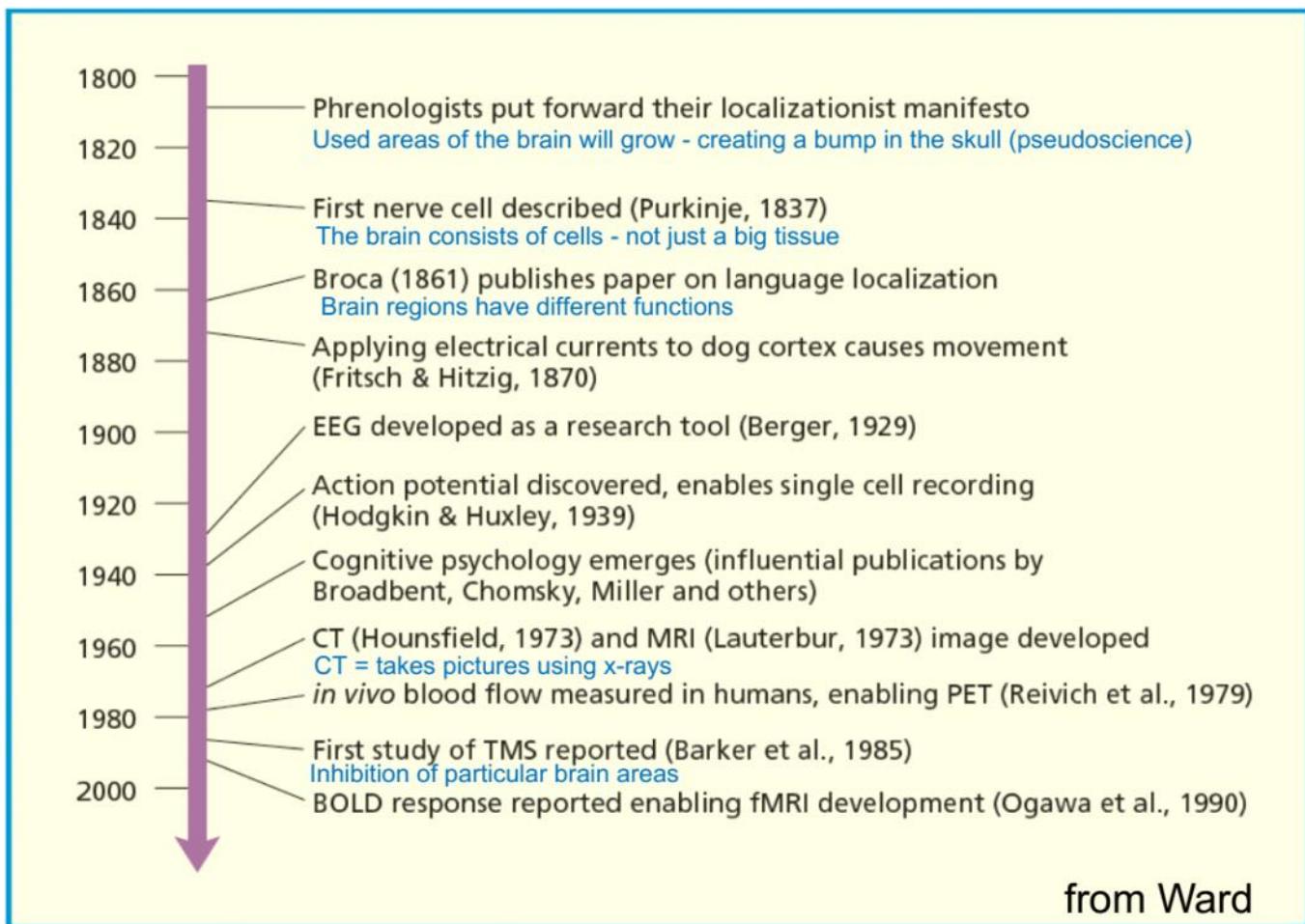


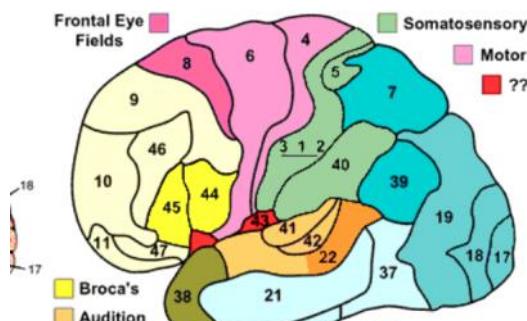
History of Neuroscience and development of methods

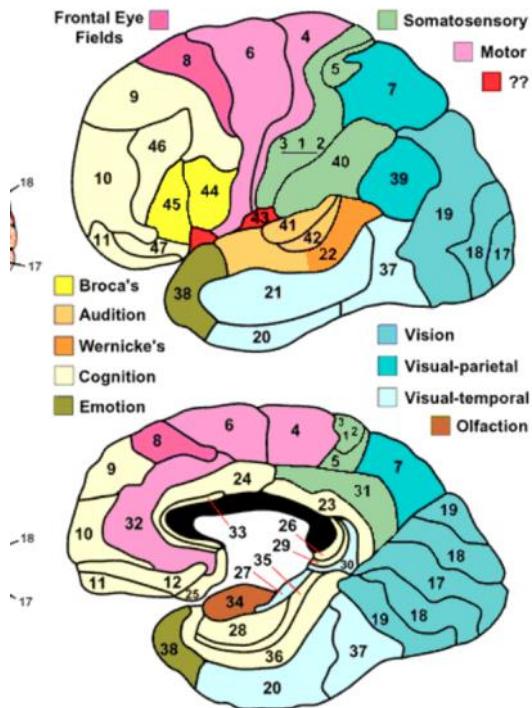
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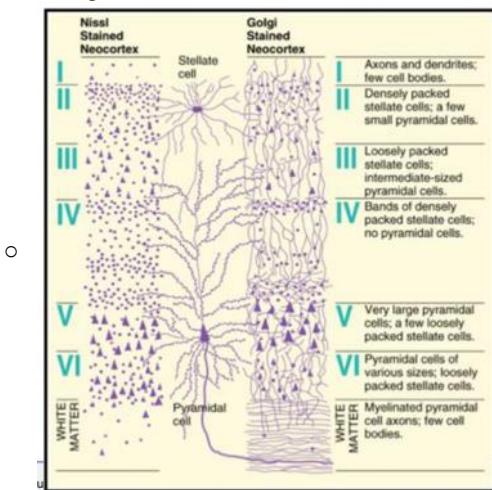
Important figures in Cognitive Neuroscience:

- **Thomas Willis:** Famous from saving a woman, that had been hanged --> fame --> used it to publish brain anatomy
 - **Phrenologist, Franz Josef Gall** (1798) publishes doctrine on brain localisation, investigating the shape of the skull as a proxy: Using different brain areas will increase grow in a area --> measurements can be done to the skull
 - o Valuable anatomical work as well
 - **Florent:** **Aggregate field theory**, Argues against localisation:
 - o Cut pigeons brains --> after removing parts of the brain, the pigeon was unable to do much --> concluded the brain works as a whole.
 - **Broca:** wins the argument, the brain is localised
 - o Investigated Leborgne who were only able to utter "tan" --> Lesion in the frontal lopes
 - **Prukinje:** described the first neuron (a big one)
 - **Nissl:** Methods were developed for investigating the brain: **the Nissl stain**
 - o Using dye on neural tissue, found cortex is organized in layers
 - o The hypothesis was: If there is a structural contrast --> also functional contrast
 - **Brodmann:** Used the Nissl stain to map the cortex --> the map that has survived, and today you refer to the areas as Brodmann area e.g. 45





- **Golgi:** The golgi stain was invented: Golgi's method stains a limited number of cells at random in their entirety -->argument for localisation
- **Cajal:** Using the golgi method found the nature of neurons as interconnections
 - o Using the two methods the structure of the cortex was discovered:



aggregate field theory (p. 7)	Flourens developed the notion that the whole brain participated in behavior, a view later known as the aggregate field theory
associationism (p. 12)	Believers of conditioning
behaviorism (p. 13)	disregards conscious thinking as relevant. It held that psychology was to be entirely concerned with external behavior and was not to try to analyze the workings of the mind that underlay this behavior. Perceptions and thought are untrustable, the only thing that can be trusted is, that you have a mind
cognitive neuroscience (p. 4)	the term <i>cognitive neuroscience</i> — fom <i>cognition</i> , or the process of knowing (i.e., what arises fom awareness, perception, and reasoning), and <i>neuroscience</i> (the study of how the nervous system is organized and functions). Tis seemed the perfect term to describe the question of understanding how the functions of the physical brain can yield the thoughts and ideas of an intangible mind.
cytoarchitectonic s (p. 8)	How cells differ beten brain regions is called cytoarchitectonics , or <i>cellular architecture</i>
empiricism (p.)	Empiricism, on the other hand, is the idea that all knowledge comes fom sensory experience, that

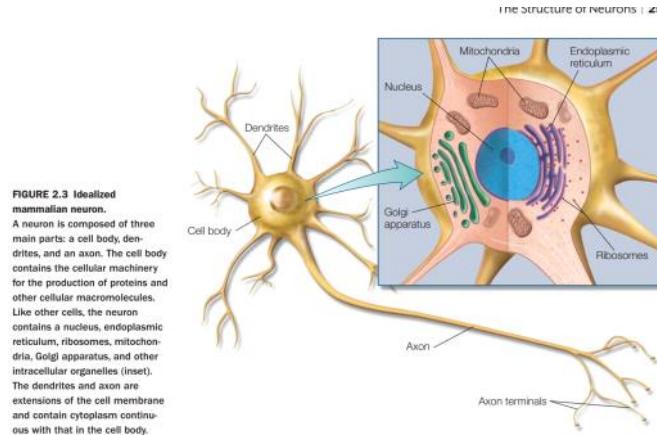
10)	the brain began life as a blank slate. Direct sensory experience produces simple ideas and concepts. When simple ideas interact and become <i>associated</i> with one another, complex ideas and concepts are created in an individual's knowledge system.
Montreal procedure (p. 13)	In collaboration with Herbert Jasper, Donald Hebb invented the Montreal procedure for treating epilepsy, in which he surgically destroyed the neurons in the brain that produced the seizures
neuron doctrine (p. 9)	Ramón y Cajal, who some call the father of modern neuroscience, was the first to identify the unitary nature of neurons and to articulate what came to be known as the neuron doctrine , the concept that the nervous system is made up of individual cells.
phrenology (p. 6)	The idea that character could be divined through palpating the skull was dubbed phrenology by Spurzheim. Phrenology is a pseudomedicine primarily focused on measurements of the human skull, based on the concept that the brain is the organ of the mind, and that certain brain areas have localized, specific functions or modules. Fra < https://www.google.dk/search?q=phrenology&oq=phrenology&aq=chrome..69i57i69i60i3i0i2.1557j0j7&sourceid=chrome&ie=UTF-8 >
rationalism (p. 10)	Rationalism grew out of the Enlightenment period and held that all knowledge could be gained through the use of reason alone: Truth was intellectual, not sensory.
syncytium (p. 9)	Golgi had believed that the whole brain was a syncytium , a continuous mass of tissue that shares a common cytoplasm.

Function of the Nervous system

Sunday, January 28, 2018 7:25 PM

The structure of neurons:

- Neurons and glial cells make up the nervous system.
- Neurons are the cells that transmit information throughout the nervous system. Most neurons consist of a cell soma (body), axon, and dendrites.
- Neurons communicate with other neurons and cells at specialized structures called synapses, where chemical and electrical signals can be conveyed between neurons.



Neuronal Signaling

- The presynaptic cell is located before the synapse with respect to information flow; the postsynaptic cell is located after the synapse with respect to information flow. Nearly all neurons are both pre- and postsynaptic, since they both receive and transmit information.
- The resting membrane potential is the difference in the voltage across the neuronal membrane during rest (i.e., not during any phase of the action potential).
- The electrical gradient results from the asymmetrical distribution of ions across the membrane. The electrical difference across the membrane is the basis of the resting potential.
- Ion channels are formed by transmembrane proteins that create passageways through which ions can flow.
- Ion channels can be either passive (always open) or gated (open only in the presence of electrical, chemical, or physical stimuli).
 - o Passive current conduction is called electrotonic conduction or decremental conduction. A depolarizing current makes the inside of the cell more positive and therefore more likely to generate an action potential; a hyperpolarizing current makes the inside of the cell less positive and therefore less likely to generate an action potential.
 - o Action potentials are an all-or-none phenomena: The amplitude of the action potential does not depend on the size of the triggering depolarization, as long as that depolarization reaches threshold for initiating the action potential.
- Voltage-gated channels are of prime importance in generating an action potential because they open and close according to the membrane potential.
- Myelin allows for the rapid transmission of action potentials down an axon.
- Nodes of Ranvier are the spaces between sheaths of myelin where voltage-gated Na⁺ and K⁺ channels are located and action potentials occur.

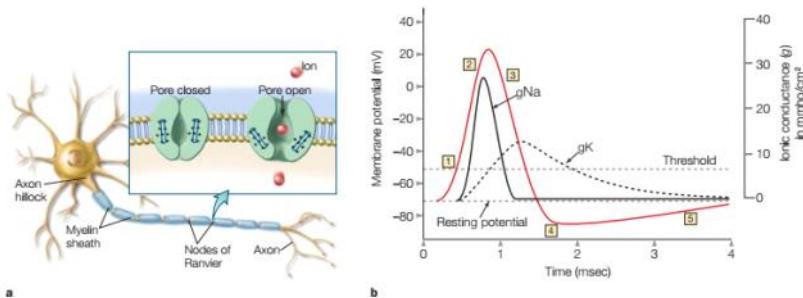


FIGURE 2.11 The neuronal action potential, voltage-gated ion channels, and changes in channel conductance.

(a) An idealized neuron with myelinated axon and axon terminals. Voltage-gated ion channels located in the spike-triggering zone at the axon hillock, and along the extent to the axon, open and close rapidly, changing their conductance to specific ions (e.g., Na⁺), alerting the membrane potential and resulting in the action potential (inset). (b) Relative time course of changes in membrane conductance to Na⁺ (gNa) and K⁺ (gK). The initial depolarizing phase of the action potential (red line) is mediated by increased Na⁺ conductance (black line), and the later repolarizing, descending phase of the action potential is mediated by an increase in K⁺ conductance (dashed line) that occurs when the K⁺ channels open. The Na⁺ channels have closed during the last part of the action potential, when repolarization by the K⁺ current is taking place. The action potential undershoots the resting membrane potential at the point where the membrane becomes more negative than the resting membrane potential.

Synaptic Transmission

- Synapses are the locations where one neuron can transfer information to another neuron or specialized non-neuronal cell. They are found on dendrites and at axon terminals but can also be found on the neuronal cell body.
- Chemical transmission results in the release of neurotransmitters from the presynaptic neuron and the binding of those neurotransmitters on the postsynaptic neuron, which in turn causes excitatory or inhibitory postsynaptic potentials (EPSPs or IPSPs), depending on the properties of the postsynaptic receptor.
- Classes of neurotransmitters include amino acids, biogenic amines, and neuropeptides.
- Neurotransmitters must be removed from the receptor after binding. This removal can be accomplished by (a) active reuptake back into the presynaptic terminal, (b) enzymatic breakdown of the transmitter in the synaptic cleft, or (c) diffusion of the neurotransmitter away from the region of the synapse.
- Electrical synapses are different than chemical synapses as they operate by passing current directly from one neuron (presynaptic) to another neuron (postsynaptic) via specialized channels in gap junctions that connect the cytoplasm of one cell directly to the other

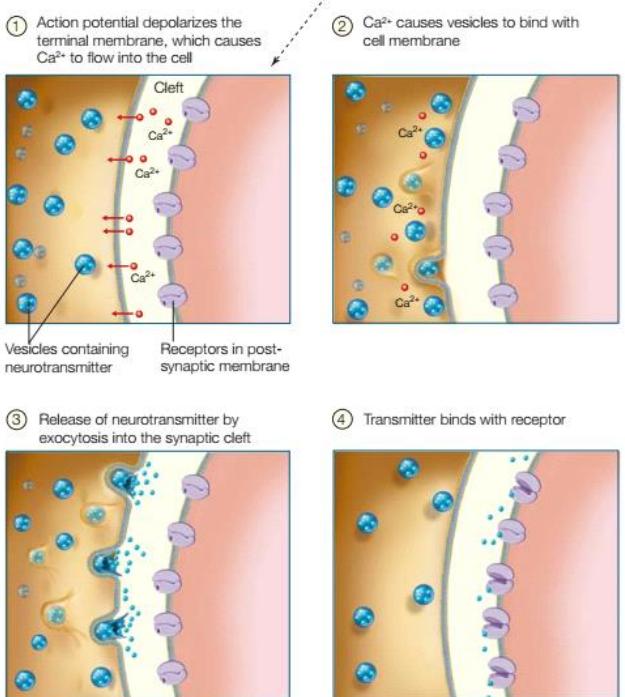
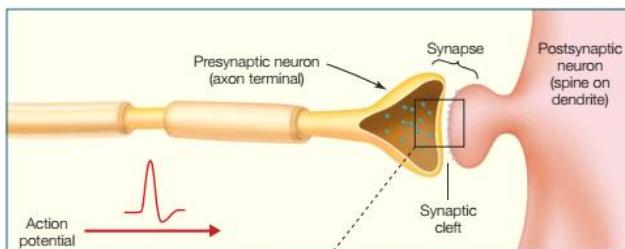


FIGURE 2.12 Neurotransmitter release at the synapse, into synaptic cleft.
The synapse consists of various specializations where the presynaptic and postsynaptic membranes are in close apposition. When the action potential invades the axon terminals, it causes voltage-gated Ca^{2+} channels to open (1), which triggers vesicles to bind to the presynaptic membrane (2). Neurotransmitter is released into the synaptic cleft by exocytosis and diffuses across the cleft (3). Binding of the neurotransmitter to receptor molecules in the postsynaptic membrane completes the process of transmission (4).

The Role of Glial Cells

- An astrocyte is a type of glial cell that helps form the blood-brain barrier.
- Astrocytes have an active role in modulating neural activity.
- Glial cells aid in the speed of information transfer by forming myelin around the axons of the neurons.
- An oligodendrocyte is a type of glial cell that forms myelin in the central nervous system.
- A Schwann cell is a type of glial cell that forms myelin in the peripheral nervous system.
- As part of the immune response of the nervous system, microglial cells are phagocytic cells that engulf damaged cells.

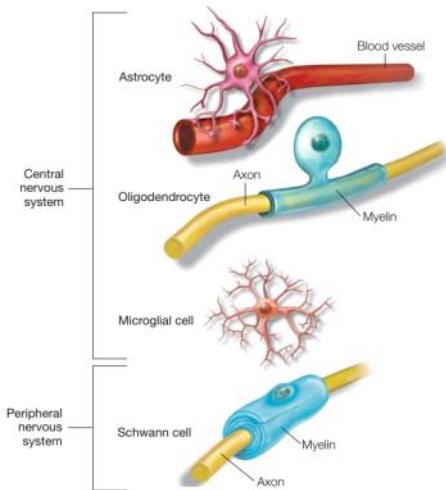


FIGURE 2.15 Various types of glial cells in the mammalian central and peripheral nervous systems.

An astrocyte is shown with end feet attached to a blood vessel. Oligodendrocytes and Schwann cells produce myelin around the axons of neurons—oligodendrocytes in the central nervous system, and Schwann cells in the peripheral nervous system. A microglial cell is also shown.

The Bigger Picture

Overview of Nervous system

- The central nervous system consists of the brain and spinal cord. The peripheral nervous system consists of all nerves and neurons outside of the central nervous system
- The autonomic nervous system is involved in controlling the action of smooth muscles, the heart, and various glands. It includes the sympathetic and parasympathetic systems.
 - o The sympathetic system uses the neurotransmitter norepinephrine. This system increases heart rate, diverts blood from the digestive tract to the somatic musculature, and prepares the body for fight-or-flight responses by stimulating the adrenal glands.
 - o The parasympathetic system uses acetylcholine as a neurotransmitter. It is responsible for decreasing heart rate and stimulating digestion.

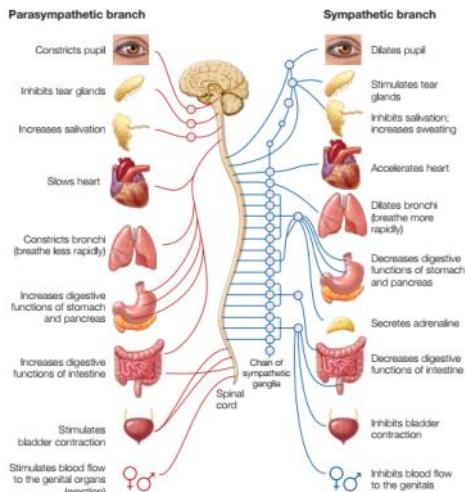
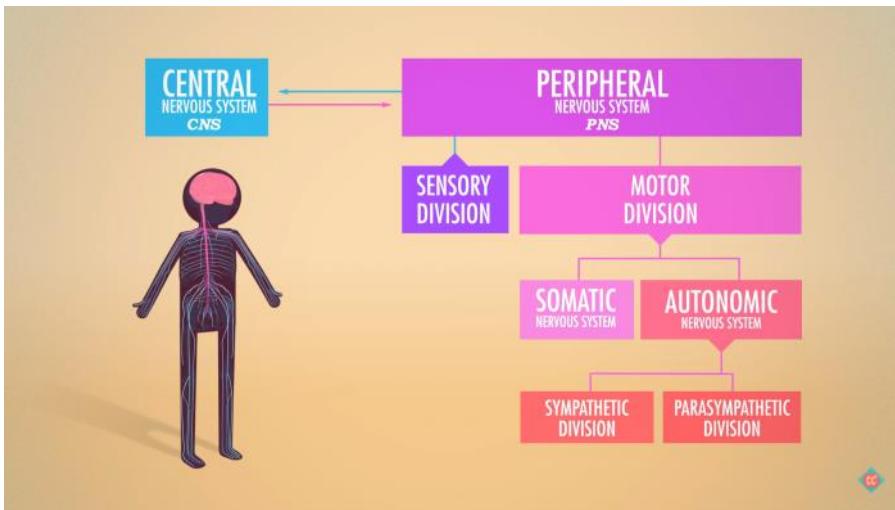


FIGURE 2.17 Organization of the autonomic nervous system, showing sympathetic and parasympathetic branches.
Please see the text for details.

- Groups of neurons are called ganglia. [nuclei in CNS - Ganglia in PNS](#)
- The cerebral cortex is a continuous sheet of layered neurons in each hemisphere.
- The axons of cortical neurons and subcortical ganglia travel together in white matter tracts that interconnect neurons in different parts of the brain and spinal cord.
- The corpus callosum is the main fiber tract that connects the two hemispheres of the brain



A Guided Tour of the brain

- Spinal cord:

- The spinal cord conducts the final motor signals to the muscles, and it relays sensory information from the body's peripheral receptors to the brain.

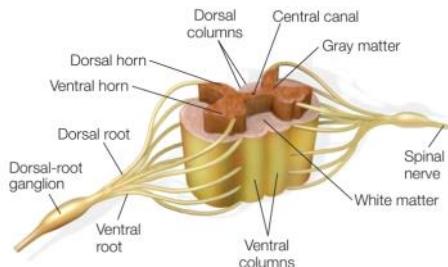
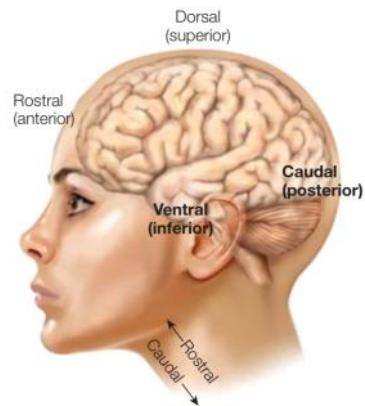


FIGURE 2.19 Gross anatomy of the spinal cord.

This cross-sectional and three-dimensional representation of the spinal cord shows the central butterfly-shaped gray matter, which contains neuronal cell bodies, and the surrounding white matter axon tracts, which convey information down the spinal cord from the brain to the peripheral neurons and up the spinal cord from peripheral receptors to the brain. The dorsal and ventral nerve roots are shown exiting and entering the cord; they fuse to form peripheral nerves. The cell bodies of peripheral sensory inputs reside in the dorsal-root ganglion and project their axons into the central nervous system via the dorsal root. The ventral horn of the spinal cord houses motor neurons that project their axons out the ventral roots to innervate peripheral muscles.

- Ventricle:



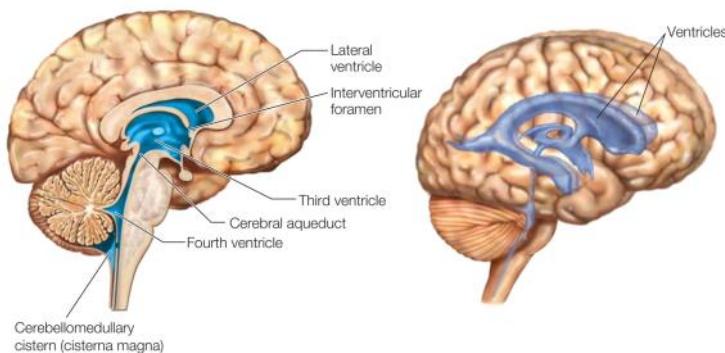


FIGURE 1 Ventricles of the human brain.
 (left) Midsagittal section showing the medial surface of the left hemisphere. (right) Transparent brain showing the ventricular system in 3D view.

The brainstem:

- We usually think of the brainstem as having three main parts: the medulla (myelencephalon), the pons and cerebellum (metencephalon), and the midbrain (mesencephalon).
- The brainstem's neurons carry out many sensory and motor processes, including visuomotor, auditory, and vestibular functions as well as sensation and motor control of the face, mouth, throat, respiratory system, and heart.
- The brainstem houses fibers that pass from the cortex to the spinal cord and cerebellum, and sensory fibers that run from spinal levels to the thalamus and then to the cortex
- Many neurochemical systems have nuclei in the brainstem that project widely to the cerebral cortex, limbic system, thalamus, and hypothalamus.
- The cerebellum integrates information about the body and motor commands and modifies motor outflow to effect smooth, coordinated movements.

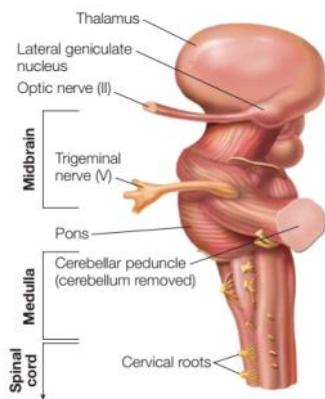


FIGURE 2.21 Lateral view of the brainstem showing the thalamus, pons, medulla, midbrain, and spinal cord.
 Anterior in the brain is at the top, and the spinal cord is toward the bottom in this left lateral view. The cerebellum is removed in this drawing.

The Diencephalon: Thalamus and Hypothalamus

- After leaving the brainstem, we arrive at the diencephalon, which is made up of the thalamus and hypothalamus. These subcortical structures are composed of groups of nuclei with interconnections to widespread brain areas.
- The thalamus is the relay station for almost all sensory information.
- The hypothalamus is important for the autonomic nervous system and endocrine system. It controls functions necessary for the maintenance of homeostasis. It is also involved in control of the pituitary gland.
- The pituitary gland releases hormones into the bloodstream where they can circulate to influence other tissues and organs (e.g., gonads).

The Telencephalon: Limbic System, Basal Ganglia, and Cerebral Cortex

- The limbic system includes subcortical and cortical structures that are interconnected and play a role in emotion.
- The basal ganglia are involved in a variety of crucial brain functions, including action selection, action gating, reward-based learning, motor preparation, timing, task switching, and more.
- **The Cerebral Cortex**

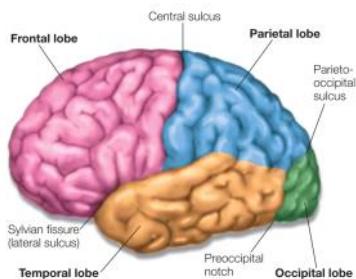


FIGURE 2.30 The four lobes of the cerebral cortex.
This is a lateral view of the left hemisphere showing the four major lobes of the brain, and some of the major landmarks that separate them.

- Gyri are the protruding areas seen on the surface of the cortex; sulci, or fissures, are the enfolded regions of cortex
- Brodmann divided the brain into distinct regions based on the underlying cytoarchitectonics.
- The lobes of the brain include the frontal, parietal, temporal, and occipital lobes.
 - o The frontal lobe is for planning, cognitive control, and execution of movements.
 - o The parietal lobe receives sensory input about touch, pain, temperature, and limb position, and it is involved in coding space and coordinating actions.
 - o The temporal lobe contains auditory, visual, and multimodal processing areas.
 - o The occipital lobe processes visual information.
 - o (The limbic lobe (not really a lobe) is involved in emotional processing, learning, and memory.)
- Topography is the principle that the anatomical organization of the body is reflected in the cortical representation of the body, both in the sensory cortex and motor cortex.
- Association cortices are those regions of cortex outside the sensory specific and motor cortical regions. Association cortex receives and integrates input from multiple sensory modalities.

Development of the Nervous system

- The nervous system develops from the ectoderm, which forms a neural plate. The neural plate becomes the neural groove and eventually the neural tube.
- Neuronal proliferation is the process of cell division in the developing embryo and fetus. It is responsible for populating the nervous system with neurons.
- Neurons and glial cells are formed from precursor cells. After mitosis, these cells migrate along the radial glial cells to the developing cortex.
- The type of cell that is made (e.g., a stellate or pyramidal cell) appears to be based on when the cell is born (genesis) rather than when it begins to migrate.
- The radial unit hypothesis states that the columnar organization in the adult cortex is derived during development from cells that divide in the ventricular region.
- A belief strongly held by most neuroscientists was that the adult brain produces no new neurons. We now know that this is not the case; new neurons form throughout life in certain brain regions.
- Synaptogenesis is the birth of new synapses; neurogenesis is the birth of new neurons.

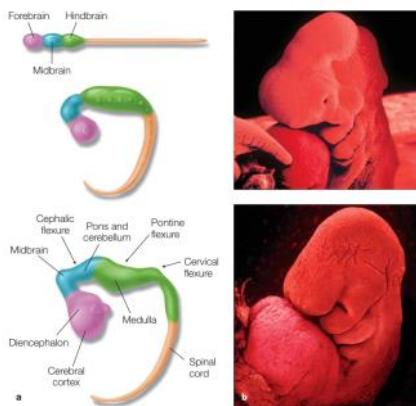
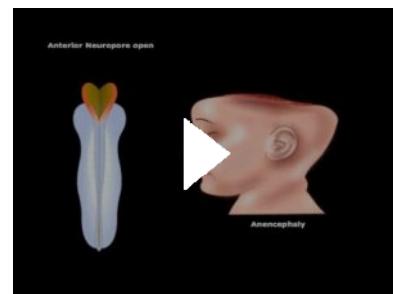


FIGURE 2.39 Early stages of embryonic development in mammals.
(a) Developing embryo. The embryo goes through a series of folds, or flexures, during development. These alterations in the gross structure of the nervous system give rise to the compact organization of the adult brain and brainstem in which the cerebral cortex overlays the diencephalon and midbrain within the human skull. (b) There is significant similarity between the gross features of the developing fetuses of mammals, as shown by this comparison of a human fetus (top) and pig fetus (bottom).

