Probabilistic mechanisms in human sensorimotor control

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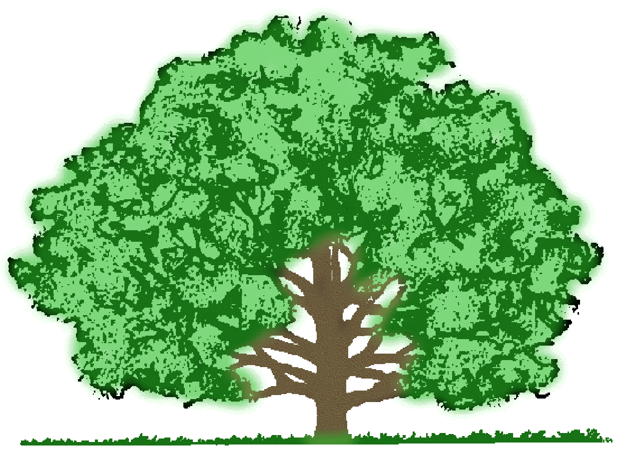
Q. Why do we have a brain?

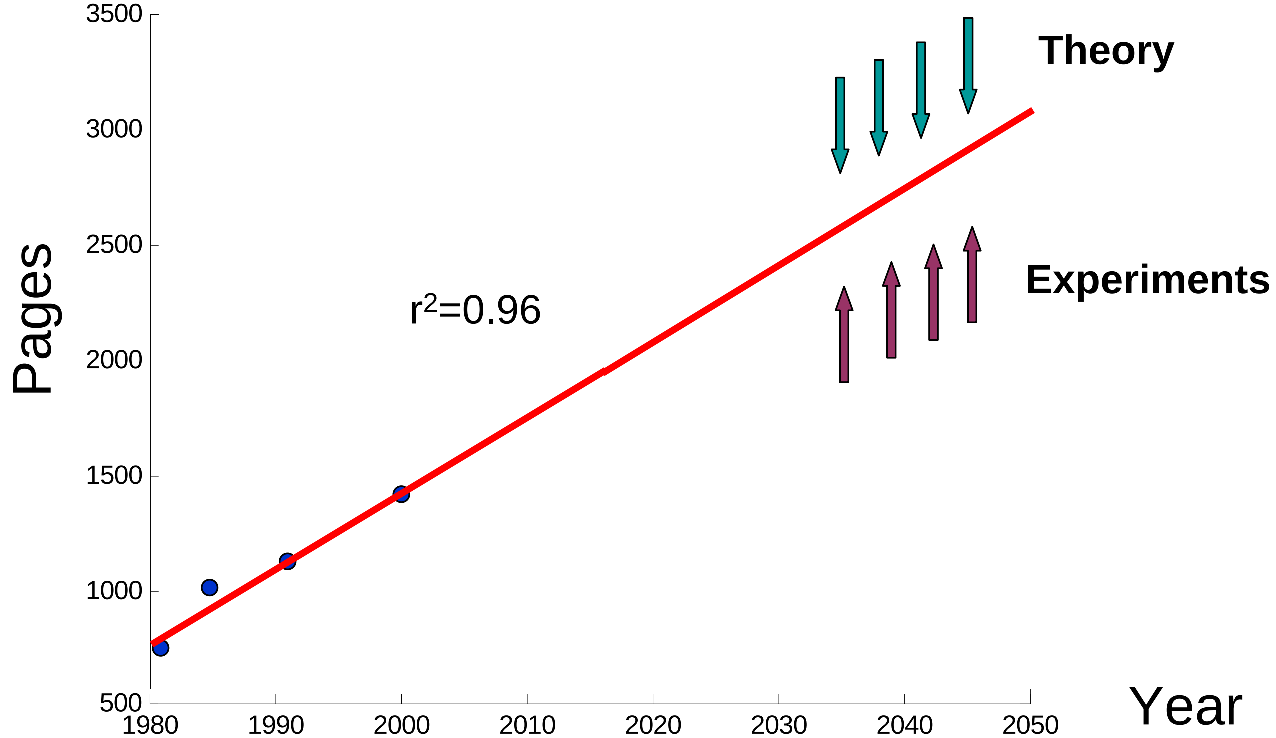
A. To produce adaptable and complex movements

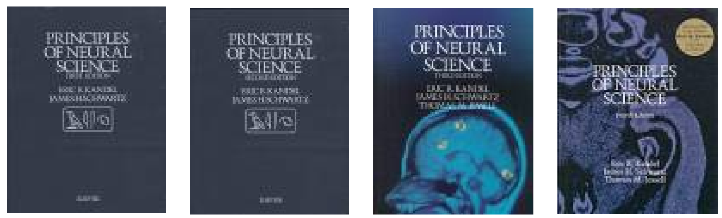
- movement is the only way we have of
  - Interacting with the world
  - Communication: speech, gestures, writing
- sensory, memory and cognitive processes ⇨ future motor outputs



Why study computational sensorimotor control?

Principles of Neural Science, Kandel et al.





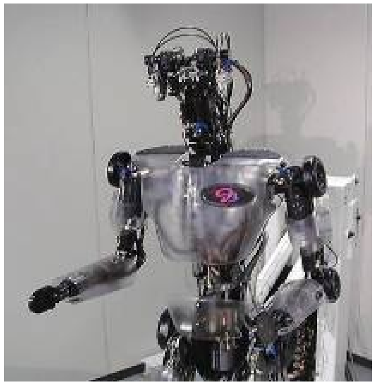
The complexity of motor control

What to move where

vs.

Moving

vs.



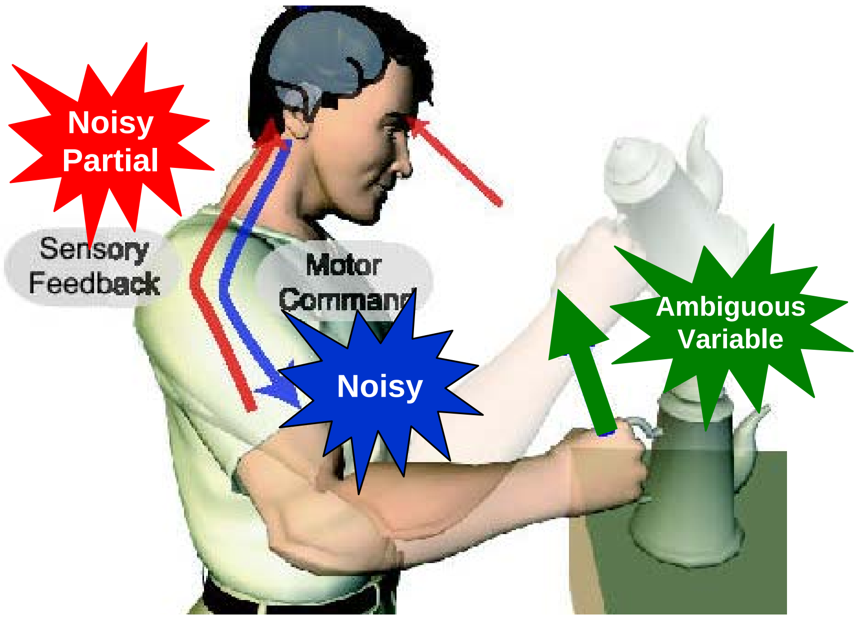
Noise makes motor control hard

Noise = randomness

The motor system is Noisy

Perceptual noise
- Limits resolution

Motor Noise
- Limits control



David Marr’s levels of understanding (1982)

1) the level of *computational* theory of the system

$$v_i^A = \frac{\partial x_i^A}{\partial x_j^B} v_j^B;$$

$$t_{ij}^A = \frac{\partial x_i^A}{\partial x_r^B} \frac{\partial x_j^A}{\partial x_s^B} t_{rs}^B;$$

$$t_{ijk}^A = \frac{\partial x_i^A}{\partial x_r^B} \frac{\partial x_j^A}{\partial x_s^B} \frac{\partial x_k^A}{\partial x_t^B} t_{rst}^B$$

2) the level of *algorithm* and representation, which are used make computations

3) the level of *implementation*: the underlying hardware or "machinery" on which the computations are carried out.

Tutorial Outline

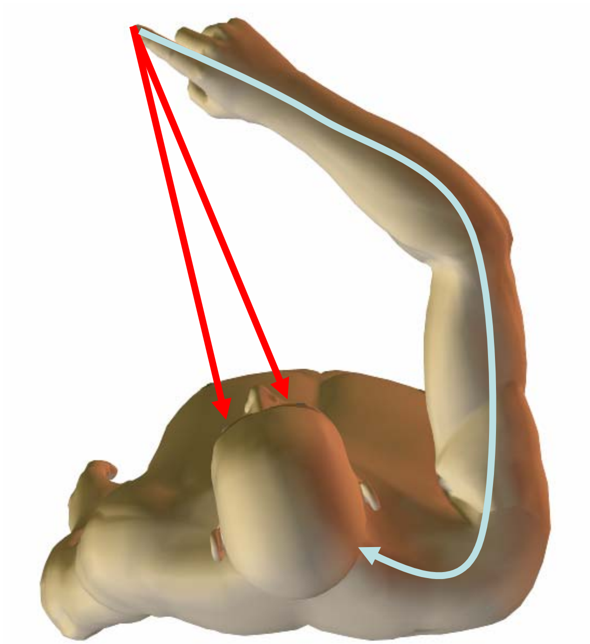
- Sensorimotor integration
  - Static multi-sensory integration
  - Bayesian integration
  - Dynamic sensor fusion & the Kalman filter
- Action evaluation
  - Intrinsic loss function
  - Extrinsic loss functions
- Prediction
  - Internal model and likelihood estimation
  - Sensory filtering
- Control
  - Optimal feed forward control
  - Optimal feedback control
- Motor learning of predictable and stochastic environments

Review papers on www.wolpertlab.com

Multi-sensory integration

Multiple modalities can provide information about the same quantity

- e.g. location of hand in space
  - Vision
  - Proprioception
- Sensory input can be
  - Ambiguous
  - Noisy
- What are the computations used in integrating these sources?



Ideal Observers

Consider n signals x_i, $i = \{1 \ldots n\}$

$$x_i = x + \varepsilon_i \qquad \varepsilon_i = N(0, \sigma_i^2)$$

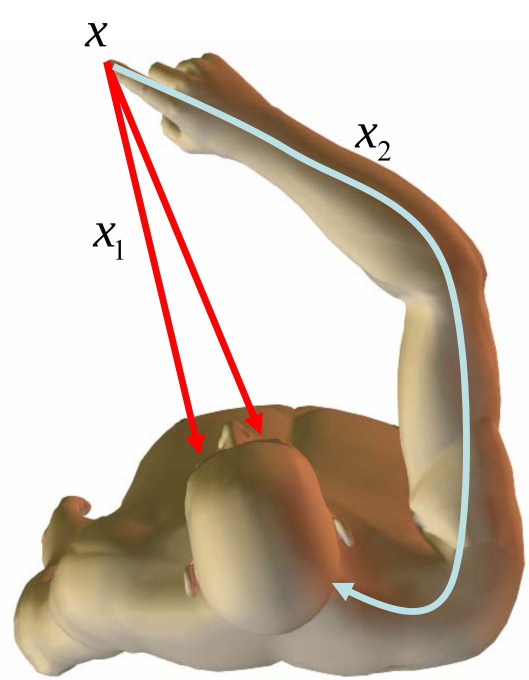
Maximum likelihood estimation (MLE)

$$P(x_1, x_2 \ldots, x_n \mid x) = \prod_{i=1}^{n} P(x_i \mid x)$$

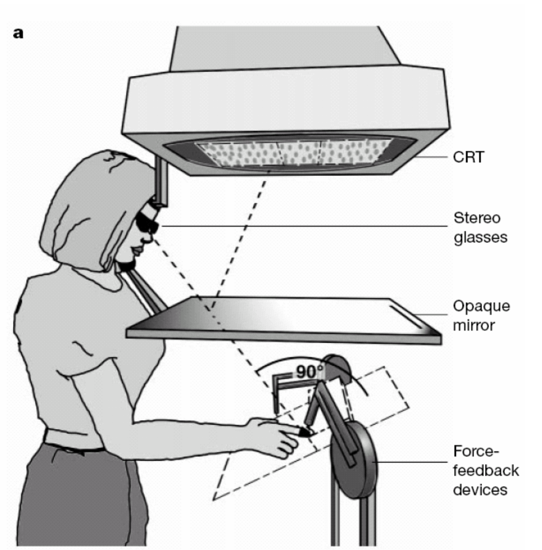
$$\hat{x} = \sum_{i=1}^{n} w_i x_i \qquad \text{with} \qquad w_i = \frac{\sigma_i^{-2}}{\left(\sum_{j=1}^{n} \sigma_j^{-2}\right)}$$

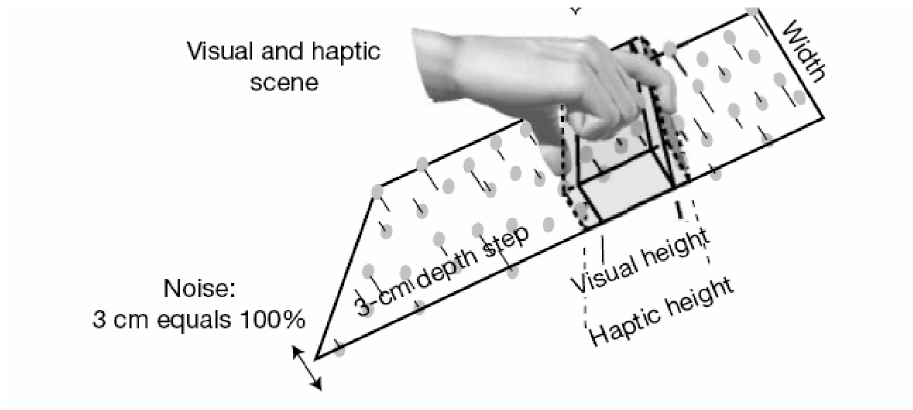
$$\sigma_{\hat{x}}^2 = \left(\sum_{j=1}^{n} \sigma_i^{-2}\right)^{-1} < \sigma_k^2 \;\; \forall k$$

Two examples of multi-sensory integration



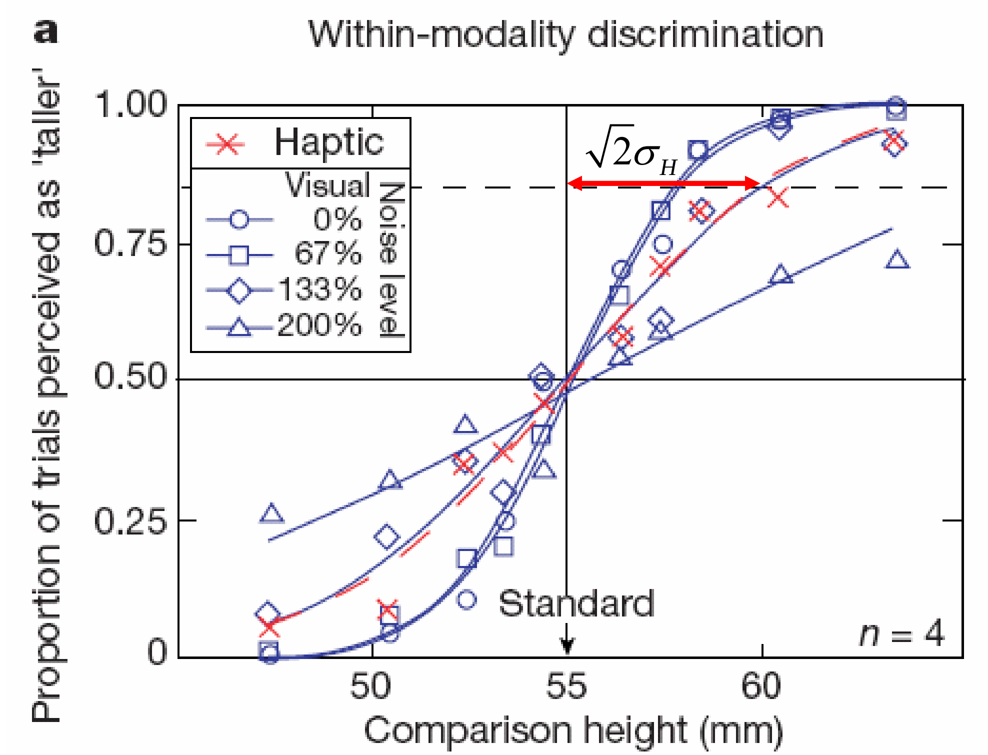
Visual-haptic integration (Ernst & Banks 2002)

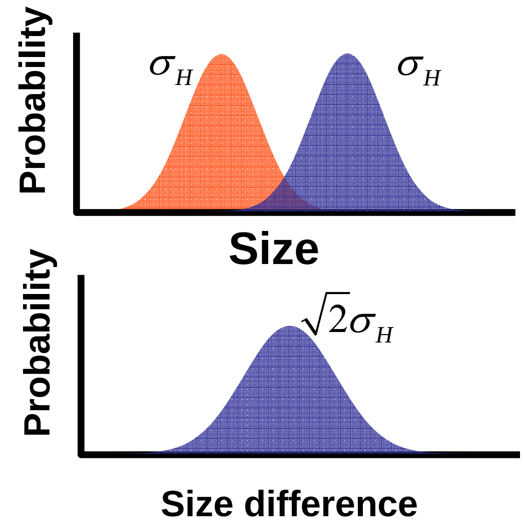




Two alternative force choice size judgment
- Visual
- Haptic
- Visual-haptic (with discrepancy)

Visual-haptic integration





Measure

- Visual reliability σ_V^2
- Haptic reliability σ_H^2
- Predict
  - Visual + Haptic noise
  - Weighting of

Visual-haptic integration

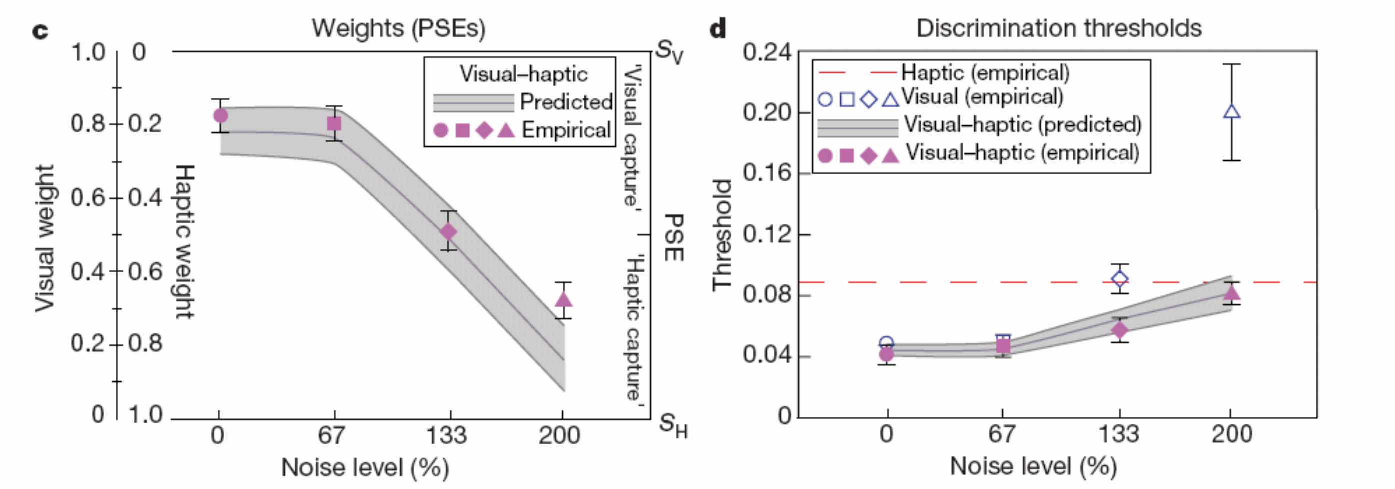
Weights

$$w_i = \frac{\sigma_i^{-2}}{\left(\sum_{j=1}^{n} \sigma_j^{-2}\right)}$$

$$w_H = \frac{\sigma_V^2}{\sigma_V^2 + \sigma_H^2} \qquad w_V = 1 - w_H$$

Standard deviation (~threshold)

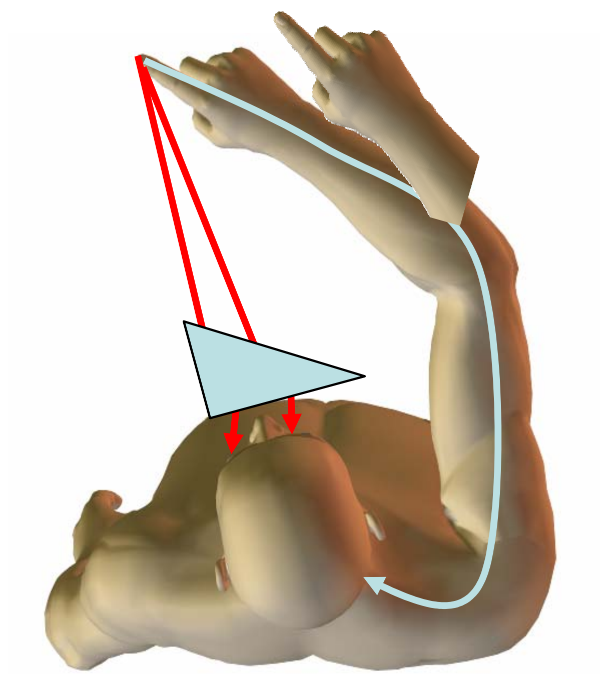
$$\sigma_{\hat{x}}^2 = \left(\sum_{j=1}^{n} \sigma_i^{-2}\right)^{-1} = \frac{\sigma_V^2 \sigma_H^2}{\sigma_V^2 + \sigma_H^2}$$

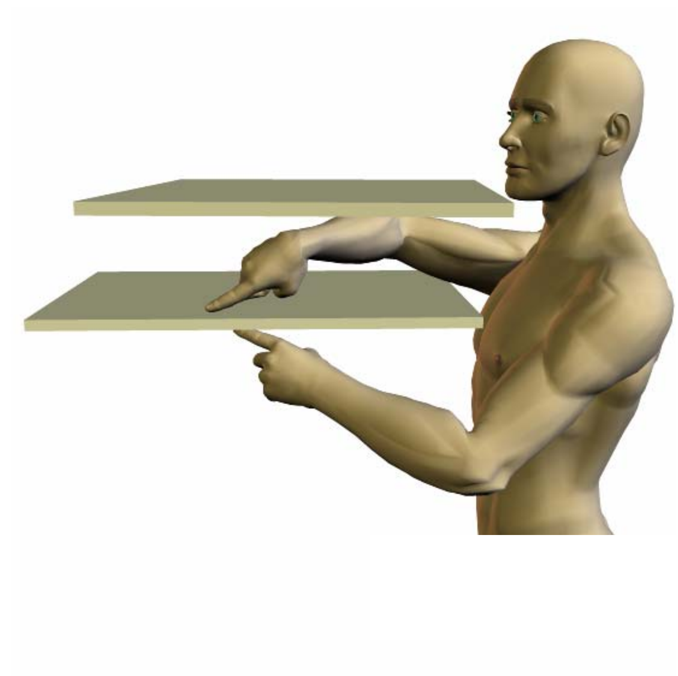


Optimal integration of vision and haptic information in size judgement

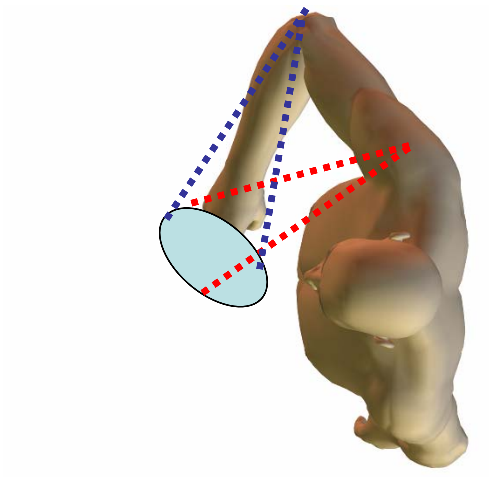
Visual-proprioceptive integration

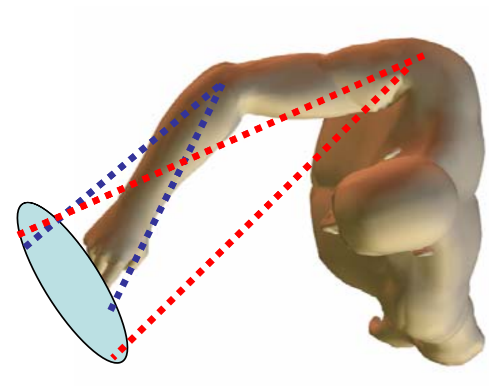
Classical claim from prism adaptation
"vision dominates proprioception"



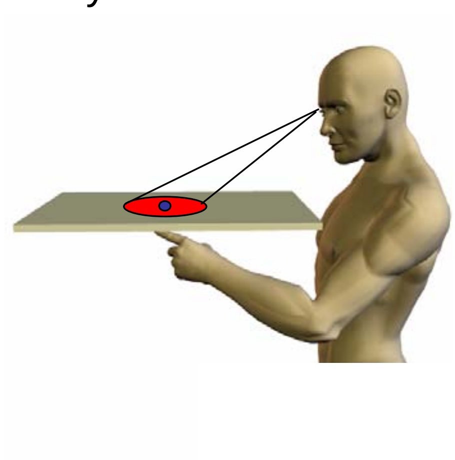


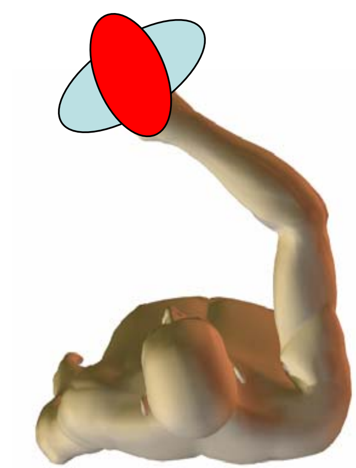
Reliability of proprioception depends on location





Reliability of visual localization is anisotropic

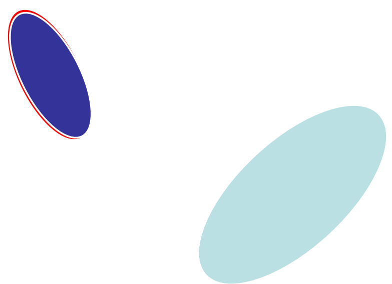




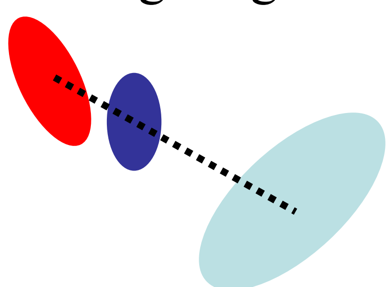
(Van Beers, 1998)

Integration models with discrepancy

Winner takes all

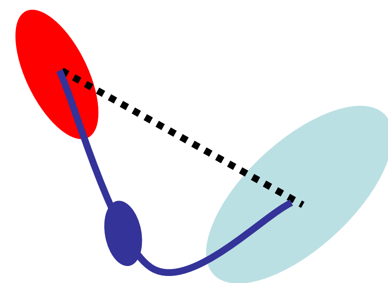


Linear weighting of mean



$\hat{\mathbf{x}} = w\mathbf{x}_V + (1-w)\mathbf{x}_H$

Optimal integration



$\hat{\mathbf{x}} = A\mathbf{x}_V + B\mathbf{x}_H$

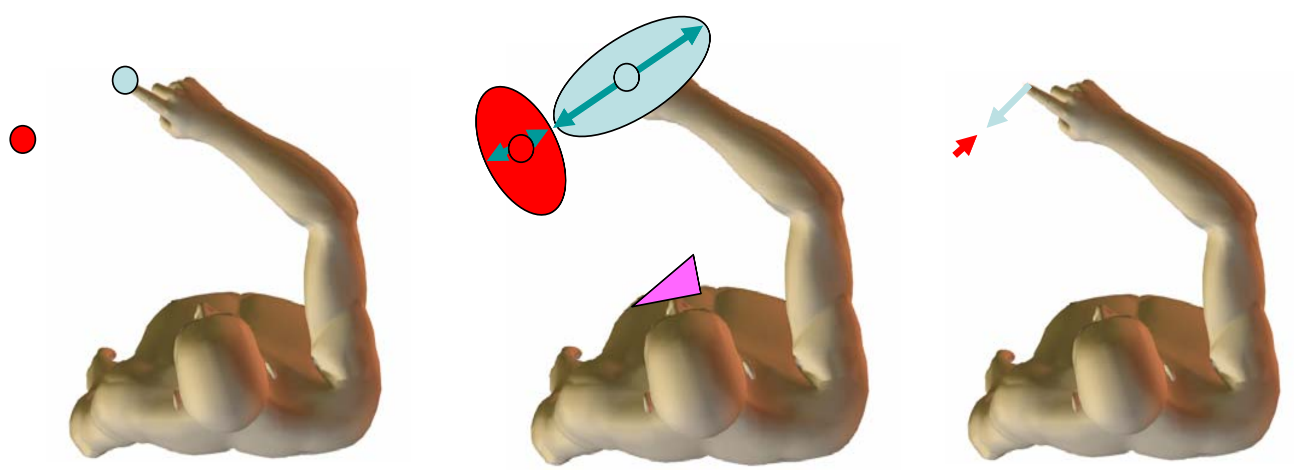
$$\Sigma_{PV} = (\Sigma_P^{-1} + \Sigma_V^{-1})^{-1}$$

$$\mu_{PV} = \Sigma_{PV}(\Sigma_P^{-1}\mu_P + \Sigma_V^{-1}\mu_V)$$

Prisms displace along the azimuth

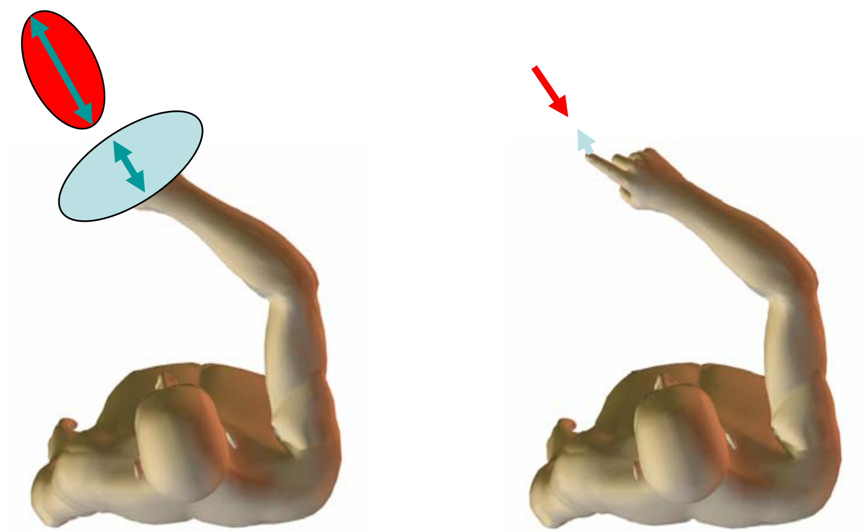
- Measure V and P
- Apply visuomotor discrepancy during right hand reach
- Measure change in V and P to get relative adaptation

Vision 0.33
Prop 0.67



(Van Beers, Wolpert & Haggard, 2002)

Visual-proprioceptive discrepancy in depth



Adaptation
Vision 0.72
Prop 0.28

Visual adaptation in depth > visual adaptation in azimuth ($p<0.01$)
> Proprioceptive adaptation in depth ($p<0.05$)

Proprioception dominates vision in depth

Priors and Reverend Thomas Bayes

1702-1761

"I now send you an essay which I have found among the papers of our deceased friend Mr Bayes, and which, in my opinion, has great merit...."

