

# The Bayesian Brain: Ideal observer models for perceptual decisions

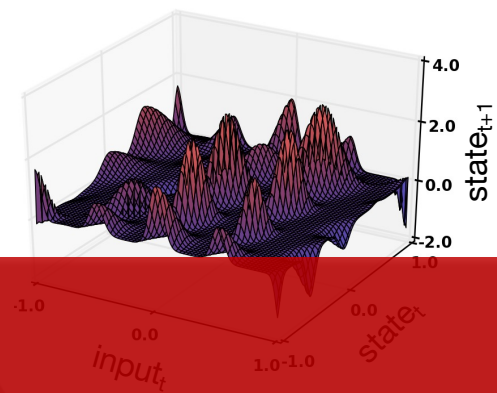
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Department of Neurobiology  
Harvard Medical School



Neuro 140  
February 6, 2024

state



?

$$\text{state}_{t+1}, \text{behavior}_{t+1} = f(\text{state}_t, \text{input}_t)$$

We need theories to constrain our hypothesis space!

How do we develop useful theories?

sensory  
inputs

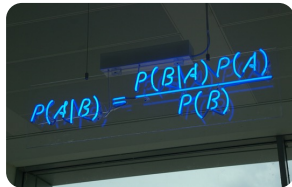
behavior



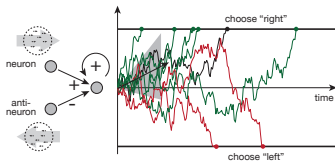
# Roadmap



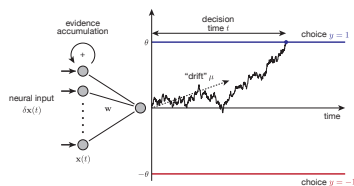
Ideal observer modeling:  
Uncertainty as guiding principle  
in AI and computational neuroscience



(Behavioral) evidence for handling uncertainty



Example 1: ideal observer models for the speed/accuracy trade-off  
in perceptual decision-making

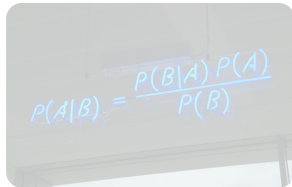


Example 2: Inference on a difference time-scale:  
Decision confidence to improve decision strategies

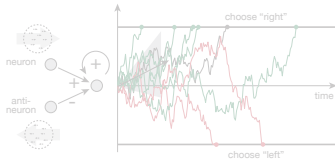
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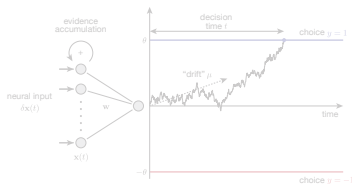
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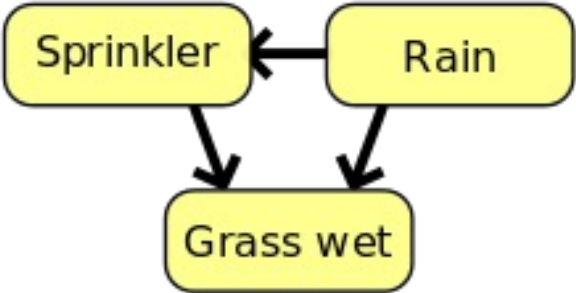


Example 1: ideal observer models for the speed/accuracy trade-off  
in perceptual decision-making



Example 2: Inference on a difference time-scale:  
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Guiding principle: information is uncertain



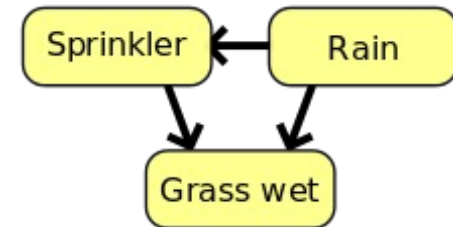
# Uncertainty handling in artificial intelligence

(a few examples)

Boltzmann machines (stochastic Hopfield networks; Hinton & Sejnowski, 1983)

Bayesian networks (Pearl, 1985)

Statistical learning theory (Vapnik & Chervonenkis, 1971)  
- brought us Support Vector Machines (Cortes & Vapnik, 1995)



Variational Bayes; MCMC; ...

...

Deep learning (~2012): initially no uncertainty

...

Variational autoencoders (Kingma & Welling, 2014; Rezende et al., 2014)

- build statistical model of inputs

Distributional reinforcement learning (Bellemare et al., 2017)

- build statistical model of long-term rewards

Diffusion models, e.g., Stable Diffusion (Sohl-Dickstein et al., 2015; Ho et al., 2020)

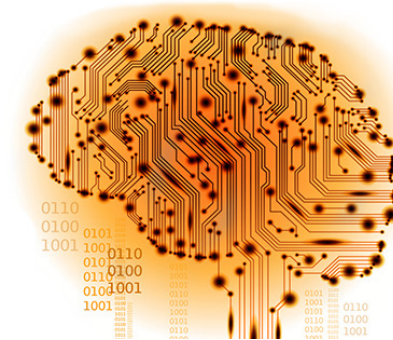
- image generation by learning to reverse stochastic diffusion process

# Ideal observer modeling

**Brain**



**AI**



today's lecture

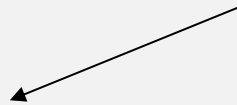
Needs to efficiently handle  
uncertain information

methods for (approximate)  
inference with uncertain  
information

"ideal observer" models

potential  
neural implementations

new algorithmic ideas  
(e.g., boltzmann machines,  
networks in general)

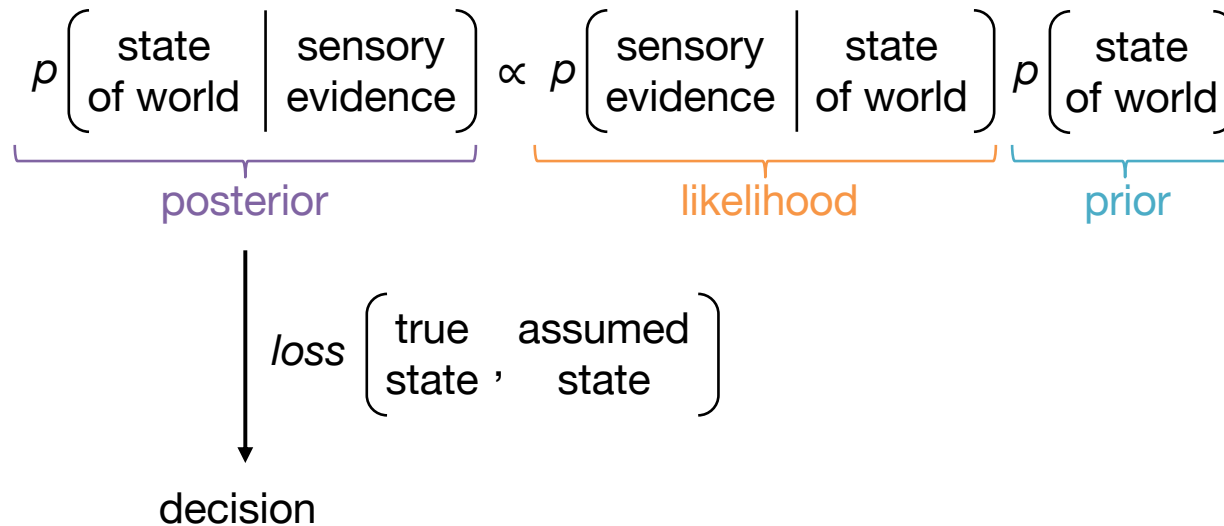


# Principled way of handling uncertainty

Using **Bayesian decision theory** to handle uncertainty



Rev. Thomas Bayes  
(1701-1761)



Pierre-Simon Laplace (*Théorie analytique des probabilités*, 1812):

*“The most important questions of life are indeed, for the most part, really only problems of probability”*

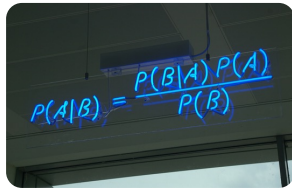
Cox’s theorem: probabilities are the only principled way to handle uncertainty (Cox, 1946)



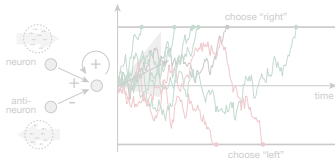
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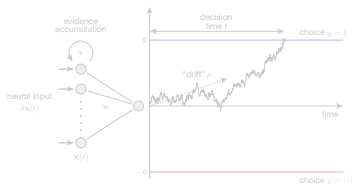
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(Behavioral) evidence for handling uncertainty



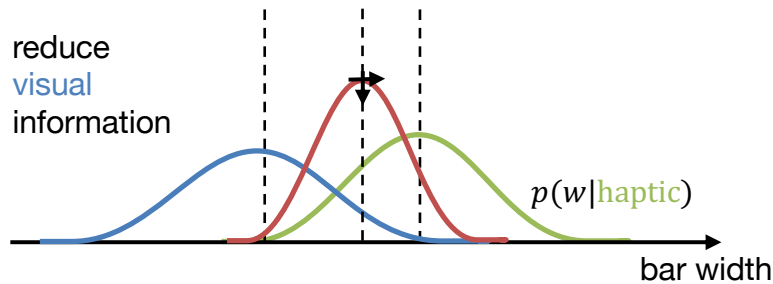
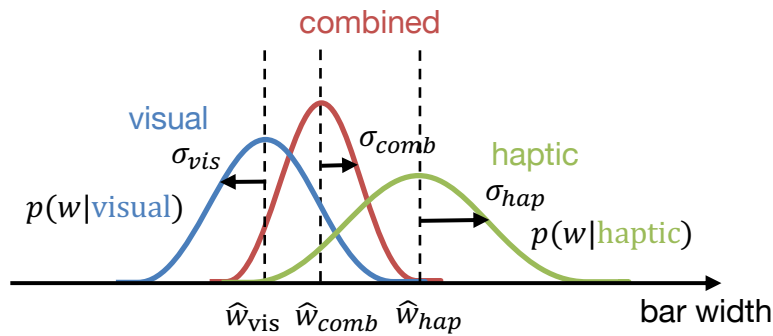
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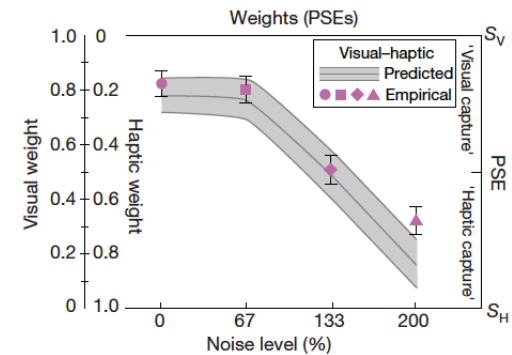
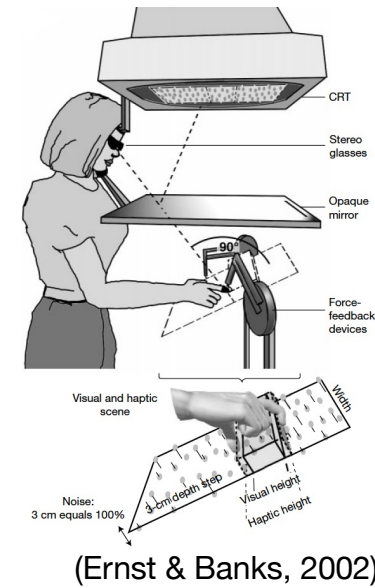
Example 2: Inference on a difference time-scale:  
Decision confidence to improve decision strategies

# Combining uncertain evidence from multiple sources

e.g. visual/auditory for object localization  
 visual/vestibular for self-motion  
 visual/haptic for bar width estimation