[Embryology of the CNS \(Easy to Understand\)](#)



[USMLE® Step 1: Neuroscience: Development of CNS Animation](#)



Neurons	Neurons are the basic signaling units that transmit information throughout the nervous system.
Glial cells	Glial cells are nonneuronal cells that serve various functions in the nervous system, some of which are only now being elucidated: Provide support, nutrition, insulation, and helps signal transmission in the nervous system

Dendrites	Dendrites are branching extensions of the neuron that receive inputs from other neurons
Spines	spines, little knobs attached by small necks to the surface of the dendrites, where the dendrites receive inputs from other neurons
Axon	axon is a single process that extends from the cell body. This structure represents the output side of the neuron
Synapse	Transmission occurs at the synapse , a specialized structure where two neurons come into close contact so that chemical or electrical signals can be passed from one cell to the next.
axon collaterals	Some axons branch to form axon collaterals that can transmit signals to more than one cell
Myelin	Many axons are wrapped in layers of a fat substance called myelin
nodes of Ranvier	Along the length of the axons, there are evenly spaced gaps in the myelin. These gaps are commonly referred to as the nodes of Ranvier
Presynaptic and postsynaptic	Neurons are presynaptic when their axon makes a connection onto other neurons, and postsynaptic when other neurons make a connection onto their dendrites.
Ion channels	Ion channels are proteins with a pore through their centers, and they allow certain ions to flow down their concentration gradients.
Ion pumps	Ion pumps use energy to actively transport ions across the membrane against their concentration gradients, that is, from regions of low concentration to regions of higher concentration.
electrochemical gradient	Difference in electrical value inside and outside the membrane
electrotonic conduction	Passive current conduction is called electrotonic conduction or <i>decremental conduction</i>
Action potential	This regenerative process is an active membrane mechanism known as the action potential . An action potential is a rapid depolarization and repolarization of a small region of the membrane caused by the opening and closing of ion channels.
Voltage-gated ion channels	The action potential is able to regenerate itself due to the presence of voltage-gated ion channels located in the neuronal membrane (Figure 2.11a, inset). These are found at the spike-triggering zone in the axon hillock and along the axon. They open and close in response to changes in the membrane potential
Threshold	We refer to this depolarized membrane potential value as the threshold for initiating an action potential
equilibrium potential	The equilibrium potential is the particular voltage at which there is no net flux of ions
Hyper depolarization	the membrane potential is even farther from the threshold required for triggering an action potential (e.g., around - 80 mV)
Absolute refractory period.	During this transient hyperpolarization state, the voltage-gated Na+ channels are unable to open, and another action potential cannot be generated. This is known as the absolute refractory period .
relative refractory period	<i>Absolute refractory period</i> is followed by the <i>relative refractory period</i> , during which the neuron can generate action potentials, but only with larger-than-normal depolarizing currents
Vesicles	a small structure within a cell, or extracellular, consisting of fluid enclosed by a lipid bilayer
Astrocytes	Astrocytes are large glial cells with round or radially symmetrical forms; they surround neurons and are in close contact with the brain's vasculature.
Blood brain barrier	The astrocytes create a barrier, called the blood-brain barrier (BBB) , between the tissues of the central nervous system and the blood
Microglial cells	Microglial cells , which are small and irregularly shaped (Figure 2.15), come into play when tissue is damaged. They are phagocytes, literally devouring and removing damaged cells
oligodendrocytes	In the central nervous system, oligodendrocytes form myelin; in the peripheral nervous system, Schwann cells carry out this task
Schwann cells	In the central nervous system, oligodendrocytes form myelin; in the peripheral nervous system, Schwann cells carry out this task
Central Nerves system	CNS can be thought of as the command-and-control center of the nervous system
Peripheral nerves system	The PNS represents a courier network that delivers sensory information to the CNS and carries the motor commands from the CNS to the muscles.
The autonomic nerves system	The autonomic nervous system (also called the autonomic, or visceral, motor system) is involved in controlling the involuntary action of smooth muscles, the heart, and various glands.
Brainstem	Consists of three parts: the medulla (myelencephalon), the pons and cerebellum (metencephalon), and the midbrain (mesencephalon). These three sections form the central nervous system between the spinal cord and the diencephalon. It contains groups of motor and sensory nuclei, nuclei of widespread modulatory neurotransmitter systems, and white matter tracts of ascending sensory information and descending motor signals
Medulla	The brainstem's most caudal portion is the medulla, which is continuous with the spinal cord (Figure 2.21). The medulla is essential for life. It houses the cell bodies of many of the 12 cranial nerves, providing sensory and motor innervations to the face, neck, abdomen, and throat (including taste) as well as the motor nuclei that innervate the heart. The medulla controls

	vital functions such as respiration, heart rate, and arousal.
Pons	Te pons, Latin for “bridge,” is so named because it is the main connection between the brain and the cerebellum. Many of the cranial nerves synapse in the pons. The pons is important for some eye movements as well as those of the face and mouth
Cerebellum	Te cerebellum (literally, “small cerebrum” or “little brain”), which clings to the brainstem at the level of the pons, is home to most of the brain’s neurons. Te cerebellum is critical for maintaining posture, walking, and performing coordinated movements. It does not directly control movements; instead, it integrates information about the body, such as its size and speed, with motor commands
Midbrain	midbrain, lies superior to the pons and can be seen only in a medial view. The midbrain also contains some of the cranial nerve ganglia and to other important structures: the superior and inferior colliculi (Figure 2.23). Te superior colliculus plays a role in perceiving objects in the periphery and orienting our gaze directly toward them, bringing them into sharper view. Te inferior colliculus is used for locating and orienting toward auditory stimuli
Thalamus	Thalamus Almost smack dab in the center of the brain and perched on top of the brainstem. Te thalamus has been referred to as the “gateway to the cortex” because, except for some olfactory inputs, all of the sensory modalities make synaptic relays in the thalamus before continuing to the primary cortical sensory receiving areas (Figure 2.24). Te thalamus is involved in relaying primary sensory information
Hypothalamus	Hypothalamus Te main link between the nervous system and the endocrine system is the hypothalamus, which is the main site for hormone production and control. Te hypothalamus controls the functions necessary for maintaining the normal state of the body (homeostasis). It sends out signals that drive behavior to alleviate such feelings as thirst, hunger, and fatigue, and it controls body temperature and circadian cycles.
The pituitary gland	The pituitary gland releases hormones into the bloodstream where they can circulate to influence other tissues and organs (e.g., gonads).
Hippocampus	hippocampus, an area located on the ventromedial aspect of the temporal lobe.
Limbic system	Limbic System Te “classical” limbic lobe (Figure 2.26) is made up of the cingulate gyrus (a band of cerebral cortex that extends above the corpus callosum in the anterior–posterior direction and spans both the frontal and parietal lobes), the hypothalamus, anterior thalamic nuclei, and the hippocampus
Amygdala	amygdala, a group of neurons anterior to the hippocampus, along with the orbitofrontal cortex and parts of the basal ganglia
Basal ganglia	Basal Ganglia Te basal ganglia are a collection of nuclei bilaterally located deep in the brain beneath the anterior portion of the lateral ventricles, near the thalamus. One summary of basal ganglia function proposes that it combines an organism’s sensory and motor context with reward information and passes this integrated information to the motor and prefrontal cortex for a decision
Sulci	Te infoldings of the cortical sheet
gyri	the crowns of the folded tissue that one observes when viewing the surface
Central sulcus	The central sulcus divides the frontal lobe from the parietal lobe
Sylvian fissure	Sylvian (lateral) fissure separates the temporal lobe from the frontal and parietal lobes
Insula	Hidden from the lateral surface view are other parts of the cerebrum, not all of which are conveniently contained in the four lobes e.g. the insula, which is located between the temporal and frontal lobe, and is, as its name implies, an island of folded cortex hidden deep in the lateral sulcus.
Prefrontal cortex	Te more anterior regions of the frontal lobe, the prefrontal cortex, take part in the more complex aspects of planning, organizing, and executing behavior—tasks that require the integration of information over time
Topography	Te spatial relationships of the body are fairly well preserved in the map of neural representations draped across these cortices, by using a principle known as topography
Somatotopy	mapping of specific parts of the body to areas of the cortex
Neocortex	neocortex: cortex that contains six cortical layers or that passed through a developmental stage involving six cortical layers
Cytoarchitectonics	Cytoarchitectonics uses the microanatomy of cells and their organization to subdivide the cortex
Association cortex	Te portion of the neocortex that is neither sensory nor motor cortex has traditionally been termed the association cortex.
synaptogenesis	synaptogenesis is the formation of synapses
Synapse elimination	Synapse elimination is a means by which the nervous system fine-tunes neural connectivity, presumably eliminating the interconnections between neurons that are redundant, unused, or do not remain functional.

Lecture 30/1

Tuesday, January 30, 2018 9:22 AM

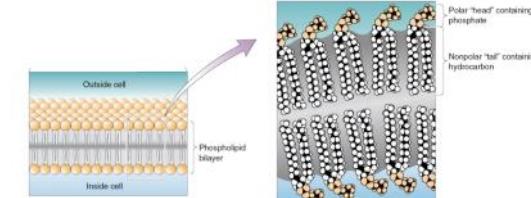
The structure of neuron:

The structure of the neuron:

- The soma includes
 - o **Cytosol**: watery fluid inside the cell
 - o **Organelles**: membrane enclosed structures within the soma
 - **Mitochondria**: generate most of the cell's supply of **adenosine triphosphate** (ATP, chemical energy) - part of the Krebs cycle (complicated cycle, main point: a single cell is a complex)
 - o **Cytoplasm**: contents within a cell membrane (e.g., organelles, excluding the nucleus)
 - Critical for polarity and receptors
- **The neural membrane**: Important to maintain electrical and chemical gradings --> important to life
 - o Structure of discrete membrane regions influences neuronal function
 - o The layer is phospholipid bi-layered

The phospholipid bi-layered membrane

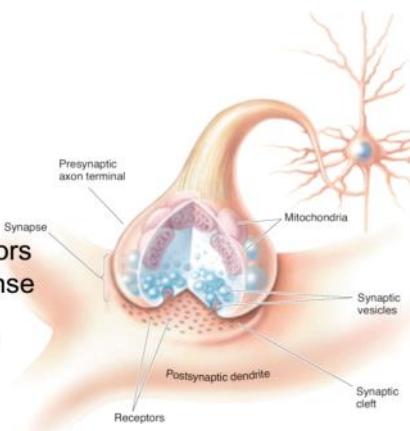
- **Hydrophilic compounds**
 - Dissolve in water due to uneven electrical charge (e.g., salt)
- **Hydrophobic compounds**
 - Do not dissolve in water due to even electrical charge (e.g., oil)
- **Lipids are hydrophobic (i.e. insulating).**
 - Contribute to resting and action potentials



- o The concentration of different ions differ across the membrane
 - The passive:
 - The membrane is more prone to allow access for some ions than others (**selective permeability**)
 - The diffusion and the electrical potential compete, since the ions are differently charged
 - The active **takes up energy**:
 - The electrical potential causes the sodium-potassium pumps to open
- o **Action potential**:
 - Difference in difference that move along the axons.
 - **Due to refractory period: Only move one way**
 - Even though the stimulation is in level, the outcome will be a number of spikes due to threshold.
 - The rate of firing determines the magnitude of the depolarisation.
- o This is a chemical neural transmission, but there is also electrical
- The chemical synaptic transmission:

Overview of Chemical Synaptic Transmission

- Neurotransmitter synthesis
 - Load neurotransmitter into synaptic vesicles
 - Vesicles fuse to presynaptic terminal
 - Neurotransmitter spills into synaptic cleft
 - Binds to postsynaptic receptors
 - Biochemical/electrical response elicited in postsynaptic cell
 - Removal of neurotransmitter from synaptic cleft
- **Neurotransmitters: Many types, some are specific to areas, some are common across areas**
 - o **Types of neurotransmitters**



- Amino acids: small organic molecules—vesicles
 - o Amines: small organic molecules—vesicles
- Peptides: short amino acid chains (proteins)—secretory granules
- Information is both between and inside neurons.

Lecture 6/2

Tuesday, February 6, 2018 8:18 AM



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Methods of Cognitive Science

Monday, February 5, 2018 8:10 PM

Cognitive Psychology and Behavioral Methods

- Cognitive psychology focuses on understanding how objects or ideas are represented in the brain and how these representations are manipulated.
- Two key concepts underlie the cognitive approach:
 1. Information processing depends on internal representations.
 2. These mental representations undergo transformations
- Fundamental goals of cognitive psychology include identifying the mental operations that are required to perform cognitive tasks and exploring the limitations in task performance

Studying the Damaged Brain

- Brain lesions, either naturally occurring (in humans) or experimentally derived (in animals), allow experimenters to test hypotheses concerning the functional role of the damaged brain region.
- Cerebral vascular accidents, or strokes, occur when blood flow to the brain is suddenly disrupted. Angiography is used to evaluate the circulatory system in the brain.
- Tumors can cause neurological symptoms either by damaging neural tissue or by producing abnormal pressure on spared cortex and cutting off its blood supply.
- Degenerative disorders include Huntington's disease, Parkinson's disease, Alzheimer's disease, and AIDS-related dementia.
- Neurological trauma can result in damage at the site of the blow (coup) or at the site opposite the blow because of reactive forces (countercoup). Certain brain regions such as the orbitofrontal cortex are especially prone to damage from trauma.
- Epilepsy is characterized by excessive and abnormally patterned activity in the brain.
- Research involving patients with neurological disorders is used to examine structure-function relationships.
 - o Single and double dissociations can provide evidence that damage to a particular brain region may result in a selective deficit of a certain cognitive operation.
- Surgical procedures have been used to treat neurological disorders such as epilepsy or Parkinson's disease. Studies conducted in patients before and after surgery have provided unique opportunities to study brain behavior relationships

Methods to Perturb (forstyrre) Neural Function

- Brain function can be perturbed by drugs, magnetic or electrical stimulation, and through genetic manipulations.
- A major drawback of drug studies, in which the drug is injected into the bloodstream, is the lack of specificity.
- Transcranial magnetic stimulation (TMS) uses magnetic pulses to transiently alter local brain physiology.
- Gene knockout technology allows scientists to explore the consequences of the lack of expression of a specific gene in order to determine its role in behavior.

Structural Analysis of the Brain

- Computed tomography (CT or CAT) uses X-rays to image the 3-D structure of the brain.
- Magnetic resonance imaging (MRI) exploits the magnetic properties of the organic tissue of the brain to image its structure. The spatial resolution of MRI is superior to CT.
- Diffusion tensor imaging (DTI), performed with magnetic resonance scanners, is used to measure white matter pathways in the brain and thus can offer information about anatomical connectivity between regions

Methods for the Study of Neural Function

- Single-cell recording allows neurophysiologists to record from individual neurons in the animal brain in order to understand how increases and decreases in the activity of neurons correlate with

- stimulation of one of the senses or behavior.
- With multiunit recording, the activity of hundreds of cells can be recorded at the same time.
 - Electroencephalography (EEG) measures the electrical activity of the brain. The EEG signal includes endogenous changes in electrical activity as well as changes triggered by specific events (e.g., stimuli or movements).
 - An event-related potential (ERP) is a change in electrical activity that is time-locked to specific events, such as the presentation of a stimulus or the onset of a response. When the events are repeated many times, the relatively small changes in neural activity triggered by these events can be observed by averaging of the EEG signals. In this manner, the background fluctuations in the EEG signal are removed, revealing the event-related signal with great temporal resolution.
 - Electrocortogram (ECoG) is similar to an EEG, except that the electrodes are placed directly on the surface of the brain.
 - Magnetoencephalography (MEG) measures the magnetic signals generated by the brain. The electrical activity of neurons also produces small magnetic fields, which can be measured by sensitive magnetic detectors placed along the scalp. MEG can be used in an event-related manner similar to ERPs, with similar temporal resolution. The spatial resolution can be superior because magnetic signals are minimally distorted by organic tissue such as the brain or skull

The Marriage of Function and Structure: Neuroimaging

- Positron emission tomography (PET) measures metabolic activity in the brain by monitoring the distribution of a radioactive tracer. The PET scanner measures the photons that are produced during decay of the tracer. A popular tracer is ^{15}O because it decays rapidly and the distribution of oxygen increases to neural regions that are active.
- Pittsburgh Compound B (PiB) is a tracer that binds to beta-amyloid and is used as an *in vivo* assay of the presence of this biomarker for Alzheimer's disease.
- Functional magnetic resonance imaging (fMRI) uses MRI to measure changes in the oxygen content of the blood (hemodynamic response). These changes are assumed to be correlated with local changes in neuronal activity.

Brain Graphs

- A brain graph is a visual model of brain organization, and can be defined either with structural or functional data. Because it can be constructed from data obtained through different types of neuroimaging methods, a brain graph is a valuable way to compare results from experiments using different methods

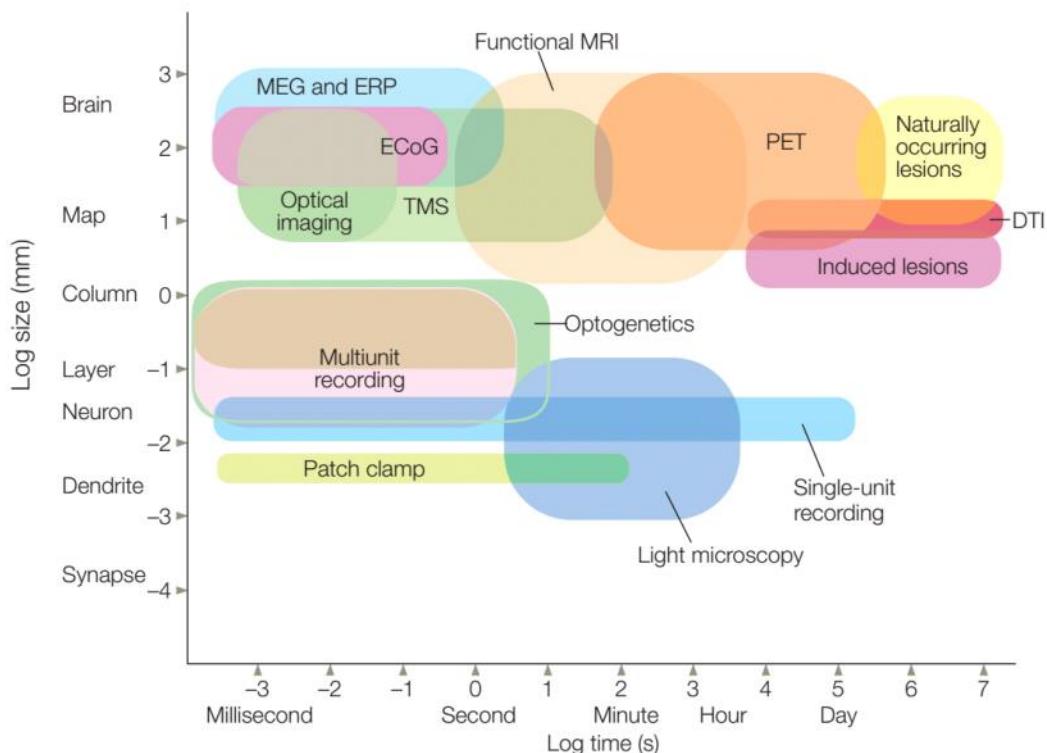
Computer Modeling

- Computer models are used to simulate neural networks in order to ask questions about cognitive processes and generate predictions that can be tested in future research

the point of Braatenberg's example is not to model a behavior; rather, it represents how a single computational change—from crossed to uncrossed wiring—can yield a major behavioral change.

Converging Methods

- Powerful insights into the structural and functional underpinnings of cognitive behavior can be gained from experiments that combine methods such as genetic, behavioral, and neuroimaging techniques



angiography (p. 79)	Angiography is a clinical imaging method used to evaluate the circulatory system in the brain and diagnose disruptions in circulation
block design experiment (p. 108)	In a block design experiment, the recorded neural activity is integrated over a “block” of time during which the participant either is presented a stimulus or performs a task.
blood oxygen level-dependent (BOLD) (p. 107)	The fMRI detectors measure the ratio of oxygenated to deoxygenated hemoglobin; this value is referred to as the blood oxygen level-dependent, or BOLD, effect
brain graph (p. 110)	A brain graph is a visual model of the connections within some part of the nervous system.
brain lesion (p. 79)	Structural damage to the white or gray matter of the brain. Lesions result from many causes, including tumor, stroke, and degenerative disorders such as Alzheimer’s disease.
cerebral vascular accident (79)	Strokes, which occur when blood flow to the brain is suddenly disrupted.
cognitive psychology (p. 74)	The study of mental activity as an information-processing problem
computed tomography (CT, CAT) (p. 91)	An noninvasive neuroimaging method that provides images of internal structures such as the brain. CT is an advanced version of the conventional X-ray. Whereas conventional X-rays compress three-dimensional objects into two dimensions, CT allows for the reconstruction of three-dimensional space from the compressed two-dimensional images through computer algorithms
deep-brain stimulation (DBS) (p. 86)	A method for treating parkinson, where electrodes are implanted in the basal ganglia and stimulate the neural activity.

degenerative disorder (p. 80)	Disorders or diseases, either genetic or environmental, in which the function or structure of the affected tissues will continue to deteriorate over time
diffusion tensor imaging (DTI) (p. 93)	A variant of traditional MRI scanners is now used to study the anatomical structure of the axon tracts that form the brain's white matter; that is, it can offer information about anatomical connectivity between regions. This method, called diffusion tensor imaging (DTI), is performed with an MRI scanner that measures the density
double dissociation (p. 84)	A double dissociation identifies whether two cognitive functions are independent of each other, something that a single association cannot do
electrocortogram (ECOG) (p. 102)	An electrocortogram (ECOG) is similar to an EEG, except that the electrodes are placed directly on the surface of the brain, either outside the dura or beneath it. Thus, ECOG is appropriate only for people who are undergoing neurosurgical treatment.
electroencephalography (EEG) (p. 99)	When populations of neurons are active together, they produce electrical potentials large enough to be measured by non-invasive electrodes that have been placed on the scalp,
Epilepsy	Epilepsy is a condition characterized by excessive and abnormally patterned activity in the brain.
event-related design (p. 108)	Event related refers to the fact that, across experimental trials, the BOLD response will be linked to specific events such as the presentation of a stimulus or the onset of a movement
event-related potential (ERP) (p. 100)	ERP graphs show the average of EEG waves time-locked to specific events such as the onset of a stimulus or response. EEG traces recorded from a series of trials are averaged together by aligning them relative to an external event, such as the onset of a stimulus or response. This alignment eliminates variations in the brain's electrical activity that are unrelated to the events of interest. The evoked response, or event-related potential (ERP), is a tiny signal embedded in the ongoing EEG that was triggered by the stimulus. By averaging the traces, investigators can extract this signal, which reflects neural activity that is specifically related to the sensory, motor, or cognitive event that evoked it—hence the name event-related potential (Figure 3.24)
functional magnetic resonance imaging (fMRI) (p. 105)	A neuroimaging method that utilizes MRI to track blood flow changes in the brain that are thought to be correlated with local changes in neuronal activity
knockout procedure (p. 90)	A key methodology is to develop genetically altered animals, using what are referred to as knockout procedures. The term knockout comes from the fact that specific genes have been manipulated so that they are no longer present or expressed.
magnetic resonance imaging (MRI) (p. 92)	A measure of the magnetic signals generated by the brain. The electrical activity of neurons also produces small magnetic fields, which can be measured by sensitive magnetic detectors placed along the scalp, similar to the way EEG measures the surface electrical activity. MEG can be used in an event-related manner similar to ERP studies, with similar temporal resolution. The spatial resolution, in theory, can be superior with MEG because magnetic signals are minimally distorted by organic tissue such as the brain or skull
magnetoencephalography (MEG) (p. 102)	As with EEG, MEG traces can be recorded and averaged over a series of trials to obtain event-related fields (ERFs). MEG provides the same temporal resolution as with ERPs, but it can be used more reliably to localize the source of the signal. Unlike electrical signals, magnetic fields are not distorted as they pass through the brain, skull, and scalp

multiunit recording (p. 97)	Techniques that allow recordings to be made in many neurons simultaneously
neural network (p. 113)	An alternative architecture that figures prominently in cognitive neuroscience is the neural network. In neural networks, processing is distributed over units whose inputs and outputs represent specific features. For example, they may indicate whether a stimulus contains a visual feature, such as a vertical or a horizontal line.
neurophysiology (p. 95)	The study of the physiological processes of the nervous system. Neural activity is characterized by physiological changes that can be described both electrically and chemically. These changes can be observed at many different levels, ranging from the gross changes recorded with EEG, to the firing of individual neurons, to the molecular changes that occur at the synapse
optogenetics (p. 72)	The method used to make neurons light sensitive. If a neuron afterwards is exposed to light, it will fire.
pharmacological studies (p. 87)	Experimental method in which the independent variable involves the administration of a chemical agent or drug. An example would be when people are given drugs that act as dopamine agonists and observations are made on their performance in decision-making tasks.
PiB (p. 106)	A radioactive compound that is used as a tracer in PET studies to label beta-amyloid, a substance that is associated with Alzheimer's Disease. The discovery of PiB provided an important biomarker for identifying people at risk for developing this disease
positron emission tomography (PET) (p. 105)	A neuroimaging method that measures metabolic activity or blood flow changes in the brain by monitoring the distribution of a radioactive tracer. The PET scanner measures the photons that are produced during the decay of a tracer
receptive field (p. 96)	The area of external space within which a stimulus must be presented in order to activate a cell. In vision, topographic representations are referred to as retinotopic. For example, cells in the visual cortex respond to stimuli that appear within a restricted region of space. In addition to spatial position, the cells may be selective to other stimulus features, such as color or shape. Cells in the auditory cortex also have receptive fields. The cell's firing rate increases when the sound comes from the region of space that defines its receptive field
regional cerebral blood flow (rCBF) (p. 106)	The distribution of the brain's blood supply, which can be measured with various imaging techniques. In PET scanning, rCBF is used as a measure of metabolic changes following increased neural activity in restricted regions of the brain.
retinotopic (p. 97)	Referring to a topographic map of visual space across a restricted region of the brain. Activation across the retina is determined by the reflectance of light from the environment. A retinotopic map in the brain is a representation in which some sort of orderly spatial relationship is maintained. Multiple retinotopic maps have been identified in the cortex and subcortex
simulation (p. 111)	A simulation is an imitation, a reproduction of behavior in an alternative medium
Single dissociation	A method used to develop functional models of mental and/or neural processes. Evidence of a single dissociation requires a minimum of two groups and two tasks. A single dissociation is present when the groups differ in their performance on one task but not the other. Single dissociations provide weak evidence of functional specialization since it is possible that the two tasks differ in terms of their sensitivity to detect group differences
Tumor	A tumor, or neoplasm, is a mass of tissue that grows abnormally and has no physiological function.
Transcranial	A noninvasive method in which a low voltage electrical current is created across the

direct current stimulation (tDCS)	brain by applying electrodes to the scalp. tDCS is hypothesized to potentiate neurons near the anodal electrode and hyperpolarize neurons near the cathodal electrode, making it less likely that the neurons fire
Transcranial magnetic stimulation	Transcranial magnetic stimulation (TMS) offers a method to noninvasively produce focal stimulation of the human brain. The TMS device consists of a tightly wrapped wire coil, encased in an insulated sheath and connected to a source of powerful electrical capacitors. Triggering the capacitors sends a large electrical current through the coil, generating a magnetic field. When the coil is placed on the surface of the skull, the magnetic field passes through the skin and scalp and induces a physiological current that causes neurons to fire.
Traumatic brain injury	Traumatic brain injury (TBI) can result from either a closed or an open head injury. In closed head injuries, the skull remains intact, but mechanical forces generated by a blow to the head damage the brain. Open head injuries happen when an object like a bullet or shrapnel penetrates the skull. With these injuries, the penetrating object may directly damage brain tissue, and the impact of the object can also create reactive forces producing coup and contrecoup. Common cause is car accident etc.
Vascular disorders	Vascular disease is a class of diseases of the blood vessels – the arteries and veins of the circulatory system of the body.
Voxels	The smallest unit of three-dimensional data that can be represented in an MRI.

Lecture 13/2

Tuesday, February 13, 2018 8:14 PM



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Hemispheric Specialization

Wednesday, February 14, 2018 11:09 AM

Anatomy of the Hemispheres

- The Wada test is used to identify which hemisphere is responsible for language before brain surgery is performed.
- The two halves of the cerebral cortex are connected primarily by the corpus callosum, which is the largest fiber system in the brain. In humans, this bundle of white matter includes more than 250 million axons.
- Two smaller bands of fibers, the anterior and posterior commissures, also connect the two hemispheres.
- The corpus callosum has both homotopic and heterotopic connections. Homotopic fibers connect the corresponding regions of each hemisphere (e.g., V1 on the right to V1 on the left), whereas heterotopic fibers connect different areas (e.g., V1 on the right to V2 on the left).
- Differences in neural connectivity and organization may underlie many of the gross asymmetries between the hemispheres.
- Ninety-six percent of humans, regardless of which hand is dominant, have a left-hemisphere specialization for language.
- The planum temporale encompasses Wernicke's area and is involved in language. The asymmetry of the planum temporale is one of the few examples in which an anatomical index is correlated with a well-defined functional asymmetry.
- Differences have been found in the specifics of cortical microcircuitry between the two hemispheres in both anterior (Broca's) and posterior (Wernicke's) language-associated cortex.

Wada test has consistently revealed a strong bias for language lateralization to the left hemisphere, because when the injection is to the left side, the patient's ability to speak or comprehend speech is disrupted for several minutes.

corpus callosum is divided on a macroscopic level into the anterior portion, called the genu, the middle portion, known as the body, and the posterior portion, called the splenium (Figure 4.7). The neuronal fiber sizes vary across the corpus callosum: Smaller fibers (~0.4 mm) are located anteriorly, gradually grading to larger fibers (5 mm) located more posteriorly

planum temporale, the cortical area at the center of Wernicke's area (involved with the understanding of written and spoken language), was larger in the left hemisphere—a pattern found in 65% of brains.

Splitting the Brain: Cortical Disconnection

- In some of the original animal studies on callosotomies, Myers and Sperry demonstrated that visual discrimination learned by one hemisphere did not transfer to the other hemisphere when the hemispheres were disconnected.
- The splenium is the most posterior portion of the corpus callosum. When the posterior half of the callosum is sectioned in humans, transfer of visual, tactile, and auditory sensory information is severely disrupted. The anterior part of the callosum is involved in the higher order transfer of semantic information.

Hemispheric Specialization

- The left hemisphere is dominant for language, speech, and major problem solving; the right hemisphere appears specialized for visuospatial tasks such as drawing cubes and other three-dimensional patterns. Thus, split-brain patients cannot name or describe visual and tactile stimuli presented to the right hemisphere, because the sensory information is disconnected from the dominant left (speech) hemisphere.
- There may be two lexicons (associations of words with specific meanings), one in each hemisphere. The right hemisphere's lexicon seems organized differently from the left hemisphere's lexicon, and these lexicons are accessed in different ways.
- The right hemisphere has been linked to one aspect of speech perception, prosody, which is the connotative aspect of oral language—the way we vary articulation to convey affect or intonation.
- Some studies show that the right hemisphere is specialized for visuospatial processing.
- The right hemisphere has special processes devoted to the efficient detection of upright faces. The left hemisphere outperforms the right hemisphere when the faces are dissimilar, and the right hemisphere outperforms the left when the faces are similar.
- Although touching any part of the body is noted by either hemisphere, patterned somatosensory information is lateralized. Thus, a split-brain patient who is holding an object in the left hand is unable to find an identical object with the right hand.
- Surprisingly, split-brain patients can use either hemisphere to direct attention to positions in either the left or the right visual field.
- The right hemisphere appears to be specialized for causal perception (the ability to detect that one object is influencing another object in both time and space), and the left hemisphere is more capable with tasks that require causal inference.
- Using Navon's stimuli, investigators showed that patients with left-sided lesions were slow to identify local targets, and patients with right-sided lesions were slow with global targets, thus demonstrating that the left hemisphere is more adept at representing local information and the right hemisphere is better with global information. [Page 151](#)
- The left hemisphere contains what Michael Gazzaniga and Joseph LeDoux have called the interpreter, a system that seeks explanations for internal and external events in order to produce appropriate response behaviors.

both hemispheres show a phenomenon called the word superiority effect (see Chapter 5). Normal English readers are able to identify the words (e.g., L) in the context of real English words (e.g., belt) than when the same letters appear in pseudowords (e.g., kelt) or nonsense letter strings (e.g., ktle). Because pseudowords and nonwords do not have lexical entries, the letters occurring in such strings do not receive the additional processing benefit bestowed on words. Thus, the word superiority effect emerges.

While the patients with right-hemisphere language exhibit a visual lexicon, it may be that each hemisphere accesses this lexicon in a different way. To test this possibility, investigators used a left-priming task. Participants were asked to indicate whether a briefly flashed uppercase letter was an H or a T. On each trial, the uppercase letter was preceded by a lowercase letter that was either an h or a t. Normally, participants respond faster to primed, when an uppercase H is preceded by a lowercase h than when it is preceded by a lowercase t.

The difference in response latency on compatible (H-H) versus incompatible (H-t) trials is taken to be a measure of letter priming. J.W., a split-brain participant, performed a lateralized version of this task in which the prime was displayed for 100 ms to either the right or the left visual field, and 400 ms later the target letter appeared in either the right or the left visual field. The results, shown in Figure 4.16, provide no evidence of letter priming for the left visual field (LVF) trials but clear evidence of priming for trials of the right visual field (RVF). Thus, the lack of a priming phenomenon in the disconnected right hemisphere suggests a deficit in letter recognition, prohibiting access to parallel processing mechanisms. J.W. exhibited a variety of other deficiencies in right-hemisphere function as well. For example, he was unable to judge whether one word was superordinate to another (e.g., furniture and chair), or whether two words were antonyms (e.g., love and hate).

The Evolutionary Basis of Hemispheric Specialization

- Hemispheric specialization is not a unique human feature, though it is most extensive in humans. The evolutionary pressures underlying hemispheric specialization—the need for unified action, rapid communication, and reduced costs associated with interhemispheric processing—exist across species.
- In general, many tasks can be performed successfully by either hemisphere, although the two hemispheres may differ in efficiency.
- The two hemispheres may work in concert to perform a task, even though their contributions may vary.

Gestures in monkeys

Splitbrain research	Research on split brainer (ruptured corpus callosum)
Wada test	A patient is given an injection of amobarbital into the carotid artery, producing a rapid and brief anesthesia of the ipsilateral hemisphere (i.e., the hemisphere on the same side as the injection; Figure 4.4). Then the patient is engaged in a series of tests related to language and memory
amobarbital	A barbiturate used to produce rapid and brief anesthesia.

Sylvian fissure	The large sulcus that defines the superior border of the temporal lobe—
Planum temporale	The cortical area at the center of Wernicke's area (involved with the understanding of written and spoken language)
Homotopic areas	Areas in corresponding locations in the two hemispheres
Corpus Callosum	The left and right cerebral hemispheres are connected by the largest white matter structure in the brain, the corpus callosum
Splendium	The corpus callosum is divided on a macroscopic level into the anterior portion, called the genu, the middle portion, known as the body, and the posterior portion, called the splenium
Heterotopic areas	Regions with different locations in the two hemispheres
Anterior commissure	A much smaller band of fibers connecting the two hemispheres
Posterior commissure	Fiber band connecting the brain hemispheres smaller than the anterior commissure, which carries some interhemispheric fibers
Hierarchical structure.	A configuration that may be described at multiple levels, from global features to local features; the finer components are embedded within the higher level components.
Interpreter	The unique specialization of the left hemisphere—the interpreter—allows our mind to seek explanations for internal and external events in order to produce appropriate response behaviors.
Modules	The general concept of modularity is that the components of a system can be categorized according to their functions
Handedness	The dominant hand

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Kan vi snakke om modules?

Lecture 20/2

Tuesday, February 20, 2018 2:18 PM



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Sensation and perception

Tuesday, February 20, 2018 2:18 PM

Senses, Sensation, and Perception

Sensation: Early Perceptual Processing

Audition

- Signal transduction from sound wave to neuronal signal begins at the eardrums. Sound waves disturb the hair cells. This mechanical input is transformed into a neural output at the cochlea. Signals are processed in the hair cells and basilar membrane of the cochlea. The cochlea sends its information in the form of neuronal signals to the inferior colliculus and the cochlear nucleus. Information then travels to the medial geniculate nucleus of the thalamus and on to the primary auditory cortex.
- Neurons throughout the auditory pathway maintain their tonotopic arrangement as they travel up to the cortex, but the tight organization is less apparent in the auditory cortices A1 and A2 when viewed with high-resolution methods.
- Sound localization is aided by the processing of differences in interaural time and interaural sound intensity, which are each coded separately in the brain.

Olfaction

- Smell is the sensory experience that results from the transduction of neural signals triggered by odor molecules, or odorants.
- Signal transduction from odorant to neuronal signal begins when the odorant attaches to an odor receptor in the olfactory epithelium. The signal is then sent to the olfactory bulb through the olfactory nerve, which projects to the primary olfactory cortex. Signals are also relayed to the orbitofrontal cortex, a secondary olfactory processing area.
- The primary olfactory cortex is important for detecting a change in external odor, and the secondary olfactory cortex is important for identifying the smell itself.
- Similar to the importance of sampling sound from two ears, we use our two nostrils to obtain different olfactory samples, varying the rate of airflow through each nostril and thus altering the rate of absorption.

The olfactory pathway is the only sensory pathway that does not send information to the thalamus.

Gustation

- Gustation and olfaction are known together as the chemical senses because the initial response is to molecules (chemicals) in the environment
- The five basic tastes are salty, sour, bitter, sweet, and umami. The perception of more complex tastes arises from the complex cortical processing of these individual tastes in areas of the brain such as the secondary gustatory cortex in the orbitofrontal region.
- Signal transduction is initiated when a taste cell in the mouth responds to a tastant by depolarizing and sends a signal to the gustatory nucleus in the dorsal medulla. From there, a signal zips to the ventral posterior medial (VPM) nucleus of the thalamus. The VPM synapses with the primary gustatory cortex found in the operculum and insula. The primary gustatory cortex connects with the secondary processing areas found in the orbitofrontal cortex.
- The orbitofrontal cortex is also involved in processing the reward value of food and the resulting motivation to eat food

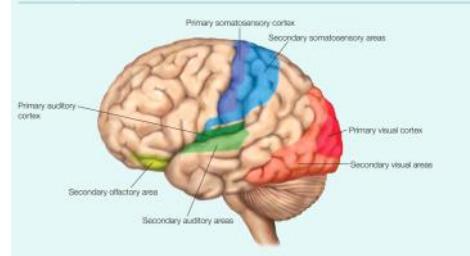
Somatosensation

- Corpuscles located in the skin respond to somatosensory touch information.
- Nociceptors (free nerve endings) respond to pain and temperature information.
- Nerve cells at the junctions of muscles and tendons provide proprioceptive information.
- Primary somatosensory cortex (S1) contains a homunculus of the body, wherein the more sensitive regions encompass relatively larger areas of cortex.
- Somatosensory representations exhibit plasticity, showing variation in extent and organization as a function of individual experience

Vision

- Light activates the photoreceptors, the rods and cones, on the retina.
- The optic nerve is formed from the axons of the ganglion cells, some of which decussate (cross over) at the optic chiasm.
- Axons in the optic nerve synapse on the LGN, and from the LGN become the optic radiations that are sent to V1.
- Ten percent of the fibers from the retina innervate non-LGN subcortical structures, including the pulvinar and superior colliculus. Visual neurons respond only to a stimulus that is presented in a specific region of space. This property is known as the receptive field of the cell.
- Visual cells form an orderly mapping between spatial location and the neural representation of that dimension. In vision, these topographic representations are referred to as retinotopic maps.
- The visual cortex is made up of many distinct regions. These regions are defined by their distinct, retinotopic maps. The visual areas have functional differences that reflect the types of computations performed by cells within the areas. For instance, cells in area V4 are sensitive to color information, and cells in V5 are sensitive to motion information.
- Humans also have visual areas that do not correspond to any region in our close primate relatives

Anatomy of the senses



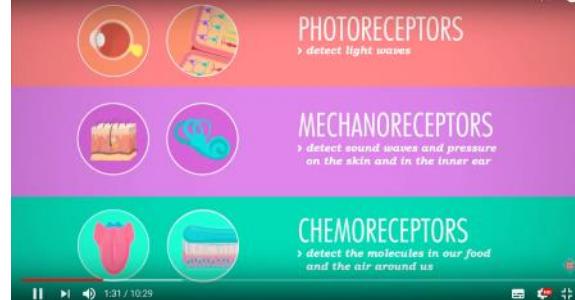
Hearing & Balance: Crash Course A&P #17



Taste & Smell: Crash Course A&P #16



Taste & Smell: Crash Course A&P #16



From Sensation to Perception

- Our percepts are more closely related to activity in higher visual areas than to activity in primary visual cortex.
- Anatomical differences among people in the size of V1 affect the extent of visual illusion.