Essay towards solving a problem in the doctrine of chances. *Philosophical Transactions of the Royal Society of London*, 1764.

Bayes rule

A = Disease **B = Positive blood test**

$$P(\underbrace{A,B}_{\text{A and B}}) = P(\underbrace{A\,|\,B}_{\text{A given B}})P(B) = \underline{P(B\,|\,A)P(A)}$$

Neuroscience

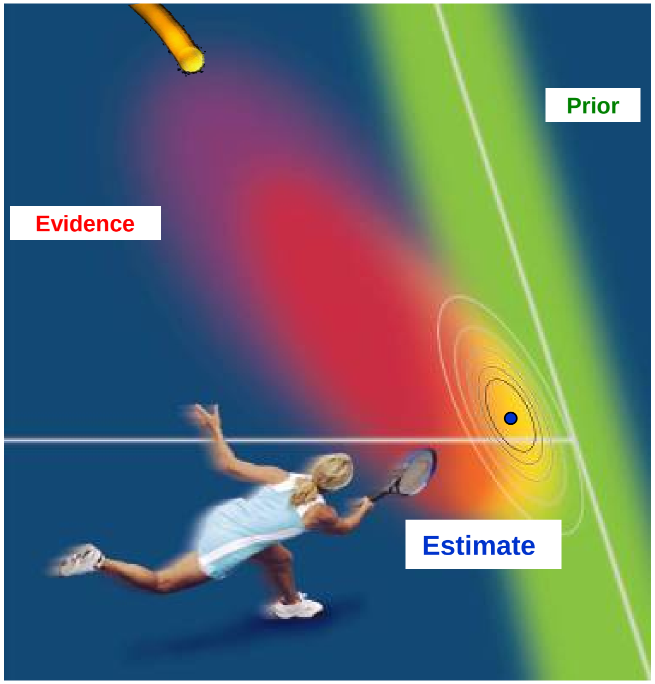
A= State of the world **B=Sensory Input**

$$\overbrace{\mathrm{P(state|sensory\ input)}}^{\text{Belief in state AFTER sensory input}} = \frac{\overbrace{\mathrm{P\,(sensory\ input|state)}}^{\text{Evidence}}\ \overbrace{\mathrm{P(state)}}^{\text{Belief in state BEFORE sensory input}}}{\mathrm{P(sensory\ input)}}$$

Posterior **Likelihood** **Prior**

Bayesian Motor Learning

Real world tasks have variability, e.g. estimating ball's bounce location



Sensory feedback (Evidence)

Combine multiple cues

to reduce uncertainty

+

Task statistics (Prior)

Not all locations are

equally likely

=

Optimal estimate (Posterior)

Bayes rule

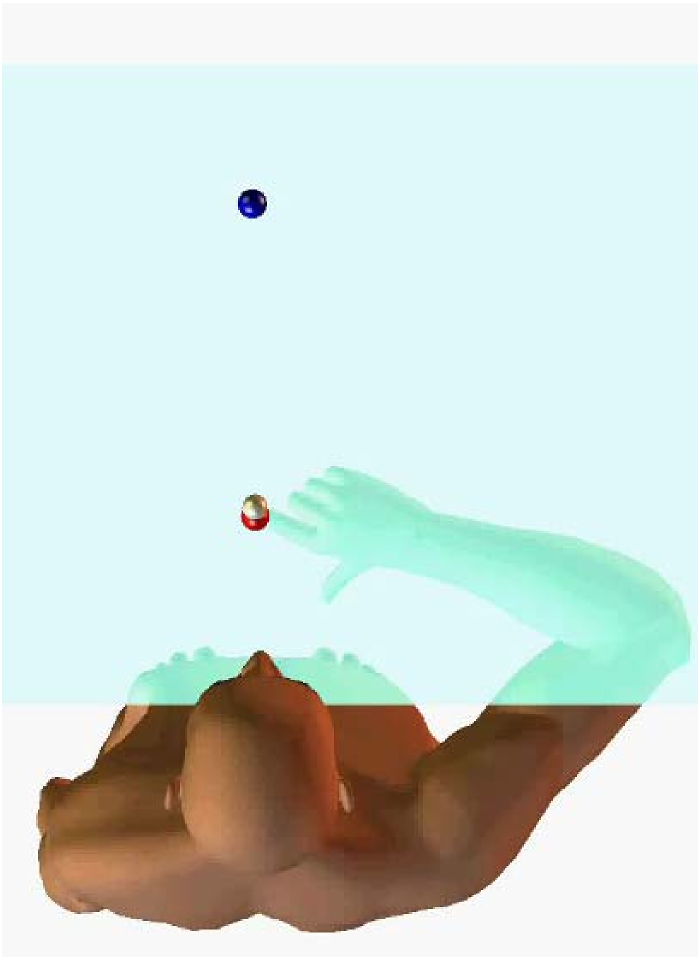
$$P(\text{state}|\text{sensory input}) \propto P(\text{sensory input}|\text{state})\, P(\text{state})$$

Does sensorimotor learning use Bayes rule?

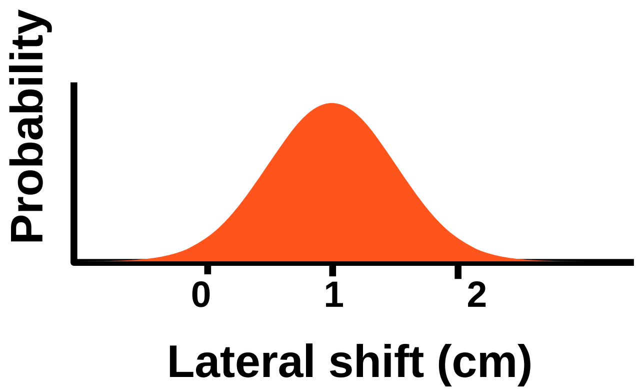
If so, is it implemented

- Implicitly: mapping sensory inputs to motor outputs to minimize error?
- Explicitly: using separate representations of the statistics of the prior and sensory noise?

Prior

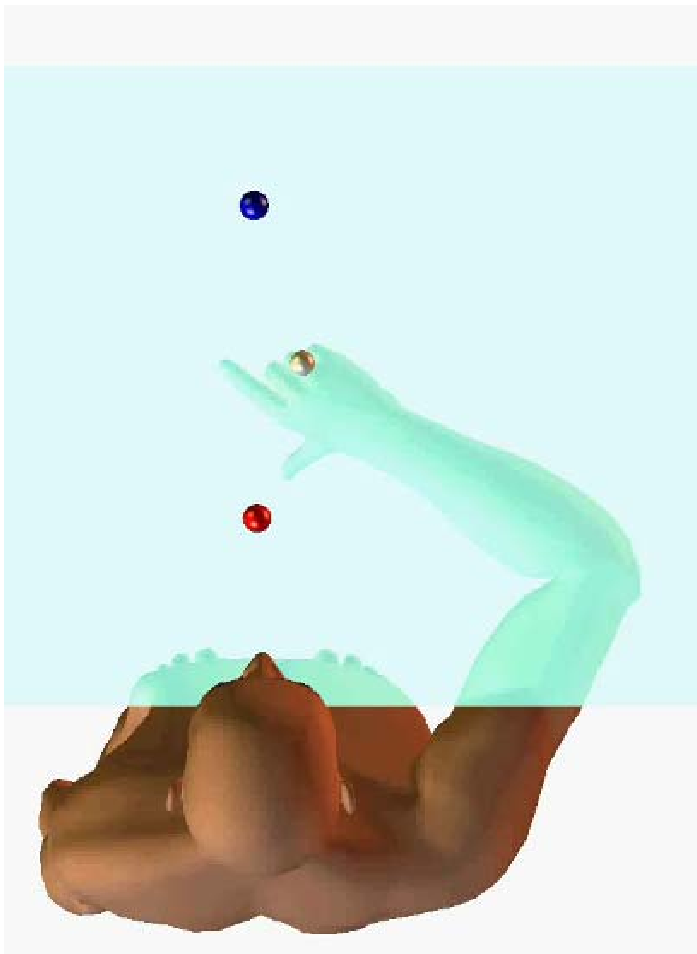


Task in which we control
1) prior statistics of the task
2) sensory uncertainty



(Körding & Wolpert, Nature, 2004)

Prior



Task in which we control
1) prior statistics of the task
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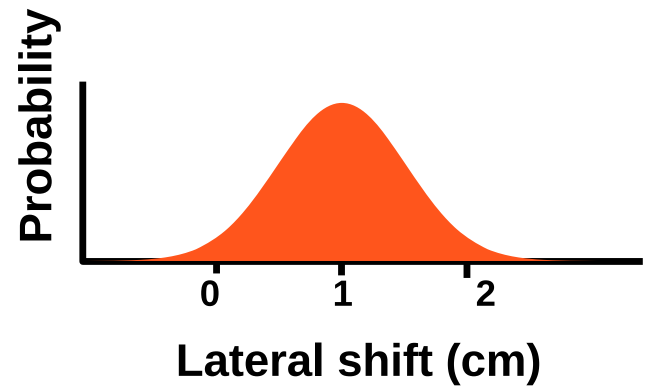
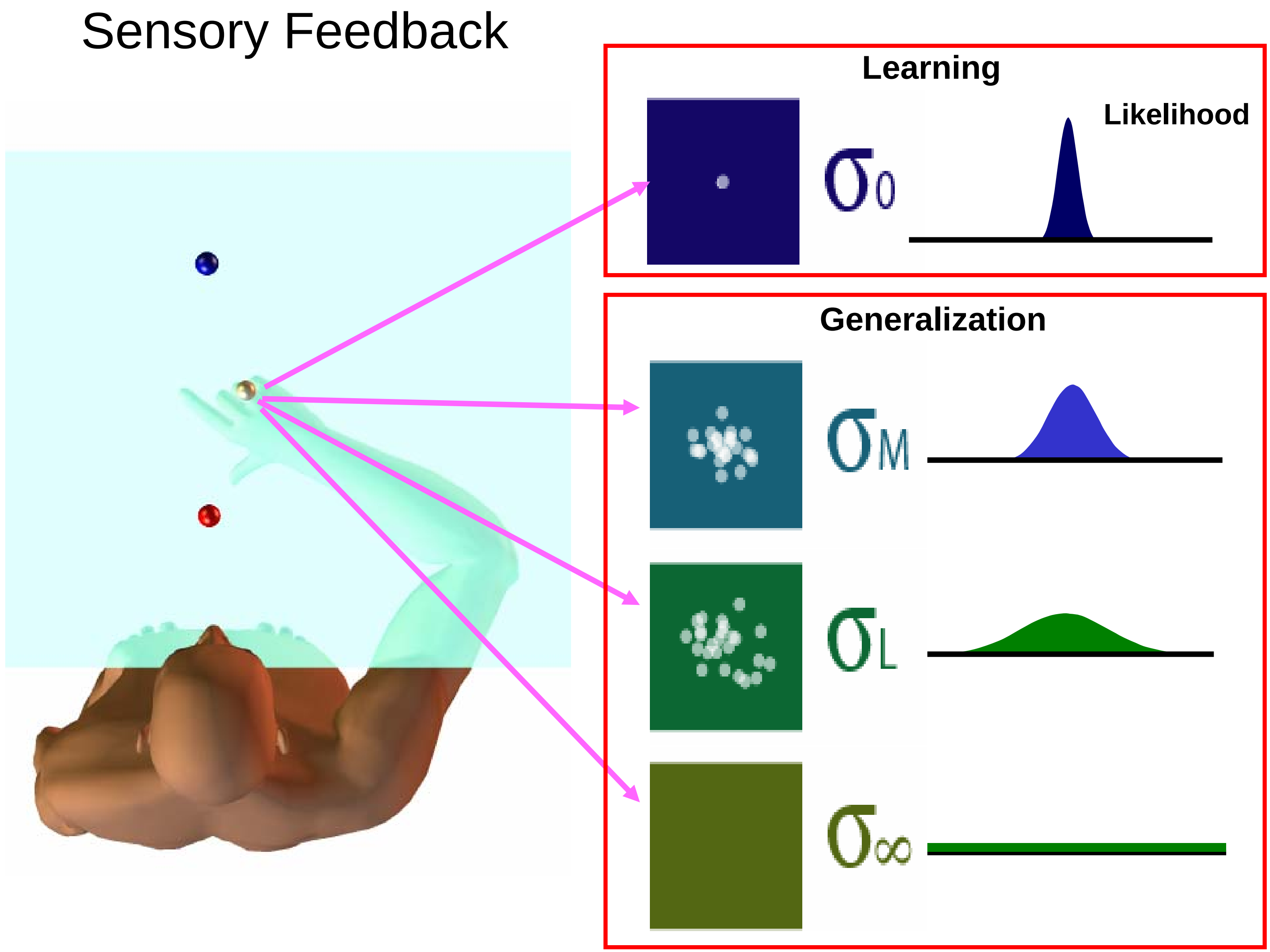
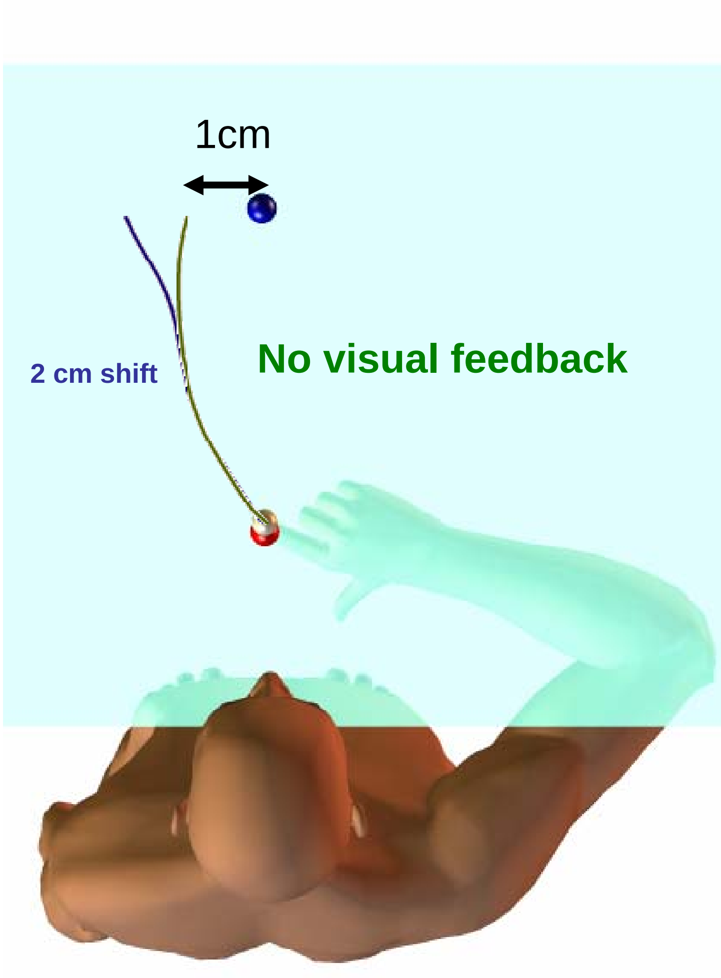


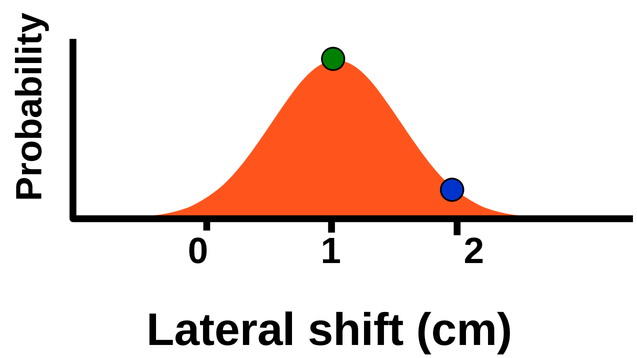
(Körding & Wolpert, Nature, 2004)



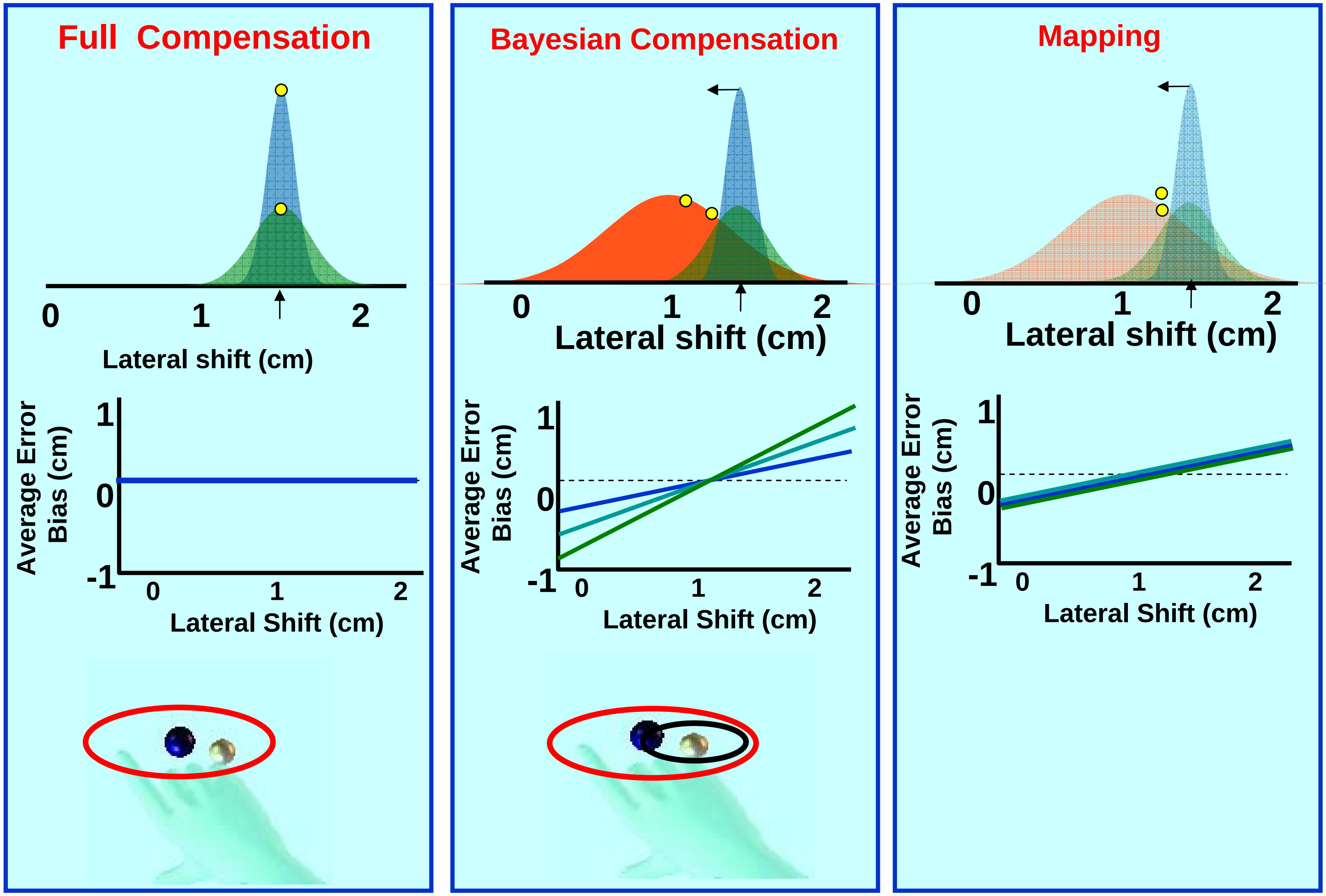
Sensory Feedback
Learning
Likelihood
σ_0
Generalization
σ_M
σ_L
σ_∞

After 1000 trials



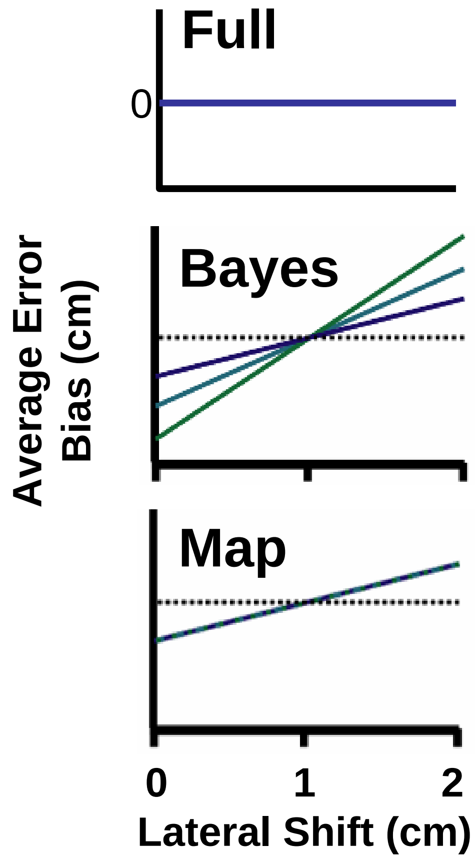


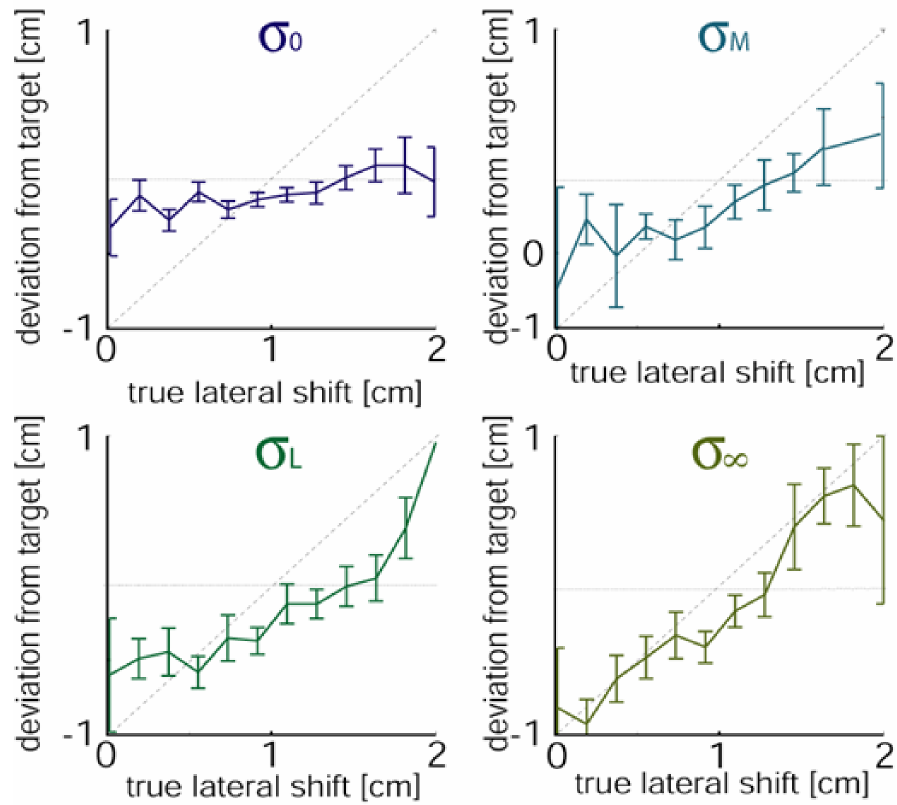
Models



Full Compensation
0
1
2
Lateral shift (cm)
Average Error Bias (cm)
1
0
-1
0
1
2
Lateral Shift (cm)
Bayesian Compensation
0
1
2
Lateral shift (cm)
Average Error Bias (cm)
1
0
-1
0
1
2
Lateral Shift (cm)
Mapping
0
1
2
Lateral shift (cm)
Average Error Bias (cm)
1
0
-1
0
1
2
Lateral Shift (cm)

