Advanced Neurotheory Course – Lecture 1

Fabio Stefanini

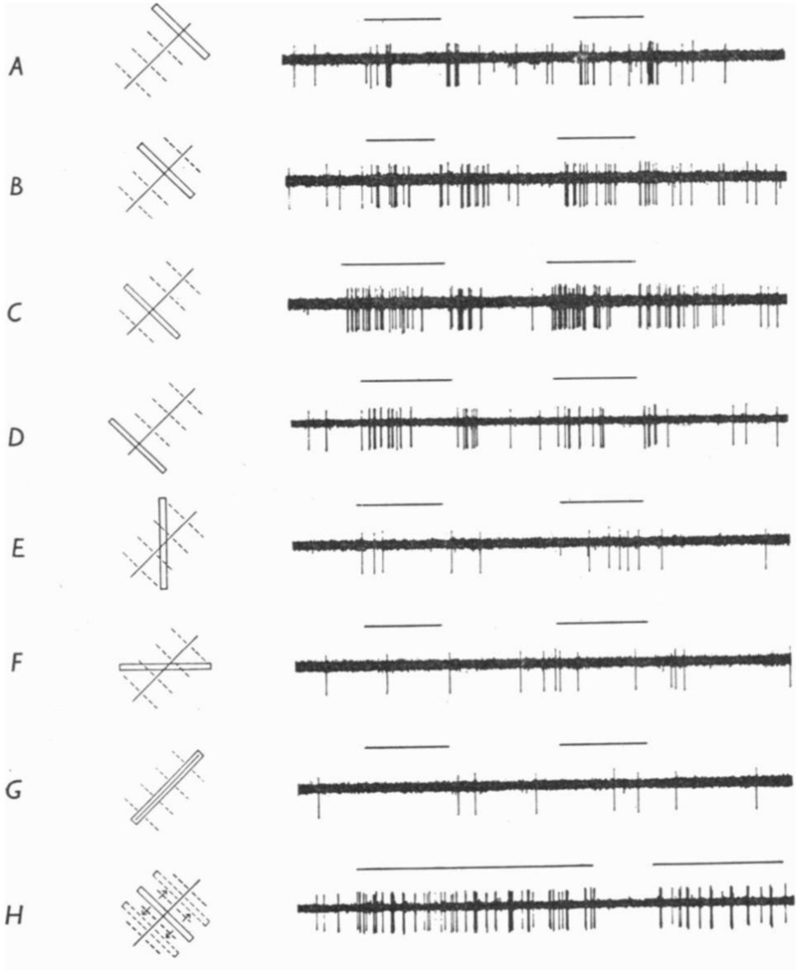
Jan 25th 2019

fs2545@columbia.edu

JLG-6D

- Rigotti, Mattia, et al. "The importance of mixed selectivity in complex cognitive tasks." *Nature* 497.7451 (2013): 585.
- Stefanini, Fabio, et al. "A distributed neural code in ensembles of dentate gyrus granule cells." *bioRxiv* (2018): 292953.
- Bernardi, Silvia, et al. "The geometry of abstraction in hippocampus and prefrontal cortex." *bioRxiv* (2018): 408633.
- Dayan, Peter, and Laurence F. Abbott. *Theoretical neuroscience*. Vol. 806. Cambridge, MA: MIT Press, 2001.

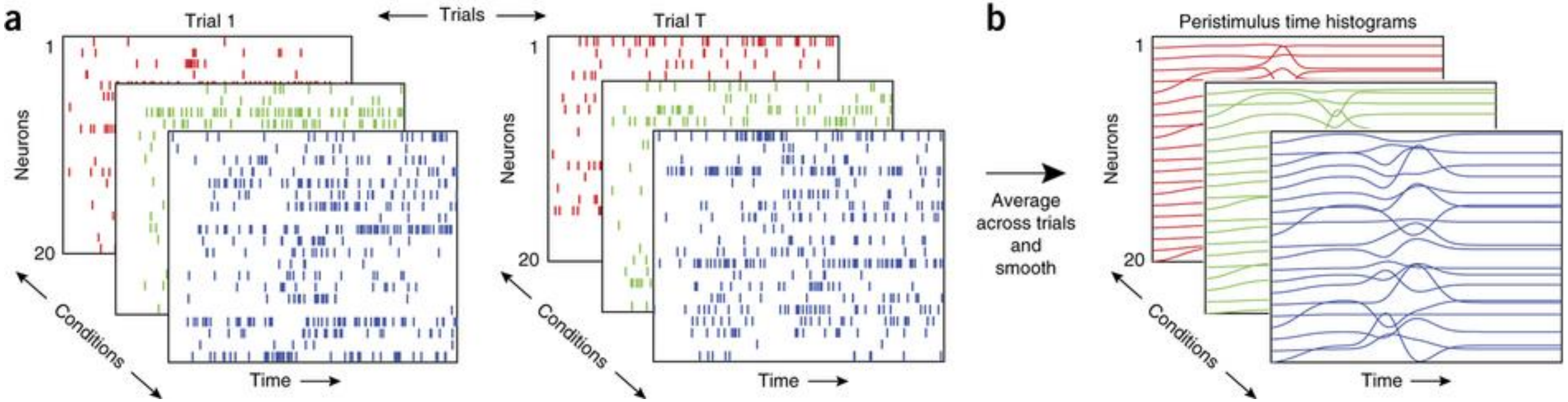
Reading neural code: the idea of tuning curves



Torsten Wiesel and
David H. Hubel
“for their discoveries concerning information processing in the visual system".

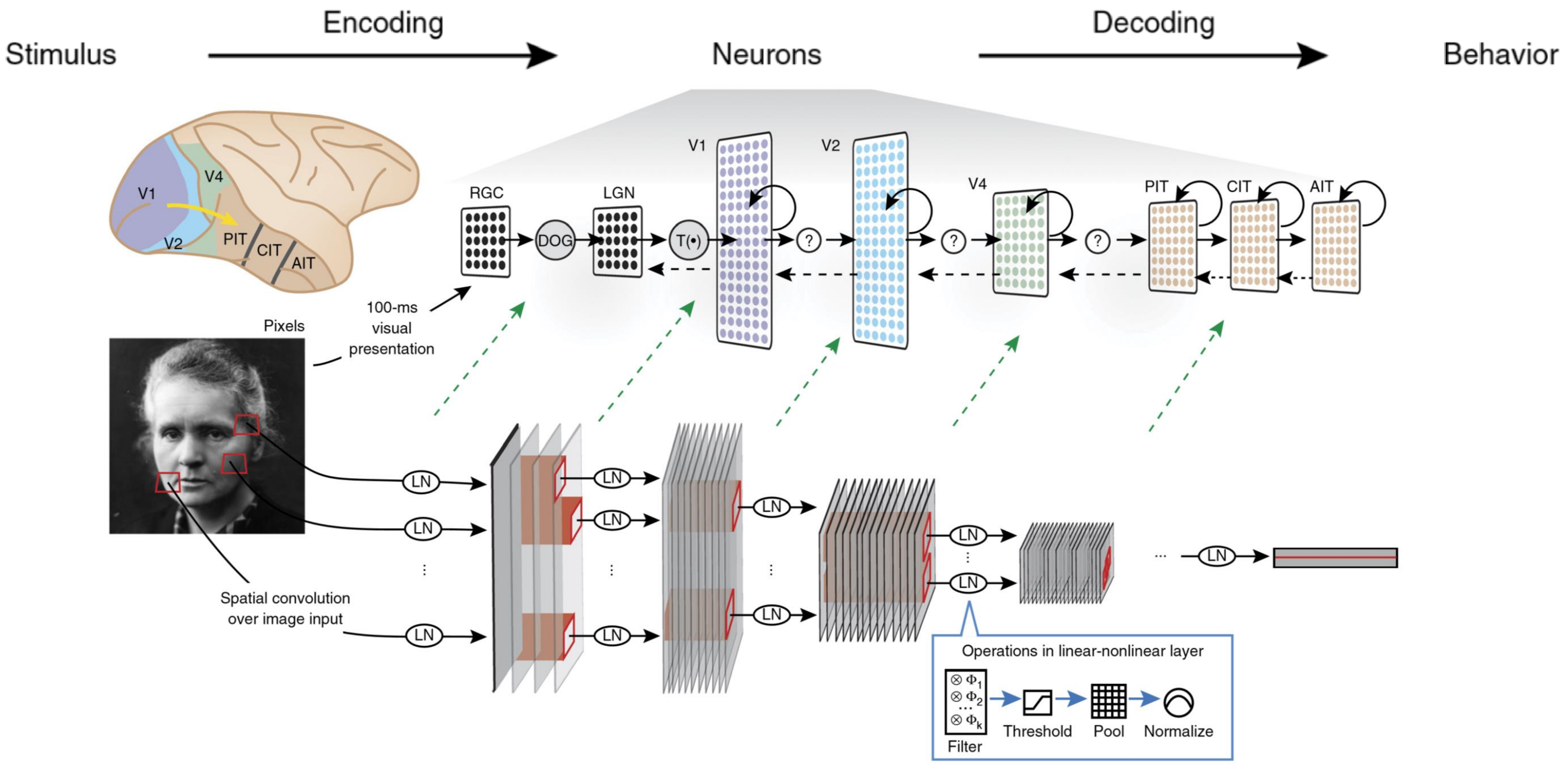
Source: YouTube, Hubel and Wiesel’s lab

Reading neural code: a lot of neurons (and trials)



J. Cunningham and B. Yu, 2014

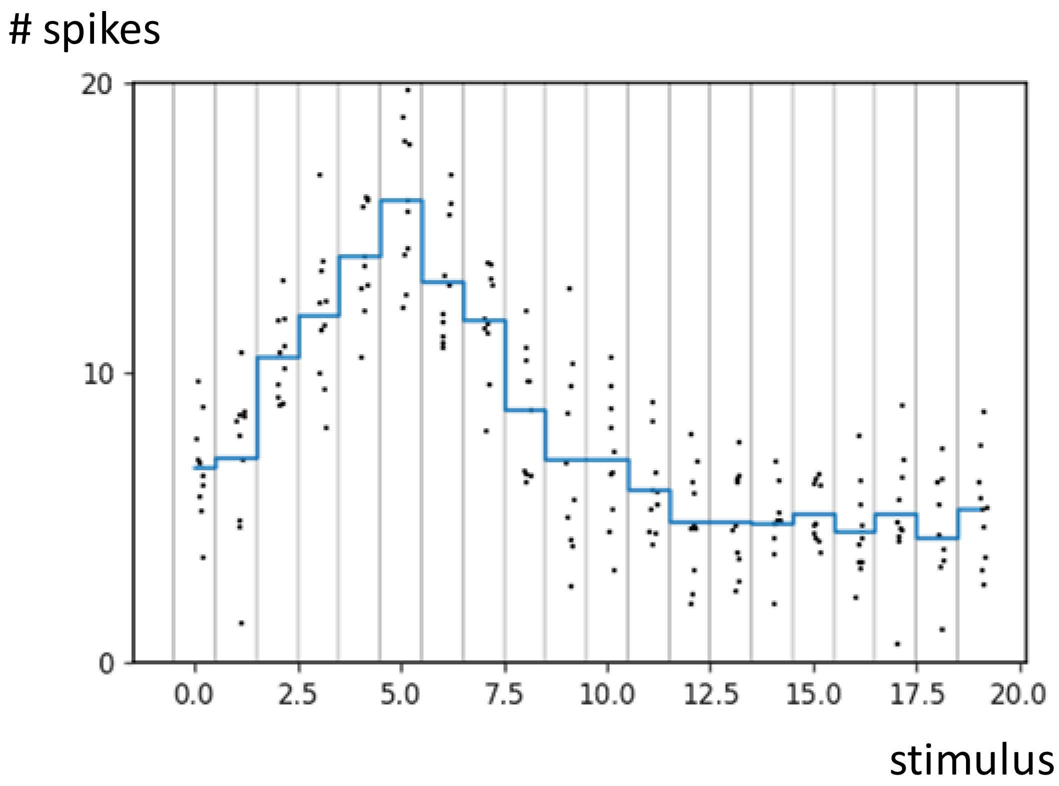
Encoding -> decoding -> understanding



Yamins and Di Carlo, *Nat. Neurosci.* 2016

Decoding: the probabilistic framework

$$p(\mathbf{r}|s)$$



Probability of response given the stimulus

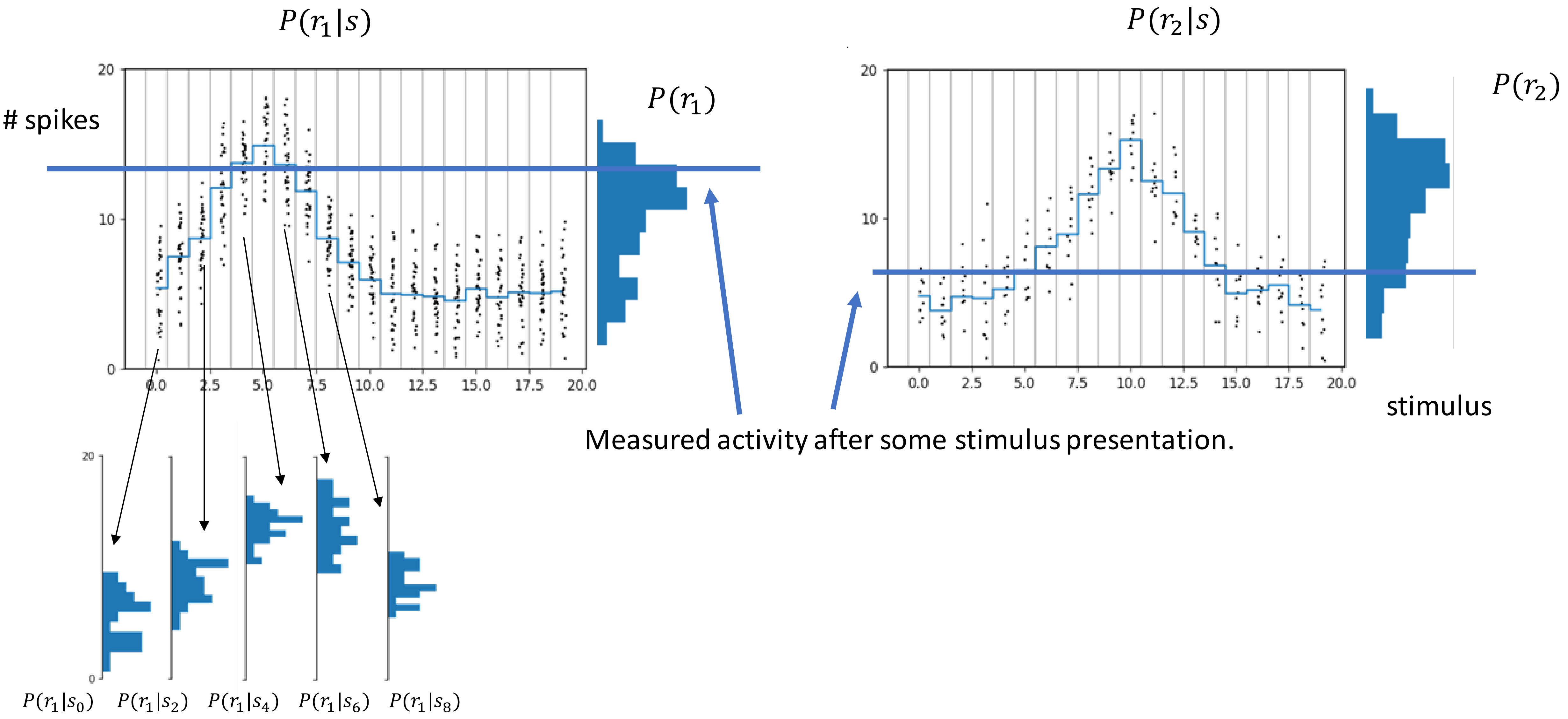
Probability of stimulus

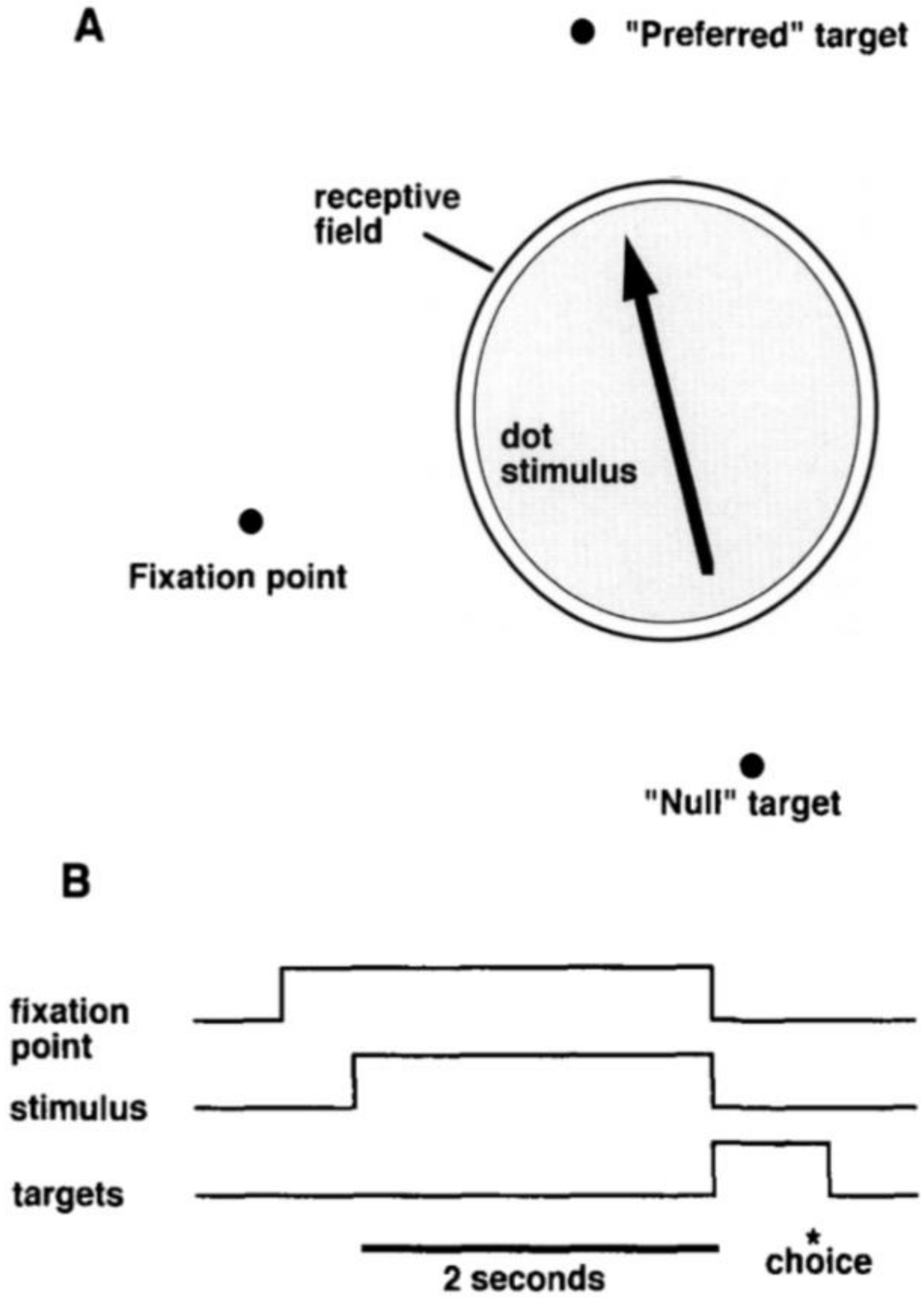
$$p(s|\mathbf{r}) = \frac{p(\mathbf{r}|s)p(s)}{p(\mathbf{r})}$$

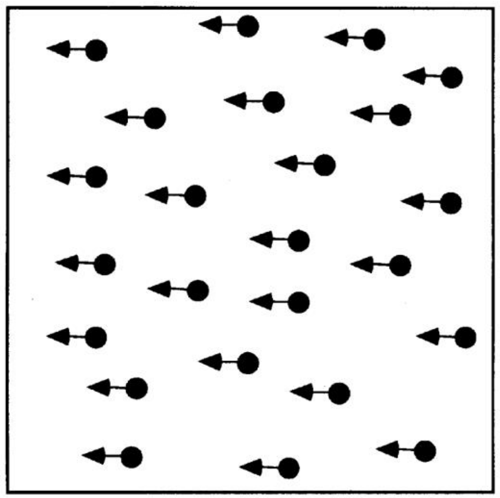
Probability of response

Decoding: the probabilistic framework

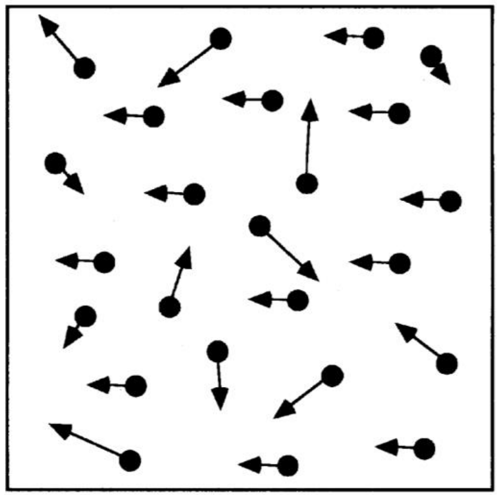
$$p(s|\mathbf{r}) = \frac{p(\mathbf{r}|s)p(s)}{p(\mathbf{r})}$$





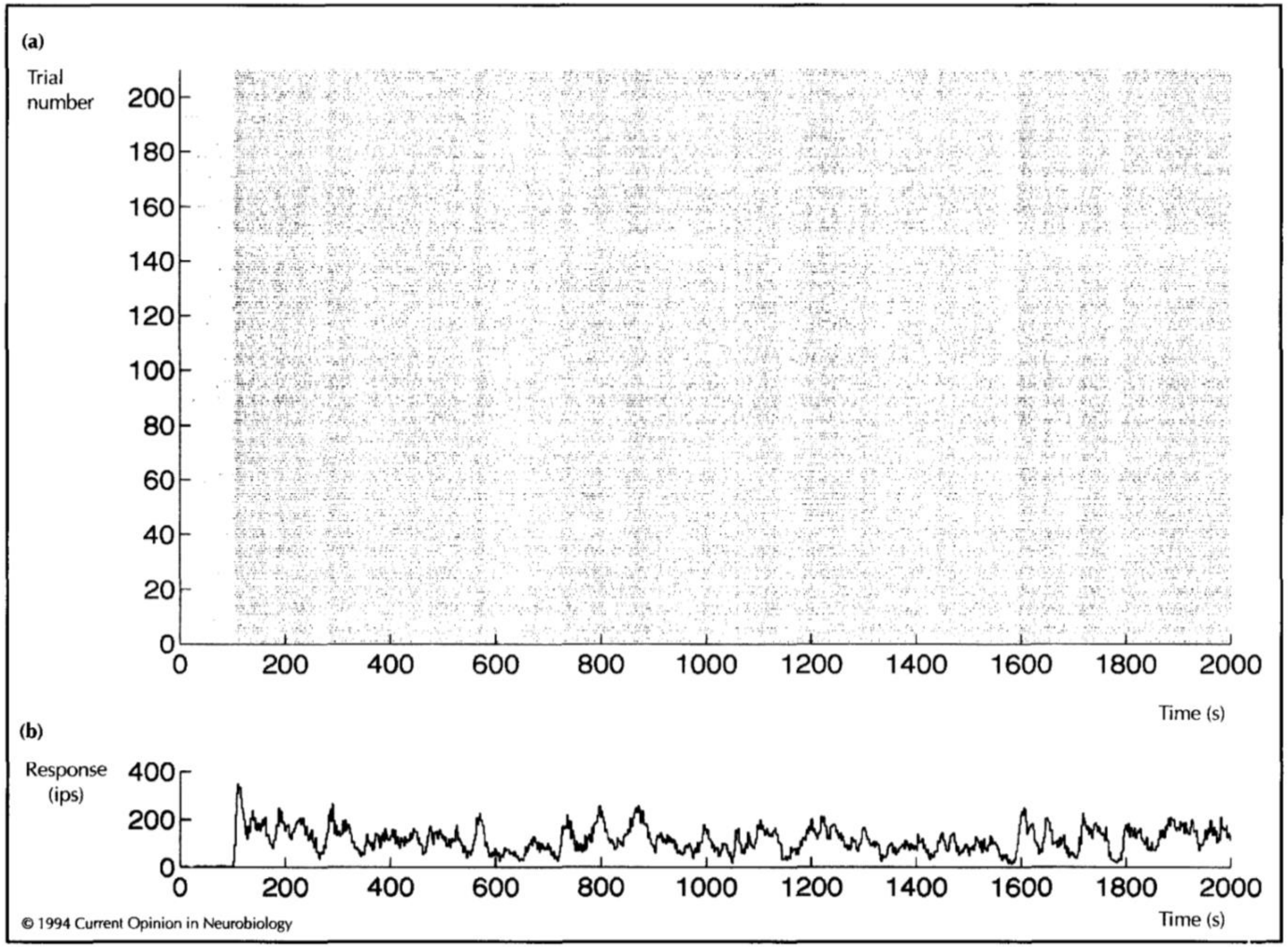


100% coherence

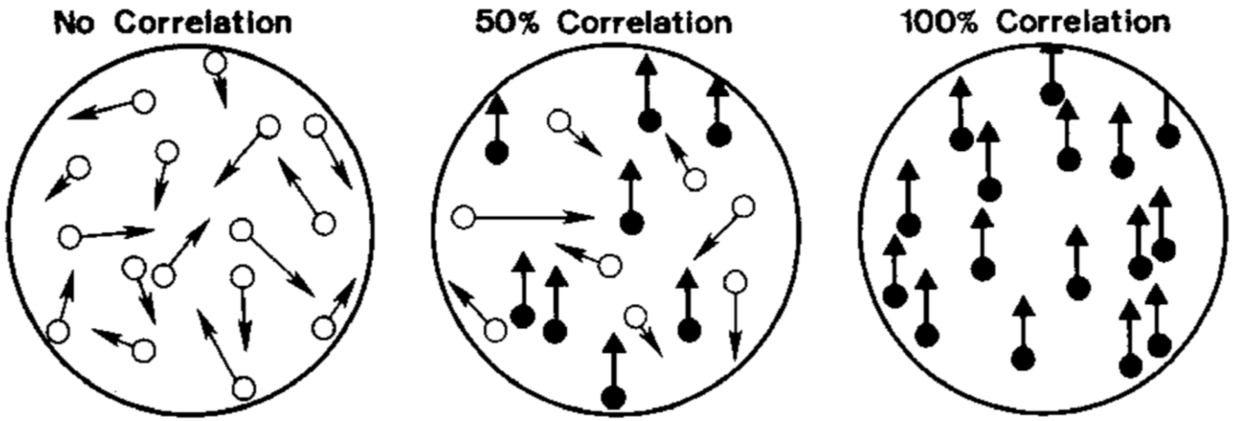


50% coherence

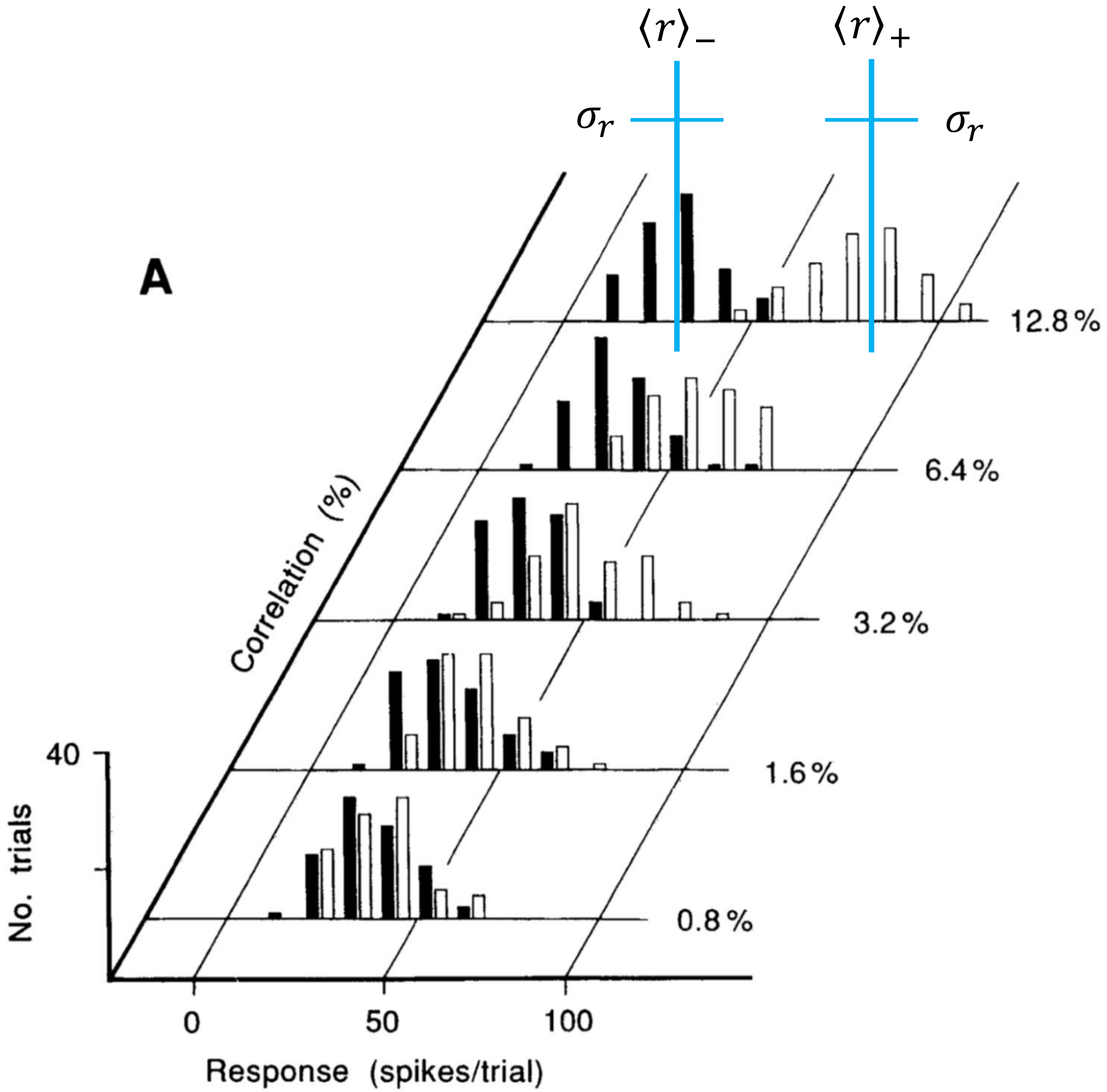
Neural responses are highly variable



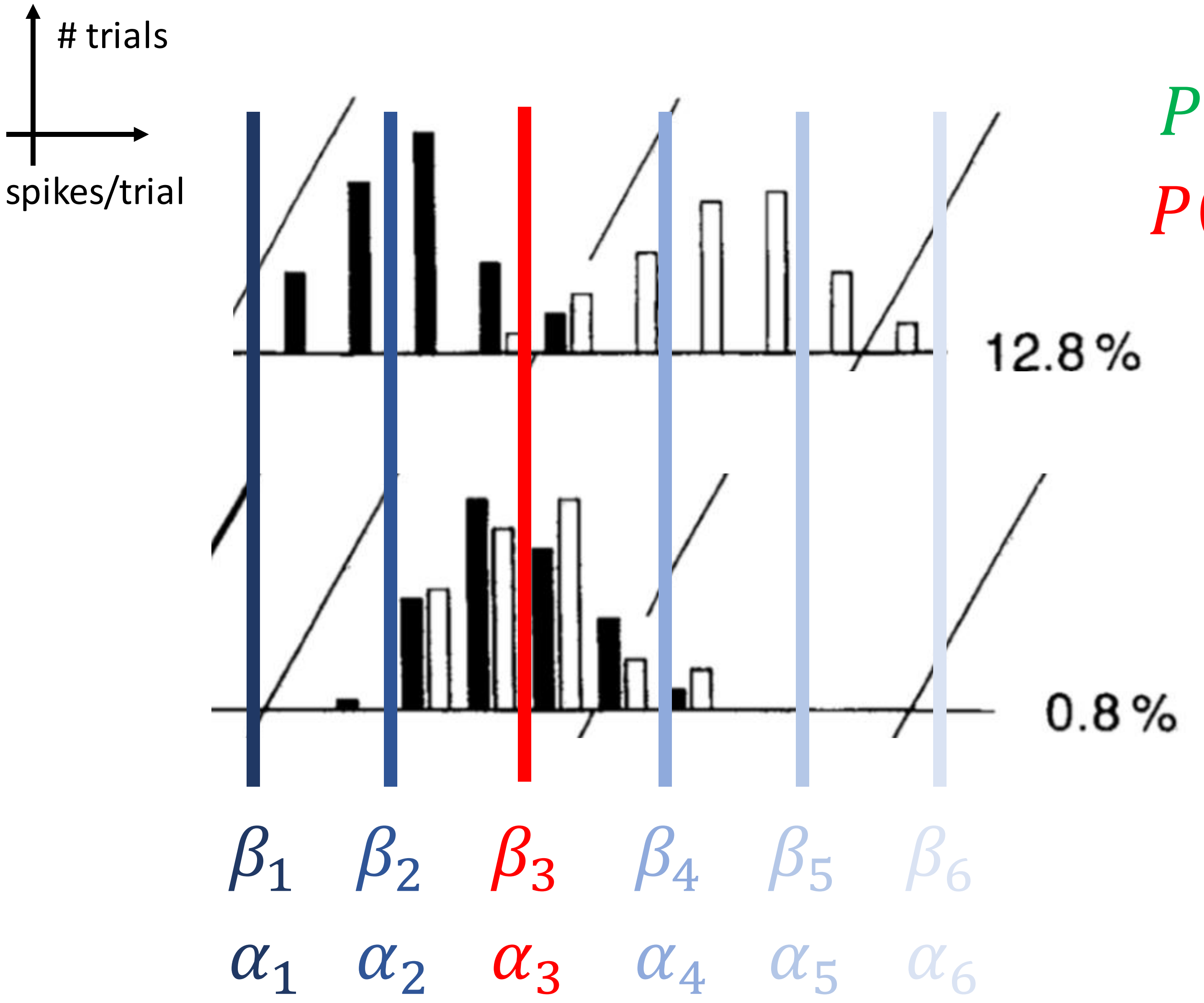
Discrimination



$$d' = \frac{\langle r \rangle_+ - \langle r \rangle_-}{\sigma_r}$$



Britten, et al. 1992



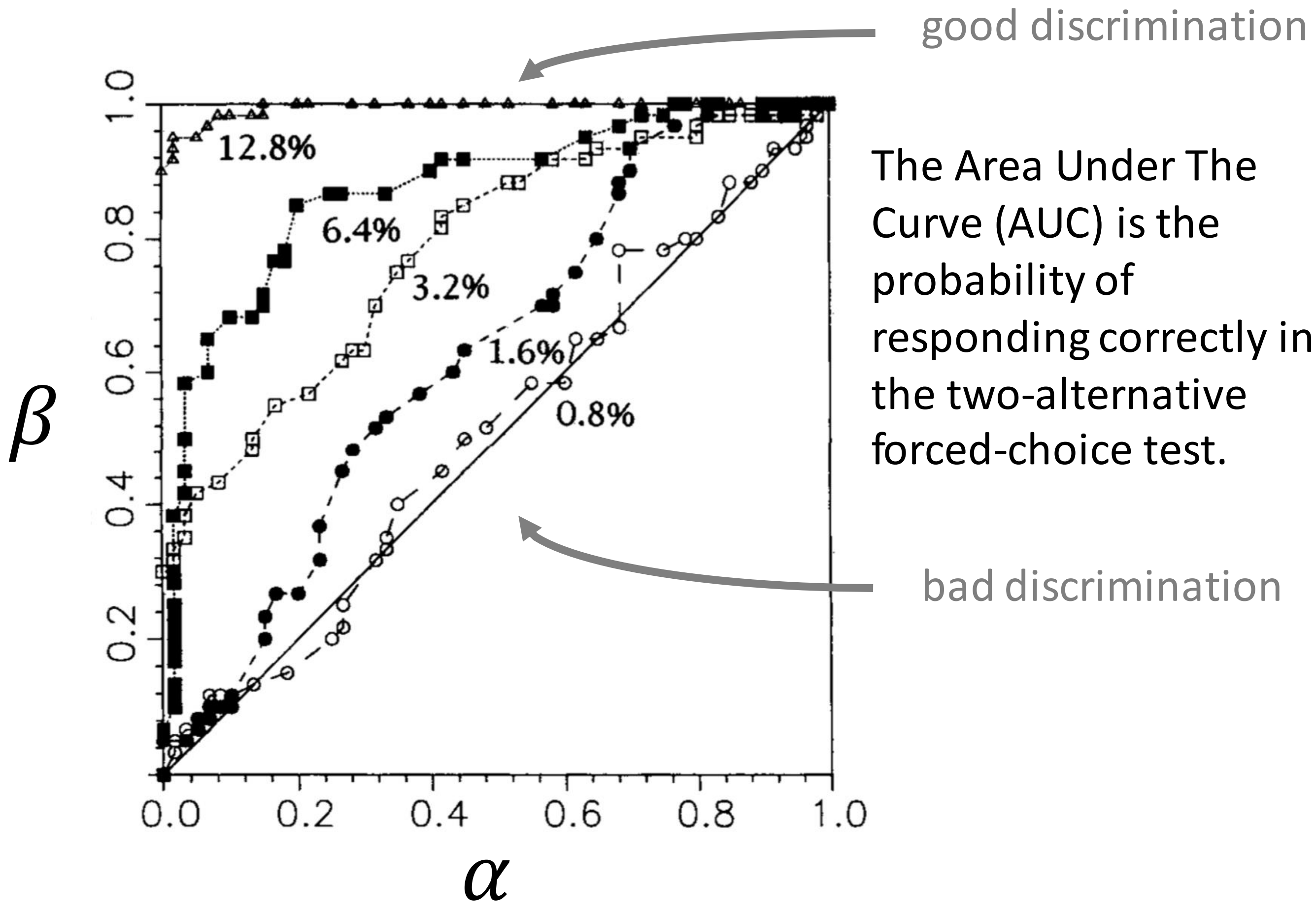
$P(r \geq z\,|+) = \beta$ hit

$P(r \geq z\,|-) = \alpha$ false alarm

stimulus	Prob. correct	Prob. incorrect
+	β	$1-\beta$
-	$1-\alpha$	α

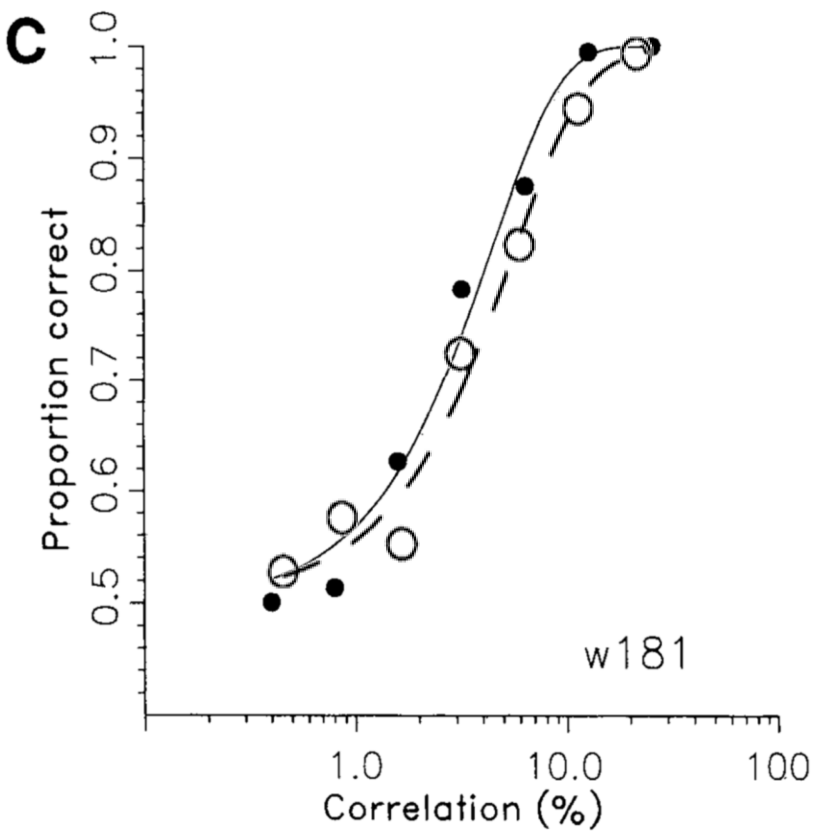
Britten, et al. 1992

ROC analysis



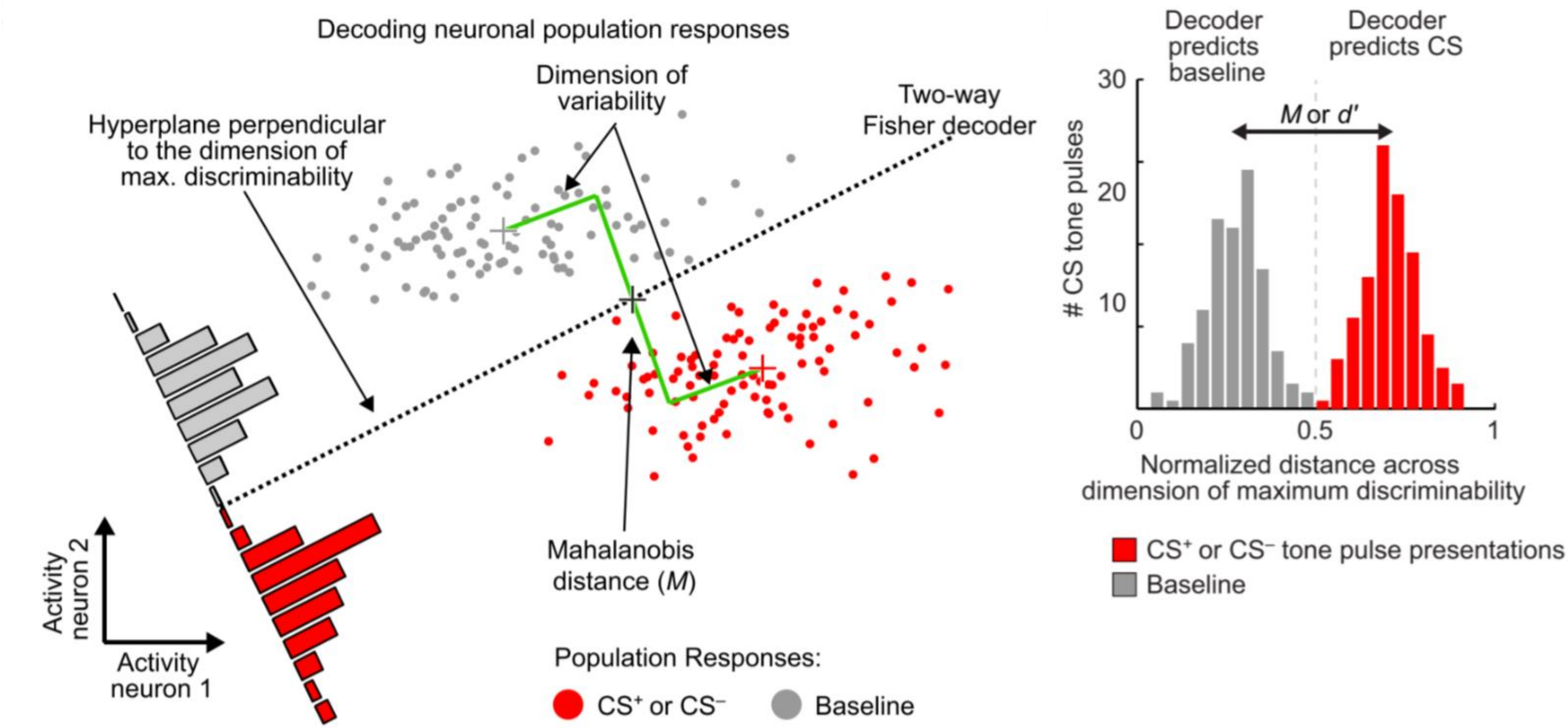
The Area Under The Curve (AUC) is the probability of responding correctly in the two-alternative forced-choice test.

