Active sensing

Ehud Ahissar
Active sensing

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

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- 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**
  - Finger pad
  - \(~200 \mu m~\)

- **audition**
  - Cochlea
  - \(10 \mu m~\)

- **vision**
  - Retina
  - \(10 \mu m~\)

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.
Vel - constant

\[ f = SF \times V \]

\[ dt = dx / V \]
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.
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.
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

- $V_{\text{eye}}$
- RF(1)
- RF(2)
- Retinal outputs
- 1
- 2
- Space
- Time
Vision: Temporal encoding due to eye movement

- Space
- Time
- Retinal outputs
- Δx
- Δt
- RF(1)
- RF(2)
- V_eye
Vision: Temporal encoding due to eye movement
Vision: Temporal encoding due to eye movement

\[ \Delta t \]

\[ \Delta x \]

\[ \text{retinal outputs} \]

\[ V_{\text{eye}} \]

RF(1)

RF(2)
Vision: Temporal encoding due to eye movement

![Diagram showing retinal outputs and temporal encoding](image)
### Spatial vs temporal coding

<table>
<thead>
<tr>
<th>Spatial</th>
<th>Temporal</th>
</tr>
</thead>
<tbody>
<tr>
<td>faster</td>
<td>better resolution</td>
</tr>
</tbody>
</table>

- scanning allows sensing in between receptors
## Passive vs Active sensing

of stationary objects

<table>
<thead>
<tr>
<th></th>
<th>Passive</th>
<th>Active</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>threshold</strong></td>
<td>low</td>
<td>high</td>
</tr>
<tr>
<td><strong>accuracy</strong></td>
<td>low</td>
<td>high</td>
</tr>
<tr>
<td><strong>Systems involved</strong></td>
<td>sensory</td>
<td>Sensory + motor</td>
</tr>
<tr>
<td><strong>coding</strong></td>
<td>spatial</td>
<td>Spatial + temporal</td>
</tr>
<tr>
<td><strong>Processing speed</strong></td>
<td>fast</td>
<td>slow</td>
</tr>
<tr>
<td><strong>Used in</strong></td>
<td>detection</td>
<td>Exploration Localization Identification</td>
</tr>
</tbody>
</table>

…
Central processing of touch

where touch begins?

• at the receptors?
• with sensor movement?
• in high brain centers?
Sensory-motor loops of the vibrissal system
Localization (‘where’)  
Identification (‘what’)  
Whisking

Sensory-motor loops of the vibrissal system

The old view

Cortex

Thalamus

Brainstem
Sensory-motor loops of the vibrissal system
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

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

Phase 1:
Firing of Motor Neuron

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)
Open-loop system

Information flows in one direction (from neurons to muscles)

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

Name:
- Muscle spindle receptors
- Golgi tendon organs
- Joint receptors

Sensitive to:
- muscle length
- muscle tension
- Flexion, extension
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

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: \( f = k_1 \theta \)
**PID control**

- **Proportional** (to the controlled variable)
- **Integral** (of the controlled variable)
- **Derivative** (of the controlled variable)

![PID Control Diagram](image)

Present \( \theta \)
Past \( \theta \)
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
- Controlled variables – motor vs sensory
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
- \( f = k_1F \)

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
- Controlled variables – motor vs sensory
Sensory-motor loops of the vibrissal system
Basic principles of closed-loop control
Set point

\[ V_d \]

\[ V_m = f(-V_s) \]
\[ V_s = g(V_m) \]
Set point

\[ V_m = f(V_d - V_s) \]
\[ V_s = g(V_m) \]
Direct control without direct connection

\[ V_m = f(V_d - V_s) \]
\[ V_s = g(V_m) \]
Nested loops

\[ V_m = f(V_d - V_s) \]

\[ V_s = g(V_m) \]
Parallel loops

\[ V_{m2} = f(V_d - V_s) V_s = g(V_{m2}) \]

\[ V_{m1} = f(V_d - V_s) V_s = g(V_{m1}) \]
Parallel loops

\[ V_m = f(V_d - V_s) \]
\[ V_s = g(V_m) \]

\[ X_m = f(X_d - X_s) \]
\[ X_s = g(X_m) \]
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

\[ V_m = \int (V_d - V_s) \, dt \]

Diagram:
- \( V_{\text{desired}} \) to \( V_{\text{motor}} \) through an integrator
- \( V_{\text{sensed}} \) from \( V_{\text{motor}} \)
- Graph showing \( V_m \) vs. \( V_m^0 \) and \( V_s \) vs. \( V_m \)
Sensory-motor loops of the vibrissal system
Sensory-motor loops of the vibrissal system
Sensory-motor loops of the vibrissal system

Diagram showing the sensory-motor loops of the vibrissal system. Key structures include:

- Primary Sensory Cortex
- Secondary Sensory Cortex
- Zona Incerta
- Thalamus
- Primary Motor Cortex
- Superior Colliculus
- Red Nucleus
- Pontine Reticular Nucleus
- Brainstem Reticular Formation
- Facial Nucleus
- Brainstem Loop
- Trigeminal Ganglion
- Trigeminal Nuclei
- VPM-dm
- VPM-vl
- POm
- Cerebellar/Olivary
- Thalamic Nuclei
- Cortical areas

Arrows indicate the flow of information between these structures, highlighting the sensory and motor pathways.
Active sensing in the vibrissal system
Sensory signal conduction
The vibrissal system
Sensory signal conduction

The vibrissal system

whisker

Meisner
Merkel
Ruffini
Lanceolate
free endings
Sensory-motor loops of the vibrissal system
Motor control of whiskers

Intrinsic muscles

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

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:
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Motor control of whiskers

Intrinsic muscles

Vibrissal proprioception

- Each follicle contains ~2000 receptors
- About 20% of them convey pure proprioceptive information
Whiskers come with different muscle sizes

Intrinsic muscles

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 …
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
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

space

time
What the whiskers tell the rat brain

Whisking

Whisker position vs. time

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Whisker position vs. time
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**Reafference:**

Their own movement

(“Whisking”)

**Exafference:**

Touch
What the whiskers tell the rat brain

Touch

Whisker position vs. time

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Whisker position vs. time

space

time

Touch
What the whiskers tell the rat brain

Touch

Whisker position vs. time

space

time
What the whiskers tell the rat brain

How can the brain use this information?

- Whisking:

  Whisker position vs. time

- 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

Finger pad  cochlea  retina

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

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

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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