

From Nerve Cells to Cognition: The Internal Cellular Representation Required for Perception and Action

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CONSIDERING THAT THE BRAIN has a hundred billion nerve cells, it is remarkable how much can be learned about mental activity by examining one nerve cell at a time. Progress has been particularly good when we understand the anatomy and the connections of the functionally important pathways. Cellular studies of the sensory systems, for example, provide important insight into how stimuli at the body's surface are translated by the brain into sensations and planned action. Analyses of vision, the sensory modality most thoroughly studied at the cellular level, show that information arrives in the brain from the retina in separate, parallel pathways, each dedicated to analyzing a different aspect of the visual image (form, movement, or color), and that these separate inputs are integrated into coherent images according to the brain's own rules.

Different modalities of perception—an object seen, a face touched, or a melody heard—are processed similarly
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by different sensory systems. Receptors in each system first analyze and deconstruct stimulus information. Receptors at the periphery of the body for each system are sensitive to a particular kind of physical event—light, pressure, tone, or chemical odorants. When a receptor is stimulated—when, for example, a receptor cell in the retina is excited by an image—it responds with a distinct pattern of firing that represents certain properties of the image. Each sensory system obtains information from the stimulus in this way and transmits this information along a pathway of cells leading to a specific region of cerebral cortex. In the cortex different unimodal regions representing different sensory modalities communicate through specific intracortical pathways with multimodal association areas, which select and combine signals into an apparently seamless perception.

The brain thus produces an integrated perception because nerve cells are wired together in precise and orderly ways according to a general plan that does not vary greatly among normal individuals. Nevertheless, the connections are not exactly the same in all individuals. As we shall learn in later chapters, connections between cells can be altered by activity and by learning. We remember specific events because the structure and function of the connections between nerve cells are modified by those events.

Neural scientists believe that a cellular approach is necessary to understand how the brain works. But it is also their conviction that this approach is not sufficient. To understand how people think, behave, feel, and act, it also is essential to understand how the integrative action of the brain—the simultaneous activity of discrete sets of neurons—produces cognition. A combination of methods from a variety of fields—cell biology, systems neural science, brain imaging, cognitive psychology, behavioral neurology, and computer science—has given rise to a functional approach to the brain called *cognitive neural science*.

In this chapter we first discuss the emergence of cognitive neural science as an integrative approach for studying behavior. We then illustrate the success of the approach by considering what has been learned about a complex mental state: the experience, both real and imagined, of the body in space and the space around it. Finally, because such experiences rely on conscious awareness and selective attention, we discuss the feasibility of a scientific approach to understanding consciousness. In subsequent parts of this book we take up in turn the five major areas of cognitive neural science: perception, action, emotion, language, and memory.

The Major Goal of Cognitive Neural Science Is to Study the Neural Representations of Mental Acts

The academic study of normal mental activity was a subfield of philosophy until the end of the nineteenth century, and the chief method for understanding the mind was introspection. By the middle of the nineteenth century this tactic had given way to experimental approaches and eventually the formation of the independent discipline of experimental psychology. In its early years experimental psychology was concerned primarily with the study of sensation: the sequence of events by which a stimulus gives rise to a behavioral response. By the turn of the century the interests of psychologists turned to the behaviors themselves—learning, memory, attention, perception, and voluntary action.

The discovery of simple experimental means for studying learning and memory—first in humans by Hermann Ebbinghaus in 1885, and a few years later in experimental animals by Ivan Pavlov and Edgar Thorndike—led to a rigorous empirical school of psychology called *behaviorism*. Behaviorists, notably J. B. Watson and B. F. Skinner, argued that behavior could be studied with the same precision achieved in the physical sciences but only if students of behavior abandoned speculation about what goes on in the mind (the brain) and focused instead on *observable* aspects of behavior. For behaviorists, unobservable mental processes, especially anything as abstract as conscious awareness, was simply deemed inaccessible to scientific study. Instead, they concentrated on evaluating—objectively and precisely—the relationship between specific physical stimuli and observable responses in intact animals. Their early successes in rigorously studying simple forms of behavior and learning encouraged them to treat all processes that intervene between the stimulus (input) and behavior (output) as *irrelevant* to a scientific study of behavior.

Thus, behaviorism largely ignored mental processes. In fact, during behaviorism's most influential period, the 1950s, many psychologists accepted the most radical behaviorist position, that observable behavior is *all* there is to mental life. As a result, the scientific concept of behavior was largely defined in terms of the limited techniques used to study it. This emphasis reduced the domain of experimental psychology to a restricted set of problems, and it excluded from study some of the most fascinating features of mental life.

Therefore it was not difficult in the 1960s for the founders of *cognitive psychology*—Frederick Bartlett, Edwin Tolman, George Miller, Noam Chomsky, Ulric
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Neisser, Herbert Simon, and others—to convince the scientific community of the narrowness of behaviorism. These early cognitive psychologists, building on the evidence from Gestalt psychology, psychoanalysis, and European neurology, sought to demonstrate that our knowledge of the world is based on our biological apparatus for perceiving the world, that perception is a *constructive* process that depends not only on the information inherent in a stimulus but also on the mental structure of the perceiver.

Thus, cognitive psychology is concerned not simply with specifying the input and output for a particular behavior, but also with analyzing the process by which sensory information is transformed into perception and action—that is, with evaluating how a stimulus leads to a particular behavioral response. Only in this way, cognitive psychologists argue, can we hope to understand the relationship between a person's actions and what that person sees, remembers, or believes. It is now clear that the behavior studied by behaviorists was largely restricted to simple reflex actions that do not require conscious mental activity. Any approach to the study of more complex behavior that fails to address mental activity is simply inadequate to account for all but the simplest components of behavior.

In redirecting scientific attention to complex mental operations, cognitive psychologists have focused on *information processing*, on the flow of sensory information from sensory receptors to its eventual use in memory and action. The cognitive approach to behavior assumes that each perceptual or motor act has an *internal representation* in the brain. Since the brain is a physical organ, an internal representation for a perceptual or motor act must have the form of a distinctive pattern of neural activity in a specific set of interconnected nerve cells that encodes the percept or the action. Looked at in this way, an internal representation is a neural representation: a representation of neural activity.

An empirical approach to internal representations, which looks at them as neural representations, has not been without its own problems, however. Once psychologists acknowledged that internal representations are an essential component of behavior, they had to come to terms with the serious problem that most mental processes are still largely inaccessible to experimental analysis. Without direct access to the neural substrates of internal representations it is difficult, if not impossible, to distinguish between rival theories. Fortunately, significant progress in the cellular analysis of the visual, somatosensory, and motor systems in intact behaving primates has allowed a beginning in the neurobiological analysis of mental processes. We now know how neural activity in different sensory and motor pathways encodes different sensory stimuli and planned actions. As we saw in [Chapter 19](#), sophisticated radiological imaging methods also permit direct visualization of the various regions of active human brain pathways in controlled behavioral experiments. By comparing the results of cellular recordings in primates with imaging in humans, we now have the power to study directly the neural representation of sensory stimuli and motor actions.

Cognitive Neural Science Integrates Five Major Approaches to the Study of Cognitive Function

Cognitive neural science is an integrative approach to the study of mental activity that emerged from five major technical and conceptual developments. First, in the 1960s and 1970s techniques for studying the activity of single cells in the brains of intact and behaving animals, including primates, were developed by Ed Evarts and by Vernon Mountcastle. Soon these techniques were used to correlate the actions of individual cells under controlled behavioral conditions. It then also became possible to stimulate small groups of cells and to increase their activity or to lesion them so as to reduce their activity. By correlating individual cells with behavior, seeing the effects of introducing activity (stimulation) and reducing activity (lesion), these studies made it possible to examine perceptual and motor processes at the cellular level while animals were engaged in typical sensory or motor behaviors. As a result, we know that the mechanisms of perception are much the same in humans and monkeys and other simpler animals.

Second, cellular studies in monkeys also led to the ability to correlate the patterns of firing of individual cells in specific brain regions with higher cognitive processes, such as attention and decision making. This changed the way behavior is studied in both experimental animals and humans. Unlike the behaviorists, we no longer focus only on the stimulus response properties of behavior; instead, we focus on the information processing in the brain that leads to a behavior.

Third, developments in systems neural science and cognitive psychology stimulated a renewed interest in the behavioral analysis of patients with lesions of the brain that interfere with mental functioning. This field had remained strong in Europe but was neglected in the United States. Patients with lesions of specific regions of the brain exhibit quite specific cognitive deficits. The behavioral consequences of brain lesions thus tell us much

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about the function of specific areas and pathways in the brain. Lesion studies have shown that cognition is not a unitary process but that there are several cognitive systems, each with many independent information-processing modules. For example, the visual system, a prototype of a cognitive system concerned with sensory perception, has specialized pathways for processing information about color, form, and movement.

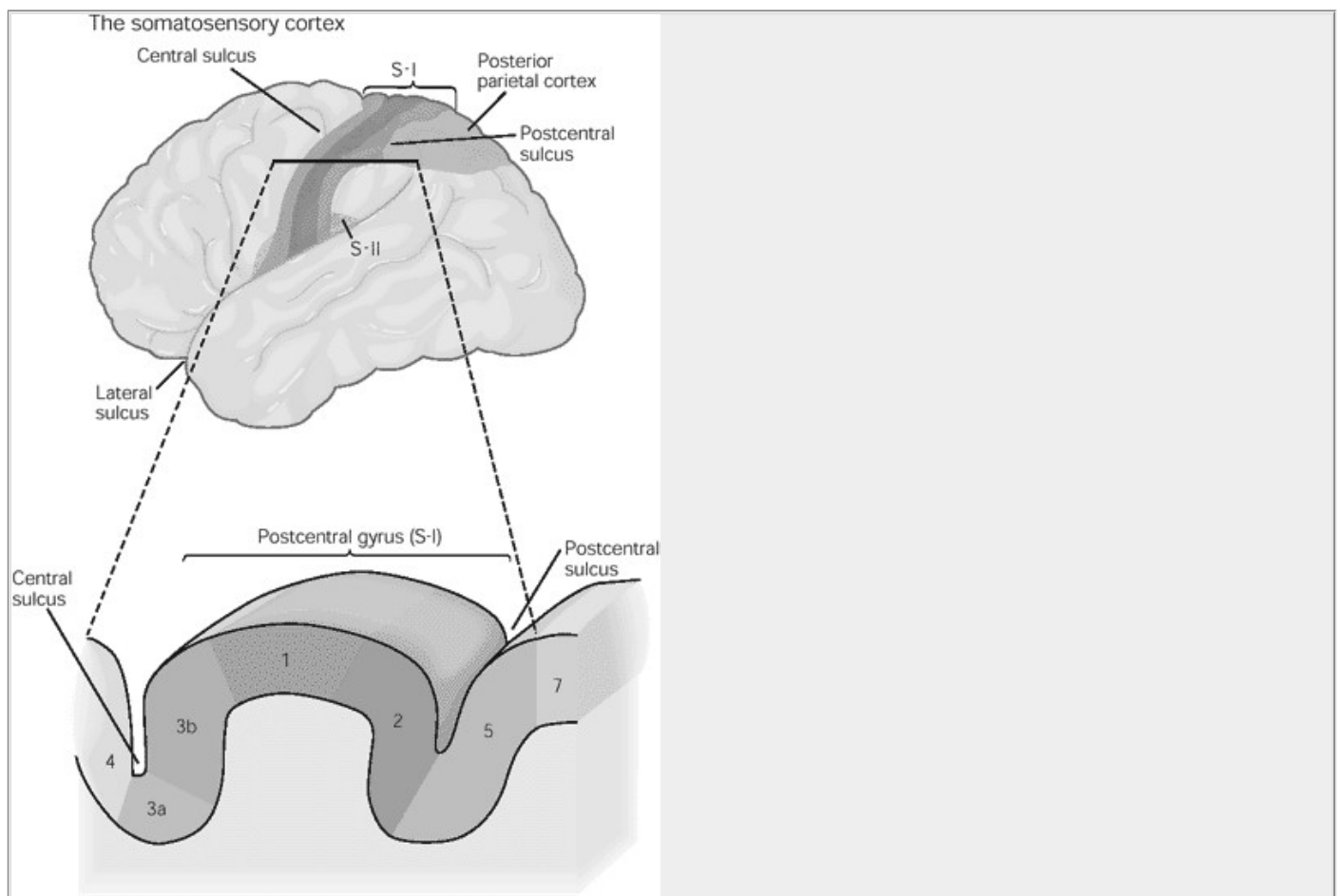


Figure 20-1 The neural architecture of the somatosensory system.

