# Chapter 1: Summary

Thomas Willis first introduced us, in the mid 1600s, to the idea that damage to the brain could influence behavior and that the cerebral cortex might ind d be the seat of what makes us human. Phrenologists expanded on this idea and developed a localizationist view of the brain. Patients like those of Broca and Wernicke later supported the importance of specific brain locations on human behavior (like language). Ramón y Cajal, Sherrington, and Brodmann, among others, provided evidence that although the microarchitecture of distinct brain regions could support a localizationist view of the brain, these areas are interconnected. Soon scientists began to realize that the integration of the brain's neural ne orks might be what enables the mind.

At the same time that neuroscientists were researching the brain, psychologists were studying the mind. Out of the philosophical theory of empiricism came the idea of associationism, that any response followed by a reward would be maintained and that these associations were the basis of how the mind learned. Associationism was the prevailing theory for many years, until Hebb emphasized the biological basis of learning, and Chomsky and Miller realized that associationism couldn't explain all learning or all actions of the mind.

Neuroscientists and psychologists both reached the conclusion that there is more to the brain than just the sum of its parts, that the brain must enable the mind—but how? e term *cognitive neuroscience* was coined in the late 1970s because fields of neuroscience and psychology were once again coming together. Neuroscience was in n d of the theories of the psychology of the mind, and psychology was ready for a greater understanding of the working of the brain. e resulting marriage is cognitive neuroscience. The last half of the 20th century saw a blossoming of interdisciplinary research that produced both new approaches and new technologies resulting in non-invasive methods of imaging brain structure, metabolism, and function.

# Chapter 2: Structure and Function of the Nervous System

## TAKE-HOME MESSAGES

- 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.

- 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 ow. 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).
- 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.
- 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.

## TAKE-HOME MESSAGES

- 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.

## TAKE-HOME MESSAGES

- 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.

## TAKE-HOME MESSAGES

- 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.
- 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 flight-or-fight responses by stimulating the adrenal glands.
- The parasympathetic system uses acetylcholine as a neurotransmitter. It is responsible for decreasing heart rate and stimulating digestion.
- Groups of neurons are called ganglia.
- 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.

## TAKE-HOME MESSAGES

- 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.
- 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 brain- stem 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.

## TAKE-HOME MESSAGES

- 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).

## TAKE-HOME MESSAGES

- The limbic system includes subcortical and cortical struc- tures 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.

## TAKE-HOME MESSAGES

- 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.
- The frontal lobe is for planning, cognitive control, and execution of movements. The parietal lobe receives sensory input about touch, pain, temperature, and limb position, and it is involved in coding space and coordinating actions.
- The temporal lobe contains auditory, visual, and multi- modal processing areas. The occipital lobe processes visual information. 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 out- side the sensory specific and motor cortical regions. Association cortex receives and integrates input from multiple sensory modalities

## TAKE-HOME MESSAGES

- 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.

# Chapter 3: Methods of Cognitive Neuroscience

## TAKE-HOME MESSAGES

- Cognitive psychology focuses on understanding how objects or ideas are represented in the brain and how these representations are manipulated.
- Fundamental goals of cognitive psychology include identifying the mental operations that are required to perform cognitive tasks and exploring the limitations in task performance.

## TAKE-HOME MESSAGES

- 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.

## TAKE-HOME MESSAGES

- 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.
- 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- behaviour relationships.

## TAKE-HOME MESSAGES

- 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 (temporarily) 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 behaviour.

## TAKE-HOME MESSAGES

- 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.

## TAKE-HOME MESSAGES

- 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 behaviour.
- 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 speci c 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.

## TAKE-HOME MESSAGES

- 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.

## TAKE-HOME MESSAGE

- A brain graph is a visual model of brain organization, and can be de ned 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.

## TAKE-HOME MESSAGE

- 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.

## TAKE-HOME MESSAGE

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

# Chapter 4: Hemispheric Specialization

## TAKE-HOME MESSAGES

- 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-de ned 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.

## TAKE-HOME MESSAGES

- 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.

## TAKE-HOME MESSAGES

- 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 hemi- sphere 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 nd an identical object with the right hand.
- Surprisingly, split-brain patients can use either hemi- sphere 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 glob- al targets, thus demonstrating that the left hemisphere is more adept at representing local information and the right hemisphere is better with global information.
- 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

## TAKE-HOME MESSAGES

- 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.

# Chapter 5: Sensation and Perception

## TAKE-HOME MESSAGES

- 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.

## TAKE-HOME MESSAGES

- 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 air ow 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.

## TAKE-HOME MESSAGES

- Gustation and olfaction are known together as the chemical senses because the initial response is to molecules (chemicals) in the environment.

  - The ve 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.

## TAKE-HOME MESSAGES

- 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.

