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"The Somatosensory System"

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THE SOMATOSENSORY SYSTEM

1. RECEPTORS

Receptors in the skin can be classified both according to the morphology of their endings and by their physiological responses to deformation. Specific receptors subserve specific sub-modalities of somatic sensation.

Slowly adapting (SA) receptors, as their name suggests, respond in tonic fashion to a maintained indentation. They convey information about static touch or pressure. SA type I receptors are the Merkel cell- neurite complex. SA type II receptors are Ruffini endings.

Rapidly adapting (RA) receptors respond phasically to maintained indentation, to its onset and offset. They respond well to oscillatory stimuli of varying depth, and convey information about flutter-vibration. Low frequency transduction in the glabrous skin is done by Meissner corpuscles, and in hairy skin by nerve endings in the hair follicle complex. High frequency transduction, in both glabrous and hairy skin, is done by the deep-lying Pacinian corpusles.

In muscles, spindle afferents with annulospiral endings provide information about muscle length. Golgi tendon organs signal muscle tension. In joint capsules, Ruffini endings signal joint angle. Together, these receptors provide information on limb position or kinesthesis.

The various kinds of encapsulated endings above are connected to large diameter, heavily myelinated, primary afferent fibers. Somatic transduction can also be done by free nerve endings on small diameter, lightly myelinated or unmyelinated primary afferent fibers. Afferent fibers are bundled in nerves, and information from a dermatome on the skin enters the appropriate level of the spinal cord.

2. ASCENDING PATHWAYS

There are two major pathways that carry somatic information through the spinal cord. In addition, the trigeminal system conveys somatic information from the face and part of the head.

A. The dorsal column - medial lemniscal system (touch-pressure, flutter-vibration and kinesthesis). Large diameter primary afferents project ipsilaterally via the dorsal columns to the nucleus gracilis (lower body) and cuneatus (upper body); collaterals enter the dorsal horn to relay to spinal reflex pathways, spinocerebellar neurons and some spinothalamic and spinoreticular neurons. Fibers representing different submodalities terminate

in different parts of the dorsal column nuclei (DCN). The dorsal column nuclei project to the contralateral thalamus - principally to the ventroposterolateral nucleus. (VPL). After leaving the DCN, the ascending axons cross the midline as internal arcuate fibers in the medulla and ascend toward the thalamus in the medial lemniscus.

B. The anterolateral system (touch, pain and temperature). Small diameter primary afferents project via Lissauer's tract to dorsal horn neurons, principally ipsilateral to the side of entry. Collaterals relay to spinal reflex pathways, and to spinoreticular, spinocervical and spinothalamic neurons.

Axons ascending toward the thalamus (spinothalamic tract fibers) are principally crossed and traverse the midline over several segments above their cells of origin. The cells of origin are found mainly in layers III-V of the spinal gray matter. Spinothalamic tract axons ascend in the anterolateral funiculus and terminate in several regions of the brain including a) the VPL nucleus of the thalamus b) the centrolateral intralaminar nucleus of the thalamus, c) the posteromedial nucleus (Pom) of the thalamus, d) various brain stem nuclei, e) the periaqueductal gray matter of the midbrain. Thus, some axons in the spinothalamic tract may send out collaterals en route to the thalamus, while others may never reach the thalamus.

C. The trigeminal system. The organization of this system is analogous to that of the segmental system ascending via the spinal cord. The primary afferents are found principally in cranial nerve V, also in nerves VII, IX, and X.

Thick, myelinated primary afferents for touch and vibration have cell bodies located in the semilunar ganglion and send a major axonal branch into the principal sensory nucleus of the V nerve, the functional equivalent of the dorsal column nuclei. Collaterals descend in the spinal tract of V to all regions of the spinal nucleus of V (particularly the magnocellular region of the caudal division) to synapse with cells projecting to the cerebellum and with "spinothalamic - like" cells.

The principal nucleus of V sends to the thalamus crossed axons (ventral trigeminothalamic tract) that ascend in association with the medial lemniscus and uncrossed axons (dorsal trigeminothalamic tract) that ascend near the central gray. These axons terminate principally in the ventroposteromedial nucleus (VPM), with a few going on to Pom.

Primary afferents for position sense (joint and muscle afferents) have cell bodies located in the mesencephalic nucleus of V. Primary afferents and interneurons of the nucleus send axons to the motor nucleus of V for masticatory reflexes. Cells of the mesencephalic nucleus of V also project to the cerebellum and perhaps to thalamus.

Smaller diameter primary afferents for pain and temperature have cell bodies located in the semilunar ganglion and send axons into the spinal tract of V. They descend to terminate mainly in the substantia gelatinosa of the caudal division of the spinal nucleus of V. The axons of the second order neurons ascend with the contralateral medial lemniscus and project to VPM, Pom and the intralaminar thalamic nuclei. They also send collaterals to the brain

stem and midbrain.

3. THE SOMATOSENSORY THALAMUS

An important aspect of organization of the somatosensory thalamus is the segregation of input from different receptor classes within nuclei and sub-nuclei. The thalamocortical projection is thus a highly parallel input to cortex.

