

18

The Organization of Cognition

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An Overall View

IN THE PREVIOUS CHAPTER WE EXAMINED how the activity of single nerve cells can be related to the internal representations required for simple cognitive tasks. In this chapter we survey the anatomical and physiological organization of the cortex that underlies the activity of populations of neurons that mediate complex aspects of cognition. For this purpose we draw on the insights that have emerged from studies of the neural mechanisms of cognition in monkeys and studies of cognitive impairment resulting from

brain injury in humans. In the following chapter we extend this analysis to premotor cortex and the control of voluntary movement. In Chapter 20 we discuss how neuroimaging studies of cognition in humans are consistent with the findings from these experimental and clinical studies.

One of the key features about cognitive functions is that they are mediated by specialized areas of neocortex that are functionally related in an orderly arrangement. This was well established in 1962 when Alexander Luria published his landmark *Higher Cortical Functions in Man*. Neurologists of Luria's generation knew that lesions at neighboring sites on the cortical surface tend to produce related symptoms. For example, lesions of the occipital cortex give rise to lower-order visual deficits (cortical blindness), whereas lesions of adjacent temporal cortex result in higher-order visual deficits (object agnosia). Similarly, lesions in the posterior sector of the frontal lobe give rise to lower-order motor deficits (weakness and paralysis), whereas more anterior lesions give rise to higher-order deficits of executive control (the prefrontal syndrome). How can these observations be explained?

Luria proposed that sensory and motor cortex comprise multiple specialized subareas that are connected hierarchically. A primary sensory area lies next to a secondary sensory area that in turn borders a tertiary area. These areas have progressively more complex functions, culminating in the integration of multiple sensory modalities in the tertiary zones. Areas in the frontal lobe concerned with motor behavior are similarly organized. The primary motor cortex lies next to a secondary motor area (the premotor cortex) that in turn borders a tertiary area, the prefrontal cortex,

Sensory : Primary → Secondary → Tertiary

Motor : Primary ← Secondary ← Tertiary

concerned with the executive control of behavior. In Luria's scheme sensory information flows into the central nervous system through a series of synaptic relays from primary to secondary to tertiary sensory areas, whereas motor commands flow from tertiary to secondary to primary motor areas. The tertiary areas at the peak of these sensory and motor hierarchies interact and are the seats of cognitive function.

More than 45 years after publication of Luria's book these general principles are still accepted. However, our understanding of the neural systems of cognition is far richer than that of Luria and his contemporaries, in large part because of newer methodologies.

Functionally Related Areas of Cortex Lie Close Together

The cortex of each cerebral hemisphere is a continuous sheet of gray matter ~~in which certain gross anatomical subdivisions are obvious~~. Within each of these lobes the cortex is further subdivided into anatomically and functionally defined areas (Figure 18–1).

Functional areas are distinguished by cellular structure, connectivity, and the physiological response properties of neurons. Identification of the functions of a cortical area requires characterizing the behavioral conditions under which its neurons are electrically active (by means of single-neuron recording) and determining its anatomical connections with other areas (by means of neuroanatomical tracers).

These invasive methods cannot be used in humans except under rare circumstances in which there is some clinical benefit. Consequently the major advances in identifying the function of anatomically or physiologically discrete areas of cortex have come from studies of animals, in particular the *macaque monkey*, a species of the macaque (*Macaca*), an Old World monkey. Old World monkeys are our closest living relatives aside from the apes; like us, they are able to carry out demanding tasks that require well-developed cognitive abilities such as attention, memory, and pattern discrimination.

In the macaque a region of cortex is defined as functionally distinct if neurons within it have similar functional properties (such as responding to similar types of visual stimulation) and common connections (such as receiving the same input from primary visual cortex). In addition, to qualify as an area of lower-order sensory or motor cortex the neurons in that area must be organized into a single, coherent neural map of the sensory or motor periphery. The number of functionally distinct areas identified by these criteria

(Figure 18–1) is much greater than the number of areas defined cytoarchitecturally because an area with anatomically similar cells may contain several functionally and connectionally distinct areas.

A few simple precepts govern the organization of functional areas in the macaque cerebral cortex: (1) all areas fall into a few major functional categories; (2) areas in a given category occupy a discrete, continuous portion of the cortical sheet; and (3) areas that are functionally related occupy neighboring sites (Figure 18–2).

organization
of fcnl areas
in mhp cerebral
cortex

Sensory Information Is Processed in the Cortex in Serial Pathways

In analyzing how the areas of the cerebral cortex act together to produce behavior it is useful to ask, as in the study of social organizations, who talks to whom? Cortical areas communicate with each other by means of bundles of axons traveling together in identifiable tracts. As a result of neuro-anatomical tracing studies in the monkey, the neural tracts (or projections) running from area to area are now well understood. A dye injected into one population of neurons is carried by axonal transport to distant clusters of neurons that can be identified because they are labeled with the dye (see Box 4–2).

These tracing studies have confirmed Luria's idea that the sensory areas of cortex are organized hierarchically. Within each sensory system (visual, auditory, etc.) signals from the periphery arrive at a primary sensory area, such as the primary visual cortex (V1), primary auditory cortex (A1), or primary somatosensory cortex (S-I).

Primary sensory areas possess four properties characteristic of their role in the early stages of information processing.

1. Their input is from thalamic sensory relay nuclei. (The thalamus is the main subcortical source of input to all areas of cortex but only some thalamic nuclei relay sensory signals).
2. The neurons in a primary sensory area have small receptive fields—the region on the receptor surface that must be stimulated in order for the neuron to fire—and are topographically arranged to form a precise map of the sensory receptor surface (retina, cochlea, or skin).
3. Injury to a part of the map causes a simple sensory loss confined to the corresponding part of the contralateral sensory receptor surface.
4. Connections to other cortical areas are limited, confined almost entirely to nearby areas that process information in the same modality.

Macques

Similar fcnl
properties

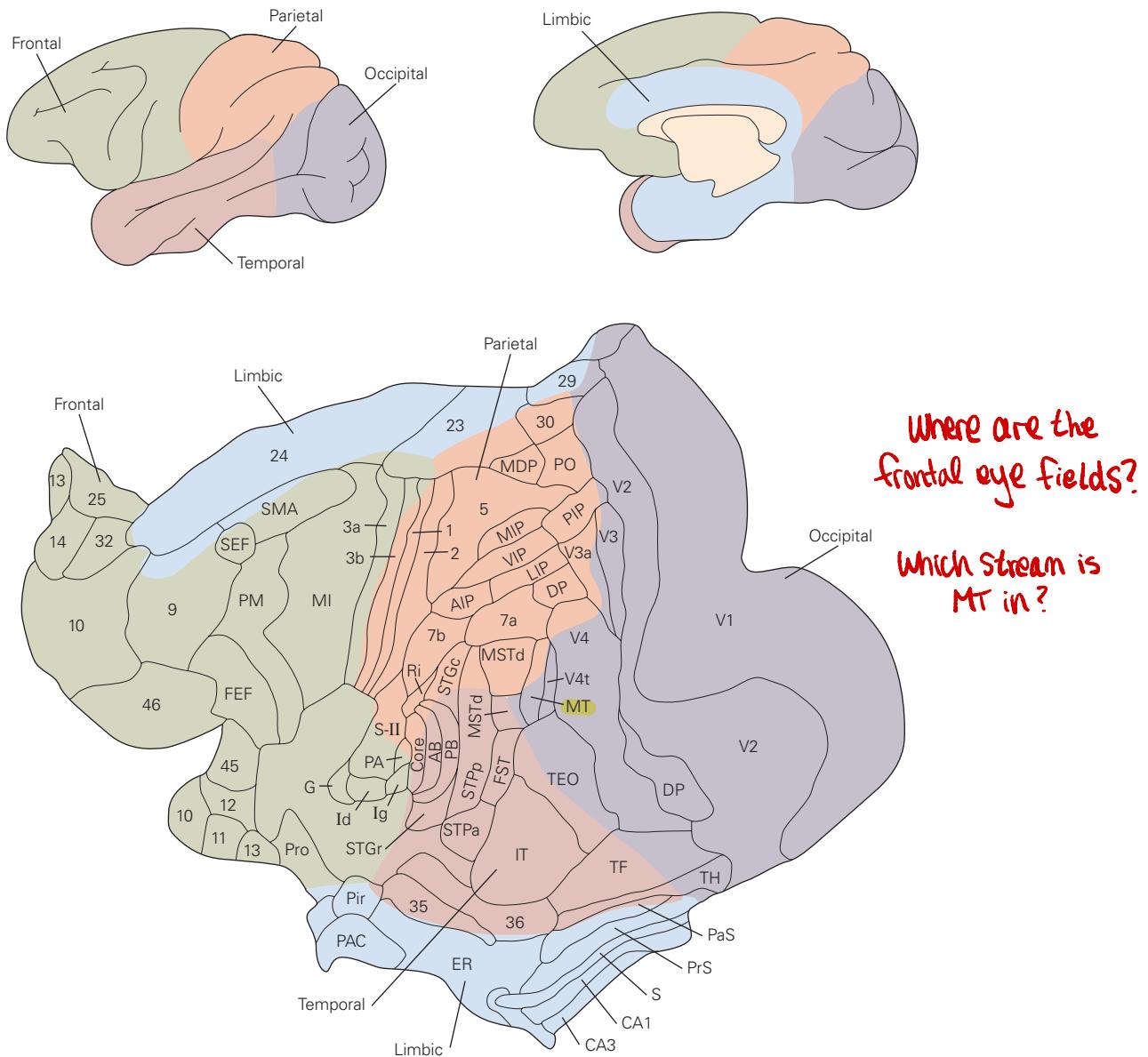


Figure 18–1 The cerebral cortex of the macaque monkey. Lateral and medial views show the location of five cortical lobes. The labeled areas on the unfolded hemisphere are those defined in physiological and anatomical studies. (Adapted, with permission, from Van Essen et al. 2001.)

