Biosystems II: Neuroscience

Sensory Systems

Lecture 5

Transformation of Neural Codes from PNS to CNS

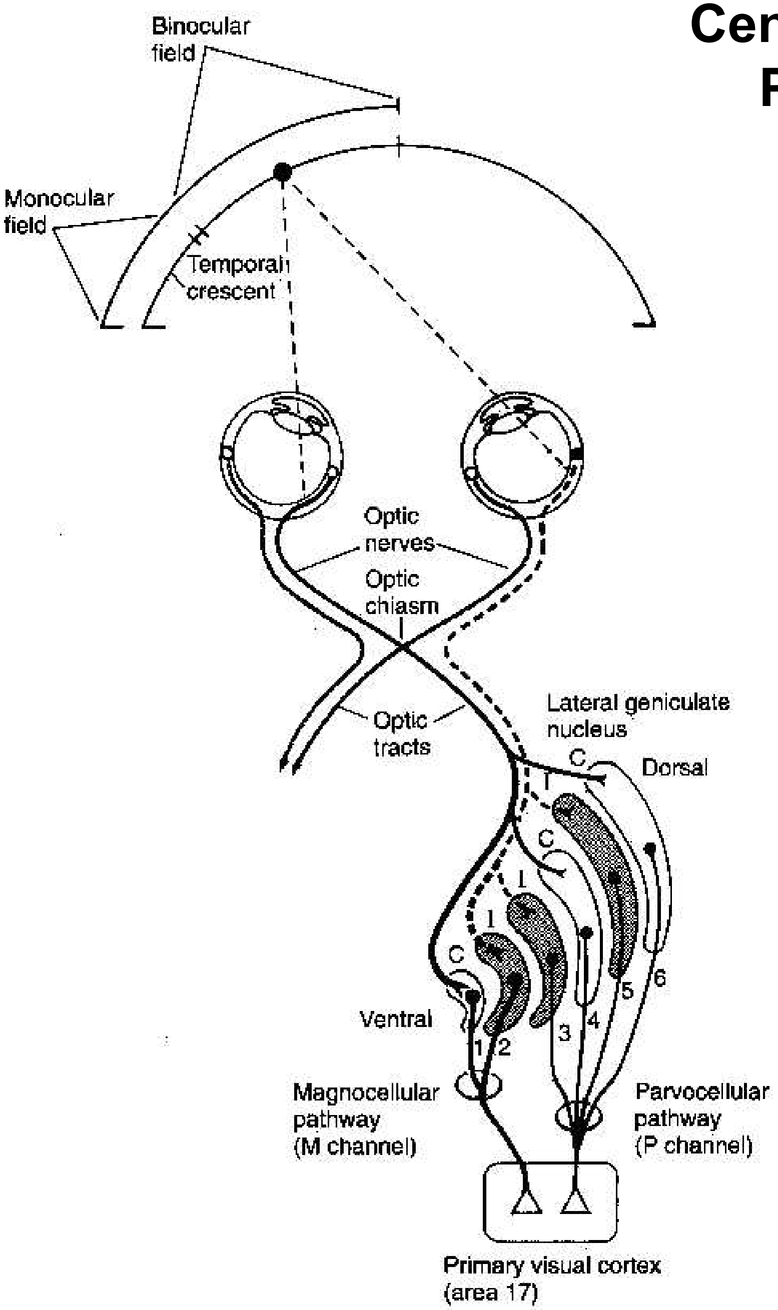
Dr. Xiaoqin Wang

Outline

1. Each sensory system consists of both parallel and hierarchical processing pathways leading from PNS to CNS and the cerebral cortex (Fig.5-1, 5-2, 5-3)
    - a). Ascending pathway (“afferent”, feed-forward)
    - b). Descending pathway (“efferent”, feed-back)
2. Cerebral cortex consists of functionally distinct areas supporting each sensory modality and other complex cognitive functions
    - a). Landmarks of cerebral cortex (Fig.5-4, 5-5)
    - b). Laminar organization of the cortex (Fig.5-6, 5-7)
3. Sensory neurons are topographically organized along the ascending pathway. Topographic maps are inherited from PNS.
    - a). Somatotopic maps (Fig.5-8, 5-9)
    - b). Retinotopic maps (Fig.5-10)
4. Neuronal properties become increasingly more complex and selective along the ascending pathway. Functional maps are created at CNS.
    - a). Increase of RF size (Fig.5-11)
    - b). Segregation of sub-modalities in cortex (Fig.5-12)
5. Cortex is organized by functional columns. Cortical columns communicate with each other via horizontal neural connections.
    - a). Ocular dominance and orientation column maps (Fig.5-13, 5-14)
    - b). Horizontal connections (Fig.5-15)
6. Hierarchical and parallel organizations of sensory processing
    - a) RF representations in somatosensory afferents and cortex (Fig.5-16, 5-17, 5-18)
    - b). Letter representations in somatosensory afferents and cortex (Fig.5-19)

Central Visual Pathway

Inputs from the right hemiretina of each eye project to different layers of the right lateral geniculate nucleus to create a complete representation of the left visual hemifield. Similarly, fibers from the left hemiretina of each eye project to the left lateral geniculate nucleus. The temporal crescent is not represented in contralateral inputs. Layers 1 and 2 comprise the magnocellular layers; layers 4 through 6 comprise the parvocellular layers. All of these project to area 17, the primary visual cortex. There are major pathways from the retina through the lateral geniculate nucleus to area 17 of the cortex, which process, in parallel, different aspects of visual information. Three major parallel pathways have been identified: one magnocellular and two parvocellular pathways. The first is concerned primarily with movement and gross features of the stimulus; the second primarily carries information on detail and form; the third is concerned with color.



Receptor

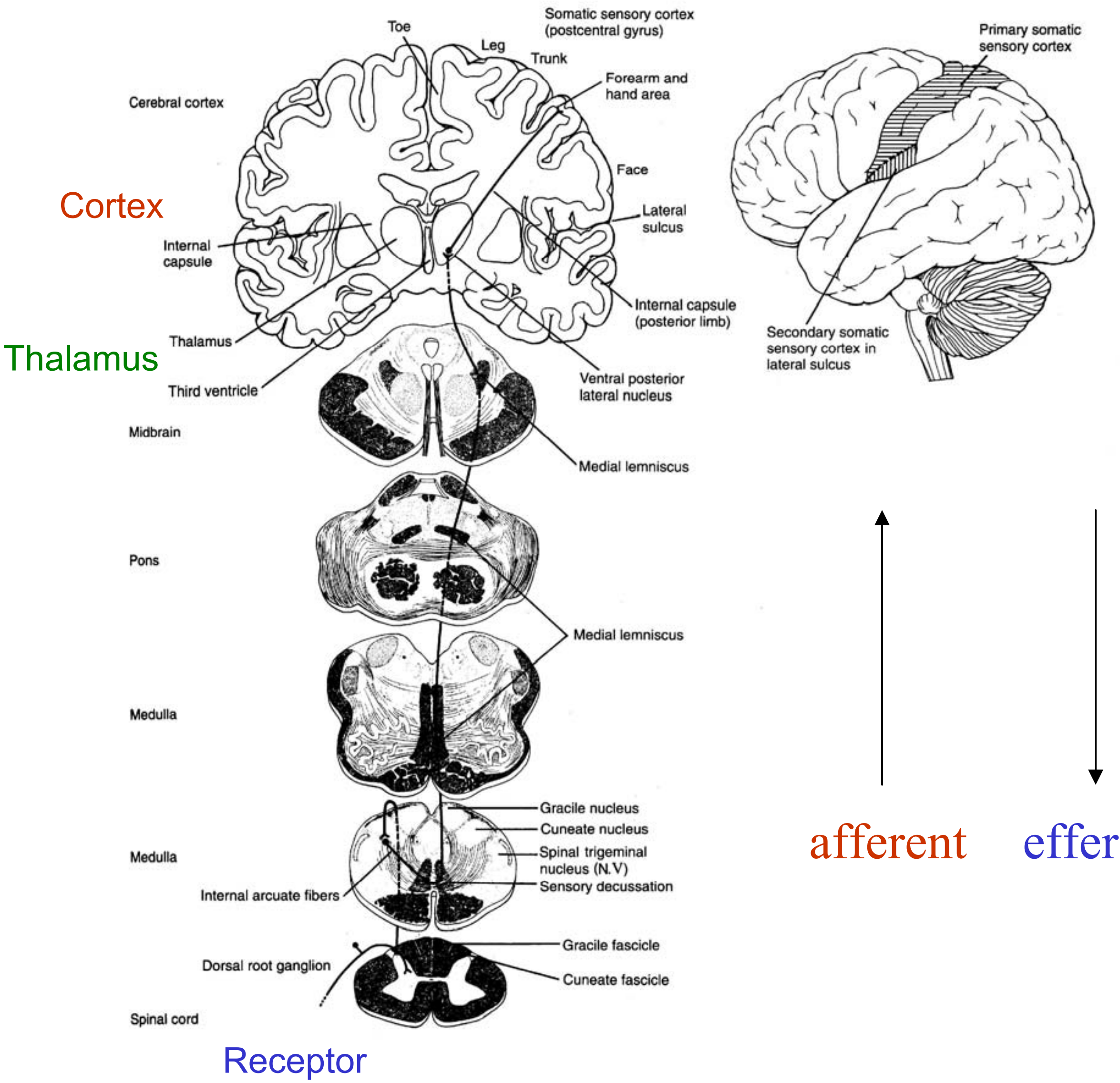
Thalamus

Cortex

Fig.5-1

Central Somatosensory Pathway

General organization of the dorsal column-medial lemniscal system, which mediates tactile sensation and limb proprioception. Three synapses are found between the periphery and the cerebral cortex in the main pathway of the system. The first synapse is made by the central processes of the dorsal root ganglion cells onto neurons in the gracile and cuneate nuclei in the lower medulla. The axons of neurons in these nuclei ascend in the medial lemniscus and synapse on neurons in the ventral posterior lateral nucleus of the thalamus. The neurons in this nucleus in turn send axons to the somatic sensory cortex. At right is a lateral view of a cerebral hemisphere illustrating the location of the primary somatic sensory cortices, which receive a direct projection from the ventral posterior nucleus of the thalamus.

