Multimodal Processing of Self-Motion Information

Non-Linear Transformations

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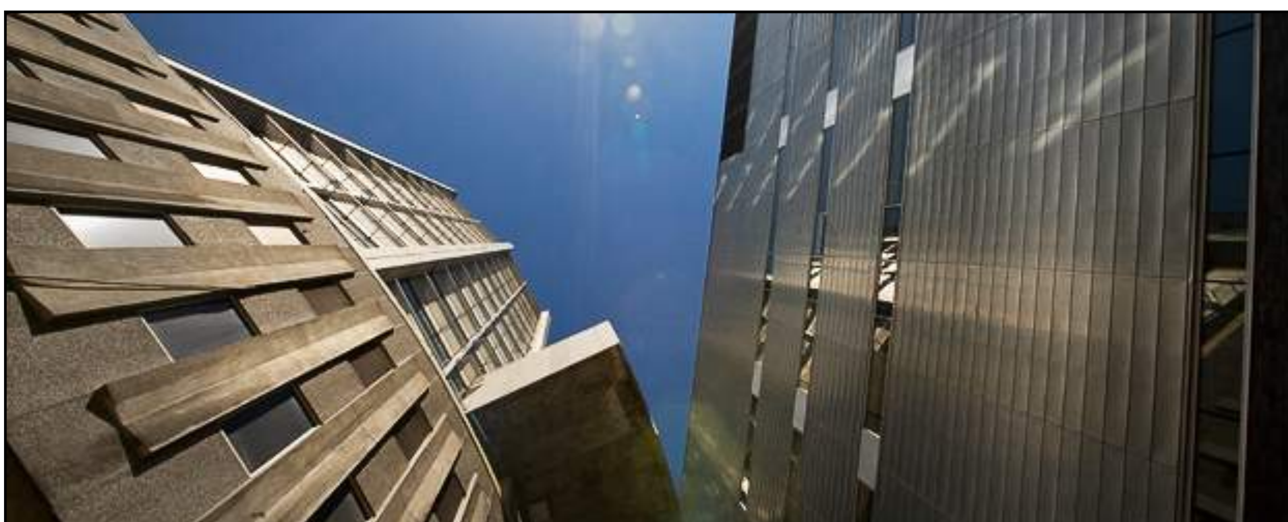
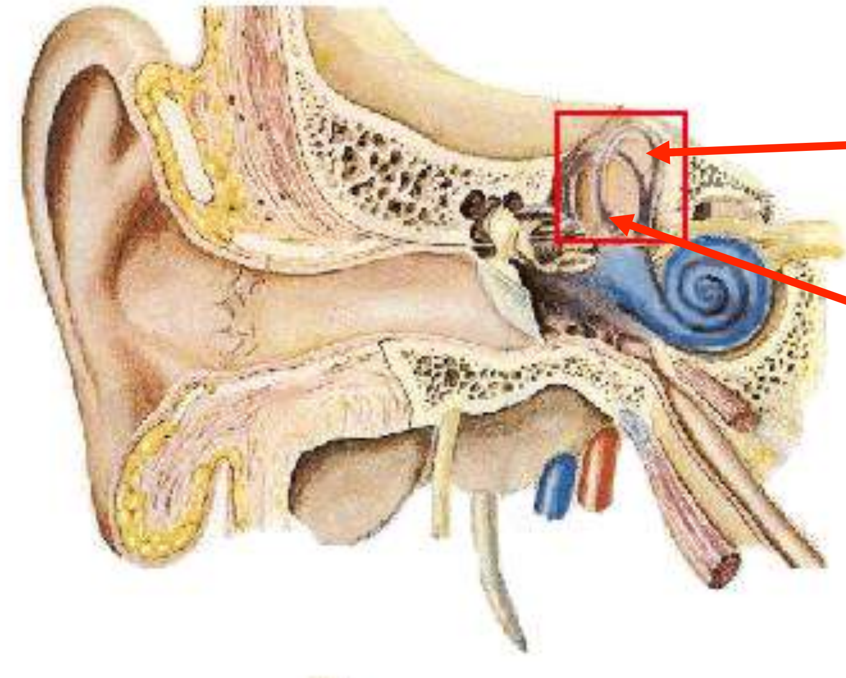


Function of the Vestibular System



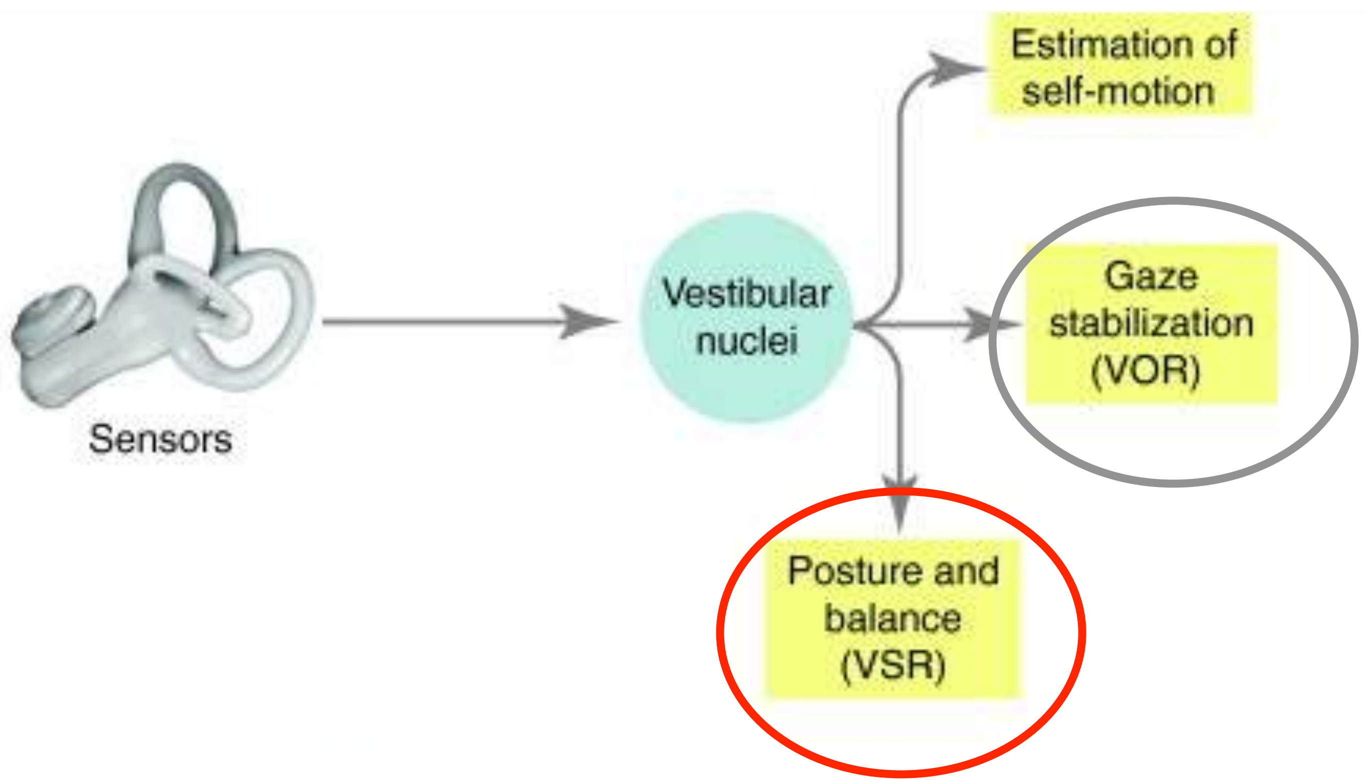
Semicircular canals
- sense angular rotation

Otoliths
- sense linear acceleration

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



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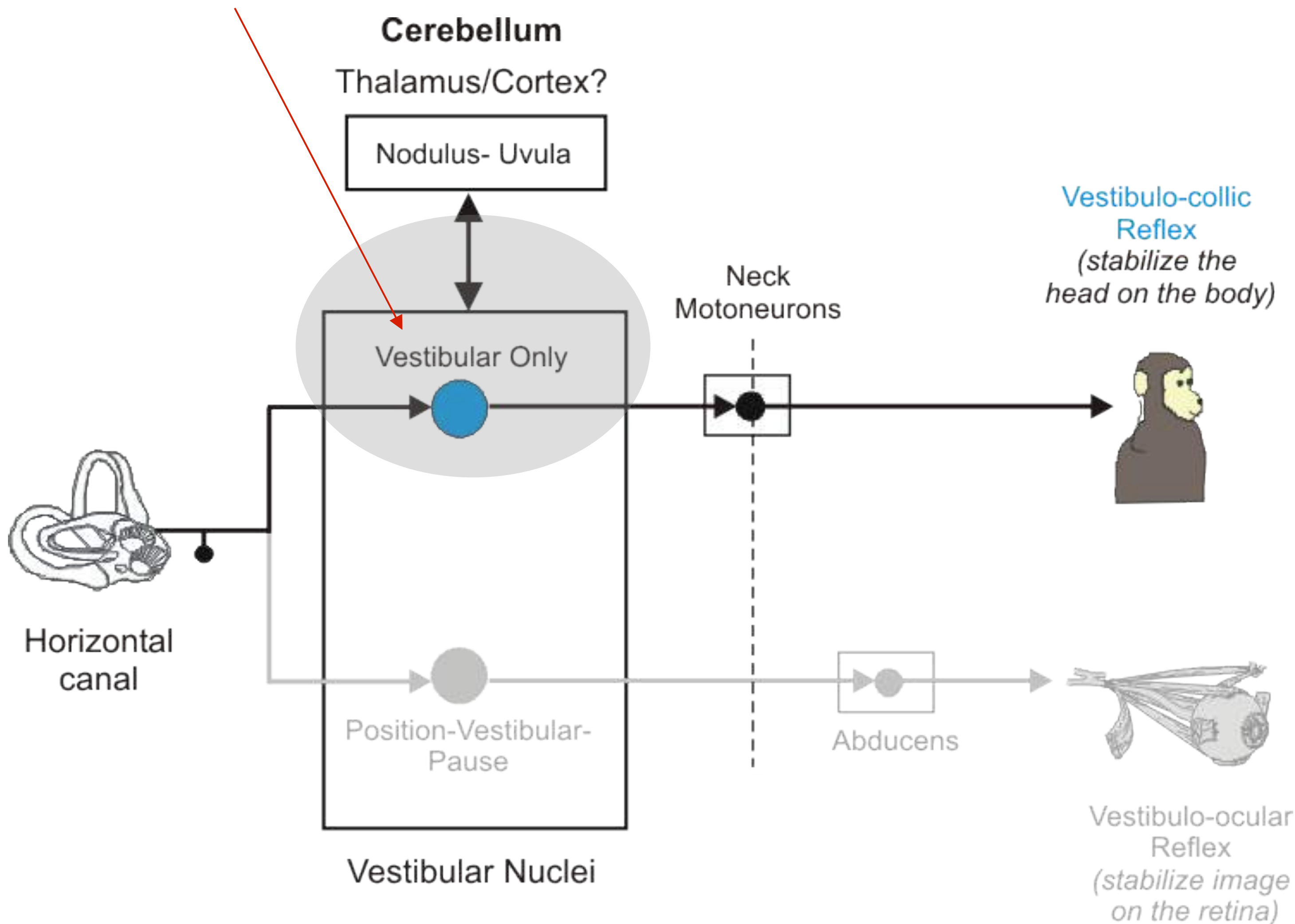


Lack of Balance after vestibular sensory loss

https://www.youtube.com/watch?v=DClAIf7rVb8

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.

Sensorimotor transformations: Vestibulo-spinal Reflexes

1. Static Non-linearities

    -Boosting non-linearity in central vestibular neurons

    -Gain fields in the vestibulo-cerebellum

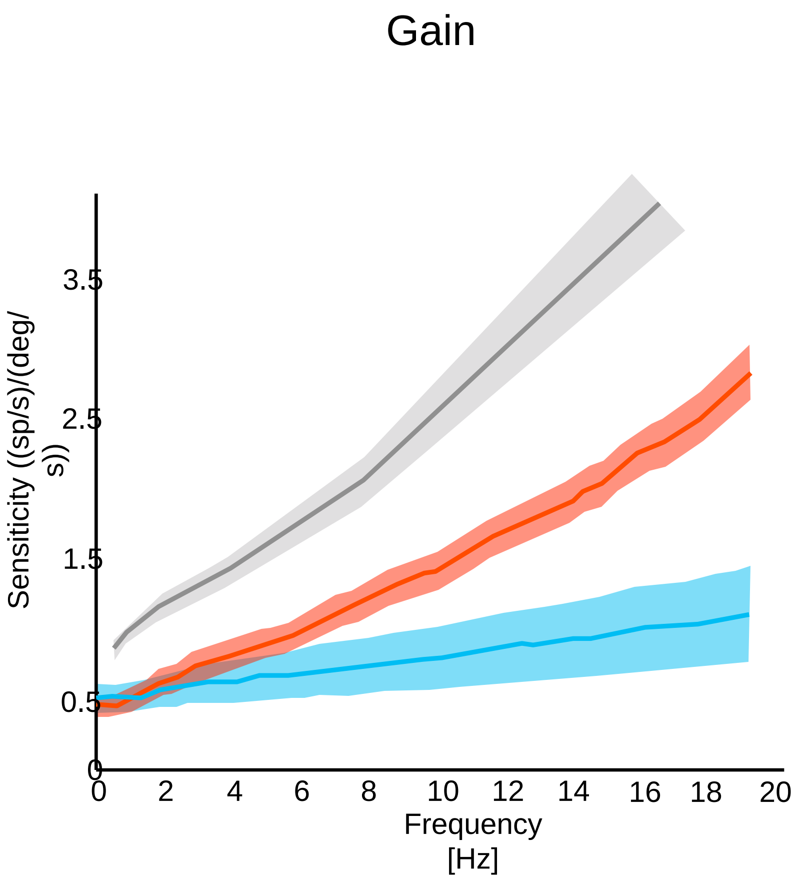
2. Dynamic Non-linearities

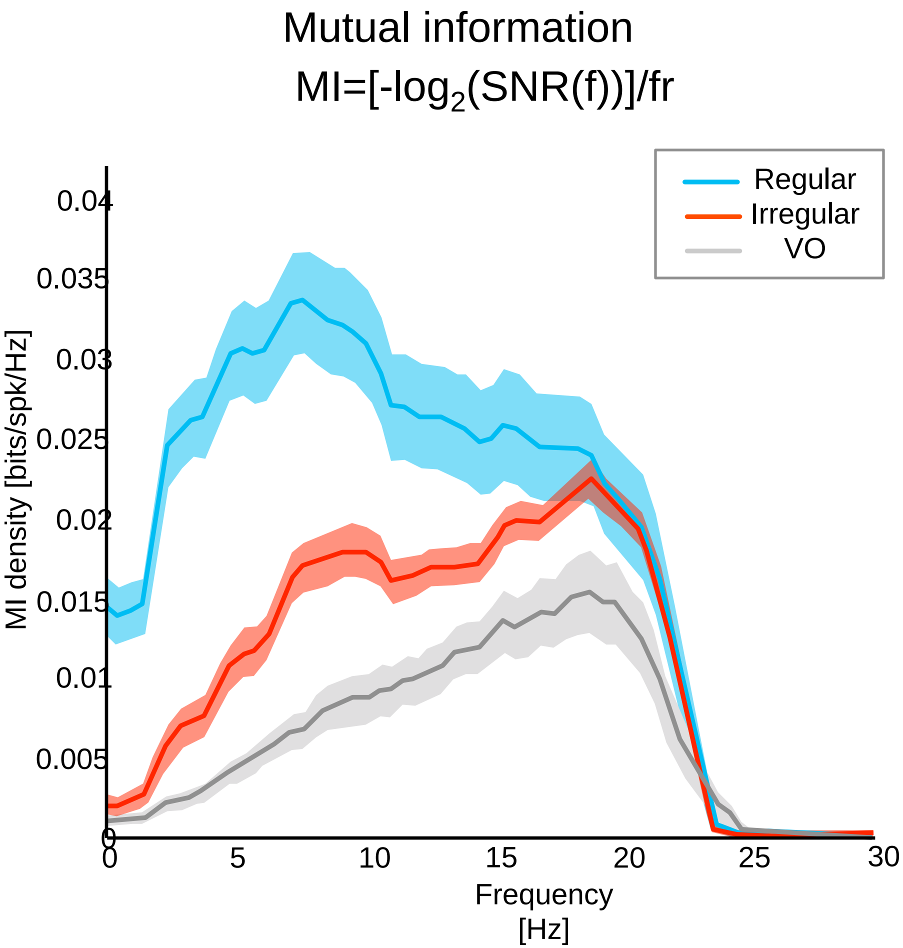
    - Suppression of Reafference and common strategies across systems

    - Learning in vestibulo-spinal reflex pathways

Recall from the last lecture:

Estimation of Gain versus Mutual Information

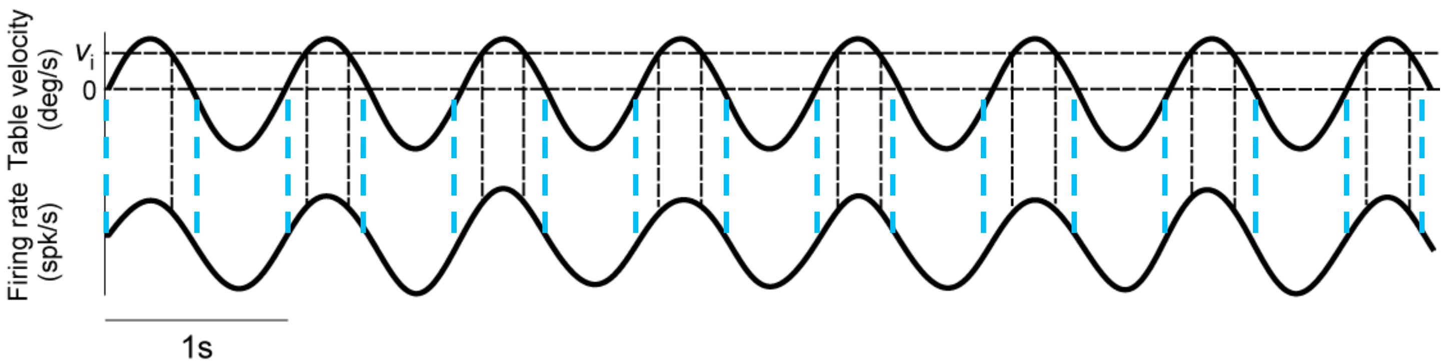




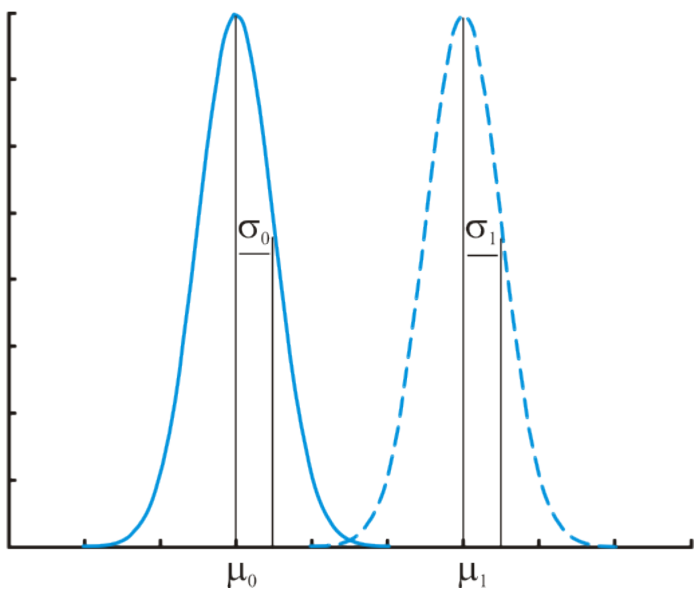
Note further that Central cells are tuned for higher frequencies, but encode less information than afferents…..

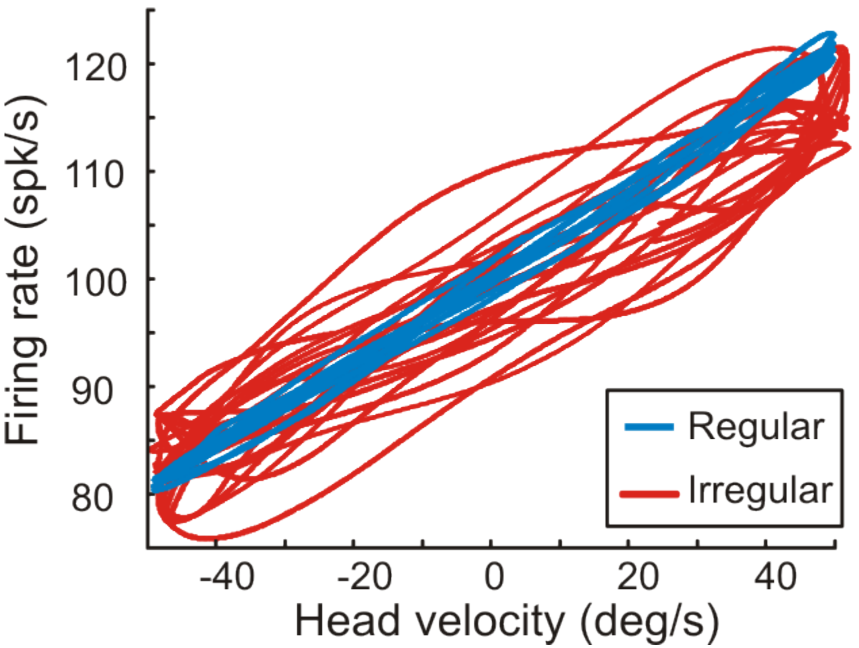
Massot, Chacron, and Cullen; 2011

Detection thresholds



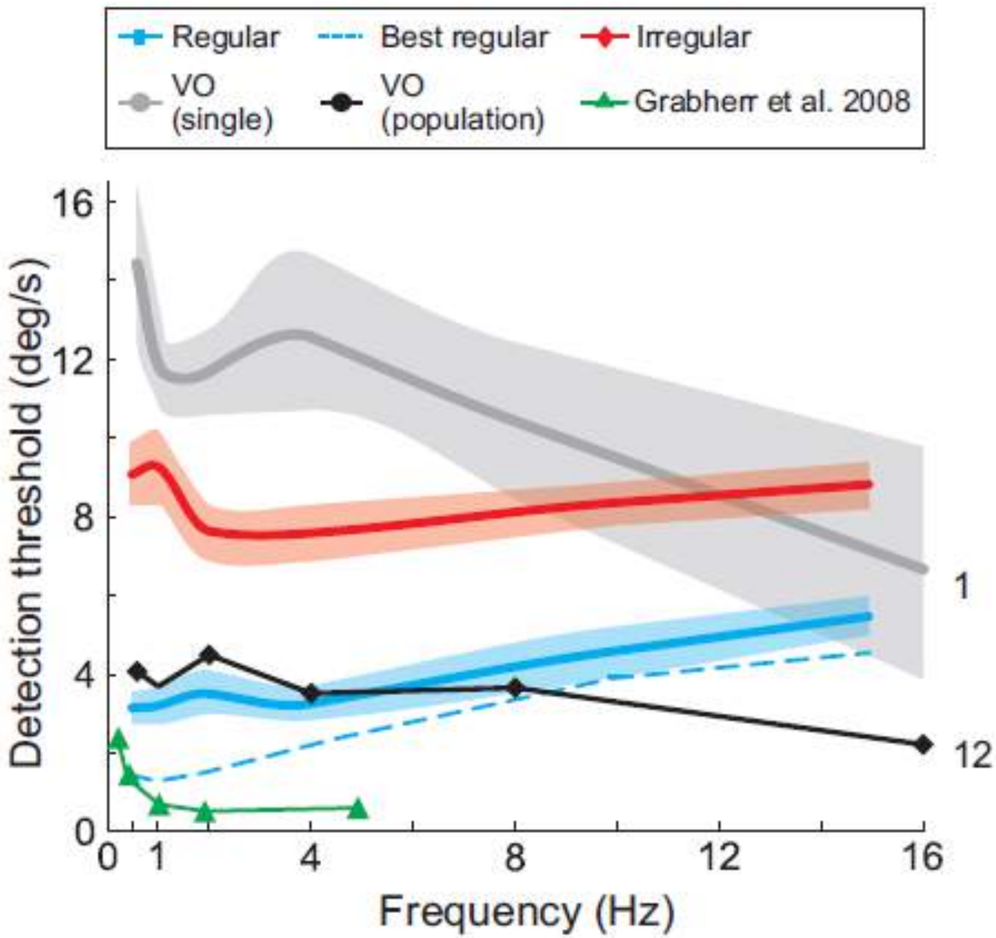
$$d' = (\mu_1 - \mu_0) / \sqrt{(\sigma_1^2 + \sigma_0^2)/2}$$



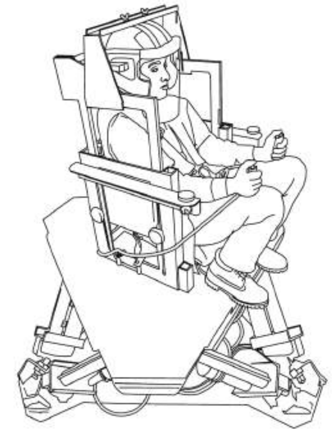


Sadeghi, Chacron, Taylor, and Cullen; J Neurosci 2007

Comparison of Detection Thresholds



Cullen, Trends in Neuroscience 2012



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?

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

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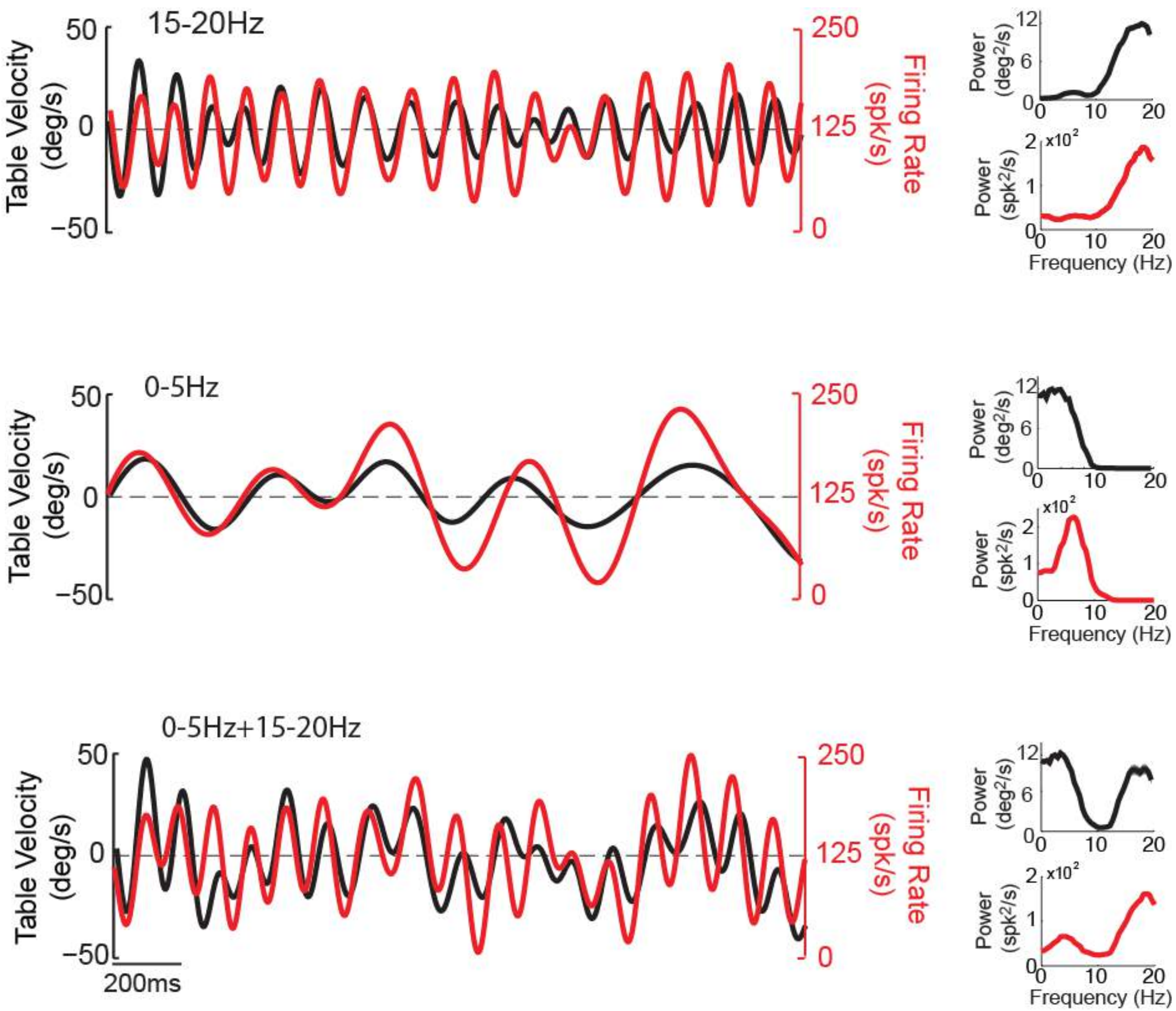
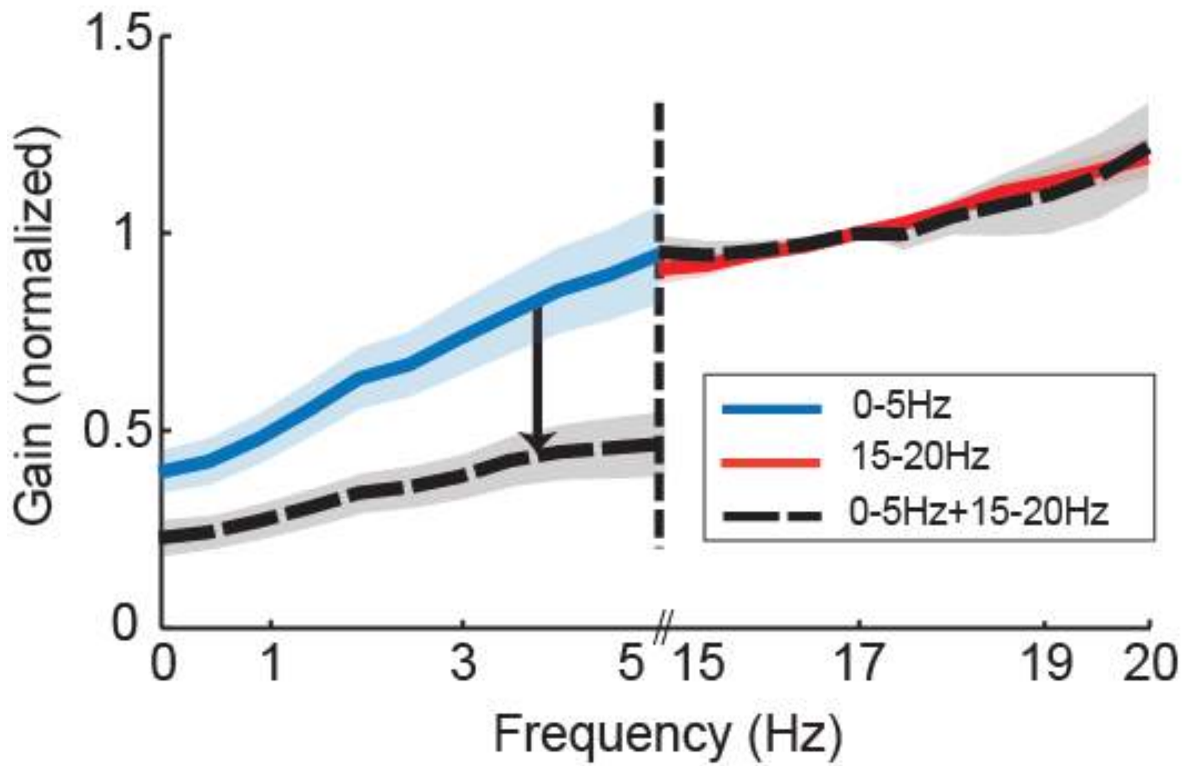
Experiment: High pass, Low Pass, and Summed Noise



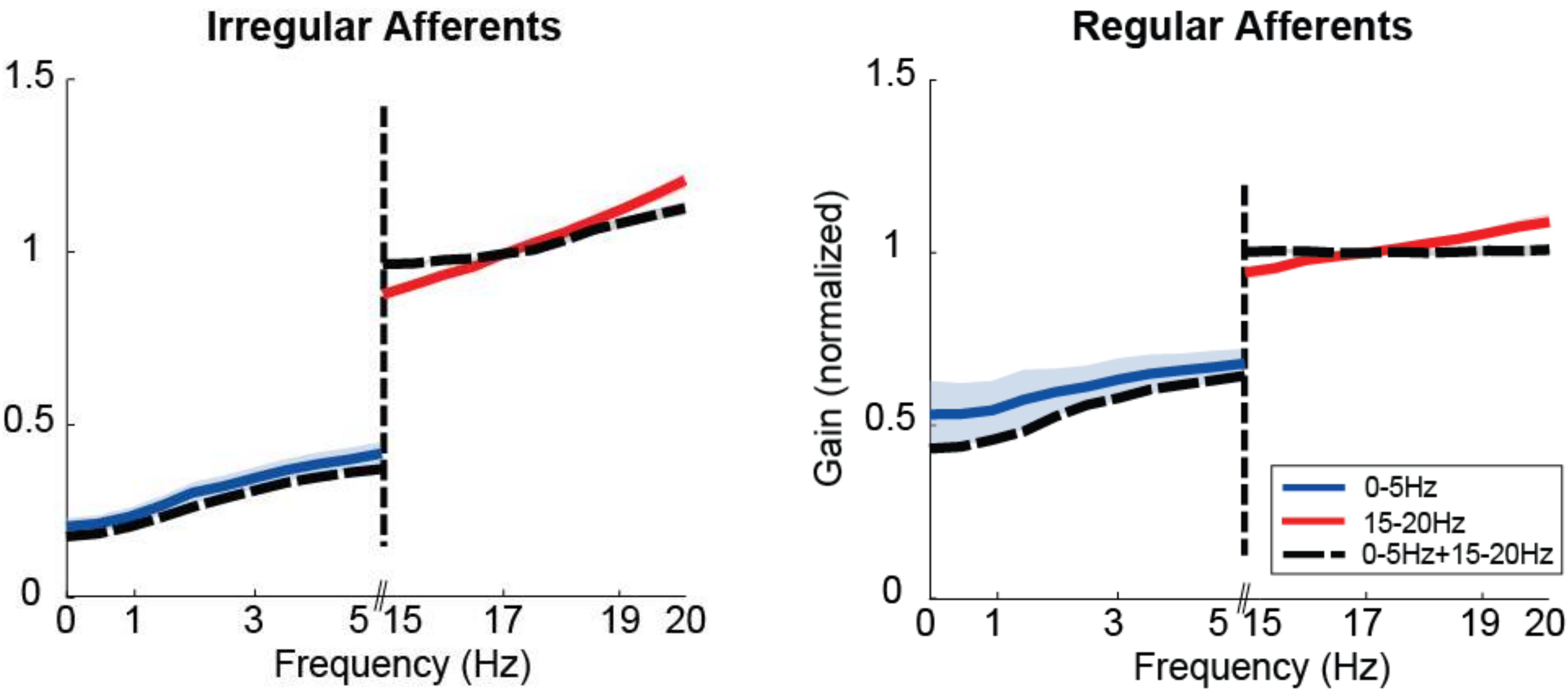
Central vestibular neurons respond nonlinearly to sums of noise stimuli.