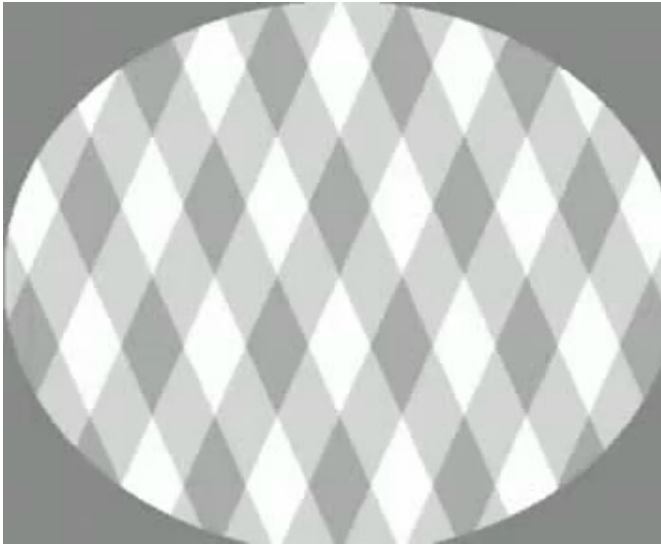


Cue combination using the laws of probability

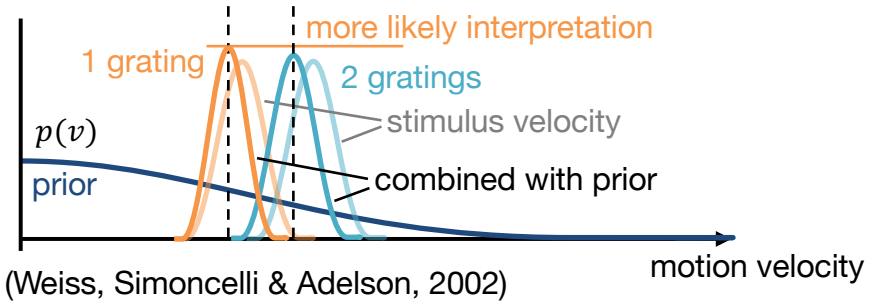
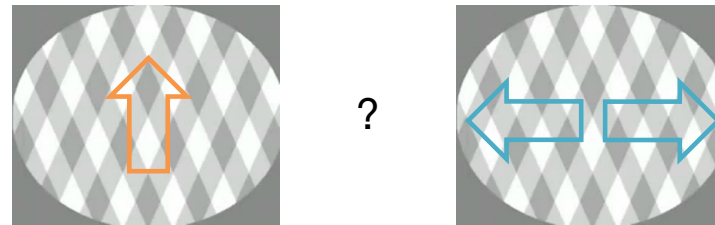


# Rely on prior information

Prior = state of the world in absence of evidence



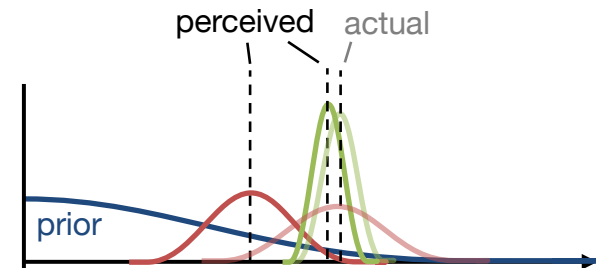
[https://www.youtube.com/watch?v=g\\_sn0WtHK1g](https://www.youtube.com/watch?v=g_sn0WtHK1g)



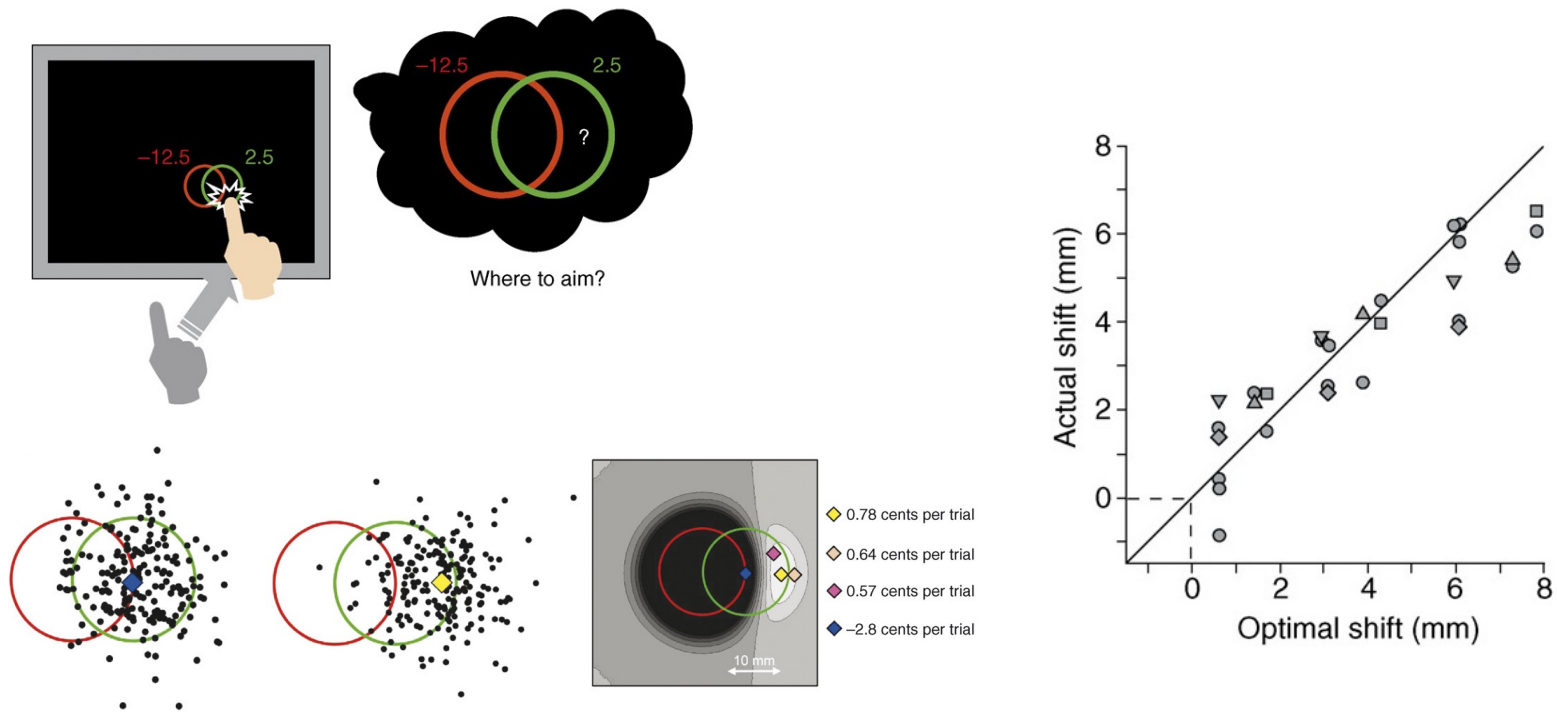
Real-world: underestimating speed in bad weather



vs.



# Sensitivity to rewards/losses



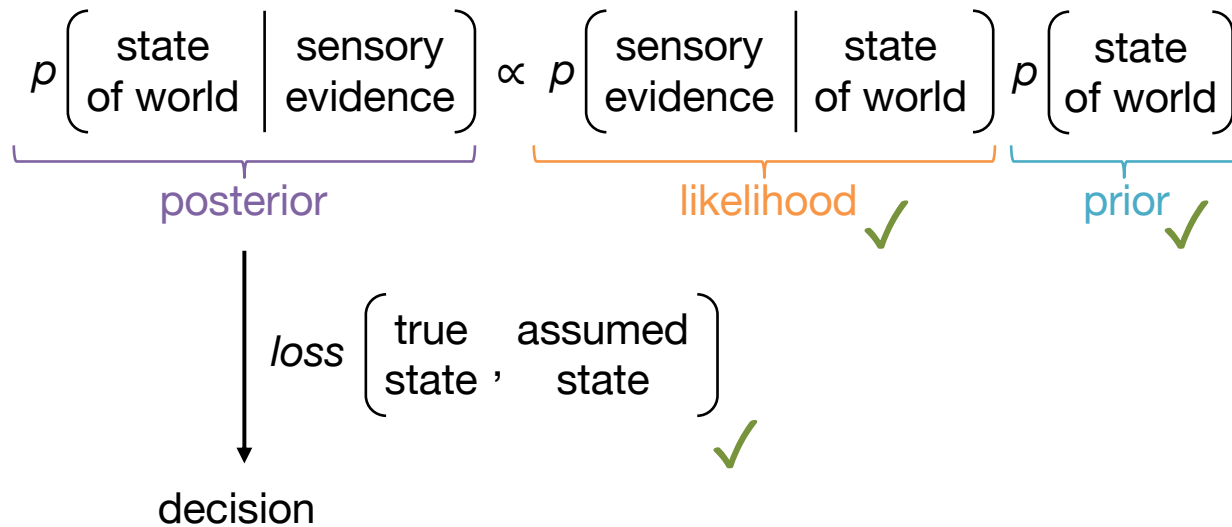
(Trommerhäuser, Maloney & Landy, 2008)

...has also been used to reverse-engineer the reward/loss function  
e.g. Körding & Wolpert (2004); Drugowitsch et al. (2012)

# Recap: Bayesian decision theory



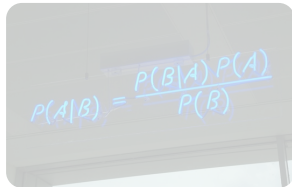
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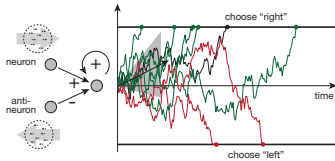
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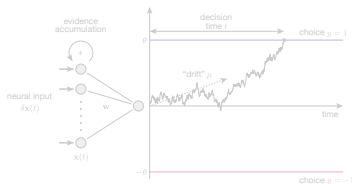
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(Behavioral) evidence for handling uncertainty



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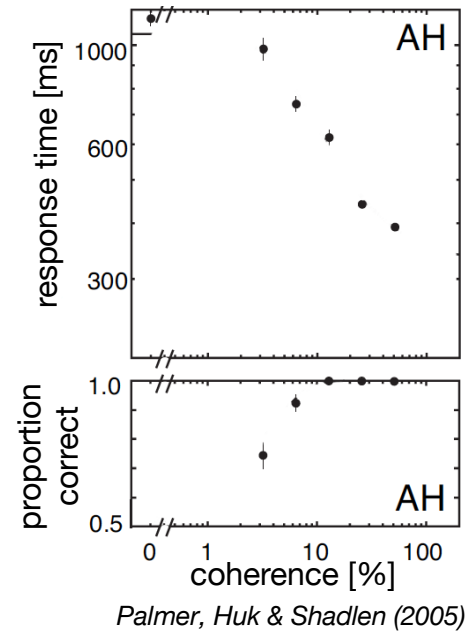
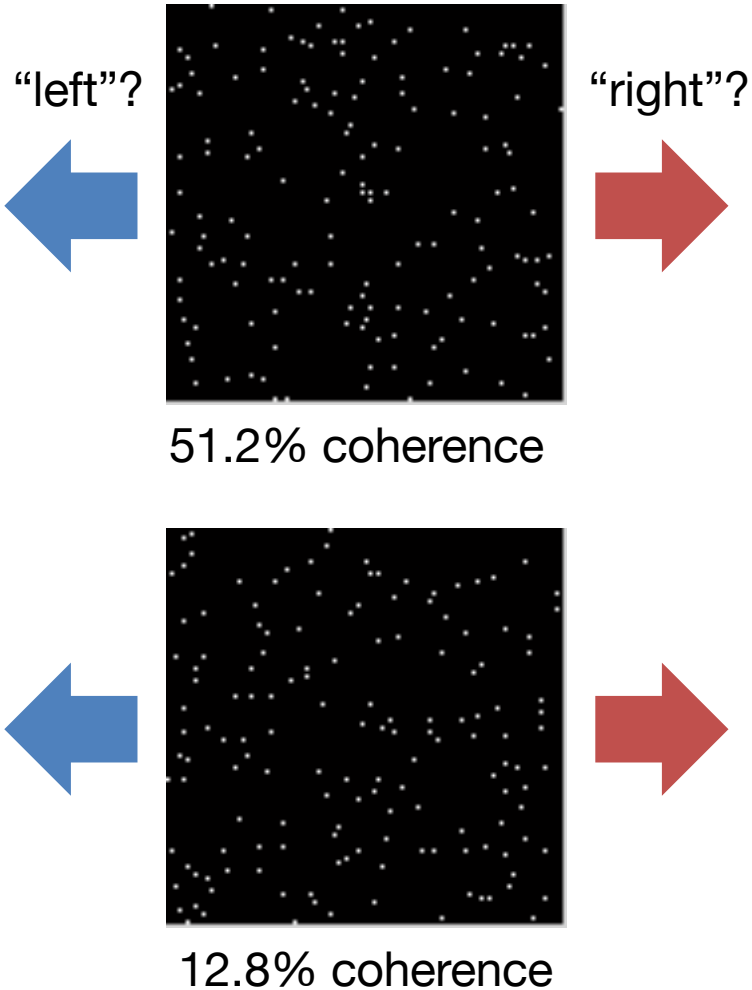
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# In the lab: the random-dot motion task

