Chapter 14:

Lateralization and Language

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A common misconception among non-scientists, popularized by the media and online quizzes, is that analytic people are “left brained” while the creatives among us are “right brained” (Chapter 1). Modern studies have concluded repeatedly that correlating brain function with behavior on this broad level is not this simple. Both hemispheres of the brain are capable of carrying out the same essential functions: processing sensory and perception information, motor communication to the body, and the storage and retrieval of memory.

However, there are some features that are slightly more focused in one hemisphere than the other. We describe these features as being **lateralized**. Many different functions have a slight preference in lateralization: for example, the right hemisphere seems slightly better at making judgments about the duration of visible stimuli or processing of low-frequency musical stimuli. Keep in mind, the left hemisphere can also perform these functions, just not quite as well as the right can.

One heavily-lateralized function is language: for most people, the production and comprehension of language is dominated by structures in the left hemisphere of the brain. This chapter deals with these particular functions.

Chapter 14 outline

14.1 Lateralization

Almost all mammals are bilaterally symmetrical, with a left half that is more or less a mirror image of the right half. The internal organs, however, often tell a different story. We have a single stomach, liver, and heart, none of which are symmetrical. Even paired organs like the lungs or kidneys, are slightly asymmetrical. The brain can most accurately be thought of as a pair of intimately-connected organs with subtle differences in function.

The brain’s two hemispheres are connected by white matter tracts which allow the two halves to communicate. The largest interhemispheric white matter tract is the **corpus callosum**, which is made up of 200-250 million axons. If you held a human brain and separated the two hemispheres dorsally along the longitudinal fissure, you would be able to see the fibers of the corpus callosum holding the two halves together. The corpus callosum is about 10 cm (~4 inches) long from anterior to posterior, and the middle part of the structure forms the dorsal-most roof of the lateral ventricles.

In addition to the corpus callosum, there are a handful of other white matter tracts that allow the hemispheres to communicate. The much-smaller **anterior commissure** is a tenth of the thickness of the corpus callosum, connects the two temporal lobes, and conveys important limbic information such as memory and emotion. The **hippocampal commissure** is one of the outputs of the hippocampus that connects the structures in the left and right hemispheres. These small white matter tracts are often used as points of reference in imaging studies or surgical dissection.

A pair of researchers, Drs. Ronald Myers and Roger Sperry, were very curious about these pathways of communication between the two hemispheres. In the 1950's, they wanted to understand how information from one visual field gets conveyed into the opposite hemisphere of the brain. To answer the question of **interhemispheric transfer**, they conducted experiments in cats. One of their early experiments presented healthy cats with two different boxes, only one of which contained food. An eyepatch was placed over one of the cat's eyes, and the cat was free to paw at one of the boxes, which if chosen correctly, would yield the food reward. At first, as expected, the cat would choose from the boxes at random, obtaining the food reward 50% of the time. Over multiple trials, as the cat began to learn which box held the food, the success rate rose to picking the rewarded box 100% of the time. When the eyepatch was then moved to the other eye, the cat performed the task correctly 100% of the time, reliably picking the box associated with food.

Then, Myers and Sperry performed a two different surgical procedures on the cats. One severed the optic chiasm, which kept visual information in the ipsilateral hemisphere. This ensured that when wearing the eye patch, visual information does not cross into both hemispheres. The other procedure to severed their corpus callosum, a process called a **corpus callosotomy** (or **commissurotomy**), which limited interhemispheric transfer after visual cortex processing. Between these two interventions, there were four groups of cats: Fully intact, optic chiasm cut, corpus callosum cut, and the experimental group with both optic chiasm and corpus callosum cut..

The box-selection behavioral experiment was then repeated. As with the intact cats, when the eyepatch was placed over one eye, the experimental cats (both chiasm and corpus callosum severed) initially guessed at the boxes, getting the reward 50% of the time. Again, as before, these animals improved their performance over repeated trials, eventually getting the

