chapter 15

The Temporal Lobes

When he was 40 years old, H. H., a successful corporate lawyer with a wife and two school-age children, was finding his job increasingly stressful. His wife was taken off guard when he suddenly announced that he was quitting his law firm. He complained of being so stressed that he simply could not remember cases on which he was working and felt that he could not continue as a lawyer. He had no plan about how he would support his family but, curiously, he seemed unconcerned about it.

A couple weeks later, H. H. shaved his hair off, donned a flowing robe, and left his family to join a fringe religious group. His wife of 15 years was stunned by this sudden change in behavior: up to this point, H. H. had been an atheist. She was notified a couple of weeks later that he had collapsed with a seizure while handing out flowers and peace pamphlets in a large U.S. airport. He was taken to a hospital in a confused state, and a neurological examination revealed a left-temporal-lobe tumor. Fortunately, it was operable and was removed.

H. H. was aphasic after his surgery, but this condition cleared in a matter of weeks. He was left with enduring word-finding difficulties, problematic only when he was tired. He continued to complain of verbal memory problems, however. And his wife said that his personality remained different from what it had been, largely because he remained religious. Eventually, H. H. successfully returned to his law firm, although with a reduced caseload from that of his pretumor days.

H. H. showed typical symptoms of temporal-lobe disorder, including radical changes in affect and personality, memory disturbance, and at least a transient disturbance of language. In this chapter, we survey the anatomy of the temporal lobe, present a theoretical model of its function, describe the basic symptoms of damage to it, and briefly describe clinical tests of temporal-lobe function.

Anatomy of the Temporal Lobe

The temporal lobe comprises all the tissue that lies below the Sylvian sulcus and anterior to the occipital cortex (Figure 15.1). Subcortical temporal-lobe structures include the limbic cortex, the amygdala, and the hippocampal formation (Figure 15.2). Connections to and from the temporal lobe extend throughout the brain.

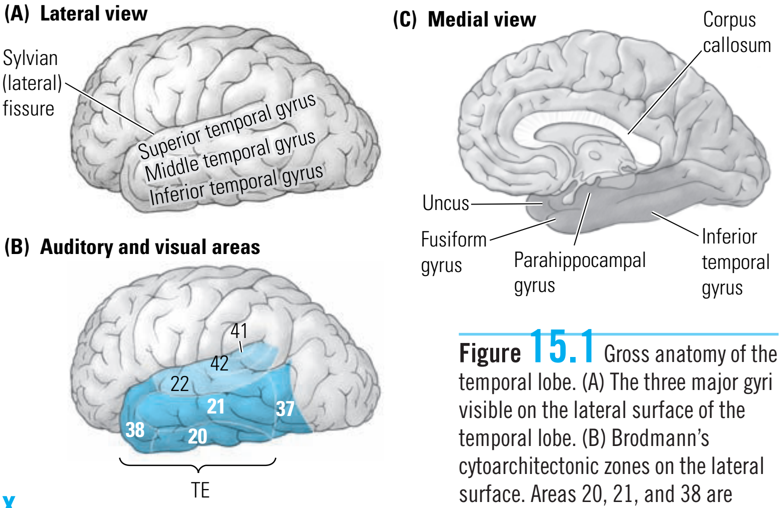


Figure 15.1 Gross anatomy of the temporal lobe. (A) The three major gyri visible on the lateral surface of the temporal lobe. (B) Brodmann's cytoarchitectonic zones on the lateral surface. Areas 20, 21, and 38 are often referred to by von Bonin and Bailey's designation TE. (C) The gyri visible on a medial view of the temporal lobe. The uncus refers to the anterior extension of the hippocampal formation. The parahippocampal gyrus includes areas TF and TH.

Subdivisions of the Temporal Cortex

Brodmann identified 10 temporal areas, but many more areas in the monkey were identified in more-recent studies (see Felleman and van Essen's map, Figure 10.19). Likely there are more areas in the human as well. We can divide the temporal regions on the lateral surface into those that are auditory (Brodmann's areas 41, 42, and 22 in Figure 15.1B) and those that form the ventral visual stream on the lateral temporal lobe (areas 20, 21, 37, and 38 in Figure 15.1B). The visual regions are often referred to as inferotemporal cortex or by von Economo's designation, TE.

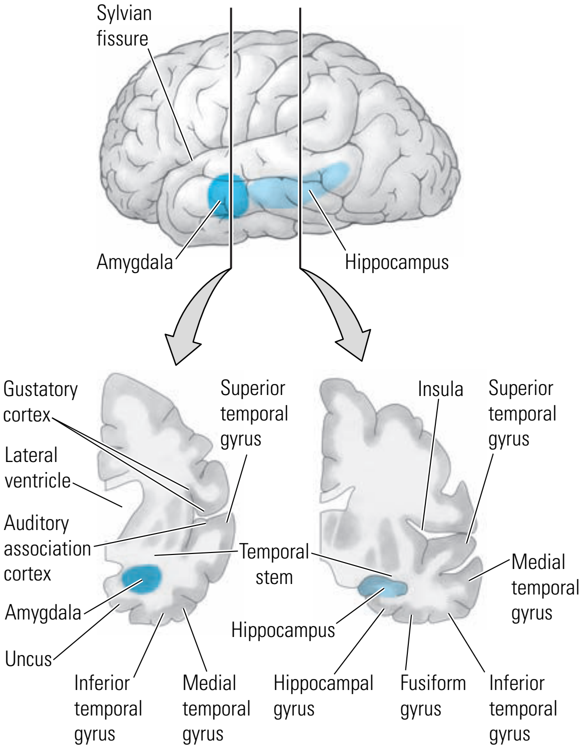
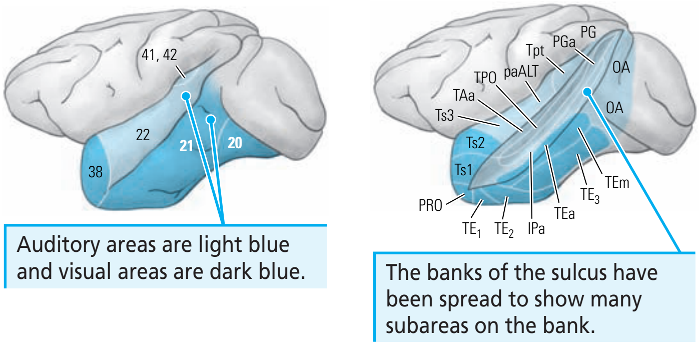


Figure 15.2 Internal structure of the temporal lobe. (Top) Lateral view of the left hemisphere illustrating the relative positions of the amygdala and hippocampus buried deep in the temporal lobe. The vertical lines indicate the approximate location of the sections in the bottom illustration. (Bottom) Frontal sections through the left hemisphere illustrating the cortical and subcortical regions of the temporal lobe.

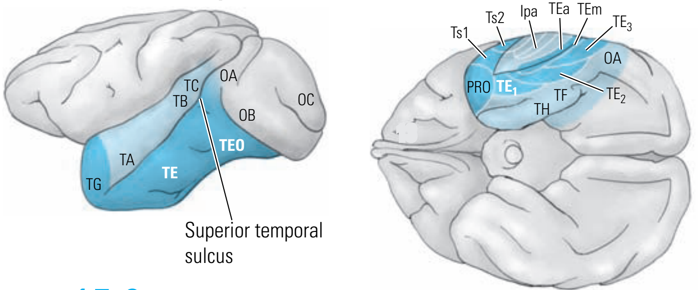
(A) Brodmann's areas **(C) Lateral view**



Auditory areas are light blue and visual areas are dark blue.

