Neurorobotic models of spatial cognition

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Outline

I. Background basic concepts
- Computational neuroscience
- Neural coding
- Population vector coding
- Firing rate neuronal model
- Unsupervised associative learning

II. Spatial cognition and its neural bases

III. Neurorobotic models of spatial cognition
Computational neuroscience & neurorobotics

**Computational neuroscience** (mathematical formalism) to model the mechanisms underlying the S-R relation and provide experimentally testable predictions.

- **Model**: set of equations \( R(S, P_1, \ldots, P_n) \)
  - Analytical solutions
  - Numerical solutions
  - Robotic validation

Experimental (empirical) approach

Set of rules:
- describing the experimental observations
- predicting/extrapolating unseen behaviour

Model of the system
Computational neuroscience & neurorobotics

Experimental neuroscience

- Complex system
- Experimental protocol
- Experimental data

Mathematical formalism

- Model
- Simulations / robotics
- Simulation data

Prediction

- Modification

in vivo, in vitro, in situ

Comparison

Overall behavior

- System network
- Local network
- Single cell
- Synapse

Computational neuroscience & neurorobotics

Experimental neuroscience ↔ Theoretical neuroscience
Maps the input into neural responses

Encoding

Stimulus

Response

Predicts the most likely stimulus that elicited an observed response

Decoding

Neuronal activity & neural coding

Micro-electrode

Regular Spiking Pyramidal Cell: Visual Response
Neuronal activity & neural coding

Action potential or ‘spike’

Neuronal activity & neural coding

Space
time
Firing rate

Adrian (1926) – Mean discharge proportional to neural selectivity

Rate coding

Spike count / $\Delta t$
(Hz or spikes/s)
Neuronal activity & neural coding

Tuning curve of V1 simple cell

Variance of the noise

Mean activity

Neuronal activity & neural coding

$f(s) = r_{\text{max}} \exp \left( -\frac{1}{2} \left( \frac{s - s_{\text{max}}}{\sigma_f} \right)^2 \right)$

$s_{\text{max}}$ : preferred orientation;
$T_{\text{max}}$ : maximal response;
$\sigma_f$ : tuning curve width (selectivity)

$a_i = f_i(\theta) + n_i(\theta)$

$n_i(\theta) \sim N(0, \sigma_i(\theta))$
Population vector decoding

One neuron

Many neurons

1. “Winner take all” decoding (competitive decoding scheme)
Population vector decoding

1. “Winner take all” decoding (competitive decoding scheme)

2. “Population vector” decoding (cooperative decoding scheme)

Many neurons

Population vector decoding


- The monkey is guided to move the lever from the center of apparatus to one of eight peripheral locations.
- Neural activities in the motor area are recorded.
Population vector decoding


\[ \hat{\mathbf{v}} = \sum_i \frac{r_i}{Z} \hat{\mathbf{c}}_i \]

- \( \hat{\mathbf{v}} \): decoded direction
- \( \hat{\mathbf{c}}_i \): preferred direction
- \( r_i \hat{\mathbf{c}}_i \): contribution from \( i \)th neuron
- \( Z = \sum r_i \): normalization factor

Cortical control of motor neuroprostheses

Goal:
Decode arm movement direction from neural activity
Cortical control of motor neuroprostheses
**Beyond firing rate coding**

Temporal coding

- **Visual system**
  e.g. Thorpe, Nature 1996; Van Rullen, Neural Comput 2001; Gollisch & M. Meister, Science 2008

- **Olfactory system**
  e.g. Whalley K, Nature Rev Neurosci 2013

- **Auditory system**
  e.g. Heil, Current Opin Neurobiol 2004

- **Somatosensory system**
  e.g. Szwed et al., Neuron 2003; Johansson & Branieks, Nat Neurosci 2004

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**Beyond firing rate coding**

"Go / No-Go categorization task"

20 ms per image, each image presented 1 time

(Thorpe et al. 1996)
Beyond firing rate coding

(Thorpe et al. 1996)

Reaction time for “Go trials” : 445 ms

94% of correct answers

(Thorpe et al. 1996)
Beyond firing rate coding

Which properties of the spike train convey information?

