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 the vestibular canal is most active.

4. List the connections for the vestibular ocular reflex.

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

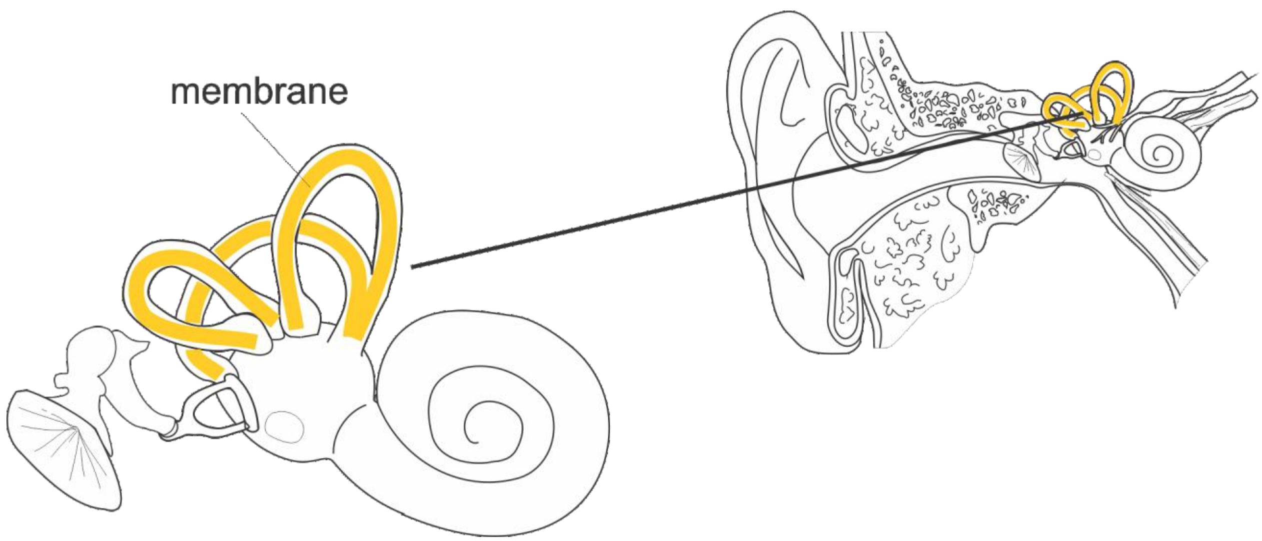
6. Contrast which parts of the cerebellar circuits act as teachers versus students.

The sense of balance originates from the labyrinth

The bony labyrinth is a convoluted system of tunnels in the skull that contains the sensors for the auditory and vestibular systems. The vestibular system is the part responsible for one's sense of balance.

The inside of these tunnels is lined with a membrane. Perilymph (somewhat similar to extracellular fluid) is found between the bone and the membrane.

Endolymph (similar to intracellular fluid e.g. high K+, low Na+) fills the inside of the membrane. It has a +80 mv charge with respect to the perilymph.



The auditory and vestibular systems have a common origin.

Aquatic animals possess a lateral line system. This organ consists of a system of tubes lined with sensory cells with hair like projections that are in communication with the surrounding water.

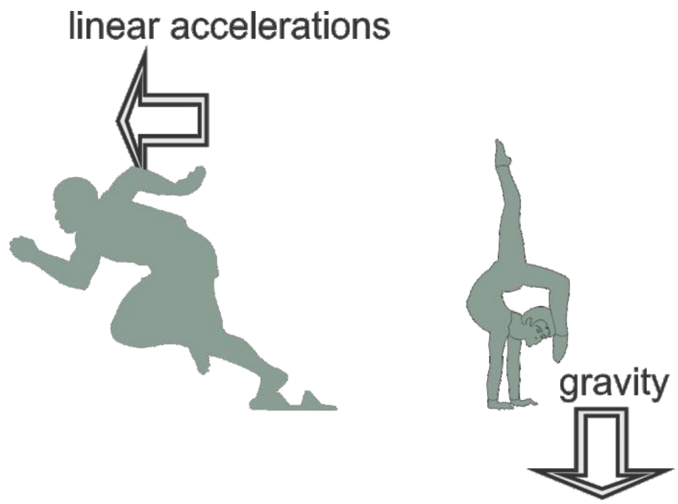
The sensory cells are activated by fluid movement in the tubes caused by:

1. Waves produced by some external disturbance in the water (the precursor of the auditory system).
2. The fish's own motion (the precursor of the vestibular system).