The anatomical labels are as follows. The numbered areas are Brodmann's areas; AB, auditory belt; AIP, anterior intraparietal area; CA₁, CA₃, cornu ammonis fields of hippocampus; Core, primary auditory cortex; DP, dorsal prelunate area; ER, entorhinal cortex; FEF, frontal eye field; FST, floor of superior temporal sulcus; G, gustatory cortex; Id, Ig, insular cortex, dysgranular and granular divisions; IT, inferotemporal cortex; LIP, lateral intraparietal area; MDP, medial dorsal parietal area; M1, primary motor cortex; MIP, medial intraparietal area;

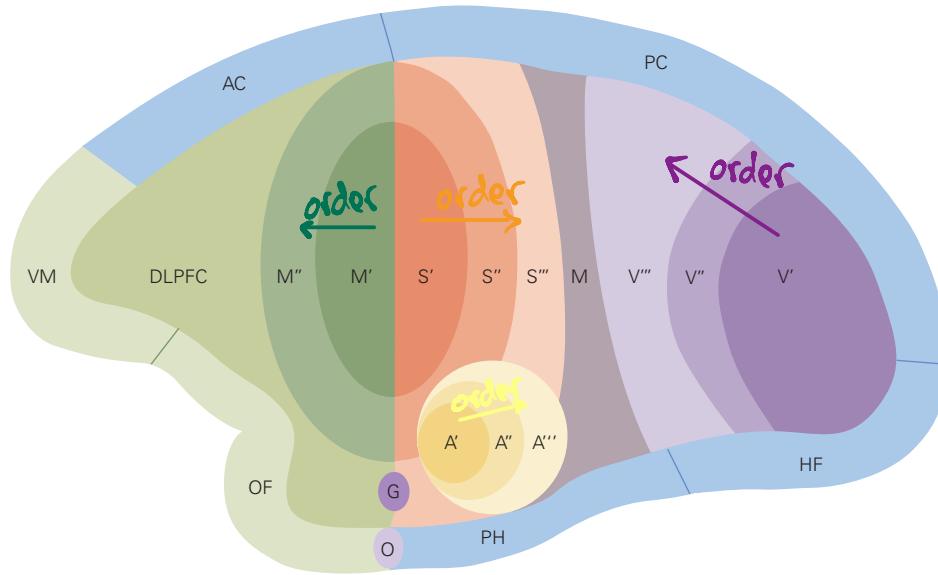
MSTd, MSTI, medial superior temporal sulcus, dorsal and lateral divisions; MT, middle temporal area; PA, postauditory area; PAC, periamygdaloid cortex; PaS, parasubiculum; PB, auditory parabelt cortex; PIP, posterior intraparietal; Pir, piriform cortex; PM, premotor cortex; PO, parieto-occipital area; Pro, orbital proisocortex; PrS, presubiculum; Ri, retroinsular area; S, subiculum; SEF, supplementary eye field; S-II, secondary somatosensory area; SMA, supplementary motor and adjacent cingulate motor areas; STGc, STGr, superior temporal gyrus, caudal and rostral divisions of auditory cortex; STPa, STPp, superior temporal polysensory area, anterior and posterior divisions; TEO, temporo-occipital area; TF, TH, parahippocampal areas; V₁, V₂, V₃, V_{3a}, V₄, V_{4t}, visual areas; VIP, ventral intraparietal area.

Primary (low)

Secondary

Tertiary (high)

order ↑



Category	Subcategory	Key	Figure 18-1
Visual	Primary	V'	V1
	Secondary	V''	V2, V3, V3a, PIP, PO, MT, V4
	Tertiary	V'''	MDP, LIP, 7a, MSTd, MSTI, FST, IT
Somatosensory	Primary	S'	3a, 3b
	Secondary	S''	1, 2, S-II
	Tertiary	S'''	5, MIP, AIP, 7b, Ri, Id, Ig
Auditory	Primary	A'	Core
	Secondary	A''	AB, PA
	Tertiary	A'''	PB, STGc, STGr
Multimodal		M	VIP, STPp, STPa
Gustatory		G	G
Olfactory		O	Pir, PAC
Motor	Primary	M'	M1
	Secondary	M''	PM, SMA, FEF, SEF, 24
Dorsolateral prefrontal	Dorsal	9, 10, 14	
	Dorsolateral	DLPFC 46	
	Ventral convexity	45	
Orbital-ventromedial prefrontal	Orbital	OF	11, 12, 13, Pro
	Ventromedial	VM	25, 32
Limbic	Anterior cingulate	AC	24
	Posterior cingulate	PC	23, 29, 30
	Hippocampal	HF	CA1, CA3, S, PrS, PaS
	Parahippocampal	PH	ER, TF, TH, 35, 36

Figure 18-2 The cerebral cortex is divided into discrete functional categories. Cortical areas in each functional category occupy a continuous physical region of the cortical sheet, shown here in a schematic version of the unfolded hemisphere in Figure 18-1. The table indicates the functionally distinct

areas within each category. Primary sensory areas send their outputs to multiple secondary sensory areas, which in turn provide inputs to tertiary (higher-order) areas. Multimodal areas are tertiary areas with significant input from more than one sensory system.

association cortex

Higher-order sensory areas have a different set of properties that are important to their role in the later stages of information processing.

1. They receive little input from the sensory relay nuclei in the thalamus; instead, their input arises from other thalamic nuclei and lower-order areas of sensory cortex.
2. Their neurons have large receptive fields and are organized into imprecise maps of the array of receptors in the periphery.
3. Injury results in abnormalities of perception and of related cognitive functions but does not impair the ability to detect sensory stimuli.
4. They are connected not only to nearby unimodal sensory areas but also to distant areas in the frontal and limbic lobes.

Thus, sensory information is processed serially, with each area in the chain carrying out certain computations and conveying the results to the next area. For example, in the ventral pathway of the visual system, which is concerned with processing information about form, the pathway begins with neurons that respond to detailed features of a visual stimulus and proceeds to neurons that encode the overall form. Receptive fields of individual neurons in the primary visual cortex (V1) span approximately 1 degree of visual angle; those of neurons in V4 (a mid-order area) span approximately 10 degrees; and those in the inferotemporal cortex (a higher-order area) span up to 100 degrees. Thus an individual neuron in V1 could be sensitive to a small detail in a face, such as an eyebrow aligned in a certain direction within its small receptive field, whereas a neuron in the inferotemporal cortex can respond to an entire face.

However, sensory pathways are not exclusively serial; in each functional pathway higher-order areas project back to the lower-order areas from which they receive input. In this way neurons in higher-order areas, sensitive to the global pattern of sensory input, can modulate the activity of neurons in lower-order areas that are sensitive to local detail. For example, top-down signals originating in the inferotemporal cortex might help neurons in V1 to resolve a detail in a part of the face.

The hierarchical chain of sensory processing leads to areas with functions so complex that they cannot be described as simply sensory. In the late 19th century Santiago Ramón y Cajal proposed that areas with sensory functions were fundamentally distinct from those with cognitive functions, calling the latter the *association cortex*. This term is rooted in the

idea that cognition depends upon our learning which of the myriad stimuli impinging on our senses are associated with one another. Modern neuroscientists apply the term *association cortex* to regions of cortex where injury causes cognitive deficits that cannot be explained by impairment of sensory or motor function alone.

Large regions of association cortex are contained within each of the four lobes and contribute to cognition in distinctive ways.

The *parietal association cortex* is critical for sensory guidance of motor behavior and spatial awareness.

The *temporal association cortex* is important for recognition of sensory stimuli and for storage of semantic (factual) knowledge.

The *frontal association cortex* plays a key role in organizing behavior and in working memory.

The *limbic association cortex* serves complex functions related to emotion and episodic (autobiographical) memory.

Association areas have much more extensive input and output connections than do lower-order sensory and motor areas. Some association areas have a variety of visual, auditory, somatosensory, and motor connections that permit them to integrate sensory modalities or to use sensory information to guide motor behavior (see Chapter 19). In addition, all association areas are interconnected by a dense network of pathways within and between the parietal, temporal, frontal, and limbic lobes.

Parallel Pathways in Each Sensory Modality Lead to Different Association Areas

In addition to being processed serially another principle of cortical organization is that the same information is processed differently in parallel pathways. In the visual system for example, two major parallel pathways terminate in different higher-order areas of cortex. The dorsal stream processes spatial information (position, motion, speed) and projects to parietal association cortex. The ventral stream processes information about form (color, shape, texture) and projects to temporal association cortex.

Dorsal and ventral pathways exist in other sensory systems as well (Figure 18–3). In the auditory and somatosensory systems dorsal pathways serve motor and spatial functions, whereas ventral pathways serve recognition functions. The dorsal-ventral division extends into frontal association cortex.

ventral → temporal AC
dorsal → parietal AC

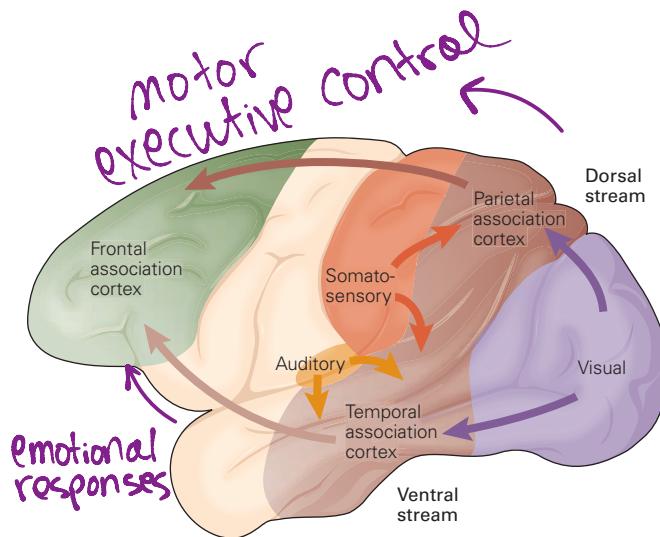


Figure 18–3 The dorsal and ventral systems of the cerebral cortex. Lower-order sensory areas send their output in parallel to parietal (dorsal stream) and temporal (ventral stream) association cortex, which in turn send their output to frontal association cortex. The parietal cortex projects primarily to dorsal areas of frontal cortex, areas that serve motor and executive control functions for which spatial information is important. The temporal cortex projects primarily to ventral regions of frontal cortex, including the orbital prefrontal cortex, areas that mediate emotional responses to things in the environment. Emotional significance can be assigned to an object only after the object has been recognized, an ability that depends on areas of the temporal lobe.

The Dorsal Visual Pathway Carries Spatial Information and Leads to Parietal Association Cortex

The parietal cortex plays a key role in the visual guidance of motor behavior and in spatial perception and cognition, that is, seeing and understanding where objects are relative to each other. These two functions are related because visuomotor control requires processing spatial information. Reaching for your coffee cup while you read the newspaper requires taking into account where the image of the cup is on your retina and where your eyes are pointing so as to determine where the cup is located relative to your hand.

The parietal cortex is ideally suited for such computations because it is connected to visual, somatosensory, and motor areas of cortex. Parietal cortex may have initially developed the capacity to represent where things are relative to the body to guide actions such as grasping, and then developed the ability to represent where things are relative to each other without reference to the body.