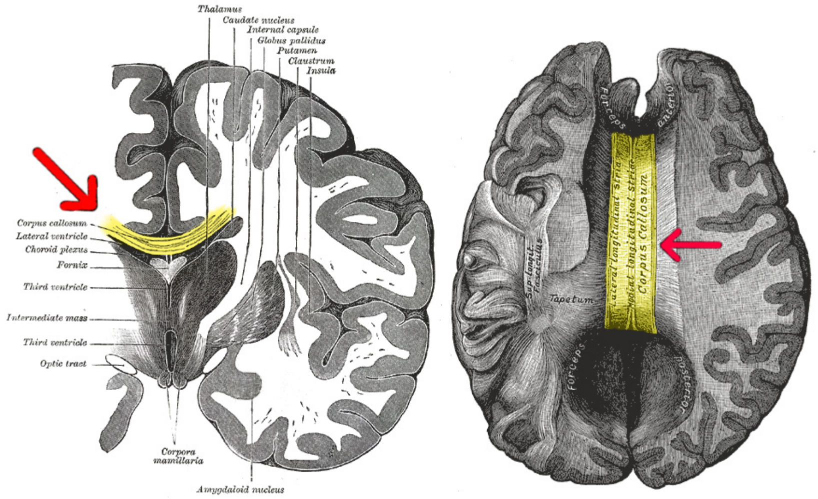

Figure 14.1 The corpus callosum, indicated in yellow with red arrow, in a coronal slice (left) and seen from the top when both hemispheres are gently pulled apart (right).

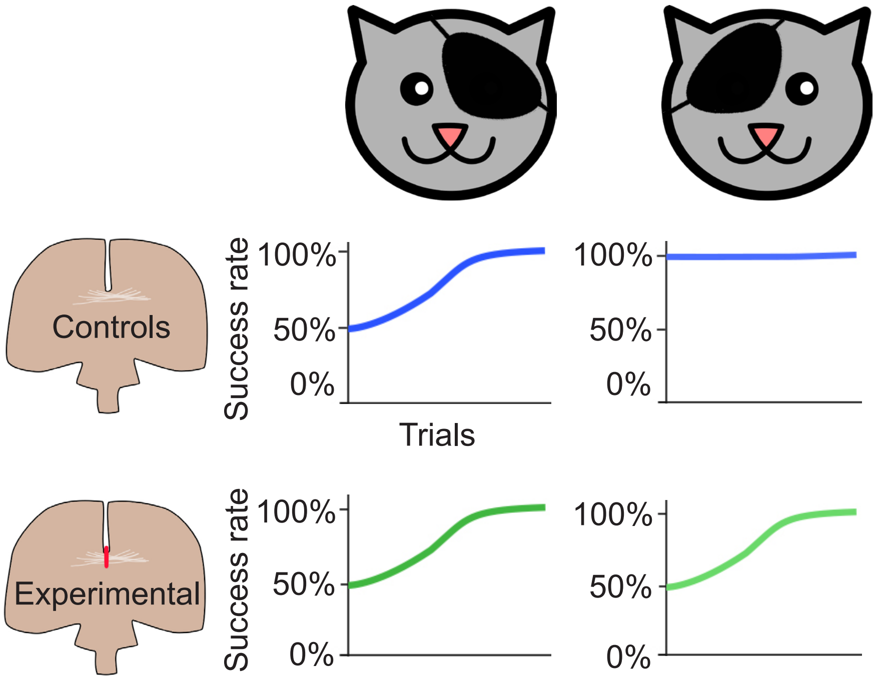

Figure 14.2 Myers and Sperry demonstrated that each hemisphere is capable of learning and storing memories independently.

reward every time. However, after the eyepatch was switched from one eye to the other, these cats essentially had to "start over" with their learning: they picked the rewarded box only 50% of the time, improving to 100% over trials. Because of the surgical procedures, the visual information and associated reward memory in one hemisphere never made it to the other half of the brain - a failure of interhemispheric transfer.

The two other control groups immediately performed at 100% after the eyepatch was switched over, just as well as the fully intact cats. When the optic chiasm was severed with the corpus callosum intact, the visual information remained in the ipsilateral hemisphere, but after processing in V1, that information passed over the corpus callosum to the contralateral hemisphere. When the corpus callosum was severed with the optic chiasm intact, the visual information made their way into both hemispheres through the optic nerve.

Myers and Sperry then extended their research to humans. Sometimes, commissurotomy is suggested for younger patients with drug-resistant epilepsy. Grand mal seizures are often characterized by uncontrolled electrical activity in one hemisphere, which then crosses the corpus callosum to the other hemisphere before "bouncing back" to the original hemisphere. During the procedure, the surgeon cuts the corpus callosum, and in doing so, keeps the atypical electrical activity isolated in one hemisphere. Patients have significantly fewer and less severe seizures following recovery from the operation.