This system is the evolutionary precursor of our inner ear.

The vestibular system has two parts.

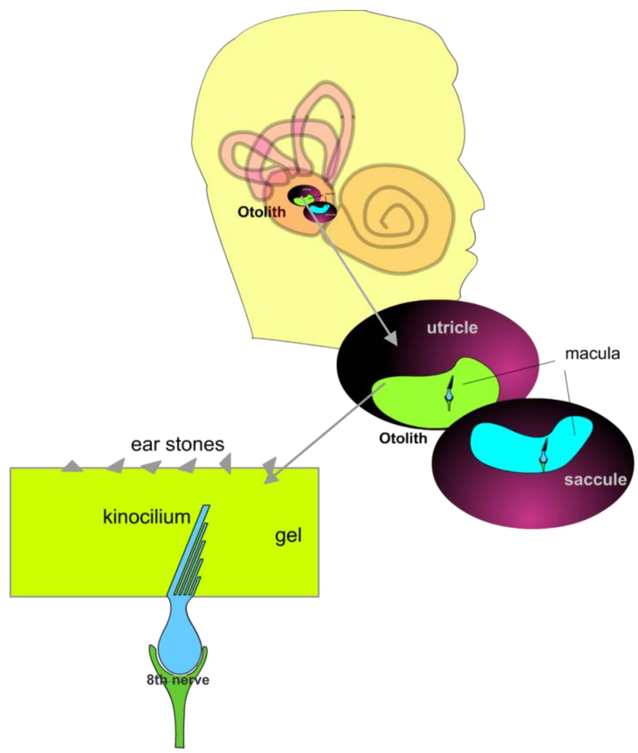
These are the otolith organs and the semicircular canals. Each has different functions.



The otolith organs have two functions:

1. The otoliths sense the head's translation (motion in a straight line).
2. They are also able to sense the head's position relative to gravity. These are the organs that tell us which way is up.

The canals detect the head's rotation (turning motion).



The anatomy of the otolith organs.

The otolith organs are two membranous sacs called the utricle and the saccule.

In each, a portion of the membrane is thickened (the macula) and contains hair cells innervated by neurons of the 8th nerve.

The hair cells project into a gelatinous substance. Calcium carbonate crystals (ear stones) are embedded in this gel.

The thickest and longest of stereocilia is the kinocilium.

How is motion transduced into neural firing?

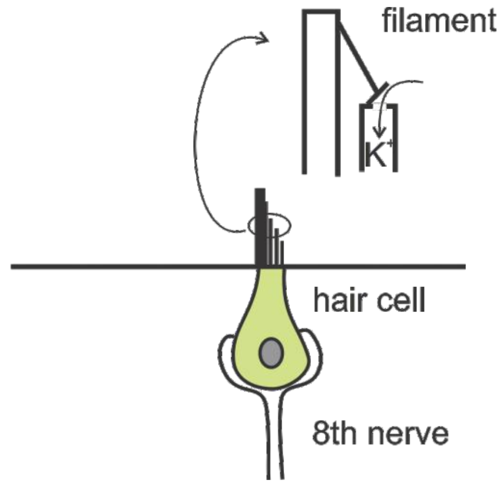
The steps are:

1) As in auditory hair cells, motion bends the hairs.

2) The filament between adjacent hairs opens ion channels allowing K^+ to enter the hair cell.

3) The hair cell depolarizes, releasing neurotransmitter

4) There is an increase in the frequency of AP's in the 8th nerve afferent.

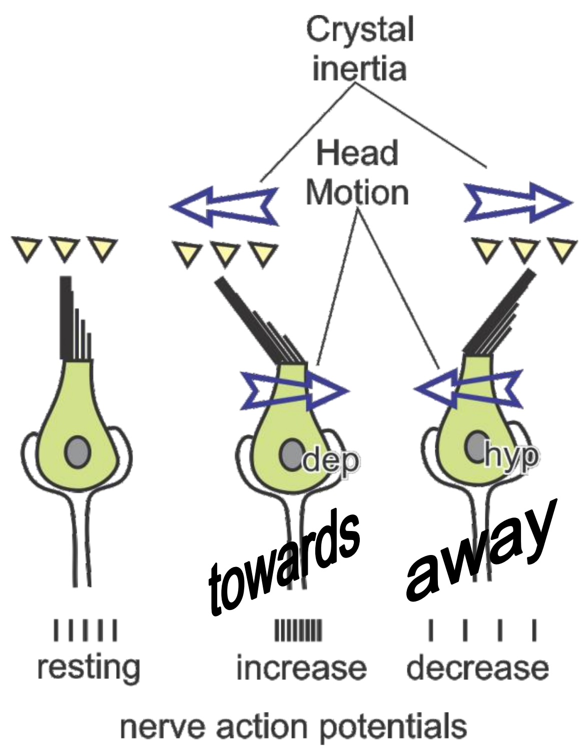


What bends the hairs?

