**(Slide 1) Lecture 17**

**Physiology of higher nervous activity**

 **(Slide 2)** Lecture plan:

1. Conditioned and Unconditioned Reflexes. Classification of Conditioned Reflexes.

2. Rules of Formation of Conditioned Reflexes.

3. Classification of Conditioned Reflexes.

4. Higher order conditioned reflexes (second, third and higher orders).

5. Systemic Character of Brain Activity. Concept of Dynamic Stereotype.

6. Theory of Formation of Temporary Connections Underlying Formation of Conditioned Reflexes.

7. Inhibition of Conditioned Reflexes.

8. Unconditioned Inhibition.

9. Protective Inhibition.

10. Conditioned (Internal) Inhibition

11. Scheme of the Functional System of Purposive Behavioral Act. Role of Individual Functional Blocks in Implementation of Behavioral Act.

**(Slide 3)** One of mechanisms of adaptation of animals and humans to the variable environment is nervous activity based on reflex mechanisms. In the process of the evolution, genetically reinforced responses (unconditioned reflexes) have been established that integrate and coordinate functions of different organs and provide adaptation of an organism. In individual life humans and higher animals develop qualitatively new reflex responses that were termed “conditioned reflexes” by I. Pavlov and were regarded by him as the most perfect form of adaptation.

**(Slide 4) Video\_Ivan Pavlov’s Dog Experiment – What is Conditioned Reflex**

**(Slide 5)** The main dynamically alternating processes in the CNS are excitation and inhibition. Their interrelations, force and localization determine controlling functions of the cortex. According to I. Pavlov, a functional unit of the higher nervous activity (HNA) is a conditioned reflex.

**(Slide 6)** Higher nervous activity is a complex of conditioned and unconditioned reflexes and of higher mental functions that provides reasonable behavior under variable natural and social conditions. First suggestions about the reflex nature of the activity of higher divisions of the brain were belong to I. Sechenov, and later on this reflex principle was extended to the mental activity of humans. Sechenov’s ideas were experimentally confirmed by I. Pavlov who developed a method of objective evaluation of functions of the higher divisions of the brain – a method of conditioned reflexes.

**(Slide 7)** I. Pavlov showed that all reflexes could be classified into two groups: unconditioned and conditioned. Comparative characteristics of unconditioned and conditioned reflexes are given in slide 6.

**(Slide 8)** Unconditioned reflexes may be simple and complex. Complex inborn unconditioned reflexes are called instincts. The characteristic feature of instincts is that they present a chain of reactions following each other in a strictly defined order.

**(Slide 9)** A conditioned reflex is a complex multicomponent reaction established on the basis of an unconditioned reflex using a preceding neutral stimulus. It has a signaling character and prepares an organism for the forthcoming unconditioned stimulus. An example is re-distribution of blood in the body, enhancement of breathing and circulation in a pre-start period (in running competitions) so that an individual gets prepared for a muscle effort before it begins.

**(Slide 10)** 1. Use of two stimuli, one of which is unconditioned (food, painful stimulus etc.) that causes an unconditioned response, and the other is conditioned, or signaling stimulus (light, sound, sight of food etc.), that signals about a forthcoming unconditioned stimulus;

2. Multiple repetition of combinations of conditioned and unconditioned stimuli (although sometimes only one combination may be enough);

3. A conditioned stimulus should precede an unconditioned one;

4. A conditioned stimulus may be any external or internal stimulus that is neutral as far as possible, causes no defense response, is not excessively strong but catching attention;

5. An unconditioned stimulus should be strong enough to form a temporary connection in the brain;

6. An unconditioned stimulus should produce a stronger excitation than a conditioned stimulus;

7. Any extra stimuli should be excluded to prevent external inhibition of a conditioned reflex;

8. An animal in which a conditioned reflex is being established, should be healthy;

9. To establish a conditioned reflex, an animal should be motivated, for example, a salivary reflex can be established only in a hungry animal because in a fed up animal this reflex will not be established.