(e.g., Newsome, Britten, Movshon & Shadlen, 1989; Roitman & Shadlen, 2002)

*“respond as quickly and accurately as possible”*





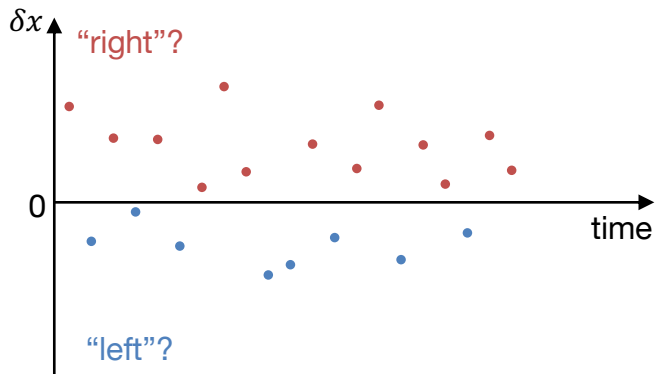
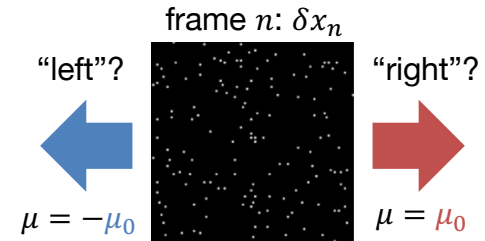
# Formalizing evidence accumulation

Latent state

$$\mu = \{-\mu_0, \mu_0\}$$

Noisy evidence per  $\delta t$

$$\delta x_n | \mu \sim N(\mu \delta t, \sigma^2 \delta t)$$



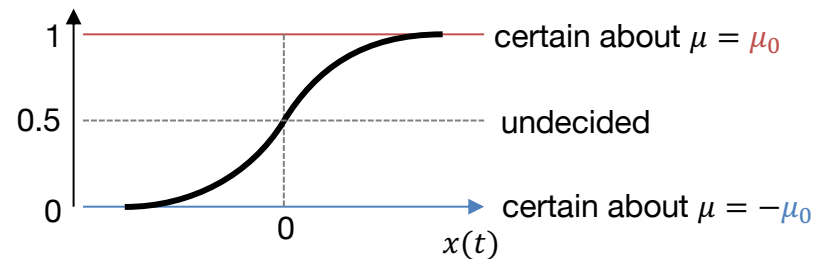
Optimal evidence accumulation: Bayes' rule

$$\underbrace{p(\mu | \delta x_{1:N})}_{\text{posterior}} \propto \underbrace{p(\delta x_{1:N} | \mu)}_{\text{likelihood}} \underbrace{p(\mu)}_{\text{prior}}$$

**Posterior belief** about motion being “right-ward” ( $\mu > 0$ )

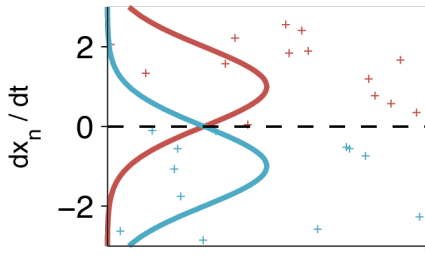
$$g \equiv p(\mu = \mu_0 | \delta x_{1:N}) = \frac{1}{1 + e^{\frac{2\mu_0 x(t)}{\sigma^2}}}$$

accumulated evidence  $\rightarrow x(t) = \sum_{n=1}^N \delta x_n$

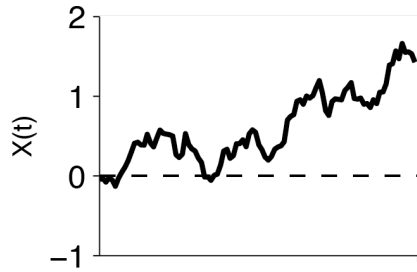


# Evidence accumulation by diffusion

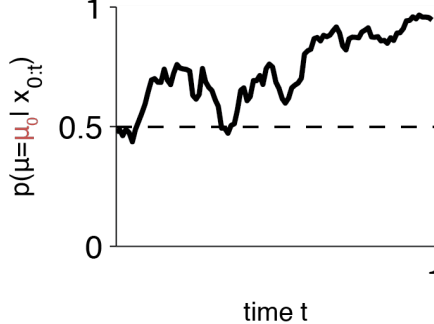
momentary evidence



accumulated evidence



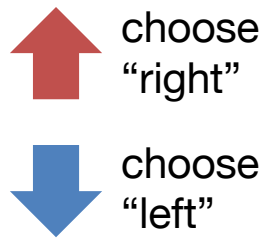
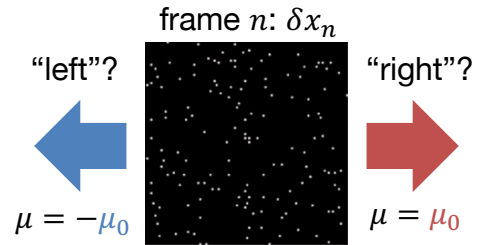
resulting posterior



$$\delta x_n | \mu \sim N(\mu \delta t, \sigma^2 \delta t)$$

$$x(t) = \sum_{n=1}^N \delta x_n$$

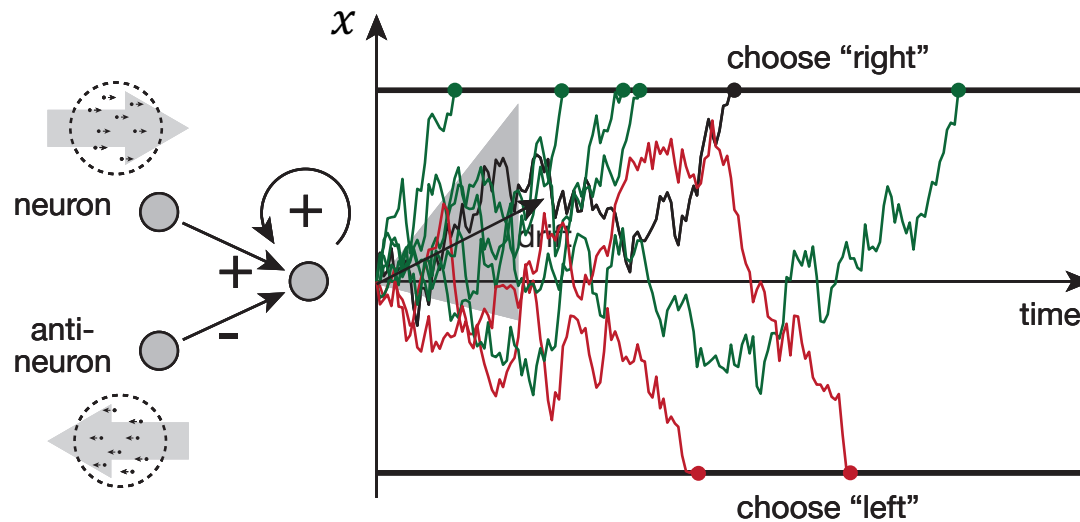
$$\frac{dx}{dt} = \mu + \sigma \eta(t)$$



make choices directly  
In space of  
accumulated evidence

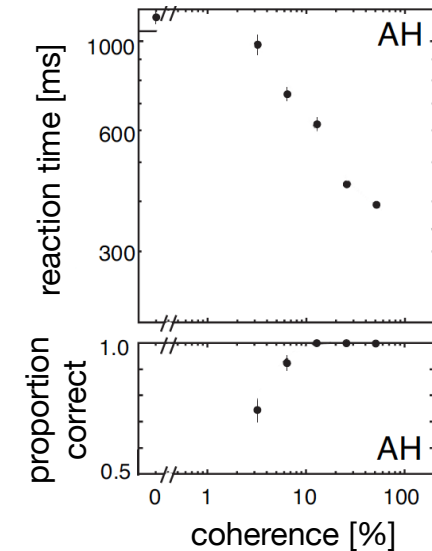
# Diffusion decision models (DDMs)

(Ratcliff, 1978)



$$\frac{dx}{dt} = \frac{\text{drift } \mu}{kc} + \frac{\text{diffusion}}{\sigma\eta(t)}$$

“coherence”      white noise process



(Palmer, Huk & Shadlen, 2005)

Works surprisingly well for, fast (<1.5s), single-stage decisions, e.g.,

Word/non-word judgments (e.g., Ratcliff & Gomez, 2004)

Numerosity judgments (e.g., Ratcliff & McKoon, 2018)

Recognition memory (e.g., Ratcliff, 1978)

...

# Deciding when to decide: decision boundaries

Free evidence: accumulate forever!

Assume: time/evidence is costly

**speed/accuracy trade-off**

**fast choices**  $\longleftrightarrow$  **slow choices**

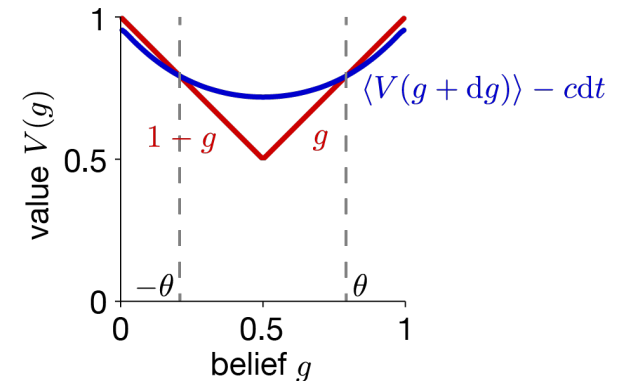
**cost** linear in time,  $ct$   
**reward** 1 for correct, 0 for incorrect

cheap expensive  
 inaccurate accurate

**Optimal trade-off:** dynamic programming (Bellman, 1960s)

After accumulating for some time  $t$ : expected "return"  $V(g(t))$   
 (recall,  $g(t) \equiv p(\mu = \mu_0 | \delta x_{1:t})$ )

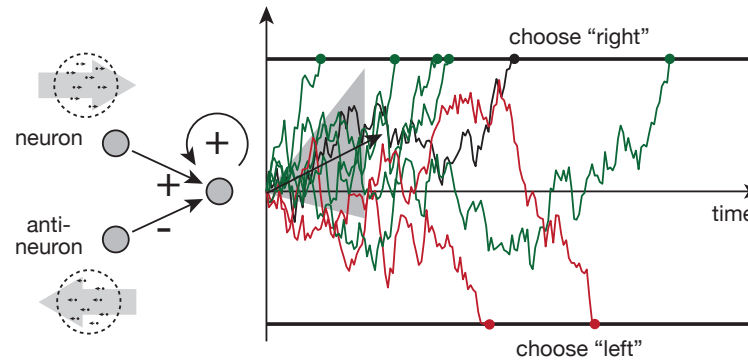
	expected return
Choosing $-\mu_0$ or $\mu_0$	$1 - g$ or $g$
Accumulating another $\delta t$	$\langle V(g + \delta g) \rangle - c\delta t$