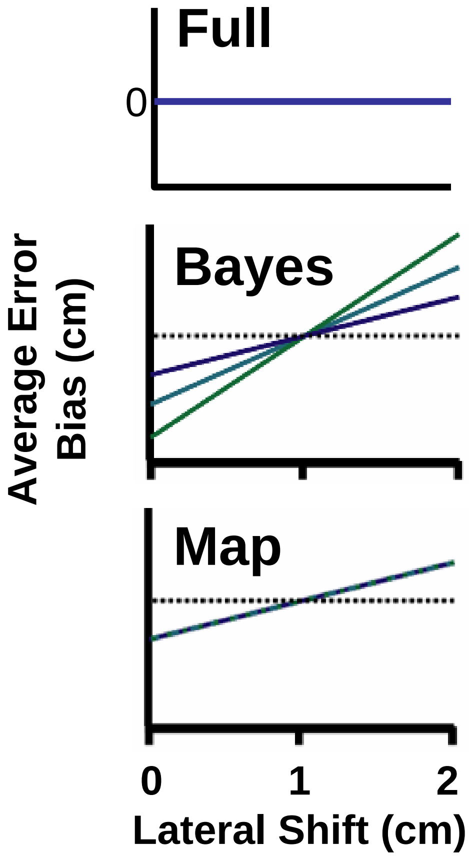
Results: single subject

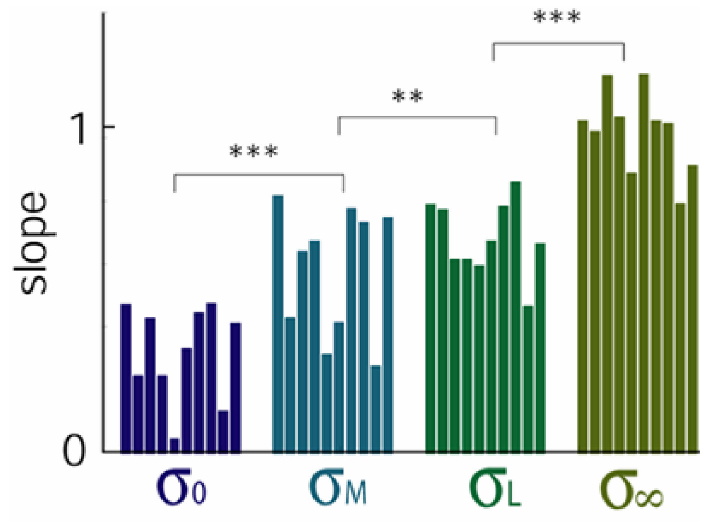


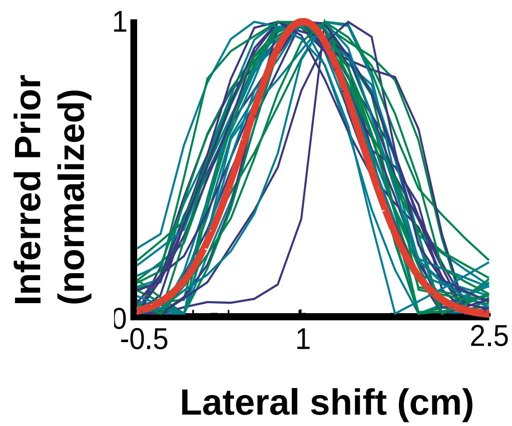


Supports model 2: Bayesian

Results: 10 subjects





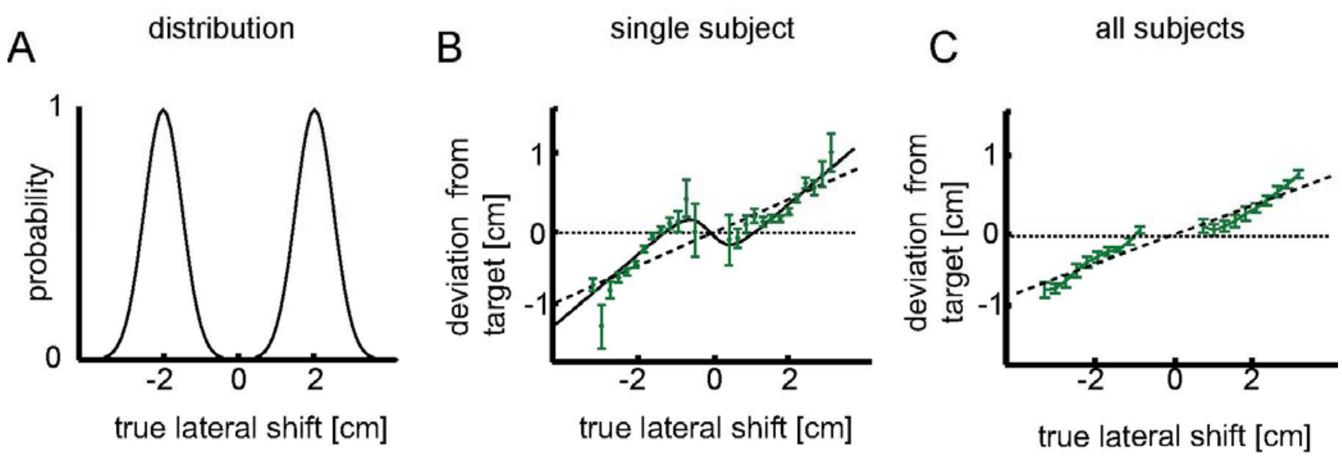


Supports model 2: Bayesian

Bayesian integration

Subjects can learn

- multimodal priors
- priors over forces
- different priors one after the other



(Körding& Wolpert NIPS 2004, Körding, Ku & Wolpert J. Neurophysiol. 2004)

Statistics of the world shape our brain

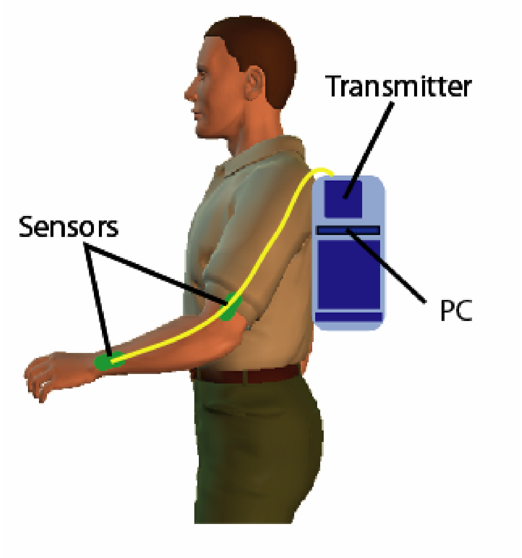
Objects

Configurations of our body

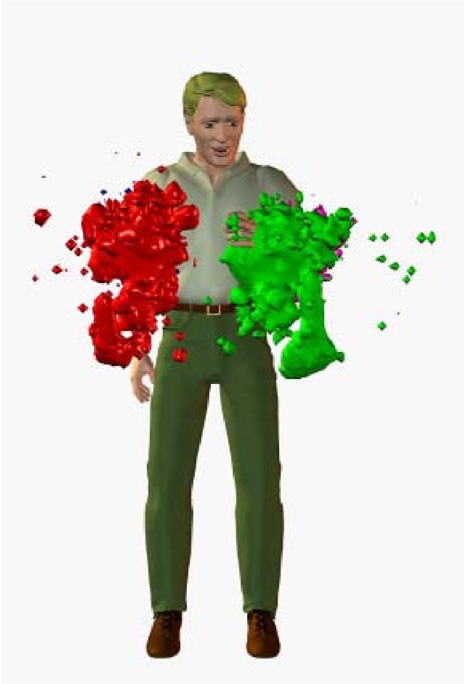
- Statistics of visual/auditory stimuli ⇨ representation visual/auditory cortex
- Statistics of early experience ⇨ what can be perceived in later life
  (e.g. statistics of spoken language)

Statistics of action

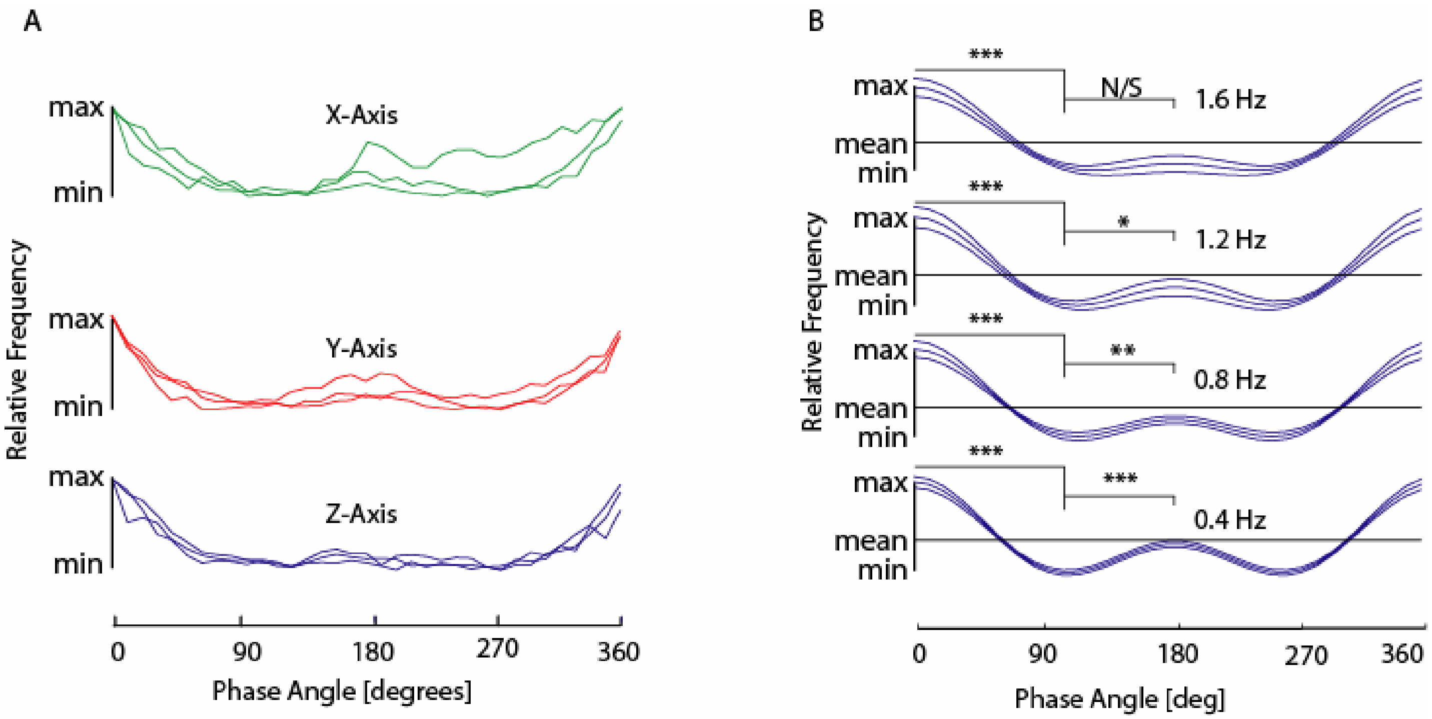
With limited neural resources statistics of motor tasks ⇨ motor performance



- 4 x 6-DOF electromagnetic sensors
- battery & notebook PC



Phase relationships and symmetry bias



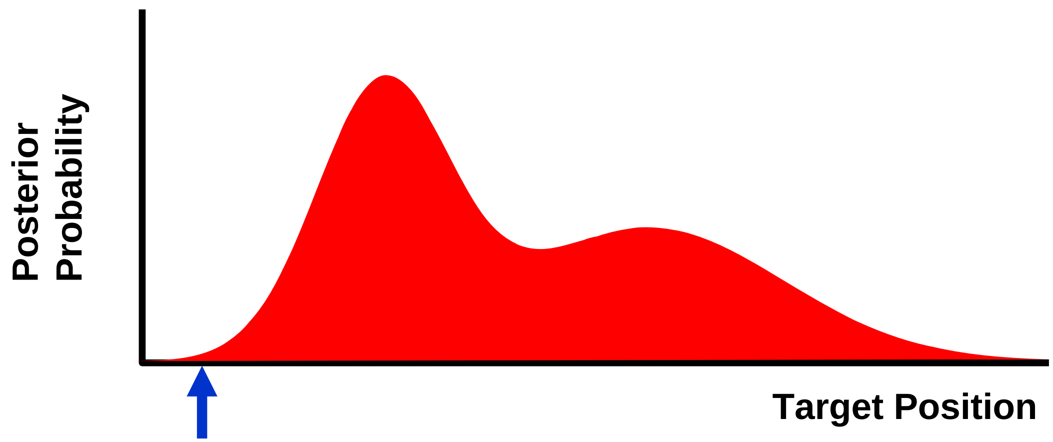
Multi-sensory integration

- **CNS**
  - **In general the relative weightings of the senses is sensitive to their direction dependent variability**
  - **Represents the distribution of tasks**
  - **Estimates its own sensory uncertainty**
  - **Combines these two sources in a Bayesian way**

- **Supports an optimal integration model**

Loss Functions in Sensorimotor system

$$\underbrace{P(\text{state}|\text{sensory input})}_{\text{Posterior}} \propto \underbrace{P(\text{sensory input}|\text{state})}_{\text{Likelihood}} \underbrace{P(\text{state})}_{\text{Prior}}$$



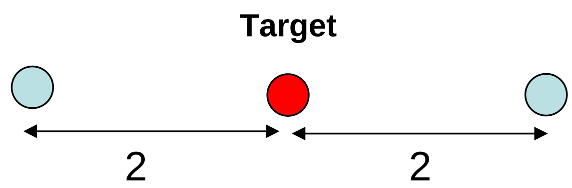
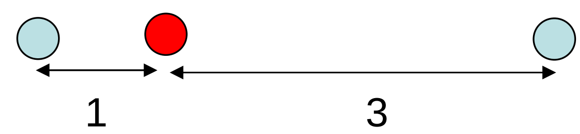
$$E[Loss] = \int Loss(state, action) P(state \mid sensory\_input)\, dsensory\_input$$

$$Bayes\ estimator \quad \hat{x}_B(s) = \arg\min_{actions} E[Loss]$$

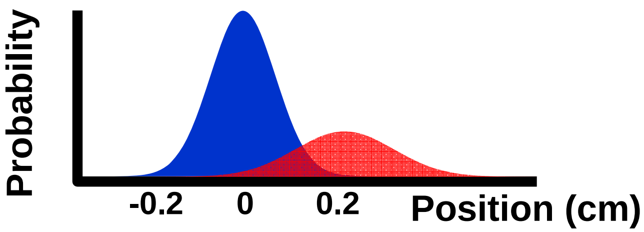
What is the performance criteria (loss, cost, utility, reward)?

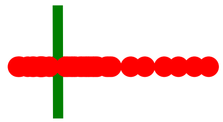
- Often assumed in statistics & machine learning
  - that we wish to minimize squared error for analytic or algorithmic tractability
- What measure of error does the brain care about?

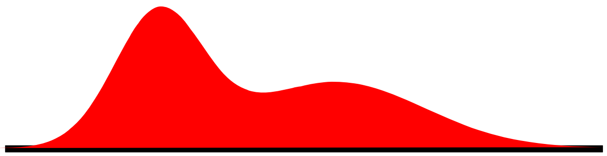
Loss function $f(error)$

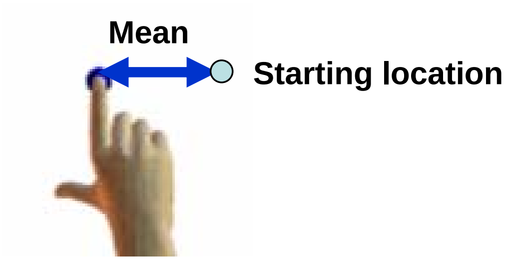
	Scenario 1	**Scenario 2**
		
$Loss = \|error\|^2$	Loss=4+4=8	Loss=1+9=10
$Loss = \|error\|$	Loss=2+2=4	Loss=1+3=4
$Loss = \|error\|^{\frac{1}{2}}$	Loss=1.4+1.4=2.8	Loss=1+1.7=2.7

Virtual pea shooter



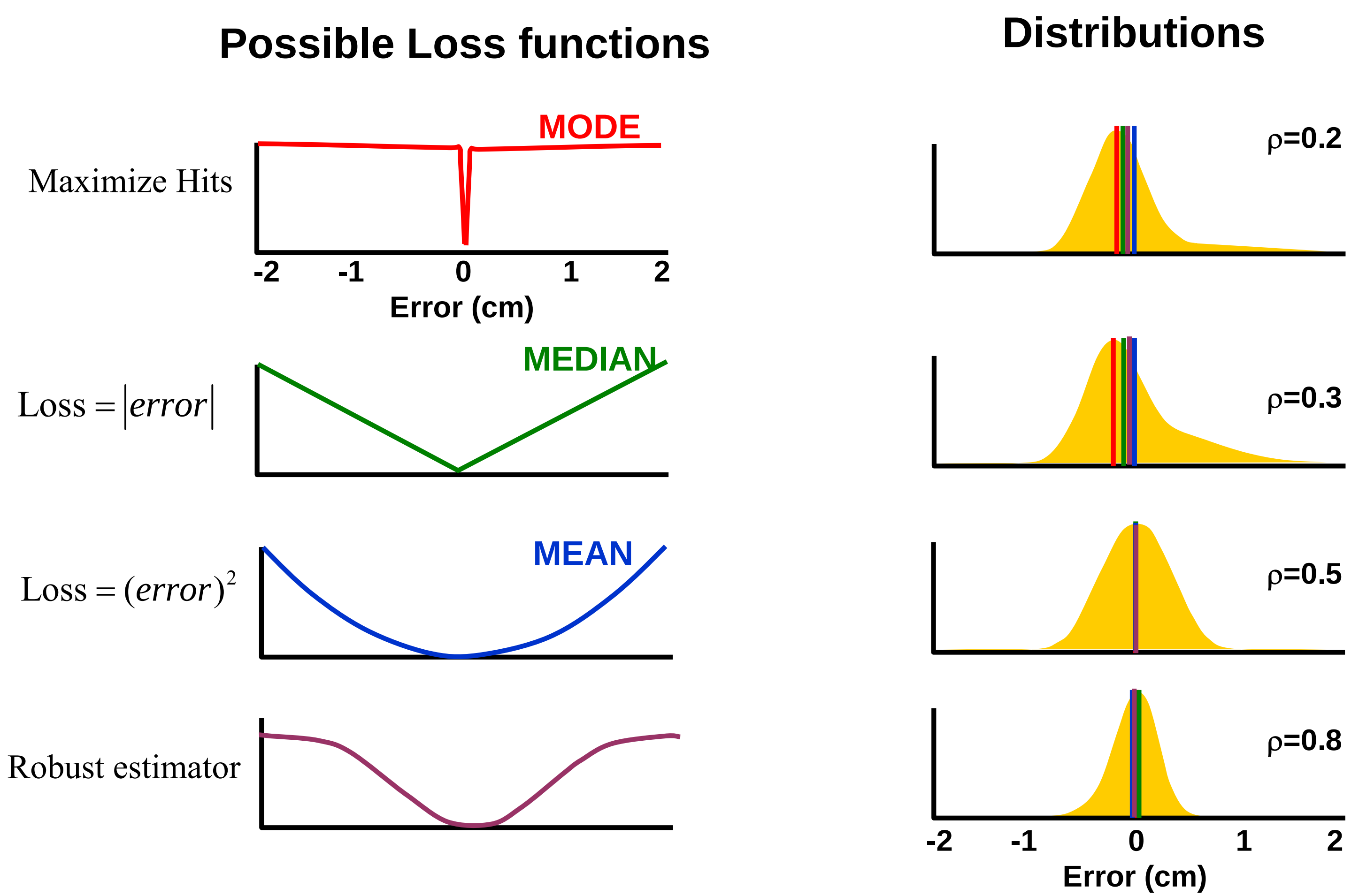




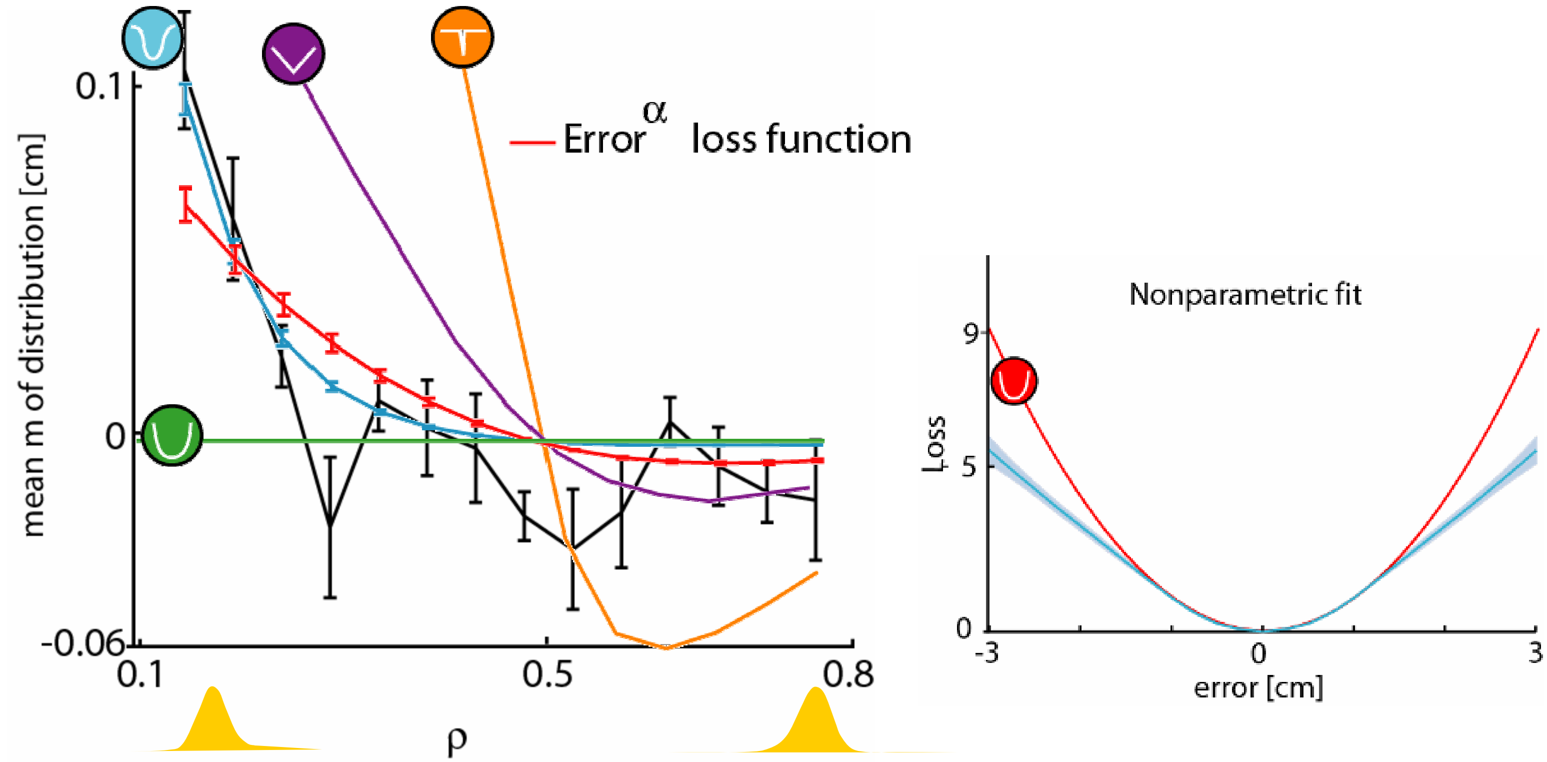


(Körding & Wolpert, PNAS, 2004)

Probed distributions and optimal means

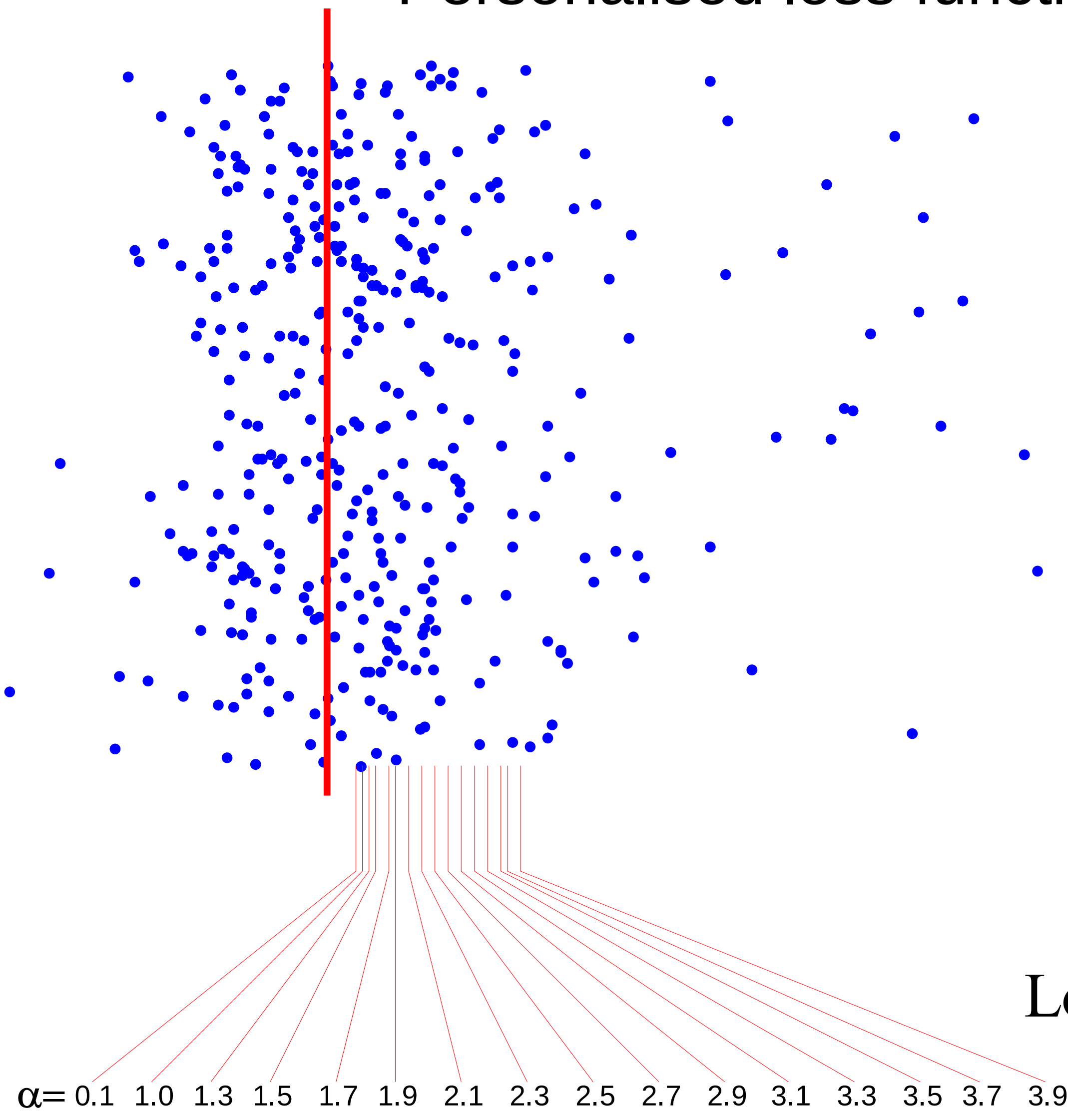


Shift of mean against asymmetry (n=8)



