MST PART Ib NEUROBIOLOGY COURSE

C. HUANG: LECTURES ON SOMATOSENSORY SYSTEMS

Topics Covered

(1) Receptors and sensory perception.
(2) Somatosensory receptors and sensory modalities.
(3) Central sensory pathways.
(4) Pain, non-specific sensory mechanisms.
(5) Clinical correlates and higher sensory processing.

Recommended textbooks


(1) RECEPTORS AND SENSORY PERCEPTION

INTRODUCTION

The term 'sensory system' refers to those parts of the nervous system that receive inputs from both the internal and external environment and conduct and process these inputs. Sensory systems thus provide mechanisms that constantly gather and process up-to-date information. All human activity is a reaction to the stimuli that act on the sensory systems of the body. The response to any particular stimulus is determined by past experience and learning. Both of these result from previous sensory inputs to the nervous system. Some of these inputs may reach consciousness and so produce a sensory experience or impression. Others remain below the conscious level, for example those responsible for monitoring and controlling the homeostatic mechanisms of the body.
SENSORY RECEPTORS

Receptors within viscera and other internal organs monitor changes in the internal environment, and are termed interoceptors. Those that detect changes in the (sometimes distant) external environment are termed exteroceptors. Stimulation of sensory receptors gives rise to a variety of simple sensations. These various primary sensations are then assembled through higher levels of integration into perceptions. We explain this specificity of sensation through the existence of specific receptor cells that are tuned to be sensitive to different forms of energy in the environment. Such modalities include:

(i) Mechanical energy: e.g. hearing (sound), balance, muscle stretch, muscle tension, somatosensory (touch, pressure).

(ii) Electromagnetic energy: e.g. vision (photons).

(iii) Chemical stimuli: e.g. taste, smell, arterial oxygen.

Within a given modality, there may be different submodalities or qualities, e.g. different wavelengths of light seen as different colours.

Sensory endings of afferent nerves may either be free nerve endings or be specialised into receptor organs. They perform the function of transduction, altering the impinging physical energy into chains of action potentials in their nerve axons.

TRANSDUCTION OF STIMULI BY SENSORY RECEPTORS

Transduction refers to the process by which different forms of stimulus are converted into electrical signals. The cell that undertakes this process is termed a sensory receptor cell.

(1) Receptor cells show highly specialised structures and function.

In a small number of cases, an entire cell may transduce the stimulus, e.g. arterial chemoreceptors. However, transduction usually takes place at a specialised site in the sensory cell. These specialisations include:

(i) microvilli in taste buds.
(ii) cilia in olfactory and visual receptors.
(iii) free nerve terminals, e.g. pain receptors in skin.
(iv) nerve terminals embedded in special structures e.g. pacinian corpuscles, muscle spindles.
The incoming energy is probably converted into electrical signals by specific molecular receptors. These often exist on structures that are small and inaccessible. One process that is relatively well understood is the effect of light in causing isomerization of the photopigment rhodopsin.

(2) The change in the molecular receptor leads to a change in the membrane potential, termed the receptor potential.

In all cases, there is an ionic channel controlled by a gating entity. For example:

(i) In a chemoreceptor, a specific molecule stimulates a receptor molecule to retract the gating particle. [closed by definition]

(ii) In a mechanoreceptor, it has been suggested that distortion of the membrane activates stretch-activated channels. [open by mechanoreceptor]

(iii) In the vertebrate photoreceptor, ion flow occurs in the dark, and is blocked when light acts on the disk membranes within the photoreceptor. [closed by default]

These changes affect ionic movements across the membrane, resulting in a change in membrane potential. The magnitude of the receptor potential is graded with stimulus size, often through a logarithmic relationship.

(3) The receptor potential gives rise to action potential discharge

(i) The sites of sensory transduction and impulse initiation are usually separated, either by some distance along the same cell body or nerve fibre, or by a synapse (or two, in the case of the visual system).

(ii) Spread of the receptor potential then takes place electronically (passively) by local current flow similar to that resulting from synaptic activity.

(iii) The end result is conversion of a graded receptor response into impulse discharge in an afferent nerve.

(4) The frequency of the resulting impulse chain is directly related to the amplitude of the receptor potential.

This is exemplified by the frog muscle spindle stretch receptor, when an applied stretch initially produces a progressively increasing rate of spike firing. This then stabilises to a lower steady level of firing.

(i) When action potentials are blocked with tetrodotoxin, the receptor potential rises to a peak during the dynamic phase of the stretch. It then falls to a lower level during static stretch.
(ii) When impulses are recorded, the instantaneous frequency of firing follows the size of the receptor potential.

The overall consequence is for sensory reception to be mapped from a continuously varying sensory domain to a neural domain of all or nothing impulses.

(5) Receptors supplement their encoding of the static features of an imposed stimulus with dynamic sensitivity properties.

Dynamic properties include:

(i) An enhanced response taking place while the stimulus is increasing.

(ii) Decline in the response during static stimulation, or adaptation.