Firing rate:

|   |   |   |   |   |   |   |   |

Spike timing:

|   |   |   |   |   |   |   |

Evoked potentials in the frontal lobe

Decision made < 150 ms

Complete visual processing < 150 ms

1-2 spikes per neuron for fast feedforward visual processing

(Thorpe et al. 1996) (Thorpe & Thorpe 2001)
Beyond firing rate coding

Is the structure of spike trains random and history-independent (Poisson)?

Can spatiotemporal correlations be informative?

The spatiotemporal structure of spike trains can be relevant to neural communication.
# Neuronal modelling

![Neuronal Image]

<table>
<thead>
<tr>
<th>Class of models</th>
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<tbody>
<tr>
<td><strong>Firing rate</strong></td>
<td>Mean activity (analog computation &amp; neural networks)</td>
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<tr>
<td><strong>Integrate &amp; Fire</strong></td>
<td>Non linear integration &amp; temporal coding</td>
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<td><strong>Hodgkin &amp; Huxley</strong></td>
<td>Biophysical properties &amp; dynamics of ionic channels</td>
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## Firing rate neuronal model

![Firing Rate Image]

Mean firing rate: \[ r = \frac{N_{\text{spikes}}}{T} \] (spikes/sec) or (Hz)
Firing rate neuronal model

\[ I_i(t) = \bar{w}_i \cdot \bar{r}(t) \cdot \varepsilon = \sum_j w_{ij} \cdot r_j(t) \cdot \varepsilon \quad \text{Synaptic input} \]

\[ \tau_i \frac{dV_i(t)}{dt} = -V_i(t) + I_i(t) \quad \text{System dynamics} \]

\[ \tau_i = 10 \text{ ms} \quad \text{Membrane time constant} \]

\[ V_i(t + \Delta t) = V_i(t) + \frac{\Delta t}{\tau_i} \cdot (-V_i(t) + I_i(t)) \quad \text{Simple integration} \]

\[ r_i(t) = f\left(V_i(t) \pm \varepsilon\right) \quad \text{Transfer function} \]
Firing rate neuronal model

Example of activity of a population of firing rate neurons

(Pouget&Snyder 2000)

(Arleo et al. 2001)

Integrate & fire model

Focus on the non linear integration properties and temporal coding

(Gerstner&Kistler 2002)

(Abbott&Dayan 2002)

\[ r = \frac{N_{\text{spikes}}}{T} \]
Integrate & fire model

Membrane ≈ RC circuit

\[ I(t) = I_k + I_c = \frac{V(t)}{R} + C \frac{dV}{dt} \]

\[ \tau = R \cdot C \]

\[ \tau \cdot \frac{dV(t)}{dt} = -V(t) + R \cdot I(t) \]

(Gerstner & Kistler 2002)
Integrate & Fire model

Example of activity of a population of I&F neurons

Computing units: neuronal modelling

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Learning: modelling synaptic plasticity

Synaptic "weights" store memories thanks to adaptation (learning)

Learning = modification of synaptic efficacy (weight)
Learning: modelling synaptic plasticity

SUPERVISED Learning

UNSUPERVISED Learning

REINFORCEMENT Learning

Unsupervised learning

Data → Learner

Discover statistical regularities in the input space and build compressed representations of the data
"Neurons that fire together wire together"

**Update rule**

\[ \Delta w_i (t) = \alpha \cdot r_i(t) \cdot r_j(t) \]

**Spike timing dependent plasticity (STDP)**

- **Hebb’s postulate:**
  - If A then B, then potentiate
  - Long-term potentiation
  - **LTP**

- **Stent’s postulate:**
  - If B then A, then depress
  - Long-term depression
  - **LTD**

**HL provides a simple formalization of the synaptic long-term potentiation (LTP) and depression (LTD) mechanisms**
**Spike timing dependent plasticity (STDP)**

Bi & Poo (1998)

**Associative memory**

AFTER LEARNING

Naïve network

Item memorized

Recall based on partial information
I. Background basic concepts

II. Spatial cognition and its neural bases

- The spatial learning problem
- Hippocampal place cells
- Head direction cells
- Entorhinal grid cells
- Multisensory integration

III. Neurorobotic models of spatial cognition

Spatial cognition

"Navigation is the process of determining and maintaining a course of trajectory from one place to another"

C. R. Gallistel (1990)
Spatial cognition

“Navigation is the process of determining and maintaining a course of trajectory from one place to another”

