The use of control theory to interpret biological motor control

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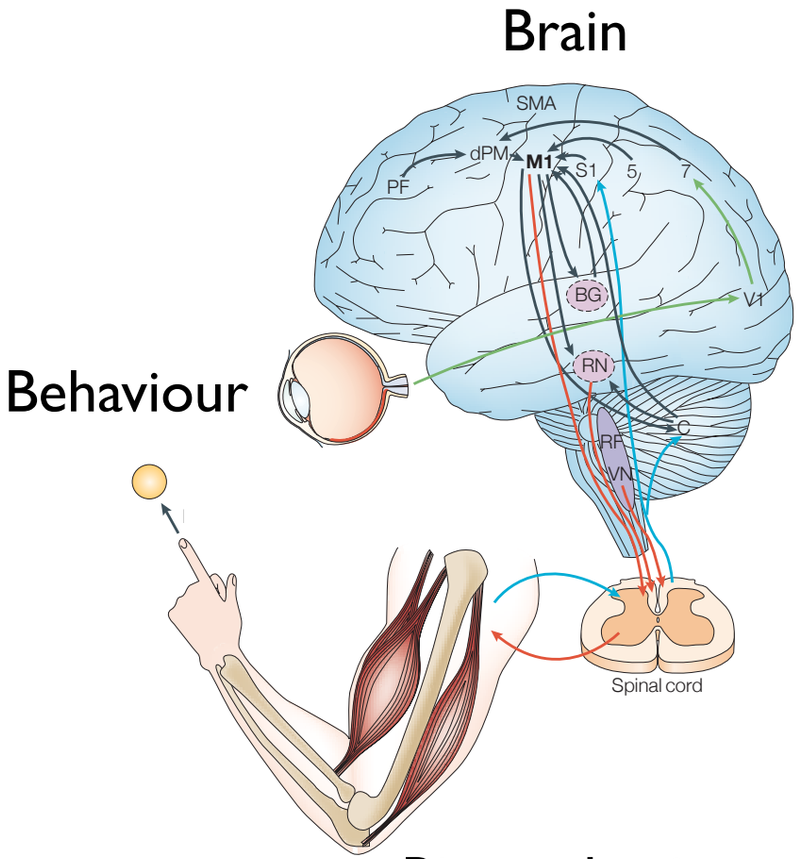
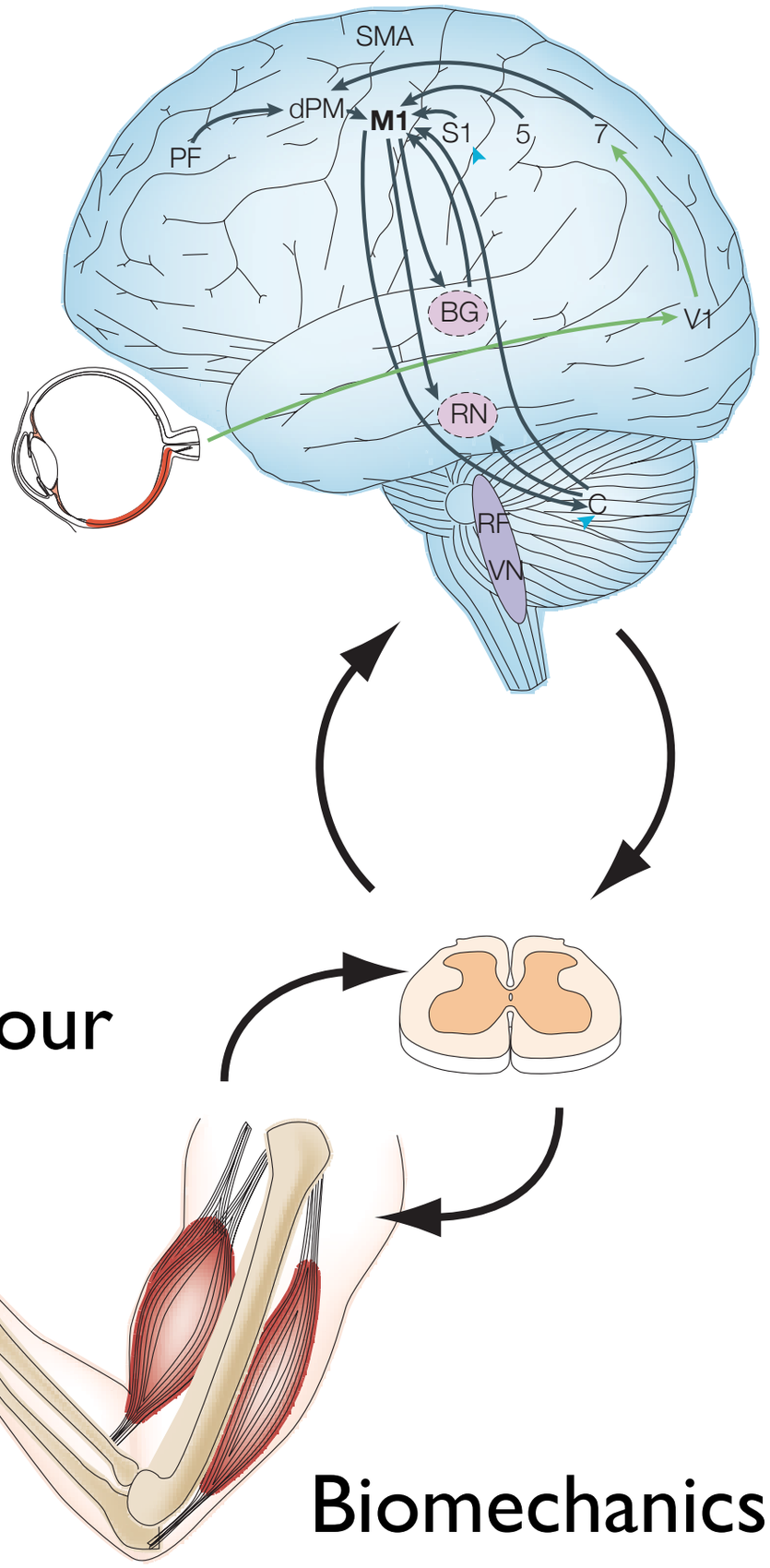
Objective: Understand function of primary motor cortex



- 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

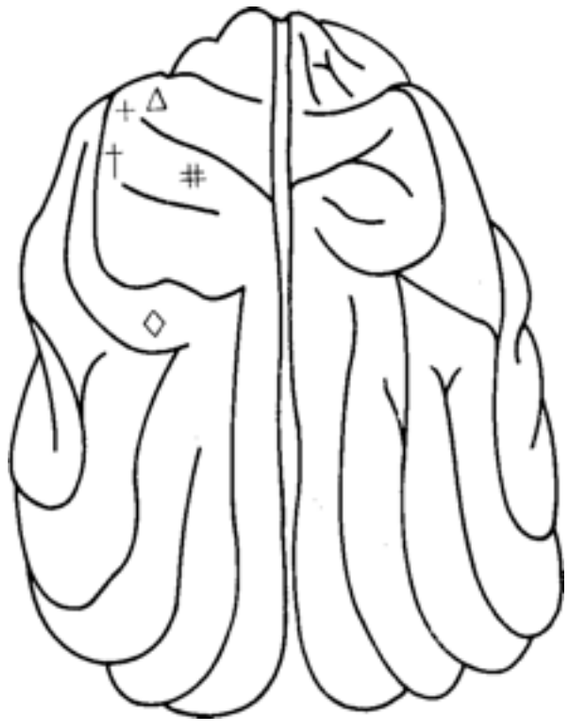


Take Home Message

- Optimal Feedback Control (OFC) as a Theory of Voluntary Control
- Stretch Responses Mirror Capabilities of Voluntary Control
- Transcortical Feedback is Important for Voluntary Control

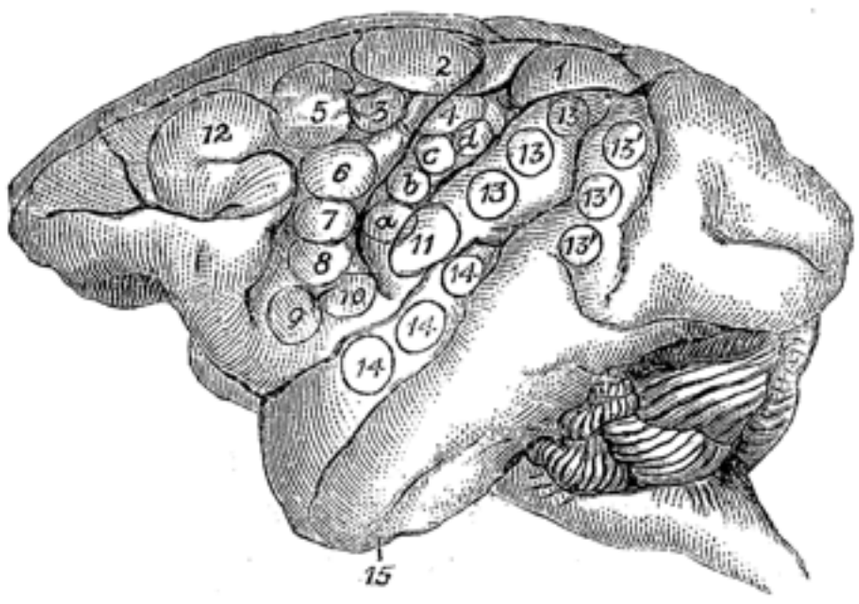
Reviews
Scott, Nature Reviews Neuroscience, 2004
Scott, TICS, 2012

Excitable cortex & evoked movements



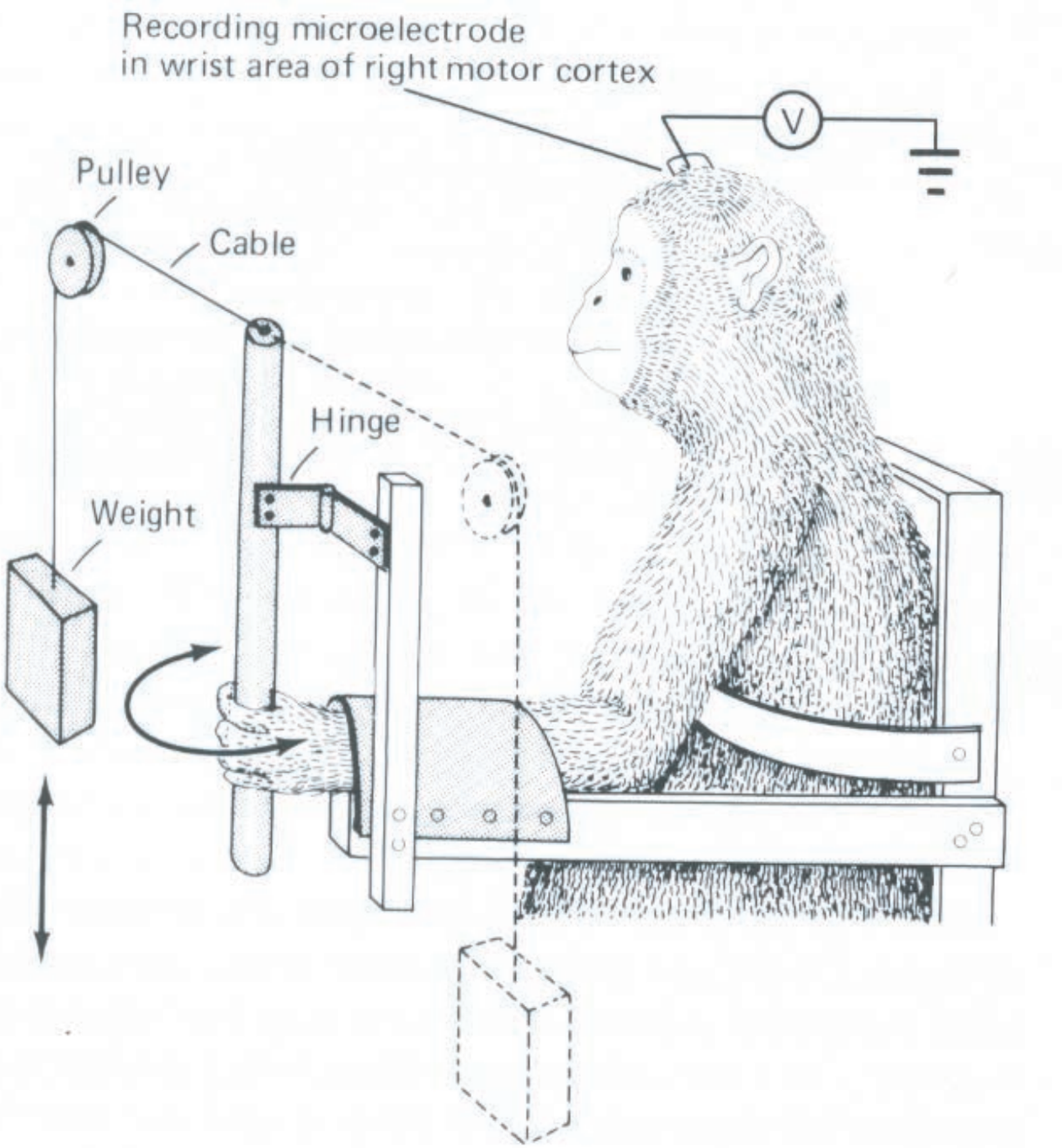
Eduard Hitzig & Gustav Fritsch (1870)

David Ferrier (1873)

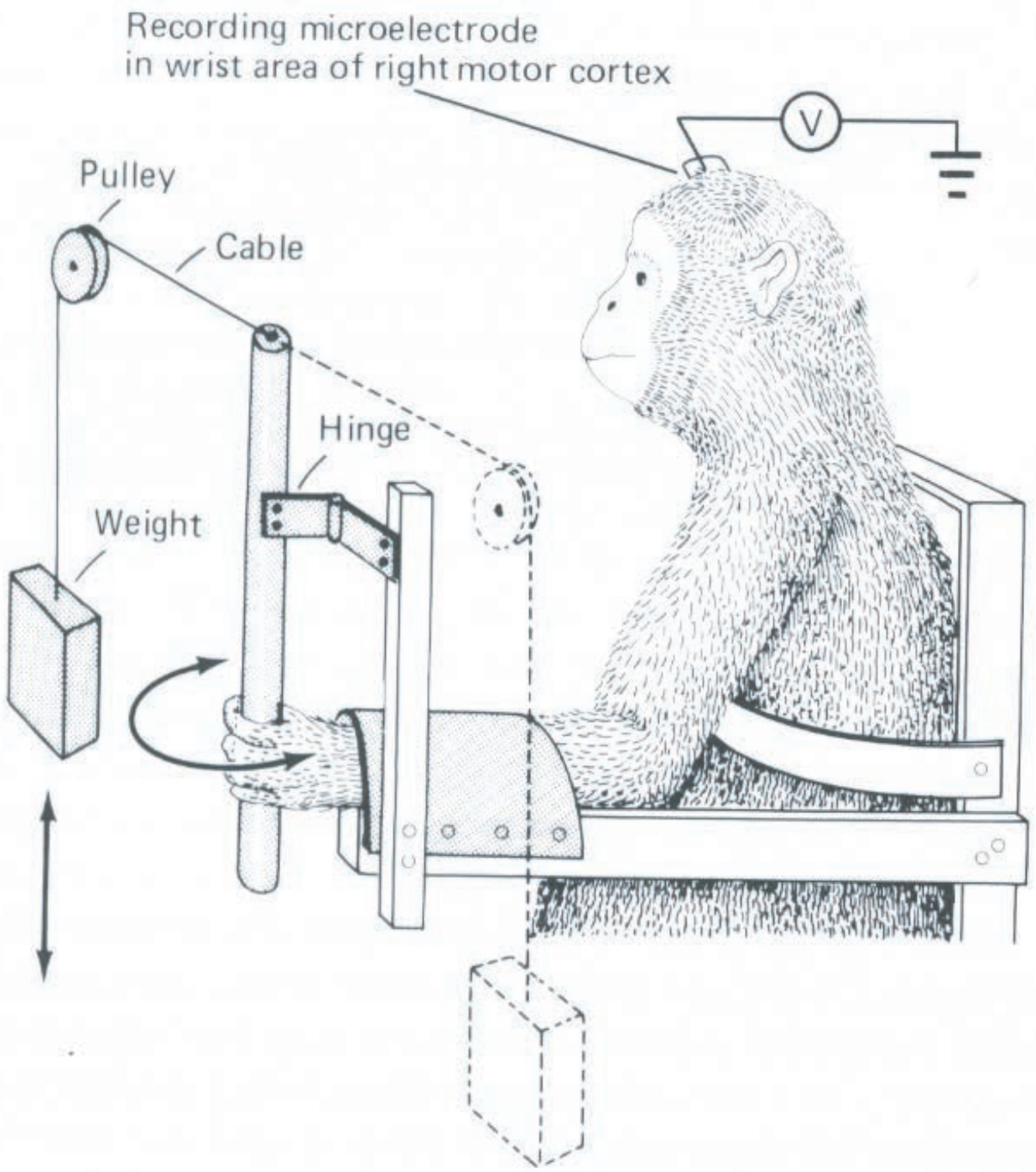


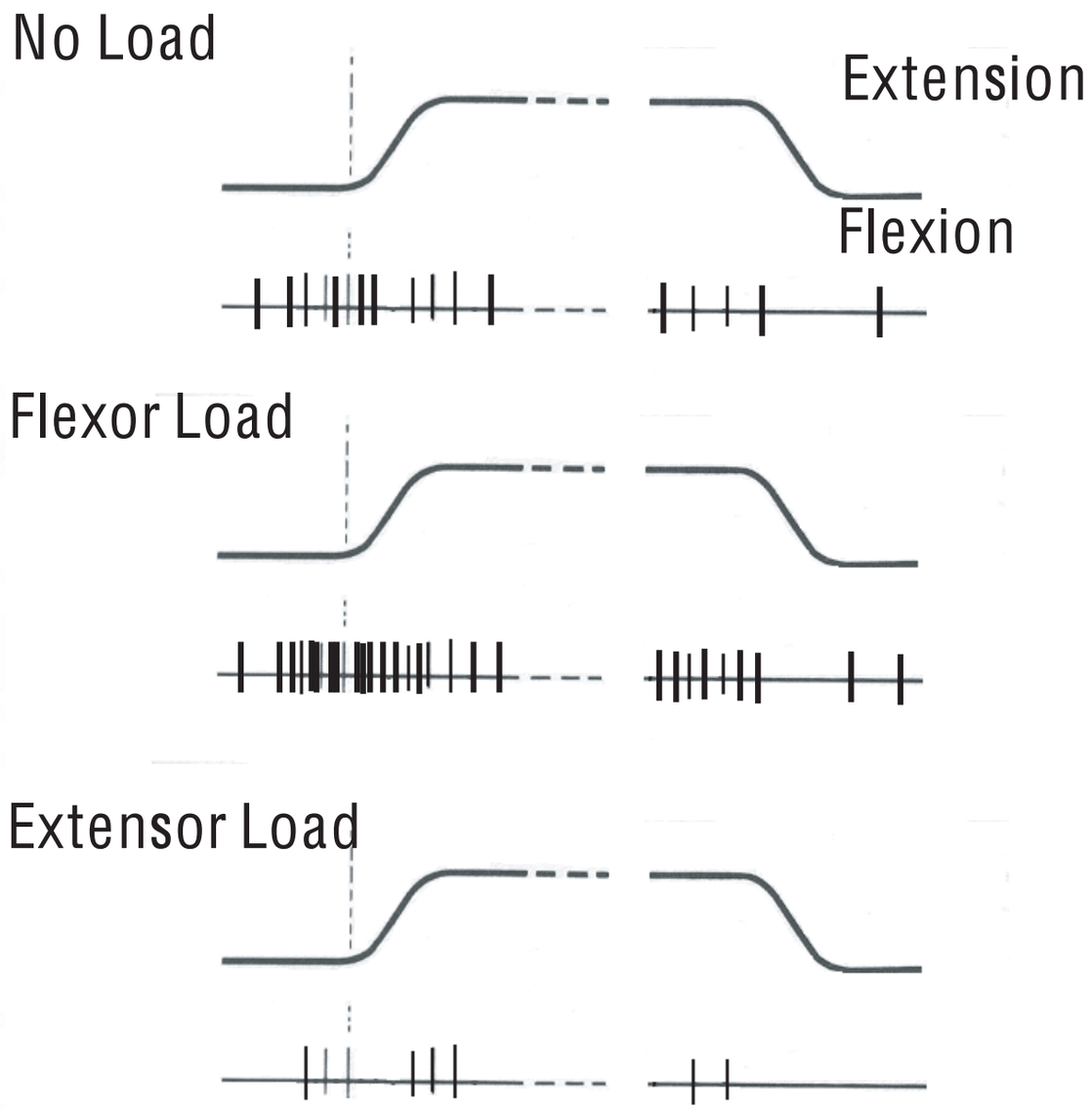
Primary Motor Cortex

Question: Muscles Versus Movements (1960s)

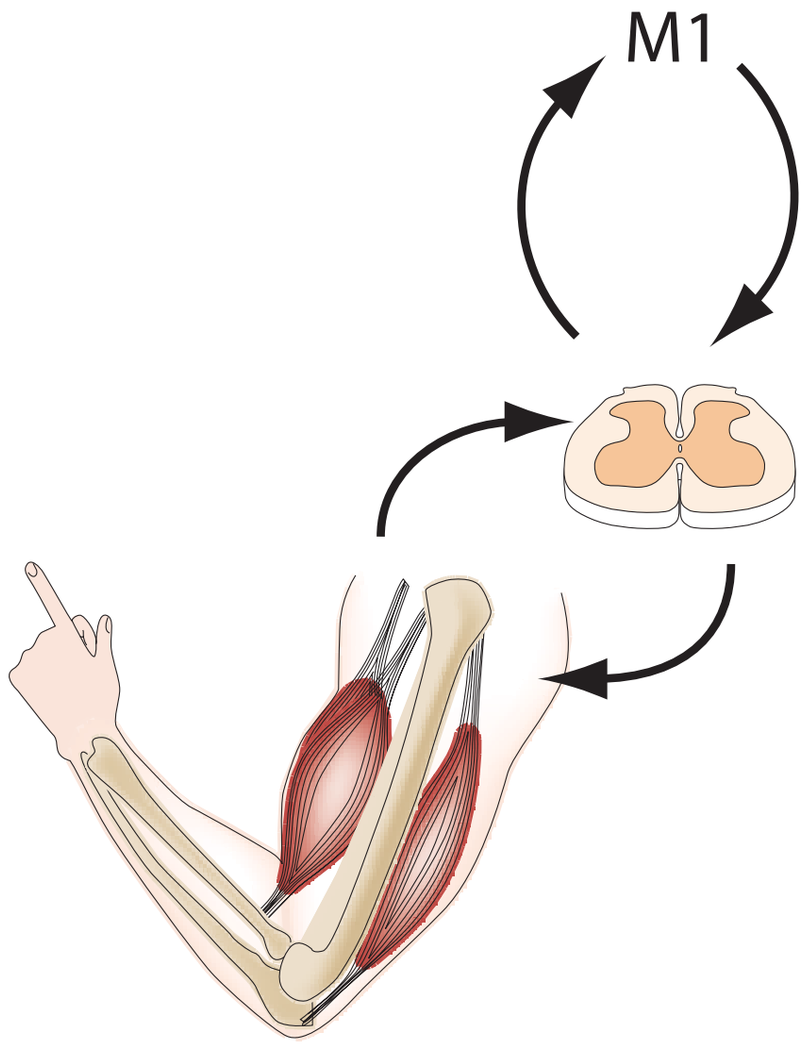


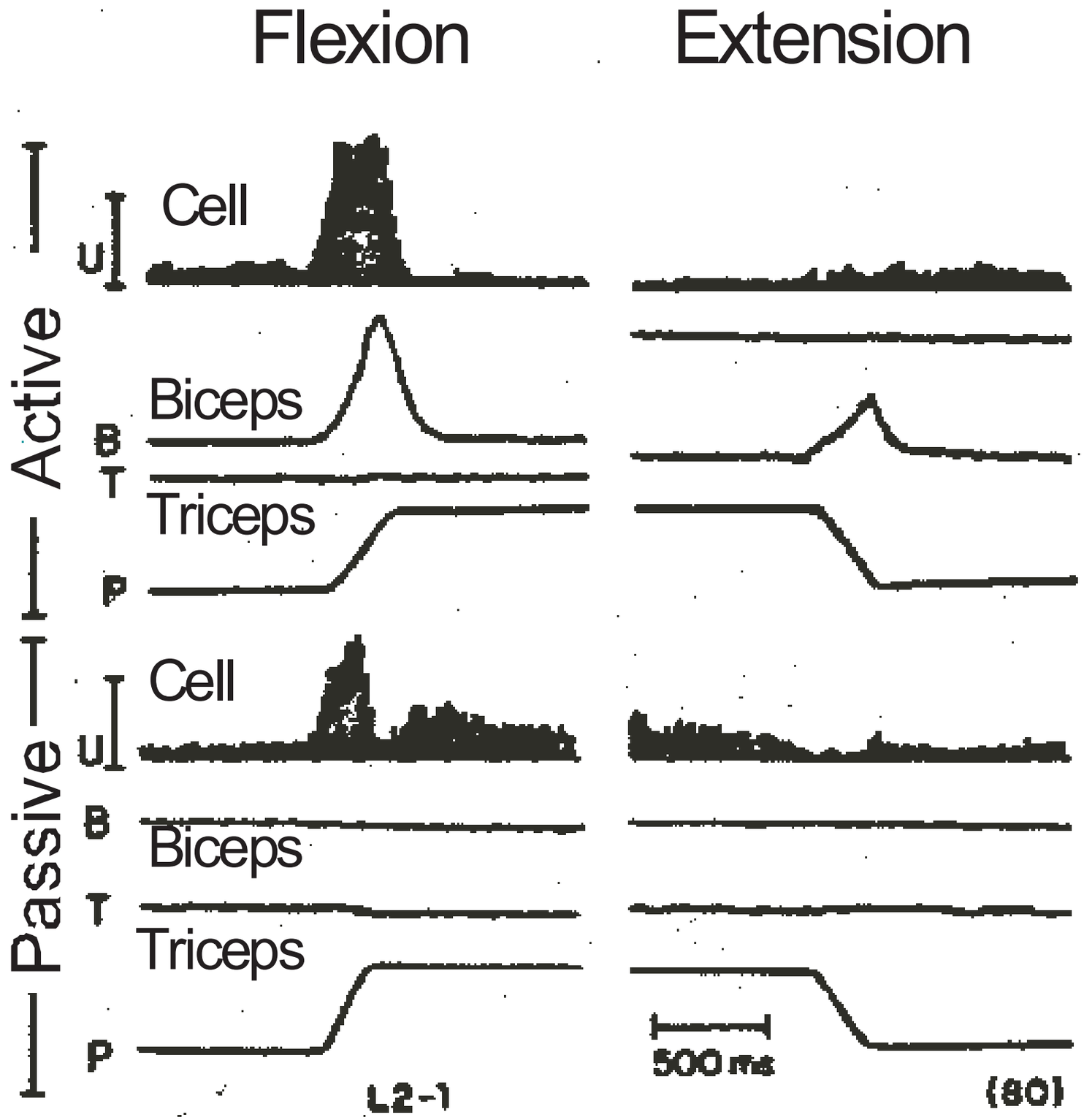
Primary Motor Cortex



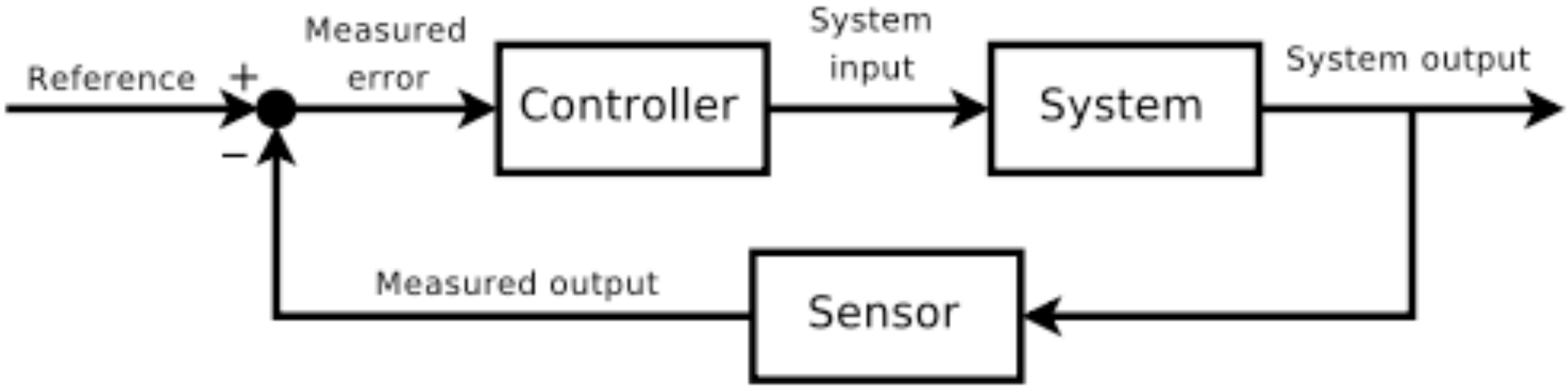


Primary Motor Cortex: Sensory Feedback

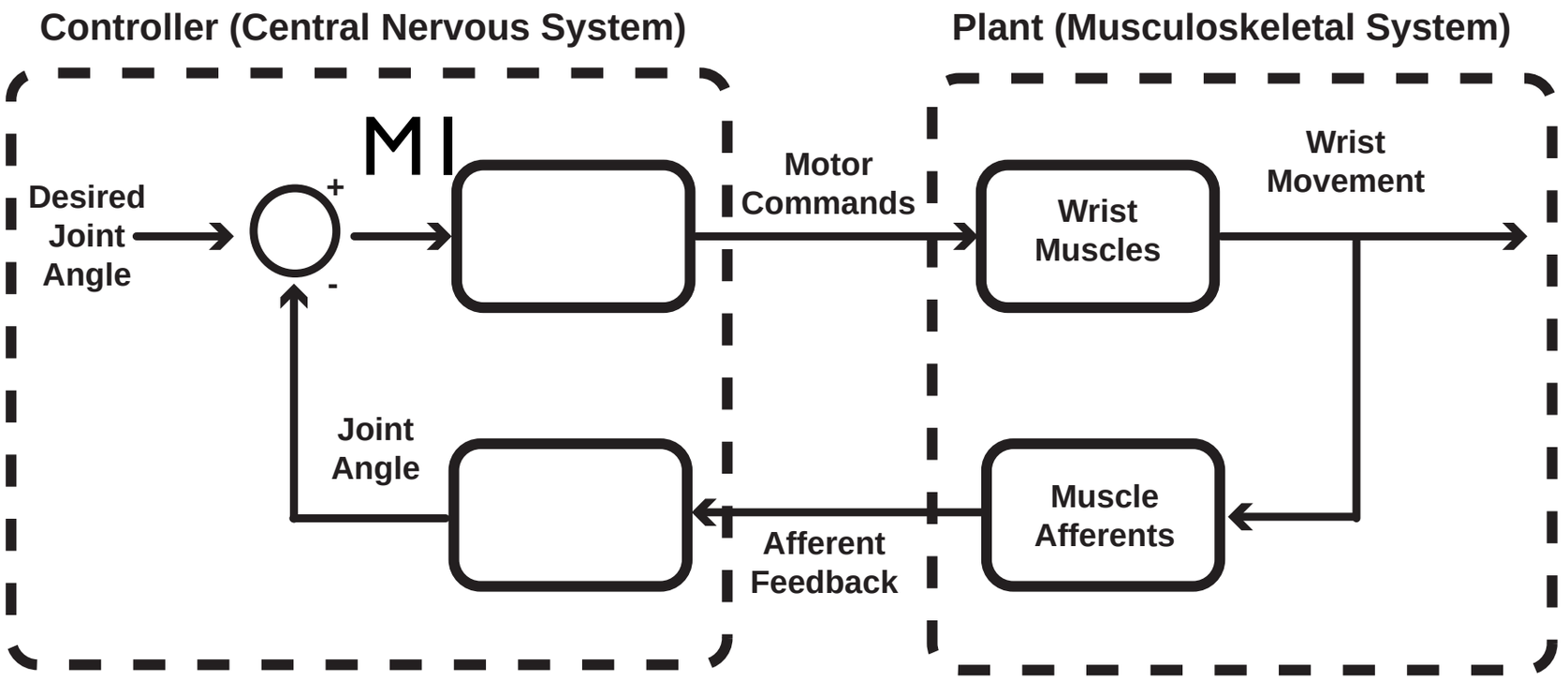




Basic Control Theory

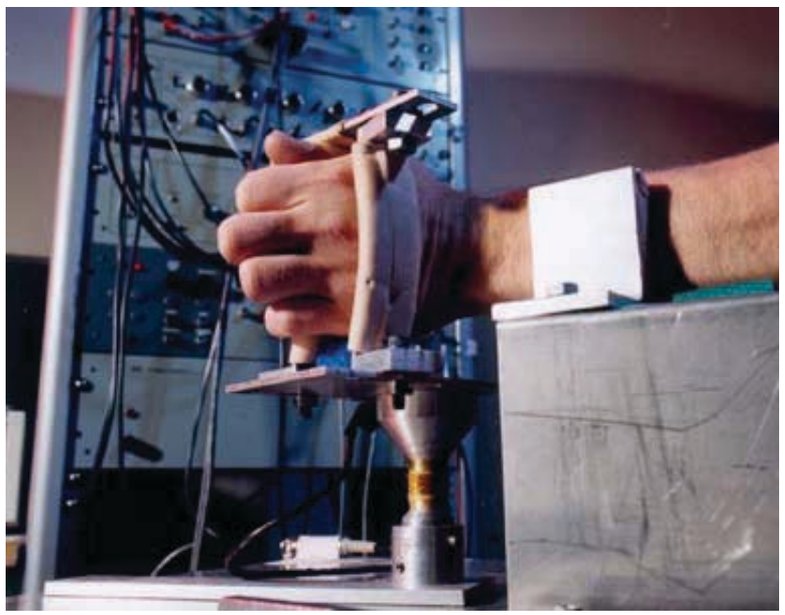


Biological Control: Control of Single-Joint wrist movements

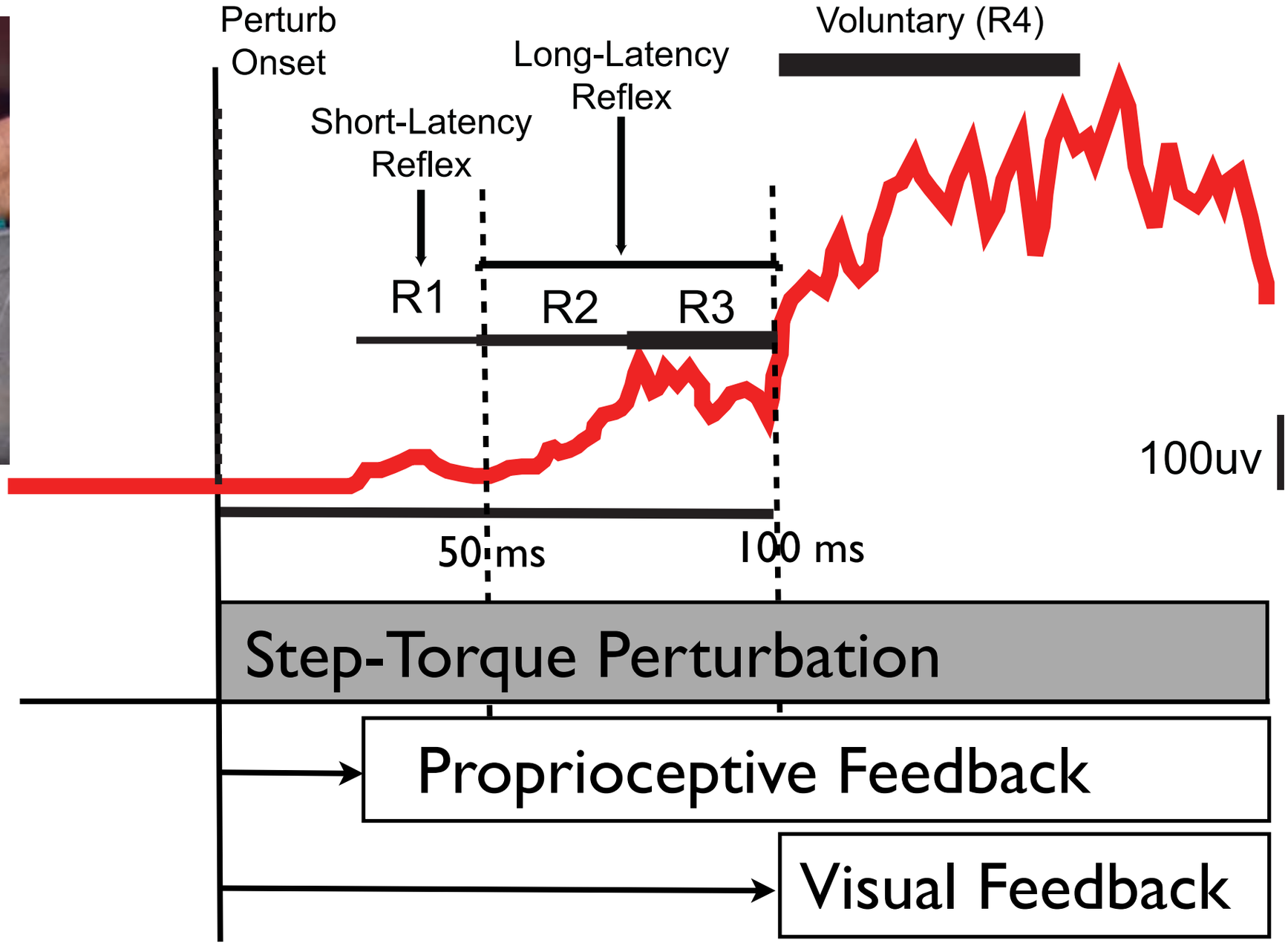


Mechanical Perturbations to Probe Feedback Control

Single-Joint Perturbation



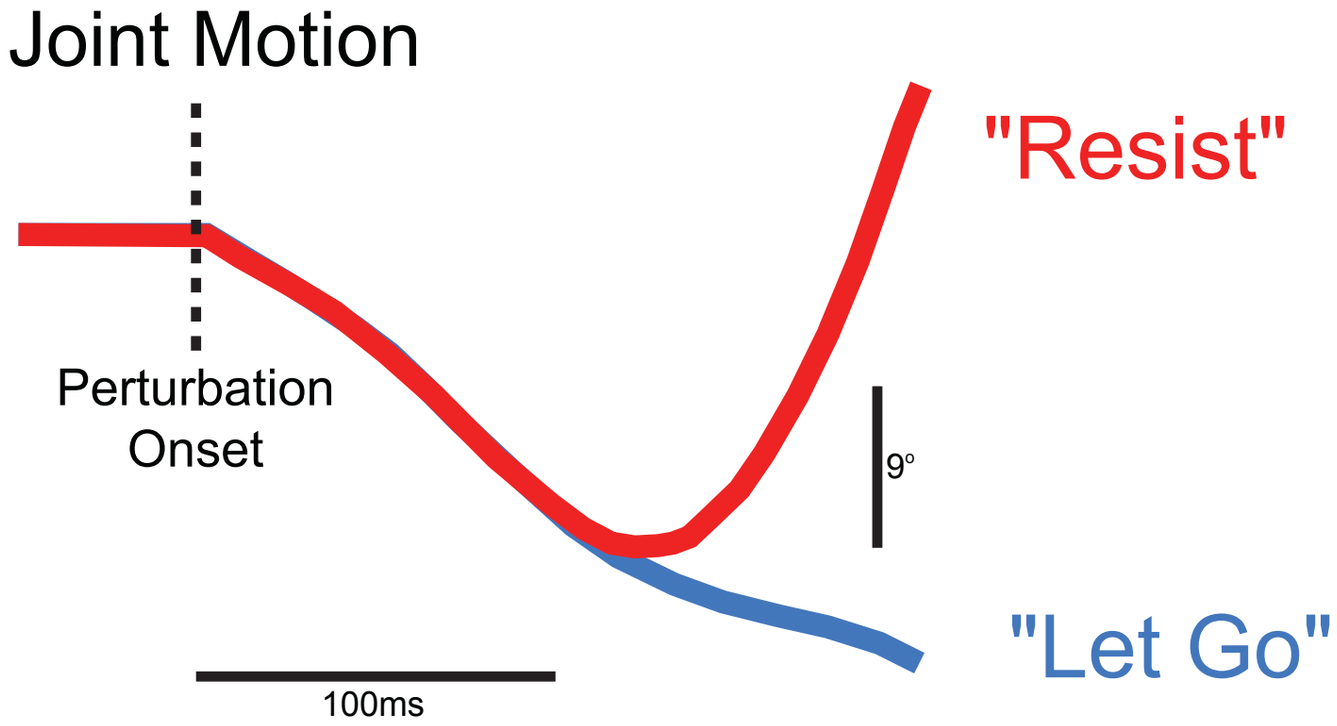
Stretch-Related Muscle Activity

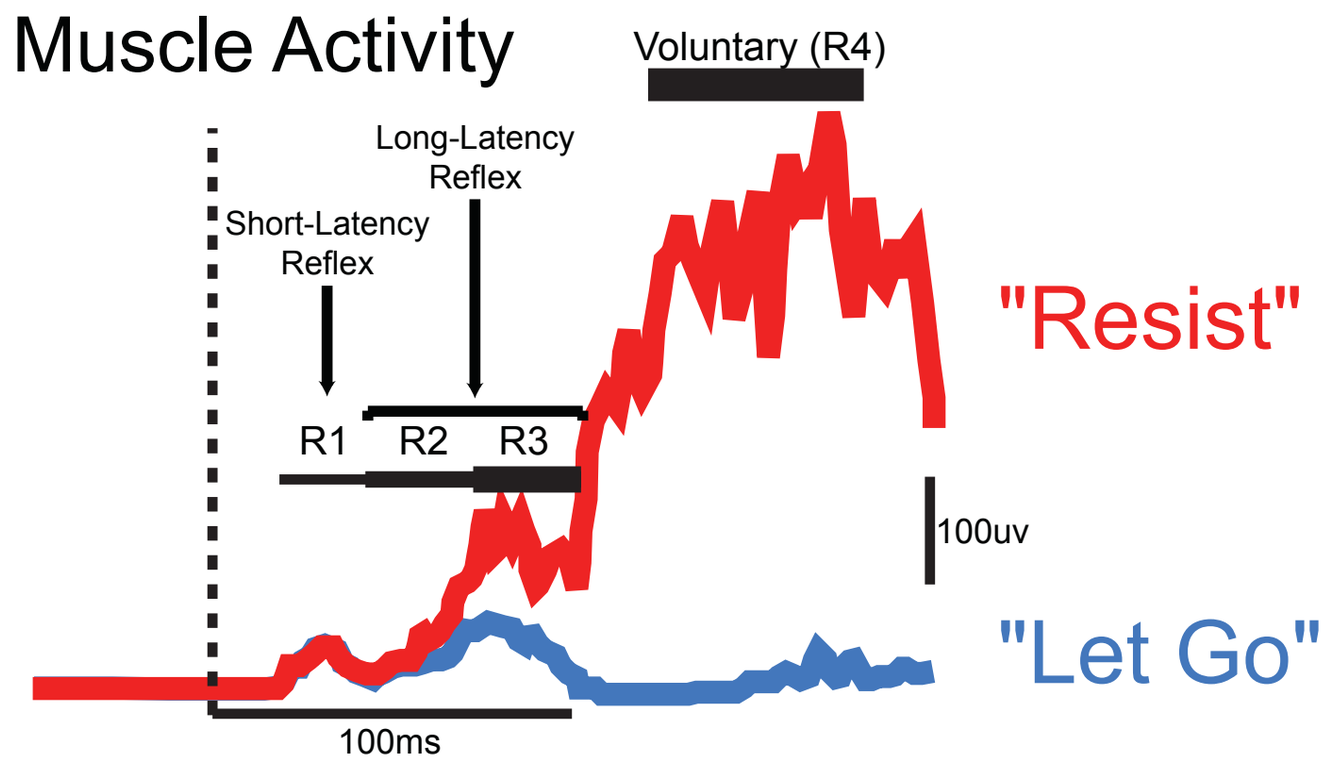


Short-latency response:
- Spinal

Long-latency response:
- Spinal and Cortical

Feedback Elicits Task Selection

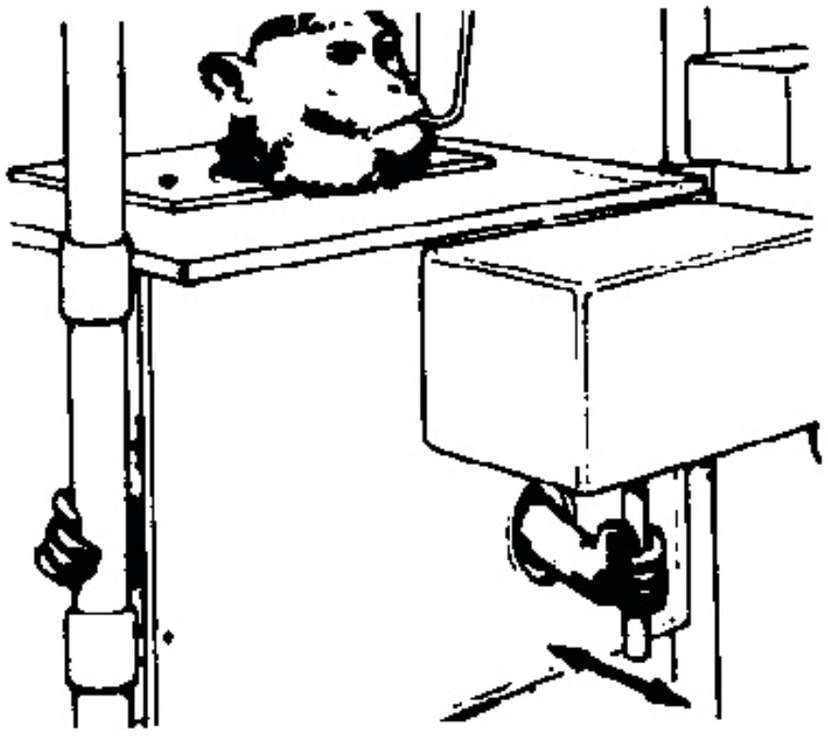




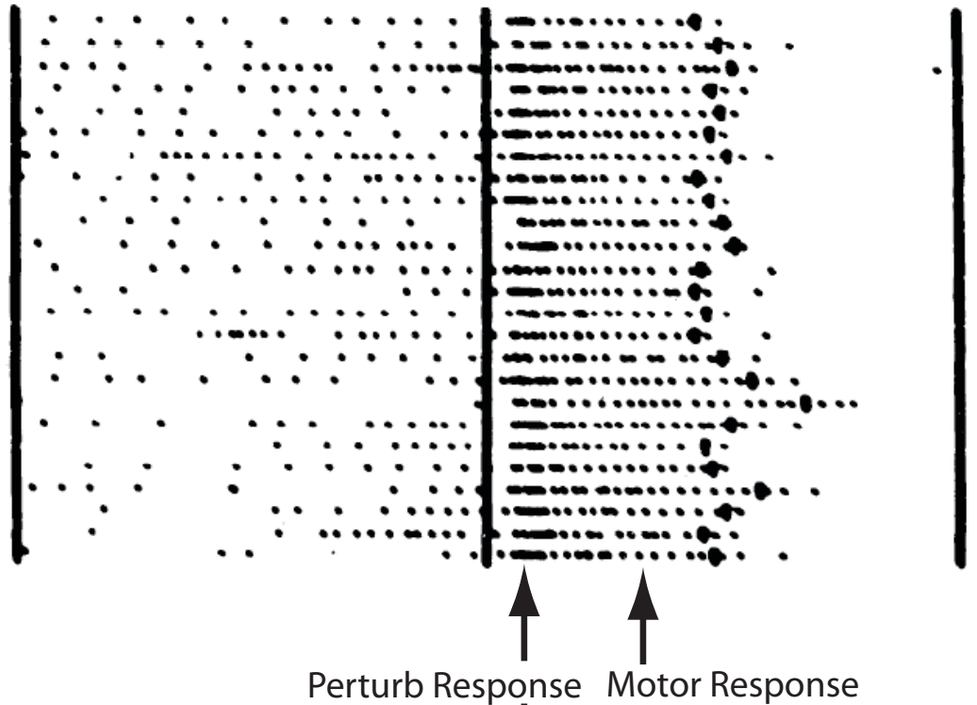
Rothwell et al., 1980

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

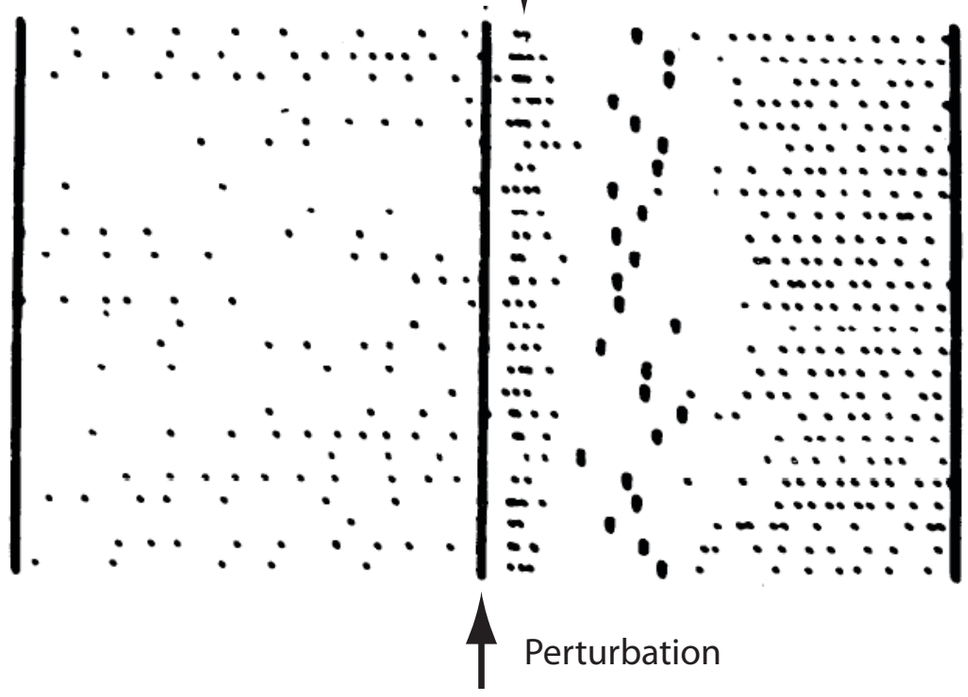
Perturbation away from body



Instruction: Pull



Instruction: Push



Evarts and Tanji, 1976

Hierarchical Model of Voluntary Control

Premotor Cortex

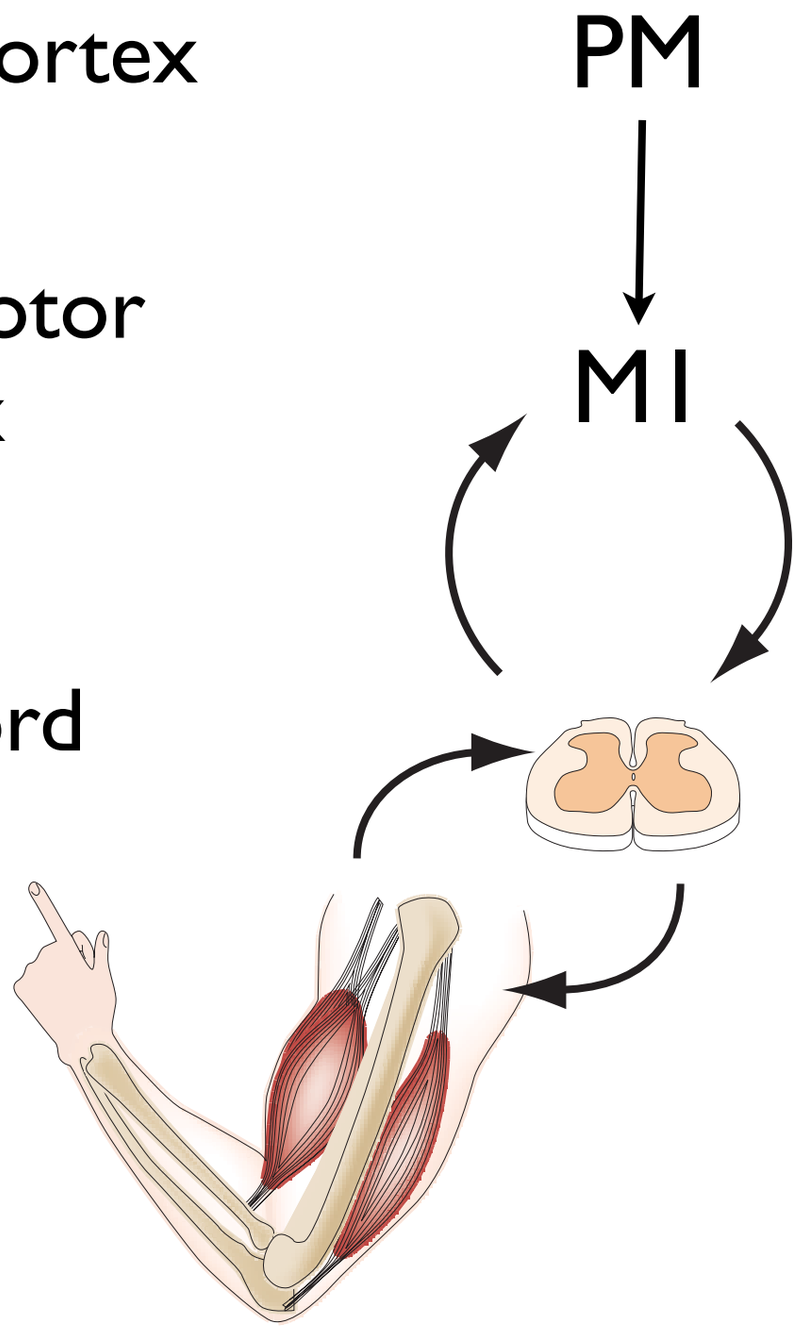
PM

Motor Planning:
Behavioural Goals (BG)

