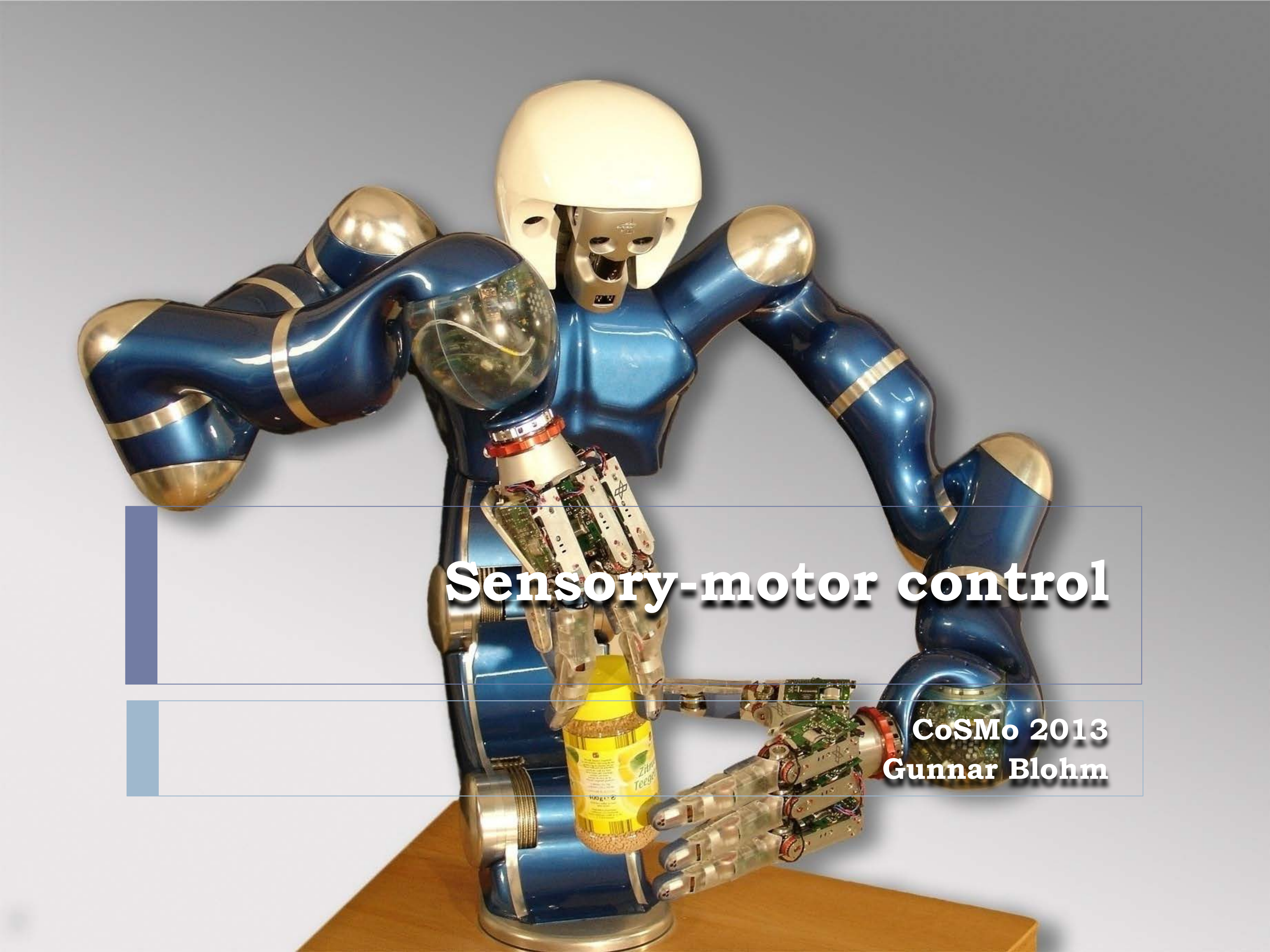


Sensory-motor control

CoSMo 2013

Gunnar Blohm

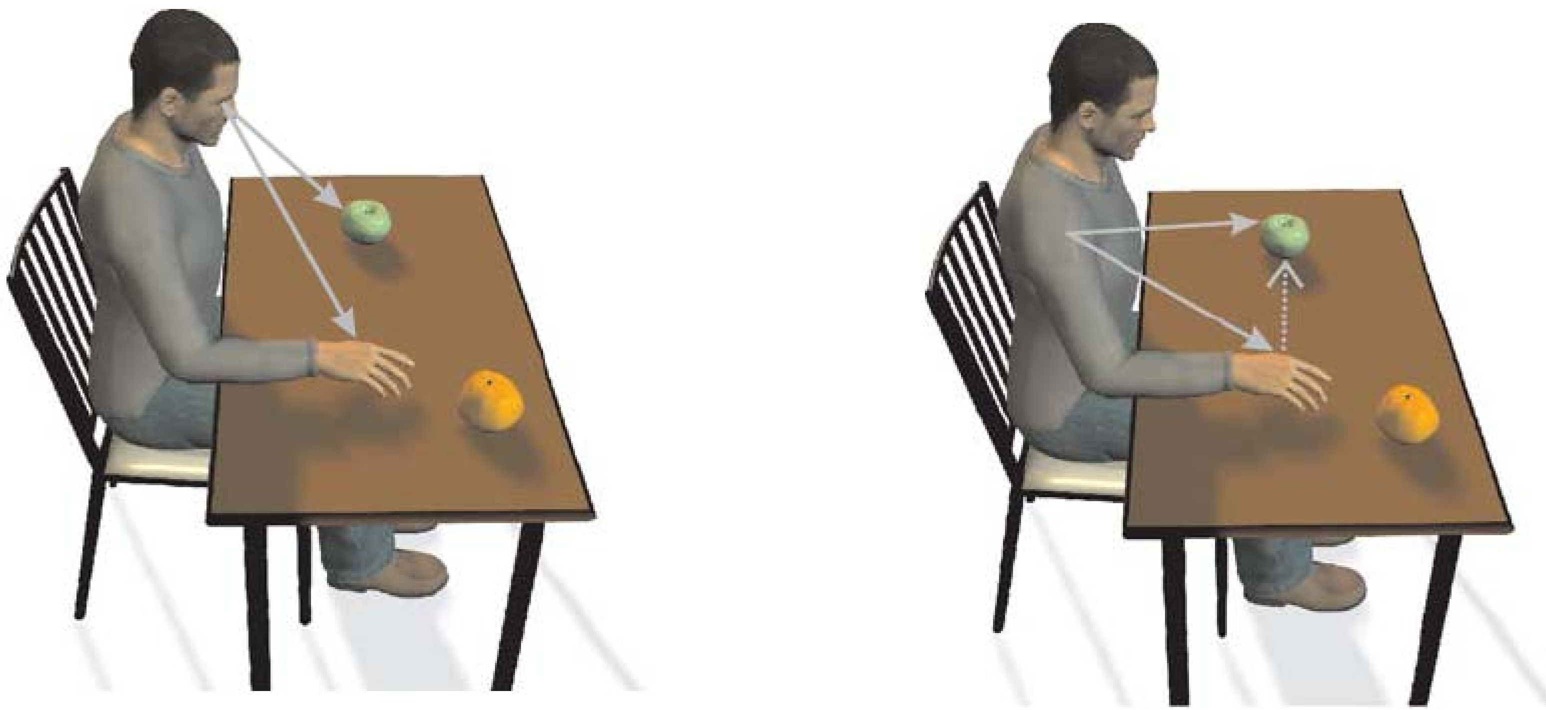
Outline

- CoSMo organization (Blohm) – Day 1
- Introduction to sensory perception
  - History, philosophy and the senses (Troje)
- Signal processing **tutorial** (Troje)
- Data sharing (Blohm & Troje)

- Sensory-motor control overview (Blohm) – Day 2
  - Problems & steps
  - Current theories & frameworks
  - Computational principles
- How to model (Blohm & Troje)
- Bayesian decoding **tutorial** (Blohm)

Motor planning & execution

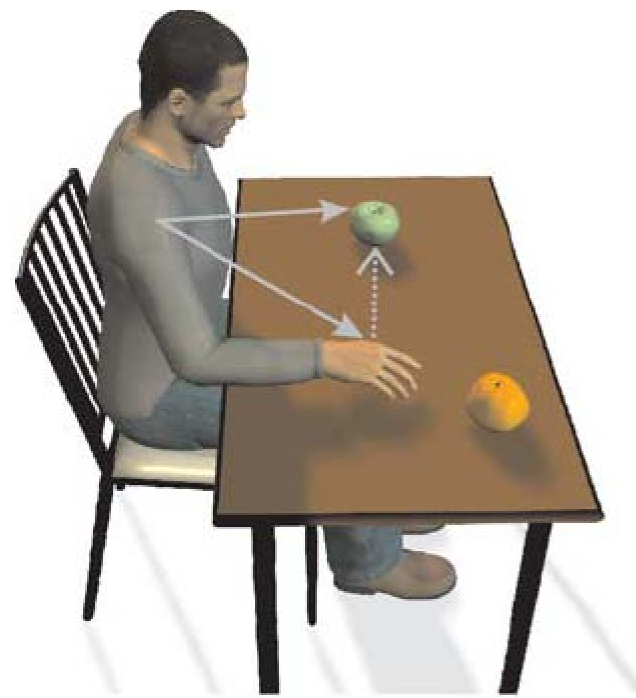
- Processes involved in the sensory guidance of action



Blohm et al. 2009

Motor planning & execution

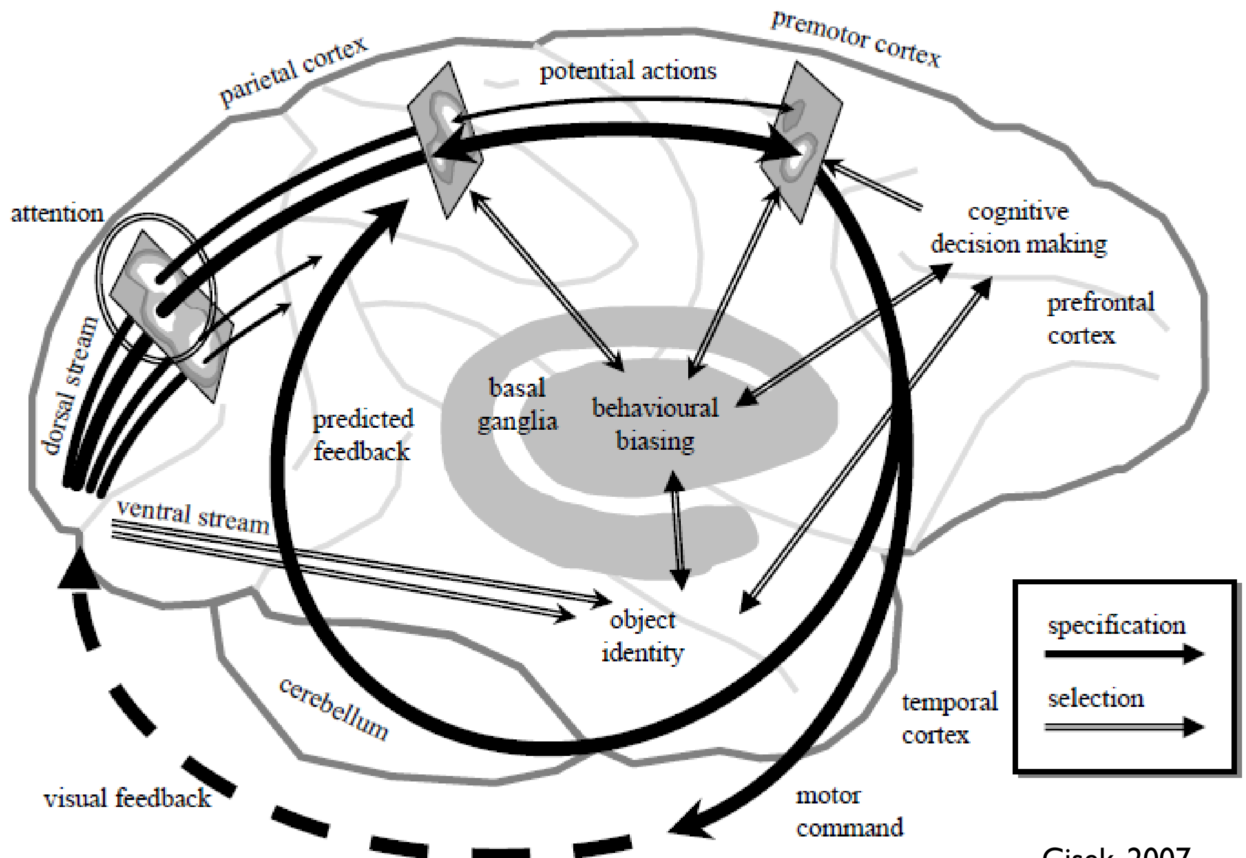
- Processes involved in the sensory guidance of action
  - Sensory processing
  - Multi-sensory integration
  - Reference frame transformations
  - Target selection
  - Decision making
    - Move or not
    - Which effector, which target
    - When to move (timing)
  - Motor planning
  - Motor control
  - Error corrections…