**(Slide 11)** Conditioned reflexes are more easily established to stimuli to which an animal is ecologically adapted. In this context, conditioned reflexes are classified into natural and artificial. Natural conditioned reflexes are established to signals inherent to the stimulus that in natural conditions induces an unconditioned reflex, e.g., sight of food, its smell, etc. All the rest conditioned reflexes are artificial, that is, they are established to factors not associated with an unconditioned stimulus, e.g., a salivary reflex to a sound.

**(Slide 12)** A stable conditioned food reflex established, for example, to light, is a first order conditioned reflex. It may be used as the basis for a second order conditioned reflex, for which a new preceding signal for example, a sound, is introduced, reinforced by the first order conditioned stimulus (in our example by light). After several combinations of sound and light the sound stimulus also starts to induce salivation. Thus, a new and a more complex mediated temporary connection is formed.

**(Slide 13)** It should be emphasized that reinforcement of the second order conditioned reflex is a conditioned stimulus of the first order reflex (light), but not an unconditioned stimulus (food), because reinforcement of both light and sound with food leads to establishment of two separate first order conditioned reflexes. A sufficiently stable second order conditioned reflex may be used to establish a third order conditioned reflex. For this a new stimulus is introduced, for example, touching the skin. Here, a touch is reinforced only by the second order stimulus (sound), which stimulates the visual center, which in turn stimulates the feeding center. Thus, a still more complex temporary connection is formed. Reflexes of higher orders (4th, 5th and 6th) can be established only in primates and humans.

**(Slide 14)** In certain situations separate conditioned reflexes may combine into complexes. If several conditioned reflexes are performed in a strictly defined sequence, and this sequence repeats many times at regular intervals, in the brain an integral system will finally establish consisting of the specific sequence of reflex responses, that is, previously separate reflexes arrange into a single complex. Neurons of the brain, despite their high functional mobility, can, nevertheless, strongly retain the sequence of responses to repeated conditioned stimulations. This is the basis of a dynamic stereotype, which actually is a stable and fixed system of responses to different conditioned signals following one another in a strictly defined sequence at definite intervals. Afterwards, application of only the first stimulus elicits the whole chain of responses.

**(Slide 15) Video\_What is Stereotype \_ Explained in 2 min**

**(Slide 16)** A dynamic stereotype is a characteristic feature of human mental activity. Many of our skills, e.g., ability to write, play musical instruments, dance and etc., are actually chains of automatic motor actions. Throughout life more complex behavioral stereotypes are established: behavioral patterns after wake up or before going to bed, working skills, resting and eating habits. Dynamic stereotypes are responsible for relatively stable patterns of social behavior, for relationships among people, for evaluation of current events and for responses to them. These stereotypes are extremely significant in life, since they permit an individual to perform many activities with the minimal tension of the nervous system. Biological sense of dynamic stereotypes is that they rid the cortical centers of the necessity to solve routine problems each time de novo and permit them to focus on more complex tasks requiring creative thinking.

**(Slide 17)** A physiological basis for conditioned reflexes is establishment of temporary functional connections at the higher levels of the nervous system. A temporary connection is a complex of neurophysiological, biochemical and ultrastructural changes in the brain induced by a combined action of conditioned and unconditioned stimuli. I. Pavlov suggested that in the process of establishment of a conditioned reflex, temporary neural connections are formed between two groups of cortical cells – cortical representatives of conditioned and of unconditioned reflexes. Excitation spreads from the center of a conditioned reflex to the center of an unconditioned reflex neuron by neuron. So, the first way of establishment of temporary connections between centers of conditioned and unconditioned reflexes is realized within the cortex.

**(Slide 18)** However, after destruction of the cortical center of the conditioned reflex the established reflex is preserved. So, it is reasonable to suggest formation of temporary connections between the subcortical center of the conditioned reflex and the cortical center of the unconditioned reflex. When the cortical representation of the unconditioned reflex is destructed, the conditioned reflex nevertheless persists. Thus, a temporary connection is likely to be established between the cortical center of the conditioned reflex and the subcortical center of the unconditioned reflex.

