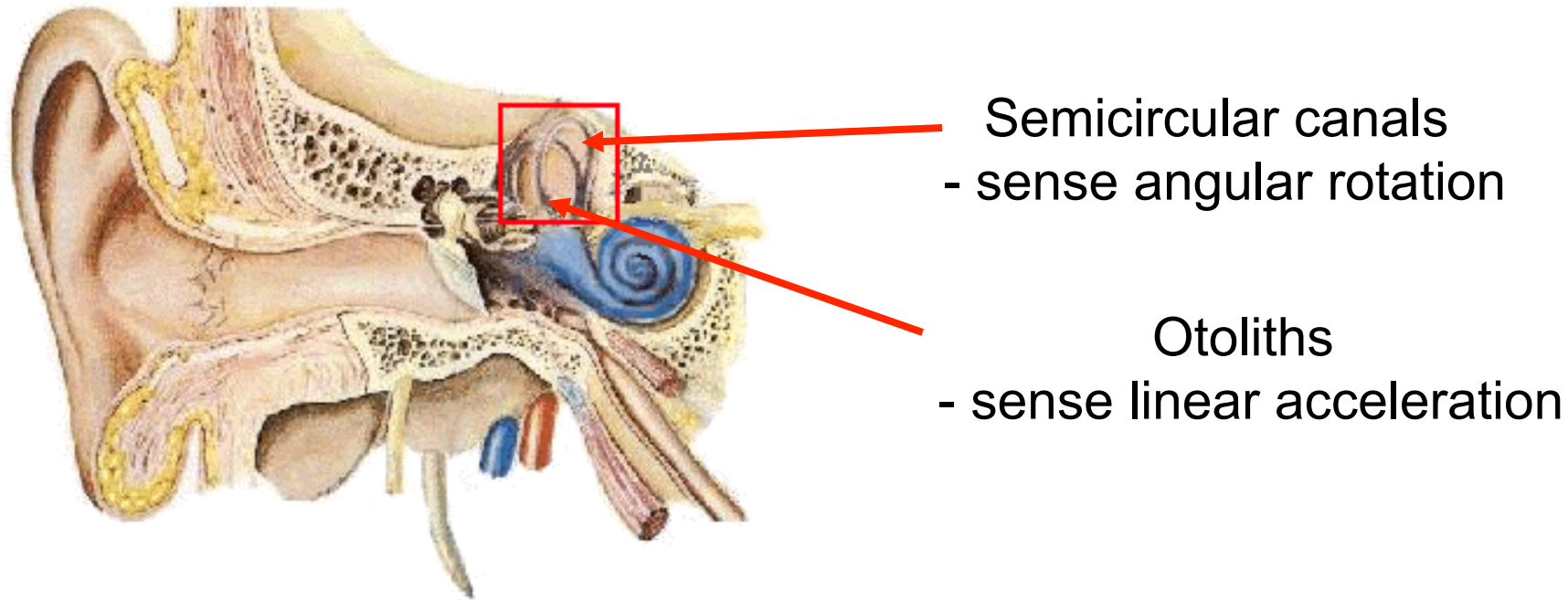


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# Non-linear sensory-motor transformations

Kathleen E. Cullen, Dept of Physiology, McGill University

# Function of the Vestibular System

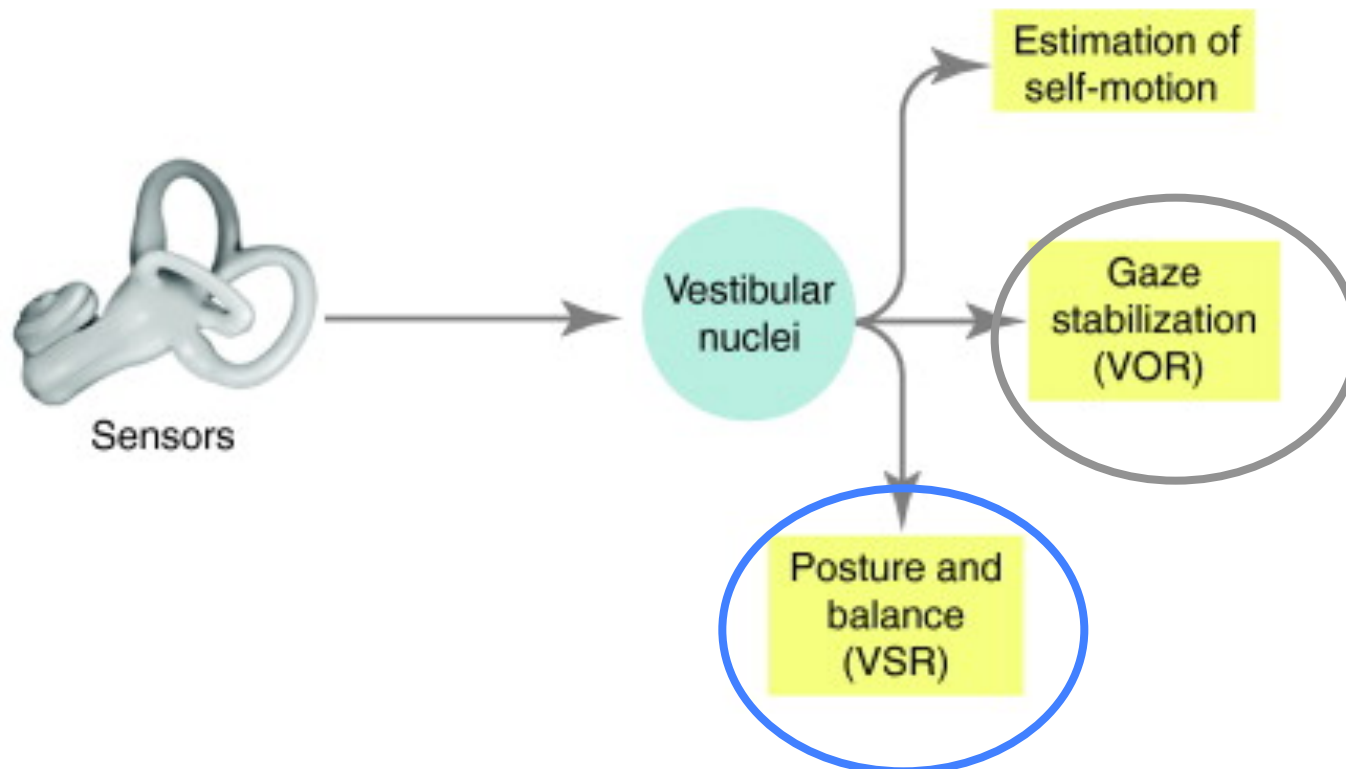


Provide information about head motion relative to space and gravity to:

- 1) Stabilize the visual axis (VOR)
- 2) Maintain head and body posture (VCR and vestibulospinal reflexes)
- 3) Compute spatial orientation or 'sense of balance'
- 4) Navigation

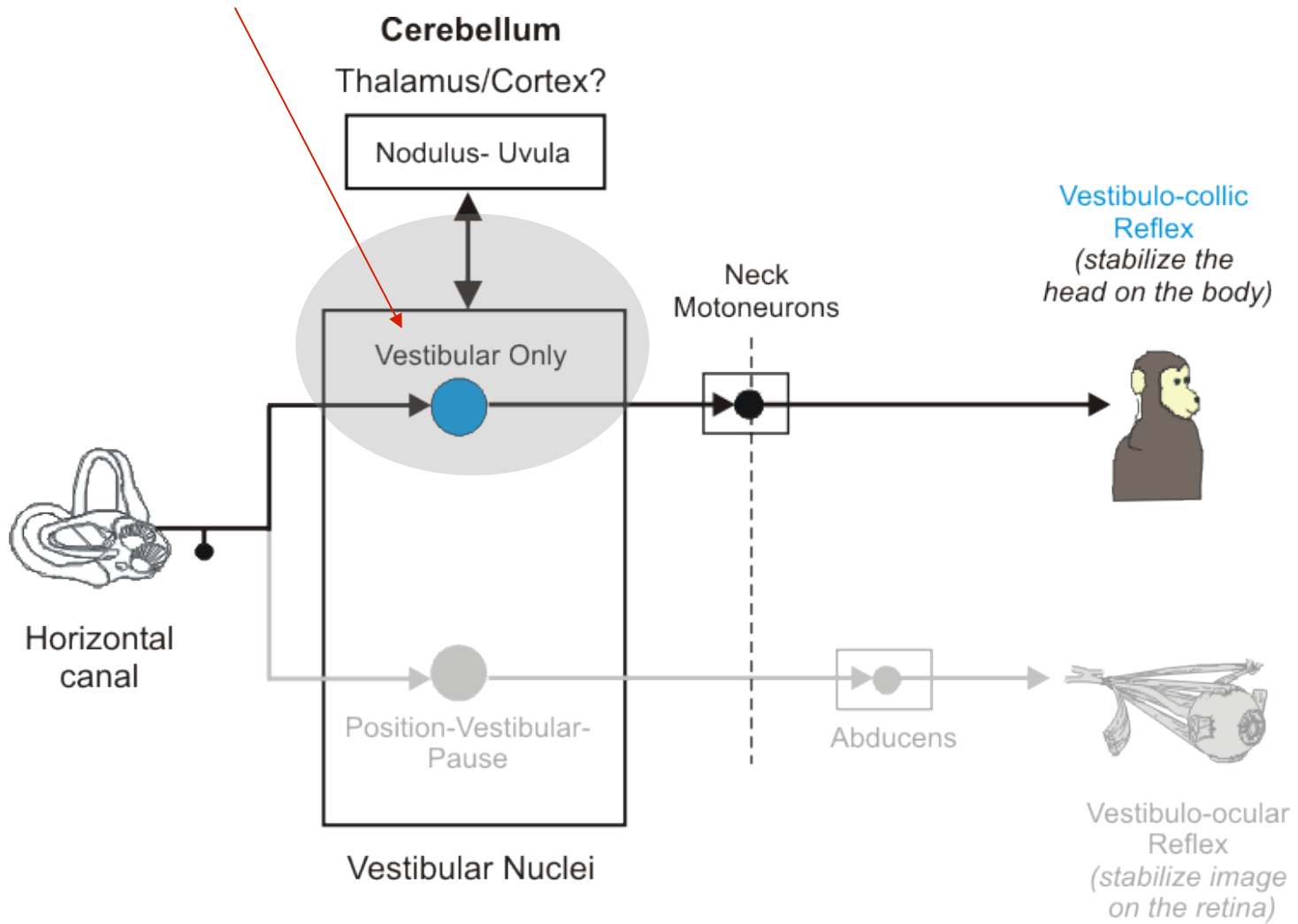
# Function of the Vestibular System

- i. The VOR,
- ii. Posture and balance, and
- iii. Higher order vestibular processing



# Function of the Vestibular System

- i. The VOR,
- ii. Posture and balance, and
- iii. Higher order vestibular processing





# Overview

Understanding how sensory pathways transmit information under natural conditions remains a major goal in neuroscience.

The vestibular system plays a vital role in everyday life, contributing to a wide range of functions from reflexes to the highest levels of perception and voluntary behavior.

Recent experiments have revealed that the sensorimotor transformations underlying postural control (i.e., via vestibulo-spinal reflexes) are characterized by significant and functionally significant non-linearities.

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# Sensorimotor transformations: Vestibulo-spinal Reflexes

## 1. Static Non-linearities

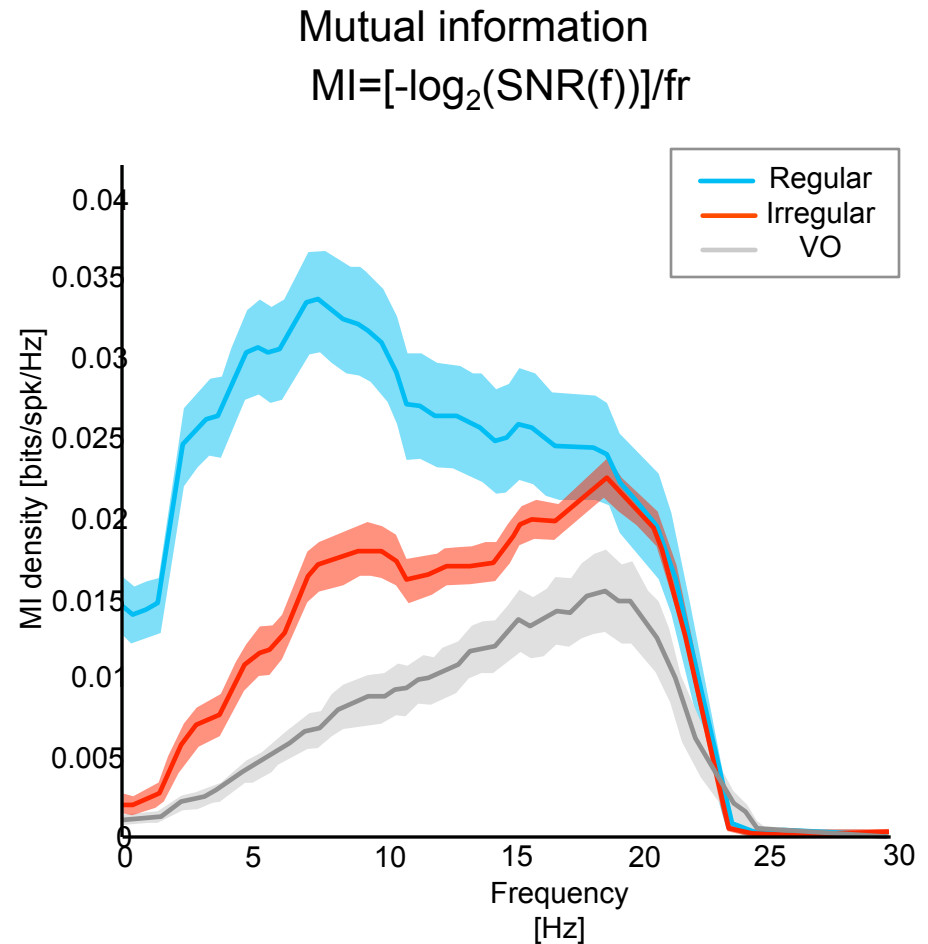
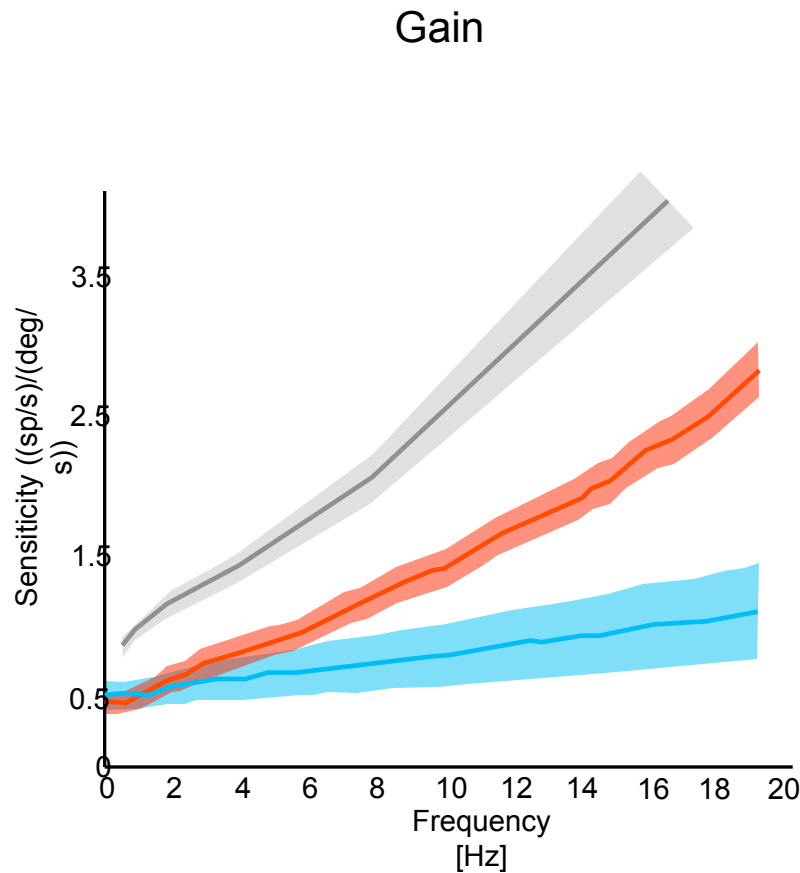
- Boosting non-linearity in central vestibular neurons
- Gain fields in the vestibulo-cerebellum

## 2. Dynamic Non-linearities

- Suppression of Reafference and common strategies across systems
- Learning in vestibulo-spinal reflex pathways

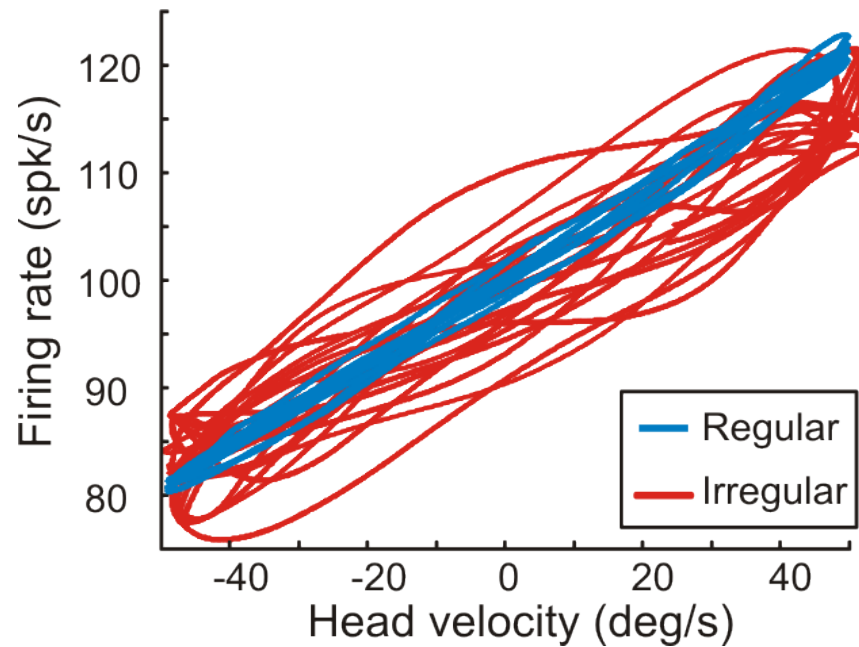
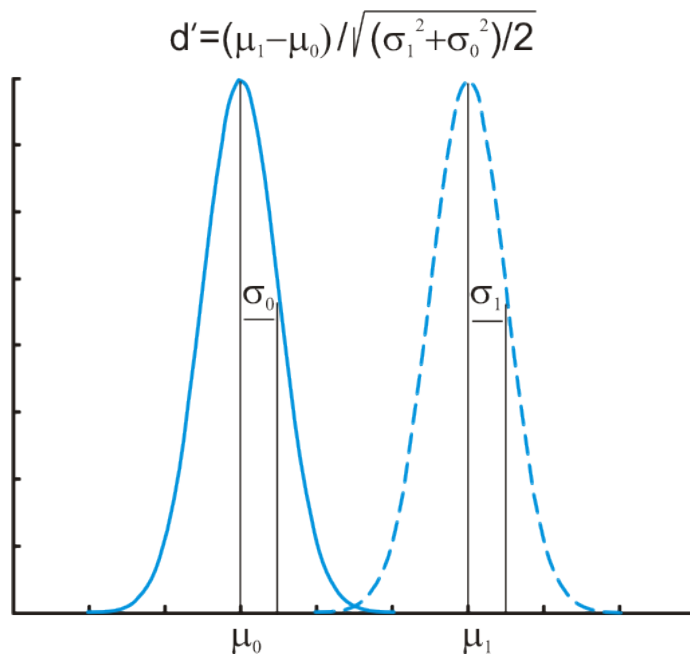
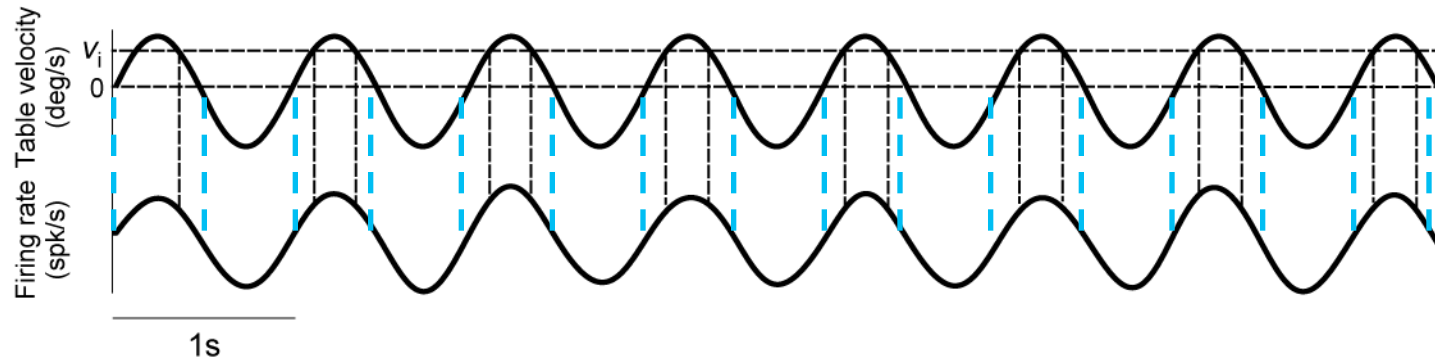
# Recall from the last lecture:

## Estimation of Gain versus Mutual Information

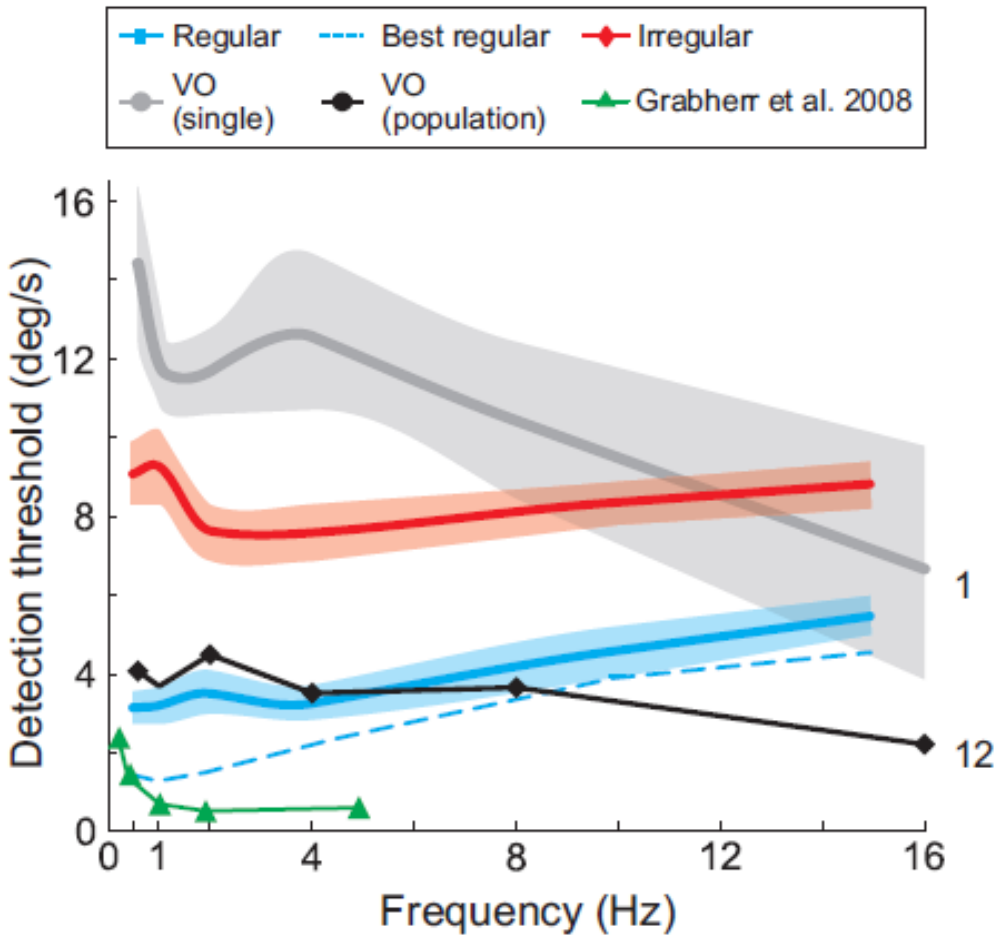
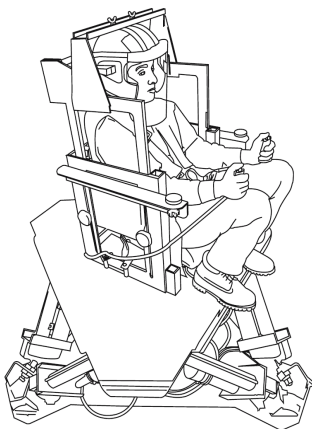


Central cells are tuned for higher frequencies,  
but encode less information than afferents.....

# Detection thresholds



# Comparison of Detection Thresholds



## Behavioral Thresholds:

Grabherr et al, 2008: ~ 0.5 -1deg/s  
Benson 1989: ~1deg/s

Thus:

So far these results suggest that the detailed time course of vestibular stimuli encoded by canal afferents during rotations is not transmitted by central neurons.

Furthermore

- At first pass, our results suggest that higher vestibular pathways must integrate information from large ( $>20$ ) central vestibular neuron populations in order to give rise to behaviorally observed detection thresholds.

- Notably, we assessed the quality of linear stimulus reconstruction by computing the coding fraction (Gabbiani, 1996; Rieke et al., 1996).

This raises the question: Is the assumption of linearity valid?

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# Sensorimotor transformations: Vestibulo-spinal Reflexes

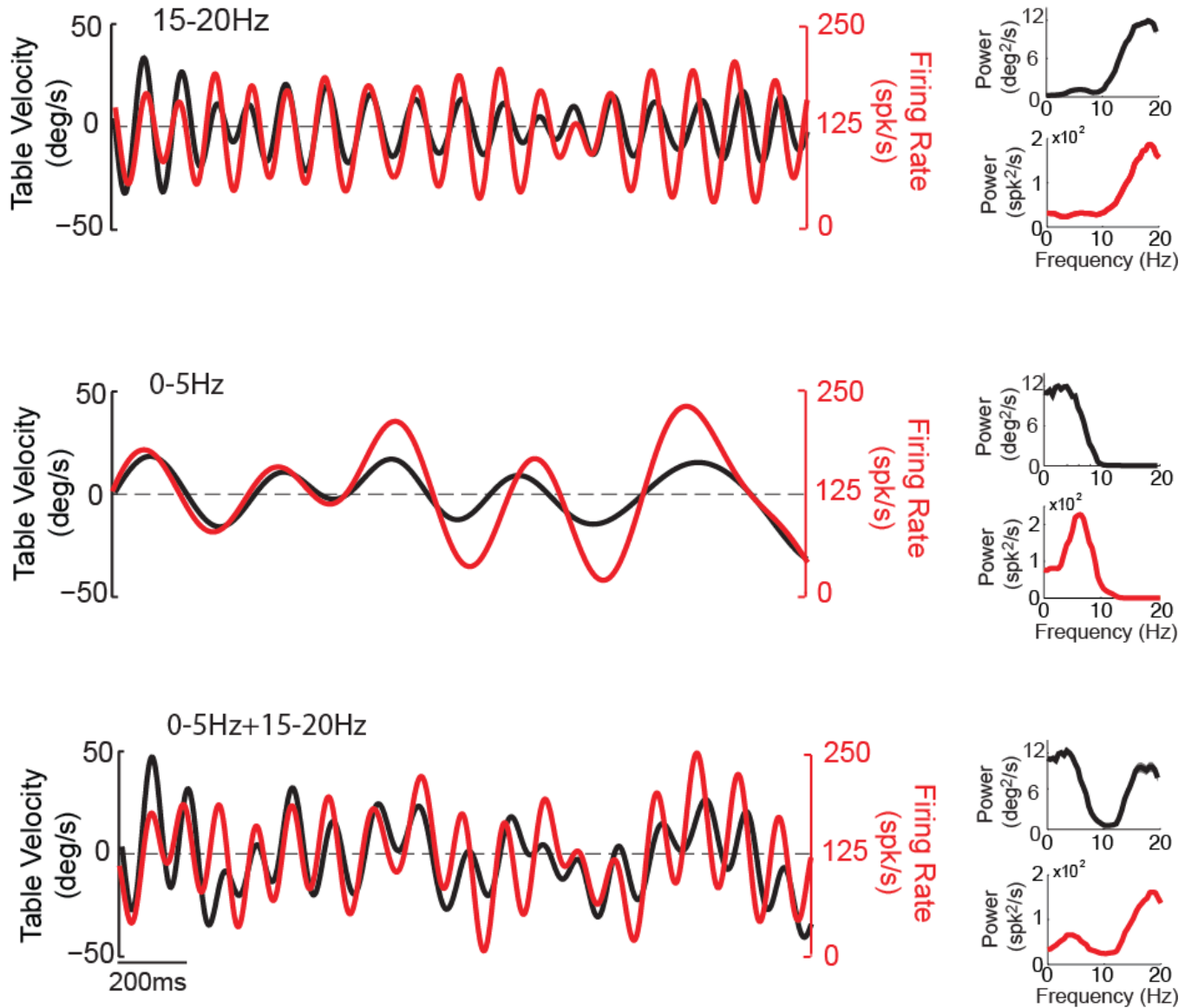
## 1. Static Non-linearities

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- Gain fields in the cerebellum

## 2. Dynamic Non-linearities

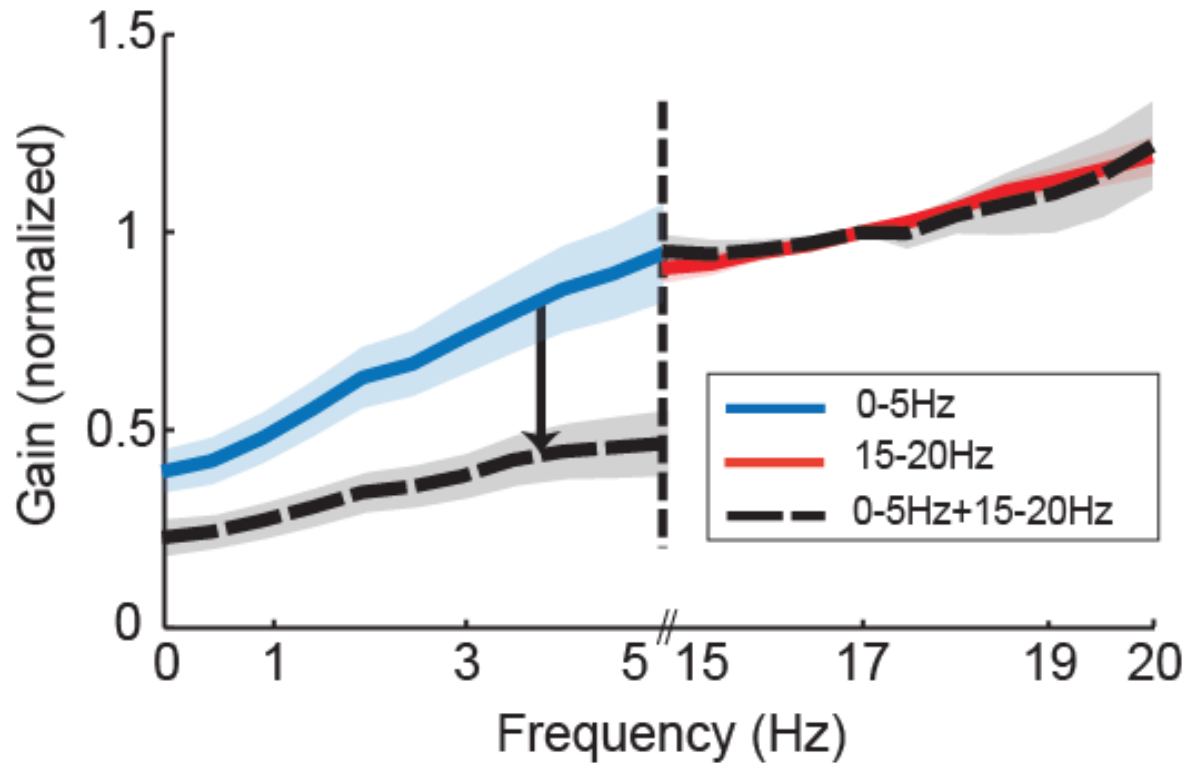
- Suppression of Reafference and common strategies across systems
- Learning in vestibulo-spinal reflex pathways

