

Optimal feedback control, efference copy & learning in sensorimotor processing

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Definition of Dynamics

In the engineering literature, the “Dynamics” of a system is composed of two equations:

$$\dot{x} = f(x, u) \quad \text{next state equation}$$

$$y = g(x) \quad \text{output equation (kinematics, sensory feedback)}$$

The state x **is** the collection of variables that are needed to define next state equation.

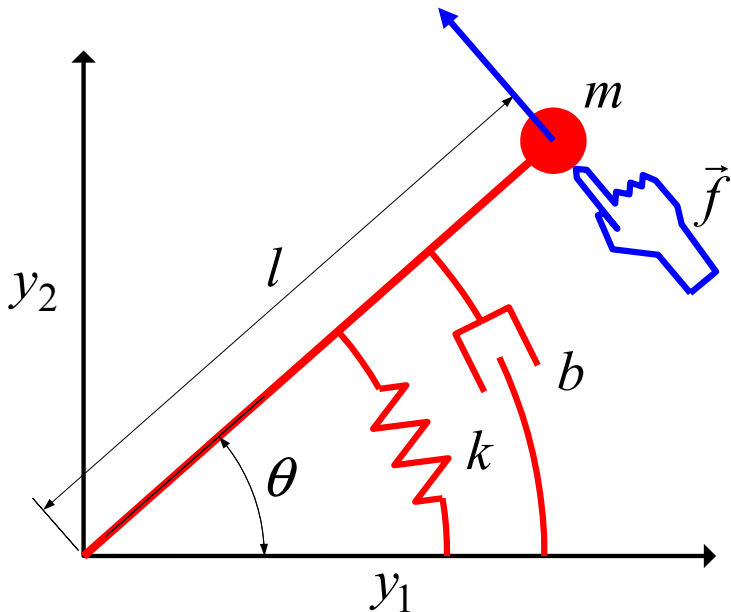
Definition of Dynamics

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The physics:

$$I\ddot{\theta} = -b\dot{\theta} - k(\theta - \theta_0) + f$$



Next state equation:

$$\begin{bmatrix} \dot{\theta} \\ \ddot{\theta} \end{bmatrix} = \begin{bmatrix} 0 & 1 \\ -kI^{-1} & -bI^{-1} \end{bmatrix} \begin{bmatrix} \theta - \theta_0 \\ \dot{\theta} \end{bmatrix} + \begin{bmatrix} 0 \\ I^{-1} \end{bmatrix} f$$

$$\dot{x} = Ax + Bf$$

The state:

$$x = \begin{bmatrix} \theta - \theta_0 \\ \dot{\theta} \end{bmatrix}$$

Output equation:

$$y = \begin{bmatrix} l \cos(\theta) \\ l \sin(\theta) \end{bmatrix}$$

Dynamics of the arm

Analytic form of the dynamics for the *two-joint* arm:

$$\begin{bmatrix} \tau_1 \\ \tau_2 \end{bmatrix} = \begin{bmatrix} I_1 + I_2 + 2l_1m_2r_2 \cos(q_2) + r_1^2m_1 + l_1^2m_2 + r_2^2m_2 & I_2 + r_2^2m_2 + r_2l_1m_2 \cos(q_2) \\ I_2 + r_2^2m_2 + l_1m_2r_2 \cos(q_2) & I_2 + r_2^2m_2 \end{bmatrix} \begin{bmatrix} \ddot{q}_1 \\ \ddot{q}_2 \end{bmatrix} \\ + \begin{bmatrix} 0 & -r_2l_1m_2 \sin(q_2) & -2r_2l_1m_2 \sin(q_2) \\ l_1m_2r_2 \sin(q_2) & 0 & 0 \end{bmatrix} \begin{bmatrix} \dot{q}_1^2 \\ \dot{q}_2^2 \\ \dot{q}_1\dot{q}_2 \end{bmatrix} + \begin{bmatrix} B_{11} & B_{12} \\ B_{21} & B_{22} \end{bmatrix} \begin{bmatrix} \dot{q}_1 \\ \dot{q}_2 \end{bmatrix} \quad (1)$$

Scheidt and Rymer, 2000

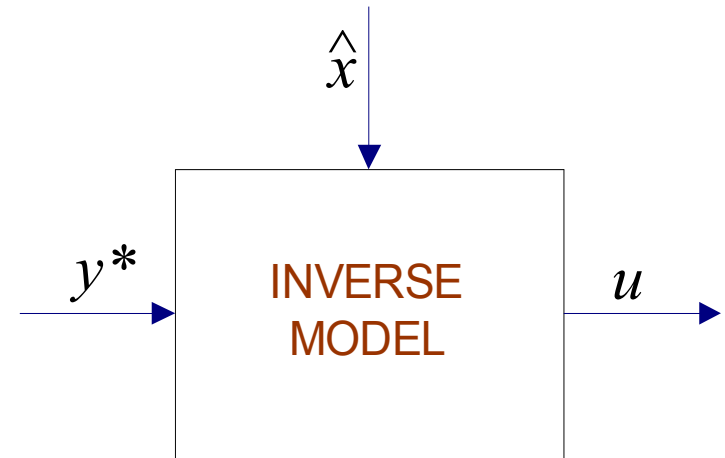
The two-joint arm is highly non-linear

Generally, we write:

$$\tau = \underbrace{D(\theta)\ddot{\theta}}_{\text{Inertia, interaction torques}} + \underbrace{C(\theta, \dot{\theta})\dot{\theta}}_{\text{Coriolis and centripetal forces}} + \underbrace{g(\theta)}_{\text{Gravity}}$$

Controlling a dynamical system

- Given a desired movement trajectory (position vs. time), what motor commands are required?
- Dynamics: $\dot{x} = f(x, u)$
- Inverse dynamics: $u = f^{-1}(\dot{x}^*, x)$
- Of course, f is not typically invertible
 - problem is “ill-posed”
- Optimal control can “regularize” problem:
 - optimal control given state $u = L(\hat{x} | \dot{x}^*)$
 - optimal estimation of state $\hat{x}(t) = K(y(t))$



Possible Input:

- desired extrinsic location of
- desired perceptual state
- desired intrinsic state (x^*)

Possible Output:

- motor unit activity
- signals to Brainstem (eye)
- signals to spinal cord (arm)

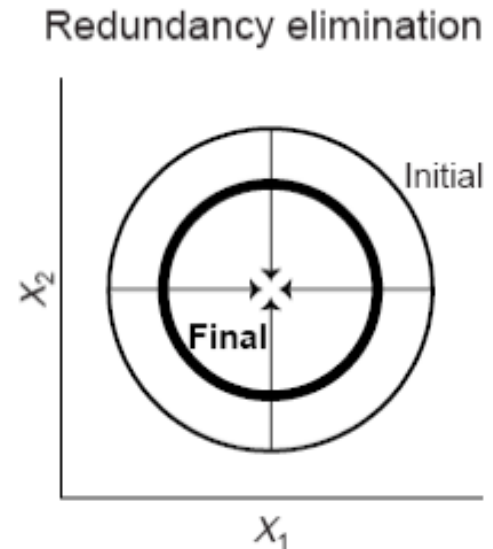
Optimal Feedback Control

- What is required to perform optimal control?
 - Optimal control given state
 - Optimal estimation of state
- No analytic solution holds for general optimal control problem
 - The two problems above are interlinked
 - Numerical solutions have been devised
- Model makes some testable behavioral predictions

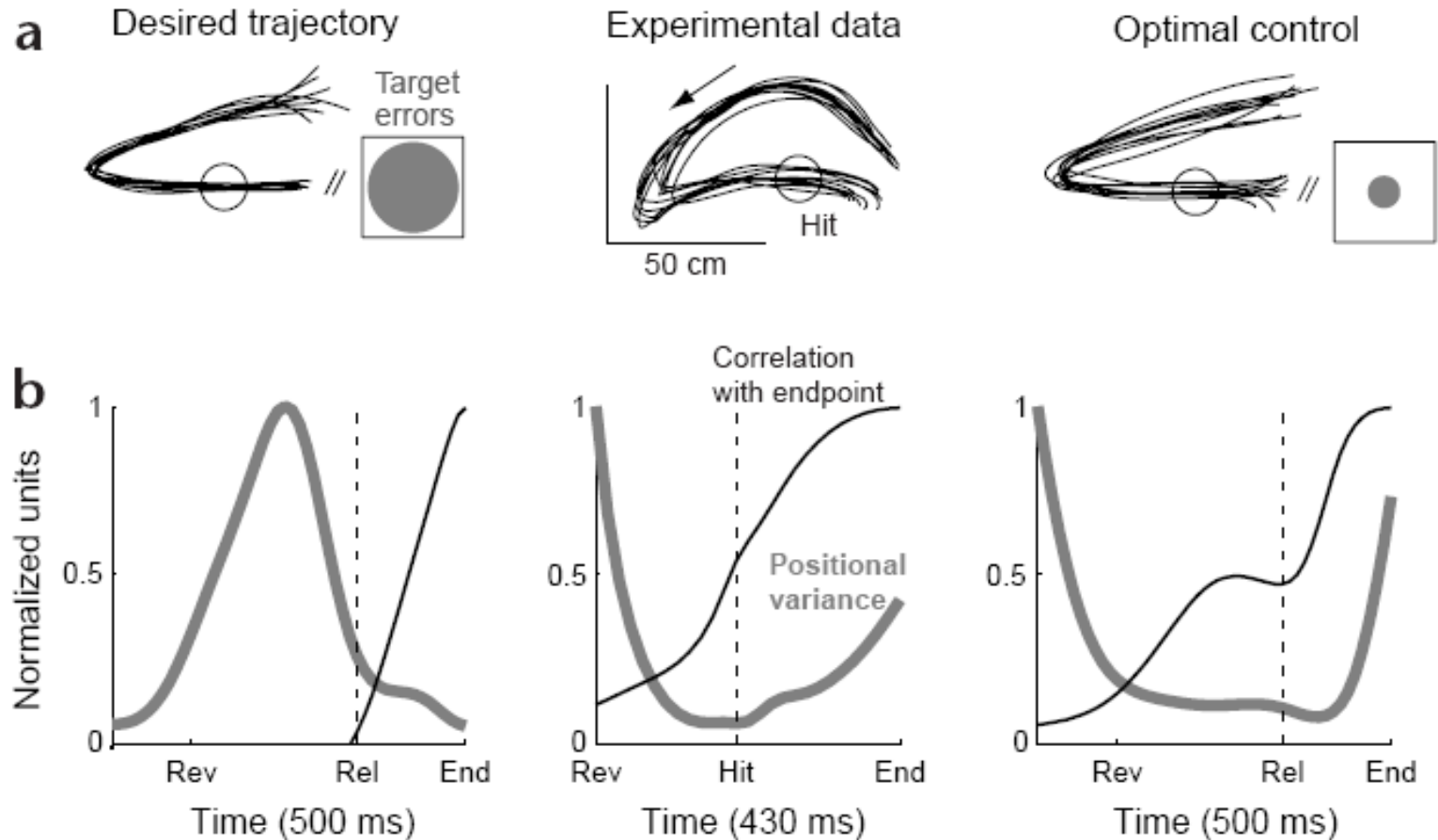
Minimum intervention principle

Assuming signal dependent noise, a general feature of optimal control emerges

Task: set X_1, X_2 so that $X_1 + X_2 = X^*$



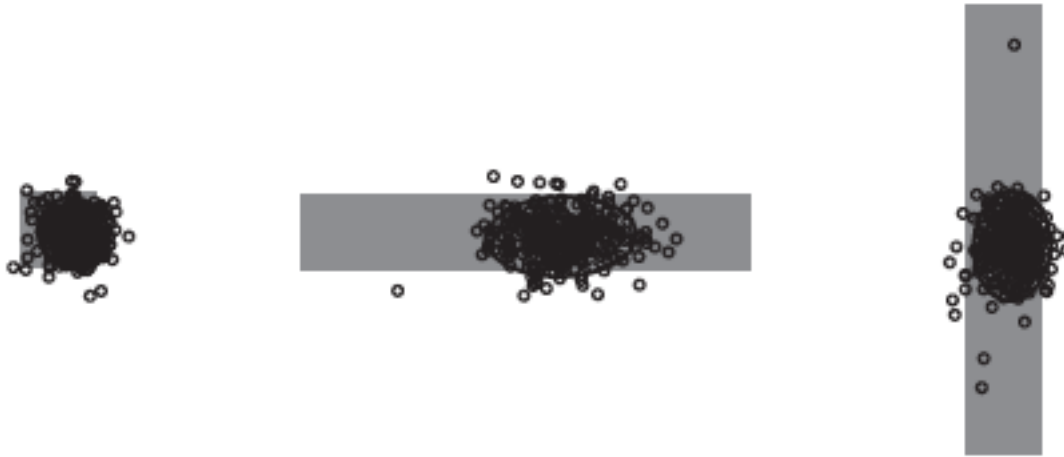
Minimum intervention principle



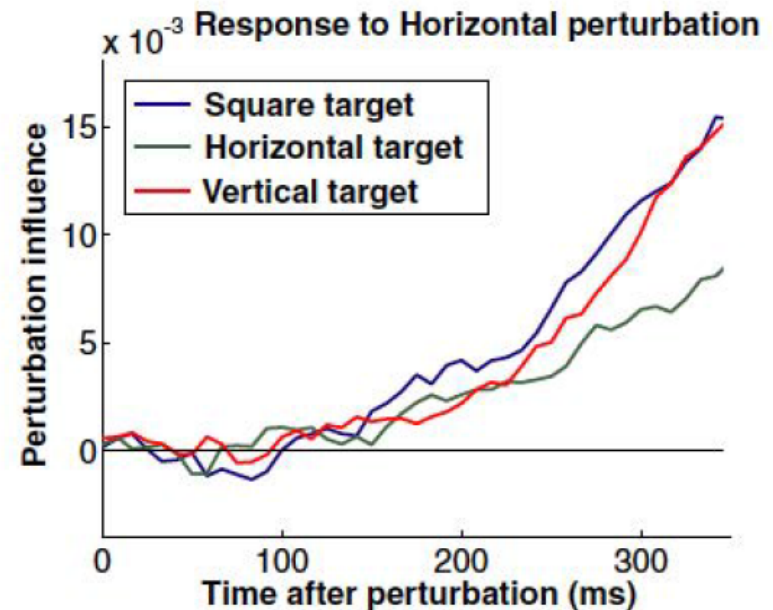
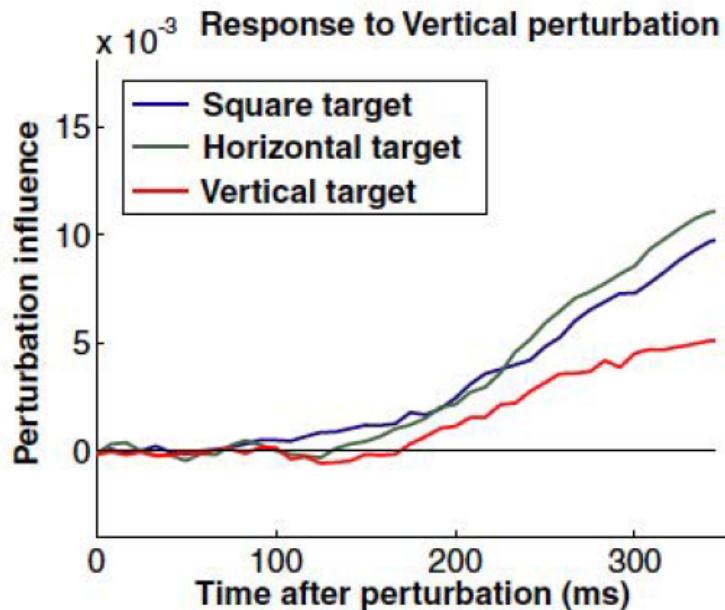
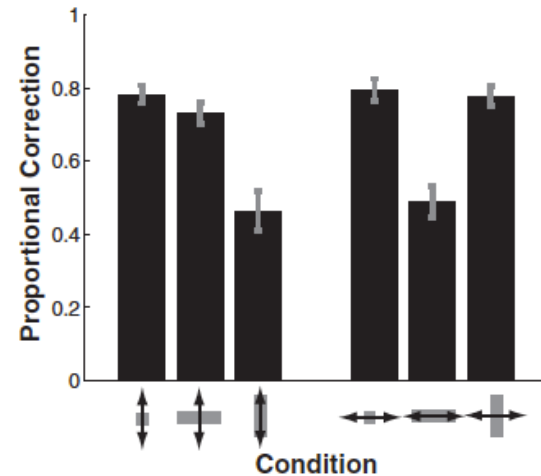
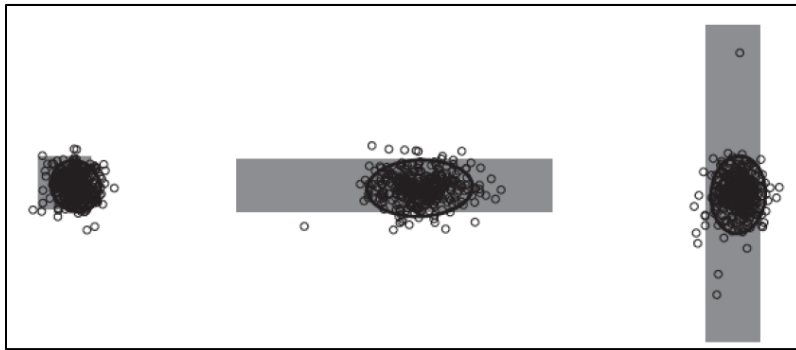
Note: the details of this “principle” rely heavily on the form of the noise model!

Minimum intervention principle

Endpoint precision with different target shapes



Minimum intervention principle



Optimal Feedback Control

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 - Optimal control given state
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- No analytic solution holds for general optimal control problem
 - The two problems above are interlinked
 - Numerical solutions have been devised
- Model makes some testable behavioral predictions
 - Minimum intervention principle
- Solution does exist for a special case:
 - Linear quadratic Gaussian control (LQG)
 - **Linear** dynamical system
 - **Quadratic** cost function
 - Additive **Gaussian** noise

Optimal Feedback Control

Linear quadratic Gaussian control (LQG)

- For a linear system with Gaussian noise

$$\dot{x}_k = Ax_{k-1} + Bu_{k-1} + v_{k-1}$$

$$y_k = Cx_k + w_k$$

v_k, w_k are white noise, Gaussian processes

and a quadratic cost function:

$$J = \sum_{k=1}^N x_k^T Q_k x_k + u_k^T R_k u_k$$

- The ***Separation Principle*** holds:
 - State estimation and optimal control can be solved independently
 - Control is performed as if had complete knowledge of state
 - “Linear-Quadratic Regulator” and “Kalman Filter”

Linear-quadratic regulator

Finite-horizon, discrete-time LQR

For a discrete-time linear system described by ^[1]

$$x_k = Ax_{k-1} + Bu_k$$

with a performance index defined as

$$J = \sum_{k=0}^N \left(x_k^T Q x_k + u_k^T R u_k \right) \quad \text{Cost function}$$

the optimal control sequence minimizing the performance index is given by

$$u_k = -F_k x_{k-1} \quad \text{Control law}$$

where

$$F_k = (R + B^T P_k B)^{-1} B^T P_k A$$

and P_k is found iteratively backwards in time by the dynamic Riccati equation

$$P_{k-1} = Q + A^T \left(P_k - P_k B (R + B^T P_k B)^{-1} B^T P_k \right) A$$

from initial condition $P_N = Q$.

Note: no output equation or feedback signals – assumes that state is known perfectly

What does this mean??

