to mentally rehearse complex sequential movements. Increased activity in the supplementary motor cortex is seen, in response to internally generated finger sequences, whereas motor sequences which are guided externally by stimuli show increased activity in the premotor cortex.

In another study, the subjects were asked to learn the same sequence of finger movements under two conditions. In one condition, the subjects became aware of the repeating sequence and were able to anticipate the next finger movement. In the other condition, subjects were distracted by another task and as a result, they were not aware of the repeating sequence. However, when the individuals engaged in this task, different brain regions were activated in these two conditions. The subjects in the first condition showed greater activity in the premotor cortex, whereas, a greater activity in the supplementary motor cortex was seen in the subjects in the second condition. This study suggested that the premotor cortex plays a more significant role in explicit motor learning, while the supplementary motor cortex mediates implicit motor learning.

A different study was conducted by Charles Gross and his colleagues. They found that a subset of pre-motor neurons also gets activated when objects are brought close to the monkey's face or hand. If the lights were then turned out, some of these neurons continued to fire even if the object was silently moved. But when the lights were turned on and the monkey saw that the object is no more present, then the firing in the neurons was seen to cease. This observation made them think that these neurons may help an organism to reach out for objects that are no longer visible.

Movements are also modulated by the basal ganglia. The basal ganglia consist of a group of interconnected forebrain nuclei, namely the caudate nucleus, putamen and globus pallidus. These are seen to be closely associated with some nuclei in the midbrain, namely the substantia nigra and subthalamic nucleus. Each of these structures receives inputs from wide areas of the cerebral cortex and sends much of their output back to the cerebral cortex. This is known as the cortex – basal ganglia – cortex loop. In humans, lesions in these regions produce movement impairments that seem quite different from the ones which are produced as a result of lesions in the pyramidal system.

The basal ganglia also receive inputs from the thalamic nuclei and the substantia nigra, in addition to information from extensive region of the cerebral cortex. Basal ganglia are broadly divided into putamen and caudate. Inputs from

the sensory motor cortical zones reach the basal ganglia via the putamen. Lesions in different areas of basal ganglia are seen to have different effects. For examples, lesions in the caudate region, impair relatively complex behaviour, whereas lesions in the putamen, show more exclusive motor impairments. They affect the strength and rate of response, rather than the direction of response.

Lesions and recordings of single neurons during motor responses in animals have provided more insight into the functioning of the basal ganglia. Animal studies have shown that each structure of the basal ganglia contains a topographic representation of body musculature. The basal ganglia are also seen to play a role in determining the amplitude and direction of actions.

The basal ganglia networks thus seem to modulate the pattern of activity, which is initiated in other brain circuits that control movements, such as motor and premotor cortical systems. Experiments also indicate that the basal ganglia are especially important in the generation of movements that are influenced by memories, in contrast to those guided by sensory control. Multiple loops that connect the basal ganglia and neocortex are also important in sensory motor learning.

The programming, timing and coordination of acts are regulated by cerebellum. In some vertebrates, the size of the cerebellum is seen to vary according to the range and complexity of movements. For instance, the size of the cerebellum is much larger in fish with extensive locomotor behaviour than in less active fish. Its size is also found to be large in flying birds, as compared with bird species that do not fly.

The outer layers of the cerebellum are called the cerebellar cortex and contain large number of multipolar cells, called Purkinje cells. The signals tend to move out of the cerebellar cortex via with the deep cerebellar nuclei. At these synapses, they produce only inhibitory postsynaptic potential. Hence, the cerebellum cortex regulates movements by inhibiting neurons.

Information from the sensory sources and from other brain motor systems reaches the cerebellar cortex. Sensory inputs refer to information obtained from the muscle and joint receptors and the vestibular, somatosensory, visual and auditory systems. The cerebellum also receives information from the brain motor systems, largely the pyramidal and non-pyramidal pathways. These motor systems also receive information from the deep nuclei of the cerebellum. Thus, the cerebellum receives elaborate information from both, system that monitor movements and systems that execute movements. It is because of this, that the cerebellum is believed to play a role in the feedback control of movements. Cerebellum plays a significant role in controlling and regulating skilled movements, particularly rapid, repeated movements that become automatic. Cerebellum is believed to contain neural programs for the control of such movements.

Based on several experiments, researchers have proposed different theories, suggesting that cerebellar circuitry includes memory like devices that might be important for motor learning. On simultaneously stimulating the climbing fibre and

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parallel fibre that provides inputs to Purkinje cells, Masao Ito (1987) observed a long-term depression of Purkinje cell. This can last as long as an hour. Such kind of memory changes in the cerebellar cortex are believed to be adaptive in nature as it involves an interaction between the vestibular and visual systems. This helps in making accommodations in the light of new information, for instance, change in the orientation of the head.

Repetitive movements are also believed to be driven by endogenous oscillators. Often, most locomotion is rhythmic in nature. For example, the flapping of wings and movement of the legs are repetitive and rhythmic in nature. In the past, theories focused on the presence of sensory feedback and reflex chain, underlying and regulating repetitive behaviours. It was believed that each act provides sensory feedback from muscles that stimulates the next component. When Sherrington tried to reduce complex behaviours into a series of simple reflexes, it was seen that eliminating the sensory feedback did not affect the basic rhythmic aspect of the act. However, at present, it is believed that endogenous oscillators tend to regulate and control repetitive and rhythmic movements. Rhythmic movements are generated by mechanisms within the spinal cord. These movements are seen to be normally modulated by feedback, but they can function independently of brain influences or afferents. This neural circuitry is responsible for generating rhythmic pattern, is known as the central pattern generator. These circuits tend to display reciprocal inhibitory innervations.

Grillner and colleagues have extensively studied how the central pattern generator regulates rhythmic locomotion. In one study, they took electromyographic records of the hind limb muscles of cats with spinal cord section and dorsal root cuts. This revealed a response known as *fictive locomotion*. This type of response involves a walking pattern that lasts for second and was seen in the cat when his single dorsal root was briefly stimulated electrically.

Different types of coordination are shown by the outputs from the spinal motoneurons. The activity of the relevant muscle shows phase relations which are similar to characteristic muscle-time differences that were observed in the movement of intact animals. Three intact adjacent spinal segments provide the minimal amount of spinal processing. This is necessary for generation of part of the locomotor rhythm. Thus, the brain does not generate the essential rhythm in the spinal cord, but it may control the onset of the rhythm and provide corrections arising from other influences, which are registered by the brain.

CHECK YOUR PROGRESS

7. Why is EMG used?
8. What is the responsibility of motoneurons?

4.12 DISRUPTION OF MOVEMENT

Different metabolic conditions can affect the chemistry and structure of the muscles. Hormones like thyroid hormones can affect the muscle chemistry and function. Its chronically low levels can produce muscle weakness and slowness of muscle contraction. Many muscle diseases involve biochemical abnormalities that lead to structural changes in muscles. These disorders are referred to as muscular dystrophy and many of the muscular dystrophies are hereditary in nature. They involve wasting of muscles. Of all the muscular dystrophies, Duchenne's muscular dystrophy is best understood.

Duchenne's muscular dystrophy is an X chromosome linked disease, which is caused by a deficit in a single gene. This gene lies on the X chromosome. Researchers began to examine the patients of Duchenne's muscular dystrophy. They found that the X chromosomes in members of families which were afflicted with the disorder had a single gene that was abnormal and was present in all boys. The abnormal gene was seen to be present on one of the two X chromosomes, carried by their mother. But the gene was normal in the father and in all unaffiliated brothers. This disorder is commonly seen in boys, usually beginning at the age of 4 to 6 years and most of these individuals tend to die within a decade.

The gene and its normal protein product are known as dystrophin. Dystrophin is produced in muscle cells, which plays a role in regulating internal calcium (Ca^{2+}) stores. When this protein is normally present, dystrophy does not result. Only half of the sons of the infected mother develop dystrophy. This is because females have two X chromosomes, of which only one X chromosome is affected. The female child has two X chromosomes. Suppose she receives the infected X chromosome from such a mother, she may not develop the disorder as the other X chromosome is normal and hence can still produce normal dystrophin. Only half of the son of this mother will receive the infected X chromosome while the other half sons will receive the normal X chromosome. The sons that receive the infected X chromosome will display the illness as these children have only one X chromosome which is infected and hence cannot produce normal dystrophin.

The defective dystrophin protein does not show any effects during the first few years of life, but dystrophy is seen in adulthood. The reason for the same is not known yet. Also, in mice, unlike humans, this condition is seen to improve even without any intervention.

Studies of the gene that encodes dystrophin suggest a very promising therapy for Duchenne's muscular dystrophy. It is believed that administering dystrophin to afflicted boys may enable their muscles to function properly. Since the muscles are usually willing to accept new genes, therefore, this may facilitate the treatment. Sometimes, a mere injection of messenger RNA for dystrophin causes muscle cells to translate the RNA and produce the protein for a brief period of time. The

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permanent establishment of a functional dystrophin gene in the muscles of Duchenne's patients may result from other gene therapies.

Poison in the body can lead to blocks in the neuromuscular junction, which can result in certain movement disorders. For instance, the venom of some highly poisonous snakes contains substances that block post-synaptic receptor sites for acetylcholine, which eventually causes neuromuscular blocks. Studying the mechanism by which venom acts in the body has increased our understanding about a disorder known as myasthenia gravis. This disorder is characterized by a profound weakness of skeletal muscles. The muscles of the head are the first to get affected and may produce symptoms like drooping of the eyelids, double vision and slowness of speech. In later stages, muscles that control swallowing and respiration may get paralyzed and may threaten life. Basic researches in animals and continuing studies in human patients have established that antibodies, directed against acetylcholine receptors cause these changes. Apparently, individuals suffering from this disease are seen to spontaneously develop these antibodies, which attack their own postsynaptic membranes. Thus, sometimes one's own immune system can attack neuromuscular junctions.

Pathology in the motoneurons of the spinal cord is likely to produce movement paralysis or weakness. These motoneurons can be destroyed by viral infection and may cause diseases like polio. Viral infection can also cause damage to the cranial motoneurons of the brain stem, which may lead to atrophy as these muscles are no longer able to contract.

Damage or injury to spinal cord may result in motor impairment. Severe damage to the spinal cord results in immediate paralysis and reflexes below the level of injury are lost. This condition is known as *flaccid paralysis*. Flaccid paralysis generally results when a massive destruction on the tissue in the spinal cord has not taken place. In this condition, below the level of injury, reflexes frequently become excessive because the intact tissue do not receive inhibitory pathways from the brain. Spontaneous improvement in the injured spinal cord is at times seen. For example, animals with spinal cord injuries were able to swim again, even without any therapeutic intervention. This feature is more commonly seen in vertebrates. However, in rats, implants of peripheral nerve or fetal nervous tissue may provide a bridge across the injury to allow reconnection of the spinal cord.

In another experiment, the spinal cord was cut in the rats, but regeneration in the cortico-spinal axons across the injury was seen. As a result, these rats were seen to regain the use of their forepaws. In fact, throughout the life span, CNS neurons of a special population are continuously produced. These neurons send out new axons that bridge the loss that may occur during the spinal injury. Regeneration in the spinal cord is also promoted by providing neurotrophic factors such as neurotrophin – 3 to severed spinal cord axons.

Damage to the motoneurons of the brain stem and spinal cord is seen to result in a syndrome known as amyotrophic lateral sclerosis (ALS) or Lou Gehrig's disease. In this disease, a progressive paralyzing in the person is seen, whereas the

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intellectual abilities remain intact. The symptoms largely depend on the level of the nervous system at which motoneurons destruction begins. The exact causes underlying the disorder are not clear but certain factors that are seen to play a role in the occurrence of this disorder are premature aging, toxic minerals, viruses, immune responses and endocrine dysfunction.

It is believed that faulty genes may underlie ALS, as nearly 10 per cent of ALS cases are hereditary, in which a clear family history of the disease is seen. This faulty gene is found to encode an enzyme—copper/zinc superoxide dismutase, that can convert highly reactive compounds into more ordinary compounds. Some investigators have hypothesized that this enzyme may protect the muscles and/or motoneurons from the cellular damage. Thus, it is possible that the nonhereditary cases of ALS might stem from the buildup of similar damage from other sources. This damage may accumulate despite the efforts of such enzymes. However, the experimental tests have failed to provide support for this hypothesis.

When scientists produced transgenic mice that, in addition to their own normal copies of the enzyme, carried a copy of the defective human gene, these animals were seen to display the ALS like syndrome. In this syndrome, their muscles tended to waste away and their motoneurons were seen to die. Eventually, this led to an early death. The abnormal gene was seen to actively damage part of the neuromuscular system. These molecular genetic changes may also lead to high levels of the transmitter glutamate. A high concentration of glutamate, (which is an excitatory amino acid) can cause neurons to die.

Strokes or injury to the human cerebral cortex results in motor impairments. For instance, injury to the cerebral cortex of the hemisphere causes paralysis or partial paralysis of voluntary movements on the contralateral side of the body. These patients also show some spasticity (reflected as the exaggeration of stretch reflexes), especially increased rigidity in response to forced movement of the limbs. These individuals may also show abnormal reflexes, such as the flaring and extension of the toes elicited by stroking the sole of the foot. A picture of symptoms tends to change over certain months following cerebral cortical injury. For instance, the initial paralysis slowly diminishes and some voluntary movements of the proximal portion of limbs return, although fine motor control of fingers is seldom regained. Damage to non-motor zones of the cerebral cortex, (for example in the parietal or frontal association cortex) is seen to result in complicated changes in motor control.

Defects in the basal ganglia can result in a variety of effects, some almost opposite to others. In some disorders, one finds presence of dramatic, persistent excess of movement, whereas in others, one may find slowness of movement and marked changes in muscle tone.

Deficits in basal ganglia results in a disease known as Parkinson's disease, named after the physician James Parkinson, who discovered it. This disease is characterized by slowness in movement, regular tremors in the hands and face at rest, rigidity in walking, loss of facial muscle tone resulting in a masklike appearance, etc. Often, these changes are progressive in nature and may take several years to

reach a maximally disabled state. Individuals suffering from Parkinson's disease also show few spontaneous actions and have great difficulty in all motor efforts, even when the motor movements are routine.

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In this disease, a progressive degeneration of cells containing dopamine, in the substantia nigra of the brain are seen, but the appearance of the symptoms is seen only after a major loss of these cells takes place. The exact cause behind the disease is still not clear. But it is speculated that subtle exposure to toxin over a long period of time is believed to underlie the development of the disorder. The disorder is generally not hereditary in nature. It is believed that a defective copy of gene that encodes alpha-synuclein, a protein normally expressed in the basal ganglia may underlie Parkinson's disease. Both research into the causes and the treatment of Parkinson's disease are still in progress. In 1960s, it was discovered that in individual with Parkinson's disease, there is a substantial loss of dopamine levels in the substantia nigra, which projects to the corpus striatum. Hence the treatment focuses on the administration of a precursor to dopamine levels of surviving cells. The substance, called L-dopa, is seen to markedly reduce symptoms in a Parkinson's patient and results in decrease in tremors and an increase in the speed of movements.

L-dopa is seen to reverse some symptoms of Parkinson's disease, but is unable to stop or reduce degeneration in the nerve cells in substantia nigra. Since the cell bodies in the brain stem continue to degenerate, hence dopamine-containing terminals in the caudate nucleus and putamen, are seen to disappear. As a result very few dopamine-containing neurons are left in the substantia nigra to be influenced by the intake of L-dopa.

