NEURAL REPRESENTATIONS OF UNCERTAINTY the sampling hypothesis

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contrast / brightness



contrast / brightness



contrast / brightness



 $3D \rightarrow 2D$ projection



contrast / brightness



 $3D \rightarrow 2D$ projection



contrast / brightness



$3D \rightarrow 2D$ projection



multiple interpretations: bistability



contrast / brightness



$3D \rightarrow 2D$ projection



multiple interpretations: bistability



aperture problem: incomplete information



contrast / brightness



$3D \rightarrow 2D$ projection



multiple interpretations: bistability

aperture problem: incomplete information







probability distribution



probability distribution



spatio-temporal neural activity patterns

 $\mathbf{r}(t,\mathbf{x})$





probability distribution



spatio-temporal neural activity patterns

 $\mathbf{r}(t,\mathbf{x})$





probability distribution







 $\mathbf{r}(t,\mathbf{x})$







4

Ν

W_{N4}

 \mathbf{X}





 \mathbf{X}

PERCEPTUAL UNCERTAINTY ↔ NEURAL VARIABILITY

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stimulus





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feature #2 intensity

feature #1 intensity



Fiser et al, TICS 2010

see also:

Hinton & Sejnowski, PDP 1986; Hinton et al, Science 1995; Dayan 1999; Hoyer & Hyvarinen, NIPS 2003, Lee & Mumford 2003



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Hoyer & Hyvärinen, NIPS 2003

Poisson-like variability (sparse coding)



Hoyer & Hyvärinen, NIPS 2003

Poisson-like variability (sparse coding)



Lee & Mumford, J Opt Soc Am A 2003

feed-back effects percept-coding neurons



Hoyer & Hyvärinen, NIPS 2003

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Berkes et al, Science 2011

average evoked = spontaneous response distributions



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Haefner et al, Neuron 2016 task-dependent changes in (co)variability



Hoyer & Hyvärinen, NIPS 2003

Poisson-like variability (sparse coding)



Lee & Mumford, J Opt Soc Am A 2003

feed-back effects percept-coding neurons



Orbán et al, Neuron 2016 stimulus-dependent changes in (co)variability

sponaneous

30

90



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Berkes et al, Science 2011

Haefner et al, Neuron 2016

task-dependent changes in (co)variability

see talks tomorrow by



Gergő Orbán



Ruben Coen-Cagli



Ralf Haefner

see talks tomorrow by



SYNAPTIC RESPONSE DISTRIBUTIONS ("synaptic sampling")
NEURAL RESPONSE DISTRIBUTIONS

see talks tomorrow by



SYNAPTIC RESPONSE DISTRIBUTIONS ("synaptic sampling")

Aitchison & Latham, arXiv 2015 plasticity \propto variability



NEURAL RESPONSE DISTRIBUTIONS

see talks tomorrow by



SYNAPTIC RESPONSE DISTRIBUTIONS ("synaptic sampling")

Aitchison & Latham, arXiv 2015 plasticity \propto variability



see talk later today by



David Kappel

Hinton & Sejnowski, PDP 1986 Hinton et al, Science 1995 Gibbs sampling by binary neurons



Hinton & Sejnowski, PDP 1986 Hinton et al, Science 1995 Gibbs sampling by binary neurons



Buesing et al, PLoS Comput Biol 2011

~Gibbs sampling by spiking neurons



Hinton & Sejnowski, PDP 1986 Hinton et al, Science 1995 Gibbs sampling by binary neurons



Buesing et al, PLoS Comput Biol 2011

~Gibbs sampling by spiking neurons



Hartmann et al, PLoS Comput Biol 2015

deterministic network



Hinton & Sejnowski, PDP 1986 Hinton et al, Science 1995 Gibbs sampling by binary neurons



Buesing et al, PLoS Comput Biol 2011

~Gibbs sampling by spiking neurons



Hartmann et al, PLoS Comput Biol 2015 Hennequin et al, NIPS 2014 PLOS Comput Biology Hennequin et al, NIPS 2014 deterministic net fast (Hamiltonian) sampling in E/I networks **Deterministic SORN** PLOS COMPUTATIONAL BIOLOGY autocorrelation 1.0А 0.5 \mathbf{W}_{vu} 0.0Н \mathbf{W}_{uv} 100 $\mathbf{0}$ t (ms)...DAHGJCJEDFHADIECBG... - Hamiltonian MSE (a.u.) ₅ Langevin $\mathbf{I}_{\mathrm{ext}}$ 0 2001000 $t \,(\mathrm{ms})$

