Outline

- CoSMo organization (Blohm) – Day 1
  - Introduction to sensory-motor control 1
    - What’s “computational”? (Thoroughman)
    - The computational neuroanatomy of the brain (Blohm)
    - What is “sensory”? (Thoroughman)
    - Sensory-to-motor transformations (Blohm)
  - Data sharing (Blohm & Thoroughman)

- Introduction to sensory-motor control 2
  - What is “motor”? (Thoroughman)
  - Target selection, motor control & learning (Blohm)
  - Prosthetics (Thoroughman)
  - What is “neuroscience”? & imaging (Thoroughman)
  - How to model (Blohm & Thoroughman)

- Matlab & Bayesian tutorials (Blohm & Thoroughman)
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
What’s “computation”?

Kurt Thoroughman
The computational anatomy of the brain

Hierarchies
Computational anatomy of the brain

\[
\log_{10} W = (1.23 \pm 0.01) \log_{10} G - (1.47 \pm 0.04)
\]

\[
r = 0.998
\]

Zhang & Sejnowski, PNAS 2000
Computational hierarchy of the brain

- Brodmann’s areas
- Functional areas
- Maps

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

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**
  - Not addressed enough!

- Models bridging Marr 1-3 are rare!
Motor planning & execution

- Processes involved in the sensory guidance of action
  - Sensory processing
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    - Move or not
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    - When to move (timing)
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Blohm et al. 2009
What’s “sensory”?  
Kurt Thoroughman
Sensory-motor transformations

Green & Cisek
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, Keith & Crawford (2009)

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...

*Gain field theory*

Constant receptive fields with gain modulation

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

Adams & Schrater
Cue combination

- Optimal Bayesian observer
  \[ p(X \mid A, V) = \frac{p(A, V \mid X) \cdot p(X)}{p(A, V)} \]

- 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

\[
\frac{1}{\sigma^2} = \frac{1}{\sigma_1^2} + \frac{1}{\sigma_2^2}
\]

\[
\sigma^2 = \frac{\sigma_1^2 \cdot \sigma_2^2}{\sigma_1^2 + \sigma_2^2}
\]

\[
\mu = \sigma^2 \cdot \left( \frac{\mu_1}{\sigma_1^2} + \frac{\mu_2}{\sigma_2^2} \right)
\]
Example: breast cancer

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

\[ P(BC+/test+) = \frac{0.0027}{0.0027 + 0.10967} = 2.4\% \]
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

\[ p(X | A,V) = \frac{p(A,V | X) \cdot p(X)}{p(A,V)} \]

- 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)
      
      \[
      x_k = F_k x_{k-1} + B_k u_k + n_k^1 \quad \quad \quad n_k^1 = N(0, Q_k)
      \]
      
      \[
      z_k = H_k x_k + n_k^2 \quad \quad \quad n_k^2 = N(0, R_k)
      \]
    
    - Initial belief (prior): uniform or some other function
    - Each observation $z_k$ can be used to update the belief

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

\[
Z_{k-1} = \{z_1 \ldots z_{k-1}\}
\]
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: $N=100$, $d=3$, $s=2 \rightarrow 10^{12}$ 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 the 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