Blohm et al. 2009

Motor planning & execution

- Processes involved in the sensory guidance of action

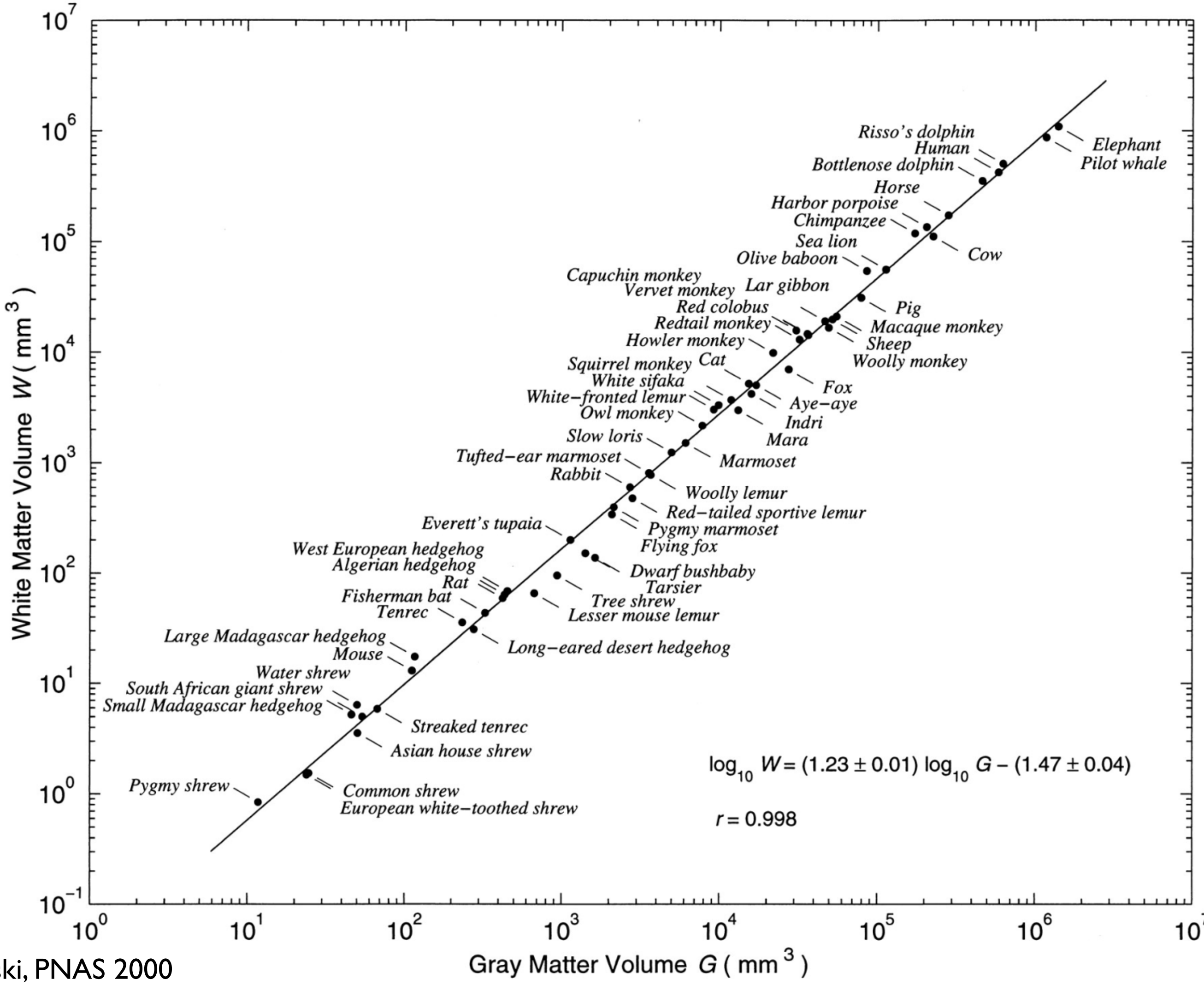


Cisek, 2007

The computational anatomy of the brain

Hierarchies

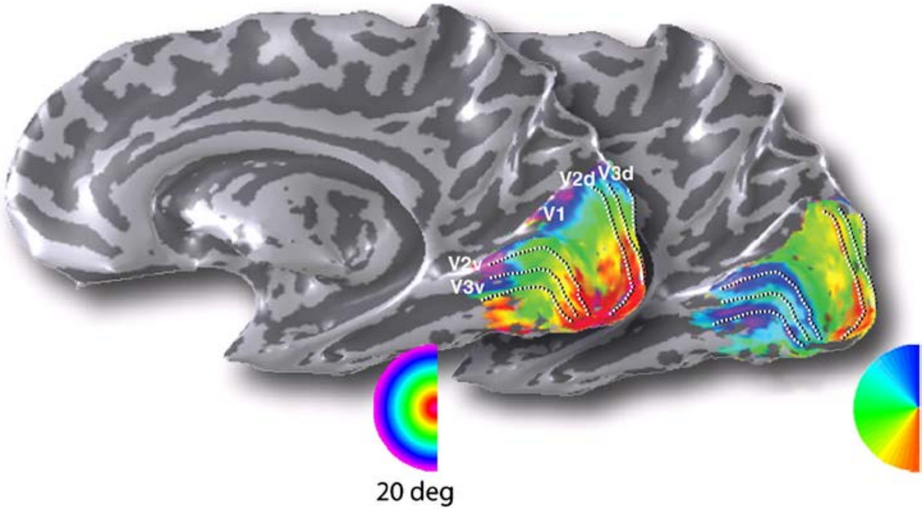
Computational anatomy of the brain



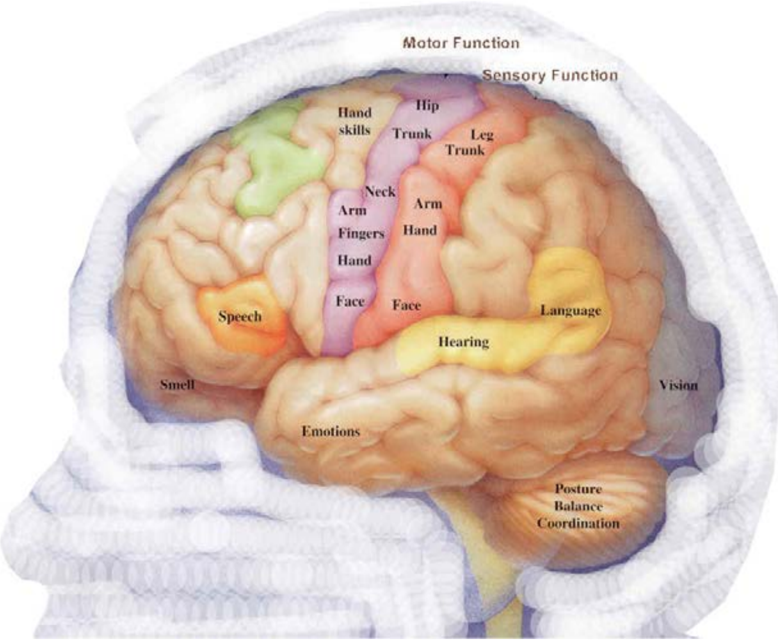
Zhang & Sejnowski, PNAS 2000

Computational hierarchy of the brain

- Brodmann's areas
- Functional areas
- Maps



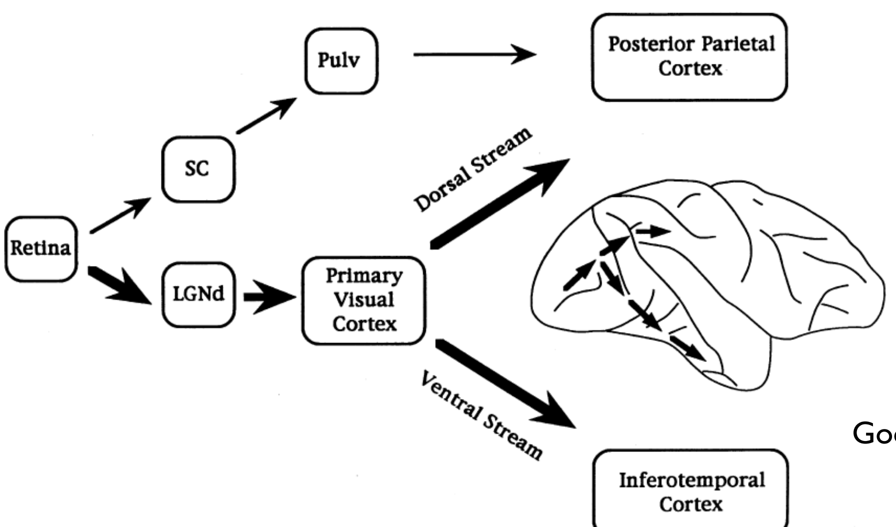
Wandell, et al., Neuron (2007)



Computational hierarchy of the brain

- Brodmann's areas
- Functional areas
- Maps
- Connectivity
- Functional pathways

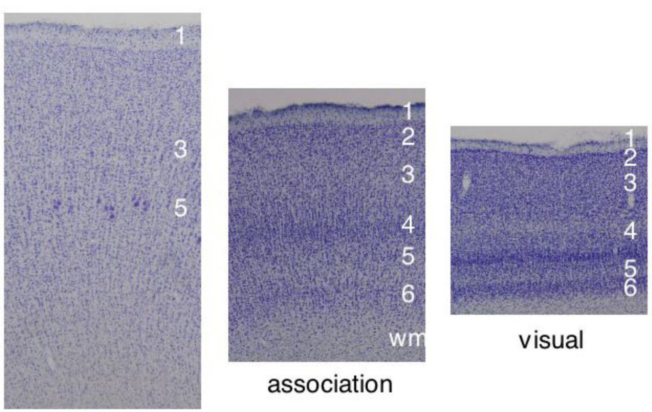
Courtesy of Kat Reinhart



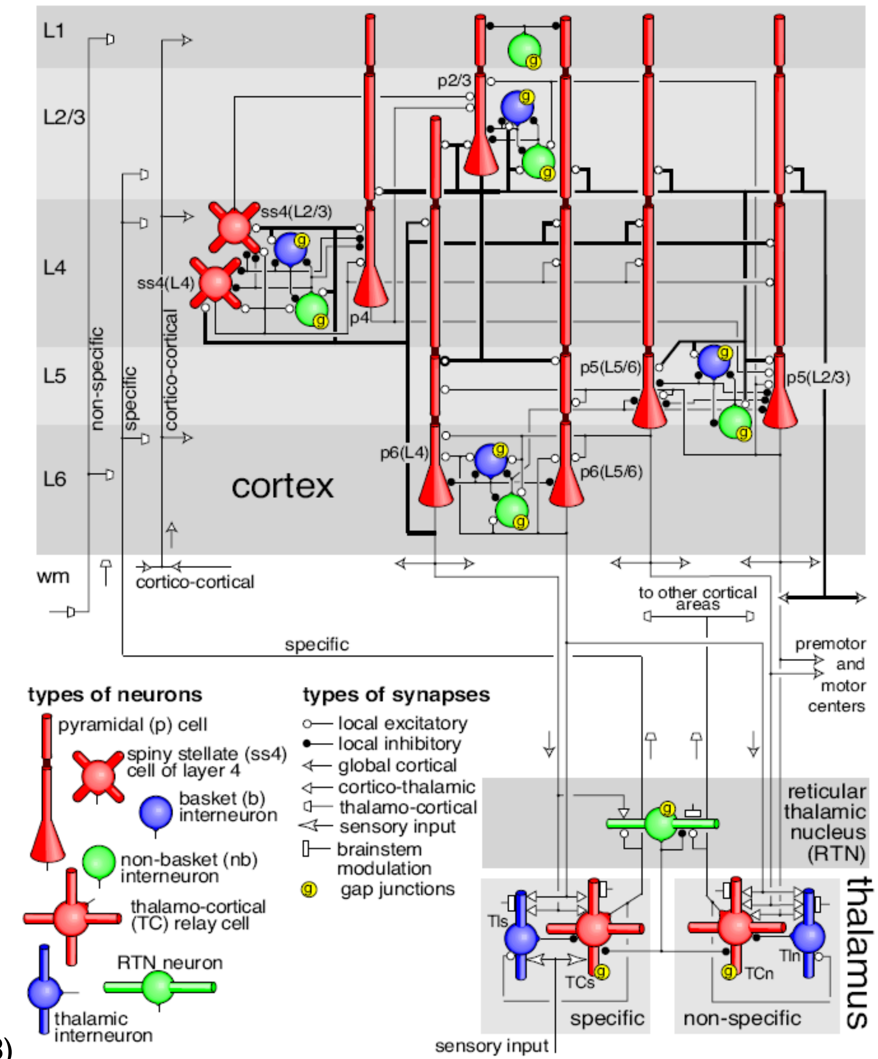
Goodale & Humphrey, 1998

Computational hierarchy of the brain

- Brodmann's areas
- Functional areas
- Maps
- Connectivity
- Functional pathways
- Detailed structure



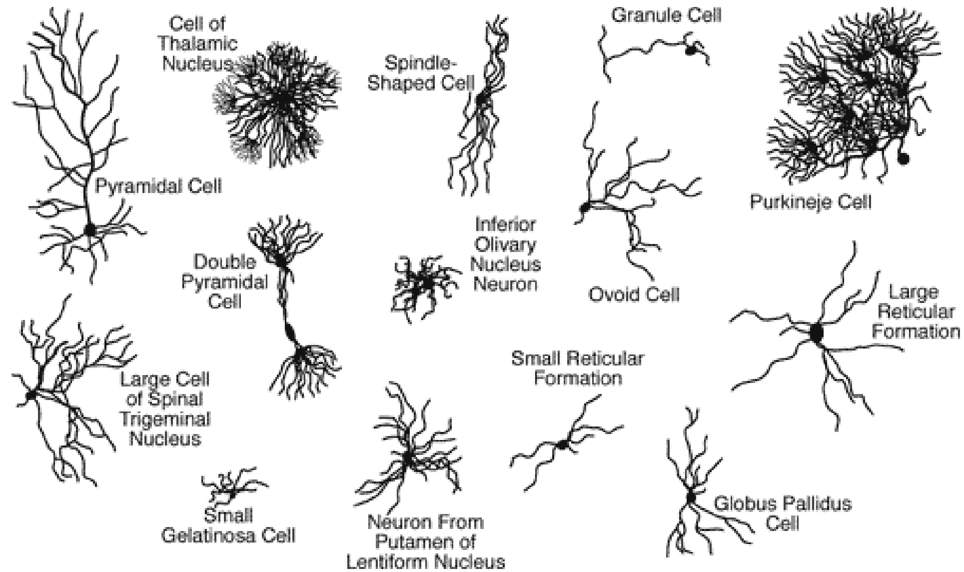
motor association visual

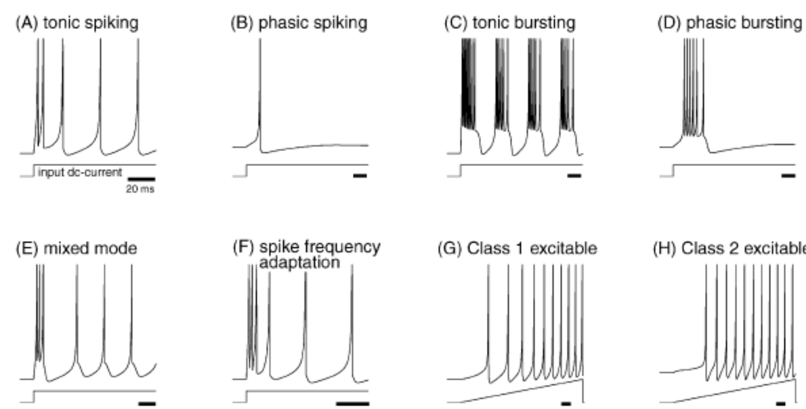


Izhikevich & Edelman PNAS (2008)

Computational hierarchy of the brain

- Brodmann's areas
- Functional areas
- Maps
- Connectivity
- Functional pathways
- Detailed structure
- Varied anatomy
- Heterogeneous behavior
- Chemical & molecular complexity
- …





Izhikevich, IEEE Transactions on Neural Networks (2004)

Levels of Marr

- Brain: hierarchy of complexities

- Computational level - 1
  - Objective?
  - How close to optimal?
  - This is what most computational neuroscience papers do!
- Algorithmic level - 2
  - Data structures?
  - Approximations?
  - Runtime?
  - Some studies get into this (computer science)
- Implementation level -3
  - Hardware? Neurons? Synapses? Molecules?
  - Not addressed enough!
- Models bridging Marr 1-3 are rare!

