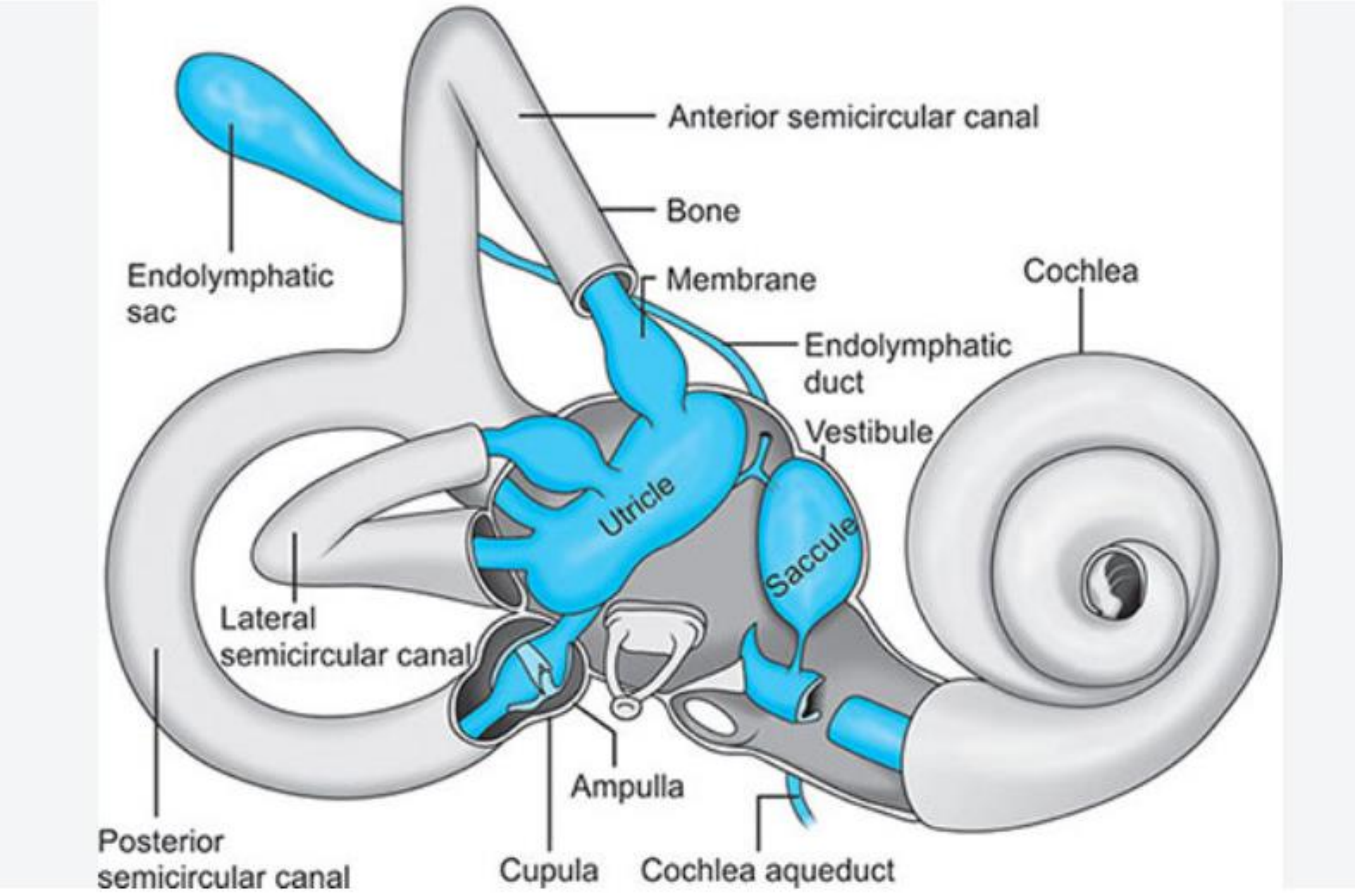
Physiology of vestibular system

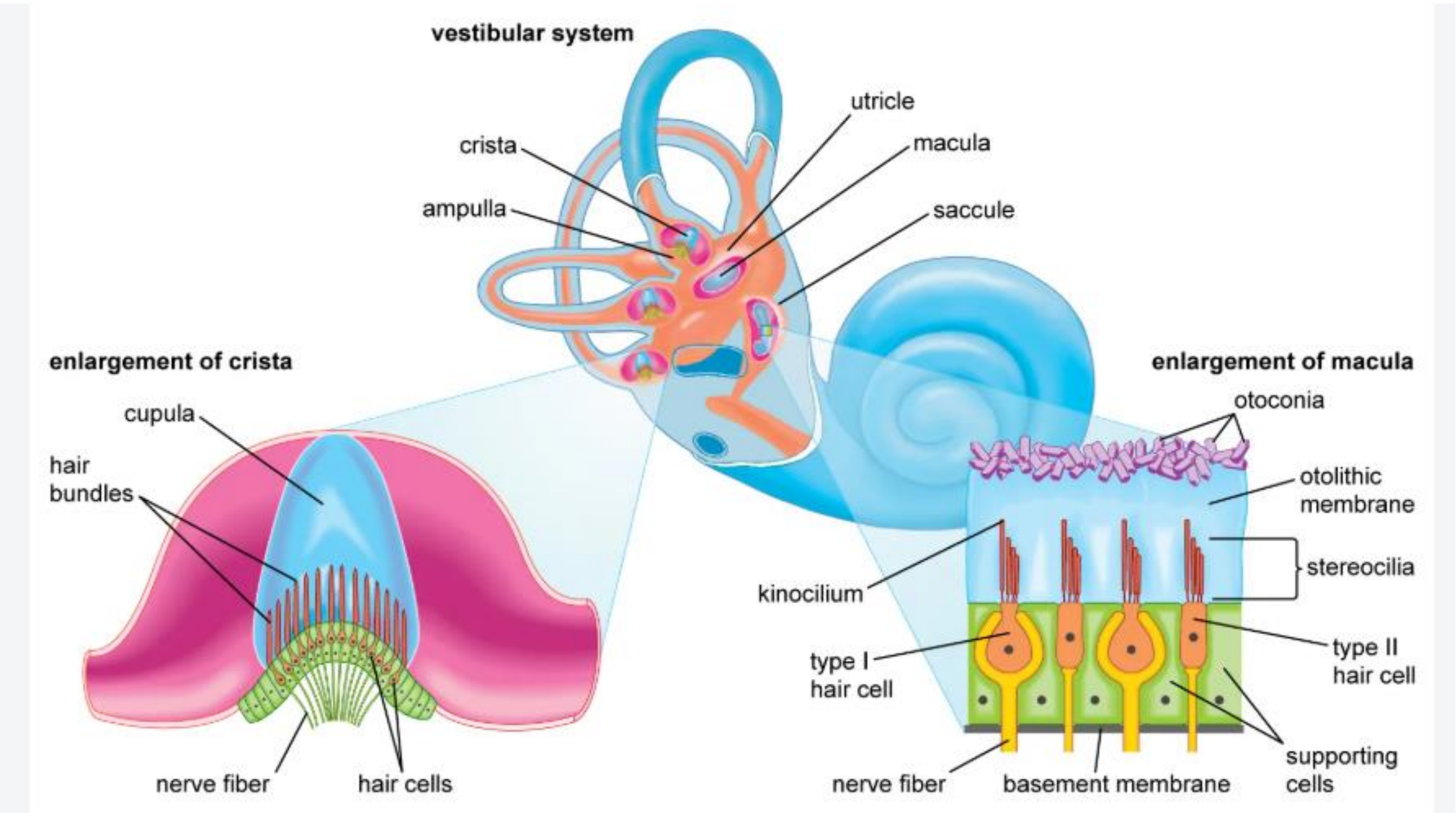
The vestibular labyrinth consists of **five** distinct sensory organs : three **cristae ampullares** (horizontal, anterior and posterior) located inside the semicircular canals and two **otolith organs** (the utricular and saccular maculae).

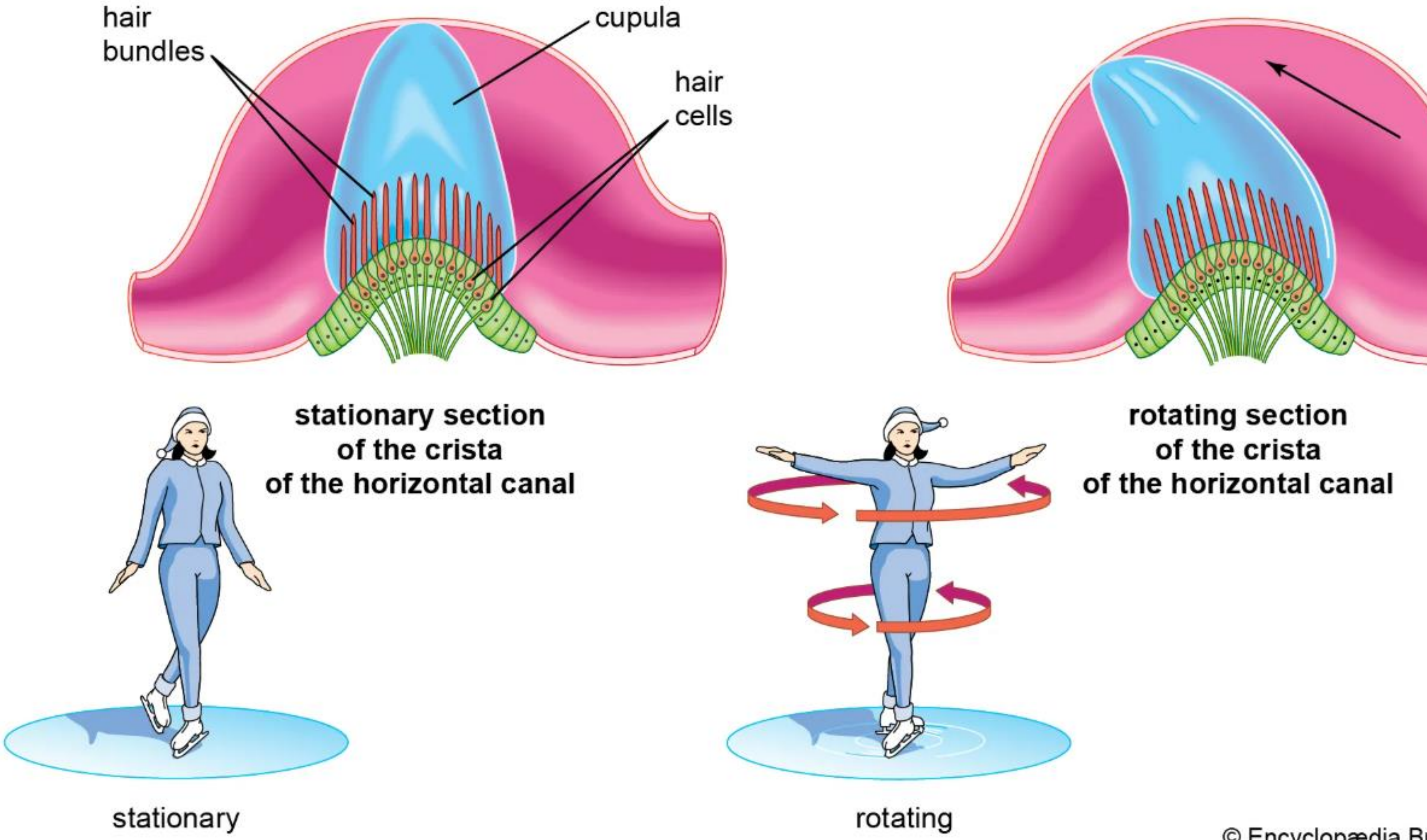
The former are sensitive to angular acceleration (head rotations); the latter to linear acceleration, such as motion in a vehicle or an elevator.