Massot, Schneider, Chacron, and Cullen,

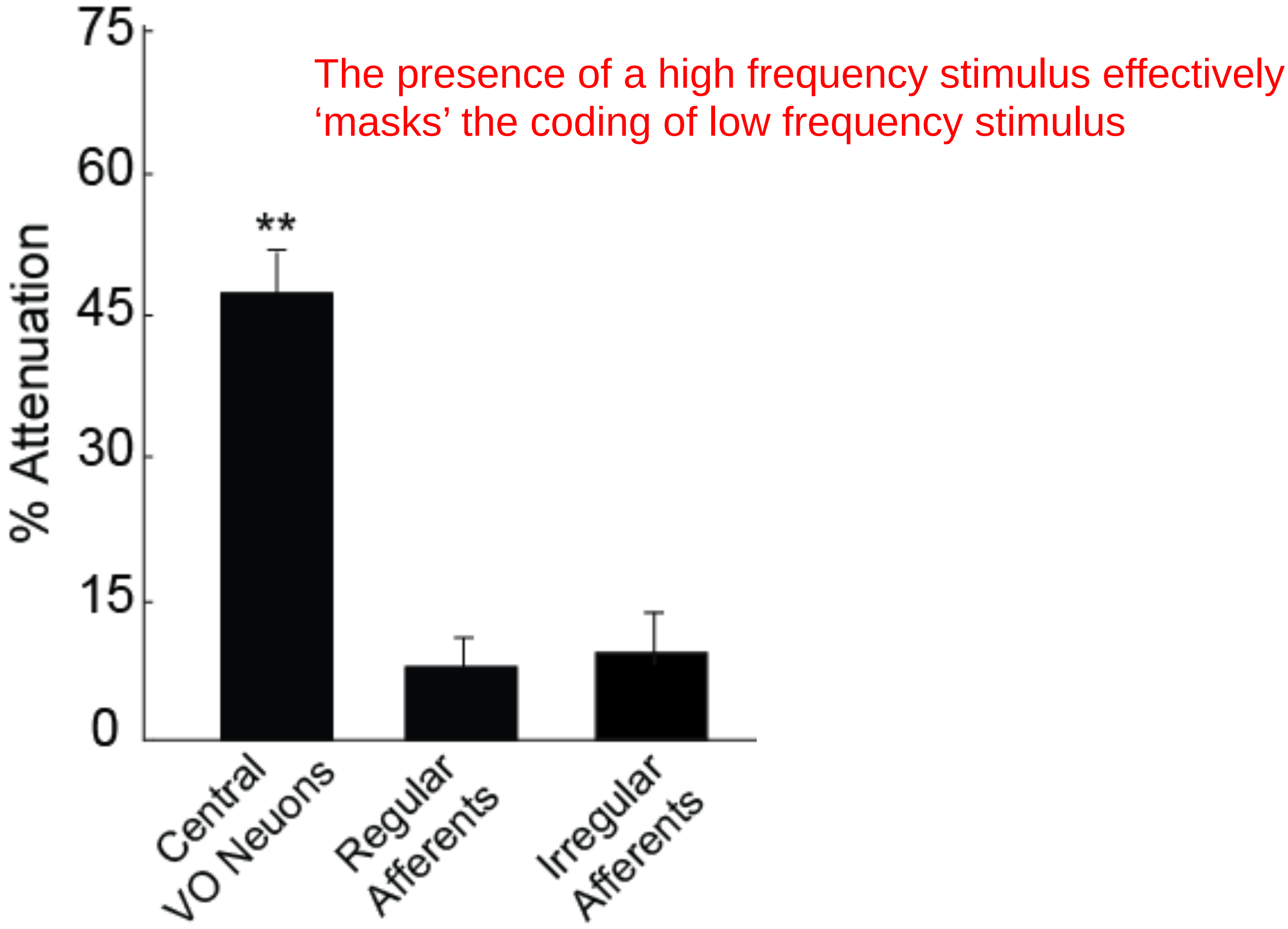
PLoS Biology 2012

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

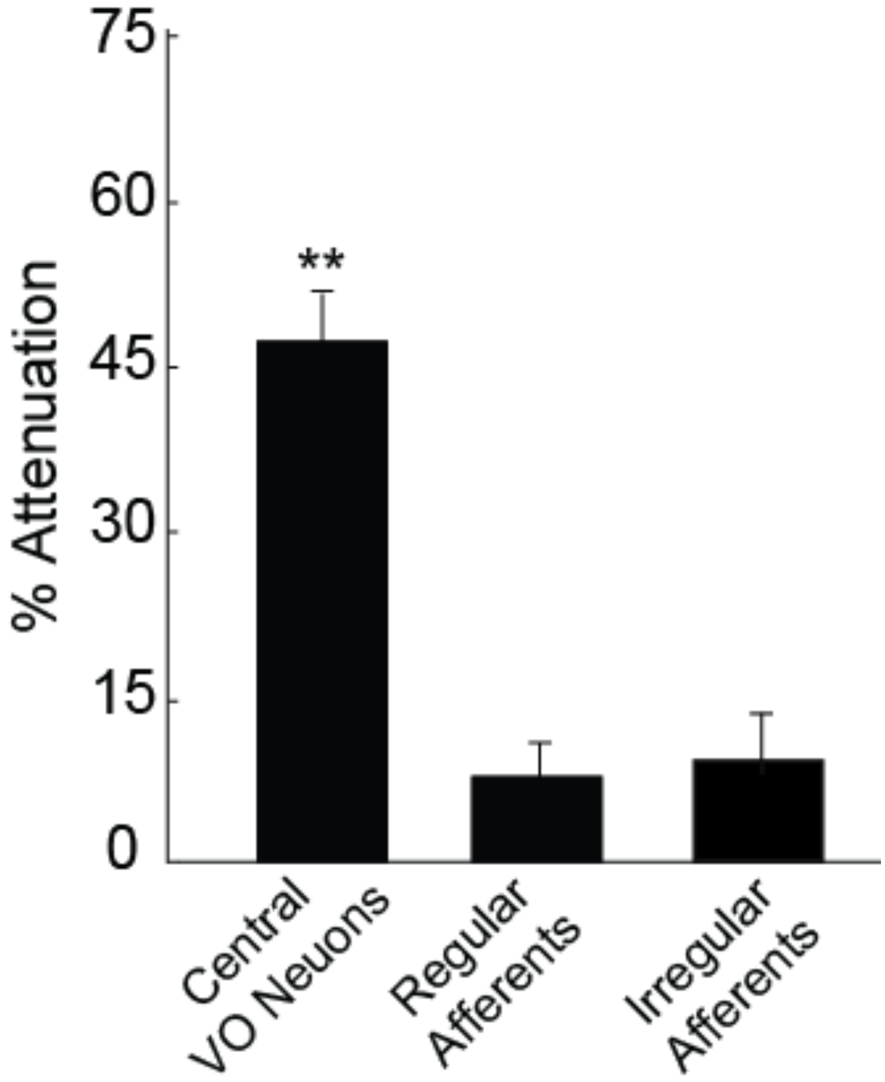


Massot, Schneider, Chacron, and Cullen,

PLoS Biology 2012



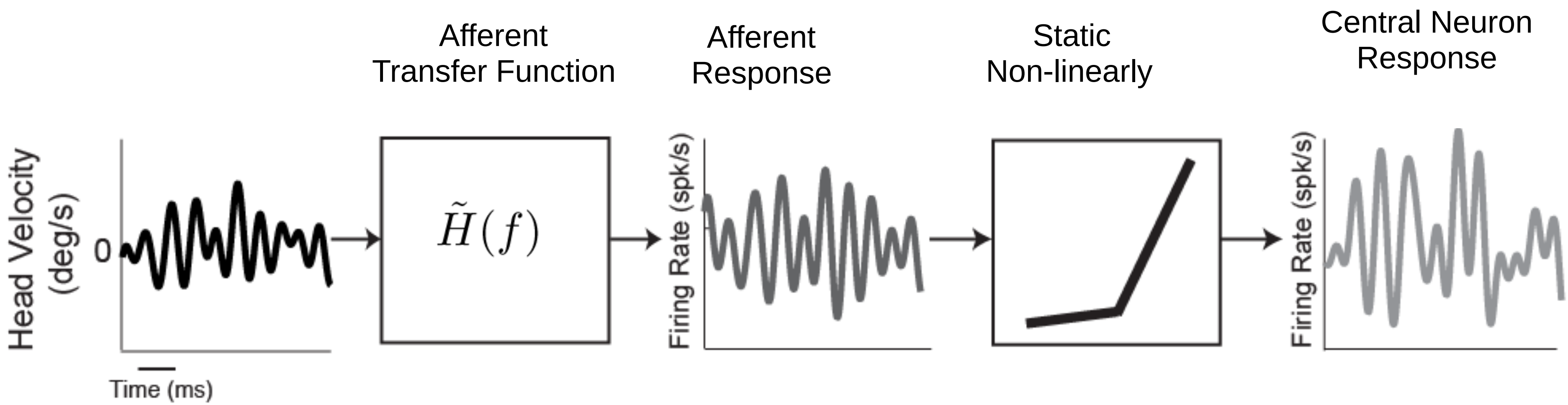
The central response nonlinearity is characterized by a strong (~50%) attenuation in neuronal sensitivity to low frequency stimuli when presented concurrently with high frequency stimuli.



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

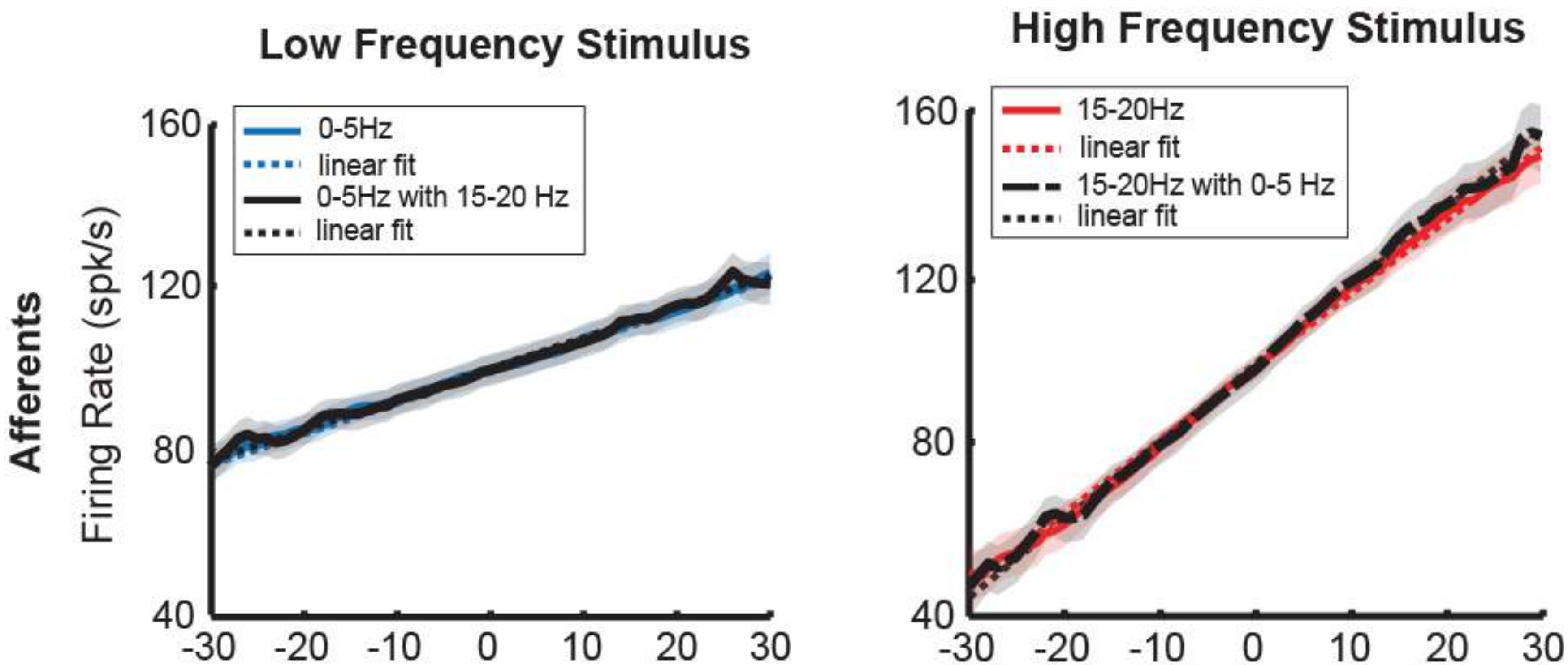
How do central vestibular neurons non-linearly Integrate their afferent input?

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



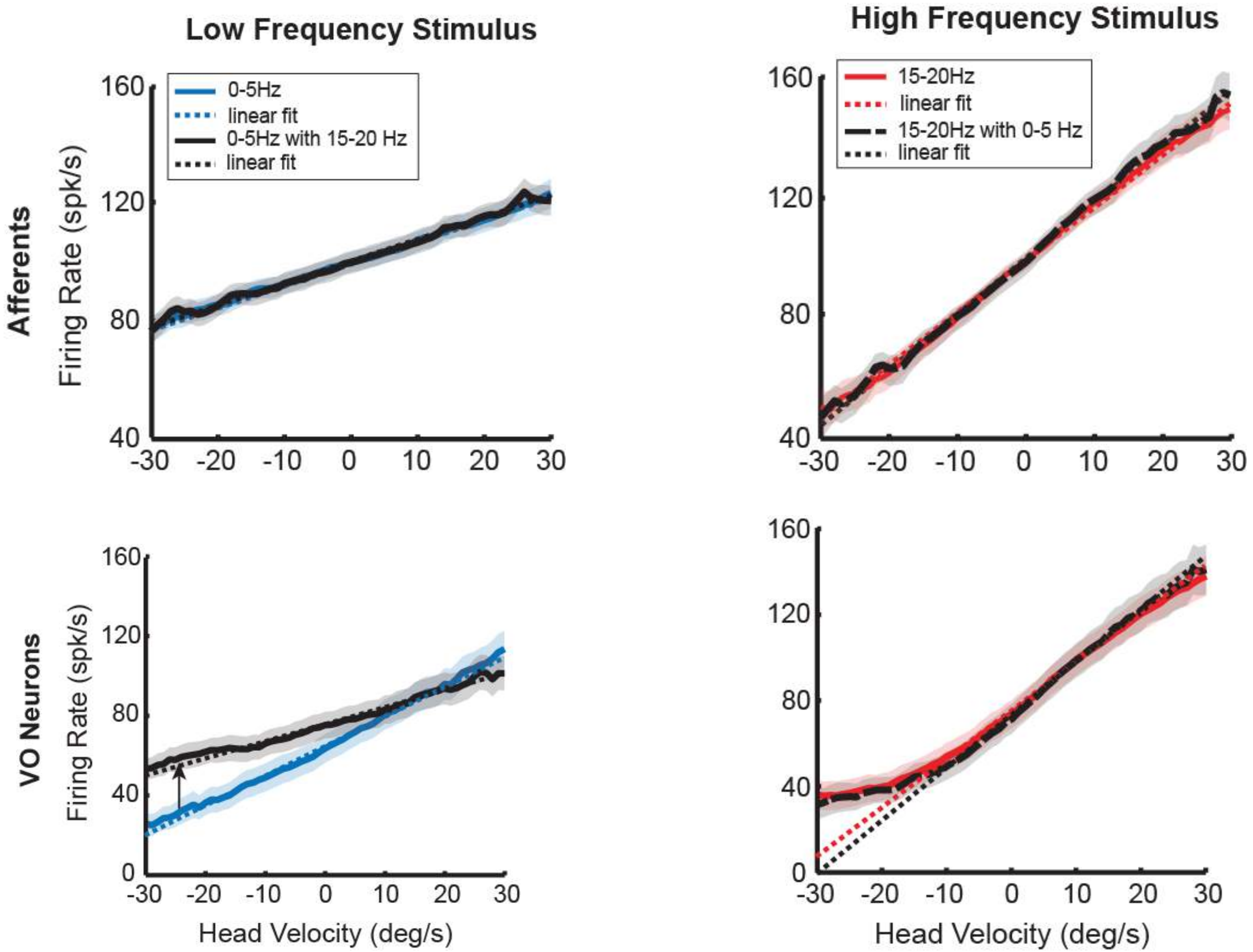
Hypothesis: A static non-linearity in the input-output relationship of central neurons accounts for attenuation of low frequency responses.

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

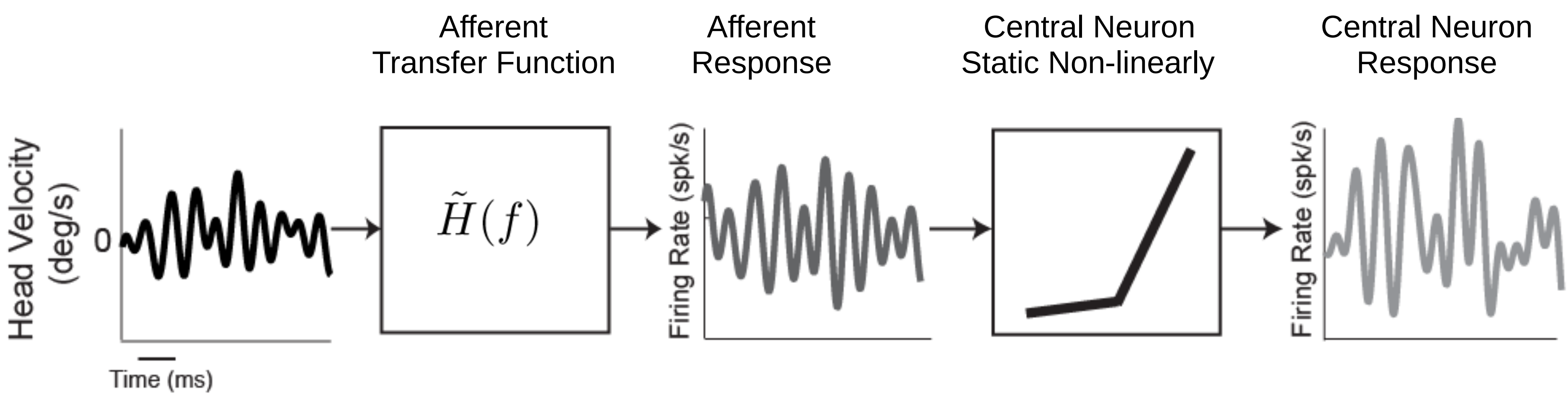


Head velocity Input (deg/sec)

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?



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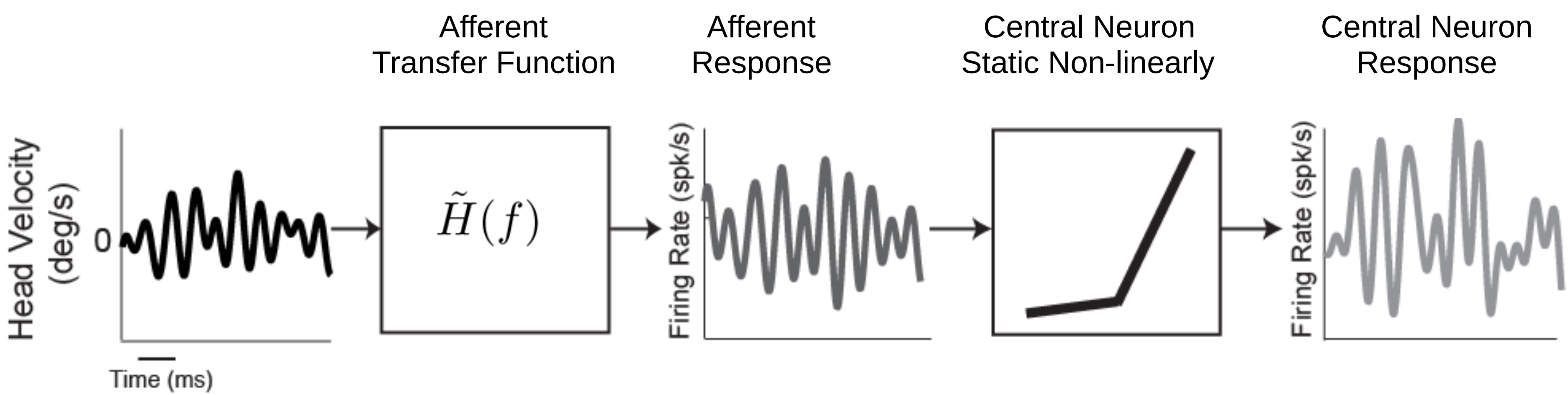
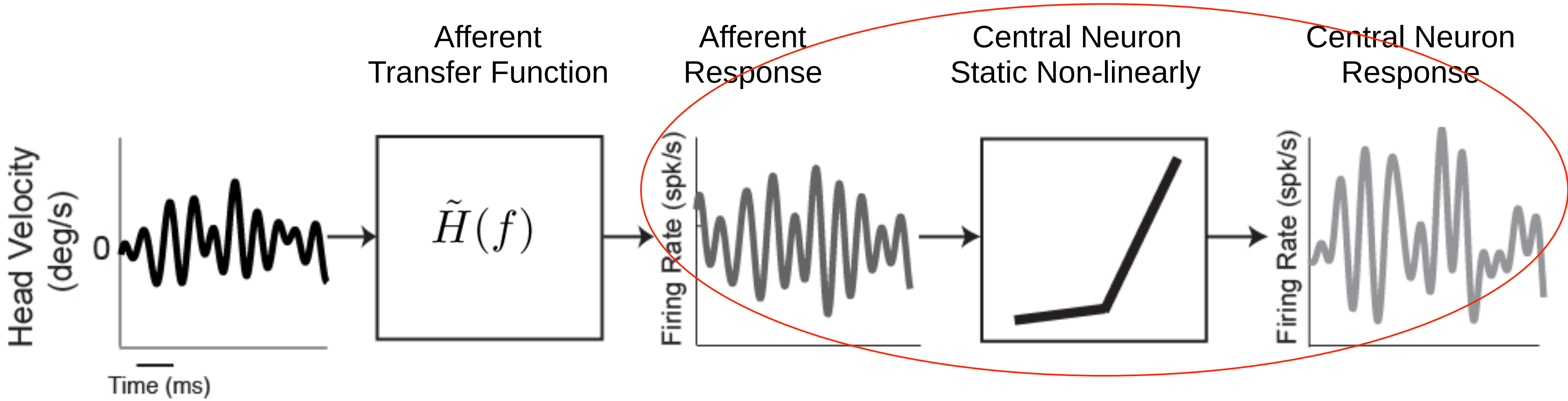


We know the relationships between

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

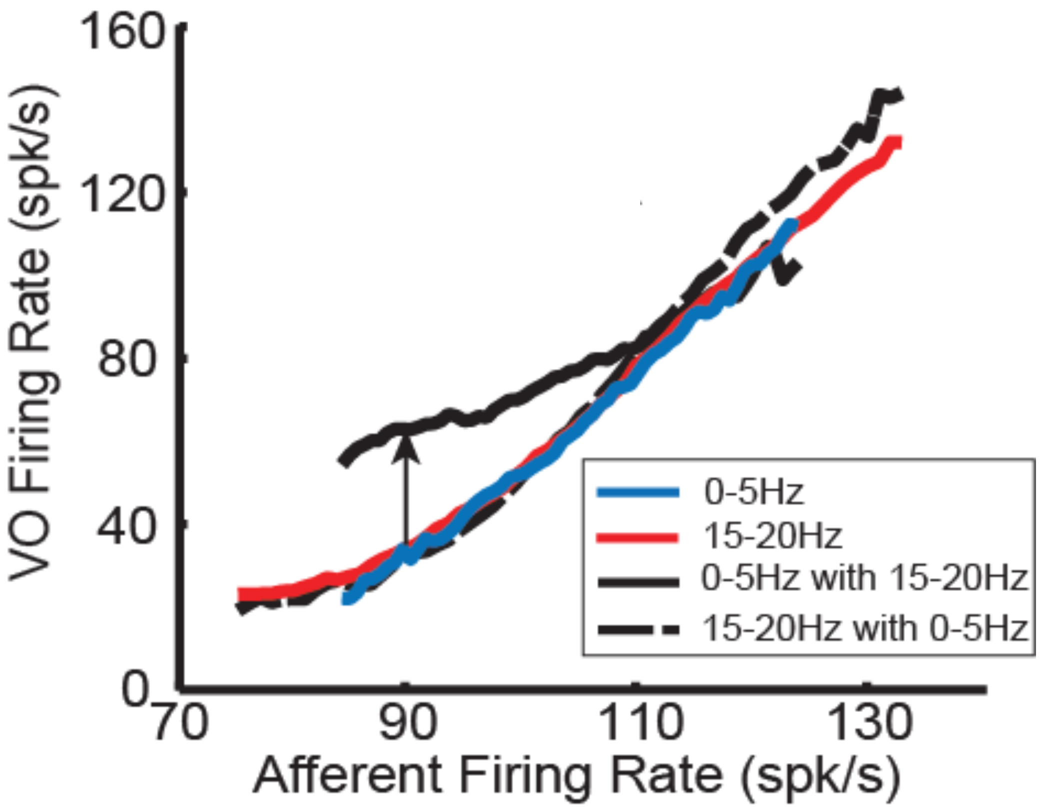
i) afferent firing rate and head velocity, and

ii) central neuron firing rate and head velocity

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

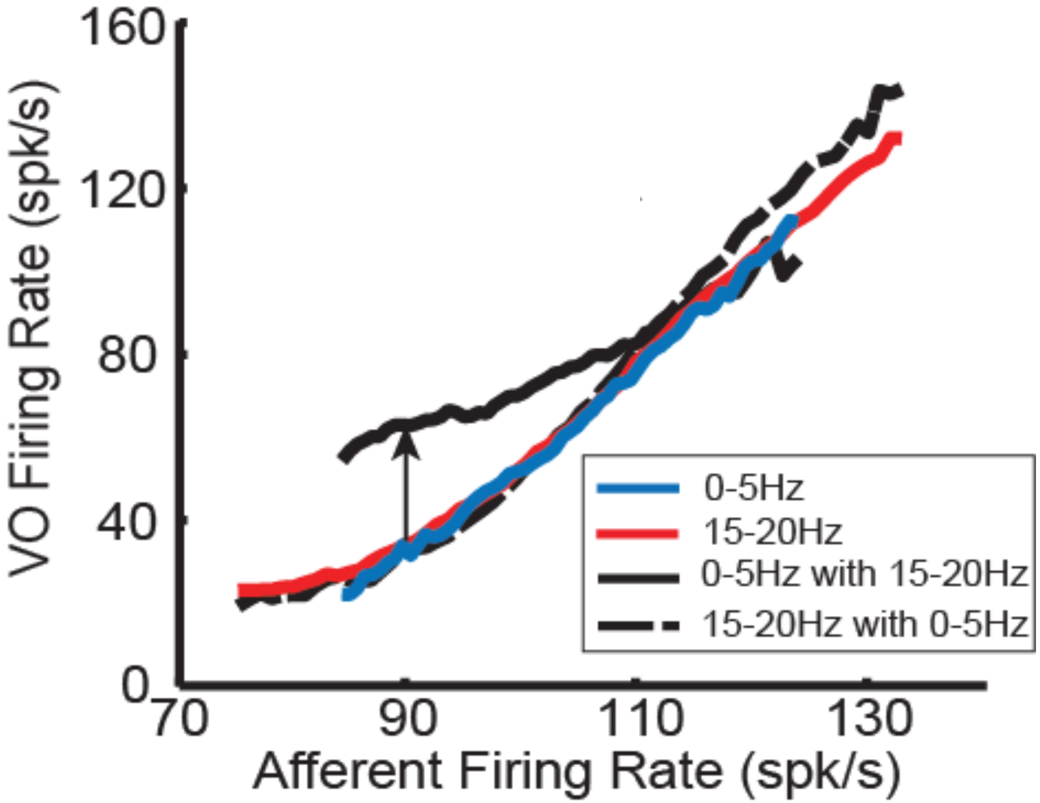
<u>afferent firing rate and central neuron firing rate</u>

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



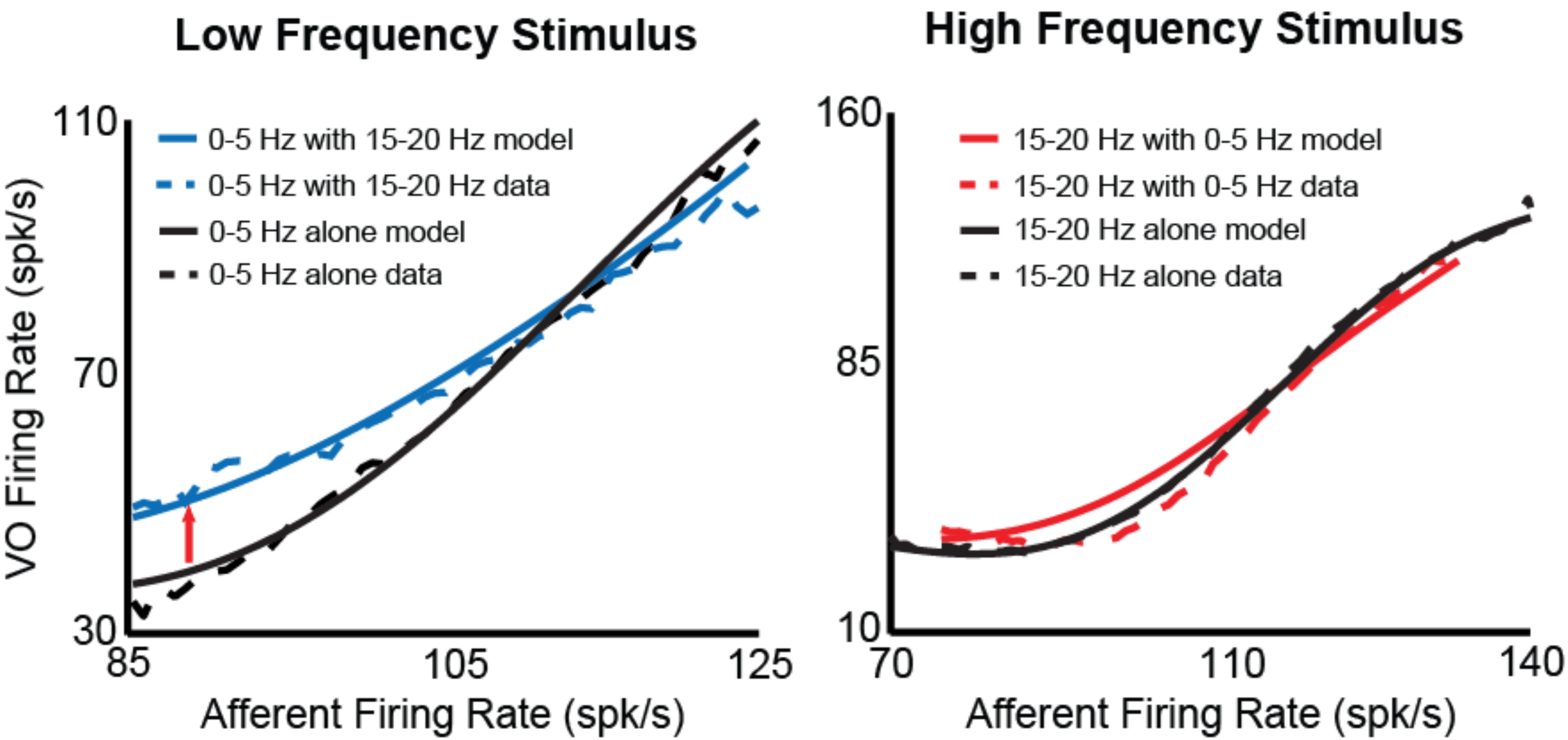
Massot, Schneider, Chacron, and Cullen, PLoS Biology 2012

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

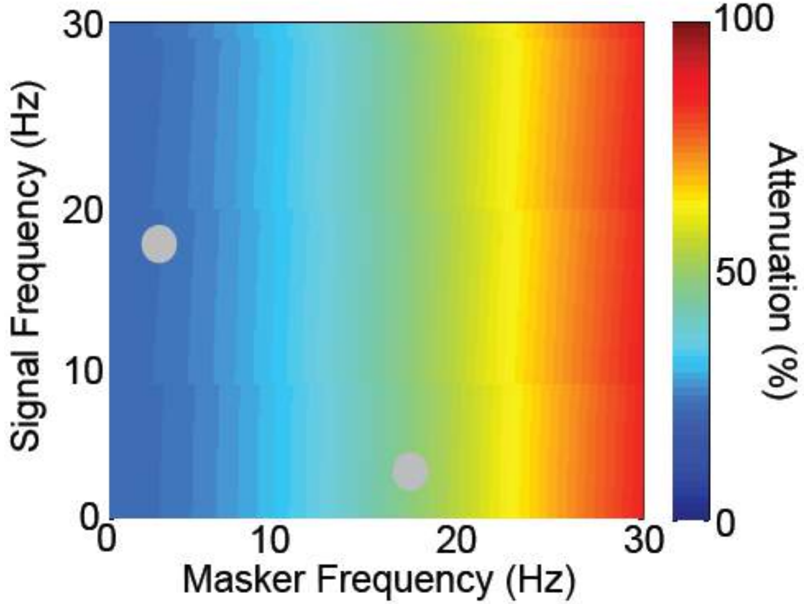


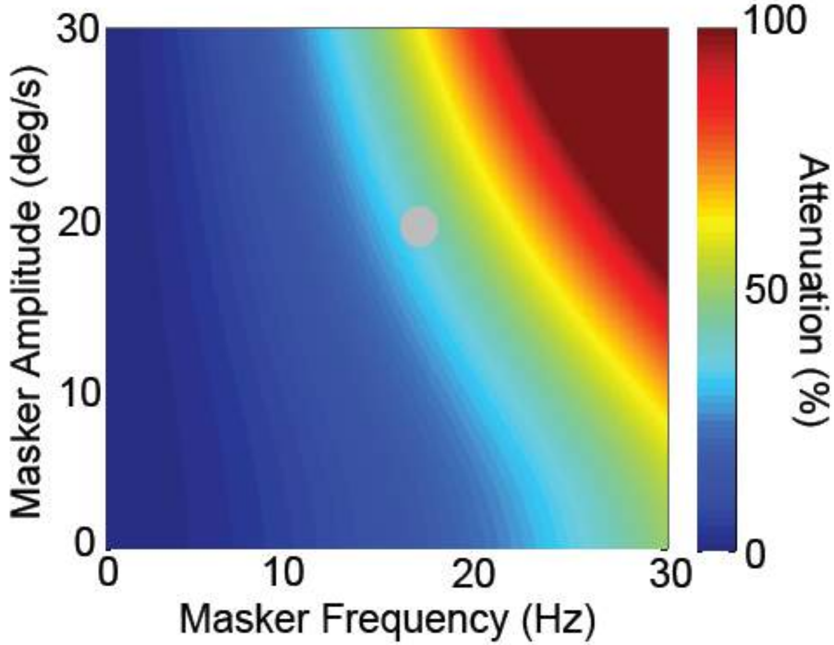
Note, curve obtained when low frequency is applied with high frequency has a lower slope. This occurs because the average central neuron firing rate is higher in this condition, than when the same stimulus is applied alone.

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



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

Massot, Schneider, Chacron, and Cullen,
PLoS Biology 2012

Summary:

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

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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?

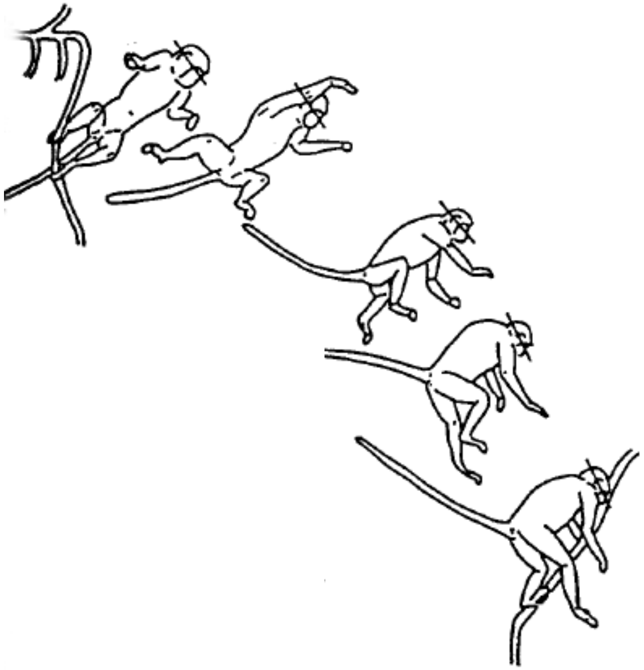
- Indeed it is not: We discovered <u>a static boosting nonlinearity</u> in the input-output relationship of central vestibular neurons accounts for this unexpected result.

- 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….