C. R. Gallistel (1990)

It looks simple but …
In 1971, O’Keefe & Dostovsky discovered the “place cells”

J. O’Keefe, Nobel Prize 2014
In 1971, O’Keefe & Dostovsky discovered the “place cells”.

J. O’Keefe
Nobel Prize 2014

Neural basis of spatial cognition

Population coding

80 simultaneously recorded place cells
Wilson & McNaughton, 1993

Neural basis of spatial cognition

Population coding

Neural basis of spatial cognition

Population coding

Wilson & McNaughton, 1993

Population coding

Wilson & McNaughton, 1993
Neural basis of spatial cognition

Hippocampal place cells...in space

Knierim et al. (2004)

In 1984, Rank discovered the "head direction cells"

J. B. Ranck, Jr.,

Head-Direction Cell in Anterior Thalamus
Neural basis of spatial cognition

Arleo et al. (2004)

Neural basis of spatial cognition

Population coding

Zugaro et al. (2003)

Arleo et al. (2001)

Peyrache et al. (2015)

Peyrache et al. (2015)
Neural basis of spatial cognition

In 2005, Edvard & May-Britt Moser discovered the “grid cells”

May-Britt & Edward Moser
Nobel Prize 2014

Maintenance of HD signal during locomotion in the vertical plane

Animal climbing up

Animal climbing down
Neural basis of spatial cognition

In 2005, Edvard & May-Britt Moser discovered the “grid cells”

Grid cells reported in mice, bats, monkeys and humans, suggesting they originated early in mammalian evolution

Taken from May-Britt Moser’ presentation
Neural basis of spatial cognition

Grid cells have at least three dimensions of variations

1. Phase

2. Scale

3. Orientation

The scale of the grid follows a dorso-ventral organization

Taken from May-Britt Moser' presentation
Neural basis of spatial cognition

Understanding neural spatial coding by focusing on the multisensory integration of environmental & internal cues
Multisensory integration

Allothetic sensory inputs

Idiothetic sensory inputs

Allothetic cues (landmarks)

Idiothetic cues (self-motion signals)
Using idiothetic cues for path integration

- Sum of \( \gamma_l \)
- Initial direction \( \theta_0 = 0^\circ \)

McNaughton et al. 2006

- Homing vector

Arleo & Rondi-Reig 2007; Etienne et al. (1998)

Müller & Wehner 1988

Multisensory integration

Environmental landmarks
Path integration
Neural basis of spatial cognition

Idiothetic cues (self-motion signals)

Allothetic cues (landmarks)

Hippocampal place cells
O’Keefe & Dostrovsky (1971)

Head direction cells
Rank (1984)

Grid cells
Hafting et al. (2005)

Border cells
Solstad et al. (2008)

Neural basis of spatial cognition

Persistence of place coding in the dark

Quirk et al. 1990

Krueger et al. 1998

LIGHT 2 min
DARK 4.5 min
DARK 5 min
DARK 5 min
DARK 5 min
LIGHT 5 min
Neural basis of spatial cognition

Persistence of place coding in the dark

Hafting et al. 2005

Neural basis of spatial cognition

Anchorage on visual landmarks and geometrical cues
Neural basis of spatial cognition

Anchorage on visual landmarks and geometrical cues

(O’Keefe & Burgess, 1996)

Anchorage on visual landmarks and geometrical cues

Zugaro et al., (2000)
Neural basis of spatial cognition

Anchorage on visual landmarks and geometrical cues

The preferred directions of all HD cells rotate simultaneously


CA3 place cell

ADN HD cell

Knierim et al., (1996)
Neural basis of spatial cognition

Anchorage on optic flow cues

rotating planetarium: 4.5°/s

Arieo et al., (2013)

Outline

I. Background basic concepts

II. Spatial cognition and its neural bases

III. Neurorobotic models of spatial cognition 1
Spatial learning model

Stressing the importance of multisensory integration

Associative Hebbian learning

place code
Place cells

direction code
HD cells

Allothetic cues
(visual landmarks)

Idiothetic cues
(path integration)

Neurorobotic methods

Khepera miniature mobile robot

CCD camera

light detector

8 IR sensors

odometer

Allothetic inputs

Idiothetic input

Arleo et al. (2000, 2001, 2004); Boucheny et al. (2005); Sheynikhovich et al. (2009); Li et al. (2019)
Neurorobotic methods

