The Physiology of the Senses
Lecture 11 - Eye Movements
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Contents

Revised 21/11/2012

Objectives

1. Explain how each of the 5 eye movements help us to see better.

2. List the action of each extra ocular muscle.

3. Explain how the same indirect pathway contributes to the proper function of both the vestibular ocular reflex and the generation of saccades.

4. Contrast the features that would allow you to differentiate the nystagmus produced by lesions that produce an imbalance versus those due to an abnormally small tonic activity.

5. Predict the effect of cerebellar plasticity on a patched good eye, after a sudden weakening of one of the eye muscles in the other eye.

Introduction

We move our eyes to help us see better. Eye movements

1) place the image of the object of interest on the part of the retina with the highest acuity, the fovea. Try to read without moving your eyes. How much of this sentence can you make out while looking at this?

2) keep the image in the eye stationary in spite of movement of the object or movements of one's head. Try shaking this page from side to side. Can you make out what it says?

There are 5 types of eye movements.

Each 1) serves a unique function and 2) has assets particularly suited to that function.

1) Saccades

If an image appears to the side, eye movements called saccades rotate both eyes so that the image falls on the fovea. Saccades are what you are using now to point the fovea at each word in this sentence. Vision is poor during saccades. To minimize this time, saccades are the fastest movements made by the body, up to 1000 degrees per second.

Get a friend. Watch their eyes while they try to make a slow saccade. You should see that they remain fast. Or they become a series of small fast saccades. Unlike a limb movement, you cannot will yourself to make a slow saccade.

2) Vergence

If you look (i.e. direct the foveae) from a far object to a near one, vergence eye movements are generated. Looking from far to near is convergence and looking from near to far is divergence.

How do saccadic and vergence eye movements differ? You may have noticed while watching your friend that vergence movements are much slower than saccades. Also during saccades both eyes rotate in the same direction. During vergence, they rotate in opposite directions.

3) Pursuit

When an object moves, the image can be kept still on the fovea by means of a pursuit eye movement (e.g. when tracking a moving ball or your finger). Watch while your friend tracks your finger as it moves slowly back and forth. Now ask your friend to try making a pursuit movement without a moving target.

When you move your finger you should see smooth pursuit eye movements. If they are not smooth, slow down your finger movements. Without a moving finger you will see a series of saccades, not a smooth pursuit movement. You cannot will yourself to make pursuit eye movements in the absence of a moving stimulus.

4) Vestibular ocular reflex (VOR)

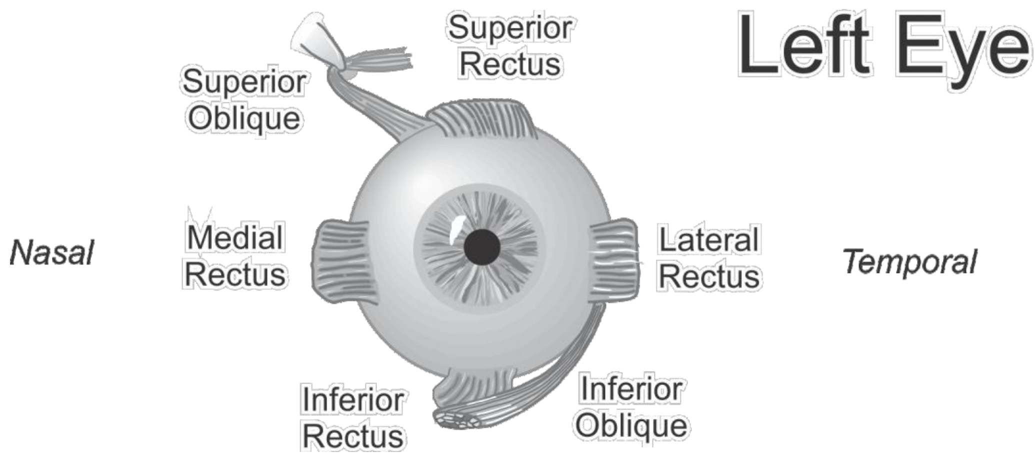
If we rotate our head, an eye movement very similar to pursuit is elicited whose function is also to keep the image still, but now on the whole retina not just the fovea. However, in spite of the fact that the movement looks similar, it is generated by a different neural circuit, the vestibular ocular reflex (VOR).

Try reading a page of text while you shake your head quickly from side to side. Compare that to reading the text while you shake the page as quickly from side to side. Notice that your reading is much better when you shake your head than when you shake the page. This is because the VOR responds much faster than the pursuit system. We will see why in this lecture. Also unlike the pursuit system, the VOR does not need a visual stimulus. It works in the dark. Rotate your head with your eyes closed. Feel your eyes move with your fingertips.

5) Optokinetic Reflex (OKR)

We have seen in the previous lecture that the VOR does not work well for slow, prolonged movements. In this case vision, through the optokinetic response (OKR), assists the VOR. The OKR is activated when the image of the world slips on a large portion of the retina and produces a sense of self motion (e.g. you sometimes feel like you are moving when sitting in a car that is stopped and a car beside you starts to move).

