Active sensing

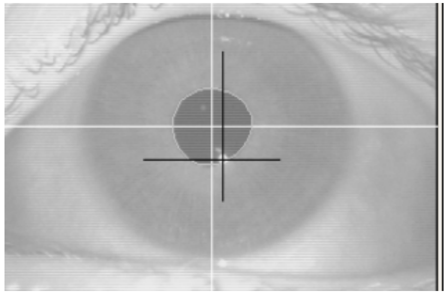
Ehud Ahissar

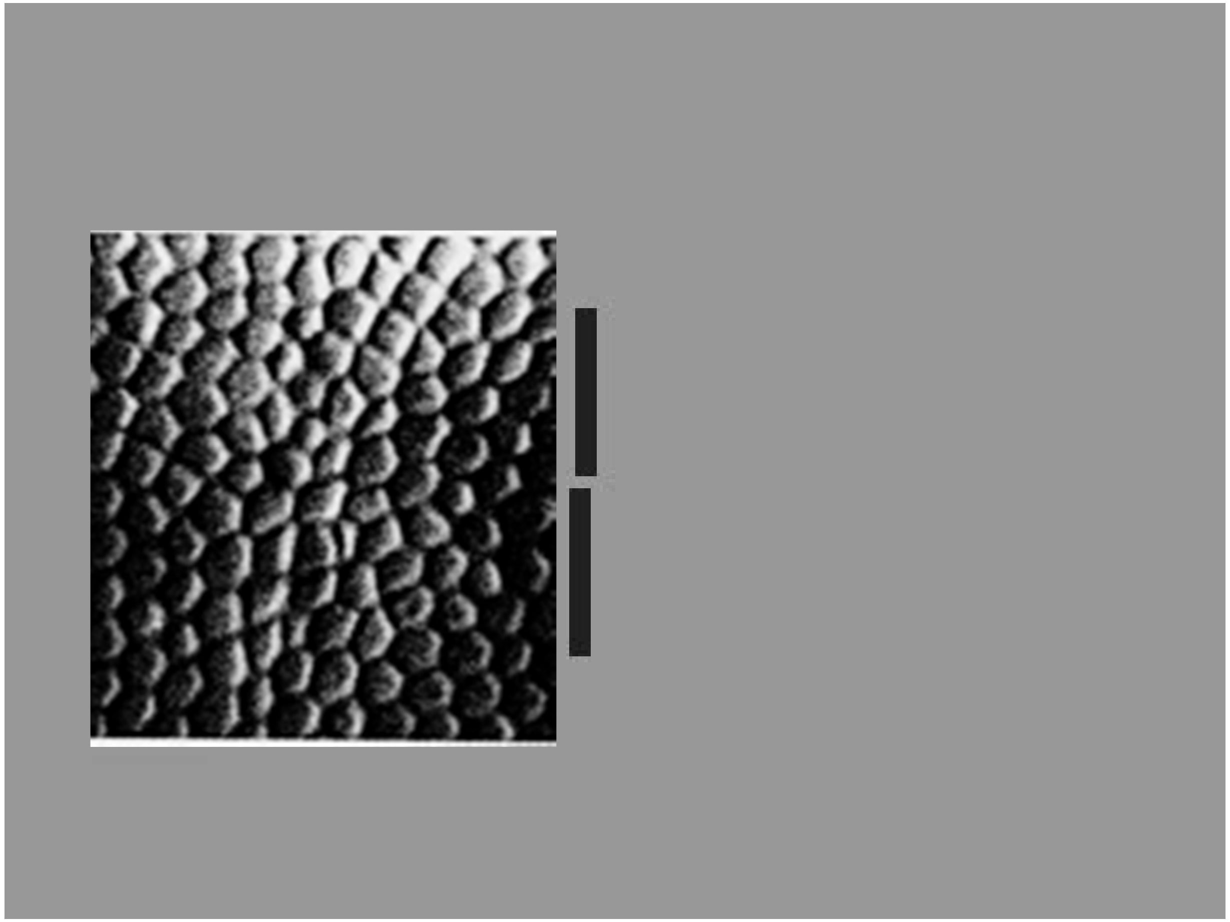
Active sensing

- Passive vs active touch
- Comparison across senses
- Basic coding principles

- Perceptual loops
- Sensation-targeted motor control
- Proprioception
- Controlled variables
- Active vibrissal touch: encoding and recoding

Eye movements during fixation

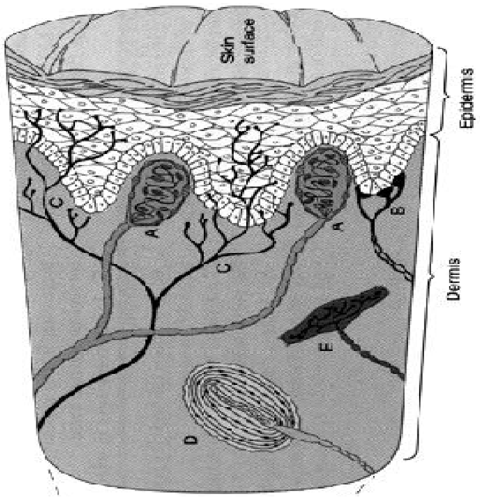




sensory encoding: *What receptors tell the brain*

Sensory organs consist of **receptor arrays**:

somatosensation **audition** **vision**

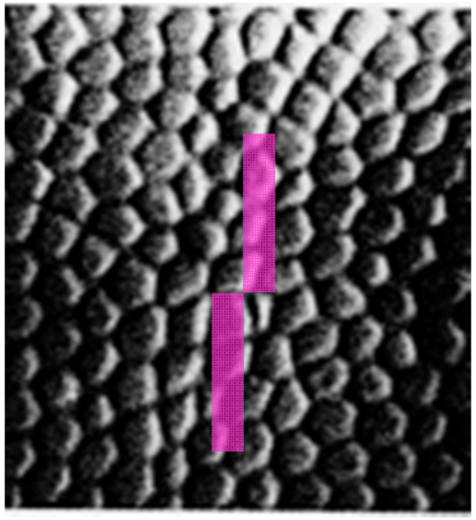


~200 µm

Finger pad

10 µm

cochlea



10 µm

retina

Spatial organization => Spatial coding (“*which* receptors are activated”)

Movements => Temporal coding (“*when* are receptors activated”)

Temporal coding in action

Coding space by time

1. Spatial frequency
2. Spatial phase

Touch: Temporal encoding of spatial features

Darian-Smith & Oke,
J Physiol, 1980

anesth. monkey,
MR fibers

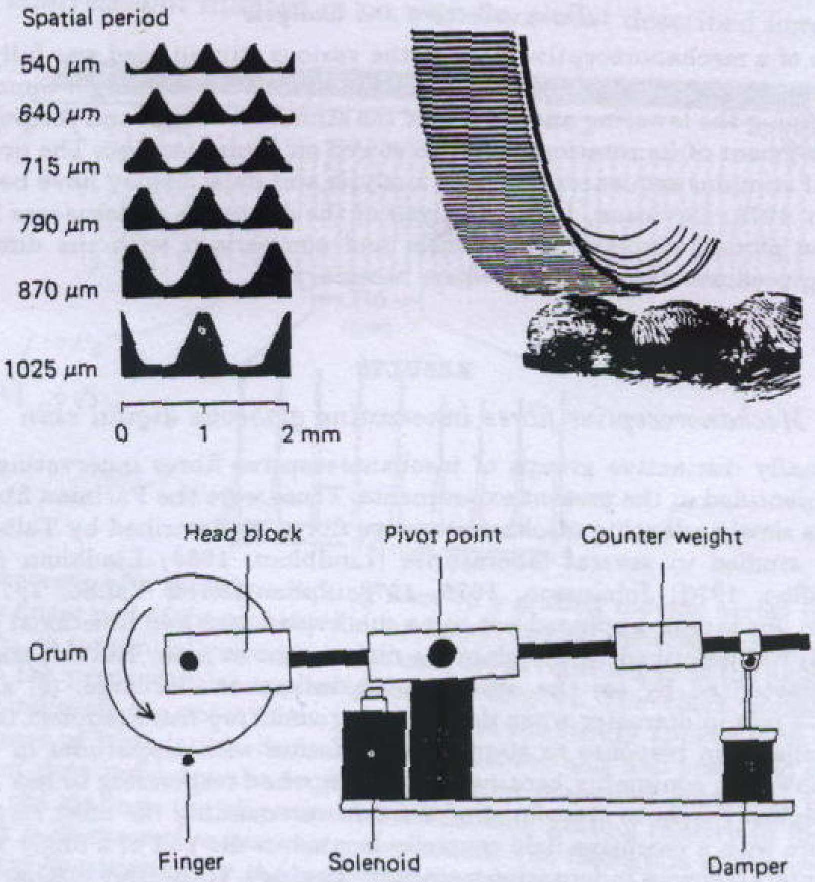


Fig. 1. Details of the stimulator used for presenting gratings to finger pad skin. The grating was mounted on a rotating drum 100 mm in diameter (upper right). The profile of each of the six gratings used is shown (upper left), along with its spatial period. The lower diagram illustrates the mechanisms for controlling the period of contact of the grating moving across the finger pad skin. *The drum was mounted at one end of a* counter-poised *lever and rotated at a preset velocity.* This drum was positioned *1 mm above the skin surface:* an actuated solenoid held the drum off the skin except for the required contact period. The perpendicular force at which the moving grating was applied to the skin during this contact period was determined by the counter-weight: this could be set in the range 20–100 g wt.

RA fiber

Vel - constant

f = SF * V

dt = dx / V

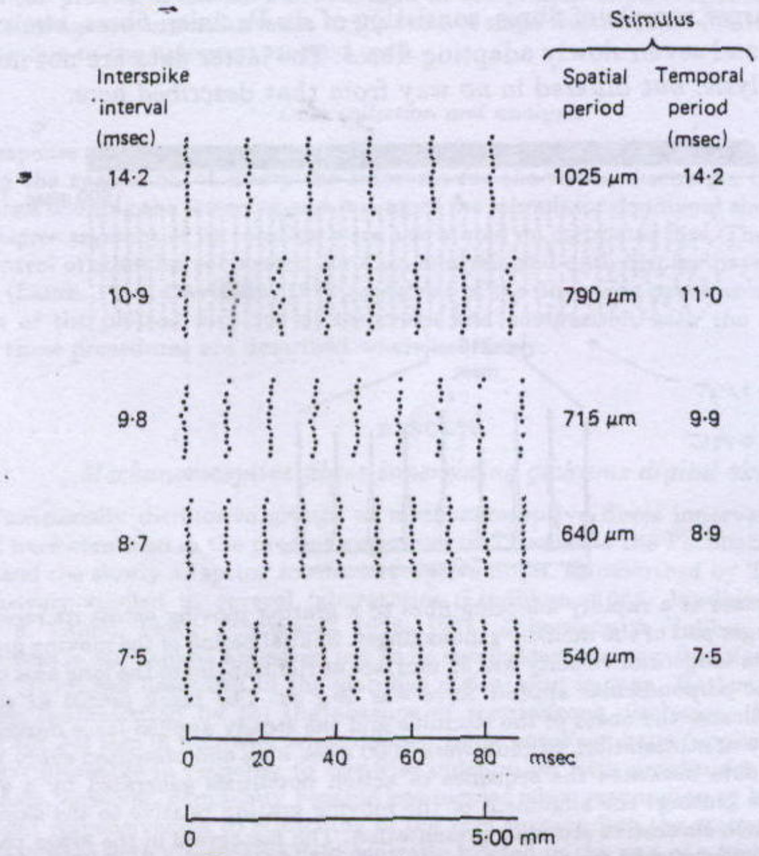


Fig. 3. Responses of a rapidly adapting fibre to different gratings moving across its receptive field on the ridged glabrous skin of terminal phalanx of thumb. The tangential velocity was 72 mm/sec in a direction at right angles to the long axis of the finger and the applied force was 60 g wt. for all records; successive stimuli were presented every 3 sec. Each row of dots indicates the occurrence of action potentials in response to a single passage of the grating across the skin; twelve successive responses are illustrated for each grating; spatial periods of these gratings are indicated on the right. The 80 msec response segment illustrated had its onset at approximately 500 msec after the beginning of stimulation, as is shown in Fig. 2. With these records there was both precise alignment of the time of occurrence of action potentials after the onset of stimulation, and also alignment relative to the instantaneous position of the grating on the skin. The stimulus spatial and temporal periods are indicated for each data block on right side of Figure. The mean interspike interval is to the left of each data block.

SA fiber

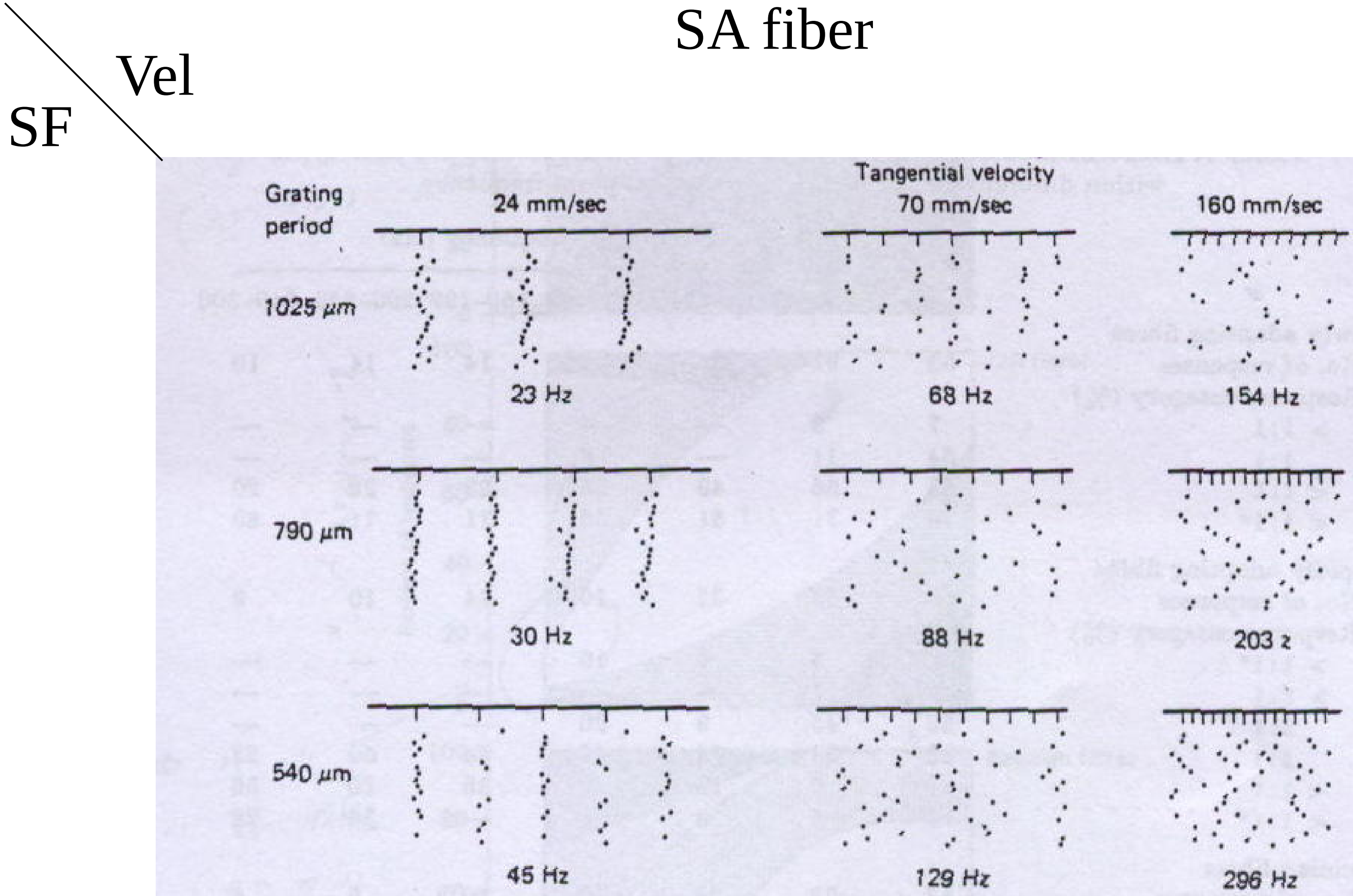


Fig. 6. Responses of a slowly adapting fibre to gratings moving across its receptive field on the finger pad of the middle finger. *The format of display of responses to* three gratings moving at three different velocities across the skin is similar to that of Figs. 4 and 5; there was, however, a small difference in the velocities used (24, 70 and 160 mm/sec) and hence a change in the stimulus temporal frequencies generated by the moving surfaces. A phase-locked discharge reflecting the stimulus temporal frequency is readily detected in the display in the range 23–68 Hz, but not at higher stimulus temporal frequencies.

RA fiber

Vel

SF

V1 V2 V3

G1

G2

G3

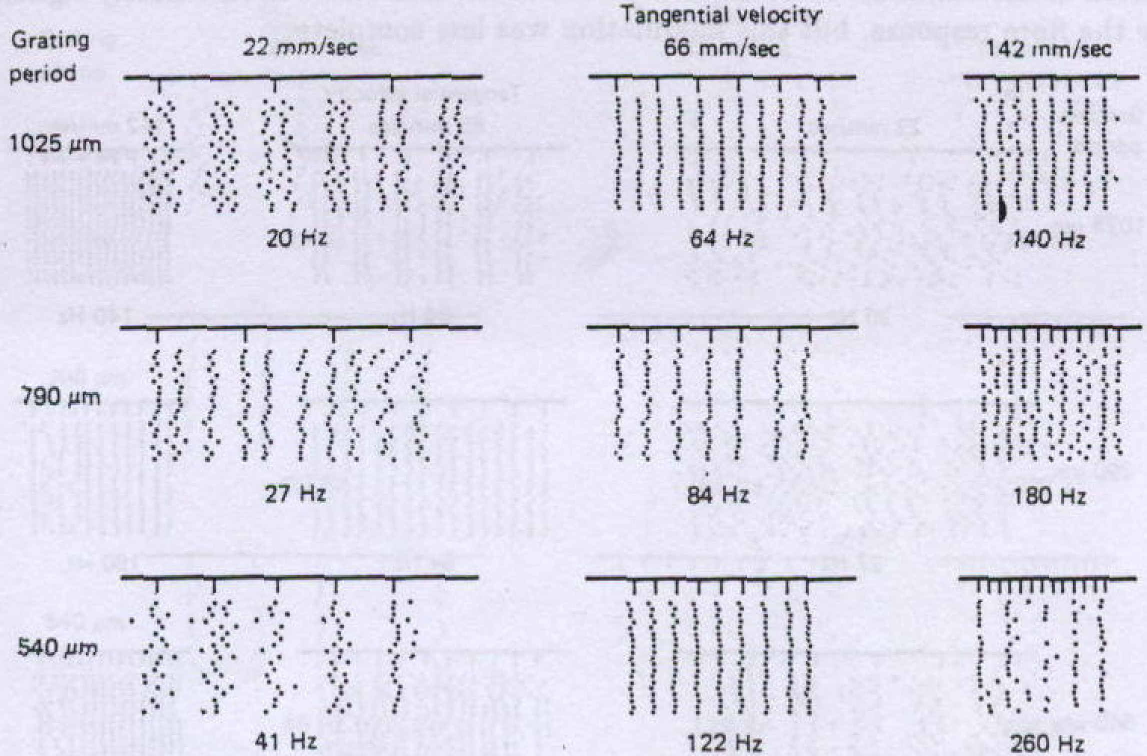


Fig. 4. Responses of a rapidly adapting fibre to three different gratings (spatial period of 1025, 790 and 540 μm) moving across the receptive field at three different velocities (22, 66 and 142 mm/sec). The fibre's receptive field was on the finger pad of the index finger. The radial force was 60 g wt. and contact area was approximately 5 × 5 mm. Each response block is a segment of the response beginning approximately 500 msec after the onset of stimulation: other response and stimulus measures were as indicated in Fig. 3. The stimulus temporal frequency is indicated by the vertical bars above each response block, and its numerical value is stated below the block. The response frequency accurately reflected the stimulus frequency in the range 64–140 Hz. At frequencies below 64 Hz the stimulus temporal frequency was represented in the modulation of discharge but not in the mean discharge frequency; at stimulus temporal *frequencies above* 140 Hz, although the response was phase-locked to the stimulus, the fibre did not respond to each successive cycle of the stimulus and hence mean *discharge frequency did not equal the stimulus temporal frequency.*

SF Vel

PC fiber

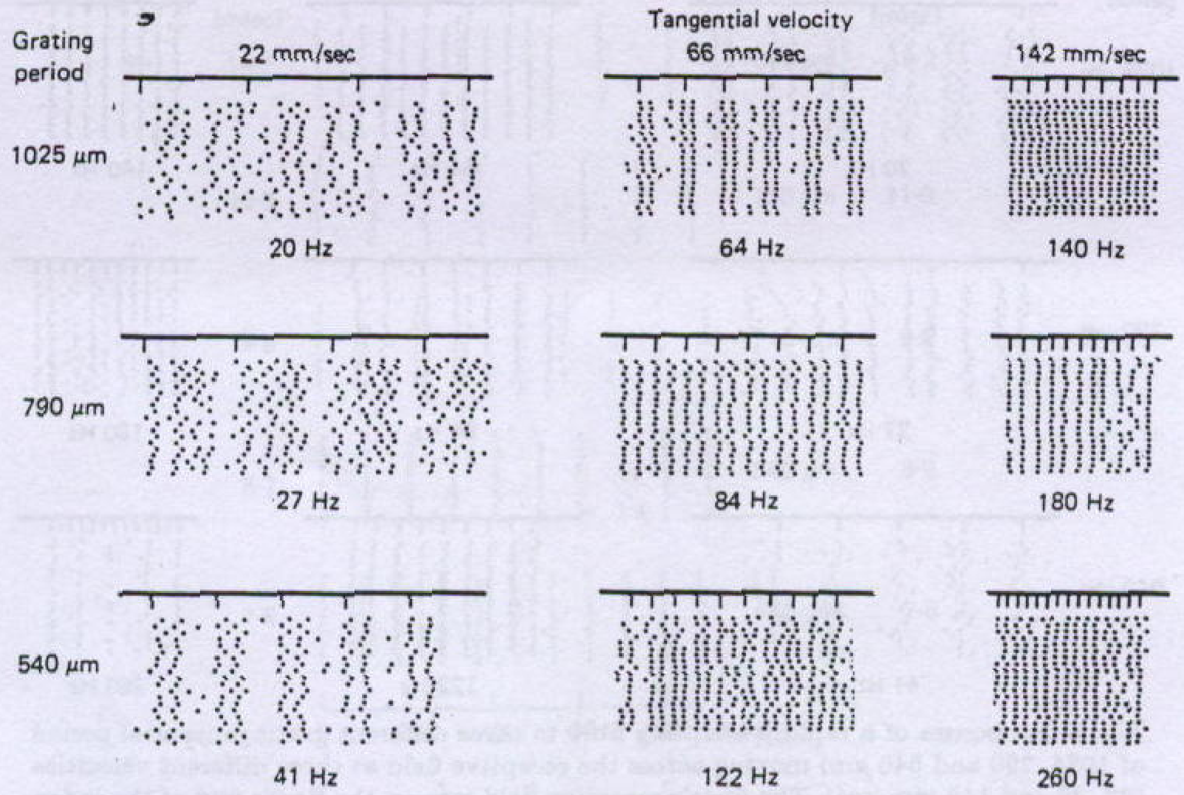


Fig. 5. Responses of a Pacinian fibre to gratings moving across part of its receptive field on the terminal pad of the index finger. The same combination of surfaces and velocities were used as in Fig. 4, and the display format is the same as in that Figure. Except with the lowest stimulus temporal frequencies (upper left corner) the fibre's response was modulated with a cycle period matching the temporal period of the stimulus. However only with stimulus temporal frequencies of 180 Hz or higher did the interspike interval match the stimulus temporal period (right column of the response blocks). In the stimulus temporal frequency range 64–140 Hz the fibre usually fired in phase twice per stimulus cycle, and at lower frequencies up to 5–7 spikes occurred within each stimulus temporal cycle.

Coding ranges

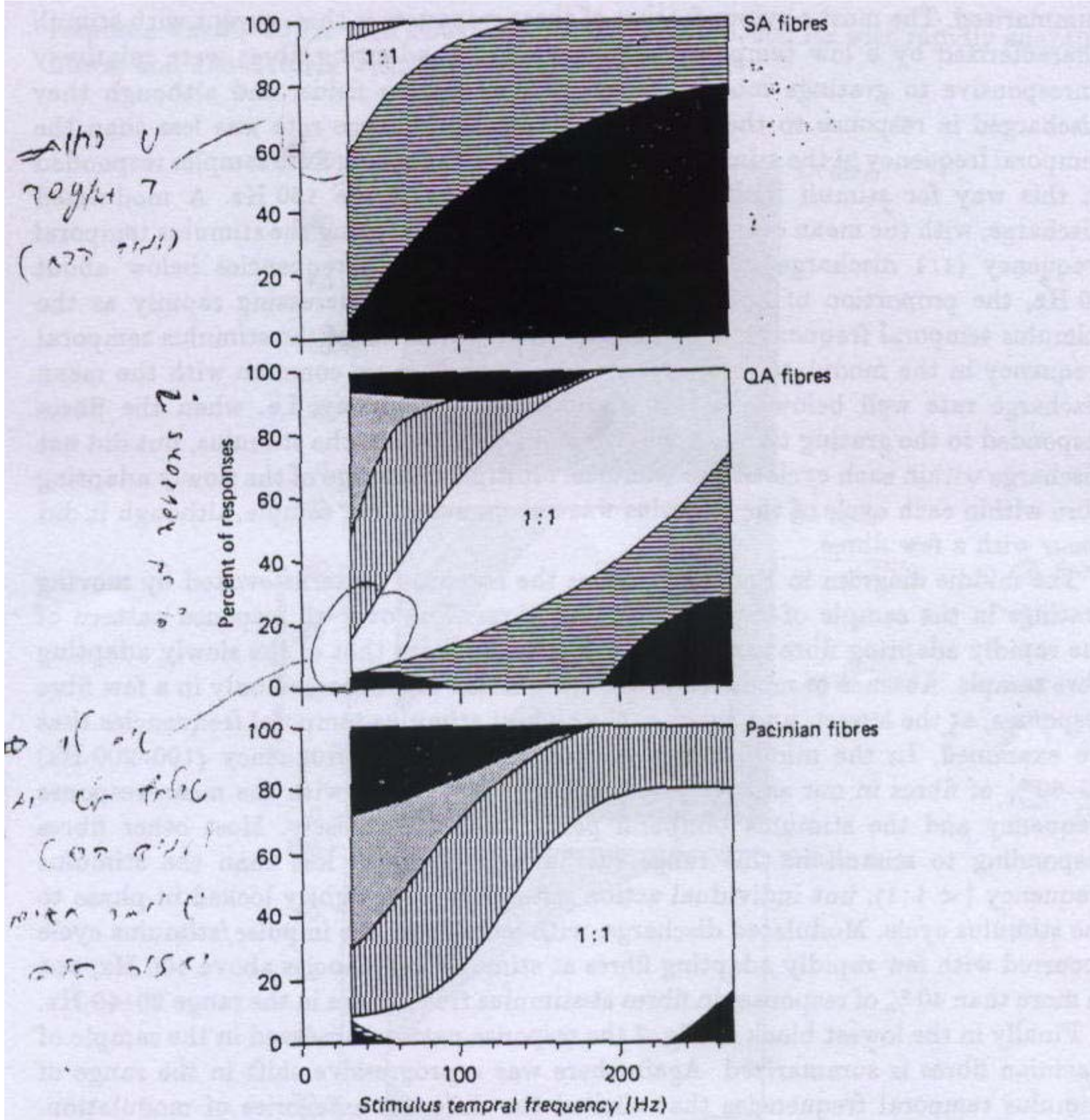
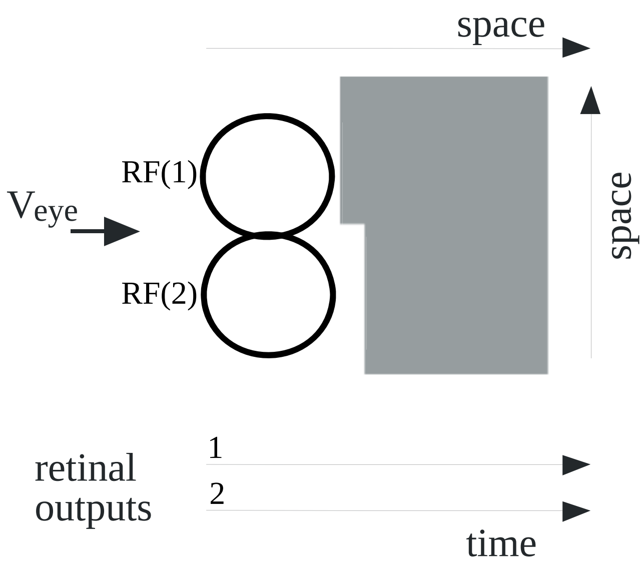


Fig. 7. Relationship of response modulation pattern to the stimulus temporal frequency

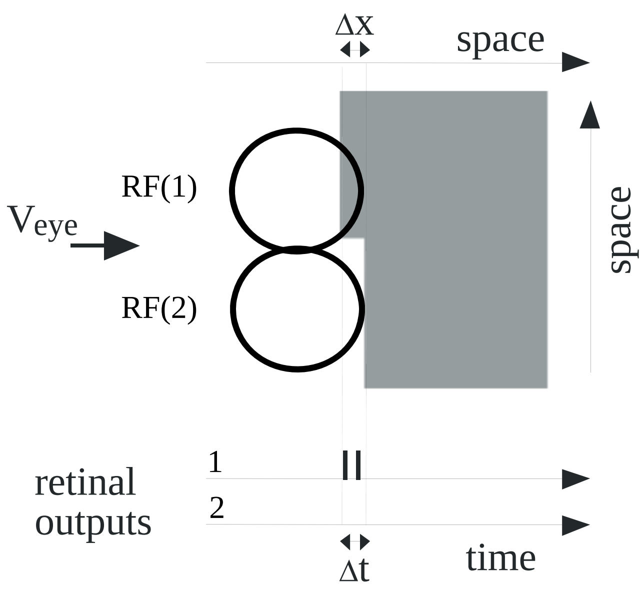
Coding space by time

1. Spatial frequency
2. Spatial phase

Vision: Temporal encoding due to eye movement



Vision: Temporal encoding due to eye movement



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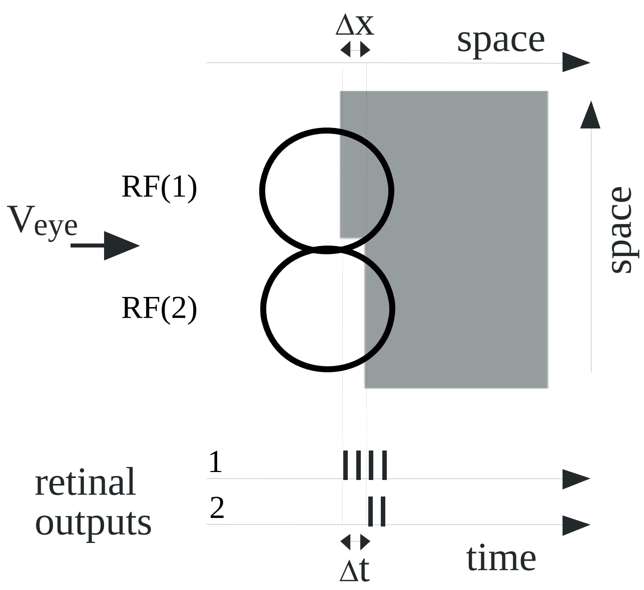
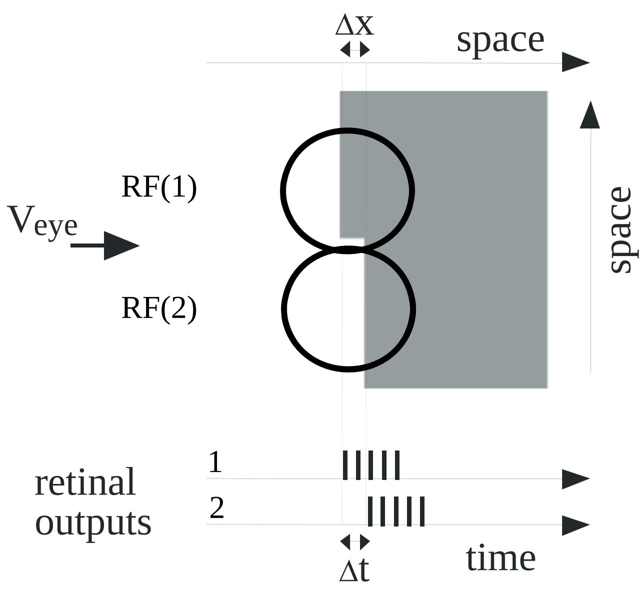
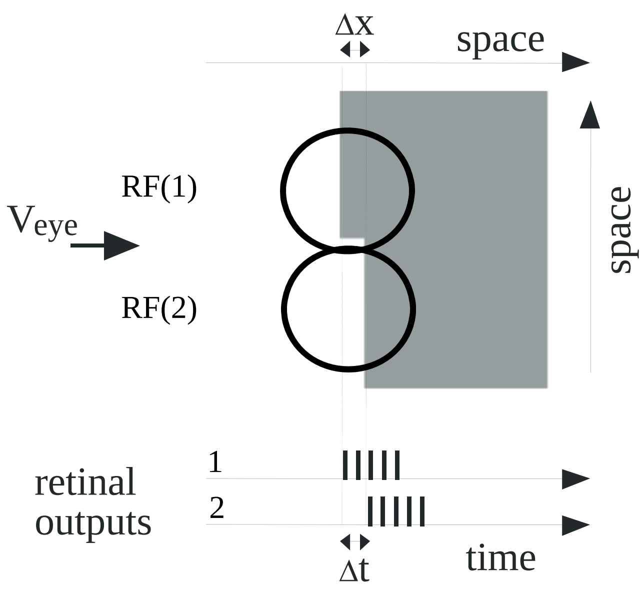


Vision: Temporal encoding due to eye movement



Vision: Temporal encoding due to eye movement



Spatial vs temporal coding

Spatial	Temporal
faster	
	better resolution

- scanning allows sensing in between receptors

Passive vs Active sensing

of stationary objects

	Passive	**Active**
threshold	*low*	*high*
accuracy	*low*	*high*
Systems involved	*sensory*	*Sensory + motor*
coding	*spatial*	*Spatial + temporal*
Processing speed	*fast*	*slow*

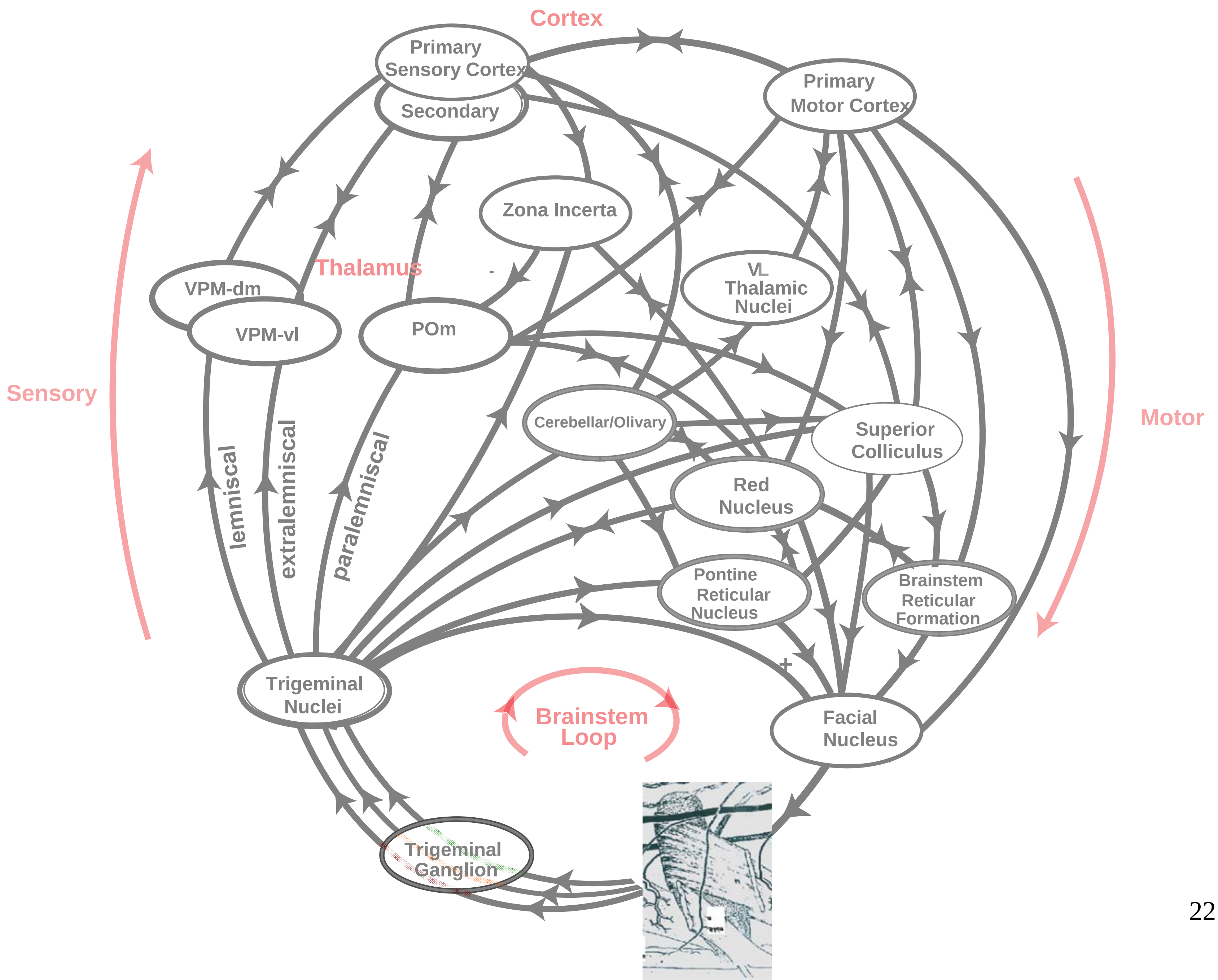
Used in	*detection*	*Exploration* *Localization* *Identification* *…*

Central processing of touch

where touch begins?