When the hairs are undisturbed, the vestibular afferents have a baseline firing rate of about 100 action potentials per second.

When the head moves, the inertia of the crystals bends the hair cells in the opposite direction. Bending all the hairs towards the kinocilium depolarizes the cell, inducing an increase in AP frequency in the 8th nerve afferents.

Bending away from the kinocilium causes hyperpolarization and reduced AP frequency.

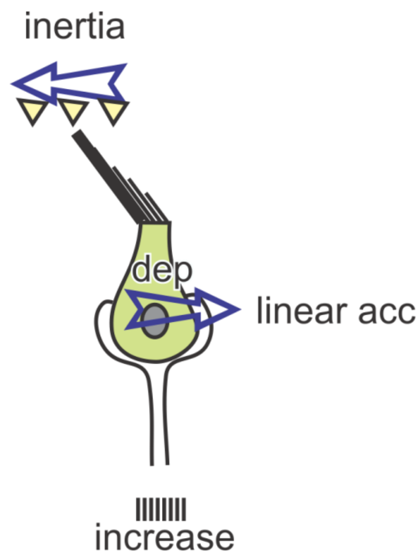


Revised 14/11/2012

Like head movements, gravity "pulls" on the crystals. When head position changes, the direction of this gravitational "pull" changes, telling you that your head is tilted.

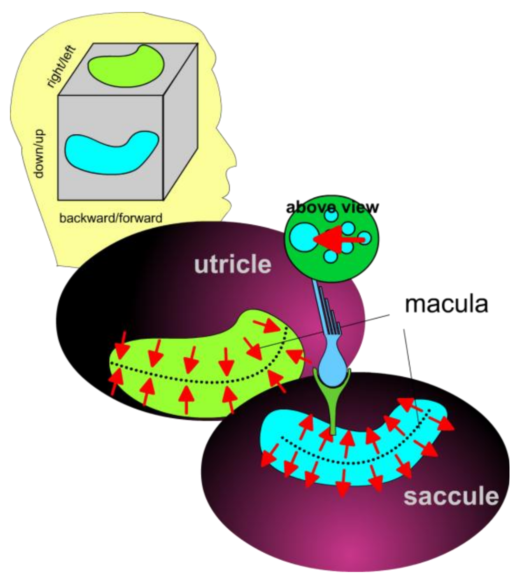
Within each macula, the kinocilium of the hair cells are oriented in all possible directions (location of kinocilium indicated by arrow).

The direction of linear acceleration or gravity is determined by which hair cells are most active.



With the head upright, the macula of the utricle is horizontal and senses left/right and forward/backward translations.

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



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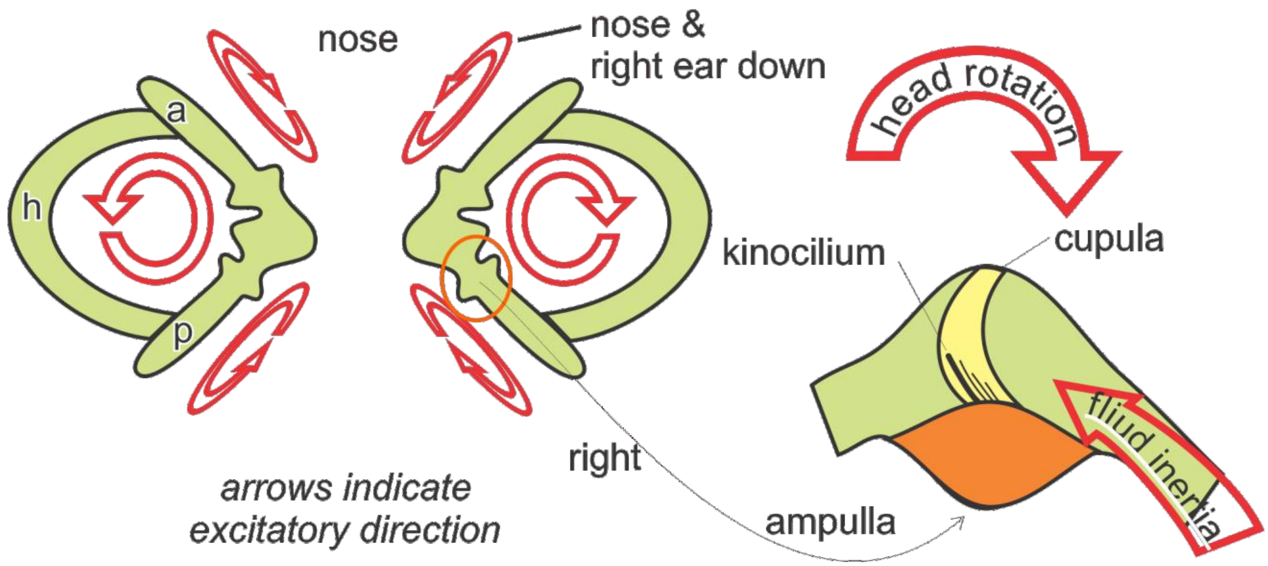
What is the functional anatomy of the semicircular canals?