In a way to find better treatment modalities to deal with Parkinson's disease, in 1980s, researchers had begun to use transplants of dopamine-containing cells, as a form of treatment in humans. In this treatment the dopamine cells of the adrenal gland are transplanted into the cerebral ventricles of patients. It was believed that these cells would release dopamine into the surrounding area, which includes the caudate nucleus. However, the clinical benefits with this intervention were seen to be minimal, which was not in agreement with the researcher's expectation.

Further research in this area, led to refinements in the treatment of Parkinson's disease. A result of one such refinement was the method of transplanting human fetal cells, which were derived from the brain into the corpus striatum. This was seen to produce remarkable symptom relief in some Parkinson's patients. In addition to improving the quality of movements, such a transplant was also seen to increase the efficacy of L-dopa treatment.

Researches on animals have shown that in such transplants, the human fetal brain stem cells become integrated into the circuitry of the corpus striatum. This causes a rewiring of damaged brains and causes a release of synaptic transmitter. These transplants have also been seen to help patients who suffer from the Parkinson's disease, which has been induced by drugs. Because of ethical reasons

associated with the use of fetal cells, researchers are trying to focus on producing cells that are genetically engineered to make dopamine.

Individuals suffering from Parkinson's disease also show cognitive and emotional changes. As the illness progresses, a cognitive decline is usually seen. Depression is equally common in Parkinson's patients. One reason for depression could be that in this disease a marked reduction in movement capabilities is seen, which can be quite stressful. Depression may also result from a diminished responsiveness of the serotonergic system. In this, depressed patients have low levels of the metabolites of serotonin, reduced activity in prefrontal cortex and mood fluctuations.

Deterioration of the basal ganglia can result in excessive movement, which results in a condition known as Huntington's disease, named after the young physician, George Huntington. Huntington's disease is hereditary in nature and usually develops over a period of 15 to 20 years. This disease is transmitted by a single dominant gene, so each child of a victim has a 50 per cent chance of developing the disease.

The symptoms of Huntington's disease usually begin to appear between the ages of 30 and 45 years. The disease is characterized by subtle behavioural changes, such as, clumsiness and twitches in fingers and face, which are often seen in the initial phase of the illness. But as the illness progresses a continuing stream of involuntary jerks are seen in the entire body. These individuals tend to show aimless movements of the eyes, jerky leg movements and writhing of the body. These significantly interfere with an individual's capacity to carry out his daily routine jobs. In later stages of the illness, marked behavioural changes like, intellectual deterioration, depression and in a minority of patients, a psychotic state that resembles schizophrenia is seen. Memory disruption and changes in visuospatial organization are equally common. Some patients show cognitive and emotional changes which can appear many years before obvious motor impairments.

In this disorder, a profound, progressive destruction of the basal ganglia, especially the caudate nucleus and the putamen is seen. Several types of cells (including neurons that contain the transmitter GABA) are particularly vulnerable. A transmitter or similar substance in the brains of these patients is likely to cause the death of these cells. Certain researchers believe that destruction of the inhibitory circuitry may underlie the disorder. Acetylcholine-containing neurons are relatively spared. According to Nancy Wexler, a gene on chromosome 4 is responsible for the disorder. In afflicted individuals, the HD gene is interrupted by a series of three nucleotides, which are repeated over and over. These repetitions can vary in length. The individual is likely to be asymptomatic, if there are less than 30 repeats, but if there are 38 or more trinucleotide repeats in the HD gene, the person will develop Huntington's disease. The longer the string of trinucleotide repeats, the earlier the symptoms of Huntington's disease appear.

When the repeats are carried by the mother, the faulty gene gets transmitted into the offspring, but in the production of sperm, a father may transmit more or

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fewer repeats than carried by him. Unfortunately, the father often transmits more repeats than he carries, to his offsprings. Thus, it is likely that the offspring of an asymptomatic father may develop Huntington's disease.

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A copy of HD with extended repeats causes degeneration of the striatum and the symptoms of Huntington's disease. Certain researchers believed that only striatal cells normally make the protein which is encoded by HD, so only these cells die when it is defective. But Huntington, whether normal or defective, is not just produced in the striatum, but throughout the brain. It is produced by both neurons and glial cells. Huntington is also made in the muscles, liver, pancreas, and testes. Thus the reason why the defective HD gene affects only striatal cells is still not clear.

A second protein has been found to bind Huntington and is called HAP-1, which is found primarily in the brain and binds the mutant version of Huntington, even more tightly than the normal version. It is possible that this increased binding kills striatal neurons. Several motor impairments may also result from cerebellar damage. Tumor in the vermis (a part of the cerebellum) causes disturbances of balance, as vermis has close connections with the vestibular system. These patients are seen to walk as if they were drunk and tend to display difficulty in even standing erect. These individuals usually place their feet widely apart in an attempt to maintain balance. The abnormalities usually involve the legs and the trunk but not the arms.

Lesions in the cerebellum make these patients see the world around them moving, whenever they move their heads. Severe alcohol intake can also cause degeneration of the cortex of the anterior lobe of the cerebellum. Damage to this region results in abnormalities of gait and posture, ataxia in legs but not in the arms, loss of coordination and swaying movements are seen. This suggests that these patients are unable to compensate normally for the usual deviations of position and posture. Damage to lateral aspects of the cerebellum causes difficulties of motor coordination. One such problem is called decomposition of movement. In this condition, gestures are broken up into individual segments, instead of being executed smoothly.

4.13 TRACING RESPONSES

Responses of an organism can be traced by making use of a *choice chamber*. This is done by introducing small invertebrate organisms into the chamber, at different starting points and observing their movements and recording their distribution after a fixed time. The investigation begins by making a null hypothesis which is then tested for significance. The organisms placed in the choice chamber may show directional responses (movement directly towards or away from particular stimuli), or behaviours such as increasing speed or increasing the turning rate. This results in overall movement out of an area and into an adjacent area. If the adjacent area is preferred, the animal reacts by reducing the speed of movement and turning rate so it is more likely to stay in preferred conditions.

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A directional response to stimuli is called *taxis* (for example phototaxis, or a phototactic response). A nondirectional response is called a *kinesis* (for example, orthokinesis). In orthokinetic responses, the rate of movement depends on the intensity of the stimulus. In klinokinetic responses, the frequency of turning depends on the intensity of the stimulus. Positive responses result in movement towards a stimulus. Negative responses result in movement away from a stimulus.

The procedure of tracing a response by using choice chambers has certain ethical issues associated with it. For example, care should be taken in placing the animals in a chamber, so that no harm is caused to them and they should be promptly returned to their natural environment or a suitable holding tank after exposure to the choice chamber.

CHECK YOUR PROGRESS

9. Which is the best understood muscular dystrophy?
10. Which syndrome is caused by damage to motoneurons of the brain stem and spinal cord?
11. What is the cause of Parkinson's disease?
12. At what age do the symptoms of Huntington's disease appear?

4.14 SUMMARY

- Sensory-motor mechanisms in human parietal cortex underlie arbitrary visual decisions.
- Motor cortex is that area of the cerebral cortex which is involved in the planning, control and execution of voluntary motor functions. It comprises of the primary motor cortex and the secondary motor cortex.
- In humans, primary motor cortex is that part of the brain which is located in the posterior portion of the frontal lobe. It functions along with pre-motor areas in the planning and execution of movements.
- A large amount of inputs are received by the secondary motor cortex, from the association cortex. Large amount of its output goes to the primary motor cortex.
- The secondary motor cortex is divided into the supplementary motor area, the premotor cortex and two cingulate motor areas.
- The function of the cerebellum is to coordinate voluntary motor movement, balance and equilibrium and muscle tone. It is situated right above the brain stem and towards the rear side of the brain.
- In comparison to the frontal and temporal lobes and brain stem, the cerebellum is protected from trauma in a better way.

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- The basal ganglia are a group of nuclei which is found on both sides of the thalamus, outside and above the limbic system. It is below the cingulate gyrus and within the temporal lobes.
- Corticofugal fibres descend through the internal capsule and pass into the brain stem, where some of them (corticobulbar fibres) terminate. Corticobulbar fibres control the activity of brain stem neurons, including motor neurons that are inside the cranial nerve nuclei.
- The performance of multiple motor tasks seems simple, though they involve a coordinated activity of thousands of motor units, in dozens of different muscles.
- In contrast, if the brain's motor control system is damaged, the performance of even simple movements can be very exhausting and difficult.
- The extrapyramidal system is composed of motor fibres which do not pass through the medullar pyramids. However, they control the movements of the body to a certain extent.
- Movement is initiated and coordinated by the motor cortex, the cerebellum and a group of structures in the inner portions of the brain. These are the basal ganglia.
- Sensory information provides critical input on the current position, velocity of body parts and spinal nerve cells (neurons). It helps in preventing opposing muscle groups from contracting at the same time.

4.15 KEY TERMS

- **Sensory motor system:** A system that controls the sensory and motor functions of an organism or the nerves controlling them
- **Stereognosis:** The ability to perceive the form of an object by using the sense of touch
- **Cerebellum:** A major division of the vertebrate brain, situated above the medulla oblongata and beneath the cerebrum in humans
- **Basal ganglia:** A group of nuclei in the brains of vertebrates, situated at the base of the forebrain and strongly connected with the cerebral cortex, thalamus and other areas
- **Betz cells:** Pyramidal cell neurons located within the fifth layer of the grey matter, in the primary motor cortex
- **Golgi tendon:** Proprioceptive sensory receptor organ that is located at the insertion point of skeletal muscle fibers into the tendons of skeletal muscle
- **Renshaw cells:** Inhibitory interneurons that one found in the grey matter of the spinal cord



- **Physiological nystagmus:** Small involuntary tremors of the eyeballs
- **Motoneurons:** Neurons located in the CNS that project their axons outside the CNS and directly or indirectly control muscles
- **Purkinje cell:** A large densely branching neuron that is the characteristic cell of the cerebellar cortex

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4.16 ANSWERS TO 'CHECK YOUR PROGRESS'

1. The three principles of sensory motor association are:
 - (i) It is hierarchically organized
 - (ii) The motor output is guided by sensory input
 - (iii) Based on learning, the nature and locus of sensory motor control can be modified
2. The key function of the dorsolateral prefrontal association cortex is to assess external stimuli and initiate appropriate reactions in response to them.
3. The primary motor cortex is present within the gyrus of the frontal lobe.
4. The cerebellum and the basal ganglia act as two very important sensory motor structures, but do not form a part of the sensory motor hierarchy.
5. Neural signals are conducted from the primary motor cortex to the motor neurons of the spinal cord via four different pathways.
6. Golgi tendon organs are usually responsible for providing the central nervous system with information about muscles tension.
7. EMG is used in the diagnosis of neuromuscular disorders. It helps in engaging in fine analysis of movements by recording the electrical activity of muscles.
8. Motoneurons are directly responsible for the excitation of muscle in the ventral region of the spinal cord and in the brain stem nuclei of several cranial nerves.
9. Of all the muscular dystrophies, Duchenne's muscular dystrophy is the best understood.
10. Damage to the motoneurons of the brain stem and spinal cord is seen to result in a syndrome known as amyotrophic lateral sclerosis (ALS) or Lou Gehrig's disease.
11. Deficits in basal ganglia result in a disease known as Parkinson's disease.
12. The symptoms of Huntington's disease usually begin to appear between the ages of 30 and 45 years.

4.17 QUESTIONS AND EXERCISES

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Short-Answer Questions

1. What are the functions of the secondary motor cortex?
2. How did Penfield and Boldrey map the primary motor cortex?
3. What role does the cerebellum play in motor learning?
4. What role do the basal ganglia play in associative learning?
5. Which structures of the brain stem tend to interact with the ventromedial cortico-brainstem-spinal tract?

Long-Answer Questions

1. List and explain various principles of the sensory motor system.
2. Explain the role played by the cerebellum and basal ganglia in the sensory motor system.
3. Explain the role played by the pyramidal and the extrapyramidal system in the control and regulation of movements.
4. Write a note on the various movement disorders that can result from damage to certain motor regions in the brain.
5. Discuss movements and their coordination from a behavioural perspective.

4.18 FURTHER READING

Pinel, John. 2008. *Biopsychology*, Fifth Edition. New Jersey: Allyn and Bacon.

Rosenzweig, M.R., A.L. Leiman, and S. M. Breedlove, 2010. *Biological Psychology: An Introduction to Behavioural, Cognitive and Clinical Neuroscience*, Second Edition. Massachusetts: Sinauer Associate Inc.

UNIT 5 REGULATION AND BEHAVIOUR

Structure

- 5.0 Introduction
- 5.1 Unit Objectives
- 5.2 Sexual Behaviour
 - 5.2.1 Stages of Reproductive Behaviour
 - 5.2.2 Regulation of Reproductive Behaviour
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- 5.3 The Two Sexes
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 - 5.3.2 Beneficial Mutations of Sexual Reproduction
 - 5.3.3 Reproductive Strategies of Male and Females
 - 5.3.4 Basic Types of Mating Systems
 - 5.3.5 Sexual Selection
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 - 5.4.1 Determination of Sex
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 - 5.4.4 Role of Gonadal Hormones
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- 5.5 Hormones and Sex
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- 5.6 Neural Mechanism of Sexual Behaviour
 - 5.6.1 Male and Female Hypothalamus: Structural Differences
 - 5.6.2 Hormonal Control of Maternal Behaviour
 - 5.6.3 Neural Control of Maternal and Paternal Behaviour
- 5.7 Summary
- 5.8 Key Terms
- 5.9 Answers to 'Check Your Progress'
- 5.10 Questions and Exercises
- 5.11 Further Reading

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5.0 INTRODUCTION

All living beings have the capability to obtain and use resources. They are capable of growing, reproducing and maintaining stable internal conditions, even when the external environment around them is undergoing constant changes. The internal environment of a living being is regulated by sensing changes in the external environment and changing the internal physiological functions that are required to survive. Behaviour can be defined as a way a living being responds to internal or environmental stimuli. The function of behaviour requires precise and accurate coordination and communication at different levels. This includes communications including cells, organ systems and whole organisms. Behavioural response is a set

of actions, which are partly determined by heredity and partly by experience. The behaviour of a living being evolves through adaptation to its environment. Functions like movement, reproduction, search for food, response to danger, etc., are based in a species' history of evolution.

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5.1 UNIT OBJECTIVES

After going through this unit, you will be able to:

- Explain sexual behaviour in organisms
- Discuss the two sexes with reference to sexual and reproductive functions
- Describe the process of sexual differentiation
- Trace the role of hormones and glands in sexual behaviour
- Explain the neural mechanism of sexual behaviour

5.2 SEXUAL BEHAVIOUR

Sexual behaviour is diverse and is determined by the complex interaction of factors such as, relationship between individuals, circumstances influencing an individual's life, his culture, his personality traits, his biological makeup as well as his general existence. It includes the perception of being a man or a woman and reflects development experiences with sex, throughout the life cycle. Sexuality encompasses all those thoughts, feelings and behaviours which are connected with sexual gratification and reproduction. These include the attraction of one person towards the other. In fact, proper sexual functioning is important to an individual's sense of well-being.

Sexuality is such an important and integral part of our lives that we often take many of its components for granted. These components may range from the requirement of two sexes for reproduction to the classification of humans into men and women, etc. Often, exceptions to our assumptions about sexuality do exist. The term sexual behaviour refers to the process of courting, copulating and cohabitating that takes place in animals and human beings. Sexual behaviour is quite complex in itself and its understanding gets further complicated by the fact that there exists a remarkable variety in it. Talking about it is still a taboo in many cultures.

Research has shown that sexual motivation and performance are not necessarily linked. In humans, this may be due to physiological or cultural factors (Robbins, 1996). Whereas, studies of animals have shown that different neural circuits underlie sexual motivation and performance (Everitt, 1990).

