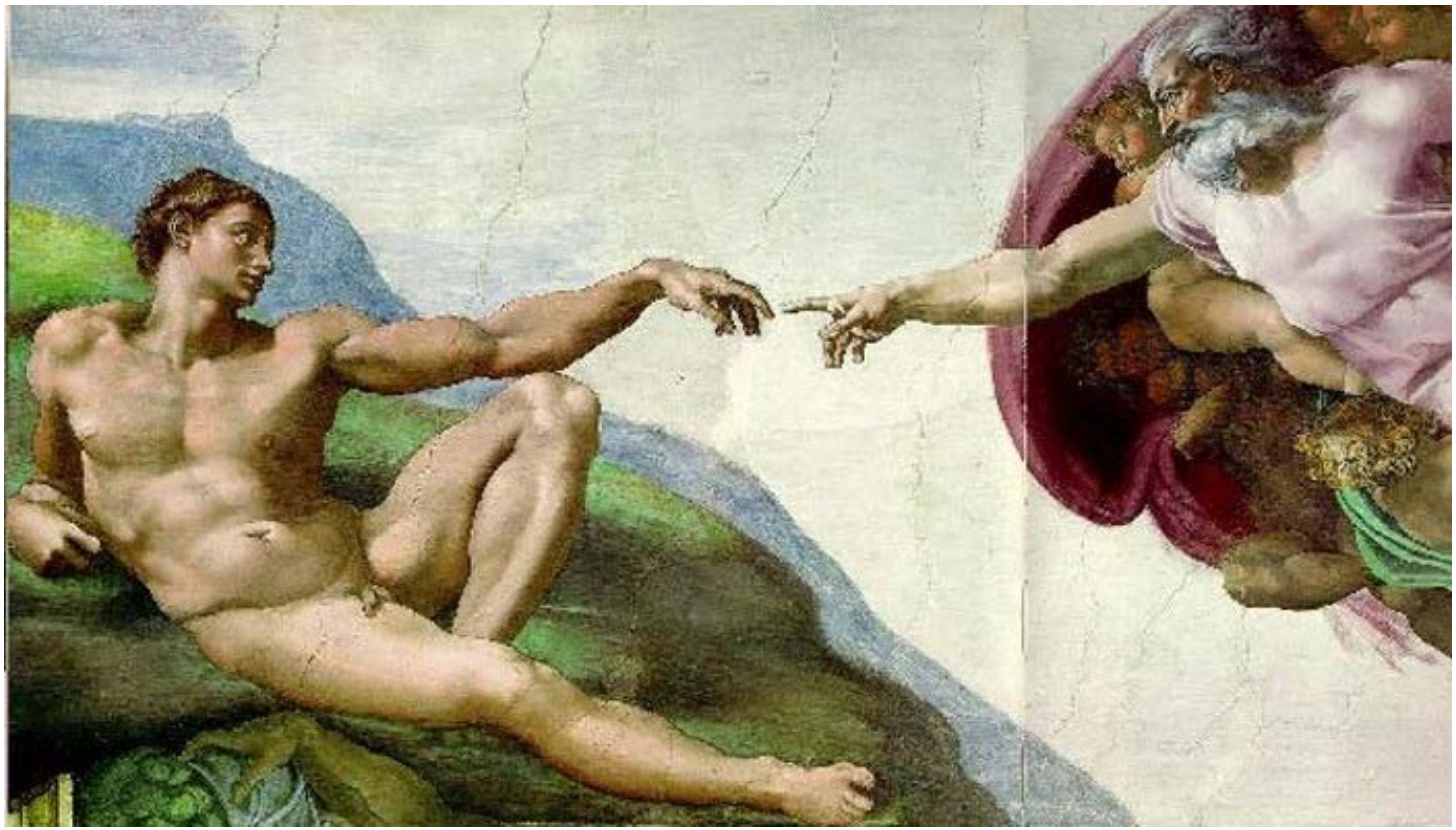
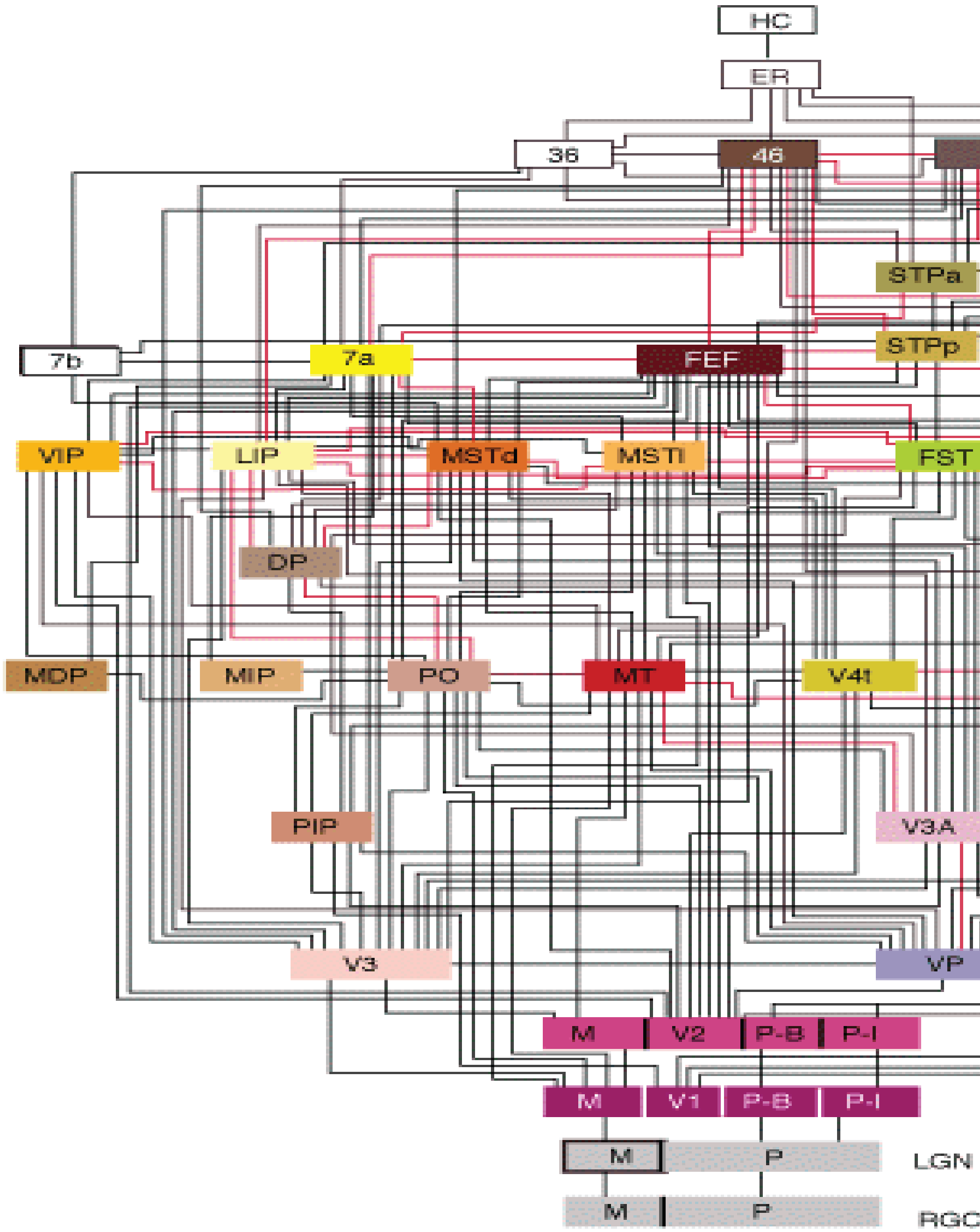
Two idiosyncratic primers on the CNS:
(1) Feedforward versus cyclic connectivity
(2) The confluence of reafference and exafference in sensation

David Kleinfeld, UCSD
21 September 2010 at the KITP
Emerging techniques in neuroscience

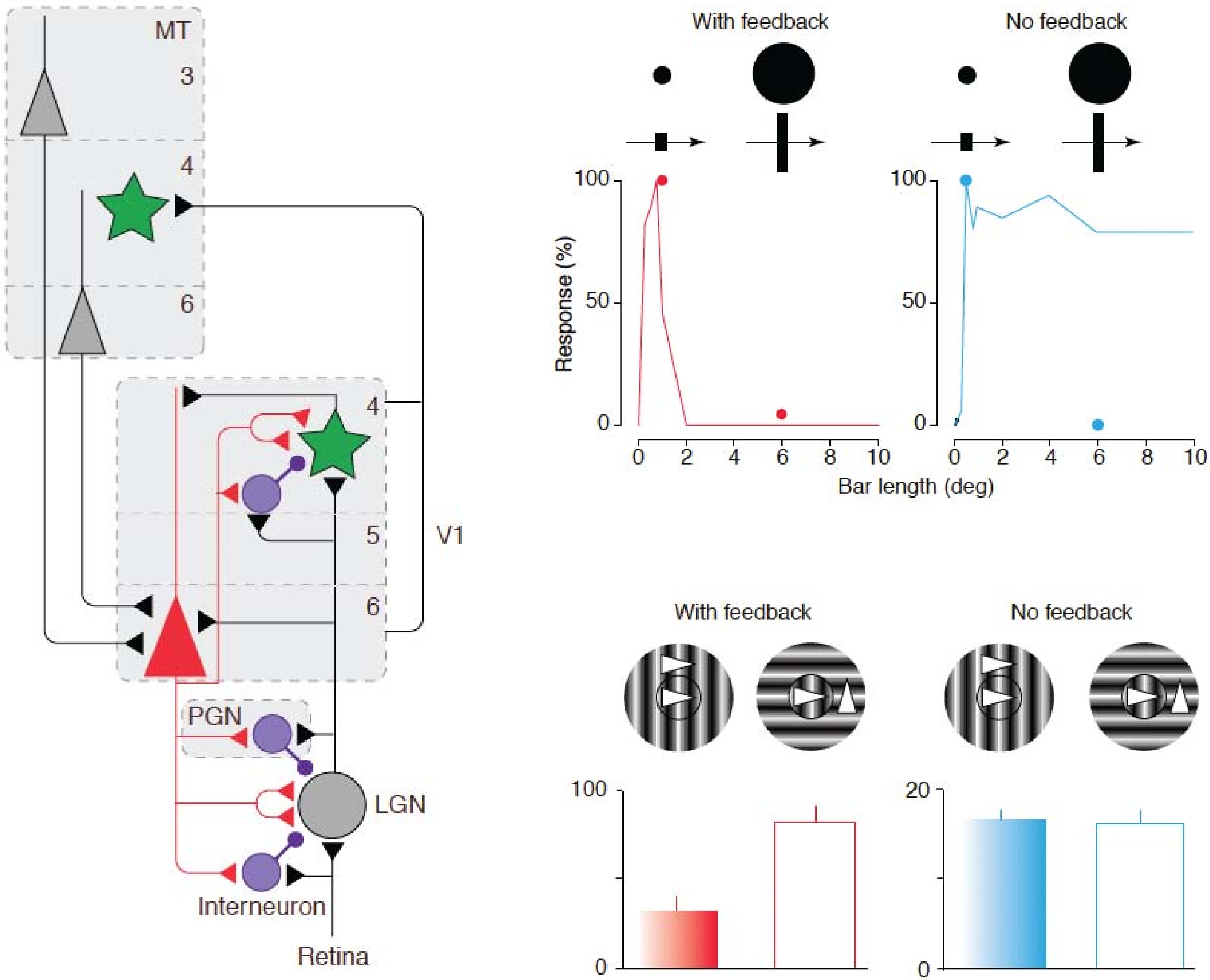


Signal flow in the classic feedforward view of visual processing

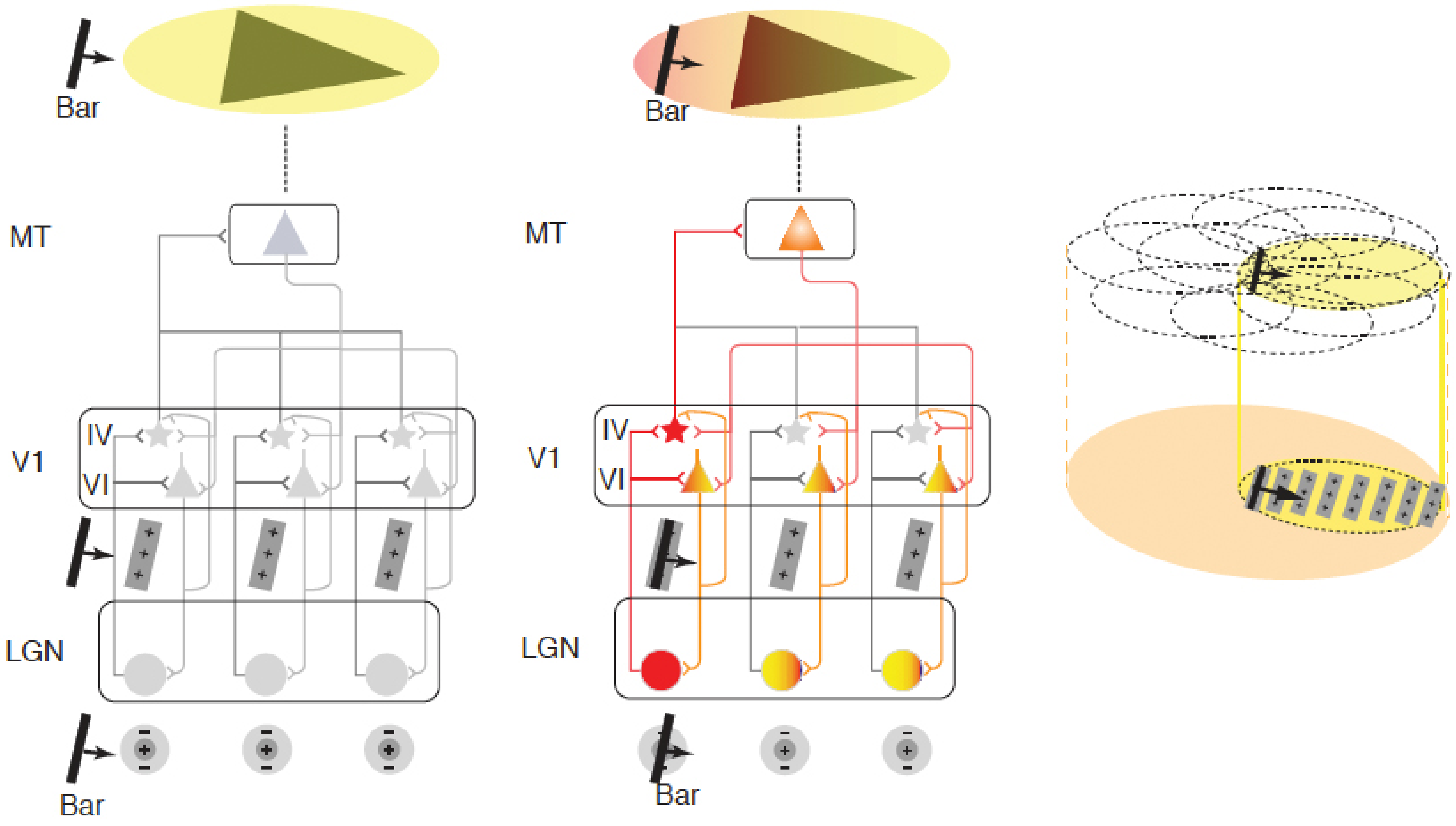


... but - all areas interact to “see” the same scene (Douglas & Martin 1991)

Feedback from V1 to the LGN

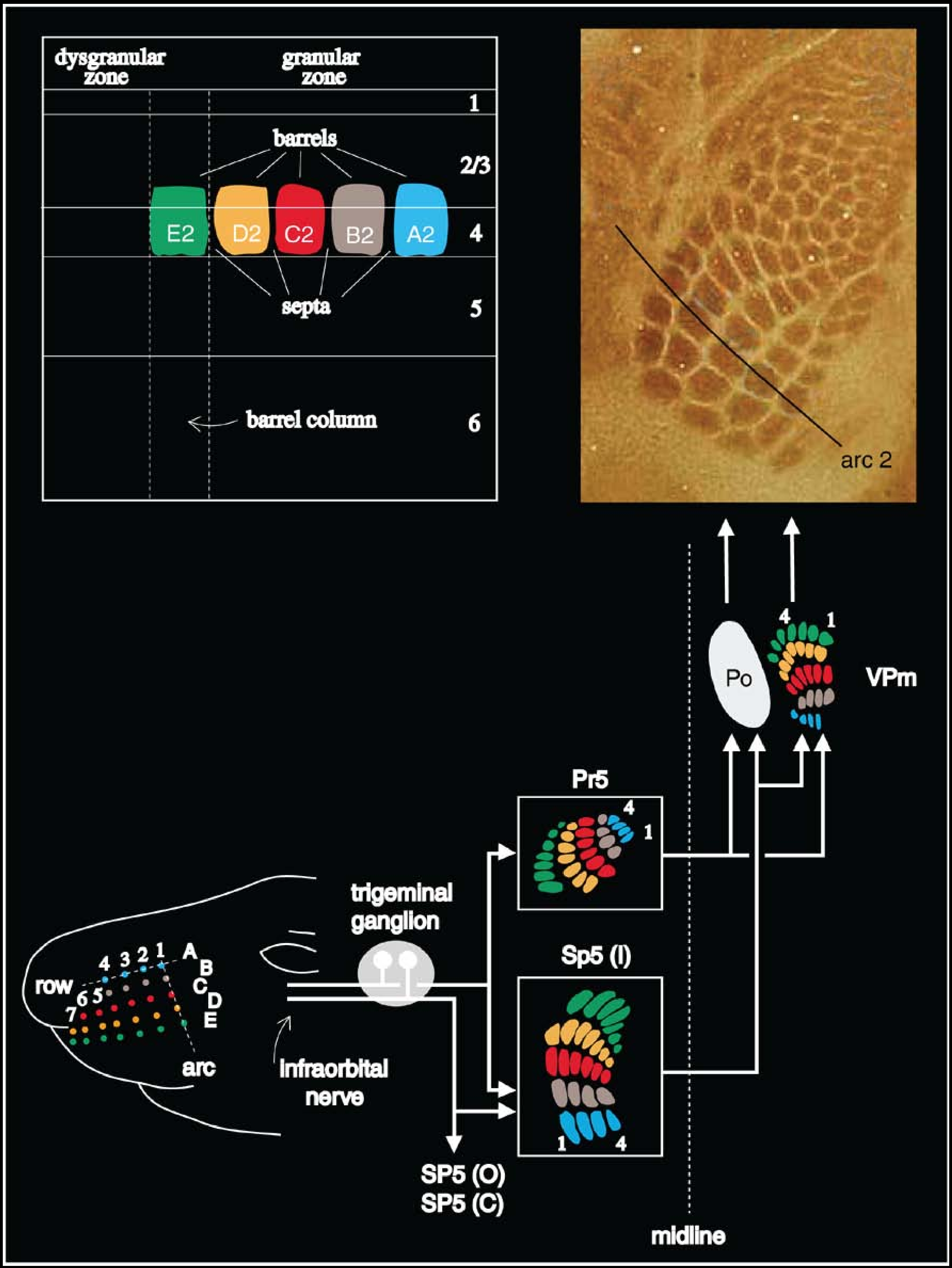


Sillito and colleagues



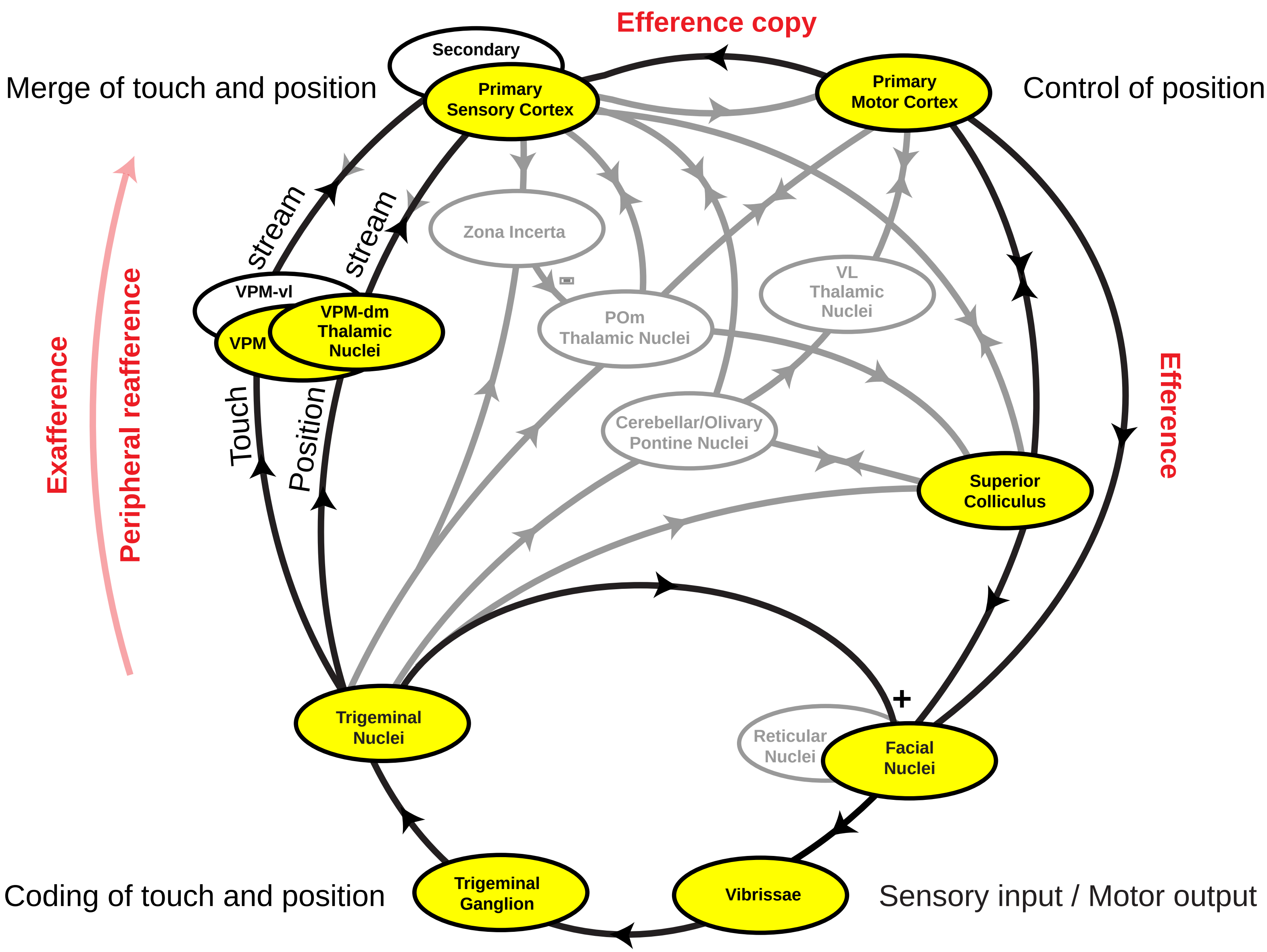
Bar
MT
IV
V1
VI
LGN
Bar
Bar
MT
IV
V1
VI
LGN
Bar