Primary Motor Cortex

M1

Convert BG into detailed patterns of motor output

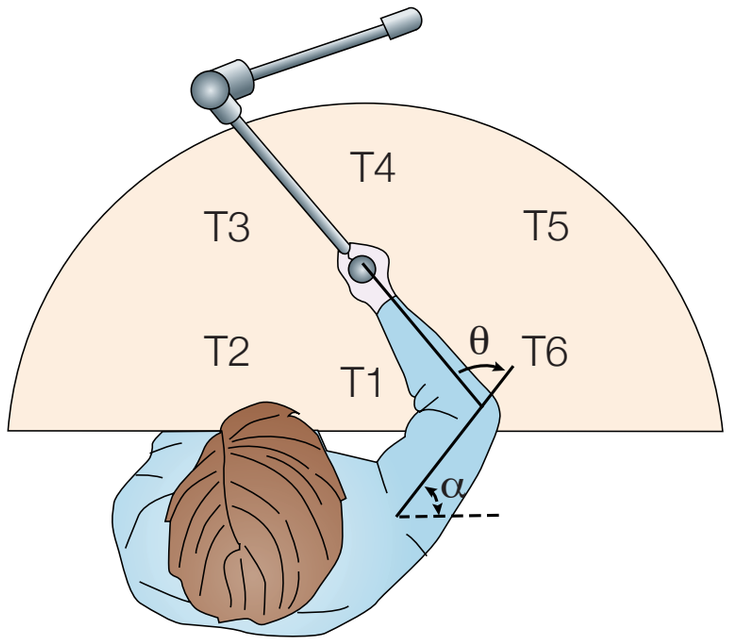


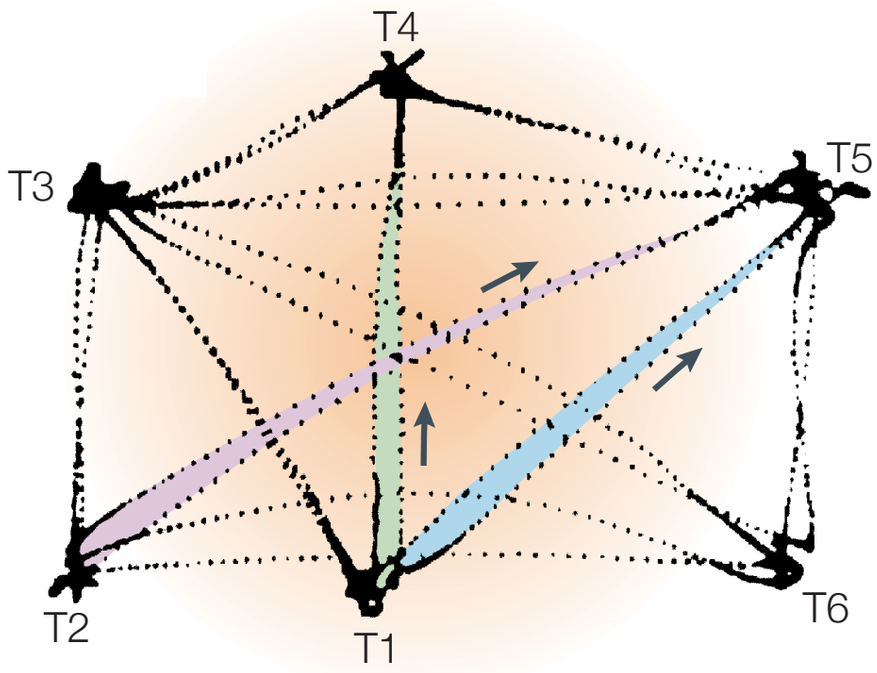
Spinal Cord

Low-level control

Inconvenient Truth about servo-control

- Delay in sensory feedback
- Intersegmental dynamics



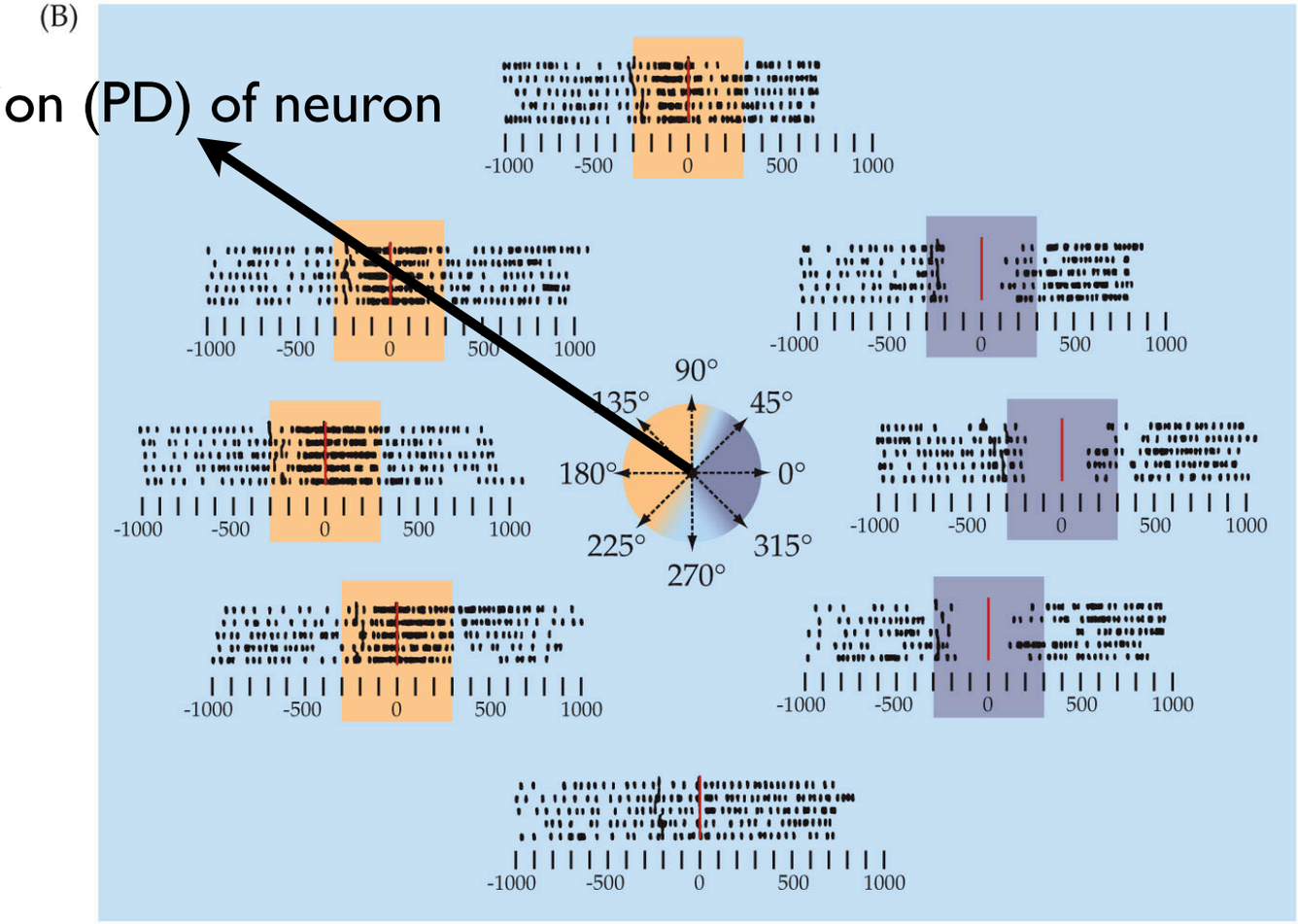


Conceptual Framework (1990s): Sensorimotor Transformations/ Coordinate Frames

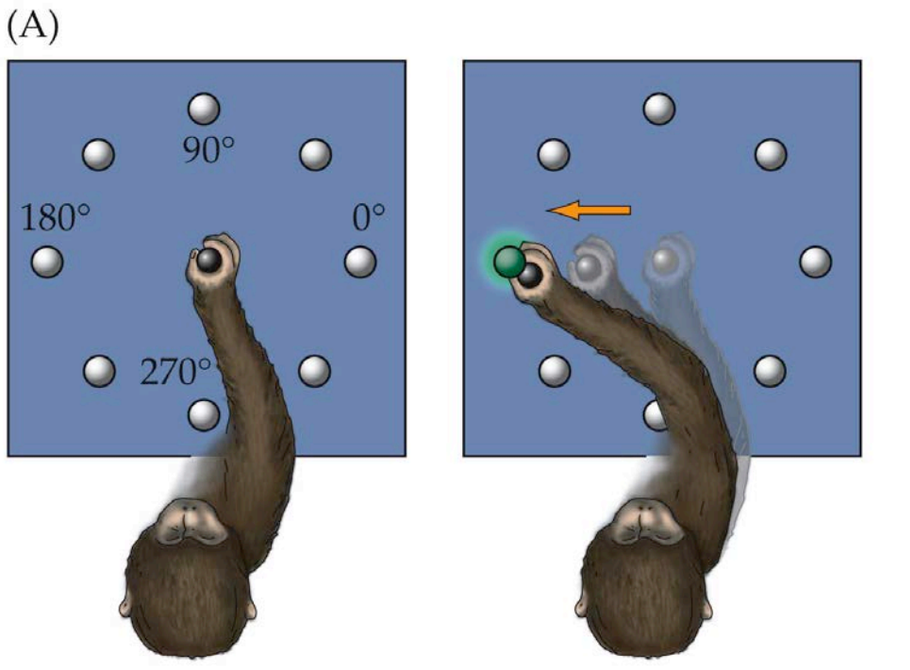
- inspired from visual system
- focus of feedforward control (open loop)
- provides penultimate goal, address control later

Obvious Question: What coordinates are represented in primary motor cortex (M1)?

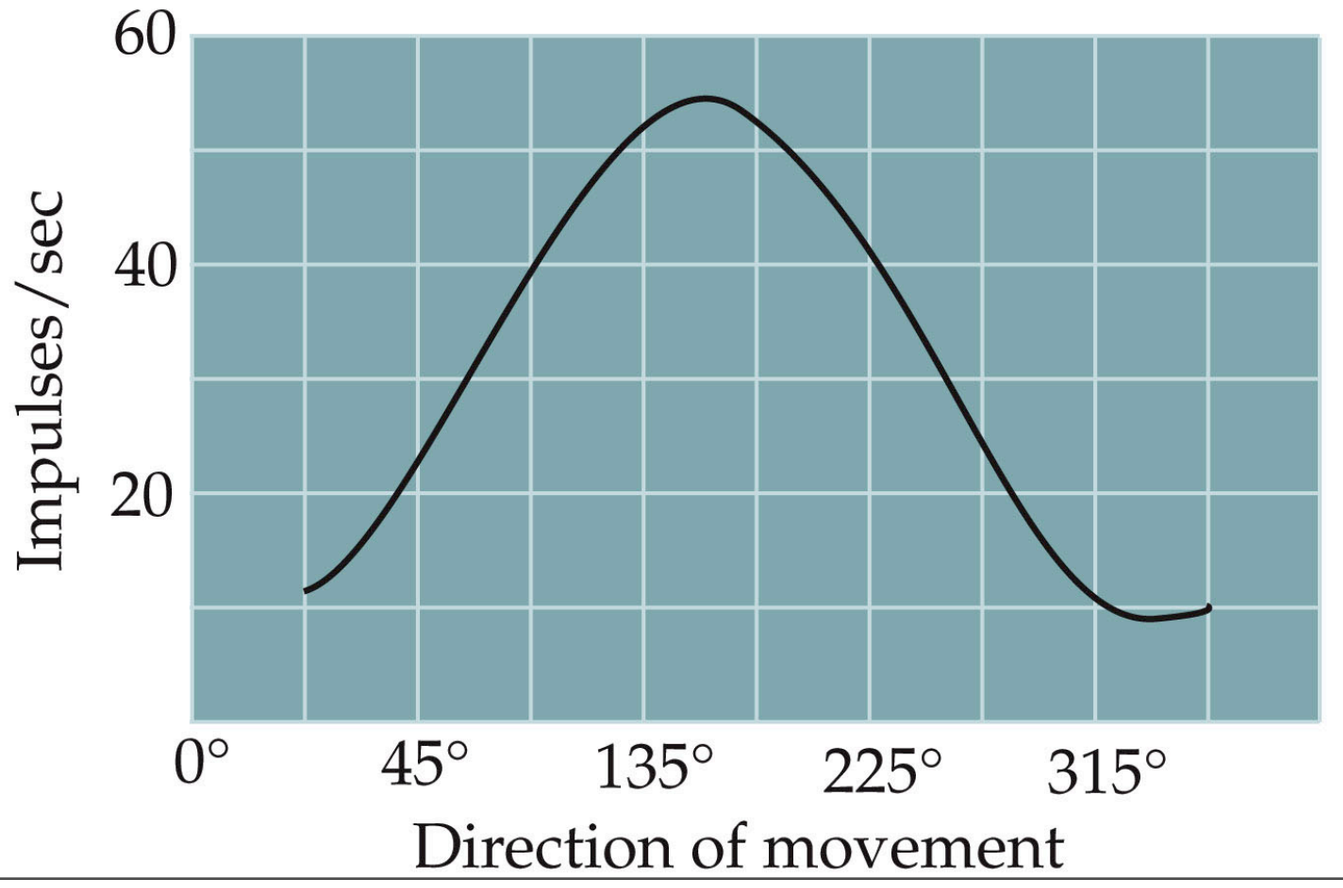
Activity of a neuron in primary motor cortex during centre-out reaching



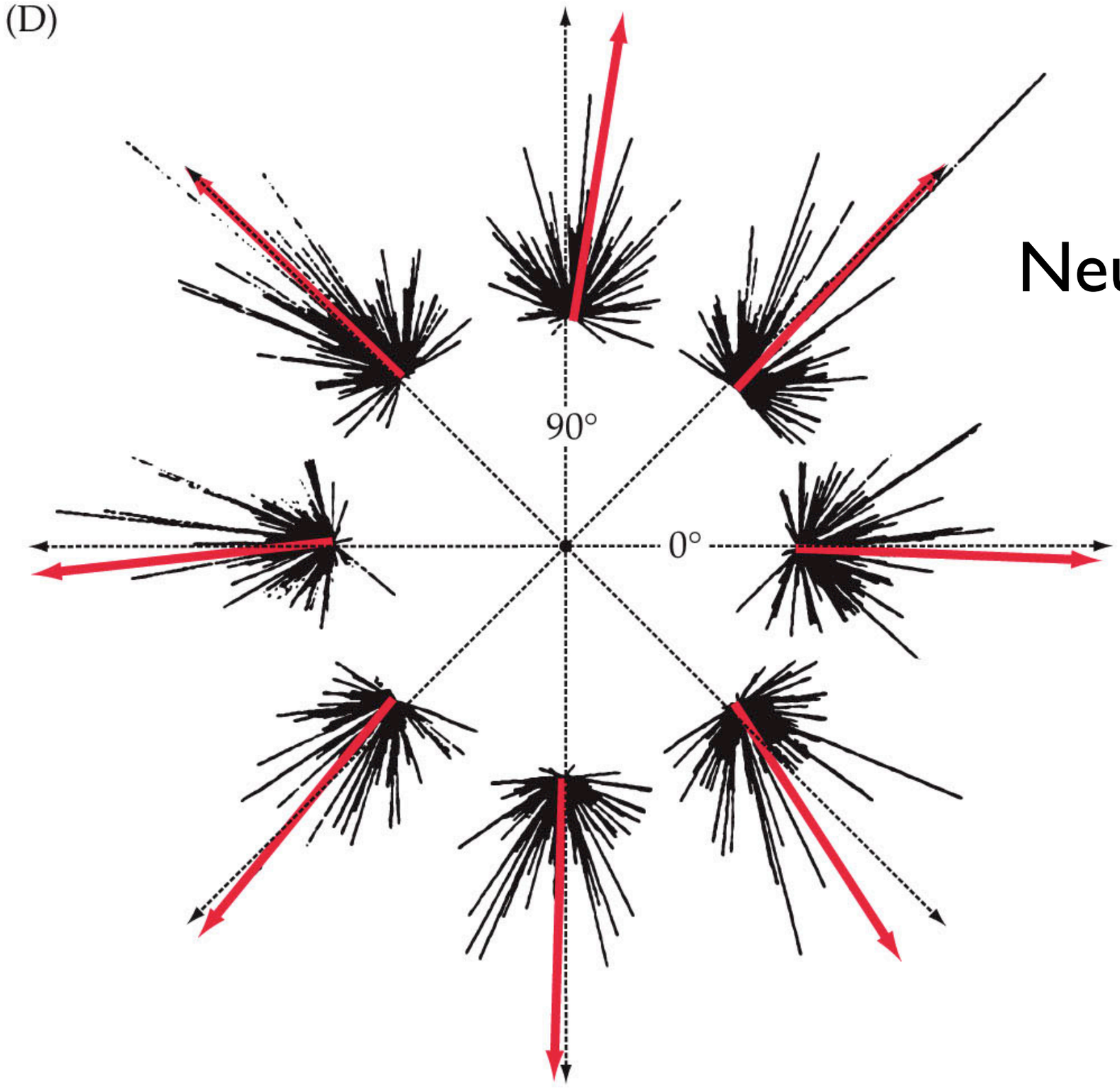
NEUROSCIENCE, Fourth Edition, Figure 17.13 (Part 2)



NEUROSCIENCE, Fourth Edition, Figure 17.13 (Part 1)

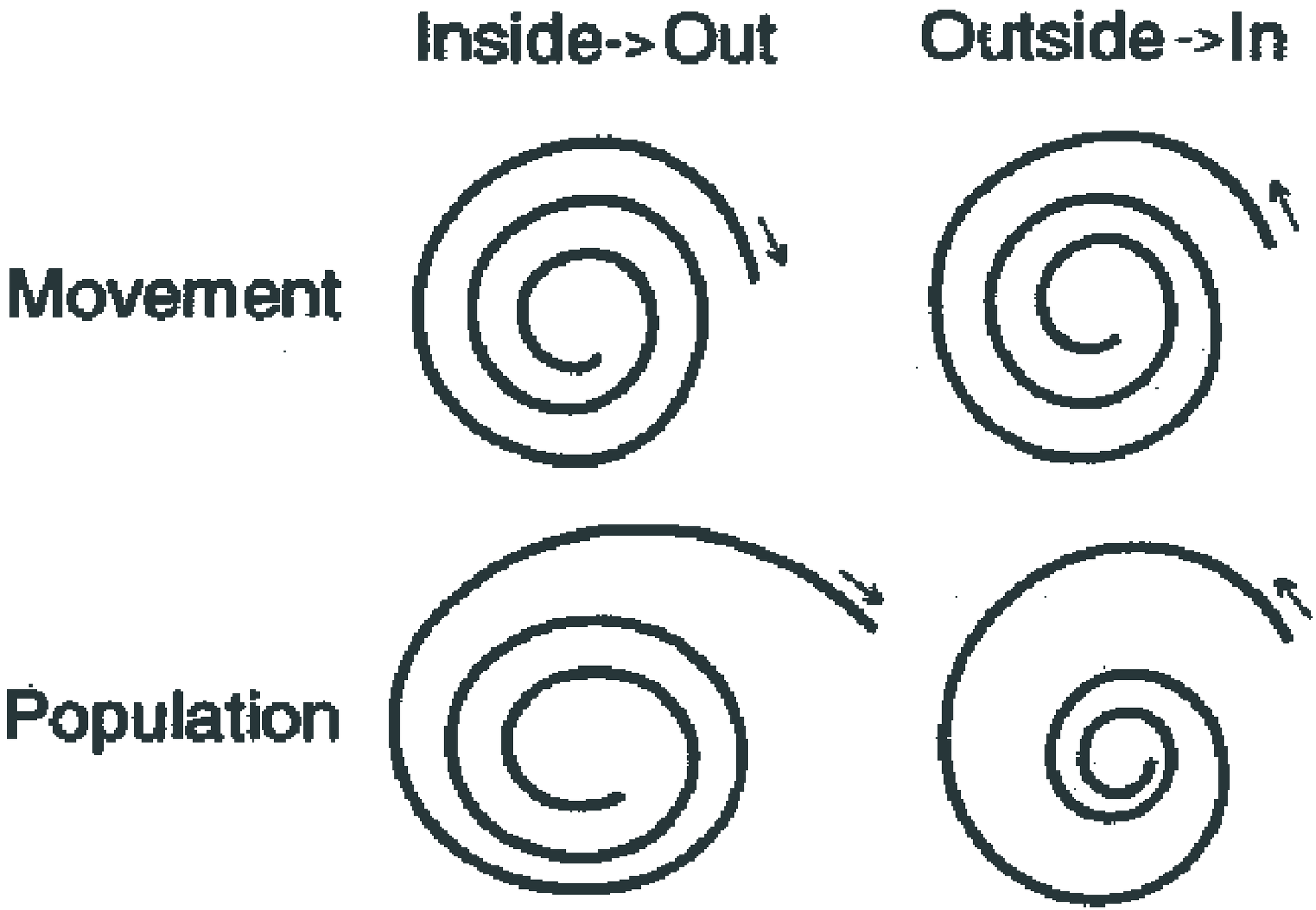


Population vectors (red) tend to point in the direction of hand motion (dashed line with arrow)



Neural coding of hand trajectory?

Instantaneous population vector predicts spiral hand motion



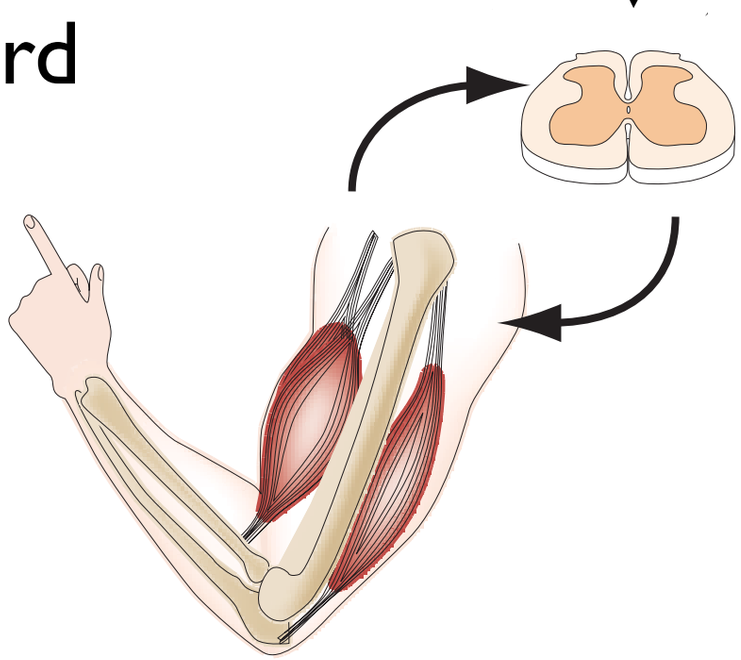
Hierarchical Model of Voluntary Control

Primary Motor Cortex

M1

Behavioural Goals (BG)

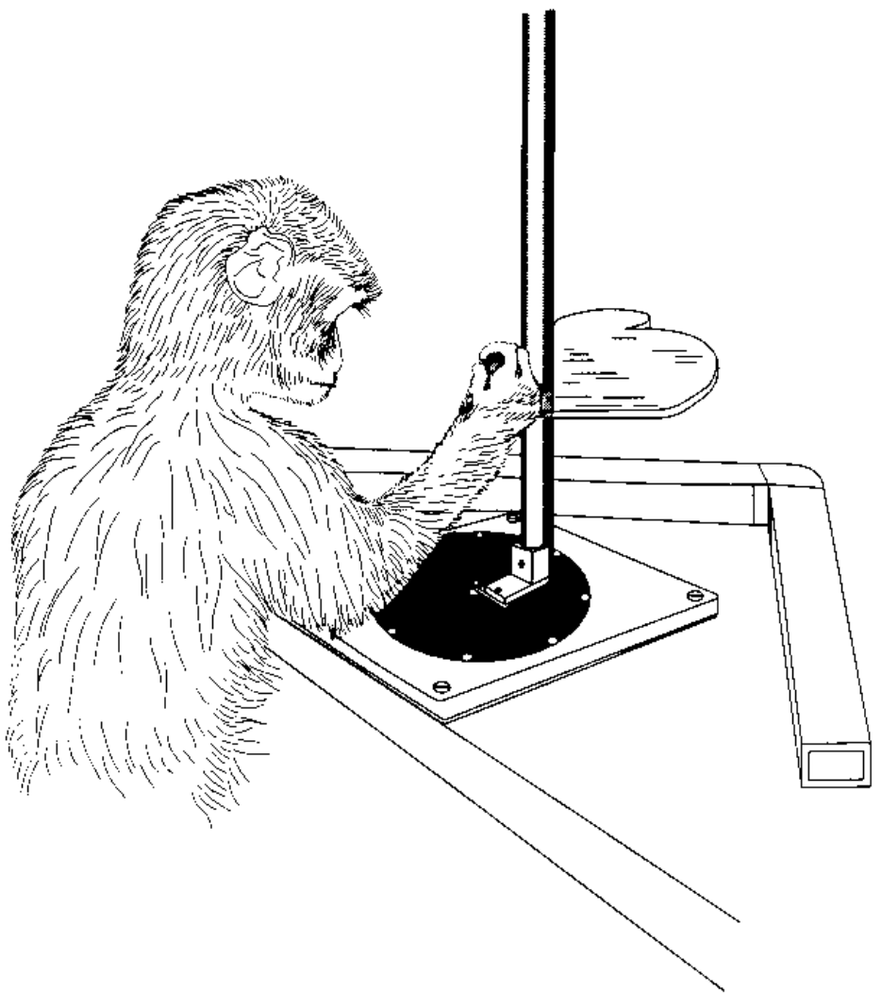
Spinal Cord



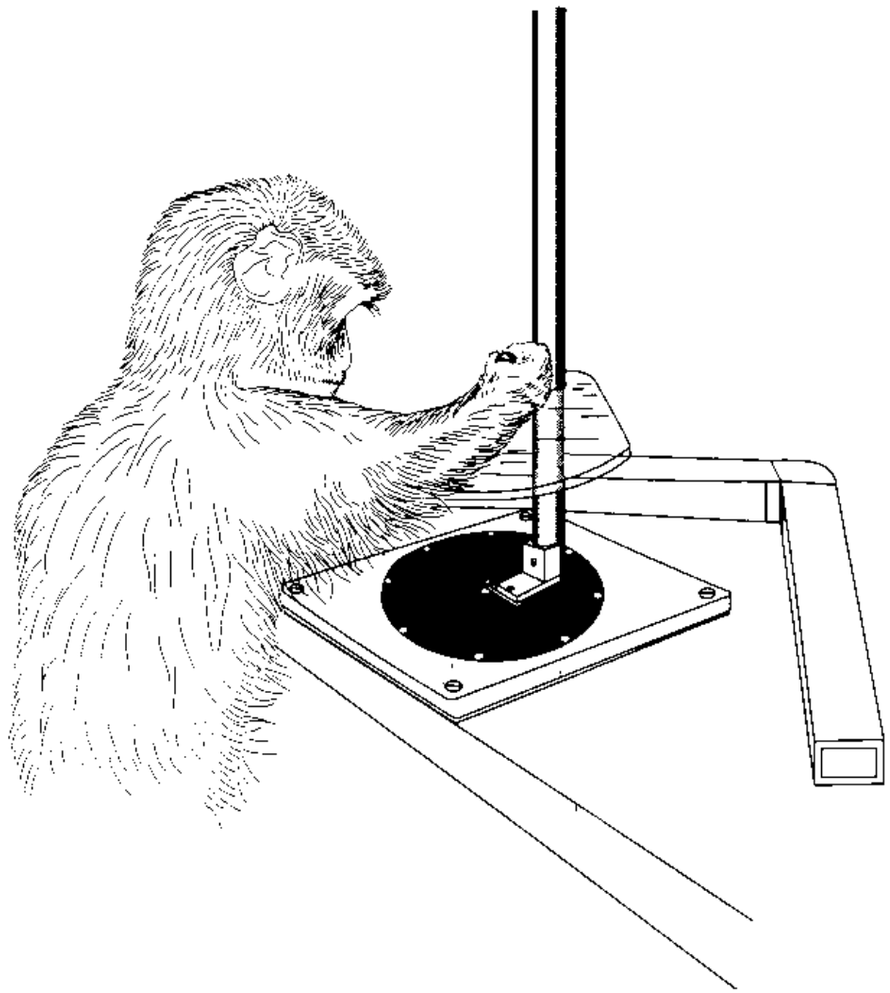
Convert BG into detailed patterns of motor output

Reaching Movements with different arm geometries

Natural



Abducted



Reaching movements with different arm geometries

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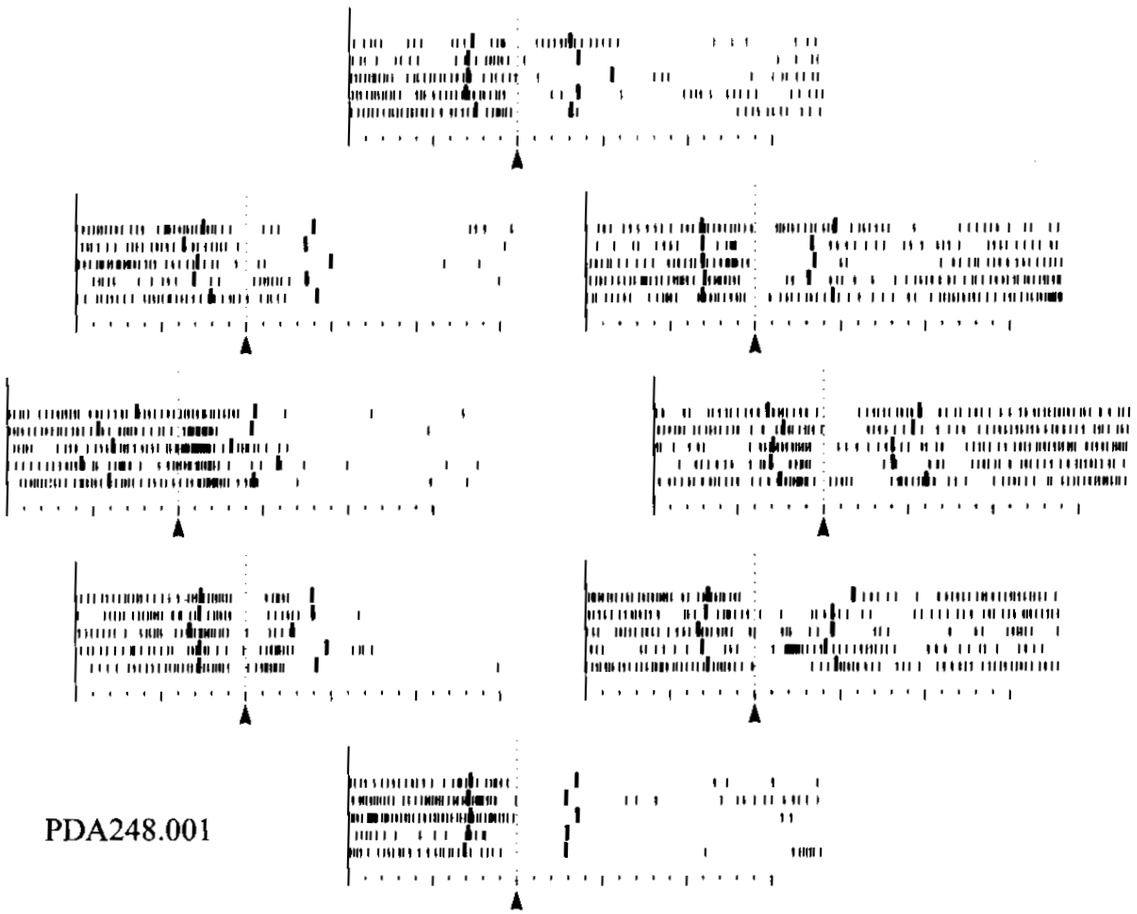
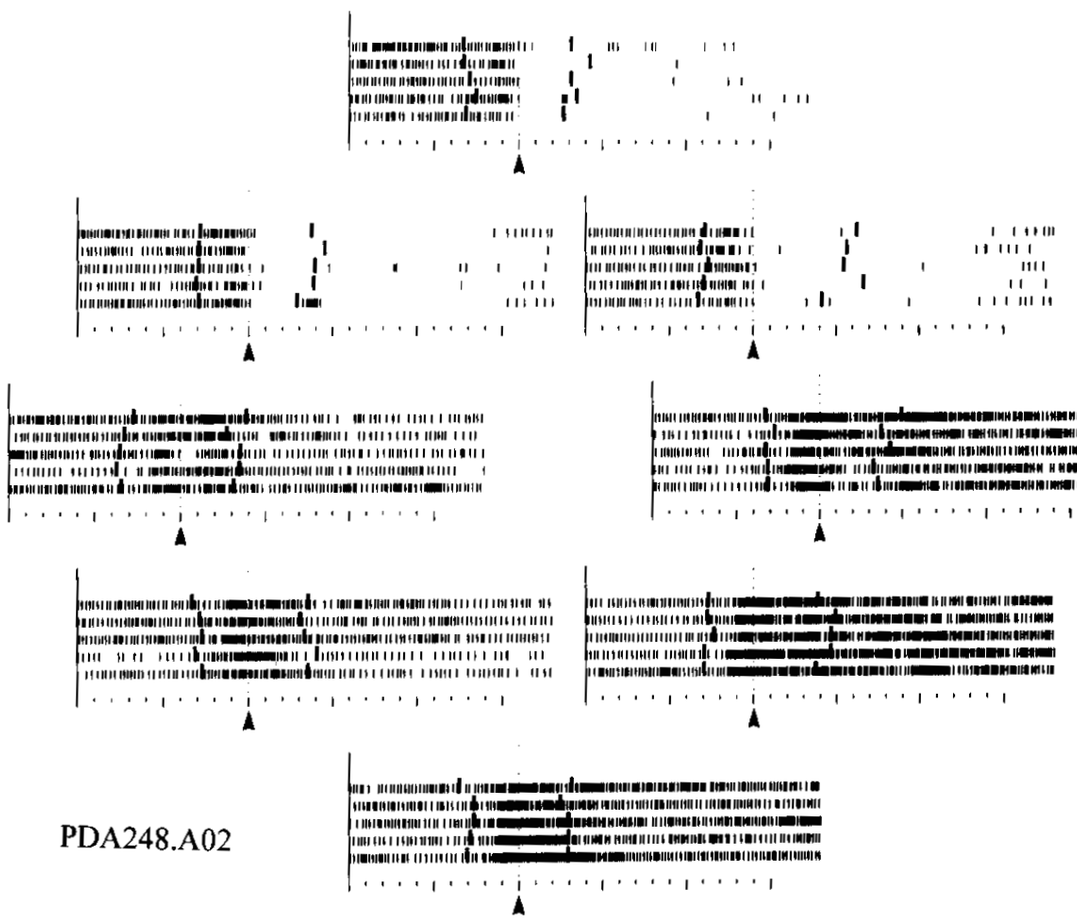
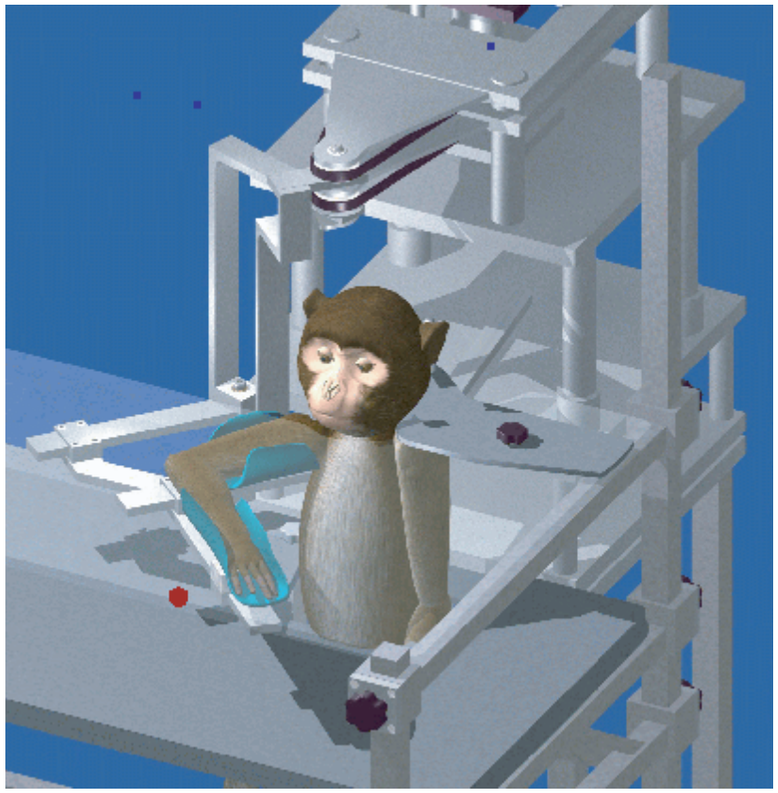


