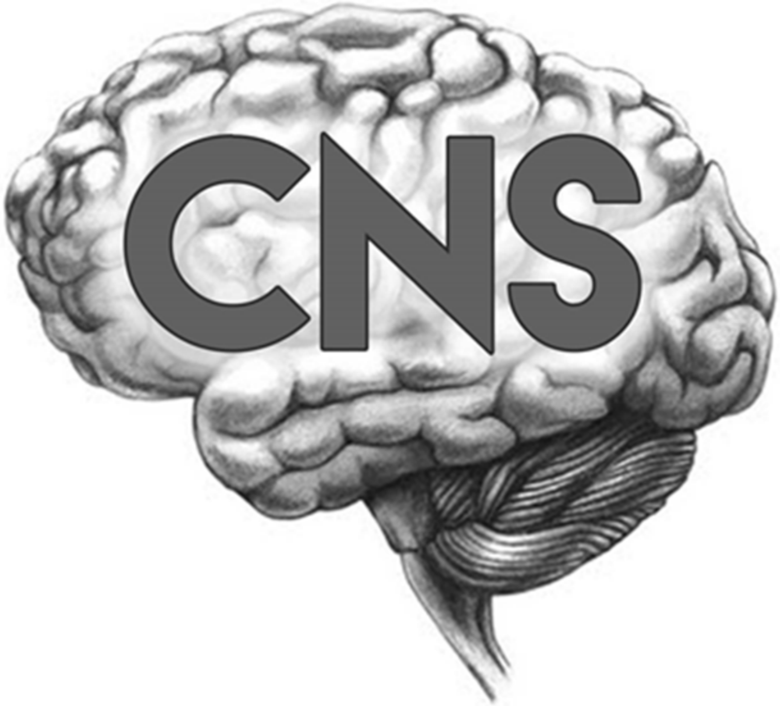

PHYSIOLOGY

☑ Sheet ○ Slide ○ Handout

Number

4

Subject

Vestibular system and cerebellum

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Date: **00/00/2016**

Price:

Notes:

→ ***The order of ideas in this sheet differs from the record.***

→ ***Topics of the lecture:***

- ***Revision of Motor systems.***
- ***Vestibular system and balance.***
- ***The cerebellum.***

→ ***You can refer to Guyton medical physiology for vestibular system topic, it is really comprehensive –pages 674-678.***

→ ***You can find these pages at the end of this sheet.***

→ ***To make things more clear, watch these two mini videos about the vestibular system: video-1, video-2.***

❖ Revision:

There are two motor systems as you know:

1. **The lateral motor system:**

   That activates the flexors.

   Made of:

A. the corticospinal tract:

→ Affects the distal flexors that are responsible for fine movements.

B. Rubrospinal tract:

→ Fibers originate from the cortex→ to the magnocellular portion of the red nucleus →to the spinal cord as a rubrospinal tract.

→ Affects the large flexors, it may also have an effect on fine movements but not as much as corticospinal.

→ It also receives some inputs from the cerebellum.

Based on the previous pieces of information:

→ Loss of rubrospinal tract →results in loss of the ability of moving the wrist but still the person can write -but not as before because wrist movements are needed for proper writing-.

→ Loss of the corticospinal tract →no ability to write but can move the wrist.

2. **The medial motor system**:

   It affects the **extensors and anti-gravity** muscles to maintain the posture.

   It includes three different tracts:

   A. **Reticulospinal tract**: it is not a crossed pathway -it is bilateral-.

   B. **Vestibulospinal tract**: It is also composed of two pathways(see slide 26):

1- Lateral vestibulospinal tract, which comes from the lateral vestibular nucleus then crosses to the other side.
2- Medial vestibulospinal tract, which comes from the medial vestibular nucleus and is a bilateraltract.

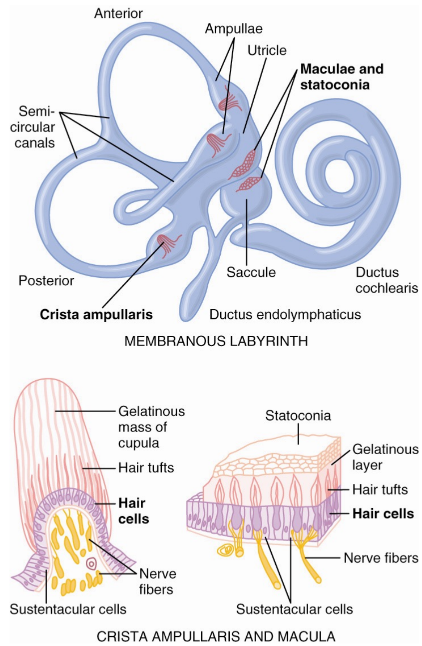
C. **Tectospinal tract:**

- ► Tectospinal pathway is a bilateral pathway.
- ► Originates from the tectum of the midbrain (سقف الدماغ المتوسط).
- ► The tectum is composed of **superior and inferior colliculi**. The superior colliculus receives inputs from the **visual tract**and gets stimulated when there is light. It sends impulses through the tectospinal tract to the muscles ofthe neck to move the head in response to the light. Thus, the response to light is done by the tectospinal tract.
- ► Whereas the response to **sounds** is the job of the **inferiorcolliculus;** the auditory pathway gives fibers to the inferior colliculus, then the inferior colliculus sends impulses to the neck muscles by the tectospinal tract to move the head towards the sound.

- Note that the lateral motor system tracts are crossed tracts and some tracts of the medial motor system as well -but not all of them-.
- Remember that each part of the CNS is topographically organized, and the input goes from one area in the cortex to the same area in the red nucleus, vestibular nuclei or spinal cord…. *An input that originates from the hand's area in the cortex is going to be sent to the area of the hand in the red nucleus for example.*
- **More about reticulospinal tract:**
  - → Remember that the reticulospinal tract is subdivided into medullary (lateral) and pontine (medial) reticulospinal tracts.
  - → Medullary reticulospinal tract is excitatory to the flexors and inhibitory to the extensors (anti-gravity muscles) while the pontine reticulospinal tract is excitatory to extensors to inhibitory for the flexors.
- **Decerebrate rigidity:**
  - → Normally, the medullary tract is stimulated by the cortex while the pontine tract is intrinsically active (i.e. it works without the need of stimulation) and these two opposing systems are in balance.
  - → When the connection between the cortex and medullary reticular formation is lost (decerebration), the medullary tract becomes inactive→ the pontine tract will work without any antagonization-no balancing for its effects- →overactivity of the extensors →decerebrate rigidity will occur.
- **Vestibular nuclei:**
  - → Are located in the brain stem.
  - → They are four in number; inferior, superior, medial and lateral.