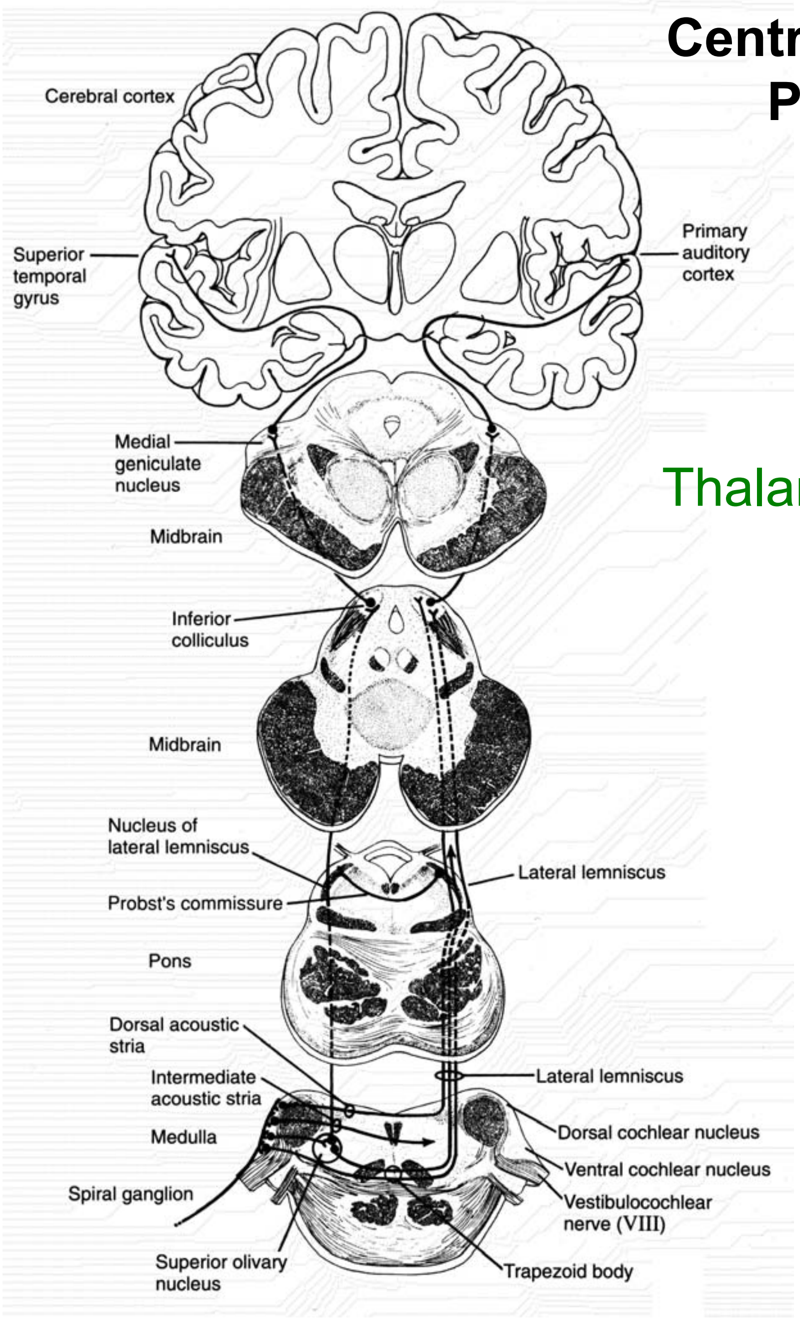


afferent ↑ efferent ↓

Fig.5-2

Central Auditory Pathway

The central auditory pathways extend from the cochlear nucleus to the primary auditory cortex. Postsynaptic neurons in the cochlear nucleus send their axons to other centers in the brain via three main pathways: the dorsal acoustic stria, the intermediate acoustic stria, and the trapezoid body. The first binaural interactions occur in the superior oliver nucleus, which receives input via the trapezoid body. The medial and lateral divisions of the superior olives nucleus are involved in the localization of sounds in space. Postsynaptic axons from the superior olives nucleus, along with axons from the cochlear nuclei, form the lateral lemniscus, which ascends to the midbrain. Axons relaying input from both ears are found in each lateral lemniscus. The axons synapse in the inferior colliculus, and postsynaptic cells in the colliculus send their axons to the medial geniculate body of the thalamus. The geniculate axons terminate in the primary auditory cortex (Brodmann's areas 41 and 42), a part of the superior temporal gyrus.



Cortex

Thalamus

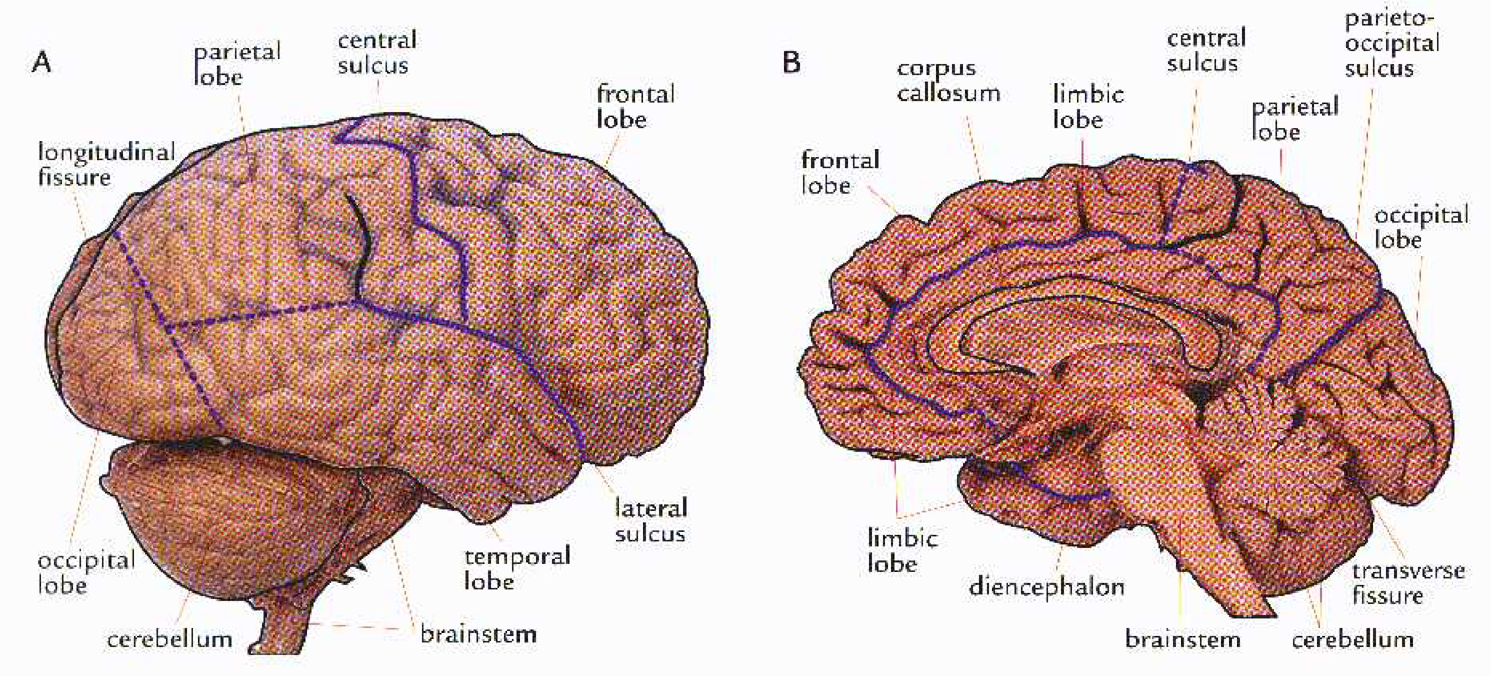
Receptor

Fig.5-3

Summary (1)

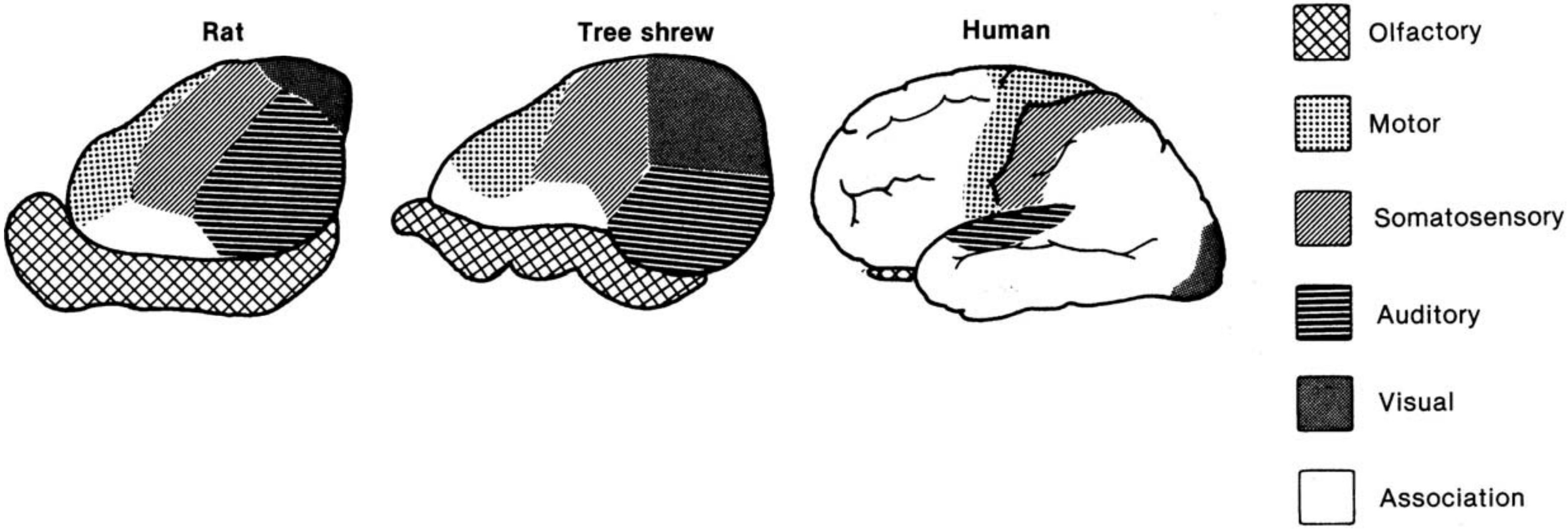
- Each sensory system consists of both parallel and hierarchical processing pathways.

Cerebral Cortex is Divided into Different Areas



Lateral and medial surfaces of the brain. A) The right lateral surface of the brain; anterior is to the right. B) The medial surface of the right half of the sagittally hemisected brain; anterior is to the left.

Organization of sensory cortex reflects the adaptation a species to the environment through evolution



Motor, sensory, and association areas of the cerebral hemispheres of three different mammalian species. All three brains are drawn the same size, even through the human brain is far larger than the other two; the relative and absolute increase in the amount of association cortex is apparent.

Fig.5-5

Cerebral cortex has six layers

Laminar organization of the cerebral cortex. Cross section of cortex stained by three different methods; the six cortical layers are indicated. The Golgi stain reveals the shapes of the arborizations of cortical neurons by completely staining a small percentage of them. The Nissl method stains the cell bodies of all neurons, showing their shapes and packing densities. The Weigert method stains muslin, revealing the horizontally oriented bands of Baillarger as well as vertically oriented collections of cortical afferents and efferents.