NEURAL CIRCUIT DYNAMICS

see talks later today by



Guillaume Hennequin



Rodrigo Echeveste



Laurence Aitchison



Cristina Savin



Jean-Pascal Pfister





Vul & Pashler, Psych Sci 2008 Vul et al, Cog Sci 2014

idiosyncrasies in decision making



see talk tomorrow by



Adam Sanborn

















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neural responses **r** to stimuli y are variable: $P(\mathbf{r}|y) = \int P(\mathbf{r}|\mathbf{x}) P(\mathbf{x}|y) d\mathbf{x}$

y

 \mathbf{X}

neural responses **r** to stimuli *y* are variable: $P(\mathbf{r}|y) = \int P(\mathbf{r}|\mathbf{x}) P(\mathbf{x}|y) d\mathbf{x}$ decoding neural responses yields a distribution: $P(y|\mathbf{r}) \propto P(\mathbf{r}|y) P(y)$

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NEURAL ARITHMETICS

Aitchison & Lengyel, Curr Opin Neurobiol, in press

	sampling	mean-field	prob. pop. code
neurons represent	variables	parameters	parameters

	sampling	mean-field	prob. pop. code
neurons represent	variables	parameters	parameters
neurons / variable	1	1	many (~100–1000)

	sampling	mean-field	prob. pop. code	
neurons represent	variables	parameters	parameters	
neurons / variable	1	1	many (~100—1000)	too many?

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distributions are represented	by iterative sampling	by iterative dynamics / instantaneously	instantaneously	

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neurons represent	variables	parameters	parameters	
neurons / variable	1	1	many (~100–1000)	too many?
distributions are represented	by iterative sampling	by iterative 	instantaneously	too slow!?

	sampling	mean-field	prob. pop. code	
neurons represent	variables	parameters	parameters	
neurons / variable	1	1	many (~100—1000)	too many?
distributions are represented	by iterative sampling	by iterative 	instantaneously	too slow!?
inference of dynamical variables	?	\checkmark	\checkmark	

	sampling	mean-field	prob. pop. code	_
neurons represent	variables	parameters	parameters	-
neurons / variable	1	1	many (~100—1000)	too many?
distributions are represented	by iterative sampling	by iterative 	instantaneously	too slow!?
inference of dynamical variables	?	\checkmark	\checkmark	
correlations (limiting factor)	(time)	×	(neurons)	

	sampling	mean-field	prob. pop. code	
neurons represent	variables	parameters	parameters	
neurons / variable	1	1	many (~100—1000)	too many?
distributions are represented	by iterative sampling	by iterative 	instantaneously	too slow!?
inference of dynamical variables	?	\checkmark	\checkmark	
correlations (limiting factor)	(time)	×	(neurons)	
cue combination	\checkmark	\checkmark	\checkmark	
	sampling	mean-field	prob. pop. code	
-------------------------------------	--------------------------	---	------------------	------------
neurons represent	variables	parameters	parameters	
neurons / variable	1	1	many (~100—1000)	too many?
distributions are represented	by iterative sampling	by iterative dynamics / instantaneously	instantaneously	too slow!?
inference of dynamical variables	?	\checkmark	\checkmark	
correlations (limiting factor)	(time)	×	(neurons)	
cue combination	\checkmark	\checkmark	\checkmark	
marginalisation	\checkmark	\checkmark	√?	

	sampling	mean-field	prob. pop. code	_
neurons represent	variables	parameters	parameters	-
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cue combination	\checkmark	\checkmark	\checkmark	
marginalisation	\checkmark	\checkmark	√?	
dynamics	stochastic	deterministic	deterministic	

	sampling	mean-field	prob. pop. code	_
neurons represent	variables	parameters	parameters	-
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inference of dynamical variables	?	\checkmark	\checkmark	
correlations (limiting factor)	(time)	×	(neurons)	
cue combination	\checkmark	\checkmark	\checkmark	
marginalisation	\checkmark	\checkmark	√?	
dynamics	stochastic	<u>deterministic</u>	<u>deterministic</u>	robustness?

