The Physiology of the Senses
Lecture 10 - Balance
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Contents

Objectives

1) Specify which anatomical aspects of otolith organs and vestibular canals make them best suited for detecting different types of motion.

2) Explain how a particular translational direction is coded by hair cells in the otolith organs.

3) Given an arbitrary head rotation, predict which vestibular canal is most active.

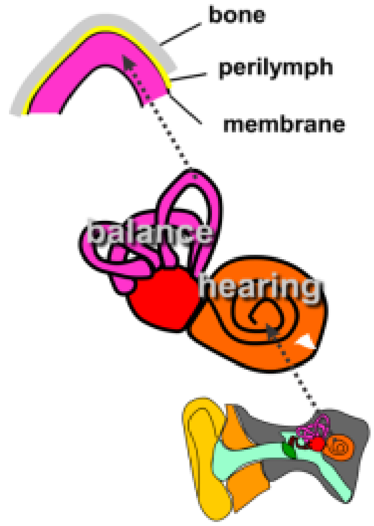
4) List the synapses in the vestibular ocular reflex.

5) Explain how the optokinetic response helps prevent dizziness and also causes it.

6) Contrast which parts of the cerebellar circuits act as teachers and which the students.

Revised 15/11/2017

The sense of balance originates in the labyrinth.



The **bony labyrinth** is a convoluted system of tunnels in the skull that contains the sensors for hearing and balance. The inside of these tunnels is lined with a membrane. The space between the bone and the membrane (Figure 10.1) contains **perilymph** a fluid somewhat similar to extracellular fluid. **Endolymph,** a fluid similar to intracellular fluid (i.e. high K+, low Na+) fills the inside of the membrane and surrounds the balance receptors. Endolymph bathes the hair cells in both the auditory and vestibular system. Endolymph has a +80 mv charge with respect to the perilymph. We will discover the importance of this voltage shortly.

Figure 10. 1 The Labyrinth and Vestibular System Inside the bony labyrinth (grey) one finds the perilymph (yellow) and inside the membrane, the endolymph (pink).

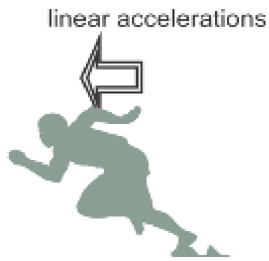
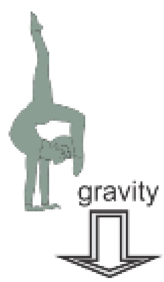
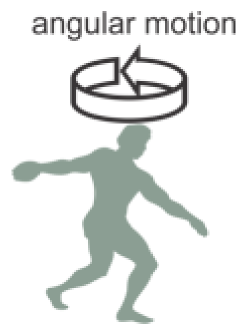
The sensors for hearing are close to those for balance because they have a common origin.

The common origin is the lateral line organ that first evolved in early fish. This organ consists of tubes that lie along the fish's side. As the fish swims, water flows through these tubes and across the sensory cells, which have hair-like projections that are bent by the water. Fluid movement in the tubes is caused by

1. waves produced by some noise in the water (the precursor of the auditory system) and
2. the fish's own motion (the precursor of balance or the **vestibular system**).

The vestibular system has two parts.

The vestibular system has two parts, the **otolith organs** and the **semicircular canals**. Each has a different function.

Otolith Organs	**Semicircular Canals**
The otolith organs have two functions: 1. The otoliths sense the head's **linear acceleration** (motion in a straight line). They sense how quickly you are accelerating forward or backward, left or right, or up or down.  2. They are also able to sense the head's position relative to **gravity**. These are the organs that tell us whether we are upside down or right side up. 	The canals detect the head's **rotation** (turning motion). 

The Anatomy of the Otolith Organs

Inside the otolith organs are two sacs called the **utricle** and the **saccule**. On the inside of each a portion of the sac is thickened and called the macula (blue and green ovals in Figure 10.2). The macula contains **hair cells** innervated by neurons of the 8th nerve.

The hair cells project into a gel. Calcium carbonate crystals (ear stones) are embedded in this gel. The purpose of the stones is to give the gel extra mass.

