

The Physiology of the Senses

Lecture 11 - Eye Movements

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Objectives

- 1) Explain how each of the 5 eye movements help us to see better.
- 2) List the action of each extraocular 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

Our eyes are arguably our most valuable sense. But our vision would be very poor if we were very unable to move our eyes. This section explores the ways in which movements of the eyes improve vision.

The iPhone 6 camera sports cinematic video stabilization which "helps to keep your shots steady. So even if you're doing something like filming while hanging off the side of a street car, your video looks as smooth as if you were gliding through the scene on a rig."

Video stabilization uses the phone's built-in gyroscope to measure and compensate for unwanted hand shaking. Our VOR have been doing this for millennia.

We move our eyes to help us see.

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 of one's head. Try shaking this page from side to side quickly. Can you make out the words?

The 5 Types of Eye Movements

In the course of evolution five eye movement systems have developed to aid vision. Each has a unique role of keeping the eye's view still and a unique way of doing it.

1) *Saccades*

If an image appears to the side on your peripheral retina, eye movements called saccades rotate both eyes so that the image falls on the foveae of each. Saccades are what you are using now to point your fovea at

each word in this sentence. Vision is poor during saccades because the image of the words is sweeping across the retina. To minimize this time of poor vision, saccades are the fastest movements the body can make, up to 1000 degrees per second.

Get a friend. Watch their eyes while they try to make a slow saccade. You should see that the saccades 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 your 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. This is because 1) the ciliary muscles, used in accommodation, are slow and 2) speed costs energy. Thus there is no advantage in making the vergence eye movements fast. Also note that during saccades both eyes rotate in the same direction. During vergence, they rotate in opposite directions.

3) Pursuit

When an object moves, its 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 (except for a few exceptions to be covered later).

4) Vestibular Ocular Reflex (VOR)

If you rotate your 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. Notice that your reading is much better while you shake your head than while you shake the page. This is because the VOR responds much faster than the pursuit system. We saw in the previous chapter that the VOR is a very short reflex. 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 chapter that the VOR does not work well for slow, prolonged head rotations. 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 OKR often elicits a sense of false 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.

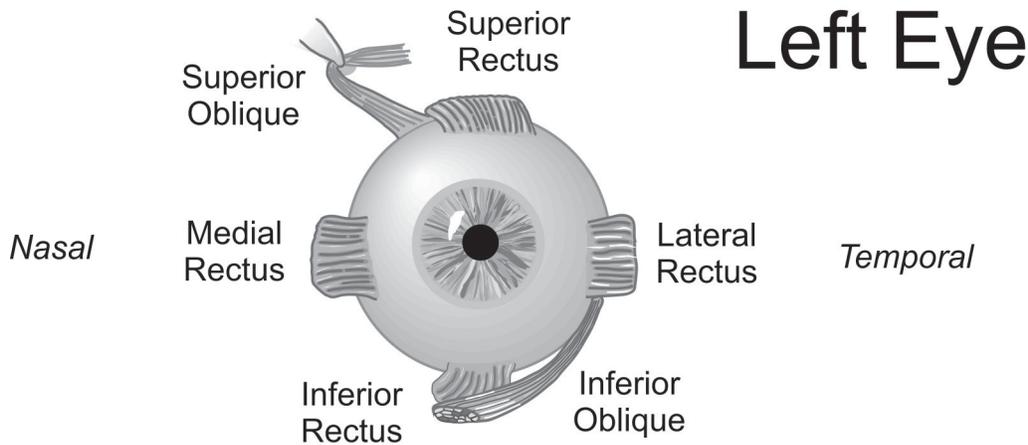


Figure 11.1 The Eye Muscles of the Left Eye Nasal (nose) is on your left and the temporal side on your right.

They act as 3 agonist/antagonist pairs.

The 6 extraocular muscles are located outside the eyeball and pull on the eyeball to turn it. When your eye points forward, 60% of the motoneurons are active in all these muscles. To look elsewhere, one of a muscle pair contracts and the other relaxes.

You need 3 pairs to allow rotations in all possible directions:

1. horizontal, the medial and lateral recti (mr and lr),
2. vertical, the superior and inferior recti (r and ir),
3. and torsional, the superior and inferior oblique (so and io).