Top: A lateral view of a cerebral hemisphere illustrates the location of the primary somatic sensory cortices in the parietal lobe. The somatic sensory cortex has three major divisions: the primary (S-I) and secondary (S-II) somatosensory cortices and the posterior parietal cortex. The relationship of S-I to S-II and to the posterior parietal cortex is seen best from a lateral perspective of the surface of the cerebral cortex. **Bottom:** A section shows the four distinct cytoarchitectonic regions of S-I (Brodmann's areas 3a, 3b, 1, and 2) and their spatial relationship to area 4 of the motor cortex and areas 5 and 7 of the posterior parietal cortex.

Fourth, new radiological imaging techniques—positron emission tomography (PET), magnetic resonance imaging (MRI), magnetoencephalography, and voltage-sensitive dyes—have made it possible to relate changes in activity in entire populations of neurons to specific mental acts in living humans (see Chapter 19).

Finally, computer science has made a distinctive contribution to cognitive neural science. Computers have made it possible to model the activity of large populations of neurons and to begin to test ideas about the role of specific components of the brain in particular behaviors. To understand the neural organization of a complex behavior such as speech, we must understand not only the properties of individual cells and pathways but also the *network properties* of functional circuits in the brain. Network properties, although dependent on the properties of individual neurons in the network, need not be identical or even similar to the properties of individual cells in the network. Computational approaches, especially when combined with *psychophysics*, the analysis of the relationship between the physical attributes of a stimulus and perception, are helpful in characterizing the system as whole, in specifying what the system is capable of doing, and in determining how the properties of the constituent cells account for system properties.

To illustrate a cognitive neural science approach to a particular problem in cognition, we consider in this chapter how objects accessible to touch are represented internally (neurally). We shall begin with the representation of *personal space*, the neural representation of the body surface. We examine how this representation arises in primary and higher-order somatosensory cortices from a map of the tactile sensibilities of the body surface, and how modification of this map by the loss of a body part can create a phantom representation. We also consider how representations of personal space are elaborated in unimodal and multimodal association cortices into a more complex *peripersonal space*, the space within arm's reach, and *extrapersonal space*, the larger environment around the body. Finally, we consider how representations of spatial relations in the association cortex of the posterior parietal lobe can give rise to *imagined* and *remembered space*.

The Brain Has an Orderly Representation of Personal Space That Can Be Studied on the Cellular Level

When we say internal representations are neural representations, it is important to note that the term "neural representation" is used in two ways. First, the term can refer simply to the anatomical organization of afferent sensory pathways in the cerebral cortex, ie, to the fact

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that afferent fibers throughout each sensory system are arranged to form topographic maps of the receptor surface. Second, the term can refer to the more complex and conceptual case of the cortical representation of the space surrounding the body. Here the representation is not topographical but dynamic, and the representation is encoded in the pattern of firing of cells that need not have any specific topographic relation to one another with respect to the receptor surface.

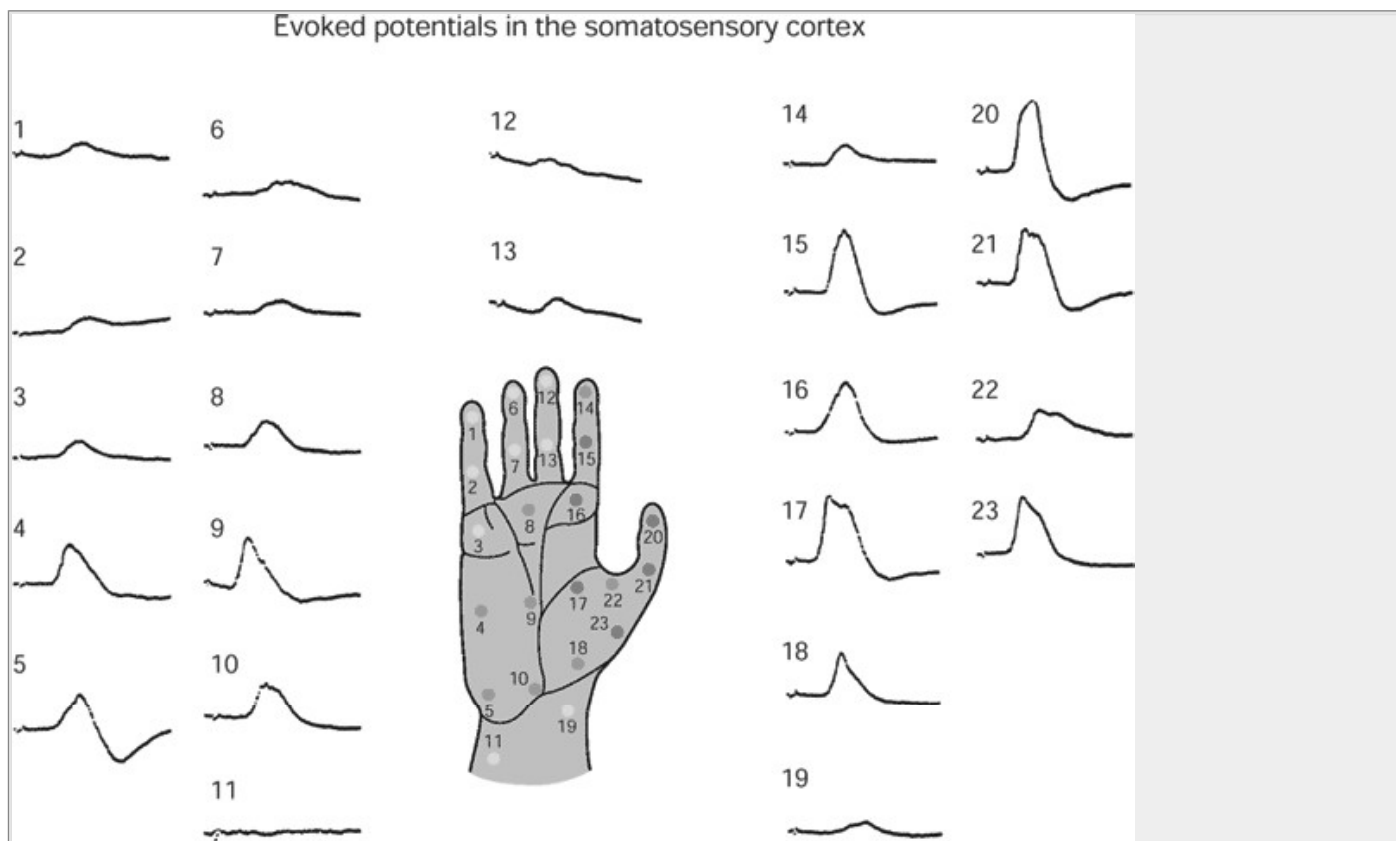


Figure 20-2 The first maps of neural representation of specific areas of the body in the somatosensory cortex were based on patterns of evoked potentials. This figure shows the evoked potentials of one large group of neurons in the left postcentral gyrus of a monkey elicited by a light tactile stimulus applied to different points on the right palm. The evoked potentials are strongest when the stimulus is applied to the thumb and forefinger (points 15, 16, 17, 20, 21, and 23). They are weakest when the stimulus is applied to the middle or the small finger (points 1, 2, 3, 12, and 13). (Adapted from Marshall et al. 1941.)

Perhaps the simplest examples of internal representations are those of the body surface (personal space). This has been extensively explored in the study of

touch and proprioception, two modalities mediated by the somatic sensory system. Touch provides us with information about our body surface as well as the properties of objects, such as their shape, texture, and solidity (see [Chapter 23](#)). Proprioception provides us with information on the static position and movement of our fingers and limbs (see [Chapter 23](#)).

In the case of touch, primary sensory neurons with receptors in the skin translate stimulus energy into neural events that initiate activity in precise pathways that include several processing stages before they terminate in the somatosensory areas of the parietal lobe of the cerebral cortex. At each processing stage in the somatosensory system—where afferent axons terminate on the cells of a nucleus—the arrangement of the inputs preserves the spatial relations of the receptors on the body surface. This topographic constancy thus creates a *neural map* of the body surface at each processing point in the somatosensory system so that neighborhood relations are preserved: information from receptors that are close to each other in the skin is conveyed to neighboring cells in each relay. In this way each bit of information in each relay is associated with activity in a specific point on the body.

Neural maps of the body surface were first obtained using gross recording and stimulation techniques on the surface of the postcentral gyrus, which was the only portion of the brain readily accessible to experimentation with the techniques available ([Figure 20-1](#)). In the late 1930s Wade Marshall found that he could produce an *evoked potential* in the cortex ([Figure 20-2](#)) by touching a specific part of the animal's body surface. Evoked potentials are recorded electrical signals that represent the summed activity of thousands of cells and are often obtained by using macroelectrodes. The evoked response method was used by Marshall, Clinton Woolsey, and

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Philip Bard to map the neural representation of the body surface in the postcentral gyrus of monkeys ([Figure 20-3](#)).

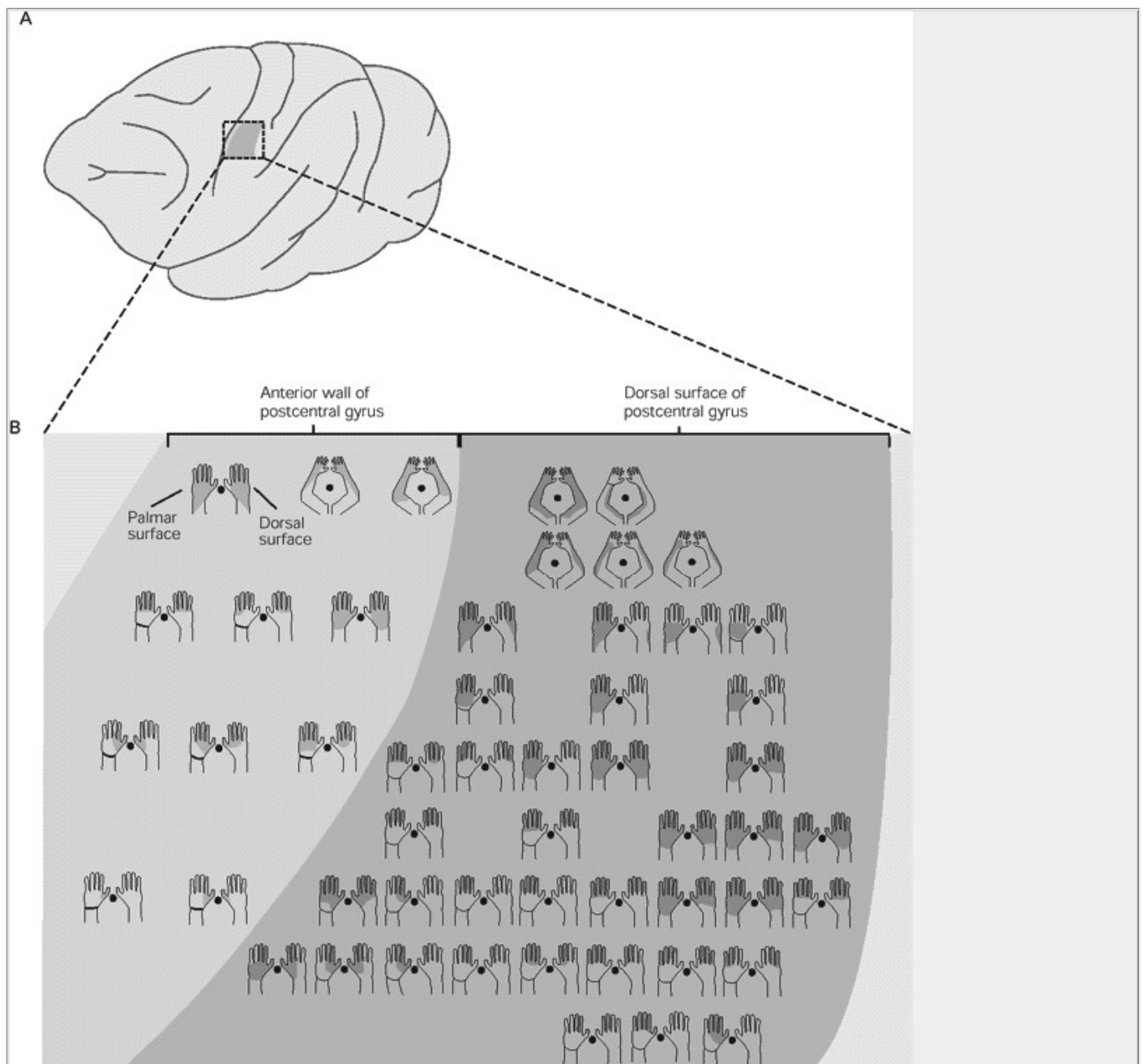


Figure 20-3 An early map of cortical responses to tactile stimulation in monkeys.