Sensorimotor transformations: Vestibulo-spinal Reflexes

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

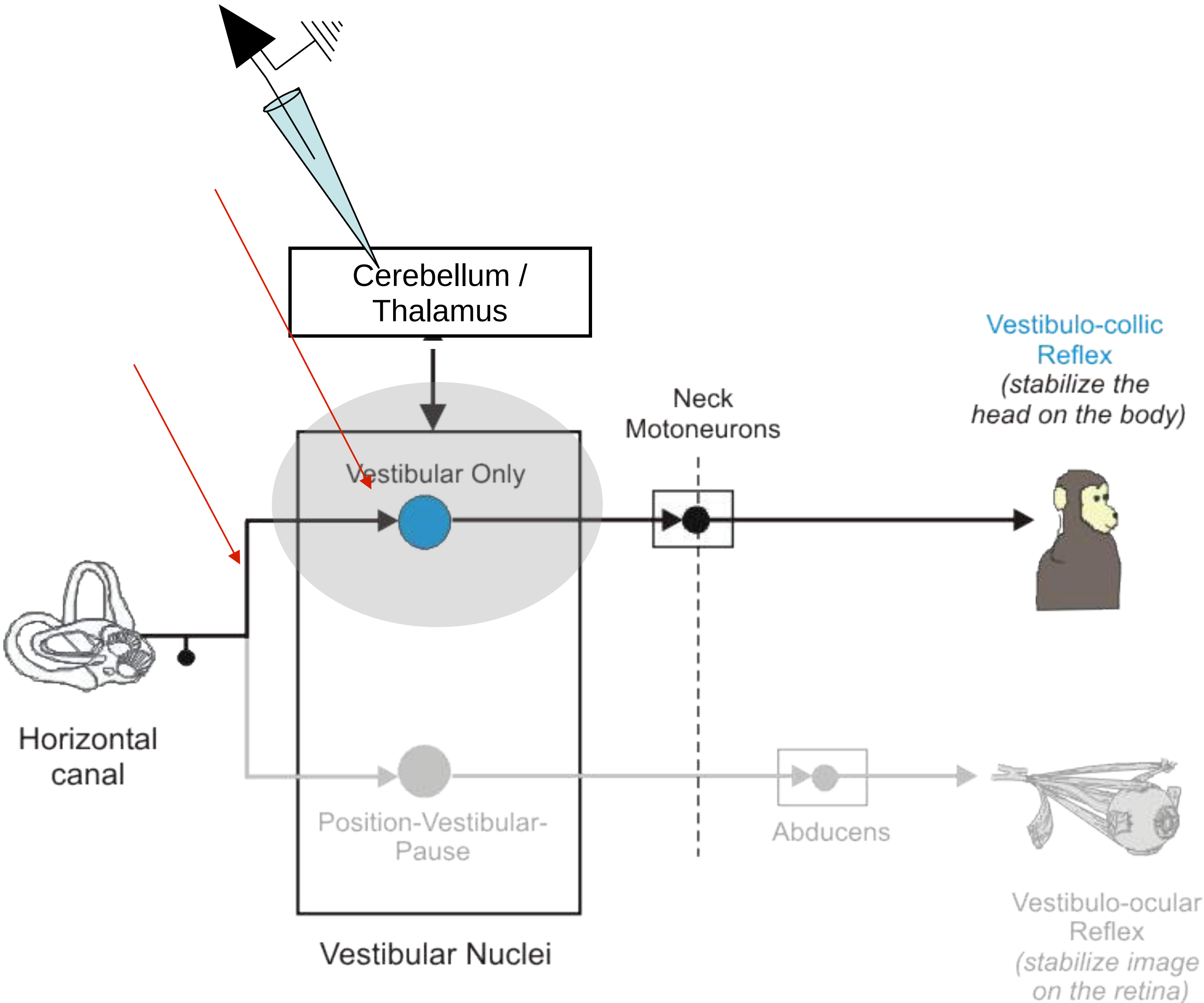
Focus on a relatively simple sensory-motor pathway with
a well-described organization

Consider the medial of the
deep cerebellar nuclei (rostral fastigial nucleus), which

1) Constitutes a major output target of the cerebellar cortex,
and in turn sends strong projections to the
  - vestibular nuclei,
  - reticular formation, and
  - spinal cord

  to ensure accurate posture and the maintenance of balance.

2) In addition, this nucleus receives sensory information including
  - vestibular, and
  - proprioceptive inputs



Cerebellum / Thalamus
Vestibulo-collic Reflex
(stabilize the head on the body)
Neck Motoneurons
Vestibular Only
Horizontal canal
Position-Vestibular-Pause
Abducens
Vestibulo-ocular Reflex
(stabilize image on the retina)
Vestibular Nuclei

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,

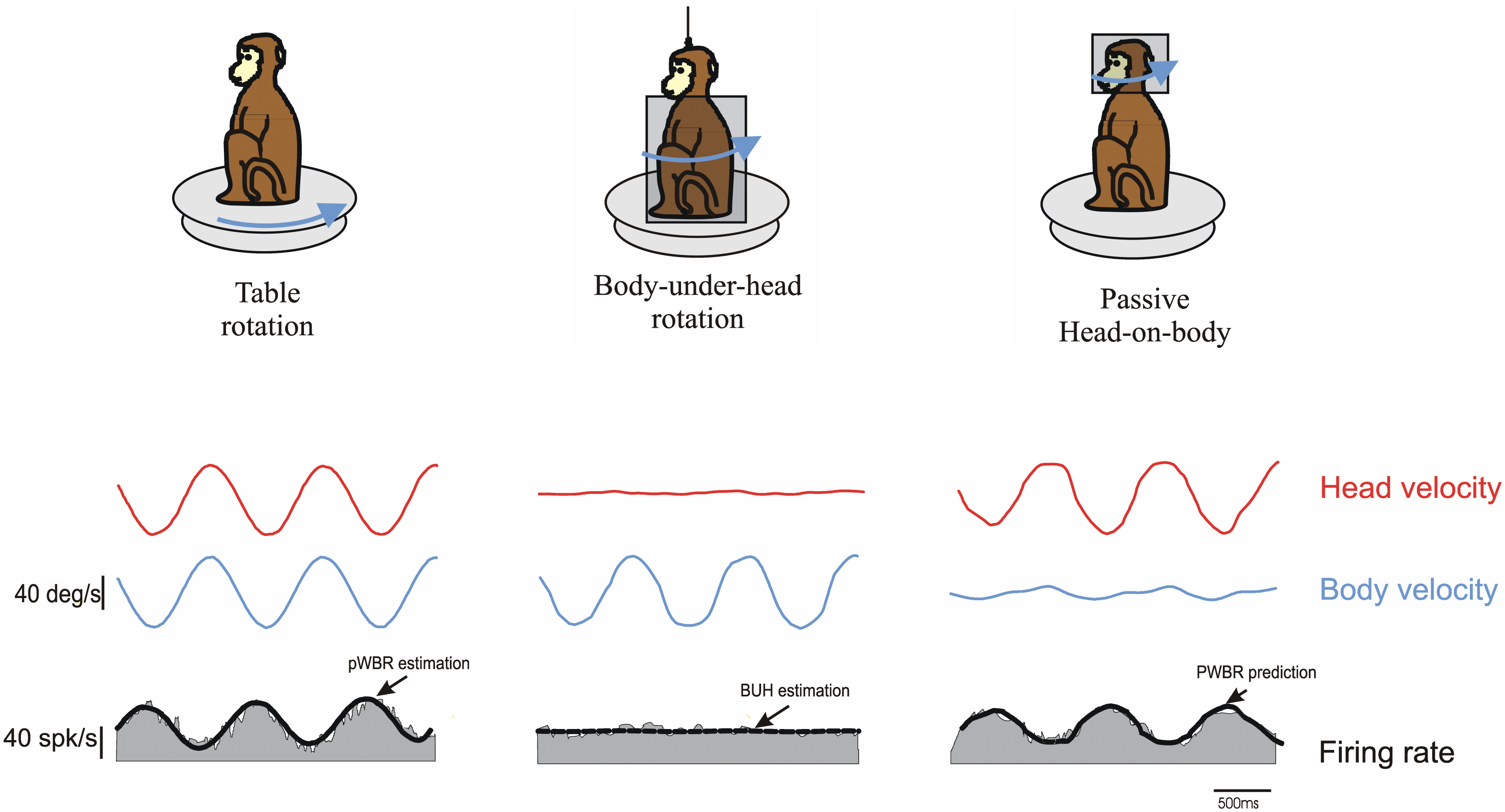
Head and body motion are encoded in two distinct channels by the output neurons of the vestibular cerebellum

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

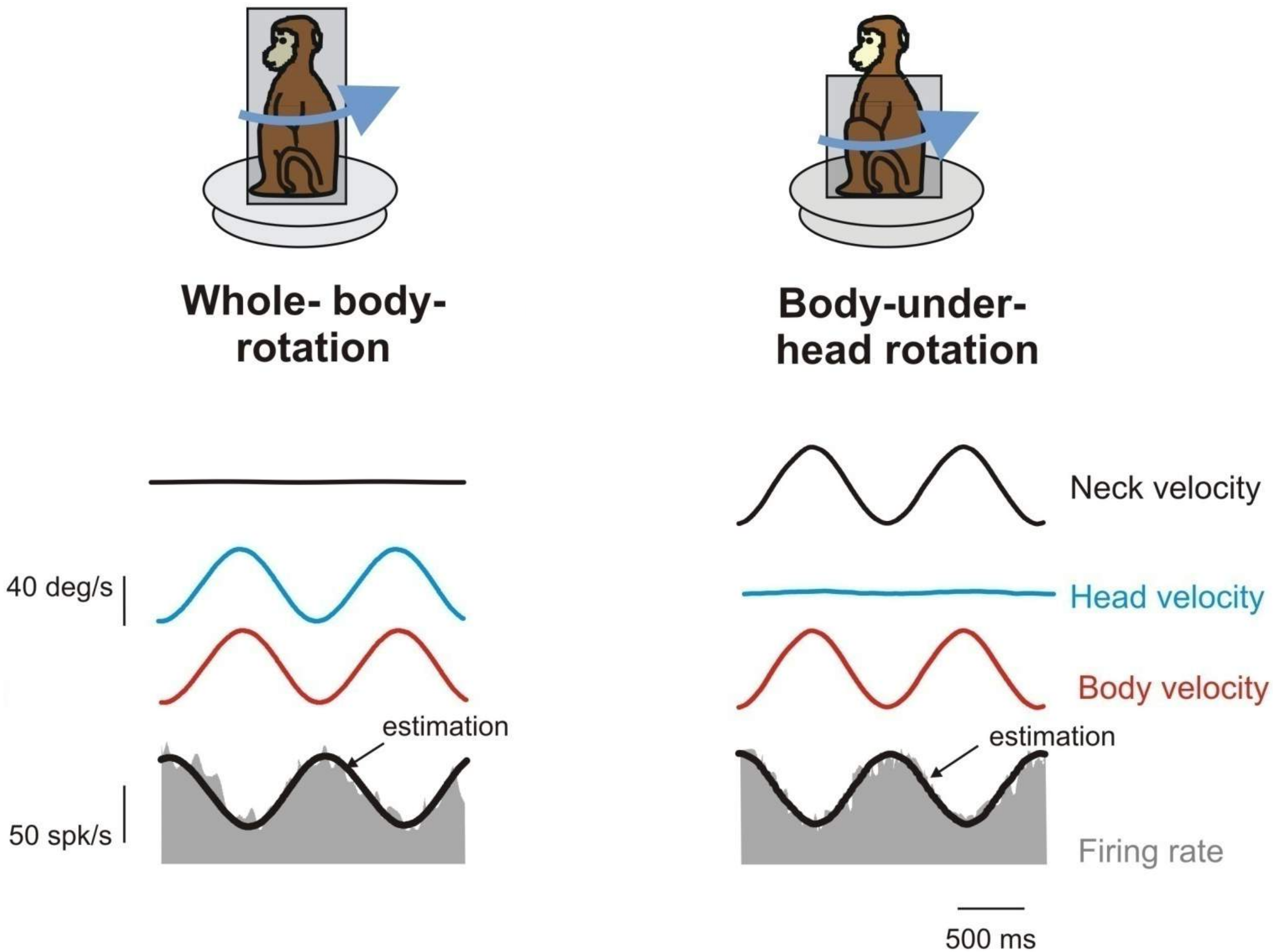
Vestibular-only cell (Unimodal)



Brooks and Cullen, J. Neurosci., 2009

Example Vestibulo-Cerebellar Neuron

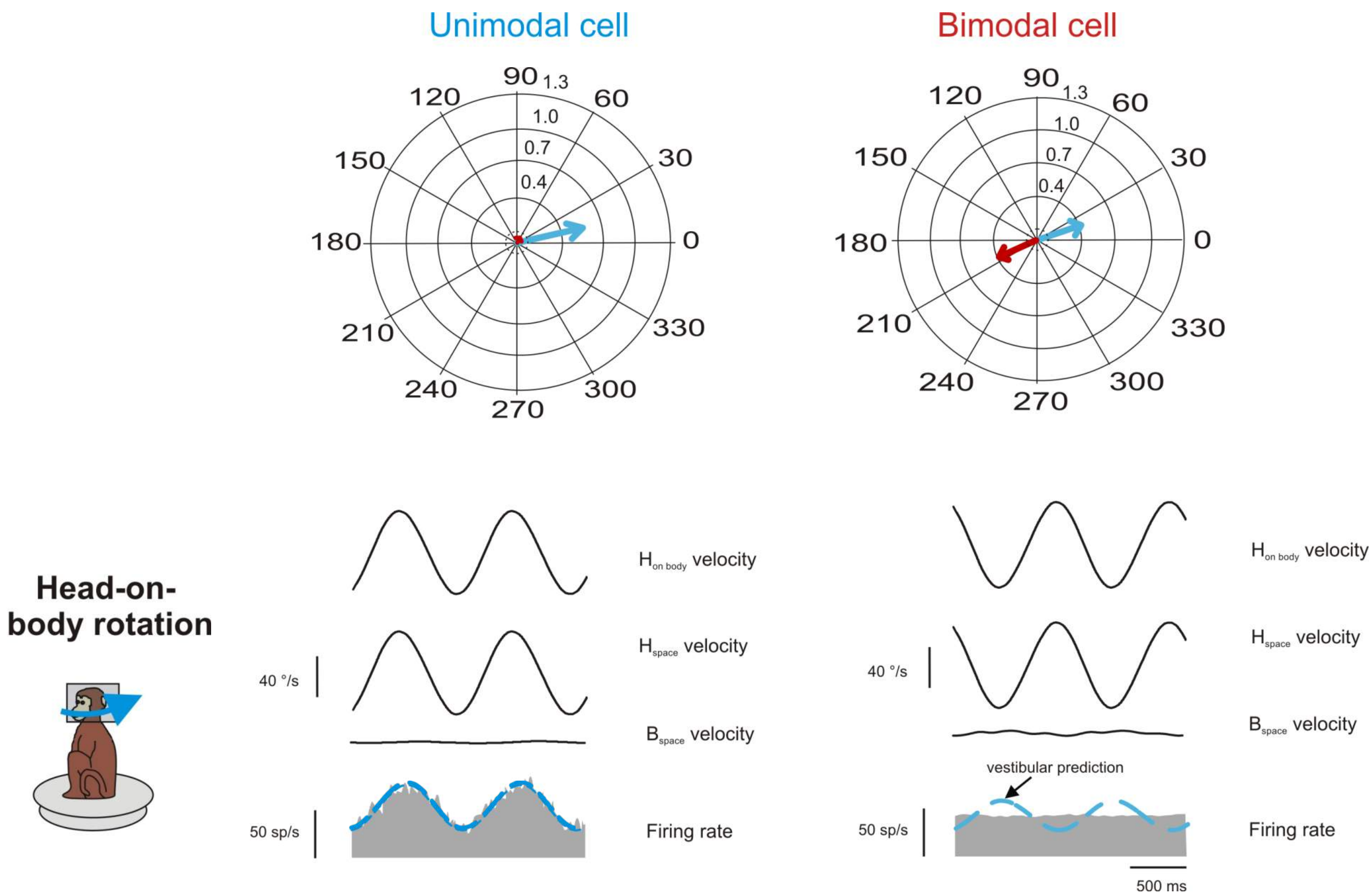
Vestibular+neck cell (Bimodal)



Brooks and Cullen, J. Neurosci., 2009

Brooks and Cullen, SFN 2007

Vestibular and neck inputs sum linearly



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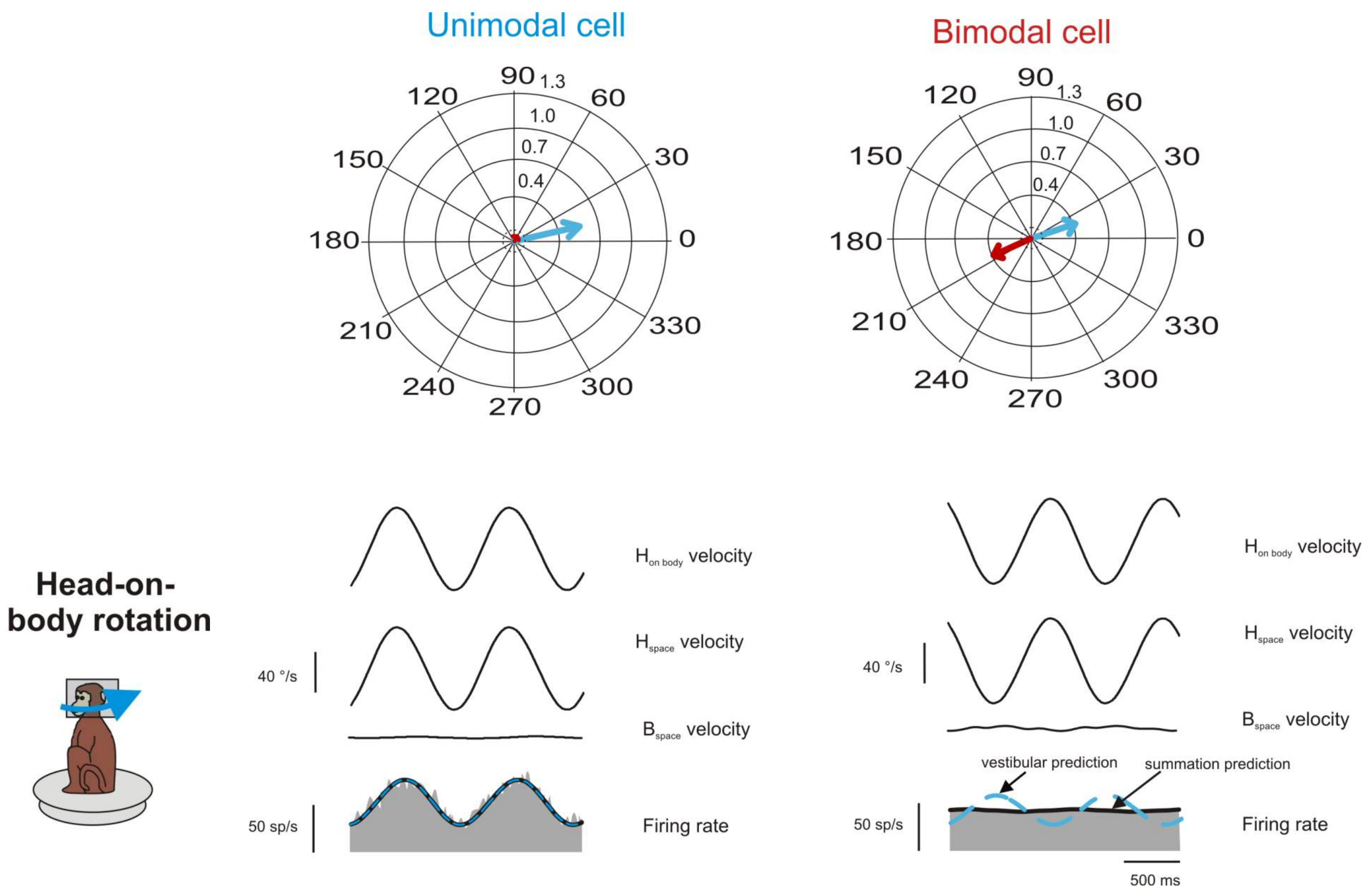
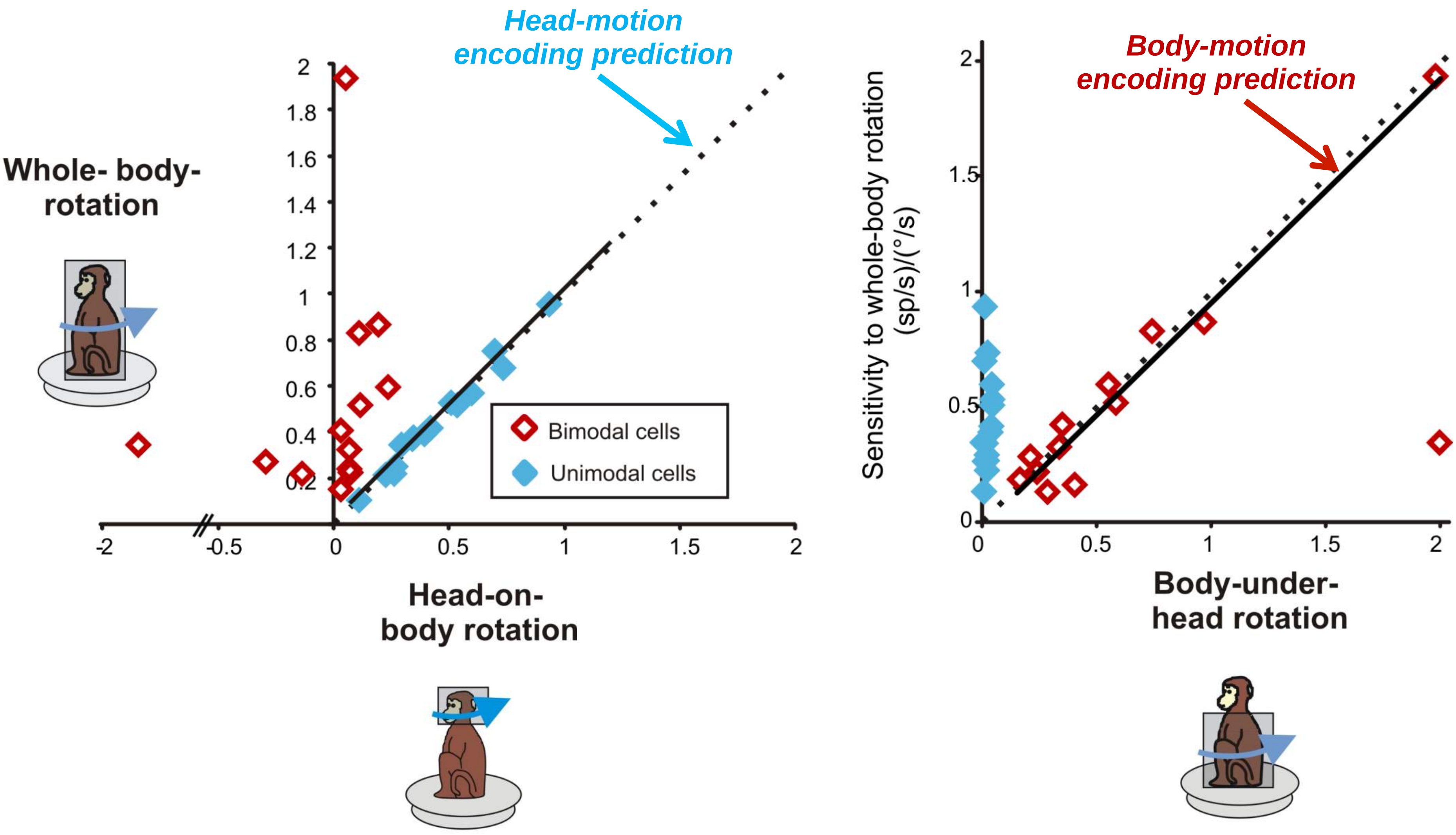


Bimodal neurons encode body motion, and unimodal neurons encode head motion



Brooks and Cullen, J. Neurosci., 2009

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

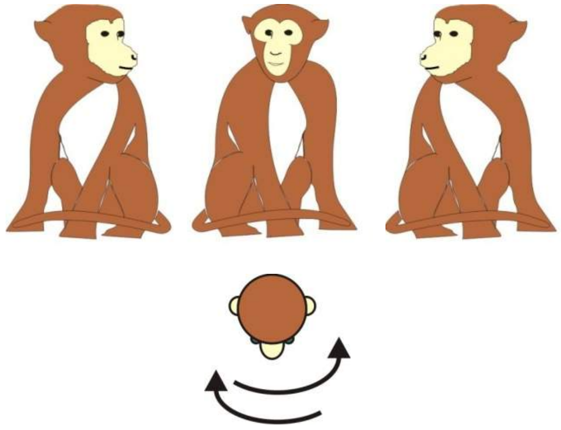
However, humans can detect movement of the body and the head separately even in darkness (Mergner et al 1981) .

Body motion perception is thought to be a result the convergence of vestibular and neck proprioception signals

1) Head motion is encoded by VN and unimodal cerebellar neurons

2) Body motion encoded by bimodal cerebellar neurons

However, the vestibular responses of bimodal neurons also depend on head-on-body position



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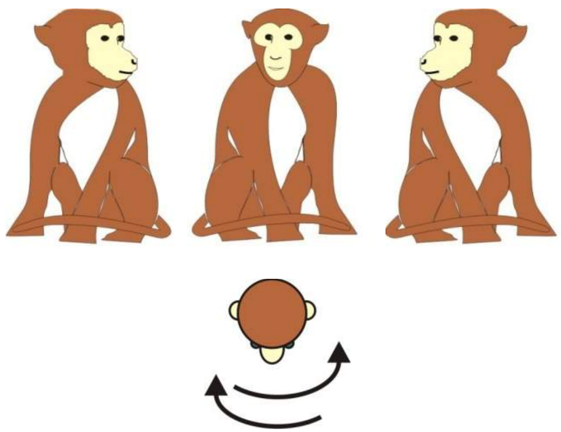
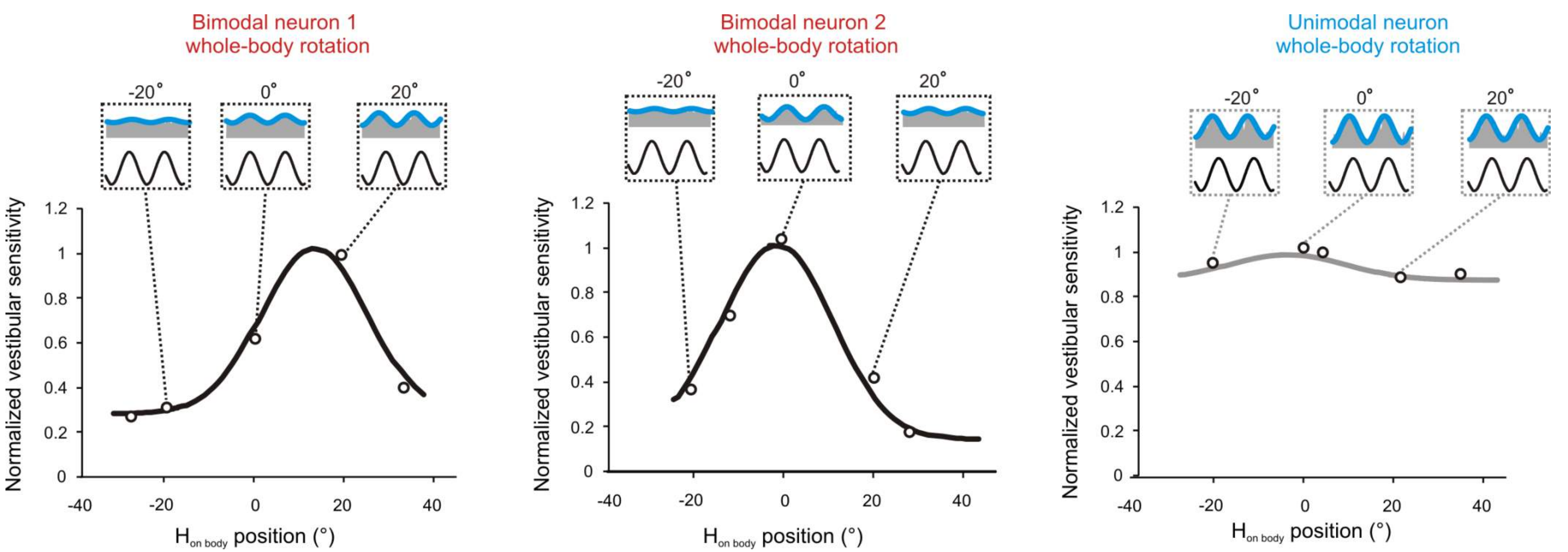
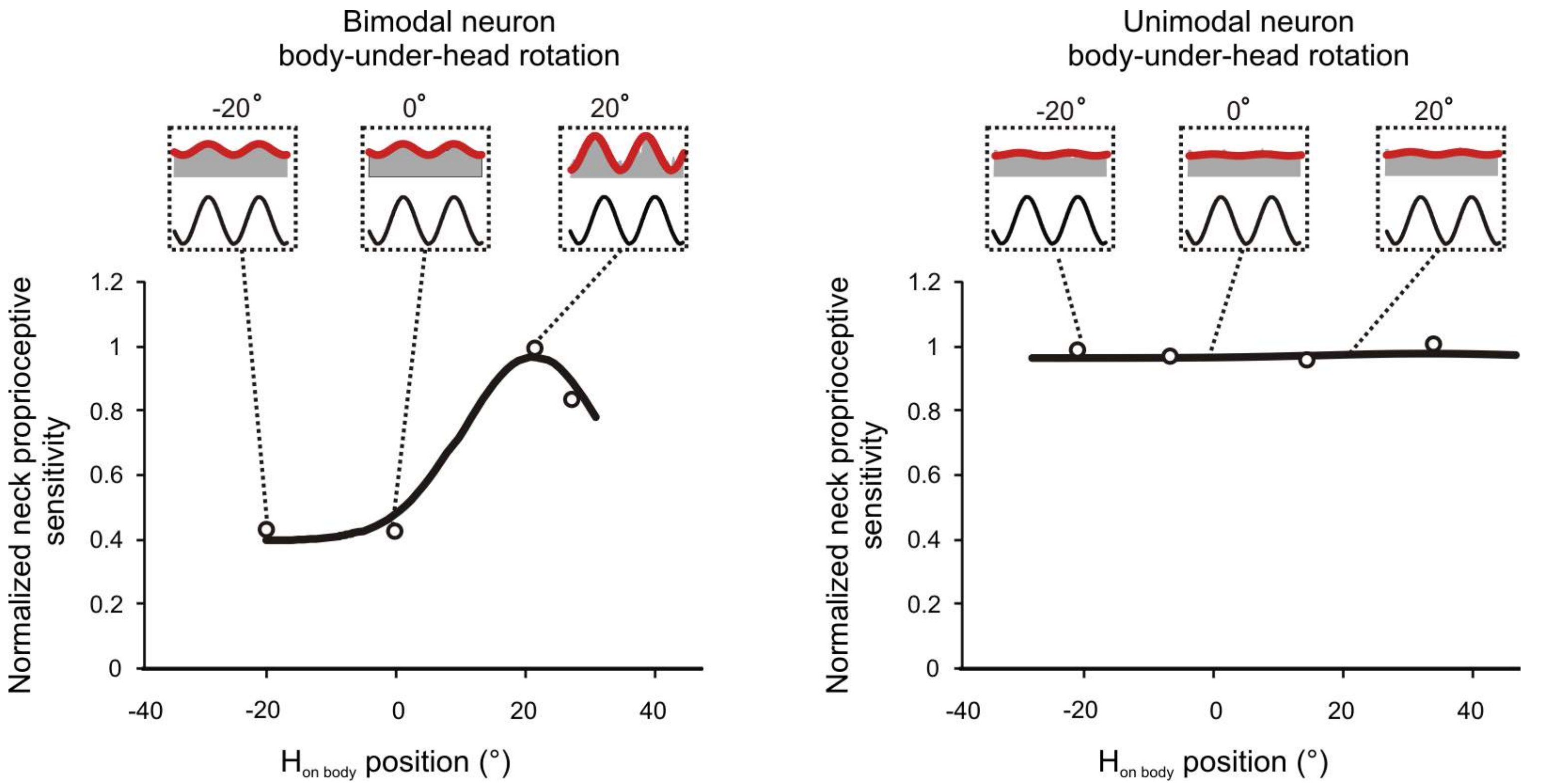
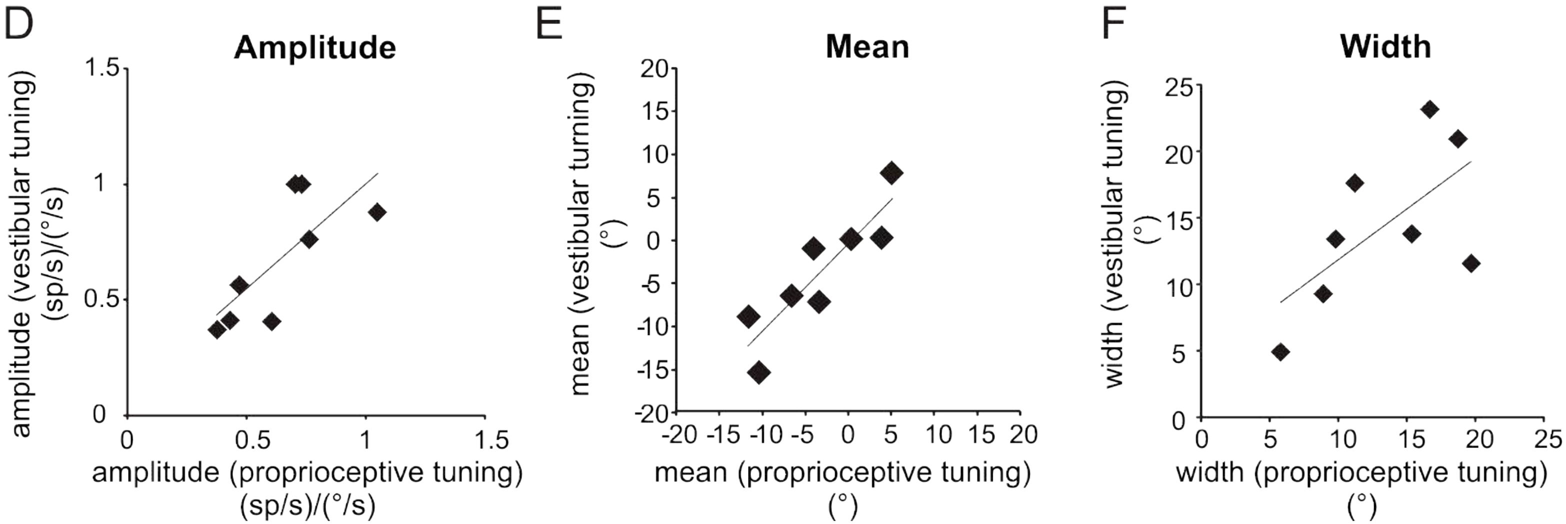




The <u>neck proprioceptive</u> responses of bimodal neurons also depend on head-on-body position

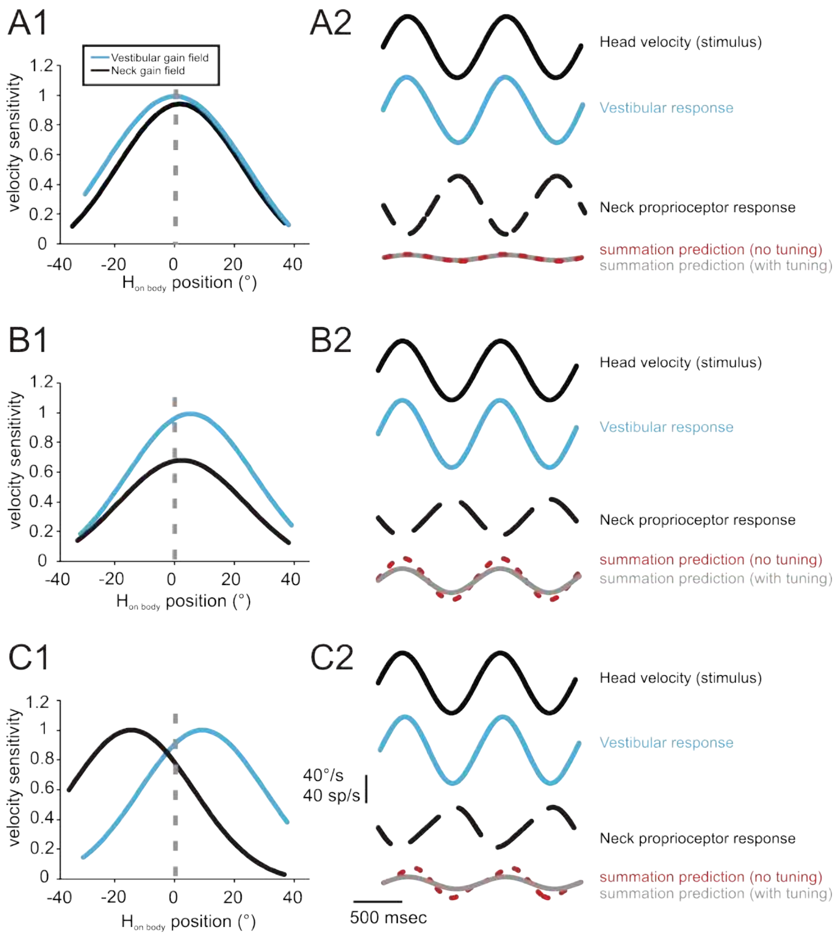


Comparison of the proprioceptive and vestibular responses of bimodal neurons further reveals similar tuning in response to changes in head-on-body position.