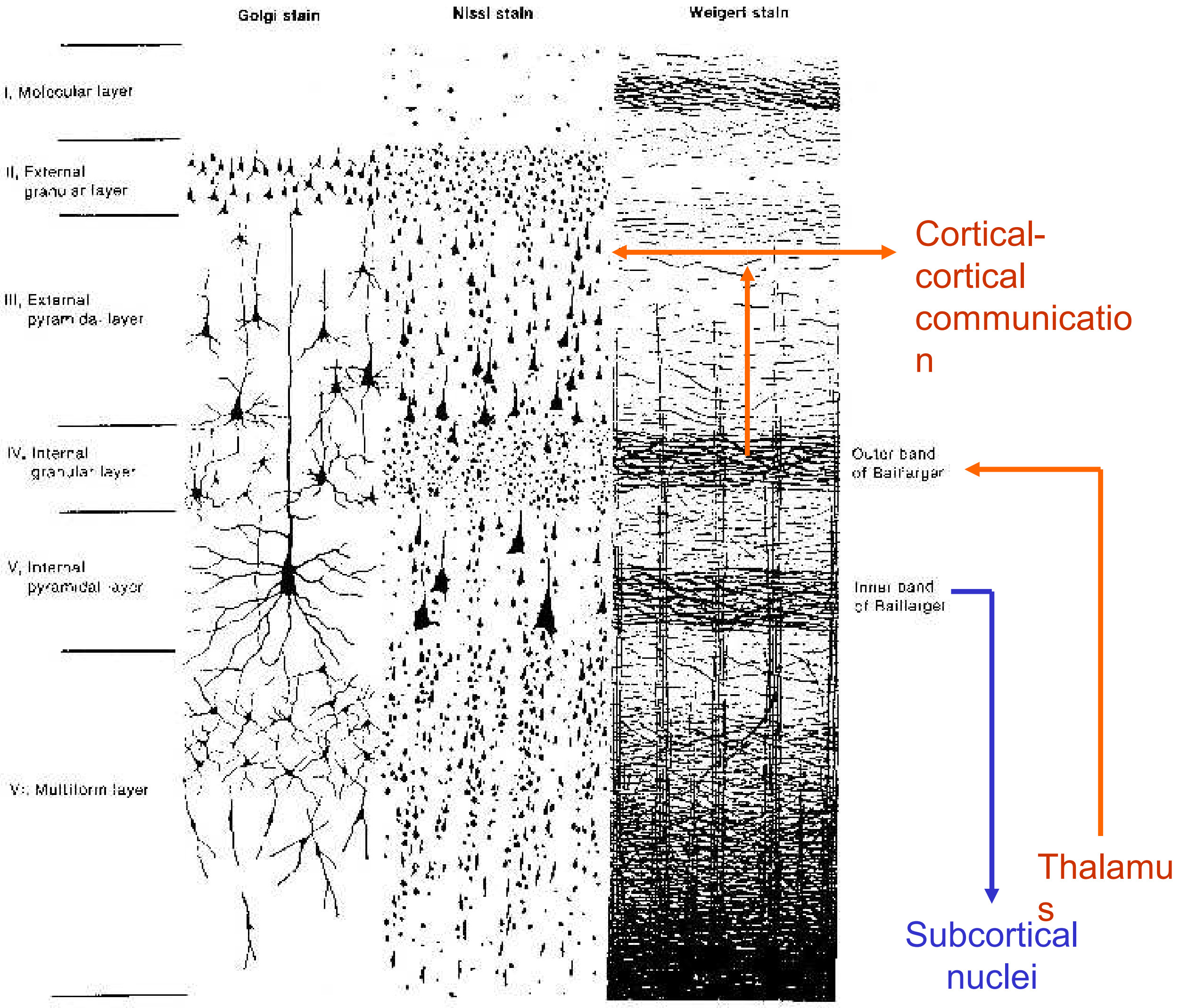


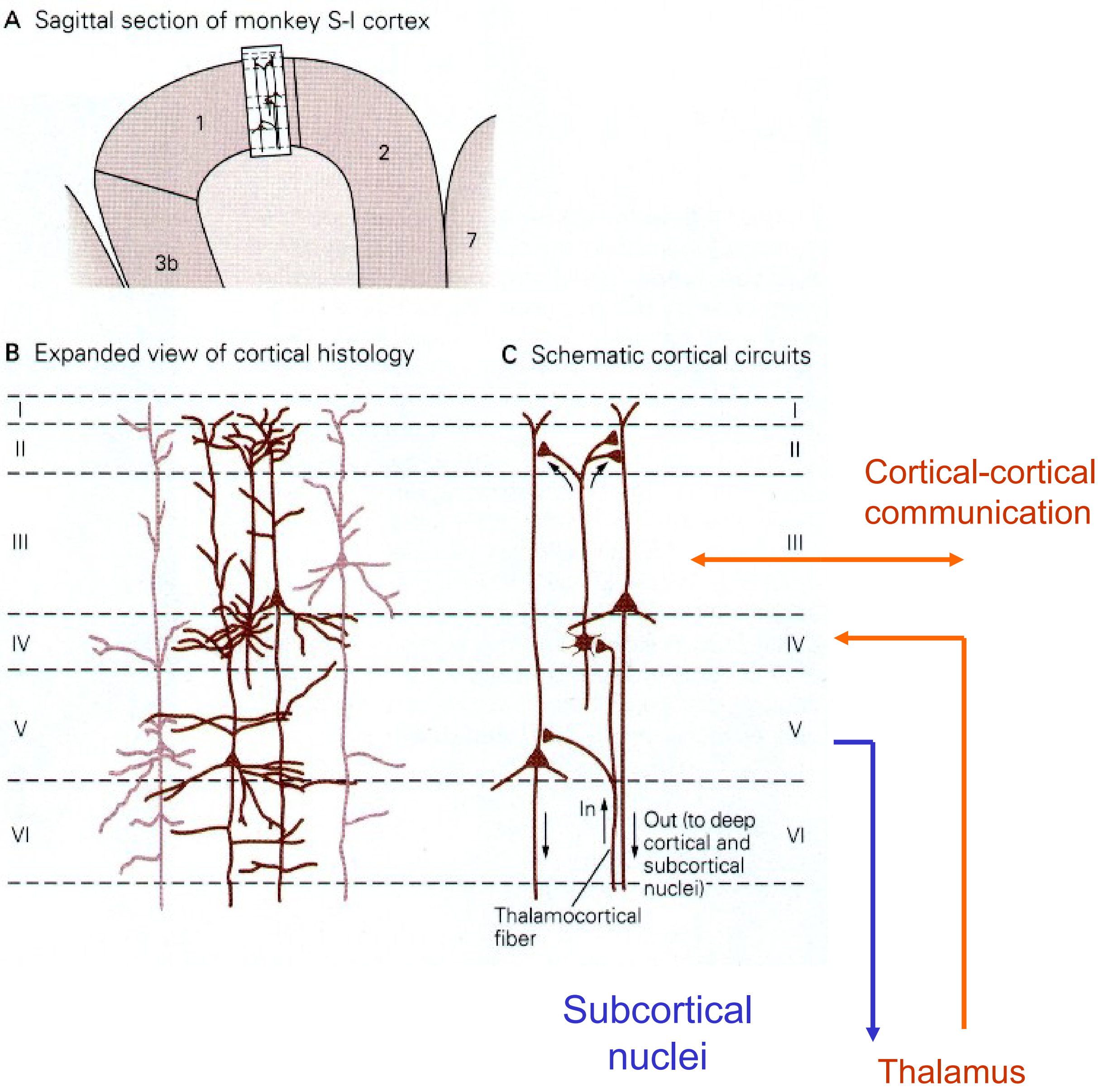
Fig.5-6

The columnar organization of cortical neurons is a consequence of the pattern of connections between neurons in different layers of cortex.

A). The dendrites and axons of most cortical neurons extend vertically from the surface to white matter, forming the anatomical basis of the columnar structure of the cortex.

B). Morphology of the relay neurons of layers III-V. Stellate neurons (small spiny cell) are located in layer IV. These neurons are the principal target of thalamocortical axons. The axons of the stellate neurons project vertically toward the surface of the cortex, terminating on the apical dendrites of a narrow beam of pyramidal cells whose somas lie in layers II III, and V above or below them. Stellate cell axons also terminate on the basal branches of pyramidal cells in layers II and III. The axons of pyramidal neurons project vertically to deeper layers of the cortex and to other cortical or subcortical regions; they also send horizontal branches within the same cortical region to activate columns of neurons sharing similar physiological properties.

C). Schematic diagram of intracortical excitatory circuits. The principal connections are made vertically between neurons in different layers.