People who have had this surgery are sometimes called **split-brain patients**, a population of patients who were extensively

Clinical connection: Agenesis of the corpus callosum

In a handful of rare cases, people can be born without a corpus callosum, a condition called **agenesis of the corpus callosum (ACC).** Some people with ACC develop atypically, experiencing seizures and poor motor control or coordination. An estimated one-fourth of people diagnosed with ACC after birth have some intellectual disability, but most have typical levels of intelligence. They may have subtle abnormal developmental traits, such as a difficulty with processing common social cues (as seen in autism). Notably, the real-life savant who served as the inspiration for the movie *Rain Man* was born with ACC.

studied by Dr. Michael Gazzaniga.. Overwhelmingly, split-brain patients are healthy with no significant changes in intelligence and no dramatic changes in personality. However, some of them do experience deficits in memory and concentration.

Among split-brain patients, very unique behavioral and cognitive deficits can be observed under specific experimental circumstances. The baseline test begins by briefly showing the patient some visual stimulus, such as a picture of a donut, only in their right visual field, which gets represented in the left visual cortex (refer back to chapter 7.2 for a reminder of the circuitry of the visual system). When asked what the patient had seen, they would report “a donut,” just as any typical person would (because the left hemisphere is highly involved in language and enables the person to report the object verbally).

In a second experiment, both of the patient’s hands are placed on a table hidden behind a screen. An object, such as an apple, is then placed in their right hand. As the patient feels that object, tactile information such as its hardness, diameter, and temperature, ascends contralaterally into the left somatosensory cortex (chapter 8). After the object is removed from their hand, the patient is asked to feel blindly through a collection of objects, all hidden behind the screen, and find a matching object. When doing this task with the right hand, they would be successful in selecting an apple (because the motor system is crossed). However, when the left hand was now tasked with reaching behind the screen to select a matching object, they would not be able to know which object to pick up because this information goes to the right somatosensory cortex (which has no knowledge of the apple). From these data, the researchers concluded that each hemisphere is independently capable of receiving their own sets of somatosensory inputs

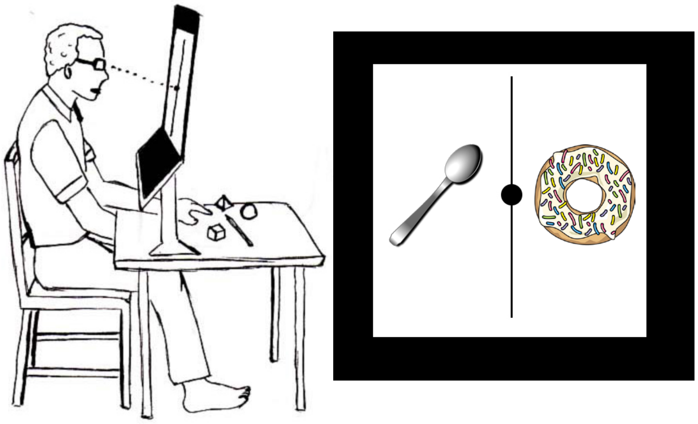

Figure 14.3 Experimental setup for studying interhemispheric transfer of visual information in humans (left). After fixation on the dot in the center of the visual field, the stimuli (right) are flashed briefly, and the patient is asked the either name the item observed, or reach behind the screen and select a matching object.

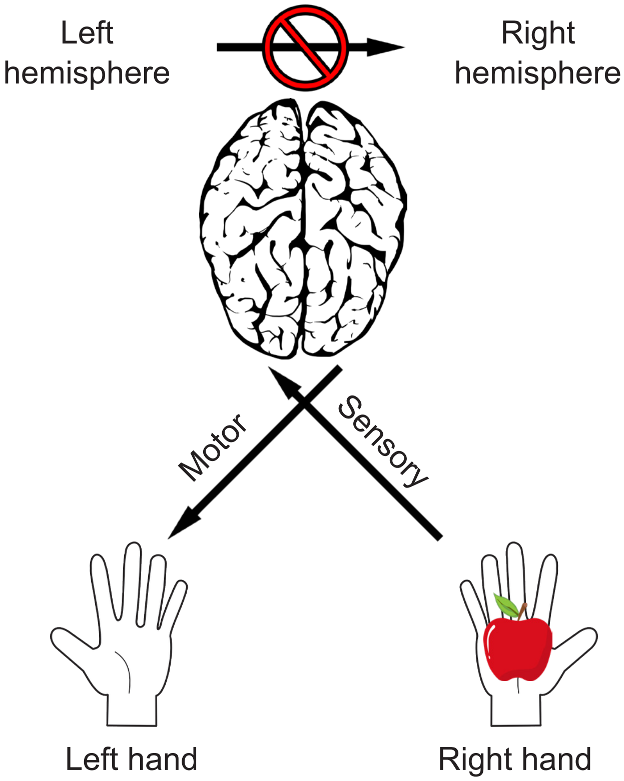

Figure 14.4 In split-brain patients, when an apple is placed in the right hand, that information ascends contralaterally but cannot cross hemispheres.

and storing their own memories. Without an intact corpus callosum, the two hemispheres are unable to share that knowledge, so the sensory and memory information that reaches the left hemisphere isn't capable of reaching the right hemisphere, which controls the left hand - so the left hand is clueless to the object placed in the right hand.