Recordings were made in the primary somatic sensory cortex (S-I). The lateral view of the brain shows the recording site (**A**). Two maps show the sites (**black dots**) in Brodmann's areas 3a and 1 that responded to stimulation of the palmar and dorsal surfaces of the right hand (**B**). At each site the **colored areas** of the hand indicate areas of stimulation that evoke a response at that site. The sites on the left side of the figure are in the anterior wall of the postcentral gyrus, corresponding roughly to areas 3b and 3a in S-I. The sites on the right side of the figure are on the dorsal surface of the postcentral gyrus, corresponding roughly to area 1 in S-I. (Adapted from [Marshall et al. 1941.](#))

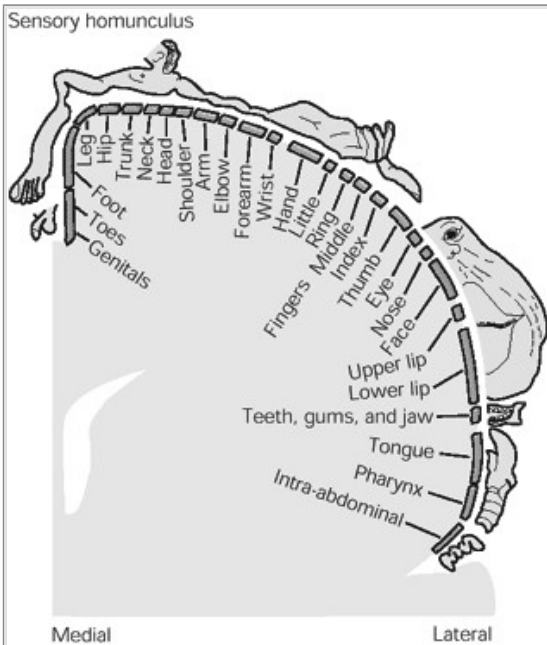


Figure 20-4 Somatic sensory and motor projections from and to the body surface and muscle are arranged in an orderly way in the cortex. The sensory map illustrated here is for Brodmann's area 1 in the postcentral gyrus of the parietal cortex. Each area within the somatosensory cortex (areas 3a, 3b, 1, and 2) contains a full representation of the body (see Figure 20-5). Parts of the body that are important for tactile discrimination, such as the tip of the tongue, the fingers, and the hand, have disproportionately large representations reflecting greater degrees of innervation. (Adapted from Penfield and Rasmussen 1950.)

The human somatosensory cortex was similarly mapped by the neurosurgeon Wilder Penfield during operations for epilepsy and other brain disorders. Working with locally anesthetized patients, Penfield stimulated various points in the primary somatosensory cortex (on the surface of the postcentral gyrus) and asked the patients what they felt. (This procedure is necessary to ascertain where the epilepsy started and therefore to avoid unnecessary damage to normal brain tissue during surgery.) Penfield found that stimulation of specific populations of cells in the postcentral gyrus served as a reasonable simulation of natural activation of these populations, producing tactile sensations in discrete parts of the opposite side of the body. From these studies Penfield constructed a map of the neural representation of the body in the primary somatosensory cortex of humans that was homologous to that obtained by Marshall, Woolsey, and Bard for the monkey.

As shown in Figure 20-4, in humans the leg is represented most medially at the crown of the skull, followed by the trunk, arms, face, and finally, most laterally (near the ear), the teeth, tongue, and esophagus. Note that in Figure 20-4 each part of the body is drawn in proportion to its relative importance in sensory perception. The face is large compared with the back of the head; the index finger is gigantic compared with the big toe, and the torso has the smallest area of all. This distortion reflects differences in innervation density in different areas of the body. Similar distortions are observed in the body representations of other animals. In rabbits, for example, the face and snout have the largest representation because they are the primary way a rabbit explores its environment (Figure 20-5).

The Cortex Has a Map of the Body for Each Submodality of Sensation

The early efforts at constructing a somatosensory map of the cortex probed only a limited area of the post-central gyrus using techniques that had poor spatial resolution. This work led to the conclusion that there was a single large representation of the body surface in the cortex. Later studies, using microelectrodes to record the responses of individual cortical neurons, revealed that there are actually four fairly complete maps in the primary somatosensory cortex, one each in Brodmann areas 3a, 3b, 1, and 2 (Figure 20-6).

Although each of the areas has essentially the same body map, each represents different types of information. Sensory information from muscles and joints, important for limb proprioception, is represented in area 3a. Information from the skin, important for touch, is represented in area 3b. This information from the skin is further processed within area 1 and then combined with information from muscles and joints in area 2. This explains why a small discrete lesion in area 1 impairs tactile discrimination, whereas a small lesion in area 2 impairs the ability to recognize the size and shape of a grasped object.

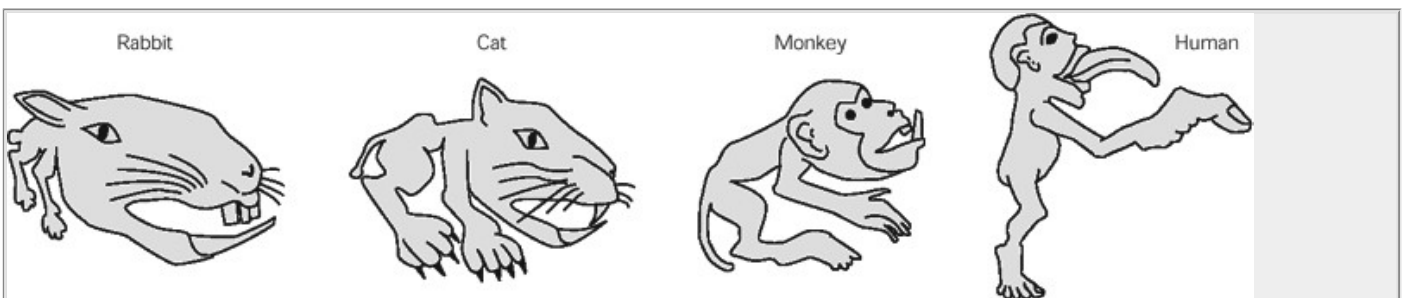


Figure 20-5 Different species rely on different parts of the body for adaptive somatosensory information. These drawings show the relative importance of body regions in the somatic sensibilities of four species, based on studies of evoked potentials in the thalamus and cortex.

The Orderliness of the Cortical Maps of the Body Is the Basis of the Accuracy of Clinical Neurological Examinations

The precision of the brain's sensorial map of the body surface, its map to the retina, the cochlea, and the olfactory epithelium (Figure 20-4), and its parallel motor map explains why clinical neurology has long been an accurate diagnostic discipline, even though for many decades it relied on only the simplest tools—a wad of cotton, a safety pin, a tuning fork, and a reflex hammer. Disturbances within the somatic sensory system can be located with remarkable accuracy because there is a direct relationship between the anatomical organization of the functional pathways in the brain and specific perceptual and motor behaviors.

A dramatic example of this relationship is the Jacksonian march, a characteristic sensory seizure first described by the neurologist John Hughlings Jackson. In this type of epileptic attack the numbness and paresthesia (inappropriate sensations such as burning or prickling) begin in one place and spread throughout the body. For example, numbness might begin at the fingertips, spread to the hand, up the arm, across the shoulder, into the back, and down the leg on the same side. This sequence is explained by the arrangement of inputs from the body in the somatosensory cortex; the seizure starts in the lateral region of the cortex, in the area where the hand is represented, and propagates across the cortex toward the midline (see Figure 20-4).

The Internal Representation of Personal Space Is Modifiable by Experience

Until recently it was simply assumed that the cortical maps of the body surface were hard wired, that the pathways from the receptors in the skin to the cortex were fixed early in development. But the cortical maps do change, even in adults, with the use of the afferent pathways. Two studies were particularly important in demonstrating this. First, a study of normal animals showed that the details of topographic maps vary considerably from one individual to another. Since this study did not separate the effects of experience from genetic endowment, a second set of experiments was carried out to determine the relative contributions of genes and experience to this variability.

In this experiment monkeys were trained to touch a rotating disk with the tips of the middle finger to obtain food pellets. After several months of touching the disk, the area in the cortex devoted to the tips of these middle fingers was greatly expanded at the expense of the adjacent proximal phalanges, which did not contact the moving surface. These results suggest that use of the finger tips strengthens the connections, somewhere along the somatosensory pathway, between the stimulated skin regions and the cortex (Figure 20-7).

Intense use or disuse produces even more dramatic changes in these connections. Several monkeys have been studied 10 years or more after an upper limb was completely deafferented by severing all sensory nerves serving the arm. In all of these monkeys the cortical representation of the face (where innervation remained intact) has expanded into the adjacent area that had represented the hand before deafferentation, so now stimulation of the face evokes responses in the area that normally represents the hand. These changes occur over a wide area of cortex: In fully one third of the map devoted to the body surface, an area of about 10 mm of cortex, the connections representing the hands and arms have been replaced by those representing the face.

What mechanisms underlie these changes? Recent evidence suggests that afferent connections to neurons in the somatic sensory cortex are formed on the basis of correlated firing. It is thought that cells that fire together wire together! Michael Merzenich and his colleagues tested this idea by surgically connecting the skin surfaces of the fingers of two adjacent digits on the hand of

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a monkey. This procedure ensures that the connected fingers are always used together and therefore increases the correlation of inputs from the skin surfaces of the adjacent fingers. Increasing the correlation of activity from adjacent fingers in this way abolishes the sharp discontinuity normally evident between the zones in the somatosensory cortex that receive inputs from these digits (Figure 20-8). Thus, the demarcation in the pattern of connections not only is genetically programmed, but also develops normally through learning, by temporal correlations in patterns of input.