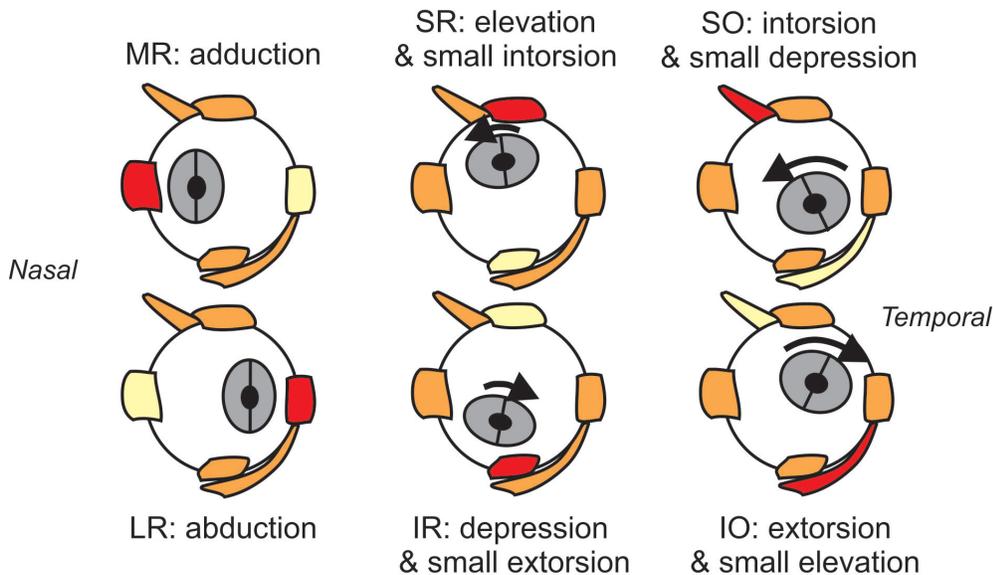


Figure 11.2 The Action of Each Eye Muscle In each the left eye is shown with the nose on your left. MR: medial rectus results in adduction, turning the eye towards the nose. LR: lateral rectus causes abduction, turning the eye away from the nose. SR: superior rectus causes elevation and a small intorsion, turning the eye upwards and counterclockwise. IR: inferior rectus causes depression and a small extorsion, turns the eye downward and clockwise. SO: superior oblique causes intorsion and a small depression, turns the eye counterclockwise and downward. IO: inferior oblique causes extorsion and a small elevation, turns the eye clockwise and upward.

The Vestibular Ocular Reflex

The Direct Path

Suppose you are playing a sport such as basketball. In order to see the players around you, every time your head turns your eyes should turn quickly in the opposite direction. To minimize the delay in this reflex the distance from the sensor to the eyes should be short. Also the number of synapses should be few. Fortunately both are true. The synapses in the VOR are at the hair cell, the vestibular nucleus (vn), motoneurons in the 6th nerve nucleus (6th), and the lateral rectus muscle (lr) (Figure 11.3). The medial rectus (mr) of the right eye is activated by a projection from the 6th to the 3rd nerve nucleus.

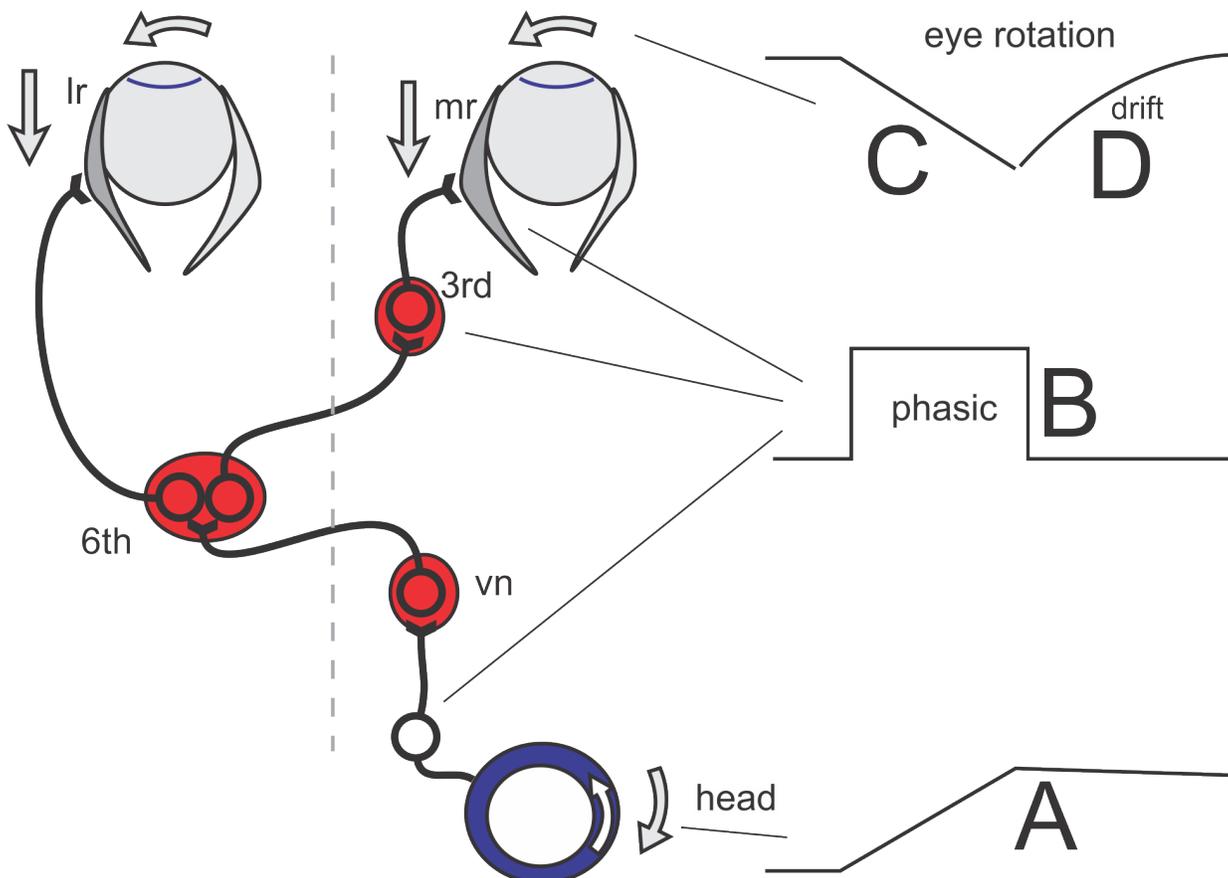


Figure 11.3 The Vestibular Ocular Reflex The rotation of the head to the right causes activation of the vestibular nucleus (vn) on the right side, the nucleus of the 6th nerve (6th) on the left side, and contraction of the lateral rectus (lr) in the left eye. As well there is activation in the nucleus of the 3rd nerve (3rd) and of the medial rectus muscle (mr). A: Rotation of the head, B: the phasic increase in activity in the vestibular nucleus, the oculomotor nuclei, and the muscles. C: the rotation of the eye to the left, and D: the drift of the eye back to the right.