The thickest and longest of hairs on hair cells is the **kinocilium**.

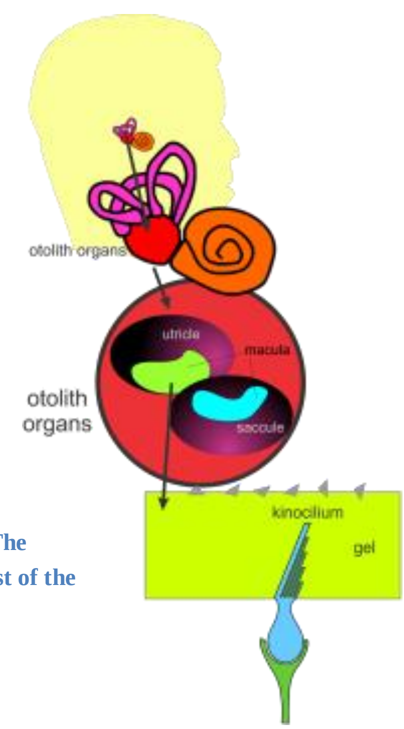


Figure 10. 2 The otolith organs consist of the utricle and saccule.

How is motion transduced into neural firing?

The steps are:
1) As in auditory hair cells, motion bends the hairs.
2) Endolymph, high in K+ and low in Na+ surrounds the hairs. Endolymph has a +80 mv charge with respect to the hair cell.
3) The filament between adjacent hairs opens ion channels. The endolymph's positive voltage pushes K+ into the negatively charged hair cell (Figure 10.3).
4) The hair cell depolarizes, releasing neurotransmitter.
5) There is an increase in the frequency of AP's in the 8th nerve afferent.

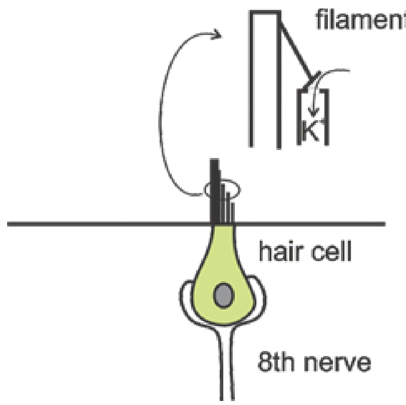


Figure 10. 3 The Hair Cell's Hairs and Filaments When the flap is opened, K+, potassium, enters the cell.

What bends the hairs?

When the hairs are undisturbed, the vestibular afferents have a resting firing rate of about 100 action potentials per second (Figure 10.4).

When the head moves, the inertia of the crystals bends the hair cells in the opposite direction. Bending all the hairs towards the tallest hair, the kinocilium, opens the ion channel and depolarizes the cell, inducing an increase in action potential frequency in the 8th nerve afferents.

Bending away from the kinocilium closes the ion channel and causes hyperpolarization and reduces the action potential frequency.

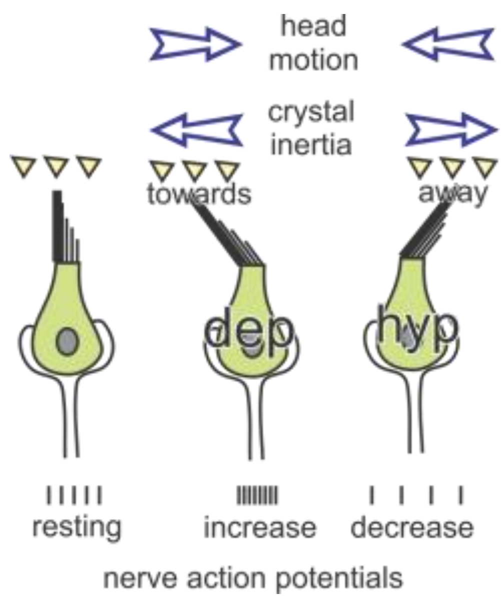


Figure 10. 4 The Effects of Motion on Hair Cells Bending the hairs toward the tallest hair increases the potential inside the cell and the rate of action potentials produced. Bending in the opposite direction produces the opposite effects.