As we have learned in Chapter 17, injury to the parietal cortex in humans results in a wide range of behavioral impairments, which can be classified into

two broad categories. In the first category are impairments of body awareness, motor control, and visual guidance of motor behavior. These deficits result from damage to dorsal parts of the parietal cortex close to and connected with the somatosensory cortex. In the second category are impairments of spatial perception and cognition. These deficits result from damage to ventral parts of parietal cortex close to and connected with the visual cortex. Thus the **parietal cortex** can be thought of as having two subdivisions: a **dorsal component serving primarily motor functions** and a **ventral component serving primarily spatial functions**.

Specific impairments in the first category include **asomatognosia**, a disorder of body awareness in which patients deny the existence of the arm or leg contralateral to the lesion or refuse to acknowledge that it belongs to them even when they can see it. Another is **ideomotor apraxia**, which arises from damage to the dominant hemisphere; patients are unable to execute certain movements such as waving goodbye, either on command or by imitation, although they may spontaneously make the same movement under circumstances that evoke it habitually. A third deficit in this category, **optic ataxia**, results from damage to the dorsomedial parietal cortex. Patients with this deficit have difficulty reaching for an object in the peripheral visual field (as when reaching for a coffee cup while reading the newspaper). The hand may go to the wrong location, or it may be misoriented when attempting to grasp the object (Figure 18–4). Patients can, however, perform a reaching task that does not depend on vision, for example touching one's own knee in the dark and can report the locations of visible objects correctly. This collection of symptoms cannot be explained by a purely motor or purely visual mechanism but instead reflects difficulty in coordinating visual input and motor output.

Specific impairments in the second category include **hemispatial neglect**. Patients with this defect are profoundly inattentive to events in the half of space opposite the injured side (see Chapter 17). Another is **constructional apraxia**, an inability to appreciate the structure and arrangement of things by looking at them. Patients suffering from constructional apraxia have difficulty arranging a set of tiles or matchsticks according to a model placed in plain view. They may also be deficient in tests of writing and drawing because these require putting marks on a page in a precise arrangement (Figure 18–5).

Injury to parietal cortex can impair cognitive tasks that require abstract spatial thinking. For example, patients with **acalculia** have trouble understanding and manipulating numbers, particularly multidigit numbers where the value of a digit depends on its place.

dorsal
2
Motor

ventral
2
Spatial

1st category
impaired
impairments
of body
awareness,
motor control,
& visual guidance

damage to
dorsal parietal
cortex close
to SSC

2nd category
impaired
impairments
of spatial
perception &
cognition

damage to
ventral parietal
cortex connect
to visual cortex

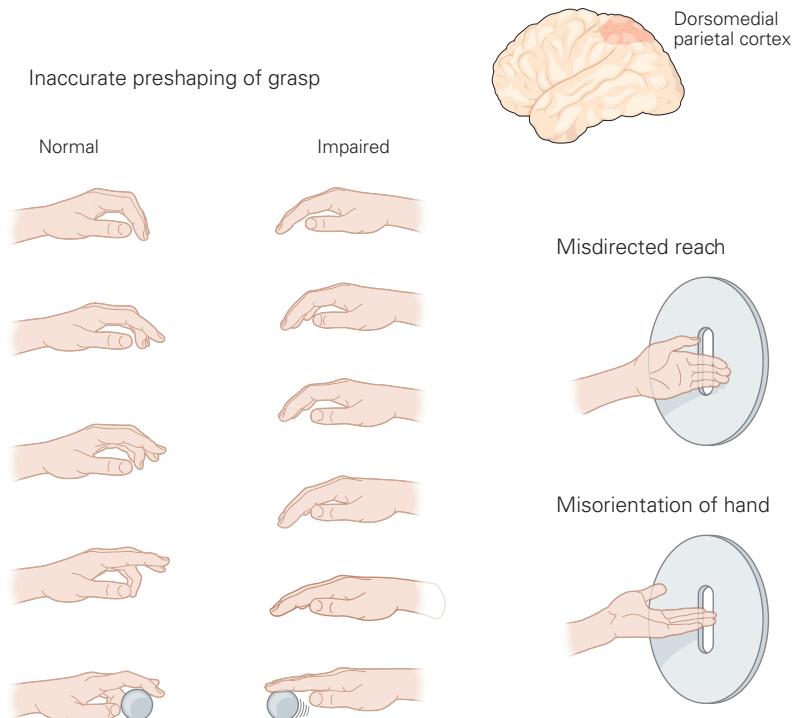


Figure 18–4 Patients with damage to the dorsomedial parietal cortex have difficulty with visually guided grasping and reaching (**optic ataxia**). When required to grasp an object, patients fail to shape their hand appropriately. When required to place their fingers through a slot in a plate, they reach to the wrong location and fail to orient the hand correctly. (Reproduced, with permission, from Jeannerod 1986 [left panels]; and Perenin and Vighetto 1988 [right panels]).

Injury to the left angular **gyrus**, a region at the lateral edge of the parietal lobe, results in **agraphia with alexia**, a condition in which patients cannot read, write, or spell and cannot understand a word spelled out orally. Reading and writing involve spatial thinking in that they depend on the ability to perceive, remember, and reproduce the sequence of letters in a word.

Although clinical observations pinpoint the parietal cortex as important for many spatially based abilities, they do not tell us about the underlying neural mechanisms. Our understanding of these mechanisms comes in large part from studies of monkeys using single-neuron recording. Four areas in the monkey's **intraparietal sulcus** have been thoroughly studied: the **lateral, ventral, medial, and anterior intraparietal** areas. Neurons in all of these areas carry spatial information, signaling the location of an object to which the monkey is paying attention or is about to direct movement. Within a given area neurons respond to one or more specific kinds of sensory stimulation (somatosensory or visual), fire in conjunction with a specific kind of movement (looking, reaching, or grasping), and encode the location of a target relative to a specific part of the body (eye, head, or hand) or the environment.

The lateral intraparietal area encodes retina-centered information about points in the visual field that the monkey has selected for attention and is involved in visual attention and eye movements. Its

neurons, like those in unimodal visual areas, have receptive fields for fixed points on the retina. Visual responses in these neurons increase when the monkey is paying attention to a stimulus in the receptive field (Figure 18–6A). This enhancement of the response occurs whether or not the monkey is planning an eye movement toward the stimulus. Neurons here also fire when the monkey is anticipating the appearance of a stimulus or remembering the location where a stimulus appeared, and some neurons fire around the time of an eye movement toward the receptive field.

The ventral intraparietal area encodes head-centered spatial information about visual and tactile stimuli and is involved in multisensory guidance of head and mouth movements. Individual neurons respond to both visual and somatosensory stimuli. Most neurons respond to tactile stimulation on the face or head and to visual stimuli presented near the receptive field. The match between somatosensory and visual receptive fields is maintained when the eyes move: The visual receptive fields are shifted so as to remain at a fixed position relative to the head (Figure 18–6B).

The medial intraparietal area encodes both retinacentered and body-centered spatial information and is involved with visually guided reaching. Neurons in this area respond to visual targets and are active when the monkey is planning and executing reaching movements. They are sensitive to the direction of reaching

Ventral
↓
head-centered
spatial info

Medial
↓
visually-guided
reaching

valley

lateral
↓
*visual
attention
&
eye movements*

mtr
?

Dorsal → Motor control of body
(close to SSC)

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Ventral → Spatial perception & cognition
(close to visual cortex)

in relation both to where the monkey is looking (right or left of the gaze) and to the body (right or left of the trunk) (Figure 18–6C).

The anterior intraparietal area encodes object-centered and hand-centered spatial information and is involved with visually guided grasping. Individual neurons are selective for objects of particular shapes and for the hand shapes required to grasp them. A neuron that fires when the monkey sees a given object will also fire when it prepares to grasp that object (Figure 18–6D).

Clinical observations in humans and electrophysiological studies in monkeys lead to two general conclusions. First, the parietal cortex is specialized for the sensory guidance of motor behavior as well as for spatial perception and cognition. Second, different regions

within the parietal cortex serve different functions: Dorsal regions close to the somatosensory cortex contribute to motor control of the body whereas ventral regions close to the visual cortex contribute to spatial perception and cognition.

The Ventral Visual Pathway Processes Information About Form and Leads to Temporal Association Cortex

The temporal association cortex, like the parietal association cortex, is a region where higher-order areas of different sensory systems share borders and are interconnected. These association areas receive information about form, sound, touch, and shape from lower-order

Anterior
↓
visually-guided
grasping

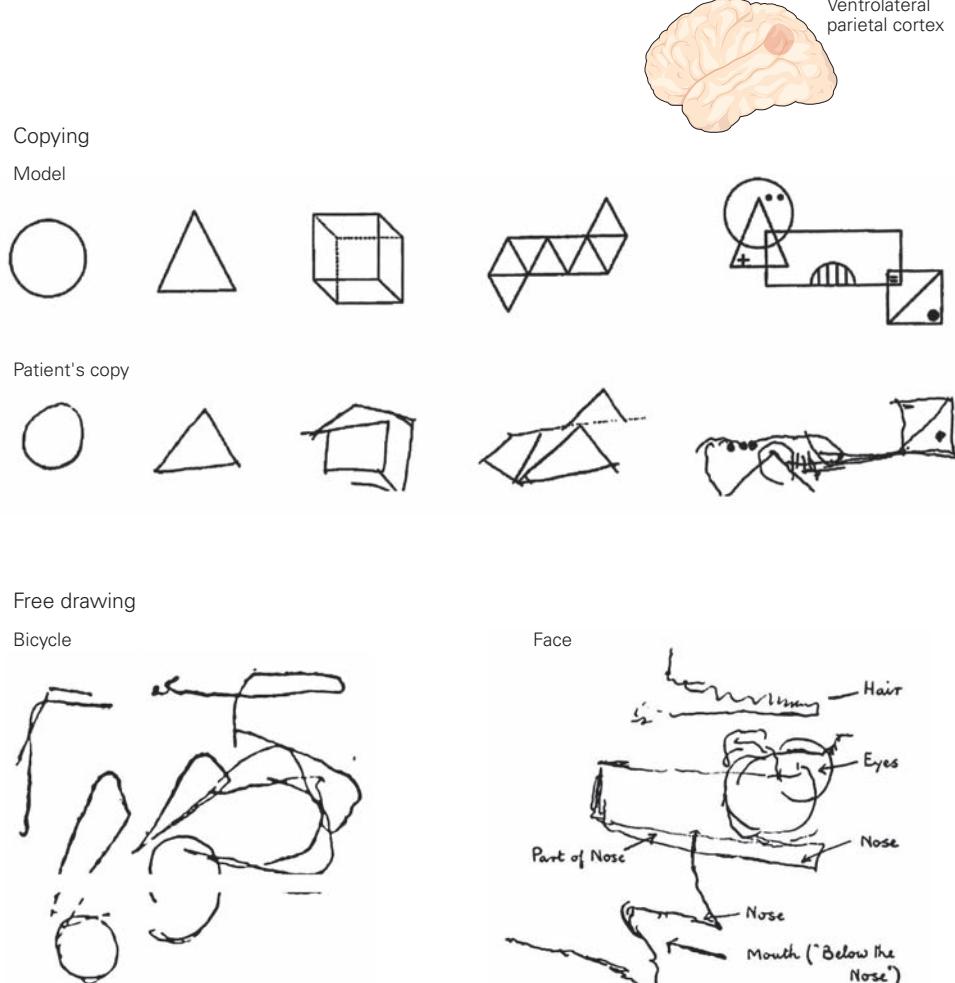
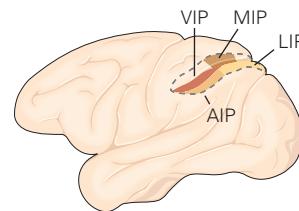