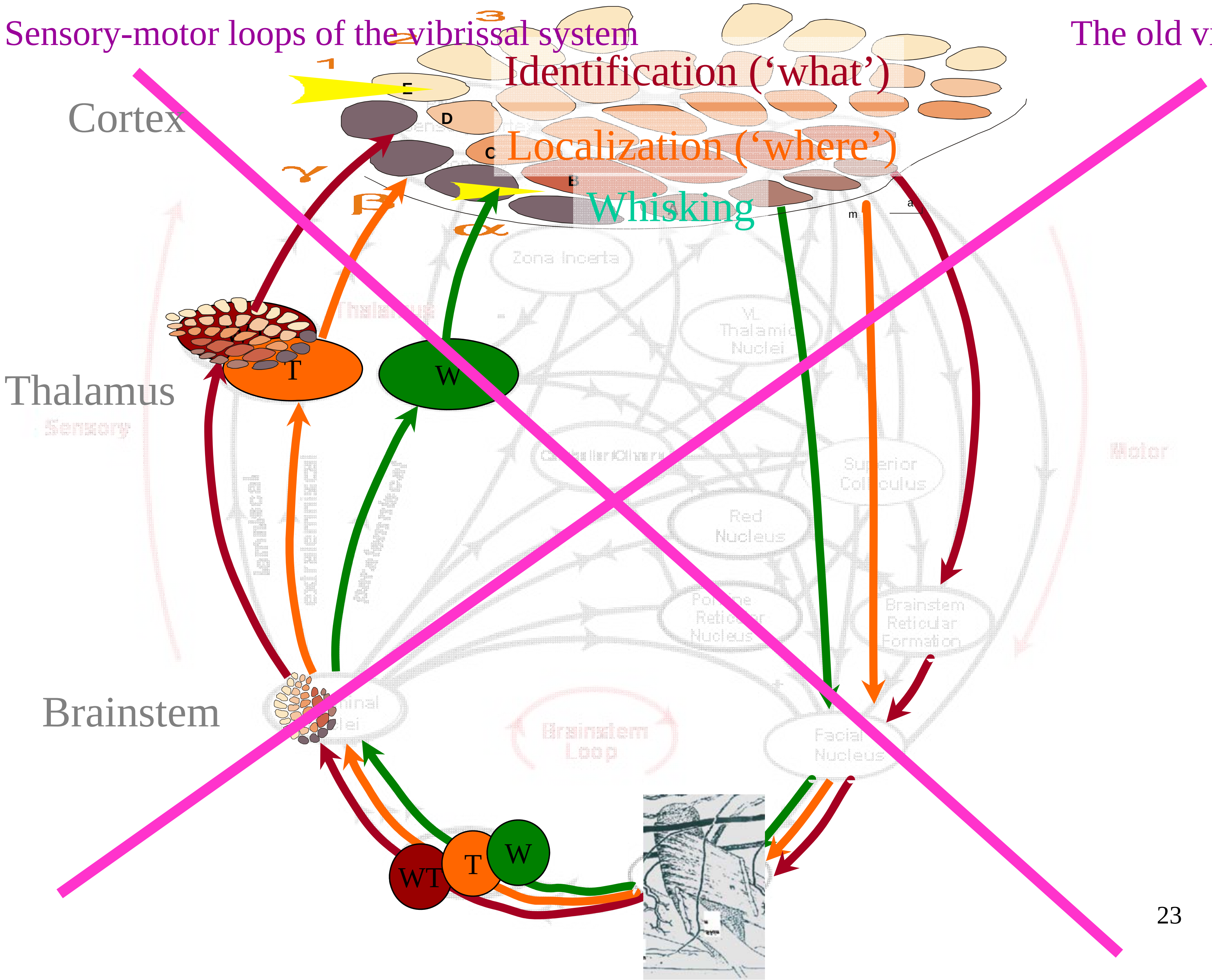
- at the receptors?
- with sensor movement?
- in high brain centers?

Sensory-motor loops of the vibrissal system

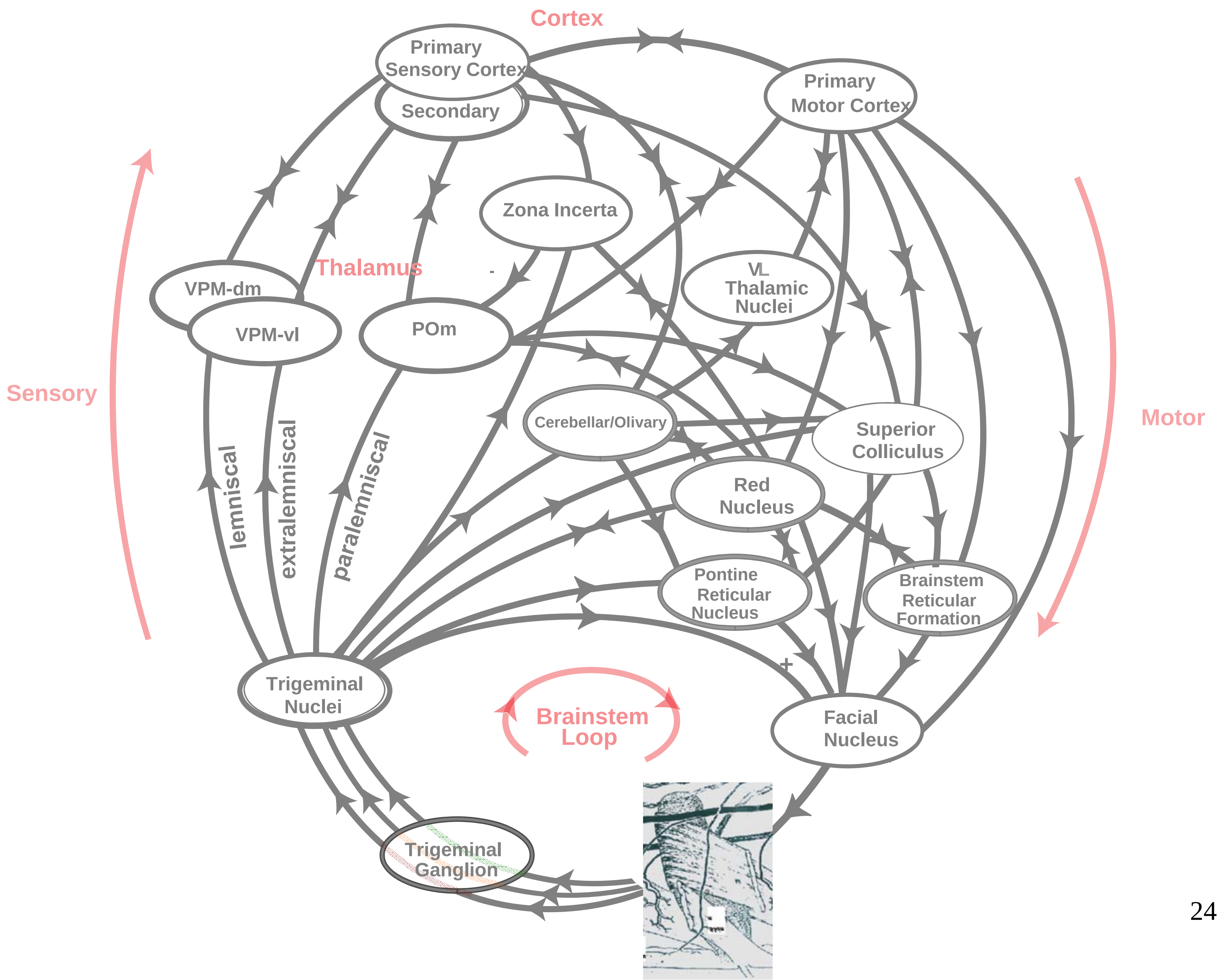


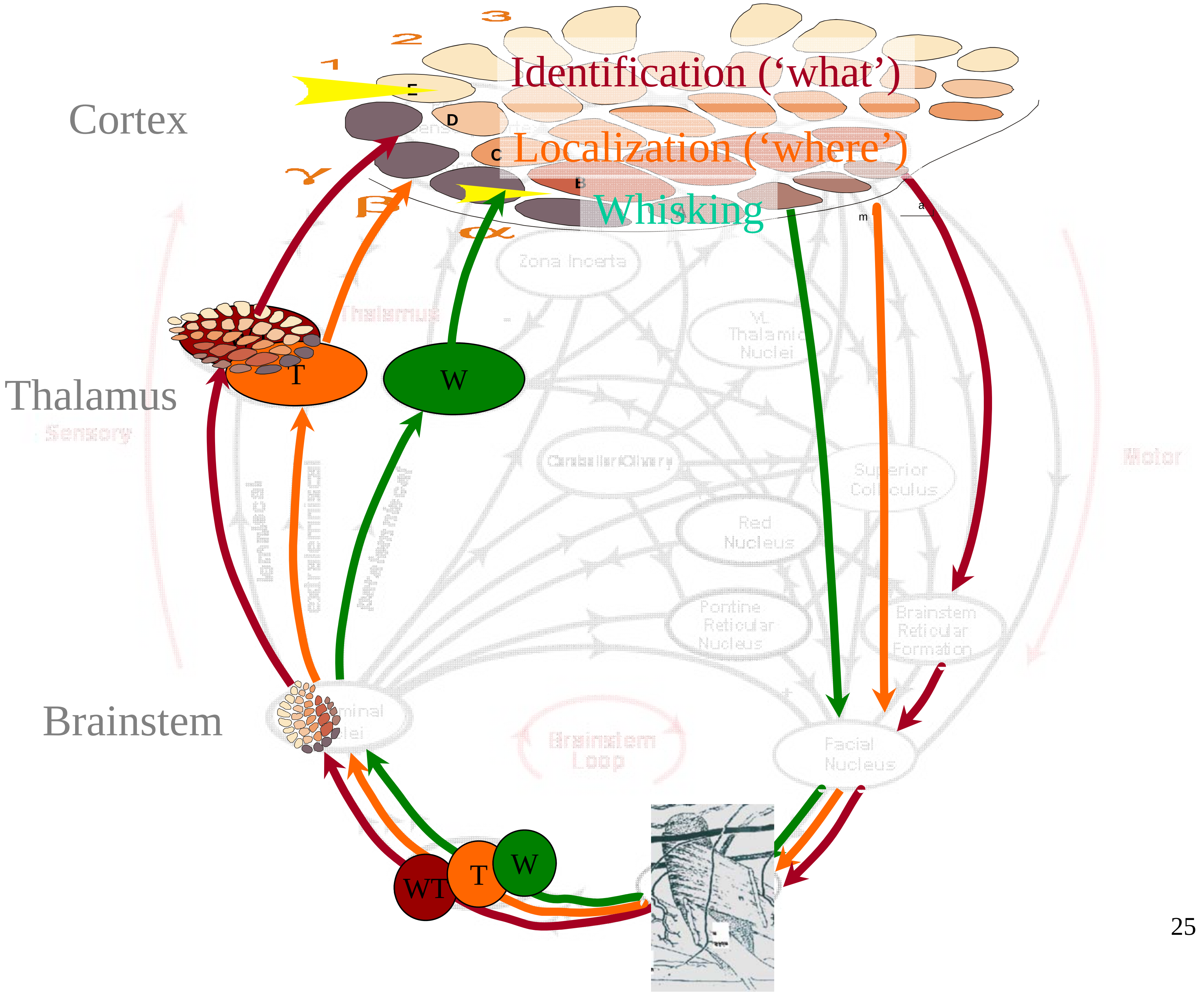
Sensory-motor loops of the vibrissal system

The old view

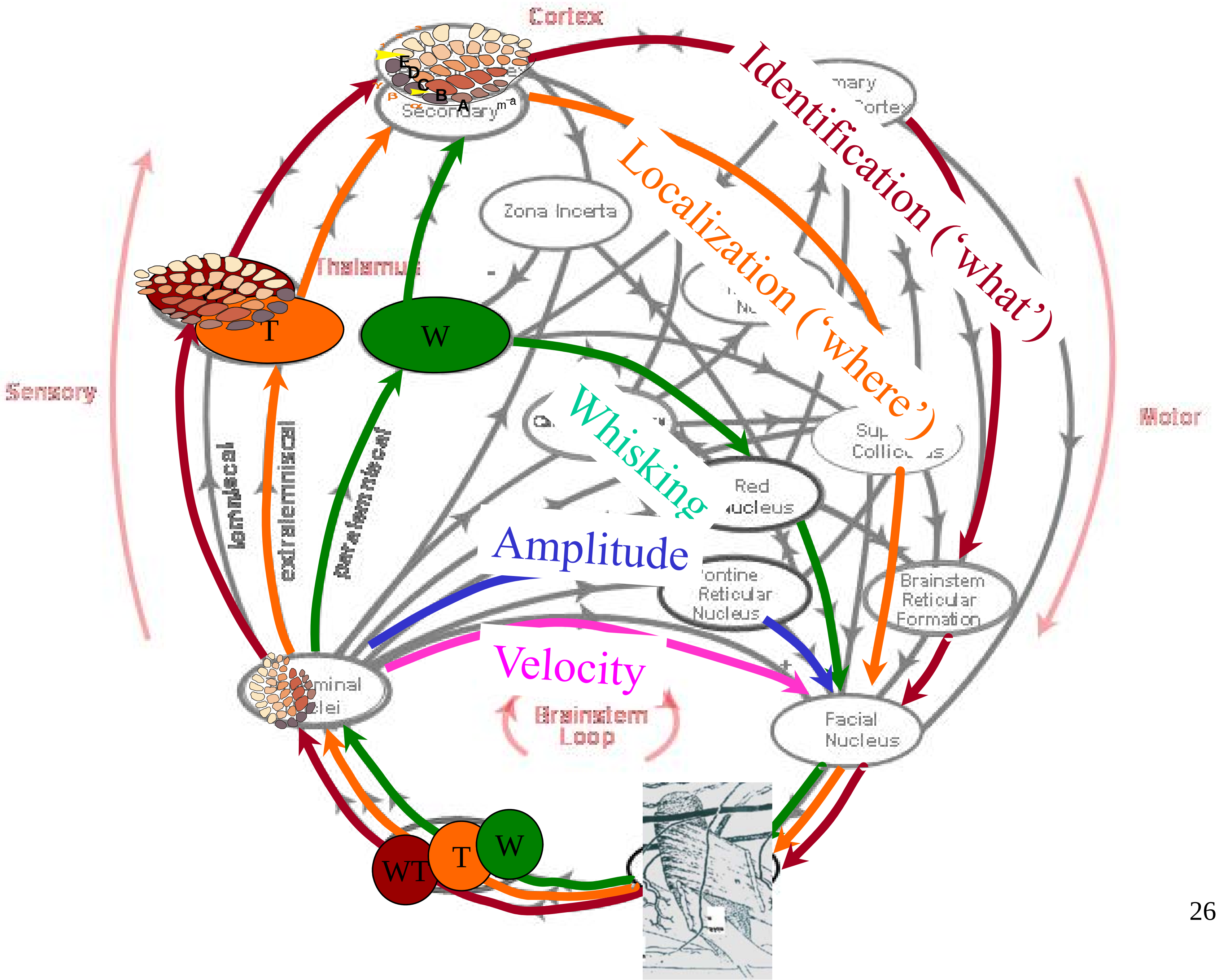


Sensory-motor loops of the vibrissal system




Cortex
Identification ('what')
Localization ('where')
Whisking
Thalamus
T
W
Brainstem
WT
T
W
Zona Incerta
VL Thalamic Nuclei
Superior Colliculus
Red Nucleus
Pontine Reticular Nucleus
Brainstem Reticular Formation
Facial Nucleus
Brainstem Loop
Motor
Sensory

Sensory-motor loops of the vibrissal system



Central processing of touch

where touch begins?

- ~~at the receptors?~~
- with sensor movement?
- in high brain centers?

Active touch does not begin at the receptors

Motor control

- Closed loops
- Proprioceptive feedback
- Reflexes – tool for probing loop function
- Controlled variables – motor vs sensory

Motor control

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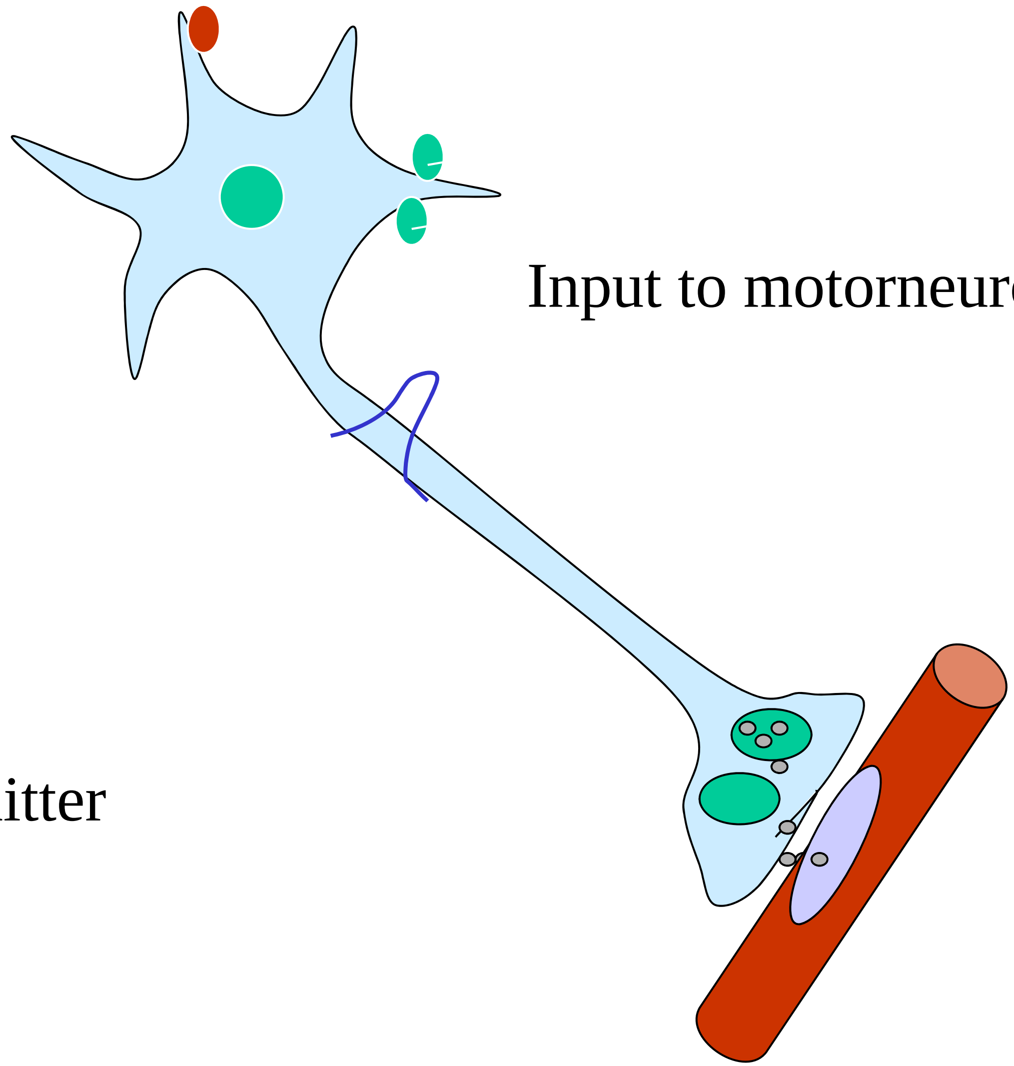
Excitation Contraction Coupling

Phase 1:
Firing of Motor Neuron

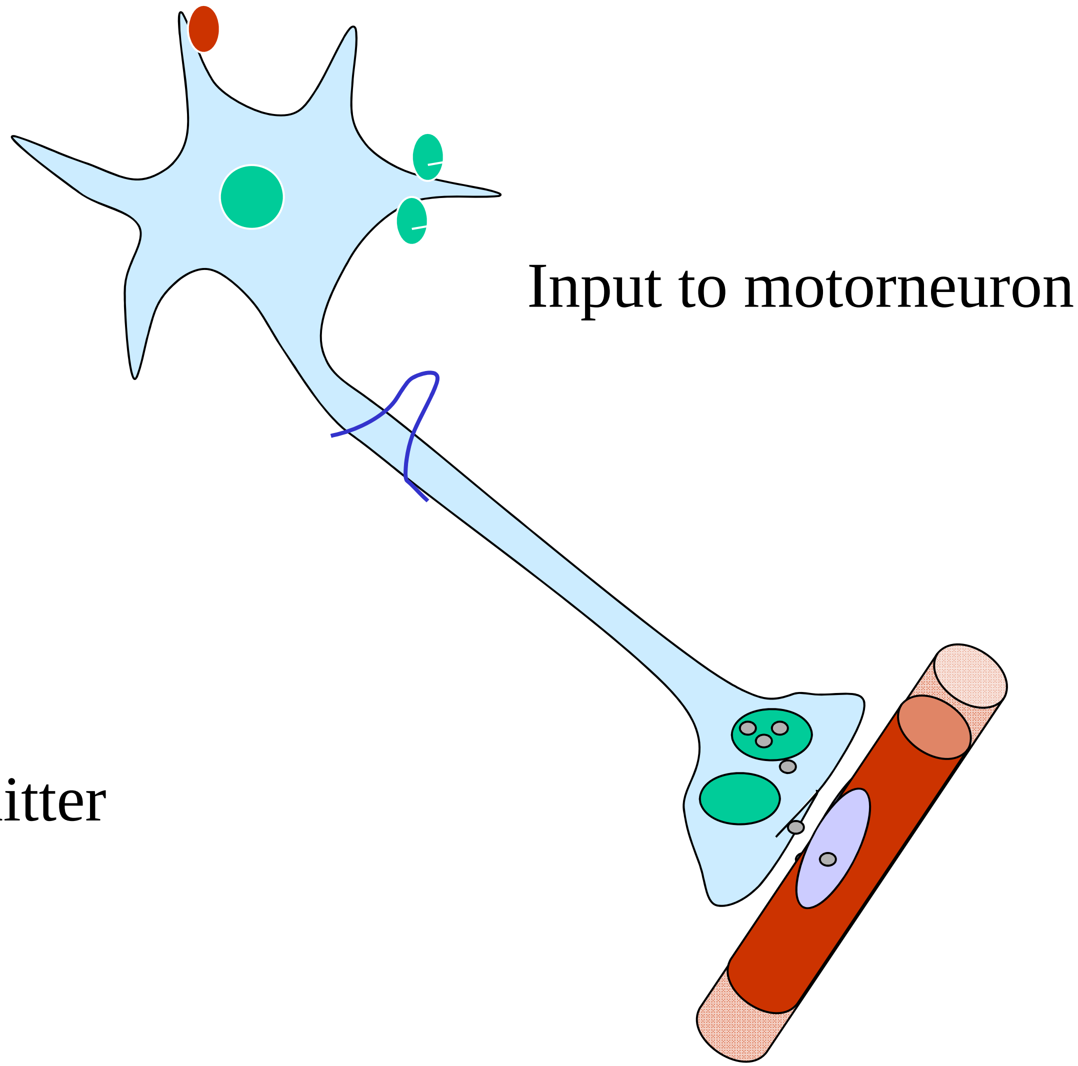


Input to motorneuron

Phase 2:
Release of Neurotransmitter

Excitation Contraction Coupling

Phase 1:
Firing of Motor Neuron

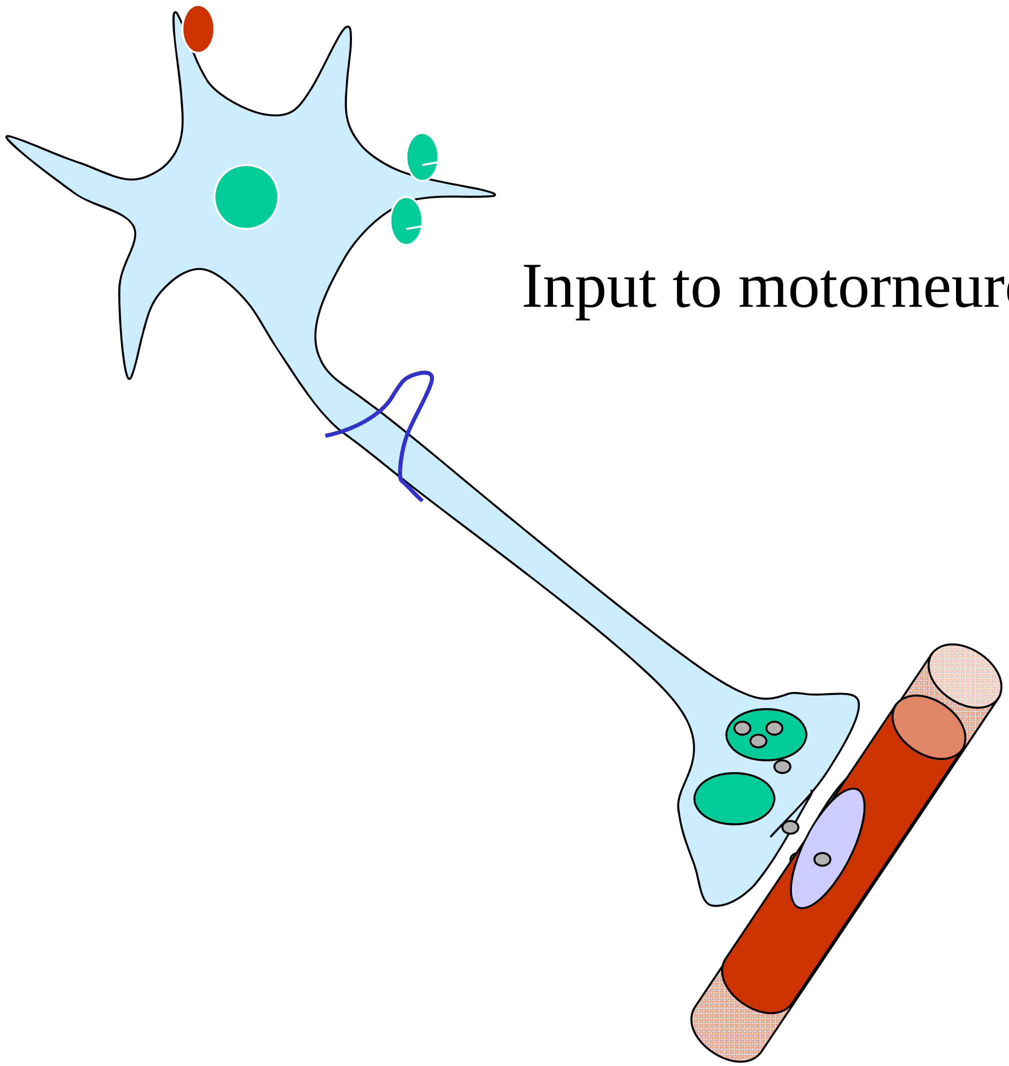


Phase 2:
Release of Neurotransmitter

Phase 3:
Muscle contraction

Open-loop system

Information flows in one direction (from neurons to muscles



Input to motorneuron

Open-loop system

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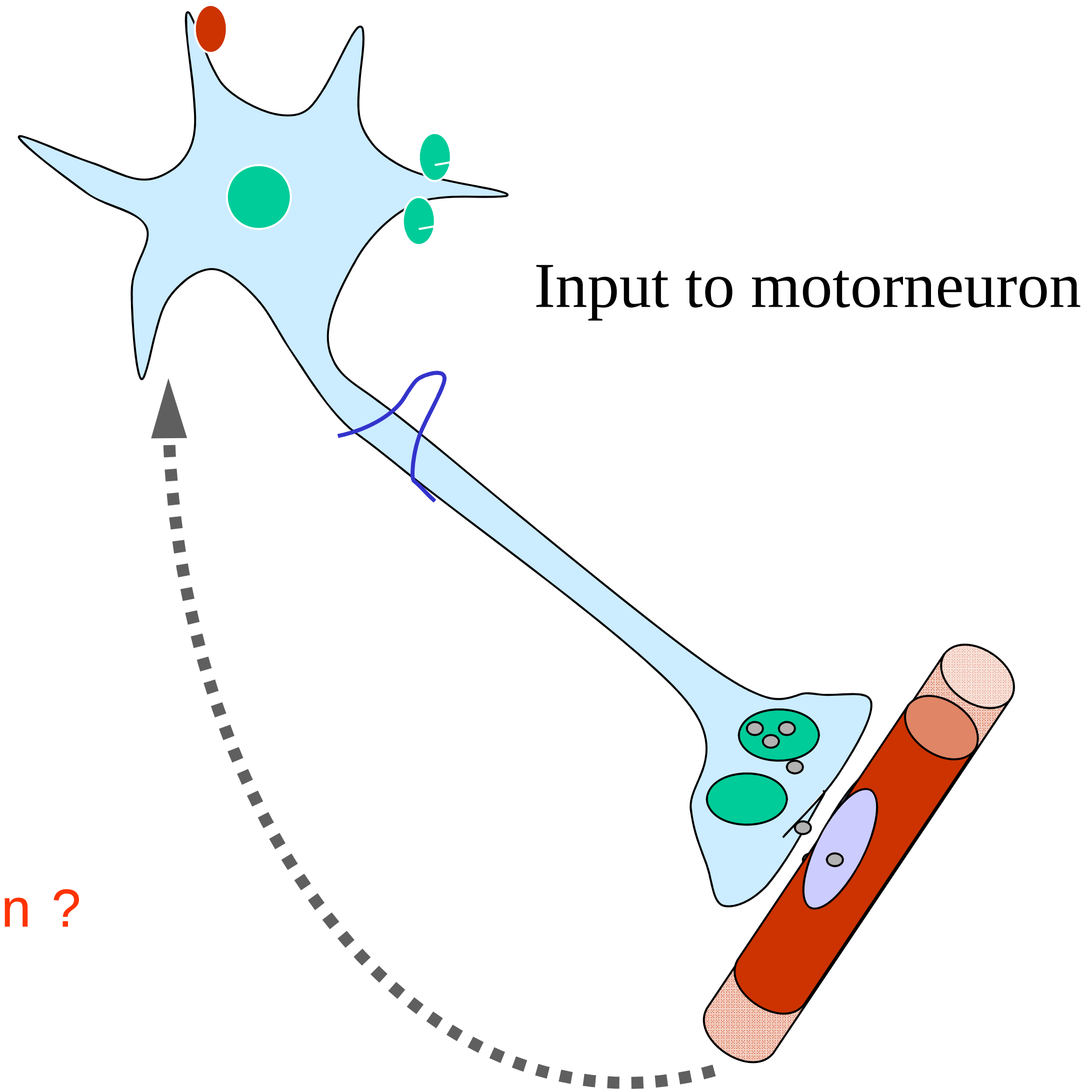


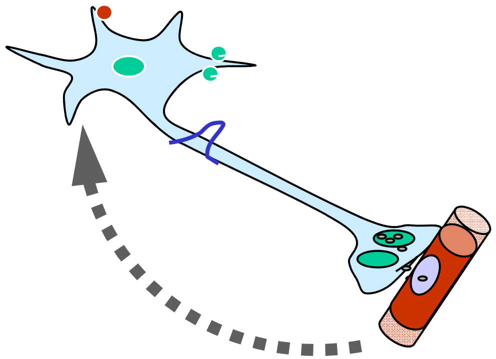
Closed-loop system

Information flows in a closed loop: from neurons to muscles and from muscles to neurons

What kind of information ?

Closed-loop system

The direct feedback from muscles and joints is mediated by **proprioceptive signals**

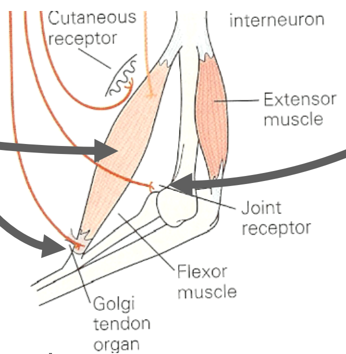


Proprioceptive receptor types

Name:	Muscle spindle receptors	Golgi tendon organs	Joint receptors
Sensitive to:	muscle length	muscle tension	Flexion, extension

Proprioceptive receptor types

Name:	Muscle spindle receptors	Golgi tendon organs	Joint receptors
Sensitive to:	muscle length	muscle tension	Flexion, extension
Location:	Fleshy part of the muscle	Between muscle and tendon	Joint capsule
	Parallel to muscle fibers	*Serial* to muscle fibers	Between bones



Proprioceptive receptor types

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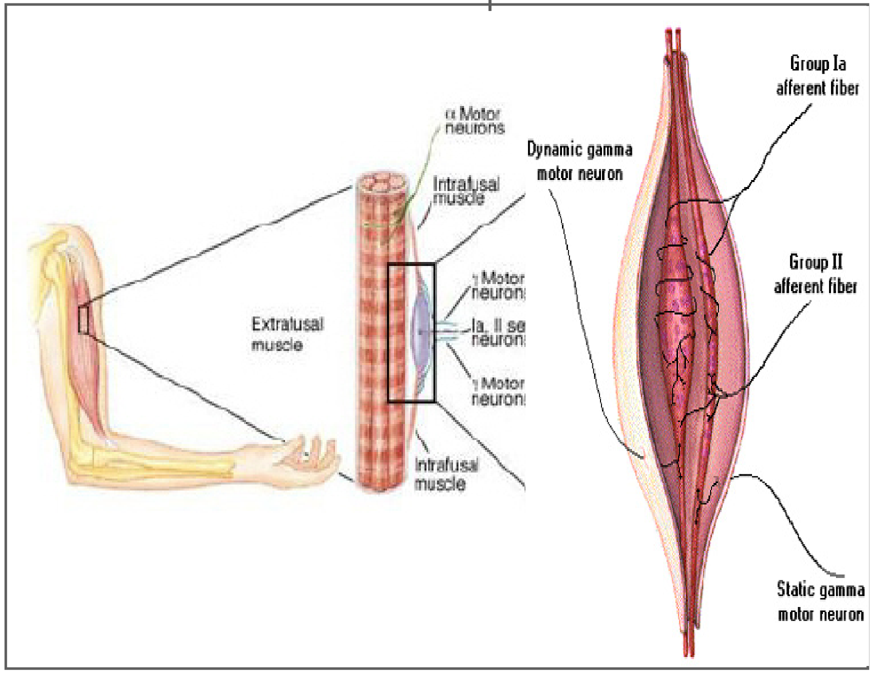
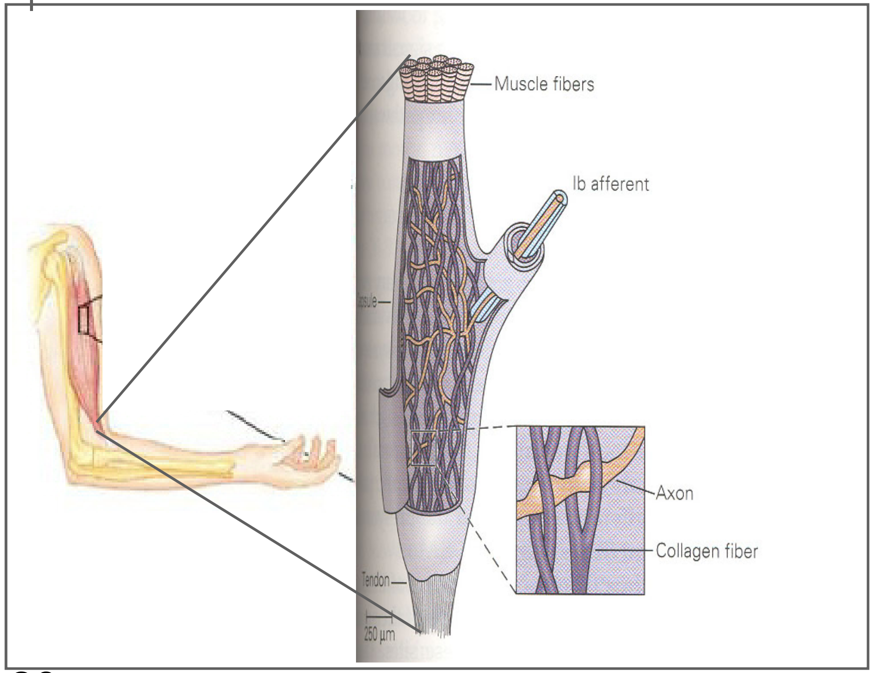




Motor control

- Closed loops
- Proprioceptive feedback
- Reflexes – tool for probing loop function
- Controlled variables – motor vs sensory

What proprioceptors encode?