In addition to head movements, gravity "pulls" on the stone crystals. When head position changes, the direction of this gravitational "pull" changes, telling you that your head is tilted (Figure 10.5).

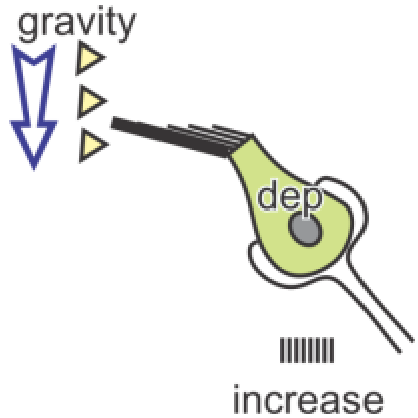


Figure 10. 5 The weight of the crystals pulls them down, as well as the attached hairs, activating the hair cell.

Within the macula of the utricle and saccule (Figure 10.6), the kinocilium of the hair cells are oriented in all possible directions on the surface of the macula (the location of kinocilium is indicated by the red arrows). The direction of linear acceleration or gravity is determined by which hair cells are most bent toward the kinocilium.

With the head upright, the **macula of the utricle** (green) is in the horizontal plane and senses left/right and forward/backward translations.

The **macula of the saccule** (blue) is on the side and senses translations in the vertical plane (up/down and forward/backward).

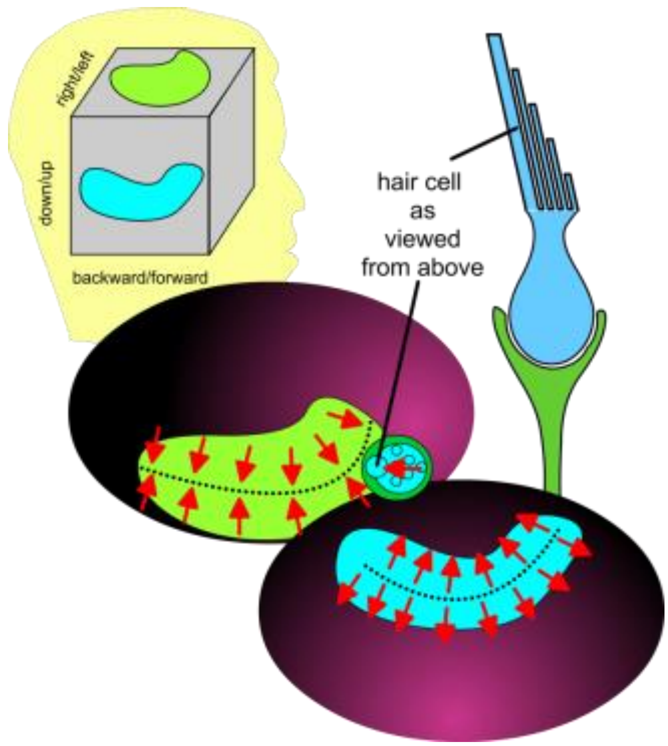


Figure 10. 6 The Orientation of the Hairs in the Otoliths
The arrow tip indicates the orientation of the kinocilium in the hair cells of the utricle (green) and saccule (blue). The box shows their orientation in the head.

The semicircular canals sense head rotation.

There are three canals on each side of your head (Figure 10.7A). One is approximately **horizontal (h)**, and the other two, **the anterior (a)** and **posterior (p)**, are vertical. All three are about perpendicular to each other and thus form three sides of a cube. Within the canals are endolymph-filled semicircular ducts and each has a swelling called the ampulla (Figure 10.7B). A pliable membrane called the cupula seals the inner diameter of the ampulla. The hairs of the hair cells project into the cupula.