Figure 18–5 Disorders of copying and drawing result from damage to the parietal cortex. Drawings of complex figures are grossly inaccurate whether drawn from a model or from

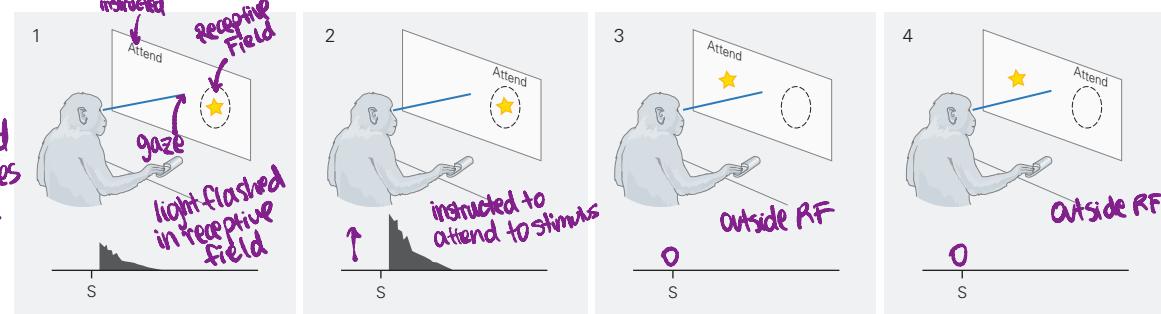
memory. The problem arises from an inability to perceive the spatial relations of the parts of an object. (Reproduced, with permission, from Critchley 1953; and Trojano and Grossi 1998.)



Receptive field characteristics

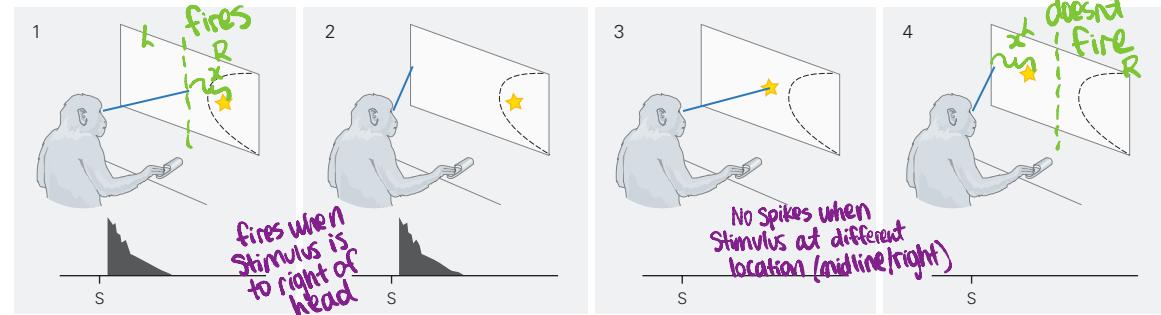
no attention = no firing

A Lateral intraparietal area



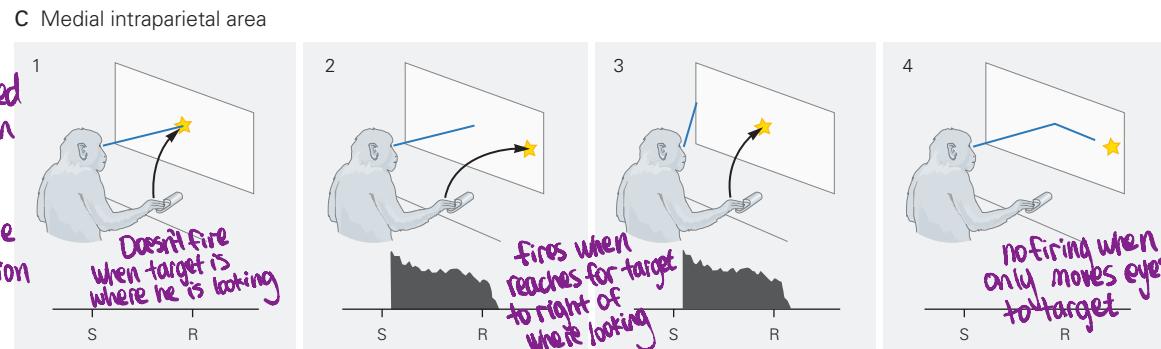
Retina-centered, attention sensitive

B Ventral intraparietal area



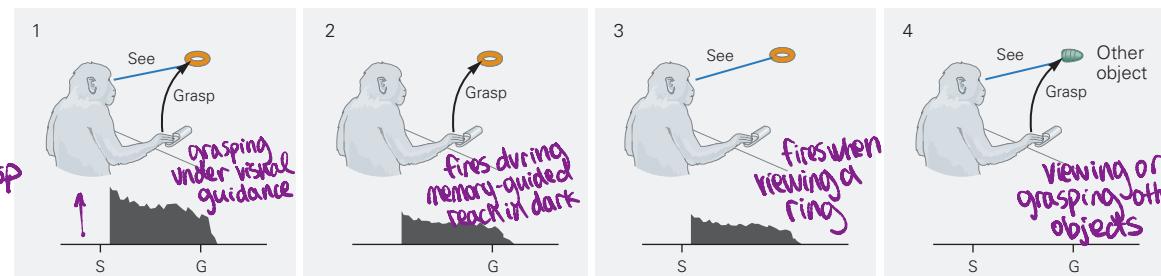
Head-centered

C Medial intraparietal area



Retina-centered direction of reach; preparation to reach

D Anterior intraparietal area



Retina-centered, object-specific viewing, grasping

IT Cortex → ventral visual pathway
(shape, color, texture)



Temporal association cortex
(object recognition)



Ventral frontal cortex
(emotional response)

visual, auditory, and somatosensory areas. For example, the **inferotemporal cortex** receives information about the shape, color, and texture of visual images through the ventral visual pathway. The temporal association cortex uses this information to mediate the recognition of objects in the environment and, through projections to the ventral frontal cortex, trigger appropriate emotional responses to them (see Figure 18–3).

Injury to the visual and auditory association areas of the temporal lobe in humans impairs recognition of the significance of sensory stimuli, resulting in a variety of perceptual deficits termed **agnosias**. Patients with **visual object agnosia**, a result of injury to a mediovelar part of the temporal cortex, cannot recognize things but can draw them (Figure 18–7). This deficit is a striking contrast to patients with parietal cortex injury, who can recognize things but often cannot draw them well (Figure 18–5). Patients with visual object agnosia may be unable to recognize objects in general or may be unable to make fine distinctions within a category of objects such as faces. An impairment in recognition specific to faces is called **prosopagnosia**.

Auditory agnosia has been described, although reports of it are rare, perhaps because the condition is associated with more disabling disorders of language comprehension. Patients with auditory agnosia, when asked to describe recordings of natural sounds, demonstrate that they are not deaf but that their ability to recognize the sounds is impaired.

Figure 18–6 Neurons in the parietal cortex of the monkey are selective for the location of objects in the visual field relative to particular parts of the body. Each histogram represents the firing rate of a representative neuron as a function of time following presentation of a stimulus. In each diagram the line emanating from the eyes indicates where the monkey is looking.

A. Neurons in the **lateral intraparietal area (LIP)** have **retina-centered receptive fields**. The strength of the visual response depends on whether the monkey is paying attention to the stimulus. The neuron fires when a light is flashed inside its receptive field (dotted circle) (1). The visual response is increased if the monkey is instructed to attend to the location of the stimulus (2). The neuron does not fire if the stimulus is presented outside the receptive field regardless of where attention is directed (3, 4).

B. In the **ventral intraparietal area (VIP)** some neurons have **head-centered receptive fields**. This is determined by keeping the head in a fixed position while the monkey is instructed to shift its gaze to various locations. This neuron fires when a light appears to the right of the midline of the head (1, 2). It does not fire when the light appears at another location relative to the

By far the most debilitating of all conditions arising from damage to the human temporal lobe is **Wernicke's aphasia**, a disorder in understanding spoken language. Wernicke's aphasia arises from damage to the superior temporal gyrus of the left hemisphere, a region corresponding to **Brodmann's area 22** (comparable in location to the auditory association cortex in the superior temporal gyrus in the monkey). It is not merely a disorder of speech comprehension but is accompanied by severe garbling of the patient's own speech. This indicates that auditory forms of words stored in the temporal lobe serve not only as templates for speech recognition but also as guides for speech production.

Semantic dementia is a degenerative disorder typically arising from pathology of the temporal cortex. Studies of patients with this disorder indicate that this part of cortex is critical not only for recognition but also for semantic memory. To have semantic knowledge of a thing means to associate the disparate pieces of information that one has accumulated about it, for example, the sound, feel, appearance, and use of a telephone. These associations are forged through experience-dependent changes in the synaptic connections among the same temporal lobe areas on which recognition depends. A patient with semantic dementia shown pictures of an ostrich and a penguin may name them simply "bird" or even "animal." The loss of detailed knowledge about things in the world emerges even in tests requiring only nonverbal responses, such as placing together pictures of things that are semantically related.

head, as on the midline or to the left (3, 4). The critical contrast is between situations 1 and 4. The retinal location of the light is the same in both (slightly to the right of the fixation point) yet the neuron fires in 1, when the stimulus is to the right of the head, but not in 4, when the stimulus is to the left of the head.