The banks of the sulcus have been spread to show many subareas on the bank.

(B) Von Bonin and Bailey's areas **(D) Ventral view**



Superior temporal sulcus

Figure 15.3 Cytoarchitectonic regions of the temporal cortex of the rhesus monkey. (A) Brodmann's areas. (B) Von Bonin and Bailey's areas. (C and D) Lateral and ventral views of Seltzer and Pandya's parcellation showing the multimodal areas in the superior temporal sulcus. The sulcus has been opened up to reveal many subareas on its banks. These subareas are normally not visible from the surface.

The sulci of the temporal lobe contain a lot of cortex, as can be seen in Figure 15.2. In particular, the Sylvian fissure contains tissue forming the *insula*, which includes the gustatory cortex as well as the auditory association cortex. The superior temporal sulcus, which separates the superior and middle temporal gyri, also contains a significant amount of neocortex, which can be divided into many subregions (Figure 15.3). The cortex of the superior temporal sulcus is multimodal, receiving input from auditory, visual, and somatic regions, as well as from the other two polymodal regions (frontal and parietal) and the paralimbic cortex.

The medial temporal region (limbic cortex) includes the amygdala and adjacent cortex (uncus), the hippocampus and surrounding cortex (subiculum, entorhinal cortex, perirhinal cortex), and the fusiform gyrus. The entorhinal cortex is Brodmann's area 28, and the perirhinal cortex comprises Brodmann's areas 35 and 36. Cortical areas TH and TF at the posterior end of the temporal lobe are often referred to as the *parahippocampal cortex* (see Figure 15.3). The fusiform gyrus and inferior temporal gyrus are functionally part of the lateral temporal cortex (see Figure 15.2).

Connections of the Temporal Cortex

The temporal lobes are rich in internal connections, afferent projections from the sensory systems, and efferent projections to the parietal and frontal association regions, limbic system, and basal ganglia. The neocortex of the left and right temporal lobes is connected by the corpus callosum, whereas the medial temporal cortex and amygdala are connected by the anterior commissure.

The results of studies on the temporal–cortical connections of the monkey reveal five distinct types of cortical–cortical connections, which are illustrated in Figure 15.4:

1. *A hierarchical sensory pathway.* The hierarchical progression of connections emanate from the primary and secondary auditory and visual areas, ending in the temporal pole. The visual projections form the ventral stream of visual processing, whereas the auditory projections form a parallel ventral stream of auditory processing (see Figure 15.4A).
2. *A dorsal auditory pathway.* Traveling from the auditory areas to the posterior parietal cortex, this pathway is analogous to the dorsal visual pathway and thus concerned with directing movements with respect to auditory information (see Figure 15.4A).

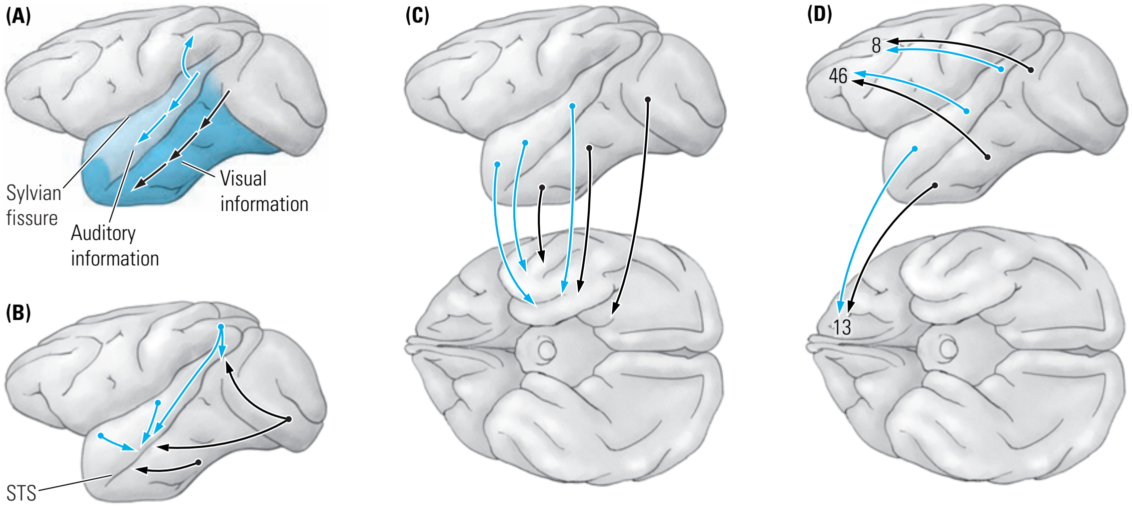


Figure 15.4 Major intracortical connections of the temporal lobe. (A) Auditory and visual information progress ventrally from the primary regions toward the temporal pole, en route to the medial temporal regions. Auditory information also forms a dorsal pathway to the posterior parietal cortex. (B) Auditory, visual, and somatic outputs go to the multimodal regions of the superior temporal sulcus. (C) Auditory and visual information goes to the medial temporal region, including the amygdala and the hippocampal formation. (D) Auditory and visual information goes to two prefrontal regions, one on the dorsolateral surface and the other in the orbital region (area 13).

3. *A polymodal pathway.* This pathway is a series of parallel projections from the visual and auditory association areas into the polymodal regions of the superior temporal sulcus (see Figure 15.4B).
4. *A medial temporal projection.* The projection from the auditory and visual association areas into the medial temporal, or limbic, regions goes first to the perirhinal cortex, then to the entorhinal cortex, and finally into the hippocampal formation or the amygdala or both (see Figure 15.4C). The hippocampal projection is a major one, forming the **perforant pathway.** A disturbance of this projection results in a major dysfunction in hippocampal activity.
5. *A frontal-lobe projection.* This series of parallel projections reaches from the association areas to the frontal lobe (see Figure 15.4D).

These five projection pathways presumably subserve different functions, which will become apparent in the next section. Briefly, the hierarchical sensory pathway probably subserves stimulus recognition; the dorsal auditory pathway may play some role in detecting the spatial location of auditory inputs; the polymodal pathway probably underlies stimulus categorization; the medial temporal projection is crucial to long-term memory; and the frontal-lobe projection is necessary for various aspects of movement control, short-term memory, and affect.

A Theory of Temporal-Lobe Function

The temporal lobe does not have a unitary function, in that it houses the primary auditory cortex, the secondary auditory and visual cortex, the limbic cortex, and the amygdala and hippocampus. On the basis of the cortical anatomy, we can identify three basic sensory functions of the temporal cortex: one concerned primarily with the processing of auditory input, another specialized for visual object recognition, and still another associated with long-term storage of sensory input (that is, memory). The hippocampus works in concert with the object-recognition and memory functions of the neocortex and plays a special role in organizing the memory of objects in space. The remaining temporal-lobe region, the amygdala, adds affective tone (that is, emotion) to sensory input and memories.

Temporal-lobe functions are best understood by considering how the brain analyzes sensory stimuli as they enter the nervous system. Imagine that you are hiking in the woods. On your journey, you notice many different birds, and you decide to keep a mental list of the species that you encounter so that you can tell your sister, who is an avid birder. As you walk along, you suddenly stop and back up—you have encountered a rattlesnake in the middle of the path. You decide to change routes and look for birds elsewhere! What temporal-lobe functions took part in your experience?