**(Slide 19)** Separation of the cortical centers of conditioned and unconditioned reflexes by transection of the cerebral cortex does not prevent establishment of a conditioned reflex. This shows the probability for formation of temporary connections between the cortical center of a conditioned reflex, the subcortical center of an unconditioned reflex and the cortical center of an unconditioned reflex.

**(Slide 20)** There exist different opinions as to the mechanisms of formation of temporary connections. A temporary connection is presumably established on the basis of the principle of dominant. Excitation focus caused by unconditioned stimulus is always stronger than that caused by a conditioned stimulus because unconditioned stimuli are always more biologically significant. Since this excitation focus is dominating, it attracts excitation from the focus of the conditioned stimulation. Once this excitation has made its way through some neuronal pathways, next time it will pass these ways much more readily (a phenomenon of “a beaten path”) due to: summation of excitations, long-term increase in excitation of synapses, increase in the amount of transmitters in synapses, formation of new synapses. All these factors create structural predispositions for facilitation of propagation of the excitation through neuronal networks.

**(Slide 21)** Another idea of the mechanism of formation of temporary connections is the theory of convergence. This theory rests on the ability of neurons to receive stimuli of different modalities. According to P. Anokhin, conditioned and unconditioned stimuli cause an extensive activation of cortical neurons through activation of the reticular formation. In result the ascending signals (from a conditioned and an unconditioned stimuli) overlap, and their excitations meet, or converge, on the same cortical neurons. This convergence of excitations results in establishment and stabilization of temporary connections between cortical representations of conditioned and unconditioned stimuli.

**(Slide 22)** To ensure adaptation and adequate behavior it is important not only to generate new conditioned reflexes and preserve them for a long time, but also to eliminate reflexes no longer needed by the body. Conditioned reflexes are eliminated by inhibition. I. Pavlov distinguished the following forms of cortical inhibition: unconditioned (inborn) and conditioned (acquired).

**(Slide 23)** This kind of inhibition of conditioned reflexes occurs immediately after action of some extra stimulus, that is, it is an inborn, unconditioned type of inhibition. There are two kinds of unconditioned inhibition: external and protective. External inhibition is induced by introduction of a new stimulus, which creates a dominating excitation focus that evokes an orientation (“what-is-it?”) reflex. Biological significance of external inhibition is that by inhibiting the current conditioned-reflex activity it permits an organism to switch over to evaluation of significance and probable danger of a new stimulus. A new stimulus, which inhibits existing conditioned reflex, is termed an external inhibitor. Repeated application of this new stimulus causes gradual diminish and finally disappearance of the orientation reflex so that it no longer inhibits conditioned reflexes. Such external inhibiting stimulus is termed an extinguishing inhibitor.

**(Slide 24)** If a new stimulus carries some biologically significant information, it inhibits conditioned reflexes every time it acts. Such constant stimulus is termed a constant inhibitor.

The biological sense of external inhibition is that it provides conditions for a more important for the moment orientation reflex caused by an emergency stimulus, and permits its fast evaluation.

**(Slide 25) Protective Inhibition.** This kind of inborn inhibition differs from external and conditioned inhibitions by the mechanism of initiation and by physiological significance. It is caused by excessive increase in strength or duration of a conditioned stimulus which start to exceed capacities of the cortical cells. This kind of inhibition has a protective significance since it prevents nerve cells from depletion. By mechanism it is similar to the phenomenon of pessimum described by N. Wedensky. Protective inhibition may be caused not only by very strong, but also by weak but persistent and monotonous stimuli. These stimuli permanently acting on the same cortical elements, lead to their depletion, and, consequently, result in protective inhibition. Protective inhibition more easily develops in an individual with a decreased working capacity, for example, after a severe infectious disease, stress, and is more common in elderly people.