The direct path of the VOR, by itself, is not enough. Why? Recall that the function of the VOR is to keep the eyes still in the world by rotating the eyes in the opposite direction to the head. During a head rotation to the right (A, in Figure 11.3), a short lasting (phasic) response (B) is seen in vestibular afferents. This is because neurons in the vn increase their activity during the turn and return to resting activity when the turn stops. The same phasic activity is seen in the motoneurons and the muscles. This rotates the eyes to the left (C). After the rotation the eyes should remain stationary, pointing to the left. But here the eyes drift back to center (D) because muscles on the turned position need a higher maintained activation to keep the eyes pointing to the left.

The Indirect Path of the VOR

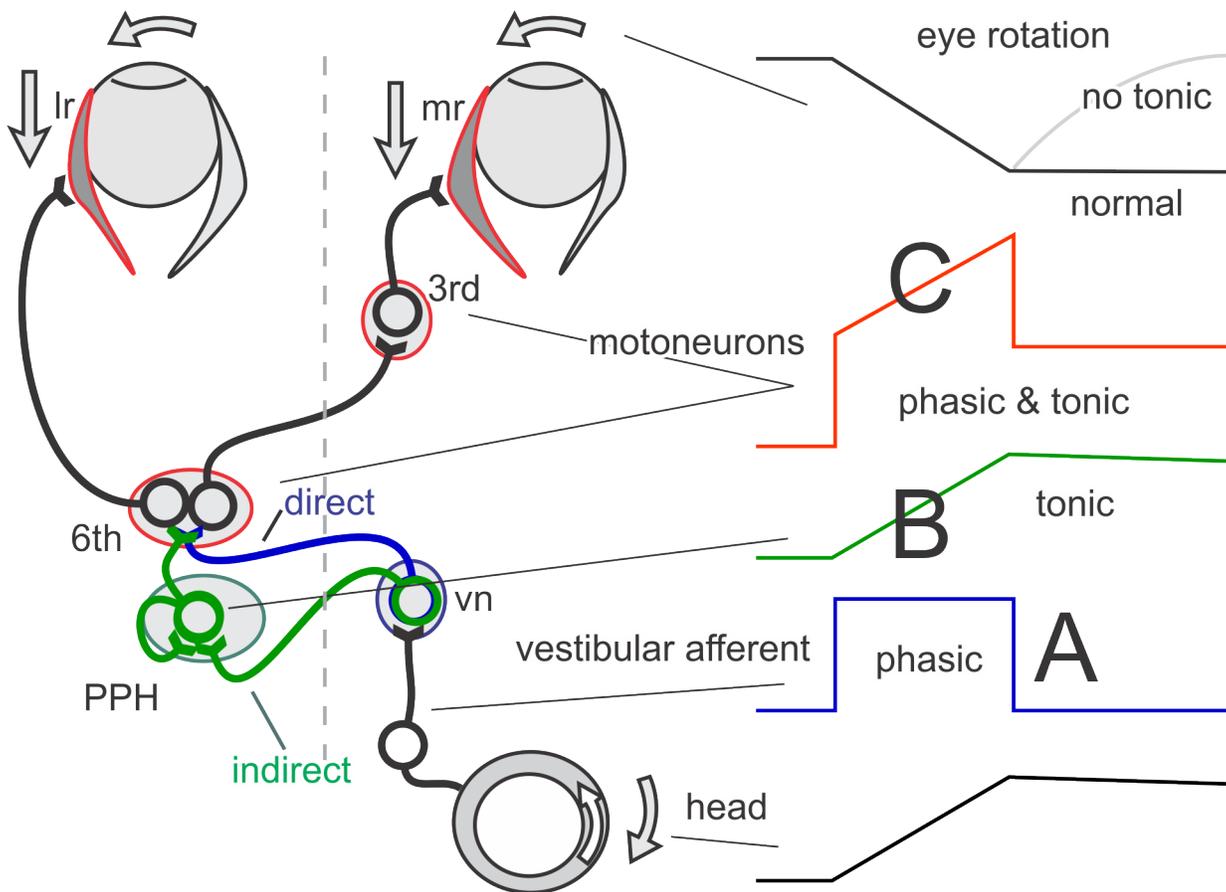


Figure 11.4 The VOR consists of a direct, as shown in Figure 11.3, and an indirect pathway. The indirect pathway, through the nucleus prepositus hypoglossi (PPH), converts the phasic activity from the canal, which is proportional to eye velocity, into a tonic activity, which is proportional to eye position and which maintains the eye at its final position after the head turn is complete. A: The phasic activity from the canal afferent, B: the tonic activity from the PPH, and C: the sum of phasic and tonic activity in the motor neurons.

From where does the required tonic input come? The **tonic** command originates via the indirect path through the nucleus prepositus hypoglossi (PPH) (Figure 11.4).