- Consider case $Q=I$, $R=0$
- Consider $Q=I$, $R=\text{scalar}$

Kalman Filter

- For linear Gaussian dynamical process:

$$x_k = Ax_{k-1} + Bu_{k-1} + v_{k-1}$$

$$y_k = Cx_k + w_{k-1}$$

$$v_k \sim N(0, V), \quad w_k \sim N(0, W)$$

- The Kalman filter is given by

Predict

Predicted (*a priori*) state estimate

$$\hat{x}_{k|k-1} = A \hat{x}_{k-1|k-1} + B u_k$$

Predicted (*a priori*) estimate covariance

$$P_{k|k-1} = A P_{k-1|k-1} A^T + V_k$$

Update

Innovation (measurement residual)

$$\tilde{y}_k = y_k - C \hat{x}_{k|k-1}$$

Innovation covariance

$$S_k = C P_{k|k-1} C^T + W_k$$

Optimal Kalman gain

$$K_k = P_{k|k-1} C S_k^{-1}$$

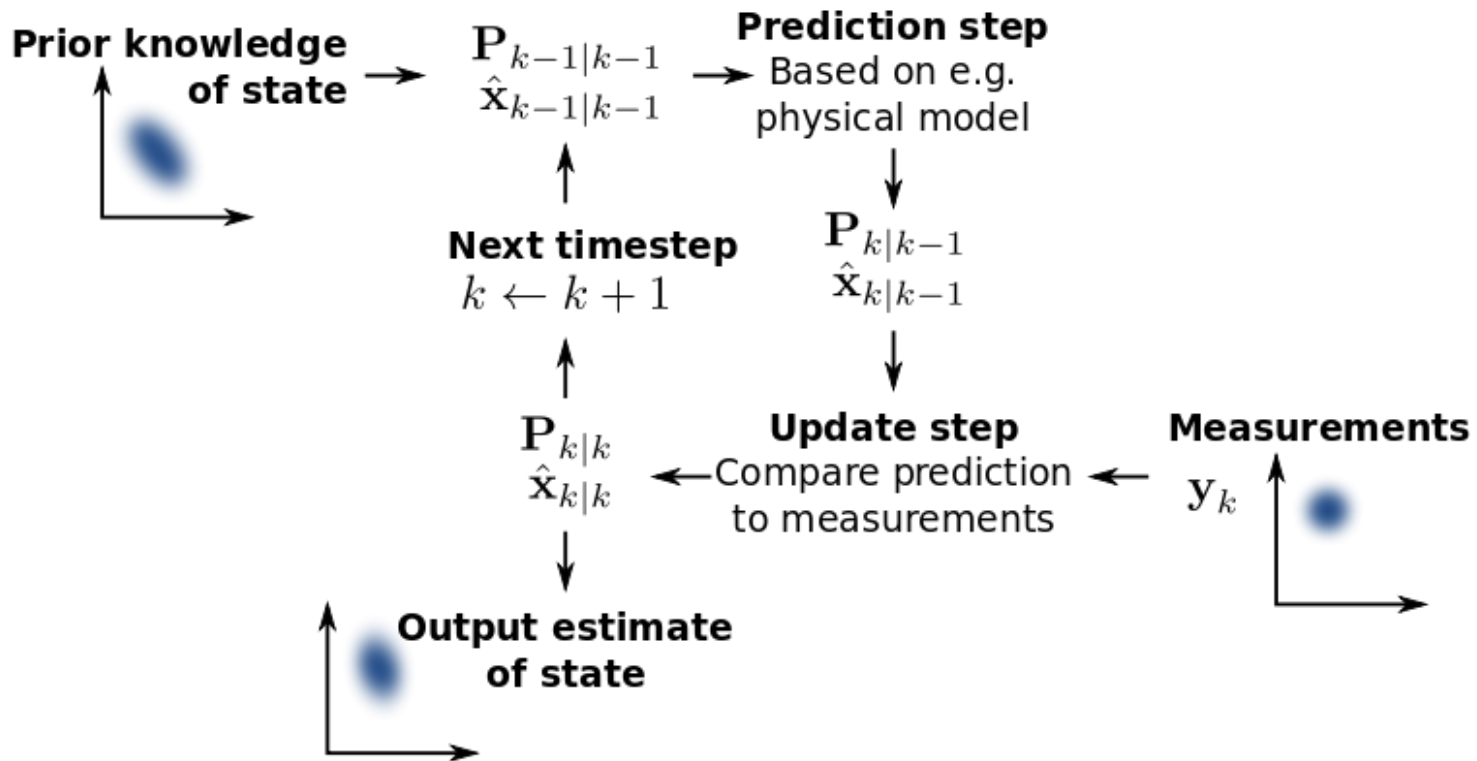
Updated (*a posteriori*) state estimate

$$\hat{x}_{k|k} = \hat{x}_{k|k-1} + K_k \tilde{y}_k$$

Updated (*a posteriori*) estimate covariance

$$P_{k|k} = (I - K_k C) P_{k|k-1}$$

Kalman Filter

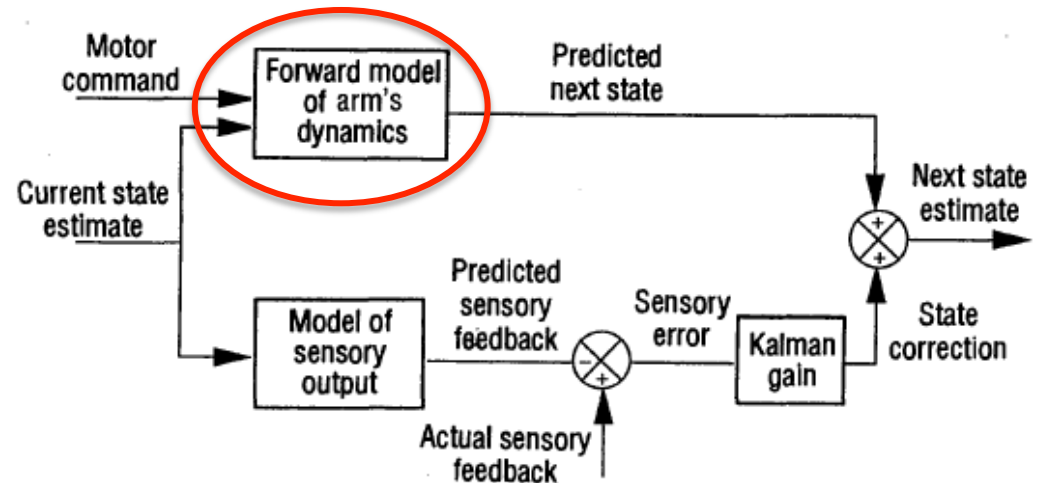


Kalman Filter

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$$\hat{x}_{k|k} = \hat{x}_{k|k-1} + K_k (y_k - C\hat{x}_{k|k-1})$$

- An example of an “internal model”:
 - “forward model” of the plant dynamics
 - “efference copy”



Sensory integration as Kalman Filter

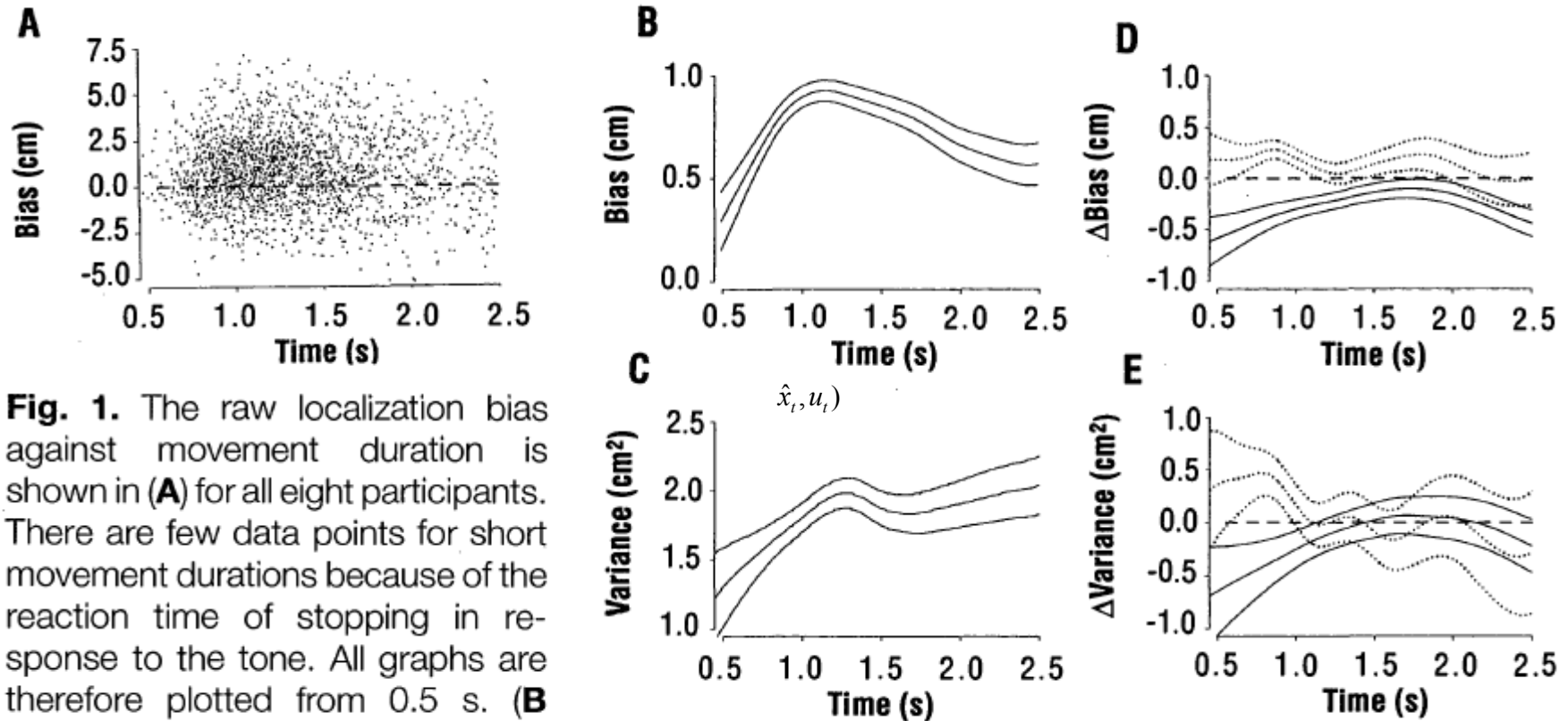
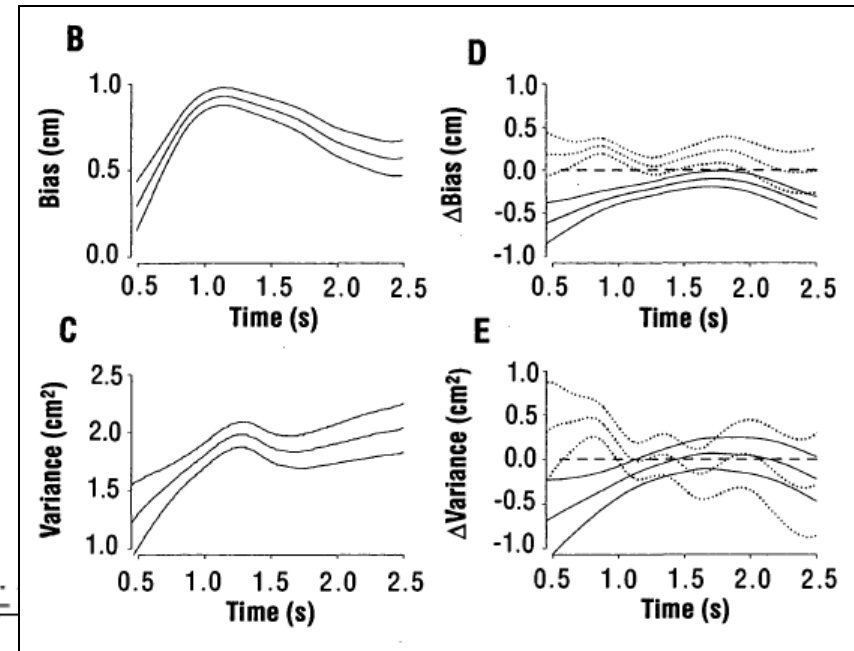
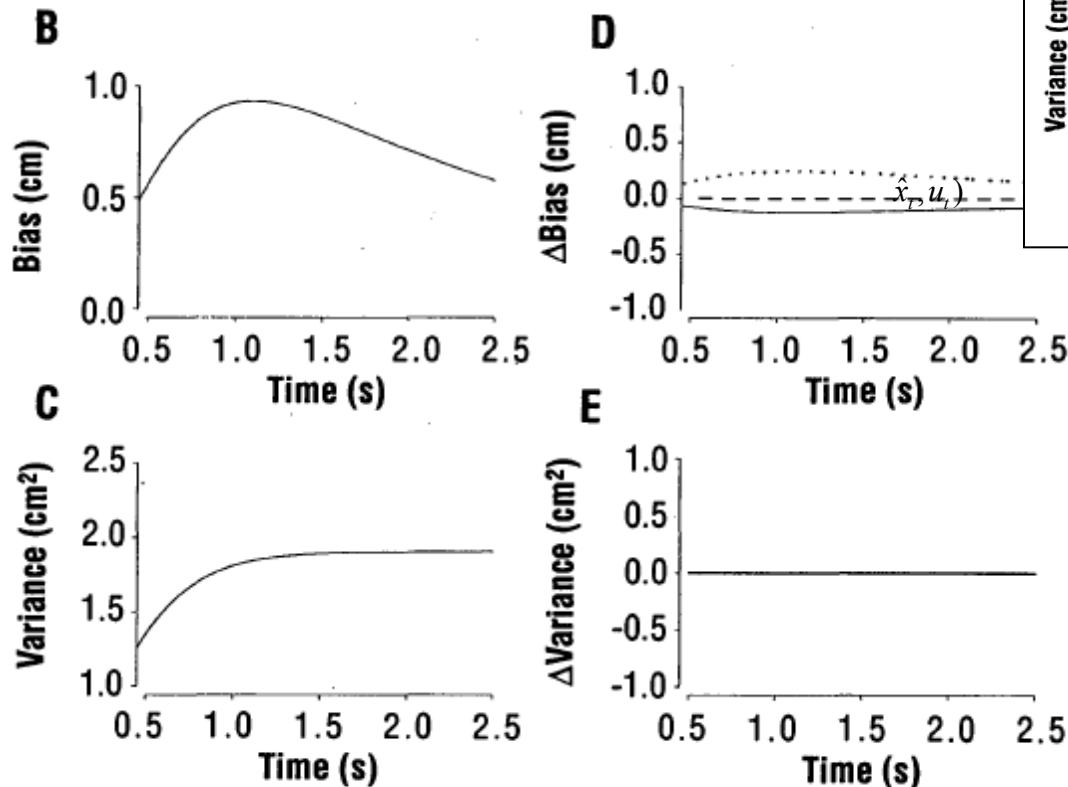


Fig. 1. The raw localization bias against movement duration is shown in (A) for all eight participants. There are few data points for short movement durations because of the reaction time of stopping in response to the tone. All graphs are therefore plotted from 0.5 s. (B through E) The main effect fits of the

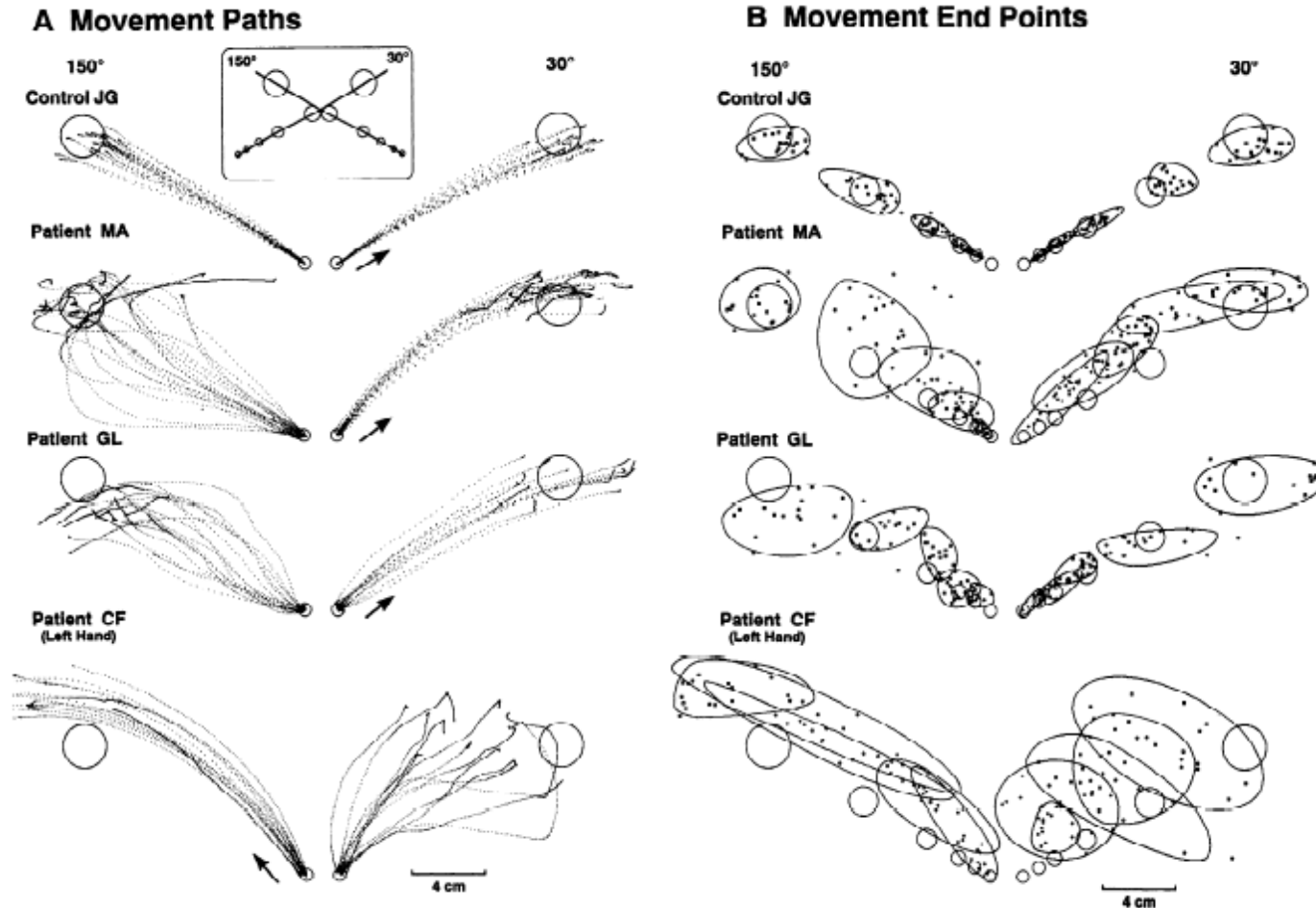
Sensory integration as Kalman Filter

To get this to work, had to assume that force output is underestimated (??)