In the next step of the experiment, a different visual stimulus, like a picture of a spoon, is presented to the left visual field, which is initially sent to the right half of the brain. When asked what they saw, they might say "nothing" or "I don't know." (because the right hemisphere is not specialized for language and the person is not able to report the object verbally). But, when the patient is asked to reach behind the screen with their left hand, they could successfully select a spoon! (Left hand is controlled by the right brain, which has knowledge of the spoon.) Their right hand, however, couldn't correctly pick a matching object (since the left brain does not have the information about the spoon). Again, these results demonstrate that each hemisphere is capable of receiving their own contralateral sensory information and storing their own sets of memory.

For most people, who have their corpus callosum intact, information is transferred rapidly between hemispheres. So, when a spoon is shown to our right brain, the left brain learns that information as well, which is why we would be able to select a matching object with our right hand.

Myers and Sperry's human studies noted an interesting difference in the ability of split-brain patients to respond verbally. When the stimulus was sent into the left hemisphere, either a visual stimulus in the right visual field or an object placed in the right hand, the patients were able to verbalize what they either saw or felt. But, when the stimulus was represented in the right hemisphere, they couldn't. Their conclusion was that the left hemisphere is much better equipped for language-related functions compared to the right hemisphere. As it turns out, language comprehension and production is heavily lateralized to the left hemisphere. For his work regarding the "effects of disconnecting the cerebral hemispheres", Dr. Sperry earned the 1981 Nobel Prize.

14.2 Language

Language is one of Homo sapiens' greatest intellectual evolutionary accomplishments. Using language, we are able to communicate very complex concepts, such as survival instructions (Don't eat those berries because they taste weird and you'll get sick) or a shared belief in the existence of complex stories (Hang stockings by the chimney and you'll get presents if you were good). Language, when used in these ways, has a powerful influence on behavior, and modern humans rely heavily on language in every aspect of society.

Components of language

Speech pathology experts have identified at least four distinct components for describing different aspects of language. The most granular unit is the **phoneme**, which is an individual sound that generally has no meaning on its own. For example, the word map can be split into three phonemes, "mm", the short "/ă/", and "p" sound.

The next larger unit of language is the **morpheme**, which is a combination of phonemes. Morphemes are capable of conveying an idea, such as "cat". Suffixes such as "-s" and "-ing" also convey ideas (plural and verbs in action, respectively) are also considered morphemes.

The **syntax** represents the next higher level of language, which is the information conveyed when words are combined in order to produce meaning at the level of phrases and sentences. For example, a statement such as "He gave a gift to his brother" contains syntactic information identical to "He gave his brother a gift", even though the organization is different. The grammatical rules of many languages tell us the order of nouns, verbs, and objects, and inappropriate deviation from these rules can change the meaning of the sentence dramatically.

Semantics refers to the understanding of meaning, especially the meaning of words in relationship to one another in a phrase, sentence, or paragraph. Extracting meaning from statements not meant to be taken literally (such as a hungry person exclaiming "I'm so hungry, I could eat a horse!") and identification of the meaning of a word under two different contexts (such as in the sentence "I held a nail between my fingers, but when I swung the hammer, I hit my nail instead.") fall under the category of semantics.

Brain structures involved with language

Whereas the left and right hemispheres of the brain are mostly symmetrical, one of the biggest asymmetries is related to the structures responsible for language. Myers and Sperry observed that split-brain people can verbally report observations made with the left brain, while having difficulty when information is stored by their right brain. This suggests that the left hemisphere is dominant for language functions. It is estimated that about 90% of right hand-dominant people and about 50% of left hand-dominant people use their left hemisphere for language related functions.

However, this does not mean that the other hemisphere does not contribute to language. The right hemisphere, for example, shows activation during the use of nonliteral language, such as in metaphor production or irony comprehension.

In addition to the split-brain patient case studies, there are several other significant pieces of evidence to support left hemispheric dominance for language.