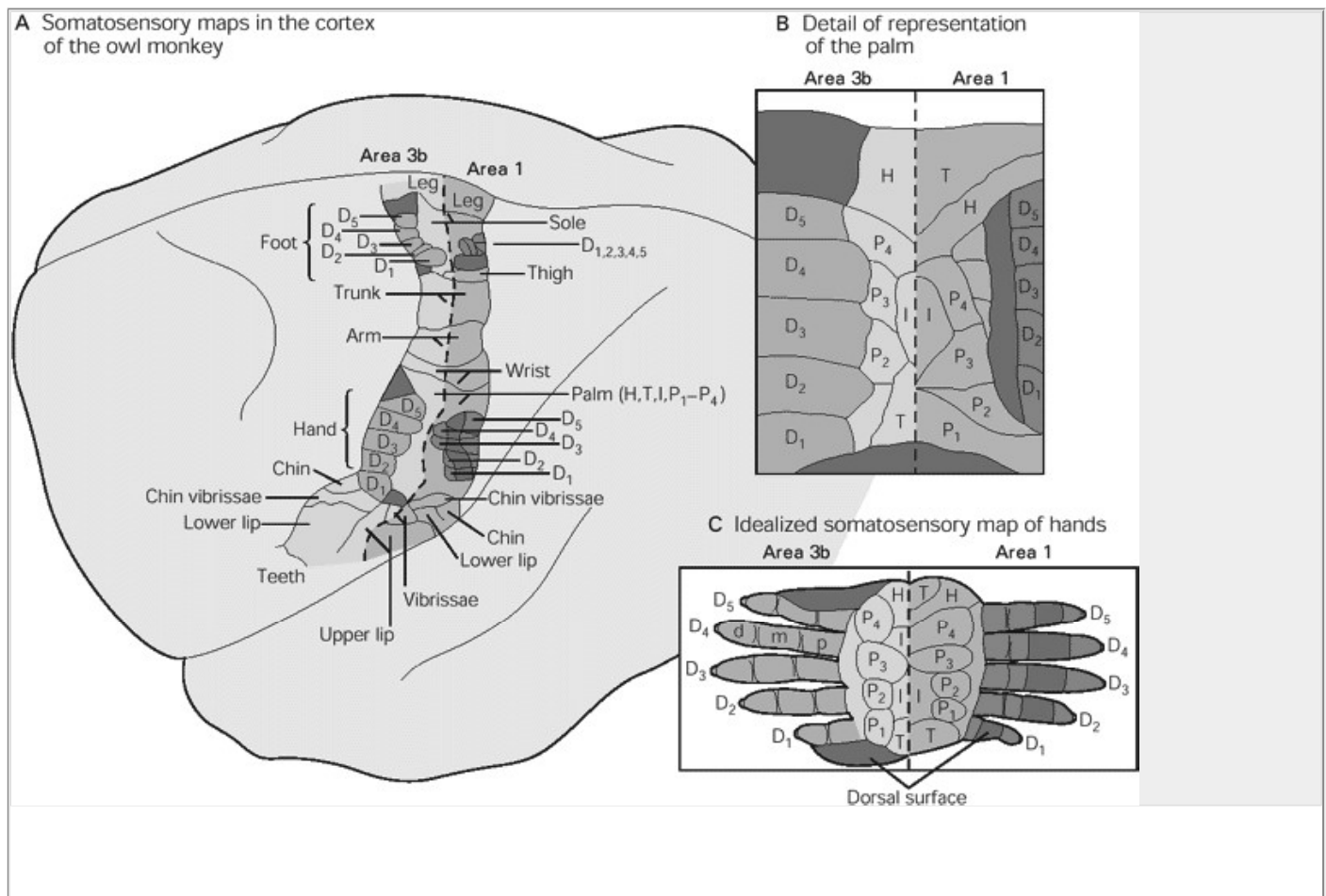


Figure 20-6 Each of the four areas of the primary somatic sensory cortex (Brodmann's areas 3a, 3b, 1, and 2) has its own complete representation of the body surface. (Adapted from Kaas et al. 1981.)

- A.** Somatosensory maps in areas 3b and 1 are shown in this dorsolateral view of the brain of an owl monkey. The two maps are roughly mirror images. Each digit of the hands and feet is individually represented (**D₁** to **D₅**).
- B.** A more detailed illustration of the representation of the glabrous pads of the palm in areas 3b and 1. These include the palmar pads (numbered in order, **P₄** to **P₁**), two insular pads (**I**), two hypothenar pads (**H**), and two thenar pads (**T**).
- C.** An idealized map of the hands based on studies of a large number of monkeys. The representations of the palm and digits reflect the extent of innervation of each palmar area in the cortex. The five digital pads (**D₁** to **D₅**) include distal, middle, and proximal segments (**d**, **m**, **p**).

The Cortical Representation of the Human Hand Area Can Be Modified

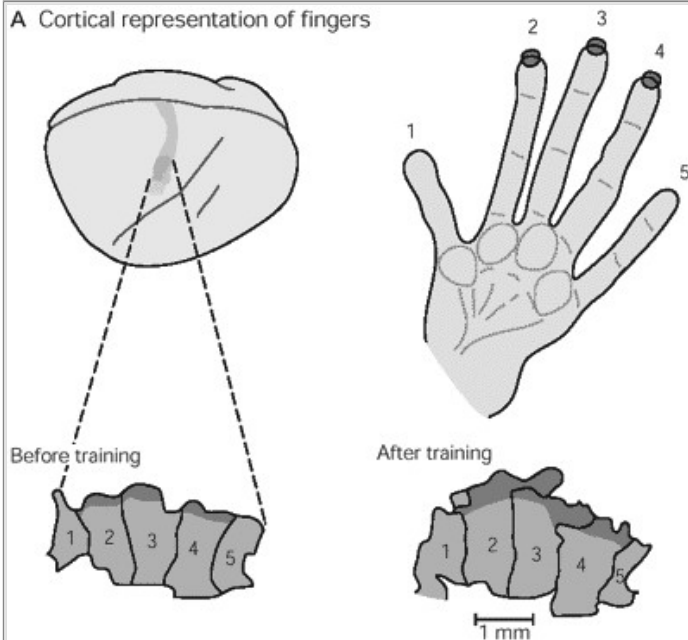
Does reorganization of afferent fibers also occur in the human brain? Magnetoencephalography can now be used to construct functional maps of the hand in normal subjects with a precision of millimeters. This imaging technique has been used to compare the hand area in the cortex of normal adult humans to that of patients with a congenital fusion of the fingers (syndactyly). Patients with this syndrome do not have individual fingers—their hand is much like a fist—so that neural activity in one part of the hand is always correlated with activity in all other parts of the hand. The size of the representation in the cortex of the syndactylic hand is considerably less than that of a normal person, and within this shrunken representation the fingers are not organized somatotopically, as are separate fingers (Figure 20-9).

When the fingers of one patient were surgically separated, however, each of the newly separate fingers became individually represented in the cortex within weeks. The new representation of the hand occupied

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3–9 mm of cortex, almost corresponding to the normal representation of the hand and the normal distance between each digit (Figure 20-10).

A Cortical representation of fingers



B Cortical receptive fields of fingers

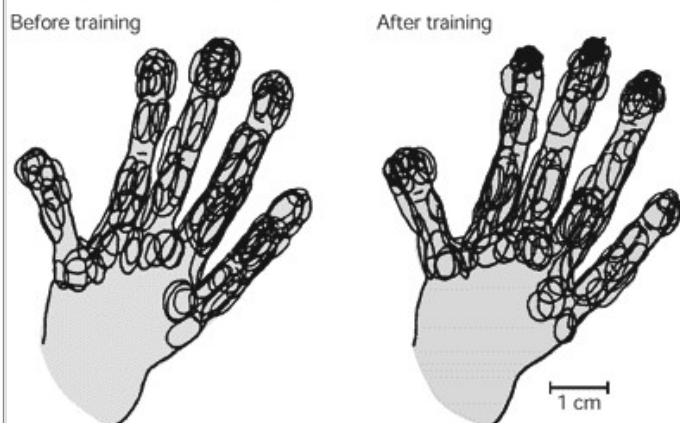


Figure 20-7 Increased use of selected fingers enlarges the cortical representation of those fingers. (Adapted from Jenkins et al. 1990).

A. The regions in cortical area 3b representing the surfaces of the digits of an adult monkey are shown before training and after training. During the period of training the monkey performed a task that required repeated use, for one hour per day, of the tips of the distal phalanges of digits 2, 3, and occasionally 4. There is a substantial enlargement of the cortical representation of the stimulated fingers after training (**brown**).

B. Cells with receptive fields on the surfaces of the digits were identified before and after training. The receptive field for a cortical neuron is the area on the skin where a tactile stimulation either excites or inhibits a cell. After training, the number of receptive fields in the distal phalanges of digits 2, 3, and 4 is larger than before learning (as indicated by the denser outlines).

The Phantom Limb Syndrome May Result From Rearrangements of Cortical Inputs

Many patients with amputated limbs continue to have a vivid sensory experience of the missing limb, a phenomenon known as the *phantom limb syndrome*. The patient senses the presence of the missing limb, feels it move around, and even feels it try to shake hands when greeting someone. People often feel terrible pain in the phantom limb. Phantom limb sensation and the pain associated with it have been attributed to impulses entering the spinal cord from the scar of nervous tissue in the stump. In fact, removing the scar or cutting the sensory nerves just above it does relieve pain in some cases.

However, recent imaging studies by Vilgancer Ramachandran of the somatosensory cortex of patients who have lost a hand suggest another explanation for phantom limb sensations. These studies show that phantom sensations are due to a rearrangement of cortical circuits. The afferent pathways adjacent to the area normally occupied by afferents from the hand expands into the latter area, just as they do in monkeys with deafferented limbs. More than half a dozen patients have now been examined, and in all of them the area of cortex that represented the hand before amputation now receives afferents from at least one other site on the skin. Ramachandran has called this *remapping of referred sensations*. These referred sensations are not distributed randomly on the body. Some of the patients have two sites of referred sensation of the lost hand, one on the face and two on the upper arm (Figure 20-11).

These referred sensations are entirely predictable from the fact that afferents from the face and upper arm, which normally lie next to those from the hand, now occupy the cortical territory previously occupied by the afferents from the amputated hand. Magneto-encephalography has been used to map the inputs to the cortex from the face, hand, and foot of some of these patients. In each there is a precise, direct correspondence between a point on the face and an individual digit (Figure 20-11A). In normal individuals afferents from an intact hand are situated between those of the face and foot. However, in the hemisphere representing the amputated limb the areas representing the face and foot abut each other in the region that formerly represented the hand. Thus, touch receptors in the face form connections with neurons in the cortex normally contacted by receptors in the missing hand.

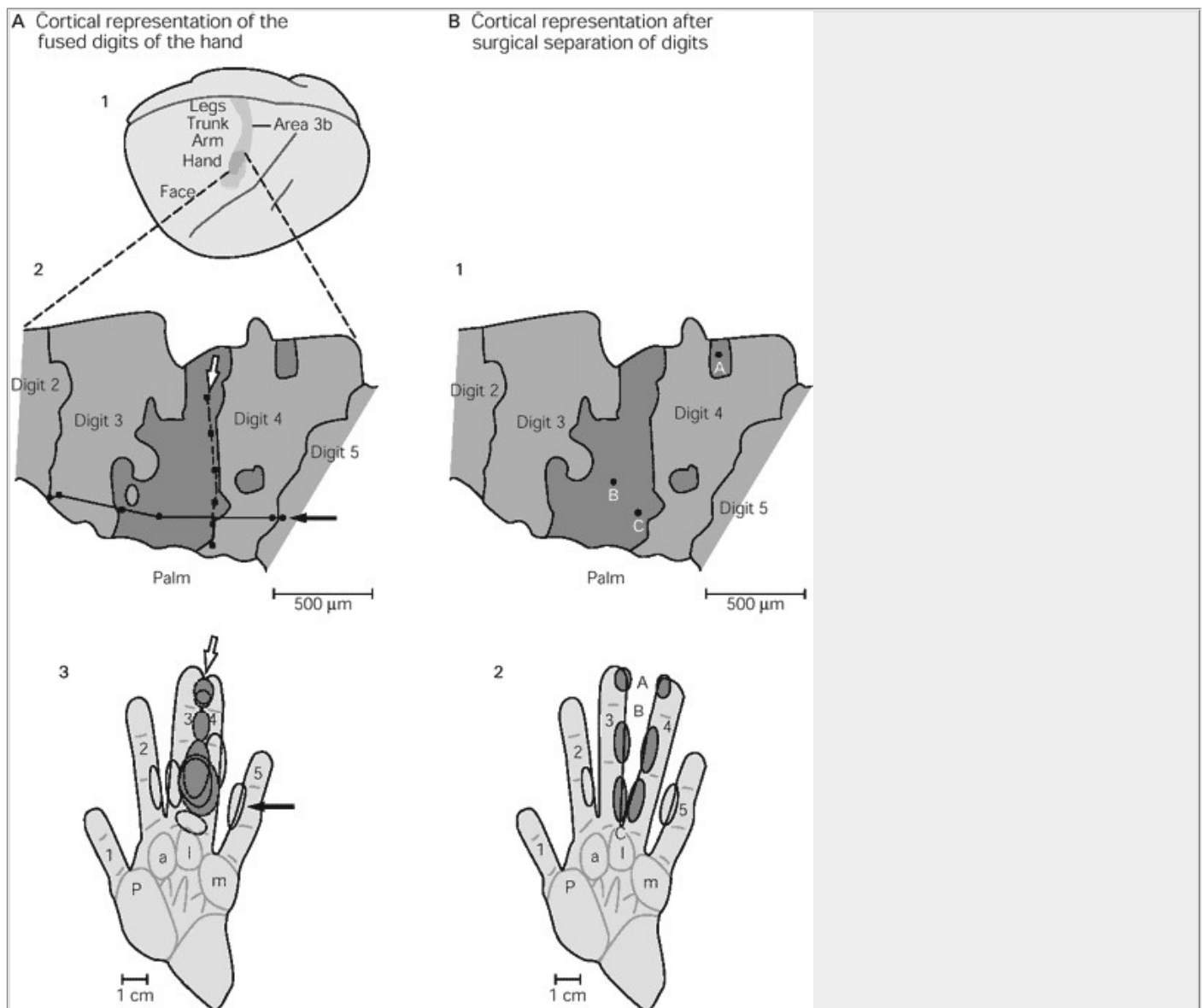


Figure 20-8 The normal discontinuities in the cortical representation of the digits of an adult owl monkey become blurred after surgical fusion of the digits. (Adapted from Clark et al. 1988.)