→ Receive inputs from the vestibular system of the inner ear.
→ The vestibular nerve emergesfrom vestibular nuclei.

❖ Vestibular system:



- To understand the mechanism by which balance is achieved, we need to know the composition of the structures that are responsible for it.
- The inner ear is composed of two parts:

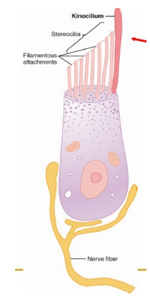
1. The auditory part (responsible for **hearing**): formed by the cochlea -*القوقعة*- which is supplied by the cochlear part of the eighth cranial nerve (vestibulocochlear).
2. The vestibular part (responsible for **balance**):
   - ♦ The vestibular apparatus is divided functionally into two parts:
     - → Part concerned with **linear acceleration** made of utricle and saccule.
     - → The other one is concerned with rotation (**angular acceleration**) and is formed by three semi-circular canals.

- These two areas are supplied by the vestibular part of the vestibulocochlear nerve.

❖ utricle قُرَيْبَةand sacculeالكُييس:

- The sensory organs of both utricle and saccule are called **maculae**. Each macula is composed of thousands of hair cells whose hairs are covered by a membraneor a gelatinous layercalled otolithic membrane(غشاء الحصيّات السمعية). And on the top of this gelatinous layer, calcium carbonate heavy crystalsare found.
- Note: calcium carbonate heavy crystalsare*known as **statoconia** -orotoliths (حُصَيَّات)-*
- Each hair cell has around 50-70 small cilia called **stereocilia**plus one large cilium, the **kinocilium,** which is located at one side of the cell. The stereocilia are arranged according to their lengths.

- These cilia are connected to each other by invisible filamentous attachments. These attachments help the cilia to move together.
  - ► When movements result in pulling the stereocilia towards the kinocilium→**the cell depolarizes**.
  - ► While when they move away from the kinocilium→**the cell hyperpolarizes**"not repolarizes; repolarization is returning back to normal".



Read the following paragraph if things are not clear yet:

- *"Because of these attachments, when the stereocilia and kinocilium bend in the direction of the kinocilium, the filamentous attachments tug in sequence on the stereocilia, pulling them outward from the cell body. This opens several hundred fluid channels in the neuronal cell membrane around the bases of the stereocilia, and these channels are capable of conducting large numbers of positive ions. Therefore, positive ions pour into the cell from the surrounding endolymphatic fluid, causing receptor membrane depolarization. Conversely, bending the pile of stereocilia in the opposite direction (backward to the kinocilium) reduces the tension on the attachments; this closes the ion channels, thus causing receptor hyperpolarization"Guyton ,12th edition, page 675*

- Different Hair cells are oriented in different directions to make it possible to sense any move in any direction -front, back, left or right-. So when the body moves in a specific direction some cells will be excited and the rest will be inhibited. *In other words; some cells are stimulated when the head bends forward, some are stimulated when the head bends backwards,others are stimulated when the head bends to one side and so on.*
- The fluid found in the in the saccule and utricle is called the **endolymph**. Its composition is similar to the intracellular fluid. Another fluid is present is called **perilymph that is concerned with hearing mechanism**.

❖ Calcium carbonate crystals:

- Under the effect of gravity, this calcified statoconiais pulled faster than the surrounding tissues and fluid because it hastwo to threetimes larger specific gravity than that of the surrounding tissues and fluid. This will make the cilia to bend ina way opposite to the direction of movement *-this is the case in linear acceleration-*.So the crystals are important to make it possible for the sensory organ to respond to changes in head position.

  Don't worry if you don't understand this, it will be explained later in this sheet.
- **Note:** the specialized cells that are responsible for all specific sensations (i.e. smell, hear, taste...) are called **hair cells**, not only those of balance.

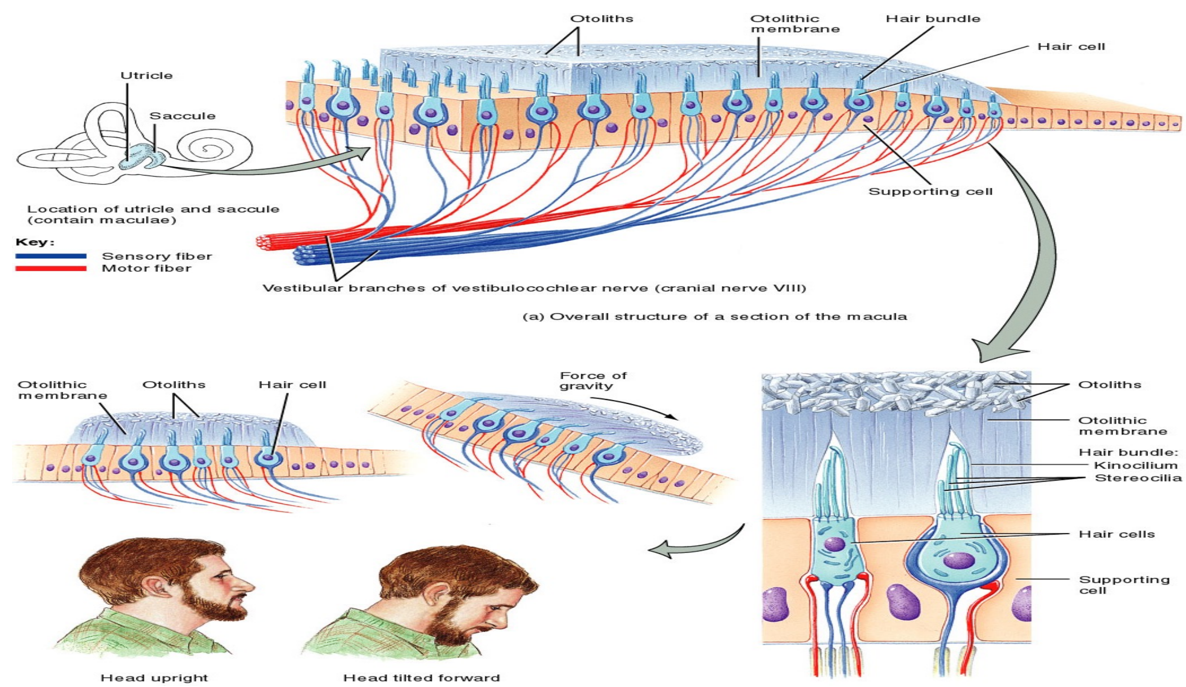
❖ The sequence of events:

- The hair cells have a basal rate of firing -they are intrinsically active- so when they are excited the rate of firing is increased-**<u>more depolarization</u>**-. While when inhibited, the rate of firing is decreased and it may become 0 -**<u>the cell is hyperpolarized-</u>**. This basal rate of firing makes the cell cable of being stimulated and inhibited just like the tone in the smooth muscles of the arterioles.

Thus there is positive and negative control.

➢ **The mechanism of static equilibrium:**

- Once there is a change in position of the head , the statoconia will move in the direction of the gravitational pull → resulting in bending of the cilia in the same direction of the pull →the hair cells, whose cilia have bent in one direction,will be more depolarized (have a higher than basal rate of firing) and get activated (excited)→ hair cells will secrete a neurotransmitter -that is probably glutamate-→the afferent fibers of the vestibular nerve will be stimulated →they will send impulses to the vestibular nuclei → and through the vestibulospinal tract impulses are transmitted to the spinal cord → finally this will cause contraction of some muscles to correct the posture and to maintain balance while changing position- *they contract in away to oppose the feeling of falling down-.*



➢ **The mechanism of equilibrium during linear acceleration:**

- *"When the body is suddenly thrust forward—that is, when the body accelerates— the statoconia, which have greater mass inertia than the surrounding fluid, fall backward on the hair cell cilia, and information of dysequilibrium is sent into the nervous centers,* *causing the person to feel as though he or she were falling backward. This automatically causes the person to lean forward until the resulting anterior shift of the statoconia exactly equals the tendency for the statoconia to fall backward because of the acceleration. At this point, the nervous system senses a state of proper equilibrium and leans the body forward no farther. Thus, the maculae operate to maintain equilibrium during linear acceleration in exactly the same manner as they operate during static equilibrium."* *Guyton, 12th edition, page 676.*

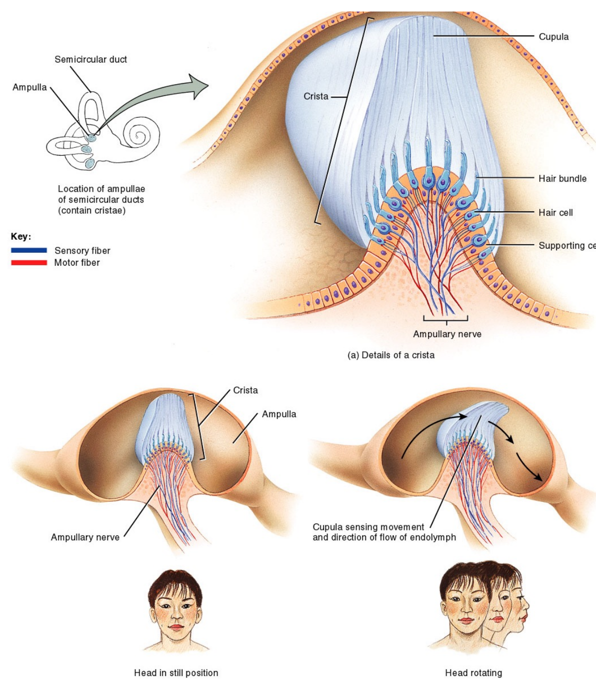
- So when the body is accelerated forward the hair cells of the maculae bend in the opposite direction, this causes one to feel as if he is falling backward. Reflexes cause the body to lean forward. *From the slides.*

❖ Semi-circular canals:

➢ The anatomy part:

There are three semi-circular ducts that are arranged at right angles to each other so that they represent all three planes in the space. These are:

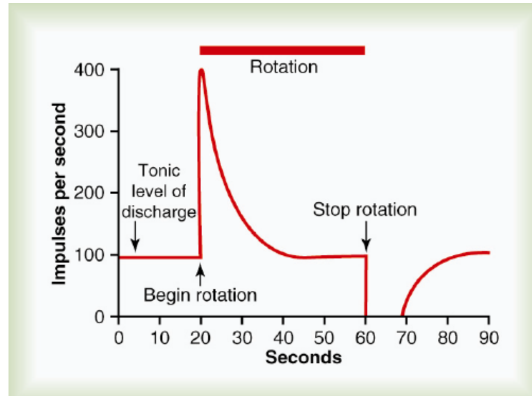
1. ***Lateral semi-circular canal (transverse)****: to detect the rotation from left to right (as when you move your head to say no).* This canal is in a transverse plane when your head is bent 45 degrees anteriorly"30 degrees in the book".
2. ***Posterior semi-circular canal:*** *to detect the movement of the head towards the shoulder.*
3. ***Anterior semi-circular canal:*** *to detect the up and down movements of the head (just like when you move your head in a yesmovement).*



- The anterior canal in the right ear and the posterior in the left ear are in the same plane. The anterior canal in the left ear and the posterior in the right ear are in the same plane.
- Thus this arrangement of these canals in both ears make the hair cells able to detect the movements in all directions (i.e. they detect rotational moves).
- The sensory organs of the semicircular canals are also hair cells that are arranged in a crest like structure called **cristae ampullaris**. On the top of the cristae ampullaris is a gelatinous layer"the doctor said it is a membrane protein" called the cupula in which the cilia of hair cells are embedded. The kinocilia of each cupula are oriented in the same direction so that bending to one direction will cause depolarization and bending to the other side will

cause hyper-polarization. At the same time, different cupulae are oriented in different directions thus they can sense any rotational movement *not the linear movements*.

- Both the crista ampullaris and macula are supplied by afferent nerves from the vestibular branch of the vestibulocochlear nerve.
- The ducts are filled with endolymph.