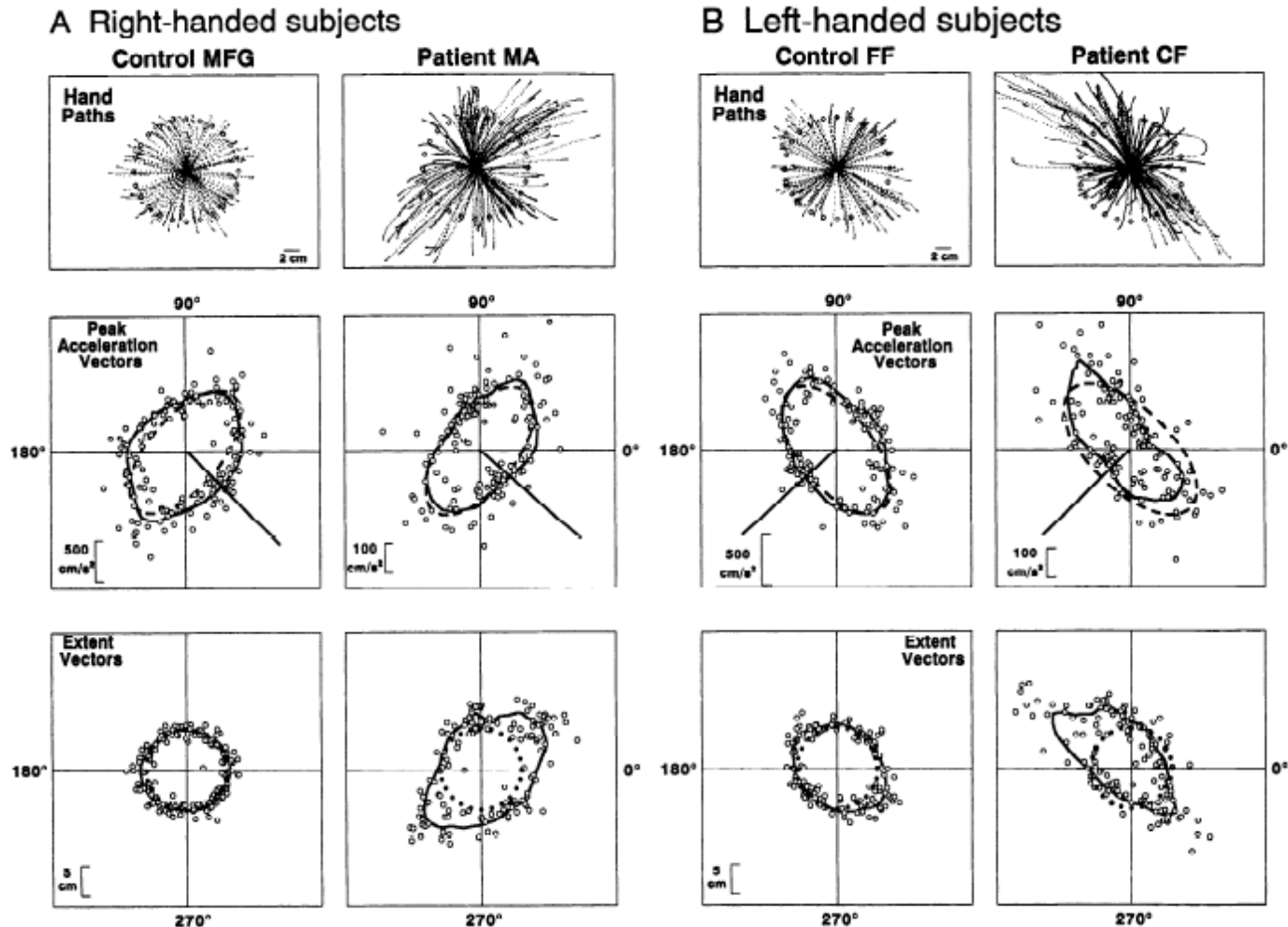


The role of proprioceptive feedback

The effect of Large Sensory Fiber Neuropathy



Effects of inertia on initial movement

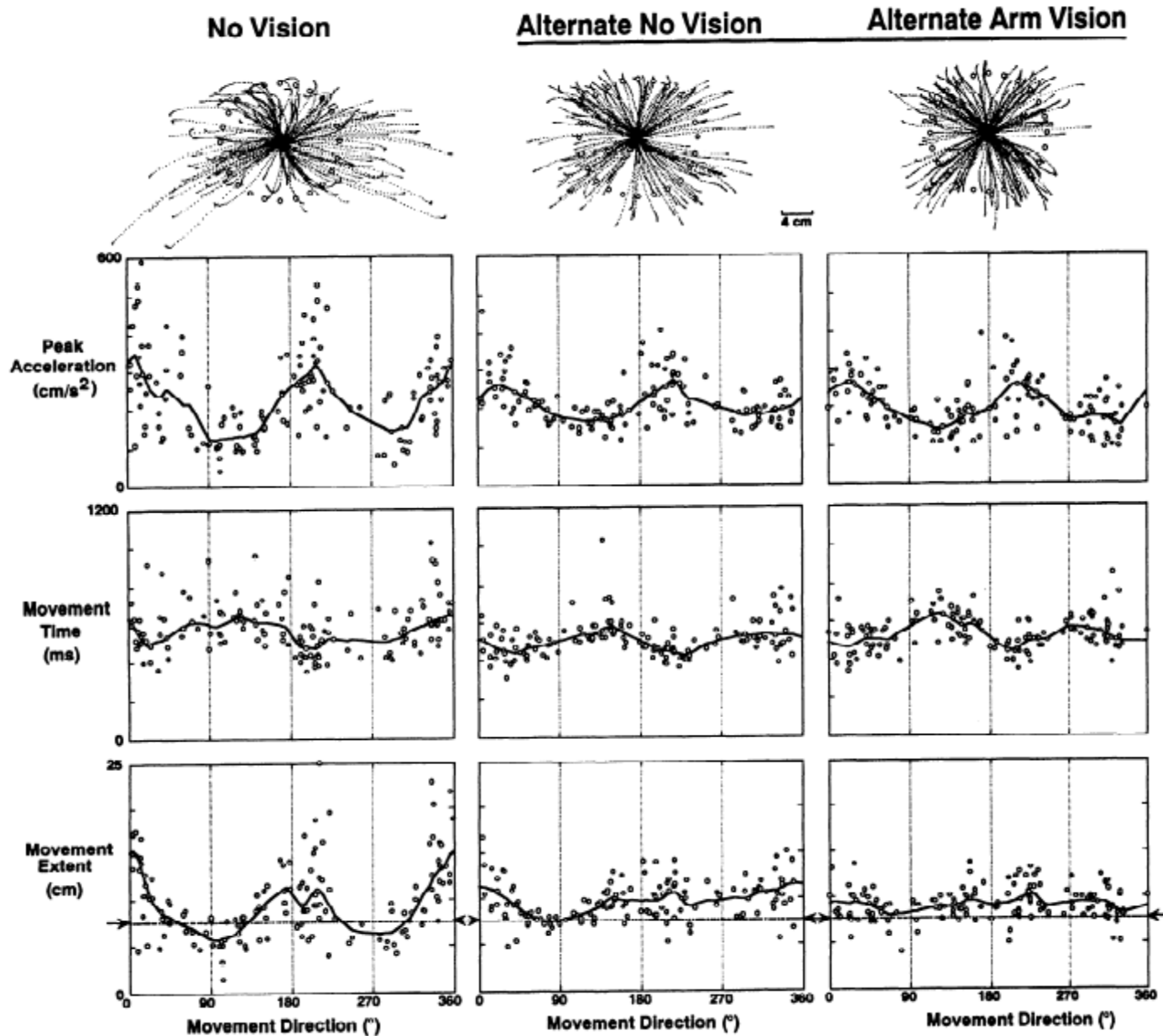


Normals compensate for inertia with movement time

Why are deafferented patients impaired?

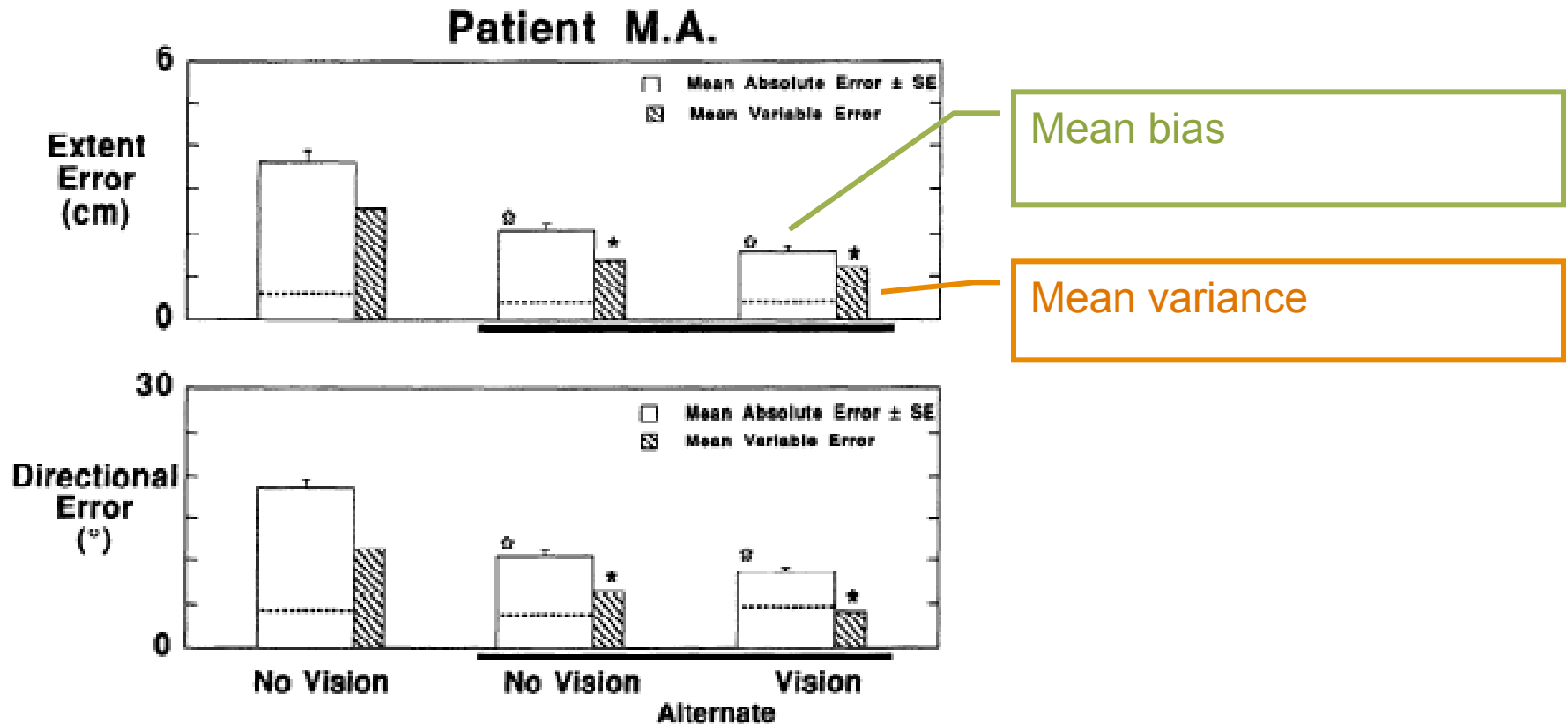
- Trouble reaching because they don't know where their hands are
- What about when they have visual feedback?

Vision helps, and the benefit persists



Ghez, Gordon,
and Ghilardi
(1995)

Vision helps, and the benefit persists



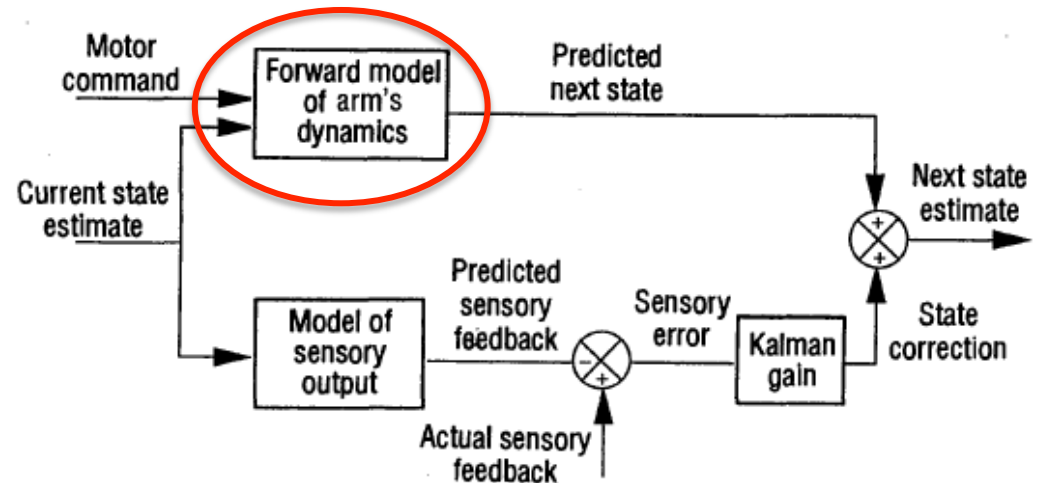
Ghez, Gordon,
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Why does prior vision help?

- For linear Gaussian dynamical process:
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- The Kalman filter: $\hat{x}_{k|k-1} = A\hat{x}_{k-1|k-1} + Bu_{k-1}$
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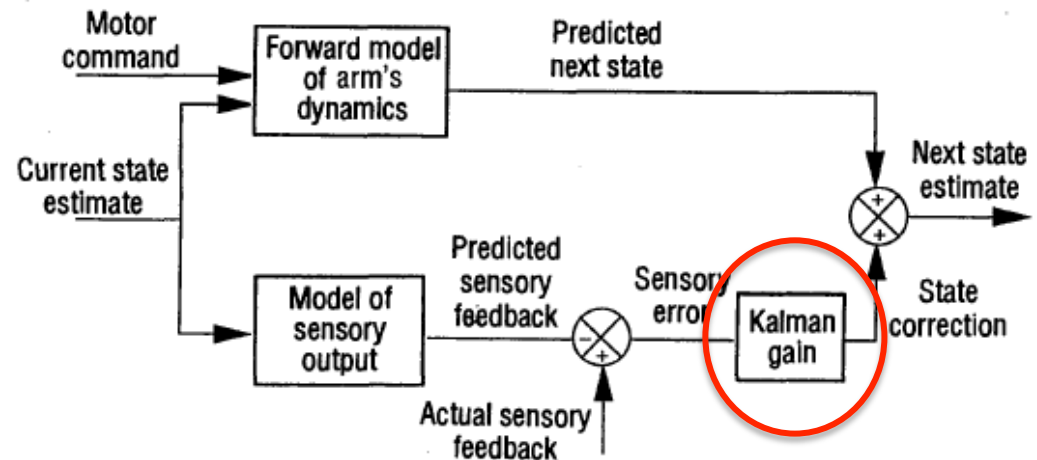


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- What does the Kalman gain do??



Optimal Estimation


How should multiple sensory inputs be combined – “sensory integration”?

If goal is *accurate perception*, it is reasonable consider the variability of each input modality:

$$\begin{array}{ll} \hat{\mathbf{x}}_{\text{vis}} & \text{has variance } \sigma_{\text{vis}}^2 \\ \hat{\mathbf{x}}_{\text{prop}} & \text{has variance } \sigma_{\text{prop}}^2 \end{array} \quad \rightarrow \quad \hat{\mathbf{x}}_c = \frac{\sigma_{\text{prop}}^2}{\sigma_{\text{vis}}^2 + \sigma_{\text{prop}}^2} \hat{\mathbf{x}}_{\text{vis}} + \frac{\sigma_{\text{vis}}^2}{\sigma_{\text{vis}}^2 + \sigma_{\text{prop}}^2} \hat{\mathbf{x}}_{\text{prop}}$$

Optimal Estimation

\hat{x}_{vis} has variance σ_{vis}^2
 \hat{x}_{prop} has variance σ_{prop}^2



$$\hat{x}_c = \frac{\sigma_{\text{prop}}^2}{\sigma_{\text{vis}}^2 + \sigma_{\text{prop}}^2} \hat{x}_{\text{vis}} + \frac{\sigma_{\text{vis}}^2}{\sigma_{\text{vis}}^2 + \sigma_{\text{prop}}^2} \hat{x}_{\text{prop}}$$

“Minimum Variance” is also “Maximum Likelihood” for the case of independent Gaussian signals

$$K_k = P_{k|k-1} C \left(C P_{k|k-1} C^T + W_k \right)^{-1} \approx \frac{\text{variance of } \hat{x}_{k|k-1}}{\left(\text{variance of } \hat{x}_{k|k-1} + \text{variance of } y \right)}$$

The Kalman gain represents the “maximum likelihood” way to combine **current sensory information** with predictions from past experience (i.e., **prior information**) ... Bayesian integration

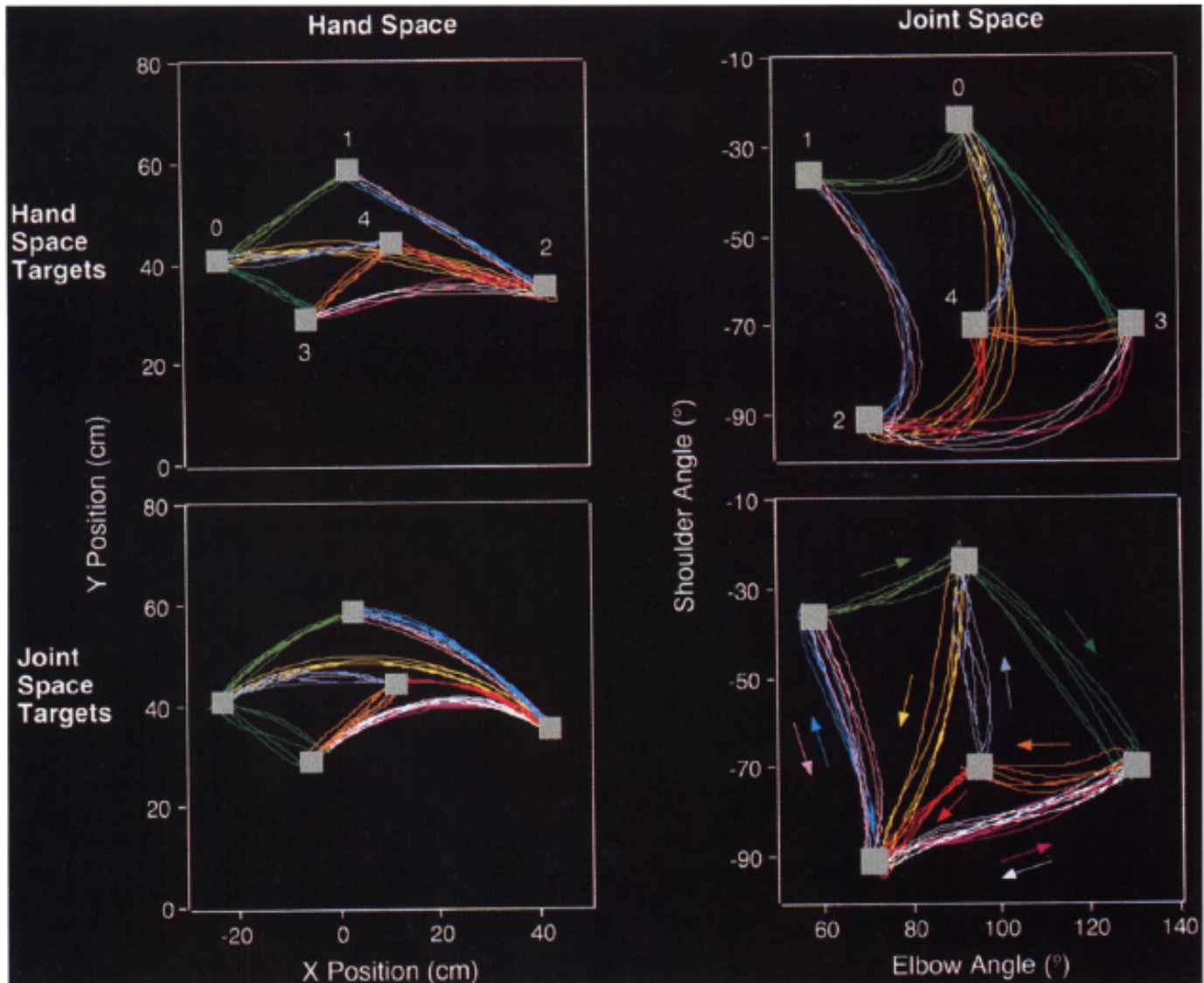
Summary so far

- Optimal feedback control
 - Minimum intervention principle
- Special case: LQG
 - Separation principle
 - Kalman filter

Learning

- Optimal control, optimal estimation require learning
- Optimal control:
 - Movements that minimize cost functions
 - Need to learn “plant”, costs, etc
- Sensory integration
 - Combine signals according to their statistics
 - Need to learn statistics
- Bayesian integration
 - Need time to acquire “prior information”
- A brief survey of sensorimotor learning

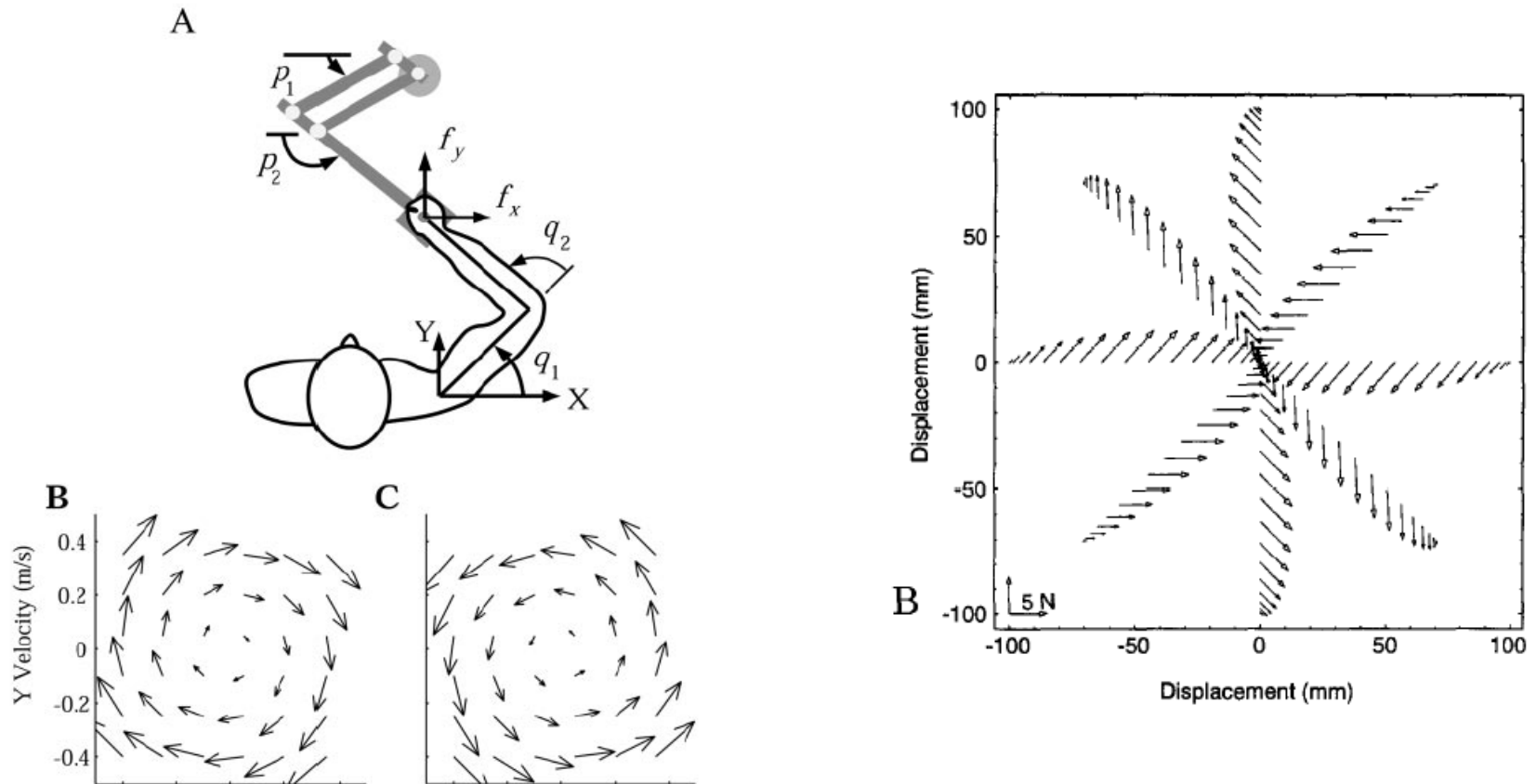
Optimality requires learning



Flanagan and Rao (1995)

Optimality requires learning

Most well-known example: reaching in a “curl-viscous” force field:



Shadmehr and Mussa Ivaldi(1994)