A. 1. A dorsolateral view of the cortex of an owl monkey shows the representation of the animal's body in area 3b of the primary somatosensory cortex. **2.** This detailed drawing of portions of the representation of the hand shows the areas for digits 3 and 4 and surrounding skin surfaces 5.5 months after surgical fusion of these digits. The areas of representation that changed after digit fusion are indicated in **brown**. Instead of the normal discontinuity between the two digits, 3 and 4, a large common area (340-1000 μm in width) now represents the parts of the digits that are fused. Stimulation of the surface of either one of the two fused digits evokes responses in cortical cells within this zone. In contrast, the discontinuity in the areas representing the fused digits and the two adjacent free digits (2 and 5) remains sharp. Evoked potentials were obtained in two series of sites corresponding to sequential stimulation of the digits in two axes: a rostral-to-caudal axis (**dashed line**) and medial-to-lateral (**solid line**). **3.** The receptive fields for the neurons at the recording sites shown in part 2. The **solid** and **white arrows** indicate sequences of stimulation corresponding to the sequences of recording sites shown in part 2.

B. Even after the fused digits are separated, the common area of representation remains. Thus, the intermingling of the representation of digits 3 and 4 is achieved centrally and does not result from peripheral regeneration that spares the site of contact. Evoked potentials were obtained at points A, B, and C in area 3b of the cortex (**1**) by stimulation of digits 3 and 4 at discrete sites (**2**).

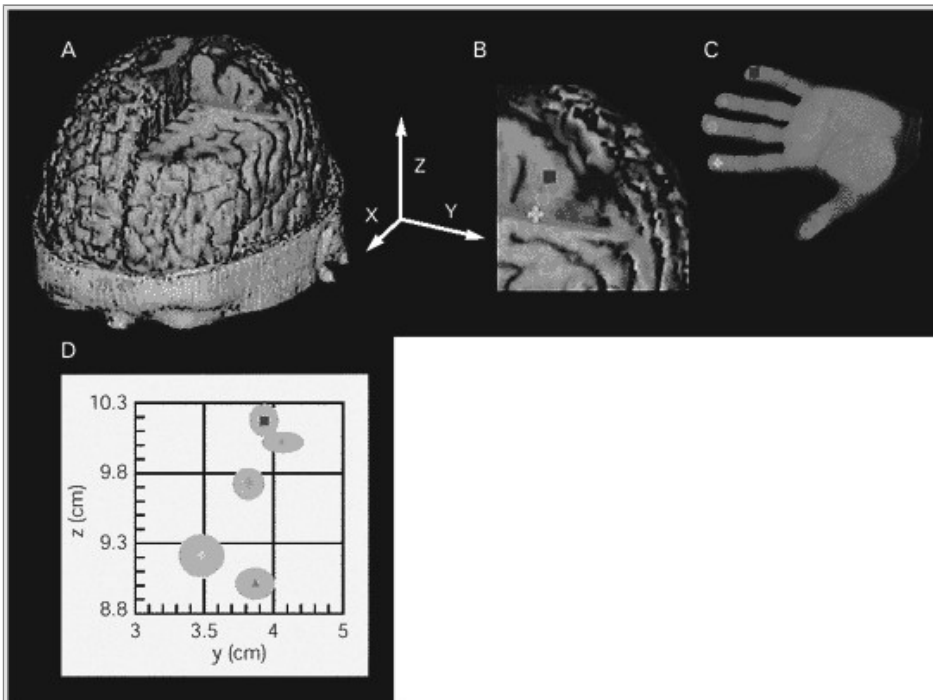


Figure 20-9 The representation of the hand in the somatosensory cortex can be determined in living subjects by means of magnetoencephalography. (From Mogilner et al. 1993.)

A-C. The areas of representation of the digits of the hand are indicated on a three-dimensional reconstruction of a subject's brain (color key is shown in C).

D. A two-dimensional plot shows the area of representation for each finger in the coronal plane. The **colored shapes** indicate averages, the **gray ovals** indicate standard errors.

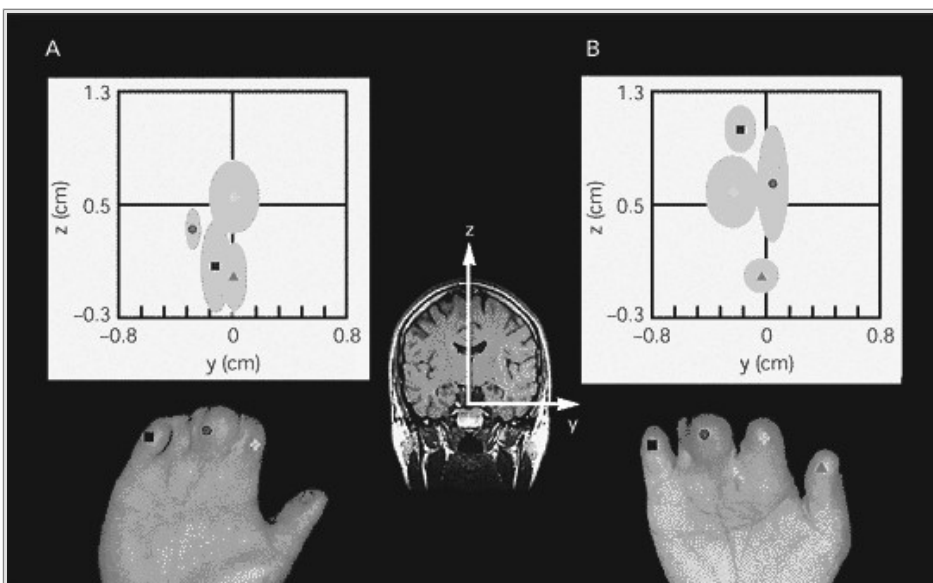


Figure 20-10 The area of representation of the hand in the somatosensory cortex changes after surgical correction of syndactyly of digits 2-5. (From Mogilner et al. 1993.)

- A.** A preoperative map of a patient with syndactyly shows that the cortical representation of the thumb, index, middle, and little fingers is abnormal and lacks any somatotopic organization. For example, the distance between sites of representation of the thumb and little finger is significantly smaller than normal.
- B.** Twenty-six days after surgical separation of the digits 2-5 the organization of the inputs from the digits is somatotopic. The distance between the sites of representation of the thumb and little finger has increased to 1.06 cm.

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Real as Well as Imagined and Remembered Extrapersonal Space Is Represented in the Posterior Parietal Association Cortex

Neurons in the primary somatosensory cortex project to higher-order somatosensory areas of the anterior parietal lobe and to the multimodal association areas in the posterior parietal cortex (Brodmann's areas 5 and 7). The posterior parietal association areas also receive inputs from the visual and auditory systems and from the hippocampus. These posterior parietal areas thus integrate somatic sensory information with other sensory modalities, an integration that is necessary for three-dimensional perception and planned manipulation of objects.

The connection between higher mental processes and signaling in nerve cells is no more clearly evident than in the posterior parietal cortex. Lesions in this area do not produce simple sensory deficits such as blindness, deafness, or loss of tactile sensibility. Rather, damage to the posterior parietal lobe produces agnosia, an inability to perceive objects through otherwise normally functioning sensory channels. The deficits with agnosia

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are complex, such as defects in spatial perception, visuomotor integration, and selective attention. The agnosias most commonly seen with lesions of the right posterior parietal visuocortex are among the most remarkable that can be seen in neurological patients. A particularly dramatic agnosia is *isostereognosis*, an inability to recognize the form of objects through touch. This agnosia is commonly accompanied by a left-sided paralysis.

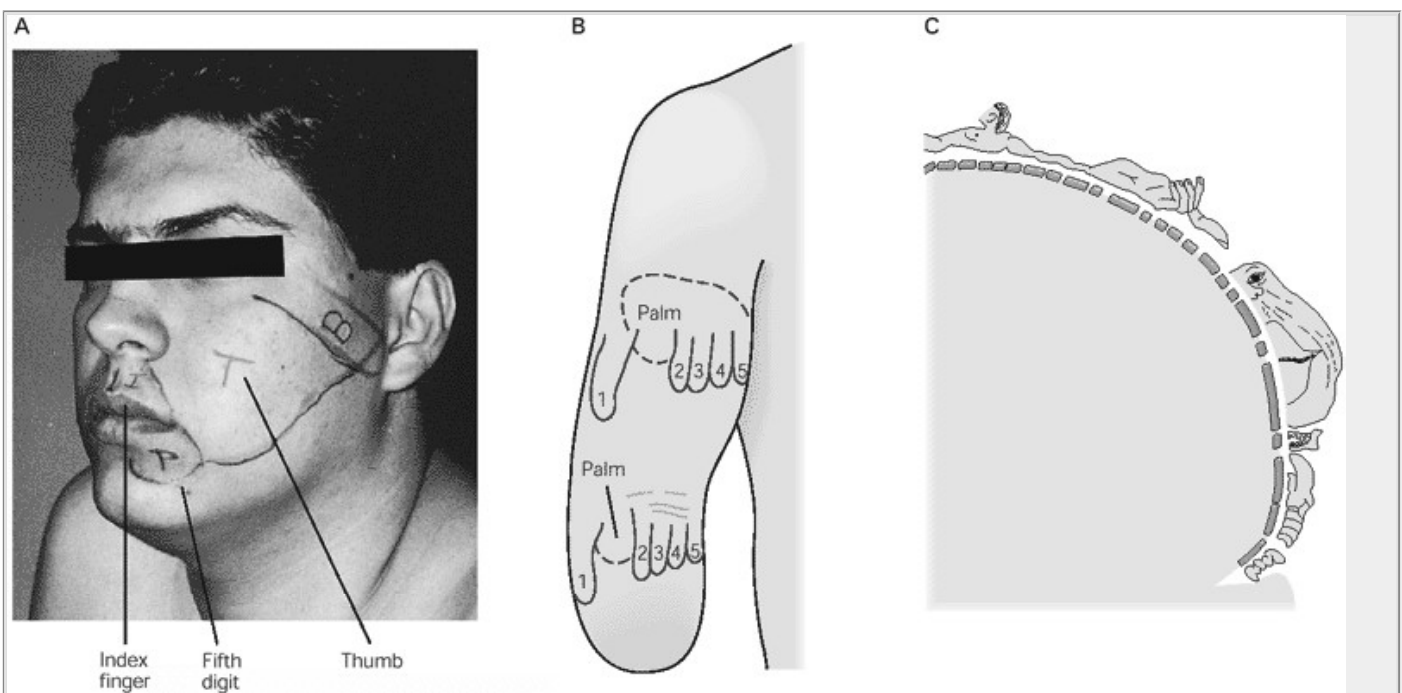


Figure 20-11 Phantom limb sensations can be evoked by touching the face. (From Ramachandran 1993.)