Male and female sexual response

- Masters and Johnson distinguished different phases of the human sexual response, including sexual excitement, plateau, orgasm, sexual satiety (Masters and Johnson, 1966).
- Despite obvious dimorphisms in external genitalia and the resulting sexual difference in expression of arousal and orgasm, men and women proceed through equivalent phases of arousal, plateau, orgasm and sexual satiety (James Pfaus, 1996).
- Both sexes report sexual fantasies and imagery and both experience genital vasocongestion, during arousal (Lechtenberg and Ohl, 1994).
- With the exception of ejaculation, more women appear to experience the same sensation of climax and resolution (Masters and Johnson, 1966).
- Ultimately, the difference lies where the brain contributes to human sexuality.

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5.2.1 Stages of Reproductive Behaviour

Reproductive behaviour can be largely divided into the following four stages:

- (i) **Sexual attraction:** is the first stage of the reproductive behaviour. Its main aim is to bring the opposite sexes (the male and the female) together. It has been seen that in many species of apes and monkeys, the male tends to get attracted by the sight of the female's skin, which swells under the influence of estrogen. Most male mammals are seen to get attracted by particular odors (also produced under the influence of the estrogen) which are produced by the females of their species. Thus, estrogen seems to play a dual function of releasing eggs (ovulation) and attracting males towards females. This facilitates the fertilization of eggs. In many species, estrogen is also seen to play another role that facilitates copulation. It stimulates the production of vaginal lubricants. In most species, copulation does not take place till the females and the males find each other sexually attractive. Hence, though sexual attraction is the first stage, but is quite essential for reproductive behaviour to take place.
- (ii) **Appetitive behaviours:** brings the couple to the second stage of reproductive behaviour. These behaviours establish, maintain or promote sexual interaction. Appetitive behaviours vary from one species to the other. In mammals, the female who engages in appetitive behaviour is said to be *proceptive*. The female may approach males, remain close to them or may show alternate approach and retreat behaviours. Whereas in rats, the females are seen to run away from the male with distinctive hopping and darting movements. This is often responded to, by the male, in terms of the mounting behaviour. In contrast to females, the male's appetitive behaviour consists of staying close to the female. In many mammals the males are seen to sniff around the female's face and vagina. However, in birds, the males are seen to engage in elaborate songs or building of nests. These appetitive behaviours

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may be exhibited just before copulation, or several days before they engage in the act of copulation.

- (iii) **Copulation:** is the third stage of reproductive behaviour. It is also known as coitus. Copulation begins with the male inserting his penis inside the female's vagina. This act is known as intromission. After intromission, the male ejaculates the semen containing sperms, inside the female. After one bout of copulation, the animals do not mate again for a certain period of time. This period is known as the refractory phase. The refractory phase varies from minutes to months, depending on the species and circumstances. However, the refractory phase is shortened in many animals, when they are provided with a new partner. This phenomenon is known as the Coolidge effect.

Copulation does not take place till the female is willing. A female that is willing for copulation is said to be sexually receptive, in heat, or in estrus. The term receptive is used only when the female displays appetitive behaviour, just before copulation. However, if they display appetitive behaviours several days before copulation, then they are said to be proceptive but not yet receptive.

When mating is likely to result in reproduction, then the females are usually seen to be receptive. Most animals are seen to breed in certain seasons. These breeding seasons tend to vary in different species. In most species, females are seen to be receptive during the breeding season.

During copulation, the sexually mature female produces gametes. These gametes are known as eggs or ova and the sexually mature male produces gametes known as sperm. When sperm and ova fuse together, then the process is known as fertilization. A single cell that results from this union of the egg and the sperm is known as a zygote. The zygote eventually divides and grows to form a new organism.

Fertilization is essential for reproduction to take place successfully. Fertilization can take place either inside (internal fertilization) or outside (external fertilization) the female body. For instance, in most fishes and frogs the males and the females release their gametes in water. In the water outside the female's body, fertilization takes place. Whereas, in most mammals, birds and reptiles, the male releases the gametes inside the female body, which results in the formation of a zygote. This zygote remains moist and ensures that the resulting offspring gains nutrients from the mother. All mammals use internal fertilization and usually give birth to young ones.

The manner of fertilization takes place differently, in different species. For instance, in mammals like the dog or humans the male penetrates his penis inside the female body. However, birds engage in internal fertilization by discharging their semen into a cloaca (the passage through which birds discharge their wastes), which contains the eggs. After the sperm reaches the ova by moving up the reproductive tract, the female bird assembles rich

nutrients and a tough shell around the zygote. This is later extruded in the form of an egg, by the bird. This process is known as oviparity. The process in which the zygote develops extensively within the female, until a well-formed individual emerges, is known as viviparity.

Copulation in rats is quite brief, where both partners are seen to get attracted towards each other by their odors. They do not remain together after copulation. Unlike other mammals, the female rat spontaneously ovulates in every 4 to 5 days and engages in proceptive behaviours, on seeing a male. Both the male and the female then produce vocalization and engage in copulation. The male tends to mount the female from the rear, grasps her hind flanks with his forelegs and tends to rhythmically thrust his hips. If the female is receptive, it tends to stand still and assume a posture known as lordosis which allows intromission. Once intromission is achieved, the male rat makes a single thrust, lasting half a second or so and then springs back off the female. During the next 6 or 7 minutes, the male rat makes about 7 to 9 such intromissions and is then seen to ejaculate while raising the front half of his body. After ejaculation, he tends to fall backwards off the female.

Following this, he is seen to immediately groom his penis with his tongue and forepaws, whereas, the female is seen to groom her vagina after remaining still for a few minutes. For the next 5 minutes, the male rat pays little attention to the female and may engage in another round of intromission if the female engages in proceptive behaviours towards him.

- (iv) **Post-copulatory behaviours:** mark the fourth stage of the copulatory behaviour. Much like copulatory behaviours, post-copulatory behaviours are seen to vary significantly from one species to the other. For instance, in some mammals, a copulatory lock is seen to occur. That is, in dogs for example, it is seen that after copulation the penis swells to such an extent that the dog is unable to remove it from within the female for about 10 to 15 minutes. Parental behaviours are also a part of the post-copulatory behaviour.

5.2.2 Regulation of Reproductive Behaviour

Much of our knowledge about the neural regulation of the reproductive behaviours comes from animal studies, largely carried out on the rats. The studies have clearly shown that the hypothalamus and steroid hormones play an important role in regulating copulatory behaviour, not only in rats but also in humans. Certain research studies which were carried out on rats showed that when the female was injected with estradiol for a few days and was then injected with progesterone, they tended to display the lordosis response. The steroid autoradiography done by the Donald Pfaff in 1997, showed that the hypothalamus contained the centers neurons that were sensitive to estrogen and progesterone. The ventromedial hypothalamus was found to be crucial for lordosis, as lesions in the ventromedial hypothalamus were found to completely abolish the lordosis response in rats. It was also seen that receptivity could be induced by placing tiny implants of estradiol in the ventromedial

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hypothalamus of rats. The estrogen hormone was seen to increase the size of the dendritic trees of the ventromedial hypothalamus neurons, within 48 hours.

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The lordosis response was also seen to diminish, when lesions were made in the grey region of the midbrain. This is because the ventromedial hypothalamus sends its axons to this region. The periaqueductal gray neurons project to the medullary reticular formation, which in turn projects to the spinal cord via the reticulospinal tract. The sensory information provided by the mounting male, in the spinal cord, evokes the motor response of lordosis. Thus, it seems that the ventromedial hypothalamus largely monitors the concentration of steroid hormones and activates the multisynaptic pathways at the right time in the ovulation cycle. This ultimately induces the spinal cord to show the motor response in the form of lordosis in rats.

Steroid hormones are also seen to activate male copulatory behaviour in rodents. These steroid sensitive neurons are seen to be present in the medial preoptic area of the hypothalamus. Lesions in the medial preoptic area are seen to abolish male copulatory behaviour in several vertebrate species. Further, small implants of androgen, in the medial preoptic area were seen to reinstate mating response in castrated males.

The small nucleus within the medial preoptic area of the hypothalamus was also found to be larger in male rats, as compared to female rats. Neurons in the medial preoptic area of the hypothalamus are seen to send their axons to the ventral midbrain, via the medial forebrain bundle. Information from the ventral midbrain is seen to reach the basal ganglia, presumably, to coordinate mounting behaviour. This information also reaches the spinal cord through a diffuse multisynaptic pathway. The various reflexes of intromission and ejaculation are in turn, mediated by the spinal cord.

Similarly, testosterone gets converted into estrogen then activates the medial preoptic area of the hypothalamus, by acting on estrogen receptors. The intromission and ejaculation reflexes are induced by the activation of the androgen receptors in the periphery and the spinal cord.

Insights into the neural regulation of the reproductive behaviour can also be obtained by studying the vomeronasal system in rats. The pheromones from the receptive female are detected by the vomeronasal organ in males. These pheromones are seen to cause arousal in male rats, which is evidenced by penile erections. The medial amygdala receives the vomeronasal information. Lesions in the medial amygdala are seen to abolish penile erections in response to receptive females. The medial amygdala sends axons to the medial preoptic area of the hypothalamus. Thus, the medial preoptic area of the hypothalamus in males appears to be involved in integrating sensory information (for example, obtained from pheromones) and in coordinating the motor patterns of copulation, when the conditions are correct.

5.2.3 Role of Pheromones

Individuals are more likely to engage in mating behaviour, when the gonadal steroid levels are adequate. The gonads play a dual function, one, of producing gametes and second, of informing the brain that the body is ready to mate. Certain hormones play a role in stimulating the mating behaviour inside the body and some hormones do so by acting outside the female body. For example, in goldfish it is seen that during ovulation, a hormone named F prostaglandin moves outside the female's body and passes through the water, to a male. On detecting F prostaglandin, the male's mating behaviour gets stimulated. In goldfish, F prostaglandin acts as both a hormone and a pheromone.

Pheromones are chemicals that are released from one individual and affect the other individual. Several species like yeast, fish, etc., are seen to release these chemicals before engaging in sexual behaviour. Pheromones can affect the other individual either slowly or rapidly. When they affect the other individual slowly, then these pheromones are said to prime the potential mate for copulation.

Pheromones can be released in water, or in air, or passed through contact between individuals. Though some of the pheromones are detected by the olfactory system, but in most species, an accessory sensory system known as the vomeronasal system has been developed. This system specifically detects pheromones. The cells in the vomeronasal organ detect pheromones and send electrical signals to the accessory olfactory bulb, in the brain. The vomeronasal organ consists of specialized receptor cells that are near but separate from the olfactory epithelium.

In mammals, two well-characterized systems of pheromones are present. They are the activation of aggression in mice and the blocking of pregnancy in several rodent species. When male mice are kept together in a cage, they engage in fights. The pheromones released in the urine of one mouse determine whether the other mouse will attack or not. The normal male mouse is not seen to attack a mouse or mice that has been castrated and is kept in the same cage with him. But the attack is seen to occur if the castrated male is smeared with urine from an intact male or female mice are injected with androgens. The pheromones are released in the urine by androgens. The male mice are seen to attack only those mice that produce pheromones, as only these mice are rivals for mating with the females.

Pheromones in the urine of male mice are also seen to accelerate puberty in young females and can halt pregnancy in mature females. The particular mix of pheromones in the urine helps the female mice to identify an individual male. In certain rodent species, if the female is exposed to pheromones from her mate's mouth and urine, then she is isolated by other members of the same species. If the urine from that male or any other male is applied to her snout, then pregnancy will be blocked. In this case, the foetus are reabsorbed by the female and she soon becomes ready for mating again. But if the female remains with the original male whose pheromones were exposed to her, from copulation on, the pregnancy

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continues. This is because the female is careful not to apply her mate's urine to her vomeronasal organ. Females are able to differentiate males by their pheromones and also tend to avoid using that male's urine, so that pregnancy continues and there is no interruption in it.

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When it comes to humans, Martha McClintock (1971) reported that menstrual cycles in women get synchronized by the pheromones passed between them. In one study, they found that women who were residing together in college dormitories were more likely to have their menstrual cycles in synchrony, than would be expected by chance. It was proposed that the females who tend to spend more time together were likely to menstruate at the same time, if the pheromones were passed between. This led to the hypothesis that these pheromones may serve as a signal of the ovulation cycle, by enabling synchronization.

Several other researches have supported the idea that women show menstrual synchrony, but it was not clear whether this synchrony took place as a result of social or pheromonal signals. Another study done by Stern and McClintock in 1998, supported the hypothesis that pheromones play a role in synchronizing the menstrual cycle. In their study, they found that the menstrual cycles in women, who have extracts of sweat from other women applied to their upper lip, were seen to get accelerated or delayed. This delay or acceleration was caused in order to synchronize their menstrual cycle with those of the women from whom the sweat was extracted.

5.2.4 Diversity of Human Sexual Behaviour

In humans, sexual behaviour involves the union of the male (the sperm) and the female gametes (the ova). In humans, fertilization takes place inside the female body (known as internal fertilization). In women, ovulation of the egg takes place in a cyclic fashion, where the ovaries release an egg in every 28 days or so. The egg released from the ovary reaches the adjacent fallopian tubes, the walls of which have specialized hair or cilia. These cilia wave back and forth, moving the egg into the uterus. In the walls of the uterus, the developing embryo gets implanted and is supported by the placenta. The placenta nourishes the embryo and the foetus.

For fertilization to take place, the egg should unite with the sperm in the fallopian tubes. Hence for fertilization to be successful, copulation should take place during a particular phase of the cycle, that is, when the ovaries release the egg. If the copulation does not take place at the right time, then the zygote may not get enough time to divide, to form an embryo that is developed sufficiently to get implanted into the walls of the uterus. The embryo that is not able to implant itself adequately, tends to drift into the connecting vagina and from there moves outside the body.

The opening of the human vagina is surrounded by folds of skin known as labia. Rostral to the vaginal opening is a mound of tissue called the clitoris. This region surrounding the vaginal opening called the vulva. To facilitate implantation

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of the newly formed embryo in most mammals, the walls of the uterus thicken. When the egg does not meet the sperm and fertilization does not take place, then in some mammals, including dogs and humans, the cells lining the uterine wall are shed and flow out with lot of blood from the vagina. This process is known as menstruation. In most mammals, the cells of the uterine wall are shed, when fertilization does not take place, but there is no visible flow of blood. For instance, all vertebrate species have ovulation cycles, but only a few mammals display menstrual cycles.

In males, sperms are produced in the testis and they mature in the adjacent, crescent shaped epididymis. Vas deferens is a small tube that is attached to the epididymis, whose muscles contract to propel the sperms into the urethra. From the urethra, both, the seminal fluid and the urine move out of the body. Several glands like the seminal vesicles, prostate and others, are joined at one common point. This is the point where the vas deferens on the left and the testes on the right, joins with the urethra.

The seminal vesicles produce and store a cloudy, viscous fluid. The prostate, which encircles the urethra at this point, produces a clear, astringent fluid and other glands contribute other fluids. The semen refers to a mixture of these fluids that are present in the urethra. During copulation, sperms are expelled from the epididymis via the vas deferens. They are expelled out of the body from the penis, during ejaculation.

A lot of diversity is seen in human sexual behaviour. Sexual behaviour in humans is as old as the evolution of mankind. In order to understand the diversity in human sexual behaviour, Alfred Kinsey began to ask his friends and colleagues about their sexual histories. His survey indicated that nearly all men engage in masturbation. The survey also indicated that oral sex was more common in people who were educated in colleges, than in those, who did not attend college. His survey also indicated that at one time or the other, many people had engaged in homosexual behaviours and nearly 10 per cent of the population preferred homosexual sex.