C. In the **medial intraparietal area (MIP)** neurons fire when the monkey is preparing to reach for a visual target and are selective for the retina-centered direction of the reach. This neuron fires when the monkey reaches for a target to the right of where he is looking (2, 3). It does not fire when he reaches for a target at which he is looking (1) or when he moves only his eyes to the target at the right (4). The physical direction of the reach is not a factor in the neuron's firing: It is the same in 1 and 3 and yet the neuron fires only in 3.

D. In the **anterior intraparietal area (AIP)** neurons fire when the monkey is looking at or preparing to grasp an object and are selective for objects of particular shapes. This neuron fires when the monkey is viewing a ring (3) or making a memory-guided reach to it in the dark (2). It fires especially strongly when the monkey is grasping the ring under visual guidance (1). It does not fire during viewing or grasping of other objects (4).

visual object agnosia

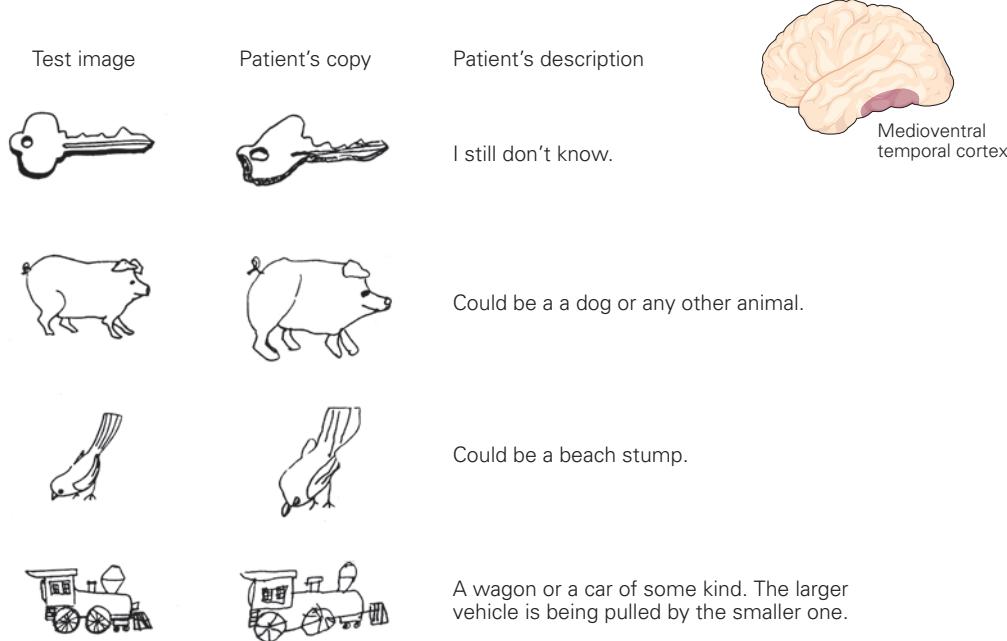


Figure 18–7 Injury to a medioventral region of temporal cortex results in visual object agnosia. When presented with the drawings shown in the left column, a patient with visual

object agnosia was able to copy them but could not accurately identify the objects. (Reproduced, with permission, from Rubens and Benson 1971.)

IT
 • not influenced by motor behavior
 • sensitive to shape, color, texture
 • largely unaffected by size / location of image

Can decode Stimulus from inferotemporal neural activity

Neurons in the temporal association cortex of monkeys become active under circumstances that suggest involvement in object recognition. The best understood area of temporal association cortex is the **inferotemporal cortex**, which occupies most of the inferior temporal gyrus and extends dorsally into the superior temporal sulcus. The activity of inferotemporal neurons, unlike neurons in the parietal cortex, is not influenced by the motor behavior of the animal. If a visual stimulus enters the neuron's receptive field and the monkey is paying attention to it, the neuron will fire at a virtually identical rate regardless of what the animal is doing or planning to do.

Inferotemporal neurons also differ from parietal neurons in that they are sensitive to the shape, color, and texture of an object in the visual receptive field. In one study individual inferotemporal neurons responded to only a few shapes out of a large test set (Figure 18–8). Because each neuron responded to different stimuli, it was possible by monitoring the activity of many neurons to determine reliably which stimulus was present on the screen. The pattern selectivity of inferotemporal neurons is largely unaffected by image size and location as long as the image falls somewhere in the neuron's typically large receptive field. This insensitivity to size and location is further evidence that the inferotemporal

cortex plays a role in shape recognition (for which location and size are irrelevant) but not in motor guidance (for which they are crucial).

Just as neurons in the inferotemporal cortex are selective for visual shapes, neurons in the auditory association cortex of the superior temporal gyrus are selective for patterns of sound. Although little studied, this region is known to contain neurons selective for particular species-specific vocalizations. Overall, the temporal association cortex plays a critical role in recognizing things and in storing some kinds of knowledge. It is not involved in the guidance of movement or in spatial perception and cognition, functions that depend instead on parietal cortex.

Goal-Directed Motor Behavior Is Controlled in the Frontal Lobe

All areas of the frontal lobe participate in the control of motor behavior but in different ways. Just as in the posterior sensory cortex, frontal areas are connected in series in a functional hierarchy (Figure 18–9). At the lower end of the chain is the **primary motor cortex** (Brodmann's area 4), also referred to as M1. Neurons here are organized into a detailed map of the body.

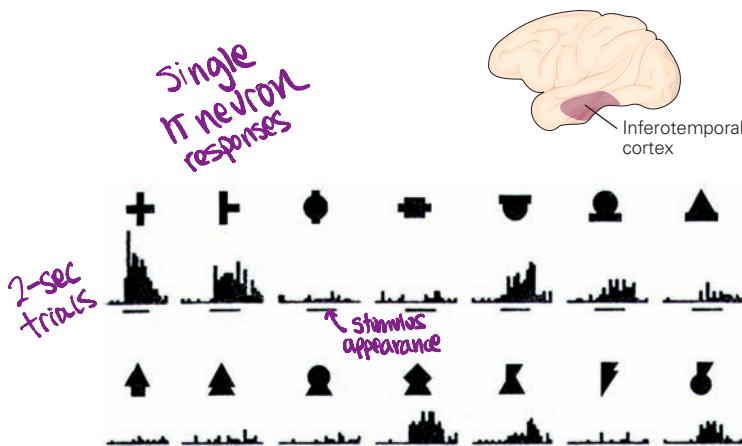


Figure 18-8 Neurons in the inferotemporal cortex of the monkey respond selectively to particular shapes. Responses of a single inferotemporal neuron are shown for 14 different silhouette shapes. The histogram under each shape represents the rate at which the neuron fired as a function of time during a two-second trial. The bar under the histogram indicates the one-second period during which the stimulus appeared. (Reproduced, with permission, from Kobatake et al. 1998.)

M1
↑
Premotor cortex
- coarse map of body
↑
Dorsolateral prefrontal cortex
- Cognitive control of motor behavior
↑
Orbital ventromedial prefrontal cortex
- emotional processes w/ executive control of behavior

The primary motor cortex has numerous subregions that produce movement of different parts of the body.

Adjacent to the primary motor cortex and reciprocally connected to it are several higher-order motor areas collectively called the **premotor cortex**. Neurons in each of these areas are arranged in a comparatively coarse map of the body. **Neuronal activity in the premotor areas reflects global aspects of motor behavior such as the combination of limbs to be used or the sequence of movements.** In addition the premotor cortex of the inferior frontal gyrus and parietal lobules contains populations of **mirror neurons** that have cognitive functions and respond to the movement of others (see Chapter 19). The premotor cortex is connected to the **dorsolateral prefrontal cortex**, which is important for cognitive control of motor behavior. This area is connected in turn to the **orbital-ventromedial prefrontal cortex**, an area involved in emotional processes associated with the executive control of behavior.

In contrast to the sensory systems, where information flows from the periphery into higher-order areas, in the **motor systems signals flow from the higher-order areas of the frontal lobe to the primary motor cortex.** Emotional processes in the orbital-ventromedial prefrontal cortex influence cognitive processes in the dorsolateral prefrontal cortex, which in turn act on spinal motor nerves through the premotor and primary motor cortex.

Prefrontal Cortex Is Important for the Executive Control of Behavior

Much of what we do in daily life depends on our ability to remember and act on intentions. Intentions can be simple or nested; they can concern particular actions or general plans, a small bit of mental arithmetic or a career path. The mental processes underlying the executive control of behavior are so diverse that it seems unlikely that they could be served by one area of the brain. Yet, remarkably, a single large region of the cerebral hemisphere, the **prefrontal cortex**, is implicated in many forms of executive control.

Patients with damage confined to the prefrontal cortex are typically normal in their perceptual ability and motor behavior and may perform normally on tests of intelligence. Yet they are unable to function effectively in daily life. Their emotional state is abnormal, and their behavior is disorganized because they lack concentration and thus are ineffective at carrying out plans. The physician John Harlow, writing in 1868, provided the first clear description of such a case. His patient, Phineas Gage, was a railroad worker who had suffered extensive prefrontal damage when blasting powder, exploding prematurely, drove a tamping iron through his head. (Figure 18–10) Formerly “a shrewd, smart business man, very energetic and persistent in pursuing all his plans,” Gage seemed transformed into another person altogether, “pertinaciously obstinate, yet capricious and vacillating, devising many plans of future operation, which are no sooner arranged than they are abandoned in turn for others appearing more feasible.”

