Biosystems II: Neuroscience

## Sensory Systems

Lecture 4

Neural Representations of Sensory Stimuli:
Concept of Receptive Field

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Outline

1. "Receptive field (RF)" describes a neuron's response boundary to a particular class of sensory stimuli

        a) RF is typically defined by mean firing rate (Fig.4-1)

        b) The size of RF varies across sensory receptor space (Fig.4-2)

        c) The size of RF depends on the threshold criterion (Fig.4-3)

2. The nature of RF depends on the stimulus and criterion used to define it (Figs.4-4, 4-5)

3. RF is usually associated with other properties of sensory stimuli (Figs. 4-6, 4-7)

4. RF may have both excitatory and inhibitory components (Figs. 4-8, 4-9)

5. Complex RF can be formed by convergence of inputs and balance between excitation and inhibition (Fig.4-10)

6. CNS neurons can extract (compute) stimulus information not explicitly encoded by sensory receptors or PNS neurons.

 - Examples: binaural processing in the auditory brainstem for sound localization (Figs.4-11, 4-12, 4-13)

# Receptive field (RF) is typically defined by mean firing rate
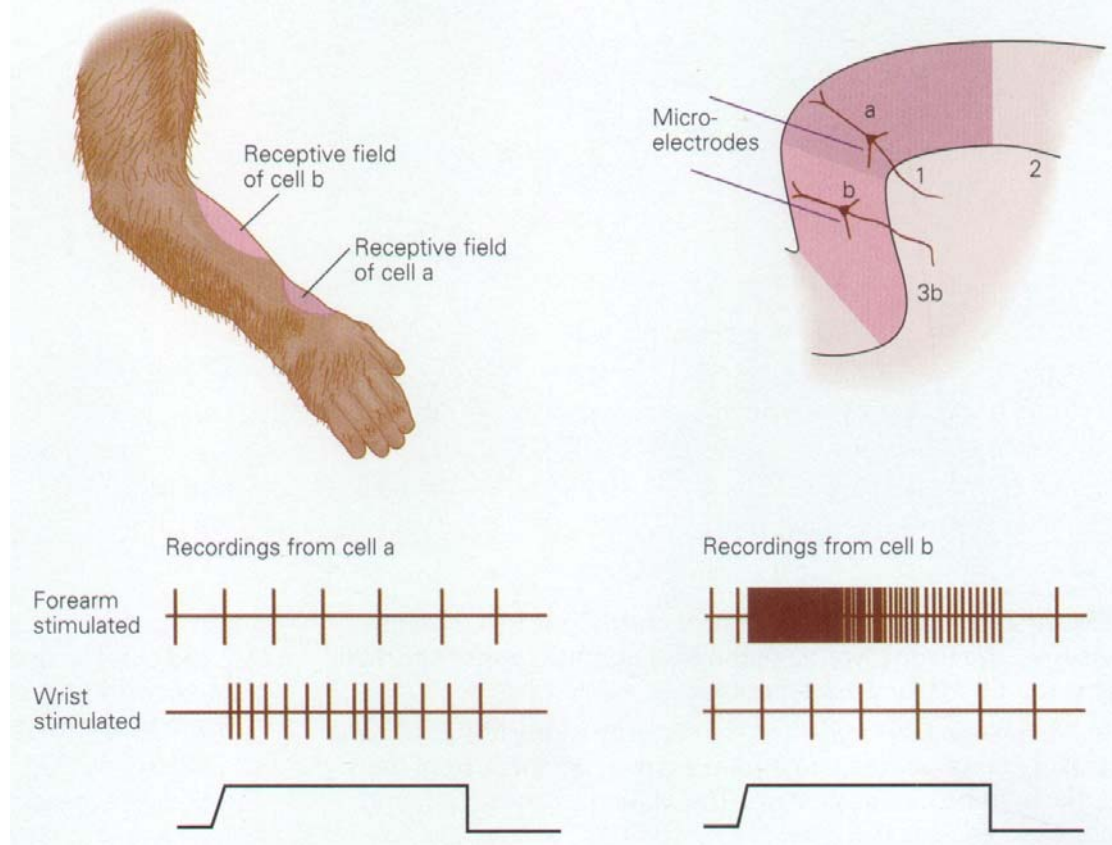
Three-dimensional functional maps of the cerebral cortex are created by examining the receptive field of adjacent cortical neurons in sequence. In this example a pair of microelectrodes are advanced into the S1 cortex. The neuron recorded at *location a* in area 1 has a sustained, slowly adapting response to pressure applied to the wrist with a small blunt probe and ceases firing when the probe is removed from the skin. It does not respond to pressure on the forearm. The neuron recorded at *location b* in area 3b responds vigorously to pressure on the forearm but not on the wrist. Note that cortical neurons, unlike sensory afferents, fire action potentials at low rates in the absence of stimuli.

Fig.4-1

Extracellular recordings are used to study neurons in the central nervous system

Much of what we know about the processing of somatic sensory information in the brain, particularly in the cerebral cortex, has been learned from studies of monkeys. The monkey has proven so useful because primates have sensory receptors identical to those of humans. Furthermore, psychophysical measurement of somatosensory discriminative abilities indicate that humans and monkeys experience the same tactile sensations in their hands when they feel vibration, palpate objects or touch a textured surface.

The techniques for studying the physiology of the cerebral cortex at the cellular level were developed by Prof. Vernon Mountcastle and his colleagues in the 1950s at Johns Hopkins University School of Medicine. Using extracellular microelectrodes (which had just become available) they recorded the electrical responses of individual neurons. Extracellular recordings reveal only the action potentials of the cell and thus, do not show synaptic activity except under certain circumstances. (Extracellular recording, however, is much simpler than intercellular recording in the intact brain because the brain pulsates, making it difficult to maintain intracellular penetrations.) Nevertheless, extracellular recording has been a useful tool in defining how sensory stimuli modulate the firing patterns of single neurons.

Microelectrode recording allows the receptive fields of several neurons at adjacent locations in the brain to be examined in sequence. By systematically moving the electrode in steps of thousandths of a millimeter, one can reconstruct a three-dimensional map of the cerebral cortex. This technique, termed micromapping, forms the experimental foundation for what we know about the columnar and somatotopic organization of the cortex.