Khepera miniature mobile robot

Arleo et al. (2000, 2001, 2004); Boucheny et al. (2005); Sheynikhovich et al. (2009)

Neurorobotic methods

PsikharpaX: the artificial rat

Meyer et al., 2005
Processing visual information

Khepera miniature mobile robot

Visual input

422 x 316 pixels

Arleo et al. (2000, 2001, 2004); Boucheny et al. (2005); Sheynikhovich et al. (2009)

Processing visual information

Modeling the orientation selectivity of V1 Simple Cells

Gabor filters

Tuning curve of V1 simple cell

8 different orientations
3 different scales

Arleo et al. (2000, 2001, 2004); Boucheny et al. (2005); Sheynikhovich et al. (2009)
Processing visual information

Modeling the orientation selectivity of V1 Simple Cells

Gabor filters

Retinotopic sampling

8 different orientations
3 different scales

Arleo et al. (2000, 2001, 2004); Boucheny et al. (2005); Sheynikhovich et al. (2009)
Odometry-based path integration

Modeling a grid-cell like network

\[ r_i(t) = \exp \left( -\frac{(\bar{s}_d(t) - \bar{s}_i)^2}{2\sigma^2} \right) \]

Arleo et al. (2000, 2001, 2004); Boucheny et al. (2005); Sheynikhovich et al. (2009)
Spatial learning model

Hippocampal place cells

Visual cues

Self-motion cues

Spatial learning model

View cells

Feature extraction

Visual cues

Processing

scale

orientation

position

Ariteo et al. (2000, 2001, 2004); Boucheny et al. (2005); Sheynikhovich et al. (2009)
Spatial learning model

Unsupervised growing Network

- if $\sum H(n-e) < A$
- then growing
- else Hebbian learning

$$W_{\text{new},ij} = H(n_e - c) \cdot \text{ran}(1)$$

$$\Delta w_{ij} = \alpha \cdot r_i \cdot r_j \cdot (1 - w_{ij})$$

Spatial learning model

Vision-based place cells

Feature extraction

Vision-based PCs

LEC

View cells

Feature extraction

Visual cues

Visual cues

Artleo et al. (2000, 2001, 2004); Boucheny et al. (2005); Sheynikhovich et al. (2009)

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Spatial learning model

Vision-based place cells

- View cells
  - Feature extraction
  - Visual cues

Position-reconstruction error based on population vector coding

Correlation between the dispersion around the center of mass and the reconstruction error

Arleo et al. (2000, 2001, 2004); Boucheny et al. (2005); Sheynikhovich et al. (2009)
Spatial learning model

Places are identified by path integration

Arleo et al. (2000, 2001, 2004); Boucheny et al. (2005); Sheynikhovich et al. (2009)

Spatial learning model

Hippocampal place cells

Hebbian learning

View cells

Feature extraction

Path integration

Self-motion cues

Arleo et al. (2000, 2001, 2004); Boucheny et al. (2005); Sheynikhovich et al. (2009)
Arleo et al. (2000, 2001, 2004); Boucheny et al. (2005); Sheynikhovich et al. (2009)

Spatial learning model

- View cells
- Feature extraction
- Path integration
- Self-motion cues
- Hebbian learning

Spatial learning model

Arleo et al. (2000, 2001, 2004); Boucheny et al. (2005); Sheynikhovich et al. (2009)
Spatial learning model

Population vector coding

Arleo et al. (2000, 2001, 2004); Boucheny et al. (2005); Sheynikhovich et al. (2009)
Population vector coding

Population activity in the dark

Normalized population firing rate

Environment (x) Environment (y)

Population vector coding

Arleo et al. (2000, 2001, 2004); Boucheny et al. (2005); Sheynikhovich et al. (2009)

Spatial learning model

Hippocampal place cells

Hebbian learning

Calibration

vision-based PCs LEC

View cells

Feature extraction

Visual cues

PI-based PCs MEC

Path integration

Self-motion cues

Arleo et al. (2000, 2001, 2004); Boucheny et al. (2005); Sheynikhovich et al. (2009)
Spatial learning model

View cells

Feature extraction

Hebbian learning

Path integration

Self-motion cues

Multisensory integration shapes exploratory behavior

Self-localization error (mm)

Arleo et al. (2000, 2001, 2004); Boucheny et al. (2005); Sheynikhovich et al. (2009)
Spatial learning model