Prism Adaptation

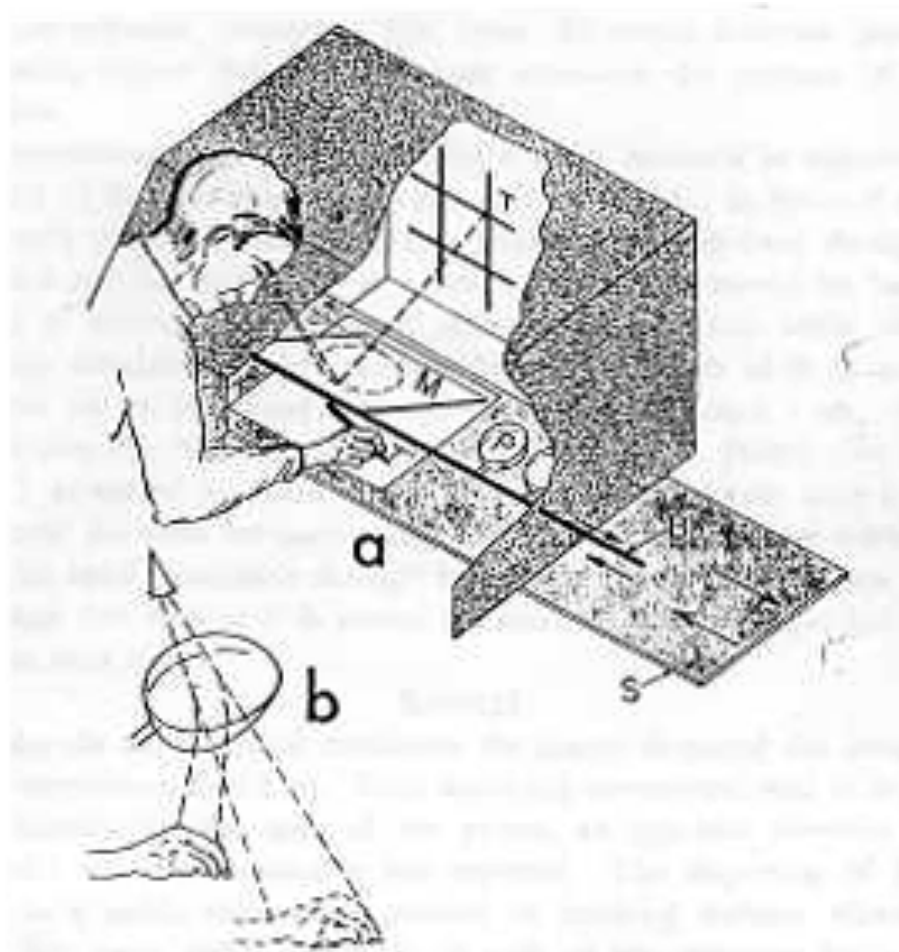
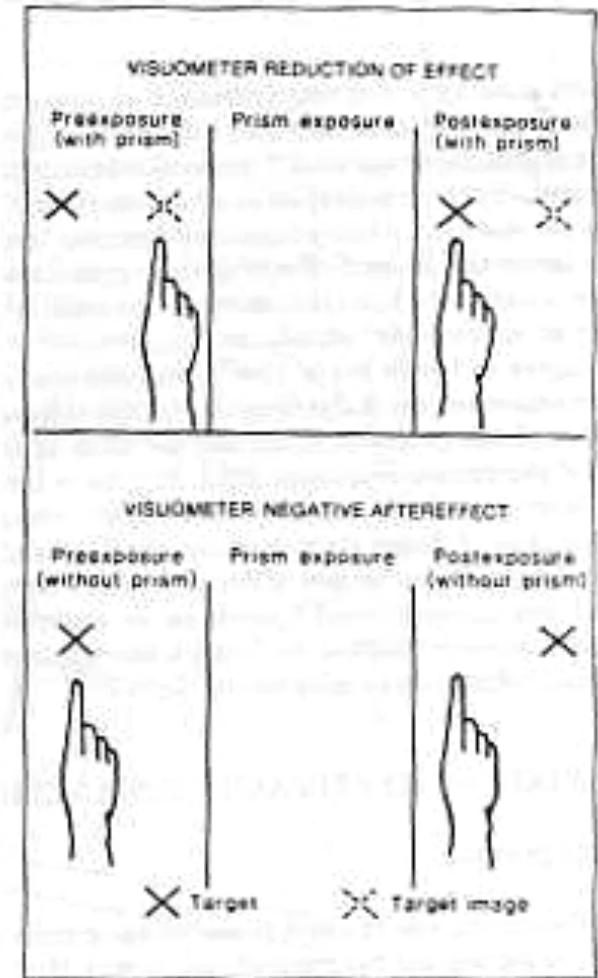


FIG. 1. Schematic representation of the apparatus.



Held and Gottlieb (1958)

What drives learning?

Task-specific learning: an error corrective learning model

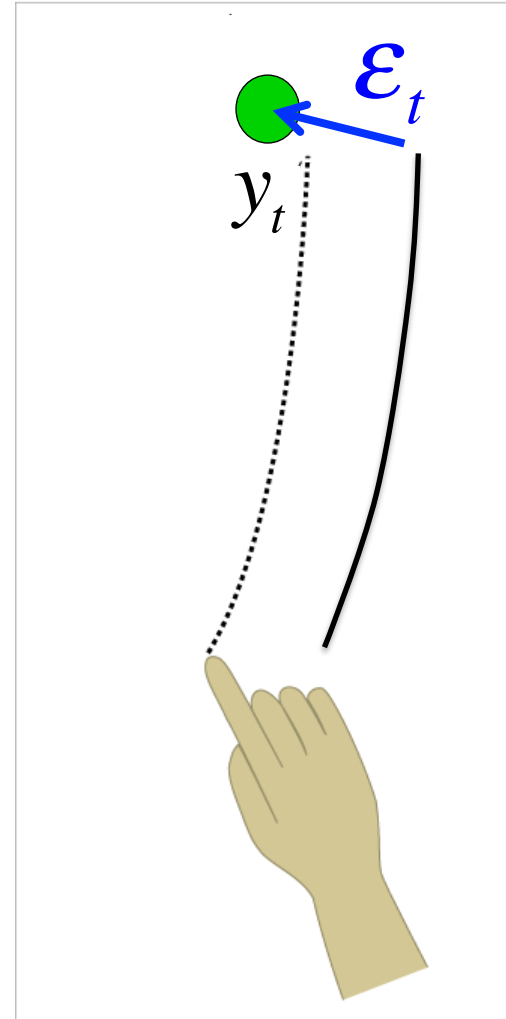
Let y_t be the reach endpoint on trial t , and the “state” x_t be the mean endpoint:

$$y_t = x_t + w_t, \quad \text{where } w_t \sim N(0, R)$$

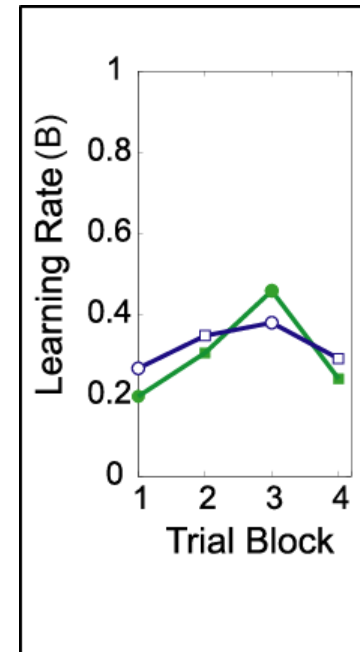
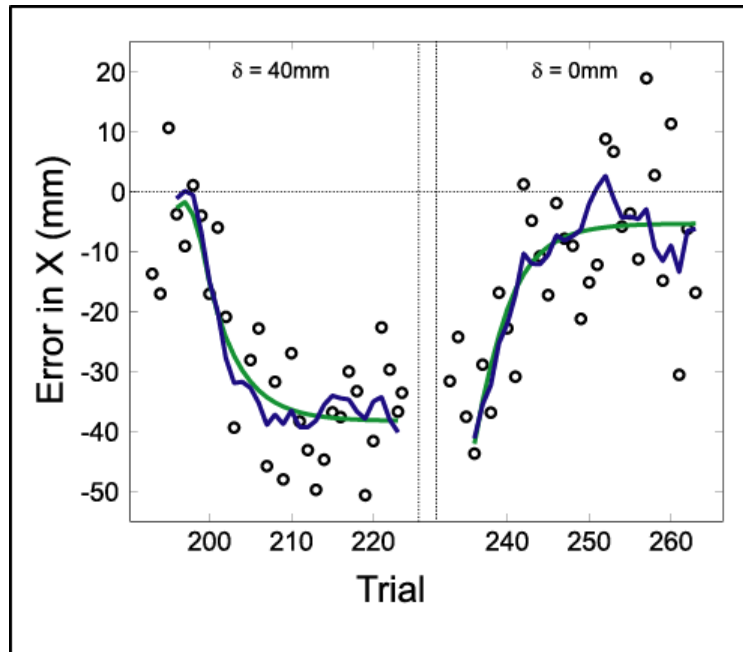
Learning can be modeled as incremental error correction driven by error ε :

$$x_{t+1} = Ax_t + B\varepsilon_t + u_t, \quad \text{where } u_t \sim N(0, Q)$$

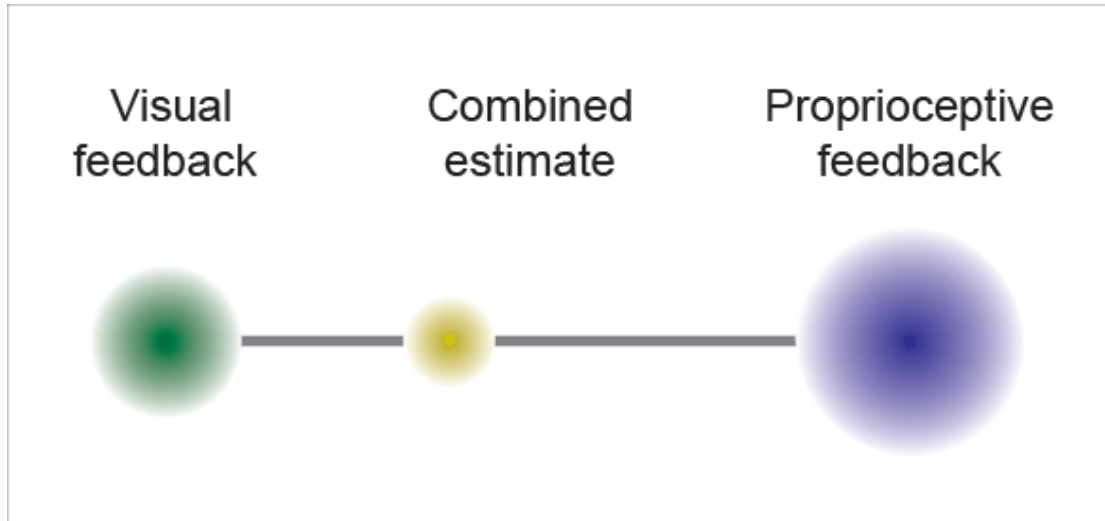
The model is a linear dynamical system
We can fit parameters to trial-by-trial
experimental data



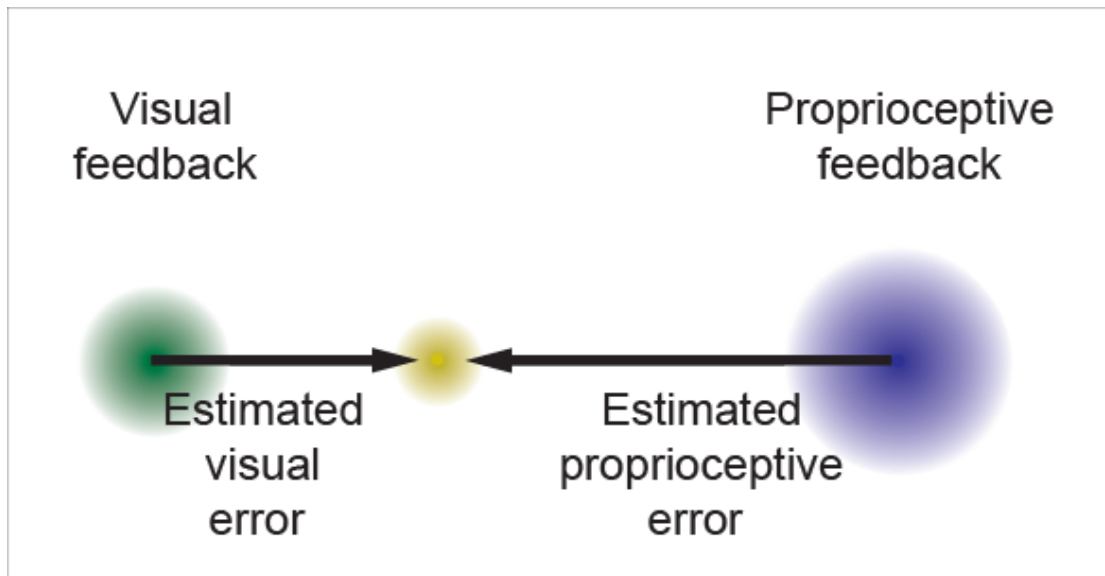
Sample Model Fits



Sensory integration is also learned



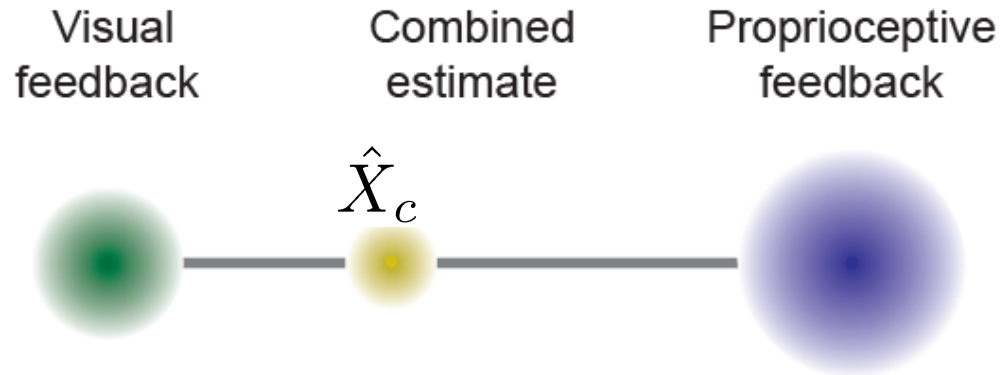
Integration



Adaptation

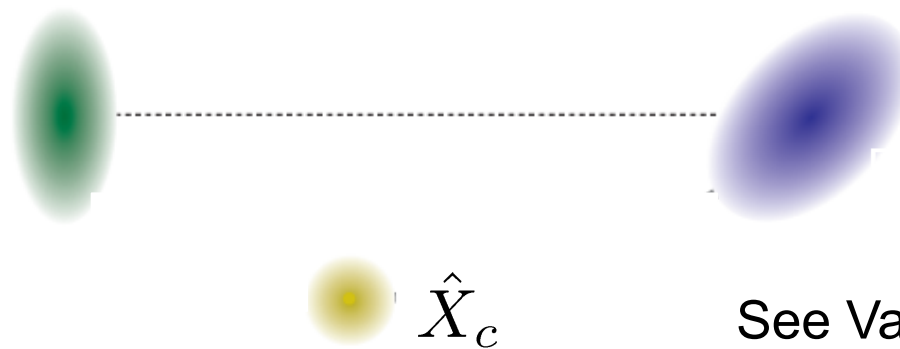
Maximum likelihood sensory integration

Sensory integration



Maximum likelihood sensory integration

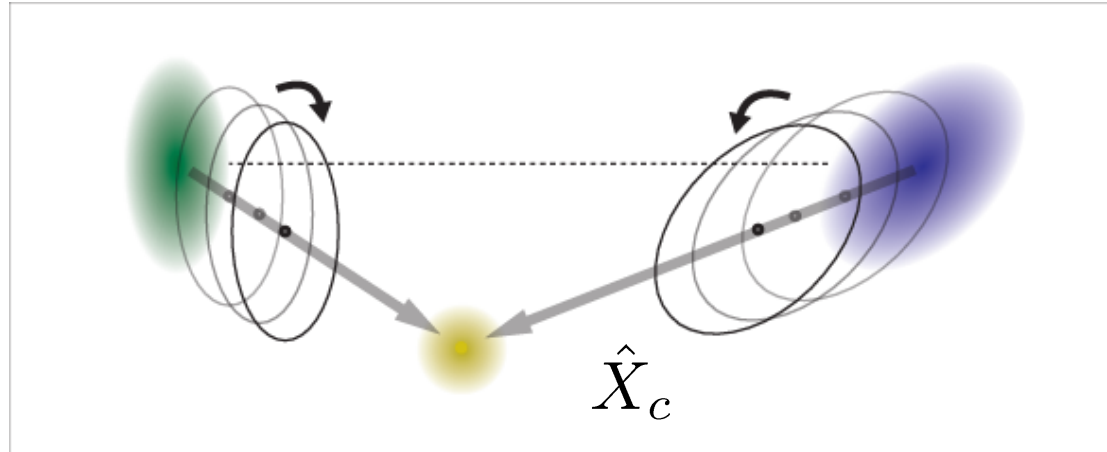
Sensory integration



See VanBeers et al., 1999

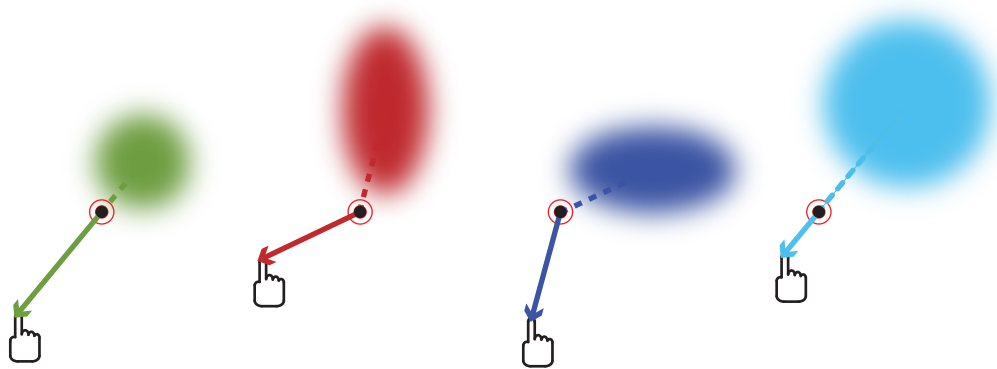
- Where does discrepancy come from?
- What happens if discrepancy persists?
 - Sensory adaptation, “recalibration” (Simani, McGuire and Sabes, 2007)
- How should the sensory modalities adapt?
 - A “credit assignment” problem

Integration and adaptation

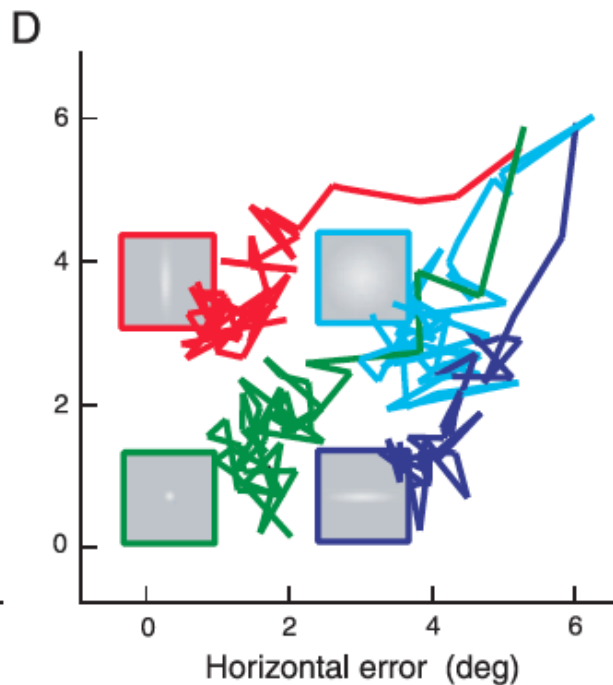
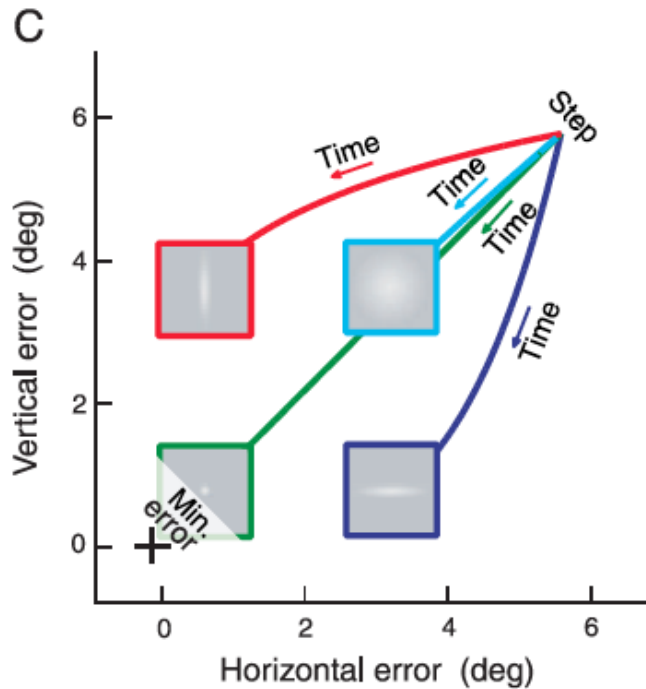