Thus receptors that signal slow and prolonged changes do so by being slowly adapting (or tonic). Those that signal brief changes are rapidly adapting (phasic) receptors.

**SENSORY PERCEPTION**

The fundamental biophysical properties outlined above have specific correlates at the psychophysical level.

(1) Sensory modalities

Muller's Law of specific nerve energies states that the nature of a sensation is determined by the sensory modality of the specific sensory nerve that is stimulated, not the sensory modality of the stimulus itself. Thus our perceptions are aware not of the objects or stimuli themselves, but of the signals transmitted by our nerves. For example a blow to the head that happens to stimulate the auditory nerve elicits the sensory experience of sound, even though the stimulus is not the usual source of energy to which the nerve is tuned. Muller's Law correlates with the specificity of the molecular transduction mechanisms in the receptor membrane.

(2) Detection

The behavioural threshold is the minimum intensity of stimulus at which it is possible for a subject to detect whether a stimulus has occurred. It needs to be compared to the threshold of the receptor for responding to some minimum amount of its specific stimulus. In general, several receptor responses must summate to produce transmission in the sensory pathway detected by a subject. For example, only a single photon is required to stimulate a single human retinal photoreceptor. However, the simultaneous activation of about 7 receptors is necessary to perceive that stimulation has occurred. Thus, in most sensory systems, the behavioural threshold is somewhat higher than the receptor threshold.
(3) Perception of intensity

This can be studied by varying the stimulus in a quantitative manner and determining the behavioural response along some quantitative scale. Such experiments show that in most sensory systems, the psychological perception of a stimulus varies in strength with the intensity of stimulation as a continuous function. The Weber-Fechner Law is one of a number of psychophysical relationships that relate neural events to the conscious discrimination of incremental changes in stimulus strength. For example, one can place small weights into the palm of the hand in a blindfolded subject. This experiment reveals that the just noticeable increment of weight, $\Delta R$ depends on the weight $R$ already present. If $\Delta S$ is the just detectable sensation:

$$\frac{\Delta R}{R} = \text{Const. } \Delta S$$

Integrating in the limit gives the Weber-Fechner Law:

$$S = a \log R + b,$$

where $a$ and $b$ are constants. Thus the sensation varies as the logarithm of the stimulus intensity.

This quantitative relationship between the psychological perception of a stimulus, and its intensity is reflected in the biophysical properties of the underlying receptors. Thus a logarithmic relationship between impulse firing and stimulus intensity exists in most sensory receptors, including:

- muscle spindles
- limulus photoreceptors
- carotid, sinus pressure receptors

(4) Spatial discrimination

 Discrimination between two spatially separated stimuli depends on the stimulation of at least two receptors which respond to stimuli in separate receptive fields. Information concerning stimulus position in space applies directly to vision and somatic sensation. It also applies to the auditory system in which different sounds affect different parts of the receptor population. This capacity can be tested psychophysically by testing for two-point discrimination of e.g. two points applied on the skin, or two points of light applied to the retina. At low intensities of stimulation, discrimination is poor. It is only in evidence at levels of intensity well above threshold.
(5) **Higher aspects of sensory perception**

These cannot be explained in terms of simple receptor properties alone. They require higher processing of sensory information by the central nervous system itself.

(i) Feature abstraction
(ii) Quality discriminations
(iii) Pattern recognition

(2) **SOMATOSENSORY RECEPTORS AND SENSORY MODALITIES**

**OCCURRENCE OF SENSORY RECEPTORS.**

Sensory receptors are situated in that part of the body where they are most likely to encounter the stimulus to which they preferentially respond. The term sensory or afferent unit covers everything from the neurone (including dorsal root ganglion, central and peripheral branches of the axons and nerve terminals) to the associated transducer element. A sensory receptor may be the structure within which a sensory nerve fibre terminates, the nerve terminal itself or a nerve terminal with an associated secondary transducer element.

**SENSORY MODALITIES**

The inputs to the central nervous system ultimately produce a sensory impression specific to the receptor stimulated. Structurally different receptors respond in different ways to specific kinds of stimulus. These sensory modalities include the five basic senses of sight, hearing, taste, smell and touch. More modalities can be added. For example, the skin not only responds to touch but also to cold, warmth, vibration and pain. Within a modality it is possible to say more about the quality of the sensory experience. The latter reflects the reaction of the receptor which responds optimally to a specific sensory stimulus. It reflects both the location of its receptive field and its specialised structure. The threshold stimulus is the minimum level of stimulation required to produce a response in a receptor. Below this level the receptor shows no response. As the stimulus intensity increases the perceived sensory experience also increases.