Mean squared error with robustness to outliers

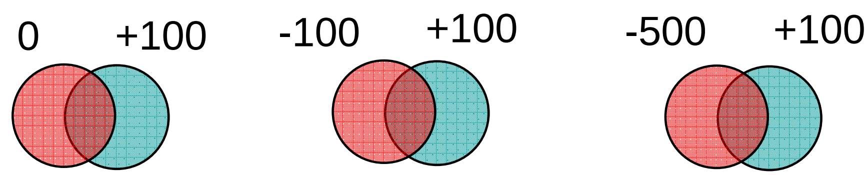
Personalised loss function

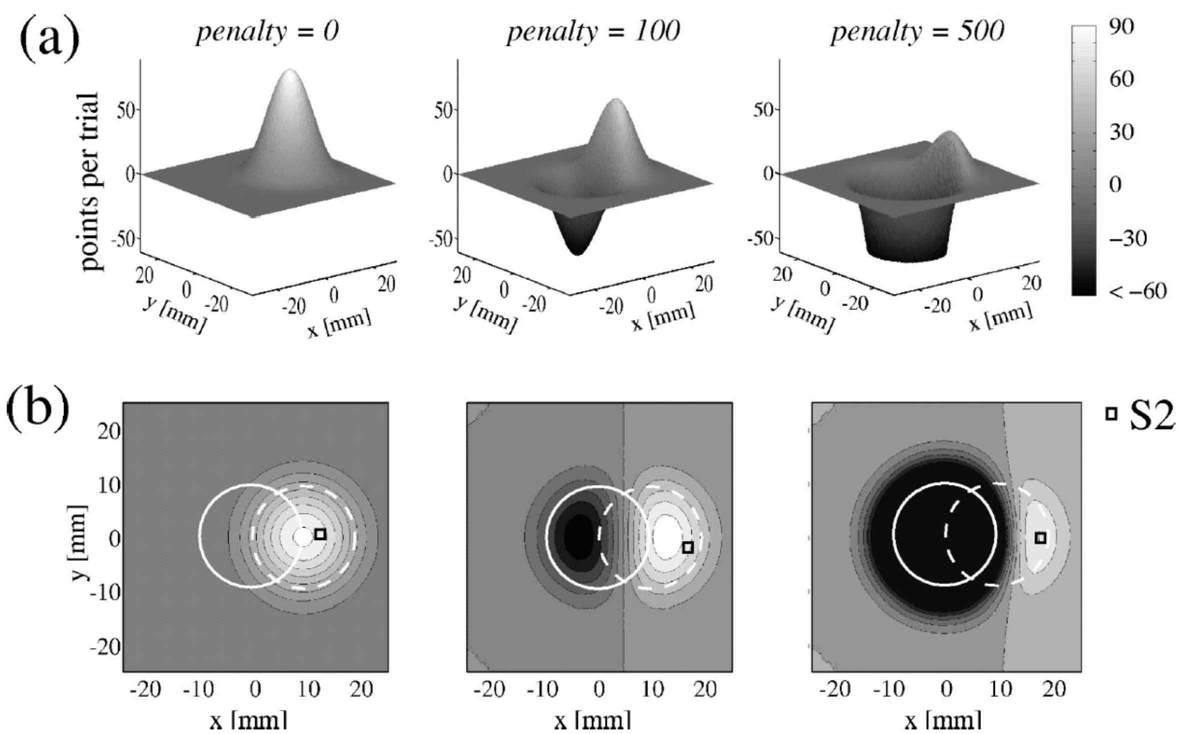


$$\text{Loss} = \sum error_i^{\alpha}$$

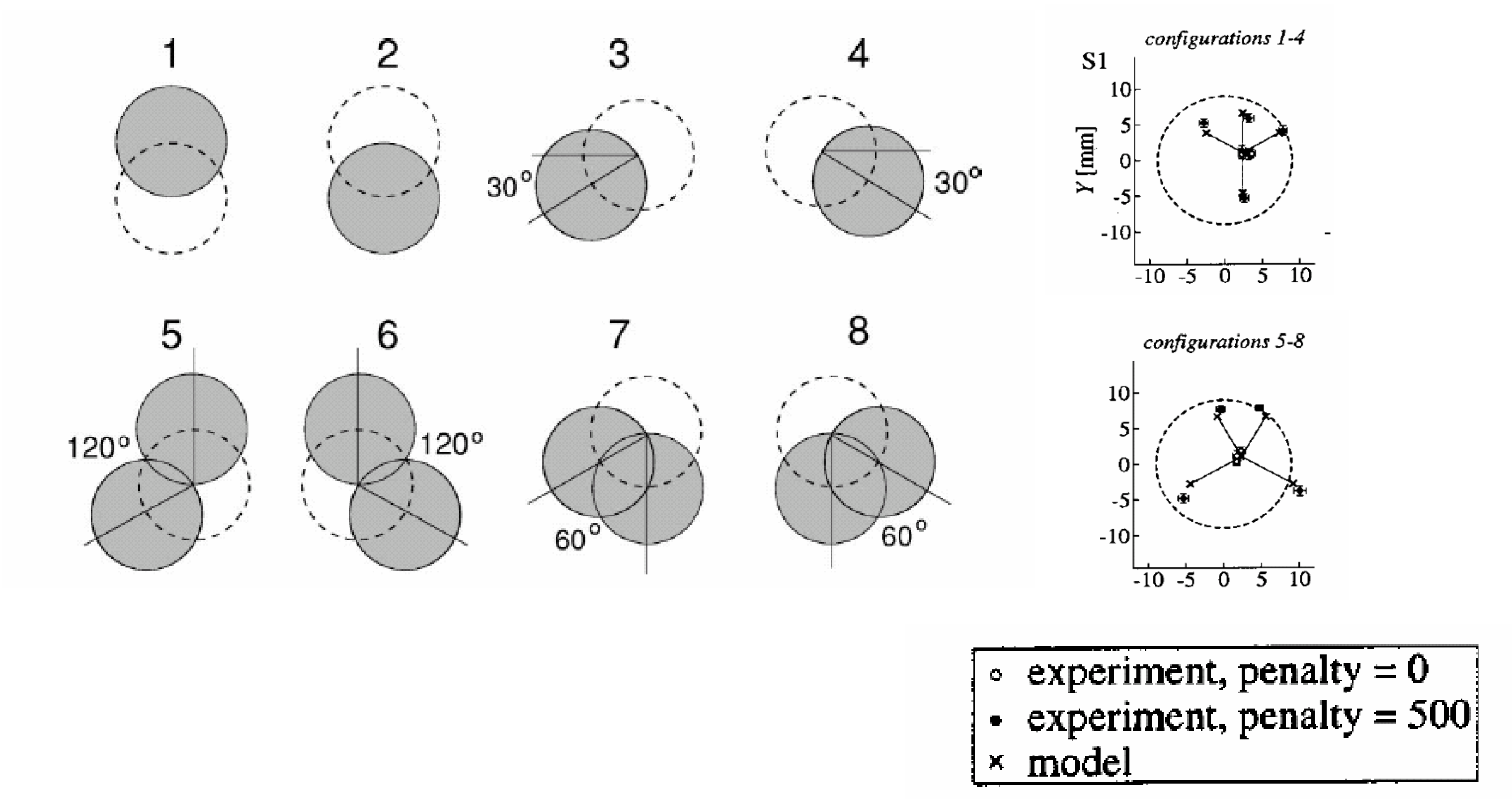
Bayesian decision theory

Imposed loss function
(Trommershäuser *et al 2003)*





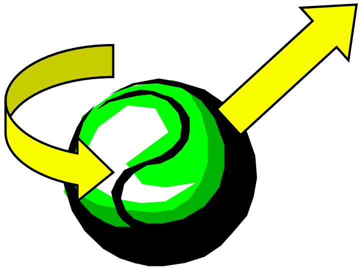
Optimal performance with complex regions



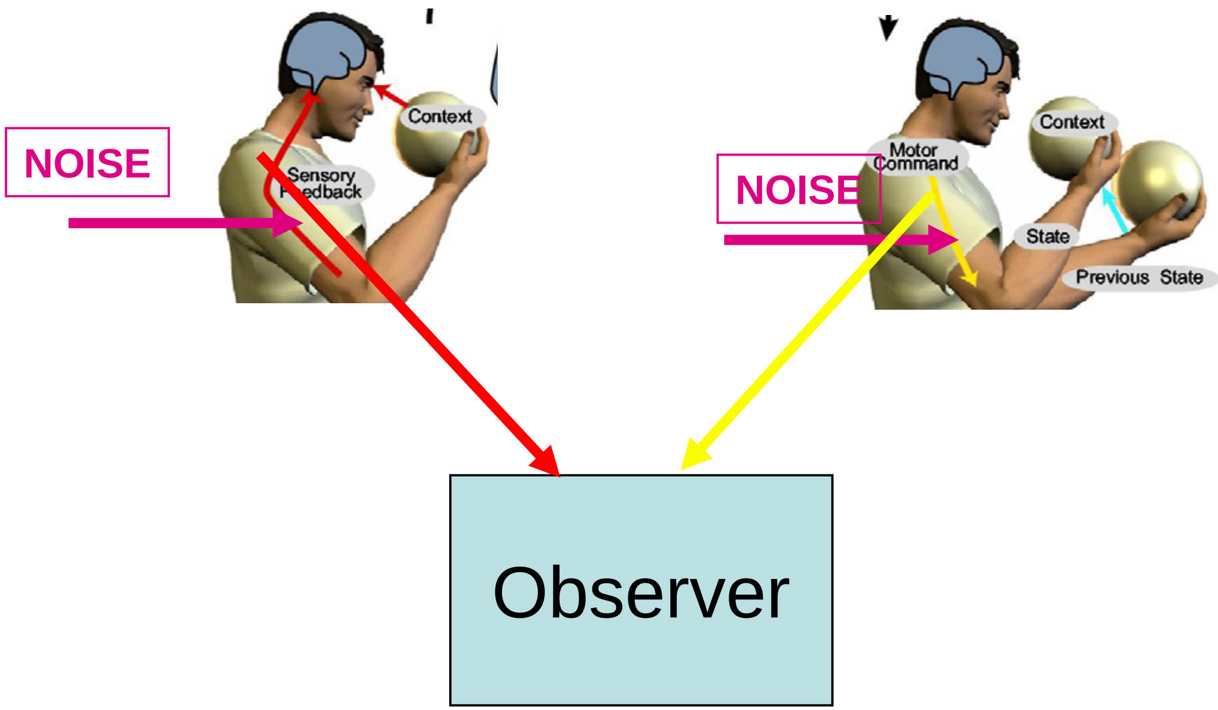
State estimation

- State of the body/world
  - Set of time-varying parameters which together with
    - Dynamic equations of motion
    - Fixed parameters of the system (e.g. mass)
  - Allow prediction of the future behaviour

- Tennis ball
  - Position
  - Velocity
  - Spin



State estimation



Kalman filter

- Minimum variance estimator
  - Estimate time-varying state
  - Can’t directly observe state but only measurement

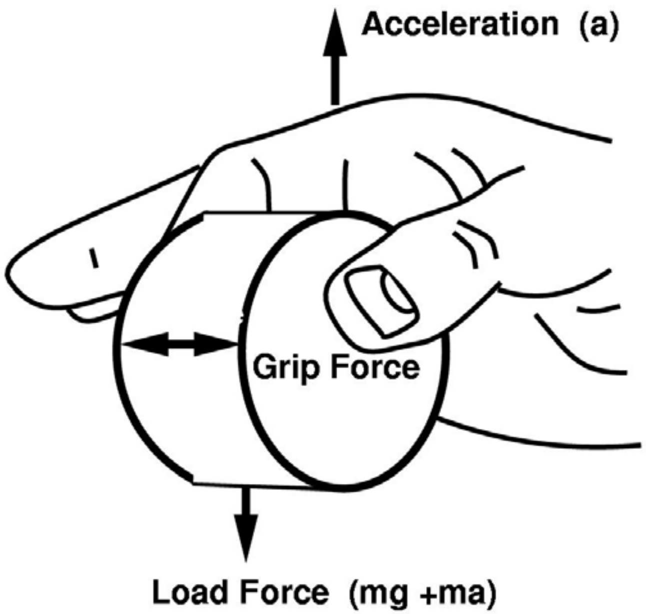
$$\mathbf{x}_{t+1} = A\mathbf{x}_t + B\mathbf{u}_t + \mathbf{w}_t$$

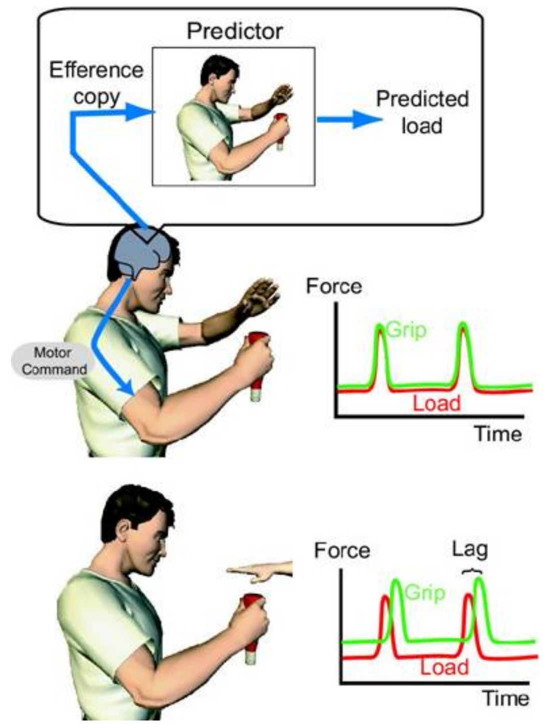
$$\mathbf{y}_{t+1} = C\mathbf{x}_t + \mathbf{v}_t$$

$$\hat{\mathbf{x}}_{t+1} = A\hat{\mathbf{x}}_t + B\mathbf{u}_t + K_t[\mathbf{y}_t - C\hat{\mathbf{x}}_t]$$

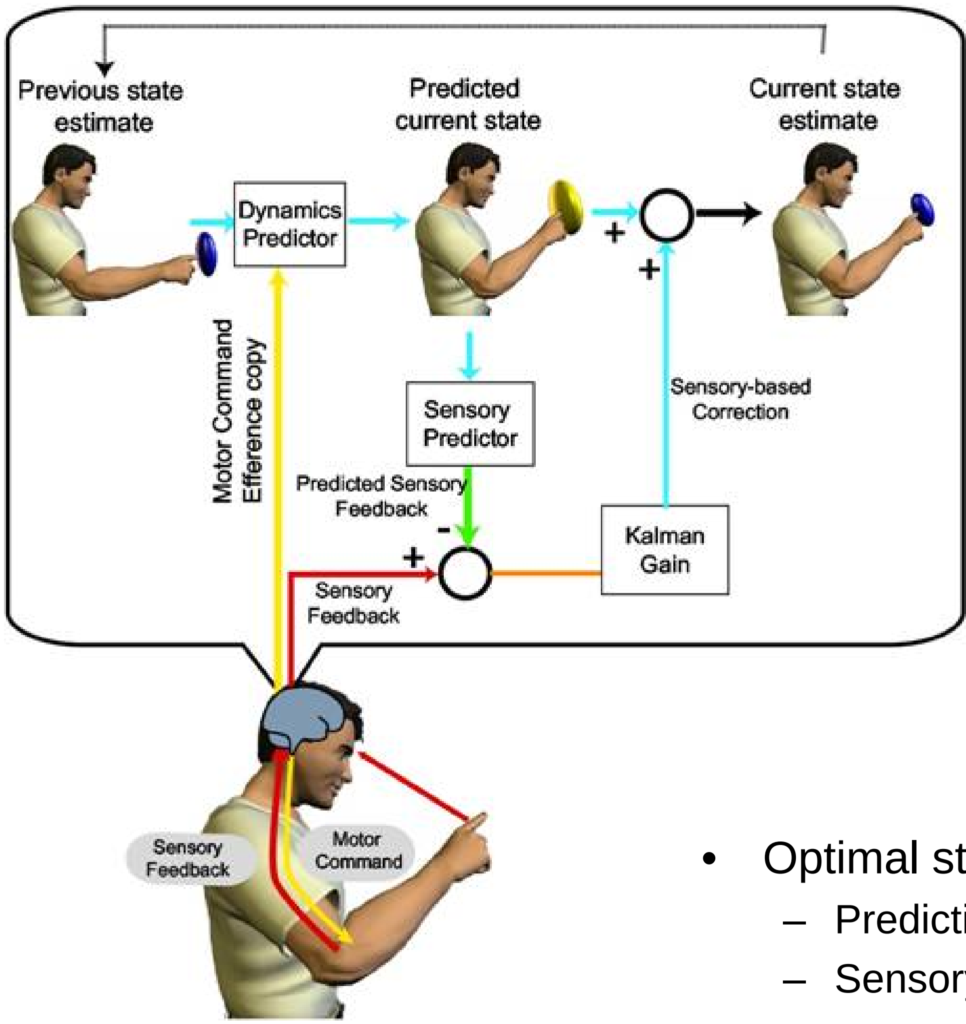
State estimation

$$\hat{\mathbf{x}}_{t+1} = \underbrace{A\hat{\mathbf{x}}_t + B\mathbf{u}_t}_{\text{Forward Dynamic Model}} + K_t[\mathbf{y}_t - C\hat{\mathbf{x}}_t]$$





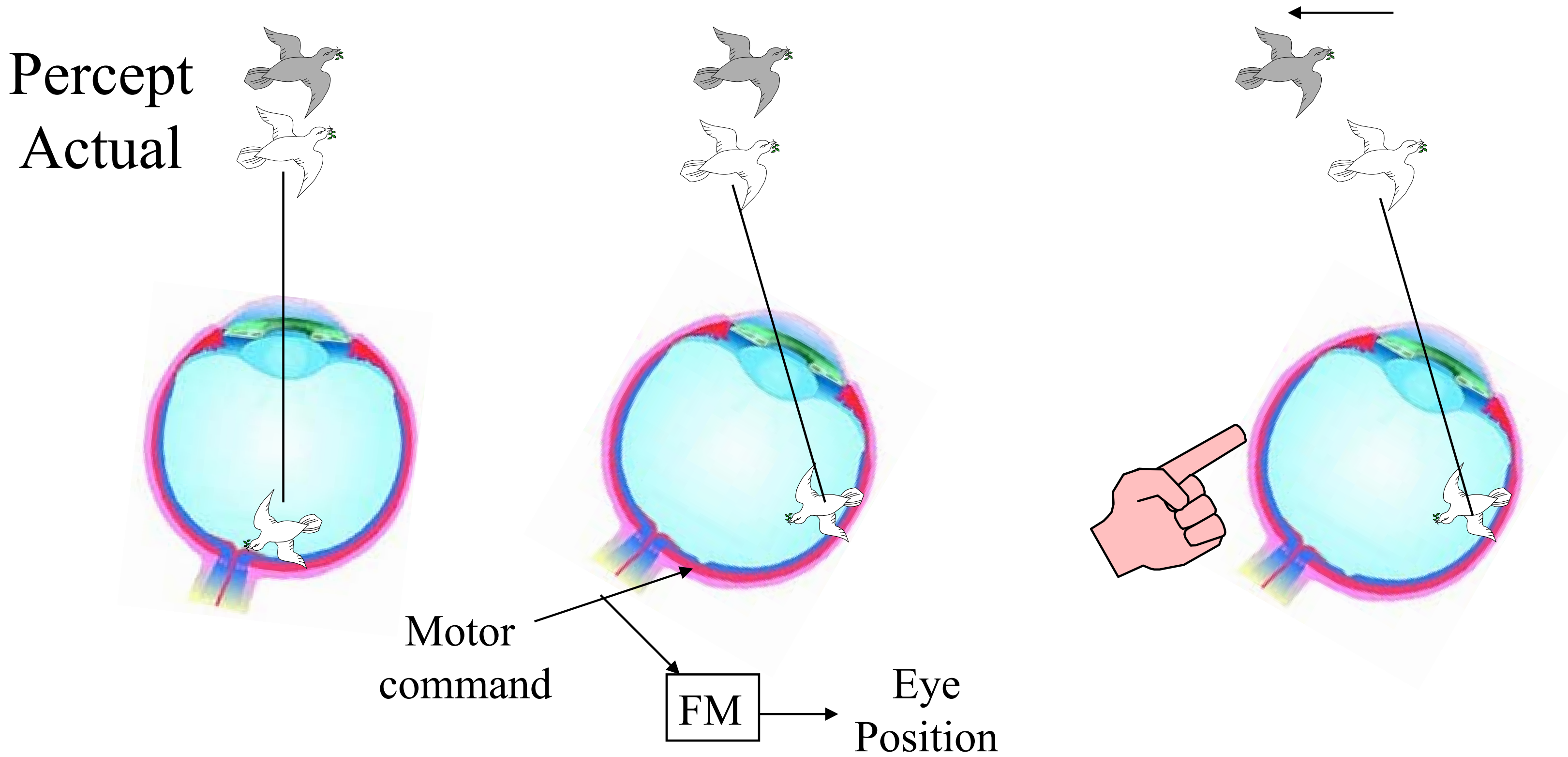
Kalman Filter



- Optimal state estimation is a mixture
  - Predictive estimation (FF)
  - Sensory feedback (FB)

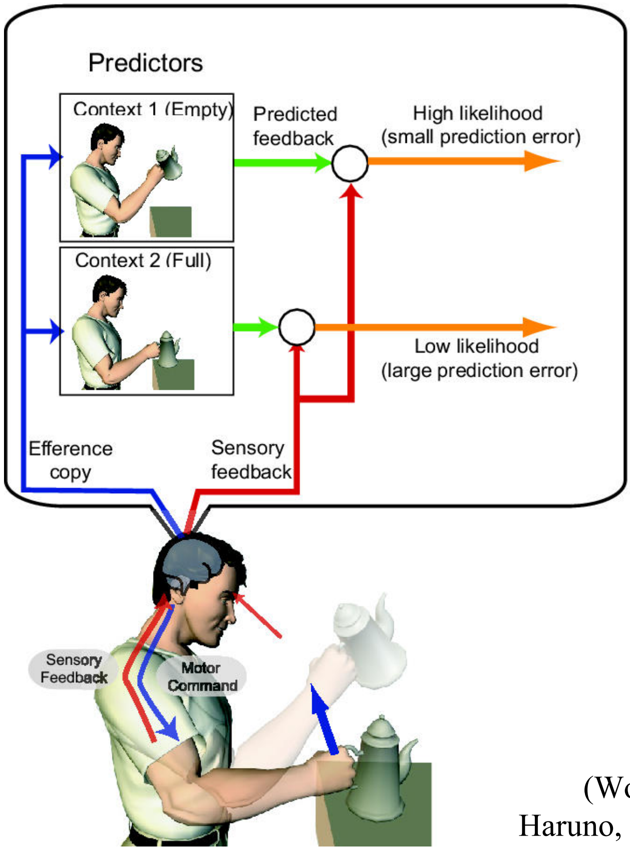
Eye position

Location of object based on retinal location and gaze direction



Sensory likelihood

$$P(\text{state}|\text{sensory input}) \propto \color{red}{P(\text{sensory input}|\text{state})}\, P(\text{state})$$

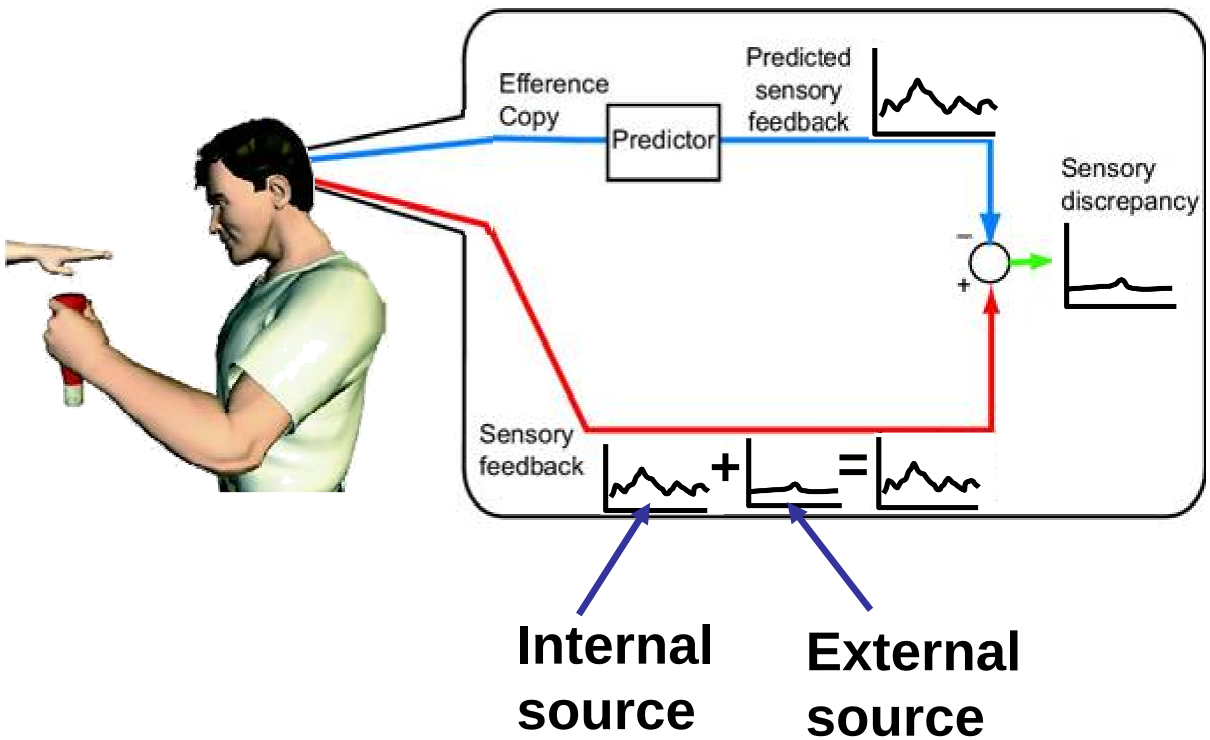


(Wolpert & Kawato, Neural Networks 1998
Haruno, Wolpert, Kawato, Neural Computation 2001)

Sensory prediction

Our sensors report

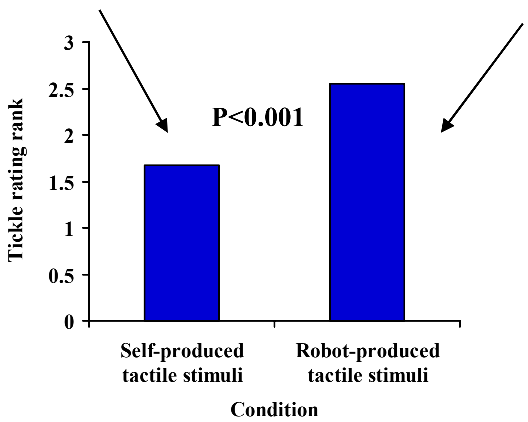
- Afferent information: changes in outside world
- Re-afferent information: changes we cause



Tickling

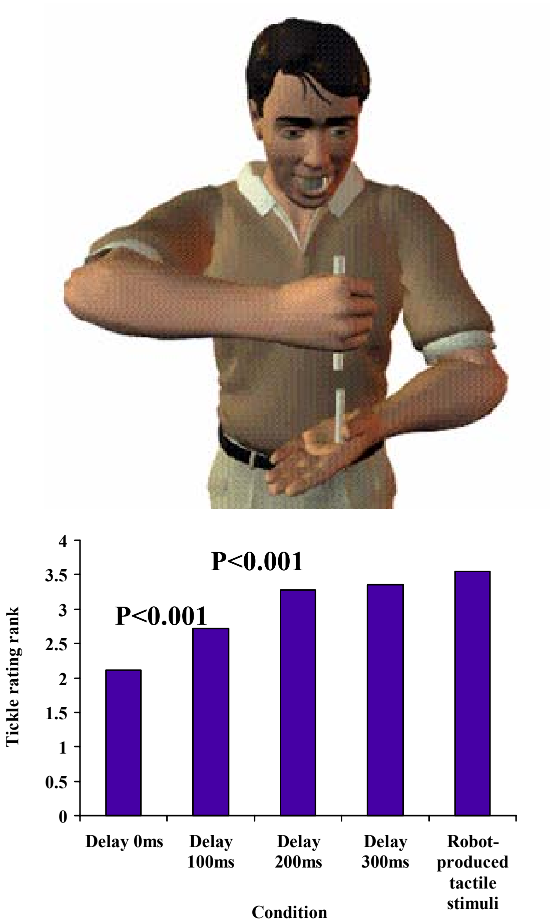
Self-administered tactile stimuli rated as less ticklish than externally administered tactile stimuli. (Weiskrantz et al, 1971)

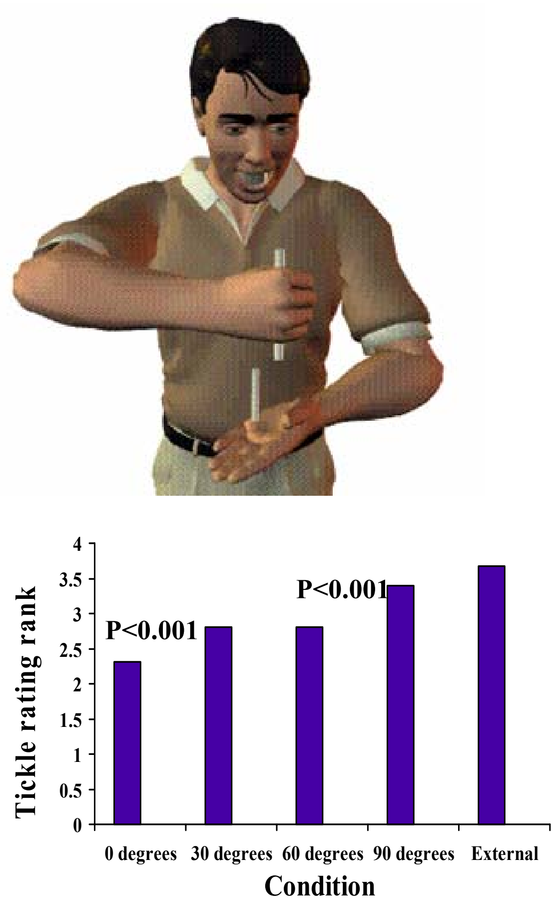
Does prediction underlie tactile cancellation in tickle?



Gain control or precise spatio-temporal prediction?