**(Slide 26)** It occurs if a conditioned stimulus stops being reinforced by an unconditioned one. It is called internal inhibition because it is realized in the structural elements of a conditioned reflex. Conditioned inhibition requires some time for formation. This kind of inhibition includes: extinctive inhibition, differentiating inhibition, delayed inhibition and the so called “conditioned inhibitor”.

**(Slide 27)** Extinctive inhibition develops when a conditioned stimulus stops being reinforced by an unconditioned one which results in a gradual disappearance (extinction) of the conditioned response. On the first application of the conditioned stimulus without reinforcement, the conditioned response occurs as usual. Repeated applications of the conditioned stimulus without reinforcement initiate an orientation response which soon extincts, and the conditioned reflex gradually disappears too.

**(Slide 28)** Differentiating (discriminative) inhibition develops in response to stimuli with characteristics similar to those of the conditioned stimulus. This kind of inhibition is based on differentiation (discrimination) between stimuli. It permits to select from similar stimuli only those that are reinforced by an unconditioned stimulus, in other words, stimuli which are more biologically significant for an organism. An example is secretion of saliva in a dog to a metronome sound with frequency of 120 beats/min. The sound with 60 beat/min frequency applied without reinforcement at first also causes salivation, but after some time the dog starts to differentiate between stimuli and does not salivate to 60 beat/min frequency.

**(Slide 29)** “Conditioned inhibitor” is a kind of differentiation inhibition. It occurs if a positive conditioned stimulus is reinforced by an unconditioned stimulus, but a combination of a conditioned stimulus and some additional neutral stimulus is not reinforced. For example, a conditioned stimulus (light) is reinforced by an unconditioned one, but a combination of light and sound (additional neutral stimulus) is not reinforced. At first, this combination evokes the same response as the light alone, but after some time it loses its signaling character, and in result the response to it disappears and remains only to conditioned stimulus (light). However, the sound acquires the inhibitory significance and in combination with other conditioned stimuli also inhibits the conditioned reflex.

**(Slide 30)** Delayed inhibition is characterized by response to a conditioned stimulus occurring immediately before application of an unconditioned stimulus. With the increase in the time interval between application of a conditioned stimulus and its reinforcement to 2-3 min., the conditioned response occurs with a longer and longer delay and finally occurs immediately before the reinforcement. A delay in the conditioned response after application of a conditioned stimulus evidences formation of delayed inhibition, with the period of delay corresponding to the period of delay in reinforcement.

**(Slide 31)** Conditioned inhibition permits the body to rid itself of many unnecessary and biologically unreasonable responses. The internal inhibition (according to P. Anokhin) is the result of a competition between two streams of excitations for the ways to effectors. For example, in extinctive inhibition of the salivary food reflex the competition is between a stream of excitations associated with the respective food reaction and excitations associated with a biologically negative reaction in the absence of reinforcement. A stronger, dominating excitation caused by dissatisfaction inhibits a weaker food-related excitation.

**(Slide 32)** Pavlov’s scientific school considers mechanisms of purposive behavior in higher animals and humans in terms of reflex theory. This means that this scientific school attempted to explain all diversity of the purposive behavior of animals and humans from the point of view of reflexes. A reflex is a mechanism of reflective activity of a human, and it terminates with a change in the state of an effector organ. Here, the extent of adaptive significance of this change does not depend on a reflex scheme. Besides, according to reflex theory, all forms of purposive behavior must be stimulus-dependent, that is, behavior must be determined by external and internal stimuli. But reasons determining purposive behavior in real life, are more complicated, and behavior sometimes cannot be explained by reflex mechanisms alone. In this context there arose a need in some theory which, without denying reflex principles of behavior could explain the logical organization of behavior on a higher level of generalization. In our opinion, such a theory was proposed by a Russian physiologist P.K. Anokhin and is called a theory of functional systems.