This nucleus converts the **phasic** vestibular input into a tonic signal, probably via a reverberating neural network. This circuit is important because it is a form of short term memory, a type of memory that is used elsewhere in the brain. This circuit is also amazing because it performs the process of integration in calculus. It counts the number of action potentials from the vestibular nucleus and generates a tonic activity proportional to this count. The vestibular nucleus signals head velocity. This circuit integrates this to head position.

Motoneurons thus receive a combined **phasic and tonic** input from:

- 1) a **phasic** command (which rotates the eye) from the direct path and
- 2) a **tonic** command (which holds the eye at its new position) from the indirect path.

Saccadic Eye Movements

In order to read this page quickly, saccades should redirect your foveas from word to word in as short a time as possible. Saccades are indeed the fastest movement the body can make with velocities up to 1000 degrees per second. These high velocities are generated by a short high frequency burst of action potentials of up to 1000 action potentials per second, the phasic component.

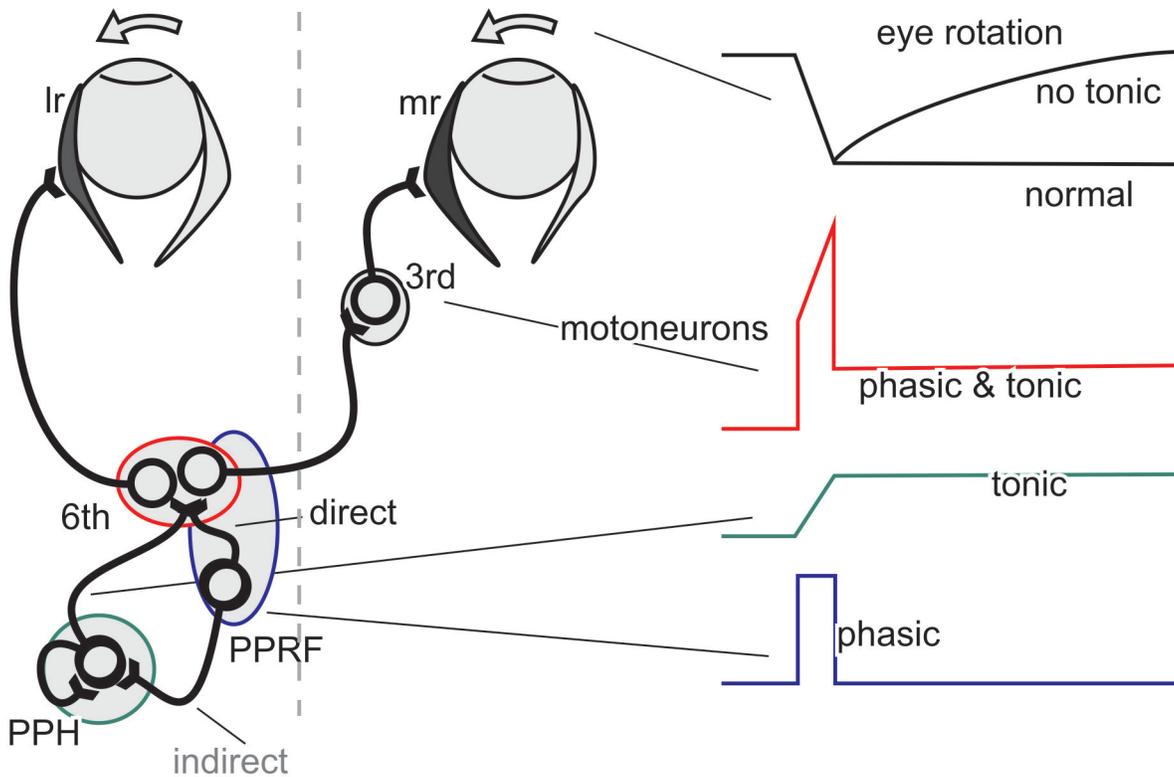


Figure 11.5 The Direct and Indirect Pathways for Saccades The same as Figure 11.4 except that the input comes from the paramedian pontine reticular formation (PPRF).

This burst originates from a structure with a long name, the **paramedian pontine reticular formation (PPRF)**, near the nucleus of the sixth cranial nerve (6th) (Figure 11.5).

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

- 1) a direct path from the PPRF which mediates the **phasic** component to move the eyes.
- 2) an indirect path, from the PPRF to PPH, which generates the **tonic** command to hold the eyes in their new eccentric position.