Bellman's equation

$$V(g) = \max\{1 - g, g, \langle V(g + \delta g) \rangle - c\delta t\}$$

# DDMs & Sequential probability ratio test



**Diffusion** Bayes-optimal evidence accumulation

**Decision-boundaries** Optimal speed-accuracy trade-off

## Sequential probability ratio test (Turning, 1940s; Wald & Wolfowitz, 1948)



accumulate  $\longrightarrow$  decide

$$p_{ij} = \prod_{k=1}^i p_i(x_k).$$

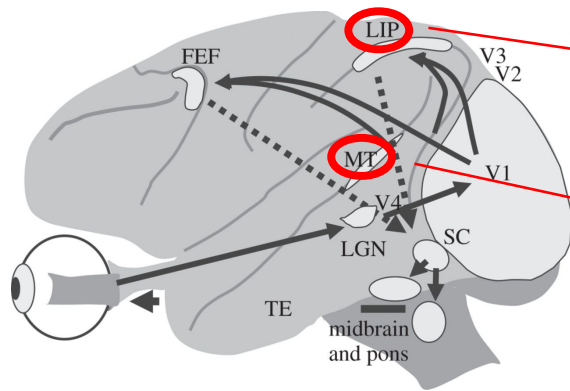
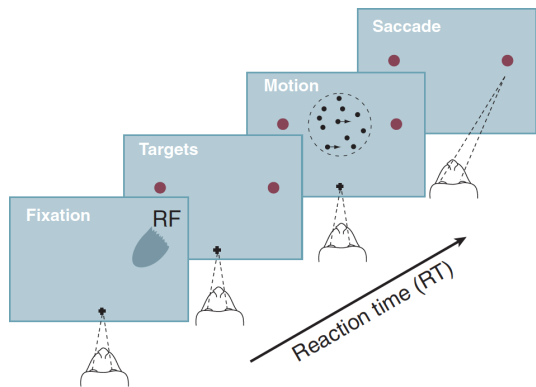
If

$\frac{p_{1n}}{p_{0n}} \geq A^*$ , the hypothesis  $H_1$  is accepted,

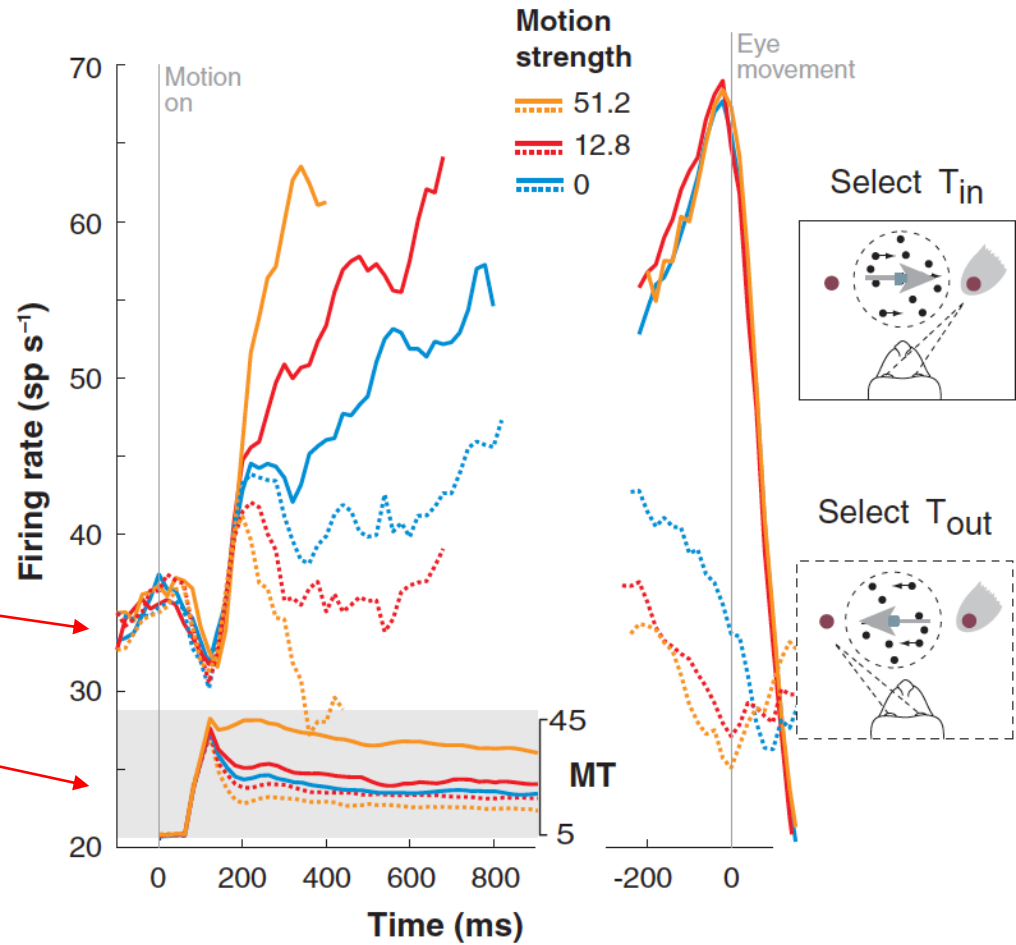
if

$\frac{p_{1n}}{p_{0n}} \leq B^*$  the hypothesis  $H_0$  is accepted.

# Neural correlates of evidence accumulation



Wurtz (2015)

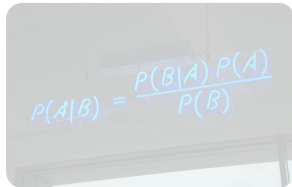


Gold & Shadlen (2007);  
LIP data from *Roitman & Shadlen (2002)*;  
MT data from *Britten (1992)*

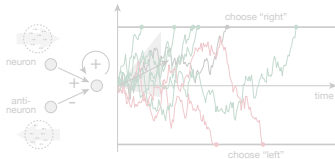
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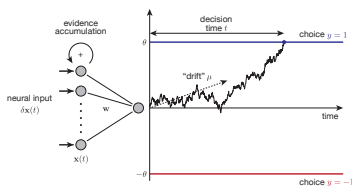
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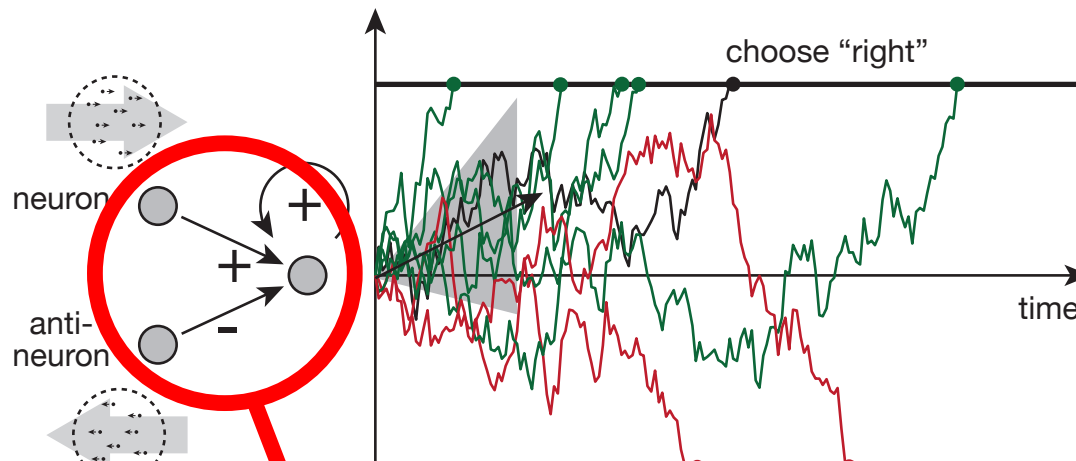


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# Extending diffusion model to higher-dimensional inputs



usually  
only 2 inputs  
Max known input weights



more realistically  
input is larger neural population  
inputs weights need to be learned

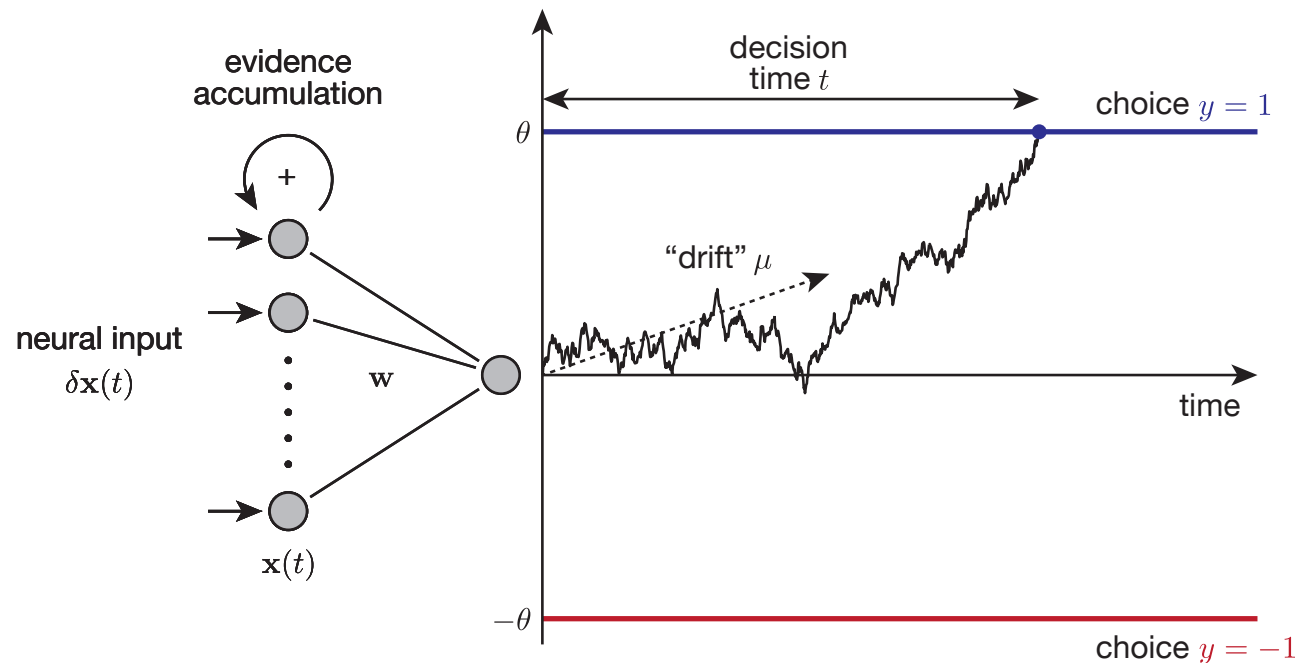
fixed, known difficulty (e.g., fixed coherence)  
(Turing, 1941; Wald & Wolfowitz, 1948)

difficulty that varies across trials  
(Drugowitsch et al., 2012)

difficulty that varies within trials, multiple sources of information  
(Drugowitsch et al., 2014; Drugowitsch, Moreno Bote & Pouget, 2014)



## A larger input population



## Learning input weights after feedback $y^*$

$$p(\mathbf{w} | \mathbf{x}, t, y^*) \propto p(y^* | \mathbf{w}, \mathbf{x}, t) p(\mathbf{w})$$

posterior belief after feedback      likelihood of weights given feedback      belief prior to feedback

$\mathbf{x}, t \xrightarrow{\mathbf{w}} y^*$

## Approximating Bayes rule

$$p(\mathbf{w}|\mathbf{x}, t, y^*) \propto \underbrace{p(y^*|\mathbf{w}, \mathbf{x}, t)}_{\text{from generative model: cumulative Gaussian likelihood}} p(\mathbf{w})$$

**INTRACHTABLE**

### Assumed density filtering

Minimizing  $KL(p||q)$  between true posterior  $p$  and Gaussian approximation  $q$

$$\underbrace{q(\mathbf{w}|\mathbf{x}, t, y^*)}_{\text{assumed Gaussian}} \approx p(y^*|\mathbf{w}, \mathbf{x}, t) \underbrace{q(\mathbf{w})}_{\text{becomes Gaussian}}$$