Deficits in Visual Perception

- Superior colliculus lesions impair the ability of an animal to orient toward the position of a stimulus (which is important for spatial orientation); visual cortex lesions impair visual acuity (which is important for object identification).
- Achromatopsia, the inability to perceive color, results from lesions to areas in and around human V4.
- These regions do not just represent color, however; they are also important for shape perception. Color is one attribute that facilitates the perception of shape.
- Akinetopsia, the inability to process motion, results from lesions to area V5 (human MT).
- As with many neurological conditions, the deficit can be quite subtle for unilateral lesions

We can conclude that the illusion—a yellowish object that is not flickering—is formed in this higher visual area (known variously as either VO or V8), indicating that although the information is sensed accurately at earlier stages within the visual stream, conscious perception, at least of color, is more closely linked to higher-area activity.

Multimodal Perception: I See What

- Some areas of the brain, such as the superior colliculus and superior temporal sulci, process information from more than one sensory modality, integrating the multimodal information to increase the sensitivity and accuracy of perception.
- When multisensory information is presented coincidentally in time and space, the multisensory neural response is enhanced. The reverse is also true; when multisensory information is not presented coincidentally in time and space, the multisensory neural response is depressed.
- People with synesthesia experience a mixing of the senses, for example, colored hearing, colored graphemes, or colored taste.
- Synesthesia is associated with both abnormal activation patterns in functional imaging studies and abnormal patterns of connectivity in structural imaging studies
-

You're Sayin' Perceptual Reorganization

- Following sensory deprivation, the function of sensory regions of the cortex may become reorganized, or exhibit what is called plasticity.
- For instance, in blind individuals, areas of the brain that are usually involved in visual function may become part of the somatosensory cortex.
- Plasticity can also be observed in healthy individuals if they are deprived of information from one sensory modality for even relatively short periods of time.

medial geniculate nucleus (MGN)	A collection of cell bodies in the medial portion of the thalamus involved in processing auditory information. Output from the MGN is directed primarily to the primary auditory cortex. Compare lateral geniculate nucleus.
multisensory integration	The integration of information from more than one sensory modality. Watching someone speak requires the integration of auditory and visual information.
inferior colliculus	A part of the midbrain that is involved in auditory processing. Compare superior colliculus.
Primary auditory cortex (A1)	The initial cortical processing area of the auditory system.
interaural time	difference in when a sound reaches each of the two ears
Tonotopic maps	an orderly correspondence between the location of the neurons and their specific frequency tuning. Cells in the rostral part of A1 tend to be responsive to low-frequency sounds; cells in the caudal part of A1 are more responsive to high-frequency sounds.
Odorants	A molecule conducted through the air that leads to activation of the olfactory receptors and may be perceived as having a smell when processed through the olfactory system. Compare tastant
Glomeruli	The neurons of the olfactory bulb
primary olfactory cortex	The initial cortical processing area for olfaction, located at the ventral junction of the frontal and temporal cortices, near the limbic cortex.
Chemical senses	Senses that interpret the environment by discriminating between the different chemicals
Primary gustatory cortex	The initial cortical processing area for gustation, located in the insula and operculum
tastant	A food molecule that stimulates a receptor in a taste cell to initiate the sensory transduction of gustation. Compare odorant.

corpuscles	A globular mass of cells that are part of the somatosensory system.
nociceptors	The least differentiated of the skin's sensory receptors, which registers pain
Proprioception	The awareness of the position of one's own body parts, such as limbs. This awareness arises from the information provided by specialized nerve cells at the linkage of the muscles and tendons
Primary somatosensory cortex or S1	The initial cortical processing area for somatosensation, including Brodmann areas 1, 2, and 3. This area of the brain contains a somatotopic representation of the body called the sensory homunculus (small man)
Secondary somatosensory cortex (S2)	The area of the brain that receives inputs from primary somatosensory cortex and processes higher level somatosensory information
retina	A layer of neurons along the back surface of the eye. The retina contains a variety of cells, including photoreceptors (the cells that respond to light) and ganglion cells (the cells whose axons form the optic nerve).
photoreceptors	A specialized cell in the retina that transduces light energy into changes in membrane potential. The photoreceptors are the interface for the visual system between the external world and the nervous system.
fovea	The central region of the retina that is densely packed with cone cells and provides high-resolution visual information.
Ganglion cells	A type of neuron in the retina. Ganglion cells receive input from the photoreceptors (rods and cones) and intermediate cells of the retina and send axons to the thalamus and other subcortical structures.
lateral geniculate nucleus (LGN)	The thalamic nucleus that is the main target of axons of the optic tract. Output from the LGN is directed primarily to the primary visual cortex (Brodmann area 17). Compare medial geniculate nucleus.
superior colliculus	A subcortical visual structure located in the midbrain. The superior colliculus receives input from the retinal system and is interconnected with the subcortical and cortical systems. It plays a key role in visuomotor processes and may be involved in the inhibitory component of reflexive attentional orienting. Compare inferior colliculus
receptive field	Visual neurons respond only to a stimulus that is presented in a specific region of space
retinotopic maps	Visual cells form an orderly mapping between spatial location and the neural representation of that dimension. In vision, these topographic representations are referred to as retinotopic maps.
Extrastriate visual areas	Visual areas that lie outside the striate cortex (Brodmann area 17, the primary visual cortex) and are considered secondary visual areas because they receive input either directly or indirectly from the primary visual cortex.
Area MT	Brain area in the middle of the temporal lobes, which has cells sensitive to color information
Area V4	Cells in V5 are sensitive to motion information
Akinetopsia	The inability to process motion
hemianopia	The loss of perception in half of the visual field
scotomas	Discrete regions of blindness
Synesthesia	The inability to differentiate between senses, word can taste of something

Lecture 27/2

Tuesday, February 27, 2018 1:06 PM



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Object recognition

Friday, March 2, 2018

10:48 AM

Principles of Object Recognition

- Sensation, perception, and recognition refer to distinct phenomena.
- People perceive an object as a unified whole, not as an entity separated by its color, shape, and details.
- Although our visual perspective changes, our ability to recognize objects remains robust.
- Memory and perception are tightly linked.
- Patients with visual agnosia are unable to recognize common objects presented to them visually. This deficit is modality specific. Patients can recognize an object when they touch, smell, taste, or hear it.

Multiple Pathways for Visual

- The ventral stream, or occipitotemporal pathway, is specialized for object perception and recognition. This is often referred to as the “what” pathway. It focuses on “vision for recognition.”
- The dorsal stream, or occipitoparietal pathway, is specialized for spatial perception and is often referred to as the “where” or “how” pathway. It focuses on “vision for action.”
- Neurons in the parietal lobe have large, nonselective receptive fields that include cells representing both the fovea and the periphery. Neurons in the temporal lobe have large receptive fields that are much more selective and always represent foveal information.
- Patients with selective lesions of the ventral pathway may have severe problems in consciously identifying objects, yet they can use the visual information to guide coordinated movement. Thus we see that visual information is used for a variety of purposes.
- Patients with optic ataxia can recognize objects but cannot use visual information to guide action. Optic ataxia is associated with lesions of the parietal cortex

Perception

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- Patients with optic ataxia can recognize objects but cannot use visual information to guide action. Optic ataxia is associated with lesions of the parietal cortex.

Computational Problems in Object Recognition

- Object constancy refers to the ability to recognize objects in countless situations, despite variation in the physical stimulus.
- Object perception may occur in a view-dependent frame of reference or a view-invariant frame of reference. In view-dependent theories, perception is assumed to be specific to a particular viewpoint. View-invariant theories posit that recognition occurs at a level that is not linked to specific stimulus information.
- The lateral occipital cortex is critical for the recognition of the shape of an object.
- The term grandmother cell has been coined to convey the notion that recognition arises from the activation of neurons that are finely tuned to specific stimuli.
- Ensemble theories, on the other hand, hypothesize that recognition is the result of the collective activation of many neurons.

Failures in Object Recognition:

- Apperceptive agnosia can be considered a problem in achieving object constancy. The patient with apperceptive agnosia may recognize an object from a typical viewpoint, but performance deteriorates when asked to name an object that is seen from an unusual viewpoint or is occluded by shadows.
- Integrative agnosia is a deficit that arises from the inability to integrate features into parts, or parts of an object into a coherent whole.
- Associative agnosia describes patients who are unable to access conceptual knowledge from visual input. Their perceptual abilities may be (relatively) intact, but they fail to link that representation to knowledge about what the object is used for, where it might be found, and so on.

The Big Picture

Category Specificity in Agnosia:

The Devil Is in the Details

Processing Faces: Are Faces Special?

- Category-specific deficits are deficits of object recognition that are restricted to certain classes of objects.
- Prosopagnosia is an inability to recognize faces that cannot be attributed to deterioration in intellectual function.
- Acquired alexia is characterized by reading problems that occur after a patient has a stroke or head trauma.
- Neurons in various areas of the monkey brain show selectivity for face stimuli.
- Similarly, specificity is observed in fMRI studies, including an area in the fusiform gyrus of the temporal lobe, the fusiform face area, or FFA.
- Analytic processing is a form of perceptual analysis that emphasizes the component parts of an object, a mode of processing that is important for reading.
- Holistic processing is a form of perceptual analysis that emphasizes the overall shape of an object, a mode of processing that is important for face perception.
- Just as the FFA is specialized for processing faces, the parahippocampal place area (PPA) is specialized for processing information about spatial relations or for classifying objects based on spatial properties (e.g., an indoor vs. outdoor scene).
- Likewise, the extrastriate body area (EBA) and the fusiform body area (FBA) have been identified as more active when body parts are viewed.

Hallucinations

STS

Mind Reading

- Encoding models are used to predict the physiological response, such as the BOLD response to a stimulus.
- Decoding models are used in the reverse manner, predicting the stimulus (or mental state) based on a physiological response such as the BOLD activity across a set of voxels.
- Mind reading may one day be used to communicate with people who are currently unable to speak.

Agnosia	A neurological syndrome in which disturbances of perceptual recognition cannot be attributed to impairments in basic sensory processes. Agnosia can be restricted to a single modality, such as vision or audition
Visual Agnosia	Inability to recognize common objects presented to them visually
Ventral (occipitotemporal) stream	The ventral stream, or occipitotemporal pathway, is specialized for object perception and recognition. This is often referred to as the “what” pathway. It focuses on “vision for recognition.”
Dorsal (occipitoparietal) stream	The dorsal stream, or occipitoparietal pathway, is specialized for spatial perception and is often referred to as the “where” or “how” pathway. It focuses on “vision for action.”
Lateral occipital	A region of extrastriate cortex that is part of the ventral pathway. Processing in LOC is essential for shape perception and recognition.

cortex (LOC)	
Object constancy	Ability to recognize an object in countless situations.
view-dependent fame of reference	Perception is assumed to be specific to a particular viewpoint.
View-invariant fame of reference	View-invariant theories posit that recognition occurs at a level that is not linked to specific stimulus information.
repetition suppression effect	The phenomenon seen during functional MRI in which the BOLD response to a stimulus decreases with each subsequent stimulus repetition
Apperceptive agnosia	A form of agnosia associated with deficits in the operation of higher-level perceptual analyses. A patient with apperceptive agnosia may recognize an object when seen from a typical viewpoint. However, if the orientation is unusual, or the object is occluded by shadows, recognition deteriorates. Compare associative agnosia.
integrative agnosia	Inability to integrate features into parts, or parts of an object into a coherent whole
Associative agnosia	failure of visual object recognition that cannot be attributed to a problem of integrating parts to form a whole, or to a perceptual limitation, such as a failure of object constancy.
category-specific deficits	Recognition impairment that is restricted to a certain class of objects. Some rare individuals demonstrate an impairment in their ability to recognize living things, yet exhibit near-normal performance in recognizing nonliving things. Such deficits are useful in the development of models about how perceptual and semantic knowledge is organized in the brain
Prosopagnosia	A neurological syndrome characterized by a deficit in the ability to recognize faces. Some patients will show a selective deficit in face perception, a type of category-specific deficit. In others, the prosopagnosia is one part of a more general agnosia. Prosopagnosia is frequently associated with bilateral lesions in the ventral pathway, although it can also occur with unilateral lesions of the right hemisphere <small>patients with prosopagnosia are able to recognize a person upon hearing that person's voice. —> Living vs. Non-Living —> FIGURE 6.24 neural network.</small>
fusiform gyrus	A gyrus located along the ventral surface of the temporal lobe. This area has been shown in neuroimaging studies to be consistently activated when people view face stimuli. Neurological lesions that include the fusiform gyrus are associated with prosopagnosia, although the damage also extends to other regions of the cortex
fusiform face area (FFA)	A functionally defined area of the brain, located in the ventral surface of the temporal lobe in the fusiform gyrus, that responds to selective stimuli, such as faces.
parahippocampal place area (PPA)	A functionally defined area of the brain (usually with fMRI), located in the parahippocampal region of the temporal lobe that shows a preferential response to stimuli depicting scenes or places.
analytic processing	Perceptual analysis that emphasizes the component parts of an object. Reading is thought to be a prime example of analytic processing in that the recognition of words requires the analysis of at least some of the component letters.
holistic processing	Perceptual analysis that emphasizes the overall shape of an object. Face perception has been hypothesized to be the best example of holistic processing, in that the recognition of an individual appears to reflect the composition of the person's facial features rather than being based on the recognition of the individual features themselves
Extrastriate body area (EBA)	A functionally-defined area in the lateral occipitotemporal cortex that has been found, in fMRI studies, to show a stronger response to images containing body parts relative to other animate and inanimate stimulus categories
Fusiform body area (FBA)	Se extrastriate body area (EBA)

One hypothesis is that many nonliving things evoke representations not elicited by living things (A. Damasio, 1990). In particular, manufactured objects can be manipulated. As such, they are associated with kinesthetic and motoric representations. When viewing an inanimate object, we can activate a sense of how it feels or of the actions required to manipulate it (Figure 6.22). Corresponding representations may not exist for living objects. Although we may have a kinesthetic sense of how a cat's fur feels, few of us have ever stroked or manipulated an elephant. We certainly have no sense of what it feels like to pounce like a cat or fly like a bird.

According to this hypothesis, manufactured objects are easier to recognize because they activate additional forms of representation. Although brain injury can produce a common processing deficit for all categories of stimuli, these extra representations may be sufficient to allow someone to recognize nonliving objects.

Decoding	Using the brain activity, which is produced by a stimulus and detected by such methods as fMRI, in order to determine the original stimulus.
Encoding model	A model of how information in the environment is represented. Encoding models are used in fMRI to predict the BOLD response to different stimuli.

Lecture 13/3

Tuesday, March 20, 2018 1:11 PM



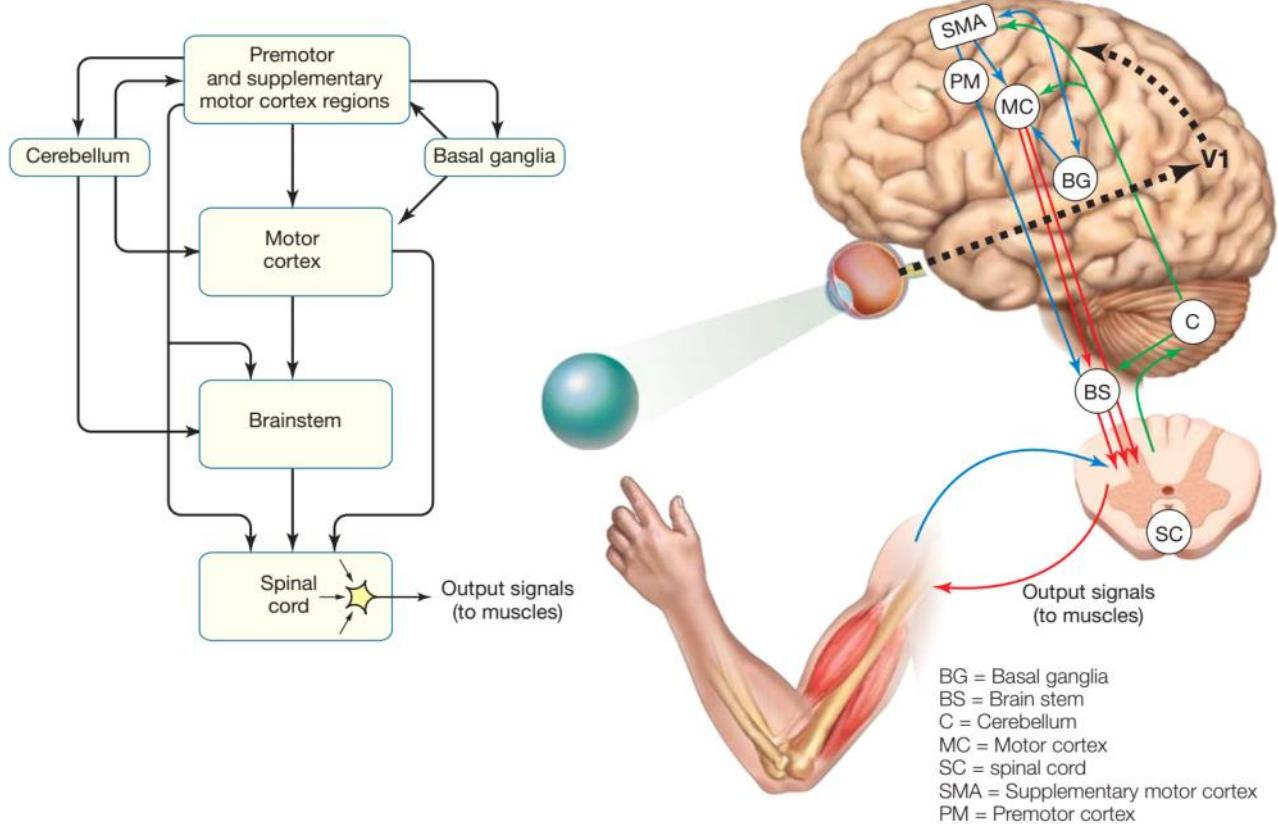
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Action

Wednesday, March 7, 2018 11:31 AM

The Anatomy and Control of Motor Structures

- Due to the hierarchical structure of the motor system, lesions on different levels affect the system differently.
 - When moving a limb both an excitatory signal and inhibitory signal is sent to the limb.
 - o Thus, to produce movement, excitatory signals to one muscle, the agonist, are accompanied by inhibitory signals to the antagonist muscle via interneurons. In this way, the stretch reflex that efficiently stabilizes unexpected perturbations can be overcome to permit volitional movement
 - In summary, the motor cortex has direct access to spinal mechanisms via the corticospinal tract. Movement can also be influenced through many other connections. First, the primary motor cortex and premotor areas receive input from many regions of the cortex by way of corticocortical connections. Second, some cortical axons terminate on brainstem nuclei, thus providing a cortical influence on the extrapyramidal tracts. Third, the cortex sends massive projections to the basal ganglia and cerebellum. Fourth, the corticobulbar tract is composed of cortical fibers that terminate on the cranial nerves
- **Take home:**
- A part of the body that can move is referred to as an effector.
 - Alpha motor neurons provide the point of translation between the nervous system and the muscular system, originating in the spinal cord and terminating on muscle fibers. Action potentials in alpha motor neurons cause the muscle fibers to contract.
 - Extrapiramidal tracts are neural pathways that project from the subcortex to the spinal cord.
 - The corticospinal or pyramidal tract is made up of descending fibers that originate in the cortex and project monosynaptically to the spinal cord.
 - Two prominent subcortical structures involved in motor control are the cerebellum and basal ganglia.
 - The primary motor cortex (Brodmann area 4) spans the anterior bank of the central sulcus and the posterior part of the central gyrus. It is the source of most of the corticospinal tract.
 - Hemiplegia is a loss of the ability to produce voluntary movement. It results from damage to the primary motor cortex or the corticospinal tract, and the deficits are present in effectors contralateral to the lesion.
 - Brodmann area 6 includes secondary motor areas. The lateral aspect is referred to as premotor cortex, and the medial aspect as supplementary motor area.
 - The primary and secondary motor cortices contain somatotopic representations, although the maps are not as well defined as is seen in sensory cortices.



Computational Issues in Motor Control

- Neurons within the spinal cord can generate an entire sequence of actions without any external feedback signal. These circuits are called **central pattern generators**.
- Descending motor signals modulate the spinal mechanism to produce voluntary movements.
- The motor system is hierarchically organized. Subcortical and cortical areas represent movement goals at various levels of abstraction

Physiological Analysis of Motor Pathways

- The neurophysiological evidence points to a more nuanced picture than we might have anticipated from our hierarchical control model. Rather than a linkage of different neural regions with specific levels in a processing hierarchy, one that moves from abstract to more concrete representations, the picture reveals an interactive network of motor areas that represent multiple features.
- Motor neurophysiologists correlate cellular activity in motor cortex with the animal's behavior.
- A common observation is that **neurons in motor areas exhibit a preferred direction**, in which the firing rate is strongest for movements in a limited set of directions.
- The population vector is a representation based on combining the activity of many neurons.
- Population vectors that provide a close match to behavior can be constructed from many motor areas, although this does not mean that all of these cells represent movement direction.
- Before movement even begins, the population vector is a reliable signal of the direction of a forthcoming movement. This finding indicates that some cells are involved in planning movements as well as executing movement.
- Neurons have dynamic properties, coding different features depending on time and context. There need not be a simple mapping from behavior to neural activity.

- The heterogeneity of responses exhibited by neurons in M1 includes both motor and sensory information.

Goal Selection and Action Planning

- The affordance competition hypothesis proposes that the processes of action selection (what to do) and specification (how to do it) occur simultaneously within an interactive neural network that continuously evolves from planning to execution.
- Action selection involves a competitive process.
- Rather than view selection and planning as serial processes, neural activity reveals that there is parallel activation of multiple goals and movement plans.
- Supplementary motor area is important for coordinating motor behavior in time (sequential movements) and between limbs (bimanual coordination).
- Parietal motor areas also show topography: Different regions of the intraparietal cortex are associated with hand, arm, and eye movements.
- Parietal motor representations are more goal oriented, whereas premotor-motor representations are more closely linked to the movement itself.
- Conscious awareness of movement appears to be related to the neural processing of action intention rather than the movement itself

The Brain–Machine Interface

- Brain–machine interface systems use neural signals to directly control robotic devices such as a computer cursor or a prosthetic device.
- BMIs offer a promising avenue for rehabilitation of people with severe movement disorders such as those resulting from spinal cord injury.
- Early BMI systems required two phases. In the first phase, neural activity was recorded while the animal produced movement and the tuning properties (such as preferred direction) were recorded. In the second phase, the output from these neurons was used to control an interface device.
- Current studies are exploring how decoders can be adapted through experience in BMI control and are looking at the stability of such systems over extended periods of time. Advances on these problems are essential for building BMI systems that will be useful in clinical settings

Movement Initiation and the Basal Ganglia

- The output from the basal ganglia, via thalamic projections, influences activity in the cortex, including the motor cortex.
- All of the output signals from the basal ganglia are inhibitory. Thus, in the tonic state, the basal ganglia dampen cortical activity.
- Movement initiation requires disinhibition: The striatal projection to the GPi inhibits an inhibitory signal, resulting in excitation at the cortex
- Striatal neurons influence the output nuclei of the basal ganglia via the direct pathway and the indirect pathway.
- Dopamine is produced in the substantia nigra pars compacta, a brainstem nucleus that projects to the striatum. It has an excitatory effect on the direct pathway and an inhibitory effect on the indirect pathway.
- Parkinson's disease results from cell death in dopamine-producing cells in the substantia nigra.
- Parkinson's disease includes disorders of posture and locomotion, hypokinesia (the absence or reduction of voluntary movement), and bradykinesia (slowness in initiating and executing movement).
- The drug L-DOPA is used in treating Parkinson's disease because it can compensate for the loss of endogenous dopamine.
- Deep-brain stimulation is a surgical technique in which electrodes are implanted in the brain. This procedure has become a novel treatment for Parkinson's disease. Implants usually are placed in the subthalamic nucleus.
- The basal ganglia may play a general function in state changes. For the motor system, a state change would correspond to the initiation of a new movement. In the cognitive system, a state change could be a change in mental set, such as when we change from one goal to another. Dopamine acts as a reinforcement signal to bias some states over others.

Action Understanding and Mirror Neurons

- Mirror neurons are neurons in premotor cortex and other areas (like the parietal lobe) that respond to an action, both when that action is produced by an animal and when the animal observes a similar action produced by another animal.
- The mirror system has been hypothesized to be essential for comprehending the actions produced by other individuals.
- The engagement of the mirror system is modulated by motor expertise.

Learning and Performing New Skills

- Sensorimotor learning is improvement, through practice, in the performance of motor behavior.
- The cerebellum is critical for error-based learning. Errors are derived from a comparison of the predicted and observed sensory information. The errors are used to update a forward model, a representation that can be used to generate the sensory expectancies for a movement.
- The predictive capacity of the cerebellum is also important for online control. By anticipating the sensory consequences of movement, it helps compensate for delays introduced by sensorimotor processing.
- The primary motor cortex is critical for the long-term retention of skills. Consolidation is enhanced by dopaminergic input to the motor cortex from the ventral tegmental area of the brainstem.
- Skill requires extensive hours of practice. Expertise is skill specific, but it may be more closely related to domain-independent factors such as motivation rather than a propensity, or inclination, for particular types of performance

Substantia nigra	A brainstem nucleus that is part of the basal ganglia. These cells are a primary source of the neurotransmitter dopamine.
Effector	Part of the body, which can move
Alpha motor neurons	Innervate muscle fibers and produce contractions of the fibers and thereby provide a physical basis for translating nerve signals into mechanical actions
Spinal interneurons	The interneurons are innervated both by afferent sensory nerves from the skin, muscles and joints and by descending motor fibers that originate in several subcortical structures
Extrapyramidal tracts	A primary source of indirect control over spinal activity modulating posture, muscle tone and movement speed.
Cerebellum	Also known as “little cerebrum.” A large, highly convoluted (infolded) structure located dorsal to the brainstem at the level of the pons. The cerebellum maintains (directly or indirectly) interconnectivity with widespread cortical, subcortical, brainstem, and spinal cord structures, and plays a role in various aspects of coordination ranging from locomotion to skilled, volitional movement.
Ataxia	Problems with sensory coordination of the distal limb movements - thus disrupting fine coordination.
Basal Ganglia	A collection of five subcortical nuclei: the caudate, putamen, globus pallidus, subthalamic nucleus, and substantia nigra. The basal ganglia are involved in motor control and learning. Reciprocal neuronal loops project from cortical areas to the basal ganglia and back to the cortex. Two prominent basal ganglia disorders are Parkinson’s disease and Huntington’s disease
Corticospinal tract	Also pyramidal tract. A bundle of axons that originate in the cortex and terminate monosynaptically on alpha motor neurons and spinal interneurons in the spinal cord. Many of these fibers originate in the primary motor cortex, although some come from secondary motor areas. The corticospinal tract is important for the control of voluntary movements.
The primary motor cortex	A region of the cerebral cortex that lies along the anterior bank of the central sulcus and precentral gyrus, forming Brodmann area 4. Some axons originating in the primary motor cortex form the majority of the corticospinal tract; others project to cortical and subcortical

	regions involved in motor control. The primary motor cortex contains a prominent somatotopic representation of the body.
Hemiplegia	The loss of voluntary movement on the contralateral side of the body
Premotor cortex	Has strong reciprocal connections with the parietal lobe, providing the anatomical substrate for external sensory-guided actions.
Supplementary motor cortex	A secondary motor area that includes the medial aspect of Brodmann area 6, just anterior to the primary motor cortex. The SMA plays an important role in the production of sequential movements, especially those that have been well learned. SMA in contrast to PM has stronger connections with the medial cortex, areas associated with internally guided personal preferences and goals.
Apraxia	A loss of praxis or skilled actions - affects motor planning. Able to perform simple gestures like creating a fist, but unable to put this into a meaningful action e.g. greeting with the wave of a hand. Two subcategories
Ideomotor apraxia	Have a rough idea of the desired action, but do not know how to execute it.
Ideational apraxia	The patient's knowledge about the intent is disrupted i.e. he is no longer able to comprehend the appropriate use of a tool.
Central pattern generators	A neural network limited to the spinal cord that produces patterned motor outputs without descending commands from the cerebral cortex or sensory feedback.
Endpoint control	A hypothesis concerning how movements are planned in terms of the desired final location. Endpoint control models emphasize that the motor representation is based on the final position required of the limbs to achieve the movement goal
Preferred direction	A property of cells in the motor pathway, referring to the direction of movement that results in the highest firing rate of the neuron. Voxels have also been shown to have preferred directions in fMRI studies, indicating that such preferences can even be measured at the cell population level of analysis
Population vector	The activity of a neuron can be described as a vector oriented to the cell's preferred direction with strength equal to its firing rate. The population vector is the sum of all the individual vectors.
Brain Machine Interface	The process where the brain sends signals to a machine in order to get it to perform an action e.g. fold laundry
Huntington's disease	Hereditary neurodegenerative disorder that appears during the fourth or fifth decade of life.
Parkinson's disease	The loss of dopaminergic neurons in the substantia nigra pars compacta. The symptoms are disorders of posture and locomotion.
Hypokinesia	The absence or reduction in voluntary movement
bradykinesia	Movements are frequently slow
Deep brain stimulation	A suggested treatment for parkinson, where an electrode is implanted into a targeted neural region usually STN. A current is passed through the electrode at high frequencies. The stimulation alters activity in the targeted regions and through the circuit.
Mirror neurons	The activity of the mirror cell is correlated with a goal-oriented action—retrieving a peanut— independent of how this information is received—by the monkey's own action, by viewing another person's action, by hearing another person's action, or by viewing only a portion of another person's action but believing that the action is taking place.
Mirror system	A distributed network of neurons that respond not only to one's own action but also to perceived actions. For instance, a mirror neuron responds when you pick up a pencil and

	when you watch someone else pick up a pencil.
Sensory motor adaption	A form of motor learning in which a learned skill is modified due to some change in the environment or agent. For example, a soccer player who adjusts her shot to compensate for a strong cross-wind is exhibiting a form of motor adaptation
Sensory motor learning	A term that refers to the acquisition of a new motor skill or capability. Motor learning can arise from maturation processes (e.g., infants crawling) or intense, dedicated practice (e.g., piano playing)
Visuomotor adaption	A form of sensorimotor adaptation in which the visual feedback is altered, resulting in a mismatch between proprioception and vision. With practice, the motor system adjusts to compensate for the mismatch
Forward model	A theoretical construct referring to the idea that the brain generates predictions of expected events. In motor control, a forward model refers to the prediction of the expected sensory consequences of a movement.

Lecture 20/3

Tuesday, March 20, 2018 1:11 PM



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EEG and Event-related potentials with a focus on language

Tuesday, March 20, 2018 1:11 PM

Luck: an Introduction to EEGs

Table 1.1 Comparison of invasiveness, spatial resolution, temporal resolution, and cost for microelectrode measures (single-unit and local field-potential recordings), hemodynamic measures (PET and fMRI), and electromagnetic measures (ERPs and ERMFs)

	MICROELECTRODE MEASURES	HEMODYNAMIC MEASURES	ELECTROMAGNETIC MEASURES
Invasiveness	Poor	Good (PET) Excellent (fMRI)	Excellent
Spatial resolution	Excellent	Good	Undefined/poor (ERPs) Undefined/better (ERMFs)
Temporal resolution	Excellent	Poor	Excellent
Cost	Fairly expensive	Expensive (PET) Expensive (fMRI)	Inexpensive (ERPs) Expensive (ERMFs)

Gazzaniga p.95-103

- Single-cell recording allows neurophysiologists to record from individual neurons in the animal brain in order to understand how increases and decreases in the activity of neurons correlate with stimulation of one of the senses or behavior.
 - With multiunit recording, the activity of hundreds of cells can be recorded at the same time.
 - Electroencephalography (EEG) measures the electrical activity of the brain. The EEG signal includes endogenous changes in electrical activity as well as changes triggered by specific events (e.g., stimuli or movements).
 - An event-related potential (ERP) is a change in electrical activity that is time-locked to specific events, such as the presentation of a stimulus or the onset of a response. When the events are repeated many times, the relatively small changes in neural activity triggered by these events can be observed by averaging of the EEG signals. In this manner, the background fluctuations in the EEG signal are removed, revealing the event-related signal with great temporal resolution.
 - Electrocorticogram (ECoG) is similar to an EEG, except that the electrodes are placed directly on the surface of the brain.
 - Magnetoencephalography (MEG) measures the magnetic signals generated by the brain. The electrical activity of neurons also produces small magnetic fields, which can be measured by sensitive magnetic detectors placed along the scalp. MEG can be used in an event-related manner similar to ERPs, with similar temporal resolution. The spatial resolution can be superior because magnetic signals are minimally distorted by organic tissue such as the brain or skull.
- p. 491-500
- In the ERP method, the N400 is a negative-polarity brain wave related to semantic processes in language, and the P600/SPS is a large positive component elicited after a syntactic and some semantic violations.
 - Syntactic processing takes place in a network of left inferior frontal and superior temporal brain regions that are activated during language processing.
 - Models of language involve unifying information from linguistic inputs or from retrieved linguistic representations with stored knowledge.