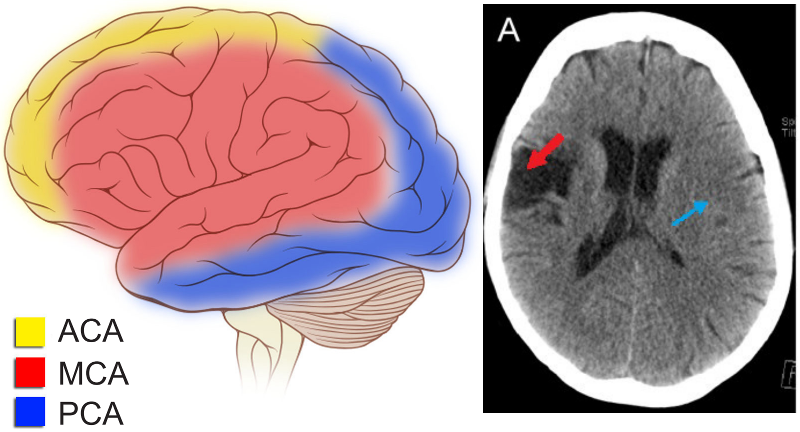

Figure 14.5 Areas of the cortex that receive blood flow from specific arteries (left). The middle cerebral artery (MCA) provides perfusion to frontal, parietal, and temporal areas that are important for language. CT scan of a patient after a stroke of the MCA, showing loss of brain tissue (red arrow, right).

People with left hemisphere lesions may lose their language capacities. A stroke of the left middle cerebral artery often leads to a variety of language related deficits. Unfortunately, similar injuries sometimes happen after brain surgery, traumatic brain injury, or brain infections, also resulting in language deficits when localized to the left hemisphere.

Experimental methods have allowed researchers to study the lateralization of language without causing any permanent damage. The **Wada test** is the most reliable method by which hemispheric lateralization of language can be determined. Named for the Japanese-born neurosurgeon Jun Wada, the test is a presurgical assessment to minimize the risk of a person losing their language capacity in the process of brain surgery. The protocol begins with the surgical team asking the patient to hold up both hands, wiggling their fingers, while counting. The patient then receives an intravenous infusion of **sodium amytal**, a GABA receptor positive allosteric modulator that acts as an anesthetic. When infused into the internal carotid artery, the drug gets delivered into just one hemisphere of the brain with little leakage into the other. When the anesthesia perfuses through the left brain, their right hand loses muscle tone and their fingers will stop moving (remember the contralateral organization of the motor control system, chapter 10.) And, if language is lateralized in this hemisphere as it is for most people, they will also be unable to count during this time. Within seconds, the anesthesia is cleared from the brain, and the wiggling and counting resume. If the patient is right hemisphere dominant for language, then they will be able to count, even though the fingers stop moving. The procedure is then repeated while the anesthetic is perfused into the other hemisphere.

The Wada test, because of its invasive nature and occasional side effects (pain, infection, and seizure or stroke in very rare cases), is used less frequently as functional brain imaging methods have become cheaper and more available through the 2000s. The fMRI is a preferred test of hemispheric dominance. To conduct these tests, a person is put into the imaging machine, then asked to perform a series of language tests, such as listing several items of a given category, or listening to a conversation in preparation for follow-up questions. During this process, the fMRI informs the medical team about which half of the brain shows greater activity during the language tests. These behavioral tests have been found to be as accurate as the Wada test in determining lateralization of language functions.

Across the language dominant hemisphere, there are a few brain regions that

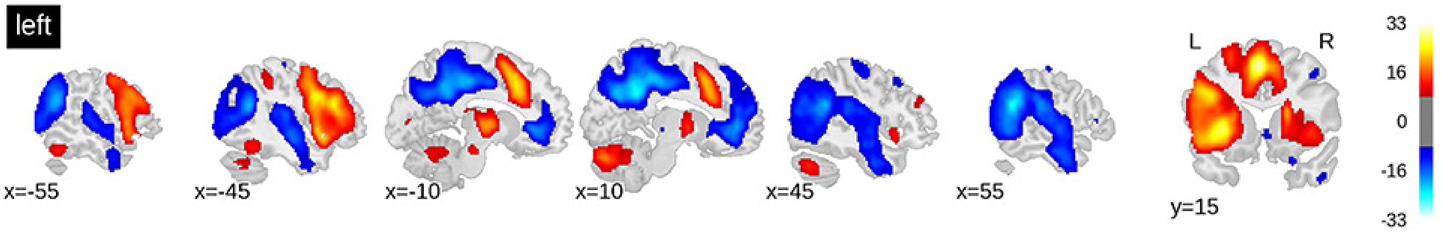

Figure 14.6 Non-invasive fMRI scans demonstrate that left hemisphere (negative x) brain areas increase in blood flow compared to right hemisphere (positive x) during the performance of language tasks. Warmer colors indicate increases in blood flow, while cooler colors represent decreases.

contribute significantly to language functions. When something goes wrong with these areas, a person may develop **aphasia**, a language disorder. It is estimated that about 180,000 new cases of aphasia are diagnosed in the United States annually. Stroke is a common cause of aphasia, but other neurological insults such as head trauma, traumatic brain injury, or subdural hematoma can induce aphasia. Just like nearly everything in biology, there is a wide range of severity, with some cases being very minor and other cases being much more severe. Speech therapy can help a patient recover from aphasia, and this progressive restoration of function is a demonstration of the brain's capacity for plasticity and remodeling.