Multisensory integration shapes exploratory behavior

Model data

Experimental data

Data by Brandner & Arleo

Arleo et al. (2000, 2001, 2004); Boucheny et al. (2005); Sheynikhovich et al. (2009)

Exploratory behavior depends on multisensory integration during spatial learning

Sheynikhovich, Grèzes, King, Arleo (2012)
Exploratory behavior depends on multisensory integration during spatial learning

Sheynikhovich, Grèzes, King, Arleo (2012)
Interplay between parallel learning systems

Multisensory integration

Episodic & procedural learning

Decision making

Multisensory integration framework to study spatial learning

Hippocampal spatial maps

Self-motion cues

Allotethic cues

Cerebellum

Interplay between parallel learning systems

Cerebellar contribution to spatial cognition

Transgenic mouse model L7-PKCI

(De Zeeuw et al., 1999)

L7-PCKI mice have a spatial learning deficit

(Burguère et al. 2005)

P < 0.001
Transgenic mouse model L7-PKCI (De Zeeuw et al., 1999)

Cerebellar model (Passot et al. 2012)

Interplay between parallel learning systems

Allothetic cues
Self-motion cues

Hippocampal spatial maps

Cerebellum

Visual landmarks

CONTROL ANIMAL

Start
Goal
**Interplay between parallel learning systems**

**Cerebellar contribution to spatial cognition**

- **Spatial learning model**
  (Passot et al. 2012)

- **Cerebellum influences the accuracy of hippocampal place maps**
  (Rochefort et al. 2011)

- **L/PKCI mice have a spatial learning deficit**
  (Burguère et al. 2005)

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**Prediction of the model**

- Coronal
  - 0P:0W
  - 0P:5W
  - 5P:0W
  - 5P:5W

- L/PKCI

**Rochefort et al. (2011)**

- WT
  - 19.9 Hz
  - 25.7 Hz
  - 35.8 Hz
  - 6.8 Hz

- L7PKCI
  - 8.6 Hz
  - 6.8 Hz
  - 4.8 Hz
  - 3.6 Hz
Interplay between parallel learning systems

Cerebellum influences the accuracy of hippocampal place maps

Spatial learning model (Passot et al. 2012)

Inaccurate spatial maps in mutants

consequences on exploratory behaviour

Prediction being tested with L. Rondi-Reig using L7-PKCI mice

Experiment: free exploration in L7PKCI mice

Collaboration with L. Rondi-Reig (IBPS, Paris)

- 4 controls and 4 mutants
- Habituation 24 hours
- Free exploration: mouse behavior recorded for 24 hours
Length and area covered by the roundtrips

- Round-trip length L
- Round-trip area S

Spatial learning model

- View cells
- Feature extraction
- Path integration
- Self-motion cues
- Hebbian learning

Arleo et al. (2000, 2001, 2004); Boucheny et al. (2005); Sheynikhovich et al. (2009)
I. Background basic concepts

II. Spatial cognition and its neural bases

III. Neurorobotic models of spatial cognition 2

Aging in Visuo-Spatial Cognition

Focus on spatial coding
Focus on active visual exploration
Aging in VISUO-SPATIAL COGNITION

PERCEPTION → ACTION

- Functional markers of mobility & autonomy loss

Previous Studies of Aging & Spatial Cognition

All based on joystick-screen tasks

- Absence of multisensory integration
- Bias due to sensorimotor impairments
- Bias due to limited field of view
- Bias due to coordinate transformations

Not ecological enough?
Ecological Spatial Navigation Experiments

streetlab

Ecological Spatial Navigation Experiments

streetlab
avec l'institut de la Vision
Ecological Spatial Navigation Experiments

Ecological Spatial Navigation Experiments
Geometry vs. Landmark Coding

N=20 young adults (range: 19-37 yrs, µ=26.25, σ=4.97, N=11 females, N=9 males)
N=20 old adults (range: 61-79 yrs, µ=71.21, σ=4.35, N=10 females, N=10 males)
Geometry vs. Landmark Coding

N=20 young adults (range: 19-37 yo, μ=26.25, σ=4.97, N=11 females, N=9 males)
N=20 old adults (range: 61-79 yrs, μ=71.21, σ=4.35, N=10 females, N=10 males)
Geometry vs. Landmark Coding

Preference for geometric cues in older adults & children

![Bar chart showing preference for geometric cues in older adults compared to children.](chart.png)

**Focusing on Gaze Dynamics**

![Diagram illustrating gaze dynamics.](diagram.png)
Gaze Dynamics & Visuospatial Coding

Can the dynamics of the visual focus of attention predict the spatial coding strategy?