Brooks and Cullen, J. Neurosci., 2009

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

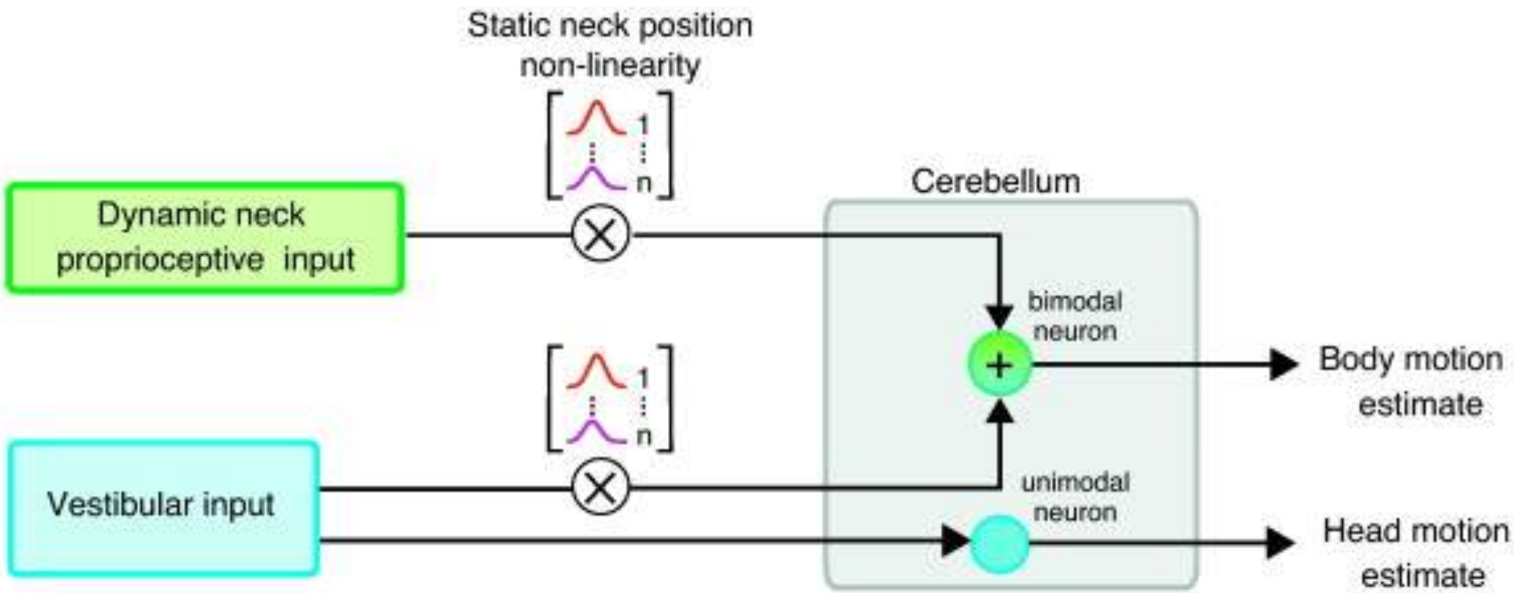


In the case of the hypothetical neuron with overlapping tuning curves (panel A), the effect of head position is effectively cancelled

Brooks and Cullen, J. Neurosci., 2009

Vestibular Cerebellar Processing:

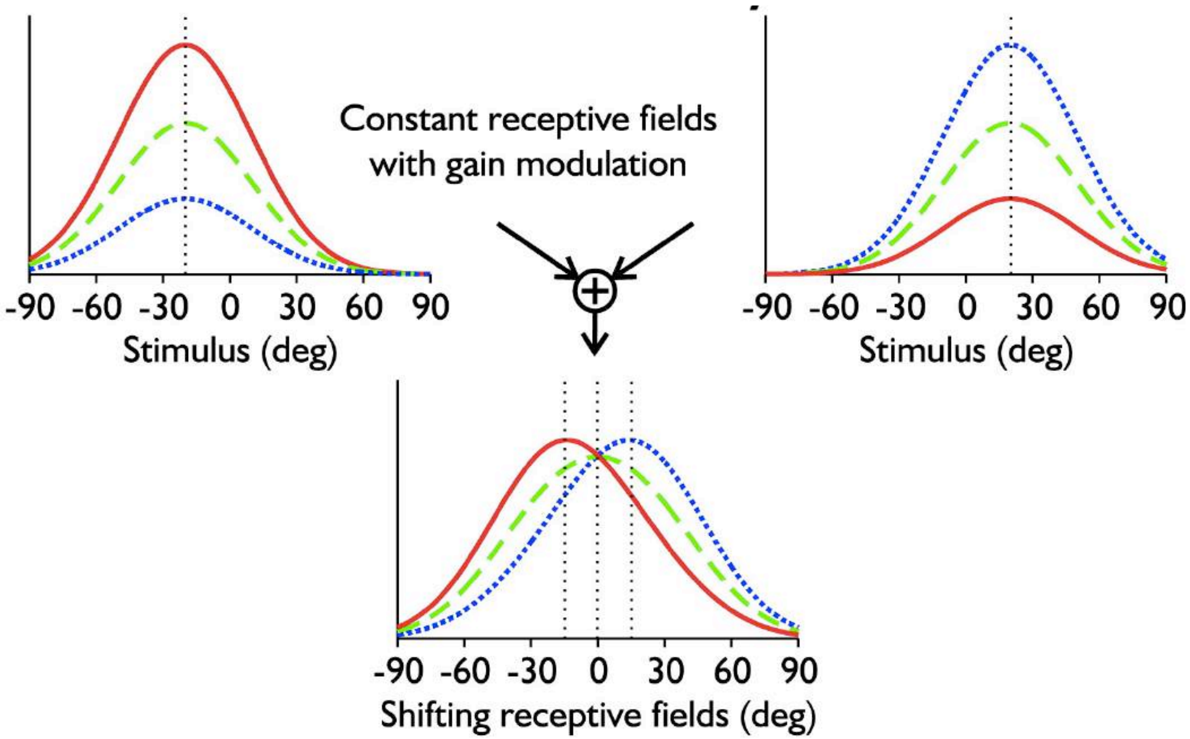
A nonlinear operation in which head-on-body position modulates the gain of vestibular and dynamic neck proprioceptive responses



Cullen, Current Opinion in Neurobiology, 2011

Vestibular Cerebellar Processing:

Relationship to the gain field theory

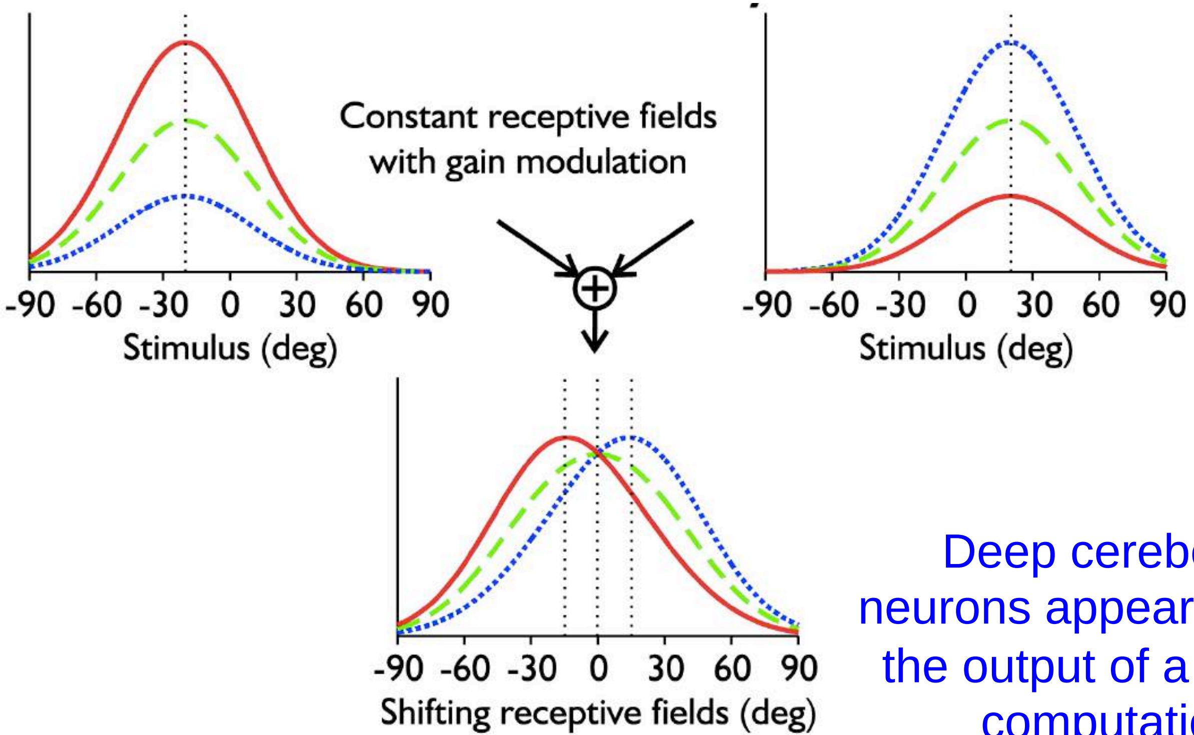


Consider the visual receptive fields of two neurons gain modulated (e.g., by eye position) in opposite ways without shifting.

- 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



Deep cerebellar neurons appear to code the output of a similar computation

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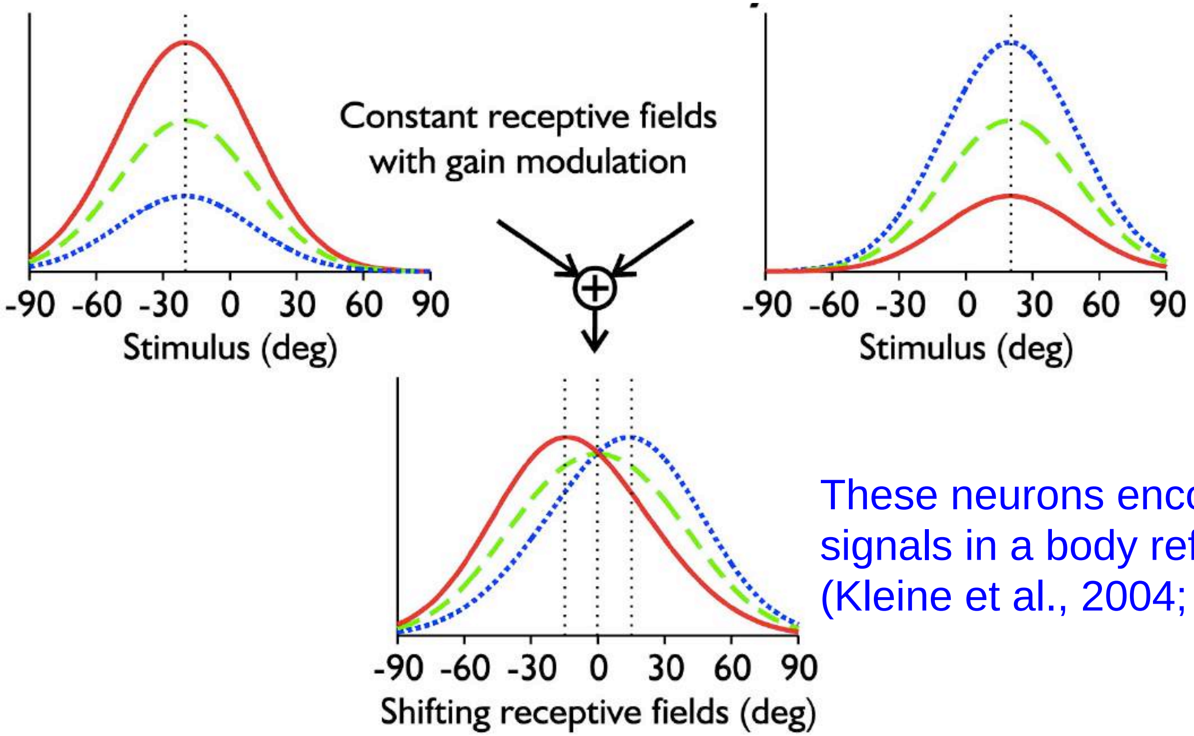
Vestibular Cerebellar Processing:

Relationship to the gain field theory



These neurons encode vestibular signals in a body reference frame (Kleine et al., 2004; Shaikh et al. 2004),

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- Eye position modulates the strength of response of the two input neurons, but does not cause them to shift.
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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.

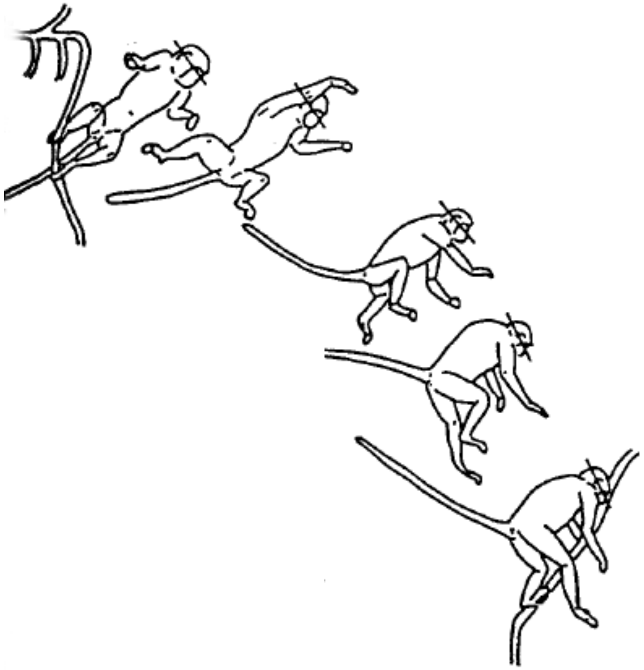
This raises the question: What is the functional significance of the observed tuning?

- 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

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   -Gain-fields in the cerebellum

2. Dynamic Non-linearities

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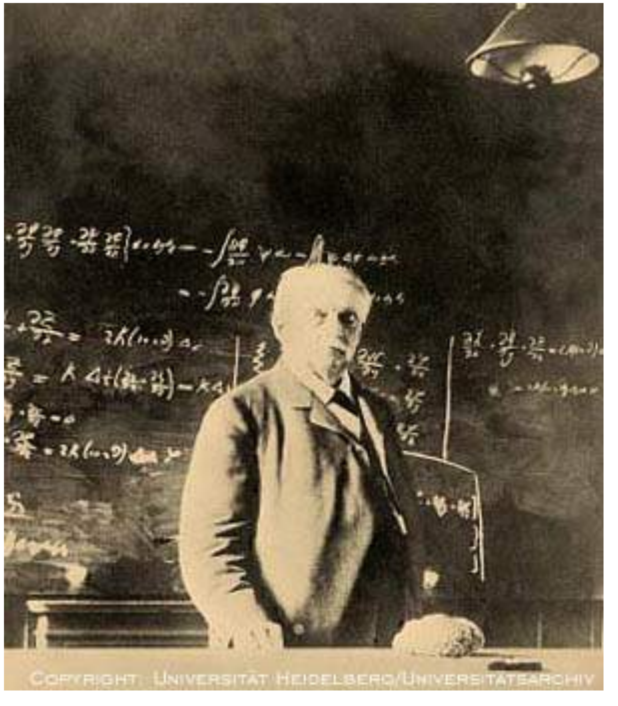
How does the vestibular system encode active self motion?

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

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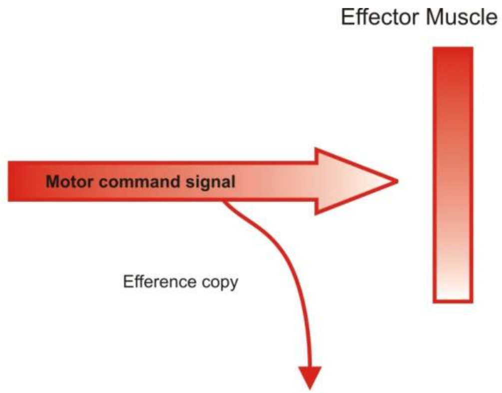
2. *Accurate Motor Control:* In the vestibular system, the central neurons that receive direct afferent input, also project to motor centers to control vestibulo-ocular and -spinal reflexes.

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.



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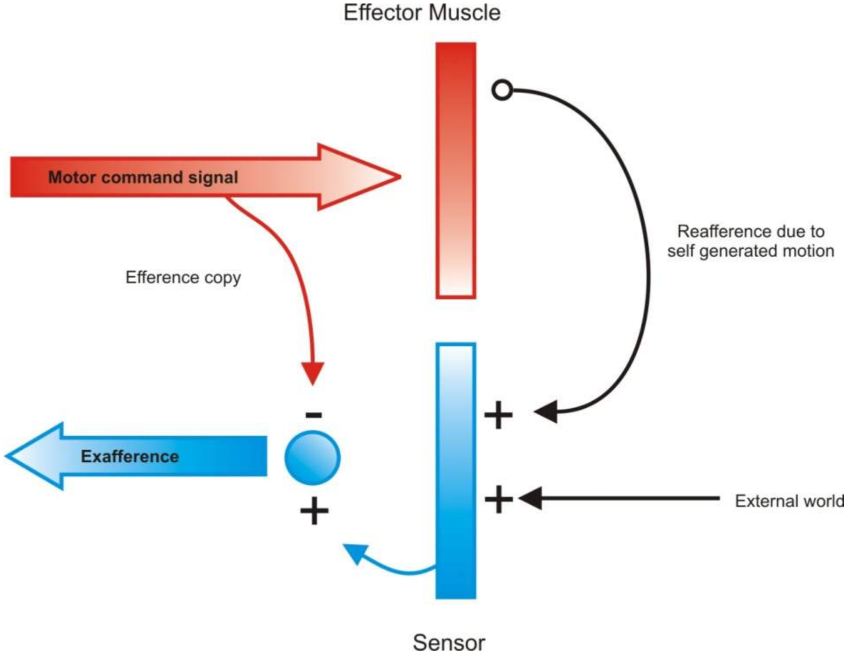

<u>As a result,</u> this anticipatory signal is then subtracted from the incoming sensory signal to selectively remove that portion due to the animal's own actions (i.e. reafference).

Computing vestibular reafference

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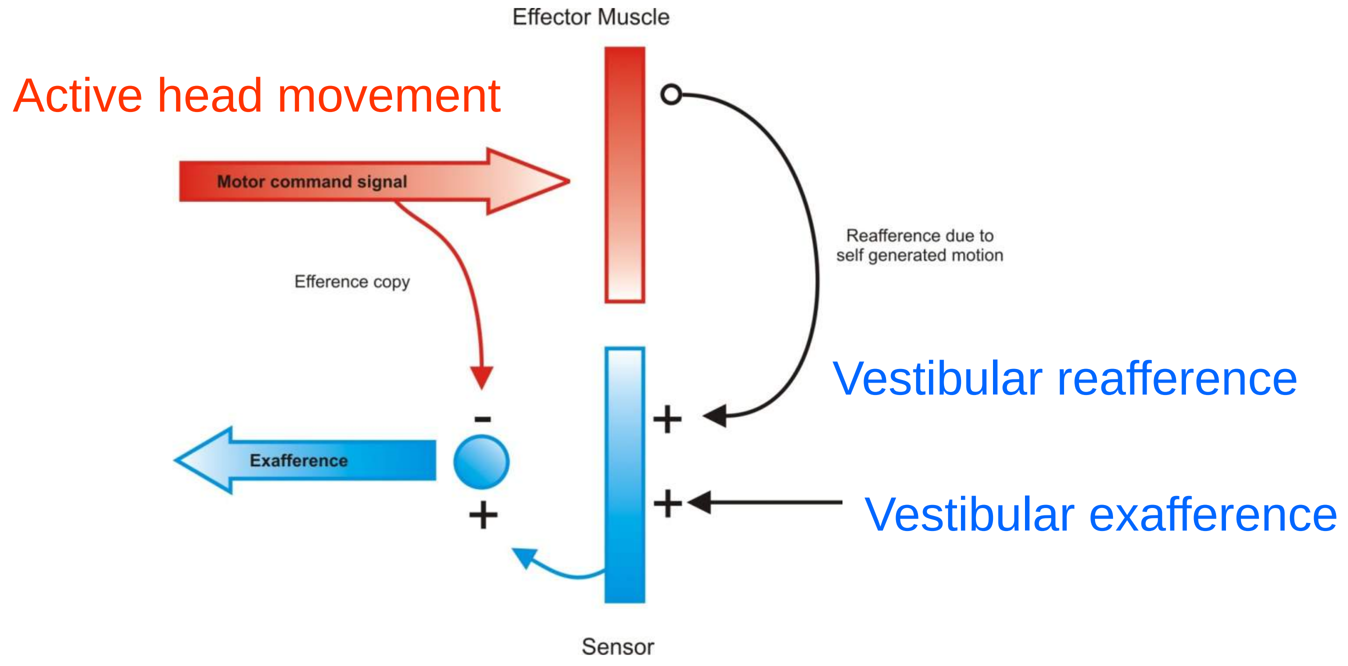
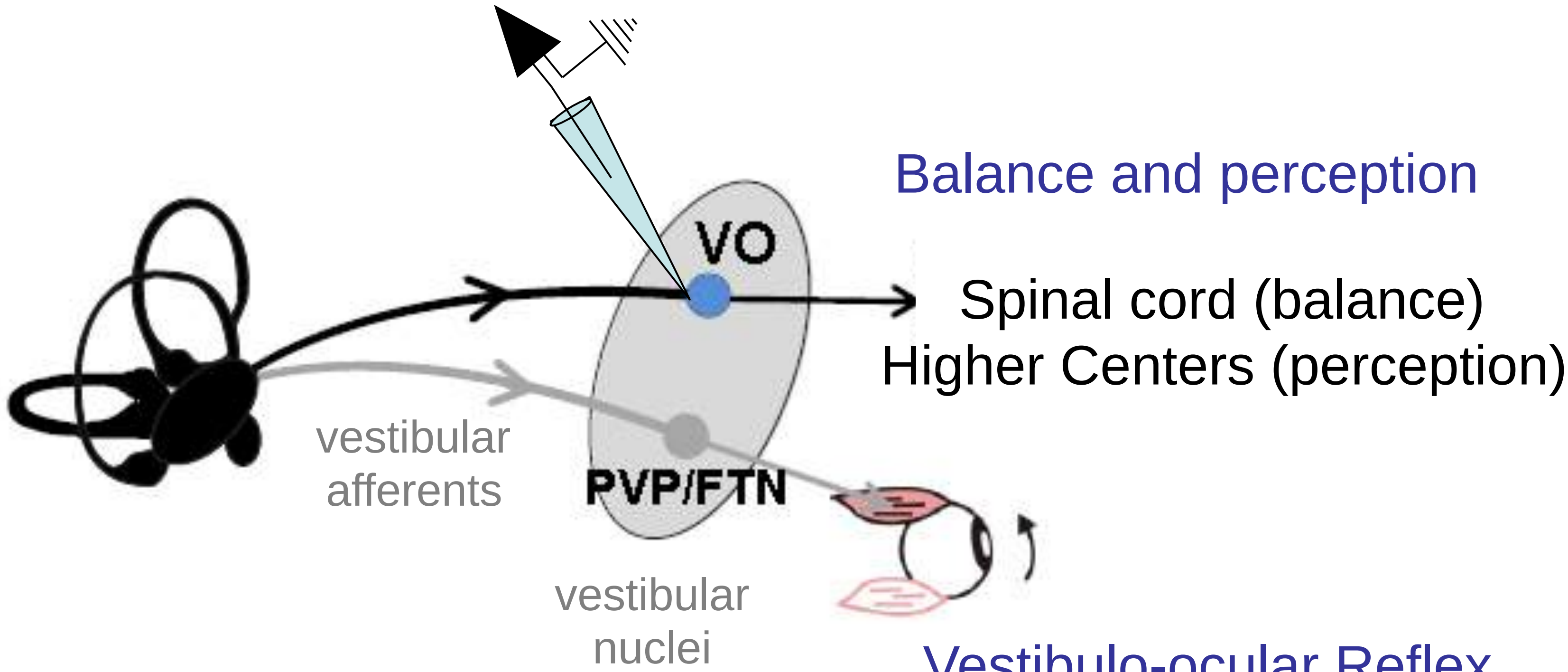


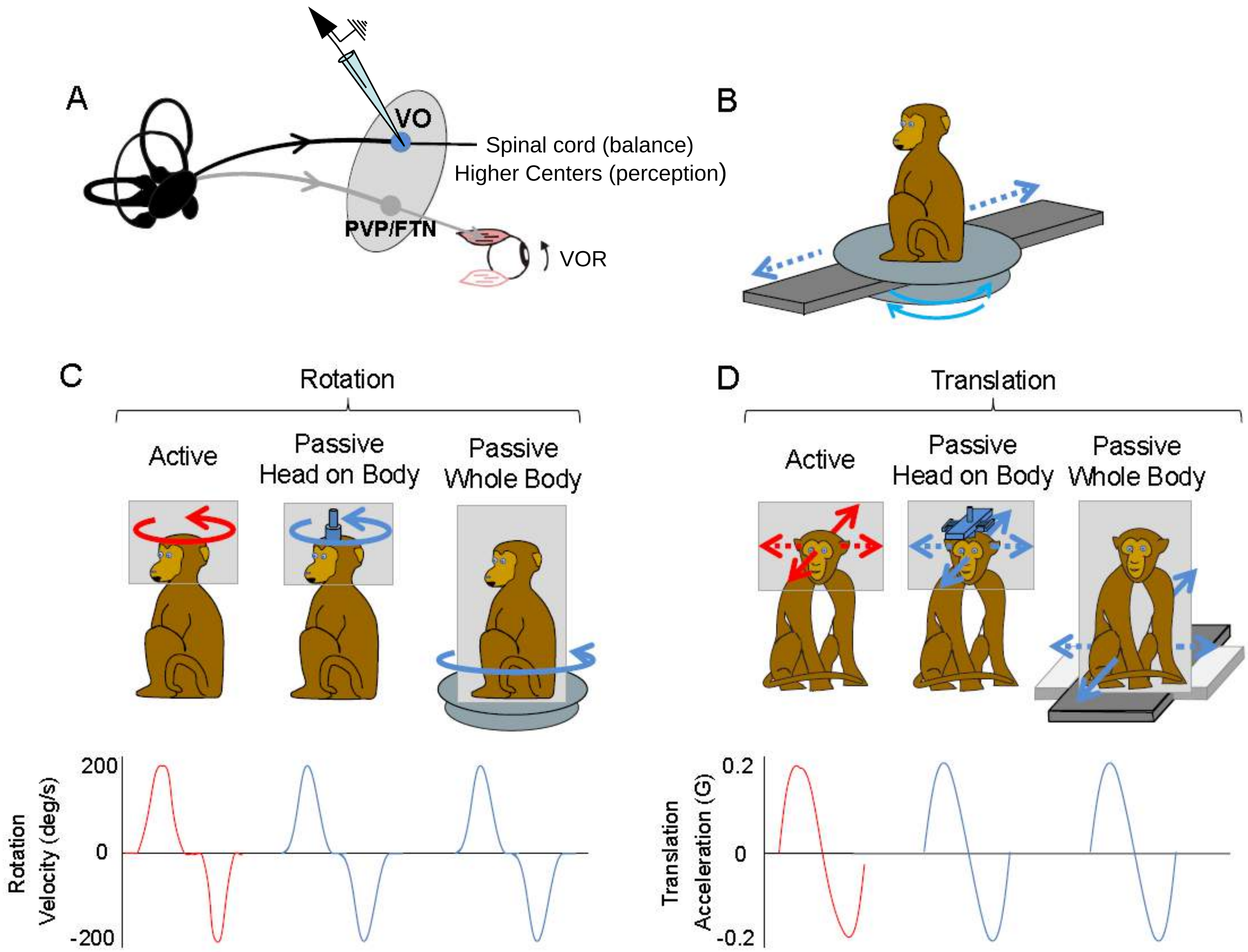
As a result, this anticipatory signal is then subtracted from the incoming sensory signal to selectively remove that portion due to the animal's own actions (i.e. reafference).

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?



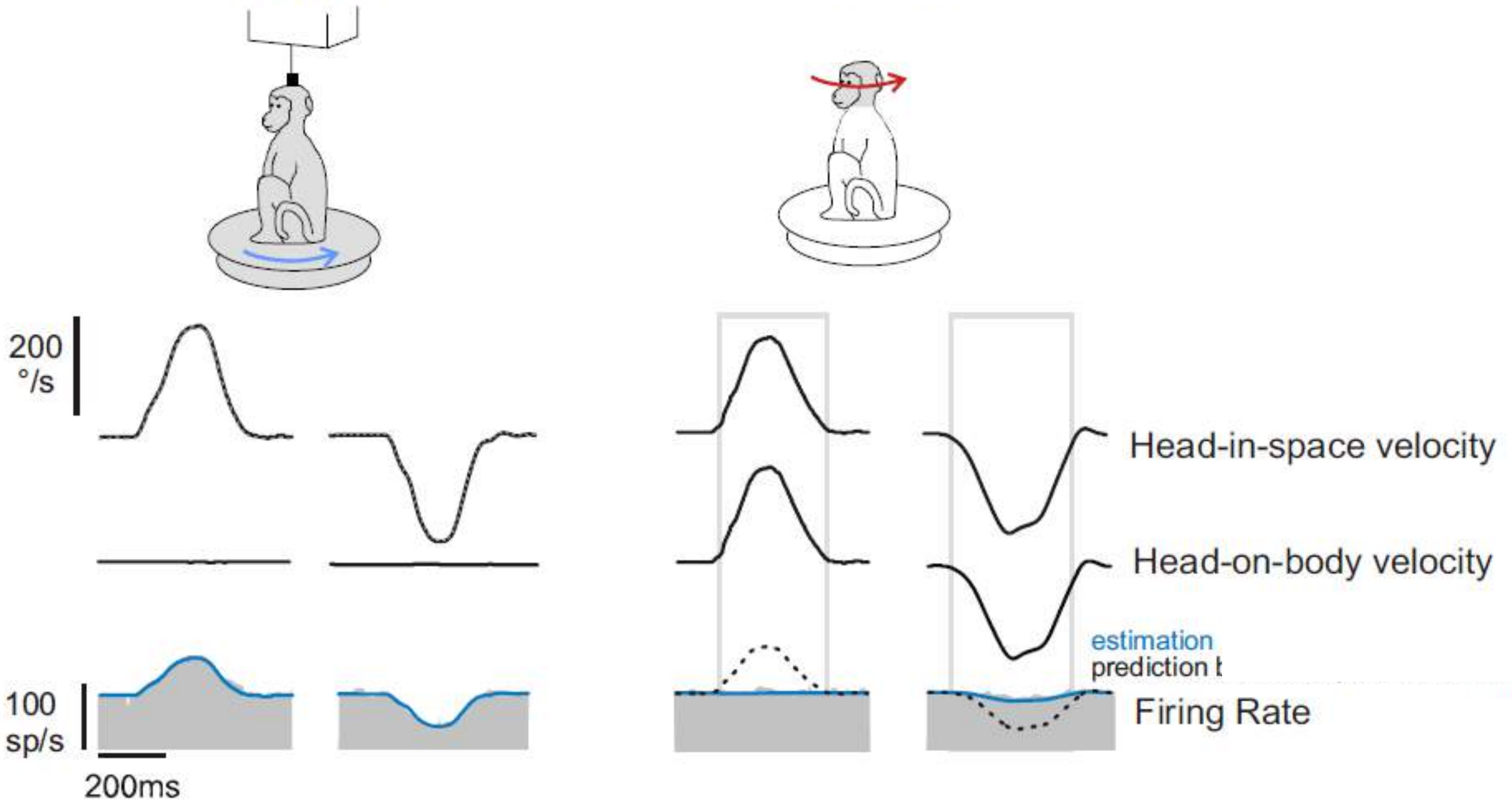
Experimental Setup



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

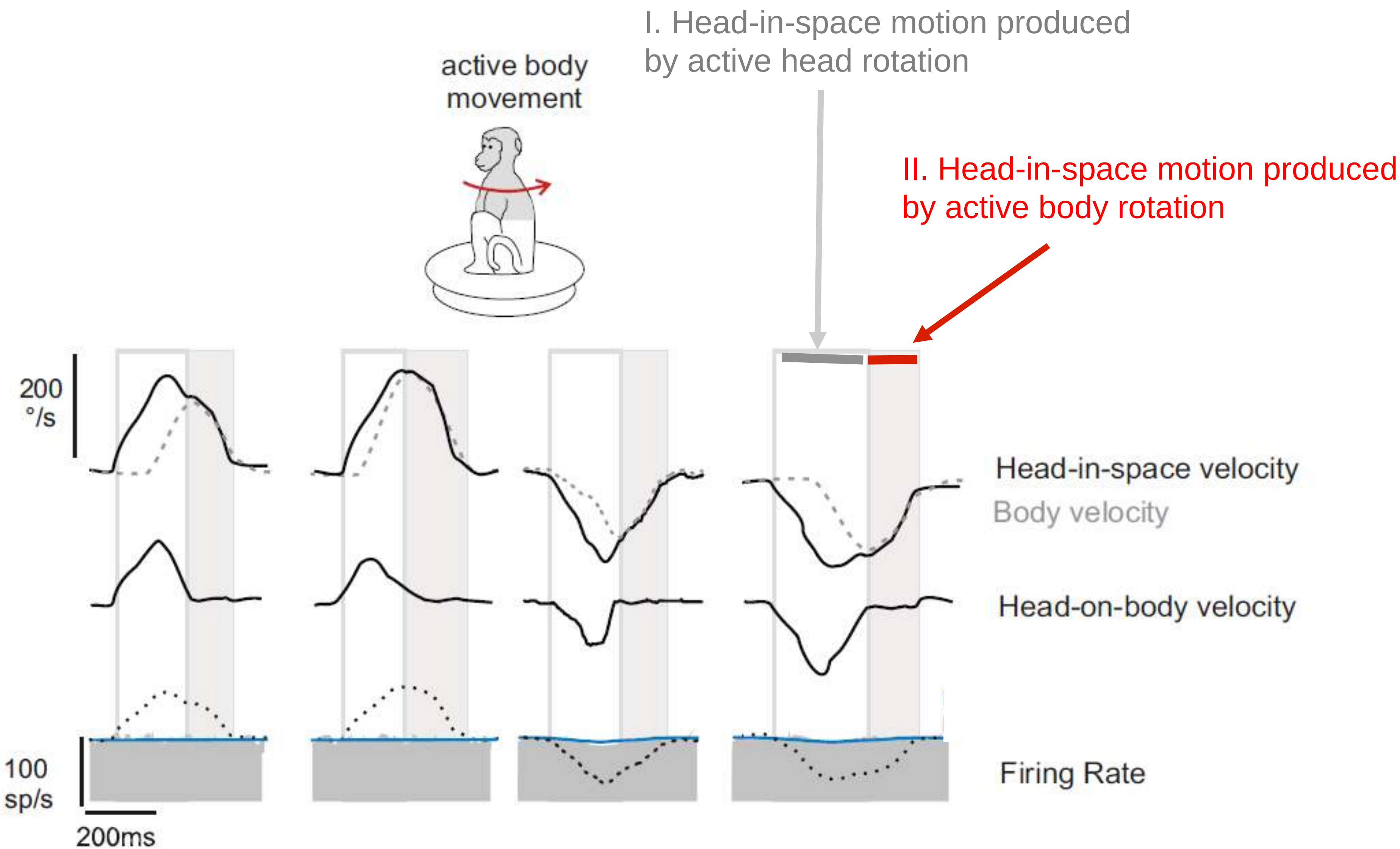
Passive Head-in-space motion

Active Head-in-space motion



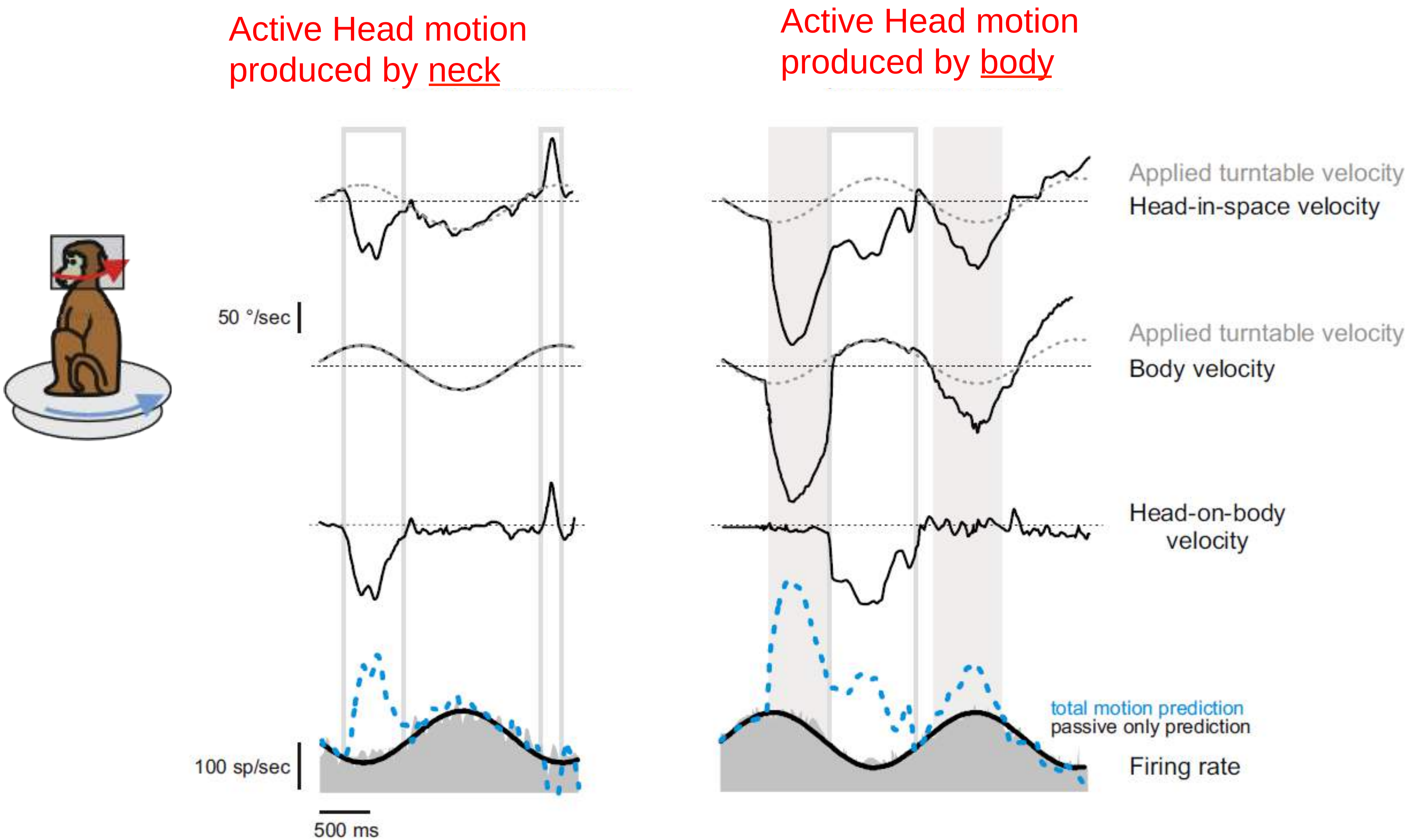
Roy and Cullen 2001, 2004

and for that produced by active body rotations.