Abducted



Scott and Kalaska JNP 1997

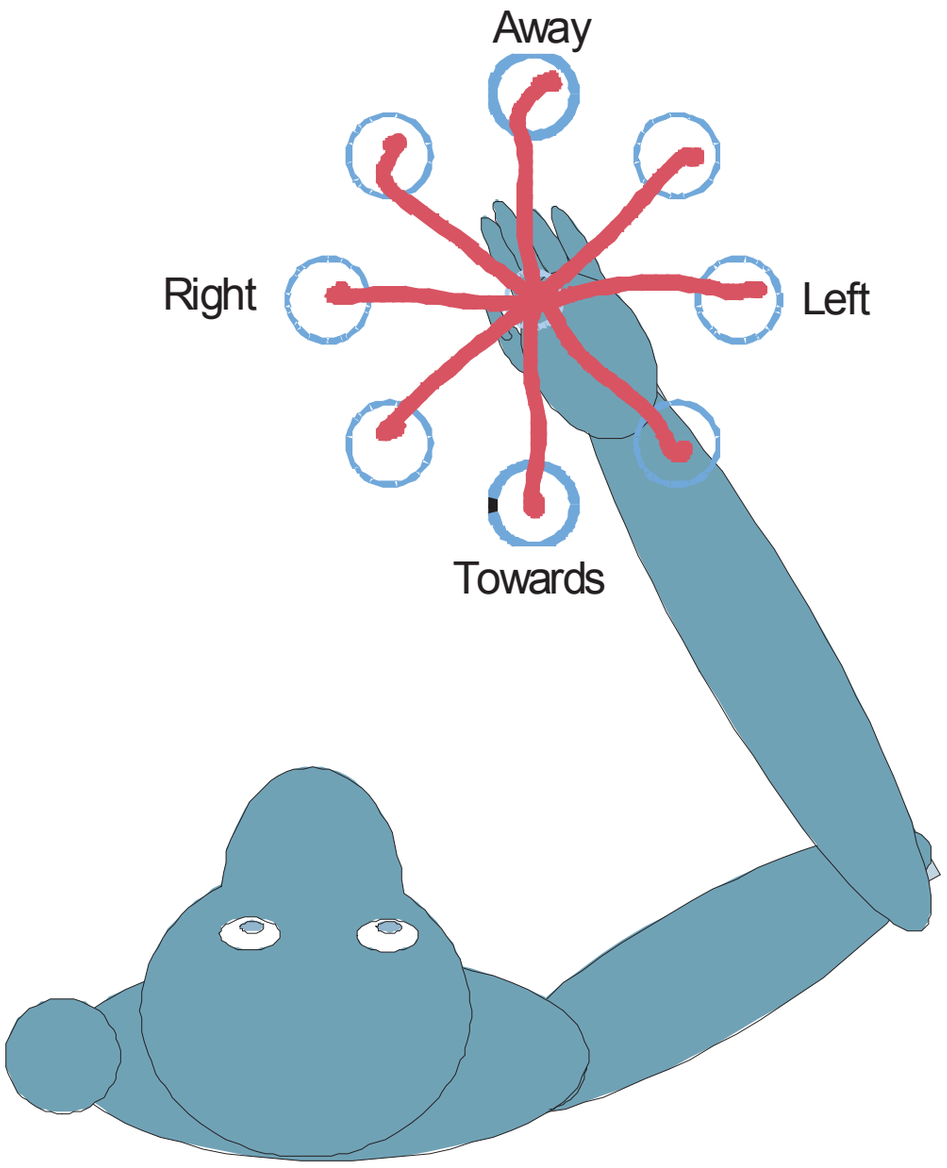
Two-dimensional Paradigm



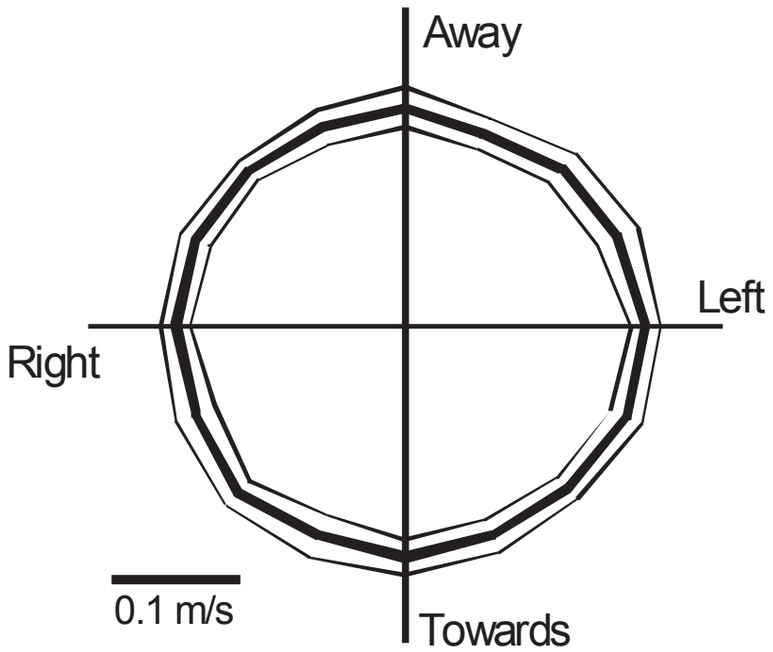
KINARM robot

- 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

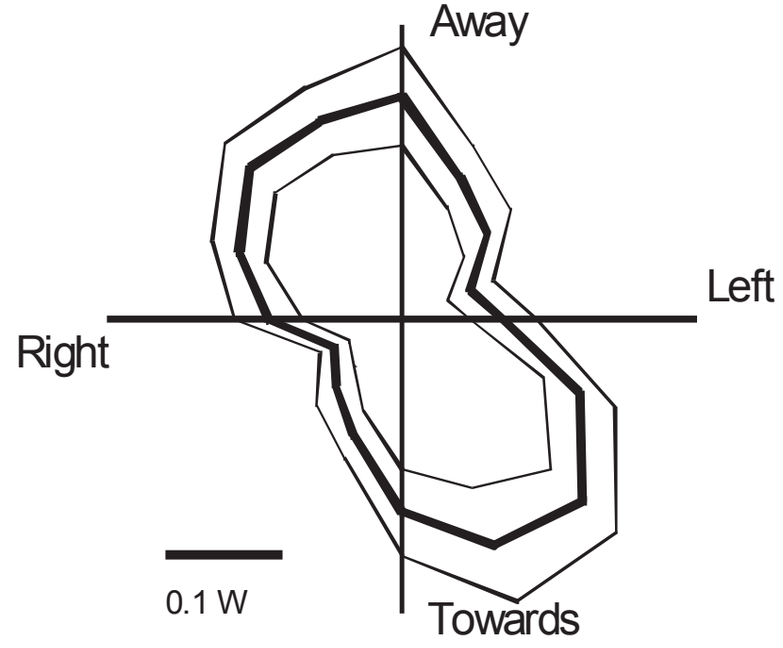
Hand Trajectory



Peak Hand Velocity

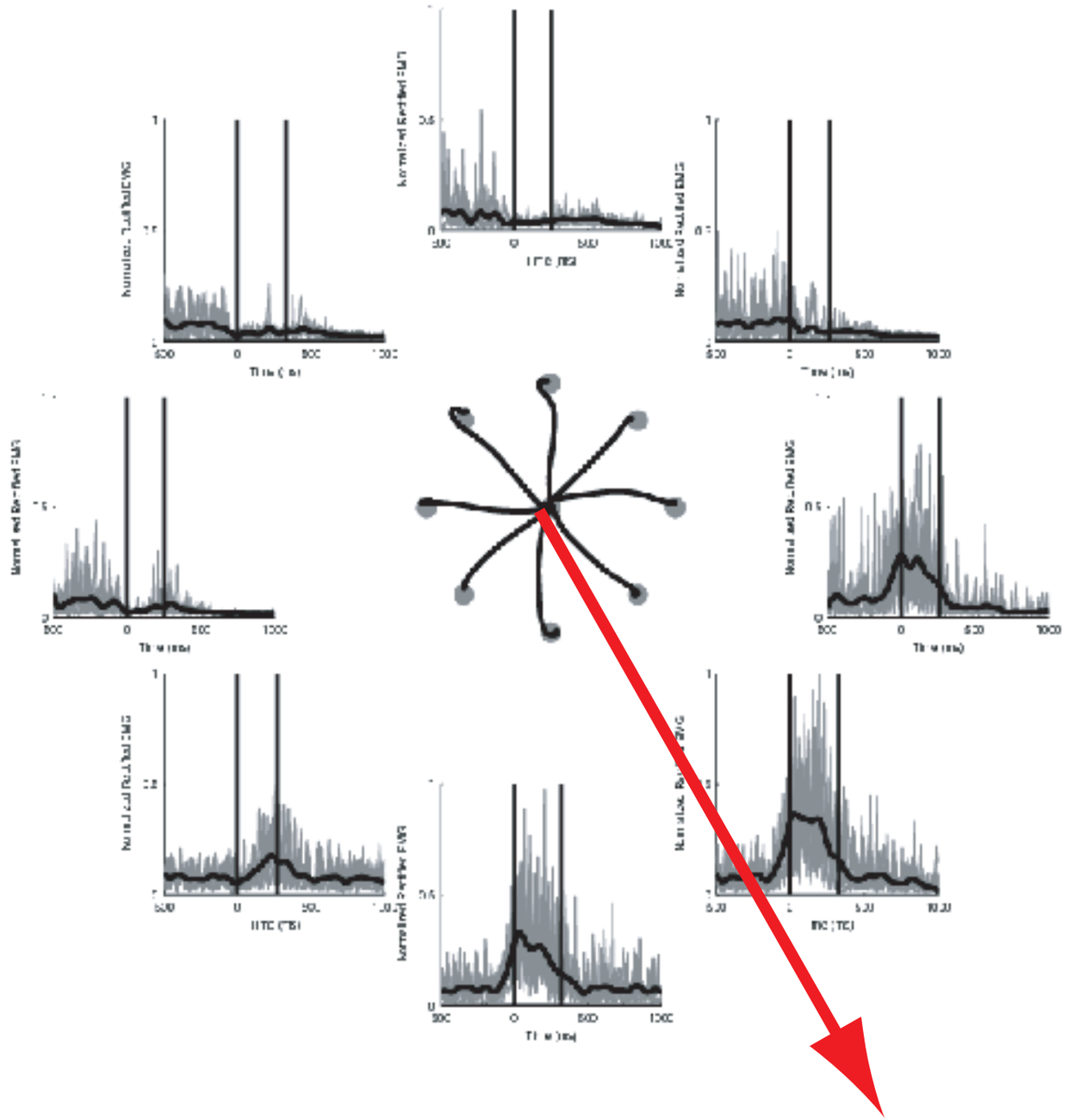


Peak Joint Power



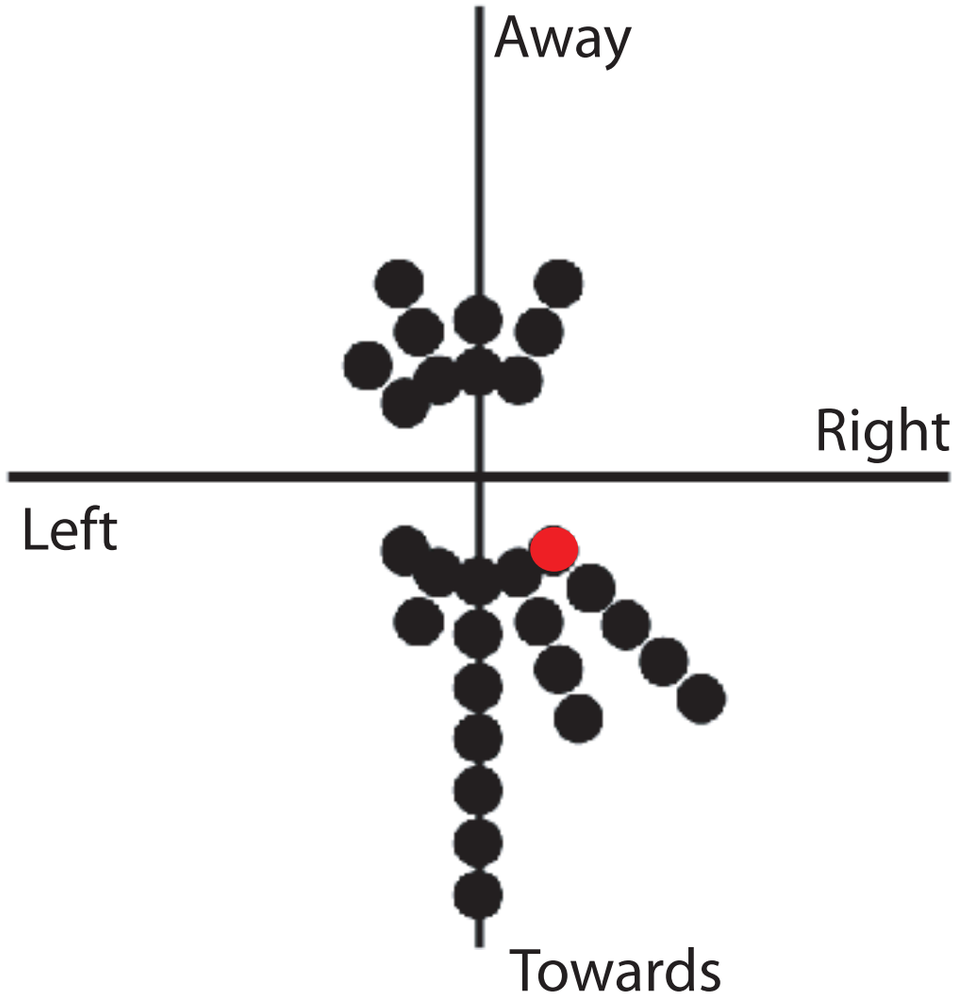
Joint Power = Angular Velocity * Torque

Posterior Deltoids: Shoulder Extensor



Preferred Direction

Distribution of Preferred Directions



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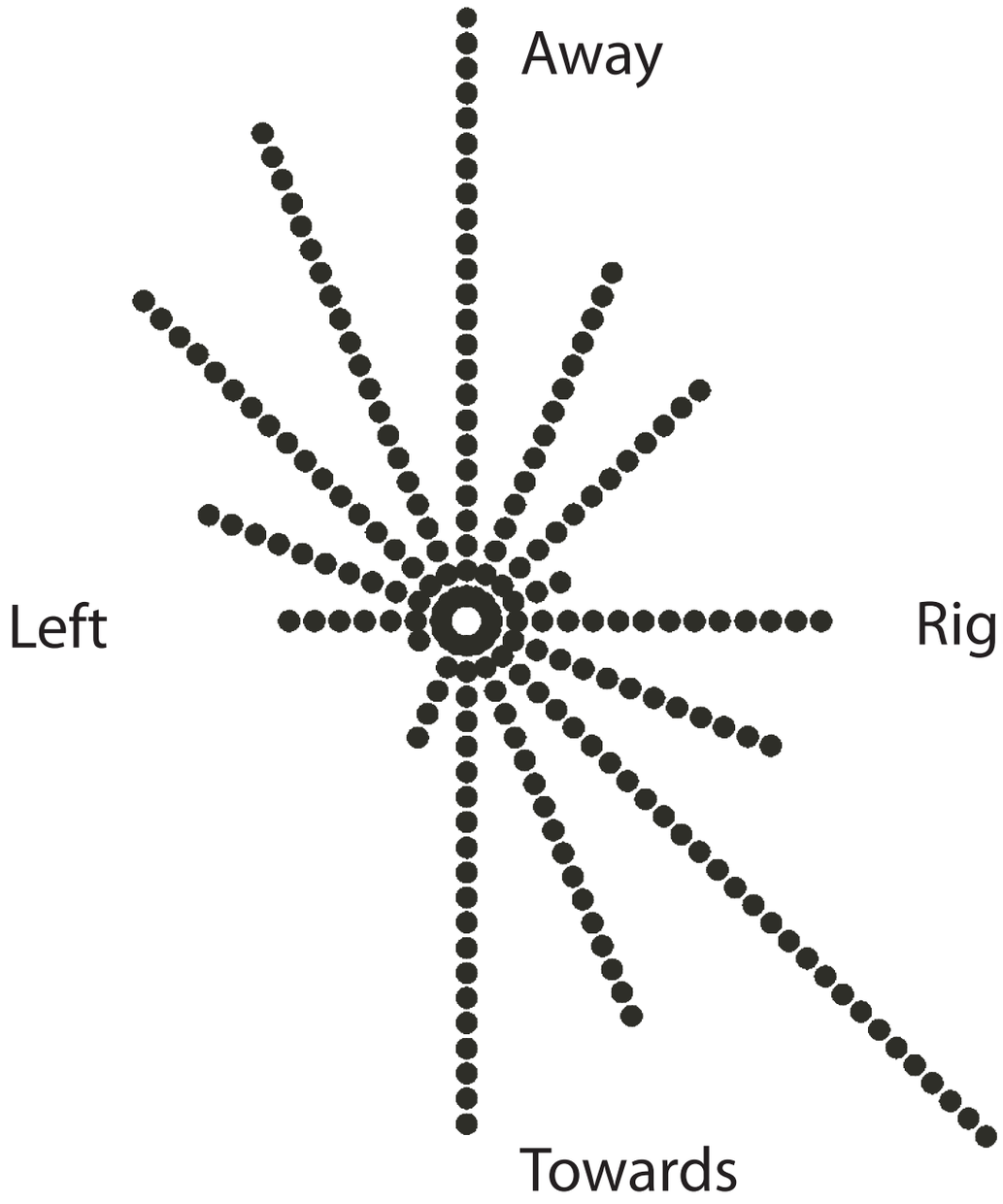
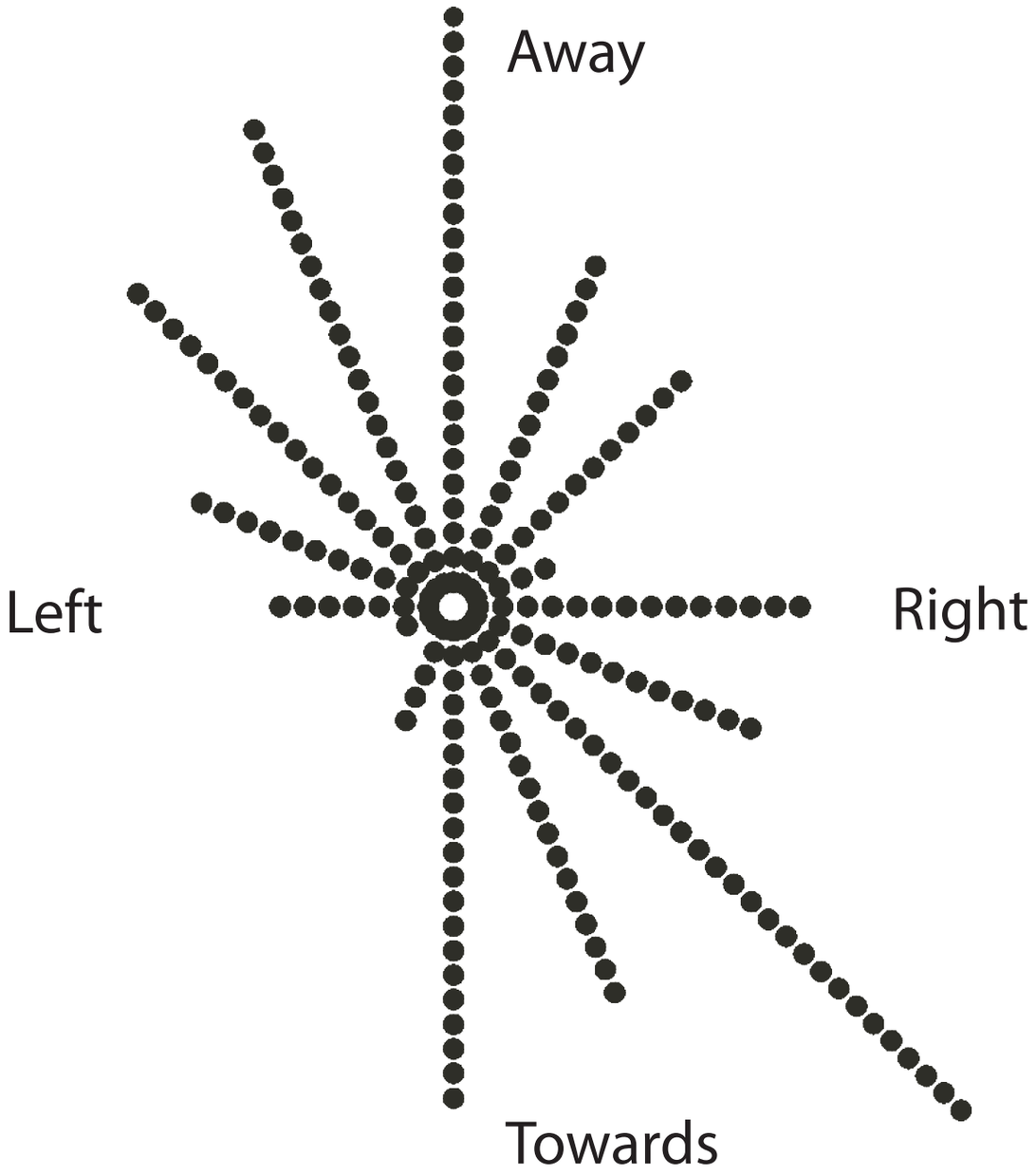
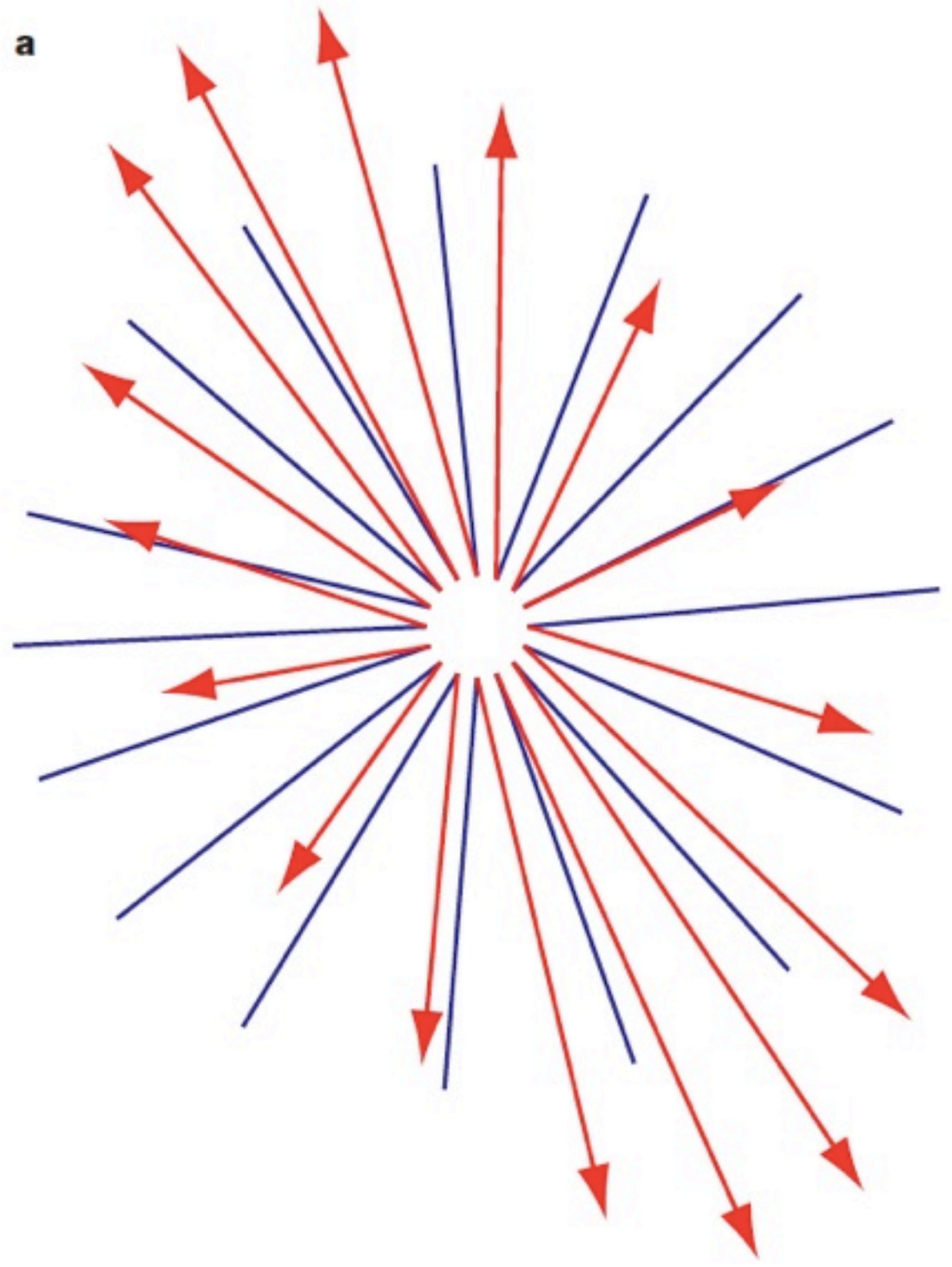


Distribution of Preferred Directions



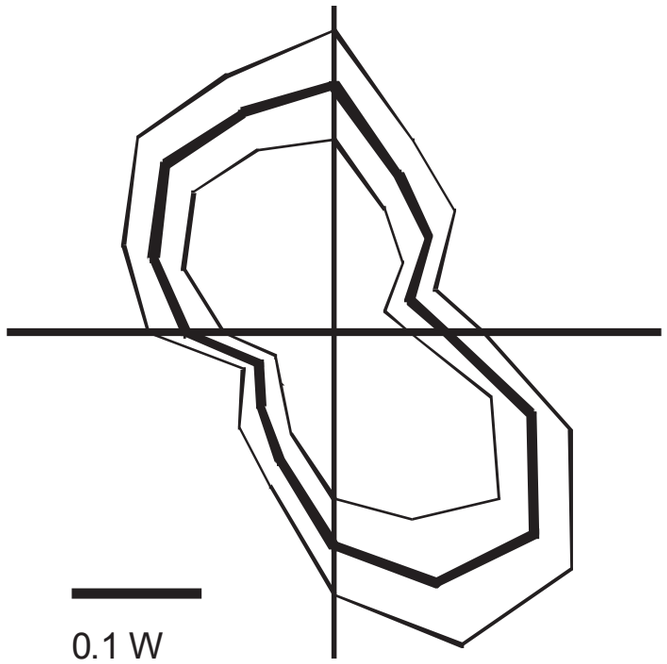
Population Vectors



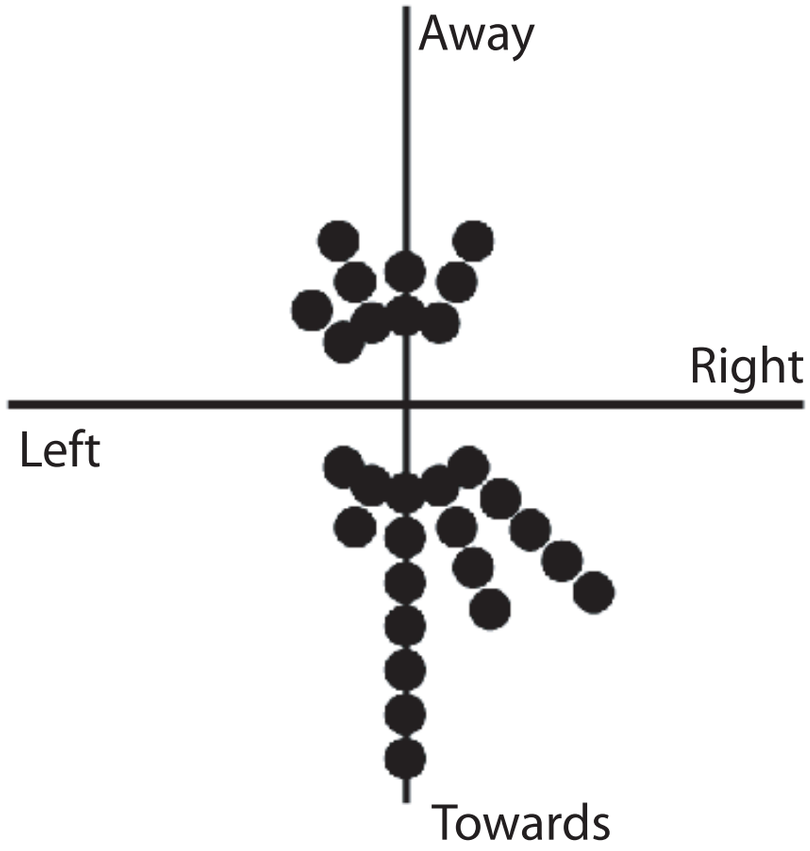
Scott et al., Nature 2001

Neural activity in M1 reflects limb mechanics:

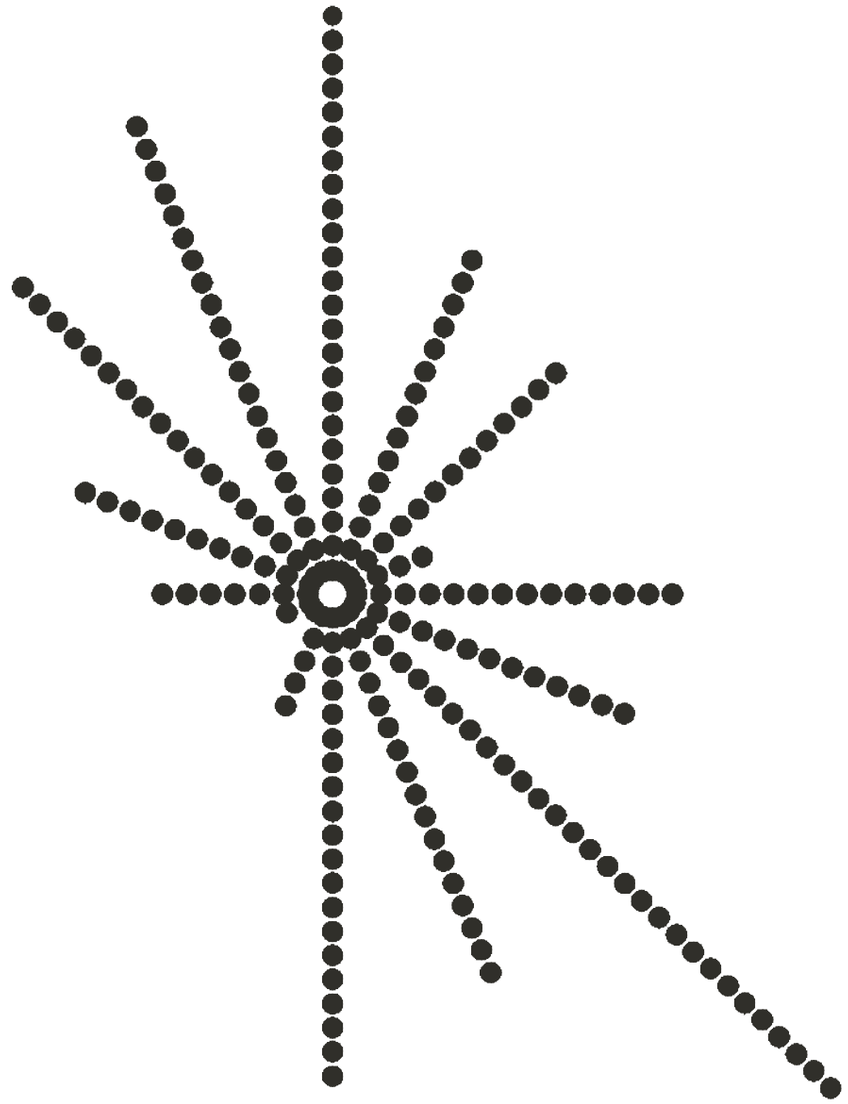
Peak Joint Power



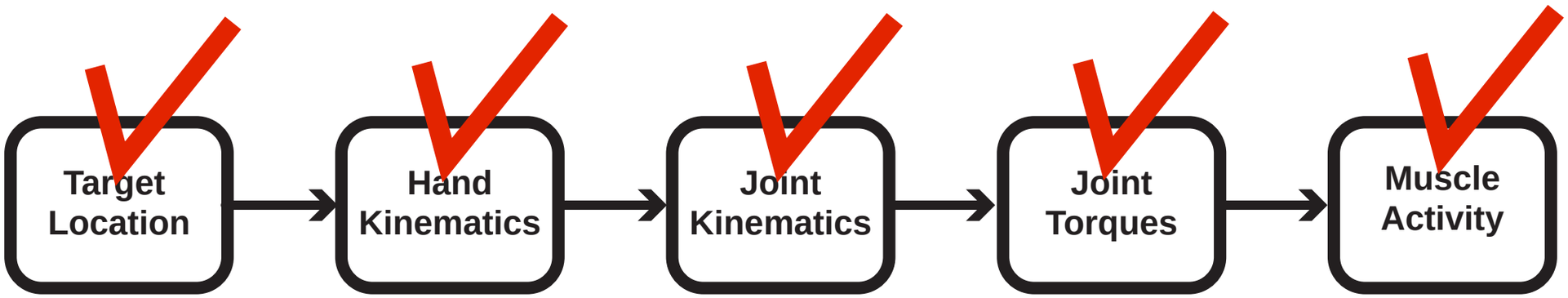
Limb Muscle Activity



M1 Cell Activity

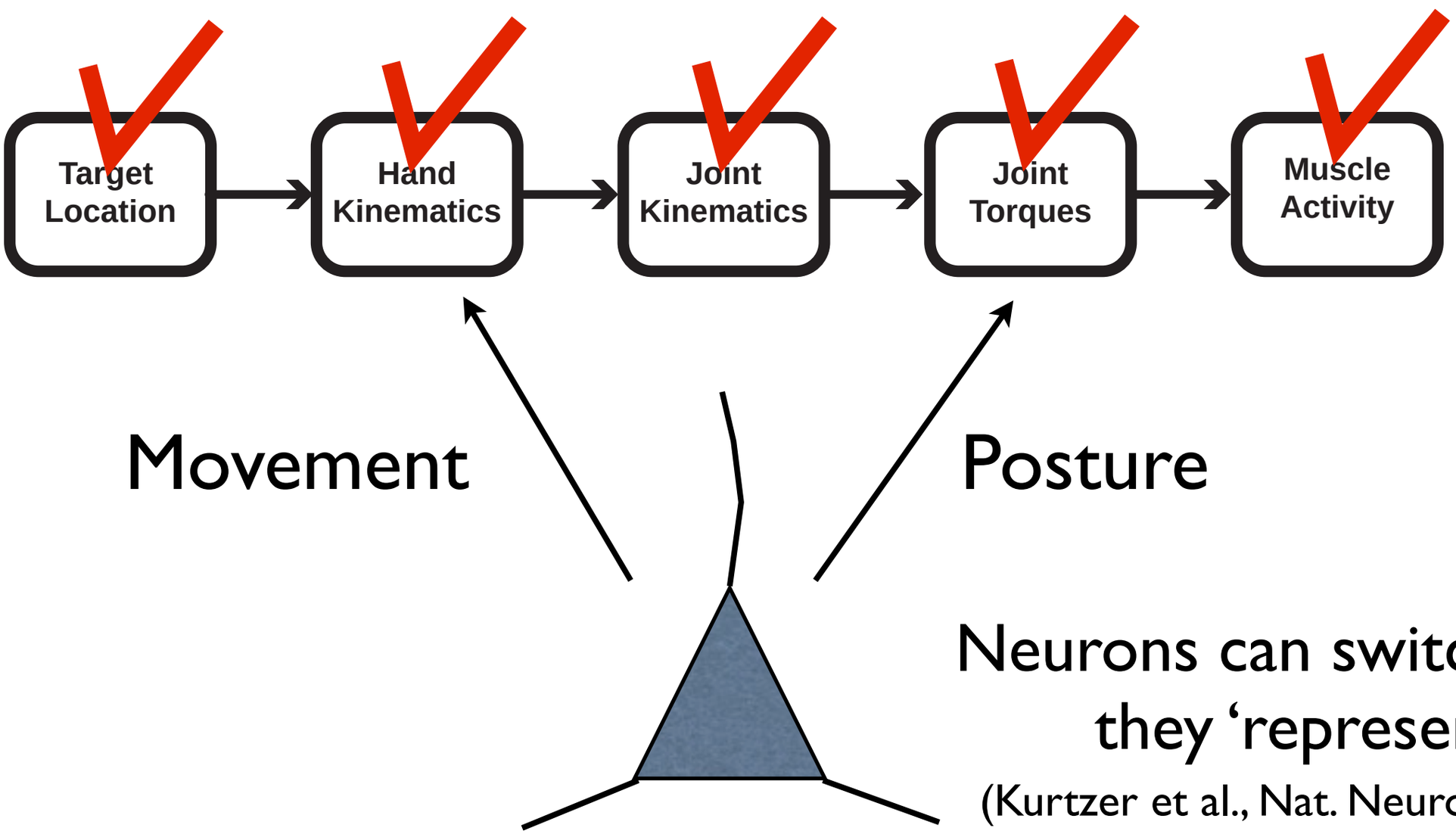


Conceptual Framework: Sensorimotor Transformations/Coordinate Frames



M1 neurons can represent all levels of information

An Inconvenient Truth about Sensorimotor Transformations/ Coordinate Frames



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)

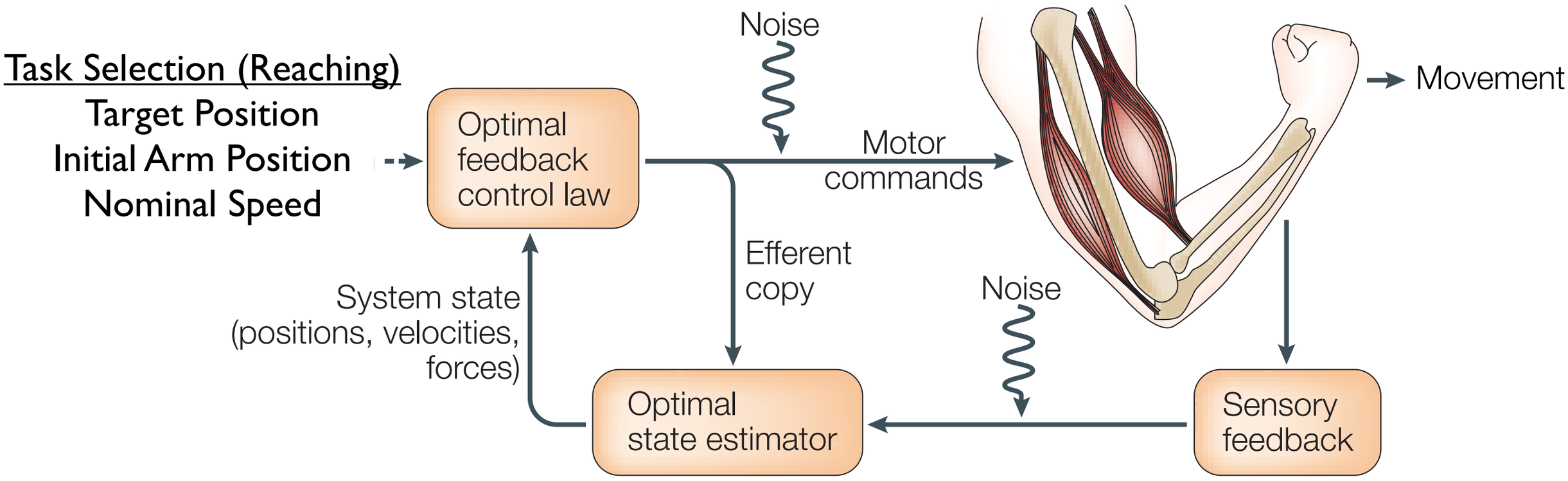
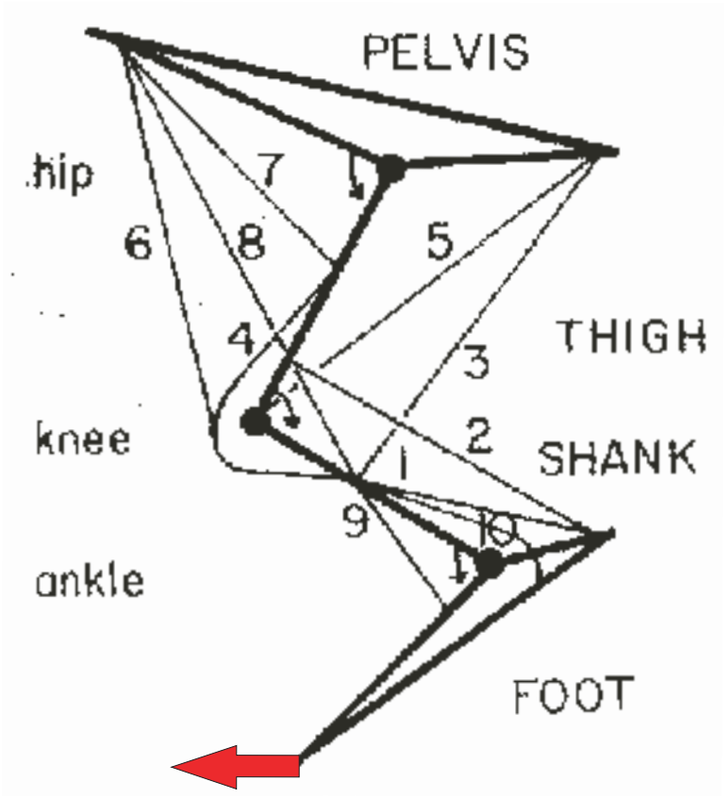


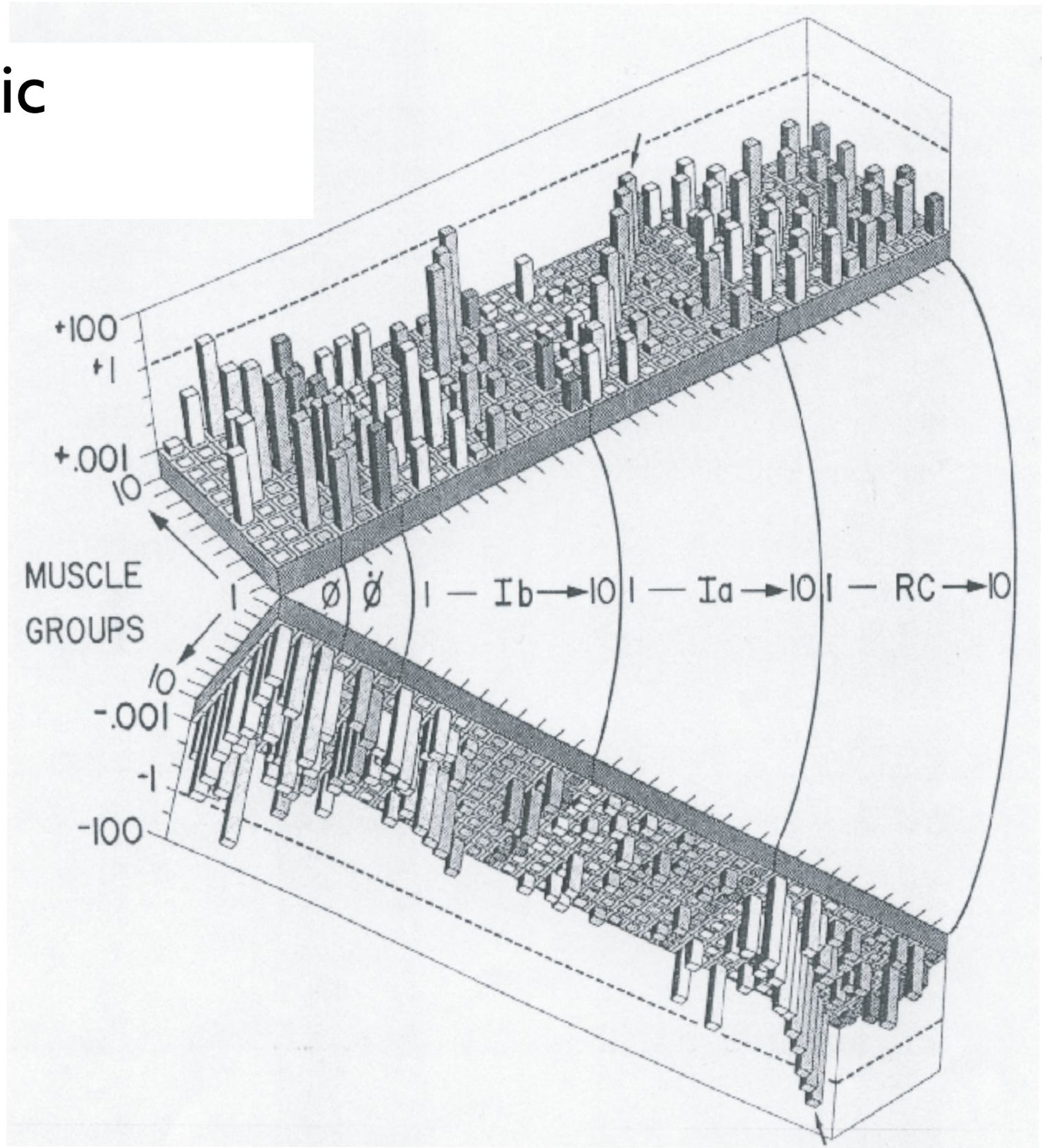
Diagram from Scott, Nat. Rev. Neurosci. 2004

Linear Quadratic Regulator



Foot slip

He, Levine, Loeb, IEEE Trans on Automatic Control 36:322-332, 1991



Optimal Feedback Control: Manages Noise

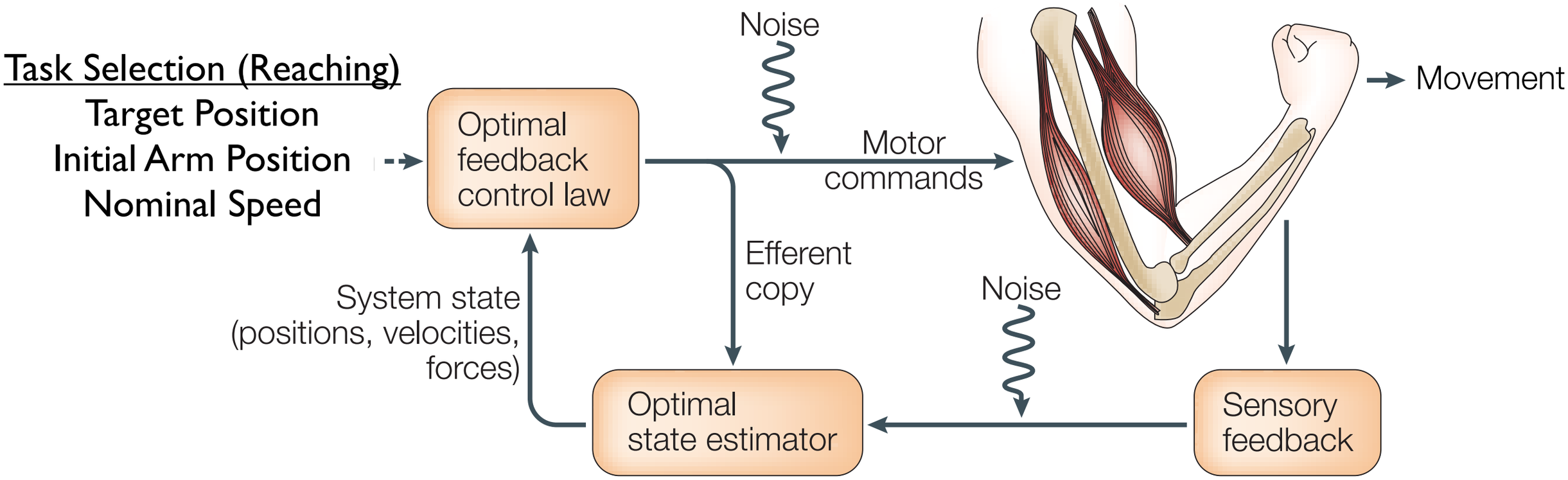
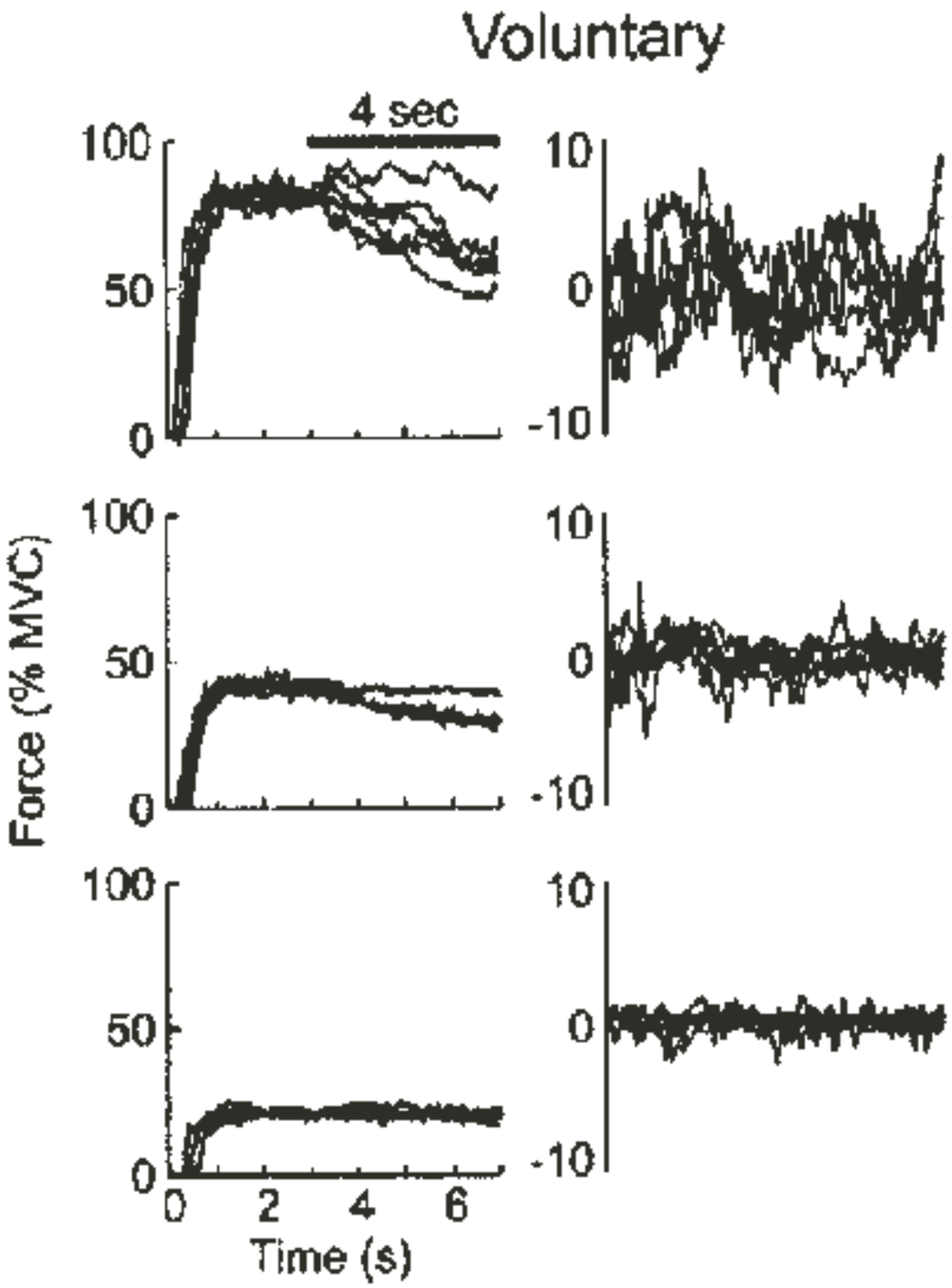
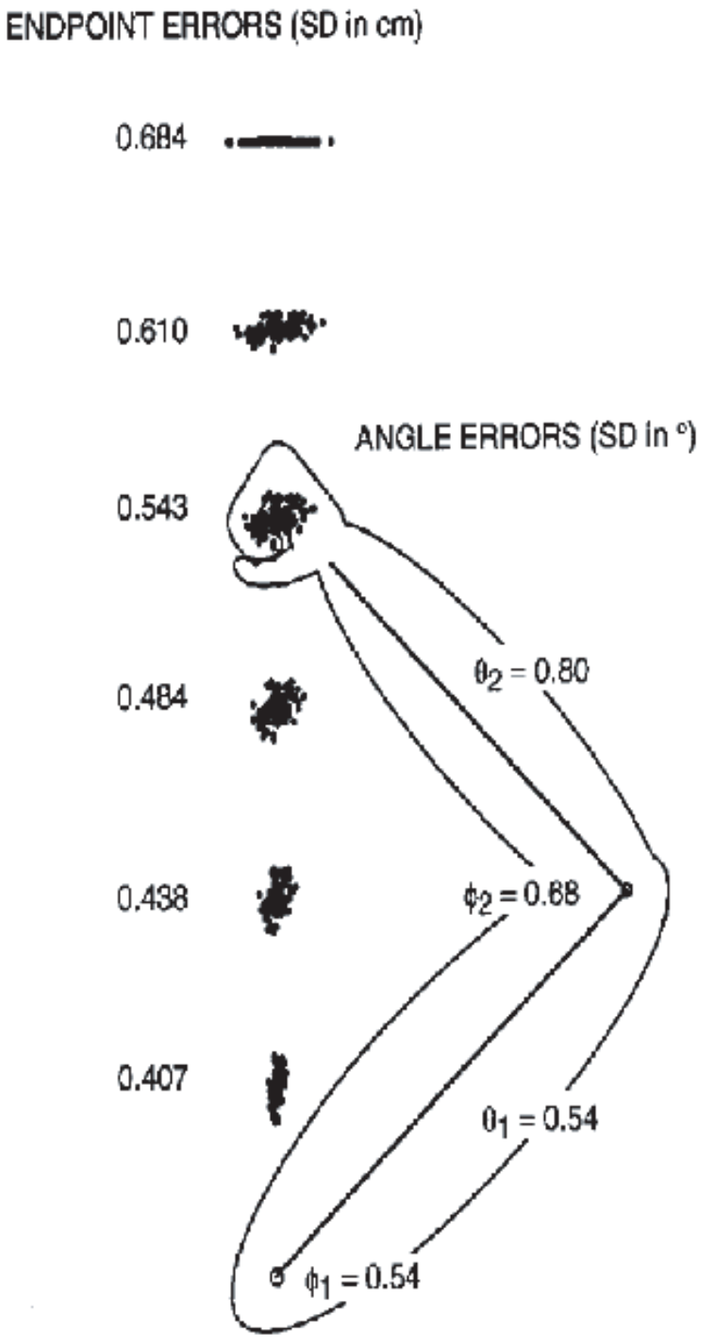


Diagram from Scott, Nat. Rev. Neurosci. 2004

Sensory and Motor Noise



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

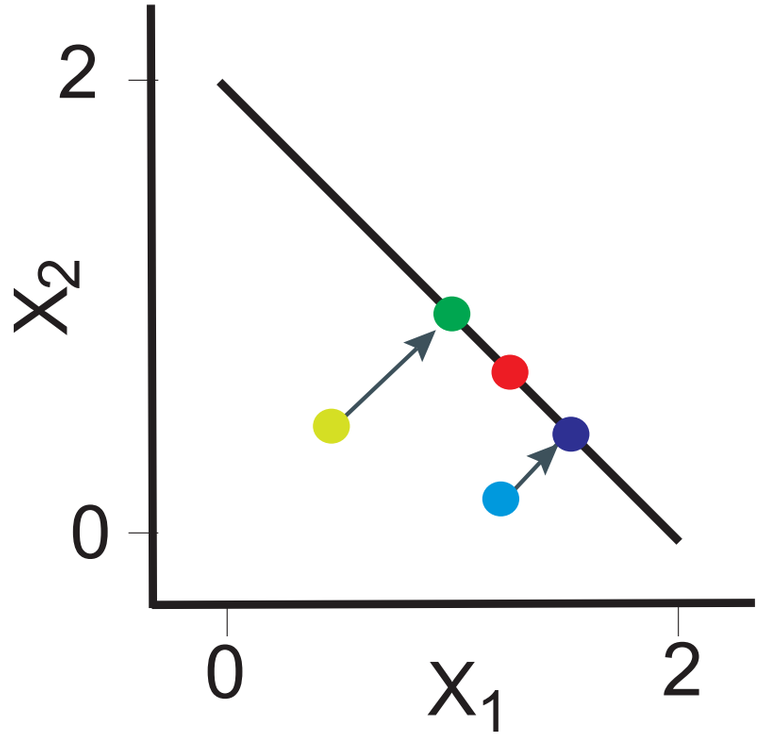
Control Problem: $X_1 + X_2 = 2$

Nominal Solution: $X_1 = X_2 = 1$ ●

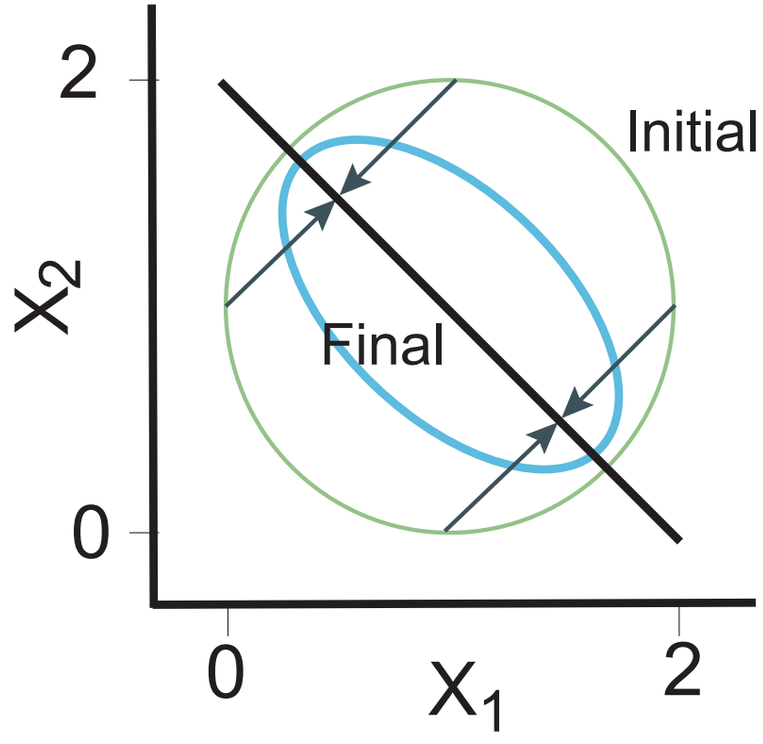
Case 1(●): $X_1 = 0.5$, $X_2 = 0.5$
Proceed to ●

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

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



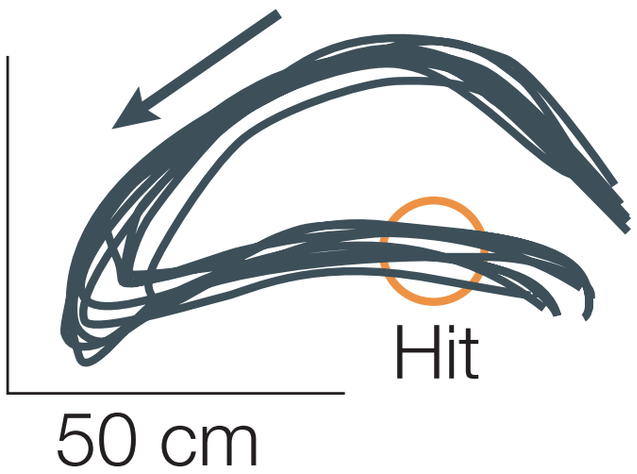
Emergent Pattern of Variability



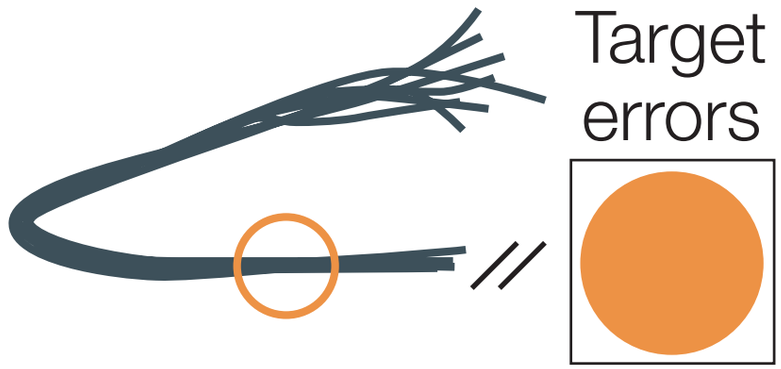
Task-dependent Corrections

Success at hitting a ping pong ball

Experimental data



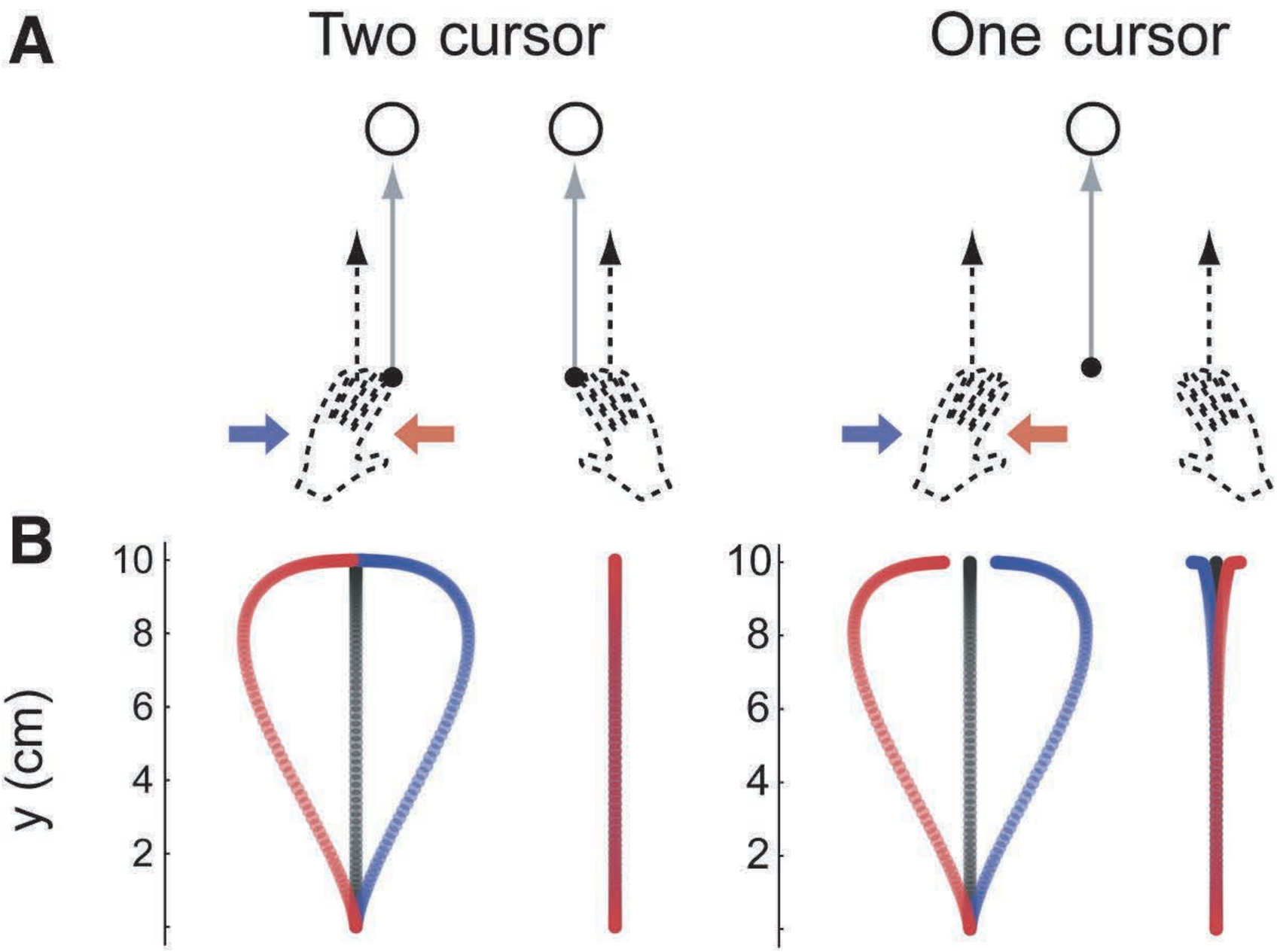
Desired trajectory



Optimal control

(Todorov and Jordan, 2002)

Optimal Feedback Control predicts flexible use of feedback

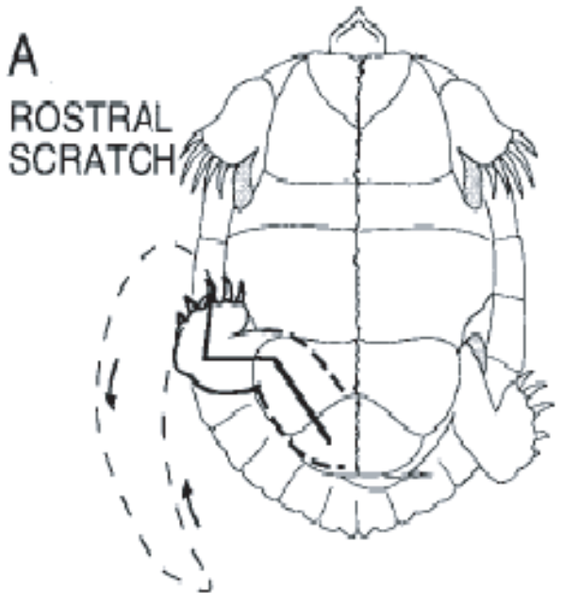


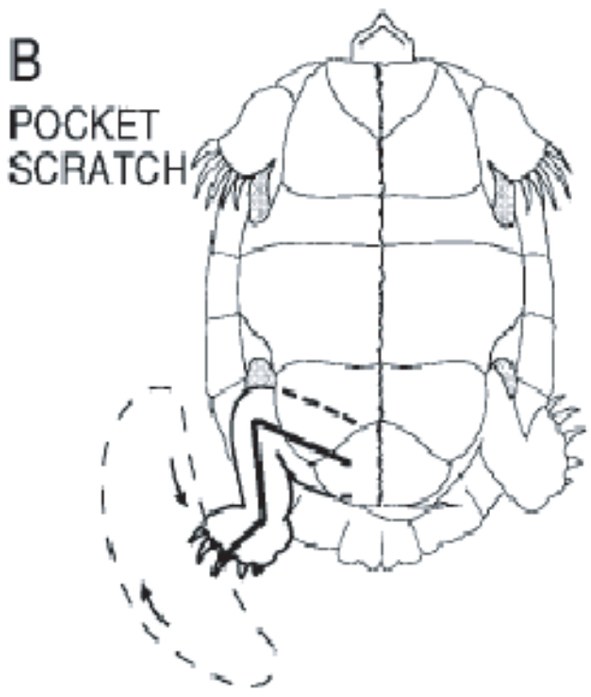
Perturb left limb DOES NOT affect right limb

Perturb left limb DOES affect right limb

Diedrichsen, Current Biology (2006)

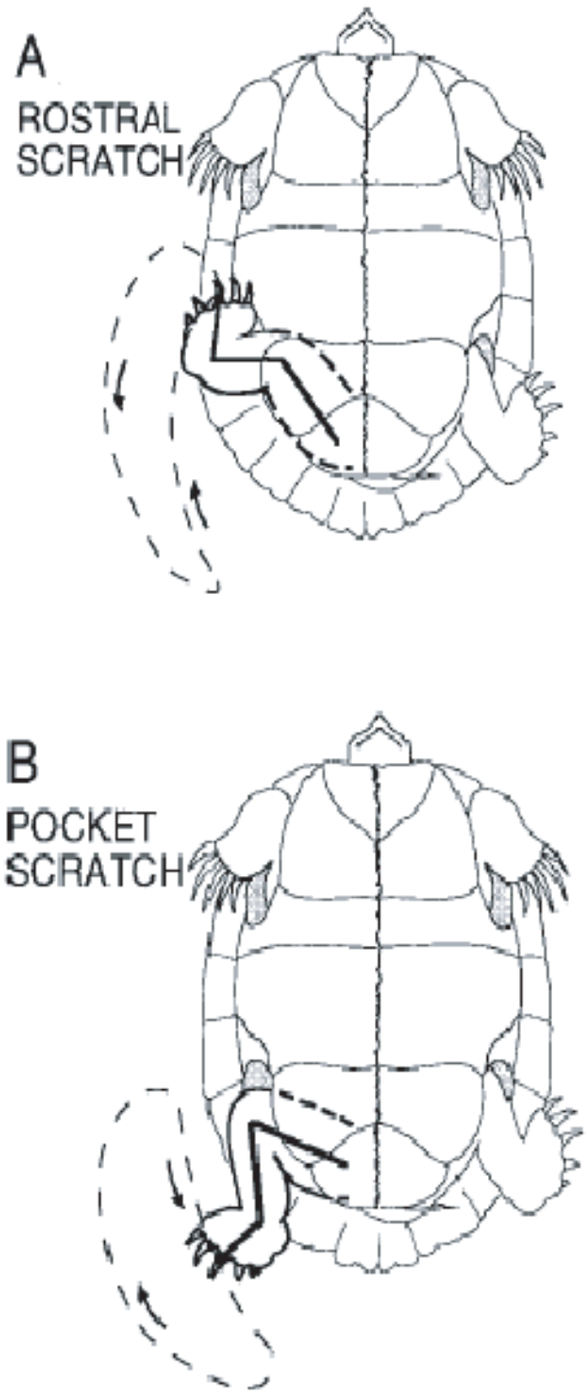
Spinalized Turtle Wiping Reflex





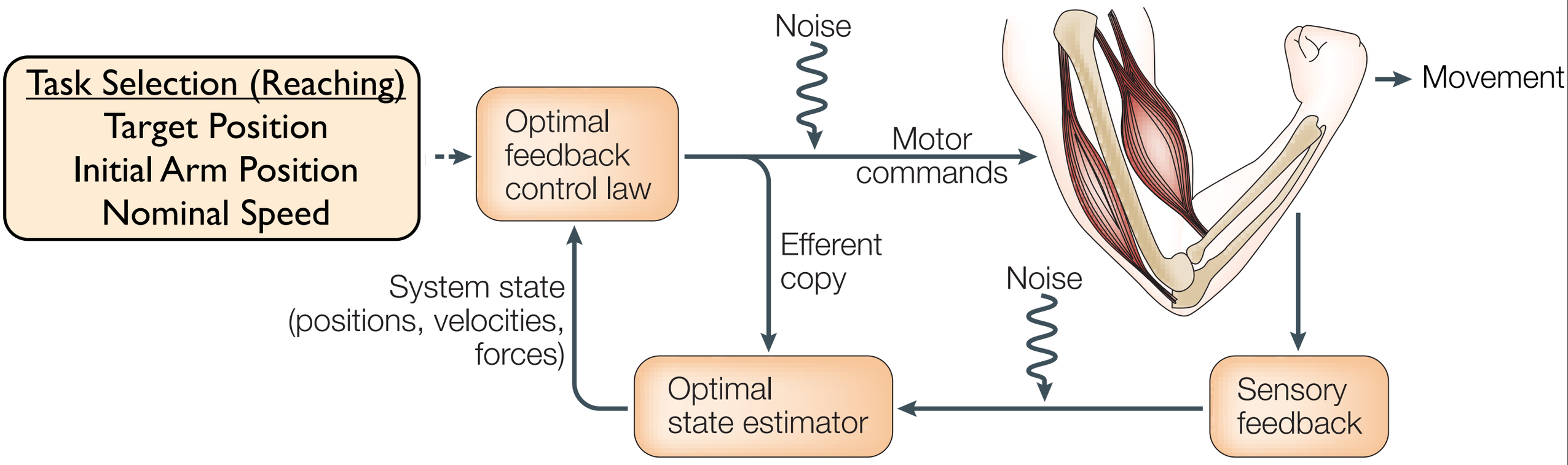
Field-Fote and Stein JNP 78:1394-1403, JNP

