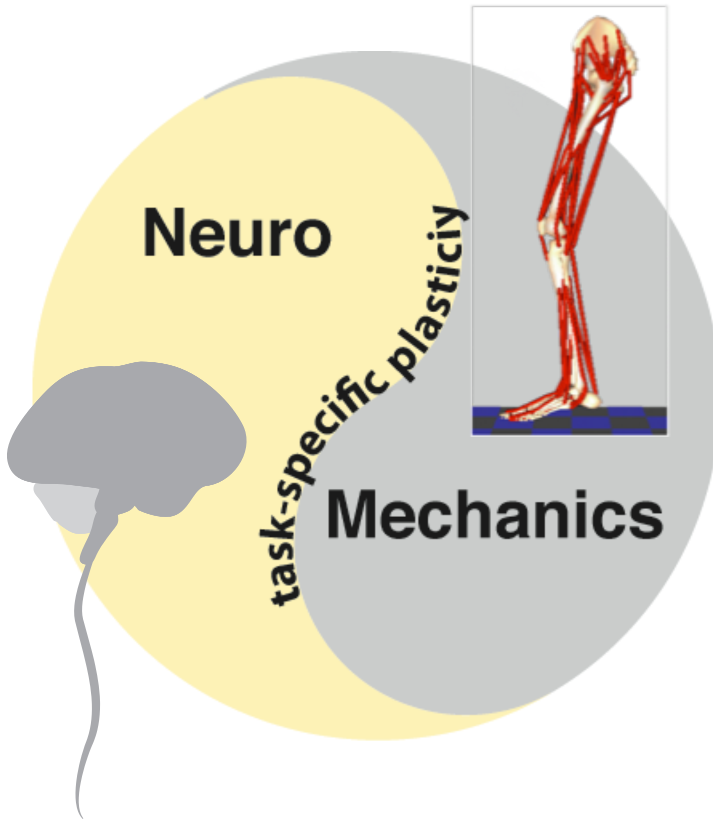
The brain and body compute together: neuromechanics of sensorimotor control

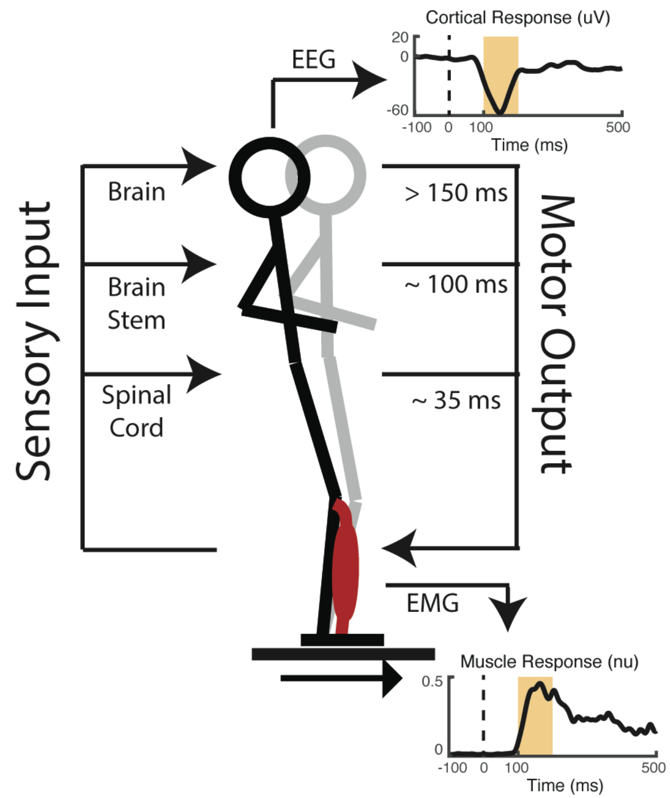


Lena H. Ting, PhD
lting@emory.edu

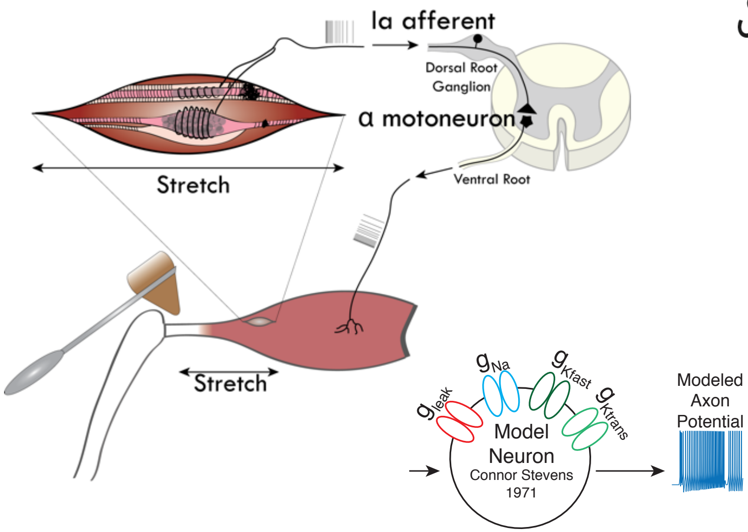
Georgia Tech
Wallace H. Coulter Department of Biomedical Engineering
at Georgia Tech and Emory University
EMORY UNIVERSITY

Multiscale neuromechanical interactions across motor, mood, mental disorders

Error assessment and perception

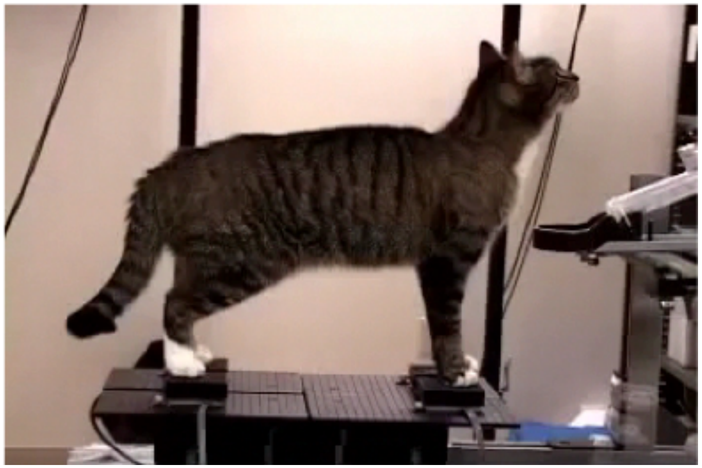


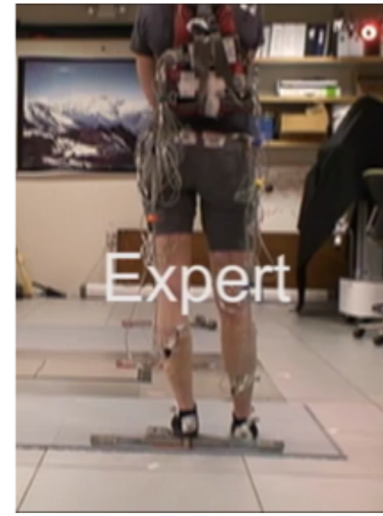
Muscle spindle sensory coding
Spinal reflex excitability