# Experiment: High pass, Low Pass, and Summed Noise

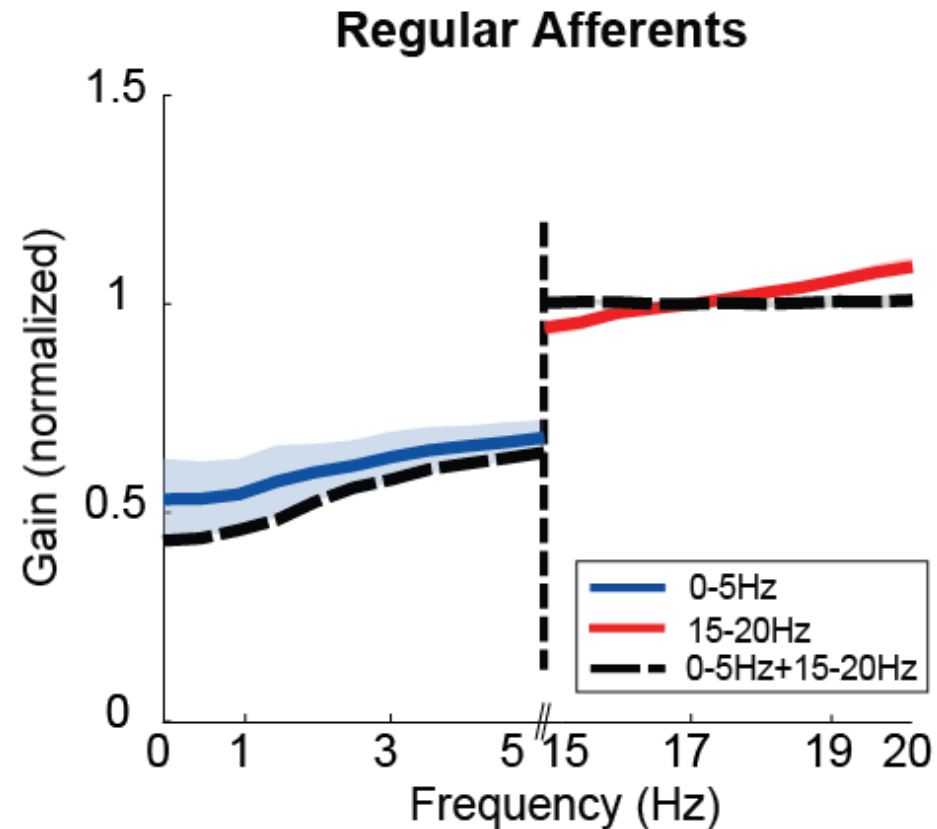
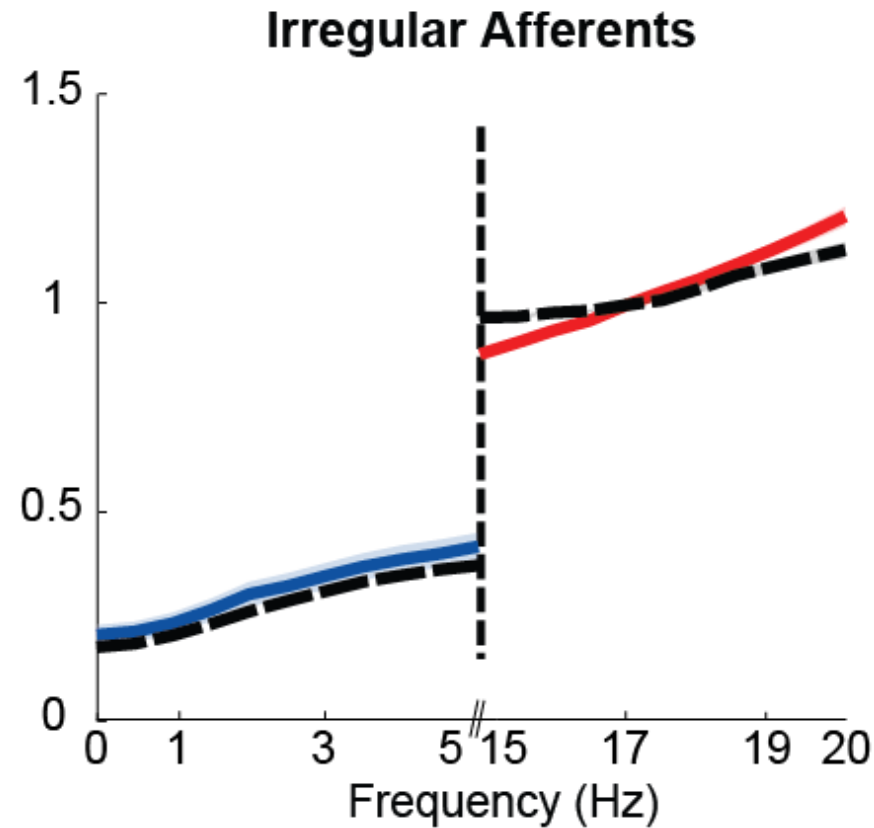


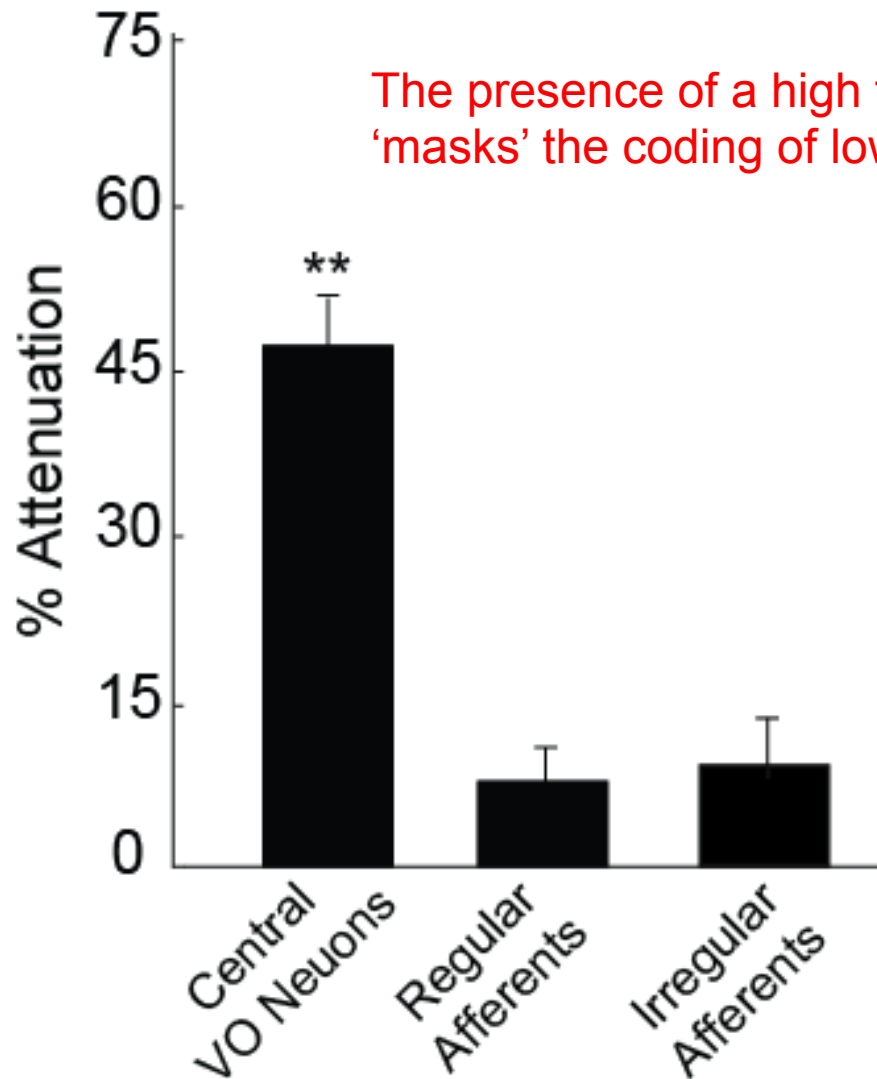


# Central vestibular neurons respond nonlinearly to sums of noise stimuli.



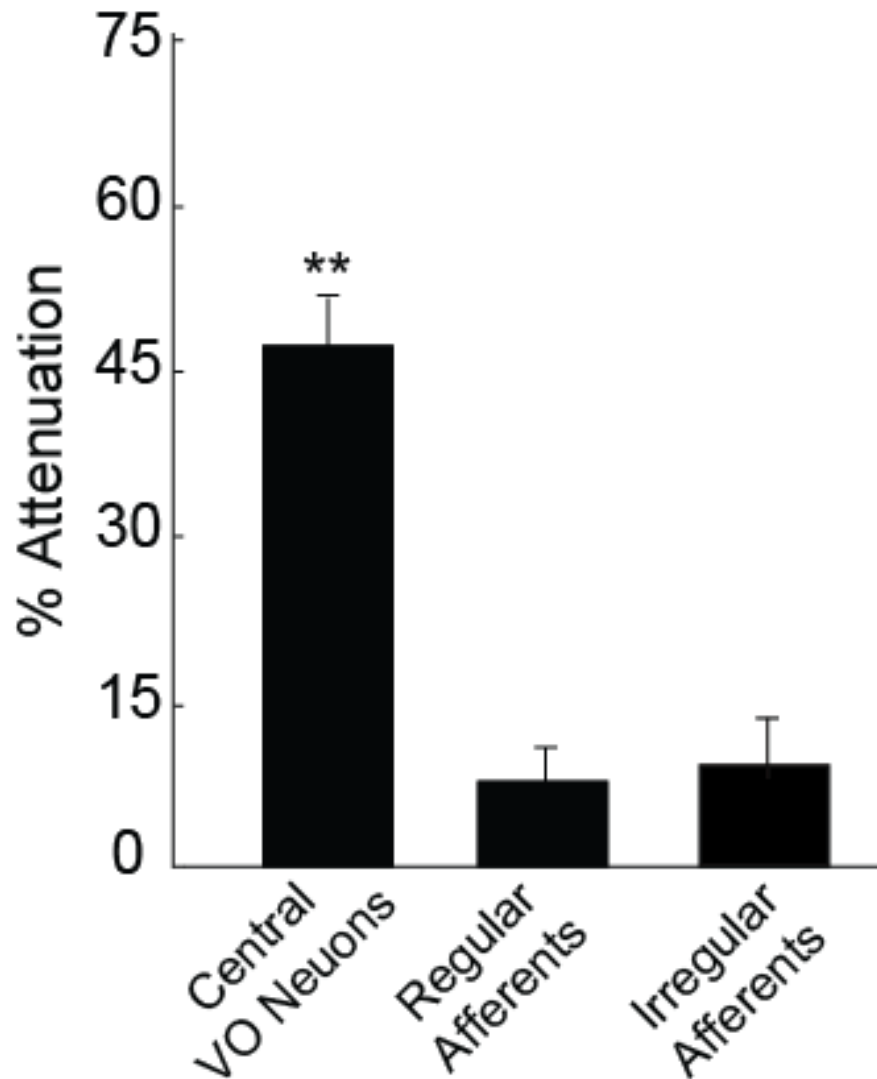
In contrast, their afferent inputs respond linearly to sums of noise stimuli.





The presence of a high frequency stimulus effectively 'masks' the coding of low frequency stimulus

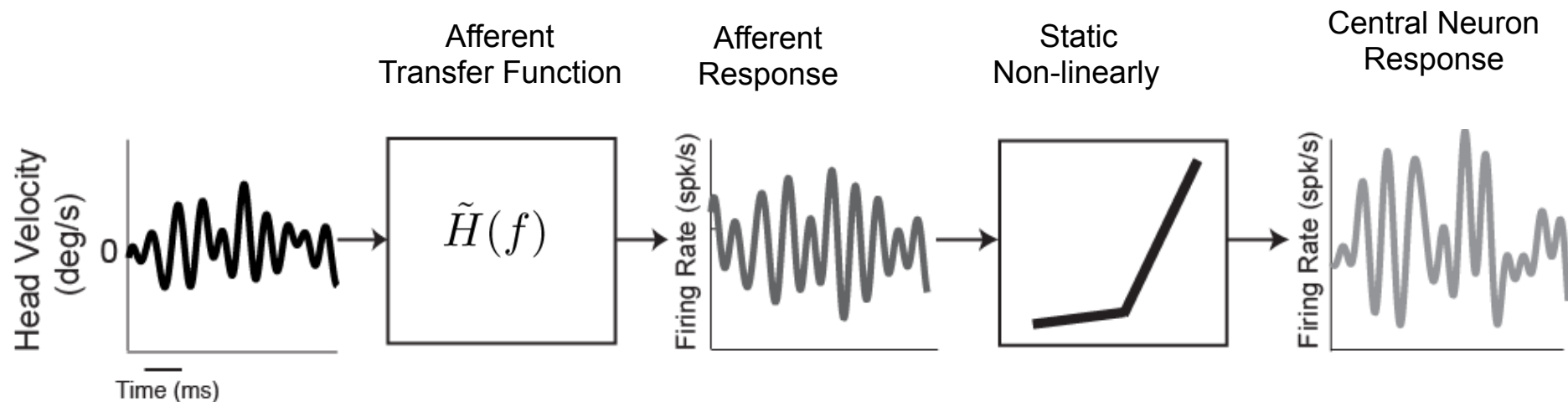
The central response nonlinearity is characterized by a strong (~50%) attenuation in neuronal sensitivity to low frequency stimuli when presented concurrently with high frequency stimuli.



A comparable attenuation in neuronal sensitivity to low frequency stimuli is observed for sums of **sinewaves** (3 Hz + 17 Hz) .

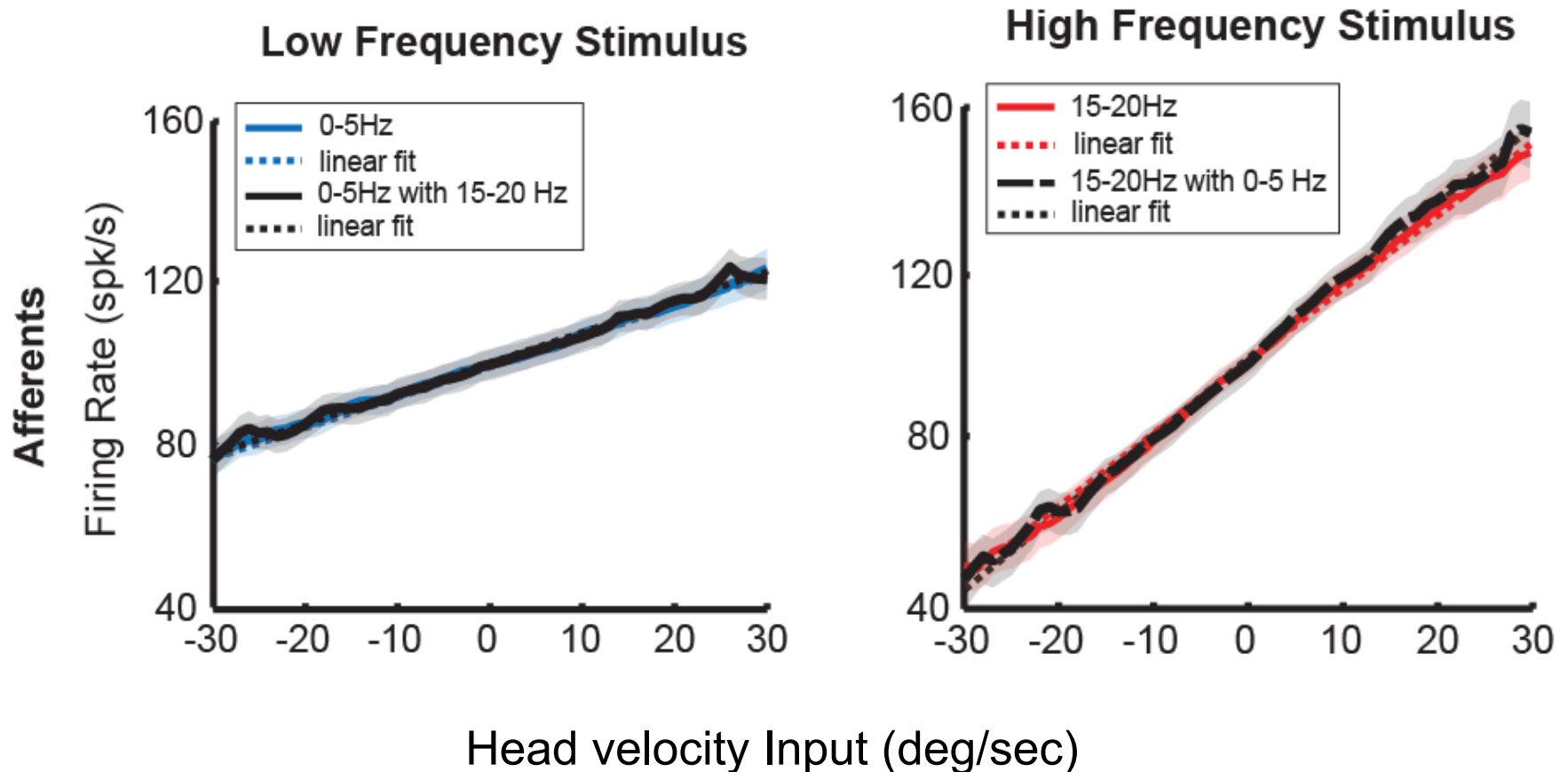
How do central vestibular neurons non-linearly  
Integrate their afferent input?

# How do central vestibular neurons non-linearly Integrate their afferent input?

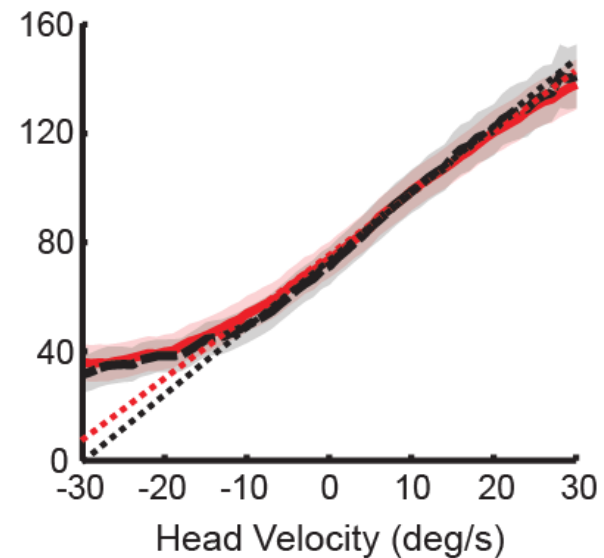
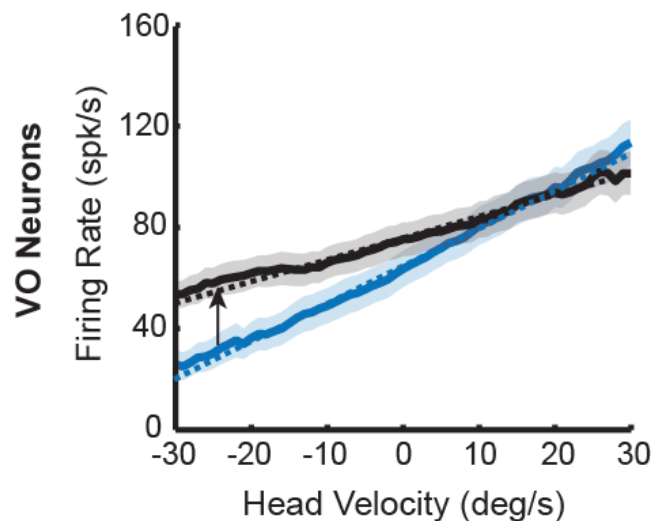
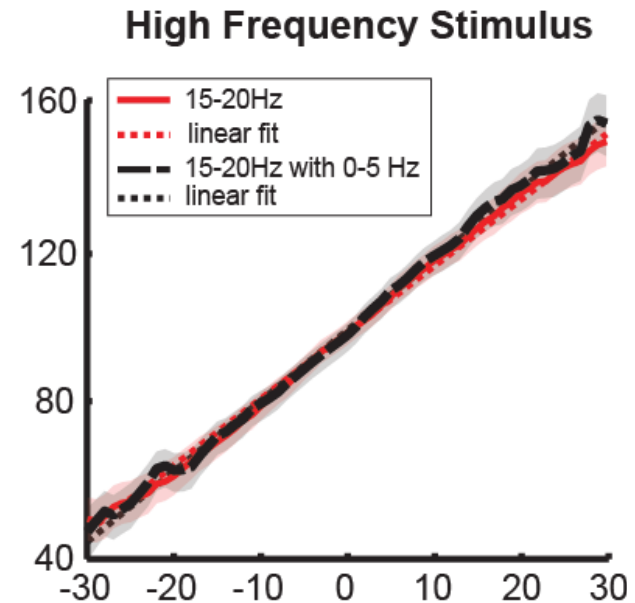
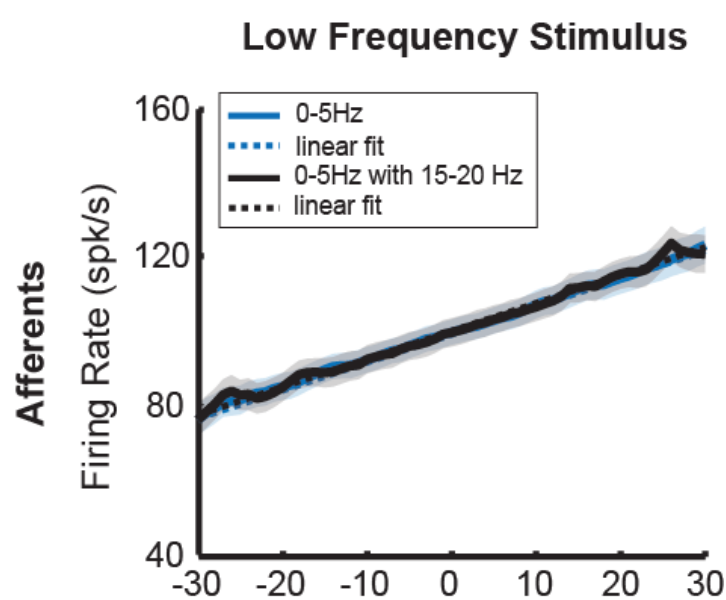


**Hypothesis:** A static non-linearity in the input-output relationship of central neurons accounts for attenuation of low frequency responses.

Afferents display a nonlinear relationship between input head velocity and output firing rate.

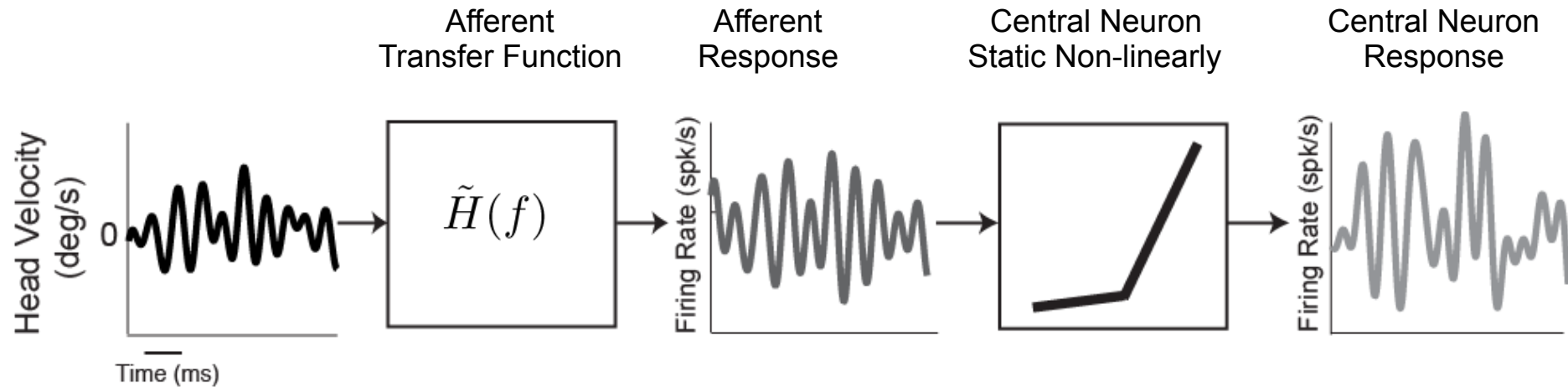


Central neurons display a nonlinear relationship between input head velocity and output firing rate.



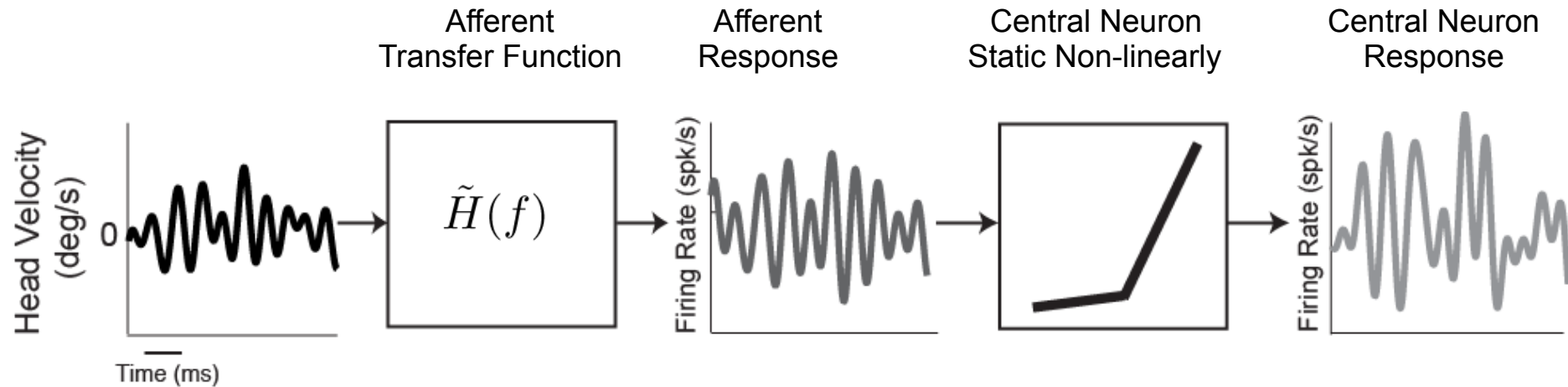


# How do central vestibular neurons non-linearly Integrate their afferent input?



**Hypothesis:** A static non-linearity in the input-output relationship of central neurons accounts for attenuation of low frequency responses.

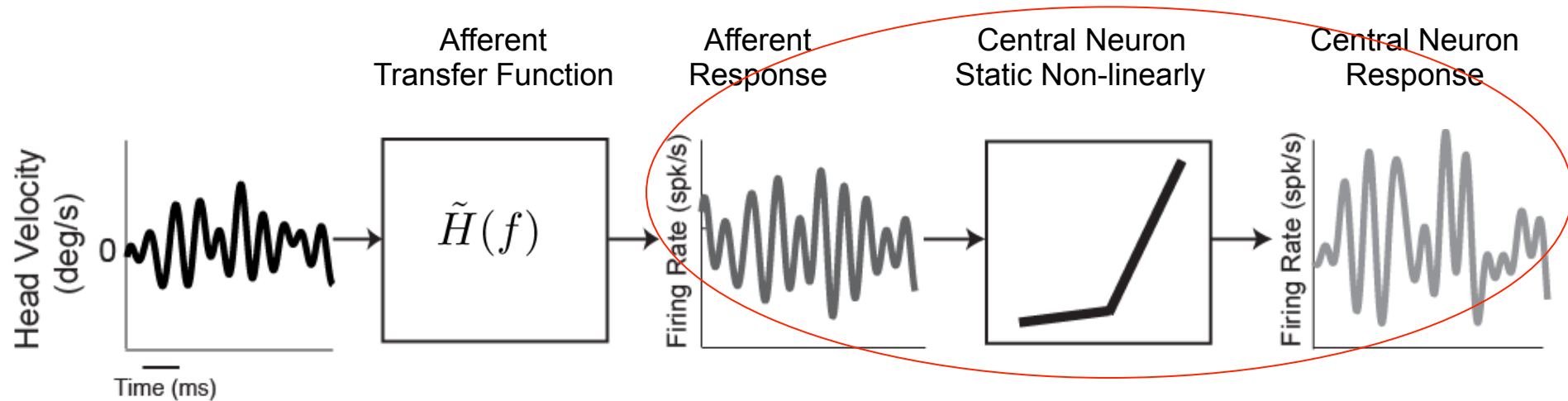
# How do central vestibular neurons non-linearly Integrate their afferent input?



We know the relationships between

- i) afferent firing rate and head velocity, and
- ii) central neuron firing rate and head velocity

# How do central vestibular neurons non-linearly Integrate their afferent input?



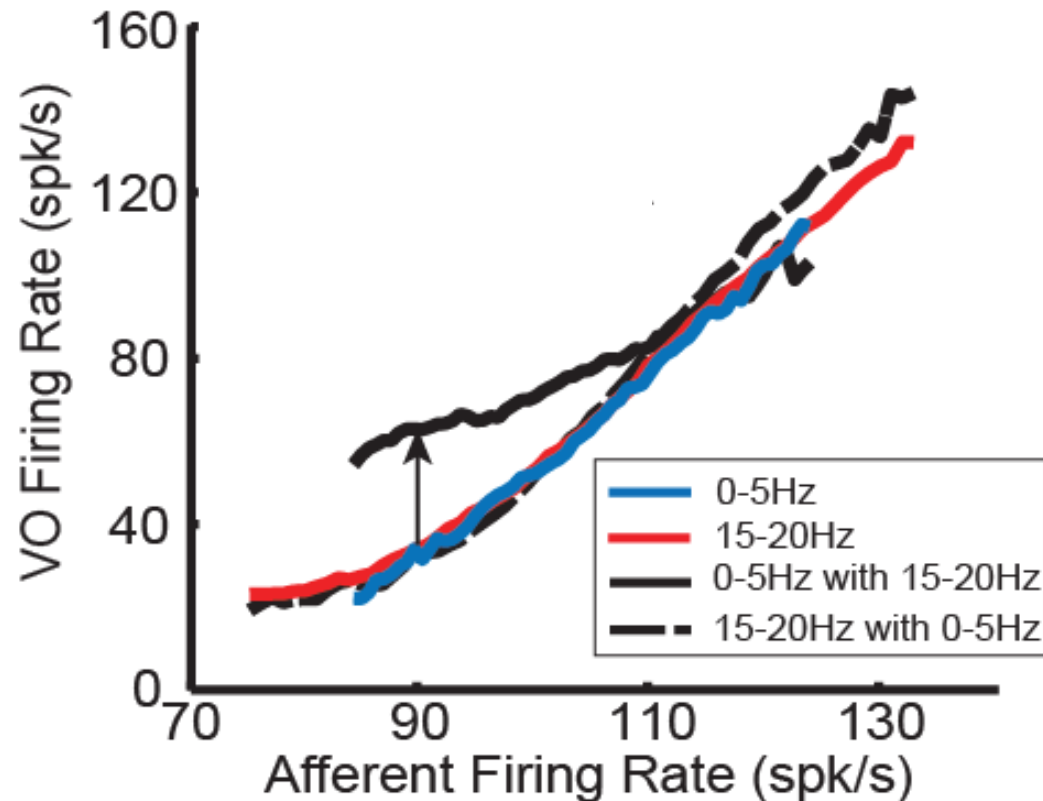
We know the relationships between

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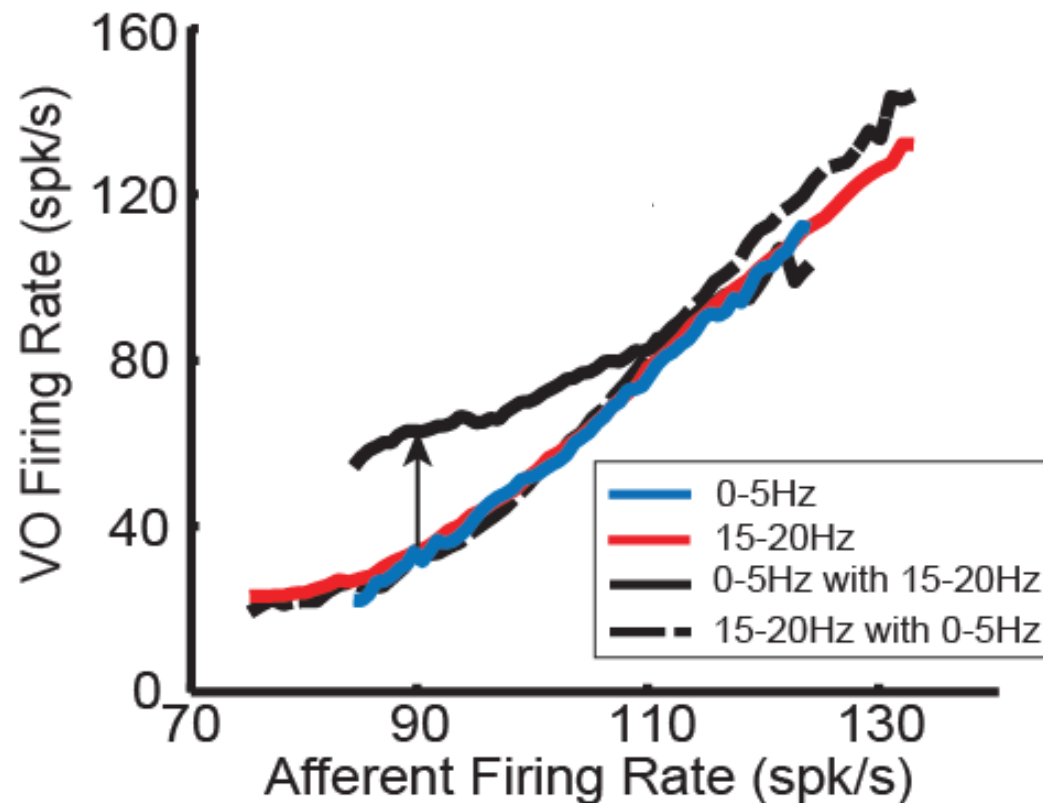
So, these relationships can be rescaled to plot the  
input-output relationship between:

afferent firing rate and central neuron firing rate

Central neurons display a static nonlinear relationship between their output firing rate and their afferent input.