Expressive (or non-fluent; or Broca's) aphasia

One of the first language-related cortical structures identified is the posterior **inferior frontal gyrus (IFG)**. Deficits in this area lead to a difficulty with the production of language.

In the 1860's, a patient named Louis Victor Lebourgne had a very unusual condition: he could only speak one syllable. For Lebourgne, the syllable "tan" meant everything, from "yes" to "no" to "hat" to "thirty-four". Lebourgne would say "tan" while gesturing emphatically, scream "TAN TAN!!" when angry, and whisper "tan" when telling secrets. Because of this, the staff at the hospital called him **Patient Tan**.

When Patient Tan died, the French physician Paul Broca performed an autopsy on the brain. Broca discovered a huge lesion about the size of a "chicken's egg" in the left hemisphere, just dorsal of the lateral fissure in the frontal lobe. Soon after, Broca performed autopsies on the brains of seven other patients with similar language difficulties, all with the same prominent injury to this portion of their frontal lobe. Because of the work that Broca did in correlating structure with function, the posterior IFG came to be called Broca's area.

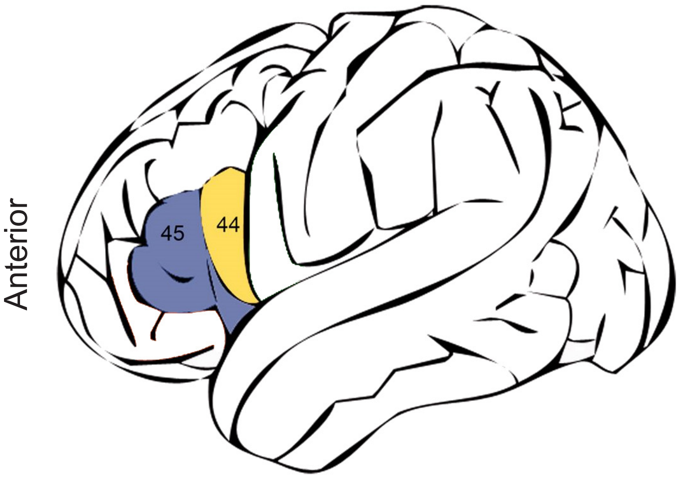

Figure 14.7 The posterior IFG, or Broca's area (labeled as 45 and 44; purple and yellow) contribute to language production.

Today, we understand that a localized injury to the IFG produces a form of aphasia called **expressive aphasia** (also called **non-fluent aphasia** or **Broca's aphasia**). These patients have difficulty expressing themselves, only speaking in short, effortful phrases, using just nouns and verbs while omitting tenses, conjunctions, and prepositions. They speak haltingly, sometimes filling the silences in their sentences with filler phrases. The patients are profoundly aware of their deficit, leading to overwhelming frustration with their inability to communicate. They know what they want to say, but often can't get it out. Interestingly, these patients do not have any significant impairment of comprehension.

Patients with IFG injury show similar expressive deficits regardless of the modality of their language. For example, when asked to write, they write slowly, using mostly nouns and verbs. Alternatively, patients who use American Sign Language also lose grammatical syntax and communicate slowly when signing!

Receptive (or fluent; or Wernicke's) aphasia

A different brain structure, called the **superior temporal gyrus** is linked to language comprehension. This area is sometimes also called **Wernicke's area**, named for the German physician named Carl Wernicke, who studied a group of patients with a different form of aphasia than Broca's. These patients had no deficits in the production of speech, but the words they used were very disorganized. They could speak complete sentences fluently, but their speech contained almost no substantial semantic content. Unlike Broca's patients, Wernicke's patients had dramatic impairments in comprehension. This language disorder is **receptive aphasia** (or **fluent aphasia**, or **Wernicke's aphasia**.)