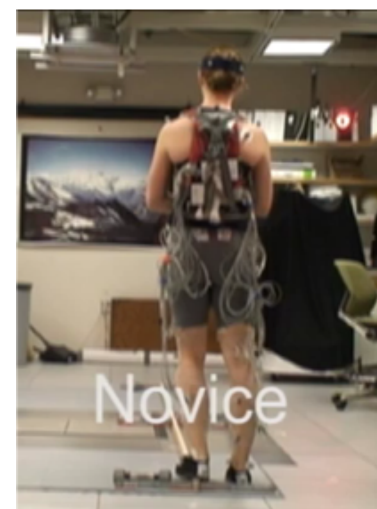
Neuromechanics of muscle coordination for balance
(a reliable indicator of motoneuron activity)

General principles about neuromechanical interactions that shape how we move

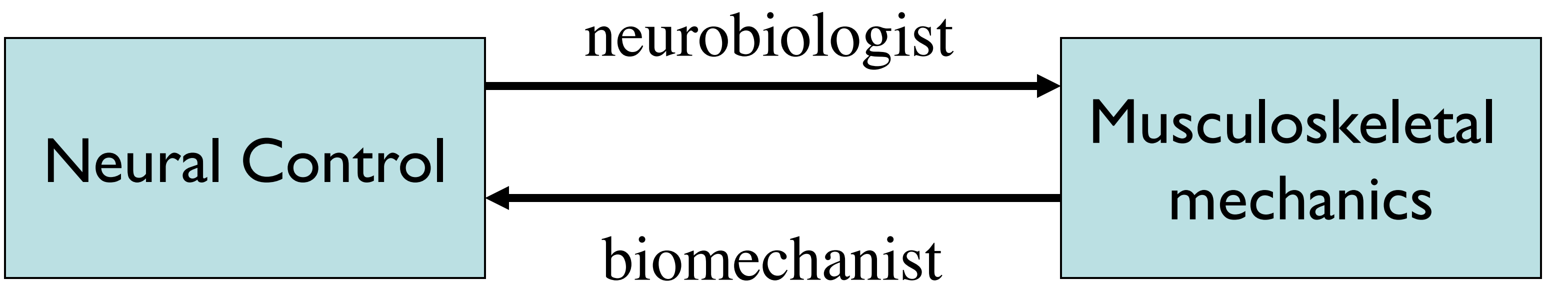




Chang and Ting, *Biology Letters* 2017



What determines the way we move?

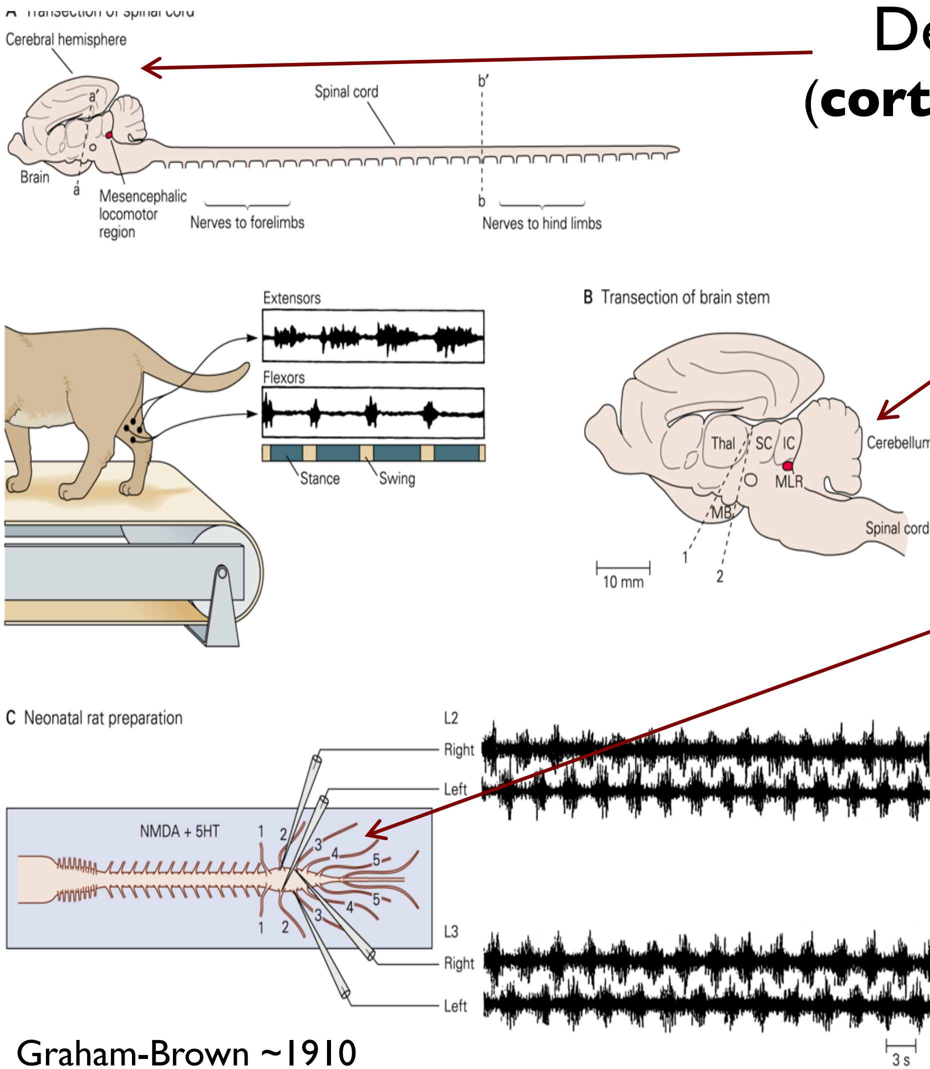


Chiel, Ting, Ekeberg, Hartmann, *Journal of Neuroscience 2009*

Neuroscience perspective

Neural control is hard, mechanics is trivial

"The brain tells the body what to do"



Graham-Brown ~1910

Decision
(**cortex**: move?)

task
command
(**brainstem:** tonic)

execution
command
(**spinal cord:** rhythmic)

cortex → brainstem → spinal cord →

…sensory feedback
and spinal reflexes too
Sherrington 1906

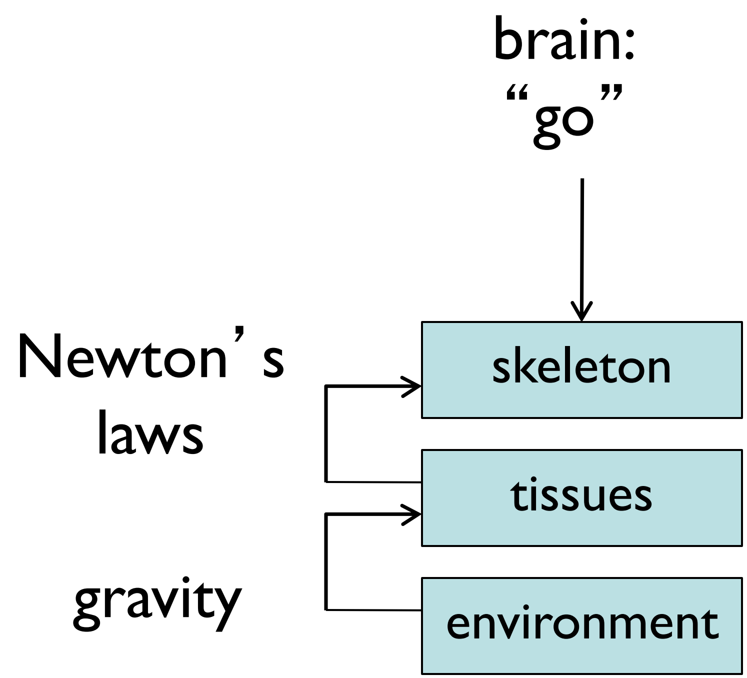
Biomechanics perspective

Mechanics is hard, control is trivial

("and therefore not interesting" – Andy Ruina)