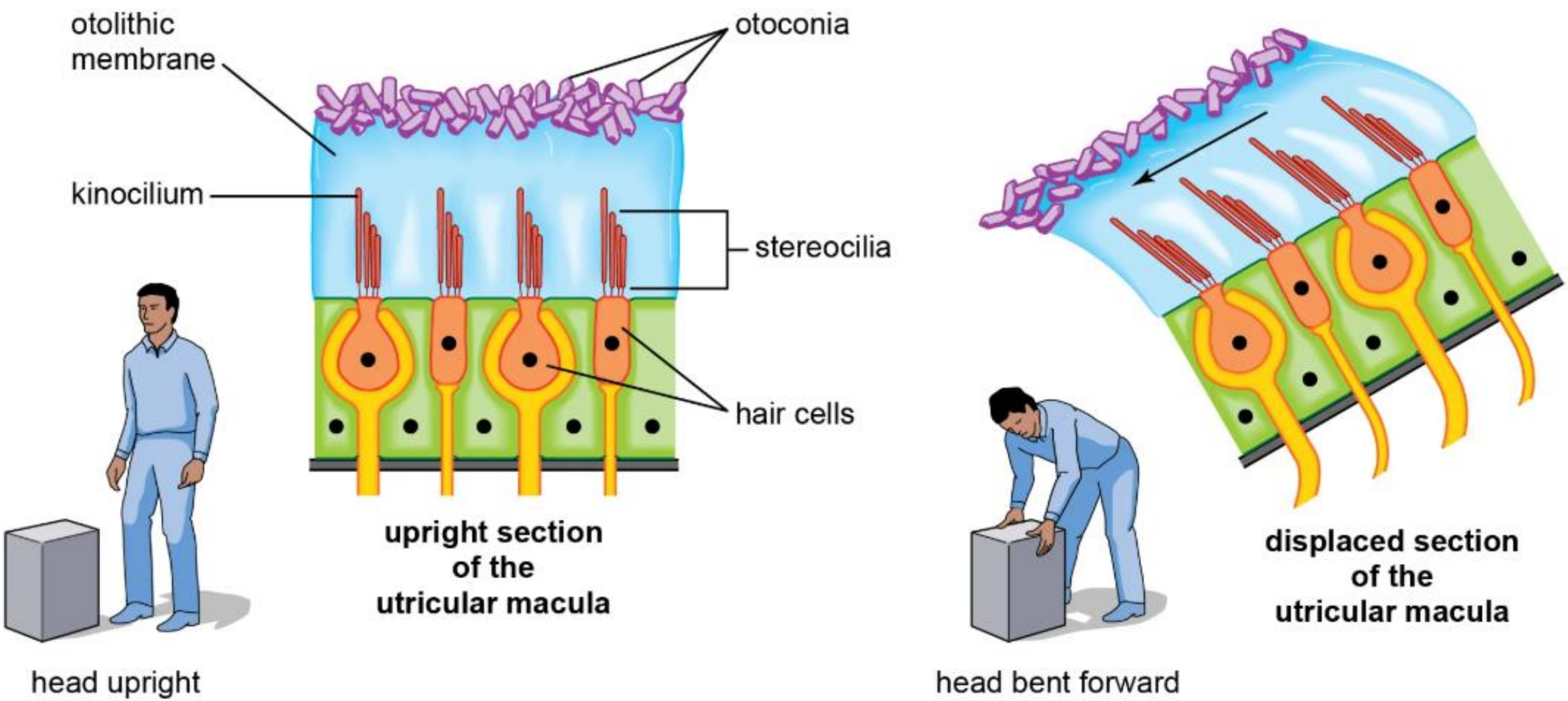
Vestibular sensory epithelia are similar in mammals, birds and reptiles, and comparative aspects have been extensively described.

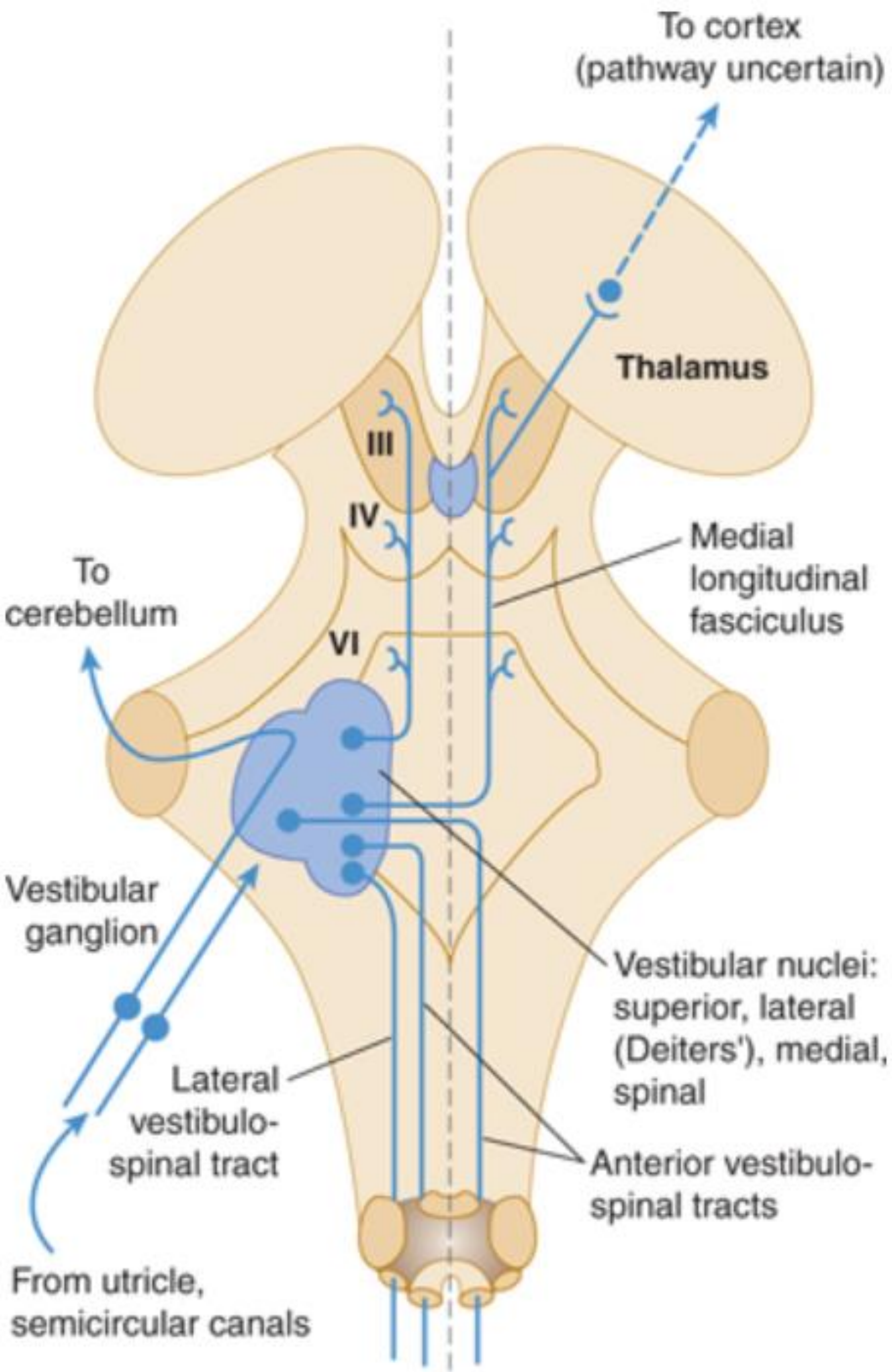
Embedded in an epithelial matrix of supporting cells are two types of sensory receptors, called hair cells.

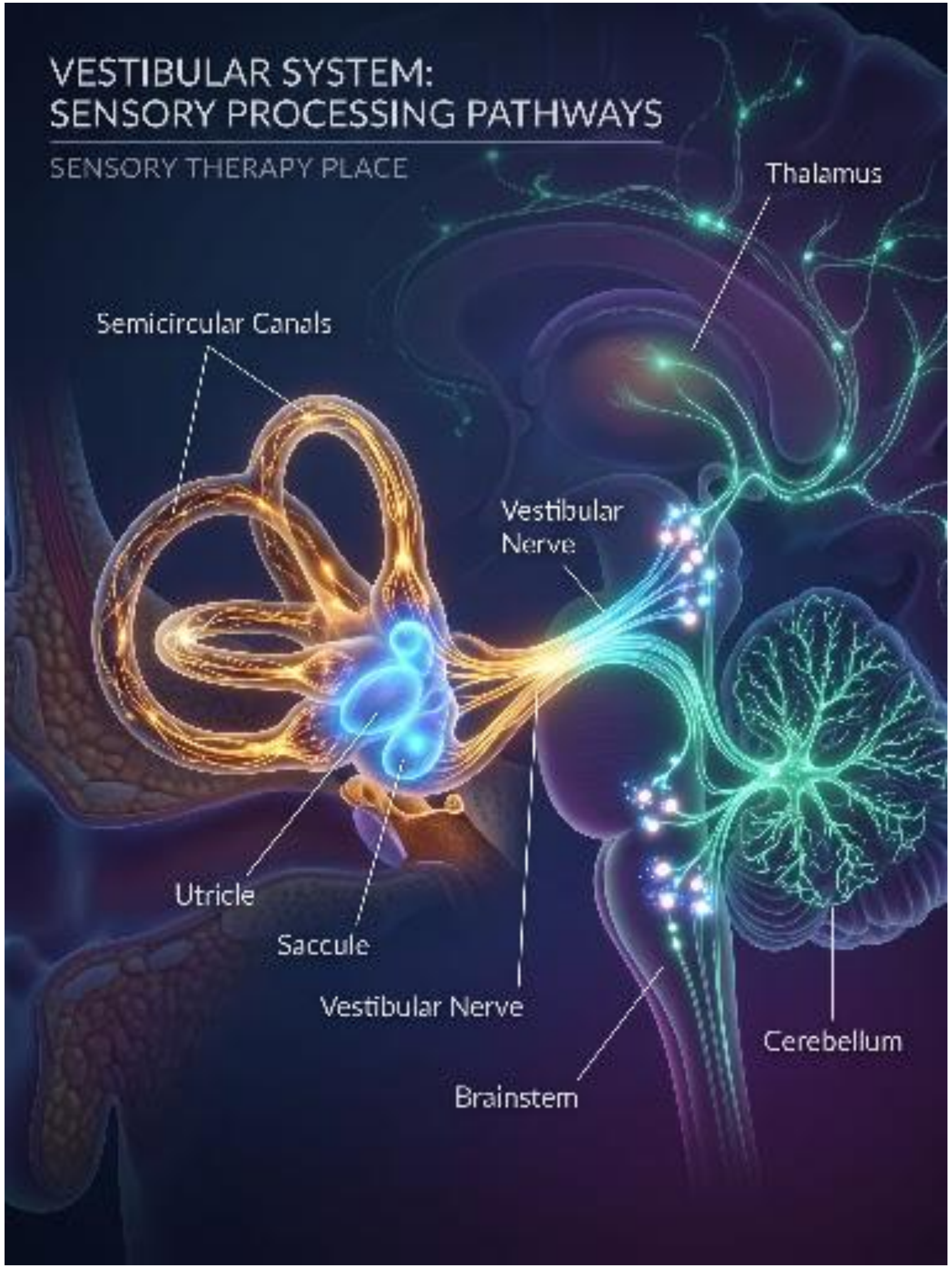

Anterior semicircular canal
Bone
Membrane
Endolymphatic sac
Cochlea
Endolymphatic duct
Vestibule
Utricle
Saccule
Lateral semicircular canal
Ampulla
Posterior semicircular canal
Cupula
Cochlea aqueduct