Classic exafferent sensory maps and pathway



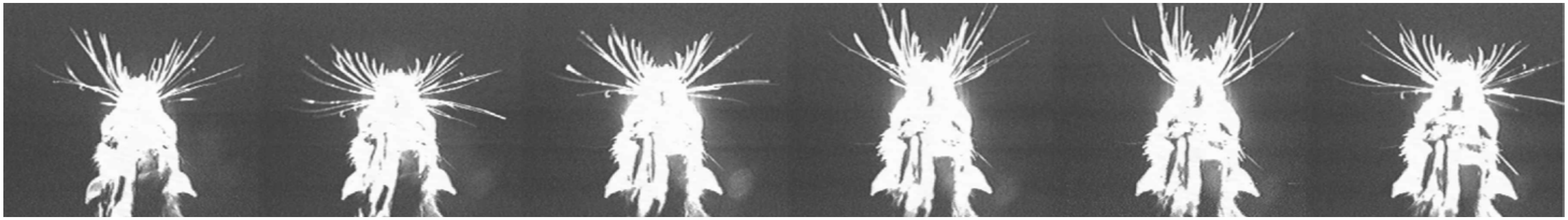
Courtesy of Martin Deschenes

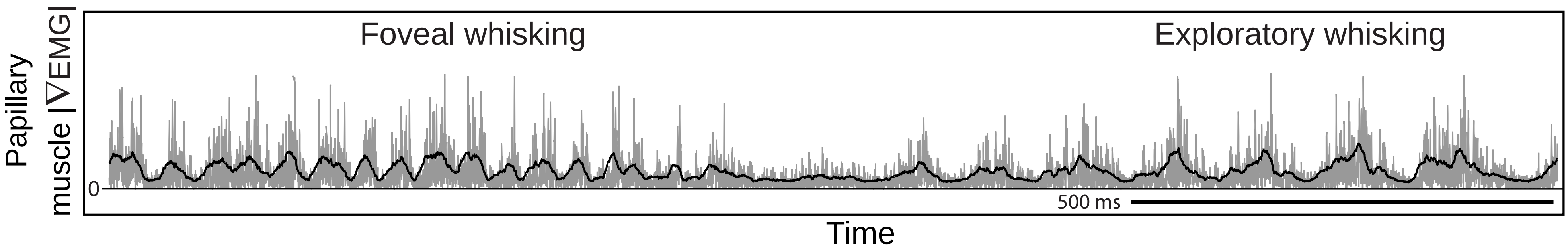
Exafference, reafference, efference, and efference copy as signals in vibrissa system loops



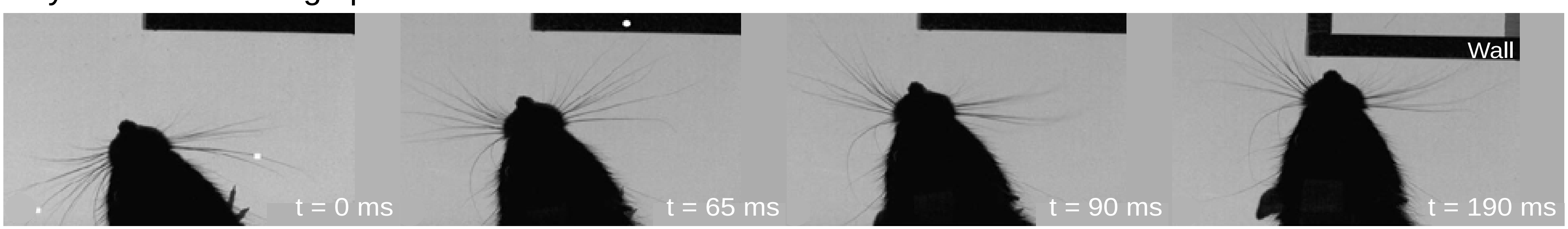
Whisking by rat: Self generated rhythmic motion and touch

Symmetric, exploratory whisking



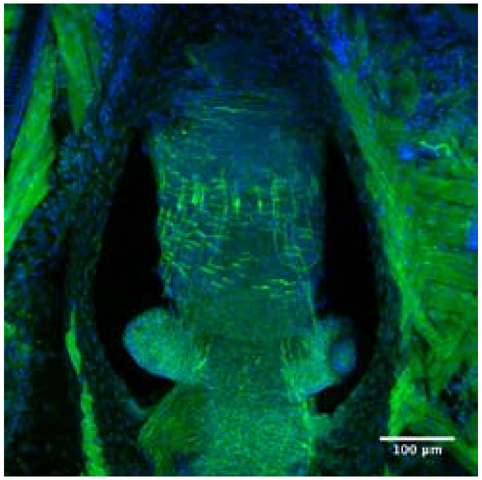


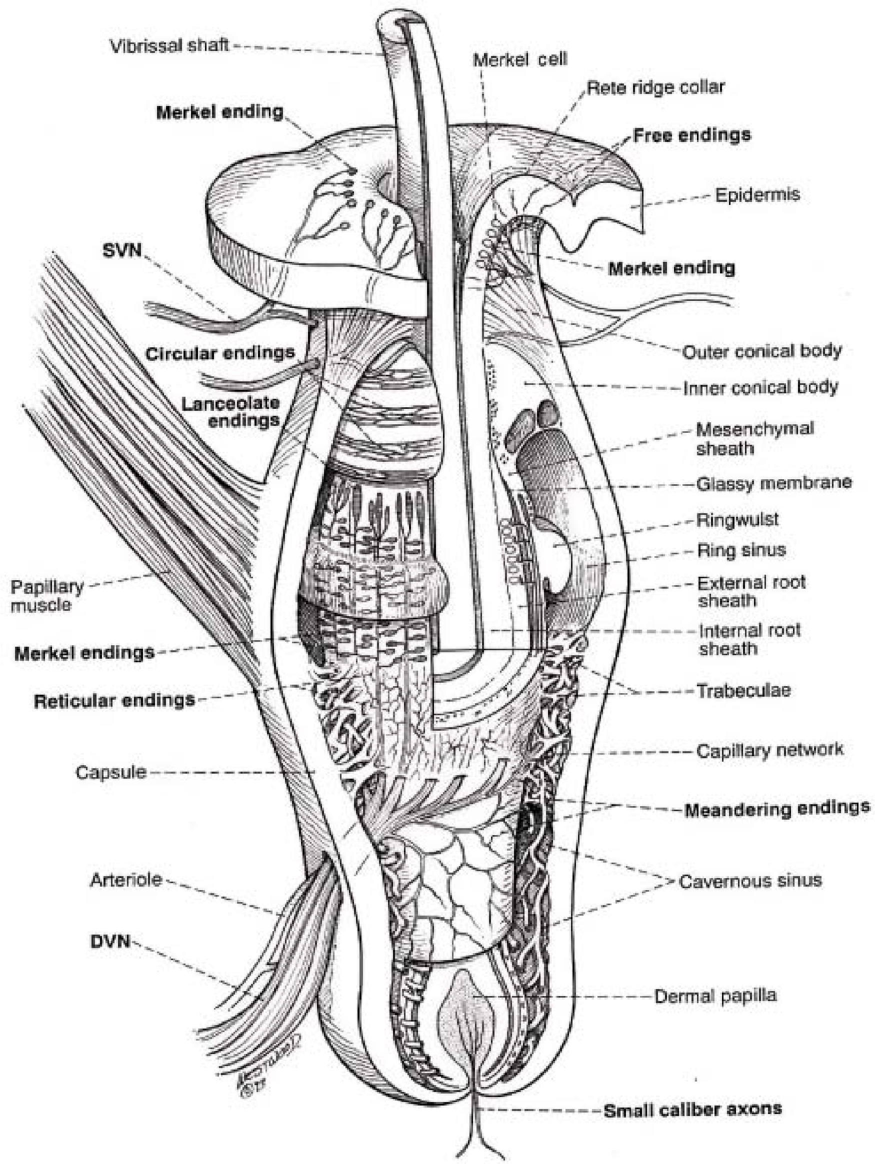
Asymmetric whisking upon contact



Berg and Kleinfeld (2003)
Towal and Hartmann (2006)
Mitchinson, Martin, Grant and Prescott (2007)

Rice's conjecture*: Mechanics and innervation of the vibrissa follicle leads to separate touch (exafferent) versus position (reafferent) signals

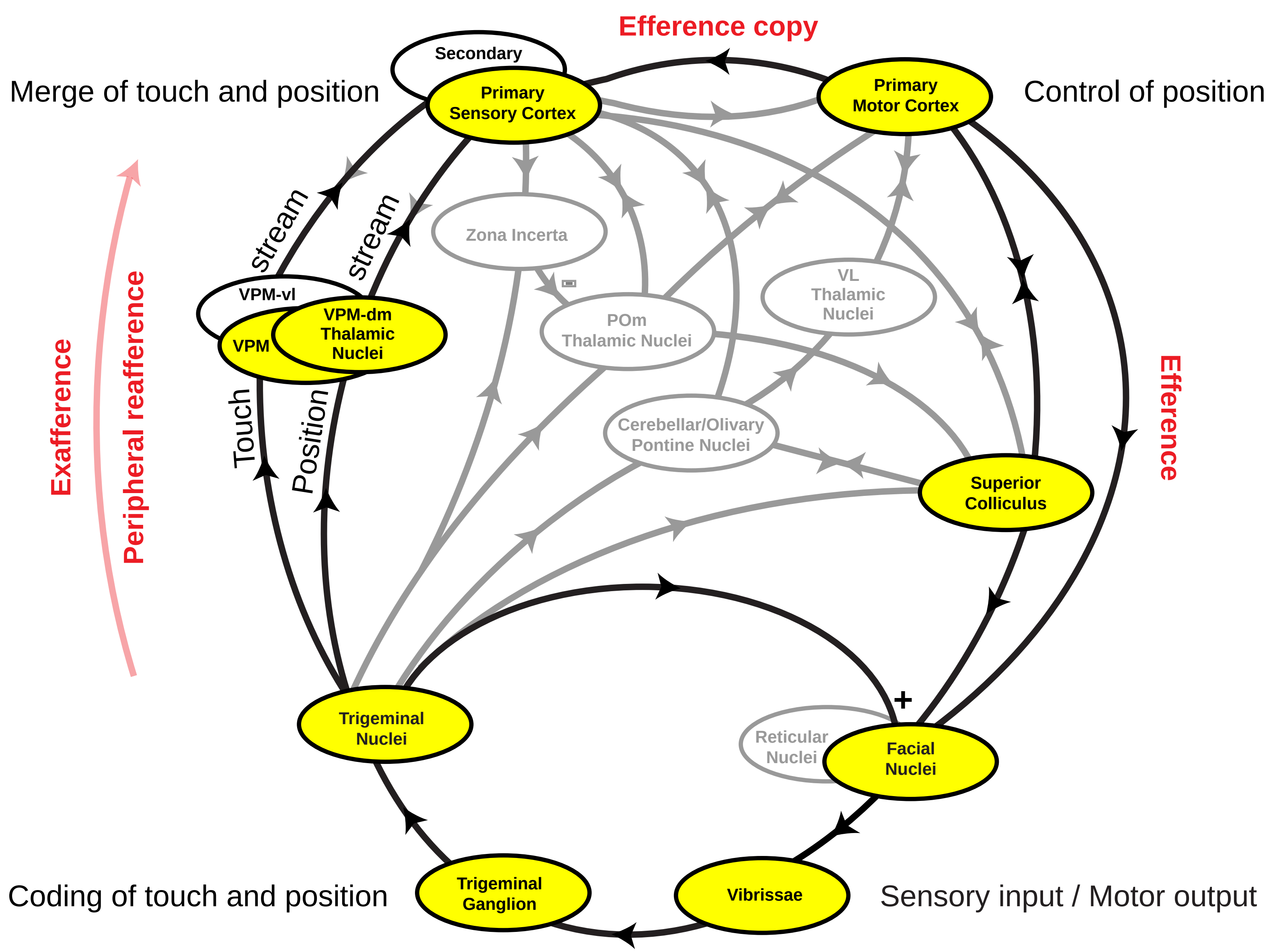




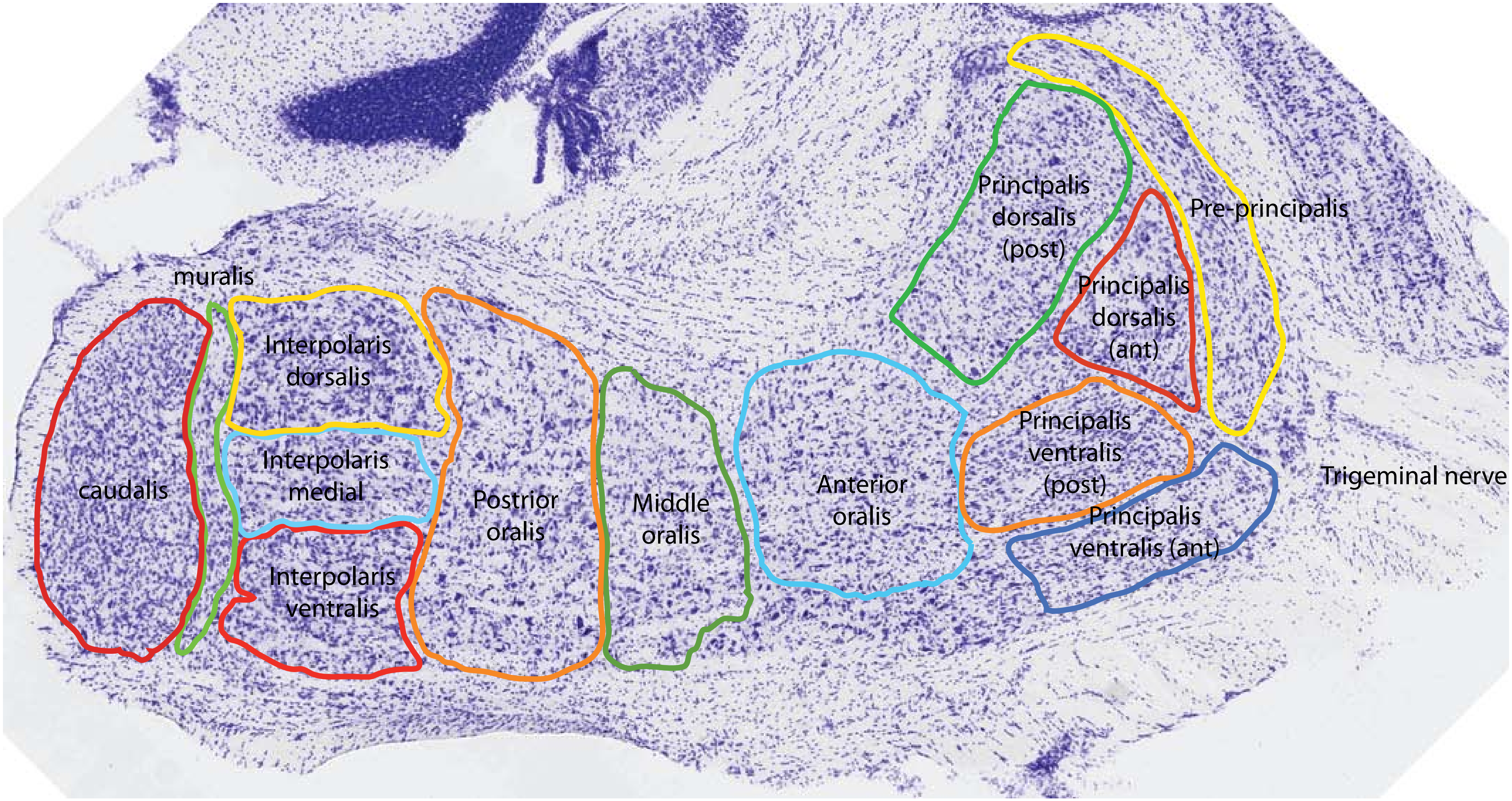
Matthews, Karten, Griesbeck & Kleinfeld - unpublished

*Rice, Kinnman, Aldskogius & Arvidsson (J Comp Neurol 1993)

Exafference, reafference, efference, and efference copy as signals in vibrissa system loops

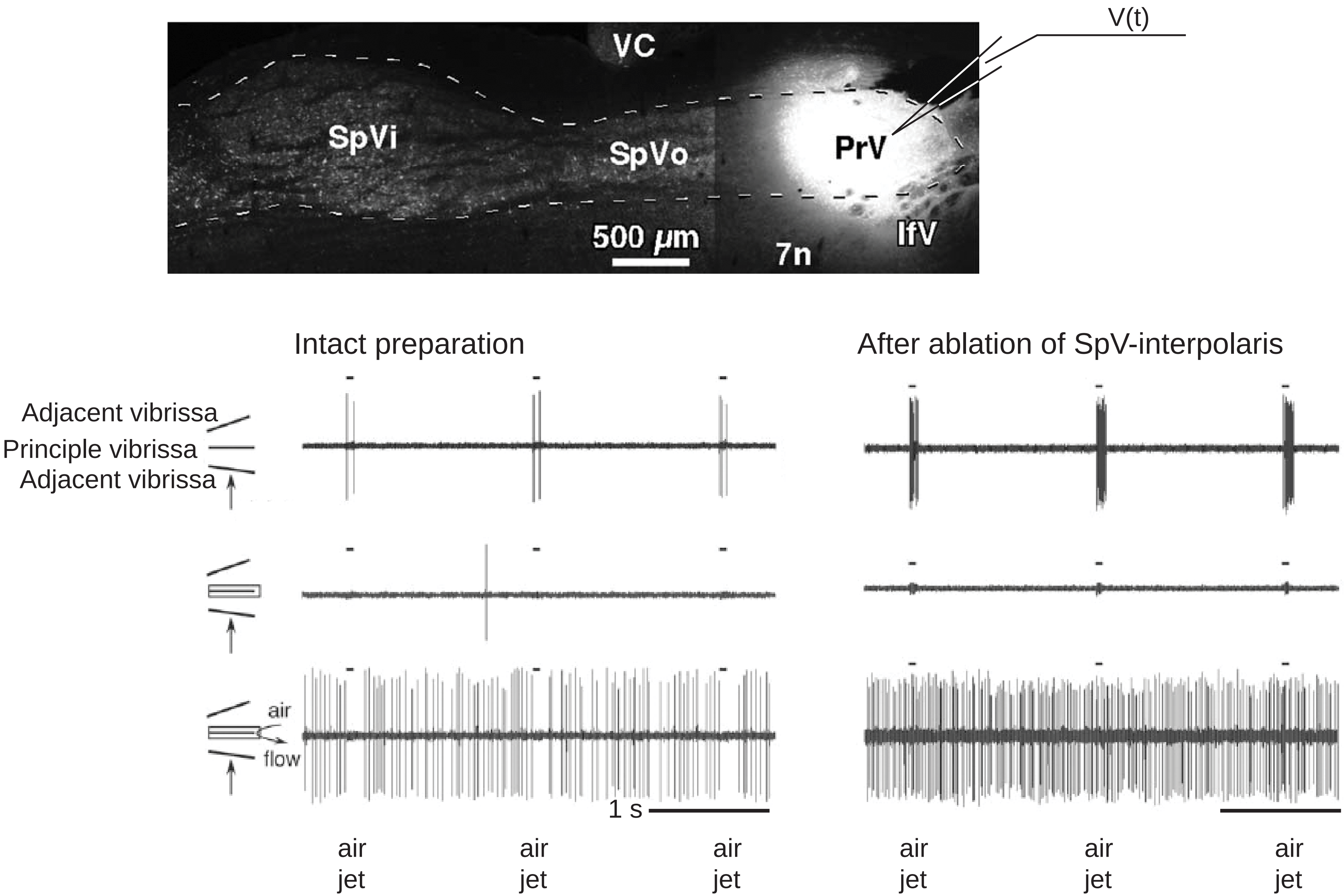


Multiple maps across the trigeminus: Interactions from SpVi to PrV



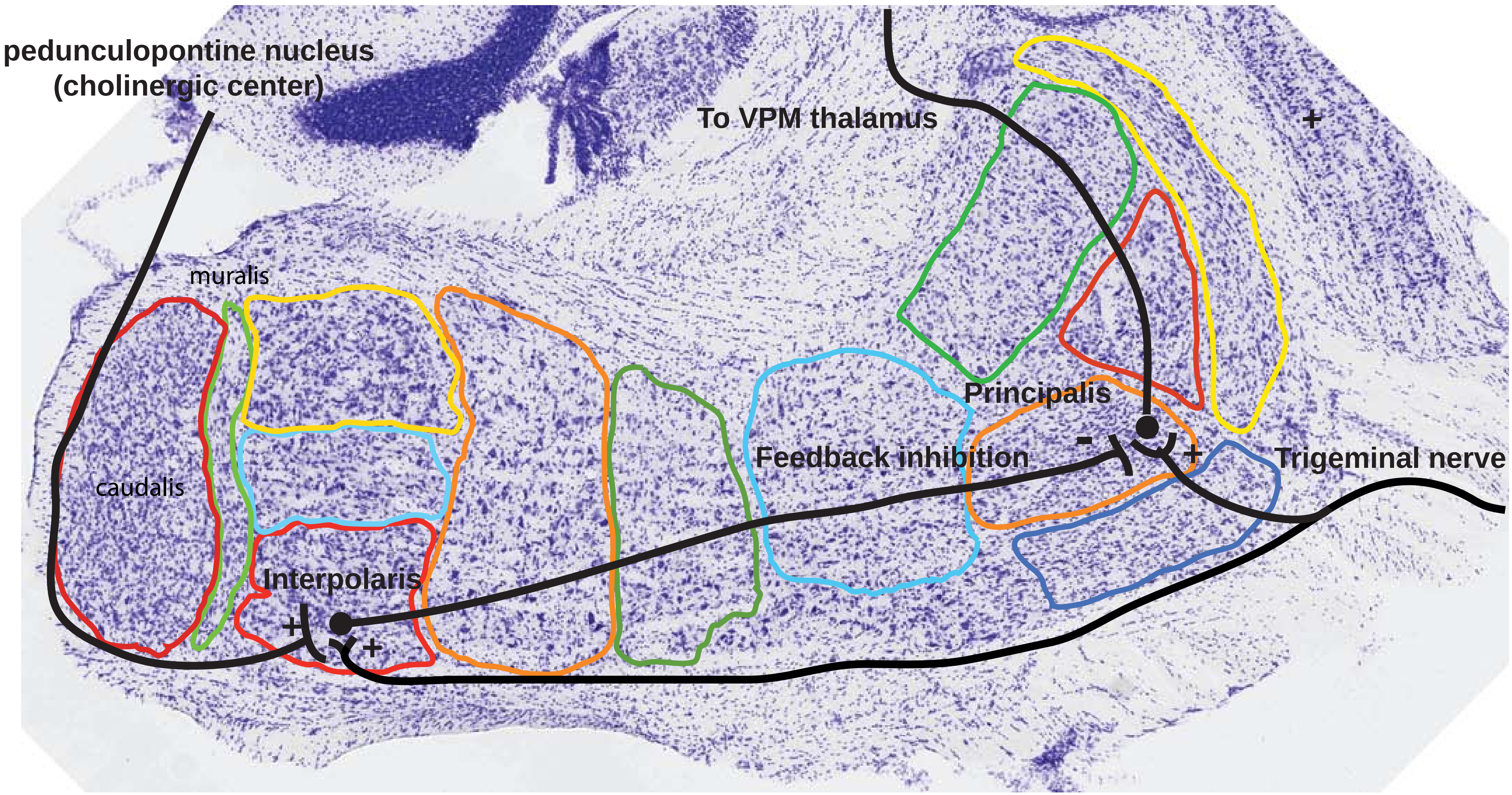
Matthews, Karten & DK (unpublished) following Deschenes, Jacquin and others