Spatio-temporal prediction

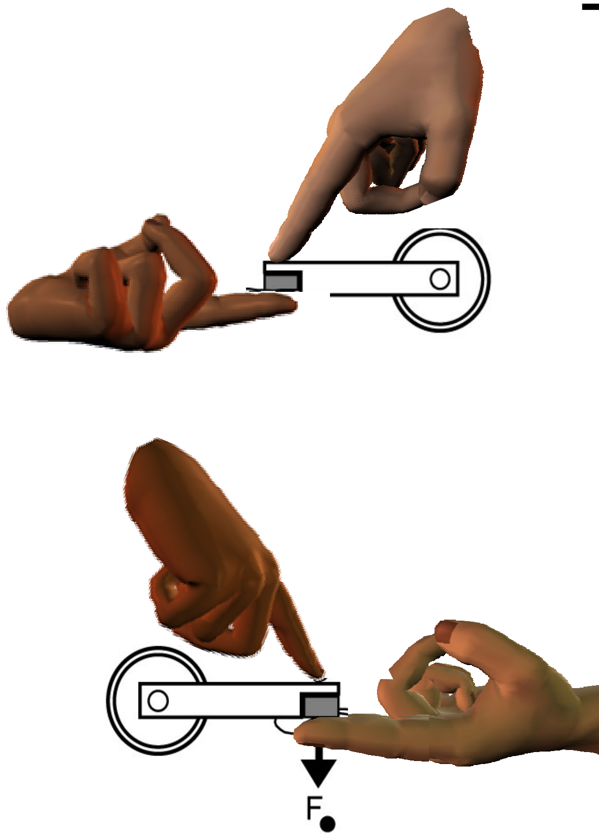




(Blakemore, Frith & Wolpert. J. Cog. Neurosci. 1999)

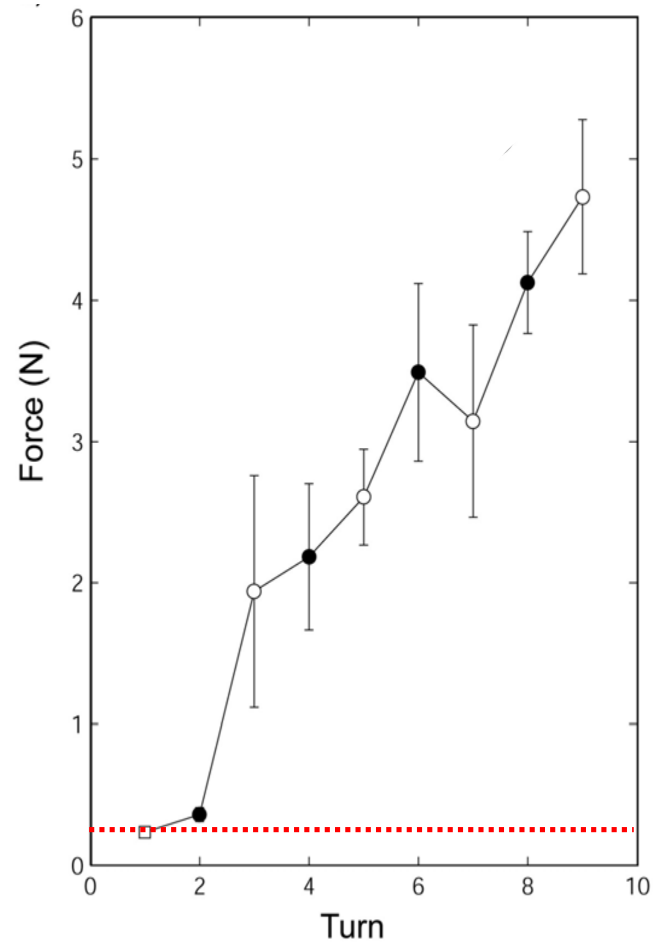
The escalation of force

Tit-for-tat

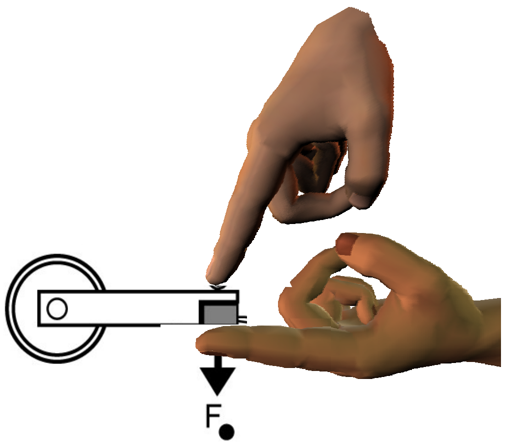


Force escalates under rules designed
to achieve parity: Increase by ~40% per turn

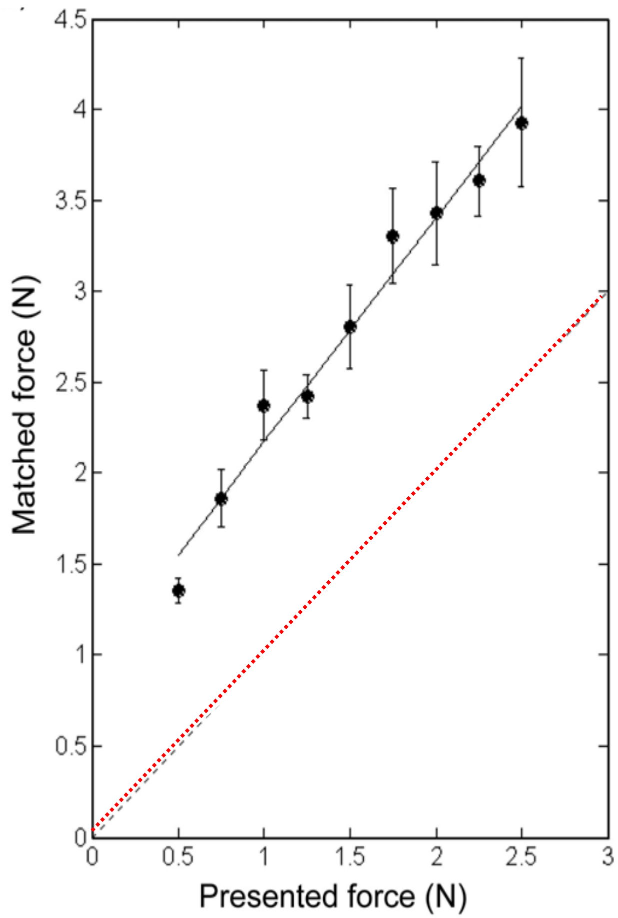
(Shergill, Bays, Frith & Wolpert, Science, 2003)



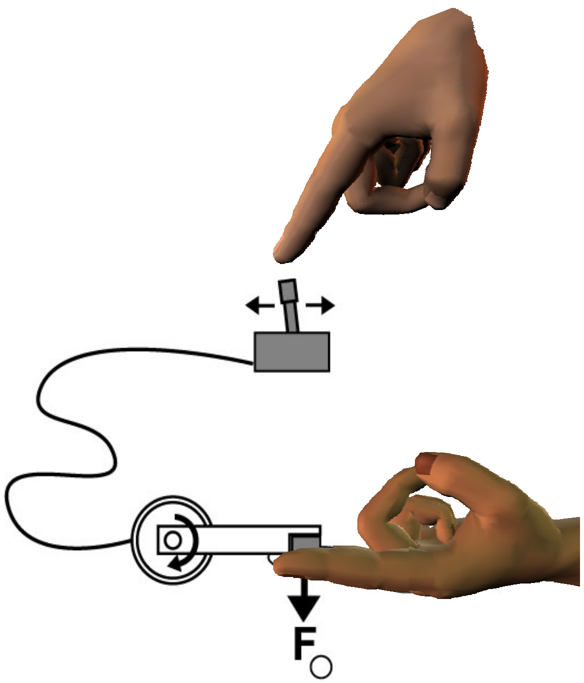
Perception of force

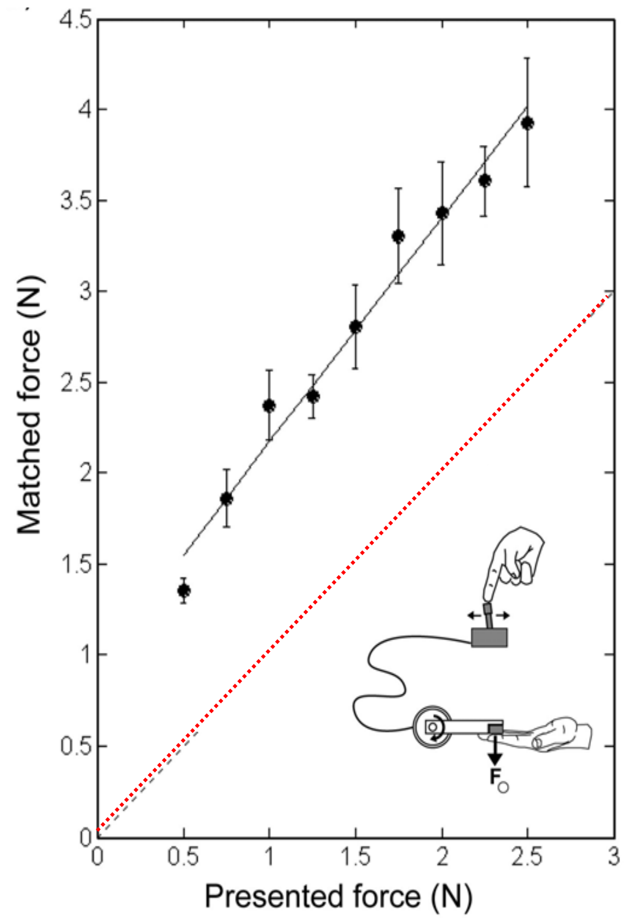


70% overestimate in force

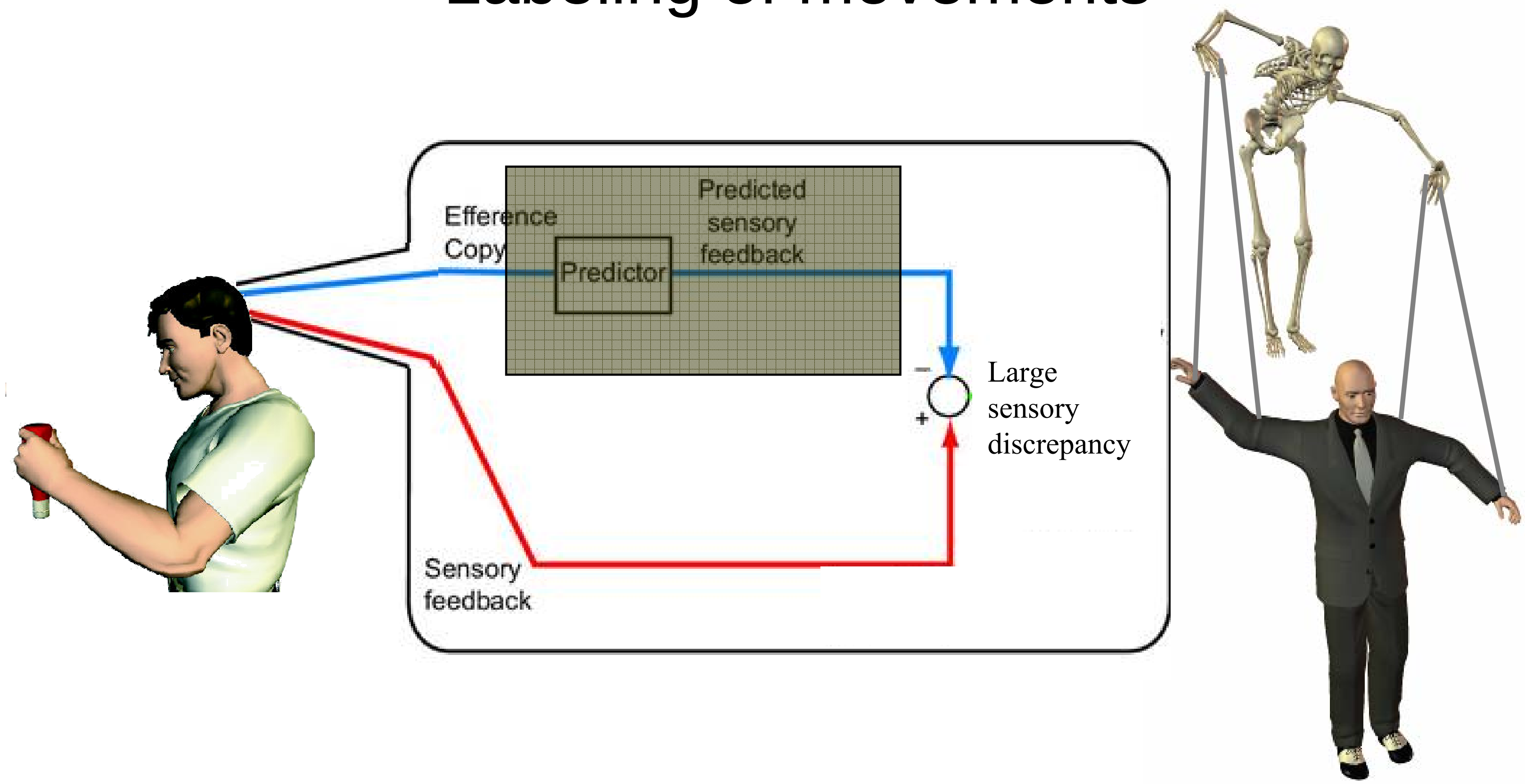


Perception of force

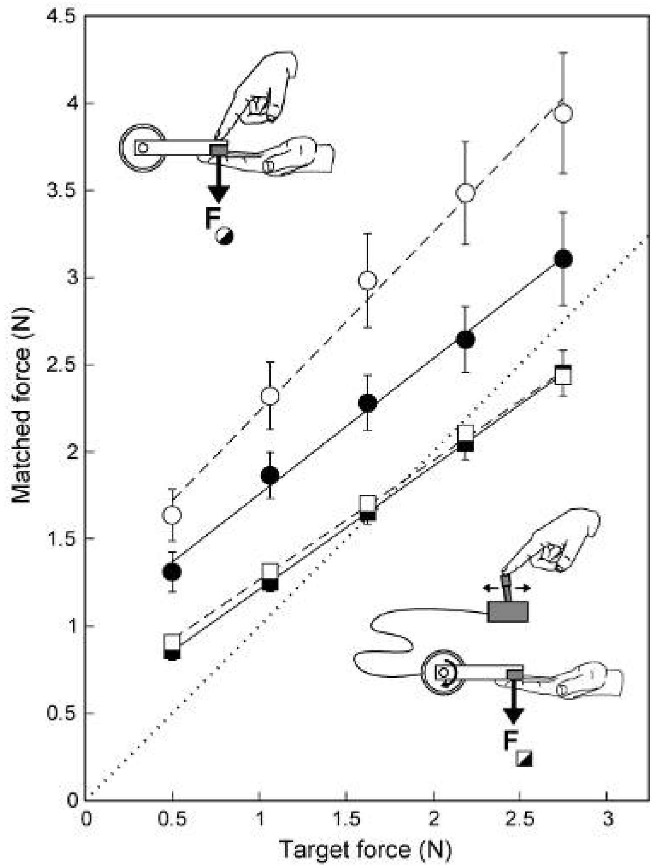




Labeling of movements



Defective prediction in patients with schizophrenic



Patients ■ ●
Controls □ ○

- **The CNS predicts sensory consequences**
- **Sensory cancellation in Force production**
- **Defects may be related to delusions of control**

Motor Learning

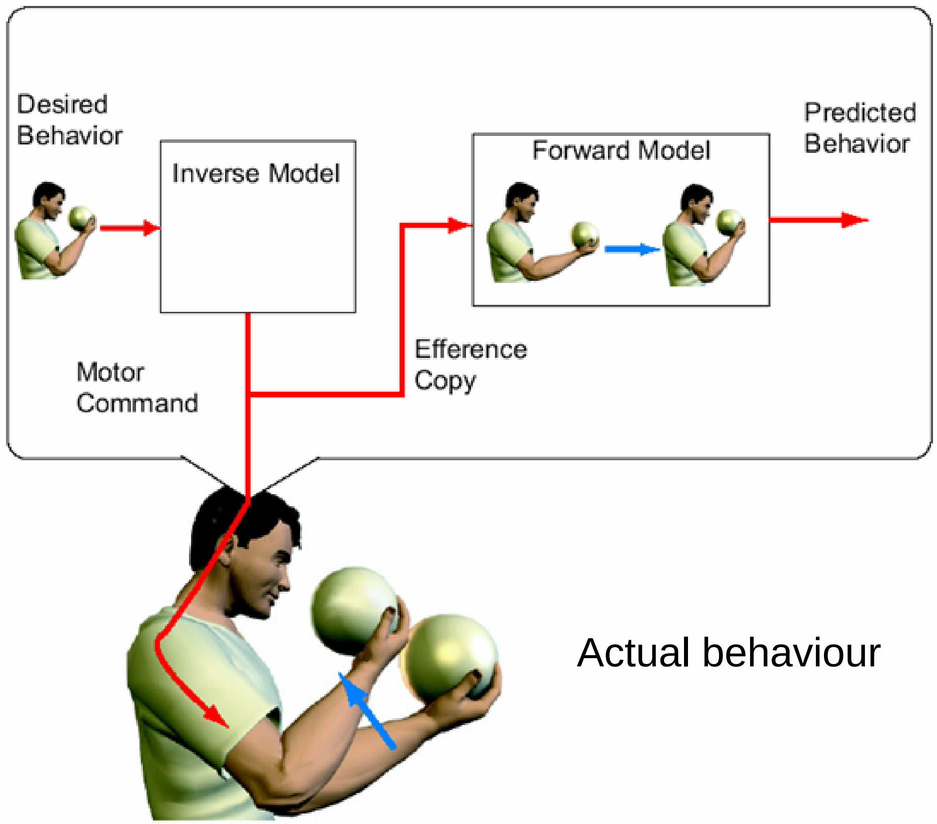
Required if:

- organisms environment, body or task change
- changes are unpredictable so cannot be pre-specified
- want to master social convention skills e.g writing

Trade off between:

- innate behaviour (evolution)
  - hard wired
  - fast
  - resistant to change
- learning (intra-life)
  - adaptable
  - slow
  - Maleable

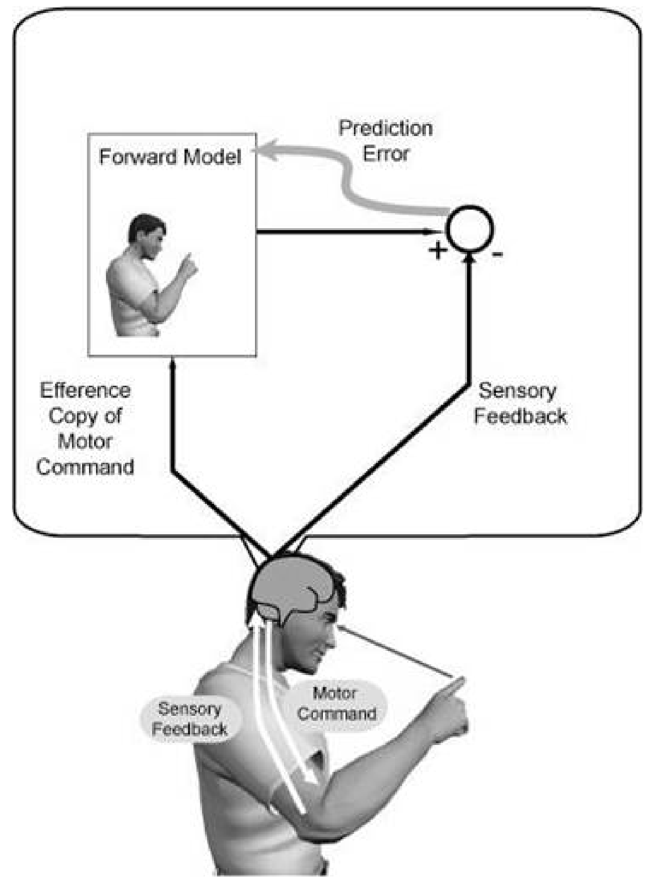
Motor Learning



Actual behaviour

Supervised learning is good for forward models

Predicted outcome can be compared to actual outcome to generate an error



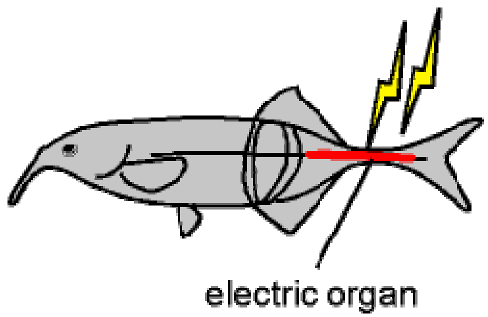
Weakly electric fish (Bell 2001)

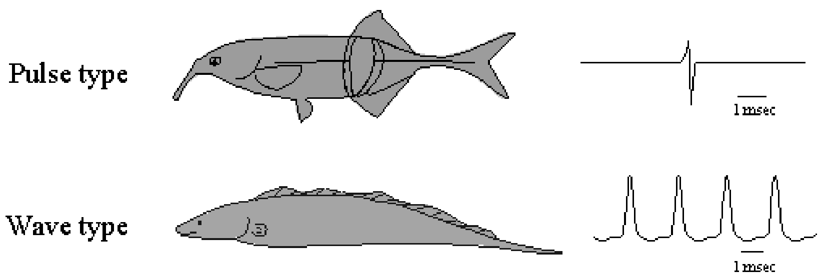
Produce electric pulses to

- recognize objects in the dark or in murky habitats
- for social communication.

The fish electric organ is composed of electrocytes,

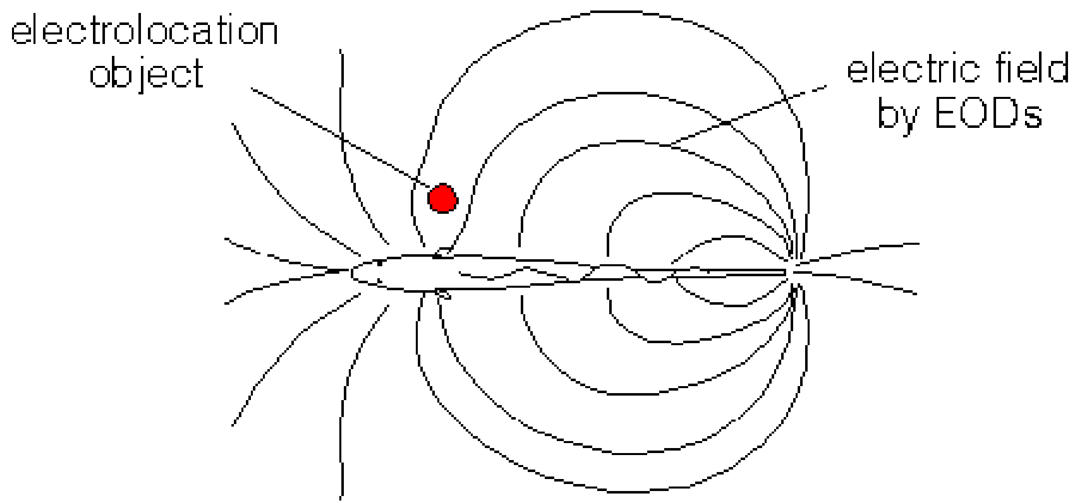
- modified muscle cells producing action potentials
- EOD = electric organ discharges
- Amplitude of the signal is between 30 mV and 7V
- Driven by a pacemaker in medulla, which triggers each discharge





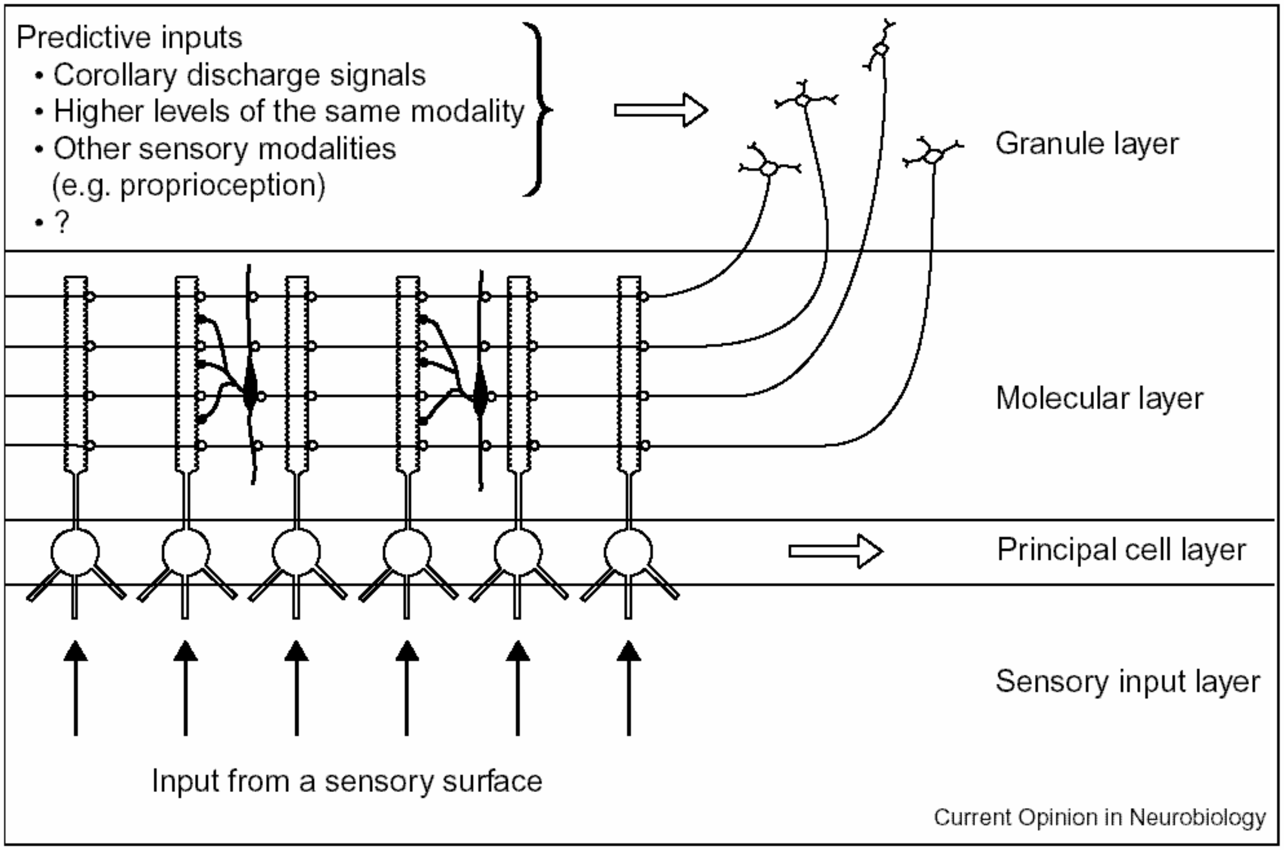
Sensory filtering

Skin receptors are derived from the lateral line system



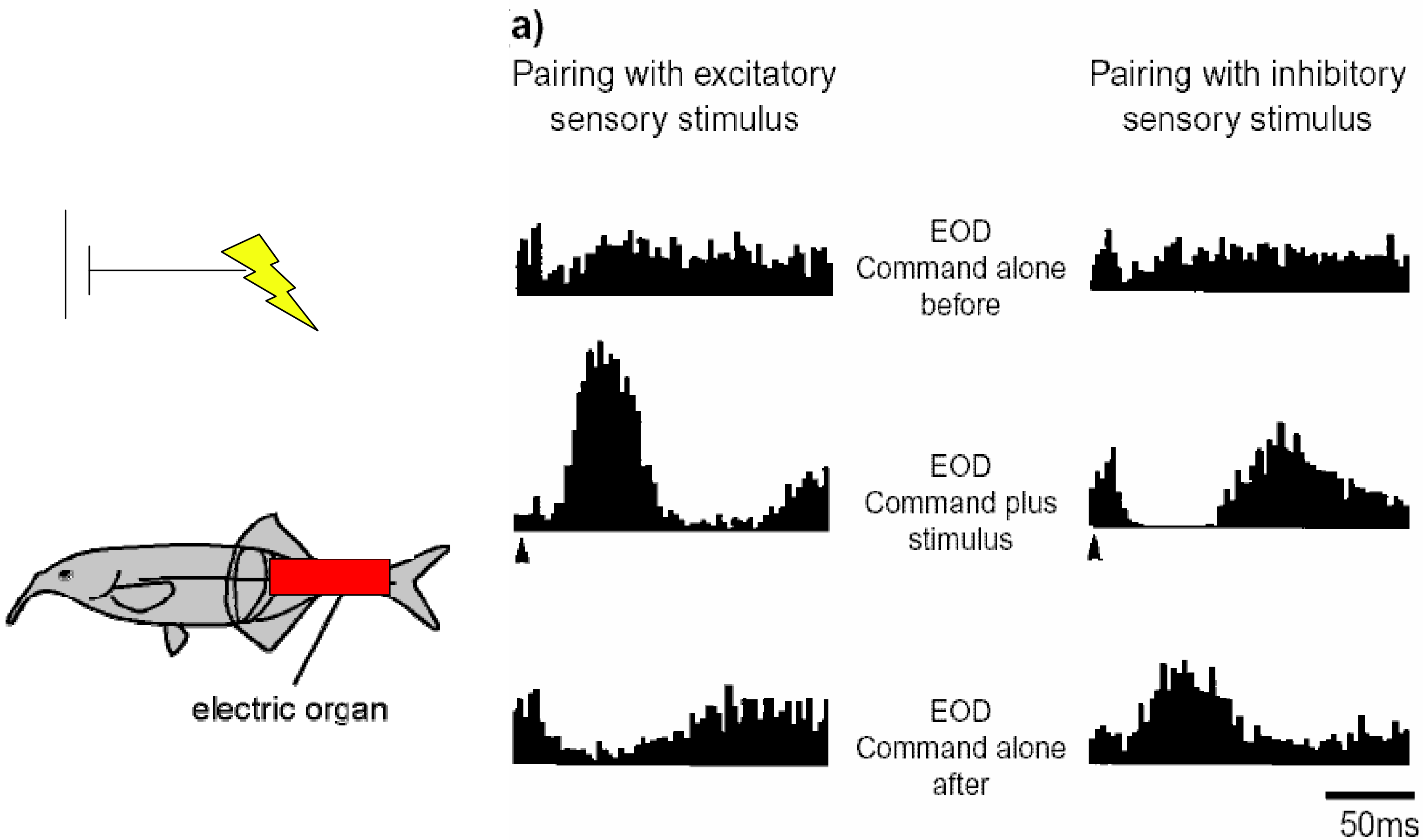
Removal of expected or predicted sensory input is one of the very general functions of sensory processing.
Predictive/associative mechanisms for changing environments