vestibular system
utricle
crista
macula
ampulla
saccule
enlargement of crista
enlargement of macula
cupula
otoconia
hair
bundles
otolithic
membrane
stereocilia
kinocilium
type I
hair cell
type II
hair cell
supporting
cells
nerve fiber
hair cells
nerve fiber
basement membrane


hair
bundles
cupula
hair
cells
stationary section
of the crista
of the horizontal canal
rotating section
of the crista
of the horizontal canal
stationary
rotating


otolithic membrane
otoconia
kinocilium
stereocilia
hair cells
upright section of the utricular macula
head upright
displaced section of the utricular macula
head bent forward

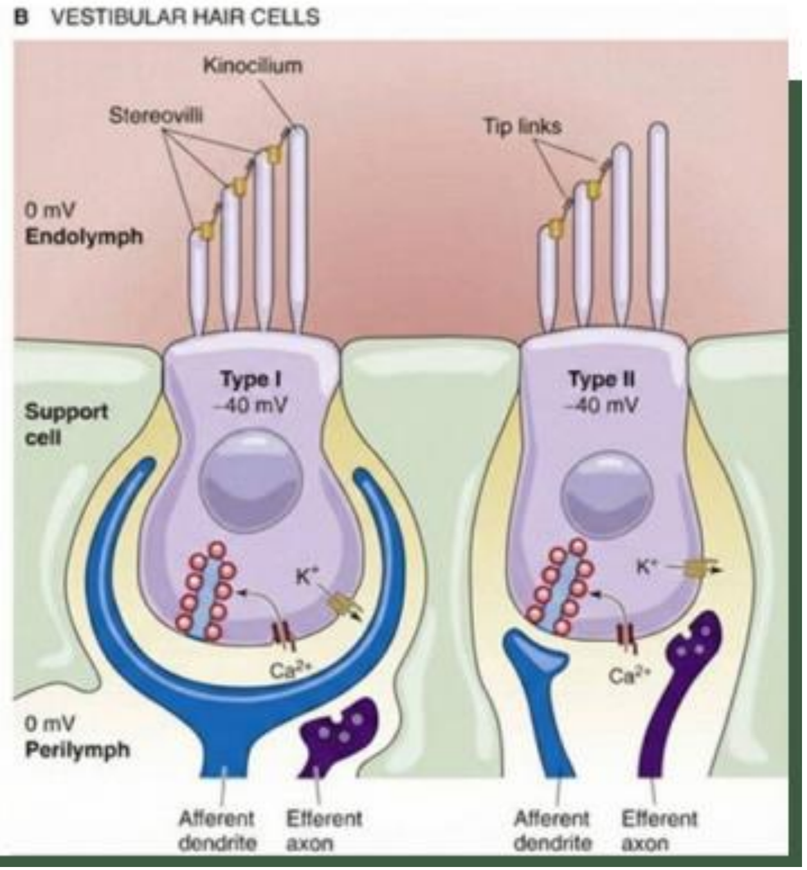

To cortex
(pathway uncertain)
Thalamus
III
IV
VI
Medial
longitudinal
fasciculus
To
cerebellum
Vestibular
ganglion
Vestibular nuclei:
superior, lateral
(Deiters'), medial,
spinal
Lateral
vestibulo-
spinal tract
Anterior vestibulo-
spinal tracts
From utricle,
semicircular canals

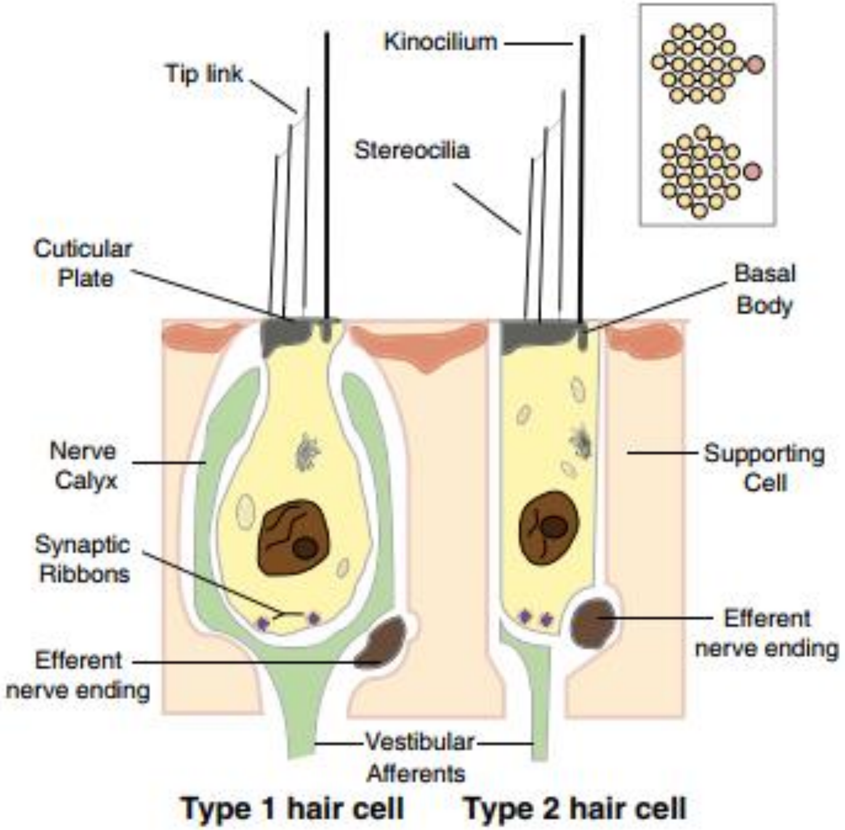

VESTIBULAR SYSTEM:
SENSORY PROCESSING PATHWAYS
SENSORY THERAPY PLACE
Thalamus
Semicircular Canals
Vestibular Nerve
Utricle
Saccule
Vestibular Nerve
Cerebellum
Brainstem

Physiology and neurophysiology of vestibular system

Neurophysiology

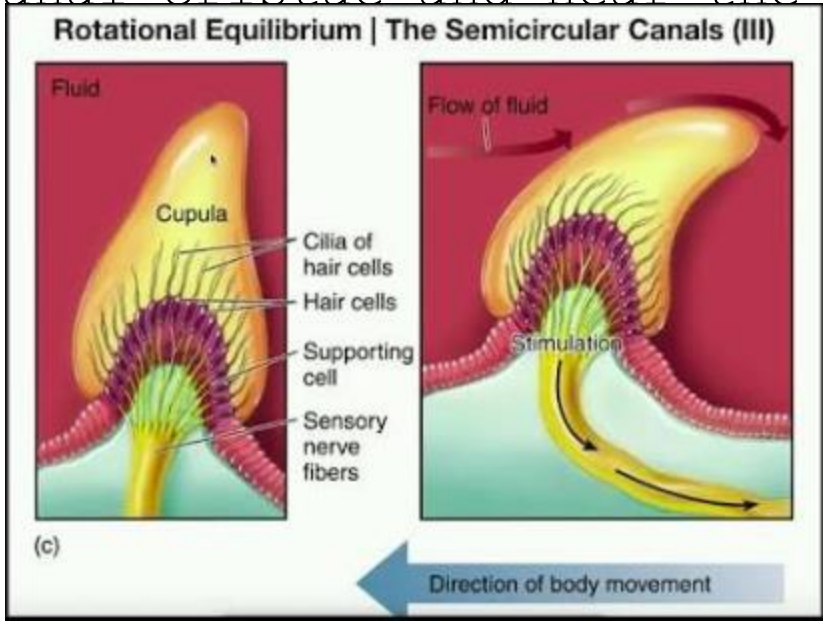
Mammalian vestibular hair cells have two flavors: type 1 and type 2