**ADAPTATION**

Slowly adapting receptors continue to respond for as long as a stimulus is applied and are often termed tonic receptors. They are responsible for awareness of the body's condition and position in relation to its surrounding environment. In contrast, rapidly adapting or phasic receptors respond to changing stimuli. Their action potential frequency is directly related to the rate of change in the amplitude of the stimulus.
All receptors show some degree of adaptation, the reduction in response with sustained stimulation. Some receptors adapt completely in a very short time whereas others only ever partially adapt even with a prolonged stimulus. For example, the Pacinian corpuscle adapts to extinction within milliseconds following the stimulus onset. In contrast, the Merkel cell-nerve terminal complex never fully adapts even after hours of stimulation. The mechanism of adaptation varies between receptors and may occur at any stage in the conversion of the stimulus. Thus at the level of the transduction process, it may involve the conductance mechanism of the receptor potential. It may also involve synaptic transmission from the secondary sensory cell to the nerve terminal or action potential generation.

RAPIDLY AND SLOWLY ADAPTING MECHANICAL RECEPTORS

The Pacinian corpuscle has been used extensively in the study of adaptation mechanisms because of its large size and accessibility. It occurs in the deeper skin layers and is 0.5 - 2.0 mm long with an onion-like lamellar structure formed of non-nervous tissue. An elongated nerve terminal passes into the centre of the corpuscle. It is highly specific in its sensitivity. It is stimulated by a short, sharp mechanical displacement, typically a 1 μm displacement occurring in 2.5 - 5.0 ms. The same stimulus extended over a longer period of time (> 20.0 ms) produces no response. The Pacinian corpuscle follows vibratory stimuli up to frequencies of 1000 Hz. These characteristic properties depend upon the numerous cellular layers that surround its central core. Their removal eliminates the response to vibration.

In contrast the response of the Merkel cell-neurite complex to mechanical stimulation persist for as long as it is stimulated. Merkel cells occur in the basal layer of the epidermis. They occur in close association with the expanded nerve terminal of afferent fibres. The Merkel cell contains dense cored membrane-bound vesicles in its cytoplasm adjacent to the nerve terminal. These may be involved in 'synaptic-like' connections between the Merkel cell and its associated nerve terminal that may have a role in the transduction process. It has been suggested that the slowly adapting response results from transmitter release which depolarises the adjacent nerve terminal. Alternatively, one may suggest that the transmitter modifies the effect of stimulation of the nerve terminal which is itself the transducer element.

SPECIFIC SENSORY UNITS

(1) Proprioceptors

The receptors responsible for the sense of position and co-ordination of different parts of the body are called proprioceptors. These include muscle spindles, Golgi-tendon organs and Ruffini endings all of which respond to tension or stretch, and Pacinian corpuscles which respond to pressure changes. Few proprioceptive stimuli reach
consciousness; many are concerned with reflex activity mediated through the spinal cord or cerebellum which in turn control or modify posture and movement.

(2) Mechanoreceptors

Exteroceptors report information about the external environment. They are therefore largely situated in the skin. They are further classified into mechanoreceptors, thermoreceptors and nociceptors. Mechanoreceptors detect skin indentation or pressure or movement of hairs. They give rise to the sensory modalities of pressure, touch, vibration and tickle. With the exception of tickle, all these receptors - Meissner's corpuscles, Merkel's discs, Pacinian corpuscles, Ruffini endings - are innervated by large diameter (5 - 12 µm), rapidly conducting (30 - 70 m s⁻¹) afferent nerve fibres. Their stimulation results in arrival of impulses at the spinal cord within milliseconds.

(3) Pain and temperature

Sensations of temperature and pain are mediated by free nerve endings of small diameter (0.5 - 10 µm) unmyelinated fibres. The fibres have slow conduction velocities around 0.5 - 2.0 m s⁻¹. Thus an impulse from the toe of an adult would then take around 1 second to reach the spinal cord. Mechanoreceptors innervated by unmyelinated fibres poorly discriminate stimulus intensity. The receptors therefore respond as threshold detectors for the presence of an object at a particular place on the skin.

(4) Thermoreceptors

The sensory modality of temperature has two qualities, cold and warmth. Warmth receptors respond maximally to temperatures slightly above body temperature. Cold receptors respond maximally to temperatures slightly below body temperature. There are specific cold-sensitive and warmth-sensitive spots in the skin and considerably more cold spots than warm spots. The histological structure of thermoreceptors is not fully known. They are probably free nerve endings. The cold receptors may be located just beneath the epidermis and the warmth receptors in the superficial layers of the dermis. Cold receptors are supplied by thin myelinated nerve fibres and warm receptors by unmyelinated fibres.

(3) CENTRAL SENSORY PATHWAYS

BASIC TERMINOLOGY IN NEUROANATOMY

(1) Neural Pathway: This refers to a chain of nerve cells linked together end-to-end which thereby convey excitation from one part of the nervous system to another.

(a) **Nerve:** a cable-like bundle of nerve fibres in the peripheral nervous system.

(b) **Fasciculus:** a bundle of nerve fibres in the central nervous system.
(c) **Fibre tract:** a cable-like bundle of fibres, all of which have a similar origin, termination and function. Fibre tracts only occur in the central nervous system, since there is no functional segregation of nerve fibres in mixed peripheral nerves.