➢ **<u>The physiology part: (please follow the figure below):</u>**

1 → Once the body starts to rotate in any direction→the endolymph in the ducts , because of its inertia, tends to remain stationary while the ducts themselves turn→this will make the fluid flow in the opposite direction of the rotation→causi 1 the cilia to bend → depolarization of the hair cells → impulses transmitted throug the afferent fibers of the vestibular nerve→ to the vestibular nuclei→ through the vestibulospi 2 tra 3 → to the spinal cord → contraction of the needed muscles to maintain balance. 4

→ With continued rotation, you reach a constant speed, at this time the endolymph will be rotating in the same speed of the ducts, thus hair cells won't be stimulated anymore and no impulses are transmitted, the excess discharge subsides back to the resting level during the next few seconds-at this time you don't feel that you are rotating-.

3 → However, when you stop rotating, the opposite happens; the ducts will stop while the endolypmhwill continue to rotate causing the cupula to bend to the opposite direction →hair cells will be hyperpolarized causing the endolymph to stop discharging entirely.

4 → After another few seconds, the endolymph stops moving and the cupula gradually returns to its resting position (basal rate of discharge).

- So you can conclude that hair cells undergo a really fast **<u>adaptation</u>** (step 2).

- Rotation of a duct in one direction causes relative movement of endolymph in the opposite direction activating the receptors in the crista ampullaris. Stop the rotation, the opposite happens. *From the slides.*

- The receptors of the rotational movement can also respond to **<u>the rate of change</u>**; i.e. the velocity of change. When the velocity is known as well as the time, the distance can be estimated.Thus these receptors can estimate the distances and the predicted position of the body after a known time. So when these receptors are damaged, this ability "predicting the positions ahead of time" will be lost. This is important for the body to know when to stop before hitting an object, if these receptors are damaged, there is no intrinsic ability to know when to stop. Actually this experiment was done in monkeys; scientists destroyed these receptors and gotthis result.

- → *"In other words, the semicircular duct mechanism predicts that dysequilibrium is going to occur and thereby causes the equilibrium centers to make appropriate anticipatory preventive adjustments. This helps the person maintain balance before the situation can be corrected."* *Guyton,12th edition, page 677.*

- This predictive function is not found in the utricle and saccule.

- This prediction mechanism is performed with the help of neck proprioceptors and the visual input. But that does not mean that these receptors don't work when you close your eyes!

****So these receptors adapt very fast and respond to the rate of change****

- *Example mentioned by the doctor:*

→ If you are riding a bus for example, then the speed of your body –and that of the cilia of the hair cells as well- is the same as the speed of the bus. If you want to get off the bus while it is moving, you will change your speed from the speed of the bus to zero but the hairs inside your inner ear are still moving in a high speed, thus to prevent falling down you will automatically decelerate gradually to maintain your balance. And if you forced your body to stop directly you will fall down.

- **Notes:**

→ There is a chemical synapse between the hair cells and the afferent fibers of the vestibular nerve.

→ Hair cells are also supplied by efferent nerve fibers. These efferent nerve fibers are corticofugal fibers for **lateral inhibition** -to make the impulses sharp and demarcated-.

Nystagmus: a dancing eye movement, could be caused by a damage in the oculomotor nerve, the vestibular system or a cerebellar disease. It is tremor of the eye and loss of the ability to fix the gaze on something.

Vestibular mechanism of stabilizing the eye:

→ There is a connection between the vestibular nuclei and the oculomotor nerve, this connection is responsible for the extraocular movements.

→ When a person changes his/her direction of movement, the vestibular system sends impulses through the vestibular nuclei to the oculomotor nerve causing the eye to move to the opposite direction. This reflex makes it possible to maintain a stable image on the retina while rotating.

→ When the vestibular system is damaged, an abnormal eye movement called **nystagmus** may result.

❖ <u>The cerebellum:</u>

- The cerebellum is the third part of the motor parts of the CNS.
- The cerebellum is located in the posterior cranial fossa.
- It was known previously as **the little brain** as it was believed that the cerebellum has no function, but they have noticed that when the cerebellum is damaged many motor functions are lost or disturbed.
- It also has many sulci and gyri.
- The cerebellum is responsible for the sequence of movements and actions and the coordination between them. It **<u>compares</u>** the actual with the intended movement and if the two do not compare favorably it corrects actualmovement based on the intended movement as the cerebral cortex never sends the exact impulses required for a movement; it sends either more or less than the needed impulses.
- The cerebellum receives inputs and sends outputs like any motor structure in the CNS.
- The main functions of the cerebellum are correction, balance, coordination of the actions and many other motor functions
- Every motor command that is released from the cortex to one of the motor tracts has a copy that is sent to the cerebellum to **monitor this command** and correct it by a tract known as **<u>corticopontocerrebellar tract.</u>**
- Remember that commands go from a specific presentation area in the cortex to the same area in the cerebellum.
- The cerebellum receives also afferent fibers form many areas; for example: it receives inputs from the inferior olive and from the vestibular nuclei in the following manner: some commands go to the lateral reticular formation and inferior olive by their tracts, and then they send these commands to the spinal cord. They also receive a feedback from the spinal cord and send it to the cerebellum to correct or monitor it.
- **<u>Parts of the cerebellum:</u>**

► **Anatomically** the cerebellum is divided into:

→ Anterior lobe.
→ Posterior lobe.
→ Flocculonodular lobe.

► **<u>Functionally</u>** ; the cerebellum is divided by longitudinal axis not by lobes;

1- **<u>Vermis</u>**:

- → This is the central part of the cerebellum.
- → It is responsible for the axial muscles such as the neck, hip, sholder and antigravity muscles…it has the representation of these muscles.
- → It receives feedback from the periphery.

2- **<u>Intermediate zone:</u>**

- → It controls the distal portion of upper and lower limps thus it has the representation of these muscles
- → It receives feedback from the periphery.

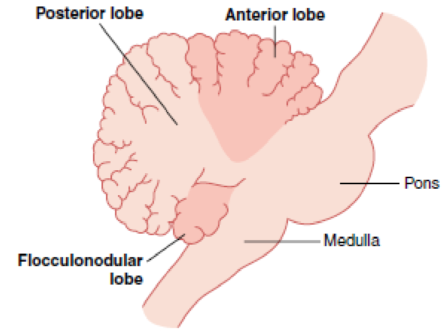


Figure 56-1 Anatomical lobes of the cerebellum as seen from the lateral side.