During reorientation

Gaze Dynamics & Visuospatial Coding

Can the dynamics of the visual focus of attention predict the spatial coding strategy?
Impact of cue reliance on spatial behavior

How does cue preference impact the use egocentric vs allocentric strategies?

N=22 young adults (range: 23-37 yo, μ=28, σ=4.28, N=13 females, N=9 males)
N=28 older adults (range: 67-81 yrs, μ=73, σ=3.9, N=17 females, N=11 males)
N=29 children (range: 10-11 yrs, μ=10, σ=0.49, N=17 females, N=12 males)

VR + eye tracking

Impact of cue reliance on spatial behavior

How does cue preference impact the use egocentric vs allocentric strategies?

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Models of aging in visuo-spatial perception & cognition

Integrated model of human aging

Scalable platform for data unification

Linking neuronal mechanisms to behavior through modeling

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Aging Human Avatar platform - An open framework

- Ageing in the early visual system
- Cerebellar ageing & vestibular-ocular reflex
- Ageing in visuo-spatial cognition

ROS: modular software architecture

Unity 3D Avatar & Environment

3D Avatar & Environment
Model of early visual system – CONVIS toolbox

Large-scale simulation of the retinal neurons with arbitrary spatiotemporal receptive fields on GPU

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Model of early visual system – CONVIS toolbox

Retina & LGN processing stage

Gradient-based parameter tuning of the retinal network based on data using deep learning algorithms

Cortical processing stage

Learning V1 receptive fields using STDP
Modelling contrast sensitivity in the presence of external noise

Huth J, Masquelier T, Arleo A (in preparation)
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CogMaster Course & INSTN2020 Part 2
Cerebellum-dependent VOR adaptation during motion

Impact of normal aging on VOR gain

Cerebellar biophysical model

Li et al., 2015

Naveros et al. (in preparation)

Luque et al. (under review)

Luque et al. (in preparation)

Li et al. (under review)

Luque et al. (in preparation)

Li et al. (under review)

Luque et al. (in preparation)

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Li et al. (under review)

Luque et al. (in preparation)

Li et al. (under review)

Luque et al. (in preparation)

Li et al. (under review)
Model of vision-based spatial learning

Li et al. (2017) CNS; Li et al. (in preparation)
Model of vision-based spatial learning

Inspiration sources...

Li et al. (2017) CNS; Li et al. (in preparation)
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Purkinje cell movie: complex spike

Reproduces Fig. 5 of De Schutter E., and Bower J.M.: An active membrane model of the cerebellar Purkinje cell. Simulation of synaptic responses. *Journal of Neurophysiology* 71: 401–419 (1994).

Visit www.cerebellum.org/models for more info and movies.

Climbing fiber activation, 0.1 ms/iframe.
Left: Membrane potential: -80 mV (blue) to 20 mV (red).
Right: Ca²⁺ concentration: 0 μM (blue) to 10 μM (red).

Produced by E. De Schutter, H. Comals, P. Franck and M. Wijnants
Copyright © Erik De Schutter Bgf-Uia, 2005.
Supervised learning

\[ \text{Update rule} \]
\[ \Delta \hat{w}(t) = -\alpha \cdot \frac{dE(t)}{d\hat{w}} \]

\[ \text{Error} \]
\[ E(\hat{w}) = \frac{1}{2} \sum_{\mu} [\tilde{t}(\mu) - \tilde{y}(\mu)]^2 \]
Reinforcement learning

Agent

Environment

action

state

reward

\[ s_t, a_t, Q(s_t, a_t), s_{t+1}, R_{t+1} \]

Temporal Difference Reinforcement Learning

Update rule

\[ \Delta w_{ij}(t) = \alpha \cdot \delta(t) \]

Teaching signal

\[ \delta(t) = R_{t+1} + \gamma \cdot \max_a Q(s_{t+1}, a) - Q(s_t, a_t) \]

is a measure of the difference between the expected reward and the actual reward