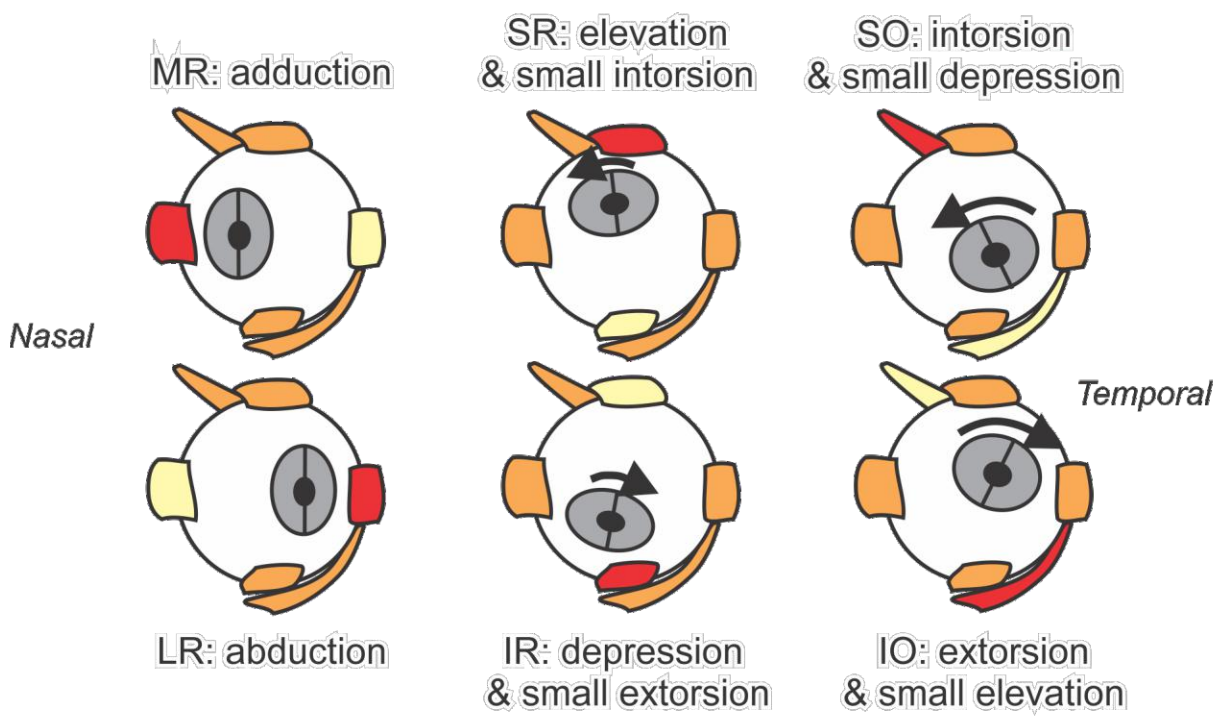
The eyes are rotated by 6 extraocular muscles



They act as 3 agonist/antagonist pairs

When your eye points forward, 60% of its motoneurons are active. To look elsewhere, one of a muscle pair contracts and the other relaxes.

You need 3 pairs to allow rotations in all three directions: horizontal, vertical and torsional.



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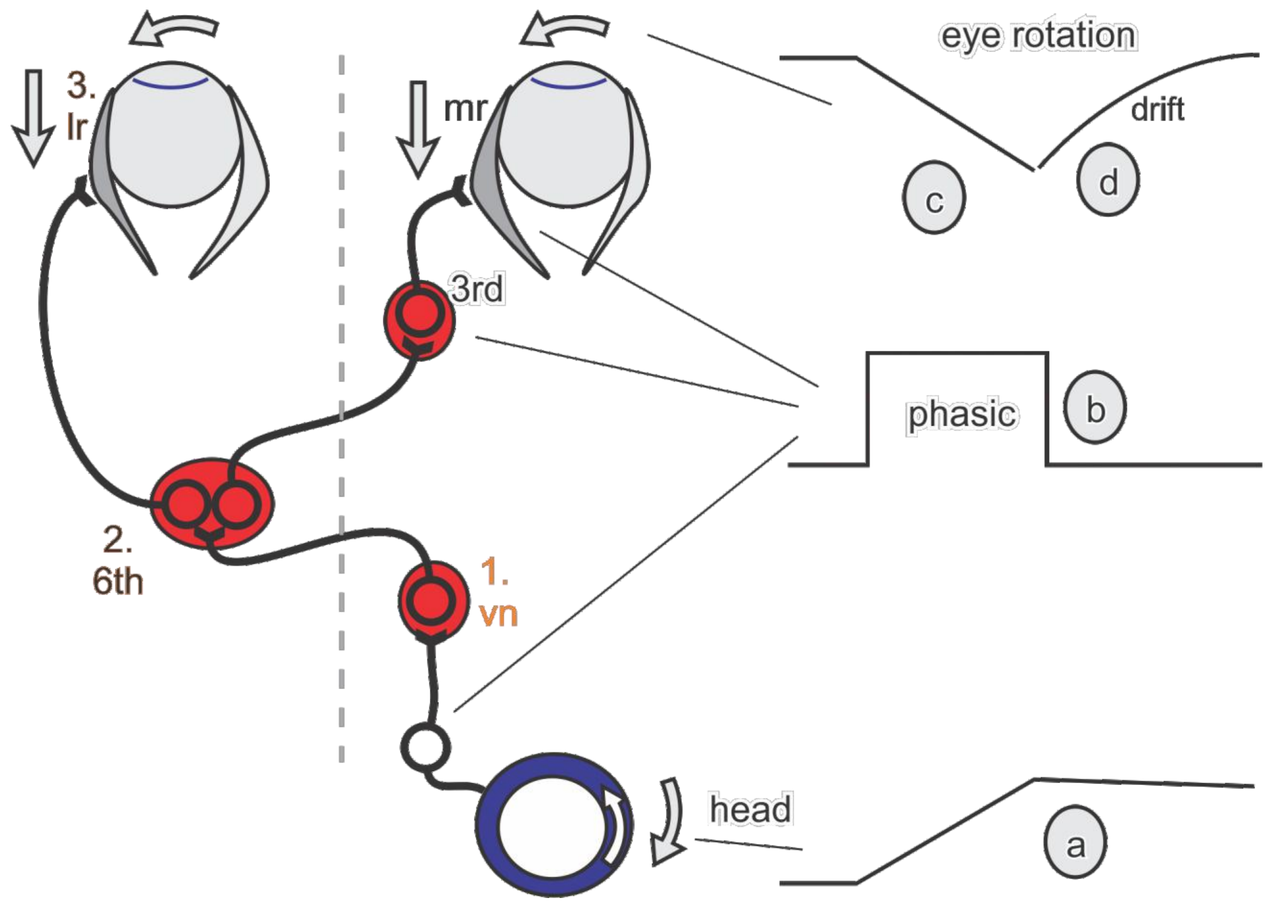
Describe the direct path of the VOR

This is a short reflex with synapses at the vestibular nucleus (vn), motoneurons (6th), and the lateral rectus muscle (lr).