Sensory Processes

As you searched for different birds, you needed to be aware of specific colors, shapes, and sizes of birds that you might encounter. This process is object recognition and is the function of the ventral visual pathway in the temporal lobe.

You also needed to be able to categorize the birds quickly, because they were often flying away, and you had to do so by using information that varied in perspective from sighting to sighting (for example, lateral view versus rear view). This process of categorization is crucial to both perception and memory and probably depends on the cortex in the superior temporal sulcus. Categorization may require a form of directed attention because certain characteristics of stimuli are likely to play a more important role in classification than others. For example, classifying two different yellow birds requires that attention be directed away from color and focused on shape, size, and other characteristics. Thus, damage to the temporal cortex leads to deficits in identifying and categorizing stimuli. There is no difficulty in locating the stimulus or in recognizing that a stimulus is present, however, because these activities are functions of the posterior parietal and primary sensory areas, respectively.

As you walked along, you also may have heard birdsong, and you needed to match songs with the visual input. This process of matching visual and auditory information is called **cross-modal matching.** It, too, is likely to depend on the cortex of the superior temporal sulcus. As you saw more and more birds, you had to form memories that you could later access. Furthermore, as you saw different birds, you needed to access their names from your memory. These processes of long-term memory depend on the entire ventral visual stream as well as the paralimbic cortex of the medial temporal region.

Affective Responses

When you encountered the snake, you first heard the rattle, which alerted you, and you stopped. As you scanned the ground, you saw and identified the snake, and your heart rate and blood pressure rose. The affective response that you exhibited is a function of the amygdala. The association of sensory input and emotion is crucial for learning because stimuli become associated with their positive, negative, or neutral consequences, and behavior is modified accordingly.

In the absence of this system, all stimuli would be treated as equivalent. Consider the consequences of failing to associate the rattlesnake, which is poisonous, with the consequences of being bitten. Or consider being unable to associate good feelings (such as love) with a specific person. Laboratory animals with amygdala lesions become very placid and do not react emotionally to threatening stimuli. For example, monkeys that were previously terrified of snakes become indifferent to them.

Spatial Navigation

When you changed routes and went elsewhere, you used the hippocampus. The hippocampus contains cells that code places in space; together, these cells allow us to navigate space and to remember where we are.

As we consider these general functions of the temporal lobes, you can see that their loss would have devastating consequences for behavior. There would be an inability to perceive or to remember events, including language. There would be a loss of affect. Note, however, that a person would be able to use the dorsal visual system to make visually guided movements and, under many circumstances, would appear rather normal.

The Superior Temporal Sulcus and Biological Motion

An additional temporal-lobe function was not included in our hiking example. Animals engage in what we can call *biological motion*, or movements that have particular relevance to a species. For example, our eyes, faces, mouths, hands, and bodies make movements that can have social meanings. We shall see that the superior temporal sulcus analyzes these types of movements.

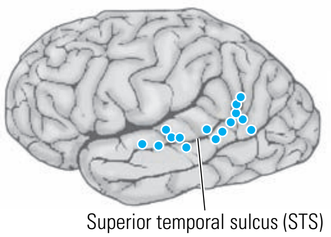
As already mentioned, the superior temporal sulcus receives multimodal inputs, and these inputs play a role in categorizing stimuli. A major category of stimuli is social perception, which includes the analysis of actual or implied bodily movements that provide socially relevant information. This information plays an important role in allowing us to develop hypotheses about the intentions of other people, an ability that is sometimes referred to as *theory of mind* or *social cognition*. For example, the direction in which a person's eyes are looking provides us with considerable information about what that person is attending (or not attending) to.

In a nice review, Allison and colleagues propose that cells in the superior temporal sulcus play a key role in social cognition. For example, cells in the monkey superior temporal sulcus respond to various forms of biological motion including the direction of eye gaze, head movement, mouth movement, facial expression, and hand movement. For social animals such as primates, knowledge about biological motion is critical information needed to guess the intentions of others. As illustrated in Figure 15.5, imaging studies show activation along the superior temporal sulcus during the perception of various forms of biological motion.

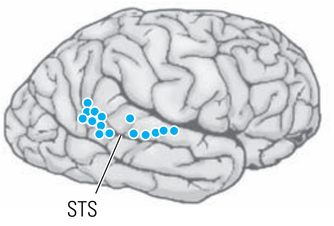
An important correlate of mouth movements is vocalization, and so we might predict that regions of the superior temporal sulcus are also implicated in the perception of species-typical sounds. In monkeys, cells in the superior temporal gyrus, which is adjacent to the superior temporal sulcus and sends connections

Figure 15.5 A summary of the activation (shaded areas) of the superior temporal sulcus (STS) region in the left (A) and right (B) hemispheres during the perception of biological motion. (After Allison, Puce, and McCarthy, 2000.)

(A) Left hemisphere



(B) Right hemisphere



to it, show a preference for "monkey calls," and imaging studies in humans have shown that the superior temporal gyrus is activated both by human vocalizations and by melodic sequences.

We could predict activation in the some part of the superior temporal sulcus in response to the combination of the visual stimulus (mouth movements) and talking or singing. Presumably talking and singing can be perceived as complex forms of biological motion. We could predict that, if people have temporal-lobe injuries that lead to impairments in analyzing biological motion, there is likely to be a correlated deficit in social awareness. Indeed, there is.

Asymmetry of Temporal-Lobe Function

The temporal lobes are sensitive to epileptiform abnormalities, and surgical removal of the abnormal temporal lobe is often of benefit in treating epilepsy. These circumstances also allow neuropsychologists to study the complementary specialization of the temporal lobes.

A comparison of the effects of left and right temporal lobectomy by Brenda Milner and her colleagues revealed that specific memory defects vary according to which side the lesion is on. Damage to the left temporal lobe is associated with deficits in verbal memory; damage to the right with deficits in nonverbal memory (for example, of faces). Similarly, left temporal lesions are associated with deficits in processing speech sounds, whereas right temporal lesions are associated with deficits in processing certain aspects of music.

Little is known, however, about the relative roles of the left and right temporal lobes in social and affective behavior. Right, but not left, temporal-lobe lesions lead to impairments in the recognition of faces and facial expression; so it seems likely that the two sides play different roles in social cognition. In fact, clinical experience dictates that left and right temporal-lobe lesions have different effects on personality.

Although the left and right temporal lobes are relatively specialized in their functions, do not be overly impressed by the apparent functional asymmetry. Substantial functional overlap is revealed in the relatively minor effects of *unilateral* temporal lobectomy, a striking result considering that such a large zone of the cerebral hemispheres is removed. Recall, for example, the striking recovery of function in H. H., whom we met at the beginning of the chapter. It is incorrect to assume, however, that removing both temporal lobes merely doubles the symptoms of damage seen in unilateral temporal lobectomy. Bilateral temporal-lobe removal produces dramatic effects on both memory and affect that are orders of magnitude greater than those observed subsequent to unilateral lesions.

