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)
Classic exafferent sensory maps and pathway

<table>
<thead>
<tr>
<th>dysgranular zone</th>
<th>granular zone</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2/3</td>
</tr>
<tr>
<td>E2  D2  C2  B2  A2</td>
<td>4</td>
</tr>
<tr>
<td>septa</td>
<td>5</td>
</tr>
<tr>
<td>barrel column</td>
<td>6</td>
</tr>
</tbody>
</table>

arc 2

Courtesy of Martin Deschenes
Exafference, reafference, efference, and efference copy as signals in vibrissa system loops

Coding of touch and position

Primary Sensory Cortex

Primary Motor Cortex

Superior Colliculus

Vibrissae

Sensory input / Motor output

Merge of touch and position

Efference copy

Exafference

Peripheral reafference

Touch

Position

VPM-vl

VPM-dm

Thalamic Nuclei

Trigeminal Ganglion

Trigeminal Nuclei

VPM

Zona Incerta

POm

Thalamic Nuclei

Cerebellar/Olivary Pontine Nuclei

Facial Nuclei

Reticular Nuclei

Control of position

Efference
Whisking by rat: Self generated rhythmic motion and touch

Symmetric, exploratory whisking

Foveal whisking

Exploratory whisking

Asymmetric whisking upon contact

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Matthews, Karten, Griesbeck & Kleinfeld - unpublished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, reaafferece, efference, and efference copy as signals in vibrissa system loops

- Sensory input / Motor output
- Coding of touch and position
- Merge of touch and position
- Control of position
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Matthews, Karten & DK (unpublished) following Deschenes, Jacquin and others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

Intact preparation

After ablation of SpV-interpolaris

Furuta, Timofeeva, Nakamura, Okamoto-Furuta, Togo, Kaneko & Deschenes (2008)
Multiple maps across the trigeminus: Interactions from SpVi to PrV

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- **Coding of touch and position:**
  - Trigeminal Nuclei
  - VPM-vl
  - VPM-dm Thalamic Nuclei
  - POm Thalamic Nuclei
  - Zona Incerta
  - Cerebellar/Olivary Pontine Nuclei

- **Sensory input / Motor output:**
  - Facial Nuclei
  - Superior Colliculus
  - Trigeminal Ganglion
  - Vibrissae

- **Exafference, reafference, efference, and efference copy:**
  - Primary Sensory Cortex
  - Primary Motor Cortex
  - Secondary Thalamic Nuclei
  - Reticular Nuclei

- **Merge of touch and position:**
  - Exafference
  - Peripheral reafference

- **Control of position:**
  - Efference copy
  - Efference
Brainstem

L6

VPM

NrT

L4
Frequency dependent shifts in time-to-peak in PO but not VPM thalamus

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**

**Coding of touch and position**

**Sensory input / Motor output**

**Merge of touch and position**

**Control of position**

**Peripheral reafference**

**Efference copy**

- **Trigeminal Nuclei**
- **VPM**
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- **Zona Incerta**
- **POm**
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- **Reticular Nuclei**
- **Superior Colliculus**
- **Vibrissae**
- **Trigeminal Ganglion**
- **Facial Nuclei**
- **Primary Sensory Cortex**
- **Primary Motor Cortex**
- **VL Thalamic Nuclei**
- **Reticular Nuclei**
S1 cortex canonical excitatory connections

input $\rightarrow$ VPM $\rightarrow$ L4 ($\rightarrow$ L2/3) $\rightarrow$ L5 $\rightarrow$ output
input $\rightarrow$ VPM $\rightarrow$ (L4 $\rightarrow$) L6 $\rightarrow$ VPM $\rightarrow$ feedback

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

To neighboring columns

From neighboring columns

To neighboring columns

From thalamus

To other brain areas

To thalamus
Existence proof of reverberation using cultures of cortical neurons
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.