monkey VS decoder

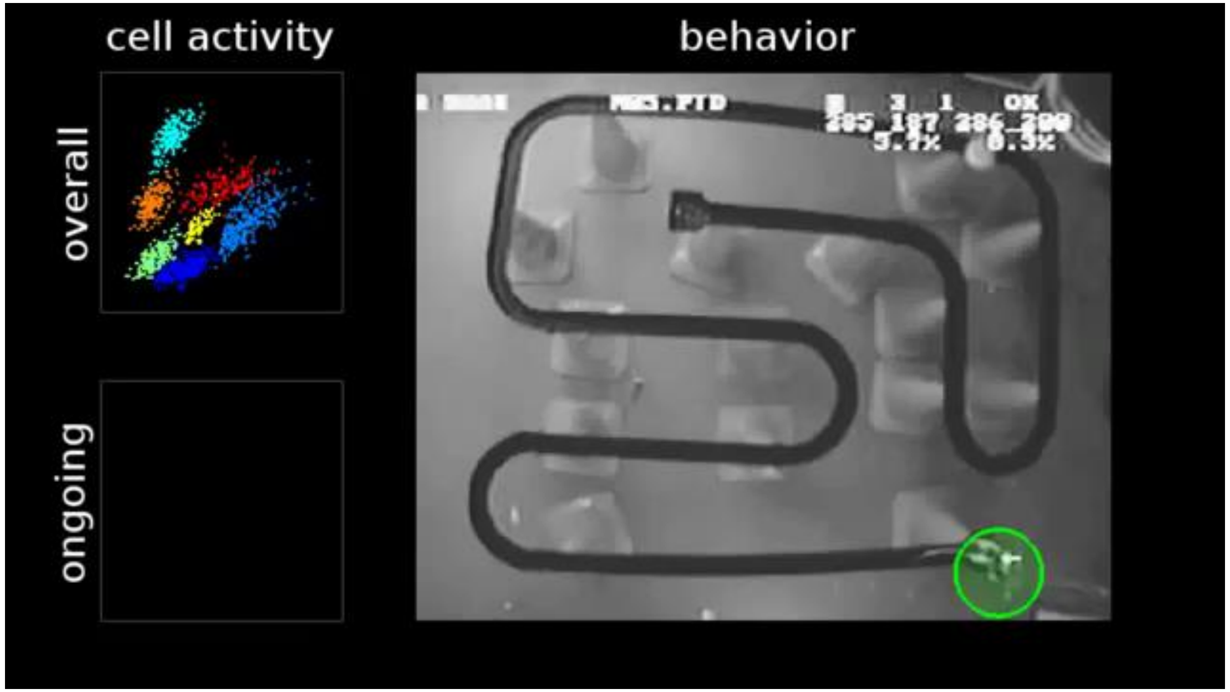


Britten, et al. 1992

Fisher Linear Discriminant Analysis



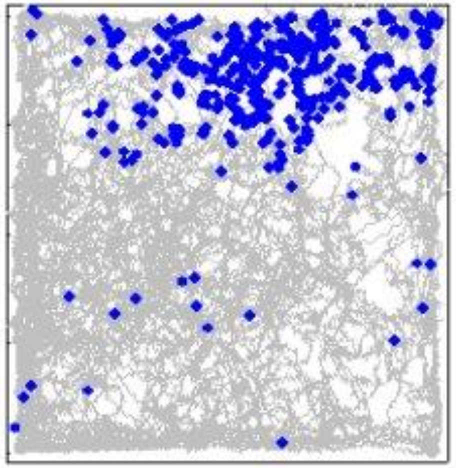
Grewe et al., 2017, *Nature*, “Neural ensemble dynamics underlying a long-term associative memory”

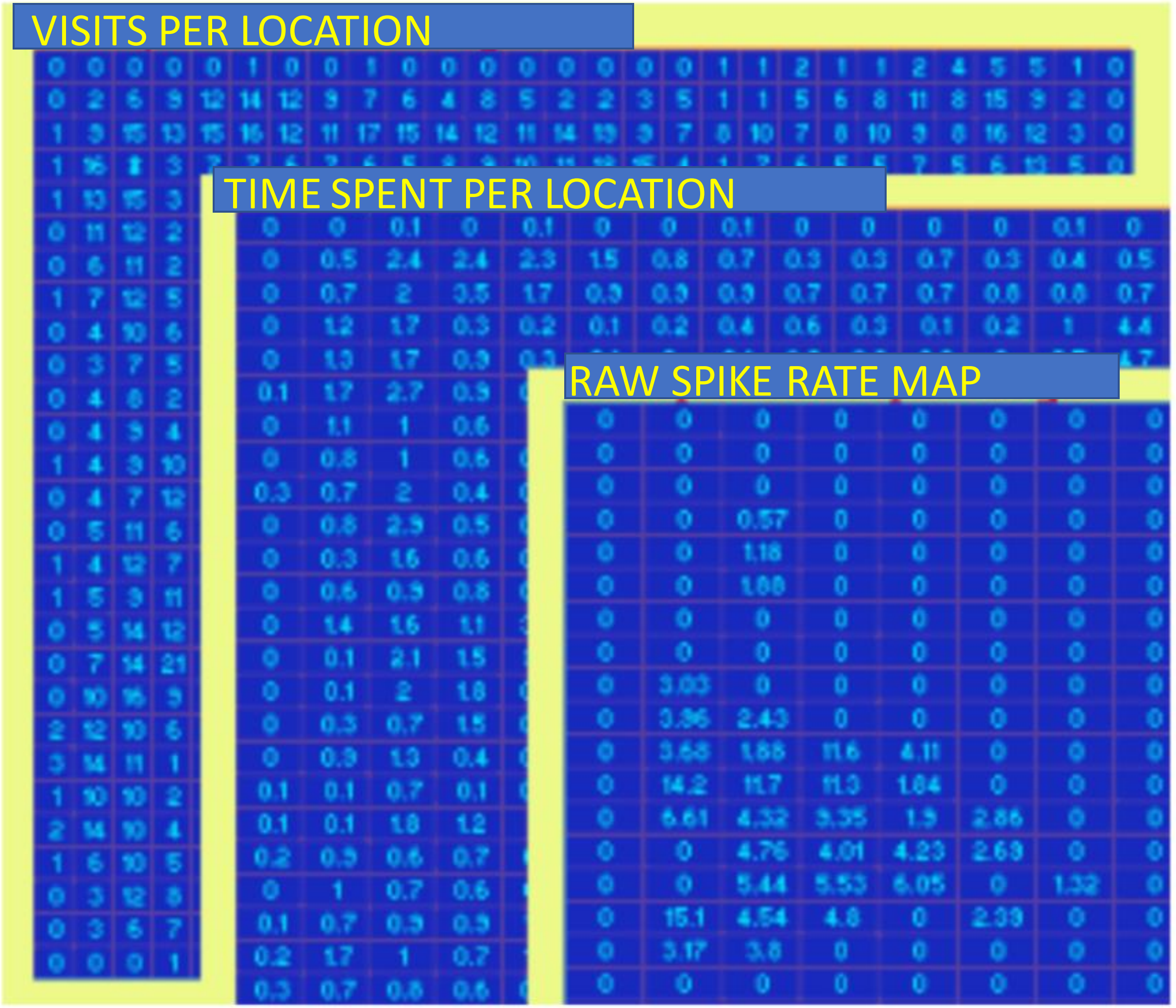


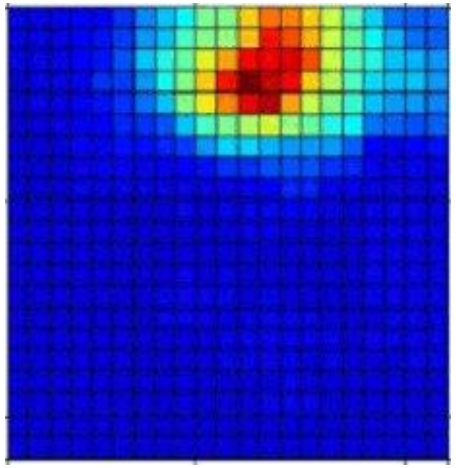
Source: YouTube, Matt Wilson’s lab

J. O’Keefe, E. Moser and M.B. Moser
“for their discoveries of cells that constitute a positioning system in the brain".

«[…] the results suggest that [the cells] were not responding to a <u>simple</u> sensory stimulus nor to a <u>specific</u> motor behavior.»

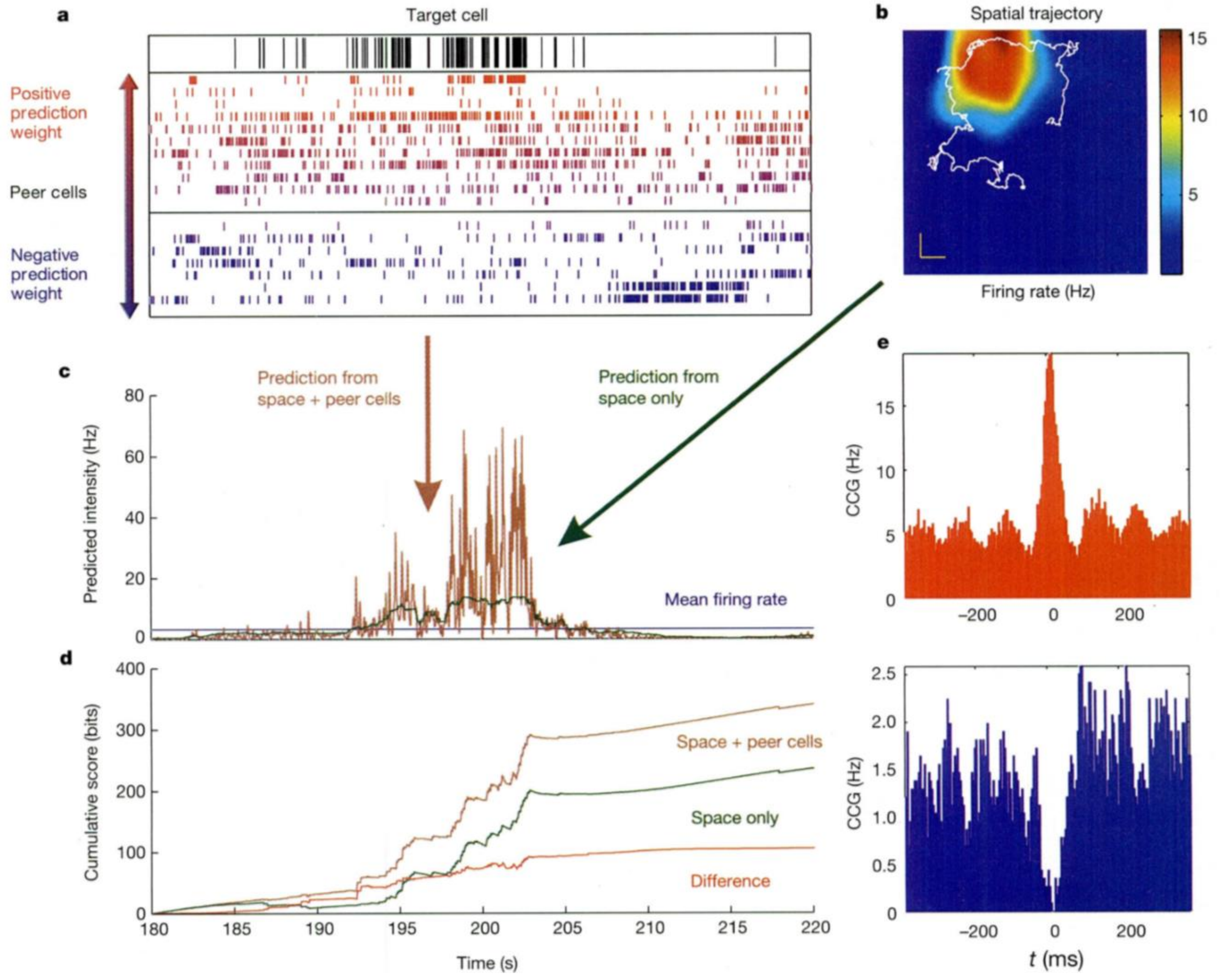






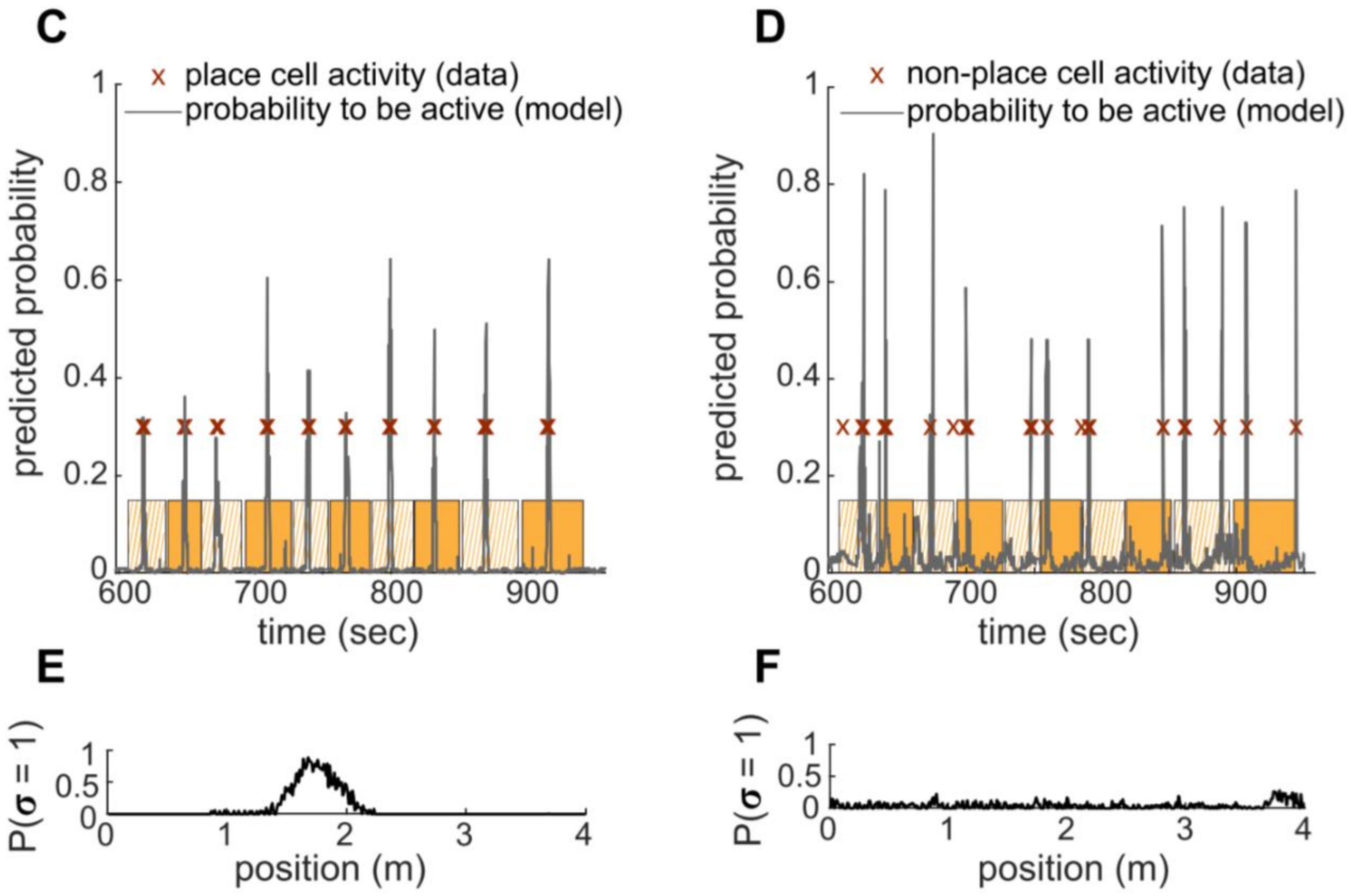
rate_i = # spikes_i / time_i

http://hargreaves.swong.webfactional.com/ ← a nice (though old) overview!



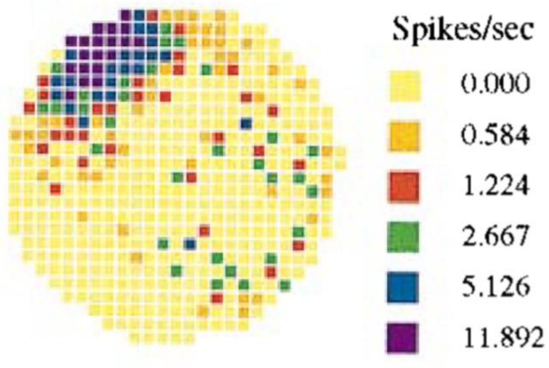
Harris, Kenneth D., et al. "Organization of cell assemblies in the hippocampus." Nature 424.6948 (2003): 552.

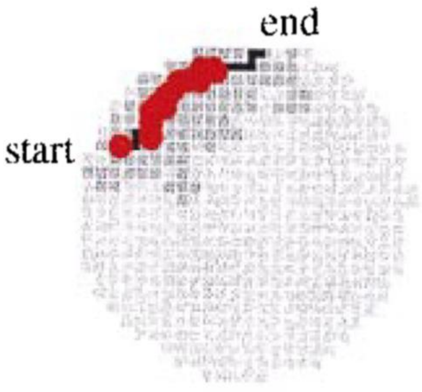
Predicting one cell's activity from that of the rest of the population

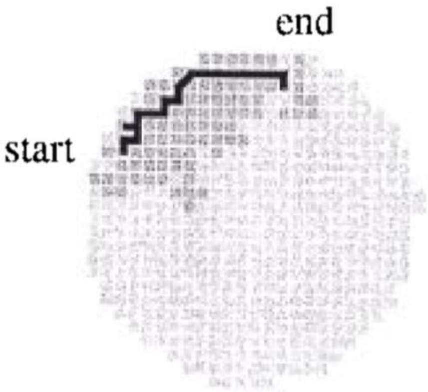


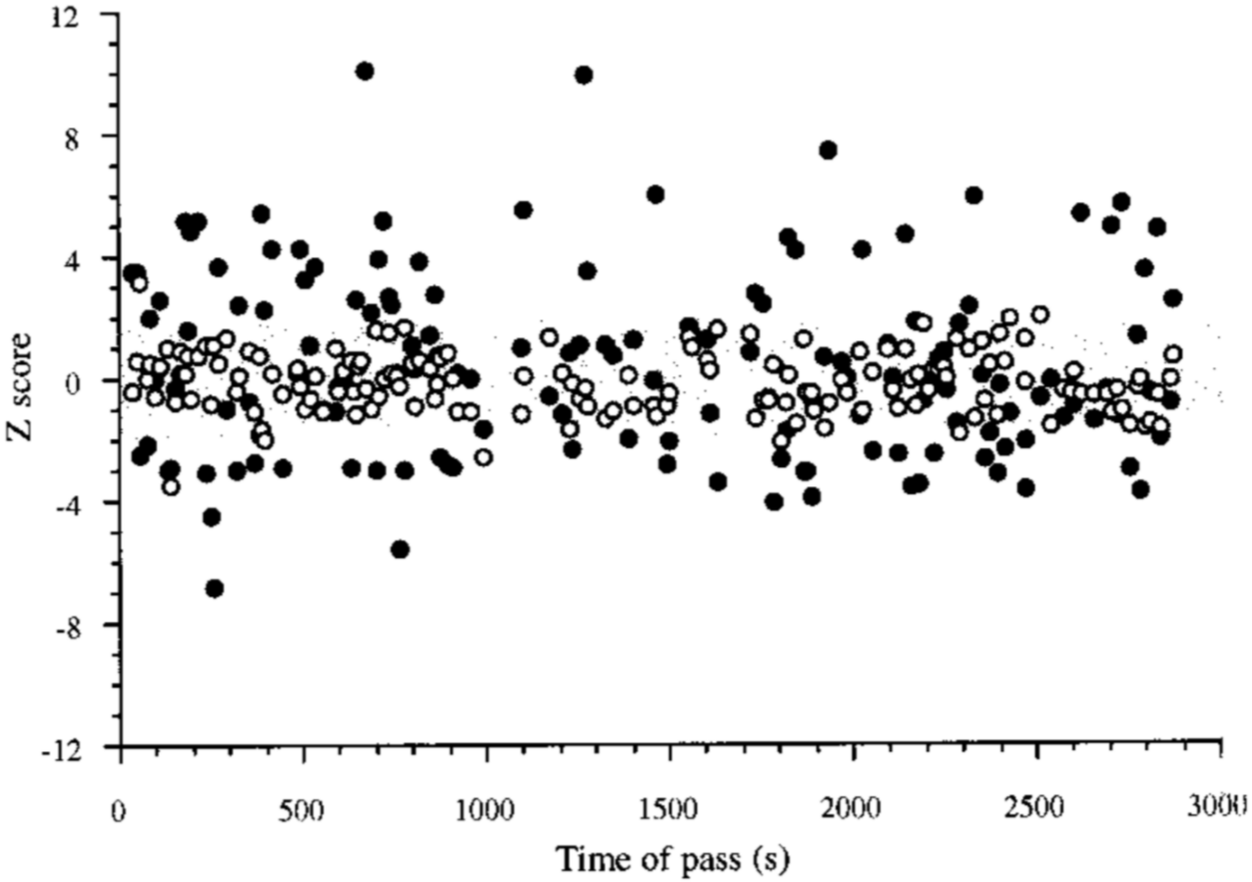
Meshulam et al., 2016, *arXiv*, "Collective behavior of place and non–place neurons in the hippocampal network"

Fenton and Muller, 1998, *PNAS*, "Place cell discharge is extremely variable during individual passes of the rat through the firing field"





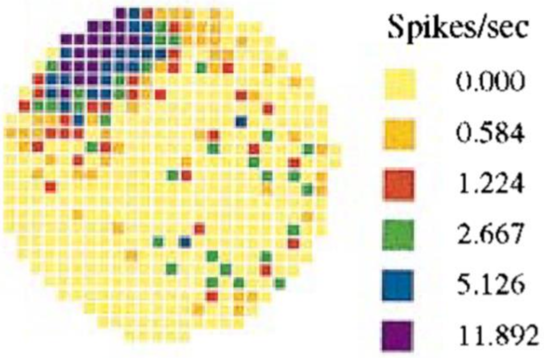


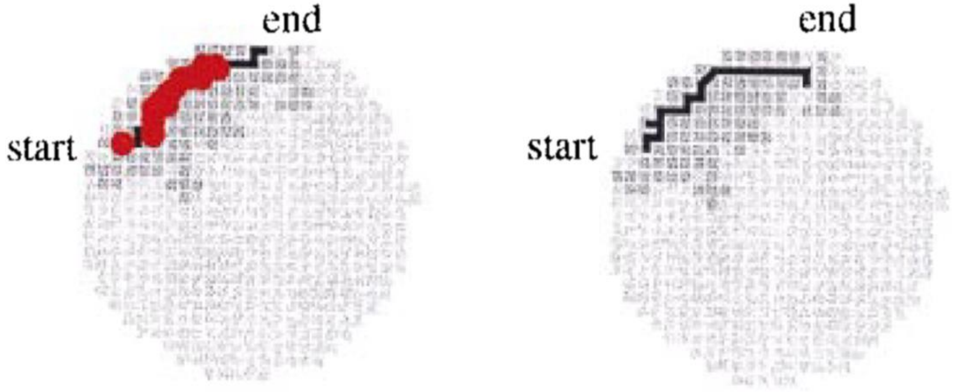


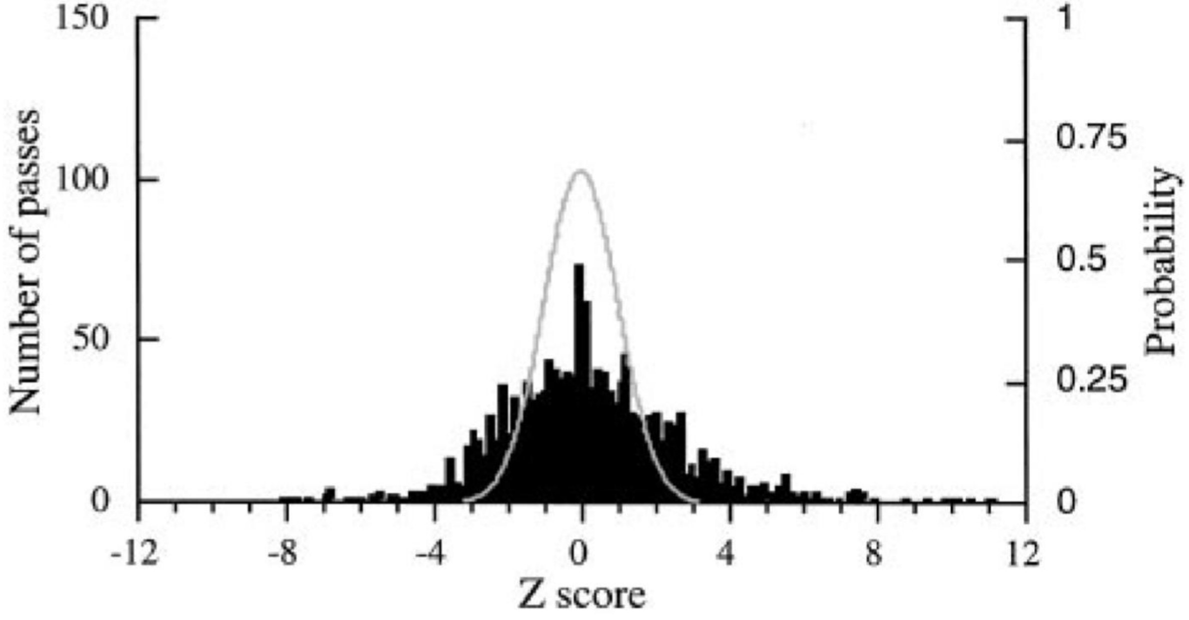
$$Z = \frac{S - N + \frac{1}{2}}{\sqrt{N}}, \quad S < N.$$

$$Z = \frac{S - N - \frac{1}{2}}{\sqrt{N}}, \quad S \geq N.$$

S = spikes at passage
N = mean (expected) number of spikes
Z = standard score of observed spikes





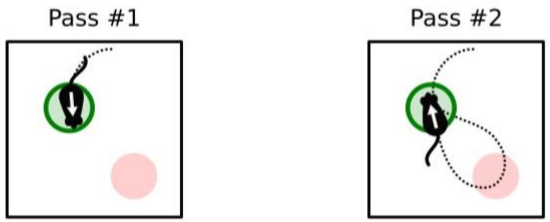


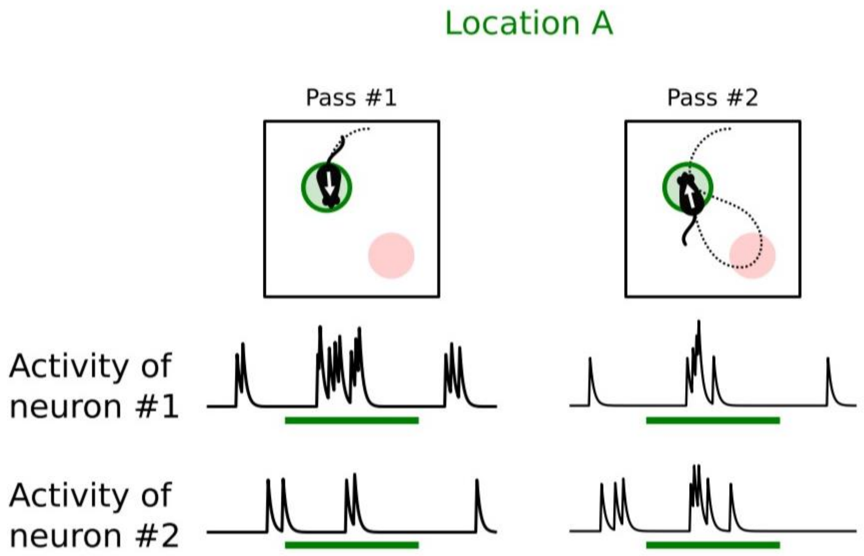
$$Z = \frac{S - N + \frac{1}{2}}{\sqrt{N}}, \quad S < N.$$

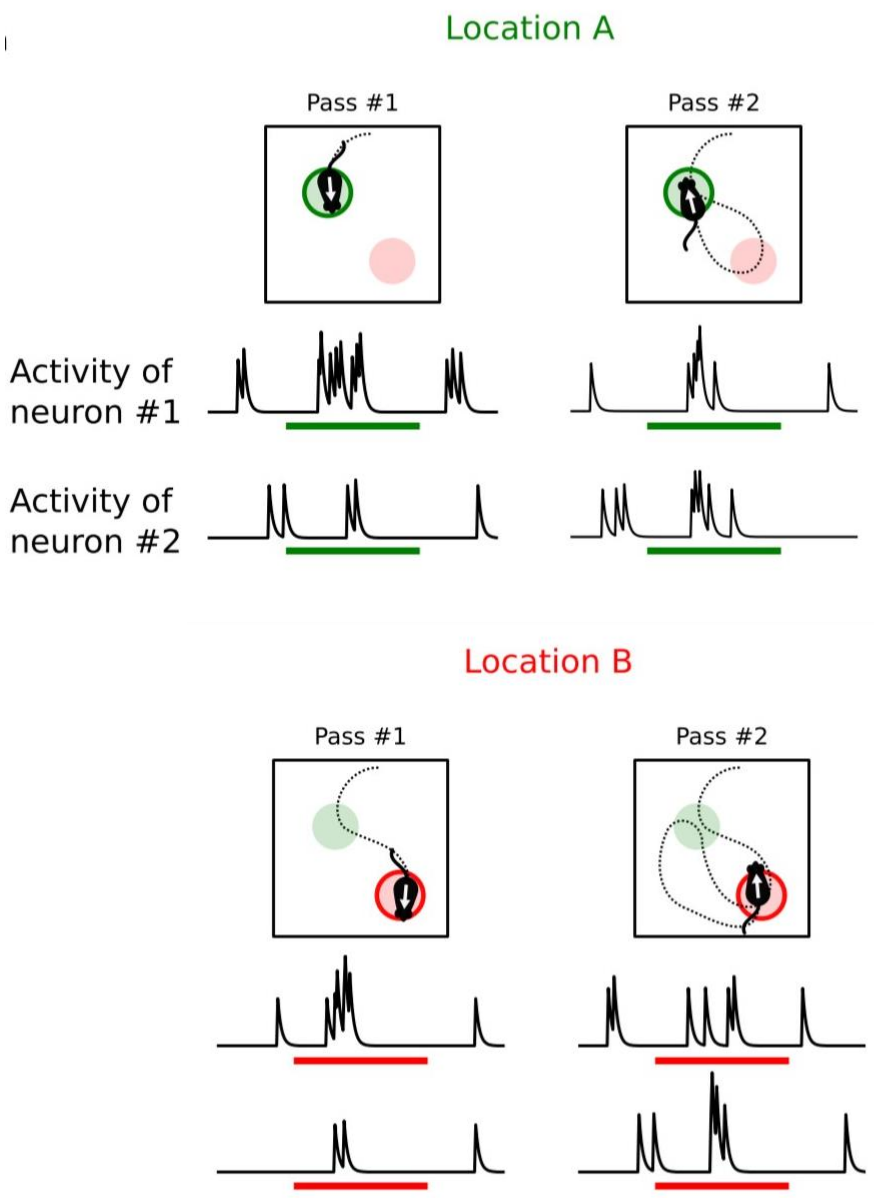
$$Z = \frac{S - N - \frac{1}{2}}{\sqrt{N}}, \quad S \geq N.$$

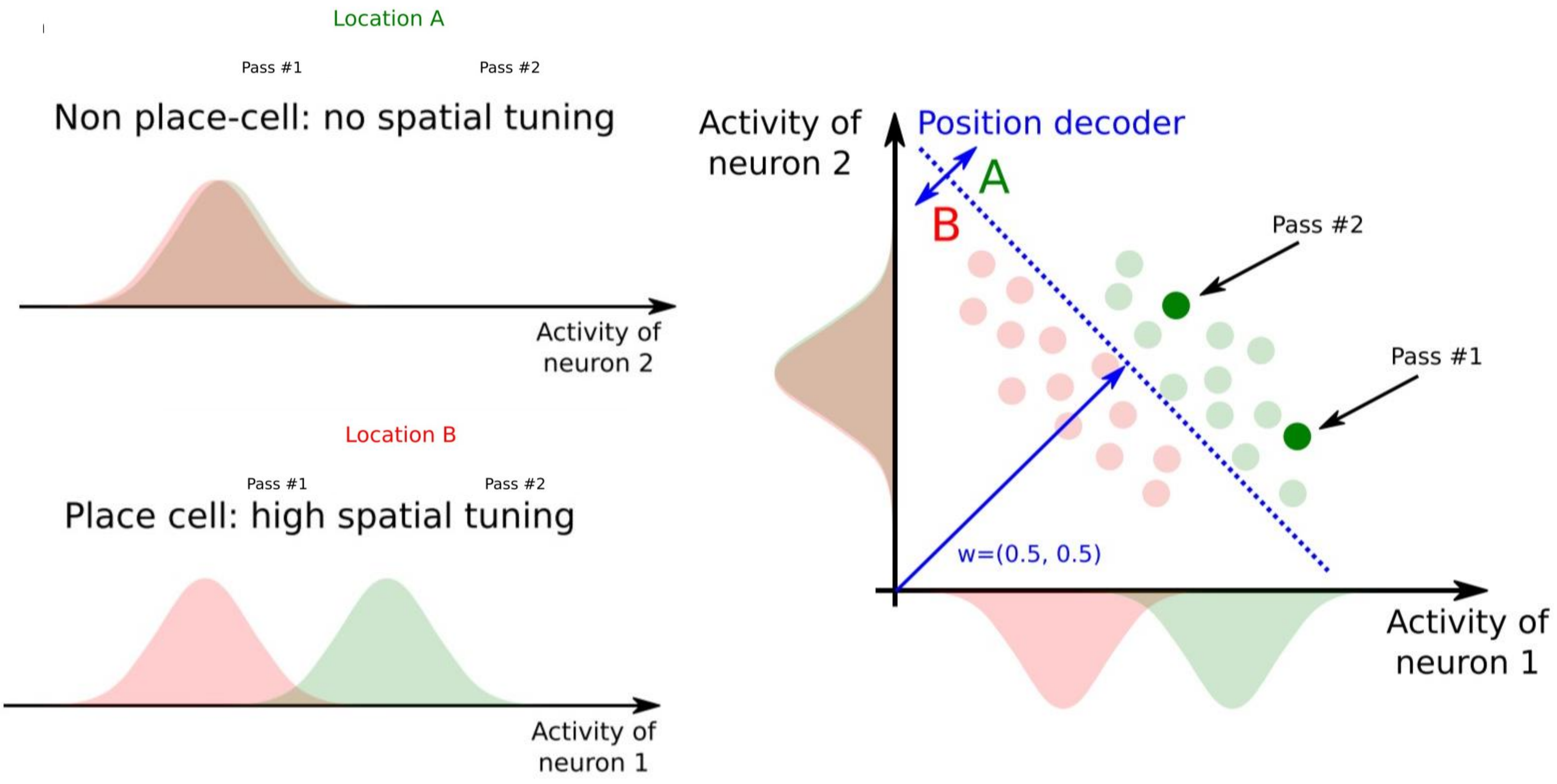
S = spikes at passage
N = mean (expected) number of spikes
Z = standard score of observed spikes