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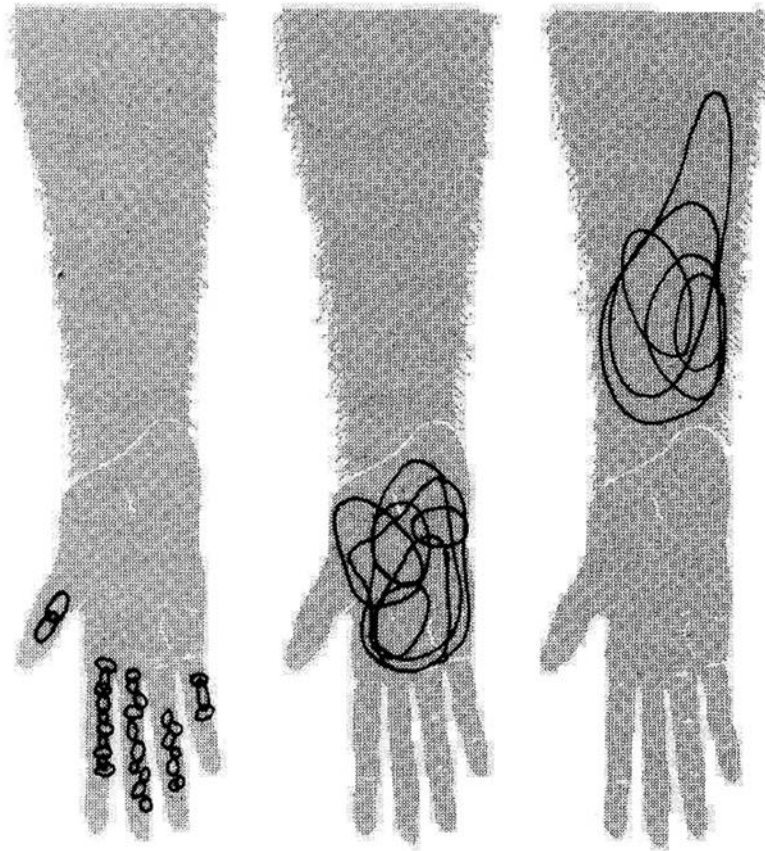
The size of RF varies across sensory receptor space, as illustrated by tactile RFs measured in different parts of skin surfaces in a monkey's arm.

Fig.4-2
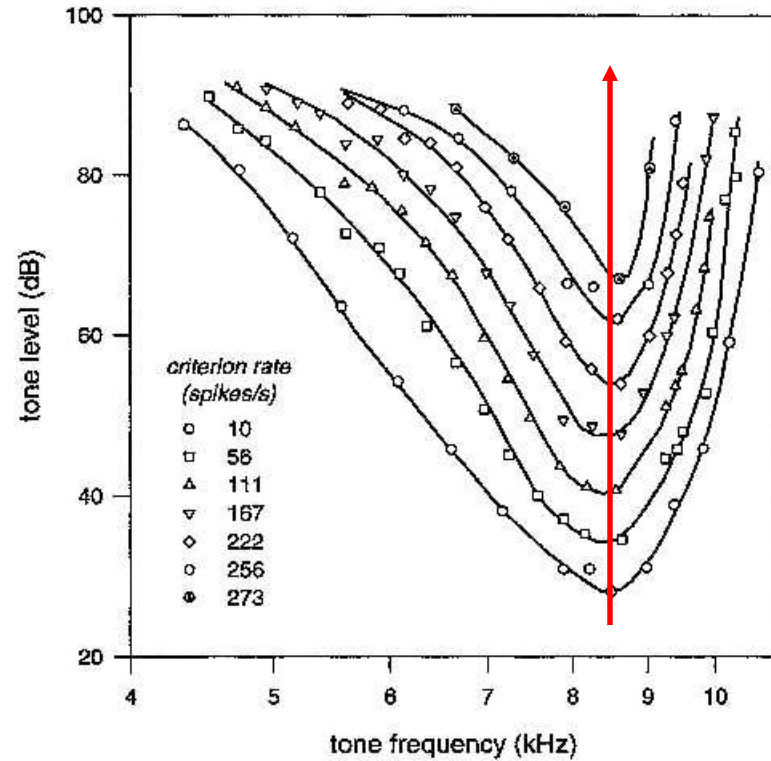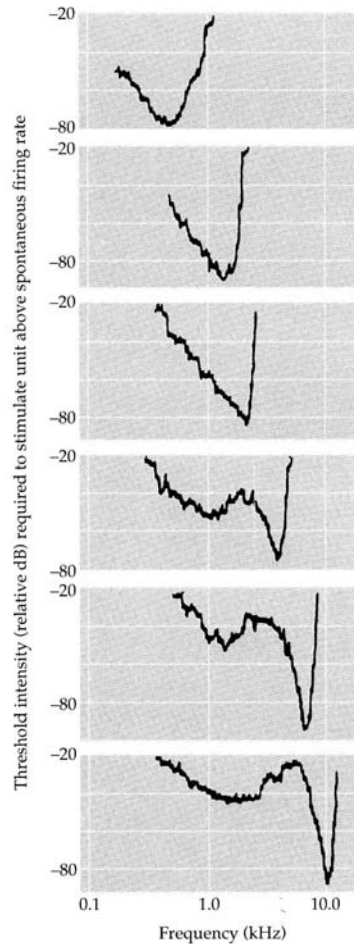
The size of RF depends on the threshold criterion. (left) Examples of RF of auditory-nerve fibers tuned to different frequencies. (right) RF of an auditory-nerve fiber defined by different criterion rates. Higher criterion rate results in smaller RF size.

Fig.4-3

Visual RF defined by spot light

Retinal ganglion cells respond optimally to contrast in their receptive fields. Ganglion cells have circular receptive fiends, with specialized center (pink) and surround (gray) regions. On-center cells are excited when stimulated by light in the center and inhibited when stimulated in the surround; off-center cells have the opposite responses. The figure shows the responses of both types of cells to five different light stimuli (the stimulated portion of the receptive field is shown in yellow). The pattern of action potentials fired by the ganglion cell in response to each stimulus is also shown in extracellular recordings. Duration of illumination is indicated by a bar above each record.

A). On-center cells respond best when the entire central part of the receptive field is stimulated (3). These cells also respond well, but less vigorously, when only a portion of the central field is stimulated by a spot of light (1). Illumination of the surround with a spot of light (2) or ring of light (4) reduces or sup- presses the cell firing, which resumes more vigorously for a short period after the light is turned off. Diffuse illumination of the entire receptive field (5) elicits a relatively weak discharge because the center and surround oppose each other's effects.