Motor planning & execution

- Processes involved in the sensory guidance of action
  - Sensory processing
  - Multi-sensory integration
  - Reference frame transformations
  - Target selection
  - Decision making
    - Move or not
    - Which effector, which target
    - When to move (timing)
  - Motor planning
  - Motor control
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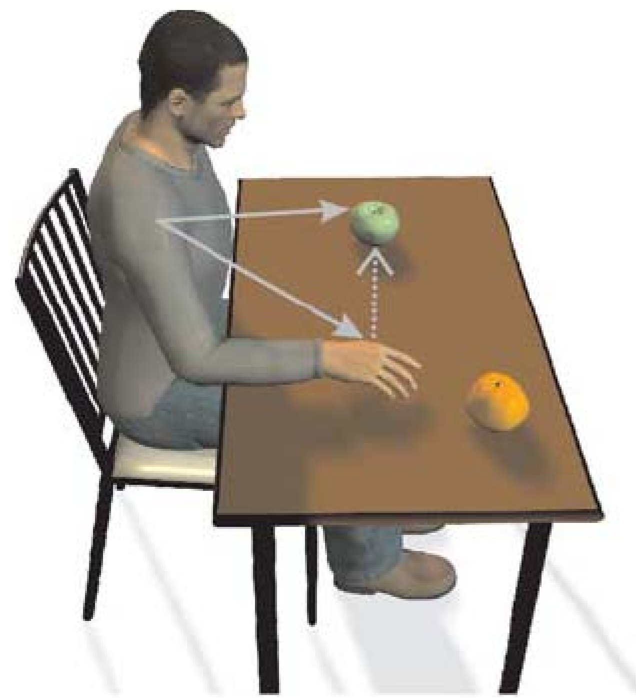


Blohm et al. 2009

Sensory-motor transformations

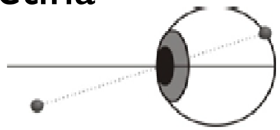
Cullen & Chacron

Sensory-motor transformations

- Justin: DLR robot – ball catching
  - Sensory ref frames ~= motor ref frame…
  - Sensory code ~= motor code…
  - Movie…

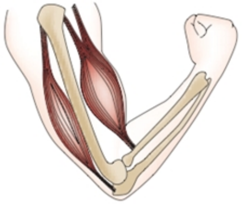
Sensory-motor transformations

- Reference frames
  - Determined by sensory and motor apparatus
    - Vision: attached to the retina

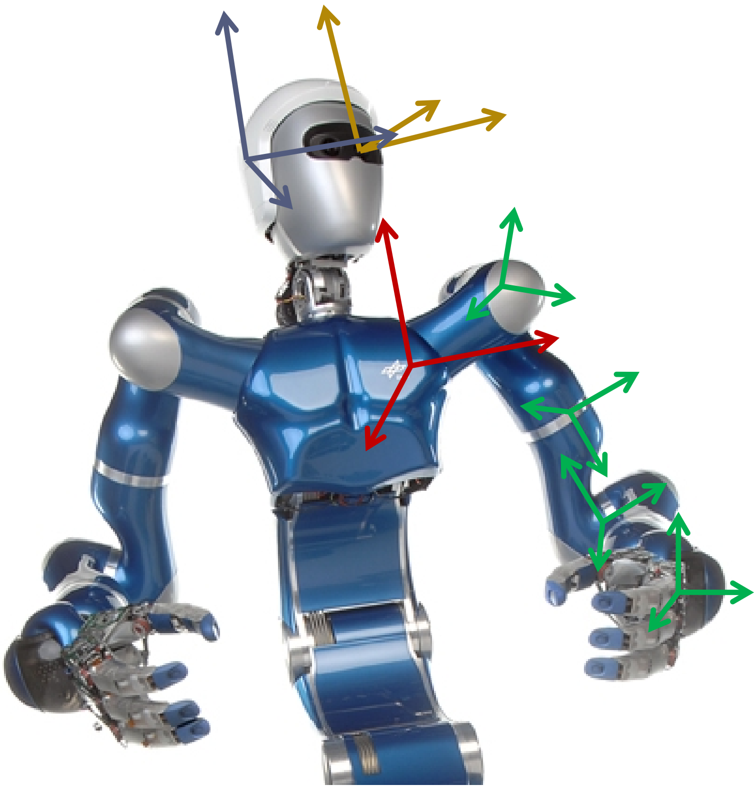


    - Audition: attached to the head

    - Proprioception:
      relative joint angles

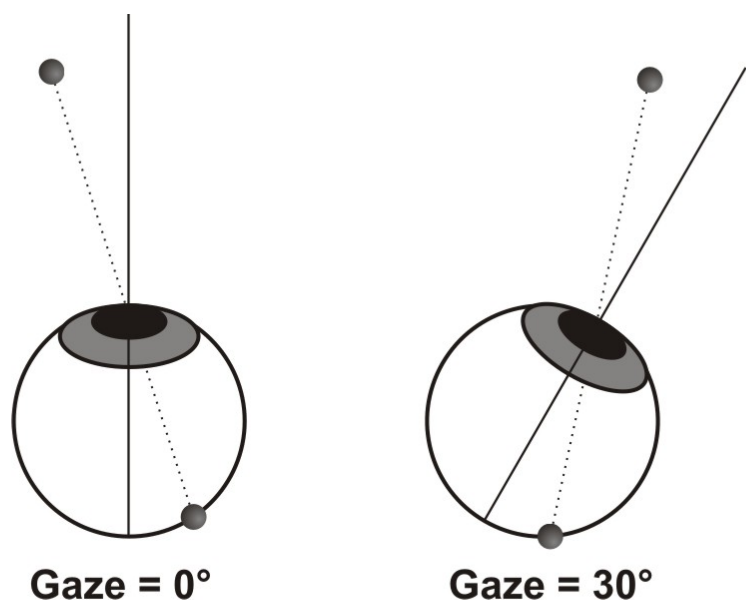


    - Arm movement: relative to attachment at shoulder



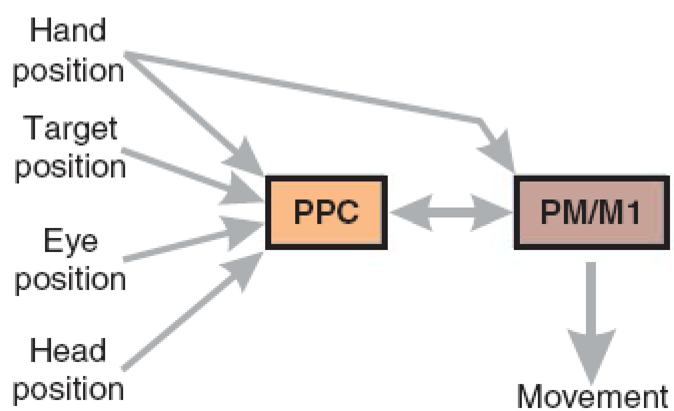
Sensory-motor transformations

- Reference frames
  - Knowledge about reference frames is required to localize sensory and motor events
    - Same retinal image – different spatial locations



Sensory-motor transformations

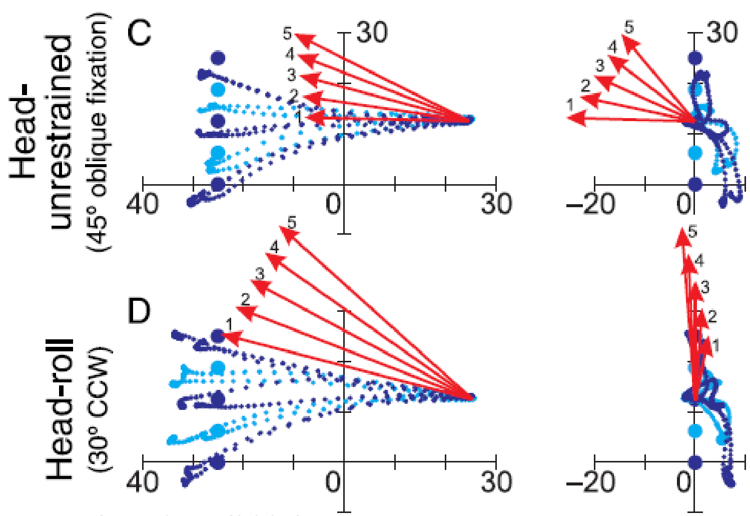
- Reference frames
  - A reference frame transformation is needed to map sensory to motor coordinates
    - Requires estimates of body geometry



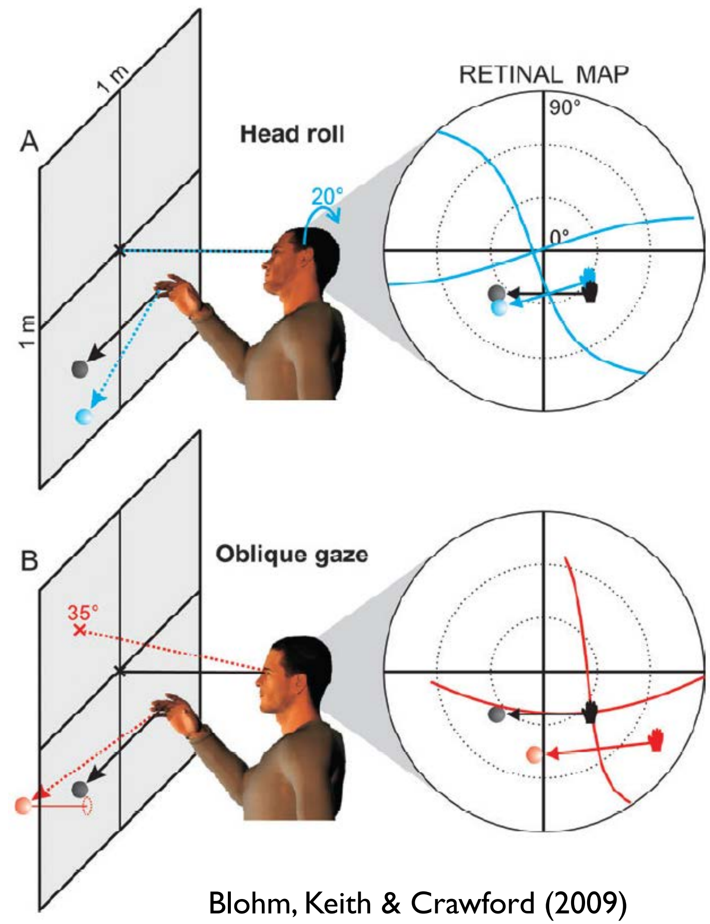
Blohm et al. 2009

Examples: reference frame transformations

- Reaching / pointing



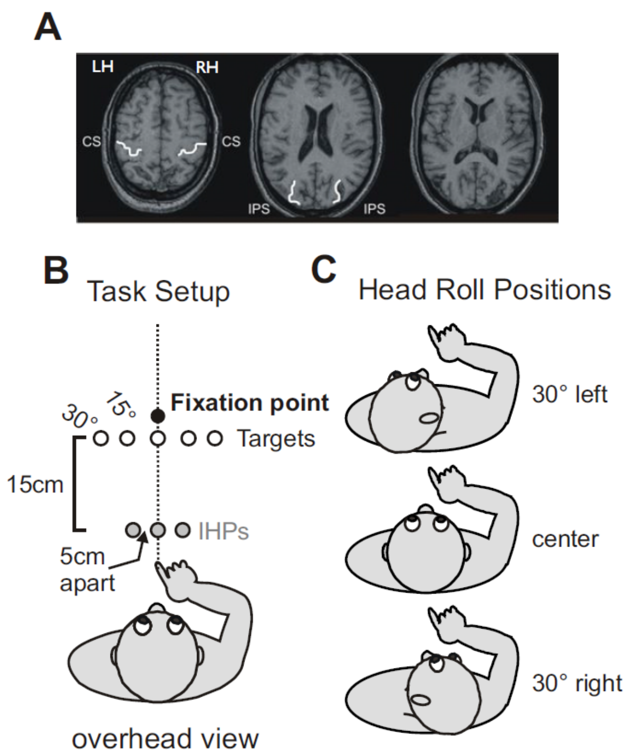
Blohm, & Crawford (2007)



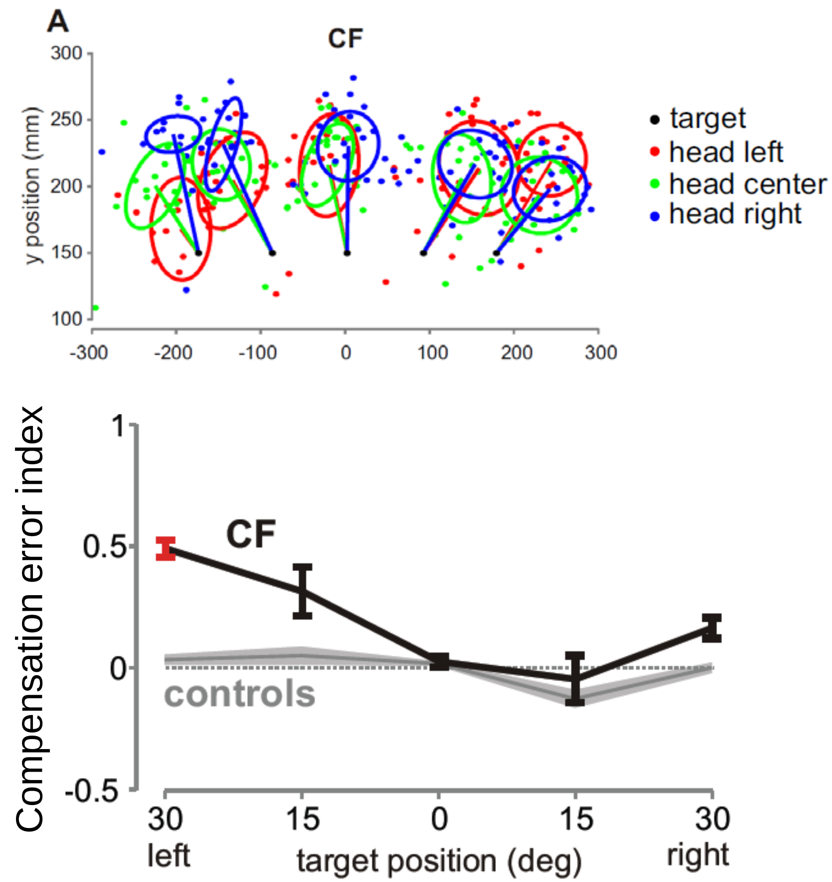
Blohm, Keith & Crawford (2009)

