The use of control theory to interpret biological motor control

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Objective: Understand function of primary motor cortex

- Muscles versus Movements (pre-1970)
- Traditional Servo Control (1970 to 1985)
- Feedforward (Open-Loop) Control (1985 to 2002)
- Optimal Feedback Control (since 2002)

Review
Scott, J. Physiology, 2008
• Optimal Feedback Control (OFC) as a Theory of Voluntary Control

• Stretch Responses Mirror Capabilities of Voluntary Control

• Transcortical Feedback is Important for Voluntary Control

Reviews
Scott, Nature Reviews Neuroscience, 2004
Scott, TICS, 2012
Excitable cortex & evoked movements

Eduard Hitzig & Gustav Fritsch (1870)

David Ferrier (1873)
Primary Motor Cortex

Question: Muscles Versus Movements (1960s)
Primary Motor Cortex

Recording microelectrode in wrist area of right motor cortex

No Load

Extension

Flexion

Flexor Load

Extensor Load
Primary Motor Cortex: Sensory Feedback

Flexion

Extension

Active

Passive

M1

Cell

Biceps

Triceps

Cell

Biceps

Triceps

L2-1

500 ms

(80)
Basic Control Theory

Biological Control: Control of Single-Joint wrist movements

Controller (Central Nervous System)
- Desired Joint Angle
- Joint Angle
- Motor Commands
- Wrist Muscles
- Wrist Movement
- Afferent Feedback
- Muscle Afferents

Plant (Musculoskeletal System)
Proprioceptive Feedback

Visual Feedback

Voluntary (R4)

100 ms

100 uv

Short-Latency Reflex

Long-Latency Reflex

Perturb Onset

R1

R2

R3

100 ms

50 ms

Step-Torque Perturbation

Proprioceptive Feedback

Visual Feedback

Single-Joint Perturbation

Stretch-Related Muscle Activity

Short-latency response: Spinal

Long-latency response: Spinal and Cortical

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Feedback Elicits Task Selection

Joint Motion

Perturbation Onset

100ms

9°

"Resist"

"Let Go"

Muscle Activity

Voluntary (R4)

Rothwell et al., 1980

Short-Latency Reflex

R1 R2 R3

Long-Latency Reflex

100ms

100uv
Context-dependent change in perturbation-related activity in primary motor cortex

Instruction: Pull

Instruction: Push

Evarts and Tanji, 1976
Hierarchical Model of Voluntary Control

Motor Planning: Behavioural Goals (BG)

Convert BG into detailed patterns of motor output

Low-level control

Premotor Cortex

Primary Motor Cortex

Spinal Cord

PM

MI
Inconvenient Truth about servo-control

- Delay in sensory feedback
- Intersegmental dynamics
Conceptual Framework (1990s):
Sensorimotor Transformations/Coordinate Frames

- inspired from visual system
- focus of feedforward control (open loop)
- provides penultimate goal, address control later

Obvious Question: What coordinates are represented in primary motor cortex (M1)?
Activity of a neuron in primary motor cortex during centre-out reaching.
Population vectors (red) tend to point in the direction of hand motion (dashed line with arrow)

Neural coding of hand trajectory?
Instantaneous population vector predicts spiral hand motion

Movement

Population

Inside→Out  Outside→In
Hierarchical Model of Voluntary Control

Primary Motor Cortex → MI → Behavioural Goals (BG)

Convert BG into detailed patterns of motor output
Reaching Movements with different arm geometries

Natural Abducted
Reaching movements with different arm geometries

Natural

Abducted

Scott and Kalaska JNP 1997
Two-dimensional Paradigm

KINARM robot

- Two-dimensional planar motor task involving shoulder and elbow
- Can apply joint- or hand-based loads
- Augmented reality system displays targets in the plane of the task
Joint Power = Angular Velocity * Torque
Posterior Deltoids: Shoulder Extensor

Distribution of Preferred Directions

Preferred Direction
Distribution of Preferred Directions

Scott et al., Nature, 2001
Distribution of Preferred Directions

Scott et al., Nature, 2001

Population Vectors

Scott et al., Nature 2001
Neural activity in M1 reflects limb mechanics:

Peak Joint Power

Limb Muscle Activity

M1 Cell Activity

0.1 W
Conceptual Framework: Sensorimotor Transformations/Coordinate Frames

M1 neurons can represent all levels of information
An Inconvenient Truth about Sensorimotor Transformations/Coordinate Frames