Spinalized Turtle Wiping Reflex



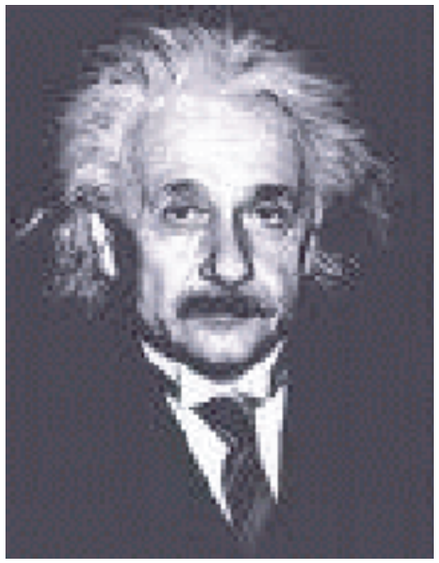
Field-Fote and Stein JNP 78:1394-1403, JNP

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)



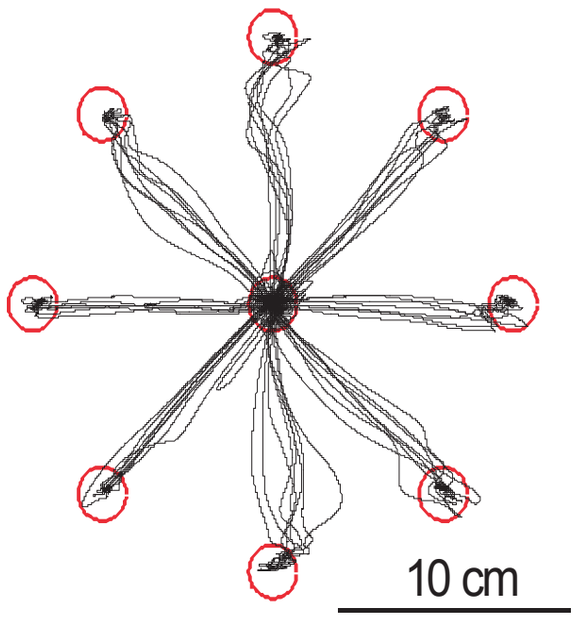
Primary Motor Cortex (M1) contributes to

Voluntary Control

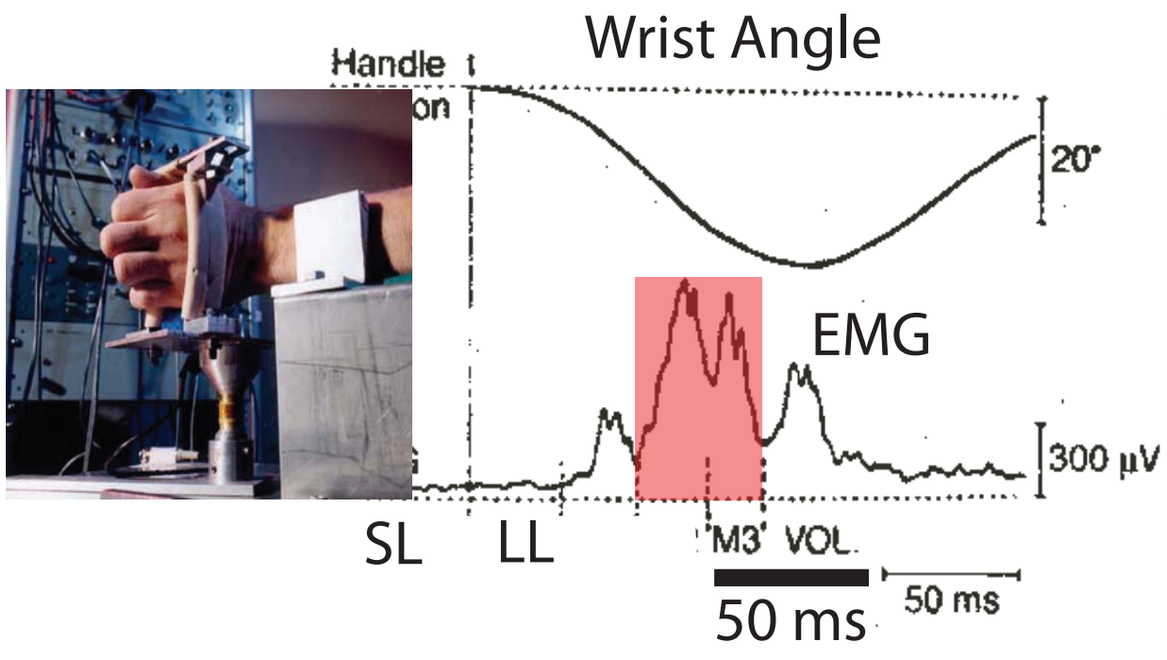


Long-Latency (LL) Reflexes

Visual-Guided Reaching

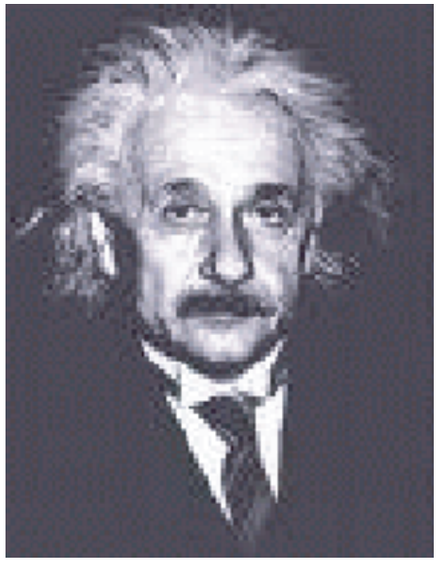


Mechanical Perturbation



Primary Motor Cortex (M1) contributes to

Voluntary Control



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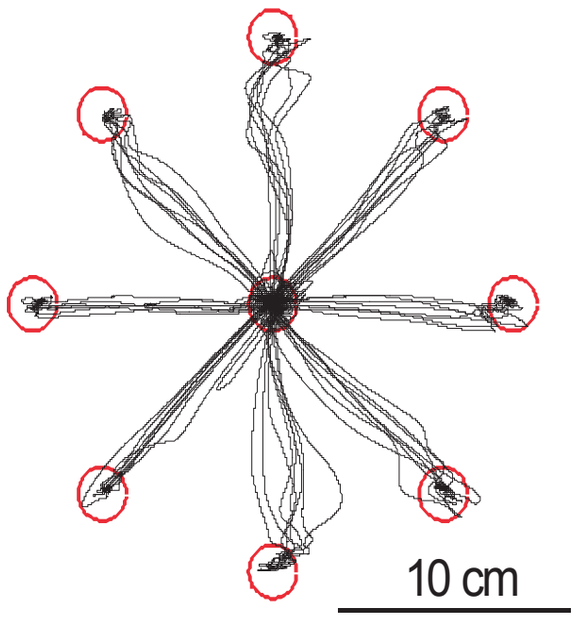
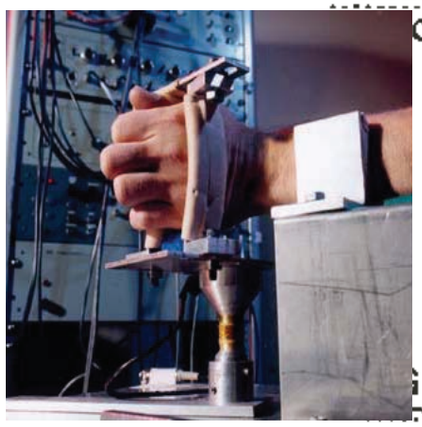
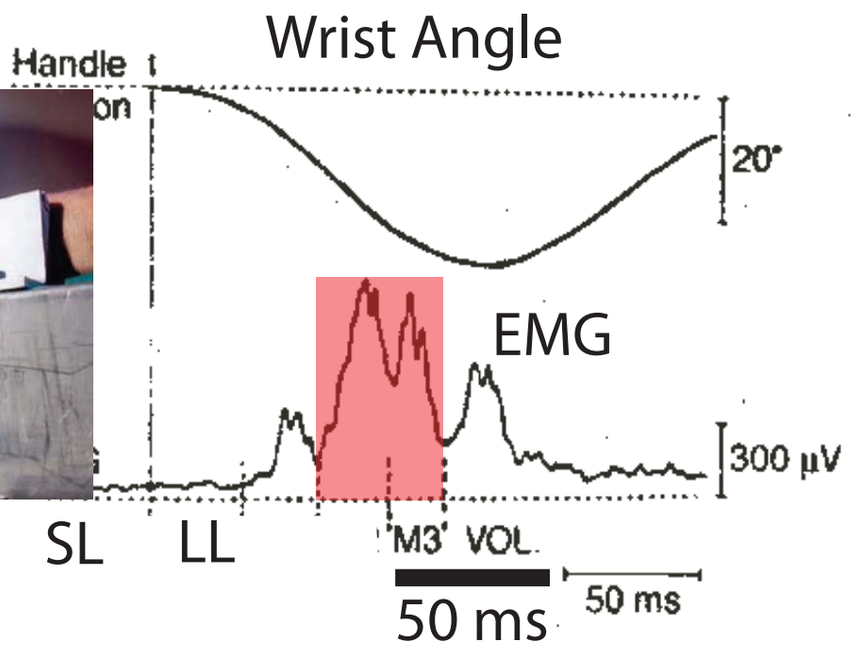
Long-Latency (LL) Reflexes

Visual-Guided Reaching



Mechanical Perturbation

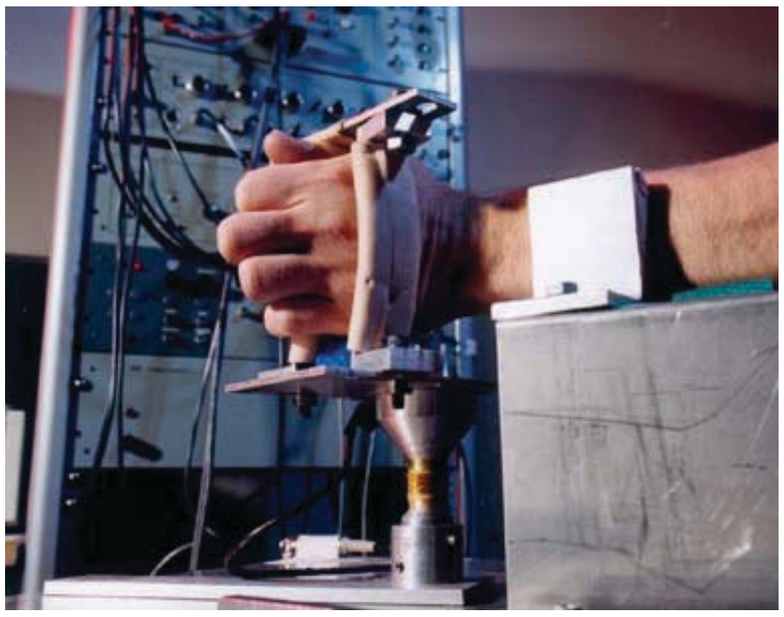




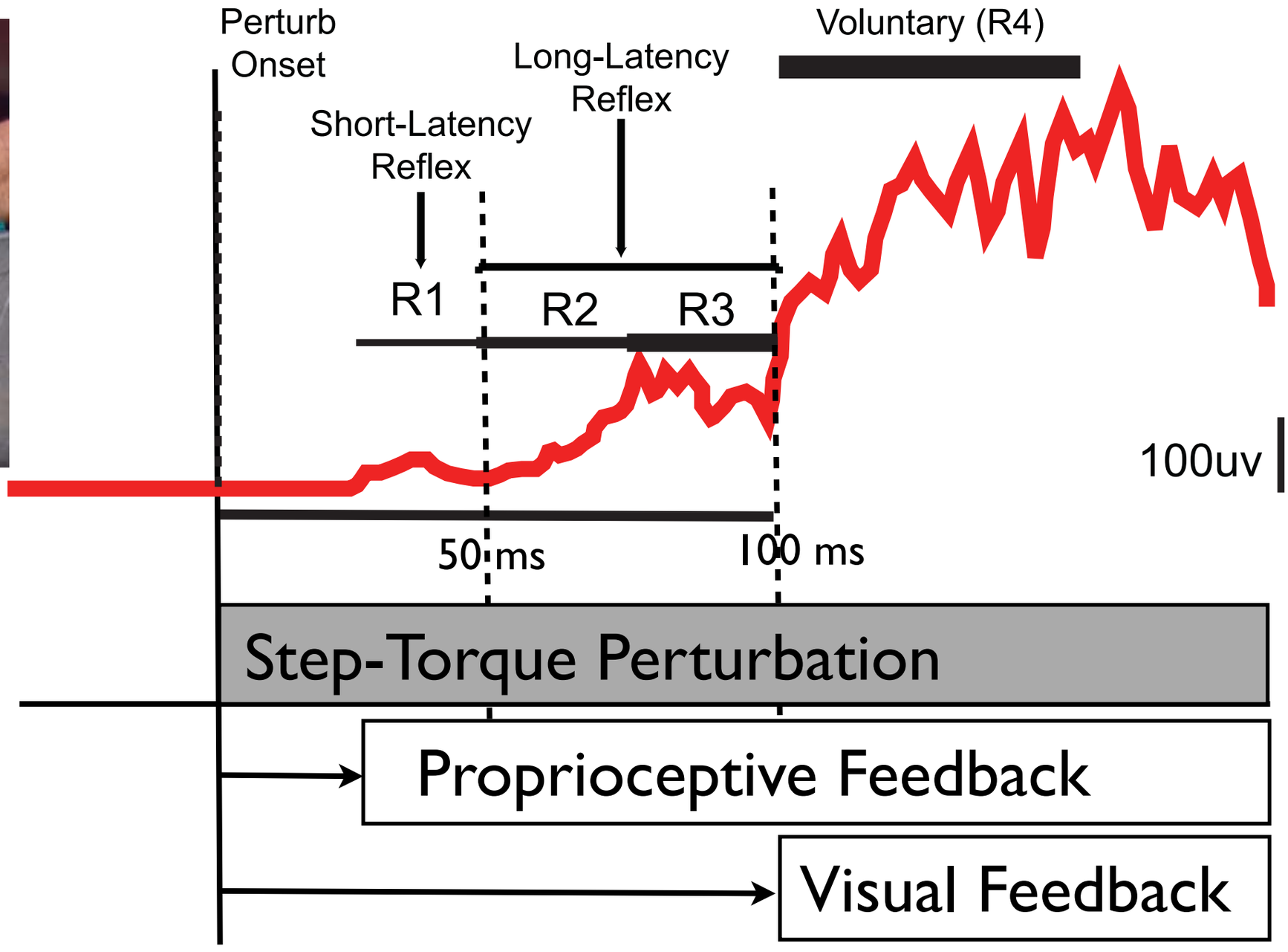
Feedback Matters for Voluntary Control!

Study stretch responses to probe voluntary control

Single-Joint Perturbation



Stretch-Related Muscle Activity

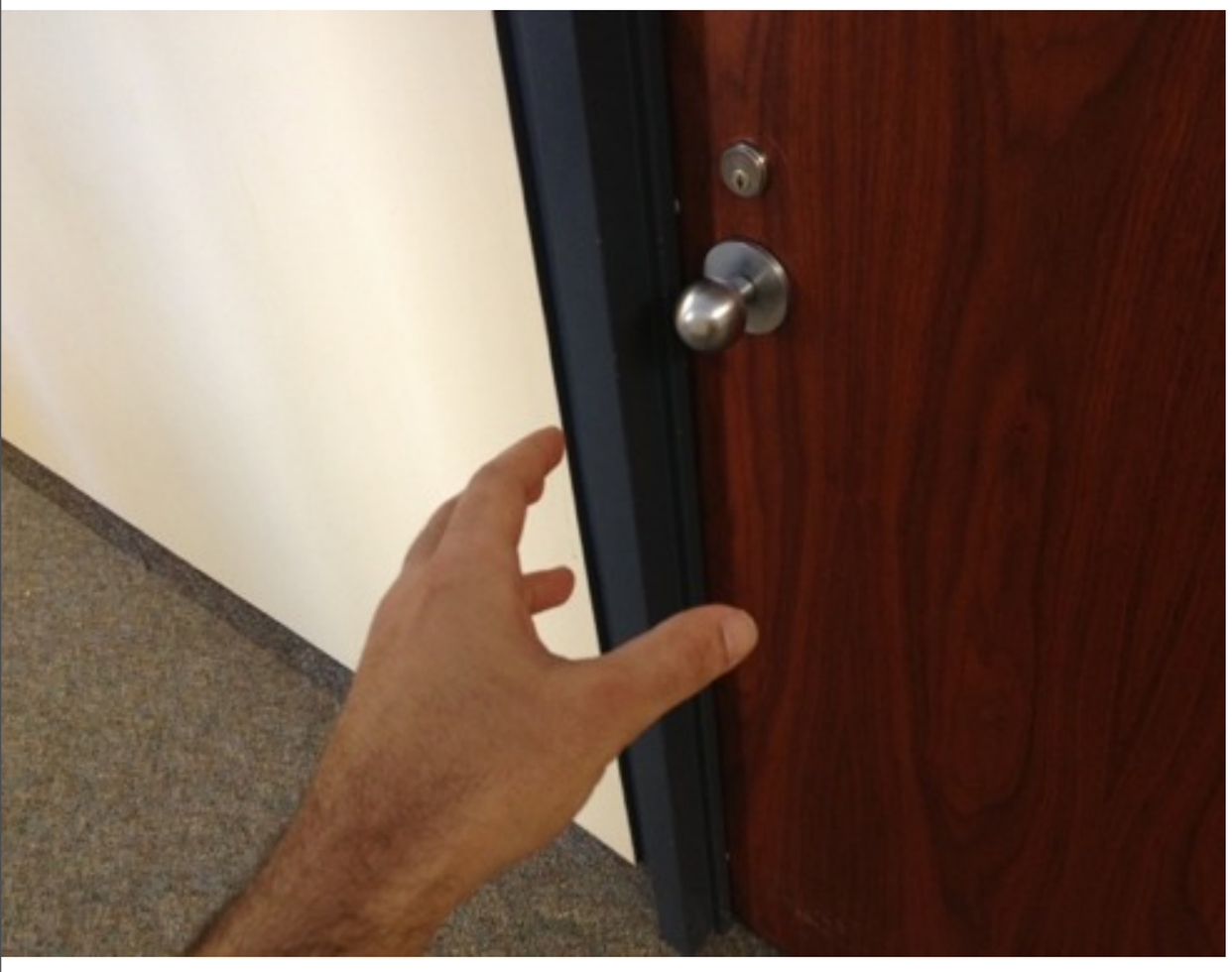


Short-latency response:
- Spinal

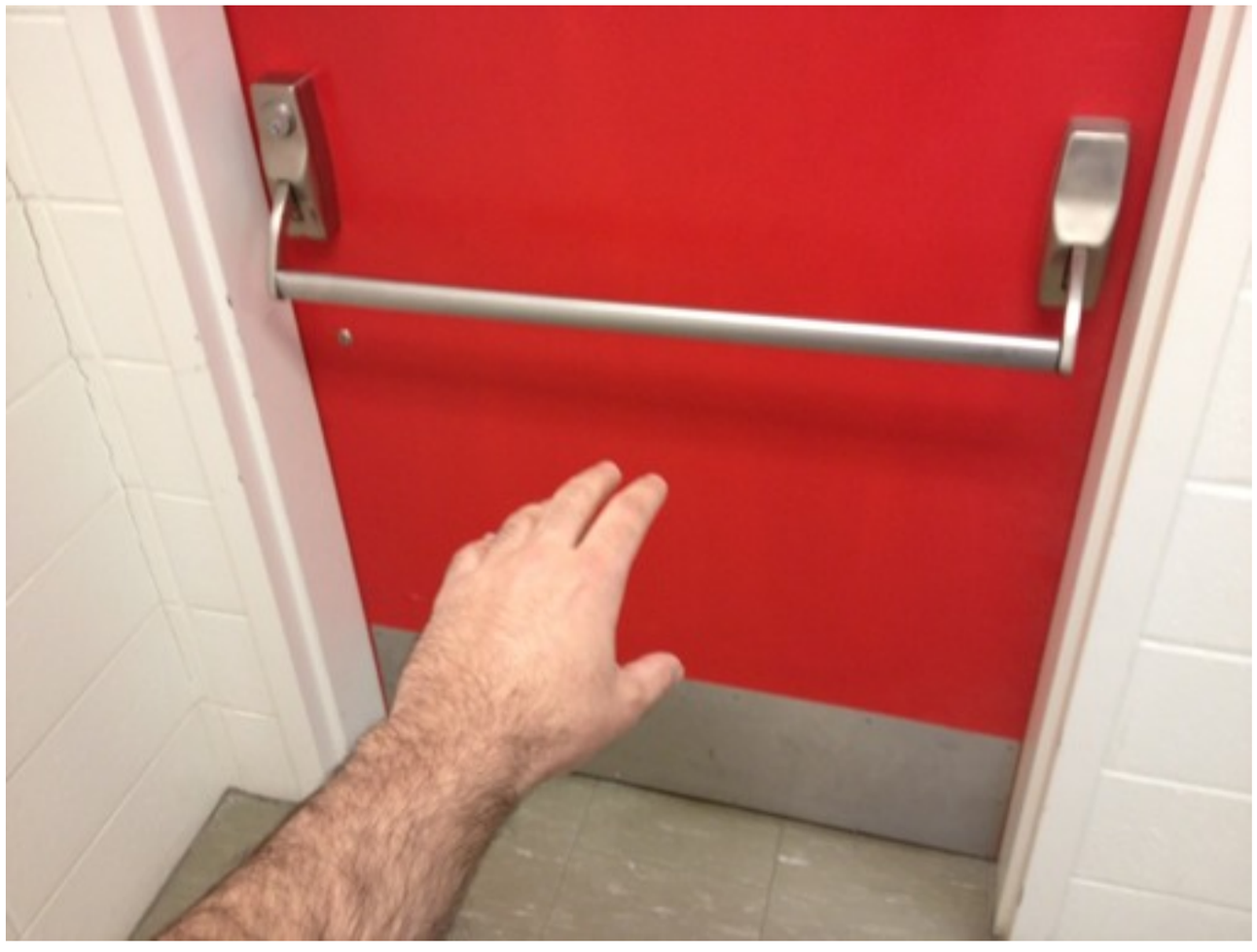
Long-latency response:
- Spinal and Cortical

Feedback corrections depend on the behavioural goal

Localized



Room for error along the bar



Feedback corrections depend on the behavioural goal

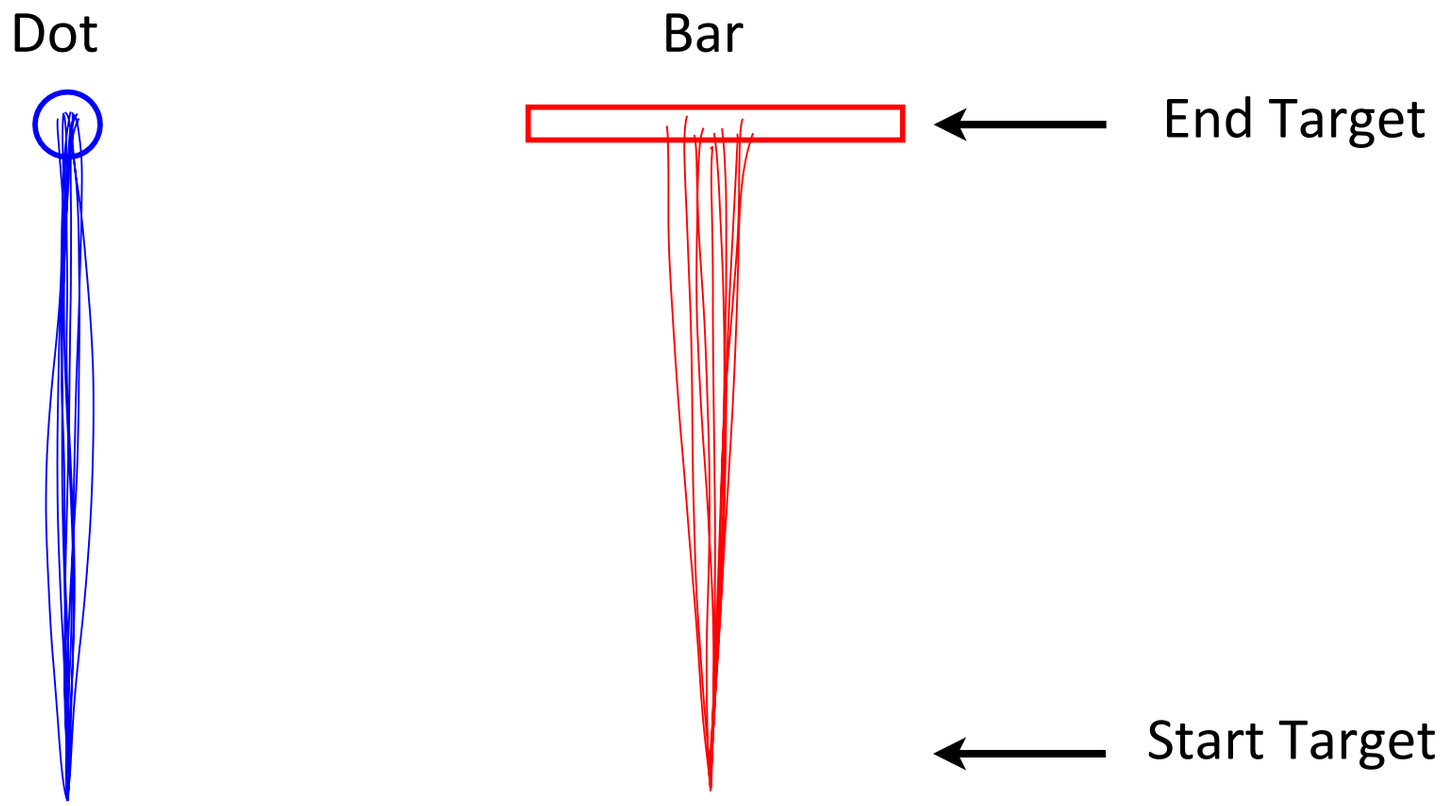
Localized

Room for error along the bar

Online corrections are influenced by the goal

Joe Nashed

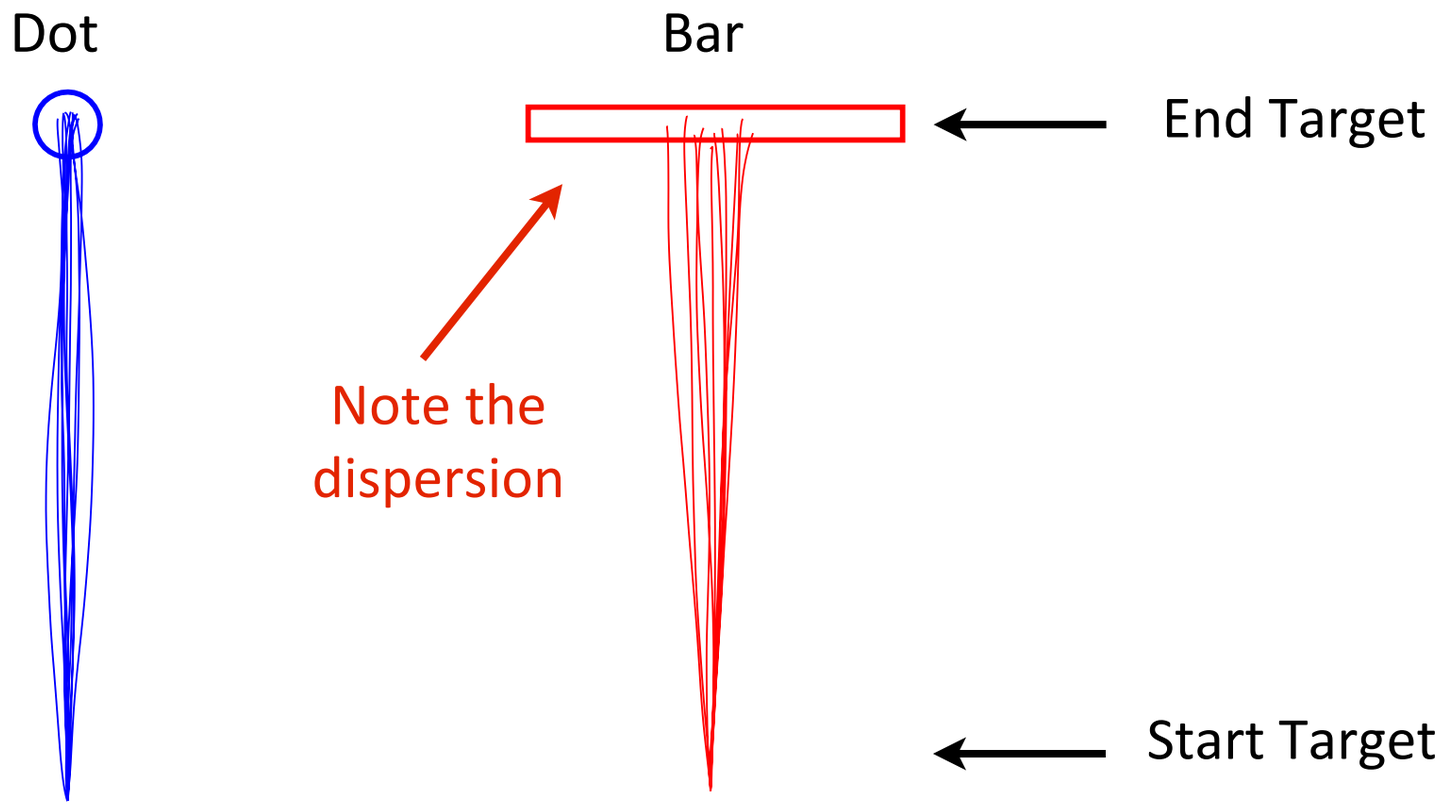
Optimal control Model



Online corrections are influenced by the goal

Joe Nashed

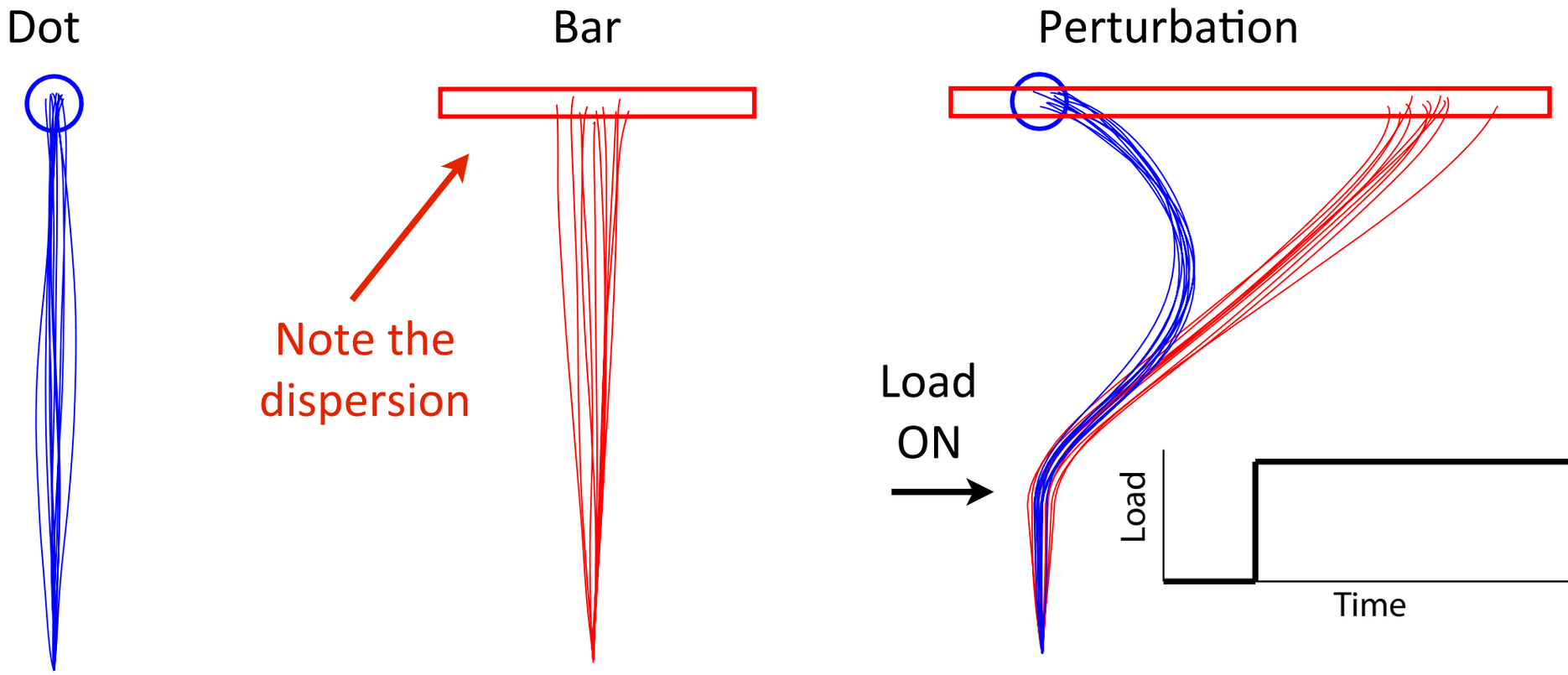
Optimal control Model



Joe Nashed

Online corrections are influenced by the goal

Optimal control Model

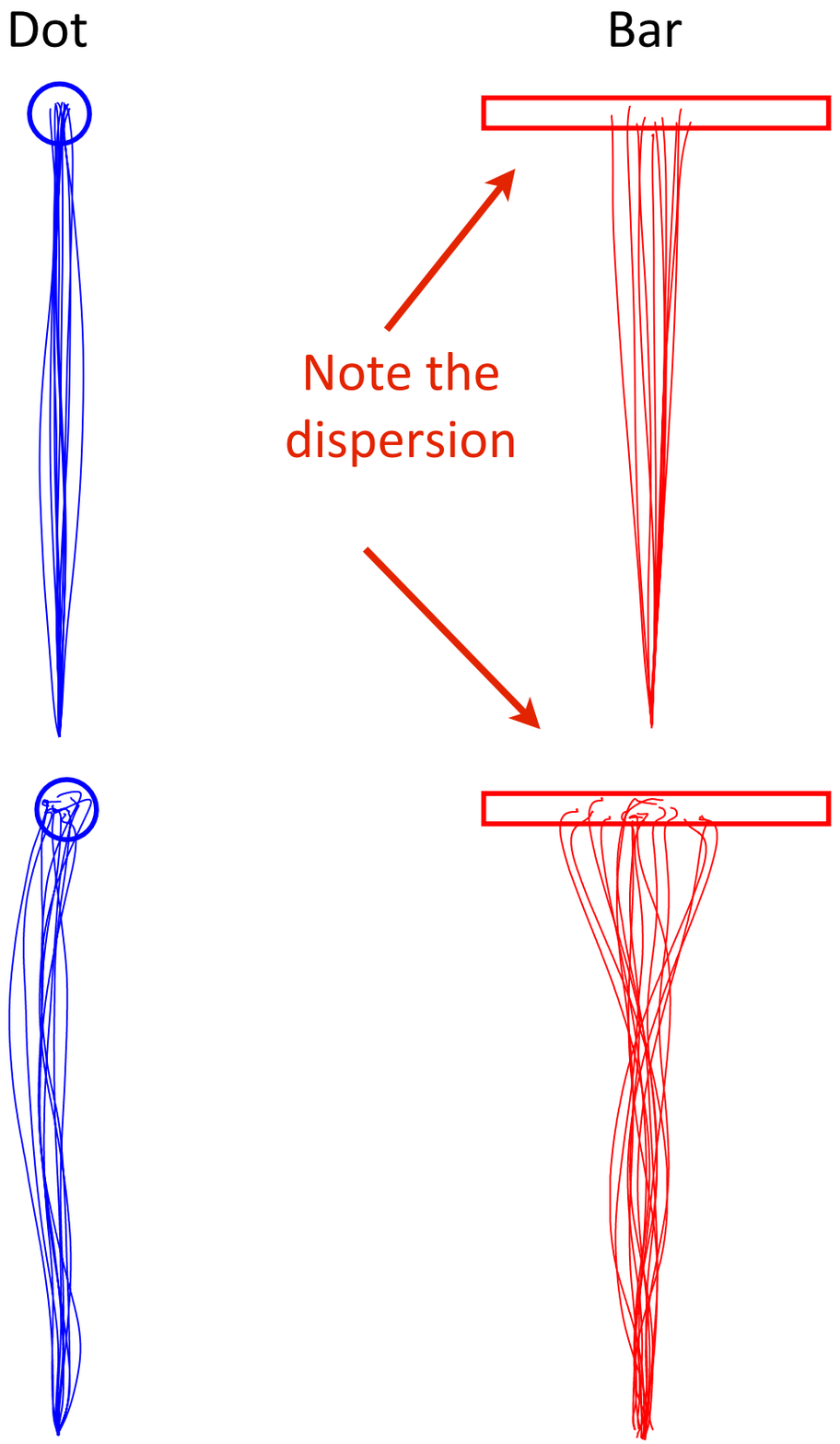


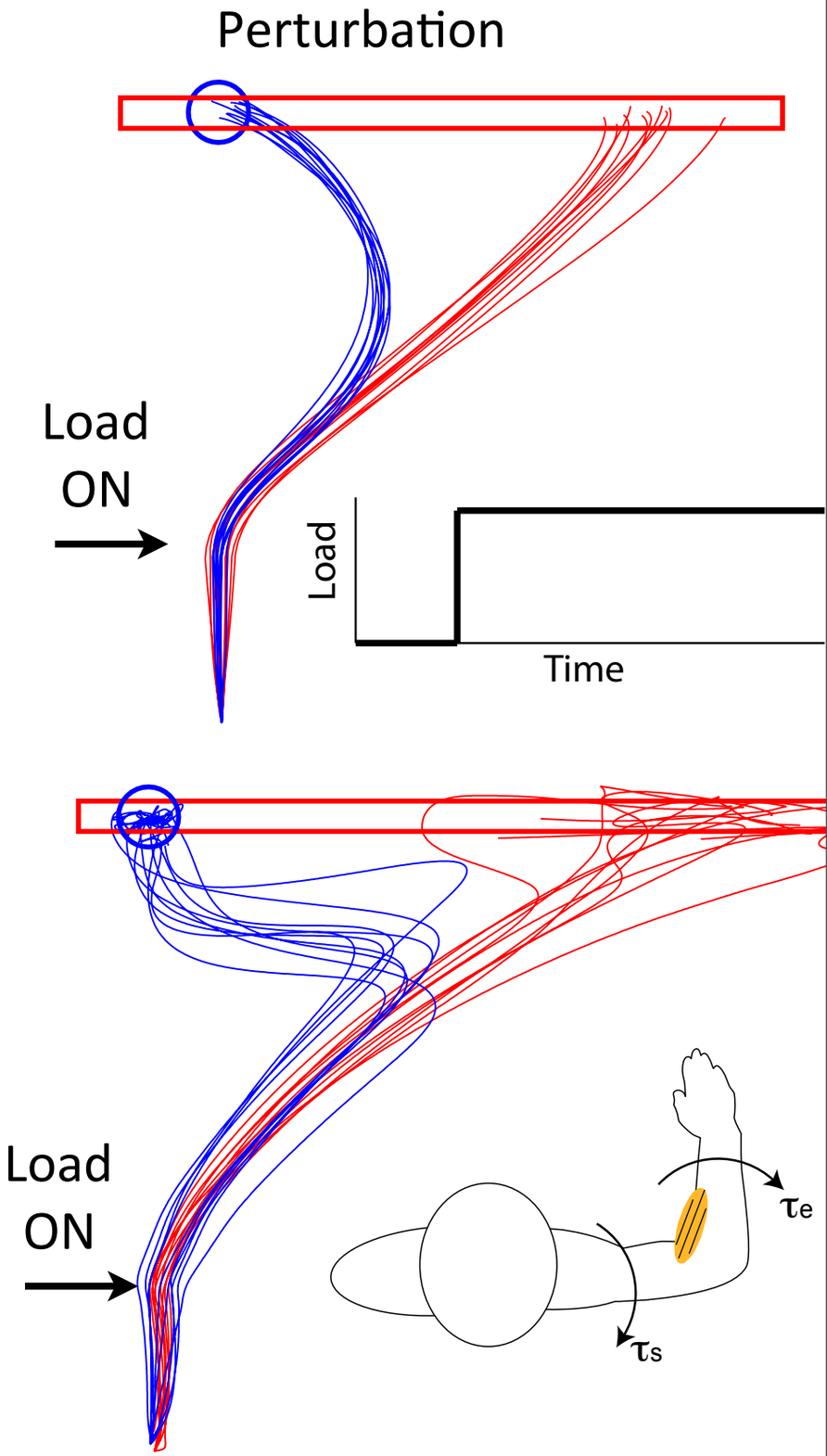
Online corrections are influenced by the goal

Joe Nashed

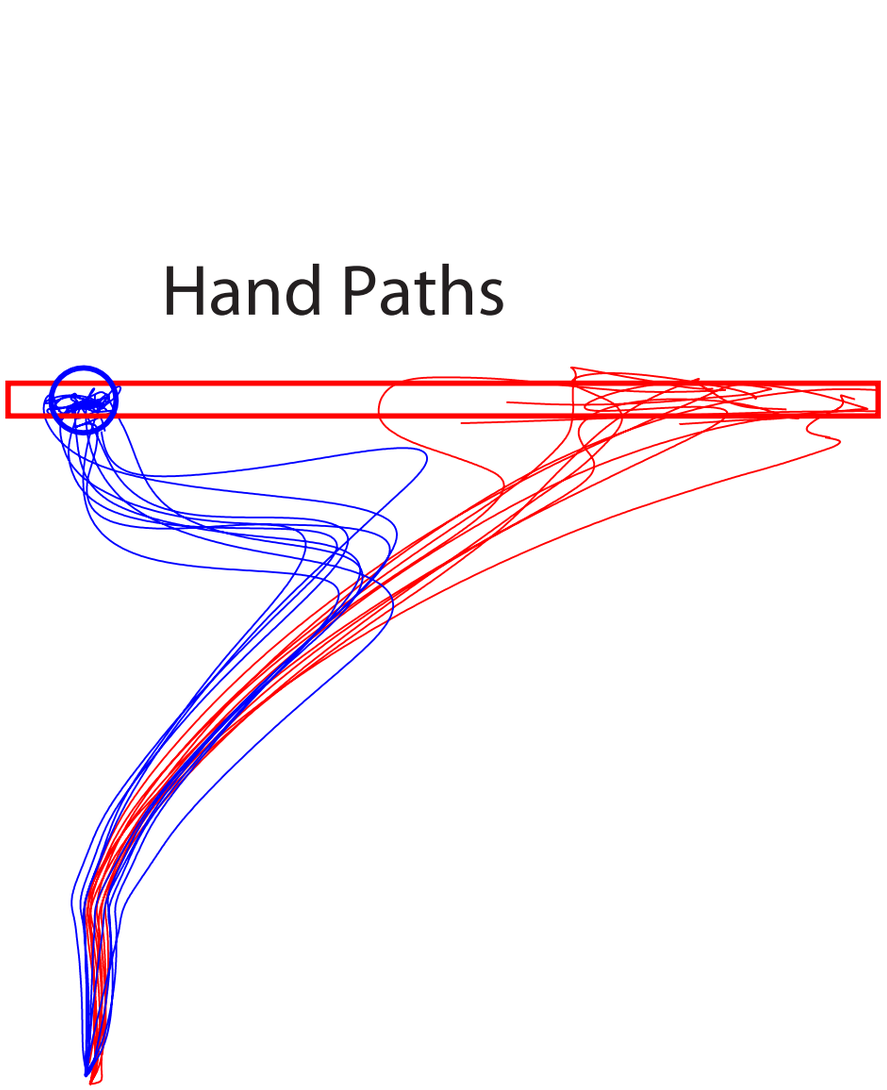
Optimal control Model

Exemplar Subject

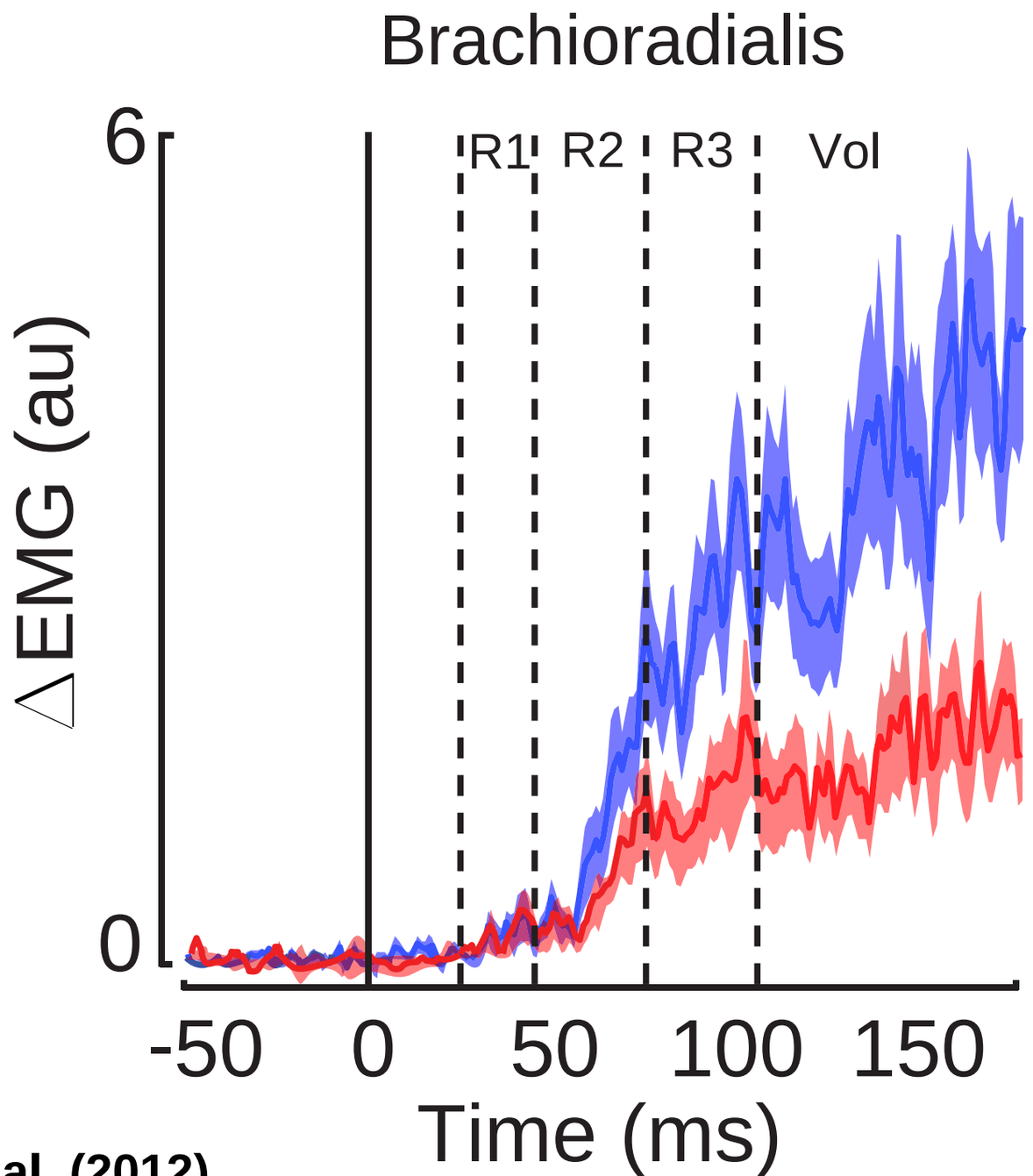




The shape of the goal influences the long latency response

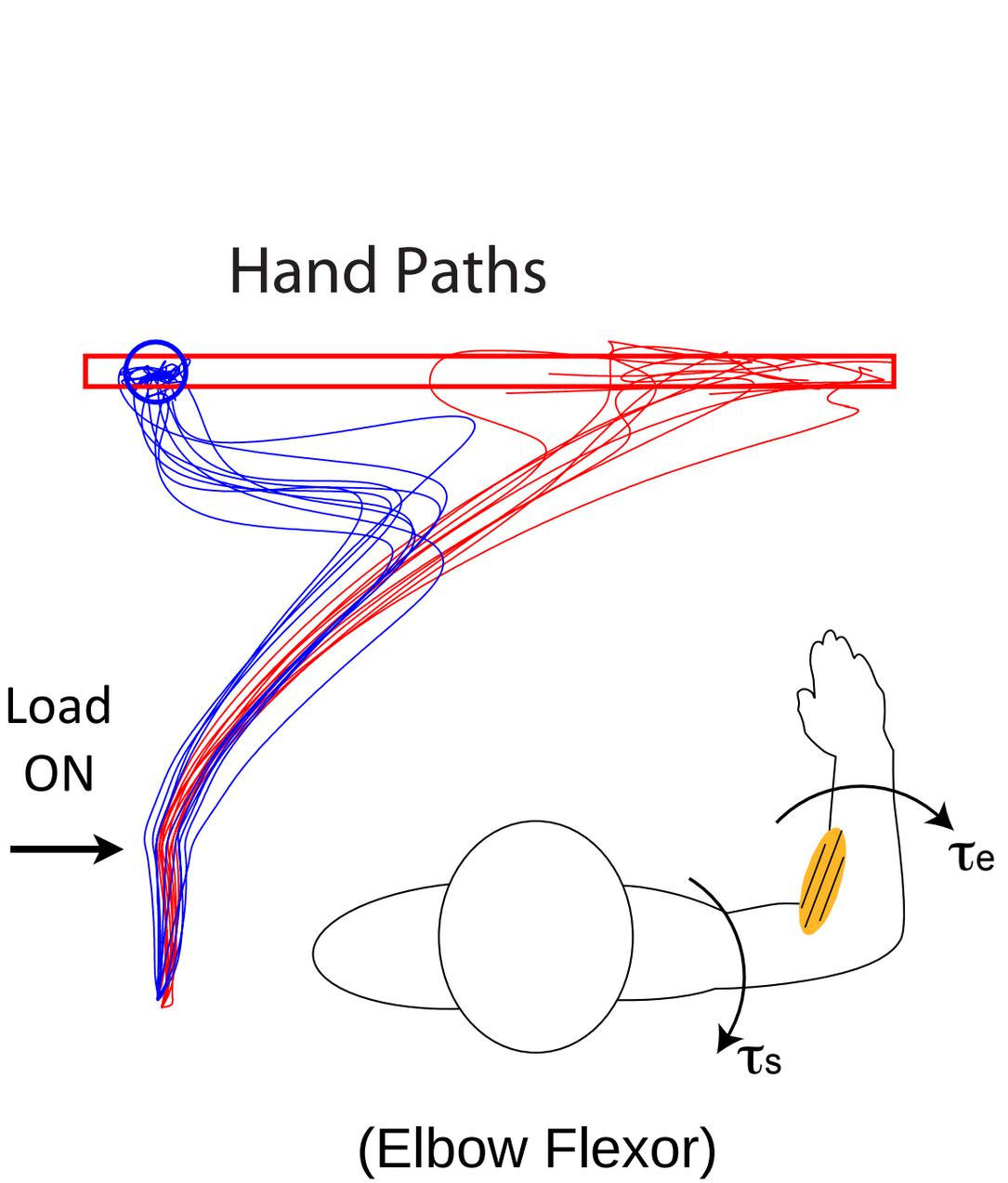


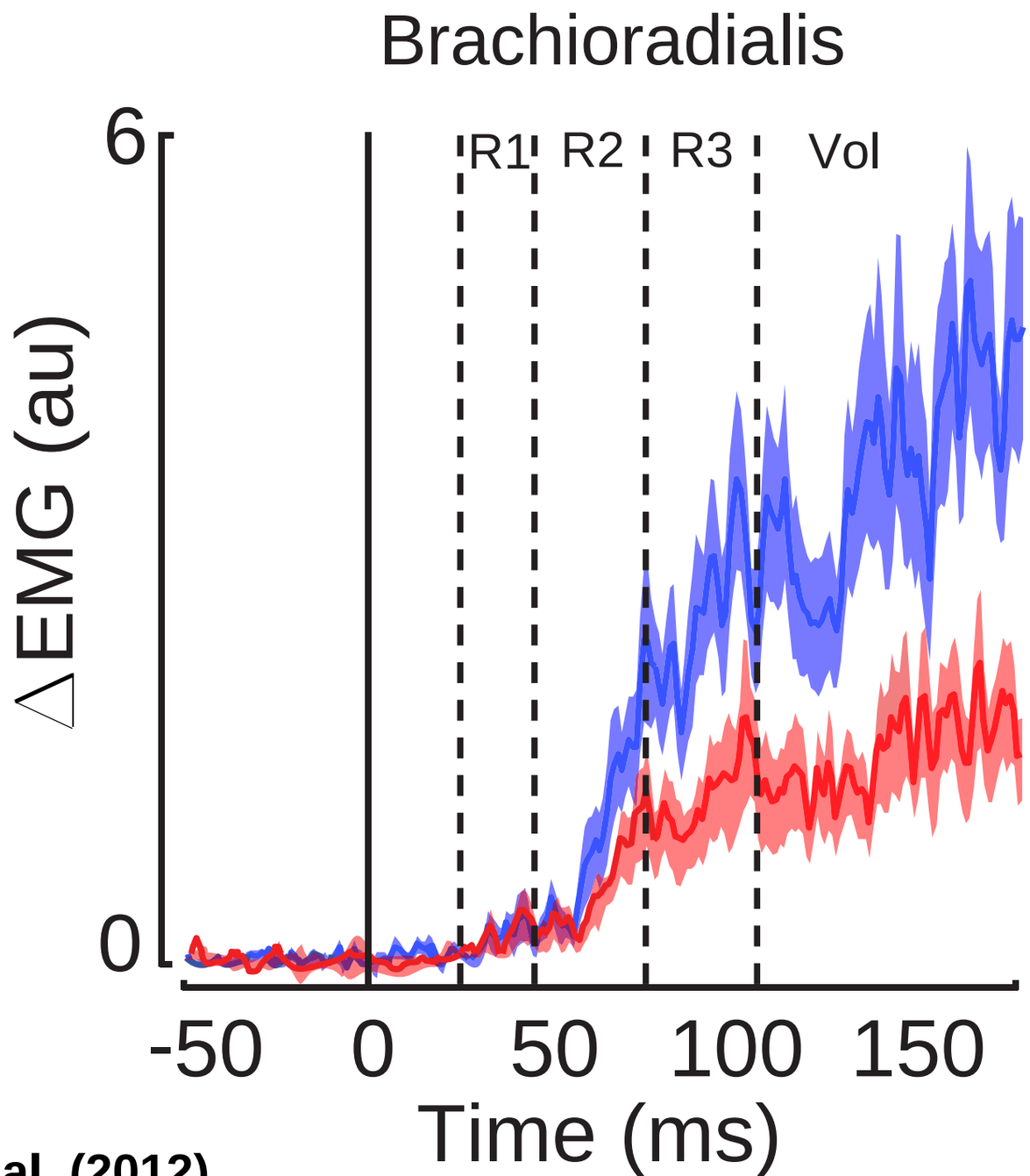
(Elbow Flexor)