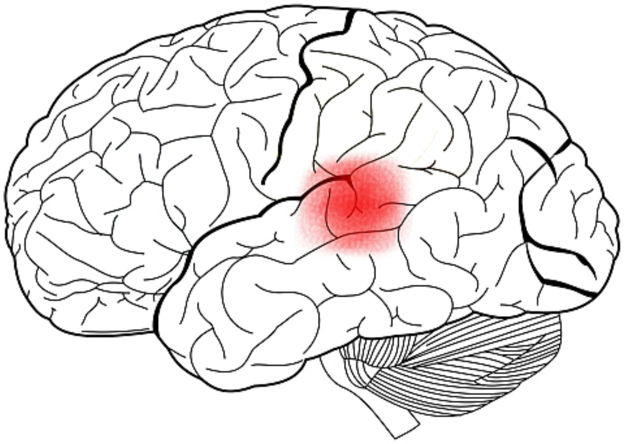

Figure 14.8 The superior temporal gyrus, or Wernicke's area (red), contributes to language comprehension.

While talking, people with receptive aphasia may create new meaningless words they are unaware of, a symptom called **paraphasia**. These words could be a mispronunciation of a word, perhaps sounding like the jumbling of syllables. They can happen at the level of the phoneme or morpheme, such as in nonwords such as "emchurch" or "plehzd". They also appear at the level of syntax, when a person substitutes a word incorrectly for another, as in the sentence "But I seem to be table you correctly, sir."

Sometimes, they experience a difficulty with recalling words, a symptom called **anomia**. This happens in the middle of a sentence, and may be difficult to catch in casual conversation, since they will often use vague language ("stuff" or "things") or use several words in a roundabout fashion to describe what they are trying to say, a behavior called **circumlocution** ("red, it's green, and yellow means be cautious, to keep people safe" instead of "traffic light.")

Conduction aphasia

Early theories suggested that communication between the STG and the IFG is important for healthy language production and comprehension. Anatomically, a band of white matter called the **arcuate fasciculus** spans these areas, originating in STG and terminating in the IFG. When this structure is injured, people develop some difficulty with repeating language they hear, a disorder called **conduction aphasia**. Generally, these patients display paraphasias when asked to repeat multisyllabic words, often switching phonemes around in a single word.

These patients have no significant deficits in language production or comprehension, presumably because their IFG and STG are still intact and healthy. Conduction aphasia is less severe than expressive or receptive aphasia.

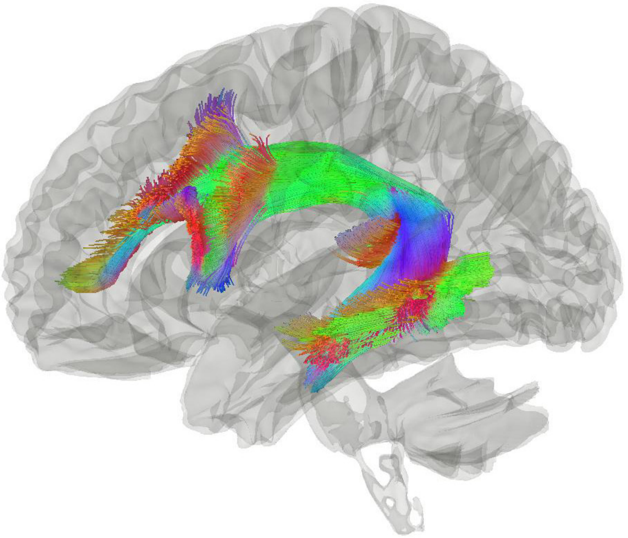

Figure 14.9 The arcuate fasciculus (colored) is a large white matter band that connects the two major language-related cortical structures.

Global aphasia

Extensive brain damage to the left IFG, STG, and arcuate fasciculus may cause the most severe form of aphasia, **global aphasia**. Patients experience both expressive and receptive deficits, usually only being able to communicate using only single words or grunts. They also struggle with repeating words spoken to them. Following a major stroke to the left middle cerebral artery, global aphasia may first present, possibly lessening in severity as the brain heals.

If their other hemisphere is spared, patients with global aphasia can learn to communicate using pantomime or facial expressions.

The Wernicke-Geschwind model

From case studies of injuries leading to aphasia, a few cortical structures emerge as being major contributors to language: the IFG, STG, and the arcuate fasciculus that connects the two. Two neurologists, Carl Wernicke and later Norman Geschwind, proposed the **Wernicke-Geschwind model**, which suggests that information is passed along through language structures in a linear pathway, and each section is responsible for a different aspect of language.