- White matter tracks in the left hemisphere connect frontal and temporal lobes to create specific circuits for speech, semantic analysis, and syntactic processing.
- Models of language production must account for the selection of the information to be contained in the message; retrieving words from the lexicon; sentence planning and grammatical encoding using semantic and syntactic properties of the word; using morphological and phonological properties for syllabification and prosody; and preparing articulatory gestures for each syllable.
- Each stage in Levelt's model for language production occurs serially, and its output representation is used for input to the next stage. It avoids feedback, loops, parallel processing, and cascades, and it fits well with the findings of ERPs recorded intracranially

Neurophysiology	The study of the physiological processes of the nervous system. Neural activity is characterized by physiological changes that can be described both electrically and chemically. The changes can be observed at many different levels, ranging from the gross changes recorded with EEG, to the firing of individual neurons, to the molecular changes that occur at the synapse
Single-cell recording	Single-cell recording allows neurophysiologists to record from individual neurons in the animal brain in order to understand how increases and decreases in the activity of neurons correlate with stimulation of one of the senses or behavior.
Receptive field	The field, where a neuron is receptive for stimulation.
Retinotopic	The primary visual cortex are arranged in similar manner as the visual field. Adjacent parts of the visual field are represented in adjacent parts in the primary visual cortex.
Multiunit-recordings	A method, which makes measurement of multiple neurons simultaneously possible.
Electroencephalography (EEG)	Electroencephalography (EEG) measures the electrical activity of the brain. The EEG signal includes endogenous changes in electrical activity as well as changes triggered by specific events (e.g., stimuli or movements).
Event-related potential	An event-related potential (ERP) is a change in electrical activity that is time-locked to specific events, such as the presentation of a stimulus or the onset of a response. When the events are repeated many times, the relatively small changes in neural activity triggered by these events can be observed by averaging of the EEG signals. In this manner, the background fluctuations in the EEG signal are removed, revealing the event-related signal with great temporal resolution.
Time frequency analysis	Amplitude i.e. power of a wave in different frequency regions varies over the course of processing.
Magnetoencephalography (MEG)	Magnetoencephalography (MEG) measures the magnetic signals generated by the brain. The electrical activity of neurons also produces small magnetic fields, which can be measured by sensitive magnetic detectors placed along the scalp. MEG can be used in an event-related manner similar to ERPs, with similar temporal resolution. The spatial resolution can be superior because magnetic signals are minimally distorted by organic tissue such as the brain or skull.
Electrocortogram (ECoG)	Electrocortogram (ECoG) is similar to an EEG, except that the electrodes are placed directly on the surface of the brain.
P600 response	Also syntactic positive shift. A positive polarity event-related potential elicited when words violate syntactic rules in sentences. Compare N400 response

Lecture 3/4

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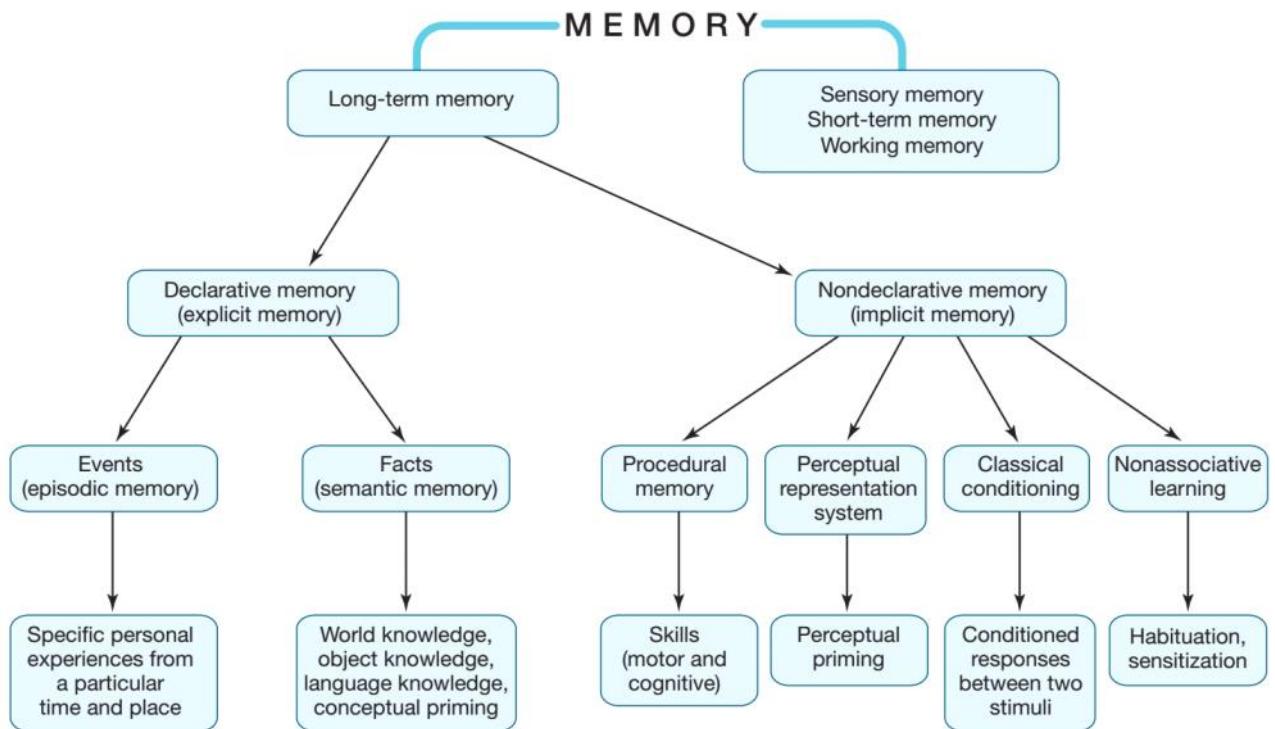
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The Anatomy of Memory

Thursday, April 5, 2018 2:16 PM

An overview of memory

The Anatomy of Memory | 301

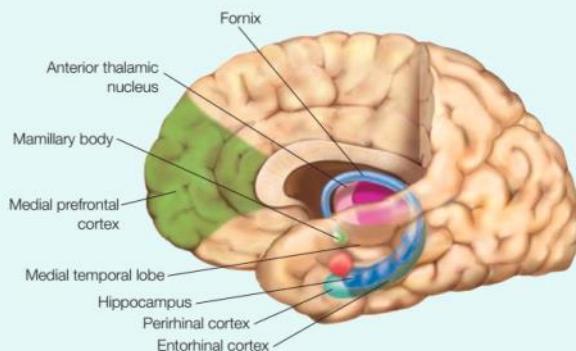


Learning and memory into three major processing stages:

1. Encoding is the processing of incoming information that creates memory traces to be stored. It has to separate steps, the first is acquisition. Sensory systems are constantly being bombarded by tons of stimuli. Most only produce a very brief transient sensory response that fades quickly (about 1000 ms after presentation) without ever reaching short term memory. During this period, however, the stimuli are available for processing. This state is known as a sensory buffer. Only some of these stimuli are sustained and make the cut into short term memory, the acquisition. The second step is consolidation, in which changes in the brain stabilize a memory over time resulting in a long term memory. This can occur over days to months, even years, and creates a stronger representation over time. There are many theories as to what is occurring when a memory is consolidated, which we discuss later in the chapter.
2. Storage is the result of acquisition and consolidation and represents the permanent record of the information.
3. Retrieval involves accessing stored information and using it to create a conscious representation or to execute a learned behavior, such as a motor act.
 - Most of the brain is involved in memory:

ANATOMICAL ORIENTATION

The anatomy of memory



The components of the medial temporal lobe memory system are shown. Other regions of the brain, such as the prefrontal cortex, are involved in storage and retrieval of memories.

The Anatomy of Memory

- Learning is the process of acquiring new information, the outcome of which is memory.
- Learning and memory have many stages, including encoding (acquisition and consolidation), storage, and retrieval.
- What is known as the medial temporal lobe memory system is made up of the hippocampus and the surrounding rhinal and parahippocampal cortices.
- Other areas involved with memory include the prefrontal cortex, the parietal cortex, and subcortical structures

Memory Deficits: Amnesia

- Anterograde amnesia is the loss of the ability to form new memories, as in the case of H.M.
- Patient H.M. developed amnesia after bilateral removal of his medial temporal lobes to treat epilepsy.
- Retrograde amnesia is the loss of memory for events that happened in the past.
- Retrograde amnesia tends to be greatest for the most recent events, an effect known as a temporal gradient or Ribot's Law.
- Patients with retrograde amnesia may have normal shortterm memory as shown by digit span tests.

Mechanisms of Memory

- Short-term forms of memory
 - o Sensory memory
 - Stored in sensory structures as short-lived neural traces
 - Echoic: Auditory memory
 - Duration: EEG/MEG and mismatch negativity shows the length of this memory to be 9-10 s
is a component of the event-related potential (ERP) to an odd stimulus in a sequence of stimuli.
 - Iconic: Visual memory
 - Duration: 300-500 ms
 - The capacity is large, even though it is short-lived
 - o Short-term memory
 - Duration: Seconds to minutes
 - Capacity: 5-10 items
 - Can be prolonged by chunking
 - Early data on short-term memory led to the development of the modal model:

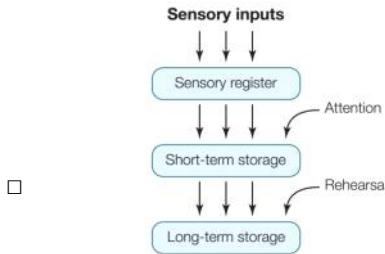


FIGURE 9.5 The Atkinson and Shiffrin modal model of memory.

Sensory information enters the information-processing system and is first stored in a sensory register. Items that are selected via attentional processes are then moved into short-term storage. With rehearsal, the item can move from short-term to long-term storage.

- At each stage the memory can be lost either by decay (information degrades and is lost over time), inference (new information displaces the old information) or a mix of the two
- The modal model have later been questioned due to double dissociations between long-term memory and short-term memory: Patients had either functioning short-term or long-term memory, but not the other way around → suggests a memory must not be held in short-term to enter long-term memory
- Working memory
 - A limited-capacity store for retaining information over the short term (maintenance) and for performing operations on the contents of this store (manipulation)
 - Three-part working memory:

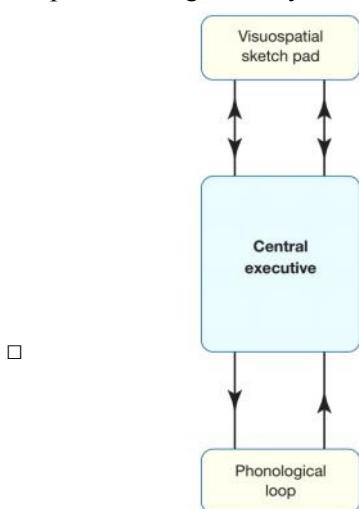


FIGURE 9.7 Simplified representation of the working memory model proposed by Baddeley and Hitch.

This three-part working memory system has a central executive that controls two subordinate systems: the phonological loop, which encodes information phonologically (acoustically) in working memory; and the visuospatial sketch pad, which encodes information visually in working memory.

- The proposed central executive mechanism is a cognitive system, a command-and-control center that presides over and coordinates the interactions between subordinate systems
- The phonological loop is a hypothesized mechanism for acoustically coding information in working memory (thus, it is modality specific)
 - ◆ Discovered: Memory inference was present when recalling an array of similar sounding words, opposed to similar looking words
 - ◆ The phonological loop might have two parts: a short-lived acoustic store for sound inputs and an articulatory component that plays a part in the subvocal rehearsal of visually presented items to be remembered over the short term.
- The visuospatial sketch pad is a short-term memory store that parallels the phonological loop and permits information storage in either purely visual or visuospatial codes.
- Long-term memory

The verbal strategy, however, proved better when the participants were required to concurrently track a moving stimulus by operating a s-lus during the retention interval. In contrast, people are impaired on verbal memory tasks (but not nonverbal memory tasks) when they are required to repeat nonsense syllables during the retention interval, presumably because the phonological loop is disrupted. Dissociations like these cannot be explained by assuming that there is a unitary memory system.

- Declarative memory (depends on the medial temporal system)
 - Episodic memory: Memories of personal experiences that we recall about our own lives
 - Semantic memory: Objective knowledge which does not include the context, where it was learned
- Non declarative memory: implicit memory (Knowledge we have no conscious access to)
 - Conditioning
 - Habituation
 - Sensitization
 - Procedural memory: memory depending on extensive and repeated practise
 - Priming: The enhanced signal due to previous stimuli

The Medial Temporal Lobe Memory System

- The medial temporal lobe is a key component in organizing and consolidating longterm memory that is permanently stored in a distributed fashion in the neocortex
- The Medial Temporal Lobe Memory System includes
 - Amygdala
 - Plays a role in emotional memories Arousal
 - Hippocampus
 - Crucial for forming new memories
 - Case: R.B. had damage in CA1 pyramidal cells and had dense anterograde amnesia
 - Involved with the storage and retrieval of contextual memory
 - E.g. place cells are situated in the hippocampus → the "where" in context memory
 - ◆ If lesioned in rats they are unable to use visual clues for locating objects
 - Equally contains neurons specific for odors and locations → the hippocampus may bind together different contextual information to form a complex contextual memory
 - Memory quality may be a critical factor for whether the hippocampus is essential for retrieval.
 - The proposal is that it plays a permanent role in retrieving detailed contextual memory, but is not necessary for retrieval once detail is lost and memory has generalized
 - Parahippocampal
 - Receive information from the visual, auditory and somatosensory association cortex and sends these inputs to the hippocampus
 - Lesions in this area will cause significant memory deficits → the hippocampus is unable to function correctly if these areas are lesioned
 - Entorhinal cortical area The EC is the main interface between the hippocampus and neocortex.
 - Perirhinal cortical area
 - Receive information from the visual, auditory and somatosensory association cortex and sends these inputs to the hippocampus
 - Lesions in this area will cause significant memory deficits → the hippocampus is unable to function correctly if these areas are lesioned
 - These areas equally process information, therefore will a lesion involving the surrounding structures be more severe than one solely in the hippocampus
- The hippocampus is critical for the formation of longterm memory.
- Cortex surrounding the hippocampus is critical for normal hippocampal function in memory.
- The delayed non-match to sample task is used to assess memory in non-human primates.
- The amygdala is not a crucial part of the system for episodic memory, but it is important for emotional memory.
- Neurons that activate when rats are in a particular place and facing a particular direction have been

404: During retrieval, the hippocampus was selectively active only for items that were actually correctly recollect (Figure 9.26), thus indicating an episodic memory. This strongly suggests that the hippocampus is involved in retrieval for episodic memories but not memories based on familiarity.

identified in the hippocampus and are called place cells. They provide evidence that the hippocampus has cells that encode contextual information.

Imaging Human Memory

- Using the subsequent-memory paradigm (our experiment) it is found that the hippocampus and the posterior parahippocampal cortex is essential for encoding
- Retrieval was recorded in an fMRI-study, participants asked to judge whether the presented word was in a previous presented wordlist. The results showed that the hippocampus was active during retrieval for correctly remembered items
- A model known as the binding of items and contexts (BIC) model proposes that the perirhinal cortex represents information about specific items (e.g., who and what), the parahippocampal cortex represents information about the context in which these items were encountered (e.g., where and when), and processing in the hippocampus binds the representations of items with their context (relational memory)
- The hippocampus is involved in encoding and retrieval for episodic memories that are recollected, whereas areas outside the hippocampus, especially the perirhinal cortex, support recognition based on familiarity

- Functional MRI evidence suggests that the hippocampus is involved in encoding and retrieval for episodic memories that are recollected. Areas outside the hippocampus, especially the entorhinal cortex, support recognition based on familiarity.
- Neuroimaging has confirmed the neural basis of memory demonstrated by animal and lesion studies and has provided some notable new findings—including, for example, evidence that the hippocampus and surrounding parahippocampal and perirhinal cortices may play different roles in memory, supporting different forms of recognition memory.
- The retrosplenial cortex in the parietal lobe appears also to be crucial for memory.
- The PHC and RSC have anatomical and functional connectivity patterns that are similar to each other and are very different from the PRC.

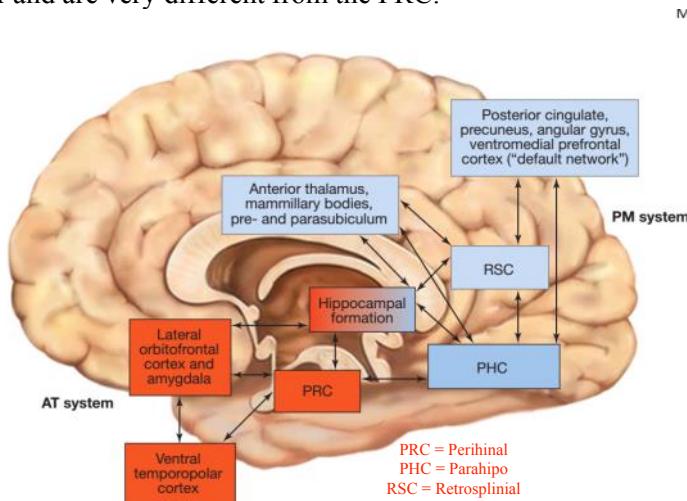


FIGURE 9.35 Model of two neocortical systems for memory-guided behavior.
The components of the anterior temporal (AT) system are shown in red. The posterior medial (PM) system is shown in blue. Regions with strong anatomical connections are indicated with arrows.

The PRC in the anterior system supports memory for items, and it is involved in familiarity-based recognition, associating features of objects, and making fine-grained perceptual or semantic discriminations. Ranganath and Richey suggest that the overall cognitive job of the anterior system (in collaboration with the amygdala, VTPC, and lateral orbitalfrontal cortex) may be to assess the significance of entities.

The PHC and RSC, which are not traditionally included in medial temporal lobe systems, support recollection-based memories, such as memory for scenes, spatial layouts, and contexts. These researchers also propose that this system, together with the other posterior medial system structures, may construct mental representations of the relationships between entities, actions, and outcomes.

Some support for this theory comes from neurological patients. Recall that along with hippocampal damage, Alzheimer's disease, with its episodic memory impairment, is associated with severe disruptions in the retrosplenial cortex, posterior cingulate, precuneus, and angular gyrus, which together are the proposed posterior medial system. In contrast, patients with semantic dementia, which is characterized by a loss of knowledge about objects, have extensive damage to the anterior temporal lobes.

Memory Consolidation

- Consolidation is the process that stabilizes a memory over time after it is first acquired. In most current models, consolidation consists of an initial rapid consolidation process, followed by a slower permanent consolidation process
- The medial temporal lobes, particularly the hippocampus, are essential for the rapid consolidation and initial storage of information for episodic and semantic memories.
- The mechanisms of the slow consolidation process, however, remain more controversial.
 - o Two main theories:
 - The standard consolidation theory: considers the neocortex to be crucial for the storage of fully consolidated long-term memories, whereas the hippocampus plays only a temporary role. In this view, the representations of an event that are distributed

throughout the cortex come together in the medial temporal lobe where the hippocampus binds them. Then, through some sort of interaction between the medial temporal lobe and the neocortex, the bound information is slowly transferred and replaced by a permanent memory trace in the neocortex.

- **The multiple trace theory:** suggests that only the long-term stores for semantic information rely on the neocortex while some aspects of episodic memory, consolidated or not, continue to rely on the hippocampus. In this formulation, a new memory trace, composed of a combination of attributes, is set down in the hippocampus every time a memory is retrieved: The more times a memory is retrieved, the more traces are set down. Remote events that have been retrieved more often have more hippocampal traces and become resistant to hippocampal damage. These traces are not exactly alike, but may differ in attributes. Slowly, the common elements of the traces are extracted into “gist” information and then stored as semantic memory elsewhere in the cortex. This theory suggests that episodic memories degrade over time and are slowly converted to semantic memory.
- Lateral and anterior regions of the temporal lobe are important for the retrieval of information from the long-term stores
- Two prominent theories of long-term memory consolidation are the standard consolidation theory and the multiple trace theory.
- Hippocampal memory consolidation is quick.
- Lesions to the anterior temporal cortex can cause severe retrograde amnesia.
- Damage to the temporal lobe outside of the hippocampus can produce the loss of semantic memory even while the ability to acquire new episodic memories remains intact.

Cellular Basis of Learning and Memory

- In Hebbian learning, if a synapse is active when a postsynaptic neuron is active, the synapse will be strengthened. Long-term potentiation is the long-term strengthening of a synapse.
- NMDA receptors are central to producing LTP but not to maintaining it.

Learning	The process of acquiring new information
Memory	Memory is created when something is learned, and this learning may occur after a single or multiple exposure to the information, experience, or actions
Sensory Memory	The sensory perception of information with a lifetime of ms to s
Short-term memory	The retention of information over seconds to minutes
Working memory	Transient representations of task-relevant information. These representations may be related to information that has just been activated from long-term memory or something recently experienced. Representations in working memory guide behavior in the present, constituting what has been called, “the blackboard of the mind.”
Long-term memory	The retention of information over the long term, from hours to days and years
Amnesia	Memory deficit or loss
Anterograde amnesia	The inability to form new longterm memories
Retrograde amnesia	The inability to recall memories from the past, sometimes temporally limited
Temporally limited	Temporally limited means to have a timelimit
Temporal gradient/Ribot's	Retrograde amnesia often tends to be greatest for most recent events. This is known as a temporal gradient/Ribot's Law

Law	
Declarative memory(explicit memory)	Memory for events and facts that can consciously be accessed
Nondeclarative memory	Knowledge to which we typically have no conscious access, such as motor and cognitive skills (procedural knowledge). For example, the ability to ride a bicycle is a nondeclarative form of knowledge. Although we can describe the action itself, the actual information one needs to ride a bicycle is not easy to describe.
Procedural memory	A form of nondeclarative memory that involves the learning of a variety of motor skills (e.g., knowledge of how to ride a bike) and cognitive skills (e.g., knowledge of how to read)
Priming	A form of learning in which behavior or a physiological response is altered because of some recent stimulus or state. Priming usually refers to changes that occur over a short-time scale; for example, hearing the word “river” primes the word “water.”
Perceptual representation system (PRS)	A form of nondeclarative memory, acting within the perceptual system, in which the structure and form of objects and words can be primed by prior experience and can be revealed later through implicit memory tests.
Transient global amnesia	A sudden, dramatic, but transient (lasting only hours) amnesia that is both anterograde and retrograde.
Relational memory	Memory that relates the individual pieces of information relevant to a particular memory and that supports episodic memories.
Distributed representations	The idea that information may be stored in large populations of neurons located in relatively widespread regions of the brain. This idea is in contrast to the idea that the representations of some items in memory are stored in a discrete, highly localized set of neurons
Hebbian learning	Hebb’s law states that, if a synapse is active when a postsynaptic neuron is active, the synapse will be strengthened; this phenomenon is known as Hebbian learning.

Emotion

Monday, April 9, 2018 10:48 AM

What Is an Emotion?

- Most psychologists agree that emotion consists of three components:
 1. A physiological reaction to a stimulus,
 2. a behavioral response, and
 3. a feeling

Neural Systems Involved in Emotion Processing

- Many parts of the nervous system are involved in our emotions
 - o Emotions are triggered by an episodic memory, in which case our memory systems are involved
 - o When emotions are triggered by an external event or stimulus (as they often are), our sensory systems play a major role
 - o The physiologic components of emotion (that shiver up the spine, or the racing heart and dry mouth people experience with fear) involve the autonomic nervous system (ANS), a division of the peripheral nervous system.
 - the sympathetic system promotes “fight or flight” arousal
 - the parasympathetic promotes “rest and digest.”
- The Papez circuit describes the brain areas that James Papez believed were involved in emotion. They include the hypothalamus, anterior thalamus, cingulate gyrus, and hippocampus. The limbic system includes these structures and the amygdala, orbitofrontal cortex, and portions of the basal ganglia.
- Investigators no longer think there is only one neural circuit of emotion. Rather, depending on the emotional task or situation, we can expect different neural systems to be involved.

Categorizing Emotions

- Most emotion researchers agree that the response to emotional stimuli is adaptive, comprised of three psychological states: a peripheral physiological response (e.g., heart racing), a behavioral response, and the subjective experience (i.e., feelings). What they don't agree on are the underlying mechanisms.
- The crux of the disagreement among the different theories of emotion generation involves the timing of these three components and whether cognition plays a role.
- In an effort to apply some order and uniformity to our definition of emotion, researchers have focused on three primary categories of emotion:
 1. Basic emotions comprise a closed set of emotions, each with unique characteristics, carved by evolution, and reflected through facial expressions.
 2. Complex emotions are combinations of basic emotions, some of which may be socially or culturally learned, that can be identified as evolved, long-lasting feelings.
 3. Dimensions of emotion describe emotions that are fundamentally the same but that differ along one or more dimensions, such as valence (pleasant or unpleasant, positive or negative) and arousal (very pleasant to very unpleasant), in reaction to events or stimuli.
- Basic emotions
 - o Innate, universal and short-lasting human emotions
 - o Paul Ekman's theory: Anger, fear, disgust, sadness, happiness, and surprise are the six basic human facial expressions and that each expression represents a basic emotional state, these emotions do not vary across cultures
 - o Additionally suggested pride and shame may be basic emotions
- Complex emotions
 - Complex emotions, such as love and jealousy, are considered to be refined, long-lasting cognitive versions of basic

- emotions that are culturally specific or individual.
- o According to Ekman parental love, jealousy etc. Is complex emotions, since they can last a lifetime
- o No universal expression exist for romantic love, therefore a complex emotions according to Ekman
- Dimensions of emotions
 - o Another way of categorizing emotions is to describe them as reactions that vary along a continuum of events in the world, rather than as discrete states.
 - o **Feldman-Barret:** Emotional reactions to a stimuli can be characterized by two factors:
 - valence (pleasant - unpleasant) and
 - Arousal (intensity of the internal emotional response)
 - o Rolls: Emotional reactions to a stimuli can be characterized by the actions and goals they motivate
 - Approach or withdrawal from a situation
- Emotions have been categorized as either basic or complex, or varying along dimensional lines.
- Six basic human facial expressions represent emotional states: anger, fear, disgust, happiness, sadness, and surprise.
- Complex emotions (such as love) may vary conceptually as a function of culture and personal experiences.
- The dimensional approach, instead of describing discrete states of emotion, describes emotions as reactions that vary along a continuum.

Theories of Emotion Generation

• Researchers do not agree on how emotions are generated, and many theories exist.

Jame-Lange: You don't run because you are afraid, you are afraid because you become aware of your bodily change when you run.

Canon-Bard: Parallel emotional systems: Fast through cortex (I'm scared) and slow through hypothalamus (sympathetic nervous system - fight or flight)

Appraisal: Richard Lazarus: Quick risk/benefit analysis of situation
Subjective: Different people have different reactions

Singer-Schachter Theory: blend of the James-Lange and appraisal theories. Singer and Schachter proposed that emotional arousal and then reasoning is required to appraise a stimulus before the emotion can be identified.

Constructivist Theories: Lisa Barrett: First we form a mental representation of the bodily changes that have been called core affect (Russell, 2003). This representation is then classified according to language-based emotion categories. Barrett suggests that these categories vary with a person's experience and culture, so there are no empirical criteria for judging an emotion

Evolutionary Psychology Approach: From this viewpoint, an emotion is not reducible to any one category of effects, such as effects on physiology, behavioral inclinations, cognitive appraisals, or filing states, because it involves coordinated, evolved instructions for all of them together.

LeDoux's High Road and Low Road: fast hardwired fight-or-flight response & slow cognition (whoa, that looks suspiciously like an Ursus arctos horribilis, good thing I've been keeping in shape) A emotion (feels scared)

The Amygdala

- The amygdala is the most connected structure in the forebrain.
- The amygdala contains receptors for many different neurotransmitters and for various hormones.
- The role that the amygdala plays in emotion is still controversial.
- The amygdala is critical for the acquisition and expression of an implicitly conditioned fear response, whereas the hippocampus is critical for the explicit conditioned fear response

Interactions Between Emotion and Other Cognitive Processes

- Fear-conditioning paradigm

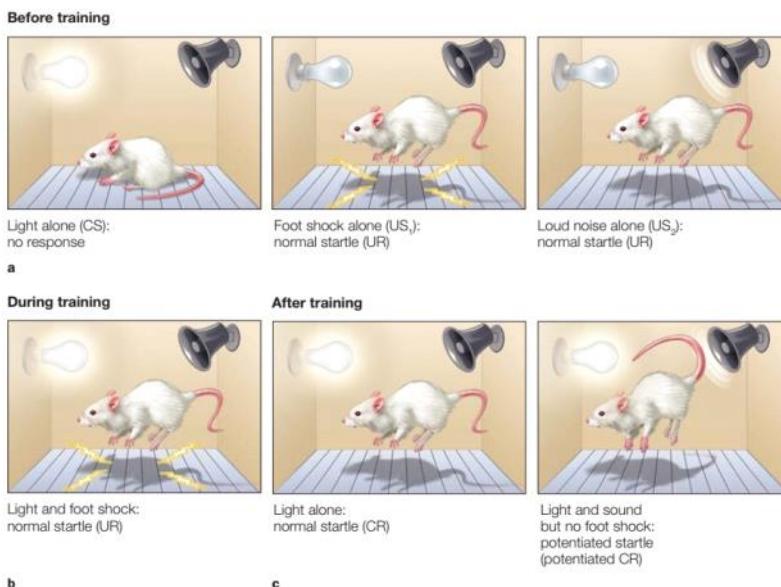


FIGURE 10.8 Fear conditioning.

(a) Before training, three different stimuli—light (CS), foot shock (US₁), and loud noise (US₂)—are presented alone, and both the foot shock and the noise elicit a normal startle response in rats. (b) During training, light (CS) and foot shock (US₁) are paired to elicit a normal startle response (UR). (c) In tests following training, presentation of light alone now elicits a response (CR), and presentation of the light together with a loud noise but no foot shock elicits a potentiated startle (potentiated CR) because the rat is startled by the loud noise and has associated the light (CS) with the startling foot shock (US).

- Two pathways for fear-conditioning:

- Superior dorsal lateral amygdala undergo changes that pair CS (conditioned stimulus) and US (unconditioned stimulus)
- The lateral nucleus is connected to the central nucleus in amygdala, which initiate an emotional response to a stimulus if it is determined dangerous
- Information about the fear-inducing stimulus reaches the amygdala through two separate but simultaneous pathways
 - One goes directly from the thalamus to the amygdala without being filtered by conscious control.
 - Signals sent by this pathway, sometimes called the low road, reach the amygdala rapidly, but are incomplete
 - At the same time, sensory information about the stimulus is being projected to the amygdala via another cortical pathway, sometimes referred to as the high road.
 - The high road is slower, but more complete
 - This route goes via the thalamus, which sends the information to the sensory cortex for finer analysis, which sends it to the amygdala

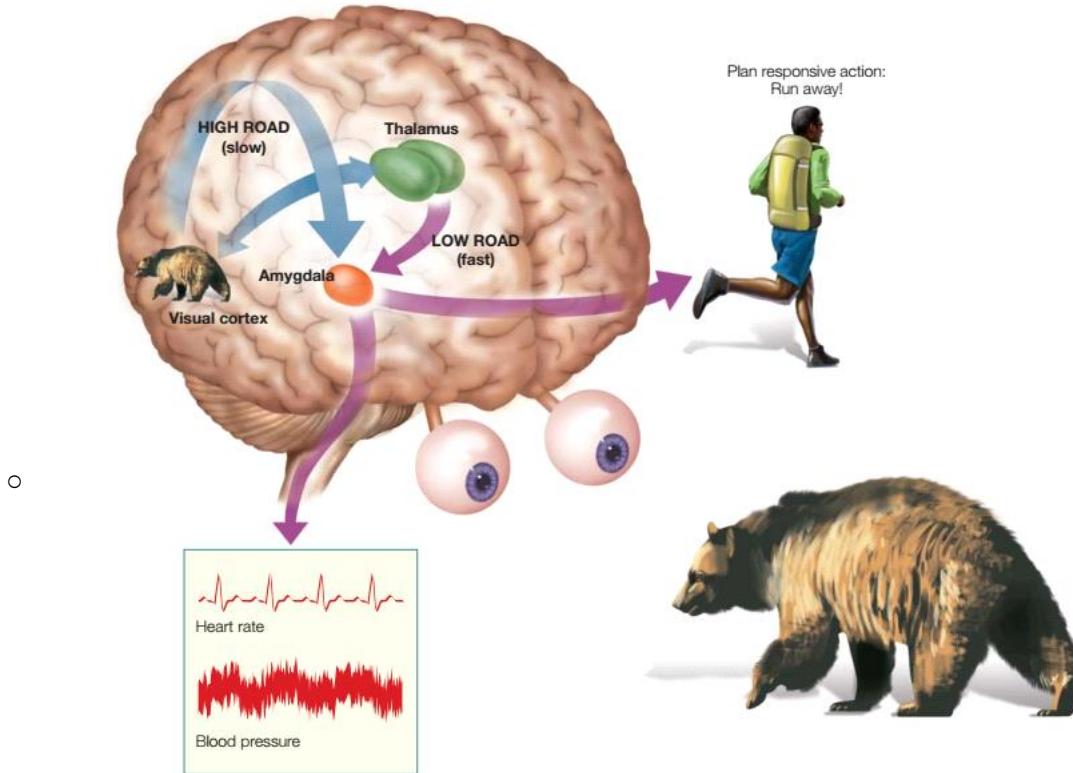


FIGURE 10.10 The amygdala receives sensory input along two pathways.

When a hiker chances upon a bear, the sensory input activates affective memories through the cortical "high road" and subcortical "low road" projections to the amygdala. Even before these memories reach consciousness, however, they produce autonomic changes, such as an increased heart rate, blood pressure, and a startle response such as jumping back. These memories also can influence subsequent actions through the projections to the frontal cortex. The hiker will use this emotion-laden information in choosing his next action: Turn and run, slowly back up, or shout at the bear?

- The role of the amygdala in learning to respond to stimuli that have come to represent aversive events through fear conditioning is said to be implicit.
 - o Learning is expressed indirectly through a behavioral or physiological response
- The amygdala is critical for indirect expression of the conditioned fear
 - o i.e. skin conductance when *told* a stimulus elicits a shock
- Explicit emotional learning
 - o Is the persistence of emotional memories related to the action of the amygdala during emotional arousal?
 - Experiment: Rats with injected with a drug to induce arousal show improved memory
 - With lesion to the amygdala this enhancement of memory is blocked
 - → Amygdala's role is modulatory: Depend on hippocampus for memory acquisition, but on the amygdala for arousal-dependant modulation
 - Studies point to the conclusion that the amygdala modulates hippocampal, declarative memory by enhancing retention by **enhancing hippocampal consolidation**, rather than by altering the initial encoding of the stimulus
 - also suggests that the amygdala can interact directly with the hippocampus during the initial encoding phase
 - o Extreme arousal or chronic stress may actually impair performance of the hippocampal memory system.
 - due to the effect of excessive stress hormones, such as glucocorticoids, on the hippocampus.
- The influence of Emotion on perception and attention
 - o When attentional resources are limited it is the arousing emotional stimuli that reach awareness
 - Amygdala plays a critical role in enhancing our attention when emotional stimuli are present and has a leading role in mediating the transient changes in visual cortical processing

- Emotion-laden stimuli receive greater attention and prior to perceptual processing
- Emotion and decision making
 - Somatic marker hypothesis: emotional information in the form of physiological arousal, is needed to guide decision making.
 - When presented with a situation that requires us to make a decision, we may react emotionally to the situation around us. This emotional reaction is manifest in our bodies as somatic markers—changes in physiological arousal.
 - Three types of emotions influence decision making:
 - 1: Your current emotional state.
 - 2: Your anticipatory emotions; the ones that occur before you make your decision.
 - 3: Based on personal experience, the emotion that you expect to feel after you have made the decision
 - Orbitofrontal cortical damage impairs the ability to respond to changing patterns of reward and punishment
 - It is difficult to reverse an association, once it's learned
 - OFC is selectively active for the magnitude of reward and punishment and for their changing patterns
 - Lesion to the OFC therefore results in poor decision making
 - People with OFC damage have normal emotional reactions to their wins and losses, but they do not feel regret.
 - Experienced feelings about a stimulus and feelings that are independent of the stimulus, such as mood states, have four roles in decision making.
 1. They can act as information.
 2. They can act as “common currency” between disparate inputs and options (you can feel slightly aroused by a book and very aroused by a swimming pool)
 3. They can focus attention on new information, which can then guide the decision.
 4. They can motivate approach or avoid behavior decisions.
- Emotion and social stimuli
 - Depending on the specific facial expression, it appears that different neural mechanisms and regions of the brain are at work, not for processing specific facial expressions per se, but more generally for processing different emotions
- TAKE-HOME MESSAGES:
 - Fear conditioning is a form of classical conditioning in which the unconditioned stimulus is aversive. It is a form of implicit learning.
 - The amygdala is heavily involved in fear conditioning (a form of implicit memory).
 - The conditioned stimulus is a neutral stimulus that, through classical conditioning, will eventually evoke a response. The unconditioned stimulus is the stimulus that, even without training, evokes a response.
 - The unconditioned response is the response naturally elicited (without training) by the unconditioned stimulus. The conditioned response is the response that is elicited (with training) by the conditioned stimulus. Usually the unconditioned response and the conditioned response are the same (e.g., the startle response in the rat), but they have different names depending on what elicits the response.
 - Patients with bilateral amygdala damage fail to acquire a conditioned response during fear conditioning, indicating that the amygdala is necessary for such conditioning to occur
 - Information can reach the amygdala via two separate pathways: The “low road” goes directly from the thalamus to the amygdala; the “high road” goes from the cortex to the amygdala.
 - The amygdala is also important for explicit memory of emotional events. First, the amygdala is necessary for normal indirect emotional responses to stimuli whose emotional properties are learned explicitly, by means other than fear conditioning. Second, the amygdala can enhance the strength of explicit (or declarative) memories for emotional events by modulating the storage of these memories.
 - The amygdala appears to be necessary for automatically deriving information from the eyes of others when identifying emotional facial expressions. This ability is especially critical for the proper identification of fear, because the defining characteristic of fear is an increase in the volume of the eye whites.
 - When looking at faces, the activity of the amygdala increases with the degree of difference

from a categorically average face.