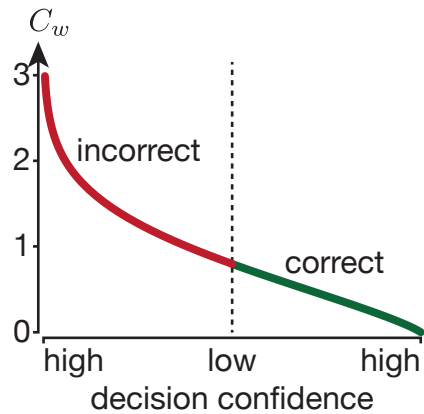
Learning of input weights: tracking mean and covariance of Gaussian

# The Bayes-(near)-optimal learning rule

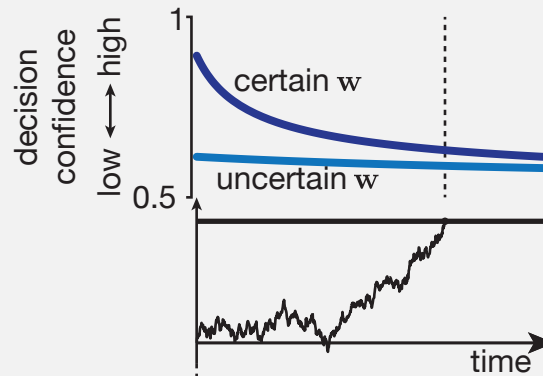
With prior belief before feedback,  $\mathbf{w} \sim \mathcal{N}(\mu_w, \beta_w \bar{\Sigma}_w)$

$$\Delta\mu_w = \frac{y^* C_w}{\sigma \sqrt{t + \frac{\sigma^2}{\sigma_\mu^2} + \beta_w \frac{\mathbf{x}^T \bar{\Sigma}_w \mathbf{x}}{\sigma^2}}}$$

monotonic function of decision confidence (points to  $C_w$ )  
 accumulated evidence (points to  $\bar{\Sigma}_w \mathbf{x}$ )  
 decision time (points to  $t$ )  
 learning rate  $\alpha_{ADF}$  (points to  $\beta_w$ )  
 weight uncertainty (points to  $\bar{\Sigma}_w$ )



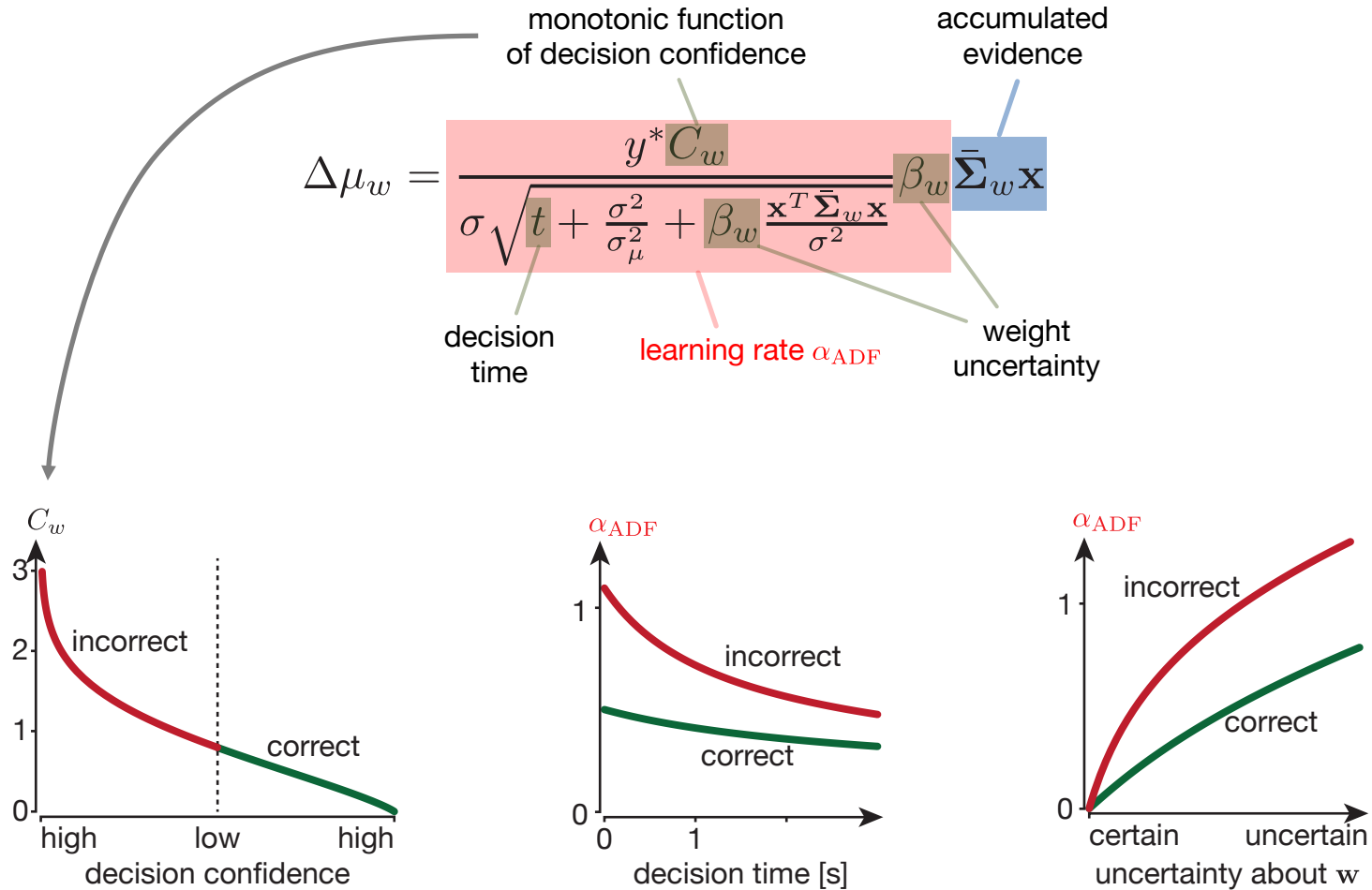
## What determines decision confidence?



- less confident due to
- slower choices (usually harder)
  - less certain about weights

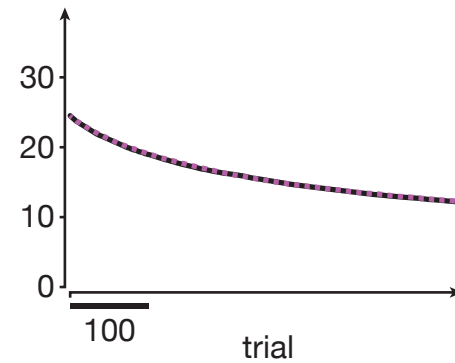
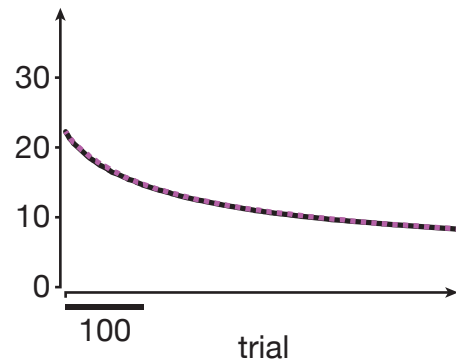
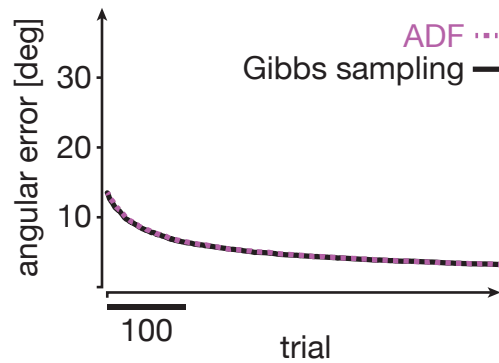
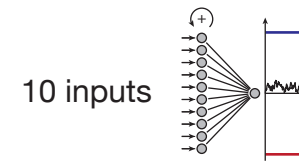
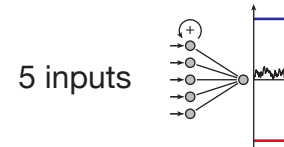
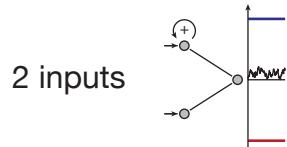
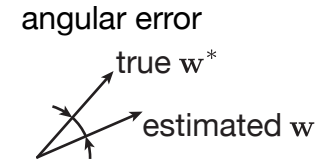
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# How good is the approximation?

Compare performance to optimal (Gibbs sampling) solution

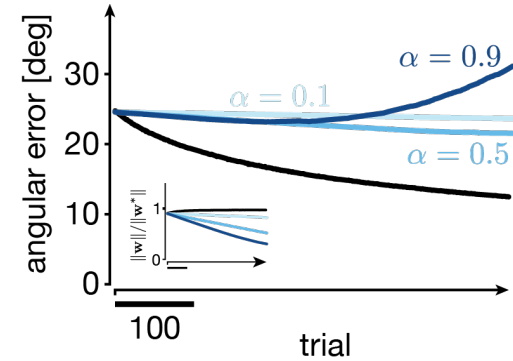
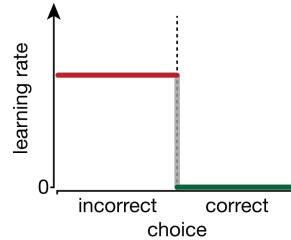


# Do we need to be probabilistic? Simpler heuristics

## Simple delta rule

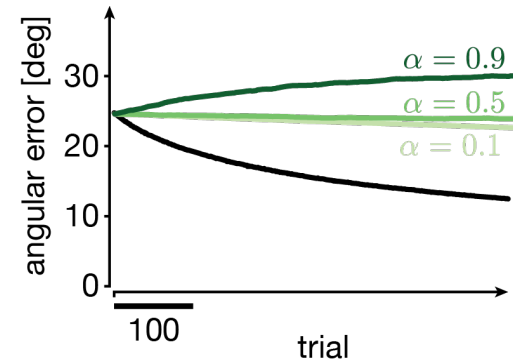
minimizes distance between chosen and correct bound

$$\Delta \mathbf{w} = \alpha \underbrace{(y^* \theta - \mathbf{w}^T \mathbf{x}(t))}_{\text{either } 2\theta \text{ or } 0} \mathbf{x}(t)$$



## Normalized delta rule

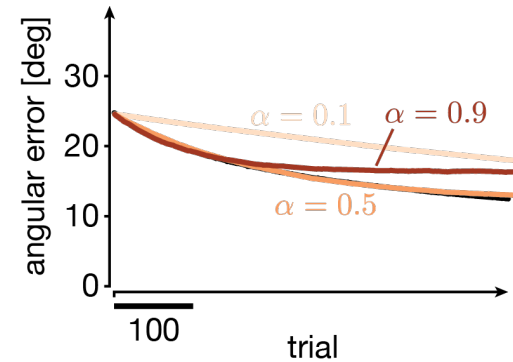
delta rule with normalization,  $\mathbf{w} \leftarrow \frac{\mathbf{w}}{\|\mathbf{w}\|} \langle \|\mathbf{w}^*\| \rangle$



## Stochastic gradient ascent

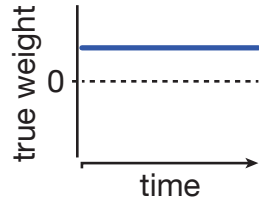
on log-likelihood

$$\Delta \mathbf{w} = \alpha \nabla_{\mathbf{w}} \ln p(y^* | \mathbf{w}, \mathbf{x}(t), t)$$