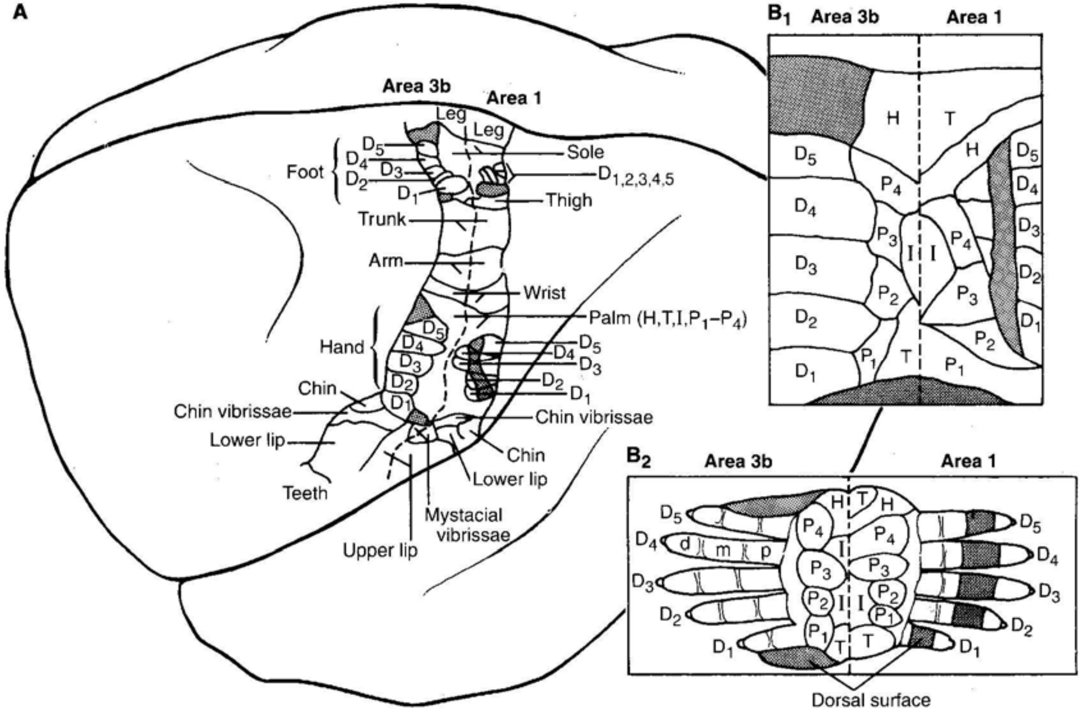
Cortical-cortical communication

Subcortical nuclei

Thalamus

Fig.5-7

Cortical Maps of Skin Surface

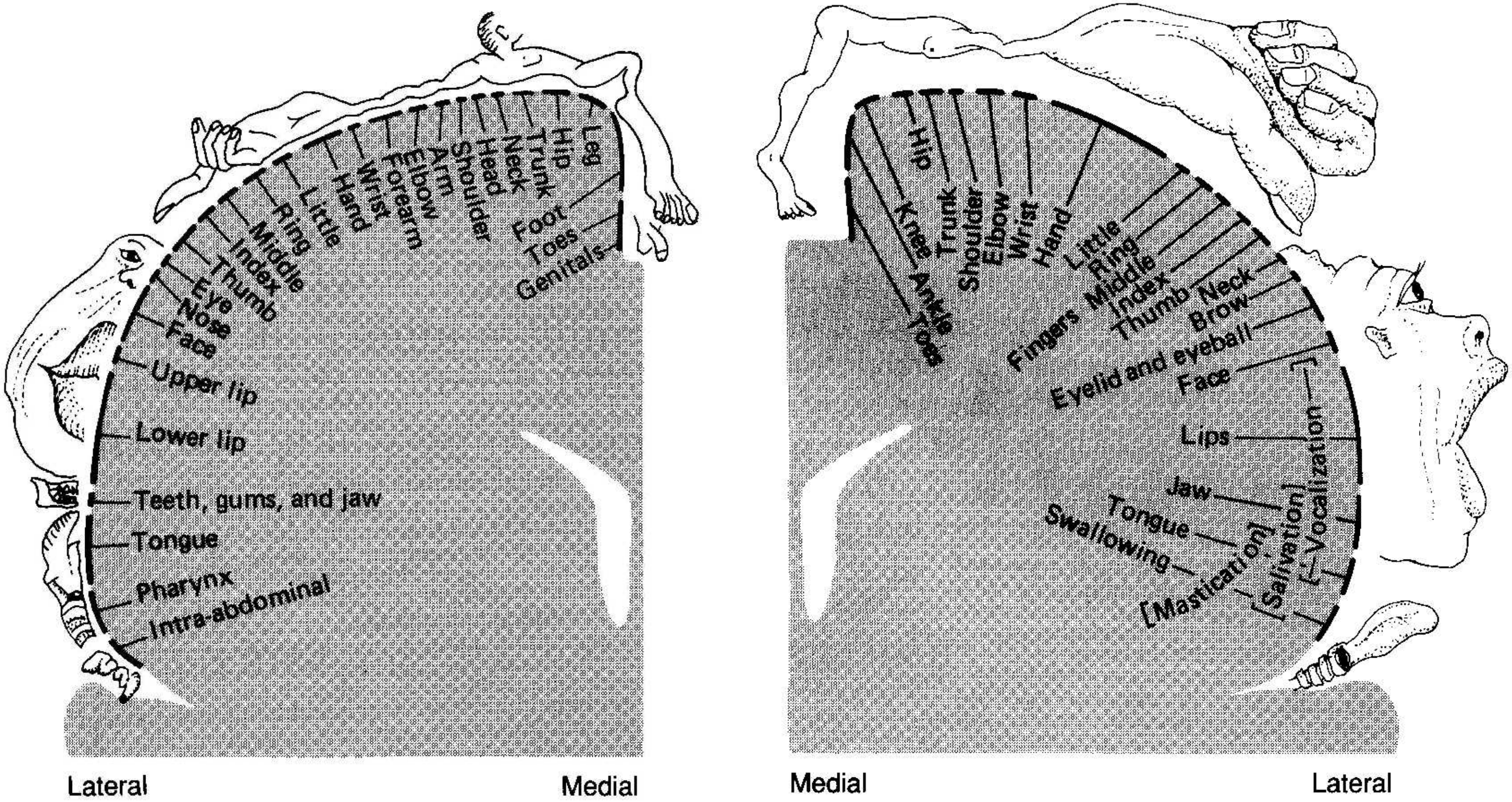


Organization of the primary somatosensory cortex. Each of the four subregions of the primary somatosensory cortex (Brodmann's areas 3a, 3b, 1, and 2) has its own complete representation of the body surface. This figure illustrates the representation for the hand and the foot in areas 3b and 1.

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. The digits of the hand and foot are numbered D_1 to D_5.

B). 1. 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, P_4 to P_1), two insular pads (I), two hypothenar pads (H), and two thenar pads (T). 2. An idealized map of the hands based on studies of a large number of monkeys. The distorted representations of the palm and digits reflect the extent of innervation of each palmar area in the cortex. The five digital pads (D_1 to D_5) include distal, middle, and proximal segments (d, m, p).

Fig.5-8



Sensory Homunculus

Motor Homunculus

Somatic sensory and motor projections from and to the body surface and muscle are arranged in the cortex in somatotopic order.

A). Sensory information from the body surface is received by the postcentral gyrus of the parietal cortex (areas 3a and 3b, and 1 and 2). Here the map for area 1 is illustrated. Areas of the body that are important for tactile discrimination, such as the tip of the tongue, the fingers, and the hand, have a disproportionately larger representation, reflecting their more extensive innervation.

B). The analogous motor map exists for the motor cortex.

Fig.5-9

Topographic Maps Maintain the Continuity of Sensory Space

Retinotopic map in primary visual cortex. Each half of the visual field is represented in the contralateral primary visual cortex. In humans the primary visual cortex is located at the posterior pole of the cerebral hemisphere and lies almost exclusively on the medial surface. (In some individuals it is shifted so that part of it extends onto the lateral surface.) Areas in the primary visual cortex are devoted to specific parts of the visual field, as indicated by the corresponding numbers. The upper fields are mapped below the calcarine fissure, and the lower fields above it. The striking aspect of this map is that about half of the neural mass is devoted to representation of the fovea and the region just around it. This area has the greatest visual acuity.

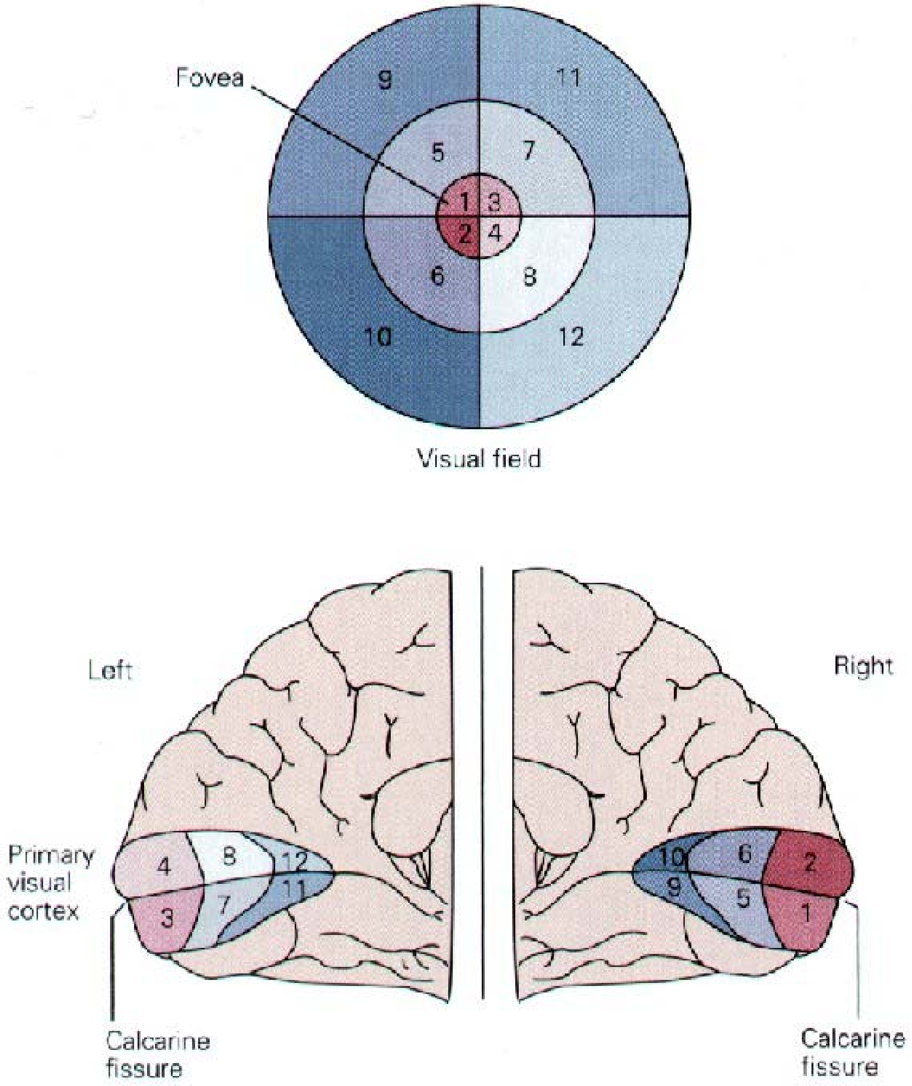


Fig.5-10

Summary (2)

- The basic organization throughout the ascending pathway is the topographical organization (" topographical map") initially established by peripheral receptors.

RF size usually increases in higher processing centers

The receptive fields of neurons in the primary somatic sensory cortex are larger than those of the sensory afferents. Each of the hand figurines shows the receptive field of an individual neuron in areas 3b, 1, 2, and 5 of the primary somatic sensory cortex, based on recordings made in alert monkeys. The colored regions indicate the region of the hand where light touch elicits action potentials from the neuron. Neurons that participate in later stages of cortical processing (Brodmann's areas 1 and 2) have larger receptive fields and more specialized inputs than neurons in area 3b. The neuron illustrated from area 2 is directionally sensitive to motion to- ward the fingertips. Neurons in area 5 of- ten have symmetric bilateral receptive fiends at mirror image locations on the contralateral and ipsilateral hand.