Location A

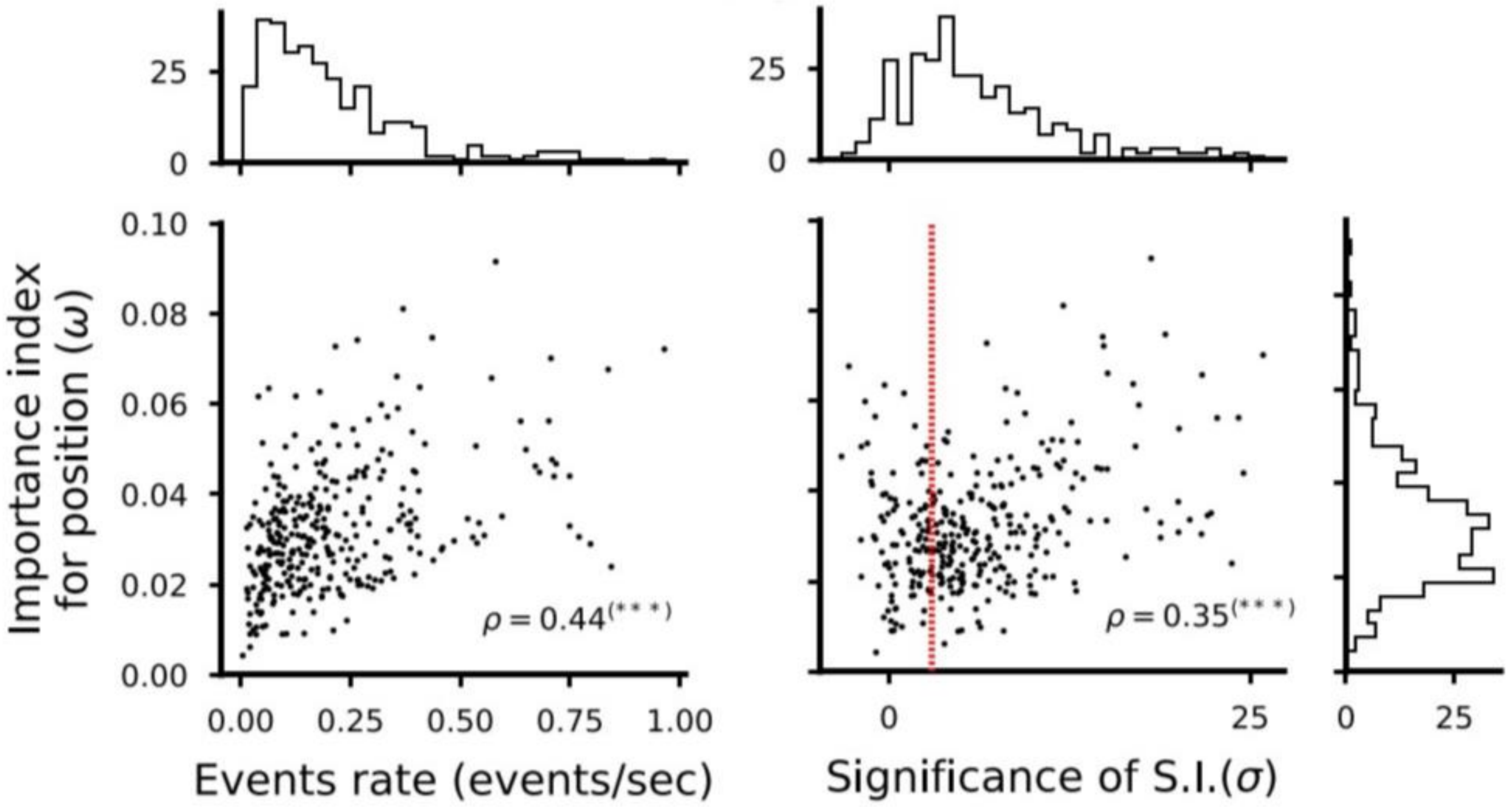


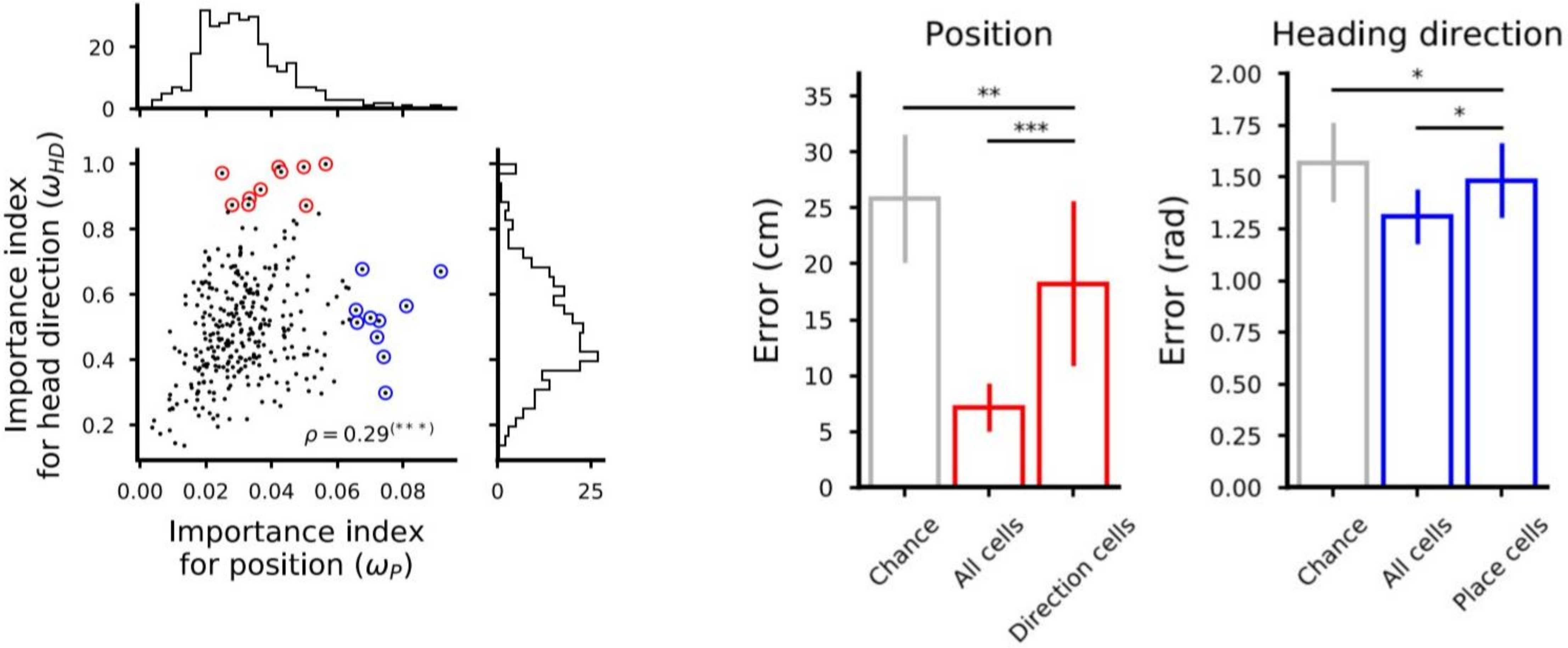

Location A
Pass #1
Pass #2
Activity of neuron #1
Activity of neuron #2


Location A
Pass #1
Pass #2
Activity of neuron #1
Activity of neuron #2
Location B
Pass #1
Pass #2

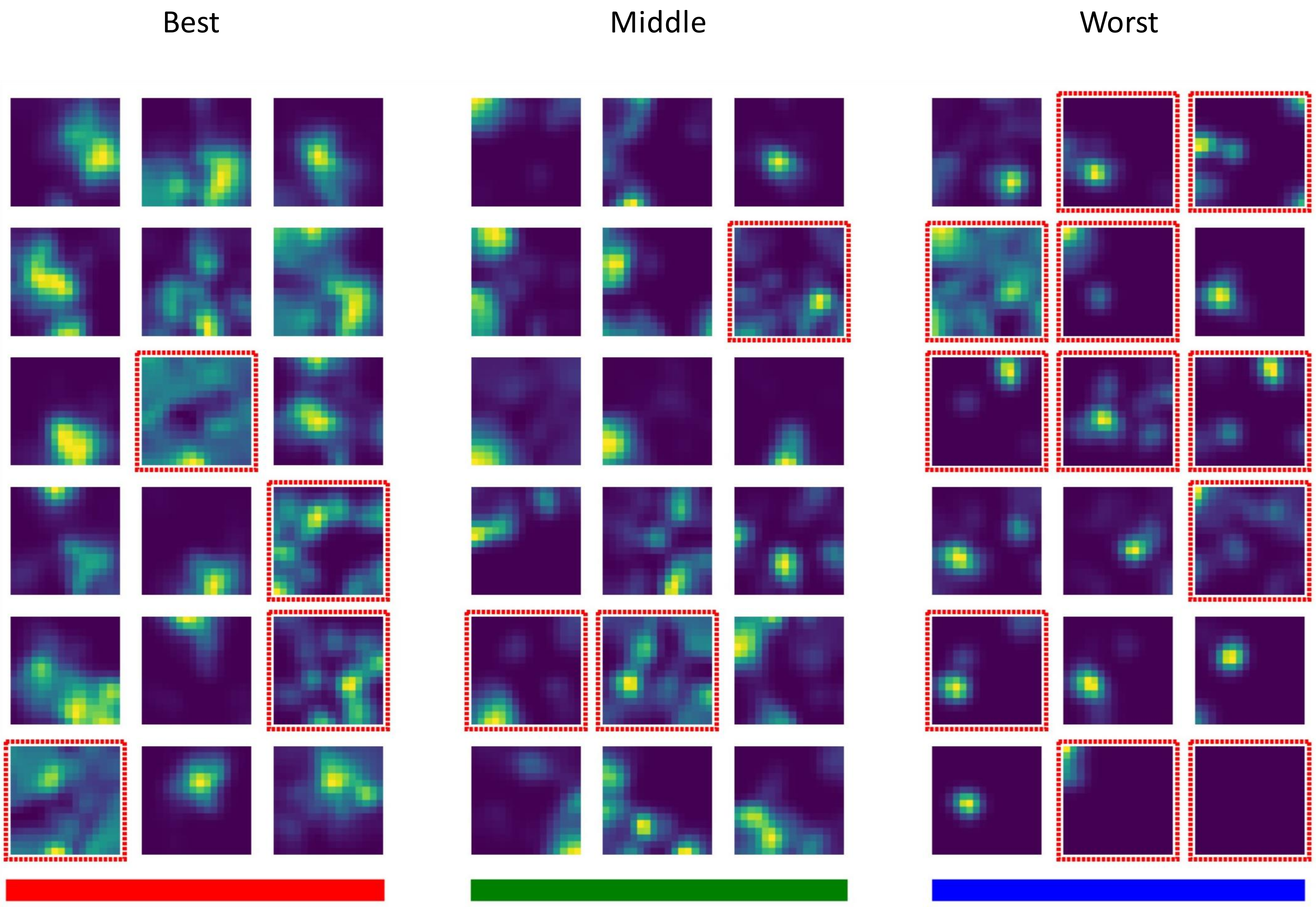


Location A
Pass #1
Pass #2
Non place-cell: no spatial tuning
Activity of neuron 2
Location B
Pass #1
Pass #2
Place cell: high spatial tuning
Activity of neuron 1
Activity of neuron 2
Position decoder
A
B
Pass #2
Pass #1
w=(0.5, 0.5)
Activity of neuron 1


25
0
0.10
0.08
0.06
0.04
0.02
0.00
Importance index
for position (ω)
$\rho = 0.44^{(***)}$
0.00
0.25
0.50
0.75
1.00
Events rate (events/sec)
25
0
$\rho = 0.35^{(***)}$
0
25
Significance of S.I.(σ)
0
25



Importance index for head direction (ω_{HD})
Importance index for position (ω_P)
$\rho = 0.29^{(***)}$
Position
Error (cm)
Chance
All cells
Direction cells
Heading direction
Error (rad)
Place cells


Best
Middle
Worst

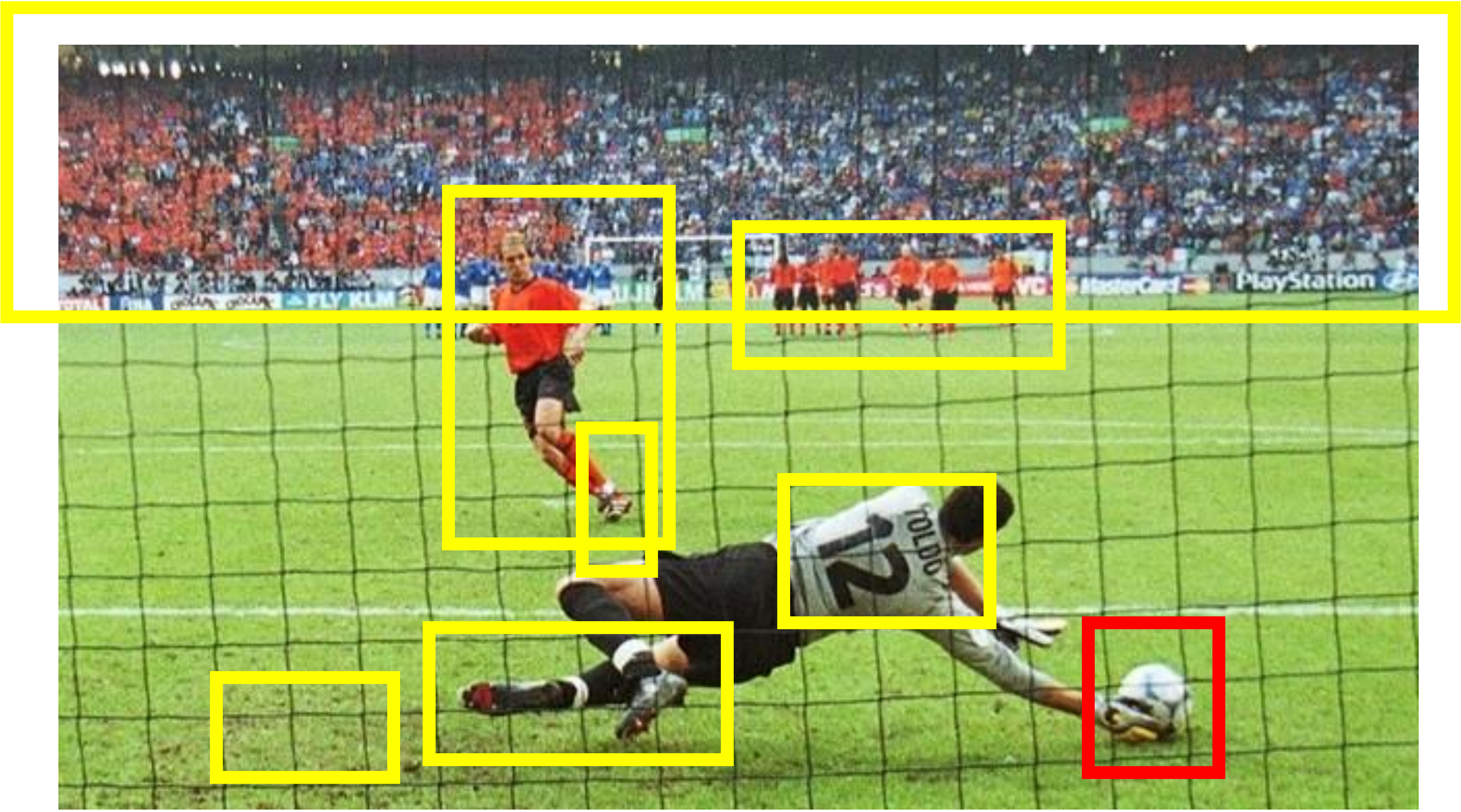
Mixed selectivity and dimensionality

Euro 2000 Semi-finals, Amsterdam Arena.
Italy – Netherlands (3-1p)
F. Toldo vs P. Bosvelt


240-2265

Umberto Boccioni –States of Mind I – Farewell (MoMa, New York)

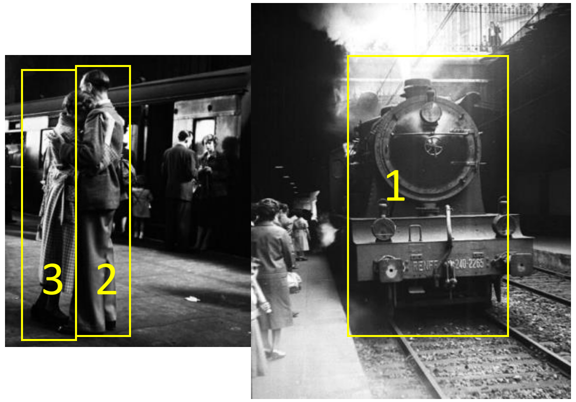
Euro 2000, Amsterdam Arena.
Italy – Netherlands (3-1p)
F. Toldo vs P. Bosvelt



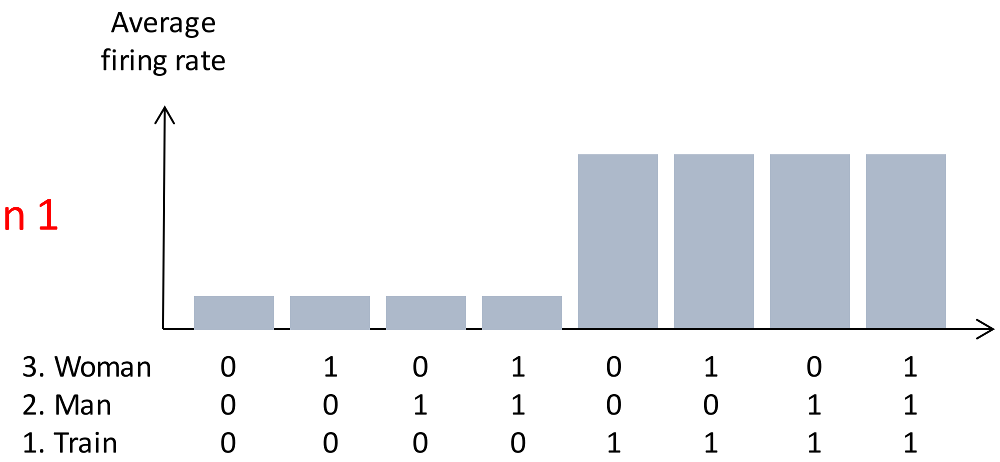
Euro 2000, Amsterdam Arena.
Italy – Netherlands (3-1p)
F. Toldo vs P. Bosvelt

Dynamism of a Soccer Player, 1913, oil on canvas, 193.2 x 201 cm (6' 4 1/8" x 6' 7 1/8"). The Sidney and Harriet Janis Collection, [Museum of Modern Art](), New York

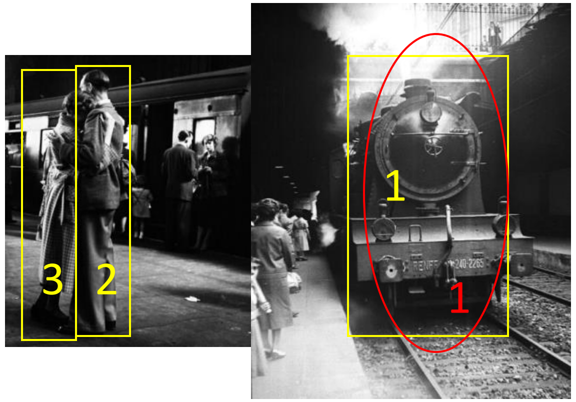
Man
Woman
Train

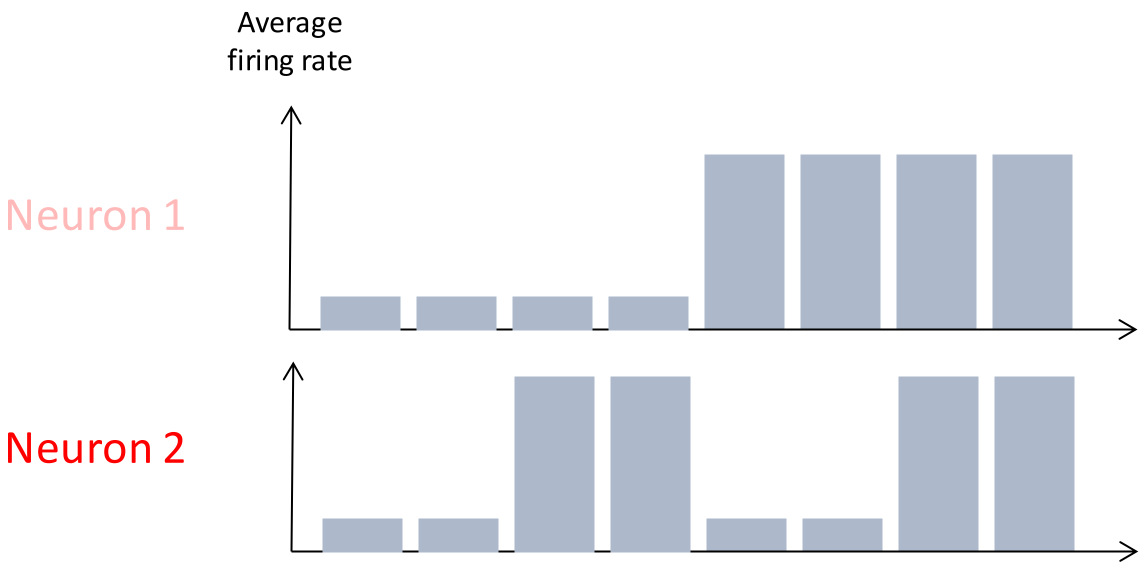


Neuron 1

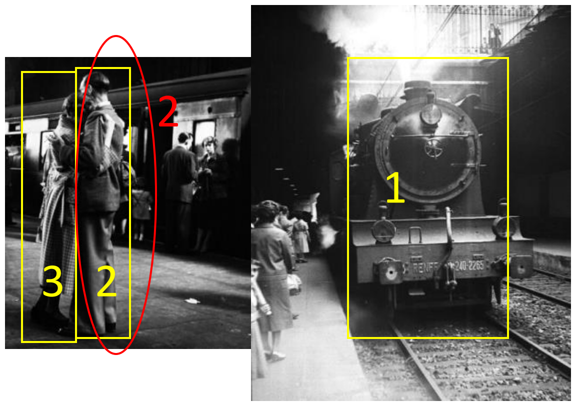


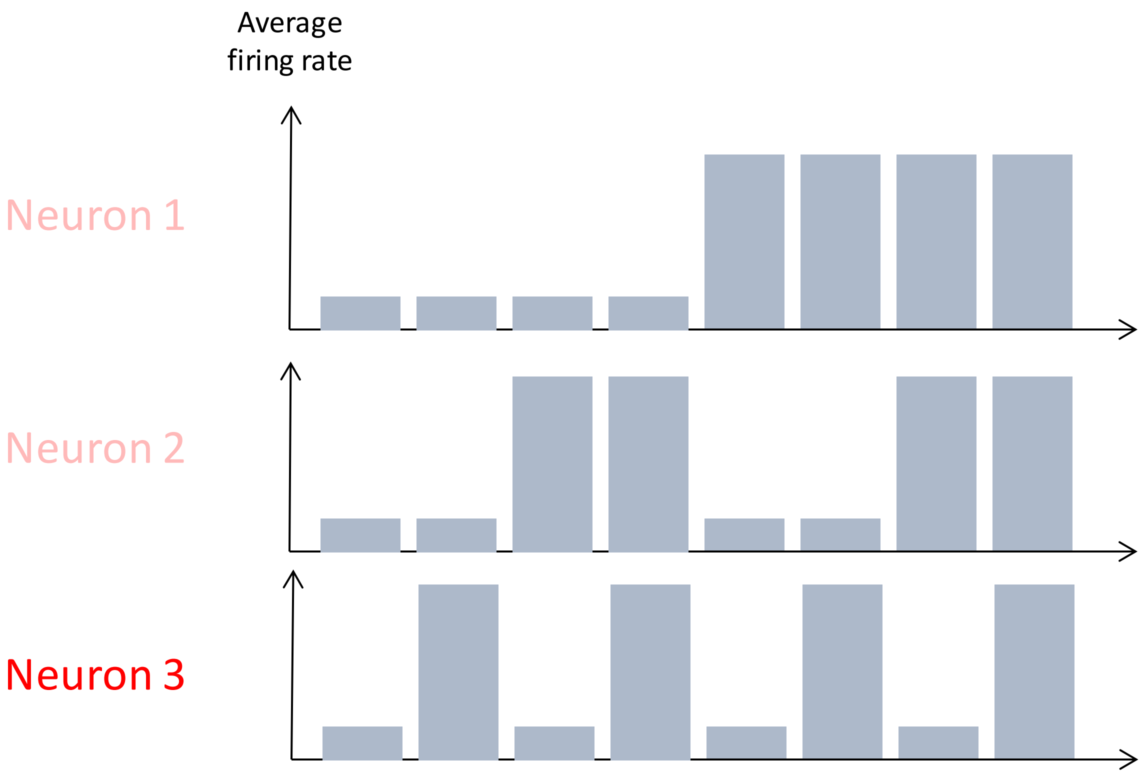
PCH=Peri-condition histogram



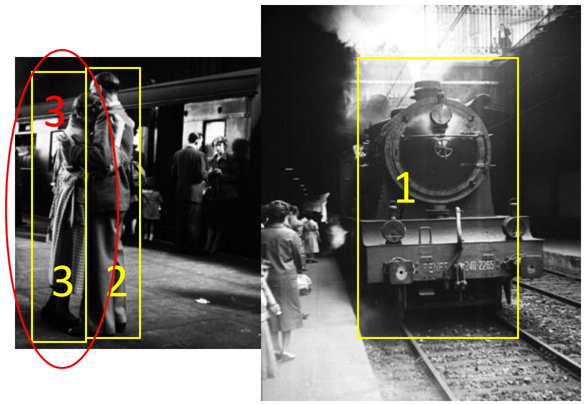


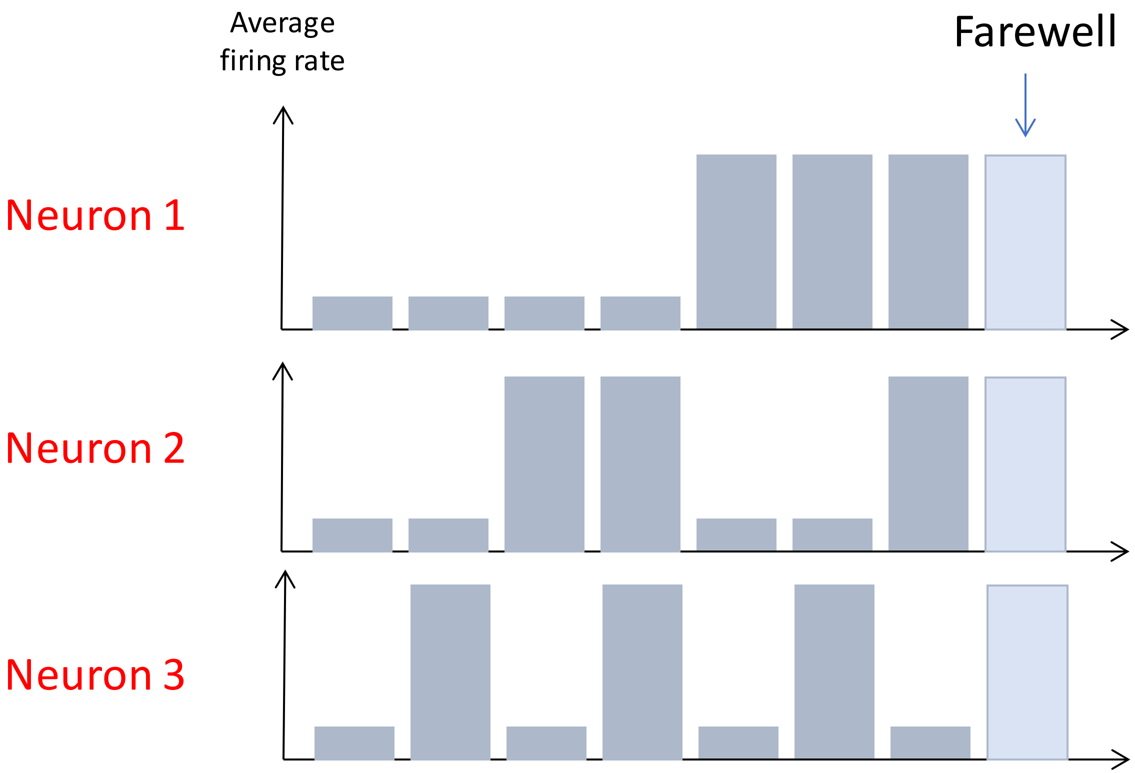
3. Woman	0	1	0	1	0	1	0	1
2. Man	0	0	1	1	0	0	1	1
1. Train	0	0	0	0	1	1	1	1





3. Woman	0	1	0	1	0	1	0	1
2. Man	0	0	1	1	0	0	1	1
1. Train	0	0	0	0	1	1	1	1





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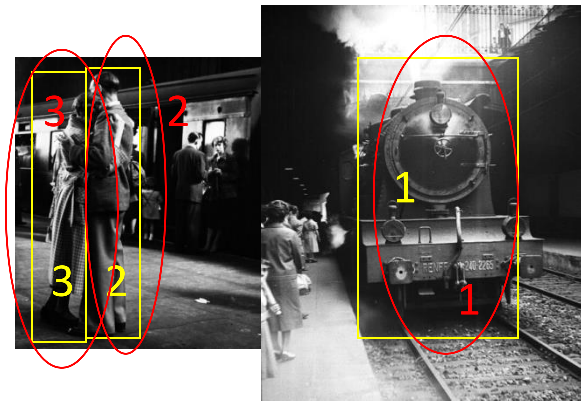
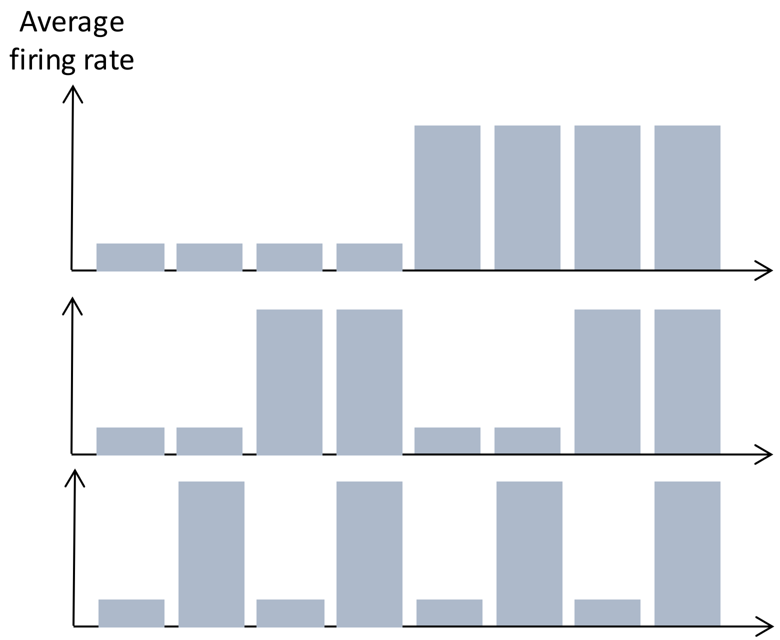
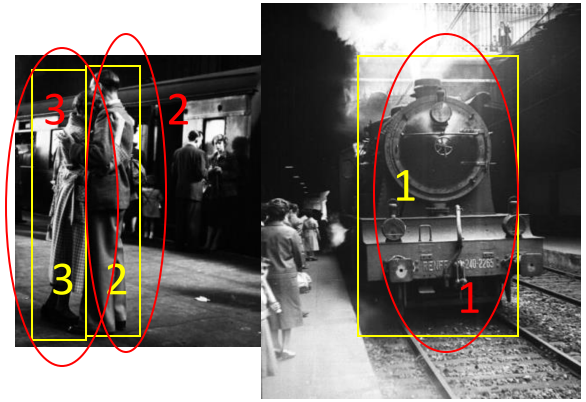
2. Man	0	0	1	1	0	0	1	1
1. Train	0	0	0	0	1	1	1	1



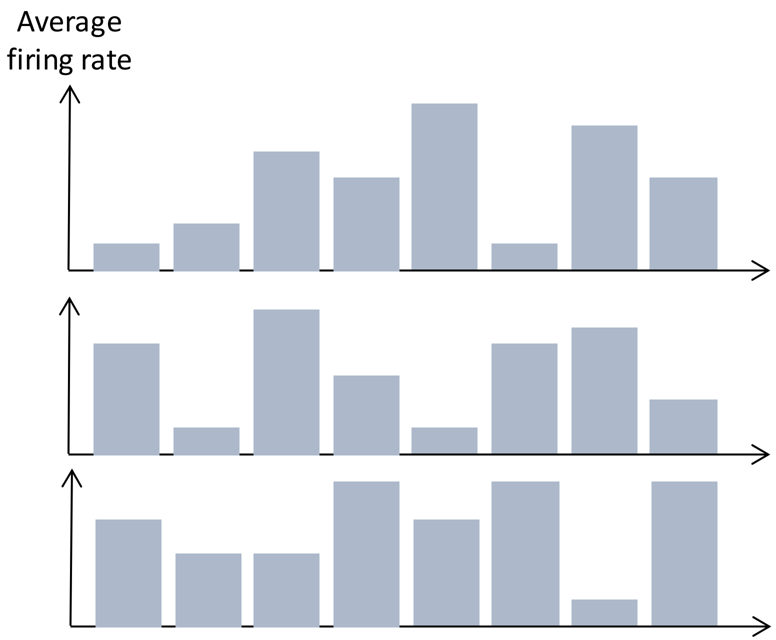
Orderly distributed representations



3. Woman	0	1	0	1	0	1	0	1
2. Man	0	0	1	1	0	0	1	1
1. Train	0	0	0	0	1	1	1	1

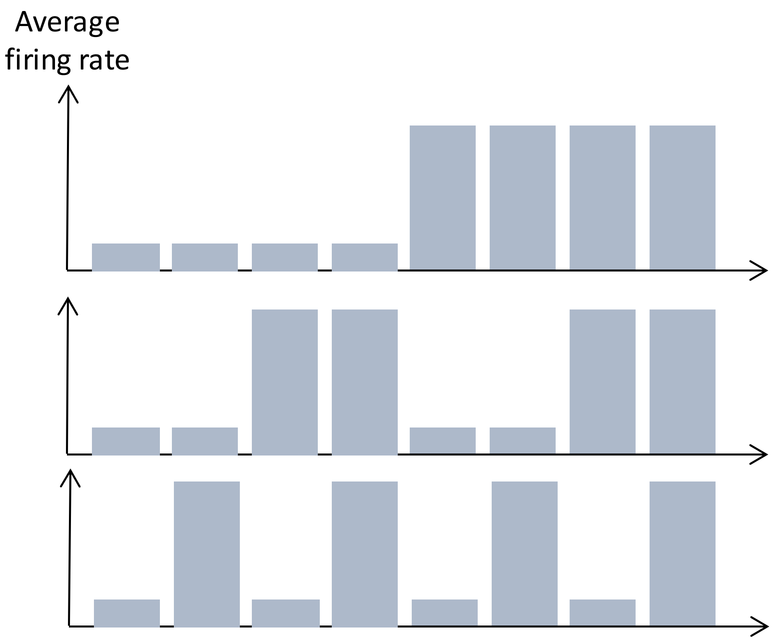


Recorded neural representations

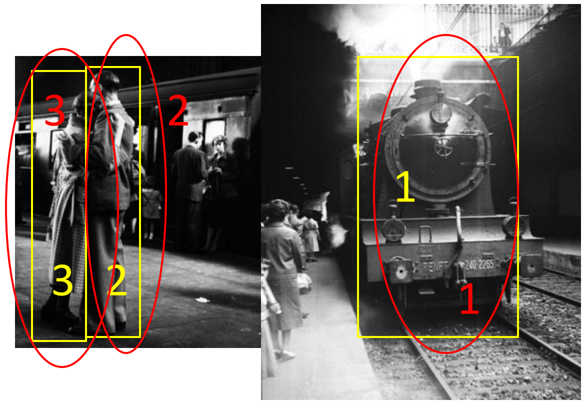


3. Woman	0	1	0	1	0	1	0	1
2. Man	0	0	1	1	0	0	1	1
1. Train	0	0	0	0	1	1	1	1

Orderly distributed representations



3. Woman	0	1	0	1	0	1	0	1
2. Man	0	0	1	1	0	0	1	1
1. Train	0	0	0	0	1	1	1	1



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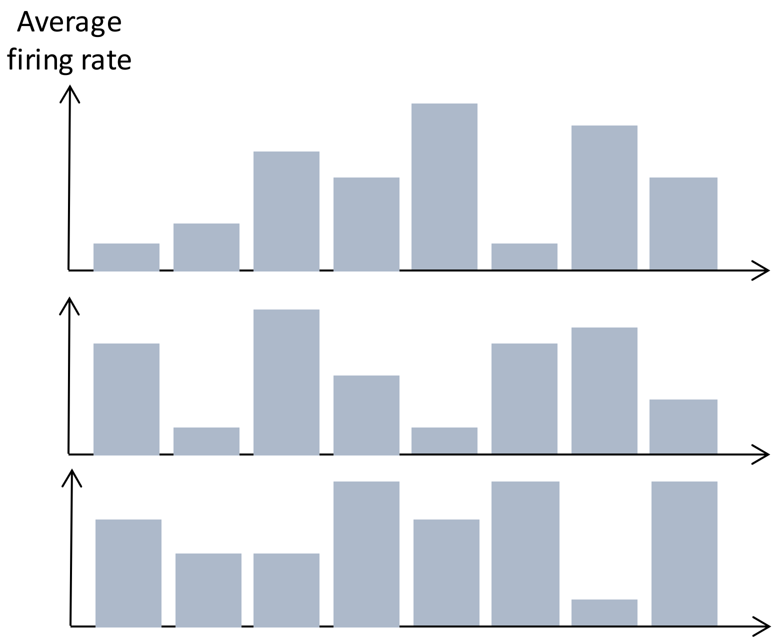
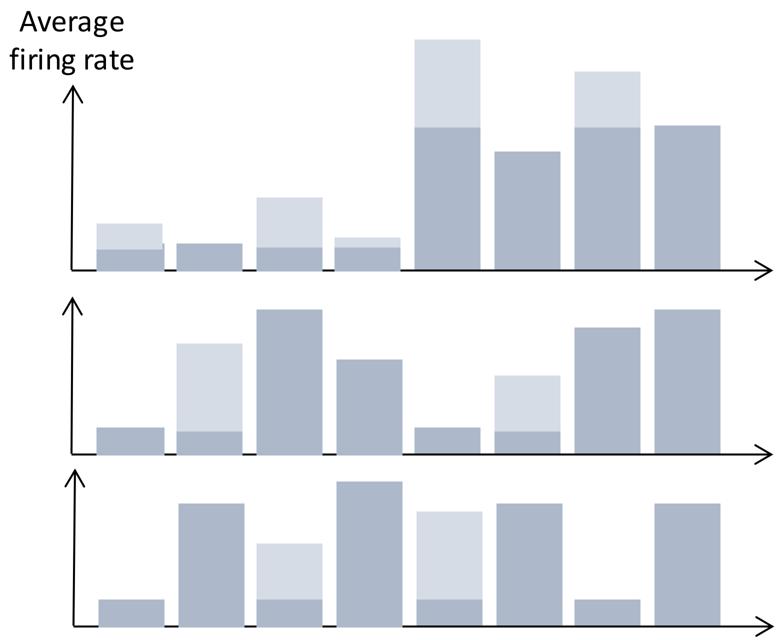
Recorded neural representations