The model begins with the simple scenario: An interviewer is asking you a question, and you answer. First, the sound information arrives into A1, the primary auditor y cortex (see chapter 8 for more details). From there, that information is processed by the STG (Wernicke's area), which then takes meaning out of those sounds. Then, that information travels across the arcuate fasciculus. Then, that information arrives at the IFG (Broca's area), where neurons carry information related to the planning of language, such as coordinating the muscle movements that create the verbal response. Finally, those signals arrive at the motor cortex, which is then responsible for sending the descending signals to control the muscles required for speech (chapter 10).

Another component of the model proposes an explanation for the following situation: You read

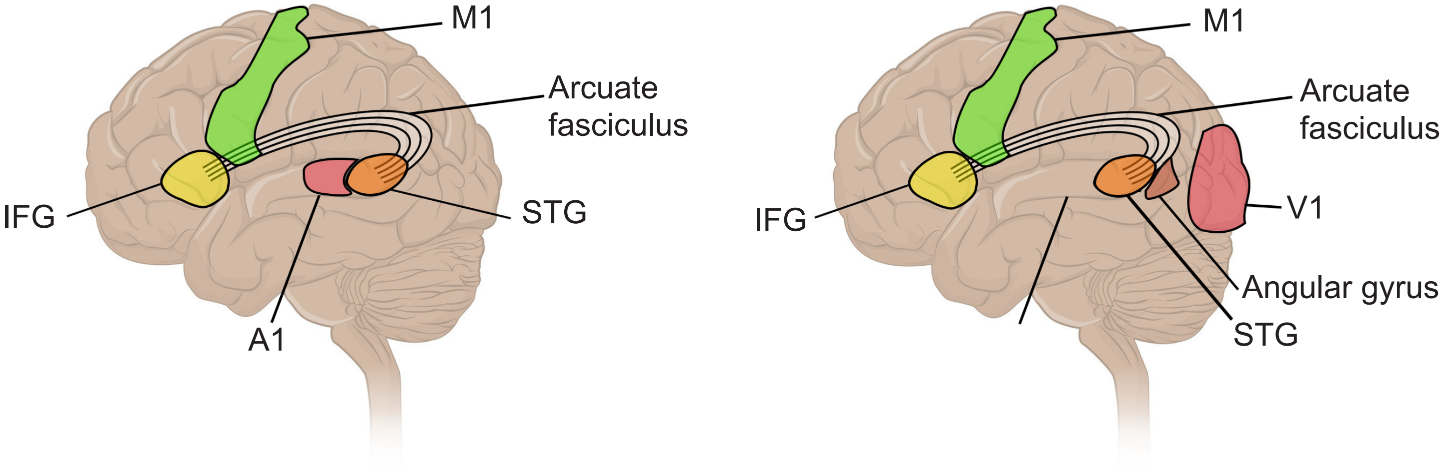

Figure 14.10 The Wernicke-Geschwind model in auditory processing and responding suggests that information signaling arrives into cortex through A1, travels through STG, IFG, then M1 (left). In a reading and responding task, the model suggests that information signaling arrives into cortex through V1, passes through circuits in the angular gyrus, then through STG, IFG, then M1 (right).

a question on a piece of paper, and answer the question verbally. Visual information arrives into the V1, the primary visual cortex. The output of the visual cortices arrives at the angular gyrus, a parietal lobe structure just posterior to the STG. From here, the signal travels through STG and continues through motor cortex, following the same pathway described above.

This Wernicke-Geschwind model was initially helpful for providing a framework for understanding language. But in modern times, we regard it as an oversimplified and outdated explanation of a complex behavior. Sometimes the model fails to accurately predict the nature of a patient's aphasia even if the locus of a lesion has been precisely identified. Furthermore, some injuries to brain areas outside of those structures identified in the model produce aphasia.

Modern research indicates that language functions are not strictly localized as described by the Wernicke-Geschwind model. Instead, language is such a complex behavior, that the interactions between these areas and more are used in language.

Clinical connection: Dyslexia

Affecting an estimated 7-20% of the population, **developmental dyslexia** is a pronounced difficulty with identification of phonemes in printed words and a related difficulty with reading unfamiliar words. Challenges appear in preschool, when learning to decode phonemes is an expected developmental milestone. These difficulties are not a result of intellectual disability. However, dyslexia is not explicitly a language disorder, since patients generally have no difficulties with comprehension of spoken word.

Genetic factors contribute to risk, but a definitive neural mechanism behind dyslexia is still unknown. There are differences in the anatomy and activity of the cerebellum and some atypical lateralization in temporal, parietal, and occipital lobes, suggesting that perhaps some atypical communication from V1 to the language areas of the brain or memory of previously-learned words contribute to symptoms.

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