Examples: reference frame transformations

- Reference frame transformation deficits in optic ataxia



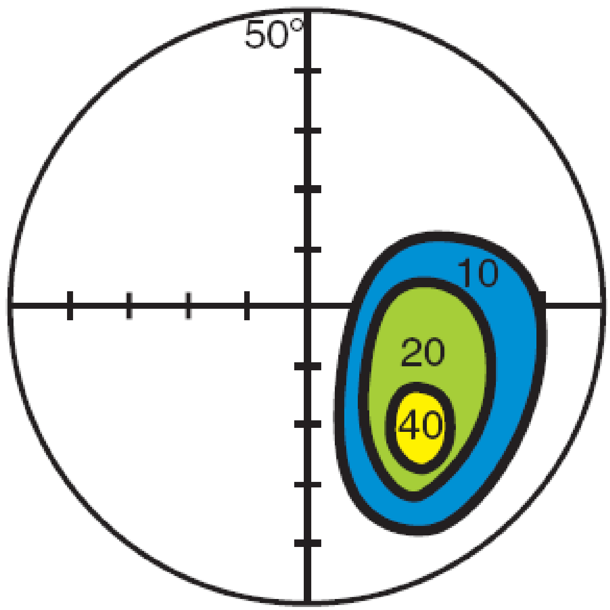
Khan, Pisella, Blohm (2013)



Current theories of sensory-motor transformations

Coding information in the brain

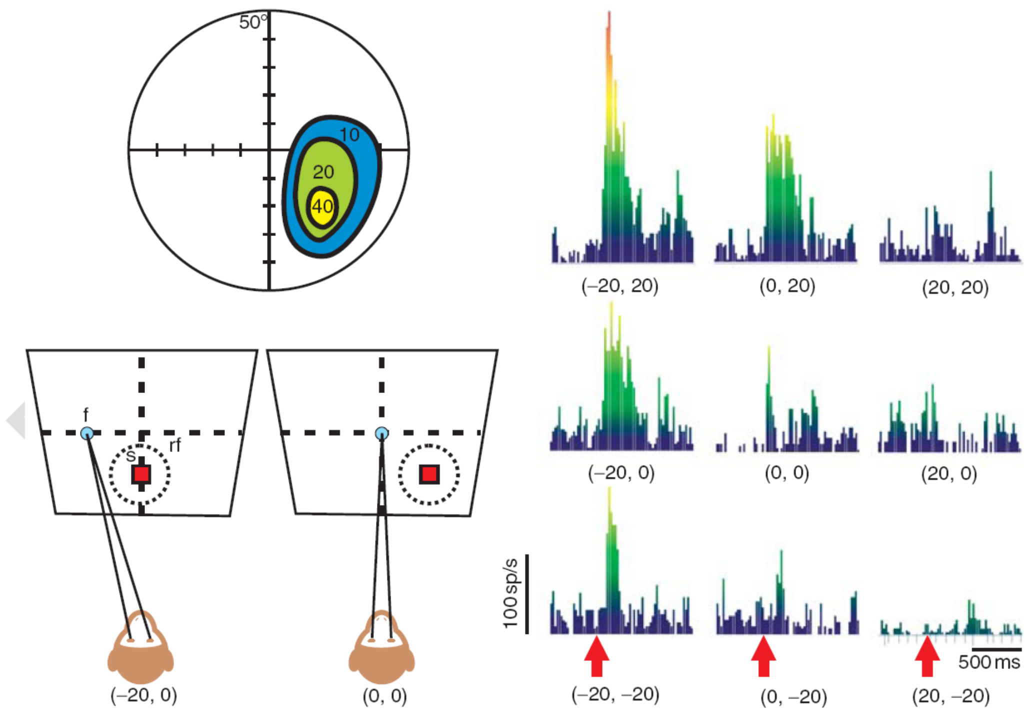
- Receptive fields
  - = activation pattern of a neuron for targets across space
    - We assume that the brain explicitly "codes" certain information
    - AND that we can decode it!



Blohm, Khan, Crawford, 2009 (adapted from Andersen, et al., 1985)

Gain modulation

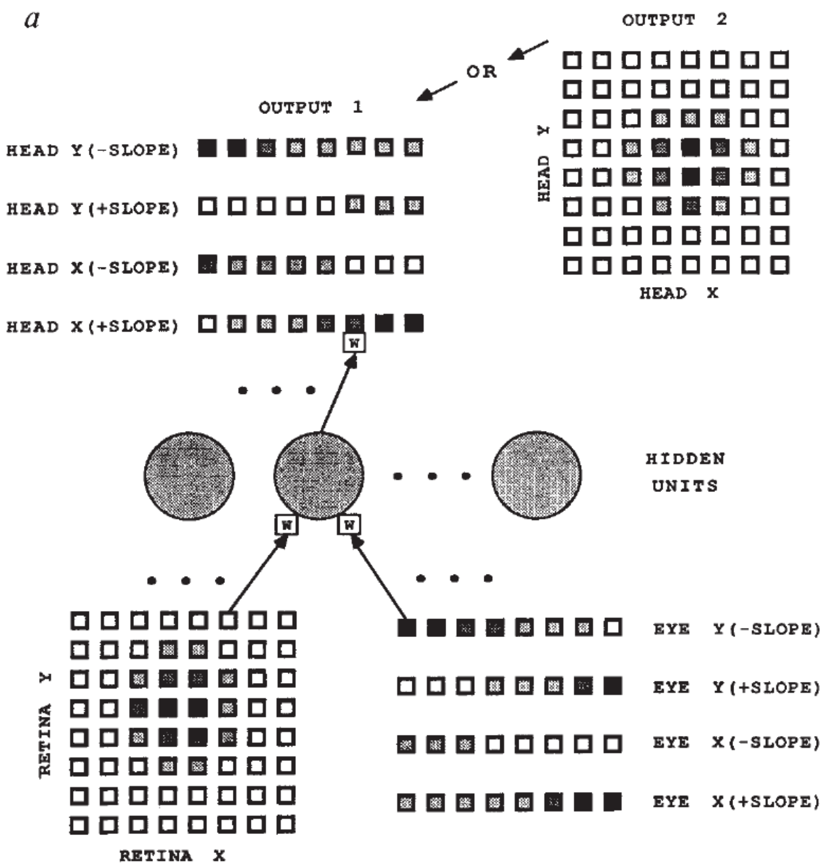
- = change of receptive field strength with secondary input
  - E.g. eye position gain modulation of visual receptive fields in posterior parietal cortex



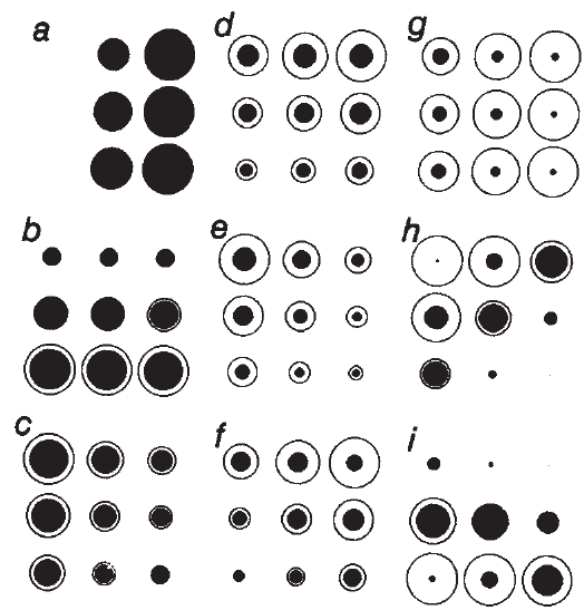
Blohm, Khan, Crawford, 2009 (adapted from Andersen, et al., 1985)

Gain modulation

- Reference frame transformations
  - Zipser & Andersen, Nature 1988

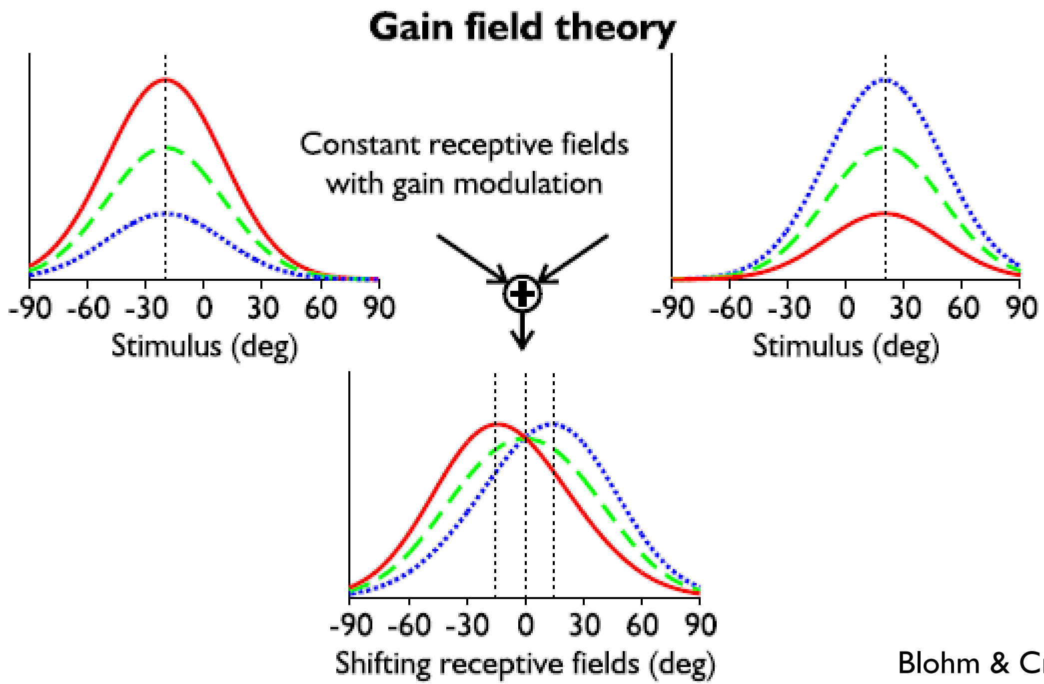


Eye position gain modulation of hidden layer units



Gain modulation

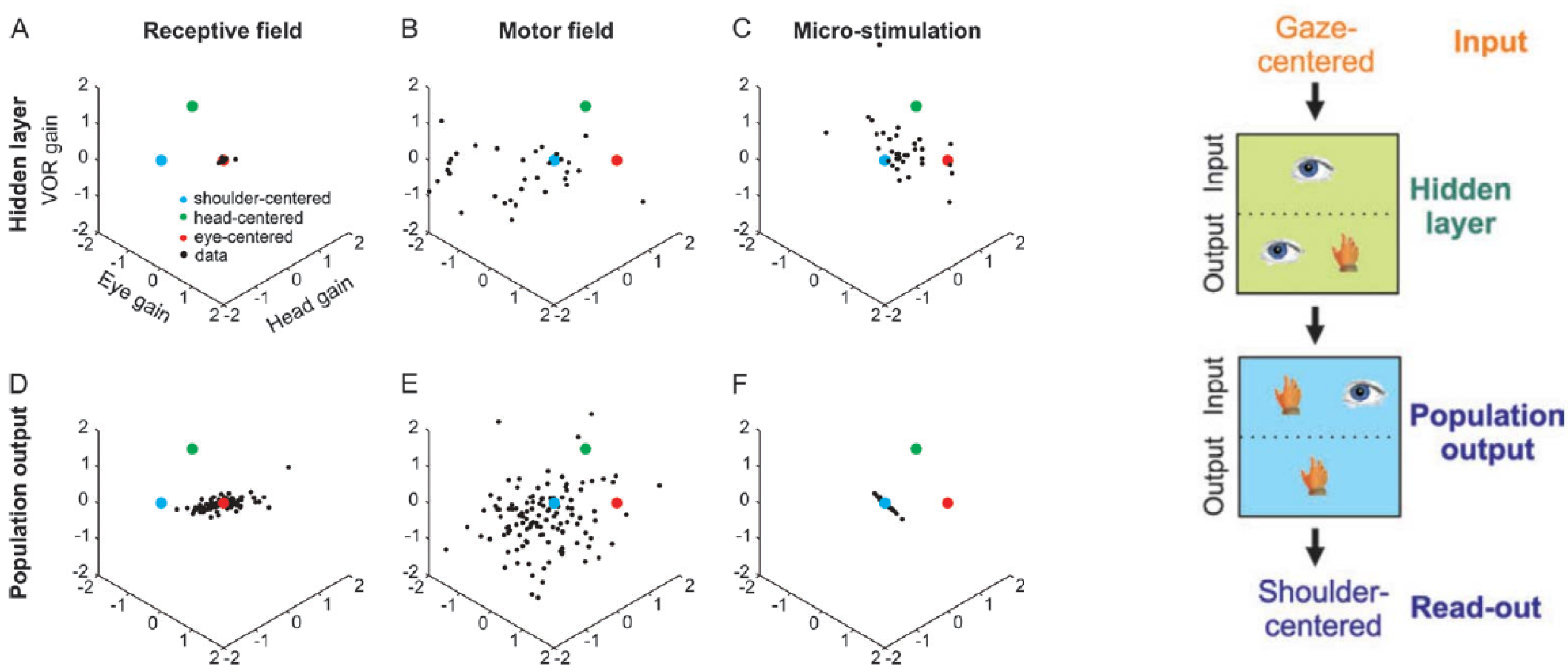
- Powerful computational means for
  - Cue combination
  - Reference frame transformations
  - Multi-sensory integration…



Blohm & Crawford, 2009

Reference frame transformations

- Reference frames based on "electrophysiological" analysis of a 3-D visuo-motor transformation network



Blohm, Keith, Crawford, 2009

Some open questions

- Are gain modulations really used by the brain?
  - Gain signals might be too slow? (Goldberg)
  - But decoding eye position is possible (Bremmer, Krekelberg)
- Do results from simple feed-forward ANNs generalize to spiking networks with complex cortical architecture?
- How can the brain carry out sensory-motor transformations of a whole scene?
  - Is that even necessary?
- How are stochastic reference frame transformations computed?
- What networks in the brain are involved for different sensory/motor systems?
  - One transformation for all sensory-motor processes?
- …

Multi-sensory integration

Introduction

- The world is highly variable
  - Sensory uncertainties
  - Noisy neural codes
  - Conflicting sensory cues (e.g. illusions)
- Questions:
  - How does the brain generate a perceptual experience despite all this uncertainty?
  - How can we infer a state (i.e. code in the brain, attribute of an object, sensory state, etc)?
  - What is the optimal way to act in this noisy world?
  - How do we decide what cue to trust and/or how much?

What is multi-sensory integration?

- Example: Ventriloquism

  Integration of vision and audition

Edgar Bergen with sidekick (Charlie McCarthy)

What is multi-sensory integration?