3. Woman	0	1	0	1	0	1	0	1
2. Man	0	0	1	1	0	0	1	1
1. Train	0	0	0	0	1	1	1	1

Orderly distributed representations



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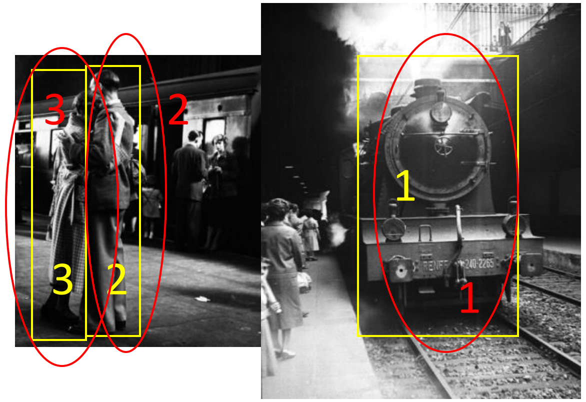
1. Train	0	0	0	0	1	1	1	1



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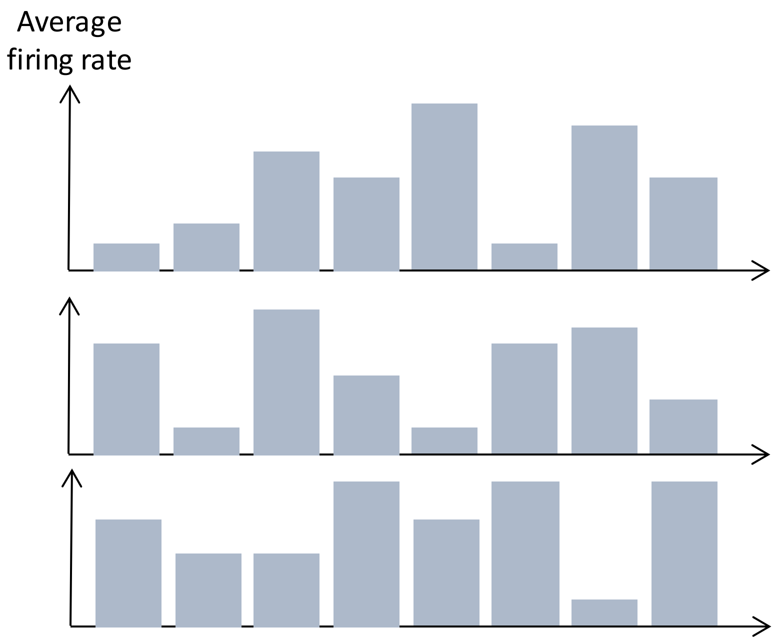
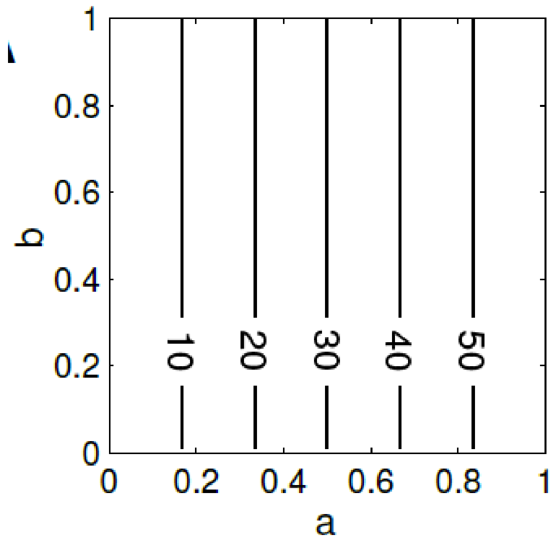
Recorded neural representations

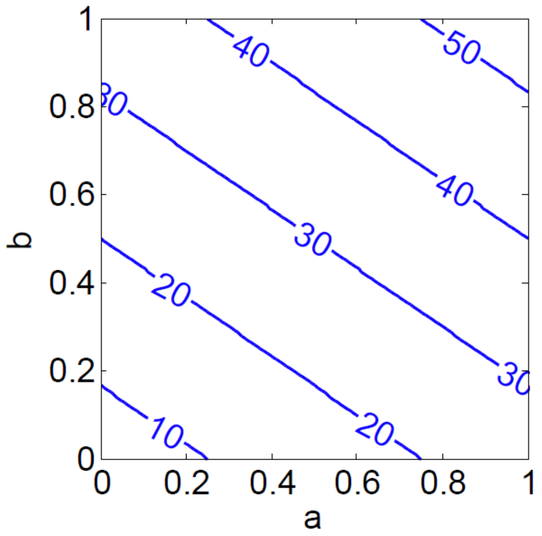


3. Woman	0	1	0	1	0	1	0	1
2. Man	0	0	1	1	0	0	1	1
1. Train	0	0	0	0	1	1	1	1

a,b = parameters of a visuo-auditory stimulus
(e.g. luminance and sound intensity)

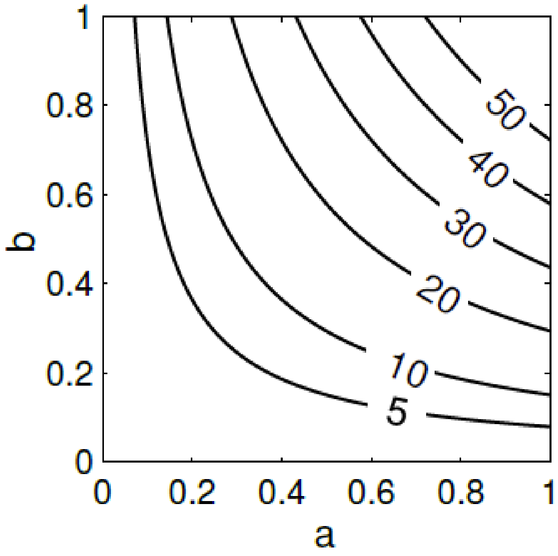


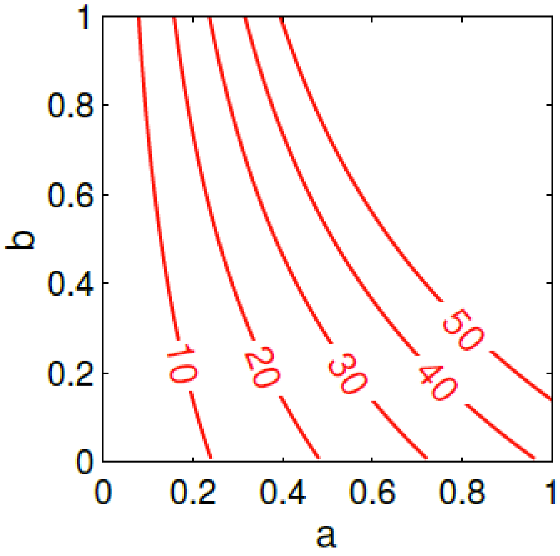
Specialized neurons (pure selectivity)



Linear mixed selectivity

Non-linear mixed selectivity neurons

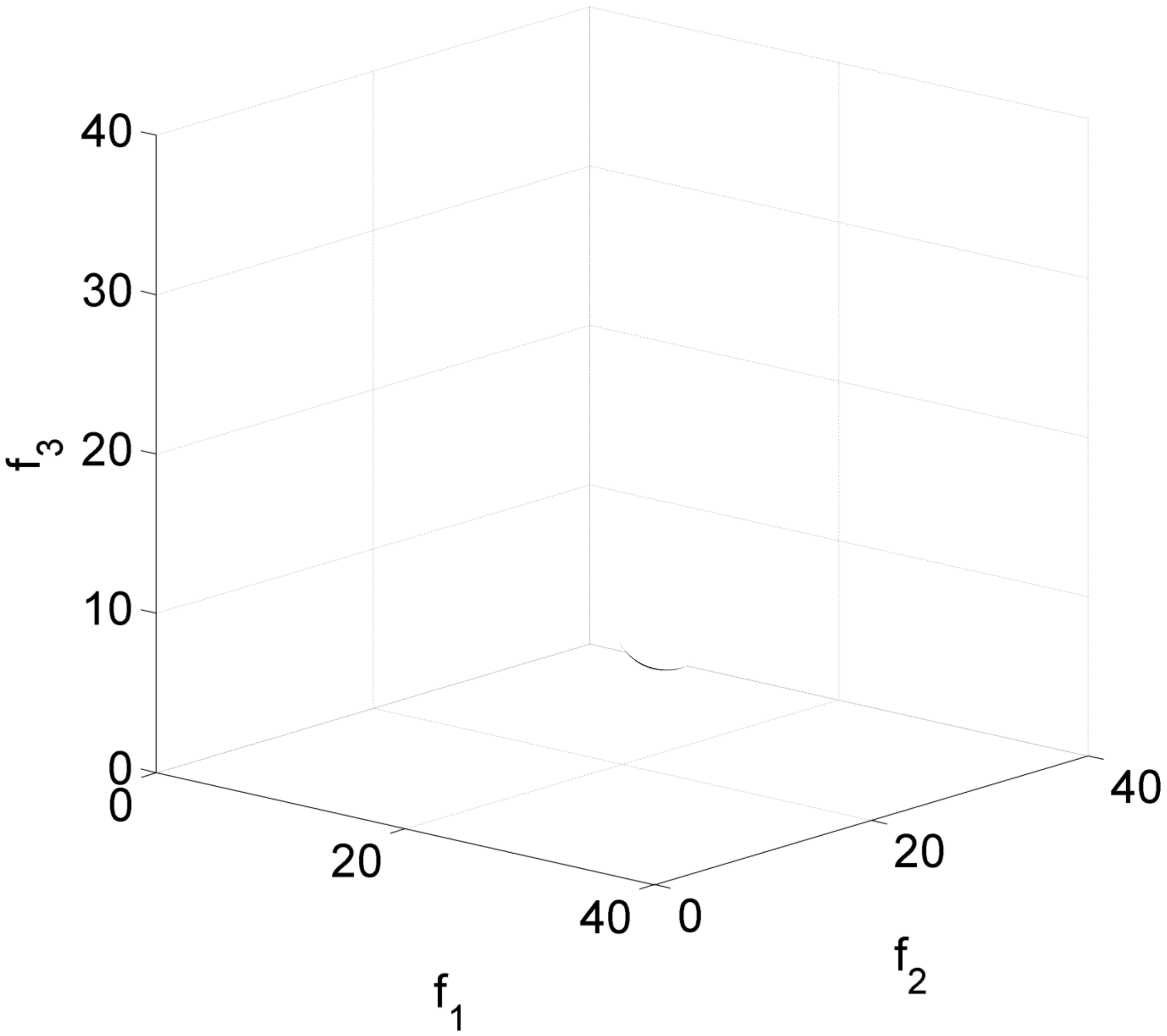




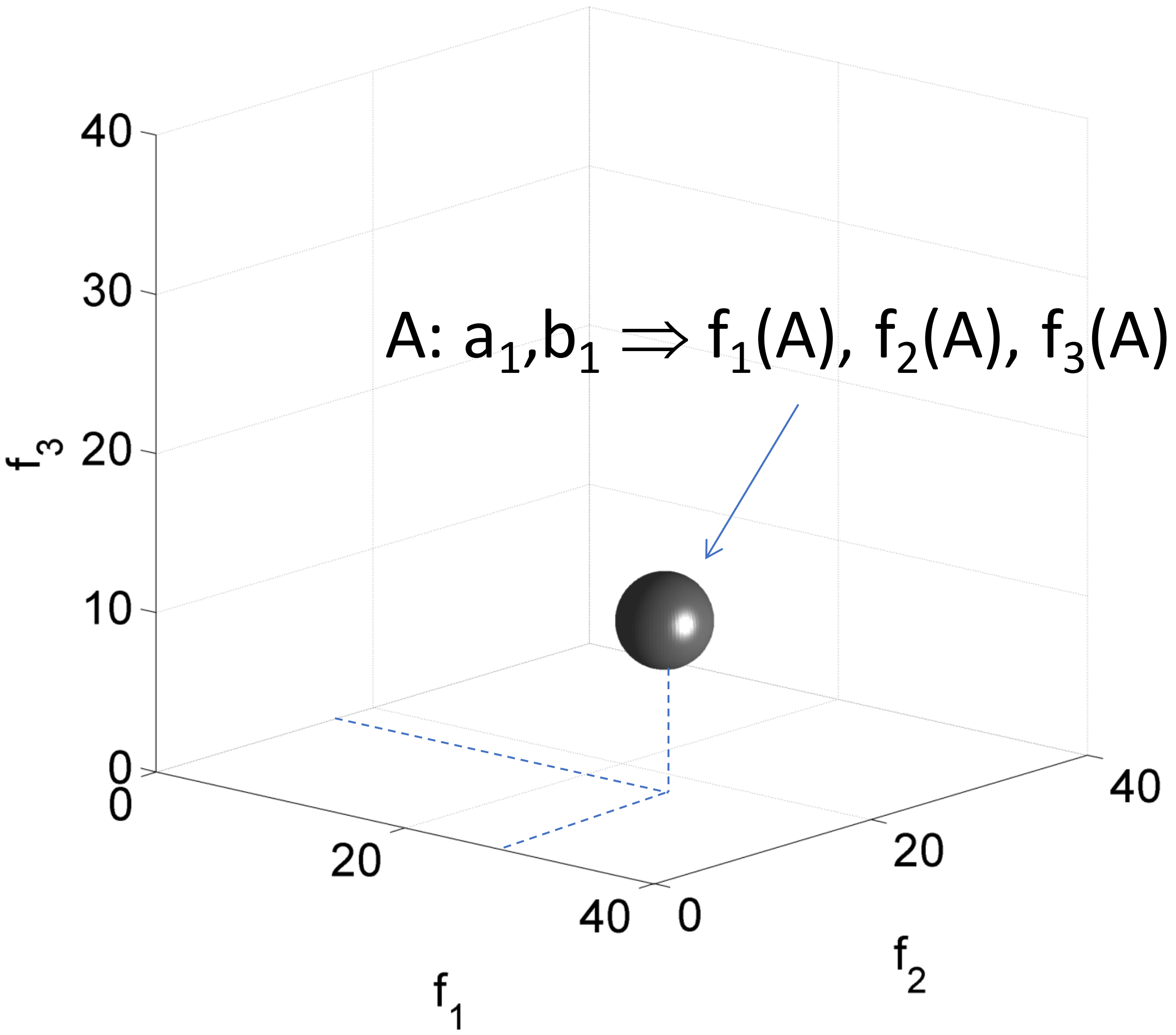
Not easily interpretable response functions

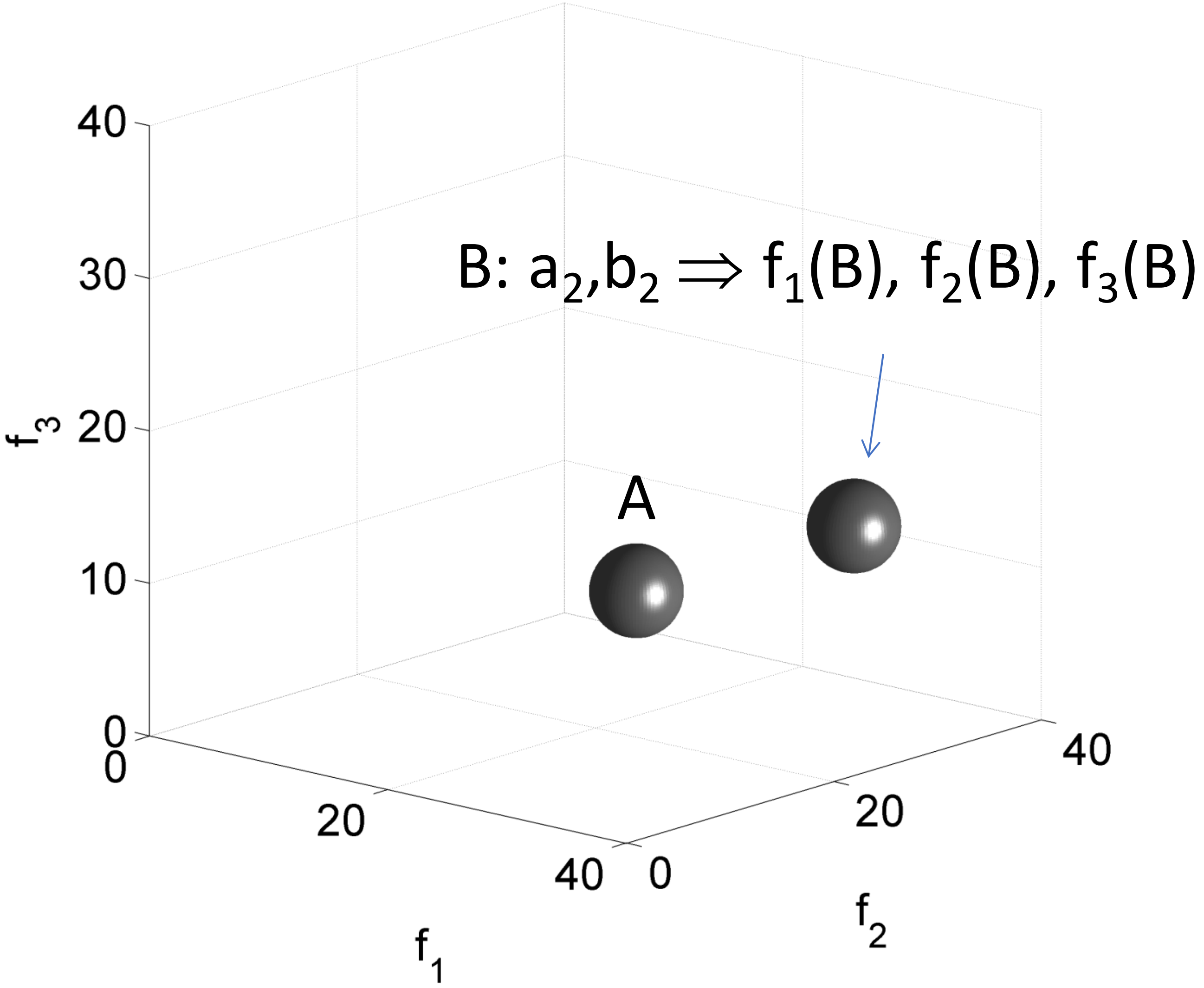
Pure selectivity neurons:
geometry of neural representations

f_1=60 a, f_2=60 b, f_3=60-50a

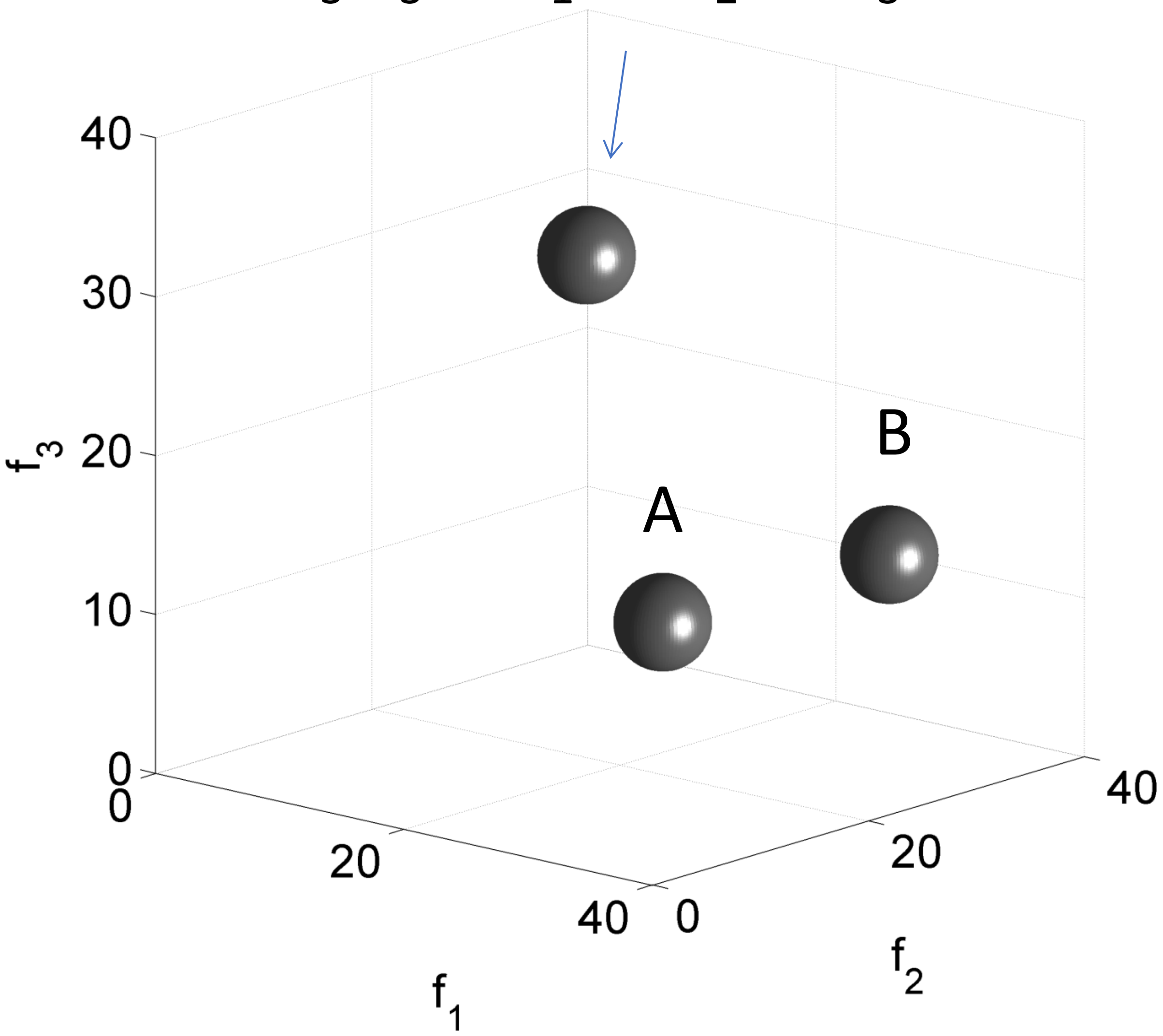


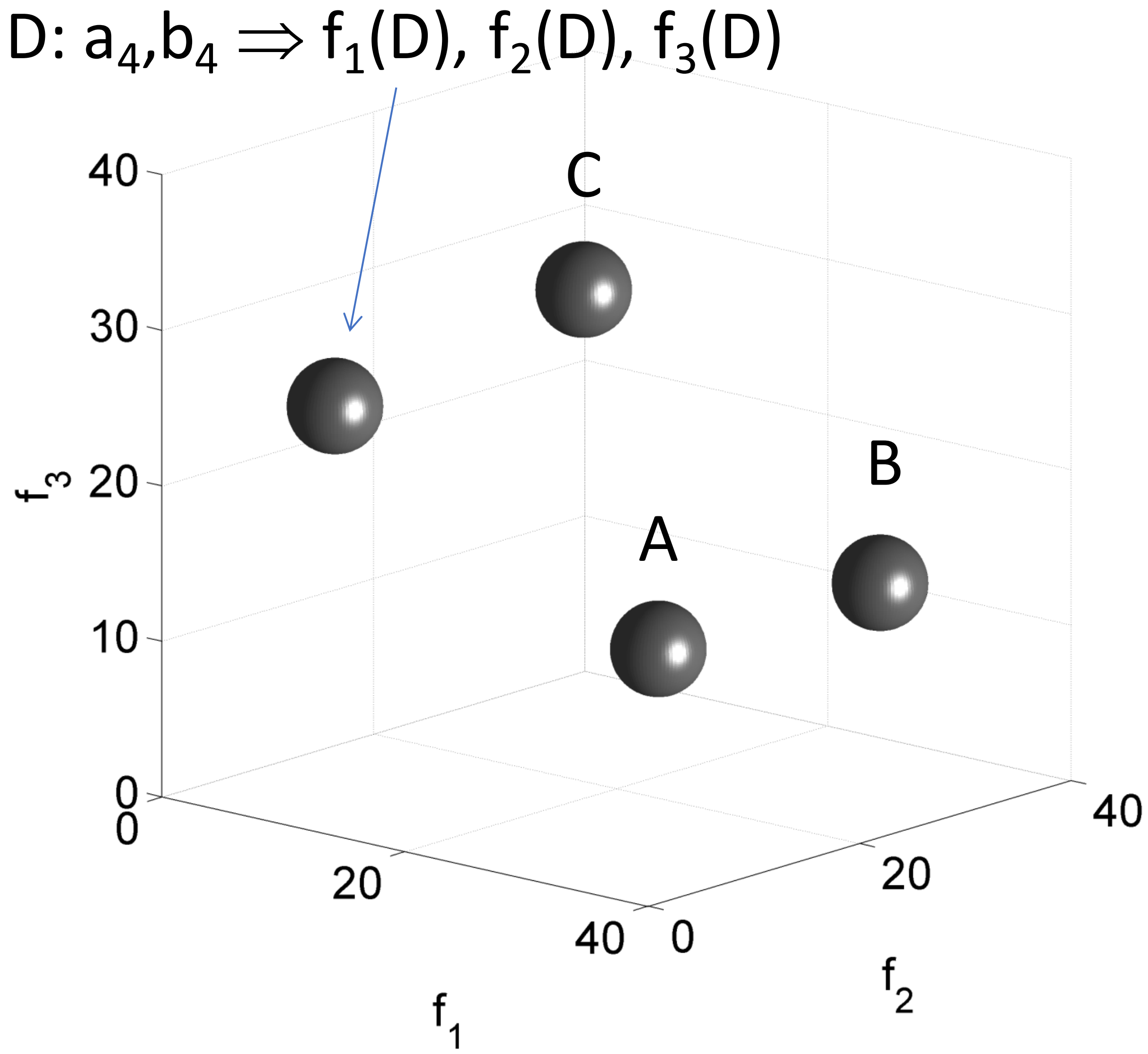
$$f_1 = 60\,a, \quad f_2 = 60\,b, \quad f_3 = 60 - 50a$$



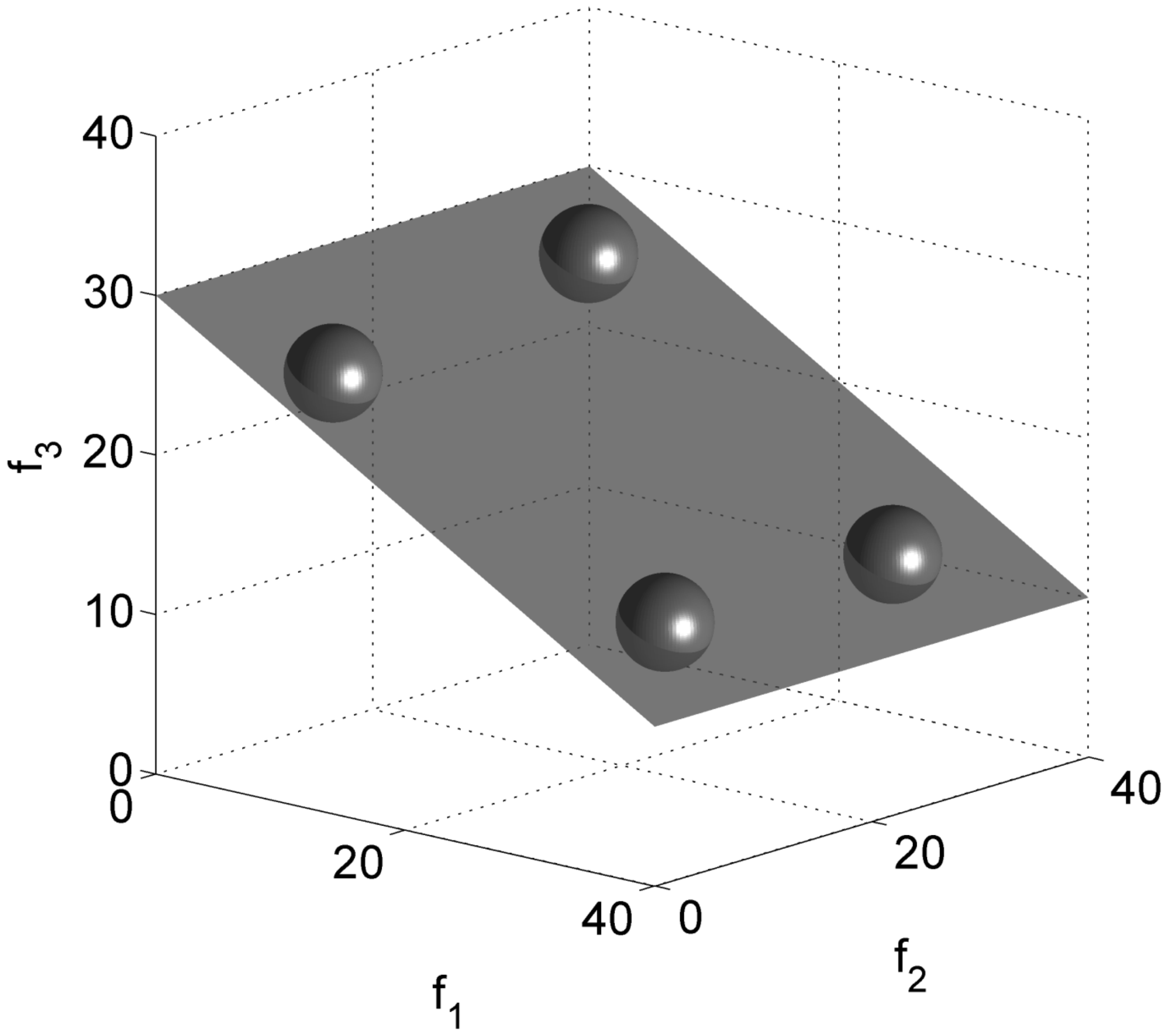

B: $a_2,b_2 \Rightarrow f_1(B), f_2(B), f_3(B)$
A
f_3
40
30
20
10
0
0
20
40
f_1
0
20
40
f_2

$$C: a_3, b_3 \Rightarrow f_1(C),\ f_2(C),\ f_3(C)$$

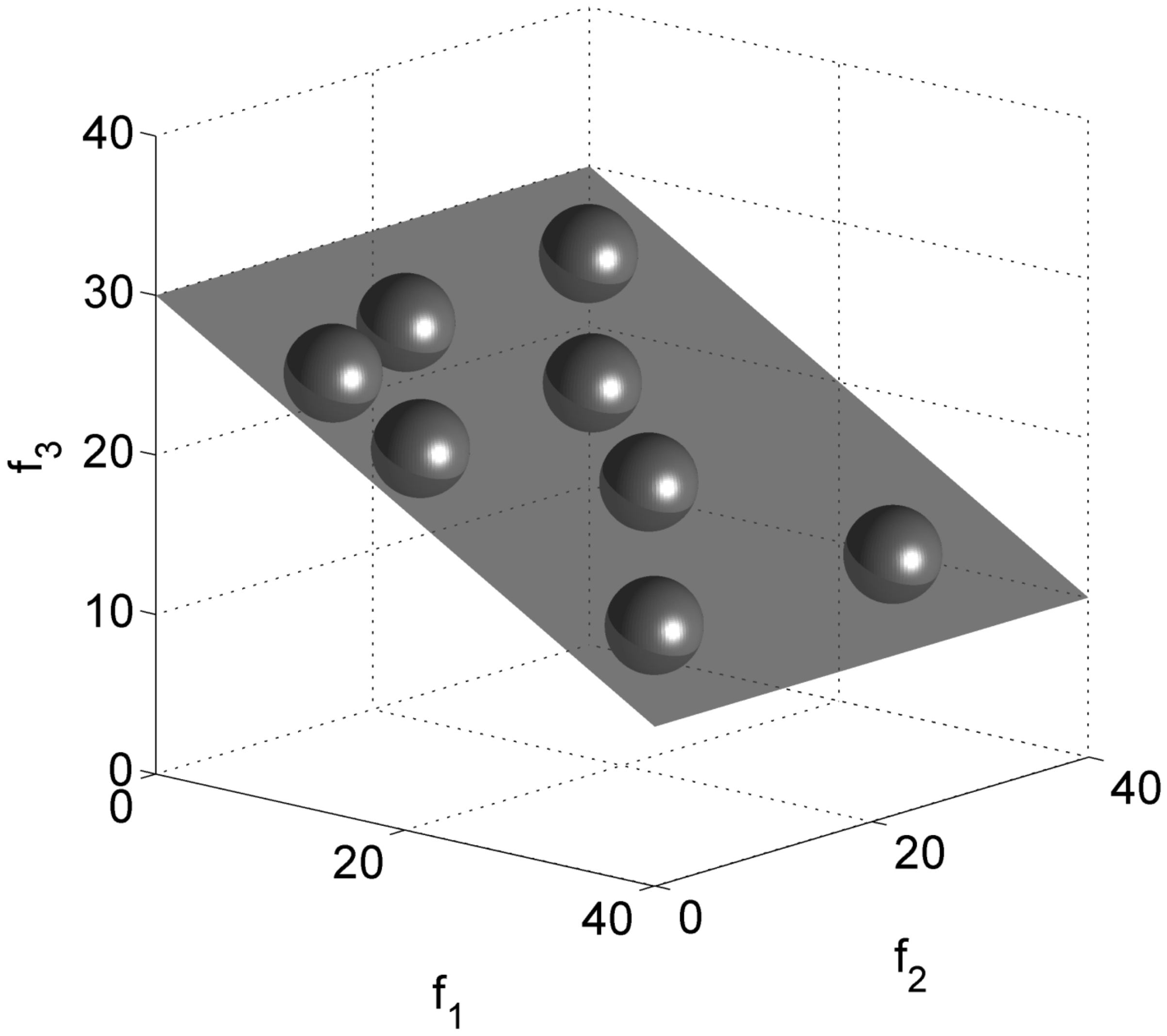




D: $a_4, b_4 \Rightarrow f_1(D), f_2(D), f_3(D)$
C
B
A
f_3
40
30
20
10
0
0
20
40
f_1
0
20
40
f_2