Later, John B. Watson studied the behavioural and physiological observations of people who had engaged in sexual intercourse or masturbation. Later, similar work was carried out by the physician, William Masters and psychologist, Virginia Johnson. Their work further enhanced our understanding about physiological responses that occur during intercourse, in various parts of our body. Their work also increased our knowledge about the time course of physiological responses and their relations to what is experienced during intercourse.

Unlike most mammals, where the male mounts the female from the rear, humans are seen to engage in face-to-face postures while having intercourse. Human beings are also seen to engage in a great variety of coital postures from session to session and even within the same session. This diversity of sexual reproductive behaviours within and between individuals differentiates humans from other species.

According to Masters and Johnson, (1996; 1970; 1975) the four relatively distinct phases of human sexual response as follows:

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- (i) **Desire phase:** consists of fantasies about sexual activity or a sense of desire to have sexual activity.
- (ii) **Excitement phase:** consists of both a subjective sense of sexual pleasure and physiological changes that accompany subjective pleasure. This includes penile erection in the male and vaginal lubrication and enlargement in the female.
- (iii) **Orgasm:** in this phase there is a release of sexual tension and a peak of sexual pleasure. In this phase, most men (during ejaculation) and most women (during copulation), experience extreme pleasurable sensations.
- (iv) **Resolution:** in this phase the individual has a sense of relaxation and well-being.

Although both men and women go through the four relatively distinct phases of human sexual response, yet typical differences are seen in the male and the female responses. One important difference is a greater variety of commonly observed sequences in women. Women show three typical patterns in their sexual response cycle, as compared to men, who have only one basic pattern. Most men, but not women, have an absolute refractory phase, following orgasm. As a result, most men cannot achieve full erection and another orgasm until some time has elapsed. The length of this time varies from person to person and can vary from few minutes to hours. Several other factors also influence the length of this time. On the other hand, most women can have multiple orgasms in rapid succession.

The sexual response pattern in males varies considerably from that in females. In males, mental, physical or both types of stimulation result in sexual excitement. In them, sexual excitement is accompanied by the penis being engorged with blood, making it erect. The rate of excitement varies in men. What may stimulate one man, may reduce excitement in the other. If stimulation continues, then the level of excitement reaches a high plateau. Most people try to extend this plateau as long as possible. This continued excitement results in an orgasm, which is triggered and accompanied by ejaculation. Once ejaculation takes place, a gradual dissipation in excitement is seen. During the resolution phase, the penis loses its erection. In the human sexual response cycle, the excitement phase and the resolution phase are the longest parts of the cycle. Typically, the plateau lasts only for a few minutes. The duration of orgasm is shorter than a minute.

In women, three patterns of sexual responses are seen. In the first pattern, during the excitement phase, the clitoris, like the penis, swells by congestion of blood vessels. Furthermore, vaginal secretion of lubricating fluids is increased and the muscles surrounding the vagina relax. In women, orgasm is marked by rhythmic muscular contractions in the muscles that surround the vagina. In most women, stimulation of the clitoris facilitates orgasm. The temporal pattern of response varies

in women and men. During intercourse, women take more time to reach an orgasm, than men. Unlike men, women do not undergo any absolute refractory phase.

In the second pattern, a high level of excitement of the plateau phase, does not quite trigger an orgasmic release. The sexual excitement is seen to dissipate gradually after a prolonged plateau period.

In the third pattern, women are seen to experience a rapid and explosive orgasm, with only a brief plateau and resolution phase. In this pattern, orgasm is seen to last for a comparatively longer period of time, than in the first pattern.

The more varied the sexual behaviour is, the more varied are the factors that influence an individual's sexual behaviour. Some of the factors that are known to influence sexual behaviour are, an individual's genetic makeup, hormone levels, past experiences and learning. Therefore, sexual therapy focuses on all these factors and aims to help the person relax and recognize the sensations which are associated with coitus. This therapy helps the partners to learn behaviours that facilitate desired effects in both partners. It also focuses on removing several myths and fears that are associated with the sexual behaviour. Many individuals believe that masturbation is not a healthy practice. However, researches have shown that masturbation may help to avoid sexual problems in adulthood.

Sexual behaviour is also crucial for an individual's well-being. Research has shown that sexual behaviour aids overall health and men who have sex often tend to live longer than men who do not. Though it is helpful, yet many severe diseases like syphilis, AIDS and gonorrhoea can be communicated through sexual intercourse. AIDS (acquired immune deficiency syndrome) is an insidious fatal disease that is caused by the HIV (human immunodeficiency virus). This virus can pass through genital, oral and anal sex. Proper use of condoms can prevent several diseases related to sexual behaviour, including AIDS. Condoms have also been seen to be effective in birth control and in preventing unwanted pregnancies.

In humans, much like rats, no correlation has been seen between the amount of androgen produced and the tendency to copulate. Some boys have to be treated with synthetic androgens, to help them develop normally, as they are unable to release gonadotropins. Gonadotropins regulate normal growth, sexual development and reproductive function. Several studies have shown that androgen is needed to stimulate sexual activity in men. Either due to reduced release of gonadotropins, or due to reduced sensitivity of the testes towards gonadotropins, low levels of androgen can sometimes cause infertility. In men who have crossed 60 years of age, a gradual decline in gonadal function is seen. The testosterone levels gradually decline as gonadotropin levels rise. Sildenafil, the anti-impotence drug which is commonly known as Viagra, tends to act directly on tissues in the penis to promote erection. This drug inhibits a second-messenger enzyme which is known as phosphodiesterase-5. Viagra does not have any effect on the androgens.

Androgens are also responsible for activating sexual interest in women, as after menopause, some women tend to report a reduced interest in sex. Other reasons for such changes may be the changes in hormonal levels at this point,

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within the individual. Also, a very low regimen of androgens is sometimes seen to revive the interest in sex, in menopausal women. Though estrogen treatment of menopausal women aids lubrication, but it does not revive interest in sexual relations, in these women.

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CHECK YOUR PROGRESS

1. What factors determine sexual behaviour?
2. List the four stages of reproductive behaviour.
3. How do steroid hormones affect rodents?

5.3 THE TWO SEXES

Men and women differ in multiple ways. There are several factors which are responsible for these differences. In the present section, we shall study hormones and their effect on the development of different characteristics, which differentiate men from women.

Most people are generally characterized as men and women, but there are some exceptions to this categorization, as people termed as gay and lesbian do exist. In several countries they are accepted. In some they are not accepted and overall, a lot of stigma is associated with these terms. If seen carefully, such exceptional cases have been present in this world since thousands of years. For instance, when we refer to Mahabharata, we are reminded about the character of Shikhandi. In addition to knowing why men and women differ, we shall also look at the reasons of development of these types characteristics.

In all mammals, sexual differentiation begins with the fertilization of the egg and the sperm, leading to the formation of the zygote. Sex is determined by the XX chromosomes present in the female and the XY chromosomes present in the male. The genetic information on the sex chromosome determines whether the zygote so formed will result in the birth of a male child, or the female child. When the two XX chromosomes come together, then a female is born but when an X and a Y chromosome come together, then a male is born. The male and the female sex are not determined by two different blueprints of the development. In reality, we all are programmed to develop female bodies but male bodies develop only when the female programme is overruled.

5.3.1 Foetal Hormones and Development of Reproductive Organs

After the six weeks of fertilization, primordial gonads (the gonadal structure) appear. It is interesting to know that this gonadal structure has been found in every foetus, regardless of their sex. This primordial gonad has an outer covering (cortex) and an internal core (medulla). Cortex has the potential to develop into an ovary and medulla has the potential to develop into testis.

After the sixth week of conception, the Y chromosome of the male triggers the synthesis of H-Y antigen and this protein causes the medulla of the primordial gonad to develop into testis. There is no counterpart of the H-Y antigen. This means that if the H-Y antigen is absent, then the cortex of the primordial gonad will automatically develop into ovaries. If H-Y antigen is injected into a female foetus, then as a result of it a female with testis will be born and if H-Y antigen is injected into a male foetus, then as a result of it a male with ovaries will be born.

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Two types of reproductive ducts develop in the sixth week after the fertilization. They are known as the male Wolffian system and the female Mullerian system. The male Wolffian system has the capacity to develop into male reproductive ducts. For example, the seminal vesicles which hold the fluid in which sperm cells are ejaculated and the vas deferens, through which the sperm cells travel to the seminal vesicles. The Mullerian system also has the capacity to develop into female reproductive ducts, for example, the uterus, the upper part of the vagina and the fallopian tubes.

The testes secretes the male sex hormones which is known as testosterone and the Mullerian inhibits the substance in the third month of male foetal development. This substance that emits testosterone and Mullerian, causes degeneration of the Mullerian system. This again causes the testes to descend into the scrotum. The scrotum refers to a sac that holds the testes outside the bodily cavity. The Wolffian development is never triggered by the sex chromosomes but is always triggered by the presence of the male sex hormone, testosterone. That is why, when during the appropriate foetal period, the testosterone hormone is injected into the genetic female, then, they are seen to develop male reproductive ducts along with the female reproductive ducts.

The differentiation of the external reproductive organs and the internal reproductive organs (i.e., the gonads and reproductive ducts) takes place differently. The male and the female internal reproductive organs are developed from different precursors, namely, the medulla for the male and the cortex for the female. Also, the male and female reproductive ducts are produced by the Wolffian and the Mullerian systems respectively. Further, each foetus develops either the internal reproductive organs of the male or the female. Much in contrast to the differentiation of the internal reproductive organs, the differentiation of the external reproductive organs (the male and the female genitals) takes place from the same precursor.

The bi-potential precursor which is responsible for differentiation of the external reproductive organs develops in the second month of pregnancy. It consists of the following four parts:

- (i) **Glans:** which grows into the head of the penis in the male, or the clitoris in the female
- (ii) **Urethral folds:** which fuse in the male, or enlarge to become the labia minora in the female
- (iii) **Lateral bodies:** which form the shaft of the penis in the male, or the hood of the clitoris in the female

- (iv) **Labioscrotal swellings:** which form the scrotum in the male, or the labia majora in the female.

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Again testosterone plays an important role in the development of external genitals, much in the same way as it does in the development of internal organs. The presence of testosterone at the appropriate stage of foetal development, leads to the development of external male genitals, from the bi-potential precursor. On the other hand, its absence leads to the development of external female genitals. Thus, in this way, the foetal hormones influence the development of reproductive organs.

5.3.2 Beneficial Mutations of Sexual Reproduction

Beneficial mutations can result from the process of sexual reproduction and can spread to other individuals in largely two ways. One way is by cloning itself and giving birth to individuals that only have its genes, including the mutated ones. This process is known as *fission* (it involves the simple splitting of one individual cell into two cells) and *parthenogenesis*, in unicellular animals and multi-cellular organisms respectively. If the mutation is especially useful, then the future generations will mostly consist of this individual's progeny. Eventually, other beneficial mutations may arise. In this manner, it is possible for a species to evolve without sexual reproduction.

The second way of spreading beneficial mutations to other individuals is through sexual reproduction. In this manner, the individual which carries the beneficial mutation (a helpful new gene) gives birth to offspring which contain both the new gene and the genes from the other individual. Some of the genes obtained from the other individual may also be beneficial. In this manner, through the process of sexual reproduction, many beneficial genes, that arise from different individuals, can come together in future generations. The biological diversity results from this mixing of beneficial genes that takes place during sexual reproduction. This process is likely to increase the chances of the future generations to survive, when faced with adversity. This is evident from the fact that certain animals are able to produce by both asexual and sexual means; for example, aphids are insects seen to reproduce by parthenogenesis, when the conditions are favourable for growth, there is ample amount of food and population is unchecked. However, they are seen to engage in sexual reproduction when the conditions are not suitable for favourable growth. Through sexual reproduction, they are seen to produce offsprings with effective swapping genes that enables them to migrate away looking for more hospitable environments. Thus, the major advantage of reproducing sexually is that one is able to produce offspring who have half their genes and have the chance of producing new genes. These new genes might enable them to survive in new conditions.

For sexual reproduction to take place, it is not essential that the species should consist of two different sexes. In many species where sexual reproduction takes place, the same organism is seen to produce both the sperms and the eggs.

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In them, sex consists of donating sperm to a partner while accepting sperms in return. Such individuals that can produce as either males or females are called hermaphrodites. Very few vertebrates are true hermaphrodites. It is likely that early during evolution, in our pre-vertebrate ancestors, the male and female roles must have become so divergent that the sexes eventually split. This resulted in some individuals who would exclusively produce sperms and other would exclusively produce eggs.

In some species, a different pattern of reproduction is seen. For example, in many species of fish, individuals spend some parts of their life behaving and reproducing as females and other parts of their life reproducing as males. Though these individuals never produce sperms and eggs at the same time, but they can be regarded as serial hermaphrodites. In some cases, this switch is seen to have reproductive advantages. For instance, many fish, when young, are reproduced as females and tend to switch to the more aggressive territorial behaviour needed to reproduce as males, when they are large enough to compete with others.

In certain other fish like the black molly, such sexual switches may result from social stimuli. For example, if all male fishes are removed from the tank, then usually the largest female transforms into a male and is able to successfully reproduce as that sex. A similar kind of such a transformation takes place in the African cichlid, *Haplochromis Burtoni*, which consists of two kinds of males. In them, the older larger male is seen to defend the territory and mate with the females. As long as such a male is present, the other males tend to remain small, inconspicuously colored and sexually inactive. But if the older male is removed, the smaller males become aggressive and one of them eventually transforms into a large, gaudily colored male that mates with other females. The male that undergoes such a transformation is usually the largest among the smaller males. This transformation is often accompanied by reduced serotonin levels in the brain and increased release of the hormone that releases gonadotropin. The increase in the release of gonadotropin hormone stimulates the testes to increase the production of steroids.

Not all the mutations in genes are beneficial. For instance, presence of only one sex X chromosome results in a syndrome which is known as the Turner's syndrome. The individuals who have Turner's syndrome are females with poorly developed, but recognizable ovaries. These individuals lack the SRY gene. In some individuals with XX chromosome, exposure to androgen *in utero* can also lead to certain masculinizing features. Certain other genetic mutations can be seen in these individuals such as congenital adrenal hyperplasia (CAH). In this condition, adrenal glands fail to produce sufficient corticoids and instead produce considerable amount of androgens. These androgen levels are usually intermediate between those of normal females and males and the new born has an 'intersex' appearance. The size of their phallus is intermediate between a normal clitoris and a normal penis. Their skin folds also resemble both, labia and scrotum. In these individuals, sometimes the opening of the vagina fails to form and sometimes the urethra opens

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somewhere along the base or length of the phallus. In them, an internal portion of vagina is present but the testes are not present in the scrotum. However, the ovaries are present and remain in the abdomen. The Mullerian duct structures are fully developed. These females are often described by their parents as being tomboyish in their nature. Although by adulthood, most of these females describe themselves as heterosexual in nature. But they are seen to be more homosexual in their orientation as compared to other women.

Another condition in which the X chromosome of the male has a defective androgen receptor gene, is known as androgen insensitivity. In this, the individual is unable to respond to androgenic hormones as they are incapable of producing the androgen receptor. In these individuals, the gonads develop as normal testes and produce MRH, which inhibits Mullerian duct structures and plenty of testosterone. In the absence of working androgen receptors, the Wolffian ducts fail to develop. The external epithelia form labia and a clitoris. These individuals look like normal females at birth and develop breasts at puberty. But in these individuals, neither the ovaries nor the uterus is present, hence these individuals are unable to menstruate. These women have a slightly shallow vagina and are infertile. But they look and behave like other women.