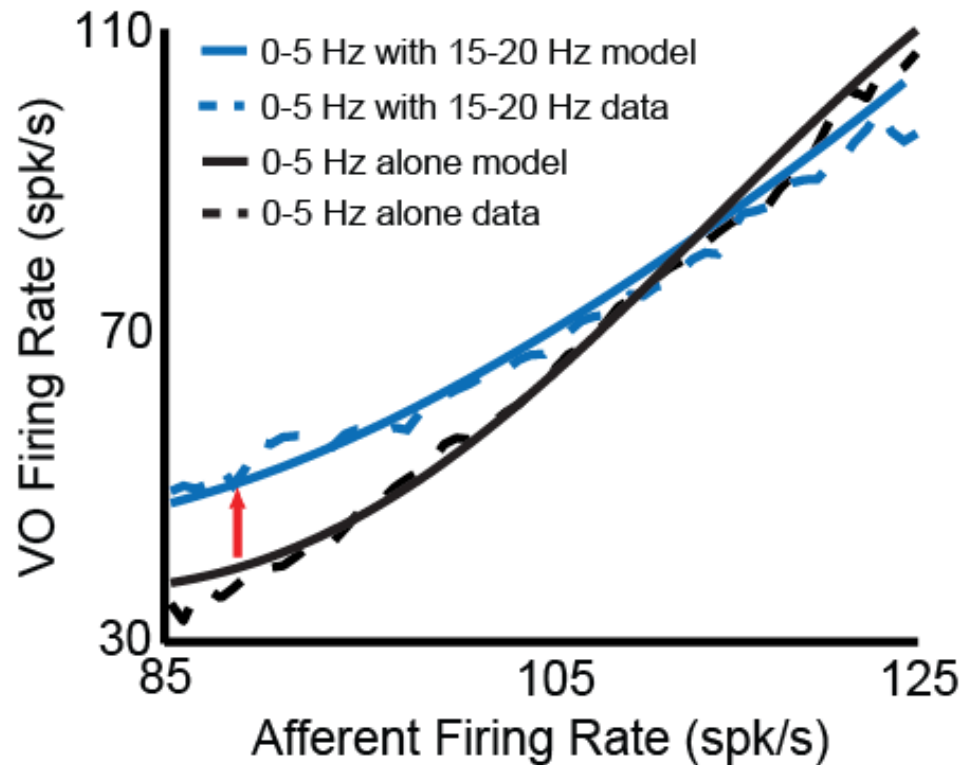
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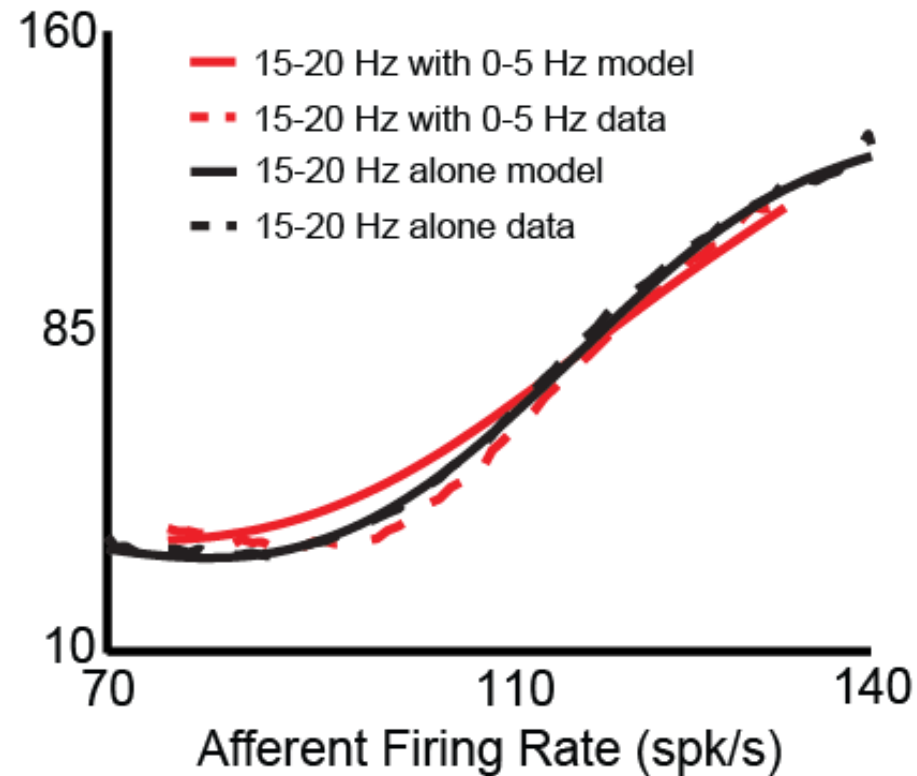
Note, curve obtained when low frequency is applied with high frequency has a lower slope. This occurs because the average central neuron firing rate is higher in this condition, than when the same stimulus is applied alone.

A simple model accurately predicts nonlinear central neuron responses to sums of low and high frequency stimuli

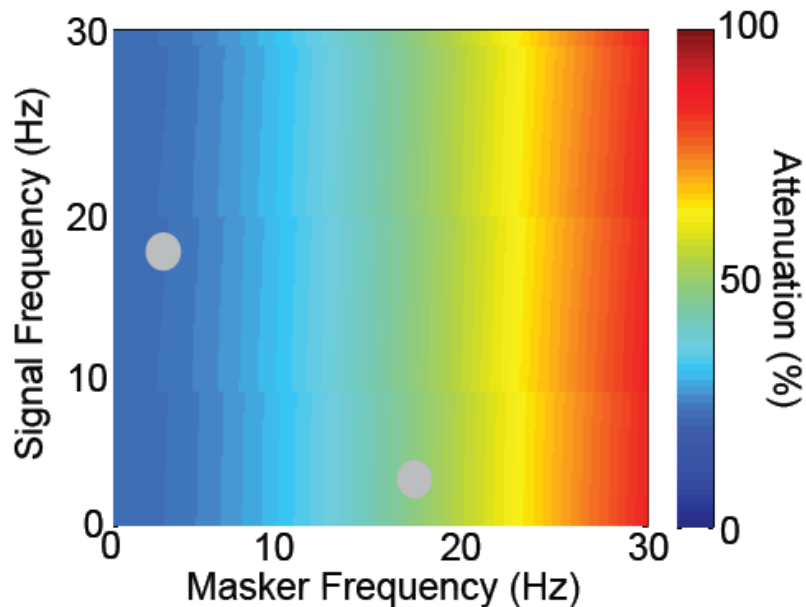
### Low Frequency Stimulus



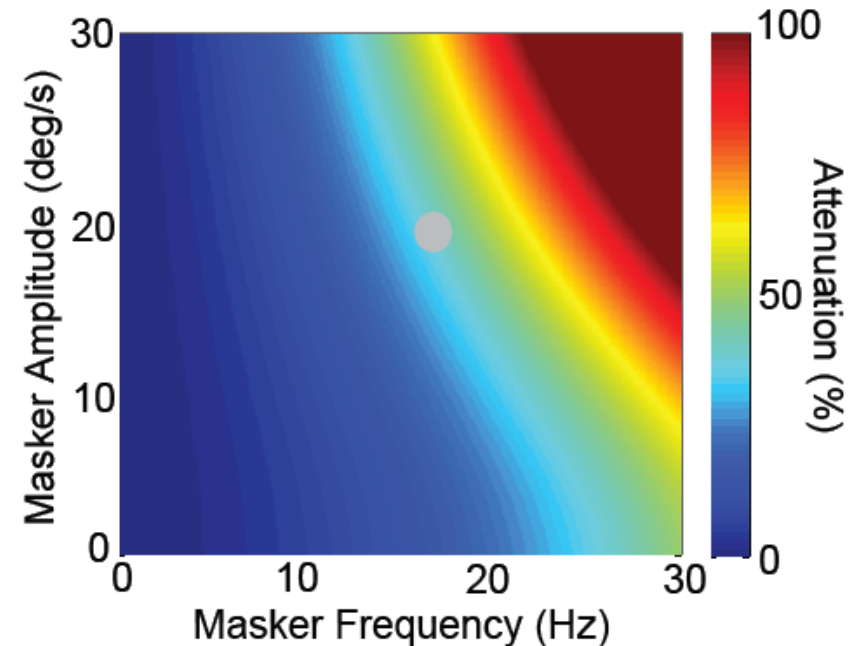
### High Frequency Stimulus



With this model, we can now predict the % gain for different stimuli



Higher frequency Maskers  
Produce greater Signal attenuation



Higher amplitude Maskers  
Also produce greater Signal attenuation

## Summary:

Thus the detailed time course of vestibular stimuli encoded by afferents during rotations is not transmitted by central neurons.

This raises the question: Is the assumption of linearity valid?



## Summary:

Thus the detailed time course of vestibular stimuli encoded by afferents during rotations is not transmitted by central neurons.

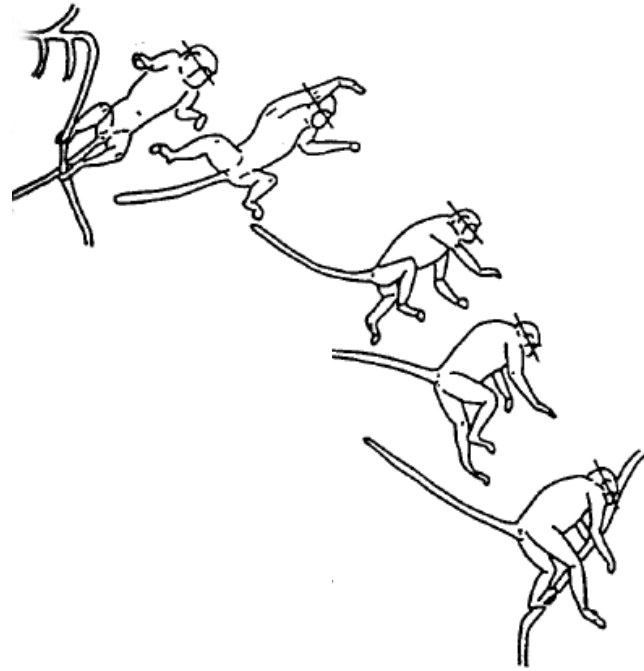
This raises the question: Is the assumption of linearity valid?

- Indeed it is not: We discovered a static boosting nonlinearity in the input-output relationship of central vestibular neurons accounts for this unexpected result.
- Notably, this nonlinear integration of afferent effectively extends the coding range of central neurons, and enables them to better extract the high frequency features of self-motion when embedded with low frequency motion during natural movements.

# Functional Role of Central Vestibular Neurons

These neurons initiate vestibulo-spinal postural reflexes.

Stabilize posture during unexpected transient disturbances, or when falling, or locomotion on uneven surfaces.



These same neurons also likely transmit self-motion information to higher level areas that contributes to perception during everyday activities

Note, however that self motion can be self-produced as well as externally applied....

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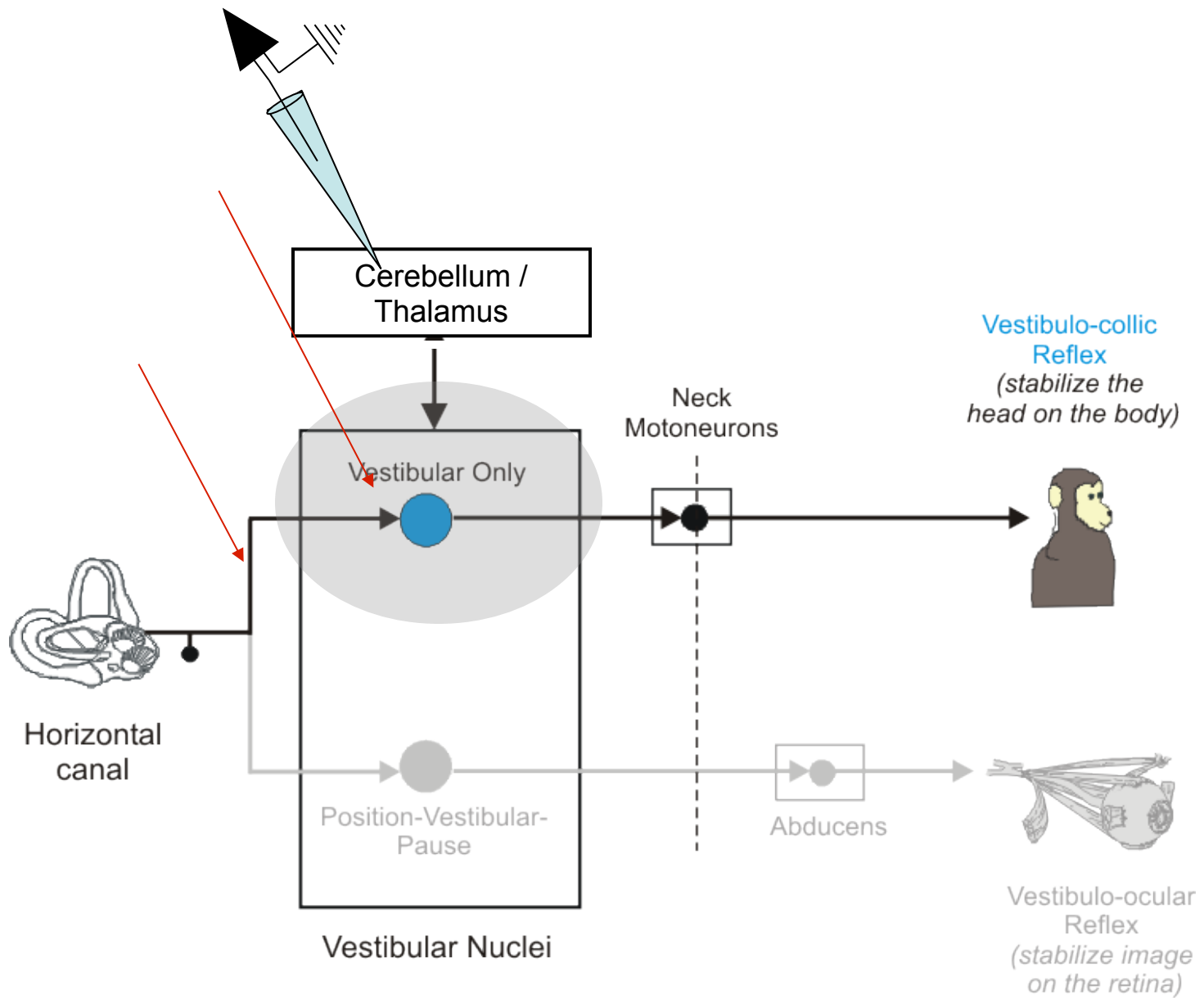
# Sensorimotor transformations: Vestibulo-spinal Reflexes

## 1. Static Non-linearities

- Boosting non-linearity in central vestibular neurons
- Gain fields in the vestibulo-cerebellum

## 2. Dynamic Non-linearities

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- Learning in vestibulo-spinal reflex pathways



## Vestibular Cerebellum:

Nonlinear processing of vestibular and proprioceptive signals underlies the accurate computation of body motion



Question:

What information does the brain need to keep track of for you to keep your balance?

During passive self-motion,

Head and body motion are encoded in two distinct channels by the output neurons of the vestibular cerebellum

Unimodal neurons

- respond to vestibular stimulation
- encode head motion

Bimodal neurons

- respond to vestibular and proprioceptive stimulation
- encode passive body motion

# Example Vestibulo-Cerebellar Neuron

## Vestibular-only cell (Unimodal)

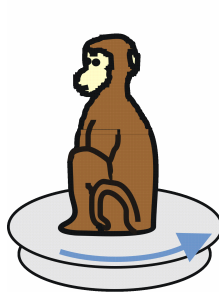
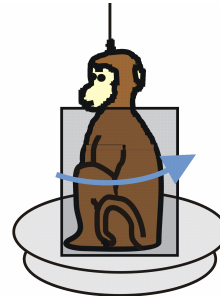
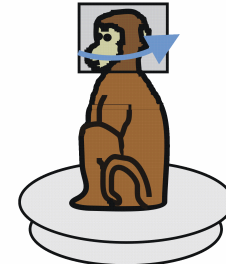


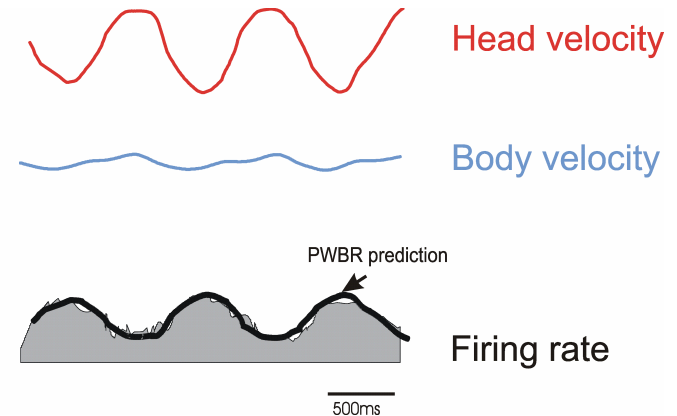
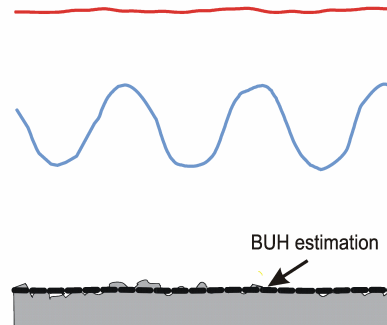
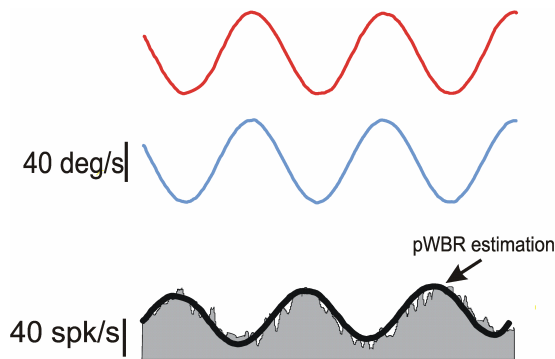
Table rotation



Body-under-head rotation

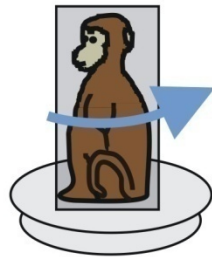


Passive Head-on-body

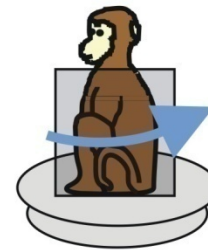
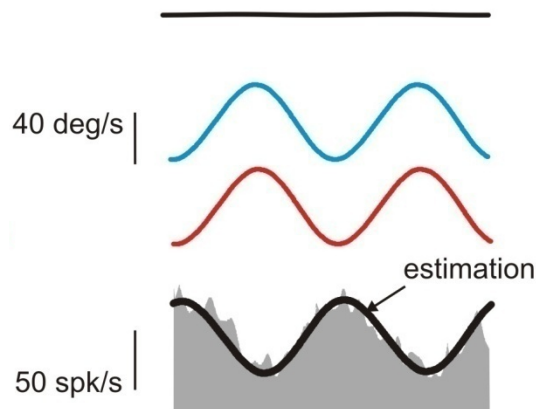


# Example Vestibulo-Cerebellar Neuron

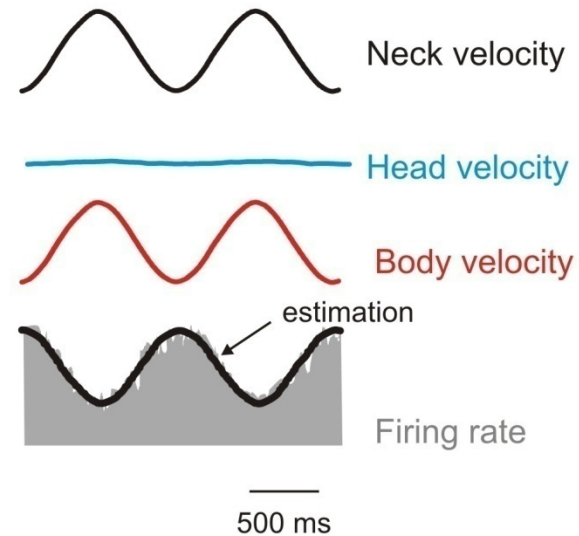
## Vestibular+neck cell (Bimodal)



**Whole- body-  
rotation**

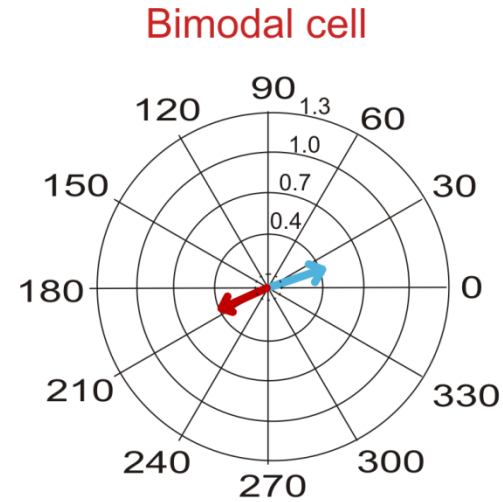
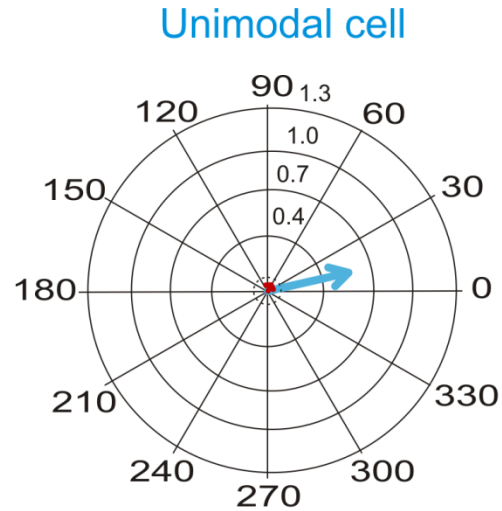


**Body-under-  
head rotation**

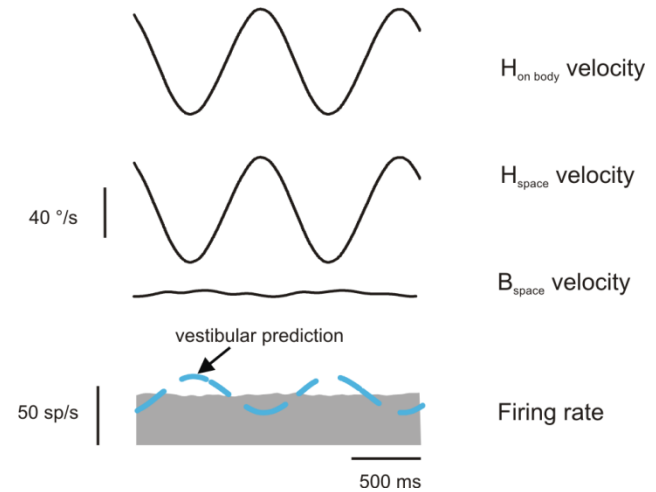
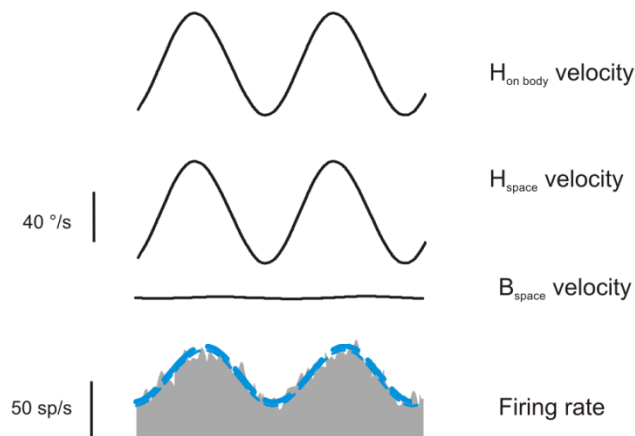
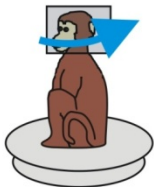




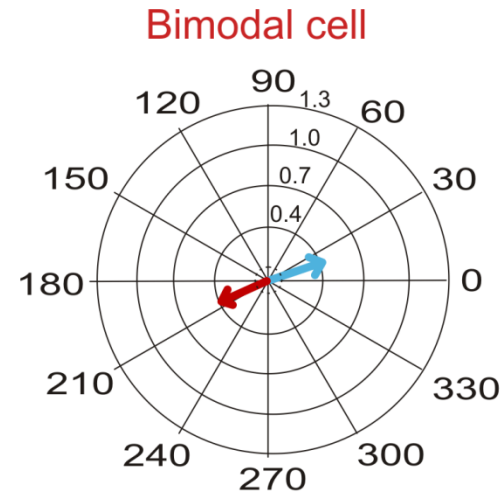
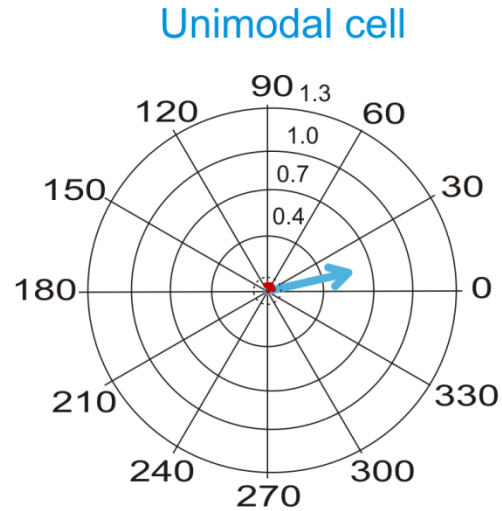
# Vestibular and neck inputs sum linearly



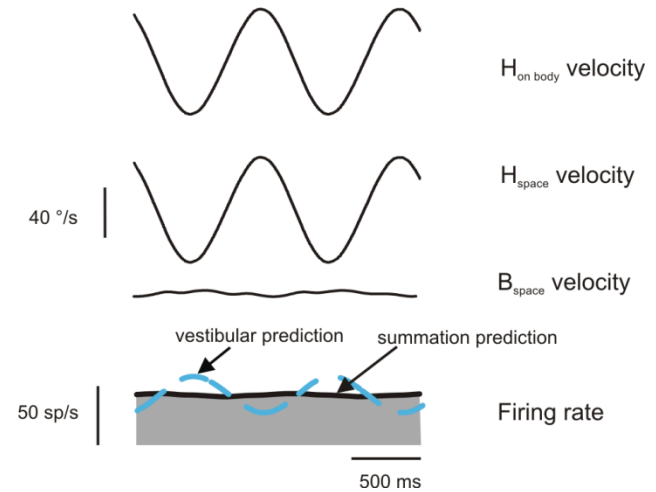
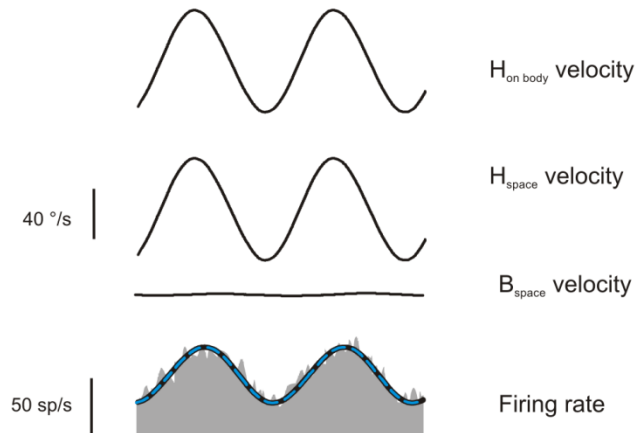
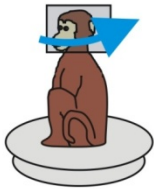
Head-on-body rotation



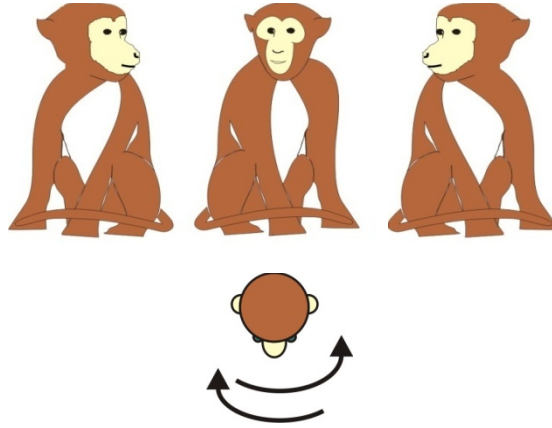
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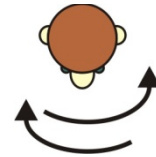
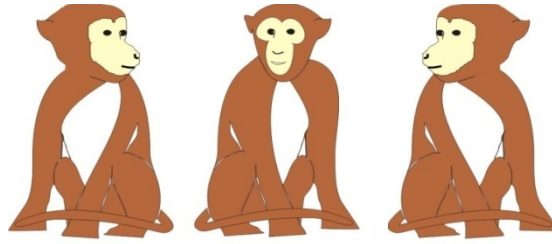
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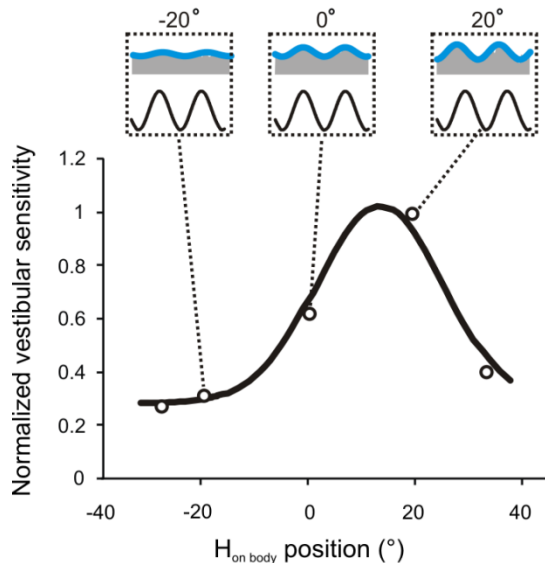
The vestibular responses of bimodal neurons depend on head-on-body position



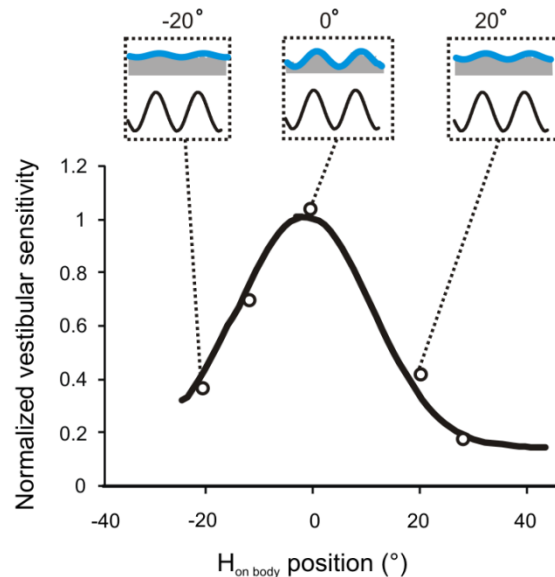
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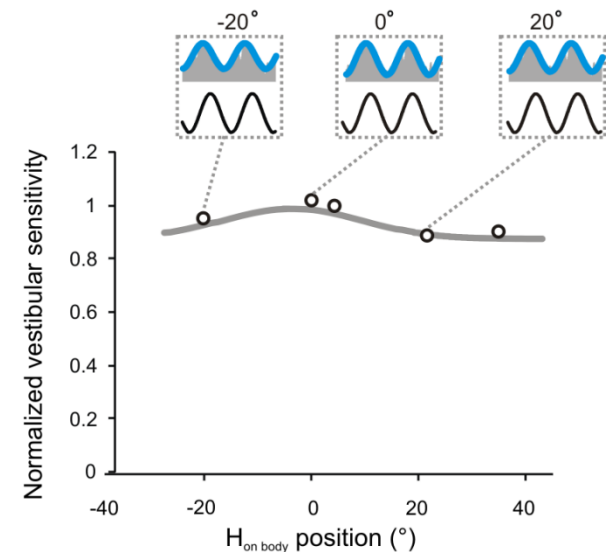
Bimodal neuron 1  
whole-body rotation