- Example: reaching
  - Evaluation of current hand position
    - Vision
    - Current joint angles (proprioception and/or efference copy)
- Noisy signal estimates

Current multi-sensory integration theory

Yu & Schrater

Mathematical framework for Bayesian integration

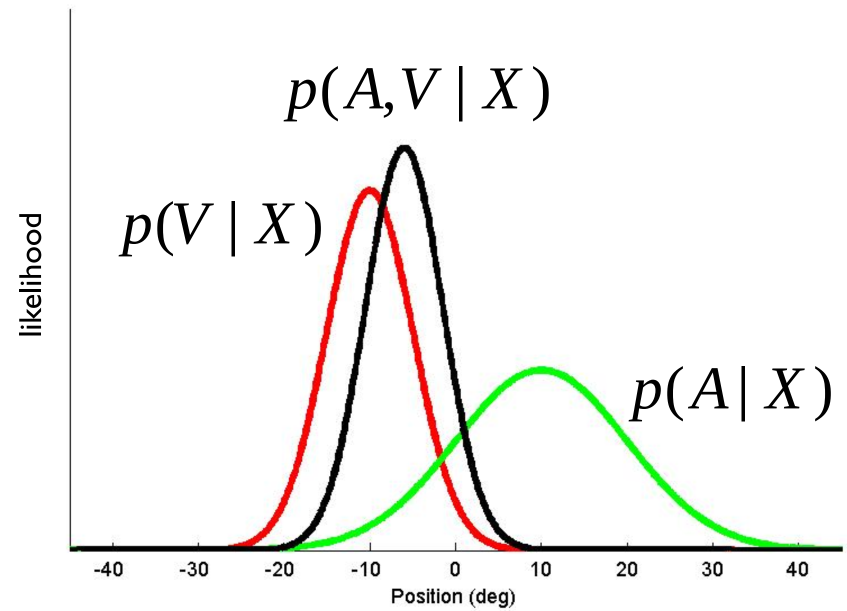
- Cue combination
  - Optimal Bayesian observer $p(X \mid A,V) = \dfrac{p(A,V \mid X)\cdot p(X)}{p(A,V)}$
  - Independent observations A, V

$$p(A,V \mid X) = p(V \mid X)\cdot p(A \mid X)$$

  - If uniform priors, then

$$p(X \mid A,V) \propto$$
$$p(V \mid X)\cdot p(A \mid X)$$

  - The brain always uses all available useful information.
  - Information from different sources is combined in a statistically optimal fashion



Bayesian integration

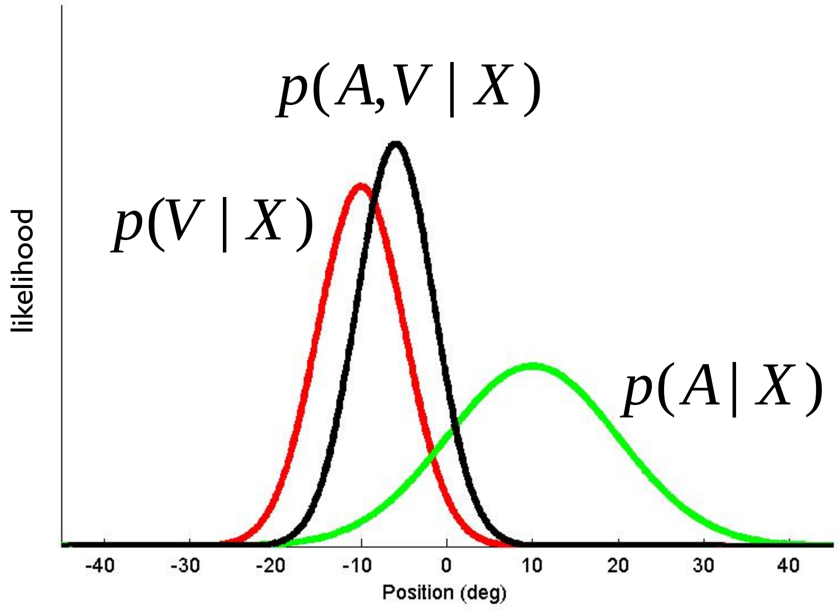
- Cue combination
  - Gaussian likelihood functions

$$\frac{1}{\sigma^2} = \frac{1}{\sigma^2{}_1} + \frac{1}{\sigma^2{}_2}$$

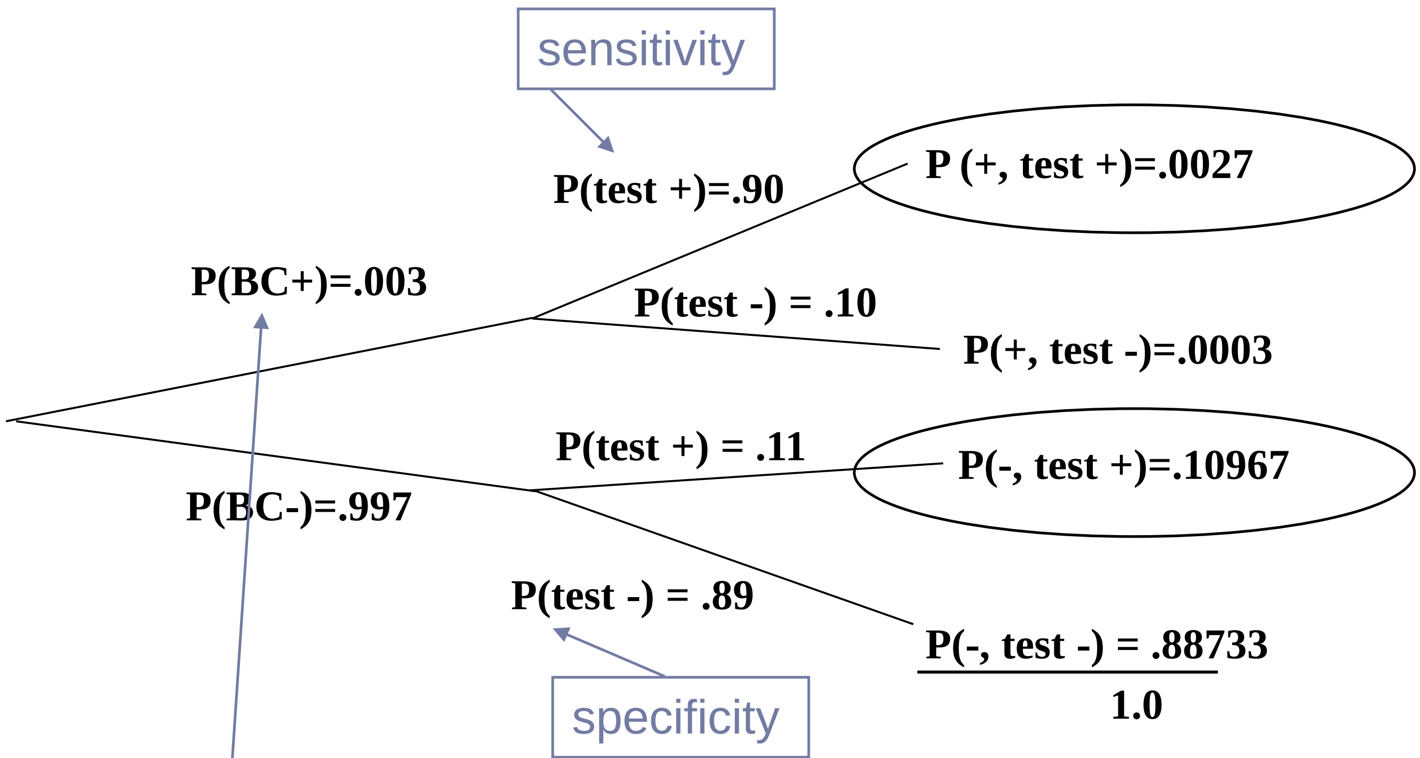
$$\Longleftrightarrow$$

$$\sigma^2 = \frac{\sigma^2{}_1 \cdot \sigma^2{}_2}{\sigma^2{}_1 + \sigma^2{}_2}$$

$$\mu = \sigma^2 \cdot \left(\frac{\mu_1}{\sigma^2{}_1} + \frac{\mu_2}{\sigma^2{}_2} \right)$$



Example: breast cancer



Marginal probabilities of breast cancer….(prevalence among all 54-year olds)

P(BC/test+)=.0027/(.0027+.10967)=2.4%

Estimation of priors?

- Based on a priori belief
- Difficulty: priors can be subjective and/or objective
- A non-uniform prior acts like a cue in cue integration

$$p(X \mid A,V) = \frac{p(A,V \mid X) \cdot p(X)}{p(A,V)}$$

- How to build an objective prior?
  - Based on prior evidence...

Estimation of priors?

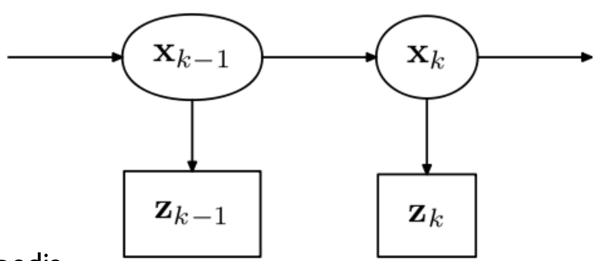
- Estimation of priors
  - Kalman filter (~1960): recursive Bayesian estimation
    - Given a hidden Markov process with state x_k (i.e. chain of events)

$$x_k = F_k x_{k-1} + B_k u_k + n_k^1 \qquad n_k^1 = N(0, Q_k)$$
$$z_k = H_k x_k + n_k^2 \qquad n_k^2 = N(0, R_k)$$

    - Initial belief (prior): uniform or some other function
    - Each observation z_k can be used to update the belief

$$p(x_k \mid z_k) = \frac{p(z_k \mid x_k) \cdot p(x_k \mid Z_{k-1})}{p(z_k \mid Z_{k-1})}$$

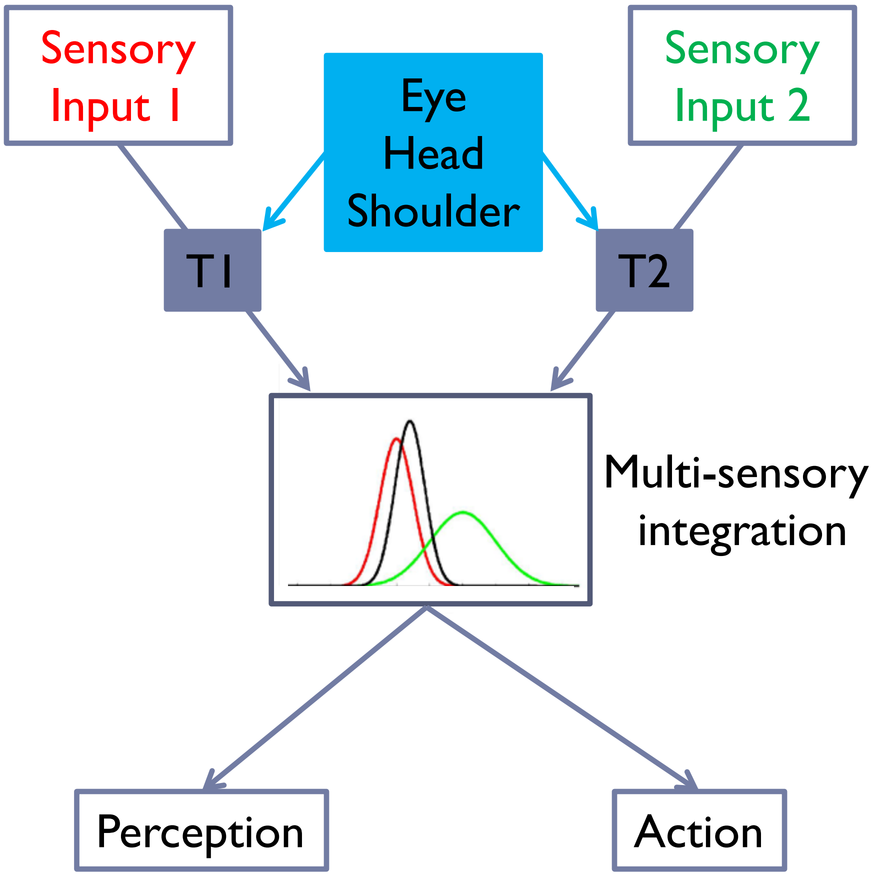
$$Z_{k-1} = \{z_1 \ldots z_{k-1}\}$$



Wikipedia

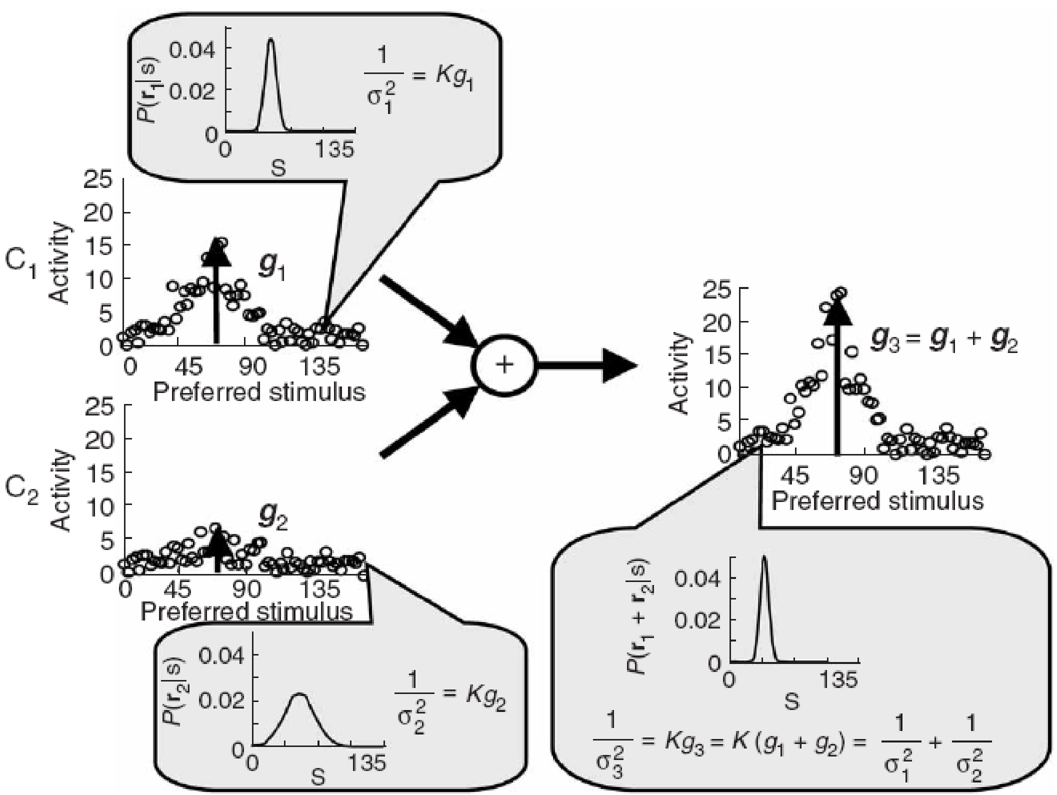
Multi-sensory integration across ref. frames

- Sensory signals have to be transformed into a common reference frame BEFORE integration
  - Transformations depend on relative orientation of eyes, head, shoulder...
  - The CNS needs to estimate eye-head-shoulder angles
- But, sensory estimations are noisy!
- Does this noise affect multi-sensory integration?