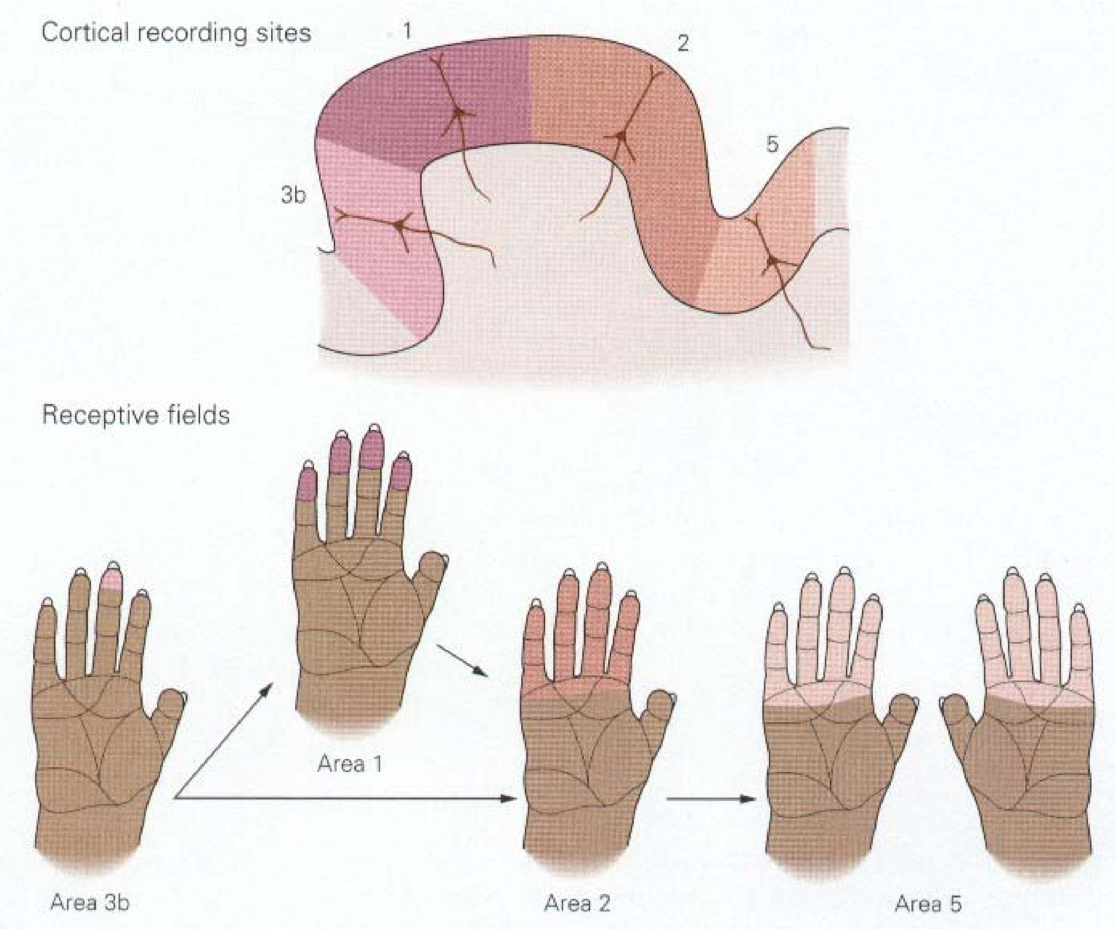


Fig.5-11

Different Sensory Modalities are Mapped into Various Cortical Areas

Segregation of sub-modalities in cortex. Each region of the somatic sensory cortex receives inputs from primarily one type of receptor.

A). In each of the four regions of the somatic sensory cortex (Brodmann's areas 3a, 3b, 1, and 2) inputs from one type of receptor in specific parts of the body are organized in columns of neurons that run from the surface to the white matter.

B). Detail of the columnar organization of inputs from digits 2, 3, 4, and 5 in a portion of Brodmann's area 3b. Alternating columns of neurons receive inputs from rapidly adapting (RA) and slowly adapting (SA) receptors in the superficial layers of skin.

C). Overlapping receptive fields from RA and SA receptors project to distinct columns of neurons in area 3b.

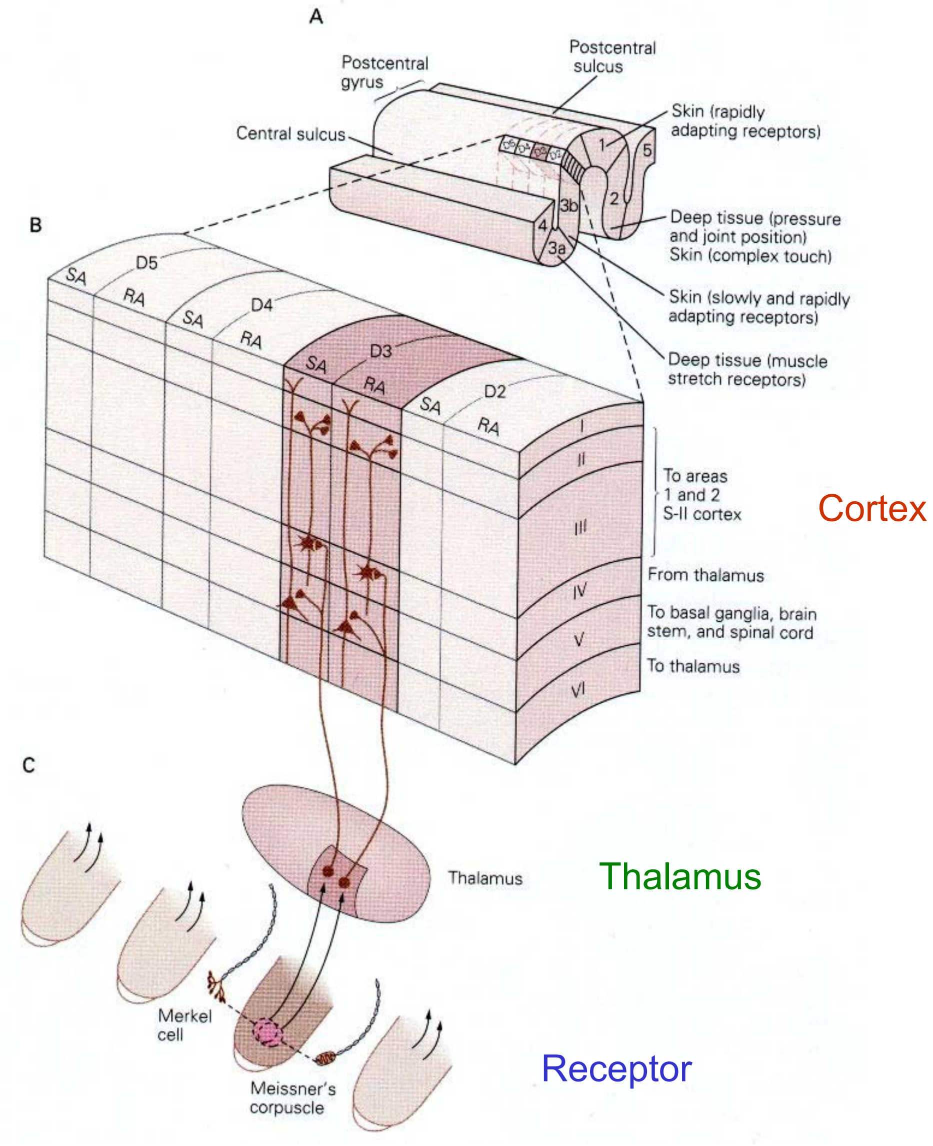


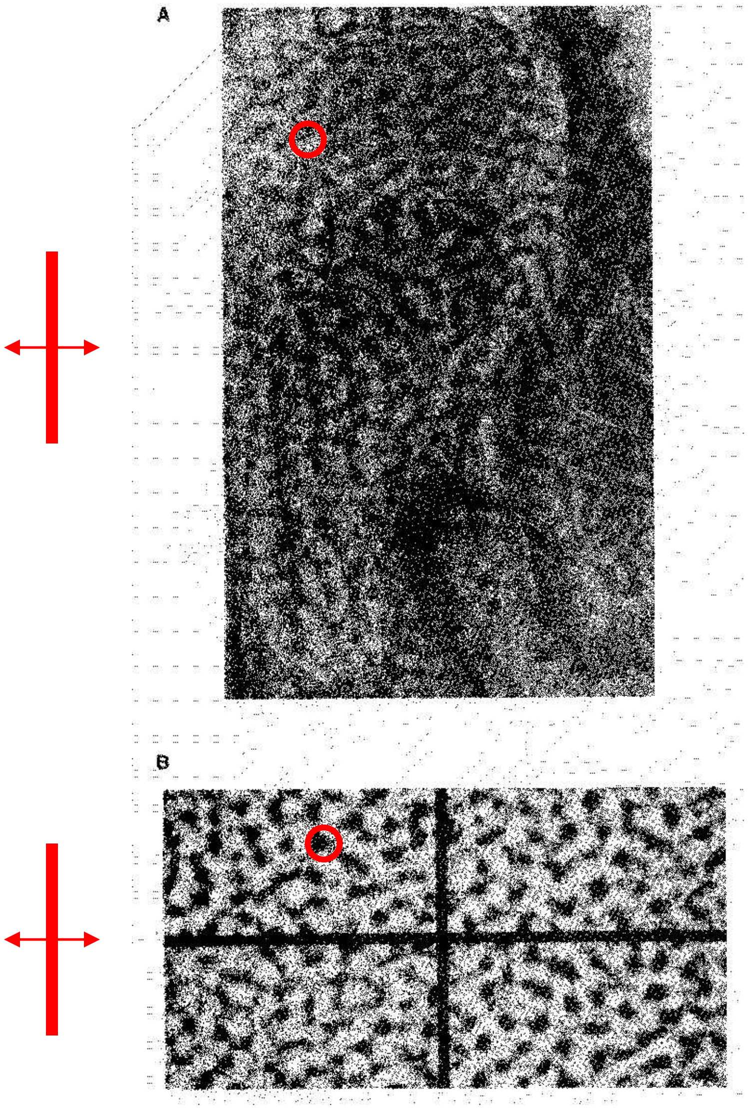
Fig.5-12

Orientation Columns in the Primary Visual Cortex

Orientations columns in the visual cortex.

A). A 2-deoxyglucose visualization of orientation columns in the visual cortex of a monkey binocularly stimulated with vertically oriented lines. Bright areas indicate those neurons responding to the stimulus. The cortex was sectioned tangentially.

B). Images of four different domains in the same cortical area of the primary visual cortex, imaged from the exposed surface of a living monkey brain with a sensitive camera. In each domain the constituent cells had the same axis of orientation. Differences in surface reflectance correspond to differences in the activity of cells. The darker areas correspond to regions of higher activity. Each view represents the pattern of activity occurring during the presentation of gratings having different orientations.



2-deoxyglucose visualization

Optical imaging

Fig.5-13

Orientation Columns in the Primary Visual Cortex

Ocular dominance and orientation column maps in primary visual cortex. Small regions of the visual field are analyzed in the primary visual cortex by an array of complex cellular units called hypercolumns.

A single hypercolumn represents the neural machinery necessary to analyze a discrete region of the visual field. Each contains a complete set of orientation columns, representing 360 degree, a set of left and right ocular dominance columns, and several blobs, regions of the cortex in which the cells are specific for color. Each ocular dominance column receives input from either the contralateral (C) or ipsilateral (I) eye via projections from cells in individual layers of the lateral geniculate nucleus that serve one or the other eye.