The medial rectus (mr) of the right eye is also activated by a projection via motoneurons in the III nerve nucleus.



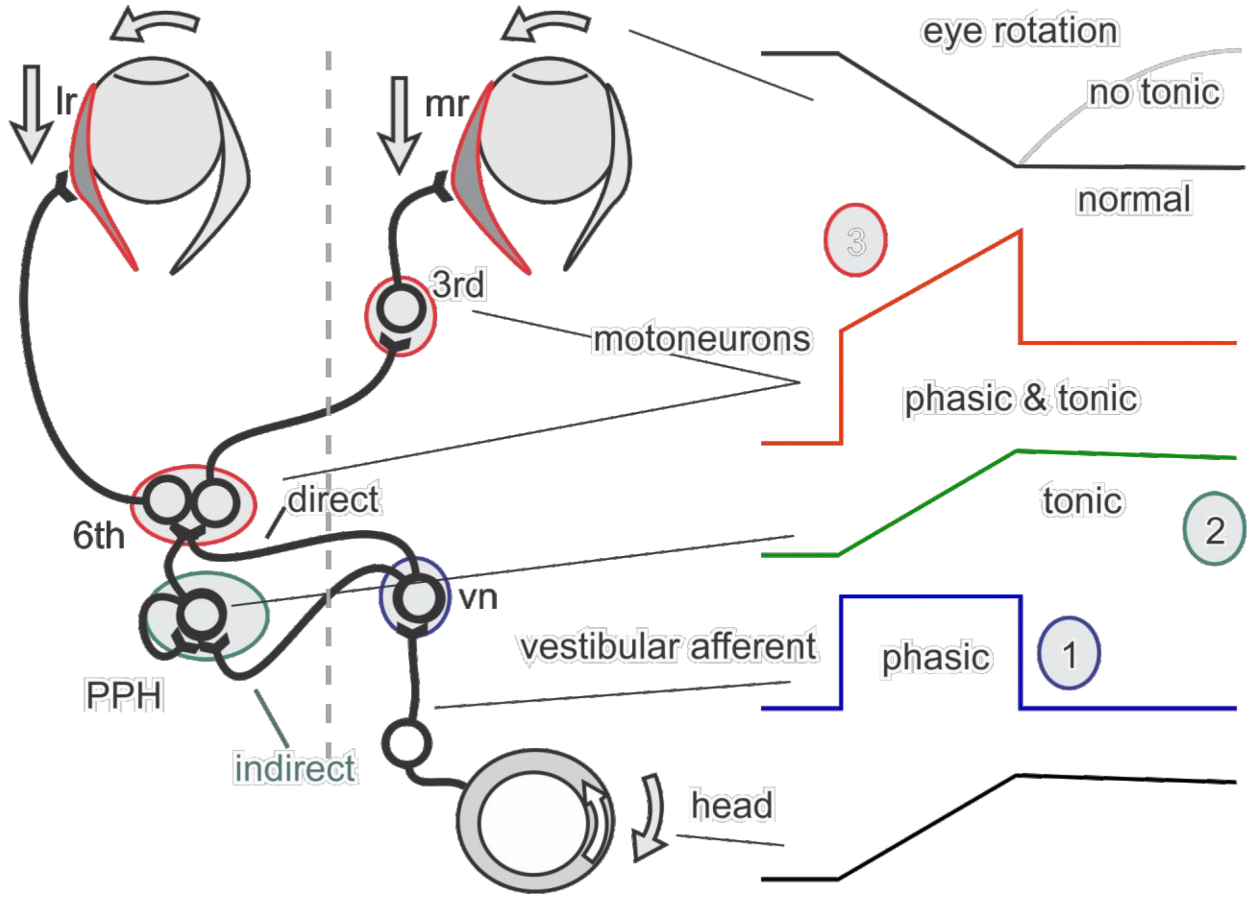
The direct path, by itself, is not enough. Why?

Recall that the function of the VOR is to keep the eyes still in space by rotating the eyes in the opposite direction to the head.

During a head rotation to the right (a), a phasic response (b) is seen in vestibular afferents (because vestibular afferents sense how fast you rotate), in the motoneurons and the muscles. This rotates the eyes to the left (c).

After the rotation you want the eyes to remain pointing to the left. But the eyes would drift back to center (d) because muscles on the left need a higher maintained activation to keep the eye rotated to the left.

Where does the required tonic input come from?



The tonic command originates via the indirect path through the nucleus prepositus hypoglossi (PPH).

This nucleus converts the phasic vestibular input into a tonic signal, probably via a reverberating neural circuit, a form of short term memory.