5.3.3 Reproductive Strategies of Males and Females

Through the gradual process of evolution, most species came to have two different sexes, which were divergent in their form and behaviour. Today most species are sexually dimorphic (that is, in them the males and the female have two different bodies). In contrast to them are sexually monomorphic species. In these species, both the sexes are different internally in the production of sperms and egg, but they look quite similar. Most vertebrate species are sexually dimorphic in nature. In them, males have larger bodies as compared to females. Further, the gametes are also seen to differ in their size. Male gametes (sperms) are small, whereas female gametes are large in size. Males are able to produce millions of sperms using the same amount of energy and nutrients, as is needed by the females to produce a single egg.

For the purpose of reproduction, females are likely to choose males that are healthy, as they are believed to carry healthy genes, in comparison to unhealthy males, as they are likely to carry harmful genes. Unlike females, males are not seen to be so selective in choosing a partner for reproduction, as they tend to produce several sperms which are sufficient to inseminate several females.

Courtship is a period during which females assess whether a particular male is a suitable partner for reproduction, or not. It indirectly involves assessing whether that particular male has more healthy or harmful genes. In mammals this decision is all the more crucial as the females tend to carry the young ones for a prolonged period within their bodies and spend lot of time in grooming and rearing them. In most vertebrates, only a minority of men who reach reproductive age succeed in mating, whereas, nearly all females who reach reproductive age manage to mate.

5.3.4 Basic Types of Mating Systems

The mating strategies across different species are seen to differ significantly. Broadly speaking, mating systems can be classified into the following four types:

- (i) **Promiscuity:** refers to a kind of a mating system in which animals (male or female) mate with several partners and do not establish long-lasting associations. In this type of mating system, there is little investment of males and females in their offspring.
- (ii) **Polygyny:** refers to a mating system in which each male mates with several females and has a long-lasting association with them. But in this type of mating, the female is seen to mate with only one male. For example, elephants, seals and gorillas show polygyny. In this type of mating system, the females spend more time in rearing the offspring as compared to males.
- (iii) **Polyandry:** refers to a mating system where a female is seen to mate with several males, but males, in contrast, are seen to mate with only one female. This type of mating system is seen in jacana. In them, the female is usually seen to be larger and more colourful than the male. Once the female jacana lays her eggs in the nest, she departs and the male is seen to incubate the eggs and raise the young ones. In this type of mating system, the males spend more time in rearing offspring, as compared to females. The term polygamy is sometimes used to refer to polygyny and polyandry collectively.
- (iv) **Monogamy:** in this type of mating, one man is seen to mate with one female exclusively and both the sexes are seen to form a long-lasting association. Both the male and the female are seen to spend a lot of time in bringing up their offsprings. Monogamy is seen to be more common in birds than in mammals. The reason for this could be because the young ones are too immature at the time of hatching and a single bird cannot provide enough food for the chicks to survive.

When we look at human beings, all the above-mentioned types of mating systems are seen prevalent in different human cultures, except promiscuity.

5.3.5 Sexual Selection

The term sexual selection refers to the selective pressures that each sex exerts on the other, because of massive competition between males and the selective selection of females, in choosing a sexual partner. Darwin used the concept of sexual selection as a special type of natural selection to explain certain features. These features could not be explained only on the basis of natural selection. These features included, presence of enormous antlers in the male moose, presence of elaborate tail features in male birds, etc. These features cannot be explained alone, on the basis of the process of natural selection, as these features do not help animals in gathering food, eluding predators and finding shelter. In fact, some of these features may act as hindrances in these activities.

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Darwin stated that the only and the main reason behind the presence of these features could be that they may help animals in procuring their mates. He found that members of the other sex displayed a preference for mates, with these features. Darwin believed that the two sexes are likely to differ all the more in their appearance, as the process of sexual selection is likely to exert different selective pressures on males and females. Sometimes, the two sexes in some species appear so different that the zoologist originally classified them as two different species. The influence of sexual selection on appearance can occur to a limited level only. This is because if the male is overly ornamented, then he may find it difficult to obtain food and to protect himself from his predators. Activities like obtaining food and protecting oneself from the predators is quite crucial for survival.

In sexual selection, individuals who demand that the potential partners display certain characteristics, or perform certain behaviours before engaging in mating are likely to benefit by passing these genes, that favour such behaviour on to their offsprings and future generations. Once a particular species begins to show preference for certain features, characteristics and behaviours, then this prejudice tends to be self-perpetuating. In this way, natural selection favours the maintenance of such mating behaviours. Because of natural selection, if female lions favour mating, with for instance, maned lions, then the females who mate with lions without manes are likely to leave their offspring, particularly their sons at a distinct disadvantage.

Although sexual selection tends to shape the reproduction process in several species, still, the extent to which the sexual selection might have influenced and shaped the process of human reproduction is not clear. The process of sexual selection is also seen to influence the control of ovulation in certain species. For instance, in frogs it is seen that more the male displays behaviours that are preferred by the female before engaging in mating, the more eggs the female is likely to release and make them available for fertilization. Similarly in rats, courtship and/or copulation is required for ovulation to take place. In lions too, only vigorous copulation over several days is essential for inducing the female to ovulate. The reproductive physiology of lionesses enforces strict evolutionary pressure on male behaviour.

In species that are seen to reproduce through the process of parthenogenesis, sexual selection is seen to influence the process of ovulation. For instance, in whiptail lizards and Amazon mollies, courtship and mating behaviour facilitate ovulation. These females are seen to release more eggs, if they are courted and go through mating behaviour. In whiptail lizards, the females are seen to take turns while mating with one another. A given female may play the role of a male at one moment, wrapping her body around the other female, pressing their cloacae together, biting her neck and so on. The same female may later play a feminine role with some other female, which acts as a male. If two female whiptail lizards are kept together in the cage, then they are seen to literally take turns. Such mock mating is seen to increase the number of eggs released and laid.

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In contrast to whiptail lizards, Amazon mollies mate not only with one another, but also with the males of closely related sailfin molly species. These males on courtship with the Amazon mollies are seen to insert their modified fin into the female and deposit sperms inside her body. The sperms do not fertilize the eggs, but the Amazon will release more eggs and later give birth to more daughters for having gone through the mock mating. The male sailfins exhibit this activity. They may even rehearse it to improve their mating later, with the female sailfin. Another reason behind this behaviour of male sailfins could be that female sailfins are seen to desire and find those males attractive, whom they see with other females of either species.

5.4 SEXUAL DIFFERENTIATION

Sexual differentiation is a process through which a particular species develops into either a male or a female, who behaves differently and has separate different and distinct bodies. In mammals, including humans, this process begins before birth and continues until the individual is capable of reproducing.

5.4.1 Determination of Sex

Sex determination refers to the process of establishing whether an individual is a male or a female. It also determines the development of male and female organs of an individual. In vertebrates, early in the development stage, each individual has a pair of indifferent gonads, which vaguely resemble both the testes and the ovaries. During the first month of gestation in humans, the indifferent gonads begin to change, either into ovaries or testes. Broadly speaking, sex determination is of the following three types: environmental sex determination, nonallosomic genic determination of sex and chromosomal determination of sex.

In environmental sex determination, certain aspects of the environment help in determining the sex of an individual. For instance, marine mollusk *crepidula* becomes a female, if reared alone. In company of a female, it develops into male. Similarly, in crocodiles and some lizards, high temperature induces male characteristics and low temperature induces female characteristics. Another mode of sex determination is the nonallosomic genic determination of sex. For instance, in bacteria, the fertility factor present in a plasmid determines sex.

Chromosomal determination of sex is different to nonallosomic Gen C determination of sex. In chromosomal determination of sex, the sex of an individual is determined by the presence of sex chromosomes. Chromosomal or allosomic determination of sex is based on the occurrence of two types of gametes, in one of the two sexes (known as heterogametes). It is of the following types:

- **XX-XY type**

In most insects and mammals, the female possesses two homomorphic sex chromosomes, named XX and the males contain two heteromorphic sex

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chromosomes, named XY, for instance, human beings have 22 pairs of autosomes and one pair of sex chromosomes. The females are homogametic, that is their ova are similar in their chromosome type and contain the XX chromosome. In contrast to it, the male gamete is heterogametic as the sperms consist of two types of chromosomes, X and Y. The sex of the offspring is determined at the time of fertilization and is determined by the sperm. The sperm is heterogametic, as the female's sex chromosomes are of XX type. As the two types of sperms (22+X and 22+Y) are produced in equal proportion, therefore, there are equal chances of getting a male or female child in a particular mating. Since the Y chromosome determines the male sex of the individual, therefore it is known as androsome.

In mammals, the Y chromosome contains a gene known as the sex-determining region, on the Y gene (SRY gene). This gene is responsible for the development of testes. The cells of indifferent gonad produce the SRY protein, if the individual has a Y chromosome. The SRY protein causes the cells in the cores of the indifferent gonad (medulla) to proliferate at the cost of the outer layers (the cortex), resulting in the development of the testis. But in the absence of the Y chromosome, the SRY protein is not produced and in that case, the cells of the cortical layers proliferate more than those of the medullary layers. This results in the formation of the AB ovary. In addition to SRY gene, certain other genes, such as WT1 (Wilm's tumor 1), SF-1 (steroidgenic factor 1), SOX9, DAX1 and MIS-12 (Mullerian Inhibiting Substance 12), are seen to play a smaller role in sexual differentiation. Defects or mutations in these genes cause failure in gonadal differentiation. This produces clinical syndromes known as intersex disorders.

- **XX-XO type**

In roundworms and some insects, the female has two sex chromosomes, XX and the male has only one sex chromosome, X. In them, the female is homogametic as it produces only one type of eggs (A+X) and the males are heterogametic as they produce two types of gamete (A+X and A+O).

- **ZW-ZZ type**

In birds and some reptiles, it the female that is heterogametic, as it produces two types of eggs (A+Z, A+W) and the male is homogametic as it produces only one type of male gametes (A+Z).

- **Z0-ZZ type**

In some butterflies and moths, it is the female that is heterogametic as it contains only one sex chromosome and produces two types of eggs (A+Z, A+0), whereas the male is homogametic as it produces similar type of sperms (A+Z).

- **Haplodiploidy**

This is a type of sex determination in which the female is diploid (as they are developed from fertilized eggs) and the male is haploid (as males are

developed parthenogenetically from unfertilized eggs). It is seen in some insects like bees, ants and wasps.

CHECK YOUR PROGRESS

4. How does sexual differentiation begin in mammals?
5. Which male sex hormone is secreted by the testes?
6. List the four parts of the bi-potential precursor.

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5.4.2 Sexual Differences

Men and women, both have almost similar kind of brain structure. But there are some differences in their brain structure. For instance, on an average, the male brain is a bit (nearly 15 per cent) larger than the female brain. Also, a higher level of baseline metabolic activity is seen in different areas of the brain of the males and the females, respectively. For instance, men show a higher level of baseline metabolic activity in the temporal lobe and the limbic system, whereas, women show a higher level of baseline metabolic activity in the cingulate gyrus. Some biological psychologists believe that these differences are responsible for the differences in the sexual behaviour, cognition and emotional functions in human beings.

Several studies have been undertaken to understand the development of sex differences in the brain. Most of these studies are conducted on rats as they are born just after 22 days of conception. During these 22 days after conception, hormones no longer influence the genital development, but certainly influence the brain development. Thus, it becomes much easier to observe and understand the effects of hormones on development of the brain, without any confounding factors that may result from the effects of hormones on the genital development.

In 1936, Pfeiffer conducted several studies on rats to understand the development of sex differences in the brain. He focused primarily on the factors that control the development of the steady and cyclic patterns of gonadotropin, which was released in males and females respectively. In one of its experiments, he took a few neonatal male and female rats and removed their gonads. In some male and female rats, the gonads were transplanted. In his studies, he found that removal of gonads in the neonatal rats of either genetic sex causes them to develop into adults with the female cyclic pattern of gonadotropin release. In contrast to it, a steady male pattern of gonadotropin release was seen in both, the intact neonatal rats and in those neonatal rats whose gonads had been removed. No effect on the pattern of hormone release was seen as a result of the transplantation of ovaries in the neonatal rats, whose gonads were removed. Based on these observations, Pfeiffer concluded that the female cyclic pattern of the release of gonadotropin, normally develops unless the preprogrammed female cyclicality is overridden by testosterone hormone during perinatal development.

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Since Pfeiffer was not aware that the release of gonadotropin from the anterior pituitary is controlled by the hypothalamus, therefore, he incorrectly concluded that the presence or absence of testicular hormones in neonatal rats, influenced the development of the pituitary. His experiments had, in fact, provided the first evidence of the role played by the perinatal androgens in the sexual differentiation of the hypothalamus. Hormonal control certainly affects several other differences between the male and female brains, for example, the presence of the perinatal testosterone is responsible for the development of male brain characteristics and its absence is responsible for the development of female brain characteristics, regardless of genetic sex.

All steroid hormones have the ability to change from one to other steroid hormone as they have similar structures. This process is known as *aromatization*. All gonadal and adrenal sex hormones are steroid hormones and are derived from one source, which is cholesterol, for instance, the testosterone hormone changes to estradiol as a result of a slight change in one ring of the testosterone molecule. This may change the ring to a benzene ring.

One particular theory proposes that perinatal testosterone do not masculinize the brain directly. In fact, masculinizing of the brain is seen to result from estradiol, that has been aromatized from perinatal testosterone. This suggests that aromatization plays a critical role in the process of masculinization of brain, in many species.

According to this theory, it was found that in many species estradiol and not testosterone, is responsible for direct masculinizing. Several reasons that support this theory come from the observation that in rats, for example, the enzyme that is necessary for aromatization of testosterone is present in neonates. It has also been seen that neonatal injections of estradiol tend to result in the masculinization of the brain. Further, the agents that tend to block the aromatization of testosterone, or block estrogen receptors, interfere with the masculinizing effect of testosterone on the brain.

This theory raises questions about how the genetic females of species whose brains are masculinized by estradiol, keep from being masculinized by their mother's estradiol, which circulates through the foetal blood supply. The answer to this question was obtained from studies which were conducted on rats which showed that their blood contains a substance known as Alpha fetoprotein. This substance tends to deactivate the estradiol which is circulating in the foetal blood during the perinatal period, by binding to it. In this case, the next question that arises is that, how does estradiol masculinize the brain of the male foetus in the presence of the deactivating effects of alpha fetoprotein. Further studies have shown that the testosterone in rats is immune to alpha fetoprotein and hence can travel unaffected from the testes to the brain, where it enters cells and then gets converted into estradiol. Since, alpha fetoprotein does not readily penetrate the blood-brain barrier; hence it is unable to break down estradiol in the brain of the rat.

Much similar to rats, in humans too, the female foetus is protected from the masculinizing effects of the mother's estrogens by the presence of the placental barrier. This placental barrier has been found to be ineffective against the effects of some synthetic estrogens like diethylstilbestrol. That is why women who have been exposed to synthetic estrogens during pregnancy tend to give birth to the female child, displaying a variety of male characteristics.

Differences in sexual orientation have been reported to have a genetic basis on several research studies that have been conducted in this area. In one study conducted by Bailey and Pillard in 1991 on homosexual males who had twin brothers, it was found that 52 per cent of the monozygotic twin brothers and 22 per cent of the dizygotic twin brothers were homosexual. They also conducted a similar study on female homosexuals who had twin sisters. The concordance rates for homosexuality were found to be 48 per cent for monozygotic twins and 16 per cent for dizygotic twins. Hamer *et al.*, in 1993, proposed that a gene for male homosexuality is localized on one end of the X chromosome. But other researchers like Rice *et al.* (1999), did not find any such gene on the X chromosomes. The search for specific genes that influence an individual's sexual orientation is still in progress.