B). The spontaneous firing of off-center cells is suppressed when the central area of the receptive field is illuminated (1, 3) but accelerates for a short period after the stimulus is turned off. Light shone onto the surround of the receptive field excites the cell (2, 4).
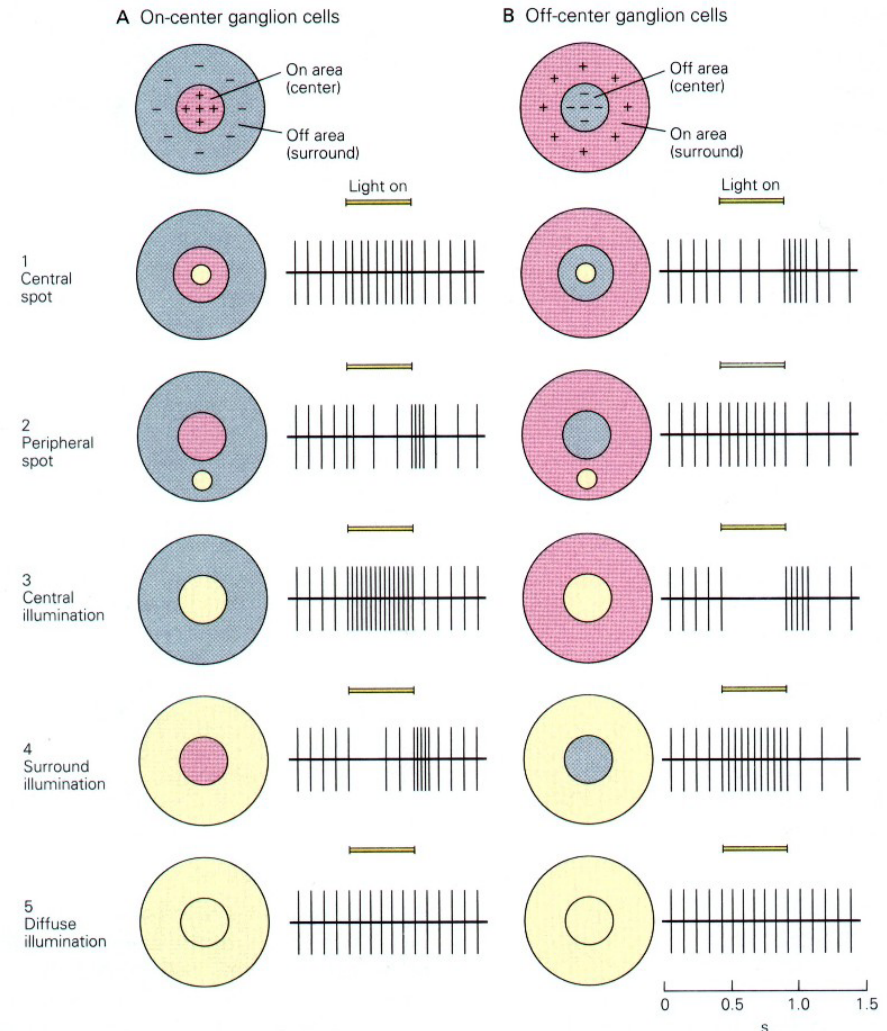

Fig.4-4

Receptive field of a simple cell in the primary visual cortex (V1). The receptive field of a cell in the visual system is determined by recording activity in the cell while spots and bars of light are projected onto the visual field at an appropriate distance from the fovea. The records shown here are for a single cell. Duration of illumination is indicated by a line above each record of action potentials.

1). The cell's response to a bar of light is strongest if the bar of light is vertically oriented in the center of its receptive field.

2). Spots of light consistently elicit weak responses or no response. A small spot in the excitatory center of the field elicits only a weak excitatory response (a). A small spot in the inhibitory area elicits a weak inhibitory response (b). Diffuse light produces no response (c).

3). By using spots of light, the excitatory or "on" areas (+) and inhibitory or "off" areas (-) can be mapped, The map of the responses reveals an elongated "on" area and a surrounding "off" area, consistent with the optimal response of the cell to a vertical bar of light.
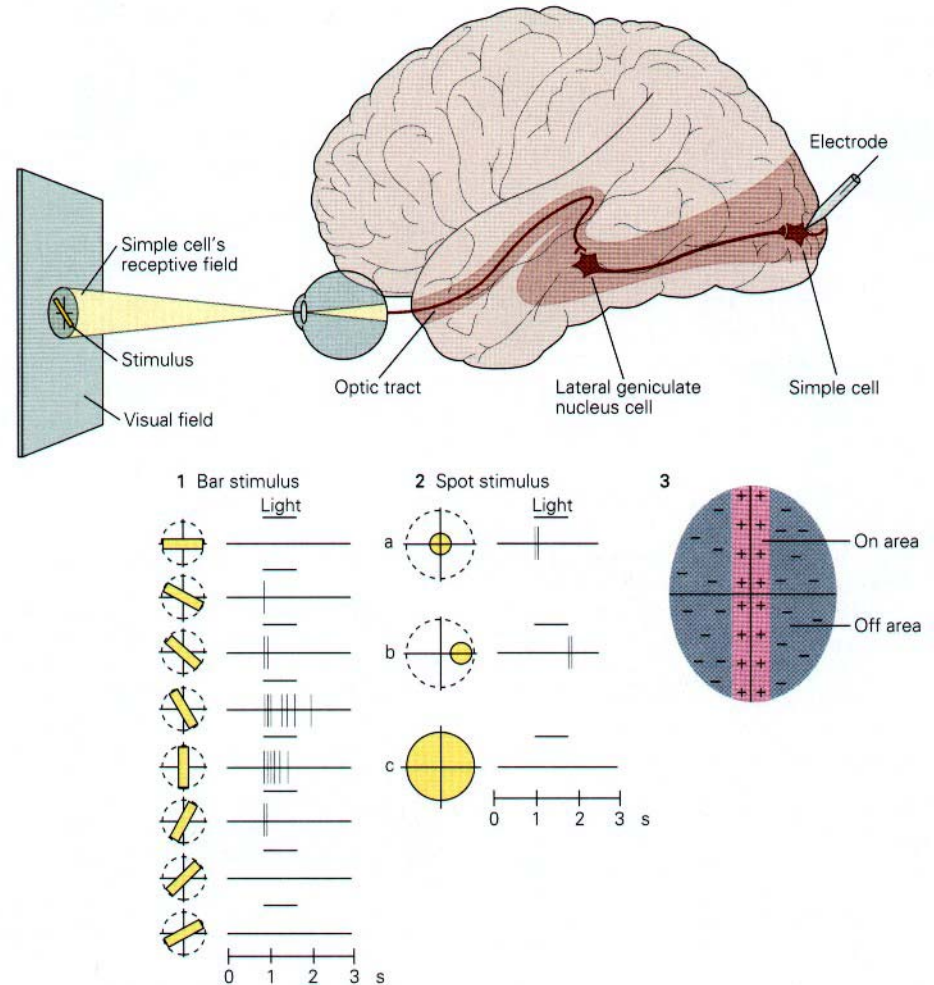
Fig.4-5