(d) **Funiculus:** a fibre tract forming an anatomically distinct column of fibres.

(2) **Ganglion or nucleus:** Neural pathways that are related functionally tend to begin or end in the same part of the nervous system. Consequently they come together to form a compact structure, in which the cell bodies of adjacent chains lie side by side. The resulting swelling is termed a *ganglion* if it is in the peripheral nervous system and a *nucleus* if it is in the central nervous system.

(3) **A relay station or synapse:** This is the part of a pathway where impulses are transferred from the end of the nerve fibre of one cell to the cell body of another. Thus, relay stations are located in nuclei, and in all ganglia except in sensory ganglia.

(4) **Commissure:** A band of grey or white matter that connects a portion of the central nervous system to its corresponding structure on the opposite side.

(5) **Decussation:** The crossing of the midline by an ascending or descending fibre bundle. Since left and right bundles are crossing the midline simultaneously, they criss-cross through each other.

**GREY MATTER**

The most marked specialisation of the internal structure of the central nervous system is a differentiation into grey matter and white matter. Grey matter contains cells bodies of neurons, whereas white matter is made up of myelinated nerve fibres.

(1) **In the spinal cord, the grey matter develops and is organised in a manner that reflects its fundamental function in receiving, processing and outputting information.**

(i) The grey matter uniformly surrounds the central canal in the embryonic spinal cord

(ii) However in the course of embryonic development it becomes concentrated at:

(a) a ventrolateral site opposite the site of exit of motor nerve roots. The cells accumulating here form the ventral or anterior horn of the spinal cord and constitute its motor nerve nuclei.
(b) a dorsolateral site opposite the site of entry of sensory nerve fibres. The cells that accumulate here form the sensory nuclei of the cord.

(iii) This leaves a H-shaped cross-piece or grey commissure.

(iv) Nerve cell bodies of the grey matter of the cord are organised to form nuclei.

(2) The spinal cord nuclei have a sensory, motor or associative function.

(i) The substantia gelatinosa forms the tip of the dorsal horn. It is made up of small cell bodies, and functions as a local associative area for the dorsal horn.

(ii) The principal sensory nucleus forms the bulk of the dorsal horn. They give rise to fibres that ascend to the brain.

(iii) The intermediate nucleus contains internuncial neurons connecting motor and sensory neurons.

(iv) The somatic motor nuclei are classified into:-

(a) The anteromedial nucleus, which forms the medial part of the ventral horn in limb-supplying segments, and the entire ventral horn elsewhere.

(b) The anterolateral nucleus of the upper limb and lower limb segments (respectively C5 - T1, L3 to S3) respectively. These contain large motor neurons that innervate muscles of the limbs.

(v) The visceral motor nuclei: the intermediolateral nucleus is located lateral to the intermediate nucleus in segments T1 - L2. The small and multipolar cells give rise to sympathetic preganglionic fibres.

(3) Similar principles apply to nuclei of cranial nerve in the brain itself.

We thus divide the nuclei as follows:

(i) Sensory nuclei: These subserve general sensory tactile and limb position functions, and visceral sensory functions from taste buds, cardiovascular and respiratory systems, and gastrointestinal tract.

(ii) Motor nuclei: These have nerve fibres that leave the central nervous systems for a range of destinations:-

(a) Somatic motor nuclei: the nerve fibres end in striated muscles derived from the mesoderm of an embryonic somite.
(b) Branchial motor nuclei: the nerve fibres innervate striated muscles derived from the mesoderm of a branchial arch.

(c) Visceral (preganglionic) motor nuclei: the nerve fibres synapse with postganglionic cells of the autonomic nervous system.

(4) Sensory and motor nuclei occupy characteristic locations in segments of the central nervous system

(i) In a spinal cord cross section:
   a) sensory nuclei occupy the dorsal horn.
   b) motor nuclei occupy the ventral horn.

The above grey matter persists as a continuous column through the hindbrain and midbrain.

(ii) In the medulla and pons, this grey matter rotates and is displaced dorsally and so lies in the floor of the IVth ventricle:
   a) The sensory nuclei lie in the lateral part of the floor of the ventricle.
   b) the somatic visceral motor nuclei lie in the medial part of the floor.
   c) the branchial motor nuclei are left behind in a ventral location in line with the ventral horn of the spinal cord.

(iii) In the midbrain, the somatic and preganglionic motor, and sensory nuclei persist, and lie ventral to the aqueduct as part of the central grey matter. However the column of grey matter containing the branchial motor nuclei has dropped out.

(5) The remaining grey matter not accounted for contributes to the reticular formation of the brain.

WHITE MATTER AND PATHWAYS

(1) Pathways link up different levels of brain and spinal cord

Any given level of the brain or spinal cord will contain:

(i) Segmental pathways. These link incoming (sensory) information with a response that involves the segment itself. They may connect ipsilateral (uncrossed pathway) or contralateral (crossed pathway) neurons.