Nashed et al. (2012)

The shape of the goal influences the long latency response

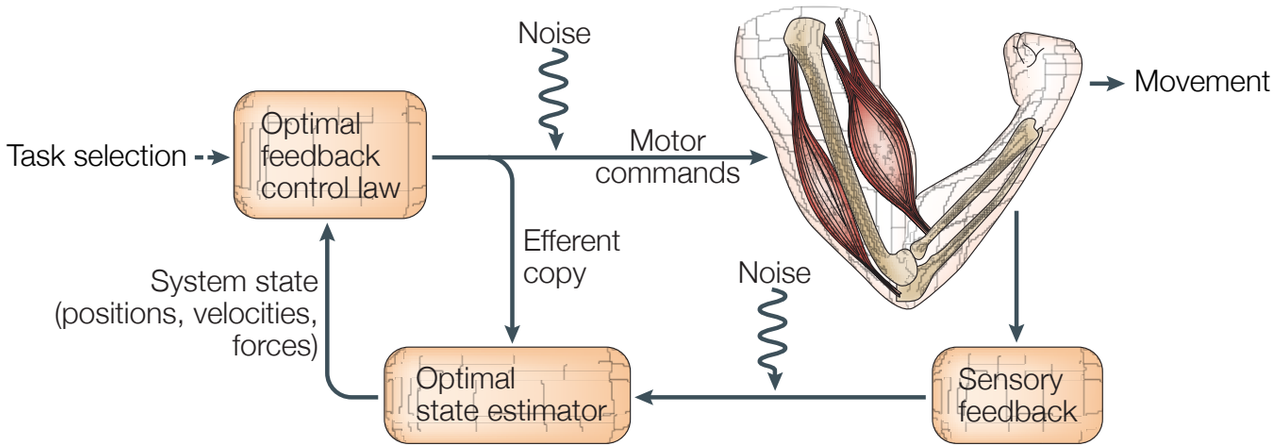


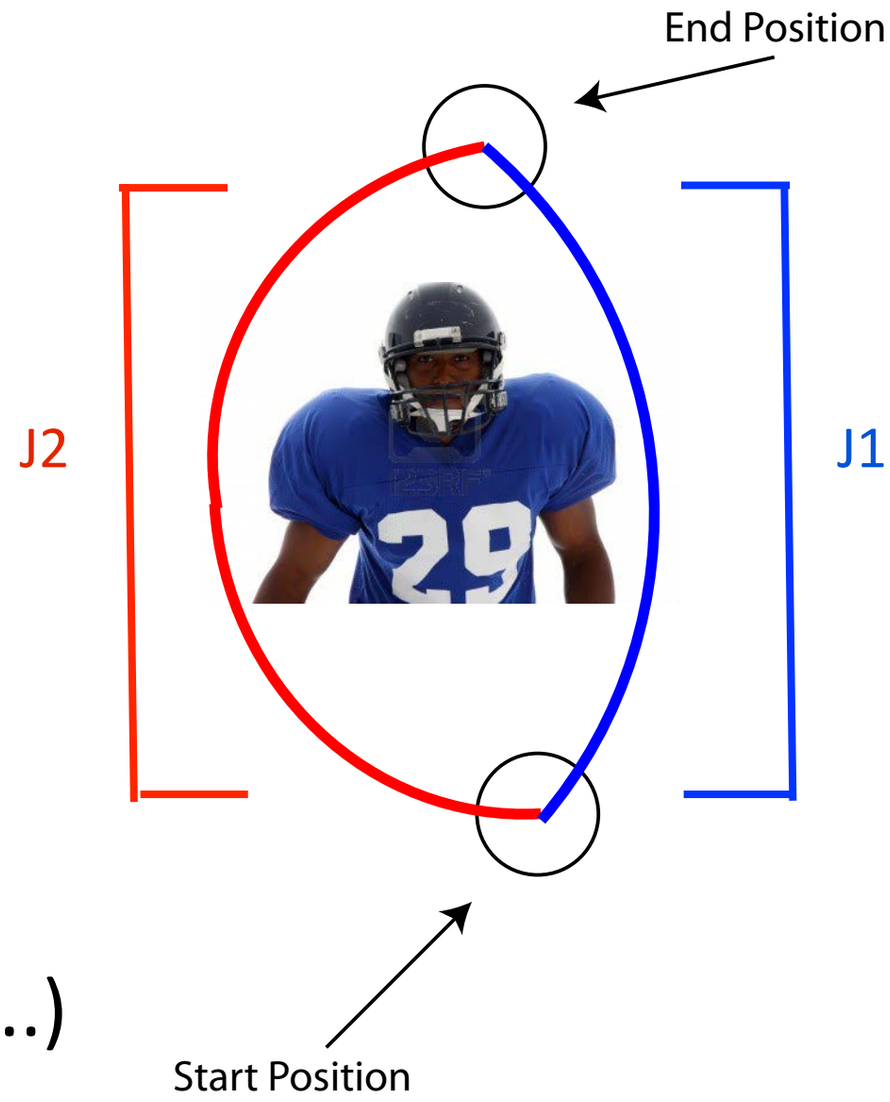


Nashed et al. (2012)

What if the player gets hit sideways?

How do you move to a goal?
Cost-to-go defines how to best reach a goal

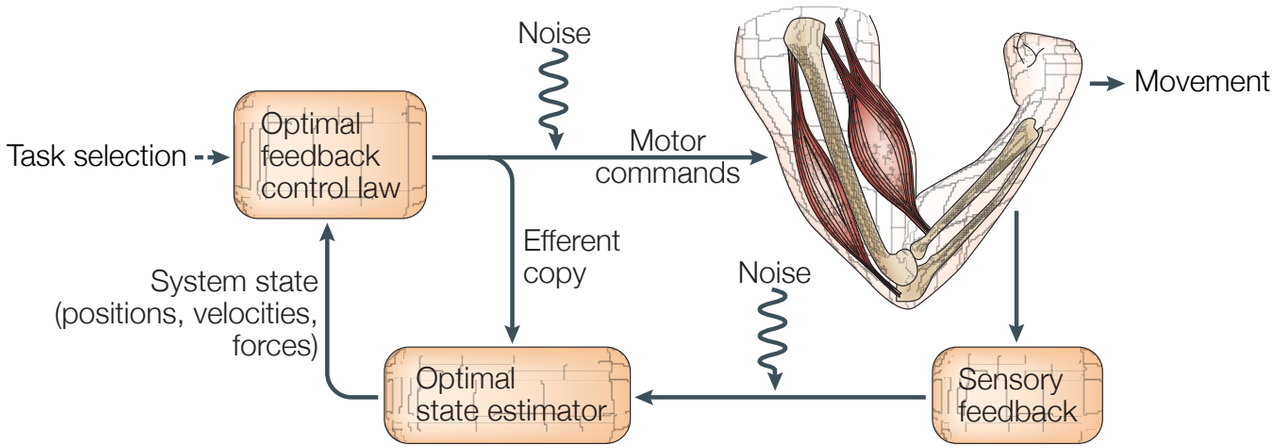


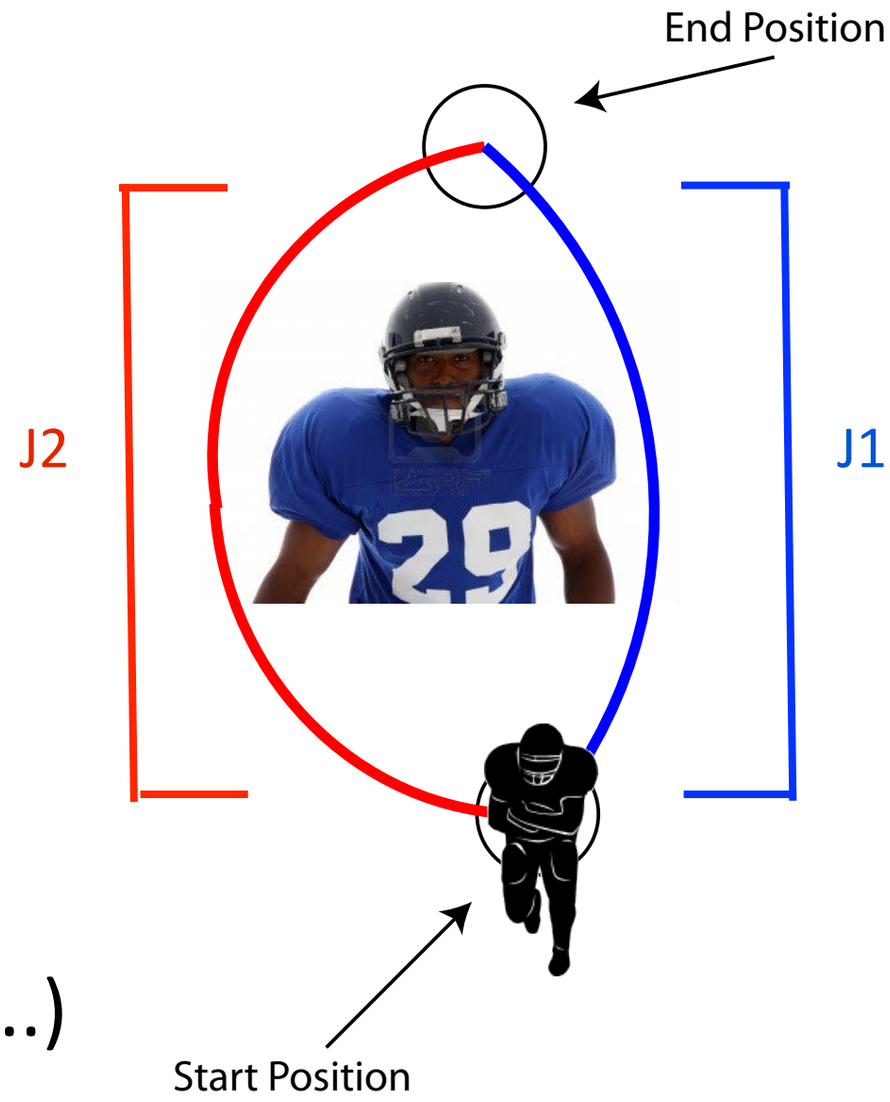


Cost-to-go: Is the total remaining cost (i.e accuracy, energy..) given the current state

J1 < J2

How do you move to a goal?
Cost-to-go defines how to best reach a goal





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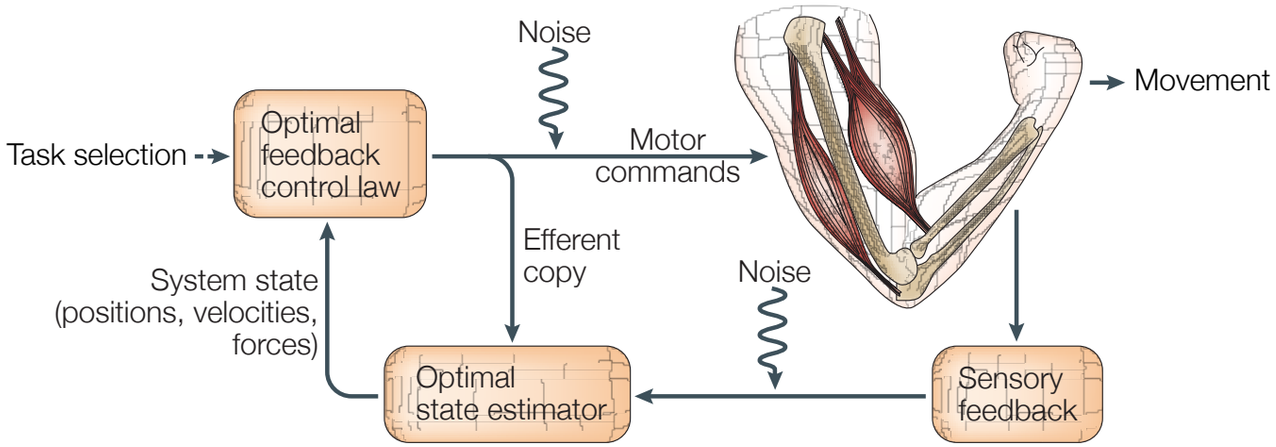

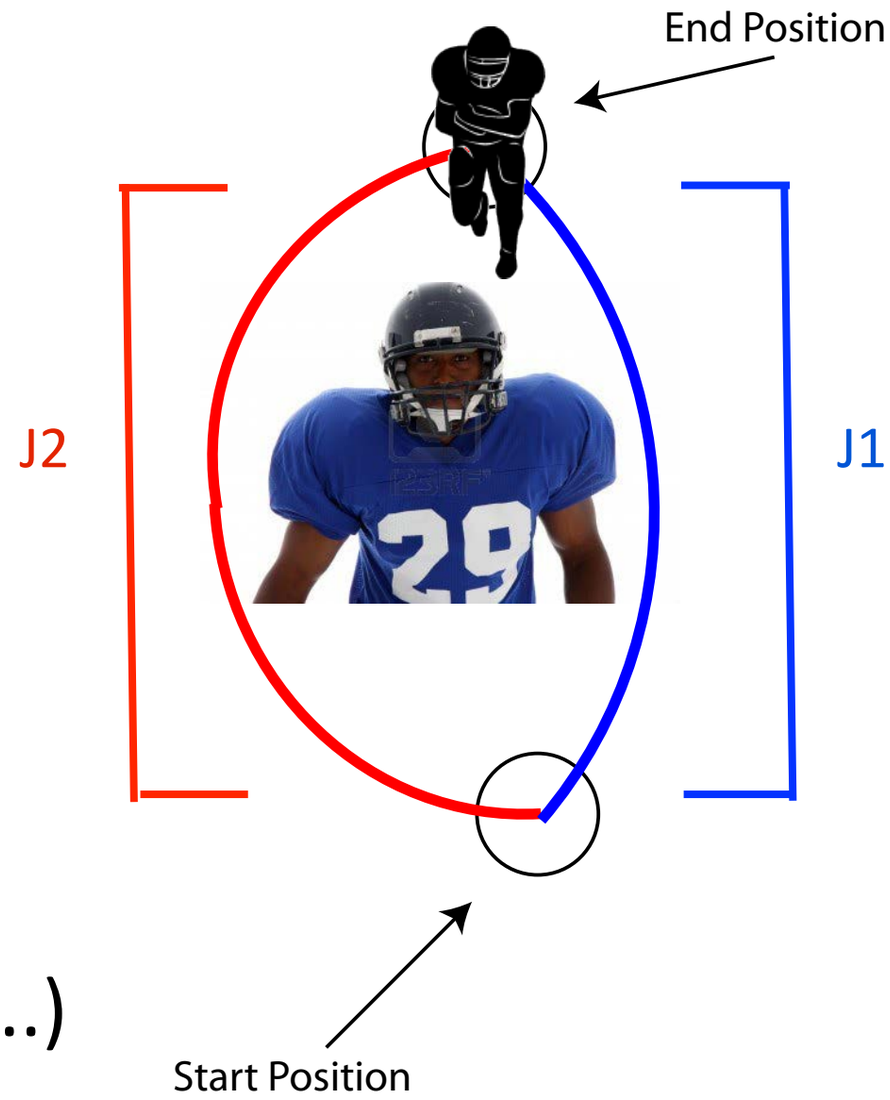

Cost-to-go: Is the total remaining cost (i.e accuracy, energy..) given the current state

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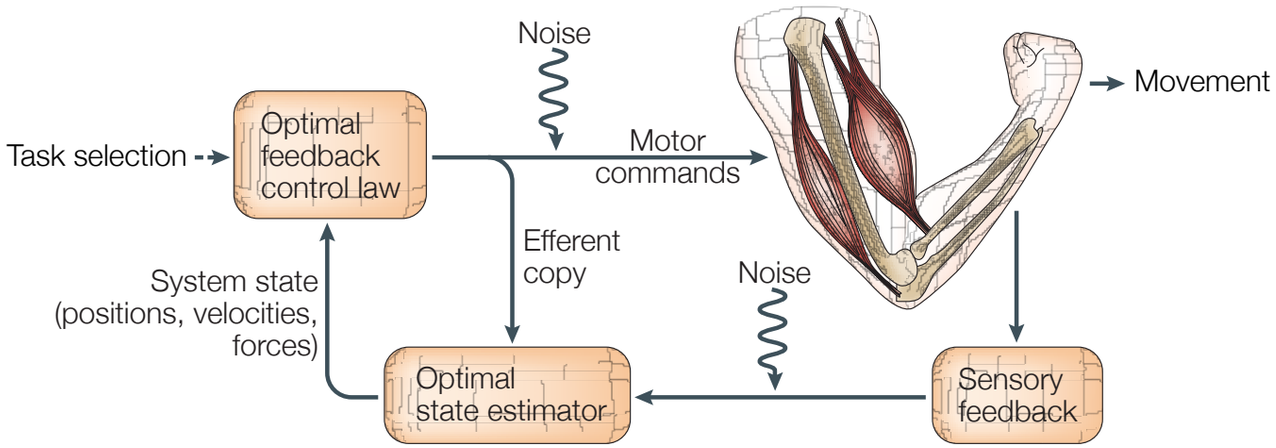
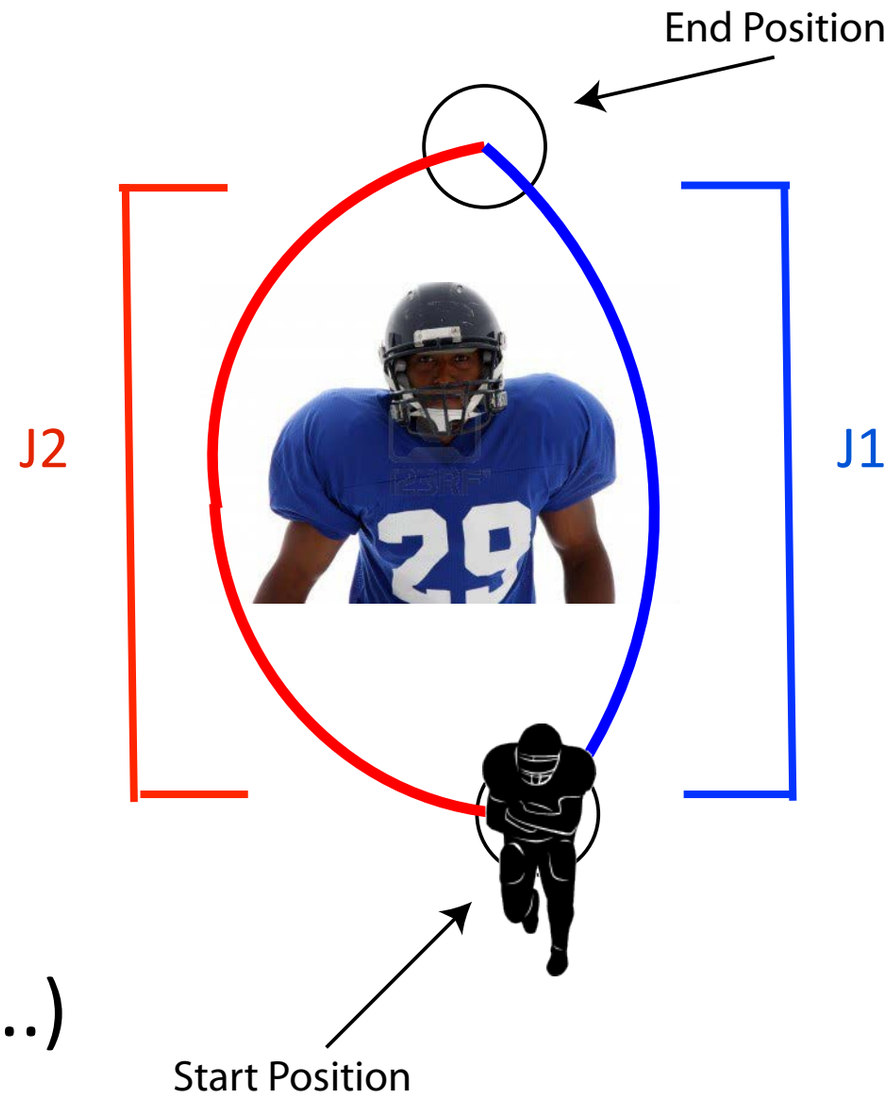
How do you move to a goal?
Cost-to-go defines how to best reach a goal





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

J1 < J2

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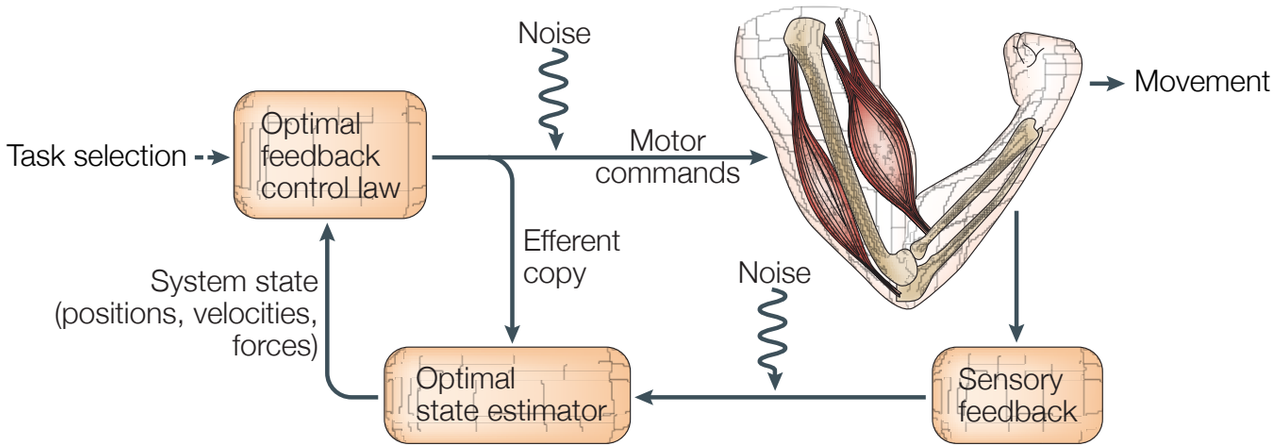
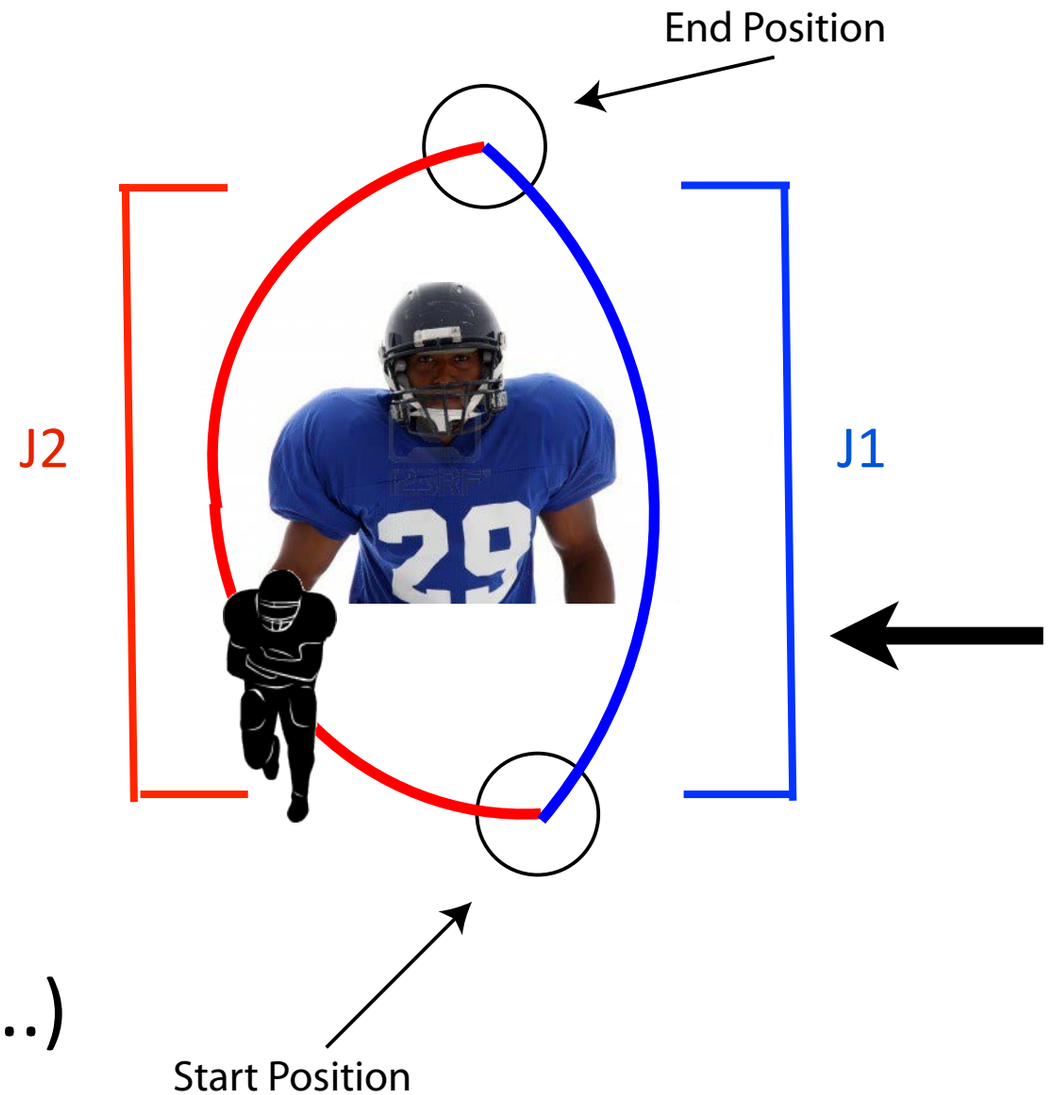
Cost-to-go defines how to best reach a goal

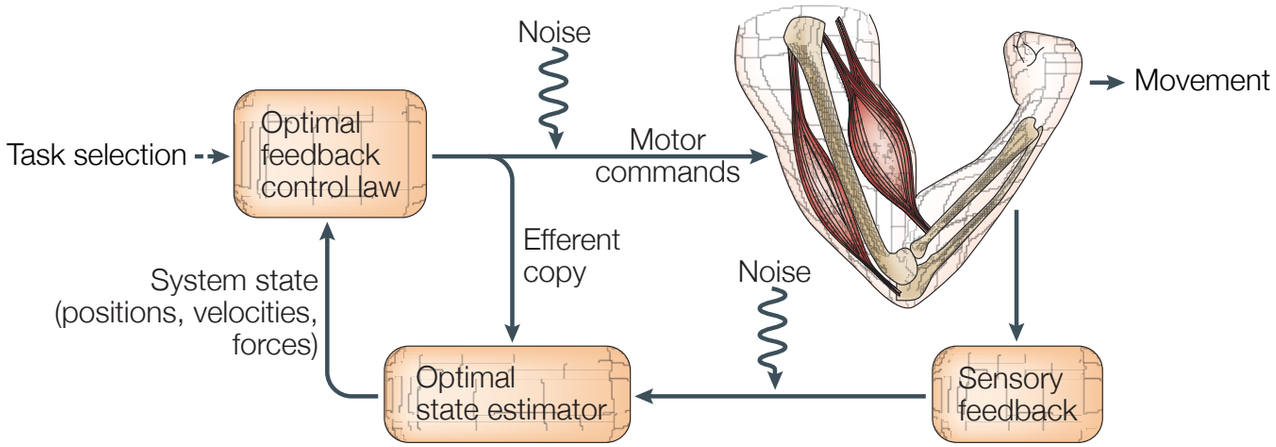


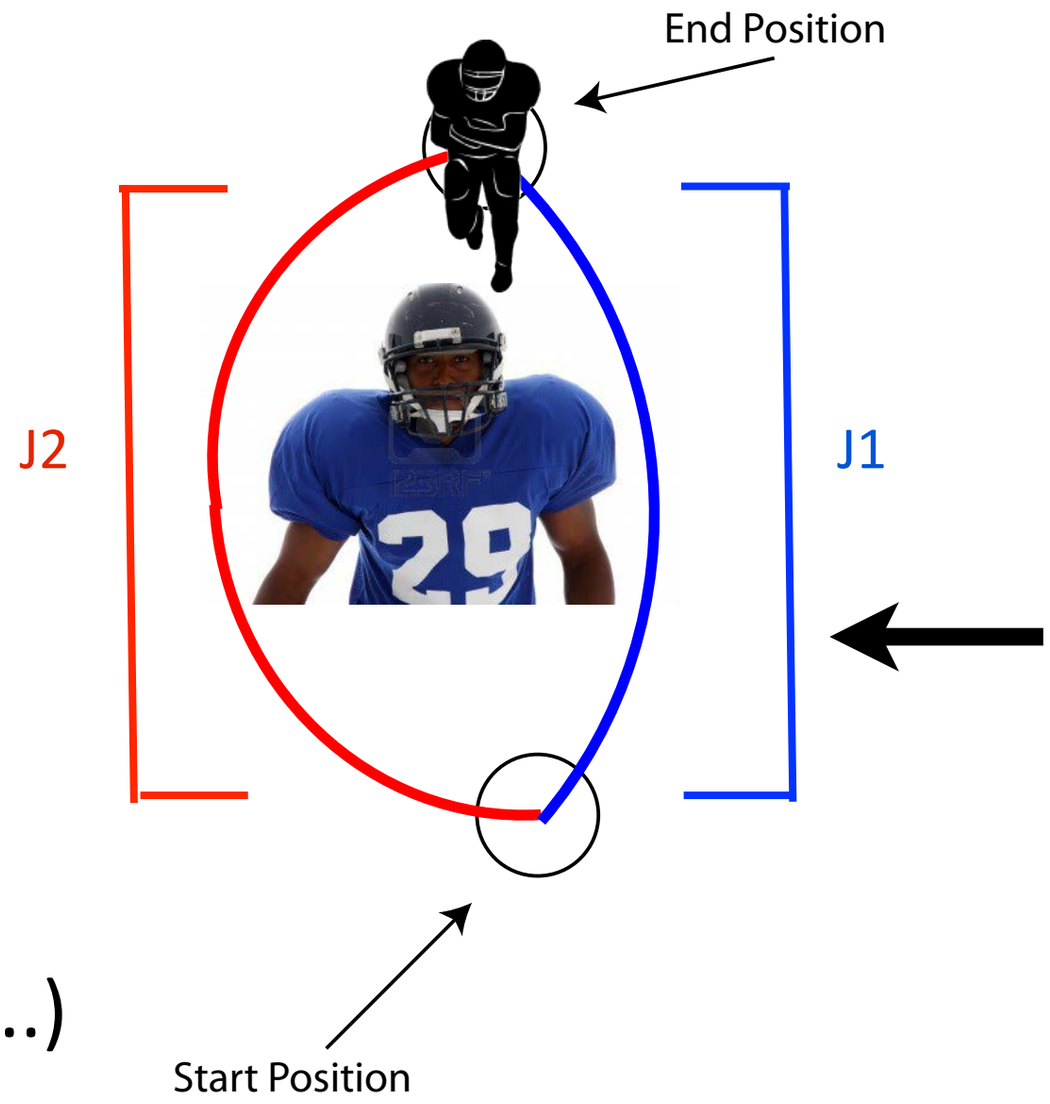


Cost-to-go: Is the total remaining cost (i.e accuracy, energy..) given the current state

J1 < J2

How do you move to a goal?
Cost-to-go defines how to best reach a goal

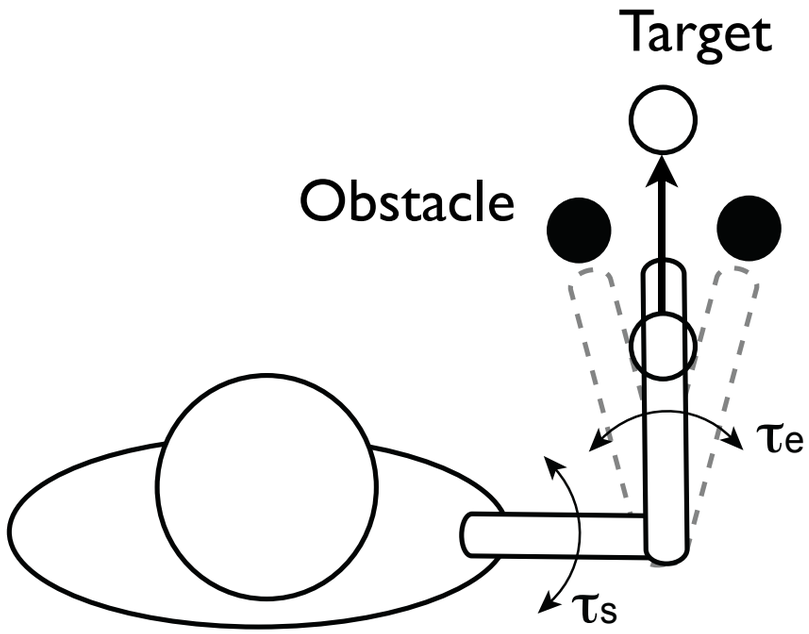


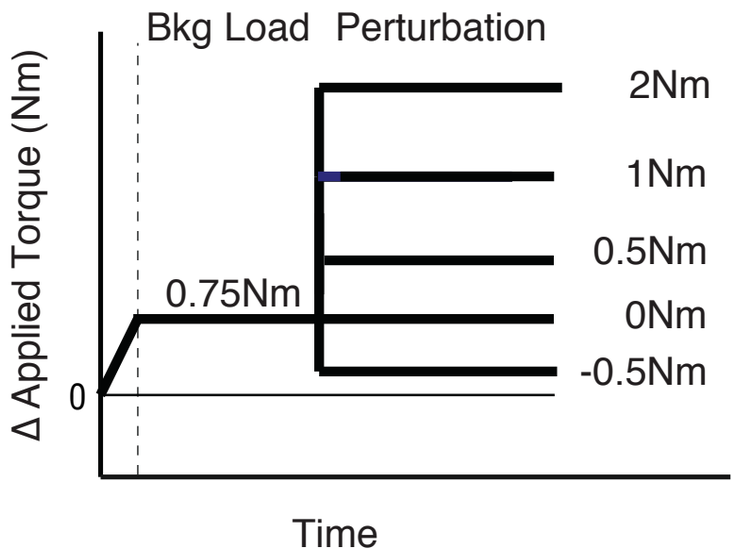


Cost-to-go: Is the total remaining cost (i.e accuracy, energy..) given the current state

~~J1 < J2~~ J2 < J1

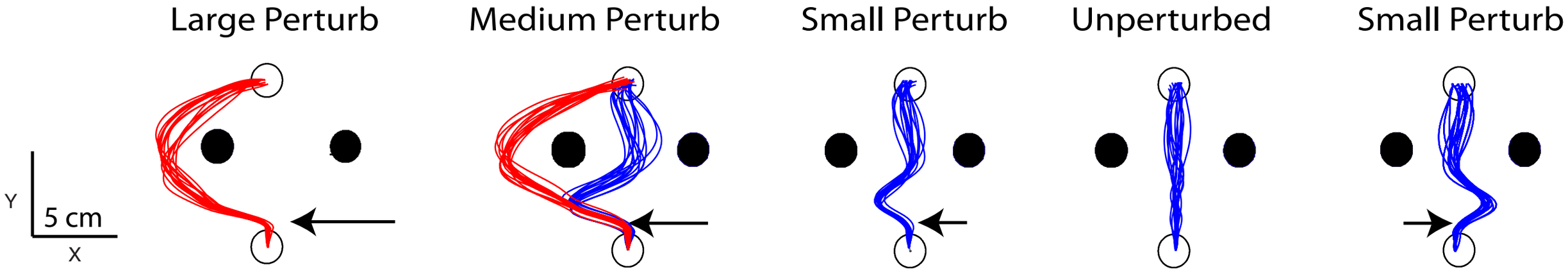
Reach to target with peripheral obstacles





Load applied to both joints

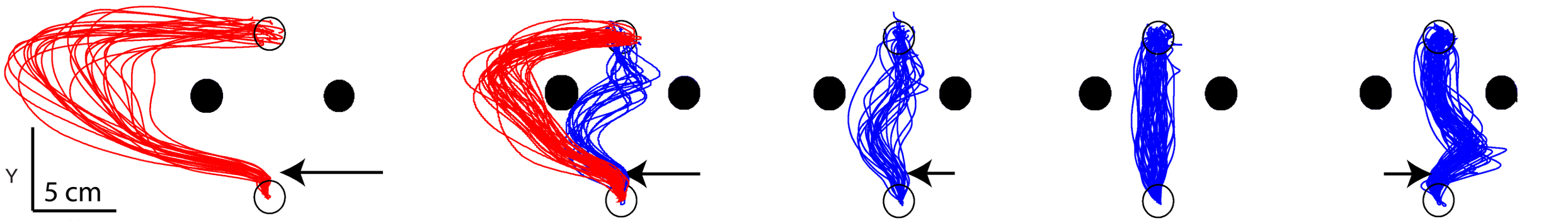
Optimal Feedback Control Model



Reach to target with peripheral obstacles

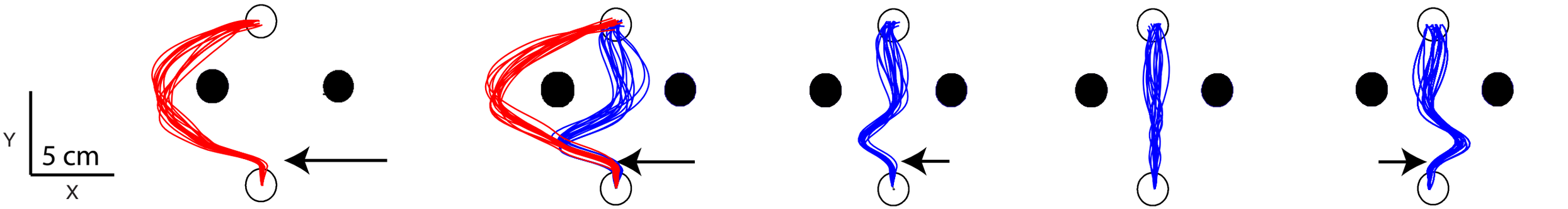
Exemplar Subject

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

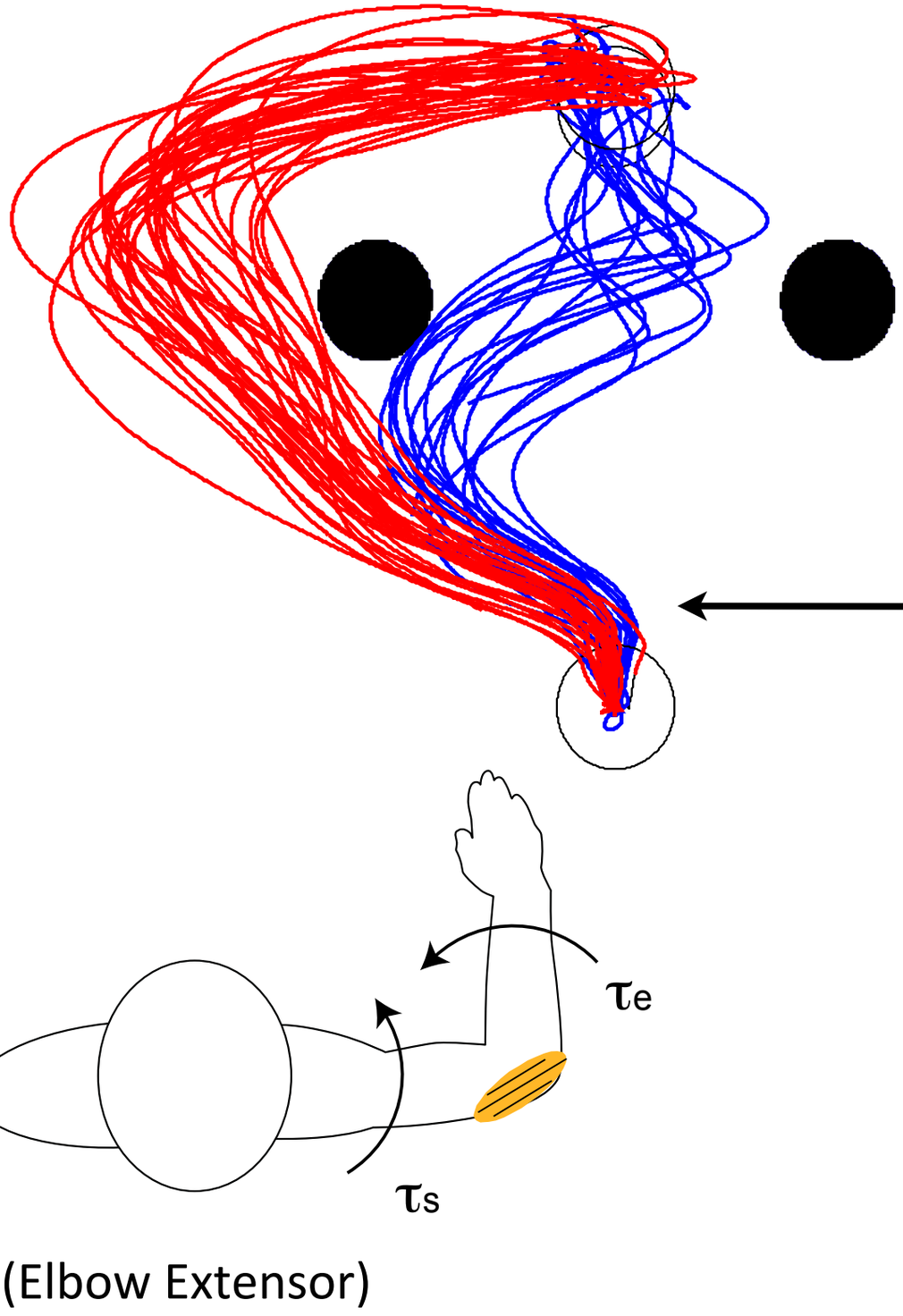


Optimal Feedback Control Model

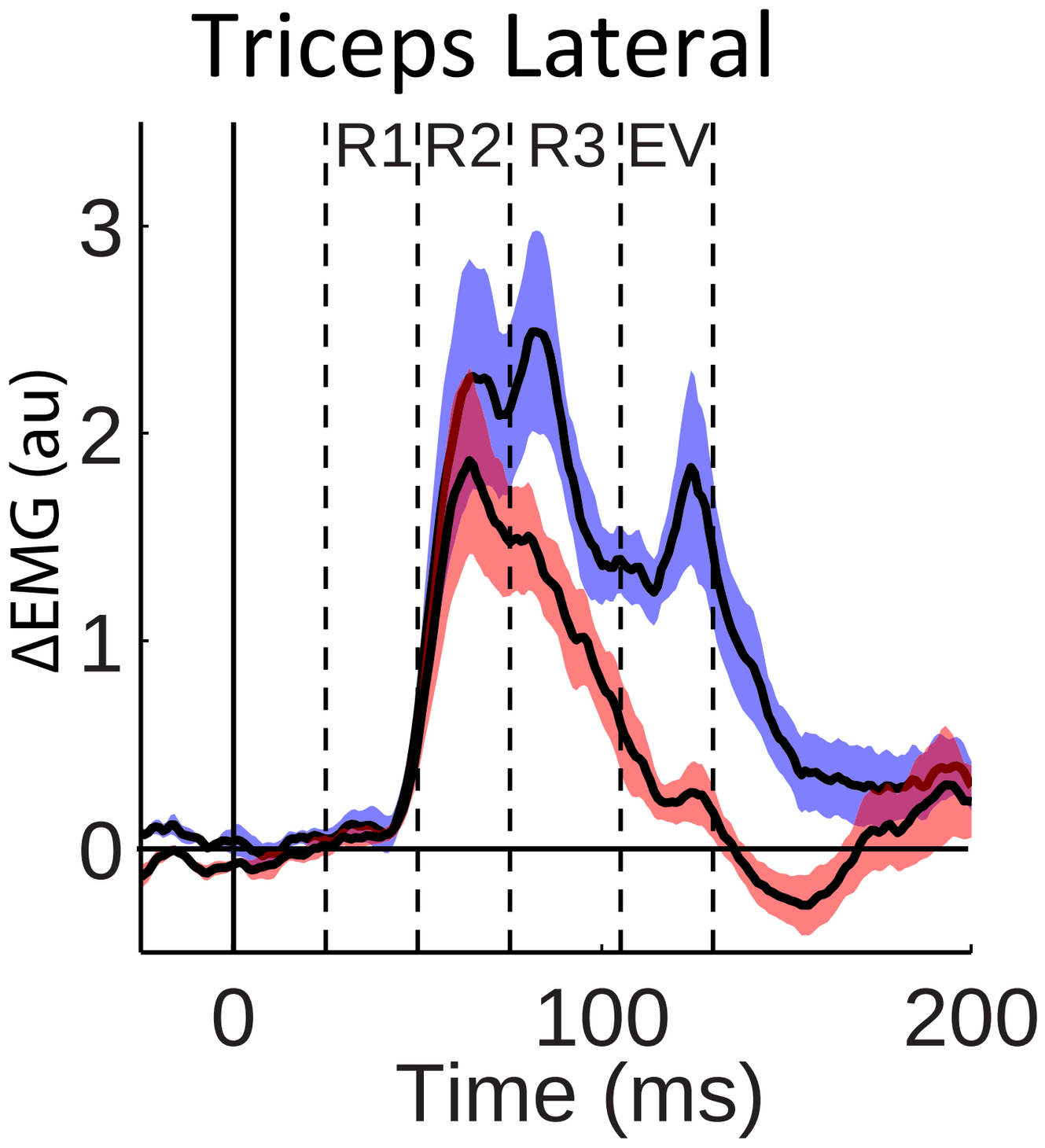
Large Perturb | Medium Perturb | Small Perturb | Unperturbed | Small Perturb



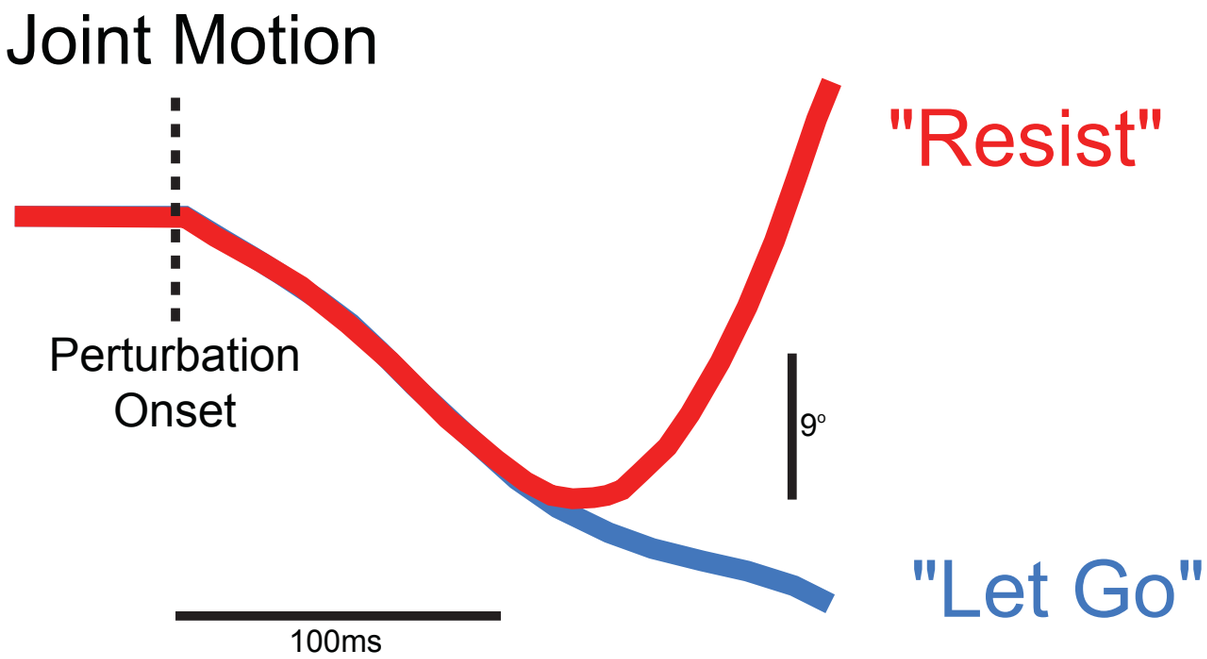
Online “decisions” made in 60ms

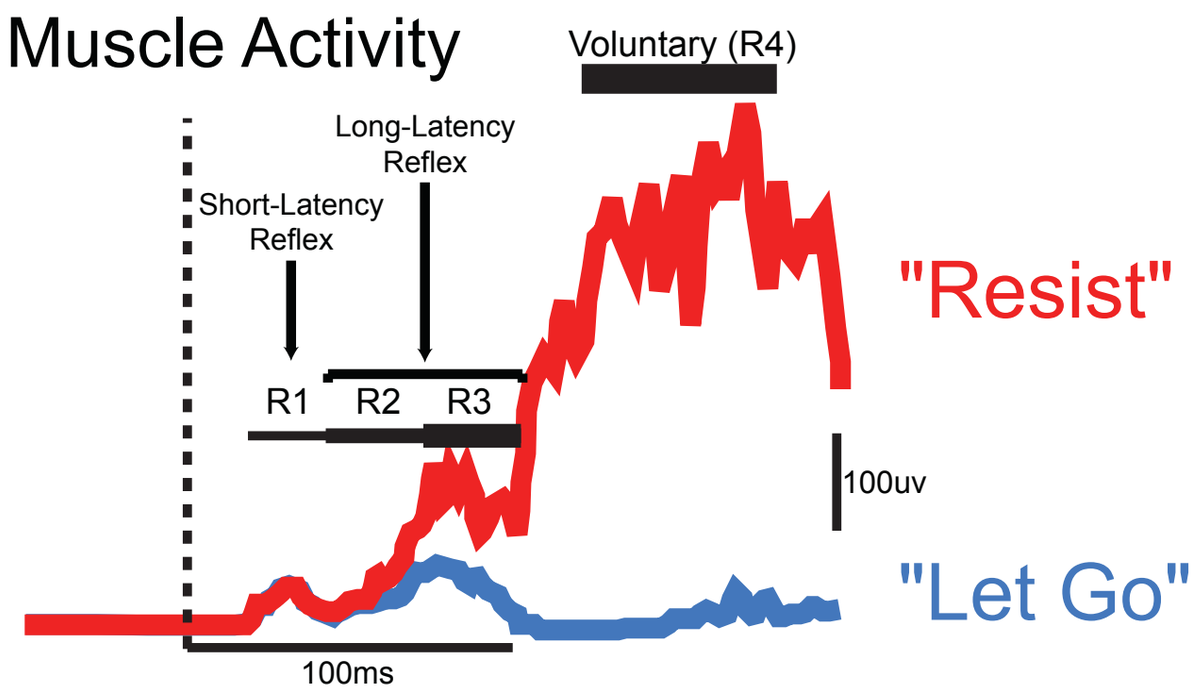


(Elbow Extensor)



