Cerebral Cortex:

Cerebral Cortex, Intellectual Functions of the Brain, Learning, and Memory

Physiologic Anatomy of the Cerebral Cortex:

The cerebral cortex consists of a relatively thin layer of neurons ranging from 2 to 5 mm in thickness with a total surface area of approximately ¼ square meter and containing about 100 billion neurons. Most cortical neurons fall into one of three categories: (1) granular (or stellate), (2) fusiform, or (3) pyramidal.
The granule cells are short-axon, local circuit neurons that utilize glutamate (excitatory) or GABA (inhibitory) as neurotransmitters. In contrast, fusiform and pyramidal neurons have long axons that project at some distance from the cortex. Fusiform cells project to the thalamus, whereas pyramidal neurons project to other locations in the same or opposite hemisphere and to a variety of subcortical locations, such as the red nucleus, basilar pons, and spinal cord. The neurons of the cerebral cortex are organized into six horizontal layers. Layer IV receives incoming sensory signals from the thalamus, whereas neurons in layer V give rise to long subcortical projections to the brain stem and spinal cord. Corticothalamic fibers originate from cells in layer VI. The corticothalamic interconnections are most significant because damage to the cortex alone seems to result in less dysfunction than occurs when both cortex and thalamus are damaged. Layers I, II, and III are specialized to receive input from and project to other parts of the cortex in the same or opposite hemisphere.

Functions of Specific Cortical Areas:

Studies have clearly shown that many areas of the cerebral cortex are specialized for specific functions. Some areas, called primary cortex, have direct connections with the spinal cord for controlling movement, whereas other primary regions receive sensory input from various thalamic nuclei that represent each of the special senses (except olfaction) and somatosensation. Secondary cortical areas are called association cortex, and they serve to interconnect various portions of the cortex in the same or opposite hemisphere.

Association Areas:

• Parieto-occipito-temporal area includes

(1) the posterior parietal area that contains the spatial coordinates for all parts of the contralateral side of the body as well as all contralateral extrapersonal space;
(2) the area for language comprehension called Wernicke’s area, which lies in the superior temporal gyrus;

(3) the area for the initial processing of visual language (reading) in the angular gyrus of the inferior parietal lobule; and

(4) an area for naming objects located in the anterior part of the occipital lobe.

• Prefrontal association area functions in close relation with motor areas of the frontal lobe to plan complex patterns and sequences of movement. Much of its input comes from the parieto-occipito-temporal association cortex, and its principal output is sent to the caudate nucleus for additional processing. It is also involved in nonmotor functions that include memoryrelated transformations related to problem solving and other internally guided behavior. It contains one specialized region, Broca’s area, which is involved in the motor aspects of speech and receives input from Wernicke’s area in the temporal lobe. Broca’s area provides output to the nearby motor cortex that controls the muscles required for speech production.

• Limbic association cortex includes the anterior pole of the temporal lobe, the ventral aspect of the frontal lobe, and a portion of the cingulate cortex. It is involved with the complex processes of emotional and motivational behavior, and it is connected with limbic system structures such as the hypothalamus, amygdala, and hippocampus.

• Facial recognition area is located on the ventromedial surfaces of the occipital and temporal lobes.

Concept of the Dominant Hemisphere:

The interpretive functions of Wernicke’s area, the angular gyrus, and the frontal motor speech areas are more highly developed in one hemisphere, the dominant hemisphere. In approximately 95% of all individuals, the left hemisphere is dominant regardless of handedness. How one hemisphere comes to be dominant is not yet understood.

Wernicke’s area is often assigned a general interpretive function because damage to this area results in the inability to comprehend spoken or written language even though the individual has no hearing deficit and may be able to read the words on a

page. Likewise, damage to the angular gyrus (with Wernicke's area intact) may leave undamaged the ability to understand spoken language, but the ability to comprehend written words is lost. This is called word blindness.
Interestingly, the area in the nondominant hemisphere that corresponds to Wernicke's area is also involved in language function. It is responsible for understanding the emotional content or intonation of spoken language. Similarly, an area in the nondominant frontal lobe corresponds to Broca's area and is responsible for imparting the intonation and inflections that give emotional color or meaning to speech. In a way, these areas are also "dominant" for a particular language function.