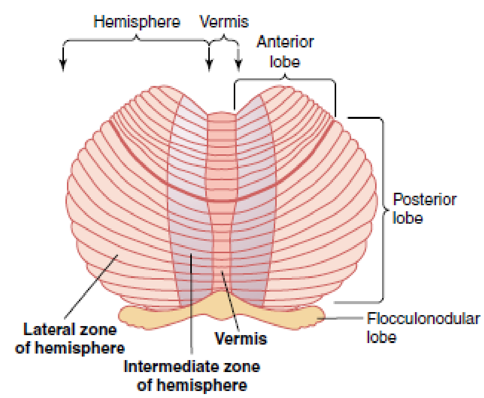


Figure 56-2 Functional parts of the cerebellum as seen from the posteroinferior view, with the inferiormost portion of the cerebellum rolled outward to flatten the surface.

3- **<u>The lateral zone:</u>**

- → It controls the sequence, timing, planning and coordination of the movements, especially for ballistic (i.e. very rapid) and programmed movements; like typing. These movements are very fast that they cannot be controlled by the cortex because it is going to take long time. Thus this part of the cerebellum programs such movements and tells the body to do them -like when you run a computer program to do a certain task and it does what it is supposed to do- .
- → In other words, if a person wants to type something, this part of the cerebellum makes something like a program for his typing movements. This program includes many actions likecontraction of the agonist (flexor) and relaxation of the antagonist (extensor) and the opposite might take place within the perfect timing and sequence.So the cerebellum makes this program and sends it to the body, it will run rapidly resulting in fast, professional typing movements. This is the concept of programming the movements.
- → Receives **No feedback** from the periphery thus there is no representation.
- → *"Without this lateral zone, most discrete motor activities of the body lose their*

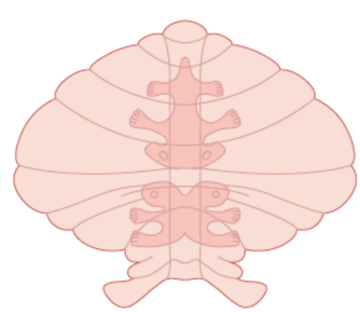


Figure 56-3 Somatosensory projection areas in the cerebellar cortex.

appropriate timing and sequencing and therefore become incoordinate." Guyton, *12th edition, page 682.*

► **Developmentally:**

A- Vesstibulocerebellar part:

- → This is mainly composed of the flocculonodular lobe.
- → Because it is the oldest part of the cerebellum -from an evolutionary point of view-, it is called **archicerebellum**.
- → It receives its impulses from the vestibular system of the inner ear, either through the vestibular nuclei OR through afferent fibers that originate in the vestibular apparatus itself→ to the vestibular nuclei →then they terminate in the flocculonodular lobe and fastigial nucleus of the cerebellum.
- → Since it's related to the vestibular system, thus it is concerned with balance and eye movements.
- → While the efferent fibers arise from fastigial nucleus→ to the vestibular nuclei carrying the corrections and monitoring commands.
- → Some efferent fibers may terminate in oculomotor nuclei which control the extra ocular muscles.
- → Also, some efferent fibers may terminate in the reticular formation of the brain stem and go through the reticulospinal tract to correct the position by controlling the anti-gravity muscles.
- → Based on that; an abnormality in this part may result in dysequilibrium, nystagmus or abnormal posture.

B- Spinocerebellum part:

- → It is made of vermis and para-vermis areas -i.e. intermediate zones-.
- → Known also as paleocerebellum.
- → Body representation is found in this part of the cerebellum.
- → Concerned with peripheral motor action thus it communicates with the spinal cord through the medial and lateral motor systems.

C- Cerebocerebellum:

- → Called the neocerebellum as it is the newest part of the cerebellum.
- → It is found in monkeys and humans.
- → It is connected with the cortex.
- → It has **No representation** of the body because it receives no inputs from down; it only receives inputs from the cortex and sends outputs to the cortex through the thalamus (VL part of it) -it does not communicate with the periphery-. *It communicates only with the cortex!*

→ It is concerned with planning and timing of the actions -onset and termination-.

❖ <u>Cerebellar nuclei:</u>

- All the deep cerebellar nuclei receive signals from two sources:
  (1) The cerebellar cortex
  (2) The deep sensory afferent tracts to the cerebellum
- All efferent fibers of the cerebellum originate from one of the nuclei.
- These deep nuclei are:

→ **Fastigial nucleus:**the deep nucleus of the vermis.

→ **Interposed nucleus:**the deep nucleus of the intermediate zonewhich is composed of globose nucleus and the emboliform nucleus.

→ **Dentate nucleus:**the deep nucleus of the lateral zone.

- **<u>Very important note:</u>** all the efferent fibers of the cerebellum originate from the deep cerebellar nuclei **except** some fibers that arise from the **<u>lateral vestibular nucleus</u>** of the medulla thus this nucleus can be considered **functionally**as a deep cerebellar nucleus. So you can notice that some afferent fibers go directly to the lateral vestibular nuclei and some efferent arise from it directly and go to the vestibulospinal tract.

Sorry for any mistakes,

Wish you all best of luck ~

Vestibular Sensations and Maintenance of Equilibrium

Vestibular Apparatus

The vestibular apparatus, shown in Figure 55-9, is the sensory organ for detecting sensations of equilibrium. It is encased in a system of bony tubes and chambers located in the petrous portion of the temporal bone, called the *bony labyrinth.* Within this system are membranous tubes and chambers called the *membranous labyrinth.* The membranous labyrinth is the functional part of the vestibular apparatus.

The top of Figure 55-9 shows the membranous labyrinth. It is composed mainly of the *cochlea* (ductus cochlearis); three *semicircular canals;* and two large chambers, the *utricle* and *saccule.* The cochlea is the major sensory organ for hearing (see Chapter 52) and has little to do with equilibrium. However, the *semicircular canals,* the *utricle,* and the *saccule* are all integral parts of the equilibrium mechanism.