Feedback Elicits Task Selection



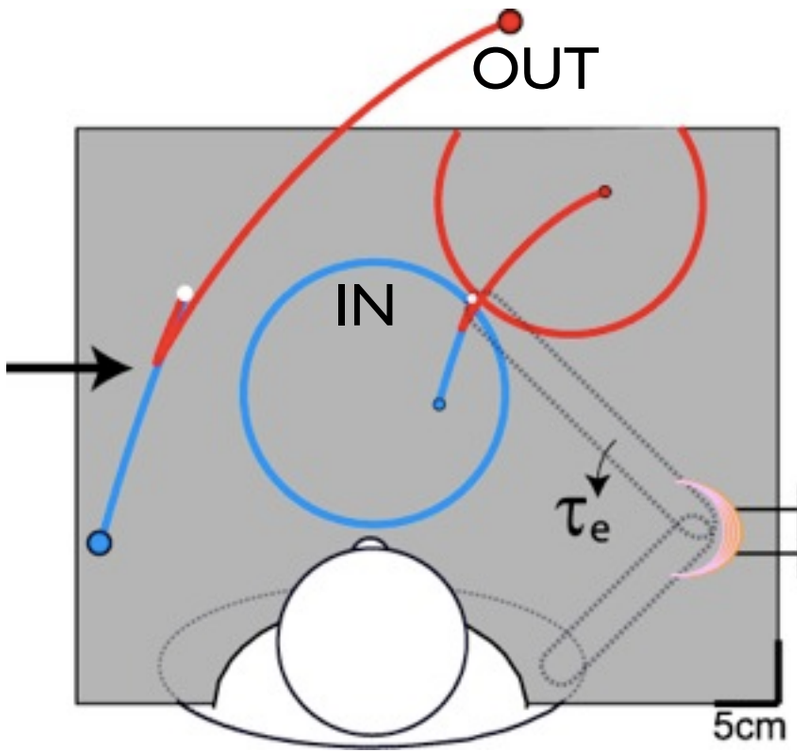


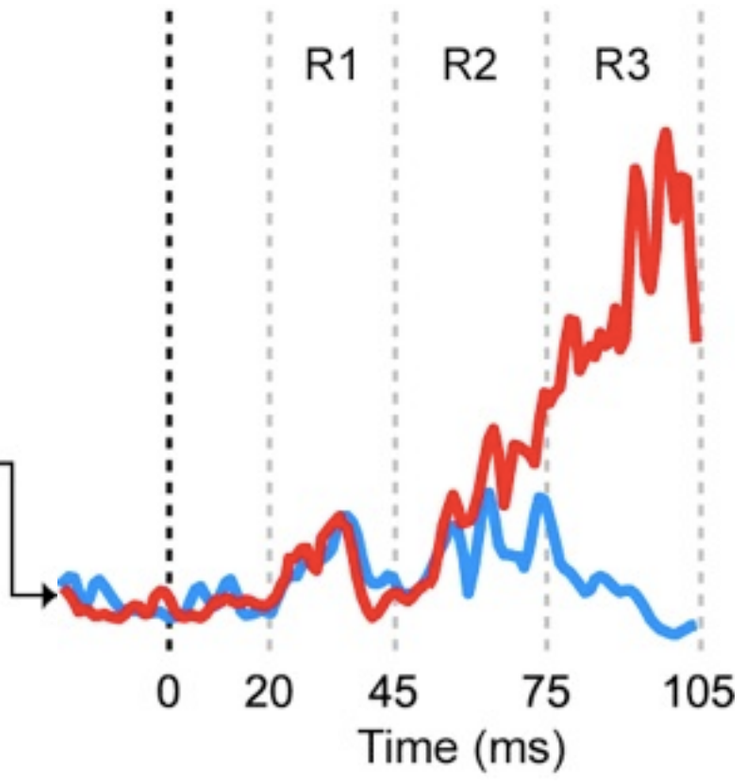
Rothwell et al., 1980

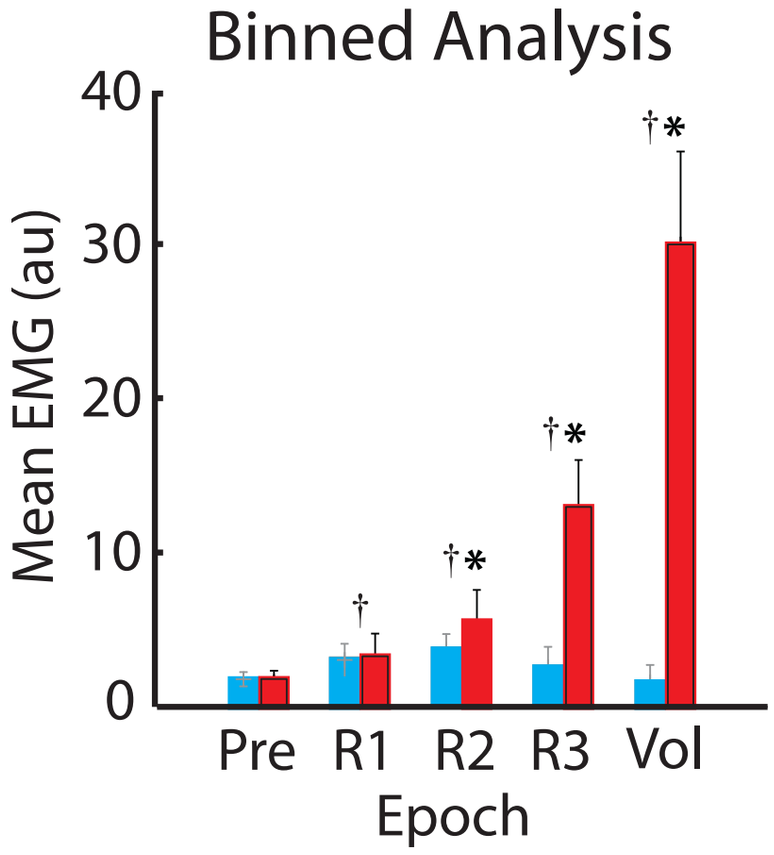
Feedback for Rapid Task Selection

Andrew Pruszynski

Spatial Analog of Resist/Let Go





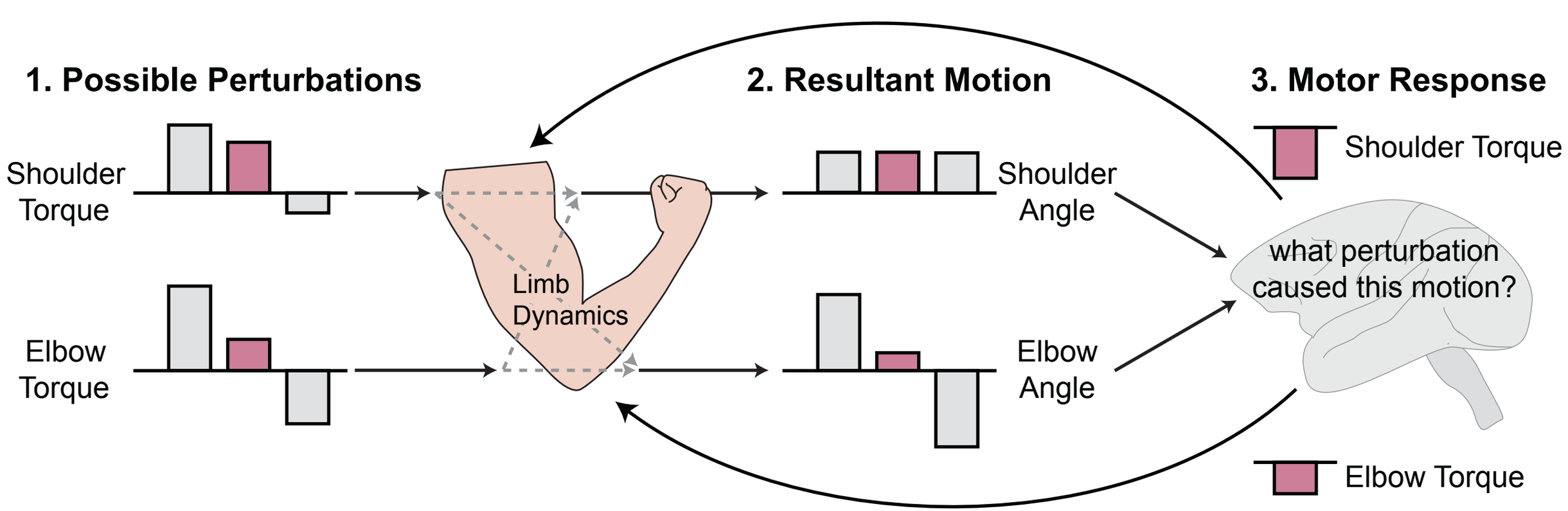


Load Applied and Must Move to Spatial Target

Pruszynski et al., JNP 2008

When do corrective responses consider limb mechanics?

Limb mechanics causes interactions between shoulder and elbow



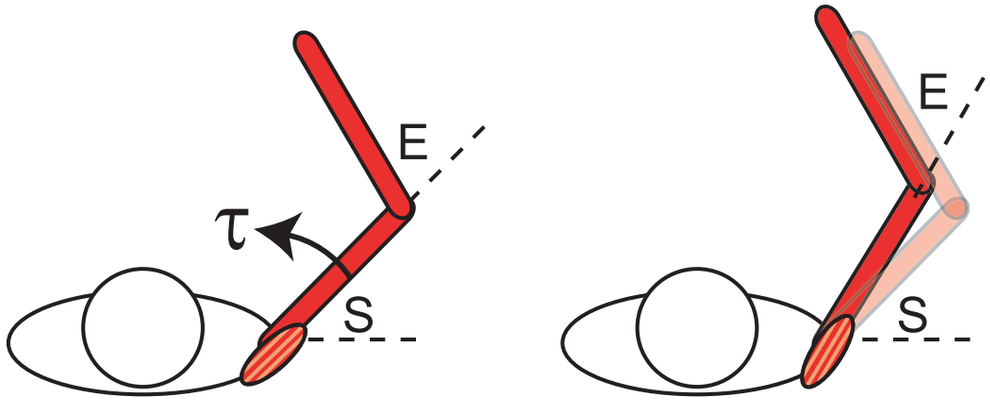
Isaac Kurtzer

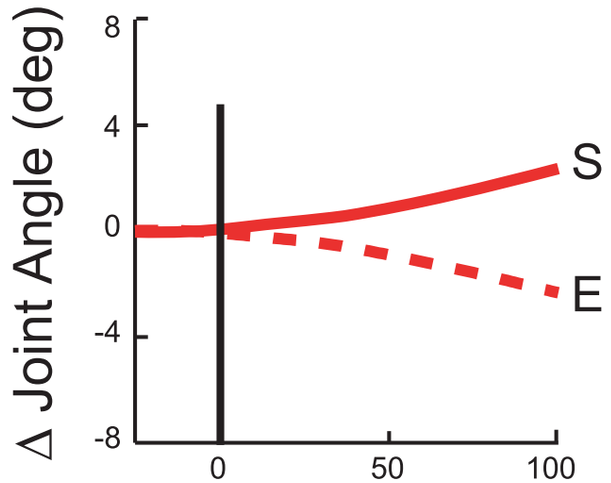
Same shoulder motion, different underlying torques

Applied Torque

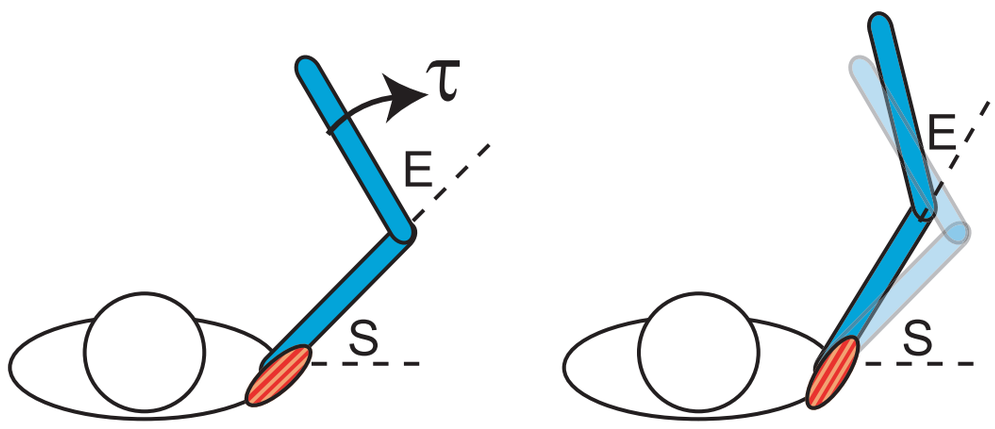
Induced Motion

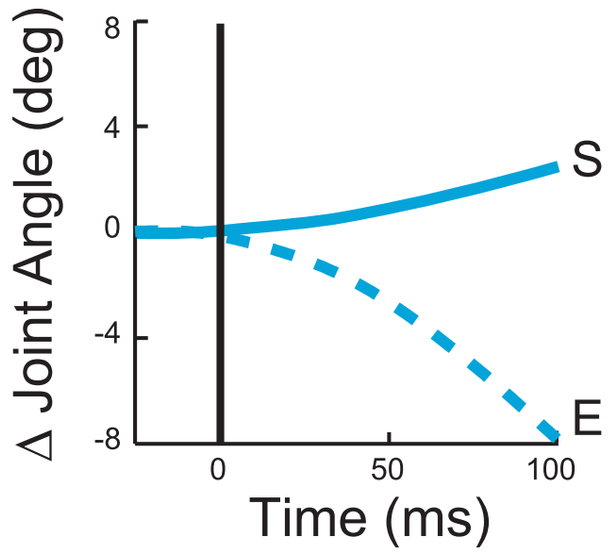
Shoulder Torque





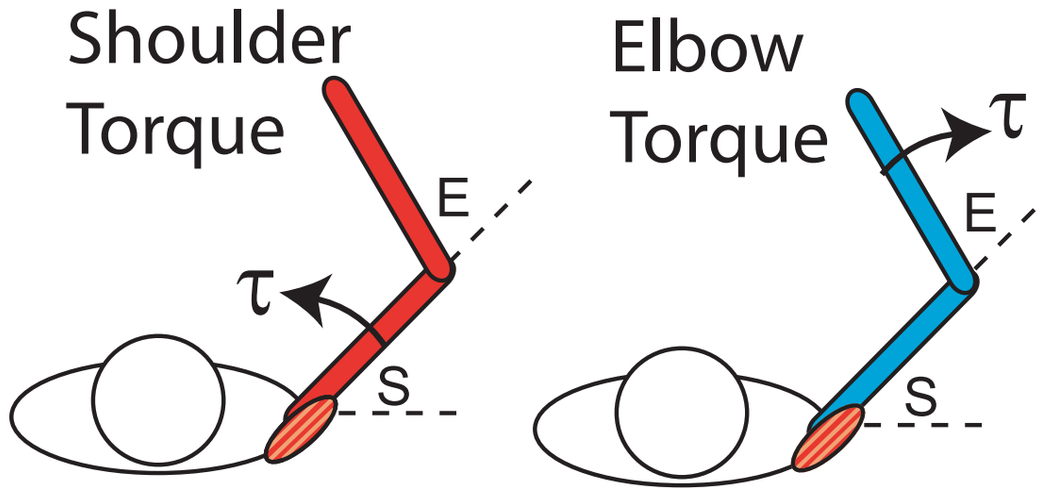
Elbow Torque

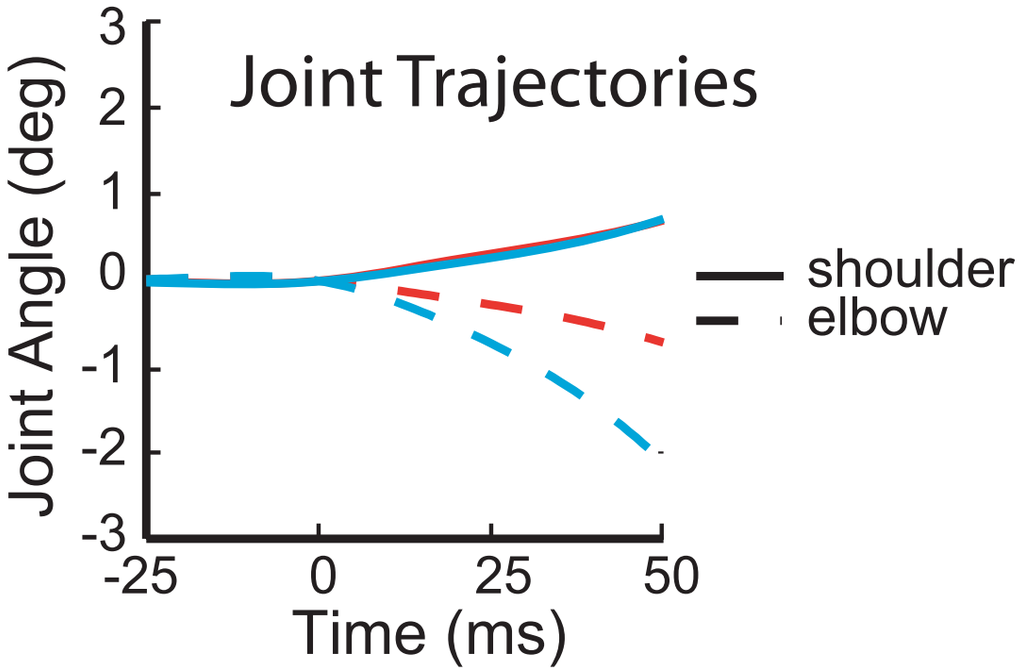




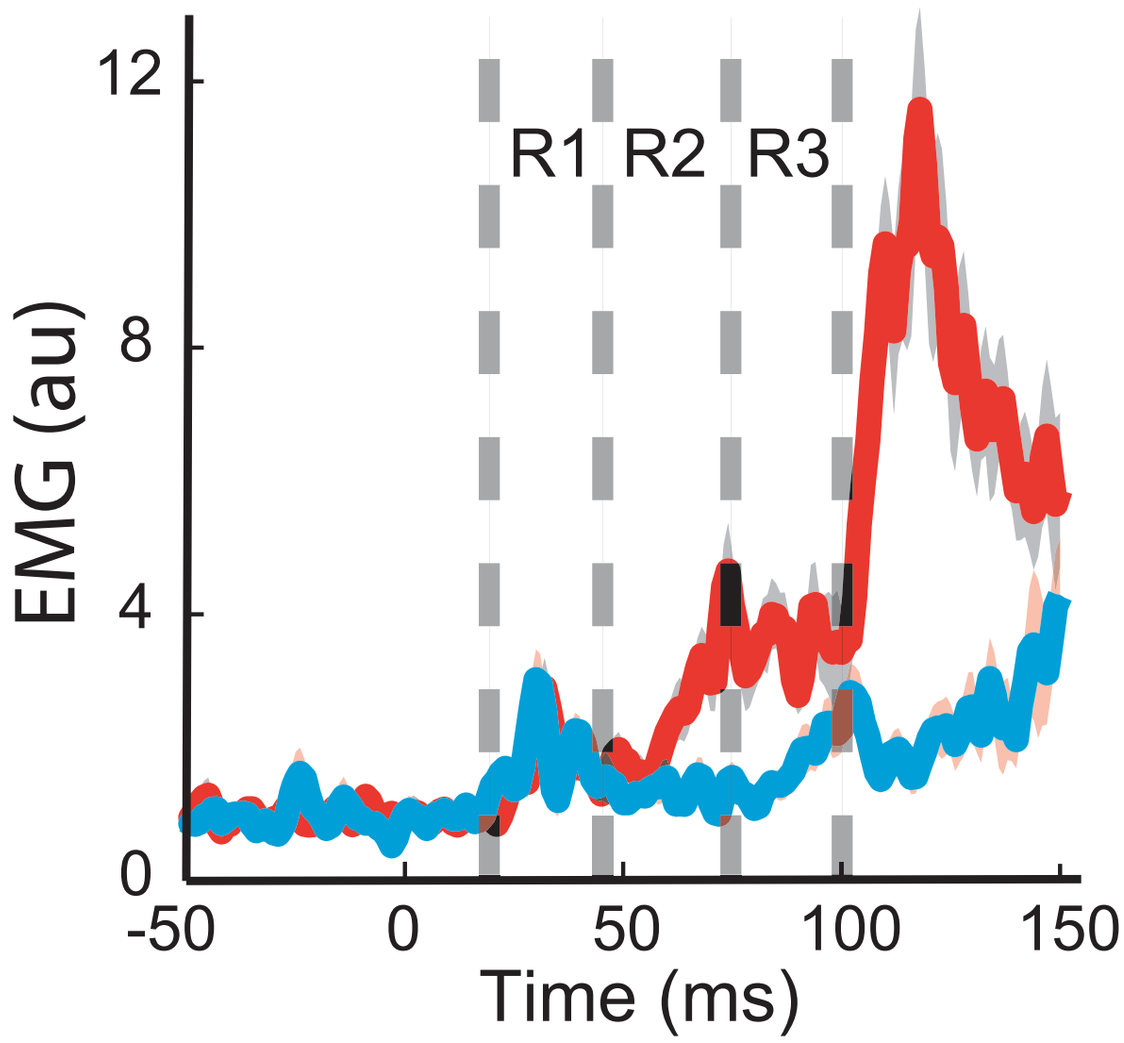
Kurtzer et al., Current Biology, 2008

Same shoulder motion, different underlying torques





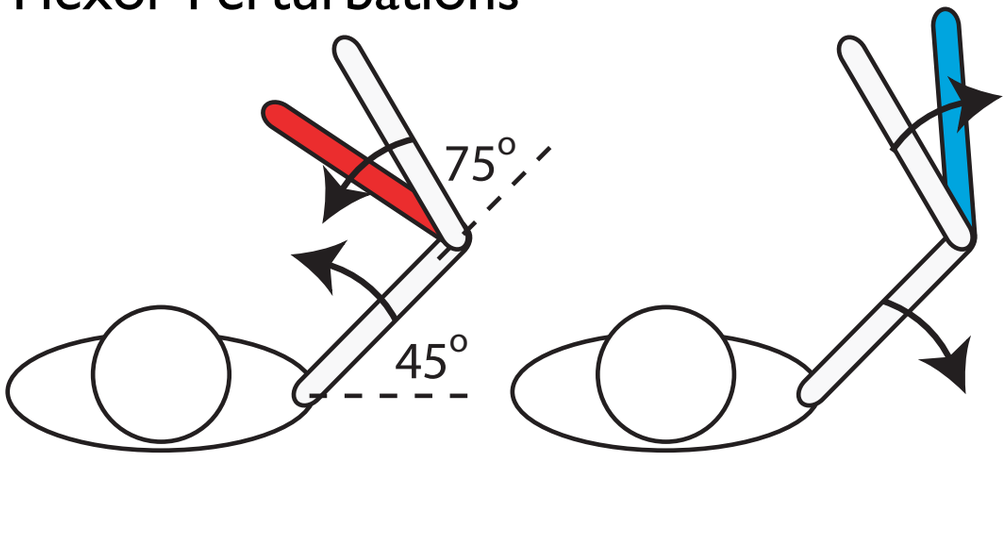
Muscle Activity

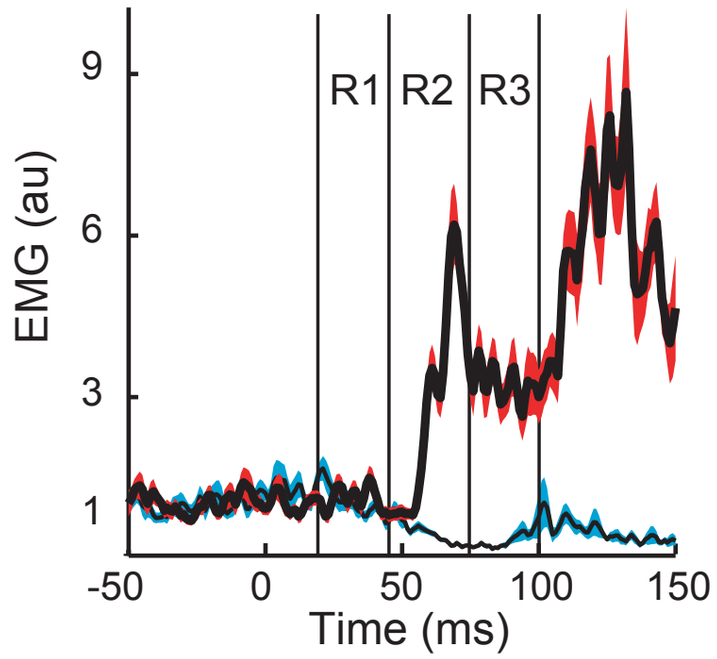


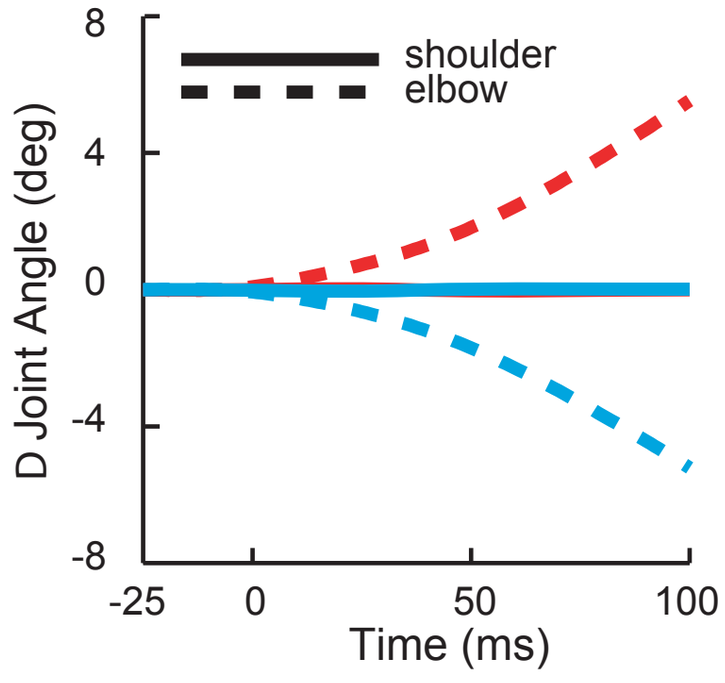
Knowledge of Limb Mechanics

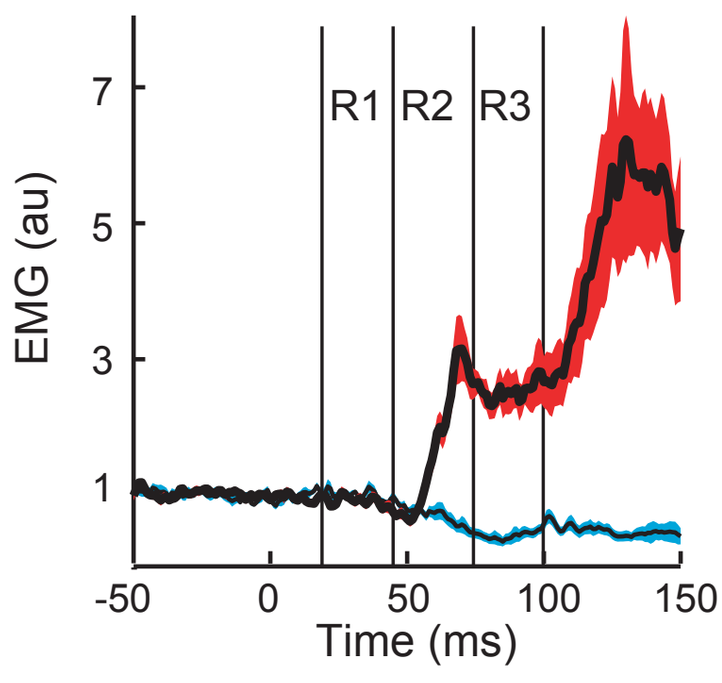
No Shoulder Motion, Opposite Shoulder Torques

Flexor Perturbations



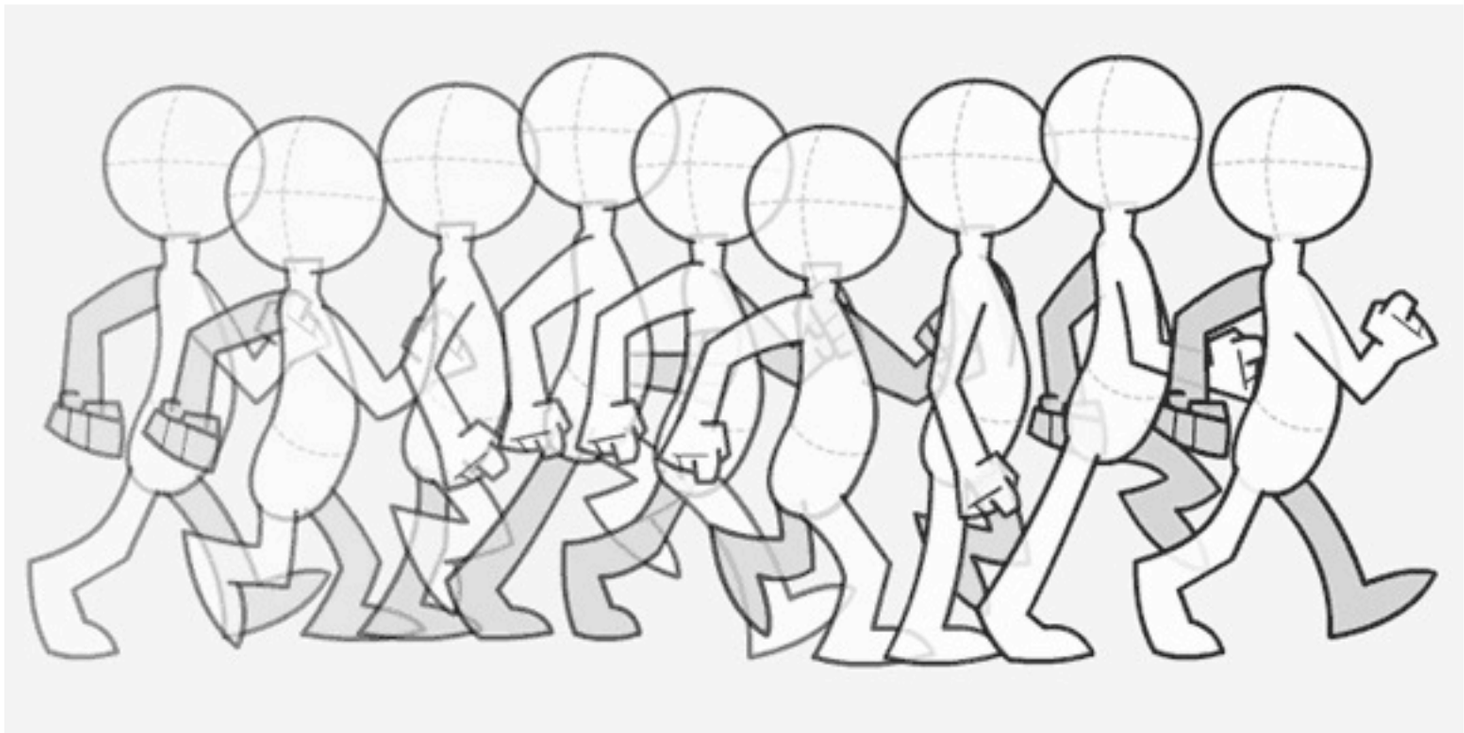






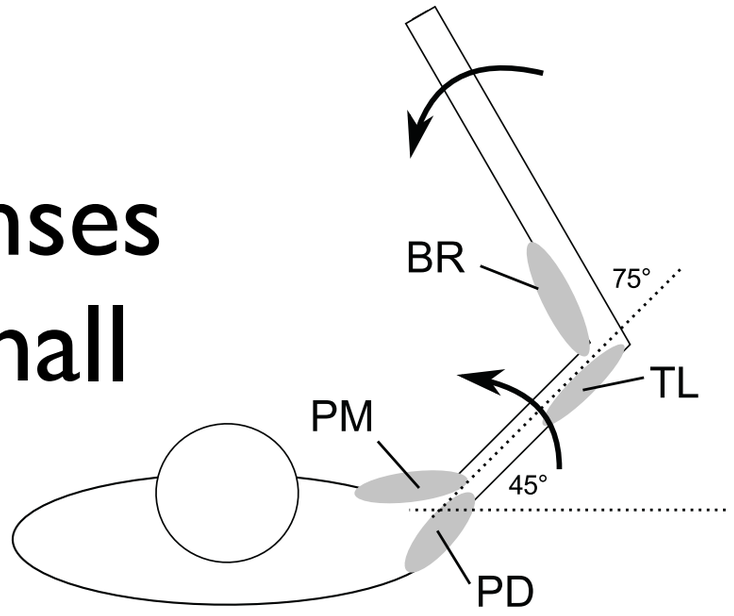
Stumble corrective response is distinct from locomotion

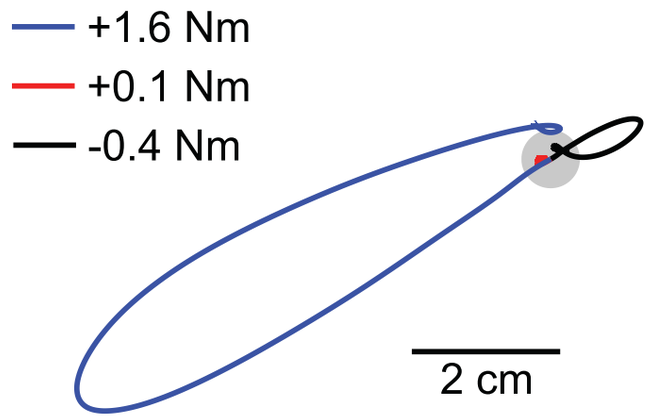
Locomotor pattern



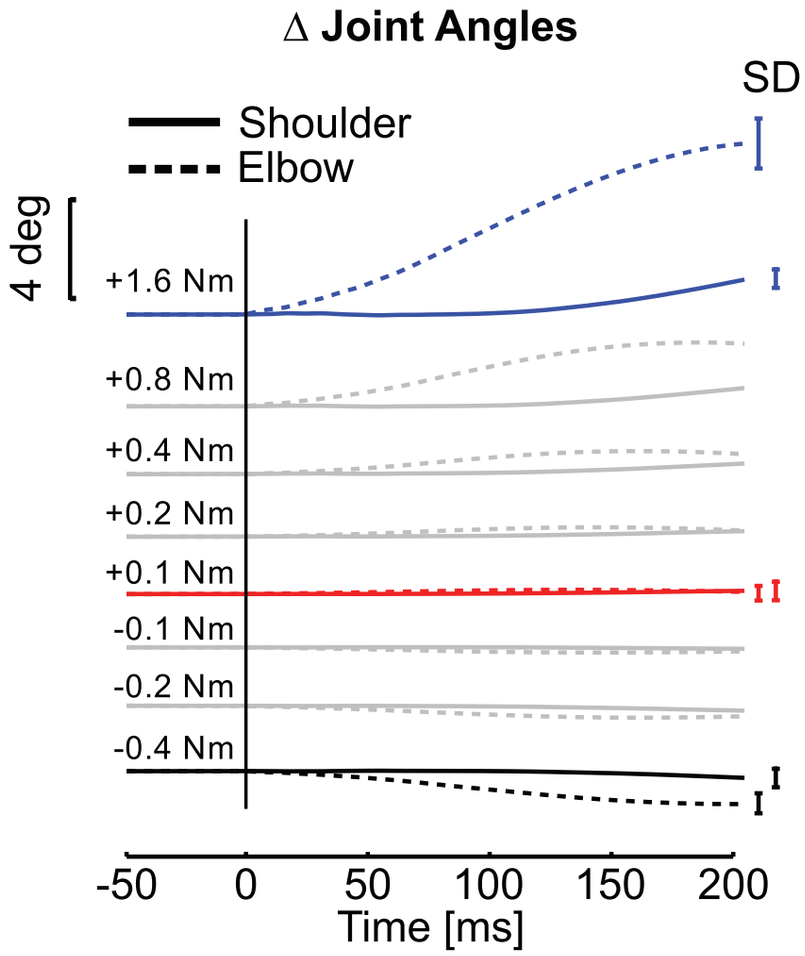
Stumble corrective response

Postural Task: Perturbation responses present for very small perturbations

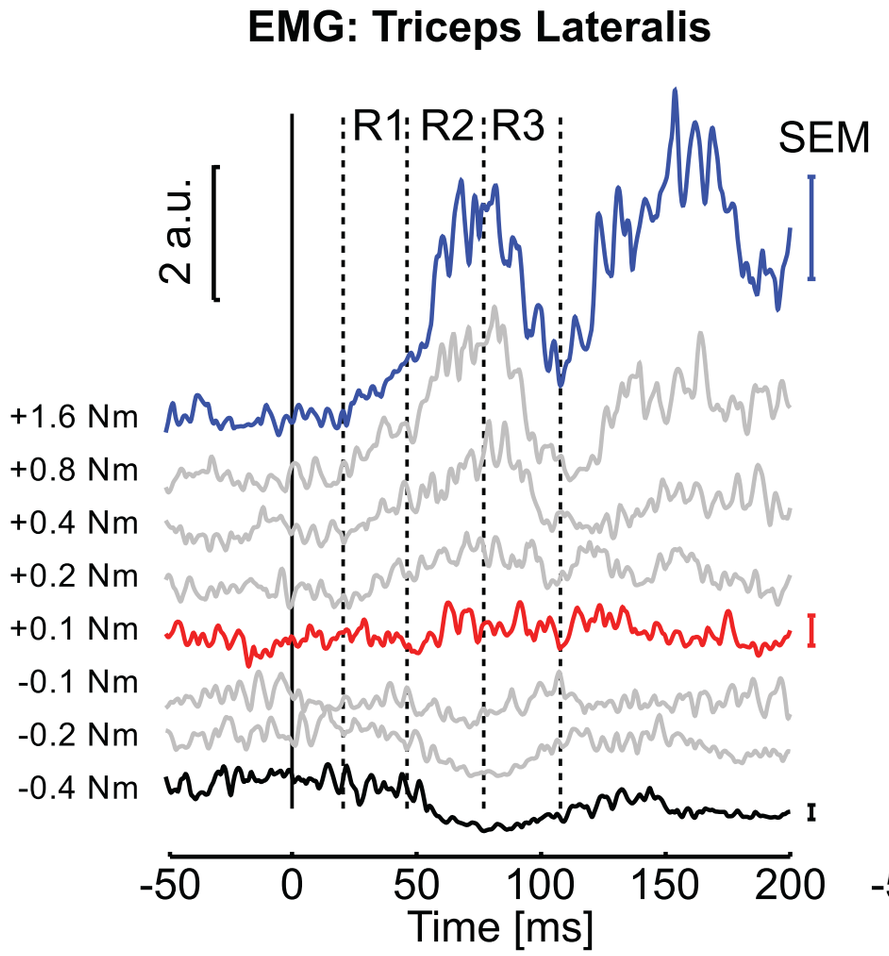




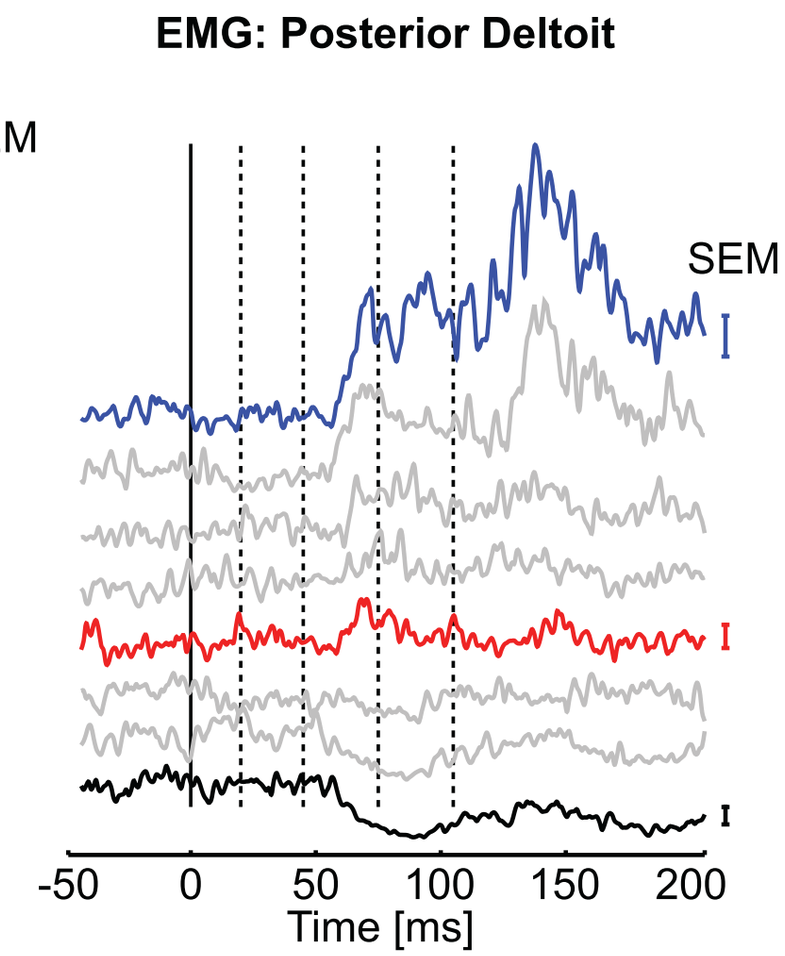
2 Nm background load



Crevecoeur et al., J Neurophysiol (2012)



Muscle stretched: Short-latency response

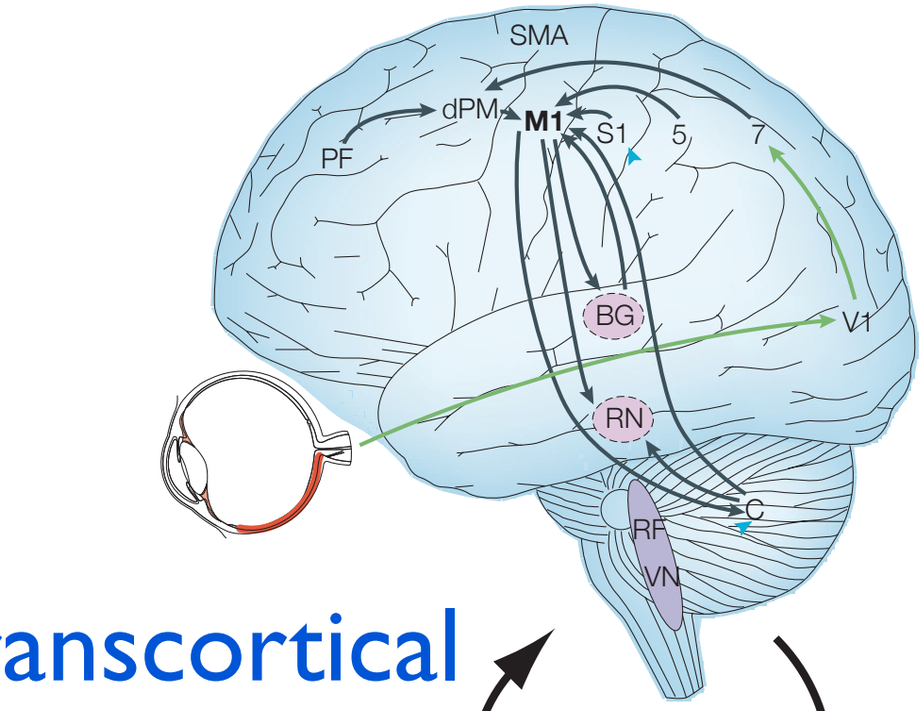


Muscle not stretched: Long-latency response

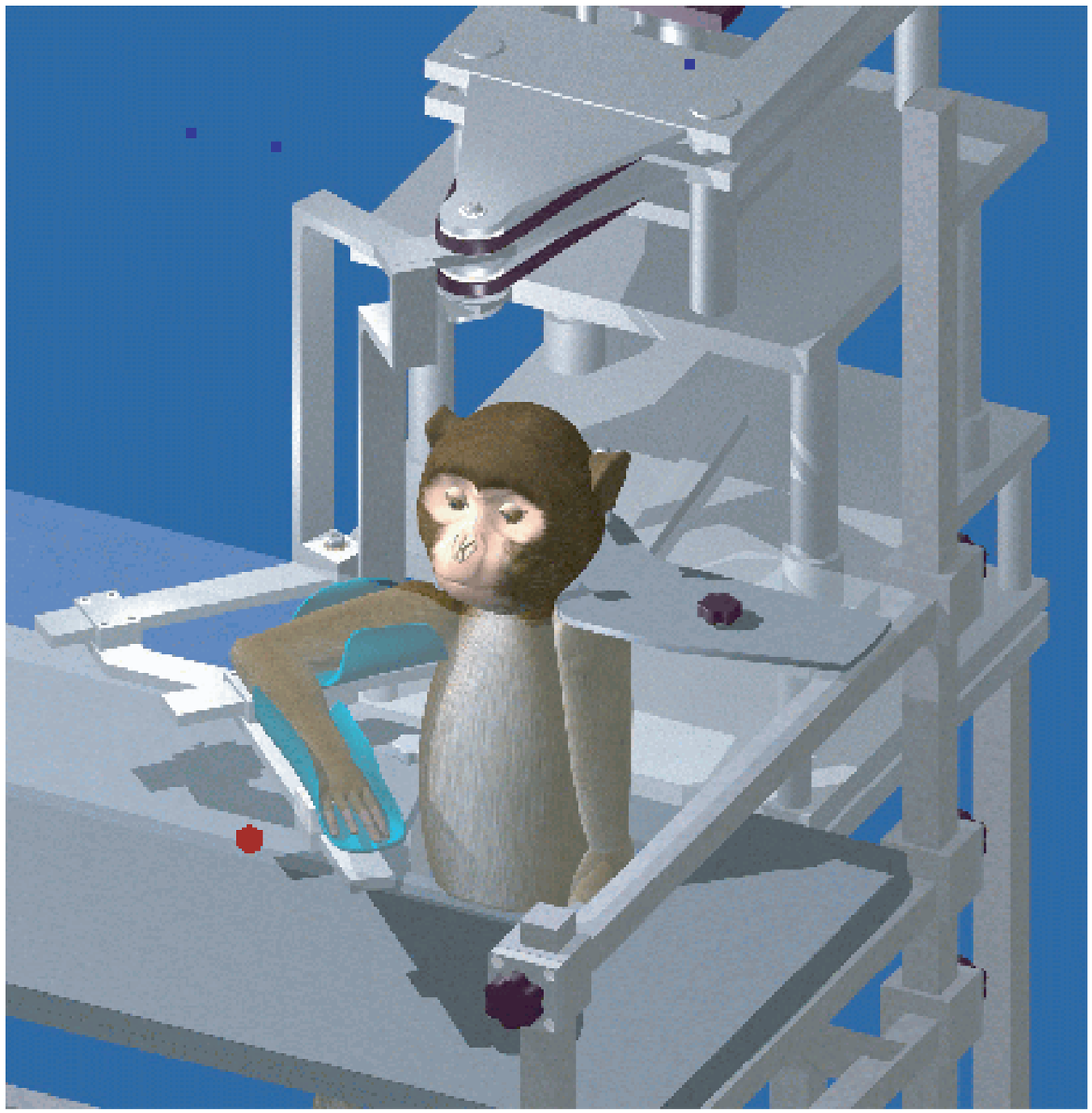
Neural Basis of Voluntary Feedback Control

Functional Properties

	SL	LL	Early Vol
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		✓	✓

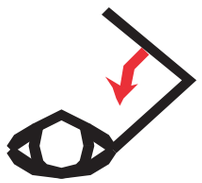


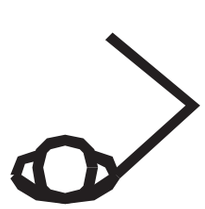
Record individual neurons in Primary Motor Cortex (M1) as they perform behavioural tasks

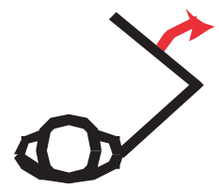


Perturbation Response during Postural Control

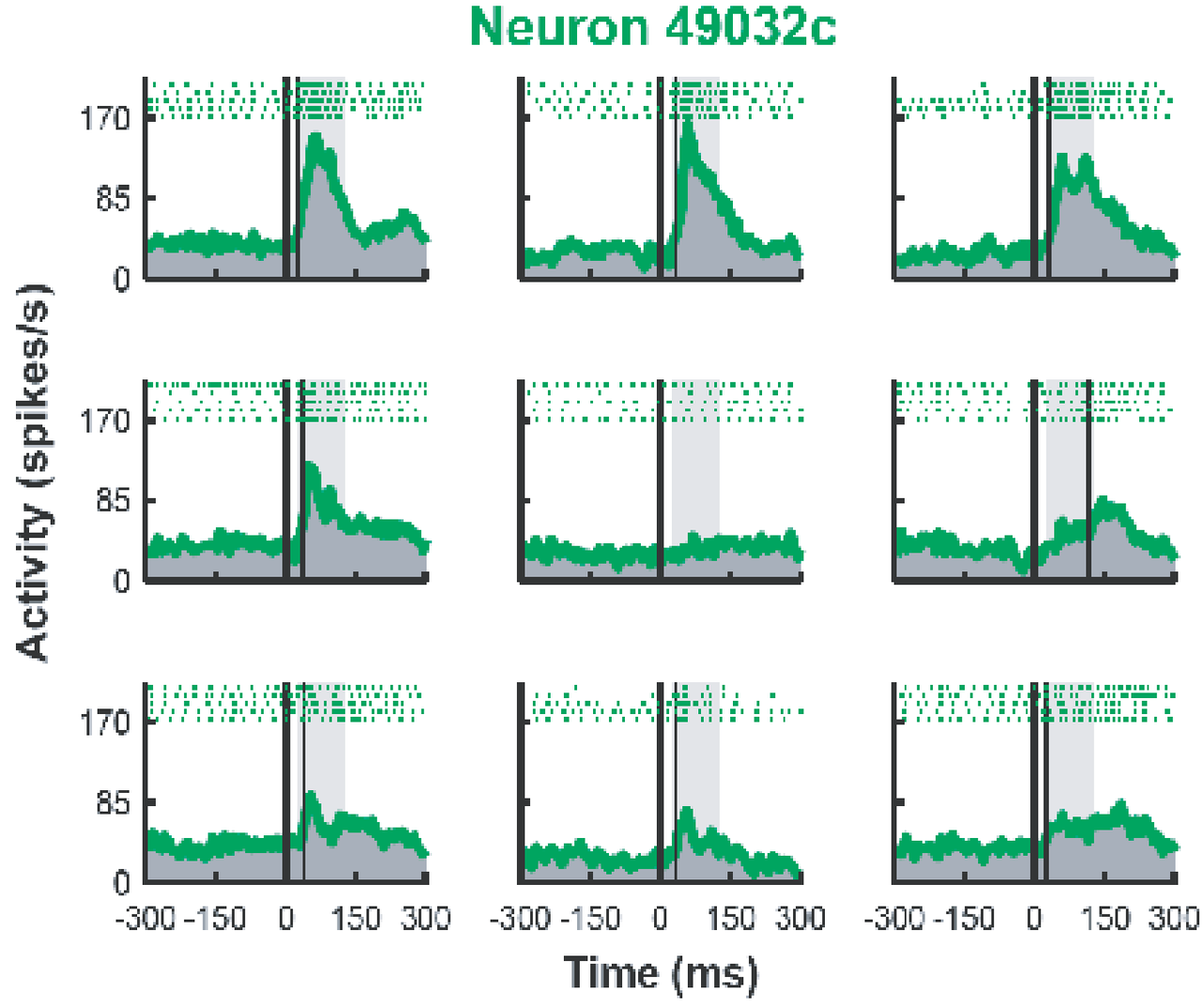
Hand Trajectories

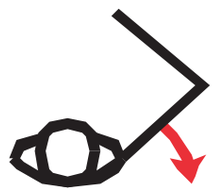


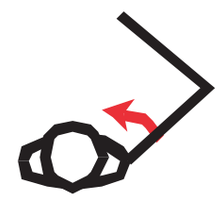




Motor Cortex Cell

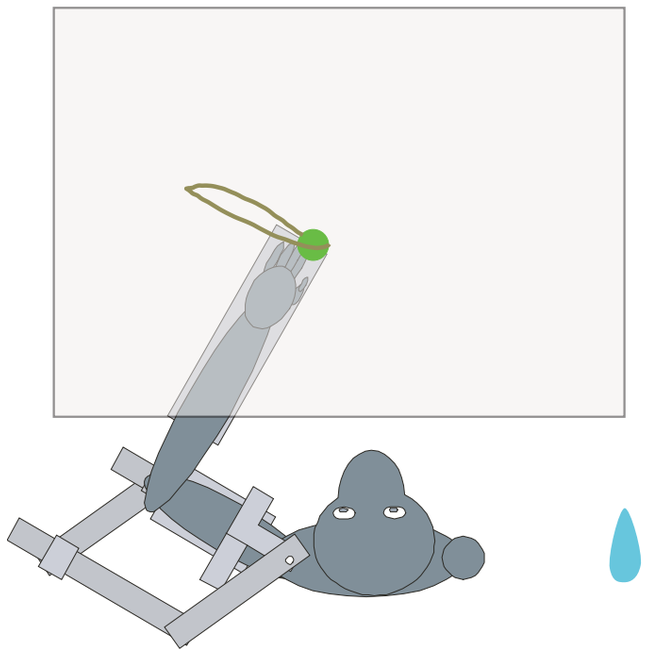


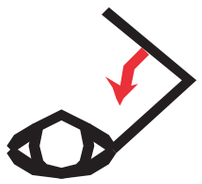


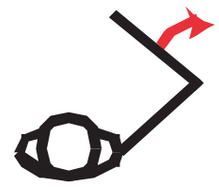


Herter et al., JNP 2008

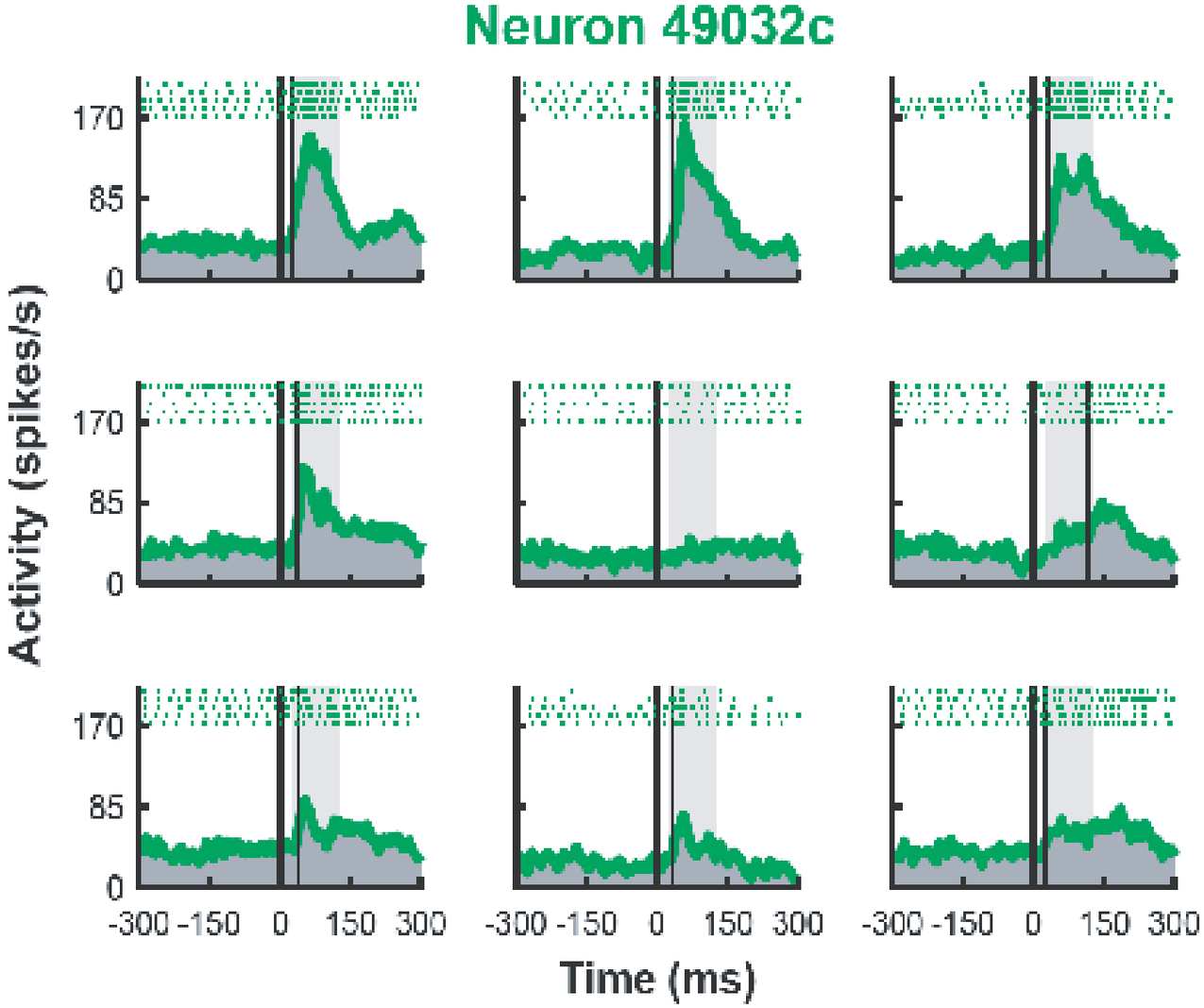
Perturbation Response during Postural Control