Higher Intellectual Functions of the Prefrontal Association Cortex:
The function of the prefrontal cortex is complex and multifactorial, and it is typically explained by describing the deficits seen in individuals with large lesions in this cortex.

• Decreased aggressiveness and inappropriate social responses. This is most apparent when lesions involve the ventral aspect of the prefrontal cortex, the limbic association area.
• Inability to progress toward goals or to carry through sequential thoughts. Prefrontal cortex gathers information from widespread areas of the brain to develop solutions to problems, whether they require motor or nonmotor responses. Without this function, thoughts lose their logical progression, and the individual loses the ability to focus attention and becomes highly distractible.
• Prefrontal cortex as the site of "working memory." The ability to hold and sort bits of information to be used in a problem-solving function is described as "working memory." By combining these stored bits of information, we can prognosticate, plan for the future, delay a response while further information is gathered, consider the consequences of actions before they are performed correlate information from many sources, and control actions in accordance with societal or

moral laws. All of these actions are considered intellectual functions of the highest order and seem to be definitive for the human experience.

Function of the Brain in Communication—Language Input and Output:

There are two aspects to communication: language input (the sensory aspect) and language output (the motor aspect). Some individuals are capable of hearing or identifying written or spoken words, but they do not comprehend the meaning of the words. This is the result of a lesion in Wernicke's area; the condition is known as receptive or sensory aphasia and may simply be called Wernicke's aphasia. If the lesion extends beyond the confines of Wernicke's area, a total inability to use language communication ensues, termed global aphasia.

If an individual is able to formulate verbal language in his or her mind but cannot vocalize the response, the condition is called motor aphasia. This indicates a lesion involving Broca's area in the frontal lobe, and the condition can also be referred to as Broca's aphasia. The defect is not in control of the musculature needed for speech but, rather, in elaboration of the complex patterns of neural and muscle activation that in effect define the motor aspects of language. Lesions that involve the corresponding language areas in the nondominant hemisphere cause sensory aprosodia (inability to comprehend the emotional qualities of speech) or motor aprosodia (inability to impart emotional content to speech).

Function of the Corpus Callosum and Anterior Commissure to Transfer Thoughts, Memories, Training, and Other Information between the Two Cerebral Hemispheres:

The corpus callosum provides abundant interconnections for most areas of the cerebral hemispheres except for the anterior portion of the temporal lobes, which are connected via the anterior commissure. Some of the more important functional connections mediated by these two fiber bundles are as follows:

• The corpus callosum allows Wernicke's area in the left hemisphere to communicate with the motor cortex in the right hemisphere. In the absence of this connection, voluntary movement of the left side of the body to a communicated command is not possible.

• Visual and somatosensory information from the left side of the body reaches the right hemisphere. Without a corpus callosum, this sensory information cannot extend to Wernicke's area in the left hemisphere. As a result, such information cannot be used for processing by Wernicke's area, and the left body and left visual field are ignored.

• Without a corpus callosum, only the left half of the brain can understand both the written and spoken word. The right side of the brain can only comprehend the written word, not verbal language. Emotional responses, however, can involve both sides of the brain (and body) if the anterior commissure is intact.

Thoughts, Consciousness, and Memory:

The neural substrates for the three processes of thoughts, consciousness, and memory are poorly understood at present. The holistic theory suggests that a thought results from patterned stimulation of the cerebral cortex, thalamus, and limbic system; each of these areas contributes its own particular character or quality to the process.

Memory—Roles of Synaptic Facilitation and Synaptic Inhibition:

Memories derive from the changes in synaptic transmission between neurons that occur as a result of previous neural activity. These changes cause new pathways, facilitated pathways, or inhibited pathways to develop in the appropriate neural circuitry. The new or altered pathways are called memory traces. Although we think of memories as positive collections of previous experiences, probably many are, in a sense, negative memories. Our minds are inundated with sensory information, and an important brain function is the ability to ignore irrelevant or extraneous information. This process is called habituation. Conversely, the brain also has the capacity to enhance or store certain memory traces through facilitation of synaptic circuits, a mechanism referred to as memory sensitization.