Proprioceptive receptor types

Name:	Muscle spindle receptors	Golgi tendon organs	Joint receptors
Sensitive to:	muscle length	muscle tension	Flexion, extension

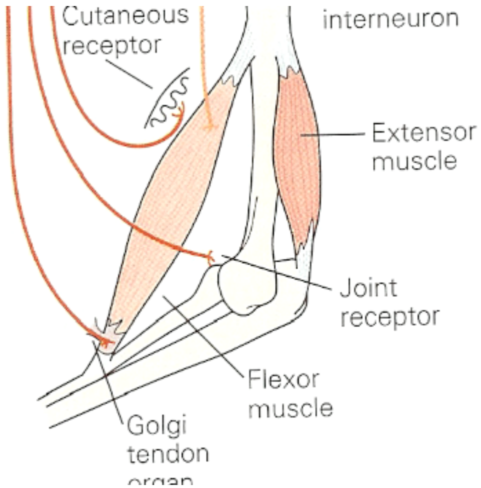
From
Arthur Prochazka,
University of Alberta

Proprioceptive receptor types

Name:	Muscle spindle receptors	Golgi tendon organs	Joint receptors
Sensitive to:	muscle length	muscle tension	Flexion, extension
Encode:		force $f = k_1 F$	

Proprioceptive receptor types

Name:	Muscle spindle receptors	Golgi tendon organs	Joint receptors
Sensitive to:	muscle length	muscle tension	Flexion, extension
Encode:	Length + velocity $f = k_1 L + k_2 V^{0.6}$	force $f = k_1 F$	angle $f = k_1 \theta$



Proprioceptive receptor types

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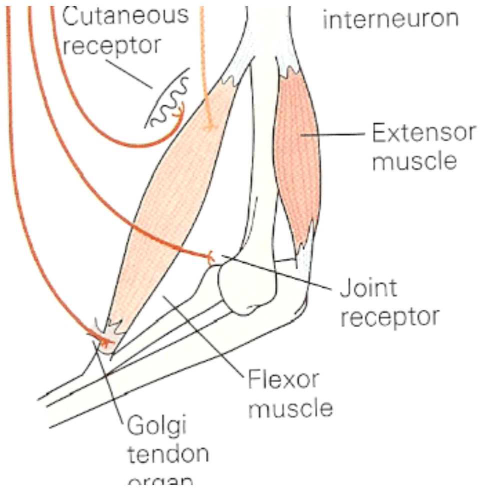
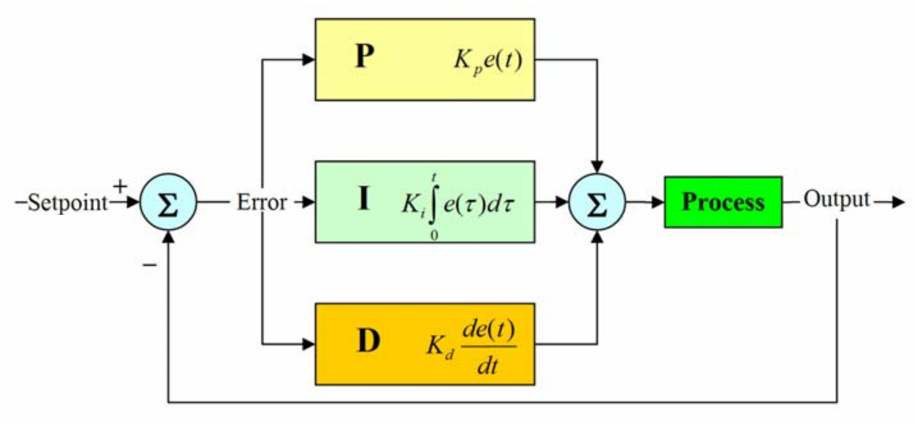
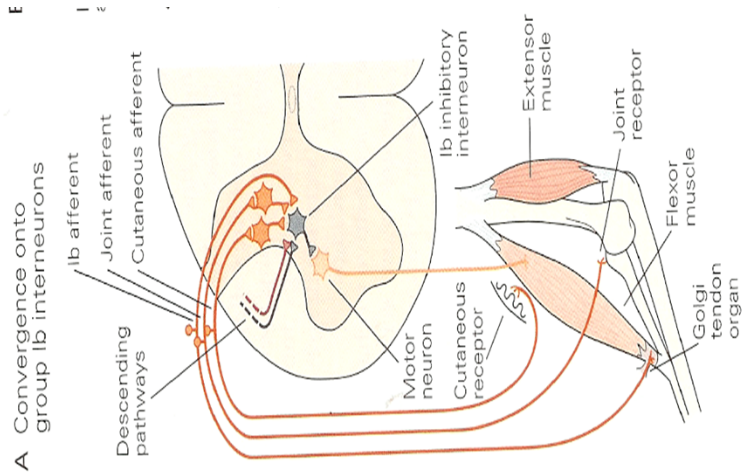
Sensitive to:	muscle length	muscle tension	Flexion, extension
Encode:	Length + velocity $f = k_1 L + k_2 V^{0.6}$	force $f = k_1 F$	angle $f = k_1 \theta$
	$\dot{\theta}$	$\ddot{\theta}$	θ



PID control

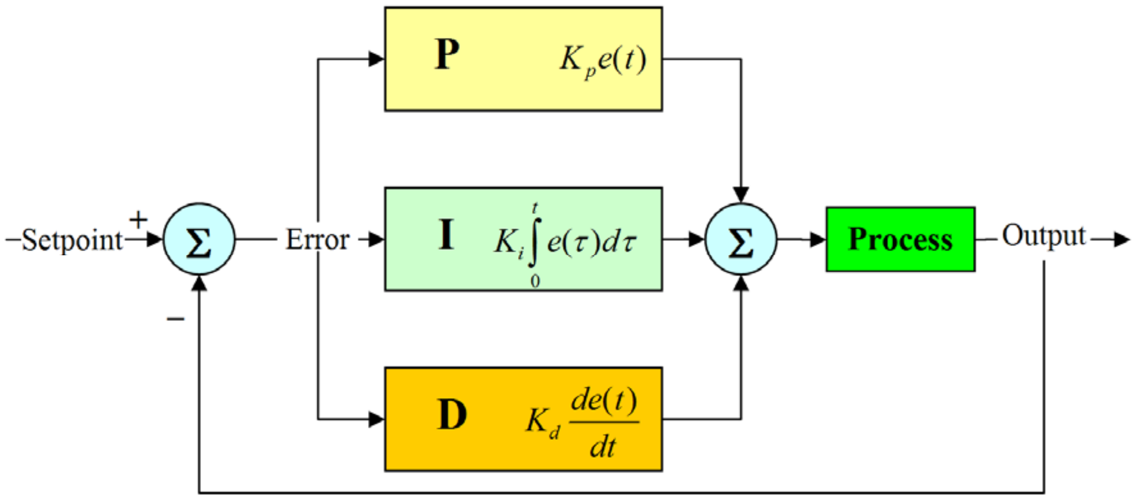
- Proportional (to the controlled variable) Present $\dot{\theta}$
- Integral (of the controlled variable) Past θ
- Derivative (of the controlled variable) Future $\ddot{\theta}$





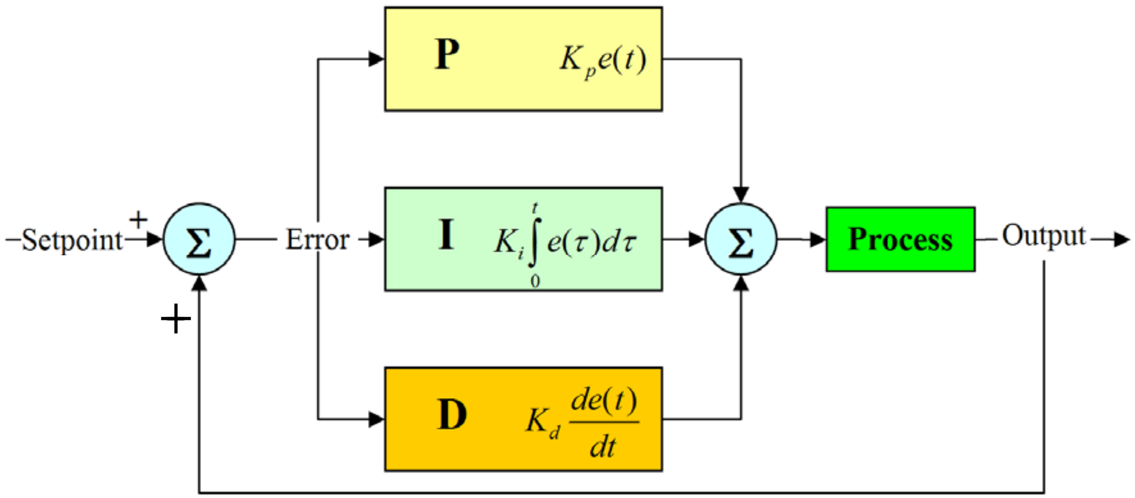
Negative feedback loop

- **Characteristic**: The effect of a perturbation is in opposite direction
- **Requirement**: The cumulative sign along the loop is negative
- **Function**: Can keep stable fixed points



Positive feedback loop

- **Characteristic**: The effect of a perturbation is in the same direction
- **Requirement**: The cumulative sign along the loop is positive
- **Function**: amplifies perturbations



Motor control

- Closed loops
- Proprioceptive feedback
- Reflexes – tool for probing loop function
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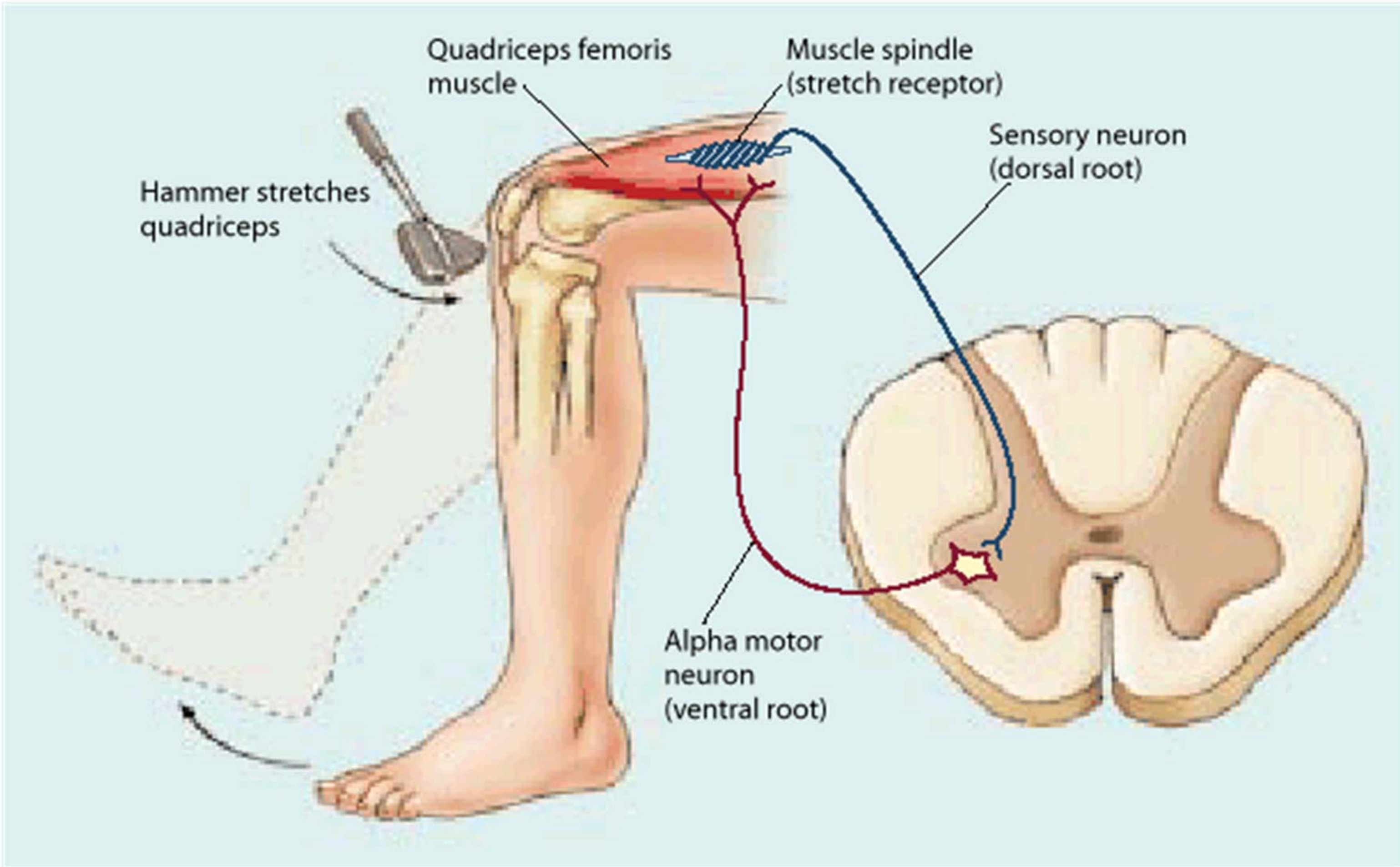
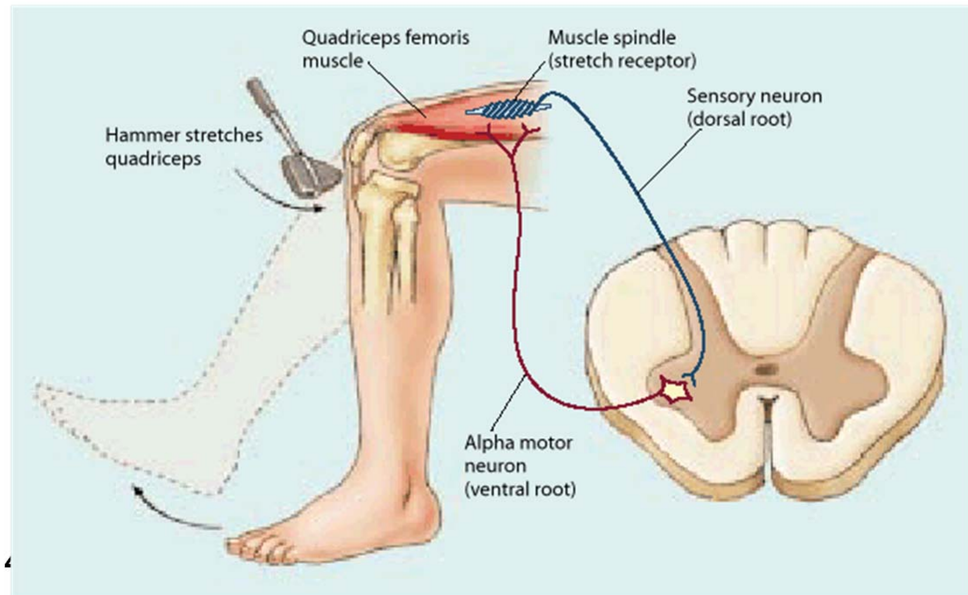
The stretch reflex probes the control function of muscle spindles



Is the loop positive or negative?

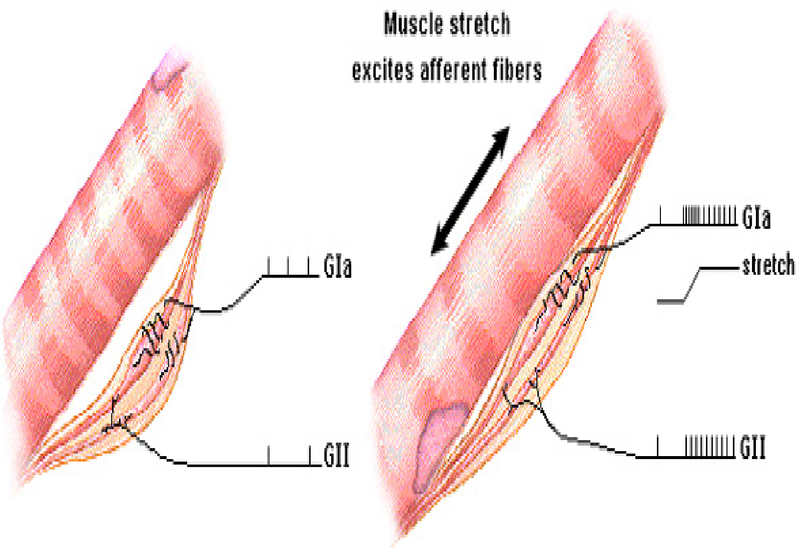
- The stroke stretches the spindle
- As a result the muscle contracts
- The result opposes the perturbation

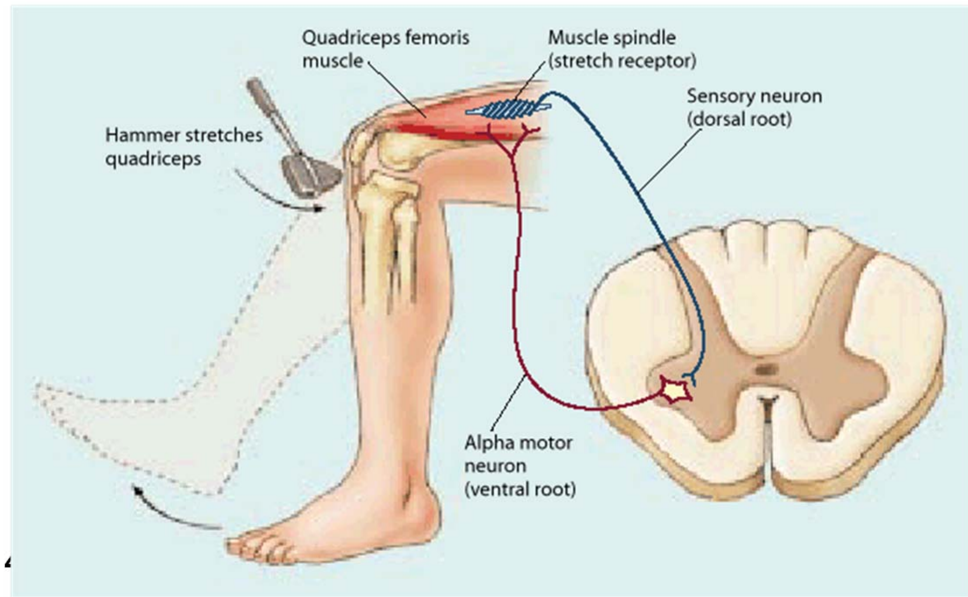
  => negative FB loop



the anatomical loop

- Muscle spindle excites the motor neuron
- Motor neuron excites muscle fibers
- Muscle contraction suppresses spindle response





Proprioceptive receptor types

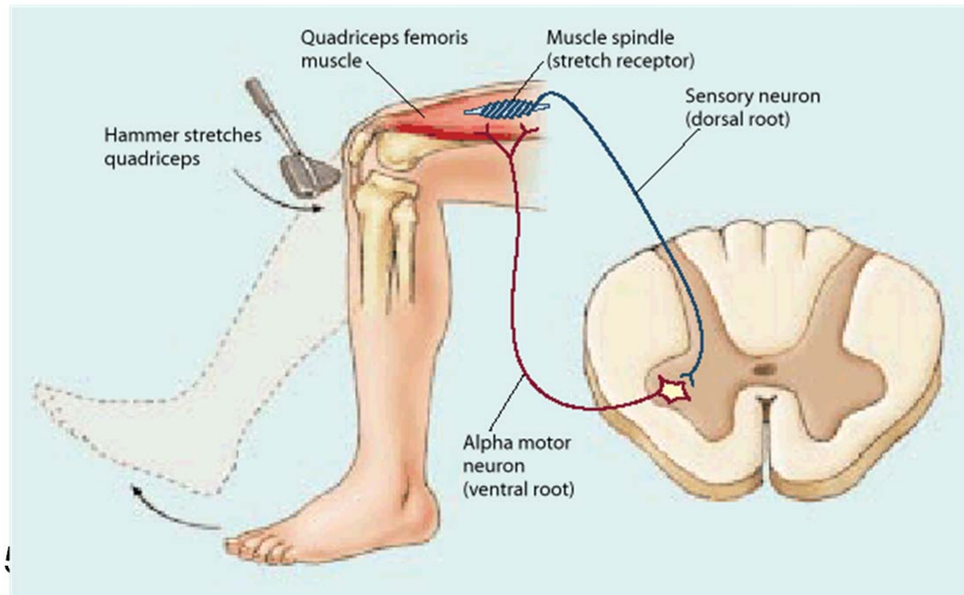
Name:	Muscle spindle receptors	Golgi tendon organs	Joint receptors
Sensitive to:	muscle length	muscle tension	Flexion, extension
Encode:		force $f = k_1 F$	

Why spindles fire at rest?

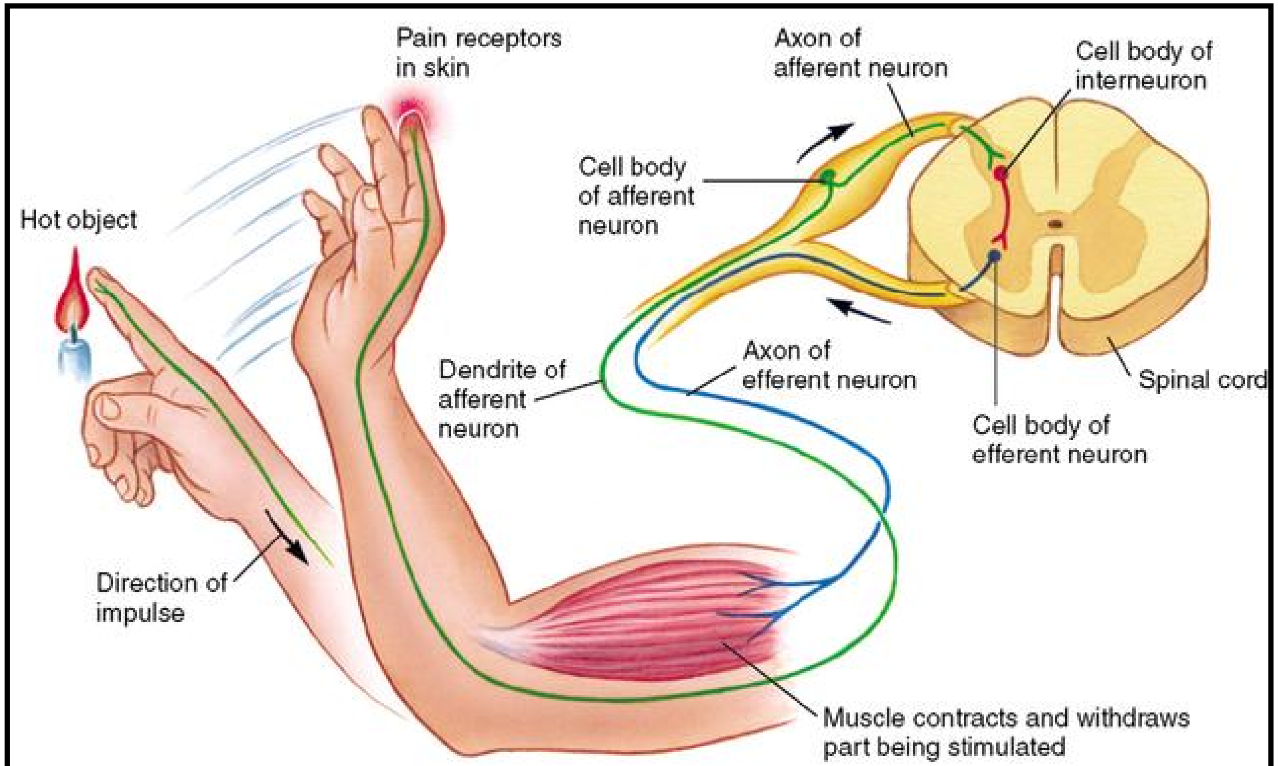
What about the flexor muscles?

Positive or negative loop?

What is the underlying circuit?



Pain reflex



Positive or negative?

What is the underlying circuit?

Motor control

- Closed loops
- Proprioceptive feedback
- Reflexes – tool for probing loop function
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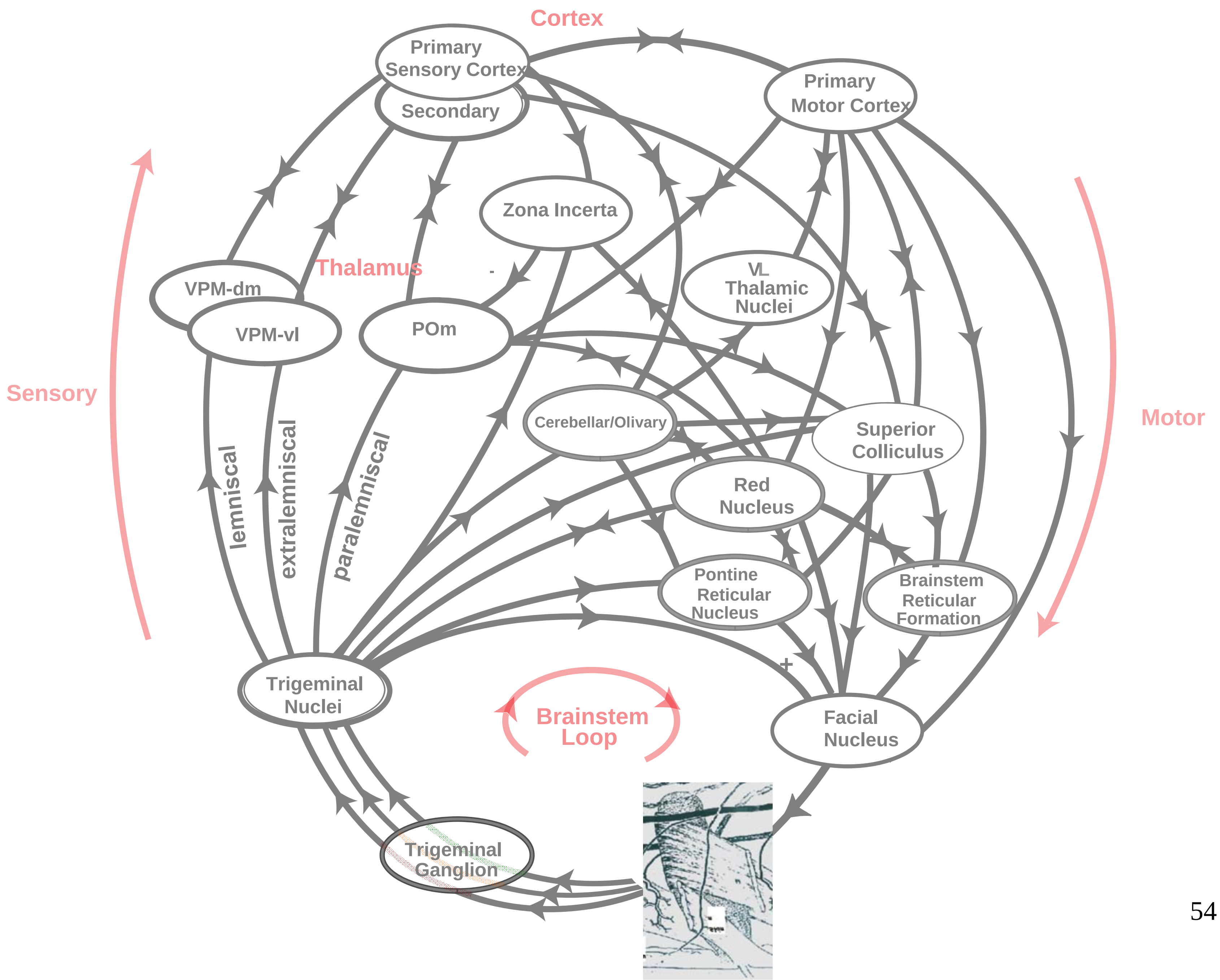
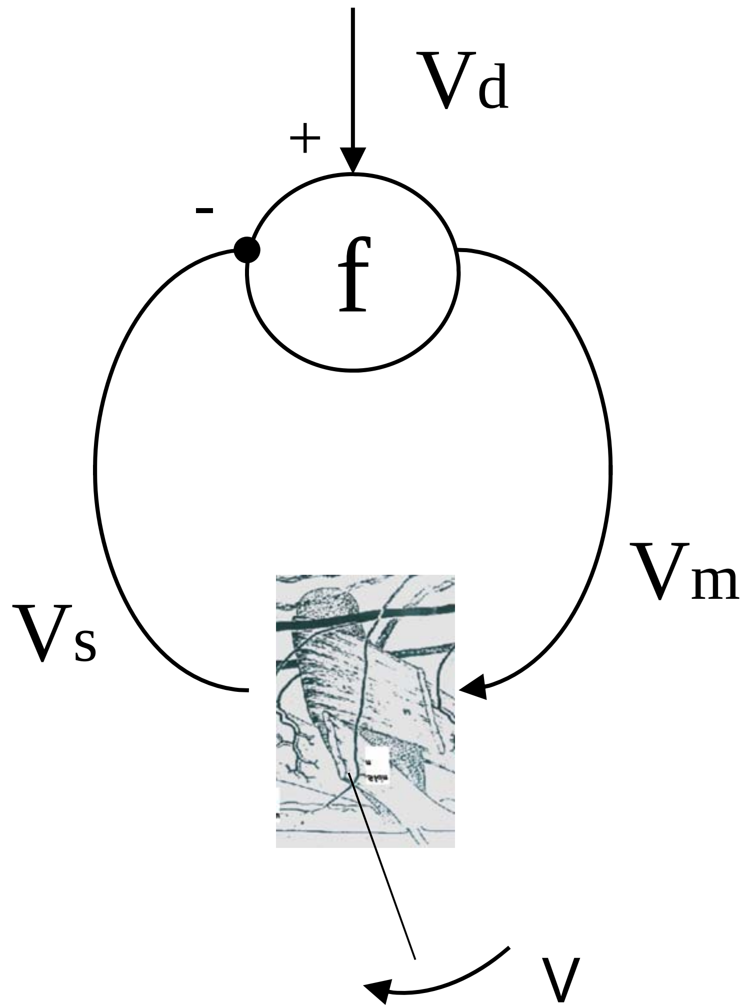
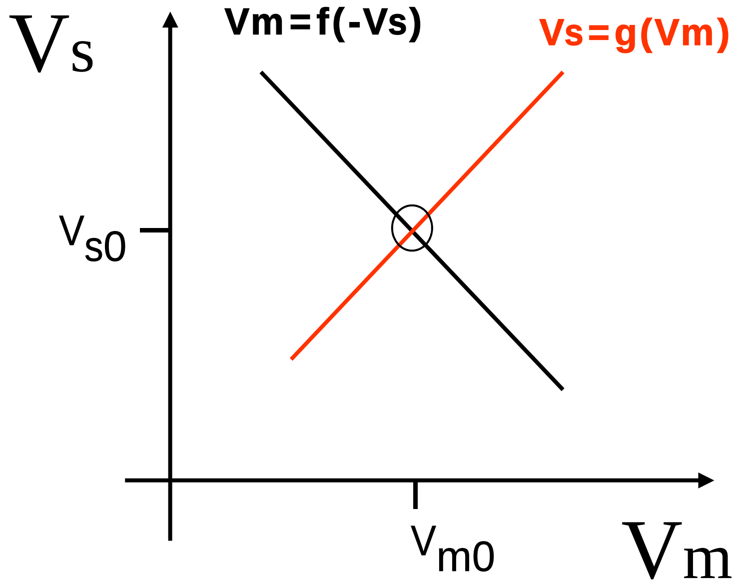
Sensory-motor loops of the vibrissal system