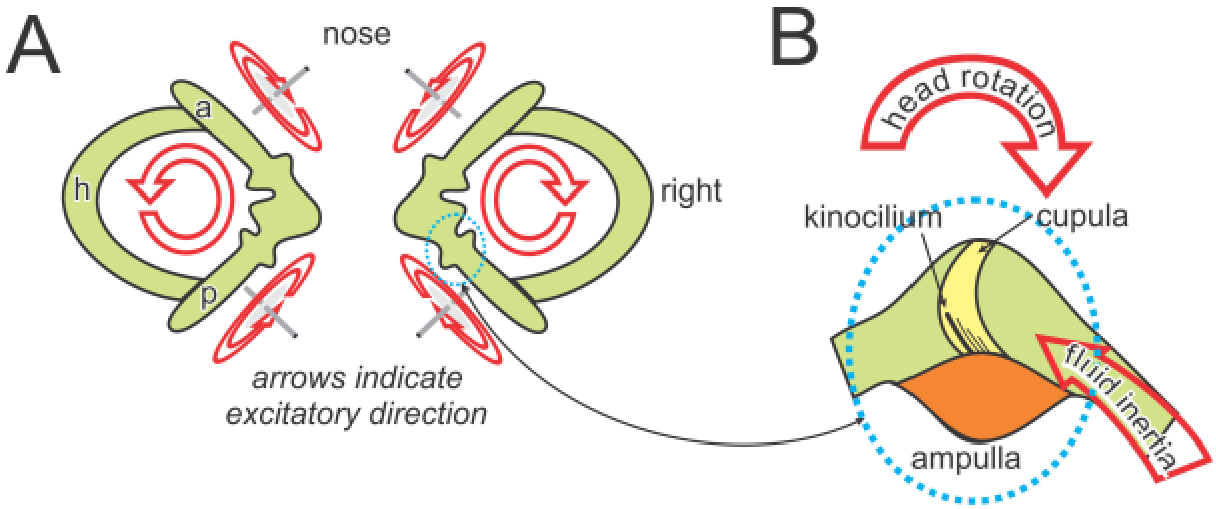


Figure 10. 7 **The Orientation of the Canals in the Head A:** the horizontal (h), anterior (a) and posterior (p) canals have different orientations (indicated by arrows). The top is towards the nose and the rightmost canals are on the right side of the head. **B:** the ampulla (shown inside the blue dotted circle contains the cupula and the hair cells. The latter become deflected during a head rotation.

How do the canals detect angular acceleration of the head?

When there is a change in speed of head rotation, the endolymph fluid lags behind, because of inertia, pushing on and distorting the cupula. The bending of the hair cell hairs causes increase or decrease of the hair cell potential, depending on whether bending occurs towards or away from the kinocilium.

How do the canals compute direction of head rotation?

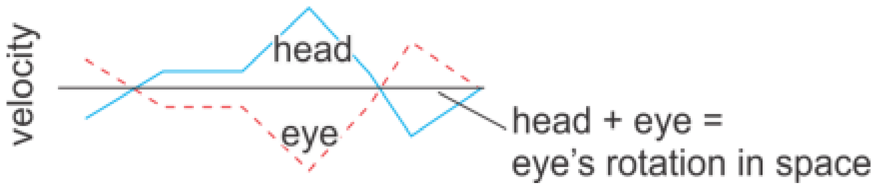
Since there are three canals on each side of the head and they are roughly perpendicular to each other, the activity in the canals decomposes all rotation into three components, so much to the right, so much downward, and so much clockwise. Also, the canals are arranged such that each canal has a partner on the other side of the head. When one partner’s hair cell potential is increased, the other’s is decreased. This is called **a push-pull organization**. When the rotation is in the plane of a canal push-pull pair, the potential of this pair’s cells are increased or decreased while the other four canals show no change. When the head rotates rightward in the plane of the horizontal canals, the potential increases in the horizontal canal on the right side of the head and decreases in the left. No change in potential occurs in the other four canals.

The anterior canal on one side and the posterior on the other also form push-pull pairs When you tip your head forward and to the left ear, in the plane of the left anterior canal, this canal's hair cells increase in potential while those of the right posterior canal decrease. No other canal changes its activity. When you tip your head forward and to the right ear, the right anterior canal's hair cell potential increases while those of the left posterior decreases.