Certain individuals also believe that homosexuals and heterosexual individuals differ with respect to the levels of sex hormones in their body. But this notion is not true and several studies have shown that both, homosexuals and heterosexuals have the same levels of circulating hormones. Also, orchidectomy has been seen to reduce sexual behaviour in both, heterosexual and homosexual males. But orchidectomy has not been seen to redirect an individual's sexual behaviour and replacement injections are seen to simply reactivate the sexual preferences that existed prior to surgery.

Homosexuals and heterosexual individuals have been reported to have neuroanatomical, neuropsychological and hormonal response differences. In some studies, but not in all, male homosexuals have been found to have a brain structure that is intermediate between female and male heterosexuals. In one study, Le Vay (1991), compared the postmortem neuroanatomy of heterosexual men, homosexual men and heterosexual women. They found that the third interstitial nucleus of the anterior hypothalamus (INAH 3) was more than twice as large in heterosexual men, as it was in women. INAH 3 was also found to be twice as large in heterosexual men, as it was in homosexual men. His findings only suggested that there may be a correlation between the sexual orientation of homosexuality and the small size of the INAH 3 nucleus. It may also be possible that a third factor may affect both, the homosexuality and the size of the INAH 3 nucleus and hence may be responsible for this correlation. Le Vay's study was found to be controversial and many other researchers have not been able to replicate the findings that were obtained by him. The search of the neural correlates underlying sexual orientation is still in process.

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Studies were conducted on nonhuman species to understand the role played by perinatal hormones in influencing the development of one's sexual orientation. These studies have led to the conclusion that in rats, pigs, zebra, finches, dogs, hamsters and ferrets, the perinatal castration of males and testosterone treatment of females, tend to induce same-sex preferences. The finding so obtained in several mammals, certainly has some relevance to humans.

But care should be taken while generalizing results which were obtained from studies conducted on non-human species and human beings. The reason for this is that there are limits to what can be applied to animals and to humans, as the cues and conditions necessary for sexual behaviour vary considerably in man and animals. A human's sexual orientation is strongly influenced by cognitive and emotional components of sexuality, which have no counterpart in laboratory animals.

Some studies have also indicated that the level of perinatal hormones influences sexual orientation in human adults. The strongest support for this view comes from the quasi-experimental study of Ehrhardt and her colleagues in 1985. They interviewed adult women whose mothers had been exposed to diethylstilbestrol during pregnancy. Diethylstilbestrol is a synthetic estrogen. These adult women reported a higher degree of sexual attraction towards other women, than towards men. This suggested that perinatal estrogen exposure does encourage homosexuality and bisexuality in women. But it was seen that the sexual behaviour of all, but one of the 30 subjects was still primarily heterosexual. This further suggested that the effects of perinatal estrogen exposure are relatively weak.

In 1996, McClintock and Herdt suggested that the emergence of sexual attraction may be stimulated by adrenal cortex steroids, as studies have suggested that most boys and girls tend to get attracted towards each other around the age of 10 years. Puberty is seen to occur at the age of 11 years in girls and at the age of 12 years for boys. It is the adrenal maturation that occurs during childhood, at the age of about 10 years.

5.4.3 Defining Gender

Most humans have distinct feminine or masculine characteristics. The term sex refers to one's biological sex (that is one's physical structure), whereas, the term gender identity refers to the sense of one's own sex. Although gender identity is typically established in early childhood, it is not necessarily stable. For instance, when individuals with 5-alpha reductase deficiency are reared as girls, they tend to assume a masculine gender identity at puberty because of the masculinizing influence of testosterone.

Usually one's gender tends to be in accordance with one's sex. But there are some individuals in whom, the biological sex and the gender identity does not seem to match. For example, a transsexual man is an individual who is biologically a man, but has the gender identity of a female and his sexual orientation is typically towards heterosexual men.

5.4.4 Role of Gonadal Hormones

Perinatal hormones influence both, the development of brain and the development of behaviour. Such influence has been studied by focusing on the role of perinatal hormones in the development of sexually dimorphic copulatory behaviours. Much of this research has been conducted on laboratory animals.

One such study was conducted by Phoenix and his colleagues in 1959, on guinea pigs. They injected pregnant guinea pigs with testosterone, thereafter they ovariectomized the female offspring. These offspring, on reaching maturity, were injected with testosterone and their copulatory behaviour was assessed. It was found that more male-like mounting behaviour was displayed by females who had been exposed to perinatal testosterone, in response to testosterone injections in adulthood, than adult females who had not been exposed to perinatal testosterone. However, when these female offspring were injected with progesterone and estradiol and mounted by males, they displayed less lordosis. Lordosis refers to the arched back posture of female rodent receptivity. This posture facilitates intromission. Thus, Phoenix and his colleagues demonstrated that the perinatal injection of testosterone masculinizes and defeminizes a genetic female's adult copulatory behaviour.

In another study which was conducted by Grady, Phoenix and Young in 1965, it was found that aromatization of perinatal testosterone to estradiol is important for both, defeminization and the masculinization of rodent copulatory behaviour. In this study, they found that lack of early exposure of male rats to testosterone, feminizes and demasculinizes their copulatory behaviour as adults. The male rats which had been castrated shortly after birth were unable to display the normal male copulatory pattern of mounting and intromission, when they were treated with testosterone and given access to the sexually receptive female. However, when these same rats were injected with estrogen and progesterone as adults they exhibited more lordosis as compared to uncastrated male rats.

It is clear that perinatal hormones play an important role in the development of normal copulatory behaviour in mammals. However, little is known about the role played by them in the development of proceptive behaviours and in the development of behaviours related to gender, which are not directly related to reproduction. The perinatal testosterone is known to affect behaviours related to gender, by disrupting the proceptive hopping, darting and ear wiggling of receptive female rats and the by disrupting the maternal behaviour of female rats. The perinatal testosterone is also known to increase the aggressiveness of female mice and the rough social play in female monkeys and rats.

While looking at the effect of perinatal hormone on behavioural development, a few points should be kept in mind. For instance, feminizing and demasculinizing effects and defeminizing and masculinizing effects do not always go together. Also, hormone treatments can enhance or disrupt female behaviour without affecting the male behaviour and vice versa. The time when the exposure to these hormones takes place, is equally important in determining its effects on the development of

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behaviour. For instance, during the sensitive period (the first 11 days after birth), a single injection of testosterone is sufficient to masculinize and defeminize the rat brain. But after the sensitive period is over, large multiple doses of the testosterone are needed to masculinize or defeminize the brain of the rat.

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Different periods in the life span of an individual can be divided into childhood, adolescence and adulthood. Childhood is the time when the levels of circulating gonadal hormones are low; the reproductive organs are immature and there are little differences in the general appearance of both males and females. Adolescence is marked by the beginning of a transitional period between childhood and adulthood. This period is known as puberty. Puberty generally begins at about 11 years of age in girls and 12 years in boys. This is the period during which a sudden spurt of growth is seen because of increased release of growth hormones. In this period, fertility is achieved and the secondary sex characteristics are also seen to develop. Secondary sex characteristics are features other than reproductive organs, which distinguish sexually mature men from sexually mature women. This period is also seen to be associated with several significant changes in the hormone levels. For instance, an increase in the release of hormones by the anterior pituitary is seen. The increased release of growth hormone is seen to act directly on bone and muscle tissue to produce a spurt in the pubertal growth. The increase in the release of gonadotropic and adrenocorticotrophic hormones causes the gonads and adrenal cortex to increase the release of gonadal and adrenal hormones. These gonadal and adrenal hormones initiate the maturation of genitals and foster the development of secondary sex characteristics. Testosterone and estrogen are important for the normal development of secondary sex characteristics.

At puberty, in men, androgen levels are seen to be higher than the estrogen levels that result in masculinization. On the other hand, in pubertal females, the level of estrogen is seen to be higher than that of androgen. This results in feminization. However, individual's that have been castrated before reaching puberty do not become sexually mature, unless they receive replacement injections of androgen or estrogen. Although it is the higher levels of androgen hormones that are responsible for masculinization, but androstenedione (an androgen that is released primarily by the adrenal cortex during puberty) is normally responsible for the growth of pubic and axillary hair (underarm hair) in females. Hence, it is not fully correct to attribute androgen as the male hormone.

5.4.5 Social Influence on Sexual Differentiation

Sexual differentiation is not only affected by hormones and one's genetic make-up, but it is also influenced by social factors, to a great extent. Sexuality is often seen as something more than just the physical sex. In fact, sexuality and total personality are entwined, thus making it impossible to speak of sexuality as a separate entity. Sexuality is seen to affect personality development and functioning to such a significant extent that the term psychosexuality can be used to describe it. Sexual activities are often used by people to gratify nonsexual needs such as dependency, aggression, power and status. Although sexual and nonsexual impulses

may jointly motivate behaviour, the analysis of behaviour depends on understanding the underlying individual motivation and their interactions.

Sexuality depends on four interrelated psychosexual factors namely, sexual identity, gender identity, sexual orientation and sexual behaviour. These are seen to affect personality development and functioning. The term sexual identity refers to a pattern of a person's biologically sexual characteristics, which includes chromosomes, external and internal genital, hormonal compositions, gonads and secondary sex characteristics. In normal development, these characteristics form a cohesive pattern that confirms the sexual identity of individuals.

The term gender identity refers to an individual's sense of maleness or femaleness. It results from an almost infinite series of clues which are derived from experiences with family members, teachers, peers and from cultural phenomenon. The term, sexual orientation, is used to describe the object of a person's sexual impulses. It includes heterosexual, homosexual and bisexual orientation. Heterosexual relationship refers to a sexual relationship between two opposite genders, for example, the relationship between a man and a woman. Homosexual relationship refers to a sexual relationship between the same genders, for example, between two men (known as gay) or two women (known as lesbians). Bisexual men and women are people who strike a sexual relationship with members of both sexes. Sexual behaviour includes an individual's desires, fantasies, pursuit of partners, autoeroticism and all activities which are engaged in expressing and gratifying sexual needs. It is a blend of psychological and physiological responses to internal and external stimuli.

Social factors are also seen to affect the sexual differentiation of the nervous system. This can be clearly seen by carefully observing the behaviour of rats. In rats the mother is seen to lick the anogenital region of each pup to elicit a spinal reflex. This causes to empty the bladder and colon. The newborn rat pups can either urinate or defecate on their own. Incidentally, in the process of licking, the mother ingests at least some of the wastes and thereby receives pheromones from the pups that affect the composition of her milk, as the pups mature. Researchers like Celia Moore and her colleagues noticed that the mother rat tends to lick the anogenital region of the male pups more often than the female pups. When the mother rat's olfactory epithelium was treated with chemicals so that she is unable to smell, then it was seen that she tended to lick all her pups less and was unable to distinguish between males and females. Such male pups who received less licking by their mother at the anogenital region, had fewer SNB cells (spinal nucleus of the bulbocavernosus), that survived around the birth. Hence the licking of the mother rat helps in the masculinization of the spinal cord.

This masculinization is actually the result of androgens, as the mother rat is able to detect male pups only by smelling androgen metabolites in their urine. This masculinization of the spinal cord can also be seen from a different view point. It can be said that the mother rat tends to treat male pups differently from her female pups.

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In humans too, in different cultures, boys and the girls are treated differently right from the time of infancy. Such differential treatment certainly has some effect on the developing brain and later contributes to sexual differences in their behaviour. There is a possibility that the older humans interacting with the baby might detect differences, resulting from the effect of prenatal androgens on the foetal brain. Hence, they may treat the baby differently. In this way, subtle differences that may be originally present may get magnified as a result of early social experiences.

One question that arises here is that whether men and women behave differently because they are treated differently, or they have different biological processes which might be immune to cultural influences. Since sex roles differ in different societies, therefore there is little reason to doubt that the sexual differentiation of the brain and the body is affected by societal influences. It is quite difficult to distinguish between the influence of prenatal and social factors on sexual differentiation.

To illustrate this point, we need to look at a rare mutation that affects the enzyme (5-alpha-reductase). This enzyme is responsible for converting testosterone to dihydrotestosterone (DHT). If an XY individual is not able to produce this enzyme, then his internal structures are still seen to develop along a masculine fashion, but the genital epithelium is unable to amplify the androgenic signal by converting the testosterone to the more active DHT. In these individuals, although the testes develop, Mullerian ducts regress and Wolffian ducts are masculinized. The phallus resembles a large clitoris. In these individuals, the phallus is slightly masculinized and the genital folds resemble labia. Although they contain the testis, but usually there is no vaginal opening. In a particular village in the Dominican Republic, babies are often born with this type of appearance and are reared in their community as girls. But at the time of puberty, the testes begin to produce more androgen and the external genitalia become more masculine. The phallus grows into a recognizable penis. Their body becomes masculine in its built, the hips narrow down and breasts do not appear. They are seen to behave like young men showing sexual interest in women. But these men never develop facial beard. They are often nicknamed as *guevedoces* by other villagers.

There may be two main reasons for the behaviour of these individuals, one could be that the prenatal testosterone may have masculinized their brain, hence at puberty, their brain may ask them to seek out for other women for sexual relationships. This explanation also suggests that social influences may have little effect in determining their behaviour and sexual orientation.

The second reason for this phenomenon could be that early hormones were not effective. Another cause for this behaviour may be that the culture simply recognizes and teaches children, that some people can start out as girls and can later change as boys. But still it becomes completely difficult to clearly state whether prenatal hormonal influences or early social influences are more important for sexual determination of the human behaviour. However, it can be certainly stated

that hormones have some effect on the developing brain and that the society reinforces and accentuates sexual differences in human beings.

5.5 HORMONES AND SEX

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Hormones are the chemicals that affect the growth of function of the reproductive organs. They also affect the development of secondary sex characteristics and the behavioural patterns of animals.

5.5.1 Neuroendocrine System and its Glands

The term neuroendocrine system refers to neuronal glands and hormones that are directly involved in sexual development and behaviour. The endocrine glands are the organs whose primary function is the release of hormones. Organs such as the stomach, liver and intestine also release hormones into the blood. These organs are also seen as a part of the endocrine system. The glands of the endocrine system are divided into exocrine glands and endocrine glands. Exocrine glands release their secretions into the target organs, through their ducts, for example, sweat glands release their chemicals into ducts. Endocrine glands are also known as ductless glands as they release their secretions directly into the blood. Their secretions are known as hormones. Hormones tend to travel via the circulatory system until they reach the target area. This area is where hormones normally exert their effect, for example, other endocrine glands or sites in the nervous system.

(i) Hormones

Most hormones can be categorized into three broad categories, namely, amino acid derivatives, peptides and proteins and steroids.

Amino acid derivative hormones are hormones are synthesized from an amino acid molecule, for example, epinephrine, which is released from the adrenal medulla and is synthesized from tyrosine. Peptide hormones are short chains of amino acids. Steroids are hormones that are synthesized from cholesterol, which is a kind of fat molecule.

Of all types of hormones, it is the steroid hormones that play a major role in sexual development and behaviour. Steroid molecules, like most of other hormones, produce their effects by binding to receptors in cell membranes. They can also readily penetrate cell membranes and produce their effects, as they are small and are fat soluble. After crossing the cell membrane, they bind with cytoplasm or nucleus and directly affect gene expression. In this fashion, steroid hormones tend to have especially diverse and long lasting effects on cellular function. Unlike steroid hormones, amino acid derivatives and peptide hormones affect gene expression by largely indirect mechanisms.

(ii) Gonads

When we talk about hormone and sex we have to talk about gonads, e.g., the male testis and the female ovaries. Testis produces sperm cells and ovaries produce

ova. After copulation or sexual intercourse, one sperm combines with one ovum. This forms a cell which is known as the zygote. The zygote contains all information which is necessary for normal growth and has the potential to develop into an adult organism.