- A.** A subject whose arm was amputated above the left elbow shows sites on his face where stimulation (brushing the face with a cotton swab) elicits sensation referred to the phantom digits. Regions of the body that evoke referred sensations are called reference fields. Stimulation of the region labeled T always evoked sensations in the phantom thumb. Stimulation of facial areas marked I, P, and B evoked sensation in the phantom index finger, pinkie, and ball of the thumb, respectively. This patient was tested four weeks after amputation.
- B.** The upper arm of a subject who experienced referred sensation in the face and in two distinct areas on the arm—one area close to the line of amputation and a second area 6 cm above the elbow crease. Each area is a precise spatial map of the lost digits; the maps are almost identical except for the absence of fingertips in the upper map. When the patient imagined pronating his phantom lower arm, the entire upper map shifted in the same direction by about 1.5 cm. Stimulating the skin region between these two maps did not elicit sensations in the phantom limb.
- C.** Portion of sensory homunculus showing how the cortical area receiving inputs from the hand is flanked by the regions devoted to the face and the arm. Rearrangement of these cortical inputs is thought to be responsible for some types of phantom limb sensation.

Patients with astereognosis show a striking deficit in the self-image of the left side of their body as well as a deficit in perceiving the external world on the left. For example, some patients will not dress, undress, or wash the affected side (*personal neglect syndrome*). Patients may even deny or disown their left arm or leg, going so far as to say, "Who put this arm in bed with me?" Because the idea of having a left limb is completely foreign to them, patients also appear to deny the existence of any paralysis in this limb and may attempt to leave the hospital prematurely since they believe nothing is wrong with them. These patients, then, seem to lose a discrete part of self-awareness.

In some patients with neglect syndrome the sensory neglect extends from personal space (the self-image of the body) to peri- and extrapersonal space (*spatial neglect*). In such cases, for example, the ability to copy the left side of a drawing is severely disturbed. The patient may draw a flower with petals on

only the right side of the plant. When asked to copy a clock, the patient may ignore the numbers on the left, or try to cram all the numbers into the right half of the clock, or draw them on one side running off the clock face (Figure 20-12).

A particularly dramatic example of spatial neglect is seen in self-portraits painted by a German artist who suffered a stroke that affected his right posterior parietal cortex (Figure 20-13). The portraits done at two months and three and a half months after the stroke showed a

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profound neglect of the left side of the face. The neglect persisted, albeit in a minor way, even when the patient had essentially recovered at nine months.

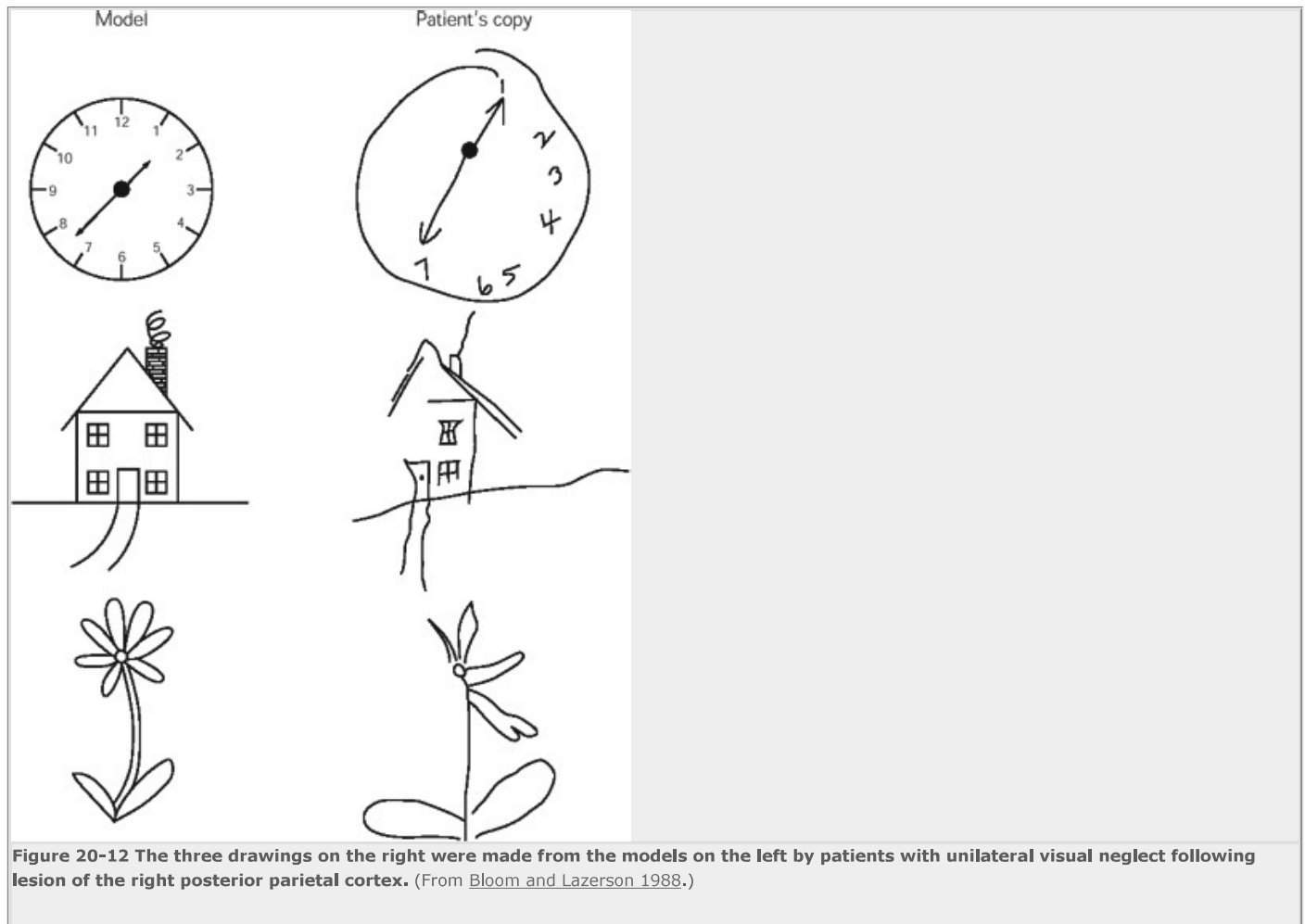


Figure 20-12 The three drawings on the right were made from the models on the left by patients with unilateral visual neglect following lesion of the right posterior parietal cortex. (From Bloom and Lazerson 1988.)

The spatial neglect of stimuli can be remarkably selective. Studies of patients with neglect syndrome following right hemisphere damage have revealed important selective deficits in the perception of the forms of objects. Such patients are unable to "see" all the parts of an object, even though the visual pathways are intact, but nevertheless are able to recognize the object (Figure 20-14). These clinical findings provided some of the first evidence that normal perceptual pathways include discrete circuits for attending to (1) the global shape of an object and (2) local components of the global shape (Figure 20-15).

Perhaps the most fascinating form of sensory neglect is *representational neglect*, in which the left or right visual field is neglected in an internal representation of a scene. This was first observed by Edoardo Bisiach in a group of patients in Milan, all of whom had injury to the right parietal lobe. As the patients were sitting in the hospital's examining room they were asked to imagine that they were standing opposite the cathedral in the city's main public square, the Piazza del Duomo, and to describe from memory the key buildings around the square. These subjects were able to identify all the buildings on the right side of the square (ipsilateral to the lesion) but could not recall the buildings on the left, even though these buildings were thoroughly familiar to them. The patients were next asked to imagine that they were standing on the steps of the cathedral, so that right and left were reversed. In this imagined position the patients were able to name the buildings they previously had been unable to identify but could not now identify the buildings they had previously named (Figure 20-16).

This suggests that memory of extrapersonal space is stored with a *body-centered* frame of reference (see Box 25-1 for a discussion of retinotopic head-centered and body-centered frames of reference). The Milan patients clearly have a complete memory of the entire public square and complete access to that memory. However, they neglect the left half of the remembered space, just as they neglect the left half of the visual field in reality, because they are unable to access and recall images associated with their left side, contralateral to the side of the lesion. Thus, memories for each half of the visual field are accessed through the contralateral hemisphere.

Recent PET scanning studies of normal subjects indicate that when subjects close their eyes and visualize an object such as the letter "a," the visualization recruits activity in the primary visual cortex, in much the same way as an actual object seen with the eyes. That is, imagined visual images are generated by the same components of the visual system as are real images produced by external stimuli. Thus, damage to the posterior parietal cortex, which impairs realtime visual perception, also impairs remembered or imagined visual imagery. Moreover, many tasks that require visual imagery from memory recruit very strong activation of the posterior parietal cortex, suggesting that in their imagination individuals orient their body with respect to the imagined figure! It is presumably this imagined orientation that is lacking in patients with representational neglect.



Figure 20-13 (Opposite) Self-portraits by an artist after damage to his right posterior parietal cortex. The portraits were drawn 2 months after a stroke (upper left), at 3.5 months (upper right), at 6 months (lower left), and at 9 months (lower right), by which time the artist had largely recovered. The early portraits show severe neglect of the side of the face opposite the lesion. (From Jung 1974.)

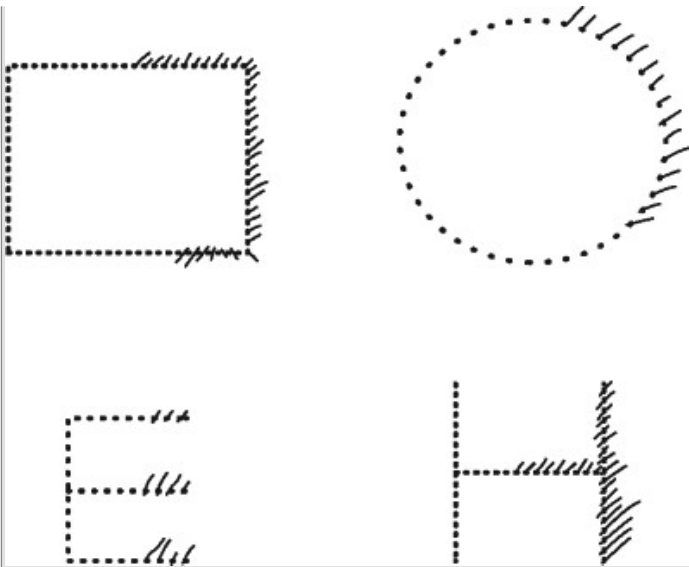


Figure 20-14 The neglect of space on the left after injury to the right posterior parietal cortex may be remarkably selective. A patient may not be visually aware of all parts of an object but still able to recognize the object. Patients with neglect after a right hemisphere stroke were shown drawings in which the shape of an object is drawn in dots (or other tiny forms). The patient was then asked to mark with a pencil each dot. In the figure here the patient was able to report accurately each shape (rectangle, circle, letter E, letter H) but when required to mark each dot with a pencil she neglected the left half of each object. (Adapted from [Marshall and Halligan 1995](#).)

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Is Consciousness Accessible to Neurobiological Analysis?

Consciousness Poses Fundamental Problems for a Biological Theory of the Mind

In studying visual neglect we are beginning to address one of the great mysteries of cognitive neural science, in fact of all science: the nature of consciousness. The special character of consciousness attracts fierce interest and debate among philosophers of mind because it is difficult for some to see how consciousness might be explained in reductionist physical terms.

To begin with, how does one define consciousness? At the beginning of this book we stated that what we commonly call the mind is simply the entire set of operations of the brain. In this sense, consciousness is fundamentally a function of the brain and therefore in principle we should be able to identify neural mechanisms that give rise to consciousness. This, of course, does not begin to tell us what to look for in the brain. We must first come to terms with the defining characteristics of consciousness if we are to develop productive neural theories of consciousness.

Consciousness is ordinarily thought of as a state of awareness. Philosophers of mind such as John Searle and Thomas Nagel ascribe three dominant features to awareness: subjectivity, unity, and intentionality.

The *subjectivity* of conscious experience is seen by Searle and Nagel as its defining characteristic and the characteristic that poses the greatest scientific challenge. Each of us experiences a world of private and unique sensations. Our own experience seems much more *real* to us than the experiences of others. Our own ideas, moods, and sensations—our successes and disappointments, joys and pains—are experienced directly, whereas we can only appreciate other people's ideas, moods, and sensations by referring to our own direct experience. Are the blue you see and the lavender you smell identical to the blue that I see and the lavender that I smell? The fact that conscious experience is uniquely personal and intensely subjective raises the question of whether it is even possible to determine objectively some common characteristics of consciousness in different individuals. If the senses ultimately produce only subjective experience, we cannot, the argument goes, use those same senses to arrive at an objective understanding of experience.