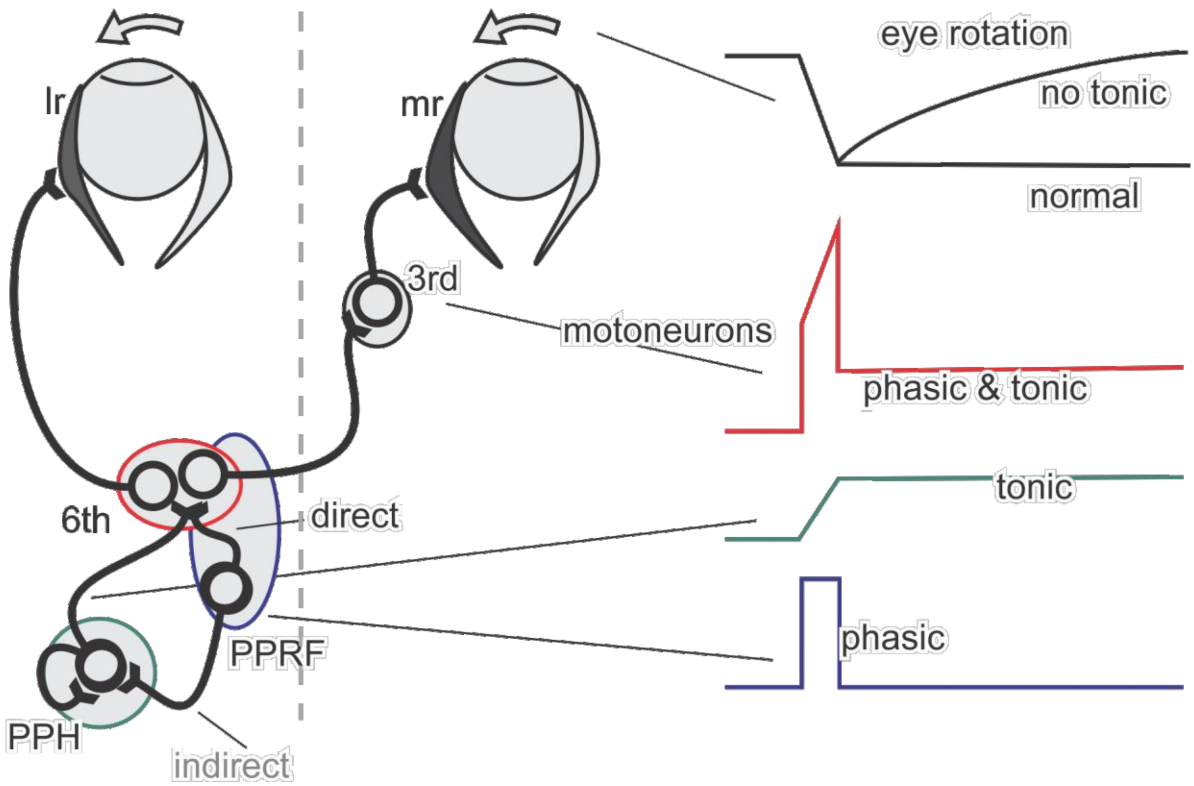
This circuit is important because it is a form of short term memory, a type of memory that is used elsewhere the brain.

This circuit is also amazing because it performs calculus. It counts the number of action potentials from the vestibular nucleus. The vestibular nucleus signals head velocity. This circuit integrates this to head position.

Motoneurons thus normally exhibit the combined phasic & tonic input from:
1) a phasic command (which rotates the eye) from the direct path and
2) a tonic command (which holds it there) from the indirect path.

Describe the generation of saccadic eye movements

Saccades redirect foveas to objects of interest, e.g. words in this sentence. Saccades are very fast (velocities up to 1000 degree/sec). These high velocities are generated by a phasic burst of action potentials per sec (up to 1000 ap/sec).



This burst of activity originates in the PPRF (paramedian pontine reticular formation, near the nucleus of the sixth cranial nerve (6th).)

The PPRF generates conjugate (both eyes) ipsilateral rotations. As in the VOR, there are two paths:

1) a direct path which mediates the phasic command to move the eyes.

2) an indirect path via PPH which generates the tonic command to hold the eyes in an eccentric position.

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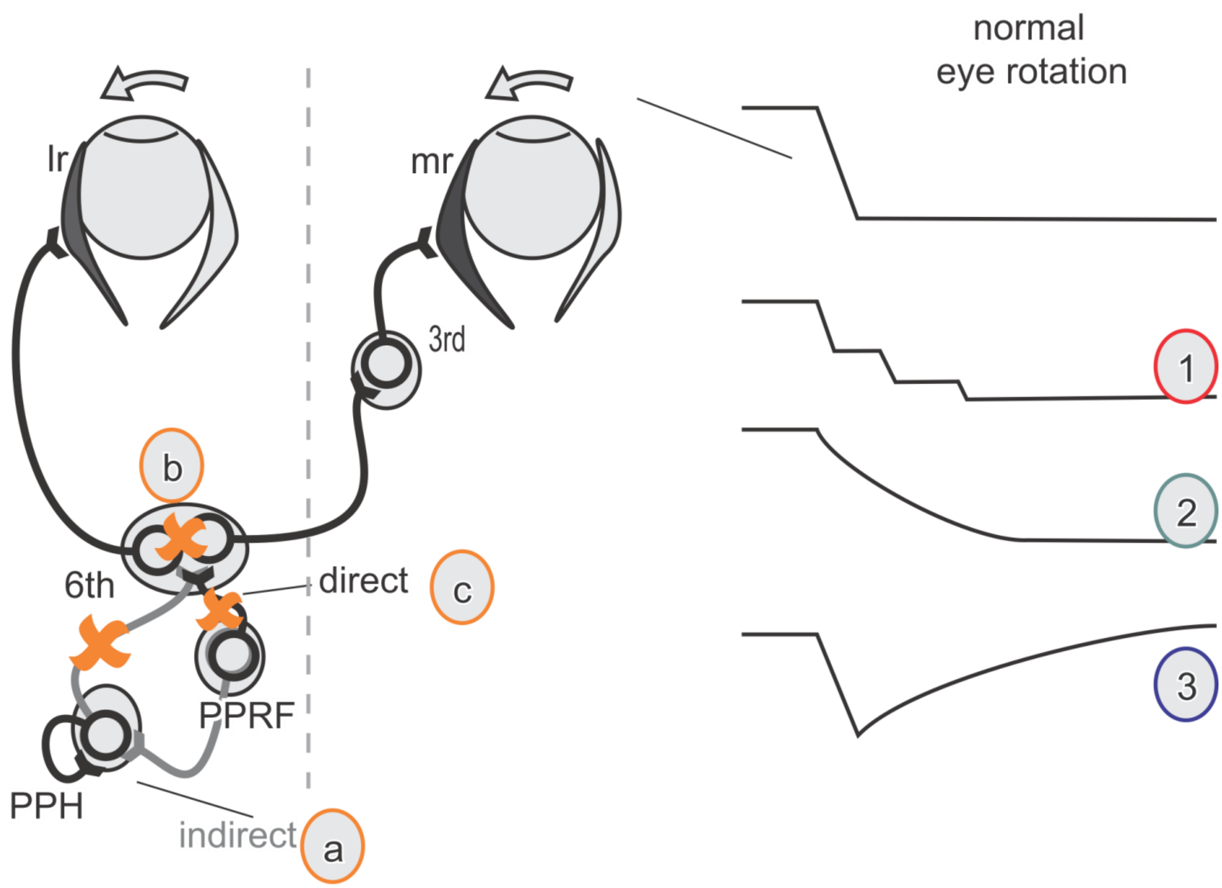
Lesions in the saccadic system