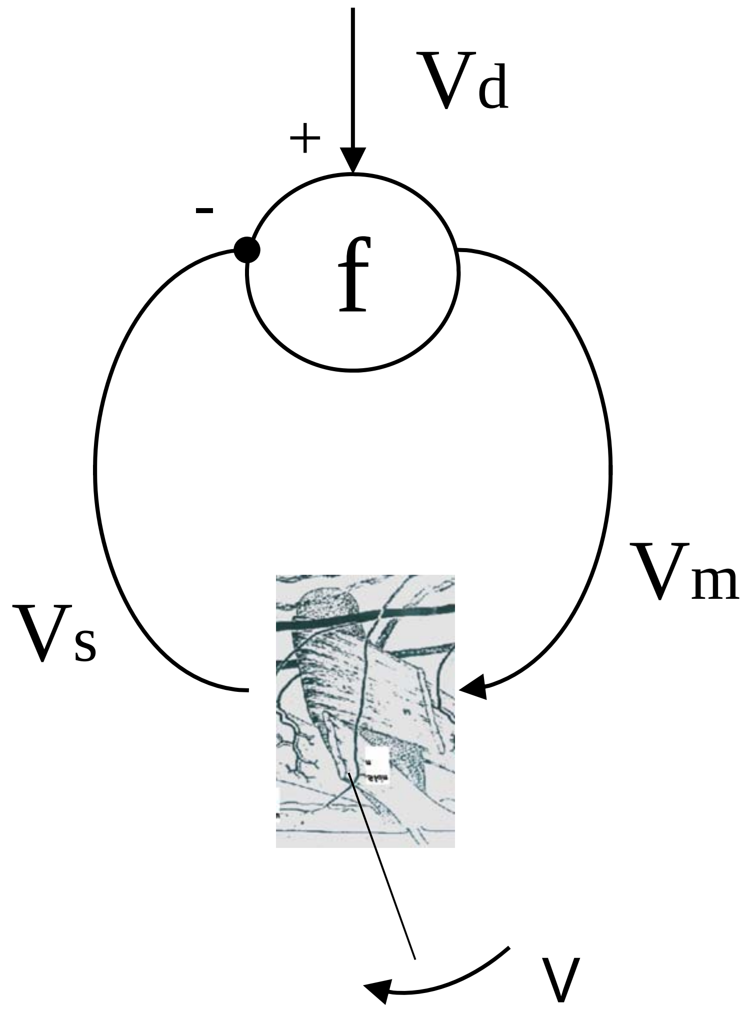
Basic principles of closed-loop control

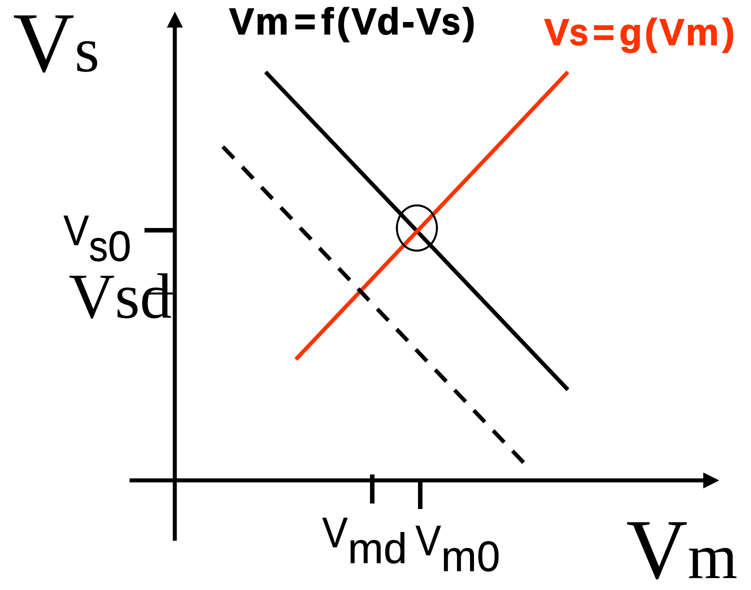
Set point



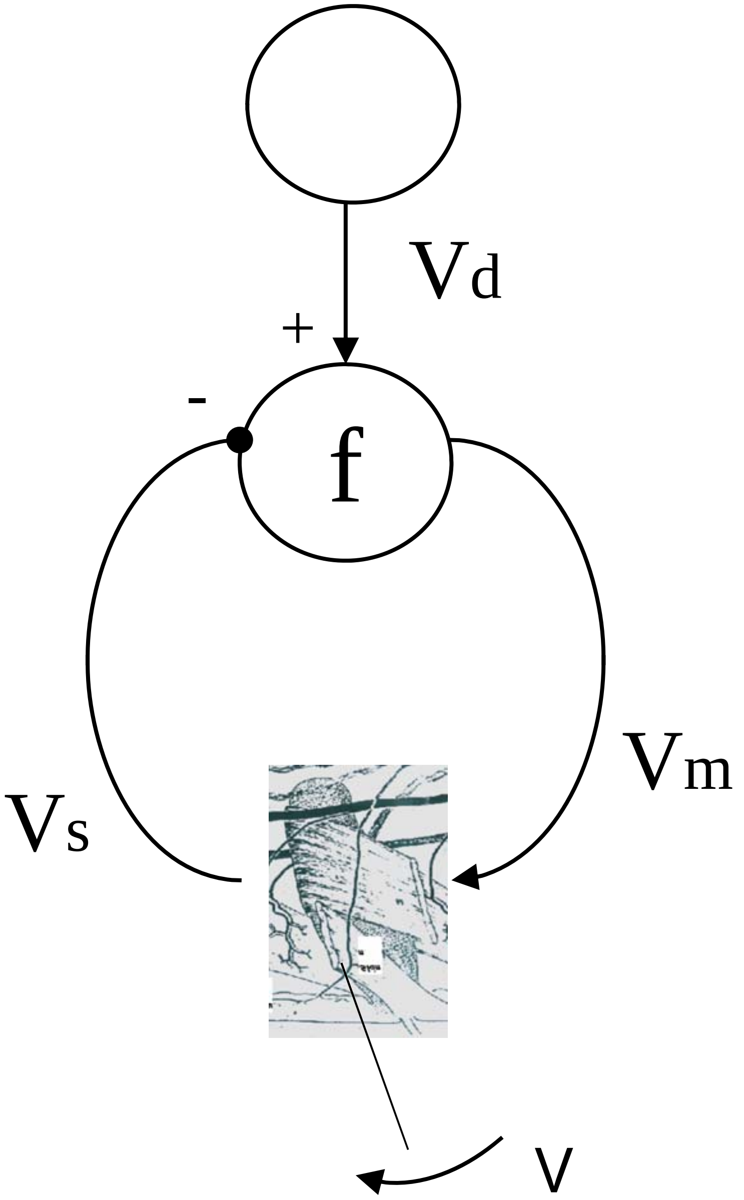


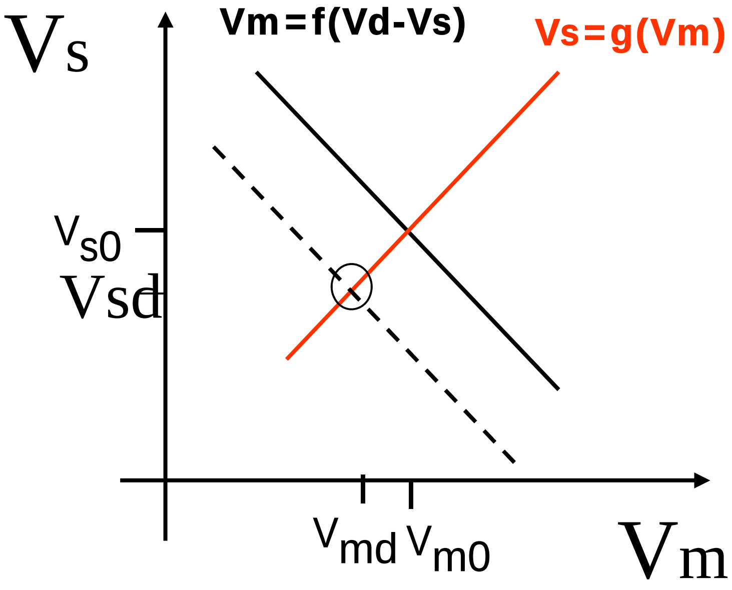
Set point



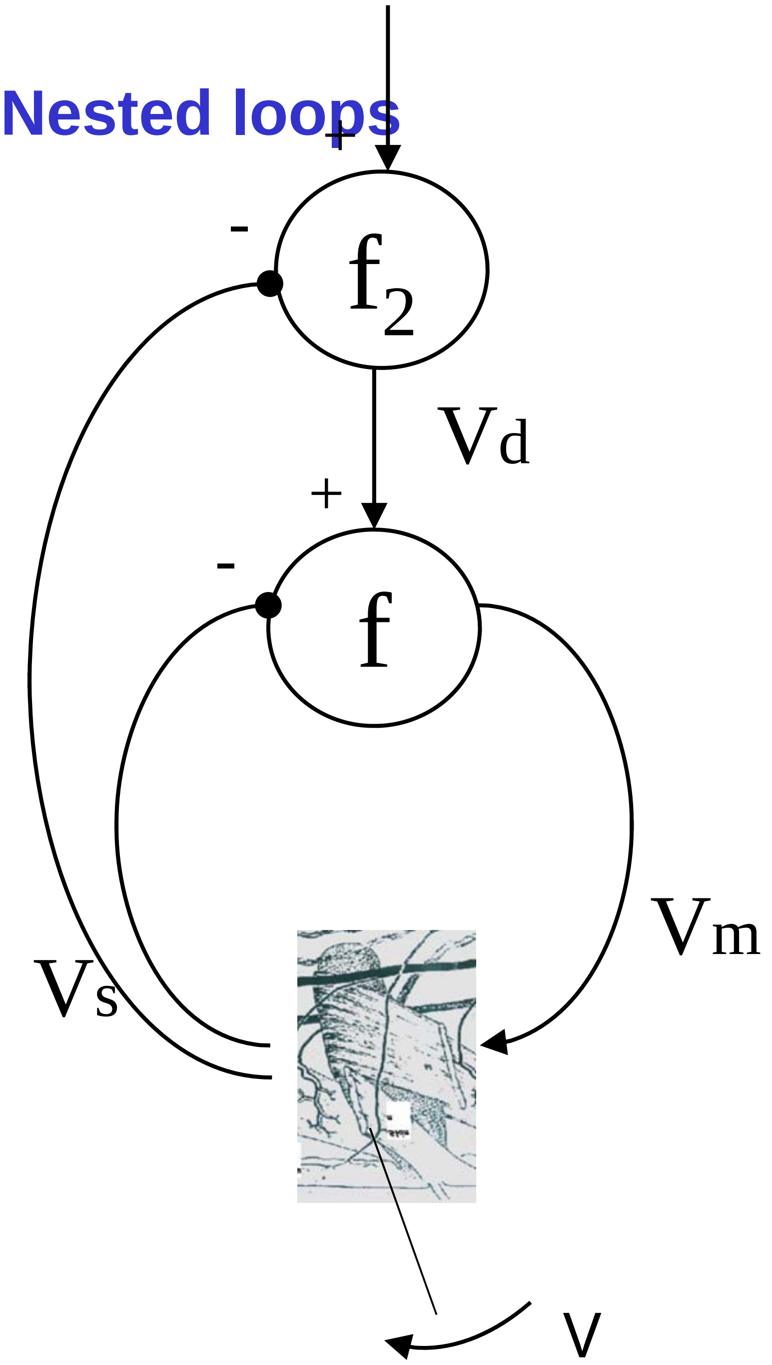


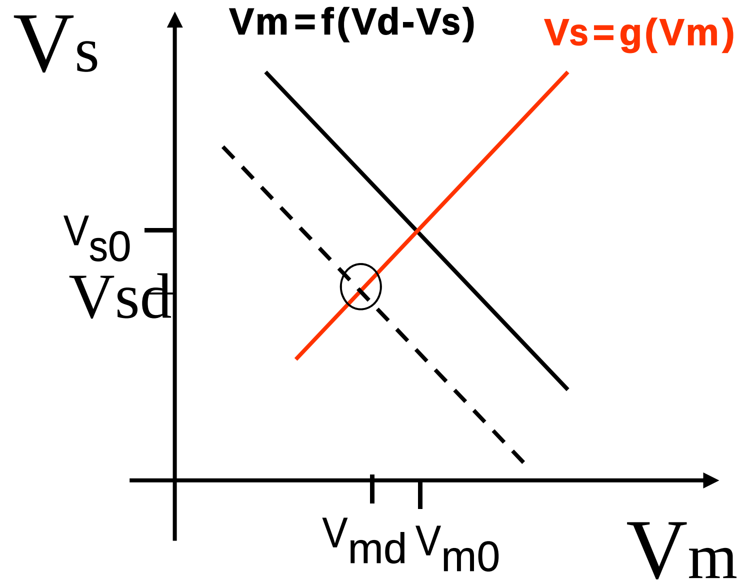
Direct control without direct connection



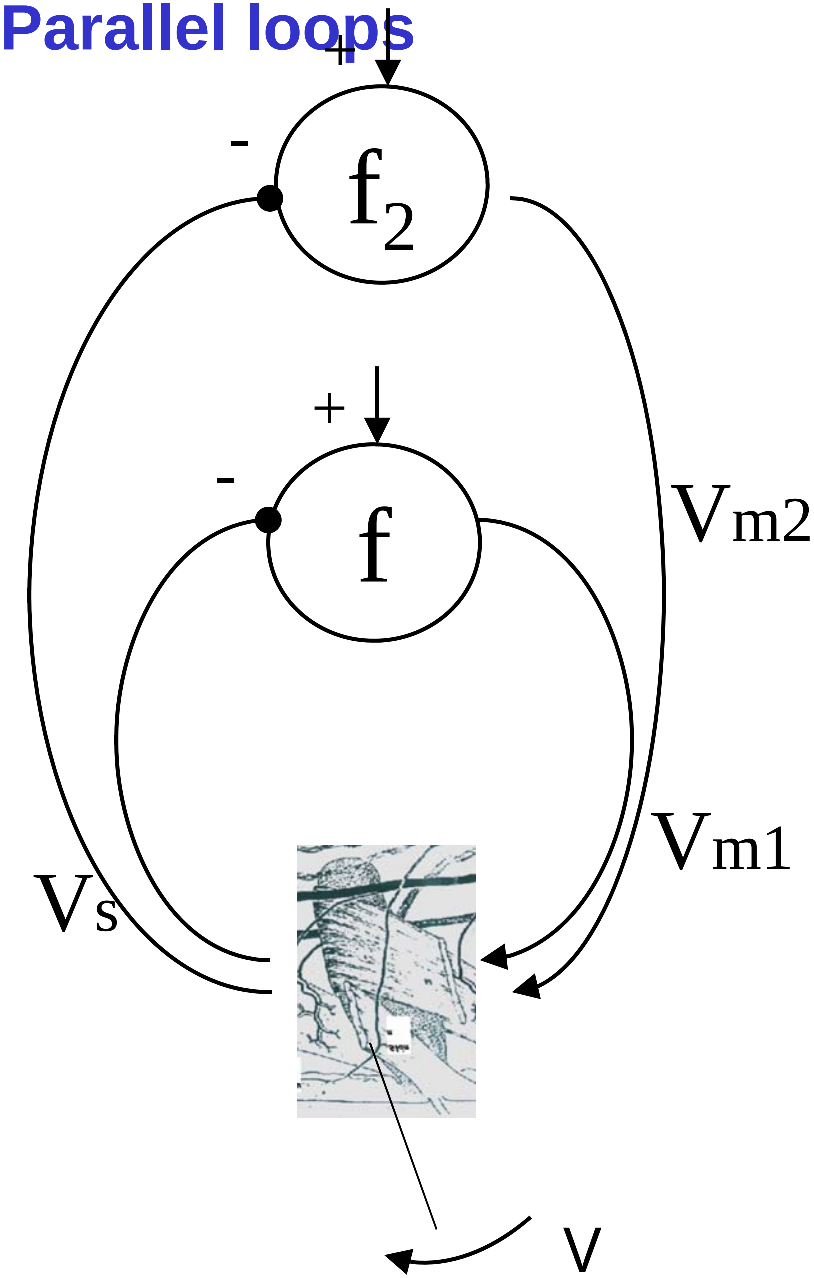


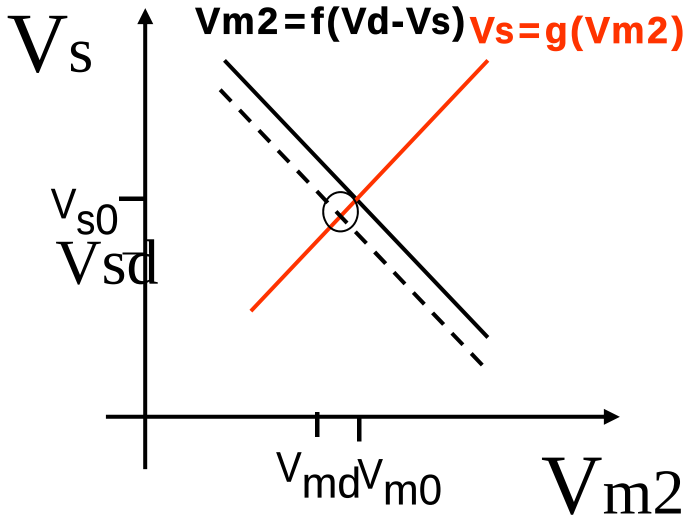
Nested loops

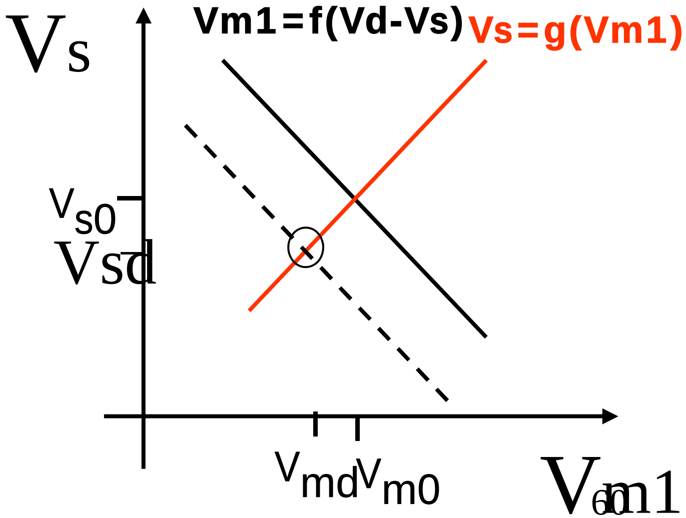




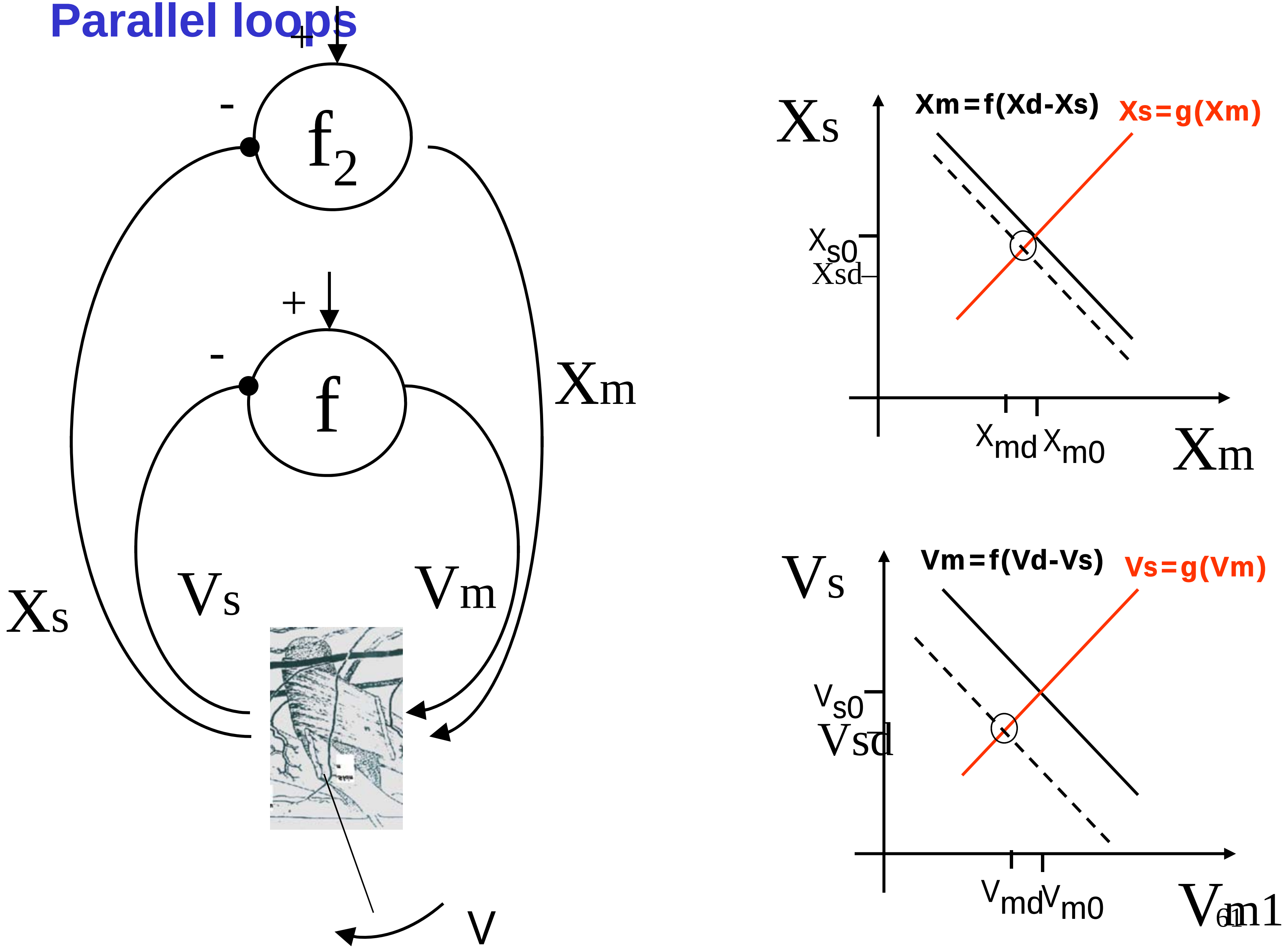
Parallel loops





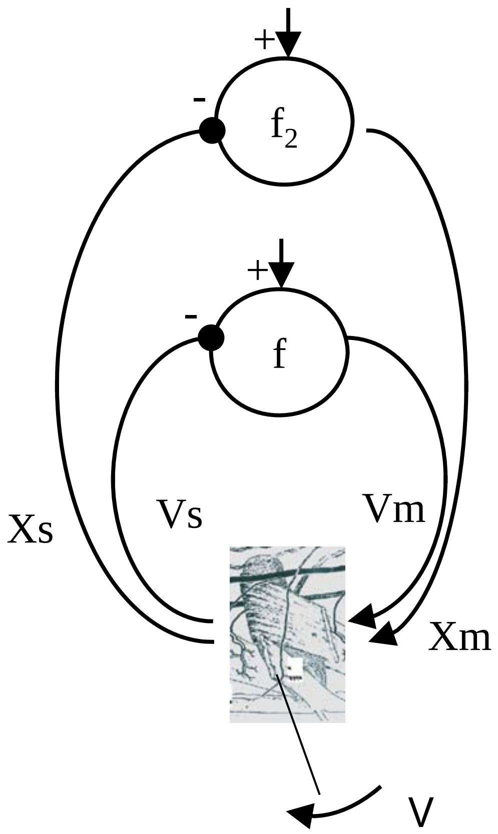


Parallel loops



Closed loops in active sensing

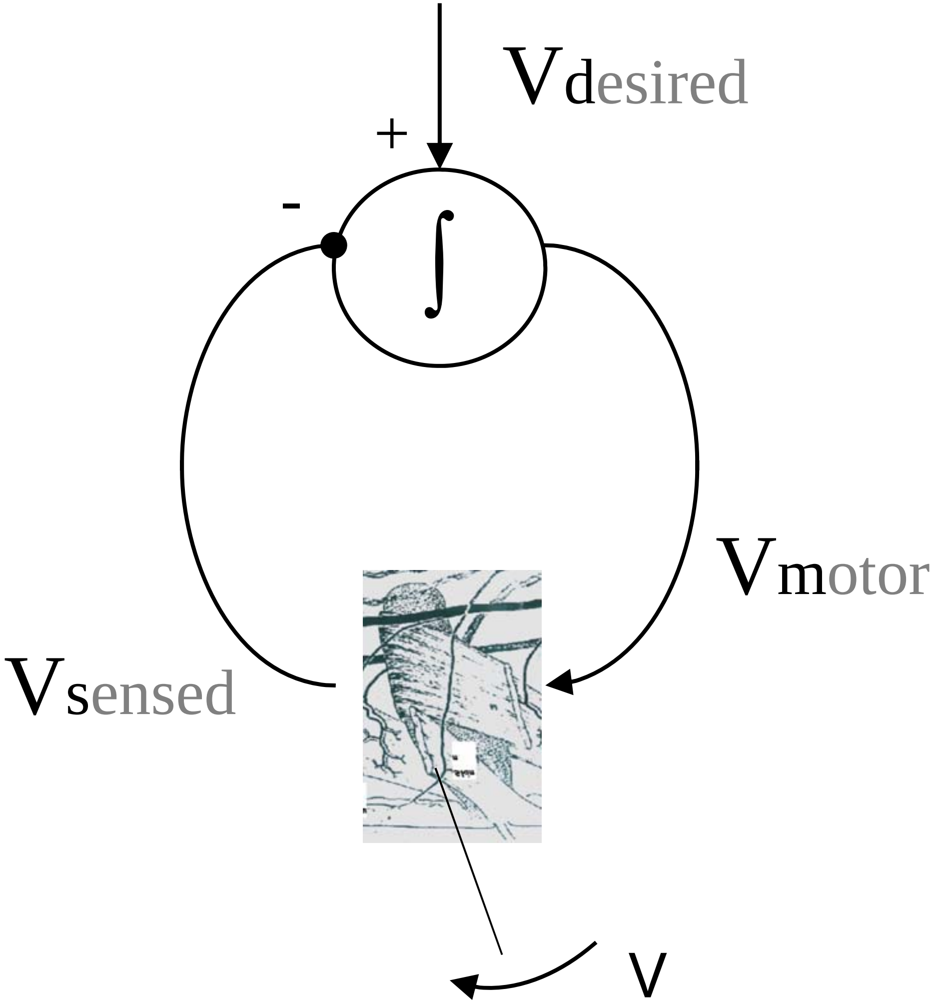
The controlled variables can be

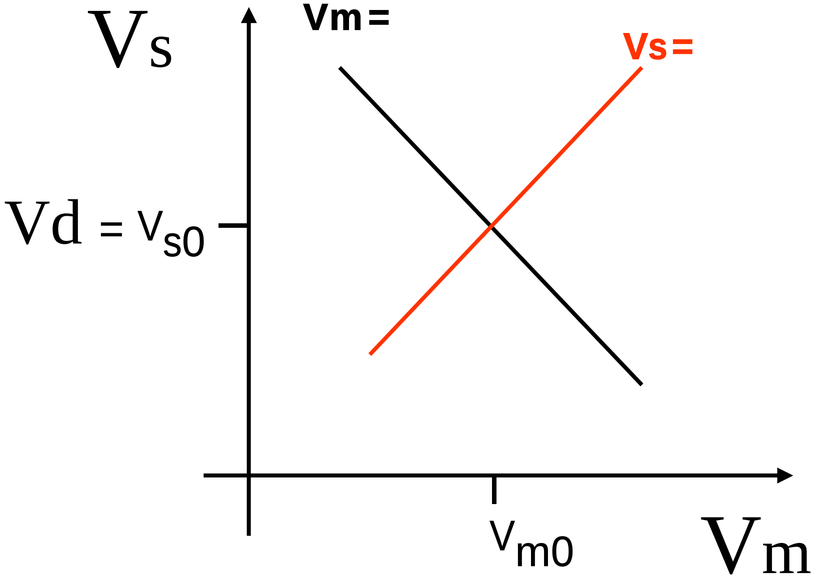


- Motor (via Xs)
  (velocity, amplitude, duration, direction, …)
- Sensory (Xs)
  (Intensity, phase, …)
- Object (via Xm – Xs relationships)
  (location, SF, identity, …)

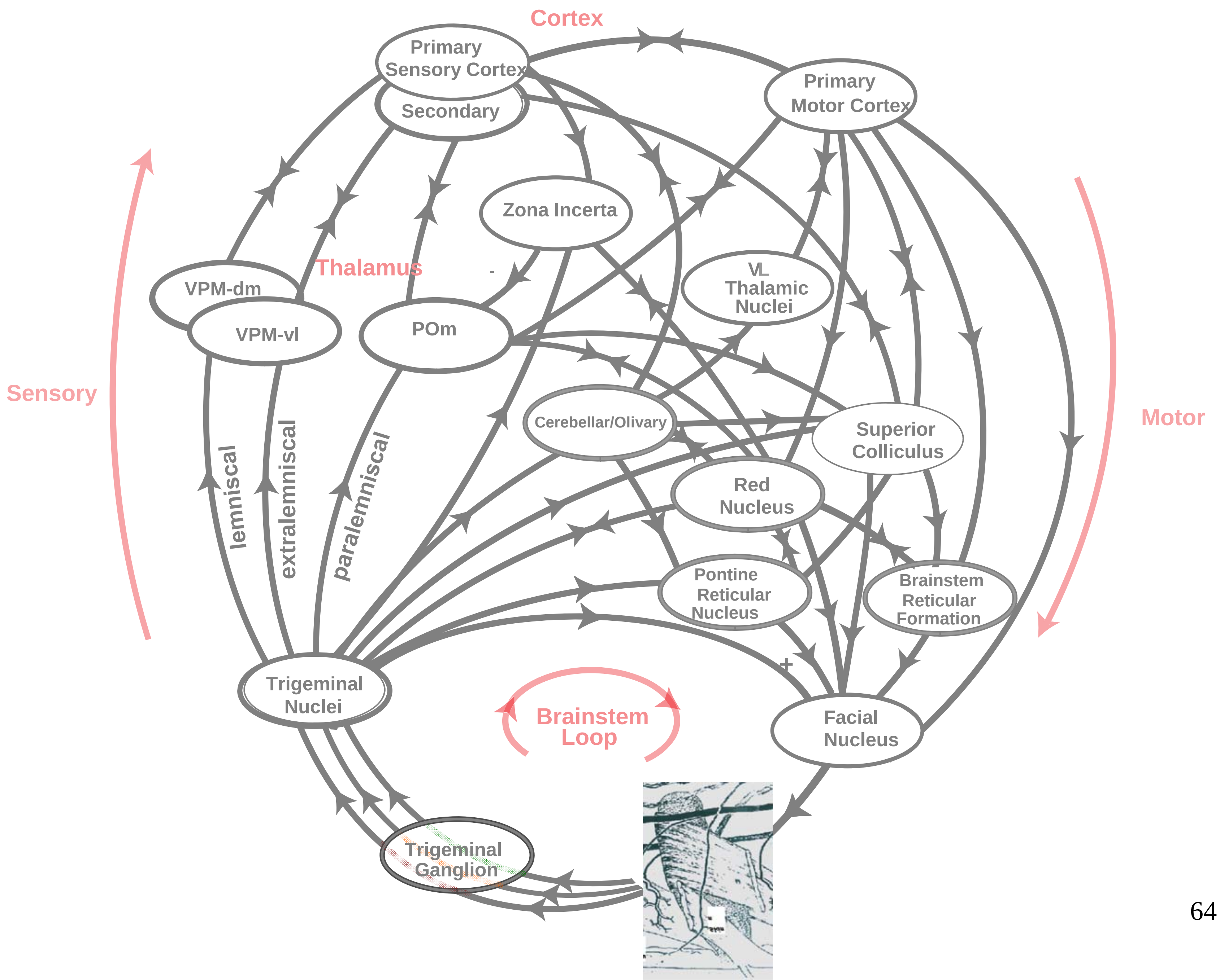
Servo control

$$Vm = \int(Vd-Vs)dt$$

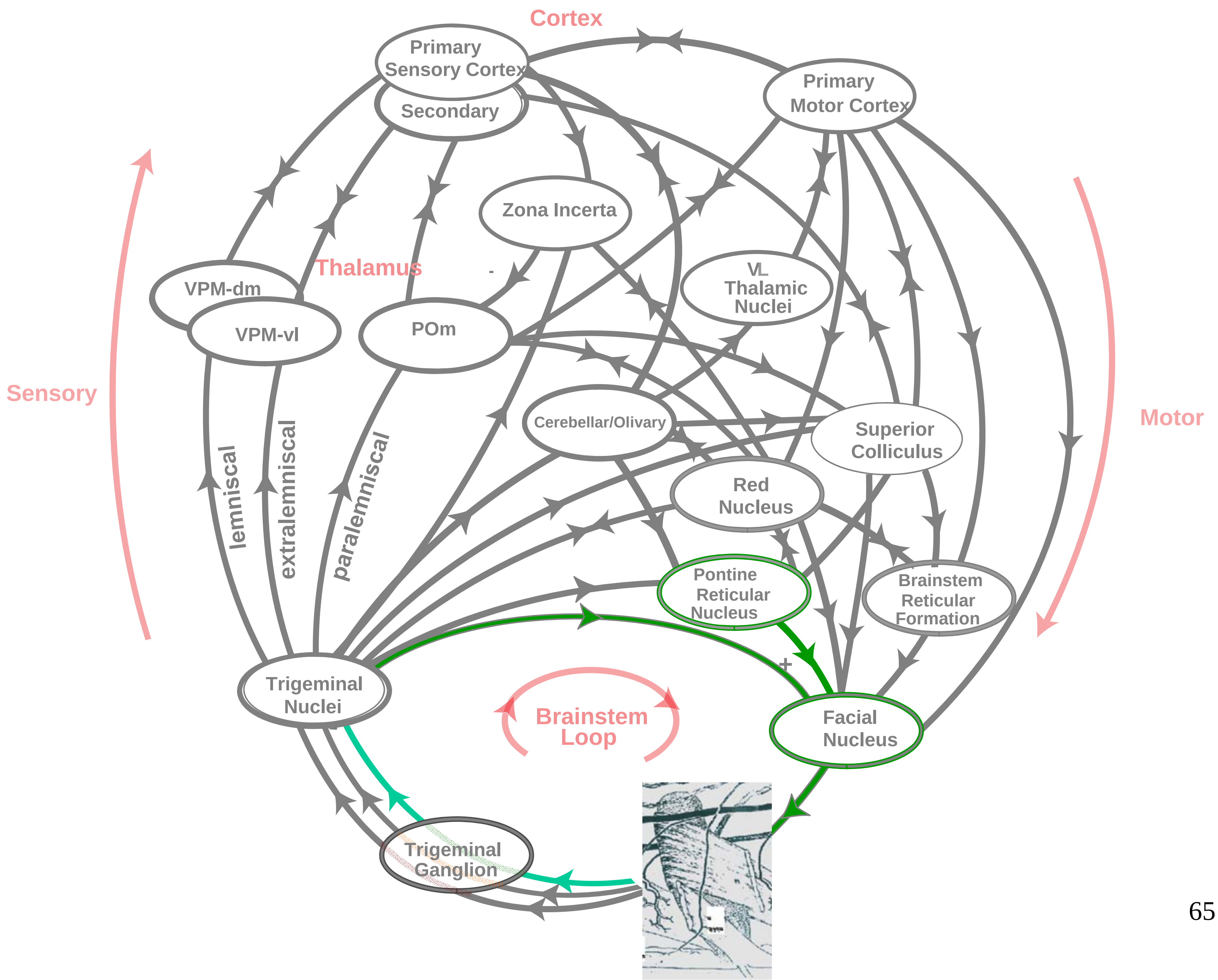




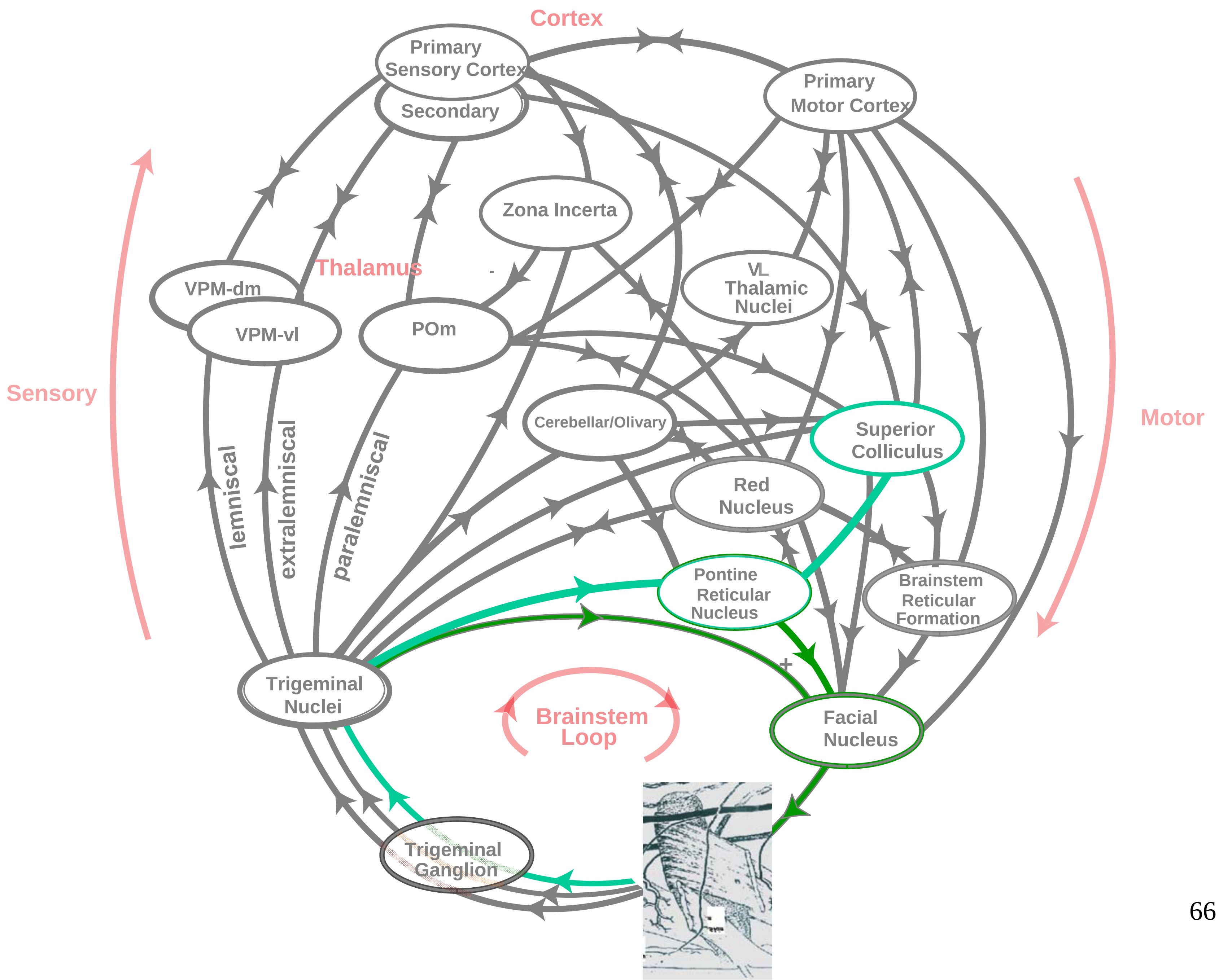
Sensory-motor loops of the vibrissal system



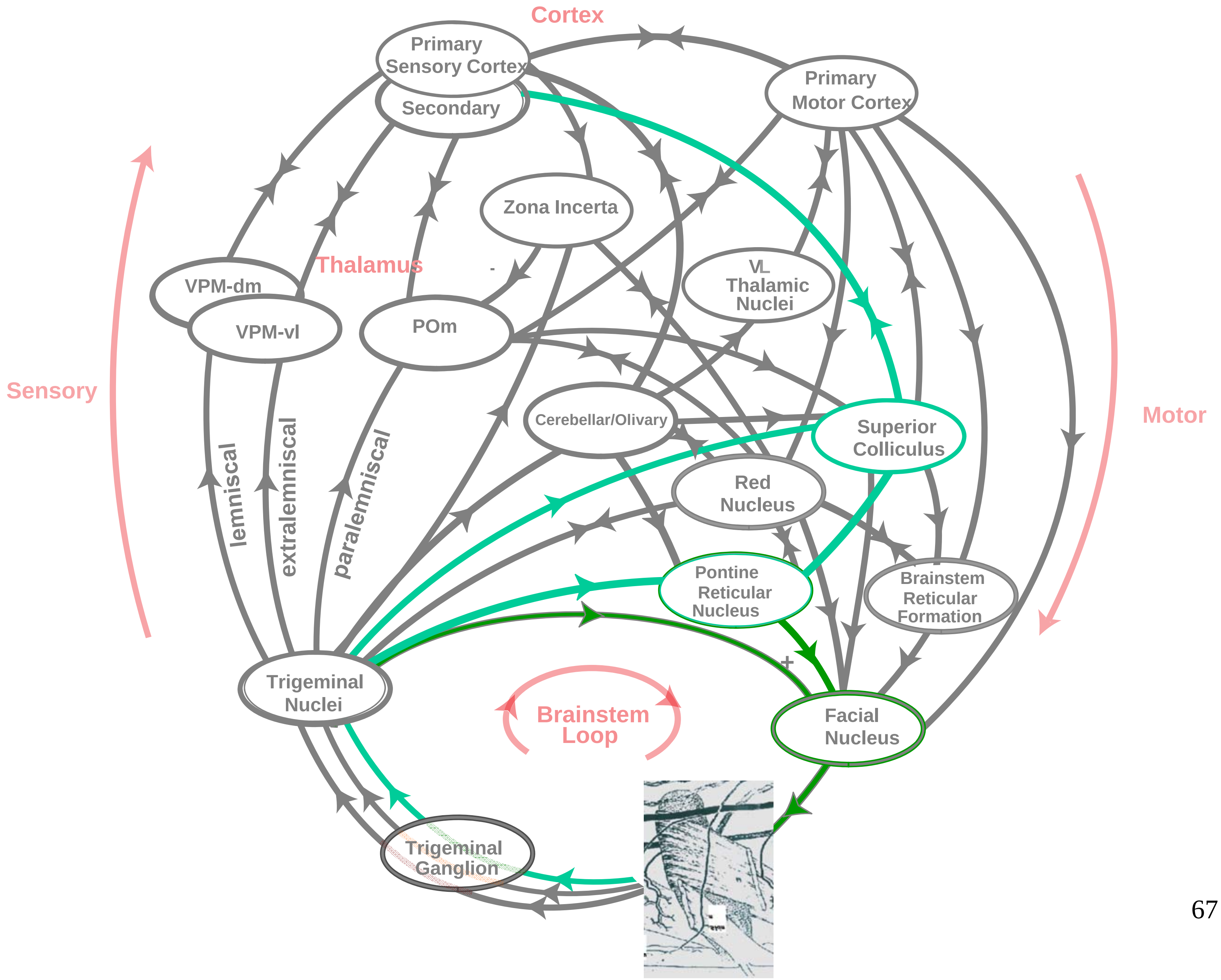
Sensory-motor loops of the vibrissal system