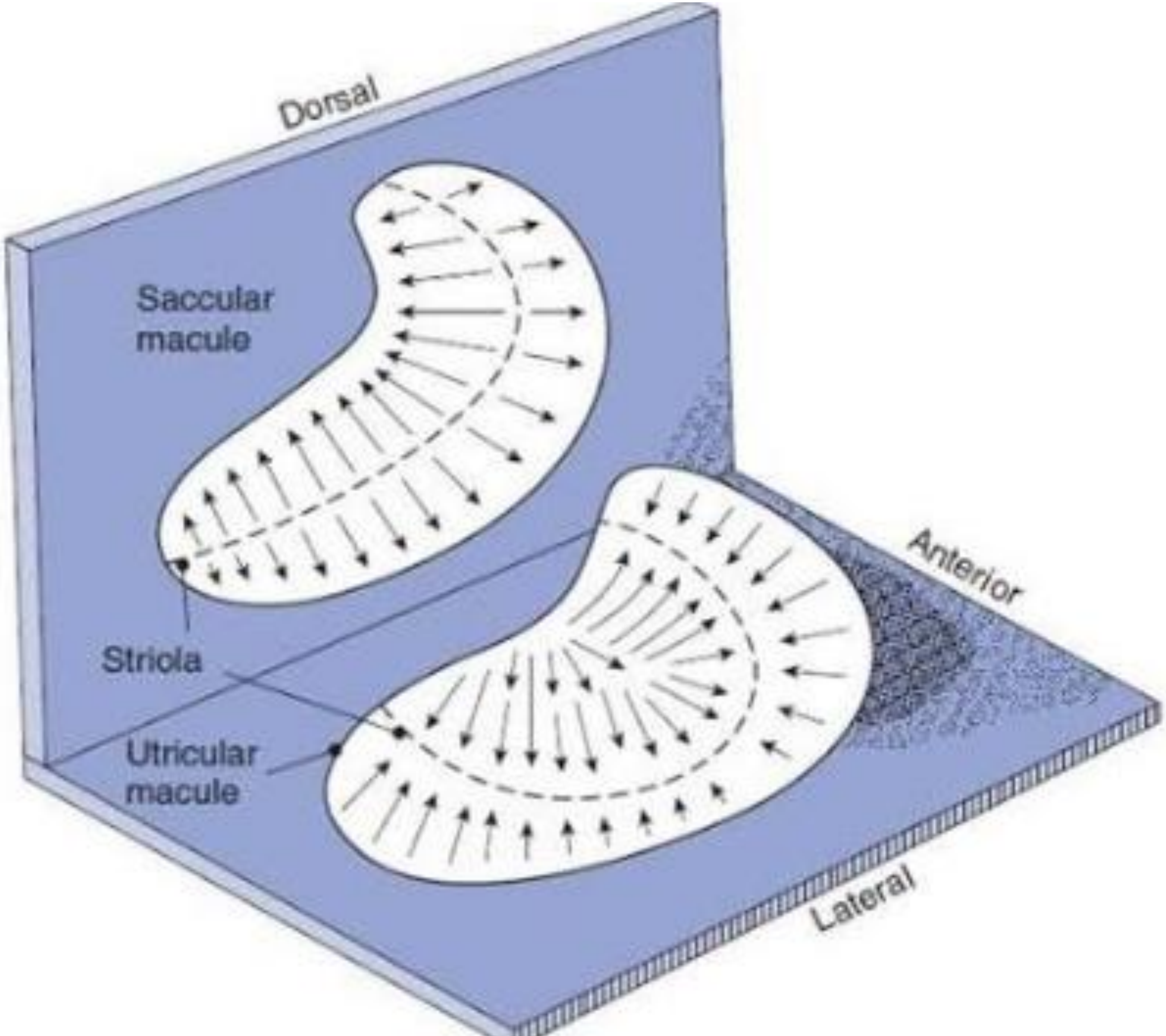




Type 1 vestibular hair cells are phylogenetically younger than type 2 and are enveloped by a calyx, an axon of a primary vestibular afferent.

These type 1 calyx hair cells are located more in the central areas of the semicircular canal cristae and near the striola of the utricle and saccule.





Dorsal
Saccular
macule
Striola
Utricular
macule
Anterior
Lateral

Type 2 bouton hair cells are located more in the periphery.

The type 1 hair cells primarily synapse on primary vestibular afferents with an irregularly spaced discharge pattern.

The type 2 hair cells primarily communicate with synapses that have afferents that discharge with a regularly spaced pattern.

Some vestibular afferents synapse on both type 1 and type 2 hair cells and are called dimorphic afferents.

Dimorphic afferents can have either regular or irregular discharge patterns and tend to discharge regularly when in the periphery and irregularly when in the central areas of the crista or near the striola.

Vestibular afferents with regular and irregular discharge patterns have a range of unique properties that can translate to clinical observations.

Gentamicin, for instance, preferentially affects the type 1 hair cells that are associated with irregularly discharging afferents.

These afferents are thought to primarily encode information about the timing of head movements, for instance, during complex stimuli such as keeping one’s gaze fixed during walking.

They are also more sensitive to high frequency stimuli and electrical currents.

These irregular afferents also are preferentially lost with aging or with chronic metabolic conditions like type 2 diabetes mellitus
.

On the other hand, regularly firing vestibular afferents (associated with type 2 hair cells) are thought to better encode the fidelity of a head movement signal but are less sensitive to more complex stimuli.

The brain is continuously comparing the firing rates of each side's vestibular afferents, with differences interpreted as head movement.

When the vestibular nuclei identify an asymmetry in firing rate between the two sides, the brain interprets this difference as a head rotation toward the side with increased firing rate.

Vestibular Physiology

The semicircular canals detect head angular (rotational) acceleration and the otoconial end organs detect head linear acceleration (translation) as well as head tilt.

Semicircular Canal Physiology

Early vestibular physiologists identified the function of the semicircular canals first in pigeons.

By studying the effects of individual canal stimulation on head movements, J.R. Ewald discovered fundamental concepts in vestibular physiology upon which we continue to rely.

One of his observations was that each semicircular canal has a preferential direction of stimulation.

The hair cells of semicircular canal cristae are arranged in a consistent pattern, such that deflection of the cupula either excites or inhibits all hair cells of the crista of that canal.

For the lateral semicircular canals, for instance, the stereocilia are arranged such that the kinocilium is closest to the vestibule, so that displacement of the cupula toward the vestibule (ampullopetal flow) excites the lateral semicircular canals.

The opposite is true for the vertical canals (superior and posterior semicircular canals).

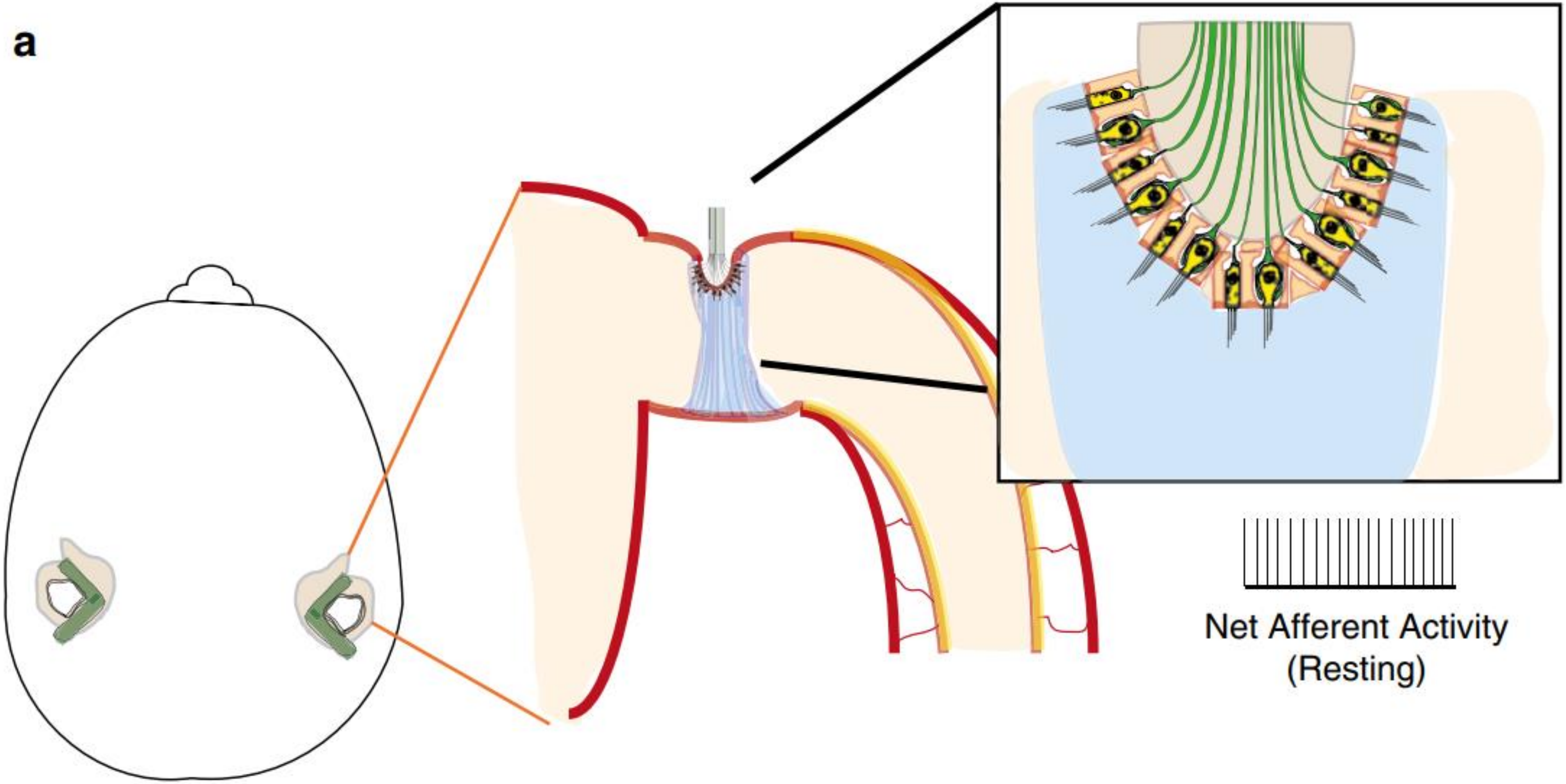
For the vertical canals displacement of the cupula away from the vestibule (ampullofugal flow) is excitatory.

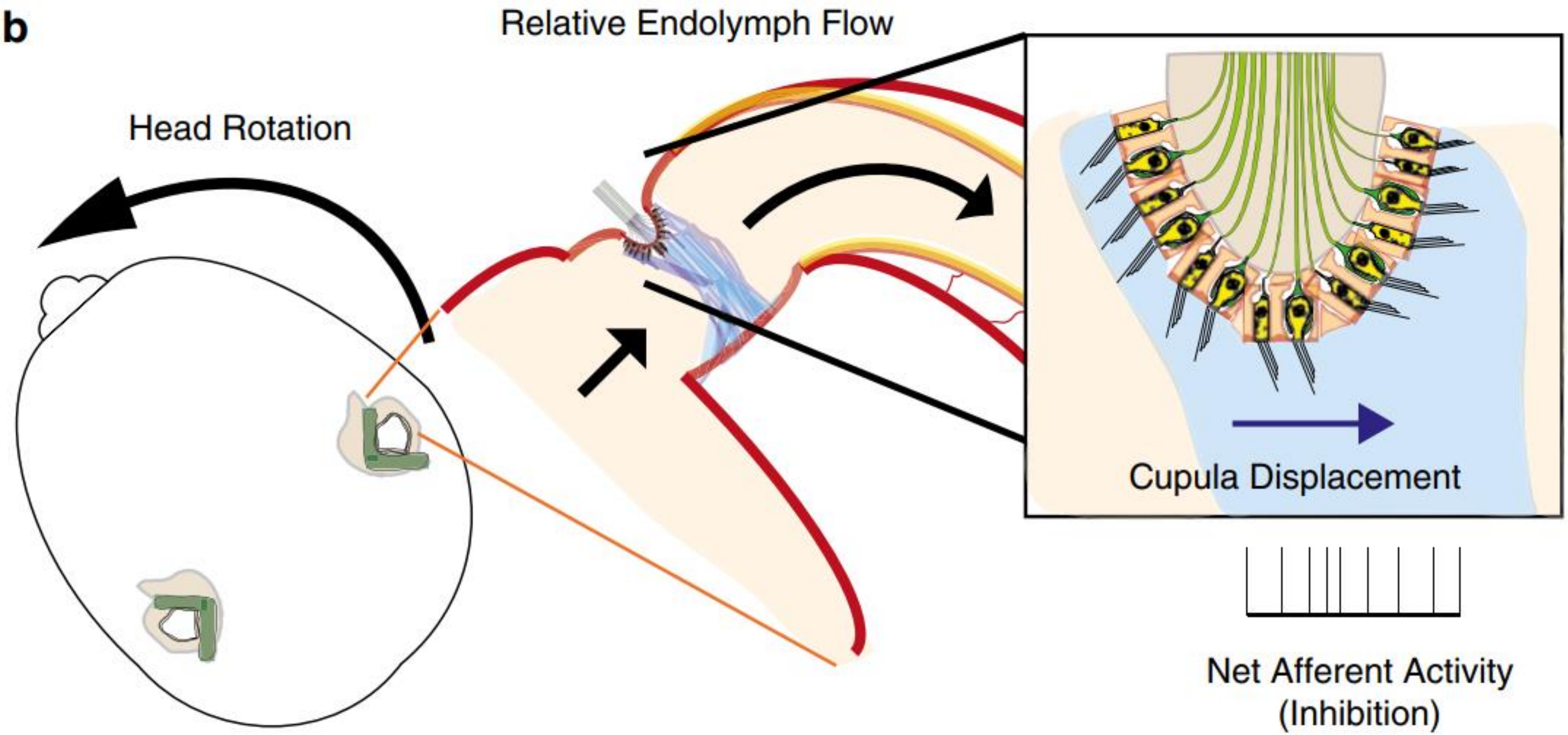
While this arrangement may seem counterintuitive, it allows for a simple rule: head rotation in the plane of each semicircular canal and toward that side is maximally excitatory to that semicircular canal.

