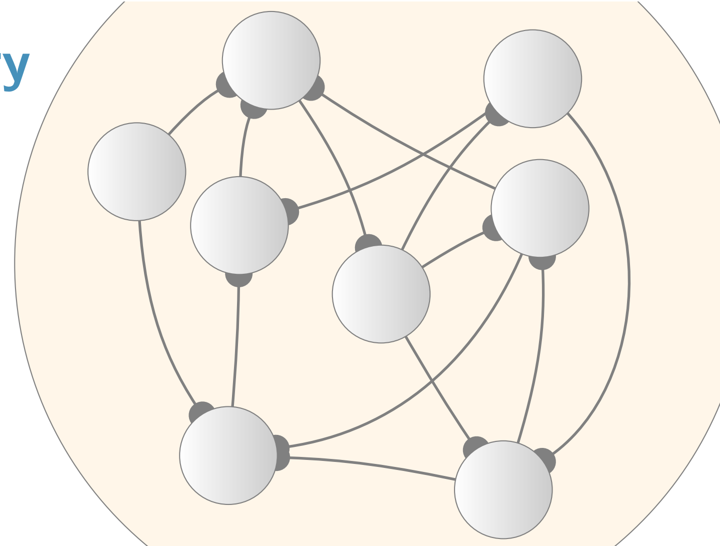
Failing to prepare is preparing to fail:

A network theory of movement preparation and execution

Guillaume Hennequin
University of Cambrige, UK



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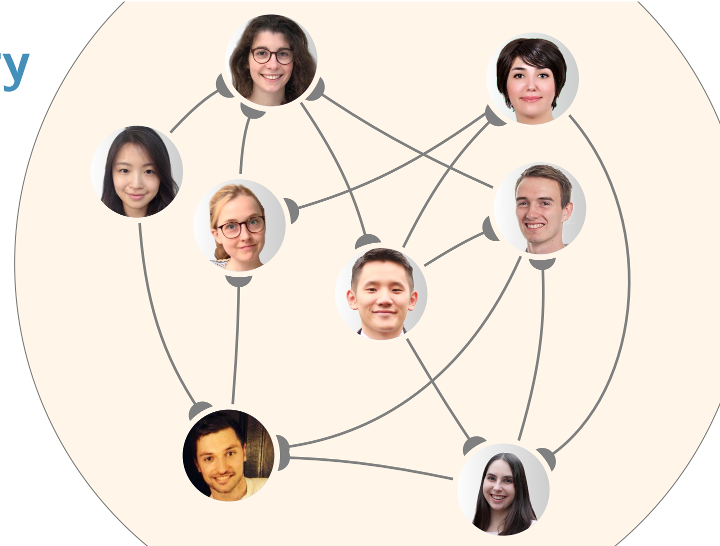

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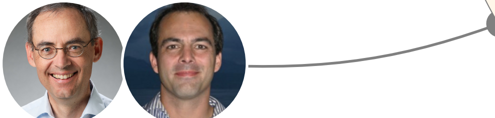
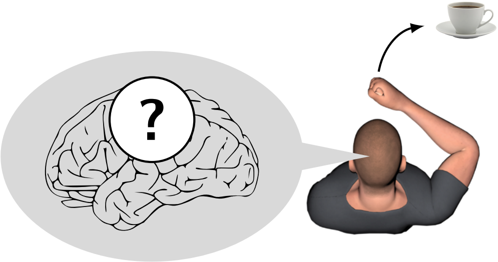


How do brains control movement?



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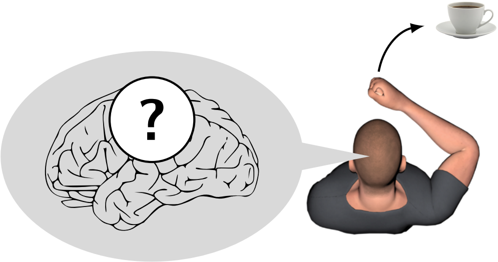

computational principles

phenomenology of neural activity

circuit mechanisms

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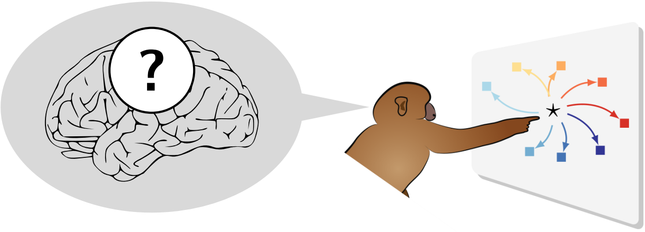

Illustration: Y.T. Kimura

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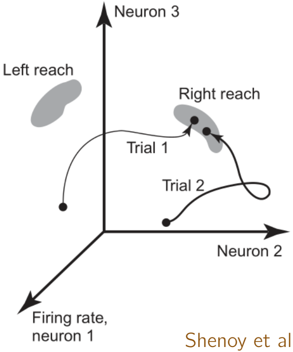

Shenoy et al. (2013)

Illustration: Y.T. Kimura

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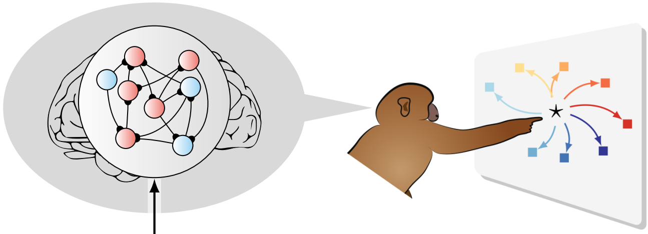

computational principles

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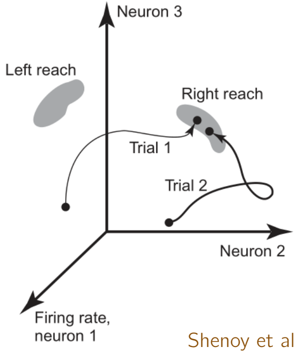
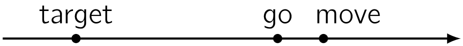
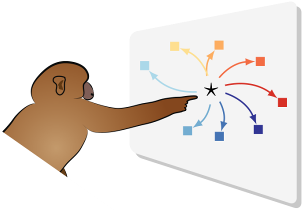
network-level theories



Shenoy et al. (2013)

delayed reaching task





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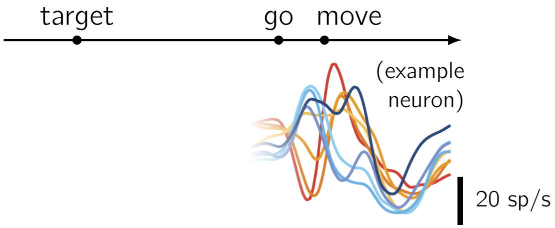

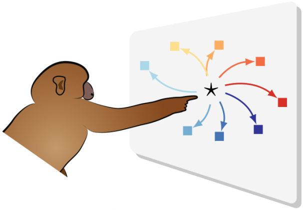

Churchland et al. (2010, 2012); Elsayed et al. (2016)

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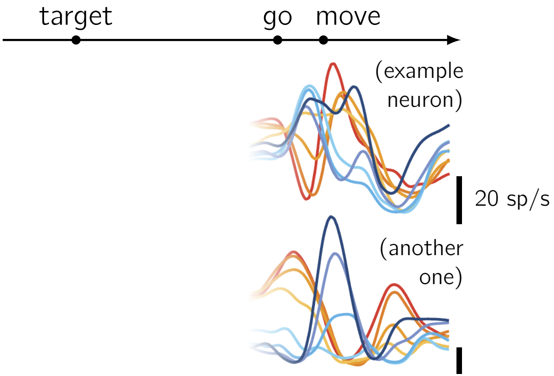

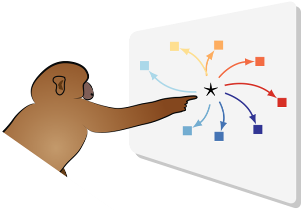

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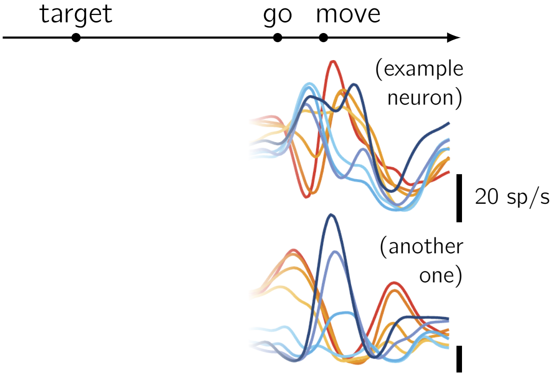
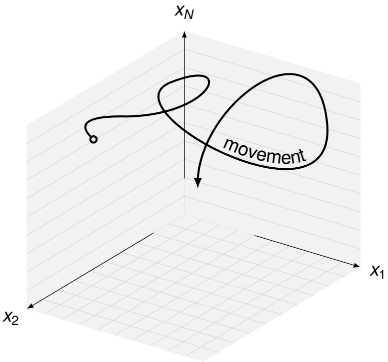


$$\frac{d\mathbf{x}}{dt} = f(\mathbf{x})$$



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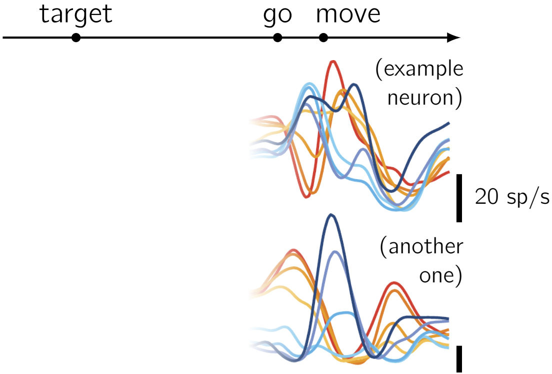

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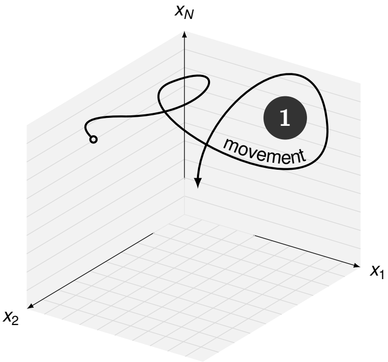
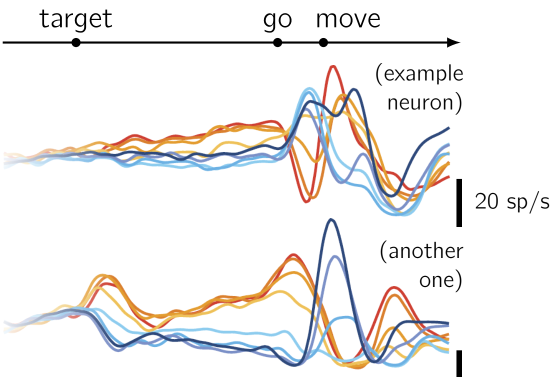


network principles underlying:

1 movement-related activity?