Spatial sharpening of vibrissal sensory input at the level of the brainstem



Furuta, Timofeeva, Nakamura, Okamoto-Furuta, Togo, Kaneko & Deschenes (2008)

Multiple maps across the trigeminus: Interactions from SpVi to PrV



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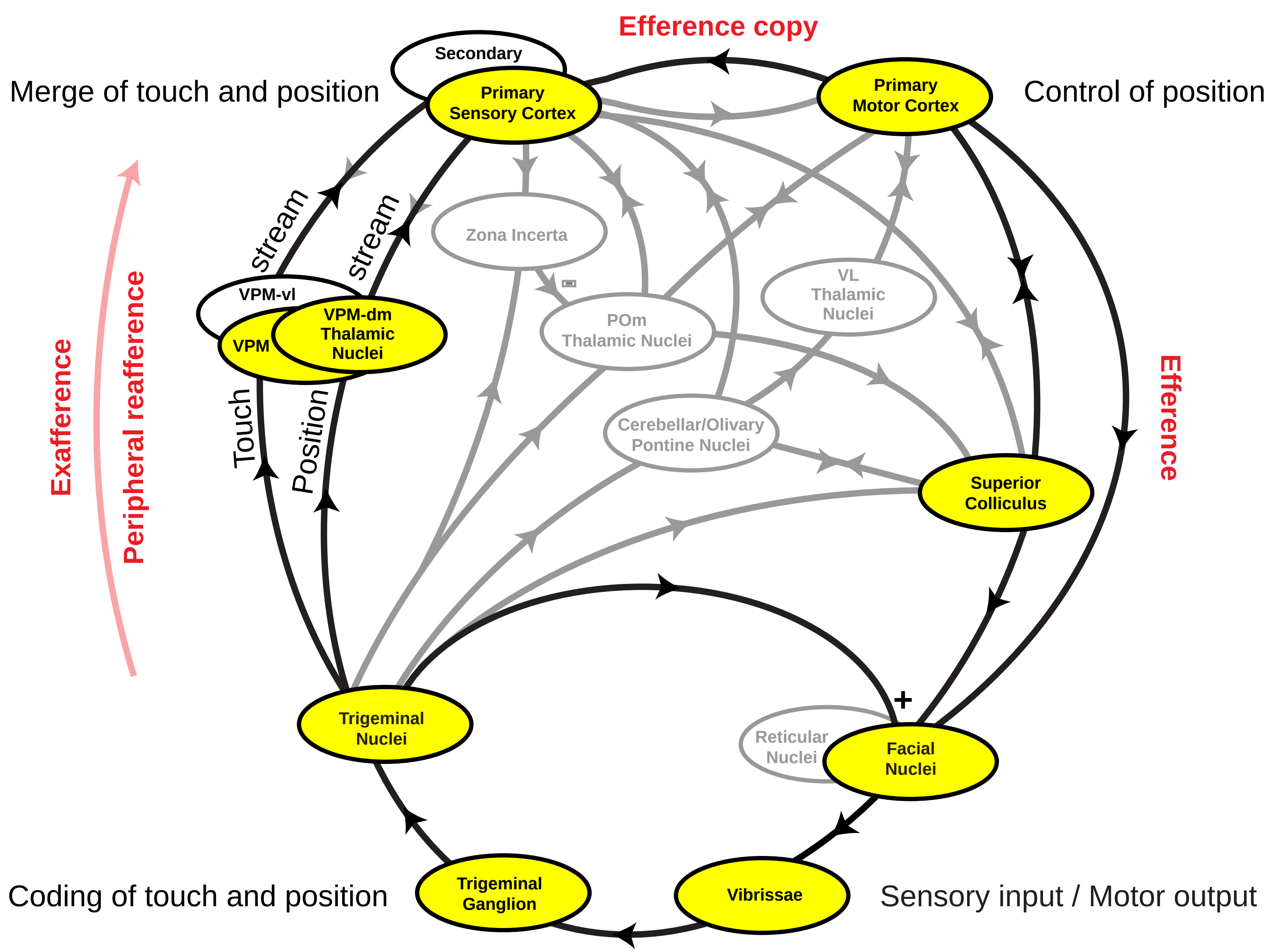
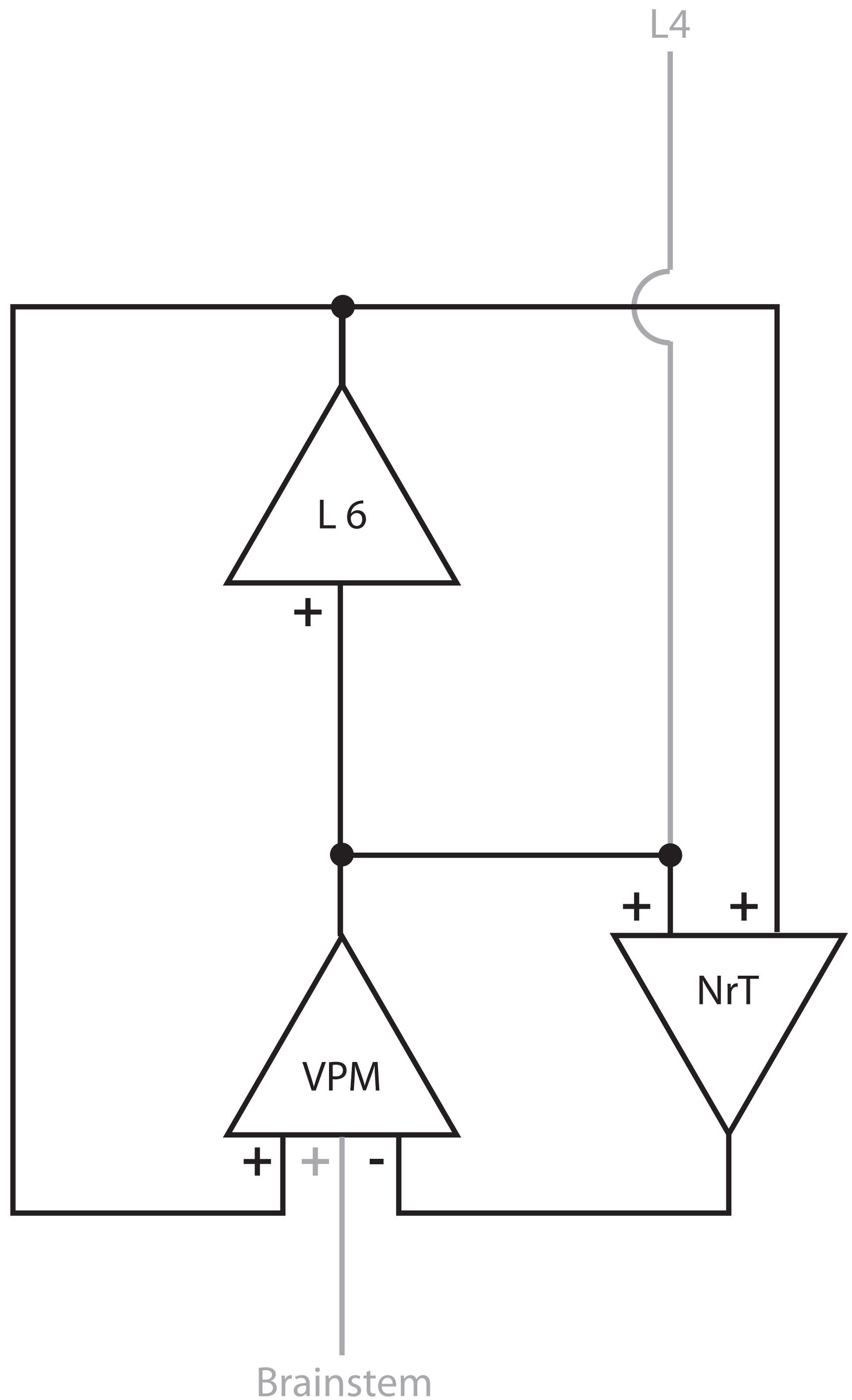
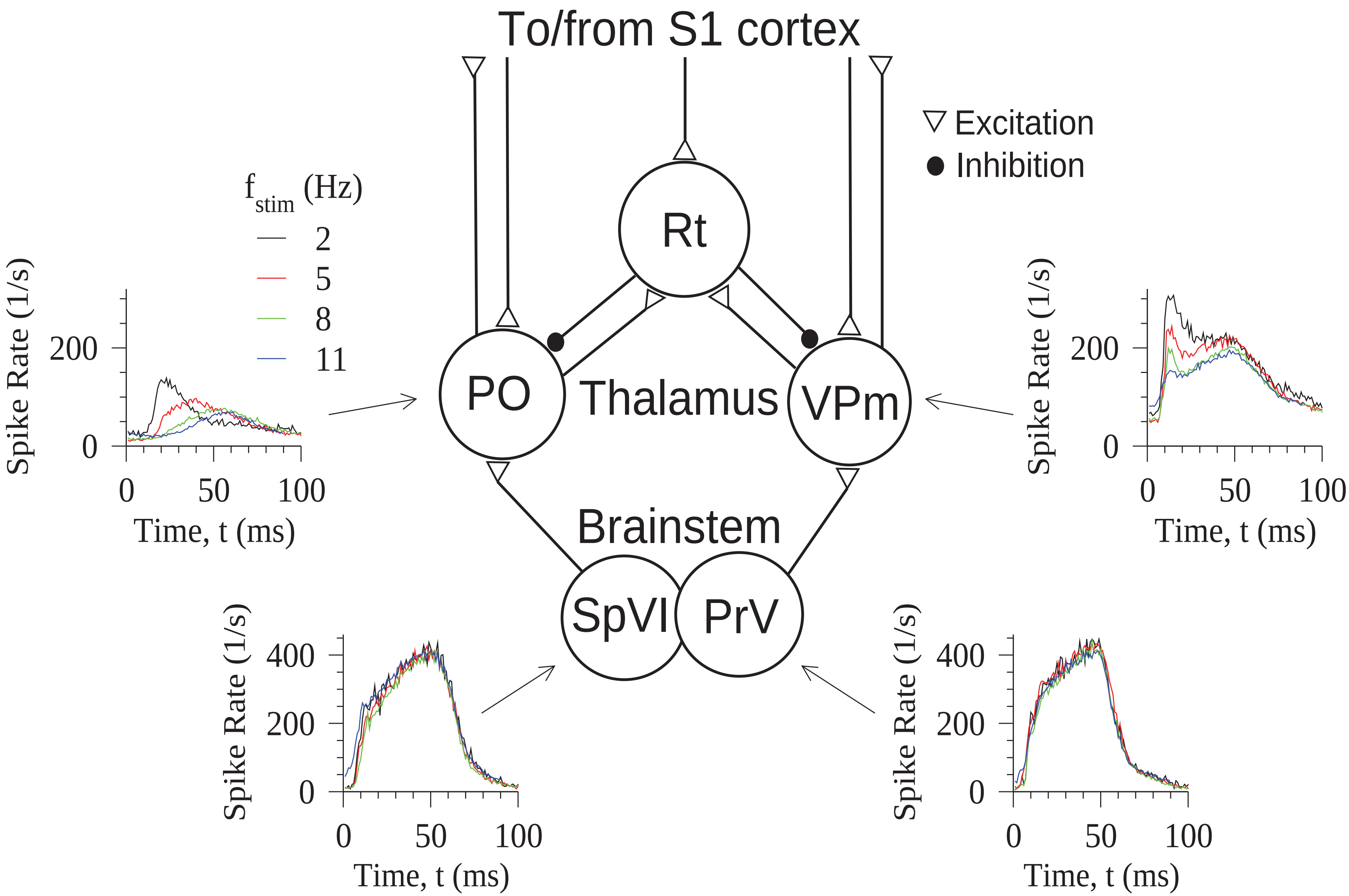




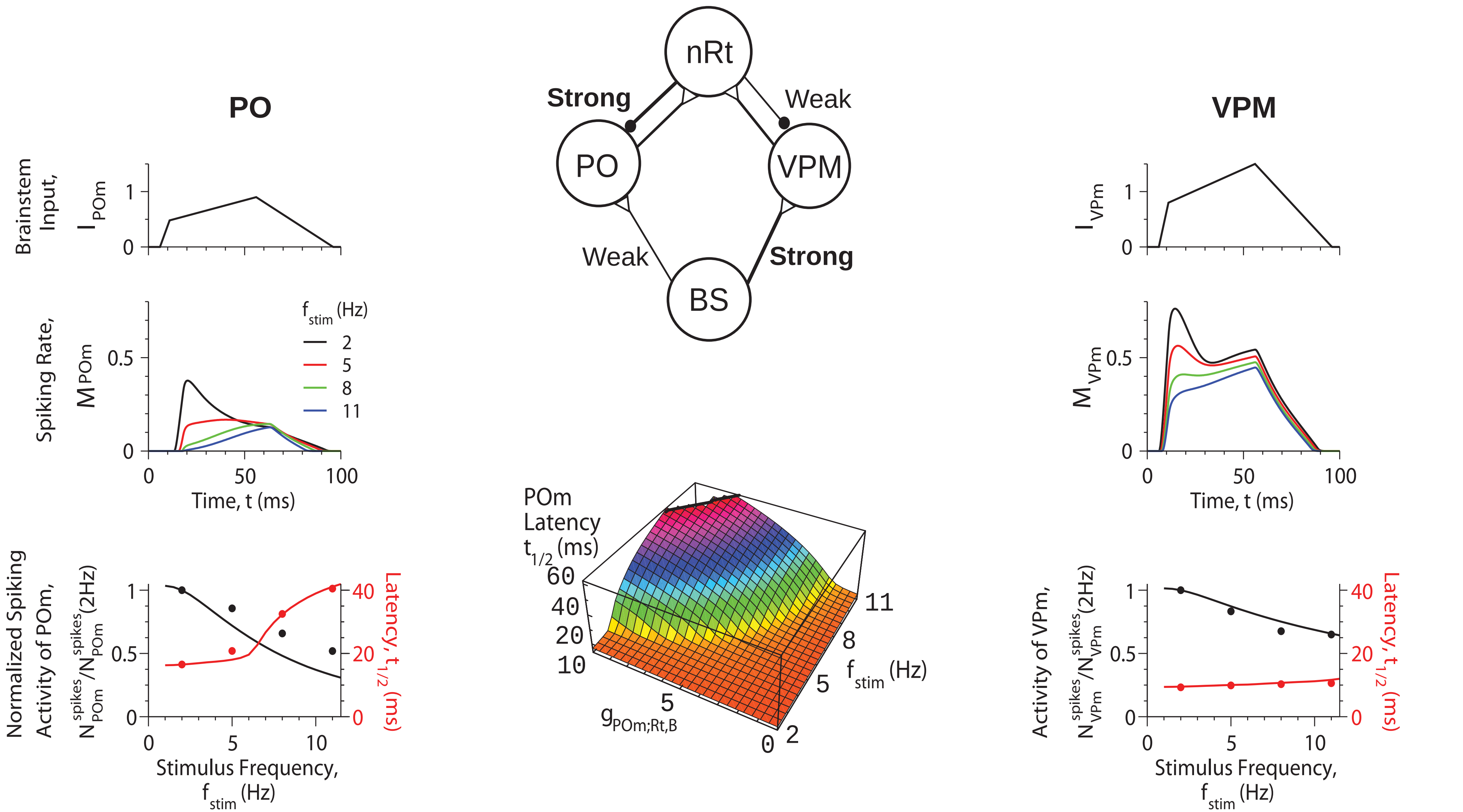
L4
L 6
+
+
+
NrT
VPM
+
+
-
Brainstem

Frequency dependent shifts in time-to-peak in PO but not VPM thalamus



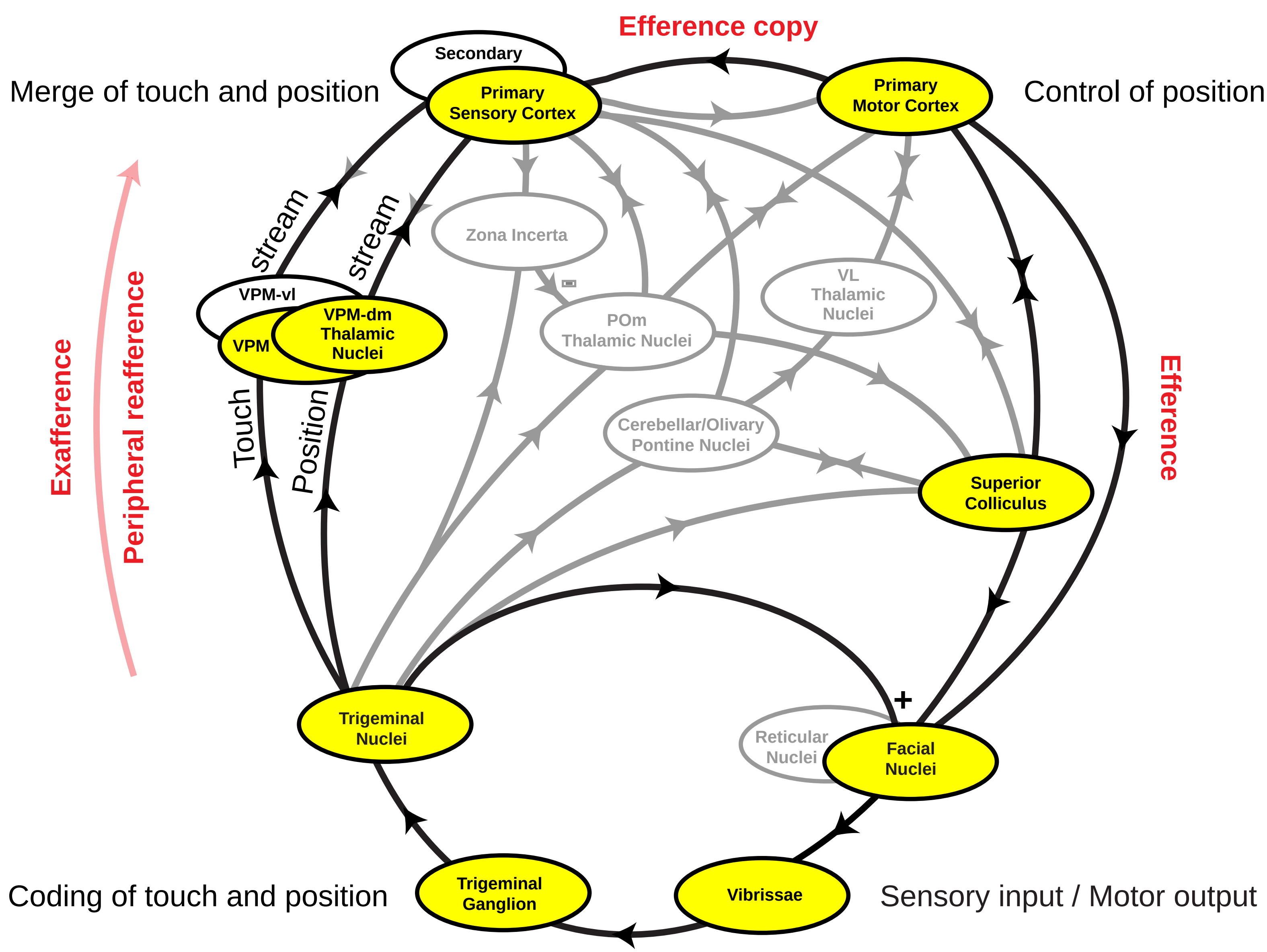
Ahissar, Sosnik & Haidarliu (2000); Sosnik, Haidarliu & Ahissar (2001).