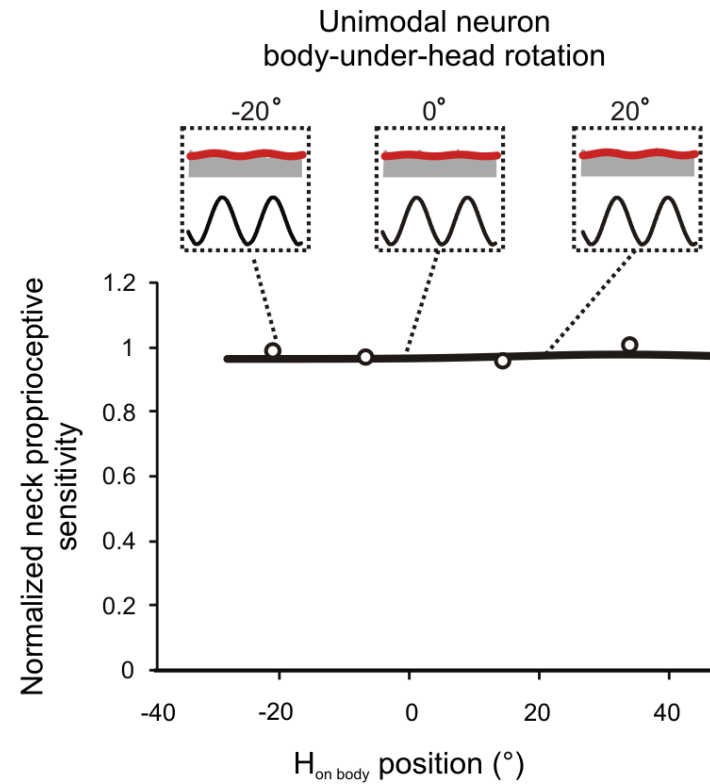
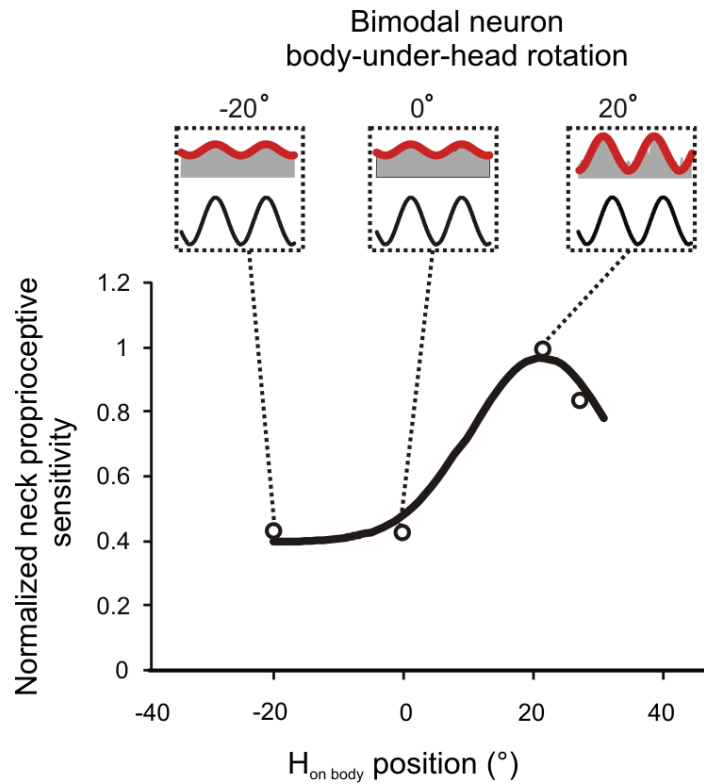
Bimodal neuron 2  
whole-body rotation



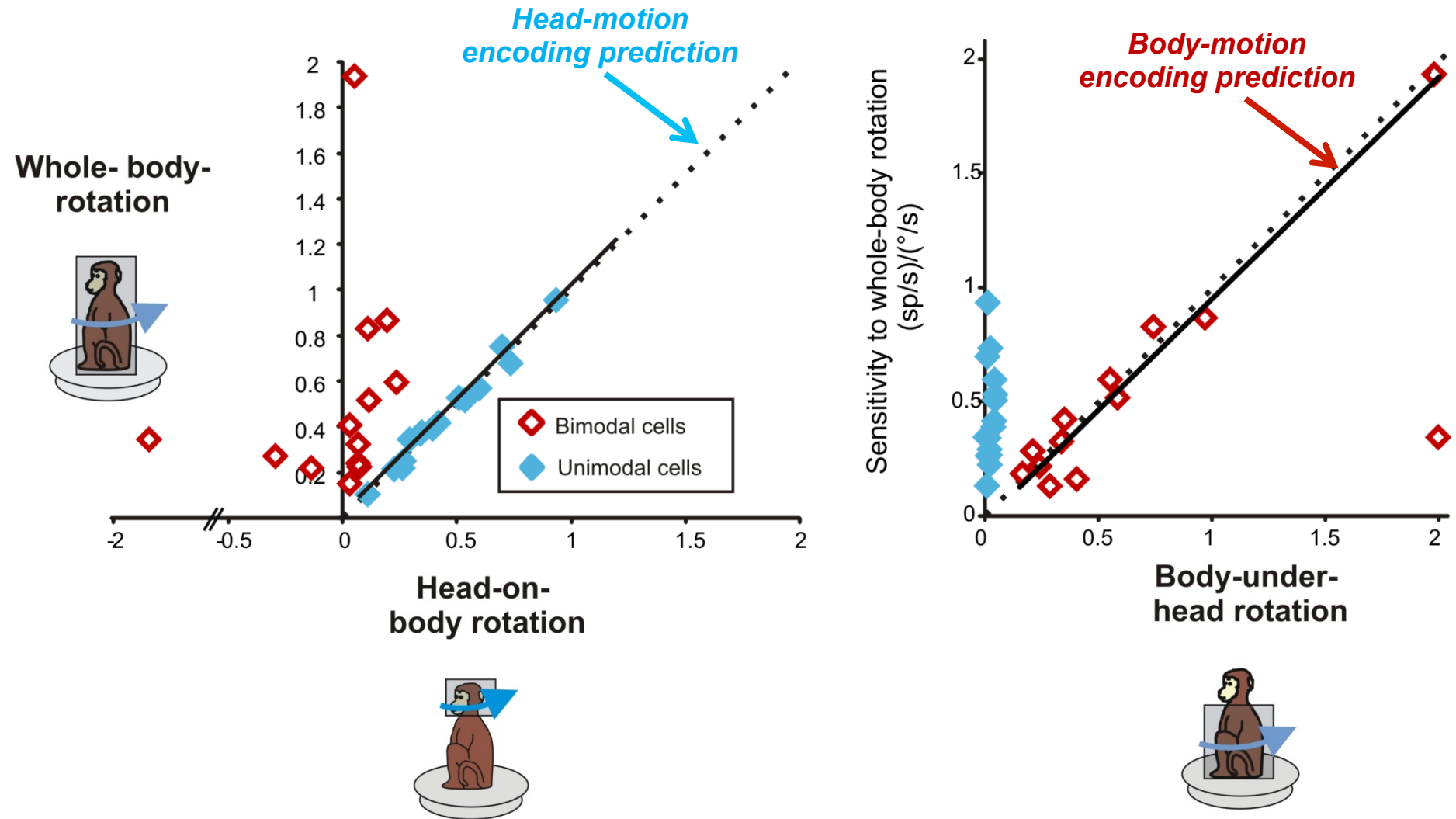
Unimodal neuron  
whole-body rotation



# The neck proprioceptive responses of bimodal neurons also depend on head-on-body position



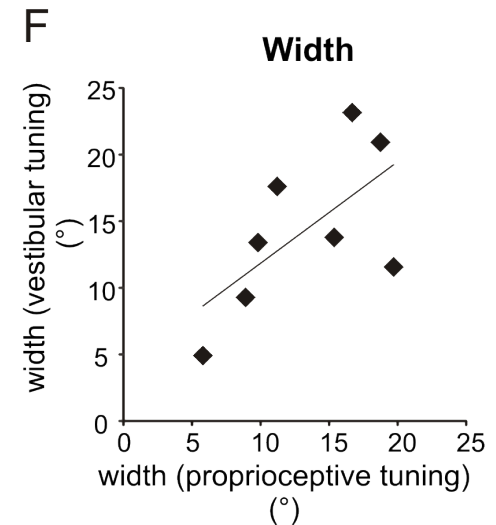
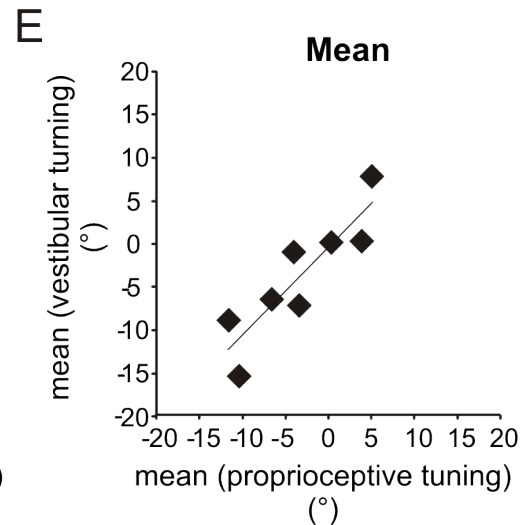
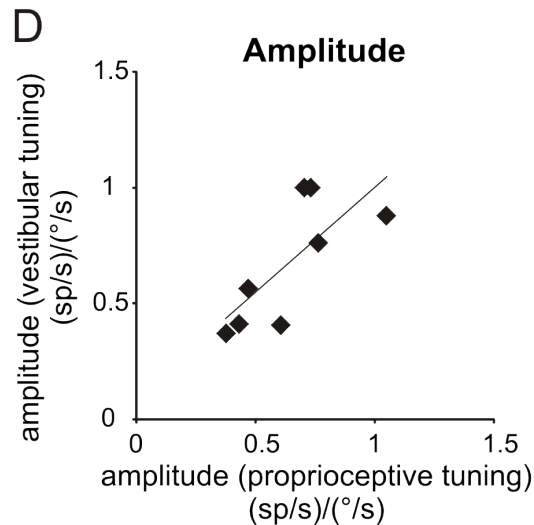
# Bimodal neurons encode body motion, and unimodal neurons encode head motion



# Neuronal representations of head versus body motion in the primate cerebellum

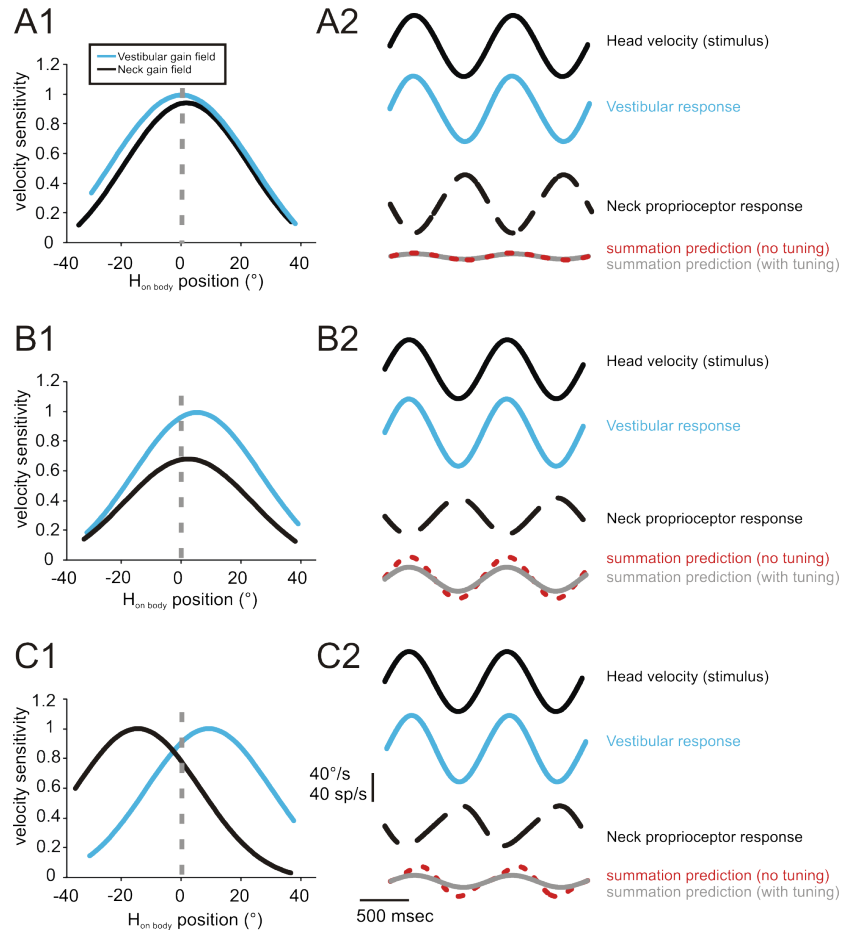
- Head motion is detected by the vestibular sensors
- No sensor directly encodes motion of the body in space
- However, humans can detect movement of the body and the head separately even in darkness (Mergner et al 1981) .
- Body motion perception is thought to be a result the convergence of vestibular and neck proprioception signals
  - 1) Head motion encoded by VN neurons and unimodal cerebellar neurons
  - 2) Body motion encoded by bimodal cerebellar neurons

Comparison of the proprioceptive and vestibular responses of bimodal neurons further reveals similar tuning in response to changes in head-on-body position.





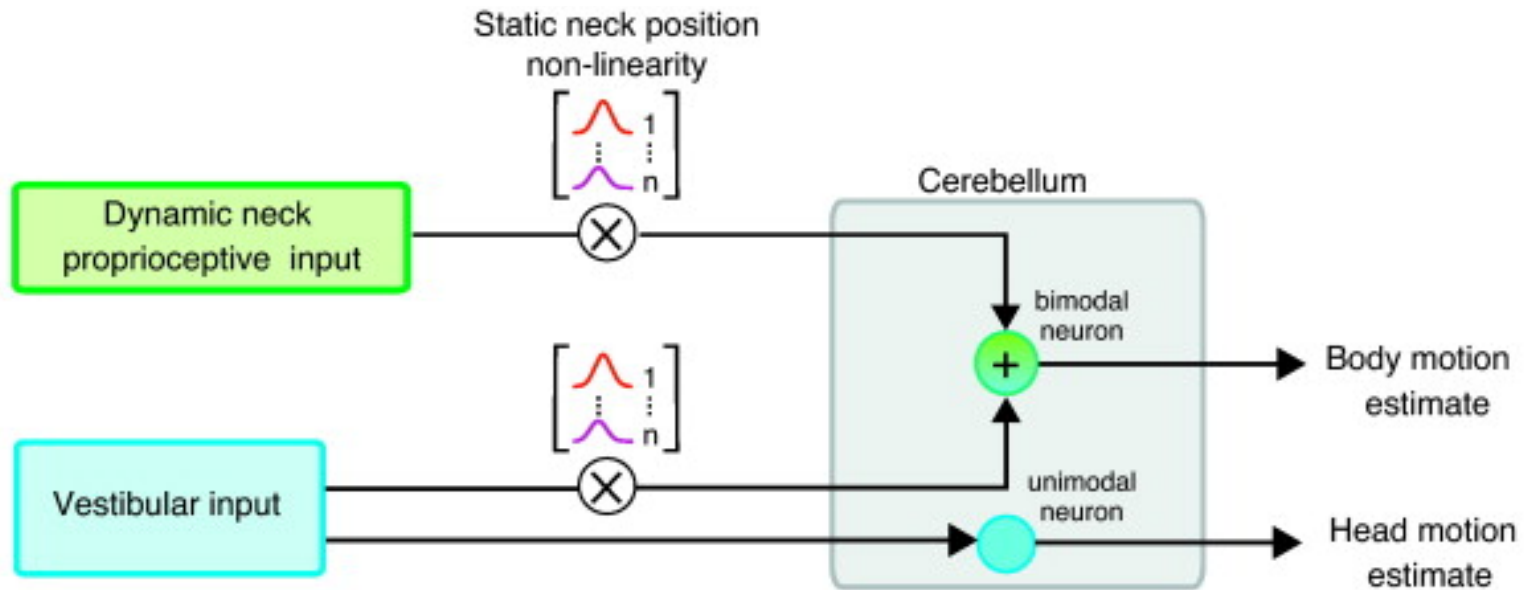
# This comparable tuning is required for bimodal neurons to encode body motion



In the case of the hypothetical neuron with overlapping tuning curves (panel A), the effect of head position is effectively cancelled

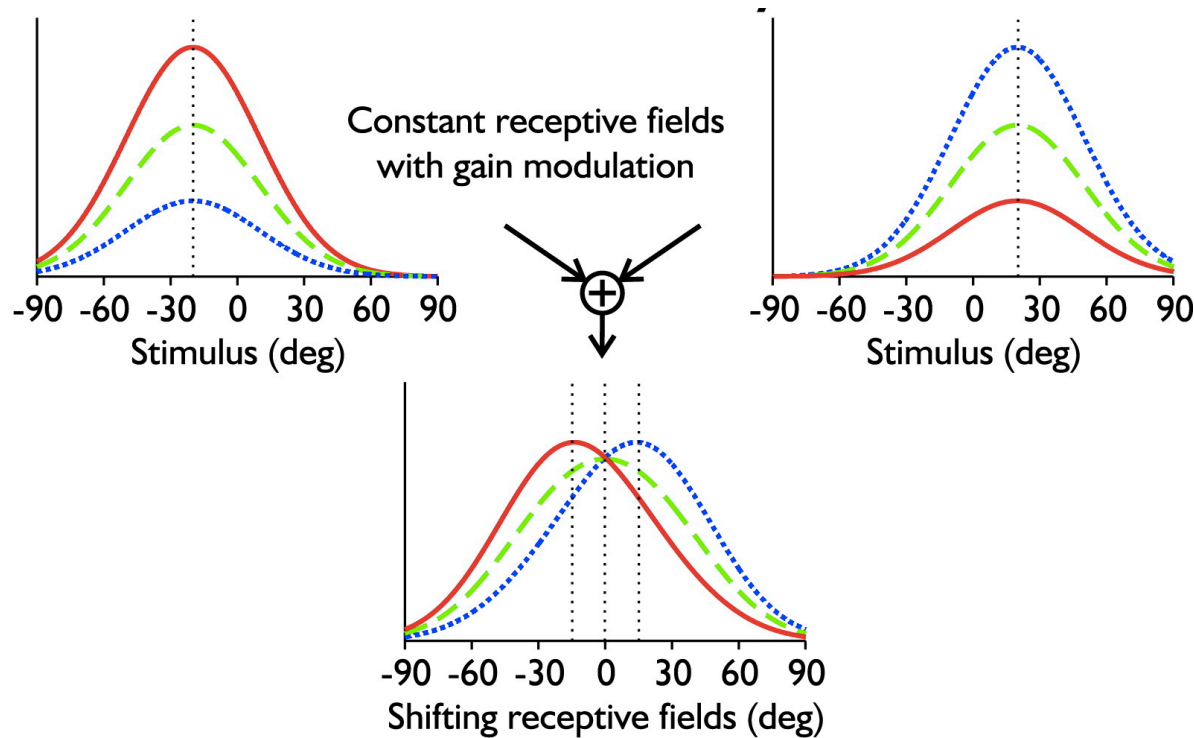
# Vestibular Cerebellar Processing:

A nonlinear operation in which head-on-body position modulates the gain of vestibular and dynamic neck proprioceptive responses



# Vestibular Cerebellar Processing:

## Relationship to the gain field theory

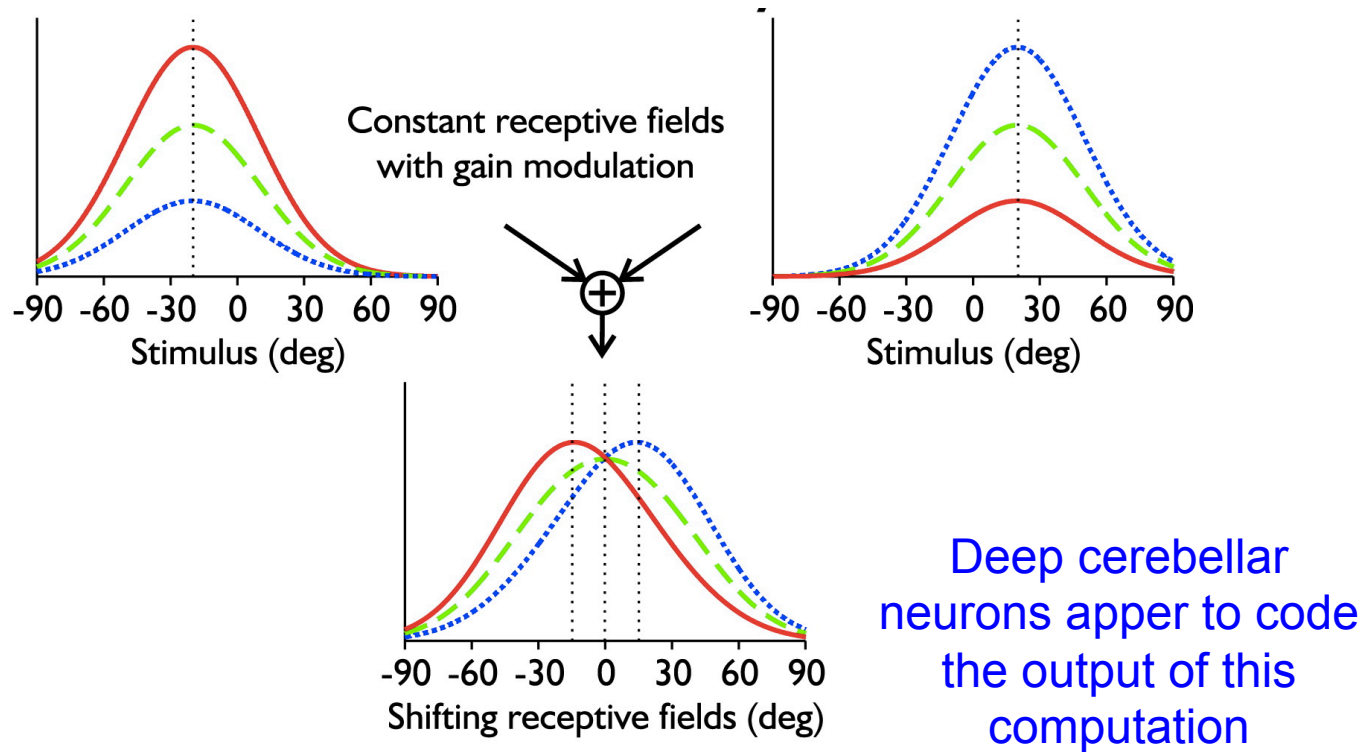


Consider the visual receptive fields of two neurons gain modulated (e.g., by eye position) in opposite ways without shifting.

- Eye position modulates the strength of response of the two input neurons, but does not cause them to shift.
- The summation of these two gain-modulated neural responses however can shift receptive fields in the output.

# Vestibular Cerebellar Processing:

## Relationship to the gain field theory

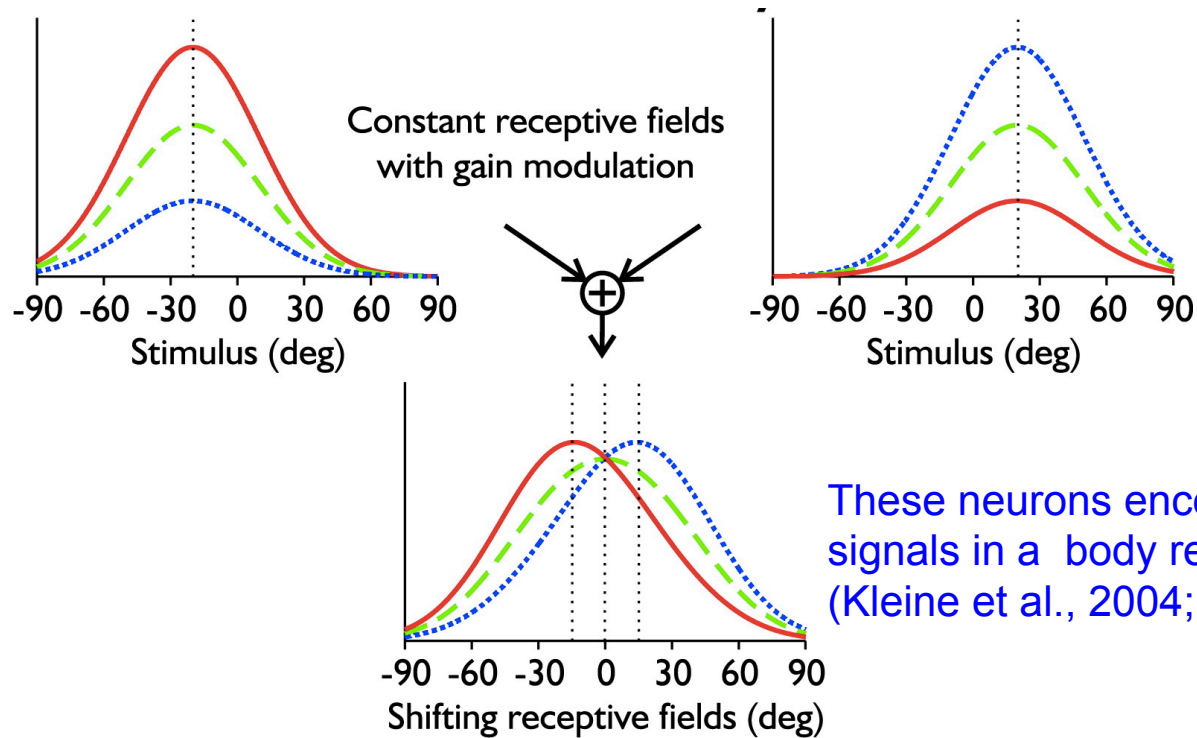


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Consider the visual receptive fields of two neurons gain modulated (e.g., by eye position) in opposite ways without shifting.

- Eye position modulates the strength of response of the two input neurons, but does not cause them to shift.
- The summation of these two gain-modulated neural responses however can shift receptive fields in the output.

## Summary:

Thus comparison of the proprioceptive and vestibular responses of bimodal neurons further revealed that neurons show tuning in response to static changes in head-on-body position.

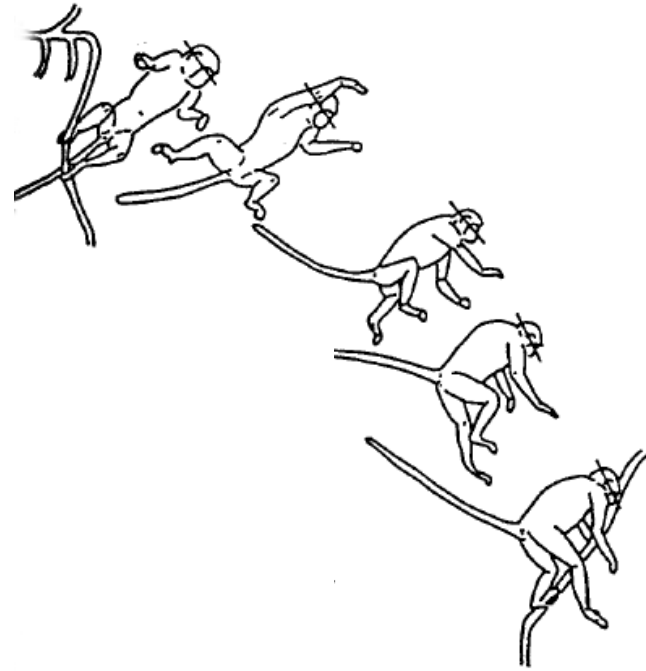
This raises the question: What is the functional significance of the observed tuning?

- To produce accurate motor control requires combining sensory signals with other postural information to transform the original sensory input from its native reference frame into another that is relevant to ongoing behavior.
- Vestibular sensory information is first encoded in a head reference frame because the sensors are located in the head. So, to generate appropriate postural responses, it is vital to integrate vestibular inputs with proprioceptive inputs.

# Functional Role of Vestibulo-cerebellar Neurons

These neurons are a vital component of vestibulo-spinal postural reflexes, they project to multiple levels of the spinal cord.

Function: Integrate vestibular and proprioceptive inputs to ensure the generation of appropriate postural responses.



This is absolutely vital, since for the same vestibular input, the appropriate postural response will depend how the head is oriented relative to the body!

Again note, however that self motion can be self-produced as well as externally applied....

---

# Sensorimotor transformations: Vestibulo-spinal Reflexes

## 1. Static Non-linearities

- Boosting non-linearity in central vestibular neurons
- Gain-fields in the cerebellum

## 2. Dynamic Non-linearities

- Suppression of Reafference and common strategies across systems
- Learning in vestibulo-spinal reflex pathways

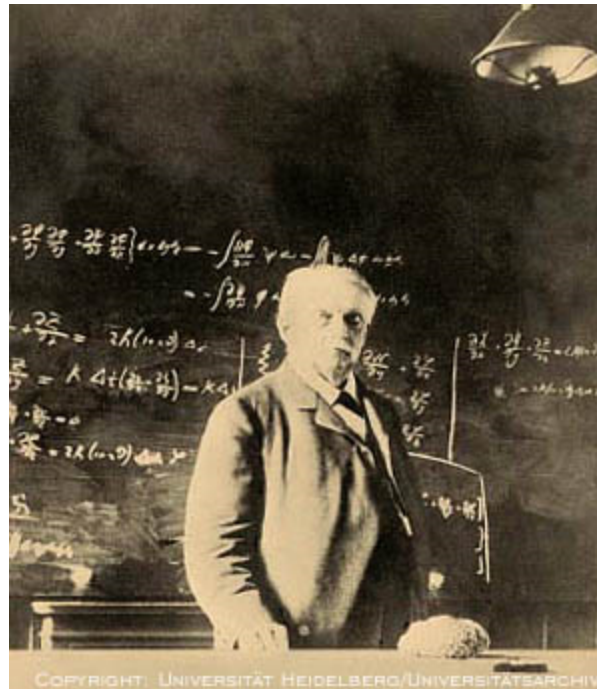


How does the vestibular system encode active self motion?



# Differential processing of self-generated versus passive stimulation

1. *Perceptual Stability*: Helmholtz (1867) made the salient observation that tapping on the canthus of the eye, results in an illusionary shift of the visual world. However, we never see the world 'shift' when we make saccades.



# Differential processing of actively-generated versus passive stimulation

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*For example, while vestibular-reflexes are essential for providing robust postural response to unexpected vestibular stimuli, they can be counter-productive when the goal is to make active head movements.*

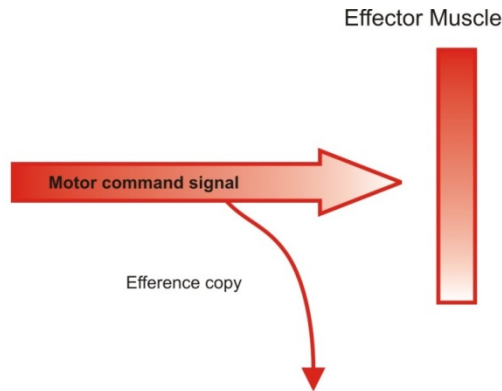
# Differential processing of actively-generated vs. passive stimulation

1. *Perceptual Stability*: Helmholtz (1867) made the salient observation that tapping on the canthus of the eye, results in an illusory shift of the visual world. However, we never see the world 'shift' when we make saccades.
2. *Accurate Motor Control*: In the vestibular system, the central neurons that receive direct afferent input, also project to motor centers to control vestibulo-ocular and -spinal reflexes.
3. Von Holst and Mittelstaedt (1950) proposed that an efference copy of the motor command was used distinguish between reafference and exafference.