# Steady-state performance

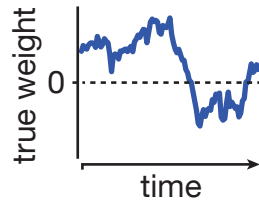
So far



stationary weights

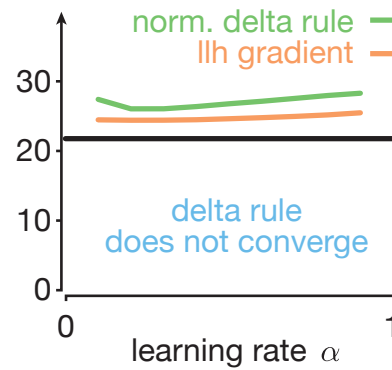
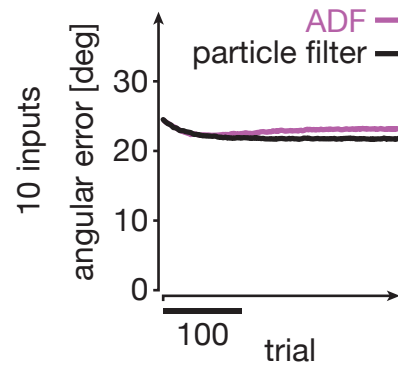
aim to learn weights

Now

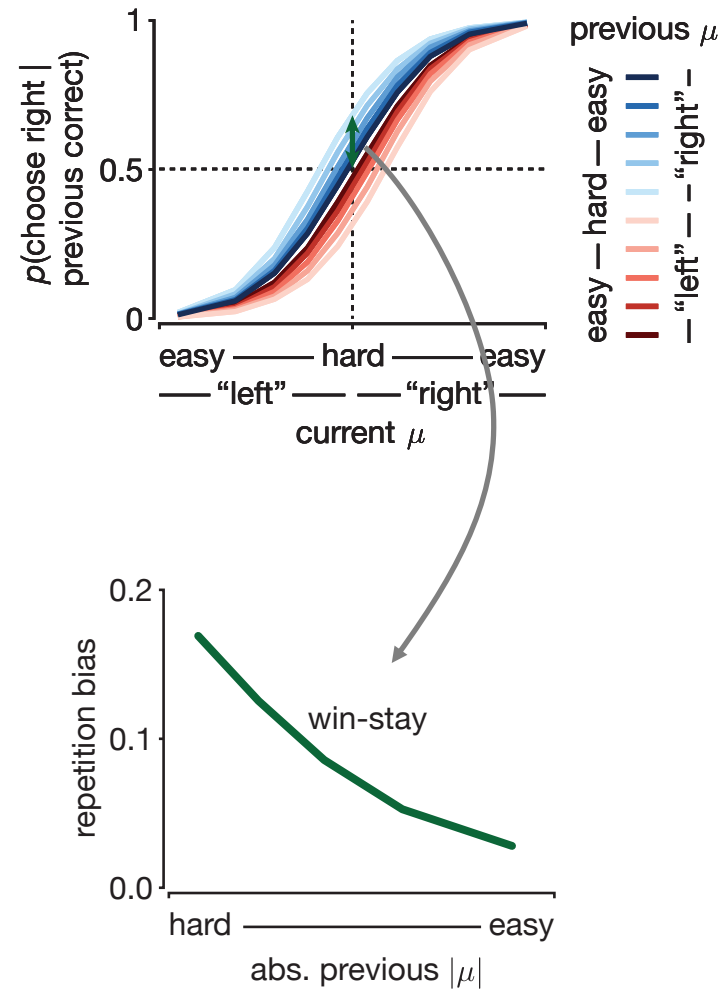
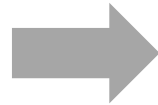
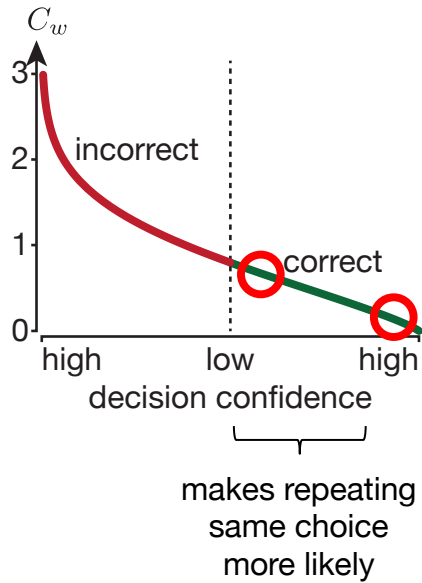


weights follow AR(1) process

aim to track changes

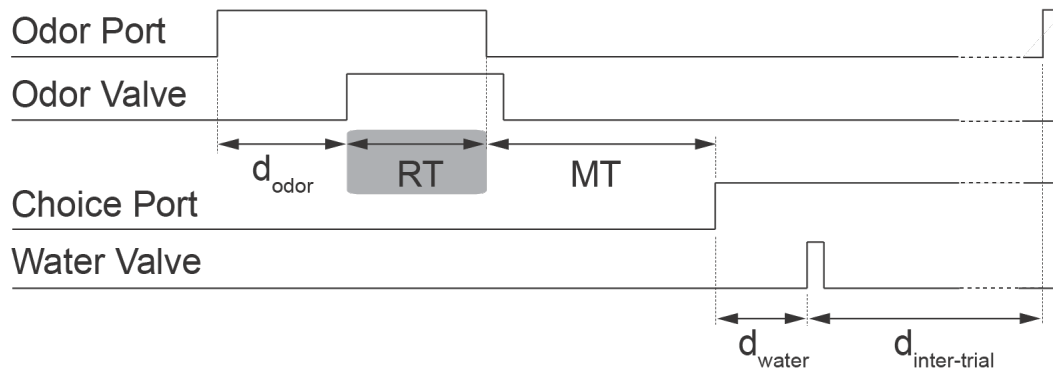
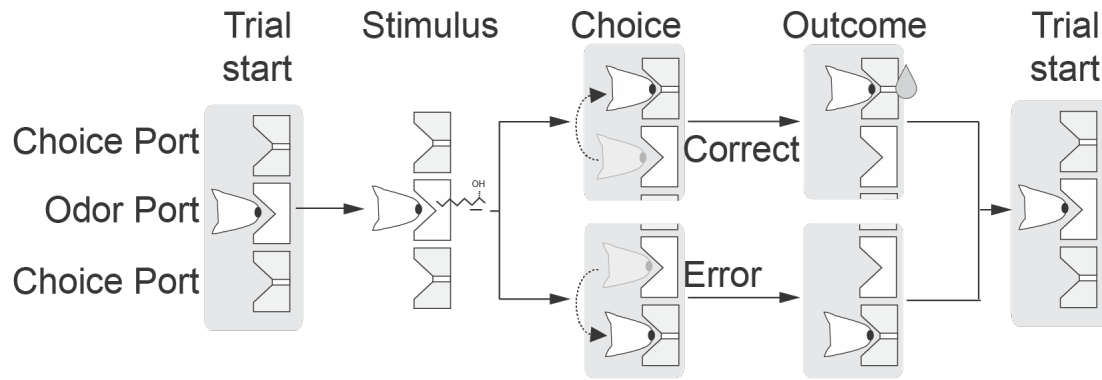


# Continual learning predicts sequential choice dependencies



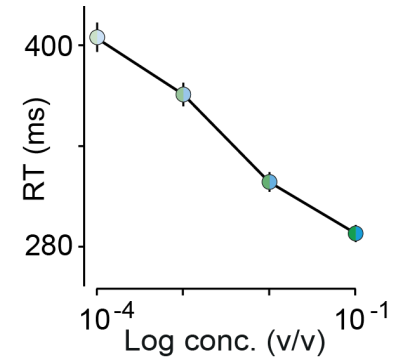
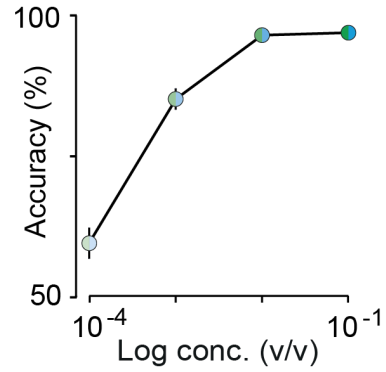
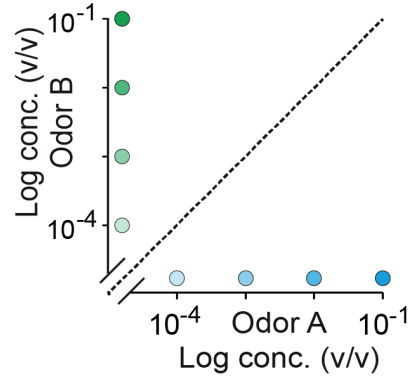


# Odor categorization/identification task

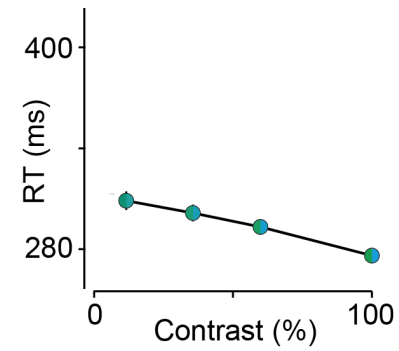
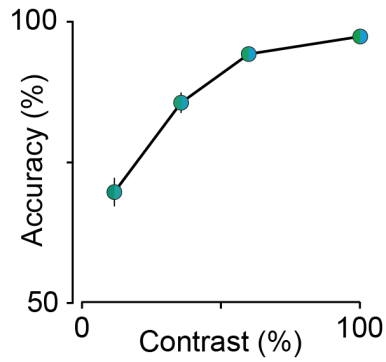
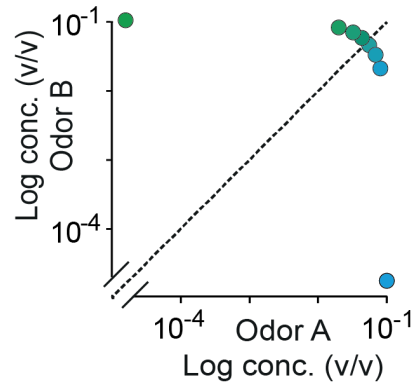


# Task conditions

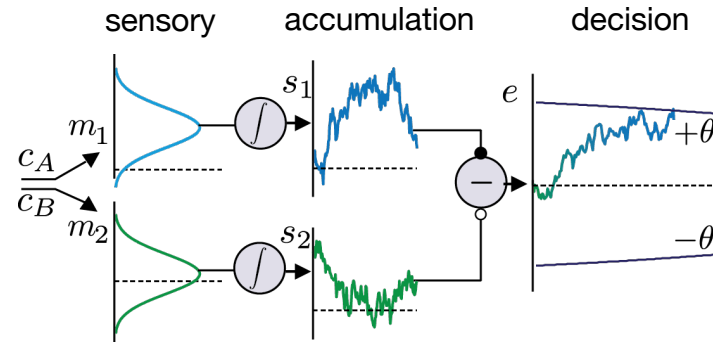
## Odor identification condition



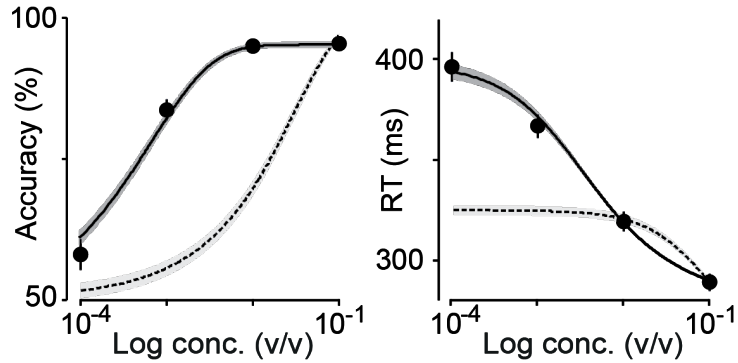
## Odor categorization condition



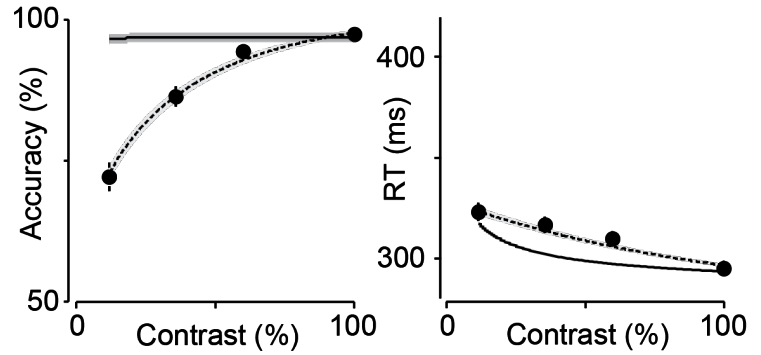
# Vanilla diffusion models can't fit both conditions