Symptoms of Temporal-Lobe Lesions

Nine principal symptoms are associated with disease of the temporal lobes: (1) disturbance of auditory sensation and perception, (2) disorders of music perception, (3) disorders of visual perception, (4) disturbance in the selection of visual and auditory input, (5) impaired organization and categorization of sensory

Table 15.1 Summary of major symptoms of temporal-lobe damage

Symptoms	Most probable lesion site	Basic reference
Disturbance of auditory sensation	Areas 41, 42, 22	Vignolo, 1969 Hécaen and Albert, 1978
Disturbance of selection of visual and auditory input	Areas TE, superior temporal sulcus	Sparks et al., 1970 Dorff et al., 1965
Disorders of visual perception	Areas TE, superior temporal sulcus, amygdala	Milner, 1968 Meier and French, 1968
Disorders of auditory perception	Areas 41, 42, 22	Samson and Zatorre, 1988 Swisher and Hirsch, 1972
Disorders of music perception	Superior temporal gyrus	Zatorre et al., 2002
Impaired organization and categorization of material	Areas TE, superior temporal sulcus	Wilkins and Moscovitch, 1978 Read, 1981
Poor contextual use	Area TE	Milner, 1958
Disturbance of language comprehension	Area 22 left	Hécaen and Albert, 1978
Poor long-term memory	Areas TE, TF, TH, 28	Milner, 1970
Changes in personality and affect	Areas TE, plus amygdala	Blumer and Benson, 1975 Pincus and Tucker, 1974
Changes in sexual activity	Amygdala, plus?	Blumer and Walker, 1975

input, (6), inability to use contextual information, (7) impaired long-term memory, (8) altered personality and affective behavior, and (9) altered sexual behavior. Table 15.1 summarizes the major symptoms of temporal-lobe damage, lists the most probable lesion sites, and cites basic references. The sections that follow sample the range of temporal-lobe disorders and their clinical assessment.

Disorders of Auditory Perception

Damage to the primary visual or somatic cortex leads to a loss of conscious sensation; so it is reasonable to predict that bilateral damage to the auditory cortex will produce *cortical deafness*, an absence of neural activity in the auditory regions. The results of neither clinical nor animal laboratory studies support this prediction, however. As the Snapshot on page 378 illustrates, auditory hallucinations, which result from spontaneous activity in the auditory regions, are essentially the opposite of cortical deafness. Auditory hallucination is the perception of sounds (hearing voices) that are not actually present. The auditory cortex does play an actual role in discriminating two forms of auditory processing—namely, rapidly presented stimuli and complex patterns of stimuli. Language is fast and must be analyzed quickly, whereas music generally contains relatively slower changes in frequency, but the ear must be sensitive to the small differences in frequency important in music.

Speech Perception

Impaired auditory processing can be seen in the difficulty that temporal-lobe patients have in discriminating speech sounds. Although related to the common complaint among patients with left-temporal-lobe damage that people

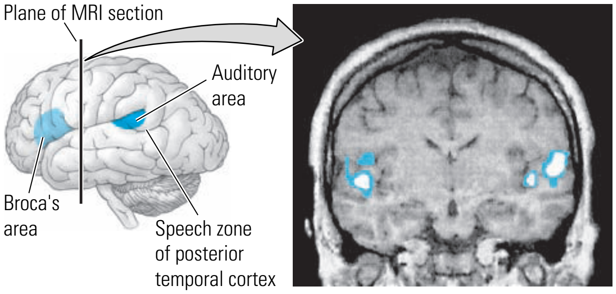
SNAPSHOT

Imaging Auditory Hallucinations

Auditory hallucinations are the most common symptom of schizophrenia, being reported by about 65% of people diagnosed with the disease. Auditory hallucinations are not simply sounds; a patient hears fully formed verbal passages that appear to be coming from an external source. The patient's thoughts are usually hostile or paranoid, as in the following example:

> Days later while in the Metropolis again, I was once more startled by those same pursuers, who had threatened me several days before. It was night-time. As before, I could catch part of their talk, but, in the theatre crowds, I could see them nowhere. I heard one them a woman, say: "You can't get away from us; we'll lay for you and get you after a while!" To add to the mystery, one of these "pursuers" repeated my thoughts aloud verbatim. I tried to elude those pursuers as before, but this time I tried to escape from them by means of subway trains, darting up and down subway exits and entrances, jumping on and off trains, until after midnight. But, at every station where I got off a train, I heard the voices of these pursuers as close as ever (L. Percy King, from a letter written in the 1940s protesting the writer's imprisonment in a mental hospital and published in Firth, 1999, p. 414)

Dierks and colleagues described an experiment with paranoid schizophrenia patients whose hallucinations could be monitored within one fMRI session. In this study, the verbal hallucinations activated the primary auditory cortex, Broca's area, and the speech zone in the posterior temporal cortex in the left hemisphere. In addition, there was some activation of the limbic areas (see the illustration above).



fMRI activation of auditory cortex during hallucinations in a schizophrenic subject. (After T. Dierks et al., 1999.)

These results suggest that the hallucinations have their origin in the patients' own inner language systems. The researchers propose that activation in the auditory cortex leads to the perception that the voices are coming from an external source. The limbic activity presumably results from the anxiety generated by hearing voices, especially hostile voices.

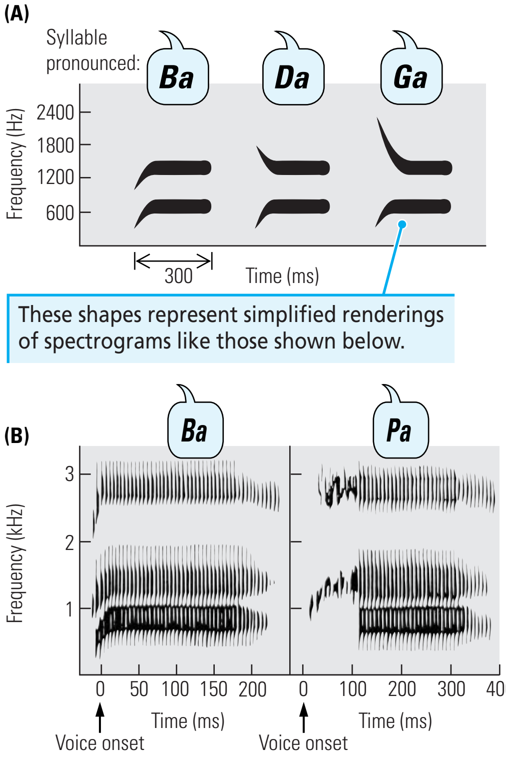
(T. Dierks, D. E. J. Kinden, M. Jandl, E. Formisano, R. Goebel, H. Lanfermann, and W. Singer. Activation of Heschl's gyrus during auditory hallucinations. *Neuron* 22:615–621, 1999.)

are talking too quickly, the problem is not so much the quickness of the speech but rather the patient's inability to discriminate sounds presented quickly. This difficulty is commonly encountered by normal people trying to learn a new language.

The problem is not just in discriminating the speech sounds, however, but also in judging the temporal order in sounds heard. If a normal subject is presented with two sounds, a temporal separation of only 50 to 60 ms is sufficient to identify which sound was presented first. Subjects with temporal-lobe lesions may require as much as 500 ms between two sounds (a 10-fold increase) to perform at the same level. Each of these audioperceptual impairments appears more severe after left-temporal-lobe lesions than after right-temporal-lobe lesions—a result suggesting that these auditory skills are especially important in the discrimination of speech sounds.