$GABA_B$ feedback from nRt to PO can realize frequency-dependent latency (Ahissar's frequency-to-time code)



Golomb, Ahissar & Kleinfeld (2006)

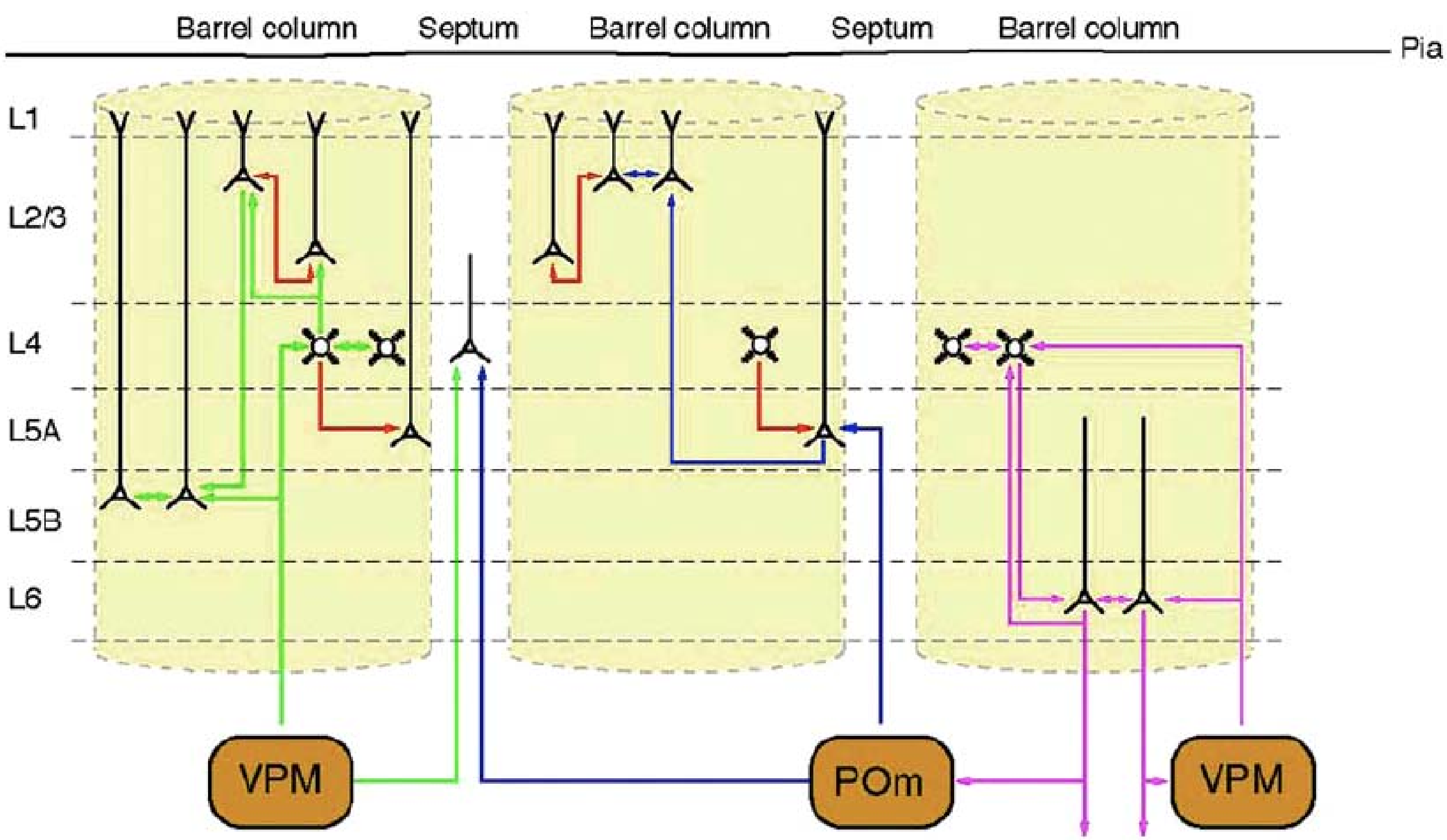
Exafference, reafference, efference, and efference copy as signals in vibrissa system loops



S1 cortex canonical excitatory connections

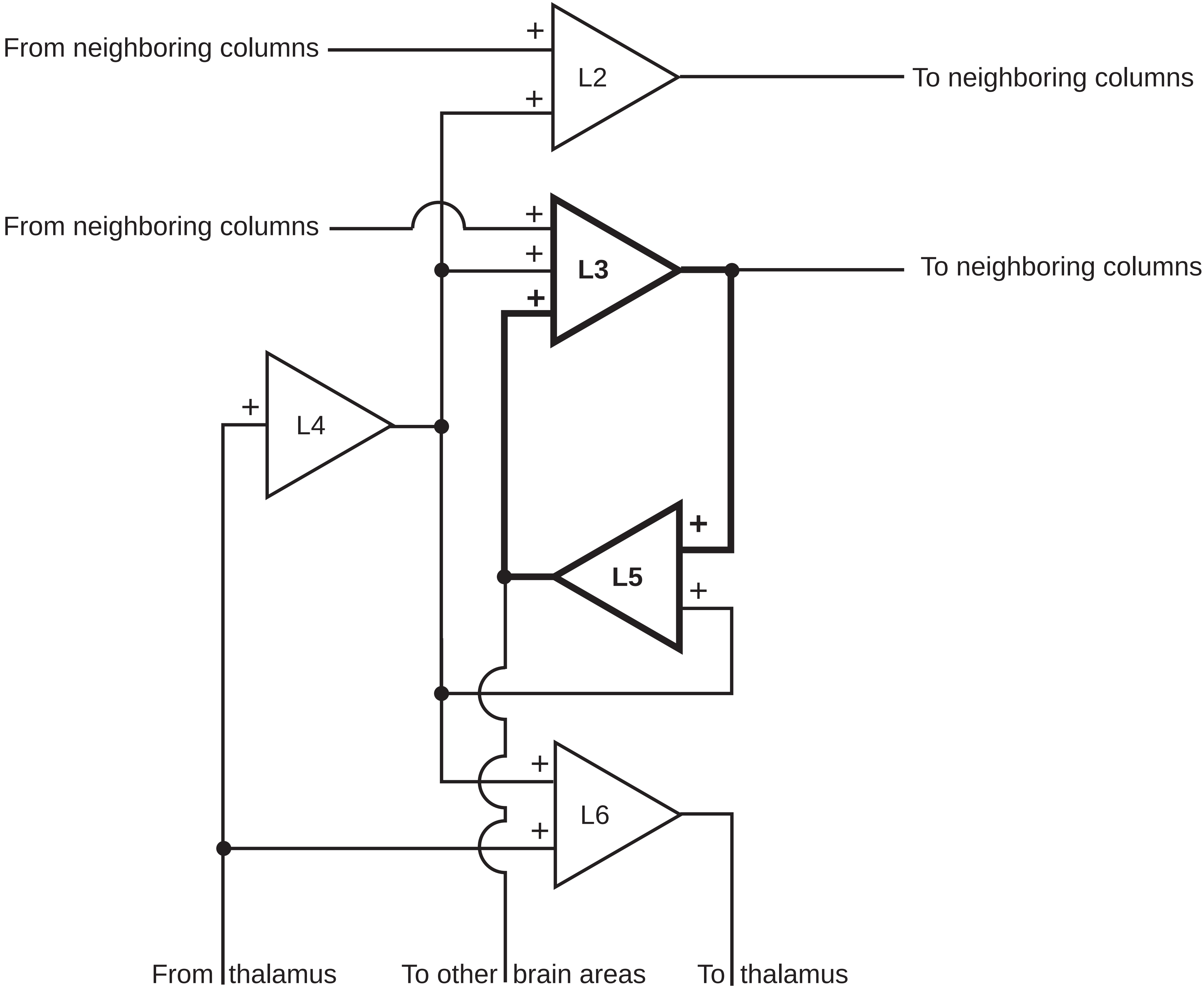
input → VPM → L4 (→ L2/3) → L5 → output

input → VPM → (L4 →) L6 → VPM → feedback

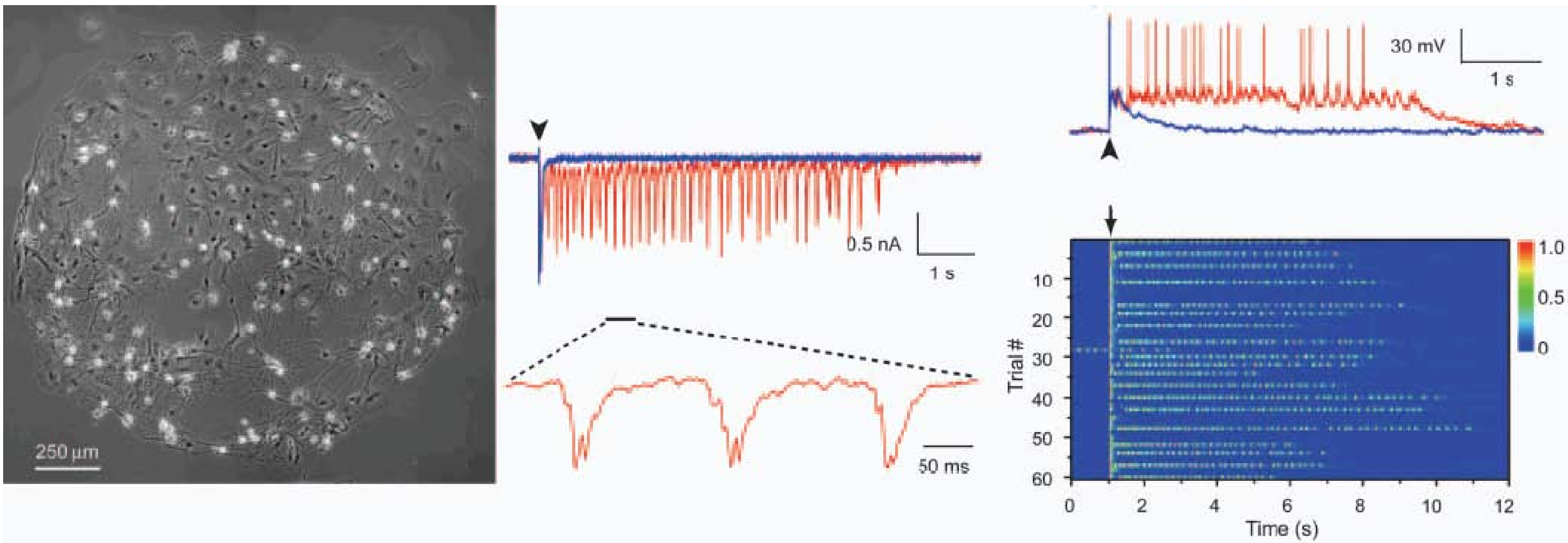


Lübke & Feldmeyer (2007)

What does this buy us computationally?
What does this imply in terms of dynamics?

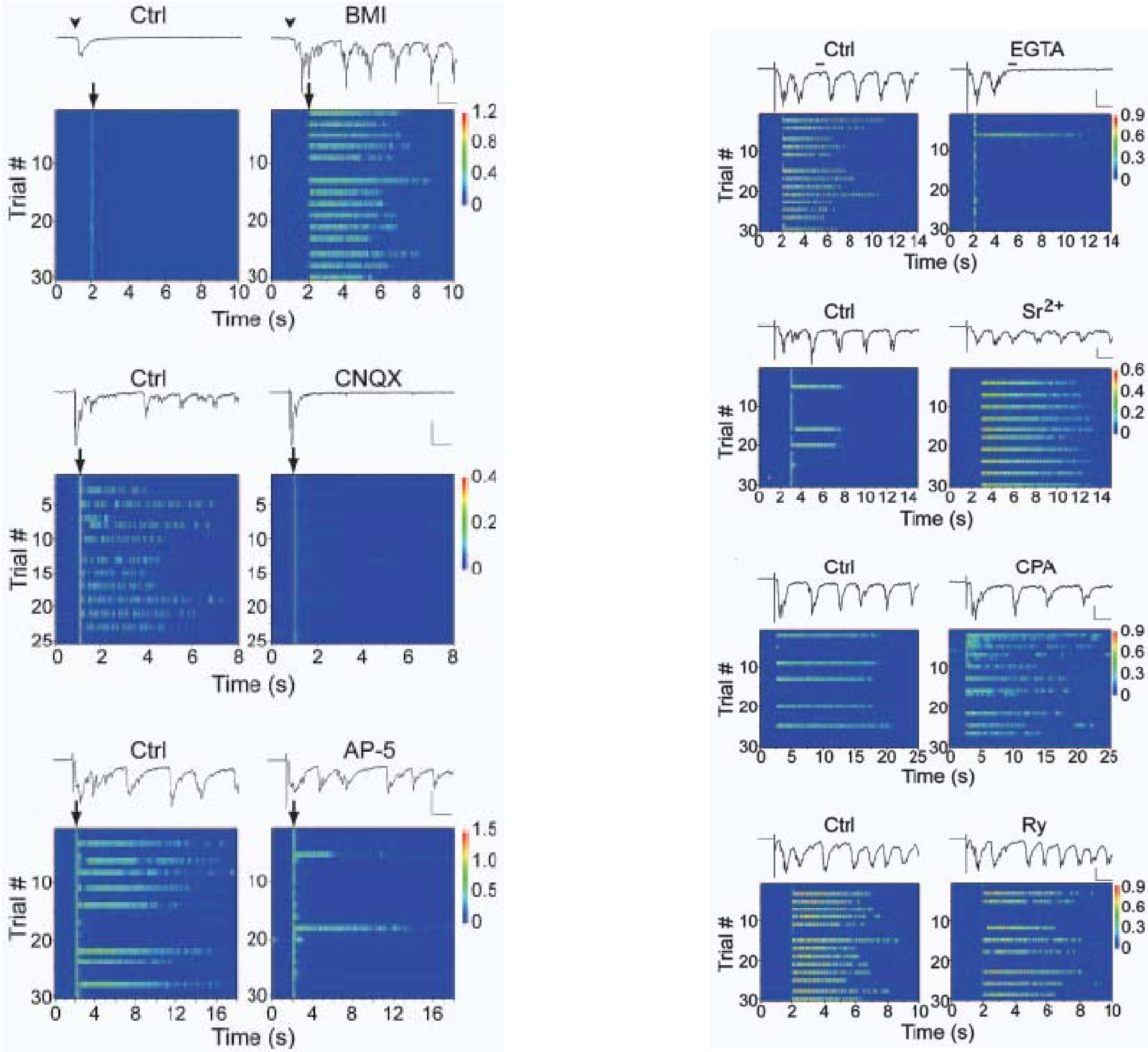

From neighboring columns
L2
To neighboring columns
From neighboring columns
L3
To neighboring columns
L4
L5
L6
From thalamus
To other brain areas
To thalamus

Existence proof of reverberation using cultures of cortical neurons



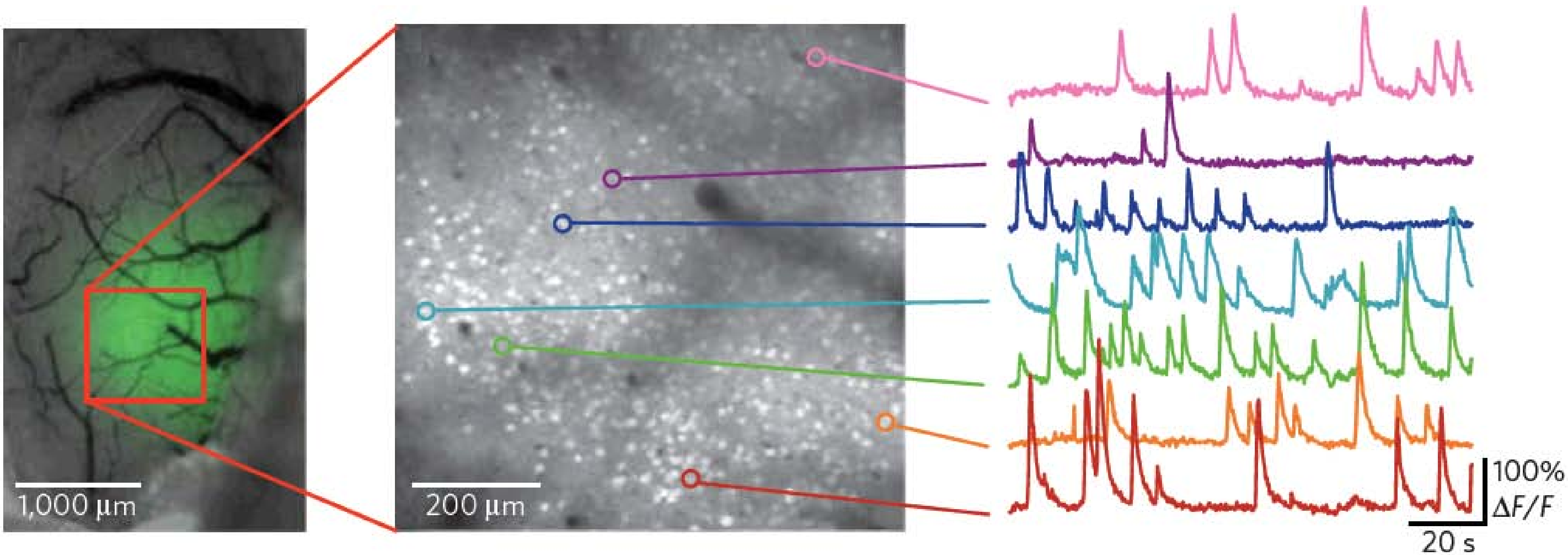
Lau & Bi (2005)

Excitatory synaptic transmission is obligatory for reverberation in cultures of cortical neurons



Lau & Bi (2005)

Despite positive feedback, many silent neurons in response to vibrissa stimulation



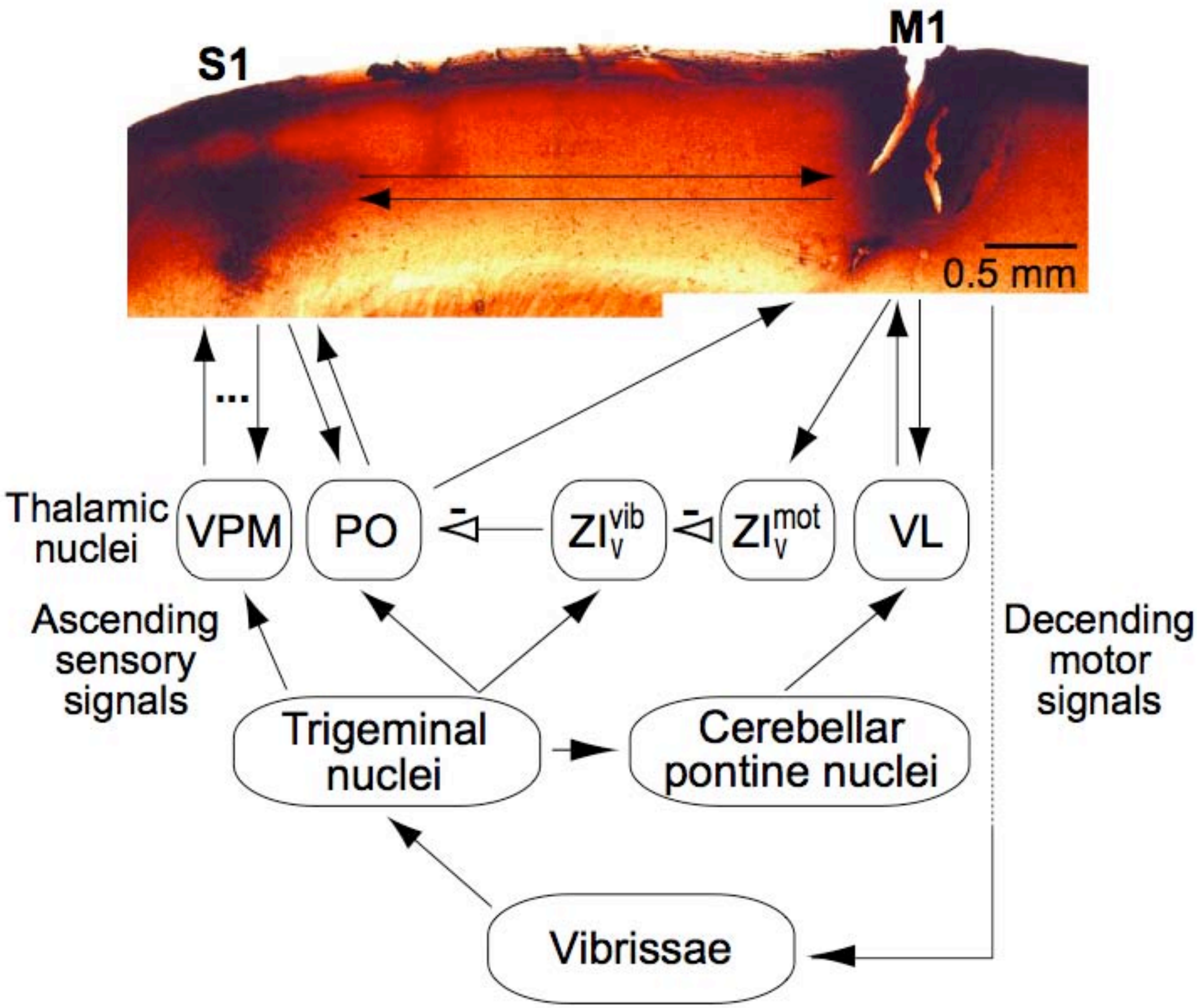
O'Connor, Huber & Svoboba (2009)

Are the cells silent for reasons of connectivity – or is the stimulus ineffective, *i.e.*, should we think in terms of trigeminal cortex?

Evidence for propagation of neuronal activation across cortex

Ferezou, Bolea & Petersen (2006)

M1 cortex gates (multi-vibrissa) vibrissae input to S1 cortex via PO



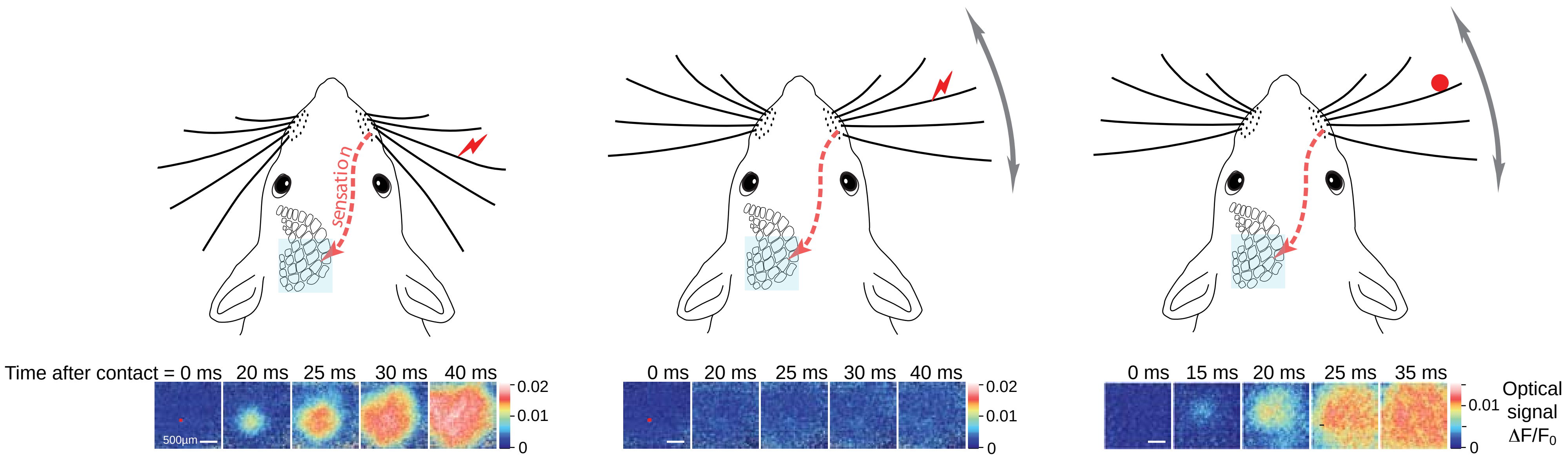
Urbain & Deschenes (2007)

Evidence that behavioral state gates sensory input during whisking

Startle mode (awake and sessile)

Exploration mode (whisking *without* contact)

Object detection mode (whisking *with* contact)