(ii) Intersegmental pathways connect the pathways of one segment with those of other segments, to make it possible for excitation entering the cord at one level to reach higher and lower levels.
(iii) **Long ascending pathways to the brain** convey sensory activity from the spinal cord to end at different parts of the brain.

(iv) **Long descending pathways** feed impulses from higher centres into the terminal part of the primary pathways in either the intermediate nucleus or the ventral horn of the spinal cord.

(2) **Ascending pathways separately convey different modalities of sensory information from spinal cord to higher centres.**

(i) **Pain and temperature pathways and the anterolateral touch pathway:** Sensory nerve fibres enter the spinal cord through the dorsal root, and synapse in the central nucleus. The postsynaptic fibres cross the midline and ascend the white matter of the spinal cord in the lateral (pain and temperature) or the ventral spinothalamic (anterolateral) tracts.

(ii) **Dorsal column touch pathway and pathways for position sense:** Branches of the sensory nerve fibres enter the spinal cord and ascend in the dorsal funiculus of the spinal cord. The first synapse is in the dorsal column nucleus in the medulla, and midline decussation takes place in the postsynaptic neurones beyond that.

(iii) **Pathways to the cerebellum:** Ipsilateral and contralateral neurons synapse in the grey matter of the spinal cord and the postsynaptic neurones ascend in the ventral and dorsal spinocerebellar tracts.

(3) **Descending pathways convey motor commands from brain to motor nuclei**

(i) **The lateral corticospinal tract:** The fibres arise from contralateral cerebral cortex and end in motor neurons in the ventral horn that innervate the limb muscles.

(ii) **The ventral corticospinal tract:** A small fibre bundle from ipsilateral and contralateral cortex, ends in neurons in the anteromedial nucleus that innervate the trunk muscles.

(4) **The long pathways link to specific higher structures in the brain**

(i) **The ascending pathways:**
   a) Always synapse once before always synapsing in the diencephalon.
   b) Will have crossed the midline once and only once before reaching the level of the diencephalon.
   c) From there, postsynaptic cells relay to specific areas in the cerebral cortex that always lie posterior to the central sulcus.
(ii) **The motor pathways:**
   a) Begin from cortical motor areas anterior to the central sulcus of the cortex.
   b) Sweep past in the internal capsule and do not synapse in the diencephalon.
   c) Cross the midline in the medulla oblongata, before proceeding down the spinal cord.

THE CEREBRAL HEMISPHERES

(1) The cerebral hemispheres are attached on either side of the diencephalon i.e. to the rostral end of the axial part of the brain.

(2) **Importance:** They provide the dominant association mechanisms for the central nervous system. They function:
   (i) to process the information collected by all the sense organs.
   (ii) to record that data for future reference (memory).
   (iii) to initiate a response in the light of that sensory information, and past experience.

(3) **Origin:** They develop close to the rostral end of the brain, beginning as a vesicle formed by the outpouching of the lateral wall of the telencephalon close to the olfactory bulb. The olfactory bulb thus differentiates into:-
   (i) the future cerebral hemisphere, the larger part, and
   (ii) the olfactory bulb proper.

(4) **Development of connecting pathways:** The fibres that connect the diencephalon and the cerebral hemisphere must pass through the caudal wall of the interventricular foramen. This connection enlarges in order to accommodate pathways that:-
   (i) ascend to the cerebral hemisphere from the brainstem and
   (ii) descend from the cerebral hemisphere to the brainstem.

Accordingly, the 'posterior' wall of the interventricular foramen becomes progressively thicker.

SENSORY PROCESSING BY THE CENTRAL NERVOUS SYSTEM

PERIPHERAL INPUTS

Peripheral information from all parts of the body, except the head, enters the spinal cord in spinal nerves. Spinal nerves also contain motor and efferent fibres. The afferent fibres enter through the dorsal roots, each of which represents a particular peripheral region. However the afferent nerve fibres regroup into new bundles in the nerve plexuses. Each peripheral nerve consequently contains fibres from several spinal nerves. Conversely
each spinal nerve contains fibres from several peripheral nerves. The area of skin supplied by a spinal nerve is therefore not sharply defined. Thus peripheral nerve transection in the extremities produces a clearly defined sensory deficit but transection of a dorsal root or spinal nerve causes only a slight sensory deficit. The sensory innervation area of a spinal nerve is called a dermatome. Dermatomes are arranged on the body surface in a sequence that corresponds to those of the spinal cord segments.

The head region is supplied by the 12 cranial nerves which enter the brain at the levels of the brain stem and diencephalon. Of these the trigeminal nerve (cranial nerve V) is a functional part of the somatosensory system. It supplies sensory fibres to the face and mouth region including skin, teeth, oral mucosa and tongue. Sensory pathways can be conveniently divided into a specific lemniscal system and a non-specific anterolateral system. In the specific sensory system the sensory input and its pathway to the sensory cortex is clearly defined. In contrast the non-specific system has no clearly defined sensory input and is excited by convergence from all sensory surfaces.