Problem: Match the lesions (a, b, c) with the eye movements (1, 2 or 3)
a) if indirect pathway or PPH is lesioned
b) if 6th n is partially damaged
c) if direct pathway is lesioned.



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What initiates a saccade?

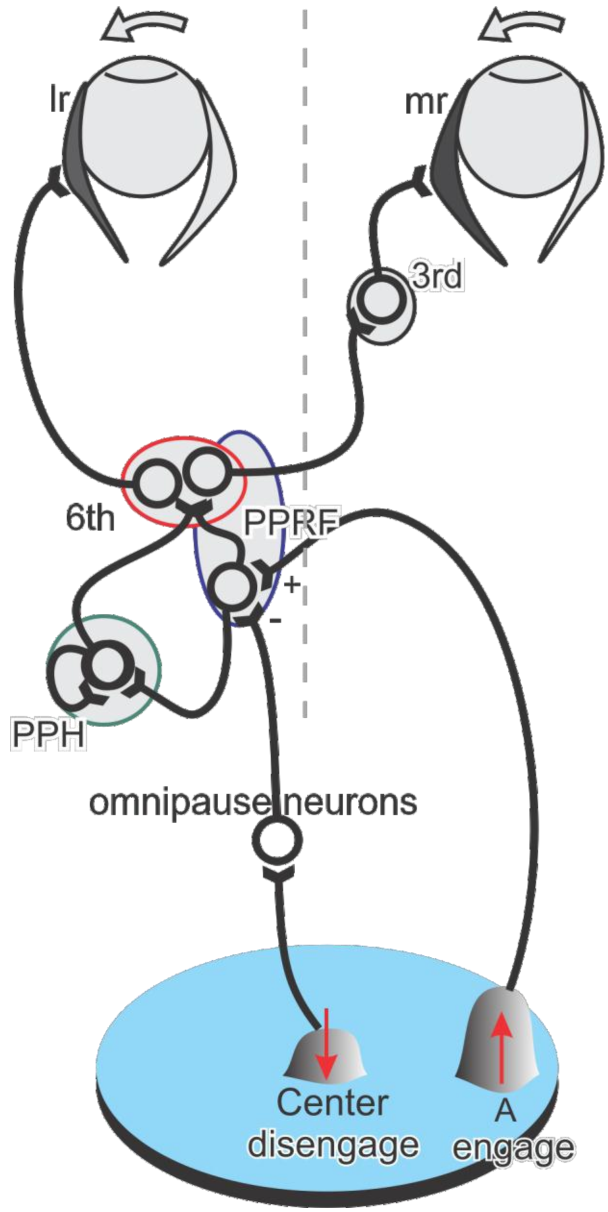
As we have seen, to make a saccade to a visual target at A, activity at the retinotopic location A in the superior colliculus (SC) must occur.

But before a saccade can begin, a hill of activity at the center must be removed. This hill of activity keeps the eyes fixating the current location.

It does this through omnipause neurons which inhibit burst neurons in the PPRF.

Thus to make a saccade, a visual stimulus produces activity at A, and at the same time the activity at the center is removed.

Then PPRF neurons are released from inhibition and driven by the collicular activity at A.



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What stops a saccade?