McGeer 1990; Collins, Wisse, Ruina 2005

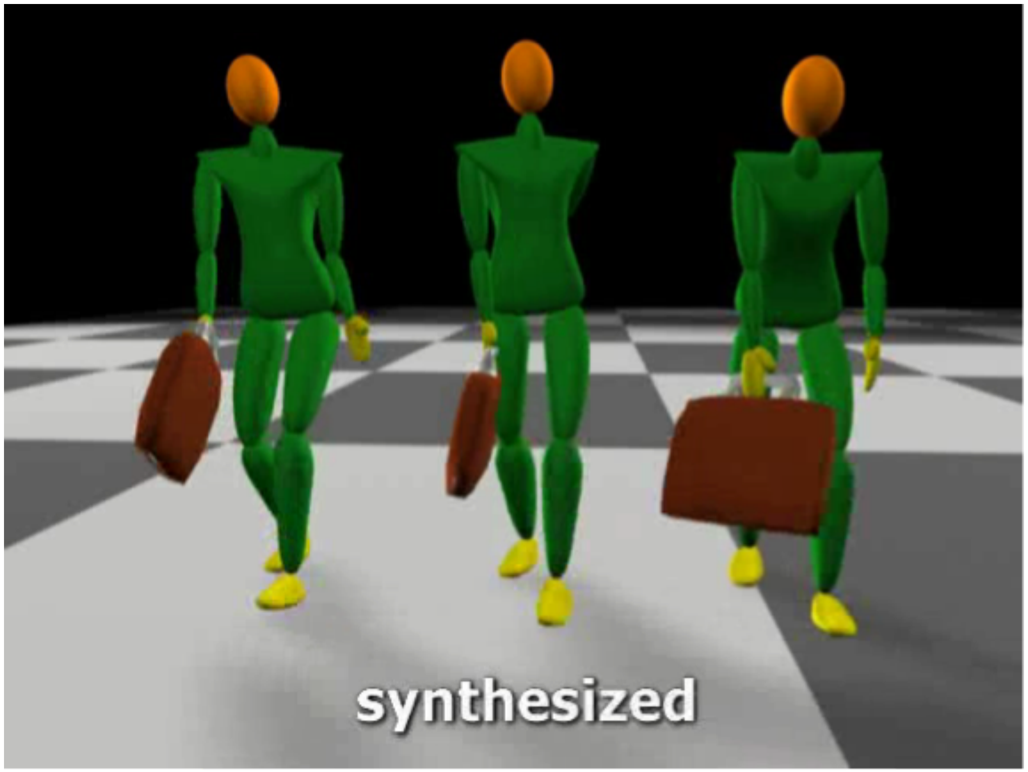
Passive dynamic walking requires almost no energy expenditure



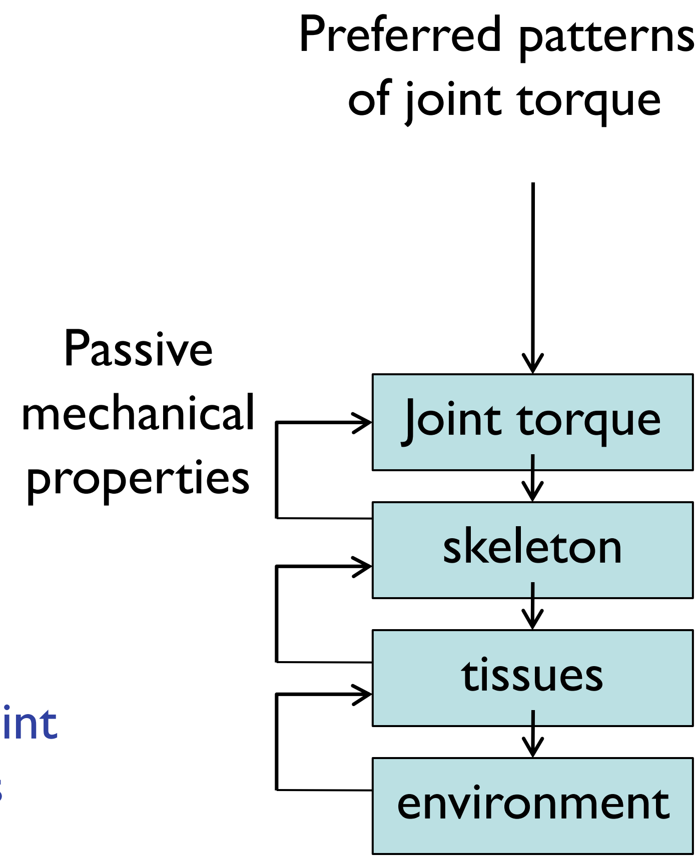
Neuromechanics perspective

Neuromechanical interactions produce characteristic and constrained motions

"Why can we recognize people by the way they walk?" – me



Liu, Hertzmann, Popovic 2005



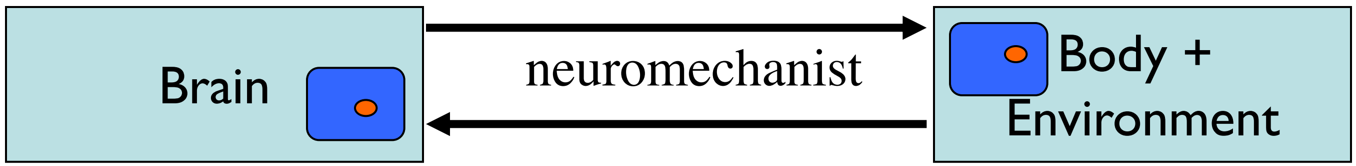
Walking simulations based on preferred patterns of joint torque also improve joint force predictions in patients

Walter …. Fregly 2014 J. Biomech Eng

VIEWPOINT

The brain has a body: adaptive behavior emerges from interactions of nervous system, body and environment Trends in Neuroscience 1997

Hillel J. Chiel and Randall D. Beer

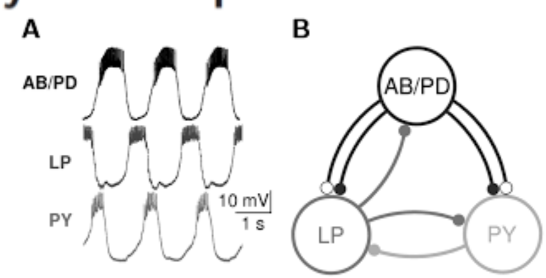


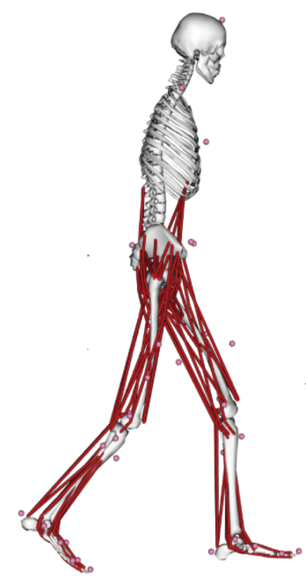
Neuromechanically feasible solutions

Individual solutions

Similar network activity from disparate circuit parameters

Astrid A Prinz, Dirk Bucher & Eve Marder
Nature Neuroscience 2004





Failure of Averaging in the Construction of a Conductance-Based Neuron Model

J Neurophysiology 2002

JORGE GOLOWASCH,[1] MARK S. GOLDMAN,[1,2] L. F. ABBOTT,[1] AND EVE MARDER[1]