- The amygdala is activated by novel stimuli independent of valence and arousal.
- Attention, perception, and decision making are all affected by emotion.

Get a Grip! Cognitive Control of Emotion

- James Gross' theory of emotional suppression: Gross hypothesized that "shutting down" an emotion at different points in the process of emotion generation would have different consequences and thus, could explain the divergent conclusions.
 - To test his theory, he compared reappraisal, a form of antecedent-focused emotion regulation, with emotion suppression, a response-focused form.
 - Results: Conscious reappraisal reduces the emotional experience; this finding supports the idea that emotions, to some extent, are subject to conscious cognitive control.

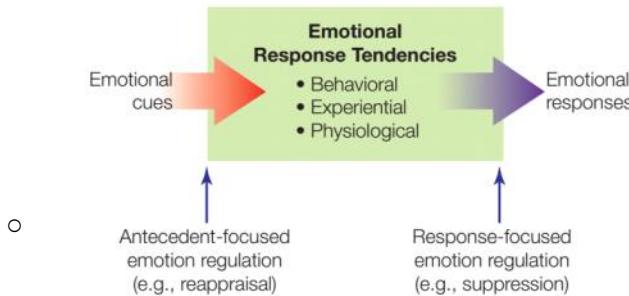


FIGURE 10.21 James Gross's proposed model of emotion.

Gross proposed a model in which emotions may be regulated either by manipulating the input to the system (**antecedent-focused emotion regulation**) or by manipulating its output (**response-focused emotion regulation**).

- Different cognitive reappraisal goals and strategies activate some of the same PFC regions as well as some regions that are different.
- Emotion regulation is complex and involves many processes.
- Emotion regulation is dependent on the interaction of frontal cortical structures and subcortical brain regions.
- Different emotion regulation strategies have different physiological effects.

Other Areas, Other Emotions

- **Insula**
 - There is a significant correlation between insular activity and the perception of internal bodily states (interoception)
 - The junction where cognitive and emotional information are integrated
 - the insula may play a broad role in integrating affective and cognitive processes, whereas the amygdala may have a more selective role in affective arousal, especially for negative stimuli
- **Disgust**
 - The anterior insula is essential for detecting and experiencing disgust
 - Results provide additional evidence that the insula is a neural correlate of disgust identification in others and of experiencing disgust directly
- **Happiness**
 - A complex phenomenon to study...
- **Love**
 - "Love is a complicated business, and it appears to light up much of the brain—but you didn't need an fMRI study to tell you that"
 - Different brain areas are associated with the processing of different emotions. The orbitofrontal cortex is activated when identifying angry facial expressions and hearing angry prosody, and the anterior insula is linked to identification and experience of disgust.
 - The insula appears to play a broad role in integrating affective and cognitive processes

Unique Systems, Common Components

- Emotion research has shifted from identifying areas that specialize in a specific emotion to characterizing how these areas interact and determining if there are any interactions common to different types of emotional experience.
- Ultimately, understanding how we perceive and experience emotion will require studying the interactions of a diverse set of neural structures.

Feeling	Many researchers claim that a feeling is the subjective experience of the emotion, but not the emotion itself.
Emotions	An affective (positive or negative) mental response to a stimulus that is comprised of a physiological response, a behavioral response, and a subjective experience (e.g., by change in heart rate, facial expression, and speech).
Emotion generation	Typically a combination of a bottom up emotional response in combination with a top down emotional response that involves memory and linguistic representation
Emotional stimulus	A stimulus that is highly relevant for the well-being and survival of the observer
Basic emotions	Basic emotions comprise a closed set of emotions, each with unique characteristics, carved by evolution, and reflected through facial expressions
Complex emotions	Complex emotions are combinations of basic emotions, some of which may be socially or culturally learned, that can be identified as evolved, long-lasting feelings.
Dimensions of emotions	Dimensions of emotion describe emotions that are fundamentally the same but that differ along one or more dimensions, such as valence (pleasant or unpleasant, positive or negative) and arousal (very pleasant to very unpleasant), in reaction to events or stimuli.
Facial expressions	The nonverbal communication of emotion by manipulation of particular groups of facial muscles. Research findings suggest six basic human facial expressions represent the emotional states anger, fear, disgust, happiness, sadness, and surprise.
Core affect	Mental representation of bodily changes
Amygdala	Groups of neurons anterior to the hippocampus in the medial temporal lobe that are involved in emotional processing.
Fear conditioning	Learning in which a neutral stimulus acquires aversive properties by virtue of being paired with an aversive event.
Attentional blink	A phenomenon often observed during rapid serial presentations of visual stimuli, in which a second salient target that is presented between 150-450 ms after the first one goes undetected.
Somatic markers	A physiological-emotional mechanism that was once theorized to help us sort through possible options and make a decision. Somatic markers were thought to provide a common metric for evaluating options with respect to their potential benefit.
Orbitofrontal cortex	A region of the frontal lobe, located above the orbits of the eyes, that is implicated in a range of functions, including perceptual processes associated with olfaction and taste, as well as those associated with monitoring whether one's behavior is appropriate.
Emotional regulation	Emotional regulation refers to the processes that influence the type of emotions we have, when we have them, and how we express and experience them. Emotion regulation processes can intervene in multiple points in the emotion generation process - some conscious, other unconscious
Affective flexibility	Processing the relevance of various stimuli depending on a person's current goals and motivation
Insula	A part of cortex known to process gustatory information.

Introspection	perception of internal bodily states
Flow	Being in the "zone" - the process of having an optimal experience

Lecture 17/4

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Language

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The Anatomy of Language

ANATOMICAL ORIENTATION

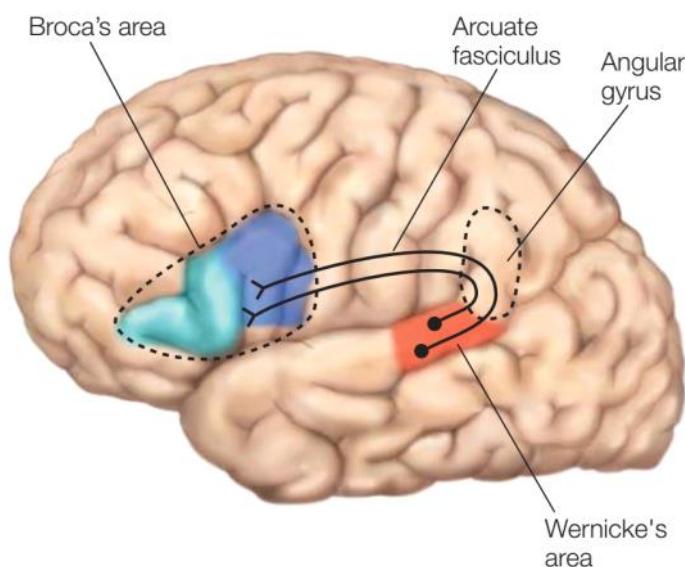
The anatomy of language

A diagram of the left hemisphere of the brain. Several regions are highlighted and labeled: Broca's area (blue) is located in the inferior frontal cortex; the Inferior frontal cortex is also labeled. The Sylvian fissure is shown as a deep groove. The Superior temporal gyrus (green) is located above the Sylvian fissure. The Supramarginal gyrus (red) and Angular gyrus (pink) are located in the parietal lobe. Wernicke's area (cyan) is located in the posterior part of the superior temporal gyrus. Lines connect the labels to their respective locations on the brain diagram.

Language processing is located primarily in the left hemisphere. Many regions located on and around the Sylvian fissure form a language processing network.

- Anomia is the inability to find the words to label things in the world. It is not a deficit of knowledge.
- A left-hemisphere network involving the frontal, parietal, and temporal lobes is especially critical for language production and comprehension.
- The right hemisphere does have roles in language, especially in processing the prosody of language.

Brain Damage and Language Deficits



- Lichtheim first described the classical localizationist model:
 - o linguistic information, word storage (A 5 Wernicke's area),
 - o speech planning (M 5 Broca's area)

- conceptual information stores (B)
 - are located in separate brain regions interconnected by white matter tracts.
 - The white matter tract that flows from Wernicke's area to Broca's area is the arcuate fasciculus.

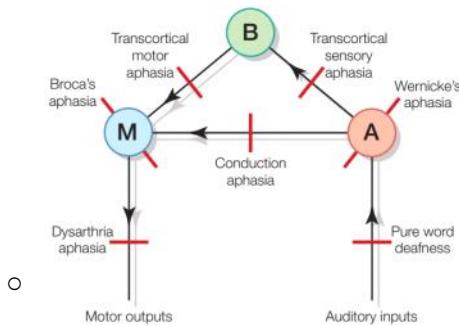


FIGURE 11.4 Lichtheim's classical model of language processing.
The area that stores permanent information about word sounds is represented by A. The speech planning and programming area is represented by M. Conceptual information is stored in area B. The arrows indicate the direction of information flow. This model formed the basis of predictions that lesions in the three main areas, or in the connections between the areas, or the inputs to or outputs from these areas, could account for seven main aphasias. The locations of possible lesions are indicated by the red line segments. A = Wernicke's area. B = conceptual information stores. M = Broca's area.

- Language disorders, generally called aphasia, can include deficits in comprehension or production of language resulting from neurological damage.
- Patients with Broca's aphasia have problems with speech production, syntax, and grammar, but otherwise comprehend what is said or written fairly well.
- The lesions that produce Broca's aphasia may not be limited to the classically defined Broca's area in the left inferior frontal cortex.
- People with Wernicke's aphasia have severe comprehension deficits but can produce relatively fluid speech; it is, however, rather meaningless. Originally linked to damage solely in Wernicke's area (the posterior superior temporal gyrus), today Wernicke's aphasia is also linked to damage outside the classic Wernicke's area.
- Aphasia can also result from damage to the connection between Wernicke's and Broca's areas (the arcuate fasciculus). Conduction aphasia is the disorder that results from such damage, and people with this type of aphasia have problems producing spontaneous speech as well as repeating speech.

The Fundamentals of Language in the Human Brain

- The mental lexicon is the brain's store of words and concepts.
- A morpheme is the smallest unit of language that has meaning.
- A phoneme is the smallest unit of sound that makes a difference to meaning.
- Semantic (meaning) relationships between words are an organizational principle of the mental lexicon.
- Syntax refers to the way in which words in a particular language are organized into grammatically permitted sentences.
- Grammar refers to the structural rules that govern the composition of words, phrases, and sentences in a particular natural language.
- Patients with neurological damage may name an item with an incorrect but semantically-related word (e.g., "animal" for "horse"), which supports the idea that the mental lexicon contains semantic networks of related meanings clustered together

The arcuate fasciculus (Latin: curved bundle) is a bundle of axons that forms part of the superior longitudinal fasciculus, an association fiber tract.

The arcuate bidirectionally connects caudal temporal cortex and inferior parietal cortex to locations in the frontal lobe.^{[1][2]} The arcuate fasciculus connects Broca's Area and Wernicke's Area.

Language Comprehension

- Perceptual analysis of linguistic input

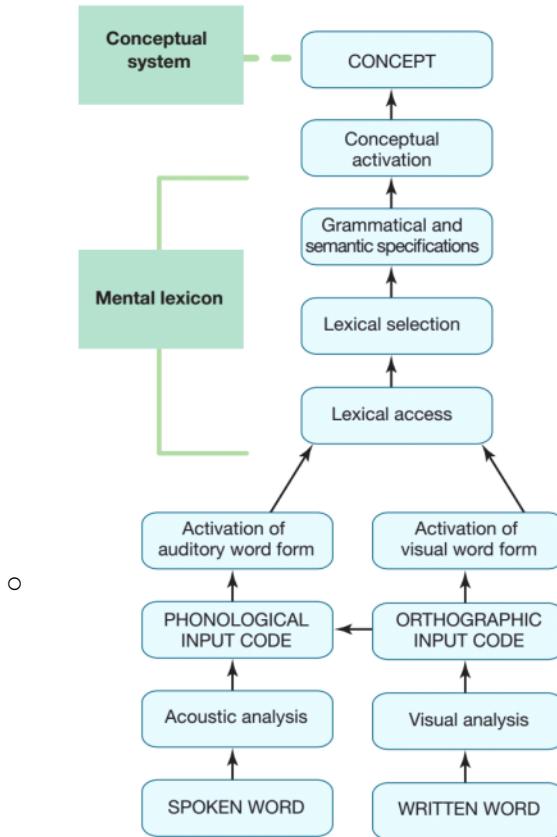


FIGURE 11.8 Schematic representation of the components involved in spoken and written language comprehension.
Inputs can enter via either auditory (spoken word) or visual (written word) modalities. Notice that the information flows from the bottom up in this figure, from perceptual identification to "higher level" word and meaning activation. So-called interactive models of language understanding would predict top-down influences to play a role as well. For example, activation at the word-form level would influence earlier perceptual processes. We could introduce this type of feedback into this schematic representation by making the arrows bidirectional (see "How the Brain Works: Modularity Versus Interactivity").

- Spoken input: Understanding speech

Language Comprehension | 483

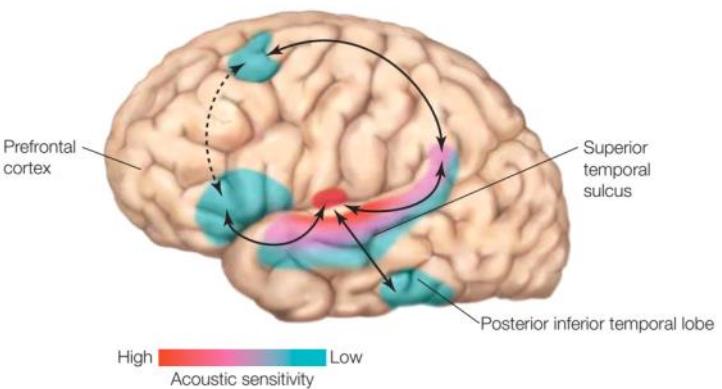


FIGURE 11.10 Brain areas important to speech perception and language comprehension.
Acoustic sensitivity decreases moving anteriorly and posteriorly away from primary auditory cortex, while speech sensitivity increases. Anterior and posterior regions of the superior temporal sulcus are increasingly speech specific. Posterior inferior temporal lobe and prefrontal regions are also important during speech processing. Heschl's gyrus (primary auditory cortex; red spot) is not speech specific, but is instead activated by all auditory inputs.

- There are no pauses between phonemes in speech that correspond to words: segmentation problem
- The prosody of speech is the rhythm and the pitch of the speaker's voice.
- Sound comprehension involves the superior temporal cortex. People with damage to this area have pure word deafness.
- Distinguishing speech from nonspeech sounds occurs in the mid-portion of the superior temporal

- sulcus (STS), but no lexical-semantic information is processed in this area.
- Spoken-word recognition processing proceeds anteriorly in the superior temporal gyrus (STG): Phoneme processing appears localized to the left mid-STG, integration of phonemes into words appears localized to the left anterior STG, and processing short phrases appears to be carried out in the most anterior locations of STS.
- Written Input: Reading words:
 - o Written-word processing takes place in occipitotemporal regions of the left hemisphere. Damage to this area can cause pure alexia, a condition in which patients cannot read words, even though other aspects of language are normal.
 - o Occipitotemporal regions of the left hemisphere may be specialized for the identification of orthographic units.
- The role of context in word recognition:
 - o Three classes of models attempt to explain word comprehension: Modular models, interactive models and hybrid models.
 - o Lexical selection can be influenced by sentence context.
 - o Lexical access and selection involve a network that includes the middle temporal gyrus (MTG), superior temporal gyrus (STG), and the ventral inferior and bilateral dorsal inferior frontal gyri (IFG) of the left hemisphere.
 - o Left MTG and STG are important for the translation of speech sounds to word meanings.
 - o Syntactic parsing is the process in which the brain assigns a syntactic structure to words in sentences.
 - o In the ERP method, the N400 is a negative-polarity brain wave related to semantic processes in language, and the P600/SPS is a large positive component elicited after a syntactic and some semantic violations

Syntactic processing takes place in a network of left inferior frontal and superior temporal brain regions that are activated during language processing

Neural Models of Language Comprehension

- Models of language involve unifying information from linguistic inputs or from retrieved linguistic representations with stored knowledge.
- White matter tracts in the left hemisphere connect frontal and temporal lobes to create specific circuits for speech, semantic analysis, and syntactic processing

Neural Models of Speech Production

- Levelts model:

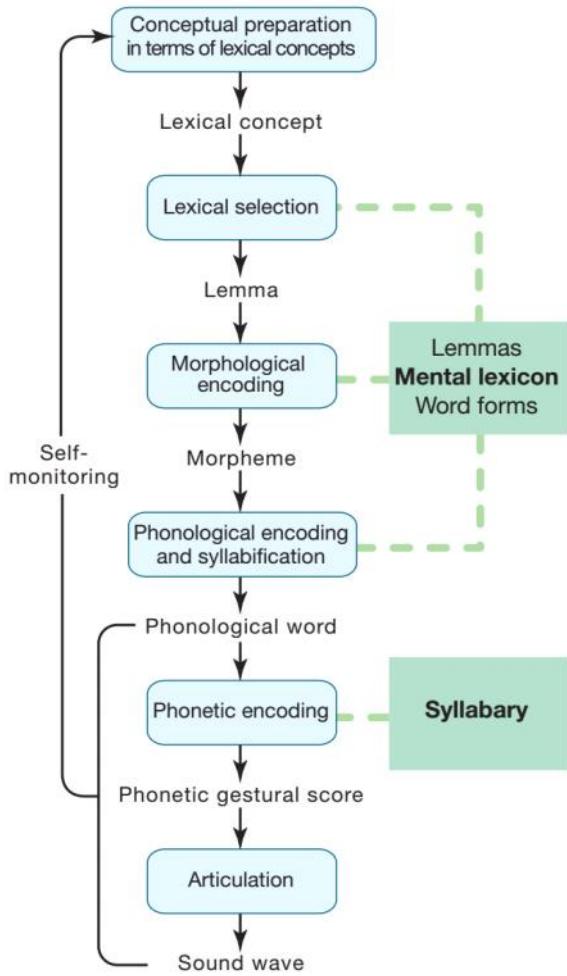


FIGURE 11.23 Outline of the theory of speech production developed by Willem Levelt.

The processing components in language production are displayed schematically. Word production proceeds through stages of conceptual preparation, lexical selection, morphological and phonological encoding, phonetic encoding, and articulation. Speakers monitor their own speech by making use of their comprehension system.

- Models of language production must account for the selection of the information to be contained in the message; retrieving words from the lexicon; sentence planning and grammatical encoding using semantic and syntactic properties of the word; using morphological and phonological properties for syllabification and prosody; and preparing articulatory gestures for each syllable.
- Each stage in Levelt's model for language production occurs serially, and its output representation is used for input to the next stage. It avoids feedback, loops, parallel processing, and cascades, and it fits well with the findings of ERPs recorded intracranially.

Evolution of Language

- Animal calls can carry meaning and show evidence of rudimentary syntax. In general, however, animal calls tend to be inflexible, associated with a specific emotional state, and linked to a specific stimulus.
- Many researchers suggest that language evolved from hand gestures, or a combination of hand gestures and facial movement.
- Areas that control hand movement and vocalizations are closely located in homologous structures in monkeys and humans

Anomia	The inability to name objects
Sylvian fissure	Also lateral fissure. A large fissure (sulcus) on the lateral surface of the cerebral cortex first described by the anatomist Franciscus Sylvius. The Sylvian fissure separates the frontal cortex from the temporal lobe below.
Wernicke's area	Area of human left posterior superior temporal gyrus: Identified by Carl Wernicke in the 19th century.
Broca's area	An area located in the left hemisphere of the frontal cortex that is important to language production
Aphasia	Broad term referring to the collective deficits in language comprehension and production that accompany neurological damage, even though the articulatory mechanisms are intact
Dysarthria	Loss of control over articulatory muscles
Speech apraxia	Deficits in the motor planning of articulations
Broca's aphasia	The oldest and perhaps best-studied form of aphasia, characterized by speech difficulties in the absence of severe comprehension problems. However, Broca's aphasics may also suffer from problems in fully comprehending grammatically complex sentences. Compare Wernicke's aphasia.
Syntax	Rules governing how words are put together in a sentence
agrammatic aphasia	Difficult producing and/or understanding the structure of sentences. Agrammatic aphasia is seen in brain-damaged patients who may speak using only content words, leaving out function words such as the and a.
Wernicke's aphasia	A language deficit usually caused by brain lesions in the posterior parts of the left hemisphere, resulting in comprehension deficits. Compare Broca's aphasia.
arcuate fasciculus	A white matter tract that connects the posterior temporal region with frontal brain regions and is believed to transmit language-related information between the posterior and anterior brain regions.
conduction aphasia	Conduction aphasics can understand words that they hear or see and can hear their own speech errors, but they cannot repair them. They have problems producing spontaneous speech as well as repeating speech, and sometimes they use words incorrectly
Global aphasia	the inability to both produce and comprehend language. Typically, this type of aphasia is associated with extensive left-hemisphere damage, including Broca's area, Wernicke's area, and regions between them.
mental lexicon	A mental store of information about words that includes semantic information (the words' meanings), syntactic information (how the words are combined to form sentences), and the details of word forms (their spellings and sound patterns)
Lexical access	refers to the stage(s) of processing in which the output of perceptual analysis activates word-form representations in the mental lexicon, including their semantic and syntactic attributes
Lexical selection	the lexical representation in the mental lexicon that best matches the input can be identified (selected)
lexical integration	integrates words into the full sentence, discourse, or larger context
morpheme	the smallest meaningful unit in a language
Phoneme	the smallest unit of sound that makes a difference to meaning.
Semantic	The way that meaning is represented in the words of a language
Semantic paraphasias	The production of a word related in meaning to the intended word (e.g., horse for cow) instead of the intended word itself. Wernicke's aphasia patients often produce semantic

	paraphasias
Alexia	Patients cannot read words, even though other aspects of language are normal.
Phonology	The way sounds of a language are organized to create meaning

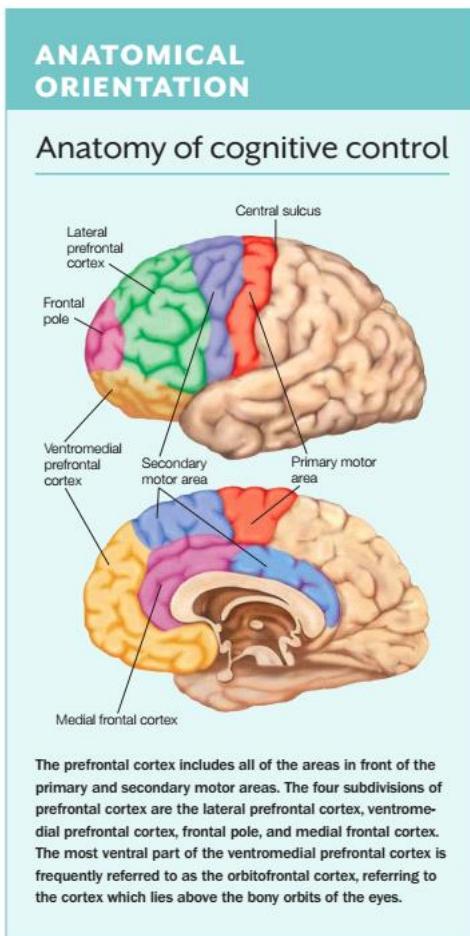
Cognitive Control

Wednesday, April 25, 2018 2:04 PM

What Is Cognitive Control?

- Cognitive control refers to mental abilities that involve planning, controlling, and regulating the flow of information processing.

The Anatomy Behind Cognitive Control



- Prefrontal cortex includes four major components: lateral prefrontal cortex, frontal pole, medial frontal cortex, and ventromedial prefrontal cortex. All are associated with cognitive control.

Cognitive Control Deficits

- The ability to make goal-directed decisions is impaired in patients with frontal cortex lesions, even if their general intellectual capabilities remain unaffected

Goal-Oriented Behavior

- Goal-oriented behaviors allow humans and other animals to interact in the world in a purposeful way.
- A goal-oriented action is based on the assessment of an expected reward and the knowledge that there is a causal relationship between the action and the reward. Goal-oriented behavior requires the retrieval, selection, and manipulation of task-relevant information.
- A habit is a response to a stimulus that is no longer based on a reward.
- Working memory consists of transient representations of task-relevant information. The prefrontal

cortex

(especially the lateral prefrontal cortex) is a key component in a working memory network.

- Physiological studies in primates show that cells in the prefrontal cortex remain active even when the stimulus is no longer present in delayed-response tasks. A similar picture is observed in functional imaging studies with humans. These studies also demonstrate that working memory requires the interaction of the prefrontal cortex with other brain regions.
- Various frameworks have been proposed to understand functional specialization within the prefrontal cortex.

Three gradients have been described to account for processing differences in prefrontal cortex:

anterior–

posterior, ventral–dorsal, and lateral–medial

As a heuristic, we can think of PFC function as organized along three separate axes

1. A ventral–dorsal gradient organized in terms of maintenance and manipulation as well as in a manner that reflects general organizational principles observed in more posterior cortex, such as the ventral and dorsal visual pathways for “what” versus “how.”

2. An anterior–posterior gradient that varies in abstraction, where the more abstract representations engage the most anterior regions (e.g., frontal pole) and the least abstract engage more posterior regions of the frontal lobes. In the extreme, we might think of the most posterior part of the frontal lobe, the primary motor cortex, as the point where abstract intentions are translated into concrete movement.

3. A lateral–medial gradient related to the degree to which working memory is influenced by information in the environment (more lateral) or information related to personal history and emotional states (more medial).

In this view, lateral regions of PFC integrate external information that is relevant for current goal-oriented behavior, whereas more medial regions allow information related to motivation and potential reward to influence goal-oriented behavior.

Decision Making

- A decision is the selection of one option among others based on the predicted value of the consequences (reward).
- Some rewards are primary reinforcers, such as food, water and sex; others are secondary reinforcers, such as money and status.
- The subjective value of an item is made up of multiple variables that include payoff amount, context, probability, effort/cost, temporal discounting, novelty, and preference.
- Single-cell recordings in monkeys and fMRI studies in humans have implicated frontal regions, including orbitofrontal cortex, in value representation
- Prediction error (PE) is the difference between the expected reward and what was actually obtained. The firing rate of dopamine neurons is correlated with prediction error.
- Prediction error is used to update value information and learning.
- All dopaminergic neurons appear to give alerting signals, but some are activated by reward value while others are activated by reward salience, which may act to control motivated behavior. Their anatomical organization appears to reflect their functional organization

Goal Planning

- Successful execution of an action plan involves three components: (a) identifying the goal and developing subgoals, (b) anticipating consequences when choosing among goals, and (c) determining what is required to achieve the goals.
- An important part of cognitive control is the ability to shift focus from one subgoal to another. People who cannot shift between subgoals are said to “perseverate.”
- Goal-oriented behavior requires the retrieval and selection of task-relevant information. The prefrontal cortex can be conceptualized as a dynamic filtering mechanism through which the task-relevant information is activated and maintained in working memory

Goal-Based Cognitive Control

- In goal-directed control, information processing is influenced by goals and the allocation of attentional resources.

- Goal-oriented behavior involves the amplification of task-relevant information and the inhibition of task-irrelevant information. Amplification and inhibition may entail separate processes given that aging selectively affects the ability to inhibit task-irrelevant information.
- Patients with prefrontal cortex damage lose inhibitory control. For example, they cannot inhibit task-irrelevant information.
- A network spanning prefrontal cortex and posterior cortex provides the neural substrates for interactions between goal representations and perceptual information. This dynamic process is revealed in studies that combine different cognitive neuroscience methods to show that, as task goals are modified, activation in perceptual areas is either increased or decreased compared to baseline conditions.
- The inhibition of action constitutes another form of cognitive control. In the stop-signal task, participants attempt to abort a planned response. The right inferior frontal gyrus and the subthalamic nucleus are important for this form of control.

Ensuring That Goal-Oriented Behaviors Succeed

Cognitive Control (executive function)	allows us to use our perceptions, knowledge, and goals to bias the selection of action and thoughts from a multitude of possibilities. Cognitive control is essential for purposeful goal-oriented behavior and decision making
Goal-oriented behavior	Behavior that allows us to interact in the world in a purposeful manner. Goals reflect the intersection of our internal desires and drives, coupled with the current environmental context
prefrontal cortex (PFC)	A region of cortex that takes part in the higher aspects of motor control and the planning and execution of behavior, perhaps especially tasks that require the integration of information over time and thus mandate the involvement of working memory mechanisms. The prefrontal cortex has three or more main areas that are commonly referred to in descriptions of the gross anatomy of the frontal lobe: the dorsolateral prefrontal cortex, the anterior cingulate and medial frontal regions, and the orbitofrontal cortex
Lateral prefrontal cortex (LPFC)	The region of the cerebral cortex that lies anterior to Brodmann area 6, along the lateral surface. This region has been implicated in various executive functions, such as working memory and response selection.
Frontal polar region (FP)	The most anterior part of the prefrontal cortex, including area 10 and parts of area 9. This region is hypothesized to play a critical role in the hierarchical representation of action goals
Orbitofrontal cortex (OFC)	A region of the frontal lobe, located above the orbits of the eyes, that is implicated in a range of functions, including perceptual processes associated with olfaction and taste, as well as those associated with monitoring whether one's behavior is appropriate
medial frontal cortex (MFC)	The medial region of the frontal cortex that includes parts of areas 24, 32, and inferior aspects of 6 and 8. The medial frontal cortex is associated with cognitive control—in particular, monitoring functions for error detection and resolving conflict
Dopamine	An organic chemical amine that in the brain functions as a neurotransmitter. It is formed from L-DOPA by removing a carboxyl group
Ventral tegmental area	A part of the dopamine system. Dopaminergic neurons originating here project through either the mesolimbic pathway, or the mesocortical pathway.
striatum	One of the nuclei of the basal ganglia. The striatum is the main receiving zone of the basal ganglia, receiving extensive inputs from the cerebral cortex and other subcortical structures. The striatum in humans is composed of the caudate and putamen nuclei.
perseveration	Persisting in a response even after being told that it is incorrect

utilization behavior	extreme dependency on prototypical responses for guiding behavior
Goal-oriented actions	based on the assessment of an expected reward or value and the knowledge that there is a causal relationship between the action and the reward
Action-outcome	When there is a causal relationship between the action and the reward
Habit	A habit is defined as an action that is no longer under the control of a reward, but is stimulus driven; as such, we can consider it automatic.
Working memory	Transient representations of task-relevant information. These representations may be related to information that has just been activated from long-term memory or something recently experienced. Representations in working memory guide behavior in the present, constituting what has been called, "the blackboard of the mind."
Delayed-response tasks	A task in which the correct response must be produced after a delay period of several seconds. Such tasks require the operation of working memory because the animal or person must maintain a record of the stimulus information during the delay period
Recency memory	the ability to organize and segregate the timing or order of events in memory
Normative decision theories	Normative decision theories define how people ought to make decisions that yield the optimal choice.
Descriptive decision theories	Descriptive decision theories attempt to describe what people actually do, not what they should do
action-outcome decisions	With an action-outcome decision, the decision involves some form of evaluation (not necessarily conscious) of the expected outcomes.
stimulus-response decisions	After we repeat that action, and if the outcome is consistent, the process becomes habitual; that is, it becomes a stimulus-response decision.
Primary reinforcer	They have a direct benefit for survival fitness. Their value, or our response to these reinforcers, is to some extent hardwired in our genetic code
Secondary reinforcers	rewards that have no intrinsic value themselves but become rewarding through their association with other forms of reinforcement
Value	An abstract entity referring to the overall preference given to a stimulus or action. The value is assumed to reflect the combination of a number of different attributes such as how much reward will be received, the likelihood of that reward, and the efforts and costs required to achieve the reward
nucleus accumbens	The ventral part of the striatum, one of the nuclei of the basal ganglia. The nucleus accumbens is associated with the reward system of the brain, showing changes in activity in response to both primary and secondary reinforcers.
mesocortical pathway	A path through which dopaminergic projections travel to reach the neocortex.
Prediction error	A theoretical construct in theories of reinforcement learning that is defined as the difference between an expected and actual outcome or reward. If the reward is greater than expected, a positive prediction occurs which can be used to increase the likelihood of the behavior. If the reward is less than expected, the negative prediction can be used to decrease the likelihood of the behavior.
Dynamic filtering	The hypothesis that a key component of working memory involves the selection of information that is most relevant, given current task demands. This selection is thought to

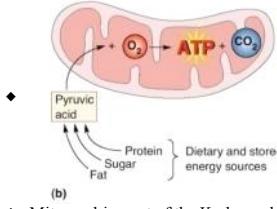
	be accomplished through the filtering, or exclusion of, potentially interfering and irrelevant information.
Inhibitory control	The hypothesis that one aspect of executive functions is the regulation of habitual responses or environmentally dictated actions by active inhibition. A loss of inhibitory control is assumed to underlie the tendency of some patients with prefrontal lesions to produce socially inappropriate behavior
Monitoring	The executive function associated with evaluating whether current representations and/or actions are conducive to the achievement of current goals. Errors can be avoided or corrected by a monitoring system. One of the hypothesized operations of a supervisory attentional system.
Anterior cingulate cortex	Anterior portion of the cingulate cortex, located below the frontal lobe along the medial surface. This region is characterized by a primitive cytoarchitecture (three-layered cortex) and is part of the interface between the frontal lobe and the limbic system. The anterior cingulate cortex is implicated in various executive functions, such as response monitoring, error detection, and attention
Supervisory attentional system	The psychological model used to explain how response selection is achieved in a flexible manner. Without the SAS, behavior is dictated by context, with the selected action being the one that has been produced most often in the current context. The SAS allows for flexible behavior by biasing certain actions based on current goals or helping to determine actions in unfamiliar situations.
Errorrelated negativit (ERN)	An electrical signal that is derived from the EEG record following an erroneous response. The ERN is seen as a prominent negative deflection in the ERP, and it is hypothesized to originate in the anterior cingulate
response conflict.	A situation in which more than one response is activated, usually because of some ambiguity in the stimulus information. It has been hypothesized that the anterior cingulate monitors the level of response conflict and modulates processing in active systems when conflict is high

Outline for: Basic neurophysiology

Tuesday, January 30, 2018 10:06 AM

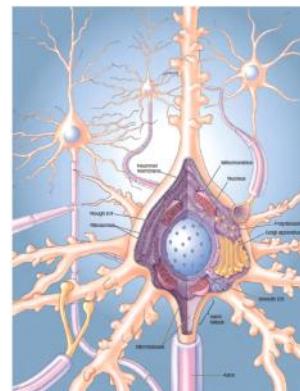
The structure of neurons:

- Neurons are the cells that transmit information throughout the nervous system.
- Most neurons consist of a cell soma (body), axon, and dendrites.
 - o The soma (body) includes
 - **Cytosol:** watery fluid inside the cell
 - **Organelles:** membrane enclosed structures within the soma
 - **Mitochondria:** generate most of the cell's supply of **adenosine triphosphate (ATP, chemical energy)**



- ◆ Mitocondria: part of the Krebs cycle (complicated cycle, main point: a single cell is a complex)

- o Cytoplasm: contents within a cell membrane (e.g., organelles, excluding the nucleus)
- o The axon is isolated by myelin
 - Myelin allows for the rapid transmission of action potentials down an axon.
 - Along the axon: **Nodes of Ranvier:** the spaces between sheaths of myelin where voltage-gated Na⁺ and K⁺ channels are located and action potentials occur.
- A membrane surrounds the neuron:
 - o Barrier that encloses cytoplasm
 - o Important to maintain electrical and chemical gradings → important to life
 - o The membrane consists of lipids
 - Lipids are hydrophobic opposed to hydrophilic, meaning they do not dissolve in water



Neuronal Signaling

- A resting neuron is more negative on the outside, than the inside around called the **resting membrane potential**, -70 mV.
 - o Due to difference in concentration of ions on the inside and the outside of the membrane
 - o Na⁺ and Cl⁻ concentrations are greater outside of the cell, and K⁺ concentrations are greater inside the cell

Outside	Inside
[K ⁺] _o = 5 mM	[K ⁺] = 100 mM
[Na ⁺] _o = 150 mM	[Na ⁺] = 15 mM
[Ca ²⁺] _o = 2 mM	[Ca ²⁺] = 0.0002 mM
[Cl ⁻] _o = 150 mM	[Cl ⁻] = 13 mM

- o **Polarized:** When a neuron has a negative membrane potential

- The neuronal membrane is peppered with transmembrane proteins enabling ions to move through the membrane
 - o **Ion channels:** Proteins selective to ions to pass through the membrane (passive)
 - Hydrophilic channel
 - Since there are many more K⁺ channels, than other channels, the membrane is more permeable for K⁺ than Na⁺
 - Two types of channels:
 - **Non-gated ion channels:** Always allows associated ions to pass through
 - **Gated ion channels (e.g. voltage gated channels):** Open or close due to change in voltage or chemical or physical stimuli
 - o **Ion pumps:** Active transport of ions across the membrane against their concentration gradients (from low to higher concentration)
 - How does the neuron maintain resting membrane potential?
 - o The answer is: Na⁺/K⁺-pump (**sodium-potassium pump**) and the fact that the **membrane is more permeable for K⁺.**
 - **Na⁺/K⁺-pump:** For each molecule of ATP that is **hydrolyzed**, the resulting energy is used to move three Na⁺-ions out of the cell and two K⁺ ions into the cell
 - To even out the concentration gradient of ions, K⁺ ions are carried out of the neuron, leaving it more negative than the outside
 - **Creating an electrochemical gradient:** More negative on the outside than the inside

- How does the signaling occur?
 - 1: Environmental stimuli occur, triggering the sodium channels to open → increasing the charge inside the membrane
 - The stimuli has to be strong enough to reach the threshold of **-55 mV**, otherwise it is a graded potential, which is a local phenomenon. **All-or-nothing phenomenon.**
 - 2: If the increase in charge inside the neuron is large enough, the gated ion channels will open, and sodium ion will rush into the neuron causing a **depolarization +40 mV**
 - A chain reaction of depolarization will move along the axon. If one area is depolarized, changing the current → causing other gated ion channels to open
 - 3: **Re polarization:** The potassium gated ion channels open, trying to even out the balance
 - 4: **Hyperpolarization:** Too many potassium leaves the neuron, until the sodium-potassium pump starts working again
- Refractory period: During this transient hyperpolarization state, the voltage-gated Na⁺ channels are unable to open, and another action potential cannot be generated → the current can go only ONE way.
- The amplitude of the action potential does not depend on the size of the triggering depolarization, as long as that depolarization reaches threshold for initiating the action potential.
 - The amplitude is determined by the **rate of firing**

Synaptic Transmission

- Neurons communicate with other neurons in the **synapses**, where chemical and electrical signals can be conveyed between neurons
 - o found on dendrites and at axon terminals or on the neuronal cell body.
- **Two kinds of transmission:**
 - Chemical synapse
 - o Release of neurotransmitters and the binding of those to the postsynaptic neuron causes excitatory or inhibitory postsynaptic potentials
 - If the potentials are excitatory or inhibitory depends on the properties of the postsynaptic receptor - not the neurotransmitter

? I thought, they worked opposingly?
Slide 43: Indikerer lidt, at den er negativt ladet??