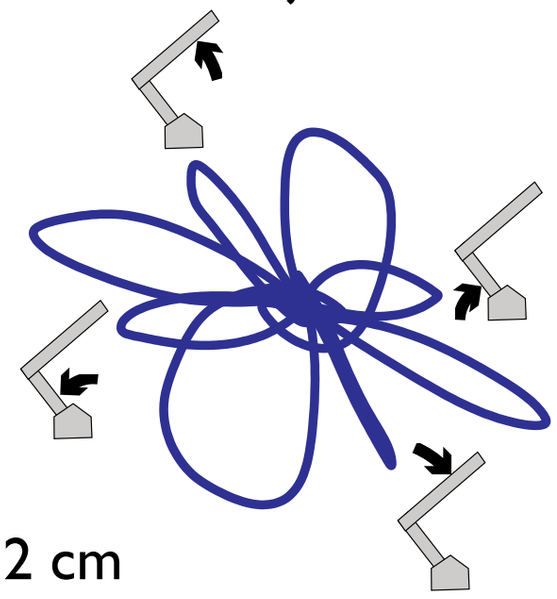


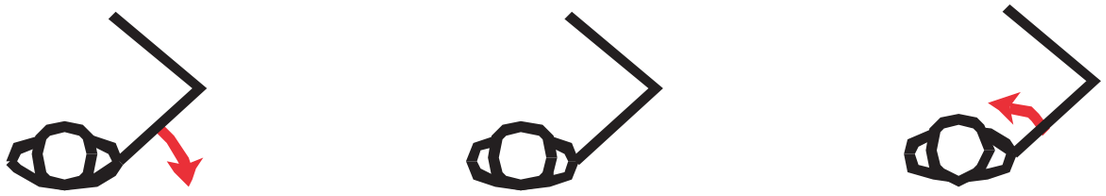


Motor Cortex Cell



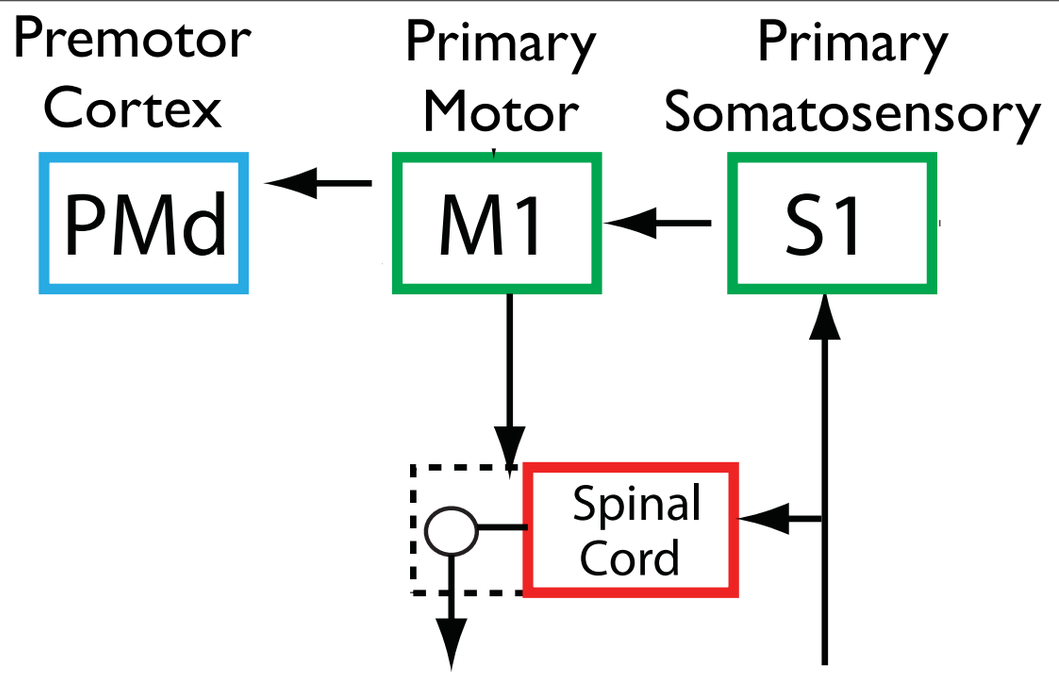
Hand Trajectories



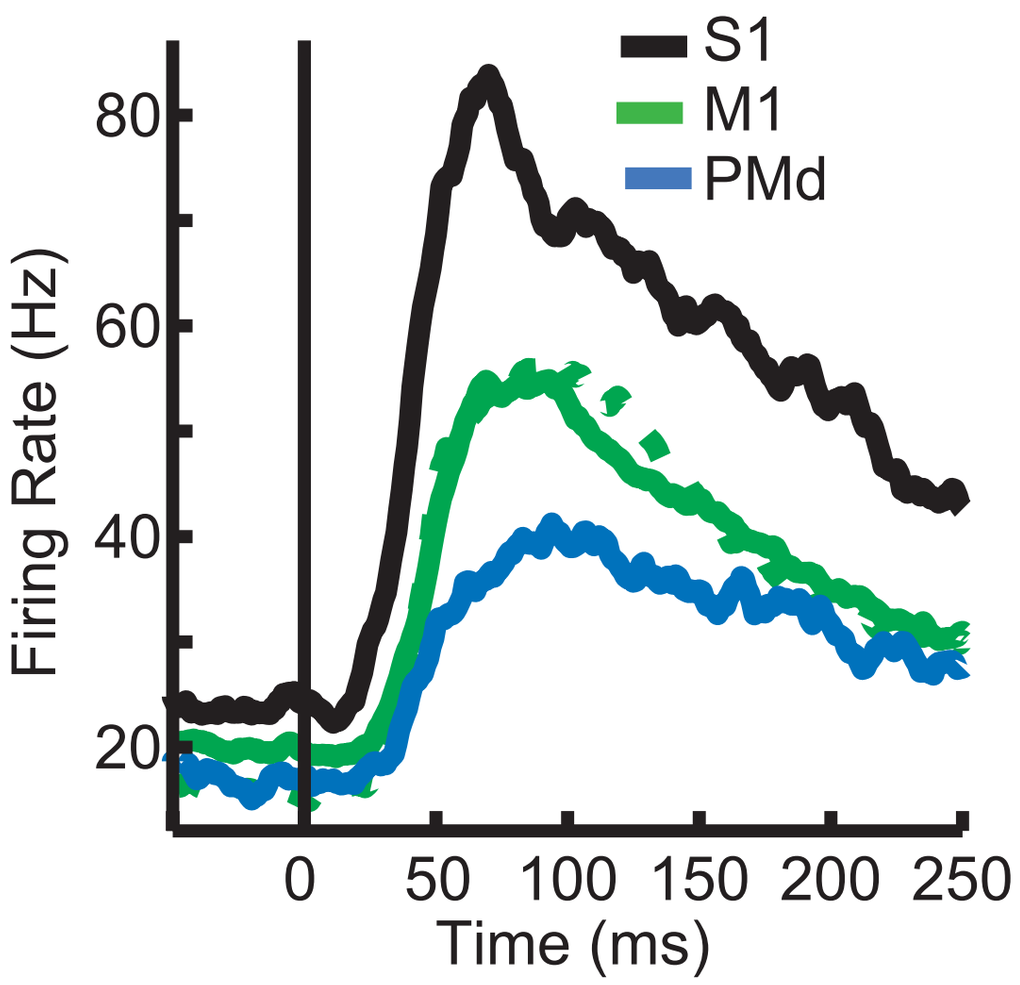


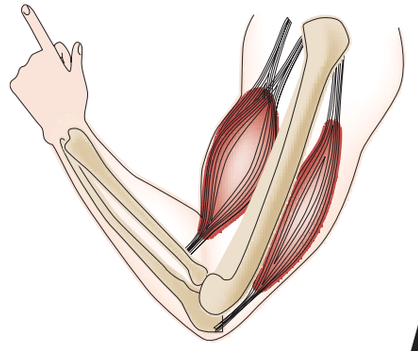
Herter et al., JNP 2008

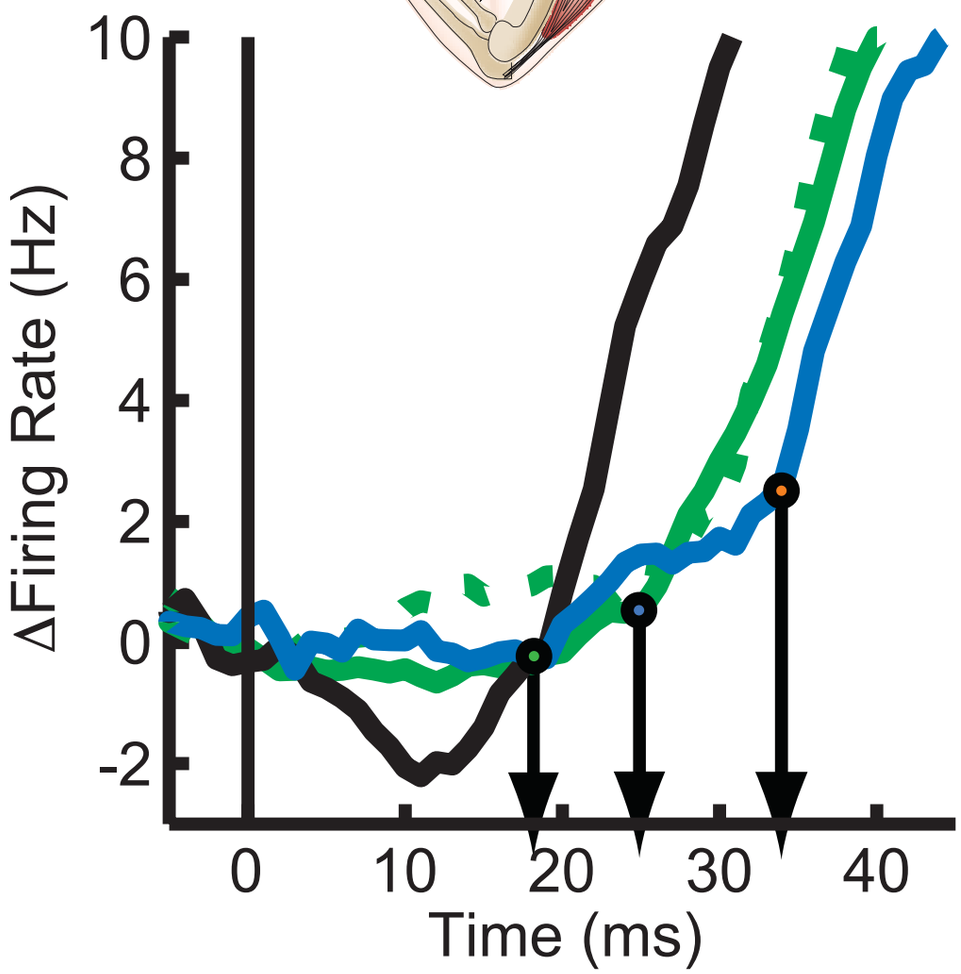
Perturbation Response during Postural Control



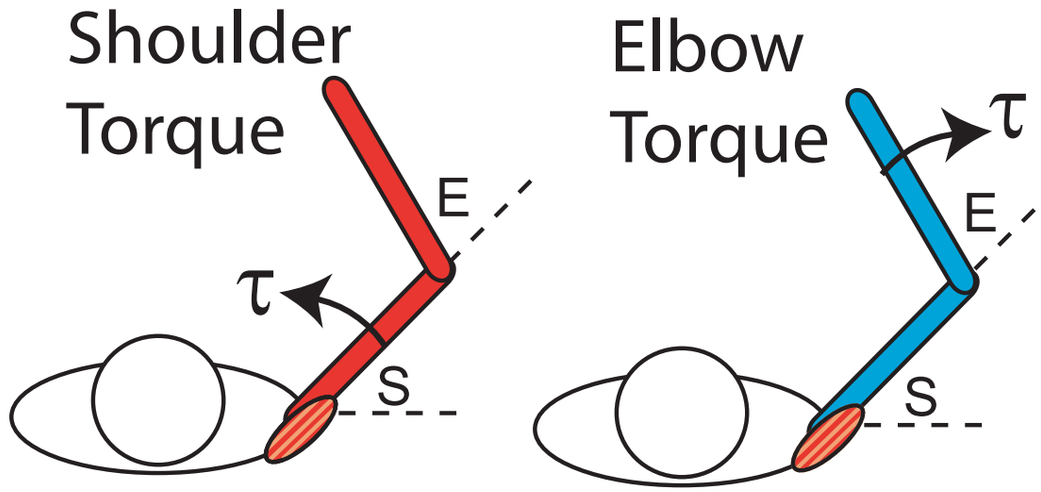
Population Responses

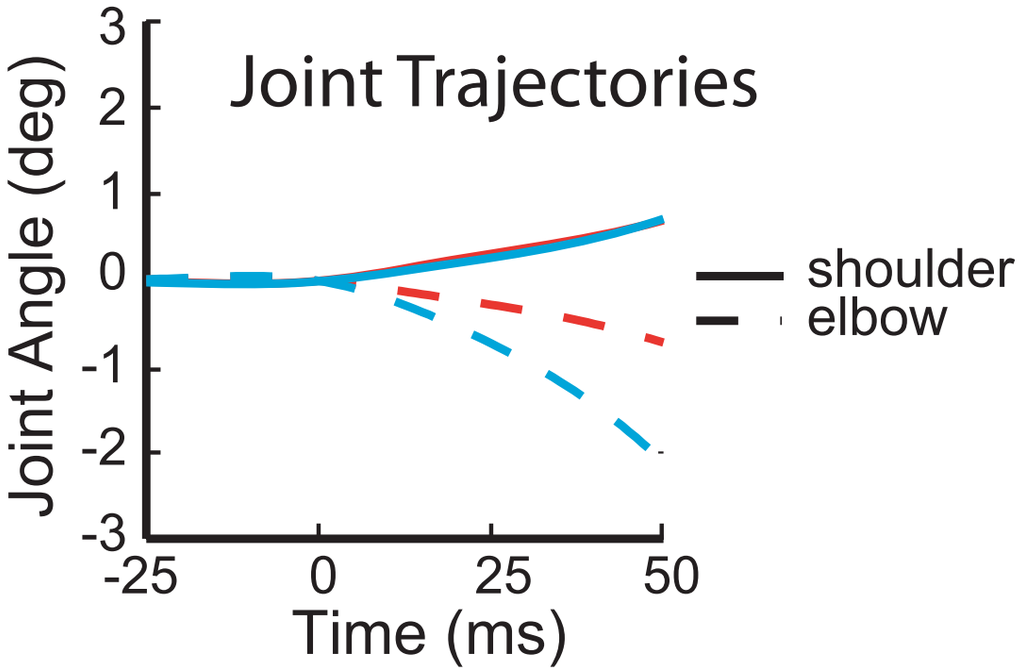




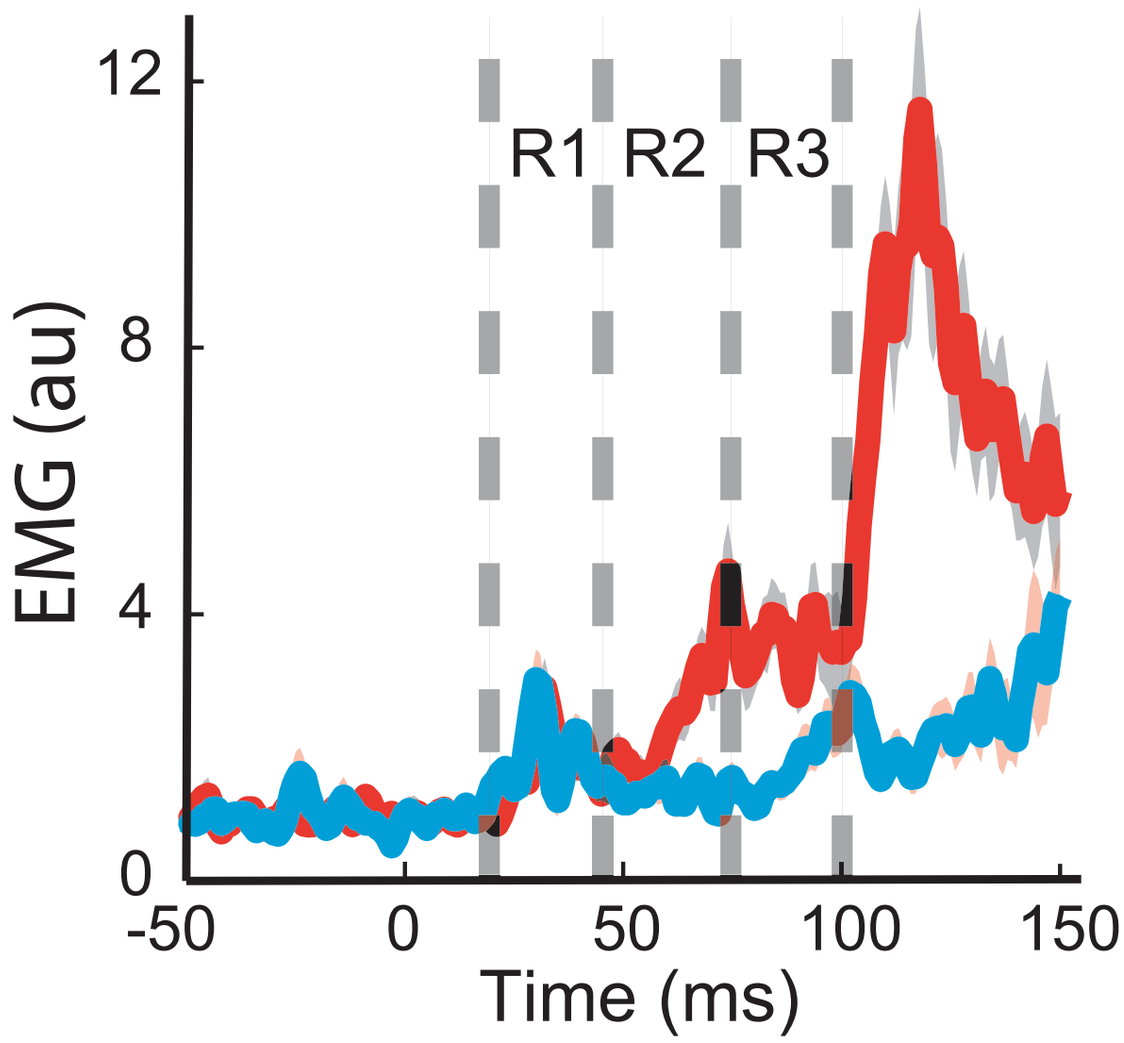


Same shoulder motion, different underlying torques





Muscle Activity

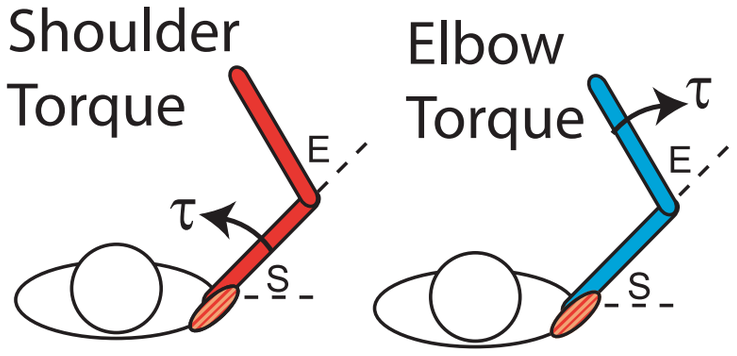


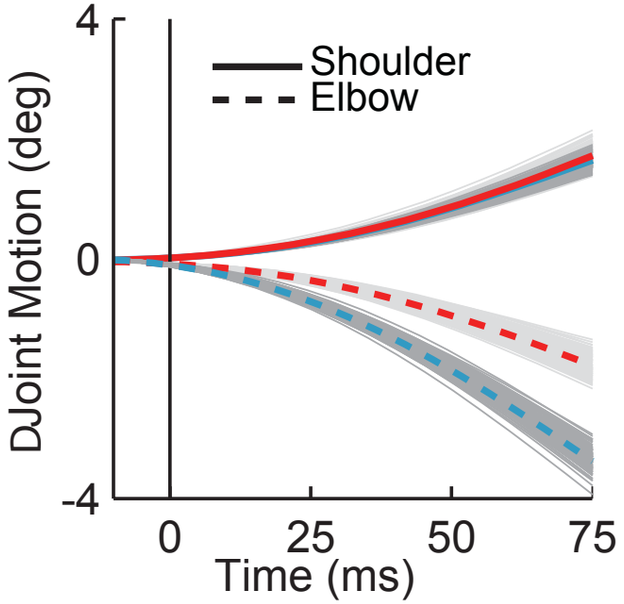
Record Shoulder-related neurons during perturbations

Andrew Pruszynski

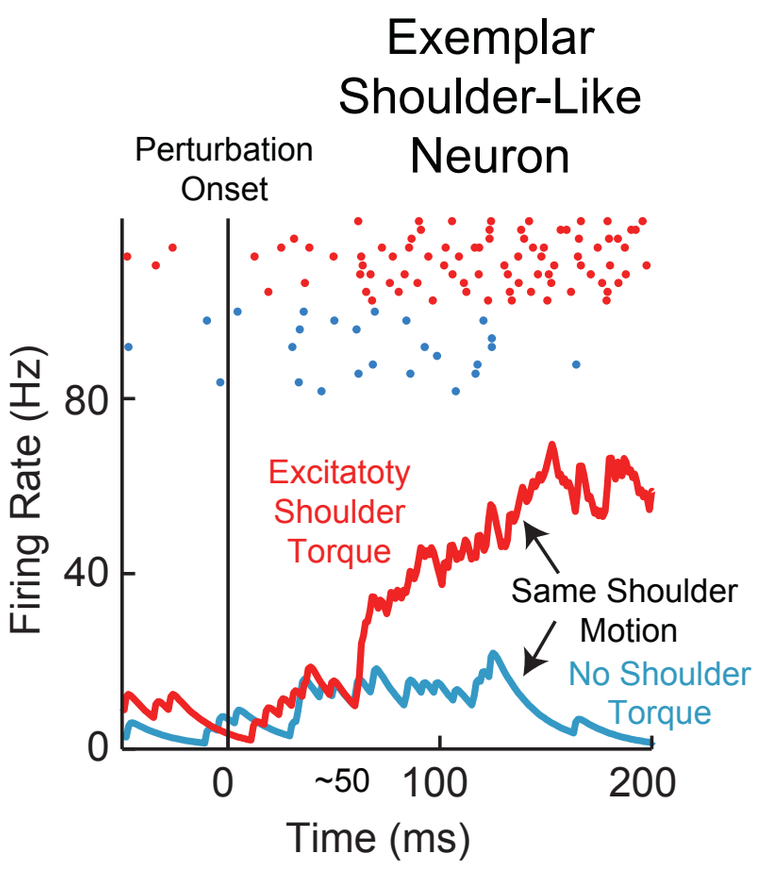
Pruszynski et al., Nature, 2011

Perturbations

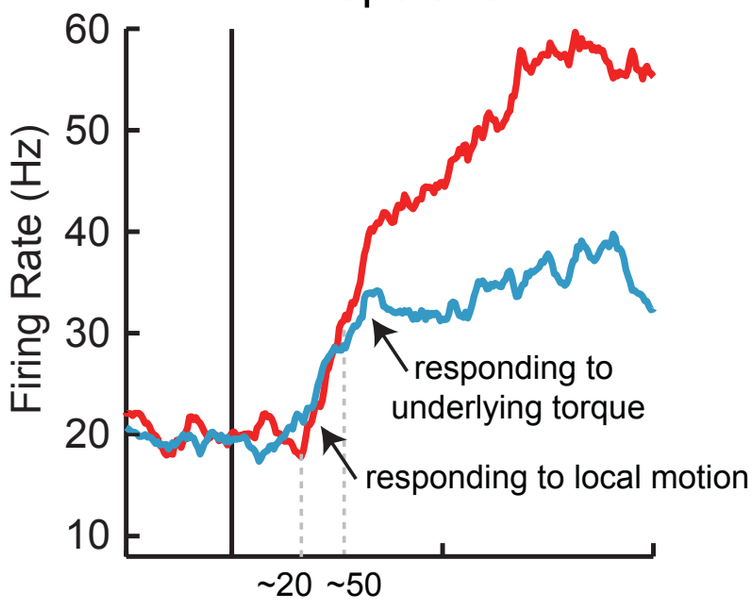




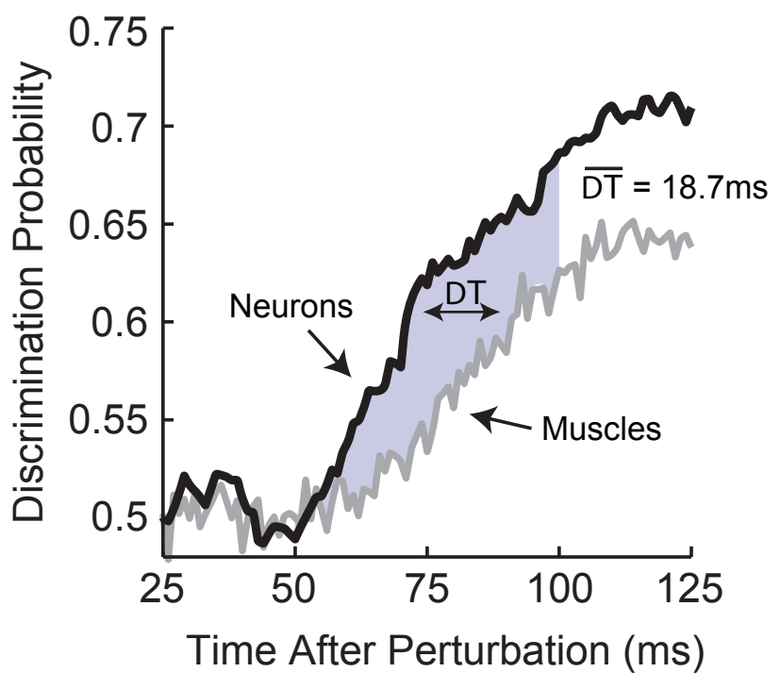
Exemplar Shoulder-Like Neuron



Neural Population

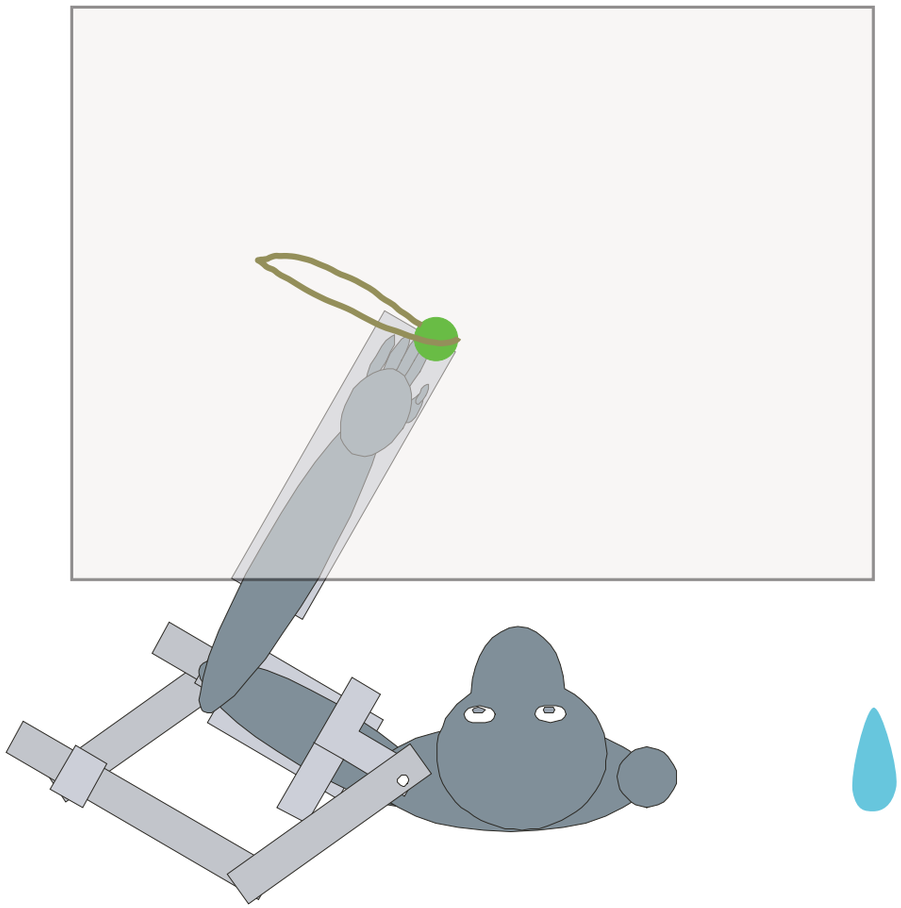


Sensitivity to Underlying Torque

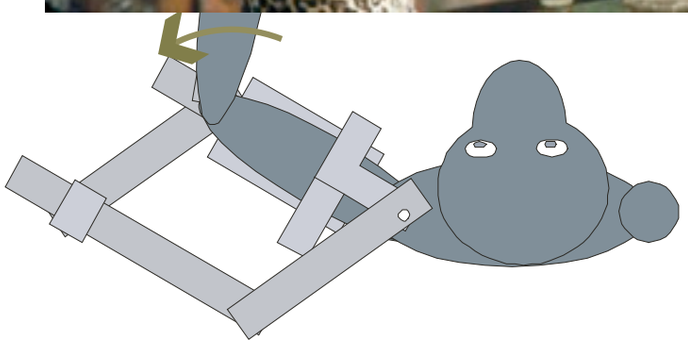


How Does Behavioural Goal Change Feedback?

Postural Control



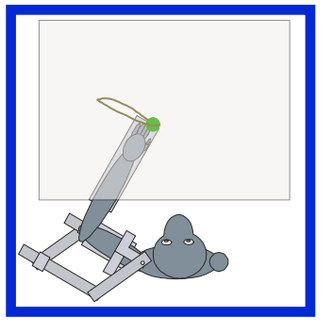
Watch Movie

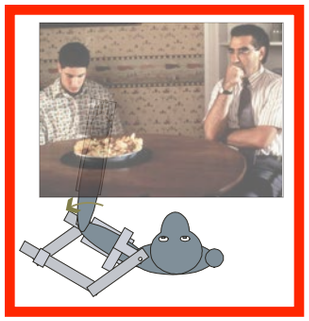


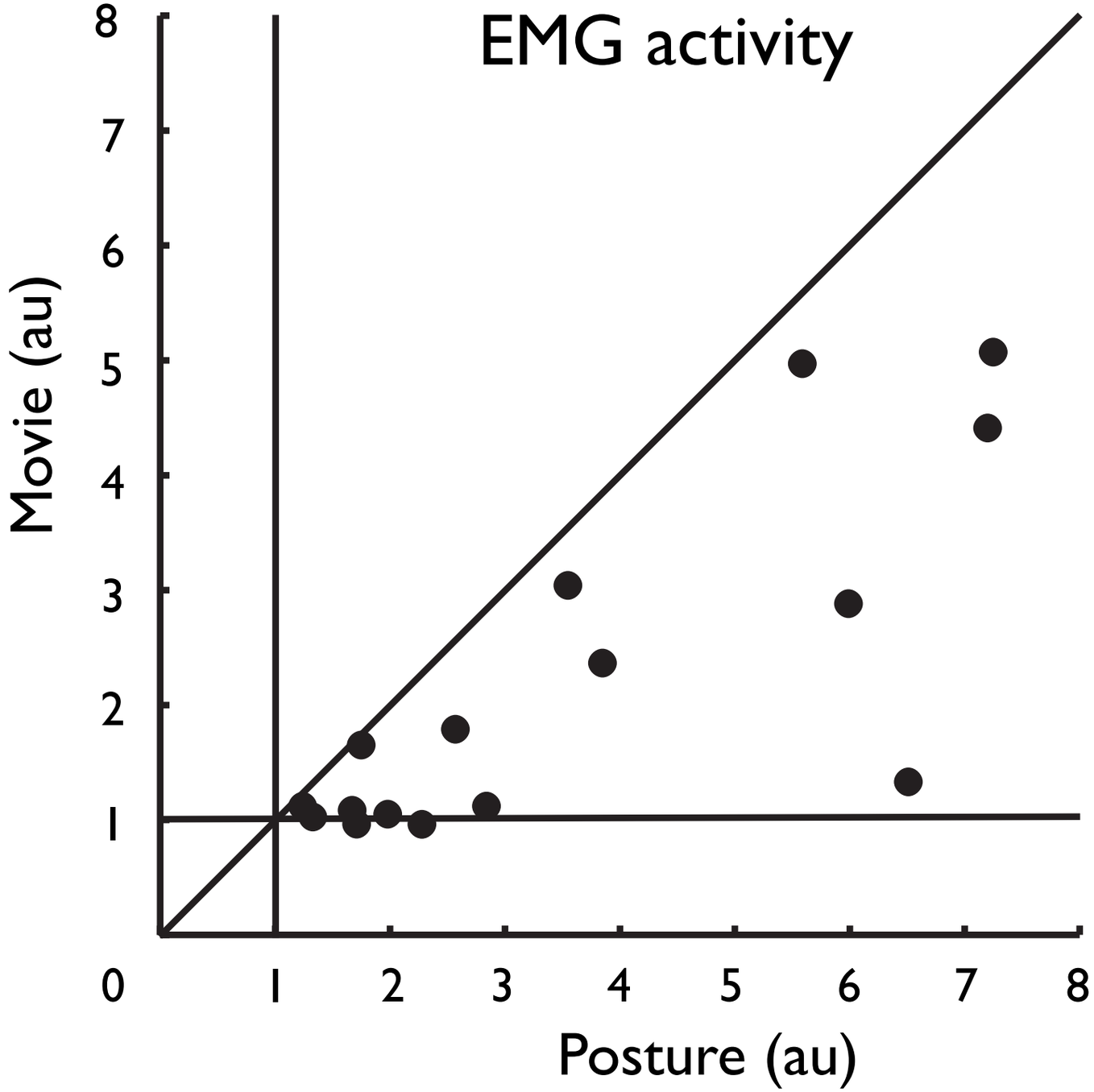
Examine muscle and neural activity across two tasks

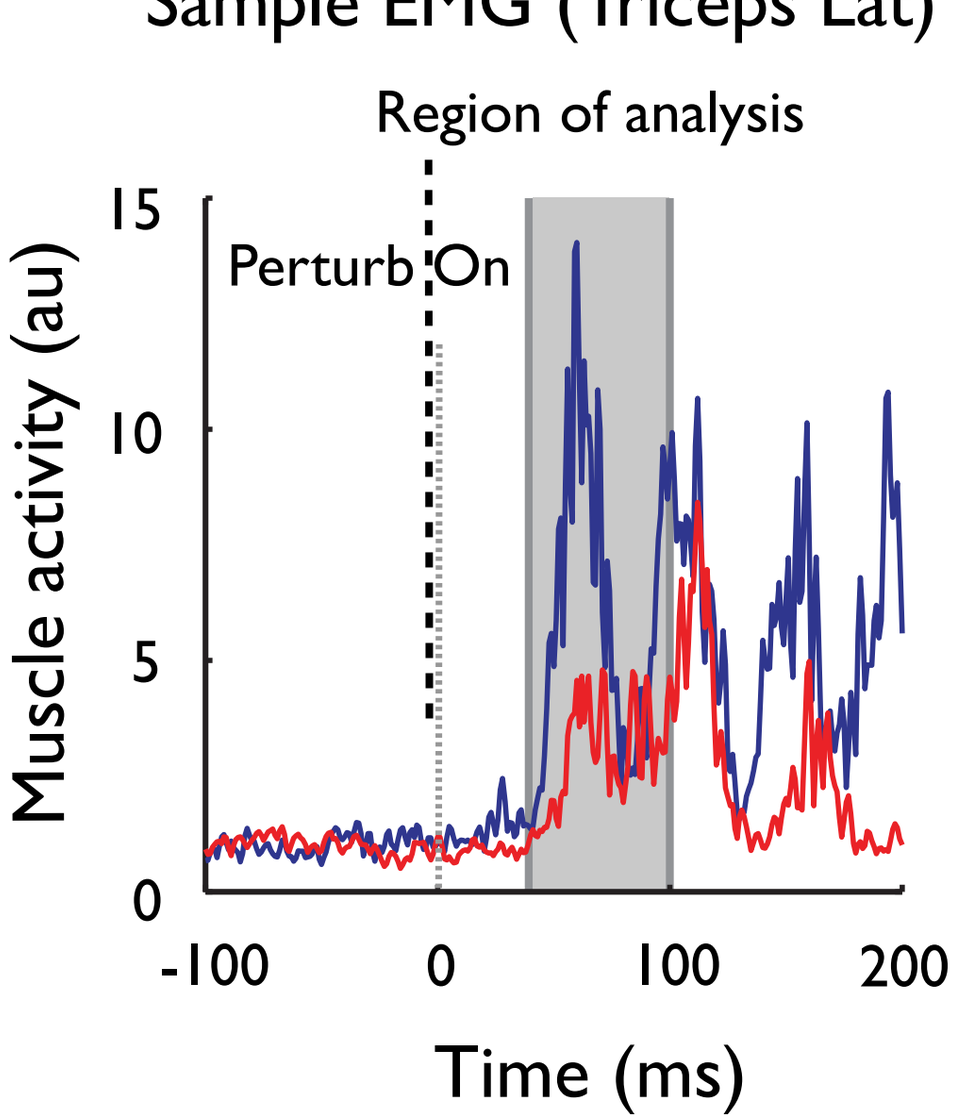
Mohsen Omrani

Stretch response reduced 50% in Movie task

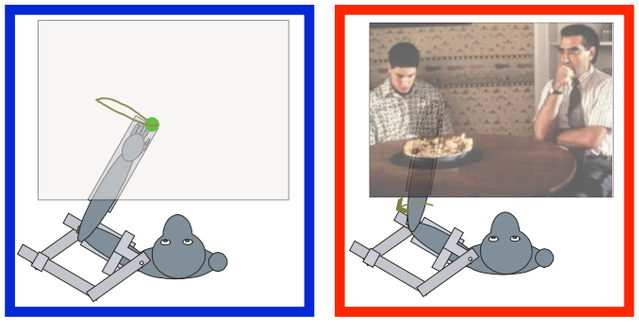








Task-dependent Change in Perturbation Related Activity in M1



Cell #1

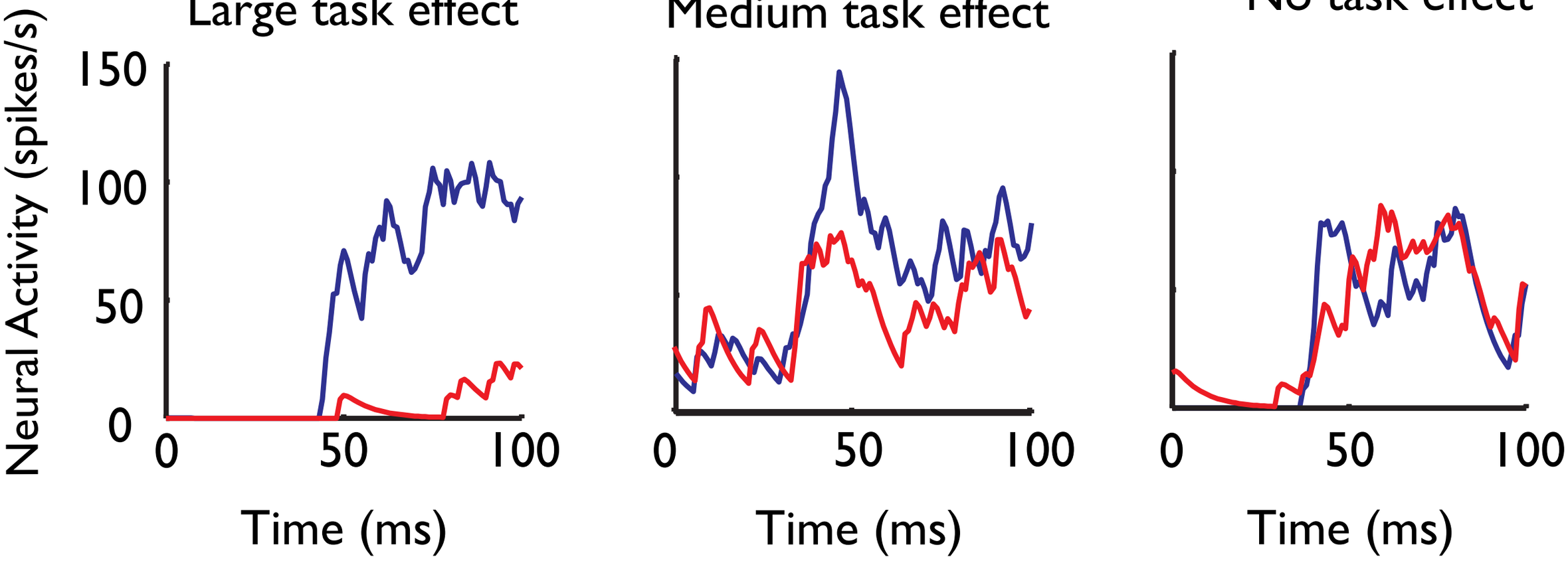
Large task effect

Cell #2

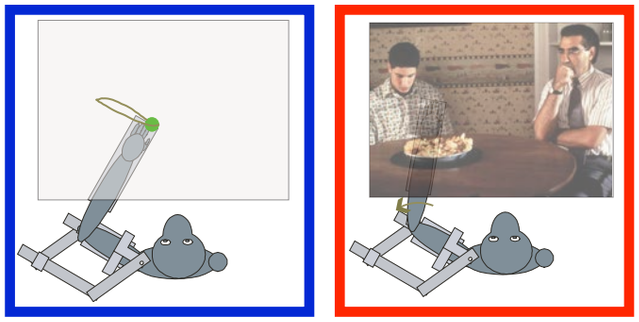
Medium task effect

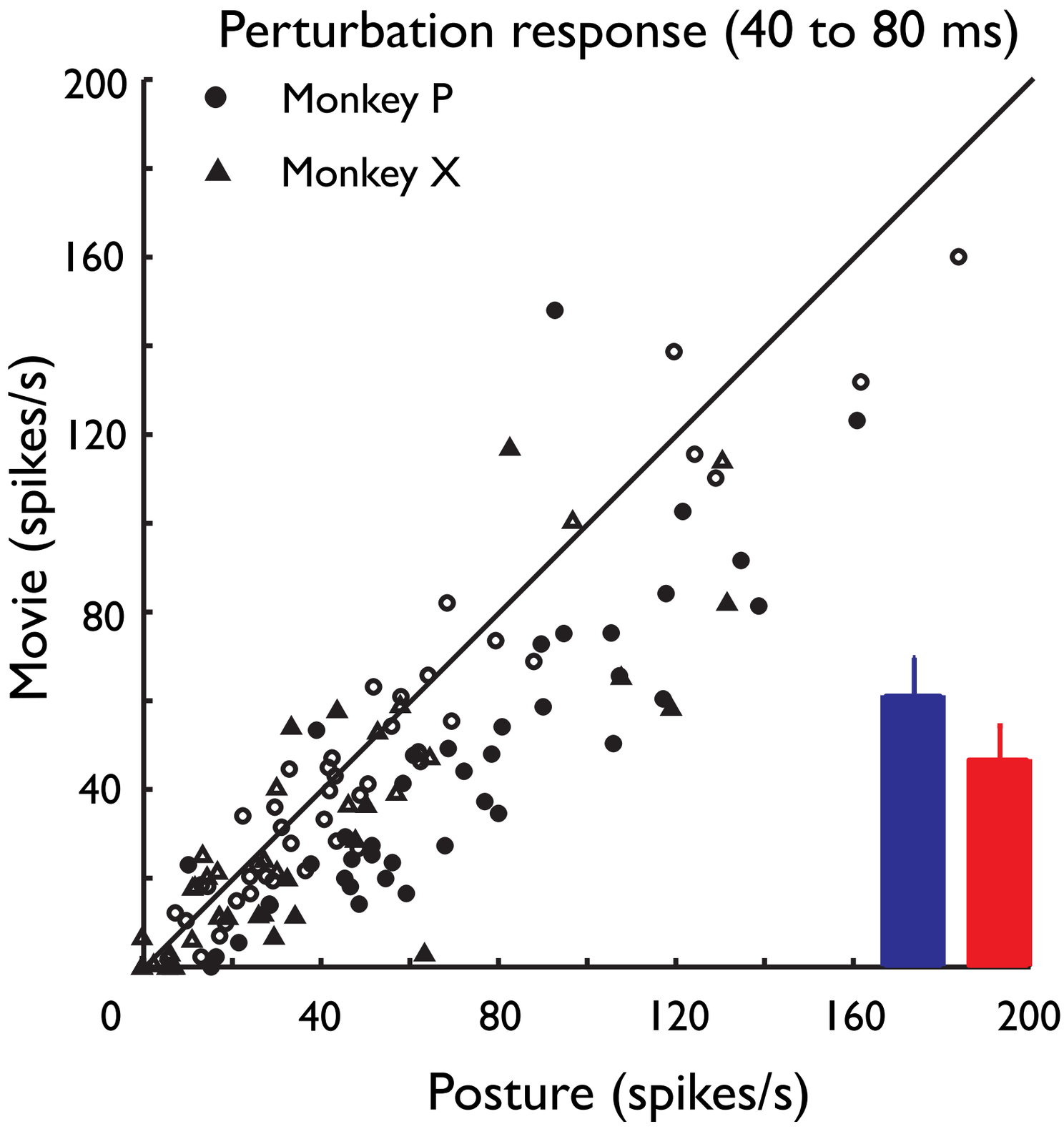
Cell #3

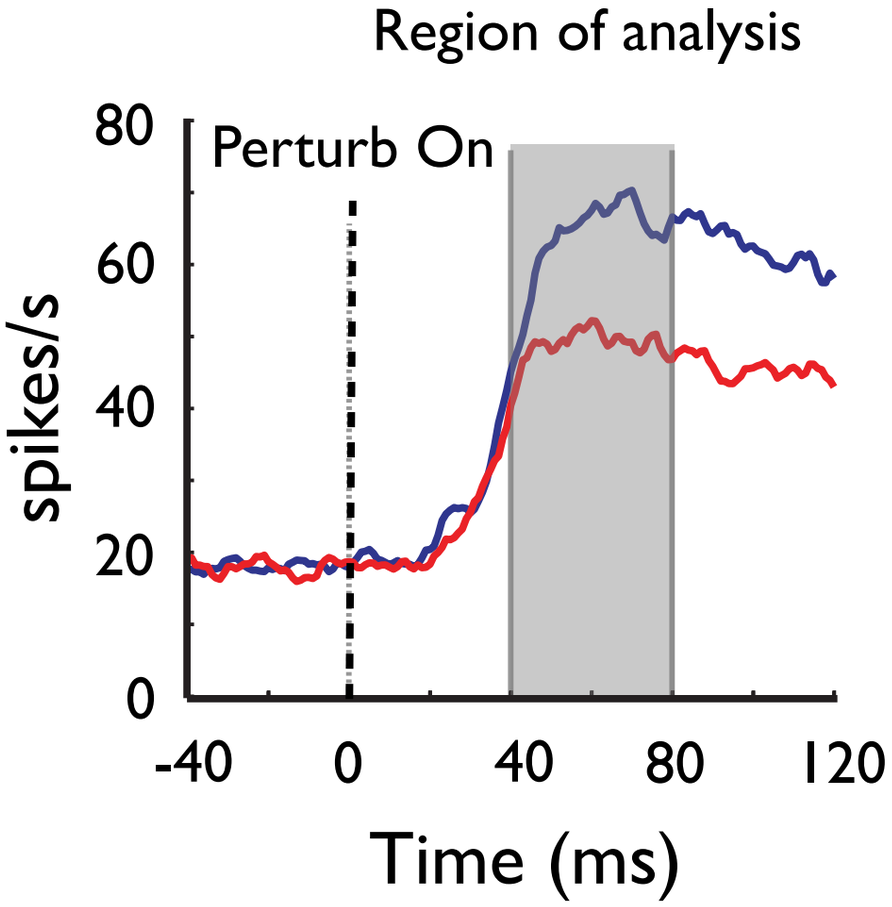
No task effect



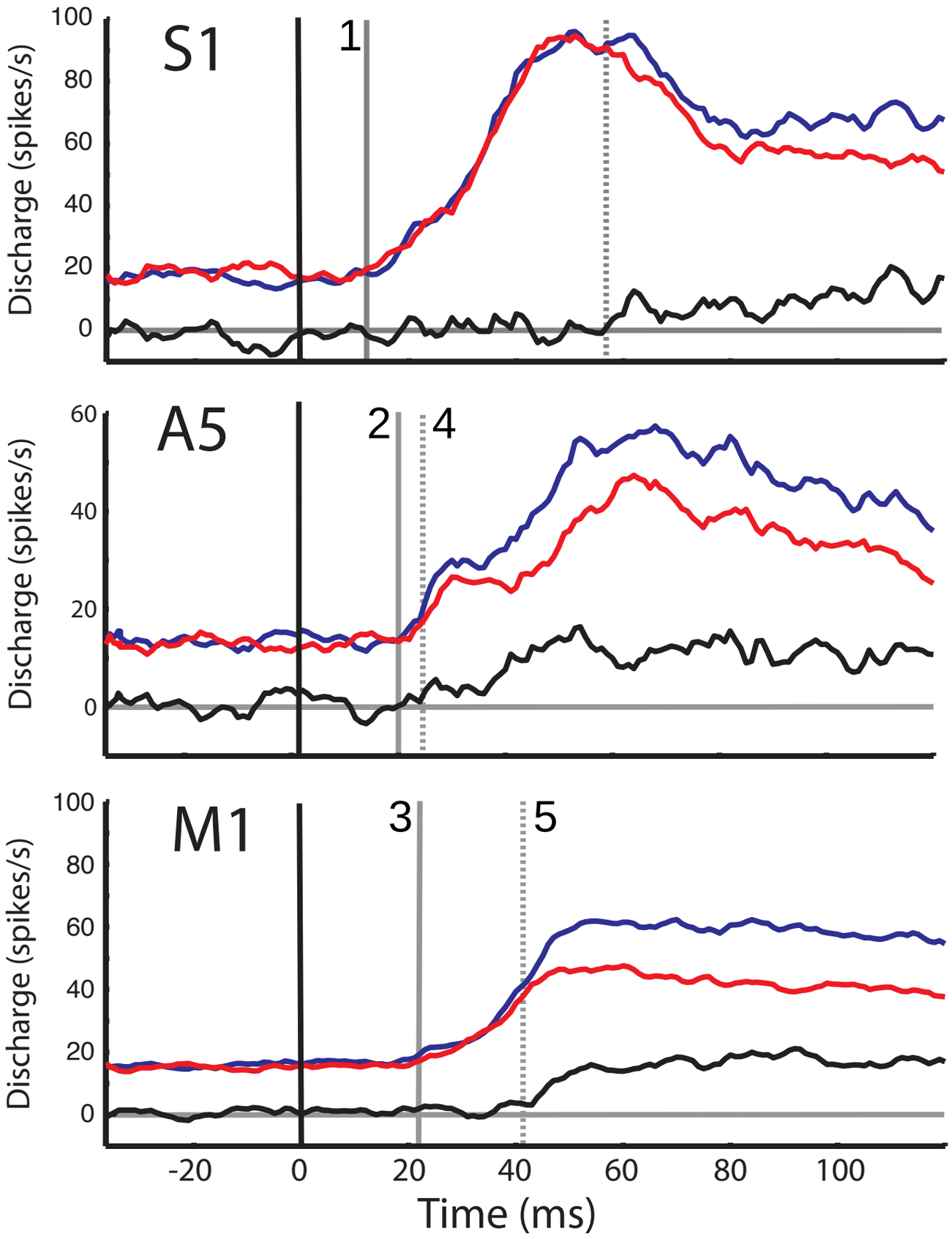
MI stretch response decreases 40% in Movie Task