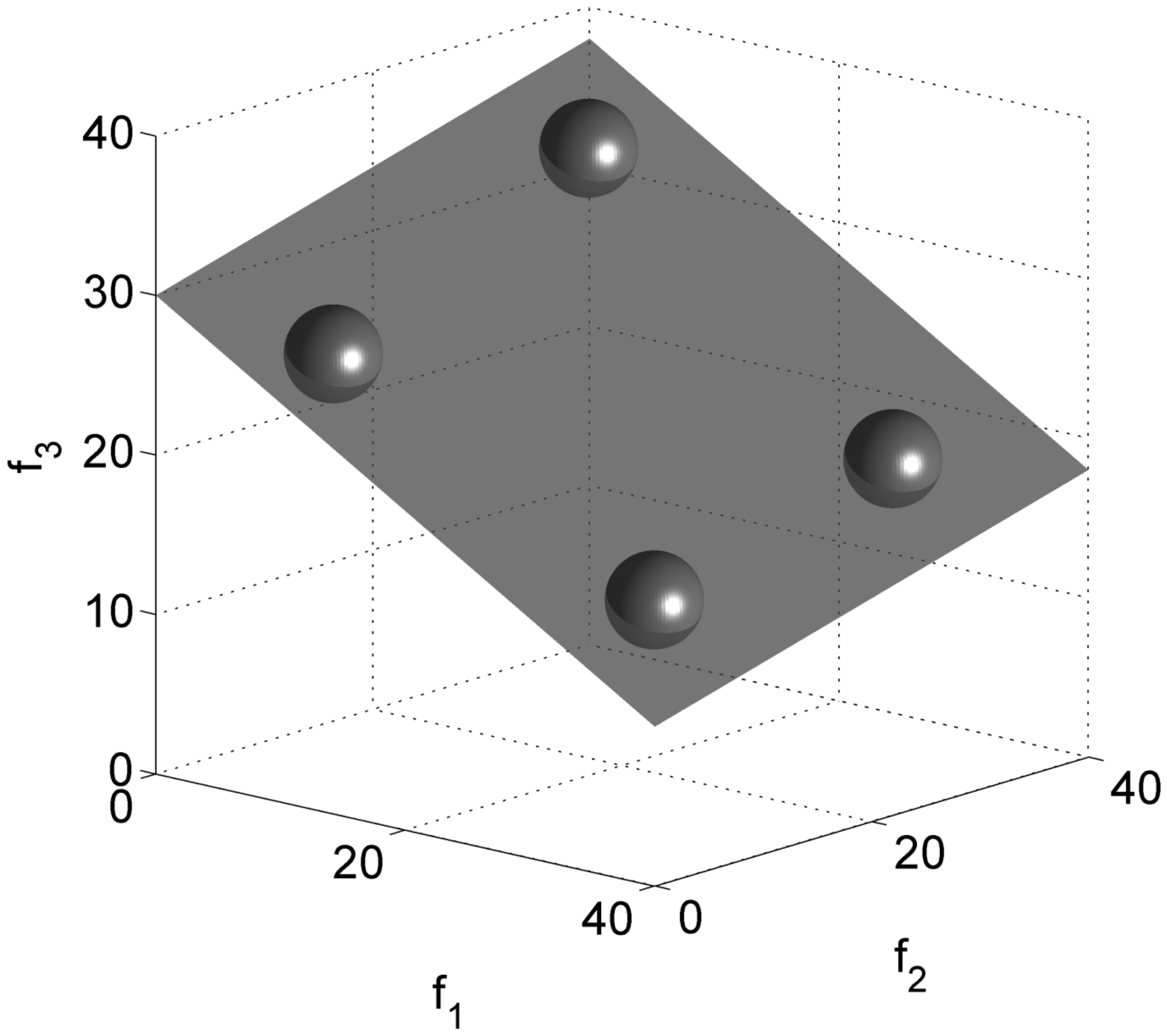


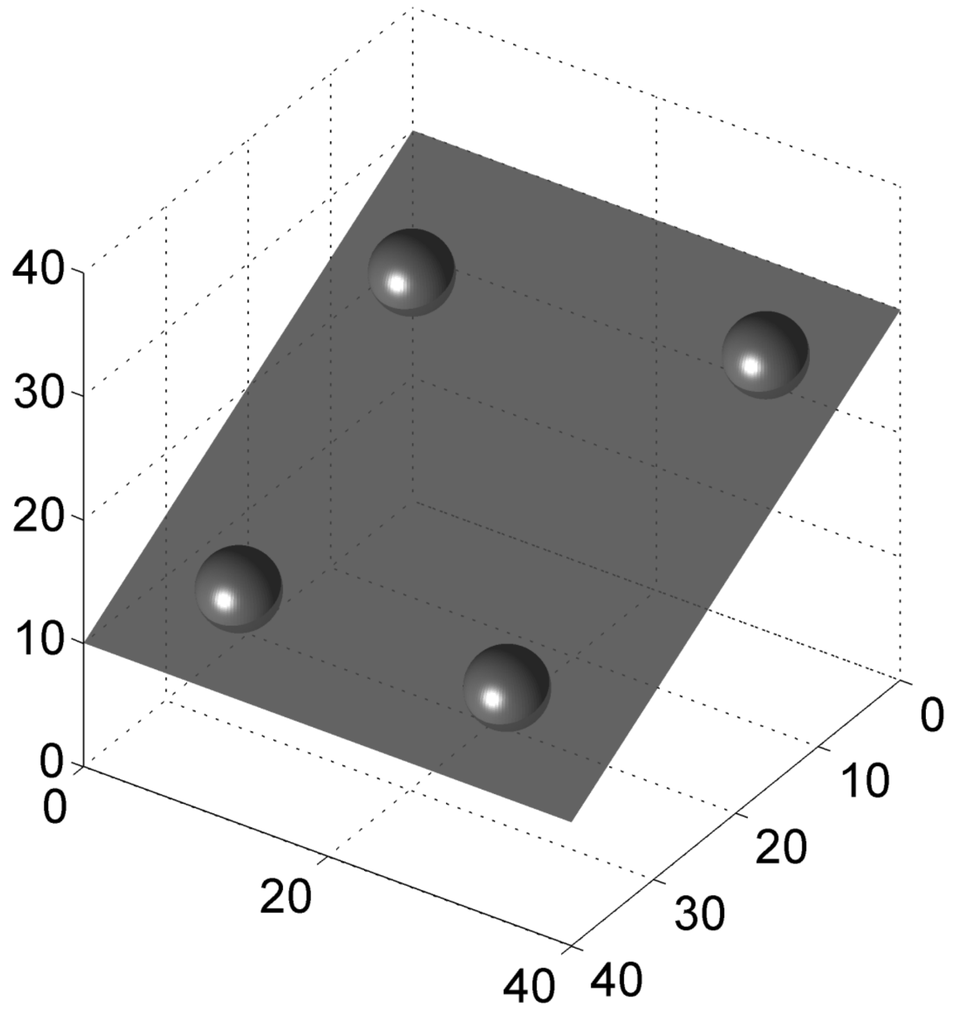
40
30
20
10
0
f_3
0
20
40
f_1
0
20
40
f_2



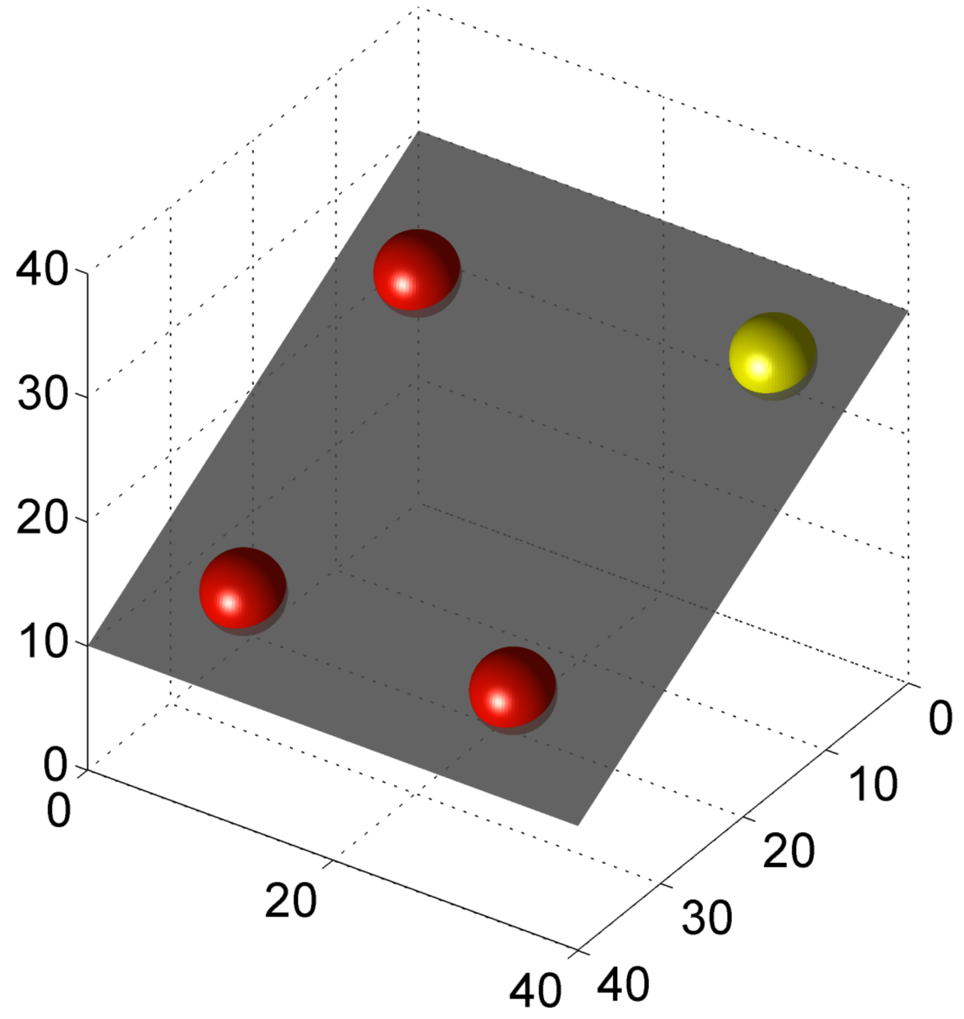
40
30
20
10
0
f_3
0
20
40
f_1
0
20
40
f_2

Linear mixed selectivity neuron: f_3=30-15a+6b

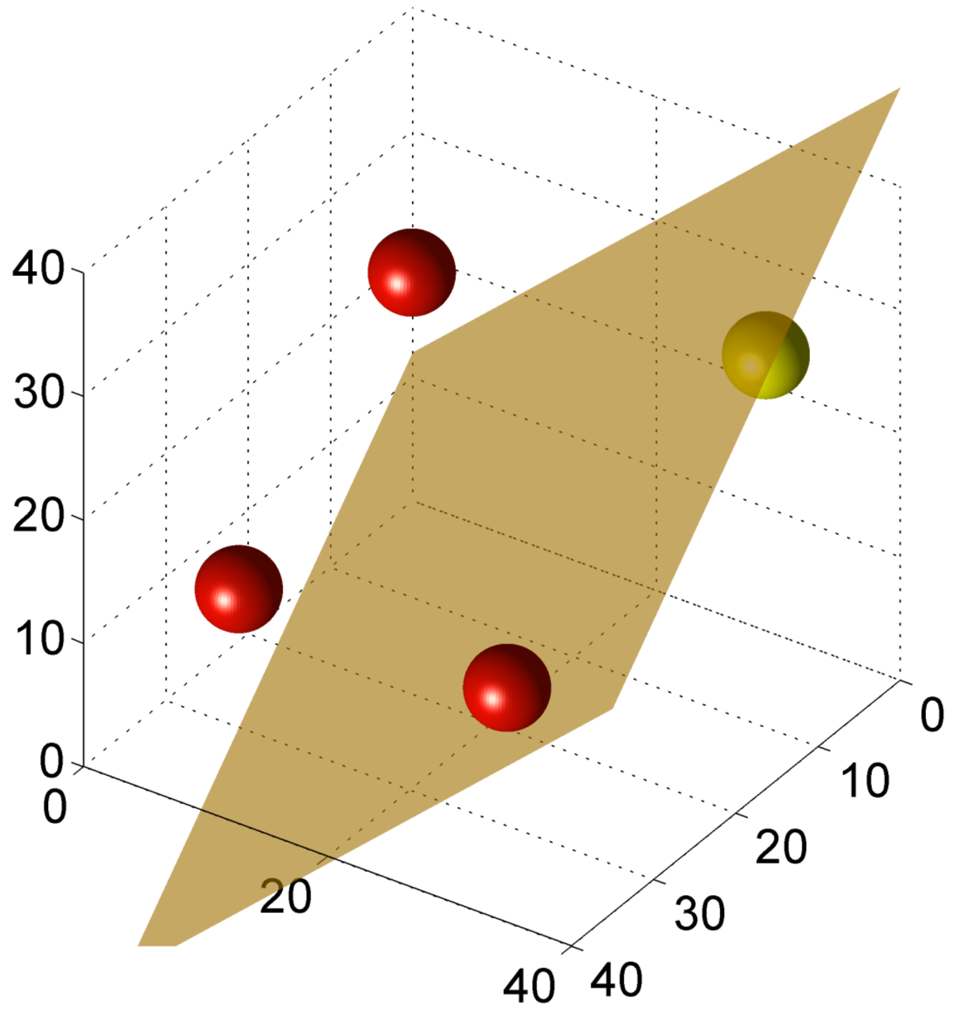




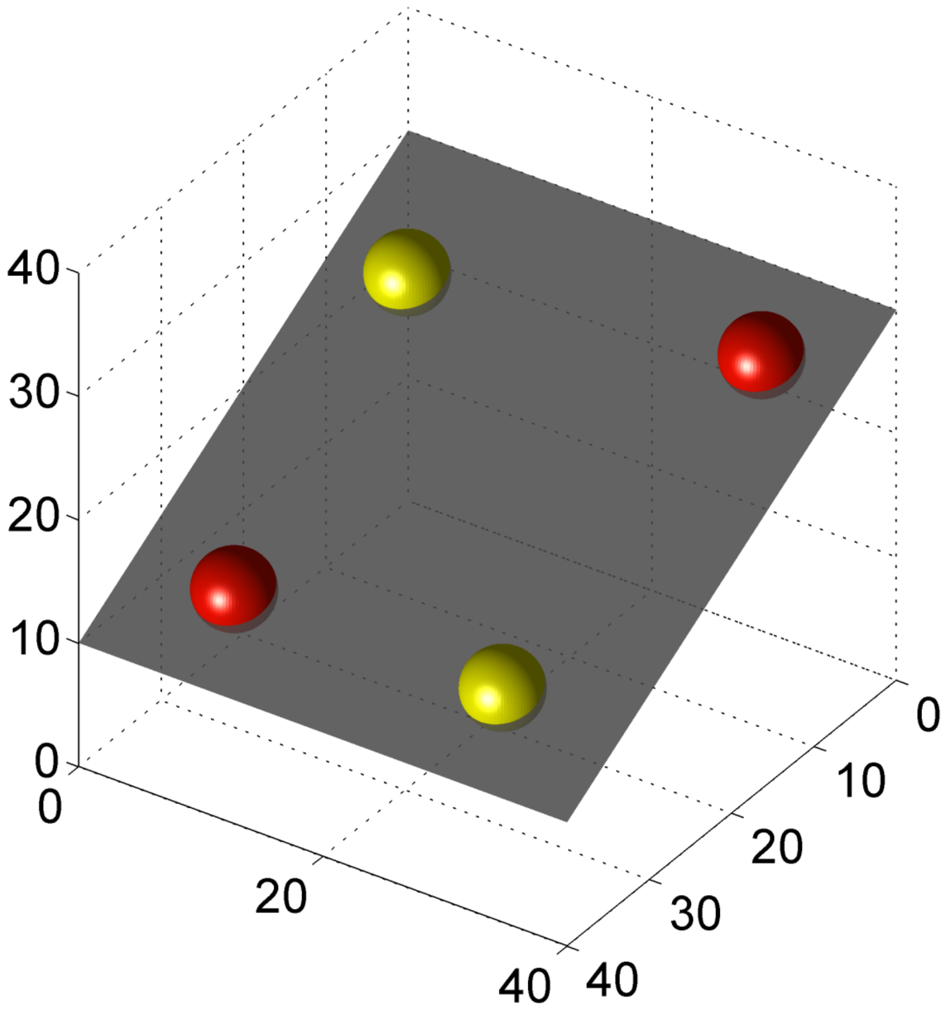
40
30
20
10
0
0
20
40
0
10
20
30
40



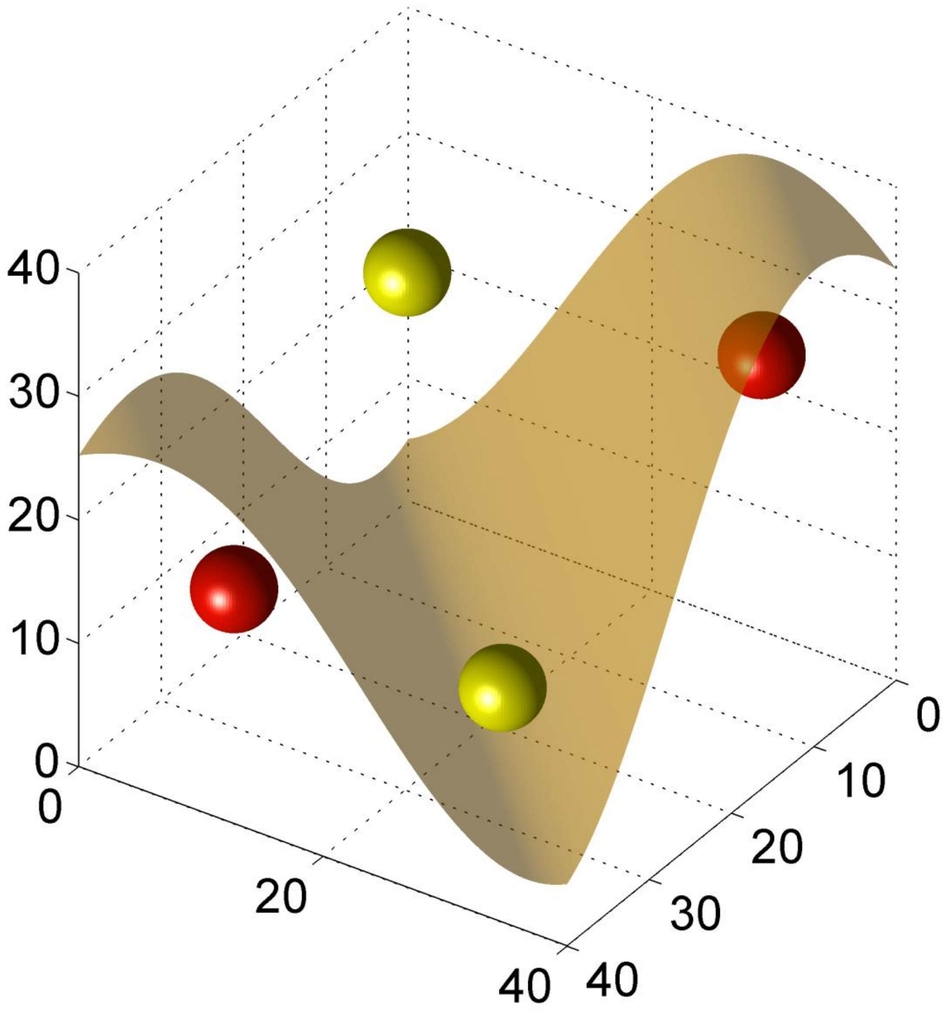
40
30
20
10
0
0
20
40
0
10
20
30
40

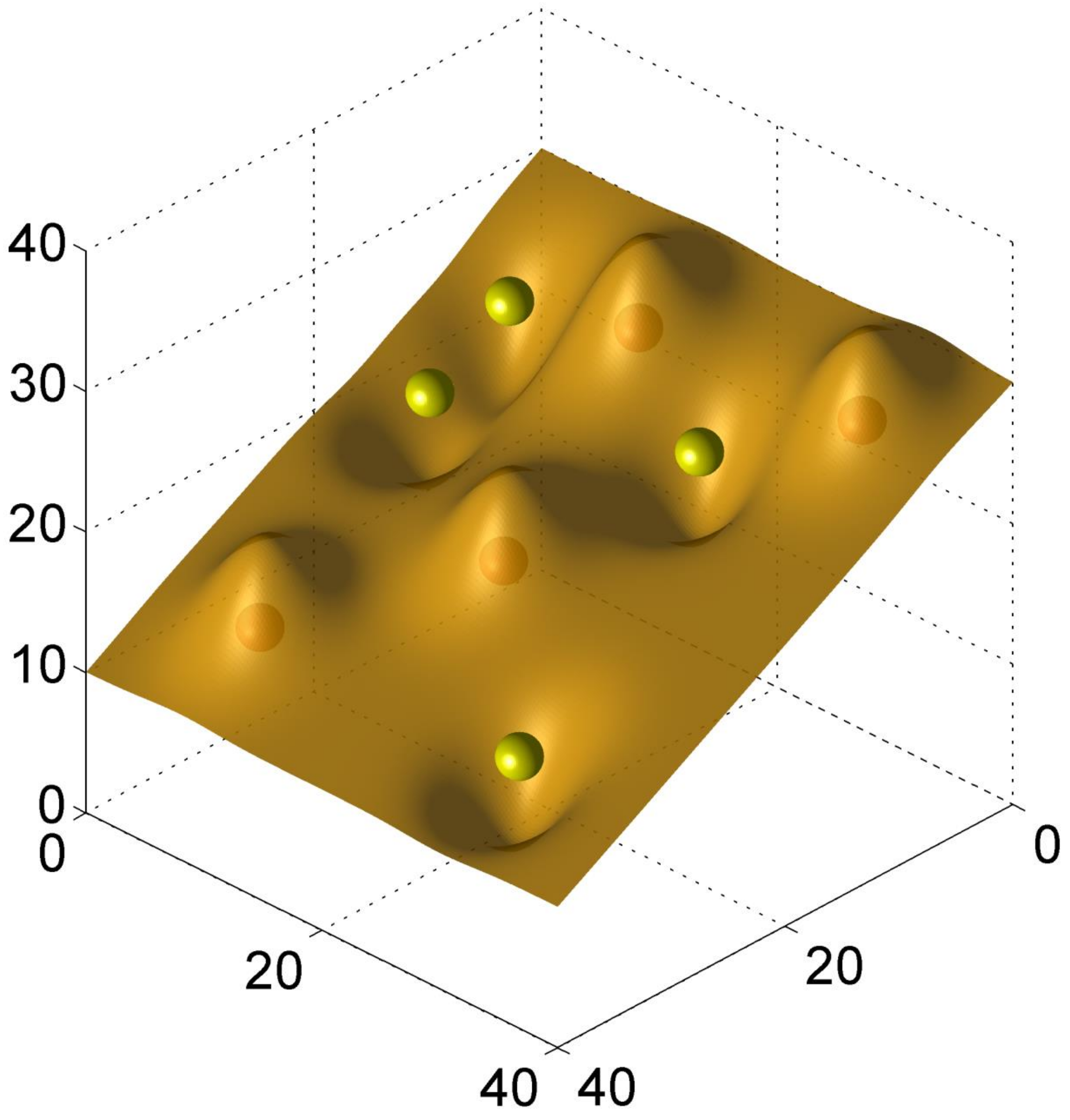


40
30
20
10
0
0
20
40
0
10
20
30
40



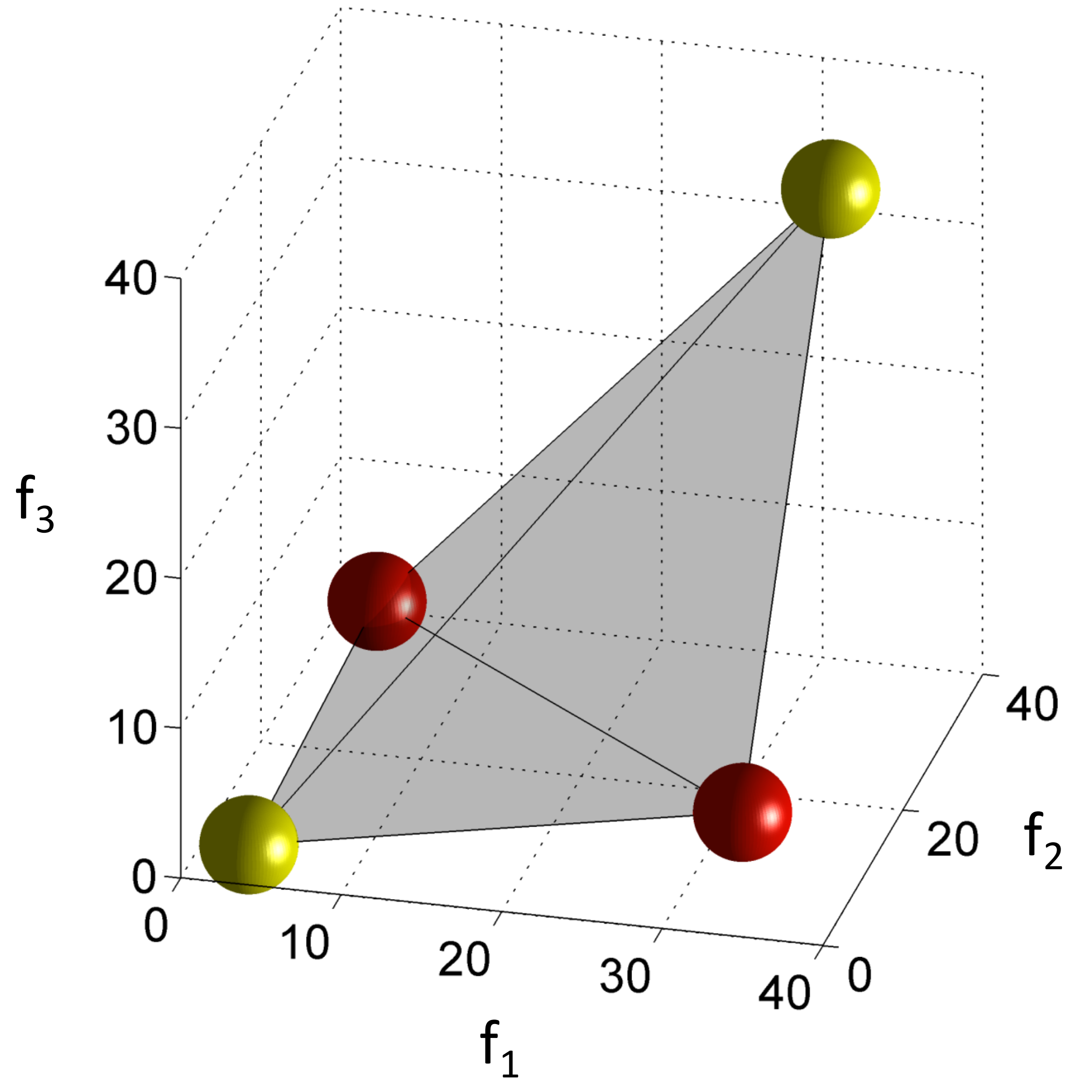
40
30
20
10
0
0
20
40
0
10
20
30
40

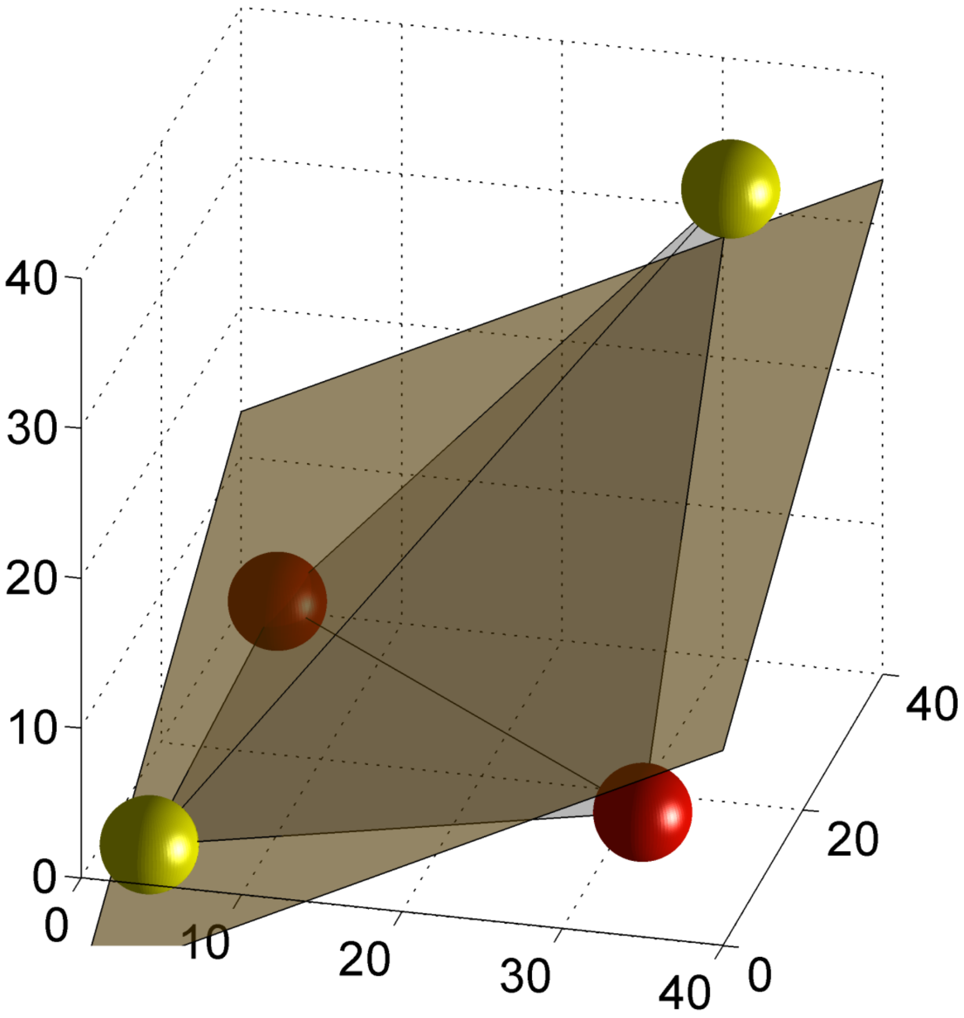

40
30
20
10
0
0
20
40
0
10
20
30
40


40
30
20
10
0
0
20
40
40
20
0

Non-linear mixed selectivity

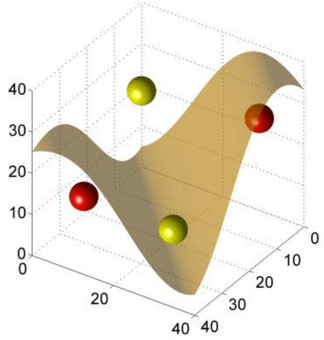
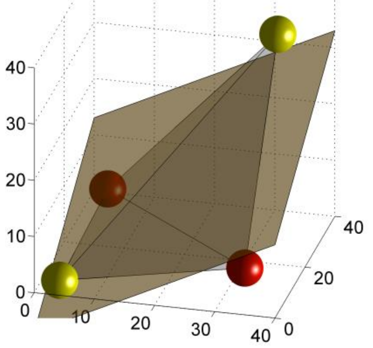
f_1=60 a, f_2=60 b, f_3=ϕ(a,b)



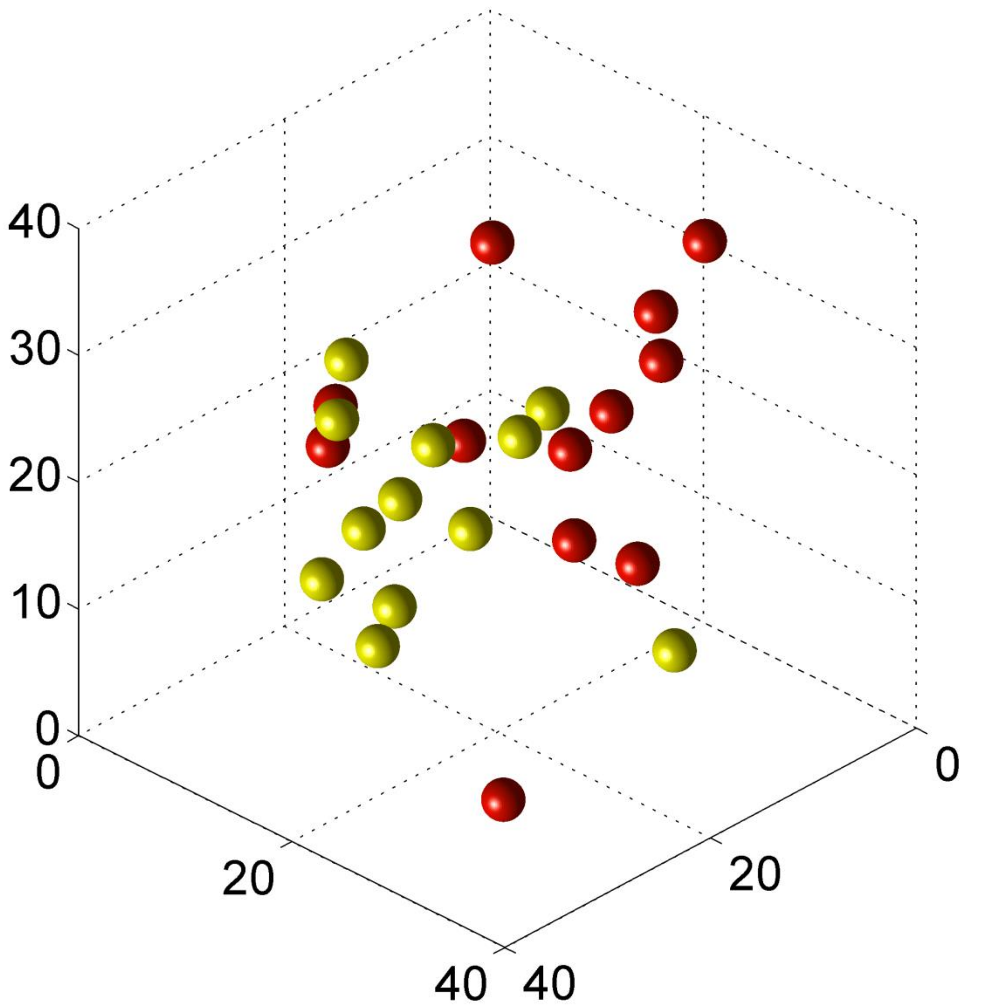


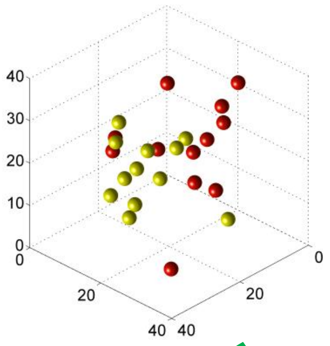
40
30
20
10
0
0
10
20
30
40
0
20
40

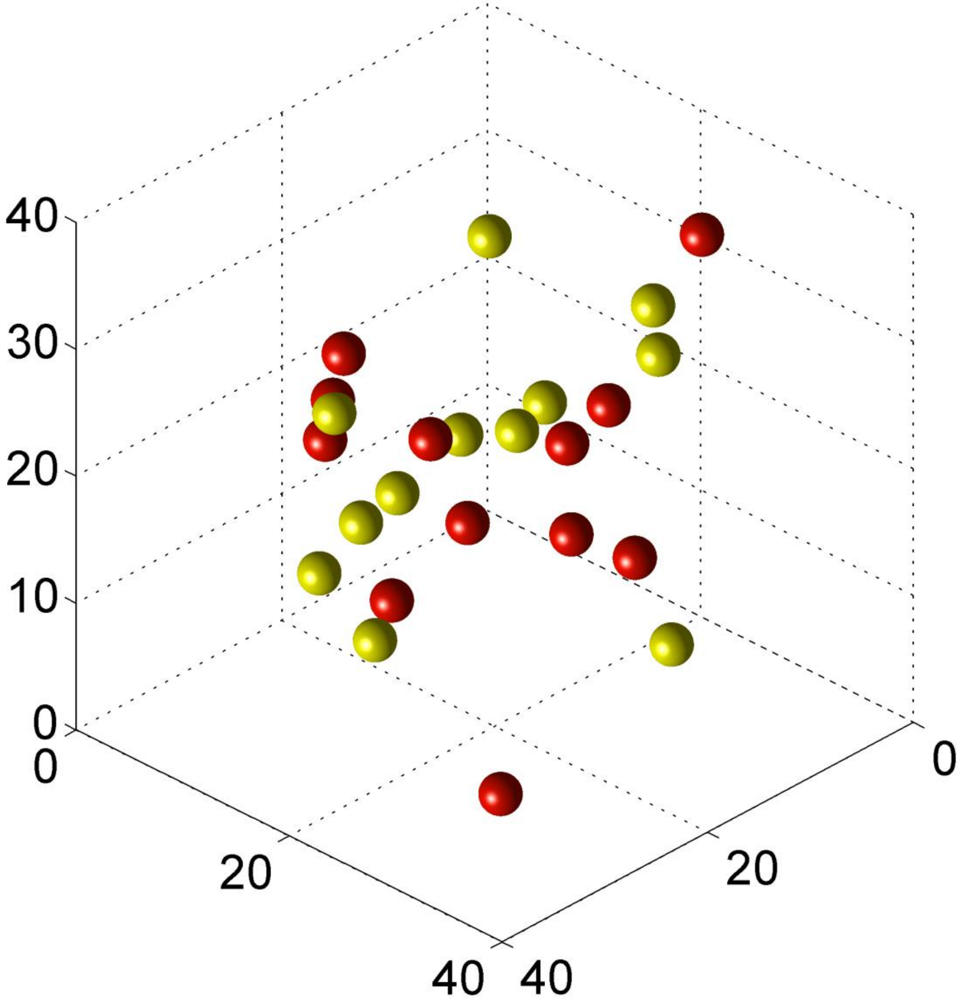
Summary

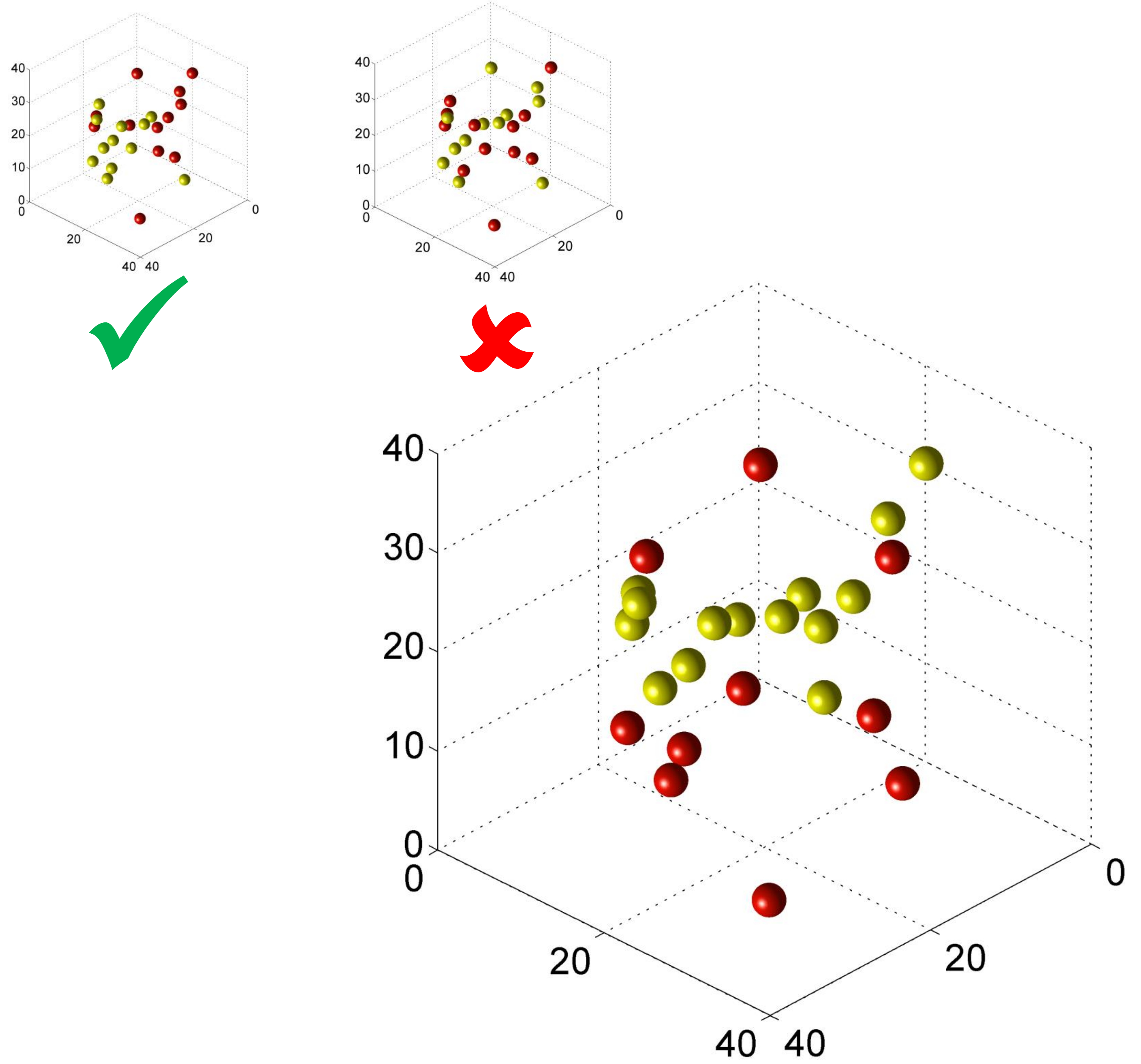
Response properties	Pure and linear mixed selectivity	Non-linear mixed selectivity
	Low dimensionality	High dimensionality
Geometry of neural representations		
Readout	Complex	Simple (linear)
Quantitative measure of the quality of neural representations	?	