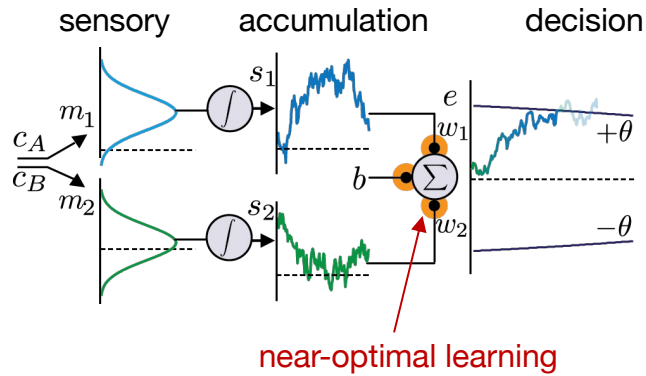
Odor identification condition



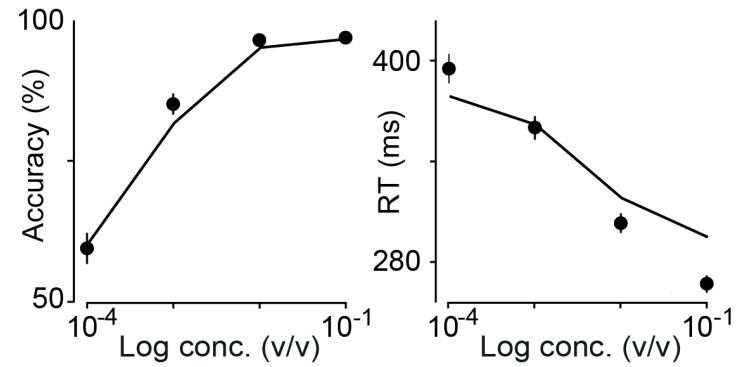
Odor categorization condition



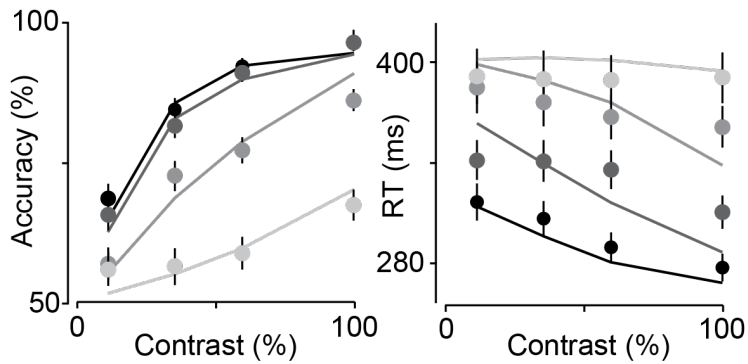
...but a learning model can



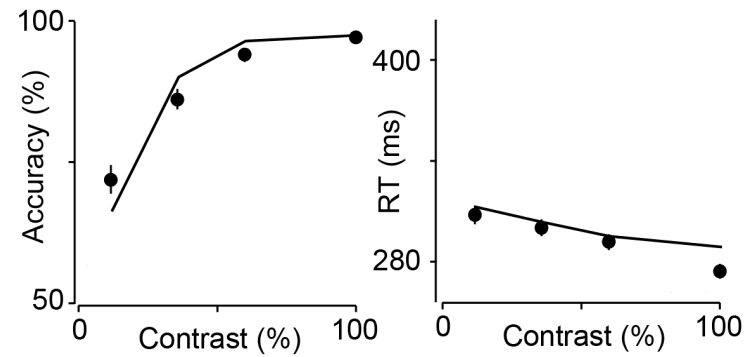
Odor identification condition



Interleaved condition



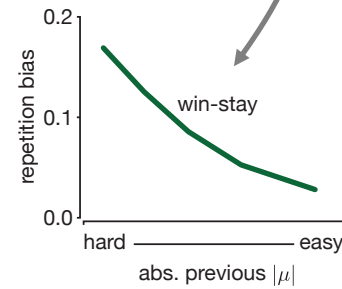
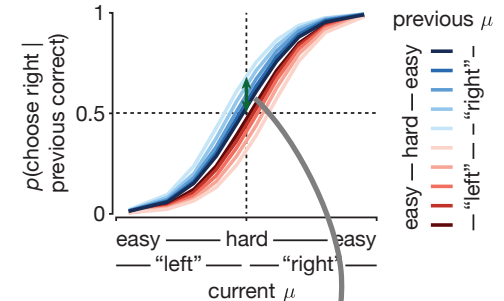
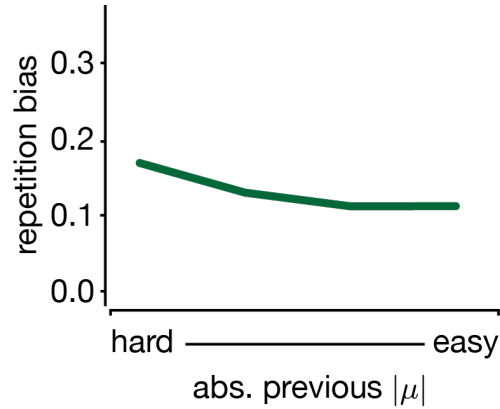
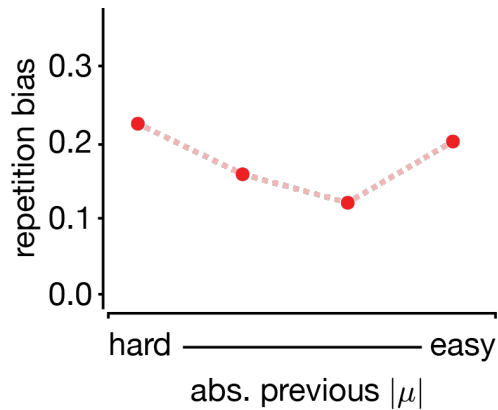
Odor categorization condition



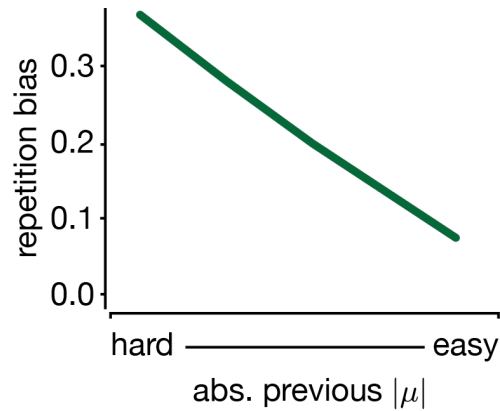
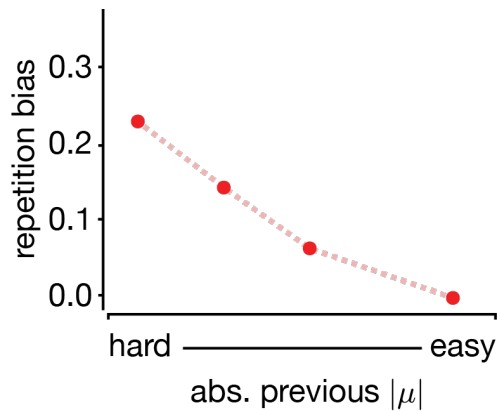
# Sequential effects

Sequential effects are not fitted, but predicted

Odor identification condition

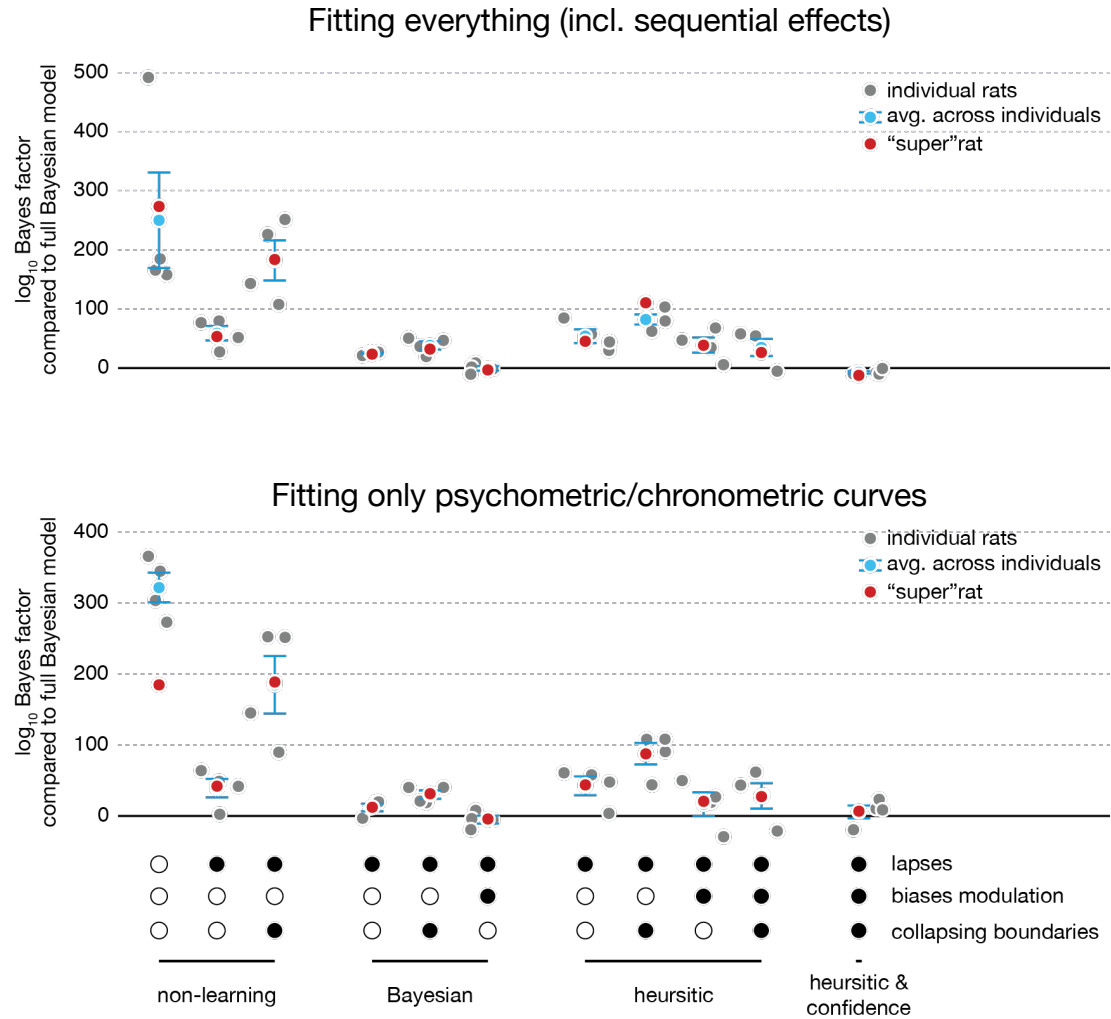


Odor categorization condition



# Simpler models fit data less well

Model comparison on psychometric/chronometric curves & sequential effects



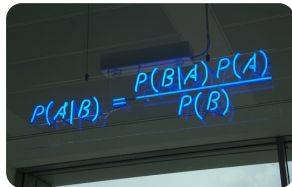
Using BIC; qualitatively same results for AIC & AICc

# Summary



Ideal observer modeling:  
Uncertainty as guiding principle  
in AI and computational neuroscience