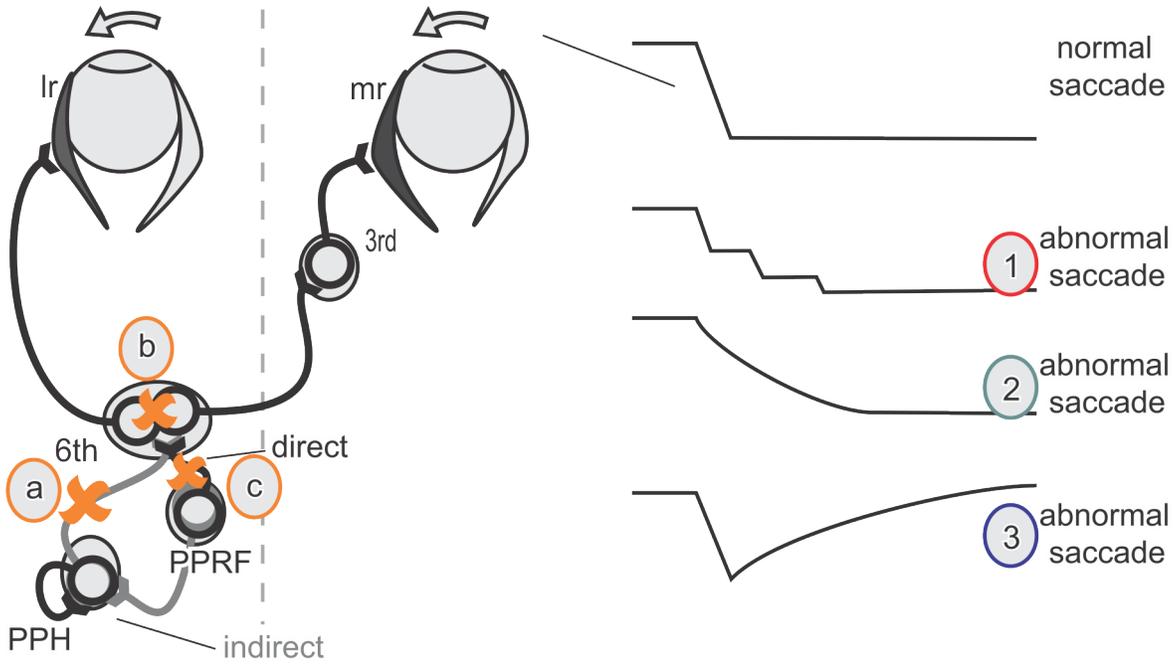
Lesions in the Saccadic System

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.



What stops a saccade?

Because saccades are very fast their duration is short lasting roughly 50 msec. for a 20 degree 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.

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 all eye movement **corollary discharge** (Figure 11.7). Because saccades are not guided by sensory feedback, they are called ballistic movements.

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 realises that this signal should originate some place close to the eye muscle. In this way corollary discharge could include 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. The 3 other eye movement types also share the PPH.

One hypothesis for what stops a saccade is the following. The eye position signal from the PPH is used to guide the activity of the hill in the SC, that starts in location A, 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 saccadic eye movement. This is a simple but elegant feedback loop.

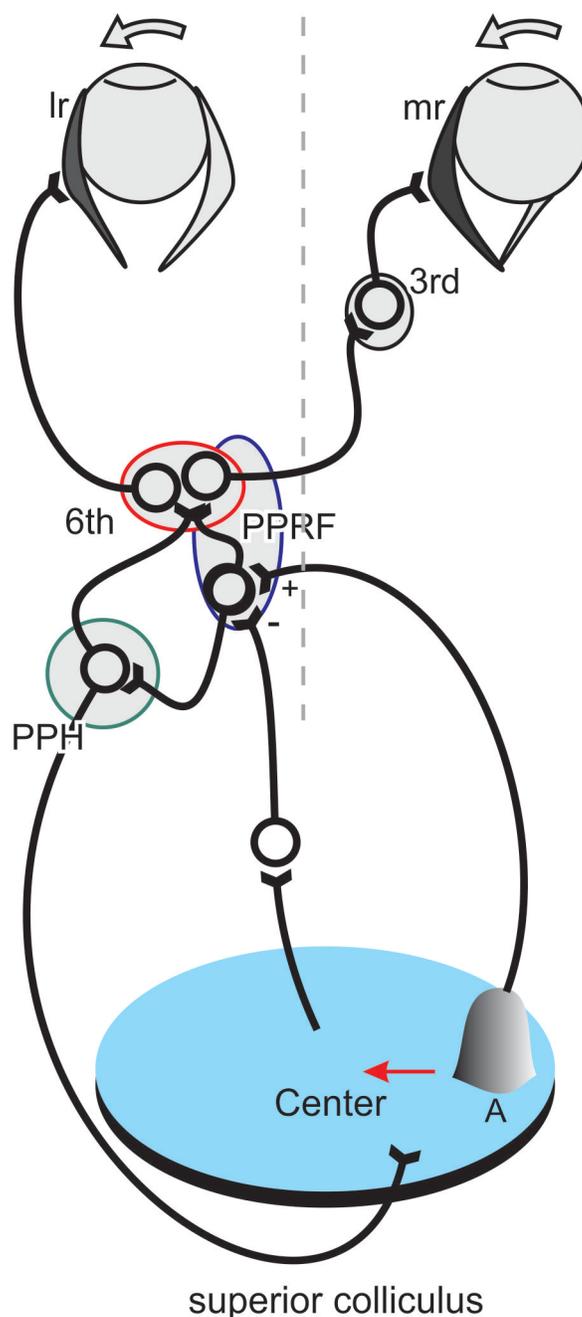


Figure 11.7 A saccade is stopped by corollary discharge from the PPH. One hypothesis is that corollary discharge guides the hill of activity from A to the center. When the hill reaches the center the omnipause neurons are activated, the PPRF inhibited, and the saccade is stopped in target.

Where Saccadic Commands Originate

Recall that 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 (Figure 11.8). It elicits a saccade (via the PPRF) so that fovea can examine the stimulus.

Also recall that the frontal eye fields (FEF) with input from the Parietal Eye Fields (PEF) and Prefrontal Cortex direct a saccade to a remembered target (Figure 11.9).

Thus the superior colliculus directs short latency involuntary saccades to an unexpected flash and the frontal eye fields direct longer latency voluntary saccades to a selected target.