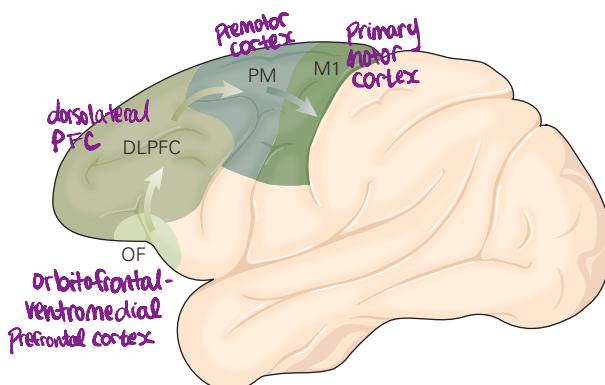


Figure 18-9 Regions of the frontal lobe are connected in series. The pathway begins in the orbitofrontal-ventromedial prefrontal cortex (OF) and from there projects to the dorsolateral prefrontal cortex (DLPFC), the premotor cortex (PM), and finally the primary motor cortex (M1). **Emotional and cognitive processes in the prefrontal cortex exert control over behavior through these connections.**

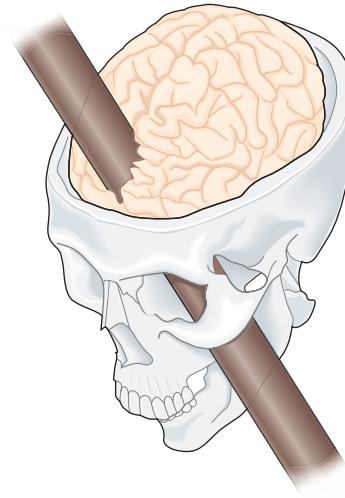
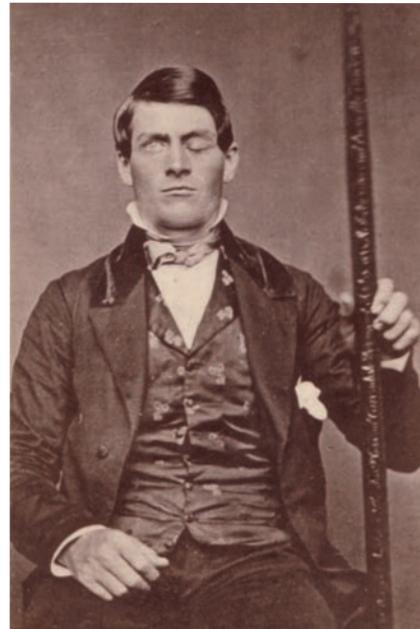
PFC Damage

- abnormal emotional state
- disorganized behavior
- flat emotional tone
- indifference to everything

Figure 18–10 A nineteenth century case revealing the dependence of personality on prefrontal cortex.

Left: Phineas Gage with the three-foot long tamping iron that was driven through his head by an explosion.

Right: A computer reconstruction of a drawing of the passage of the tamping iron through Gage's brain. This injury resulted in severe personality changes that illuminated our understanding of the function of the frontal lobes. (Adapted, with permission, from Bechara et al. 1994.)



Patients with prefrontal damage are unable to travel on their own because they will board whatever bus comes along first. They are unable to wait on tables in a restaurant because they lack the ability to respond to competing demands. One patient, an accomplished cook before sustaining brain damage, was able to use familiar recipes but could not follow new ones. If she went out to buy food she might be gone for hours, having coffee with a friend and forgetting all about the task at hand.

Emotional tone following prefrontal injury typically is characterized by flatness, shallowness, and indifference. This may take the form of loss of religious feeling, loss of appreciation for literature or music, insensitivity to the feelings of others, or indifference to the financial consequences of one's own actions.

Similar emotional changes occur in nonhuman primates. The observation by Charles Jacobsen that chimpanzees with prefrontal lesions no longer became enraged when they failed to perform simple tasks led the Portuguese neurosurgeon Egas Moniz to introduce prefrontal lobotomy as a last-resort treatment for uncontrollable behavioral problems in patients with mental illness. This treatment was ultimately abandoned because of its devastating and irreversible damage to the patient's personality. Although cognitive and affective problems often occur together, cognitive deficits are especially pronounced after injury to dorsolateral prefrontal cortex, whereas emotional abnormalities are especially pronounced after orbital-ventromedial injury.

Dorsolateral Prefrontal Cortex Contributes to Cognitive Control of Behavior

Injury to the **dorsolateral prefrontal cortex** results in **cognitive deficits** that are manifested in a number of objective tests ranging from the very complex to the remarkably simple. An example of a complex test is to send patients on a shopping expedition with a set of specific instructions on where to go and what to buy. Typically, patients do not comply with the instructions, break accepted rules of social interaction, proceed inefficiently, and consequently fail to obtain all of the items specified.

A simple test that is highly sensitive to dorsolateral prefrontal damage is the **Wisconsin Card Sort Test**. Subjects are given a deck of cards printed with symbols and must select one card at a time and place it next to one of four samples. Told only whether each choice is correct or incorrect, they must discover by trial and error whether the correct choice is based on the number of symbols on the card, their shape, or their color (Figure 18–11). Patients with lesions of the dorsolateral prefrontal cortex persist in using an unsuccessful strategy, making so-called perseverative errors. They also make capricious errors, abandoning a successful rule unnecessarily. It is as if conscious oversight of behavior has been weakened, releasing habitual or random responses that are normally suppressed. It is easy to see how this condition could give rise to erratic behavior in everyday tasks.

PFC damage in NHPs
• no longer enraged when failing at simple tasks

dorsolateral PFC → Cognitive deficits

Orbital-Ventromedial PFC → Emotional abnormalities

Cognitive deficits:

- following instructions
- making perseverative & capricious errors
- verbal fluency

Tests of verbal fluency are also sensitive indicators of dorsolateral prefrontal injury. When instructed to write down as many five-letter words as possible beginning with the letter "R" within a limited period of time, patients with prefrontal lesions produce relatively few words and sometimes break the rule by generating words with fewer or more letters than the required number. Asked about what it is like to perform this task, one patient said: "My brain becomes a blank. I completely run out of words. I can't think any more."

Studies of nonhuman primates have helped us understand the functions of the prefrontal cortex. Systematic study of prefrontal contributions to cognition began with Jacobsen's demonstration in the 1930s that chimpanzees with prefrontal lesions do poorly in delayed-response tasks. In a typical delayed-response task the animal is allowed to watch while

food is placed under one of two objects and a curtain is drawn. After a delay the curtain is raised, and the animal is allowed to lift one of the two objects. If the animal chooses the object covering the piece of food, it is allowed to retrieve and eat the food. The success rate is lower in animals with prefrontal lesions than in normal controls, especially with long delays. Later studies in macaque monkeys showed that this deficit results specifically from injury to the dorsolateral prefrontal cortex in and around the principal sulcus, roughly coincident with Brodmann's area 46.

Single-cell recordings in the prefrontal cortex of monkeys have cast light on why neuronal activity here is important to delayed-response performance. The ocular delayed-response task has been widely used in such investigations. Early in each trial, while the monkey is looking at a spot projected in the center of a screen, an image flashes briefly in the periphery of the screen. After the peripheral image has been extinguished the monkey must continue to fixate the central spot until it goes off, which is the instruction to look to the peripheral location where the image had appeared. During the delay period some neurons in the dorsolateral prefrontal cortex are active; these neurons are selective for specific locations. For example, a neuron may fire strongly when the monkey is planning to move to the left but only weakly when movement to the right is planned. This neuronal activity during the delay between a stimulus and the response maintains information on the location of the stimulus after it has vanished.

Is such activity in the prefrontal cortex related specifically to planning movements or to a more general function such as working memory? (Working memory is the ability to hold information in mind and manipulate it mentally, as when dialing a telephone number or doing mental arithmetic.) To answer this question, researchers carried out single-cell recordings in monkeys that had to remember information without planning a specific movement. Under these conditions some prefrontal neurons were active (Figure 18–12), indicating that prefrontal cortex is not concerned exclusively with planning movement. Nevertheless, working memory and executive control of movement may be related because both depend on the ability to retain information over time. Presumably a patient who is sent to buy food but ends up going off with a friend is unable to hold in her mind the plan with which she set out.