Speech differs from other auditory input in three fundamental ways:

1. Speech sounds come largely from three restricted ranges of frequencies, which are known as *formants.* Figure 15.6A illustrates sound spectrograms of different two-formant syllables. The dark bars indicate the frequency bands seen in more detail in Figure 15.6B, which shows that the syllables differ both in the onset frequency of the second (higher) formant and in the onset time of the consonant. Notice that vowel sounds are in a constant frequency band, but consonants show rapid changes in frequency.
2. The same speech sounds vary from one context in which they are heard to another, yet they are all perceived as being the same. Thus, the sound spectrogram of the letter “d” in English is different in the words “deep,” “deck,” and “duke,” yet a listener perceives all of them as “d.” The auditory system must have a mechanism for categorizing varying sounds as equivalent, and this mechanism must be affected by experience, because a major obstacle to learning foreign languages in adulthood is the difficulty of learning equivalent sound categories. Thus, a word’s spectrogram depends on context—the words that precede and follow it. (There may be a parallel mechanism for musical categorization as well.)



These shapes represent simplified renderings of spectrograms like those shown below.

Figure 15.6 Speech sounds. (A) Schematic spectrograms of three different syllables, each made up of two formants. (B) Spectrograms of syllables differing in voice onset time. (After Springer, 1979.)

3. Speech sounds change very rapidly in relation to one another, and the sequential order of the sounds is critical to understanding. According to Liberman, we can perceive speech at rates of up to 30 segments per second, although normal speech is on the order of 8 to 10 segments per second. Speech perception at the higher rates is truly amazing, because it far exceeds the auditory system’s ability to transmit all the speech as separate pieces of auditory information. For example, nonspeech noise is perceived as a buzz at a rate of only about 5 segments per second. Clearly, language sounds must be recognized and analyzed in a special way by the brain, much as the echolocation system of the bat is specialized in the bat brain. It is likely that the special mechanism for speech perception is in the left temporal lobe. This function may not be unique to humans, because the results of studies in both monkeys and rats have shown specific deficits in the perception of species-typical vocalizations after temporal lesions.

The fact that left-temporal-lobe lesions alter the perception of speech sounds ought not to be surprising: since the time of Wernicke, lesions of the left temporal association cortex (primarily area 22) have been known to produce aphasia (see Chapter 1). The classical view of Wernicke’s aphasia is that it is associated with disturbed recognition of words, the extreme form being “word deafness”—an inability to recognize words as such despite intact hearing of pure tones.

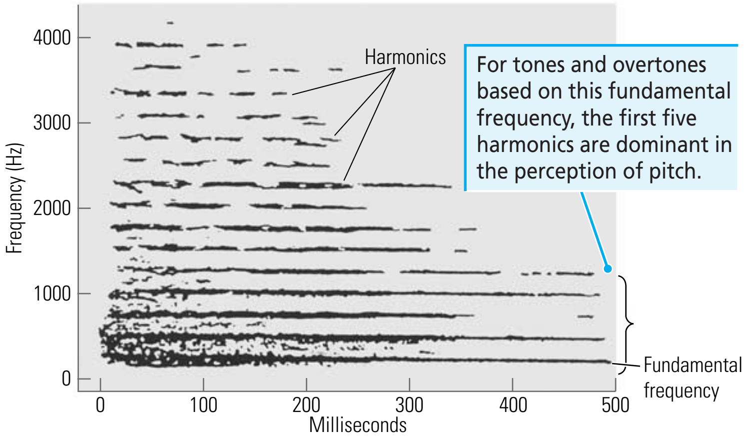
Music Perception

The second category of auditory deficit is in processing sounds related to music. Musical sounds may differ from one another in three aspects: loudness, timbre, and pitch.

- *Loudness* refers to the magnitude of a sensation as judged by a given person. Loudness, although related to the intensity of a sound as measured in decibels, is in fact a subjective evaluation described by such terms as "very loud," "soft," "very soft," and so forth.
- *Timbre* refers to the distinctive character of a sound, the quality by which it can be distinguished from all other sounds of similar pitch and loudness. For example, we can distinguish the sound of a violin from that of a trombone even though they may play the same note at the same loudness.
- *Pitch* refers to the position of a sound in a musical scale, as judged by the listener. Pitch is clearly related to frequency. Consider the note middle C, described as a pattern of sound frequencies as depicted in Figure 15.7. The amplitude of acoustic energy is conveyed by the darkness of the tracing in the figure. The lowest component of this note is the *fundamental frequency* of the sound pattern, which is 264 Hz, or middle C. The sound frequencies above the fundamental frequency are known as *overtones* or *partials*. The overtones are generally simple multiples of the fundamental (for example, 2 × 264, or 528 Hz; 4 × 264, or 1056 Hz), as can be seen in Figure 15.7. Those overtones that are multiples of the fundamental are known as *harmonics*.

The classic view, dating to Hermann Helmholtz in the late 1800s, held that pitch perception depends on the fundamental frequency, and the overtones provide timbre. This view now appears to be incorrect. If the fundamental frequency is removed from a note by means of electronic filters, the overtones are sufficient to determine the pitch of the fundamental frequency—a phenomenon known as *periodicity pitch*. The ability to determine pitch from the overtones alone is probably due to the fact that the difference between the frequencies of the various harmonics is equal to the fundamental frequency (for example, 792 Hz − 528 Hz = 264 Hz = the fundamental). The auditory system can determine this difference, and we perceive the fundamental frequency.

Figure 15.7 Spectrographic display of the steady-state part of middle C (264 Hz) played on a piano. Bands of acoustical energy are present at the fundamental frequency, as well as at integer multiples of the fundamental (harmonics). (After Ritsma, 1967.)



For tones and overtones based on this fundamental frequency, the first five harmonics are dominant in the perception of pitch.

The primary auditory cortex of the right temporal lobe appears to make this periodicity pitch discrimination. For example, Zatorre found that patients with right temporal lobectomies that include the primary auditory cortex are impaired at making pitch discriminations when the fundamental is absent but normal at making such discriminations when the fundamental is present. Right temporal lesions that spare the primary auditory cortex or left temporal lobectomies do not impair performance. Zatorre suggested that the right temporal lobe has a special function in extracting pitch from sound, regardless of whether the sound is speech or music. In regard to speech, the pitch will contribute to "tone" of voice, which is known as **prosody.**

Other aspects of music are also specially processed in the right temporal lobe. The simplest is the perception of timbre, which is impaired by right temporal lesions. In addition, more-complex aspects of music, such as scales, chords, and progressions, are all constructed from single musical notes. Although speculative, it seems likely that we humans develop a "musical store" much as we develop a "syntactic store" of words. Thus, when we encounter a musical scale or progression, we recognize it as such. The mechanism of such a hypothetical store is unknown, but it may be a function of the right auditory association cortex.

Finally, Liegeois-Chauval and colleagues point out that distinct musical processes may depend on specific cortical sites in the superior temporal gyrus (see Figure 15.2). Thus, in their study of patients with temporal lobectomies, these investigators found that rhythm discrimination was most affected by right posterior superior temporal gyrus damage, whereas distinguishing meter (for example, distinguishing a waltz and a march) was more affected by anterior damage to either temporal lobe.

Although it is tempting to compartmentalize music and language on opposite sides of the brain, it seems unlikely that the brain is specifically designed to treat them differently; rather, certain characteristics of musical and language input are probably analyzed selectively by the two hemispheres. Zatorre emphasized the key difference: the left hemisphere is concerned more with speed and the right hemisphere with distinguishing frequency differences, a process called *spectral sensitivity*.

Disorders of Music Perception

The fact that the brain appears to have neural networks dedicated to the processing of language and music leads to the conclusion that both language and music have biological roots. Although this conclusion seems obvious for language, it is less obvious for music, which has often been perceived as an artifact of culture. But considerable evidence suggests that humans are born with a predisposition for processing music.