**(Slide 33)** A functional system is a dynamic arrangement of central and peripheral structures and mechanisms that are coordinated to achieve useful adaptive results. In this situation a useful adaptive result acts as a system-forming factor, for the sake of which the system is constructed. According to P. Anokhin, a functional system of a purposive behavioral act has the following structure:

Afferent synthesis is the first stage of formation of a purposive behavioral act. This stage provides answers to four questions:

What is needed by an organism? How can it be achieved? How can it be done in the given situation? When can it be done?

The first question arises in connection with a biological demand for something which evokes motivation.

A biological demand is a non-compensated change in some homeostatic parameters, for example, in levels of glucose, lipids, amino acids.

**(Slide 34)** The term “motivation” is taken from psychology where it means “attraction to something”. In a more specific sense motivation is a well-realized need (demand).

**(Slide 35)** In physiology motivation is understood as an emotionally colored condition of an organism based on a certain demand and manifested by selective excitation of certain structures of the central nervous system and by purposive behavior aimed at elimination of the initial demand. As soon as the motivational excitation is formed and becomes dominant, memory mechanisms are activated which retrieve from certain brain structures the information about earlier behavior of an organism in a similar situation. Thus, the answer to the second question is associated with activation of memory mechanism.

**(Slide 36)** The third question is answered by evaluation of information entering an organism in result of activation of different sensory systems by stimuli coming from external environment. This information is called a “situational afferentation”. At last, realization of a purposive behavioral act is associated with a specific starting (triggering) stimulus (in the scheme – “starting ((triggering)) afferentation”).

**(Slide 37)** Decision-making is the stage of formation of the behavioral act associated with restrictions of the liberty of an organism. After the stage of afferent synthesis is completed, it becomes clear what is required for an organism, how it can be achieved, how it can be done in the given situation and when it can be done. However, every specific situation suggests several options of behavior, and at this stage of decision-making the most suitable one is selected.

**(Slide 38)** Efferent synthesis (program of behavior) is the stage of generation of a specific pattern of behavior which must lead to achievement of the useful adaptive result for an organism. Simultaneously, an acceptor of the result of behavior is formed. Acceptor of the result of behavior (action) is a functional block that stores information about parameters of the ideal model of the desired result. Besides, the acceptor of behavioral result compares parameters of the actual result with the parameters of the ideal model of the result.

**(Slide 39)** There may be two variants of comparison of parameters of the actual result with the ideal model. The first variant – parameters of the actual result fully coincide with those of the ideal model. P. Anokhin called this situation “match”. This situation produces positive emotions which “confirm” that the behavior that has led to this result was correct. Positive emotions indicate achievement of the useful adaptive result, and the functional system completes its function. The second variant – parameters of the actual result do not meet the parameters of the ideal model. P. Anokhin called this situation “mismatch”. Mismatch generates negative emotions which indicate a failure in achievement of the result. In this context there may occur either an enhancement of behavior aimed at achievement of the required result, or cessation of the behavior due to inability to achieve the required result. P. Anokhin linked the above processes occurring in acceptor of the behavioral result with physiological mechanisms of emotions, and called the theory explaining the origin of emotions in terms of processes occurring in an acceptor of behavioral result, “a biological theory of emotions”.

**(Slide 40)** Lesson assignment:

Lauralee Sherwood. Fundamentals of Human Physiology.

Pages: 124 – 128.

Questions that we will analyze for a lesson on this topic:

1. Conditioned and Unconditioned Reflexes. Classification of Conditioned Reflexes.

2. Rules of Formation of Conditioned Reflexes.

3. Classification of Conditioned Reflexes.

4. Higher order conditioned reflexes (second, third and higher orders).

5. Systemic Character of Brain Activity. Concept of Dynamic Stereotype.

6. Theory of Formation of Temporary Connections Underlying Formation of Conditioned Reflexes.

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9. Protective Inhibition.

10. Conditioned (Internal) Inhibition

11. Scheme of the Functional System of Purposive Behavioral Act. Role of Individual Functional Blocks in Implementation of Behavioral Act.

Finish for today

The full lecture is at the indicated website.

**Thank you for attention**