RF is usually associated with other properties of sensory stimuli

The receptive fields of primate retinal ganglion cells have two concentrically organized regions, a center and an antagonistic surround. This fundamental organization is expressed in two basic forms: In an on-center cell, light falling on the center excites the cell while light falling on the surround inhibits it. In an off-center cell, light falling on the center inhibits the cell while light falling on the surround excites it. Different types of ganglion cells are distinguished by the sizes of their receptive fields and by the ways in which their centers and surrounds integrate signals from the different classes of cones.
A). M cells constitute about 8% of all ganglion cells. Even the smallest center receives inputs from several cones. The spectral sensitivities of center and surround differ little, if at all.
B). P cells constitute about 80% of all ganglion cells. Two sub-types are defined by the organization of cone inputs. The "red-green" opponent type receives inputs only from L and M cones, whereas the "yellow-blue" type receives input from all three classes of cones. Within the red-green class different connections to cones give rise to multiple cell subtypes: on- or off-center cells, and centers with L or M cone inputs. The cone inputs to the surround are less firmly established, but are generally thought to arise from the class that does not feed the center. In cells in and near the fovea the center of the receptive field receives input from a single cone; in more peripheral regions of retina several cones provide input to the center. Less is known about the structure of the receptive fiends of the blue- yellow type of P cell. The antagonistic mechanisms seem to overlap more, possibly because chromatic aberration defocuses short-wavelength light, and center and surround are harder to distinguish. Cells in which S cones contribute the "off " signal are rare.
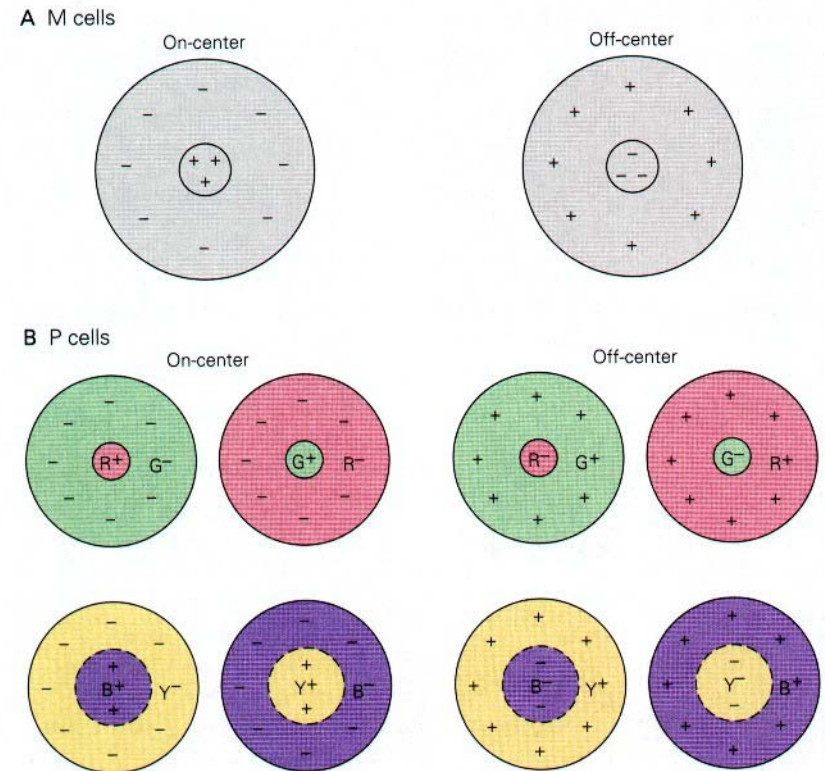

Fig.4-6

Signal processing properties of neurons are linked to their RF properties

The firing patterns of mechanoreception in the superficial layers of the skin encode the texture of objects rubbed across the skin.

A). 1. The nerve responses to textures are measured with the hand immobilized. The receptive field of a single receptor on a monkey's finger is stimulated with an embossed array of raised dots on a rotating drum. The pattern moves horizontally over the receptive field as the drum rotates The experimenter thus controls the speed of movement and the location of the dot pattern in the receptive field. The pattern is moved laterally on successive rotations to allow the dots to cross the medial, central, and lateral portions of the receptive field on successive rotations. The composite response of an individual nerve fiber to successive views of the raised dots simulates the distribution of active and inactive nerve fibers in the population. 2. Sequential action potentials discharged by individual receptors during each revolution of the drum are represented in spatial event plots in which each action potential is a small dot, and each horizontal row of dots represents a scan with the pattern shafted laterally on the finger.

B). Spatial event plots of three types of mechanoreception to dot patterns with different spacing. Slowly adapting Merkel disk receptors and rapidly adapting Meissner's corpuscles differentiate between dots and blank space when the spacing of the dots exceeds the receptive field diameter. A receptor fires bursts of action potentials for each dot, spaced by silent intervals. As the dots are brought closer together, the resolution of individual dots blurs. Pacinian corpuscles do not distinguish texture patterns because their receptive fields are larger than the dot spacing.
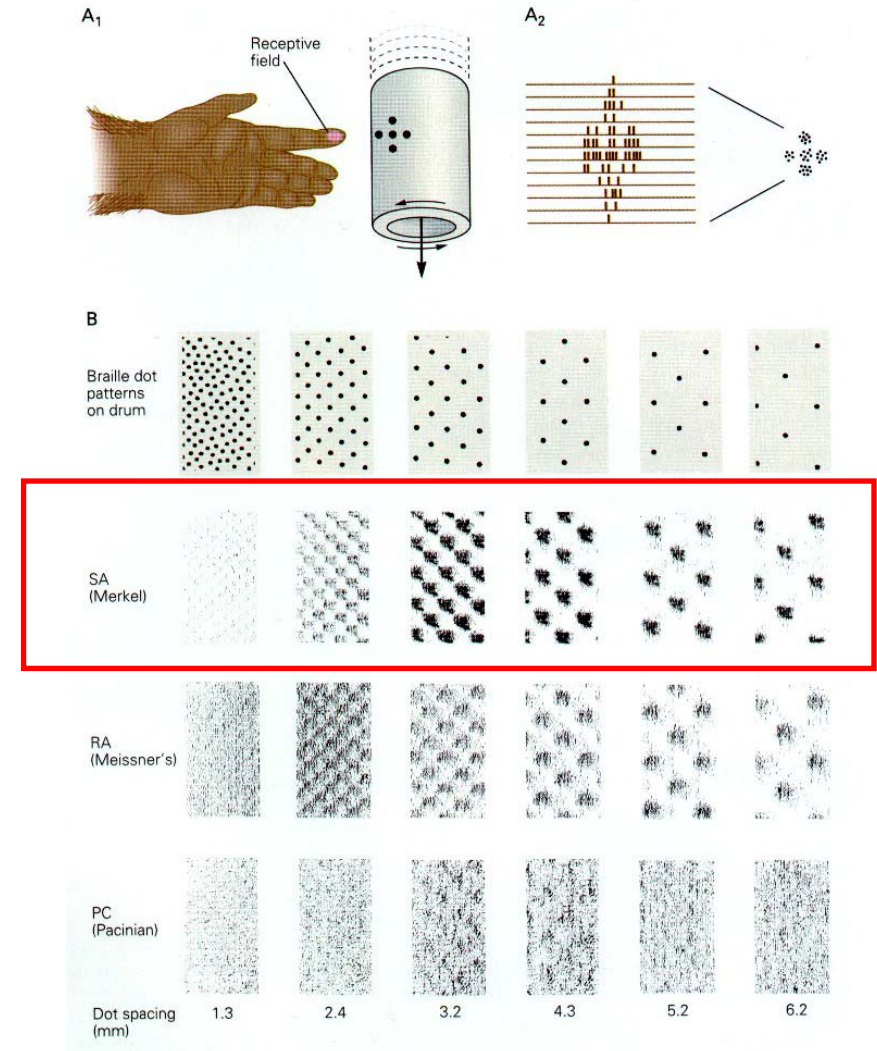