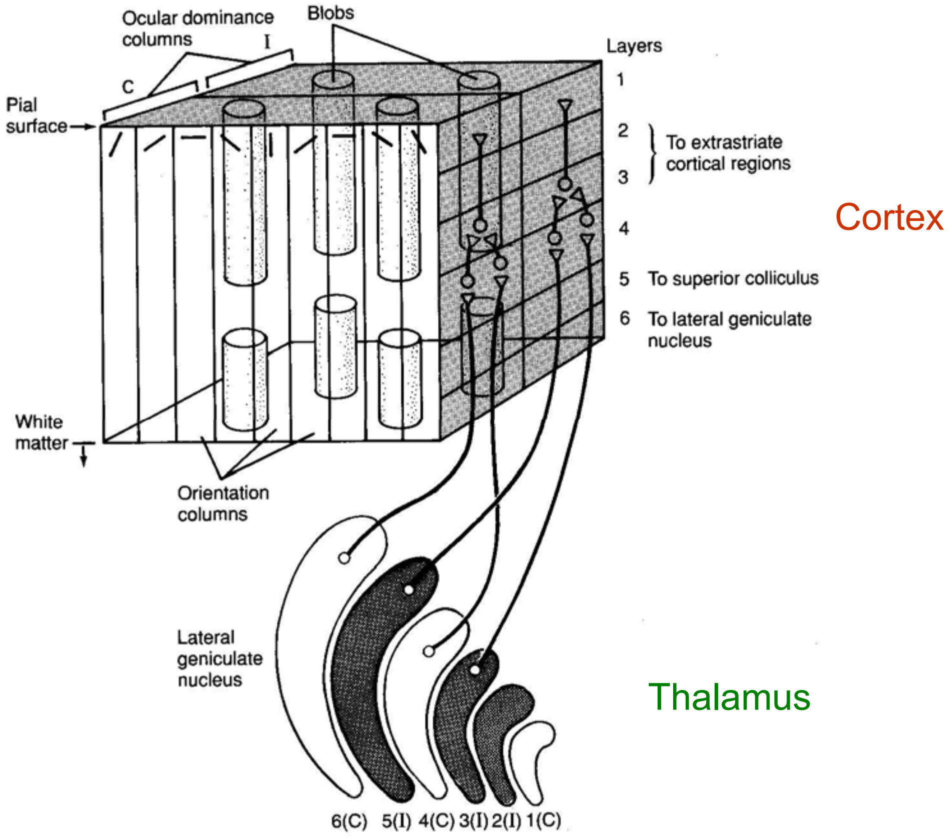


Fig.5-14

Orientation columns are linked by horizontal connections

Columns of cells in the visual cortex with similar funding are linked through horizontal connections.

A). A camera lucida reconstruction of a pyramidal cell injected with horseradish peroxidase in layers 2 and 3 in a monkey. Several axon collaterals branch off the descending axon near the dendritic tree and in three other clusters (arrows), The clustered collaterals project vertically into several layers at regular intervals, consistent with the sequence of functional columns of cells.

B). The horizontal connections of a pyramidal cell, such as that shown in A, are functionally specific. The axon of the pyramidal cell forms synapses on other pyramidal cells in the immediate vicinity as well as pyramidal cells some distance away. Recordings of cell activity demonstrate that the axon makes connections only with cells that have the same functional specificity (in this case responsiveness to a vertical line).

C). 1. A section of cortex labeled with 2-deoxyglucose shows a pattern of stripes representing columns of cells that respond to a stimulus with a particular orientation. 2. Microbeads injected into the same site as in 1 are taken up by the terminals of neurons and transported to the cell bodies. 3. Superimposition of the images in 1 and 2. The clusters of bead-labeled cells lie directly over the 2-deoxyglucose-labeled areas, showing that groups of cells in different columns with the same axis of orientation are connected.

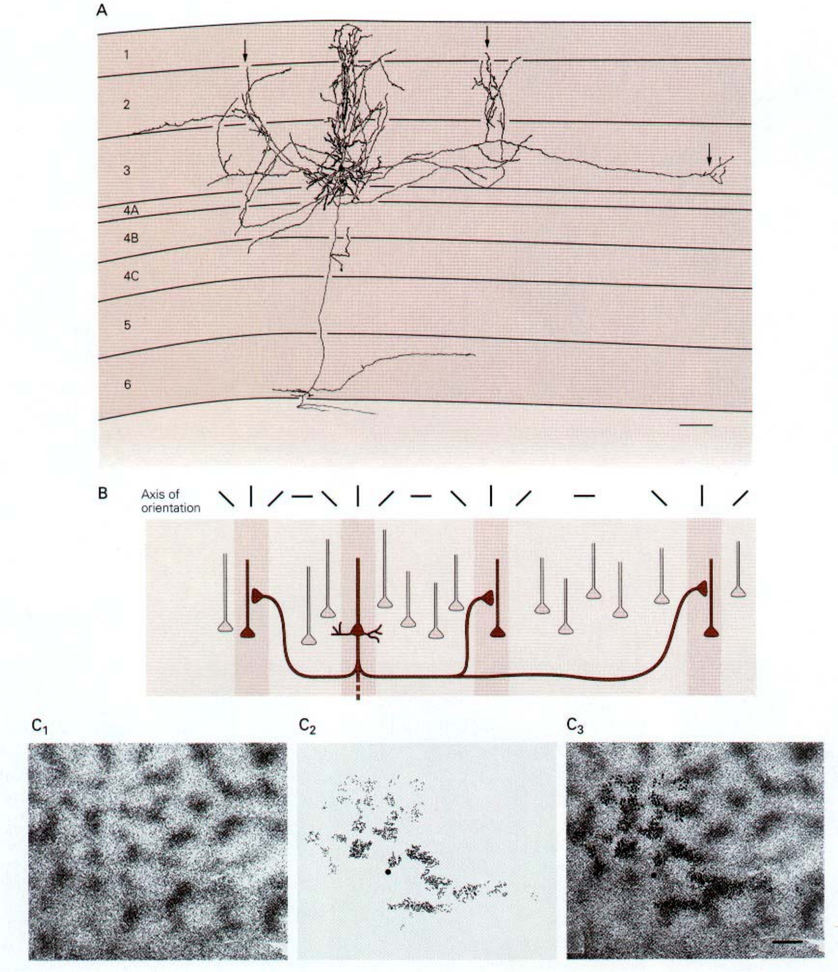
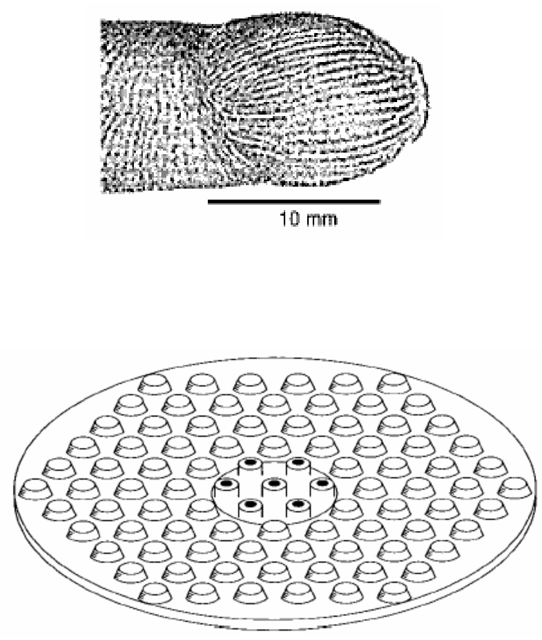


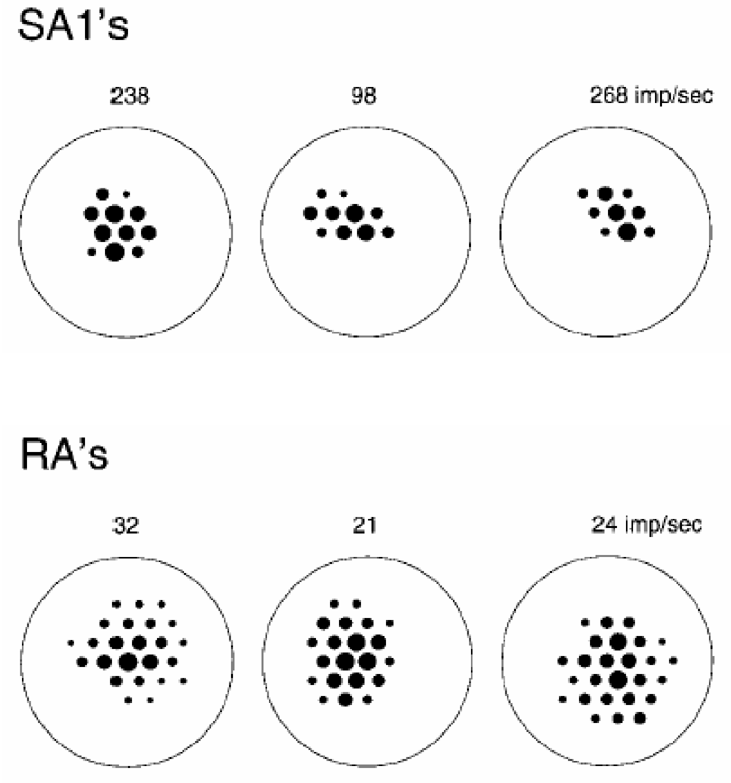
Fig.5-15

Summary (3)

- Functional maps are created at the CNS.

Tactile RF of Mechanoreceptive Afferents





(*Left*) Stimulus array. Seven active probes driven by linear motors occupy the central, 7 locations of a larger hexagonal array of static probes spaced at 1.0-mm intervals (center to center). Active probes are cylindrical rods, 0.5-mm diam. The passive probes are truncated cones raised 0.85 mm above the background with sides sloped at 60° relative to the base. Active and passive probes are both 0.5 mm in diameter where they contact the skin. The array illustrated here is smaller than the actual array (13 mm diam.).