- An iterative version of Expectation-Maximization (EM) algorithm (Ghahramani, 1995)
- Can also formulate as a Kalman filter (brain is trying to estimate “bias”)
- Somewhere in-between supervised and unsupervised learning
- Again, this is the **normal state**

Integration and adaptation



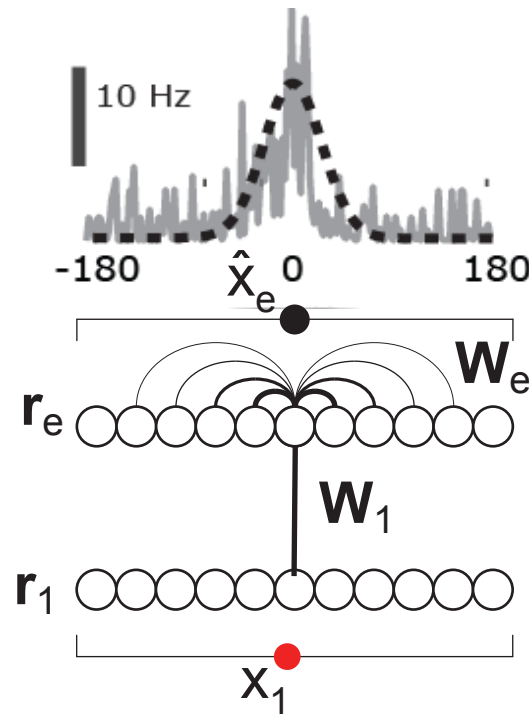
Visual shifts with different uncertainty



result in different pattern of adaptation

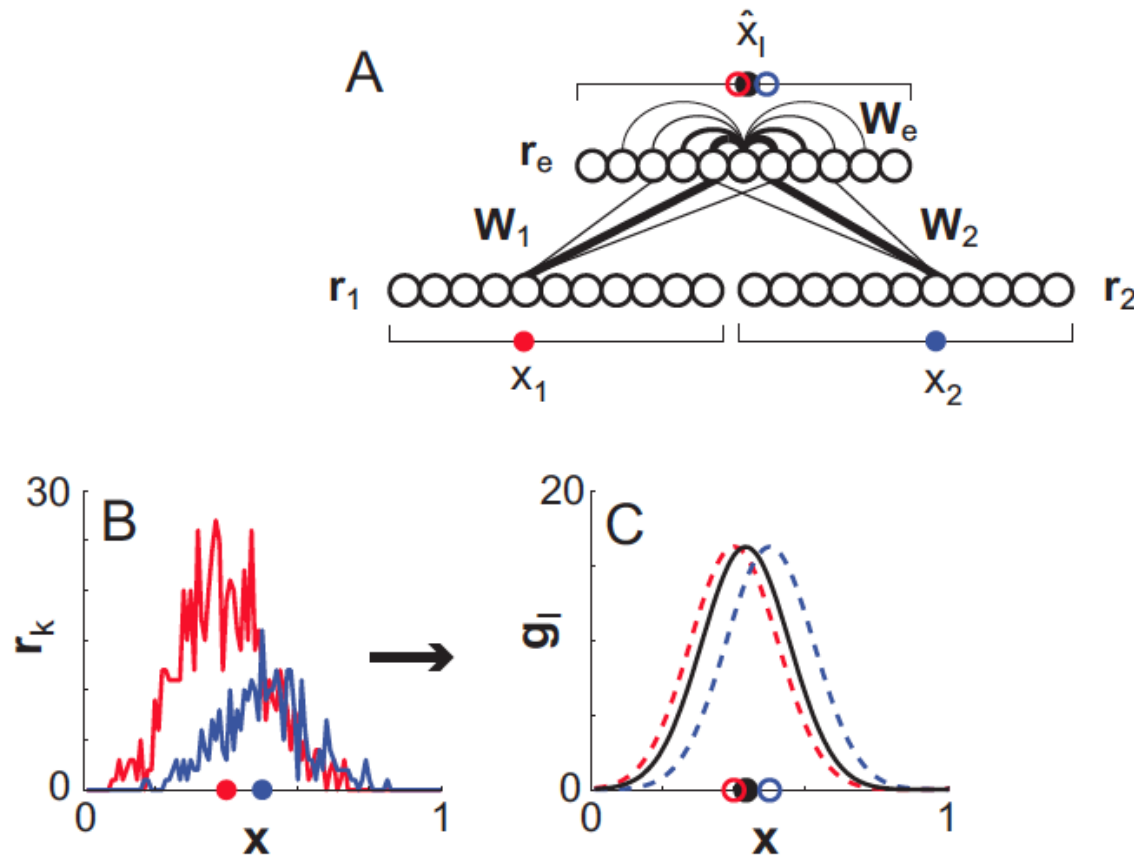
Adaptive sensory integration

- Network performs ML integration



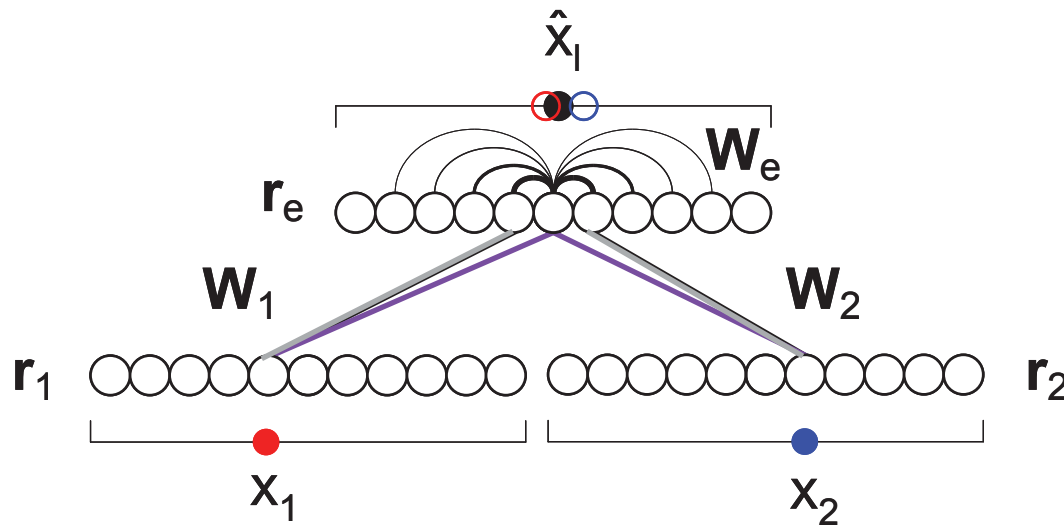
Adaptive sensory integration

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Adaptive sensory integration

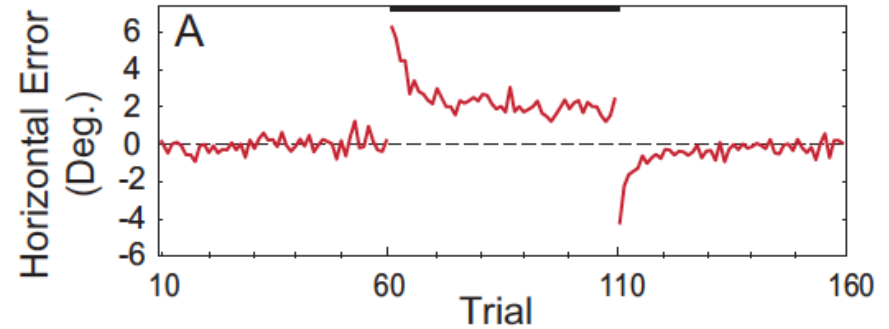
- Network adapts, using same scheme as EM model (integrated estimate as “teacher”)
 - Hebbian learning at the inputs



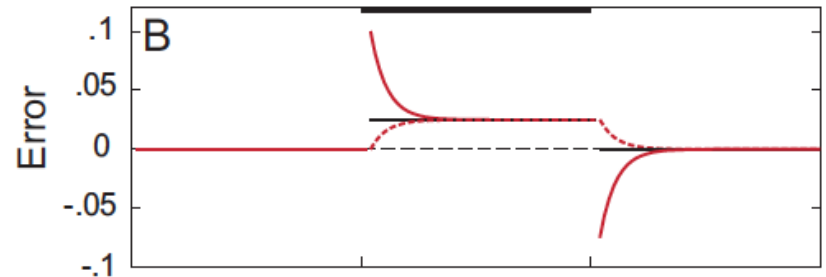
Adaptive sensory integration

Models capture
temporal dynamics of
learning

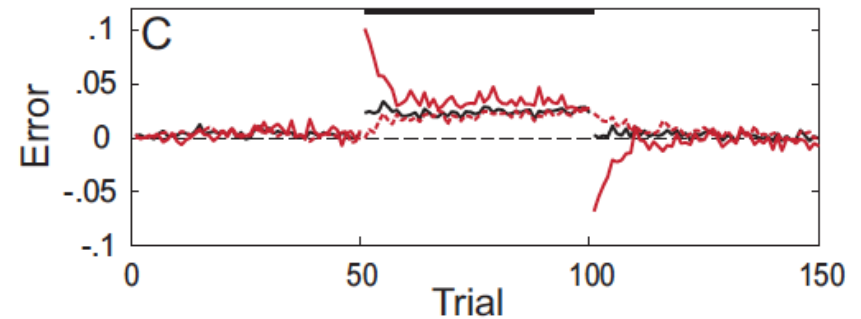
EXPERIMENTAL
DATA



EM
MODEL



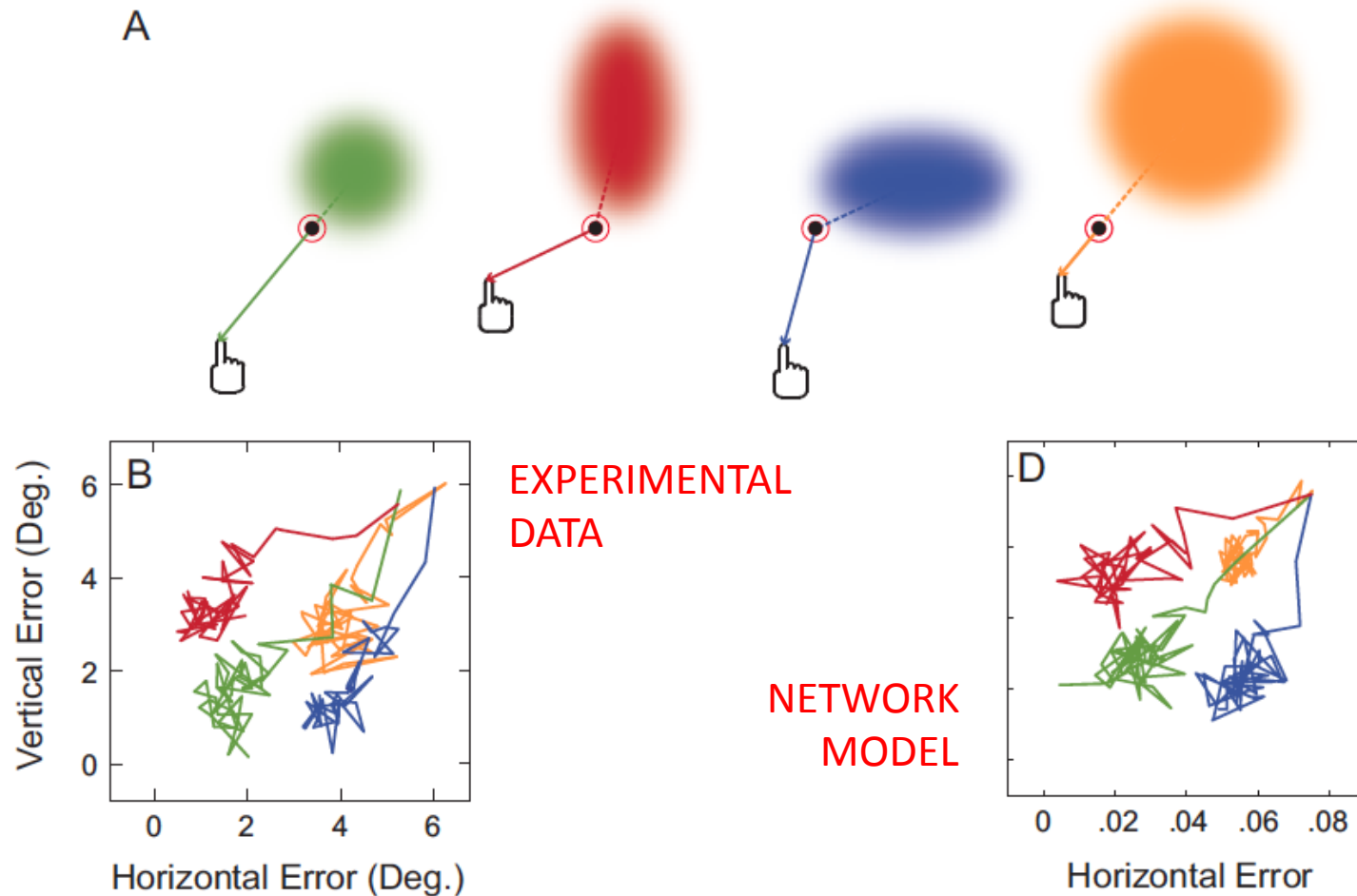
NETWORK
MODEL



Biddle Snead and Sabes, *unpub.*

Adaptive sensory integration

Models capture spatial dynamics of learning, learning spatial anisotropy *de novo*



Burge and Banks, J Vision (2007)

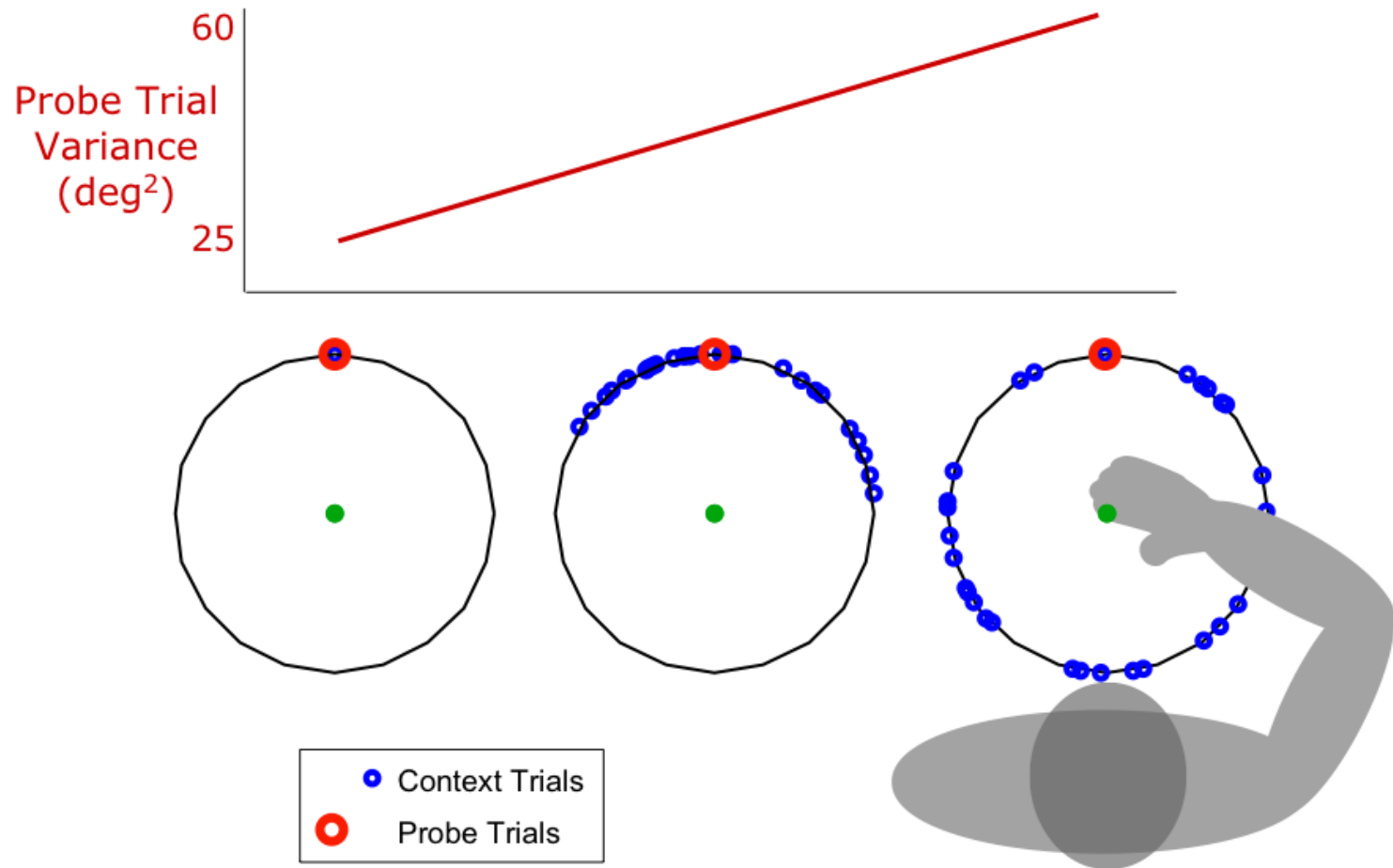
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Incorporating recent experience through learning