Churchland et al. (2010, 2012); Elsayed et al. (2016)

delayed reaching task



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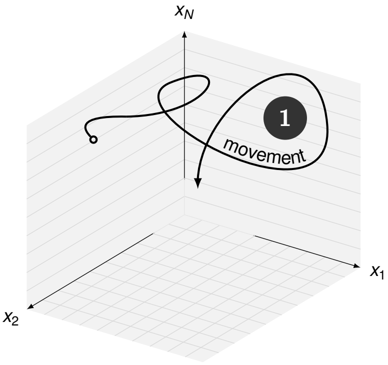

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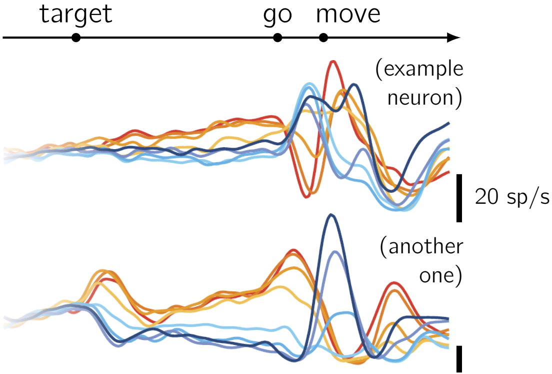

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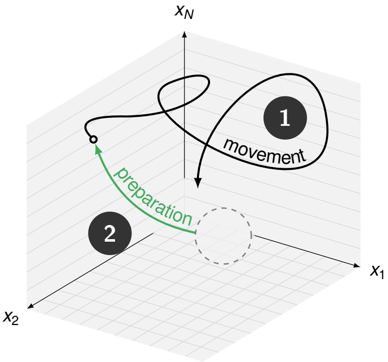
$$\frac{d\mathbf{x}}{dt} = f(\mathbf{x}, \mathbf{u})$$



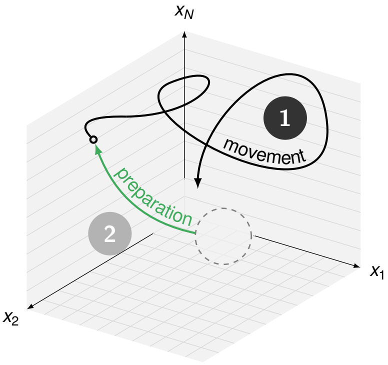
network principles underlying:

1. movement-related activity?
2. preparatory activity?

1

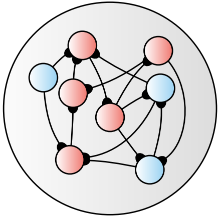
network dynamics
for movement generation

- off-the-shelf models of cortical dynamics struggle to produce M1-like activity
- new model class with detailed E/I balance generate M1-like activity transients
- simple learning rules can construct such networks



Hennequin et al., *Neuron* (2014)
Li et al., *in prep*

$$\tau \frac{d\mathbf{x}}{dt} = -\mathbf{x}(t) + \mathbf{W}\,\phi[\mathbf{x}(t)] + \text{input}$$



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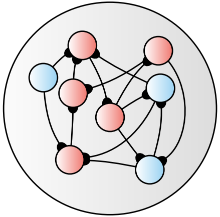
momentary change of population activity vector

decay

recurrent connectivity

firing rate nonlinearity



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what connectivity
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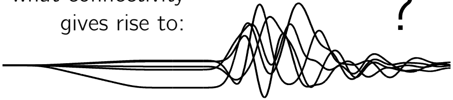

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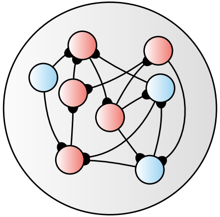

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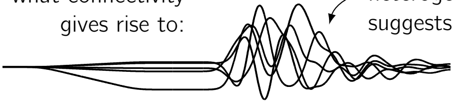
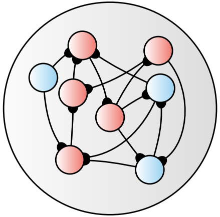


complexity /
heterogeneity
suggests disorder



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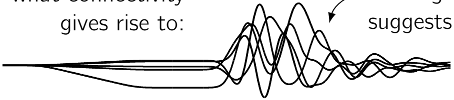

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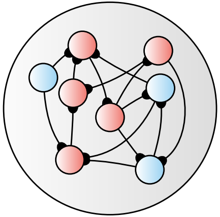
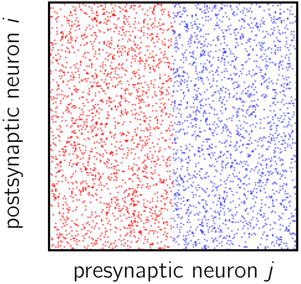


Rajan and Abbott (2006)

connectivity matrix **W**



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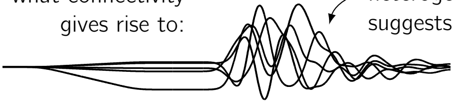

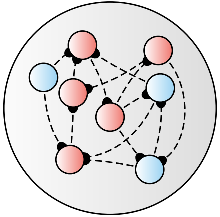

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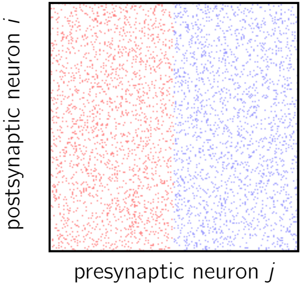

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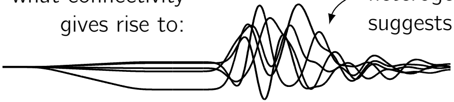

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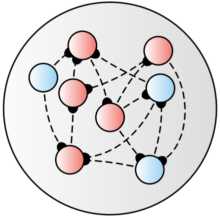

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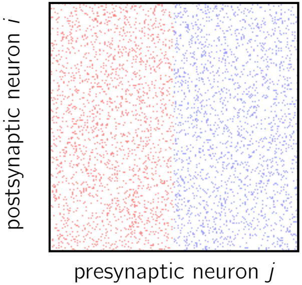
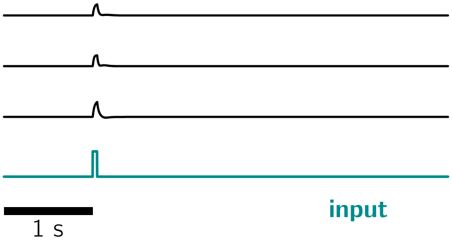


weak connectivity: stable but simple dynamics



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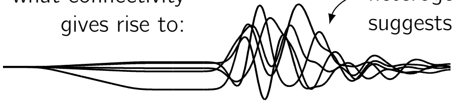
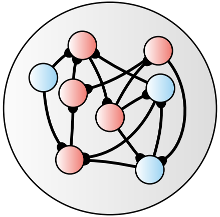


complexity / heterogeneity suggests disorder



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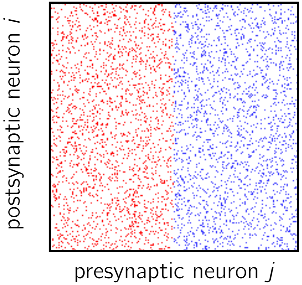
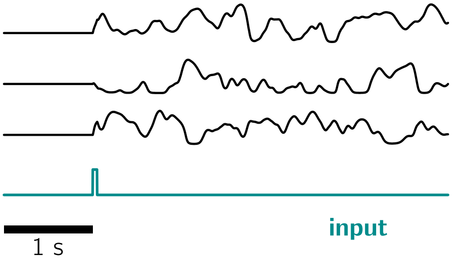


strong connectivity: complex but chaotic dynamics



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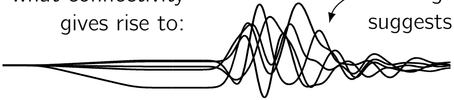

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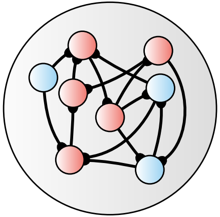

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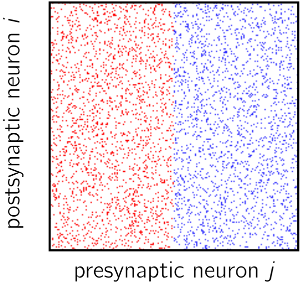

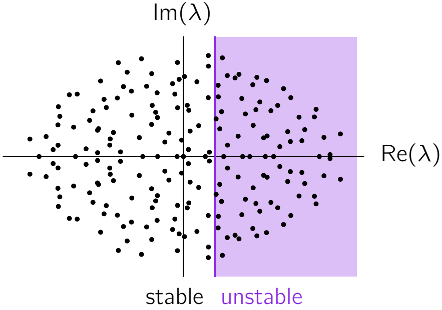

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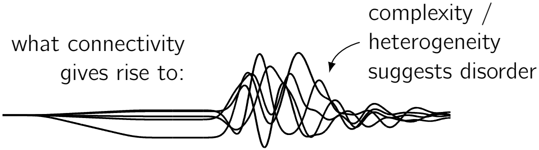

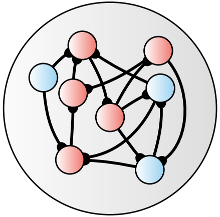

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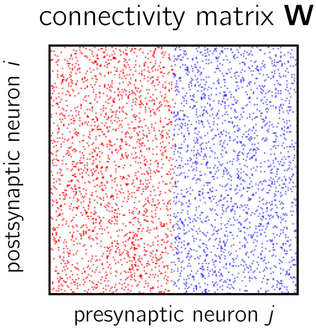

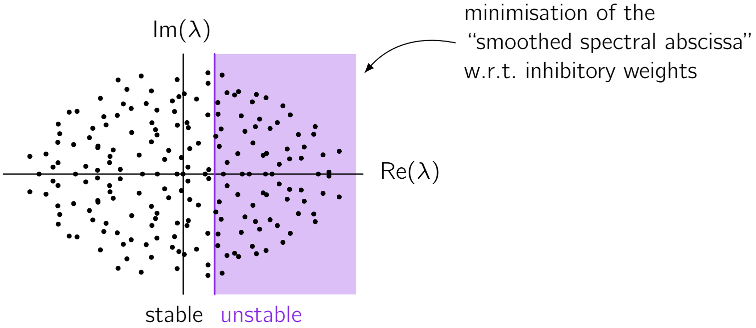

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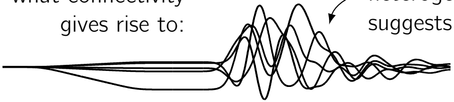
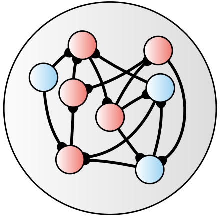


complexity / heterogeneity suggests disorder



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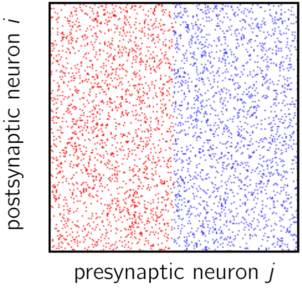

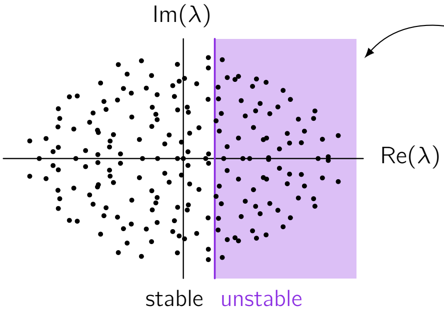

minimisation of the "smoothed spectral abscissa" w.r.t. inhibitory weights

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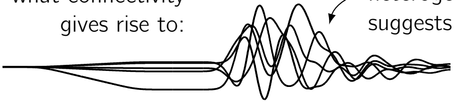

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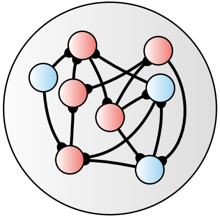

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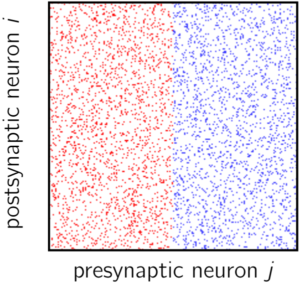

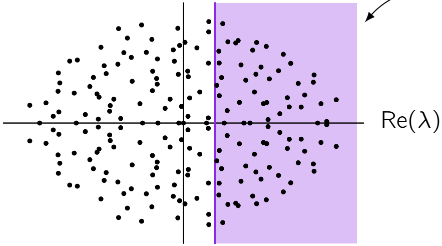

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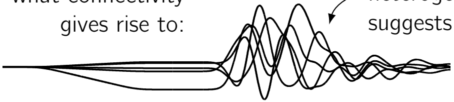