(*Right*) RF maps of 3 typical SA1 (*Top panel*) and 3 typical RA (*Bottom panel*) afferents. Area of each • is proportional to the mean impulse rate evoked by the stimulus at that location relative to the rate evoked by the 500-µm stimulus at the hot spot (displayed above each pair of RFs). RA impulse rates are lower because the RA afferents responded only during the transient phase of the 200-ms indentation period. (From Vega-Bermudez and Johnson (1999)

Fig.5-16

Tactile RF of Area 3b of Somatosensory Cortex

RF structures observed in area 3b. Each *panel* gives a typical example of the type, the total number of RFs fitting the description, and their percent of the total RF sample (*n* = 247). The types are shown in decreasing order of frequency. *A*, A single inhibitory region located on the trailing (distal) side of the excitatory region. *B*, A region of inhibition located on one of the three nontrailing sides of the excitatory region. *C*, Two regions of inhibition on opposite sides of the excitatory region. *D*, Inhibition on three sides of the excitatory region. *E*, Inhibition on two contiguous sides of the excitatory region. *F*, A complete inhibitory surround. *G*, An excitatory region only. *H*, RF dominated by inhibition. *I*, RFs not easily assigned to one of the preceding categories. (From DiCarlo, Johnson and Hsiao 1998)

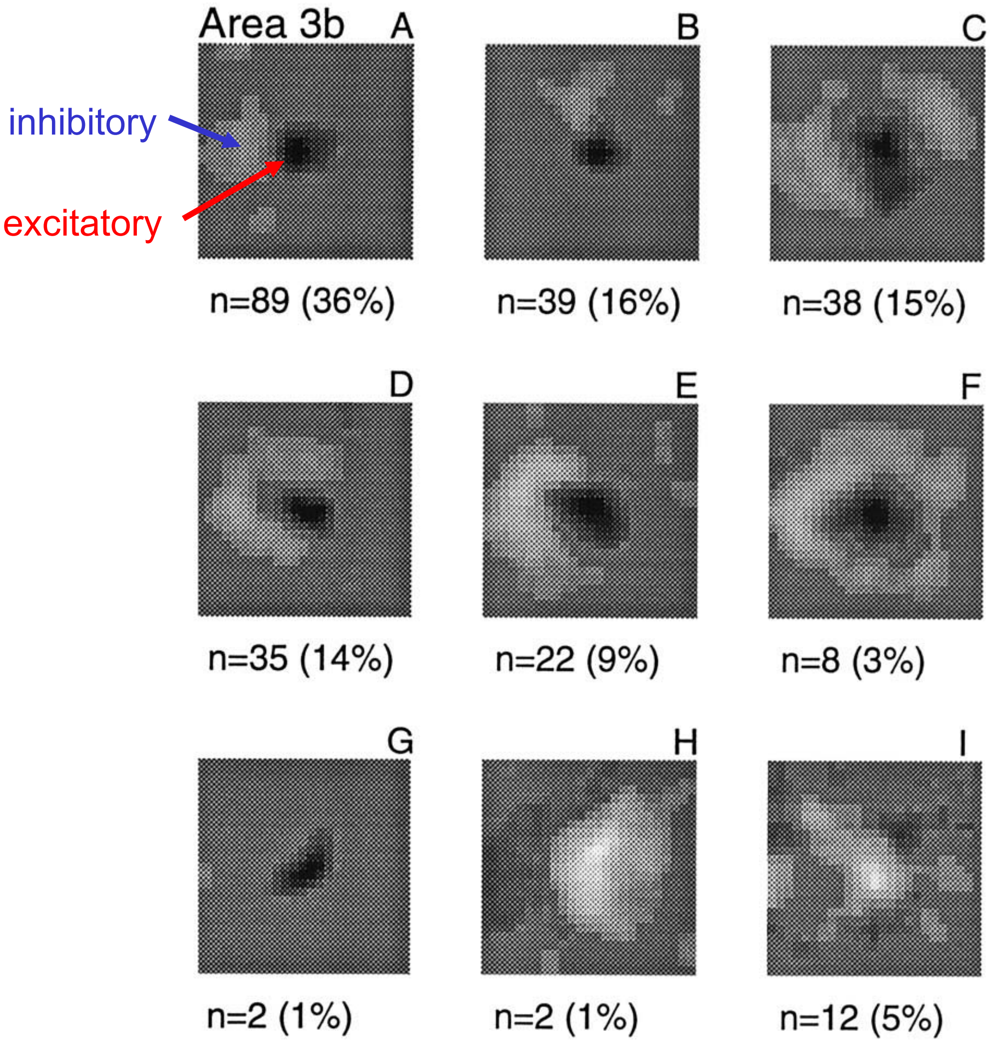
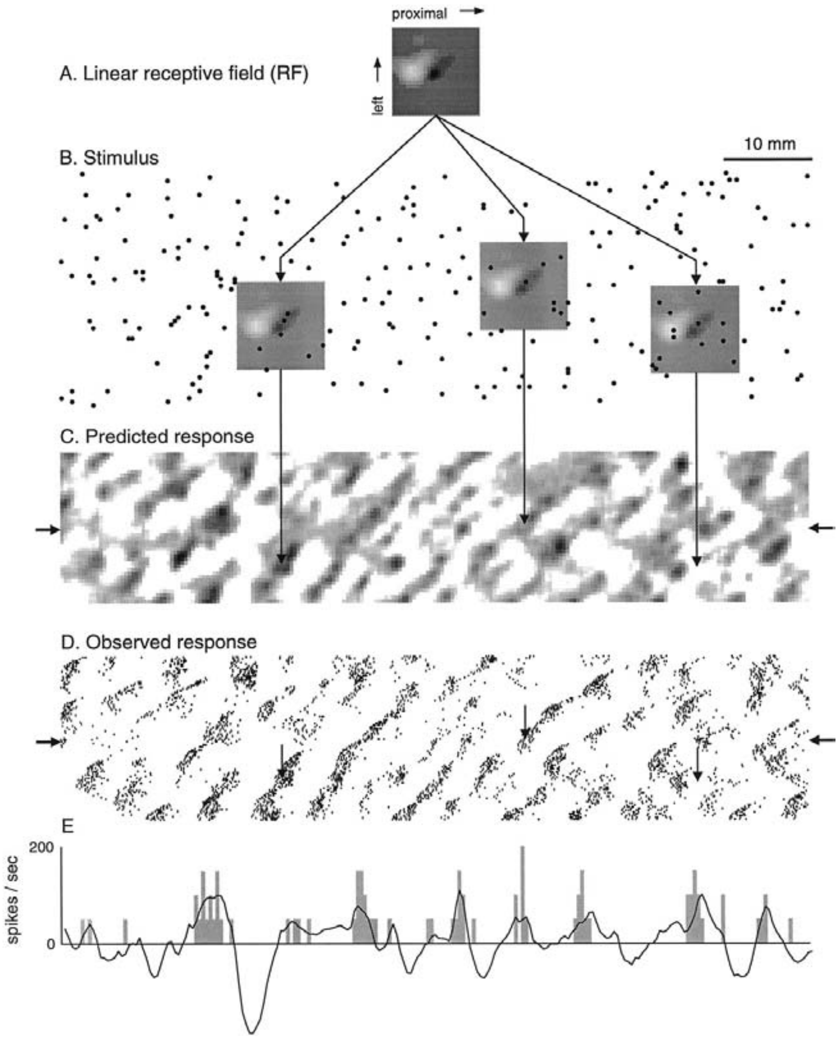


Fig.5-17

Measuring tactile RF using random dots

A typical neural response and the resulting RF estimate. *A*, RF estimate. The *gray scale* represents the grid of weights (25 × 25 bins = 10 × 10 mm) that best described the response of the neuron to the random dot stimulus pattern. The RF diagram is meant to represent excitatory and inhibitory skin regions viewed through the back of the finger as the finger points to the *left* and the stimulus pattern moves from *right* to *left* under the finger. The background *gray* level (50% *black*) represents the region where dots had no (linear) effect on the neural response, with darker levels representing excitatory regions where dots increased the probability of firing and lighter levels representing regions where dots decreased the probability of firing. *B*, A portion of the random dot stimulus pattern with the RF superimposed at three locations. The intensity of the RF *gray scale* has been reduced so the *stimulus dots* can be seen. *C*, Neural impulse rates predicted by convolving the RF (*A*) with the random dot stimulus (*B*) and by clipping negative values to zero. Darker regions correspond to higher predicted rates. The *arrows* extending from *B* to *C* point to the predicted impulse rates for each of the three RF positions in *B*. *D*, Observed response of this neuron. Each *tick mark* indicates the occurrence of a single spike. The plotted position of each spike was determined by the location of the stimulus pattern at the instant the spike occurred (SEP). The three *vertical arrows* indicate the responses at the stimulus locations corresponding to the three predicted responses in *C*. *E*, Predicted (*black line*) and observed (*gray histogram*) impulse rates in a single scan are indicated by the *arrows* at the *sides* of *C* and *D*. Predicted rates <0 correspond to periods in which the summed inhibitory effects exceed the summed excitatory effects. (From DiCarlo, Johnson and Hsiao 1998)

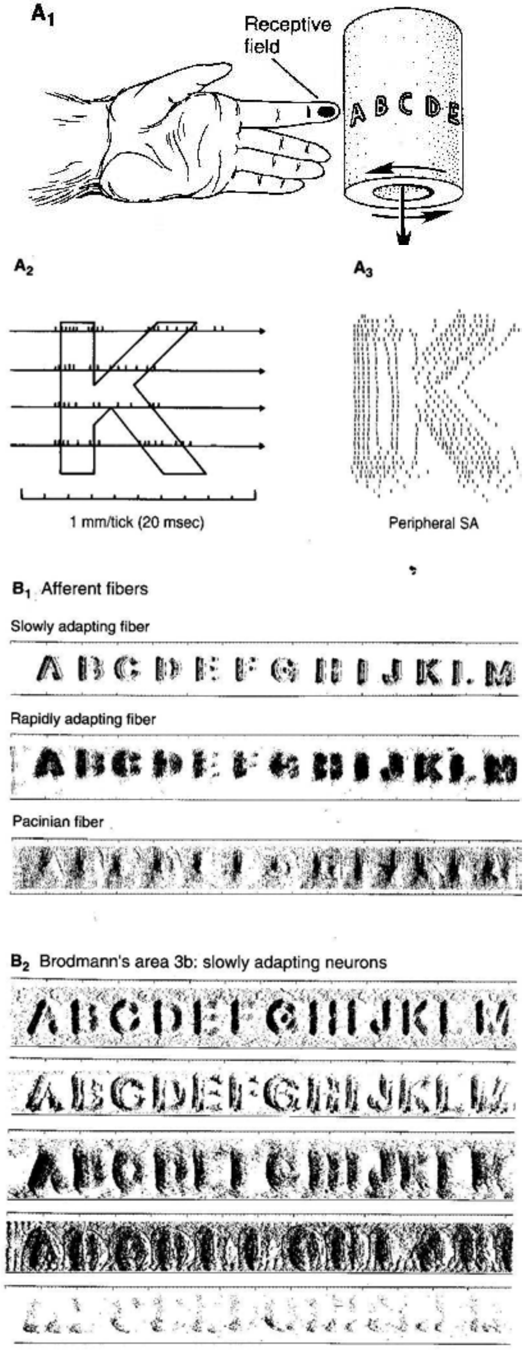


Neural Representation of Letter Shapes: PNS to CNS

Letter representations in somatosensory system. The spatial characteristics of embossed letters are represented in the discharge of cutaneous mechanoreception and neurons in primary somatic sensory cortex.