The Vestibular Ocular Reflex (VOR)

The otoliths and canals activate many postural reflexes. These connect to muscles in your legs, trunk and arms and keep you upright. Another key reflex is one that turns the eyes, the **vestibular ocular reflex (VOR)**. The important function of the VOR is to stabilize the retinal image during rotations of the head. To maintain a clear image, requires keeping the eye still in space in spite of any head translation or rotation. For example, when the head rotates with a certain speed and direction, the eyes must rotate with the same speed but in the opposite direction (Figure 10.8). The ratio of the eye and head rotations is called the gain of the VOR. The ideal gain is -1. This gain keeps the image of the world stationary on the retina. Many of the newer smartphones use Optical Image Stabilization for the same reason.

Figure 10. 8 Rotations of the eye should cancel those of the head. If the eye rotation (red) in the head is the opposite of that of the head (blue) the eye will stay still (black flat line).



Explain the neural mechanism for a horizontal VOR.

When the head rotates rightward, the following occurs (Figure 10.9):

1) The right horizontal canal hair cells depolarize (potential increases) while those of the left hyperpolarize (potential decrease).
2) The right vestibular afferent activity increases, while activity of the left decreases.
3) The right vestibular nucleus' activity increases while that in the left decreases.
4) In the cranial nerve (motoneurons to extraocular muscles), neurons in the left 6th and right 3rd nerve nuclei fire at a higher frequency.
5) Those in the left 3rd and right 6th nerve nuclei fire at a lower frequency.
6) The left lateral rectus (lr) extraocular muscle and the right medial (mr) rectus contract.
7) The left medial rectus and the right lateral rectus relax.
8) Both eyes rotate leftward.

Notice the push-pull organization, an increase on one side is accompanied by a decrease on the other.

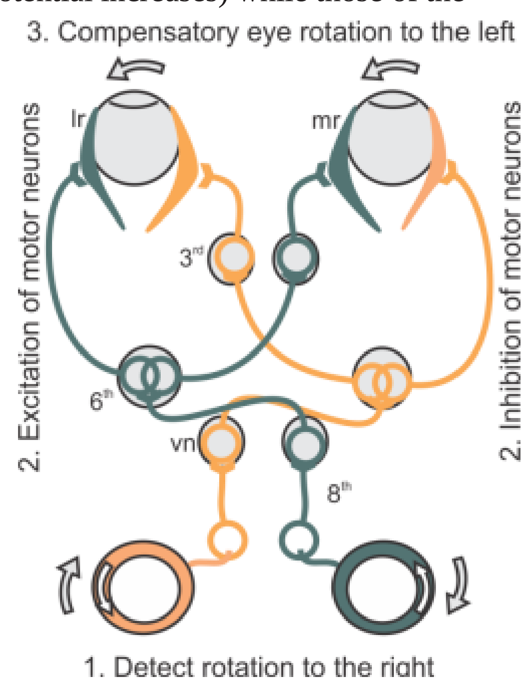


Figure 10. 9 The Horizontal VOR Turning the head to right (green) activates the right horizontal canal, the right vestibular nucleus ((vn), the motoneurons in the left 6th nerve nucleus (6th), left lateral rectus (lr), the right medial rectus (mr), and both eyes turn to the left. The mirror images neurons (orange) show an inhibition of activity when turning right.

Why do we get dizzy?

During normal head rotations, the eye rotates opposite to the head, canceling the motion of the head. This stabilizes the image of the world on the retina (Figure 10.10).

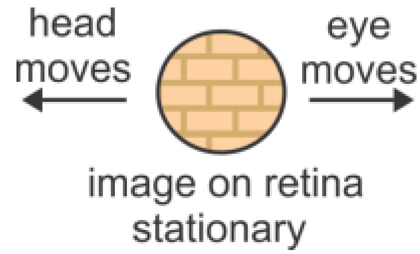


Figure 10. 10 The Normal Vestibular Ocular Response Head motion in one direction is canceled by eye rotation in the other, resulting in a stationary image on the retina.