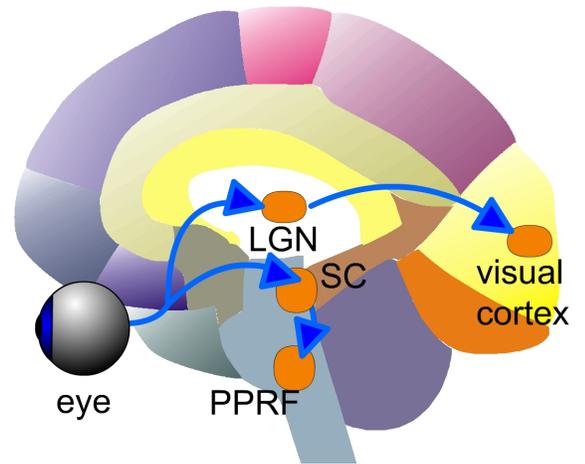


Figure 11.8 The short latency pathway for saccades is through the superior colliculus (SC).

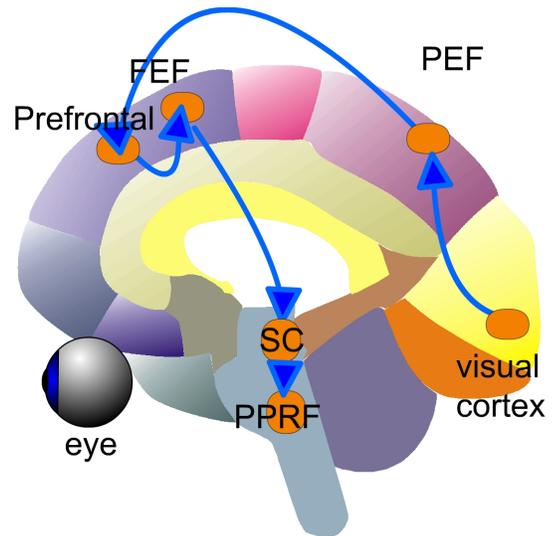


Figure 11.9 The longer latency pathway for saccades is through the parietal eye fields, prefrontal cortex, and frontal eye fields.

*The cerebellum calibrates saccades.
(and all other movements)*

It is important that the size of saccades be accurate. For reading quickly it is necessary to jump to the next word in as few saccades as possible. It is also important that the saccades in each eye be equal in order that each fovea end up looking at the same word. It is very difficult to read when you see double. Let's see what happens if saccades are not equal.

1. Normally saccades in the two eyes are equal (conjugate) and reasonably accurate (Figure 11.10.1).

2. Immediately after a paralysis that weakens the right eye's medial rectus muscle, the leftward saccades in the right eye are too small. The patient is now strabismic and sees double.

3. Often the visual system suppresses the image in the weak eye in the patient continues to make small saccades in the right eye. The normal eye is often patched to prevent that. This is done to encourage the brain to increase the drive to the weaker muscle. After the normal eye is patched, saccade amplitude gradually increases over the next few days in both eyes. This is because a larger command is sent to motoneurons of both eyes. In the right unpatched eye (the one with weaker muscle) saccades become normal if the paralysis is not too severe. In the normal patched left eye, however, saccades become too large.

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

This recalibration arises from the cerebellum a structure located under the posterior part of the cortex and a repair shop for reflex responses.

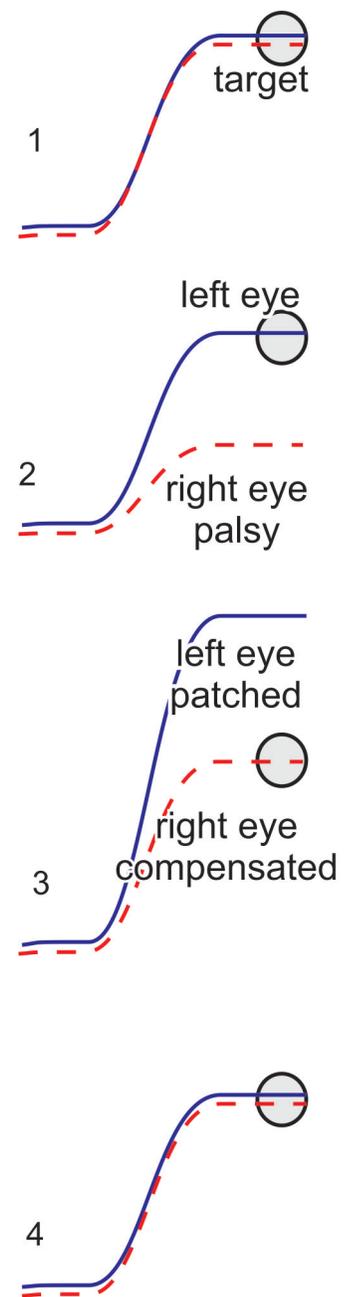


Figure 11.10 **The cerebellum calibrates saccades.** 1. Saccades are equal in the two eyes. 2. The weakened right eye makes small saccades while those in the left eye are normal. 3. The right eye is trained to make normal saccades but now those of the left eye, which is patched, become too large. 4. When the left eye's patch is removed its movements again become normal.

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 (Figure 11.11). Normal nystagmus is seen during large head rotations. The VOR generates the slow phases. This keeps your eye pointing on a target. Head nystagmus is a rhythmic back and forth movement of the head often seen in birds such as pigeons and turkeys. A bird's head rapidly moves forward and then holds still while the body catches up. During the hold period, the image of the world is stationary and clearly visible on the bird's retina.

When the slow phase reaches the furthest the eye muscle can turn, edge of oculomotor range, a saccade (quick phase) is generated in the opposite direction to new target. The frequency of saccades increases when you voluntarily look in the direction of rotation because now saccades interrupt the VOR more often.