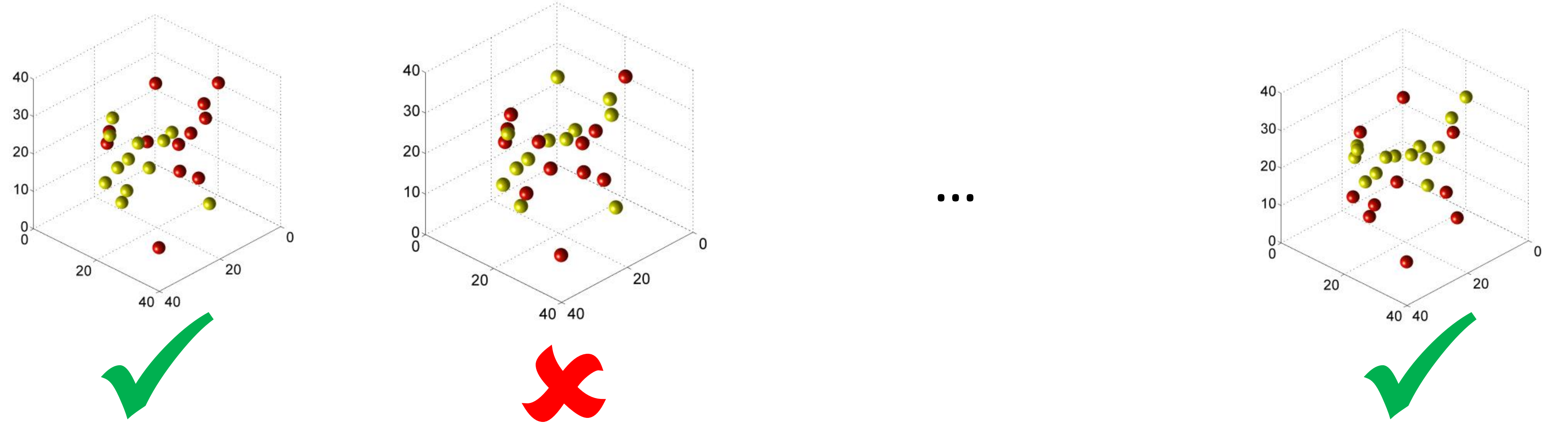
N= Number of neurons (number of axes)
p= number of spheres (p<N, p=max dimensionality)



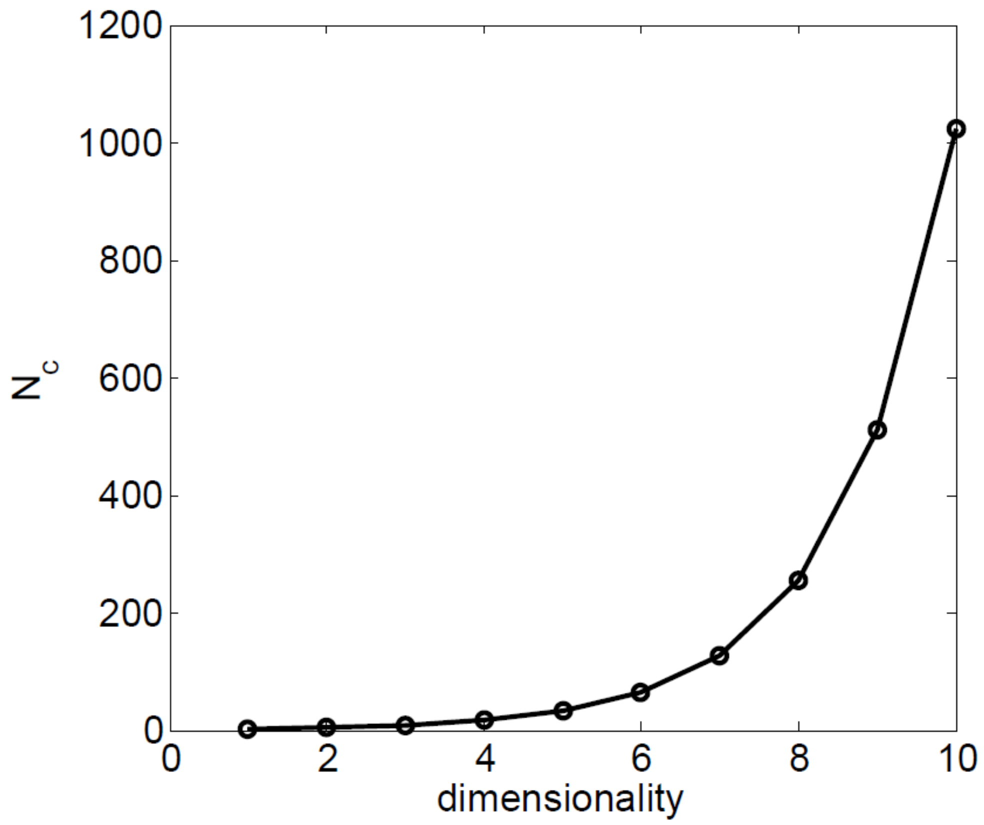

40
30
20
10
0
0
20
40
40
20
0


40
30
20
10
0
0
20
40
40
20
0

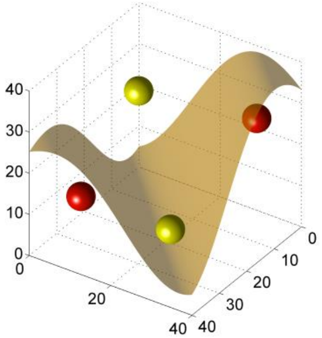
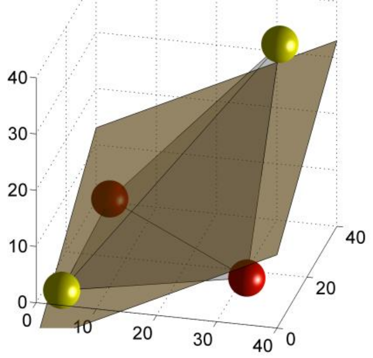

40
30
20
10
0
0
20
40
40
20
0



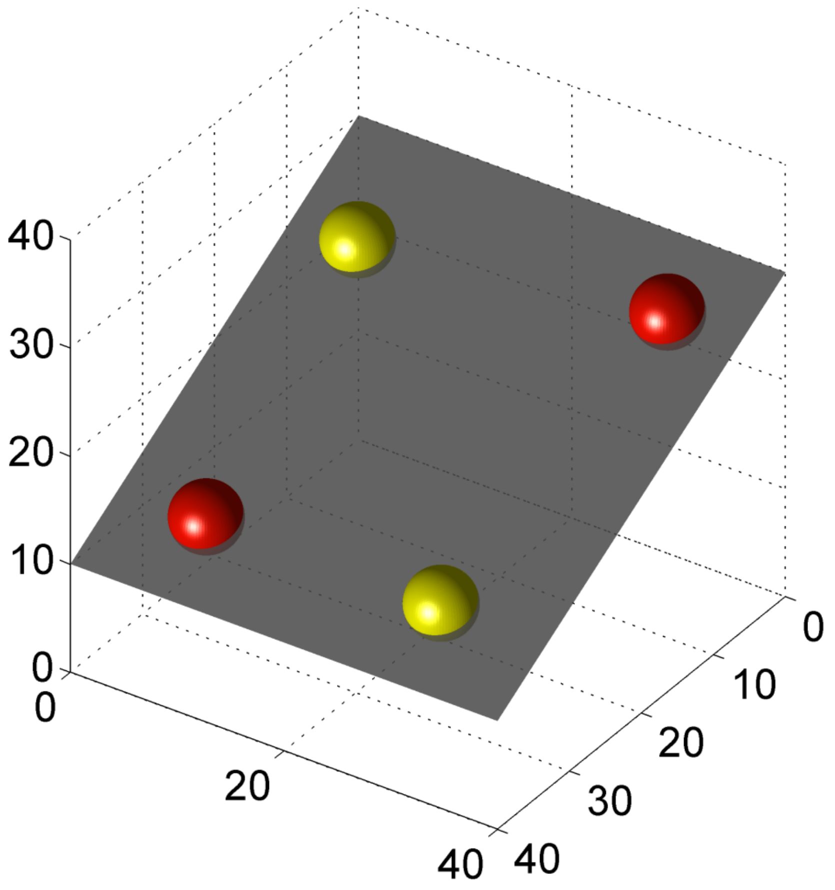
N_c = Number of binary classifications that are implementable by a simple linear readout



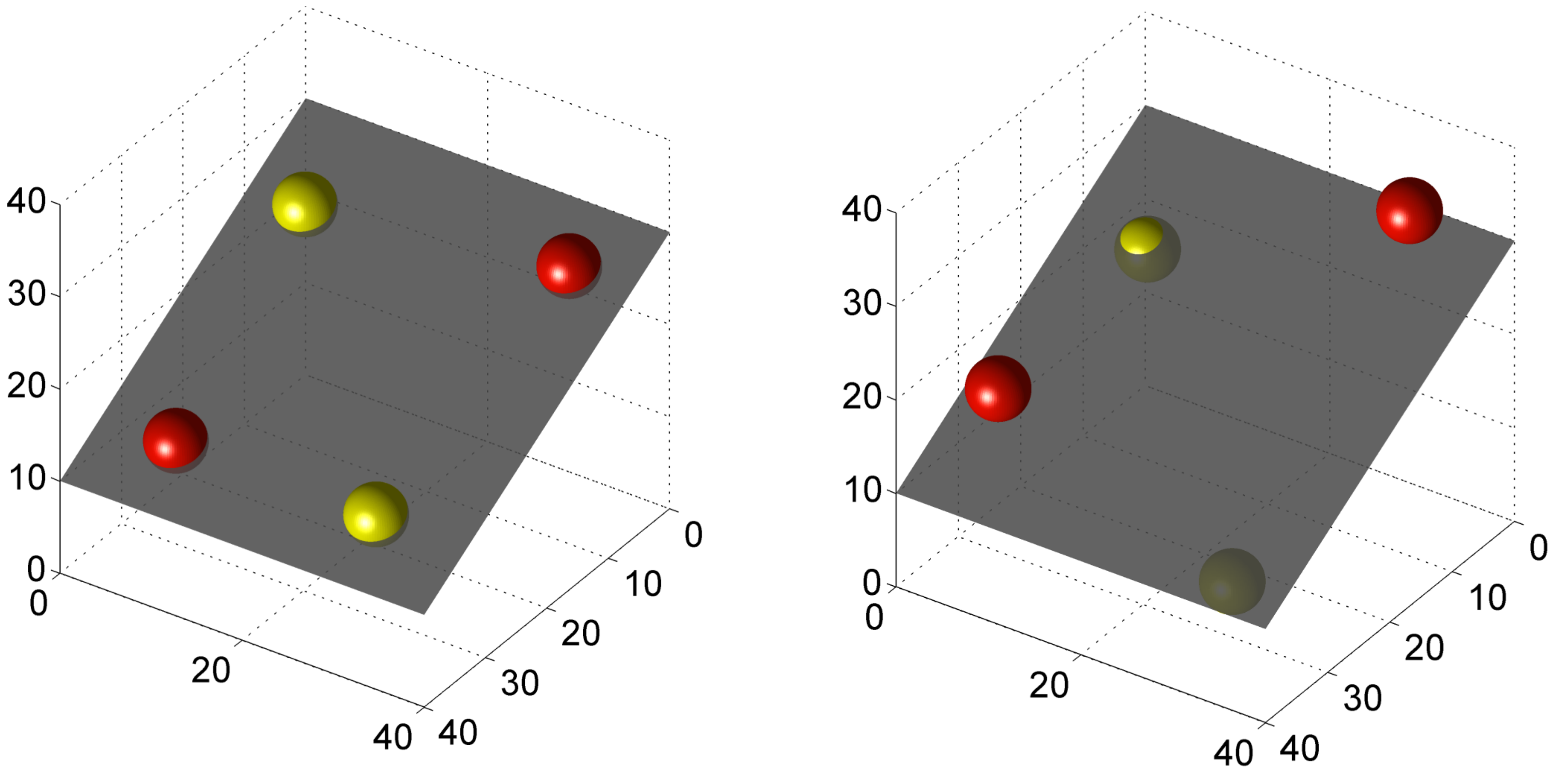
Summary

Response properties	Pure and linear mixed selectivity	Non-linear mixed selectivity	
Geometry of neural representations	Low dimensionality 	High dimensionality 	$d \approx \log(N_c)$
Readout	Complex	Simple (linear)	
Quality of neural Representations: N_c	Low	High	$N_c \approx \exp(d)$

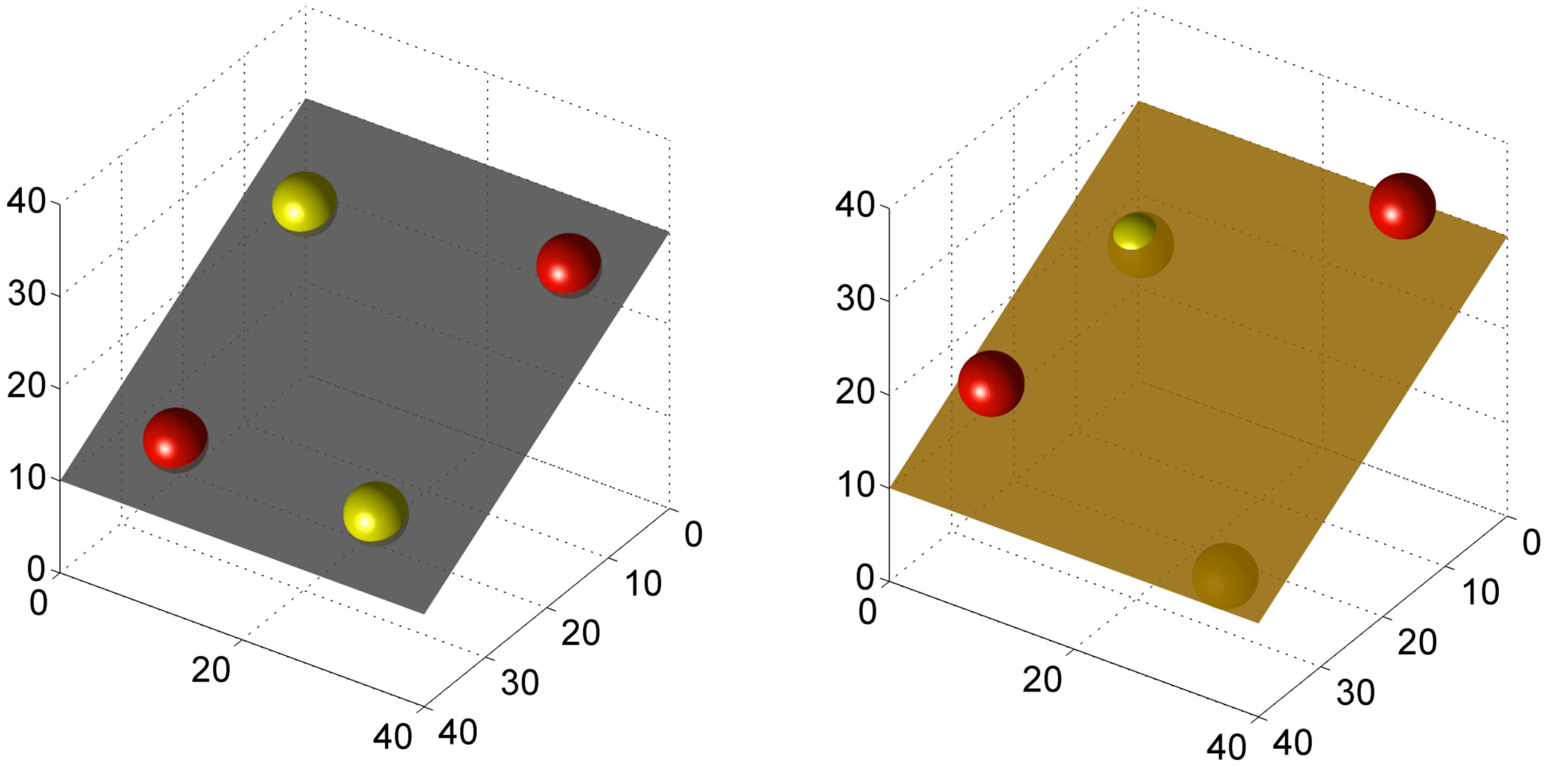
Low dimensional with noise may look high dimensional



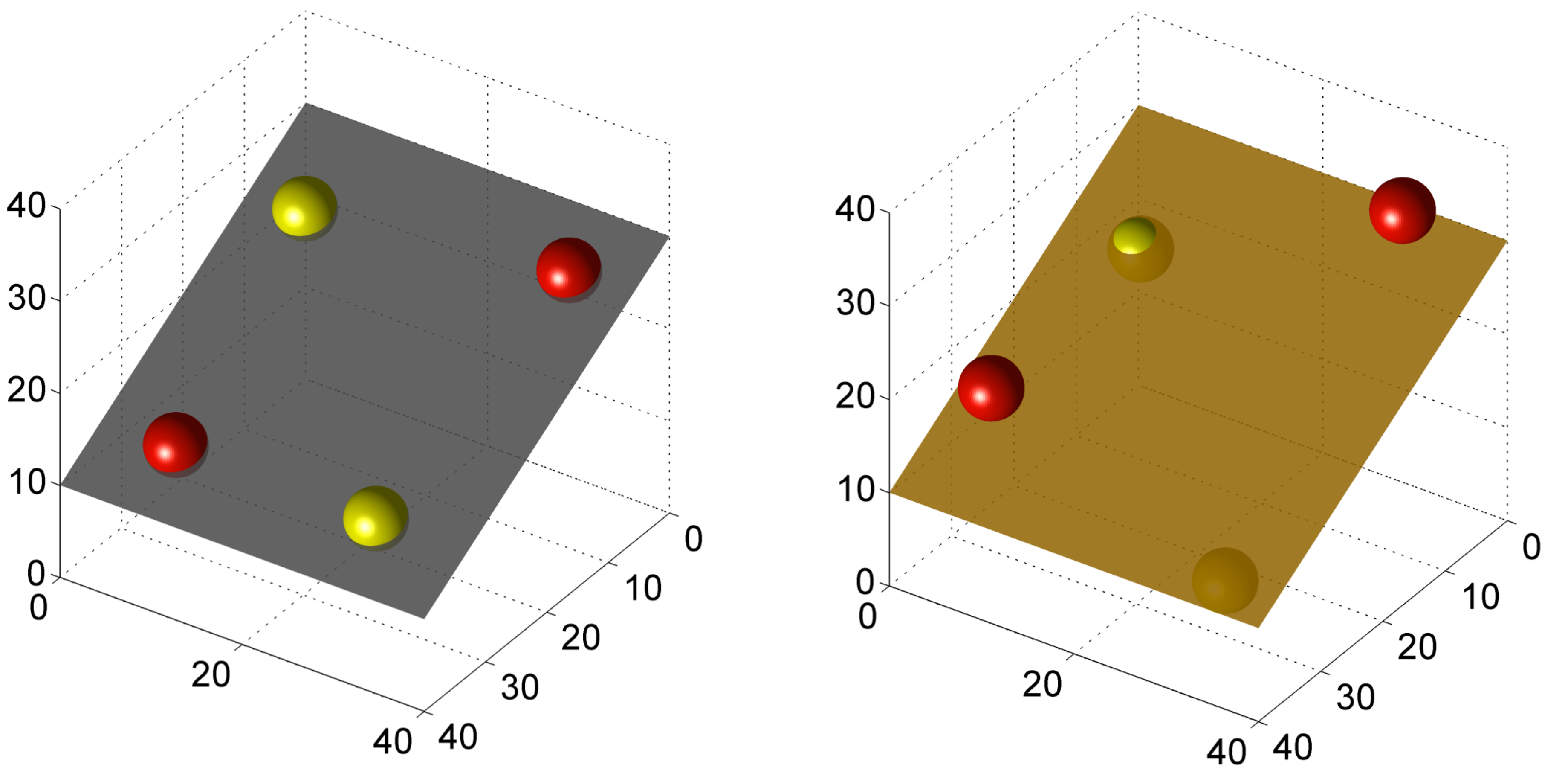
Low dimensional with noise may look high dimensional



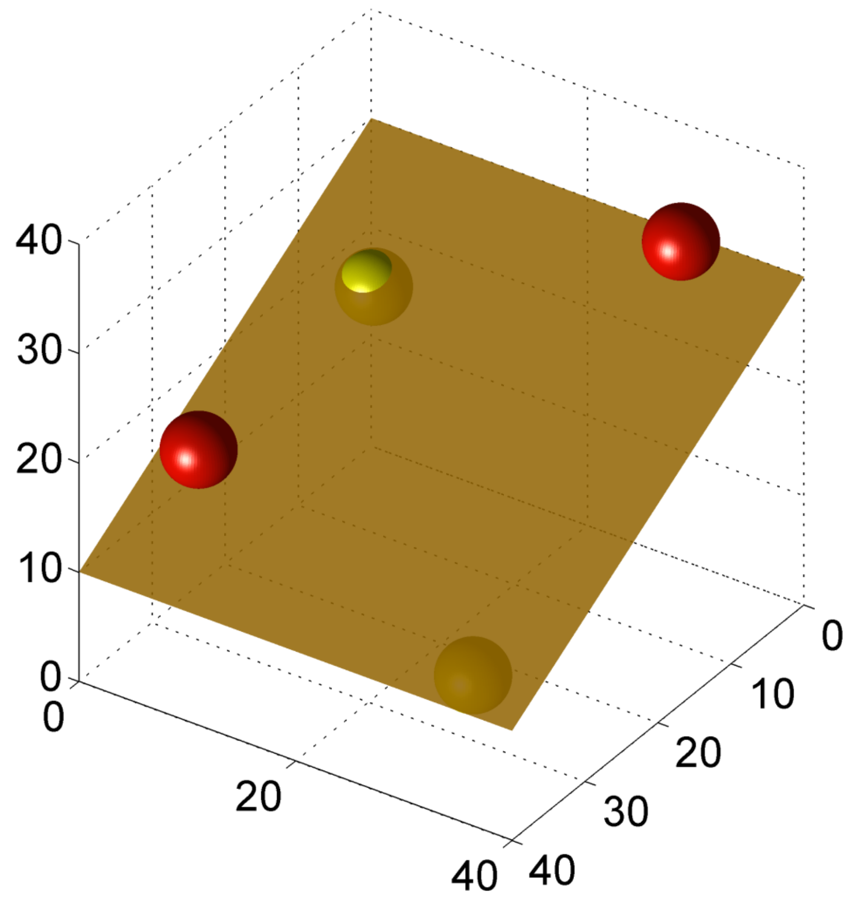
Low dimensional with noise may look high dimensional



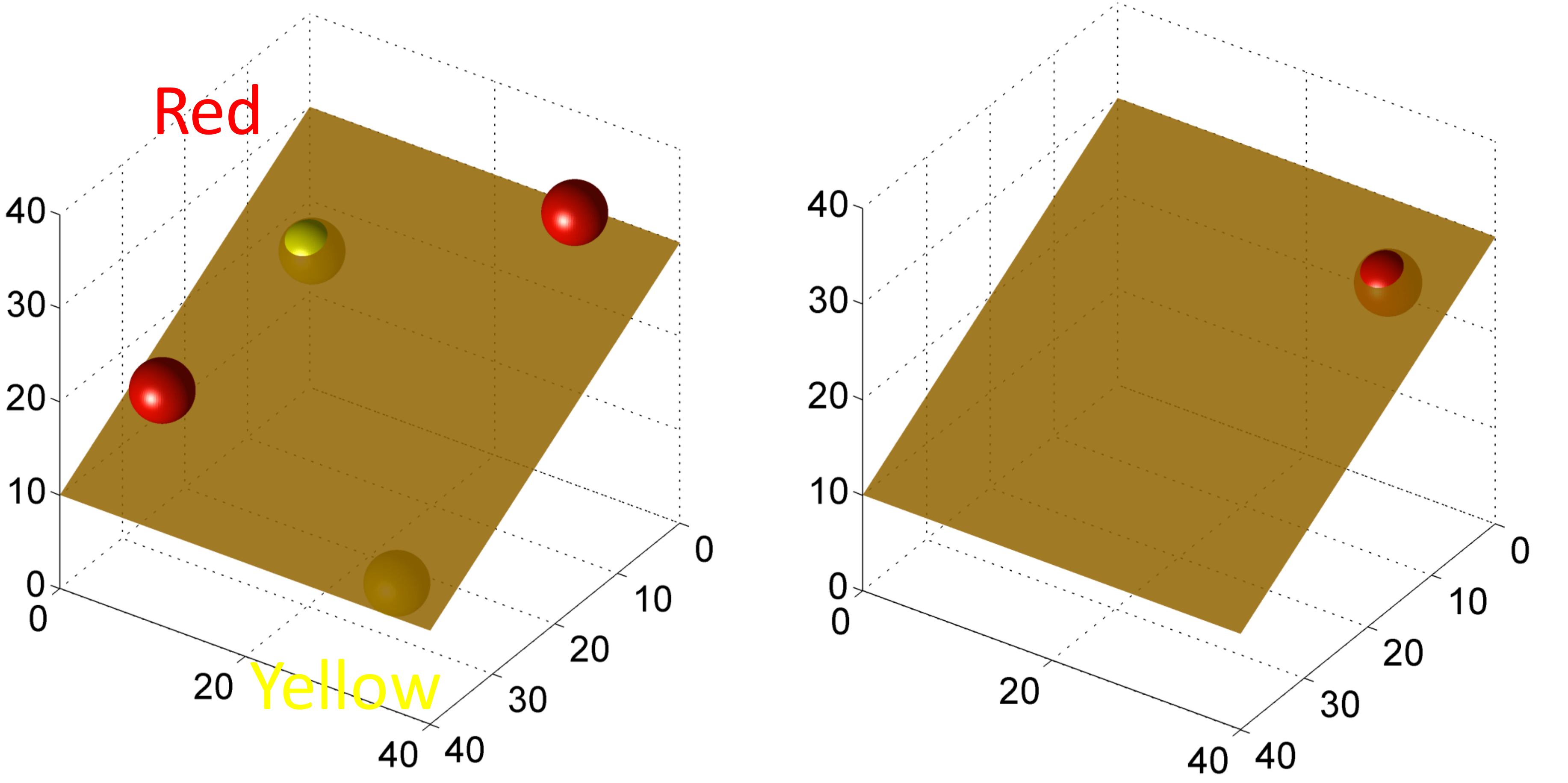
Low dimensional with noise may look high dimensional



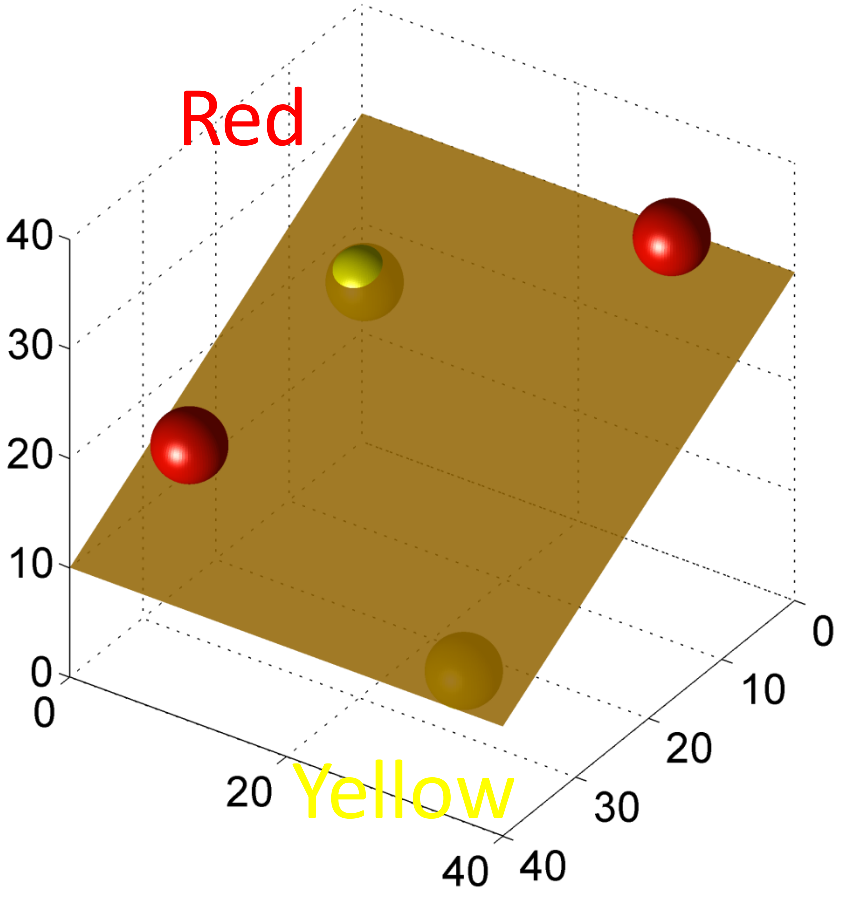
Low dimensional with noise may look high dimensional

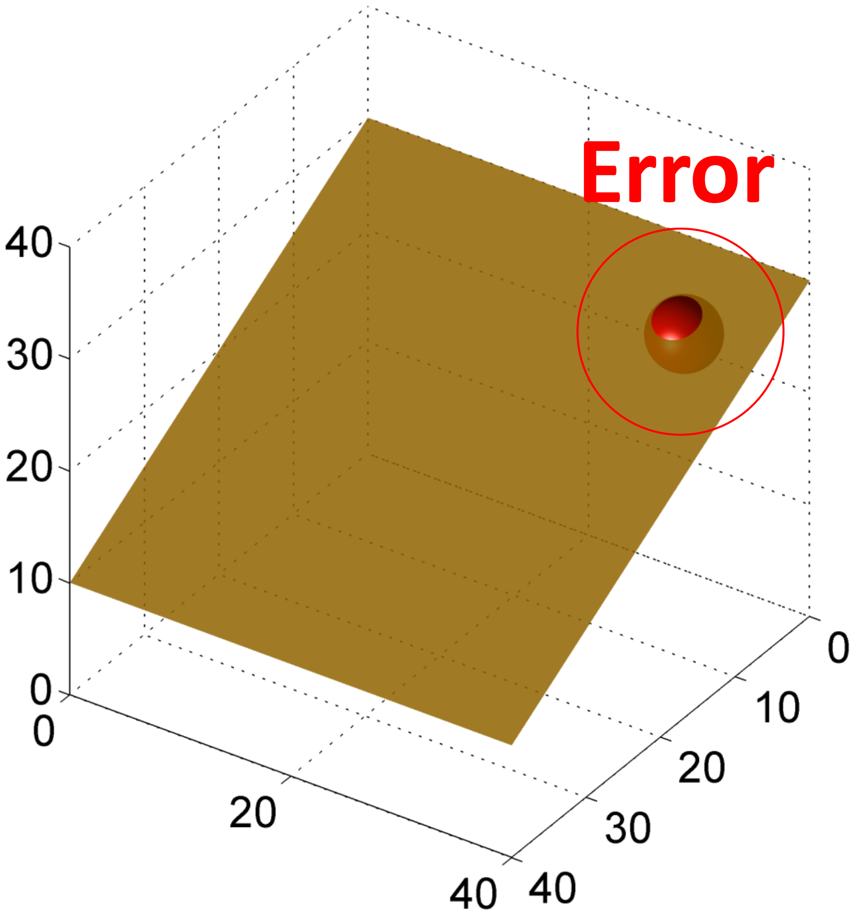


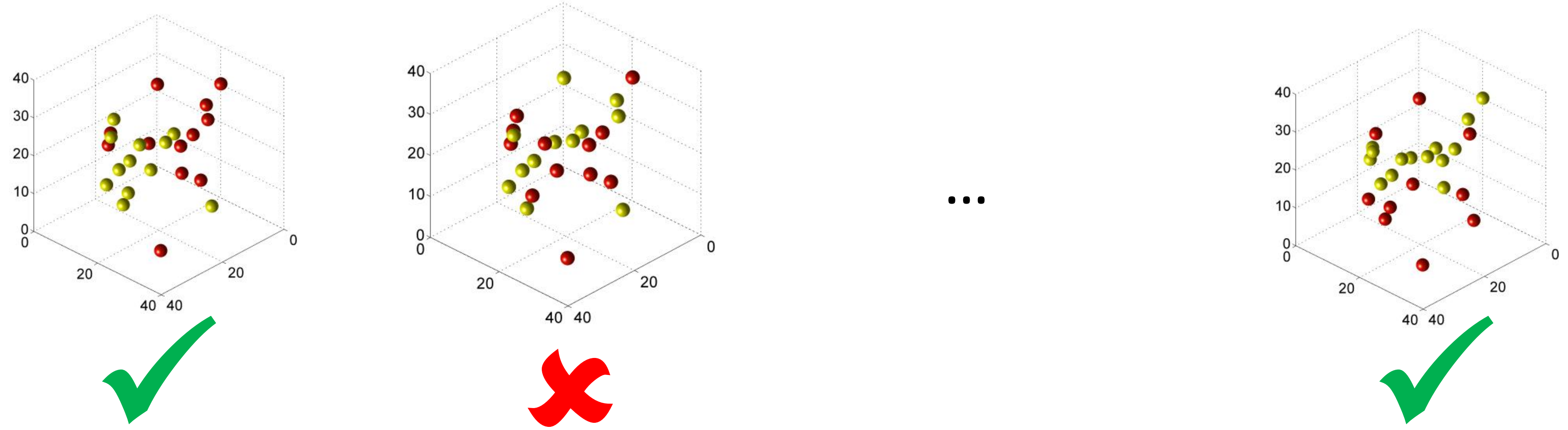
Low dimensional with noise may look high dimensional



Low dimensional with noise may look high dimensional





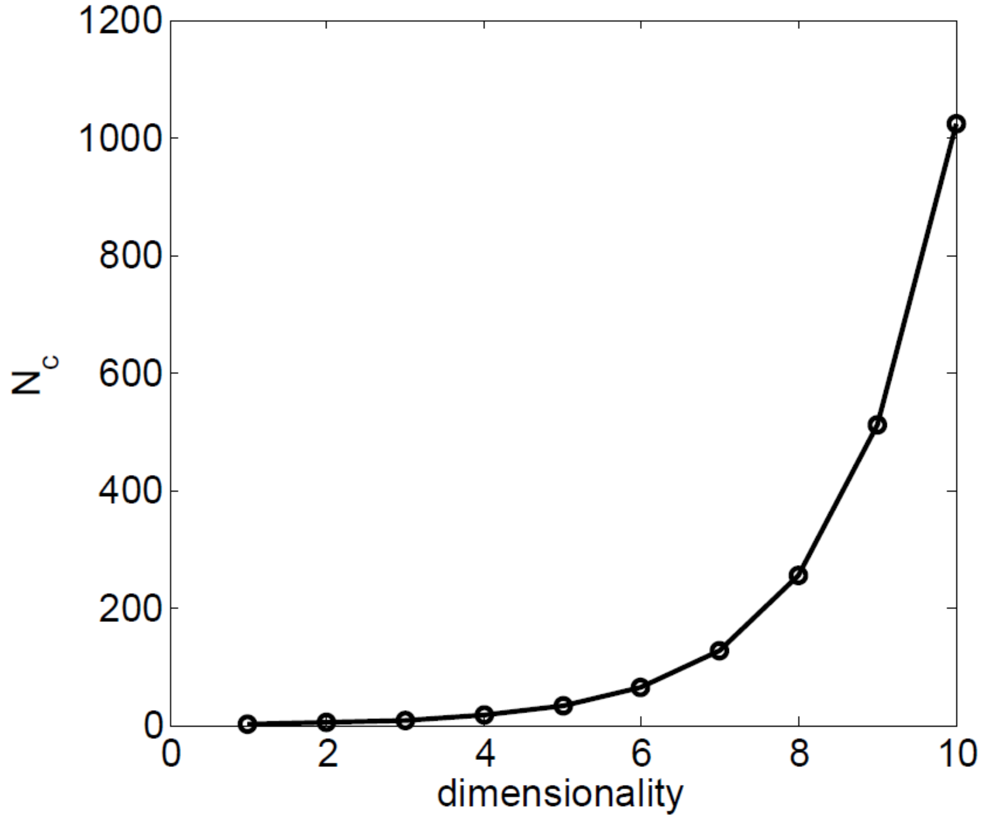


N_c = Number of binary classifications that are implementable by a simple linear readout

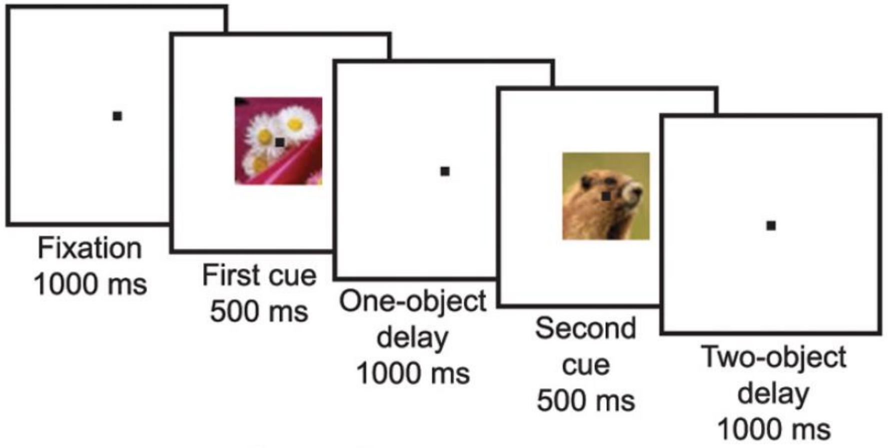
Implementable

⇔

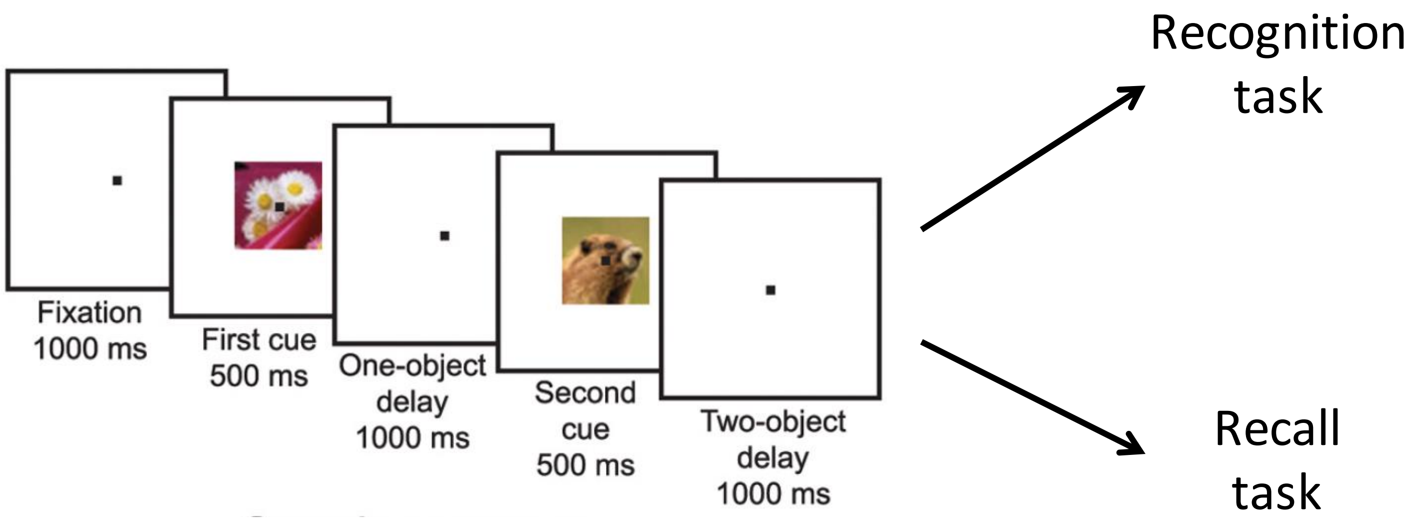
Cross Validated Performance> θ



Neural representations in PFC

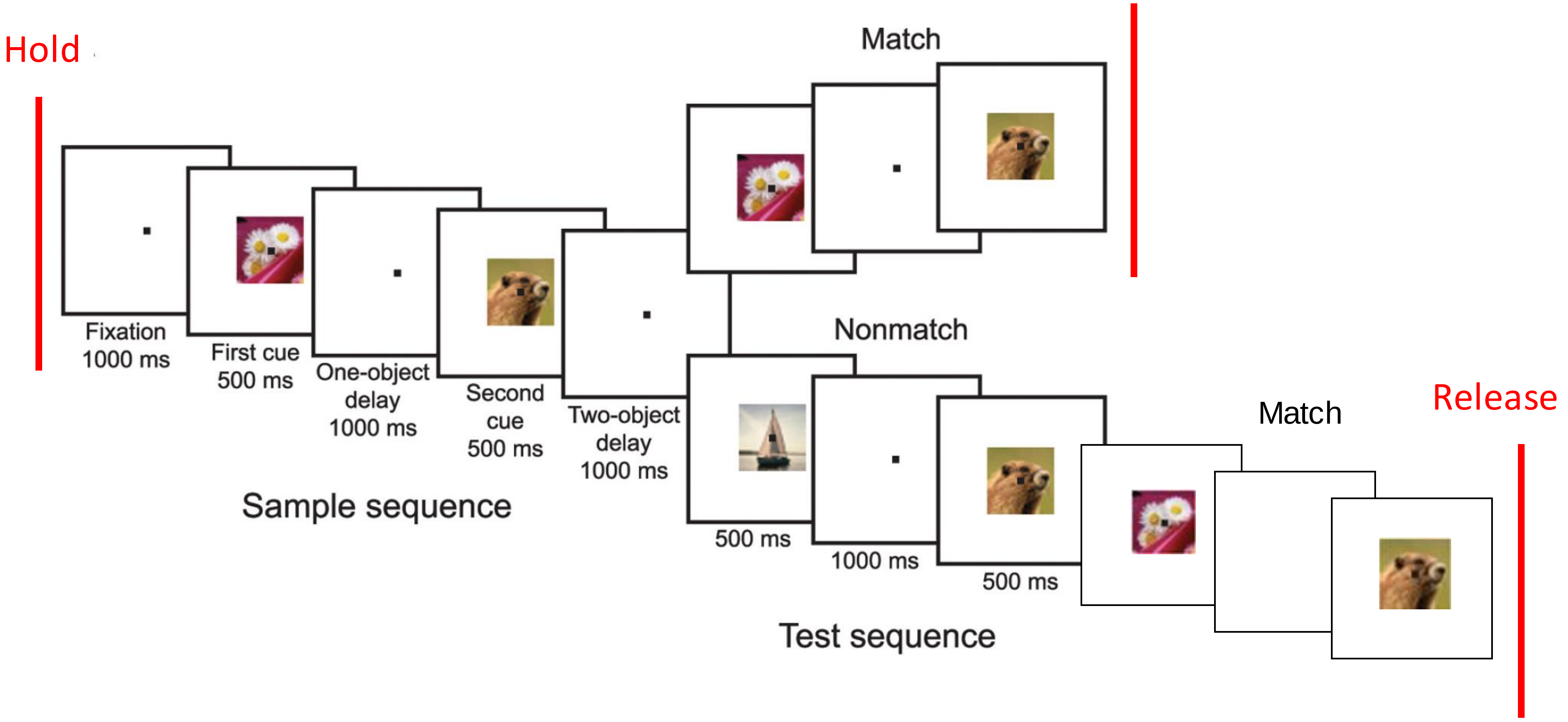


Warden, M.R. and Miller, E.K. (2010) *Journal of Neuroscience,* 30(47):15801-15810.