When you turn your head, the cupula in you canal becomes deflected, signalling that you are turning. During a prolonged head rotation (20sec or more), the elasticity of the cupula gradually restores it to its upright position. The drive to the VOR stops and, if your eyes are closed, you falsely sense that you are stationary. If you then open your eyes, you see that the world moving and you feel dizzy (Figure 10.11).

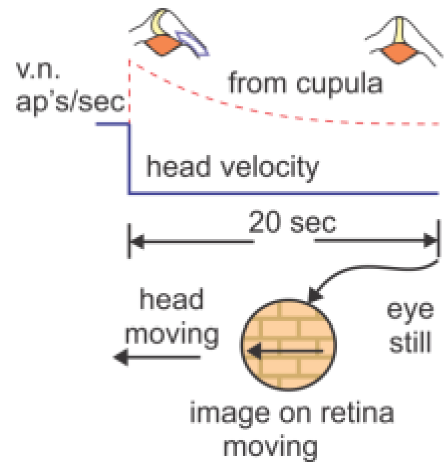


Figure 10. 11 Prolonged rotations make you dizzy. After 20 sec of rotation, the cupula springs back to its upright position signalling that you are stationary. If you now open your eyes you will see that in fact you are still rotating and you will feel dizzy. Top red dashed line: activity of hair cells. Blue line: head rotation.

Visual input, on its own, can drive the VOR, the optokinetic response (OKR), but the OKR takes time to build up. When the visual scene on your retina starts to move (retinal slip) the OKR kicks in producing a rotation of the eyes in the opposite direction. Thus an initial slip of the world in the eye's view is followed by a stabilized image. This initial retinal slip can elicit a false perception of motion. For example when you look out a car window and see an adjacent car start to move you often sense yourself move. The visual input comes from MSTd, which senses **optic flow**, the visual motion produced when you move. The signal from vision and the cupula is combined in the vestibular nuclei (Figure 10.12) and then sent to the thalamus. The thalamus then projects to the primary somatosensory cortex where activity elicits the subjective sense of self-motion.

Many do not become very dizzy during a prolonged rotation if they keep their eyes opened and fixate on stationary objects around them. This is because the visual input compensates for loss of vestibular drive. Visual input builds up as the vestibular input dies away, as the cupula is restored to its normal position. The net result is that the eye's view of the world remains stable (Figure 10.12). A ballet dancer avoids becoming g dizzy by spotting. Although the body spins continuously, the head rotates more rapidly and then is briefly still. This prevents adaptation of the cupula.

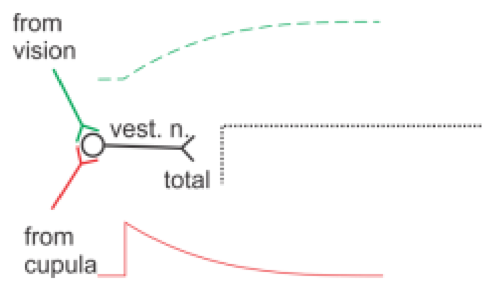


Figure 10. 12 Visual and vestibular signals combine to compute a correct estimate of head velocity. Green dashed visual input of optic flow. Red solid: vestibular estimate of head velocity. Black dotted: The combined correct estimate.

Motion sickness occurs when the two signals are in conflict. Suppose you are inside the cabin of a boat during a storm. Your vestibular afferents sense that you are moving. Because you and the cabin are moving together, the visual system senses that you are still. The visual and vestibular signals are in conflict. To avoid motion sickness the best solution is to go out on the deck and look at the horizon. Here both signal the same motion. Similarly, the best way to get motion sickness in a car is to sit in the backseat and read. The best way of avoiding motion sickness is to sit in the front seat and look out the front window.

One theory for the feeling of nausea that sometimes accompanies dizziness is that the brain interprets this conflict as poisoning and responds by eliciting vomiting to clear the poison.

More Cases of Feeling Dizzy

You can imagine that, as your life goes by, some neurons involved in the VOR may die or malfunction or the eye muscle strength may decrease. This would lower the VOR gain.

If you change the prescription on your glasses (with an increase or decrease in magnification), the change in optics changes the VOR gain you need. You initially may feel dizzy because of the retinal slip when wearing your glasses.