Brooks and Cullen, under review

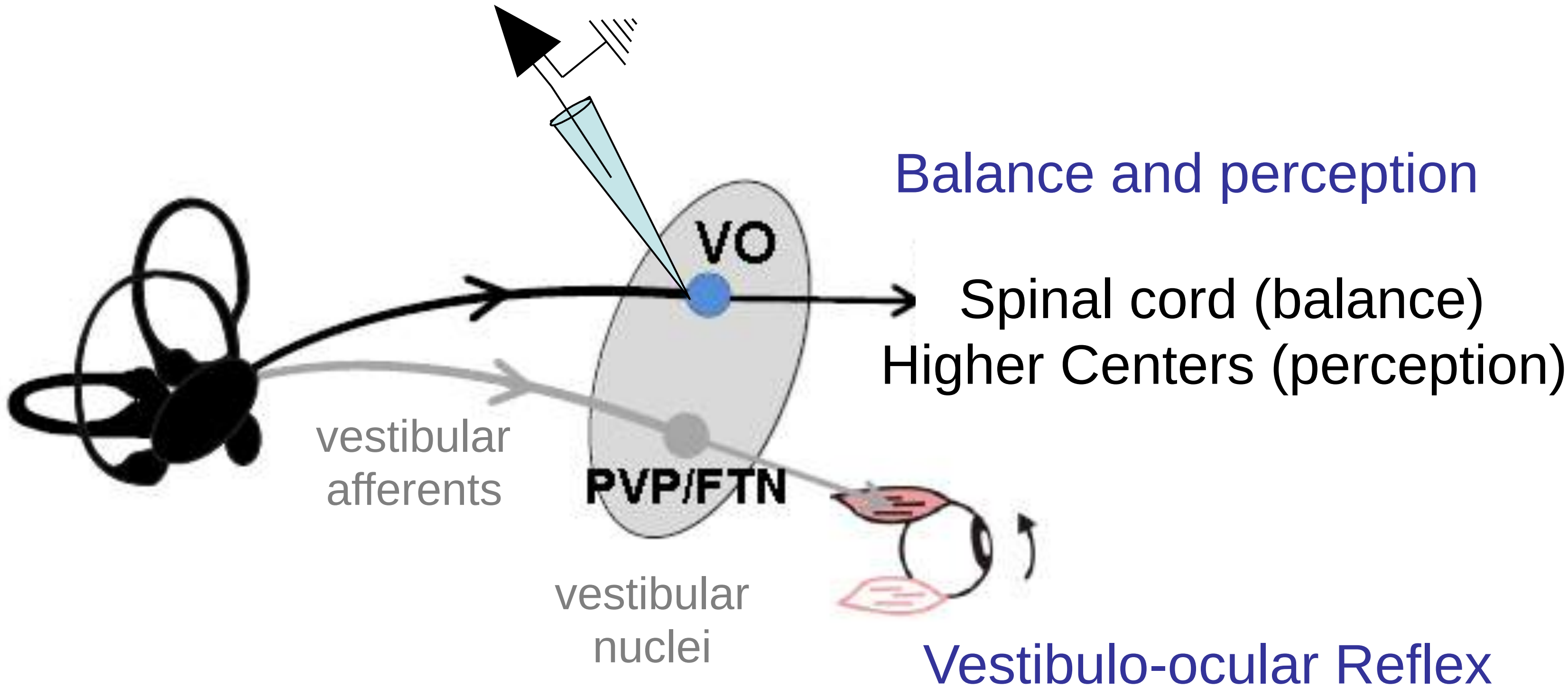
Moreover, neurons selectively encode passive motion during concurrent active/passive movements



Roy and Cullen, J. Neurosci., 2001

Brooks and Cullen, under review

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



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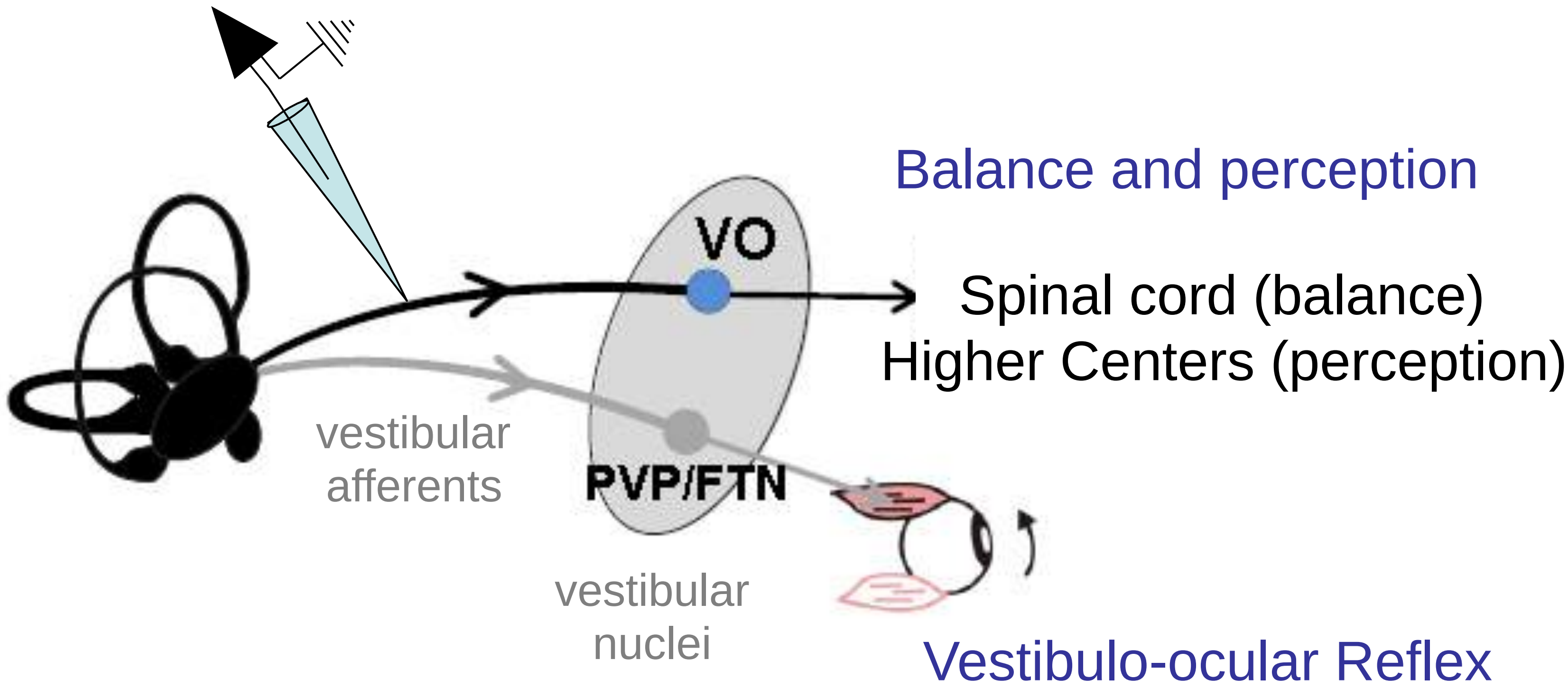
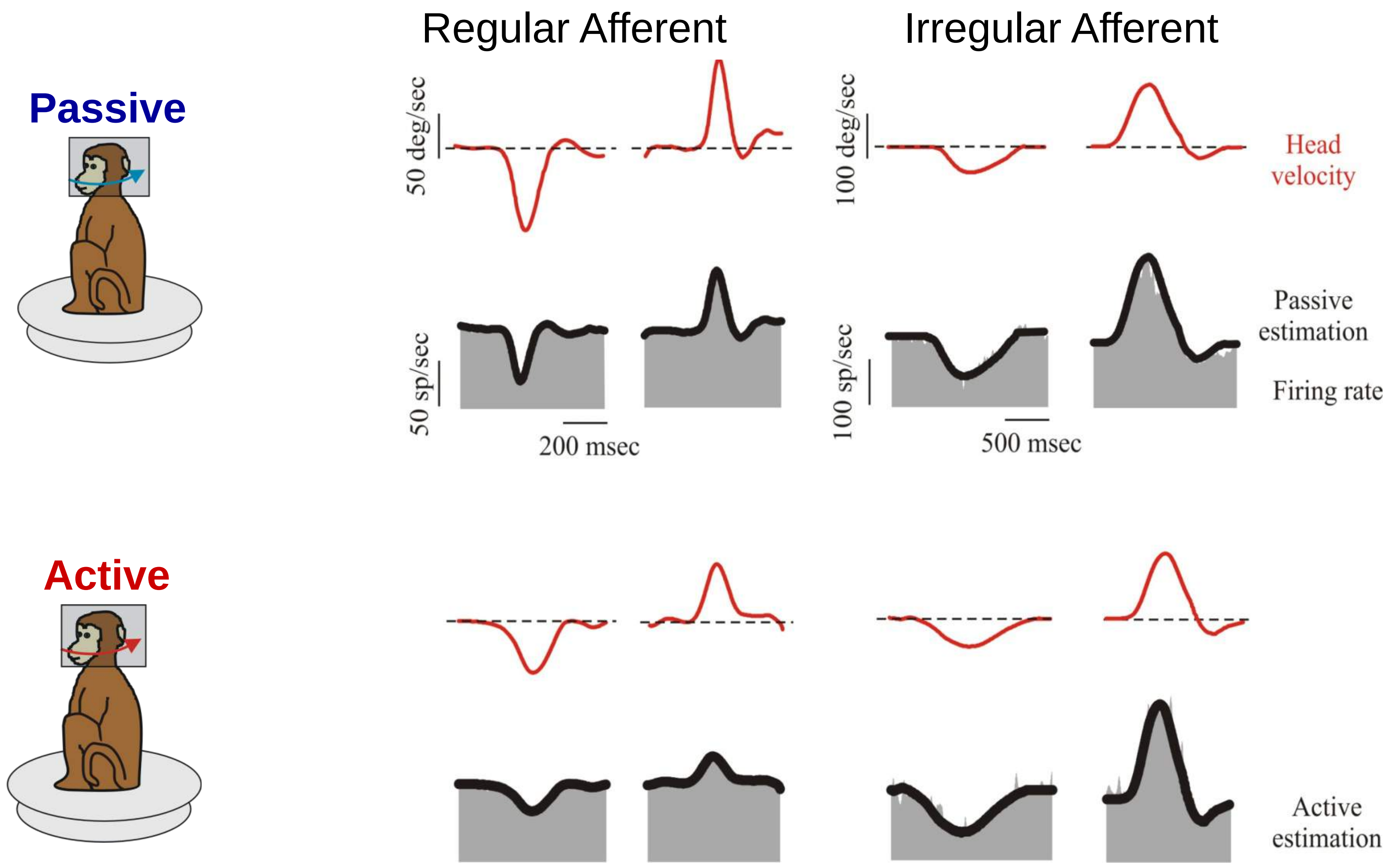


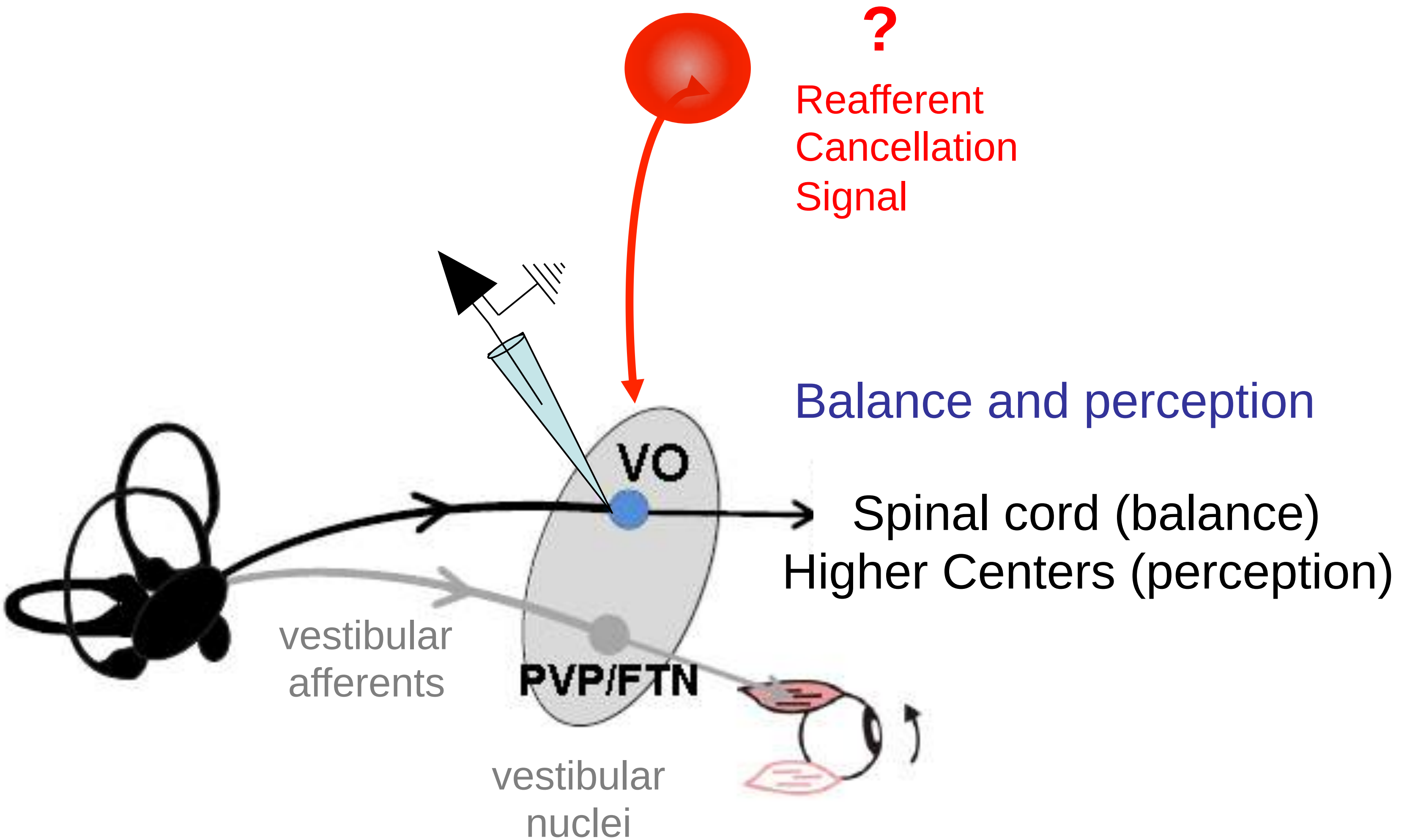
This distinction is not observed at the previous stage:

Vestibular afferents similarly encode active and passive motion



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

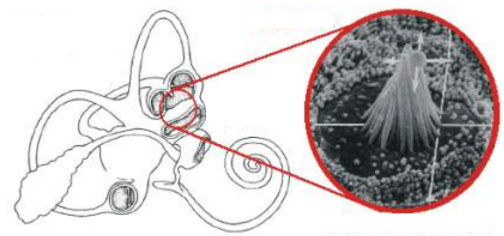
Where and how does the brain make this distinction between active and passive head motion?



During Passive Movements:

The Vestibular Sensors are Activated

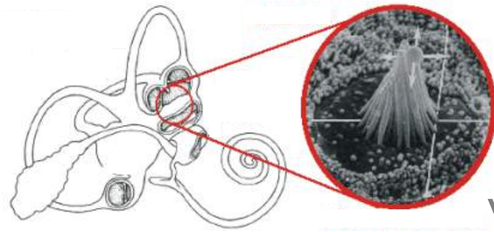
Passive
Whole-Body
Rotation



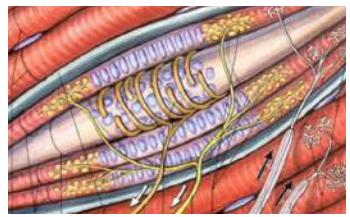
Vestibular

During active movements:

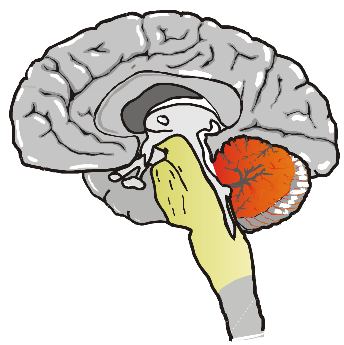
Additional information is available for distinguishing between passive vs. active motion



Vestibular



1. Proprioception

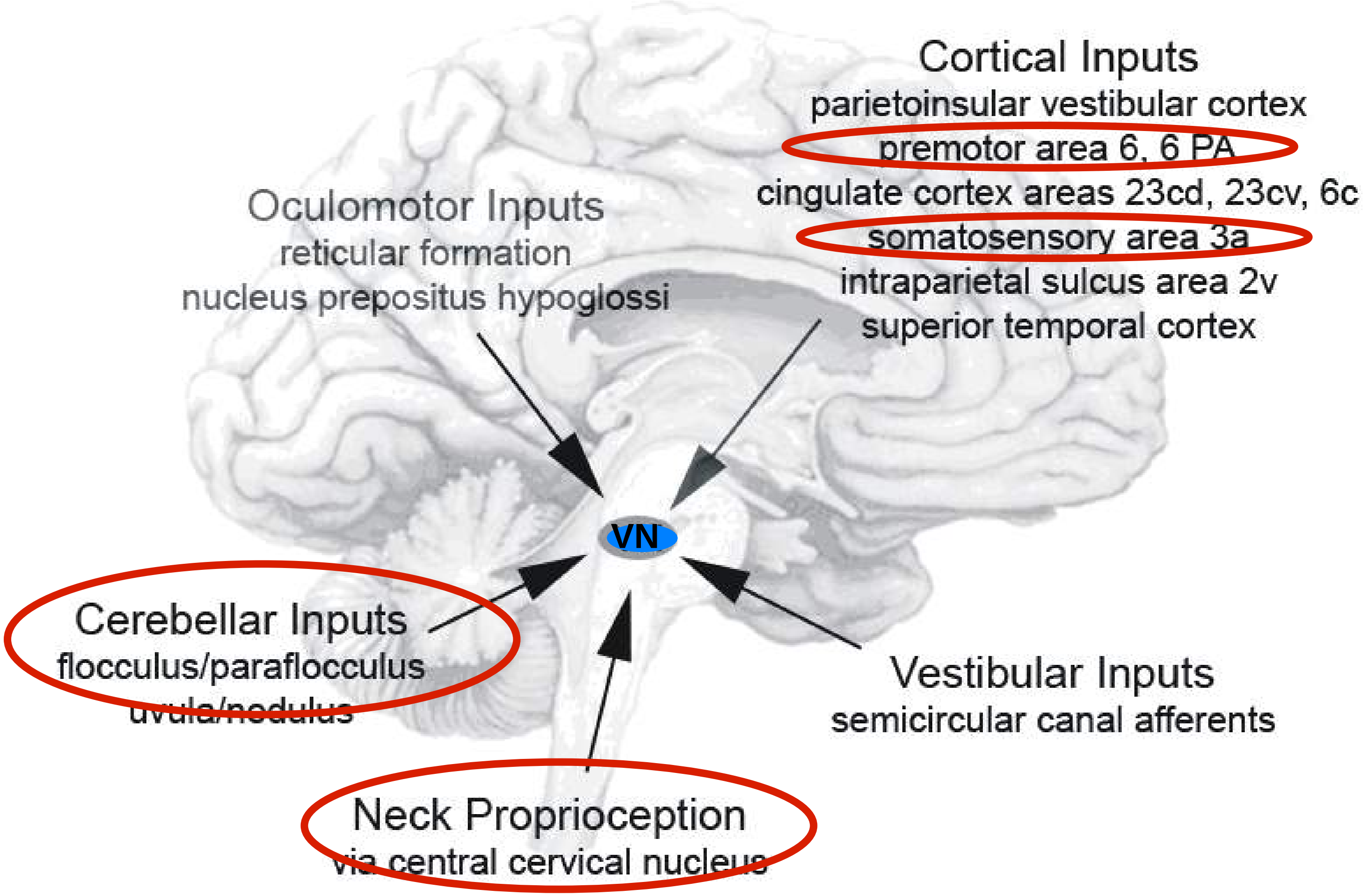


2. Motor Command

3. Knowledge

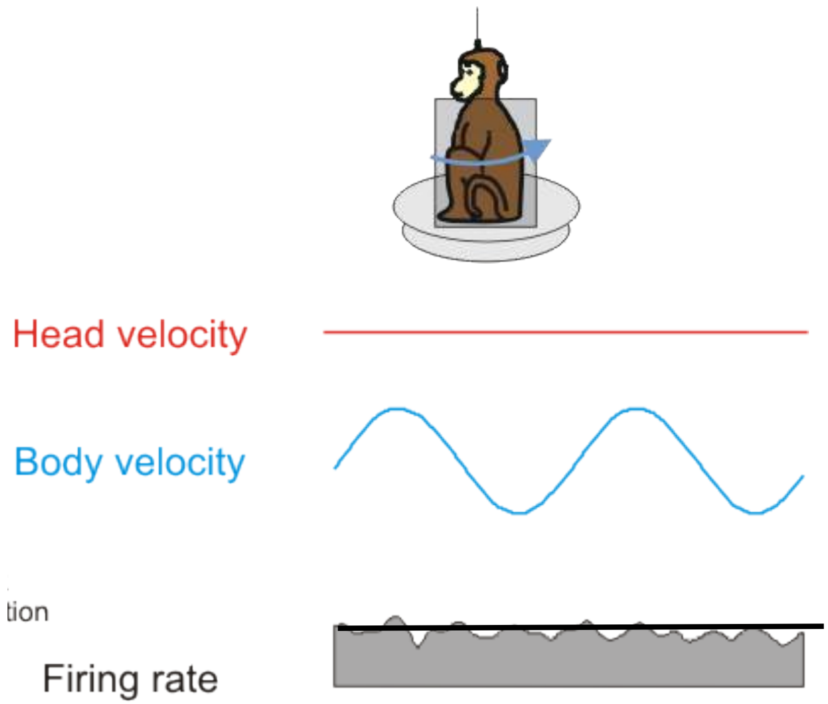
Active Self-motion

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

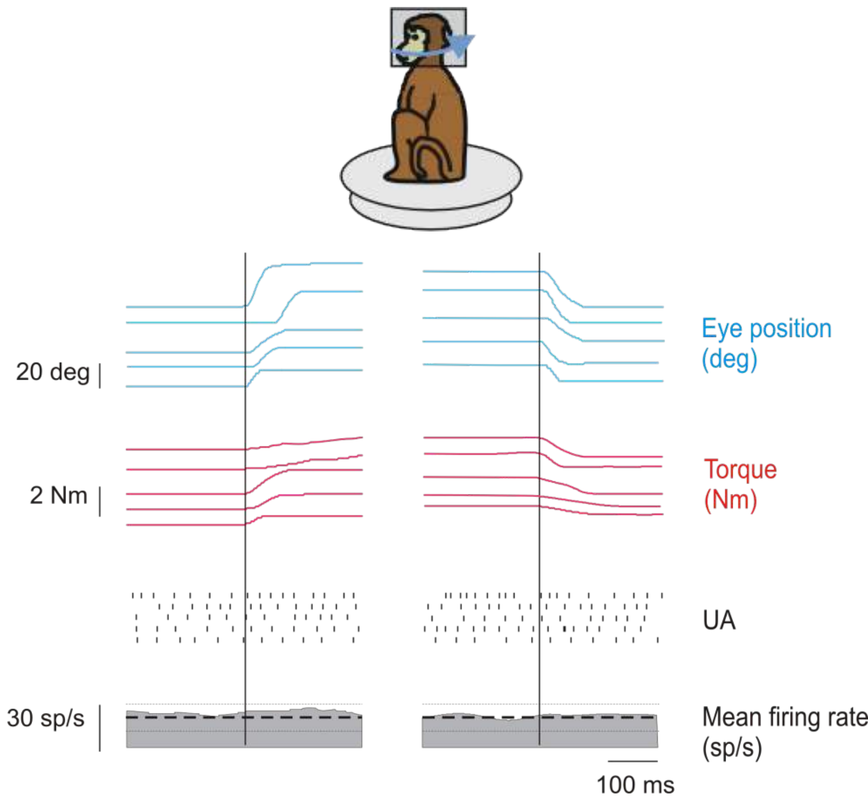


Cancellation of self-produced stimulation is **not** directly mediated by proprioceptive or by motor efference copy inputs

Passive stimulation of neck proprioceptors



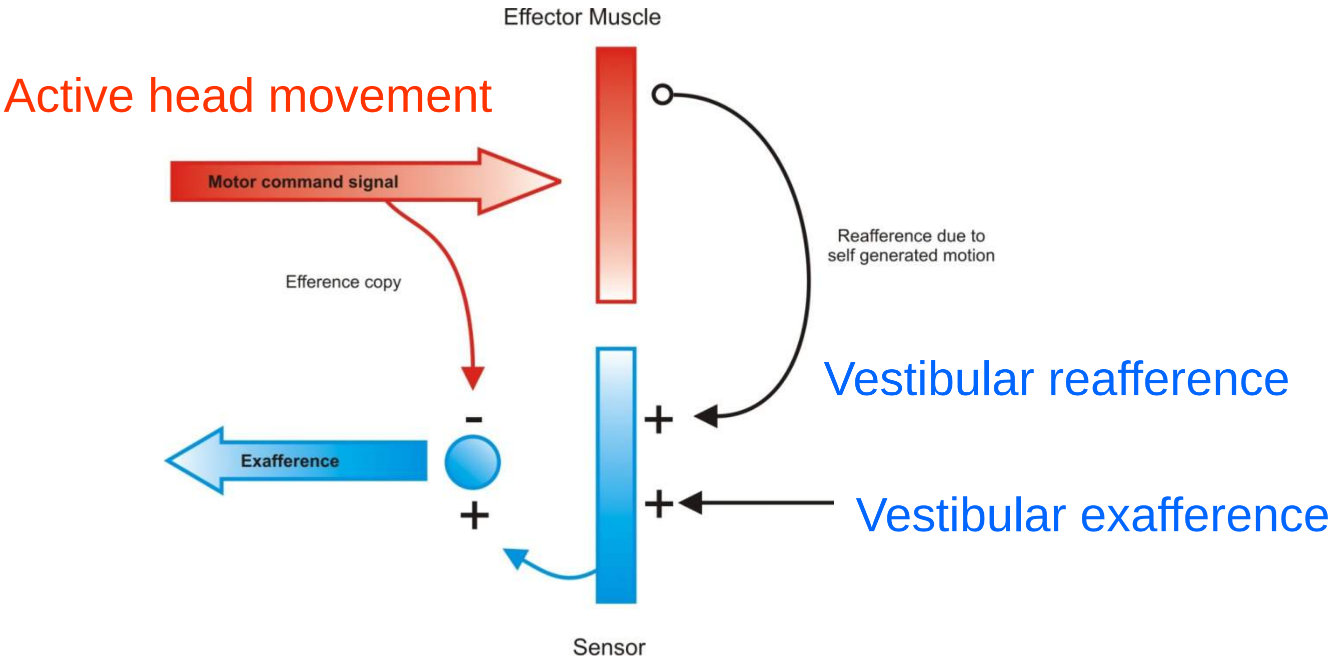
Generation of motor efference copy without head motion