*Handling uncertainty by Bayesian decision theory*

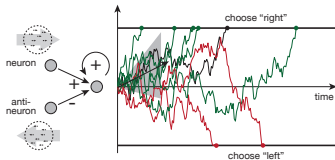


(Behavioral) evidence for handling uncertainty

*Reliability-weighted cue combination*

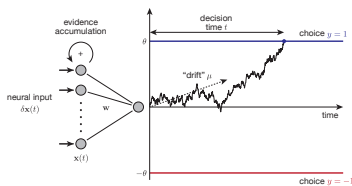
*Use of prior information for uncertain evidence*

*Loss-sensitive decision-making*



Example 1: ideal observer models for the speed/accuracy trade-off  
in perceptual decision-making

*Optimal speed-accuracy trade-off by diffusion models*



Example 2: Inference on a difference time-scale:  
Decision confidence to improve decision strategies

*Bayes-optimal learning is confidence-weighted*

*Provides computational role for decision confidence*

*Predicts sequential choice dependencies for continual learning*

Drugowitsch et al. (2012). The Journal of Neuroscience

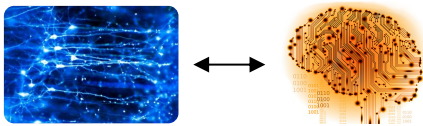
Drugowitsch et al. (2019). PNAS

Mendonça et al. (2020). Nature Communications

# Ideal observer models as hypothesis generators



Brain is too high-dimensional to fully explore by experiments

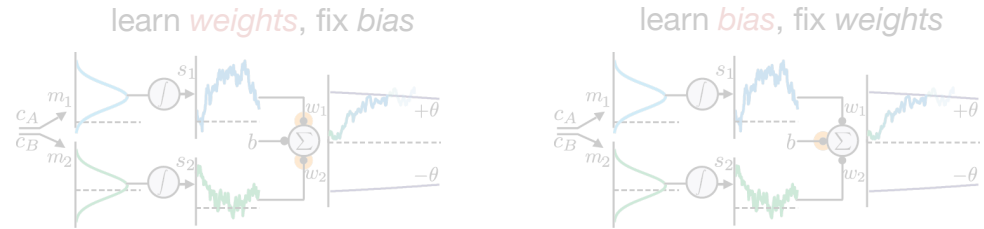


Use of ideal observer models to generate hypotheses of brain function

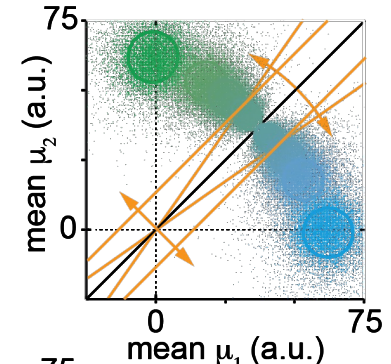
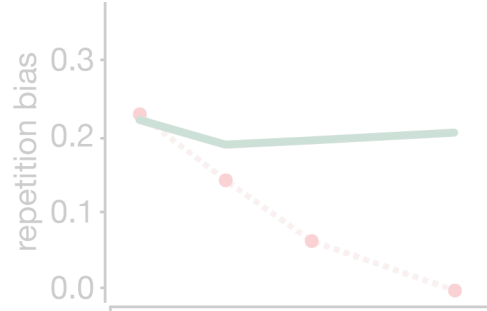
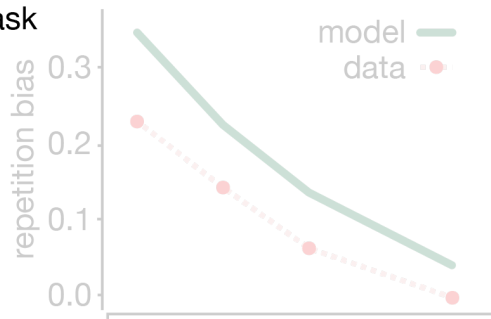


Further questions?

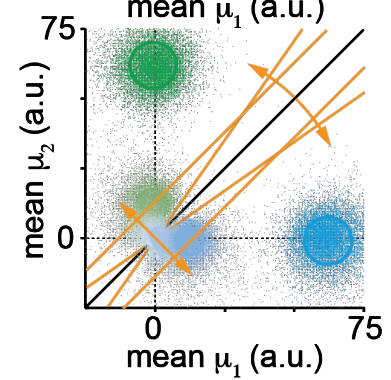
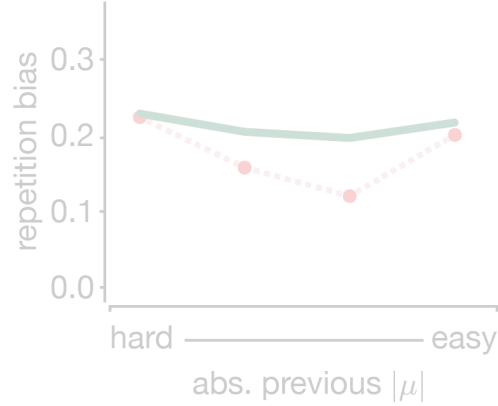
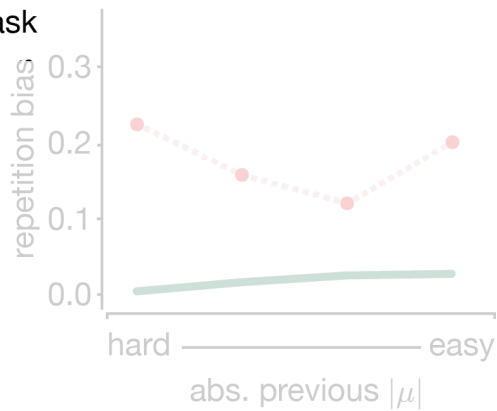
# Do rodents learn both weights *and* biases?



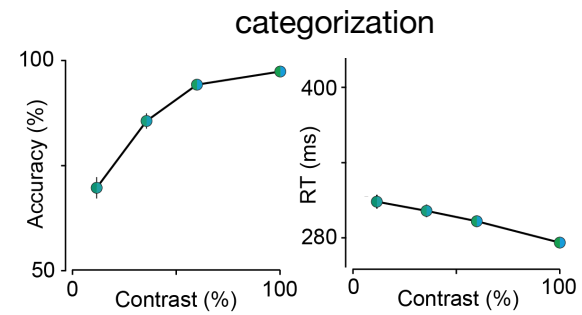
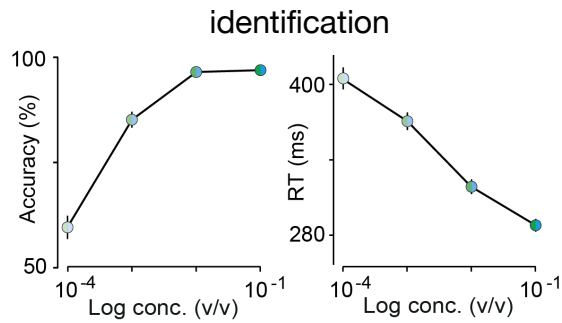
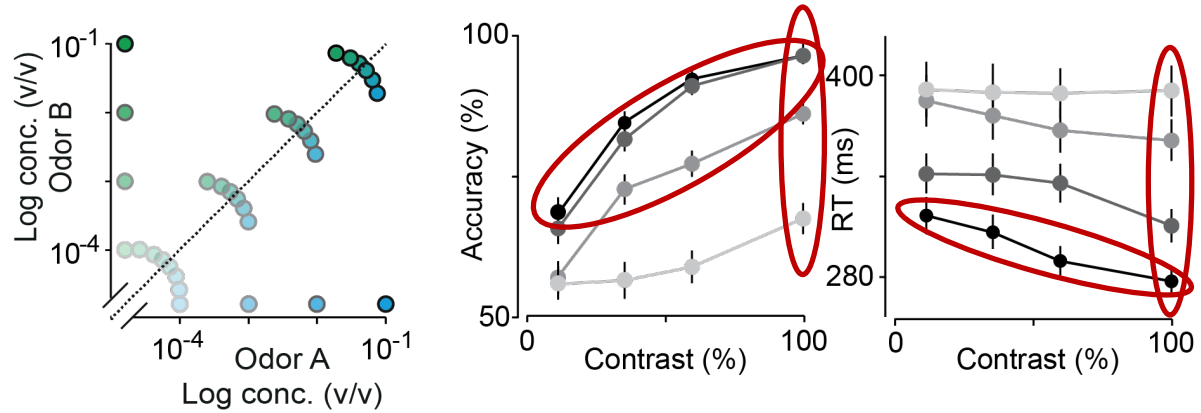
categorization task



identification task



# Simple parameter adjustment across blocked conditions?



## Confidence-weighting only for diffusion models?

For diffusion models

$$p(\mathbf{w}|\mathbf{x}, t, y^*) \propto p(y^*|\mathbf{w}, \mathbf{x}, t) p(\mathbf{w})$$

More generally, following choice  $y$  after observing  $\mathbf{x}$

after correct choices,  $y = y^*$

$$p(\mathbf{w}|\mathbf{x}, \text{choice}) \propto p(y = \text{choice}|\mathbf{w}, \mathbf{x}, \text{choice}) p(\mathbf{w})$$

after incorrect choices,  $y \neq y^*$

$$p(\mathbf{w}|\mathbf{x}, \text{choice}) \propto (1 - p(y = \text{choice}|\mathbf{w}, \mathbf{x}, \text{choice})) p(\mathbf{w})$$

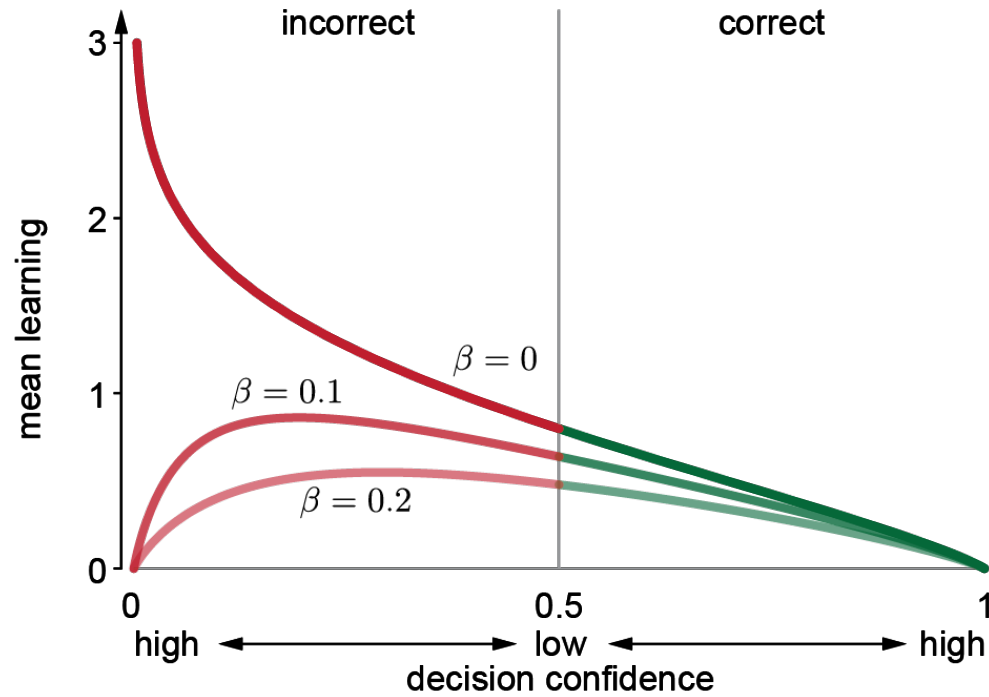
decision confidence

What about  $N$ -AFC with  $N > 2$ ?

Feedback is *correct/incorrect*: again **decision confidence**

Feedback is *correct choice*: need full posterior  $p(y|\mathbf{w}, \mathbf{x})$  for all  $y$

# Confidence trumps imperfect feedback



$\beta$  = probability of inverted feedback

Further questions?