- DLPFC
- Primary Sulcus
- Brodmann's Area 46

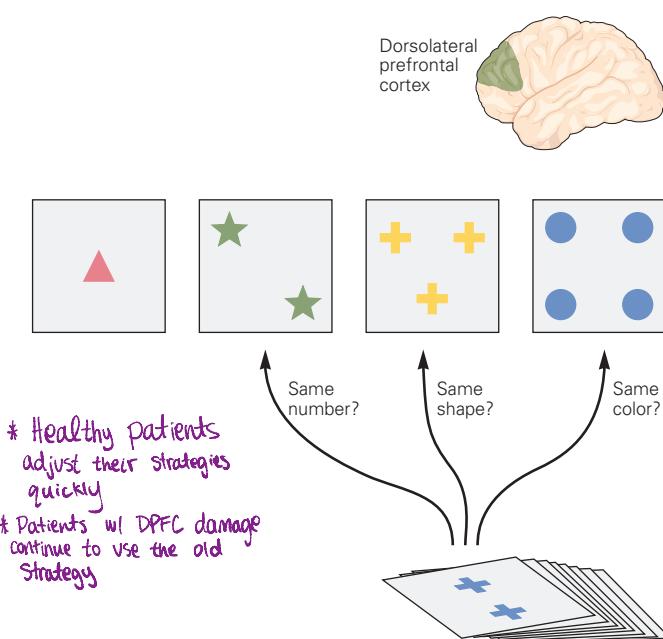


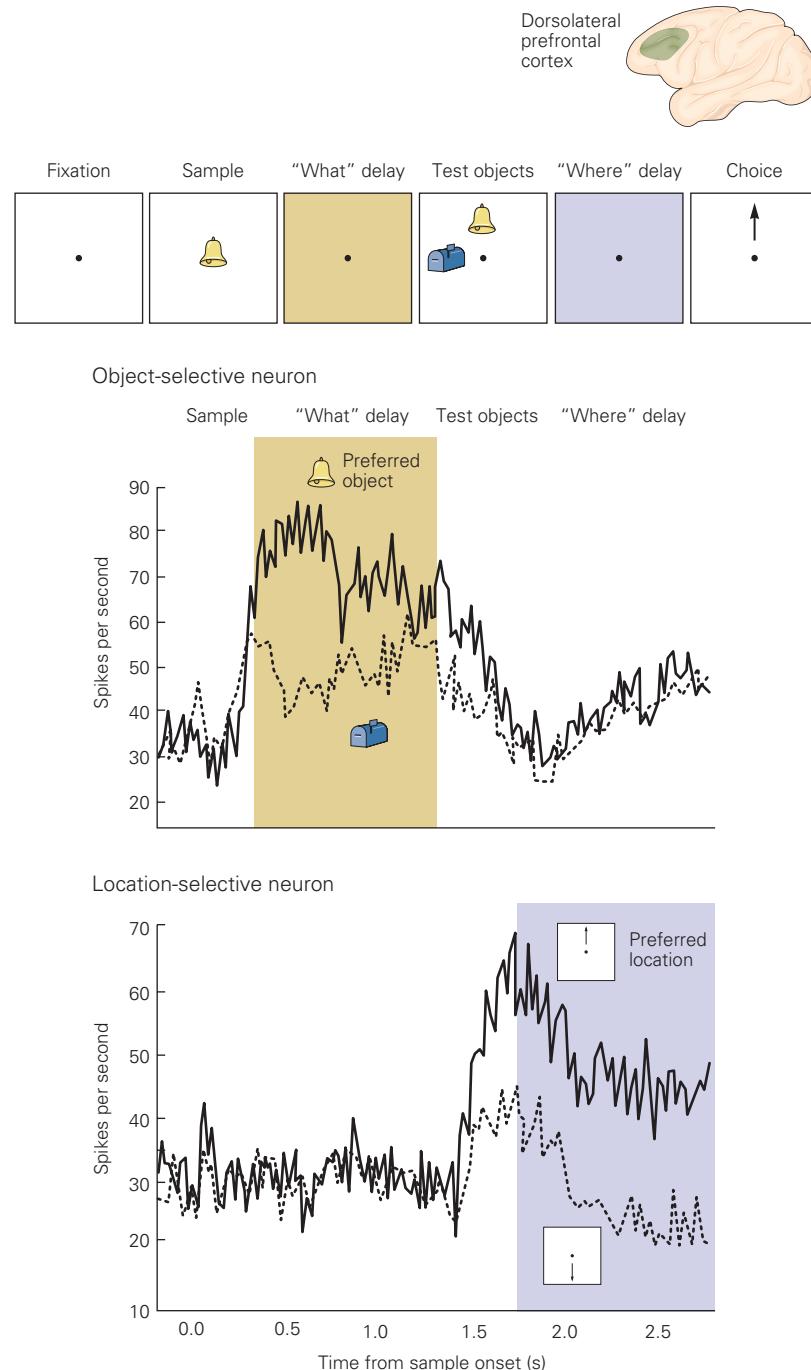
Figure 18–11 The Wisconsin Card Sort Test evaluates cognitive deficits resulting from damage to dorsolateral prefrontal cortex. The patient selects one card at a time from the deck, places it next to one of the samples, and is told whether the choice was correct or incorrect. The patient must determine by trial-and-error whether the correct strategy is to place the card next to the sample with symbols of the same number (two), the same shape (crosses), or the same color (blue). The rule according to which the tester announces choices to be correct or incorrect changes intermittently and without warning. Healthy subjects rapidly adjust their strategy, but patients with prefrontal damage typically continue to use the old strategy long after it has ceased to be effective. (Reproduced, with permission, from Milner and Petrides 1984.)

Orbital-Ventromedial Prefrontal Cortex Contributes to Emotional Control of Behavior

The orbital-ventromedial prefrontal cortex plays a critical role in Goal-Directed behavior because of its

Figure 18–12 Neurons in the dorsolateral prefrontal cortex of a monkey are involved in holding information in working memory. In the experiment illustrated here a trial begins with the monkey looking at a small spot in the center of the screen. Then a sample object (in this case a bell) appears briefly. The screen is then left blank for a period during which the monkey has to fixate a central spot and remember what object was presented (the “what” delay). Two test objects are then displayed at different locations on the screen (in this case the bell at the screen’s top and a mailbox at the screen’s left). The monkey has to recognize the object matching the previous sample (the bell) and note its location at the top of the screen. The display then vanishes and a second delay period ensues during which the monkey has to fixate the spot in the screen center and remember where the matching object was presented (the “where” delay). At the end of the delay four dots are displayed in the periphery and the fixation spot is extinguished. To complete the trial successfully the monkey has to make an eye movement to the dot at the location where the matching object appeared (the top of the screen in this example).

The firing rate of two neurons is shown as a function of time during the trial. During the “what” delay (requiring the monkey to remember what image had been presented) a typical object-selective prefrontal neuron was more active when the monkey was remembering a bell than a mailbox. During the “where” delay (requiring the monkey to remember where to make an eye movement) a typical location-sensitive neuron was more active when the monkey was preparing to shift his gaze upward than downward. (Reproduced, with permission, from Rao et al. 1997.)



connections to three neural systems: (1) It is linked strongly to the hypothalamus and amygdala, subcortical structures that mediate homeostatic drive states such as hunger and thirst and instinctual drive states such as those that underlie fear, aggression, and mating. Through these connections it has access to information about various drives. (2) It receives input from

every sensory system including the gustatory and olfactory systems. Through these inputs it has access to information about objects such as their color, texture, and taste that allow recognition and appropriate emotional responses. (3) It projects to the dorsolateral prefrontal cortex, which in turn projects to premotor cortex. Through this pathway it is in a position to

OVMPFC:

- 1) Linked to hypothalamus/amygdala
- 2) Receives input from all sensory systems
- 3) Projects to DLPFC

trigger appropriate behavior. For example, if hunger were strong and a nearby fruit had the color, texture, and taste of ripeness, then the orbital-ventromedial prefrontal cortex could trigger eating.

In some patients with injury to the orbital-ventromedial prefrontal cortex motivational factors are severely affected although cognitive impairments are relatively minor. One such patient, called EVR, performed at normal or above normal levels on numerous tests of cognitive ability, including the Wisconsin Card Sort Test. Yet in day-to-day life he was incapacitated in part by impaired decision making. His indecisiveness in selecting a restaurant exemplifies the problems that beset him. It could take him hours to choose a

restaurant as he drove to each one and carefully considered the relative merits of the menu, seating plan, and atmosphere.

Patients like EVR fail in clinical tests of decision making as well. In the Gambling Task the participant selects at will one card at a time from any of four decks. With some selections the subject receives a reward, with others a penalty is imposed. The schedule of rewards and penalties is such that decks A and B deliver larger individual rewards but lower net returns. Healthy subjects learn by trial and error to avoid these bad decks and to select from decks C and D instead. EVR showed the opposite pattern, persisting in a losing strategy (Figure 18–13). Presumably he did so because he lacked

Emotional deficits:

- Impaired decision making
- Lack of aversive emotional response to risky/bad situations

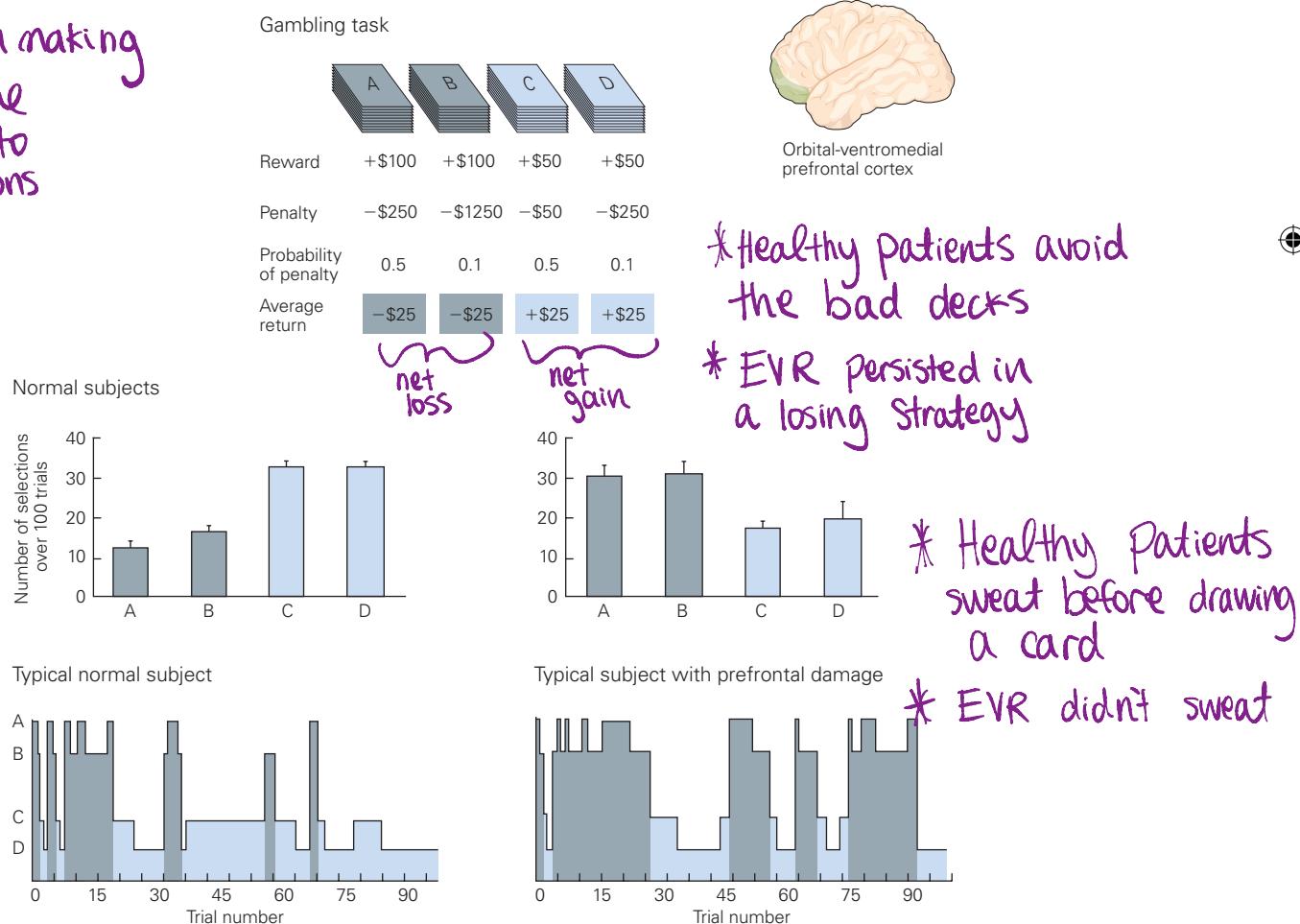


Figure 18–13 Injury to the orbital-ventromedial prefrontal cortex impairs anticipation of the consequences of decisions. This impairment is evident in a gambling task. Choosing cards from two stacks (A and B) leads to a net loss whereas choosing from the other two (C and D) leads to a net gain.

Healthy subjects learn by trial and error to make the majority of their choices from stacks C and D. Patients with damage to the orbital-ventromedial prefrontal cortex do not adjust their strategy over time to maximize the reward. (Reproduced, with permission, from Bechara et al. 1994.)

$\uparrow p \text{ preference} = \uparrow \text{FRs}$

an aversive emotional response to the poor returns of decks A and B. Unlike healthy participants, who show apprehension by sweating when they prepare to take a card from a bad deck, EVR showed no skin conductance response before selecting a card.