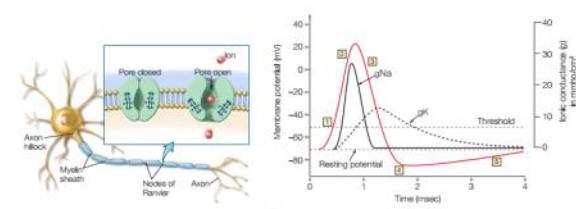
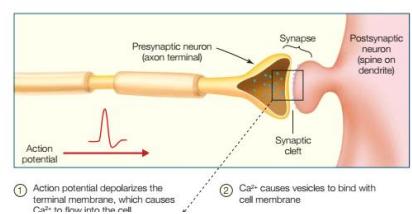


FIGURE 2.11 The neuronal action potential, voltage-gated ion channels, and changes in channel conductance.
(a) An idealized neuron with myelinated axon and axon terminals. Voltage-gated ion channels located in the spike-triggering zone of the axon hillock, and along the extent to the axon, open and close rapidly, changing their conductance to specific ions (e.g., Na⁺), altering the membrane potential and resulting in the action potential (depolarization). (b) Graph of changes in membrane voltage over an action potential. The initial depolarizing phase of the action potential (red line) is mediated by an increase in Na⁺ conductance (black line), and the later repolarizing, descending phase of the action potential is mediated by an increase in K⁺ conductance (dashed line) that occurs when the K⁺ channels open. The Na⁺ channels have closed during the last part of the action potential, when repolarization by the K⁺ current is taking place. The action potential undershoots the resting membrane potential at the point where the membrane becomes more negative than the resting membrane potential.

Chemical synapse:



- Chemical synapse.
 - o Release of neurotransmitters and the binding of those to the postsynaptic neuron causes excitatory or inhibitory postsynaptic potentials
 - If the potentials are excitatory or inhibitory depends on the properties of the postsynaptic receptor - not the neurotransmitter
 - o The process: Neurotransmitter synthesis → Load neurotransmitter into synaptic vesicles → Vesicles fuse to presynaptic terminal → Neurotransmitter spills into synaptic cleft → Binds to postsynaptic receptors → Biochemical/electrical response elicited in postsynaptic cell → Removal of neurotransmitter from synaptic cleft

Removal of neu
rotransmitters: can be accomplished by (a) active reuptake back into the presynaptic terminal, (b) enzymatic breakdown of the transmitter in the synaptic cleft, or (c) diffusion of the neurotransmitter away from the region of the synapse.

- Electrical synapse:
 - o Pass current directly from one neuron (presynaptic) to another neuron (postsynaptic) via specialized channels in gap junctions that connect the cytoplasm of one cell directly to the other

- The Role of Glial Cells

- Glial cells = nonneuronal cells that serve various functions in the nervous system: Provide support, nutrition, insulation, and helps signal transmission in the nervous system
- Types of glial cells:
 - o Astrocyte: helps form the blood-brain barrier.
 - o Oligodendrocyte: forms myelin in the central nervous system, which aids the speed of information transfer = **Nodes of Ranvier**
 - o Schwann cell: forms myelin in the peripheral nervous system.
 - When axons are myelinated, it is possible to change the current for one part of the axon to the next, leaping from each node of Ranvier to the other = **Saltatory conduction**

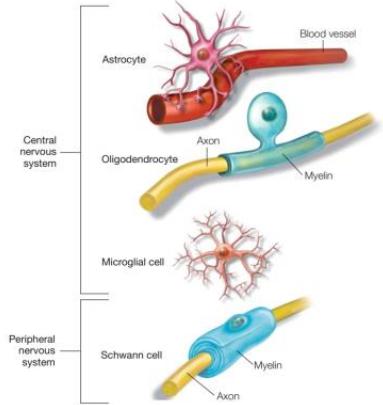


FIGURE 2.15 Various types of glial cells in the mammalian central and peripheral nervous systems.
An astrocyte is shown with end feet attached to a blood vessel. Oligodendrocytes and Schwann cells produce myelin around the axons of neurons—oligodendrocytes in the central nervous system, and Schwann cells in the peripheral nervous system. A microglial cell is also shown.

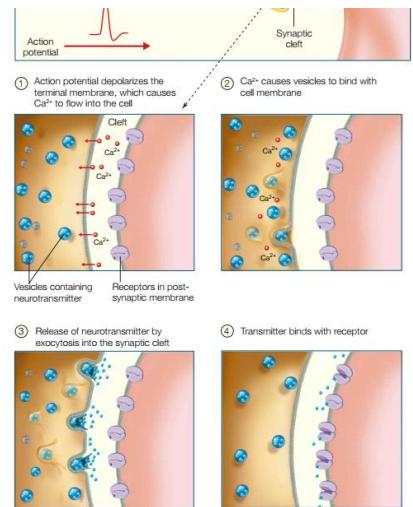


FIGURE 2.12 Neurotransmitter release at the synapse, into synaptic cleft.
The synapse consists of various specializations where the presynaptic and postsynaptic membranes are in close apposition. When the action potential invades the axon terminals, it causes voltage-gated Ca^{2+} channels to open (1), which triggers vesicles to bind to the presynaptic membrane (2). Neurotransmitter is released into the synaptic cleft by exocytosis and diffuses across the cleft (3). Binding of the neurotransmitter to receptor molecules in the postsynaptic membrane completes the process of transmission (4).

Outline for: Neuroanatomical Overview

Tuesday, February 6, 2018 10:52 AM

Why learn neuroanatomy?

- The structure implies function, which is what we are investigating
 - If damage to the same area create similar deficits → evidence for structure-function
- Connections between areas may be functionally relevant to see interconnections e.g. structures important for language
- Inspiration for development of AI

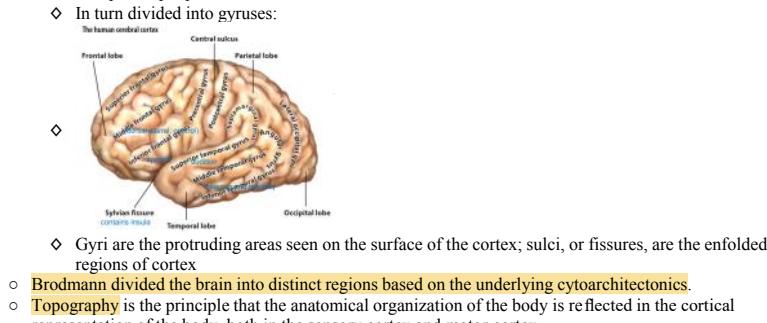
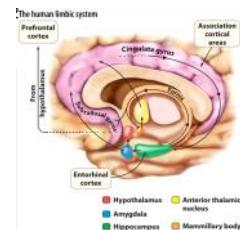
The Bigger Picture

- Overview of Nervous system

- The central nervous system: Brain and spinal cord.
 - o Nucleus: Neurons buried in white matter, which is relatively compact arrangements of nerve cell bodies and their connection
 - o The white matter: Axon and glial cells forming tracts interconnecting the brain (white by myelin)
 - o The grey matter: neurons arranged in layers forming a sheet tissue
- The peripheral nervous system: All nerves and neurons outside of the central nervous system
- The autonomic nervous system: Involved in controlling the action of smooth muscles, the heart, and various glands.
 - o Subdivided into sympathetic and parasympathetic systems:
 - The sympathetic system uses the neurotransmitter norepinephrine. This system increases heart rate, diverts blood from the digestive tract to the somatic musculature, and prepares the body for fight-or-flight responses by stimulating the adrenal glands.
 - The parasympathetic system uses acetylcholine as a neurotransmitter. It is responsible for decreasing heart rate and stimulating digestion.
- Navigation of the brain:
 - Directions referred to as:
 - o Ventral: Towards the belly
 - o Dorsal: Towards the back
 - o Rostral: Towards the beak
 - o Caudal: Towards the tail
 - Sections of the brain:
 - o Coronal section
 - o Horizontal section
 - o Sagittal section

The CNS (central nervous system): Brain and spinal cord

- Mammalian brains although they differ in size, built after similar principles (evidence for nurture in the nature vs. Nurture -debate)
- The human brain is not particularly special:
 - o Humans have larger brains, but it is the same scale between brain areas as in other primates
 - Einstein had a small brain → considered a genius
 - o The cerebral cortex, which is said to be larger than other primates, does not contain many neurons compared to the cerebellum
 - Maybe the superiority is in its connectivity in the cortex, which consists of a high amount of white matter.
- Brain autonomy:
 - o **Telencephalon:** Most cognitive processes take place here (most interesting to us)
 - Subdivided into: Limbic System, Basal Ganglia, and Cerebral Cortex
 - The **limbic system** includes subcortical and cortical structures that are interconnected and play a role in emotion.
 - The **basal ganglia** are involved in a variety of crucial brain functions, including action selection, action gating, reward-based learning, motor preparation, timing, task switching, and more.
 - The **Cerebral Cortex**
 - o The cerebral cortex is a continuous sheet of layered neurons in each hemisphere.
 - o Divided into lobes:
 - ◊ Frontal lobe: planning, cognitive control, and execution of movements
 - ◊ Parietal lobe: receives sensory input about touch, pain, temperature, and limb position, and it is involved in coding space and coordinating actions
 - ◊ Temporal lobe: contains auditory, visual, and multimodal processing areas.
 - ◊ Occipital lobe: processes visual information.
 - ◊ In turn divided into gyres:

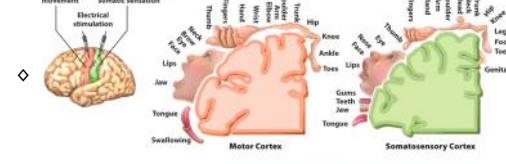


◊ Gyri are the protruding areas seen on the surface of the cortex; sulci, or fissures, are the enfolded regions of cortex

o Brodmann divided the brain into distinct regions based on the underlying cytoarchitectonics.

o Topography is the principle that the anatomical organization of the body is reflected in the cortical representation of the body, both in the sensory cortex and motor cortex.

◊ Adjacent part of the body has adjacent brain areas: e.g. sensation and motor cortex is closely connected



◊ Same principles in visual cortex: Adjacent area of the fovea has adjacent localization in the occipital lobe.

- Association cortices are those regions of cortex outside the sensory specific and motor cortical regions.

o Receives and integrates input from multiple sensory modalities

o Brainstem:

▪ Subdivided into three main parts: the medulla (myelencephalon), the pons and cerebellum (metencephalon), and the midbrain (mesencephalon).

Brainstem:

Lateral view of the brainstem showing the thalamus,

- Association cortices are those regions of cortex outside the sensory specific and motor cortical regions.

- o Receives and integrates input from multiple sensory modalities

- o Brainstem:

- Subdivided into three main parts: the medulla (myelencephalon), the pons and cerebellum (metencephalon), and the midbrain (mesencephalon).
- **Mesencephalon (midbrain):**
 - Processing visual and auditory data
 - Generation of reflexive somatic motor responses
 - **The tectum** (latin: roof): Dorsal part of the midbrain, involved in involuntary visual and auditory processing
 - **The tegmentum** (latin: the covering): Medial part of the midbrain, which is primary area for dopamine syntheses including several nuclei e.g. substantia nigra (motor dopamine system) and ventral tegmental area (cognition/emotion/reward system)
- **Metencephalon**
 - **Cerebellum** (little brain)
 - ◆ Integrates information about the body and motor commands and modifies motor outflow to effect smooth, coordinated movements
 - ◆ Receives: motor outputs and sensory inputs describing body position, inputs from vestibular projections involved in balance, auditory and visual inputs, also project to the cerebellum from the brainstem.
 - ◆ Sends: via thalamus to the motor and premotor cortex, via nuclei of the brainstem to descending projections to the spinal cord.
 - **Pons**
 - ◆ Relay sensory information to thalamus

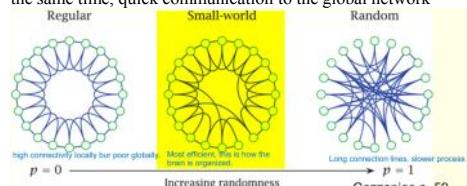
- The brainstem's neurons carry out many sensory and motor processes, including visuomotor, auditory, and vestibular functions as well as sensation and motor control of the face, mouth, throat, respiratory system, and heart.
- The brainstem houses fibers that pass from the cortex to the spinal cord and cerebellum, and sensory fibers that run from spinal levels to the thalamus and then to the cortex
- Many neurochemical systems have nuclei in the brainstem that project widely to the cerebral cortex, limbic system, thalamus, and hypothalamus.

- o **Diencephalon:** Subcortical structures are composed of groups of nuclei with interconnections to widespread brain areas.

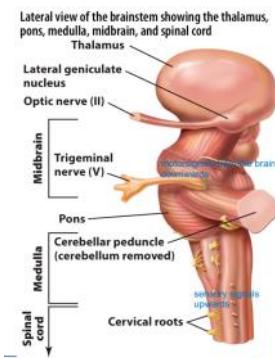
- Subdivided into
 - **Thalamus:**
 - ◆ Relay station for almost all sensory information (Gateway to the cortex)
 - ◆ Divided into several nuclei that act as specific relays for incoming sensory information
 - **Hypothalamus:** Important to autonomic nervous system
 - ◆ Control pituitary gland, which releases hormones into the bloodstream where they can circulate to influence other tissues and organs (e.g., gonads).
 - ◆ Involved in maintenance of body temperature, sleep and drives (emotions)

- o **Ventricles**

- Structures used as landmarks for fMRI scans
- Functions: cushioning (the brain has no skeleton → need for ventricles in order to release the pressure from the skull to the brain), getting rid of waste material
- o **The corpus callosum:** Main fiber tract that connects the two hemispheres of the brain
- o Most primitive towards ventral and most complex towards dorsal? (debatable, since cognition can affect the reptile brain e.g. breath can be held)
- o Connections of the brain:
 - **Small world architecture:** The brain is constructed in a manner that allows both a high degree of local efficiency and at the same time, quick communication to the global network



Brainstem:

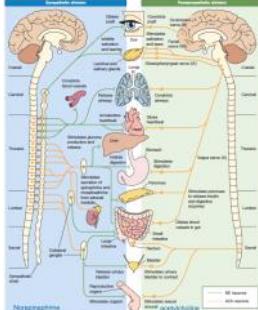


- **Spinal cord:**

- o The spinal cord conducts the final motor signals to the muscles, and it relays sensory information from the body's peripheral receptors to the brain.
 - Ventral part (towards the belly): Conducts the final motor signals to the muscles,
 - Dorsal part (towards the back): Relays sensory information from the body's peripheral receptors to the brain.
- CNS is connected to the vasculature of the brain by the blood-brain barrier (BBB):
 - o Astrocytes restricts the diffusion of objects (such as bacteria) and large hydrophilic molecules in the blood from entering the brain,
 - o Allows small hydrophobic molecules such as oxygen, carbon dioxide, and hormones.
 - o Many neuroactive agents, such as dopamine and norepinephrine cannot cross the BBB.
 - o Plays a vital role in protecting the central nervous system from blood-borne agents

- **The ANS (autonomic nervous system):**

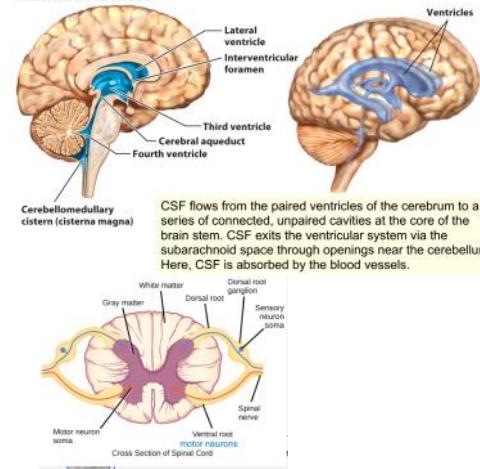
- Two divisions: Parasympathetic vs. Sympathetic nervous system



- **Development of the Nervous system**

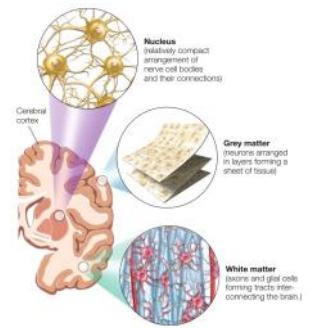
- Already after a few days of gestation, the embryo has developed into a disklike structure with three distinct layers:
 - **Endoderm (ventral):** gives rise to many of the internal organs, such as digestive system
 - **Mesoderm (middle):** gives rise to the skeleton and the muscles

Ventricles of the human brain

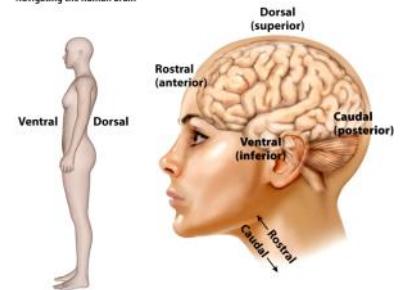
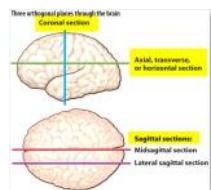


- Ectoderm (dorsal): from which the skin and all nerves are created.
- After 18 days the ectoderm begins to thicken, and the neural plate develops.
- A few days later a groove is created, as the neural plate begins to fold
 - Subsequently the folds fuse dorsally, forming the neural tube.
 - The entire CNS is created from the walls of this tube, and the hollow inside becomes the fluidfilled ventricles.
- In the rostral end of the neural tube, three swellings occur:
 - The whole brain derives from these three primary vesicles
 - Prosencephalon or forebrain: Differentiates into the diencephalon (differentiates into the thalamus (through which almost all information in the brain pass) and the hypothalamus (involved in hormonal control of body and brain)) the two telencephalic vesicles (which turn into the cerebral hemispheres) and optic vesicles
 - Mesencephalon or midbrain: differentiates dorsally into the tectum (latin: "the roof"), involved in eye-movement and sound processing; and ventrally into the tegmentum (latin: "the covering").
 - Rhombencephalon or hindbrain:
 - o Rostal hindbrain: differentiates into the cerebellum ("the little brain") involved in execution of motor programs, pons (latin: "the bridge") relays information between cortex and cerebellum
 - o Caudal hindbrain: differentiates into the medulla oblongata, where the corticospinal tract decussates.

CNS:



Navigating the human brain



Outline for: fMRI and other methods

Tuesday, February 13, 2018 5:49 PM

Different approaches for studying the brain:

- Methods for the Study of Neural Function:
 - o **Single-cell recording:** Allows recordings from individual neurons i.e. measures membrane potential.
 - Often used on animals due to invasiveness
 - o **Multineuronal recording:** The activity of hundreds of cells can be recorded at the same time.
 - o **Electroencephalography (EEG):** Measures the electrical activity of the brain.
 - **An event-related potential (ERP):** A change in electrical activity that is time-locked to specific events based on averaging of experimental stimuli. (Good temporal resolution)
 - o **Electrocorticogram (ECOG):** Similar to an EEG, except that the electrodes are placed directly on the surface of the brain.
 - o **Magnetoencephalography (MEG):** measures the magnetic signals generated by the brain.
 - The electrical activity of neurons also produces small magnetic fields, which can be measured by sensitive magnetic detectors placed along the scalp.
 - MEG can be used in an event-related manner similar to ERPs, with similar temporal resolution. (The spatial resolution can be superior because magnetic signals are minimally distorted by organic tissue such as the brain or skull)
- The methods of neural function relies on cognitive subtraction
 - o Compare a task involving a particular cognitive component to a task similar task that does not involve the associated area of the brain
 - o Challenge: When you add a cognitive component to your low level processing task, they often change.
 - o Examples on cognitive subtraction: You can subtract anything, but is it meaningful?
 - Peterson et al. PET study of single-word processing
 - Die Hard 4.0 vs Italian for Beginners Might not be comparable : Different languages etc.
- Methods for study of structure of the brain
 - o **Computed tomography (CT or CAT)** uses X-rays to image the 3-D structure of the brain.
 - o **Magnetic resonance imaging (MRI)** exploits the magnetic properties of the organic tissue of the brain to image its structure (anatomy)
 - An MR-scanner consists of multiple magnets
 - The main magnet creates a strong stable magnetic field, which is always on.
 - ◆ 10000 stronger than the earth's magnetic field
 - The gradient coils make the main field vary slightly for localisation purposes
 - ◆ The scanner vibrates, which is the source of the noise
 - Radio Frequency (RF) coils produce and send radio waves
 - Radio Frequency (RF) coils receive radio waves
 - The structural MRI relies on different types of tissue have different types of relaxation (the realignment of the molecules' spin to the magnetic field of the MR-scanner)
 - The spatial resolution of MRI is superior to CT.
 - o **Diffusion tensor imaging (DTI)**, performed with MR-scanners, is used to measure white matter pathways in the brain and thus can offer information about anatomical connectivity between regions
 - Water diffuse in all directions, if unhindered i.e. hydrophobic materials
 - In white matter, it can only diffuse along fiber tracts

The Marriage of Function and Structure: Neuroimaging

- o **Positron emission tomography (PET):** Measures metabolic activity in the brain by monitoring the distribution of a radioactive tracer.
 - Procedure:
 - A substance are labelled with a radioactive isotope of some sort.
 - ◆ A popular tracer is ^{15}O because it decays rapidly and the distribution of oxygen increases to neural regions that are active.
 - The substance is injected into the bloodstream or inhaled (depend on the wished type of measurement)
 - ◆ For the measurements of the perfusion scans often used water injected into the bloodstream (stays within the bloodstream)
 - ◆ fMRI is often used for this types of measurements today
 - ◆ For oxygen metabolism scans often used oxygen, since it is able to cross the blood-brain barrier (inhaled)
 - The substance enters the brain, emits a positron, which meets with a negatively charged electron.
 - The electron and the positron merge, and gamma radiation is released.
 - This radiation can be picked up by the scanner and be used to tell where the substance went.
 - Downsides in PET: Radioactive tracers (limited exposure), poor temporal resolution, very expensive
- o **Functional magnetic resonance imaging (fMRI):** uses MRI to measure changes in the oxygen content of the blood (hemodynamic response). These changes are assumed to be correlated with local changes in neuronal activity. (function)
 - fMRI measures the BOLD-effect, which relies on three assumptions:
 - 1: When a brain area becomes more active the surrounding blood vessels dilate in order to attract more oxygenated blood
 - 2: Water molecules have a spin, giving it magnetic properties. The magnet from the MR-scanner forces the molecules into alignment. When radio waves are emitted this cause disturbance in the alignment with the magnetic field from the MR-scanner. When the emission of radio waves stop, the molecules will realign with the grand magnetic field and while doing so emitting radio waves. The signal starts of strong due to alignment between the spin of the molecules, the later desynchronization will cause the signal to fade.
 - 3: Deoxygenated blood opposed to oxygenated blood causes disturbances in the magnetic fields, which cause water molecules to desynchronize faster.
 - ERGO: Activation of a brain area → the vessels to widen → more oxygenated blood → less magnetic field disturbances → the spin of the water molecule synchronizes for a longer period of time → the signal wished measured stays for a longer period of time
 - The BOLD signal has a significant delay relative to stimulus onset and onset of neural spiking

PET:
FMRI pretty much replaced this technique, besides studying Raclopride/dopamine
(Was an early study technique - which might be why dopamine is so well studied and considered important today!)

Albert Gede (Head of CFINN before it was called CFINN), said that we look under the streetlight when we lost our key on our way home, not because we know it's there, but because it's where we're able to look

Raclopride - A dopamine antagonist (Occupies places in the brain where there could otherwise be dopamine. Tells you about the binding potential of dopamine)

•
Plus many other things..

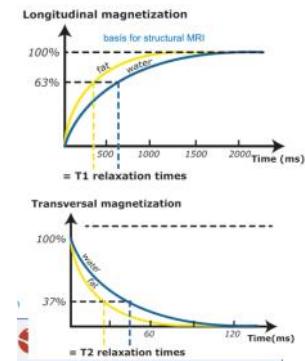
Beta amyloid plaques - PiB(Pittsburgh compound B) may be used in studies of Alzheimer's disease..

Different signal types: Relaxation as vectors

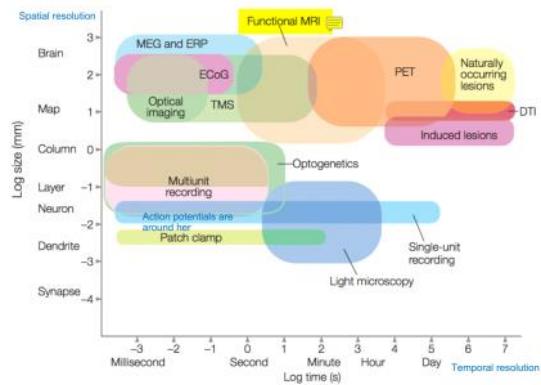


- T1 is the regaining of length on the z-axis
- T2 is the decrease in length on the x/y-plane
- Different types of tissue have different T1 and T2 relaxation

Different tissue types have different T1 and T2 relaxation rates

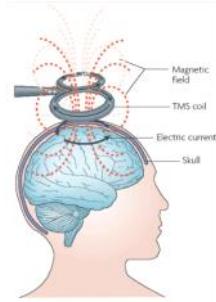
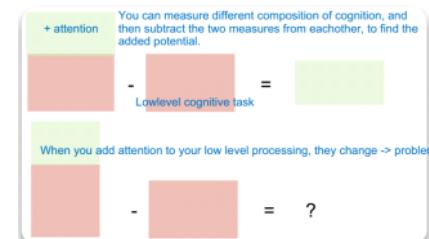


- Over time the scanner signal drifts causing the baseline signal intensity to vary
- Every method has its advantages:



Another method for studying the function: Damaged Brain

- Research involving patients with neurological disorders is used to examine structure–function relationships.
 - Single and double dissociations can provide evidence that damage to a particular brain region may result in a selective deficit of a certain cognitive operation.
 - Single dissociation: If a patient is impaired on a particular task (task A), but relatively spared on task B
 - Double dissociation: If one patient is impaired on a particular task (task A) but relatively spared on task B and another patient is impaired on task B, but relatively spared on task A
- Types of damaged brains:
 - **Brain lesions**, either naturally occurring (in humans) or experimentally derived (in animals), allow experimenters to test hypotheses concerning the functional role of the damaged brain region.
 - **Cerebral vascular accidents, or strokes**, occur when blood flow to the brain is suddenly disrupted.
 - **Tumors** can cause neurological symptoms either by damaging neural tissue or by producing abnormal pressure on spared cortex and cutting off its blood supply.
 - **Degenerative disorders** include Huntington's disease, Parkinson's disease, Alzheimer's disease, and AIDS-related dementia.
 - **Neurological trauma** can result in damage at the site of the blow (coup) or at the site opposite the blow because of reactive forces (contrecoup). Certain brain regions such as the orbitofrontal cortex are especially prone to damage from trauma.
 - **Epilepsy** is characterized by excessive and abnormally patterned activity in the brain.
- Surgical procedures have been used to treat neurological disorders such as epilepsy or Parkinson's disease. Studies conducted in patients before and after surgery have provided unique opportunities to study brain behavior relationships



Outline for: Hemispheric Specialization

Tuesday, February 20, 2018 1:09 PM

Anatomy of the hemispheres:

- The hemispheres are connected by:
 - o **Corpus callosum** (primarily): The largest fiber system in the brain
 - In humans, this bundle of white matter includes more than 250 million axons.
 - Divided into: Genu, body and splenium
 - However, no clear landmarks to define the separation
 - When the posterior half of the callosum is sectioned in humans, transfer of visual, tactile, and auditory sensory information is severely disrupted.
 - The anterior part of the callosum is involved in the higher order transfer of semantic information.
 - The connections in corpus callosum can be homotopic and heterotopic connections.
 - Homotopic fibers connect the corresponding regions of each hemisphere
 - Heterotopic fibers connect different areas
 - The brain areas connect accordingly in corpus callosum
 - e.g. the connection between posterior brain areas pass through the posterior part of the corpus callosum
 - ?
 - **Corpus callosum allows synchronization**
 - Generally the body size correlate with size of corpus callosum
 - No one knows why...
 - o Two smaller bands of fibers: Primarily connects the subcortical parts of the brain
 - **Anterior commissure**: connects regions of the temporal lobes including the amygdalae
 - **Posterior commissure**: contains fibers that contribute to the pupillary light reflex
 - Differences in neural connectivity and organization may underlie many of the **gross asymmetries between the hemispheres**.
 - Both lateralization in structure and function:
 - o **Structure**: Certain areas are overdimensionized in the left hemisphere. Likely due to the development of language in this hemisphere
 - o **Function**: See below

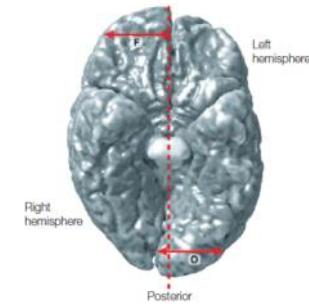


FIGURE 4.5 Anatomical asymmetries between the two cerebral hemispheres.
View looking at the inferior surface of the brain; note that the left hemisphere appears on the right side of the image. In this computer-generated reconstruction, the anatomical asymmetries have been exaggerated.

There are functional differences between the right and left amygdala. In one study, electrical stimulations of the right amygdala induced negative emotions, especially fear and sadness. In contrast, stimulation of the left amygdala was able to induce either pleasant (happiness) or unpleasant (fear, anxiety, sadness) emotions. Other evidence suggests that the left amygdala plays a role in the brain's reward system.

Lateralization in function

- During the second half of the 20th century, lateralization studies became very popular → numerous amount of studies to support whatever thesis
 - o "Despite all we have learned about hemispheric difference and specializations, the fundamental mystery remains today" - Gazzaniga
- The most acknowledged lateralizations: Speech, vision,
- **Speech**: Left lateralization
 - o 96% of humans, regardless of handedness, have a left-hemisphere specialization for language
 - However, exceptions are found: The Wada test is used to identify which hemisphere is responsible for language before brain surgery is performed.
 - o Lesions in left hemisphere can lead to aphasia
 - e.g. Sarah Scott: Typical symptoms of Broca's aphasia: **Telegram-style utterances**, lack of words, but meaningful utterances
 - o **Planum temporale** (Wernicke's area) is usually larger in the left hemisphere
 - Seldom example on an anatomical index is correlated with a well-defined functional asymmetry?
 - Experiment: Correlation between cognitive scores and symmetry of the planum temporale
 - Results: VERY small correlation, if there is a connection between function and structural differences
 - o Differences have been found in the specifics of cortical microcircuitry between the two hemispheres in both anterior (Broca's) and posterior (Wernicke's) language associated cortex.
- **Vision**: The right hemisphere receives input from the left part of the visual field and vice versa
 - o Split-brain patients cannot name or describe visual and tactile stimuli presented to the right hemisphere, because the sensory information is disconnected from the dominant left (speech) hemisphere.
 - They will, however, be able to choose a corresponding object using the hands → they are aware of the object, though an inability to name it
- **Other lateralizations from the book**:
 - o There may be two lexicons (associations of words with specific meanings), one in each hemisphere.
 - The right hemisphere's lexicon seems organized differently from the left hemisphere's lexicon, and these lexicons are accessed in different ways.
 - o The right hemisphere has been linked to one aspect of speech perception, prosody, the way we vary articulation to convey affect or intonation.
 - o Some studies show that the right hemisphere is specialized for visuospatial processing.
 - o The right hemisphere has special processes devoted to the efficient detection of upright faces.
 - The left hemisphere outperforms the right hemisphere when the faces are dissimilar, and the right hemisphere outperforms the left when the faces are similar.
 - o Although touching any part of the body is noted by either hemisphere, patterned somatosensory information is lateralized.
 - **A split-brain patient who is holding an object in the left hand is unable to find an identical object with the right hand.**
 - o Surprisingly, split-brain patients can use either hemisphere to direct attention to positions in either the left or the right visual field.
 - o Patients with left-sided lesions were slow to identify local targets, and patients with right-sided lesions were slow with global targets
 - The left hemisphere is more adept at representing local information and the right hemisphere is better with global information.
 - o The left hemisphere contains "the interpreter"
 - A system that seeks explanations for internal and external events in order to produce appropriate

65% had bigger left planum temporale • 24% were symmetric

These numbers still hold up, pretty well
But there has been 100s of thousands studies on this the last few decades - So you'll be able to find the data you want

out of dozens of split-brain patients who have been carefully examined, only six showed clear evidence of residual linguistic functions in the right hemisphere. And even in these patients, the extent of right-hemisphere language functions is severely limited and restricted to the lexical aspects of comprehension.