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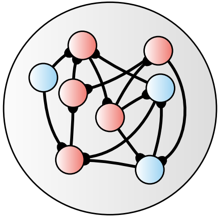

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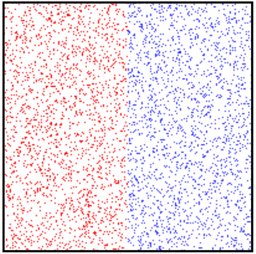
connectivity matrix $\mathbf{W}$

postsynaptic neuron i



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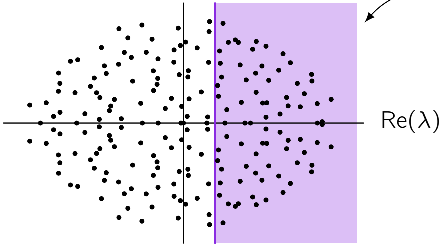

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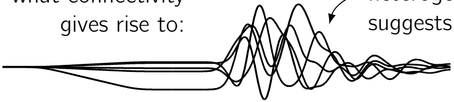

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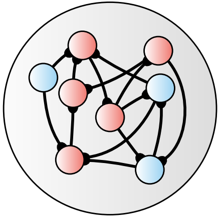

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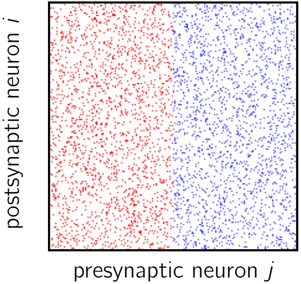

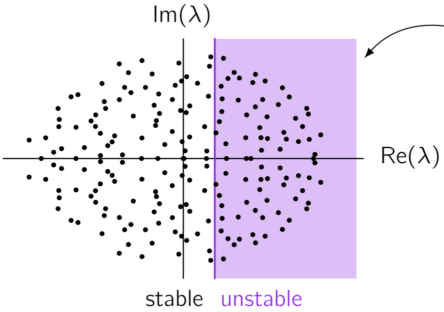

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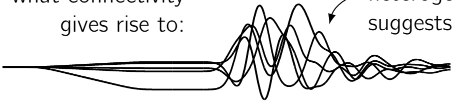

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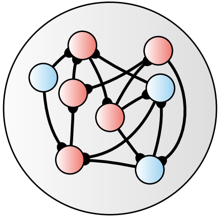

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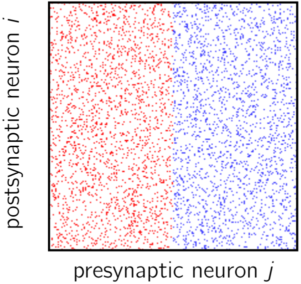

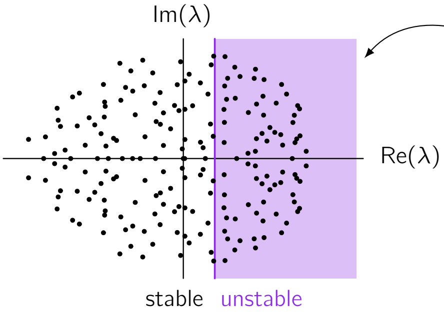

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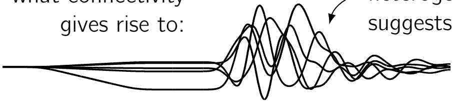

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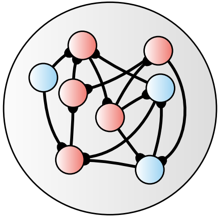

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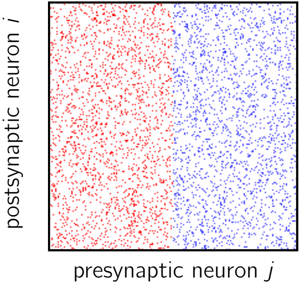

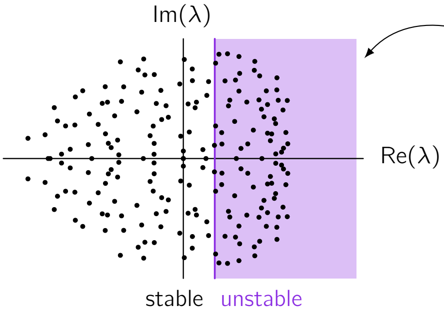

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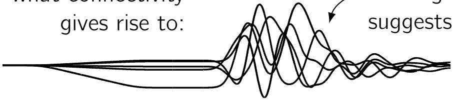

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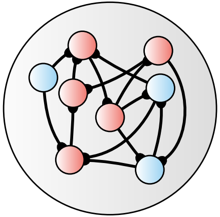

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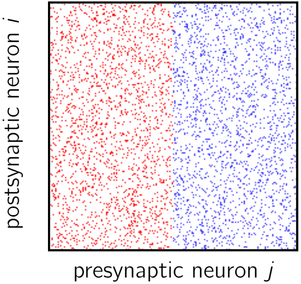

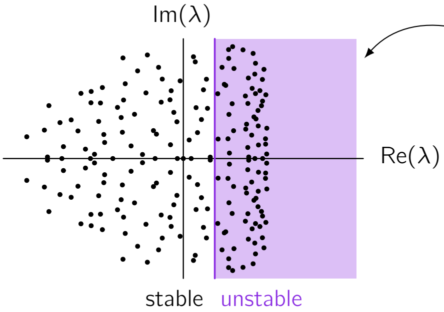

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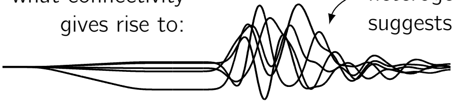

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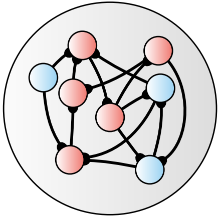

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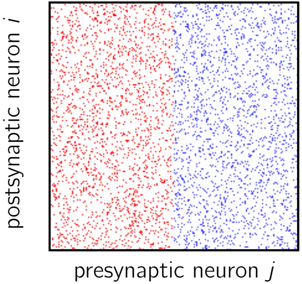

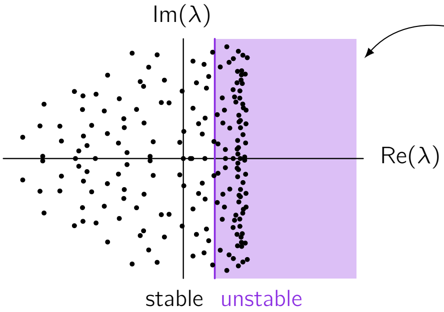

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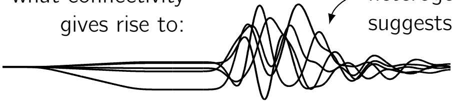

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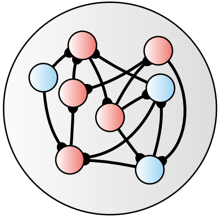

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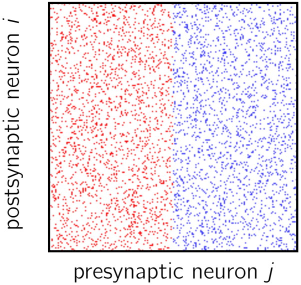

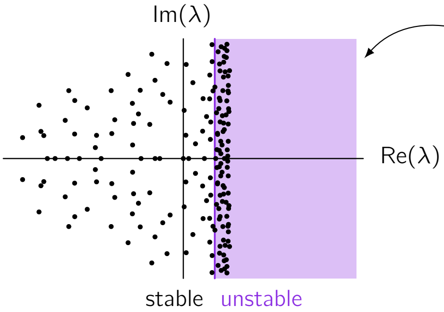

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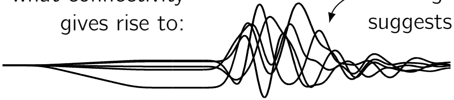

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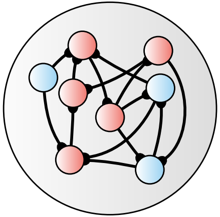

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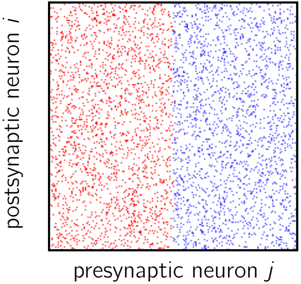

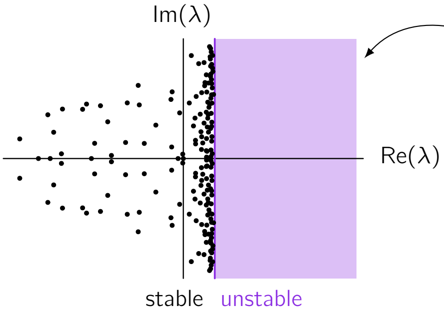

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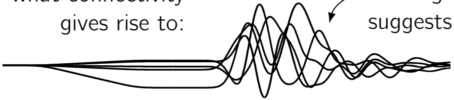

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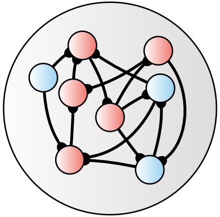

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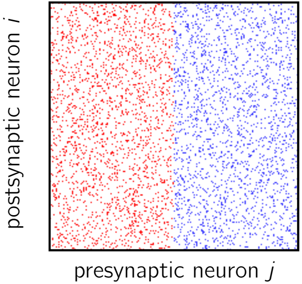

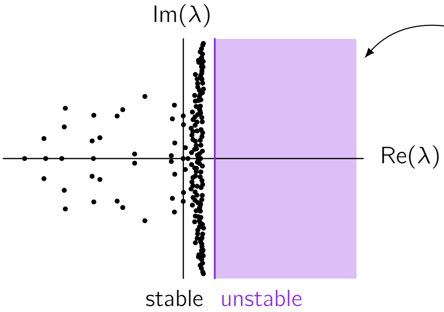

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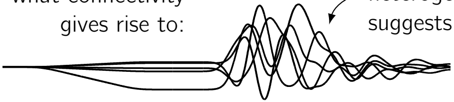

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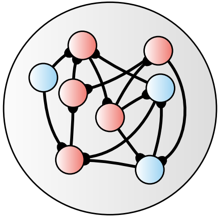

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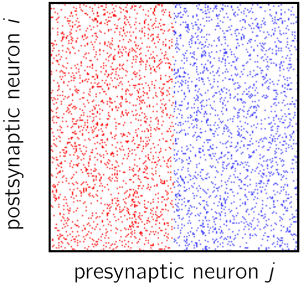

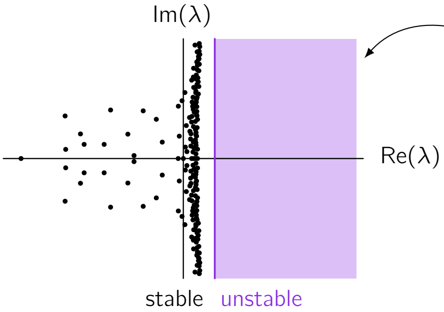

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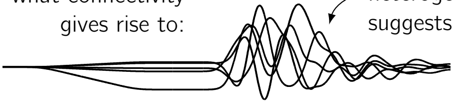

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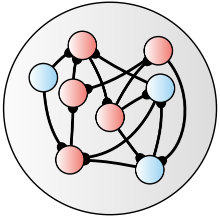

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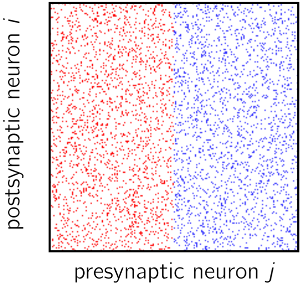