Single-neuron recordings in monkeys have shown that orbitofrontal cortex activity reflects the value of anticipated rewards. In a typical testing situation the monkey is seated in front of a pair of levers. A cue presented above one lever tells the monkey what reward

he will receive if he presses the lever. During the delay before the animal is permitted to respond, single neurons in the orbitofrontal cortex fire at a rate that reflects the monkey's preferences: If the animal likes raisins, most of the neurons will fire strongly when the monkey anticipates receiving a raisin (Figure 18–14).

When contextual factors alter the value the monkey attaches to a given food, the rate of neuronal firing in the orbitofrontal cortex shifts to reflect this fact. For example, neuronal responses decline as the monkey

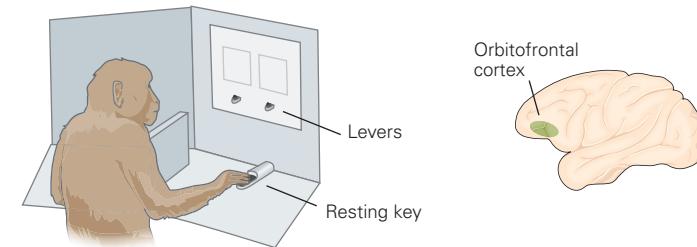
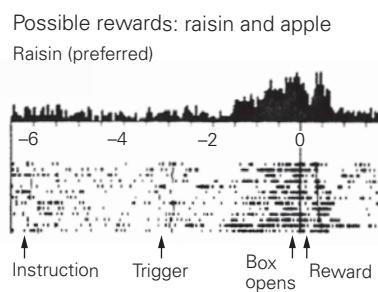
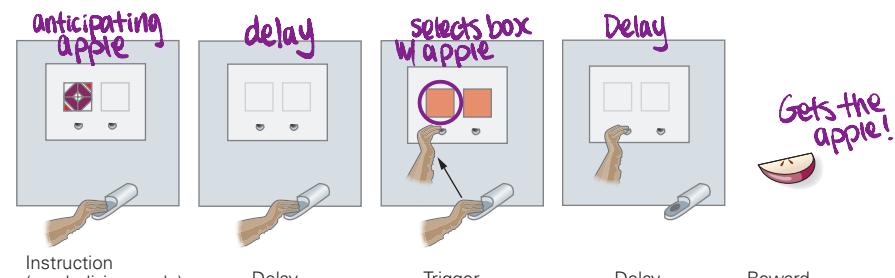


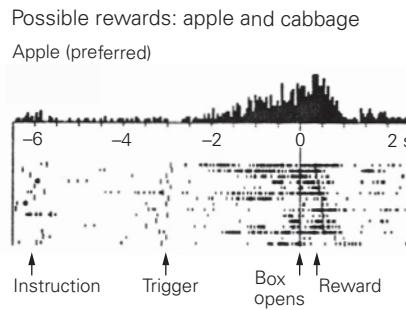
Figure 18–14 Neurons in the orbitofrontal cortex of a monkey signal the subjective value of an expected reward. In the experiment illustrated here the monkey sat facing a display screen with two buttons. He initiated a trial by depressing a lever with his hand. A symbol then appeared above one of the two buttons indicating a particular food would be available by pressing that button (instruction). After a delay a pair of squares appeared (trigger), a cue to the monkey to push one button. After a further delay the door of a food box opened, giving him access to the predicted reward. The histograms are from an orbitofrontal neuron that fired as the time for reward approached but only if the expected reward was the preferred food of a pair of alternatives. The monkey preferred raisins over apples and apples over cabbage (determined by his choices on trials, not shown, when he was allowed to choose between alternatives). Each histogram indicates the average firing rate across many trials. The rows of dots underneath each histogram represent action potentials fired on individual trials. (Reproduced, with permission, from Tremblay and Schultz 1999.)



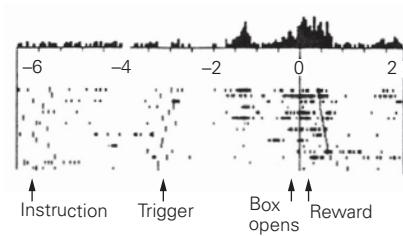
Apple

Without looking at neuronal responses, how do you know a monkey's preferred treat?

Different monkeys like different snacks



Cabbage



Do monkeys actually prefer raisins over apples?

becomes **satiated**. They can also increase or decrease when the subjective value of a given food is increased or decreased by pairing it with alternatives that the monkey likes less or more. A typical neuron fires strongly or weakly when the monkey anticipates a piece of apple, depending on whether the alternative is a less preferred food (a piece of cabbage) or a more preferred food (a raisin). The relation between single-neuron studies in the monkey and clinical observations of patients with orbital-ventromedial prefrontal damage is clear. The **loss of neurons that signal the appetitive value of anticipated rewards might well give rise to decision-making problems such as difficulty in selecting a restaurant.**

Limbic Association Cortex Is a Gateway to the Hippocampal Memory System

The cortex at the edge of the cortical surface forms a ring that is visible in a medial view of the hemisphere. Because it coincides with the edge (or limbus) of the cortical surface this ring is termed the **limbic lobe** or **limbic association cortex** (Figure 18–15).

Several decades ago it was thought that the limbic lobe association cortex, together with a collection of subcortical structures including the amygdala and hypothalamus, formed a unitary system, the “limbic system,” that served homeostatic and instinctual drives (see Chapters 47 and 48). This classic description certainly applies to the orbital and ventromedial prefrontal areas described in the preceding section. These two areas belong to the limbic lobe, are strongly connected to the amygdala and hypothalamus, and contribute to

emotional processes. Other limbic lobe regions, however, are not concerned with emotions. For example, the **hippocampal formation** which is part of the limbic lobe contributes directly to **episodic memory**, a memory more for episodes and events than for emotion.

The hippocampal formation consists of the hippocampus and the **subiculum** to which it is linked. The **hippocampal formation** mediates the formation of long-term memories and is critical for memory consolidation. Injury to it results in **anterograde amnesia**; patients are unable to form new memories but retain old memories. As we shall learn in Chapters 65 and 66, the **hippocampus** is thought to store memories temporarily through long-term synaptic plasticity. The hippocampus then transfers these memories to **neocortex** by inducing a replay in parietal, temporal, and frontal association cortex of activity patterns elicited by recent events. As a result, these cortical areas ultimately form their own stored representations of the events. Memories stored in the cortex are not dependent on the hippocampus and survive its loss.

The other divisions of the limbic lobe (see Figure 18–15) serve as intermediaries between the hippocampal formation and the frontal, parietal, and temporal association areas. Their individual functions are not yet well understood nor is it understood how the functions they serve are different from those of neighboring frontal, parietal, and temporal areas.

An Overall View

The unimodal sensory and motor areas of the cerebral hemisphere occupy only a small part of the cortical sheet. Adjoining and surrounding them are large regions of association cortex where cognitive processes occur. Basic principles governing the organization and operation of association cortex have emerged from comparing the results of human **clinical studies** and physiological and anatomical studies in monkeys.

The **two main principles of cortical organization** are **serial and parallel processing**. In posterior cortex sensory information is extracted in a series of unimodal areas with increasingly complex functions. Each sensory modality (visual, auditory, or somatosensory) is processed in a chain of cortical areas leading outward from the primary sensory area. Parallel dorsal and ventral subdivisions of each hierarchy process aspects of sensory information important for spatial behavior and for stimulus identification. Within each sensory modality, areas that process spatial information form a **dorsal stream** leading to **parietal association cortex** whereas areas that process feature information form a **ventral stream** leading to **temporal association cortex**.

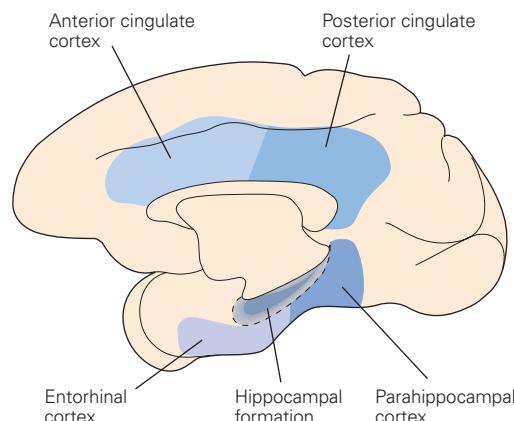


Figure 18–15 The limbic lobe includes the hippocampal formation. The hippocampal formation, including the hippocampus and subiculum complex, plays a decisive role in episodic memory. The functions of the other limbic areas on the medial surface are not well understood.

hippocampal formation
↓
memory for episodes & events

Serial

Parallel

dorsal → Parietal AC → spatial info
Ventral → temporal AC → feature info

*injury to
parietal cortex:
body awareness,
motor control,
visual guidance*

*injury to
temporal lobe:
agnosias,
Wernicke's aphasia,
semantic memory*

*dorsolateral
injury:
disorganized
behavior &
distractibility*

*orbital - VM
PFC injury:
failure to put
value on
expected consequence
of action*

The parietal association cortex, in addition to receiving convergent input from multiple sensory systems, is also strongly linked to motor areas in the dorsal frontal lobe. In humans injury to the parietal cortex results in disorders of body awareness, motor control, visual guidance of behavior, spatial vision, and spatial cognition. In monkeys parietal neurons fire in response to sensory stimuli and during motor behavior; their firing is selective for the spatial attributes of both objects and actions.

The temporal association cortex, in addition to receiving input from multiple sensory systems, is strongly linked to areas in the ventral frontal lobe concerned with emotion and cognition. In humans injury to the temporal lobe creates the agnosias (disorders of recognition), Wernicke's aphasia (a disorder of speech comprehension), and the degradation of semantic memory. Thus the functions of temporal cortex include recognizing things and storing knowledge about them. In monkeys temporal neurons fire in response to sensory stimuli, and their firing is selective for the features of objects that are important for recognition.

The frontal association cortex consists of the dorsolateral and ventromedial prefrontal areas. These areas play a critical role in the executive control of behavior. The dorsolateral prefrontal cortex is important for maintaining intention. In humans injury to this region results in disorganized behavior and distractibility. In monkeys neuronal activity in this region represents working memory or plans of action.

The orbital-ventromedial prefrontal cortex contributes to motivational states by representing the emotional value of objects that might become targets of action. Injury to this cortex in humans results in a failure to place a value on the expected consequences of an action. In monkeys neuronal activity in this region encodes the value of expected rewards.

The limbic association cortex, through its connections with the hippocampus, plays an important role in long-term episodic memory formation.

Carl R. Olson
Carol L. Colby

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