Infants show learning preferences for musical scales and are biased toward perceiving the regularity (such as harmonics) on which music is built. Peretz argued that one of the strongest bits of evidence favoring the biological basis of music is that a surprising number of people have a condition known as *congenital amusia*. They are tone deaf. Apparently, amusic people have an abnormality in their neural networks for music, and no amount of training makes much difference. In fact, we have a colleague whose parents were both music teachers and, to the chagrin of her parents, she is amusic. She likes to note that she knows that the national anthem is being played because people stand up!

Liegeois-Chauvel and colleagues studied musical processing in a large group of patients with temporal lobectomies and found that injury to the right superior temporal gyrus impairs various aspects of processing necessary for discriminating melodies. In addition, a dissociation between the roles of the posterior and anterior regions of the superior temporal gyrus on different aspects of musical processing suggests their relative localization within the superior temporal gyrus.

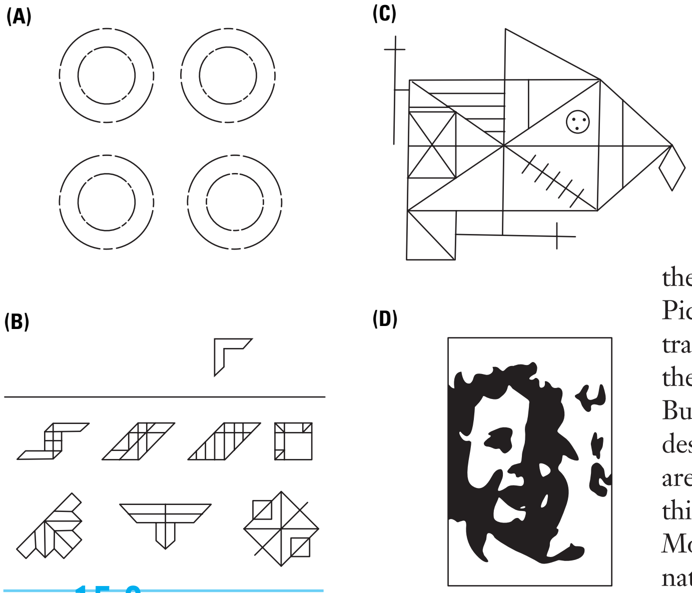


Figure 15.8 Tests for visual disorders. (A) Meier and French's test, in which the subject must identify the drawing that is different. (B) Sample of the Gottschaldt Hidden-Figures Test, in which the task is to detect and trace the sample (upper drawing) in each of the figures below it. (C) Rey Complex-Figure Test, in which the subject is asked to copy the drawing as exactly as possible. (D) Sample of the Mooney Closure Test, in which the task is to identify the face within the ambiguous shadows.

Disorders of Visual Perception

Although persons with temporal lobectomies do not normally have large defects in their visual fields, they do have deficits in visual perception. Such deficits were first demonstrated by Milner, who found that her patients with right temporal lobectomies were impaired in the interpretation of cartoon drawings in the McGill Picture-Anomalies Test. For example, one item illustrating a monkey in a cage features an oil painting on the wall of the cage—an obvious oddity or anomaly. But, although patients with right temporal lesions can describe the contents of the cartoon accurately, they are impaired at recognizing the anomalous aspects of this picture and others. Similarly, on a test such as the Mooney Closure Test or tests requiring the discrimination of complex patterns (Figure 15.8), patients with temporal-lobe damage perform very poorly.

Facial Recognition and Biological Motion

One of the most interesting visual perceptual deficits is in facial perception and recognition. When one of us (B. K.) and his associates presented patients with the split-faces test (see Figure 13.17), they found that those with right temporal-lobe resections fail to show a bias for that part of the face falling in the left visual field, suggesting that these patients perceive faces abnormally. This conclusion is consistent with reports that patients with right temporal-lobe damage are impaired at the recognition and recall of faces or photographs of faces.

Furthermore, these patients do not appear able to perceive subtle social signals such as discreet but obvious glances at one's watch, a gesture often intended as a cue to break off a conversation. Presumably the patients fail to perceive the significance of the visual signal. Facial signals are a form of biological motion, the analysis of which we have seen to be a function of the temporal lobe.

The description of deficits in visual perception in people with temporal-lobe injury is consistent with the hypothetical role of the inferior temporal cortex in the ventral visual stream (see Chapter 13). An extensive literature shows that monkeys with inferior temporal lesions have severe and selective deficits in learning tasks that require the visual recognition of objects. Furthermore, inferior temporal cortex neurons in monkeys have long been known to have selective characteristics, such as a preference for faces or hands.

These preferences may be quite specific. For example, Perrett and colleagues showed that neurons in the superior temporal sulcus may be responsive to particular faces seen head-on, faces viewed in profile, posture of the head, or even particular facial expressions. More recently, Perrett also showed that some superior temporal sulcus cells are maximally sensitive to primate bodies that are moving in a particular direction, another characteristic biological motion (Figure 15.9). This finding is quite remarkable because the basic configuration of the stimulus is identical as the body moves in different directions; it is only the direction that changes.

STS neurons in the observing monkey respond more strongly to an approaching body…

…than to the same body moving in other directions or standing still.

Figure 15.9 Neuronal sensitivity to direction of body movements. (Top) Schematic representation of the front view of a body. (Bottom) The histogram illustrates a greater neuronal response of superior temporal sulcus (STS) neurons to the front view of a body that approaches the observing monkey compared with the same body views when the body is moving away to the right and to the left or is static. (After Perrett et al., 1990.)

Activation of Inferior Temporal Neurons

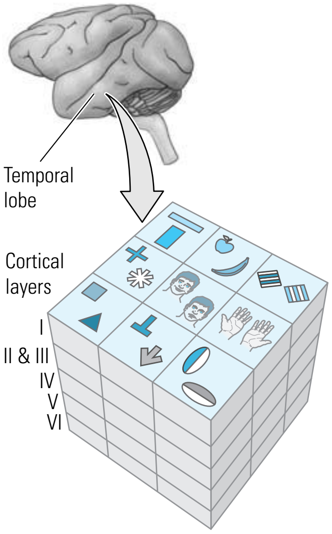
One problem with the identification of specialized temporal visual neurons is that the dedication of specific temporal cortex cells for every possible object feature in the world is impractical. Tanaka approached this problem by attempting to determine the features that are critical for activating neurons in the monkey inferior temporal cortex. He and his colleagues presented many three-dimensional animal and plant representations to find the effective stimuli for given cells. Then they tried to determine the necessary and sufficient properties of these cells.

Tanaka found that most cells in area TE require rather complex features for activation. These features contain a combination of characteristics such as orientation, size, color, and texture. Furthermore, as illustrated in Figure 15.10, he found that cells with similar, although slightly different, selectivity tend to cluster vertically in columns.

Organizationally, the cortex has an important vertical component (see Chapter 10), but the neurons organized in columns in the temporal cortex are not identical in their stimulus selectivity. Thus it seems likely that an object is not represented by the activity of a single cell but rather by the activity of many cells within a columnar module. This important finding provides an explanation for the phenomenon of stimulus equivalence—that is, the common observation that an object viewed at different orientations remains the same object. Tanaka speculates that the representation of objects by multiple cells in a columnar module in which the selectivity varies from cell to cell and effective stimuli largely overlap can provide a way for the brain to minimize the effect of small changes in input images.

Figure 15.10 Schematic representation of the columnar organization in area TE. Cells with similar but slightly different selectivity cluster in elongated vertical columns, perpendicular to the cortical surface.

Neurons in the temporal lobe form columns that respond to categories of shapes.