Bayesian computations in population codes

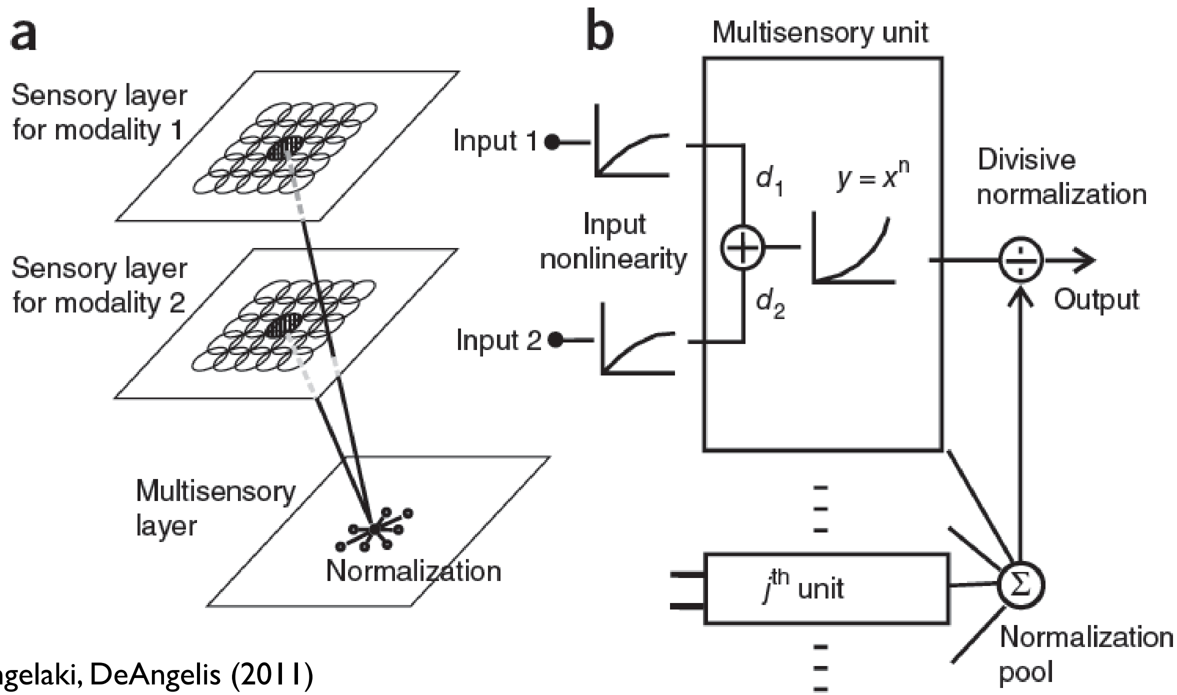
- Representing uncertainty with population codes
  - Probabilistic population codes
    - Poisson-like neural noise
    - Variance inversely related to gains of population code



Ma et al. (2006)

Neuronal implementation?

- Divisive normalization & marginalization
  - Relevant for sensory processing, visual search, object recognition, multi-sensory integration, coordinate transformations, navigation, inference, motor control, etc…



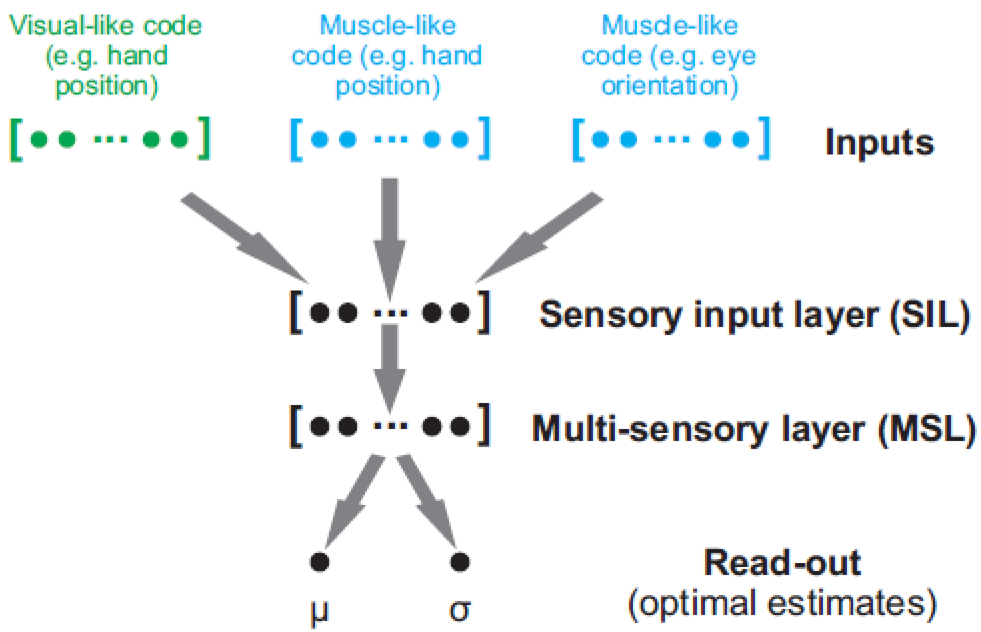
Ohshiro, Angelaki, DeAngelis (2011)

Problems with explicit divisive normalization

- The curse of dimensionality
  - $N^{(ds)}$ neurons needed
    - N: neurons along each dimension
    - d: # dimensions
    - s: # signals to be combined
  - Example: N=100, d=3, s=2 → 10^{12} neurons needed!
- Network connectivity constraints
  - Huge connectivity - # connections for each neuron > # neurons
  - Precise structure required – extraordinary regularity
- Representation of population coding
  - All input and output codes must be the same (Weak Fusion Model)
  - Mixture of different codes is not trivial
- Alignment of population codes
  - Perfect alignment of codes required

A possible alternative: implicit approximate normalization (IAN)

- In machine learning, marginalization is known as the *partition function problem*.
  - Explicit partition functions are typically impossible to compute, but non-probabilistic approaches allow for solutions.



Standage, Lillicrap, Blohm (in preparation)

Some open questions

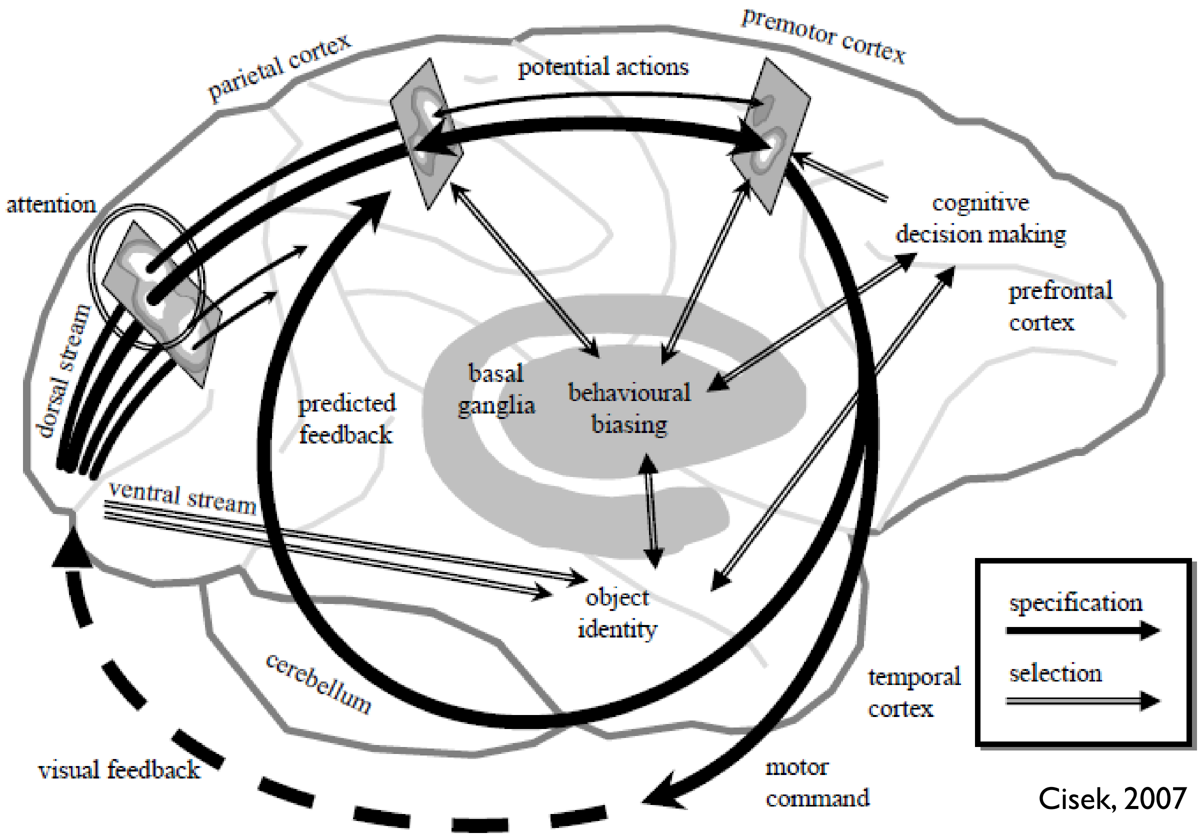
- How is multi-sensory integration carried out in t he brain?
  - Cortically, sub-cortically – different anatomy
  - Causal integration
  - Mechanisms
  - Neural implementation
- How does the brain make sure that unrelated signals are not integrated
  - In multi-modal areas, i.e. almost the whole brain!
- Is the brain just a big Kalman filter?
- How are statistics represented/stored/learned/recalled?
  - Variances, priors

Target selection & decision making

Yu & Schrater

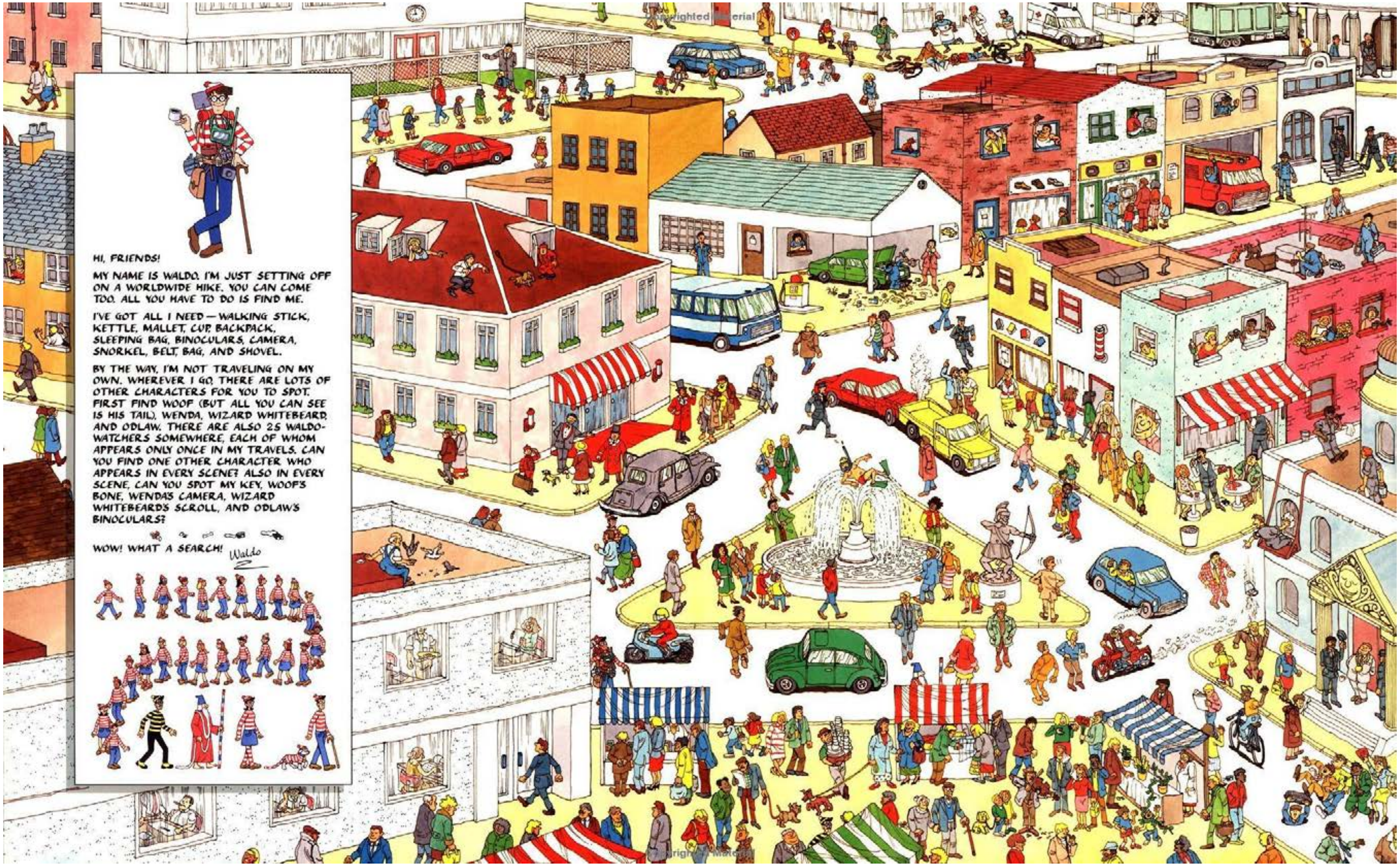
Motor planning & execution

- Target selection and decision making are integral part of motor planning and execution!