Roy and Cullen, J. Neurosci., 2001

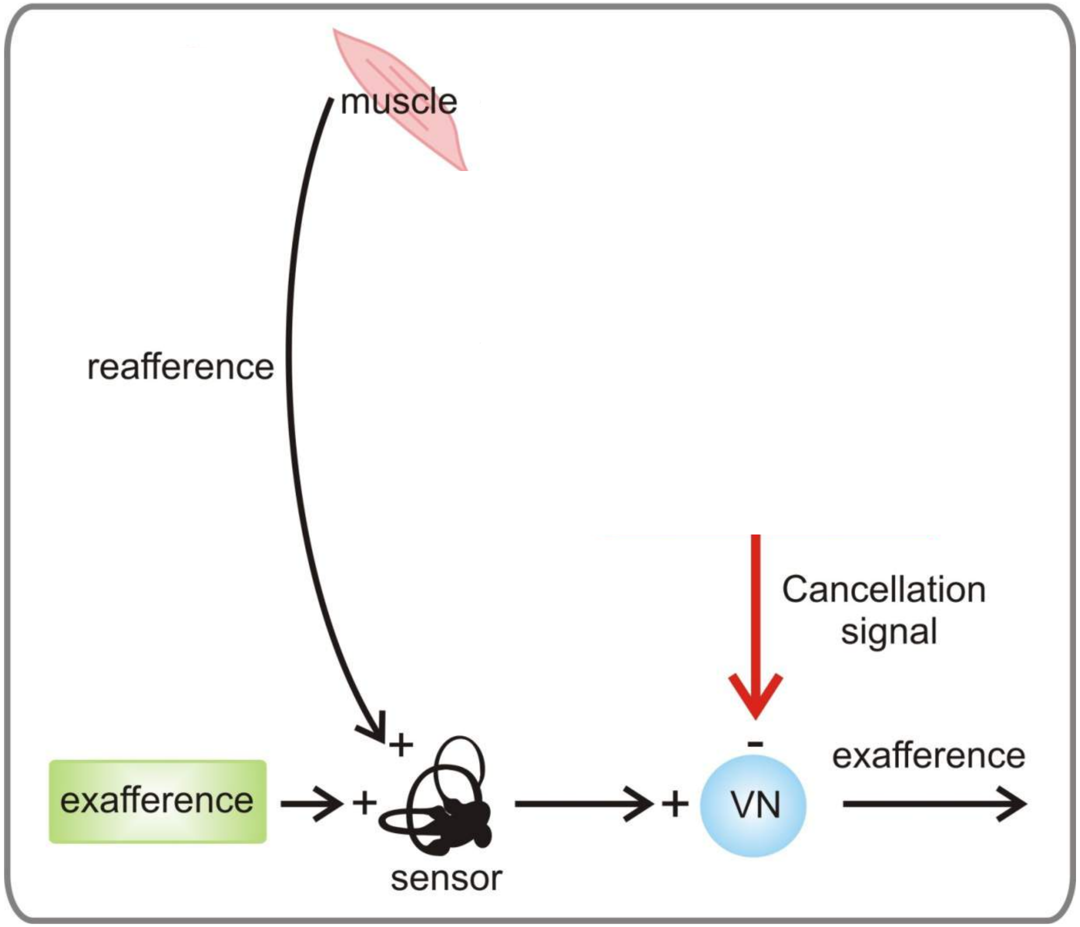
Roy and Cullen, J. Neurosci., 2004

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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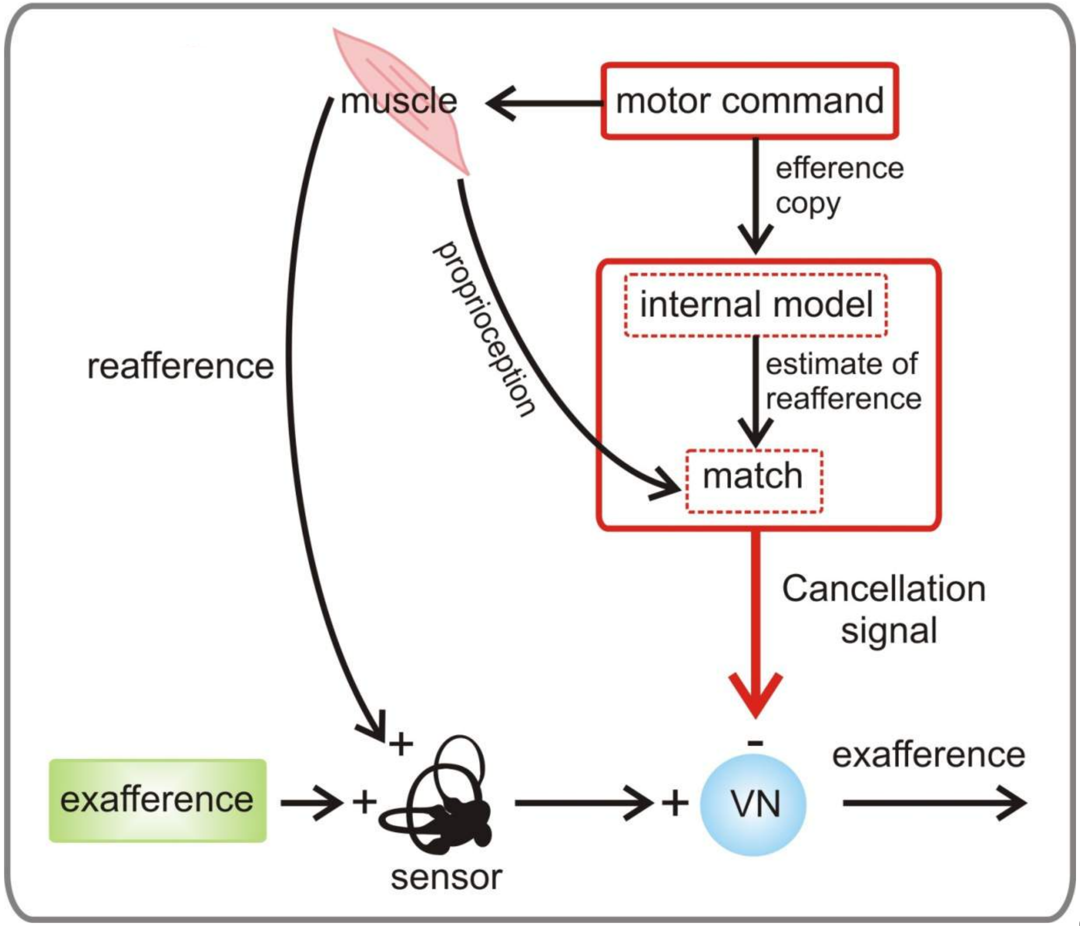
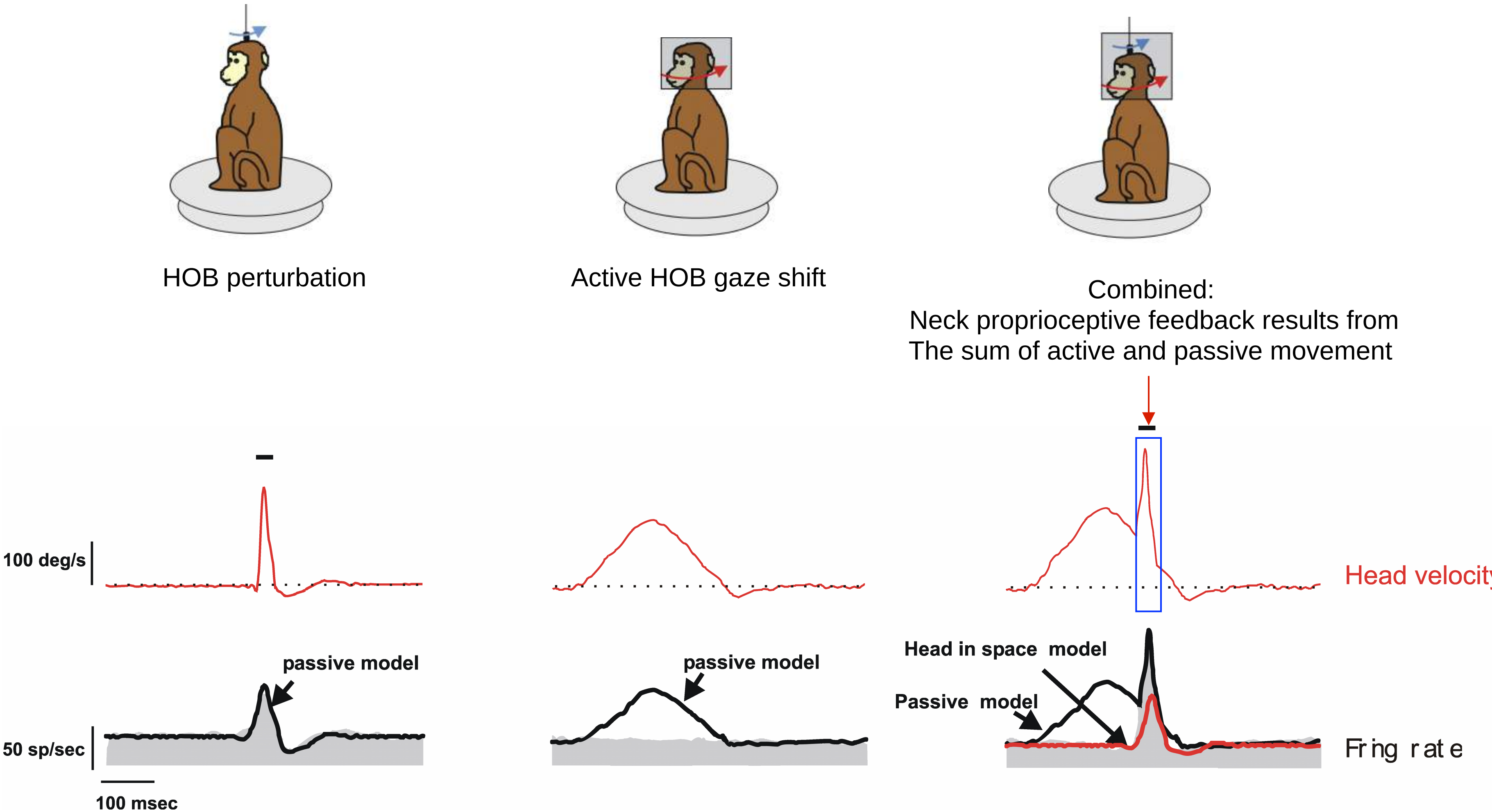


Cullen,
Trends in Neuroscience 2012

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



Brooks and Cullen, under review

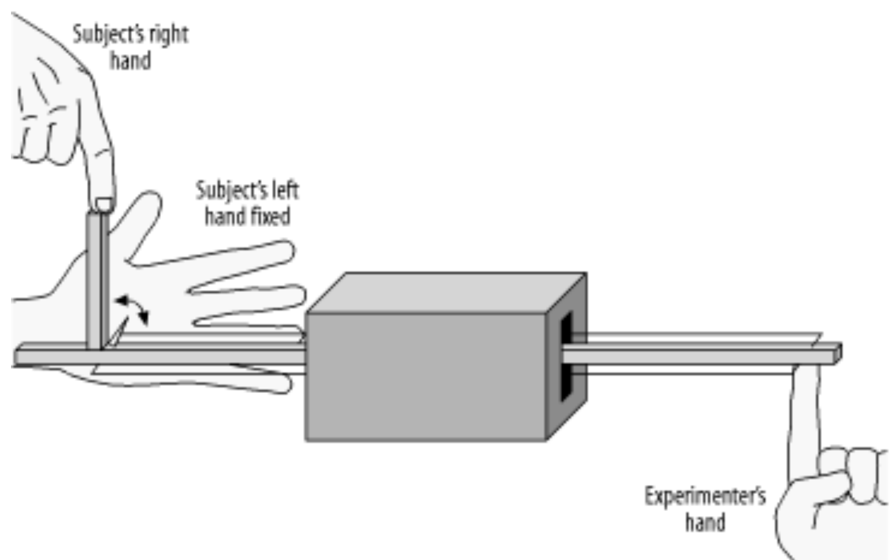
Is this a Common Strategy among Sensory Systems?

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.



Blakemore et al., *J Cogn Neurosci*., 1999

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.

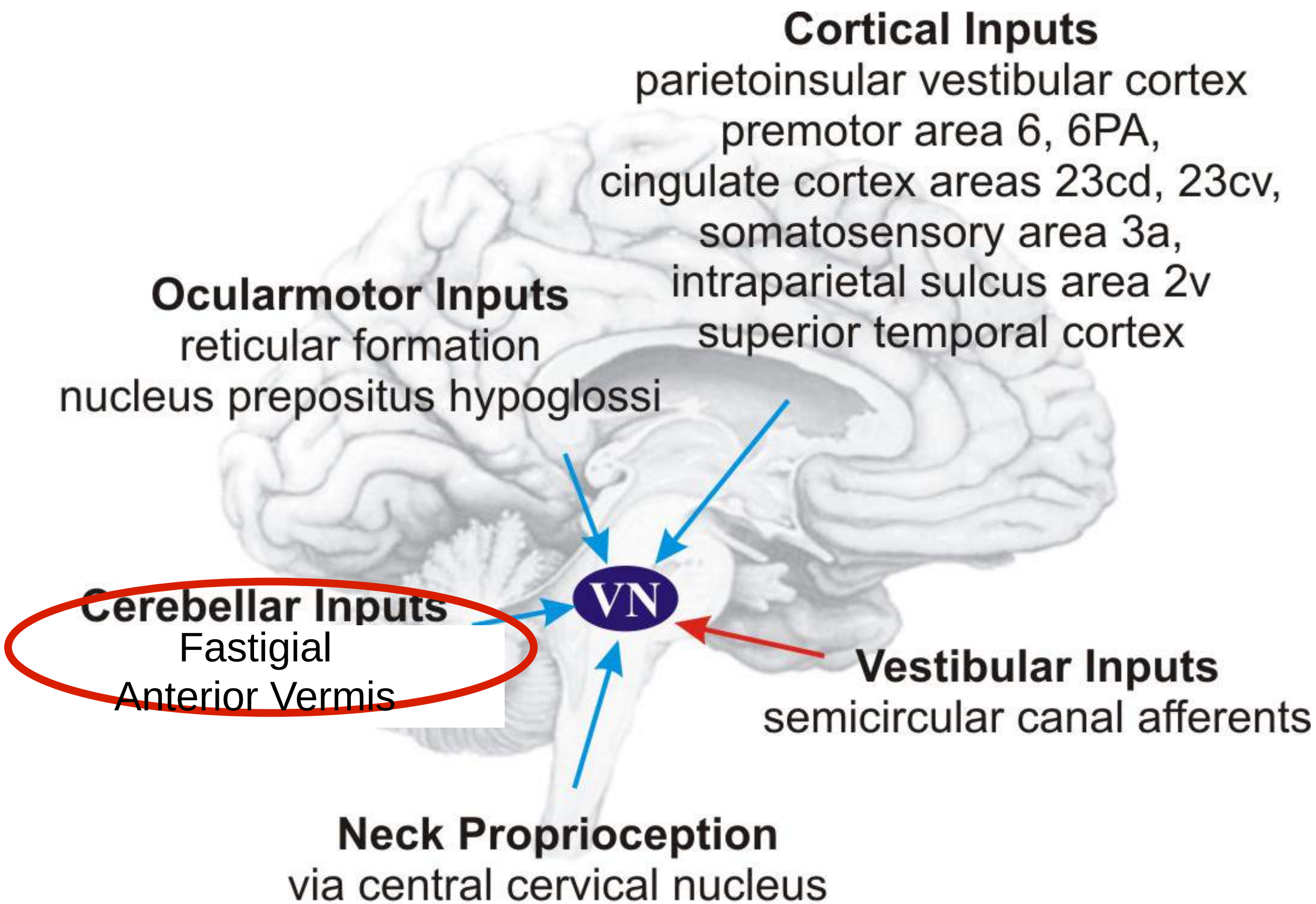
   The cerebellum-like electrosensory lobes provide the signal that is used to cancel the sensory response to self-generated stimulation (Bell and colleagues).

2. fMRI studies in humans

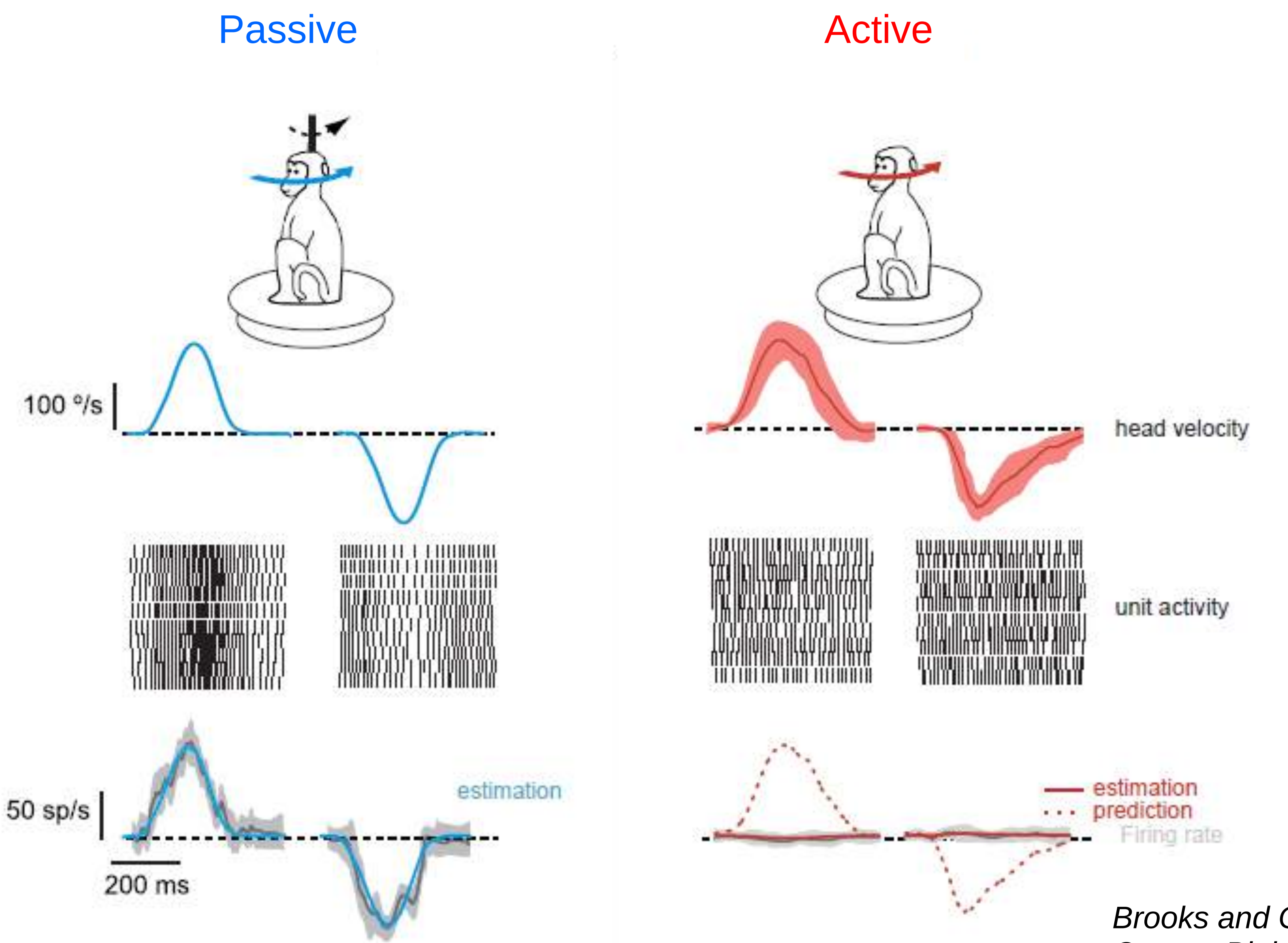
   Suggest that the cerebellum serves a similar role in the suppression of tactile stimulation during self-produced tickle (Blakemore, Wolpert and colleagues).

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

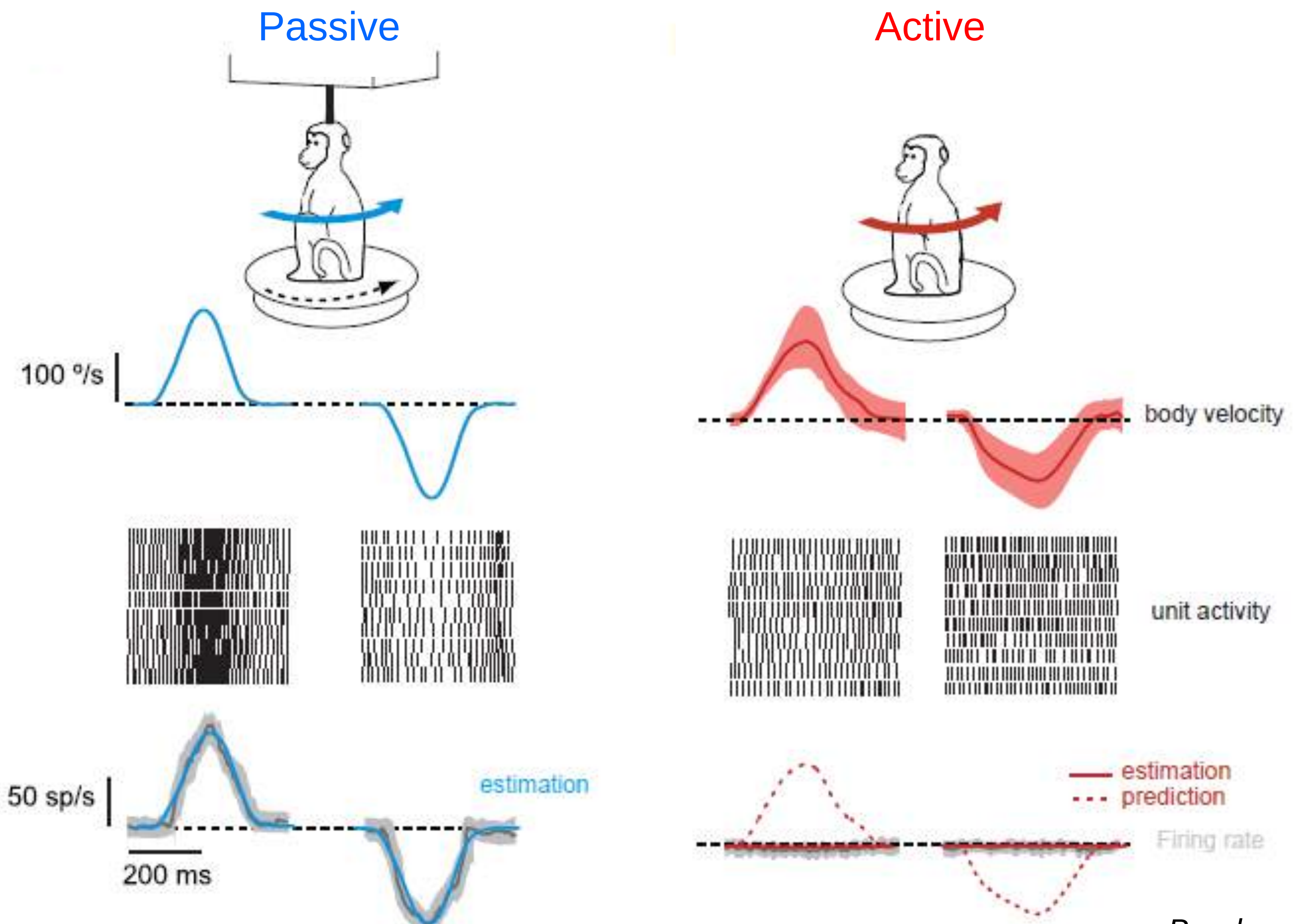


During active motion, Unimodal Neurons no longer encode head-in-space motion



Brooks and Cullen, Current Biology 2013

and Bimodal Neurons no longer encode Body motion

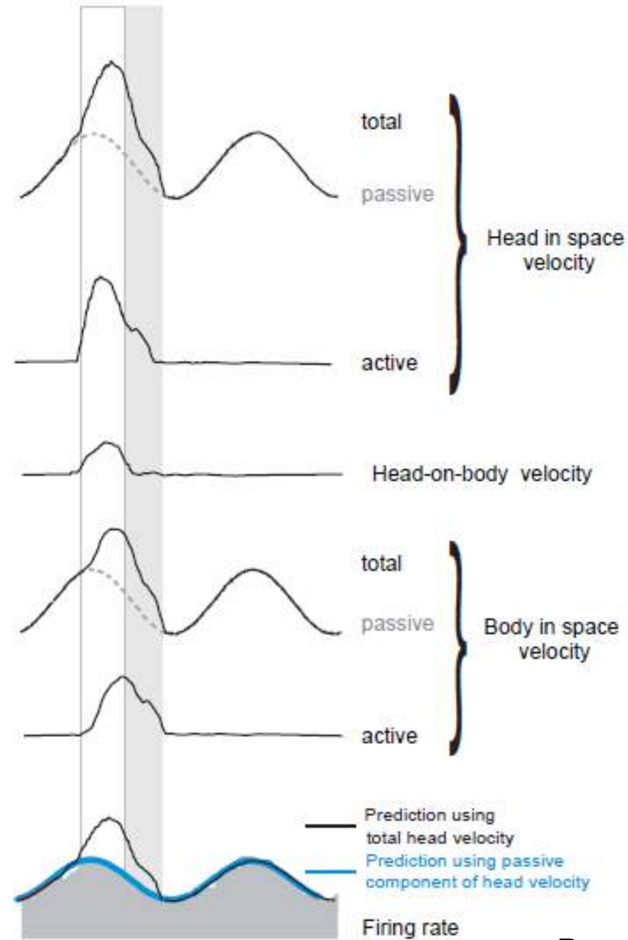


Brooks and Cullen, Current Biology 2013

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

Passive head motion and
Active head motion

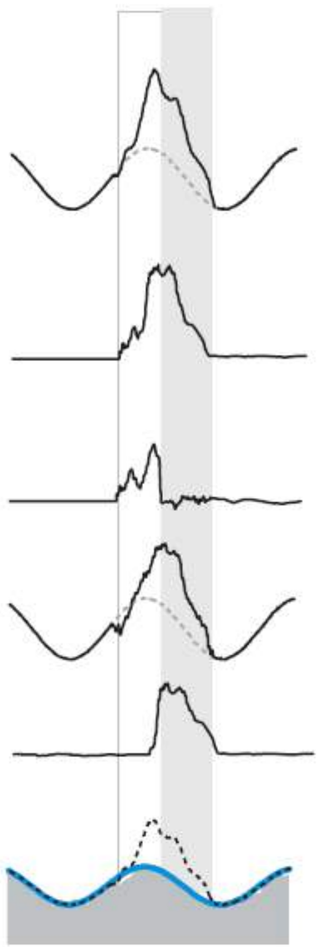
Passive head motion and
Active head motion



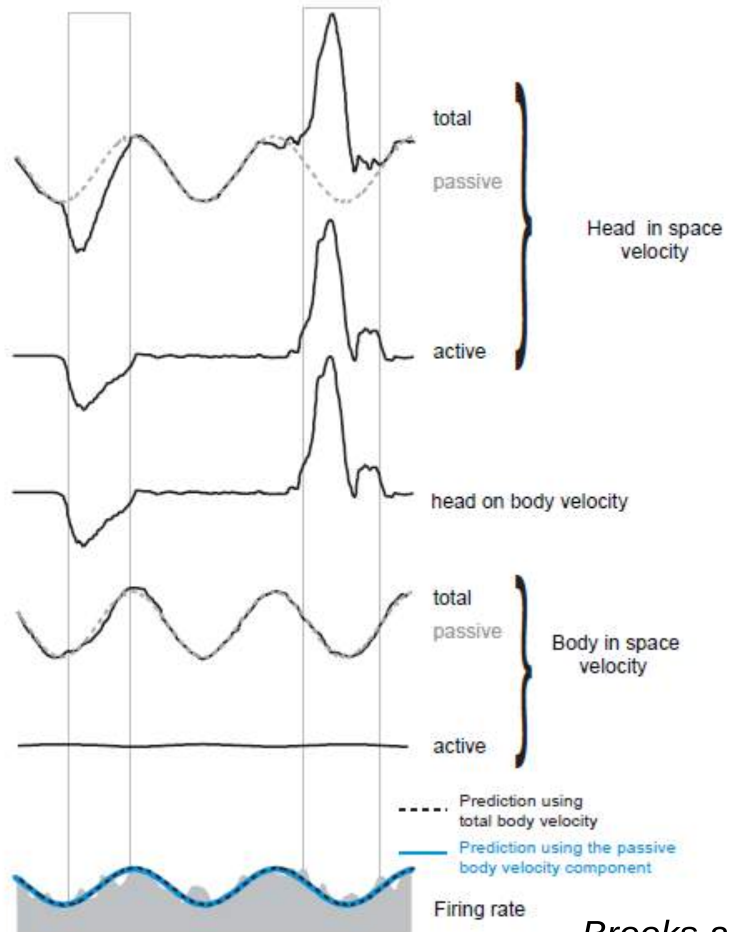
Brooks and Cullen, Current Biology 2013

And, bimodal neurons selectively encode passive body motion

Passive body motion and
Active body motion



Passive body motion and
Active body motion



Brooks and Cullen, Current Biology 2013

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.

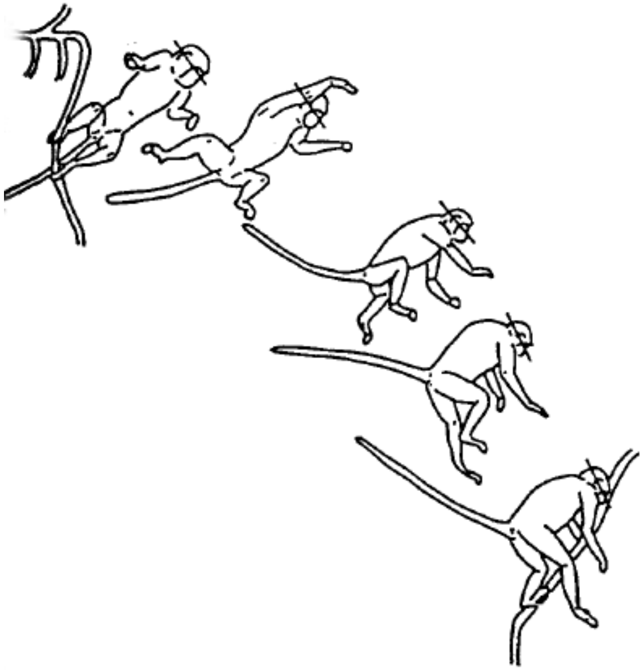
- Moreover, this central cancellation mechanism is highly adaptable.

- 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:

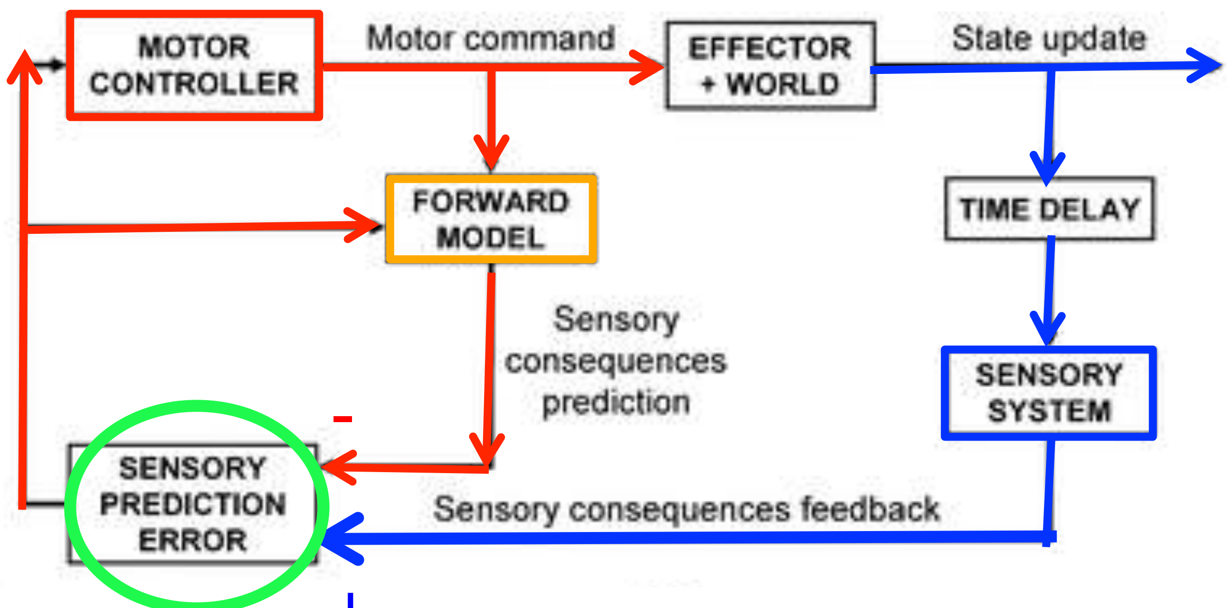
Suppression of vestibular reafference occurs when proprioceptive feedback <u>matches</u> that expected as a result of the motor command
(as during normal active movements)

If this is true,

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

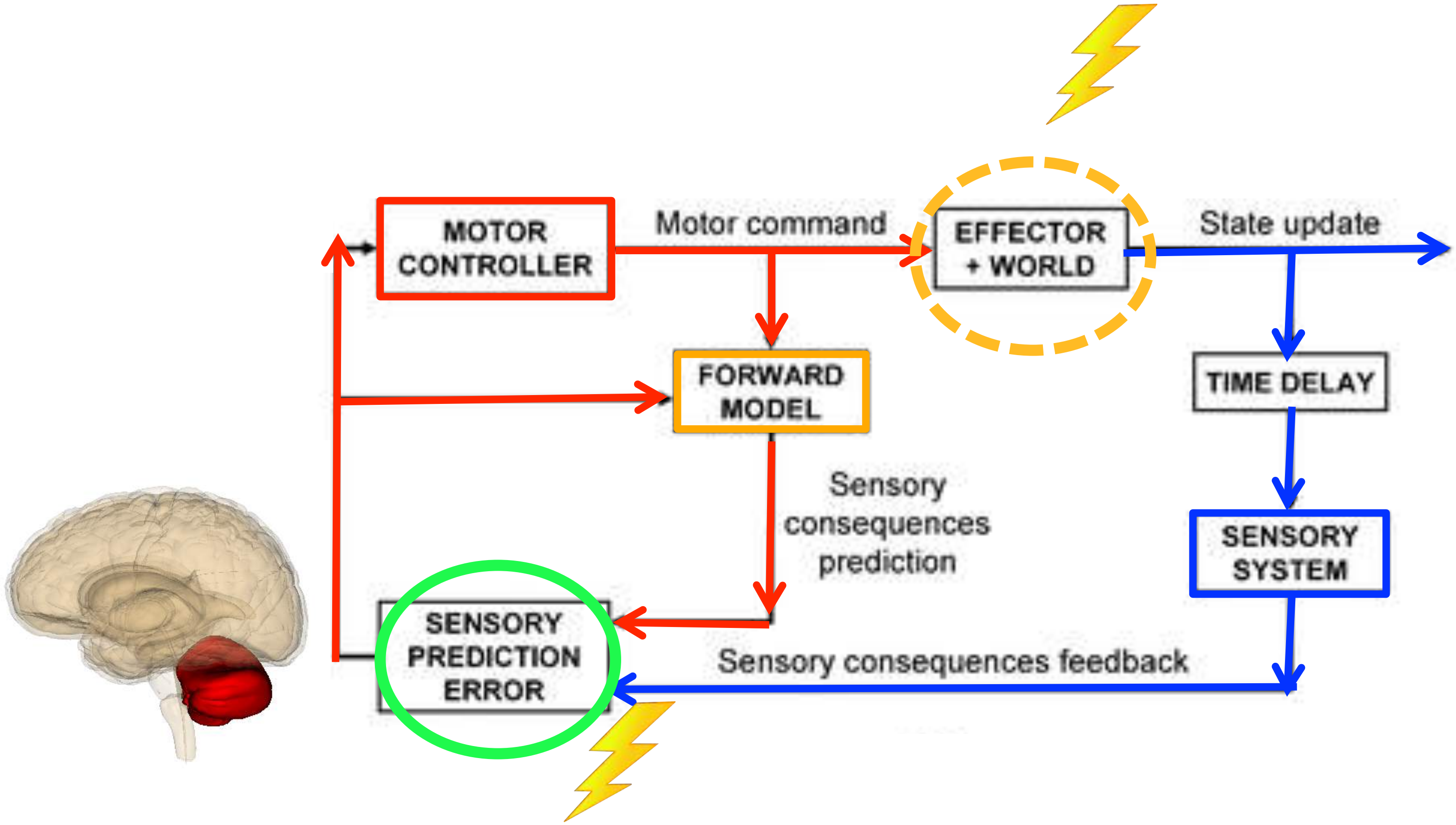
To acquire new skills and maintain mastered skills,
our brain must coordinate the responses of neurons and neural circuits with changes in motor performance.

There is accumulating evidence that the brain does this by computing an estimate of the expected sensory consequences of movement (forward model), and then comparing this estimate to the actual sensory feedback to compute the _sensory prediction error_.



In everyday life, sensory prediction errors occur not only as a result of:

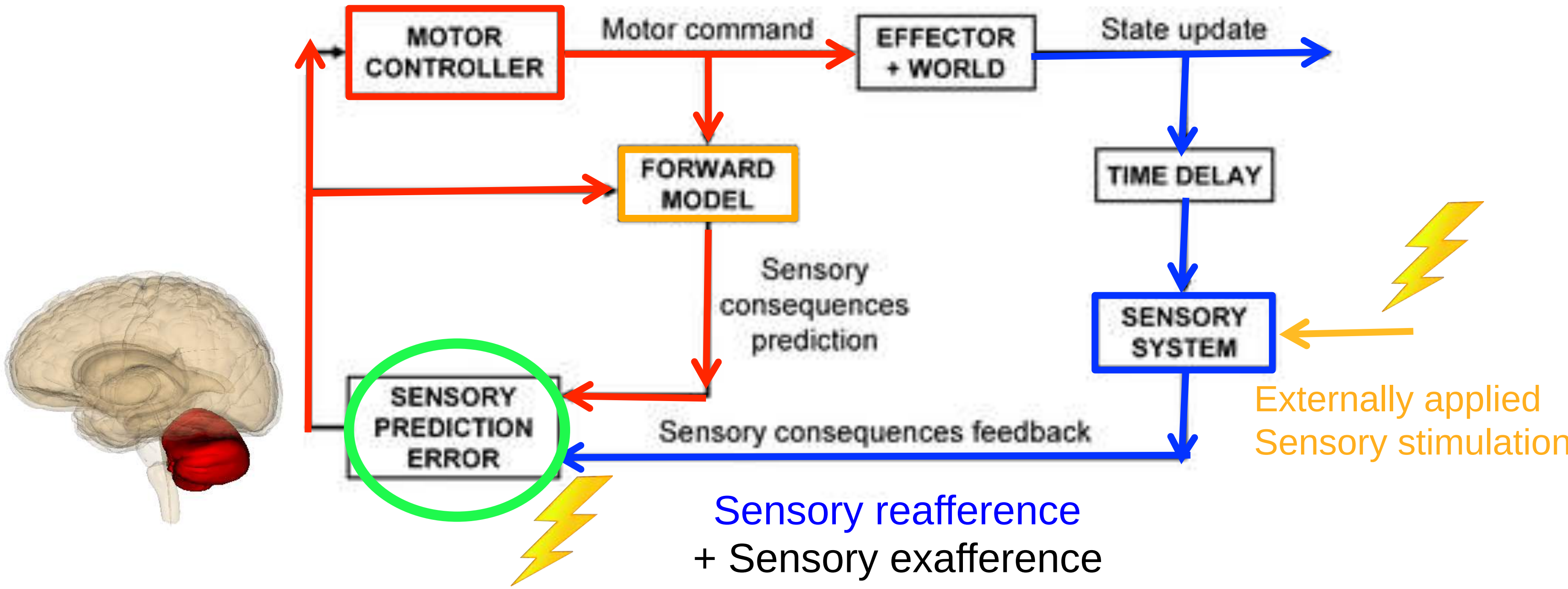
1) Changes in the effector /or world (muscle strength, load, etc.)
   (e.g. for the learning required to maintain accurate motor performance),



In everyday life, sensory prediction errors occur not only as a result of:

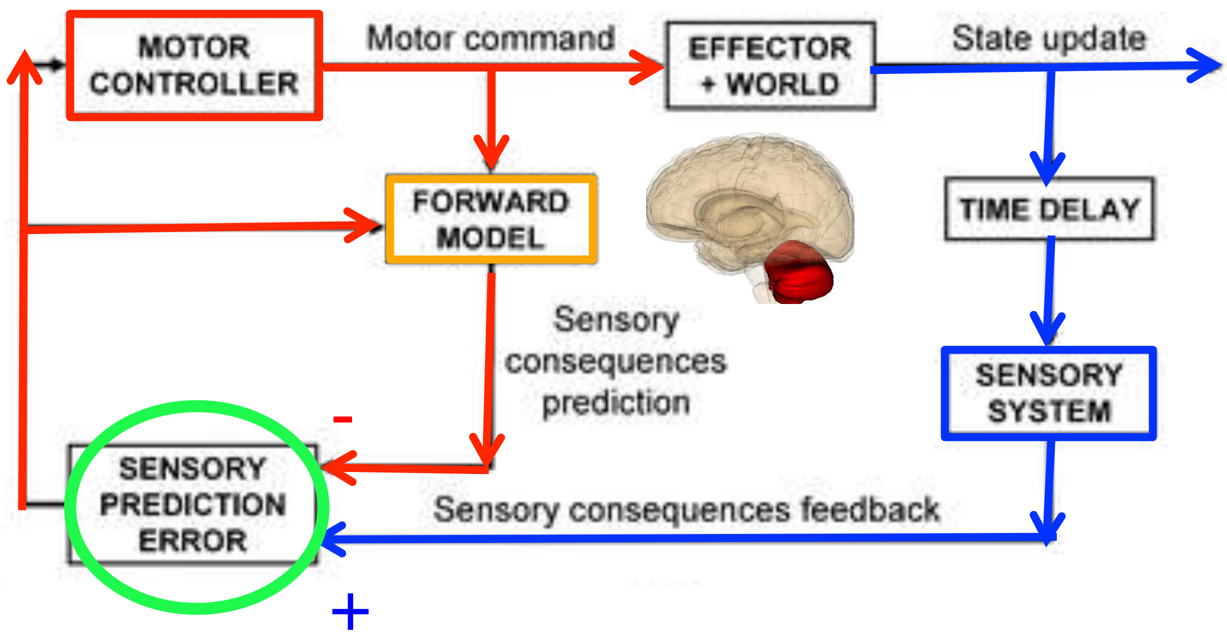
1) Changes in the effector /or world (muscle strength, load, etc)
(e.g. for the learning required to maintain accurate motor performance)
<u>but also when…</u>

2) Sensory stimulation is externally generated rather than self-generated
(e.g., sensory exafference versus reafference).