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

O’Connor, Huber & Svoboba (2009)
Evidence for propagation of neuronal activation across cortex

Active touch
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)
- Strong response to passive stimulation

Exploration mode (whisking without contact)
- Gating or suppression yields weak response to passive stimulation

Object detection mode (whisking with contact)
- Strong response to active touch

Ferezou, Bolea & Petersen (2006)
Exafference, reafference, efference, and efference copy as signals in vibrissa system loops

Coding of touch and position

Sensory input / Motor output

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Control of position

Merge of touch and position

Peripheral reafference

Exafference

Efference

Efference copy

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

Cerebellar/Olivary Pontine Nuclei

Reticular Nuclei

Touch stream

Position stream

Exafference

Peripheral reafference

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Exafference

Peripheral reafference
Brainstem slice preparation captures sensorimotor feedback circuitry

Nguyen and Kleinfeld (2005)
Fast, transient, positive feedback in the brainstem vibrissa sensorimotor loop *in vitro*

Nguyen and Kleinfeld (2005)
Fast, transient, positive feedback in the brainstem vibrissa sensorimotor loop in vivo

Nguyen and Kleinfeld (2005)
Rats can detect contact to a single vibrissa (Hutson and Masterson 1986)
Vibrissa contact leads to transient increase in EMG during contact task
(force ~ EMG)
Facial Motoneurons: Arbitrators (~40 inputs) or power transistors?
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Emerging techniques in neuroscience
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

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.

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

- **Sensory input / Motor output**
- **Coding of touch and position**
- **Merge of touch and position**
- **Control of position**

**Nodes and Connections**
- Primary Sensory Cortex
- Primary Motor Cortex
- Secondary Thalamic Nuclei
- Zona Incerta
- VL Thalamic Nuclei
- POm Thalamic Nuclei
- Cerebellar/Olivary Pontine Nuclei
- Superior Colliculus
- Facial Nuclei
- Reticular Nuclei
- VPM-dm Thalamic Nuclei
- VPM-vl VPM

**Pathways**
- Exafference
- Peripheral reafference
- Efference copy

**Streams**
- Touch stream
- Position stream
- Exafference
- Reafference
- Efference copy
Evidence for exafferent (touch) versus reafferent (position) channels

--- Exafferent pathway ---

PrV (single vibrissa response) → VPM (VPM "lemniscal" pathway) → nRT → S1 (barrels) → Cortex

--- Reafferent Pathway ---

PrV (multiple vibrissae response) → VPMdm (VPMdm pathway) → nRT → M1 → Cortex

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?

Interacting phase & touch signals

Non-interacting phase & touch signals

versus
Vibrissa touch response is conditioned on phase in the whisk cycle

Trial averaged free whisking response

Trial averaged touch response

Touch response versus phase in whisk cycle

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

\[ \theta(t) = \theta_{\text{midpoint}} + \Delta \theta \cos \phi(t) \]

where

\[ \phi(t) = 2\pi f_{\text{whisk}} t + \phi_{\text{whisk}} \]
Is the vibrissa touch response conditioned solely by phase?

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

Yes! - tuning depends on phase, $\phi$, and not angular position, $\theta$
Fairhall’s dilemma*: Efficiency versus ambiguity in coding

**Position coding of angle**
\[ \theta(t) = \theta_{\text{midpoint}} + \Delta\theta \cos \phi(t) \]

*Unambiguous but inefficient*

**Phase coding: Position normalized by whisking amplitude and offset**
\[ \phi(t) = \left[ 2\pi f_{\text{whisk}} t + \phi_{\text{touch}} \right] \mod 2\pi \]

*Efficient but ambiguous*

**Color labels angle**

**Color labels phase**

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

**Slow parameters, \( \theta_{\text{midpoint}} \) and \( \Delta\theta \), appear in M1 cortex (Hill, Curtis & Kleinfeld - in progress)*
Spiking in M1 cortex in relation to rhythmic whisking in air

Electromyogram of mystacial muscles

Videography (vibrissa position and identity)
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?
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Thank you!