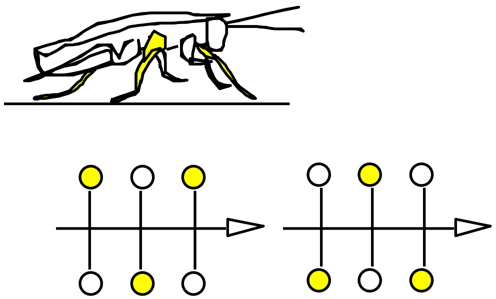
after Ting and McKay *Current Opinion in Neurobiology 2007;* Tresch and Jarc *Current Opinion in Neurobioogy 2009*

The Journal of Experimental Biology 202, 3325–3332 (1999)

TEMPLATES AND ANCHORS: NEUROMECHANICAL HYPOTHESES OF LEGGED LOCOMOTION ON LAND

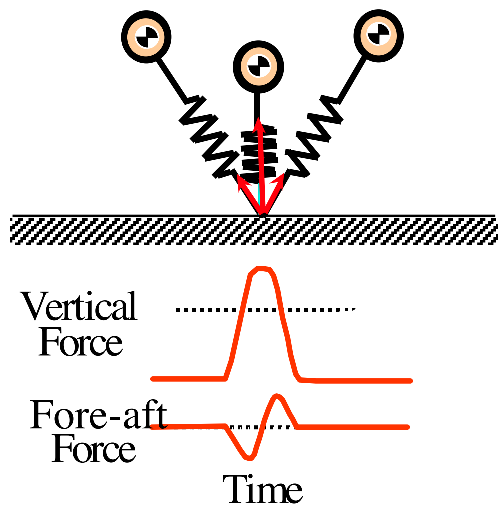
R. J. FULL[1,*] AND D. E. KODITSCHEK[2]

SIX-Legged

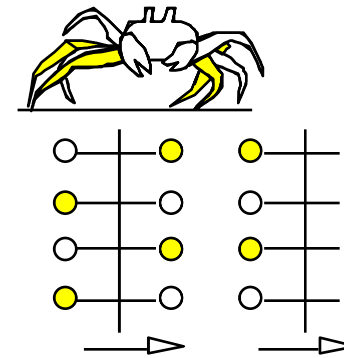


Cockroach

Common template

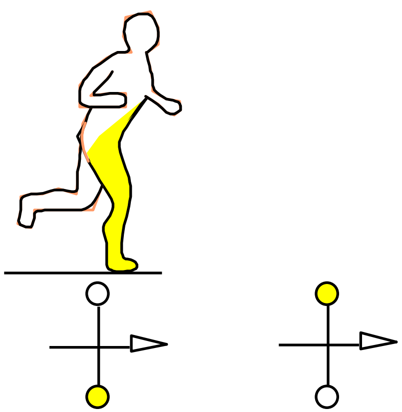


EIGHT-Legged



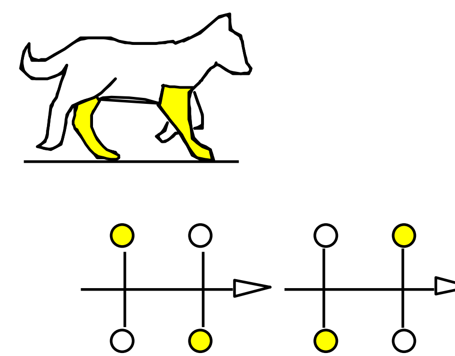
Crab

TWO-Legged



Human

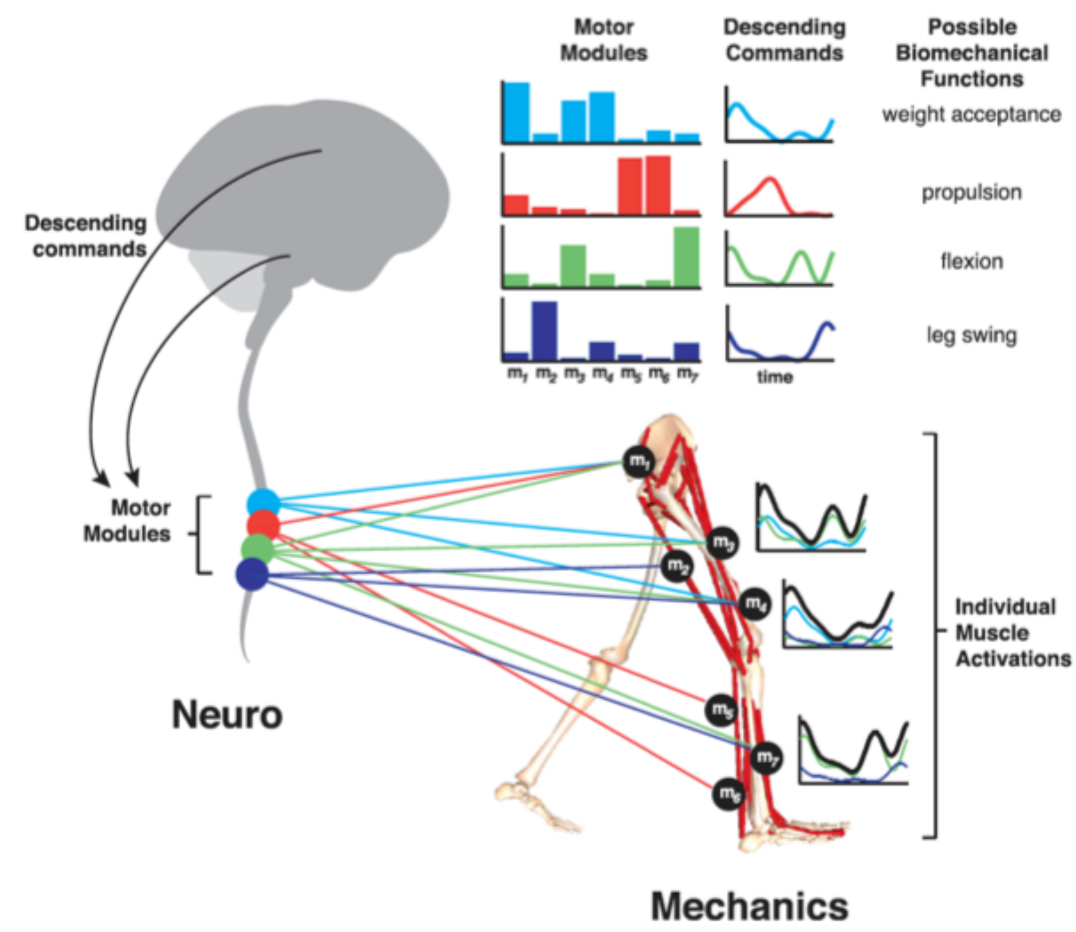
FOUR-legged



Dog

Marc Raibert MIT Leg Lab 1980s

Principles of hierarchal and modular sensorimotor control for robustness and flexibility leading to individuality



Ting et al. Neuron, 2015
Ting and McKay Current Opinion in Neurobiology 2008

Brain and computation bootcamp: Why movement matters

- Sensorimotor control as the canonical decision-making process
  - How to rapidly and robustly achieve behavioral goals by coordinating the same motor apparatus in different ways?
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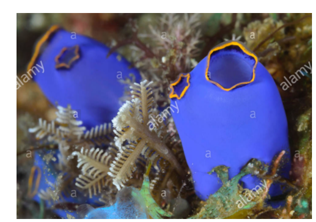
Why do we have brains?