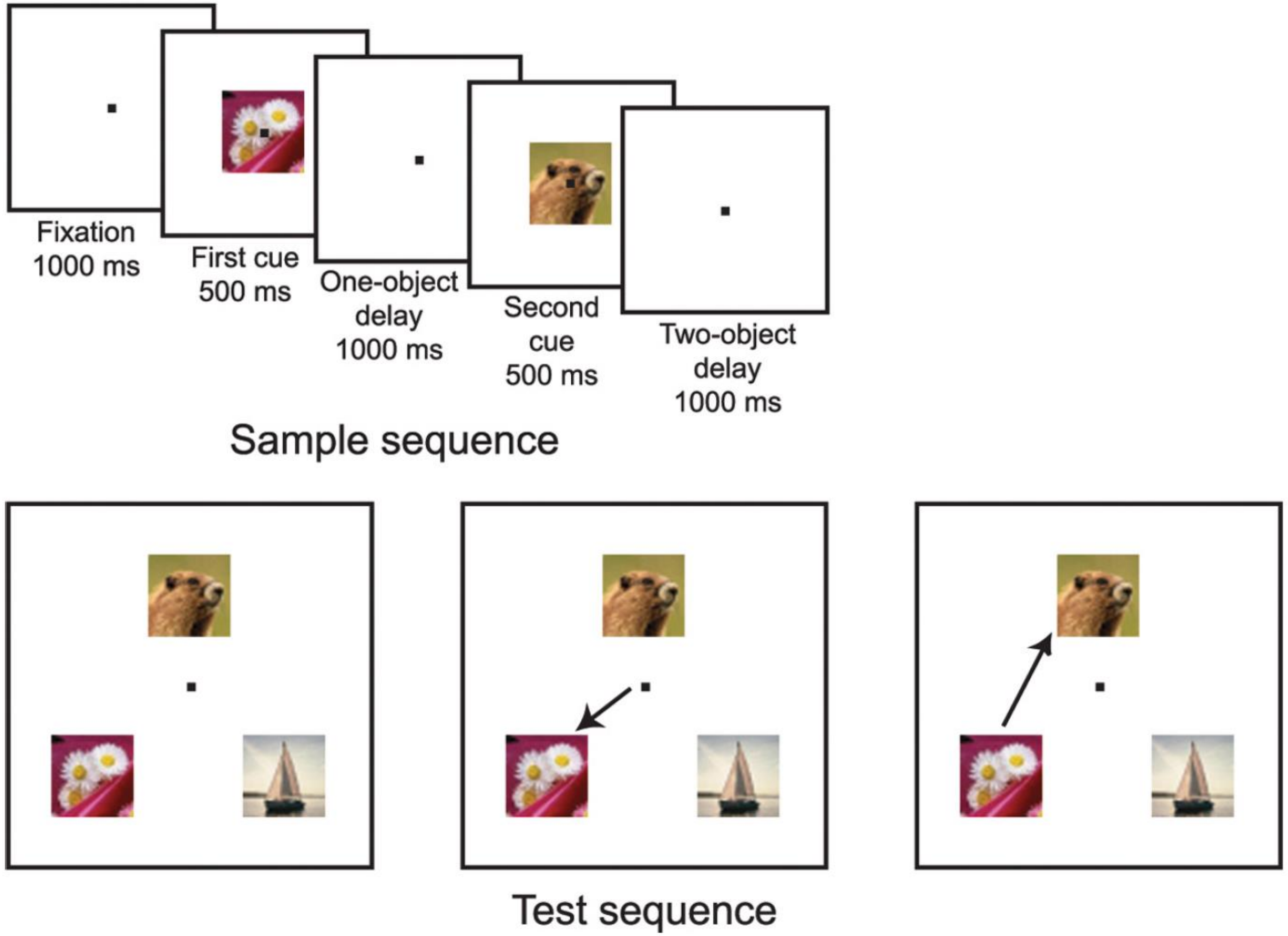


Warden, M.R. and Miller, E.K. (2010) *Journal of Neuroscience,* 30(47):15801-15810.

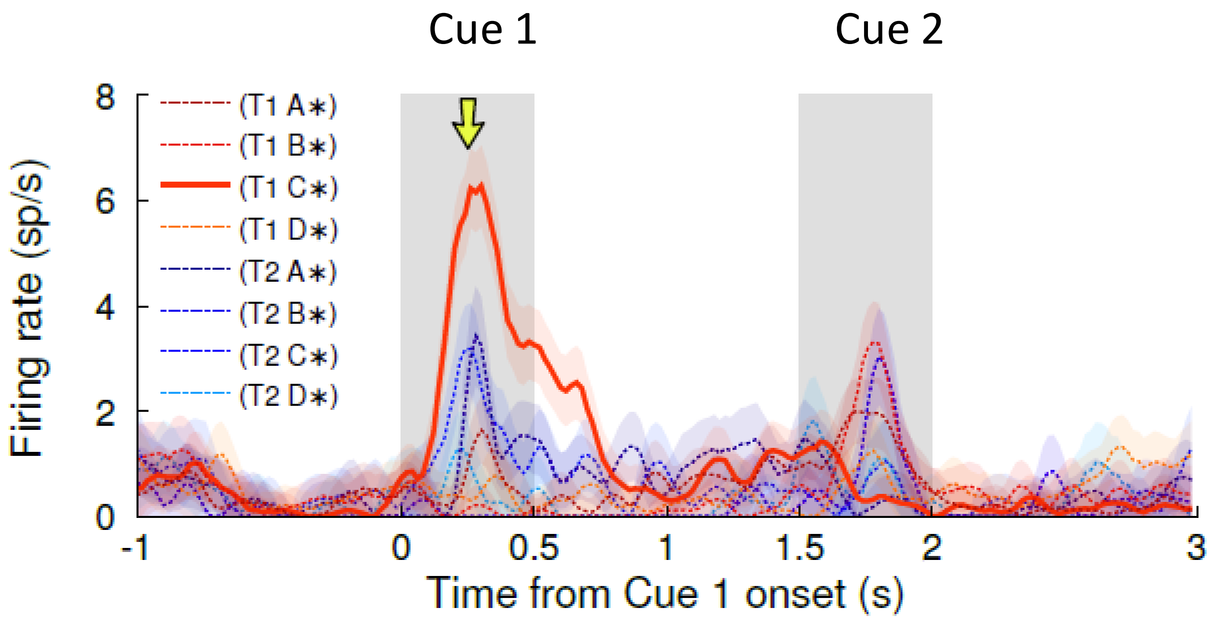
Recognition Task

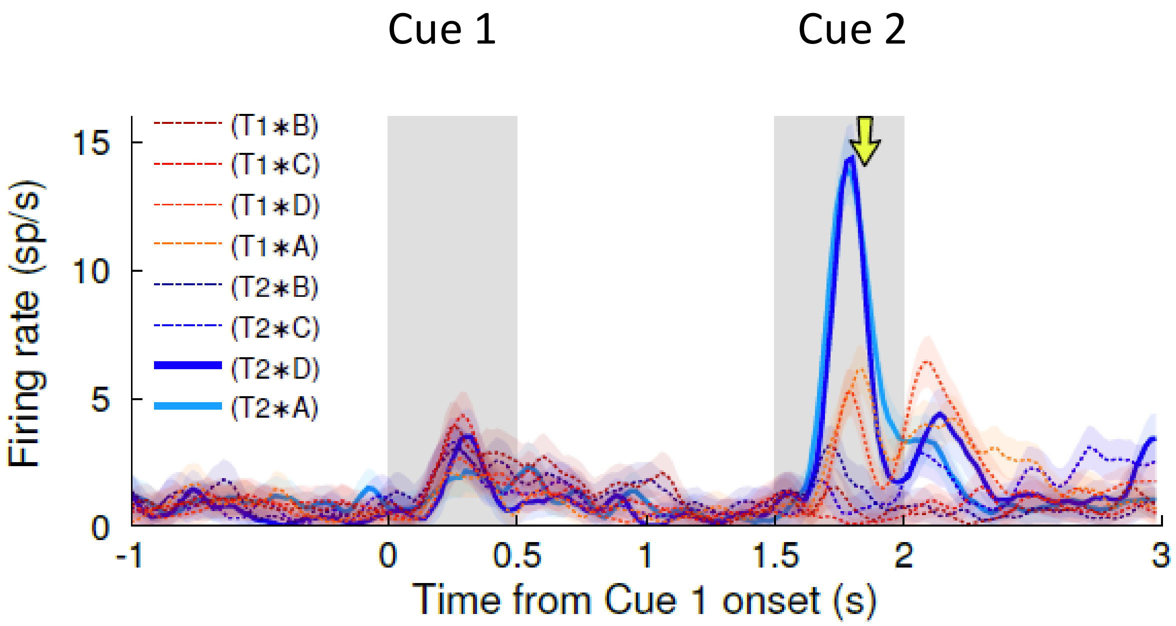


Recall Task

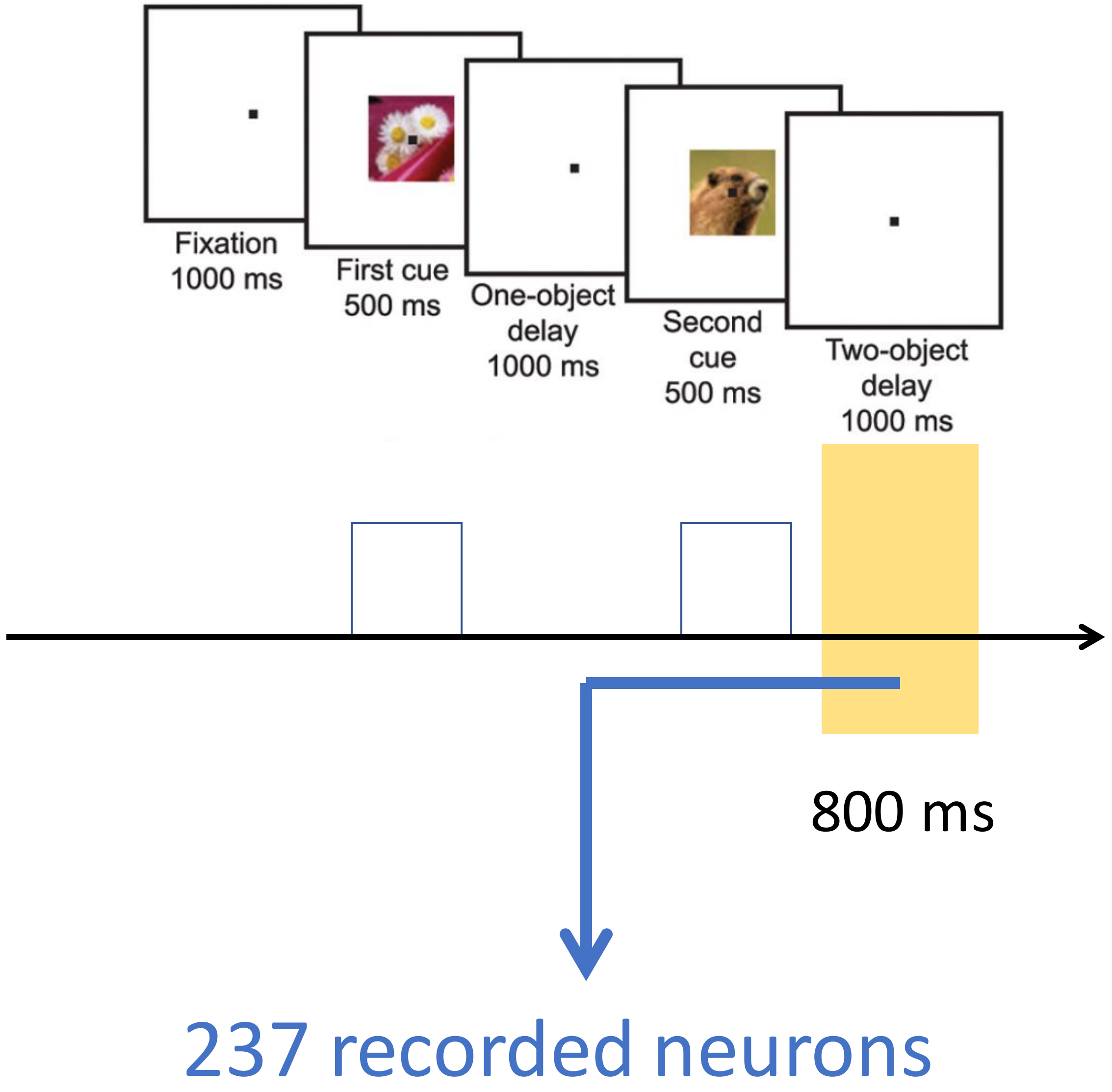

Fixation
1000 ms
First cue
500 ms
One-object
delay
1000 ms
Second
cue
500 ms
Two-object
delay
1000 ms
Sample sequence
Test sequence

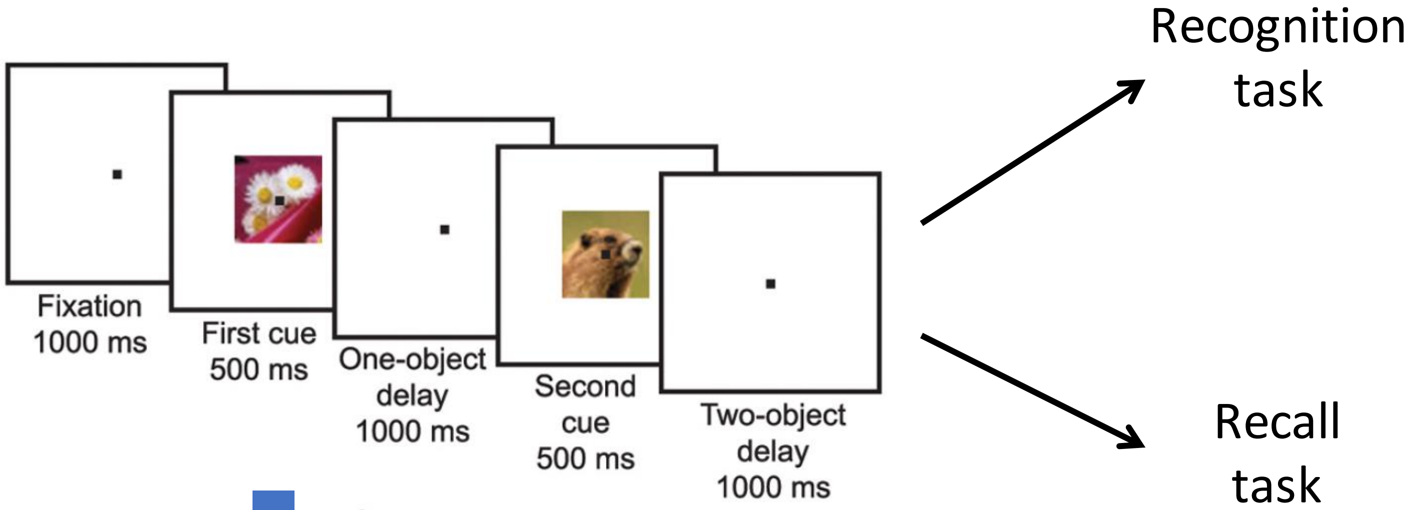
Mixed selectivity neurons





Cue 1
Cue 2
(T1∗B)
(T1∗C)
(T1∗D)
(T1∗A)
(T2∗B)
(T2∗C)
(T2∗D)
(T2∗A)
Firing rate (sp/s)
15
10
5
0
-1
0
0.5
1
1.5
2
3
Time from Cue 1 onset (s)


Fixation
1000 ms
First cue
500 ms
One-object
delay
1000 ms
Second
cue
500 ms
Two-object
delay
1000 ms
800 ms
237 recorded neurons



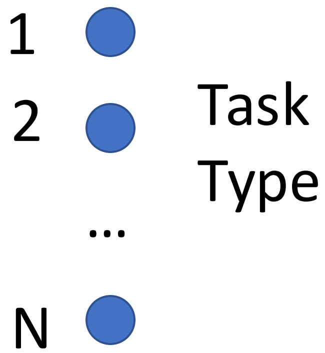
Cue 1 identity
4 visual objects

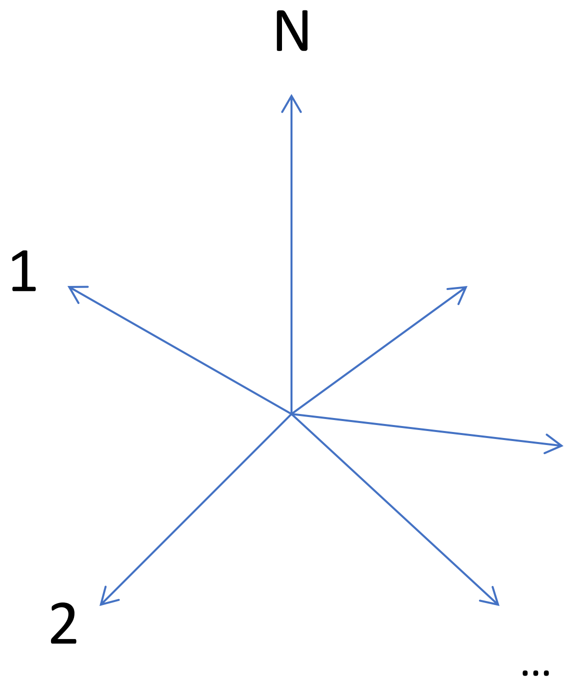
Cue 2 identity
3 visual objects

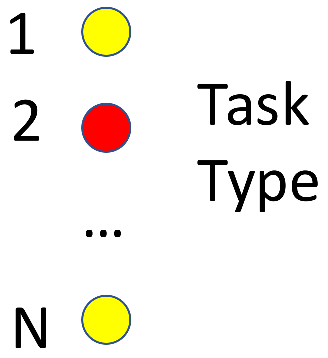
Task Type
2 tasks

4x3x2 = 24 conditions (max dimensionality)

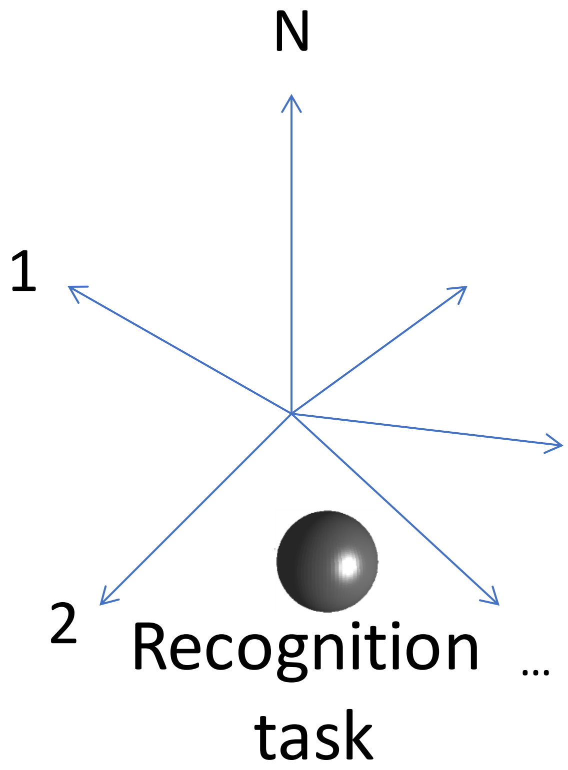
dimensionality in the case of pure selectivity neurons


1
2
…
N
Task
Type

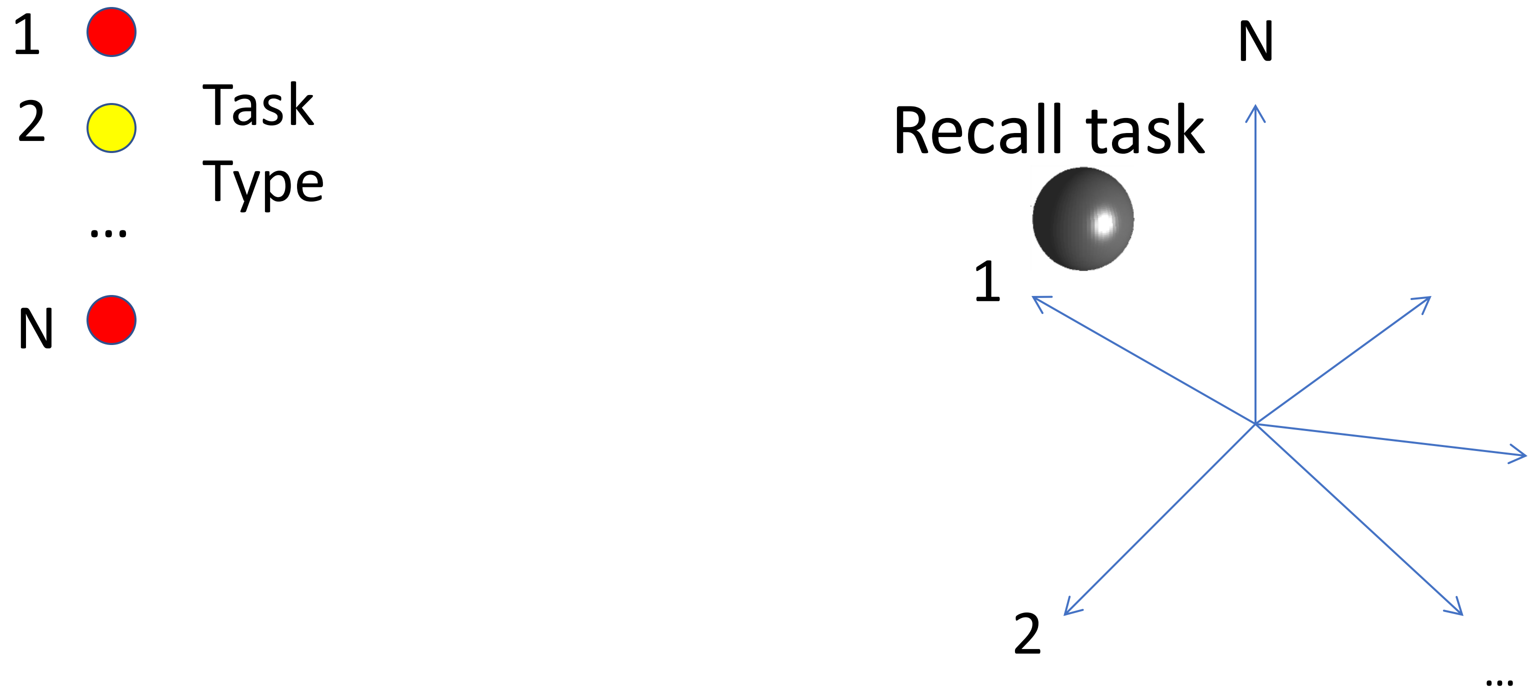

N
1
2
…

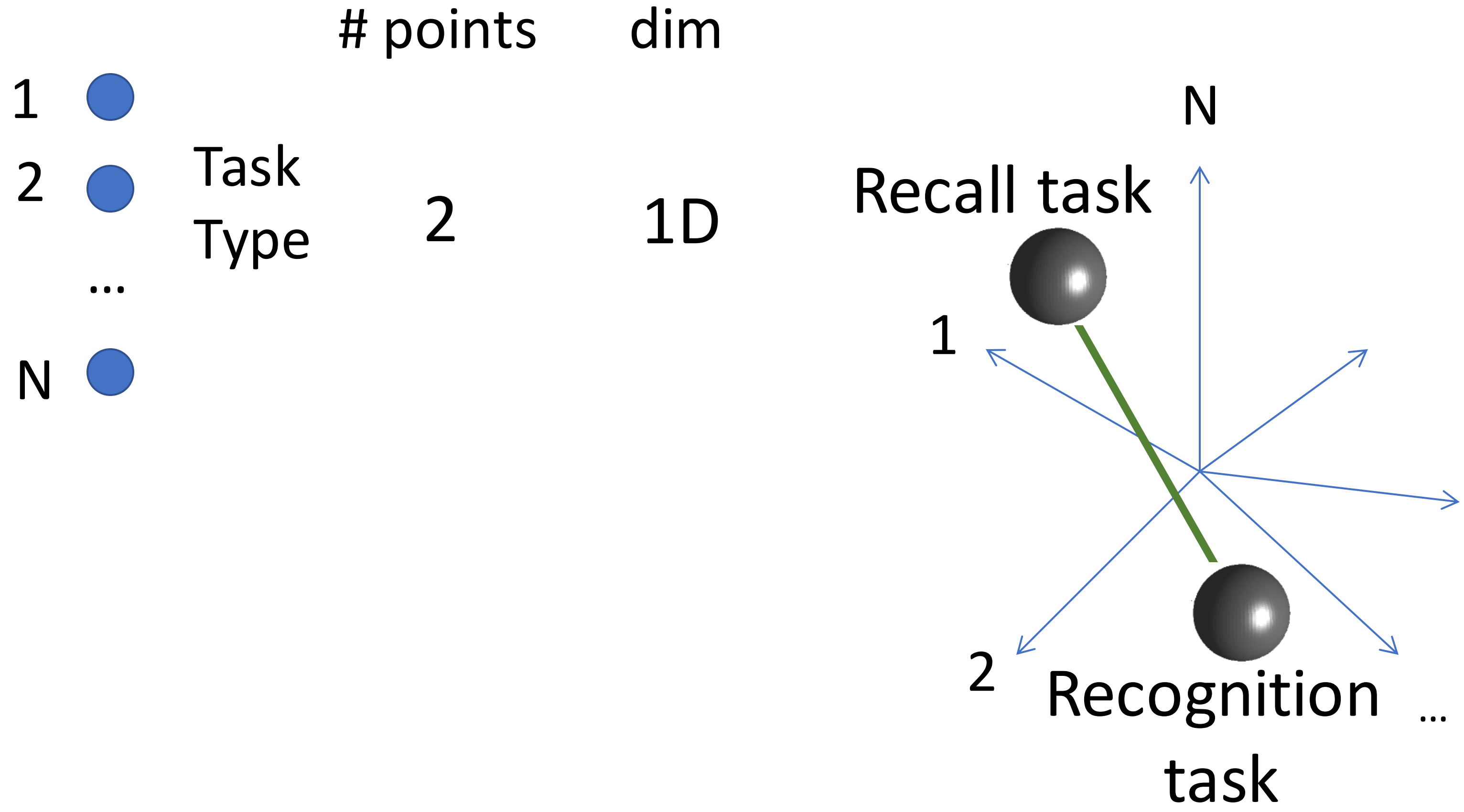


1
2
...
N
Task
Type



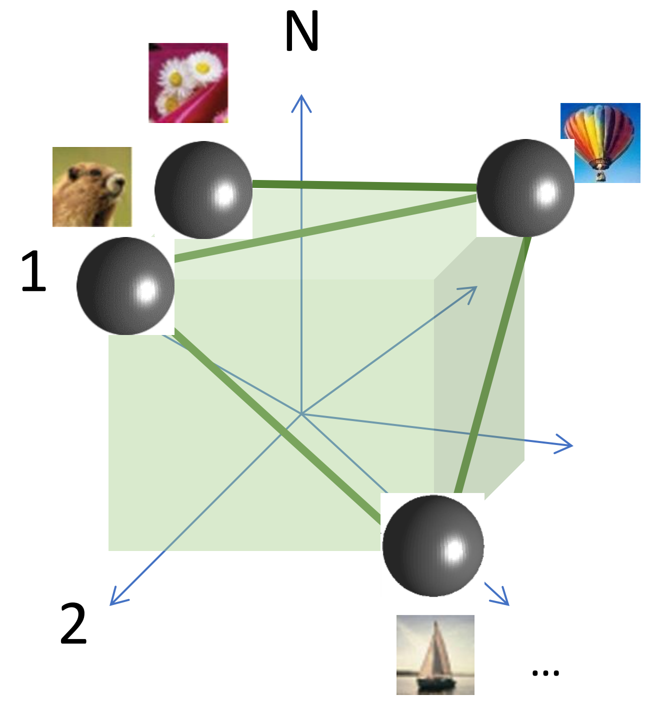
N
1
2
...
Recognition
task


1
2
...
N
Task
Type
N
Recall task
1
2
...

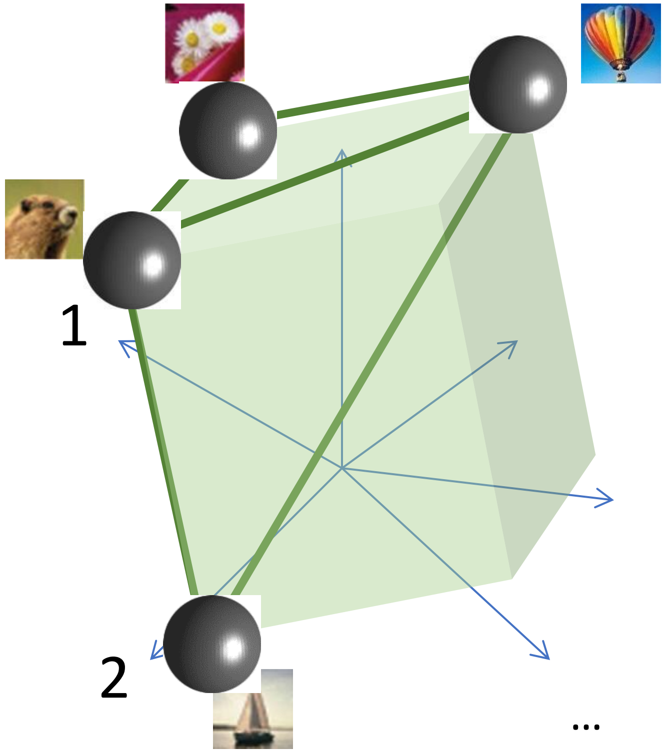


points
dim
1
2
...
N
Task
Type
2
1D
N
Recall task
1
2
Recognition
task
...