"Maculae"—Sensory Organs of the Utricle and Saccule for Detecting Orientation of the Head with Respect to Gravity. Located on the inside surface of each utricle and saccule, shown in the top diagram of Figure 55-9, is a small sensory area slightly over 2 millimeters in diameter called a *macula.* The *macula of the utricle* lies mainly in the *horizontal plane* on the inferior surface of the utricle and plays an important role in determining orientation of the head when the head is upright. Conversely, the *macula of the saccule* is located mainly in a *vertical plane* and signals head orientation when the person is lying down.

Each macula is covered by a gelatinous layer in which many small calcium carbonate crystals called *statoconia* are embedded. Also in the macula are thousands of *hair cells,* one of which is shown in Figure 55-10; these project *cilia* up into the gelatinous layer. The bases and sides of

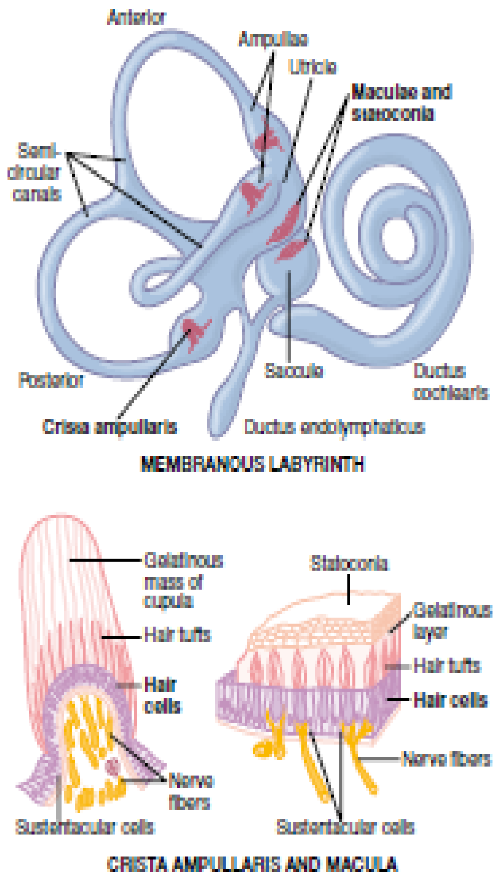


Figure 55-9 Membranous labyrinth and organization of the crista ampullaris and the macula.

Figure 55-10 Hair cell of the equilibrium apparatus and its synapses with the vestibular nerve.

the hair cells synapse with sensory endings of the *vestibular nerve.*

The calcified statoconia have a *specific gravity* two to three times the specific gravity of the surrounding fluid and tissues. The weight of the statoconia bends the cilia in the direction of gravitational pull.

Directional Sensitivity of the Hair Cells—Kinocilium. Each hair cell has 50 to 70 small cilia called *stereocilia*, plus one large cilium, the *kinocilium*, as shown in Figure 55-10. The kinocilium is always located to one side, and the stereocilia become progressively shorter toward the other side of the cell. Minute filamentous attachments, almost invisible even to the electron microscope, connect the tip of each stereocilium to the next longer stereocilium and, finally, to the kinocilium.

Because of these attachments, when the stereocilia and kinocilium bend in the direction of the kinocilium, the filamentous attachments tug in sequence on the stereocilia, pulling them outward from the cell body. This opens several hundred fluid channels in the neuronal cell membrane around the bases of the stereocilia, and these channels are capable of conducting large numbers of positive ions. Therefore, positive ions pour into the cell from the surrounding endolymphatic fluid, causing *receptor membrane depolarization.* Conversely, bending the pile of stereocilia in the opposite direction (backward to the kinocilium) reduces the tension on the attachments; this closes the ion channels, thus causing *receptor hyperpolarization.*

Under normal resting conditions, the nerve fibers leading from the hair cells transmit continuous nerve impulses at a rate of about 100 per second. When the stereocilia are bent toward the kinocilium, the impulse traffic increases, often to several hundred per second; conversely, bending the cilia away from the kinocilium decreases the impulse traffic, often turning it off completely. Therefore, as the orientation of the head in space changes and the weight of the statoconia bends the cilia, appropriate signals are transmitted to the brain to control equilibrium.

In each macula, each of the hair cells is oriented in a different direction so that some of the hair cells are stimulated when the head bends forward, some are stimulated when it bends backward, others are stimulated when it bends to one side, and so forth. Therefore, a different pattern of excitation occurs in the macular nerve fibers for each orientation of the head in the gravitational field. It is this "pattern" that apprises the brain of the head's orientation in space.

Semicircular Ducts. The three semicircular ducts in each vestibular apparatus, known as the *anterior, posterior,* and *lateral (horizontal) semicircular ducts,* are arranged at right angles to one another so that they represent all three planes in space. When the head is bent forward about 30 degrees, the lateral semicircular ducts are approximately horizontal with respect to the surface of the earth; the anterior ducts are in vertical planes that project *forward and 45 degrees outward,* whereas the posterior ducts are in vertical planes that project *backward and 45 degrees outward.*

Each semicircular duct has an enlargement at one of its ends called the *ampulla,* and the ducts and ampulla are filled with a fluid called *endolymph.* Flow of this fluid through one of the ducts and through its ampulla excites the sensory organ of the ampulla in the following manner: Figure 55-11 shows in each ampulla a small crest called a *crista ampullaris.* On top of this crista is a loose gelatinous tissue mass, the *cupula.* When a person's head begins to rotate in any direction, the inertia of the fluid in one or more of the semicircular ducts causes the fluid to remain stationary while the semicircular duct rotates with the head. This causes fluid to flow from the duct and through the ampulla, bending the cupula to one side, as demonstrated by the position of the colored cupula in Figure 55-11. Rotation of the head in the opposite direction causes the cupula to bend to the opposite side.

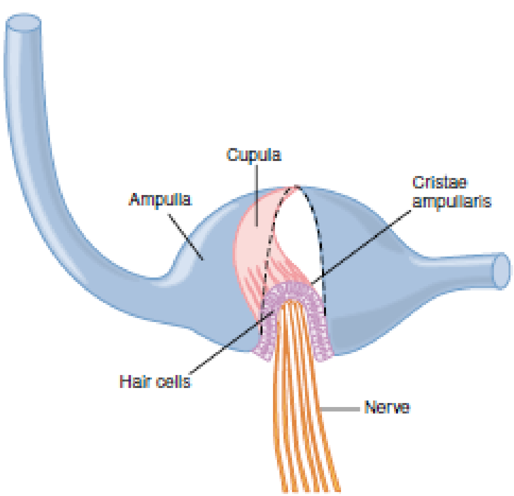


Figure 55-11 Movement of the cupula and its embedded hairs at the onset of rotation.