Movement

Posture

Neurons can switch what they ‘represent’
(Kurtzer et al., Nat. Neurosci. 2005)
Optimal Feedback Control as a model of voluntary motor control (Todorov and Jordan, 2002)

Diagram from Scott, Nat. Rev. Neurosci. 2004
Linear Quadratic Regulator

Optimal Feedback Control: Manages Noise

Task Selection (Reaching)
- Target Position
- Initial Arm Position
- Nominal Speed

Optimal feedback control law

System state (positions, velocities, forces)

Optimal state estimator

Noise

Motor commands

Sensory feedback

Movement

Diagram from Scott, Nat. Rev. Neurosci. 2004
Sensory and Motor Noise

Voluntary

ENDPOINT ERRORS (SD in cm)

ANGLE ERRORS (SD in °)

Hamilton et al., JNP 2003
Scott and Loeb, J. Neurosci. 1994
Key feature of OFC is that errors are only corrected if they affect the goal, otherwise they are ignored.

Control Problem: $X_1 + X_2 = 2$
Nominal Solution: $X_1 = X_2 = 1$

Case 1(●): $X_1 = 0.5, X_2 = 0.5$
Proceed to ▲

Case 2(■): $X_1 = 1.2, X_2 = 0.8$
Stop

Case 3(▲): $X_1 = 1.2, X_2 = 0.4$
Proceed to ¤

Emergent Pattern of Variability
Task-dependent Corrections

Success at hitting a ping pong ball

Experimental data

Desired trajectory

Optimal control

50 cm

Hit

Target errors

(Todorov and Jordan, 2002)
Optimal Feedback Control predicts flexible use of feedback

A

Two cursor

One cursor

B

Perturb left limb DOES NOT affect right limb

Perturb left limb DOES affect right limb

Diedrichsen, Current Biology (2006)
Spinalized Turtle Wiping Reflex

Field-Fote and Stein JNP 78:1394-1403, JNP
Spinalized Turtle Wiping Reflex

Field-Fote and Stein JNP 78:1394-1403, JNP
If optimal feedback control is a good model of voluntary control, then features of this control should be present in neural circuitry (Scott, Nat. Rev. Neurosci. 2004)
Primary Motor Cortex (M1) contributes to

Voluntary Control

Visual-Guided Reaching

Long-Latency (LL) Reflexes

Mechanical Perturbation

Wrist Angle

EMG

50 ms
Primary Motor Cortex (M1) contributes to

Voluntary Control

Long-Latency (LL) Reflexes

Visual-Guided Reaching

Mechanical Perturbation
Feedback Matters for Voluntary Control!

Study stretch responses to probe voluntary control

Single-Joint Perturbation

Short-latency response: Spinal
Long-latency response: Spinal and Cortical

Proprioceptive Feedback
Visual Feedback

Short-Latency Reflex
R1
R2
R3
100 ms
50 ms
100 ms

Long-Latency Reflex

Voluntary (R4)

Step-Torque Perturbation

Proprioceptive Feedback
Visual Feedback
Feedback corrections depend on the behavioural goal

Localized

Room for error along the bar
Feedback corrections depend on the behavioural goal

Localized

Room for error along the bar
Online corrections are influenced by the goal

Optimal control Model

Joe Nashed

Start Target
End Target
Online corrections are influenced by the goal

Optimal control Model

Note the dispersion

Start Target

End Target

Joe Nashed
Online corrections are influenced by the goal

Optimal control Model

Note the dispersion

Load ON

Load

Time
Online corrections are influenced by the goal

Optimal control Model

Exemplar Subject

Note the dispersion
The shape of the goal influences the long latency response

Hand Paths

(Elbow Flexor)

Nashed et al. (2012)
The shape of the goal influences the long latency response

Nashed et al. (2012)
What if the player gets hit sideways?
How do you move to a goal?
Cost-to-go defines how to best reach a goal.

Cost-to-go: Is the total remaining cost (i.e. accuracy, energy..) given the current state.
How do you move to a goal?