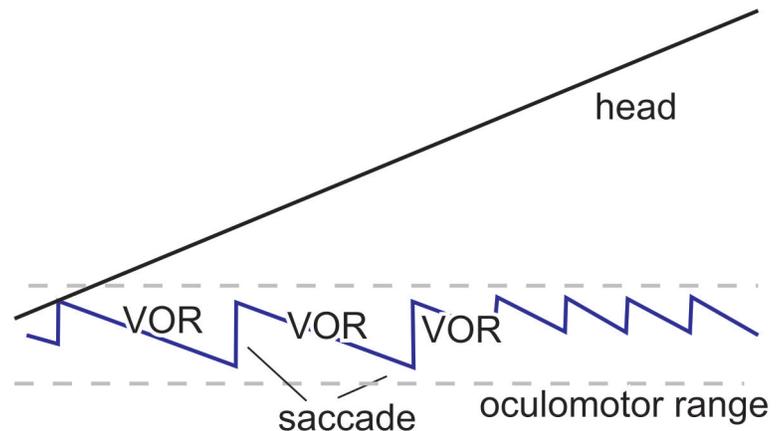


Figure 11.11 Normal nystagmus, seen while the head is turning, consists of a slow phase (VOR) and a quick phase (saccade). The head position (top) changes at the same velocity but opposite direction as the VOR. Saccades occur when the eye position reaches the oculomotor range and becomes more frequent if one looks in the direction one is turning.

Nystagmus is also seen with lesions.

Two main types are:

a) Imbalance in the VOR

This is similar to the nystagmus produced in a normal subject when the head was turning to the right, except in this case the nystagmus occurs when the head is still (Figure 11.12).

Normally when the head turns to the right, the activity of the right horizontal canal is increased and the VOR drives the eye to the left. A lesion of the left horizontal canal would produce the same imbalance.

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 (Figure 11.13). In contrast to the nystagmus seen in 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.



Figure 11.12 Abnormal nystagmus is caused by an imbalance in the VOR.



Figure 11.13 Abnormal nystagmus is also caused by a lesion in the PPH.

Vergence Eye Movements

Vergence prevents double vision (diplopia). Vergence eye movements are the slowest to develop during childhood. The movements are linked to accommodation reflex (the reflex that changes the eye's lens properties) (Figure 11.14).

On viewing an object at a different distance the eyes

1) converge or diverge to eliminate retinal disparity (seeing double)

2) accommodate (lens becomes more round or flat) to eliminate blur and

3) the pupils become smaller to reduce the blur. At the beginning of each vergence movement the target is initially out of focus. To bring this target into better focus the pupils transiently constrict, thus increasing the depth of field.

Either blur or retinal disparity will generate vergence (Figure 11.15). The strongest response is elicited when the image is blurred and there is retinal disparity.

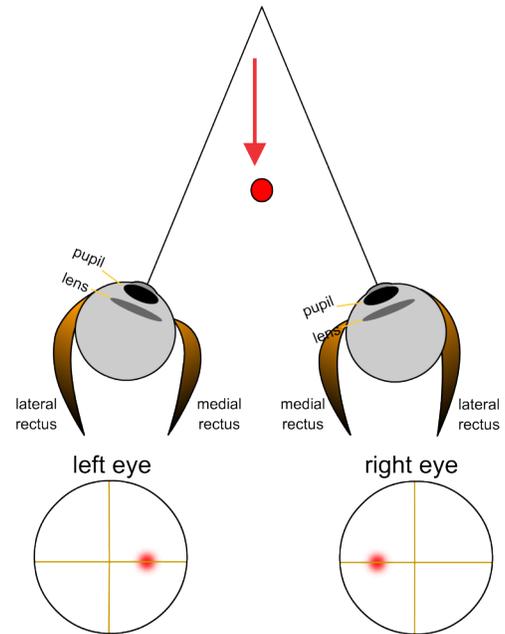


Figure 11.14 At the beginning of the convergence of the eyes onto a nearer target the eye's view shows a retinal disparity and an initial blur.

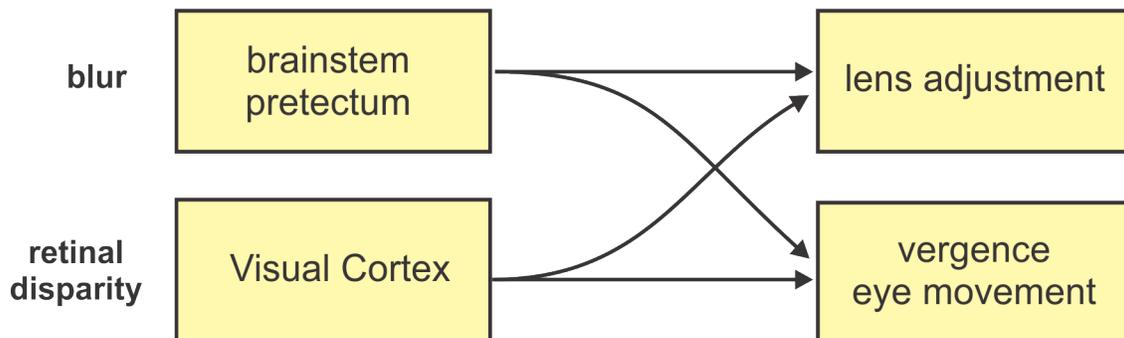


Figure 11.15 Blur and retinal disparity drive accommodation and vergence. A signal of blur from the retina arrives at the pretectum, a structure in front of the superior colliculus, and contracts or relaxes the ciliary muscles changing the lens curvature. A signal of retinal disparity, or double vision, activates visual cortex and produces vergence eye movements. The combination of the blur and disparity produces a more rapid response.