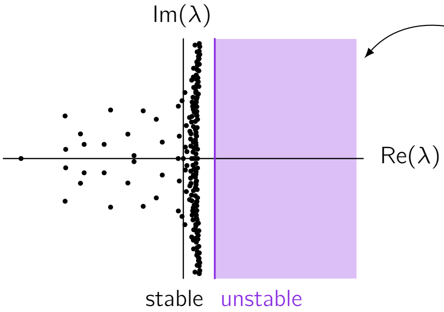

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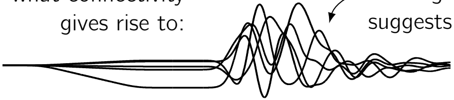

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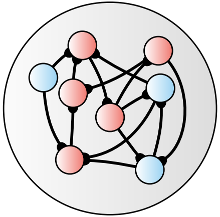

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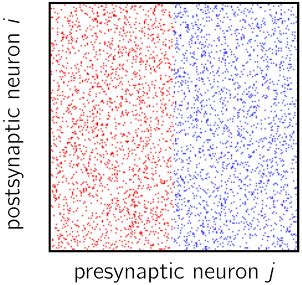

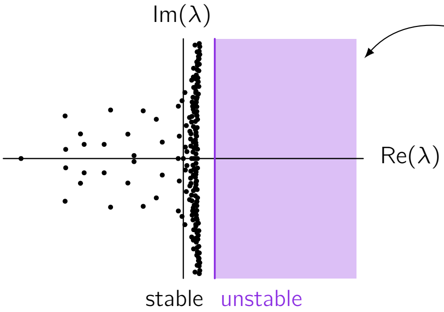

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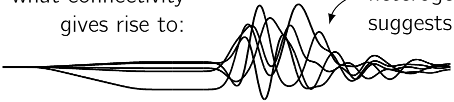

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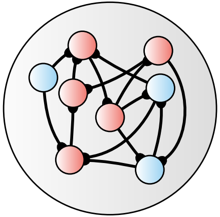

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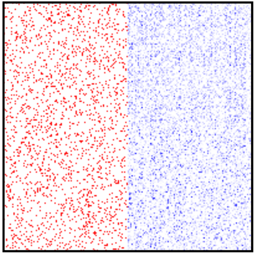
postsynaptic neuron i



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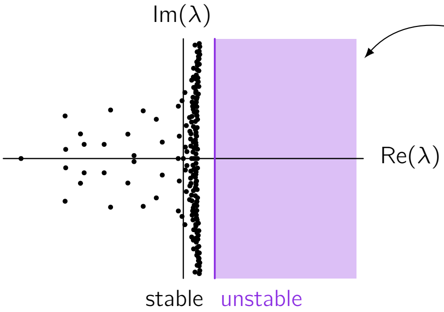

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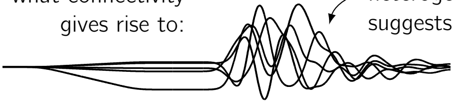
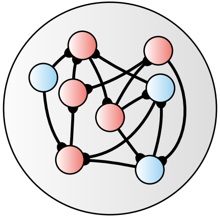


complexity / heterogeneity suggests disorder



Rajan and Abbott (2006)
Sompolinsky et al. (1988)
Kadmon and Sompolinsky (2015)
Mastrogiuseppe and Ostojic (2017)
Ahmadian et al. (2015)
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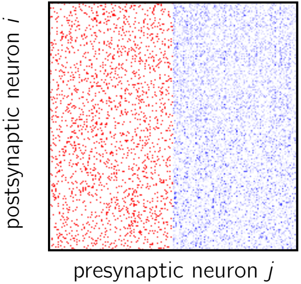
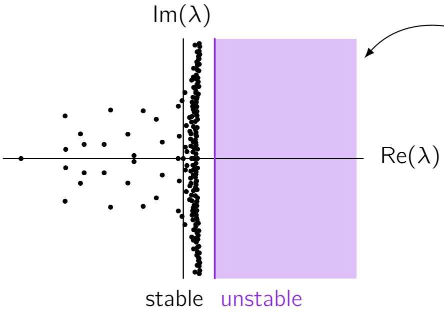
connectivity matrix **W**



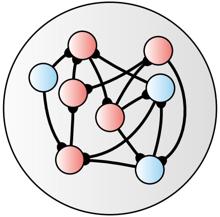


minimisation of the "smoothed spectral abscissa" w.r.t. inhibitory weights

⇒ precisely balanced 'nonnormal' network with rich transient behaviour

Murphy and Miller (2009)
Hennequin et al. (2012)
Bondanelli & Ostojic (2020)

$$\tau \frac{d\mathbf{x}}{dt} = -\mathbf{x}(t) + \mathbf{W}\,\phi[\mathbf{x}(t)] + \text{input}$$



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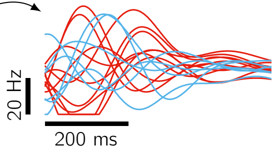
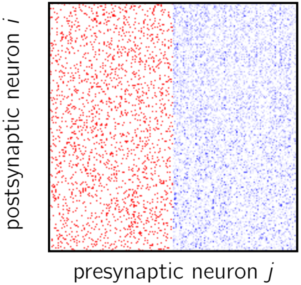
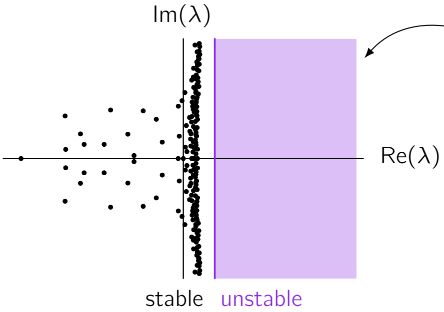
autonomous response to privileged initial condition



connectivity matrix $\mathbf{W}$





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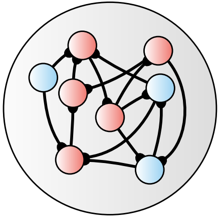

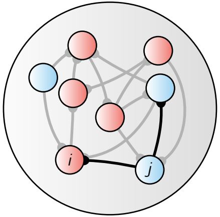

Hebbian ISP

$\Delta|W_{ij}| \propto \phi(x_j)(x_i - \alpha)$

Xizi Li

Vogels*, Sprekeler*, et al. (2011)
Luz and Shamir (2012)
Vogels et al. (2013)
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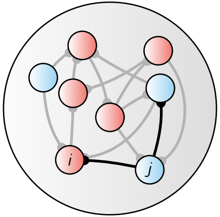
Li et al. (in prep)



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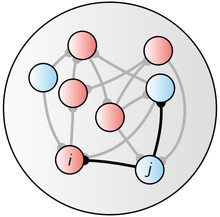

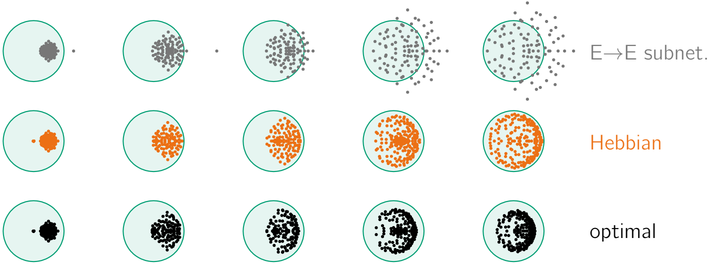

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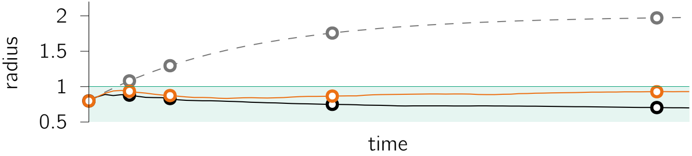

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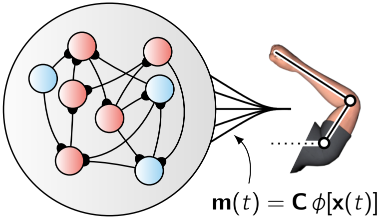
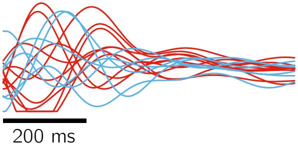
Hebbian ISP enables unsupervised construction of high-dimensional inhibition-stabilised networks

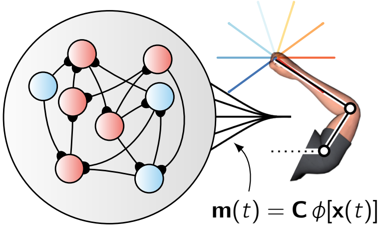


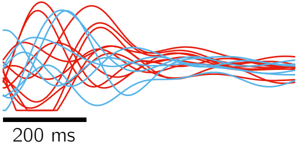


Li & Todorov (2004)
Kao et al., *Neuron* (2021)

Calvin Kao

fix the ISN; optimise readout and initial conditions





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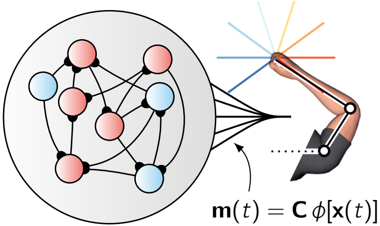

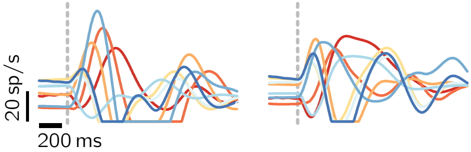

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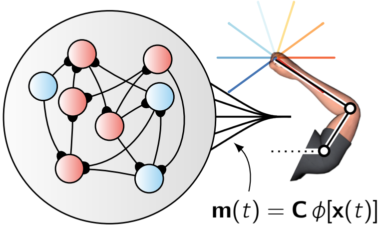

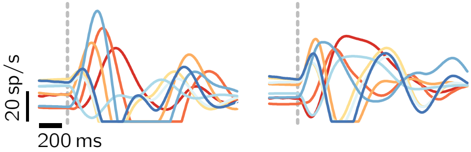

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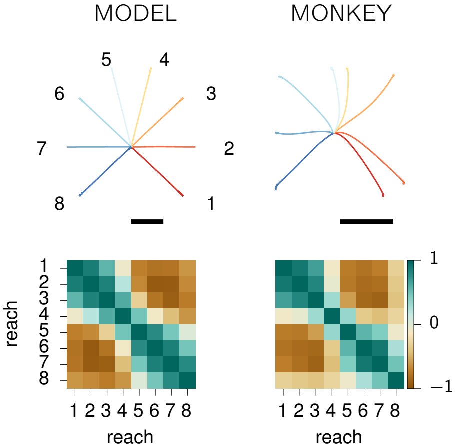
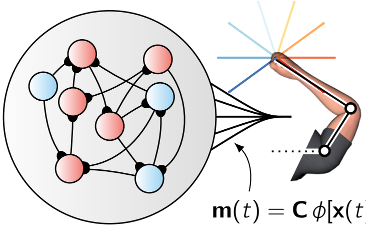


data from Churchland, Kaufman, et al.

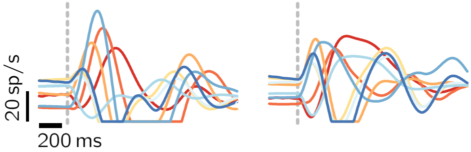
Calvin Kao

similar structure in initial conditions

fix the ISN; optimise readout and initial conditions



$\mathbf{m}(t) = \mathbf{C}\,\phi[\mathbf{x}(t)]$



Li & Todorov (2004)
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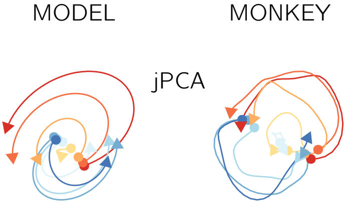
Calvin Kao

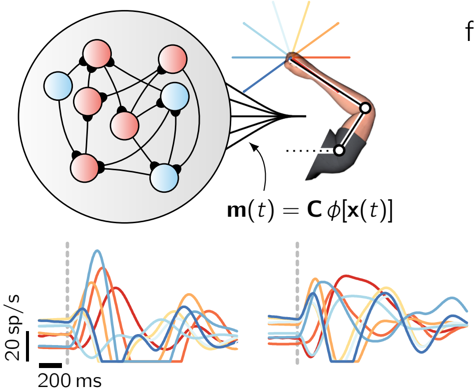


data from Churchland, Kaufman, et al.