# Computing sensory reafference

This proposal is based on the idea that:

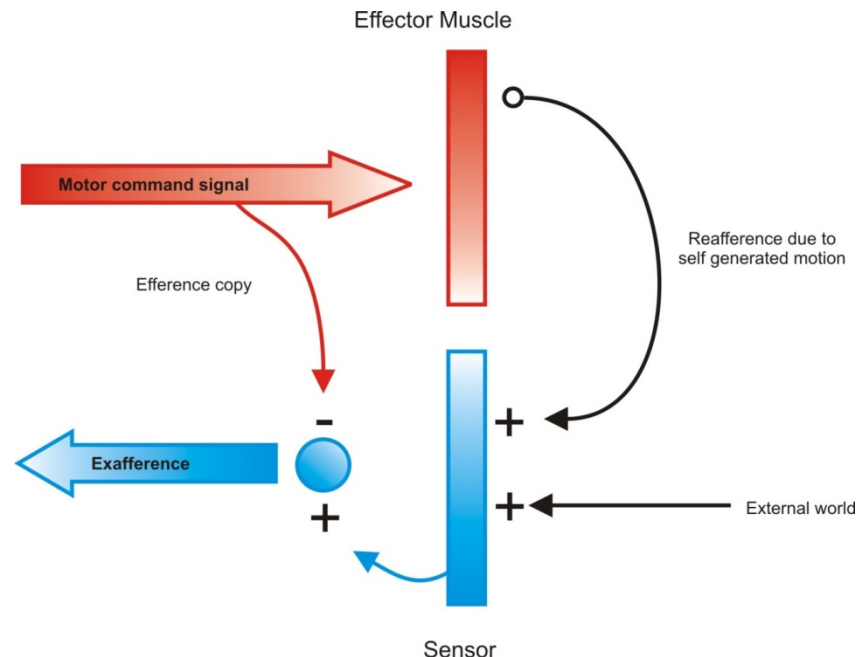
First, during active movements, the central nervous system sends a parallel “efference copy” of the motor command to sensory areas.



# Computing sensory reafference

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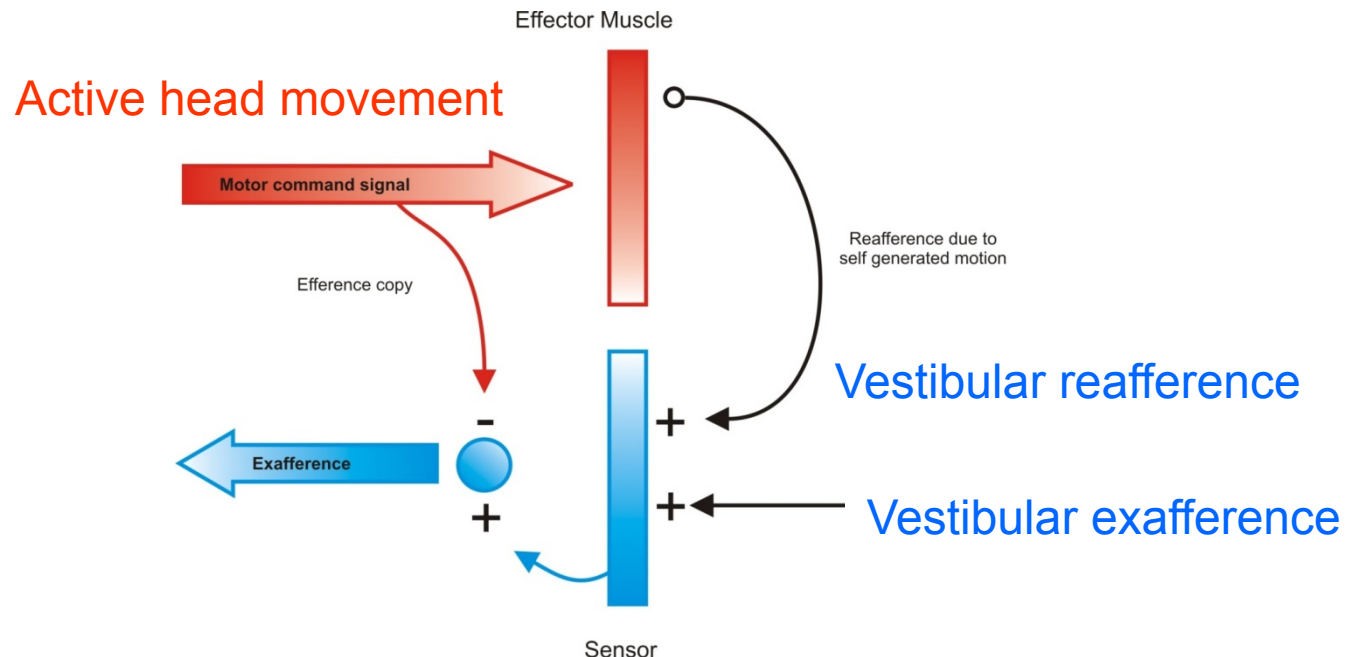


As a result, this anticipatory signal is then subtracted from the incoming sensory signal to selectively remove that portion due to the animal's own actions (i.e. reafference).

# Computing vestibular reafference

This proposal is based on the idea that:

First, during active movements, the central nervous system sends a parallel “efference copy” of the motor command to sensory areas.



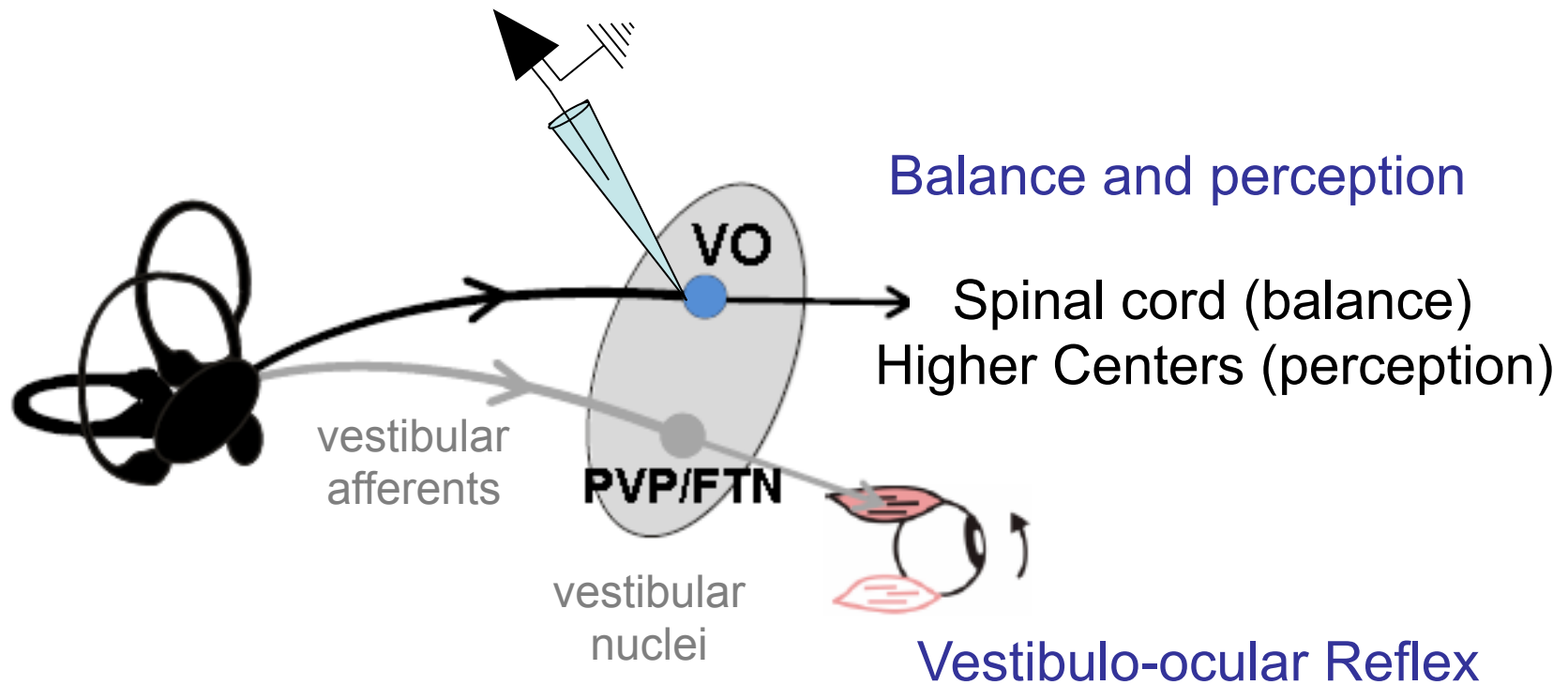
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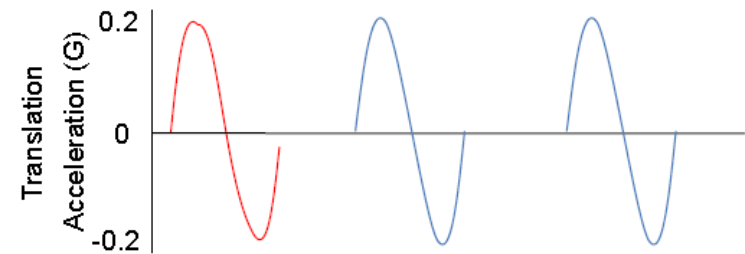
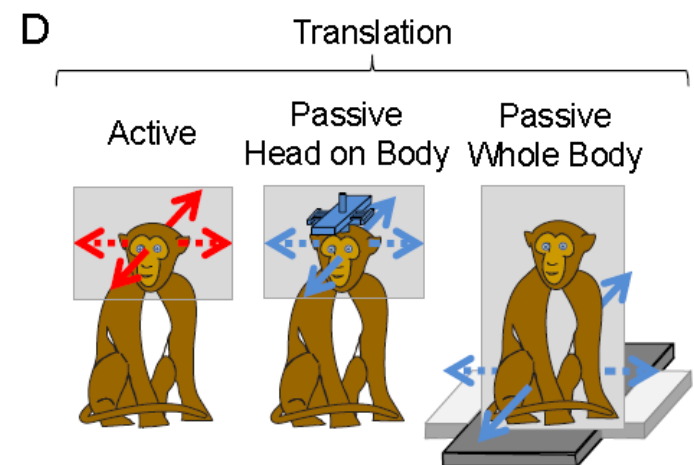
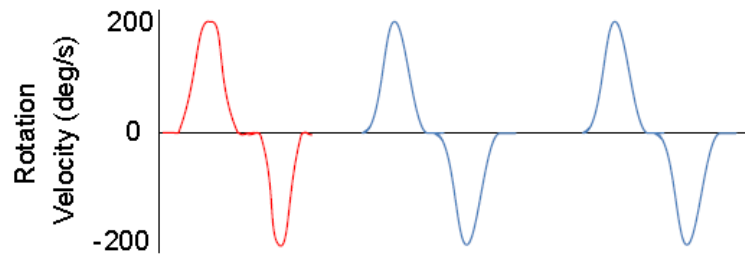
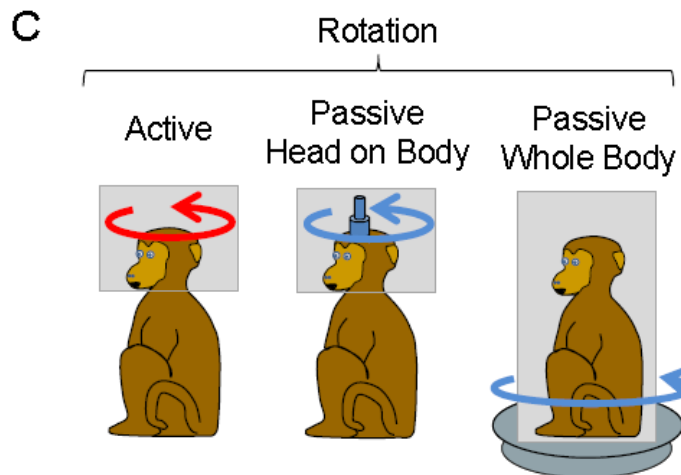
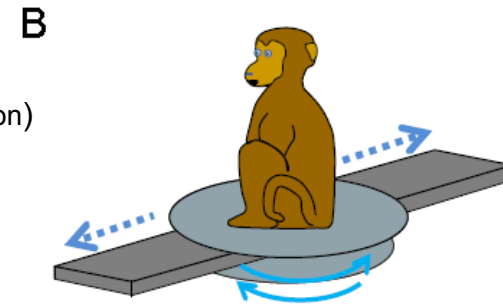
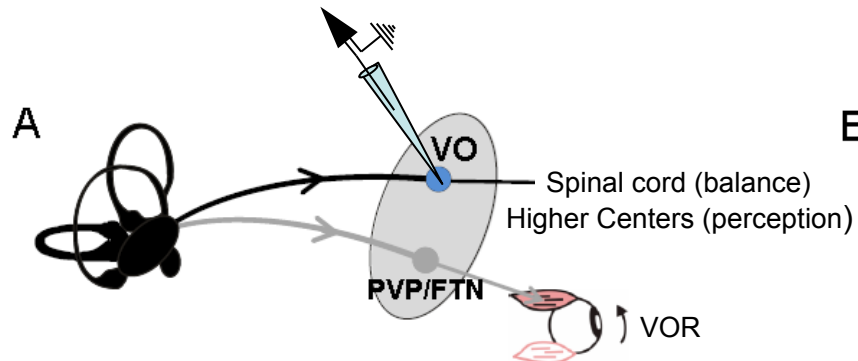
# Differential processing of actively-generated Versus passive stimulation: The vestibular system



Where and how does the brain make a distinction between active and passive head motion?

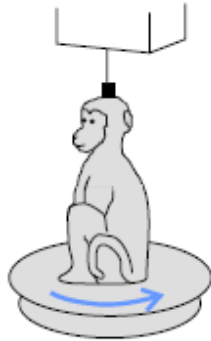


# Experimental Setup

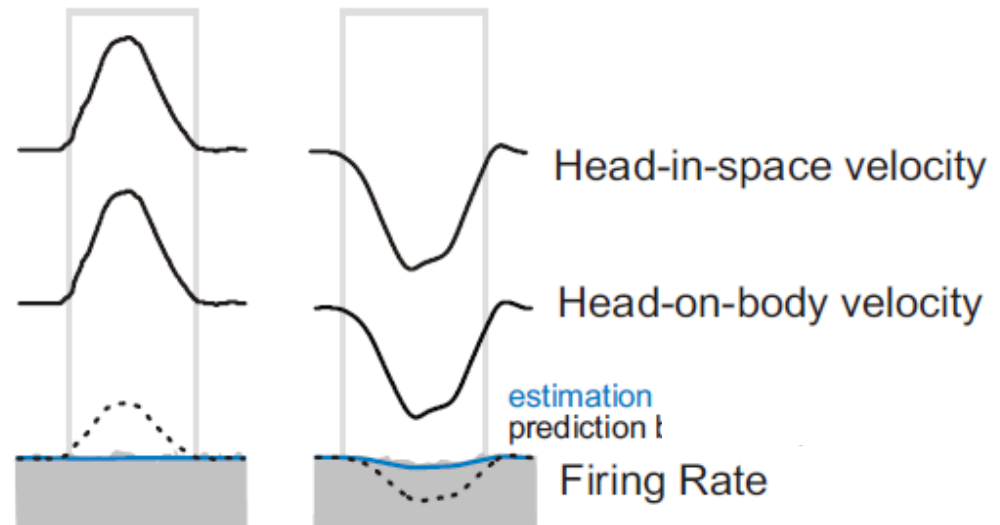
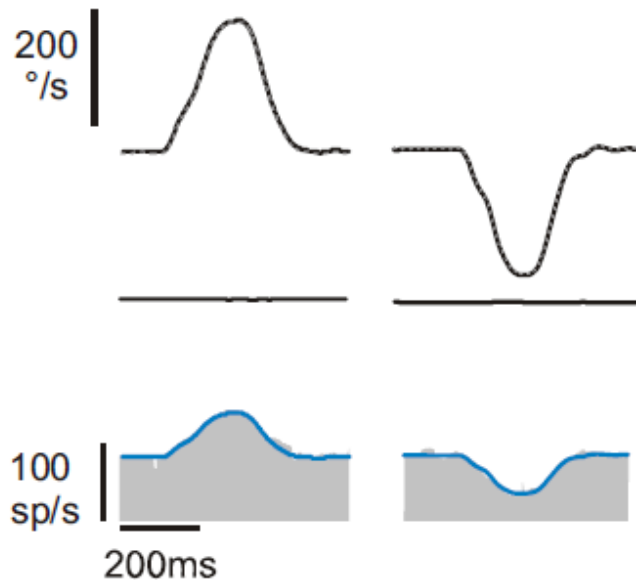


First: Vestibular reafference is suppressed for head-in-space motion produced by **active** head-on-body rotations.

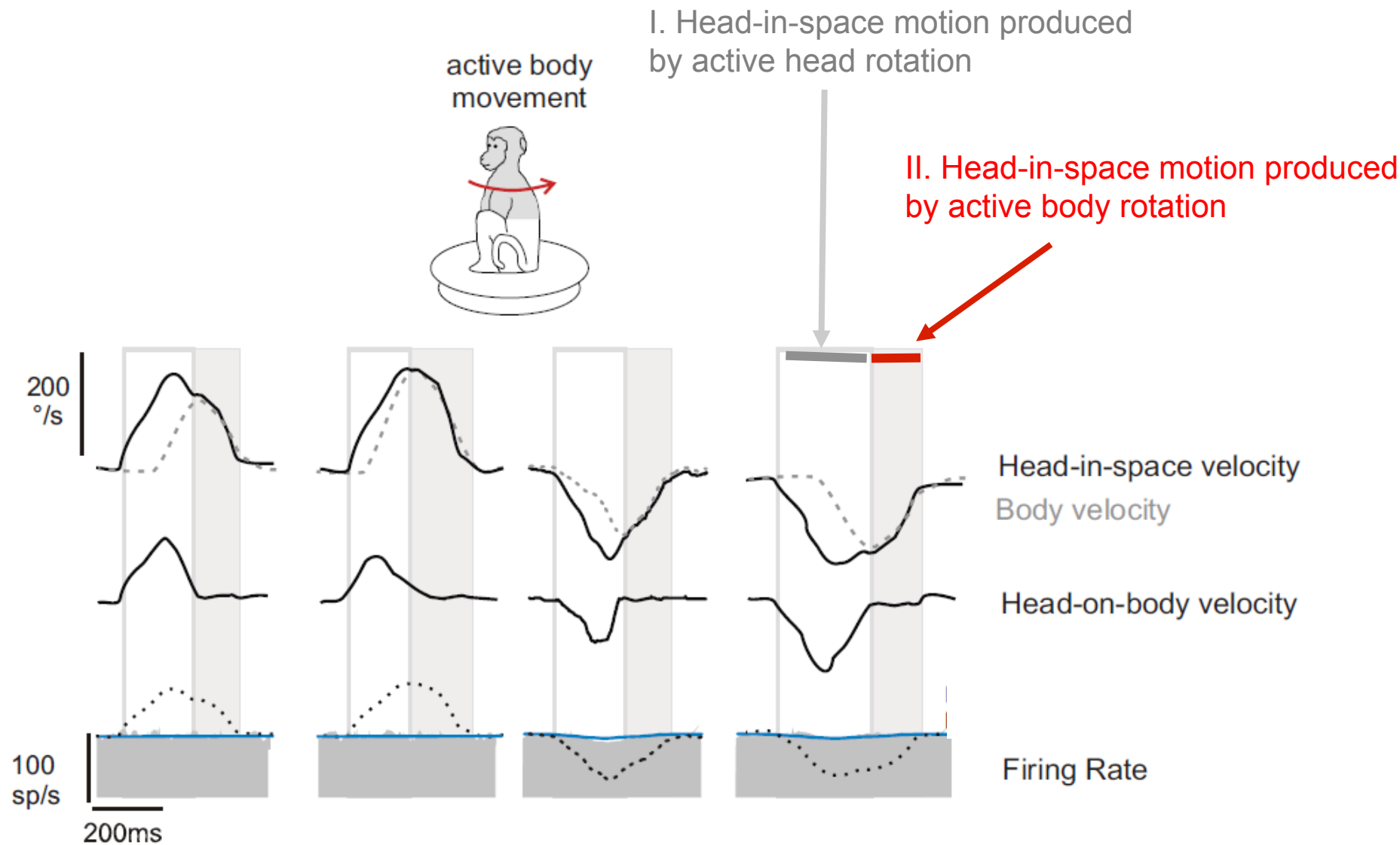
Passive Head-in-space motion



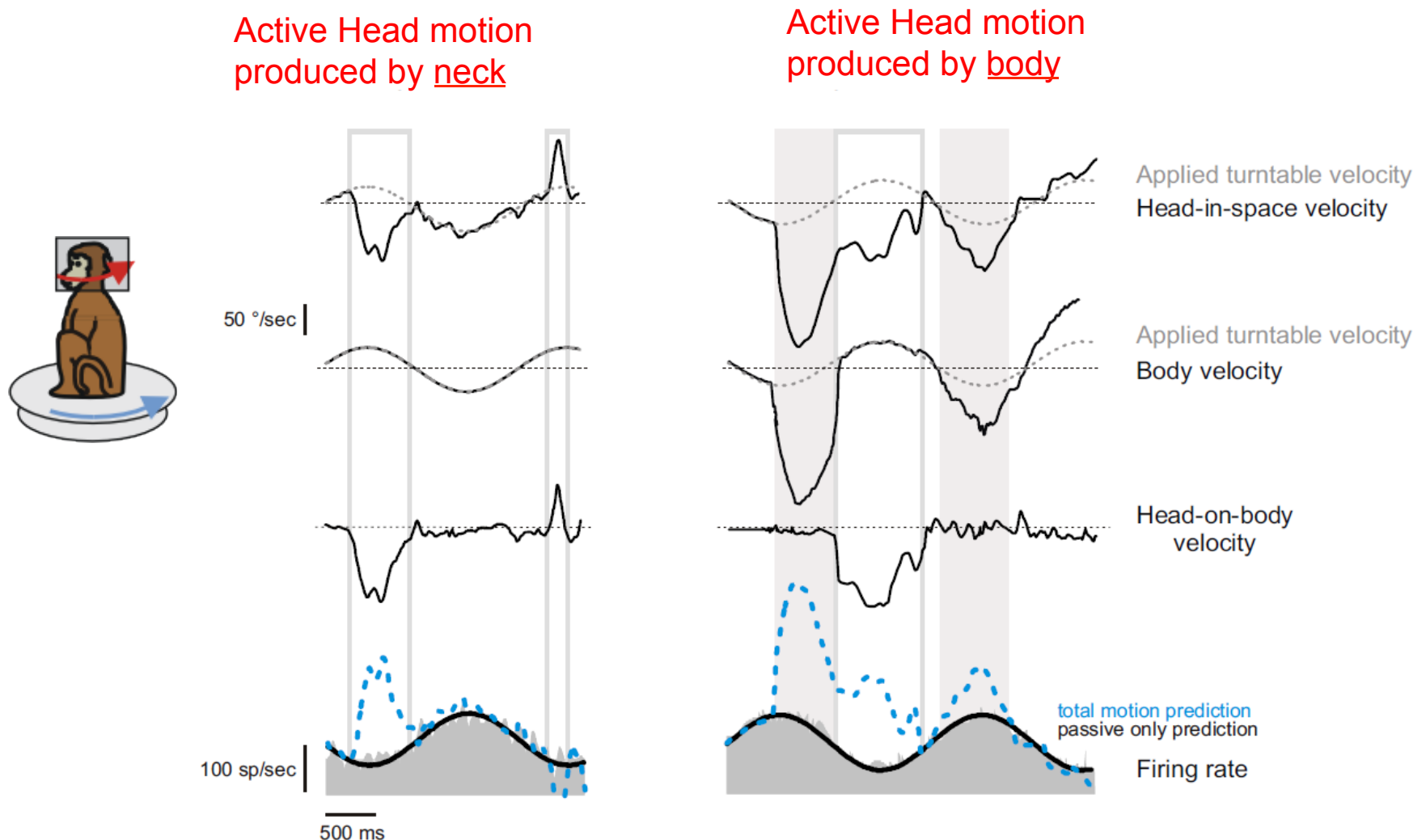
Active Head-in-space motion



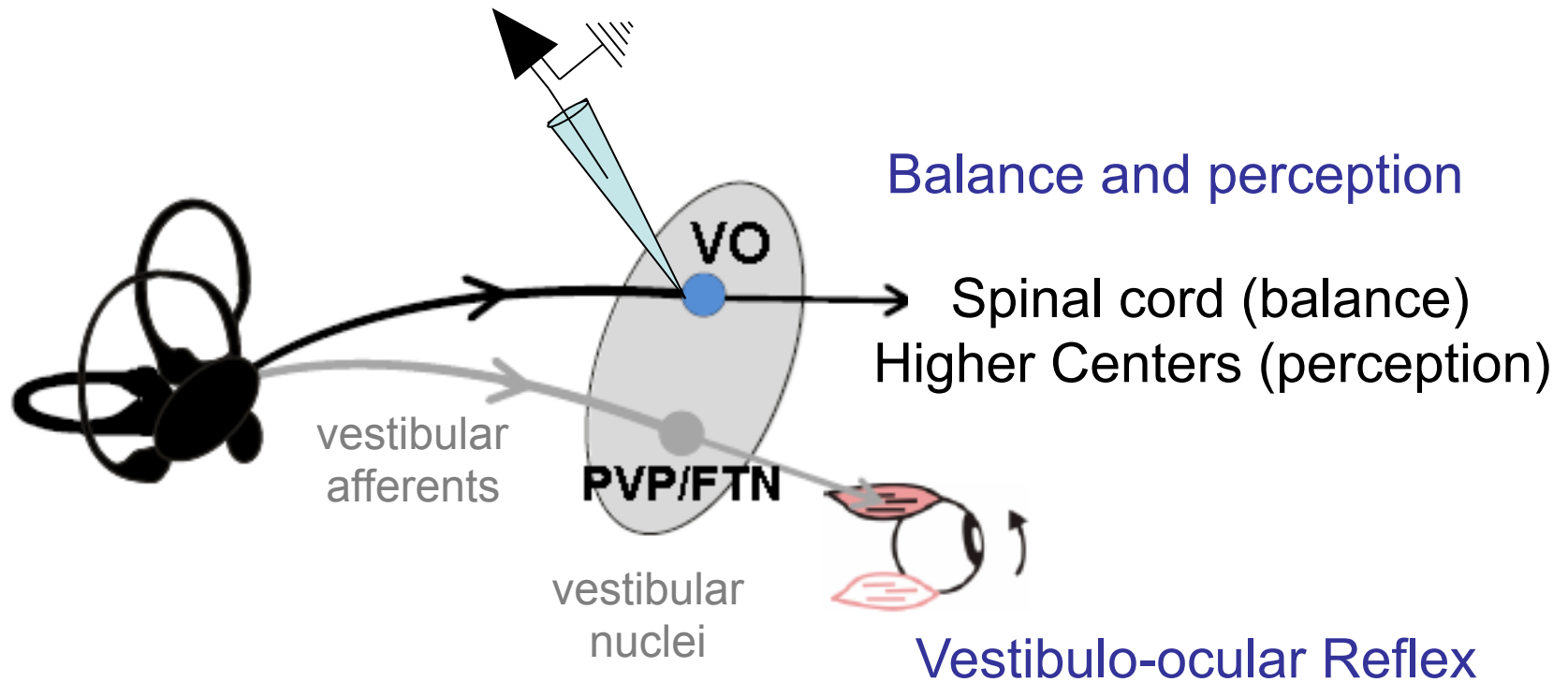
and for that produced by **active body** rotations.



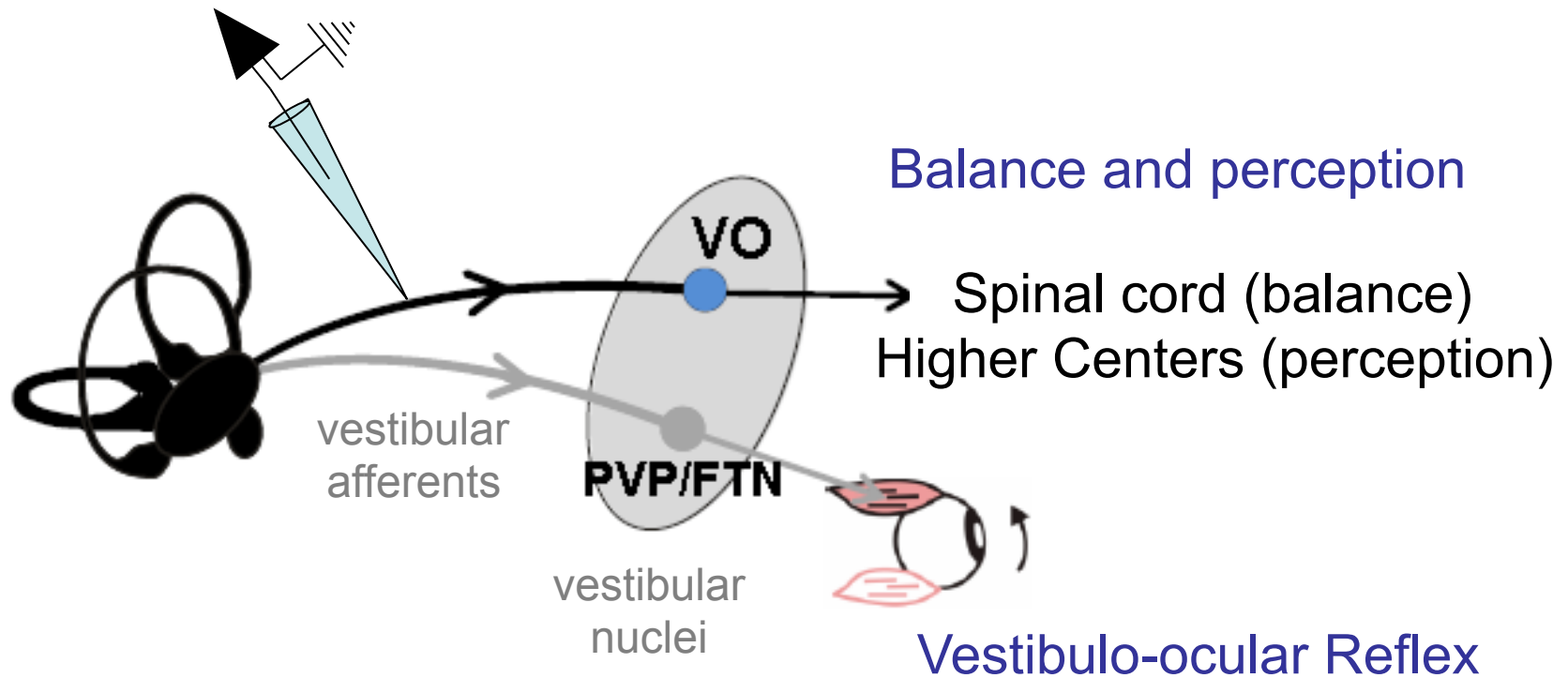
# Moreover, neurons selectively encode **passive** motion during concurrent active/passive movements



Where and how does the brain make this distinction between active and passive head motion?



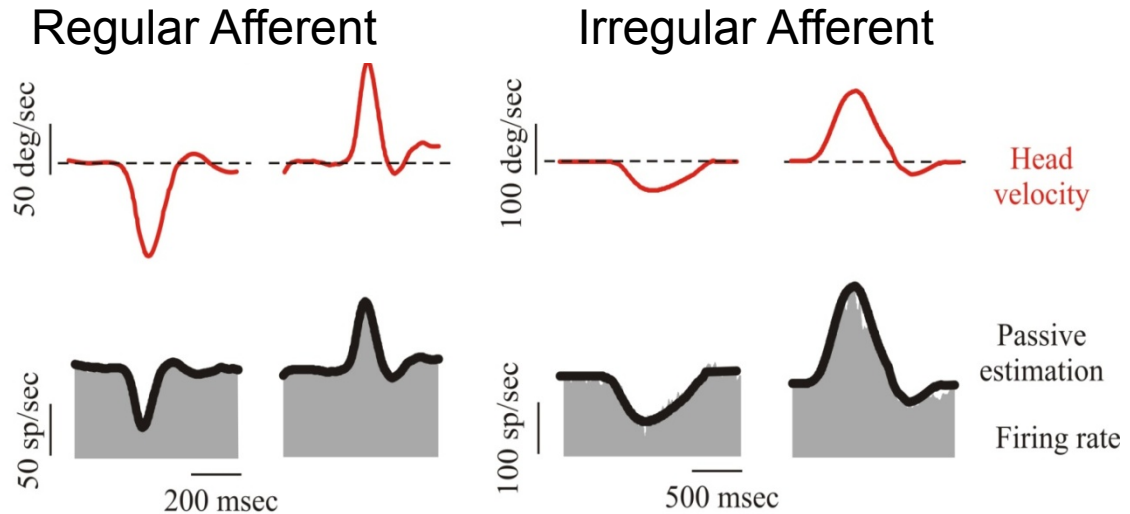
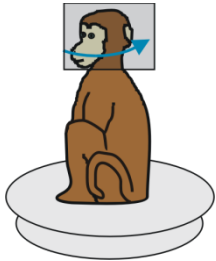
Where and how does the brain make this distinction between active and passive head motion?