Sensory-motor loops of the vibrissal system



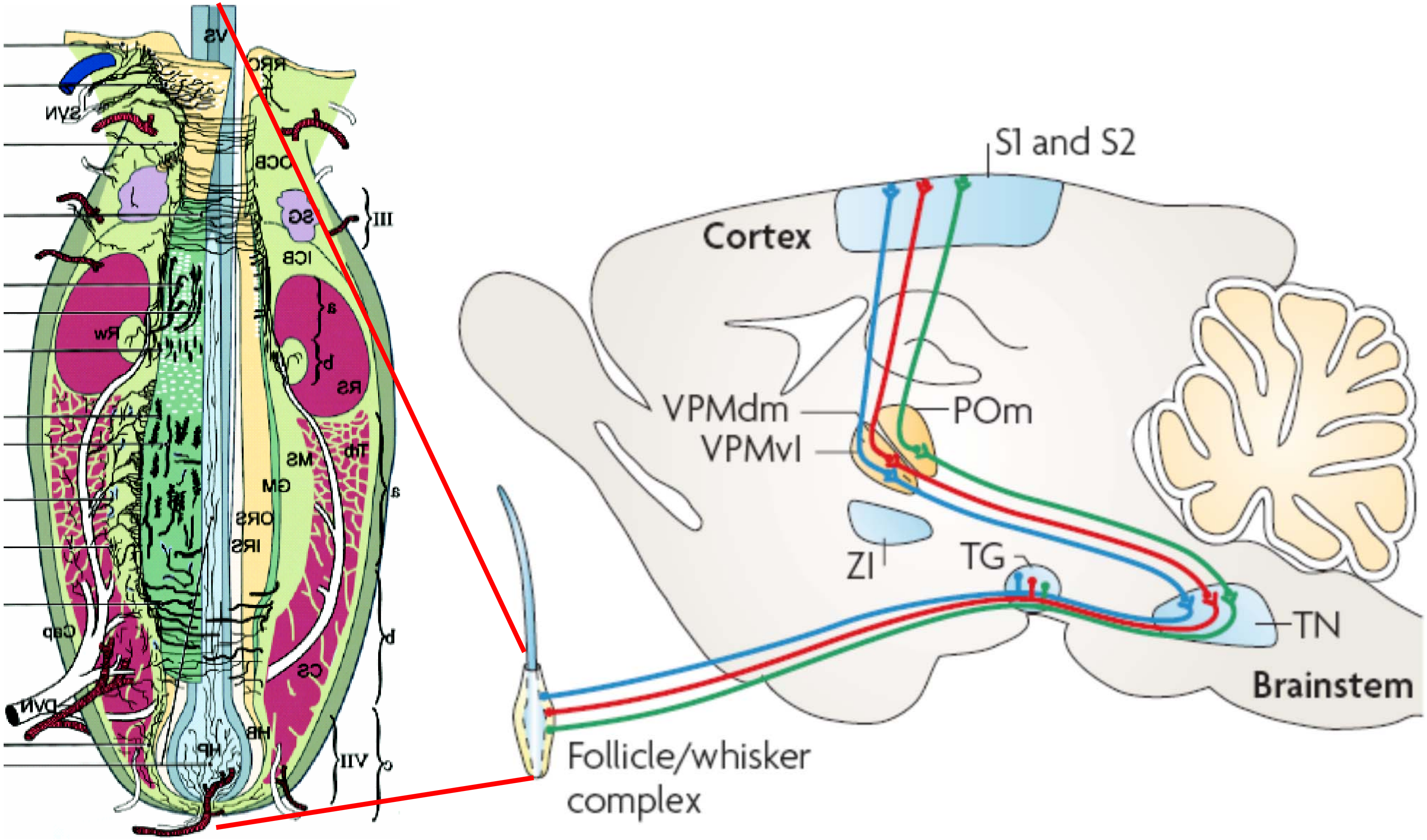
Sensory-motor loops of the vibrissal system



Active sensing
in
the vibrissal system

Sensory signal conduction

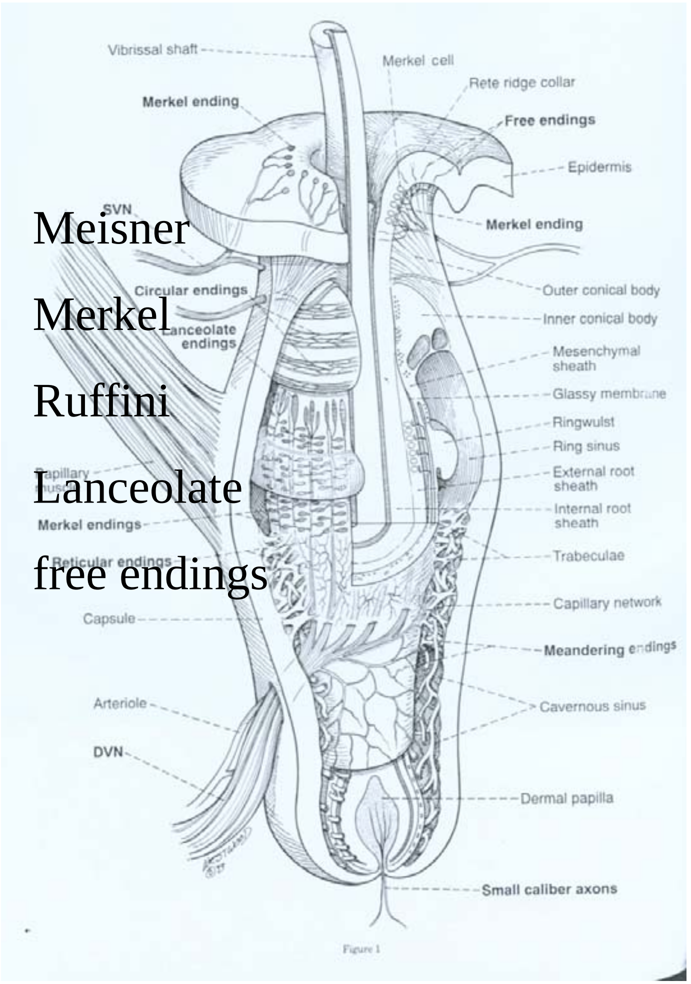
The vibrissal system

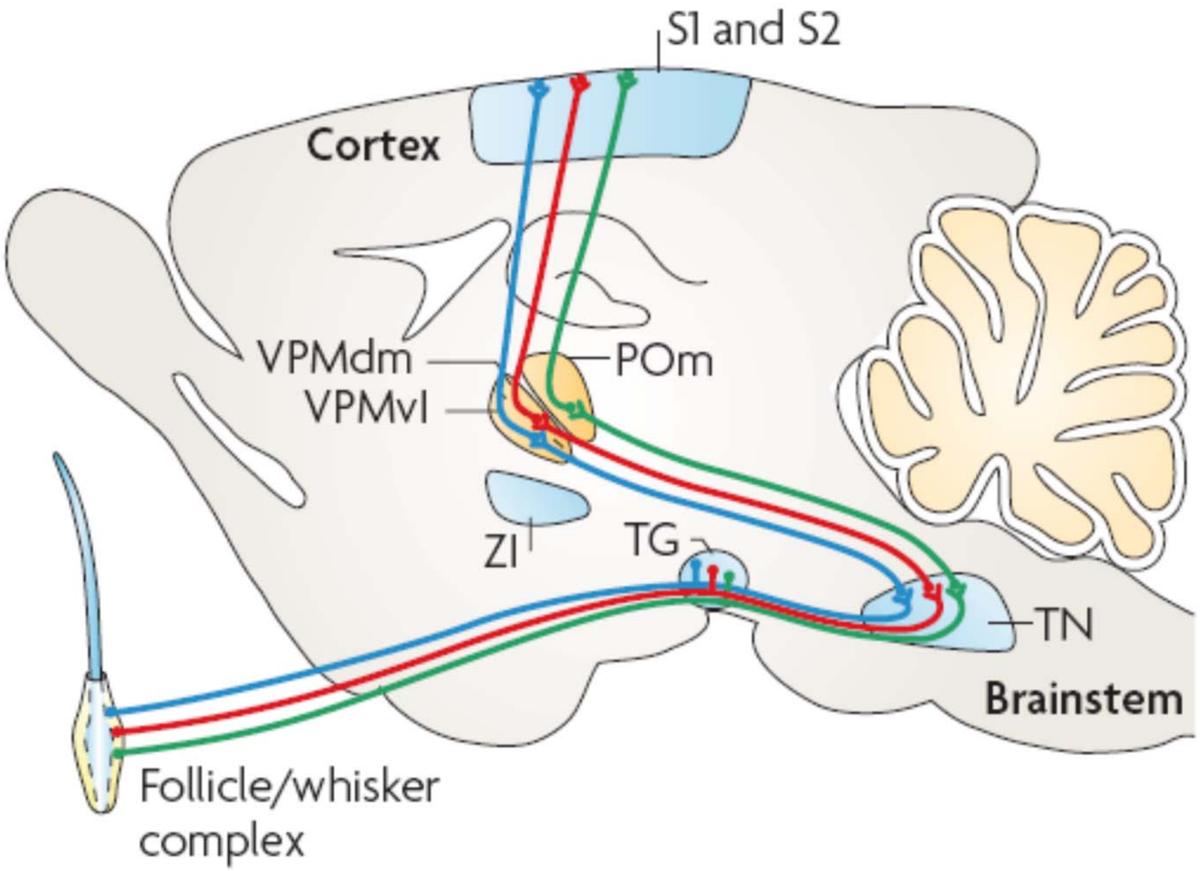


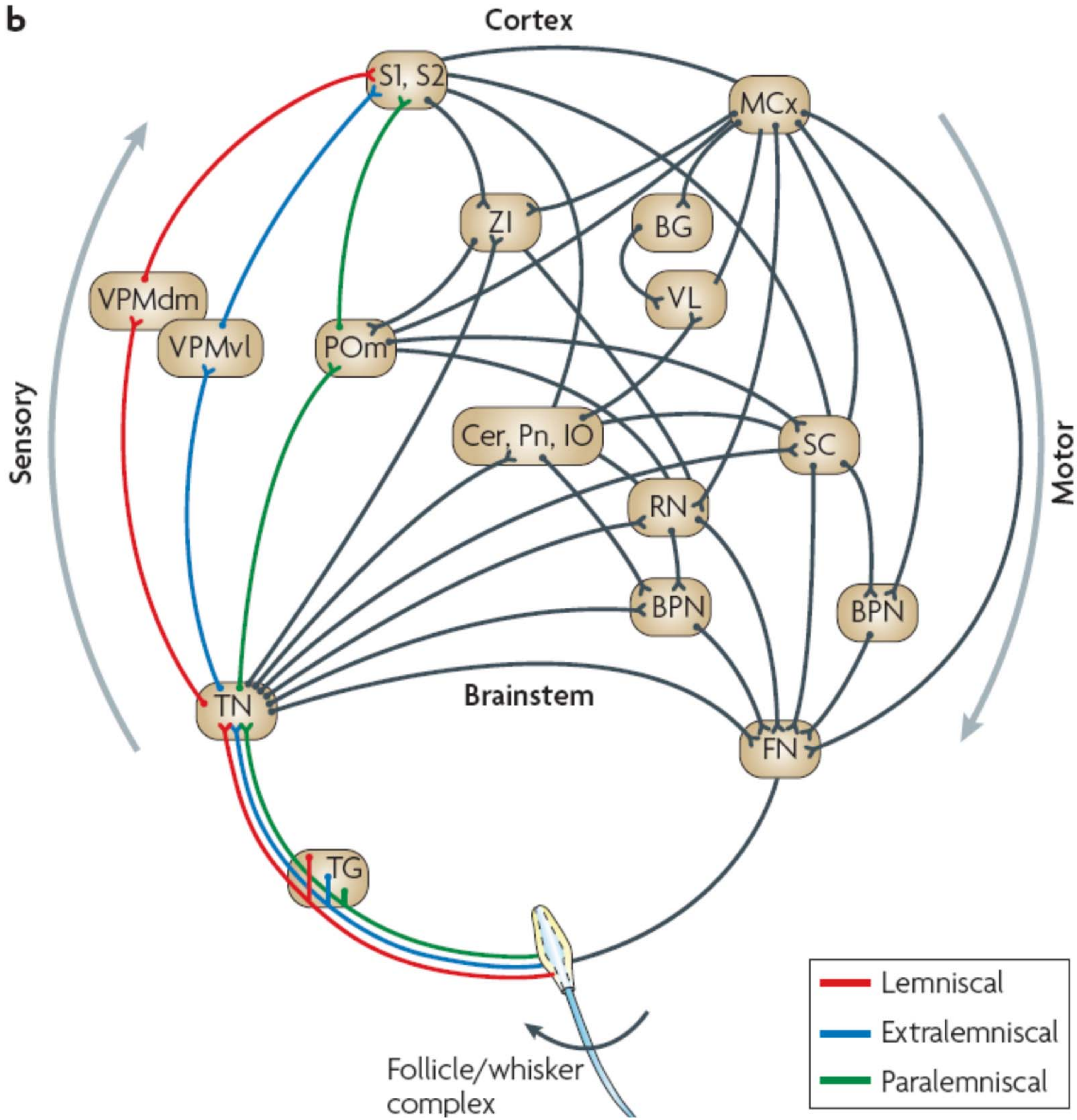
Sensory signal conduction

The vibrissal system

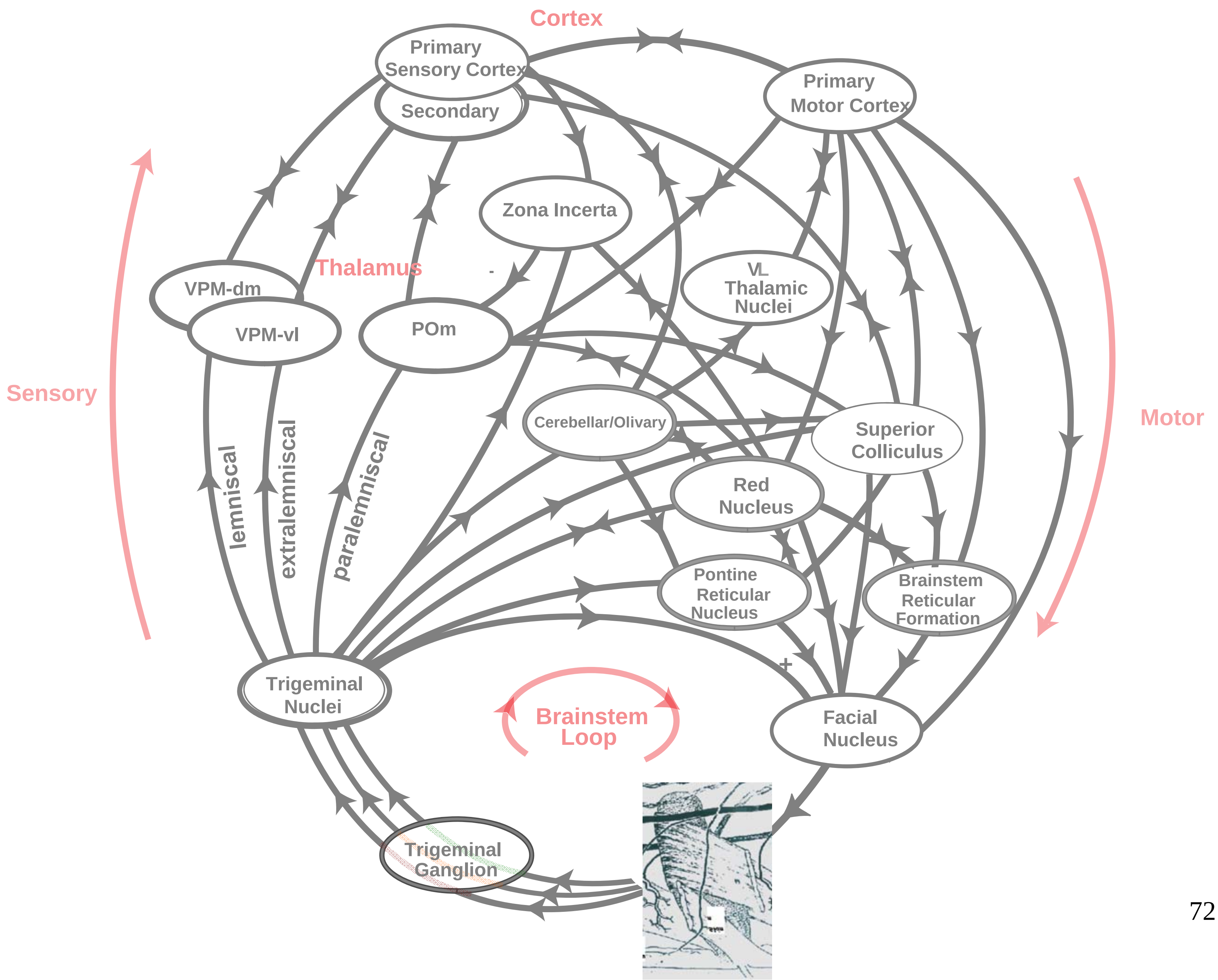
whisker





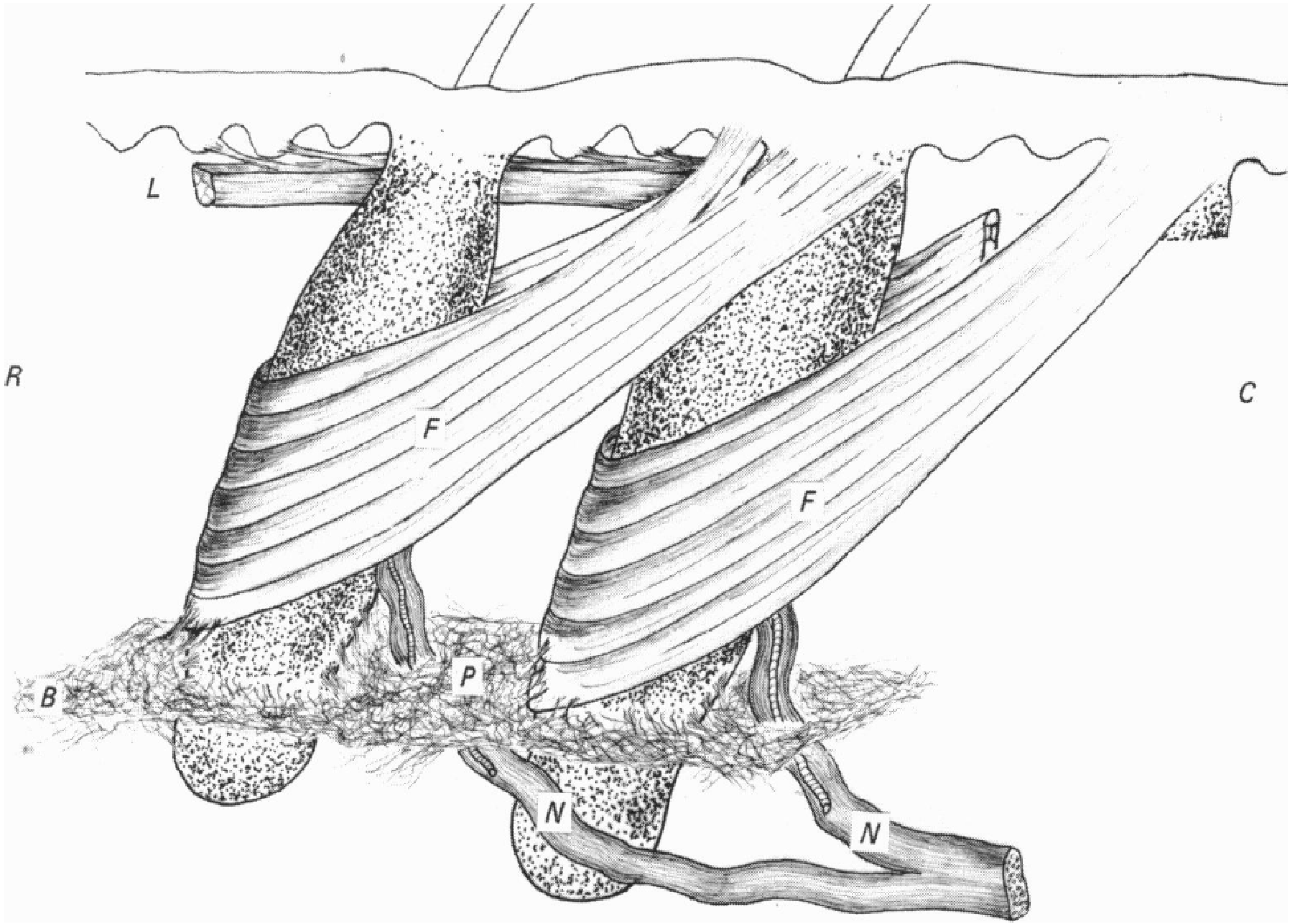

b
Cortex
S1, S2
MCx
ZI
BG
VL
VPMdm
VPMvl
POm
Cer, Pn, IO
SC
RN
BPN
BPN
Sensory
Motor
Brainstem
TN
FN
TG
Follicle/whisker complex
Lemniscal
Extralemniscal
Paralemniscal

Sensory-motor loops of the vibrissal system



Motor control of whiskers

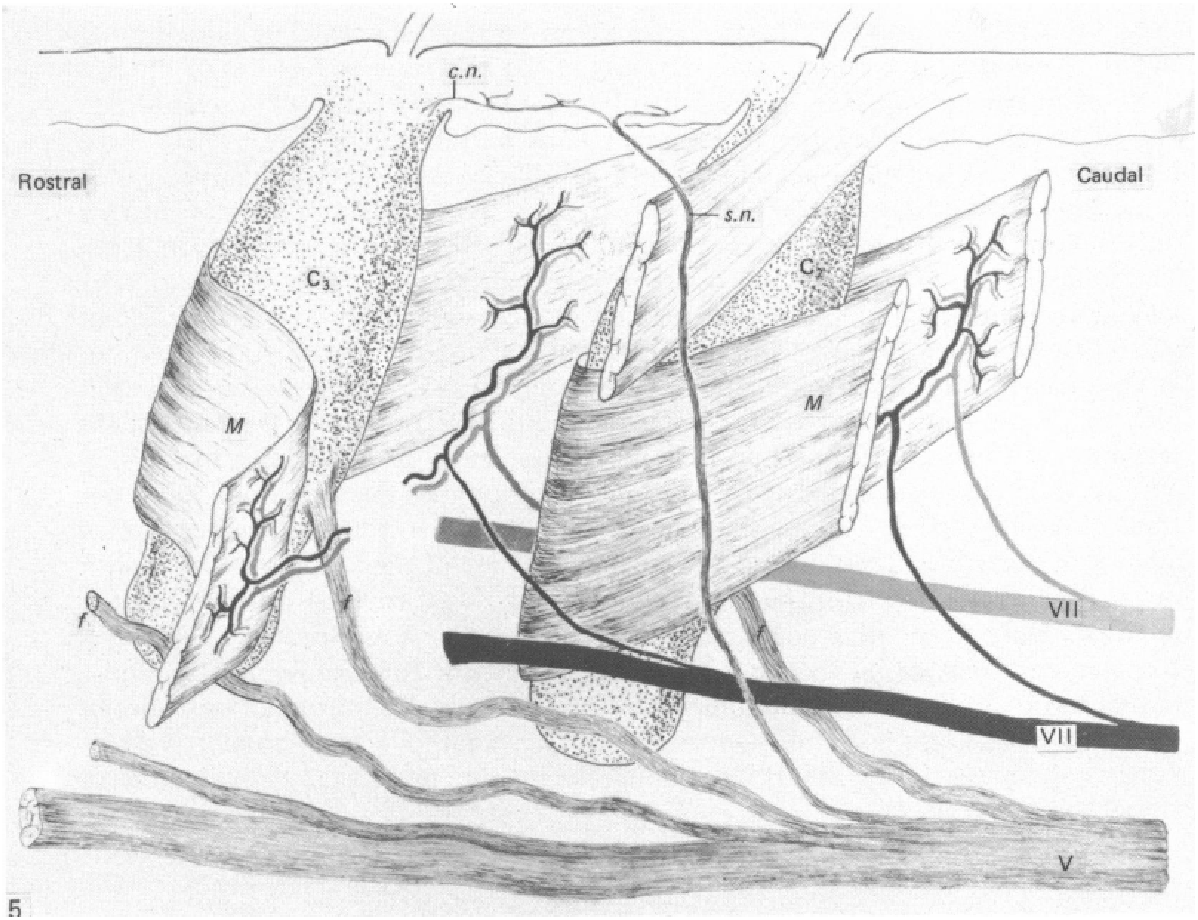
Intrinsic muscles



Dorfl J, 1982, J Anat 135:147-154

Follicle as a motor-sensory junction

- Motor signals move the follicle and whisker
- Follicle receptors report back details of self motion = proprioception
- Plus perturbations of this motion caused by the external world



Dorfl J, 1985, J Anat 142:173-184

Reception of neuronal signals in the brain

Exteroception – reception of the external world via the six senses: sight, taste, smell, touch, hearing, and balance

Interoception: reception of the internal organs of the body

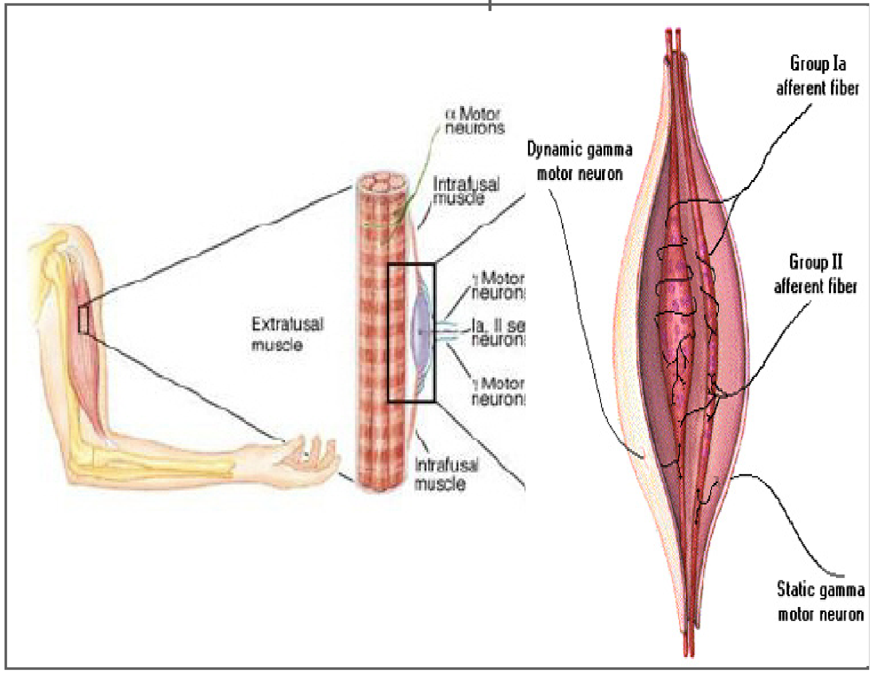
Proprioception (from "one's own" and reception) reception of the relationships between the body and the world.

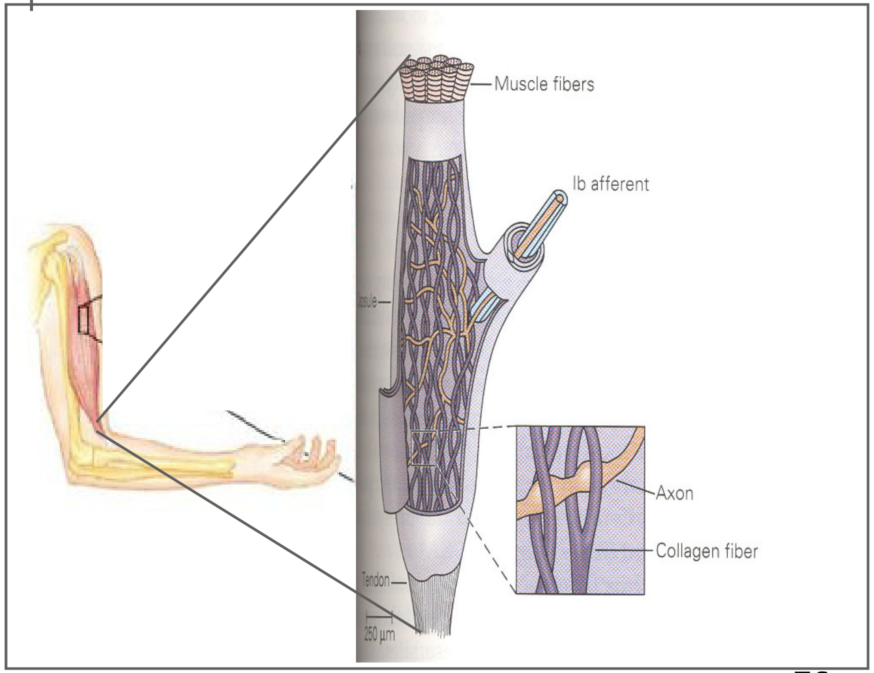
Afferent signals that relate to the external world contain:

- **Reafferent** (self-generated) sensory signals
- **Exafferent** (externally generated) sensory signals

Proprioceptive receptor types

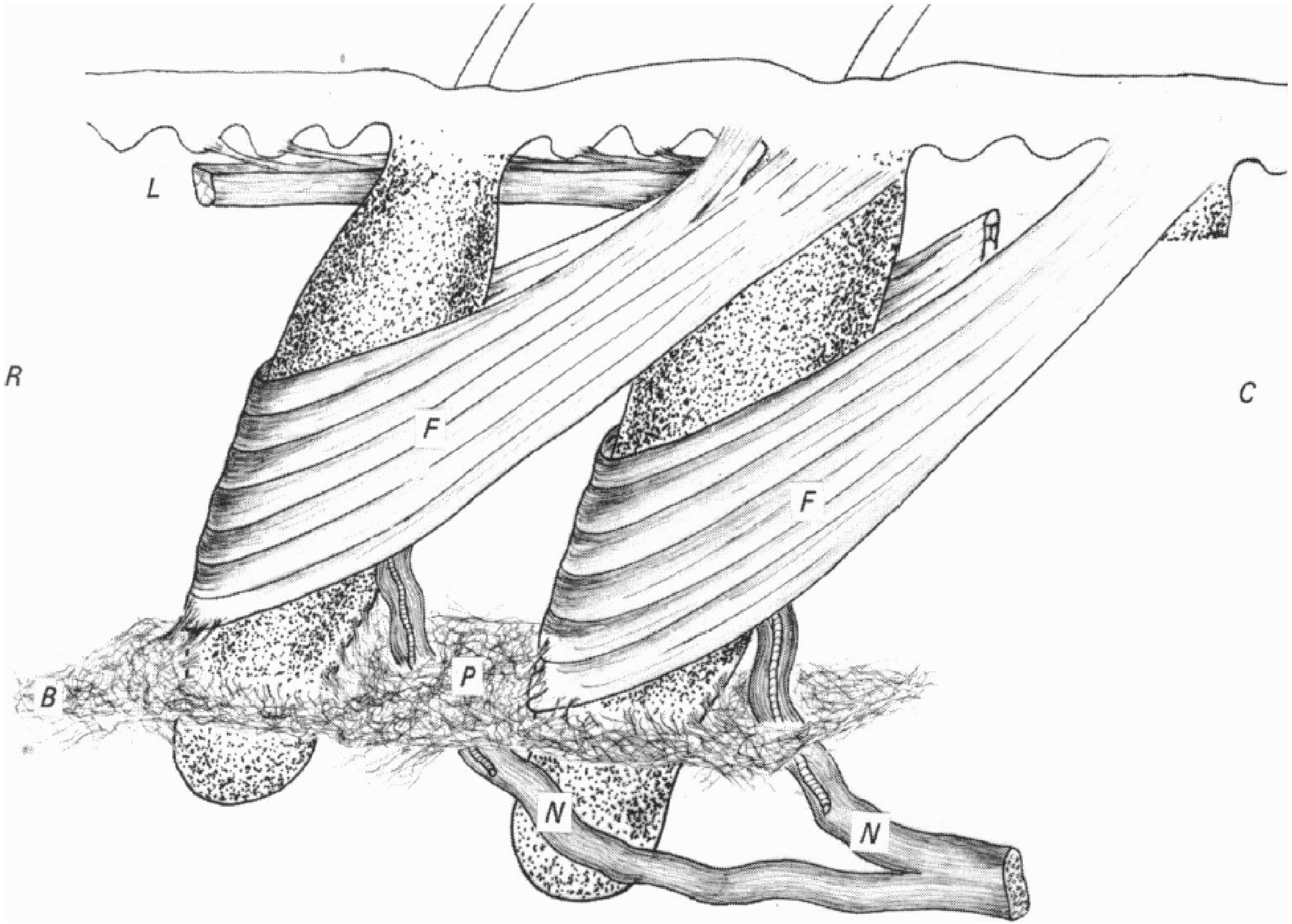
Name:	Muscle spindle receptors	Golgi tendon organs	Joint receptors
Sensitive to:	muscle length	muscle tension	Flexion, extension





Motor control of whiskers

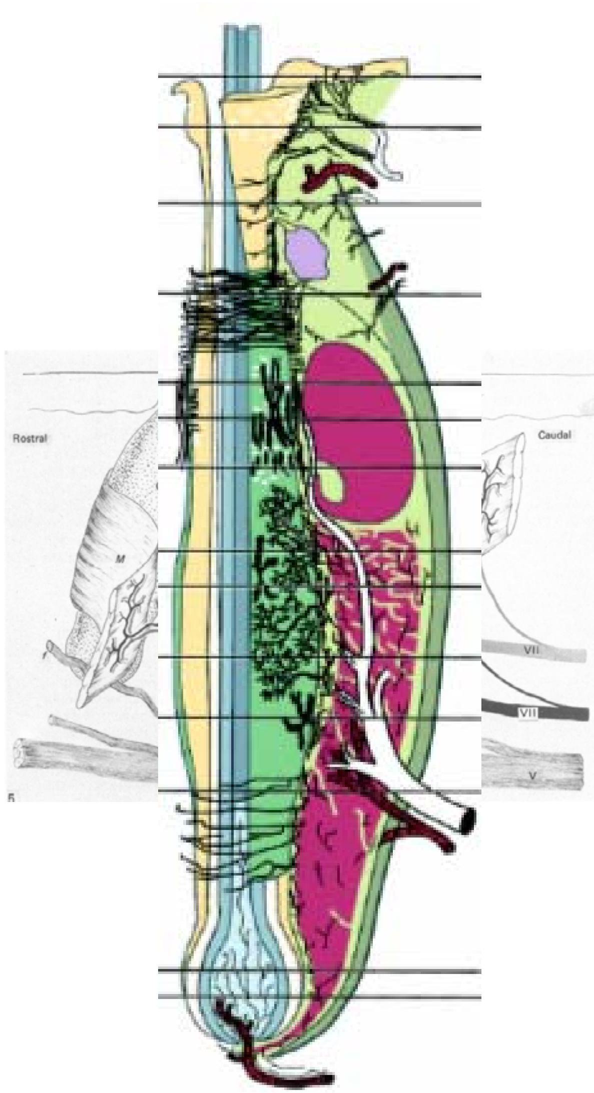
Intrinsic muscles



Dorfl J, 1982, J Anat 135:147-154

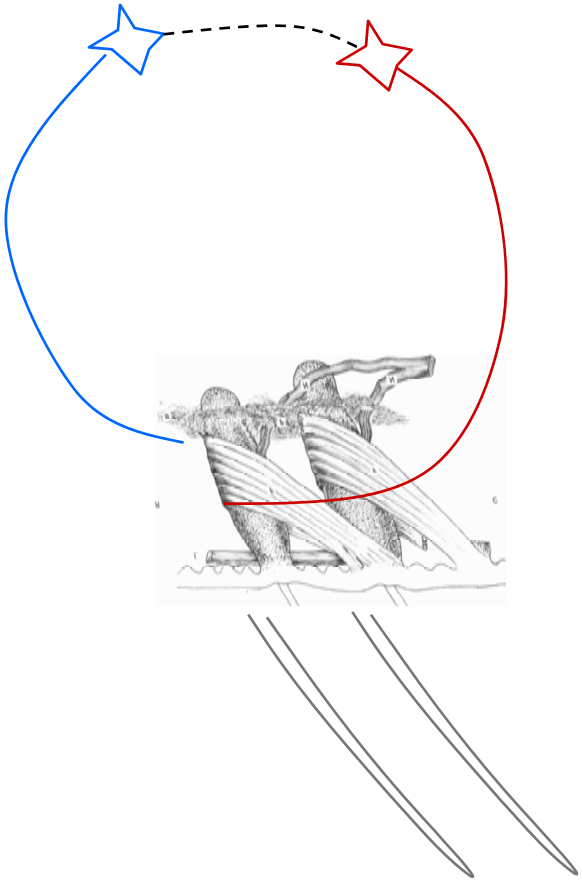
Vibrissal proprioception

- Each follicle contains ~2000 receptors
- About 20% of them convey pure proprioceptive information