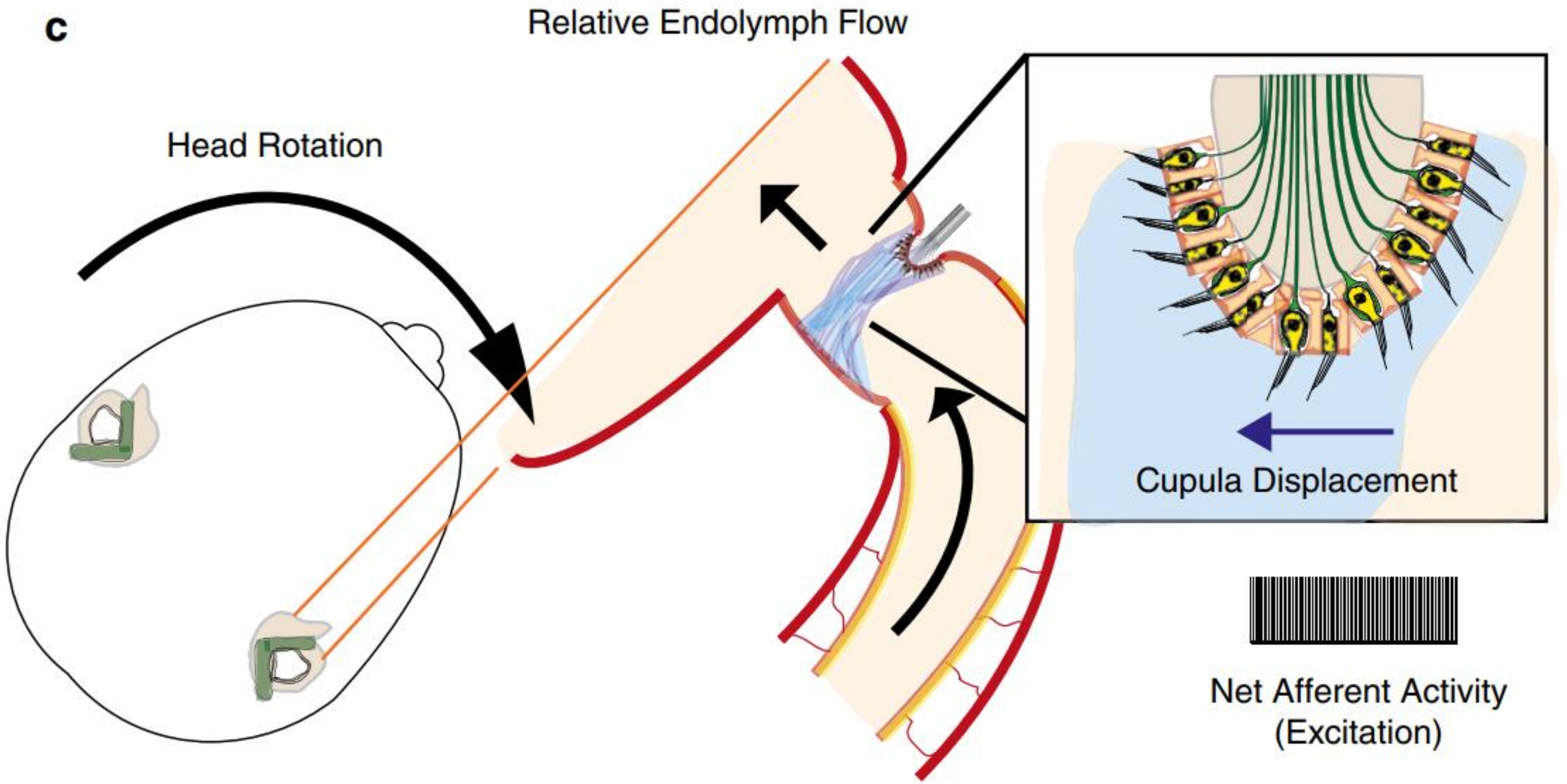
To further understand how semicircular canals are preferentially excited by a head rotation in that plane and toward that side, it is helpful to consider what occurs in the cupula during a head rotation.

As the head turns or rotates, both the labyrinth and head rotate in the same direction in a space fixed reference frame (i.e., when looking at the head from above, both seem to be moving through space.

a




b
Relative Endolymph Flow
Head Rotation
Cupula Displacement
Net Afferent Activity
(Inhibition)


c
Relative Endolymph Flow
Head Rotation
Cupula Displacement
Net Afferent Activity
(Excitation)

Physiology of the semicircular canals.

At rest, vestibular afferents maintain resting discharge activity (a).

In a head frame of reference, during a head angular acceleration (head rotation), the head with the labyrinth and endolymph rotate to either the left (b) or to the right (c).

Due to inertia, there is relative endolymph flow in the opposite direction that induces deflection of the lateral semicircular canal cupula.

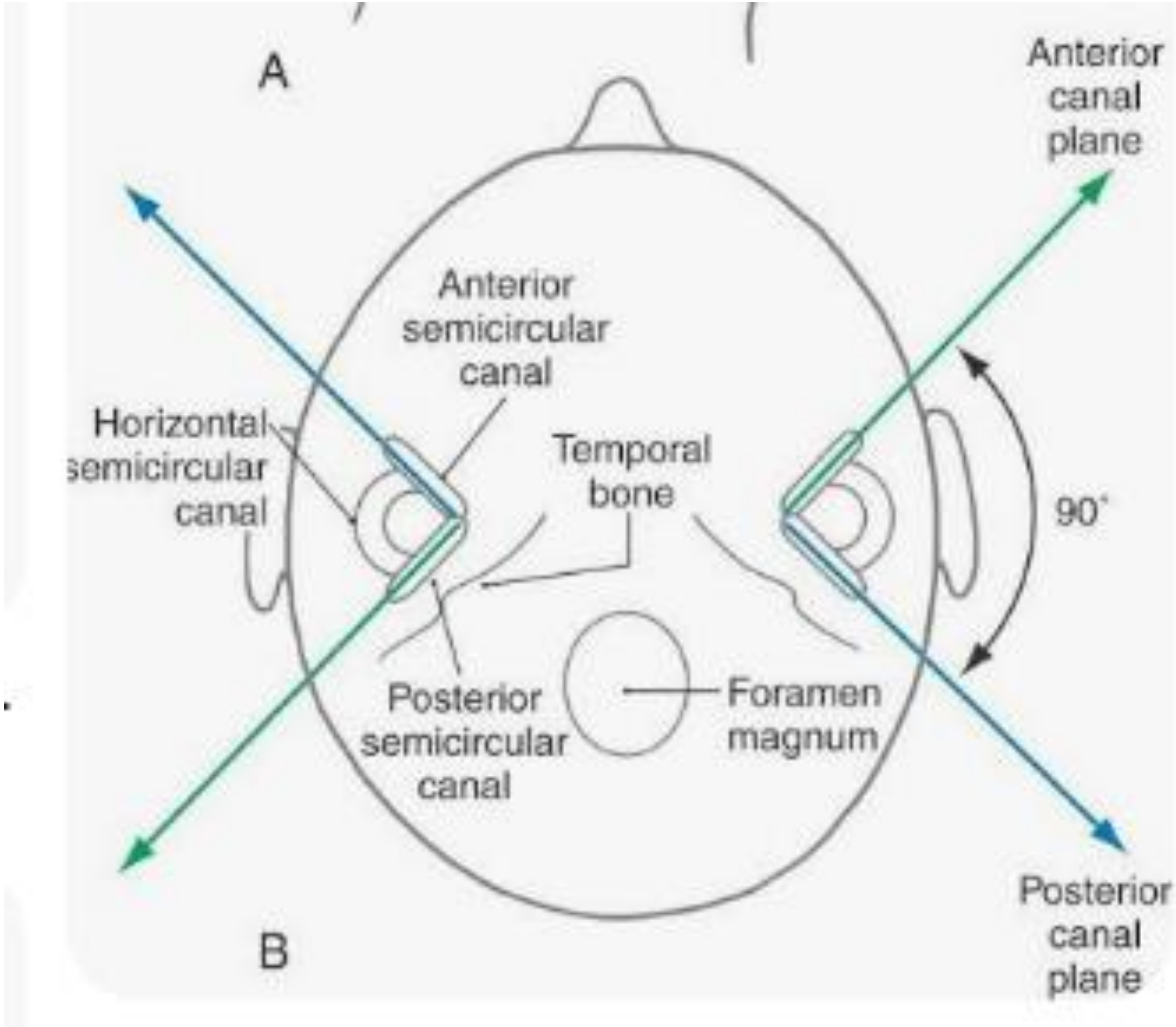
From a cupula frame of reference, the cupula is either deflected in an inhibitory direction (b), resulting in decreased vestibular afferent discharge, or an excitatory direction (c), resulting in