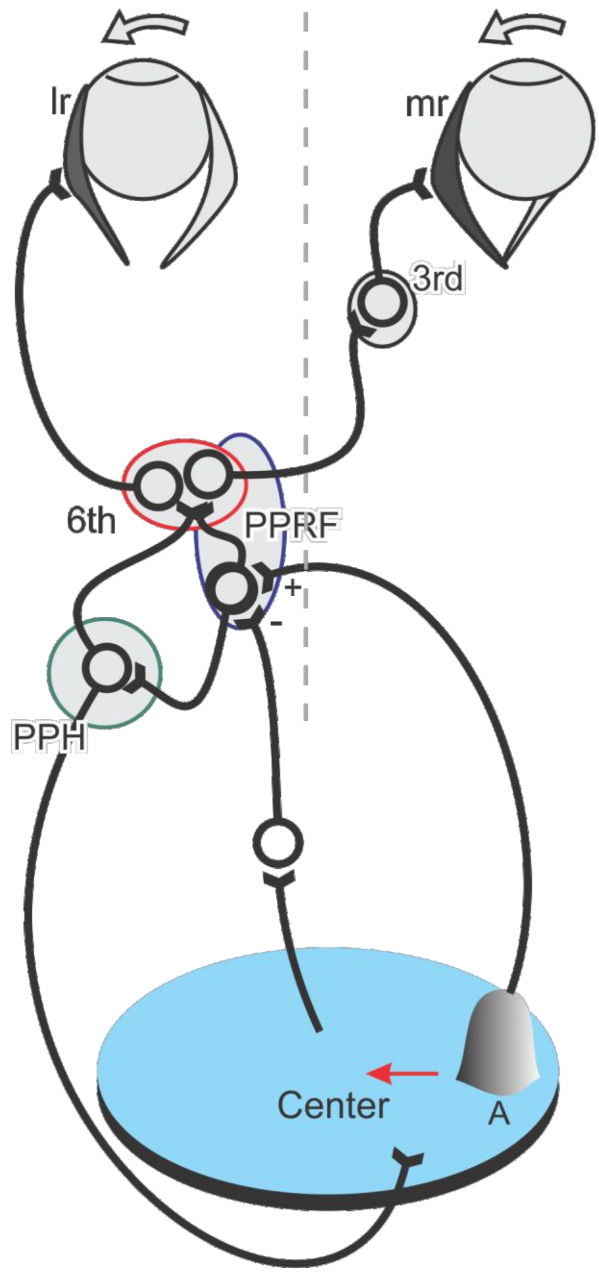
Saccades are very fast and of a short duration, (lasting roughly 50 msec. for a 20^{O} saccade). Visual feedback would arrive too late to stop the saccade. It takes 50 msec. for visual information to reach the visual cortex. Proprioceptive information would likewise take too long.

Because saccades are not guided by sensory feedback, they are called ballistic movements. Like guided missiles, the saccadic system uses an internal sense of eye position to guide and stop saccades. An internal estimate of eye position is generated by the PPH which is the origin of the corollary discharge.

At first it may seem surprising that corollary discharge comes from way down deep in the brain stem and not some cortical structure. But if one thinks about it, one would want it some place close to the eye muscle. In this way it could easily monitor all the signals that are sent to the eye muscles and thus move the eyes.

As we saw, the PPH is shared by the VOR and saccades. It is also shared by the 3 other eye movement types.

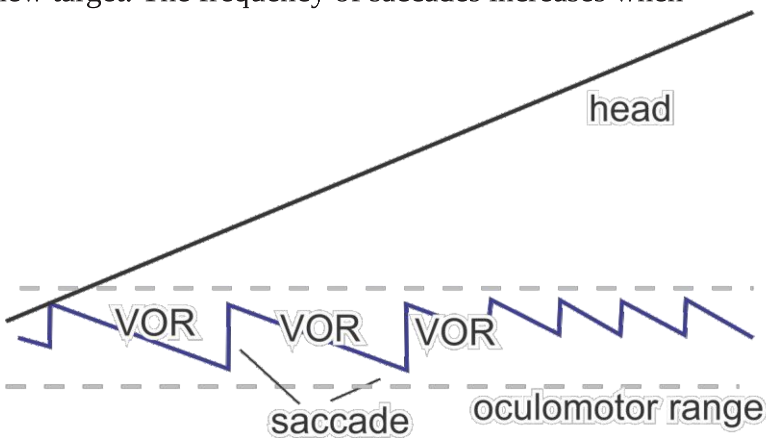
One hypothesis is that this eye position signal is used to guide the activity of the hill in the SC back to the central foveal representation. When the hill returns to the foveal representation, omnipause neurons are reactivated, PPRF burst activity stops and so does the saccade.



What is nystagmus?

Nystagmus is a rhythmic back and forth movement of the eyes. Usually the movement in one direction is fast and slow in the opposite direction. Normal nystagmus is seen during large head rotations. The VOR generates the slow phases. This helps keep your eye on a target.

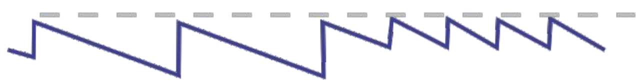
When an eye approaches the edge of oculomotor range, a saccade (quick phase) is generated in the opposite direction to new target. The frequency of saccades increases when you look in the direction of rotation because saccades interrupt the VOR more often.



Nystagmus is also seen with lesions.

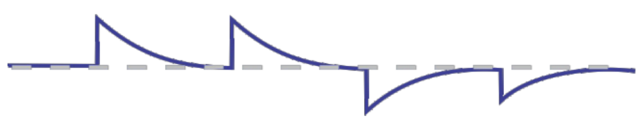
Two main types are:

a) imbalance in the **VOR**



This looks like normal nystagmus but can occur when the head is still. Here the drive is not from head motion but from an vestibular imbalance. Recall that the VOR is a push-pull system and the afferents have tonic drive which normally cancels bilaterally. Unilateral lesions (vestibular organ, afferents, nuclei etc.) disrupt this balance.

b) Tonic activity too small



This is often caused by lesion of the PPH (tone generator) or of the cerebellar flocculus which normally tunes up PPH. In contrast to a), here the slow phase i) shows an exponential (not linear) drift to a position of rest (often centre) and ii) its direction switches when the patient looks in the opposite direction.

The cerebellum calibrates saccades (and all other movements)

1. Normally saccades in the two eyes are equal (conjugate) and reasonably accurate.

2. Immediately after a palsy that weakens the right MR, saccades in the right eye are too small. The patient sees double.