Patient studies suggest that the <u>cerebellum</u> plays an important role in estimating the sensory consequences of motor commands (i.e., forward model), which are compared with the actual sensory feedback.

In turn, the computed <u>*sensory prediction error*</u> maintains movement accuracy.



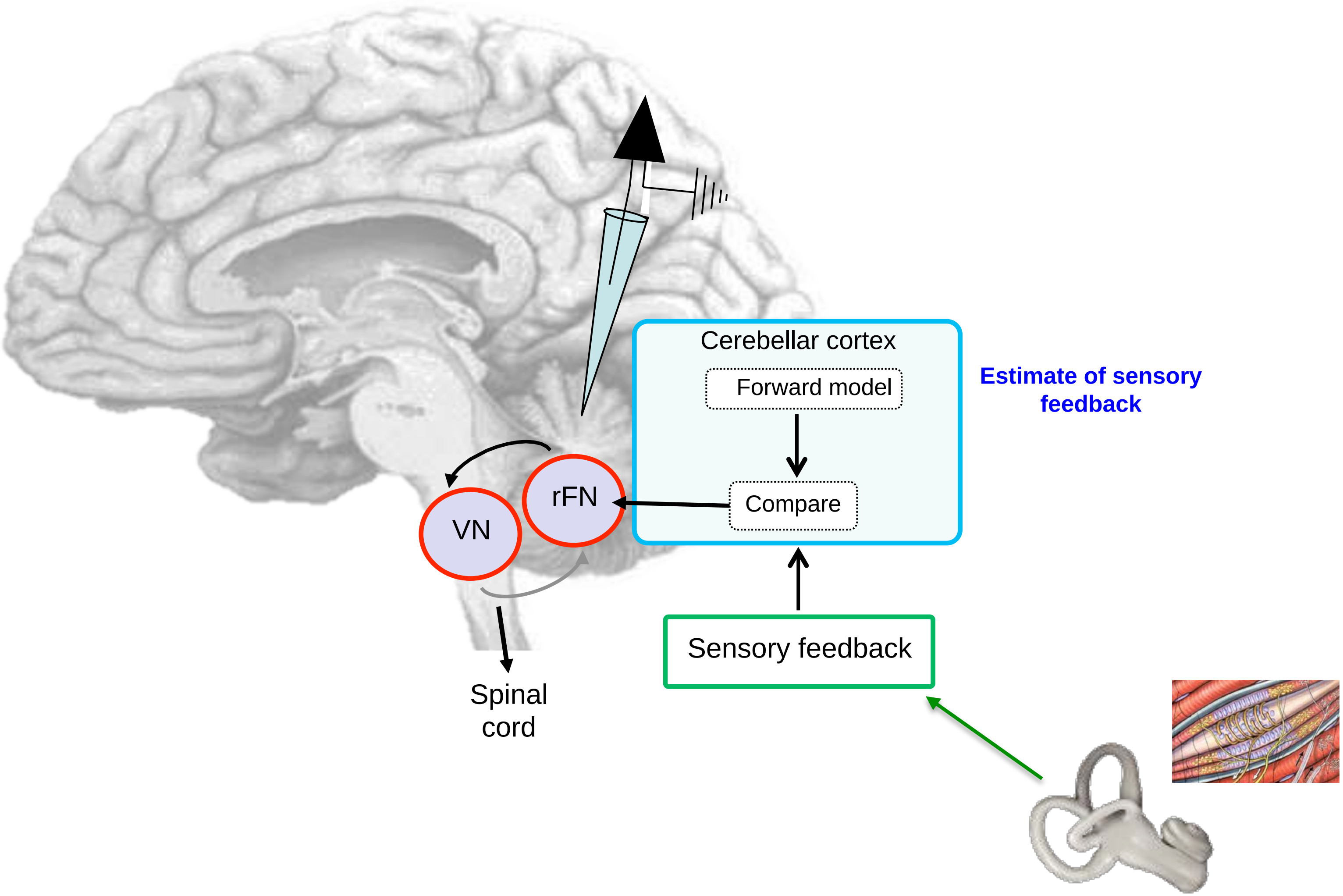
Our current hypothesis:

During active movement, suppression of sensory reafference occurs when sensory feedback matches that expected as a result of the motor command
(as during normal active movements)

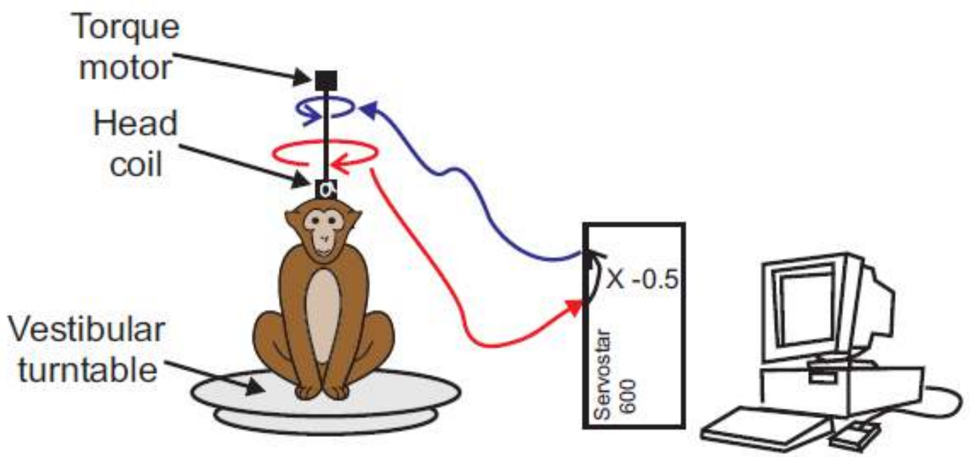
If this is true,

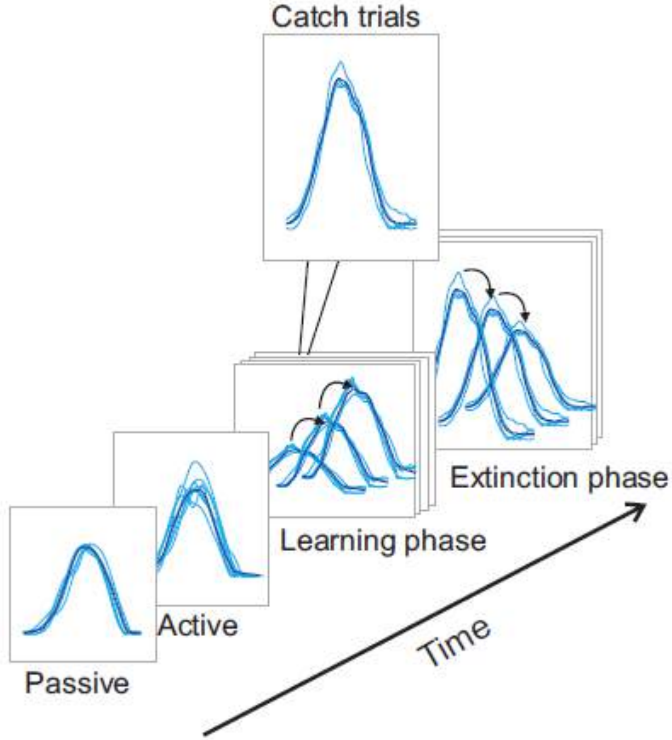
then reafferent suppression should not occur when the relationship between motor commands and sensory reafference is altered.

To test this prediction, we recorded from neurons during <u>active self-motion,</u> and this time altered the relationship between the motor command and sensory reafference.



Experiment: Change the relationship between motor command and sensory reafference via application of resistive torque

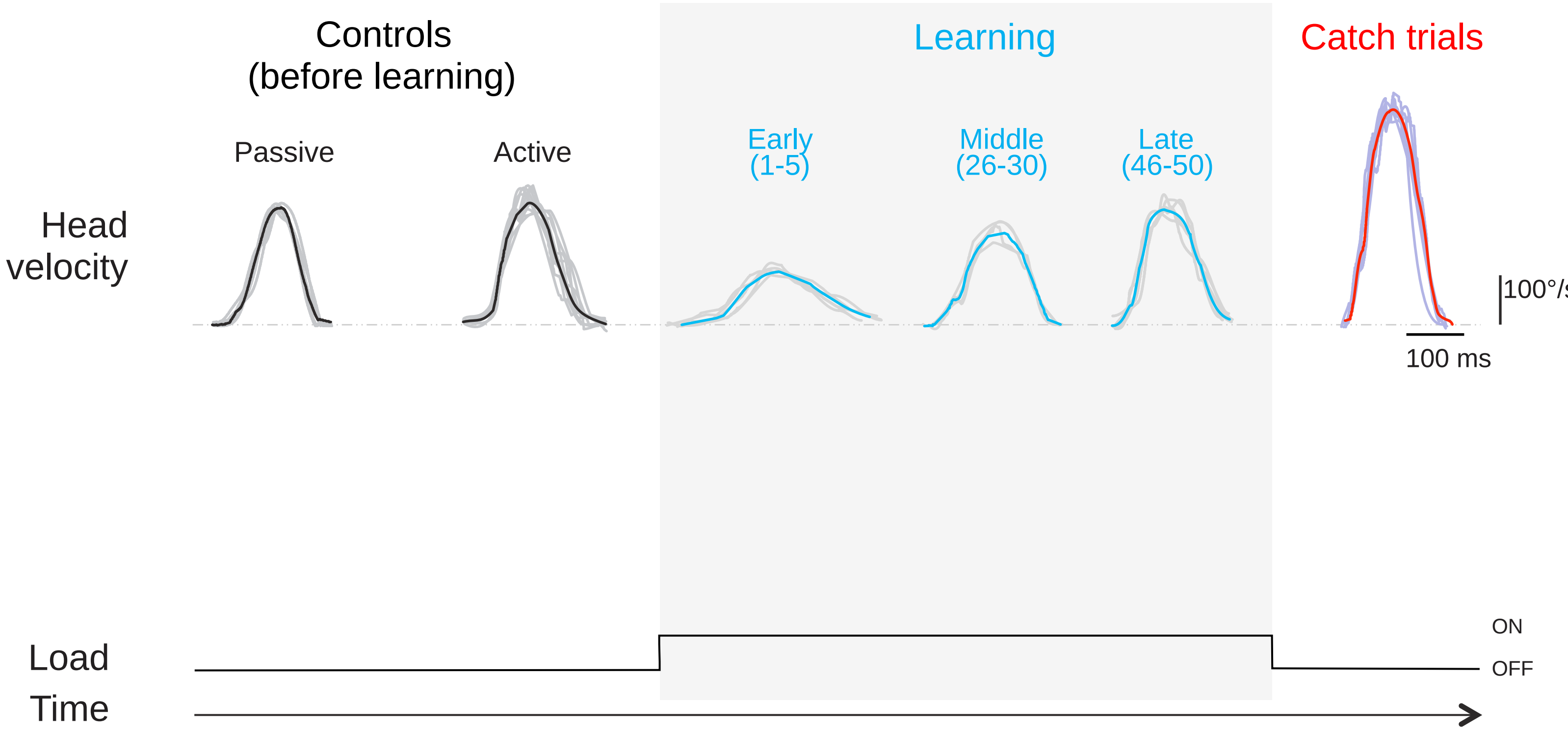




Brooks, Carriot, and Cullen, Nature neuroscience

Experiment: Change the relationship between motor command and sensory reafference via application of resistive torque

Behaviour:



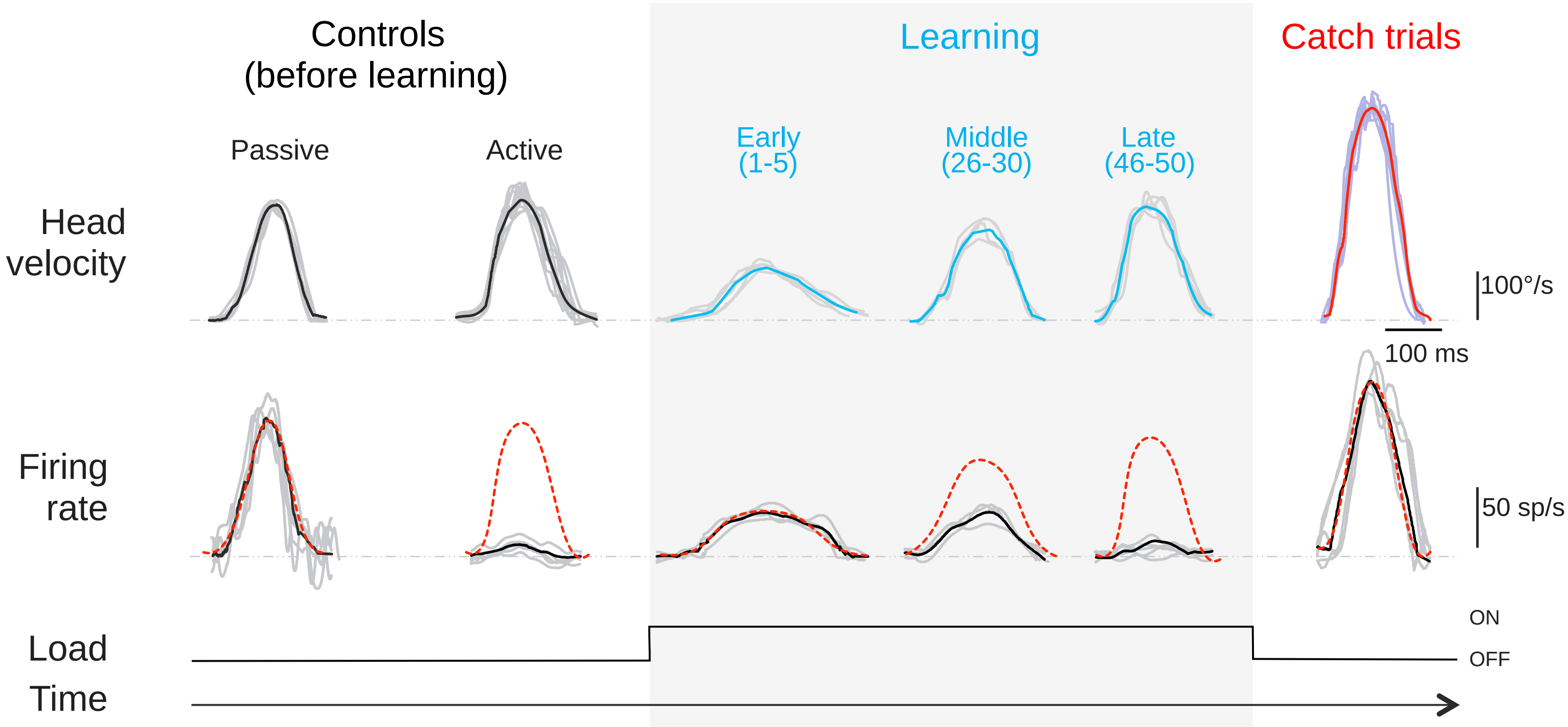
The time course of Behavioural Adaptation

1) The animal learns to adapt after ~50 movements.
2) Head overshoots the initial trajectory once resistance is removed.

Brooks, Carriot, and Cullen, Nature neuroscience

Experiment: Change the relationship between motor command and sensory reafference via application of resistive torque

Neurons:



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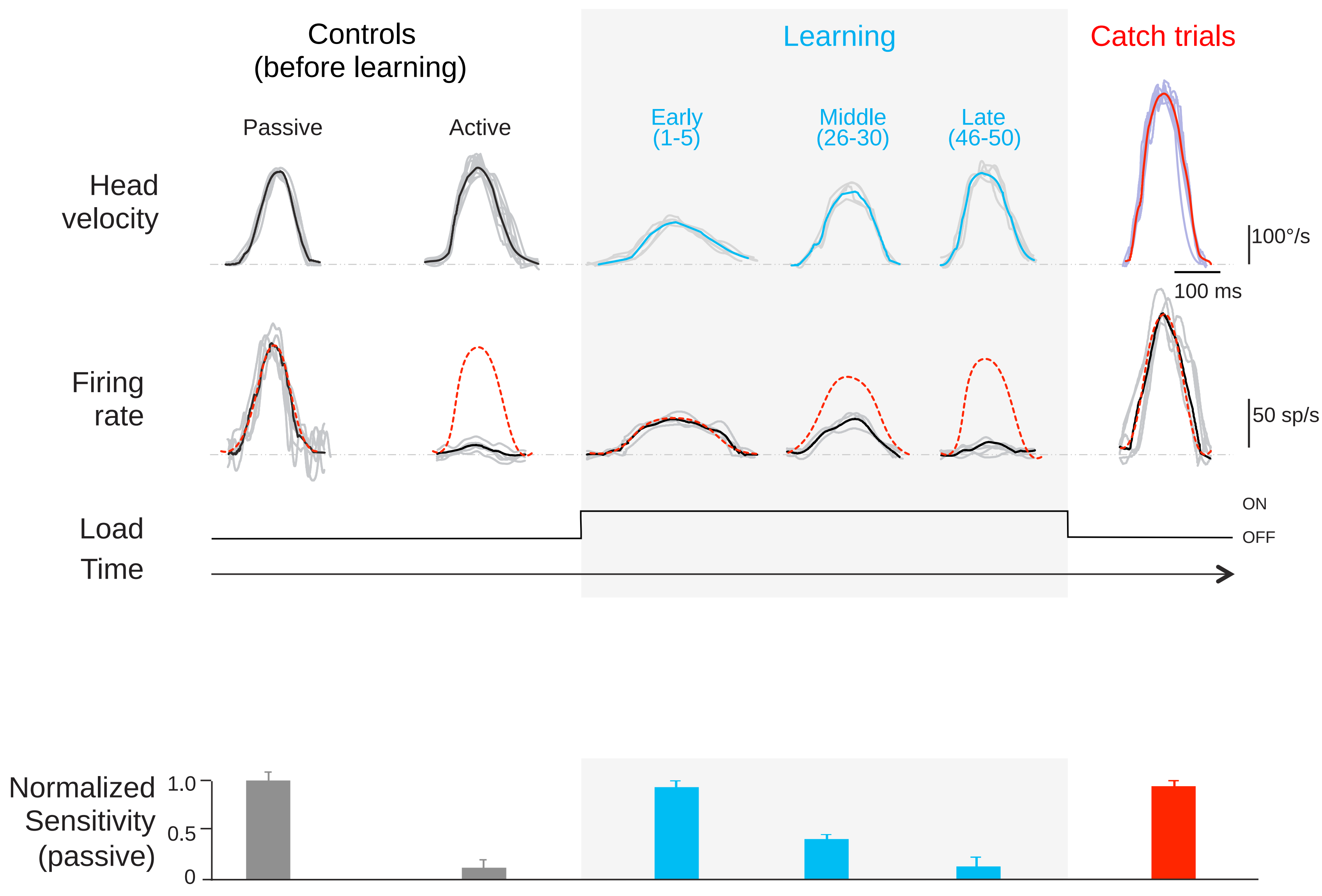

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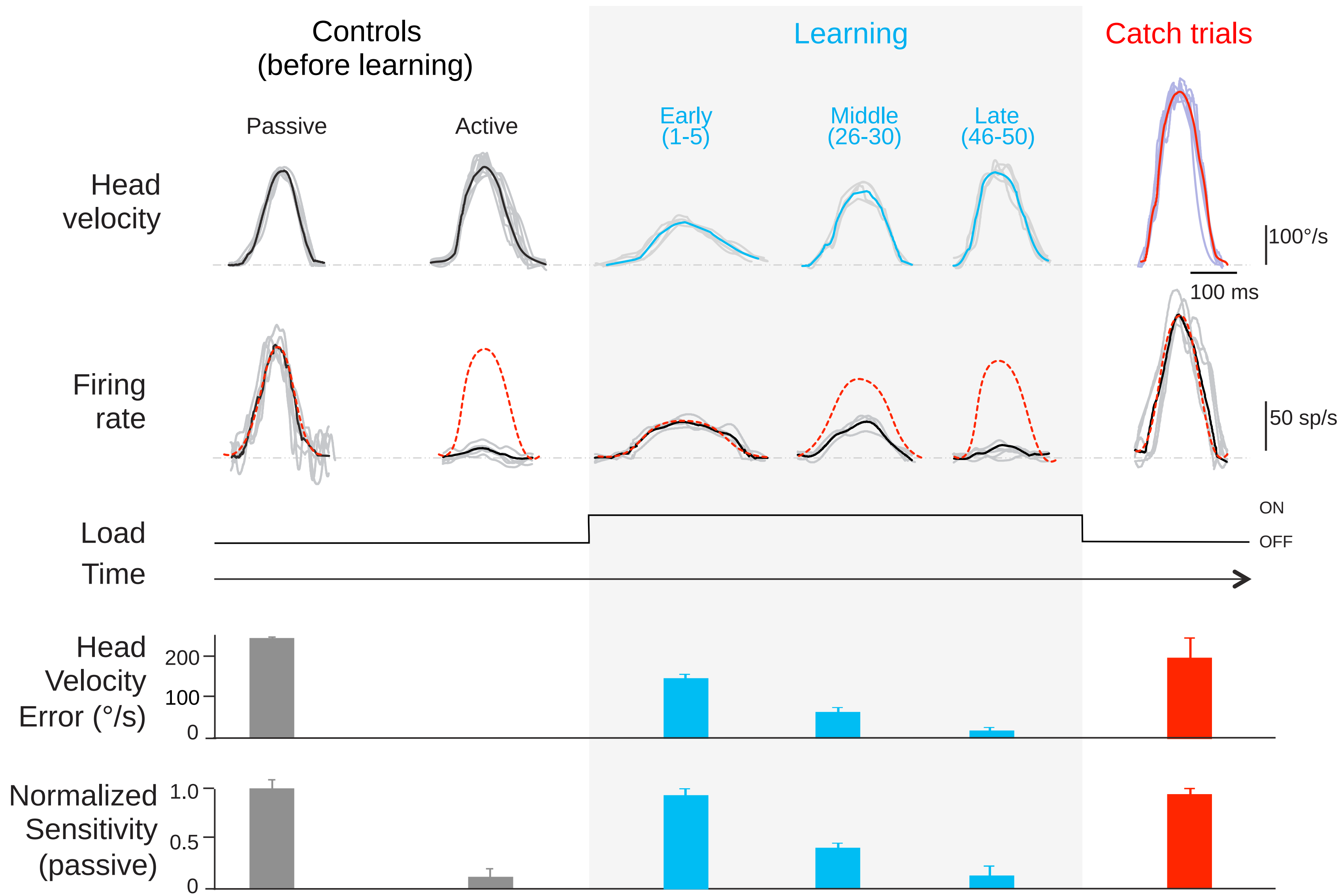
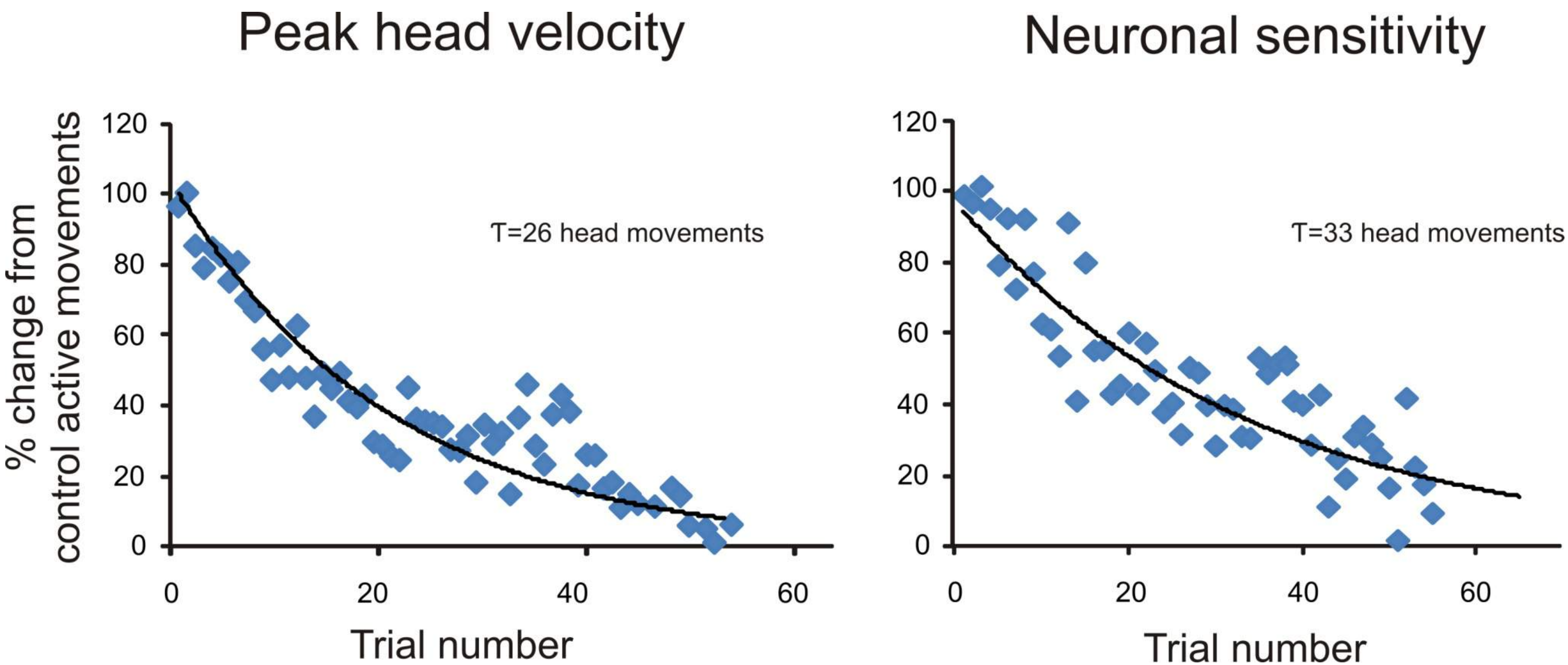


The time course:

of behavioural and neuronal adaptation are comparable



Brooks, Carriot, and Cullen, Nature neuroscience

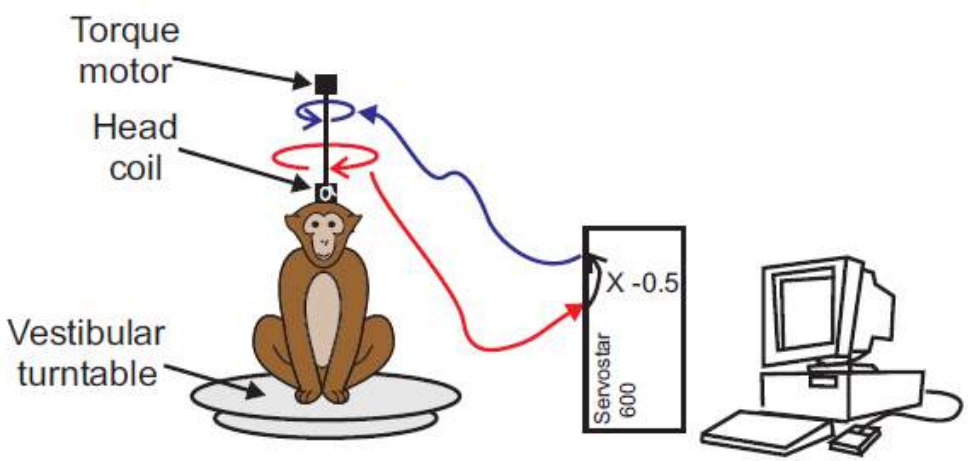
Our current hypothesis:

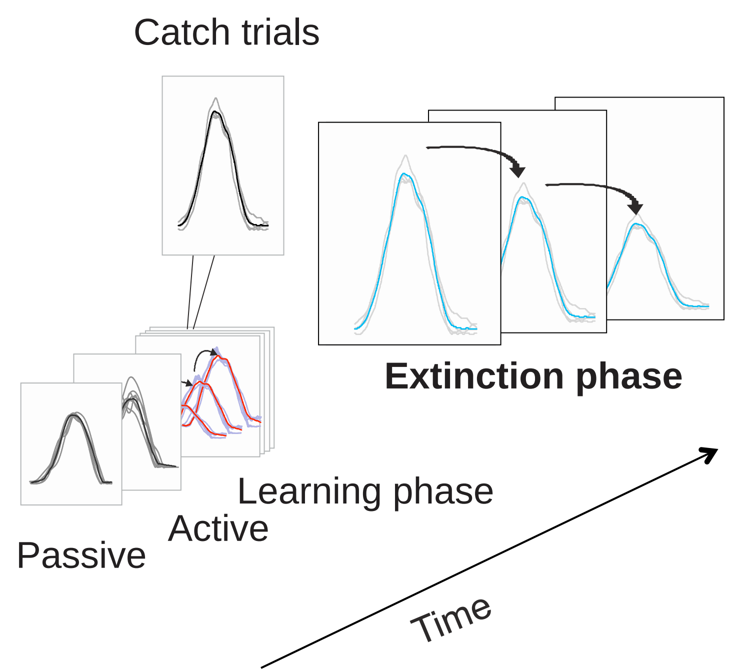
During active movement, suppression of sensory reafference occurs when sensory feedback matches that expected as a result of the motor command
(as during normal active movements)

Additionally, if this is true,

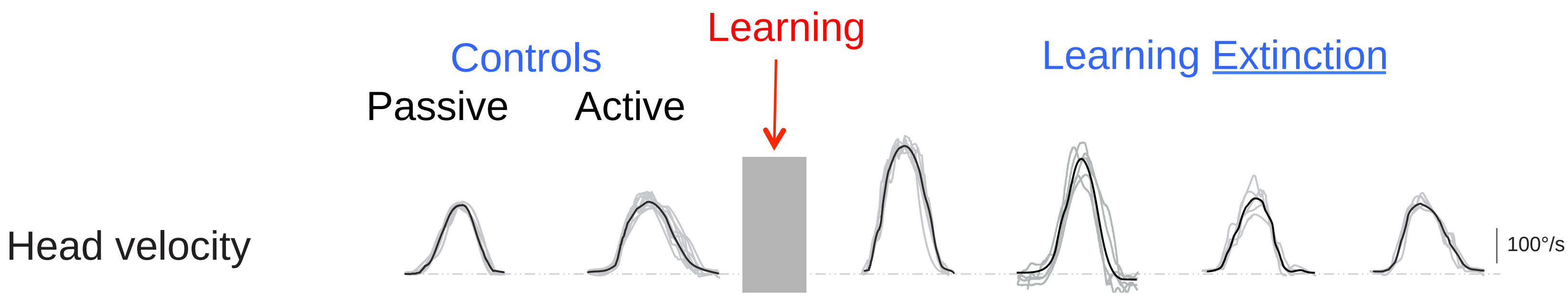
Then reafferent suppression should also not occur when the relationship between motor command and movement is altered after learning has occurred and the load is then permanently removed (i.e., during learning extinction).

Experiment: Change the relationship between motor command and sensory reafference via the removal of resistive torque





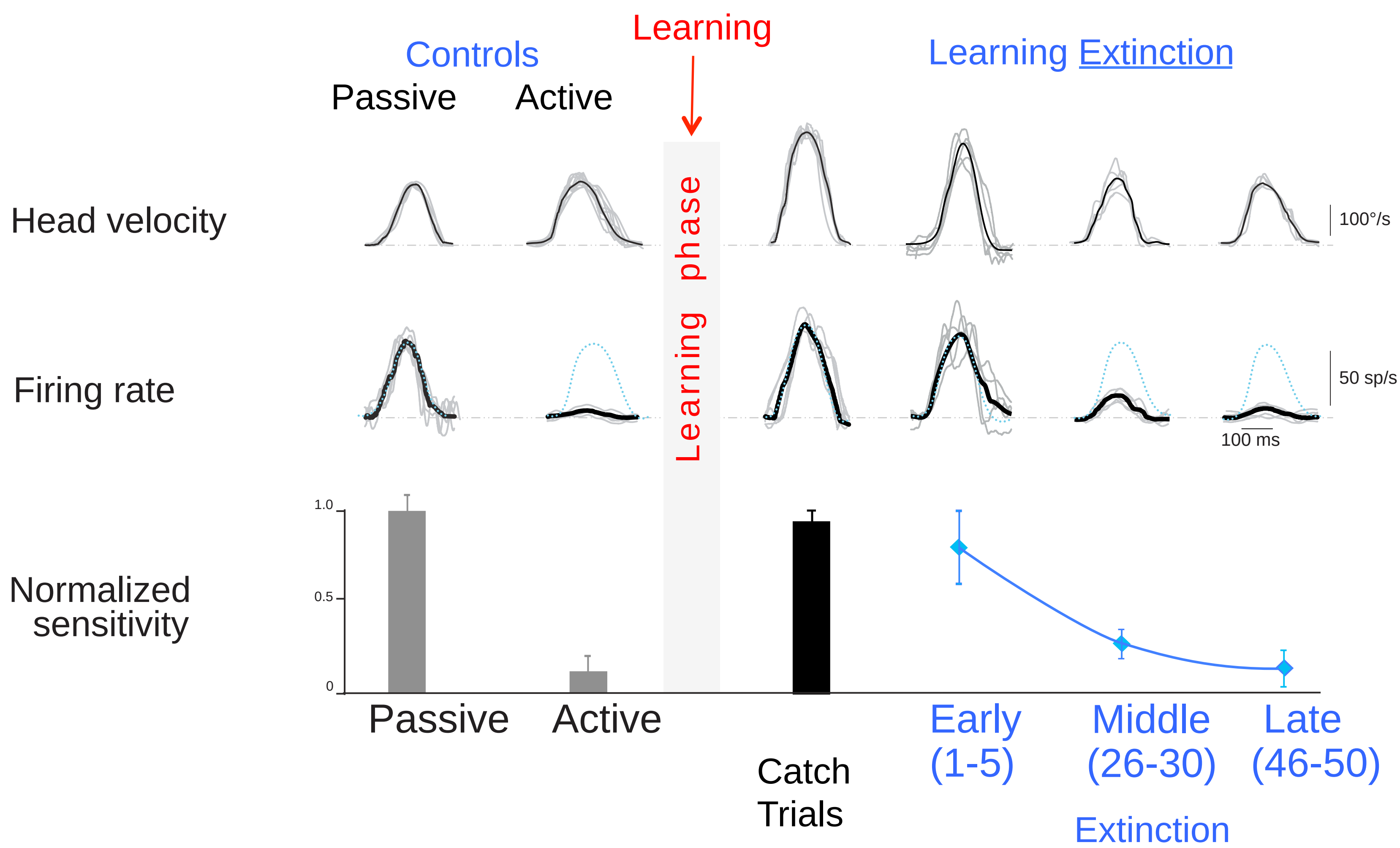
Experiment: Change the relationship between motor command and sensory reafference via the <u>removal</u> of resistive torque



The time course of Behavioural Adaptation

1) The animal learns to adapt after ~50 movements.
2) Head overshoots the initial trajectory once resistance is removed.
3) Then learning is quickly extinguished.