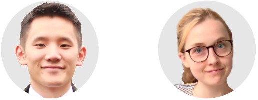
activity rotates
at the population level

Churchland*, Cunningham*, et al. (2012)

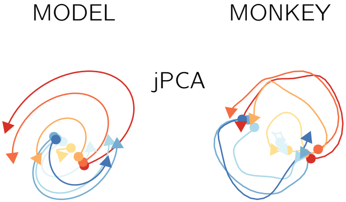
fix the ISN; optimise readout and initial conditions



Li & Todorov (2004)
Kao et al., *Neuron* (2021)



Calvin Kao Virginia Rutten



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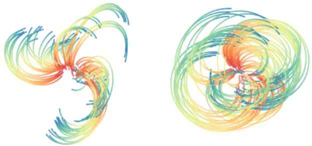
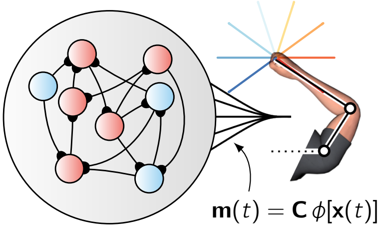
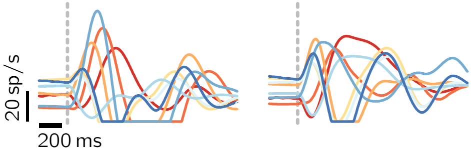


see also:
Rutten et al., *Neurips* (2020)





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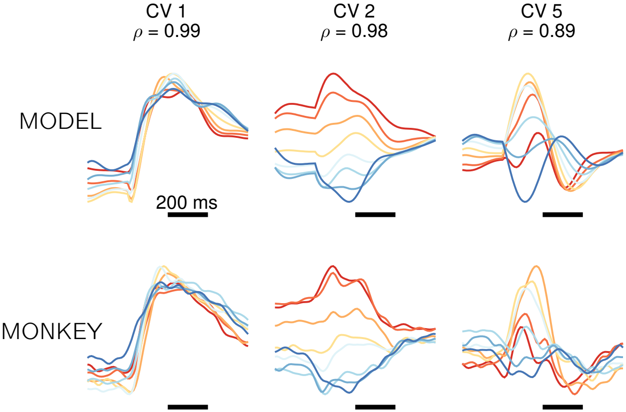


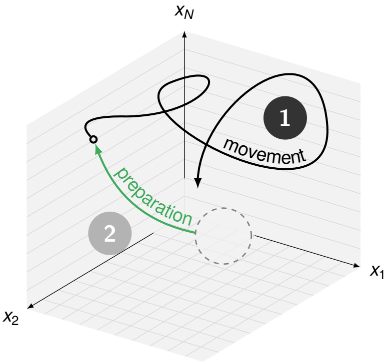
monkey and model embed similar signals

see also Sussillo et al. (2015)

1

network dynamics
for movement generation

- off-the-shelf models of cortical dynamics struggle to produce M1-like activity
- new model class with detailed E/I balance generate M1-like activity transients
- simple learning rules can construct such networks



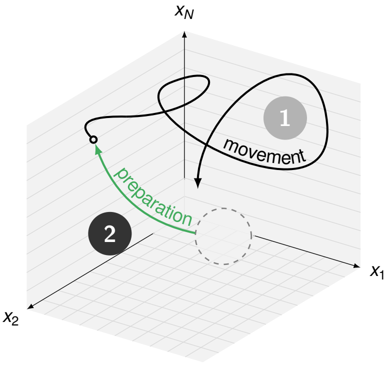
Hennequin et al., *Neuron* (2014)
Li et al., *in prep*
Stroud et al., *Nat Neurosci* (2018)

Jake Stroud

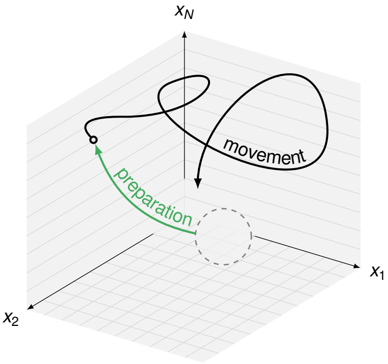
2

a network theory of
motor preparation

- preparation is important
  (failing to prepare...)
- formalised as optimal anticipatory control
- realised in gated thalamo-cortical loops



Kao et al., *Neuron* (2021)

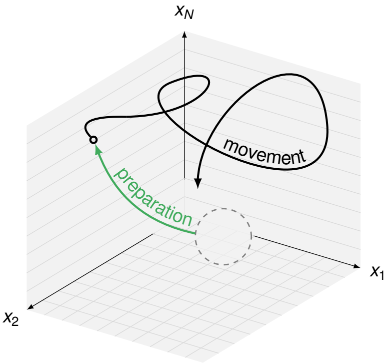


x_N
movement
preparation
x_1
x_2

Churchland et al. (2007)

Empirically:

- neural perturbations during the delay period increases reaction time (RT)



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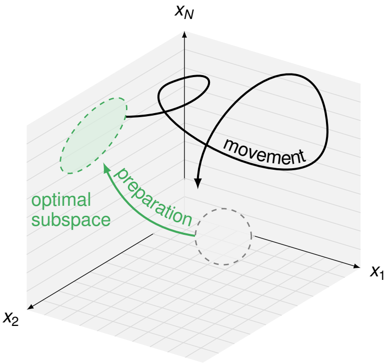

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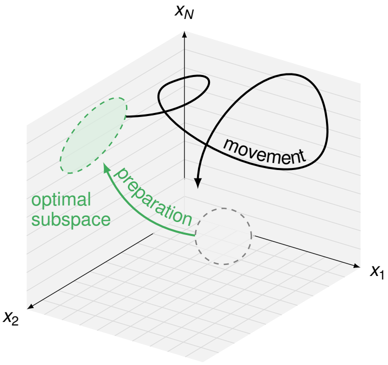

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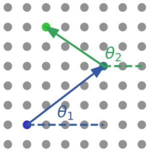
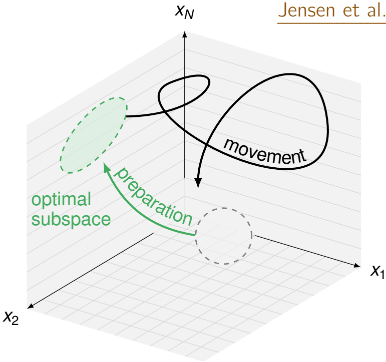


continuous reaching for 30+ min



Kris Jensen Calvin Kao Jasmine Stone

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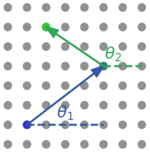

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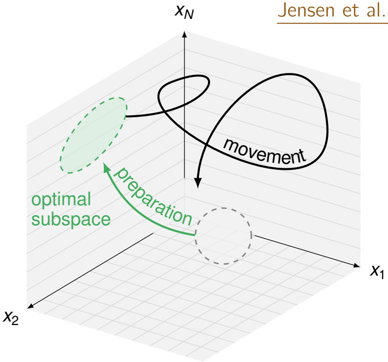
scalable, fully-Bayesian GPFA
(here: 10M+ datapoints)

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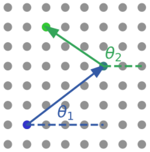

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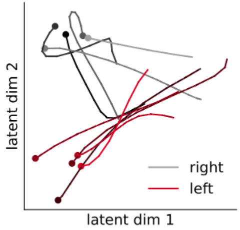

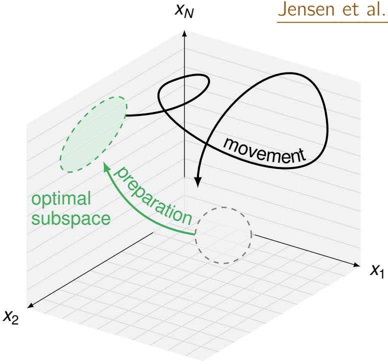


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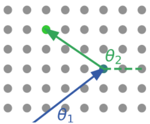

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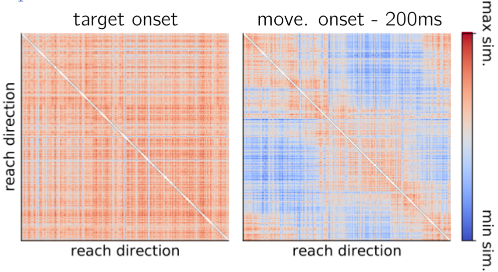

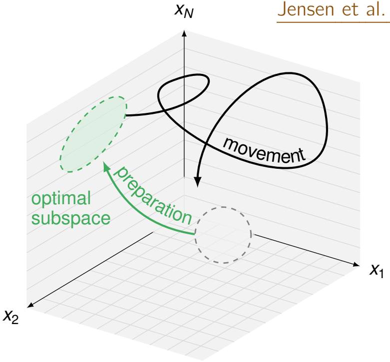

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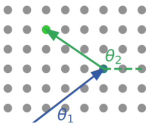

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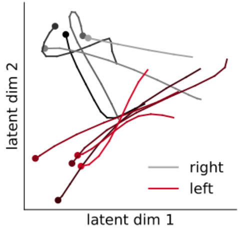

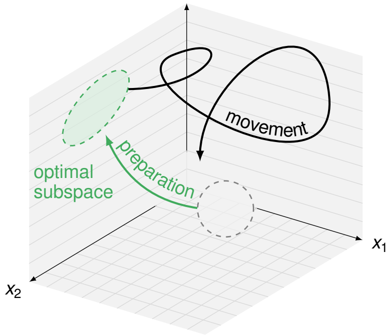


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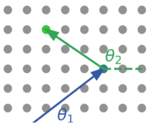

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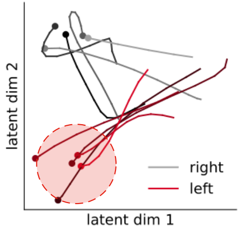

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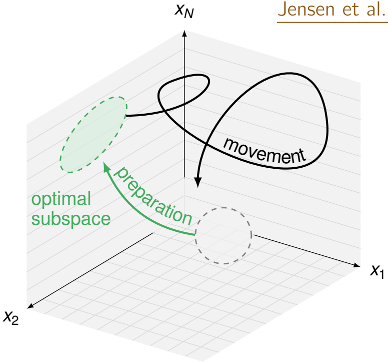

Kris Jensen Calvin Kao Jasmine Stone

Empirically:

Churchland et al. (2007)
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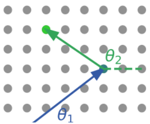
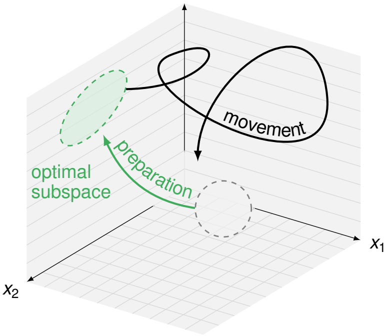
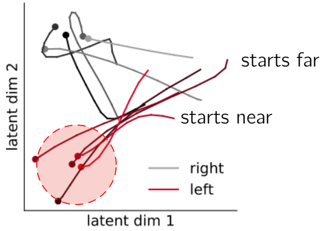


continuous reaching for 30+ min

scalable, fully-Bayesian GPFA
(here: 10M+ datapoints)





Kris Jensen   Calvin Kao   Jasmine Stone

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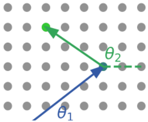