The *unitary nature* of consciousness refers to the fact that our experiences come to us as a unified whole: All of the various sensory modalities are melded into a single conscious experience. Thus, when we sit down to dinner we feel the chair against our back, hear the sound of music in the background, and taste the fruity flavor of the wine as a single experience. Our perceptions not only appear whole for the instant of the experience, but they appear to be whole and continuous over time. When we speak to our dinner partners we do so in whole sentences and pay little if any attention to the process of constructing the sentence, yet we are aware that we are completing an idea. Finally, consciousness has *intentionality*. Our experiences have meaning beyond the physical sensations of the moment. Our mind can connect with and represent the range of our experiences.

In earlier times these special features of consciousness led many philosophers to a dualistic view of mind, a view that the body had a physical existence but the mind did not, and therefore the mind was not a proper subject of the natural sciences. Now almost all contemporary philosophers of mind agree that what we call consciousness derives from physical properties of the brain. Since consciousness has properties that other brain functions do not (subjectivity, unity, and intentionality), a physicalist explanation of consciousness poses a formidable scientific problem.

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Some philosophers of mind, such as Colin McGinn, believe that consciousness is simply not accessible to empirical study because there are limits to human cognitive capacities that reflect inherent and insurmountable limitations in the architecture of the brain. Searle and Nagel, on the other hand, believe that consciousness is accessible to analysis by human mental processes and that we have been unable to account for it because it is an *emergent property* of the brain and therefore unlike any property of the brain that we understand—indeed unlike any other subject of scientific inquiry. Finally, some philosophers, for example Daniel Dennett, deny that there is any problem at all. Dennett argues, much as did the neurologist John Hughlings Jackson a century earlier, that consciousness is not a discrete operation of the brain but is simply the outcome of the computational workings of the association areas of the brain.

Of the three features of consciousness, the major difficulty, as we have said, derives from its subjective qualities. The precise difficulty is illustrated by Nagel and Searle in the following way. Assume we succeed in studying a person's consciousness by recording the electrical activity of neurons in a region known to be important for consciousness while that person carries out a particular task requiring conscious attention. How do we then analyze the results? Can we say that the firing of a group of neurons *causes* a private subjective experience? Can we say that a burst of action potentials in the thalamus and somatic sensory cortices causes someone to consciously perceive an object in his or her hand and to tell whether the object is round or square, hard or malleable?

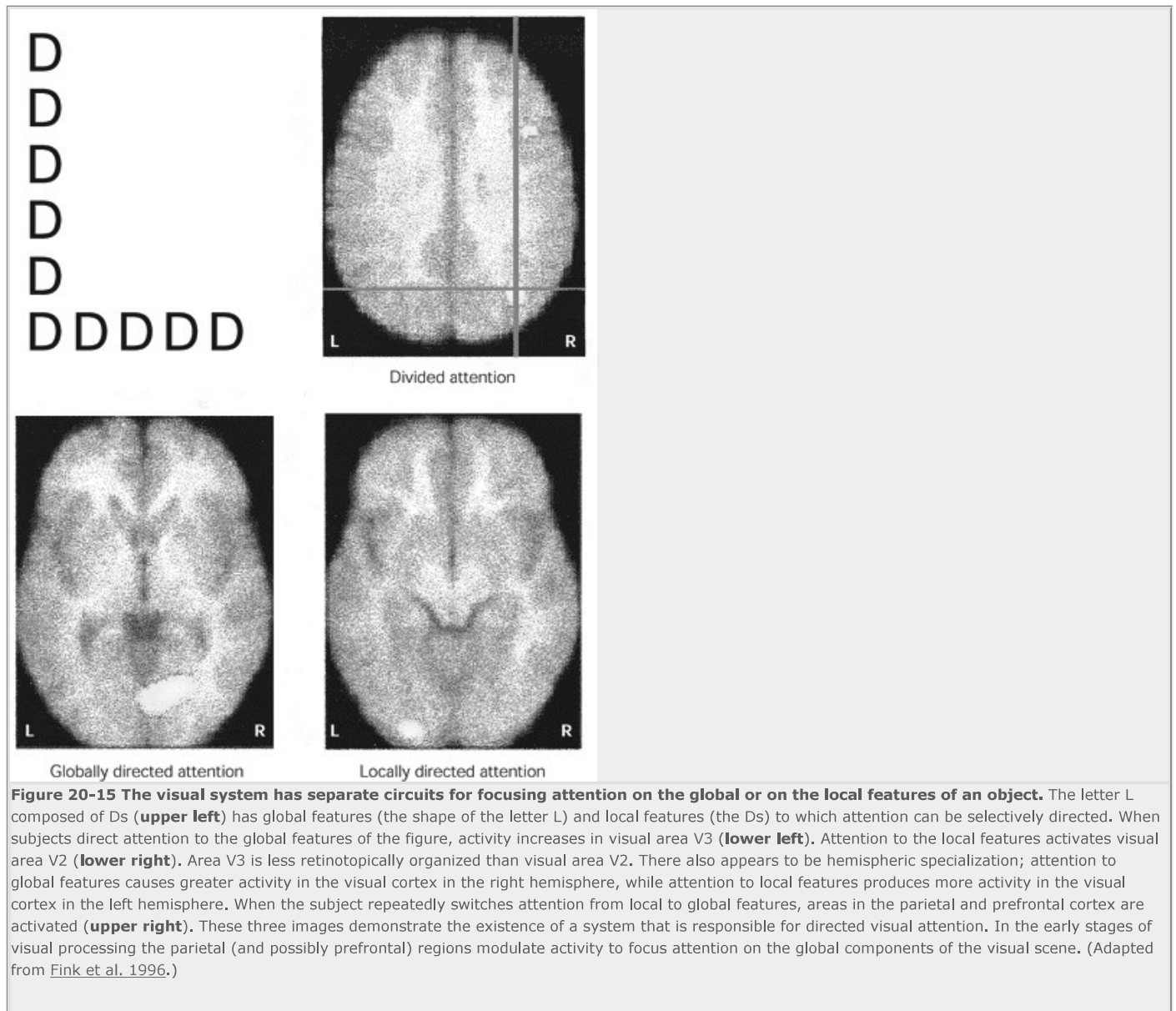
What empirical grounds do we have for believing that when a mother looks at her infant child, the firing of cells in the inferotemporal cortex concerned with face recognition give rise to her perception of her child's face?

We as yet do not know how the firing of specific neurons leads to conscious perception even in the most simple case. In fact, according to Searle, we completely lack an adequate theoretical model of how an *objective* phenomenon—electrical signals in a person's brain—can cause a *subjective* experience such as pain. Because consciousness is irreducibly subjective, it lies beyond the reach of science as we currently practice it.

Since science, as we currently practice it, is essentially a reductionist approach to events, it cannot, according to Nagel, address consciousness without a significant change in method, one that would allow the demonstration and analysis of the *elements* of subjective experience. These elements are likely to be basic components of brain function much as atoms and molecules are basic components of matter. According to Nagel, object-to-object reductions are not problematic because we understand, at least in principle, how the properties of a given type of matter arise from the molecules of which it is made. What we lack in a science of consciousness are rules for extrapolating subjective properties

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(consciousness) from the properties of objects (interconnected nerve cells). Nagel argues that our complete lack of insight into the elements of subjective experience should not prevent us from discovering rules that relate conscious phenomena with cellular processes in the brain. In fact, it is only through the accumulation of cell-biological information that we will have the data necessary to think intelligently about a more fundamental type of reduction, from the physical to the subjective. It is only after we have developed a theory that supports this more fundamental reduction that we will be able to tackle the problem of relating specific neural activity to specific subjective experiences. To arrive at that theory, we will first have to discover the elementary components of subjective consciousness. This discovery, Nagel argues, will be of enormous magnitude and implication and one that may require a revolution in biology and most likely a complete transformation of scientific thought.



Despite Philosophical Cautions, Neurobiologists Have Adopted a Reductionist Approach to Consciousness

The aim of most neural scientists working on consciousness is more modest than that envisaged by Nagel. They are not necessarily working toward a revolution in scientific thought. Although neural scientists must struggle with the difficulties of defining consciousness experimentally, these difficulties do not appear to be totally forbidding. This optimism is due in part to the fact that neural scientists are not immediately concerned with the subjective and unitary nature of consciousness.

This attitude of most neural scientists is perhaps best expressed by the physicist Steven Weinberg: "I don't see how anyone but George will ever know how it feels to be George. On the other hand, I can readily believe that at least in principle we will be able to explain all of George's behavior reductively, including what he says about what he feels, and that consciousness will be one of the emergent higher-level concepts appearing in this equation."

Indeed, neural scientists have been able to make considerable progress in understanding the neurobiology of perception without having to account for

individual experience. The philosopher Patricia Churchland reminds us that cognitive neural scientists have made progress in understanding the neural basis of perception of color without addressing whether each of us sees the same blue. Since considerable progress has been made in understanding color perception without having to account for its subjective qualities, or *qualia*, perhaps the question about qualia is itself not so meaningful within a neurobiological approach to behavior. As we shall learn in later chapters, the brain does indeed *construct* our perception of an object, but the resulting perception is not *arbitrary* and appears to correspond to independently determined physical properties of the objects. What we do not understand is how action potentials give rise to meaning. Why is it that you see a *face* when the neurons of the inferotemporal cortex fire action potentials?



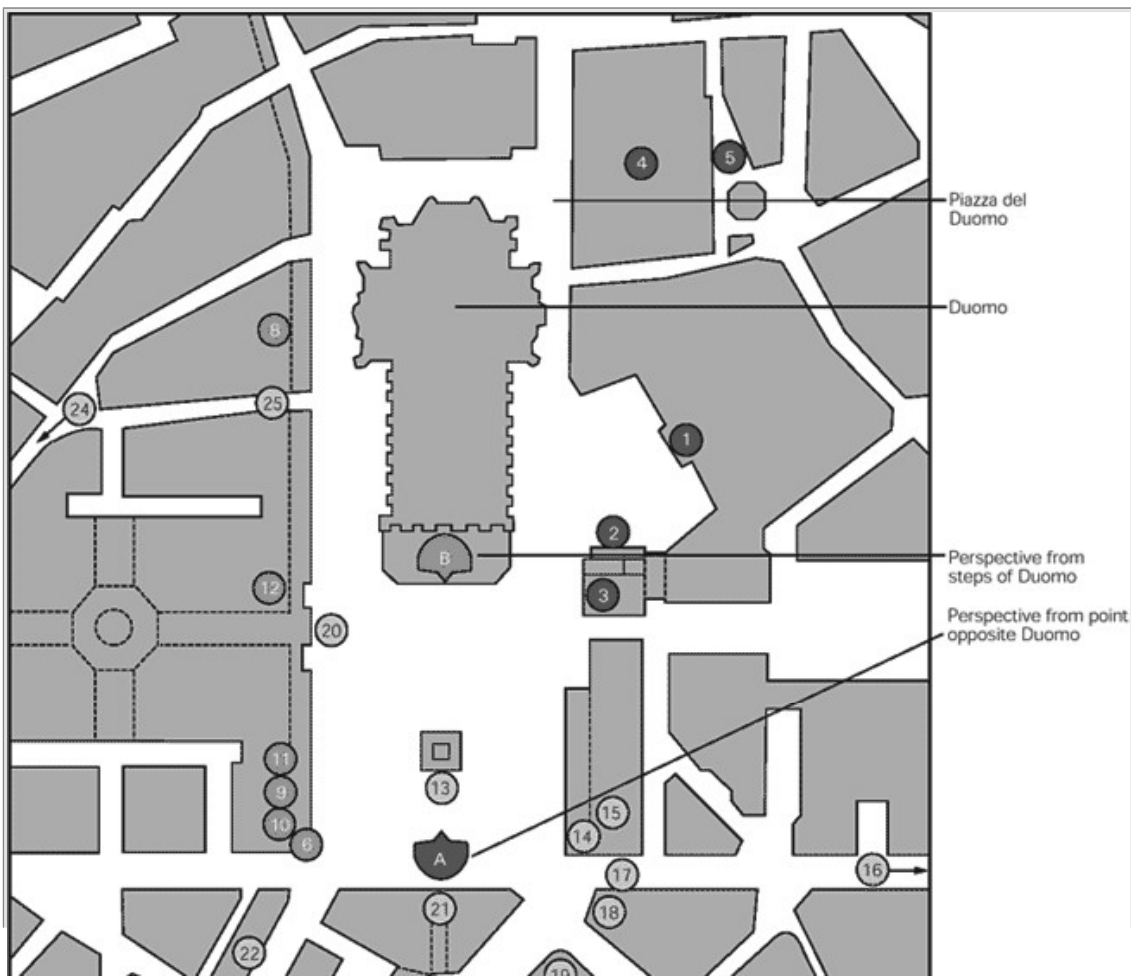
Figure 20-16 When patients with lesions of the right posterior parietal cortex were asked to recall from memory landmarks bordering the Piazza del Duomo in Milan, they were able to describe those on the right but neglected those on the left. The blue circles in the map on the opposite page represent landmark buildings recalled from **perspective A**, the point opposite Duomo; the **green** circles represent landmark buildings recalled from **perspective B** on the steps of the Duomo. (Based on Bisiach and Luzzatti 1978.)