**SPECIFIC SENSORY SYSTEMS**

**Dorsal column pathway**

Some degree of functional regrouping occurs as the central processes of the first sensory neurone enter the spinal cord. Fibres concerned with proprioception, fine touch and vibration bifurcate immediately on entering the dorsal white column into short descending and long ascending branches. The ascending branches contribute collaterals to the dorsal grey horn. They then ascend ipsilaterally in the dorsal funiculus to the medulla oblongata. The entering fibres displace fibres that previously entered the cord at a lower level medially. Hence fibres from the lower limbs lie in the medial part of the dorsal column in the fasciculus gracilis. Those from the upper limbs lie in the more lateral fasciculus cuneatus. These fibres terminate in the nucleus gracilis and the nucleus cuneatus respectively in the medulla.

Second order neurones in the nuclei gracilis and cuneatus give off axons which curve ventrally, across the midline of the medulla as internal arcuate fibres in the medial lemniscus. The latter maintains a topographical fibre arrangement. The medial lemniscus rotates through 90 degrees as it ascends through the pons.

The second order neurones terminate in the ventral postero-lateral nucleus of the thalamus. From here, tertiary neurones project to the parietal lobe of the sensory cortex. Fibres from the upper body project to the lateral aspect of the postcentral gyrus with representation of the leg, foot and anogenital region passing to the medial surface of the hemisphere.
Anterolateral pathway

A second fibre group also enters the dorsal white column of the spinal cord and bifurcates into ascending and descending branches. These convey the appreciation of light touch and pressure. The short descending fibres contribute collateral branches to the dorsal grey horn. The ascending fibres also give off collaterals to the dorsal grey horn as they pass upwards for six to eight segments. Second order neurones cross the midline following synapses in the dorsal grey horn. They cross close to the central canal in the ventral grey and white commissure to form the ventral spinothalamic tract. A single fibre therefore diverges its effect over several spinal segments. This convergence of excitation into the second order neurones reduces discriminative capacity but also reduces excitation threshold. Fibres of the ventral spinothalamic tract terminate in the ventral postero-lateral nucleus of the thalamus. Tertiary neurones pass from the thalamus into the internal capsule and end in the sensory cortex.

Trigeminal system

A distinct set of sensory pathways supplies the head. Trigeminal nerve fibres carry touch and tactile discrimination. They terminate in the chief sensory nucleus of the trigeminal nerve. Postsynaptic fibres then pass to the ventral posterosomedial nucleus of the thalamus via the trigeminothalamic tract. Tertiary neurones then proceed to the cortex. The trigeminal fibres that subserve pain and temperature also enter the pons but then travel downwards in the spinal tract of the trigeminal nerve to end in the nucleus of the trigeminal spinal tract. This tract extends caudally as far as the second cervical segment of the spinal cord. Their efferent fibres also form part of the trigeminotectal tract, cross the midline and travel rostrally to the thalamus.

Representation of the parts of the face in the descending root of the trigeminal nerve is inverted. Thus a lesion of the lower end of the root in the upper cervical cord only abolishes or reduces pain and temperature. It does not influence touch sensation over the area supplied by the ophthalmic division of the trigeminal nerve of the same side of the face.

The primary sensory neurones for facial proprioception are unusual. Their cell bodies occur in the mesencephalic nucleus of the trigeminal nerve rather than a peripheral sensory ganglion. A single process passes to proprioceptors in the area supplied by the trigeminal nerve. A small branch from this single process synapses with a cell in the reticular formation. The latter cell produce axons that either pass upwards to join the trigeminotectal tract or pass to the motor nucleus of the trigeminal nerve to elicit reflex activity.
(3) PAIN: NON-SPECIFIC SENSORY MECHANISMS

Pain is one of the most common and disturbing of human experiences. It informs us of potentially tissue-damaging stimuli and accordingly assumes an important protective role. Individuals vary widely in their response to painful stimuli. The reaction to a painful stimulus varies from time to time depending upon circumstances even in the same individual.

PAIN RECEPTORS

Damaging intensities of natural stimulation applied to the skin stimulate both mechano- and thermoreceptors. However both these receptor systems are driven to maximal activity by much less intense stimuli. They therefore cannot mediate pain but may alter the sensory quality of the pain experienced. The specific structures that sense pain are called nociceptors. There are two types of nociceptor: (i) Mechanical nociceptors respond to squeezing of the skin or to its penetration by sharp objects. (ii) Thermal or mechanothermal nociceptors respond maximally to severe thermal stimuli with a threshold of approximately 45°C.

Mechanical nociceptors can be innervated by either myelinated or unmyelinated fibres. The fastest fibres conduct at velocities around 50 m s\(^{-1}\). Mechanothermal nociceptors have unmyelinated fibres peripherally, but a small number acquire myelination more proximally in the peripheral nerve. Their conduction velocity is 10 m s\(^{-1}\) or less. This distribution of conduction velocities results in two kinds of pain. A needle pushed into the skin produces a sharp readily localised initial pain which rapidly fades when the stimulus is withdrawn. However a more diffuse delayed pain follows and this fades only slowly. The first pain is conveyed to the central nervous system in fast conducting fibres; the second pain is carried in the slow conducting, small diameter, unmyelinated fibres.