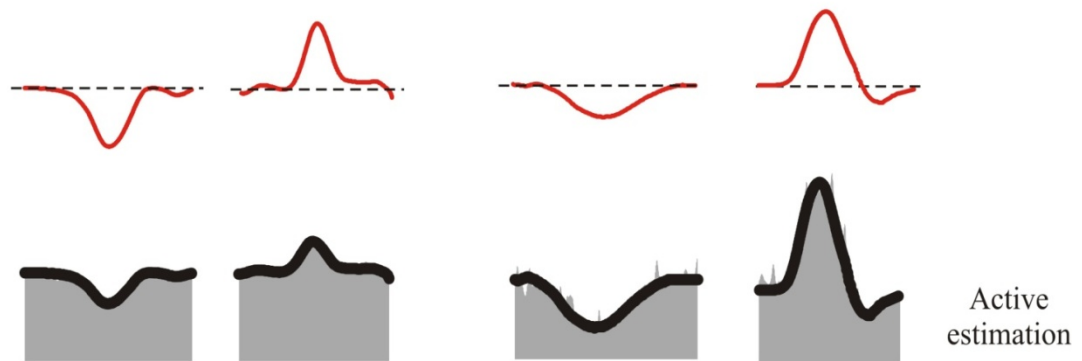
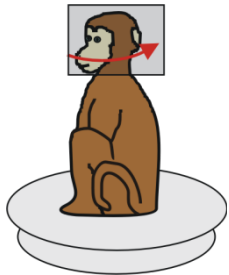


This distinction is not observed at the previous stage:  
Vestibular afferents similarly encode active and passive motion

**Passive**

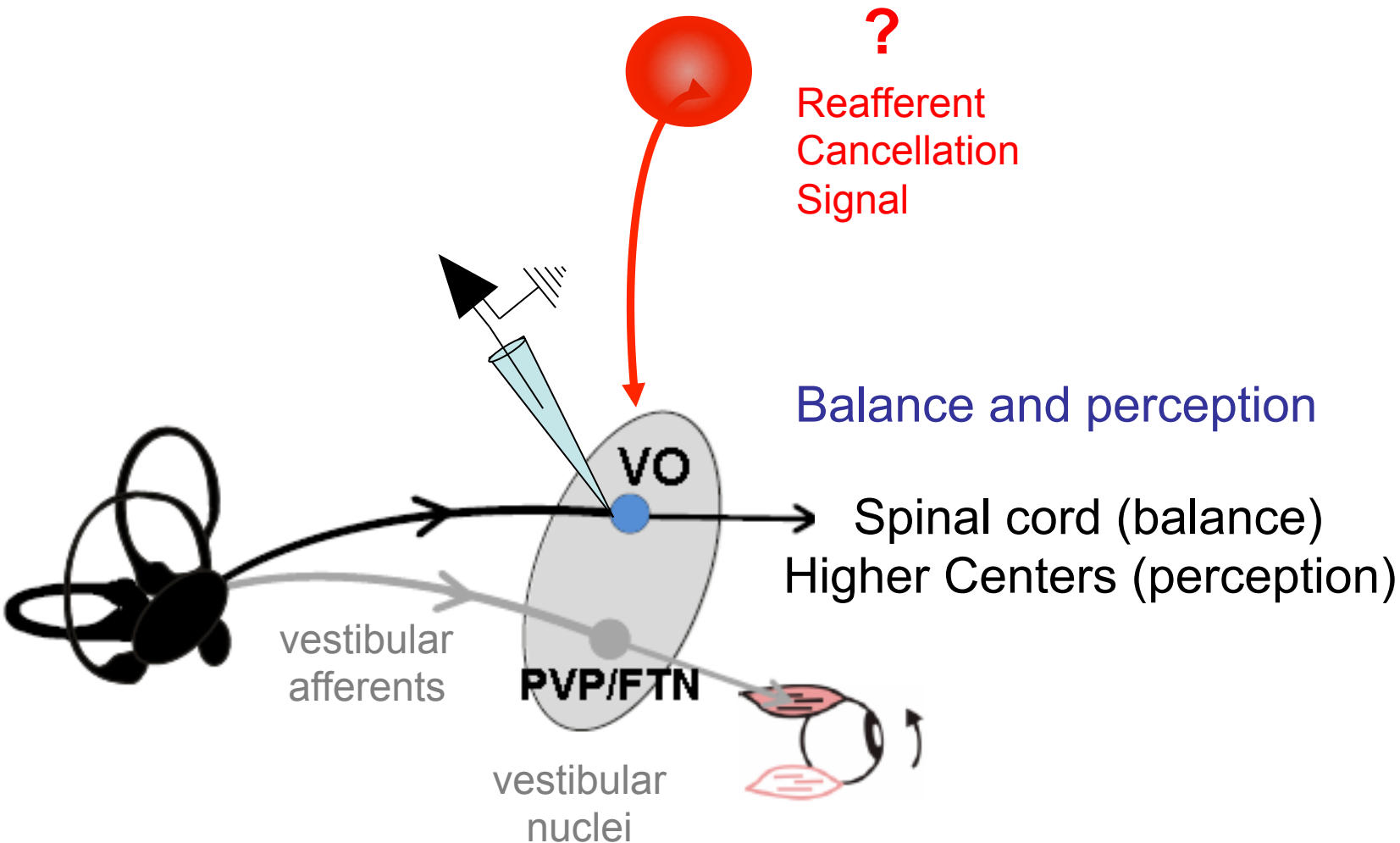


**Active**



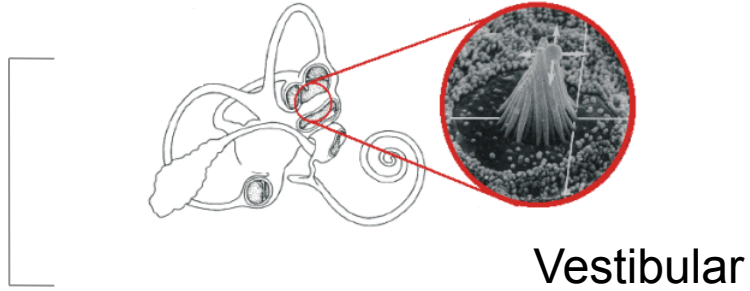
$$\text{Eq: } \text{FR}(t) = \text{bias} + g_v \dot{H}(t) + g_a \ddot{H}(t)$$

Where and how does the brain make this distinction between active and passive head motion?



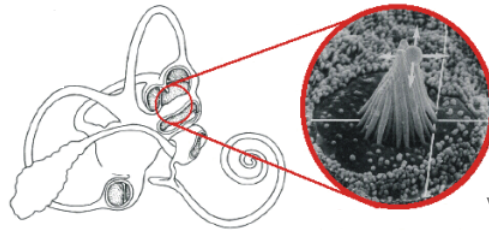
# During Passive Movements: The Vestibular Sensors are Activated

Passive  
Whole-Body  
Rotation

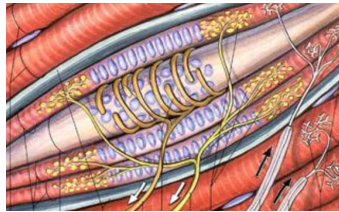


During active movements:

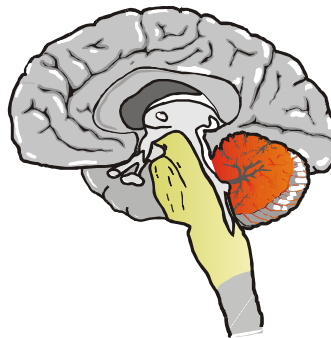
Additional information is available for distinguishing  
between passive vs. active motion



Vestibular



1. Proprioception



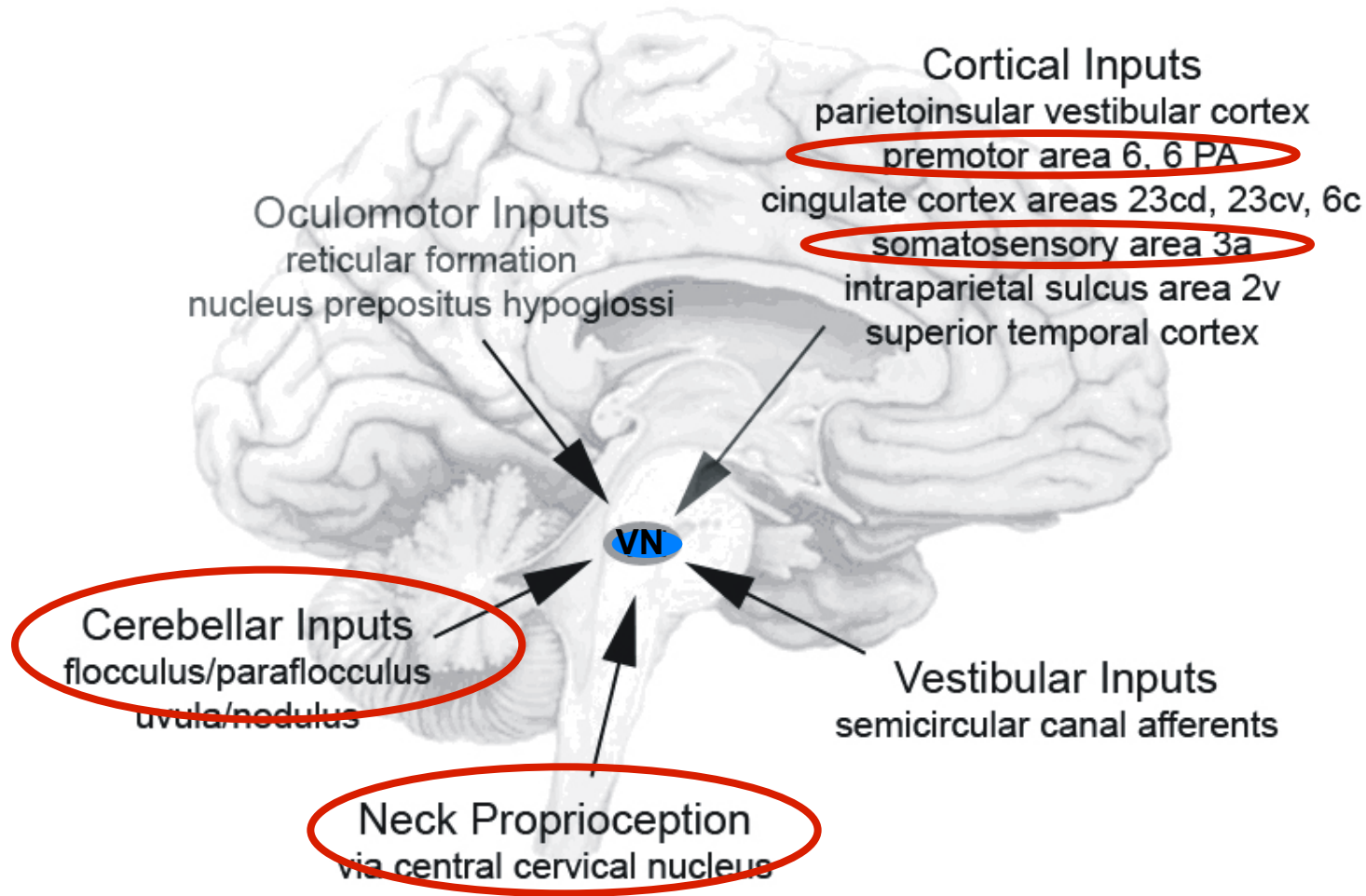
2. Motor  
Command



3. Knowledge

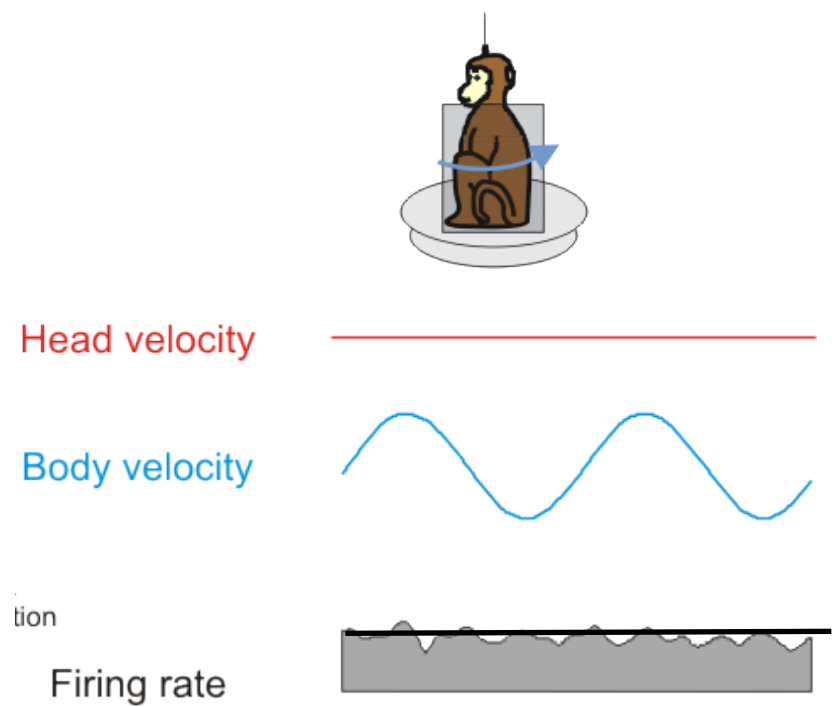
Active  
Self-motion

Multimodal information is available from many sources that could potentially cancel vestibular information

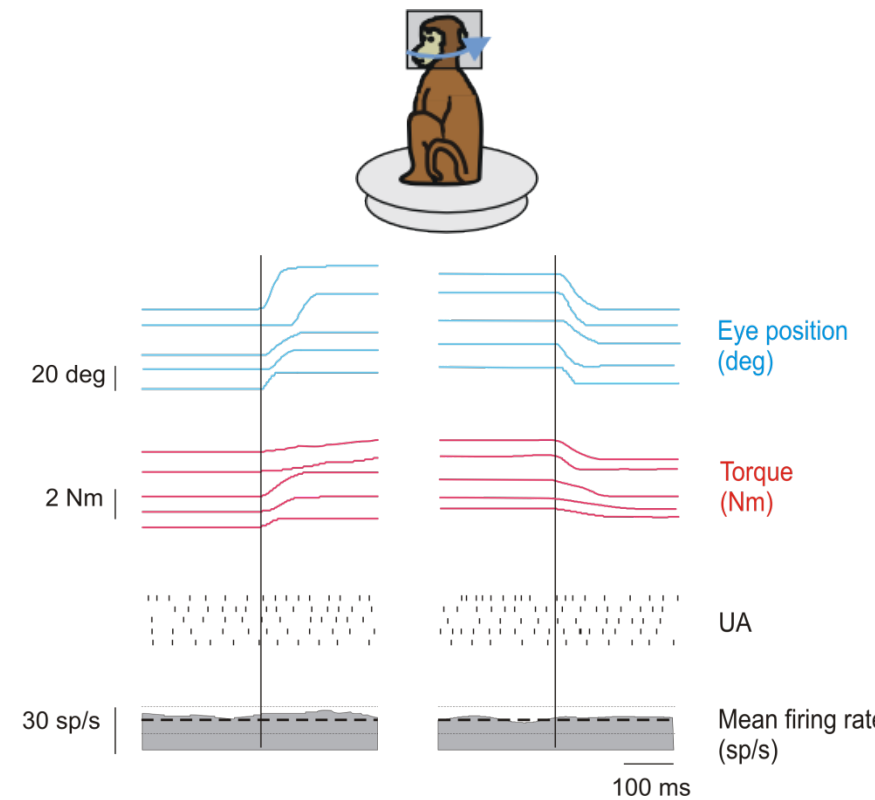


# Cancellation of self-produced stimulation is **not** directly mediated by proprioceptive or by motor efference copy inputs

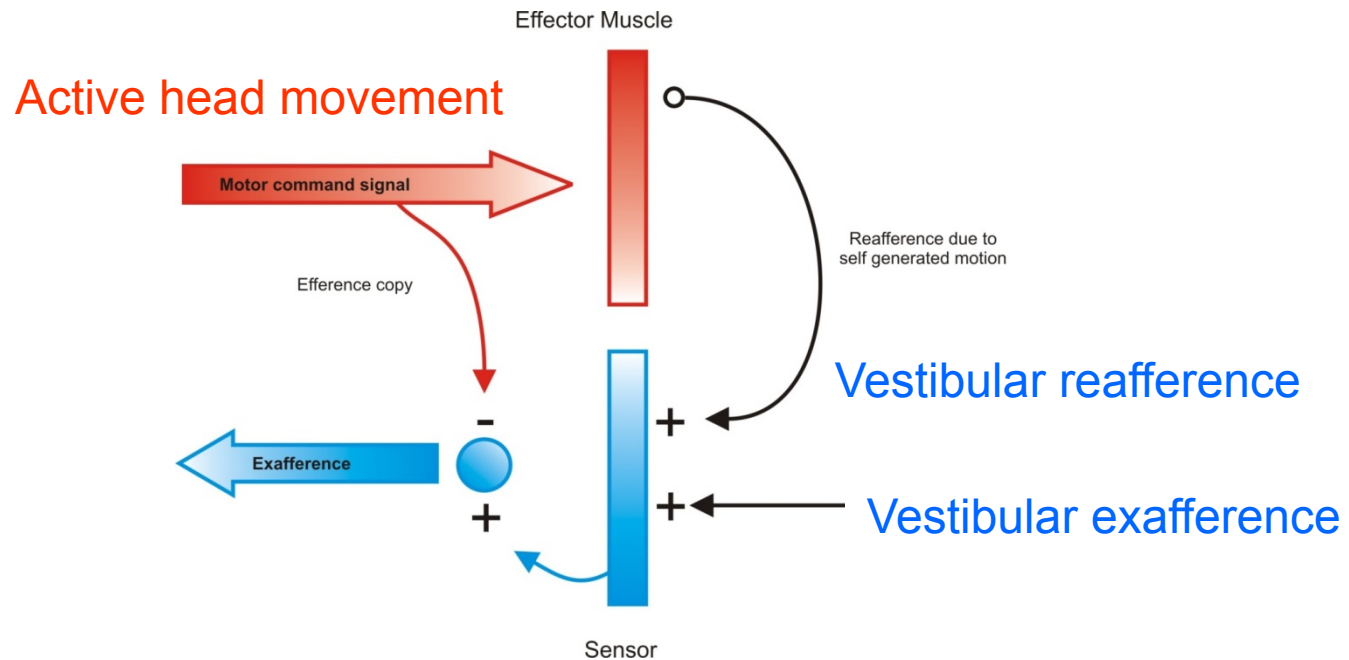
Passive stimulation of neck proprioceptors



Generation of motor efference copy without head motion

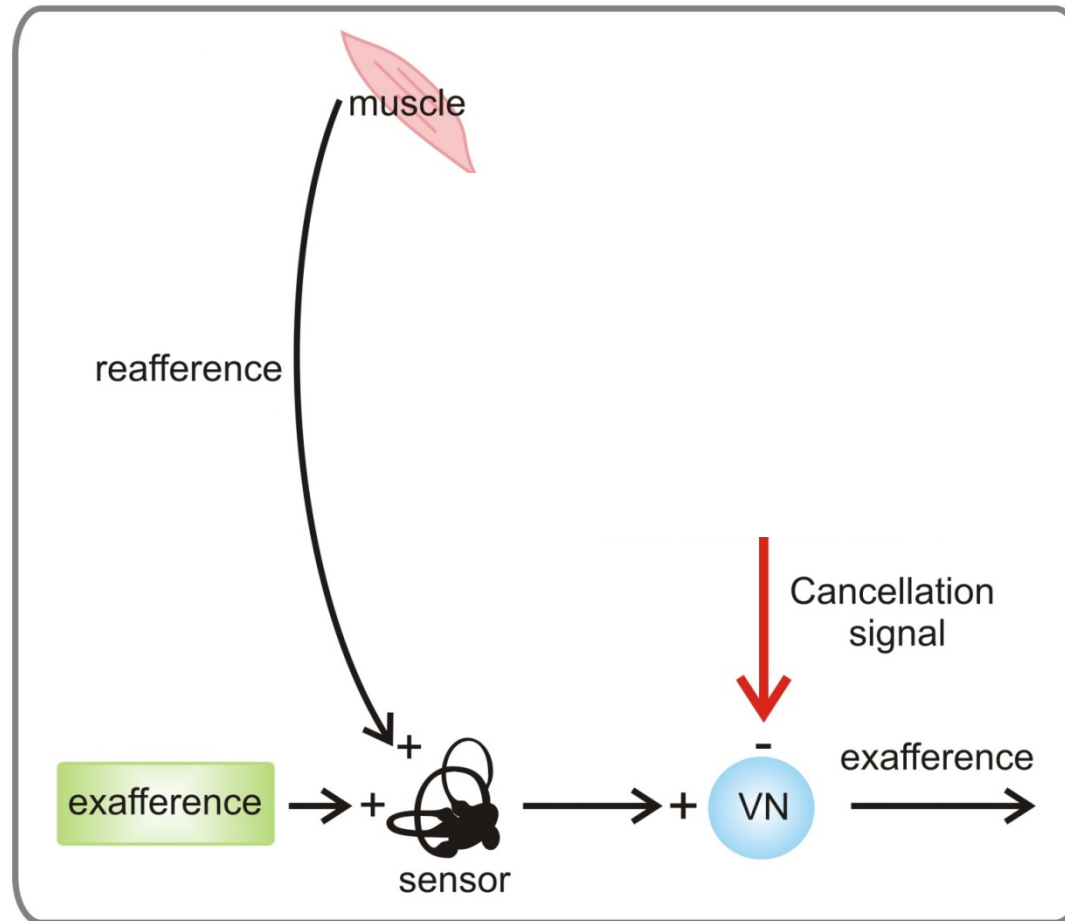


# Computing vestibular reafference



# The current working model:

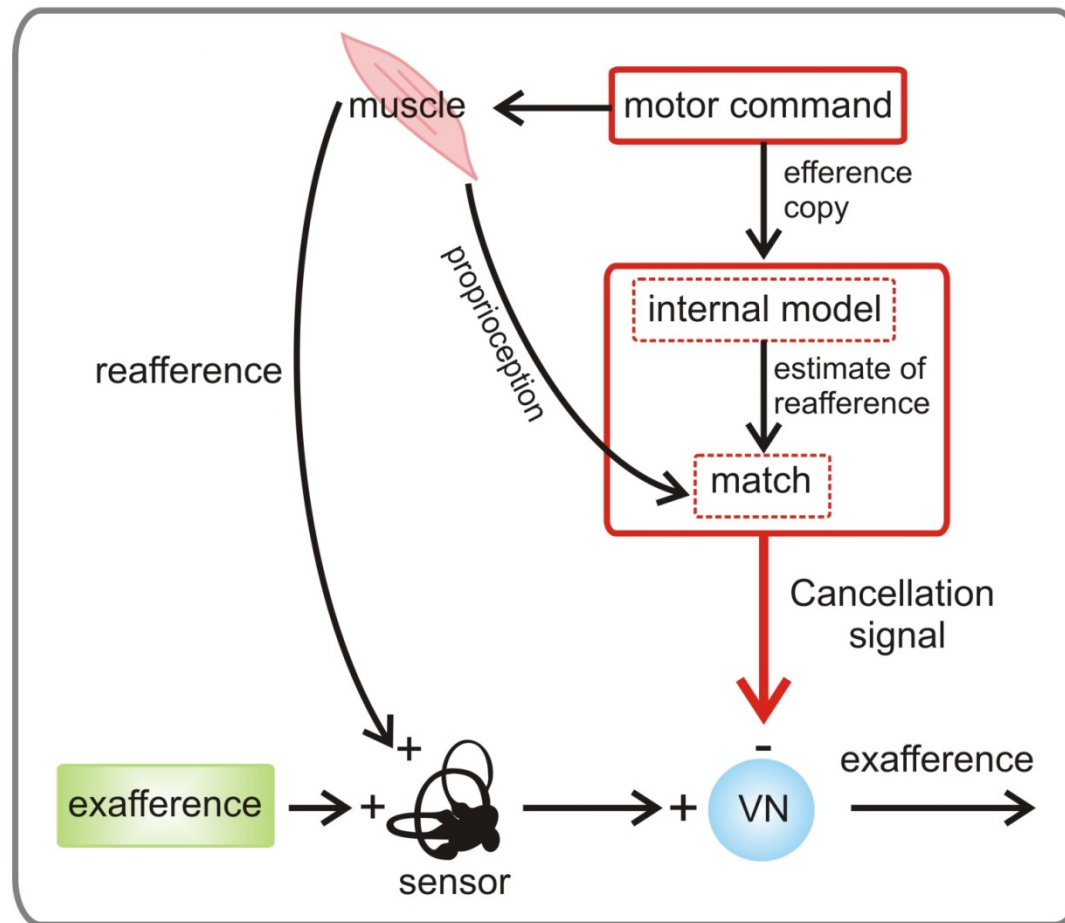
A central cancellation signal is produced if neck proprioceptor activation matches that expected as a result of the voluntary head movement.





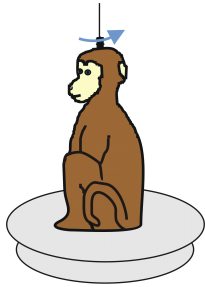
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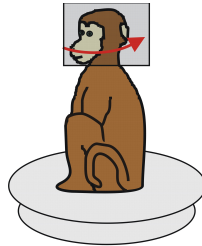


## Test of the model:

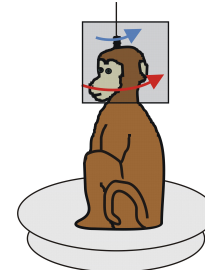
There should be no cancellation if neck proprioceptive activation does not match that expected during the generation of a active head motion



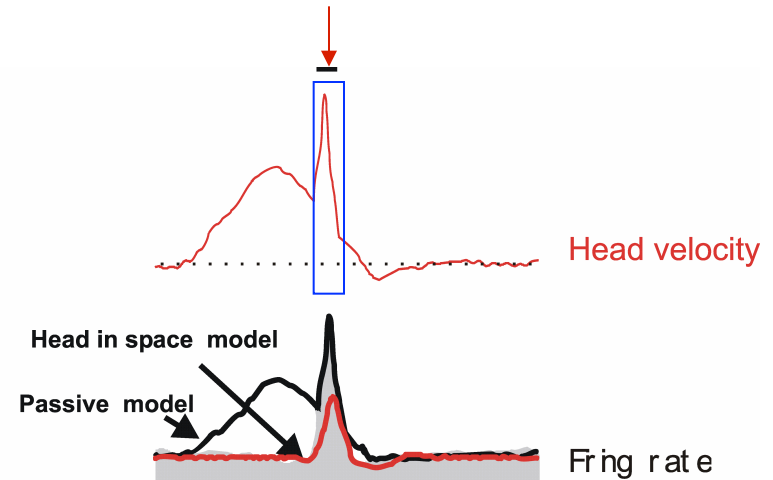
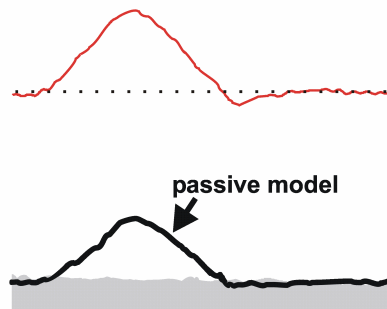
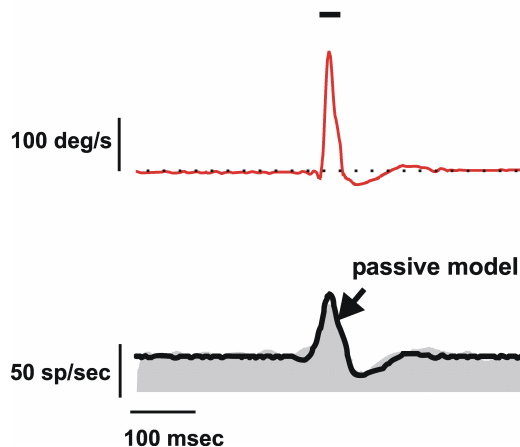
HOB perturbation



Active HOB gaze shift



Combined:  
Neck proprioceptive feedback results from  
The sum of active and passive movement



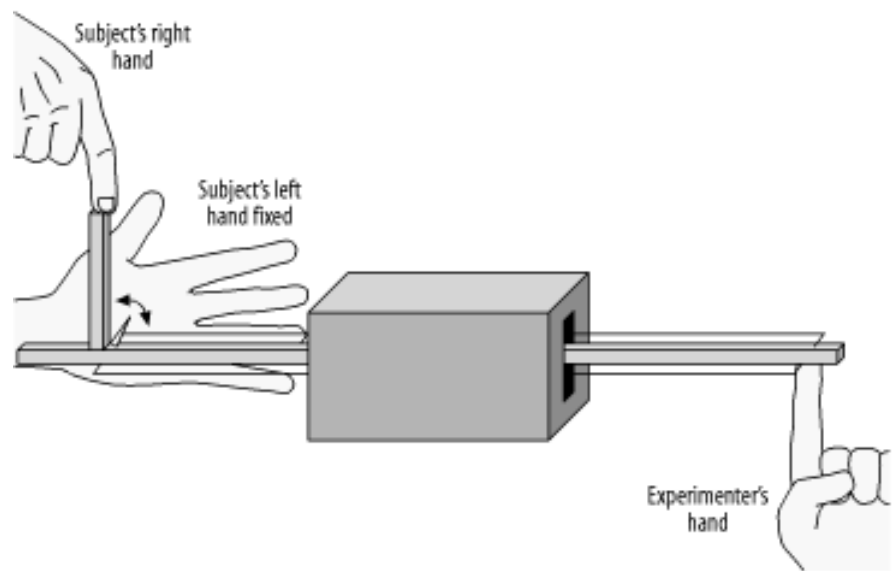
# Is this a Common Strategy among Sensory Systems?

Consider the question: *Why can't you tickle yourself?*

Wolpert and colleagues developed a tickle robot to rigorously address this critical question.

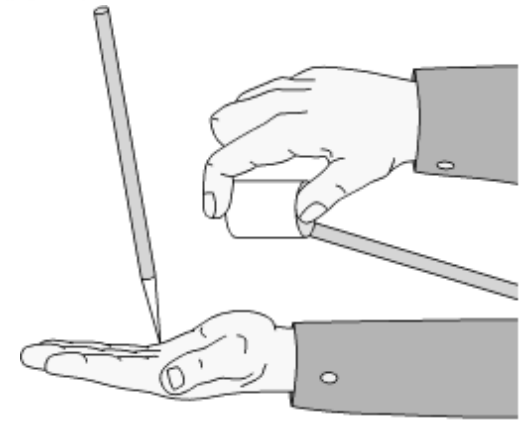
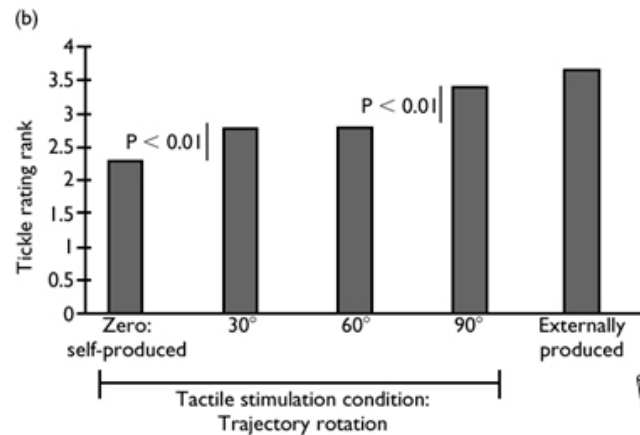
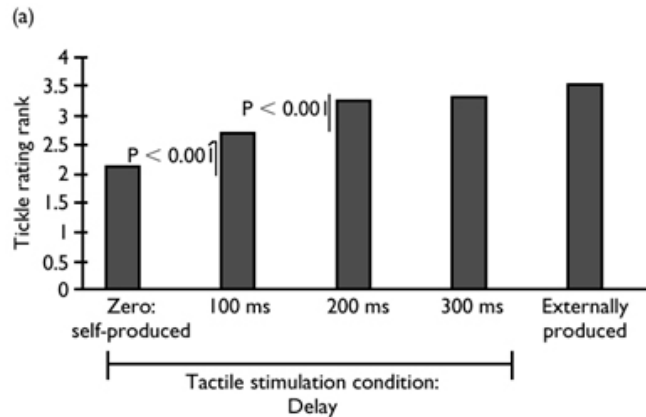
Condition 1: the experimenter produces the stimulus to touch the participant's left hand.

Condition 2: The participant self-produces the touch stimulus of his left hand using his right hand.



# Is this a Common Strategy among Sensory Systems?

Condition 3: Introduction of a temporal or spatial mismatch (i.e. a delay or rotation, respectively) between the causal action and the resultant stimulation resulted in lower ratings of tickliness .