Cost-to-go defines how to best reach a goal

**Cost-to-go**: Is the total remaining cost (i.e., accuracy, energy..) given the current state

\[ J_1 < J_2 \]
How do you move to a goal?
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\[
J_1 < J_2
\]
How do you move to a goal?
Cost-to-go defines how to best reach a goal

**Cost-to-go**: Is the total remaining cost (i.e. accuracy, energy..) given the current state
Reach to target with peripheral obstacles

Optimal Feedback Control Model

Load applied to both joints

Target

Obstacle

\( \tau_e \)

\( \tau_s \)

\[ \text{Bkg Load} \quad \text{Perturbation} \]

\begin{align*}
2 \text{Nm} \\
1 \text{Nm} \\
0.5 \text{Nm} \\
0 \text{Nm} \\
-0.5 \text{Nm}
\end{align*}

\[ \text{Time} \]

\[ \Delta \text{Applied Torque (Nm)} \]

5 cm

0.75 \text{Nm}

Large Perturb

Medium Perturb

Small Perturb

Unperturbed

Small Perturb

X

Y

Applied Load

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Reach to target with peripheral obstacles

Exemplar Subject

Large Perturb | Medium Perturb | Small Perturb | Unperturbed | Small Perturb

Optimal Feedback Control Model

Large Perturb | Medium Perturb | Small Perturb | Unperturbed | Small Perturb

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Online “decisions” made in 60ms

Triceps Lateral

(Elbow Extensor)

Time (ms)

\( \Delta \text{EMG (au)} \)

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Feedback Elicits Task Selection

Joint Motion

Perturbation Onset

"Resist"

"Let Go"

100ms

100uv

Muscle Activity

Voluntary (R4)

Long-Latency Reflex

Short-Latency Reflex

R1

R2

R3

"Resist"

"Let Go"

100ms

Rothwell et al., 1980

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Feedback for Rapid Task Selection

Spatial Analog of Resist/Let Go

Rapid Motor Responses are Goal-Directed

Load Applied and Must Move to Spatial Target

Andrew Pruszynski

Binned Analysis

Mean EMG (au)

Pruszynski et al., JNP 2008
When do corrective responses consider limb mechanics?

Limb mechanics causes interactions between shoulder and elbow

1. Possible Perturbations
   - Shoulder Torque
   - Elbow Torque

2. Resultant Motion
   - Shoulder Angle
   - Elbow Angle

3. Motor Response
   - Shoulder Torque
   - Elbow Torque

What perturbation caused this motion?
Do rapid motor responses (reactions) have knowledge of limb mechanics?

Kurtzer et al., Current Biology, 2008
Same shoulder motion, different underlying torques

Muscle Activity

Shoulder Extensor Muscle (PD)

Joint Trajectories

EMG (au)
Knowledge of Limb Mechanics

No Shoulder Motion, Opposite Shoulder Torques

Flexor Perturbations
Stumble corrective response is distinct from locomotion

Locomotor pattern

Stumble corrective response
Postural Task: Perturbation responses present for very small perturbations

Muscle stretched: Short-latency response
Muscle not stretched: Long-latency response

Crevecoeur et al., J Neurophysiol (2012)
Neural Basis of Voluntary Feedback Control

Functional Properties

- Muscle Stretch
- Termination of RMR
- Compensate for Gain Scaling
- Knowledge of Limb Mechanics
- Task Dependency (Bimanual)
- Spatial Target Properties
- Spatial Target Location
- Redirect around Obstacles
- Modified during Motor Adaptation

SL  LL  Early Vol

TRANSCORTICAL

SPINAL
Record individual neurons in Primary Motor Cortex (M1) as they perform behavioural tasks
Perturbation Response during Postural Control

Motor Cortex Cell

Hand Trajectories

Herter et al., JNP 2008
Perturbation Response during Postural Control

Motor Cortex Cell

Neuron 49032c

Hand Trajectories

Activity (spikes/s)

Time (ms)

Herter et al., JNP 2008
Perturbation Response during Postural Control

Population Responses

- S1
- M1
- PMd

Time (ms)
0 50 100 150 200 250
0 20 40 60 80
Firing Rate (Hz)

Time (ms)
0 10 20 30 40
0 2 4 6 8
ΔFiring Rate (Hz)

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Same shoulder motion, different underlying torques

Muscle Activity

Shoulder Extensor Muscle (PD)

Joint Trajectories

EMG (au)

Time (ms)

Shoulder Torque

Elbow Torque

Joint Angle (deg)

Time (ms)

-3

-2

-1

0

1

2

3

-25

0

25

50

R1 R2 R3

Time (ms)

-50

0

50

100

150

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Record Shoulder-related neurons during perturbations

Andrew Pruszynski

Firing Rate (Hz)

Exemplar Shoulder-Like Neuron

Shoulder Torque

Elbow Torque

Neural Population

Sensitivity to Underlying Torque

Pruszynski et al., Nature, 2011
How Does Behavioural Goal Change Feedback?