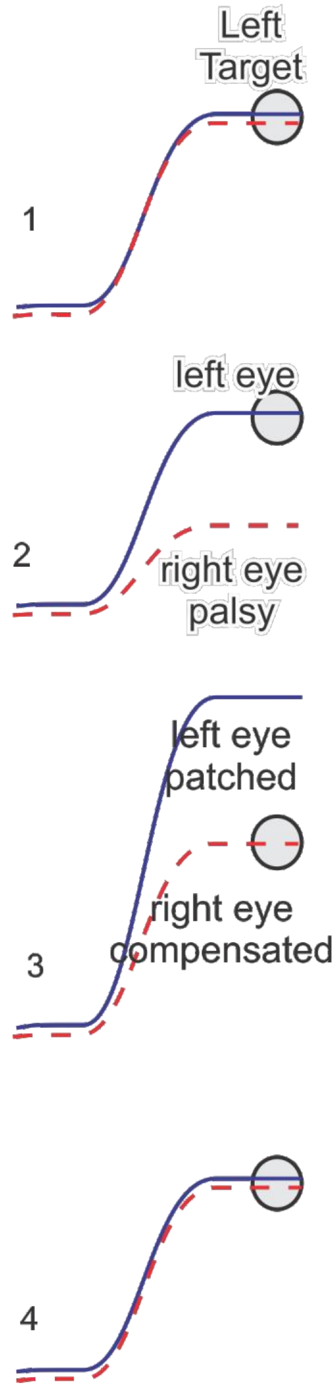
3. It is common in strabismus to patch normal eye. This is done to encourage the brain to increase the drive to the weaker muscle. Often after the normal eye is patched, saccade amplitude adapts over the next few days. It increases in both eyes. In the right unpatched eye, the one with weaker muscle, saccades become normal. In the normal patched left eye, however, saccades become too large. This is because a larger command is sent to motoneurons of both eyes.

4. If the patch is removed from the left eye, only the left eye adapts. It becomes normetric because a smaller command is somehow sent to only this muscle.

This recalibration arises from the vermis of the cerebellum. Palsies persist only if:

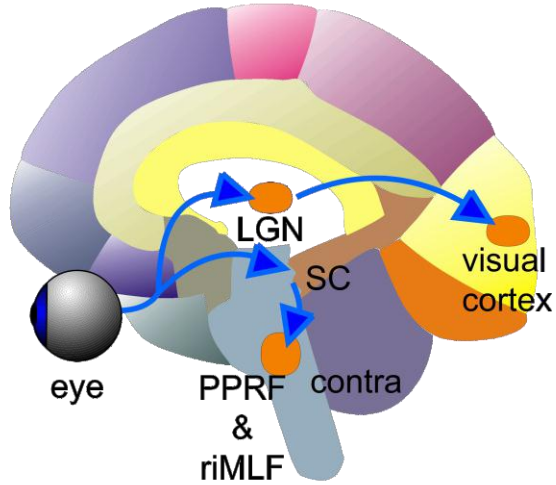
1) they exceed the repair capabilities of the cerebellum (e.g. total paralysis) or

2) the cerebellar "repair shop" is damaged.



Where do the saccadic commands come from?

The eye's ganglion cells project to both the visual cortex (via LGN) and the superior colliculus.



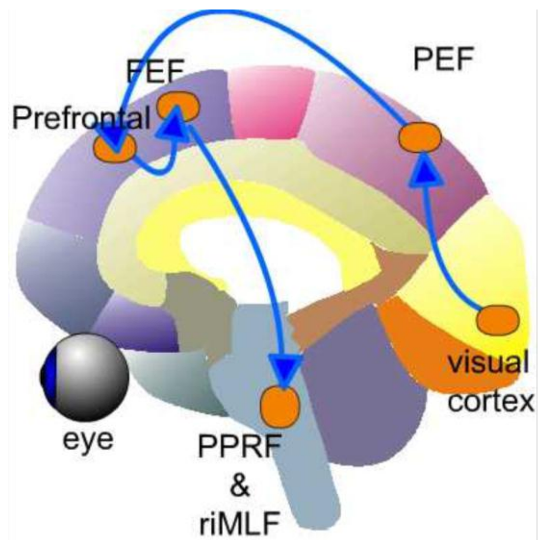
The superior colliculus responds to flashing/moving stimuli in the peripheral retina. It elicits a contralateral saccade (via the contra lateral pprf or riMLF) so that fovea can examine the stimulus.

Also recall from session 6 that the frontal eye fields (FEF) with input from the Parietal Eye Fields (PEF) and Prefrontal cortex direct a saccade to a remembered target.

In summary:

The superior colliculus directs short latency involuntary saccades to an unexpected flash.

The frontal eye fields direct longer latency voluntary saccades to a remembered target.



Vergence eye movements

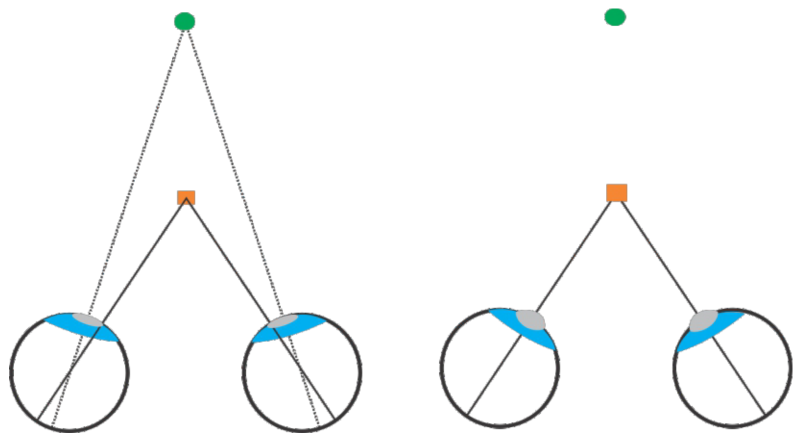
These are the slowest to develop during childhood.

The movements are linked to accommodation reflex (the reflex that changes the eye's lens properties).