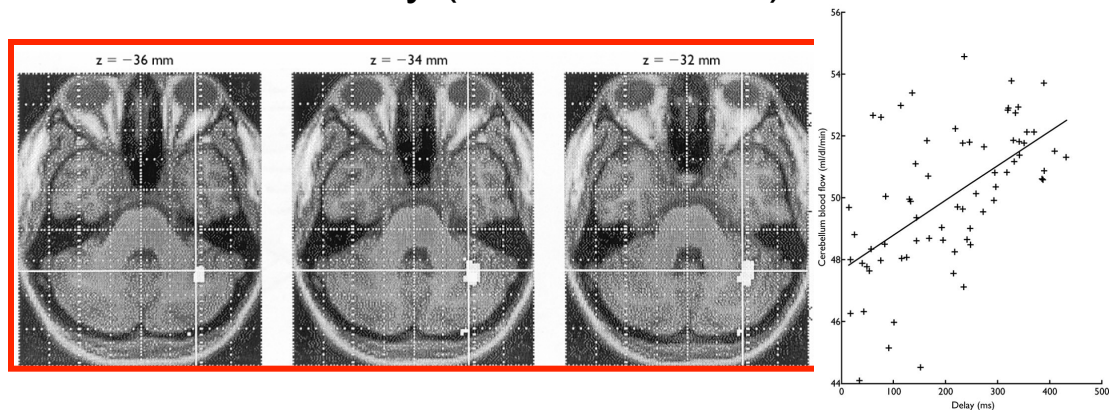


# Neural Correlates of Sensory Cancellation

## Human

For the same touch stimulus, activity in the right lateral cerebellar cortex showed a positive correlation with delay (i.e. more tickle).

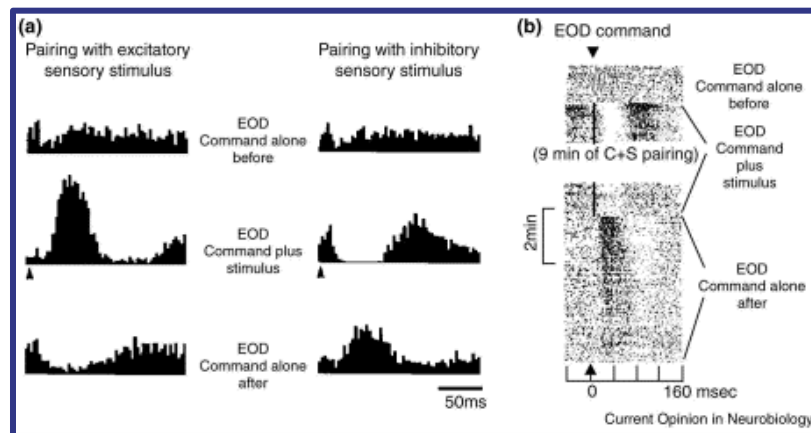
Blakemore et al.,  
*Neuroreport*, 2001



## Electric Fish

Block EOD with curare, but the motor command that would normally elicit an EOD is still produced. When artificial experimental stimuli is paired with motor command, ELL neurons are modulated.

Bell., *Curr Opin Neurobiol.* 2001



## Neural Correlates of Sensory Cancellation:

Together these studies suggest that the cerebellum is involved in signaling the sensory discrepancy between the predicted and actual sensory consequences of movements.

*Consistent with the proposal that:*

The cerebellum is involved in predicting the specific sensory consequences of movements, thereby providing the signal that is used to cancel the sensory response to self-generated stimulation.

## The Big Open Question:

What mechanism support the comparison between sensory inputs and motor commands that are required for the distinction between active and passive motion at the level of the vestibular nuclei?

# Support for the proposal that the cerebellum plays a role in the cancellation of vestibular reafference

## 1. Evidence from work in electric fish.

The cerebellum-like electrosensory lobes provide the signal that is used to cancel the sensory response to self-generated stimulation (Bell and colleagues).

## 2. fMRI studies in humans

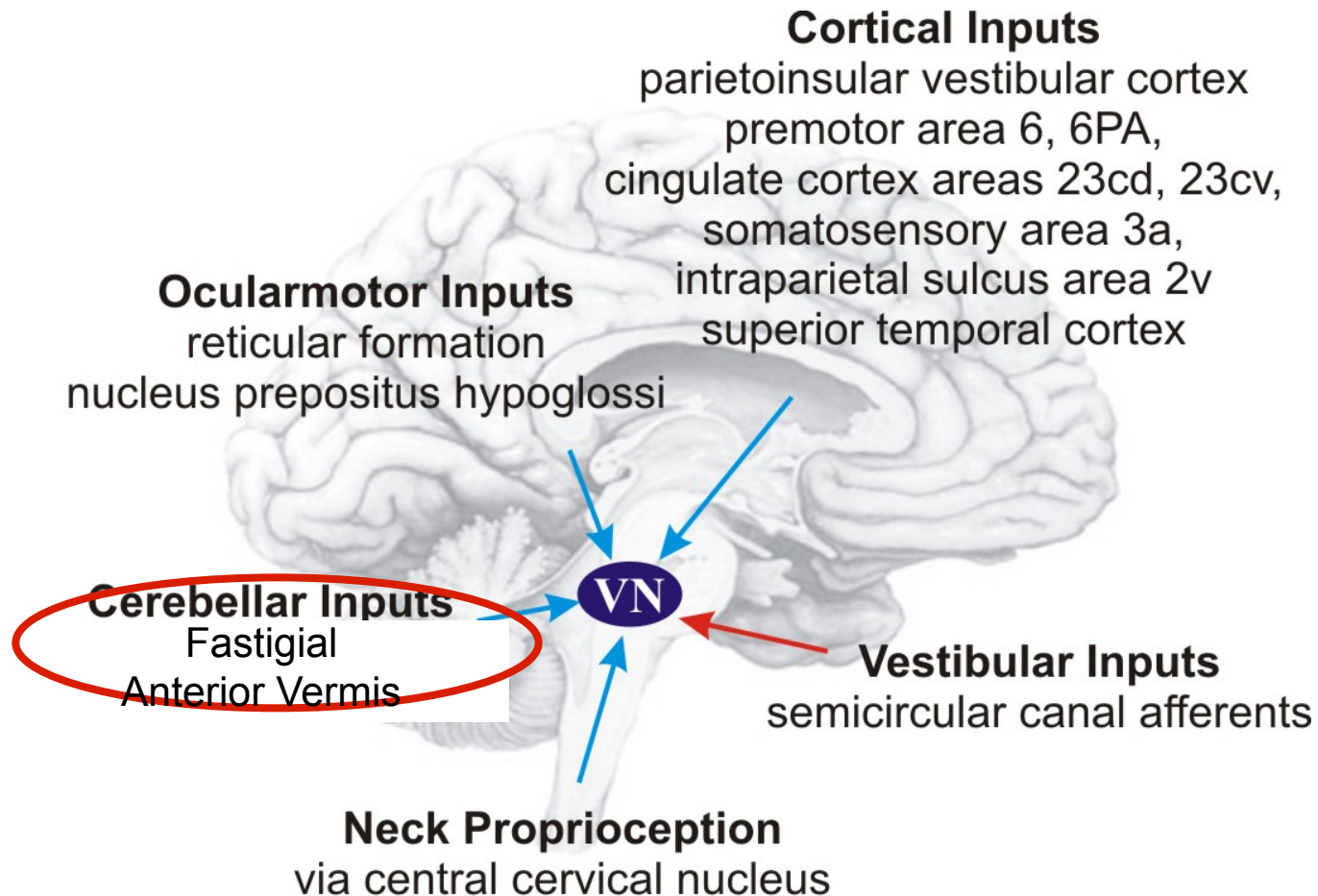
Suggest that the cerebellum serves a similar role in the suppression of tactile stimulation during self-produced tickle (Blakemore, Wolpert and colleagues).

## 3. We have now begun to study whether the vestibular cerebellum might play a role in the cancellation of vestibular reafference.

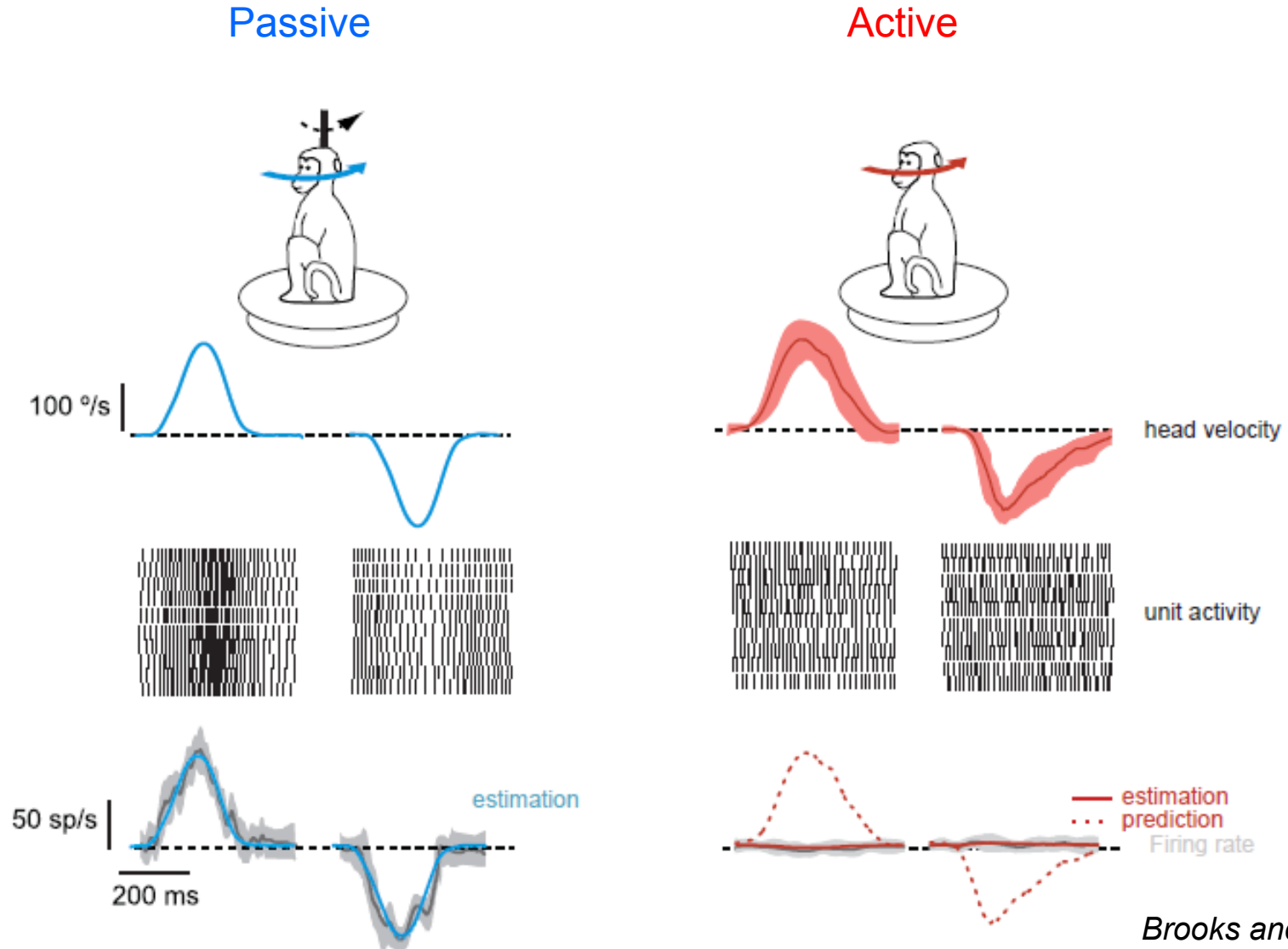


# The Vestibular Nuclei:

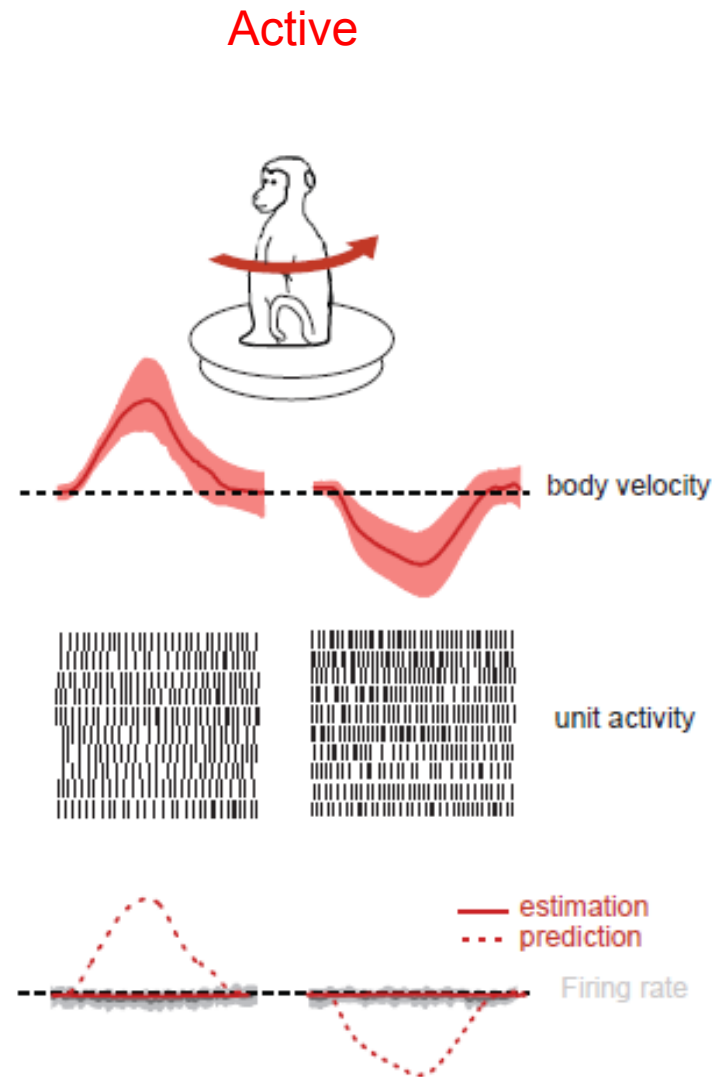
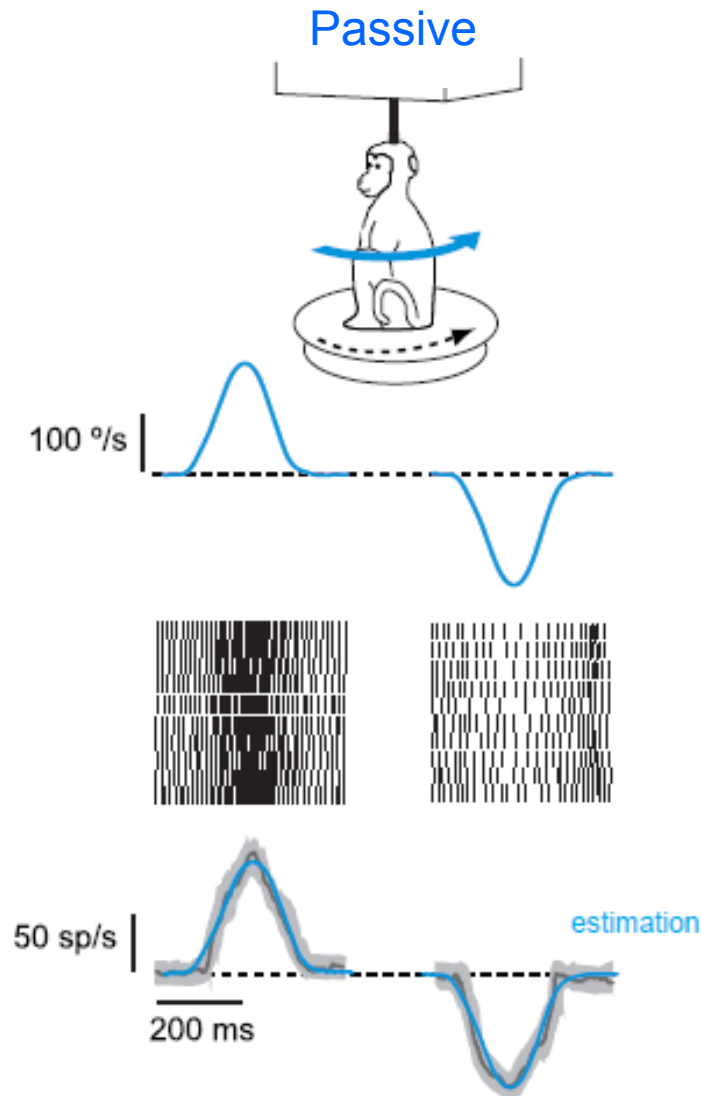
## Processing is convergent and multimodal



# During active motion, Unimodal Neurons no longer encode head-in-space motion

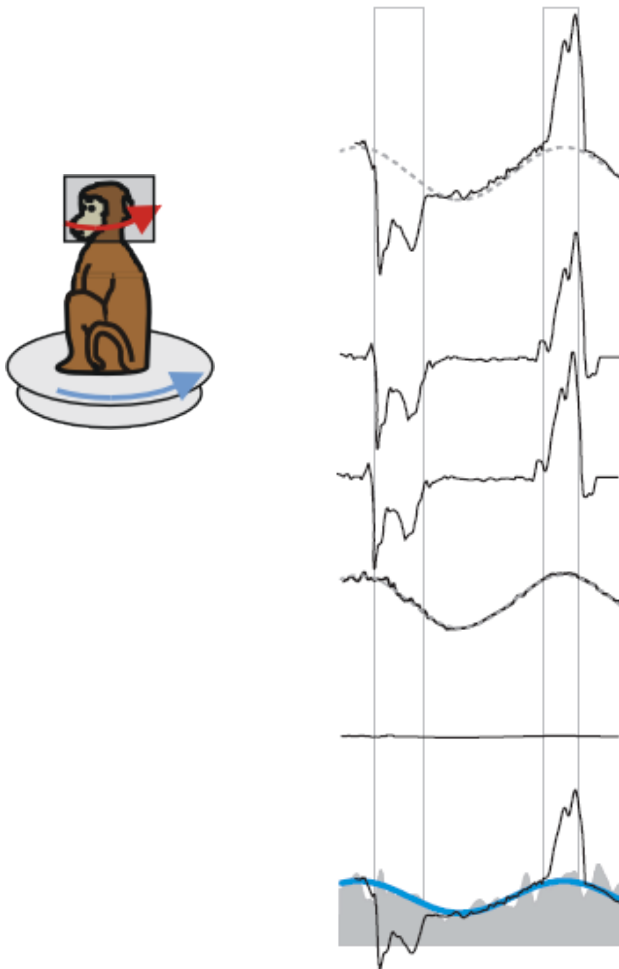


# and Bimodal Neurons no longer encode Body motion

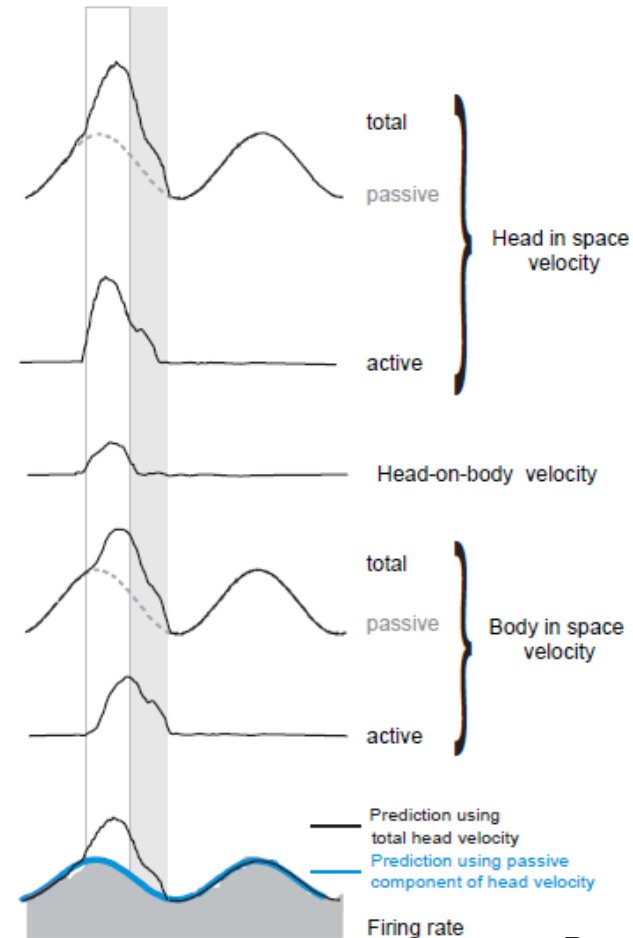


Moreover, during concurrent active/passive movements unimodal neurons selectively encode **passive head** motion

Passive head motion and  
Active head motion

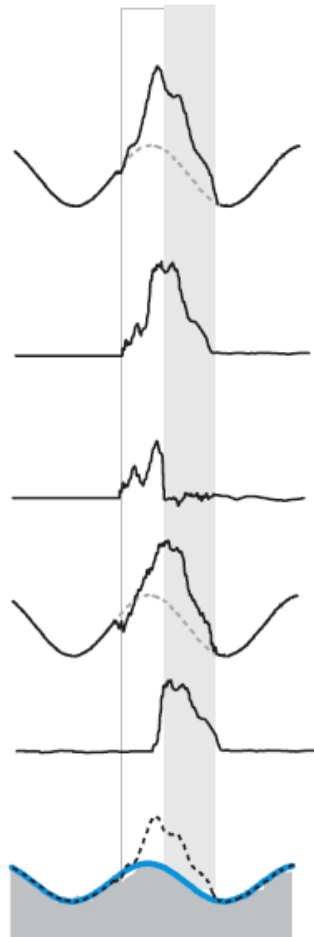
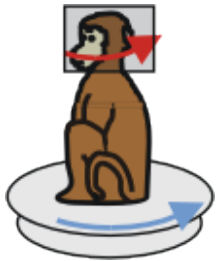


Passive head motion and  
Active head motion

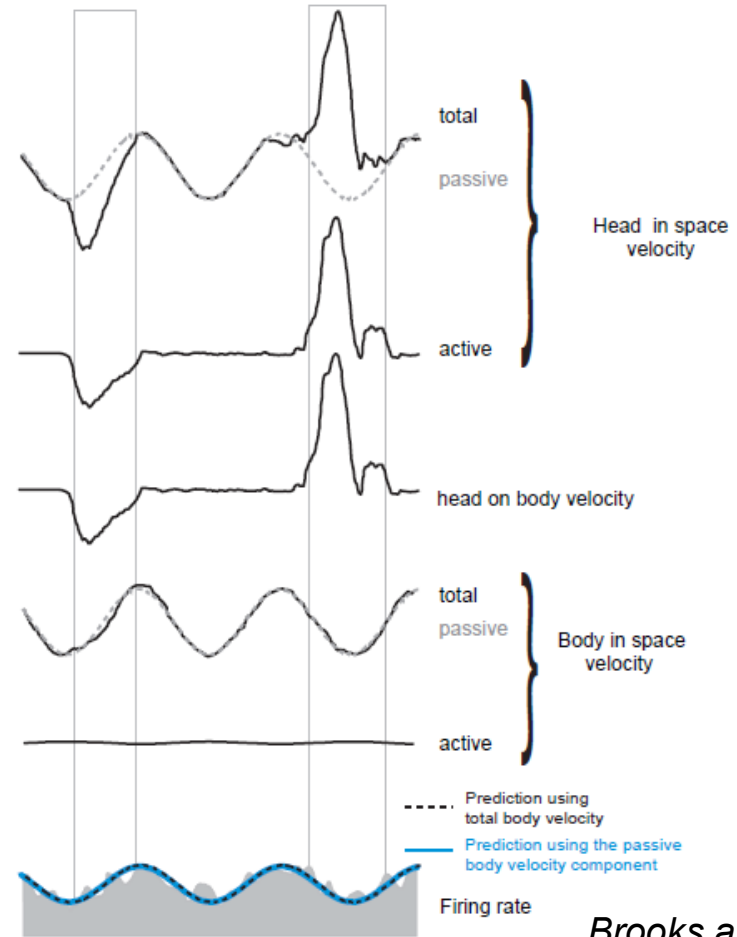


# And, bimodal neurons selectively encode **passive body** motion

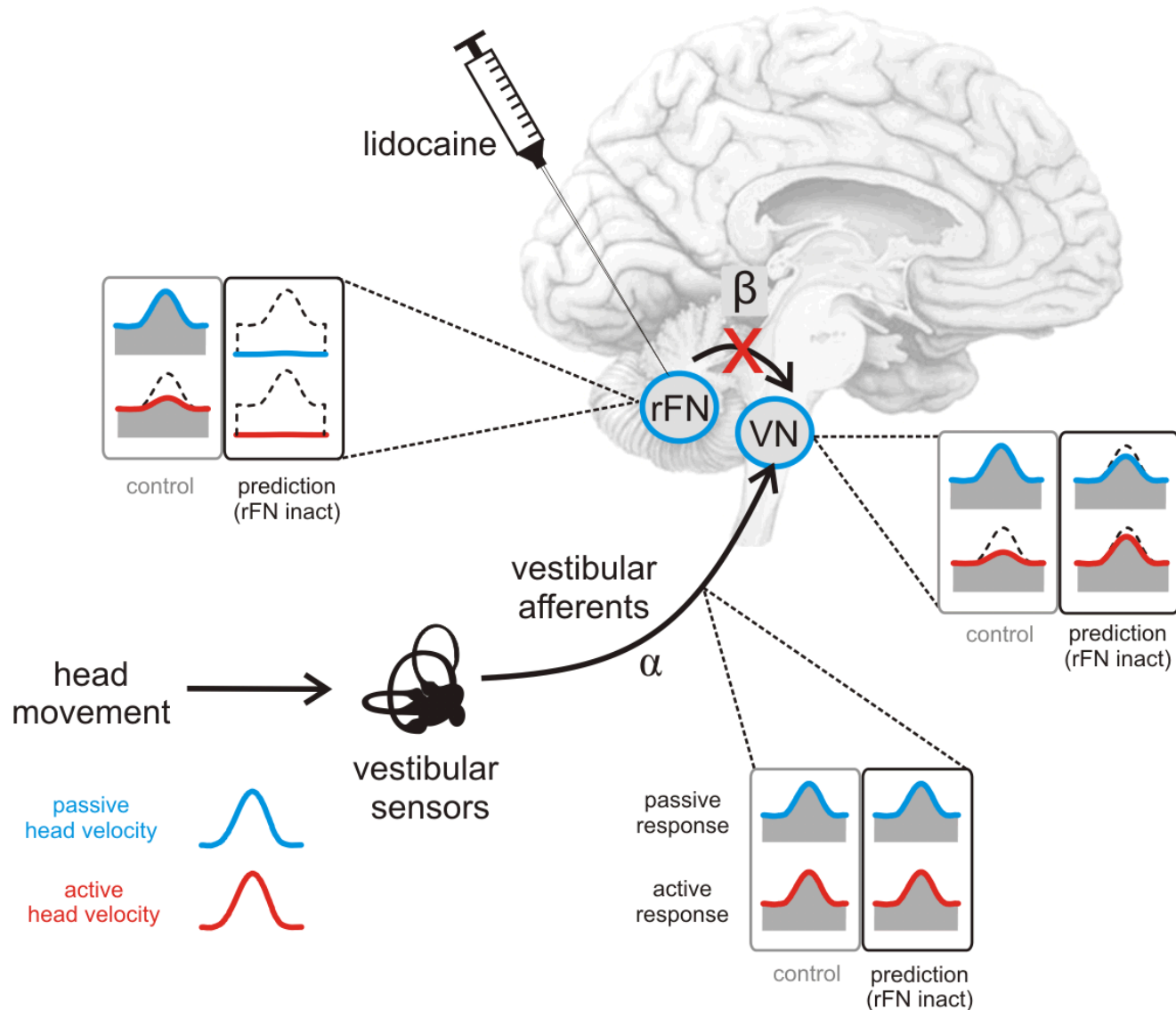
## Passive body motion and Active body motion



## Passive body motion and Active body motion

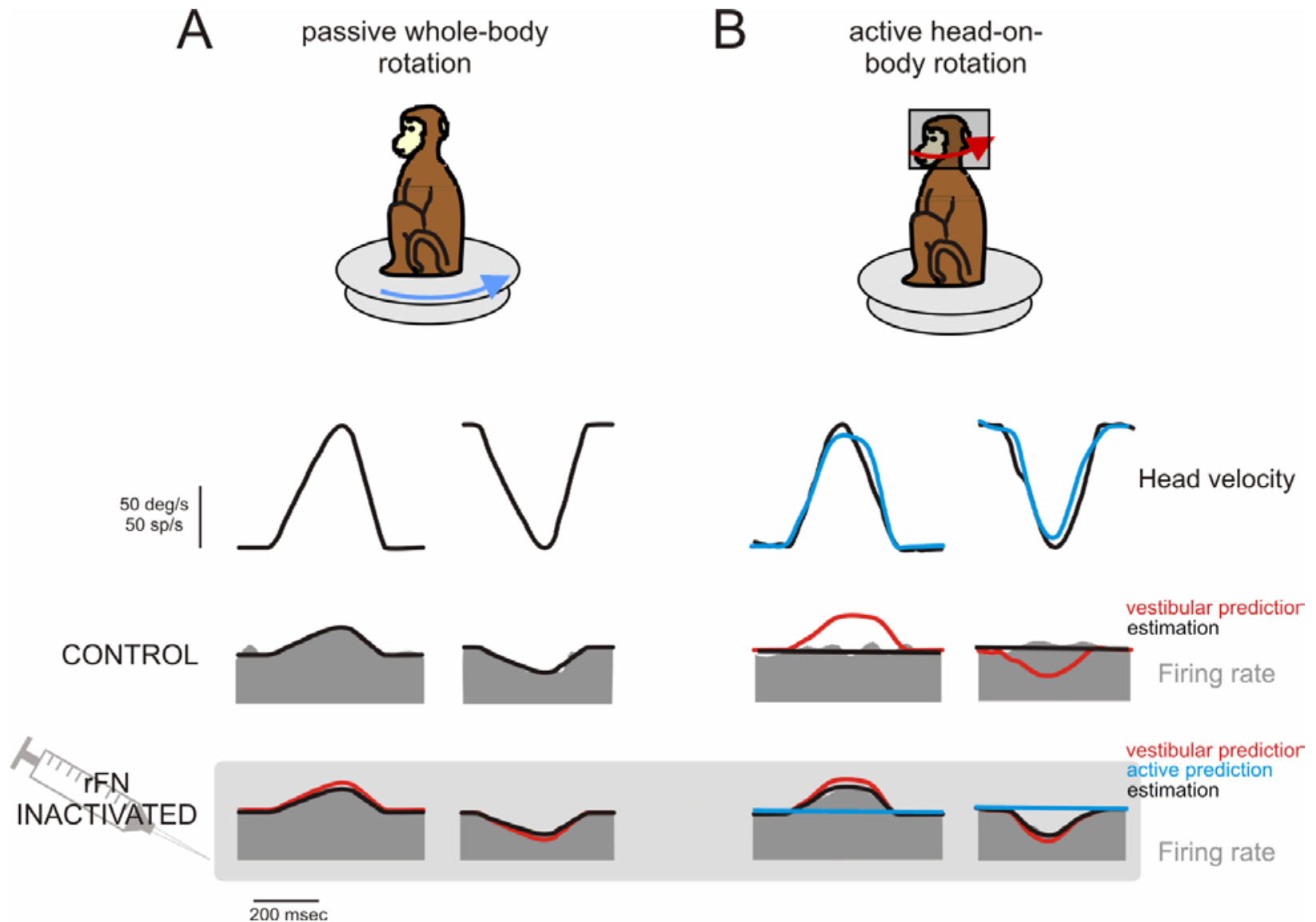


# What is the functional significance of the differential processing of active vs. passively motion by the cerebellum?



# Effect of cerebellar inactivation on VO neuron responses

Neuron now shows comparable responses to active and passive motion consistent with a role for the cerebellum in reafferent suppression.



## Summary:

Our results suggest that while vestibular afferents robustly encode both active and passive head motion, central neurons respond preferentially to passive motion.

This raises the question: What mechanism governs the differential encoding of active vs. passive motion?



## Summary:

Our results suggest that while vestibular afferents robustly encode both active and passive head motion, central neurons respond preferentially to passive motion.