Although Churchland concedes that the subjectivity of consciousness makes the neurobiology of consciousness especially difficult, she does not believe the problem is in principle insurmountable. To begin with, although most simple percepts, such as the shape of an object felt in the hand, are subjective to some degree, the subjective quality of perception does not prevent a third person from objectively evaluating experimental data about what the perceiver actually is perceiving. Some characteristics of perception, even specific qualia, can therefore be correlated with the same patterns of neuronal activity in different subjects and under a variety of circumstances. If one can discern a detailed correlation

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between a particular neural event and a mental event, that description should be a sufficient first approximation of how neural events can give rise to a mental event by any reasonable standards of scientific explanation.



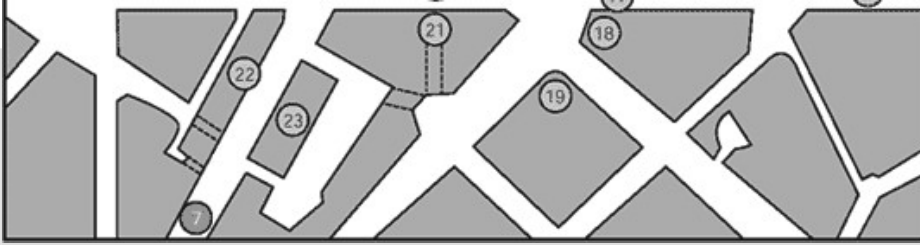


Figure. No Caption Available.

Thus the initial task is to focus on neural correlates of consciousness, by locating within the brain neurons whose activity correlates best with conscious experience, and to determine the neural circuits to which they belong. Having done that, we may be in a position eventually to meet Searle's and Nagel's higher demands: to develop a theory of the correlations we discover empirically in order to state the *laws of correlation* between neural phenomena and subjective experience.

The unitary nature of consciousness emphasized by Searle and Nagel may also not be an obstacle to fashioning a neurobiology of the mind. The unity of consciousness—our continuous and connected experience of events—must depend on the brain's ability to link discrete spatial or temporal events into a single experience. If that is so, is there a difference in principle between the sequencing of notes in a birdsong and the sequencing of words in a sentence? In each case the brain has a template of a unified sequence of utterances. If the neural representation of a sequence like a birdsong can be successfully analyzed, why should a sequence like a sentence be, in principle, less tractable to neurobiological analysis?

Finally, neurobiologists believe that consciousness has many forms, presumably mediated by a different neural system. For example, the *alert state*—the change that occurs when a person awakens or when a person who could not respond to commands becomes able to respond to commands—is thought to involve activation of the thalamus and cortex by neurons of the brain stem and its reticular formation. Alertness itself is thought to be a family of states that differ by degrees of alertness (heightened attention, indifference, inattention, sleepiness) and are influenced by mood (surprise, anger). As we shall learn in [Chapter 45](#), variations in alertness may, in part, be mediated by the components of the major modulatory systems of the brain stem—the cholinergic, dopaminergic, serotonergic, and noradrenergic systems—acting on the thalamus and cerebral cortex. Finally, alertness can be general or focused, as when we selectively attend to one object in the external world to the exclusion of others.

We will likely gain a general understanding of the neurobiology of consciousness by studying these distinct states in their simplest form and by relating well-defined characteristics of one state to the cellular changes that parallel the state. Thus, rather than grapple with the broad concept of consciousness, neurobiology approaches the problem of consciousness by studying tractable, well-defined components of consciousness, such as selective attention, to which we now turn. (See also [Appendix D](#).)

Selective Attention Is a Testable Component of Consciousness

The phenomenon of selective attention is a particularly useful starting point for the scientific study of consciousness. At any given moment we are aware of only a small fraction of the sensory stimuli that impinge upon us. As we look out on the world we focus on specific objects or scenes that have particular interest and exclude others. Let us say you raise your eyes from this book to look at someone entering the room. Now you are no longer attending to the words on this page. Nor are you attending to the decor of the room or other people in the room. This selective focusing of the sensory apparatus on one element out of many is an essential feature of all sensory processing, as William James first noted in his *Principles of Psychology* (1890):

Millions of items... are present to my senses which never properly enter my experience. Why? Because they have no *interest* for me. *My experience is what I agree to attend to*.... Everyone knows what attention is. It is the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects of trains of thought. Focalization, concentration of consciousness are of its essence. It implies withdrawal from some things in order to deal effectively with others.

Research on visual perception has shown that selective attention is actually a series of behaviors. For example, Michael Posner distinguishes four components of selective attention when an organism orients to a novel stimulus: (1) disengagement or release from the present focus of attention, (2) movement to a new location, (3) engagement at the new location, and usually (4) a sustained state of alertness.

Cellular studies of the posterior parietal cortex in monkeys have provided important insight into the neural mechanisms of selective attention. Like neurons in other visual areas, parietal neurons respond to the presence of a visual stimulus in the receptive field (see [Chapter 27](#) for a description of visual receptive fields). A remarkable observation by Robert Wurtz, Michael Goldberg, and their colleagues indicates that the strength of this response depends on whether the animal is paying attention to the stimulus ([Figure 20-17](#)). When the animal's gaze is fixed away from the stimulus, there is a moderate response to the appearance of a visual stimulus. But when the monkey has to attend to the stimulus, the same retinal input elicits a much larger response. This enhancement is consistent with observations

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that the parietal cortex contributes to selective attention to the location of objects in space. It occurs independently of the type of response the animal makes to the stimulus. The firing rate of the neuron increases by the same amount whether the animal merely looks at the stimulus or reaches toward it while looking elsewhere.

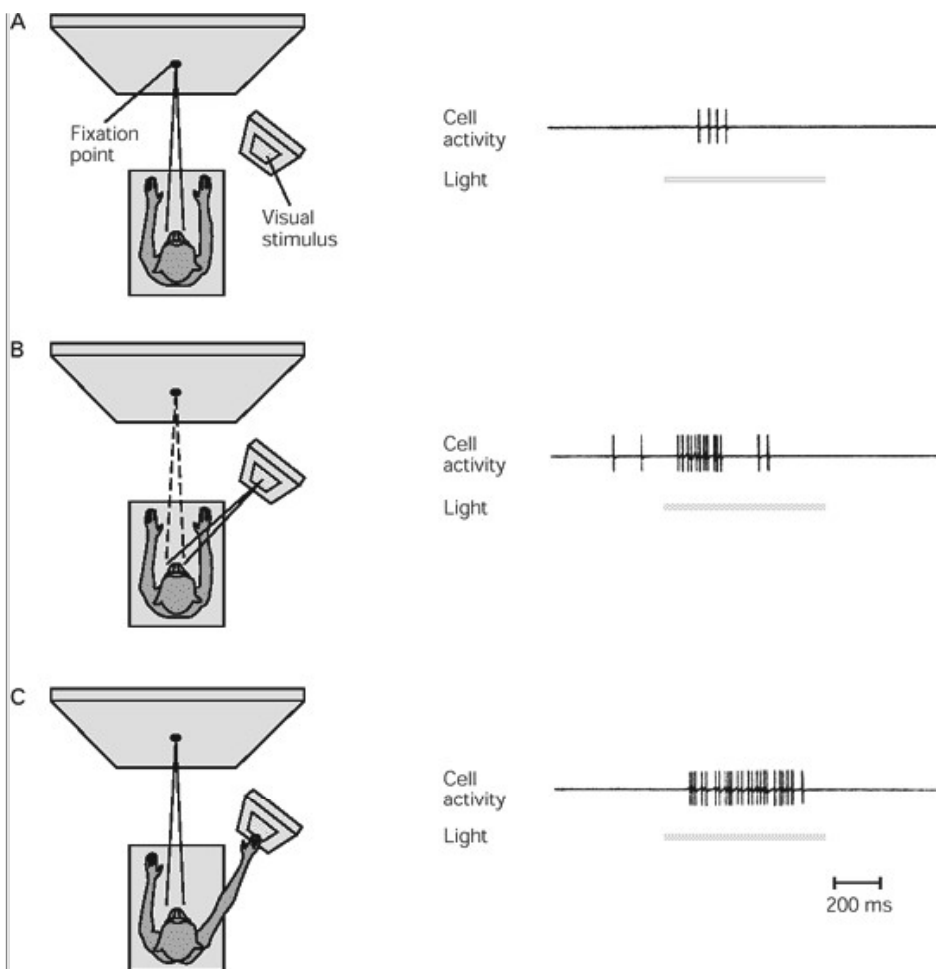


Figure 20-17 Neurons in the posterior parietal cortex of a monkey respond more effectively to a stimulus when the animal is attentive to the stimulus. (From Wurtz and Goldberg 1989.)

- A.** A spot of light elicits only a few action potentials in a cell when the animal's gaze is fixed away from the stimulus.
- B.** The same cell's activity is enhanced when the animal takes visual notice of the stimulus through saccadic eye movement.
- C.** The cell's activity is further enhanced when the monkey touches the spot but without moving his eyes.

This independence indicates that the increase in firing rate is related specifically to attention rather than to the preparation of a motor response. However, the posterior parietal cortex does make connections with structures in the prefrontal cortex that are involved in the planning and execution of movements of the eyes and the hands. Studies by Richard Anderson indicate that one of the functions of selective attention is the intention to direct a movement of the hand or eye to a location. Here we see a central issue in the study of cognition: how a percept leads to a voluntary act.

Selective attention enhances the responses of neurons in many brain areas. Neurons in the frontal cortex and superior colliculus, for example, discharge more briskly when the animal attends to the stimulus. Cells in the visual processing area of the temporal cortex also respond more strongly to attended objects. These effects of attention are evident throughout the visual system.

This type of evidence suggests that selective attention sharpens our sensory machinery, an obvious advantage in planning movement. Following up on this view, Francis Crick and Christof Koch have proposed that the attentional signals that modulate neurons in the visual system originate in the prefrontal cortex, the multimodal association area concerned with planning and motor strategies

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Neural scientists are thus beginning to address aspects of the fundamental question of consciousness by focusing on a specific, testable problem: What neural mechanisms are responsible for focusing visual attention? The solution to this specific problem, which is on the horizon, will most certainly enhance our understanding of sensory perception in general but may also contribute to the development of a biological theory of consciousness.

An Overall View

To come to grips with the biological processes of cognition we must move beyond the individual neuron and consider how information is processed in neural networks. This requires not only the methods and approaches of cellular and systems neuroscience but also the insights of cognitive psychology.

Studies of the sense of touch and its cortical representation in the anterior regions of the parietal lobe provide elementary examples of the internal representation of the body surface and of peripersonal space. This representation is not fixed, but can be modified by experience. Analysis of modifications of this representation in the posterior parietal association cortex indicates that attentiveness is a factor in integrating the representation of the body with vision and movement, an integration that allows a representation of personal space to be further integrated with a representation of extrapersonal space. Thus, the representation of the body becomes related to the representation of visual space, whether actual, imagined, or remembered, and it is within this integrated representation that the conscious self functions. It is therefore perhaps not surprising that the Russian neuropsychologist A. R. Luria suggested that portions of the parietal lobe constitute the most distinctly human aspects of cortical organization.

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