On viewing a near object the eyes

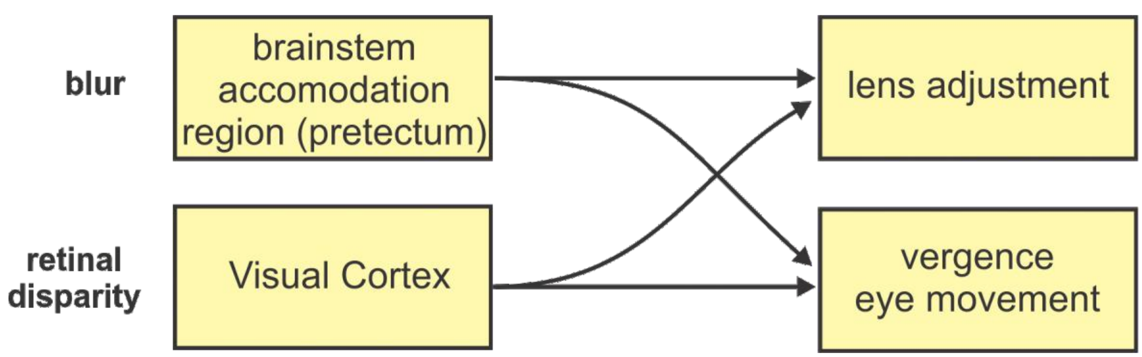
1) converge to eliminate retinal disparity (seeing double)

2) accommodate (lens becomes more round) to eliminate blur.



Either blur or retinal disparity will generate vergence.

The strongest response is elicited when the image is blurred and there is retinal disparity.



Pursuit eye movements

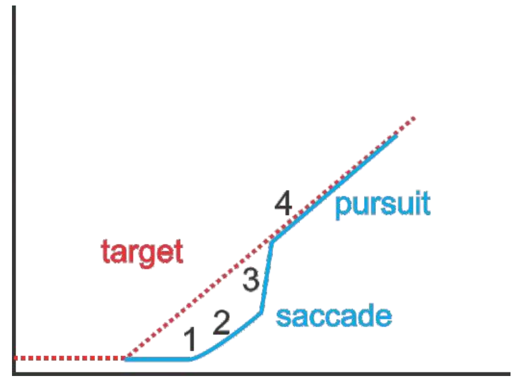
If a target starts to move,

1) there is a neural delay as the signal passes from the eye, through this long pathway to the brainstem and the muscles,

2) a pursuit movement is generated,

3) a saccade helps the eye catch up to the target, and

4) finally, if pursuit is perfect, the fovea fixates the moving object.



The sequence of structures that are used to generate pursuit eye movements is:

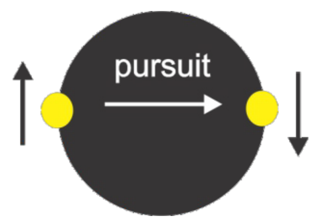
Neurons in the eye, V1, and MT respond to the speed of retinal slip. Neurons in MSTl, the cerebellum, and the brain stem code the speed of the eye movement.

Normally a visible moving target is required to initiate a pursuit movement. However there are exceptions to this rule. Some examples of stimuli that elicit pursuit are tracking:

1) the center of the wheel when all you see are two small lights on the rim in a dark room.

2) a moving auditory stimulus.

3) your finger with your eyes closed.

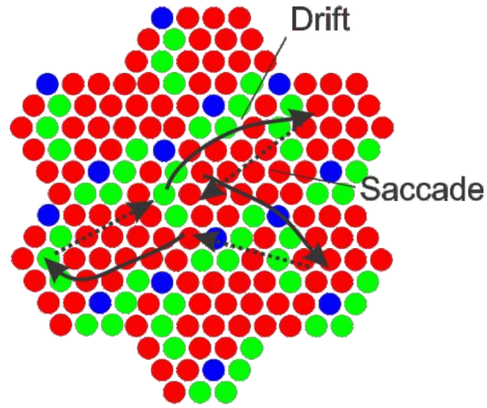


Fixation

During fixation, the eye's fovea is examining the target image.

Surprisingly the eye is not still. If one looks closely, one can see miniature movements, a fraction of a degree in size, consisting of rapid saccades and a slow drift.

The figure shows how these movements move the retina's cones across the target image.



One might think that these tiny movements would impair vision. However they appear to be essential for vision. If the target image is artificially stabilised on the retina, it disappears.

Summary: the function and characteristics of the five eye movement types.

OLD SYSTEMS:

Their purpose is to keep the images in the background still on the entire retina when the head moves (e.g. reading signs while walking).

VOR

- The VOR keeps the image of the world stationary on the entire retina.
- The VOR response is fast because it is a short reflex.
- But it responds poorly during a prolonged rotation (because the cupula adapts).
- The VOR remains calibrated by the cerebellum.

Optokinetic system

- Optokinetic reflex helps the VOR during prolonged rotations.
- This reflex is slow to get going, but that's all right because the VOR is fast.
- Best elicited by large full field visual stimulus which elicits a sensation of self-motion.

NEW SYSTEMS:

Their purpose is to bring the image of a selected object onto the fovea and keep it there.

Saccades

- Saccades point the fovea at an object of interest.
- Saccades are very fast and accurate, maximizing the time the eye is still and able to examine the visual details.
- You have no voluntary control over their speed.

Pursuit

- Pursuit keeps the fovea pointing at a moving target, e.g. a ball.
- Pursuit is reflexive. You cannot will a pursuit in the absence of a moving target (but this moving target need not be visual).
- Pursuit is slower than VOR because its pathway has many more synapses.

Vergence

- Vergence points both foveae at a near or far target.
- Vergence prevents double vision (diplopia).
- During vergence, the eyes rotate in opposite directions (disconjugate).

See problems and answers posted on

http://www.tutis.ca/Senses/L11EyeMovements/L11EyeMovementsProb.swf