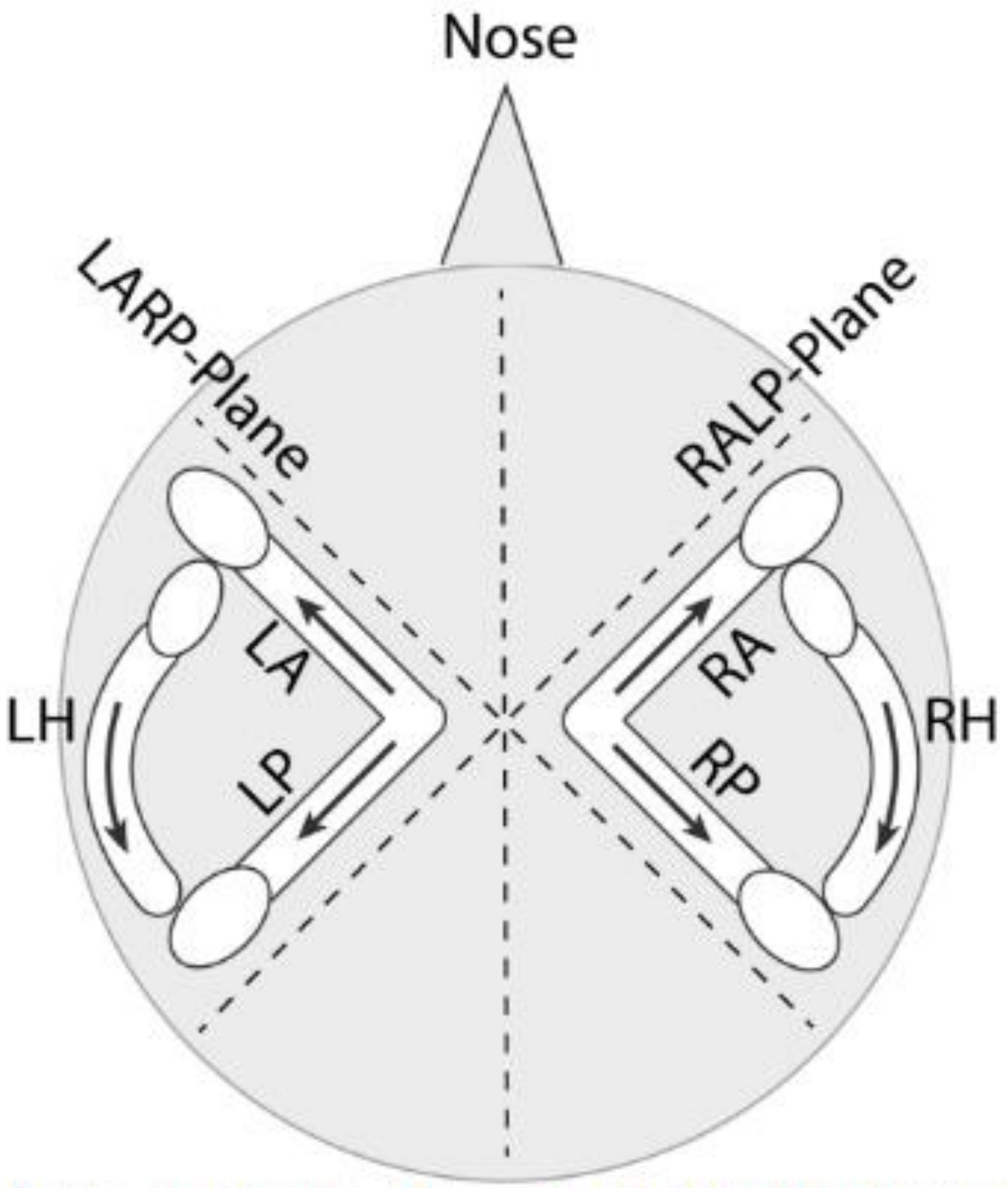
However, due to viscosity of the endolymph and elasticity of the cupula, there is relatively less movement of the cupula.

From a canal-fixed reference frame (i.e., if one was standing in the cupula), therefore, it appears the cupula is being deflected in the direction opposite the head rotation.

It is this relative motion of the cupula that the brain uses to determine the direction to which the head is rotating.

Recall that the semicircular canals are organized as coplanar pairs with the canals of the opposite ear.


A
Anterior canal plane
Anterior semicircular canal
Horizontal semicircular canal
Temporal bone
90°
Posterior semicircular canal
Foramen magnum
B
Posterior canal plane


Nose
LARP-Plane
RALP-Plane
LA
LP
LH
RA
RP
RH

The left superior (or anterior) semicircular canal is coplanar with the right posterior semicircular canal (LARP plane) and the right superior (or anterior) semicircular canal is coplanar with the left posterior semicircular canal (RALP plane).

As a result, any head rotation will excite one side and inhibit the other.

For the lateral semicircular canals, horizontal head rotations toward the side of the canal stimulates that canal, while simultaneously inhibiting the contralateral lateral semicircular canal.

The superior canal is excited by head rotations that are downward and to the side in the plane of the canal, and the posterior canal is excited by head rotations that are upward and to the side in the plane of that canal.

Another of Ewald’s observations was that excitation provides stronger stimuli to semicircular canals than inhibition.

This asymmetry in sensitivity to excitation and inhibition occurs because of the resting firing rate of vestibular afferents described above.

If we assume that a baseline firing rate for a vestibular nerve afferent at rest is approximately 100 spikes per second , this rate can increase to several hundred spikes per second during excitation, but can only decrease to zero during inhibition.

This creates an imbalance such that excitation imparts a greater vestibular stimulus than inhibition.

Otolith Physiology

The presence of otoconia on the surface of the utricular and saccular maculae allow these organs to sense linear accelerations.

Otoconia increase the density of the macula. With head translation the otoconial membrane lags with inertia behind the head movements and with head tilt it falls with gravity like a slab avalanche.

The hair cells embedded within the gelatinous layer deflect as the otoconial membrane lags with inertia or falls with gravity.

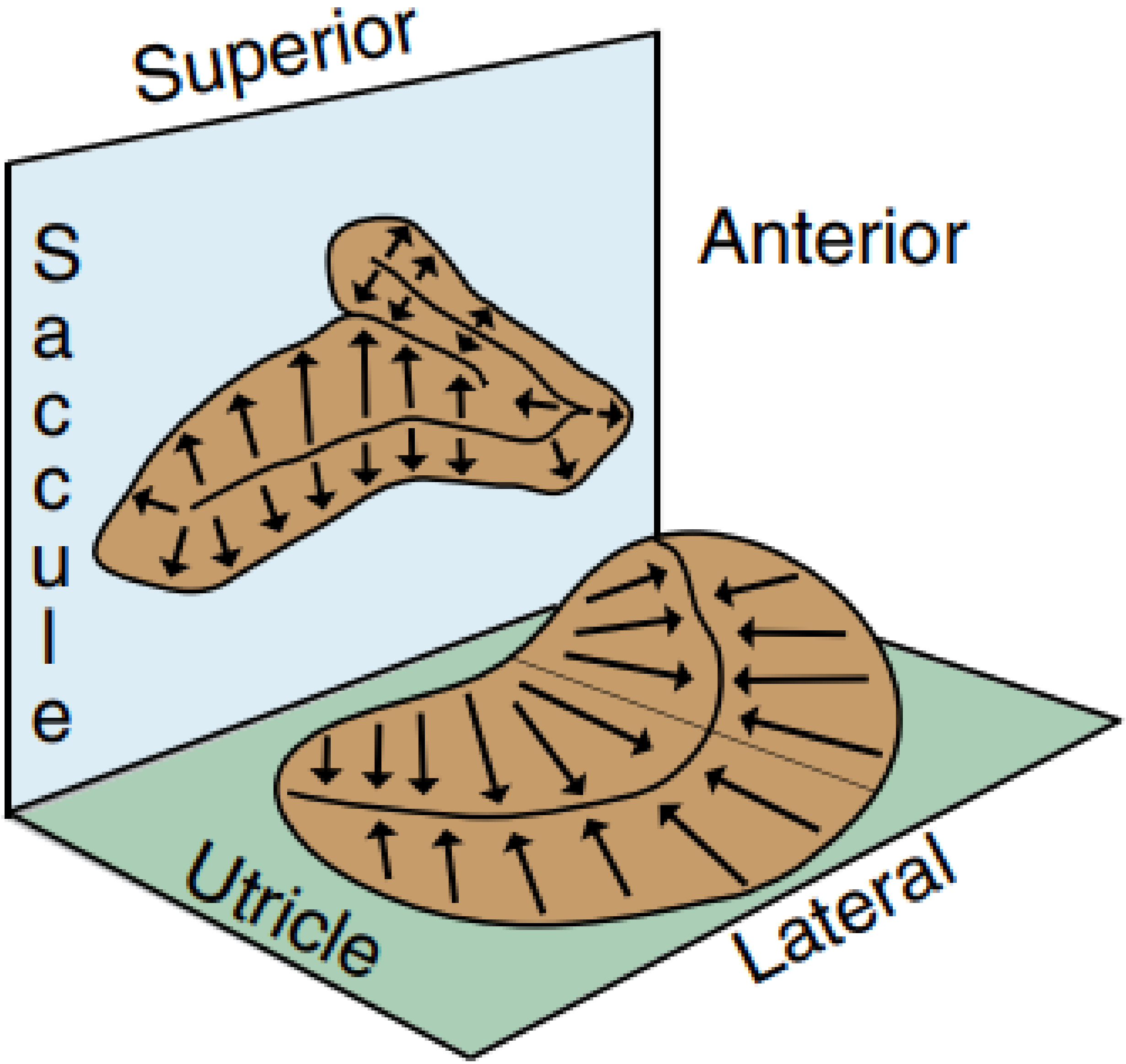
Unlike hair cells in the semicircular canal cristae, the hair cells of the otoconial organs do not have uniform polarity across their surface.

The directions of relative movement of the otoconial membrane that preferentially stimulate macular hair cells are represented by sensory force vectors.

Despite the pattern of sensory force vectors, the forces imparted on the otoconial membrane by linear acceleration are uniform, creating a symphony of activation and inhibition in the otoconial organs even within the same macula.

The brain interprets direction and magnitude of the head movement from the patterns of stimulation and inhibition .