This raises the question:

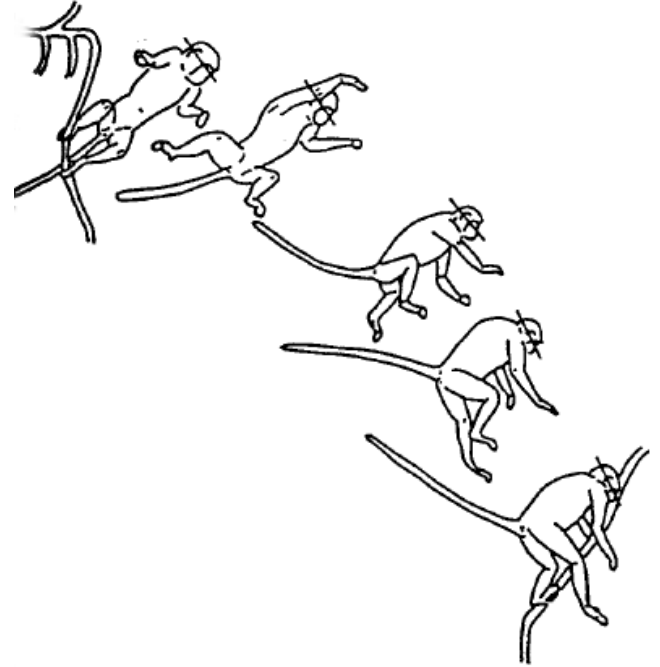
How is reafferent vestibular stimulation suppressed?

- A cancellation signal is generated when the activation of proprioceptors matches the motor-generated expectation.
- Moreover, this central cancellation mechanism is highly adaptable.
- Cerebellar output neurons provide an explicit representation of unexpected motion, that contributes to the cancellation of vestibular reafference.

# Functional Role of Central Vestibular Neurons

Neurons at the first central stage of vestibular processing:

- Detect specific features via non-linear transformations of their afferent input
- Respond preferentially to passive (versus active) motion



---

# Sensorimotor transformations: Vestibulo-spinal Reflexes

## 1. Static Non-linearities

- Boosting non-linearity in central vestibular neurons
- Gain-fields in the cerebellum

## 2. Dynamic Non-linearities

- Suppression of Reafference and common strategies across systems
- Learning in vestibulo-spinal reflex pathways

## Current hypothesis:

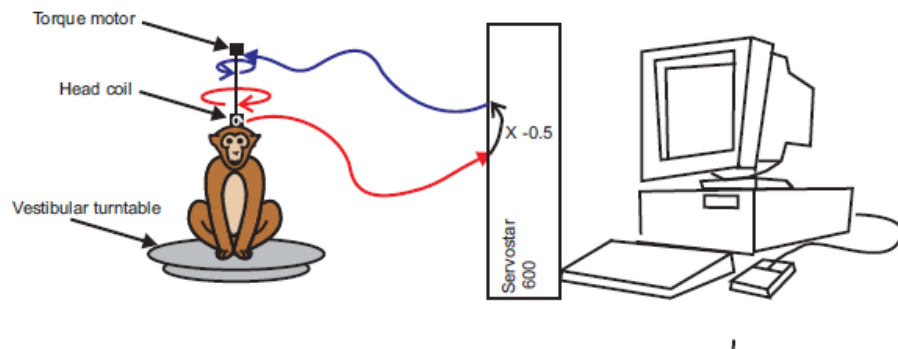
Suppression of **vestibular reafference** occurs when proprioceptive feedback matches that expected as a result of the motor command  
(as during normal active movements)

If this is true,

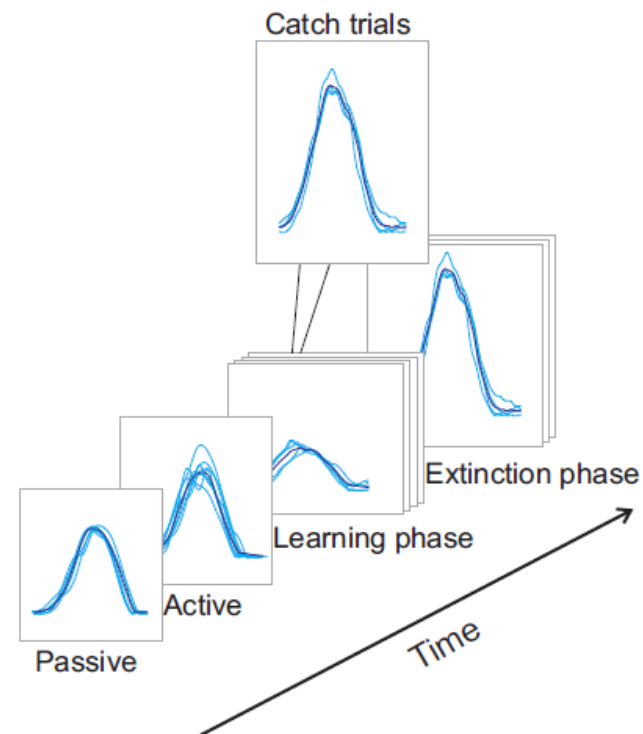
then reafferent suppression should not occur when the relationship between motor commands and sensory reafference is altered.

**Experiment:** Change the relationship between motor commands and sensory reafference  
via application of resistive torque: **Behavior**

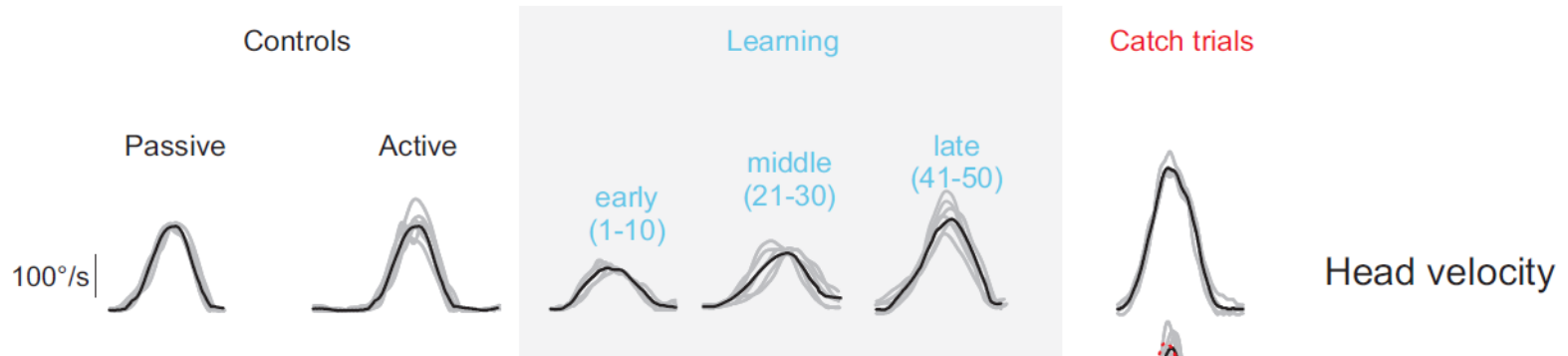
A



B



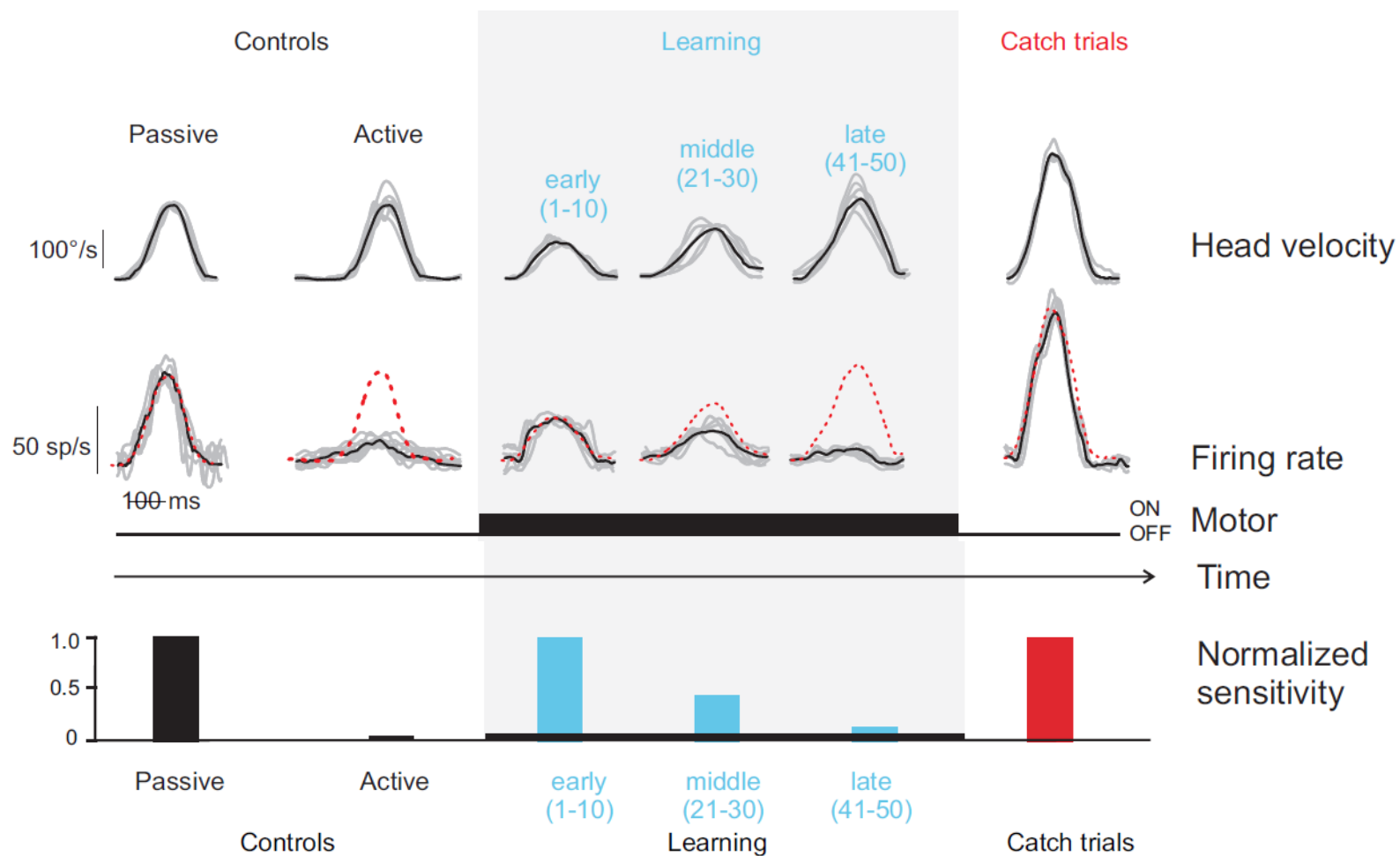
**Experiment:** Change the relationship between motor commands and sensory reafference via application of resistive torque: **Behavior**



## The time course of Behavioral Adaptation

- 1) The animal learns to adapt by trial 10.
- 2) Head overshoots the initial trajectory once resistance is removed.

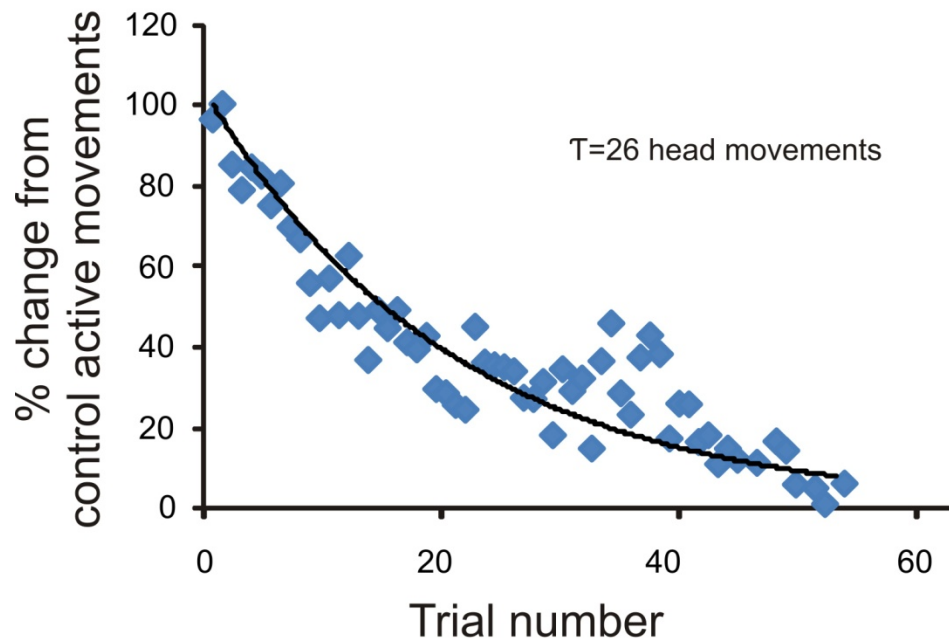
**Experiment:** Change the relationship between motor commands and sensory reafference via application of resistive torque: **Neurons**



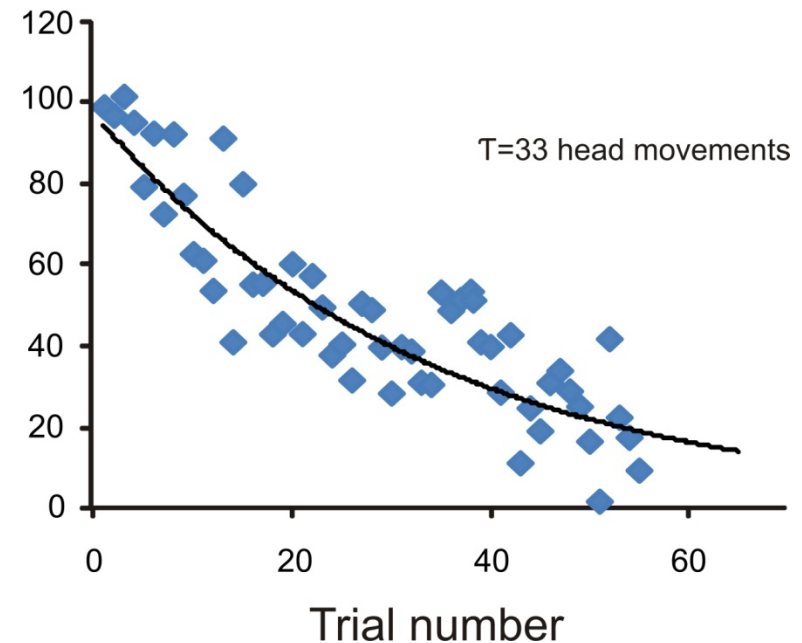
# The Time Course:

Of Behavioural and Neuronal Adaptation are Comparable

## Peak head velocity



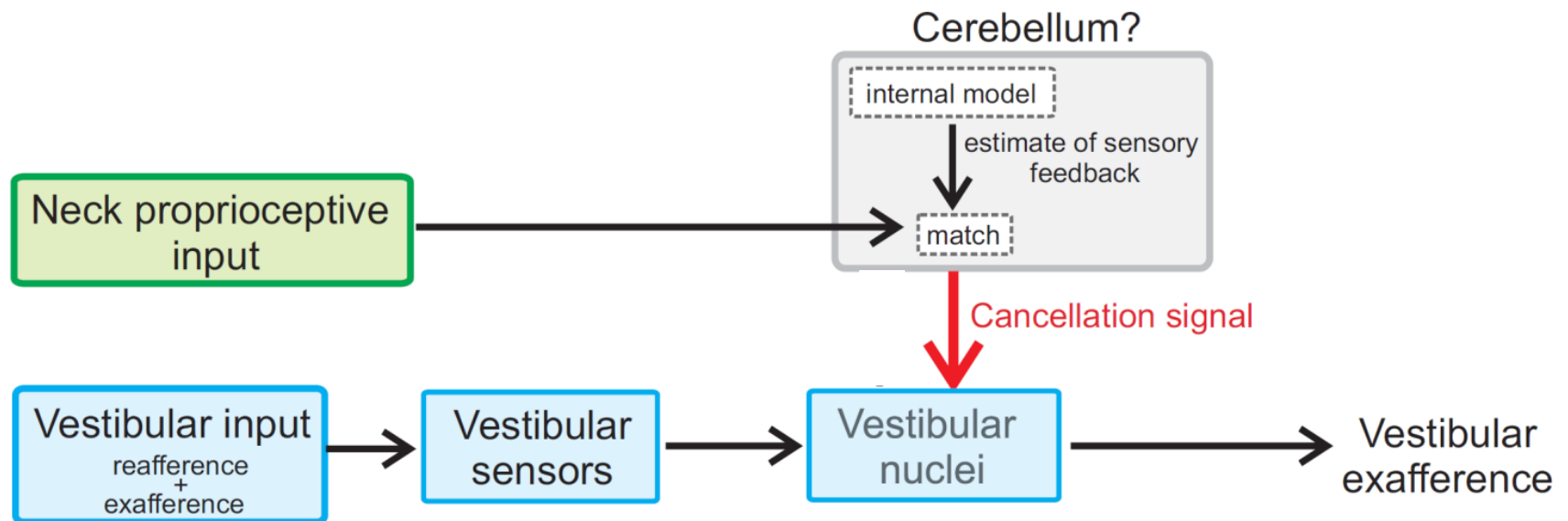
## Neuronal sensitivity





## Current hypothesis:

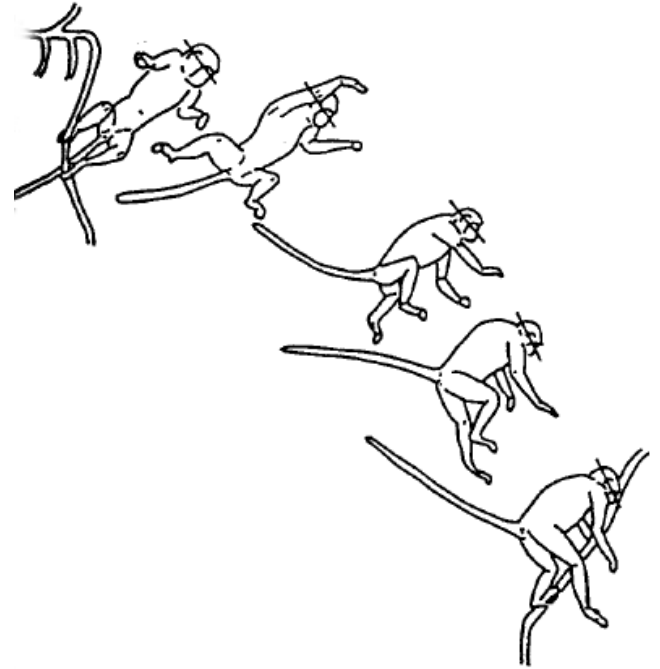
Suppression of vestibular reafference occurs when proprioceptive feedback matches that expected as a result of the motor command (as during normal active movements):



# Functional Role of Central Vestibular Neurons

Neurons at the first central stage of vestibular processing:

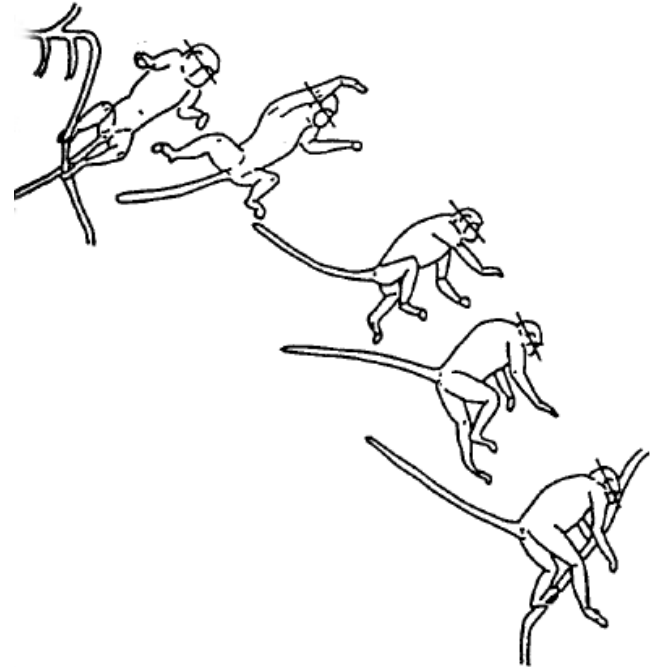
- Detect specific features via non-linear transformations of their afferent input



# Functional Role of Central Vestibular Neurons

Neurons at the first central stage of vestibular processing:

- Detect specific features via non-linear transformations of their afferent input
- Respond preferentially to passive (versus active) motion

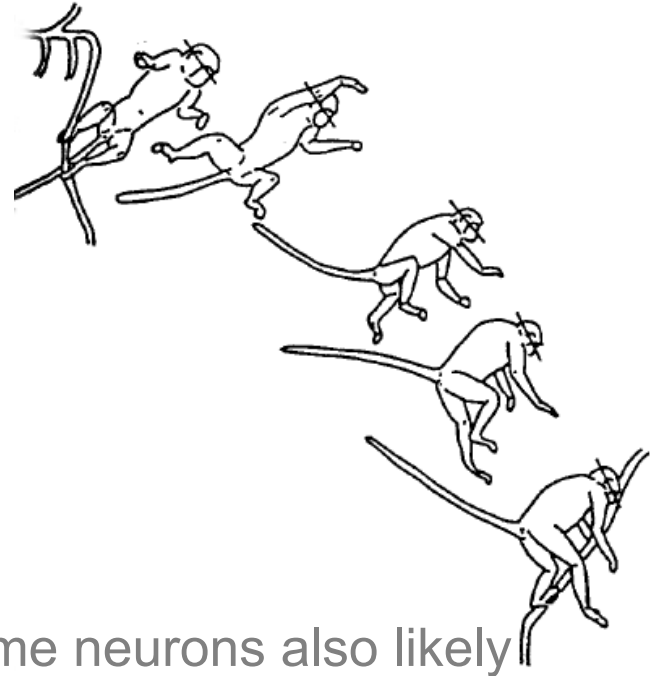


# Functional Role of Central Vestibular Neurons

Neurons at the first central stage of vestibular processing:.

- Detect specific features via non-linear transformations of their afferent input
- Respond preferentially to passive (versus active) motion
- Internal model updated with a few movements

Stabilize posture during unexpected transient disturbances, or when falling, or locomotion on uneven surfaces.



These same neurons also likely transmit self-motion information to higher level areas that contributes to perception during everyday activities



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# Sensorimotor transformations: Vestibulo-spinal Reflexes

## 1. Static Non-linearities

- Boosting non-linearity in central vestibular neurons
- Gain fields in the vestibulo-cerebellum

## 2. Dynamic Non-linearities

- Suppression of Reafference and common strategies across systems
- Learning in vestibulo-spinal reflex pathways

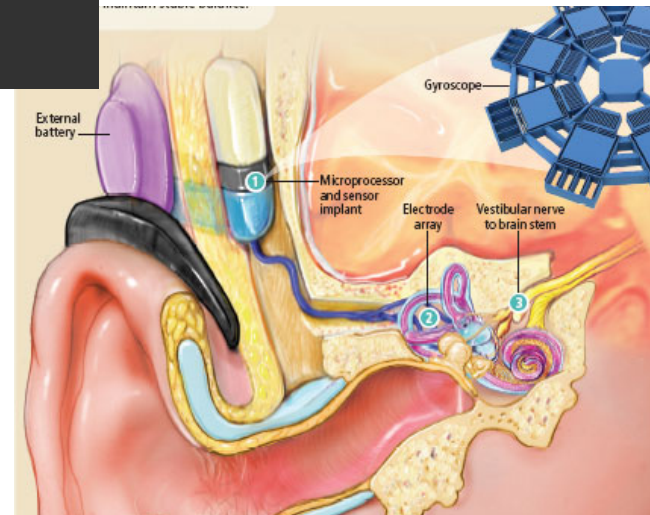
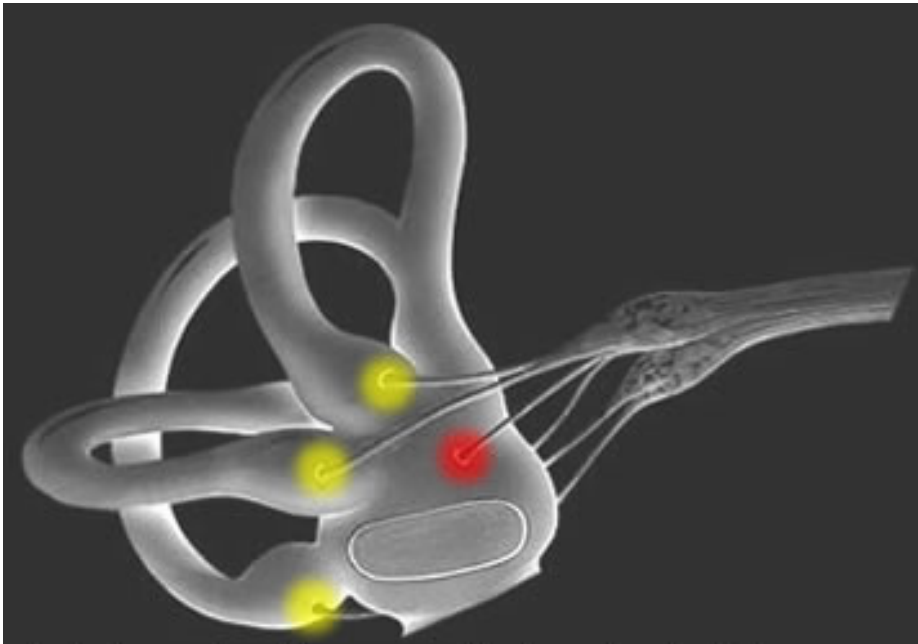
# Non-linear sensory-motor transformations

## Vestibulo-spinal pathways



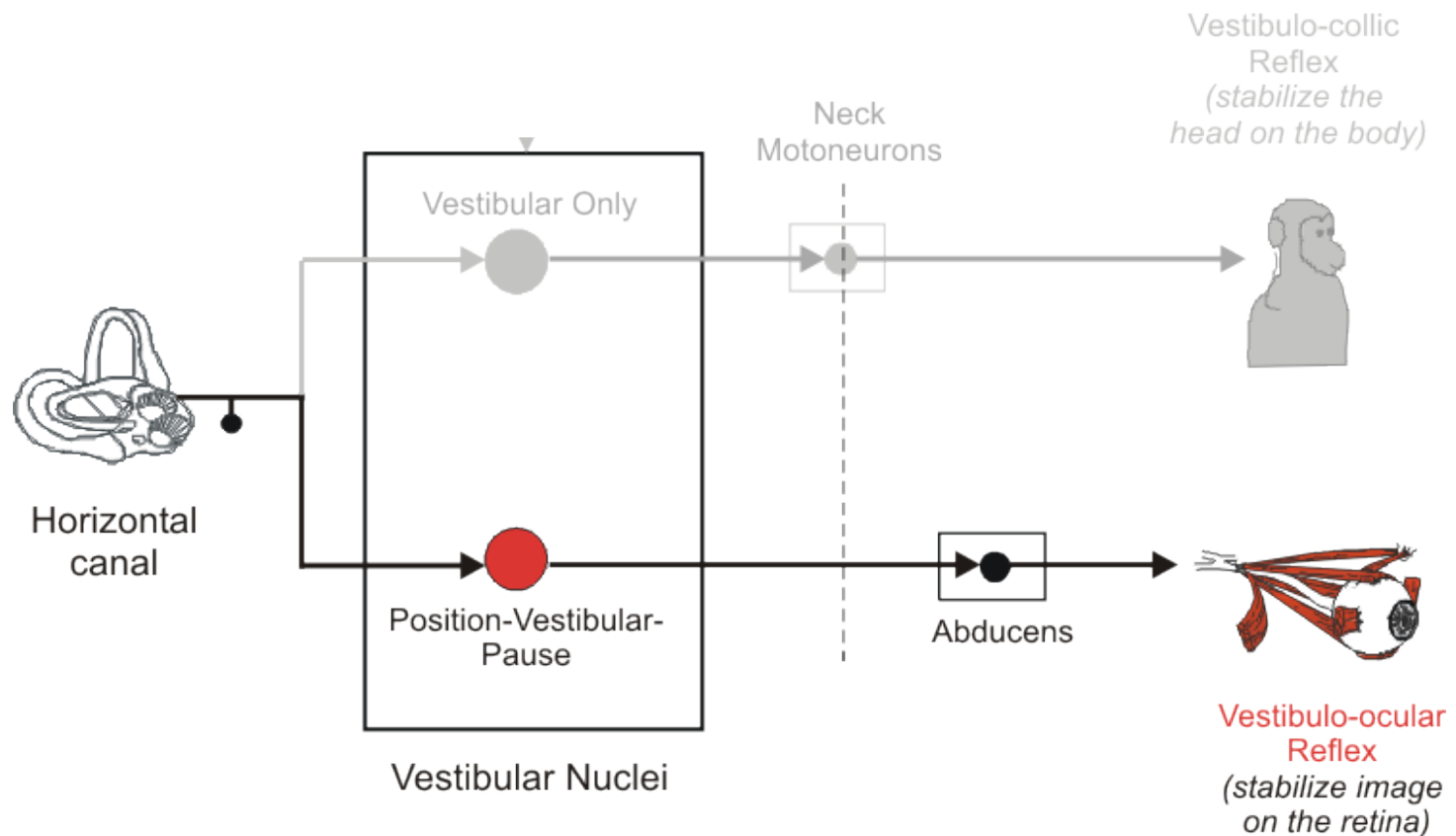
# Vestibular compensation:

## Neurophysiology of Vestibular Compensation Neural Correlates of Prosthetic Stimulation



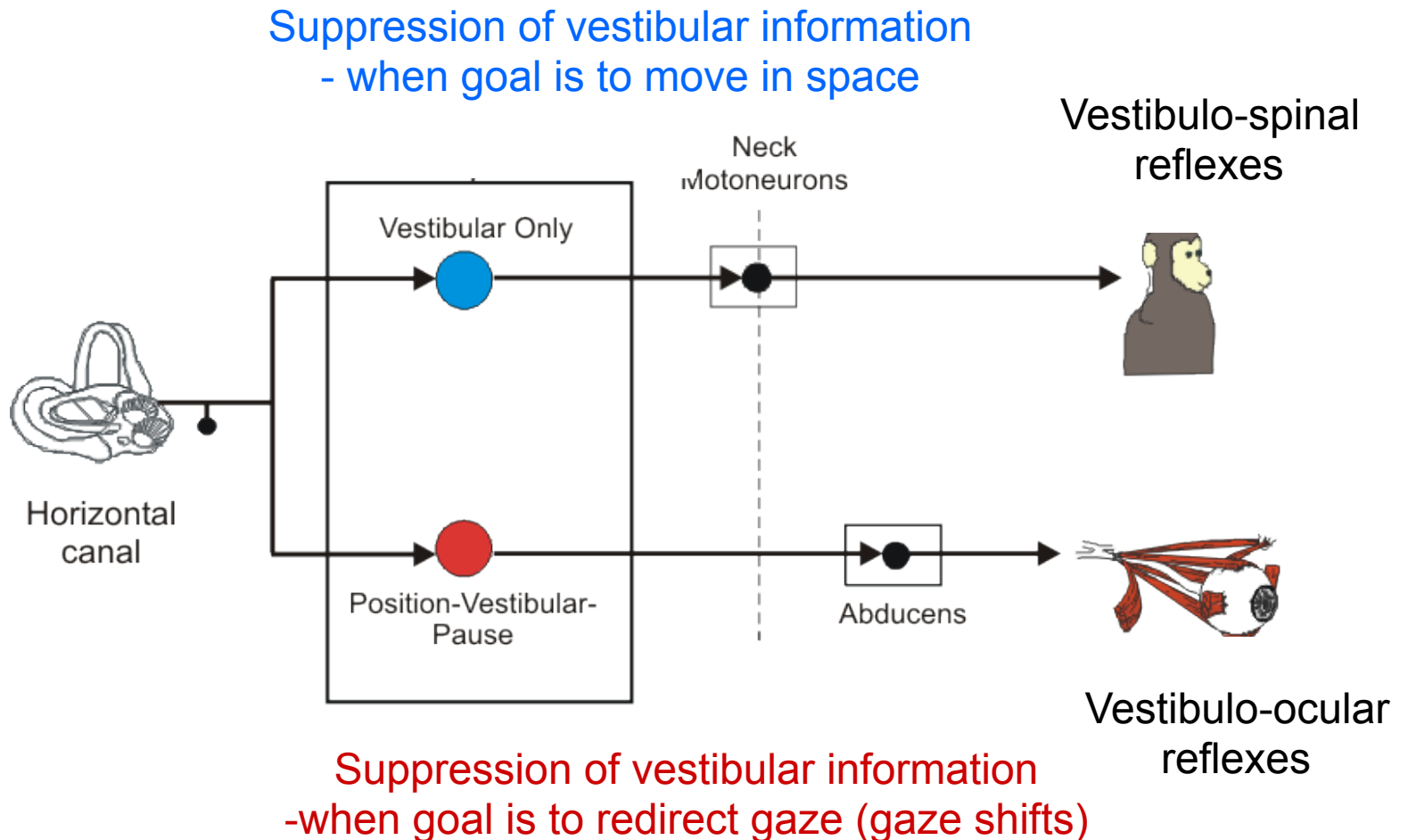
Is the differential processing of active and passively generated vestibular stimulation a general feature of all early vestibular pathways processing?

No, Consider the neurons that produce the VOR





This differential processing by different cell classes in the vestibular nuclei is consistent their functional roles:



## Gain field theory