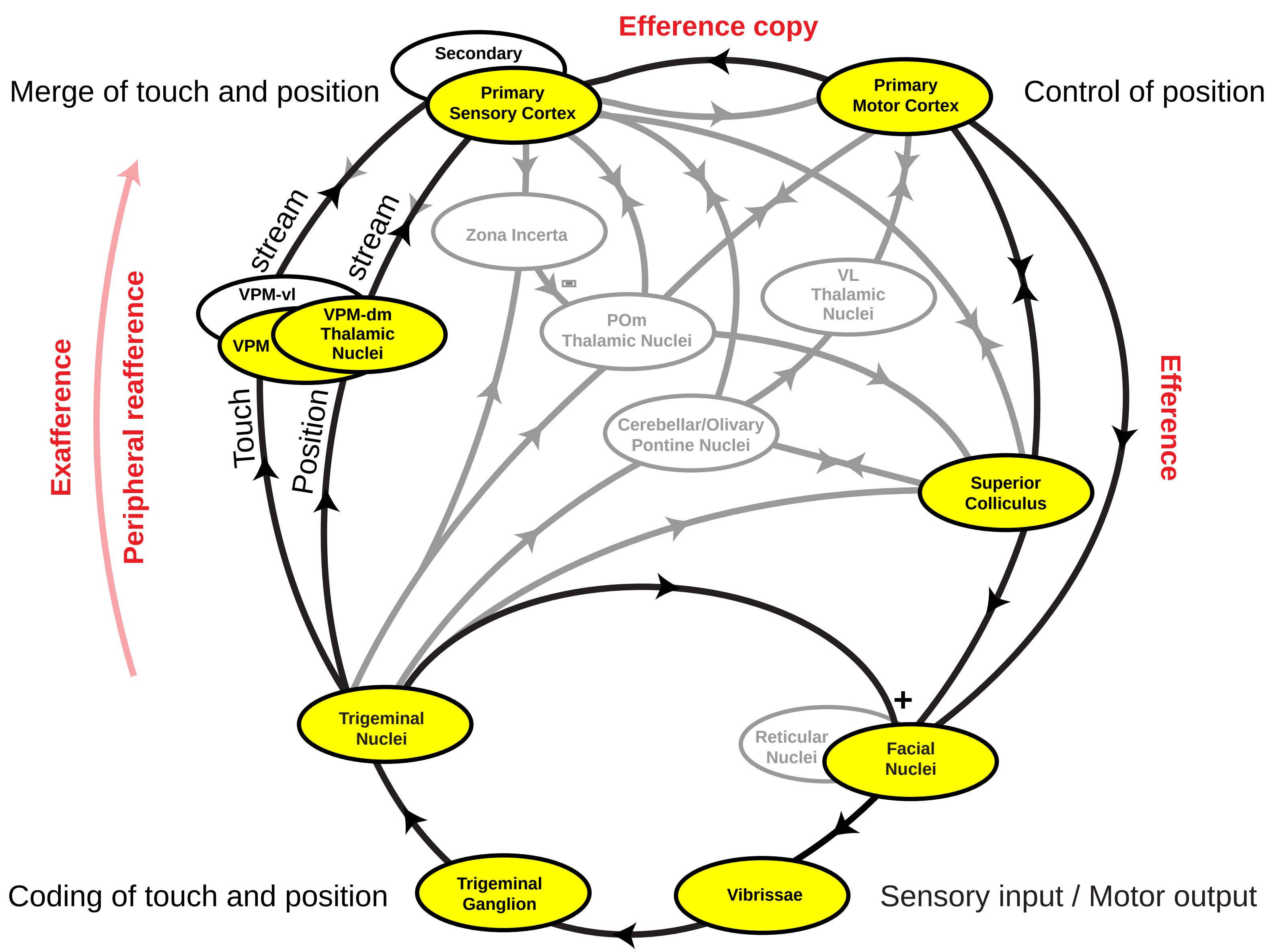
Strong response to passive stimulation

Gating or suppression yields *weak* response to passive stimulation

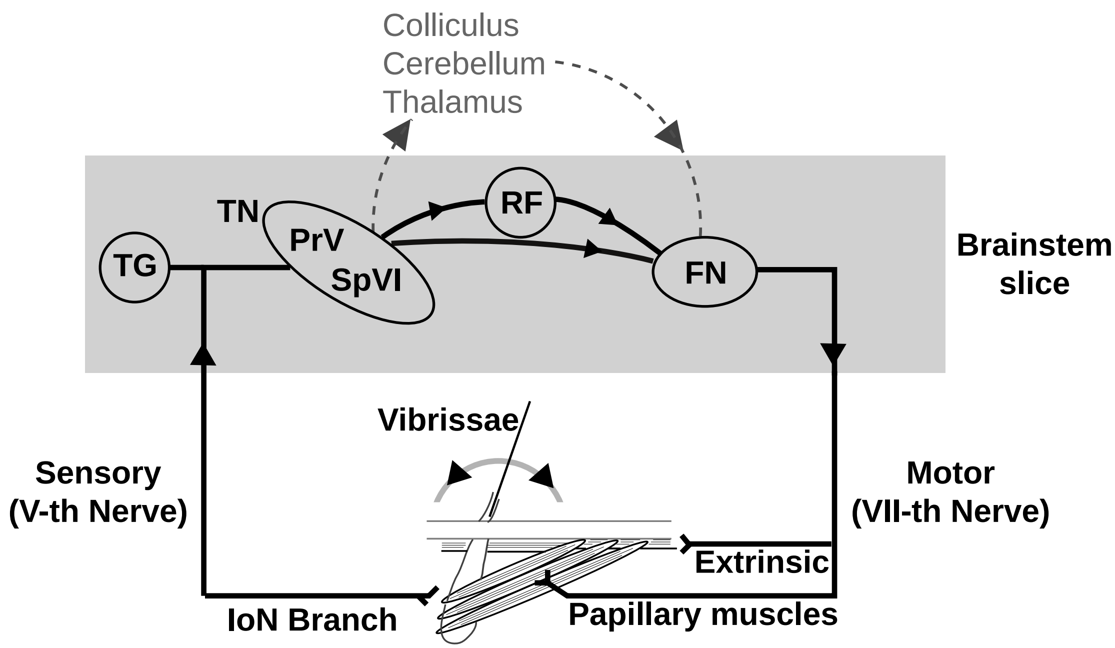
Strong response to active touch

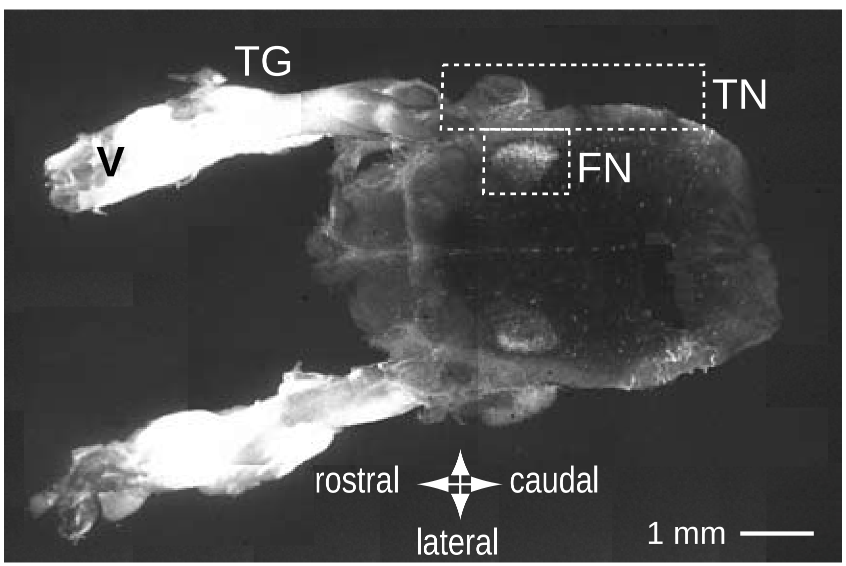
Ferezou, Bolea & Petersen (2006)

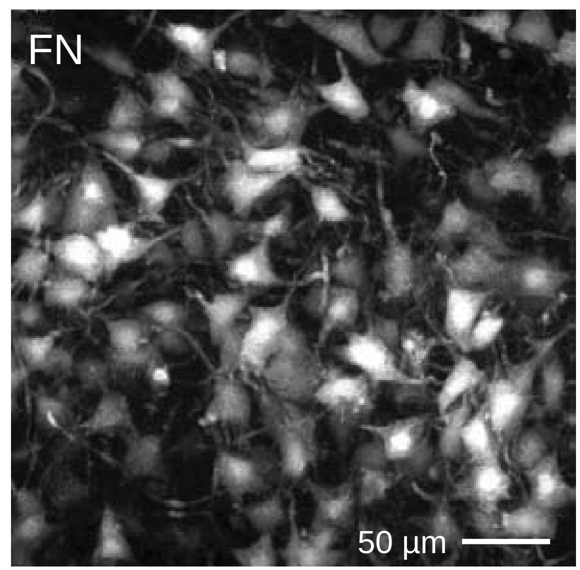
Exafference, reafference, efference, and efference copy as signals in vibrissa system loops



Brainstem slice preparation captures sensorimotor feedback circuitry

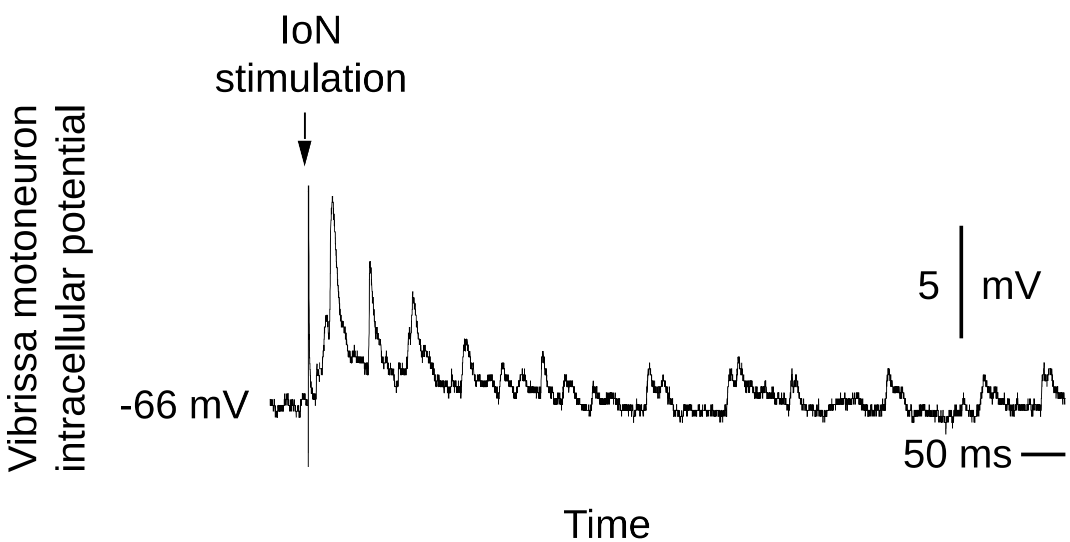


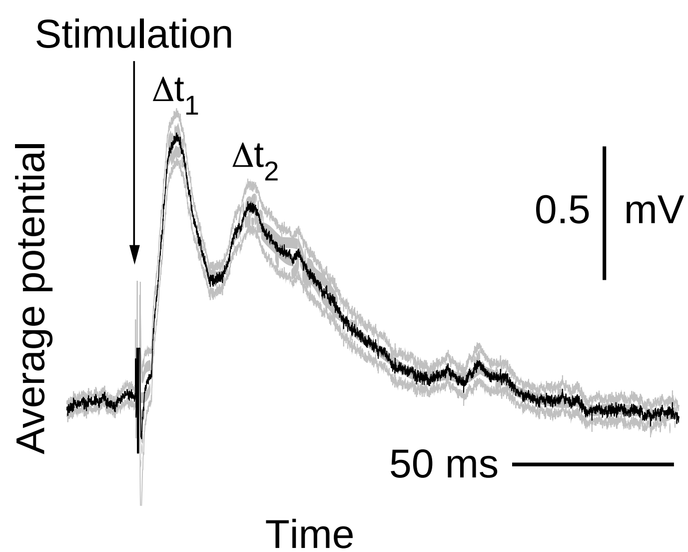




Nguyen and Kleinfeld (2005)

Fast, transient, positive feedback in the brainstem vibrissa sensorimotor loop *in vitro*





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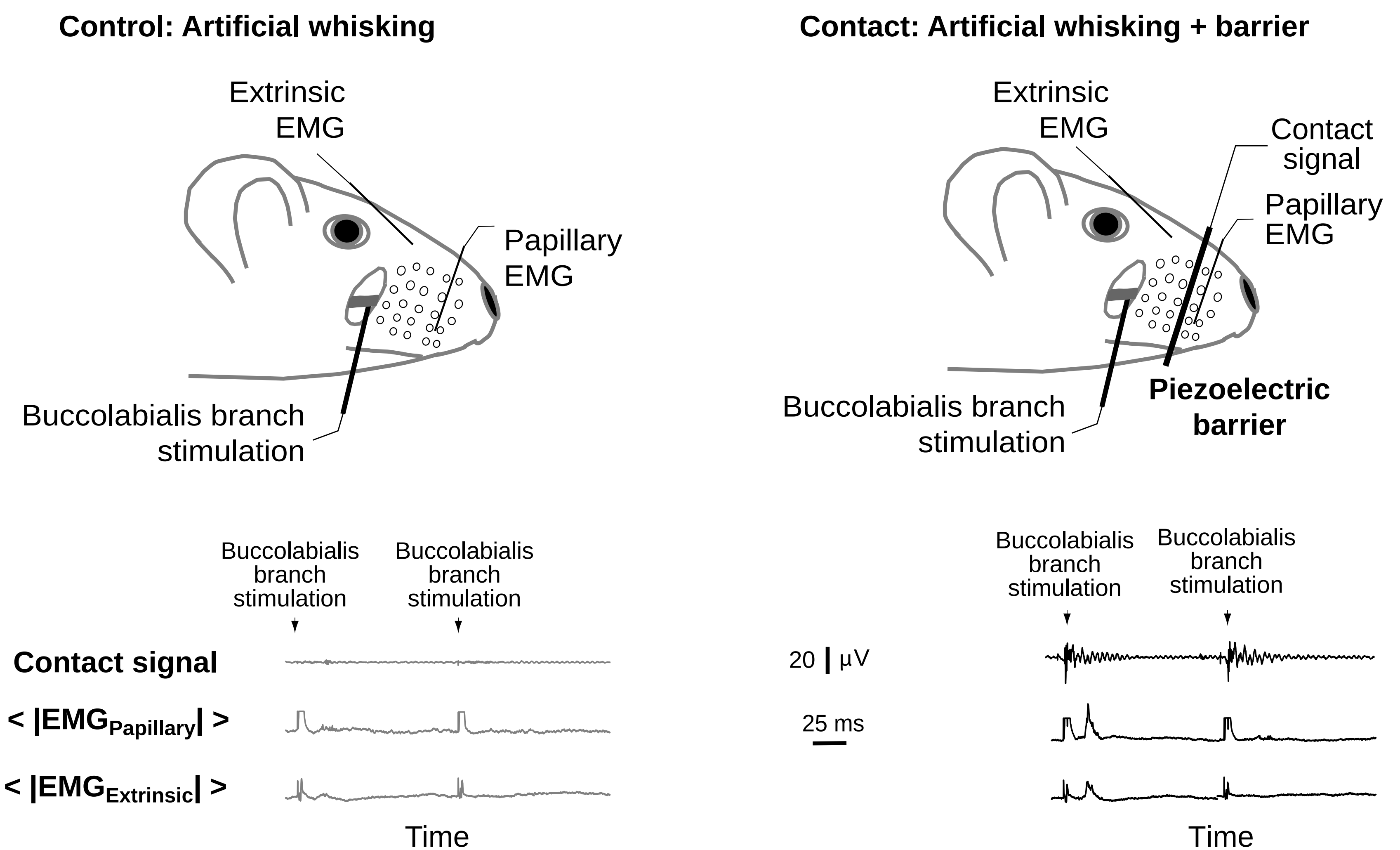
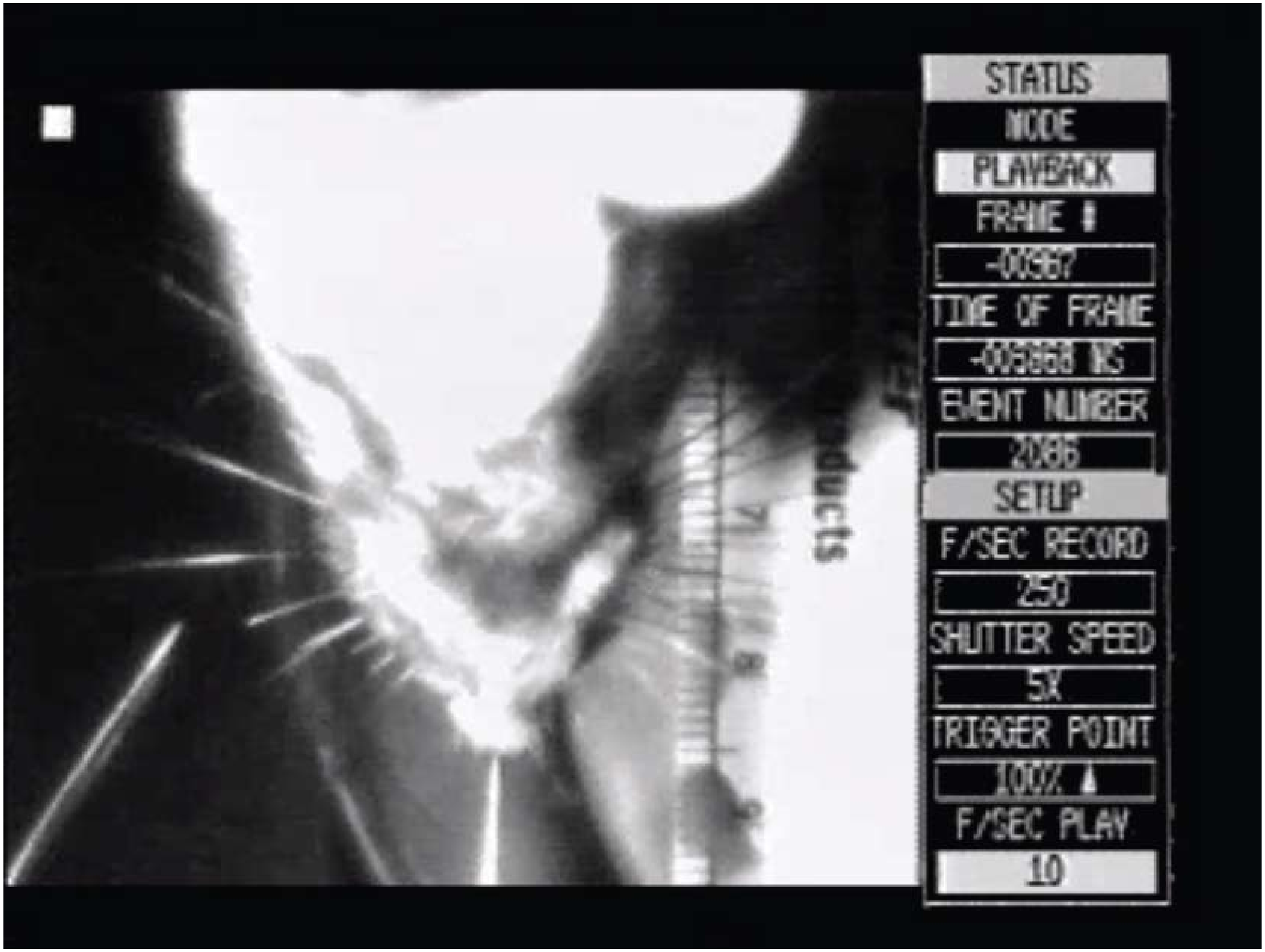


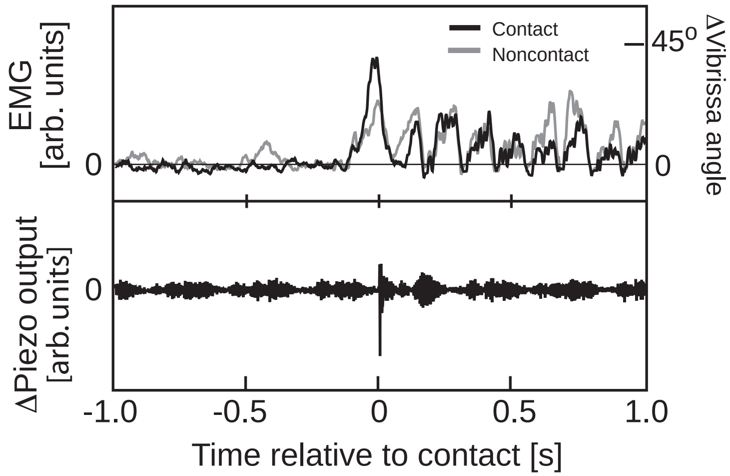
Nguyen and Kleinfeld (2005)

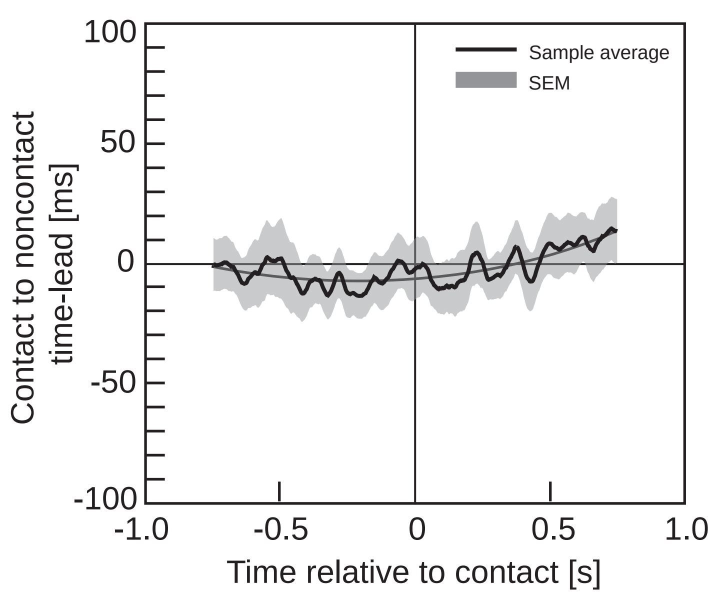
Rats can detect contact to a single vibrissa (Hutson and Masterson 1986)

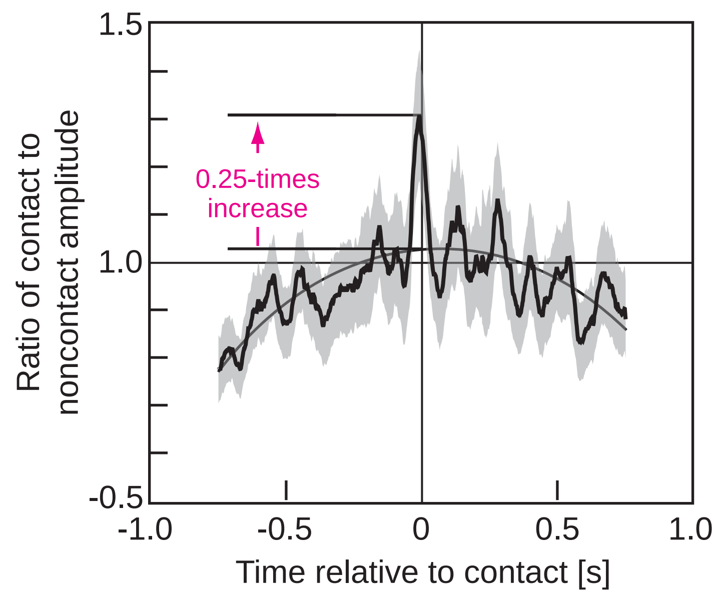


Sachdev, Berg, Champney, Kleinfeld and Ebner (2003)

Vibrissa contact leads to transient increase in EMG during contact task (force ~ EMG)