## TAKE-HOME MESSAGES

- 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 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.

## TAKE-HOME MESSAGES

- 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.

## TAKE-HOME MESSAGES

- The visual cortex is made up of many distinct regions. These regions are de ned by their distinct, retinotopic maps. The visual areas have functional differences that re ect 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.

## TAKE-HOME MESSAGES

- 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.

## TAKE-HOME MESSAGES

- 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.

## TAKE-HOME MESSAGES

- 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 coincidently in time and space, the multisensory neural response is enhanced. The reverse is also true; when multisensory information is not presented coincidently in time and space, the multisensory neural response is depressed.

## TAKE-HOME MESSAGES

- People with synesthesia experience a mixing of the senses, for example, colored hearing, colored graphemes, or colored taste.
- Synthesia is associated with both abnormal activation patterns in functional imaging studies and abnormal patterns of connectivity in structural imaging studies.

## TAKE-HOME MESSAGES

- 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.

# Chapter 6: Object Recognition

## Principles of Object Recognition

- Sensation, perception, and recognition refer to distinct phenomena.
- People perceive an object as a uni ed 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 Perception

- 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 elds that include cells representing both the fovea and the periphery. Neurons in the temporal lobe have large receptive elds 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 informa- tion 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.

## 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 speci c 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 nely tuned to speci c stimuli.
- Ensemble theories, on the other hand, hypothesize that recognition is the result of the collective activation of many neurons.

## Failures in Object Recognition: The Big Picture

- 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 de cit 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.

## 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, speci city 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 identi ed as more active when body parts are viewed.

### 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.

# Chapter 7: Attention

## TAKE-HOME MESSAGES

- Attention is the ability to focus awareness on one stimulus, thought, or action while ignoring other irrelevant stimuli, thoughts, and actions.
- Arousal is a global physiological and psychological brain state, whereas selective attention describes what we attend and ignore within any specific level (high vs. low) of arousal.
- Attention in influences how we process sensory inputs, store that information in memory, process it semantically, and act on it.

## TAKE-HOME MESSAGES

- Unilateral spatial neglect may result from damage to the right parietal, temporal, and/or frontal cortices, as well as subcortical structures. This kind of damage leads to reduced attention to and processing of the left-hand side of scenes and objects.
- Neglect is not the result of sensory deficits, because visual field testing shows that these patients have intact vision. Under the right circumstances, they can easily see objects that are sometimes neglected.
- A prominent feature of neglect is extinction, the failure to perceive or act on stimuli contralateral to the lesion (contralesional stimuli) when presented simultaneously with a stimulus ipsilateral to the lesion (ipsilesional stimulus).
- Neglect affects external personal hemispace and objects as well as internal memory for objects arrayed in space.

## TAKE-HOME MESSAGES

- Attention involves both top-down (voluntary), goal-directed processes and bottom-up (reflexive), stimulus-driven mechanisms.
- Attention can be either overt or covert.
- According to early-selection models, a stimulus need not be completely perceptually analyzed before it can be selected for further processing or rejected as irrelevant. Broadbent proposed such a model of attention.
- Late-selection models hypothesize that attended and ignored inputs are processed equivalently by the perceptual system, reaching a stage of semantic (meaning) encoding and analysis where selection may occur.
- Our perceptual system contains stages at which it can process only a certain amount of information at any given time, what are called limited-capacity stages which result in *processing bottlenecks*. Attention limits the information to only the most relevant, thereby preventing overload of the limited-capacity stages.
- Cuing tasks, where the focus of attention is manipulated by the information in the cue, are often used to study the effect of attention on information processing.

- Spatial attention is often thought of metaphorically as a “spotlight” of attention that can move around as the person consciously desires, or that can be reflexively attracted by salient sensory events.

## TAKE-HOME MESSAGES

- Spatial attention in influences the processing of visual inputs: Attended stimuli produce greater neural responses than do ignored stimuli, and this process takes place in multiple visual cortical areas.
- Highly focused spatial attention can also modulate activity in the visual system in the subcortical relay nuclei in the thalamus, thereby providing strong evidence for early- selection models of attention.
    - Reflexive attention is automatic and is activated by stimuli that are conspicuous in some way. Reflexive attention also results in changes in early sensory processing, although only transiently.
    - A hallmark of reflexive attention is inhibition of return— the phenomenon in which the recently reflexively at- tended location becomes inhibited over time such that responses to stimuli occurring there are slowed.
    - Extrastriate cortical regions specialized for the perceptual processing of color, form, or motion can be modulated during visual attention to the individual stimulus features.
    - Selective attention can be directed at spatial locations, at object features, or at an entire object.
- Current models suggest that two separate frontoparietal cortical systems direct different attentional operations during sensory orienting: *a dorsal attention network*, con- cerned primarily with orienting attention, and *a ventral attention network*, concerned with the nonspatial aspects of attention and alerting. The two systems interact and cooperate to produce normal behavior.
- The dorsal frontoparietal attention network is bilateral and includes the superior frontal cortex, inferior parietal cortex (located in the posterior parietal lobe), superior temporal cortex, and portions of the posterior cingulate cortex and insula.
- The ventral network is strongly lateralized to the right hemisphere and includes the posterior parietal cortex of the temporoparietal junction (TPJ) and the ventral frontal cortex (VFC) made up of the inferior and middle frontal gyri.
- In addition, there are subcortical networks that include the superior colliculi and the pulvinar of the thalamus.