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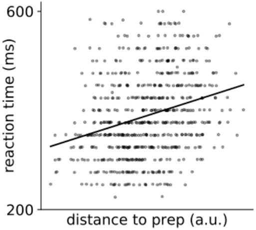
$r = 0.28$



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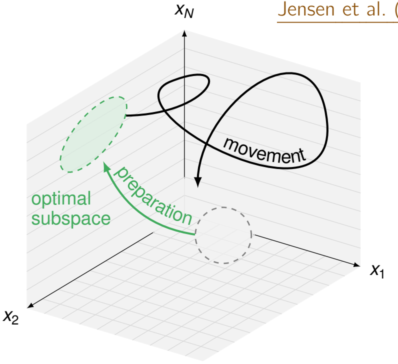
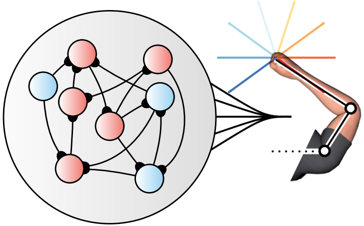
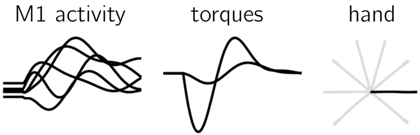


Kris Jensen Calvin Kao Jasmine Stone

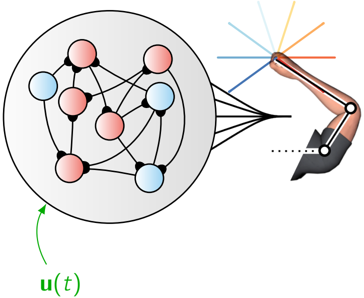


how do we get there?



$$\tau \frac{d\mathbf{x}}{dt} = -\mathbf{x}(t) + \mathbf{W}\,\phi[\mathbf{x}(t)] + h$$

Kao et al., *Neuron* (2021)



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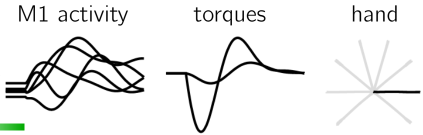

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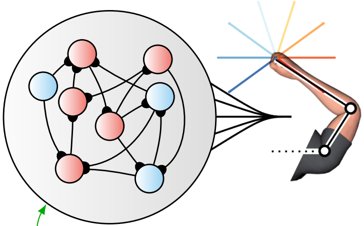

$\mathbf{u}(t)$

how do
we get
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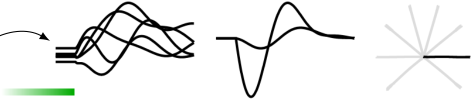

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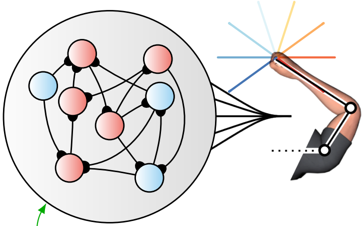
200 ms

simplest "naive" strategy:
constant $\mathbf{u}$ to
establish right fixed point

Kao et al., *Neuron* (2021)



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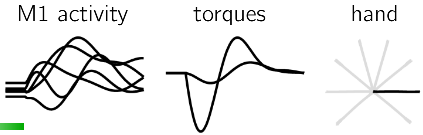

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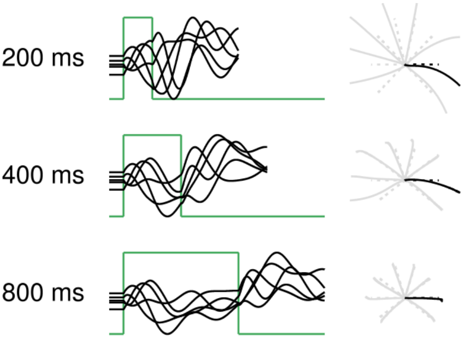
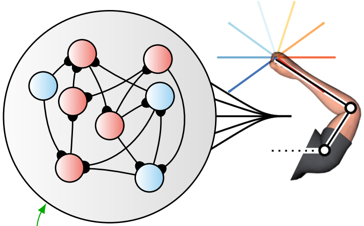


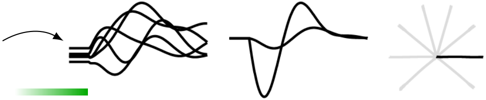
Kao et al., *Neuron* (2021)



$\mathbf{u}(t)$

how do we get there?

M1 activity | torques | hand



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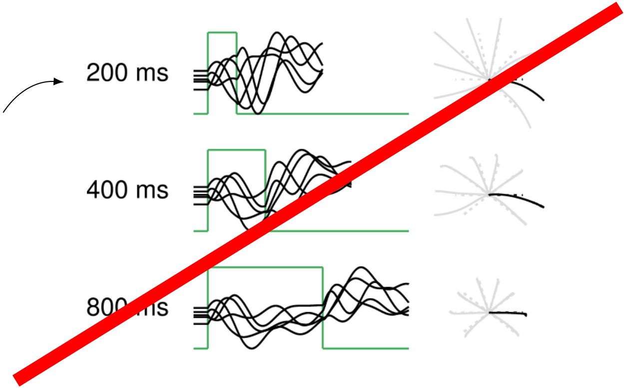
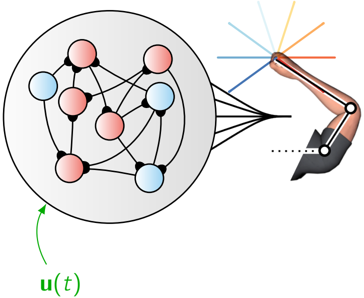


also conflicts with:
Kaufman et al. (2014)
Elsayed et al. (2016)

Kao et al., *Neuron* (2021)



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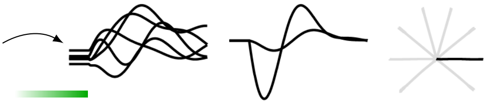

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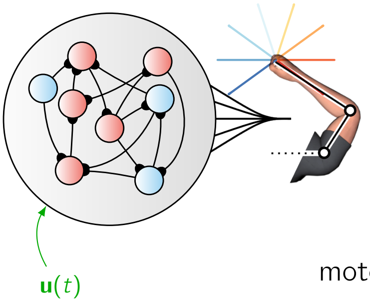

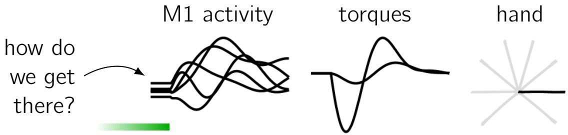

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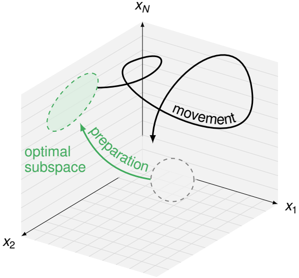
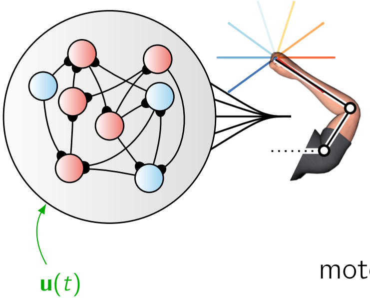
motor preparation as <u>optimal anticipatory control</u>:

choose $\mathbf{u}(t)$ so as to "be ready for movement, rapidly"



Kao et al., *Neuron* (2021)



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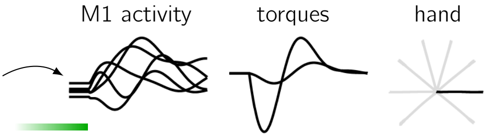

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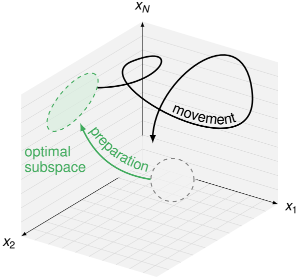
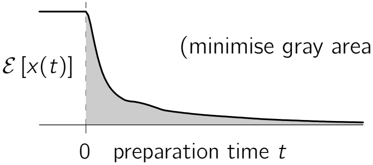
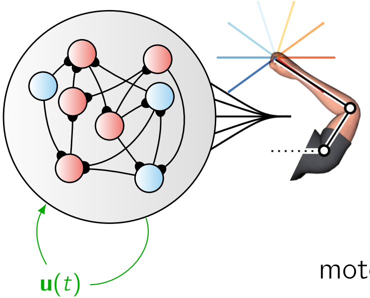
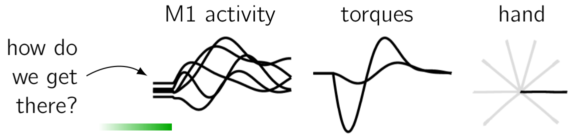


(minimise gray area + control effort)



Kao et al., *Neuron* (2021)





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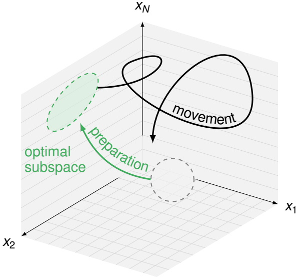
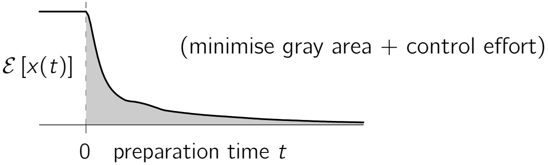
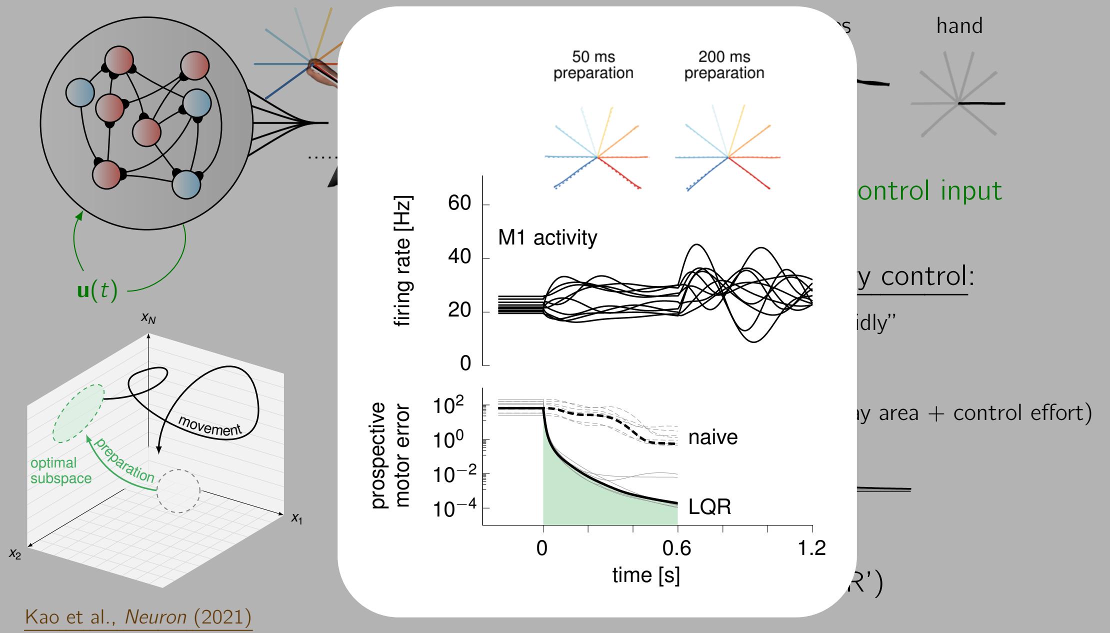