Fig.4-7

RF may have both excitatory and inhibitory components

The receptive field of a higher-order neuron in the dorsal column nuclei has a characteristic pattern of excitation and inhibition that increases spatial resolution.

A). Many peripheral receptors converge onto a single second-order sensory neuron in the dorsal column nuclei. As a consequence, the excitatory receptive field of the central neuron is made up of the receptive fields of all the presynaptic cells.

B). The receptive field of a neuron in the dorsal column nuclei and in the ventral posterior nuclei of the thalamus typically has a central excitatory receptive field surrounded or flanked by an inhibitory region. The addition of inhibitory interneurons (gray) narrows the discharge zone. Feed-forward inhibition sharpens the representation of a puncture stimulus by limiting the spread of excitation through convergent neural networks. On either side of the excitatory region the discharge rate is driven below the resting level by inhibition.

C). The asymmetric distribution of inhibitory interneurons produces lateral inhibition. In this schematic network stimulation in the upper portion of the receptive field produces strong excitation of the relay neuron. Stimulation of the lower portion of the receptive field inhibits firing because the interneurons produce feed- forward inhibition. Stimulation in the zone of overlap of excitation and inhibition reduces the responsiveness of the relay neuron to the stimulus. Lateral inhibition is particularly important for feature detection.
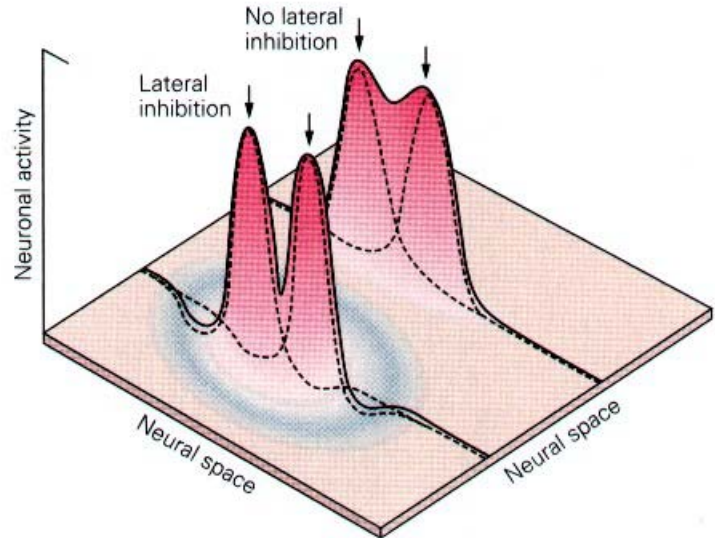

A Convergent excitation

B Surround inhibition

C Lateral inhibition

Fig.4-8
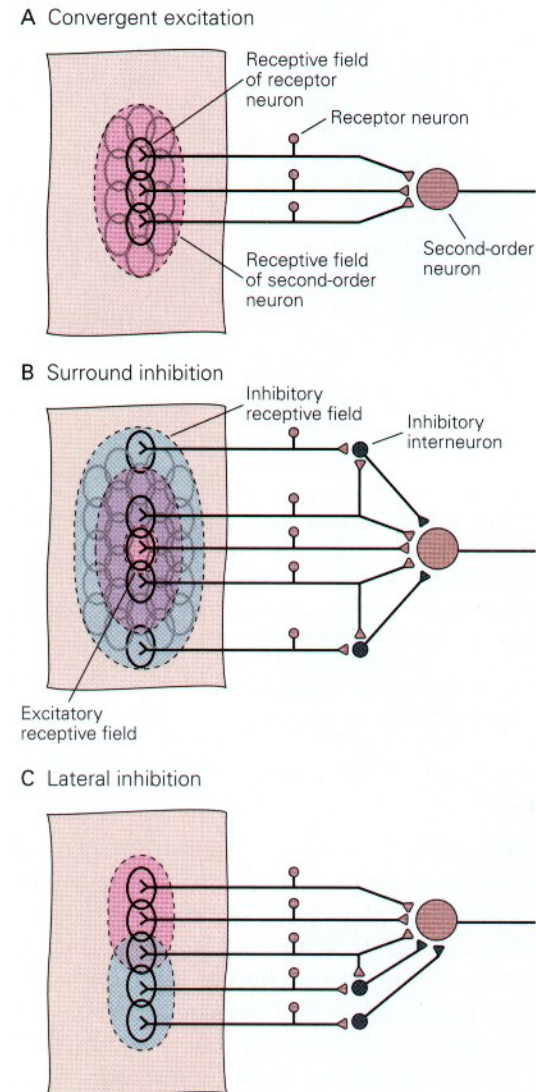
Inhibition helps to sharpen stimulus selectivity