Touch and vibration information is carried by axons originating in the dorsal column nuclei and the principal nucleus of V to central parts of VPL and VPM. In at least VPL, there is a segregation of neurons that represent different types of receptors. Information originating from stretch receptors is carried (by axons originating in DCN) to the ventral posterior oral nucleus (VPO), just rostral to VPL and VPM. Information originating from deep structures (joints, fascia, periosteum) is carried by axons originating in the DCN to the ventral posterior superior nucleus (VPS), just dorsal to VPL and VPM.

Temperature and pain information is relayed by axons of the spinothalamic tract and from the caudal division of the spinal trigeminal nucleus to perhaps the rostral and caudal extermities of VPL and VPM, and to Pom.

4. SOMATOSENSORY CORTEX

The somatosensory cortex of the postcentral gyrus in monkeys, known earlier as "SI," consists of 4 different cytoarchitectonic areas that form medial-lateral oriented bands of tissue. Each area represents principally one modality and gets input from corresponding parts of the ventral posterior nuclear complex (VPL, VPM, VPO, VPS). These areas and the inputs they receive are:

(a) area 3a - stretch receptors from muscle; input from VPO.
(b) area 3b - cutaneous receptors; input from VPL and VPM (more numerous slowly adapting receptors than areas 3b; no Pacinian input).
(c) area 1 - cutaneous receptors; input from VPL and VPM (less numerous slowly adapting receptors than area 3b; includes Pacinian input).
(d) area 2 - cutaneous input from areas 3b and 1, and thalamic input from VPS (receptors from deep structures - joints, fascia, periosteum).

Some VPL neurons project to both areas 3b and 1; some neurons project only to area 1 or only to area 3b. There are 4 separate body representations in the postcentral cortex, one in each cytoarchitectonic area (3a, 3b, 1, 2). The cutaneous representations in areas 3b and 1 are particularly well defined. The representations cannot be described as a "homunculus." Within area 3b, a modular segregation of neurons receiving input from slowly adapting and rapidly adapting cutaneous receptors can be distinguished.

The maps of the skin surface in cortex are not static entities but are dynamic, subect to use-dependent changes throughout life, including adulthood.

The "SII" region in the monkey, in the parietal operculum on the upper and

inner banks of the Sylvian sulcus, consists of several different cortical areas. "SII proper" receives input from the postcentral "SI" region and from the ventroposterior complex of the thalamus. The region caudal to this receives input from the posteromedial nucleus (Pom) of the thalamus and may be important in the conscious perception of pain.

5. PAIN

A. Receptors

a. Most if not all pain receptors are free nerve endings that, when activated by stimuli that have the potential to damage tissue, evoke sensations of pain.

b. Superficial pain, from the skin: the first sensation of "pricking pain" is well localized, of short duration, and is mediated by A fibers. The second sensation of "burning pain" is less localized, more prolonged, and is mediated by C fibers.

c. Deep pain, from muscles, bones, joints, or connective tissue has a diffuse aching character and is served by both A and C fibers.

d. Itch is served by C fibers and can be evoked by a variety of externally applied stimuli (mechanical, chemical) or by intradermal release of chemical mediators such as histamines.

B. Central Projections

a. Primary pain afferents enter the dorsal root, bifurcate and ascend and descend for 1 - 3 segments in Lissauer's tract, and terminate largely in lamina I and the substantia gelatinosa. Neurons in other laminae can extend their dentrites into these laminae and hence can receive pain input as well.

b. Second order cells project through the spinothalamic tract (see earlier section on anterolateral system).

c. The gate-control hypothesis for pain suggests that small diamater pain fibers and large diameter touch fibers have antagonistic effects on cells in the substantia gelatinosa. These cells in turn project to and regulate the firing of cells deeper in the dorsal horn. Activity in pain fibers keeps the gate open while activity in touch fibers closes the gate. Recent evidence suggests that this hypothesis needs to be modified.

C. Descending Control of Pain Transmission

Neurons in the midbrain periaqueductal and periventricular gray matter excite neurons in the raphe nuclei of the brainstem that produce serotonin. Serotonergic fibers descend in the dorsolateral funiculus to activate enkephalin containing interneurons in the substantia gelatinosa. These cells appear to presynaptically inhibit incoming substance P - containing pain fibers, thereby reducing the central transmission of pain. The endogenous opiates (such as enkephalin) conceivably occupy the same receptors on pain fibers as morphine, accounting for the analgesic affects of enkephalin.

D. Treatment of Pain

a. Neurosurgical procedures, such as sectioning dorsal roots (rhizotomy); transection of the spinothalamic tract in the spinal cord (cordotomy).

b. Electrical stimulation of the skin by electrodes overlying the spinal cord or implanted against the dorsal columns. This presumably stimulates large diameter fibers that impede the flow of pain information centrally.

c. Electrical stimulation of the midbrain periaqueductal gray. This presumably releases enkephalin or other endogenous opiates in the dorsal horn that reduce the transmission of pain impulses.

d. Aspirin-like drugs that inhibit the synthesis of protaglandins thereby reducing the sensitivity of nociceptive receptors.