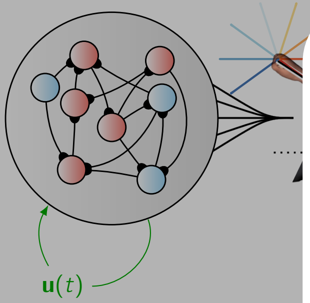


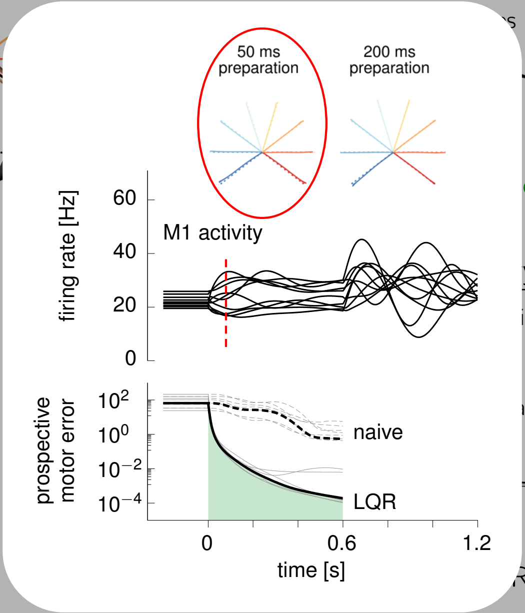
optimal solution = state feedback ('LQR')

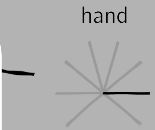
Kao et al., *Neuron* (2021)



u(t)
x_N
x_1
x_2
movement
preparation
optimal
subspace
50 ms
preparation
200 ms
preparation
M1 activity
firing rate [Hz]
60
40
20
0
prospective
motor error
10^2
10^0
10^{-2}
10^{-4}
naive
LQR
0
0.6
1.2
time [s]
hand
ontrol input
y control:
idly"
ay area + control effort)
R')
Kao et al., *Neuron* (2021)







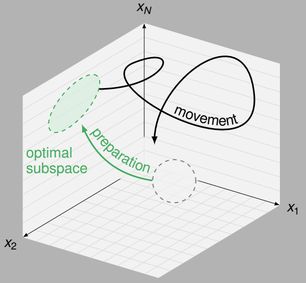
ontrol input

y control:

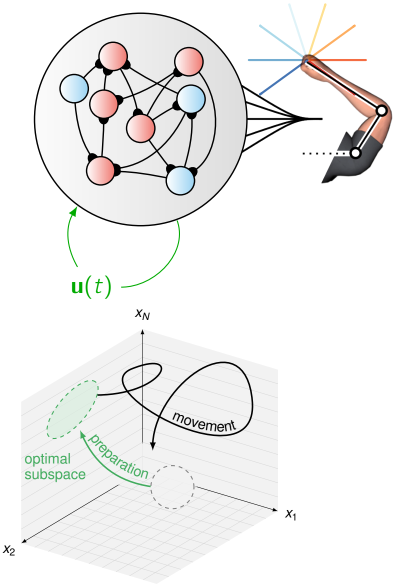
idly”

y area + control effort)

R’)



Kao et al., *Neuron* (2021)



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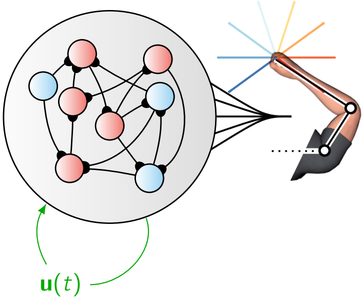

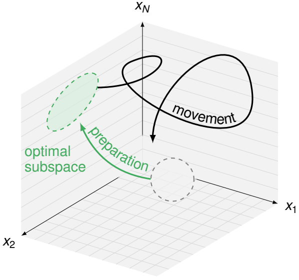

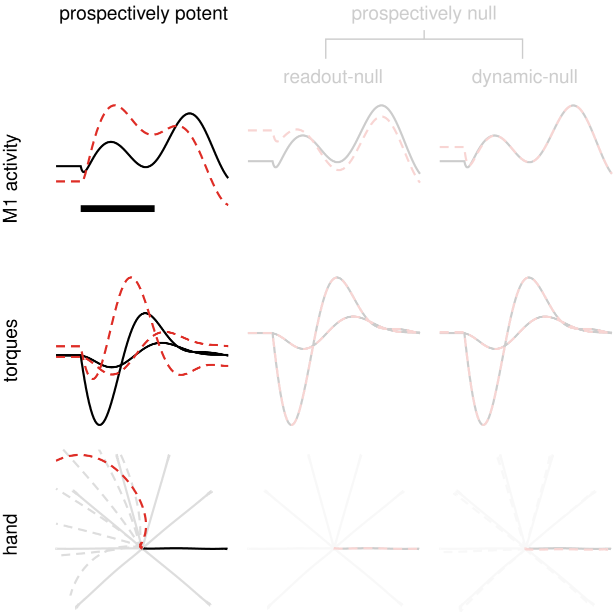

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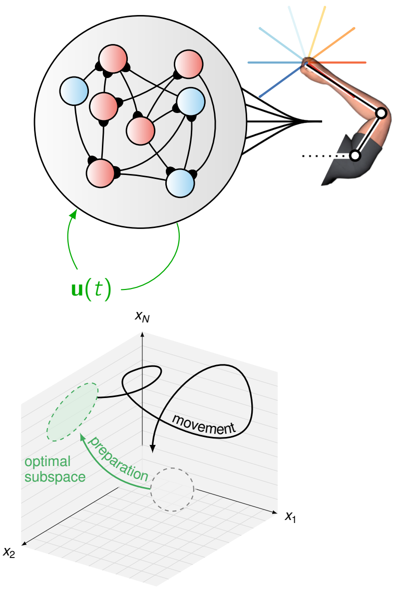

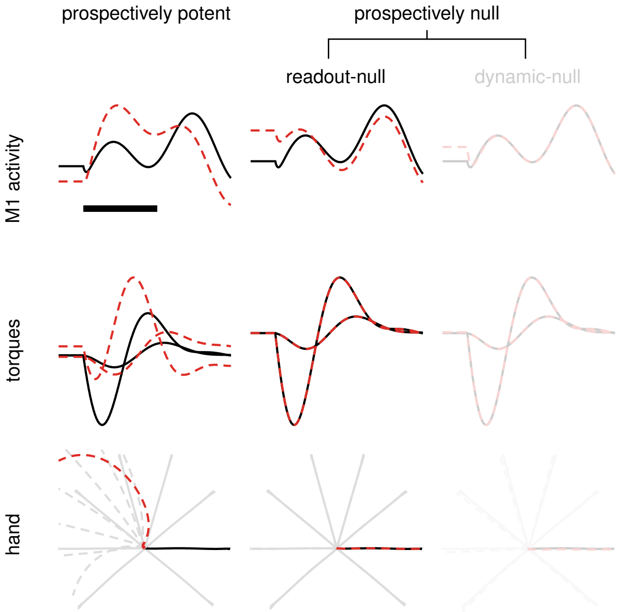

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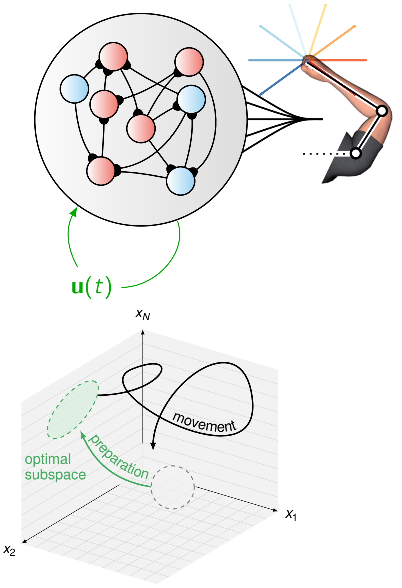

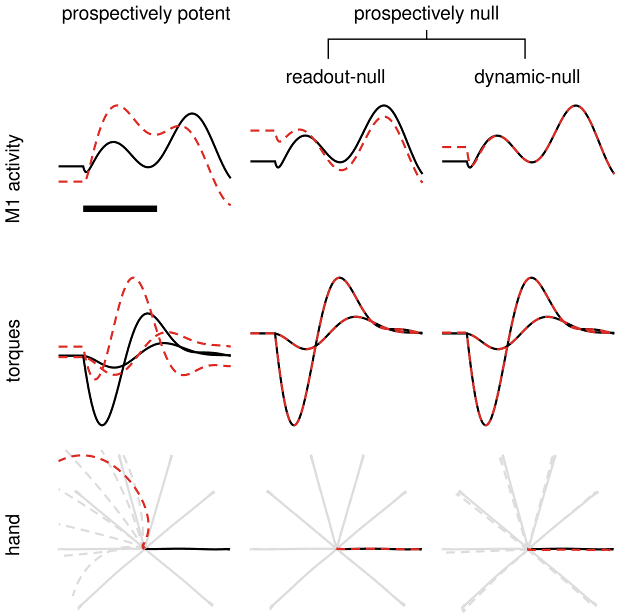

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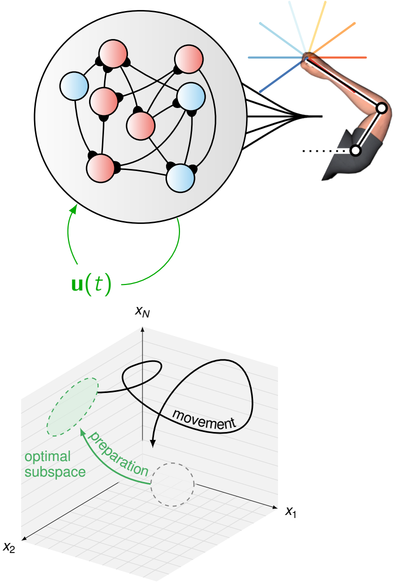
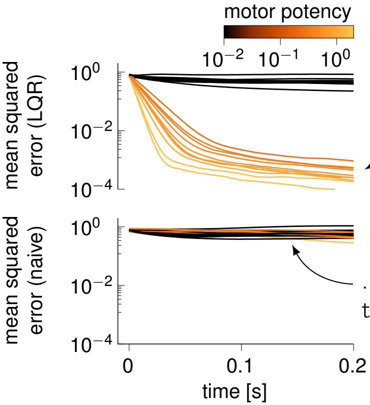


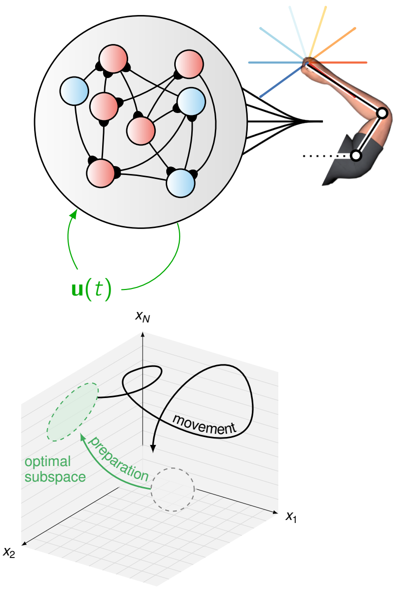


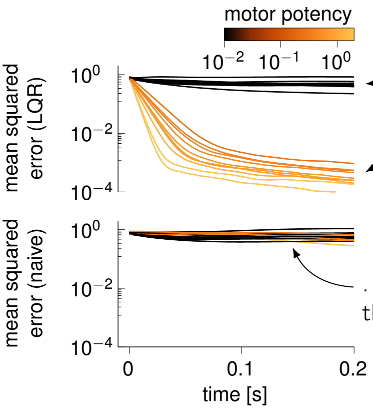
optimal, selective elimination of errors in potent dimensions. . .

c.f. also Li, Daie, et al. (2016)

. . . not observed in the naive strategy

Kao et al., *Neuron* (2021)





explains away
intriguing results
of perturbation exps.