A One-point stimulus
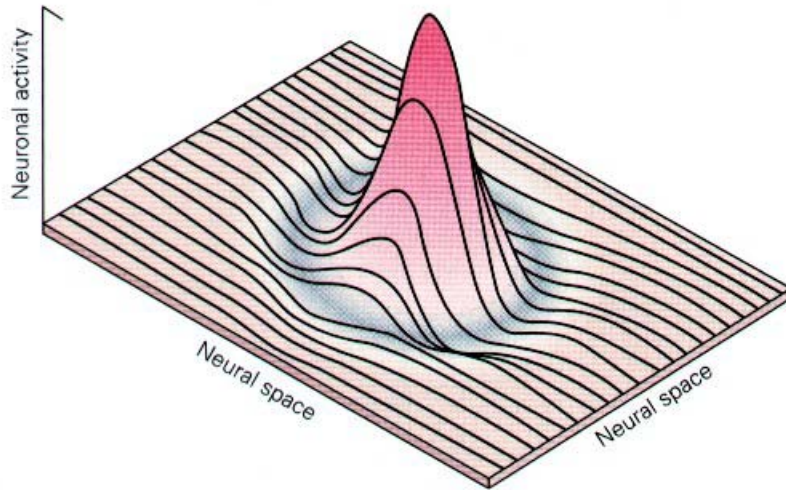
B Two-point stimulus

Two-point discrimination depends on separation of the signals from each source.
A). Stimulation of a single point on the skin activates one population of cells in the cortex. Maximal activity is in the center of the population. These neurons are surrounded by a band of neurons whose firing rates are depressed below normal tonic levels by the actions of interneurons that form lateral inhibitory networks.
B). Stimulation of two adjacent points activates two populations of receptors, each with a peak of activity (dotted lines). Normally the convergence of the two active populations in the central nervous system would result in a single large group of undistinguished inputs (all excitatory). However, lateral inhibitory networks suppress excitation of the neurons between the points, sharpening the central focus and preserving the spatial clarity of the original stimulus (solid line).
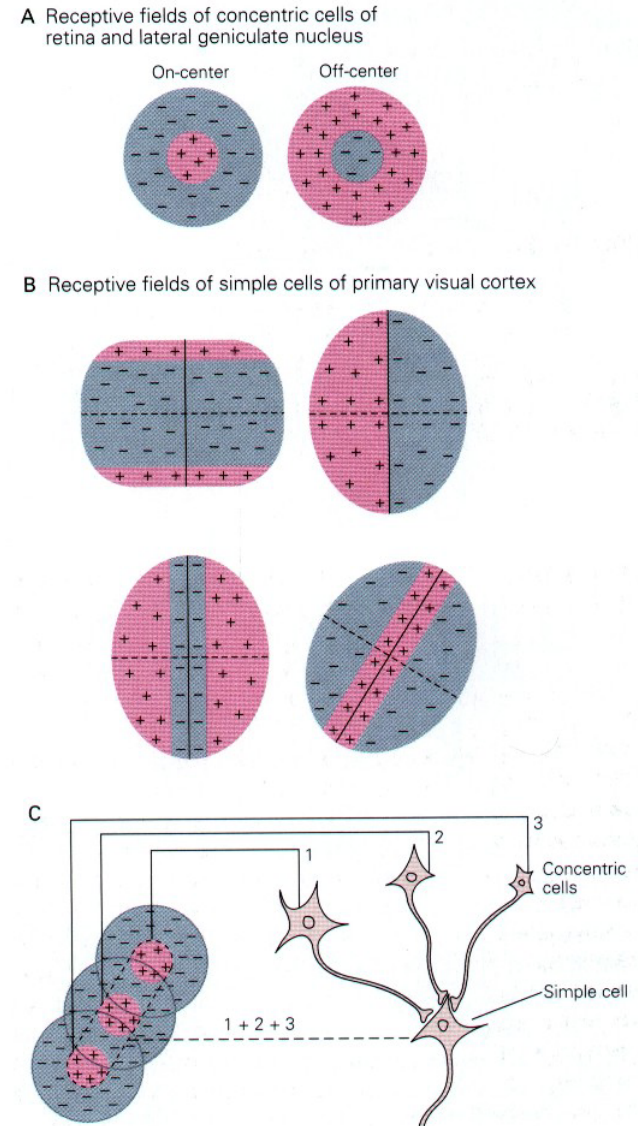
Fig.4-9

Complex RF can be formed by convergence of inputs and balance between excitation and inhibition

The receptive fields of simple cells in the primary visual cortex are different and more varied than those of the neurons in the retina and lateral geniculate nucleus.
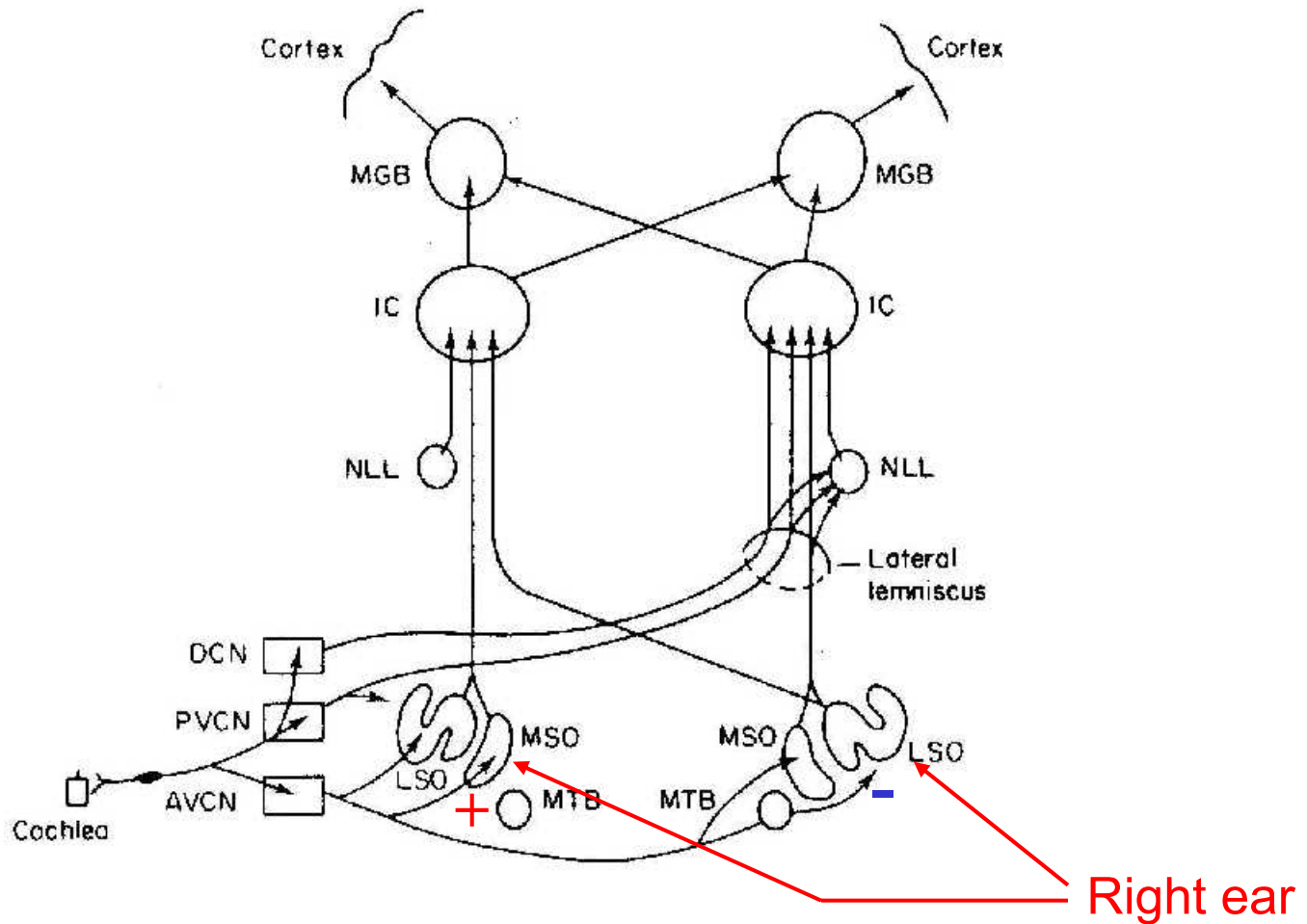**A).** Cells of the retina and lateral geniculate nucleus fall into two classes: on-center and off-center. The receptive fields of these neurons have a center-surround organization due to antagonistic excitatory (+) and inhibitory (-) regions.
B). The receptive fields of simple cells in the primary visual cortex have narrow elongated zones with either excitatory (+) or inhibitory (-) flanking areas. Despite the variety, the receptive fields of simple cells share three features: (1) specific retinal position, (2) discrete excitatory and inhibitory zones, and (3) a specific axis of orientation.
C). Model of the organization of inputs in the receptive field of simple cells proposed by Hubel and Wiesel. According to this model, a simple cortical neuron in the primary visual cortex receives convergent excitatory connections from three or more on-center cells that together represent light falling along a straight line in the retina. As a result, the receptive field of the simple cortical cell has an elongated excitatory region, indicated by the colored outline in the receptive field diagram. The inhibitory surround of the sample cortical cells is probably provided by off-center cells whose receptive fiends (not shown) are adjacent to those of the on-center cells.