CLINICAL VARIANTS OF PAIN SENSATION

Pain that arises from the skin is termed superficial pain; pain from muscles, bones, joints and connective tissue is called deep pain. Initial pain initiates rapid protective reflexes such as withdrawal of the hand when something hot is touched. Deep pain, is dull and poorly localised and often causes a vague feeling of unpleasantness and illness. It can produce autonomic reflex responses such as nausea, sweating and reduced blood pressure.

Projected pain

Direct nociceptive stimulation produces an unpleasant sensation interpreted by the central nervous system as arising from that area of skin innervated by the relevant nerve. For example, a sharp blow applied to the ulnar nerve at the elbow joint, produces a sensation of 'pins and needles' in the medial half of the hand. Projected pain also results when herniation of a damaged intervertebral disc causes spinal nerve compression as it leaves the spinal cord.
Referred pain

Nociceptive afferents from the dermatome and from the associated internal organ converge upon neurones in the pain pathway. Pain impulses that originate from internal organs are carried back to the central nervous system via sympathetic fibres. Such afferent (sensory) fibres enter the spinal cord in the dorsal root along with other sensory fibres that represent the cutaneous area, or dermatome supplied by the spinal nerve. The experienced visceral pain becomes referred to the skin surface within the associated dermatome of the spinal nerve. Angina pectoris is an important example of referred pain. It originates in the heart but appears to come from the chest and radiates down a narrow strip along the inside of the arm. A further consequence of such convergence is an increase in sensitivity (hyperpathia) of the skin in the associated dermatome. This results from an increased excitability of interneurones by the visceral impulses. Consequently, a given painful stimulus to the skin causes an increased activity within the central nervous system.

PAIN AND TEMPERATURE PATHWAYS

The central processes of pain and temperature fibres enter the dorsolateral fasciculus. Ascending and descending processes extend over one or two spinal cord segments. They then give rise to numerous collateral branches that terminate in the substantia gelatinosa. Activity in the pain pathway may be modified by inhibitory inputs from sensory fibres in the dorsal white columns. Thus rubbing an area of skin previously subjected to a blow or shaking ones hand after burning a finger partially relieves the experienced pain. The second order neurones arise in the dorsal grey horn. These cross the midline in the grey and white commissures. They next ascend in the lateral spinothalamic tract in the ventrolateral white matter of the cord to the medulla. They are then joined by the ventral spinothalamic tract and the spinotectal tract to form the spinal lemniscus which lies lateral to the medial lemniscus. This passes through the pons to the midbrain where spinotectal fibres pass to the superior colliculus. Fibres in the lateral spinothalamic tracts terminate in the ventral posterolateral nucleus of the thalamus. From here third order neurones pass to the sensory cortex.

NON-SPECIFIC SENSORY SYSTEM

Connections

Spinoreticular fibres occur within the ventrolateral white matter of the spinal cord. These fibres are largely uncrossed. They pass to the brain stem and then synapse on cells of the reticular formation. The reticular formation occupies a considerable part of the brain stem and is an important component of the non-specific system. It has numerous afferent and efferent connections that involve the entire central nervous system. It receives inputs from spinoreticular fibres, the corresponding tracts of the spinal trigeminal

Now hear this: dorsal column - fine touch
corticospinal - pain/temperature and less discriminative touch
nucleus and all other afferent cranial nerves, and therefore all sense organs. It also receives inputs from the motor and sensory parts of the cerebral cortex, the thalamus and hypothalamus. Its efferent projections are equally diverse. These descend to the spinal cord, and ascend via the non-specific thalamic nuclei to the cortex, the hypothalamus and the limbic system.

It is therefore apparent that there are alternative routes for sensory inputs from the spinal cord. The direct 'specific' route involves the medial and spinal lemnisci and projects to the ventral posterior thalamic nuclei. The indirect 'non-specific' or extralemniscal route gains access to other thalamic nuclei via polysynaptic pathways before reaching the central cortex.

**Importance**

Although still not fully understood, the non-specific system may function in:

(a) Control of the level of consciousness and of alertness by influencing the overall activity of cortical neurones. This could involve the ascending reticular activating system.

(b) Production of appropriate emotional responses to sensory stimuli particularly painful stimuli carried in the ventrolateral white matter. Such information is relayed to the limbic system.

(c) Regulatory functions such as cardiovascular, respiratory, swallowing, coughing and sneezing reflexes which involve the co-ordination of afferent and efferent systems.

(d) Involvement in motor mechanisms responsible for support and co-ordination.