Ames et al. (2014)
Sauerbrei et al. (2020)

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elimination of errors
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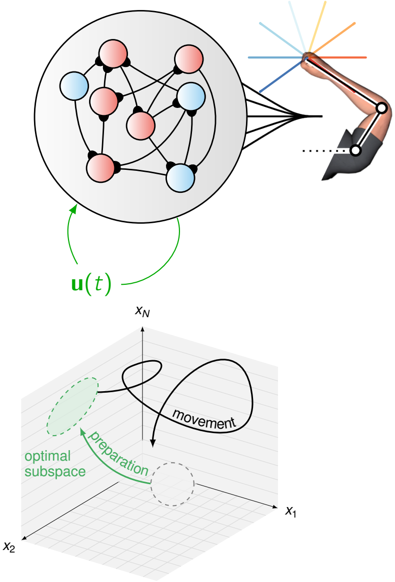
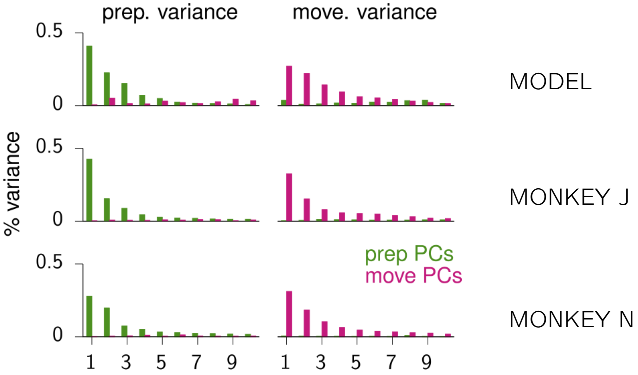
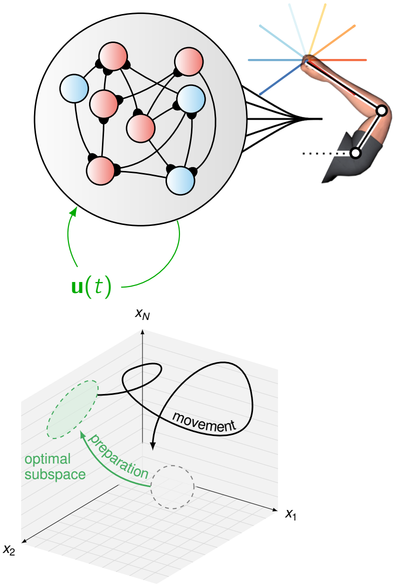


Kao et al., *Neuron* (2021)

optimal preparation also explains orthogonality between preparatory and movement subspaces:

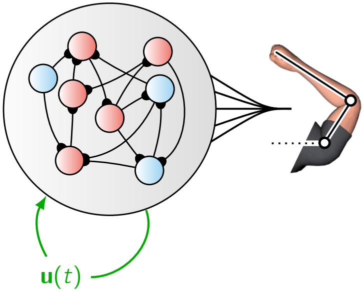


Elsayed et al. (2016)



Kao et al., *Neuron* (2021)

algorithm ⟶ circuit implementation?



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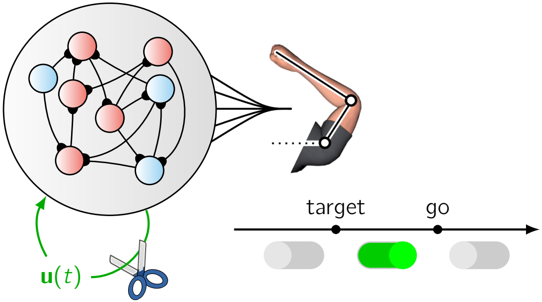

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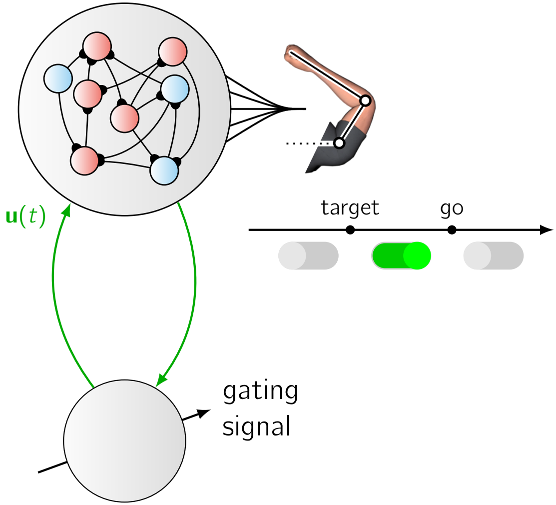
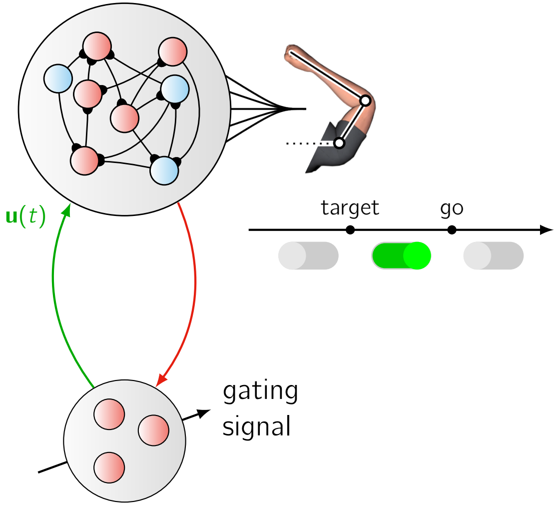


Guo et al. (2017)

Kao et al., *Neuron* (2021)

see also: Logiaco et al., *Cell Reports* (2021)



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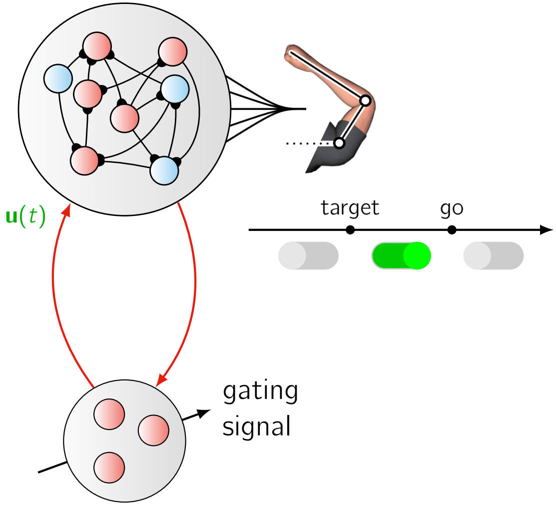

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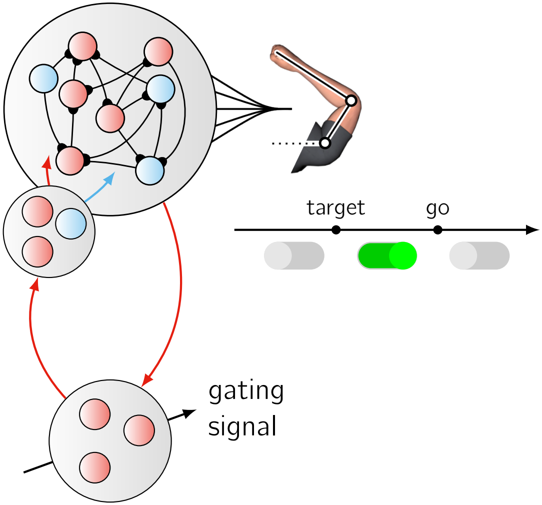

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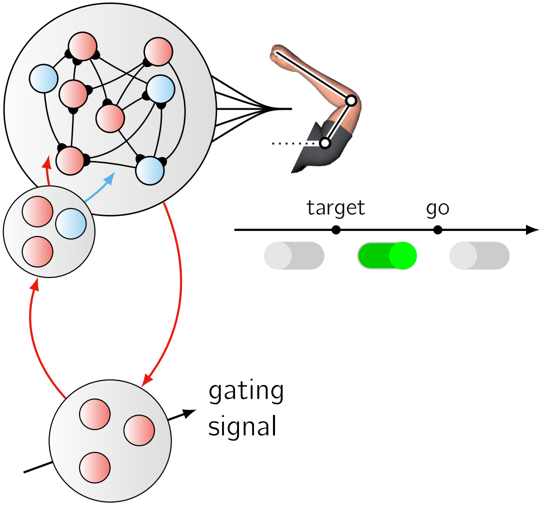
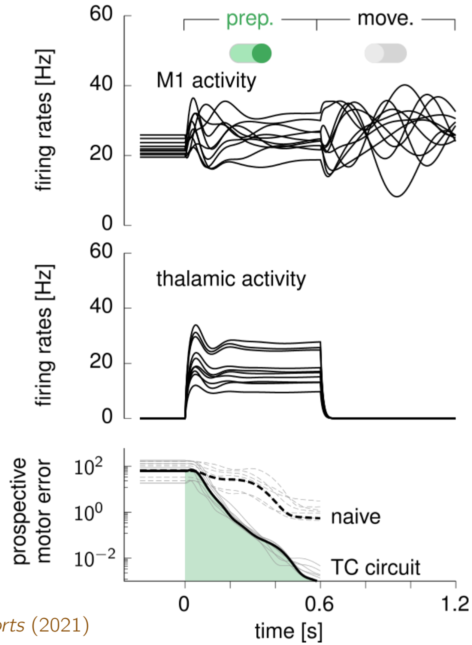
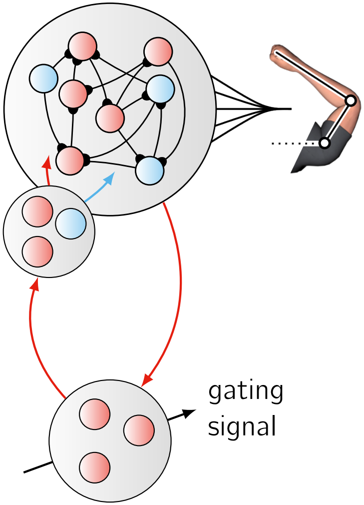




Kao et al., *Neuron* (2021)

Guo et al. (2017)
see also: Logiaco et al., *Cell Reports* (2021)



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  - ISN dynamics account for salient dynamical structure in M1 activity during movement

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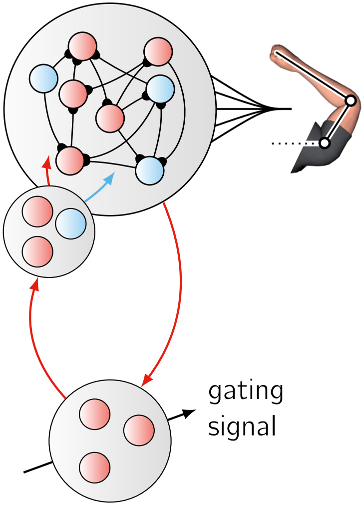

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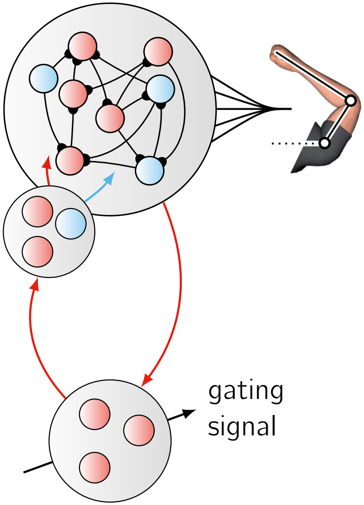

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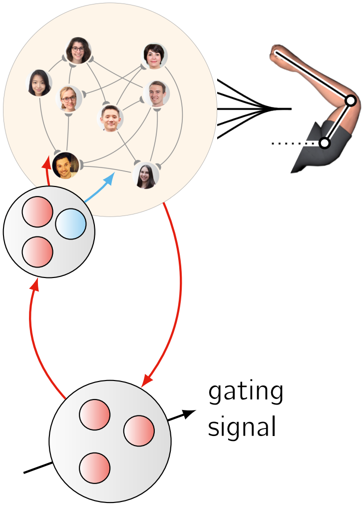

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Swiss National Science Foundation
Wellcome Trust

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