There are three canals in each side. One is approximately horizontal (h), and the other two, the anterior (a) and posterior (p), are aligned vertically and are about perpendicular to each other. Within the canals are endolymph-filled semicircular ducts which open at both ends to the otoliths. Each duct has a swelling at one of these junctions called the ampulla. A pliable membrane called the cupula seals the inner diameter of the ampulla. The hairs of the hair cells project into the cupula.



How does this structure 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.

Bending of the stereocilia causes excitation or inhibition of the hair cell depending on whether bending occurs towards or away from the kinocilium.

How does the labyrinth compute direction of head rotation?

Since there are three canals on each side that are roughly orthogonal to each other, they can decompose a rotation into three components much as we do when we say that a direction is so much to the right, so much upward, 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 is maximally excited, the other is maximally inhibited. This is called push-pull organization.

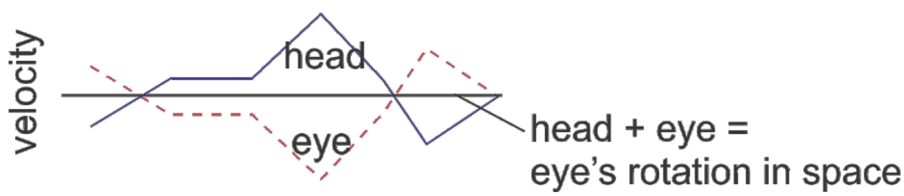
When the head rotates rightward, excitation occurs in the right horizontal canal on the right side of the head and inhibition occurs in the left.

The anterior canal on one side and the posterior on the other also form push-pull pairs.

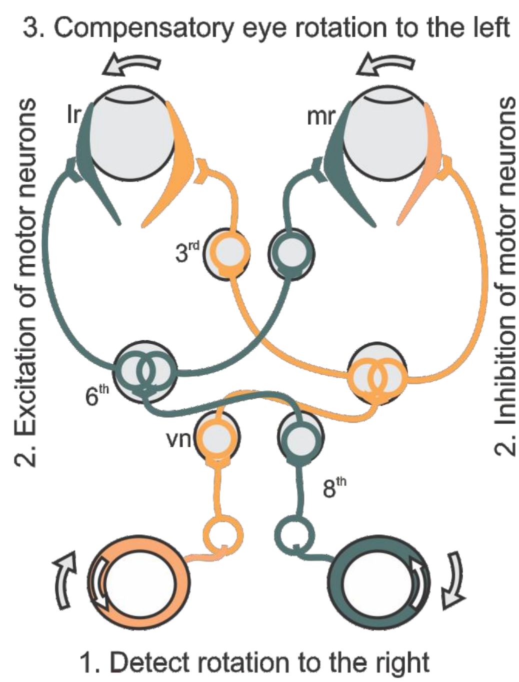
The vestibular ocular reflex (VOR).

The otoliths and canals activate many reflexes. These connect to your legs, trunk and arms for postural support. A key reflex is the vestibular ocular reflex (VOR).

The function of the VOR is to stabilize the retinal image during rotations of the head. This requires maintenance of stable eye position in space during any head **translation** or **rotation**. For example, when the head rotates with a certain speed and direction, the eyes should rotate with the same speed but in the opposite direction. The ratio of the eye and head rotations is called the gain of the VOR. The ideal gain is -1. This gain keeps the eye stationary in space.