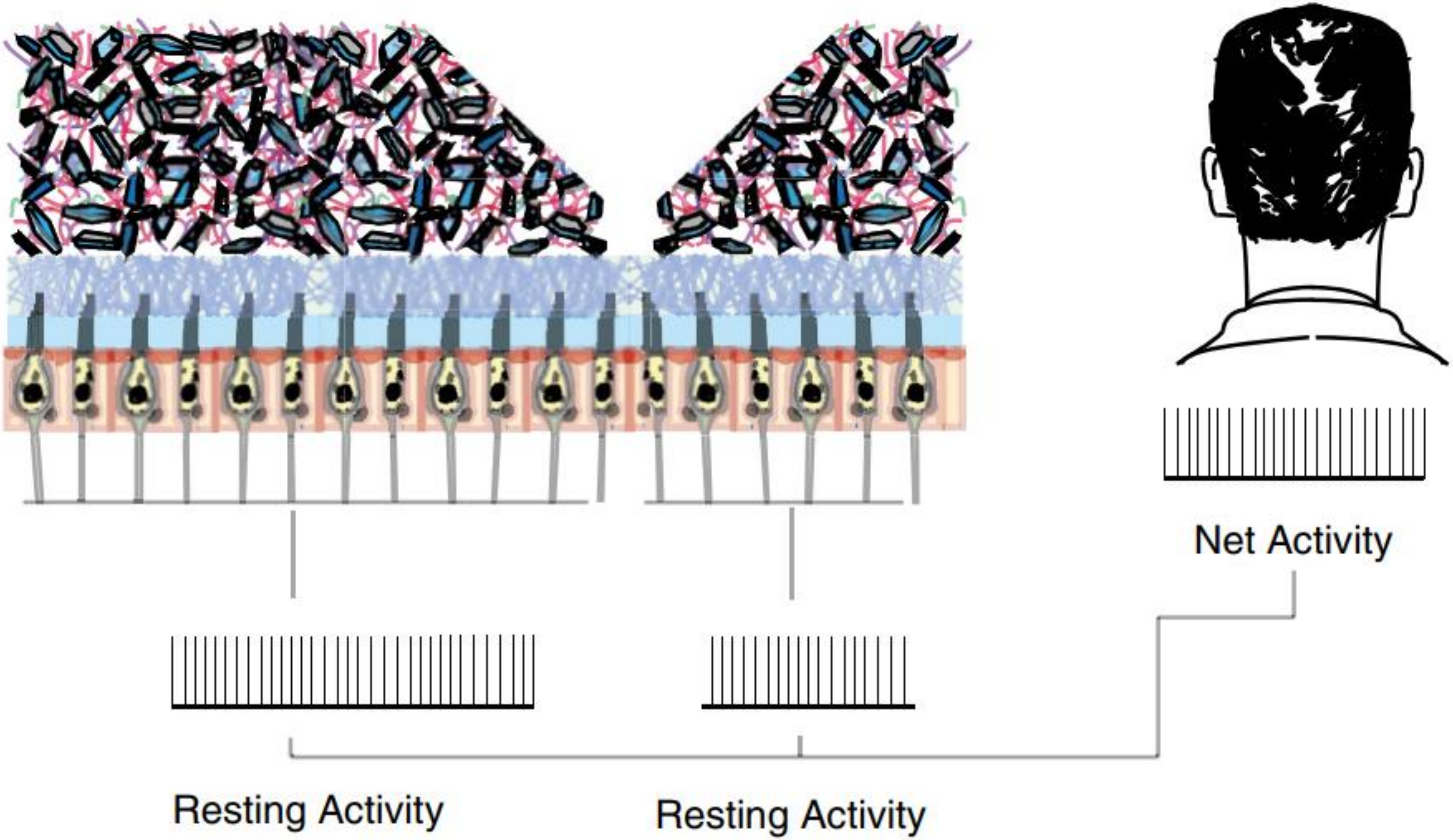
b



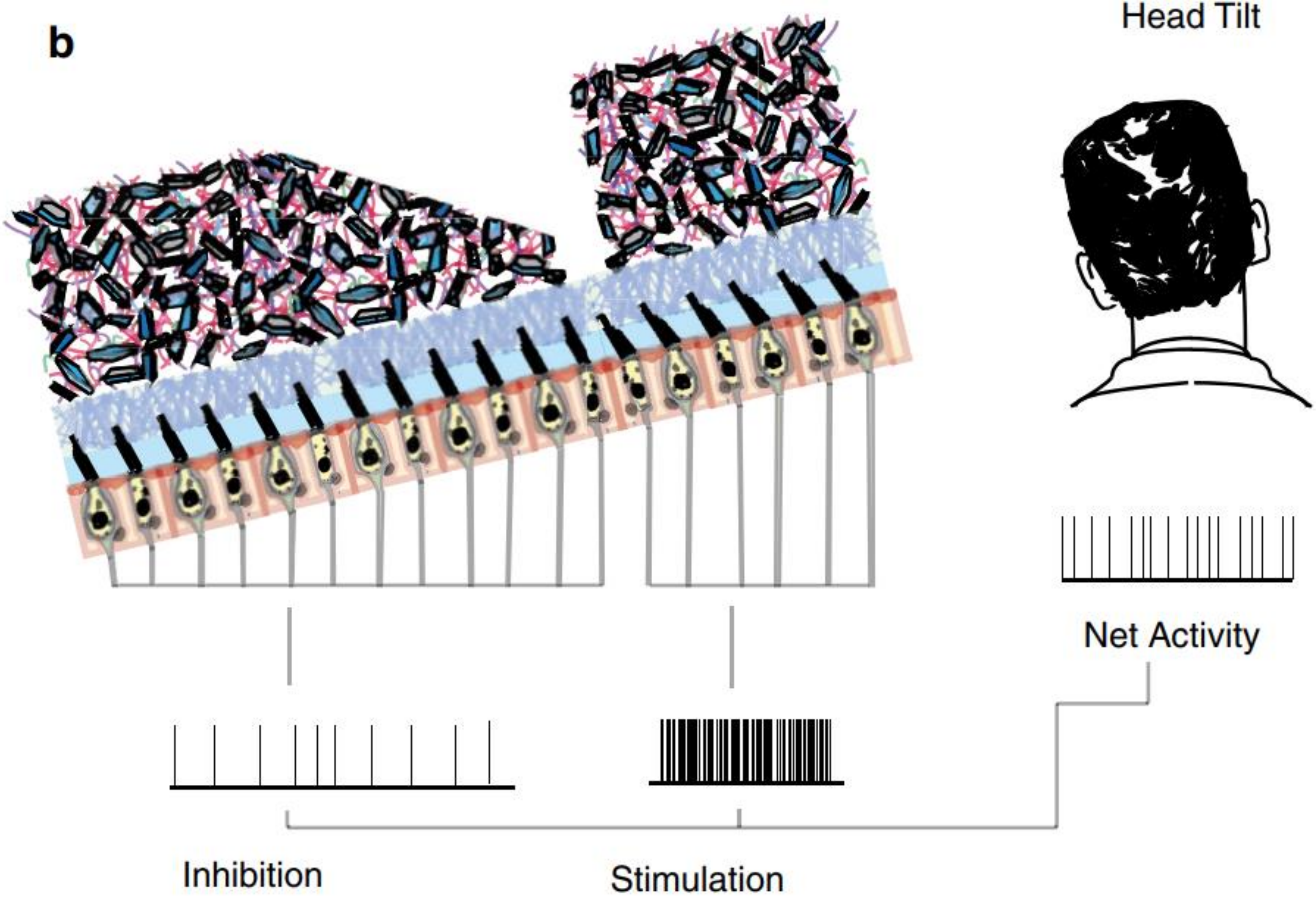
(b) In the utricular macula the kinocilia are directed toward the striola,

whereas in the saccule they are directed away from the striola.

a



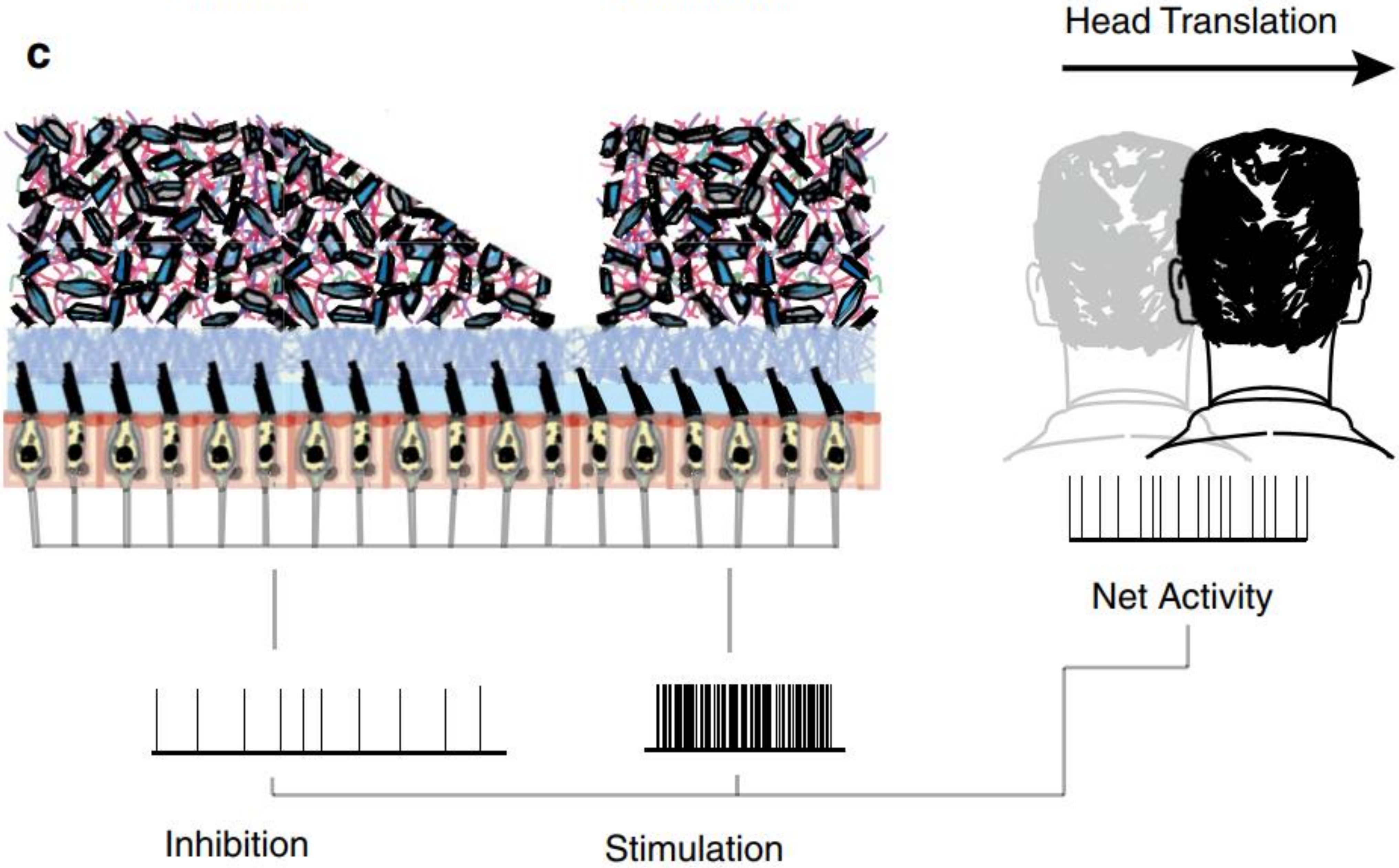
Physiology of the otoconial organs (a) At rest there is a baseline firing rate of otolithic afferents of the utricle (shown) and saccule.


b
Head Tilt
Net Activity
Inhibition
Stimulation

With left head tilt (b) the otoconial membrane falls with gravity, resulting in a portion of the hair cells being deflected in an excitatory direction and others deflected in an inhibitory direction.

This information is synthesized in the vestibular nucleus.

c



(c) If a person translates to the right, the same net force is transmitted to the otoconial membrane, resulting in the same activity as a head tilt to the left (b).

The brain uses input from the semicircular canals to distinguish a head tilt from a translation.

The utricle primarily senses lateral tilt and head translation, while the saccule senses front-to-back tilt and translation in line with gravity.

Vestibular Reflexes

In order for us to see an object clearly, the object of interest must remain steady on the fovea, a central portion of the retina that permits the highest visual acuity.

Small deviations off the fovea creates a large decrease in visual acuity, so that when an object moves across the retina, it appears blurred.

There are several types of eye movements that function to get an image to the fovea or to keep it there.

Saccades (rapid eye movements that take the eyes from one point to another) and **quick vergence** (rapid movement of both eyes to either a near or far target) are two types of eye movements that bring objects to the fovea.

Smooth pursuit (a visually induced reflex to track a moving object).

and the **vestibulo-ocular reflex (VOR)** keeps an image on the fovea once it is there.

For slow-moving objects, smooth pursuit adequately keeps an object steady on the fovea.