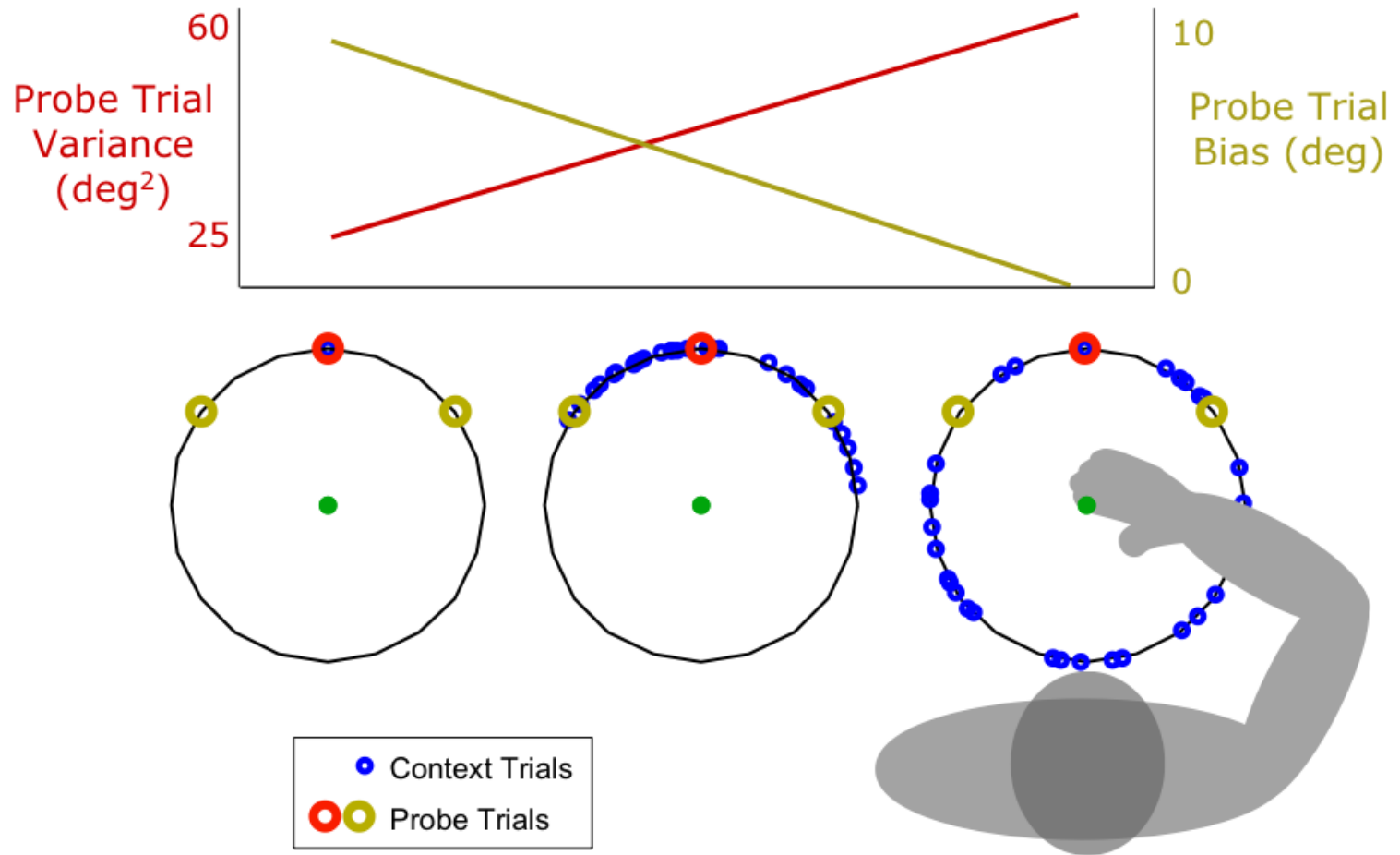
Tim Verstynen

Incorporating recent experience through learning



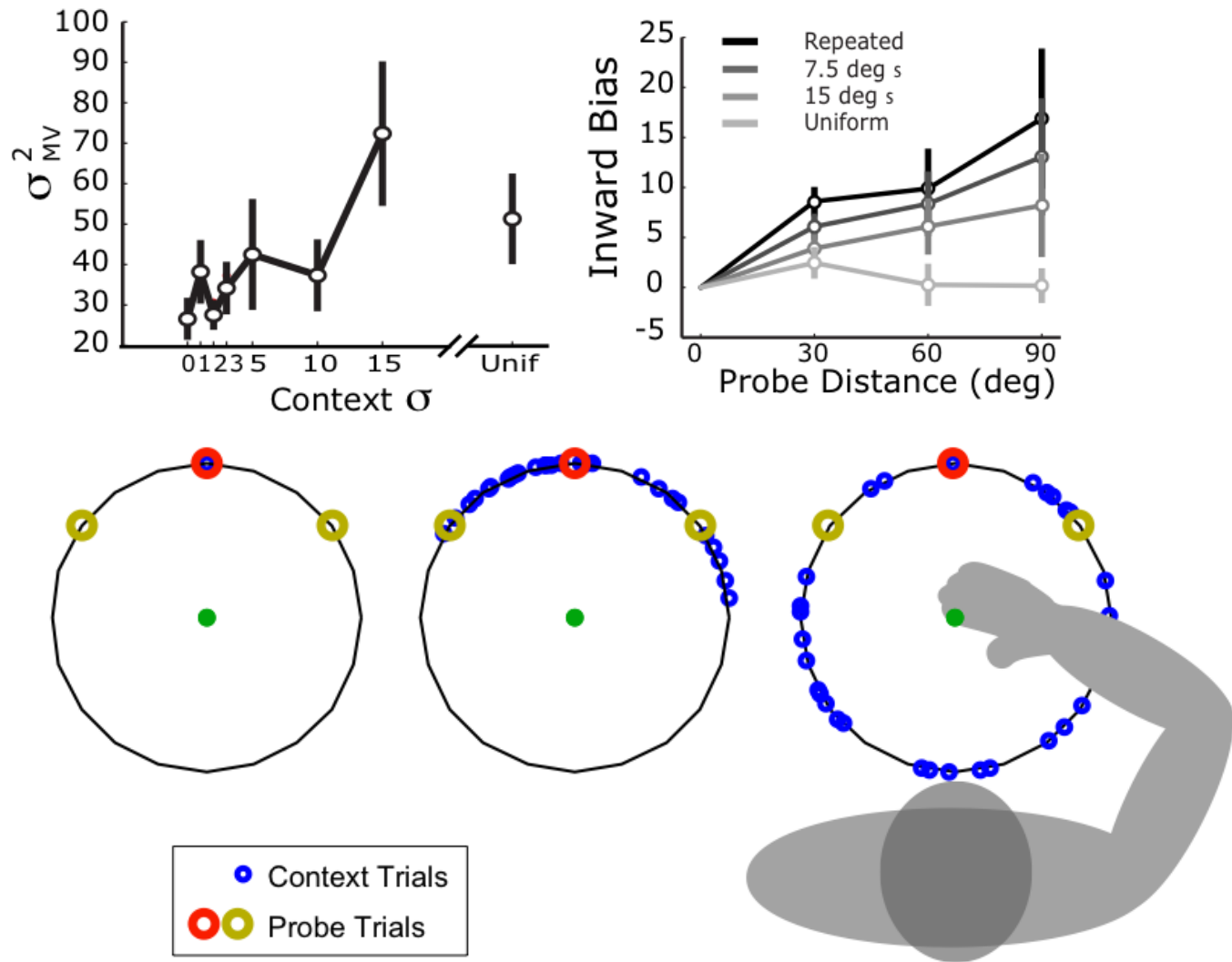
Practice makes perfect on a short timescale ... but at a cost.

Incorporating recent experience through learning



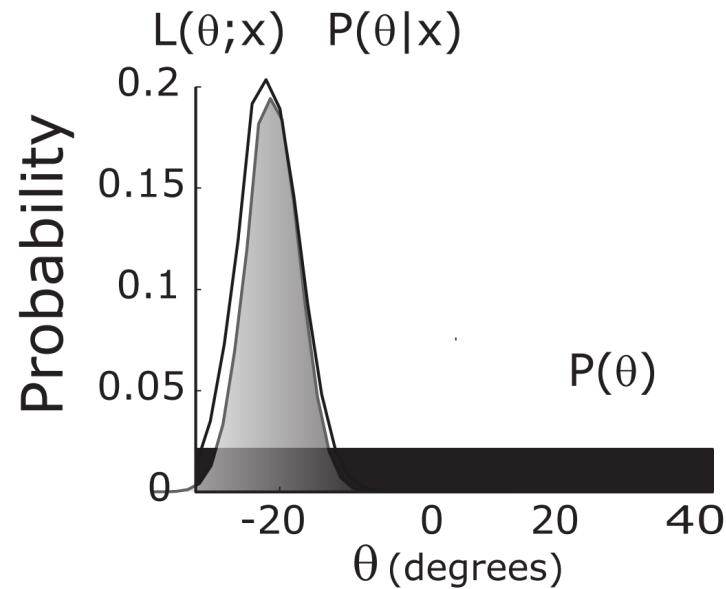
There is a bias-variance tradeoff

Incorporating recent experience through learning

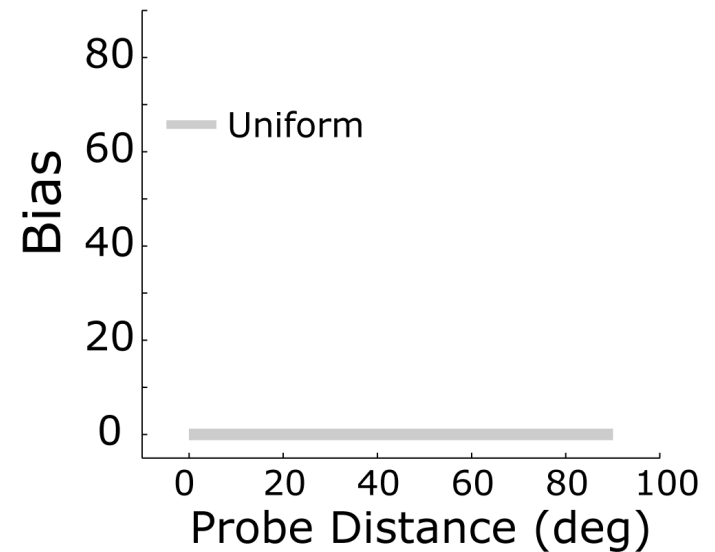
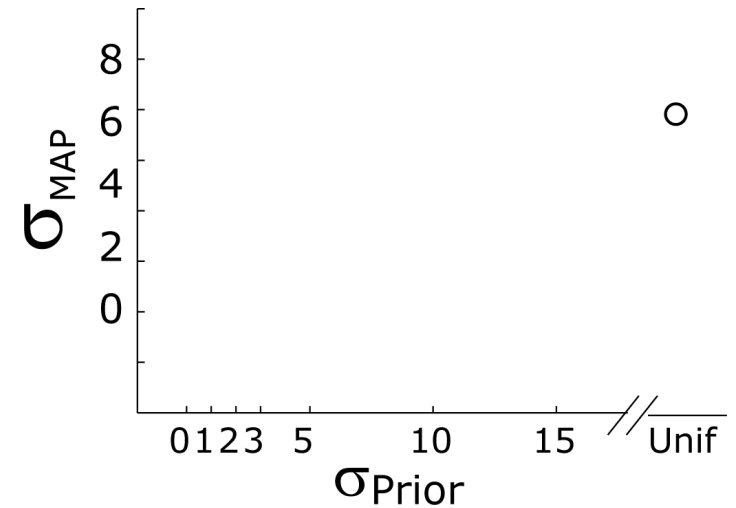


What causes this bias-variance tradeoff?

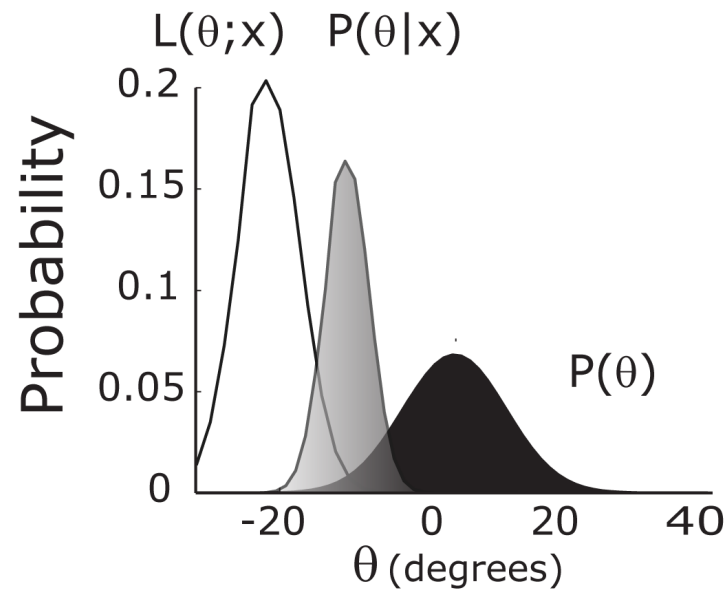
Bayesian integration of prior data



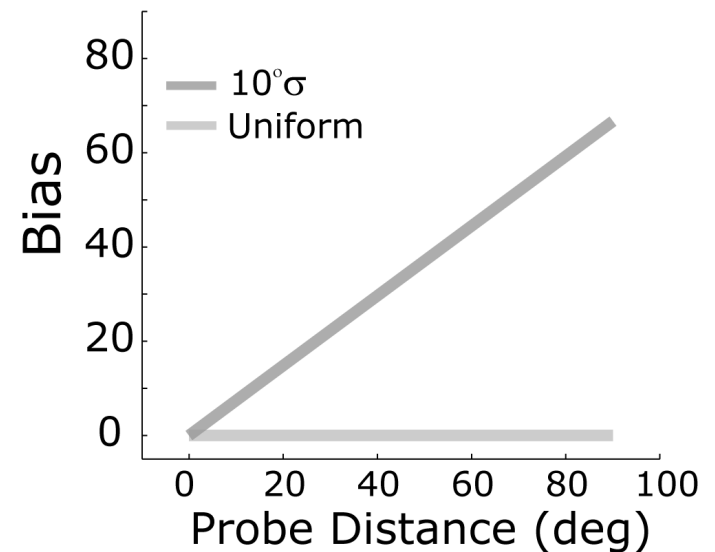
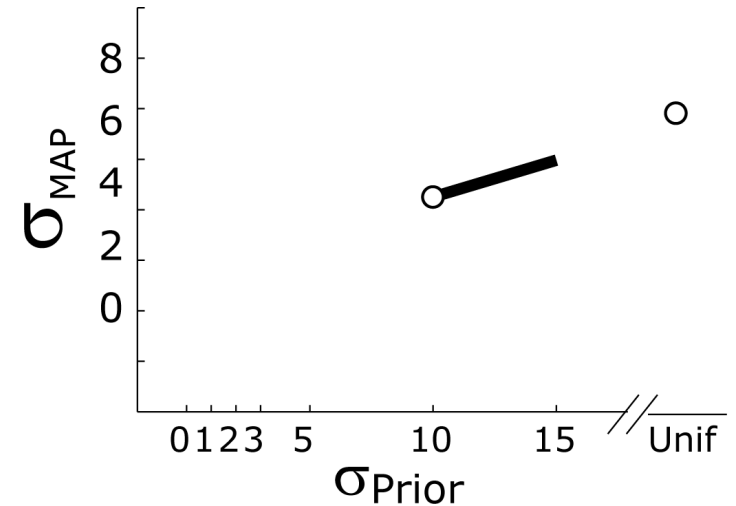
$$\text{Posterior: } P(\theta|x) \propto L(\theta; x)P(\theta)$$



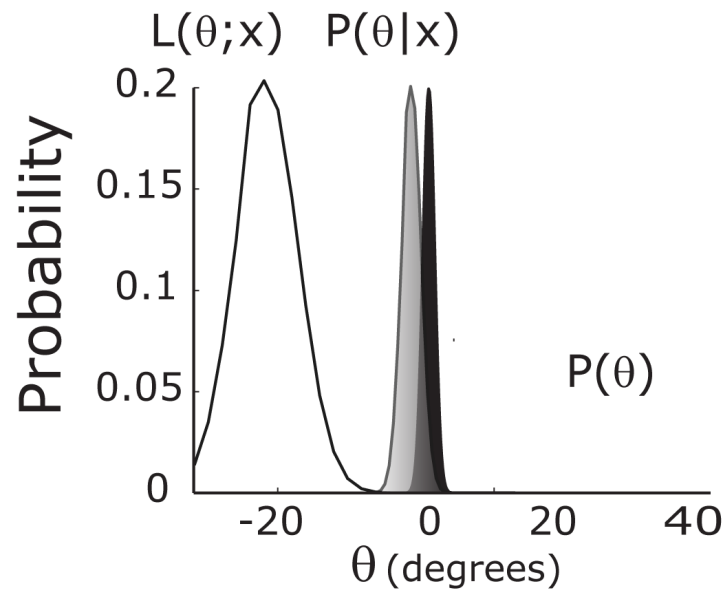
Bayesian integration of prior data



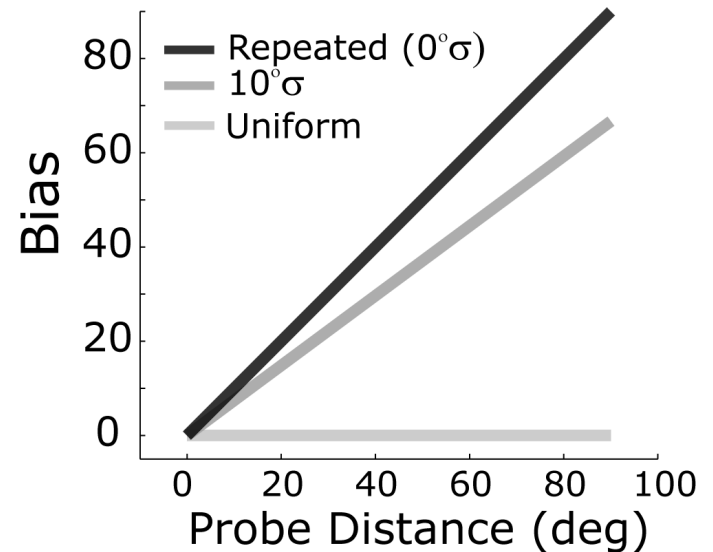
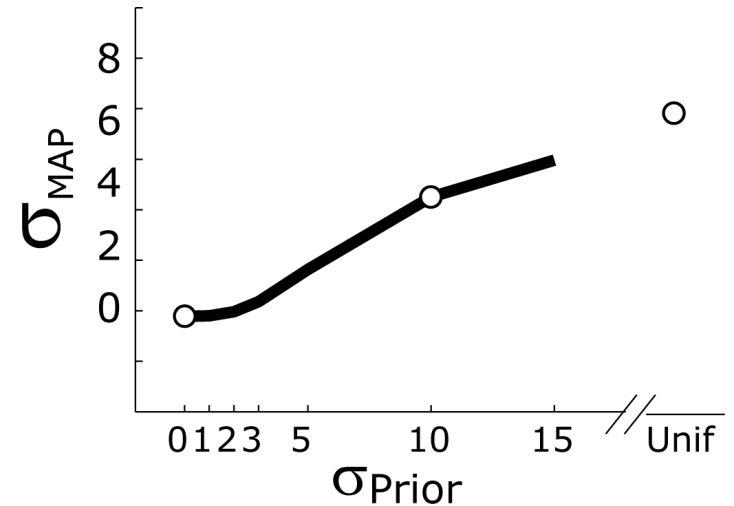
Posterior: $P(\theta|x) \propto L(\theta;x)P(\theta)$



Bayesian integration of prior data

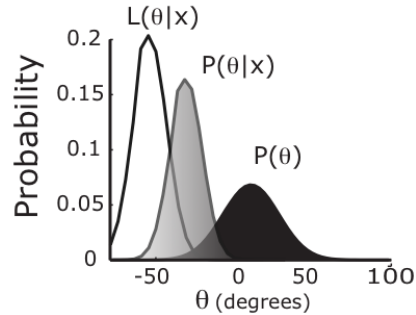


$$\text{Posterior: } P(\theta|x) \propto L(\theta; x)P(\theta)$$

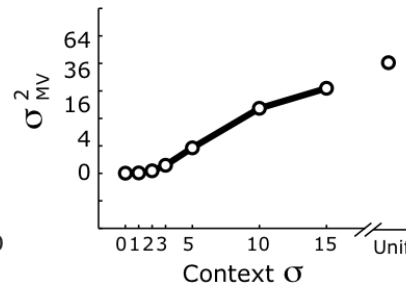


Comparison of data and Bayesian model

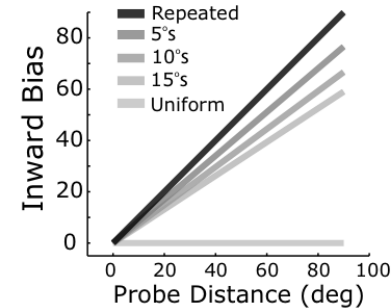
Normative Model



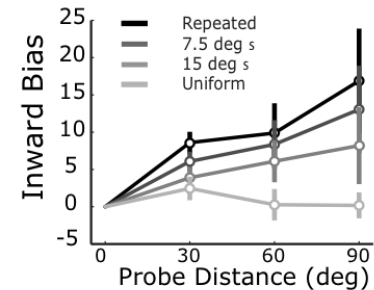
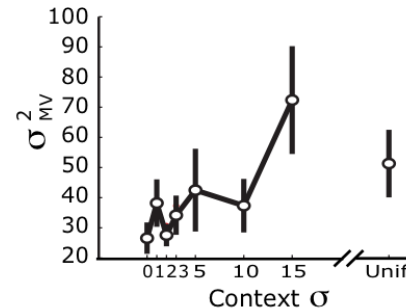
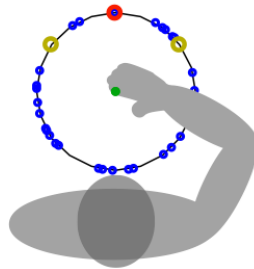
Variance Effects



Bias Effects



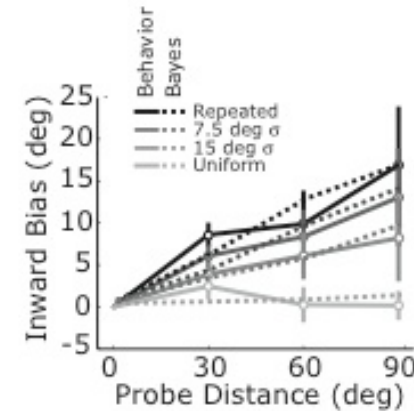
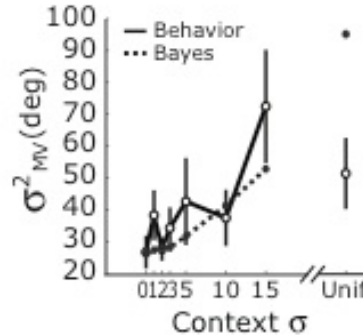
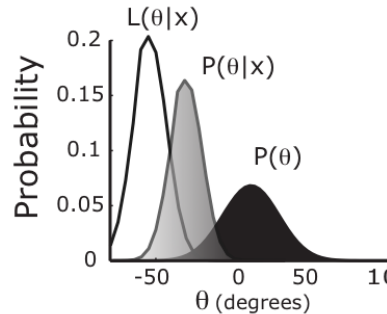
Data



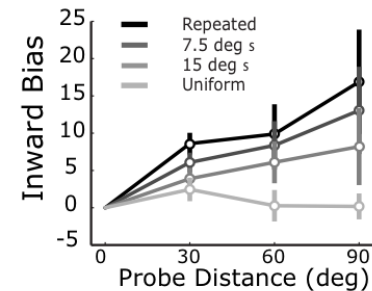
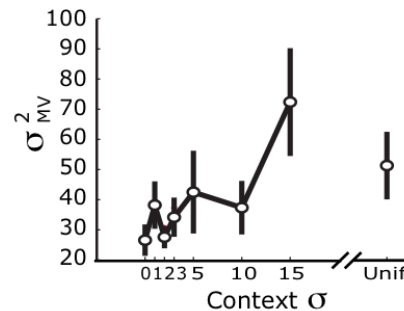
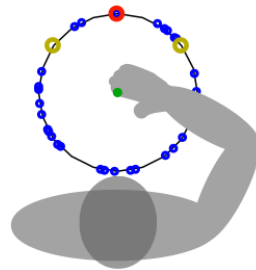
- Experimentally observed bias-variance tradeoff is **qualitatively** consistent with Bayesian integration
- Not **quantitatively** accurate
- But it doesn't take learning into account