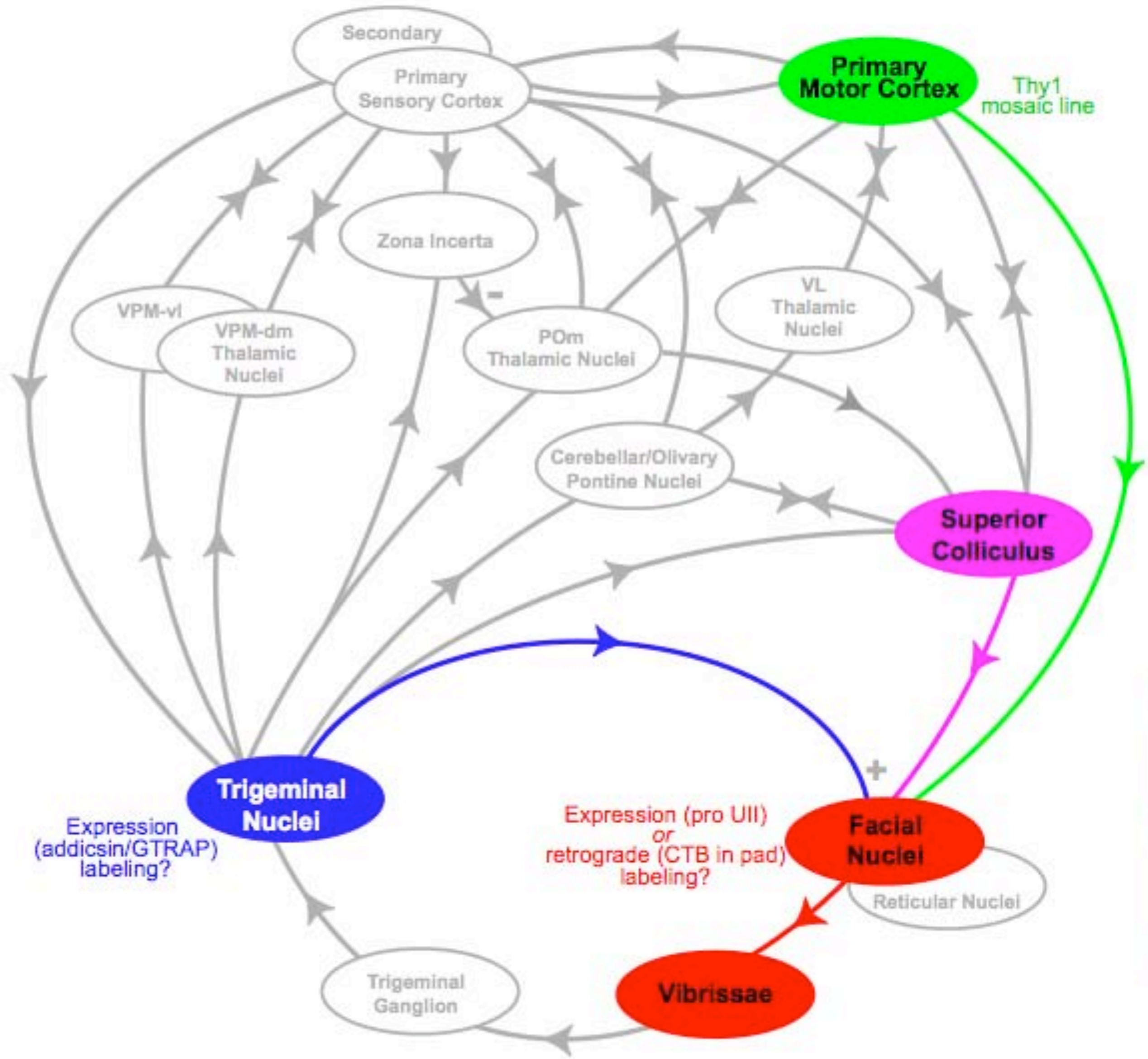




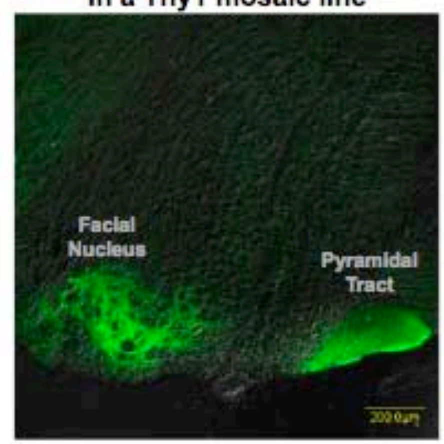


Sachdev, Berg, Champney, Kleinfeld and Ebner (2003)

Facial Motoneurons: Arbitrators (~40 inputs) or power transistors?



M1 cortex to FN projections in a Thy1 mosaic line



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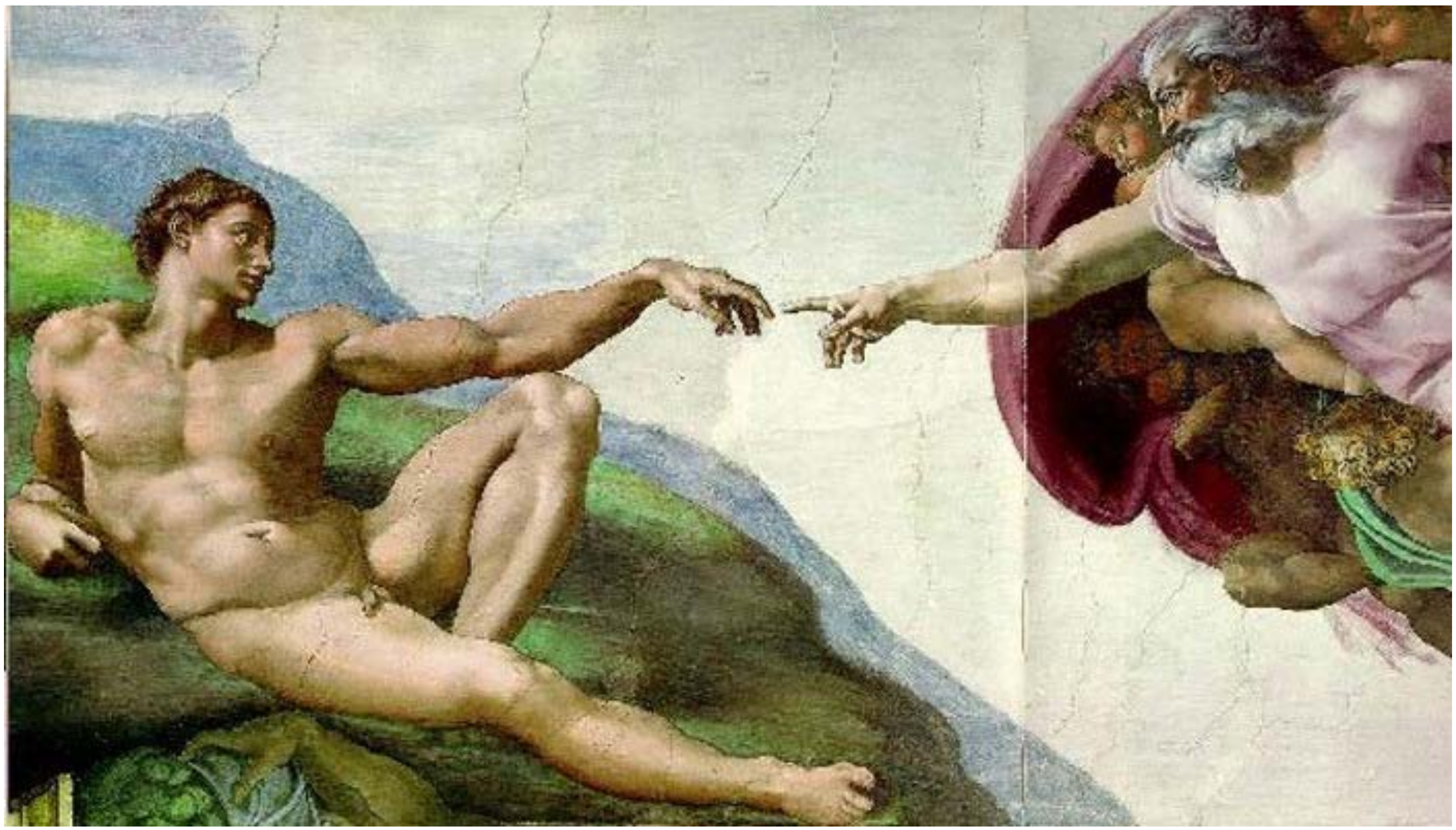
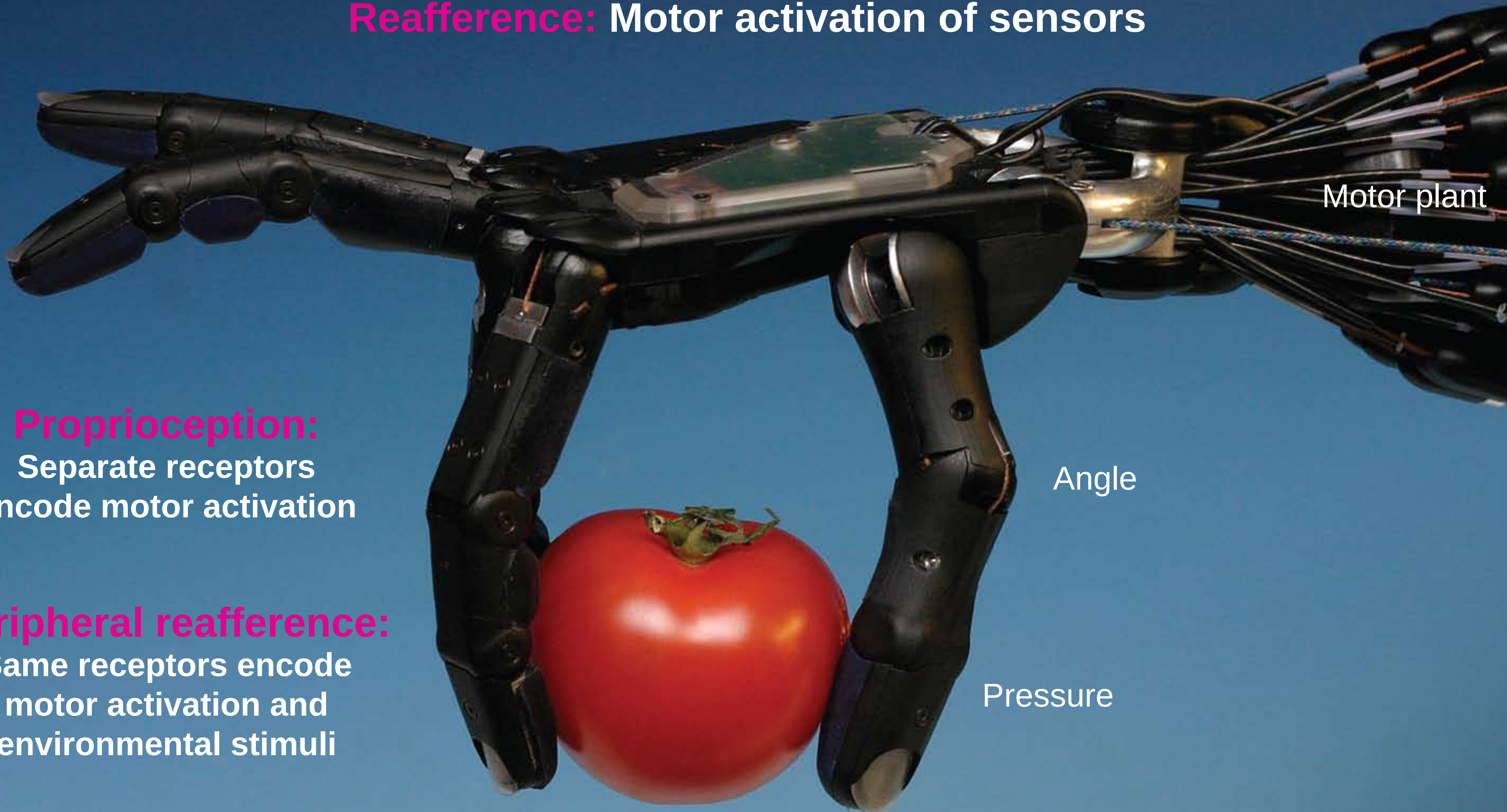


von Holst’s classification of sensory signals*

Exafference: Environmental activation of sensors

Reafference: Motor activation of sensors



Proprioception:
Separate receptors encode motor activation

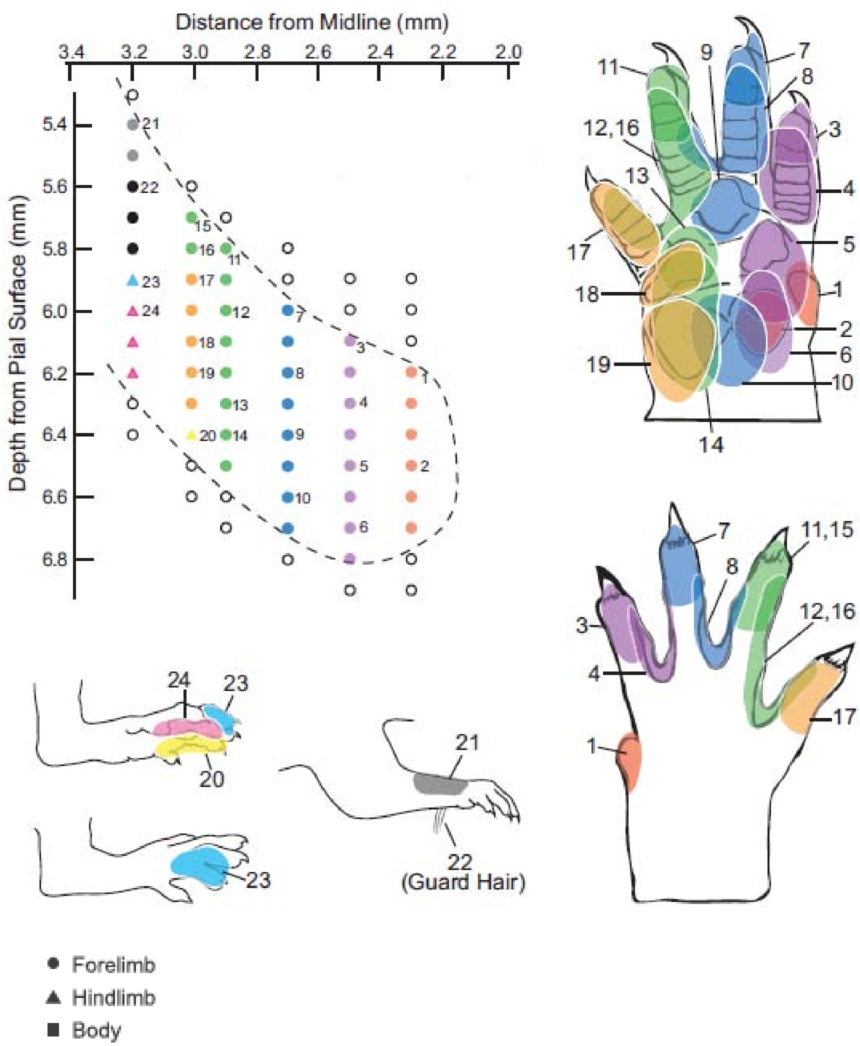
Peripheral reafference:
Same receptors encode motor activation and environmental stimuli

Efference copy: Intended motor execution

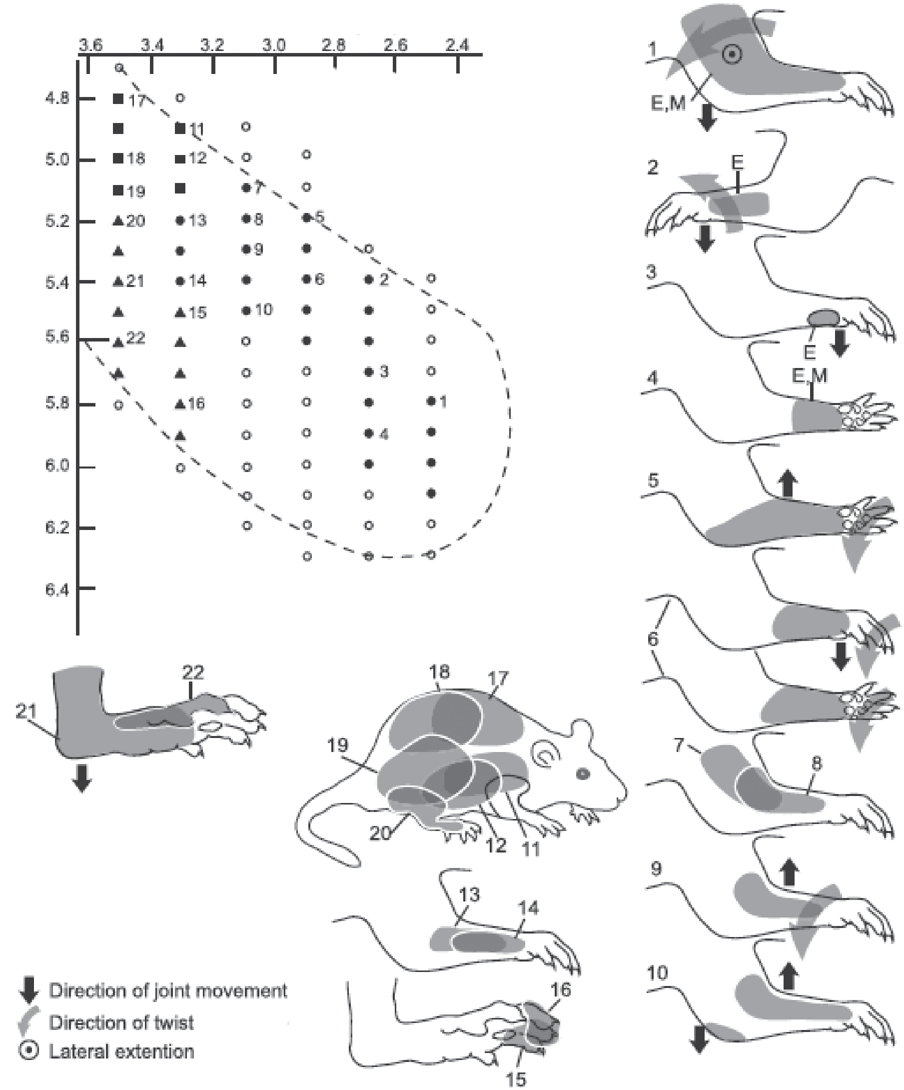
*British Journal of Animal Behavior (1954)
Shadow Robot Company Ltd.

Adjacent cutaneous and proprioceptive maps in rat VPL thalamus

Exafference



Reafference - proprioception



Francis, Xu & Chapin (2008)

Lesson

Thalamus contains maps of both exafference, *e.g.*, somatotopy, and reafference, *e.g.*, joint movement.

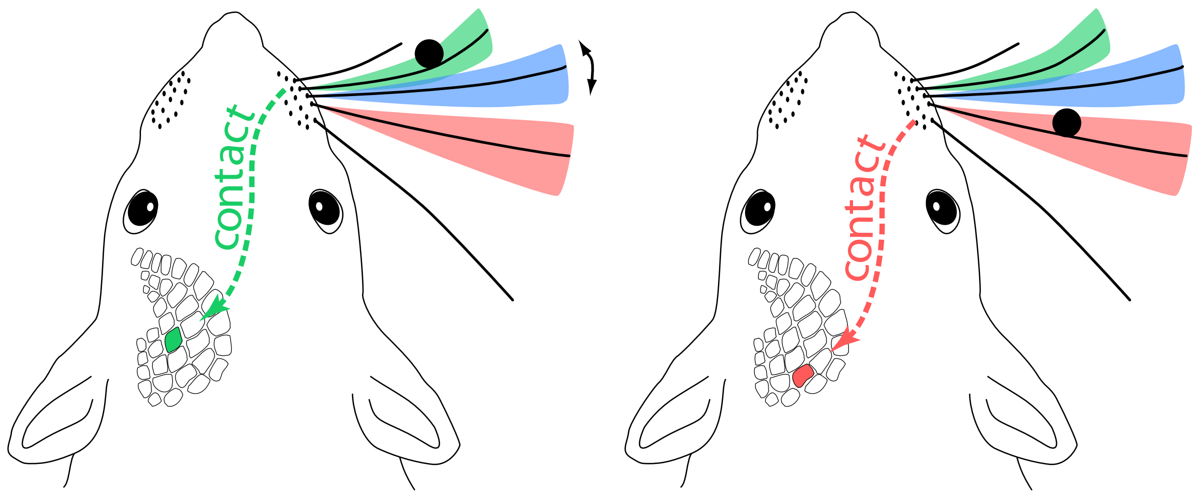
Query

Where do signals from the exafference and reafference merge?

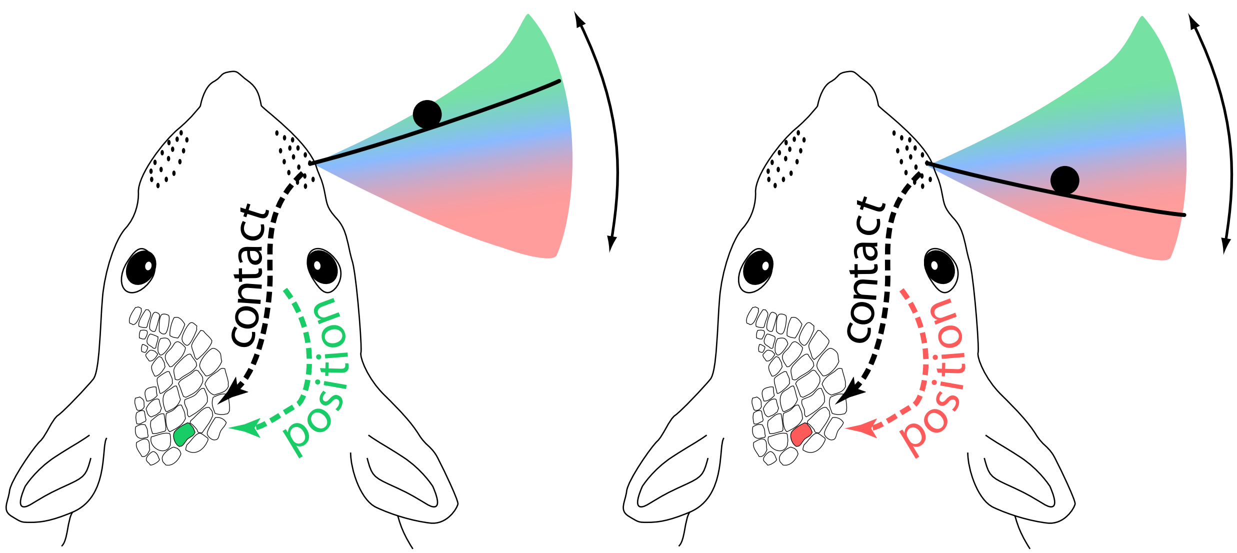
(Vibrissa sensorimotor system as a locus for study)

What class of algorithms are used to decode object location?