To interact with the world, i.e. move

- Motor and cognitive decision-making toward goals :
  - Interpret ambiguous sensory data
  - Coordinate body parts
  - Weigh cost and criteria
  - Adapt to behavioral contexts
- Costs and constraints are physical in movement
- Neurons: costly and slow
- Cognitive, emotional, and other brain functions support movement
  - *Side note:* enteric nervous system, i.e. "little brain"

Dan Wolpert

~100 neurons
tunicate larvae



<100 neurons
adult tunicate

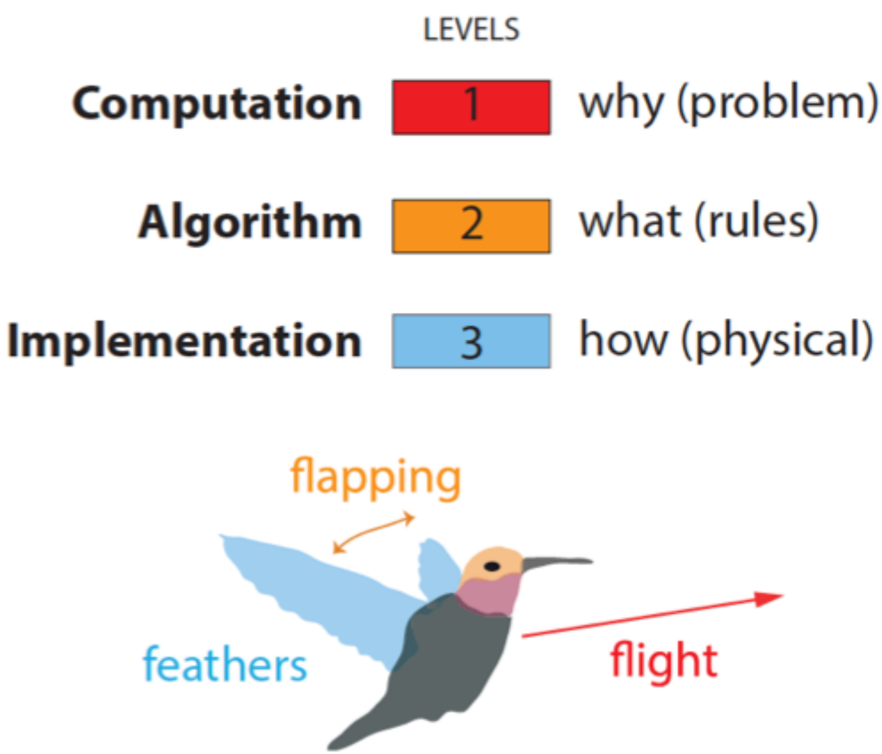
CellPress

Neuron
Perspective

2017

Neuroscience Needs Behavior: Correcting a Reductionist Bias

John W. Krakauer,[1,*] Asif A. Ghazanfar,[2] Alex Gomez-Marin,[3] Malcolm A. MacIver,[4] and David Poeppel[5,6]

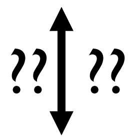


Marr 1982/2010

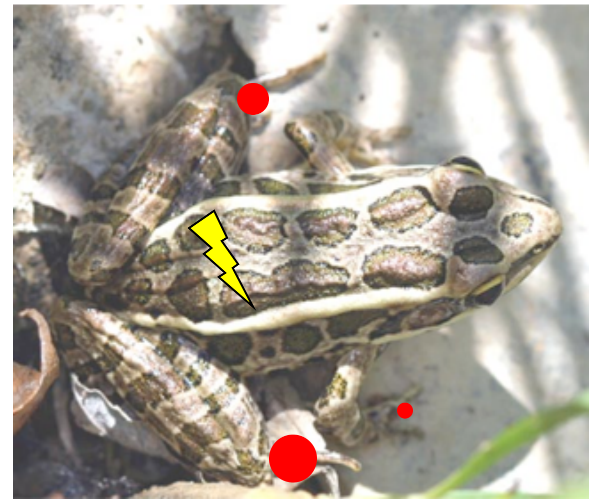
- What is the brain trying to do?
- What are the organizational principles?
- What mechanisms are available?
- How are they coordinated to produce behavior?

Example of “simple” motor decision
Frog spinal cord wiping reflex

- **Task/problem:** wipe skin
  - Abstract, goal-directed



- **Implementation:**
  - Multiple movement patterns achieve the same task
    - Leg wipes the irritated area regardless of starting position
    - Hold one leg down activates the other
  - Within a movement: Repetition without repetition
    - Bernstein 1968,



Emilio Bizzi et al MIT

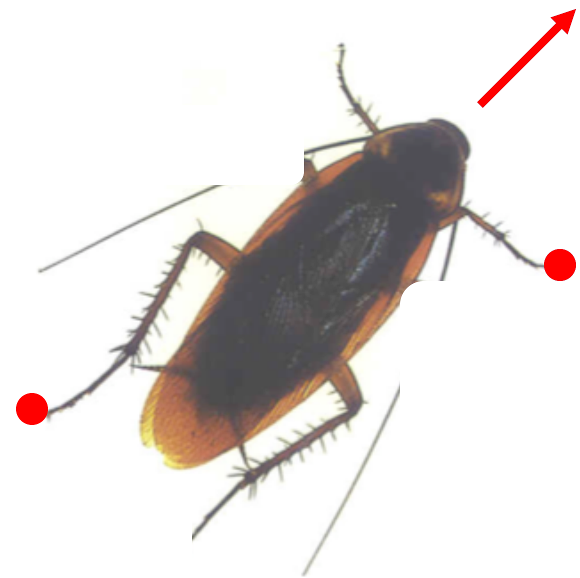
	LEVELS	
Computation	1	why (problem)
Algorithm	2	what (rules)
Implementation	3	how (physical)