Primary afferent terminate in cerebellar-like structures



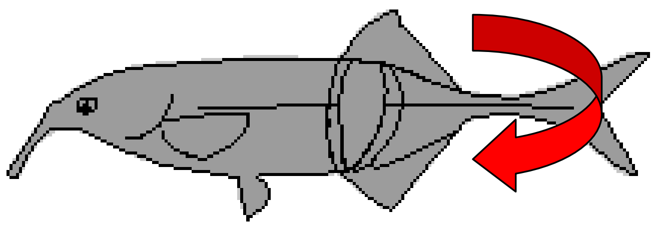
Primary afferents terminate on principal cells either directly or via interneurons

Block EOD discharge with curare

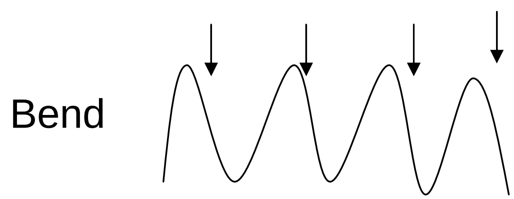


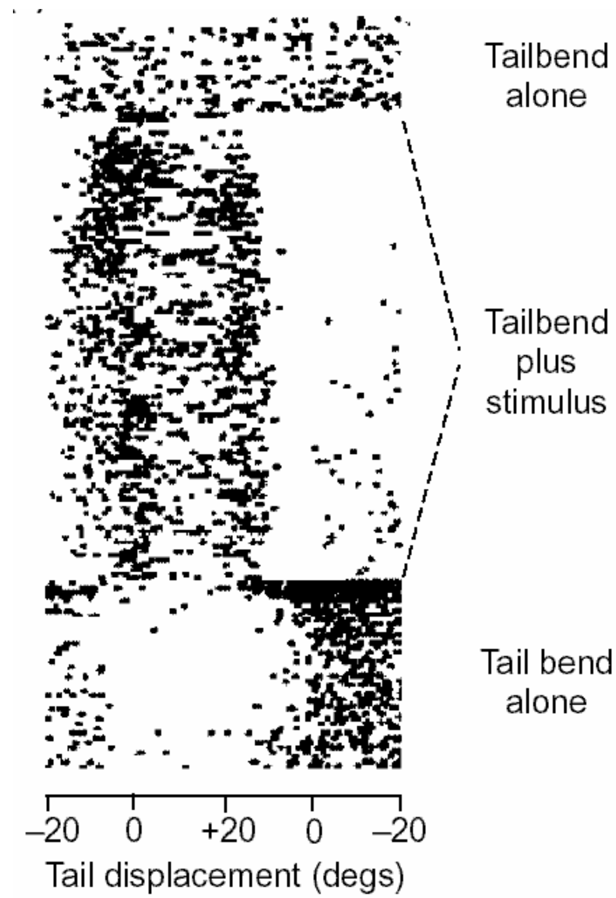
Specific for Timing (120ms), Polarity, Amplitude & Spatial distribution

Proprioceptive Prediction



Tail bend affects feedback
Passive Bend phase locked
to stimulus:



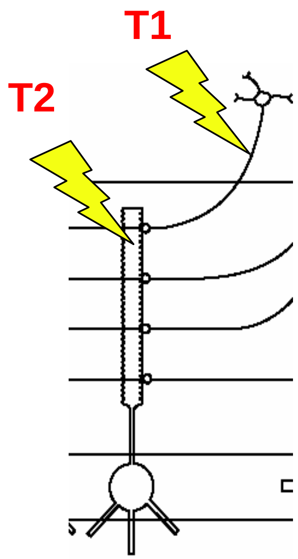


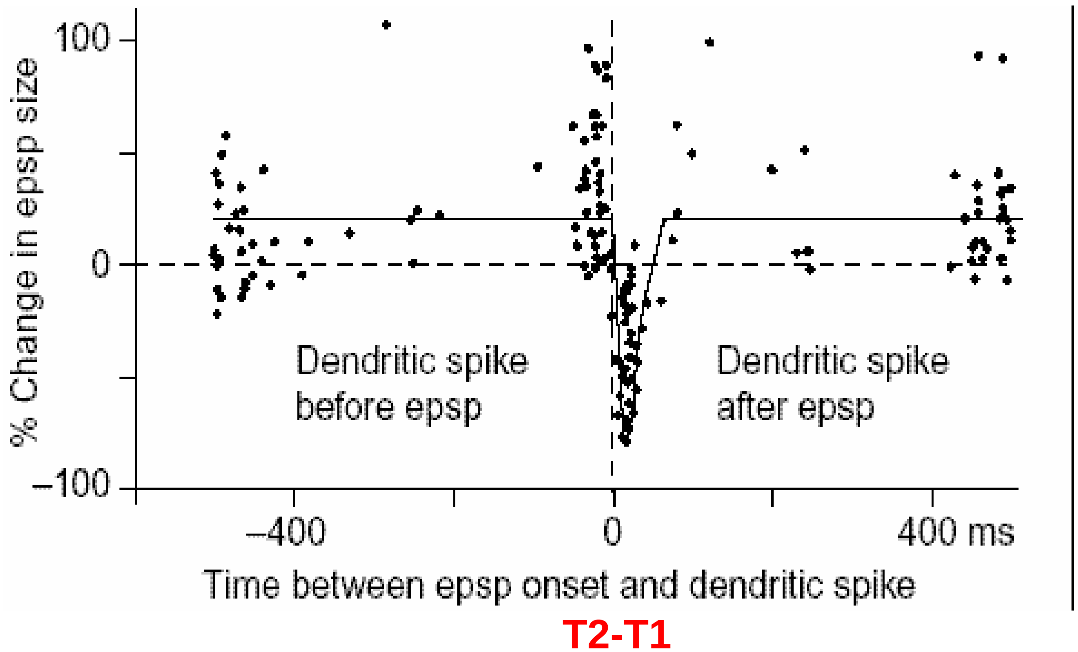
Learning rule

Changes in synaptic strength requires principal cell spike discharge

Change depends on timing of EPSP to spike

Anti-Hebbian learning

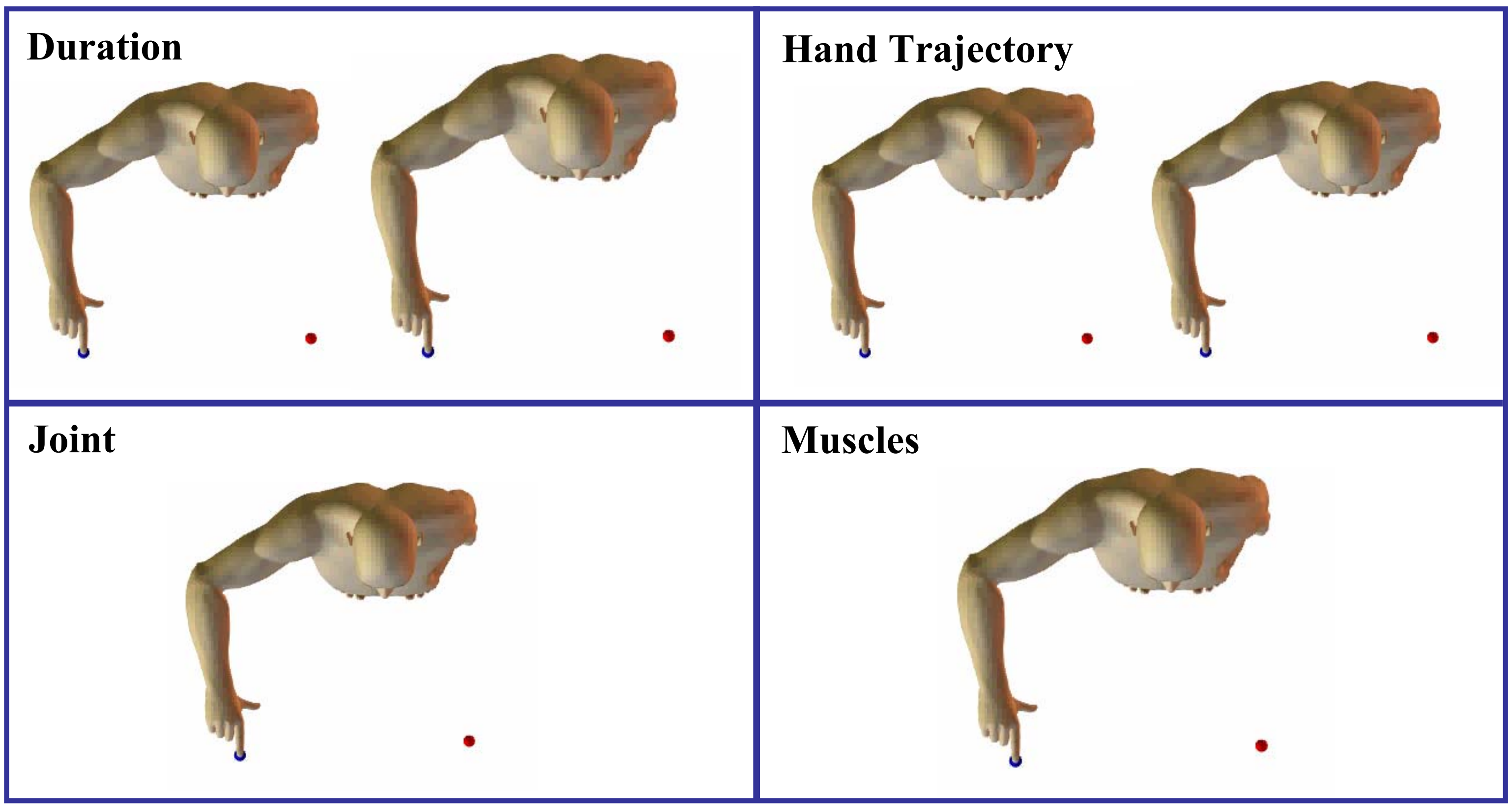




- **Forward Model can be learned through self-supervised learning**
- **Anti-hebbian rule in Cerebellar like structure of he electric fish**

Motor planning (what is the goal of motor control)

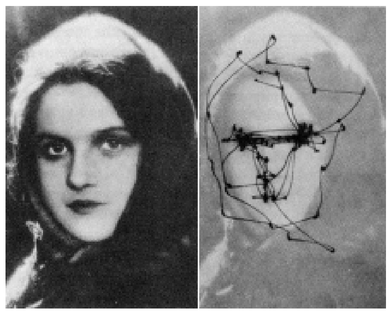
- Tasks are usually specified at a symbolic level
- Motor system works at a detailed level, specifying muscle activations
- Gap between high and low-level specification
- Any high level task can be achieved in infinitely many low-level ways

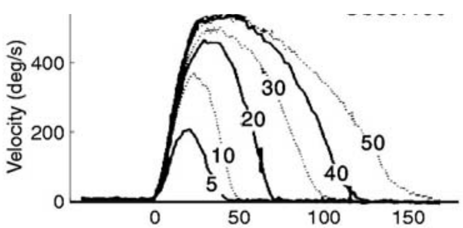


Motor evolution/learning results in stereotypy

Stereotypy between repetitions and individuals

Eye-saccades

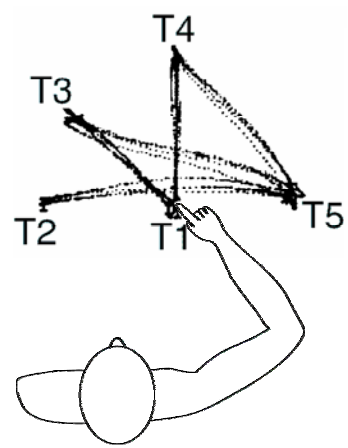


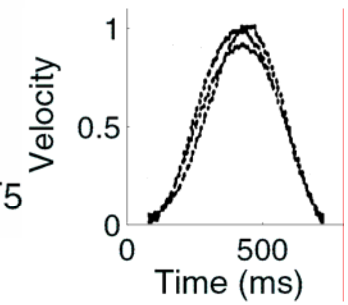


Time (ms)

- Main sequence
- Donder's law
- Listings Law

Arm- movements





- 2/3 power law
- Fitts' law

Models

HOW models

- Neurophysiological or black box models
- Explain roles of brain areas/processing units in generating behavior

WHY models

- *Why* did the *How* system get to be the way it is?
- Unifying principles of movement production
  - Evolutionary/Learning
- Assume few neural constraints

The Assumption of Optimality

Movements have evolved to maximize fitness

- improve through evolution/learning
- every possible movement which can achieve a task has a cost
- we select movement with the lowest **cost**

$$\textbf{Overall cost} = \text{cost}_1 + \text{cost}_2 + \text{cost}_3 \ldots$$

Optimality principles

- Parsimonious performance criteria
  ➔Elaborate predictions
- Requires
  - Admissible control laws
  - Musculoskeletal & world model
  - Scalar quantitative definition of task performance – usually time integral of f(state, action)

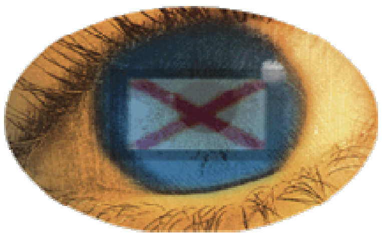
Open-loop

- What is the cost
  - Occasionally task specifies cost
    - Jump as high as possible
    - Exert maximal force
  - Usually task does not specify the cost directly
    - Locomotion well modelled by energy minimization
    - Energy alone is not good for eyes or arms

What is the cost?

Saccadic eye movements

- little vision over 4 deg/sec
- frequent 2-3 /sec
- deprives us of vision for 90 minutes/day



⇒Minimize time

Arm movements

Movements are smooth

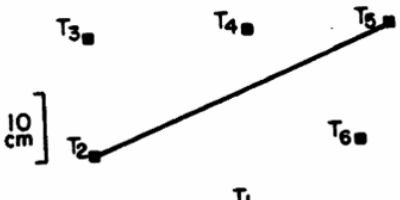
– Minimum jerk (rate of change of acceleration) of the hand (Flash & Hogan 1985)

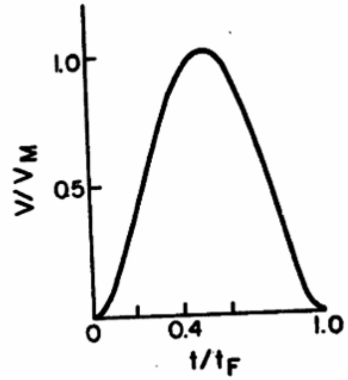
$$Cost = \int_0^T \dddot{x}(t)^2 + \dddot{y}(t)^2 \, dt$$

$$x(t) = x_0 + (x_0 - x_T)(15\tau^4 - 6\tau^5 - 10\tau^3)$$

$$y(t) = y_0 + (y_0 - y_T)(15\tau^4 - 6\tau^5 - 10\tau^3)$$

$$\tau = t / T$$

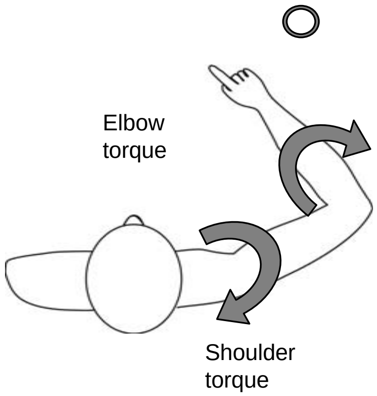


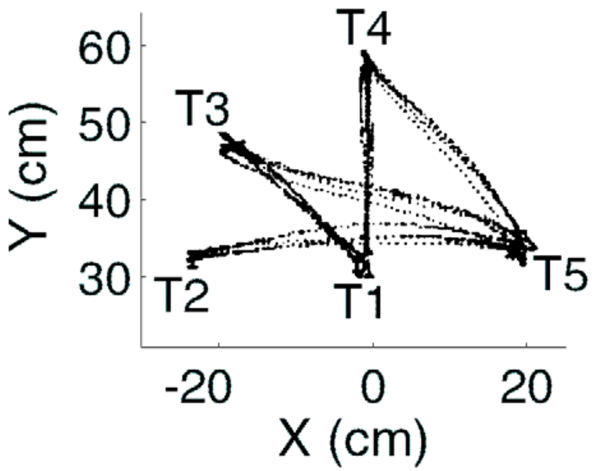


Smoothness

- Minimum Torque change (Uno et al, 1989)

$$Cost = \int_0^T \dot{\tau}_s(t)^2 + \dot{\tau}_e(t)^2 \, dt$$



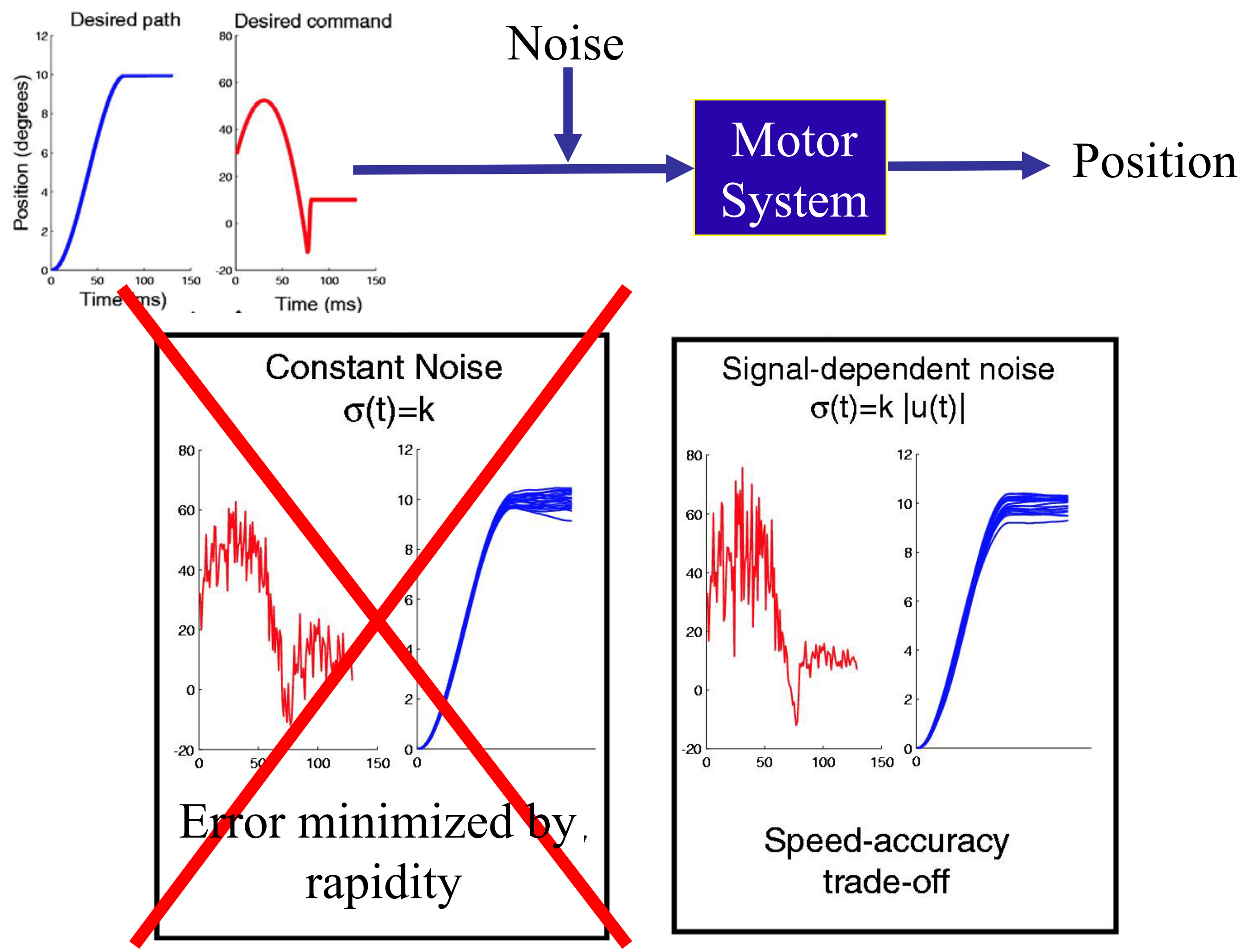


The ideal cost for goal-directed movement

- Makes sense - some evolutionary/learning advantage
- Simple for CNS to measure
- Generalizes to different systems
  - e.g. eye, head, arm
- Generalizes to different tasks
  - e.g. pointing, grasping, drawing

→ Reproduces & predicts behavior

Motor command noise

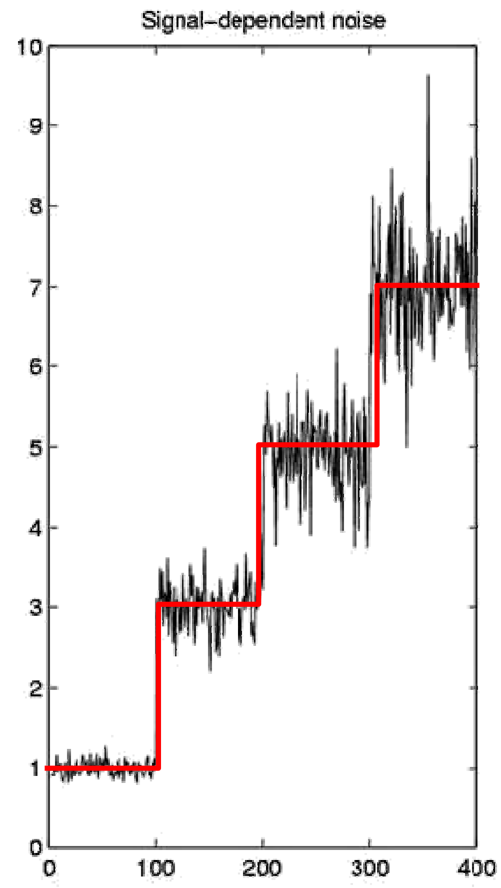


Fundamental constraint=Signal-dependent noise

- Signal-dependent noise:
  - Constant coefficient of variation
  - SD (motor command) ~ Mean (motor command)

- Evidence from
  - Experiments: SD (Force) ~ Mean (Force)
  - Modelling
    - Spikes drawn from a renewal process
    - Recruitment properties of motor units

(Jones, Hamilton & Wolpert , J. Neurophysiol., 2002)



Task optimization in the presence of SDN

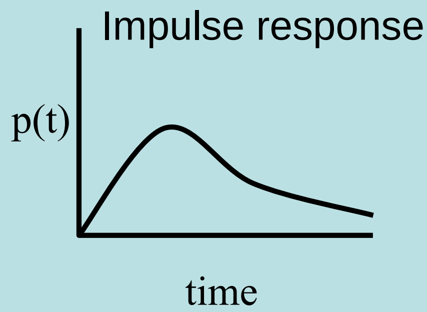
An average motor command $\Rightarrow$ probability distribution (statistics) of movement.