Tanaka and others have described two other remarkable features of inferior temporal neurons in monkeys. First, the stimulus specificity of these neurons is altered by experience. In a period of 1 year, monkeys were trained to discriminate 28 complex shapes. The stimulus preferences of inferior temporal neurons were then determined from a larger set of animal and plant models. In the trained monkeys, 39% of the inferior temporal neurons gave a maximum response to some of the stimuli used in training. This percentage compared with only 9% of the neurons in naive monkeys.

This result is exciting, because it shows that the temporal lobe's role in visual processing is not determined genetically but is subject to experience even in the adult. We can speculate that this experience-dependent characteristic allows the visual system to adapt to different demands in a changing visual environment. This feature is important for human visual recognition abilities that have very different demands in forests from those on open plains or in urban environments. In addition, experience-dependent visual neurons ensure that we can identify visual stimuli that were never encountered in the evolution of the human brain.

The second interesting feature of inferior temporal neurons is that they may not only process visual input but also provide a mechanism for the internal representation of the images of objects. Fuster and Jervey first demonstrated that, if monkeys are shown specific objects that are to be remembered, neurons in the monkey cortex continue to discharge during the "memory" period. These selective discharges of neurons may provide the basis of working memory for the stimuli. Furthermore, the discharges of these neurons may provide the basis for imagery. That is, the discharge of groups of neurons that are selective for characteristics of particular objects may provide a mental image of the object in its absence.

Disturbance of Selection of Visual and Auditory Input

We must select which inputs to process from the wealth of information in our environment. This selectivity is generally not conscious, because the nervous system automatically scans input and selectively perceives the environment. (Conscious control can be exerted, of course, as when you search for a mailbox to post a letter.)

Selectivity in auditory perception is best illustrated by the problem of listening to two conversations simultaneously. Because it is impossible to process the two competing inputs concurrently, the auditory system adopts one of two strategies: either one conversation is ignored or attention shifts back and forth from one conversation to the other. In either case, there is a selection of input. Selective perception in the visual system operates similarly. For example, because it is not possible to watch all floor events at a gymnastics meet simultaneously, either we focus our attention entirely on one event or shift it from one event to another.

Let us now consider the person with temporal-lobe damage. Selection of both auditory and visual input is impaired, which is ordinarily demonstrated only by special testing procedures. Selective attention to auditory input can be tested by dichotic listening (see Chapter 11). Recall that, when subjects are presented with two words simultaneously, one to each ear, normal subjects report more of the words presented to the right ear; if tonal sequences are presented dichotically, there will be a left-ear advantage.

This left-ear advantage is maintained in patients with temporal-lobe lesions, but left-temporal-lobe lesions result in an overall drop in the number of words recalled. One explanation for this effect is that the nervous system has difficulty focusing selectively on the input into one ear and attempts to process all the input concurrently; as a result, performance drops significantly.

Analogous findings are reported for visual input. If two different visual stimuli are presented simultaneously, one to each visual field, damage to the left temporal lobe impairs recall of content of the right visual field, but damage to the right temporal lobe impairs recall of content in *both* visual fields. Again, it may be that the nervous system is now unable to focus on distinctive features of the stimuli to allow efficient perception and storage of the input. In regard to visual input, however, it is noteworthy that right temporal lesions produce bilateral deficits, whereas left temporal lesions produce unilateral ones. This difference implies that the right temporal lobe may have a greater role than the left in selective attention to visual input.

Organization and Categorization

Asked to learn a list of words such as "dog, car, bus, apple, rat, lemon, cat, truck, orange," most of us will organize the words into three different categories—animals, vehicles, and fruit. If the list is later recalled, the items are likely to be recalled by category, and recall of the categories is likely to be used as an aid in recall of the items.

The ability to organize material is especially important for language and memory. For example, categorizing makes it possible to comprehend complex, extended sentences, including both the meaning of individual clauses and the information inferred from them. Organization of sensory input appears to be a function of the temporal lobes. Patients with left temporal lobectomies are impaired in their ability to categorize even single words or pictures of familiar objects.

Thus, patients have difficulty placing words or pictures into discrete categories, even when they are requested to, and they also have difficulty in using categories that most of us use automatically. For example, Milner has found that, when these patients are given a category name (such as animal) and are asked to recall exemplars of the category (such as dog, cat, rat), they have difficulty, even though they are fluent in other types of tests. Given that these patients have difficulty in simple types of categorization tasks studied in the laboratory, you can imagine that their difficulty in spontaneous organization may represent a significant deficit in cognition, especially in memory for complex material.

Neurolinguists propose that another type of categorization may take place in the left temporal lobe. Semantic categories are hierarchies of meaning in which a single word might belong to several categories simultaneously. For example, a duck belongs to the categories animal, bird, and waterfowl. Each of these categories is a refinement of the preceding one. Patients with posterior temporal lesions may show dysphasic symptoms in which they can recognize the broader categorization but have difficulty with the more specific ones.

Using Contextual Information

The meaning of identical stimuli can vary, depending on the context. For example, a word such as "fall" can refer to a season or to a tumble, depending on the context. Similarly, context may be a major cue for facial recognition. Most of us have encountered someone completely out of context (for example, while in Paris you encounter a clerk from your neighborhood store at home) and have been unable to recall who the person is until information about the context is provided.

A more complex example of extracting meaning from context is found in social situations. The interpretation of events, and indeed our role in events, depends on the social context. Thus, stimuli may be interpreted in one way when we are with our parents and in a different way when we are with our peers, an ability that is referred to as social cognition. (We return to social cognition in Chapter 22.) A simple example of the use of contextual information can be found in the McGill Picture-Anomalies Test described in the section on visual perceptual deficits. The only clue to the correct choice in the McGill anomalies is the context.

Memory

Interest in the temporal lobes' function in memory was stimulated in the early 1950s by the discovery that bilateral removal of the medial temporal lobes, including the hippocampus and amygdala, results in amnesia for all events after the surgery (**anterograde amnesia**). It is now clear that both the medial temporal regions and the temporal neocortex are important for memory functions (see Chapter 18).

Damage to the inferior temporal cortex specifically interferes with conscious recall of information, the extent of the memory disturbance increasing in direct proportion to the amount of temporal-lobe damaged. Lesions of the left temporal lobe result in impaired recall of verbal material, such as short stories and word lists, whether presented visually or aurally; lesions of the right temporal lobe result in impaired recall of nonverbal material, such as geometric drawings, faces, and tunes. Two case histories demonstrate the roles of the left and right temporal lobes in memory.

Mr. B., age 38, was suffering from an astrocytoma in the left temporal lobe. Before onset, he had been a successful executive in an oil company and was noted for his efficiency. As his tumor developed, he became forgetful, and at the time of hospital admission his efficiency had dropped drastically; he had begun to forget appointments and other important events. Forgetfulness had become such a problem that he had begun to write notes to himself to cover his memory problem, but he often mislaid the notes, leading to even greater embarrassment.

On formal tests of memory Mr. B. had special difficulty in recalling short stories read to him a few minutes earlier. In one test, he was read the following story from the Wechsler Memory Scale and was asked to repeat it as exactly as possible. "Anna Thompson of South Boston, employed as a scrub woman in an office building, was held up on State Street the night before and robbed of $15. She had four little children, the rent was due and they had not eaten for two days. The officers, touched by the woman's story, made up a purse for her."