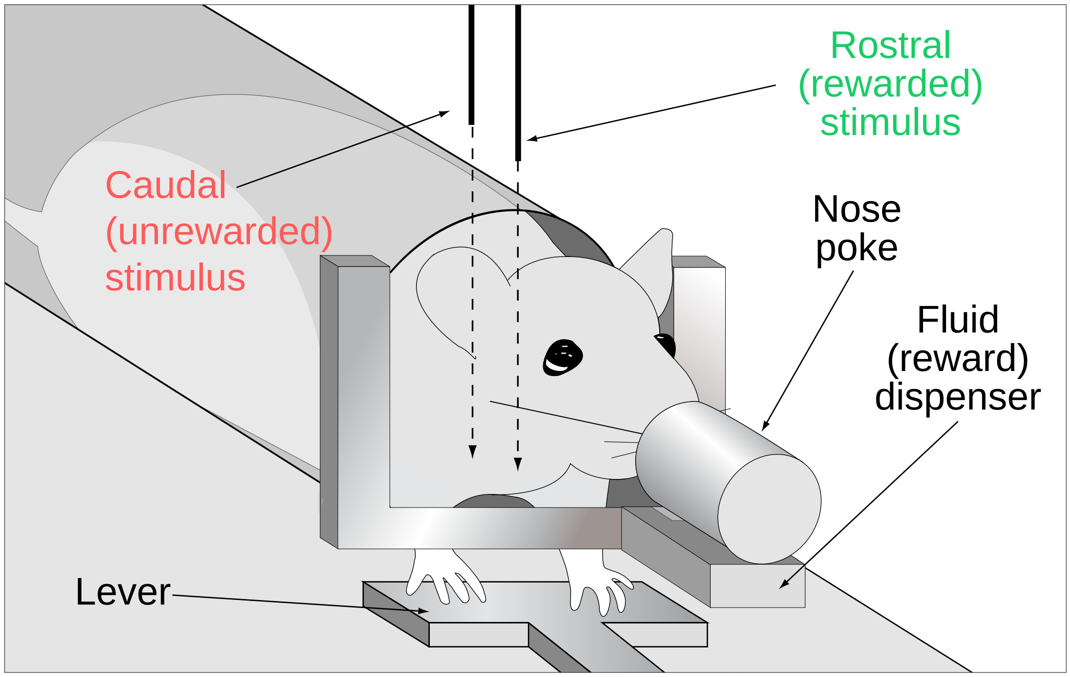
Labeled line and triangulation schemes: Require multiple vibrissae

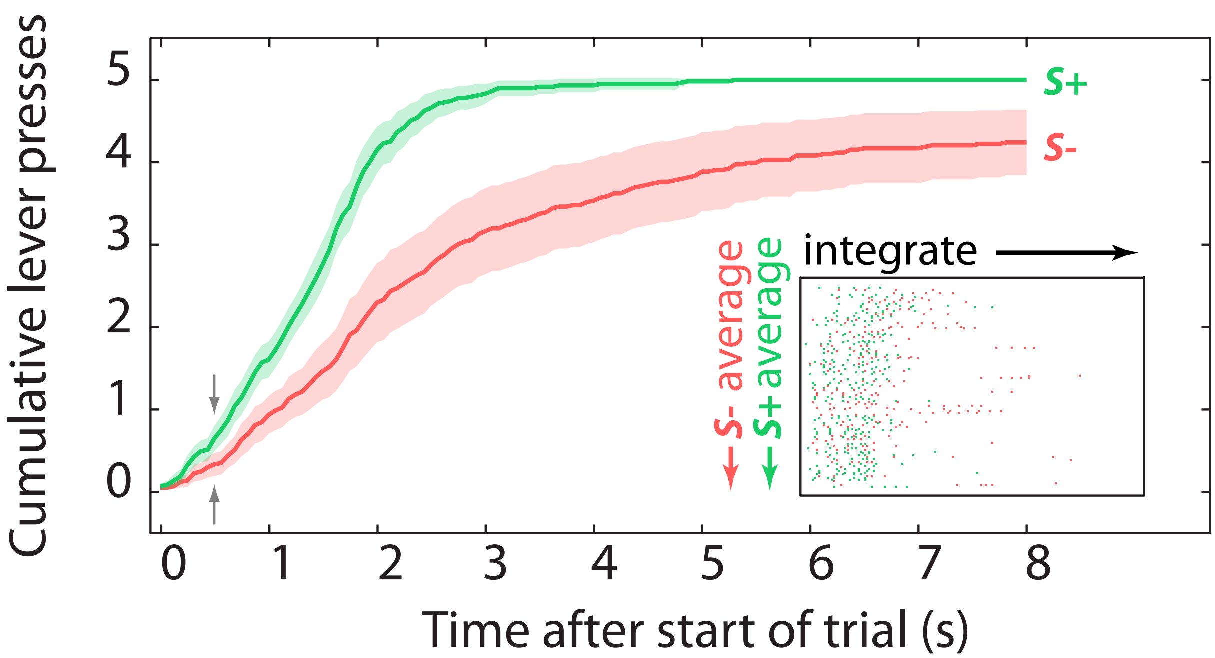


Reafference or efference copy (reference) schemes: Require only a single vibrissa



Rats can distinguish angular position, relative to their face, with a single vibrissa





Mehta, Whitmer, Figueroa, Williams and Kleinfeld (2007)

Lesson

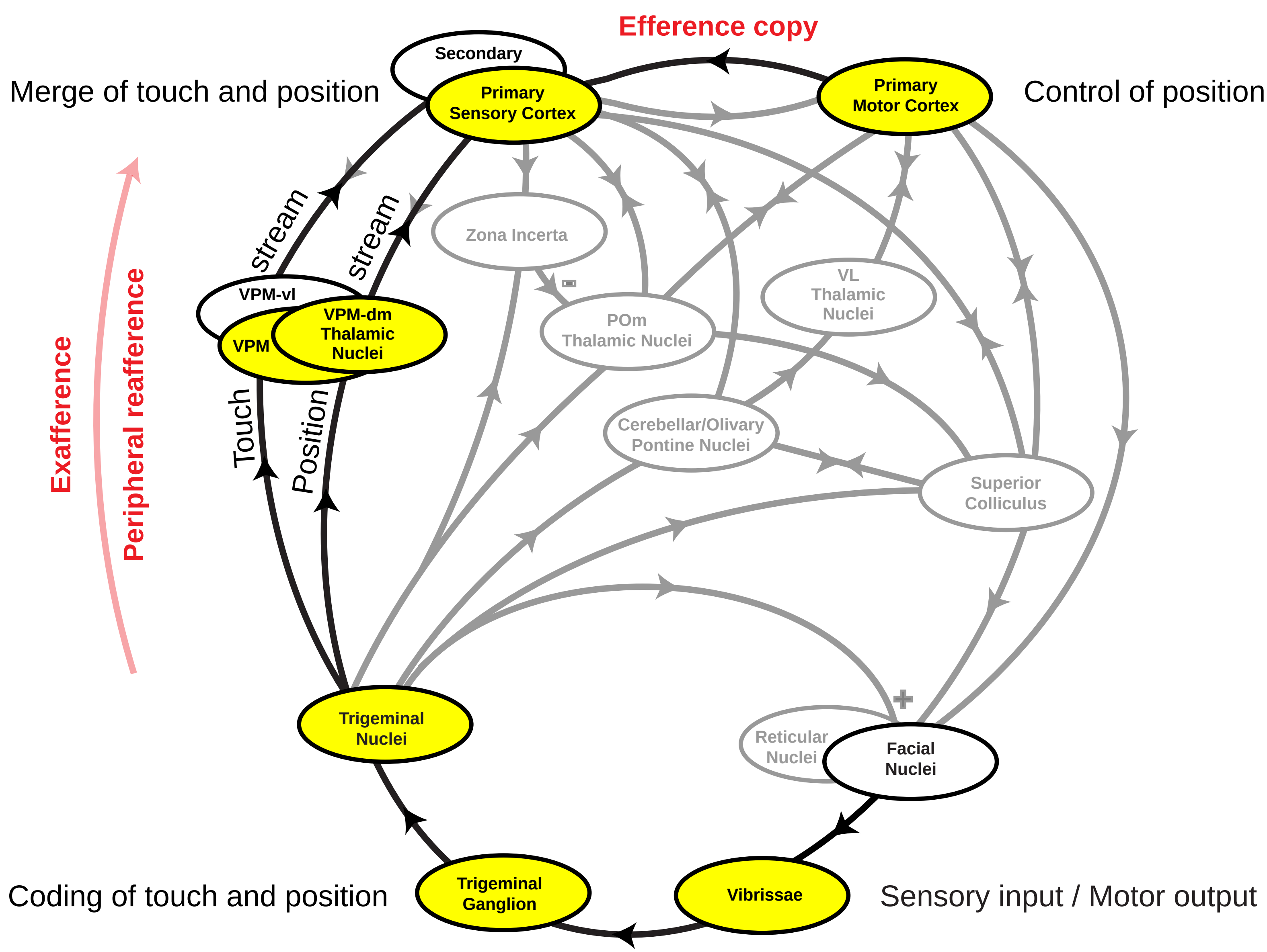
Rats can detect location in face-centered coordinates

Implies that rats can code the azimuthal position of a vibrissae.

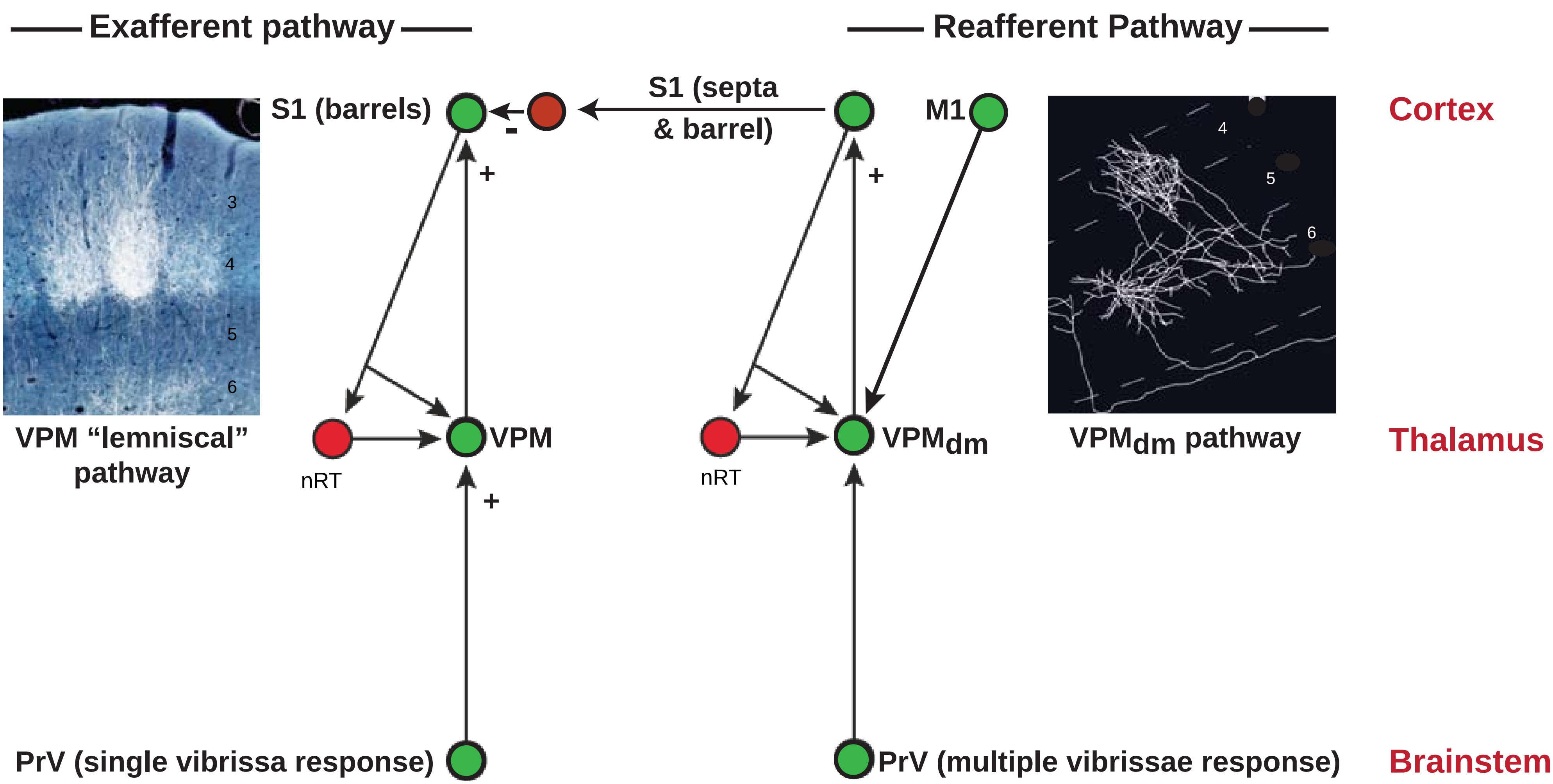
Query

What is the neurological basis of position signals?

Exafference, reafference, and efference copy in the vibrissa system



Evidence for exafferent (touch) versus reafferent (position) channels



Urbain & Deschenes (2007); Moore, Deschenes & Kleinfeld (in progress); Exafference ~ VPM; Reafference ~ VPM-dm

Yu, Derkikmam, Haidarliu & Ahissar (2006); Exafference ~ VPM; Reafference ~ PO

Masri, Bezdudnaya, Trageser & Keller (2008); Exafference ~ VPM; Reafference ~ *not* PO

Lesson

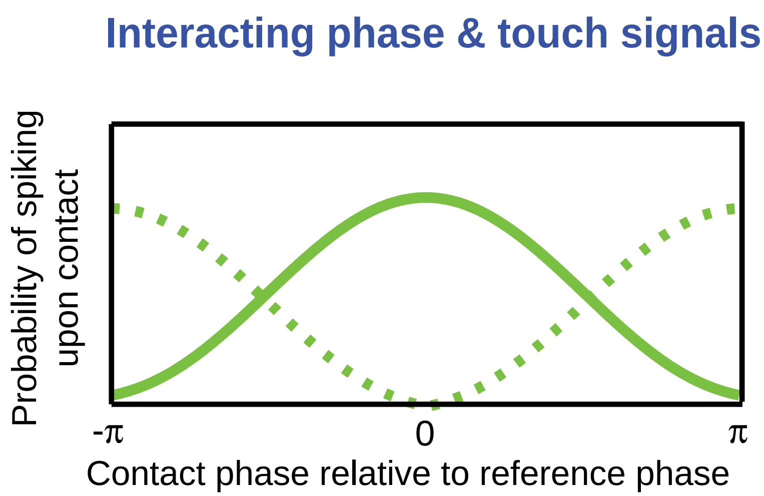
Vibrissa position is derived from peripheral reafference

Touch and position signals form independent streams.

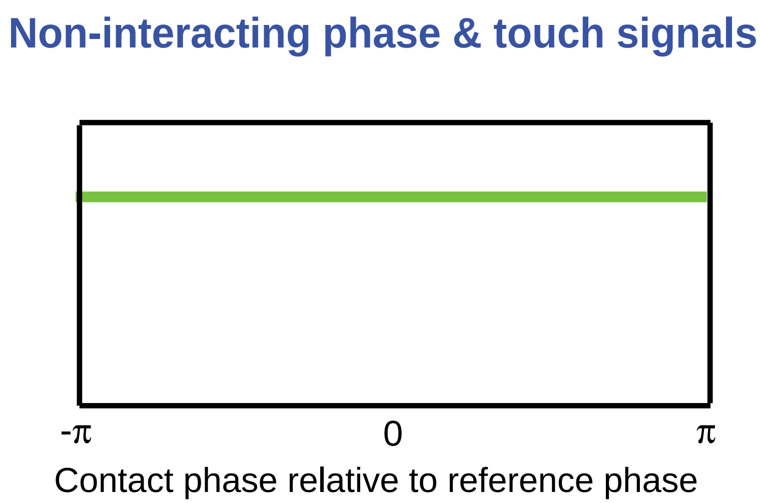
Query

What is the basis for the merge of position and touch?

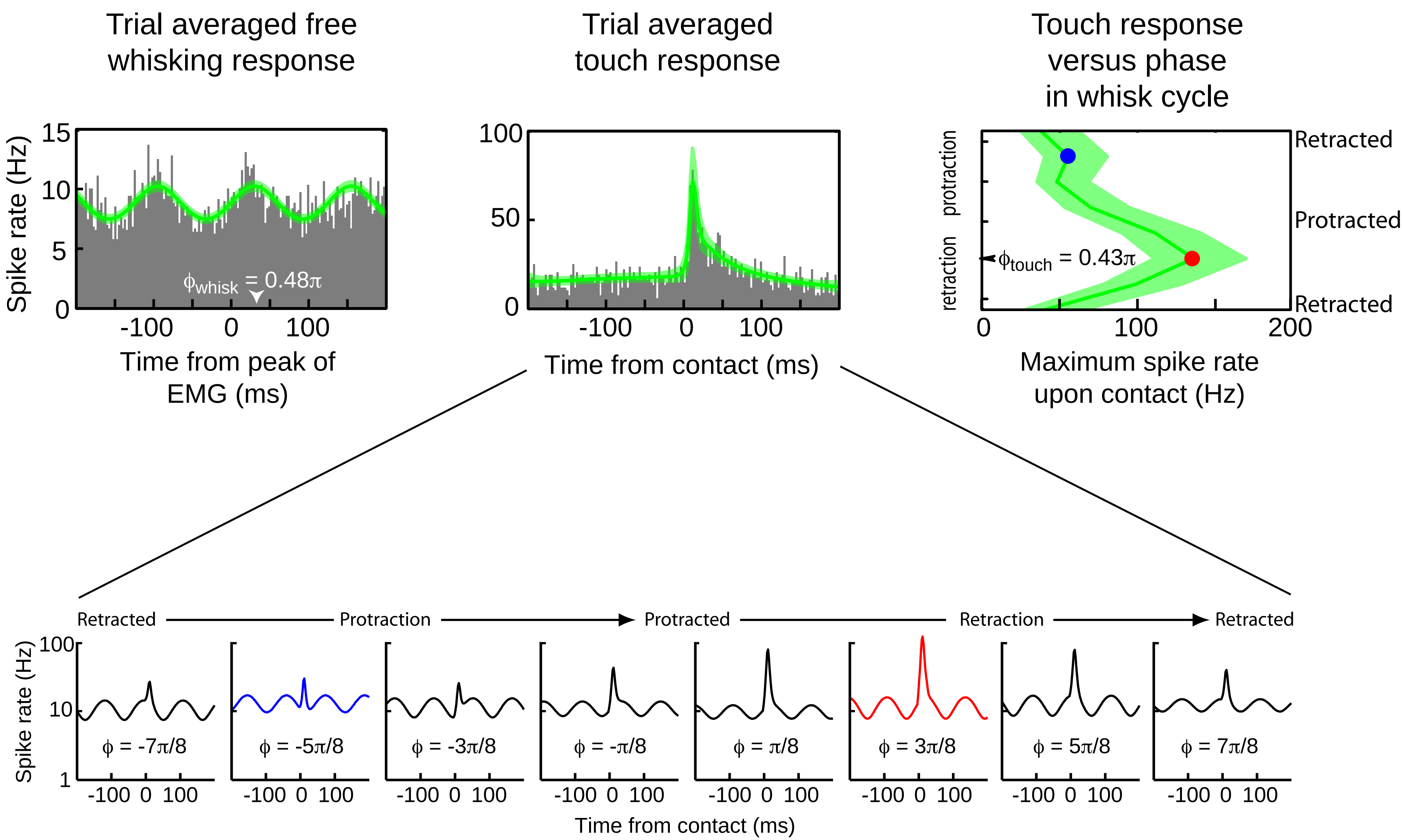
Is vibrissa touch response conditioned on phase in the whisk cycle?



versus

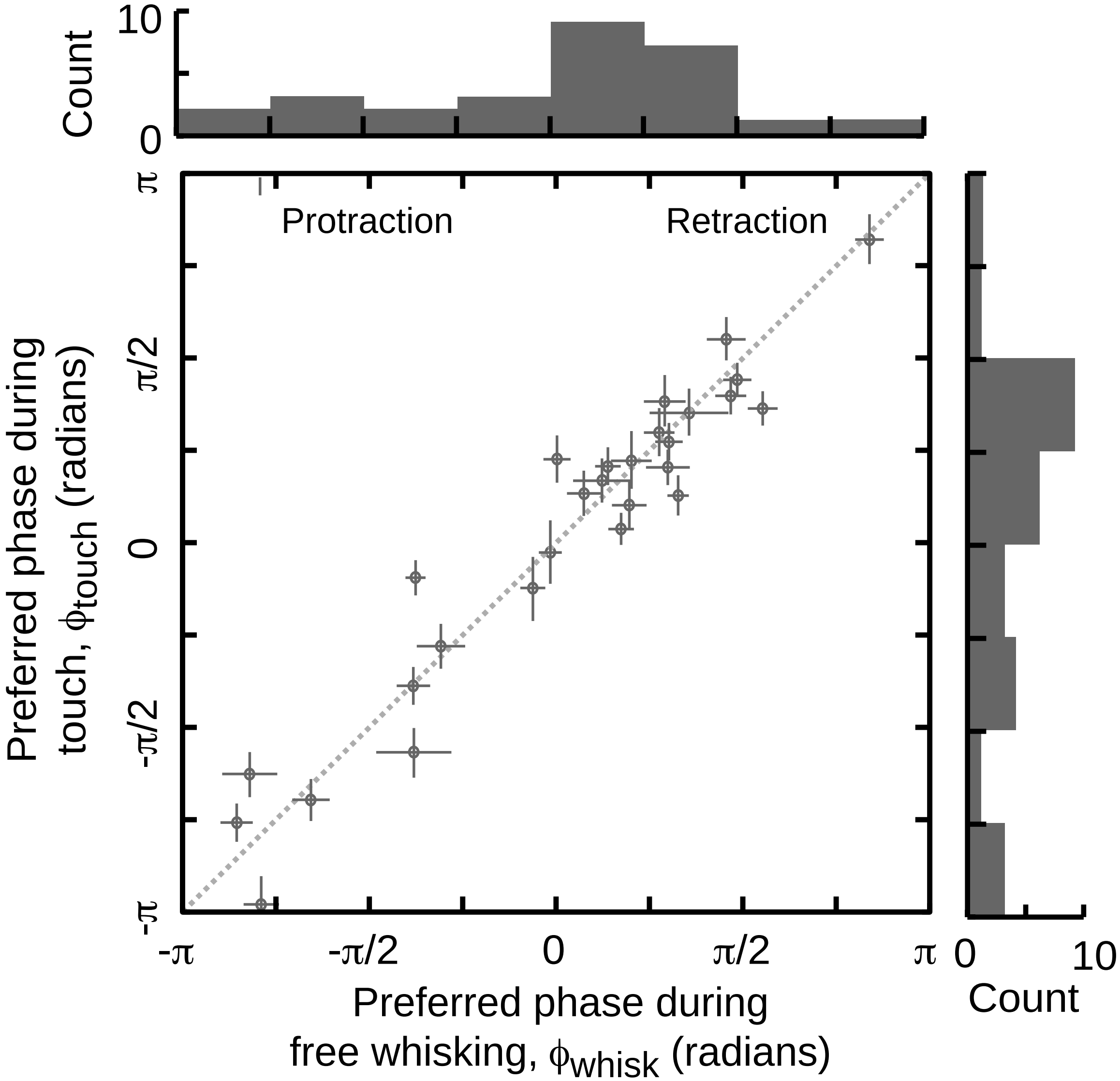


Vibrissa touch response is conditioned on phase in the whisk cycle



Curtis and Kleinfeld (2009)

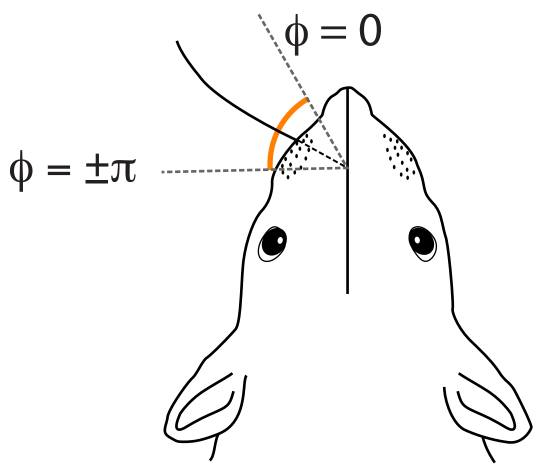
All phases are represented in the coding of touch conditioned on phase in the whisk cycle

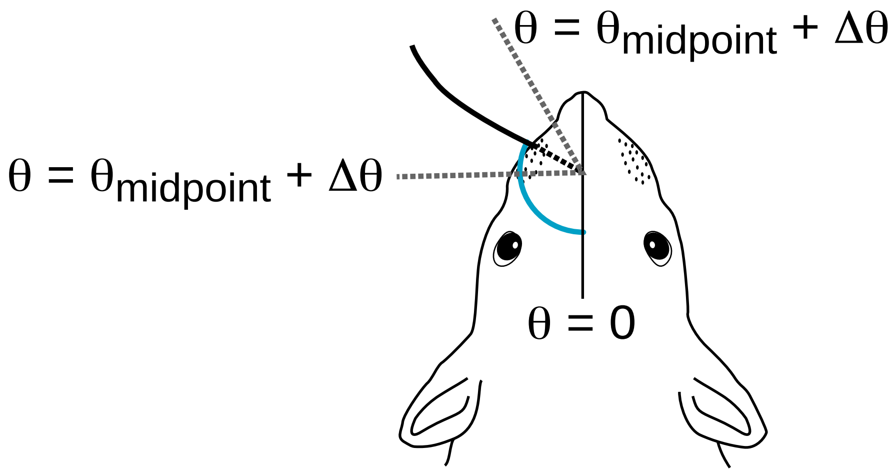


Curtis and Kleinfeld (2009)

Is the vibrissa touch response conditioned solely by phase?