Example of "simple" motor decision
Cockroach running

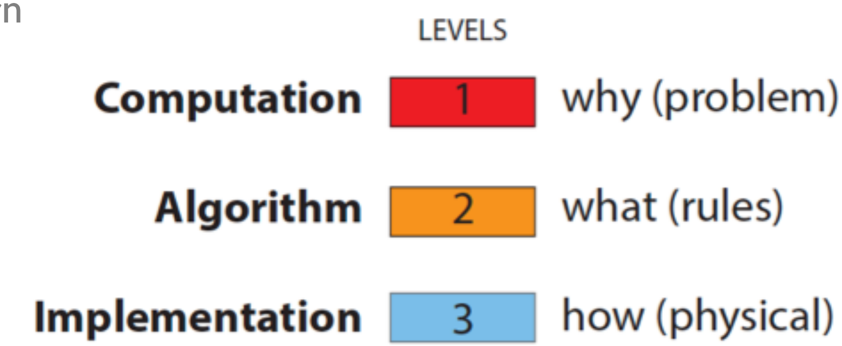
- **Task/problem:** run!
  - Abstract, goal-directed

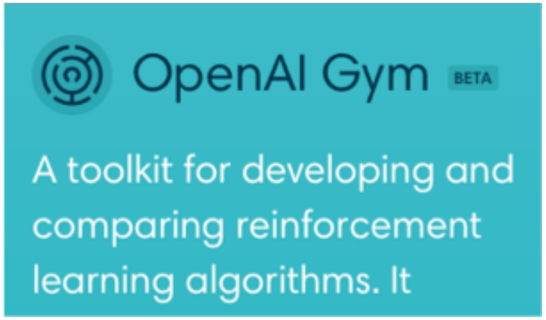
?? ↕ ??

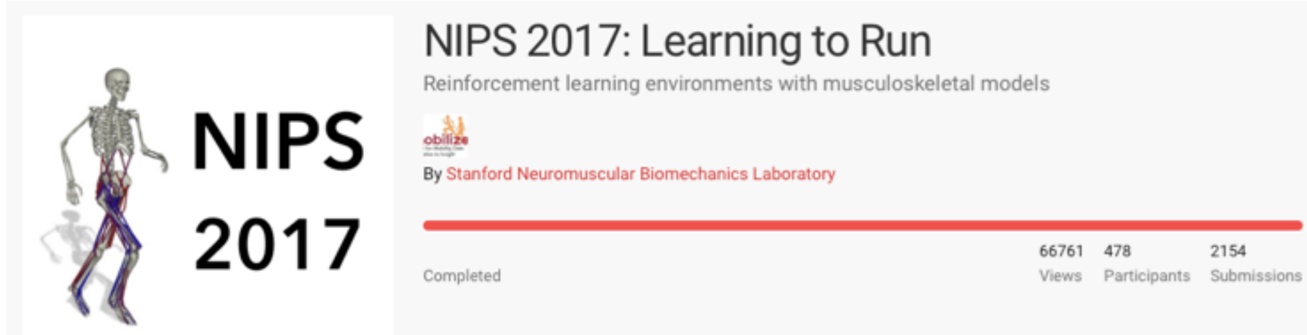
- **Implementation:**
  - Multiple movement patterns achieve the same task
    - Tripod gait pattern
    - Remove legs: switches to diagonal pattern
  - Within a movement: Repetition without repetition
    - Bernstein 1968,

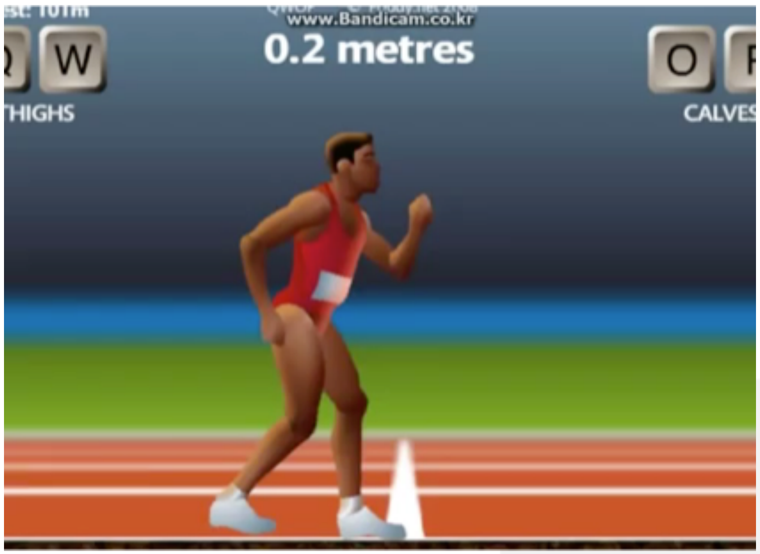


Bob Full UC Berkeley



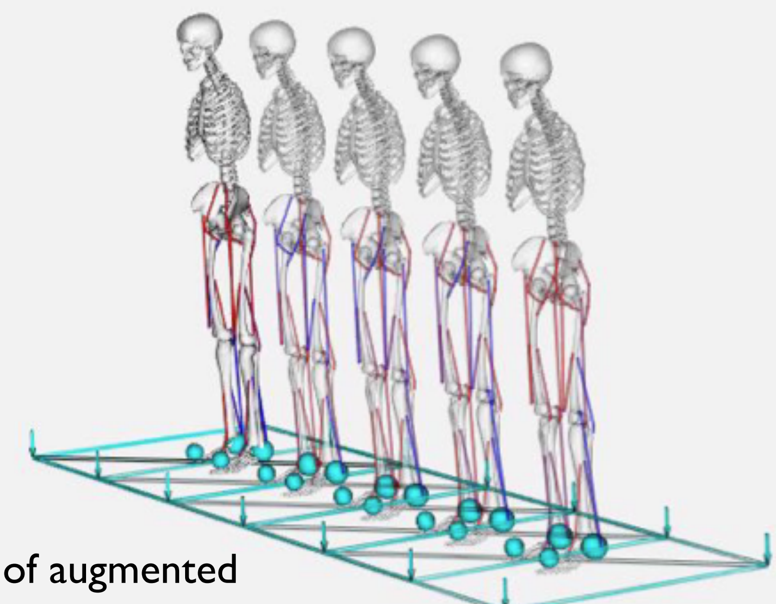






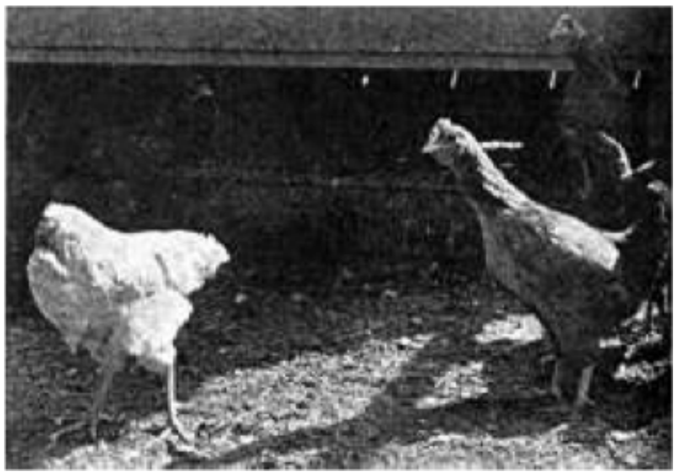
QWOP http://www.foddy.net/Athletics.html