It is obvious that some memories last only a few seconds, whereas others last hours, days, months, or years.

Consequently, three categories of memories have been described:

(1) short-term memories last only seconds or minutes unless they are converted to long-term memory;

(2) intermediate long-term memory lasts days to weeks but is eventually lost; and

(3) long-term memory, which once stored, can be recalled years later or for a lifetime.

Short-Term Memory:

Short-term memory is typified by the memory of a new telephone number recalled for a few seconds or minutes as one continues to think about the number. Several theories concerning the substrate for this mechanism are under investigation:
(1) this type of memory is due to continuous neural activity in a reverberating circuit,

(2) it occurs as a result of activation of synapses on presynaptic terminals that typically result in prolonged facilitation or inhibition, and

(3) the accumulation of calcium in axon terminals may eventually lead to enhanced synaptic output from that terminal.

Intermediate Long-Term Memory:

This memory can result from temporary chemical or physical changes in either the presynaptic or postsynaptic membrane that can persist for a few minutes up to several weeks. Some experimental observations on such mechanisms have come from studies in the snail Aplysia. Stimulation of a facilitator terminal at the same time as activation of another sensory input causes serotonin to be released at synaptic sites on the sensory terminal. Stimulation of serotonin receptors activates adenyl cyclase in the main sensory terminal, resulting in the formation of cyclic adenosine monophosphate (cAMP), which causes release of a protein kinase and leads to phosphorylation of a protein that blocks potassium channels in the sensory terminal. Decreased potassium conductance causes prolongation of action potentials that reach the sensory terminal, which in turn allows increased calcium to enter the sensory terminal, resulting in increased neurotransmitter release from the sensory terminal, thereby facilitating transmission at this synapse.

Long-Term Memory:

Long-term memory is thought to result from structural changes at the synapse that enhance or suppress signal conduction. These structural changes include

(1) an increase in the number of synaptic vesicle release sites,

(2) an increase in the number of available synaptic vesicles,

(3) an increase in the number of synaptic terminals, and

(4) changes in the shape or number of postsynaptic spines.

Consolidation of Memory:

For memories to be converted to long-term memory, they must be consolidated; that is, they must initiate the chemical or structural changes that underlie the formation of a long-term memory. In general, 5 to 10 minutes is required for minimal consolidation, whereas 1 hour or more may be needed for strong consolidation. The mechanism of rehearsal is thought to represent the consolidation process.

Rehearsal of the same information again and again in the mind potentiates the transfer from short-term to long-term memory. Over time, the important features of sensory experience become progressively more fixed in memory stores. Also during consolidation, memories are codified into various classes of information. For example, new and old experiences relative to a topic are compared for similarities and differences, and it is the latter information that is stored.

Roles of Specific Brain Parts in the Memory Process:

Lesions of the hippocampus lead to anterograde amnesia, or the inability to form or store new memories. Memories formed prior to the onset of the lesion are not affected; the reason for this appears to be that the hippocampus (and the dorsomedial thalamic nucleus) is connected to the so-called punishment and reward centers. That is, our experiences may be associated in the hippocampus with pleasure or punishment, and that is the substrate for initiating the memory process. The loss of long-term memory occurs with thalamic lesions and, in some instances, with damage to the hippocampus. The hypothesis is that the thalamus may be part of the mechanism that searches the memory hippocampal lesions do not have difficulty learning physical skills that require only manual repetition and do not involve verbalization or other types of symbolic higher order intelligence. This suggests that memory mechanisms for functions are distributed in more than one brain location stores and “reads” them. Interestingly, individuals with hippocampal lesions do not have difficulty learning physical skills that require only manual repetition and do not involve verbalization or other types of symbolic higher order intelligence. This suggests that memory mechanisms for functions are distributed in more than one brain location.