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Each cell of the human body has 23 pairs of chromosomes. But the sperm cells and the ova contain half the number of chromosomes, present in other cells. That is, they contain one member of each of the 23 pairs. When sperm and the ova combine, then the zygote so formed ends up having full complement of 23 pairs of chromosomes. It has one of each pair from the father and one of each pair from the mother.

It is quite interesting to know that sex of a child is determined by the father's sperm. The woman's ova has X chromosome in each pair and half of the man's sperm have X chromosomes and the other half of them have Y chromosomes. If during fertilization XX chromosomes bind then female child is born and if X chromosome combines with a Y chromosome, then a male child is born.

(iii) Sex steroids

Gonads also produce many other hormone than just producing ova and sperm cells. Androgens and estrogens are two main classes of gonadal hormones which are released by the testes and ovaries. Testosterone is the most common estrogen. It is a misconception that androgen creates maleness and estrogen creates femaleness, as adult ovaries release more estrogen than androgen and adult testes release more androgen than estrogen.

Both, ovaries and testes also produce another set of hormones known as progestin. The most commonly known progestin is progesterone, which is important during pregnancy in females, but in males its function is not clear. The adrenal cortex is the outer layer of the adrenal gland. Though this is mainly responsible for the regulation of glucose and salt levels in blood, it also produces small amounts of sex steroids.

Limbic nuclei also contain many steroid receptors. Steroid hormones from gonads influence a variety of neural processes, including sexual behaviour. During the critical period of early development, steroids induce differentiation among masculine phenotypes (Breedlove 1992). After puberty, the more transient activational effects of steroid hormones regulate neuroendocrine function and behaviour. In most mammalian species, gonadal steroids are essential for both, male and female maturing behaviour (Pfaff et al 1994). Sexual activity in females is regulated by a combination of estrogen and progesterone (Pfaff et al 1994). The role of steroid hormones in human sexuality is more complicated (Mc Conaghy, 1993). Testosterone replacement to hypo gonadal men increases the occurrence of sexual thoughts and women are seen to initiate intercourse more often, when steroids are elevated around the time of ovulation. However, castration in males and ovariectomy in females, does not abolish sexuality completely. Androgens tend to enhance sexuality of both, men and women.

5.5.2 Hormones of the Pituitary Gland

The pituitary gland is known as a master gland because it produces hormones whose primary function is to influence the release of hormones from other glands. The hormones released by the pituitary gland are known as tropic hormones. For example, gonadotropin is a pituitary tropic hormone that acts on gonads and stimulates the release of gonadal hormones.

Pituitary gland develops during the embryological development. It is divided into anterior and posterior pituitary gland. The posterior pituitary gland develops from a small outgrowth of hypothalamic tissue that eventually comes to dangle from the hypothalamus of the end of pituitary stalk. On the other hand, the anterior pituitary gland develops from the same embryo tissue into the roof of mouth. During the course of the development, it moves upward and joins the posterior pituitary. The tropic hormones are released by the anterior pituitary. Hence it shall be more correct to call the anterior pituitary as the master gland, rather than calling the pituitary gland in general, the master gland.

The endocrine system of the male and female work differently. In women, the release of gonadal and gonadotropic hormones occurs in a cyclic manner, which repeats itself in 28 days. This 28 day cycle controls the menstrual cycle in women. Unlike women, the release of gonadal and gonadotropic hormones in males occurs in a steady fashion. Hence their levels are more or less same each day. It was earlier believed that the difference in the pattern of release of gonadal and gonadotropic hormones in men and women may result from inherent difference between male and female anterior pituitary. But Harris (1955) found in his studies, that removal and transplant of anterior pituitary does not affect the cyclic or steady release of hormones.

(i) Neural control of the pituitary gland

Much of the research on sexual behaviour has been conducted on birds and animals that breed only in specific seasons. It has been found that seasonal variations in the lightening conditions trigger hormonal changes which are related to breeding. For instance, it has been found that by reversing the lightening conditions in which the birds and animal live, (by sending them across the equator) their breeding season can be reversed. This suggests that visual inputs to the nervous system play a role in controlling the release of tropic hormones from the anterior pituitary.

It is well established, by the stimulation and lesion studies, that the hypothalamus controls and regulates the anterior pituitary. However, its means of control are still unknown. Unlike the posterior pituitary, the anterior pituitary does not receive any neural input from the hypothalamus or from any other neural structure

(ii) Control of the anterior and posterior pituitary by the hypothalamus

Hypothalamus controls the anterior and the posterior pituitary in two different ways. The two main hormones which are released by posterior pituitary glands are vasopressin and oxytocin. These are peptide hormones and are synthesized in

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the cell bodies of neurons, in the para-ventricular nuclei and supra-optic nuclei of the hypothalamus. They are then transported along the axons of these neurons, to their terminals in the posterior pituitary and are stored there until the arrival of action potentials. The action potentials cause them to be released into the blood stream. The neurosecretory cells are the neurons that release hormones into the blood stream. The oxytocin hormone stimulates the contractions of the uterus during labor and is responsible for the ejection of the milk from the mother's breast, during suckling. The vasopressin hormone (also known as the anti-diuretic hormone) facilitates the reabsorption of water by the kidneys.

Harris, in 1955, suggested that the release of hormones from the anterior pituitary was itself regulated by hormones which were released from the hypothalamus. This hypothesis was supported by two findings. One supporting evidence, was the discovery of a vascular network or the hypothalamo-pituitary portal system. This system tended to carry hormones from the hypothalamus to the anterior pituitary. It was seen that there was a network of hypothalamic capillaries that were seen to feed a bundle of portal veins. These veins carried blood down the pituitary stalk into another network of capillaries in the anterior pituitary. The second finding that supported the hypotheses was that, the release of anterior pituitary hormones, tends to get disrupted when the portal veins of the pituitary stalk are cut. The release of hormones from the anterior pituitary takes place smoothly, only when the damaged veins get regenerated.

(iii) Discovery of hypothalamic releasing hormones

The release of anterior pituitary hormone is regulated by the hormones which are released by the hypothalamus. The hormones of the hypothalamus that stimulate the release of hormones from the anterior pituitary are known as the releasing factors and those that inhibit the release of an anterior pituitary hormone are known as inhibitory factors.

Guillemin and Schally won the nobel prize in 1977, for their breakthrough research. Guillemin and his colleagues isolated the thyrotropin releasing hormone from the hypothalamus of sheep and Schally and his colleagues isolated the same hormone from the hypothalamus of a pig. Soon, the releasing factors were known as releasing hormones, as the term hormone is known as a factor or substance until it has been isolated and its chemical structure has been identified.

The study of these hormones was not easy as they are produced in very small amount in the organisms. It was essential to obtain these releasing and inhibiting factors as they enabled both, Guillemin and Schally to determine the chemical composition of the thyrotrophic releasing hormone and this knowledge further enabled them to develop methods for synthesizing larger quantities of the hormone for research and clinical use. Schally's and Guillemin's isolation of thyrotropin releasing hormone, confirmed that hypothalamic releasing hormones controls the release of hormones from the anterior pituitary. Thus, this provided the major impetus for the isolation and synthesis of several other releasing hormones.

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The isolation of hormones that release gonadotropins was of direct relevance to the study of sex hormones. Schally and his group began to isolate the hormones that release gonadotropins. This releasing hormone stimulates the release of both of the anterior pituitary's gonadotropins, namely, the follicle stimulating hormone (FSH) and the luteinizing hormone (LH). All releasing hormones and tropic hormones are peptides.

5.5.3 Regulation of Hormone Levels

Brown, (1994) stated that the release of hormones was regulated by the three kind of signals:

- Signal from the nervous system
- Signal from hormones
- Signal from non hormonal chemicals in the blood

Except anterior pituitary gland, all other endocrine glands are regulated by the central nervous system. Endocrine glands which are located in the brain, like pituitary and pineal glands, are regulated by cerebral neurons. Those located outside the central nervous system are controlled by the autonomic nervous system usually by both its sympathetic and parasympathetic branches, which tend to have opposite effects on the release of hormones.

The regulation of hormones is also influenced by one's experiences, which are usually mediated by signals from the nervous system. This means that hormonal explanations do not in any way, rule out experiential explanations; they may be different parts of the same mechanism.

Hormonal regulation is not a one-way traffic flow. It is influenced by the signals which are obtained from other hormones, using a feedback loop system. The main function of the feedback system is to maintain stable blood levels of the hormones. Circulating hormones often provide feedback to the same structures that influence the release of hormones. For example, when the levels of gonadal hormones increase, then they send a feedback to the hypothalamus and pituitary. This causes them to decrease the release of subsequent gonadal hormone factors and gonadal hormones. And similarly, when the levels of gonadal hormones fall, then they again send a feedback to the hypothalamus and pituitary, to increase the release of subsequent gonadal hormone factors and gonadal hormones. In this way, the levels of the hormone in the blood remain stable.

The levels of circulating chemicals like glucose, calcium and sodium in the blood, influence the release and regulation of particular hormones. For instance, increased blood glucose levels increase the release of insulin from the pancreas and the insulin in turn reduces the blood glucose levels.

In 1987, Kirsch has found that hormones are released several times in a day and they do not last more than a few minutes. Changes in the frequency and duration of the hormone pulses are known to regulate the level of hormones in blood. Hence, when a pattern of the male hormone is released and it is said to be

steady, then it simply means that there are no major systematic changes in the circulation of the levels of gonadal hormones. It does not mean that the levels never vary at all.

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In short, hypothalamus and hypothalamopituitary portal system of the brain, control the hormones that release gonadotropins. The hormones that release gonadotropin stimulate the anterior pituitary to release gonadotropin, which is carried by the circulatory system to the gonads. Gonads release androgens, estrogens and progestin. The levels of these hormones in blood provide feedback to the pituitary and hypothalamus, which in turn regulates the subsequent release of gonadal hormone.

CHECK YOUR PROGRESS

7. State the source from which all gonadal and adrenal sex hormones are derived.
8. What are the ages of puberty in boys and girls?
9. What do perinatal hormones influence?

5.6 NEURAL MECHANISM OF SEXUAL BEHAVIOUR

Hypothalamus is an important part of the brain which is responsible for the sexual behaviour, as gonadotropin release is controlled by the hypothalamus. This particular discovery caused researchers to focus on the study of the neural bases of sexual behaviour. Sexual function is dependent on the coordinated activity of sensory, endocrine, cortex, limbic structures and the peripheral nervous system (Lechtemberg and Ohl, 1994). The limbic system plays an important role in the sexuality of both men and women. Research has focused on a network of limbic nuclei which include the preoptic area, hypothalamus and amygdala. Most regions are densely interconnected and each contains large number of neurons that have steroid receptors (Cottingham and Pfaff, 1986). This clearly indicates that the limbic nuclei that control sexual behaviour, responds to both neural inputs and humoral cues.

INAH 3 is a small hypothalamic nucleus. Levay found that INAH 3 was significantly larger in heterosexual men, whereas the nucleus was of comparable size in women and male homosexuals. This discovery evoked lot of controversy and led to further research in this area. This particular study and several other researches in this area suggest that there are biological markers of homosexuality. (Hofman *et al.* 1990) and homosexuality runs in families (Pillord and Wenrich 1986), with a high concordance in monozygotic twins (Whitam *et al.* 1993).

The nuclei of amygdala can be grouped into corticomedia amygdale (CMA) and basolateral amygdale (BLA). The CMA is more closely connected to the preoptic area and the hypothalamus, than the BLA. CMA also has abundant steroid

receptors and steroid metabolic enzymes. It is through CMA, that odour cues from the olfactory bulbs gain access to midline hypothalamic nuclei. These odour cues are known to play a role in human sexuality. Destruction of CMA abolishes male sexual behaviour in species that rely heavily on chemosensory stimuli.

Unlike CMA, BLA is connected to orbitofrontal cortex, dorsomedial thalamic nucleus and circuits of ventral striatum that subserve motivation and reward (Sims and Williams, 1990). The BLA is also linked to the autonomic nervous system to coordinate autonomic response to emotional events. It appears to play an important role in attaching emotional significance to sensory stimuli. In one study, Blumer, in 1970, found that temporal lobe lesions produce hypersexuality. All these observations thus indicated that the function of amygdala in human sexuality is to focus and channelize appropriate sexual behaviour.

In addition to the amygdala, the cortical areas that are seen to participate in sexual functioning are the orbitofrontal cortex and the cingulate gyrus. These structures are connected to the hypothalamus and amygdala and control complex behaviours. For example, the stimulation of cingulate gyrus produces sexual hallucinations and erection and damage of the prefrontal cortex can cause hypo or hyper sexuality.

Ventral tegmental area (VTA) and nucleus accumbens are seen to play an important role in sexual motivation and reward. VTA receives projections from the preoptic area and BLA sends efferents to the nucleus accumbens. Thus, it appears that the ventral striatum may underlie reinforcing aspect of sexual behaviour; although its specific role in humans is not known.

5.6.1 Male and Female Hypothalamus: Structural Differences

The male hypothalamus and the female hypothalamus are known to function differently in their control of anterior pituitary hormones. The male hypothalamus is responsible for steady release whereas the female hypothalamus is responsible for cyclic release of hormones. In 1971, structural differences between the male and female hypothalamus were discovered in rats by Raisman and Field. In 1978, Gorski and his colleagues discovered a nucleus in the medial preoptic area of the hypothalamus of the rat. This nucleus was known as the sexually dimorphic nucleus. This nucleus was found to be several times larger in males, as compared to that in females.

It has been seen that the size of the sexually dimorphic nuclei of male and female rats is the same, at the time of birth. But soon after birth, in a few days, the size of the sexually dimorphic nuclei in the male grows at a high rate, but the female sexually dimorphic nuclei does not grow. The growth of the male sexually dimorphic nuclei is triggered by estradiol, which has been aromatized from testosterone. That is why, castrating a day old rat results in a significantly reduced size of their sexually dimorphic nuclei, as adults. However, when a four day old rat is castrated, then comparatively the size of the sexually dimorphic nuclei is relatively larger than the castrated one day old rat. Whereas, when a neonatal female rat is injected

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with testosterone, then a significant increase in the size of the sexually dimorphic nuclei is seen. The overall size of the sexually dimorphic nucleus is seen to diminish only slightly, in male rats that are castrated in adulthood, with specific areas of the nucleus displaying significant degeneration.

The size of the rat's sexually dimorphic nucleus in males, tends to correlate with the rat's levels of testosterone and aspects of its sexual activity (Anderson *et al.* 1986). In a study conducted by Dejonge *et al.* (1989), it was found that bilateral lesions in the sexually dimorphic nucleus, cause little disruption in the male rat's sexual behaviour. The specific function of this nucleus is still quite unclear.

The discovery of the sexually dimorphic nuclei in rats also brought forward some other sexual differences in the hypothalamic anatomy of both sexes of mammals. For instance, in humans, nuclei in the preoptic, suprachiasmatic and anterior regions of the hypothalamus are found to be substantially larger in men, than in women.

(i) Hypothalamus and male sexual behaviour

Male sexual behaviour is largely governed by the medial preoptic area of the hypothalamus, which includes the sexually dimorphic nucleus. Projections of the preoptic area and hypothalamus extend to midbrain nuclei. This controls the motor aspects of sexual arousal and copulation (Pfaff *et al.* 1994).

Hull *et al.*, in 1999, found that destruction of the medial preoptic area of the hypothalamus abolishes sexual behaviour in the males of all mammalian species. In contrast, medial preoptic area lesions do not eliminate female sexual behaviours, but they tend to eliminate sexual behaviour in males. Also, bilateral medial preoptic lesions tend to abolish male copulatory behaviour in both sexes. Malsbury, in 1971 and Rodriguez Monzo *et al.*, in 2000, found that electrical stimulation of the medial preoptic area elicits copulatory behaviour in male rats. Whereas, Davidson, in 1980, found that copulatory behaviour can be reinstated in castrated male rats by implanting testosterone in medial preoptic area of the hypothalamus.