Cisek, 2007

Complex environments



The brain's approach

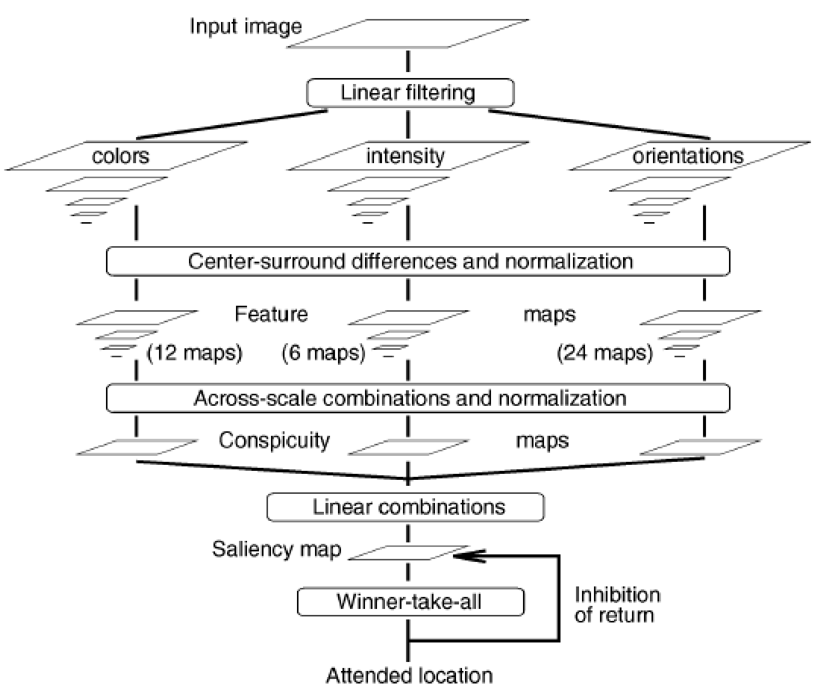
- Selective attention – interaction between
  - Bottom-up (determined by the brain's processing capabilities)
  - Top-down (voluntary)
- Goal: further process only what might be of importance

- Decide & act?

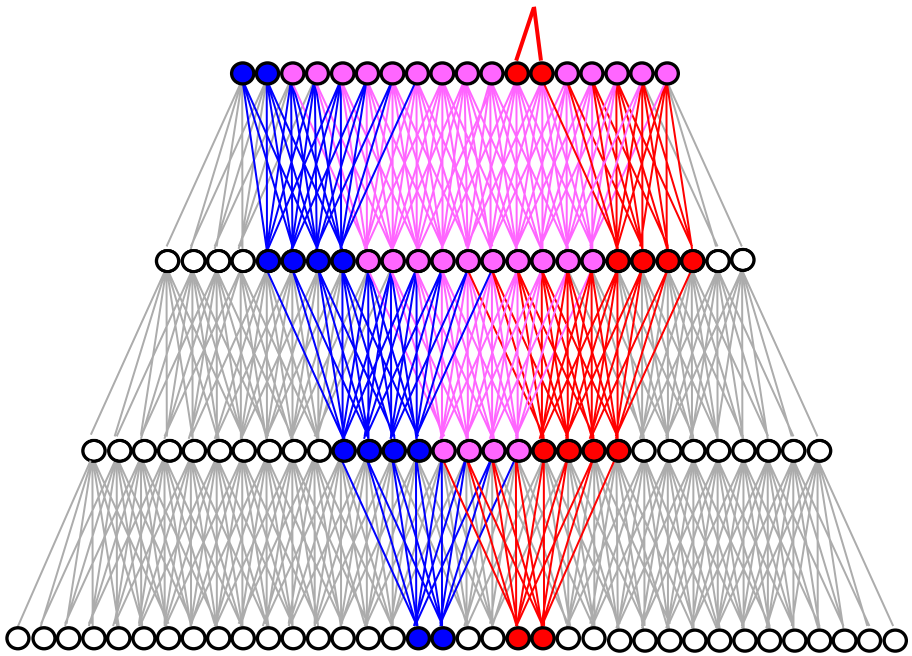
- Attention, target selection & decision making processes interact with/are part of almost ALL sensory-motor processes
  - But they are often ignored, especially by the motor control community…

Current theories

- Attention



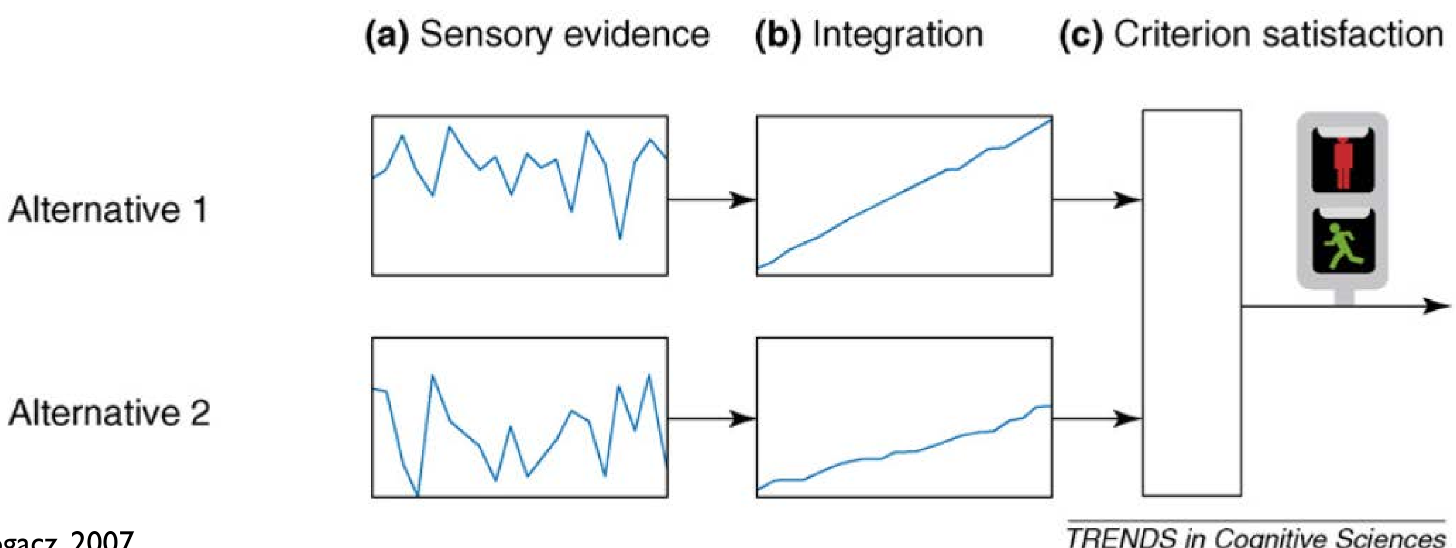
Itti et al., 1998



Tsotsos, et al. 1990

Current theories

- Target selection
  - Through the interaction of bottom-up and top-down attention
- Decision making
  - Different versions of rise-to-threshold models



Bogacz, 2007

Current theories

- Target selection
  - Through the interaction of bottom-up and top-down attention
- Decision making
  - Different versions of rise-to-threshold models
- Computational principles at work?
  - Competitive processing
  - Divisive normalization
  - Gain modulation

Some open questions

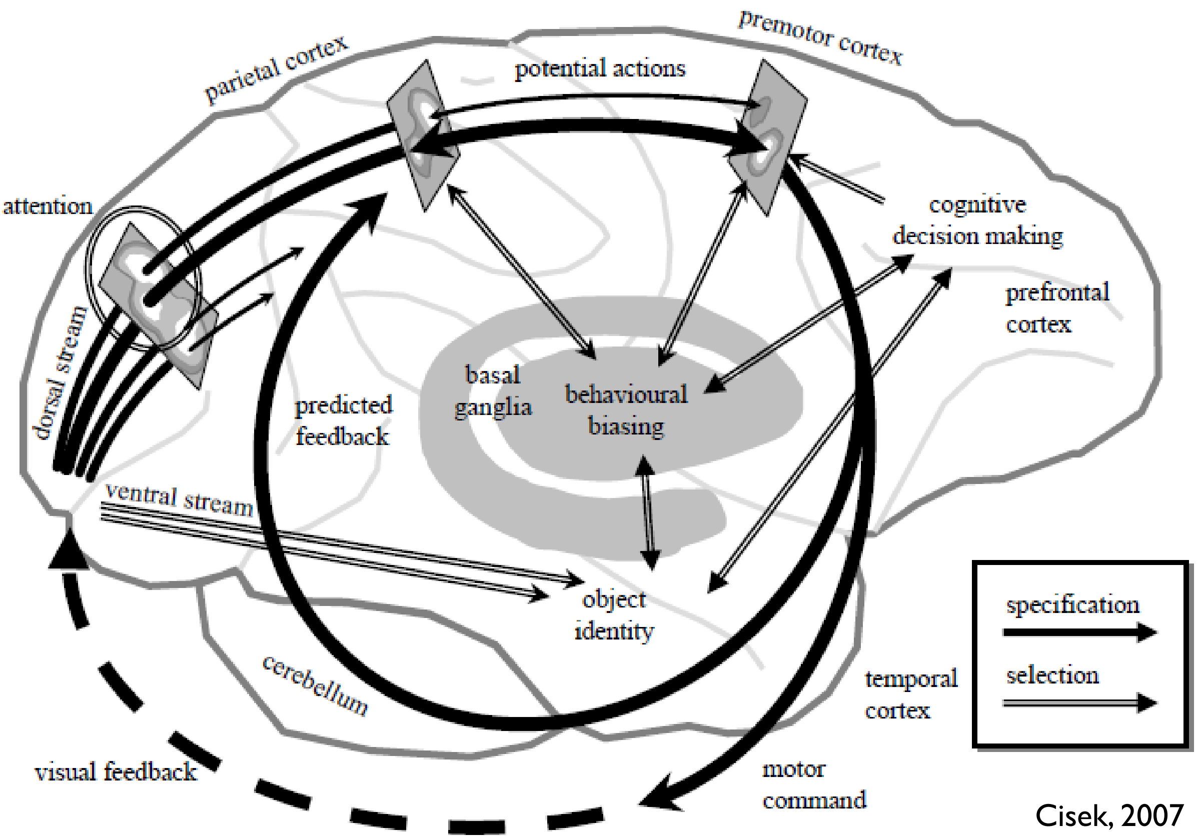
- Is there such a thing as a fixed decision threshold?
- How are multi-alternative decision computed by the brain?
- Is there one "decision system" or one for each effector?
- Are decision processes separable from motor planning?
- How do we learn to make decisions?
- The theory only captures optimal decisions
  - No "irrational" influences (e.g. emotions)
- A lot of the computational neurocircuitry is still unknown…

Motor planning, motor control & error corrections

Ting & Scott

Motor planning & execution

- Planning, execution and error correction are all part of the same system

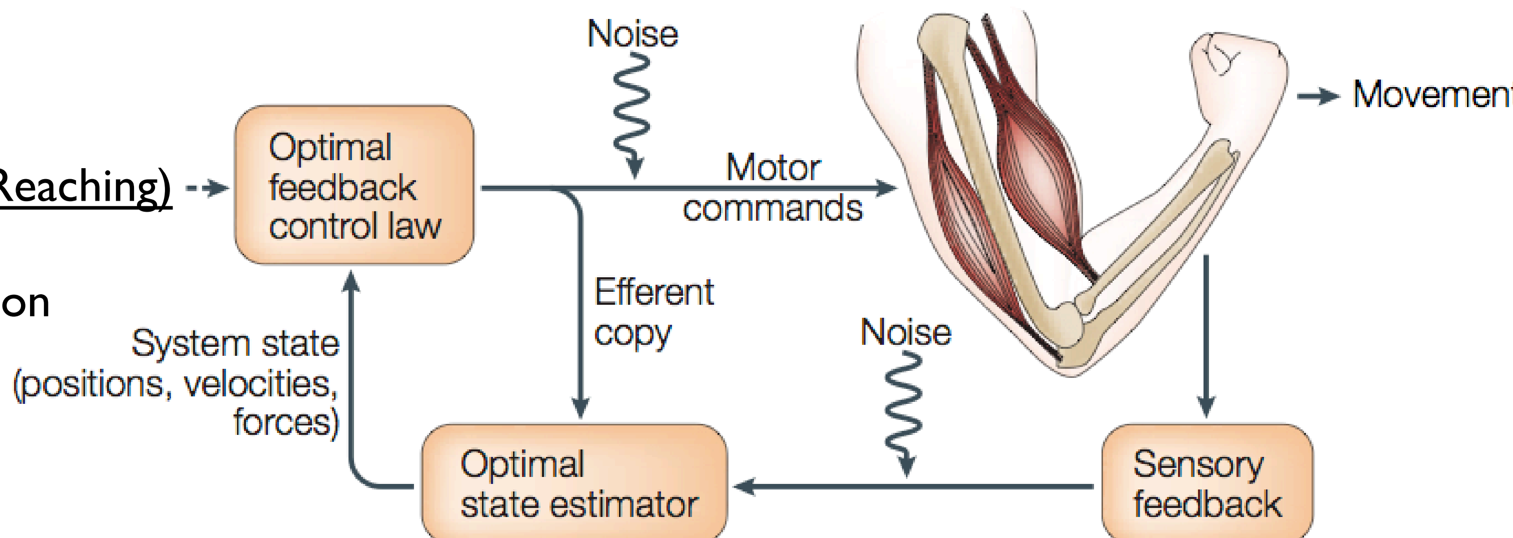


Cisek, 2007

Motor planning & control

- Motor planning is the result of all previous steps…
  - Sensory processing
  - Transformations & multi-sensory integration
  - Target selection & decision making
- Motor control
  - Different theories have been discussed in the past, but today only optimal feedback control is considered.