Mr. B. recalled: "A woman was robbed and went to the police station where they made her a new purse. She had some children too." This performance is very poor for a person of Mr. B.'s intelligence and education. On the other hand, his immediate recall of digits was good; he could repeat strings of seven digits accurately. Similarly, his recall of geometric designs was within normal limits, illustrating the asymmetry of memory functions, because his right temporal lobe was intact.

Ms. C. illustrates the complement of Mr. B.'s syndrome. She was a bright 22-year-old college student who had an indolent tumor of the right temporal lobe. When we first saw her, after surgery, she complained of memory loss. She was within normal limits on formal tests of verbal memory, such as the story of Anna Thompson, but was seriously impaired on formal tests of visual memory, especially geometric drawings. For example, in one test she was shown geometric designs for 10 seconds and then asked to draw them from memory. Ten minutes later, she was asked to draw them again. She had difficulty with immediate recall (Figure 15.11) and, after 10 minutes, was unable to recall any of the drawings.

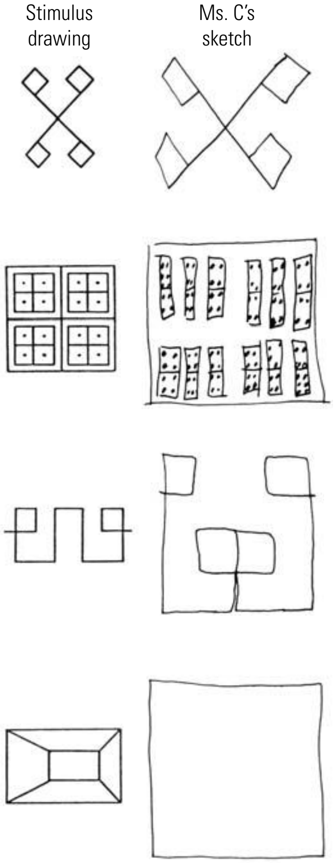


Figure 15.11 Impaired recall of geometric figures by Ms. C. In each set shown, the drawing at the left is the original stimulus and the drawing at the right is Ms. C.'s sketch made immediately after viewing each figure for 10 seconds. Note that Ms. C.'s impairment is worse with the more complex figures. Ms. C. was unable to recall even the simplest figure 10 minutes after viewing it.

Affect and Personality

Although temporal-lobe disorder has been associated with disturbance of affect in humans for nearly 100 years, knowledge about the details of this role is still surprisingly fragmentary. Wilder Penfield and others reported that stimulation of the anterior and medial temporal cortex produces feelings of fear, an effect also occasionally obtained from stimulating the amygdala. Recall, too, that H. H.'s wife complained that H. H.'s personality was different after his tumor and surgery from what it had been before.

Temporal-lobe epilepsy has traditionally been associated with personality characteristics that overemphasize trivia and the petty details of daily life. Pincus and Tucker described several symptoms of this personality, including pedantic speech, egocentricity, perseveration in discussions of personal problems (sometimes referred to as "stickiness," because one is stuck talking to the person), paranoia, preoccupation with religion, and proneness to aggressive outbursts. This constellation of behaviors produces what is described as *temporal-lobe personality*, although very few people combine all these traits.

Similar personality traits arise after temporal lobectomy. There appears to be a relative asymmetry in the symptoms, with right temporal lobectomy more likely to be associated with these personality traits than left temporal lobectomy. This observation has not been quantified, however, and warrants further study.

Clinical Neuropsychological Assessment of Temporal-Lobe Damage

A number of standardized assessment tools have proved sensitive and valid predictors of temporal-lobe injury (Table 15.2). Like the clinical neuropsychological tests of parietal-lobe function reviewed in Chapter 14, these tests do not assess all possible temporal-lobe symptoms, but it would be highly unusual for a person to perform normally on all these tests if there were damage to either temporal lobe.

- Auditory and visual processing capacity can be assessed by using dichotic listening and the McGill Picture-Anomalies Test. The picture-anomalies task is not as sensitive an indicator today as it was when first used in the 1950s, perhaps because video-based home entertainment has made the

Table 15.2 **Standardized clinical neuropsychological tests for temporal-lobe damage**

Function	Test	Basic reference
Auditory processing capacity	Dichotic words and melodies	Sparks et al., 1970
Visual processing capacity	McGill Picture Anomalies	Milner, 1958
Verbal memory	Revised Wechsler Memory Scale; logical stories and paired associates	Milner, 1975
Nonverbal memory	Rey Complex Figure	Taylor, 1969
Language	Token	de Renzi and Faglioni, 1978

average person more sophisticated visually. Nevertheless, a poor score on this test almost invariably denotes right temporal abnormality.

- The best test of general verbal memory ability is the revised Wechsler Memory Scale. However, because the Wechsler memory quotient is affected by nonspecific disorders of attention, two subtests—paired associates and logical stories—are often used as a purer measure of verbal memory capacity. The paired-associates subtest requires a subject to learn a series of word pairs (for example, north–south, cabbage–pen) such that, when one word is read (north, cabbage), its paired-associate word (south, pen) can be recalled. An example of the logical memory test was presented in reference to Mr. B.'s verbal memory defect.
- The Rey Complex-Figure Test has proved to be one of the best for evaluating nonverbal memory function of the right temporal lobe (see Figure 15.8C). A printed copy of a complex geometric pattern is placed before the subject with the instructions, "Copy the drawing as accurately as you can." Forty-five minutes later, the subject is asked to reproduce as much of the figure as he or she can remember. Although the scoring criteria provide an objective measure of nonverbal memory, the test has the drawback that depressed or poorly motivated subjects may perform poorly, not because of right temporal-lobe damage but because they refuse to try to recall the figure. There is no easy solution to this problem, because all tests of nonverbal memory are subject to this complication.
- A deficit in language comprehension could be the result of a lesion in any of the language zones of the left hemisphere (that is, in the parietal, temporal, or frontal lobes). No current neuropsychological assessment tool can localize the area of damage within the left hemisphere. For this reason, we once again recommend the token test as the test of choice for language comprehension.

Summary

The temporal lobe can be divided into four functional zones for auditory processes (superior temporal gyrus), visual processes (inferior temporal cortex), and the integration of these processes for emotion (amygdala) and spatial navigation and spatial and object memory (hippocampus and associated cortex).

The processing of auditory information is specialized for two characteristics: speed and frequency. Language processing requires analysis of rapid changes in sounds but, because people talk at different pitches (that is, high squeaky voices versus deep resonant voices), the understanding of language sounds can tolerate differences in frequencies. In contrast, music is relatively slower than language, but differences in frequency are critical. The left temporal lobe is more concerned with speed, whereas the right is more concerned with complex frequency patterns. Damage to the auditory regions of the temporal lobe produces deficits in the recognition of language (primarily left) and music (primarily right), as well as in sound localization.

The temporal lobe adds two features to both auditory and visual information—namely, tone (affect) and categorization. These aspects are important for understanding sensory input as well as for using it in biologically relevant ways, such as in biological motion. Whereas the parietal lobe processes spatial location with respect to movement, the temporal lobe uses spatial location as a feature of object recognition and in the development of memories for object location. Damage to the visual regions of the temporal lobe disrupt the recognition of complex visual stimuli, such as faces. Damage to medial temporal regions produces deficits in affect, personality, spatial navigation, and object memory.

Neuropsychological analyses of temporal-lobe functions utilize tests that are sensitive to discrete temporal-lobe injuries. Such tests include those of auditory processing (dichotic listening), visual processing (object recognition), memory (both verbal and nonverbal), and language.

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