Comparison of data and adaptive model

Normative Model



Data

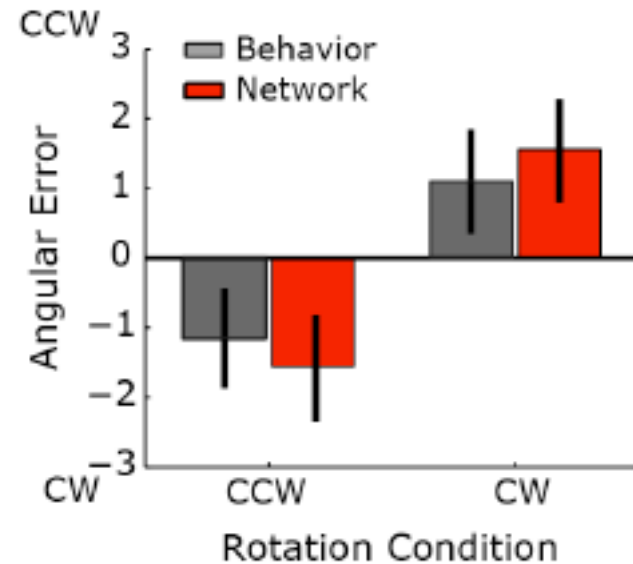
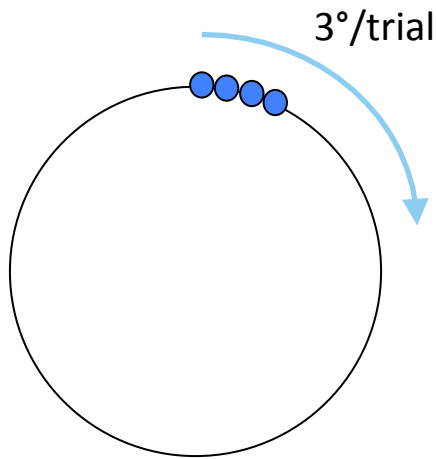


- Simple adaptive Bayesian model:

$$\begin{aligned}\mu_t &= (1 - \alpha)\mu_{t-1} + \alpha\theta \\ \sigma_t^2 &= (1 - \alpha)\sigma_{t-1}^2 + \alpha(\mu - \theta)^2\end{aligned}$$

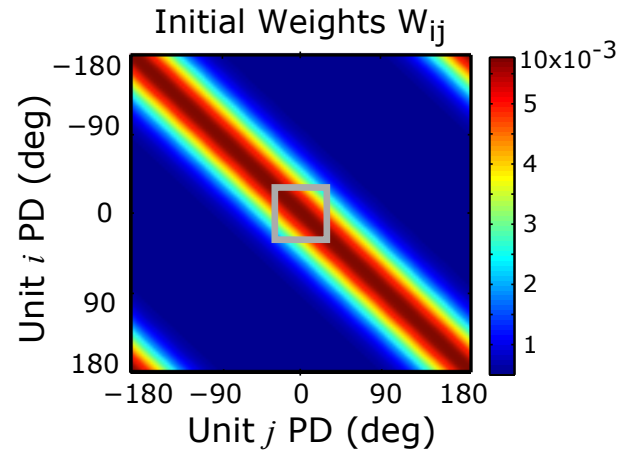
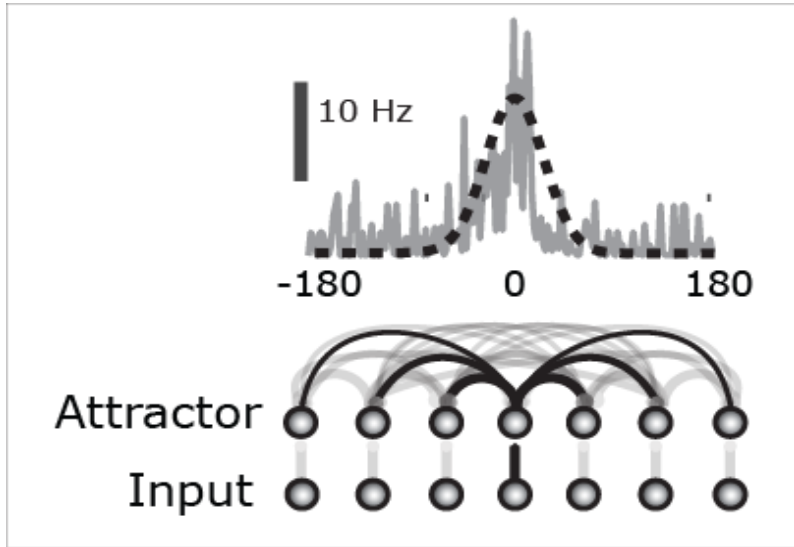
- Simple **(normative)** adaptive model captures data fairly well
- How can you distinguish this model from alternatives?

Not just guessing



- Not just a “cognitive strategy”, e.g. guessing where the target is
- Another experiment where guessing makes a different prediction than an “automatic” process

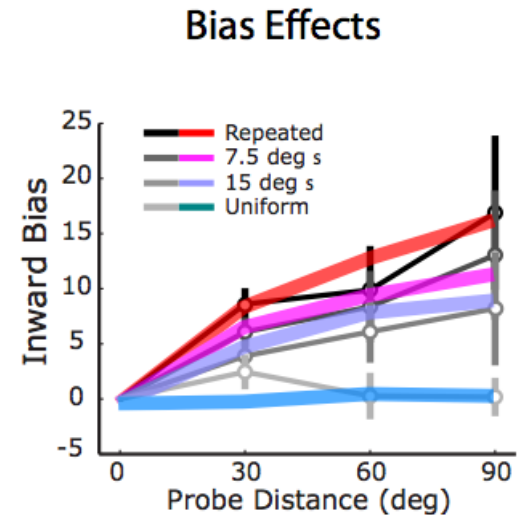
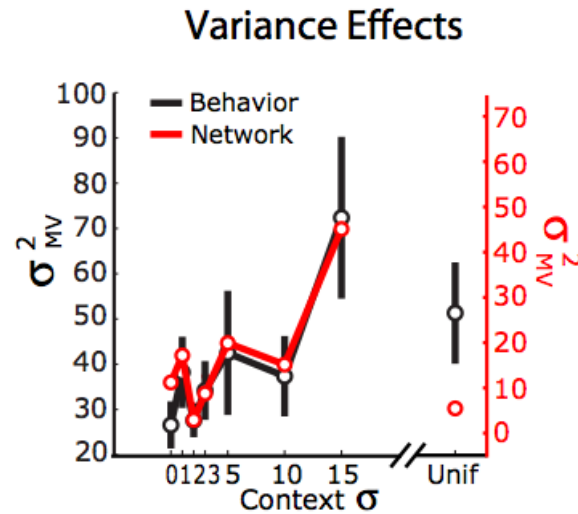
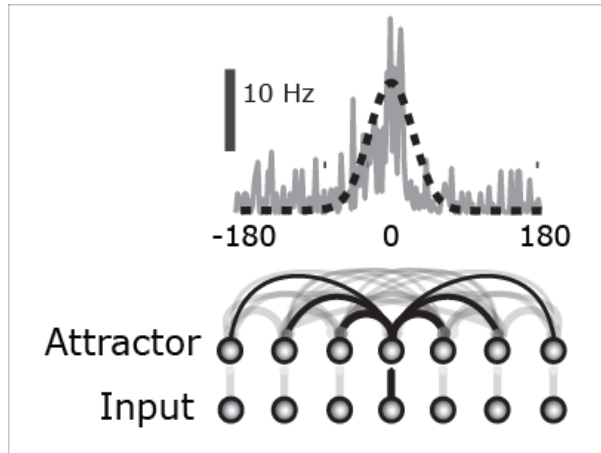
Network model: associative learning as adaptive prior



Deneve, Latham, Pouget (1999)

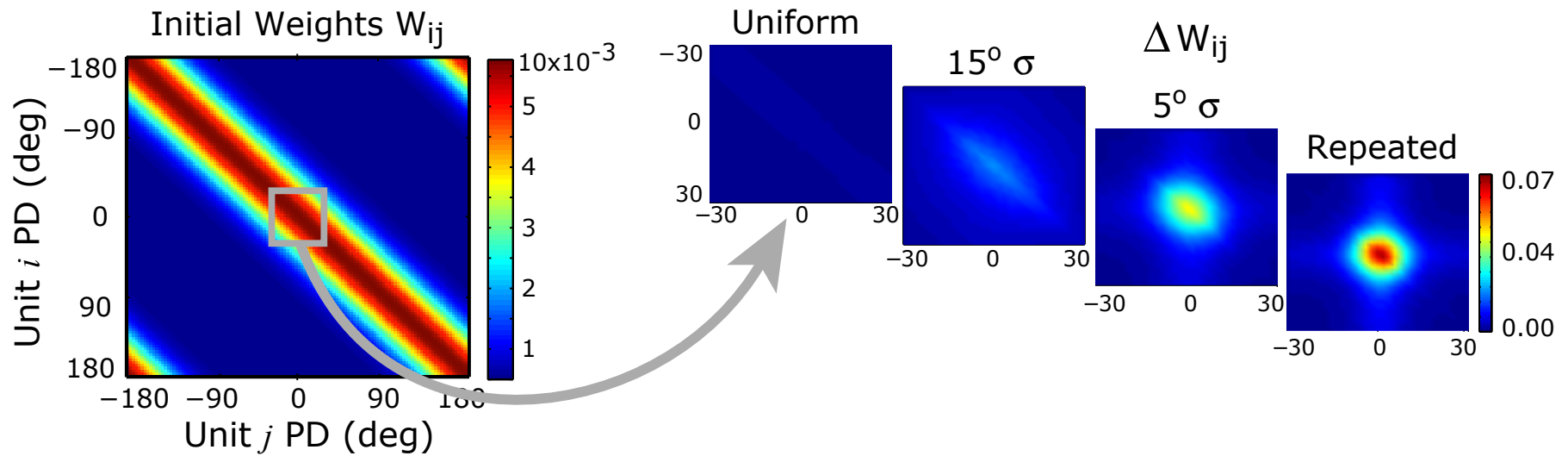
- Associative (Hebbian) learning in lateral connections
 - Recent activity patterns (experiences) reshape connectivity
 - New connectivity reshapes “energy landscape”
 - We show that network acts Bayesian:
 - Train with one context, test with various input gains
 - Get variance and bias as predicted
 - See also Wu and Amari (2005)

Network model: associative learning as adaptive prior



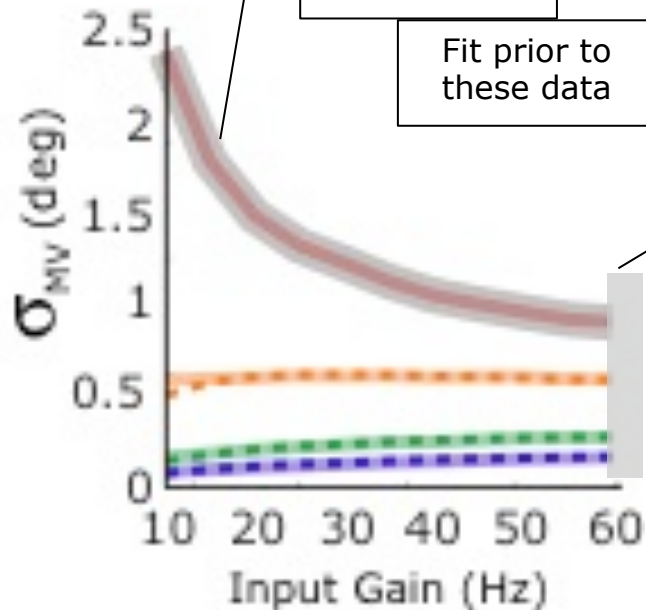
- Good match to experimental results when network experiences same trial sequence as subjects
- Associative (Hebbian) learning in lateral connections
 - Recent activity patterns (experiences) reshape connectivity
 - New connectivity reshapes “energy landscape”
 - Network acts Bayesian

Learning due to changes in network weights



Network mimics Bayesian estimation

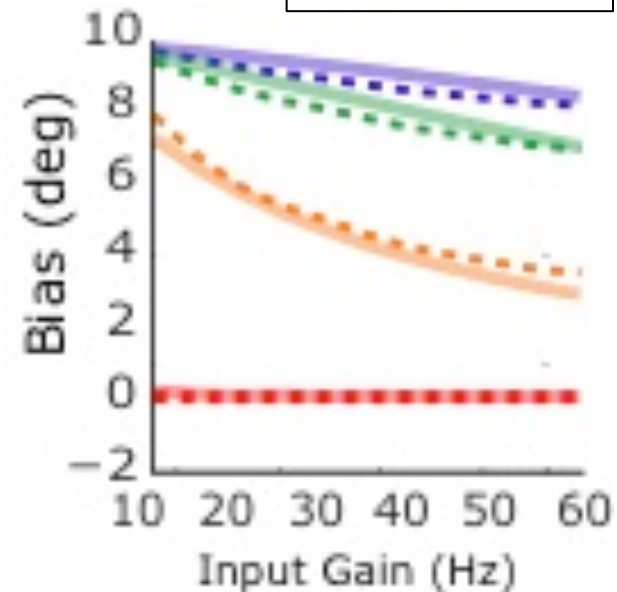
1. Model network variance



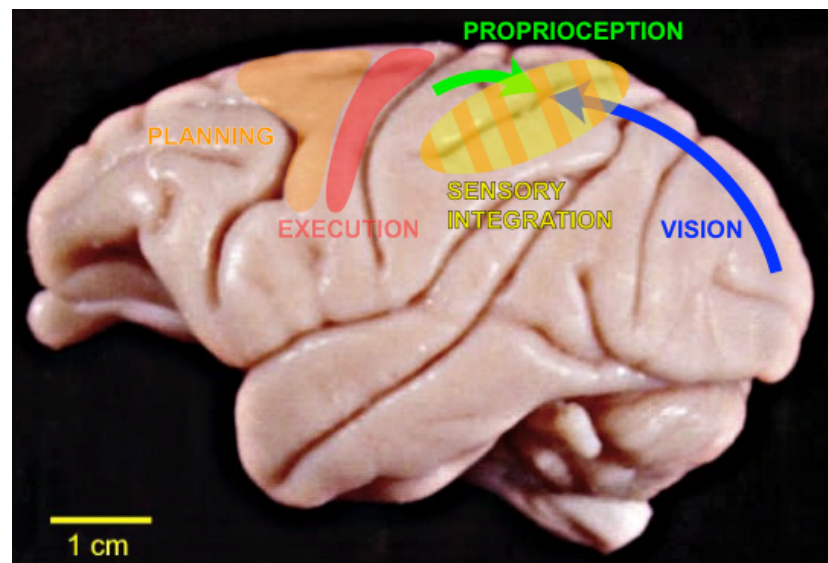
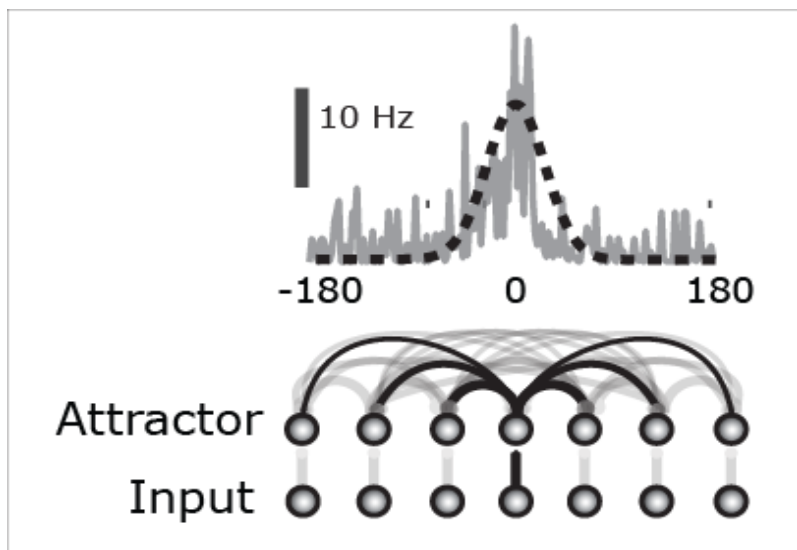
Fit likelihood to these data

Fit prior to these data

2. Predict bias

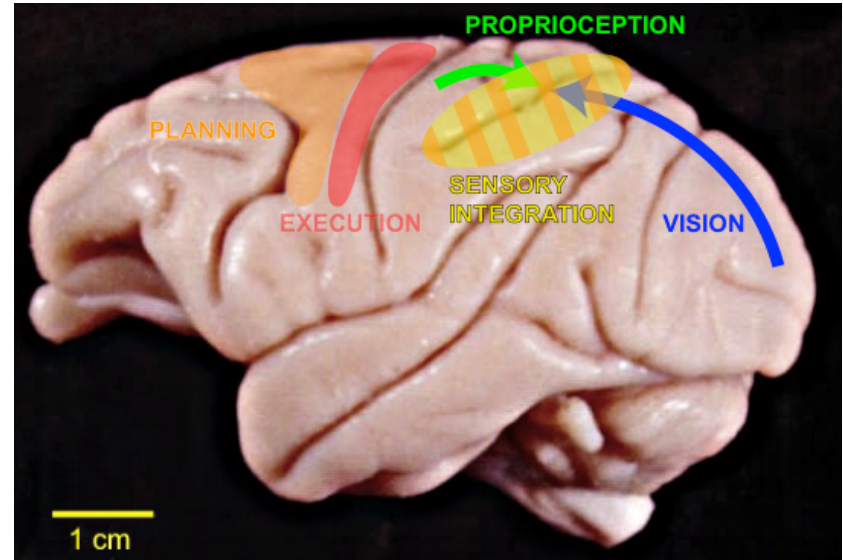
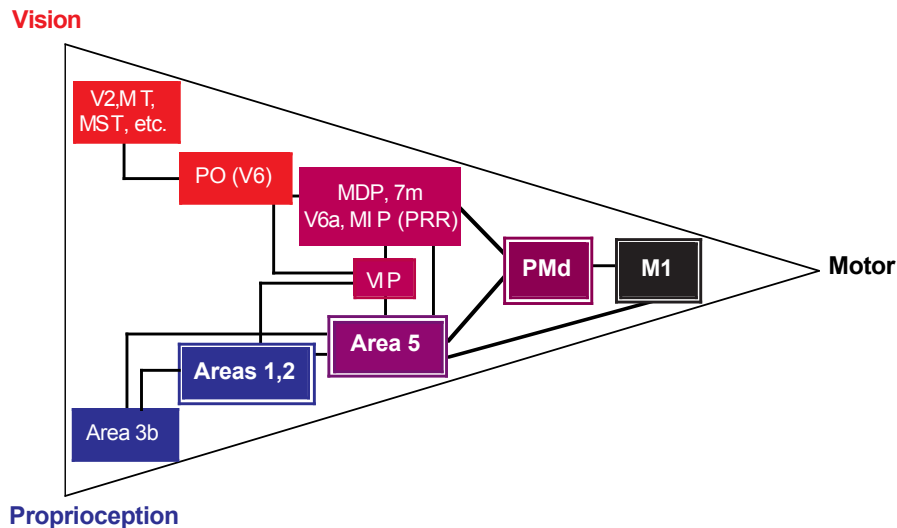


Network implementation sensorimotor processing



- Good news: simple line-attractor (with Hebbian learning) can implement key elements of sensorimotor processing: sensory integration, Bayesian inference, and coordinate transformations
- Bad news: these models are too simple to explain real fronto-parietal circuits
 - Hand-wired to work with simple representations

Network implementations of the building blocks



- Good news: simple line-attractor (with Hebbian learning) can implement key elements of sensorimotor processing: sensory integration, Bayesian inference, and coordinate transformations
- Bad news: these models are too simple to explain real fronto-parietal circuits
 - Hand-wired to work with simple representations
 - No preservation of statistical information – can't combine hierarchically
- Perhaps these limitations can be overcome with more sophisticated architectures and learning algorithms

Sensory integration as statistical model-building

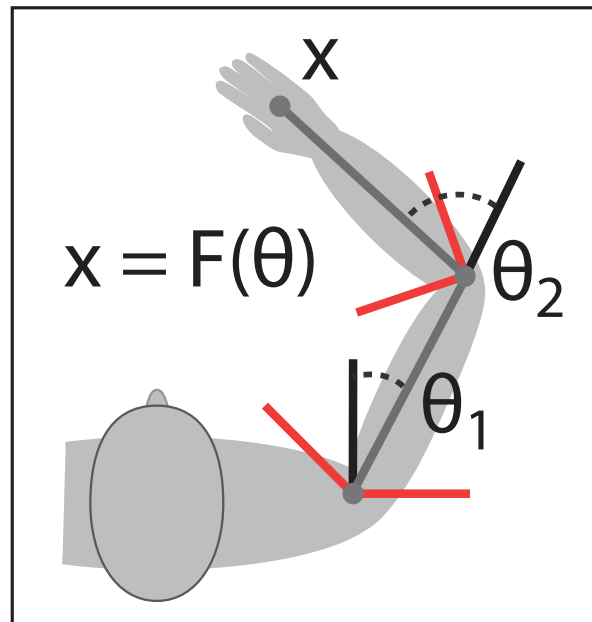
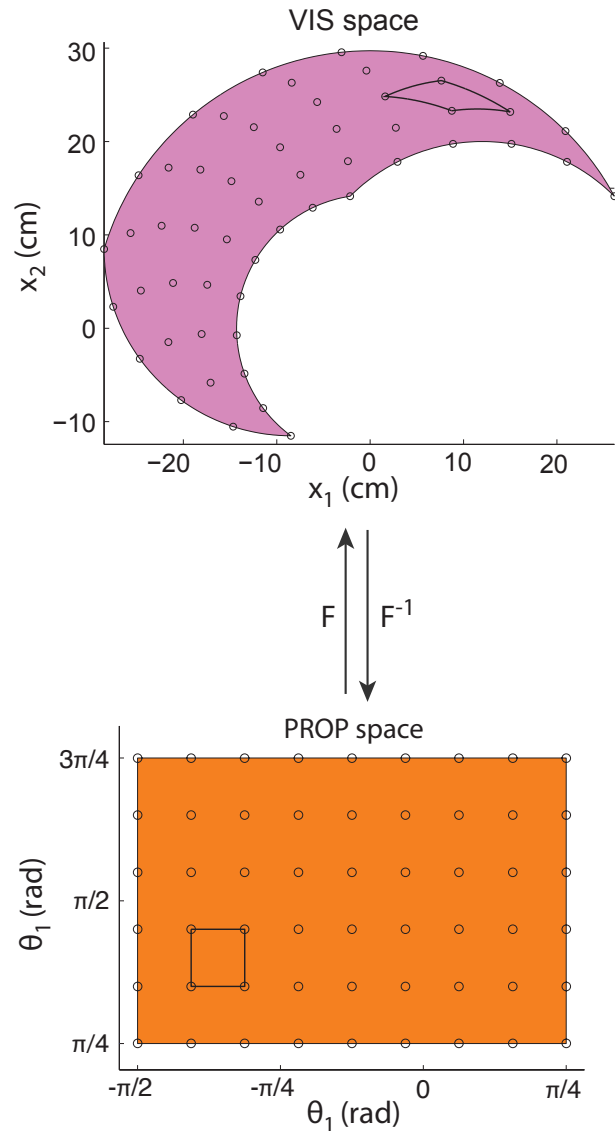