The reason behind why males with medial preoptic lesions stop copulating is not clear, but they tend to approach receptive females vigorously and are seen to make clumsy attempts to mount them. This indicates that they wish to copulate, but are unable to do so. In one study, Everitt and Stacey, in 1987, studied the effects of medial preoptic lesions on male rats which had been trained to press a lever to gain access to females, which were receptive. The female was dropped into the test chamber, through a trap door in the ceiling. It was seen that male rats continued to press the lever at a high rate to receive the female rat, following lesion in the medial preoptic area. However, they were unable to copulate with the female. In contrast, orchidectomized males stopped pressing the lever.

Further research showed that the medial preoptic area appears to control male sexual behaviour, via the lateral tegmental field. The lateral tegmental field tends to project into an area of the midbrain. In reality, the destruction of this tract disrupts the sexual behaviour of male rats. The copulatory act is seen to correlate

with the activity of individual neurons in the lateral tegmental field of male rats, for instance, during intromission, a high rate of firing is seen in the lateral tegmental field.

The medial preoptic area seems to act quite differently in female mammals, than men. The destruction of this area abolishes copulatory behaviour in males but does not do so in females. However, in females it is certainly seen to reduce the amount of time females choose to spend with sexually active males.

(ii) Hypothalamus and female sexual behaviour

When it comes to the female sexual behaviour, a different part of the hypothalamus, known as the ventromedial nucleus is seen to play an important role. It is seen that the electrical stimulation of the ventromedial nucleus facilitates the sexual behaviour of female rats. Similarly, lesions in this area are seen to result in significant reduction in the sexual behaviour of female. In fact, bilateral lesions in the ventromedial nucleus, cause female rats attack males who become too ardent and do not display lordosis.

An injection of progesterone is seen to bring an ovariectomized female rat (that received an injection of estradiol 48 hours before) into estrus. Progesterone by itself does not induce estrus, therefore estradiol affects the nervous system in a certain way, by enabling progesterone to exert its effect. This priming effect appears to be mediated by a considerable increase in the number of progesterone receptors that occur in the ventromedial nucleus and the surrounding area, following an estradiol injection. The estradiol acts by entering the ventromedial nucleus and influencing gene expression. It has also been seen that microinjection of estradiol and progesterone directly into the ventromedial nucleus, tends to induce estrus in the ovariectomized female rats.

The ventromedial nucleus is seen to influence the sexual behaviour of female rats by mediating its effects through a tract. This tract descends into the periaqueductal gray of the tegmentum. Destruction of this tract and lesions in the periaqueductal gray are seen to eliminate female sexual behaviour. In short, research on rodents suggests that tracts that run from the hypothalamus to the mesencephalon, play important roles in sexual behaviour. Male sexual behaviour is seen to be influenced by a tract that runs from the medial preoptic area to the lateral tegmental field and female sexual behaviour is influenced by a tract that runs from the ventromedial nucleus to the periaqueductal gray of the tegmentum.

5.6.2 Hormonal Control of Maternal Behaviour

Maternal behaviour is seen to be influenced not just by gonadal steroids, but also by several other endocrine hormones that are known to play a role in a human sexuality, such as, oxytocin, prolactin and hormones that release gonadotropin. For example, an increase in the circulation of prolactin is seen in male rats, during contact with a receptive female. However, hyper prolactinemia diminishes libido and sexual performance. Prolactin effects may be the result of reduced reproductive

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neuroendocrine function, suppression of dopamine in MPOA and direct effects of prolactin in neural tissue.

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From the posterior pituitary, a hormone named oxytocin is released at orgasm and is believed to contribute to sexual satiety (Meisel and Sachs, 1994). It is also known to reinforce pleasurable activities. The hormone that releases gonadotrophin has been reported to potentiate mating in male rats, but its effects are seen to be minimal. Thus, the major role of neuroendocrine hormone is still not clear.

Another hormone that is known to play a significant role in sexual desire in both, men and women, is testosterone. This hormone is believed to be connected with libido in both men and women. In fact, exogenous hormonal administration can cause external genital development which is inconsistent with the foetal sex development. For example, if pregnant women receive sufficient exogenous androgen, a female foetus possessing an ovary can develop external genitalia resembling those of male foetus.

DES (Diethylstilbestrol), an adonegic steroid, was prescribed in the 1950s and 1960s, for pregnant women who failed to conceive. However, the drug was seen to have negative effects, for instance, the women who were injected with the steroid suffered from uterine and cervical abnormalities and reproductive track abnormalities.

5.6.3 Neural Control of Maternal and Paternal Behaviour

Most neurotransmitters that act in CNS to regulate sexuality, also affect elements of the peripheral nervous system that control genital responses (Sachs et al 1994). Moreover, sex steroid hormones can influence levels of neurotransmitters (Wood and Newman, 1995). The following neurotransmitters play an important role in sexual functioning:

Monoamine system: include neurotransmitters like dopamine, norepinephrine and serotonin. Catecholamines, particularly dopamine, play a major role in sexuality. Dopamine promotes libido and sexual performance through actions in the ventral striatum and preoptic area. Dopamine agonist including amphetamine and cocaine, are initially seen to promote sexual functioning, which is followed by a progressive decline in libido and sexual performance with increasing dependence. In contrast, dopamine agonist used clinically as antipsychotic drugs and tranquilizers may cause delayed or painful ejaculation in men and anorgasmia in women.

Norepinephrine is also seen to play an important role in sexual functioning, for instance, alpha-antagonists delay normal copulatory sequence and beta-receptors blockers cause impotence, largely through peripheral actions on adrenergic control of blood flow to the penis. Evidence indicates that the adrenergic system is responsible for ejaculation. Depletion of serotonin is seen to enhance male sexual behaviour. SSRIs (Selective Serotonin Reuptake Inhibitor), therefore produces sexual dysfunction in men and women (Ohl 1994). SSRIs are also known to decrease libido, delay orgasm and inhibit erectile function (Gitlin 1994). MAOIs and tricyclic antidepressants also cause sexual dysfunction.

Opioids: have contrasting effects on libido and sexual performance (Pfans, 1996), as compared to the monoamine system. In rats, opioid infusion into MPO A, decreases mating. However, when delivered in nucleus accumbens, opioids enhance sexual motivation. Endogenous opioids tend to suppress sexual activity. Human studies show a similar pattern. Although heroin and morphine initially heighten sexual gratification, their continued use causes insidious deterioration of sexual response in men and women. In addition, prolonged use of heroine can compromise sexual function by depressing the activity of the reproductive endocrine system.

GABA: is seen to inhibit sexual behaviour possibility through actions in the preoptic area. However, the exact role played by GABA in human sexuality is largely unexplored. Several other neurotransmitters that have been implicated in the regulation of sexual behaviour are, acetylcholine, galanin, chole cystokinin (CCK), vasoactive intestinal polypeptide, substance P, vasopressin, neuropeptide Y (NPY), angiotensin, cortico tropin releasing factor (CRF), nitric oxide, etc. At present, the exact role played by these neurotransmitters in regulating sexual behaviour is still not clear.

Since neurotransmitters play a significant role in influencing and regulating an organism's sexual behaviour, therefore neurotransmitter imbalance, whether naturally occurring or drug induced, can influence sexual function peripherally and centrally. For example, prescription of drugs that impair sexuality include, antidepressants, antihypertensives, neuroleptics and antiepileptics. In fact, drug induced sexual dysfunction is a major cause of drug non-compliance.

In addition to the role played by the neurotransmitters, sexual dimorphism is seen in the nervous system of various species, based on the differences in the number, size and shape of the neurons, as well as the number of synapses. This sexual dimorphism in the nervous system was demonstrated by Fernando Nottebohm and Arthur Arnold, who conducted their study on regions of the brain that controlled singing in canaries and finches in zebras. The sections of the brain of the male and the female showed that the nuclei that control song are five to six times larger in volume, in males than in females. In this species the males are seen to produce elaborate songs and female produce only simple songs.

Birds produce songs through a specialized muscular organ called the syrinx, which is wrapped around the air passage. The muscles of the syrinx control the frequency of sounds produced, by changing the tension of membranes around the air passage. The motoneurons of the twelfth cranial nerve, control these muscles. The corresponding nucleus receives most of its innervations from robustus archistriatum (a nucleus in the brain), which in turn receives most of its innervations from the nucleus of the higher vocal center (HVC). The electrical stimulation of the nucleus elicits song snippets and the lesions of the HVC abolish complex songs in canaries and zebra finches. The songs also get disrupted by lesions in the Robustus Archistriatum (RA). It is seen that if the hatching female is exposed either to testosterone, or to estradiol, her HVC and RA are seen to grow larger in adulthood. If we continue to give testosterone to this female as an adult, then the nuclei still

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become larger and the female is likely to sing much like the male zebra finch. But if the female zebra finch is treated with androgen, only at adulthood, then they are unable to sing like their male counterparts. Hence, it can be concluded that early hormone organizes a masculine song system and the adult hormone activates the system to produce songs.

In female canaries, androgen treatment in adulthood for a few weeks is sufficient to make them sing. Androgens treatment in them is also seen to cause the HVC and the RA to become larger in volume. The dendrites of neurons in those regions grow to make new synaptic connections. Unlike zebra finches, canaries are seasonal breeders whose reproductive system is not active at the time of fall. As a result the male canaries have high androgen levels in spring and summer, as compared to fall and winter. With the varying levels of androgen, the singing and the volumes of the HVC and the RA also vary. This is due to the size of the nuclei growing larger in summer and in spring, than in the fall and the winter season. As a result, the male canaries engage in elaborate songs, thus increasing their chances of gaining a mate for the purpose of reproduction.

Similar studies found that the number of synapses in the pre-optic area of the hypothalamus, of male and female rats is different. Within the pre-optic area, a nucleus known as the sexually dimorphic nucleus of the POA (SND-POA), was found to be 4 to 5 times larger in male rats, as compared to that female rats. Roger Gorski and his colleagues found that males who were castrated at the time of their birth had much smaller SND-POAs in adulthood, whereas, females who were given androgen treatment at the time of their birth had larger (like males) SDN-POA as adults. The size of SND-POA was not seen to get altered by the castration of male rats, in adulthood. However, later researches demonstrated that the testosterone which is converted to estrogen masculinizes the SND-POA hormone in the brain. For instance, androgen-insensitive rats have a masculine SND-POA, despite their feminine exterior, as their estrogen receptors are normal.

Research in this area has also shown the presence of sexual dimorphism in the spinal cord of mammals. The neural mechanisms controlling sexual response in males and females were found to be different in mammals. For example, the striated bulbocavernosus (BC) muscles are absent in females, but are present in males. The BC muscles surround the base of the penis and are innervated by motoneurons in the spinal nucleus of the bulbocavernosus (SNB). Unlike females who have fewer motoneurons in the region of the spinal cord, male rats have about 200 SNB cells.

A few days before birth the females have as many SNB cells as the males. And on the day before birth, female rats have BC muscles attached to the base of the clitoris. These muscles are nearly as large as those of males that are innervated by motoneurons in the SNB region. But in the days just before and after birth, many SNB cells and the BC muscles die, especially in females. But, if a single injection of androgen is delivered to a new born female rat, then some of the SNB motoneurons and their muscles do not die. The BC muscles and the SNB

motoneurons are seen to die if the new born rats are castrated, along with the prenatal blockade of androgen receptors. Similarly, in rats that are sensitive to androgen, BC muscles are not present and only few SNB cells are present.

All male mammals have BC muscles, but in non-rodents, the motoneurons are found in a slightly different spinal location and are known as Onuf's nuclei. In nearly all mammals, the BC is larger in men, than in women and men have more Onuf's motoneurons, than women.

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5.7 SUMMARY

- Sexual dimorphism is the systematic difference, in form, between individuals of different sex in the same species.
- Scientific studies have proved that pheromones are one of the keys to physical attraction between two sexes of the same species.
- Pheromones are transmitted as part of the process of attraction that is caused between creatures of the same species.
- The characteristics and features of the two sexes exhibit the differences that occur during the process of our development, from infancy through adolescence and into adulthood.
- Fetal sexual differentiation is an array of complex activities that are precisely and actively programmed. These activities occur at fixed and crucial stages of fetal life. These activities involve both, genetic and hormonal factors which lead to sexual dimorphism, observed at the time of birth of an organism.
- Sex hormone is a chemical substance which is produced by a sex gland or other organ that has an effect on the sexual orientation of an organism. Like many other hormones, sex hormones may also be artificially synthesized. However, this artificial synthesis also has major and damaging side effects.
- Sex steroids play important and diverse roles in the regulation of structure and function of the central nervous system. Early in life, steroids shape the structure of sensitive areas of the brain, especially those involved in the control of reproductive behaviour and ovarian function.

5.8 KEY TERMS

- **Ovulation:** The process of production of an egg from the ovary
- **Copulation:** The activity of having sex
- **Lordosis:** An abnormal inward (forward) curvature of the vertebral column
- **Steroids:** Chemical substances that are used to treat diseases and at times used by sports people to improve their performance

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- **Hypothalamus:** A basal part of the diencephalon, governing autonomic nervous system
- **Pheromones:** Chemical substances that are produced by one animal of a species, to attract other animal of the same species
- **Zygote:** A single cell that develops into a person or animal, formed by the joining together of a male and a female gamete
- **Parthenogenesis:** A process in which an unfertilized egg develops into a new individual
- **Wolffian duct:** A paired organ found in mammals including humans, during embryogenesis
- **Mullerian duct:** A pair of ducts in an embryo, which in a female, develops into the oviducts, uterus, cervix and upper vagina

5.9 ANSWERS TO 'CHECK YOUR PROGRESS'

1. Sexual behaviour is determined by the complex interaction of factors such as, relationship between individuals, circumstances influencing an individual's life, his culture, his personality traits, his biological makeup as well as his general existence.
2. The four stages of reproductive behaviour are:
 - (i) sexual attraction
 - (ii) appetitive behaviour
 - (iii) copulation
 - (iv) post-copulatory behaviour
3. Steroid hormones are also seen to activate male copulatory behaviour in rodents.
4. In all mammals, sexual differentiation begins with the fertilization of the egg and the sperm, leading to the formation of the zygote.
5. The testes secrete the male sex hormone which is known as testosterone.
6. The bi-potential precursor consists of the following four parts:
 - (i) Glans
 - (ii) Urethral folds
 - (iii) Lateral bodies
 - (iv) Labioscrotal swellings
7. All gonadal and adrenal sex hormones are steroid hormones and are derived from one source. This source is cholesterol.
8. Puberty is seen to occur at the age of 11 years in girls and at the age of 12 years in boys.

9. Perinatal hormones influence both, the development of brain and the development of behaviour.

5.10 QUESTIONS AND EXERCISES

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Short-Answer Questions

1. What is lordosis?
2. What are the different means of passing pheromones between individuals?
3. According to Masters and Johnson, which are the four phases of human sexual response?
4. What is the Wolffian system?
5. List the basic types of mating systems.
6. Define haplodiploidy.

Long-Answer Questions

1. Explain the regulation of reproductive behaviour.
2. Write a note on the diversity of human sexual behaviour.
3. Write note on the reproductive strategies of males and females.
4. What are the different basic types of mating systems? Describe them.
5. What is the role of hormones in sexual differentiation?

5.11 FURTHER READING

Pinel, John. 2003. *Biopsychology*, Fifth edition. New Jersey: Allyn and Bacon.

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