			# points	dim
1 2 N	● ● … ●	Task Type	2	1D
1 2 N	● ● … ●	Cue1	4	3D



	# points	dim
Task Type	2	1D
Cue1	4	3D
Cue2	4	3D



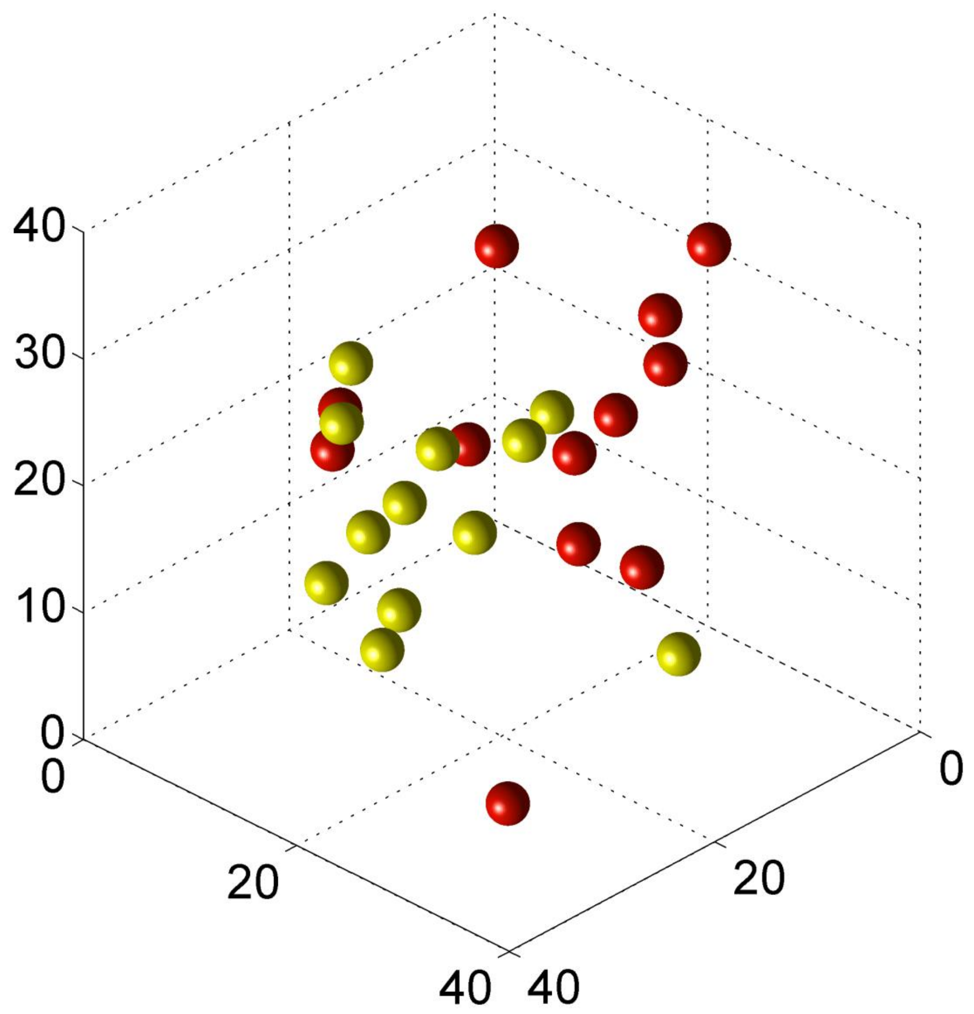
		# points	dim
Task Type	1 2 … N	2	1D
Cue1	1 2 … N	4	3D
Cue2	1 2 … N	4	3D

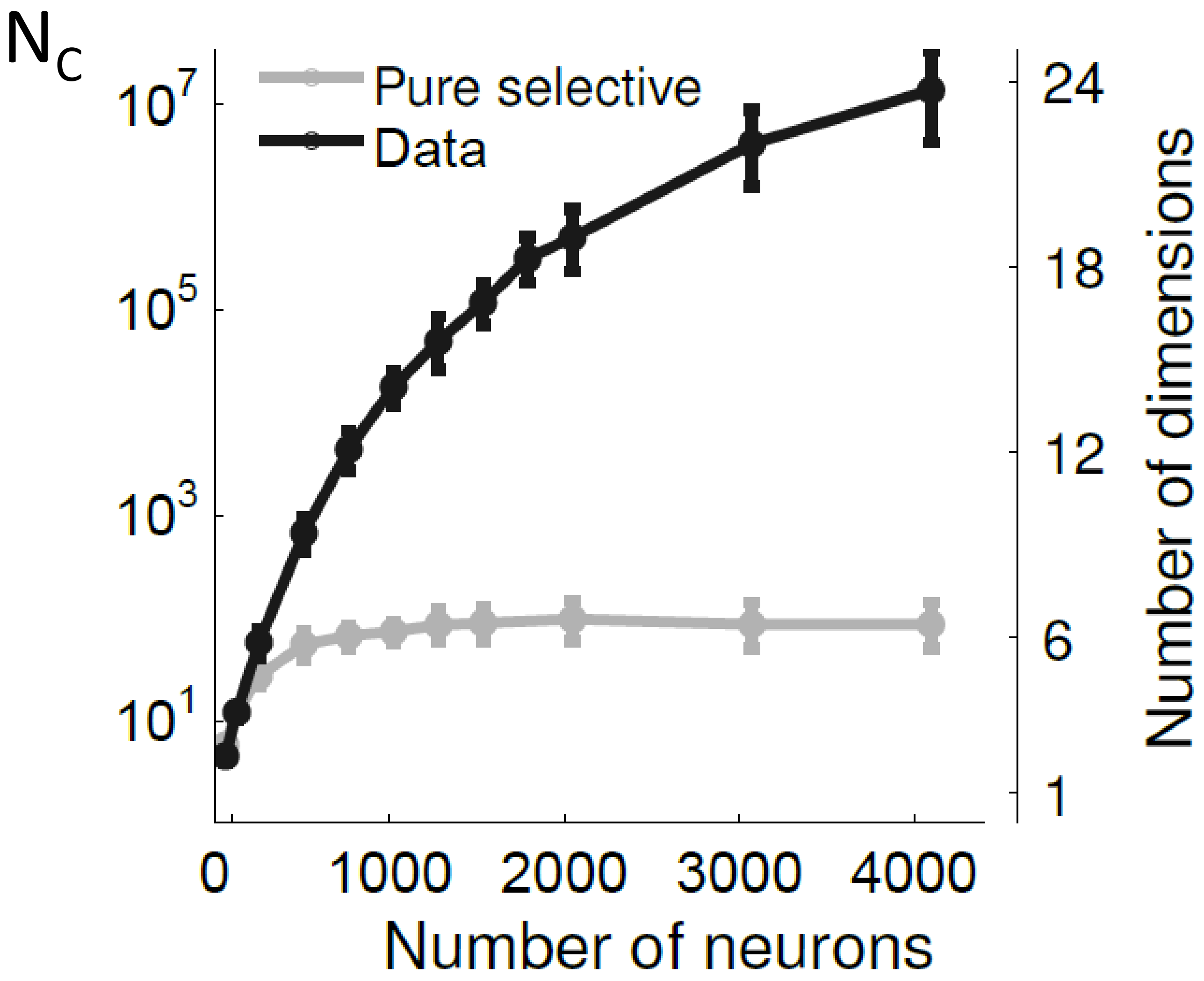
# of conditions = 24

dim = 1+3+3+1 = 8

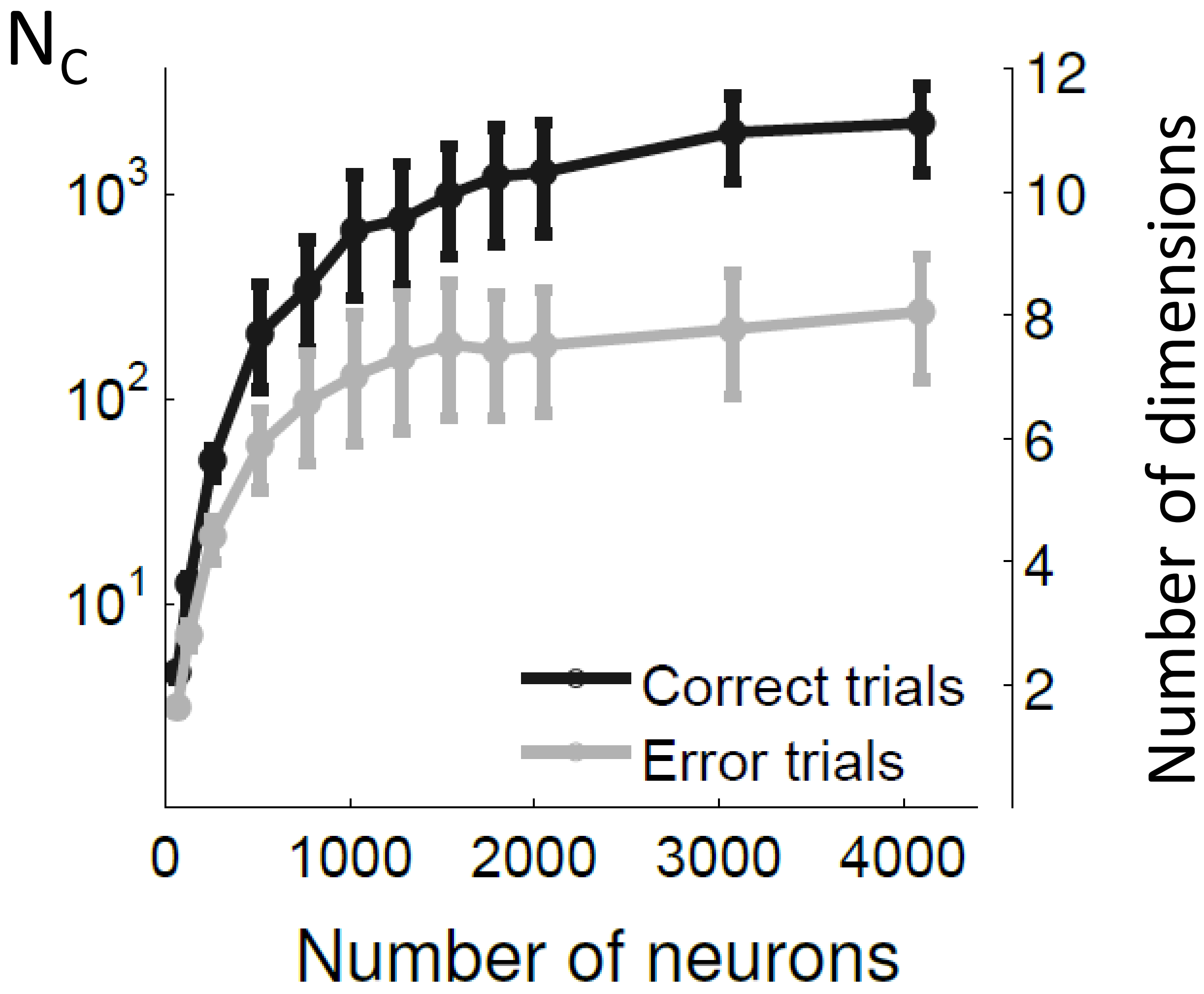
N= 237 (number of axes), p = 24

$2^{24} \approx 17 \times 10^6$ Possible binary classifications (colorings)



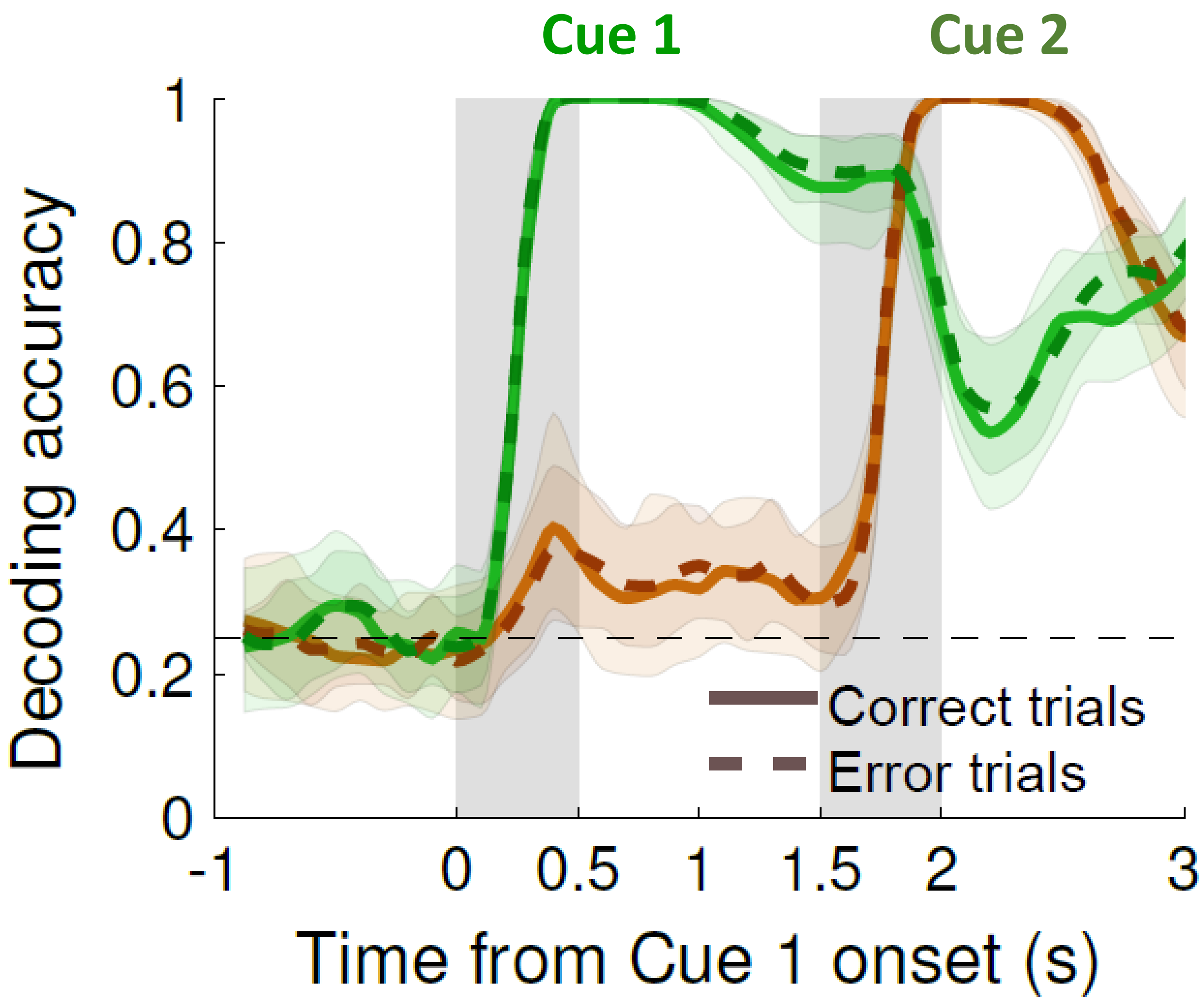


Rigotti, Barak, Warden, Wang, Daw, Miller, Fusi, *Nature* 2013



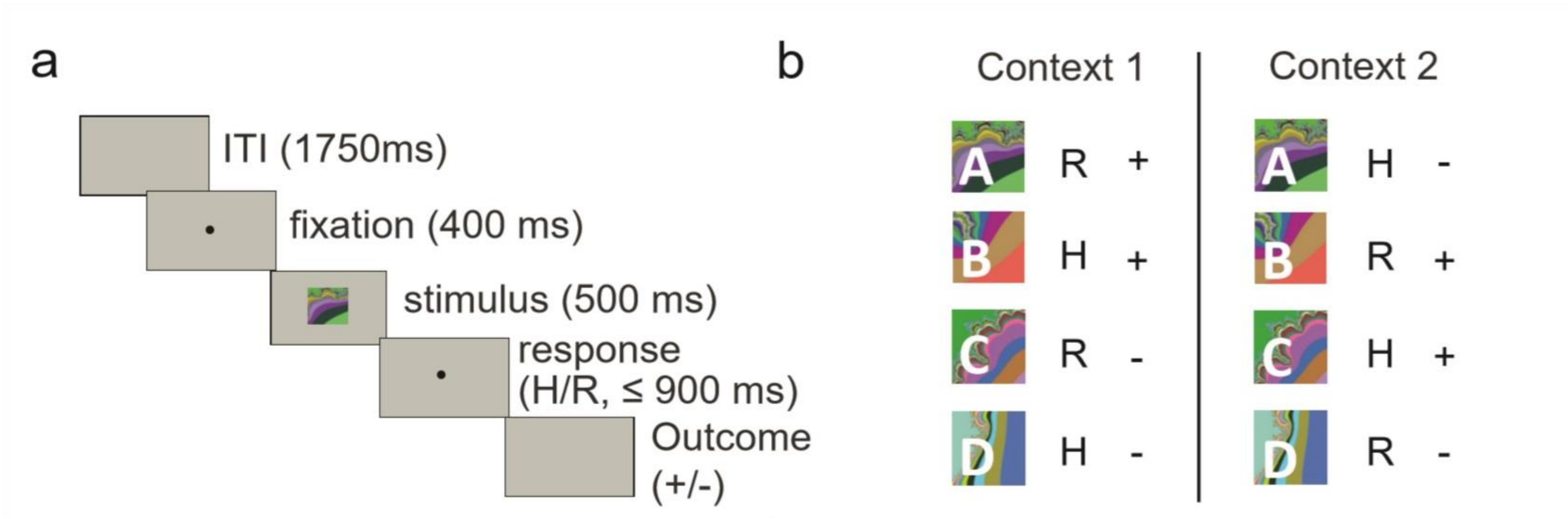
Rigotti, Barak, Warden, Wang, Daw, Miller, Fusi, *Nature* 2013

Decoding Cue 1 and Cue 2 in the error trials

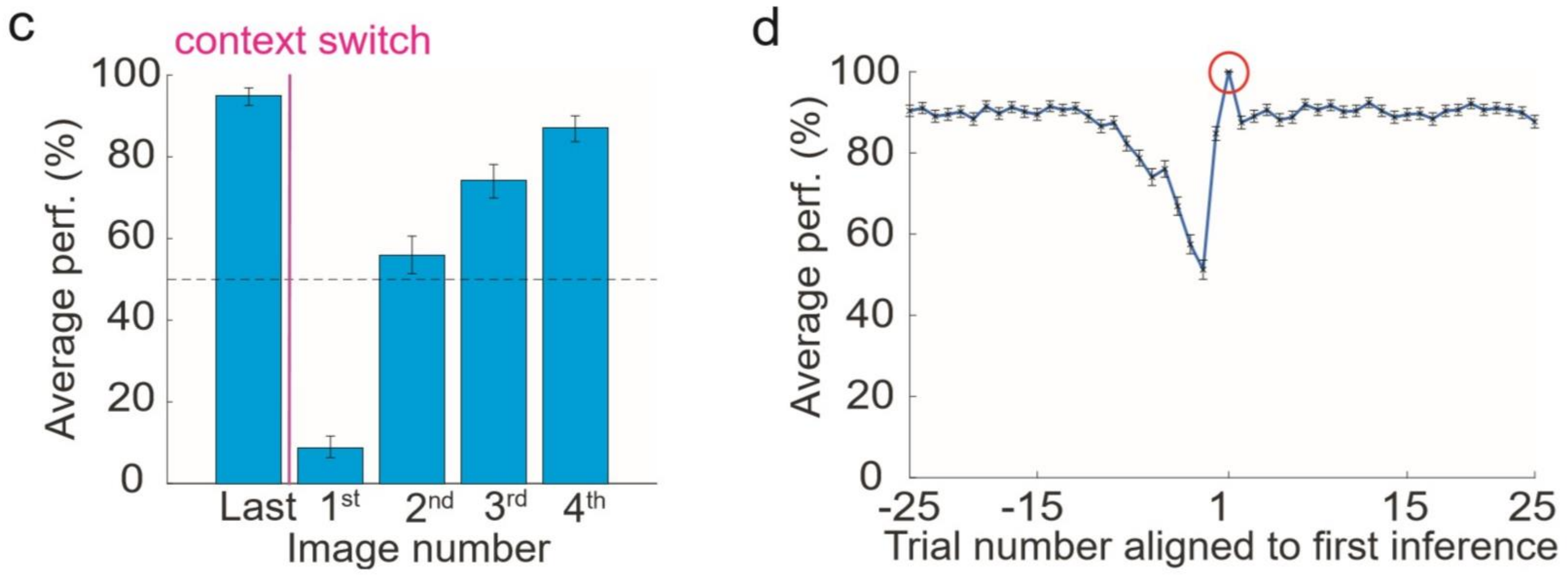


What is the same in correct and error trials

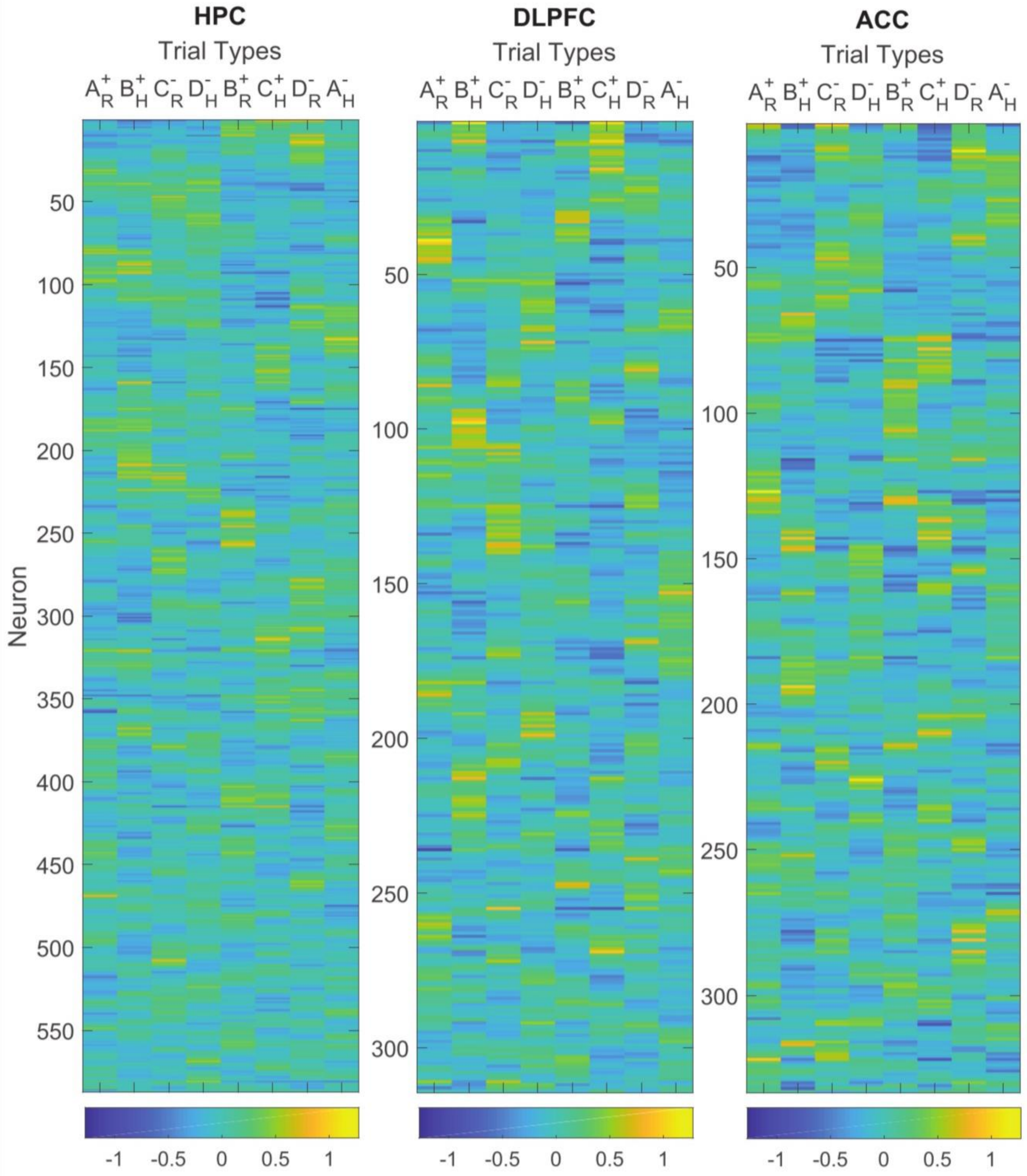
- Same decoding accuracy
- Same number of trials
- Same average firing rate
- Same distribution of firing rates
- Same coding level



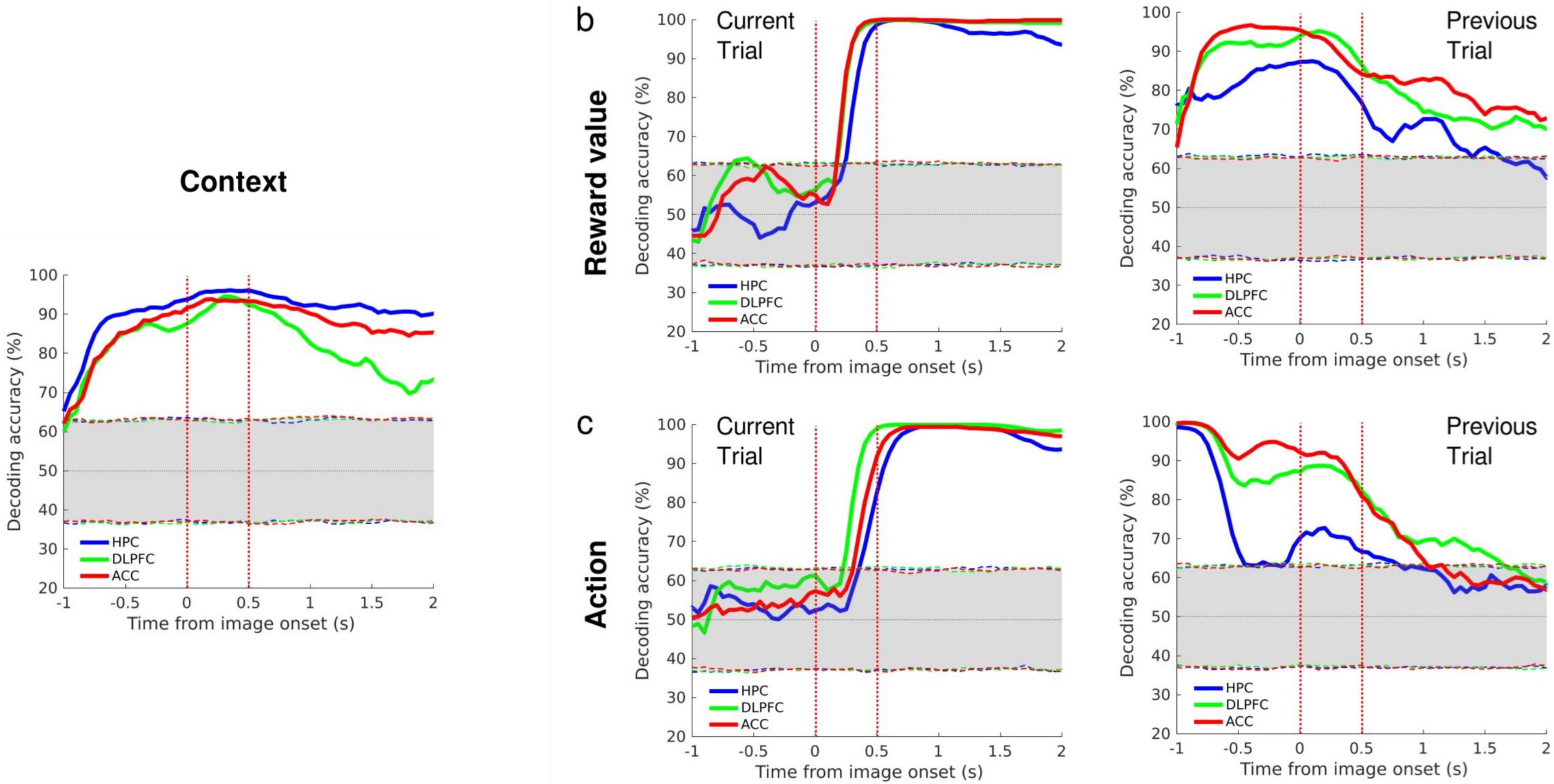
Bernardi, Silvia, et al. "The geometry of abstraction in hippocampus and prefrontal cortex." *bioRxiv* (2018): 408633.



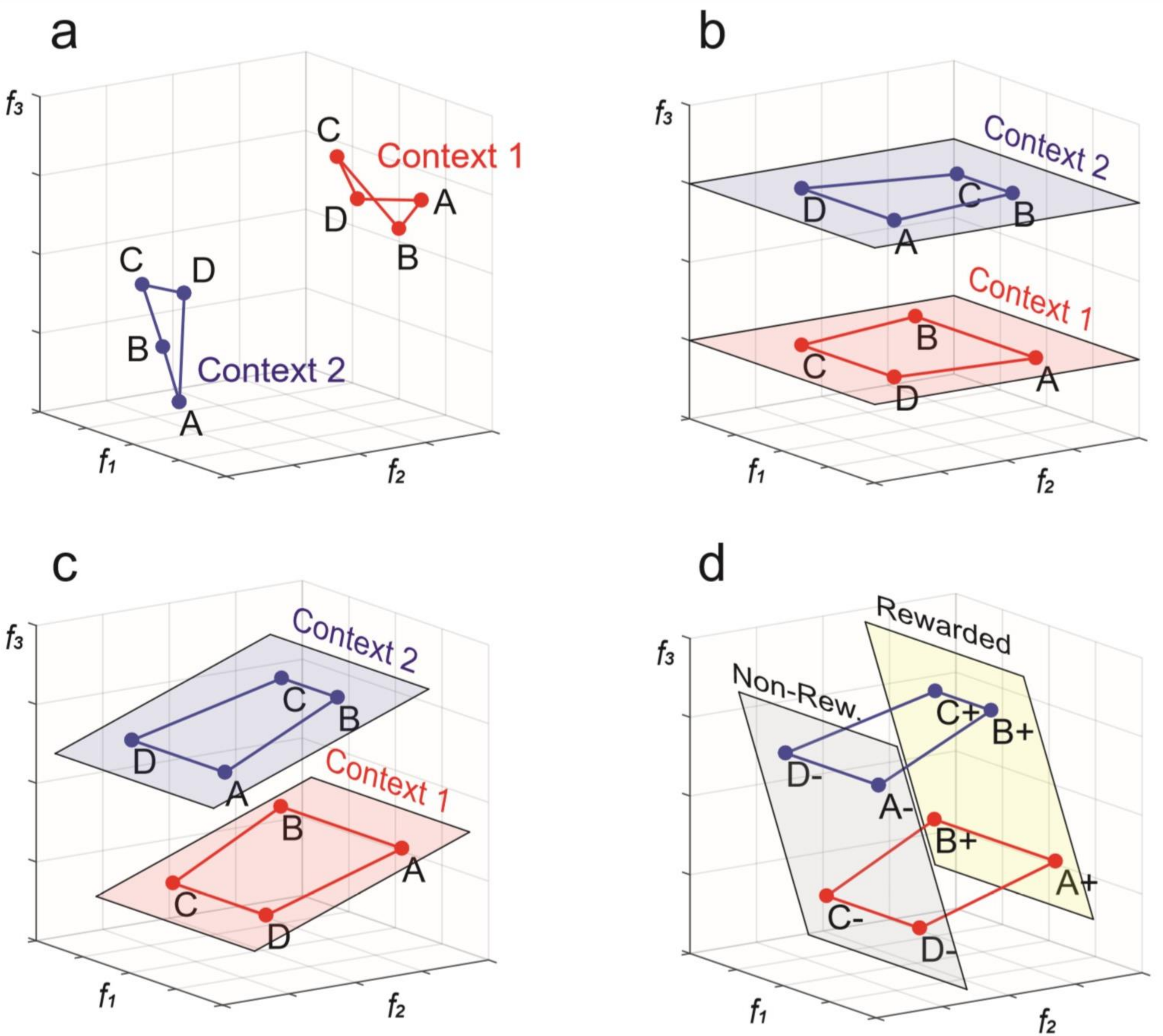
c
context switch
Average perf. (%)
100
80
60
40
20
0
Last
1st
2nd
3rd
4th
Image number
d
Average perf. (%)
100
80
60
40
20
0
-25
-15
1
15
25
Trial number aligned to first inference



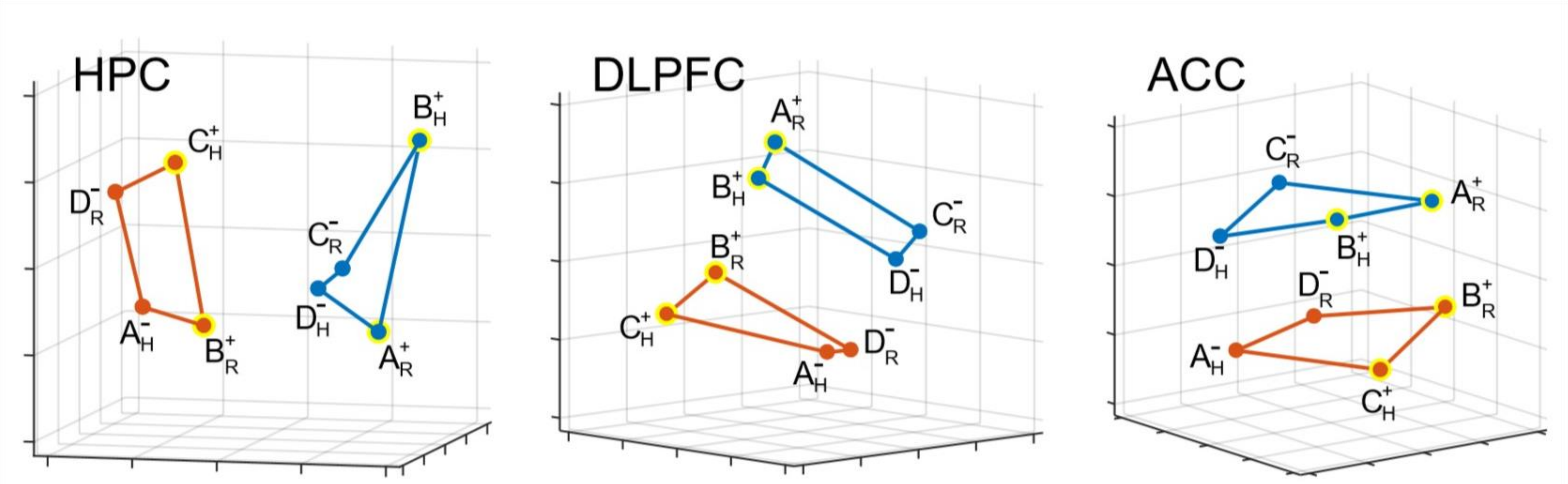
HPC
DLPFC
ACC
Trial Types
A^+_R B^+_H C^-_R D^-_H B^+_R C^+_H D^-_R A^-_H
Neuron
50
100
150
200
250
300
350
400
450
500
550
-1
-0.5
0
0.5
1



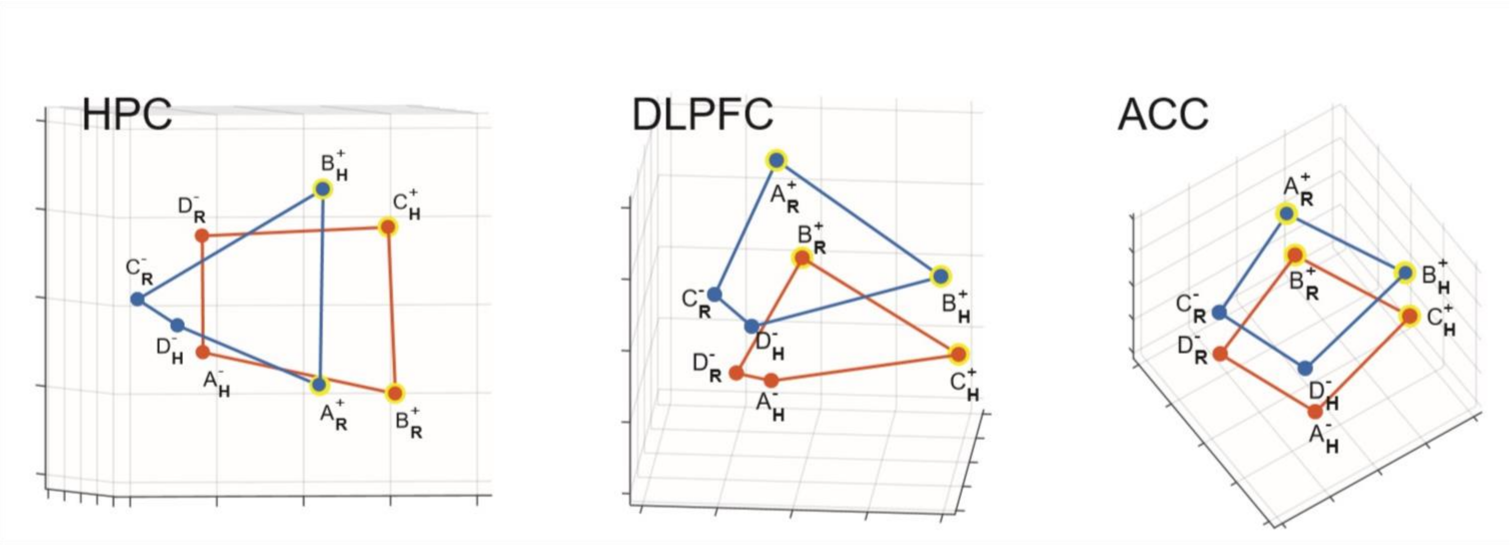
Context
b
Reward value
c
Action
Current Trial
Previous Trial
Decoding accuracy (%)
Time from image onset (s)
HPC
DLPFC
ACC

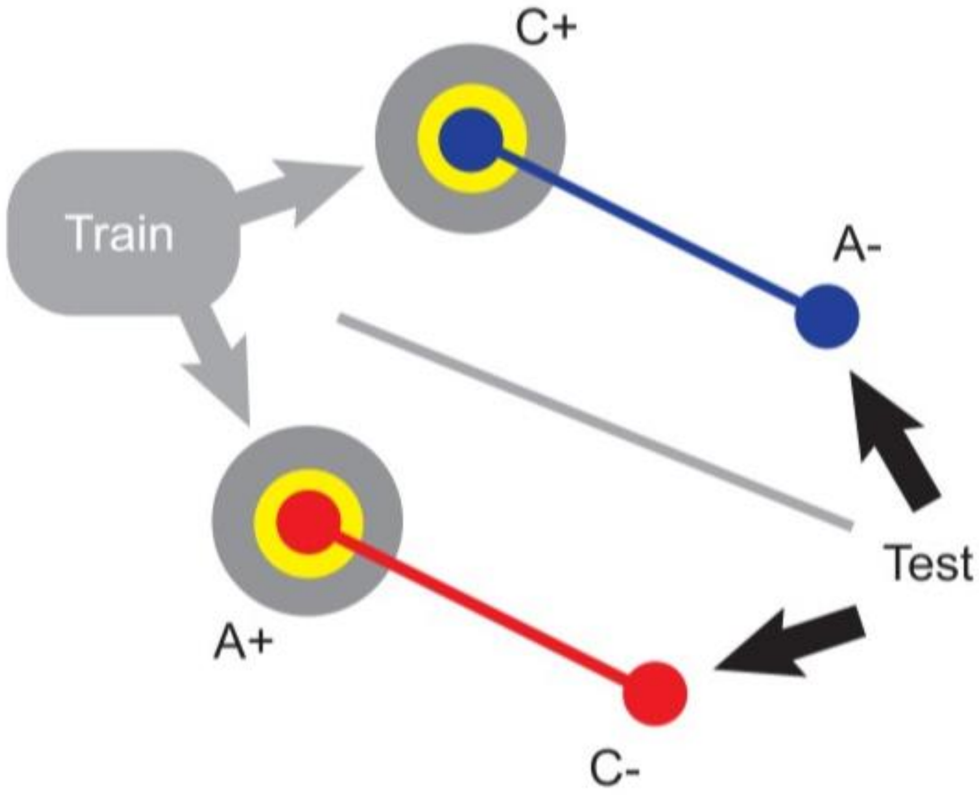


a
b
c
d
Context 1
Context 2
Rewarded
Non-Rew.
A
B
C
D
A+
B+
C+
A-
C-
D-
f_1
f_2
f_3

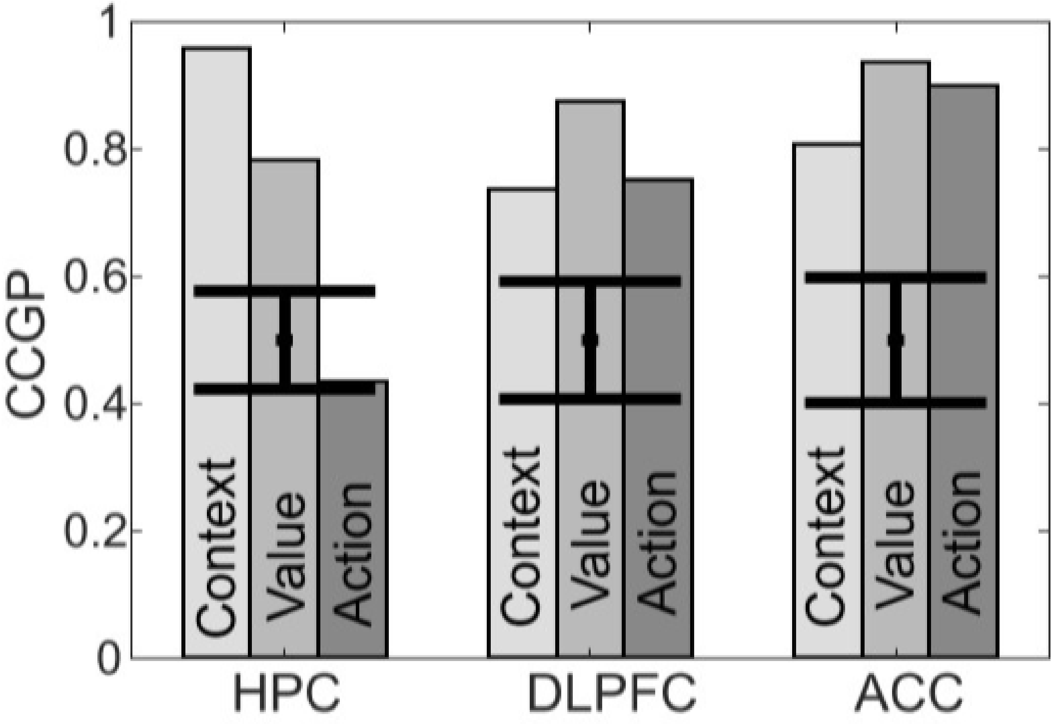


HPC
DLPFC
ACC


HPC
B^{+}_{H}
D^{-}_{R}
C^{+}_{H}
C^{-}_{R}
D^{-}_{H}
A^{-}_{H}
A^{+}_{R}
B^{+}_{R}
DLPFC
A^{+}_{R}
B^{+}_{R}
C^{-}_{R}
B^{+}_{H}
D^{-}_{H}
D^{-}_{R}
A^{-}_{H}
C^{+}_{H}
ACC
A^{+}_{R}
B^{+}_{R}
B^{+}_{H}
C^{-}_{R}
C^{+}_{H}
D^{-}_{R}
D^{-}_{H}
A^{-}_{H}


C+
Train
A-
Test
A+
C-

C


1
0.8
0.6
0.4
0.2
0
CCGP
Context
Value
Action
Context
Value
Action
Context
Value
Action
HPC
DLPFC
ACC

Summary

- Neuron tuning as variable encoding
- Statistical approaches to decode single variables from single neurons and neural populations
- The role of untuned neurons
- The geometry of neural representations in high dimensional spaces

Exercise

Generate neural data in the space of N hypothetical neurons and analyze their geometry as follows.

Choose P conditions in the space of neural representations according to an abstract or random scheme of high or low dimensionality. Each of those represent a certain combination of T task variables. Finally, embed the neural representations in the space of neurons by rotating them with a unitary matrix PxN. Generate M datapoints for each condition (i.e., trials). Use decoding strategies to analyze the dimensionality and the geometry of the neural representations.

You can use scikit-learn on the publicly available jupyter notebook server at https://129.236.163.8:1818 Password: \`neur0theory\`

or install it with Anaconda from www.anaconda.com