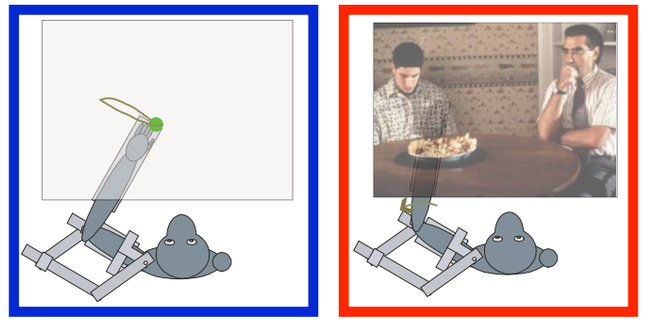






Perturbation Responses





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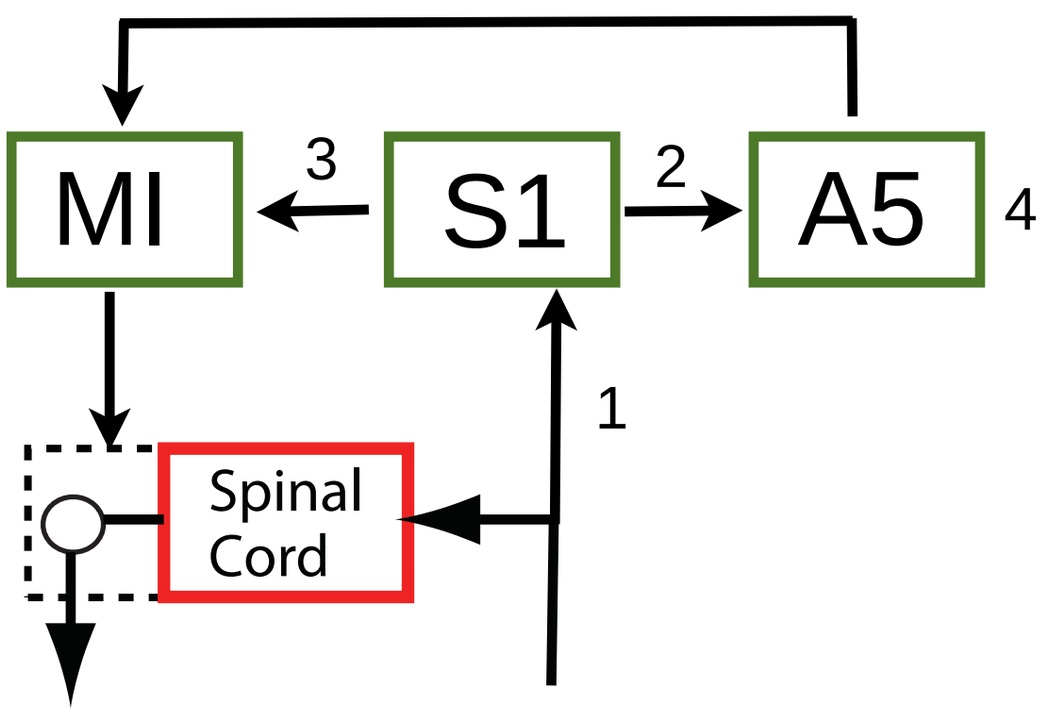
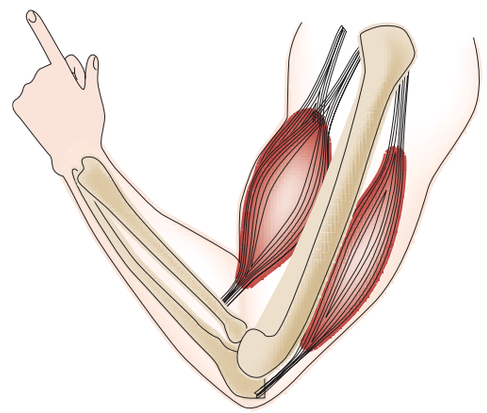


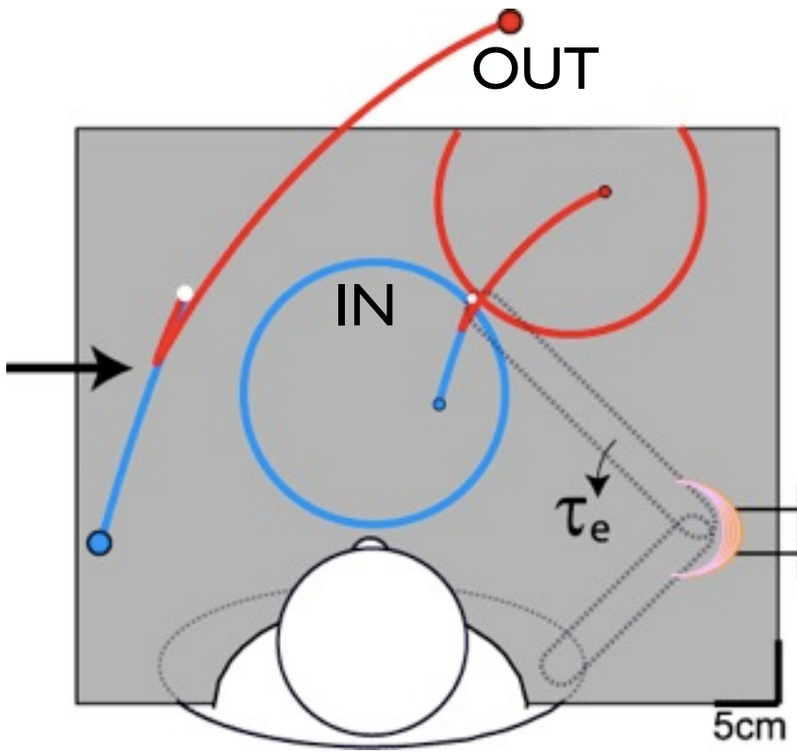


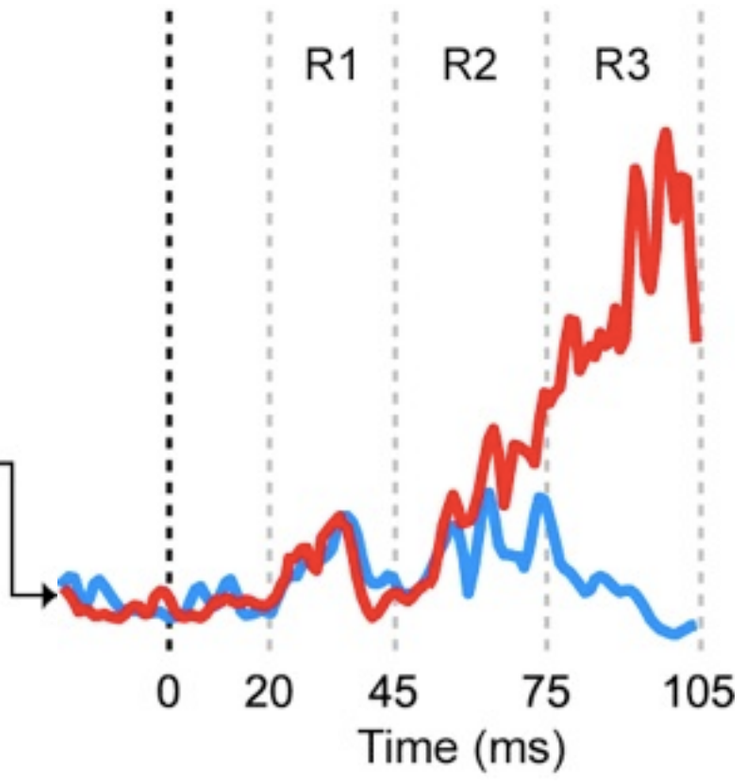
S1 - Primary Somatosensory Cortex
A5 - Parietal Area 5
M1 - Primary Motor Cortex

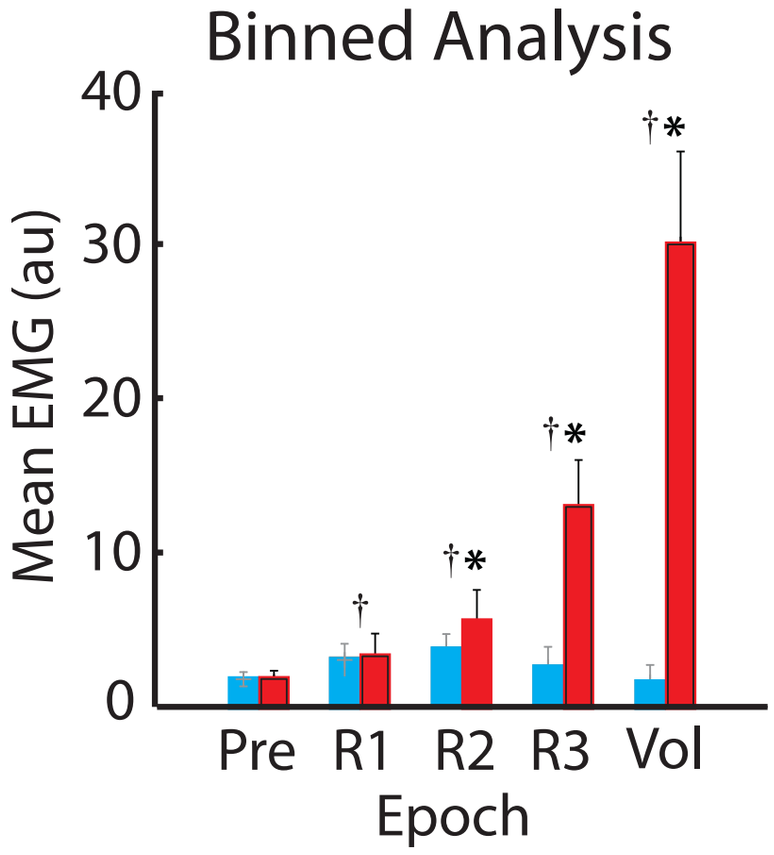
Feedback for Rapid Task Selection

Andrew Pruszynski

Spatial Analog of Resist/Let Go

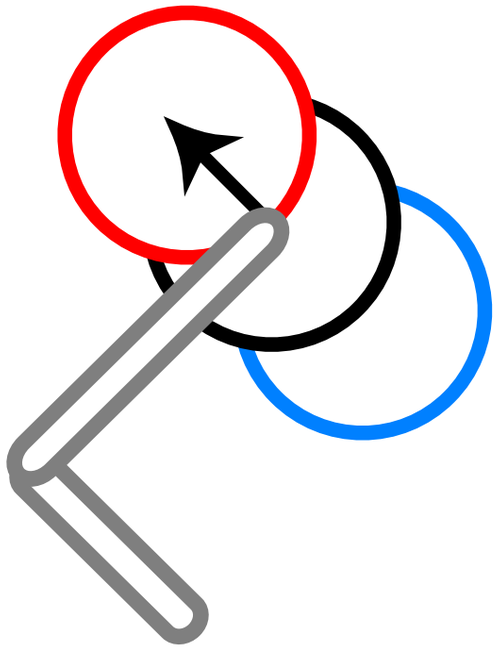






Load Applied and Must Move to Spatial Target

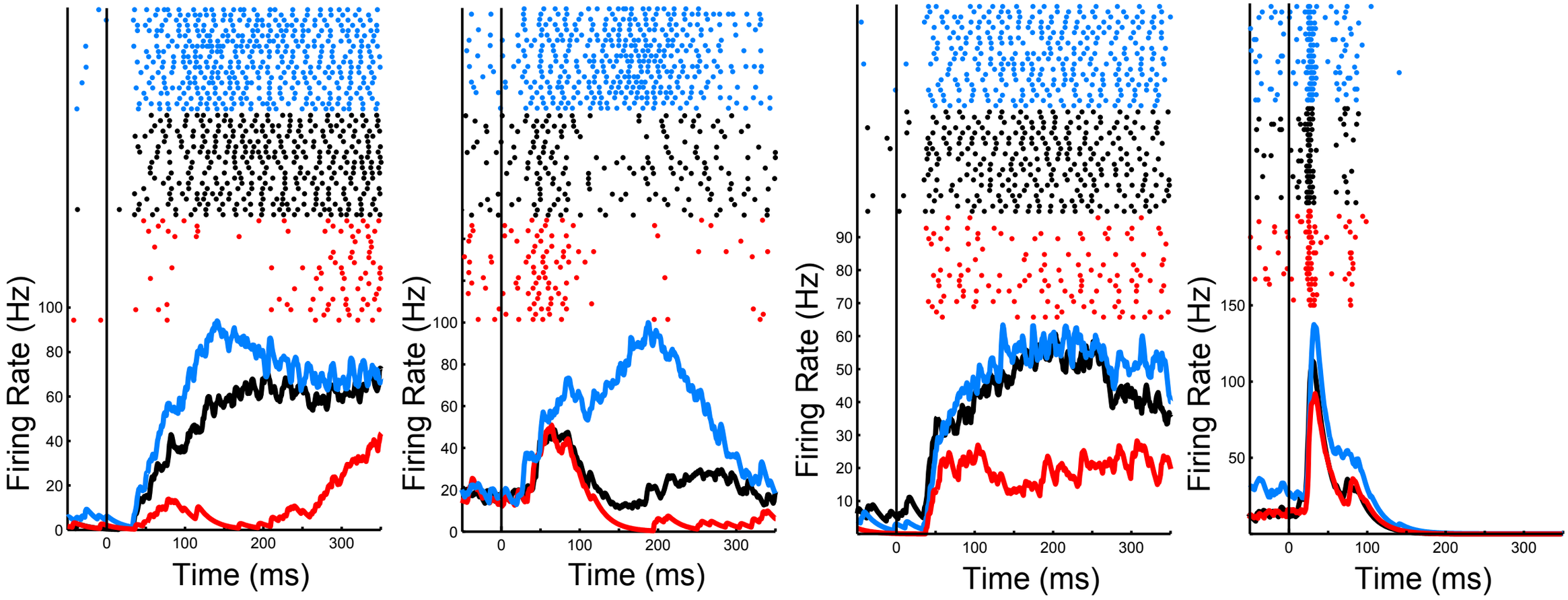
Pruszynski et al., JNP 2008



Goal-Directed Responses in Motor Cortex

Primary Motor Cortex

dorsal Premotor Cortex



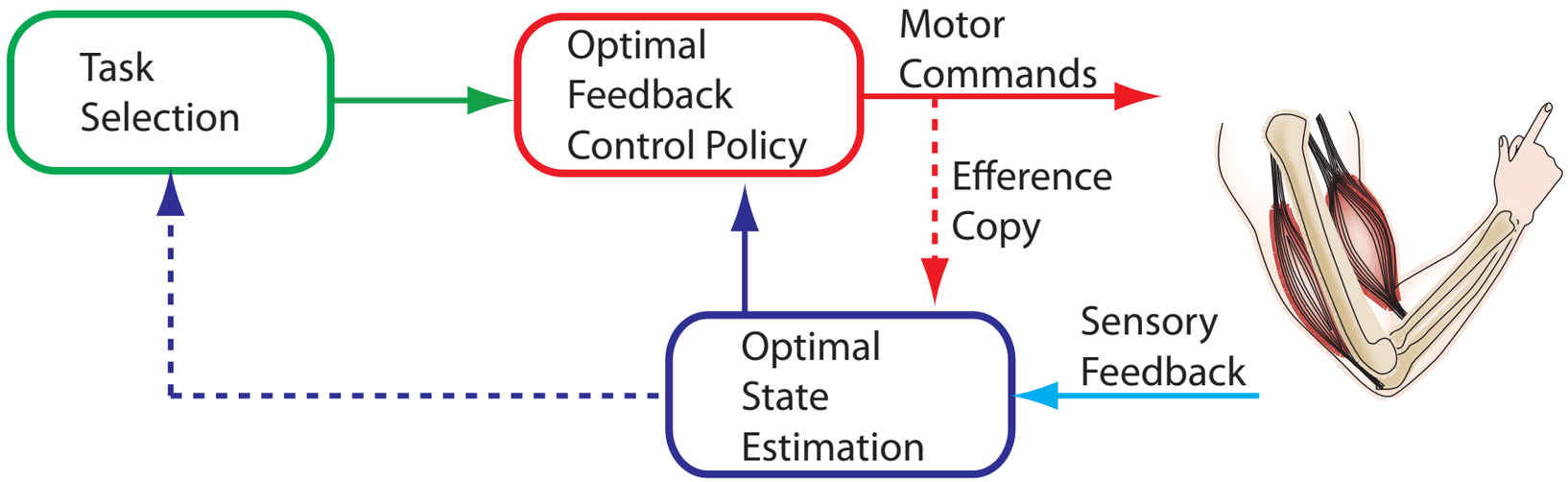
M1 Neuron (20080627b, +5mm)

M1 Neuron (20080627d, +5mm)

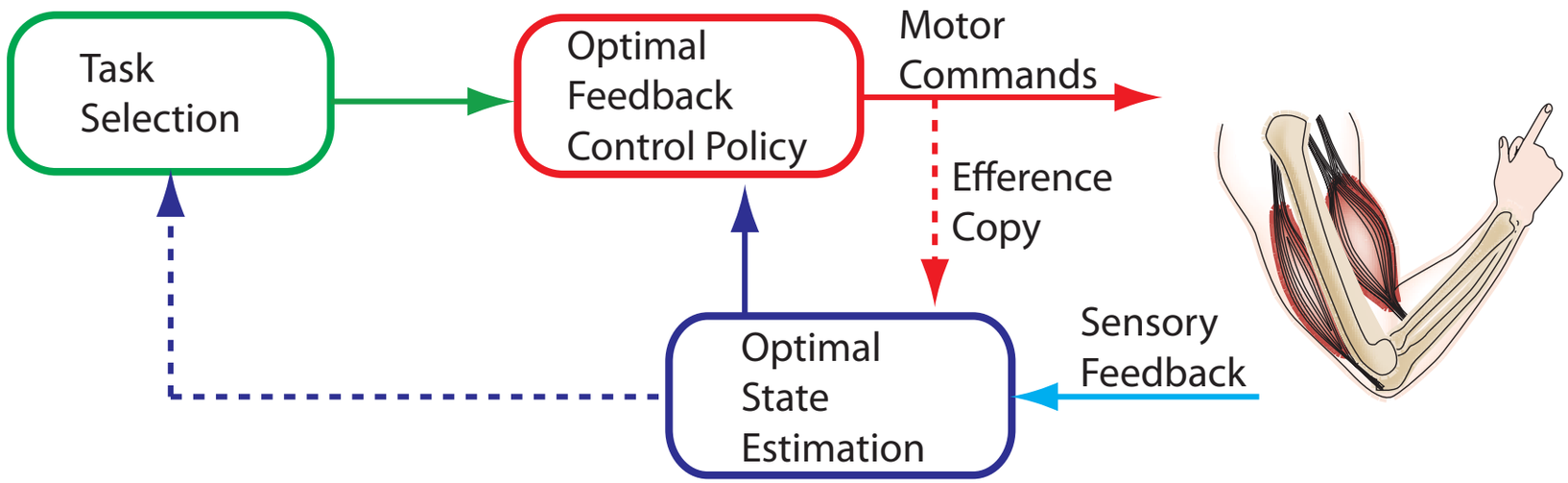
PMd Neuron (20080930d, +7mm)

PMd Neuron (20081017d, +10mm)

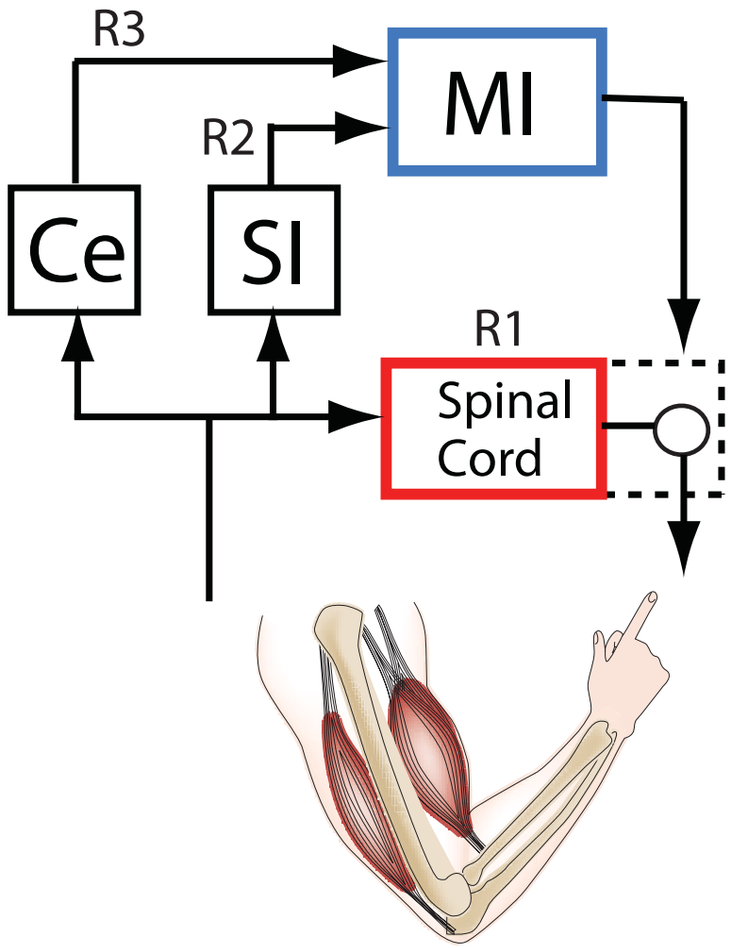
Neural Implementation of OFC-like control

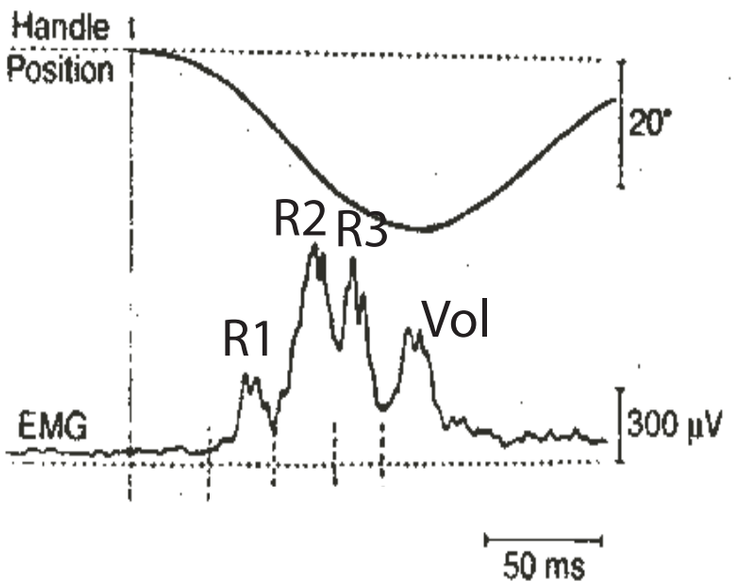


Neural Implementation of OFC-like control

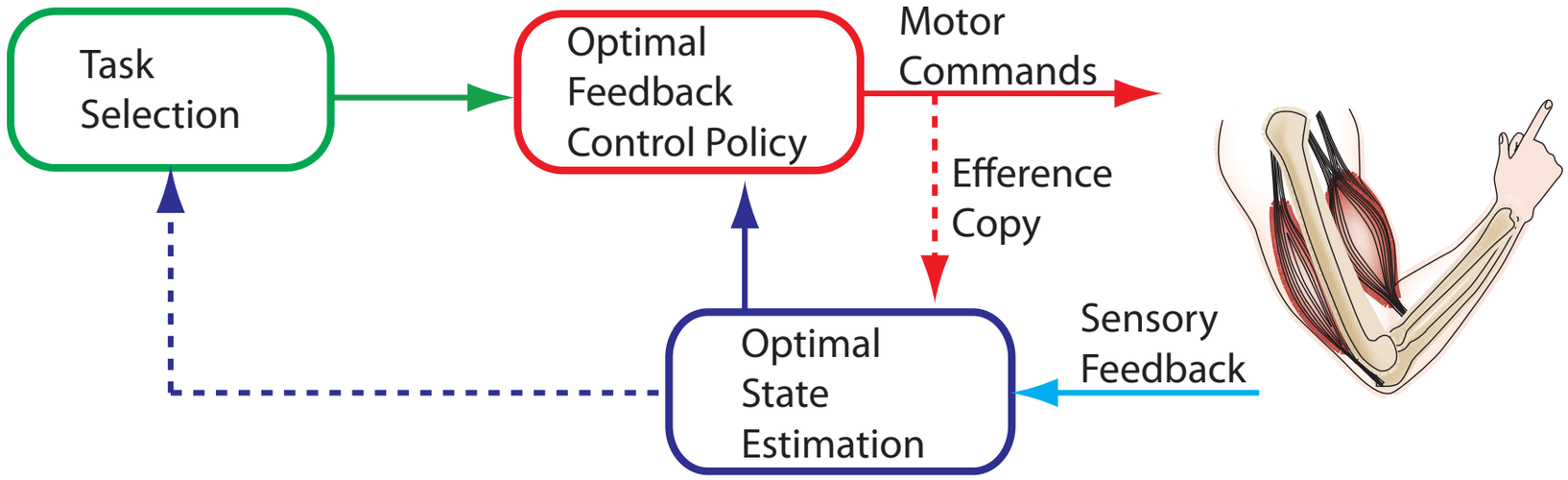


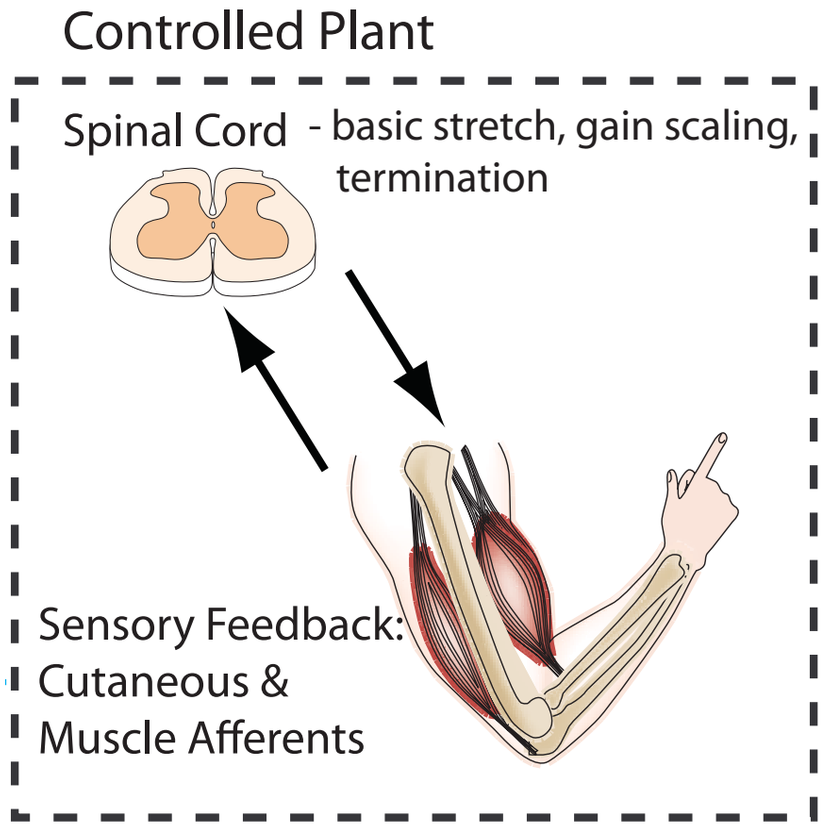
Traditional view of stretch response pathways

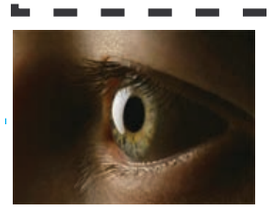




Neural Implementation of OFC-like control

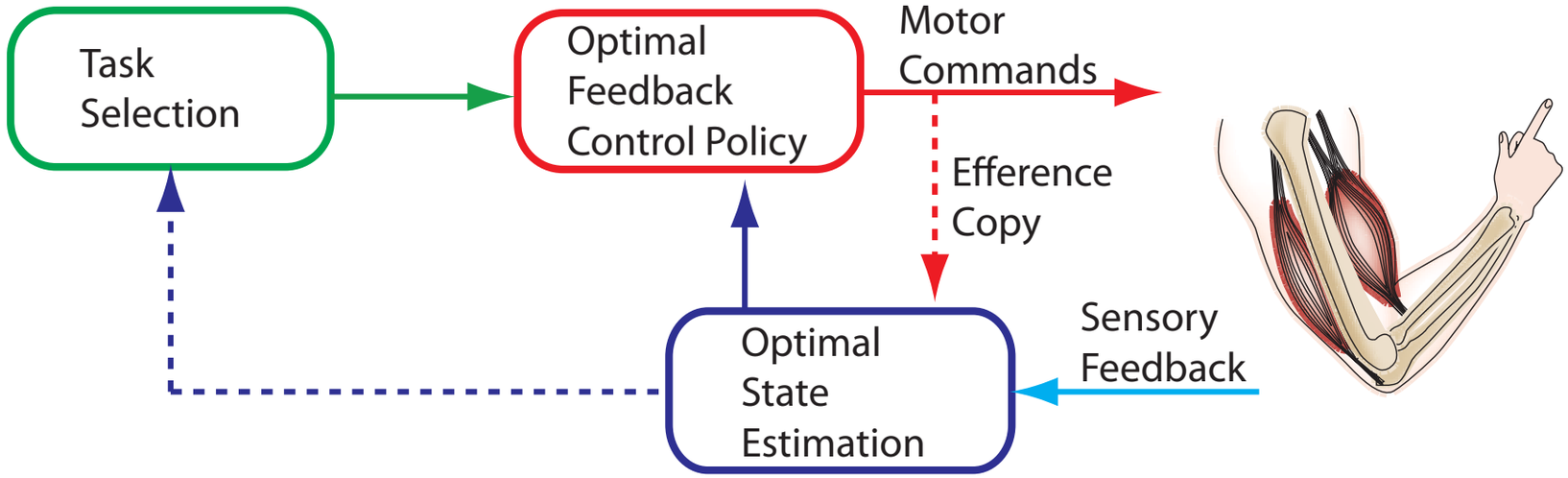


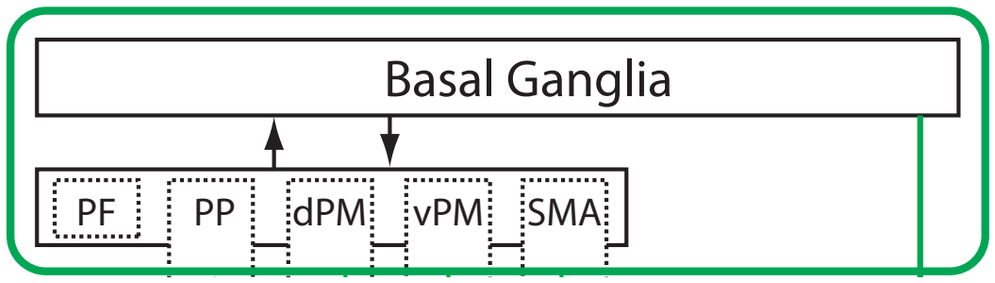


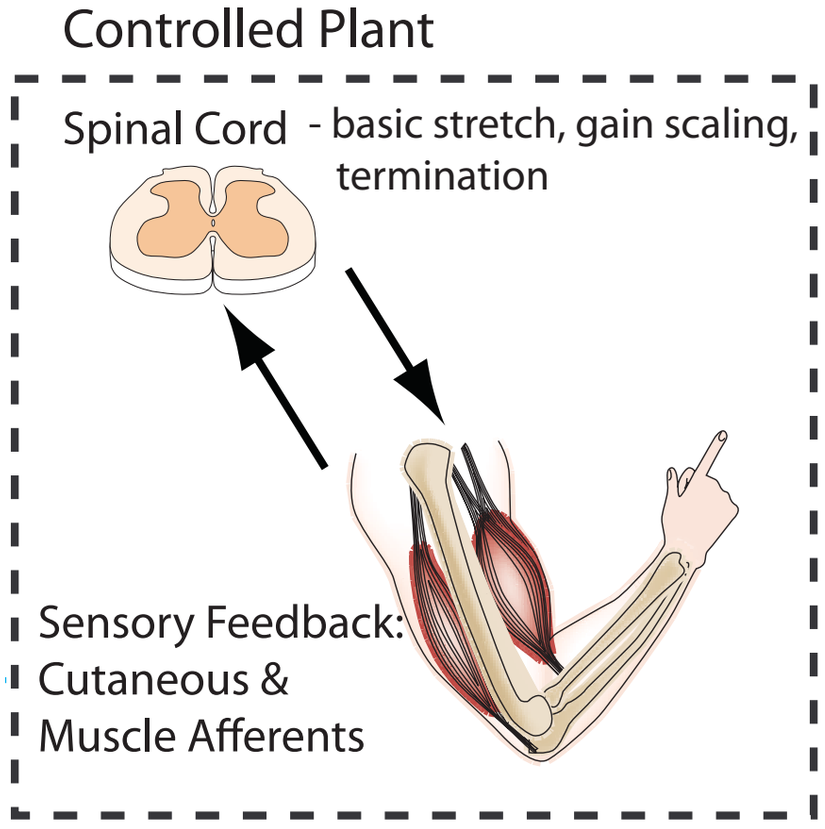


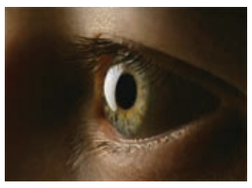
Scott, TICS 2012

Neural Implementation of OFC-like control



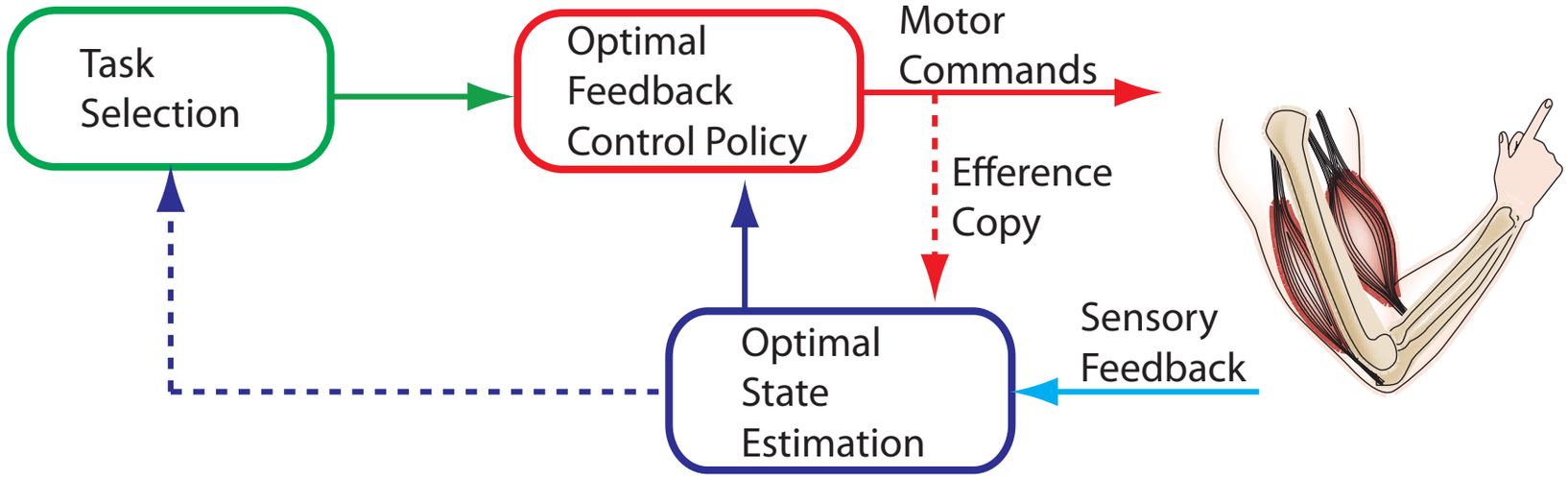


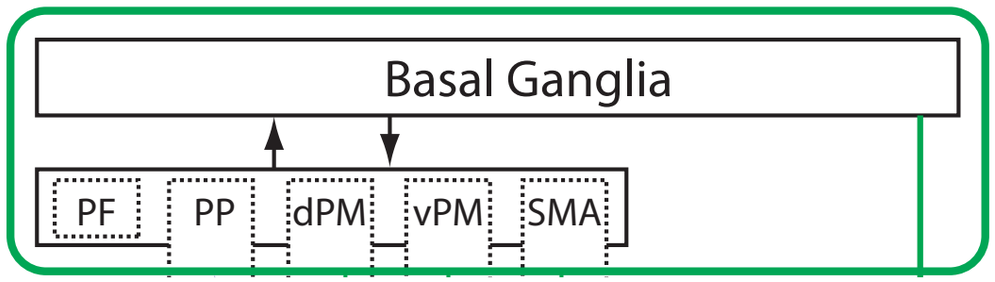


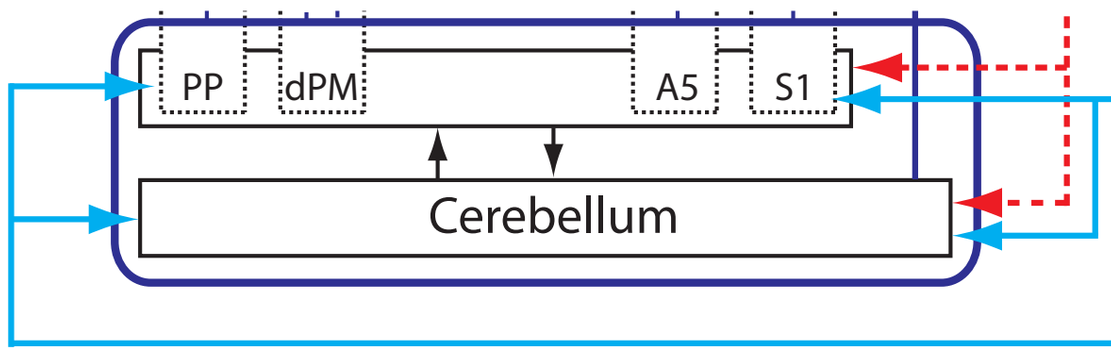


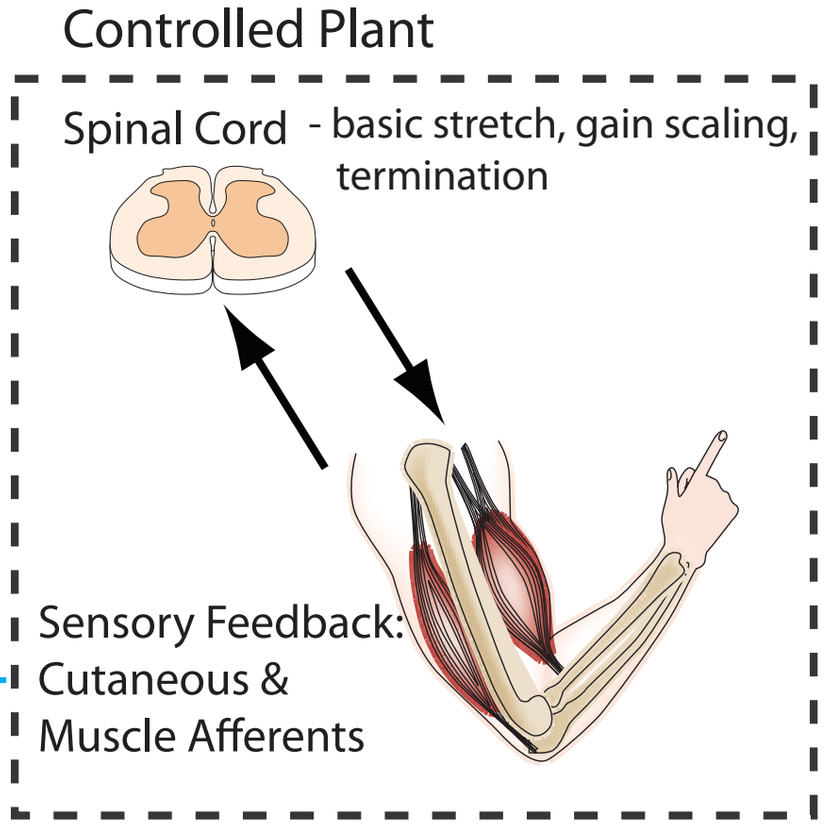
Scott, TICS 2012

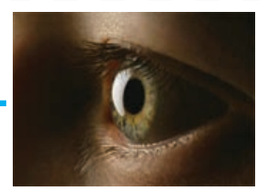
Neural Implementation of OFC-like control





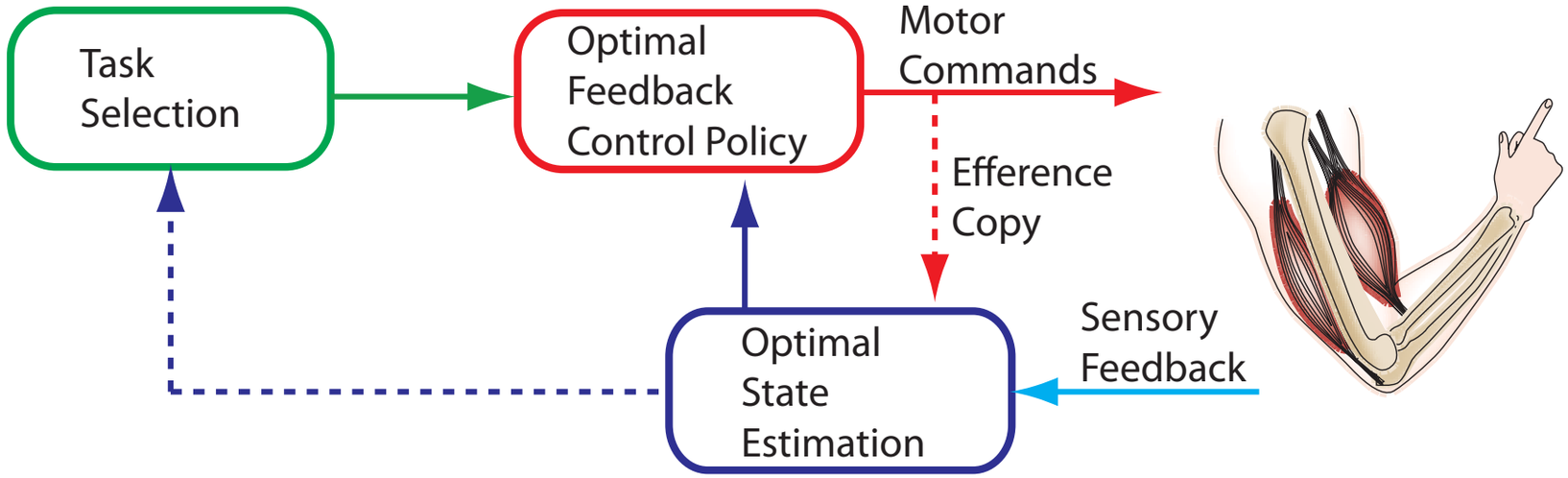


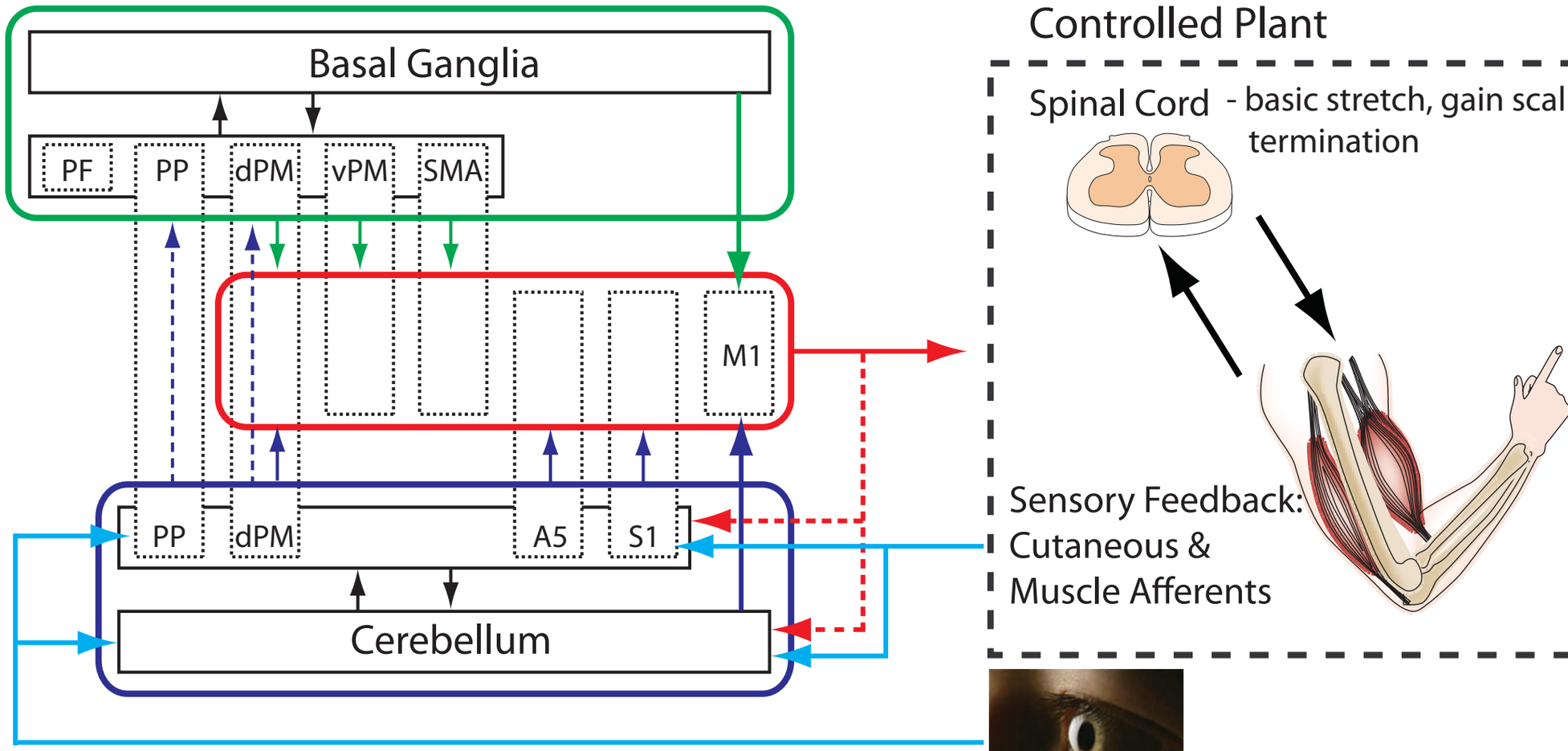




Scott, TICS 2012

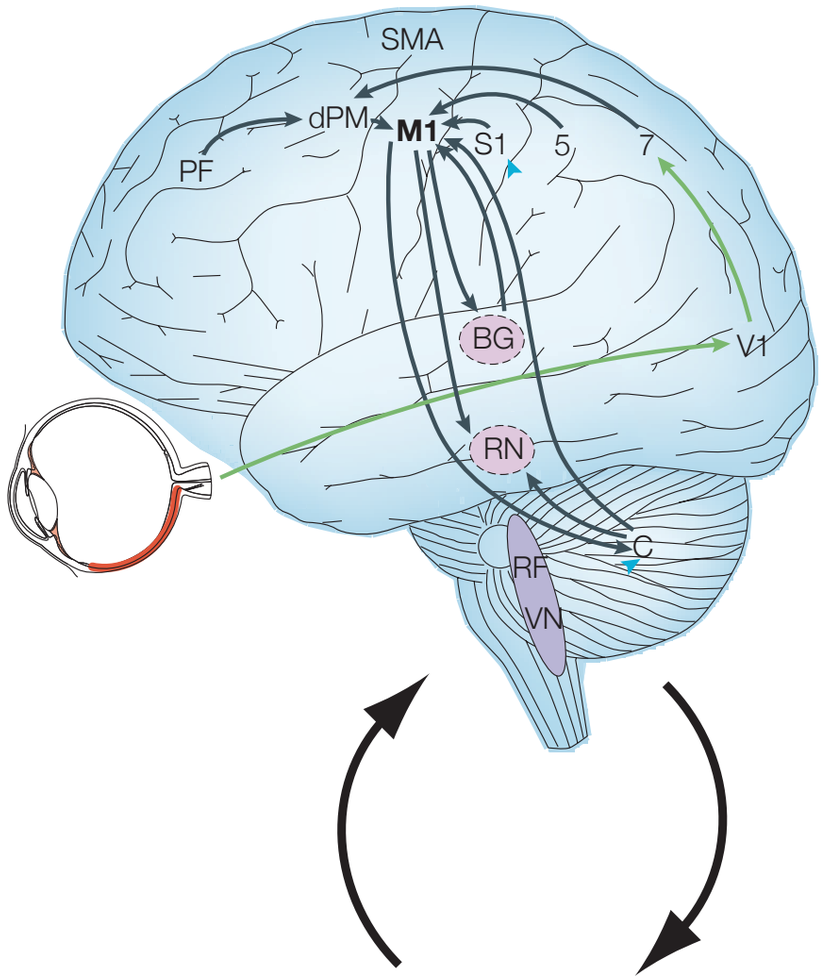
Neural Implementation of OFC-like control



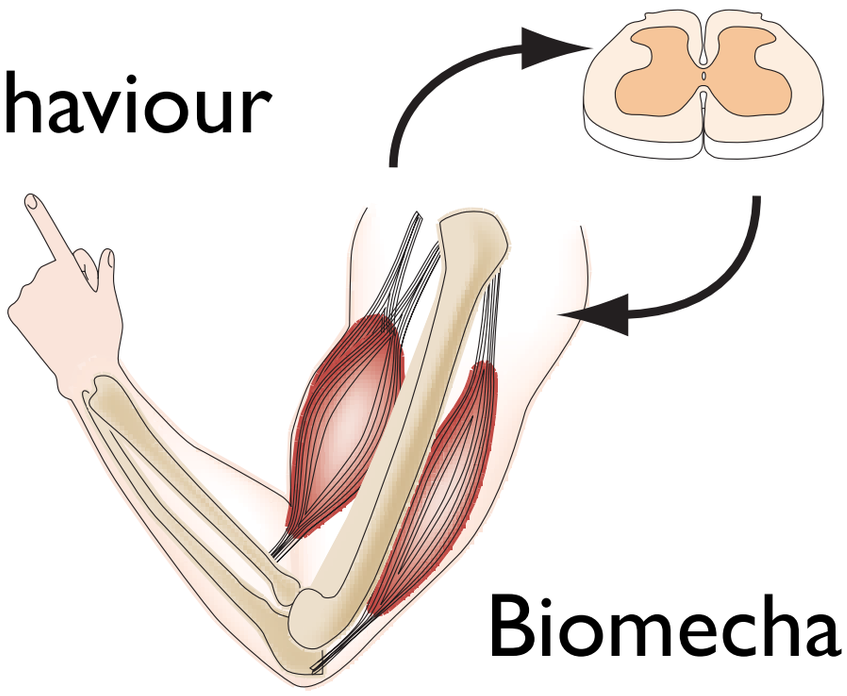


Scott, TICS 2012

Brains



Behaviour



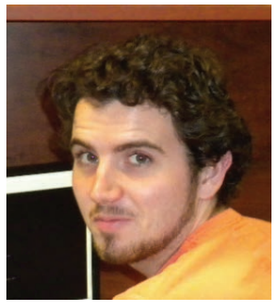
Biomechanics

Take Home Message

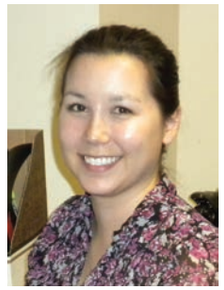
- Optimal Feedback Control (OFC) as a Theory of Voluntary Control
- Stretch Responses Mirror Capabilities of Voluntary Control
- Transcortical Feedback is Important for Voluntary Control

Clinical Research Group


Mary Jo Demers


Teige Bourke


Catherine Lowrey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