Interestingly, the left and right lexicons of these special patients can be nearly equal in their capacity, but they are organized quite differently. For example, both hemispheres show a phenomenon called the word superiority effect (see Chapter 5). Normal English readers are better able to identify the words (e.g., L) in the context of real English words (e.g., belt) than when the same letters appear in pseudowords (e.g., kelt) or nonsense letter strings (e.g., ktle). Because pseudowords and nonwords do not have lexical entries, letters occurring in such strings do not receive the additional processing benefit bestowed on words. Thus, the word superiori effect emerges.

While the patients with right-hemisphere language exhibit a visual lexicon, it may be that each hemisphere accesses this lexicon in a different way. To test this possibility, investigators used a lexical priming task. Participants were asked to indicate whether a briefly flashed uppercase letter was an H or a T. On each trial, the uppercase letter was preceded by a lowercase letter that was either an h or a t. Normally, participants are significantly faster, or primed, when an uppercase H is preceded by a lowercase h than when it is preceded by a lowercase t.

no evidence of left hemisphere priming for left visual field (LVF) trials but clear evidence of priming for trials of the right visual field (RVF). Thus, the lack of a priming phenomenon in the disconnected right hemisphere suggests a deficit in left hemisphere recognition, prohibiting access to parallel processing mechanisms. J.W. exhibited a variety of other deficits in right-hemisphere function as well. For example, he was unable to judge whether one word was superordinate to another (e.g., furniture and chair), or whether two words were antonyms (e.g., love and hate).

response behaviors.

Studies on lateralization

- Development of the studies on lateralization is based on research on split-brainers
 - A notion being: The corpus callosum is often only ruptured on those with the need e.g. epilepsy patients, whose brains may already be damaged
- Evidence on lateralization is also found in normal brains:
 - Facial expressions: Both hemispheres can generate spontaneous facial expressions, but you need your left hemisphere to produce voluntary facial expressions → People appear to have two neural systems for controlling facial expressions
 - Handedness is phenomenon
 - Ocular dominance: 97 % have a dominant eye, the phenomenon is correlated with handedness
 - Situs inversus: Due to asymmetrical motions of protein cilia in a structure called “the node” on the ventral surface of embryos in early stages of development the heart develop in the right side of the body
 - The drawing experiment: Tendency for Danish speakers to imagine them in a left-to-right manner corresponding to the reading direction:
 - The dichotic listening task: Often a right ear dominance, this is typically the ear shadowed during the task

The Evolutionary Basis of Hemispheric Specialization

- Hemispheric specialization is not a unique human feature, though it is most extensive in humans.
 - o The evolutionary pressures underlying hemispheric specialization—the need for unified action, rapid communication, and reduced costs associated with interhemispheric processing—exist across species.
- In general, many tasks can be performed successfully by either hemisphere, although the two hemispheres may differ in efficiency.
- Sarah Scott improves her ability to speak over the years → redundant areas of the brain, functions happen multiple places
 - o Evolution doesn't remove the old solution even though it has found a new

Outline for: Perception focus on hearing

Tuesday, February 27, 2018 1:05 PM

Audition

- Audition is more than detection of sounds: Involves constructing a model of the world
 - o What objects do sounds correspond to?
 - o Which location do they come from?
- The nature of sound: Sound is movement of molecules in the air
 - o A tone can be either pure or more complex
 - Pure tones: Only has energy in a certain frequency and is constant over time
 - Example: Sine wave
 - More complex sounds: Has energy in multiple frequencies, which varies over time i.e. sum of sinusoids
 - Example: White noise most complex sound: The energy is randomly distributed over frequencies and fluctuates over time - difficult to predict (high entropy)
 - In speech is vowels more like pure tones with higher harmonics, whereas the consonants are more like white noise.
 - o Changed in air pressure have the characteristic properties: amplitude and frequency
 - Frequency: Number of oscillations
 - High frequency waves are perceived as having a higher pitch
 - Intensity: The amplitude of the waves
 - High-intensity waves are perceived as louder sound
 - Pitch and volume are psychological properties, whereas frequency and amplitude are physical properties
 - → Not a one-to-one mapping e.g. the example of the missing fundamental, where the same a note with 1000 Hz is perceived even though only the overtones are played
- Transformation of sound to neural signals:
 - o The pathway through the ear:
 - 1: Outer ear
 - The pinnae: The outer part of the ear shaped to amplify certain frequencies and cause delay in sound due to reflections of sound on the shapes of the pinnae → important for locating sound
 - The ear canal: The canal the sound travels along upto the ear drum
 - 2: Middle ear:
 - Converts airborne vibrations from the ear drum to liquid-borne vibrations in the inner ear
 - The ossicles - the malleus, incus and stapes (three small bones) amplify sound pressure by acting as levers, and by applying the force on a smaller area (The oval window).
 - This enables sound to produce movement inside the fluid-filled space of the cochlea
 - ◆ The ossicles equally serve as an active volume control: By contracting the tensor tympani muscle and the stapedius muscle, the chain of the ossicles becomes more rigid thereby adjusting reactions to louder sounds.
 - 3: Inner ear:
 - The inner ear converts the liquid-borne sounds to neural impulses
 - Consists of
 - ◆ Vestibular System: Important for maintaining balance
 - ◆ Cochlea: Signals are processed in the hair cells and basilar membrane of the cochlea.
 - In the basilar membrane: Sound pressure travels from the base of the scala vestibuli, where it is initiated at the oval window by the stapes, through the helicotrema, and down the scala tympani, where it makes the membrane at the round window move.
 - Low frequencies travel far along the basilar membrane, whereas high frequencies travel shorter.
 - Explain the phenomenon, tinnitus. The hair cells first in the beginning of the basilar membrane are more exposed to sound, if overstimulated they lay down, leaving a constant activation of the high-frequency cells
 - Sound produces motion in the basilar membrane relative to the tectorial membrane - thereby bending the hairs (stereocilia) on the hair cells
 - o The pathway from the ear
 - The cochlea sends its information in the form of neuronal signals to the inferior colliculus and the cochlear nucleus. Information then travels to the medial geniculate nucleus of the thalamus and on to the primary auditory cortex.
 - All auditory nuclei (except the cochlear nuclei) receive input from both ears

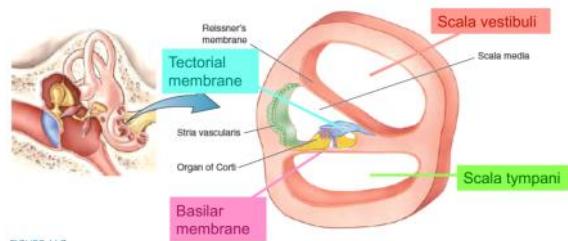
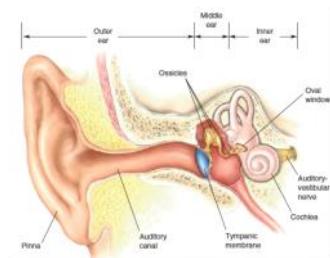
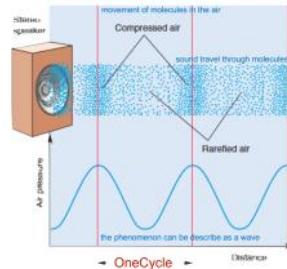
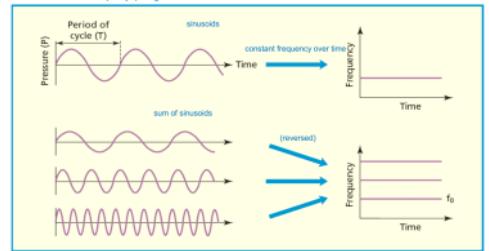


FIGURE 11.7

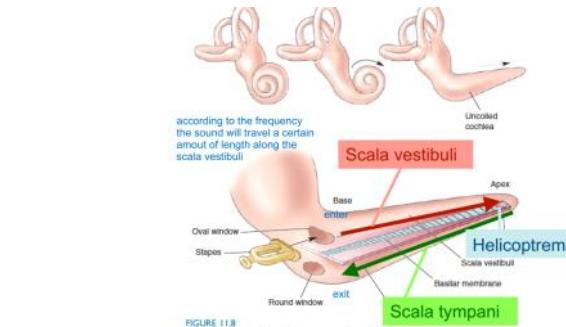
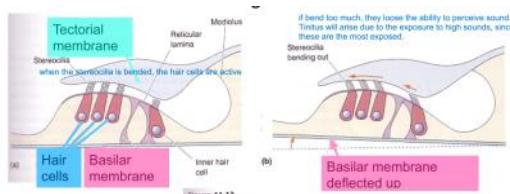
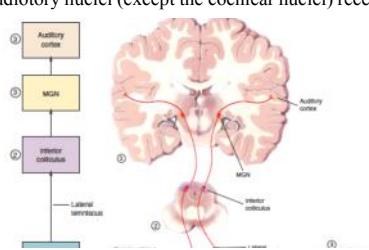


FIGURE 11.8



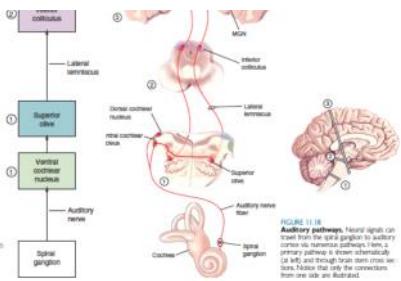
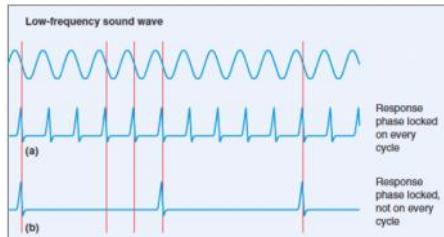


FIGURE 11.18
Auditory pathways. Facial signals can travel to the brain via two pathways to auditory cortex via numerous pathways. Item 2 shows the direct pathway from the cochlea to the brainstem. Item 3 shows the more complex pathway via the auditory nerve, which crosses the midline to the opposite side of the brainstem. Labels that apply to both pathways are shown in bold.

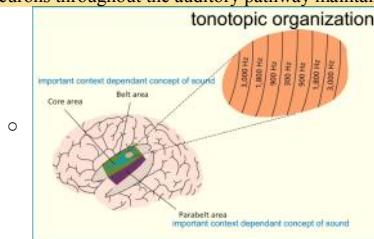
- Frequency and intensity is encoded, when perceiving sound:

- o Frequency tuned neurons in the auditory nerve.
- o Intensity is coded in the firing rates and in the number of active neurons
- o The volley principle allows one-to-one mapping to a certain degree: When more than one cell (as in (b)) go together to give the whole series of waves in a phaselocked manner. This is possible only up to 4kHz.



- o Above this frequencies are represented by tonotopy alone: The fact that particular neuron fires, instead of the tops corresponding to frequency

- Neurons throughout the auditory pathway maintain their tonotopic arrangement as they travel up to the cortex



- Sound localization is aided by the processing of differences in interaural time and interaural sound intensity, which are each coded separately in the brain.
- For localization of sound: see slide
- For summary: See slide

Similarities to the visual system:

COMPARISONS BETWEEN THE AUDITORY AND VISUAL SYSTEMS		
	Auditory system	Visual system
Thalamo-cortical route	Medial geniculate nucleus projects to primary auditory cortex	Lateral geniculate nucleus projects to primary visual cortex
Organizing principle of early neural processing	Tonotopic organization (orderly mapping between sound frequency and position on cortex)	Retinotopic organization (orderly mapping between position on retina and position on cortex)
Temporal and spatial sensitivity	Temporal > Spatial fast	Spatial > Temporal
Functional specialization of feature processing	Less well documented in the auditory domain	Well documented for color and movement
Higher-order context-dependent pathways	Evidence for separate auditory pathways for "what" versus "where"/"how" (maybe signal is mixed between hemispheres)	Evidence for separate visual pathways for "what" versus "where"/"how"

Outline for: Object recognition

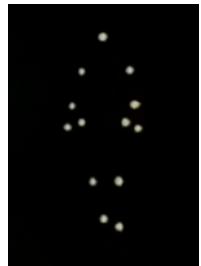
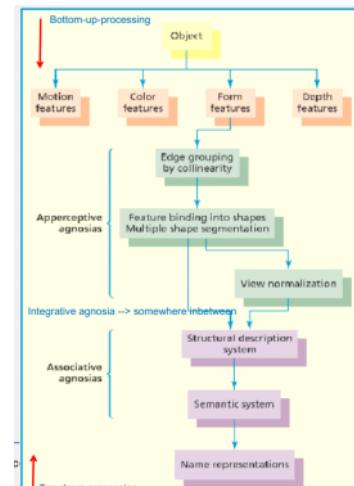
Monday, March 12, 2018 8:23 AM

Principles of Object Recognition

- Memory and perception are tightly linked.
- Sensation, perception, and recognition refer to distinct phenomena.
- People perceive an object as a unified whole, not as an entity separated by its color, shape, and details.
- Although our visual perspective changes, our ability to recognize objects remains robust → object constancy
 - o Object constancy refers to the ability to recognize objects in countless situations, despite variation in the physical stimulus
 - Words do not have object constancy - when shown a mirrored image of a word, the brain does not get "bored"
 - o Disproves the template matching model: A vast amount of templates should be stored in order to hold up.

Visual perception in the brain

- "What"-pathway: The ventral stream (occipitotemporal pathway) is specialized for object perception and recognition.
 - o Lesions of the ventral pathway may have severe problems in consciously identifying objects, yet they can use the visual information to guide coordinated movement.
- "Where"-pathway: The dorsal stream (occipitoparietal pathway) is specialized for spatial perception
 - o Lesions of the dorsal pathway can recognize objects but cannot use visual information to guide action (Optic ataxia)
 - Reaching for something: she gropes about like a person trying to find a light switch in the dark
- The parietal lobe: Neurons have large, nonselective receptive fields that include cells representing both the fovea and the periphery.
- The temporal lobe: Neurons have large receptive fields that are much more selective and always represent foveal information.
 - o Posterior to anterior
- The lateral occipital cortex is critical for the recognition of the shape of an object.



Biological motion

As predicted, house perception did not depend on whether the test items were presented in isolation or as an entire object, but face perception did (Figure 6.34b). Participants were much better at identifying an individual facial feature of a person when that feature was shown in conjunction with other parts of the person's face.

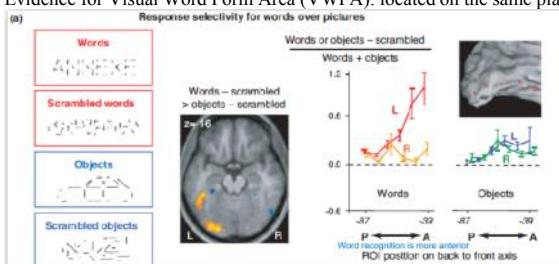
Types of object recognition

Holistic vs. Analytic processing

- Holistic processing is a form of perceptual analysis that emphasizes the overall shape of an object, a mode of processing that is important for face perception.
 - o The Margaret Thatcher illusion is a product of the holistic processing of faces
 - o Different objects may depend more or less on holistic analysis
- Analytic processing is a form of perceptual analysis that emphasizes the component parts of an object, a mode of processing that is important for reading.

Word recognition

- Words can be processed holistically or by its parts
 - o Difficult words often by its parts → the sounds to shape a full word
 - o Shorter words are recognized as a hole → word superiority effect
- Evidence for Visual Word Form Area (VWFA): located on the same place as FFA except it is left lateralized



- o The activation was greater for words than for scrambled words
- o The more it could be a word → the more activity in the VWFA e.g. er more likely than XS

Face recognition

- Multiple face recognition modules:
 - o Fusiform Face Area (FFA): Ventral part of the temporal lobes
 - Important for recognition of faces
 - o Superior temporal sulcus (STS): Involved in face perception in monkeys
 - Hypothesis: STS is important for social interactions
 - o Study, which detangles the difference between FFA and STS: Gazzaniga p. 252

Biological motion (a separate phenomenon): A particular type of motion involving humans, which is processed in a separate module

- o Biological motion is perceived as dots in a pattern
 - o Movement, activity and gender can often be deduced from these patterns

Deficits in object recognition

- Agnosia (lack of knowledge): the inability to recognize objects, when using a given sense e.g. vision, even though the sense is basically intact
 - o When using other senses, the knowledge of the object can be accessed → opposed to amnesia
 - Case: G.S. Unable to access the knowledge of a viewed lockpad, the hands, however, know the function of it and starts to rotating.
 - o Types of agnosia (the distinctions differ):
 - Apperceptive agnosia: Inability to achieve object constancy (referring to the ability to recognize objects in a vast number of orientations)
 - Objects can often be recognized in their prototypical orientation, however not in unusual views
 - Usually occurs with posterior hemisphere lesions
 - Integrative agnosia: Inability to make holistic perception (see figure)
 - Unable to use gestalt principles to group a percept into objects
 - Case: H.J.A: Unable to transform objects from a picture into a scene. Recognizes a dog, a tree (a christmastree), the door → unable to see it is an indoors scene
 - Associative agnosia: The inability to assign meaning to objects
 - Patients can perceive objects, but do not recognize them

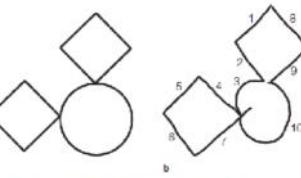


FIGURE 6.19 Patients with integrative agnosia do not see objects holistically.
Patient C.K. was asked to copy the figure shown in (a). His overall performance (b) was quite good; the two diamonds and the circle can be readily identified. However, as noted in the text, the numbers indicate the order he used to produce the segments.

Face perception tasks involve within-category discriminations; object perception tasks typically involve between-category discriminations. Perhaps the deficits in prosopagnosia patients reflect a more general problem in perceiving the subtle differences that distinguish the members of a common category.

In patient literature fails to support this hypothesis, however. For example, a man who became a sheep farmer (W.J.)



- Case: FRA could not name the objects, but was capable of colouring them
- **Prosopagnosia:** The inability to recognize faces (another type of agnosia)
 - Often caused by bilateral occipitotemporal lesions
 - In unilateral cases right hemisphere lesions are more prominent → face recognition is lateralized to the right hemisphere
 - Double dissociation between prosopagnosia and visual agnosia: face and object perception happens in two different modules
 - Case: WJ was unable to recognize his family, but still able to recognize his sheep
 - Case: CK could recognize faces, but not objects. Example: picture to the right (able to recognize the face, when the picture is turned upside down, but not the vegetables in the upright position)
- **Agnosias rarely occur alone**
 - The pattern of the occurrences:

Table 6.2 Patterns of Co-occurrence of Prosopagnosia, Object Agnosia, and Alexia	
Pattern	Number of Patients
Deficits in all three	21
Selective deficits	
Face and objects	14
Words and objects	15
Faces and words	1 (possibly) <small>May be due to lateralization effects</small>
Faces alone	35
Words alone	Many described in literature
Objects only	1 (possibly)

Other visual deficits:

- **Achromotopsia:** The inability to perceive colors
 - Retinal color blindness: A genetic inability to distinguish certain colors predominantly in males
 - Cerebral achromotopsia: Rare condition due to lesions in V4 (a module in the ventral pathway associated with colour perception)
 - Unilateral lesions give contralateral color deficits (most often)
 - Bilateral lesions → rare
- **Akinetopsia:** The inability to perceive motion, the world is perceived similar to stop-motion-movies
 - Due to bilateral lesions in V5 (a module in the dorsal pathway associated with motion perception)
 - ONLY occurs with bilateral lesions
- **Optic ataxia:** The inability to use visual information to guide movement coordination
- **Acquired alexia:** Characterized by reading problems that occur after a patient has a stroke or head trauma.

Outline for: The Acting Brain

Tuesday, March 20, 2018 3:49 PM

Action and perception is closely intertwined

- Perception is a means to action
- Action is a means to perception

The Anatomy and Control of Motor Structures

- Primary motor pathways in the brain:
 - o Premotor and supplementary motor cortex regions:
 - Initiate movement: Receive input from many regions of the cortex by way of corticocortical connections (descending fibers that originate in the cortex and project monosynaptically to the spinal cord)
 - o Motor Cortex: Goal-directed plans turn into concrete executable form anterior <> Posterior frontal lobe
 - o Brainstem → Spinal Cord → Muscles: The plan from the motor cortex goes via the brainstem to the spinal cord and becomes an output in the muscles
 - Some cortical axons terminate on brainstem nuclei, thus providing a cortical influence on the extrapyramidal tracts (neural pathways that project from the subcortex to the spinal cord)
 - The cortex sends massive projections to the basal ganglia and cerebellum.
- Brain areas relevant for movement
 - o Actions involves almost the entire brain:



- o Frontal lobes:
 - Involved in coordination of cognition generally (both external actions and internal thoughts)
 - Damage to this region does not impair physical movement but actions become inappropriate or disorganized
 - Involved in selection and maintenance of goals and responses
 - **ddsd**: Executes all voluntary movements of the body
 - The primary and secondary motor cortices contain somatotopic representations, although the maps are not as well defined as is seen in sensory cortices.
 - The homunculus was first discovered by Penfield (1950), who used electrical stimulation of the motor cortex to initiate movement
 - The homunculus emphasizes important features of the human being: "Humans manipulate objects and talk about it", Mikkel
 - The front eye field: Voluntary movement of eyes
- o Two prominent subcortical structures involved in motor control:
 - Cerebellum: Monitor action online
 - Basal ganglia: modulates the force and likelihood of an action
 - Consists of dopaminergic neurons
 - Parkinson's disease is proof that the dopamine circuit is crucial for movement
 - Occur due to damage of the subthalamic nucleus

- From brain to muscle:
 - o Extrapiramidal tracts and corticocortical connections connect the brain to the spinal cord
 - o Spinal Cord:
 - The cervical enlargement: Motor neurons that innervate muscles of the arm
 - The lumbar enlargement: Neurons that innervate the muscles of the leg
 - o Alpha motor neurons provide the point of translation between the nervous system and the muscular system, originating in the spinal cord and terminating on muscle fibers.
 - o Action potentials in alpha motor neurons cause the muscle fibers to contract
 - The neurotransmitter: acetylcholine
 - o Action includes two signals: Excitatory signal and inhibitory signal
 - To produce movement, excitatory signals to one muscle, the **agonist**, are accompanied by inhibitory signals to the **antagonist** muscle via interneurons.
 - In this way, the stretch reflex that efficiently stabilizes unexpected perturbations can be overcome to permit volitional movement
 - o Motor cortex neurons show directional tuning: Neurons are responsive for movement in a particular direction
 - Experiment: Monkeys moves a lever towards the light in a multi-unit recording
 - Result: Neurons in the motor cortex are activated for certain directions
 - Population vector: The outcome outcome direction is determined by the sum of directional neurons
 - o A part of the body that can move is referred to as an effector
 - o Are movement plans based on the trajectory or the goal of the movement?
 - Experiment: Monkeys had their afferent (feedback) input severed, and was to move towards targets in the dark
 - Manipulation: An opposing force sometimes stopped the initial movement (the monkey was unaware)
 - Result: Movements still ended up in the right place, suggesting endpoint control
 - From muscle to brain
 - o Proprioceptive neurons constitute a feedback system, where bodily sensation of location in space is send

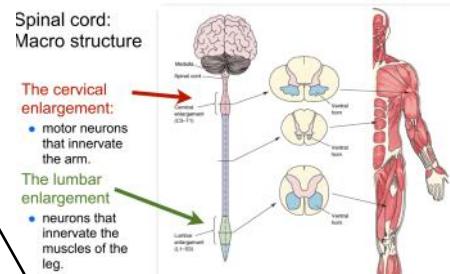
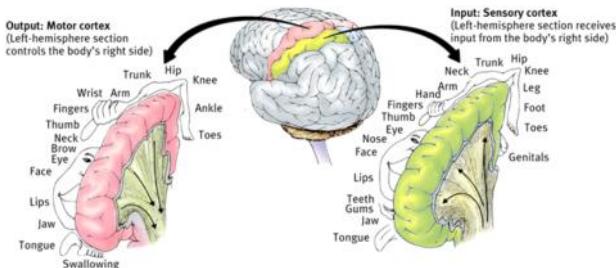
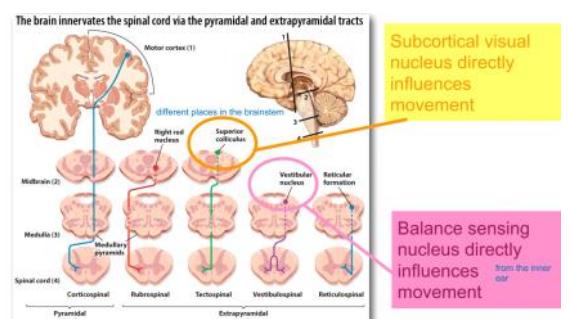
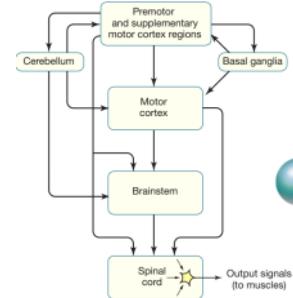


FIGURE 8.25 Differential neuro-chemical alterations in Huntington's and Parkinson's diseases.

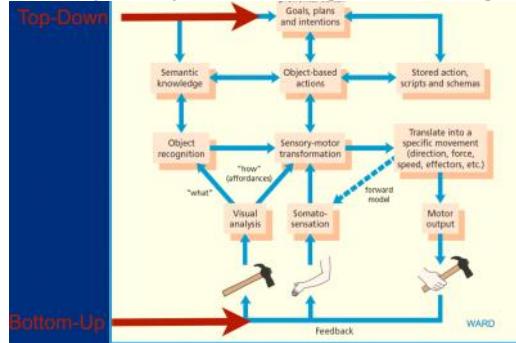
As in Figure 8.23, green links indicate excitatory projections, and red links indicate inhibitory projections. (a) In Huntington's disease, the inhibitory projection along the indirect pathway from the striatum to the external segment of the globus pallidus (GPi) is reduced. The net consequence is reduced inhibitory output from the internal segment of the globus pallidus (GPI) and thus an increase in cortical excitation and movement. (b) Parkinson's disease primarily reduces the inhibitory activity along the direct pathway, resulting in increased inhibition from the GPi to the thalamus and thus a reduction in cortical activity and movement.

to the brain

- o Proprioceptive neurons:
 - o Muscle spindles (stretch receptor): Becomes active, when the muscles stretches
 - Mechano-receptors:
- o The primary motor cortex and the primary somatosensory areas are intertwined i.e. in the sensation of pain an action is required or when linking together the position of an object in retinal space with the position of the limbs in bodily space = sensory-motor transformation

- The motor system is hierarchically organized. Subcortical and cortical areas represent movement goals at various levels of abstraction

- o Descending motor signals modulate the spinal mechanism to produce voluntary movements.



- o Higher cognitive mechanisms in action include:
 - The goals, plans and intentions of an individual
 - Stored semantic knowledge of objects and their uses
 - Stored motor programs for specific objects (e.g. lifting cups) and schemas for familiar situations (e.g. making tea)
- o More basic cognitive mechanisms in action include:
 - Object recognition (ventral “what” route)
 - Locating an object in space (dorsal “where” or “how” route)
 - Linking object shape and location with limb positions and motor commands (sensorymotor transformation)
 - Knowledge of the present state of the body (somatosensation) and position of limbs in space (proprioception)
 - Selecting a specific movement (direction, force etc.)
 - Generating the movement
 - Monitoring the progress and outcome of the action (feedback)
- o Forward model:
 - The cerebellum receives a copy of motor signals being sent to the muscles
 - It also receives massive feedback from the sensory system
 - By comparing, the cerebellum checks if the movement is coordinated e.g. if you hit the nail or not
 - The forward model is the reason for you not being able to tickle yourself, the somatosensory system already known what you are up to

- Why is action computationally difficult?

- o Infinite number of motor solutions for picking up an object, e.g. in terms of joint positions and Trajectories
- o However, some motor functions are stored routines of actions and action sequences that minimize the problem
 - Neurons within the spinal cord can generate an entire sequence of actions without any external feedback signal. These circuits are called central pattern generators.
 - e.g. same handwriting used for blackboard writing and regular writing

- Is the brain necessary in movement? Lower motor processing

- o Many processes happen independently of the brain e.g. reflexes
 - Experiment: Sherrington and Brown disconnected the spinal cord from the cortex in a cat and found it could still walk → motor neurons and stretch receptors work together independently of the brain

- Doing nothing is also an action

- o Given that the world is never stable, doing nothing is a fairly complex task
 - The vestibular system consists of semi-circular canals, which allows different dimensions of movements to be evaluated.
 - The haircells of the vestibular system respond to gravity rather than sound
 - This can be used for coding any orientation of the head

Deficits in movement:

- Hemiplegia: Loss of the ability to produce voluntary movement
 - o Results from damage to the primary motor cortex or the corticospinal tract, and the deficits are present in effectors contralateral to the lesion.
- Parkinson:
- Huntington:

The Brain-Machine Interface

- Brain-machine interface systems use directional neurons to directly control robotic devices such as a computer cursor or a prosthetic device.
- Early BMI systems required two phases.
 - o In the first phase, neural activity was recorded while the animal produced movement and the tuning properties (such as preferred direction) were recorded.
 - o In the second phase, the output from these neurons was used to control an interface device.
- Current studies are exploring how decoders can be adapted through experience in BMI control and are looking at the stability of such systems over extended periods of time. Advances on these problems are essential for building BMI systems that will be useful in clinical settings
 - o Current implants are temporary due to inflammation risks

- Brodmann area 6 includes secondary motor areas. The lateral aspect is referred to as premotor cortex, and the medial aspect as supplementary motor area.

Computational Issues in Motor Control

Physiological Analysis of Motor Pathways

- The neurophysiological evidence points to a more nuanced picture than we might have anticipated from our hierarchical control model. Rather than a linkage of different neural regions with specific levels in a processing hierarchy, one that moves from abstract to more concrete representations, the picture reveals an interactive network of motor areas that represent multiple features.
- Motor neurophysiologists correlate cellular activity in motor cortex with the animal's behavior.
- A common observation is that neurons in motor areas exhibit a preferred direction, in which the firing rate is strongest for movements in a limited set of directions.
- The population vector is a representation based on combining the activity of many neurons.
- Population vectors that provide a close match to behavior can be constructed from many motor areas, although this does not mean that all of these cells represent movement direction.
- Before movement even begins, the population vector is a reliable signal of the direction of a forthcoming movement. This finding indicates that some cells are involved in planning movements as well as executing movement.
- Neurons have dynamic properties, coding different features depending on time and context. There need not be a simple mapping from behavior to neural activity.
- The heterogeneity of responses exhibited by neurons in M1 includes both motor and sensory information.

Goal Selection and Action Planning

- The affordance competition hypothesis proposes that the processes of action selection (what to do) and specification (how to do it) occur simultaneously within an interactive neural network that continuously evolves from planning to execution.
- Action selection involves a competitive process.
- Rather than view selection and planning as serial processes, neural activity reveals that there is parallel activation of multiple goals and movement plans.
- Supplementary motor area is important for coordinating motor behavior in time (sequential movements) and between limbs (bimanual coordination).
- Parietal motor areas also show topography: Different regions of the intraparietal cortex are associated with hand, arm, and eye movements.
- Parietal motor representations are more goal oriented, whereas premotor-motor representations are more closely linked to the movement itself.
- Conscious awareness of movement appears to be related to the neural processing of action intention rather than the movement itself

Movement Initiation and the Basal Ganglia

- The output from the basal ganglia, via thalamic projections, influences activity in the cortex, including the motor cortex.
- All of the output signals from the basal ganglia are inhibitory. Thus, in the tonic state, the basal ganglia dampen cortical activity.
- Movement initiation requires disinhibition: The striatal projection to the GPi inhibits an inhibitory signal, resulting in excitation at the cortex
- Striatal neurons influence the output nuclei of the basal ganglia via the direct pathway and the indirect pathway.
- Dopamine is produced in the substantia nigra pars compacta, a brainstem nucleus that projects to the striatum. It has an excitatory effect on the direct pathway and an inhibitory effect on the indirect pathway.
- Parkinson's disease results from cell death in dopamine-producing cells in the substantia nigra.
- Parkinson's disease includes disorders of posture and locomotion, hypokinesia (the absence or reduction of voluntary movement), and bradykinesia (slowness in initiating and executing movement).
- The drug L-DOPA is used in treating Parkinson's disease because it can compensate for the loss of endogenous dopamine.
- Deep-brain stimulation is a surgical technique in which electrodes are implanted in the brain. This procedure has become a novel treatment for Parkinson's disease. Implants usually are placed in the subthalamic nucleus.
- The basal ganglia may play a general function in state changes. For the motor system, a state change would correspond to the initiation of a new movement. In the cognitive system, a state change could be a change in mental set, such as when we change from one goal to another. Dopamine acts as a reinforcement signal to bias some states over others.

Action Understanding and Mirror Neurons

- Mirror neurons are neurons in premotor cortex and other areas (like the parietal lobe) that respond to an action, both when that action is produced by an animal and when the animal observes a similar action produced by another animal.
- The mirror system has been hypothesized to be essential for comprehending the actions produced by other individuals.
- The engagement of the mirror system is modulated by motor expertise.