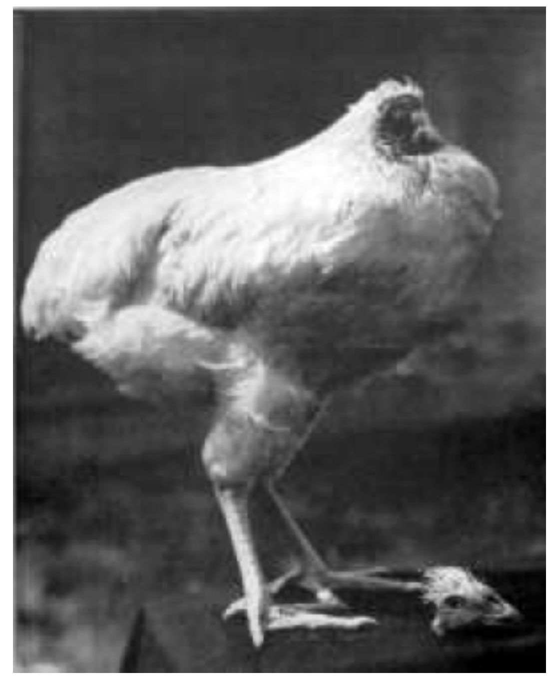
- Our bodies are multifunctional, requiring complex neural control
- The same system is reconfigured for walking, running, dancing…



Reinforcement learning using neuroevolution of augmented topologies (NEAT); Unpublished, van de Woue, de Groote

MIKE THE HEADLESS CHICKEN





- No cortex
- Half a brainstem
- Lived for years

http://www.mikettheheadlesschicken.org

Brain and computation bootcamp: Why movement matters

- Sensorimotor control as the canonical decision-making process
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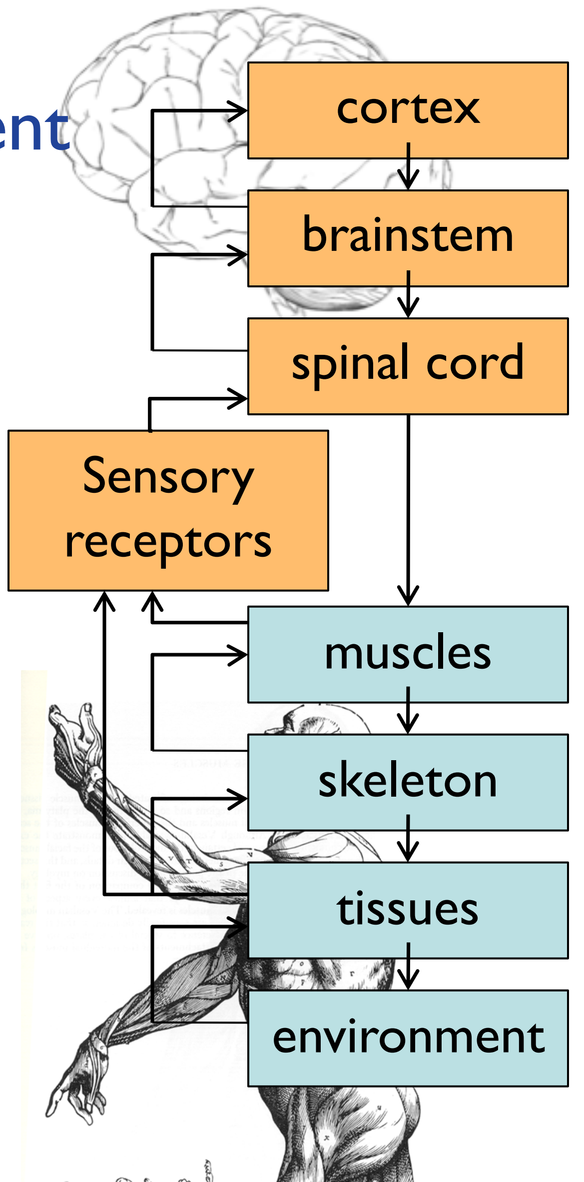
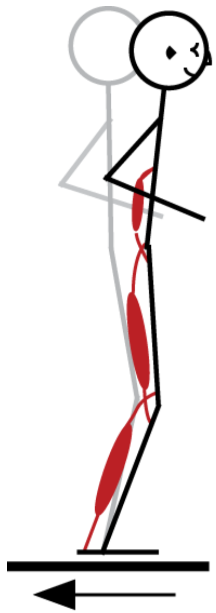
Neural control of movement is hierarchical

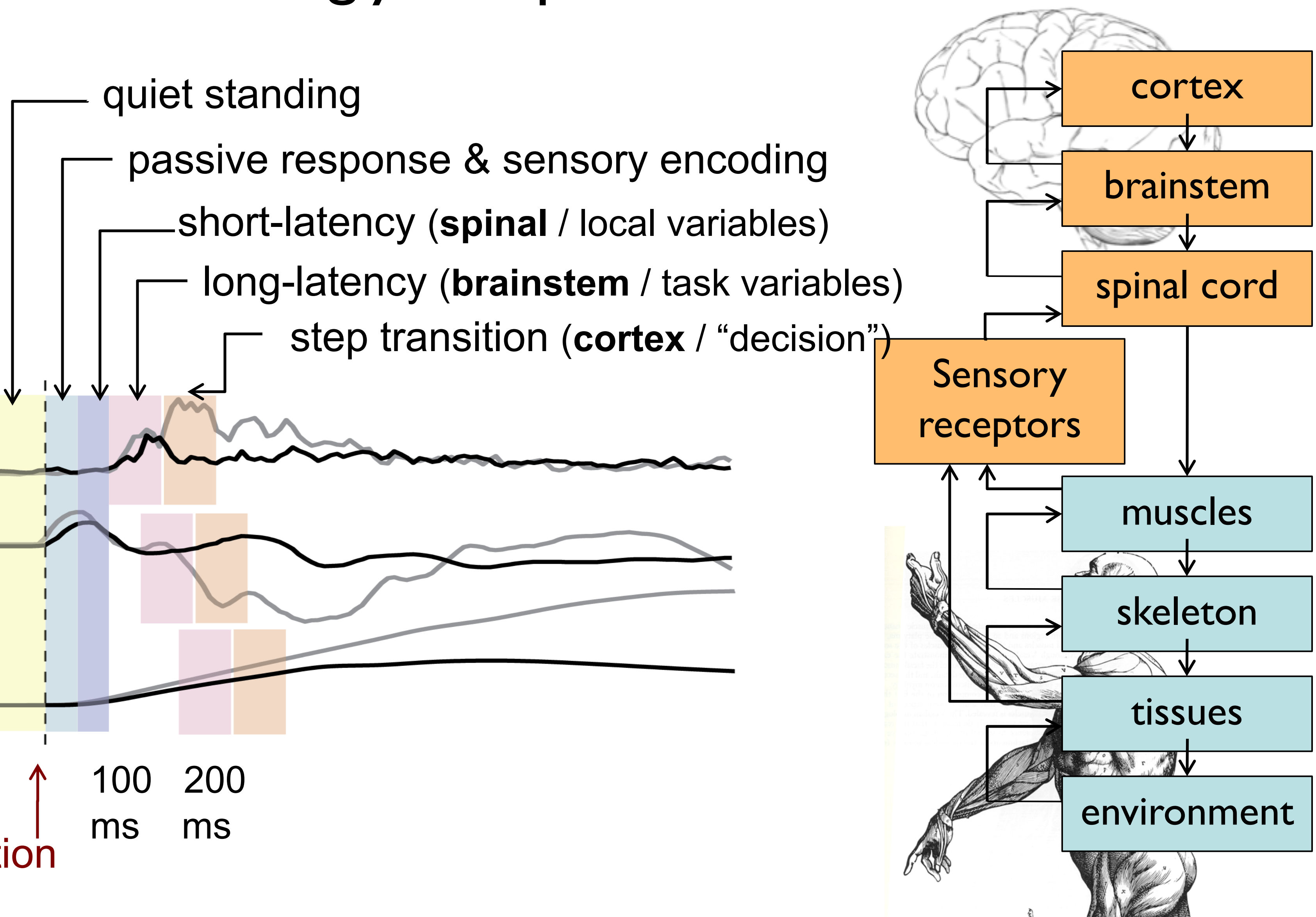
- Broadly, three categories of movement
  - Reflexive (spinal cord)
    Tendon-tap reflex, withdrawal reflex
  - Automatic/Rhythmic (brainstem)
    Locomotion, breathing, balance
  - Voluntary (cortex)
    Reaching, talking, manipulating objects