<u>Task Selection (Reaching)</u>
Target Position
Initial Arm Position
Nominal Speed



Scott, 2004

Mathematical formulation

Sensory state of our body and the world we interact with

motor command

motor noise

$$\mathbf{x}^{(k+1)} = A\mathbf{x}^{(k)} + C\mathbf{u}^{(k)} + \boldsymbol{\varepsilon}_u^{(k)}$$

What we can observe about the state

sensory noise

$$\mathbf{y}^{(k)} = B\mathbf{x}^{(k)} + \boldsymbol{\varepsilon}_y^{(k)}$$

Cost to minimize

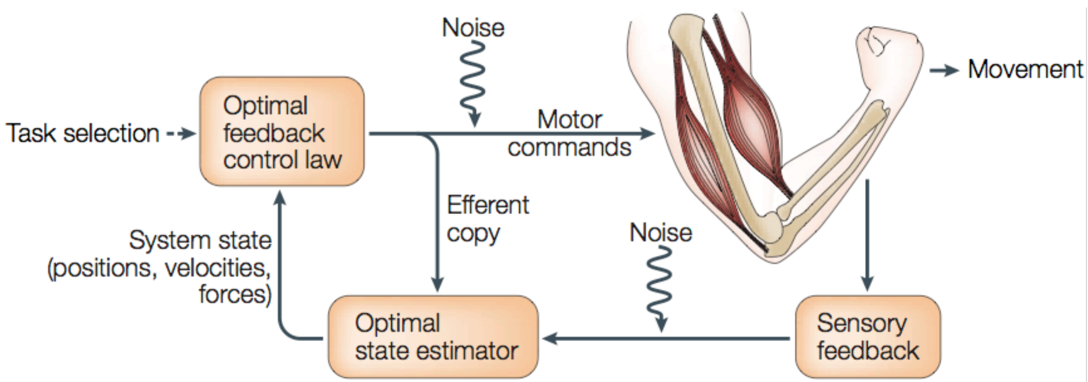
$$J = \sum_{k=0}^{p-1} \mathbf{u}^{(k)T} L^{(k)} \mathbf{u}^{(k)} + \mathbf{y}^{(k+1)T} T^{(k+1)} \mathbf{y}^{(k+1)}$$

Feedback control policy

$$\mathbf{u}^{(k)} = G^{(k)} \hat{\mathbf{x}}^{(k)}$$

Belief about state

$$\hat{\mathbf{x}}^{(k+1)} = \hat{A}\hat{\mathbf{x}}^{(k)} + \hat{A}K^{(k)}\left(\mathbf{y}^{(k)} - \hat{\mathbf{y}}^{(k)}\right) + \hat{C}\mathbf{u}^{(k)}$$

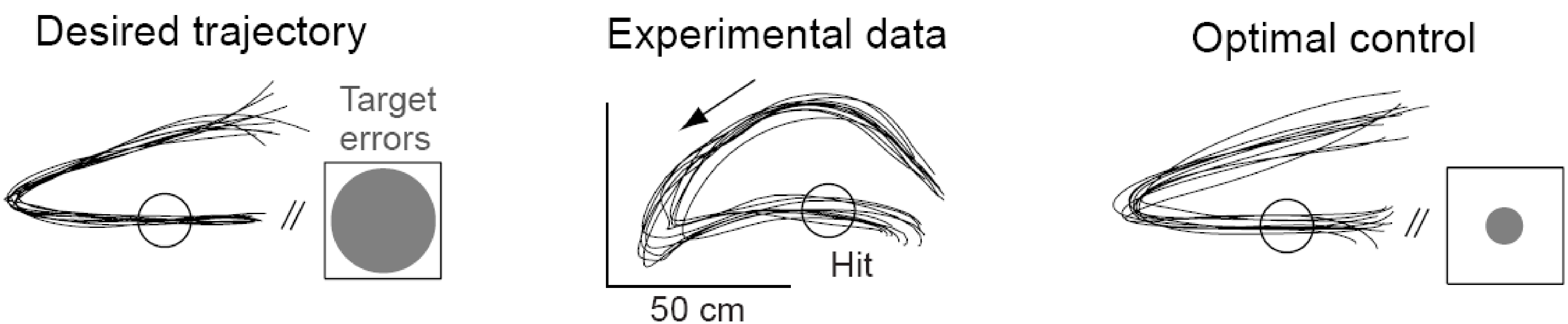


Predicted sensory consequences

Measured sensory consequences

Optimal feedback control

- Example: tennis



Torodov & Jordan, 2002

- Optimal control reproduces backward swing

Some open questions

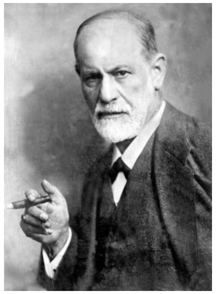
- Does the brain directly control muscles or does it simplify the control problem?
  - Muscle synergies (Ting)
  - Reflexes (Scott)
  - …
- Optimal control theory is a normative model, but how is it implemented in the brain?
  - How do networks produce optimal movements?
  - What is controlled? End position, angles, muscles…
- How can multiple motor plans be computed in parallel?
- Are error corrections controlled by a separate system or are they integral part of the optimal control loop?

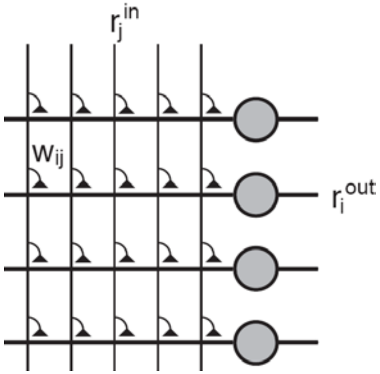
Adaptation & learning

Tweed & Smith

Hebbian learning

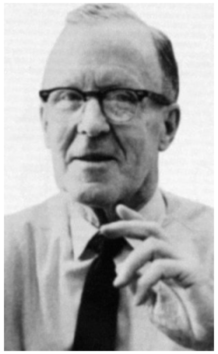
- Sigmund Freud (1888)
  - Law of association by simultaneity





Trappenberg 2010

- Donald O. Hebb (1949)
  - Functional implementation of learning
  - "When an axon of a cell A is near enough to excite cell B or repeatedly or persistently takes part in firing it, some growth or metabolic change takes place in both cells such that A's efficiency, as one of the cells firing B, is increased."
  - Activity-dependent plasticity that depends on pre- and post-synaptic activity is called Hebbian plasticity / learning
  - Neurons i and j connect with weights w_{ij}: weights adapt

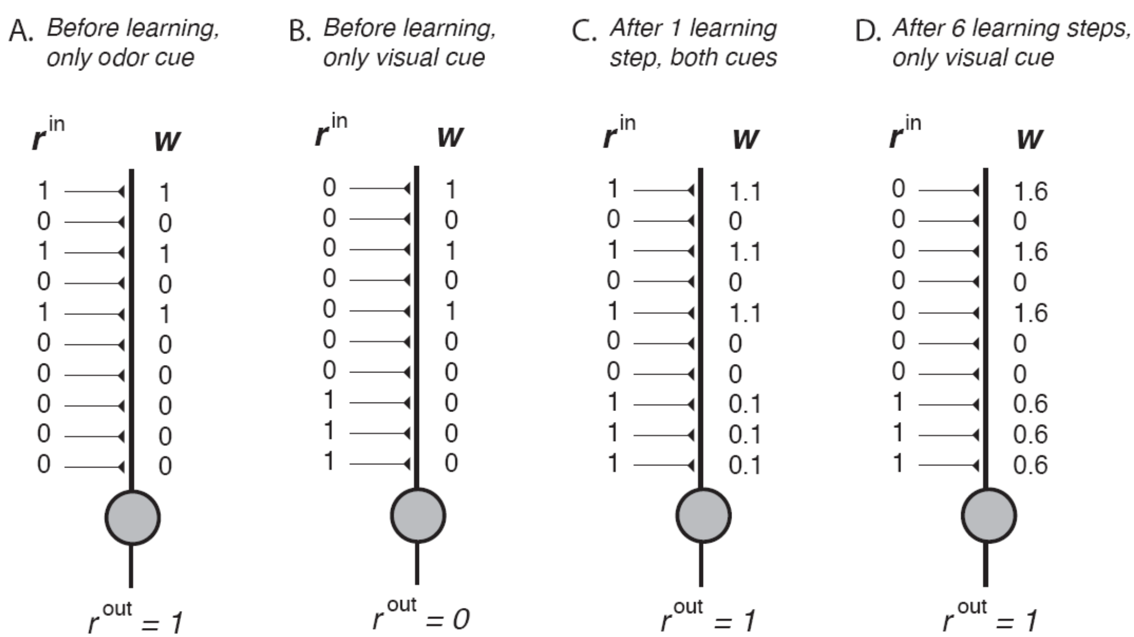


Hebbian learning

- Associative memory
  - Human memory $\neq$ computer memory
    - Computer: 1-bit failure is fatal!
    - Human: fault-tolerant
  - Humans learn associations
    - Associations can trigger memories based on related information
    - Partial information is sufficient to recall memories
    - Associative memory is essential for human cognitive processes
  - Synaptic plasticity leads to associations

Hebbian learning

- Associative memory (example)
  - Initially: only odor selective
  - Partial input sufficient (pattern completion)
  - Adaptation: increase w_i by $\Delta w = 0.1$ if a pre- synaptic firing is paired with a post-synaptic firing
  - Learning leads to association



$$r^{out} = \left(\sum_i \omega_i r_i > \theta \right)$$

Threshold $\theta = 1.5$

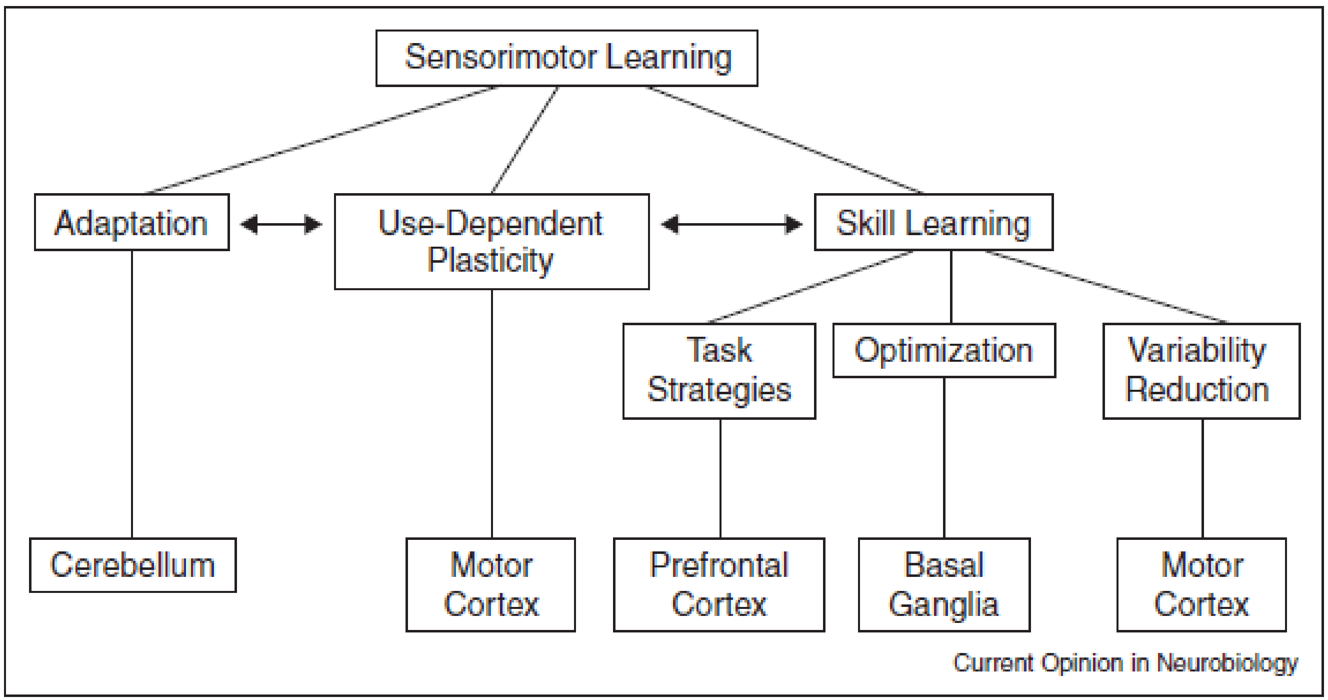
Trappenberg 2010

Hebbian learning

- Associative memory features
  - Recall from partial input: pattern completion
    - Relies on distributed stimulus representation
    - Based on (at least) partial overlap (similarity) between stimulus and weight vectors: dot product $\mathbf{r} \cdot \mathbf{w}$ is a measure of similarity
    - Generalization: output node responds to all pattern similar to trained pattern
  - Extraction of central tendencies
    - Weight vector **w** represents average of training set = prototype
    - Noise reduction through the use of prototypes
  - Robustness to degradation
    - Loss or inaccuracy of parts (synapse, neuron) does not affect system
    - This fault tolerance is essential in biological systems

Learning theories

- Learning results in behavioral changes
  - Definition: "Any relatively permanent change in behavior that occurs as a result of experience."

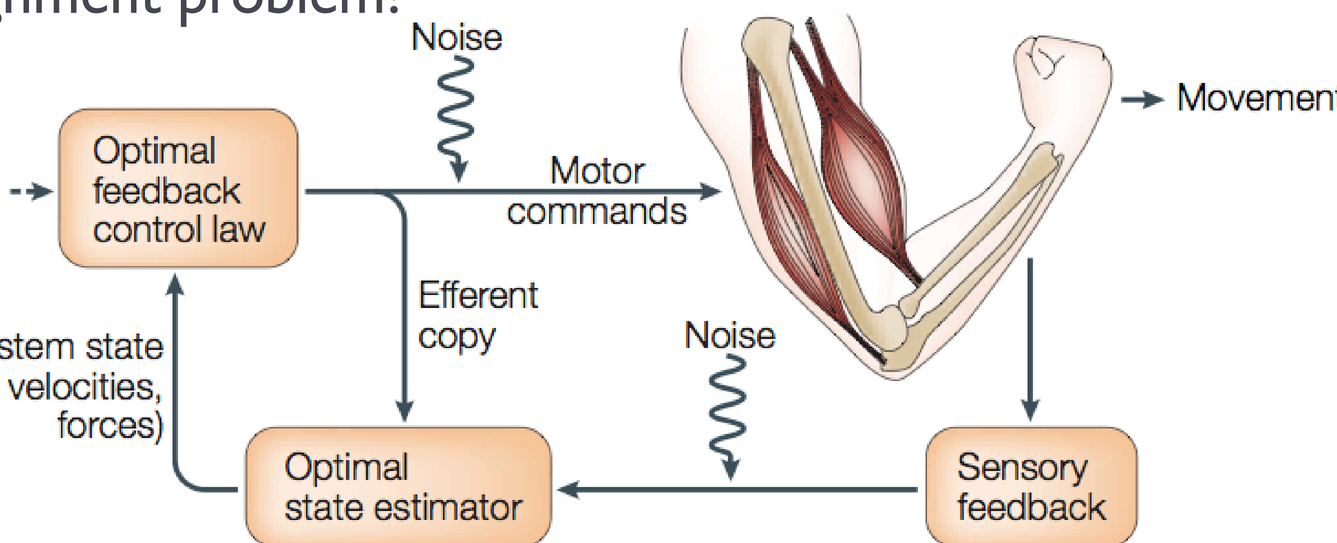


Krakauer & Mazzoni 2011

Learning theories

- Learning results in behavioral changes
  - Error-based learning: what went wrong?
    - Initial state?
    - OFC – inverse model?
    - State estimation – forward model? …
  - Credit assignment problem!

<u>Task Selection (Reaching)</u>
Target Position
Initial Arm Position
Nominal Speed



Scott, 2004

Some open questions

- Big gap between synaptic learning theories and behavioral changes!
  - Role of reward / punishment
  - Where in the brain's computational hierarchy does learning occur?
  - How does the learned state remain stable?
- Synaptogenesis / synaptic pruning are poorly understood
  - What triggers them?
  - Relationship to behavior
- Where and when does behavioral learning / adaptation occur?
  - Cortex vs. cerebellum
  - Time scales: quick adaptation vs. consolidation
  - Credit assignment problem
- We have no learning theory that works at the detailed whole brain spiking network level…

That’s it folks!