Postural Control

Watch Movie

Examine muscle and neural activity across two tasks
Stretch response reduced 50% in Movie task
Task-dependent Change in Perturbation Related Activity in M1

Cell #1
Large task effect

Cell #2
Medium task effect

Cell #3
No task effect
MI stretch response decreases 40% in Movie Task

Perturbation response (40 to 80 ms)
- Monkey P
- Monkey X

Region of analysis

Movie (spikes/s)
- Posture (spikes/s)
- Time (ms)
Perturbation Responses

S1 - Primary Somatosensory Cortex
A5 - Parietal Area 5
M1 - Primary Motor Cortex

Discharge (spikes/s)

Time (ms)

Spinal Cord

S1 - Primary Somatosensory Cortex
A5 - Parietal Area 5
M1 - Primary Motor Cortex

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Feedback for Rapid Task Selection

Spatial Analog of Resist/Let Go

Load Applied and Must Move to Spatial Target

Pruszynski et al., JNP 2008

Andrew Pruszynski

**Binned Analysis**

<table>
<thead>
<tr>
<th>Epoch</th>
<th>Pre</th>
<th>R1</th>
<th>R2</th>
<th>R3</th>
<th>Vol</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean EMG (au)</td>
<td>0</td>
<td>10</td>
<td>20</td>
<td>30</td>
<td>40</td>
</tr>
</tbody>
</table>

Pruszynski et al., JNP 2008
Goal-Directed Responses in Motor Cortex

Primary Motor Cortex

dorsal Premotor Cortex

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Neural Implementation of OFC-like control

Task Selection \rightarrow \text{Optimal Feedback Control Policy} \rightarrow \text{Motor Commands}

Optimal State Estimation \rightarrow \text{Sensory Feedback}

Motor Commands \rightarrow \text{Efference Copy}

Cutaneous & Muscle Afferents

Controlled Plant

Spinal Cord - basic stretch, gain scaling,

Basal Ganglia

Cerebellum

SMAPF PP dPM vPM

PP A5 S1

M1
dPM

Scott, TICS 2012

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Neural Implementation of OFC-like control

Traditional view of stretch response pathways
Neural Implementation of OFC-like control

Task Selection → Optimal Feedback Control Policy → Motor Commands

Optimal State Estimation

Efference Copy → Sensory Feedback

Controlled Plant

Spinal Cord - basic stretch, gain scaling, termination

Sensory Feedback: Cutaneous & Muscle Afferents

Scott, TICS 2012
Neural Implementation of OFC-like control

Task Selection  →  Optimal Feedback Control Policy  →  Motor Commands

Optimal State Estimation

Motor Commands

Sensory Feedback:
Cutaneous & Muscle Afferents
Controlled Plant: Spinal Cord - basic stretch, gain scaling, termination

Basal Ganglia

PP  PP  dPM  vPM  SMA

Spinal Cord

Sensory Feedback: Cutaneous & Muscle Afferents

Scott, TICS 2012
Neural Implementation of OFC-like control

Task Selection → Optimal Feedback Control Policy → Motor Commands

Optimal State Estimation

Sensory Feedback: Cutaneous & Muscle Afferents

Controlled Plant
Spinal Cord - basic stretch, gain scaling, termination

Sensory Feedback: Cutaneous & Muscle Afferents

Scott, TICS 2012
Neural Implementation of OFC-like control

Task Selection → Optimal Feedback Control Policy → Motor Commands

Optimal State Estimation

Sensory Feedback:
Cutaneous & Muscle Afferents

Controlled Plant
Spinal Cord - basic stretch, gain scaling, termination

Sensory Feedback: Cutaneous & Muscle Afferents

Basal Ganglia
PP PP dPM vPM SMA

Cerebellum
PP dPM A5 S1

M1

Scott, TICS 2012
Optimal Feedback Control (OFC) as a Theory of Voluntary Control

Stretch Responses Mirror Capabilities of Voluntary Control

Transcortical Feedback is Important for Voluntary Control

Take Home Message
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