Controlling the statistics of action

Given SDN, Task $\equiv$ optimizing f(statistics)

Finding optimal trajectories for linear systems

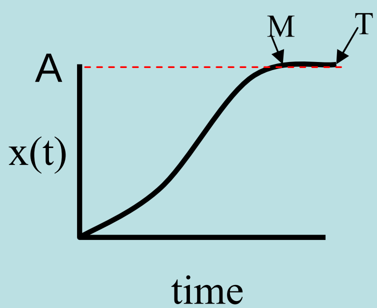
System



Signal-dependent noise

$$\sigma_u^2(t) = k^2 u^2(t)$$

Constraints



$$E[x(M)] = \int_0^M u(\tau)\, p(M-\tau)\, d\tau = A$$

$$E[x^{(n)}(M)] = \int_0^M u(\tau)\, p^{(n)}(M-\tau)\, d\tau = 0$$

Cost

$$Var[x(T)] = \int_0^M Var[u(\tau)\, p(T-\tau)]\, d\tau = \int_0^M Var[u(\tau)]\, p^2(T-\tau)\, d\tau$$

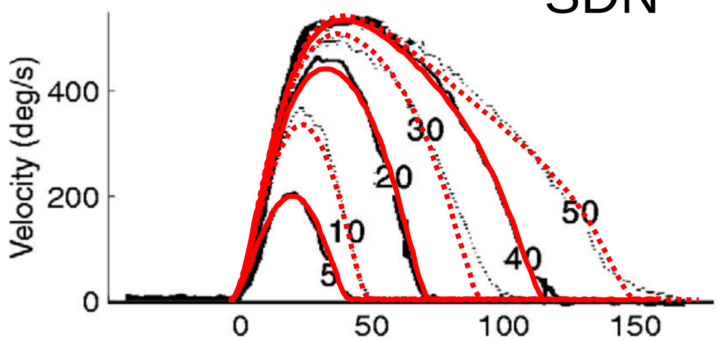
$$= \int_0^M k^2 u^2(\tau)\, p^2(T-\tau)\, d\tau = \int_0^M w(\tau) u^2(\tau)\, d\tau$$

Linear constraints with quadratic cost:
can use quadratic programming or isoperimetric optimization

Saccade predictions

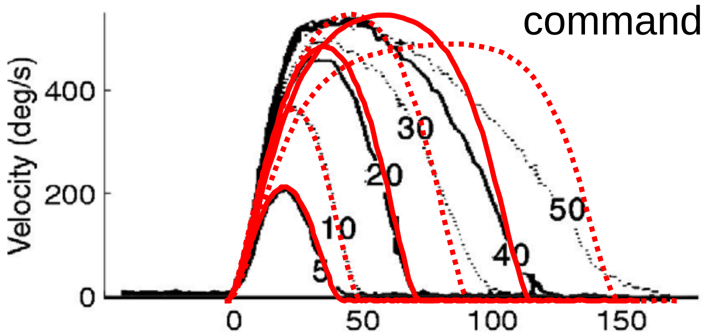
3rd order linear system

SDN

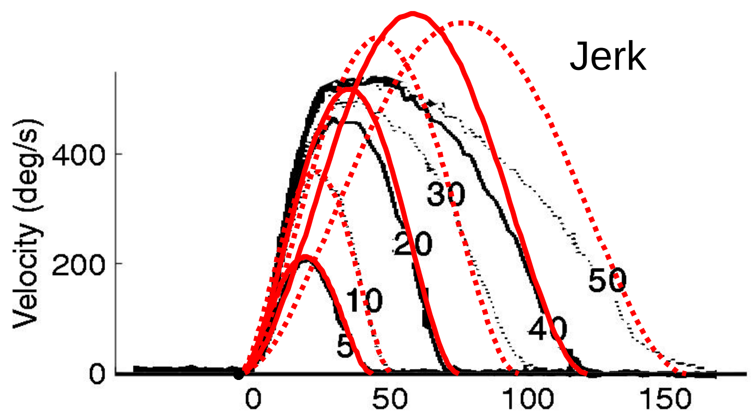


$$u(t) = \frac{k_1 e^{\frac{(t-M)}{\tau_1}} + k_2 e^{\frac{(t-M)}{\tau_2}} + k_3 e^{\frac{(t-M)}{\tau_3}}}{(\tau_2-\tau_3)\tau_1 e^{\frac{t-T}{\tau_1}} + (\tau_3-\tau_1)\tau_2 e^{\frac{t-T}{\tau_2}} + (\tau_1-\tau_2)\tau_1 e^{\frac{t-T}{\tau_3}}}$$

Motor command

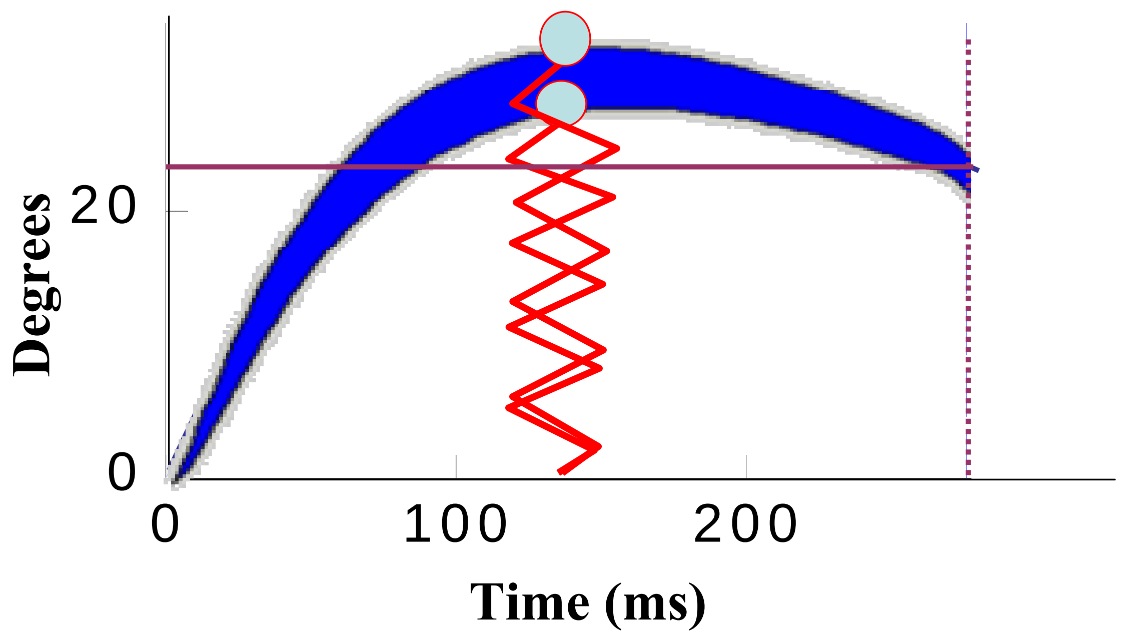


Jerk

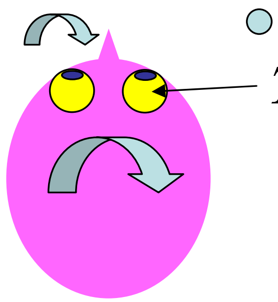


Prediction: very slow saccade

22 degree saccade in 270 ms (normally ~ 70 ms)



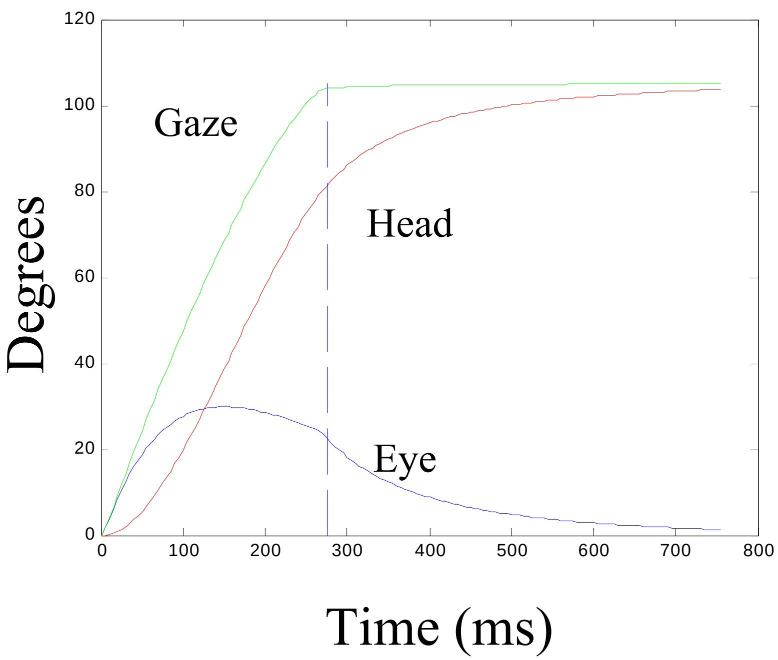
Head free saccade

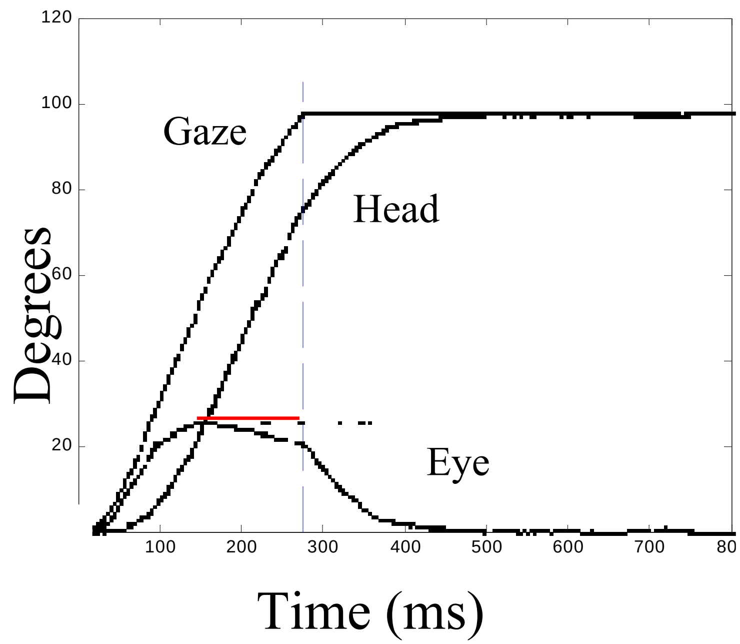


$T_{1=0.15}$ $T_{2=0.08}$

$T_{1=0.3}$ $T_{2=0.3}$

Free parameter, eye:head noise

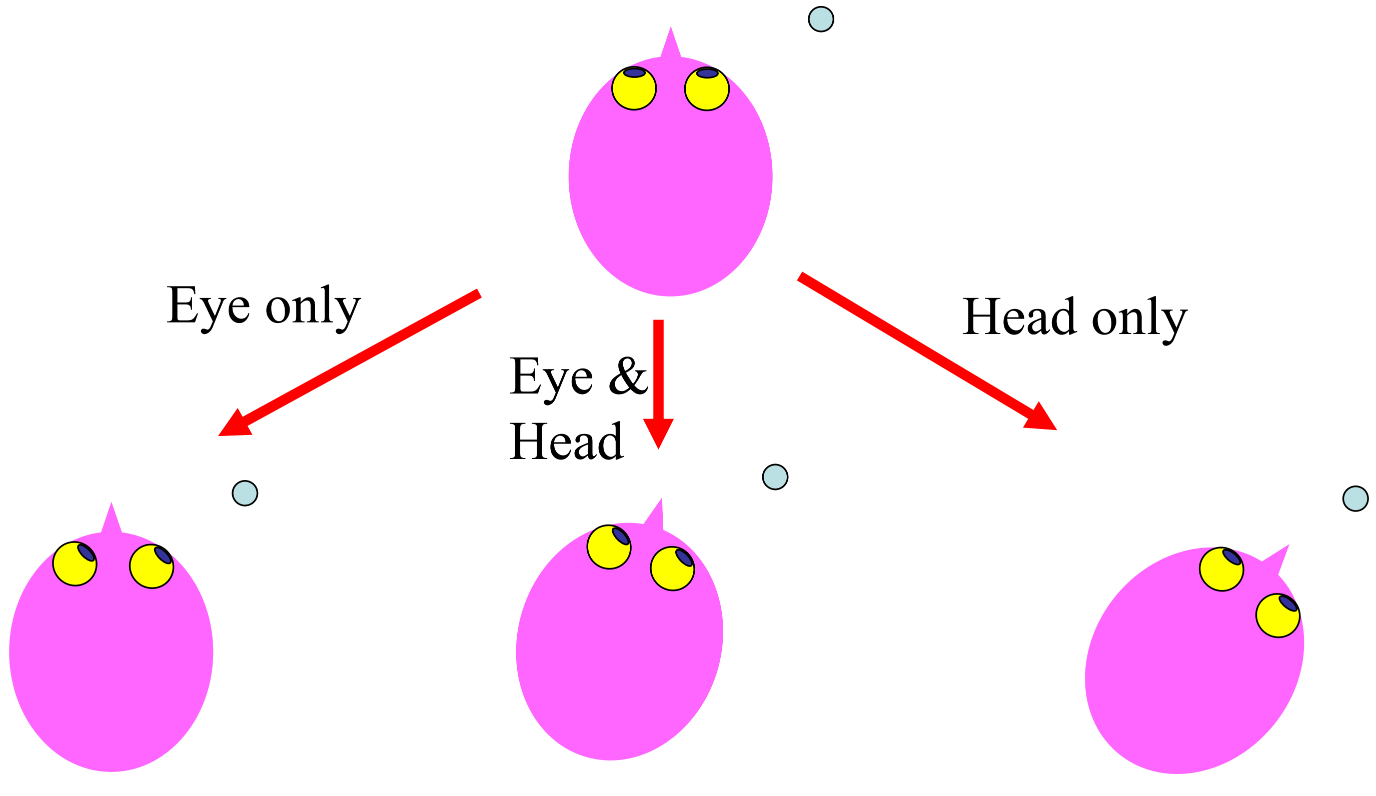




(Tomlinson & Bahra, 1986)

Coordination: Head and eye

For a fixed duration (T), $Var(A)=k\,A^2$

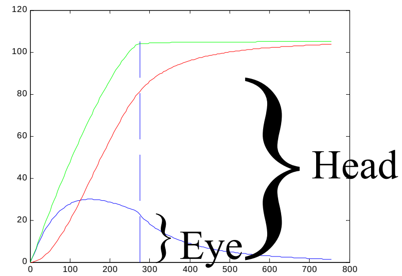


$Var(A)=k\,A^2$

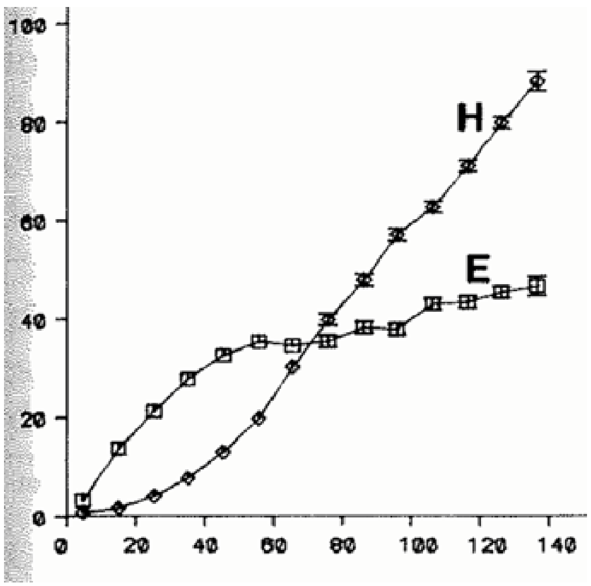
$Var(A)= k\,(A/2)^2 + k\,(A/2)^2$
$= k\,A^2/2$

$Var(A)=k\,A^2$

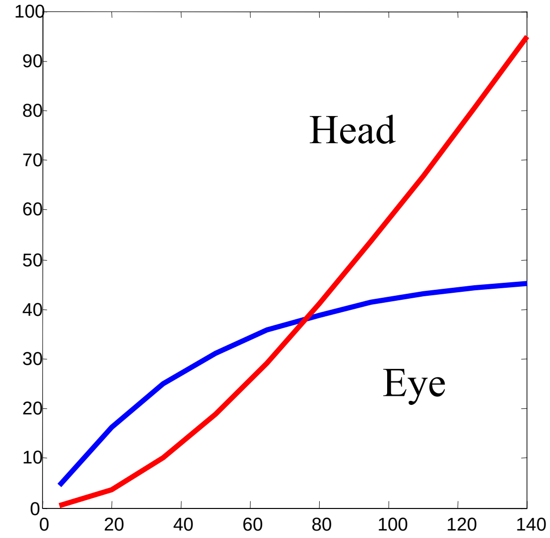
Movement extent vs. target eccentricity



Angular deviation at acquisition

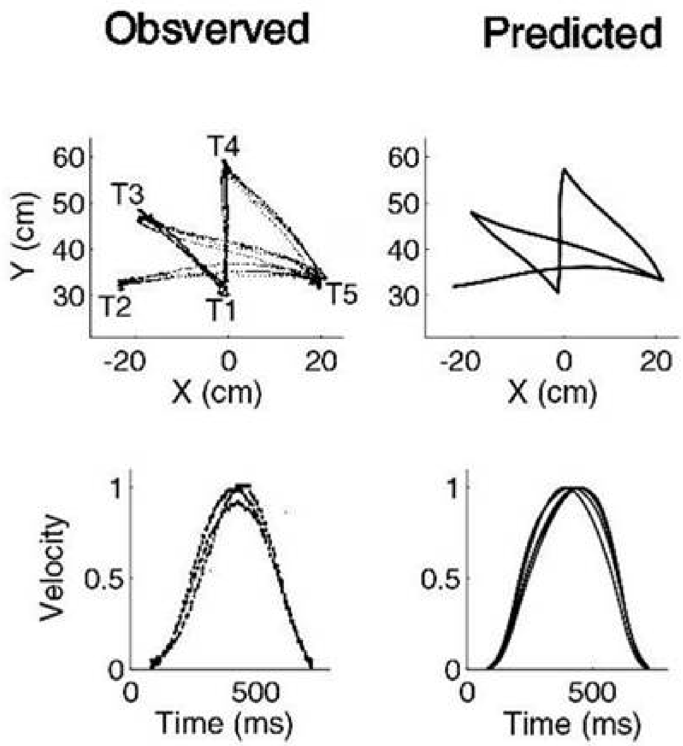


Gaze amplitude



Gaze amplitude

Arm movements



Smoothness

Non smooth movement
⇒ requires abrupt change in velocity
⇒ given low pass system
⇒ large motor command
⇒ increased noise

Smoothness ⇒ accuracy

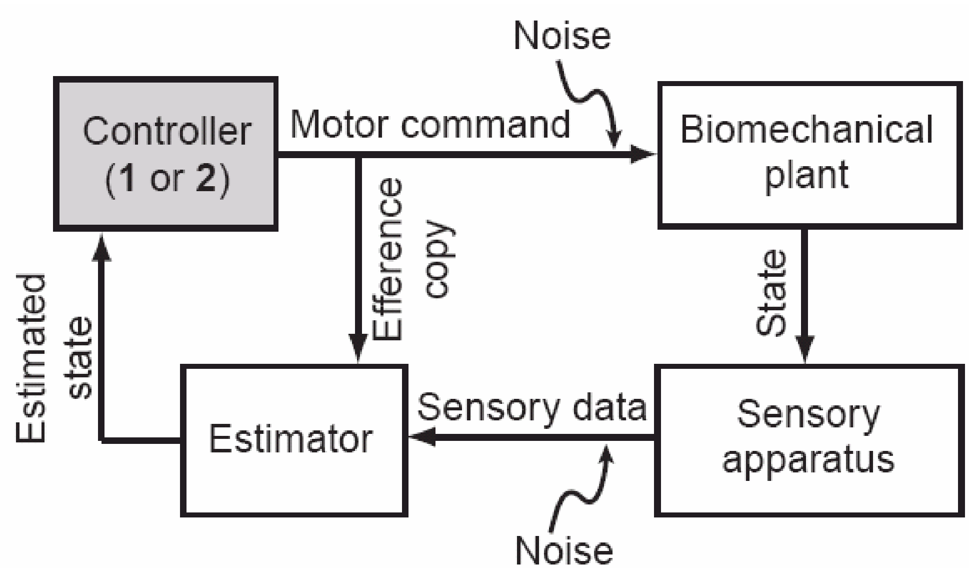
Drawing (⅔ power law) **f=path error**
Obstacle avoidance **f= limit probability of collision**

Feedforward control

- •Ignores role of feedback
- •Generates desired movements
- •Cannot model trial-to-trial variability

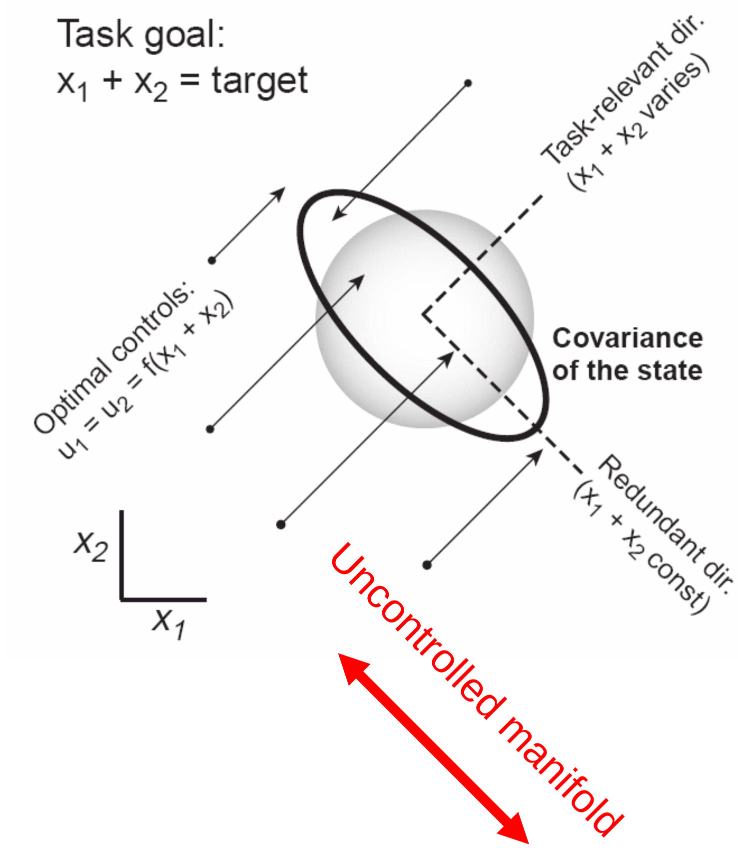
Optimal feedback control (Todorov 2004)

- Optimize performance over all possible feedback control laws
- Treats feedback law as fully programmable
  - command=f(state)
  - Models based on reinforcement learning optimal cost-to-go functions
  - Requires a Bayesian state estimator



Minimal intervention principle

- Do not correct deviations from average behaviour unless they affect task performance
  - Acting is expensive
    - energetically
    - noise
  - Leads to
    - uncontrolled manifold
    - synergies



Optimal control with SDN

- Biologically plausible theoretical underpinning for both eye, head, arm movements
- No need to construct highly derived signals to estimate the cost of the movement
- Controlling statistics in the presence of noise

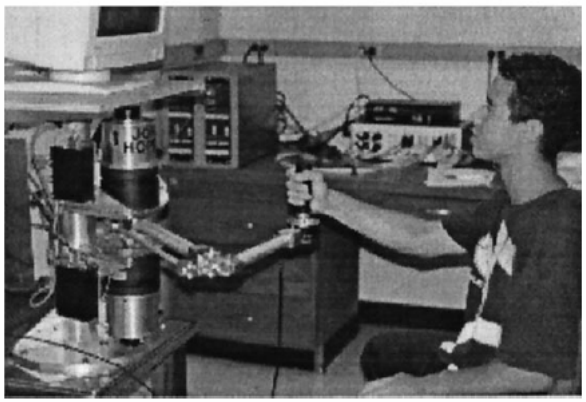
What is being adapted?

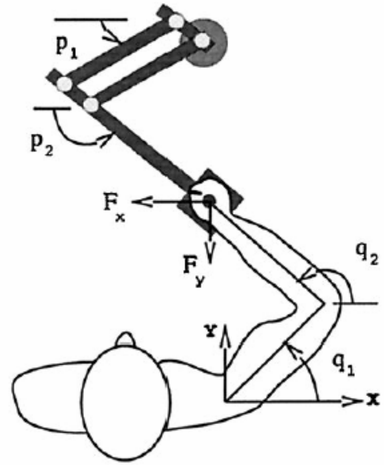
- Possible to break down the control process:

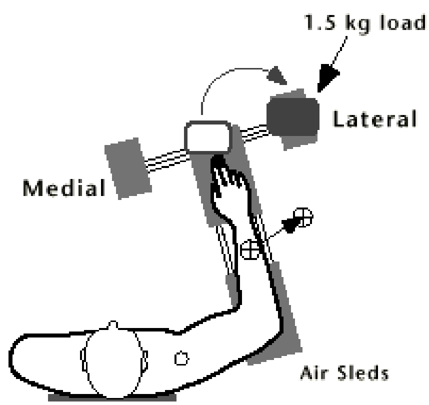
- Visuomotor rearrangements
- Dynamic perturbations
- [timing, coordination , sequencing]

- Internal models captures the relationship between sensory and motor variables

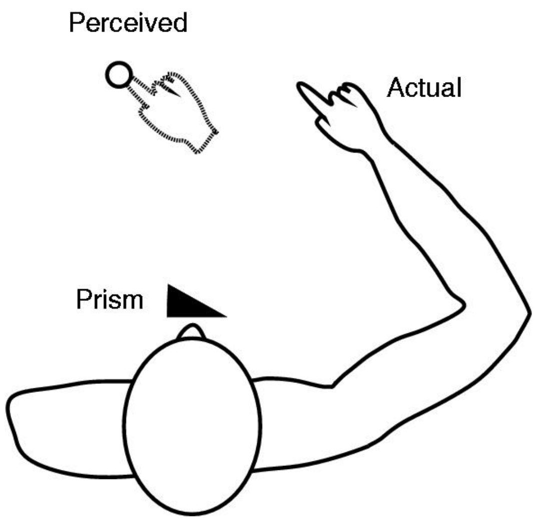
Altering dynamics

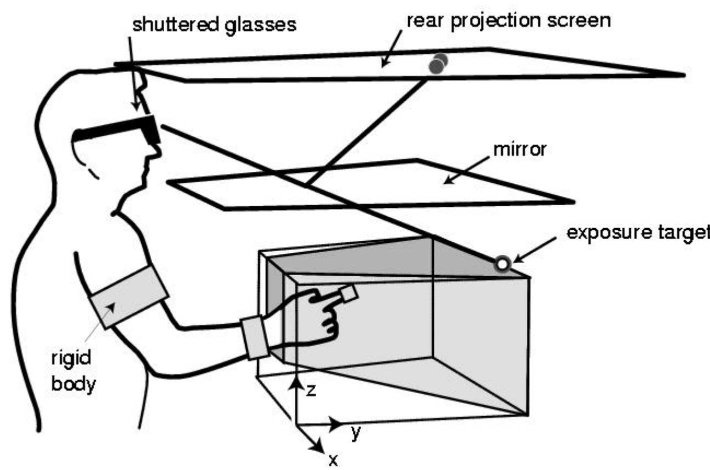




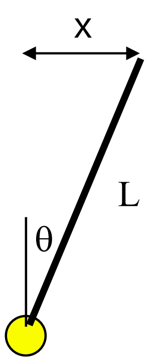


Altering Kinematics





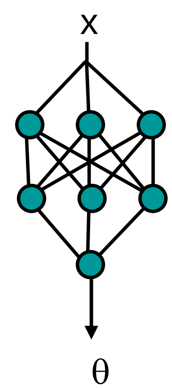
Representation of transformations



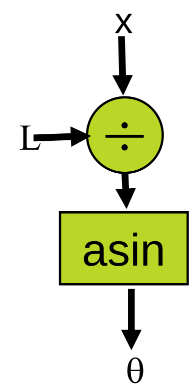
Look-up Table

x	θ
1	10
3	35
.	.
.	.