Explain the neural mechanism for a horizontal VOR.



right

When the head rotates rightward, the following occurs.

The right horizontal canal hair cells depolarize, the left hyperpolarize.

The right vestibular afferent activity increases, the left decreases.

The right vestibular nucleus' activity increases, the left decreases.

In the cranial nerves (motoneurons to extraocular muscles), neurons in the left 6^{th} & 3^{rd} fire at a higher frequency.

Those in the left 3^{rd} and right 6^{th} fire at a lower frequency.

The left lateral rectus (lr) extraocular muscle and the right medial (mr) rectus contract.

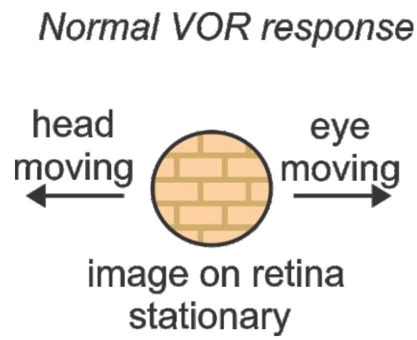
The left medial rectus and the right lateral rectus relax.

Both eyes rotate leftward.

Notice the push-pull organization.

Why do we get dizzy?

During normal head rotations, the eye rotates opposite to the head, thus canceling the motion of the head. This tends to stabilize the image of the world on the retina.

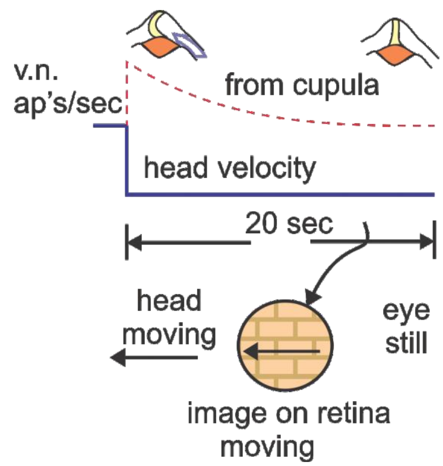


During very prolonged head rotations in the dark, the elasticity of the cupula gradually restores it to its upright position.

The drive to the VOR stops (falsely telling the brain that one is stationary).

If at this point you open your eyes, you see the world moving and you feel dizzy.

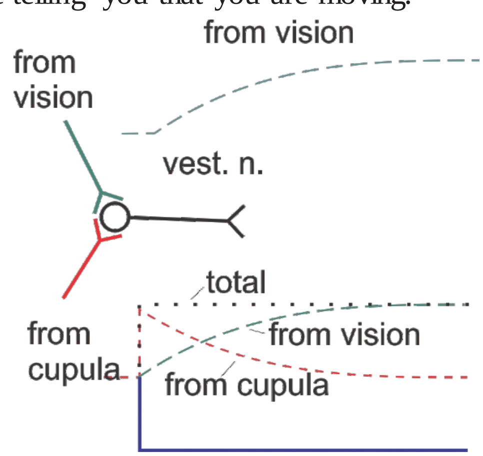
Visual input on its own can drive the VOR (the optokinetic response) but it takes time to build up. An initial slip of the world in the eye's view followed by a stabilized image as the optokinetic response kicks in.



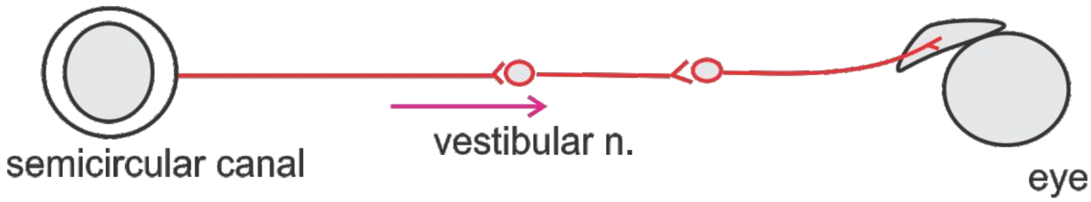
This visual input can elicit a false perception of motion (e.g. when looking out a car window and an adjacent car starts to move).

Many do not become very dizzy during a prolonged rotation if they keep their eyes opened. During a prolonged head rotation with the eyes open, both vestibular and visual input reach the vestibular nuclei. Visual input builds up as vestibular dies away. Thus the visual input compensates for the loss of cupula drive. The net result is that the eye's view of the world remains stable.