For faster movements, however, such as the head movements during walking, smooth pursuit fails, and we need a faster reflex.

The vestibular system primarily drives fast reflexes. For quick movements such as those imposed on the head during walking or running, the eyes must move with the appropriate speed and timing in order to compensate for the movement of the head.

Furthermore, postural reflexes are needed to adjust for sudden changes in head position.

The vestibulo-ocular and vestibulo-spinal reflexes are critical for maintaining both clear vision and stable posture during both planned and unplanned head movements.

Vestibulo-Ocular Reflexes

Projections from the vestibular system to oculomotor nuclei serve to keep images steady on the fovea while the head is rotating, tilting, or translating through space.

The angular VOR is classically recognized as a three-neuron arc that includes the vestibular afferent, an interneuron, and an oculomotor neuron.

Its purpose is to keep an image fixed on the retina during an angular head rotation, and it does so with great accuracy.

The extraocular muscles are roughly aligned with the orientations of the semicircular canals.

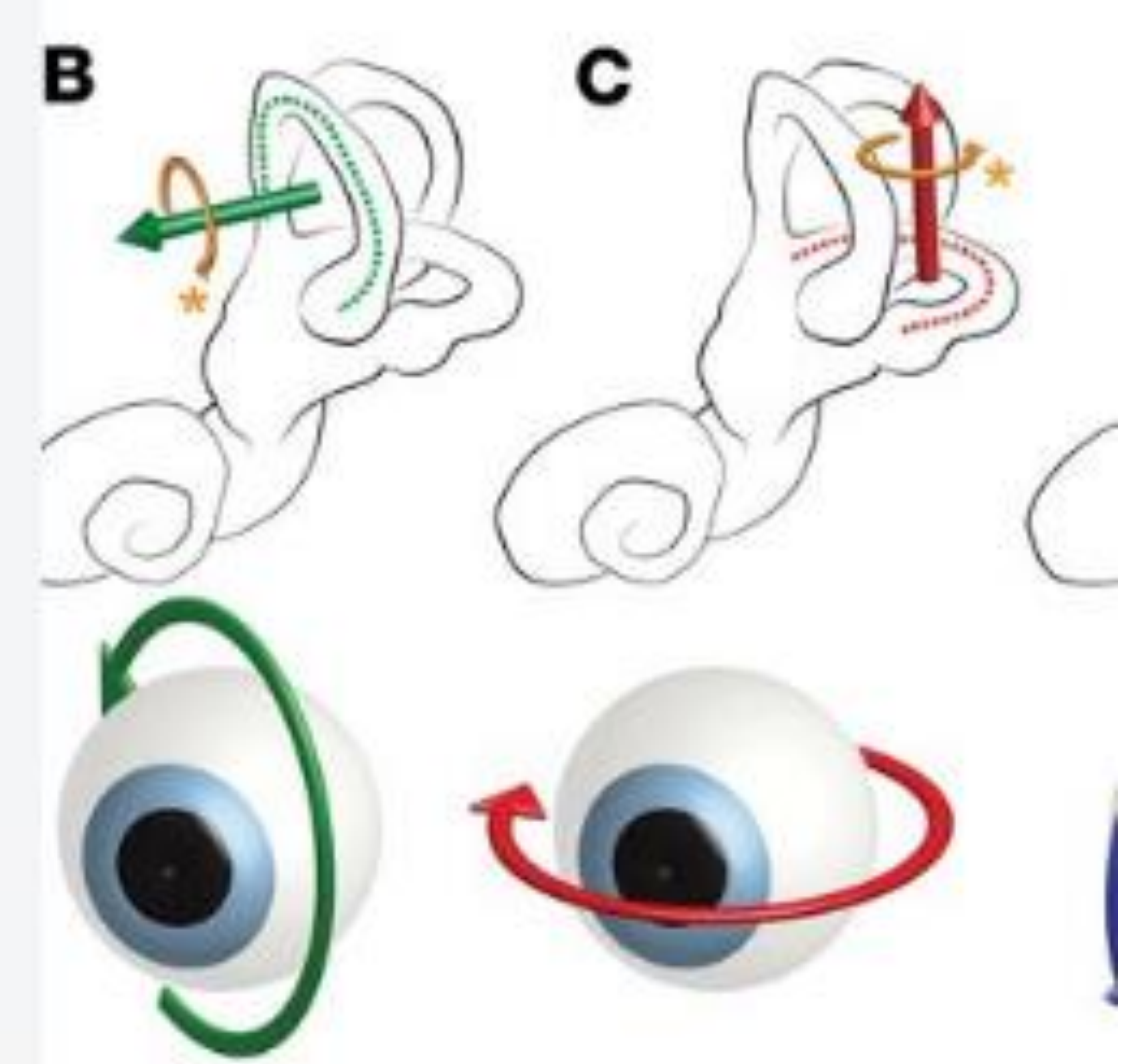
Horizontal

Left Anterior/Right Posterior
(LARP)

Right Anterior/Left Posterior
(RALP)

Eye muscle-semicircular canal alignment.

For each semicircular canal plane (lateral, LARP and RALP), the extraocular muscles are approximately aligned in corresponding planes to facilitate rapid eye rotation in response to head rotation and supporting Ewald's first law holds that stimulation of a semicircular canal causes an eye movement in the plane of that canal.


B
C

This contributes to any head rotation rapidly translating into an accurate eye rotation.

The angular VOR is among the fastest human reflexes, with a response latency of approximately 8 ms .

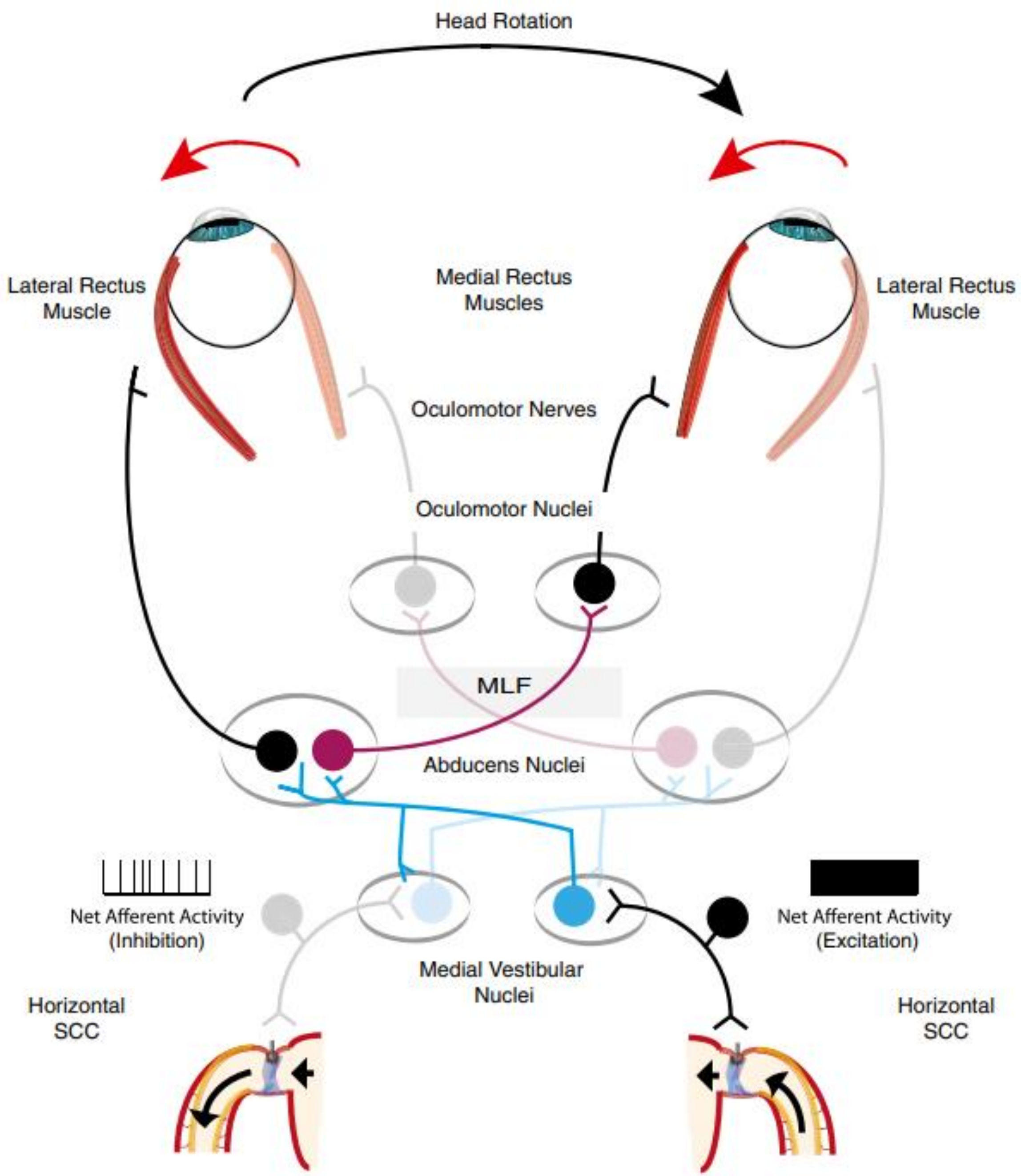
The rate limiting step in neural transmission is the synapse. There are only three neurons between the end organ’s highly sensitive hair cell mechanoreceptor and the corresponding fast contractions of the extraocular muscles.

For comparison, the latency of smooth pursuit is approximately 100 ms.

Visually induced reflexes are too slow to provide compensatory eye movements during quick head movements.

For a rightward horizontal head rotation, there is relative excitation of the right lateral semicircular canal afferents and an accompanying increase in firing activity at the right medial vestibular nucleus.

This sends excitatory projections to the contralateral left lateral rectus and the ipsilateral right medial rectus via the medial longitudinal fasciculus, while simultaneously inhibiting the contralateral left medial rectus and the ipsilateral right lateral rectus .


Head Rotation
Lateral Rectus Muscle
Medial Rectus Muscles
Lateral Rectus Muscle
Oculomotor Nerves
Oculomotor Nuclei
MLF
Abducens Nuclei
Net Afferent Activity (Inhibition)
Net Afferent Activity (Excitation)
Medial Vestibular Nuclei
Horizontal SCC
Horizontal SCC

The net result is a vestibular-induced eye movement to the left.

For a rightward head rotation, the eyes should drift to the left in order to keep the object stable on the fovea.

Since the semicircular canals are coplanar, the mirror image occurs on the contralateral side.

The same rightward head rotation leads to inhibition of the left lateral semicircular canal, resulting in inhibition of the left medial rectus and right lateral rectus.

it is important to recall that for any head movement one side is being excited, while the other is being inhibited.

Although excitation is stronger than inhibition, the inhibitory contribution from the contralateral side accounts for why patients with loss of vestibular function on one side can still generate a VOR response to some slower head rotations ipsilateral to their lesioned side.

This same push-pull pathway also exists for the vertical canals, with their neural projections ending on extraocular muscles that align with the vertical canals that are being stimulated or inhibited during the head rotation.