Touch referenced to phase vs. **Touch referenced to position**





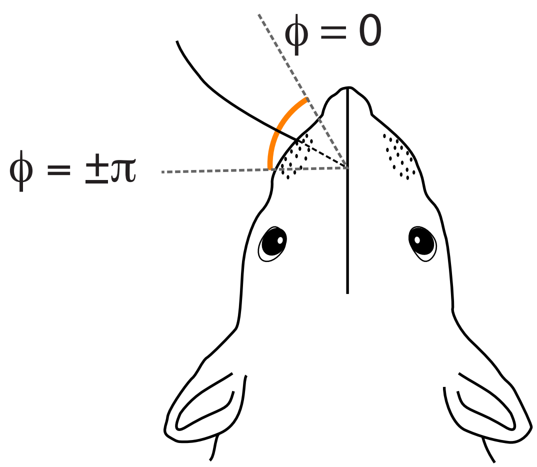
$$\theta(t) = \theta_{midpoint} + \Delta\theta \; cos \; \phi(t)$$

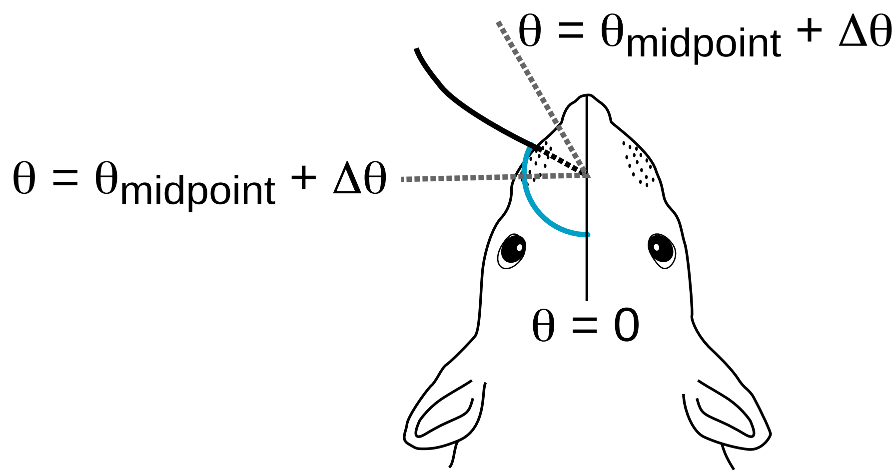
where

$$\phi(t) = 2\pi f_{whisk} t + \phi_{whisk}$$

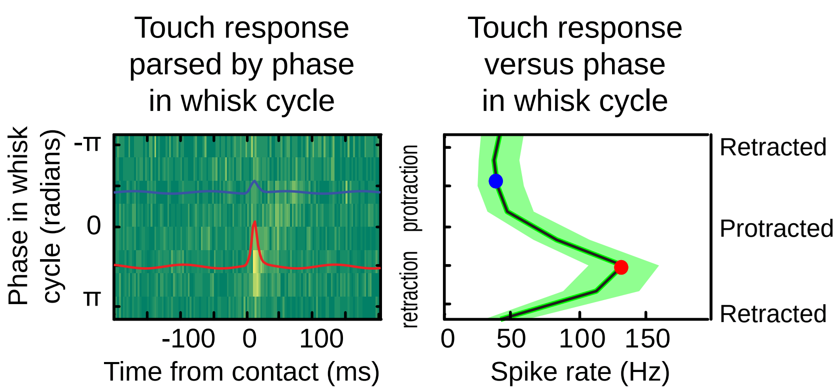
Is the vibrissa touch response conditioned solely by phase?

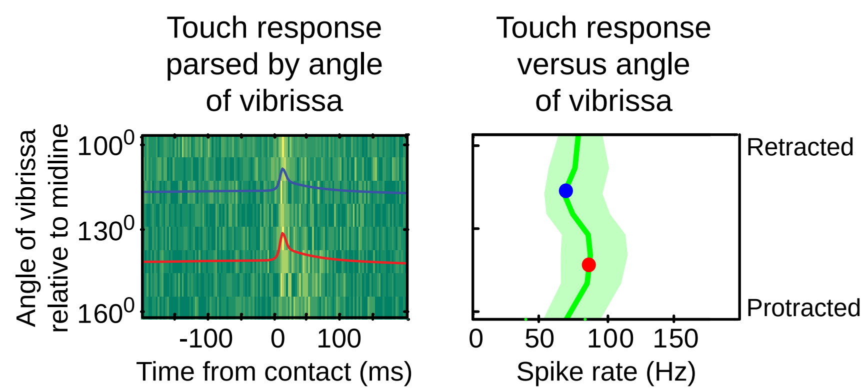
Touch referenced to phase vs. Touch referenced to position





Yes! - tuning depends on phase, ϕ, and not angular position, θ





Curtis and Kleinfeld (2009)

Fairhall's dilemma*: Efficiency versus ambiguity in coding

Position coding of angle

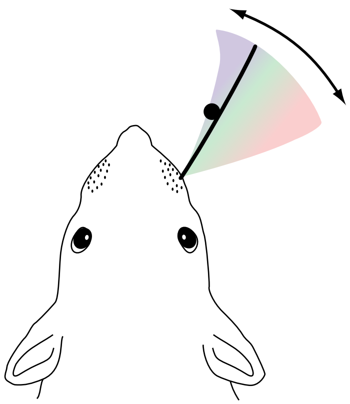
$\theta(t) = \theta_{midpoint} + \Delta\theta \, cos \, \phi(t)$

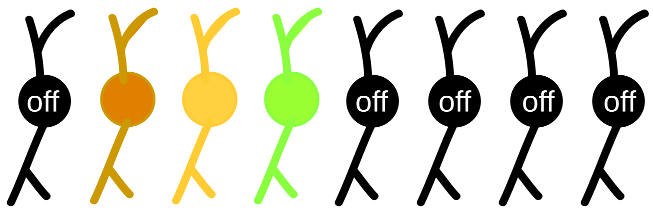
Unambiguous but inefficient

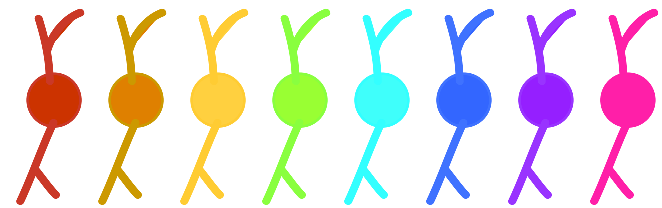
Phase coding: Position normalized by whisking amplitude and offset**

$\phi(t) = [\, 2\pi \, f_{whisk} t + \phi_{touch} \,] \; modulo \; 2\pi$

Efficient but ambiguous

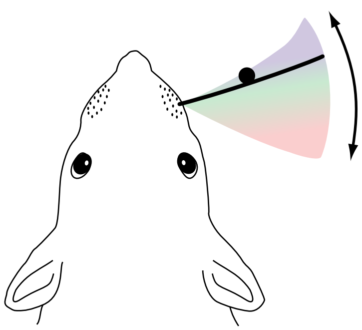


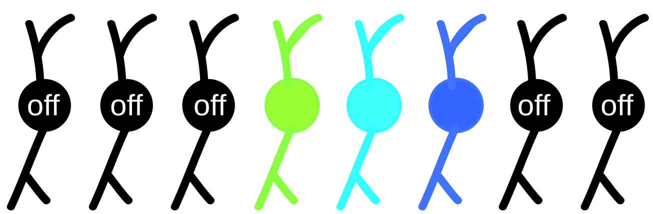


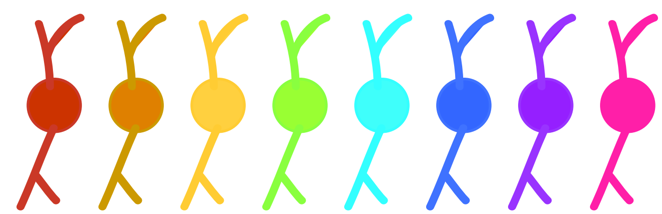


Color labels angle

Color labels phase



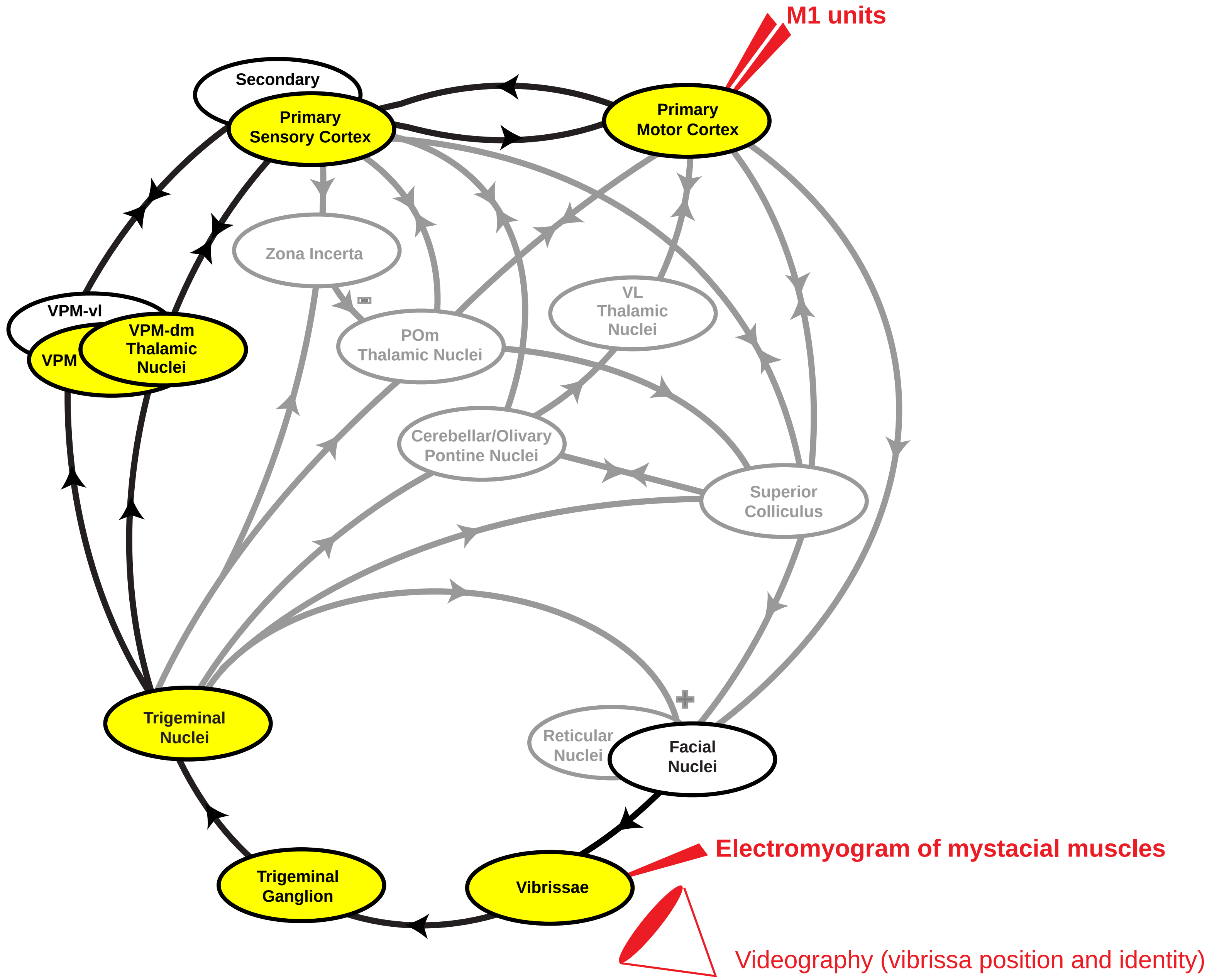




*Fairhall, Lewen, Bialek & de Ruyter Van Steveninck (Nature 2001)

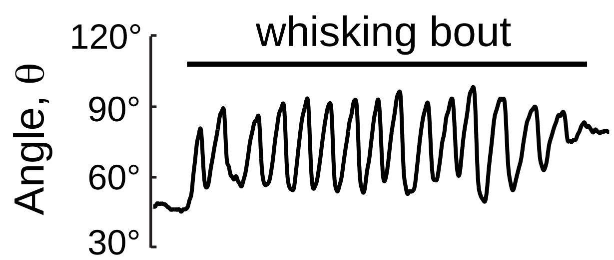
**Slow parameters, $\theta_{midpoint}$ and $\Delta\theta$, appear in M1 cortex (Hill, Curtis & Kleinfeld - in progress)

Spiking in M1 cortex in relation to rhythmic whisking in air

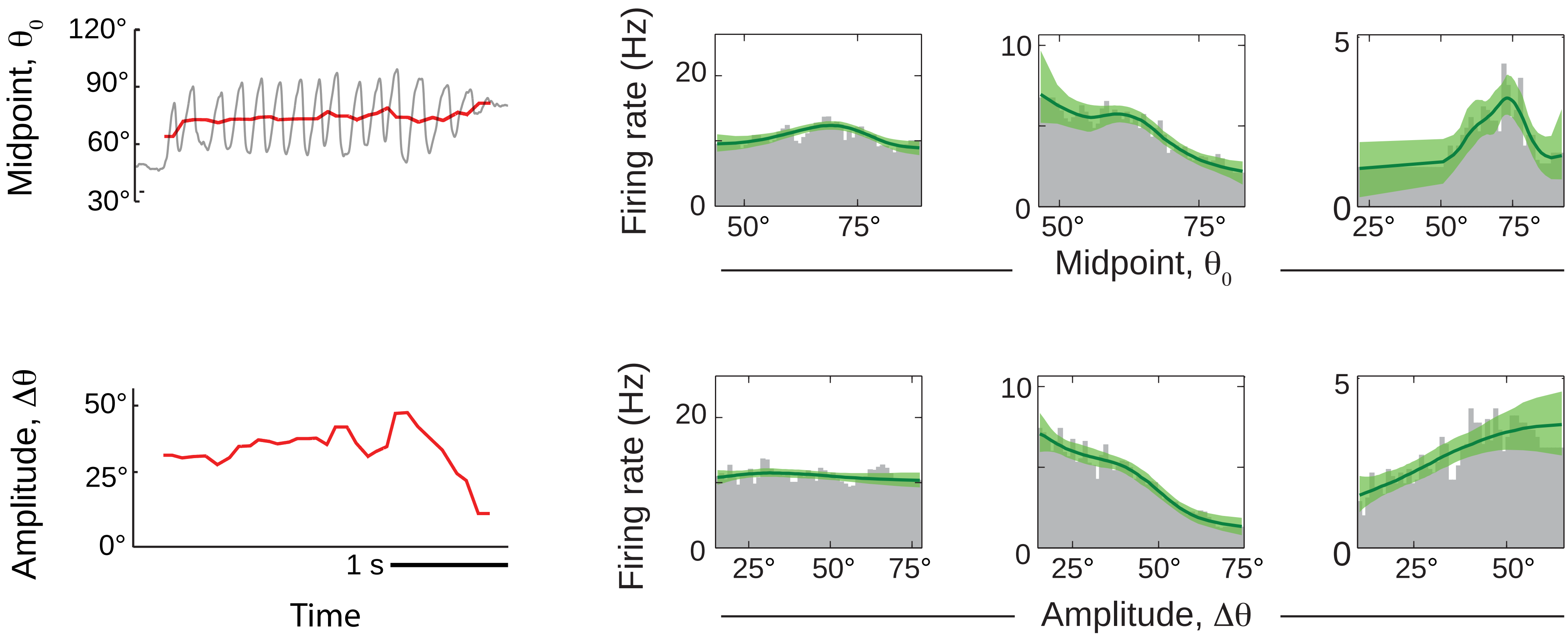


Weak coding of amplitude and midpoint by single units in M1 cortex

Decompose whisking bout



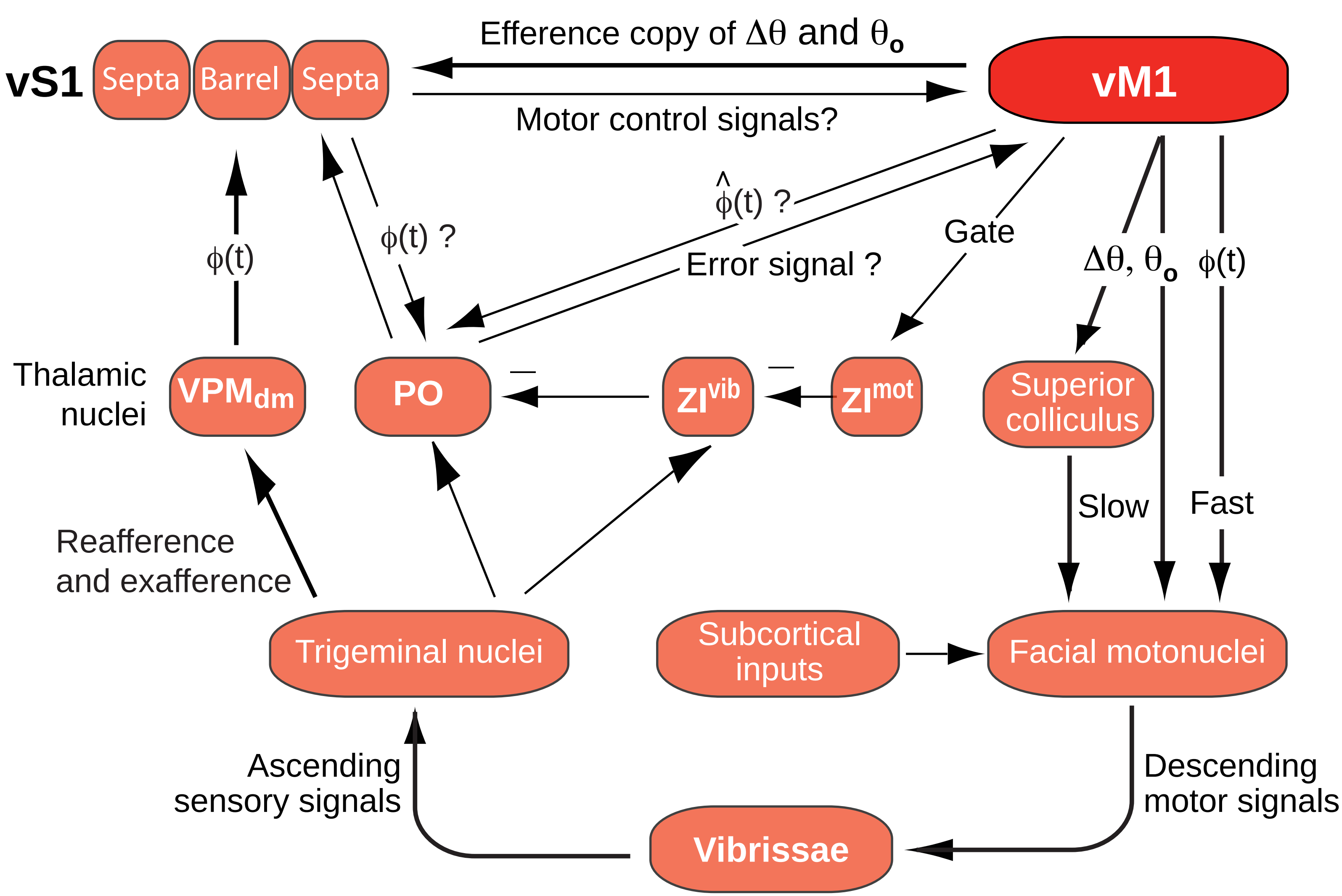
into amplitude, midpoint, and phase



Yet pooling of individual units can lead to sharp positional coding

Hill, Curtis & Kleinfeld (manuscript in preparation)

Confluence of touch and the phase of vibrissa motion in S1
Representation of the range of vibrissa motion in M1



Open issue:How does sensory input modulate whisking?

Two idiosyncratic primers on the CNS:
(1) Feedforward versus cyclic connectivity
(2) The confluence of reafference and exafference in sensation

Thank you!