A Receptive fields of concentric cells of retina and lateral geniculate nucleus

On-center   Off-center

B Receptive fields of simple cells of primary visual cortex

C

Concentric cells

Simple cell

1 + 2 + 3

Fig.4-10

The main ascending auditory pathways of the brainstem. Many minor pathways are not shown. Abbreviations: AVCN, anteroventral cochlear nucleus; PVCN, posteroventral cochlear nucleus; DCN, dorsal cochlear nucleus; LSO, lateral superior olivary nucleus; MSO, medial superior olivary nucleus; MTB, medial nucleus of trapezoid body; IC, inferior colliculus ; MGB, medial geniculate body; NLL, nucleus of the lateral lemniscus.

Fig.4-11

CNS neurons can extract (compute) stimulus information not explicitly encoded by sensory receptors or PNS neurons
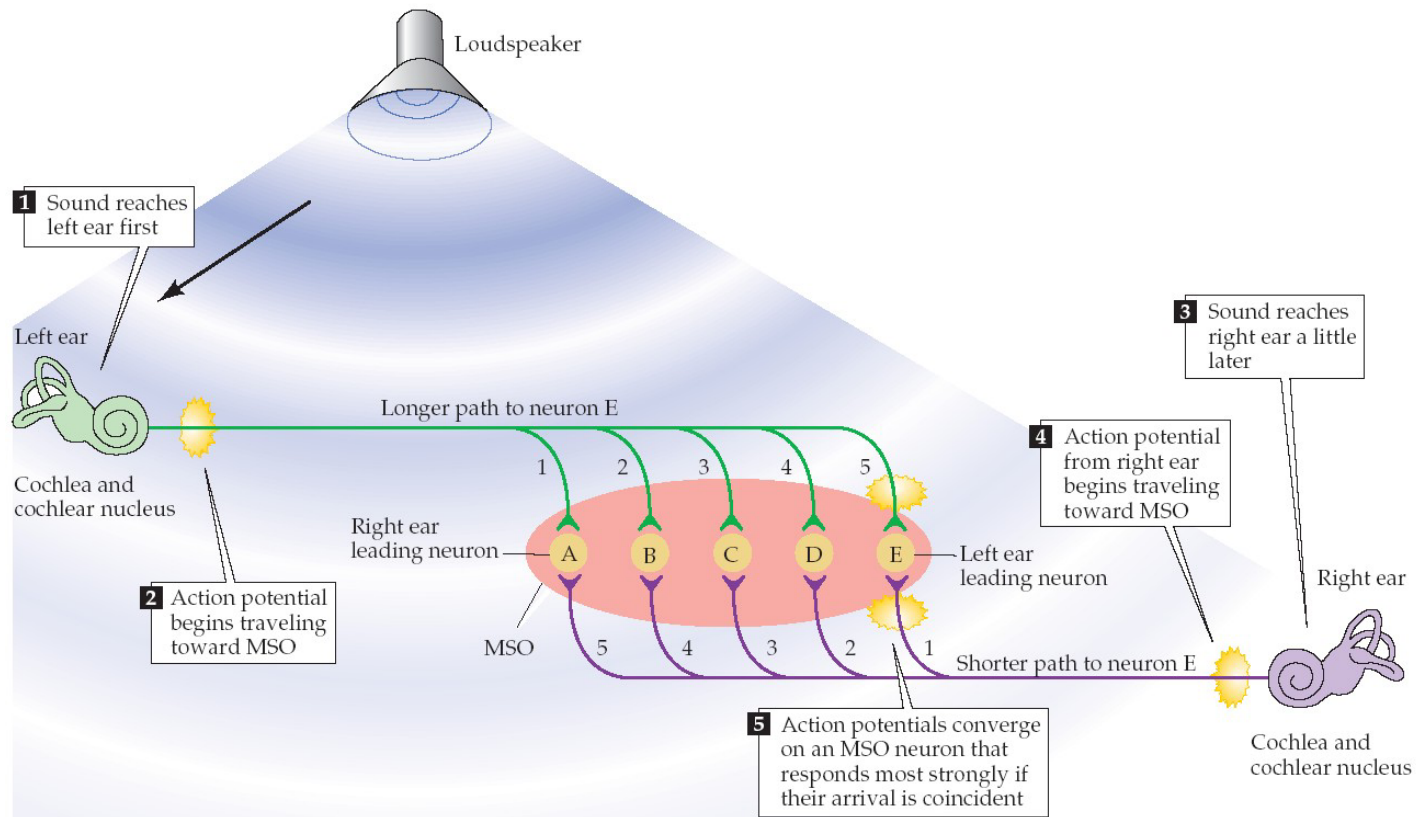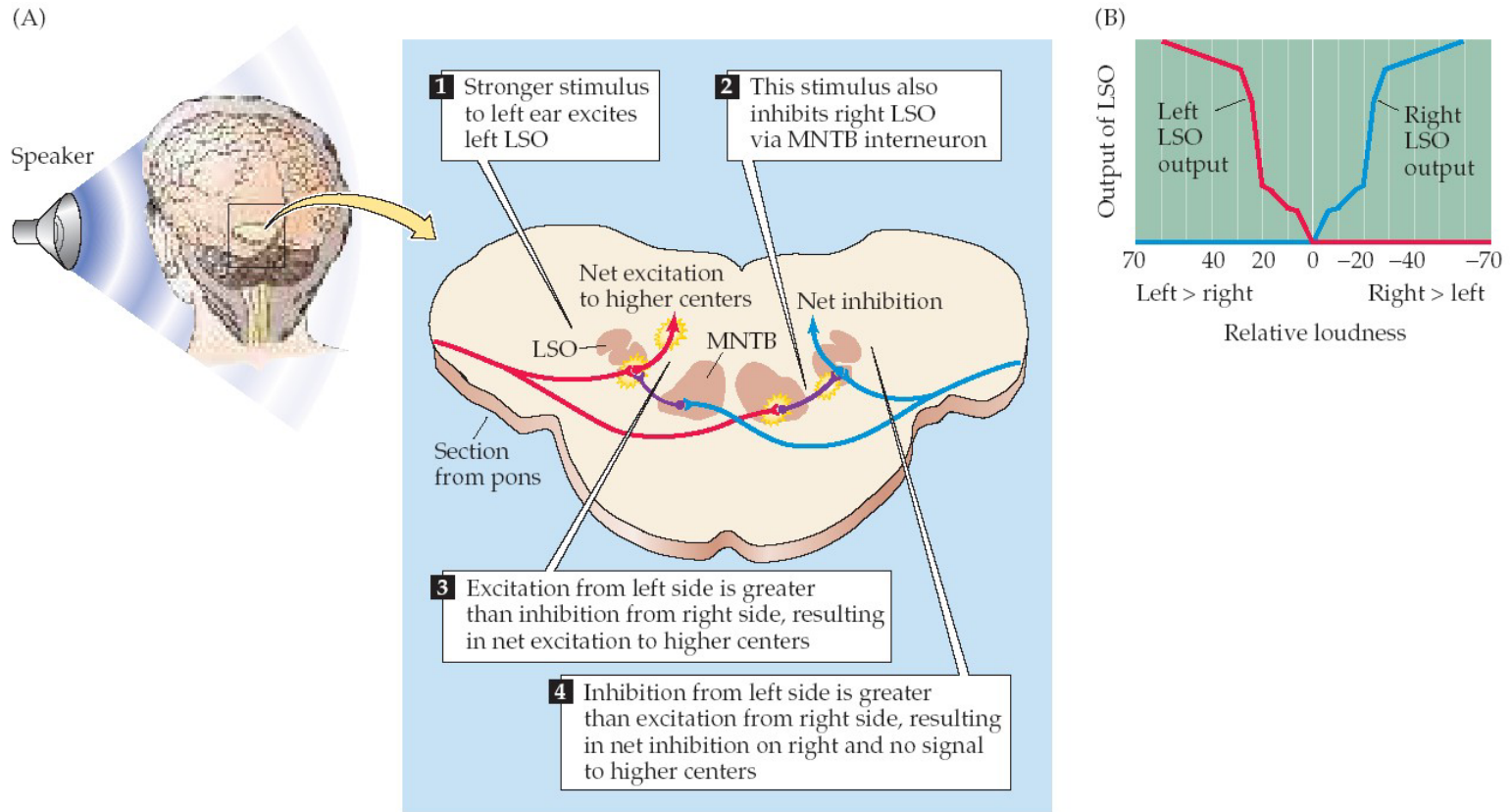

Diagram illustrating how the medial superior olive (MSO) computes the location of a sound by interaural time differences. A given MSO neuron responds most strongly when the two inputs arrive simultaneously, as occurs when the contralateral and ipsilateral inputs precisely compensate (via their different lengths) for differences in the time of arrival of a sound at the two ears. The systematic (and inverse) variation in the delay lengths of the two inputs creates a map of sound location: in this model, **E** would be most sensitive to sounds located to the left, and **A** to sounds from the right; C would respond best to sounds coming from directly in front of the listener.

Fig.4-12

(A)

Speaker

1 Stronger stimulus to left ear excites left LSO

2 This stimulus also inhibits right LSO via MNTB interneuron

Net excitation to higher centers

Net inhibition

LSO

MNTB

Section from pons