Into the cupula are projected hundreds of cilia from hair cells located on the ampullary crest. The kinocilia of these hair cells are all oriented in the same direction in the cupula, and bending the cupula in that direction causes depolarization of the hair cells, whereas bending it in the opposite direction hyperpolarizes the cells. Then, from the hair cells, appropriate signals are sent by way of the *vestibular nerve* to apprise the central nervous system of a *change in rotation* of the head and the *rate of change* in each of the three planes of space.

Function of the Utricle and Saccule in the Maintenance of Static Equilibrium

It is especially important that the hair cells are all oriented in different directions in the maculae of the utricles and saccules so that with different positions of the head, different hair cells become stimulated. The "patterns" of stimulation of the different hair cells apprise the brain of the position of the head with respect to the pull of gravity. In turn, the vestibular, cerebellar, and reticular motor nerve systems of the brain excite appropriate postural muscles to maintain proper equilibrium.

This utricle and saccule system functions extremely effectively for maintaining equilibrium when the head is in the near-vertical position. Indeed, a person can determine as little as half a degree of dysequilibrium when the body leans from the precise upright position.

Detection of Linear Acceleration by the Utricle and Saccule Maculae. When the body is suddenly thrust forward—that is, when the body accelerates—the statoconia, which have greater mass inertia than the surrounding fluid, fall backward on the hair cell cilia, and information of dysequilibrium is sent into the nervous centers, causing the person to feel as though he or she were falling backward. This automatically causes the person to lean forward until the resulting anterior shift of the statoconia exactly equals the tendency for the statoconia to fall backward because of the acceleration. At this point, the nervous system senses a state of proper equilibrium and leans the body forward no farther. Thus, the maculae operate to maintain equilibrium during linear acceleration in exactly the same manner as they operate during static equilibrium.

The maculae *do not* operate for the detection of linear *velocity.* When runners first begin to run, they must lean far forward to keep from falling backward because of initial *acceleration,* but once they have achieved running speed, if they were running in a vacuum, they would not have to lean forward. When running in air, they lean forward to maintain equilibrium only because of air resistance against their bodies; in this instance, it is not the maculae that make them lean but air pressure acting on pressure end-organs in the skin, which initiate appropriate equilibrium adjustments to prevent falling.

Detection of Head Rotation by the Semicircular Ducts

When the head suddenly begins to rotate in any direction (called *angular acceleration*), the endolymph in the semicircular ducts, because of its inertia, tends to remain stationary while the semicircular ducts turn. This causes relative fluid flow in the ducts in the direction opposite to head rotation.

Figure 55-12 shows a typical discharge signal from a single hair cell in the crista ampullaris when an animal is rotated for 40 seconds, demonstrating that (1) even when the cupula is in its resting position, the hair cell emits a tonic discharge of about 100 impulses per second; (2) when the animal begins to rotate, the hairs bend to one side and the rate of discharge increases greatly; and (3) with continued rotation, the excess discharge of the hair cell gradually subsides back to the resting level during the next few seconds.

The reason for this adaptation of the receptor is that within the first few seconds of rotation, back resistance to the flow of fluid in the semicircular duct and past the bent cupula causes the endolymph to begin rotating as rapidly as the semicircular canal itself; then, in another 5 to 20 seconds, the cupula slowly returns to its resting position in the middle of the ampulla because of its own elastic recoil.

When the rotation suddenly stops, exactly opposite effects take place: The endolymph continues to rotate while the semicircular duct stops. This time, the cupula bends in the opposite direction, causing the hair cell to stop discharging entirely. After another few seconds, the endolymph stops moving and the cupula gradually returns to its resting position, thus allowing hair cell discharge to return to its normal tonic level, as shown to the right in Figure 55-12. Thus, the semicircular duct transmits a signal of one polarity when the head *begins* to rotate and of opposite polarity when it *stops* rotating.

"Predictive" Function of the Semicircular Duct System in the Maintenance of Equilibrium. Because the semicircular ducts do not detect that the body is off balance in the forward direction, in the side direction, or in the backward direction, one might ask: What is the semicircular ducts' function in the maintenance of equilibrium? All they detect is that the person's head is *beginning* or *stopping* to rotate in one direction or another. Therefore, the function of the semicircular ducts is not to maintain static equilibrium or to maintain equilibrium during steady directional or rotational movements. Yet loss of function of the semicircular ducts does cause a person to have poor equilibrium when attempting to perform *rapid, intricate changing* body movements.

The function of the semicircular ducts can be explained by the following illustration: If a person is running forward rapidly and then suddenly begins to turn to one side, *he or she will fall off balance a fraction of a second later* unless appropriate corrections are made *ahead of time*. But the maculae of the utricle and saccule cannot detect that he or she is off balance until *after* this has occurred. The semicircular ducts, however, will have already detected that the person is turning, and this information can easily apprise the central nervous system of the fact that the person *will* fall off balance within the next fraction of a second or so unless some *anticipatory correction* is made.

In other words, the semicircular duct mechanism *predicts* that dysequilibrium is going to occur and thereby causes the equilibrium centers to make appropriate anticipatory preventive adjustments. This helps the person maintain balance before the situation can be corrected.

Removal of the flocculonodular lobes of the cerebellum prevents normal detection of semicircular duct signals but has less effect on detecting macular signals. It is especially interesting that the cerebellum serves as a "predictive" organ for most rapid movements of the body, as well as for those having to do with equilibrium. These other functions of the cerebellum are discussed in the following chapter.

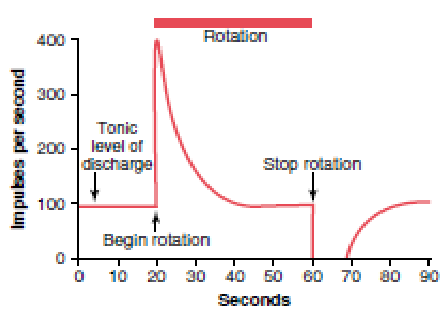


Figure 55-12 Response of a hair cell when a semicircular canal is stimulated first by the onset of head rotation and then by stopping rotation.