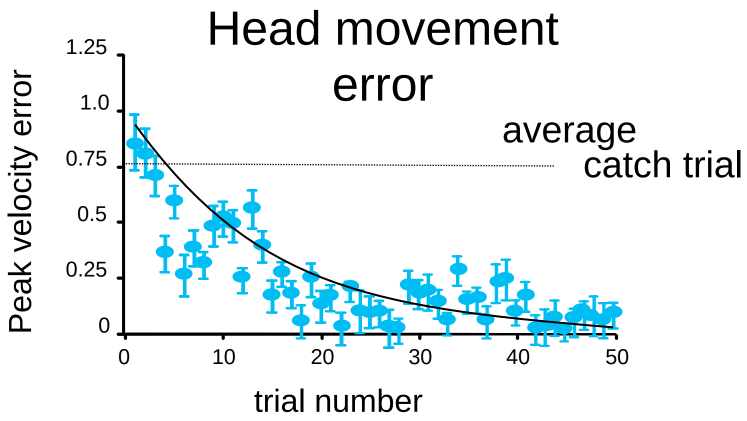
Experiment: Change the relationship between motor command and sensory reafference via the removal of resistive torque

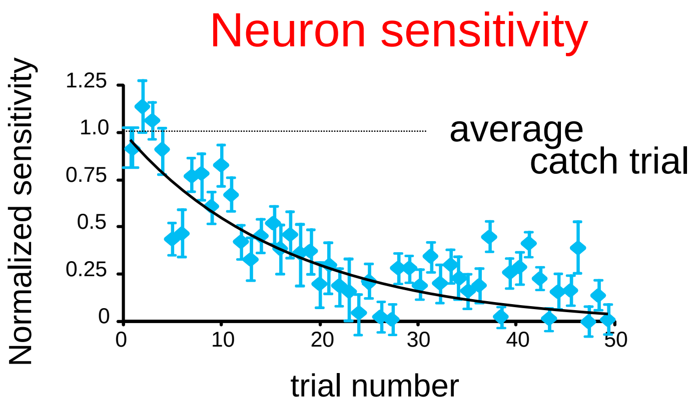


The time course:
of behavioural and neuronal extinction are also comparable

Consistent with previous studies, the extinction of learning occurs faster than the initial learning itself.

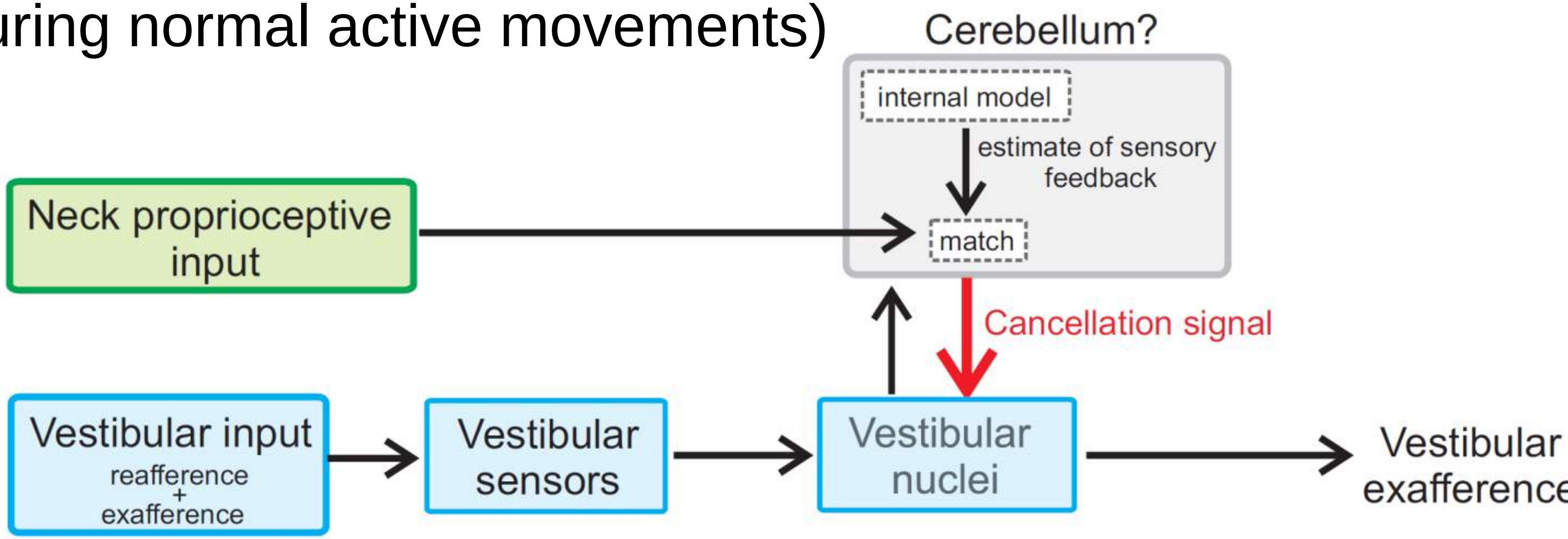
Likewise, the time course of the suppression of neuronal responses was faster (~30 %) for the extinction of learning compared to the initial learning.





Current hypothesis:

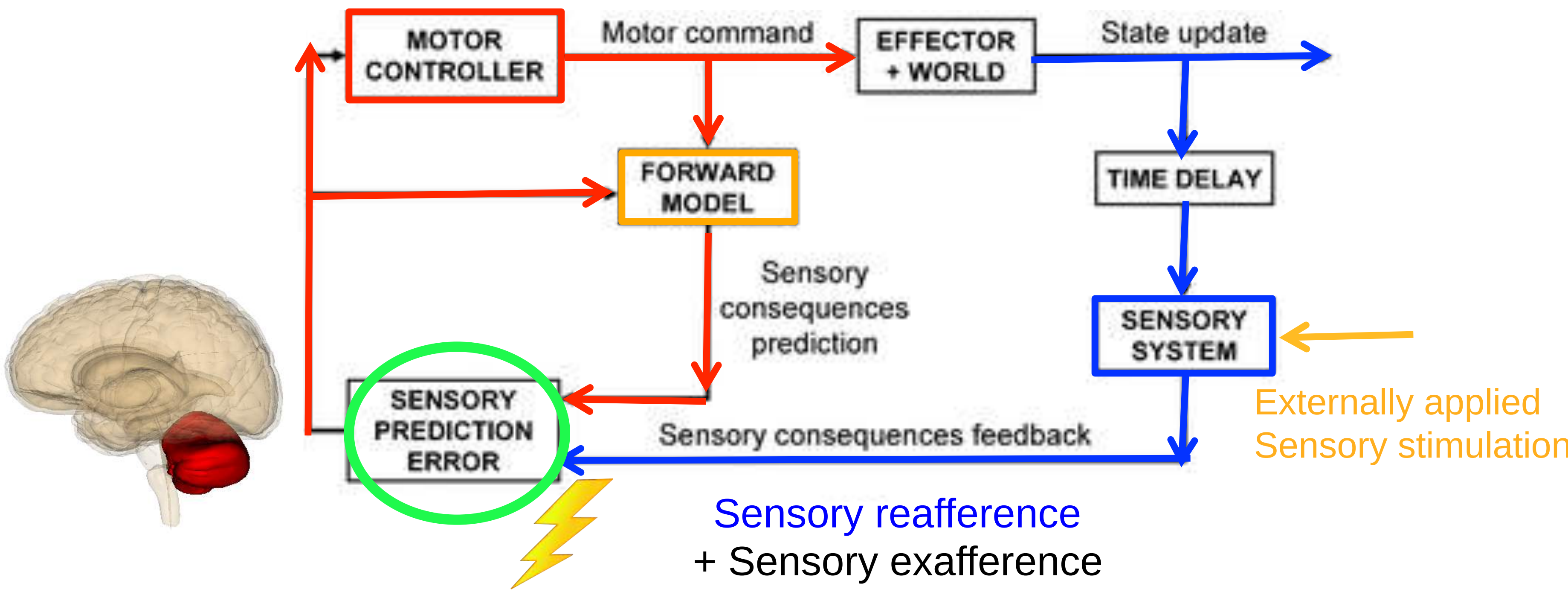
Suppression of vestibular reafference occurs when proprioceptive feedback <u>matches</u> that expected as a result of the motor command
(as during normal active movements)



Indeed, our data consistent with this proposal, reafferent suppression does not occur when the relationship between motor commands and sensory reafference is altered.

Sensory prediction errors occur as a result of both:

1) Changes in the effector /or world (muscle strength, load, etc)
   (e.g. motor learning is required to maintain accurate motor performance)
2) Sensory stimulation is externally generated rather than self-generated
   (e.g., sensory exafference versus reafference).



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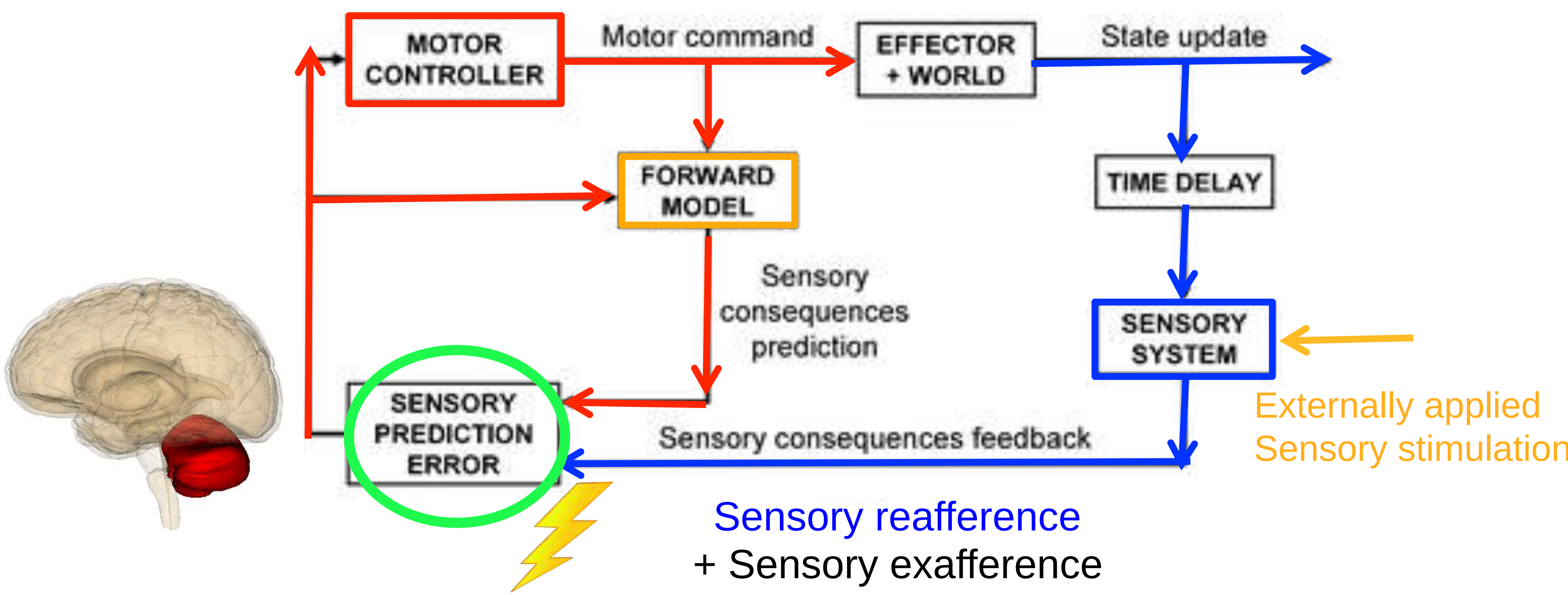

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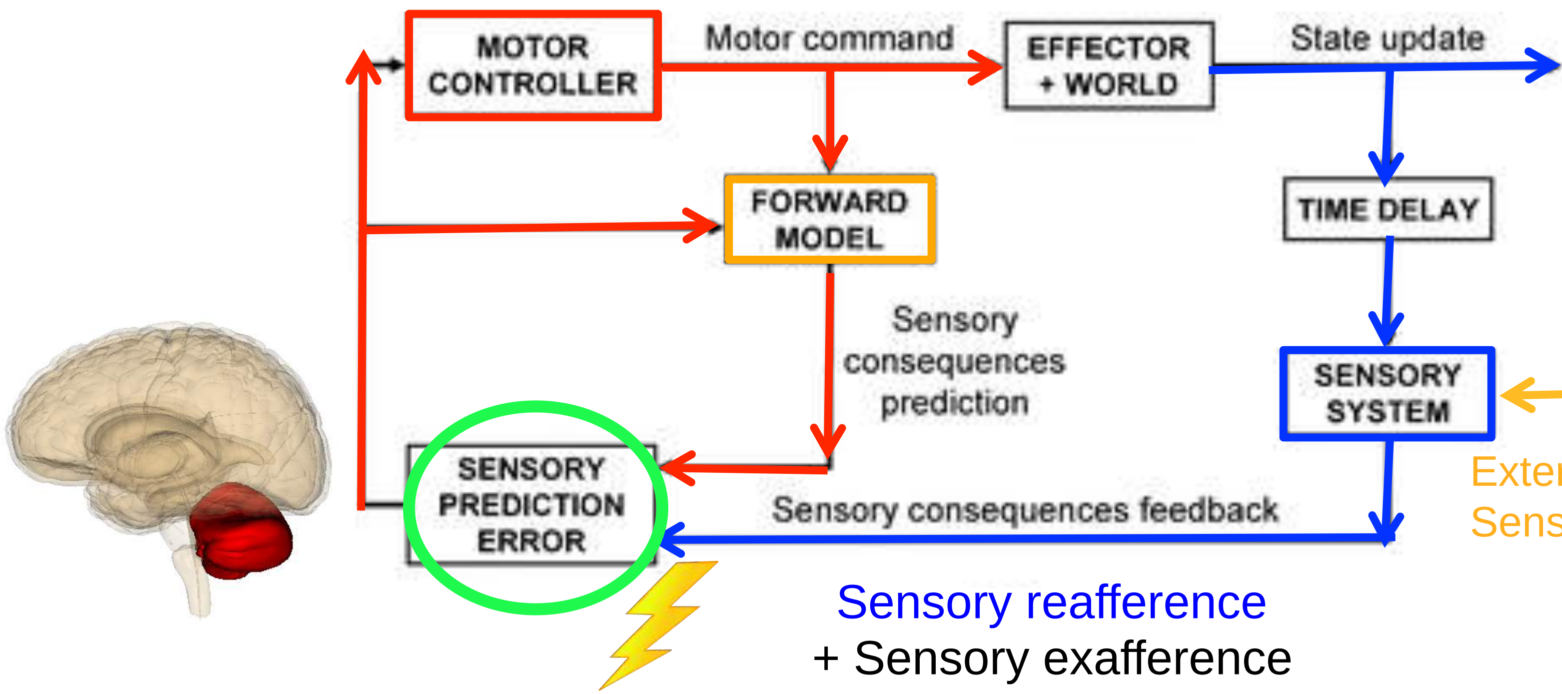
Rapid updating in the cerebellum allows that the motor system to learn to expect unexpected sensory input



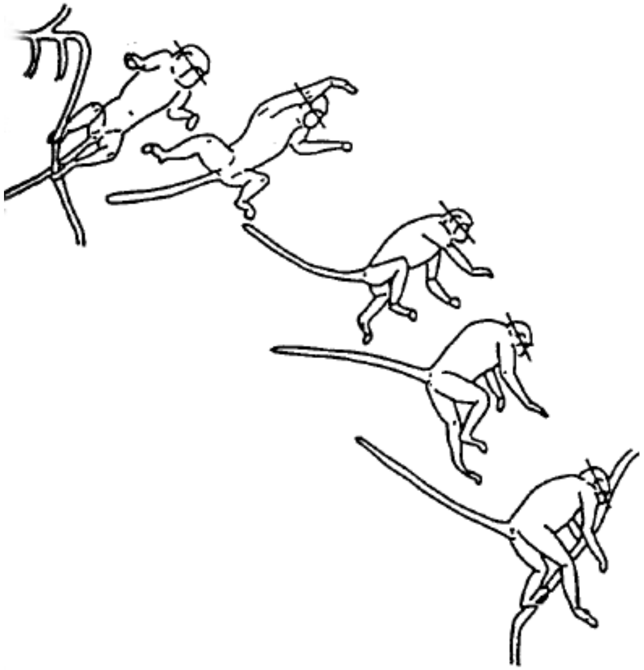
Externally applied Sensory stimulation

Sensory reafference
+ Sensory exafference

Functional Role of Central Vestibular Neurons

Neurons at the first central stage of vestibular processing:

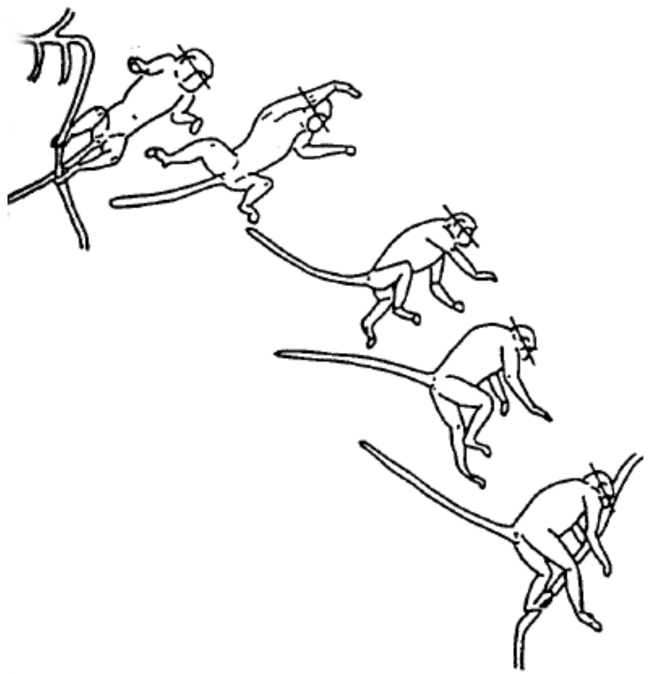
- Detect specific features via non-linear transformations of their afferent input



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

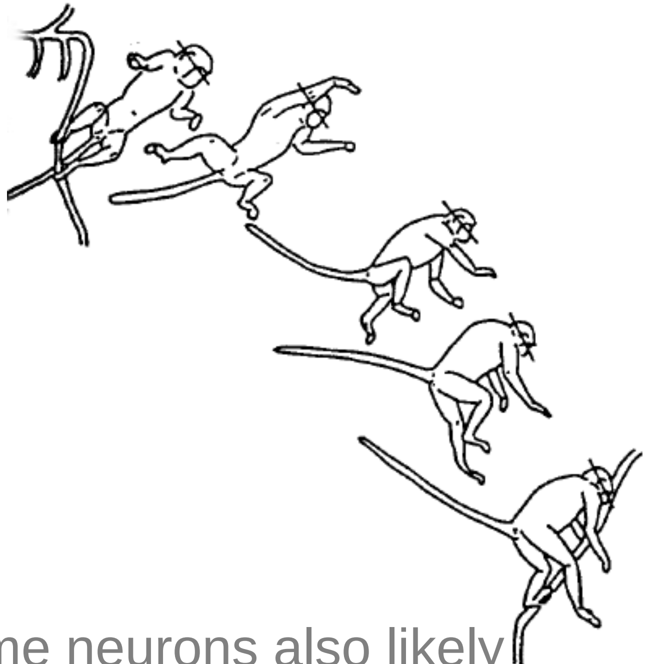


Functional Role of Central Vestibular Neurons

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.



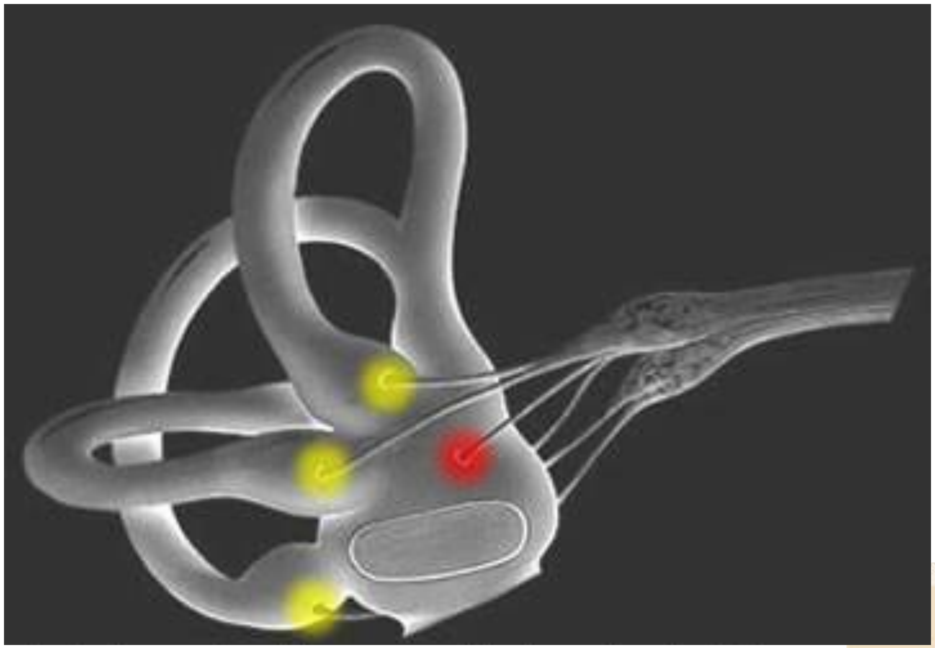
These same neurons also likely transmit self-motion information to higher level areas that contributes to perception during everyday activities

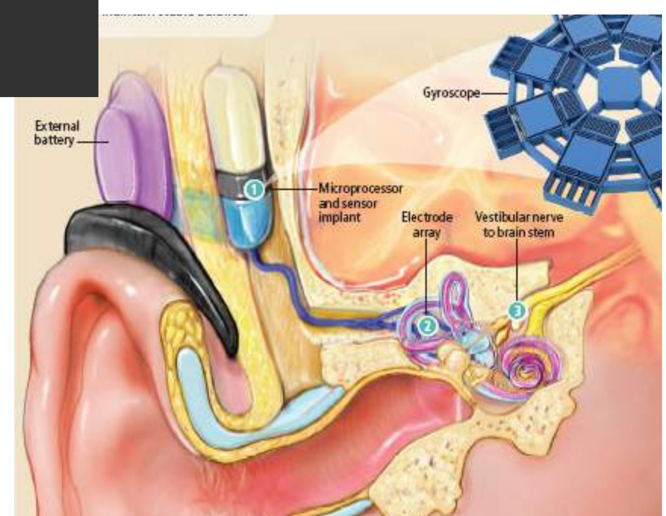
Non-linear sensory-motor transformations
Vestibulo-spinal pathways

Vestibular compensation:

Neurophysiology of Vestibular Compensation

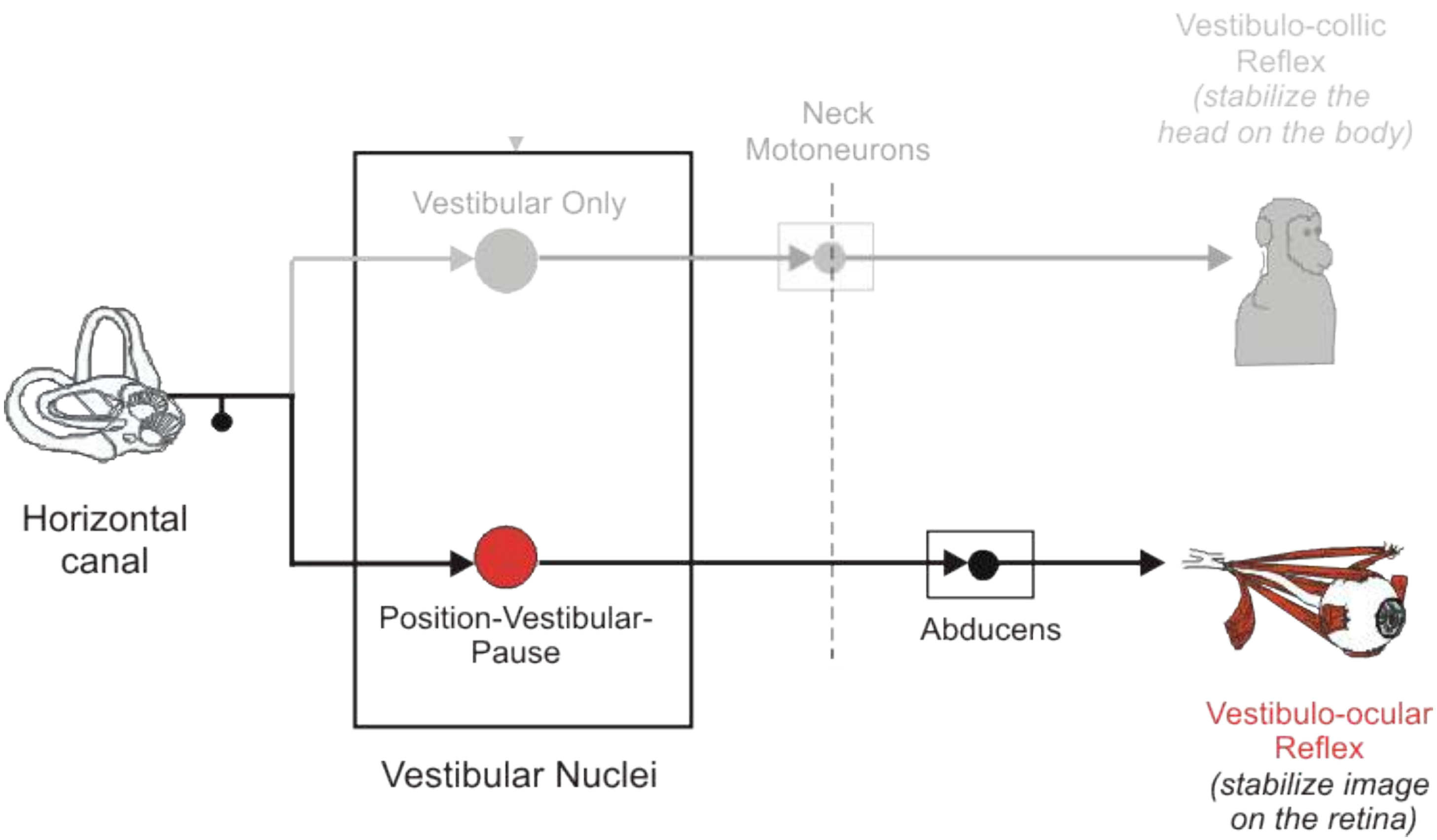
Neural Correlates of Prosthetic Stimulation





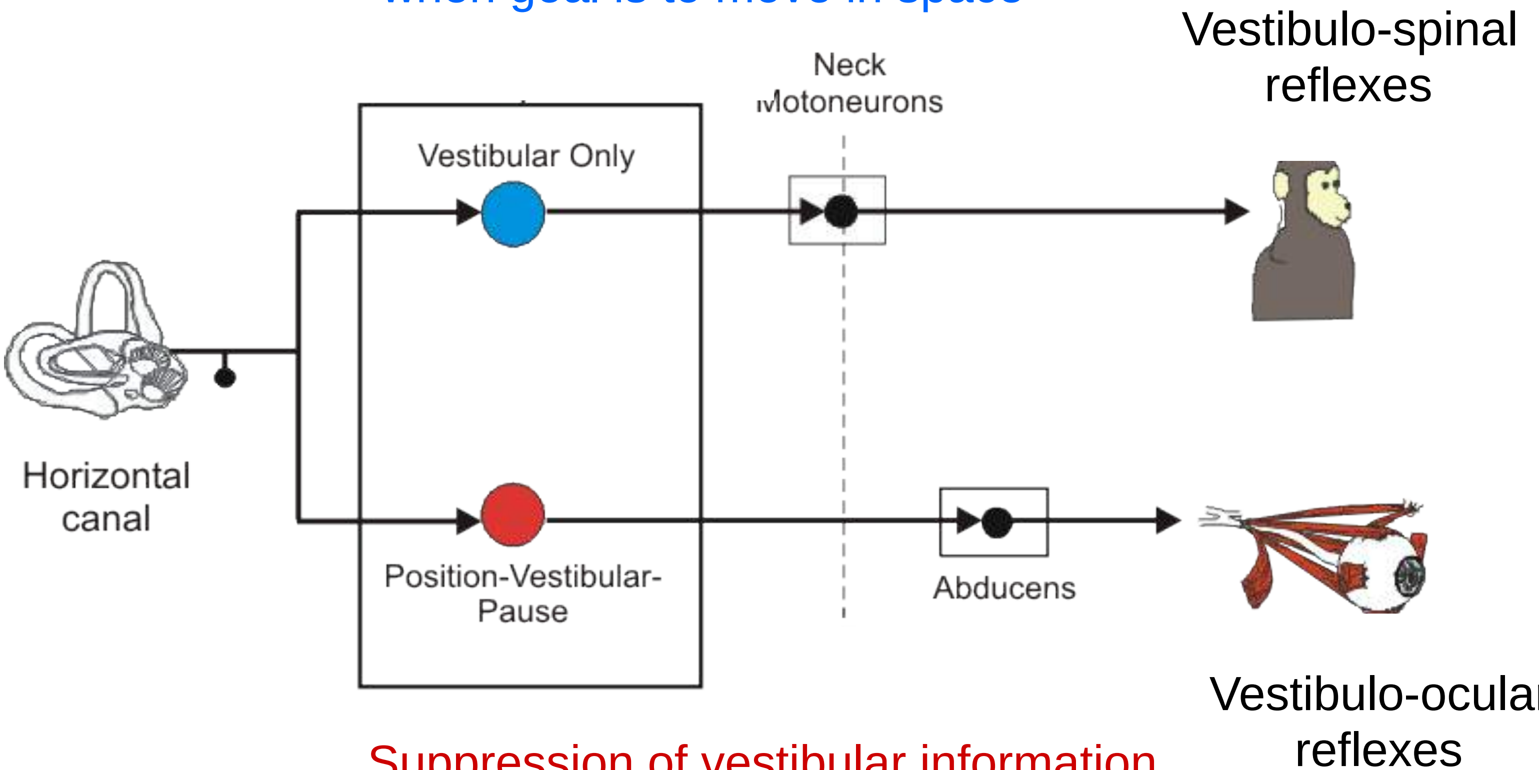
Is the differential processing of active and passively generated vestibular stimulation a general feature of all early vestibular pathways processing?

No, Consider the neurons that produce the VOR

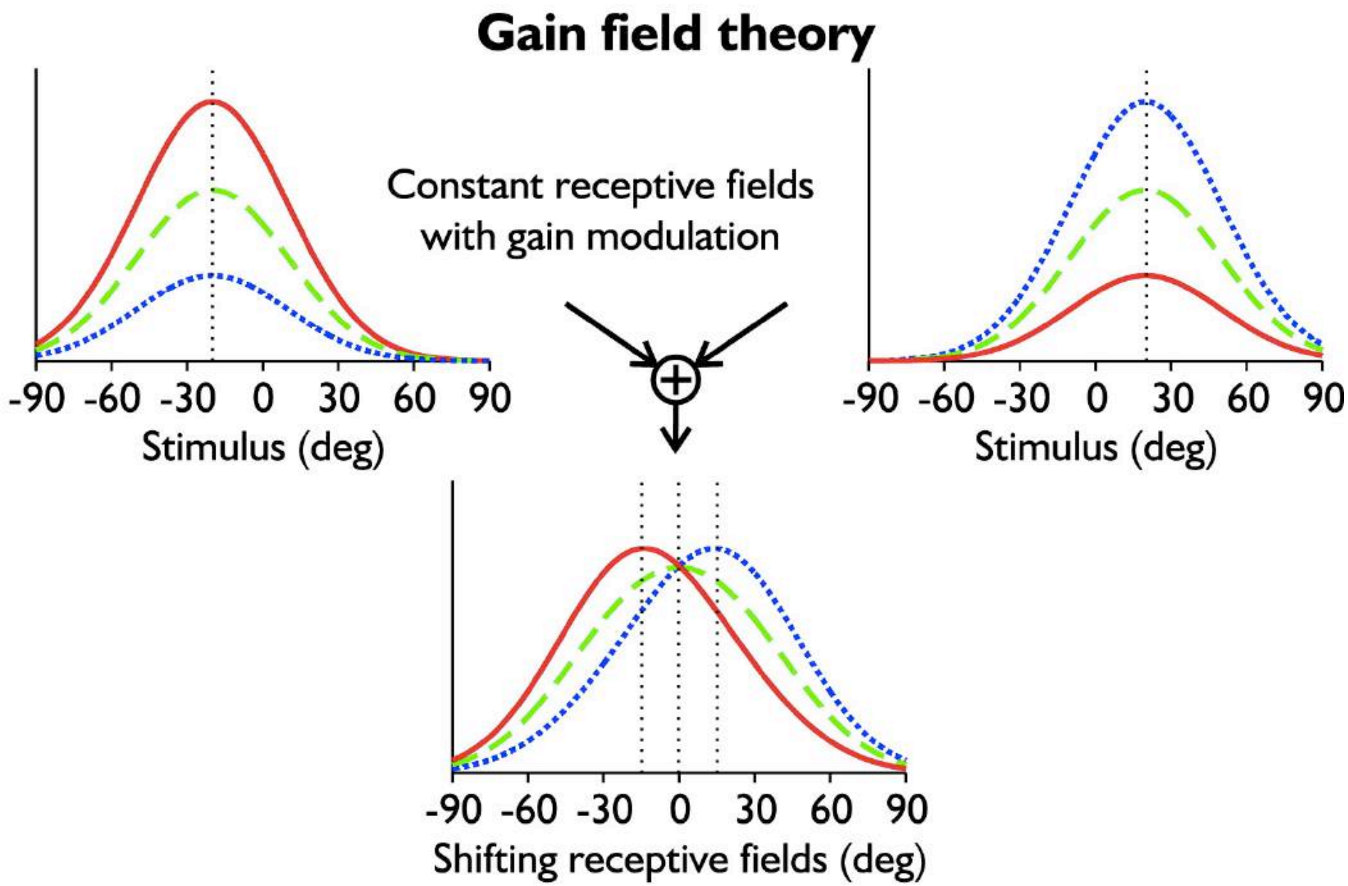


This differential processing by different cell classes in the vestibular nuclei is consistent their functional roles:

Suppression of vestibular information
- when goal is to move in space



Suppression of vestibular information
-when goal is to redirect gaze (gaze shifts)


Gain field theory
Constant receptive fields
with gain modulation
-90 -60 -30 0 30 60 90
Stimulus (deg)
-90 -60 -30 0 30 60 90
Stimulus (deg)
-90 -60 -30 0 30 60 90
Shifting receptive fields (deg)