Pursuit Eye Movements

When playing games like basketball it is important to keep one eyes on the ball. To do this requires pursued eye movements. Try tracking you're moving finger as it goes back and forth in front of your face. Notice how clear the image of the finger is when tracking it with your fovea. Notice also that while you make a pursuit eye movement, the image of the room around you slips on your retina eliciting your optokinetic reflex. In order to pursue a visual object the optokinetic reflex must be suppressed. The sequence of structures that are used to generate pursuit eye movements is shown in Figure 11.17.



Figure 11.16 Retinal slip is received in primary visual cortex and area MT. This is converted to a command proportional to the desired speed of a pursuit movement in MSTI, the cerebellum and the brainstem.

Neurons in the eye, V1, and MT respond to the speed of retinal slip. Neurons in MSTI, the cerebellum, and the brain stem code the speed of the pursuit movement. Lesions in MSTI produce pursuit deficits.

After a target starts to move (Figure 11.17),

2) there is a neural delay as the signal passes from the eye, through the long pathway in the cortex and then the muscles (Figure 11.16),

3) then a pursuit movement is generated, 4) but because of the delay the object is no longer on the fovea and a saccade is required to bring it back to the fovea, and finally,

5) if pursuit is perfect, the fovea fixates on the moving object.

Normally a visible moving target is required to initiate a pursuit movement. However there are exceptions to this rule. With practice one can learn to imagine and pursue a moving target in each of the above cases:

- 1) a moving auditory stimulus
- 2) your moving finger with your eyes closed.

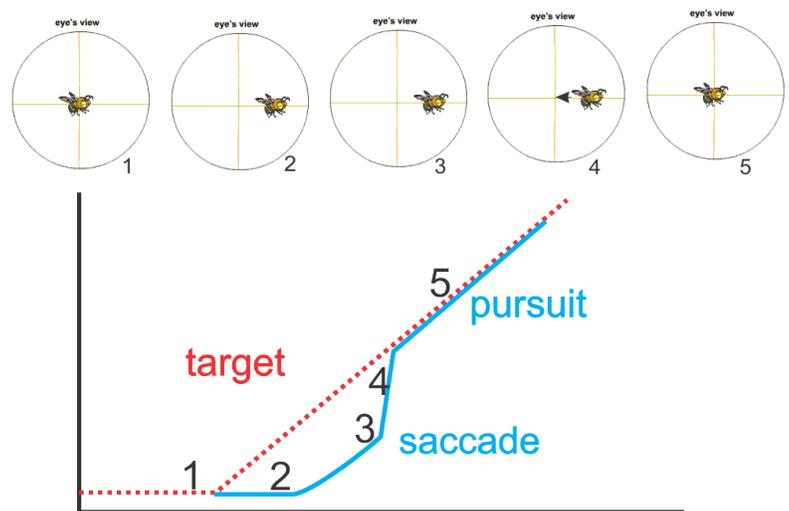


Figure 11.17 The Stages of a Pursuit Eye Movement 1.

Before pursuit begins, the target is on the fovea, 2. when the target starts to move in a shifted away from the fovea, 3. pursuit movement stabilizes the object on the retina's periphery, 4. a saccade redirects the target toward the fovea and 5, a pursuit movement maintains the moving target stationary on the fovea.

Fixation

During fixation, the eye's fovea is examining the target image. Surprisingly, the eye is not still during this fixation (Figure 11.18). If one looks closely, one can see miniature movements, a fraction of a degree in size, consisting of rapid saccades and slow drifts. 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, our perception of this image fades from sight. One hypothesis is that the movements enhance the perception of fine details beyond the resolution predicted by the spacing between the fovea's cones.

Summary

Five eye movement types can be subdivided into the two old systems that serve functional needs of the entire retina and developed before the evolution of a specialized fovea and the three new systems that developed more recently with the evolution of the fovea in order to assist its function.

OLD SYSTEMS:

These developed first in the course of evolution. Their purpose is to keep the images in our environment still on the entire retina when the head moves.

VOR

- 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 reflex

- 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.
- This reflex is best elicited by a large, full field visual stimulus that can elicit a sensation of self-motion.

NEW SYSTEMS:

These three movements developed with the evolution of the fovea. The purpose of all three is to bring the image of a selected object onto the fovea or 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

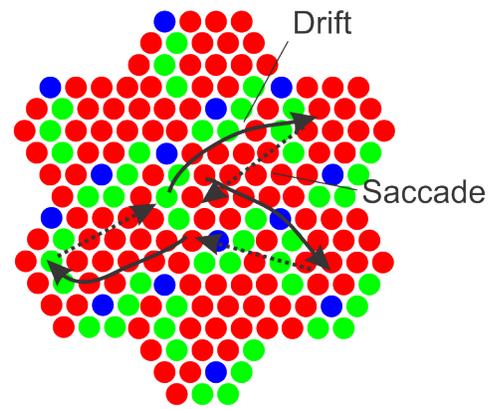


Figure 11.18 Small saccades and drifts are observed during fixation. A few of the retina's 3 cone types, as seen on the retina, are displaced by saccades (dotted lines), or drift (solid lines).

- 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>