	sampling	mean-field	prob. pop. code	_
neurons represent	variables	parameters	parameters	
neurons / variable	1	1	many (~100–1000)	too many?
distributions are represented	by iterative sampling	by iterative 	by iterative dynamics / instantaneously stantaneously	
inference of dynamical variables	?	\checkmark	\checkmark	
correlations (limiting factor)	(time)	×	(neurons)	
cue combination	\checkmark	\checkmark	\checkmark	
marginalisation	\checkmark	\checkmark	√?	
dynamics	stochastic	<u>deterministic</u>	deterministic	robustness?
neural variability for computation	useful	harmful	harmful	

	sampling	mean-field	prob. pop. code	
neurons represent	variables	parameters	parameters	
neurons / variable	1	1	many (~100–1000)	too many?
distributions are represented	by iterative sampling	by iterative dynamics / instantaneously	by iterative dynamics / instantaneously istantaneously	
inference of dynamical variables	?	\checkmark	\checkmark	
correlations (limiting factor)	(time)	×	(neurons)	
cue combination	\checkmark	\checkmark	\checkmark	
marginalisation	\checkmark	\checkmark	√?	
dynamics	stochastic	<u>deterministic</u>	<u>deterministic</u>	robustness?
neural variability for computation	useful	harmful	harmful	
learning	\checkmark	√?	?	

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	sampling	mean-field	prob. pop. code
variability	\checkmark	×	\checkmark

	sampling	mean-field	prob. pop. code
variability	\checkmark	×	\checkmark
noise correlations	\checkmark	×	\checkmark

	sampling	mean-field	prob. pop. code
variability	\checkmark	×	\checkmark
noise correlations	\checkmark	×	\checkmark
stimulus-dependent variability & correlations	\checkmark	×	×

	sampling	mean-field	prob. pop. code
variability	\checkmark	×	\checkmark
noise correlations	\checkmark	×	\checkmark
stimulus-dependent variability & correlations	\checkmark	×	×
spontaneous activity	\checkmark	×	×

	sampling	mean-field	prob. pop. code
variability	\checkmark	×	\checkmark
noise correlations	\checkmark	×	\checkmark
stimulus-dependent variability & correlations	\checkmark	×	×
spontaneous activity	\checkmark	×	×
correlation of (signal, noise & spont) correlations	\checkmark	×	_

	sampling	mean-field	prob. pop. code
variability	~	×	\checkmark
noise correlations	\checkmark	×	\checkmark
stimulus-dependent variability & correlations	\checkmark	×	×
spontaneous activity	\checkmark	×	×
correlation of (signal, noise & spont) correlations	\checkmark	×	
transients	\checkmark	\checkmark	?

	sampling	mean-field	prob. pop. code
variability	\checkmark	×	\checkmark
noise correlations	\checkmark	×	\checkmark
stimulus-dependent variability & correlations	\checkmark	×	×
spontaneous activity	\checkmark	×	×
correlation of (signal, noise & spont) correlations	\checkmark	×	_
transients	\checkmark	\checkmark	?
oscillations	\checkmark	?	?

	sampling	mean-field	prob. pop. code
variability	\checkmark	×	\checkmark
noise correlations	\checkmark	×	\checkmark
stimulus-dependent variability & correlations	\checkmark	×	×
spontaneous activity	\checkmark	×	×
correlation of (signal, noise & spont) correlations	\checkmark	×	_
transients	\checkmark	\checkmark	?
oscillations	\checkmark	?	?
ramping(?) for evidence integration	?	\checkmark	\checkmark

	sampling	mean-field	prob. pop. code
variability	~	×	\checkmark
noise correlations	\checkmark	×	\checkmark
stimulus-dependent variability & correlations	\checkmark	×	×
spontaneous activity	\checkmark	×	×
correlation of (signal, noise & spont) correlations	\checkmark	×	_
transients	\checkmark	\checkmark	?
oscillations	\checkmark	?	?
ramping(?) for evidence integration	?	\checkmark	\checkmark
spiking neurons	\checkmark	\checkmark	\checkmark

Lengyel et al, arXiv 2015















...

cell #2

response

cell #1 response







A GRADUAL REFINEMENT OF THE REPRESENTATION OF UNCERTAINTY

A PSYCHOPHYSICAL TEST

A PSYCHOPHYSICAL TEST





1100 ms















A PSYCHOPHYSICAL TEST



quality of information available: quality of probabilistic representation: error-uncertainty correlation

error (uncertainty)



quality of probabilistic representation: error-uncertainty correlation

















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SANITY CHECKS: BASIC RESPONSE

uniform spread



SANITY CHECKS: BASIC RESPONSE

60⁰

500

30⁰

1000

0⁰

uniform spread

reliable, no strong bias





SANITY CHECKS: BASIC RESPONSE

uniform spread

reliable, no strong bias

180



no time to deliberate...



drawing time mean: 450±110 ms std: 160±30 ms

A WELL-CALIBRATED PROBABILISTIC

a single subject:



A WELL-CALIBRATED PROBABILISTIC

a single subject:



all subjects:



A WELL-CALIBRATED PROBABILISTIC

a single subject:



all subjects:



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average uncertainty & error





significant

Lengyel et al, arXiv 2015



Lengyel et al, arXiv 2015



EFFECTS OF TASK DIFFICULTY Lengyel et al, arXiv 2015



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EFFECTS OF TASK DIFFICULTY Lengyel et al, arXiv 2015



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EFFECTS OF TASK DIFFICULTY Lengyel et al, arXiv 2015



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 \mathcal{D} : observation

















 x^* behaves as if sampled from $P(x|\mathcal{D})$

$$E[\mu_{x}] = x^{*}$$
$$E\left[(\mu_{x} - x^{*})^{2}\right] = \sigma_{x}^{2}$$
$$E\left[(\mu_{x} - x^{*})^{4}\right] = (\kappa_{x} + 3) \sigma_{x}^{4}$$



for **any** consistent probabilistic representation:

 x^* behaves as if sampled from $P(x|\mathcal{D})$

$$E[\mu_{x}] = x^{*}$$
$$E\left[(\mu_{x} - x^{*})^{2}\right] = \sigma_{x}^{2}$$
$$E\left[(\mu_{x} - x^{*})^{4}\right] = (\kappa_{x} + 3)\sigma_{x}^{4}$$

no parametric assumptions about $P(x|\mathcal{D})$ or $P(\sigma_x^2)$

EXACT, STATIC PROBABILISTIC REPRESENTATION



EXACT, STATIC PROBABILISTIC REPRESENTATION





 $\varepsilon^2 = \varsigma$









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EVIDENCE INERGEBRIG BINNTEGRATION Lengyel et al, arXiv 2015

EVIDENCE INERGEARCIENNTEGRATION

Lengyel et al, arXiv 2015

 $\mathcal{D}_1 \longrightarrow P(x|\mathcal{D}_1)$
EVIDENCE INEREGRATION Lengyel et al, arXiv 2015

 $\mathcal{D}_{1} \rightarrow P(x|\mathcal{D}_{1})$ \downarrow $\mathcal{D}_{2} \rightarrow P(x|\mathcal{D}_{1}, \mathcal{D}_{2})$

EVIDENCE INEREGRATION

 $\mathcal{D}_1 \longrightarrow P(x|\mathcal{D}_1)$ $\mathcal{D}_2 \longrightarrow \mathrm{P}(x|\mathcal{D}_1,\mathcal{D}_2)$ $\mathcal{D}_n \longrightarrow \mathbf{P}(x|\mathcal{D}_1, \mathcal{D}_2, \dots \mathcal{D}_n)$ x x^*

EVIDENCE INEREGRATION



EVIDENCE INERGEBRIG BINNTEGRATION Lengyel et al, arXiv 2015



assumptions:

with time, posterior becomes

- narrower and more centred on x^* $\sigma_{\rm x}^2 \propto 1/n \iff \varsigma \propto 1/n$

– more Gaussian-like $\kappa_{\rm x} \propto 1/n$

EVIDENCE INEREGRATION



EVIDENCE INTEGRATION + BEHAVIOURAL NOISE



EVIDENCE INTEGRATION + NOISE









SAMPLING-BASED REPRESENTATION



assumption: independent samples from the posterior

 $x_i \overset{\text{i.i.d.}}{\sim} \mathrm{P}(x|\mathcal{D})$

SAMPLING-BASED REPRESENTATION



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SAMPLING-BASED REPRESENTATION Lengyel et al, arXiv 2015



assumption: $x_i \overset{\text{i.i.d.}}{\sim} \mathrm{P}(x|\mathcal{D})$

independent samples from the posterior

SAMPLING-BASED REPRESENTATION



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mean squared error





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EFFECTS OF TIME

300

presentation time (msec)

400

12

10

8

600



50 75 100

133

200

167

EFFECTS OF TIME





error-uncertainty correlation



sampling

sampling

* is a simple and powerful way of representing uncertainty (MCMC, particle filters)

sampling

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provides a natural account of

sampling

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- provides a natural account of
 - neural variability

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 - behavioural idiosyncrasies

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a new paradigm to obtain trial-by-trial measure of uncertainty: humans' representation of uncertainty

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a new paradigm to obtain trial-by-trial measure of uncertainty: humans' representation of uncertainty

✤ is well calibrated, multidimensional & uses a unitary scale

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- reflects hallmarks of sampling (2-3 ms / sample)

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ACKNOWLEDGEMENTS





Marjena Popović



Adám

Koblinger