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 are telling you that you are moving. Because you and the cabin are moving together, the visual system senses that you are not moving. To avoid motion sickness the best bet is to go out on the deck and look at the horizon.



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



Does the VOR gain need to be adjusted?

The gain of the VOR (eye rotation / head rotation) should normally have a magnitude one in order to have zero retinal slip. You can imagine that, as your life goes by, some neurons involved in this reflex may die or malfunction. This would lower the VOR gain. You need something to re-adjust the gain of the VOR.

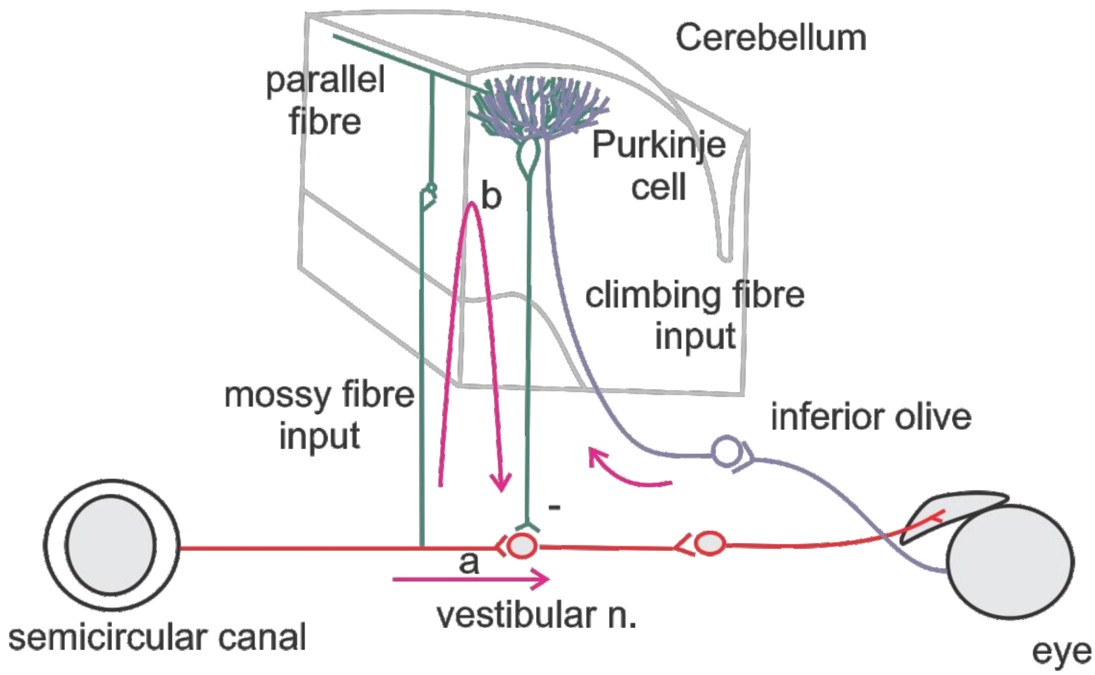
Disorders that cause a change in VOR gain:

1. 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 when wearing your glasses.
2. If your eye muscles become weaker, the VOR gain will become less than normal.
3. Disorders in gain produced by a change of vestibular input:

Disorders experienced if you have abnormal vestibular input:

1. Subjects cannot read signs while walking because the VOR fails to stabilize the eyes.
2. Subjects have difficulty standing with their eyes closed because the vestibular spinal reflexes fail to assist posture.

Most often, all of the above only produce a transient defect because the VOR is continuously adjusted and fine-tuned.



What adjusts the VOR?

The VOR is the combination of two pathways

a) the direct pathway through the vestibular n to the eye muscles.
b) the indirect pathway through the cerebellum. This involves mossy fibers, parallel fibers, and Purkinje cells which inhibit the vestibular n.

Thus the VOR gain is determined by the difference between the direct and indirect paths. The cerebellum's task is to keep this difference at the optimal value (usually 1) in spite of all the damage that may occur to the various parts of the VOR.

What teaches the cerebellum?

The visual signal arising from retinal slip provides an error signal to teach the VOR. This error signal is sent via the inferior olive to the cerebellar flocculus. Here climbing fibre input to Purkinje cells appears to produce plastic changes in the connections between parallel fibers and Purkinje cells.

The cerebellum acts like a repair shop because it makes similar re-adjustments to most reflexes.

See problems and answers posted on

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