Non-physical Parameters
$\theta = f(x, \omega)$



Physical Parameters
$\theta = \mathrm{acos}(x/L)$



High storage
High flexibility
Low Generalization

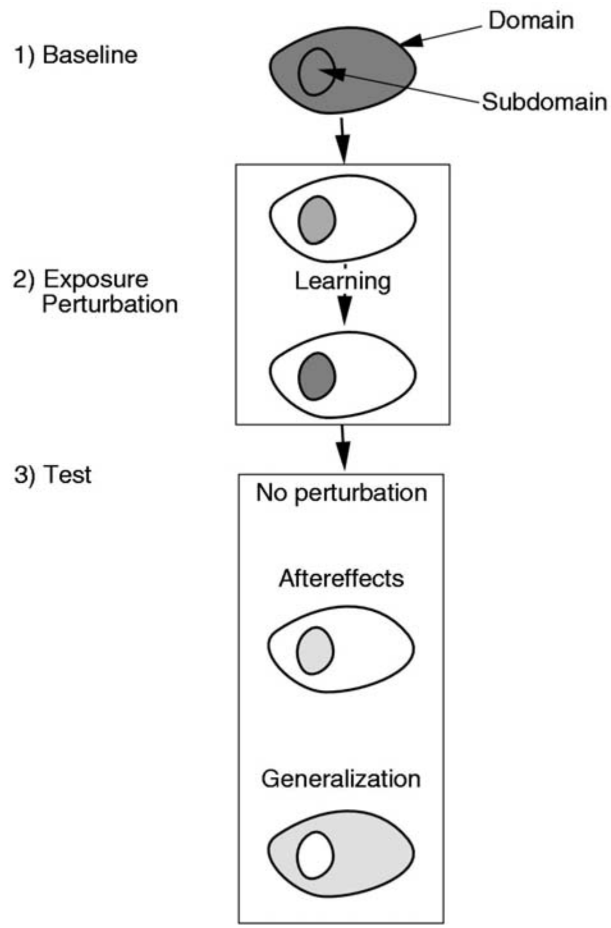
Low storage
Low flexibility
High Generalization

Generalization paradigm

- Baseline
  - Assess performance over domain of interest
  - (e.g. workspace)

- Exposure
  - Perturbation: New task
  - Limitation: Limit the exposure to a subdomain

- Test
  - Re-assess performance over entire domain of interest



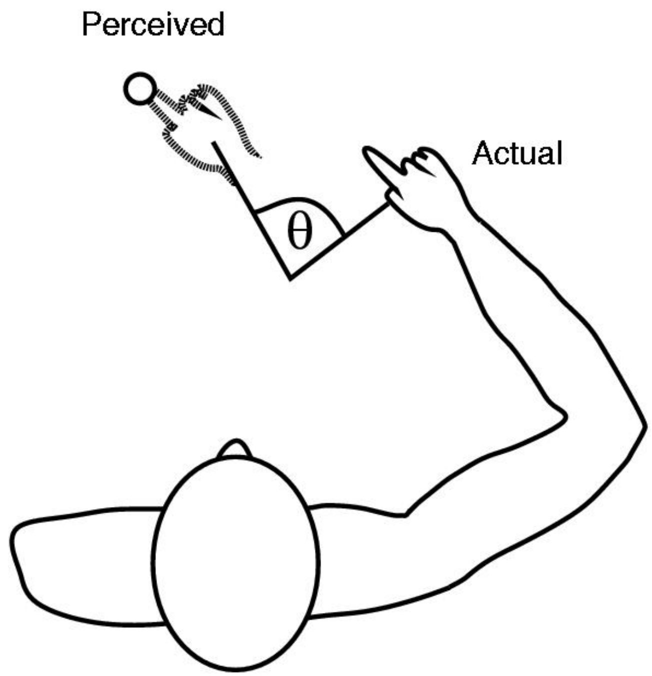
Difficulty of learning

(Cunningham 1989, JEPP-HPP)

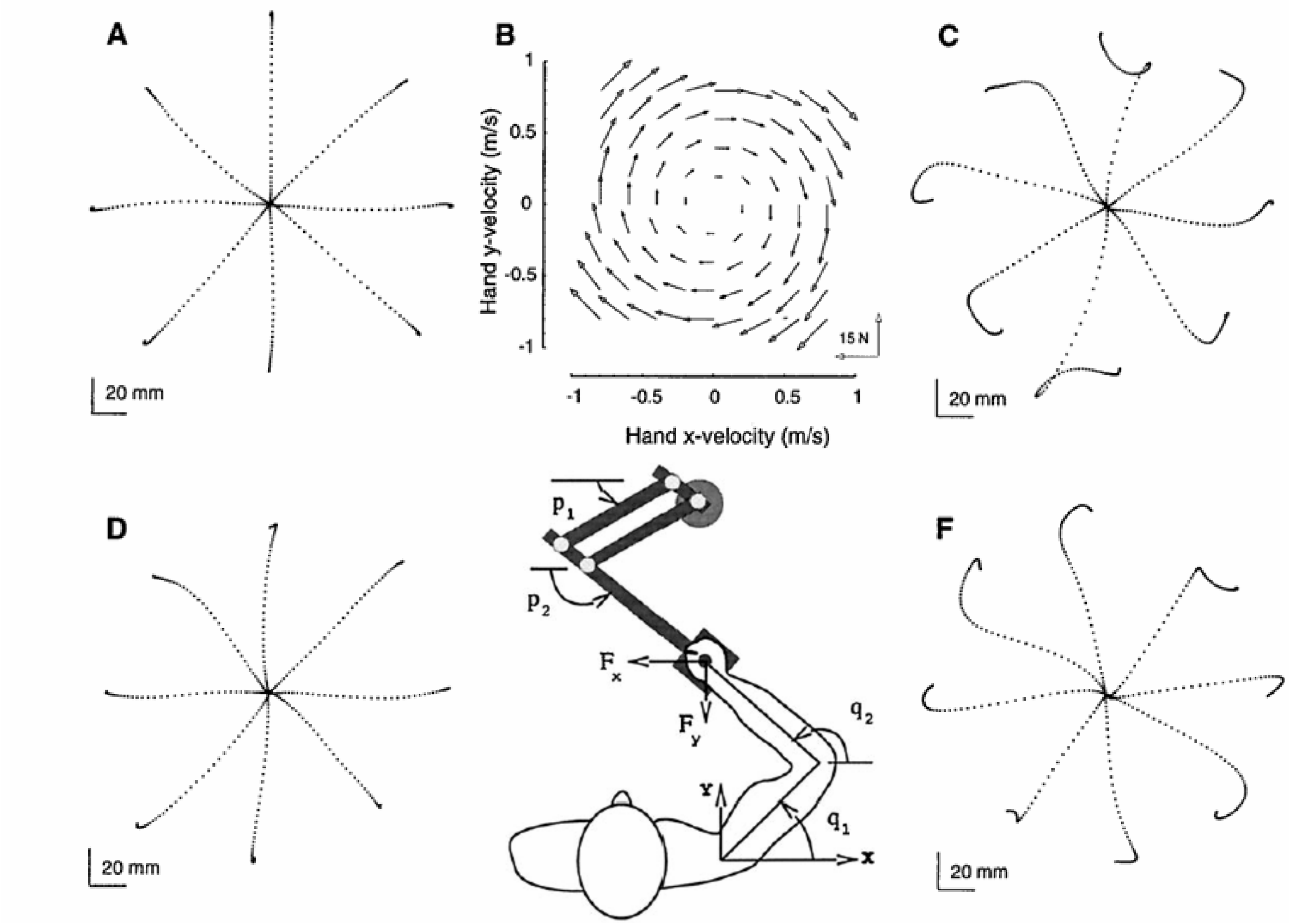
- Rotations of the visual field from 0—180 degrees

Difficulty
- increases from 0 to 90
- decreases from 120 to 180

- What is the natural parameterization



Viscous curl field



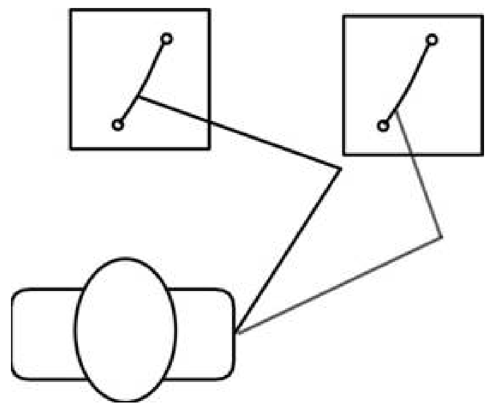
(Shadmehr & Mussa-Ivaldi 1994, J. Neurosci.)

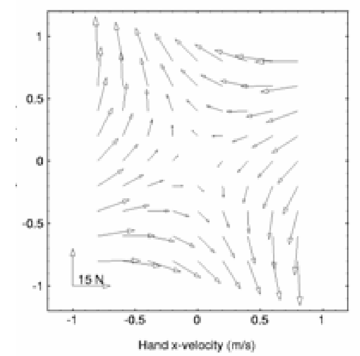
Representation from generalization: Dynamic

1. Test: Movements over entire workspace

2. Learning
   - Right-hand workspace
   - Viscous field

3. Test: Movements over left workspace





Two possible interpretations

force = f(hand velocity)

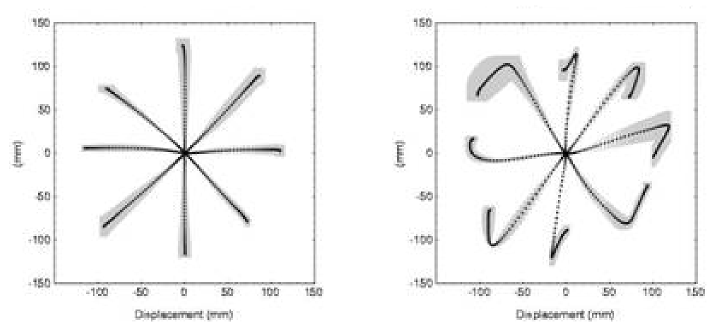
or torque=f(joint velocity)

Joint-based learning of dynamics

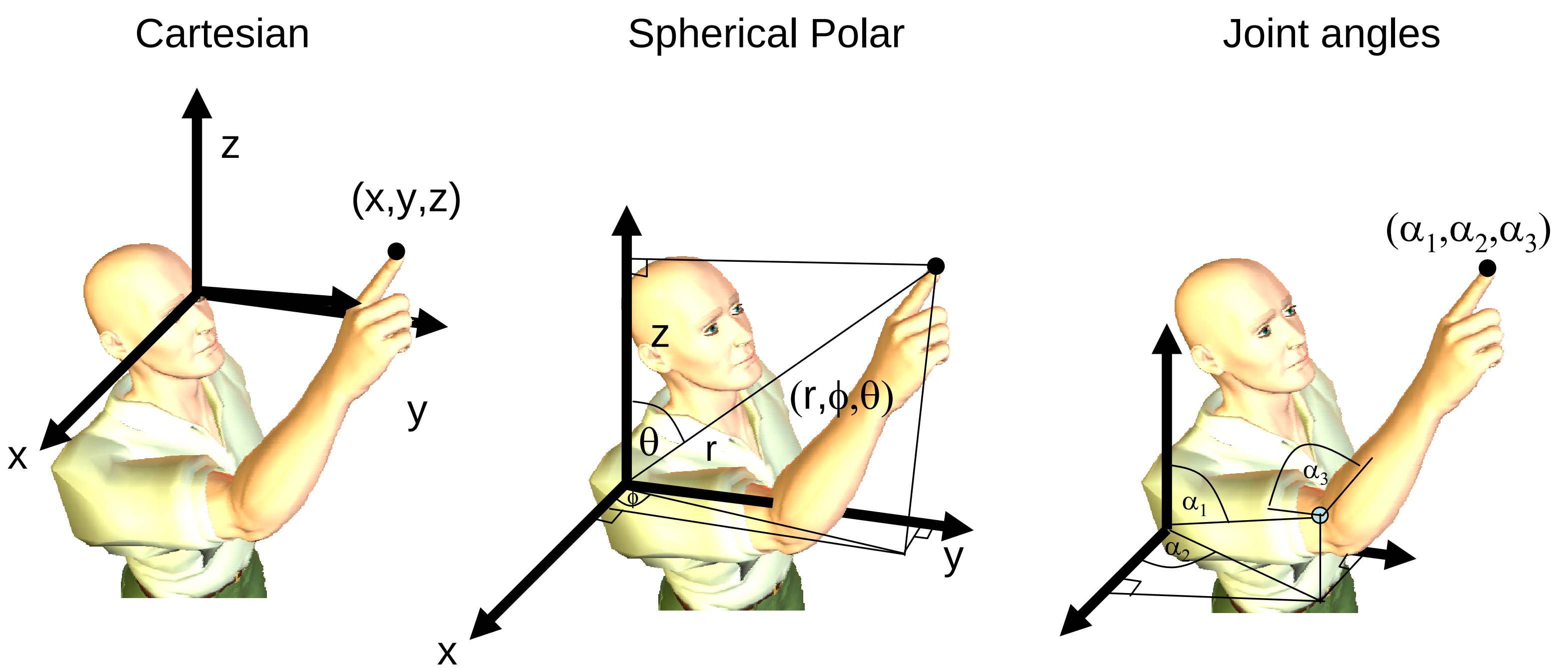
(Shadmehr & Mussa-Ivaldi 1994, J. Neurosci.)

Left hand workspace

Before **After with Cartesian field**



Visuomotor coordinates

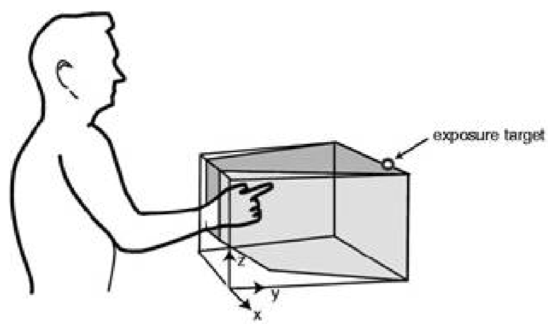


Representation- Visuomotor

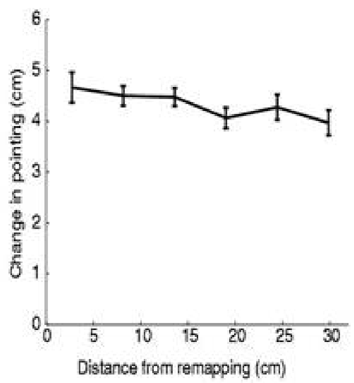
1. Test: Pointing accuracy to a set of targets

2. Learning
   - visuomotor remapping
   - feedback only at one target

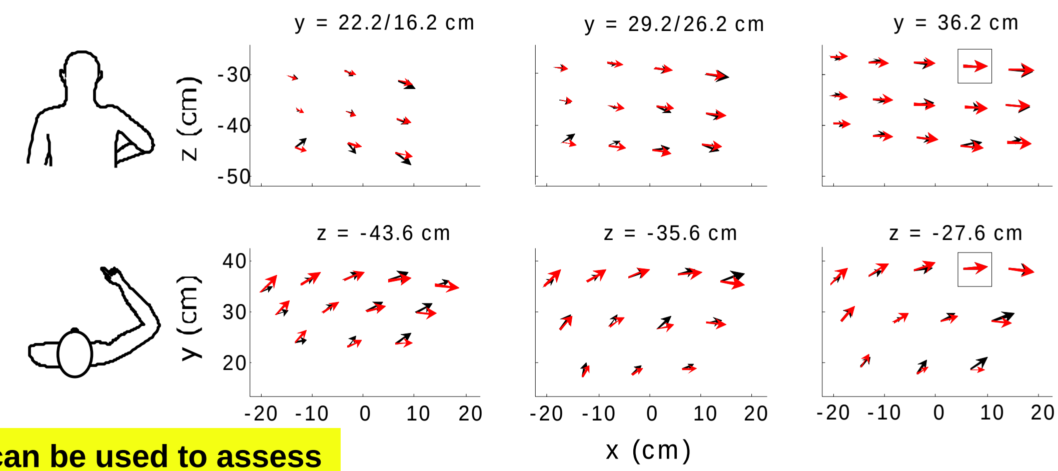
3. Test: Pointing accuracy to a set of targets



Predictions of eye-centred spherical coordinates



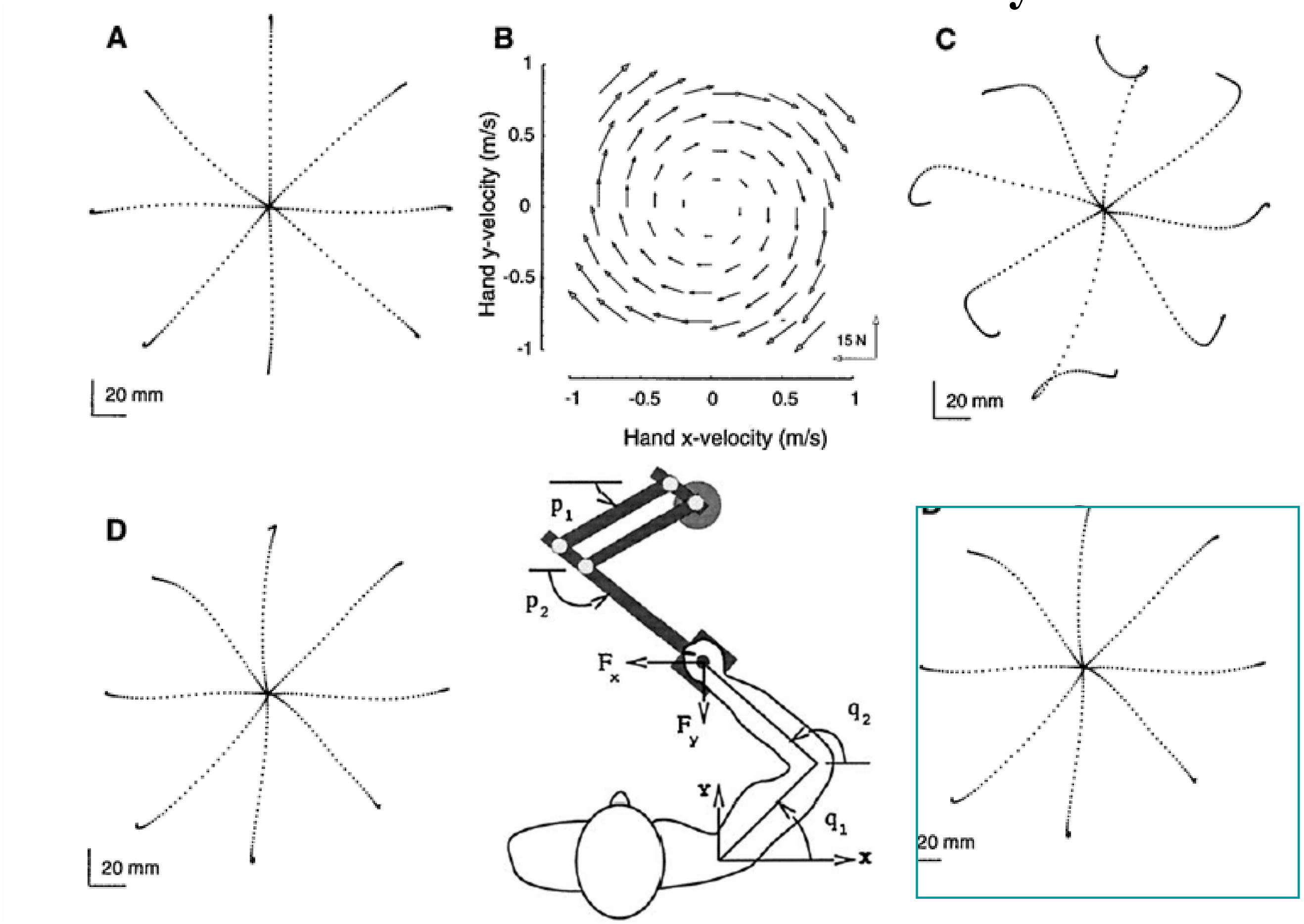
(Vetter et al, J. Neurophys, 1999)



- **Generalization paradigms can be used to assess**
  - **Extent of generalization**
  - **Coordinate system of transformations**

Altering dynamics: Viscous curl field

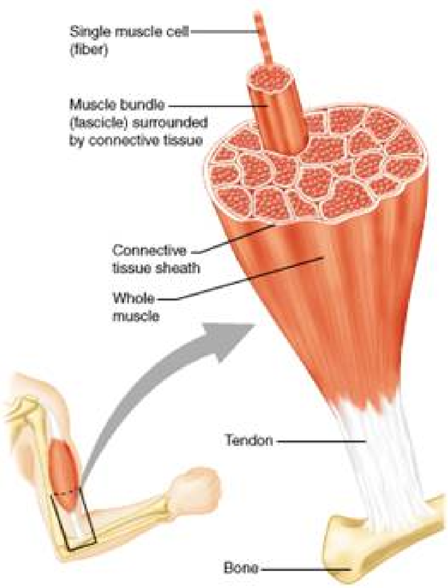
Before **Early with force**

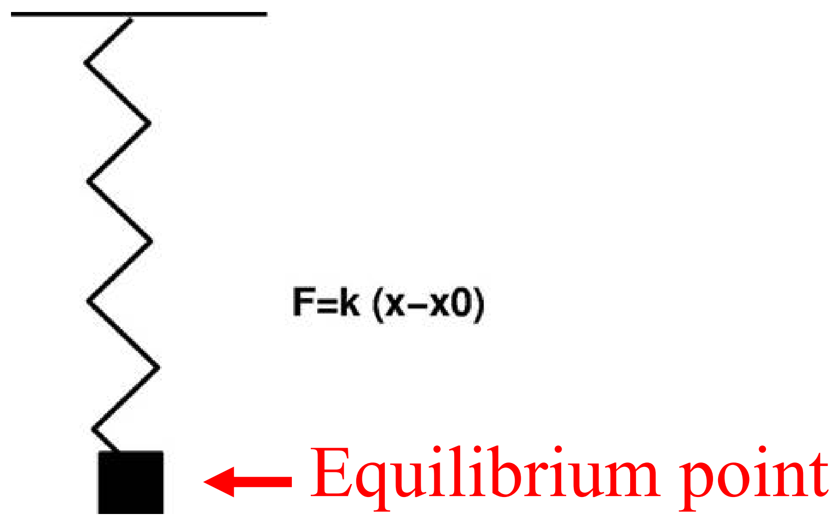


Late with force **Removal of force**

Stiffness control

A muscle activation levels sets the spring constant *k* (or resting length) of the muscle

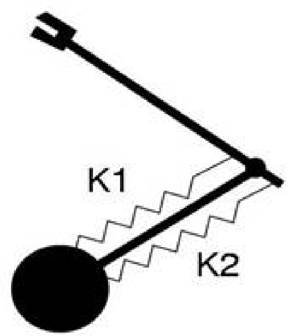


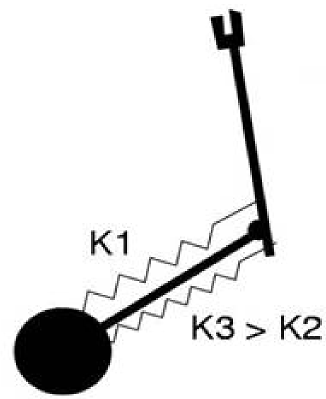


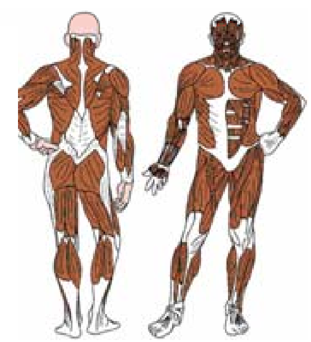
Equilibrium point control

- Set of muscle activations ($k_1,k_2,k_3\ldots$) defines a posture
- CNS learns a spatial mapping
  - e.g. hand positions $\longrightarrow$ muscle activations

    $(x,y,z) \longrightarrow (k_1,k_2,k_3\ldots)$

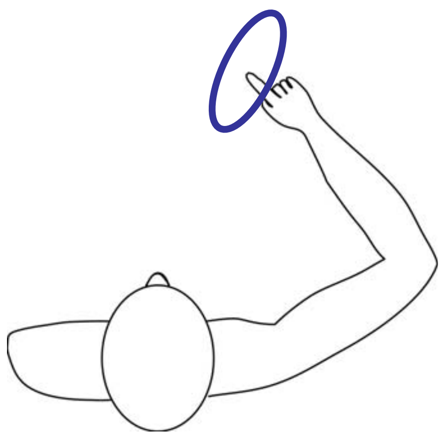




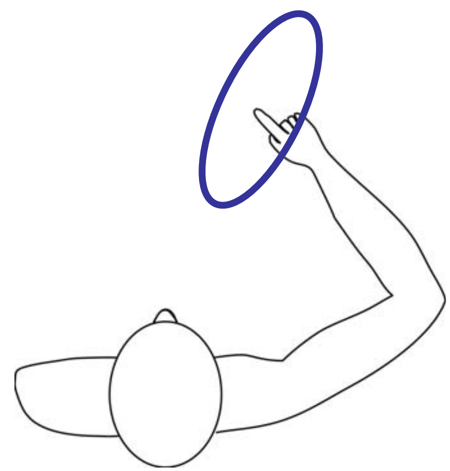


Equilibrium control

Low stiffness

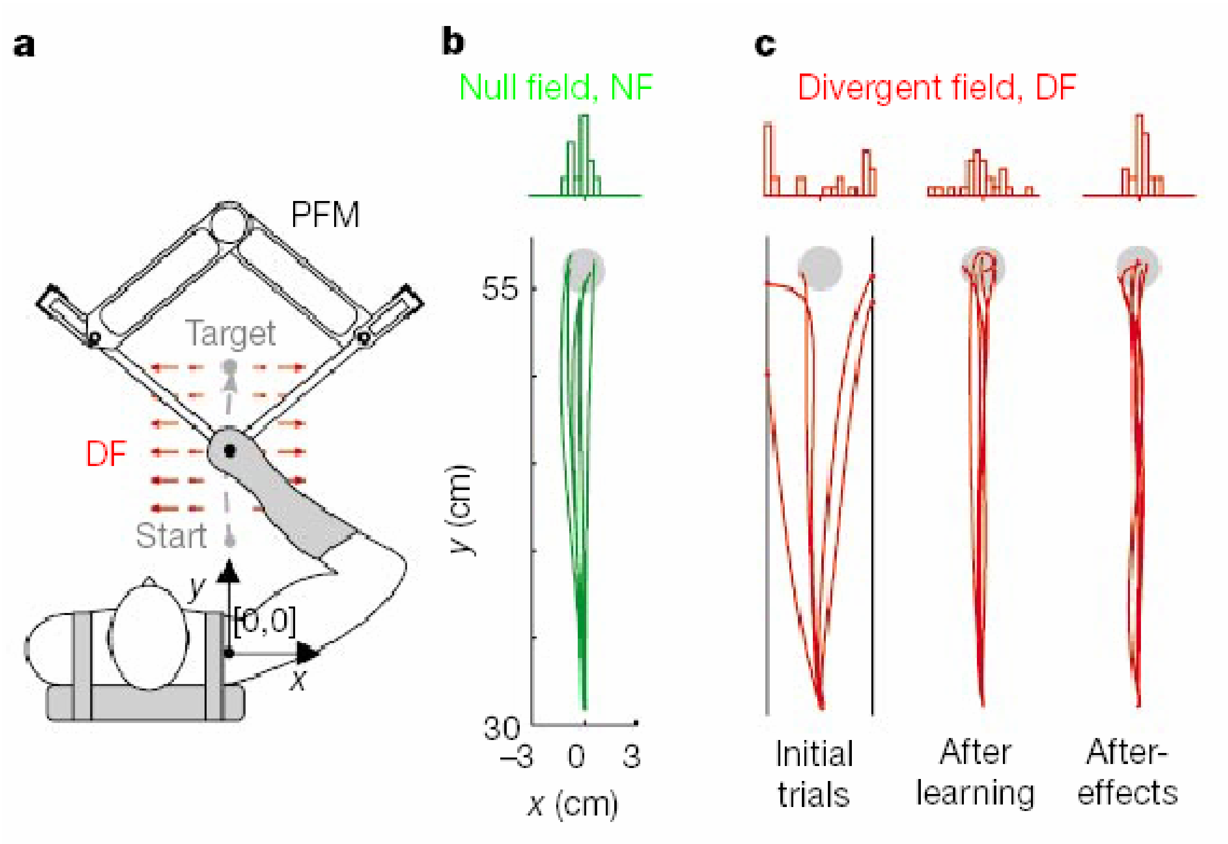


High stiffness



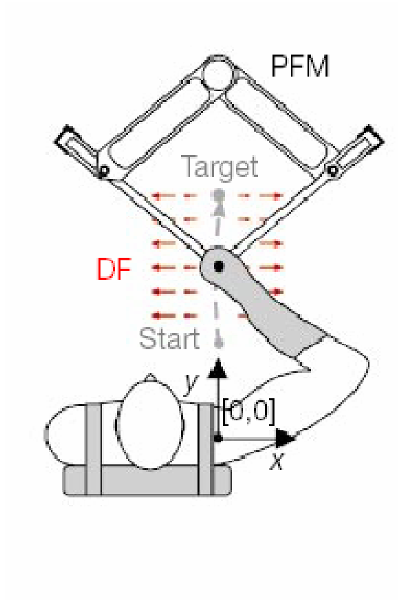
The hand stiffness can vary with muscle activation levels.

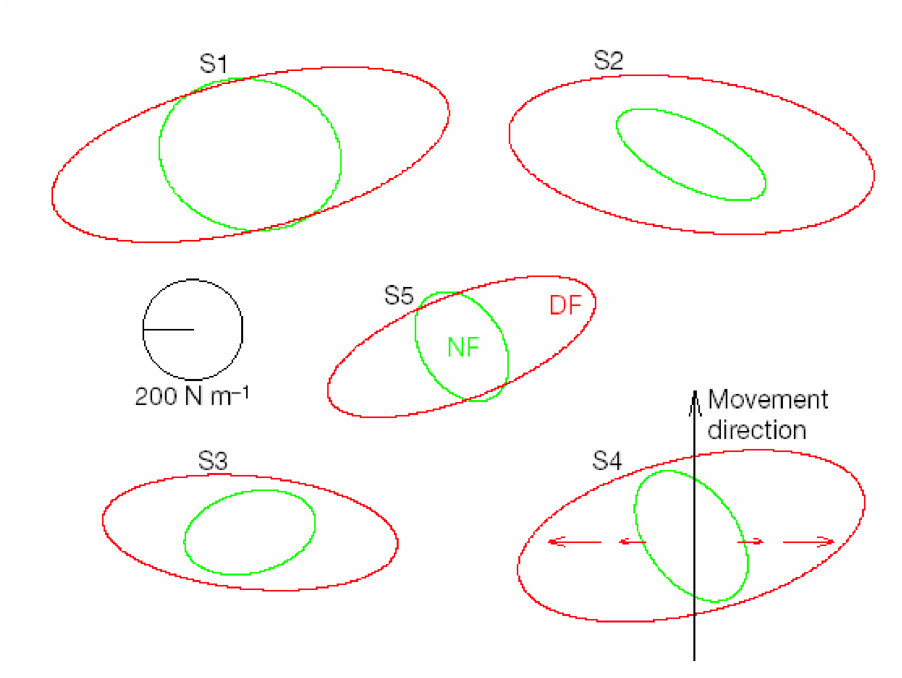
Controlling stiffness



Burdet et al (Nature, 2002)

Stiffness ellipses





- **Internal models to learn stable tasks**
- **Stiffness for unpredictable tasks**

Summary

- Sensorimotor integration
  - Static multi-sensory integration
  - Bayesian integration
  - Dynamic sensor fusion & the Kalman filter
- Action evaluation
  - Intrinsic loss function
  - Extrinsic loss functions
- Prediction
  - Internal model and likelihood estimation
  - Sensory filtering
- Control
  - Optimal feed forward control
  - Optimal feedback control
- Motor learning of predictable and stochastic environments

Wolpert-lab papers on www.wolpertlab.com

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