Joseph Makin



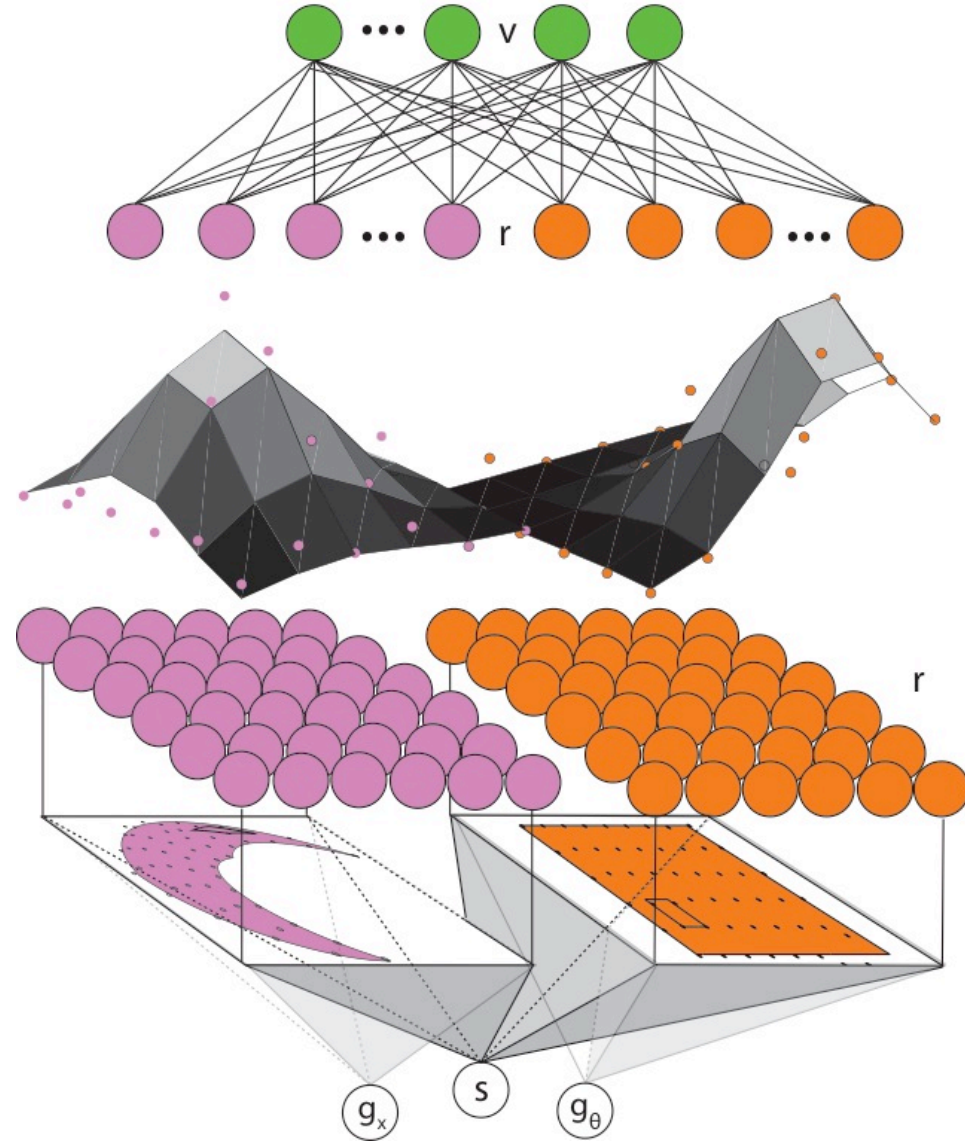
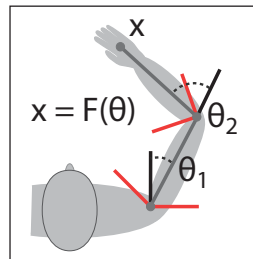
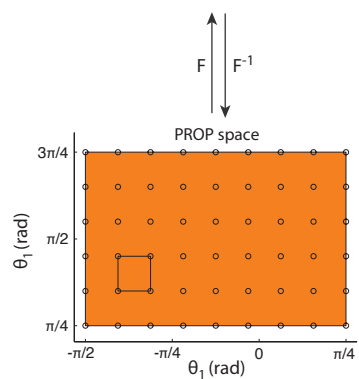
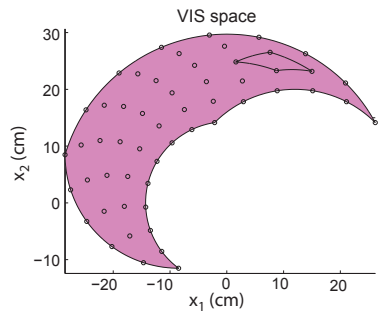
Matthew Fellows

Sensory integration as statistical model-building



Sensory integration as statistical model-building

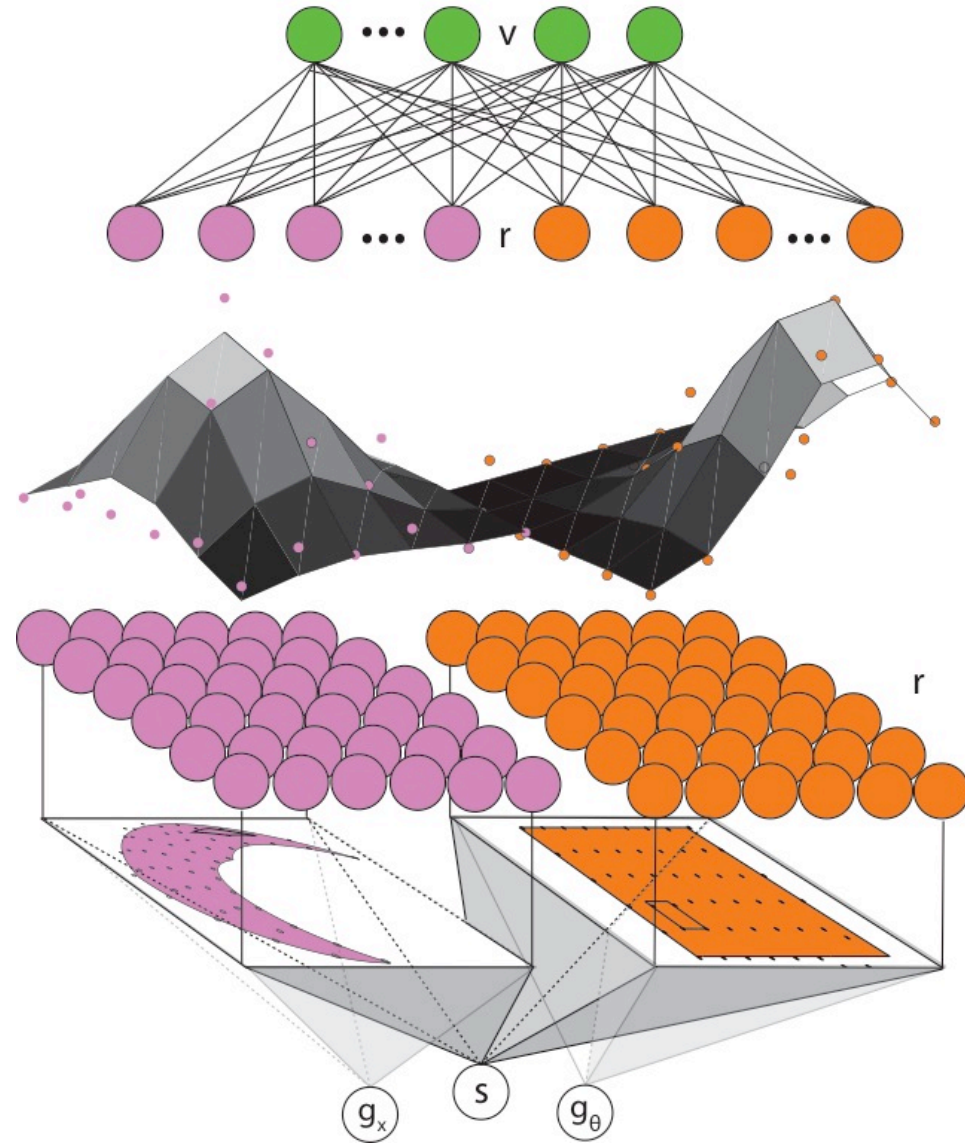
- Restricted Boltzmann Machine
- Contrastive divergence (Hinton et al)



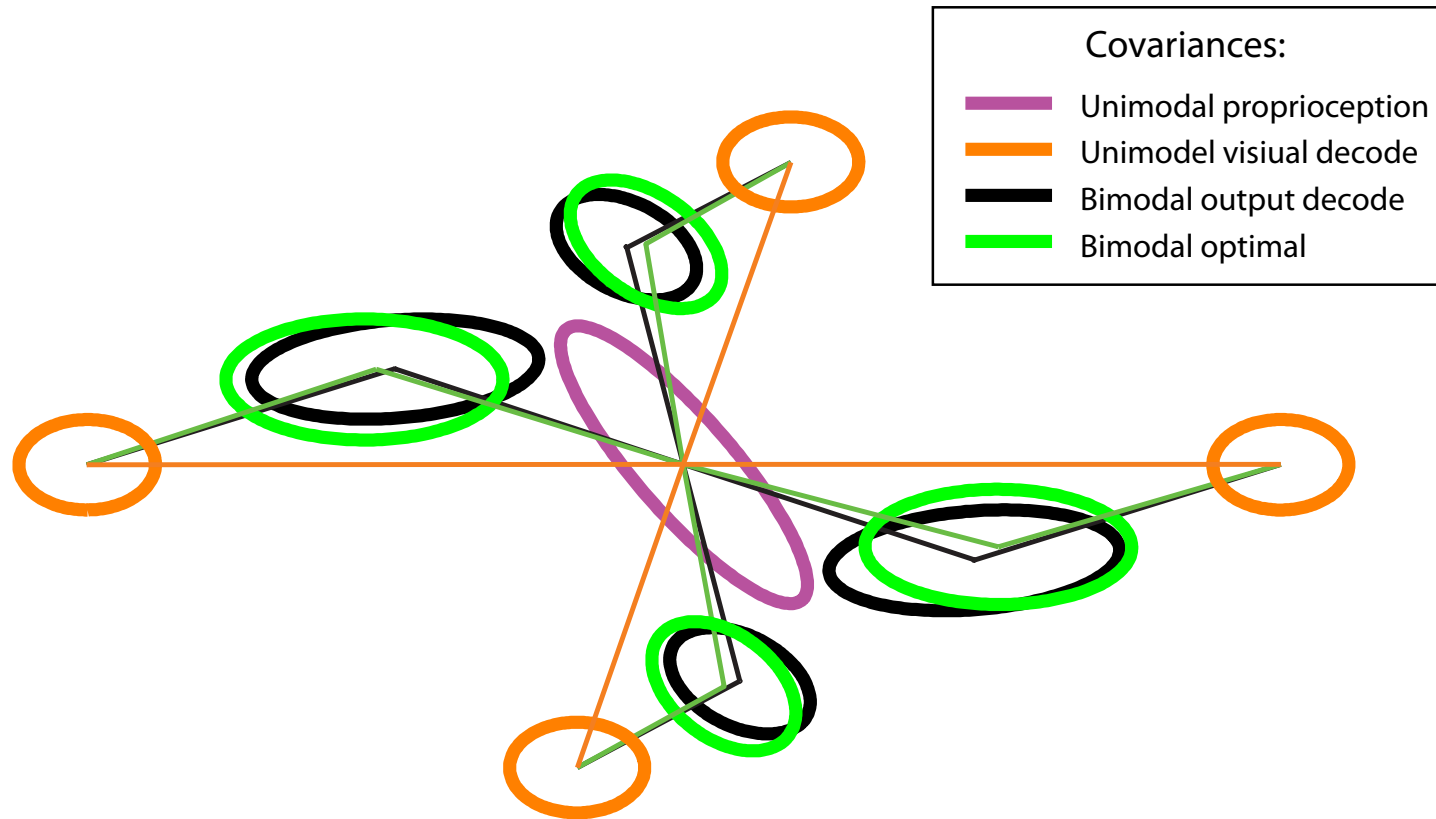
Sensory integration as statistical model-building

Network learns *de novo* the statistical relationships between the inputs:

- Integration



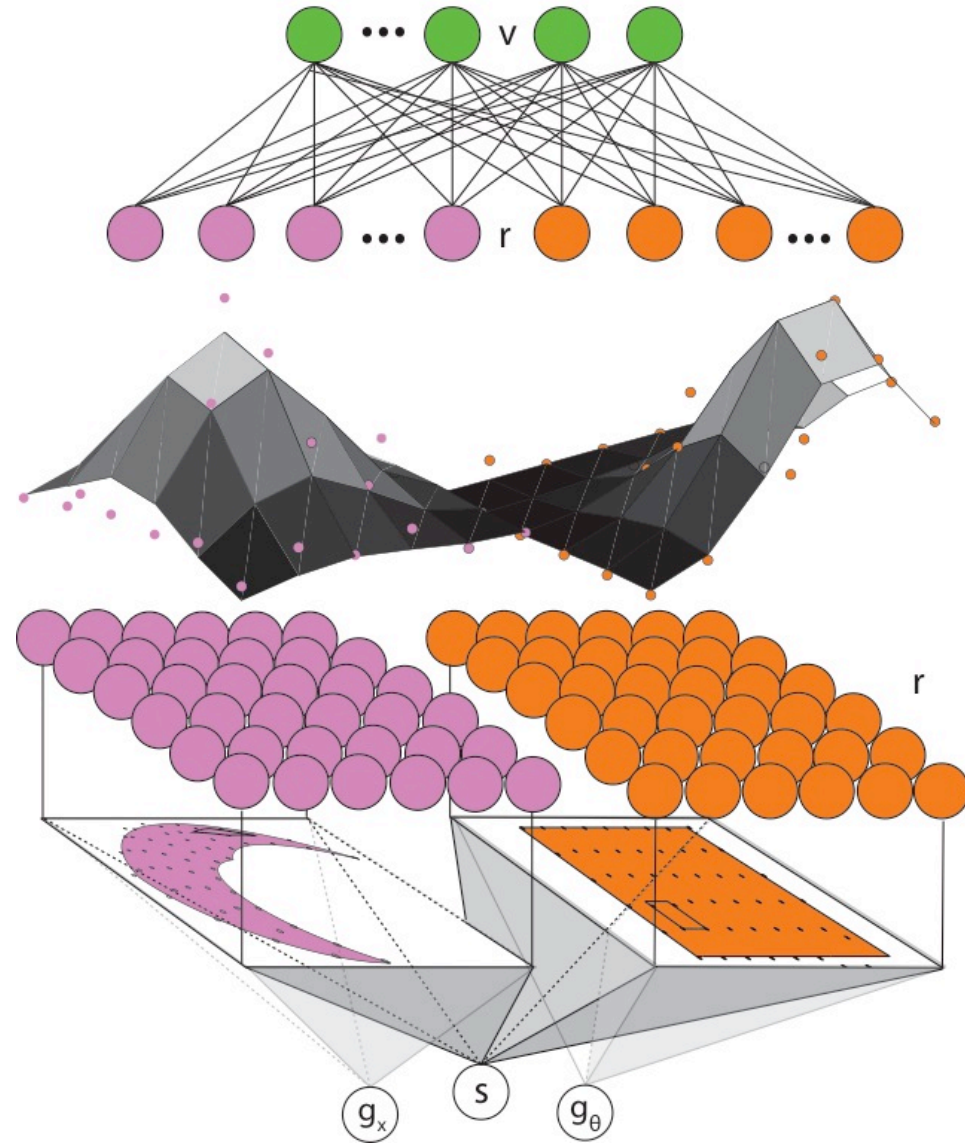
Maximum Likelihood sensory integration



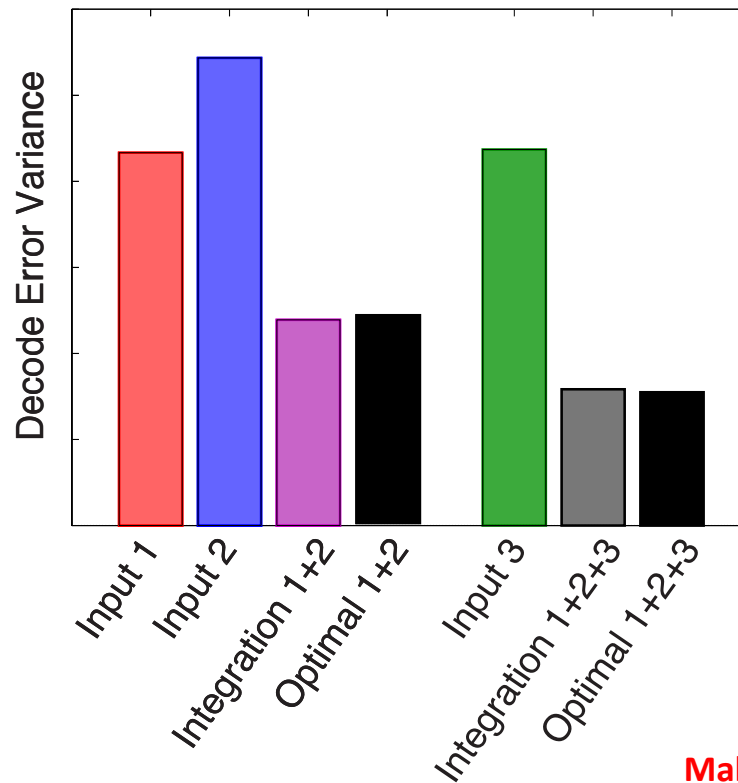
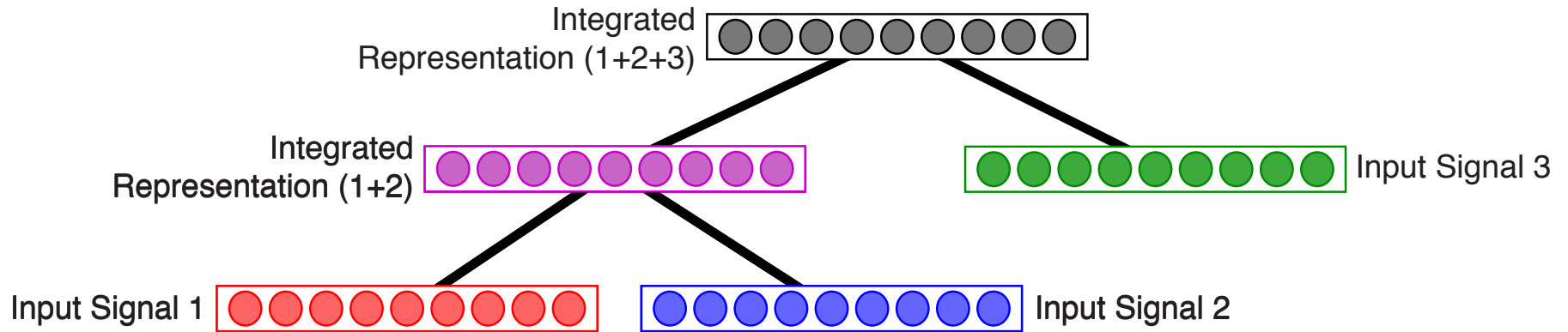
Sensory integration as statistical model-building

Network learns *de novo* the statistical relationships between the inputs:

- Integration
- Sensory transformation
- Bayesian priors
- Hierarchical combination



Hierarchical composition



Sensory integration as statistical model-building

- Results:
 - Integration of signals related via a non-linear transformation
 - Learns priors
 - Learns additive transformations
 - Can be composed hierarchically
 - See also Yildirim and Jacobs *Vis. Res.* (2012)
- Other learning algorithms are also likely to work
 - Key is the ability to learn from the local statistics in incoming signals
- Composition and the ability to handle more complex representations – candidate schema for the posterior parietal cortex?