A). 1. Embossed letters on a cylindrical drum are used to study the spatial pattern of neuronal activity in mechanoreception innervating the finger tip and, in separate experiments, in cortical neurons in Brodmann's areas 3b and 1. Letters of the alphabet are repeatedly swept across a receptive field in the finger tip of a monkey by rotating the drum. The action potentials evoked by each letter in single afferent fibers (or cortical neurons) are plotted in spatial event plots. 2. Spatial event plots are constructed as follows. Embossed letters (about 6.0 mm high and 500 um in relief) are swept (50 times at 50 mm/s) across a given location within the receptive field of a single neuron innervating the finger pad, thereby producing action potentials. The drum is rotated and the stimulus is moved across the receptive field from proximal to distal (vertical bar of the K entered the receptive field first on each sweep). After each sweep, the drum is then shifted vertically within the receptive field by 200 um and swept again. The time of occurrence of each action potential relative to adjacent stimulus position markers is recorded and ordered from top to bottom so as to assign a spatial location relative to the stimulus surface. 3. In an actual spatial event plot for the letter K, each action potential in A_2 is presented as a dot.

B). 1. Spatial event plots reconstructed from the afferent fibers from three types of receptors in a monkey: slowly adapting (top), rapidly adapting (middle), and pacinian corpuscle (bottom). 2. Spatial event plots reconstructed from five slowly adapting neurons in area 3b of an awake monkey. (From K. O. Johnson et al.)



Afferents

Cortex

Fig.5-19

Summary (4)

- Neural coding of a sensory stimulus is progressively transformed from an isomorphic (faithful) representation at the PNS to a non-isomorphic representation at the CNS (i.e., transformation from physical dimensions to neural dimensions).

Summary of Lecture 5

- Each sensory system consists of both parallel and hierarchical processing pathways.

- The basic organization throughout the ascending pathway is the topographical organization ("topographical map") initially established by peripheral receptors.

- Functional maps are created at the CNS.

- Neural representation of a sensory stimulus is progressively transformed from an isomorphic representation at the PNS to a non-isomorphic representation at the CNS (i.e., transformation from physical dimensions to neural dimensions).

Prof. Kenneth O. Johnson
(1938-2005)

Kenneth Johnson, Professor of Neuroscience and Biomedical Engineering and Director of the Krieger Mind/Brain Institute of the Johns Hopkins University, passed away on May 15, 2005. Ken was an outstanding scientist who devoted his career towards understanding the neural mechanisms of perception. He was one of the first Ph.D. students to receive a degree from the Biomedical Engineering Department of the Johns Hopkins University. Throughout his career he was a strong advocate for using quantitative methods to understand how the brain works.

The late 1960s was an extremely exciting time in neuroscience. The method of single unit recording was in its infancy and with Vernon Mountcastle, who was Ken's thesis advisor at Hopkins, Ken decided to study the neural basis of behavior. Vernon had shown that the neural mechanisms underlying behavior could be studied directly and he had pioneered a new approach of studying the brain by combining psychophysical studies in humans with neurophysiological studies in non-human primates. Ken adopted this approach to use in his studies for his entire career.

Early on, Ken formalized and expanded on the ideas of neural coding in a landmark series of papers that provided a theoretical basis for linking neural representations to sensory discrimination performance (Johnson, 1980a,b). The theory is based on a working model that begins with the transduction of sensory stimuli by peripheral receptors into an initial neural representation of the external world. Ken viewed this initial representation as being relatively simple and considered it to be like a photographic neural image, where each afferent fiber is like a pixel in a video screen conveying information about local spatial and temporal patterns. These neural images are transmitted along the ascending pathways to synapse on neurons in the central nervous system where they are transformed through successive synaptic stages into a form that is suitable for memory and perception. In those papers Ken describes how to study the neural coding problem in subjects performing two-alternative forced choice tasks (2AFC). In these tasks subjects are presented successively with pairs of stimuli and are asked to indicate whether the stimuli were the same or different. The aim of these experiments is to determine the thresholds for behavior. Then neurophysiological experiments are performed on non-human primates using the exact same stimuli and stimulus conditions. The aim of these experiments is to determine how the stimuli are represented in the population response of the neurons. The neural code is then studied by hypothesizing plausible neural measures that can account for the psychophysical behavior. All possible codes are tested and only those codes that cannot be falsified remain. For example, in the 2AFC task, codes that predict discrimination performance that is worse than the observed behavior are rejected. The aim of neural coding studies is to eliminate potential codes until only a single code remains.

Over the years, Ken and his colleagues applied this paradigm to study a wide range of somatic perceptions, including the perception of temperature, vibration, two-dimensional form, and roughness. Here I will briefly describe a few of those studies. The first study that Ken performed was of the neural mechanisms of vibration intensity (Johnson, 1974). While psychophysical studies had shown that the subjective magnitude estimate of vibratory intensity rises linearly with amplitude, neurophysiological studies had found that the responses of peripheral afferent fibers to vibrations of different intensity is piecewise linear (resembles a staircase shaped function) and as such there was no simple one-to-one relationship between the neural responses and behavior. Ken recorded from over a hundred peripheral rapidly adapting (RA) fibers, reconstructed the population activity to vibrations of varying intensity, and tested a wide range of candidate neural codes. He narrowed the number of potential codes down to three simple measures that, like behavior, increased linearly with intensity. The codes that remained were: 1) total impulse frequency, 2) total number of active fibers, and 3) total number of entrained fibers.

Ken then left Johns Hopkins and joined Ian Darian-Smith at the University of Melbourne where they applied this approach to the perception of temperature. They found that the stimulus information encoded in the population of warm fibers is marginally greater than that needed for subjects' ability to judge changes in stimulus intensity (Johnson et al., 1979). A lesson that he learned from these and the vibratory studies is that finding a single neural code for simple behavioral tasks is difficult because for simple tasks, the dimensional space of potential codes is very large and consequently there is no objective basis for choosing one code over another.

Ken then turned his attention to more complex aspects of tactile perception. In an important series of studies with John Phillips, they showed that tactile spatial form is coded by the slowly adapting type I afferents (SA1). In these studies they performed psychophysical studies using gaps, gratings of various widths, and embossed letters of varying height to show that the spatial resolution on the fingertip is about 1 mm (Johnson and Phillips, 1981). In the neurophysiological studies they recorded from the three afferents that innervate the skin and found that only the responses from the SA1 afferents could account for the psychophysical performance (Phillips and Johnson, 1981a). In a related study they constructed a continuum mechanics model of the skin and found that the local stimulus determining the SA1 response is the maximum compressive strain at the receptor terminal (Phillips and Johnson, 1981b). These studies were the first to provide a role for the SA1 afferent fibers in perception and laid the groundwork for Ken's research at Johns Hopkins for the next 25 years.

The study of spatial form required that Ken and John develop a new kind of tactile stimulator. The result was a rotating drum stimulator that scanned two-dimensional patterns across the skin and mimicked the interaction that occurs between the finger and embossed patterns during scanning. Using this method, Ken, John, and I generated neural images and demonstrated how spatial information in the form of embossed letters and dots is represented in the peripheral afferents and in neurons in primary, and later in the secondary, somatosensory cortex (Phillips et al., 1988). This study showed clearly that in the periphery, RA and especially SA1 afferents have isomorphic responses and that Pacinian afferents transmit no spatial information. The role of the SA1 afferents in form processing was further supported by psychophysical studies showing that letters that are often confused during letter discrimination tasks have similar peripheral neural images in the SA1 responses (Vega-Bermudez et al., 1991). Furthermore the psychophysical studies showed that: 1) performance in active and passive scanning is the same and 2) the subjects' performance is unaffected by changes in scanning velocity. In the cortical studies we showed that neurons in primary somatosensory cortex have highly structured non-isomorphic responses and that there is a further loss of isomorphism in neurons in SII cortex. This study supported the notion that spatial information is transformed by neurons in the somatosensory cortex into a form that underlies memory and perception. In another study we showed that neurons in somatosensory cortex, especially SII, are greatly affected by the animal's focus of attention (Hsiao et al., 1993) and that attention modifies not only the firing rate but also the degree of synchronous firing between neurons (Steinmetz et al., 2000). These were some of the first studies to show the effects of selective attention in the somatosensory system.

For the next 15 years Ken set out to uncover the structure of the receptive fields of cortical neurons. While initial neural modeling studies (Bankman et al., 1990) indicated that neurons in S1 cortex had receptive fields composed of excitatory and inhibitory subregions, it was not until the late 1990s in a series of studies with Jim DiCarlo (DiCarlo et al.,1998, 1999, 2000) that we characterized, for the first time, the spatiotemporal receptive fields of neurons in area 3b. These studies demonstrated: 1) the variety of receptive field structures in SI cortex, 2) that neurons in area 3b tend to have receptive fields composed of a central excitatory region surrounded by one or more inhibitory regions, and 3) that there is a region of delayed inhibition that overlaps the excitatory region. These studies showed how spatial form is initially transformed in the somatosensory cortex.

Closely related to these studies of form processing were a series of studies of roughness perception in which the ideas of neural coding were fully explored and tested. There were four main studies in this series (see Johnson et al., 2002 for a review) of which I will only describe the first. In this study (Connor et al., 1990), Ken, John, Ed Connor, and I studied the neural coding of roughness perception using embossed dot patterns as stimuli. What made this study unique was that we had observed that the perception of roughness forms a non-monotonic inverted "U" shaped function of dot spacing. This was fortunate because it gave us the ability to test and reject a wide range of potential neural codes. The outcome was that roughness is based on the spatial variation in firing rates among SA1 afferents spaced about 2 mm apart. So far this neural code has stood up against all challenges and has been shown to have a consistent relationship with behavior over a large number of surfaces. Remarkably, in all four studies the relationship between the neural code and perception was linear which suggests that perception may be based on linear mechanisms. An exciting outcome of this study was that the neural code predicts that there are neurons with excitatory and inhibitory subregions identical to a subset of the receptive fields of S1 neurons. These results showed that form and texture are processed along common neural pathways.

Ken's research has had a broad influence on neuroscience. For example the studies of form processing led to the development of a medical device for testing spatial acuity in patients with nerve damage. He is also responsible for the idea of neural population vector coding that has been used extensively in neurophysiological studies of perception and the motor system.

When Ken passed away he left an active, functioning lab. Three papers from the lab have just been accepted for publication. Two of those are on the mechanisms of vibratory adaptation; the other is on the mechanisms of selective attention. In addition, several papers will soon be published based on the responses from a 400 probe tactile stimulator that Ken had been developing for the last 10 years. His dream had been to use this stimulator to present a broad range of spatiotemporal patterns to the skin.

Ken was a brilliant scientist and teacher who could see to the heart of problems. He has left us with a clear understanding of how information is organized and processed by the peripheral afferents, the roles that they play in perception, and corresponding neural codes that are used in the nervous system (Johnson, 2001). Furthermore, he showed how spatial information is transformed and processed in somatosensory cortex.

(By Dr. Steven Hsiao)