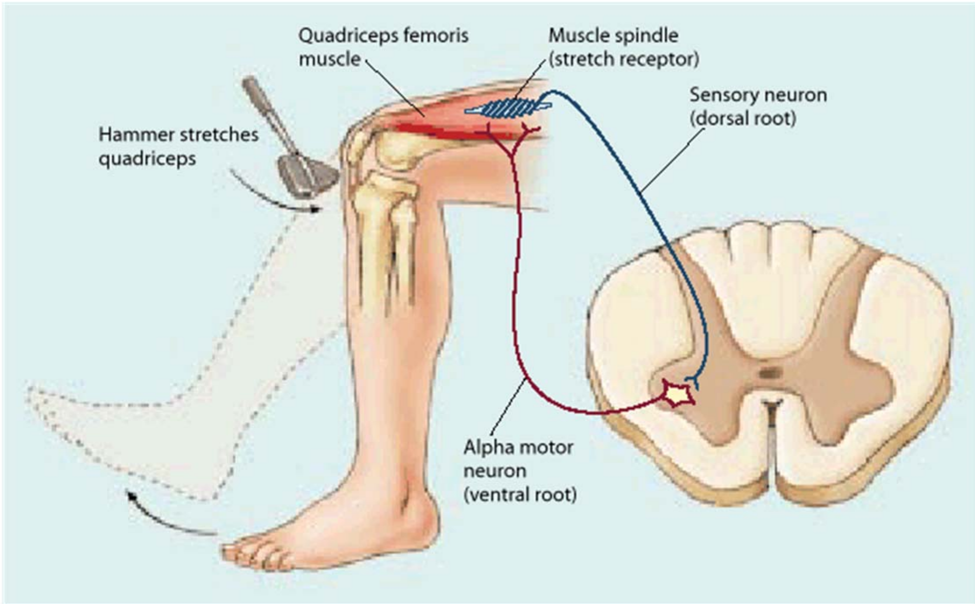
Vibrissal system

Proprioceptive loop

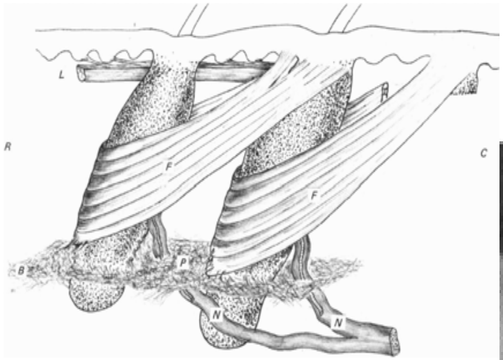


Skeletal system

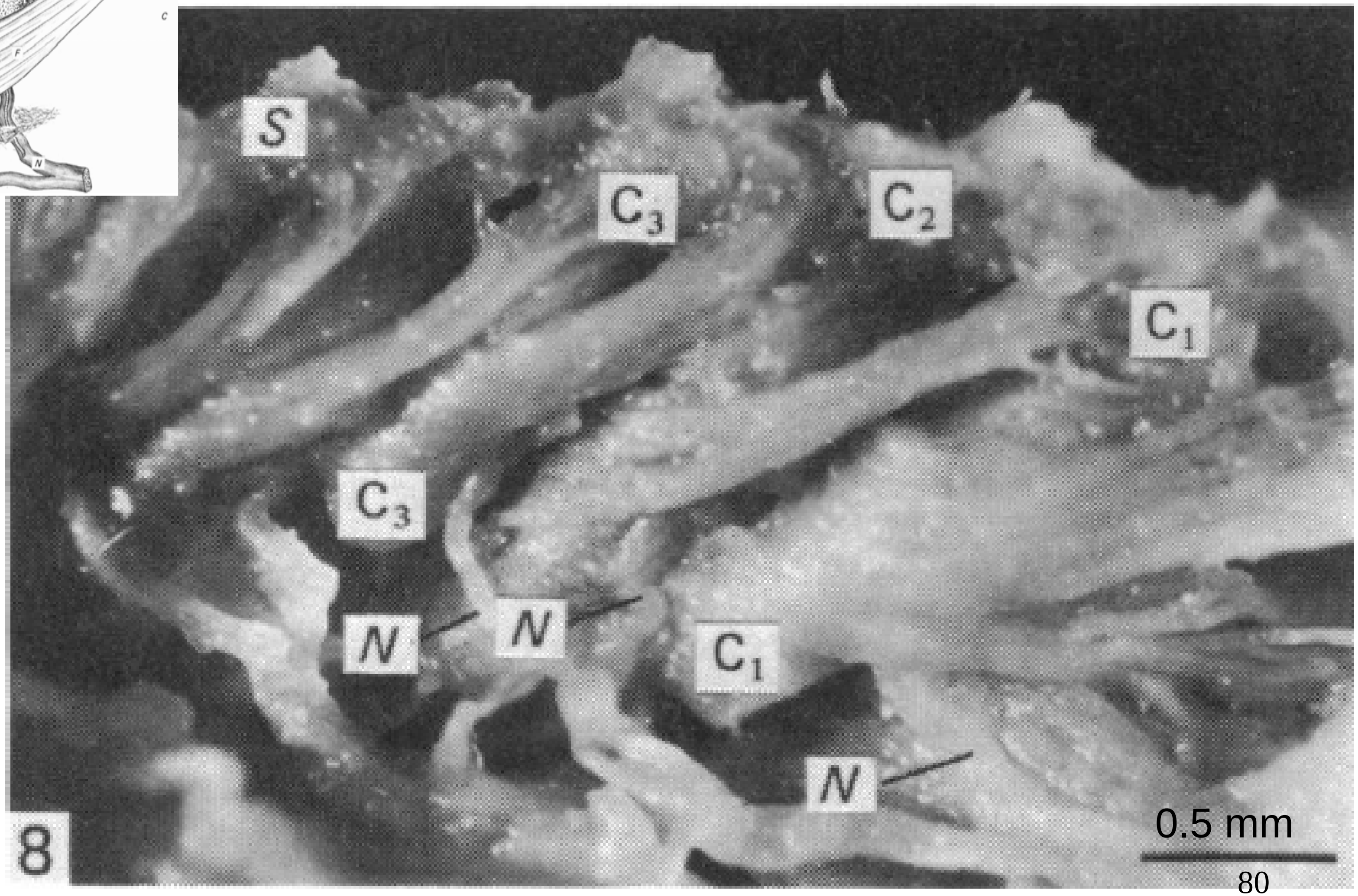
Proprioceptive loop



Whiskers come with different muscle sizes

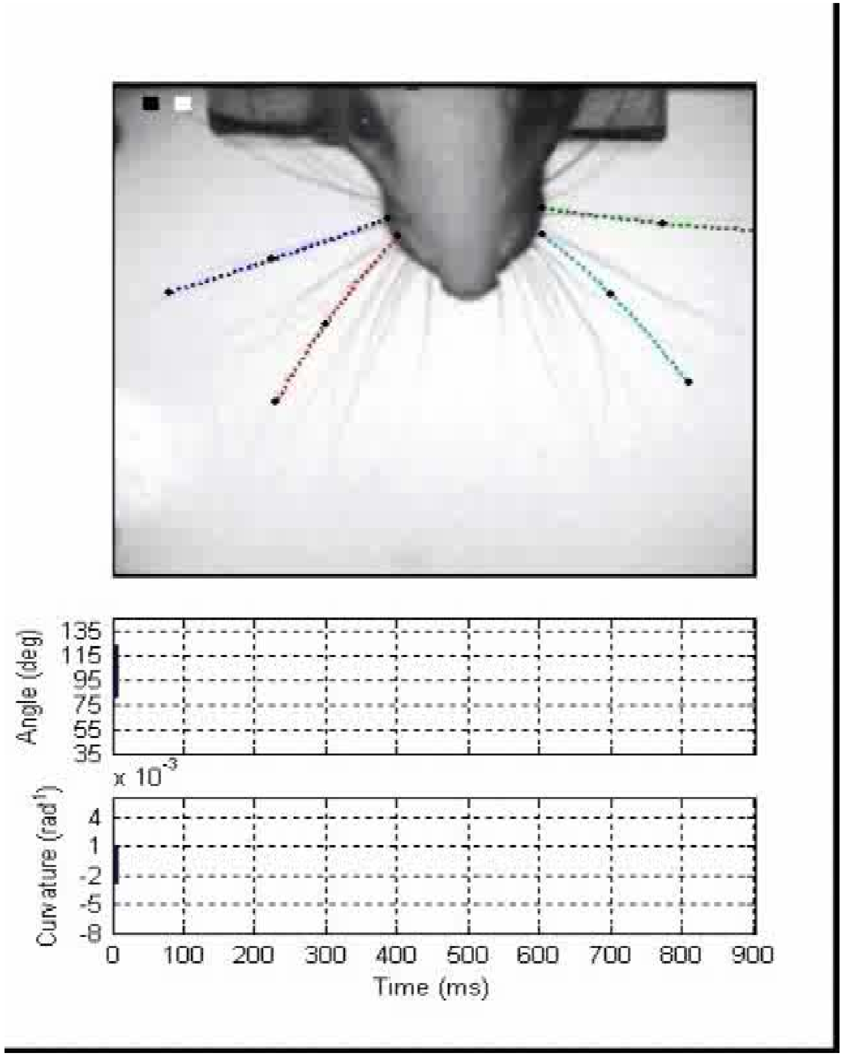


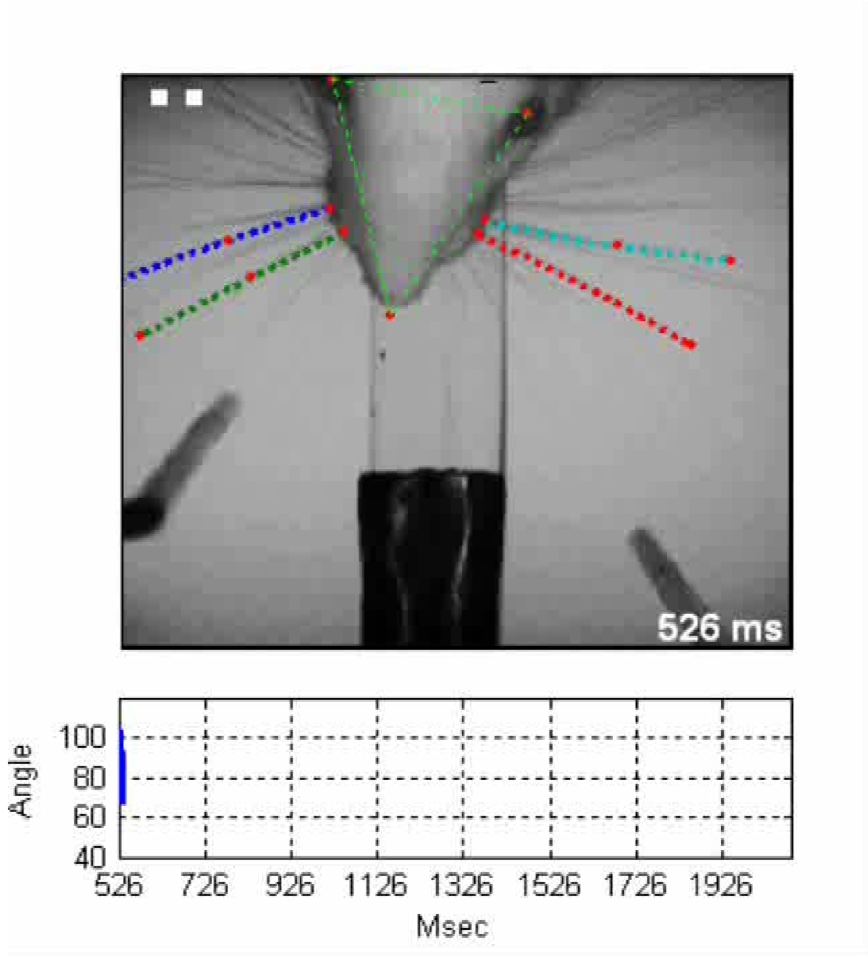
Intrinsic muscles



Dorfl J, 1982, J Anat 135:147-154

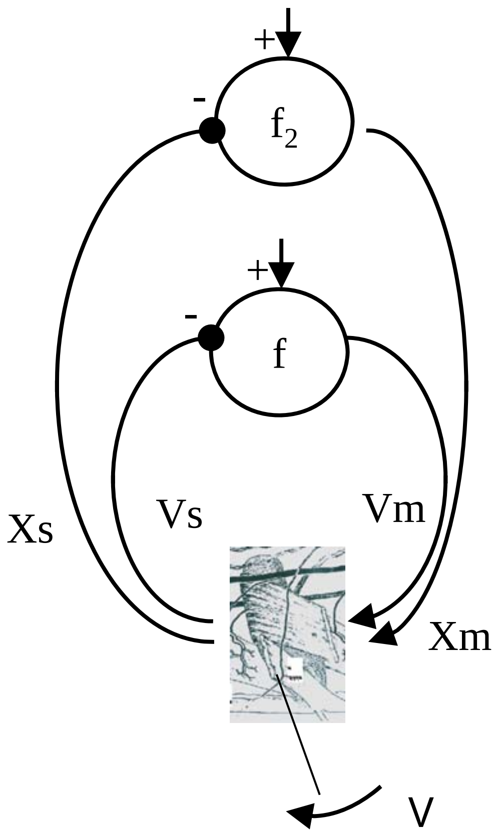
Whisking behavior – reflections of control loops





Closed loops in active sensing

The controlled variables can be

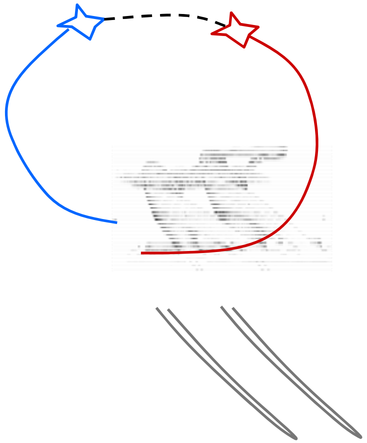


- Motor (via Xs)
  (velocity, amplitude, duration)
- Sensory (Xs)
  (Intensity, phase, …)
- Object (via Xm – Xs relationships)
  (location, SF, identity, …)

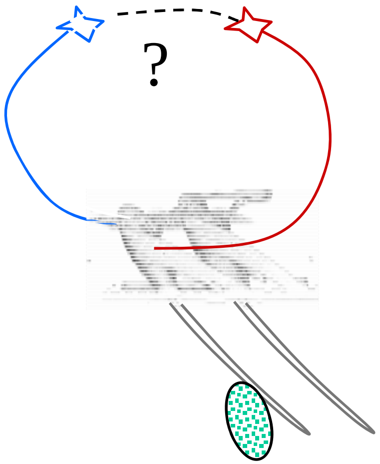
- **Tradeoffs**
- **Controlled versus modulated variables**
- **How to figure it out?**
  perturbations …

Vibrissal system

Proprioceptive loop

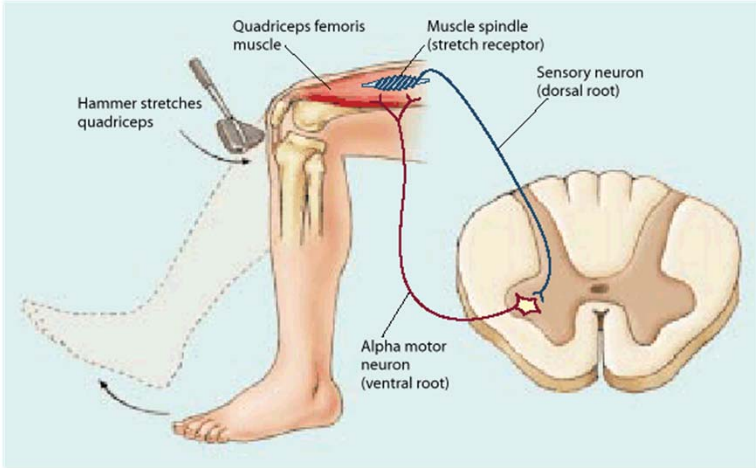


Contact loop

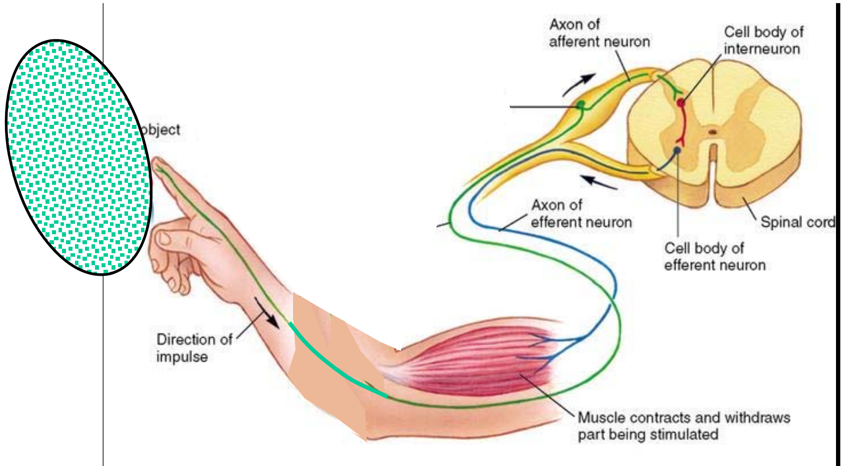


Skeletal system

Proprioceptive loop

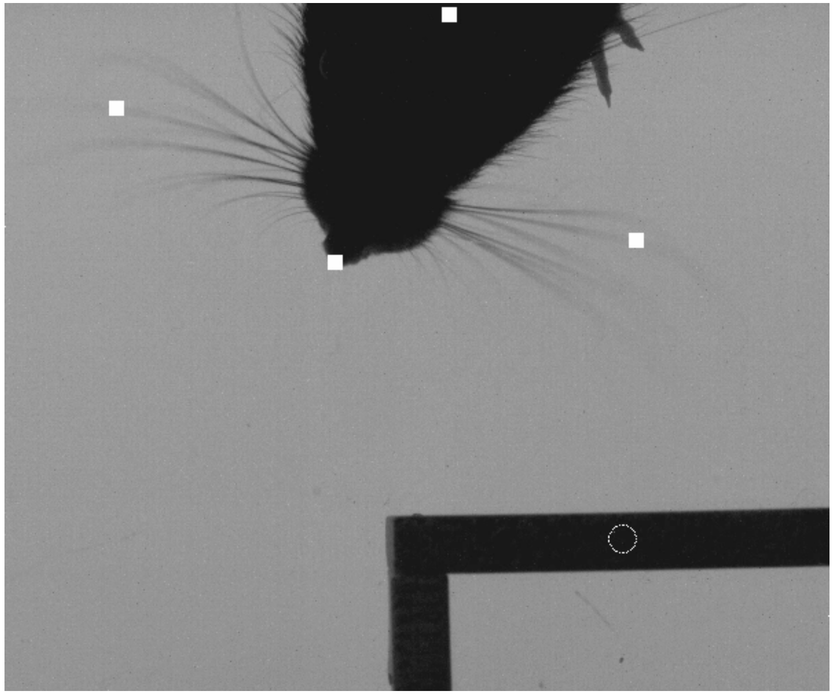


Contact loop

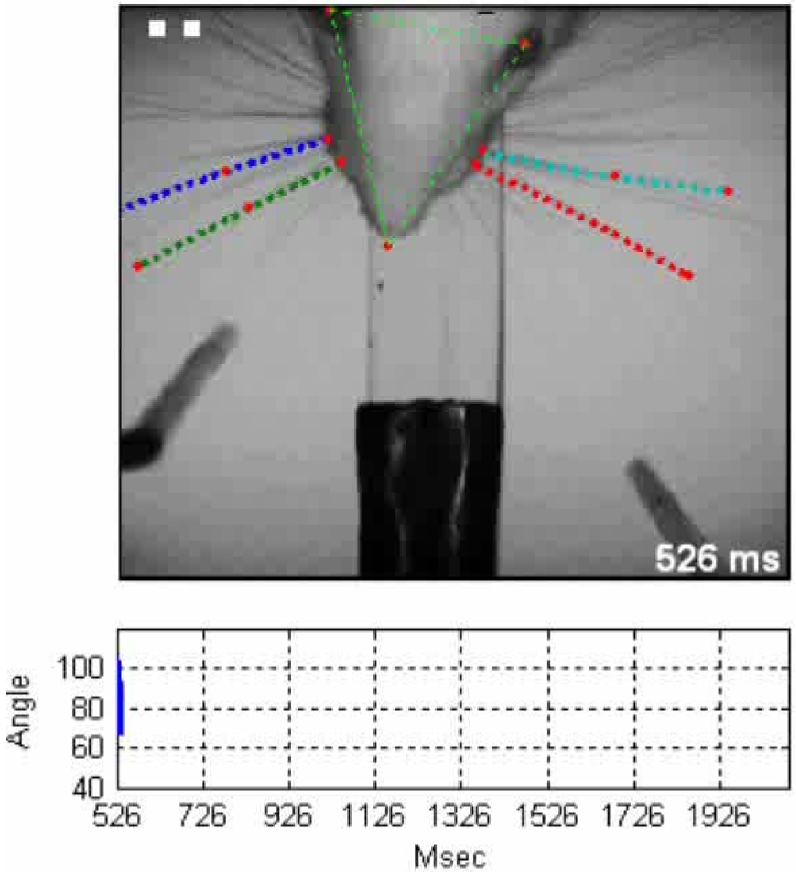


Loop sign – effect of context

Negative contact loop



Positive(?) contact loop



Mitchinson, Martin, Grant, Prescott (2007)
Proc R Soc Biol Sci

Perception of external objects

Object localization

- What signals must the brain process in order to infer a location of an external object in space?
- Reafferent + exafferent signals

Mimicry of active touch

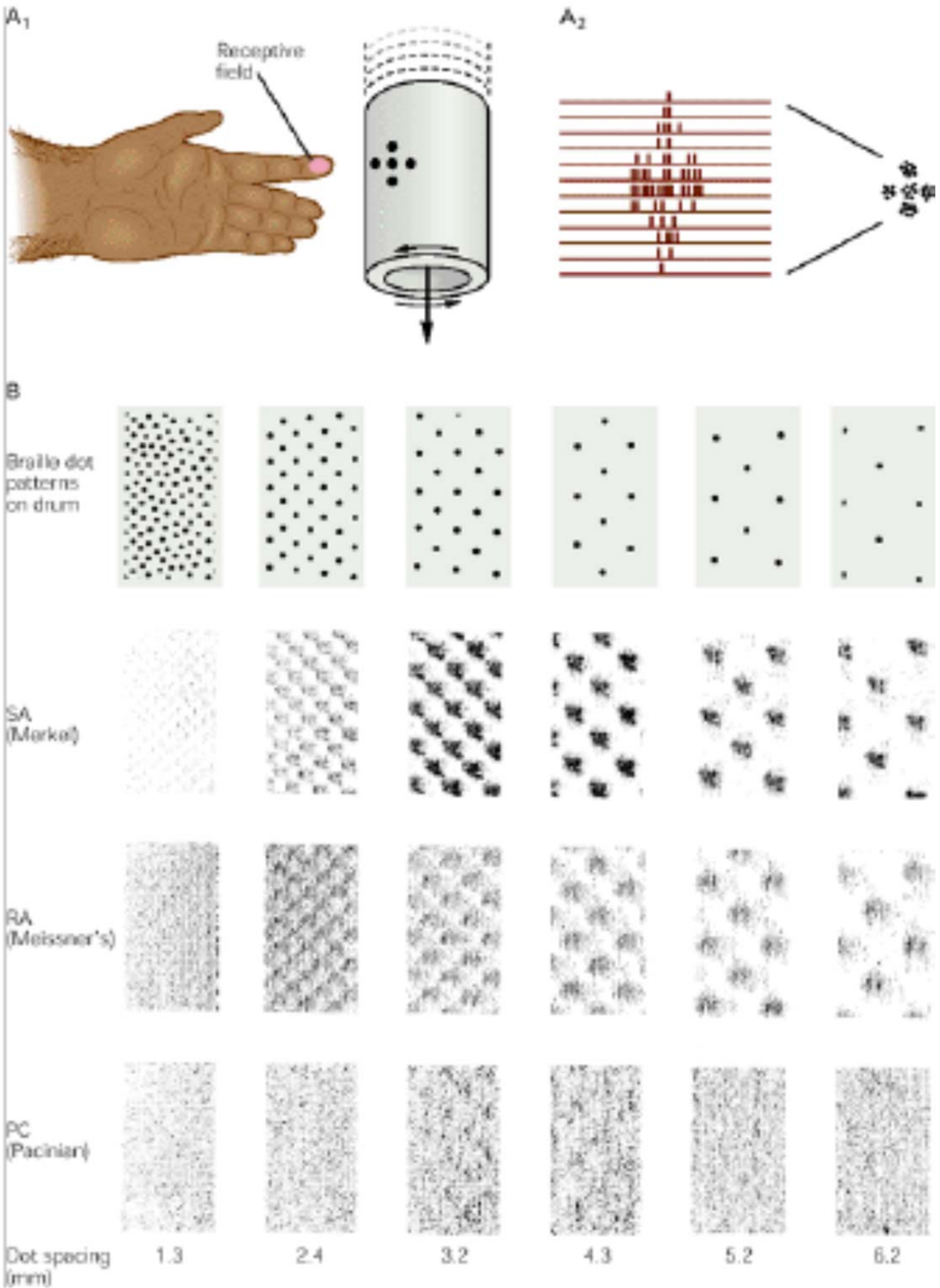


Figure 22-8 The firing patterns of mechanoreceptors in the superficial layers of the skin encode the texture of objects rubbed across the skin.
A. 1. The nerve responses to textures are measured with the hand immobilized. The receptive field of a single receptor on a monkey's finger is stimulated with an embossed array of raised dots on a rotating drum. The pattern moves horizontally over the receptive field as the drum rotates. The experimenter thus controls the speed of movement and the location of the dot pattern in the receptive field. The pattern is moved laterally on successive rotations to allow the dots to cross the medial, central, and lateral portions of the receptive field on successive rotations. The composite response of an individual nerve fiber to successive views of the raised dots simulates the distribution of active and inactive nerve fibers in the population. 2. Sequential action potentials discharged by individual receptors during each revolution of the drum are represented in spatial event plots in which each action potential is a small dot, and each horizontal row of dots represents a scan with the pattern shifted laterally on the finger.
B. Spatial event plots of three types of mechanoreceptors to dot patterns with different spacing. Slowly adapting Merkel disk receptors and rapidly adapting Meissner's corpuscles differentiate between dots and blank space when the spacing of the dots exceeds the receptive field diameter. A receptor fires bursts of action potentials for each dot, spaced by silent intervals. As the dots are brought closer together, the resolution of individual dots blurs. Pacinian corpuscles do not distinguish texture patterns because their receptive fields are larger than the dot spacing. (Reproduced from Connor et al. 1990.)

What the whiskers tell the rat brain

Reafference:

Their own movement

(“Whisking”)

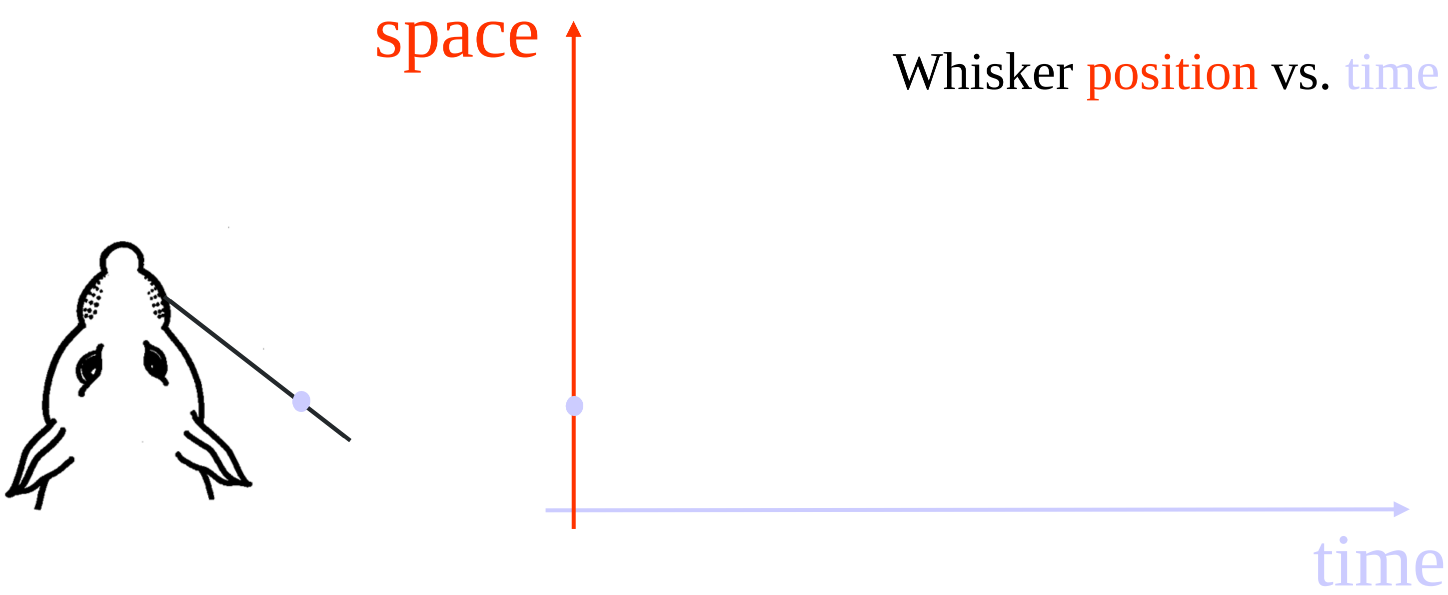
Exafference:

Touch

What the whiskers tell the rat brain

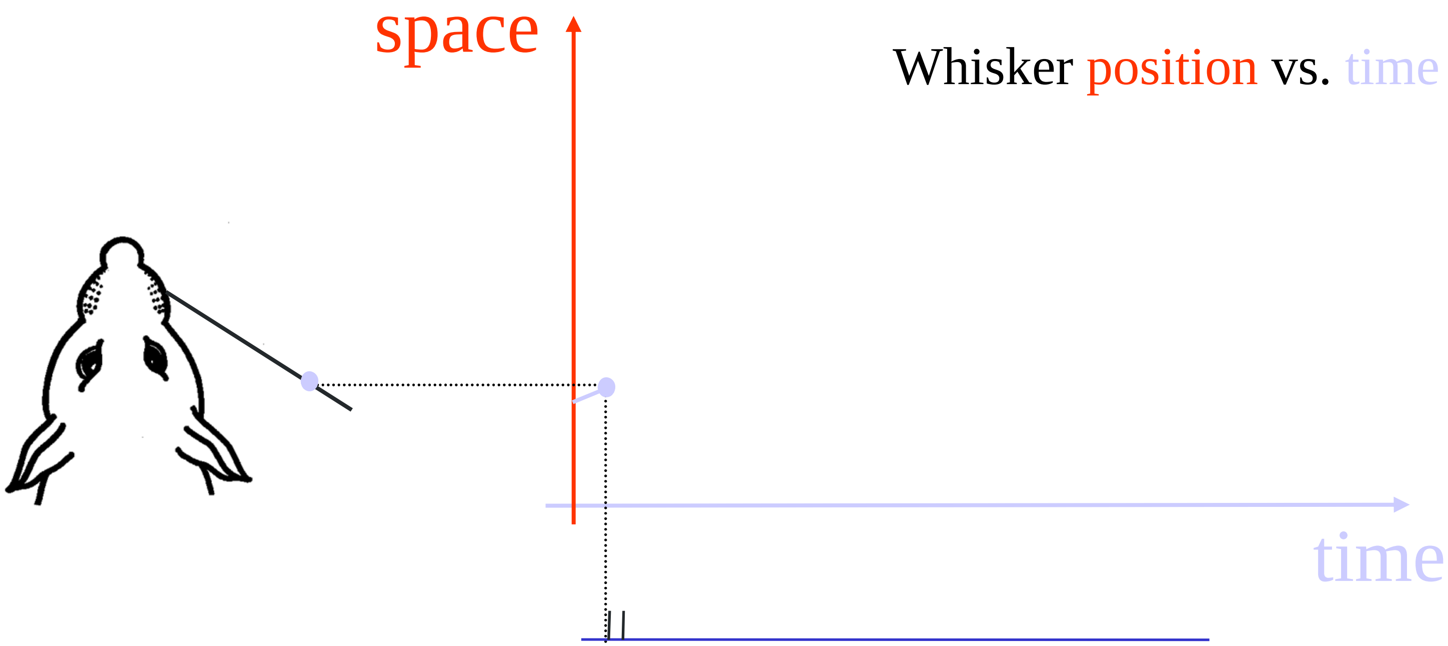
Whisking

Whisker position vs. time



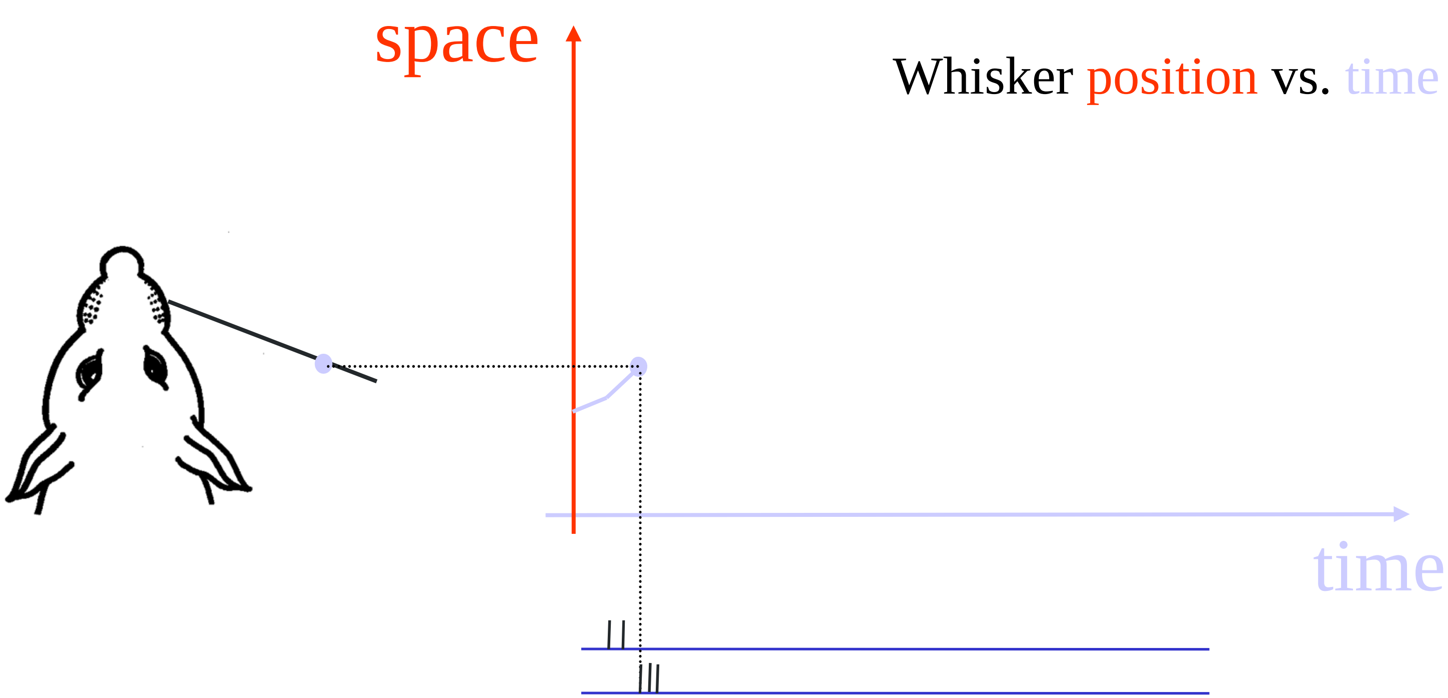
What the whiskers tell the rat brain

Whisking



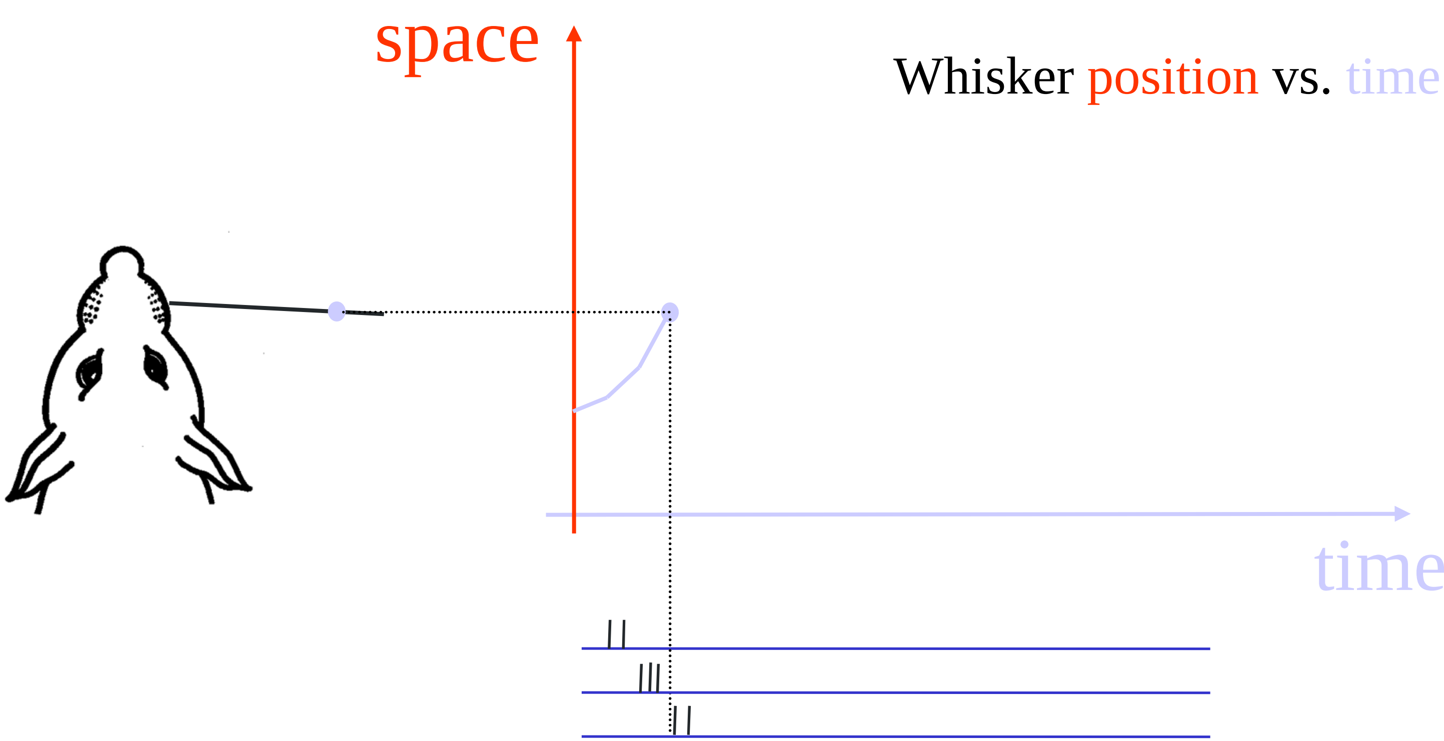
What the whiskers tell the rat brain

Whisking



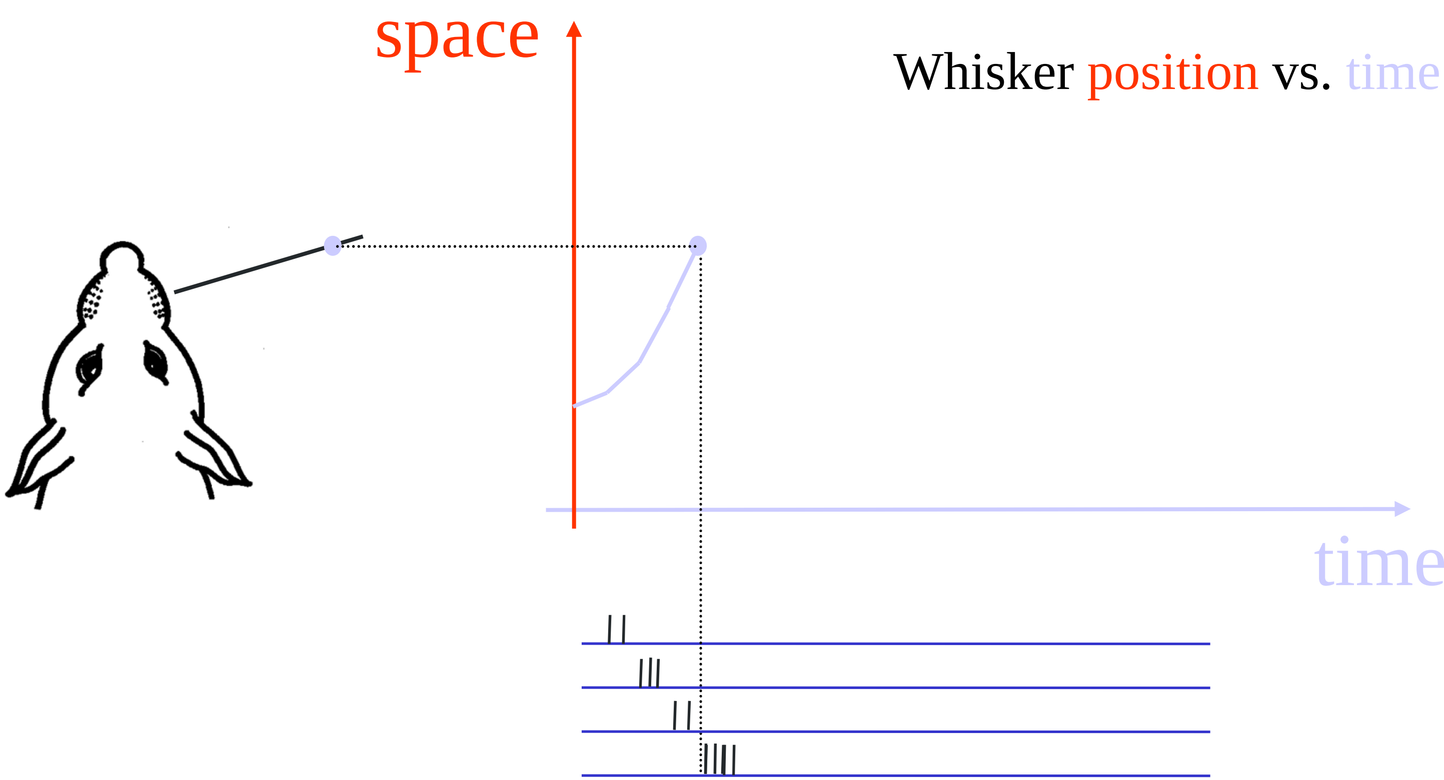
What the whiskers tell the rat brain

Whisking



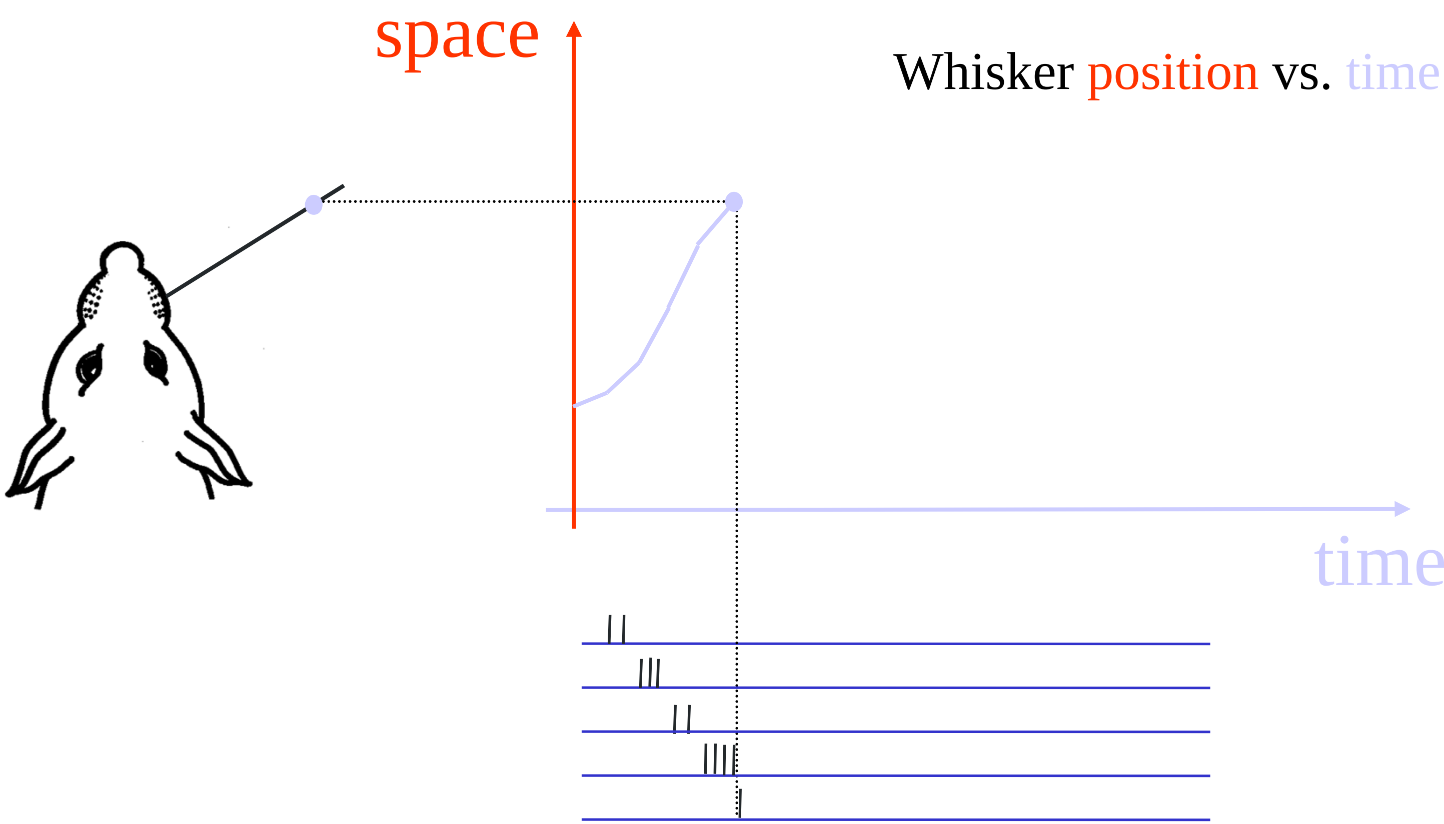
What the whiskers tell the rat brain

Whisking



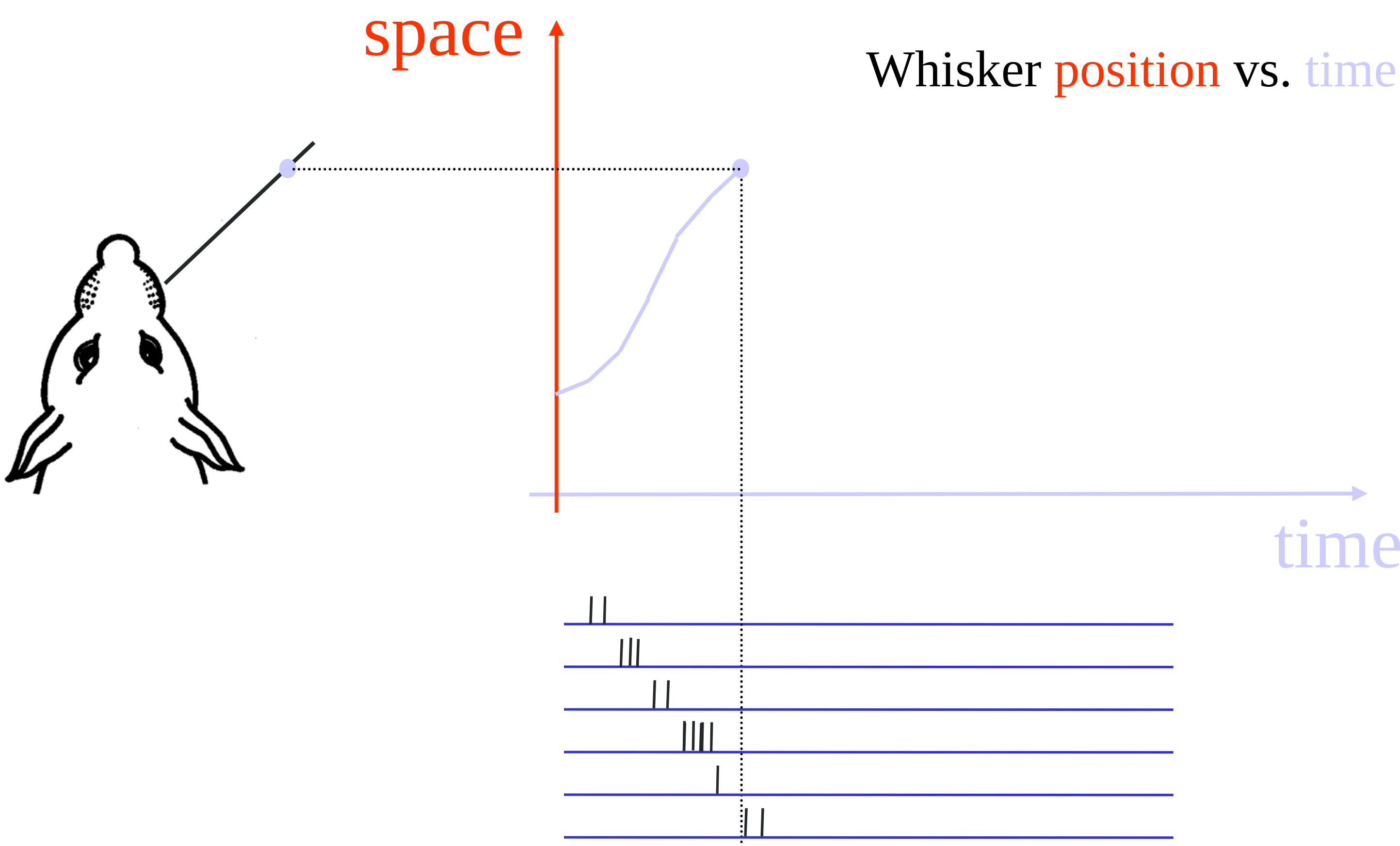
What the whiskers tell the rat brain

Whisking



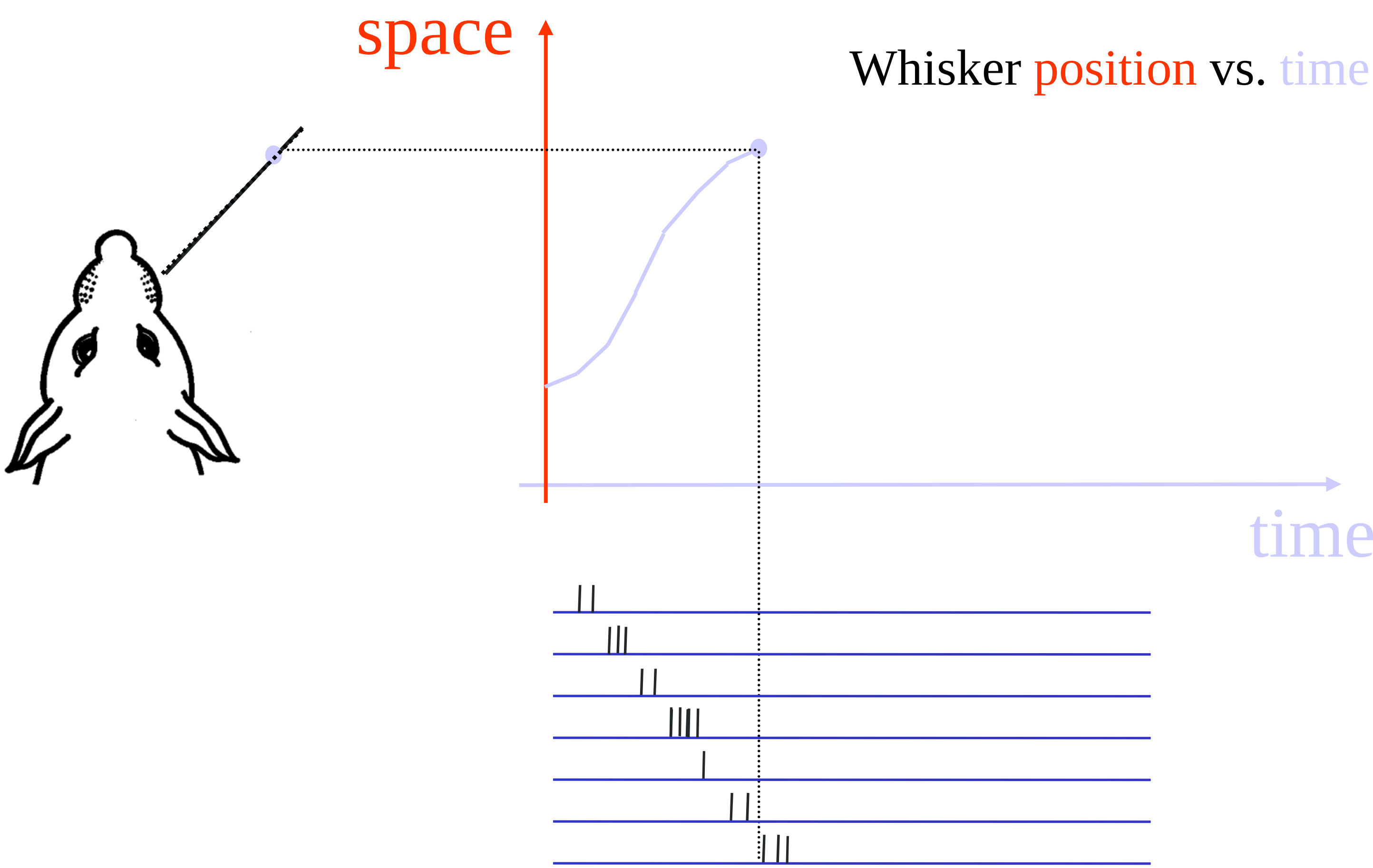
What the whiskers tell the rat brain

Whisking



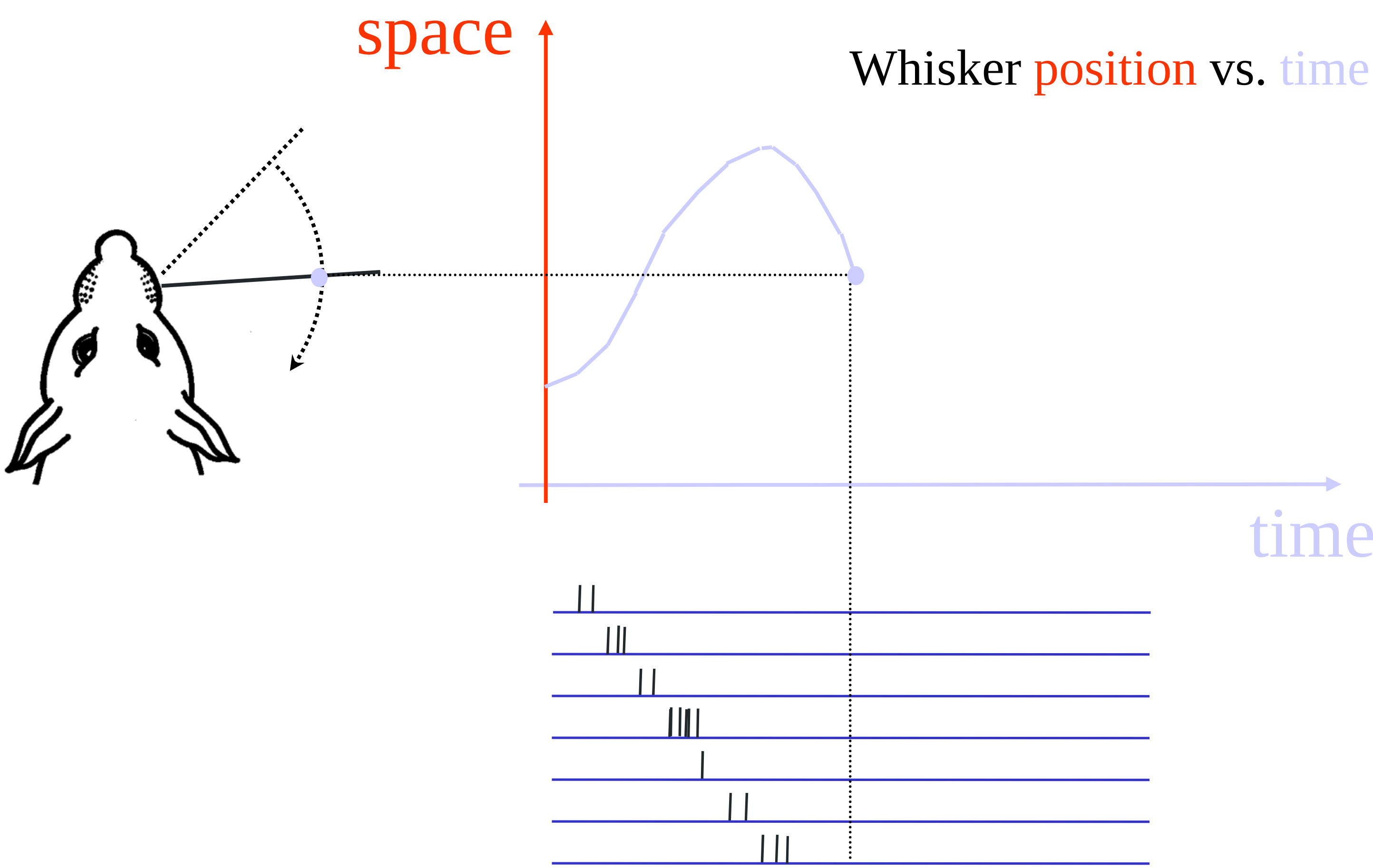
What the whiskers tell the rat brain

Whisking



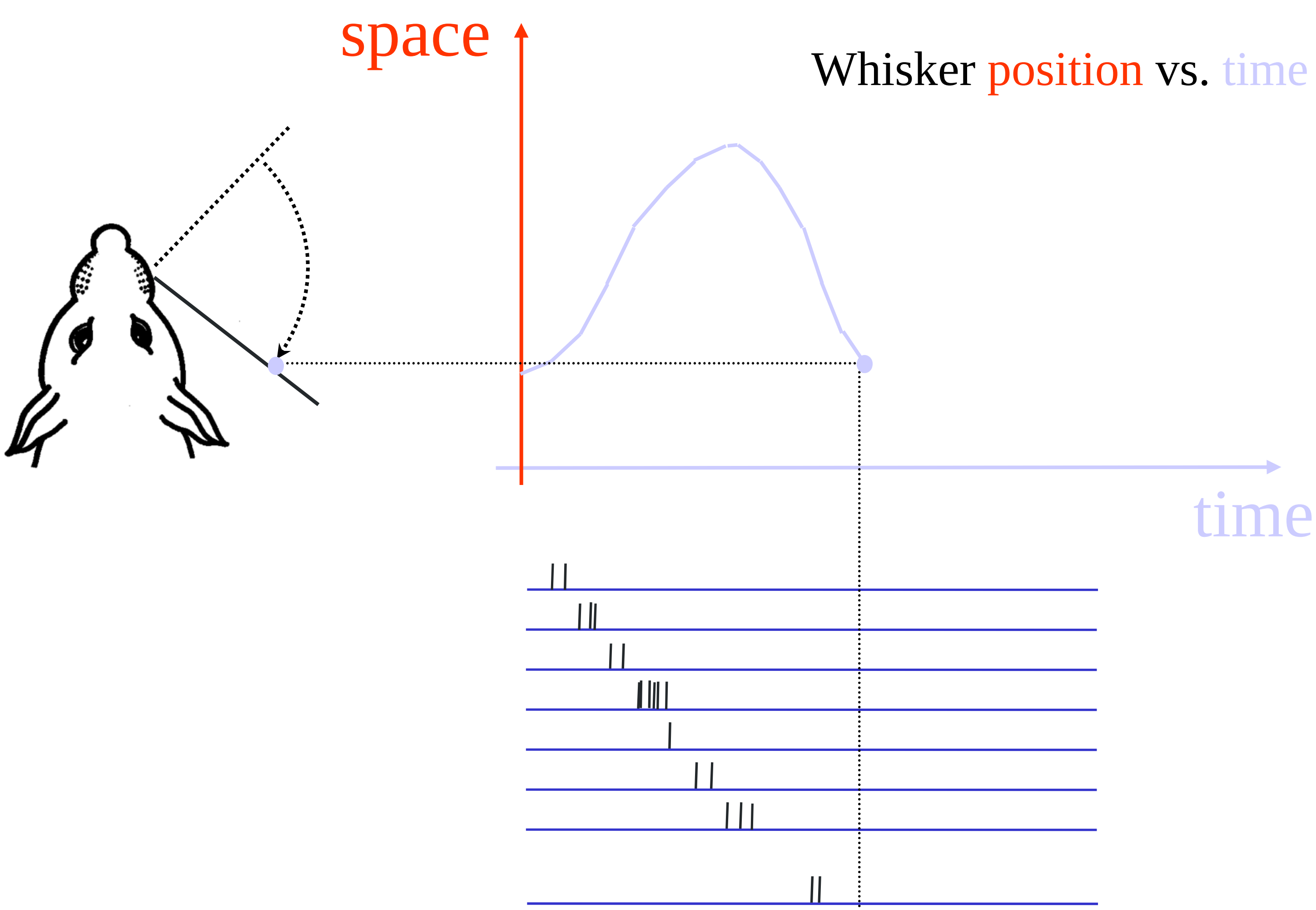
What the whiskers tell the rat brain

Whisking



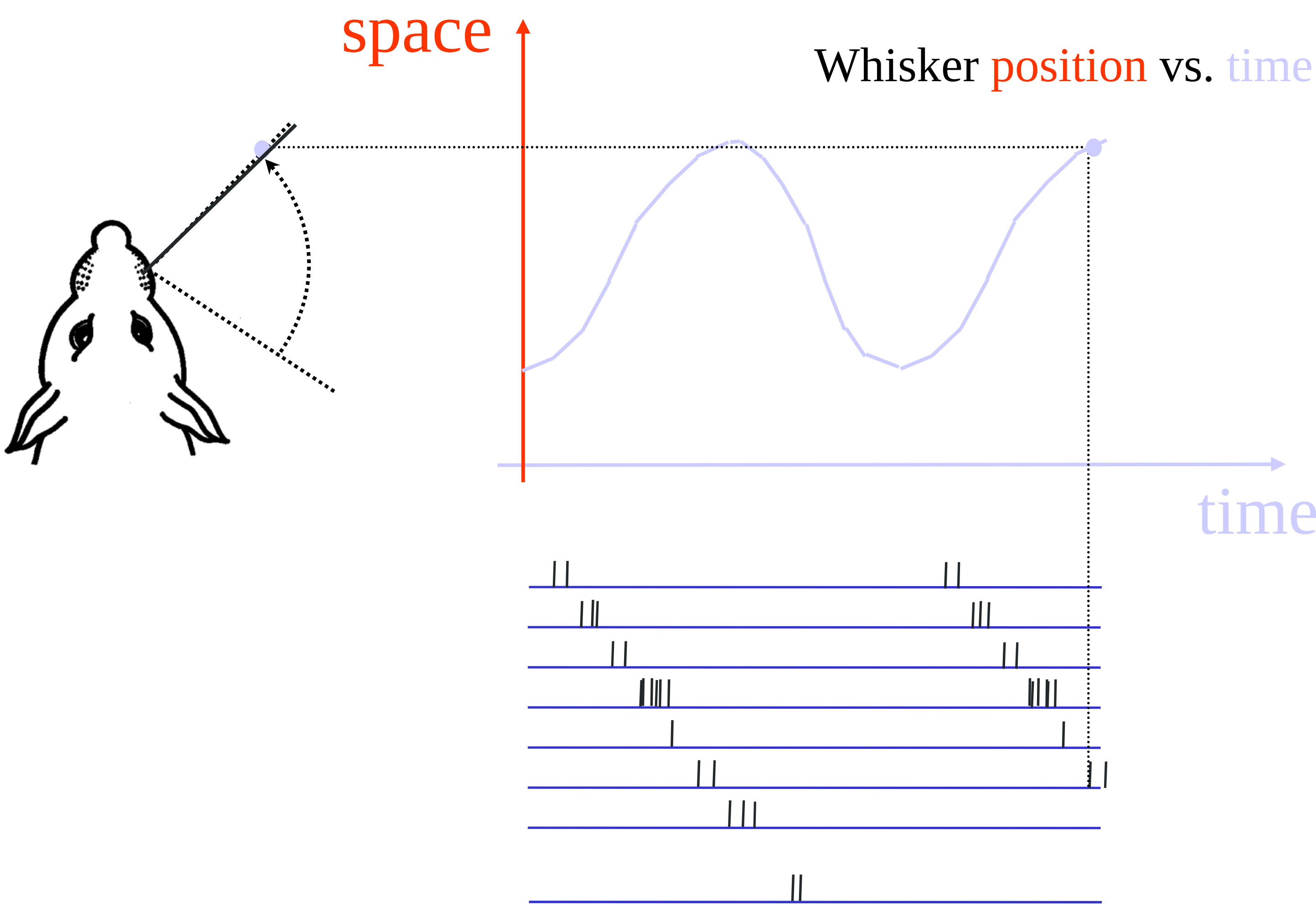
What the whiskers tell the rat brain

Whisking



What the whiskers tell the rat brain

Whisking



What the whiskers tell the rat brain

Reafference:

Their own movement

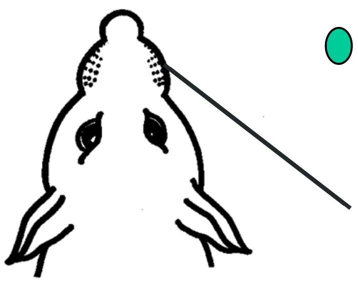
("Whisking")

Exafference:

Touch

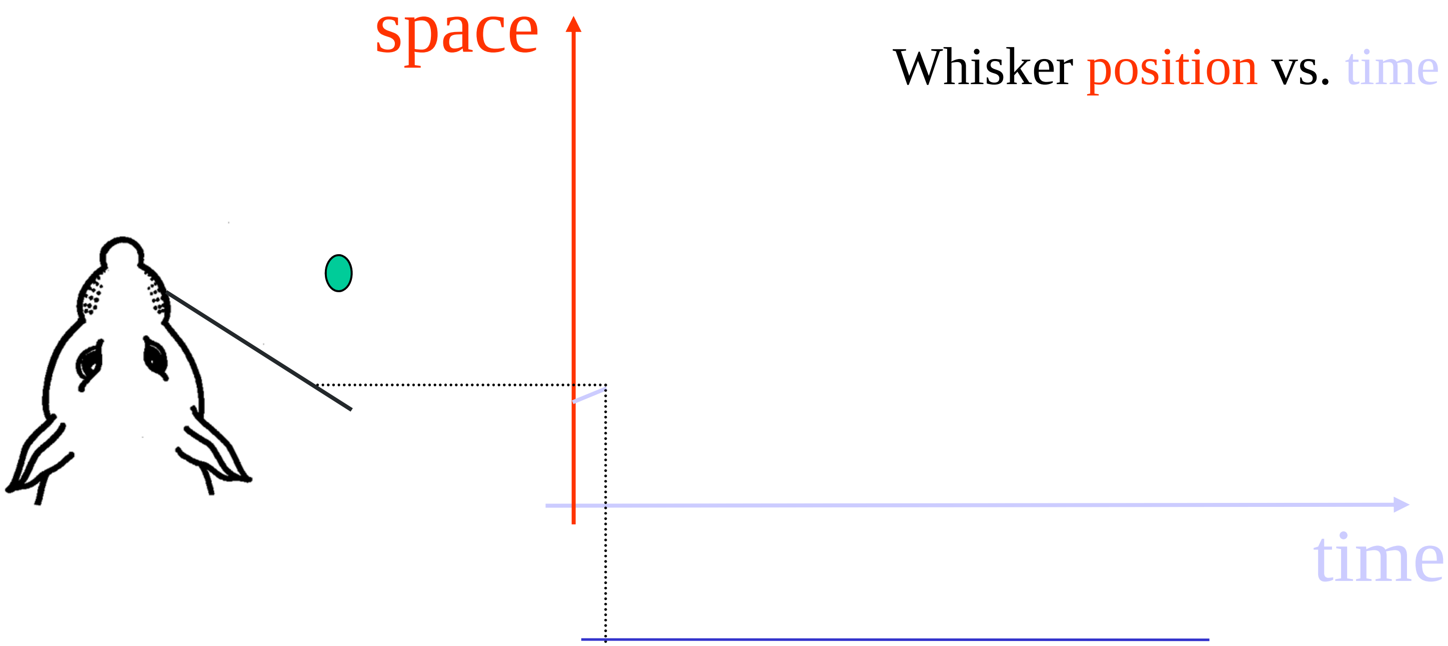
What the whiskers tell the rat brain

Touch



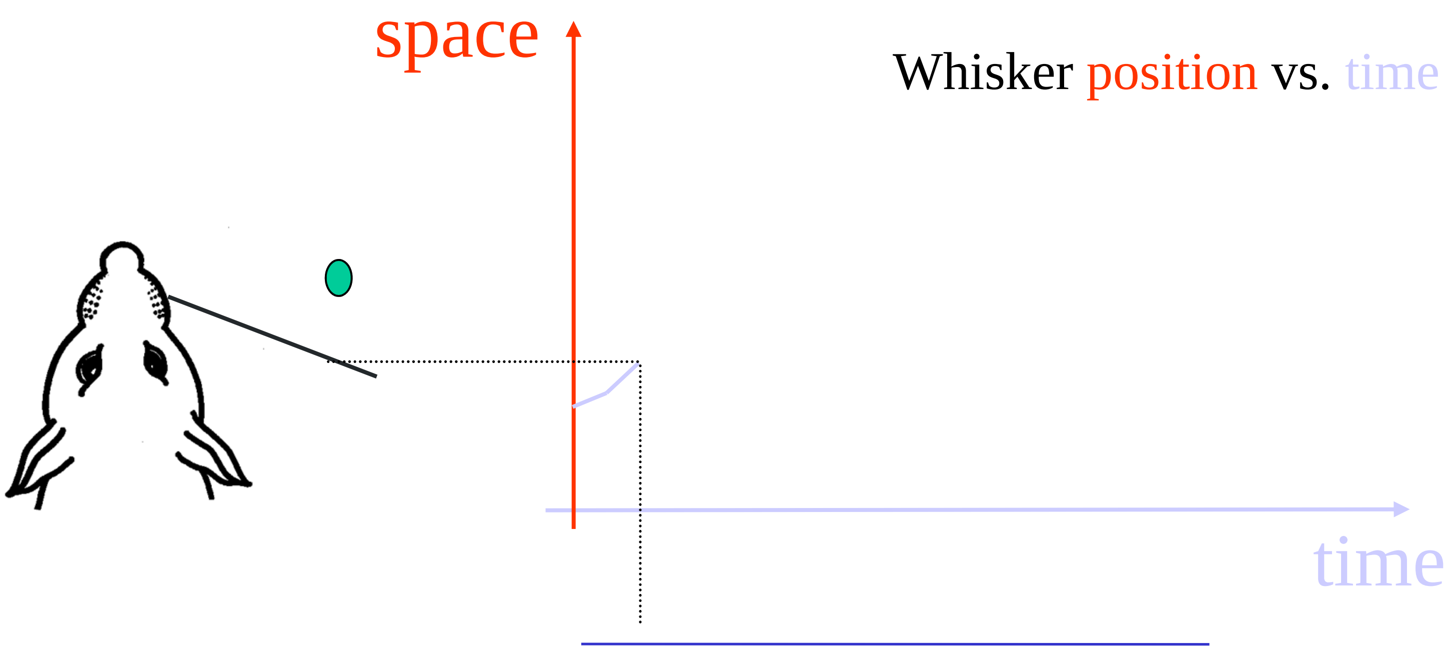
What the whiskers tell the rat brain

Touch



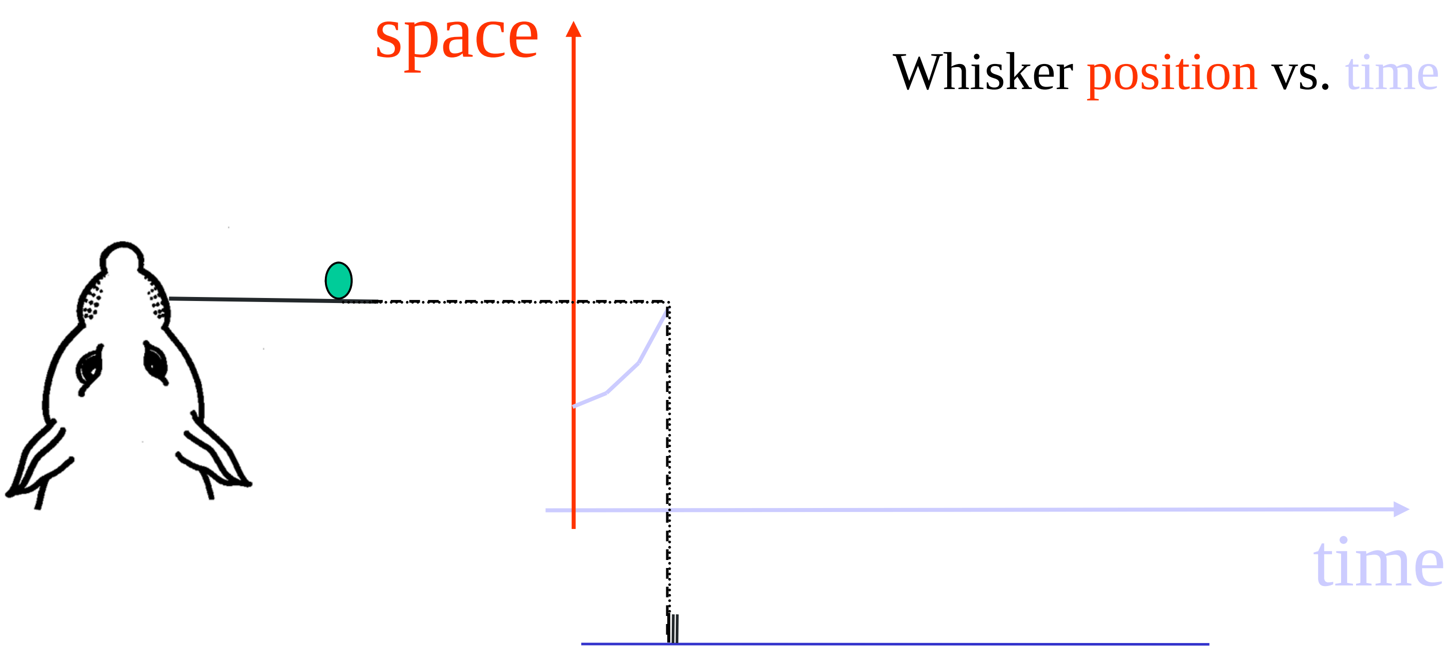
What the whiskers tell the rat brain

Touch



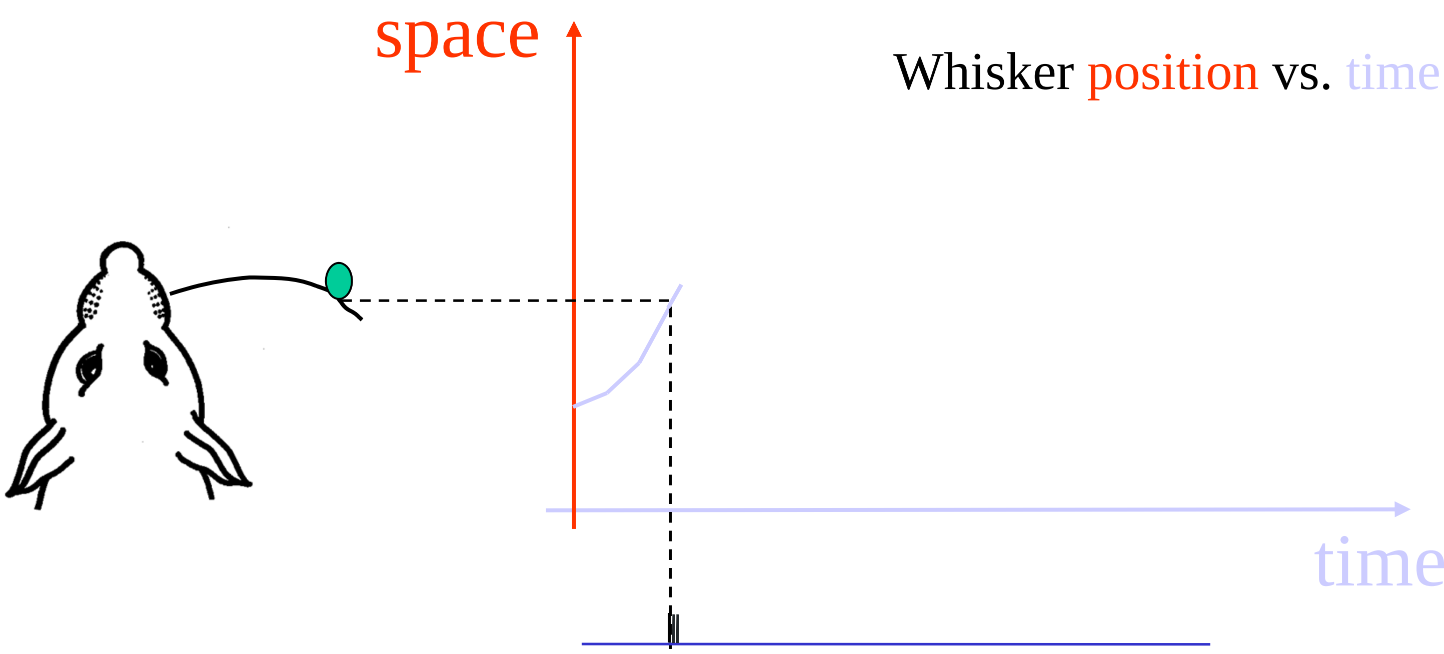
What the whiskers tell the rat brain

Touch



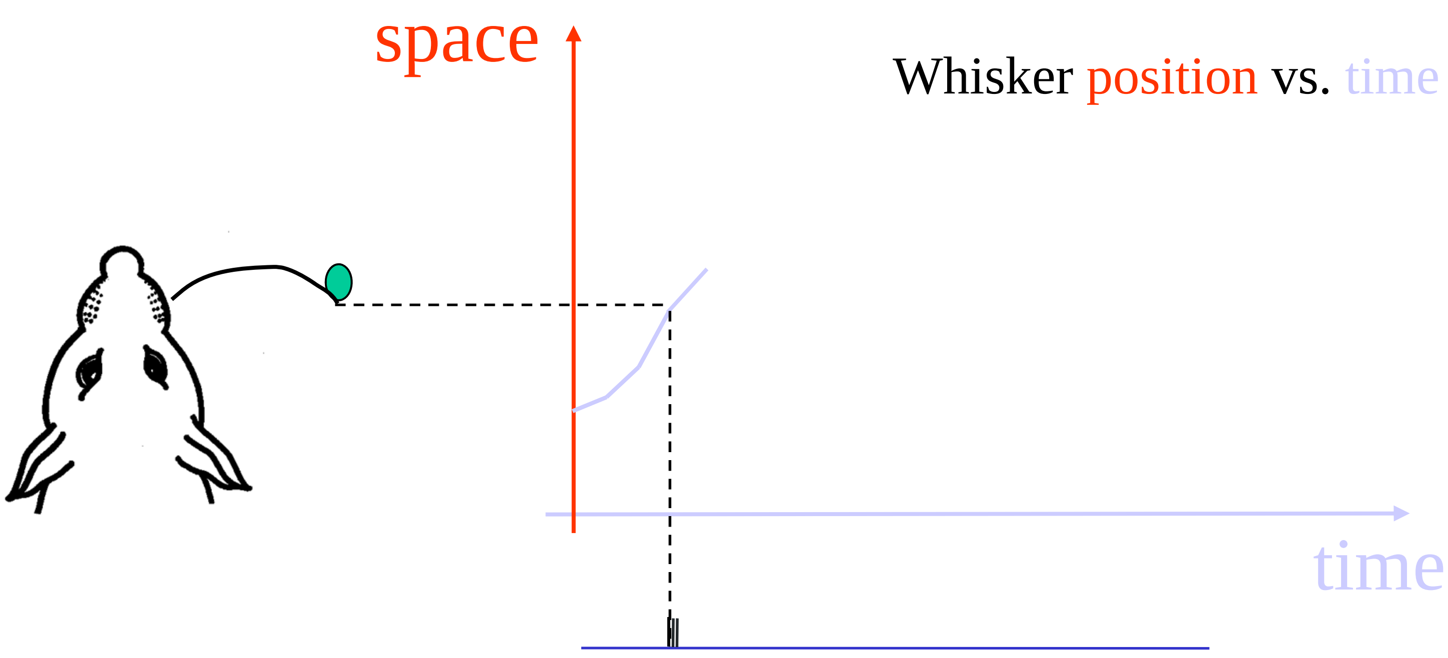
What the whiskers tell the rat brain

Touch



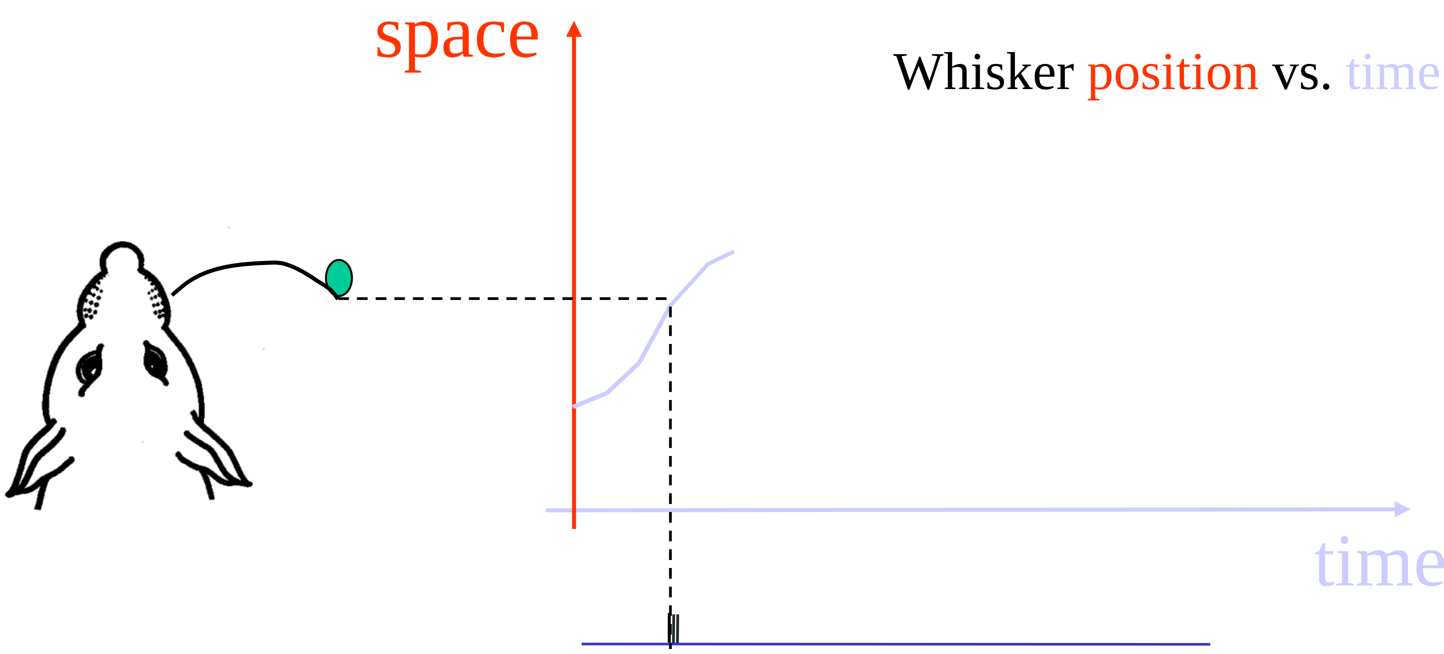
What the whiskers tell the rat brain

Touch



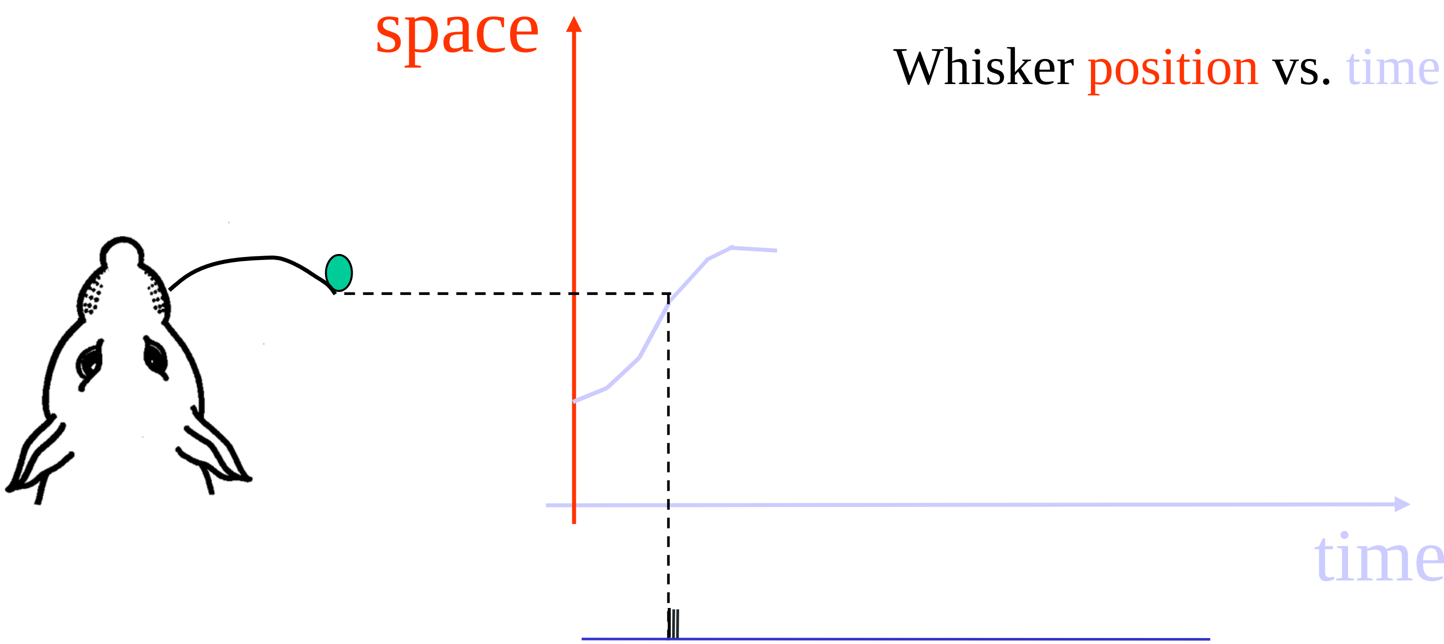
What the whiskers tell the rat brain

Touch



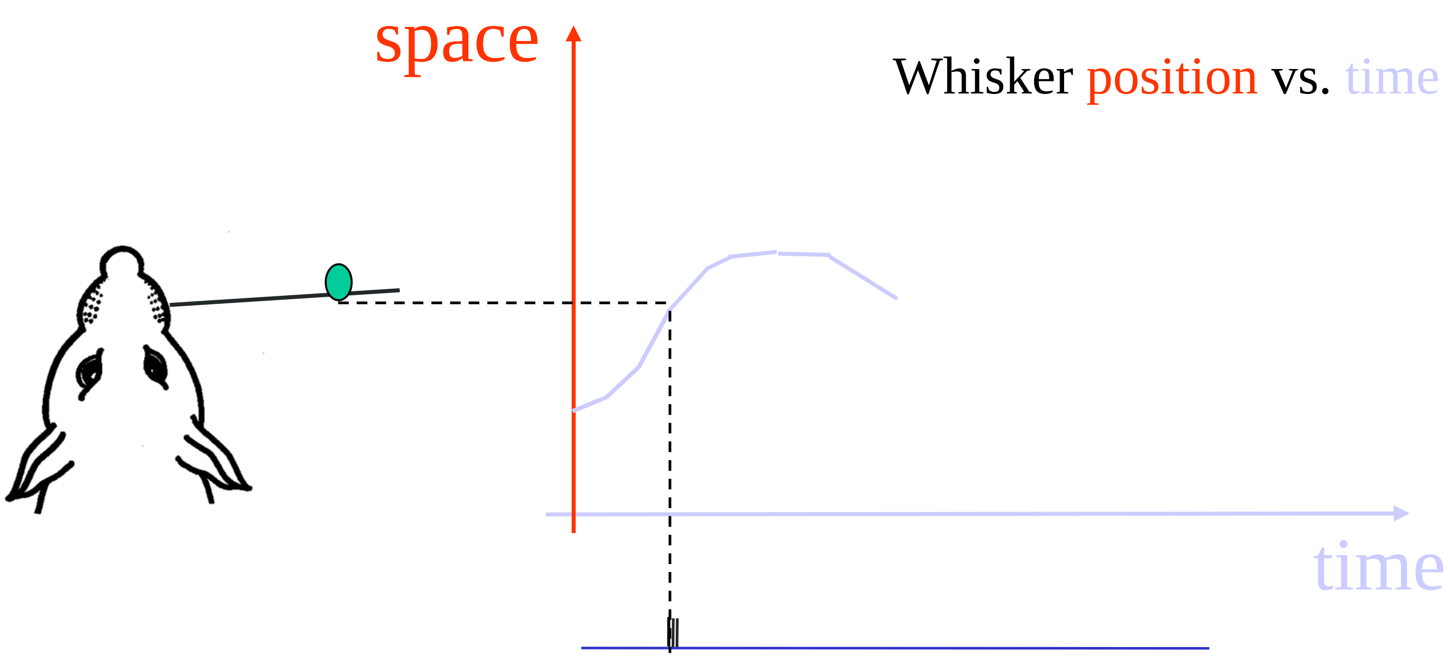
What the whiskers tell the rat brain

Touch



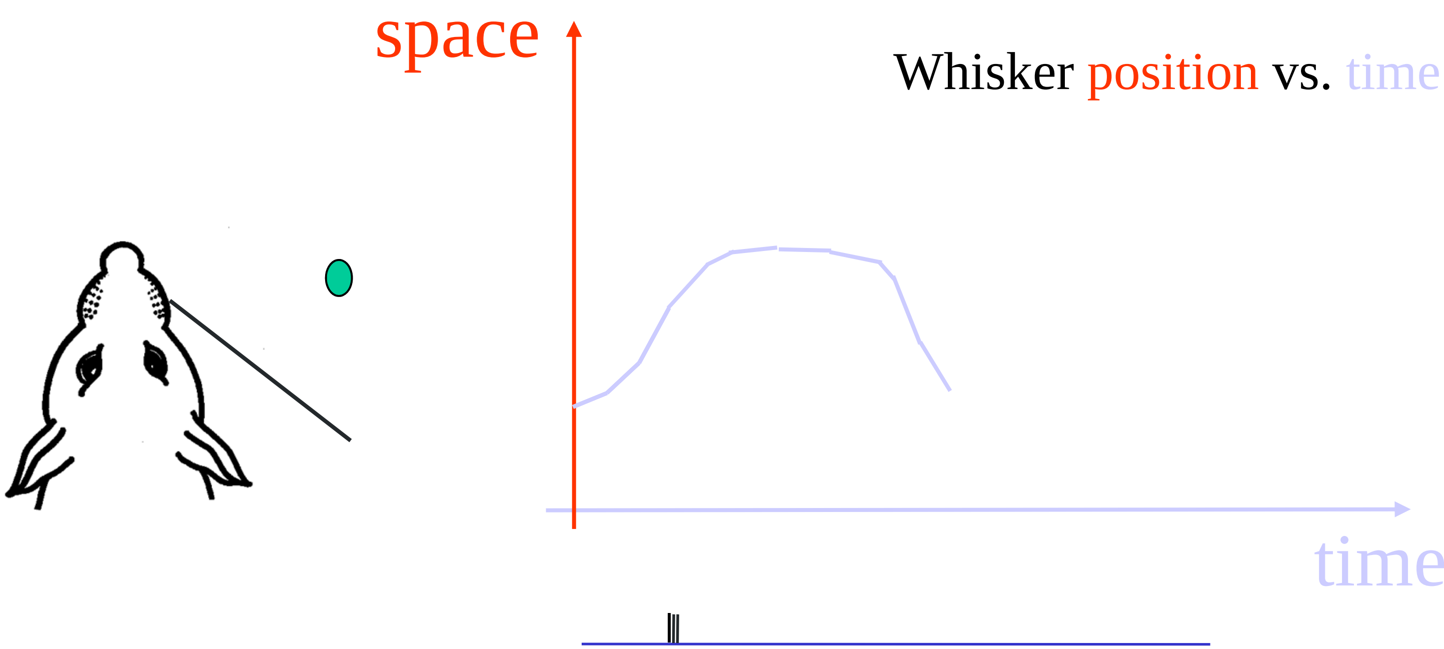
What the whiskers tell the rat brain

Touch



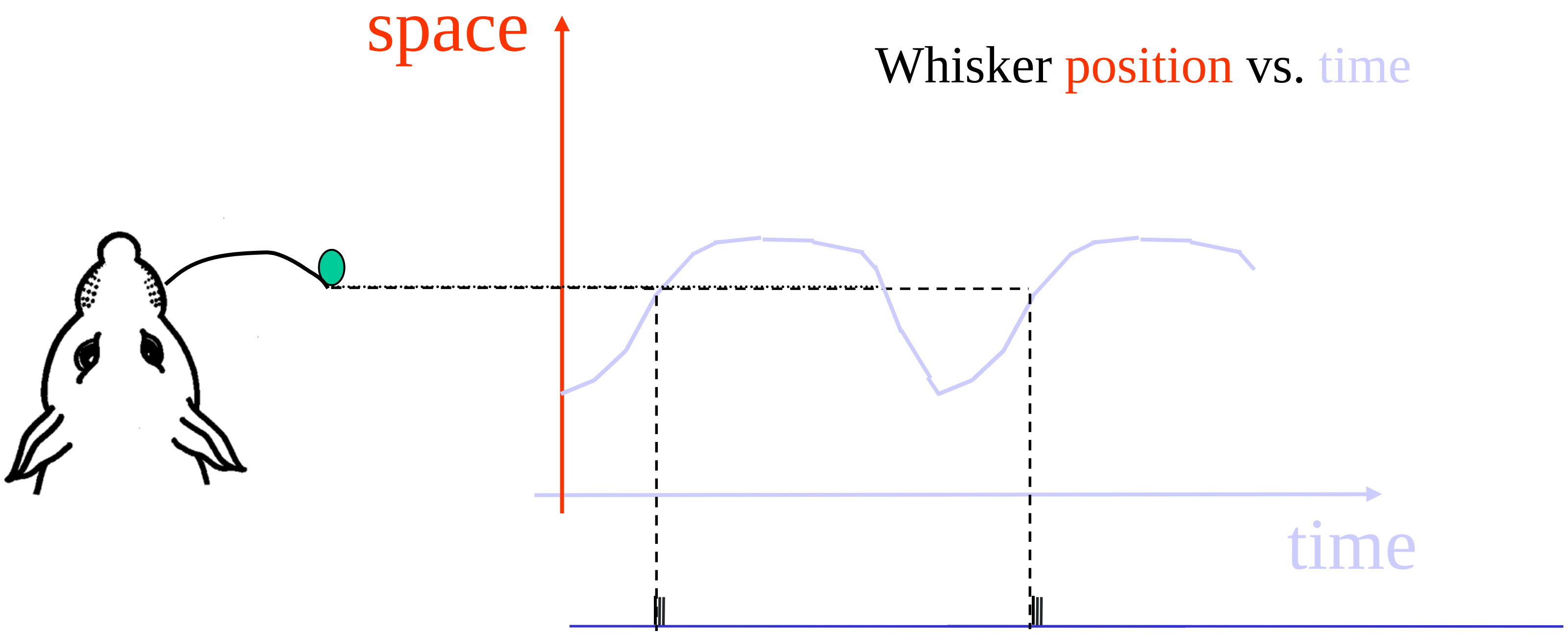
What the whiskers tell the rat brain

Touch



What the whiskers tell the rat brain

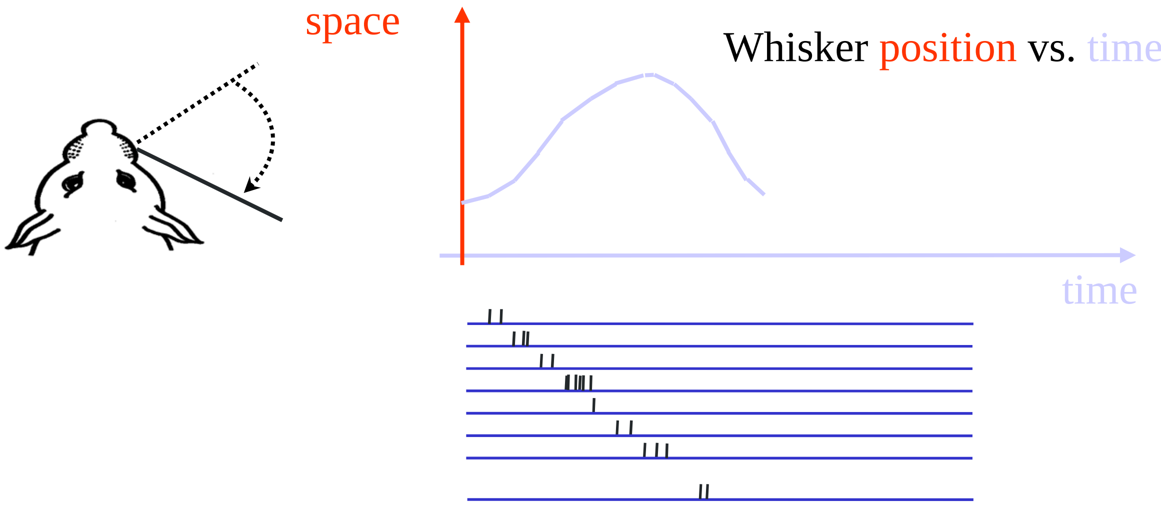
Touch



What the whiskers tell the rat brain

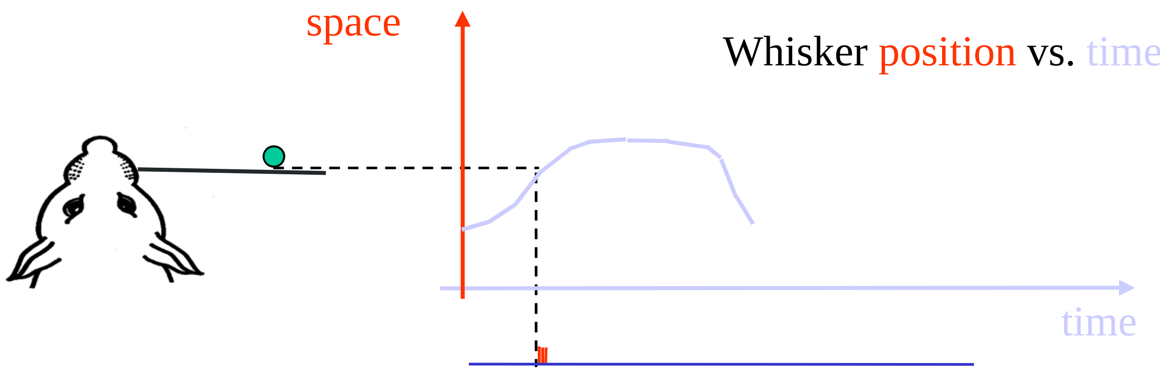
How can the brain use this information?

- Whisking:



- Touch:

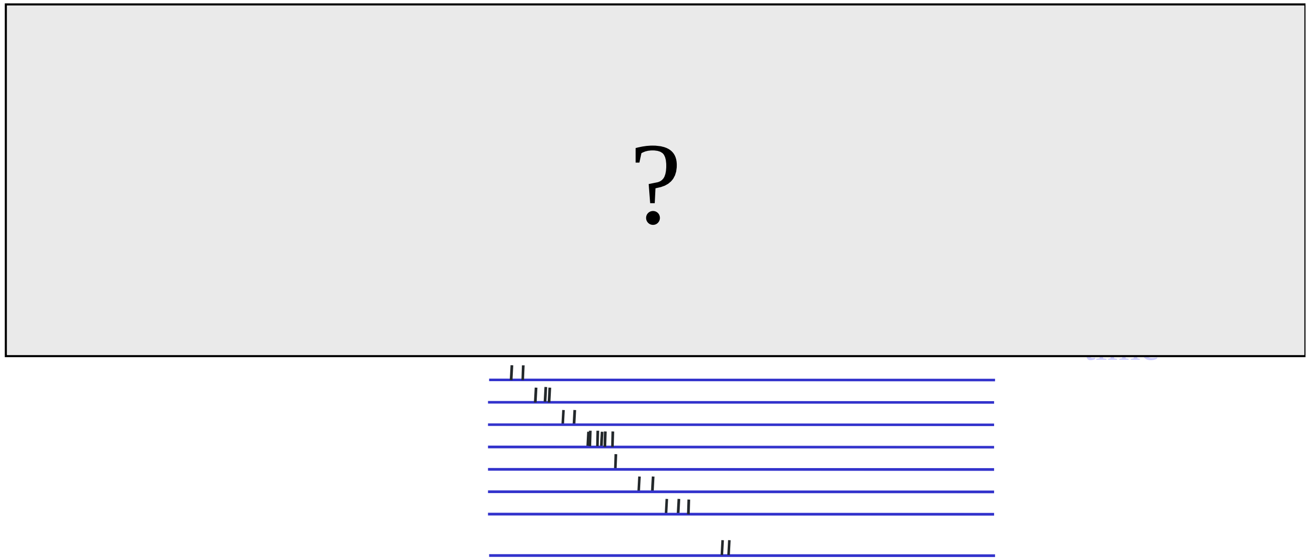
contact with object



What the whiskers tell the rat brain

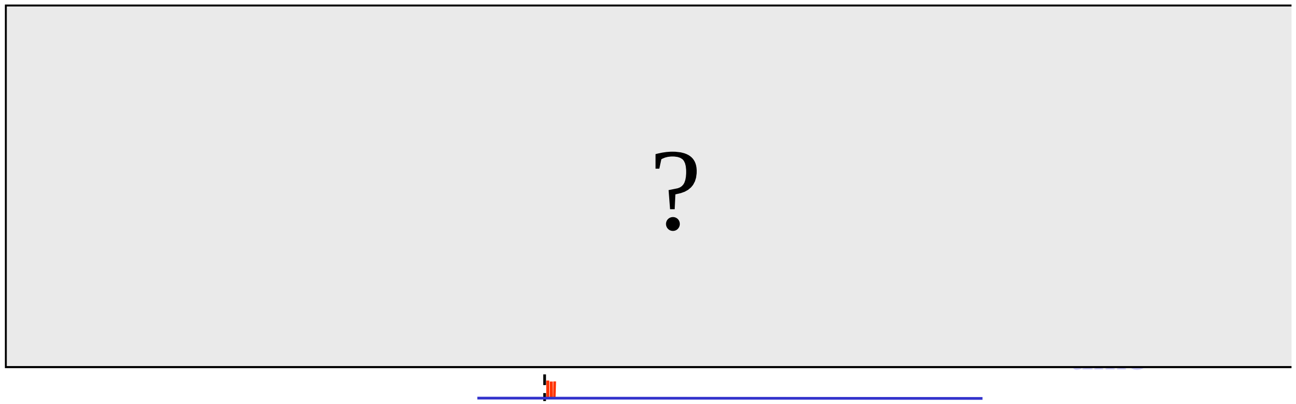
How can the brain use this information?

- Whisking:



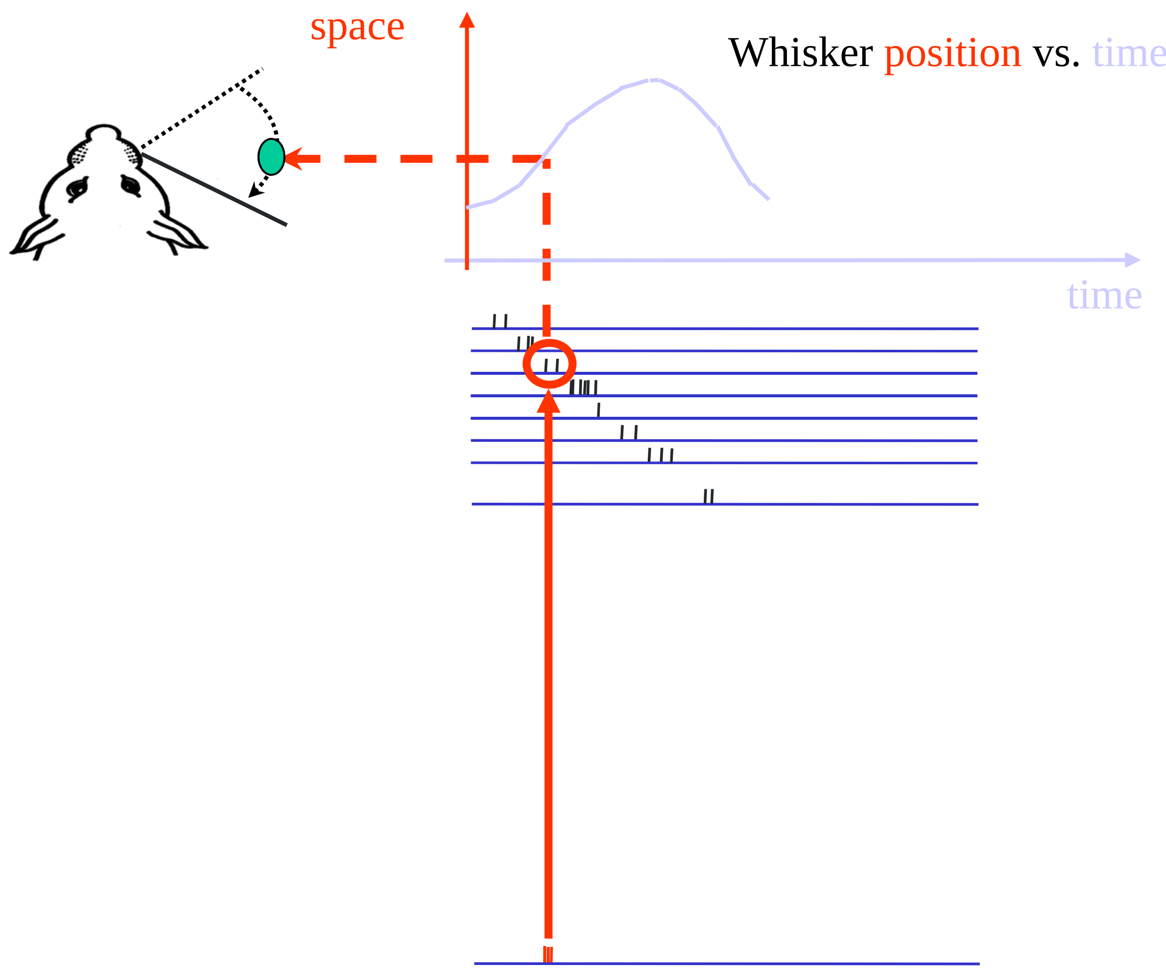
- Touch:

contact with object



How can the brain extract the location of the object

- Whisking:

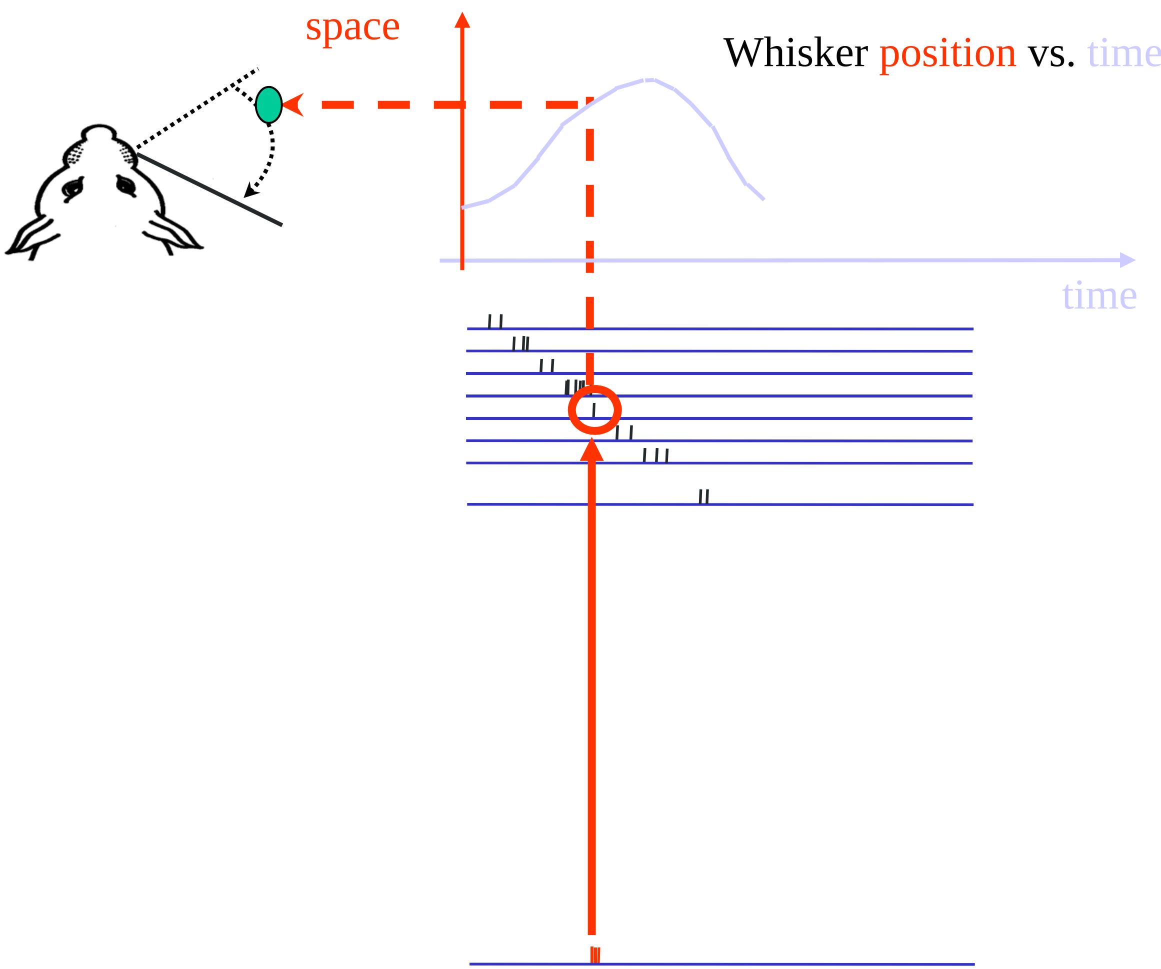


- Touch:

contact with object

How can the brain extract the location of the object

- Whisking:



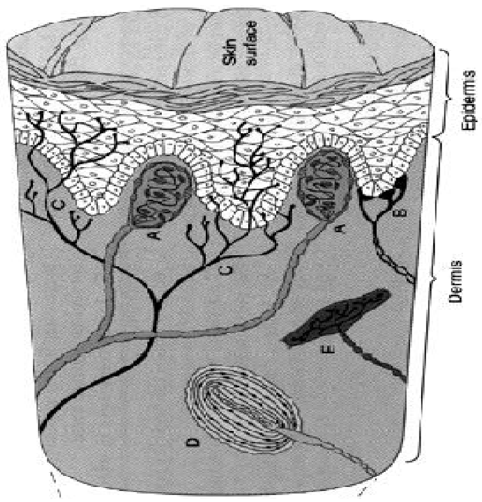
- Touch:

contact with object

sensory encoding: *What receptors tell the brain*

Sensory organs consist of **receptor arrays**:

somatosensation **audition** **vision**

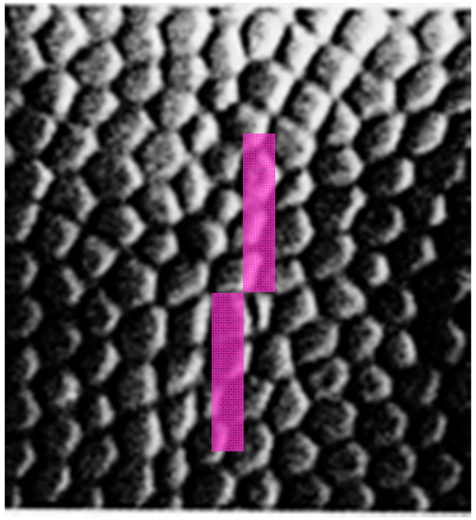


~200 µm

Finger pad

10 µm

cochlea



10 µm

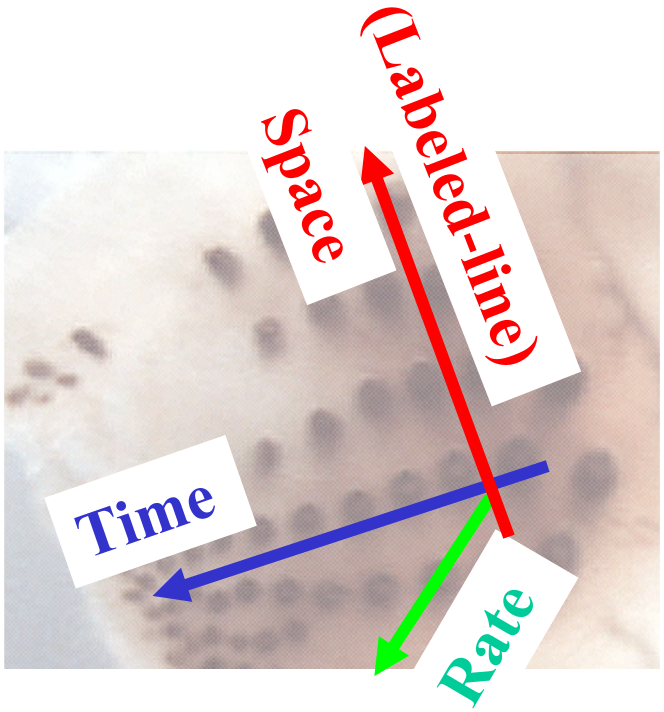
retina

Spatial organization => Spatial coding (“*which* receptors are activated”)

Movements => Temporal coding (“*when* are receptors activated”)

Orthogonal coding of object location

- Vertical object position is encoded by space
- Horizontal object position is encoded by time
- Radial object position is encoded by rate



Active sensing

The End