Vestibular Mechanisms for Stabilizing the Eyes

When a person changes his or her direction of movement rapidly or even leans the head sideways, forward, or backward, it would be impossible to maintain a stable image on the retinas unless the person had some automatic control mechanism to stabilize the direction of the eyes' gaze. In addition, the eyes would be of little use in detecting an image unless they remained "fixed" on each object long enough to gain a clear image. Fortunately, each time the head is suddenly rotated, signals from the semicircular ducts cause the eyes to rotate in a direction equal and opposite to the rotation of the head. This results from reflexes transmitted through the *vestibular nuclei* and the *medial longitudinal fasciculus* to the *oculomotor nuclei*. These reflexes are described in Chapter 51.

Other Factors Concerned with Equilibrium

Neck Proprioceptors. The vestibular apparatus detects the orientation and movement *only of the head*. Therefore, it is essential that the nervous centers also receive appropriate information about the orientation of the head with respect to the body. This information is transmitted from the proprioceptors of the neck and body directly to the vestibular and reticular nuclei in the brain stem and indirectly by way of the cerebellum.

Among the most important proprioceptive information needed for the maintenance of equilibrium is that transmitted by *joint receptors of the neck.* When the head is leaned in one direction by bending the neck, impulses from the neck proprioceptors keep the signals originating in the vestibular apparatus from giving the person a sense of dysequilibrium. They do this by transmitting signals that exactly oppose the signals transmitted from the vestibular apparatus. However, *when the entire body* leans in one direction, the impulses from the vestibular apparatus *are not opposed* by signals from the neck proprioceptors; therefore, in this case, the person does perceive a change in equilibrium status of the entire body.

Proprioceptive and Exteroceptive Information from Other Parts of the Body. Proprioceptive information from parts of the body other than the neck is also important in the maintenance of equilibrium. For instance, pressure sensations from the footpads tell one (1) whether weight is distributed equally between the two feet and (2) whether weight on the feet is more forward or backward.

Exteroceptive information is especially necessary for the maintenance of equilibrium when a person is running. The air pressure against the front of the body signals that a force is opposing the body in a direction different from that caused by gravitational pull; as a result, the person leans forward to oppose this.

Importance of Visual Information in the Maintenance of Equilibrium. After destruction of the vestibular apparatus, and even after loss of most proprioceptive information from the body, a person can still use the visual mechanisms reasonably effectively for maintaining equilibrium. Even a slight linear or rotational movement of the body instantaneously shifts the visual images on the retina, and this information is relayed to the equilibrium centers. Some people with bilateral destruction of the vestibular apparatus have almost normal equilibrium as long as their eyes are open and all motions are performed slowly. But when moving rapidly or when the eyes are closed, equilibrium is immediately lost.

Neuronal Connections of the Vestibular Apparatus with the Central Nervous System

Figure 55-13 shows the connections in the hindbrain of the vestibular nerve. Most of the vestibular nerve fibers terminate in the brain stem in the *vestibular nuclei,* which are located approximately at the junction of the medulla and the pons. Some fibers pass directly to the brain stem reticular nuclei without synapsing and also to the cerebellar fastigial, uvular, and flocculonodular lobe nuclei. The fibers that end in the brain stem vestibular nuclei synapse with second-order neurons that also send fibers into the cerebellum, the vestibulospinal tracts, the medial longitudinal fasciculus, and other areas of the brain stem, particularly the reticular nuclei.

The primary pathway for the equilibrium reflexes begins in the vestibular nerves, where the nerves are excited by the vestibular apparatus. The pathway then passes to the vestibular nuclei and cerebellum. Next, signals are sent into the reticular nuclei of the brain stem, as well as down the spinal cord by way of the vestibulospinal and reticulospinal tracts. The signals to the cord control the interplay between facilitation and inhibition of the many antigravity muscles, thus automatically controlling equilibrium.

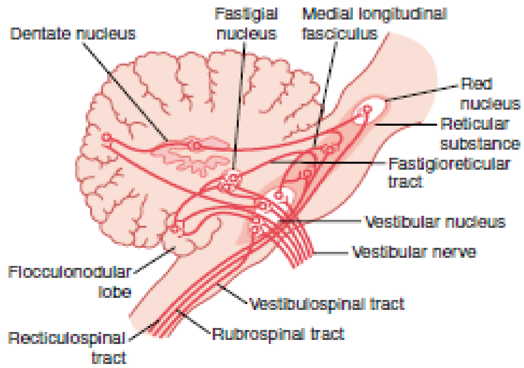


Figure 55-13 Connections of vestibular nerves through the vestibular nuclei (*large oval white area*) with other areas of the central nervous system.

The *flocculonodular* lobes of the cerebellum are especially concerned with dynamic equilibrium signals from the semicircular ducts. In fact, destruction of these lobes results in almost exactly the same clinical symptoms as destruction of the semicircular ducts themselves. That is, severe injury to either the lobes or the ducts causes loss of dynamic equilibrium during *rapid changes in direction of motion* but does not seriously disturb equilibrium under static conditions. It is believed that the *uvula* of the cerebellum plays a similar important role in static equilibrium.

Signals transmitted upward in the brain stem from both the vestibular nuclei and the cerebellum by way of the *medial longitudinal fasciculus* cause corrective movements of the eyes every time the head rotates, so the eyes remain fixed on a specific visual object. Signals also pass upward (either through this same tract or through reticular tracts) to the cerebral cortex, terminating in a primary cortical center for equilibrium located in the parietal lobe deep in the sylvian fissure on the opposite side of the fissure from the auditory area of the superior temporal gyrus. These signals apprise the psyche of the equilibrium status of the body.

Functions of Brain Stem Nuclei in Controlling Subconscious, Stereotyped Movements

Rarely, a baby is born without brain structures above the mesencephalic region, a condition called *anencephaly.* Some of these babies have been kept alive for many months. They are able to perform some stereotyped movements for feeding, such as suckling, extrusion of unpleasant food from the mouth, and moving the hands to the mouth to suck the fingers. In addition, they can yawn and stretch. They can cry and can follow objects with movements of the eyes and head. Also, placing pressure on the upper anterior parts of their legs causes them to pull to the sitting position. It is clear that many of the stereotyped motor functions of the human being are integrated in the brain stem.