**5 CLINICAL CORRELATES AND HIGHER SENSORY PROCESSING**

**HIGHER SENSORY PROCESSING: PERCEPTION**

The psychophysical relationships between the applied stimulus and the resultant sensory experience have been extensively studied. This relationship underpins the neurological clinical examination, and is required to relate applied stimuli to their perception by the patient. Stimulation of a receptor system triggers a sensory impression. Combinations of different sensory impressions become correlated and experienced at the same time. For example, an object placed in the hand of an individual imparts a sensation of its weight, size, temperature and texture. This combination of sensory impressions enables identification of the object through the individual subject's cognitive capacity and previous experience. This combination of sensations with past experience to thereby
interpret our environment is called perception. The sensory experience that results from the stimulation of any particular receptor system is probably identical between individuals. However, past experiences and learning vary with individuals. We thus perceive the world in a unique and personal way and this must be allowed for when performing neurological examinations. Thus meaningful testing of sensory function or interpret action of abnormalities in sensory perception, is absolutely dependent upon the patient's cooperation. Conversely, patients may report slight variations in the perceived stimuli which are not clinically significant.

COMMON SENSORY ABNORMALITIES

Peripheral nerve lesions

A knowledge of the cutaneous distribution of the various peripheral nerves and of the nerve plexuses that they form is required to localise the site of a peripheral lesion responsible for an abnormal sensation. If the affected nerve innervates a large cutaneous area, sensory loss is complete in a central area. However, tactile loss is more extensive than loss of pain and temperature sensation in the surrounding zone. In contrast, the loss of a small nerve may produce no obvious sensory abnormality because of the considerable overlap in skin areas supplied by adjacent peripheral nerves. This also applies to involvements of individual sensory roots. Thus the dermatome supplied by a single sensory root also receives overlapping innervation from neighbouring roots. A distinct cutaneous sensory loss then only results when several roots are affected. In this case the extent of the sensory loss will clearly indicate the roots which are involved. For this reason a good understanding of dermatome distribution is essential in clinical neurology.

Spinal cord lesions

The sensory abnormalities that result from a spinal cord lesion depend very much upon which sensory pathways are affected. Total spinal cord transection abolishes all sensation below the segmental level of the transection. Cord hemisection abolishes tactile discrimination. It reduces touch and position sense on the same side of the body as the lesion. The sensory deficit will extend as far as the dermatome level of the cord segment that corresponds to the level of the lesion. These is a corresponding loss of pain and temperature sensation on the contralateral side. Pain and temperature fibres ascend for a few segments in the posterior horn before they cross to the contralateral spinthalamic tract. The 'sensory level' for these modalities therefore is a few spinal segments lower. Spinal cord transection or hemisection also affects motor pathways.

Tabes dorsalis

Tabes dorsalis affects the sensory roots at their point of entry into the cord. To a lesser extent, it also affects the spinthalamic tracts as well as causing degeneration of the dorsal white columns. Patients consequently experience a sensory ataxia. There is a loss

*Brown-Séquard syndrome

Brown & Zuckerkandl were the first to report it in Britain in 1854.
of proprioceptive input and this results in an unsteady faltering gait particularly when visual control over posture is removed. There is often some pain loss because of the involvement of the spinothalamic tracts. Tendon reflexes may be lost due to a break in the sensory side of the reflex arc.

Syringomyelia

Syringomyelia causes degeneration in the central grey matter of the spinal cord, usually in the cervical region. This affects the decussating pain and temperature as well as light touch and pressure fibres. This produces a dissociated anaesthesia in which pain and temperature sensation is lost but discriminative touch and position sense is preserved. This sensory loss is often unilateral and affects the whole of one upper limb and shoulder and ends in the midline of the trunk with a sharp lower border.

Brain stem lesions

These produce sensory impairment readily interpreted on an anatomical basis. Involvement of the descending tract of the trigeminal nerve causes a dissociated sensory loss in the face due to loss of pain and temperature fibres within the descending tracts. A pontine lesion can affect the chief sensory nucleus of the trigeminal nerve. This will cause a sensory impairment in one side of the face. Involvement of the ascending sensory tracts may produce a hemianesthesia - a loss of touch sensation generally. It may also produce a hemianalgesia or a loss of pain sensation of the trunk and limbs on the opposite side of the body.

Thalamic lesions

Lesions within the thalamus can also produce a unilateral hemianesthesia and hemianalgesia as well as producing a spontaneous unpleasant pain particularly on the anaesthetic side.

Cortical lesions

Lesions of the sensory cortex often give rise to paraesthesia or sensations of tingling, pins and needles, or complex sensations such as feelings that tight bands are tied around a part of the body or as if water was being trickled over the skin. The paraesthesia spreads across the body in a manner that corresponds closely to the somatotopic representation in the sensory cortex. Lesions of portions of the postcentral gyrus often produce no impairment of pain sensibility and little impairment of touch. However, there is a considerable loss of position sense and tactile discrimination and of the ability to recognise form and texture (astereognosis) in the corresponding part of the opposite half of the body. Figures written upon the skin cannot be recognised and the threshold for two-point discrimination is raised.