3 Excitation from left side is greater than inhibition from right side, resulting in net excitation to higher centers

4 Inhibition from left side is greater than excitation from right side, resulting in net inhibition on right and no signal to higher centers

(B)

Output of LSO

Left LSO output

Right LSO output

70   40   20   0   −20 −40   −70

Left > right   Right > left

Relative loudness

Lateral superior olive (LSO) neurons encode sound location through interaural intensity differences. (A) LSO neurons receive direct excitation from the ipsilateral cochlear nucleus; input from the contralateral cochlear nucleus is relayed via inhibitory interneurons in the MNTB. (B) This arrangement of excitation-inhibition makes LSO neurons fire most strongly in response to sounds arising directly lateral to the listener on the same side as the LSO, because excitation from the ipsilateral input will be great and inhibition from the contralateral input will be small. In contrasts, sounds arising from in front of the listener, or from the opposite side, will silence the LSO output, because excitation from the ipsilateral input will be minimal but inhibition driven by the contralateral input will be great. Note that LSOs are paired and bilaterally symmetrical; each LSO only encodes the location of sounds arising on the same side of the body as its location,

Fig.4-13

Summary of Lecture 4

1. Each sensory neuron has a receptive field (RF). The nature of a RF depends on the stimulus and criterion used to define it.

2. Complex RF is achieved by convergence of inputs and balance between excitatory and inhibitory components.

3. CNS neurons can extract (compute) stimulus information not explicitly encoded by sensory receptors or PNS neurons.