If you have an abnormal vestibular input you may experience the following disorders:
1) difficulty reading signs while walking because the VOR fails to stabilize the eyes and
2) difficulty standing with your eyes closed because the vestibular spinal reflexes, on their own, fail to assist posture correctly.

Most often, these disorders only produce a transient defect because the VOR is continuously adjusted and fine-tuned.

What adjusts the VOR?

The VOR is the combination of three pathways (Figure 10.13):

1) the direct pathway through the vestibular nucleus to the eye muscles.
2) the indirect pathway through the cerebellum. This involves the mossy fibers, then parallel fibers, and finally Purkinje cells which inhibit the vestibular nucleus.
3) retinal slip, the teacher, via input through the climbing fibers, changes the strength of connections between parallel fibers, that fire at the same time, and Purkinje cells.

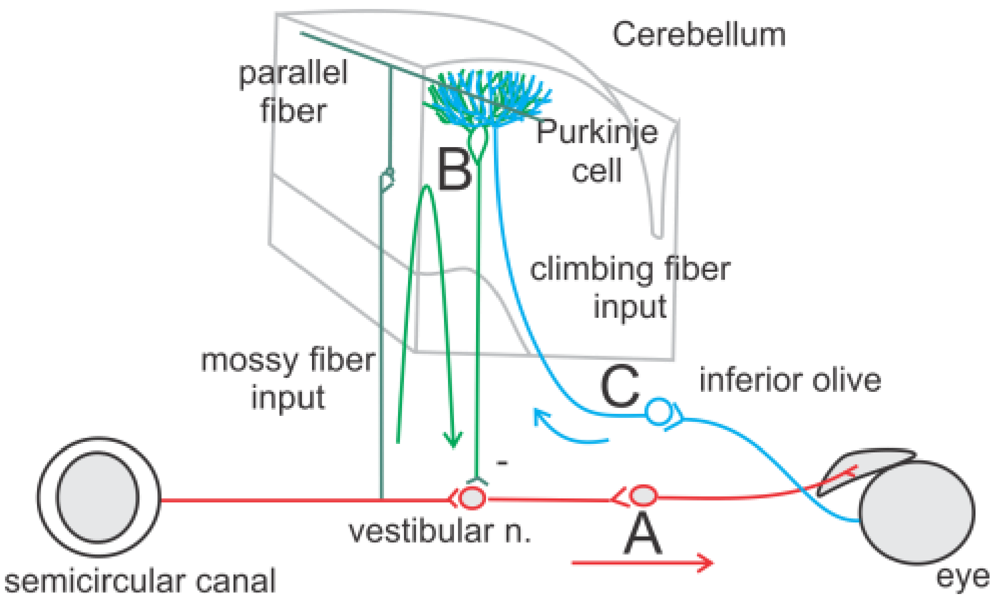


Figure 10. 13 **The Cerebellar Repair Shop A:** the direct pathway (red). **B:** the indirect pathway (green) through the cerebellum subtracts a correction. **C:** the climbing fiber input modifies the strength of the indirect pathway.

The VOR gain is determined by the difference between the direct and indirect paths. The cerebellum's task is to keep this difference optimal in spite of all the changes that may occur to the various parts of the direct VOR.

What teaches the cerebellum?

When VOR is not working properly (e.g. the eye is not rotating enough or too much) a slip of the image is detected by the retina and sent to the cerebellum via the inferior olive climbing fiber input. This is the teacher's input, which semi-permanently alters the synapses of the students; that of all concurrently activated parallel fibers. This increases or decreases the cerebellar inhibition of the vestibular nucleus. When the activity of the vestibular nucleus is just correct, the retinal slip stops and the teacher is silenced. The cerebellum acts like a repair shop. It makes similar re-adjustments to all our reflexes.

Alcohol and many drugs affect the function of the brain and this repair shop. It is thus not surprising that when the repair shop malfunctions, the VOR becomes uncalibrated, and one feels dizzy.

See problems and answers posted on

http://www.tutis.ca/Senses/L9Auditory/L9AuditoryProb.swf