Learning and Performing New Skills

- Sensorimotor learning is improvement, through practice, in the performance of motor behavior.
- The cerebellum is critical for error-based learning. Errors are derived from a comparison of the predicted and observed sensory information. The errors are used to update a forward model, a representation that can be used to generate the sensory expectancies for a movement.
- The predictive capacity of the cerebellum is also important for online control. By anticipating the sensory consequences of movement, it helps compensate for delays introduced by sensorimotor processing.
- The primary motor cortex is critical for the long-term retention of skills. Consolidation is enhanced by dopaminergic input to the motor cortex from the ventral tegmental area of the brainstem.
- Skill requires extensive hours of practice. Expertise is skill specific, but it may be more closely related to domain-independent factors such as motivation rather than a propensity, or inclination, for particular types of

According to Hickok:

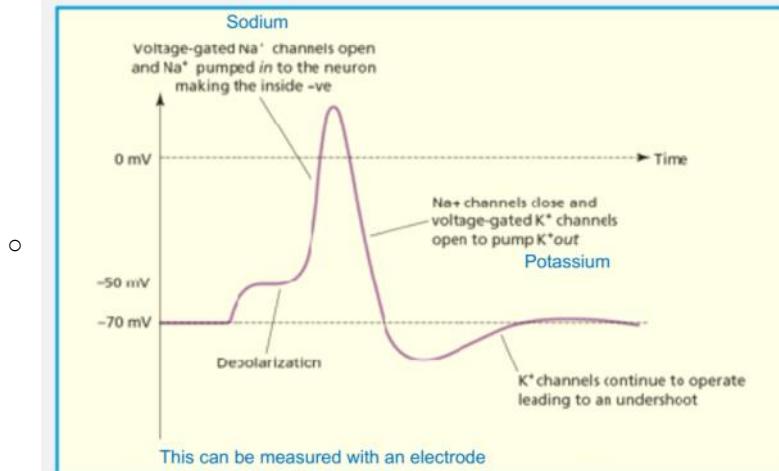
- There is no direct evidence in monkeys that mirror neurons support action understanding.
- Mirror neurons are not needed for action understanding
- Macaque mirror neurons and mirror-like brain responses in humans are different
- Action execution and action understanding dissociate in humans
- Damage to the hypothesized human mirror system does not cause action understanding deficits

performance

Outline for: EEG and event-related potentials

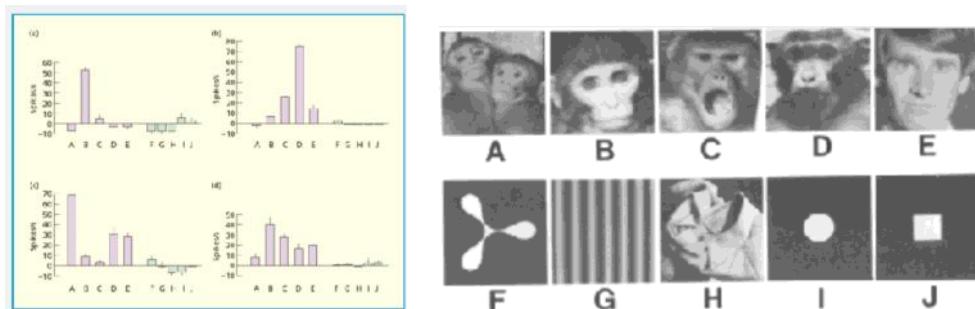
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- Methods in electrophysiology
 - These methods only record the activity, they do not stimulate neural activity
 - Invasive methods (participants often only animals):
 - Intracellular recording: A recording from the inside of the cell
 - Extra-cellular recording: A recording from the outside of the cell
 - Electrocorticogram (ECoG) is similar to an EEG, except that the electrodes are placed directly on the surface of the brain.
 - The measurements is either single-cell or multiple-cell recordings
 - Single-cell recordings: Records increases and decreases in the activity of individual neurons
 - This can be put in relation to stimulation of one of the senses or behavior
 - Single cell recordings are conducted on humans in very few cases:
 - ◆ Experiment: Epilepsy patient navigated through a virtual town while single cell recordings were conducted to reveal the existence of place cells
 - Most single cell recordings are done on animal:
 - ◆ Experiment: Electrodes implanted in the visual cortex of a cat revealed neuron with edge-detector functions.
 - ◆ Experiment: Electrodes implanted in rats' brains revealed place cells - cells, that respond to different locations independent of orientation.
 - With multiunit recording, the activity of hundreds of cells can be recorded at the same time.
 - Non-invasive methods:
 - Magneto-encephalography: measures the magnetic signals generated by the brain.
 - The electrical activity of neurons also produces small magnetic fields, which can be measured by sensitive magnetic detectors placed along the scalp.
 - MEG can be used in an event-related manner similar to ERPs, with similar temporal resolution. The spatial resolution can be superior because magnetic signals are minimally distorted by organic tissue such as the brain or skull.
 - MEG is expensive opposed to EEG
 - Electro-encephalography: Measures the electrical activity of the brain.
 - The EEG signal includes endogenous changes in electrical activity as well as changes triggered by specific events (e.g., stimuli or movements).
 - Event-related potential (ERP): A change in electrical activity that is time-locked to specific events, such as the presentation of a stimulus or the onset of a response. When the events are repeated many times, the relatively small changes in neural activity triggered by these events can be observed by averaging of the EEG signals. In this manner, the background fluctuations in the EEG signal are removed, revealing the event-related signal with great temporal resolution.
 - Electrophysiology measures electrical signalling (real brain activity)
 - Electrical signalling: Action potentials, that travels through the neural network

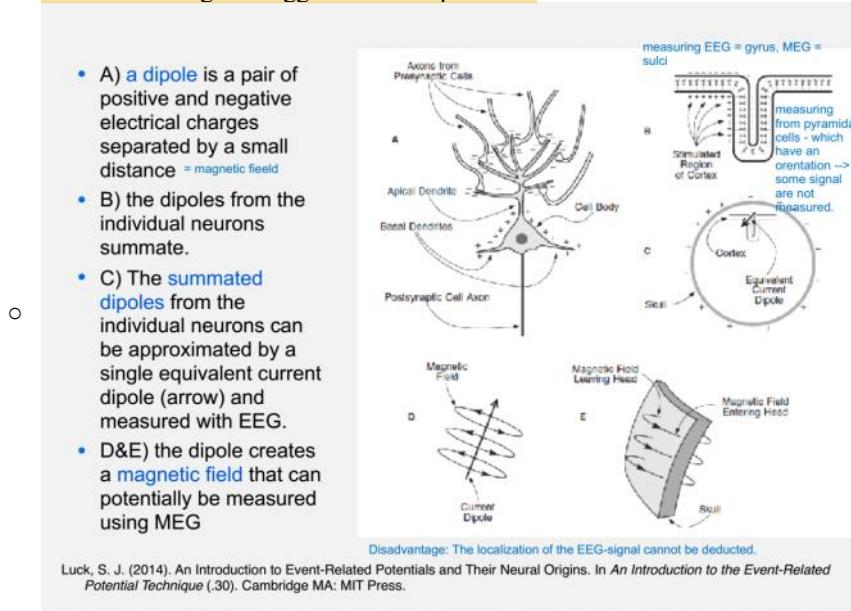


- Opposed to e.g. fMRI and PET, which investigate surrogate measures of brain activity, such as blood flow.
- Electrophysiology and measurements of neural activity have given rise to investigate, how information is represented in the brain
 - Rolls and Deco summarize three:
 - Local representation: All information about a stimulus/event is carried by one of the neurons e.g. a grandmother cell
 - Fully distributed representation: All the information about a stimulus/event is carried by all the neurons of a given

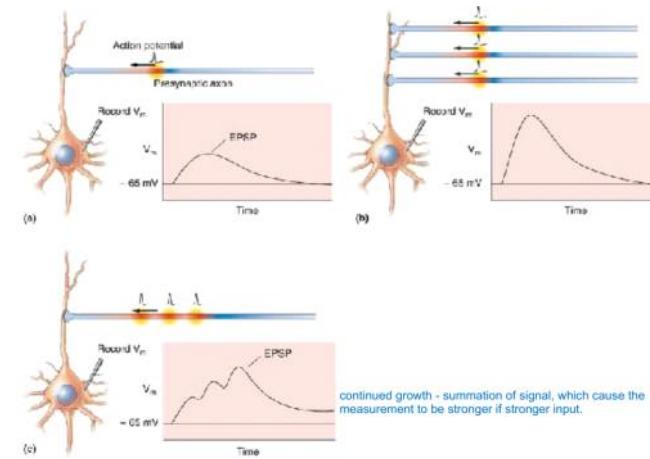
- population. The pattern of activation is what make up the representation
- Spares distributed representation: A population of neurons make up together the representation (inbetween solution)
 - Sparse distributed representation is most recognized, since some functional localization e.g. fusiform face area are discovered which questions the validity of the thesis of fully distributed representation. Equally the local representation is problematic, since the existence of population vectors
 - Example on distributed neural representations:



- How does EEG/MEG work?
 - Different neural codings
 - Rate coding: That a stimulus is associated with an increased firing rate e.g. the Hally Berry-neuron
 - Temporal coding: That a given stimulus is associated with greater synchronisation of firing across different neurons (e.g. integration)
 - Two types of synchronization:
 - One neuron is the catalyst for a group of neurons, which starts firing
 - A population of neurons are constantly active, sometimes the neurons synchronize
 - If two regions start firing in synchrony e.g. without general increase in firing rate, then this may indicate that some kind of information integration is taking place
 - The analysis of synchronization is called oscillation rate analysis, which is the typical approach, when processing EEG data
 - Temporal coding cannot be measured with fMRI, since an increased synchronization does not necessarily follow an increased BOLD-response
 - Synchronization and summation makes a signal
 - Summation: The process that determines whether or not an action potential will be triggered by the combined effects of excitatory and inhibitory signals, both from multiple simultaneous inputs (spatial summation), and from repeated inputs (temporal summation). Depending on the sum total of many individual inputs, summation may or may not reach the threshold voltage to trigger an action potential



- Whether the effect is positive or negative just implies the direction of the dipole
- EPSP summates, when...



- Advantage vs. Disadvantage in EEG

- Spatial resolution of EEG measurements
 - The number, location and magnitude of electrical sources are unknown, therefore there is an infinite number of ways the measured signal could have arisen (inverse problem)
 - Due to the “inverse problem” of getting from a surface measure to its origin(s), the spatial resolution of EEG is poor.
- EEG is cheaper than MEG (and fMRI and PET)
- Great temporal resolution

- Oscillation-based Analyses

- Neurons tend to fire in synchrony with each other; but at different rates (frequencies)
- Different oscillation frequencies characterise the different phases of sleep-wake cycle
- Different frequencies also characterise certain cognitive functions
 - Increased alpha (7-14Hz) linked to visual attention (inhibition)
 - Increased gamma (30Hz+) linked to perceptual grouping

Name	Amplitude (μV)	Frequency (Hz)	Associated Behavior	Representative Samples
Alpha	20-200	8 – 13	Awake, resting state	
Beta	~100	14 – 30, can be as high as 50	Beta I – Attention Beta II – Intense, mental activity	
Theta	~100	4 – 7	Emotional stress	
Delta	~100	< 3.5	Deep sleep, serious disease	

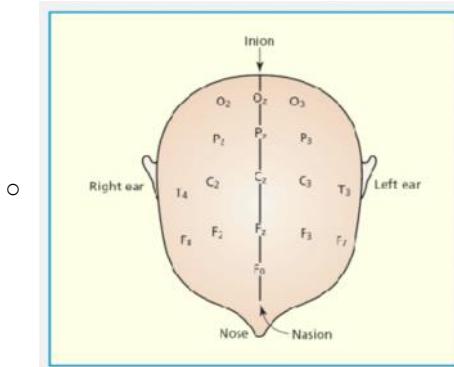
- Averaging the oscillations reduces the effects of random neural firing and artefacts and allows the signal to be put in relation to some aspect of an event (ERP)

- Different peaks approximately reflect the functioning of different cognitive stages
 - Not a simple relationship between ERP peak and cognition, because each peak is a sum of different electrical activities (many constalations could cause the outcome)
- Different components found by EEG:
 - The effect of mismatch negativity occurs, when a sound is unexpected relative to preceding sounds. This can be distinguished on the ERP signal.
 - The effect equally found in Hungarian and Finish phonemes. The languages have similar phonemes - the longer from the standard - the larger the mismatch negativity
 - The effect was also found during playing a piece of music → mismatch negativity is linked to expectation
 - N400 is a robust component of a negative-polarity brain wave related to semantic processes in language
 - Reading creates anticipations of a certain sentences finish, if violated the N400 effect occurs
 - Slower than mismatch negativity and requires attention
 - Different parameters predict the amplitude of the N400
 - A repeated word is more predictable than an unrepeated word
 - Context constrains possible words late in sentence but less in the beginning

- Frequent words are more predictable than infrequent words
 - Meaning is predictable
 - Experiment: The peanut in love: The peanut was in love gives smaller N400 than the peanut was salted
 - The linguistic system is flexible, according to the context, we are able to assign human values to objects
 - P600/SPS is a large positive component elicited after a syntactic and some semantic violations.
 - Mikkel says: Controversial: In general, the later the component is in time, the more skeptical one should be. 600 ms is loong time in terms of brain processes

- Practical execution of EEG measurements:

- The 10-20 system of electrodes are used in a typical EEG/ERP experiment
 - Recording sites in the 10-20 system:



- THERE IS A VIDEO IN MIKKEL SLIDE

Outline for: Memory - mangler

Tuesday, April 24, 2018 9:00 AM

Outline for: Emotion - mangler

Tuesday, April 24, 2018 9:00 AM

What Is an Emotion?

- Most psychologists agree that emotion consists of three components:
 1. A physiological reaction to a stimulus,
 2. a behavioral response, and
 3. a feeling

Neural Systems Involved in Emotion Processing

- Many parts of the nervous system are involved in our emotions
 - o Emotions are triggered by an episodic memory, in which case our memory systems are involved
 - o When emotions are triggered by an external event or stimulus (as they often are), our sensory systems play a major role
 - o The physiologic components of emotion (that shiver up the spine, or the racing heart and dry mouth people experience with fear) involve the autonomic nervous system (ANS), a division of the peripheral nervous system.
 - the sympathetic system promotes “fight or flight” arousal
 - the parasympathetic promotes “rest and digest.”
- The Papez circuit describes the brain areas that James Papez believed were involved in emotion. They include the hypothalamus, anterior thalamus, cingulate gyrus, and hippocampus. The limbic system includes these structures and the amygdala, orbitofrontal cortex, and portions of the basal ganglia.
- Investigators no longer think there is only one neural circuit of emotion. Rather, depending on the emotional task or situation, we can expect different neural systems to be involved.

Categorizing Emotions

- Most emotion researchers agree that the response to emotional stimuli is adaptive, comprised of three psychological states: a peripheral physiological response (e.g., heart racing), a behavioral response, and the subjective experience (i.e., feelings). What they don't agree on are the underlying mechanisms.
- The crux of the disagreement among the different theories of emotion generation involves the timing of these three components and whether cognition plays a role.
- In an effort to apply some order and uniformity to our definition of emotion, researchers have focused on three primary categories of emotion:
 1. Basic emotions comprise a closed set of emotions, each with unique characteristics, carved by evolution, and reflected through facial expressions.
 2. Complex emotions are combinations of basic emotions, some of which may be socially or culturally learned, that can be identified as evolved, long-lasting feelings.
 3. Dimensions of emotion describe emotions that are fundamentally the same but that differ along one or more dimensions, such as valence (pleasant or unpleasant, positive or negative) and arousal (very pleasant to very unpleasant), in reaction to events or stimuli.
- Basic emotions
 - o Innate, universal and short-lasting human emotions
 - o Paul Ekman's theory: Anger, fear, disgust, sadness, happiness, and surprise are the six basic human facial expressions and that each expression represents a basic emotional state, these emotions do not vary across cultures
 - o Additionally suggested pride and shame may be basic emotions
- Complex emotions
 - Complex emotions, such as love and jealousy, are considered to be refined, long-lasting cognitive versions of basic

- emotions that are culturally specific or individual.
- o According to Ekman parental love, jealousy etc. Is complex emotions, since they can last a lifetime
- o No universal expression exist for romantic love, therefore a complex emotions according to Ekman
- Dimensions of emotions
 - o Another way of categorizing emotions is to describe them as reactions that vary along a continuum of events in the world, rather than as discrete states.
 - o Feldman-Barret: Emotional reactions to a stimuli can be characterized by two factors:
 - valence (pleasant - unpleasant) and
 - Arousal (intensity of the internal emotional response)
 - o Rolls: Emotional reactions to a stimuli can be characterized by the actions and goals they motivate
 - Approach or withdrawal from a situation
- Emotions have been categorized as either basic or complex, or varying along dimensional lines.
- Six basic human facial expressions represent emotional states: anger, fear, disgust, happiness, sadness, and surprise.
- Complex emotions (such as love) may vary conceptually as a function of culture and personal experiences.
- The dimensional approach, instead of describing discrete states of emotion, describes emotions as reactions that vary along a continuum.

Theories of Emotion Generation

- Emotions are made up of three psychological components—a physiological response, a behavioral response, and a subjective feeling—that have evolved to allow humans to respond to significant stimuli. The underlying mechanisms and timing of the components are disputed
- Researchers do not agree on how emotions are generated, and many theories exist
- James-Lange Theory: William James proposed that the emotions were the perceptual results of somatovisceral feedback from bodily responses to an emotion-provoking stimulus
 - o e.g. you are afraid, because you tremble
- Cannon-Bard Theory: An emotional stimulus was processed by the thalamus and sent simultaneously to the neocortex and to the hypothalamus that produced the peripheral response. Thus the neocortex generated the emotional feeling while the periphery carried out the slower emotional reaction
 - o The neuronal and hormonal feedback processes are too slow to precede and account for emotions
- Appraisal theory: A group of theories in which emotional processing is dependent on an interaction between the stimulus properties and their interpretation.
 - o e.g. Lazarus proposed a version of appraisal theory in which emotions are a response to the reckoning of the ratio of harm versus benefit in a person's encounter with something.
- Singer-Schahter theory: Emotional arousal and then reasoning is required to appraise a stimulus before the emotion can be identified
- Constructivist theories: Emotion emerges from cognition as molded by our culture and language
- Evolutionary Psychology approach : Emotions are conductors of an orchestra of cognitive programs that need to be coordinated to produce successful behavior
- LeDoux's high road and low road: humans have two emotion systems operating in parallel. One is a neural system for our emotional responses that is separate from a system that generates the conscious feeling of emotion.

The Amygdala

- The amygdala is the most connected structure in the forebrain.
- The amygdala contains receptors for many different neurotransmitters and for various hormones.
- The role that the amygdala plays in emotion is still controversial.
- The amygdala is critical for the acquisition and expression of an implicitly conditioned fear response, whereas the hippocampus is critical for the explicit conditioned fear response

Interactions Between Emotion and Other Cognitive Processes

- Fear-conditioning paradigm

- Two pathways for fear-conditioning:
 - o Superior dorsal lateral amygdala undergo changes that pair CS (conditioned stimulus) and US (unconditioned stimulus)
 - o The lateral nucleus is connected to the central nucleus in amygdala, which initiate an emotional response to a stimulus if it is determined dangerous
 - o Information about the fear-inducing stimulus reaches the amygdala through two separate but simultaneous pathways
 - One goes directly from the thalamus to the amygdala without being filtered by conscious control.
 - Signals sent by this pathway, sometimes called the low road, reach the amygdala rapidly, but are incomplete
 - At the same time, sensory information about the stimulus is being projected to the amygdala via another cortical pathway, sometimes referred to as the high road.
 - The high road is slower, but more complete
 - This route goes via the thalamus, which sends the information to the sensory cortex for finer analysis, which sends it to the amygdala
- The role of the amygdala in learning to respond to stimuli that have come to represent aversive events through fear conditioning is said to be implicit.
 - o Learning is expressed indirectly through a behavioral or physiological response
- The amygdala is critical for indirect expression of the conditioned fear
 - o i.e. skin conductance when told a stimulus elicits a shock
- Explicit emotional learning
 - o Is the persistence of emotional memories related to the action of the amygdala during emotional arousal?
 - Experiment: Rats with injected with a drug to induce arousal show improved memory
 - With lesion to the amygdala this enhancement of memory is blocked
 - → Amygdala's role is modulatory: Depend on hippocampus for memory acquisition, but on the amygdala for arousal-dependant modulation
 - Studies point to the conclusion that the amygdala modulates hippocampal, declarative memory by enhancing retention by enhancing hippocampal consolidation, rather than by altering the initial encoding of the stimulus
 - also suggests that the amygdala can interact directly with the hippocampus during the initial encoding phase
 - o Extreme arousal or chronic stress may actually impair performance of the hippocampal memory system.
 - due to the effect of excessive stress hormones, such as glucocorticoids, on the hippocampus.
- The influence of Emotion on perception and attention
 - o When attentional resources are limited it is the arousing emotional stimuli that reach awareness
 - Amygdala plays a critical role in enhancing our attention when emotional stimuli are present and has a leading role in mediating the transient changes in visual cortical processing
 - o Emotion-laden stimuli receive greater attention and priorit perceptual processing
- Emotion and decision making
 - o Somatic marker hypothesis: emotional information in the form of physiological arousal, is needed to guide decision making.
 - When presented with a situation that requires us to make a decision, we may react emotionally to the situation around us. This emotional reaction is manifest in our bodies as somatic markers—changes in physiological arousal.
 - o Three types of emotions influence decision making:

- 1: Your current emotional state.
 - 2: Your anticipatory emotions; the ones that occur before you make your decision.
 - 3: Based on personal experience, the emotion that you expect to feel after you have made the decision
- Orbitofrontal cortical damage impairs the ability to respond to changing patterns of reward and punishment
 - It is difficult to reverse an association, once it's learned
- OFC is selectively active for the magnitude of reward and punishment and for their changing patterns
 - Lesion to the OFC therefore results in poor decision making
 - People with OFC damage have normal emotional reactions to their wins and losses, but they do not feel regret.
- Experienced feelings about a stimulus and feelings that are independent of the stimulus, such as mood states, have four roles in decision making.
 1. They can act as information.
 2. They can act as "common currency" between disparate inputs and options (you can feel slightly aroused by a book and very aroused by a swimming pool)
 3. They can focus attention on new information, which can then guide the decision.
 4. They can motivate approach or avoid behavior decisions.
- Emotion and social stimuli
 - Depending on the specific facial expression, it appears that different neural mechanisms and regions of the brain are at work, not for processing specific facial expressions per se, but more generally for processing different emotions
- TAKE-HOME MESSAGES:
 - Fear conditioning is a form of classical conditioning in which the unconditioned stimulus is aversive. It is a form of implicit learning.
 - The amygdala is heavily involved in fear conditioning (a form of implicit memory).
 - The conditioned stimulus is a neutral stimulus that, through classical conditioning, will eventually evoke a response. The unconditioned stimulus is the stimulus that, even without training, evokes a response.
 - The unconditioned response is the response naturally elicited (without training) by the unconditioned stimulus. The conditioned response is the response that is elicited (with training) by the conditioned stimulus. Usually the unconditioned response and the conditioned response are the same (e.g., the startle response in the rat), but they have different names depending on what elicits the response.
 - Patients with bilateral amygdala damage fail to acquire a conditioned response during fear conditioning, indicating that the amygdala is necessary for such conditioning to occur
 - Information can reach the amygdala via two separate pathways: The "low road" goes directly from the thalamus to the amygdala; the "high road" goes from the cortex to the amygdala.
 - The amygdala is also important for explicit memory of emotional events. First, the amygdala is necessary for normal indirect emotional responses to stimuli whose emotional properties are learned explicitly, by means other than fear conditioning. Second, the amygdala can enhance the strength of explicit (or declarative) memories for emotional events by modulating the storage of these memories.
 - The amygdala appears to be necessary for automatically deriving information from the eyes of others when identifying emotional facial expressions. This ability is especially critical for the proper identification of fear, because the defining characteristic of fear is an increase in the volume of the eye whites.
 - When looking at faces, the activity of the amygdala increases with the degree of difference from a categorically average face.
 - The amygdala is activated by novel stimuli independent of valence and arousal.
 - Attention, perception, and decision making are all affected by emotion.

Get a Grip! Cognitive Control of Emotion

- James Gross' theory of emotional suppression: Gross hypothesized that "shutting down" an emotion at different points in the process of emotion generation would have different consequences and thus, could explain the divergent conclusions.

- To test his theory, he compared reappraisal, a form of antecedent-focused emotion regulation, with emotion suppression, a response-focused form.
- Results: Conscious reappraisal reduces the emotional experience; this finding supports the idea that emotions, to some extent, are subject to conscious cognitive control.
- Different cognitive reappraisal goals and strategies activate some of the same PFC regions as well as some regions that are different.
- Emotion regulation is complex and involves many processes.
- Emotion regulation is dependent on the interaction of frontal cortical structures and subcortical brain regions.
- Different emotion regulation strategies have different physiological effects.

Other Areas, Other Emotions

- Insula
 - There is a significant correlation between insular activity and the perception of internal bodily states (interoception)
 - The junction where cognitive and emotional information are integrated
 - the insula may play a broad role in integrating affective and cognitive processes, whereas the amygdala may have a more selective role in affective arousal, especially for negative stimuli
- Disgust
 - The anterior insula is essential for detecting and experiencing disgust
 - Results provide additional evidence that the insula is a neural correlate of disgust identification in others and of experiencing disgust directly
- Happiness
 - A complex phenomenon to study...
- Love
 - "Love is a complicated business, and it appears to light up much of the brain—but you didn't need an fMRI study to tell you that"
 - Different brain areas are associated with the processing of different emotions. The orbitofrontal cortex is activated when identifying angry facial expressions and hearing angry prosody, and the anterior insula is linked to identification and experience of disgust.
 - The insula appears to play a broad role in integrating affective and cognitive processes

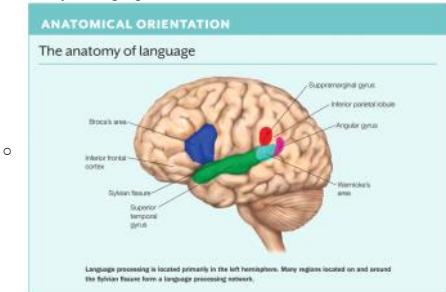
Unique Systems, Common Components

- Emotion research has shifted from identifying areas that specialize in a specific emotion to characterizing how these areas interact and determining if there are any interactions common to different types of emotional experience.
- Ultimately, understanding how we perceive and experience emotion will require studying the interactions of a diverse set of neural structures.

Outline for: Language

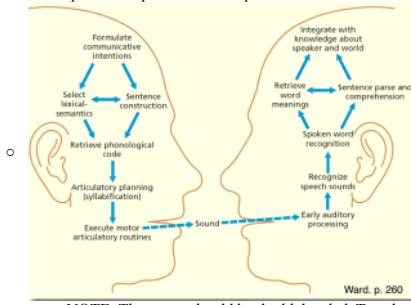
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- The anatomy of language



- The perisylvian region including the highlighted areas above is the main region for language
 - Especially, the left hemisphere is critical for language production and comprehension.
 - The right hemisphere does have roles in language, especially in processing the prosody of language

- A model of speech comprehension and production



- NOTE: The arrow should be doubleheaded. Top-down processing changes the bottom-up perception - we predict

- Speech comprehension

- Models of language involve unifying information from linguistic inputs or from retrieved linguistic representations with stored knowledge.
- White matter tracts in the left hemisphere connect frontal and temporal lobes to create specific circuits for speech, semantic analysis, and syntactic processing.
- Spoken-word recognition processing proceeds anteriorly in the superior temporal gyrus (STG). Phoneme processing appears localized to the left mid-STG, integration of phonemes into words appears localized to the left anterior STG, and processing short phrases appears to be carried out in the most anterior locations of STS.
- Distinguishing speech from nonspeech sounds occurs in the mid-portion of the superior temporal sulcus (STS), but no lexical-semantic information is processed in this area.
- Segmentation problem: No pauses between phonemes in speech that correspond to words, who do we segregate?
- Written Input: Reading words:
 - Written-word processing takes place in occipitotemporal regions of the left hemisphere. Damage to this area can cause pure alexia, a condition in which patients cannot read words, even though other aspects of language are normal.
 - Occipitotemporal regions of the left hemisphere may be specialized for the identification of orthographic units.

- Speech production:

- Models of language production must account for the selection of the information to be contained in the message; retrieving words from the lexicon; sentence planning and grammatical encoding using semantic and syntactic properties of the word; using morphological and phonological properties for syllabification and prosody; and preparing articulatory gestures for each syllable.
- Levels model
 - Each stage in Levelt's model for language production occurs serially, and its output representation is used for input to the next stage. It avoids feedback, loops, parallel processing, and cascades, and it fits well with the findings of ERPs recorded intracranially.
- Lexical selection can be influenced by sentence context.
- Lexical access and selection involve a network that includes the middle temporal gyrus (MTG), superior temporal gyrus (STG), and the ventral inferior and bilateral dorsal inferior frontal gyri (IFG) of the left hemisphere.
- Left MTG and STG are important for the translation of speech sounds to word meanings.
- Syntactic parsing is the process in which the brain assigns a syntactic structure to words in sentences.
- Syntactic processing takes place in a network of left inferior frontal and superior temporal brain regions that are activated during language processing

- Deficits in language

- Anomia: inability to find the words to label things in the world (not a deficit of knowledge)
- Dysarthria: Loss of control of articulatory muscles
 - A muscle deficit - not an aphasia
- Apraxia: Articulatory planning deficit
- Aphasia: Language deficits over and above motor and articulatory problems
 - Broca's aphasia:
 - Broca investigated the patient "Tan", named so, since it was the only word he uttered → lesions in Broca's area
 - Brocas aphasia not always linked to Broca's area lesions
 - Symptoms:
 - ◆ Slow, effortful speech
 - ◆ Speech articulation problems
 - ◆ Grammatical problems
 - Wernicke's aphasia:
 - "(...) deduced that a lesion of the auditory center in the first temporal convolution would leave people fluent, but unable to understand speech or use words properly. In other words, such a lesion would abolish sound images" (Klangbilder)
 - Originally linked to damage solely in Wernicke's area (the posterior superior temporal gyrus), today Wernicke's aphasia is also linked to damage outside the classic Wernicke's area.
 - Symptoms:
 - ◆ Able to talk fluently, but with no understanding of semantics
 - ◆ Repetition is faulty

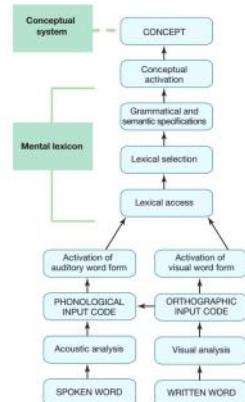


FIGURE 11.8 Schematic representation of the components involved in spoken and written language comprehension. Inputs can enter via either auditory (spoken word) or visual (written word) modalities. Notice that the information flows from the bottom up in this figure, from perceptual information to "higher-level" conceptual activation. So-called interactive models of language understanding would predict top-down influences to play a role as well. For example, activation at the word-form level would influence earlier perceptual processes. We could introduce this type of feedback into this schematic representation by making the arrows bidirectional (see "How the Brain Works: Modularity Versus Interactivity").

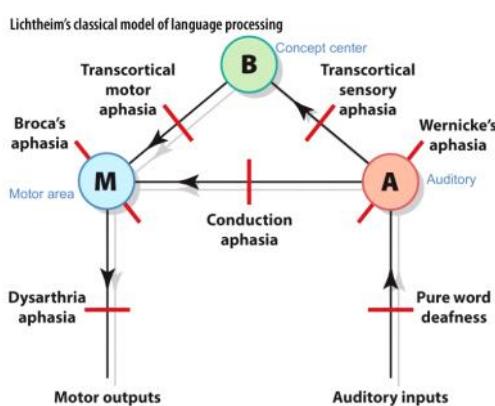


Table 20.1 Characteristics of Types of Aphasia

- Original linked to damage solely in Wernicke's area (the posterior superior temporal gyrus), today Wernicke's aphasia is also linked to damage outside the classic Wernicke's area.
- Symptoms:
 - Able to talk fluently, but with no understanding of semantics
 - Repetition is faulty
 - No motor symptoms
- The classical model of language processing:
 - Different aphasias can be explained in term of disruptions of connections between three different areas:
 - linguistic information, word storage (A 5 Wernicke's area),
 - speech planning (M 5 Broca's area)
 - conceptual information stores (B)
 - The areas are located in separate brain regions interconnected by white matter tracts.
 - NOTE: Everyone agrees the model has flaws, it is however often still applied
 - Flaws:
 - Broca's aphasic patients also have some problems in comprehension
 - A deficit in "motor images" doesn't explain one of the main symptom (agrammatism)
 - Many patients who meet criteria for Broca's aphasia have damage in temporal lobes not Broca's area (Dronkers)
 - Wernicke's aphasic patients also have problems in speech production (e.g. neologisms)
 - Wernicke's area involved in a variety of functions, including linking acoustic information with visual and motoric information
- If the Lichtenheim model is assumed it will result in 7 different types of aphasia:
 - Cortical motor aphasia
 - Lesion to M (Broca's aphasia)
 - "Speech comprehension is intact, but the patient presents either muteness or a vocabulary limited to a few words. Spontaneous speech and repeating as well as the voluntary mental sounding out of the word are not possible"
 - Cortical sensory aphasia
 - Lesion to A (Wernicke's aphasia)
 - "Cortical sensory aphasia is characterized by lack of comprehension of speech and inability to repeat it. However, the patient is able to speak spontaneously, and while vocabulary is unlimited, it is characterized by frequent word-transposition, that is, paraphasia (saying another word, than you meant to say, either syntactic, phonologically or semantic related)"
 - Conduction aphasia
 - Lesion between A and B
 - "Conduction aphasia is primarily characterized by negative symptoms. If motor or sensory aphasia is not evident, but speech is paraphasic, presenting word-transposition, on may predict a disturbance in conduction between centers a and b."
 - Everything has to go through meaning, which inhibits the ability to repeat non-sense words
 - Transcortical motor aphasia
 - Lesion between M and B
 - "Transcortical motor aphasia. This is the form on which Lichtheim's nomenclature founders. He interprets this type as aphasia in spite of retained ability to speak, which, however, is restricted to repeating. There is loss of spontaneous speech but no evidence of impairment in speech comprehension."
 - Subcortical motor aphasia
 - Lesion between M and motor outputs
 - "Subcortical motor aphasia. This form is differentiated from the preceding type by the complete integrity of the wordconcept. The muteness is the same as that found in type 4. The patient is able to indicate the number of syllables [contained in a word corresponding to an object presented to him]."
 - Transcortical sensory aphasia
 - Lesion between B and A
 - "Transcortical sensory aphasia. Impairment in comprehension of speech with preservation of the ability to repeat it. Symptoms of paraphasia are evident in spontaneous speech."
 - Subcortical sensory aphasia
 - Lesion between A and auditory inputs
 - "Subcortical sensory aphasia presents the same lack of comprehension of the spoken word and the same impairment in word mimicry. Spontaneous speech, however, is fully maintained, because the word-concept remains intact."
- NOTE: No aphasia related to area B, indicating this is not an area
- Classical models are insufficient to understanding neural basis for language

Evolution of Language

- Animal calls can carry meaning and show evidence of rudimentary syntax. In general, however, animal calls tend to be inflexible, associated with a specific emotional state, and linked to a specific stimulus.
- Many researchers suggest that language evolved from hand gestures, or a combination of hand gestures and facial movement.
- Areas that control hand movement and vocalizations are closely located in homologous structures in monkeys and humans

Motor outputs			Auditory inputs		
Table 20.1 Characteristics of Types of Aphasia					
Type of Aphasia	Site of Brain Damage	Comprehension	Speech	Impaired Repetition	Paraphasic Errors
Broca's	Motor association cortex of frontal lobe	Good	Nonfluent, agrammatical	Yes	Yes
Wernicke's	Posterior temporal lobe	Poor	Fluent, grammatical, meaningless	Yes	Yes
Conduction Global	Arcuate fasciculus Portions of temporal and frontal lobes	Good Poor	Fluent, grammatical Very little	Yes Yes	—
Transcortical motor area	Frontal lobe anterior to Broca's	Good	Nonfluent, agrammatical	No	Yes
Transcortical sensory	Cortex near junction of temporal, parietal, and occipital lobes	Poor	Fluent, grammatical, meaningless	No	Yes
Anomic	Inferior temporal lobe	Good	Fluent, grammatical	No	—

Bear, M. F., Connors, B. W., & Paradiso, M. A. (2016). Neuroscience - Exploring the Brain 4th ed., p. 627. Lippincott Williams & Wilkins.