# Chapter 8: Action

## The Anatomy and Control of Motor Structures

- 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 bers. Action potentials in alpha motor neurons cause the muscle bers to contract.
- Extrapyramidal tracts are neural pathways that project from the subcortex to the spinal cord.
- The corticospinal or pyramidal tract is made up of de- scending bers 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 de cits 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 de ned 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

- 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 ring 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 speci- cation (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 coordinat- ing 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 rst 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, in uences 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 in uence 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.
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- 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.

# Chapter 9: Memory

## TAKE-HOME MESSAGES

- 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 sys- tem 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.

## TAKE-HOME MESSAGES

- 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 retrogade amnesia may have normal short- term memory as shown by digit span tests.

## TAKE-HOME MESSAGES

- Traditional memory theories include two main distinctions about how we learn and retain knowledge: by how long the information is retained and by what type of information the knowledge contains.
- Memory classified by duration includes sensory memory, lasting only seconds at most; short-term memory, lasting from seconds to minutes; and long-term memory, lasting from days to years.
- Echoic memory is sensory memory for audition; iconic memory is sensory memory for vision.
- Working memory extends the concept of short-term memory: It contains information that can be acted on and processed, not merely maintained by rehearsal.
- Long-term memory is split into two divisions de ned  by content: declarative and nondeclarative. Declarative memory is knowledge that we can consciously access, including personal and world

knowledge. Nondeclarative memory is knowledge that we cannot consciously access, such as motor and cognitive skills, and other behaviors derived from conditioning, habituation, or sensitization.

- Declarative memory can be further broken down into epi- sodic and semantic memory. Episodic memory involves conscious awareness of past events; it is our personal, autobiographical memory. Semantic memory is the world knowledge that we remember even without recollecting the specific circumstances surrounding its learning.
- Procedural memory is a form of nondeclarative memory that involves the learning of various motor and cognitive skills. Other forms of nondeclarative memory include perceptual priming, conditioned responses, and non- associative learning.
- Different types of information may be retained in partially or wholly distinct memory systems.

## TAKE-HOME MESSAGES

- The hippocampus is critical for the formation of long- term 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 epi- sodic 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 identified in the hippocampus and are called place cells. They provide evidence that the hippocampus has cells that encode contextual information.

## TAKE-HOME MESSAGES

- Functional MRI evidence suggests that the hippocampus is involved in encoding and retrieval for episodic memories that are recollected. Areas outside the hippocam- pus, 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 parahip- pocampal 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.

## TAKE-HOME MESSAGES

- 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.

## TAKE-HOME MESSAGES

- 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.

# Chapter 10: Emotion

## TAKE-HOME MESSAGES

- 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.

## TAKE-HOME MESSAGES

- 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.
- 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.

## TAKE-HOME MESSAGES

- 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.

## 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.

## TAKE-HOME MESSAGES

- 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.

## TAKE-HOME MESSAGES

- 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.

## TAKE-HOME MESSAGE

Ultimately, understanding how we perceive and experience emotion will require studying the interactions of a diverse set of neural structures.

# Chapter 11: Language

## TAKE-HOME MESSAGES

- Anomia is the inability to find the words to label things in the world. It is not a de cit 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.

## TAKE-HOME MESSAGES

- Language disorders, generally called aphasia, can include de cits 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 de ned Broca's area in the left inferior frontal cortex.
- People with Wernicke's aphasia have severe comprehension deficits but can produce relatively uid 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 dam- age 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.

## TAKE-HOME MESSAGES

- 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.

## TAKE-HOME MESSAGES

- There are no pauses between phonemes in speech that correspond to words.
- 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 process- ing 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.

## TAKE-HOME MESSAGES

- 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.

## TAKE-HOME MESSAGES

- Three classes of models attempt to explain word comprehension: *Modular models, interactive models* and *hybrid models*.
- 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.
- 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.

## TAKE-HOME MESSAGES

- 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.

## TAKE-HOME MESSAGES

- 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 syllabi cation 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.

## TAKE-HOME MESSAGES

- 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.