- But all voluntary movement requires coordinated automatic and reflex neural control



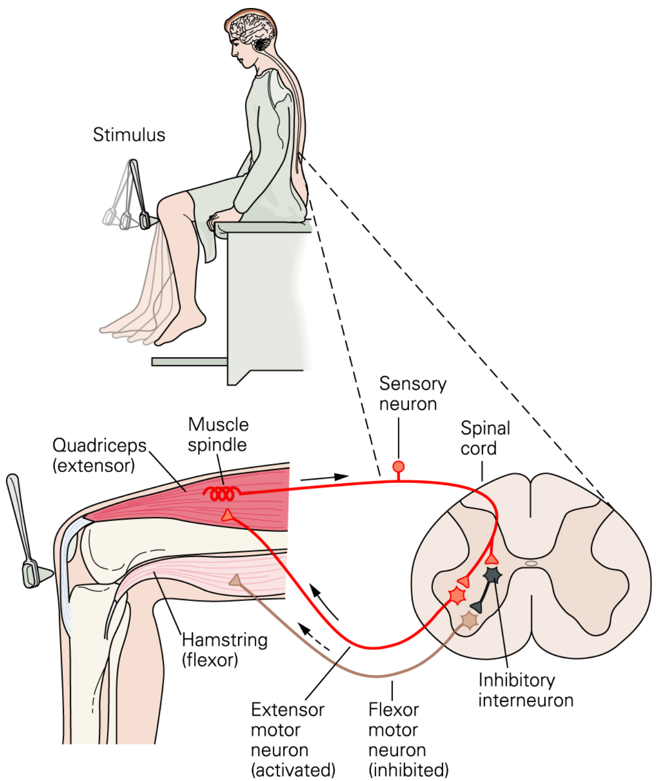
Speed is of the essence:
Increasingly complex actions with time



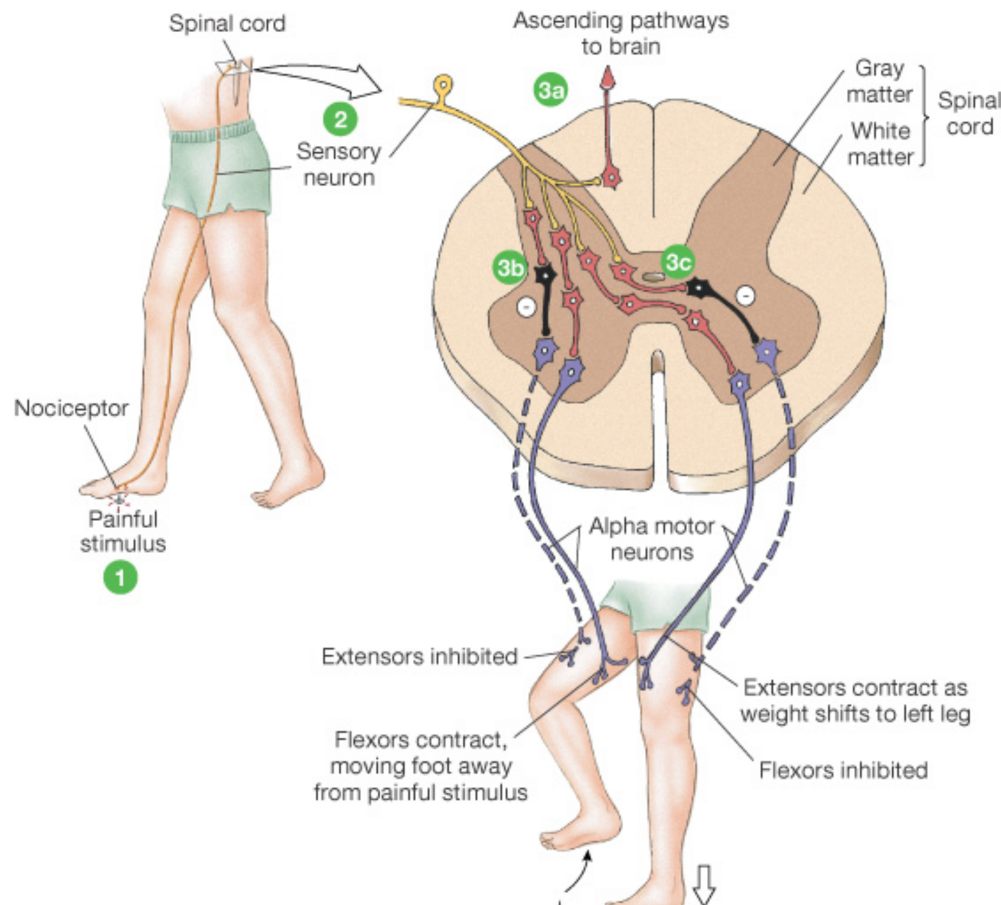


Spinal reflexes rapidly transform sensory information into meaningful motor outputs

Stretch reflex



Flexion reflex

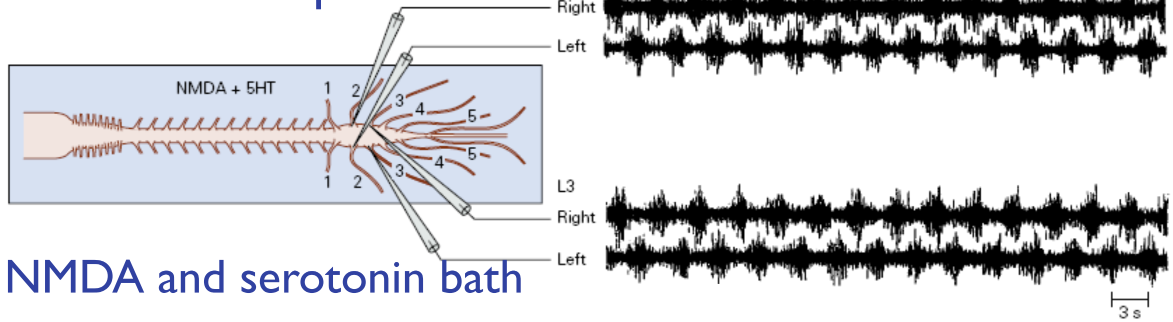


Spinal reflexes are modulated by context, adaptation, emotion, movement, cognitive tasks….

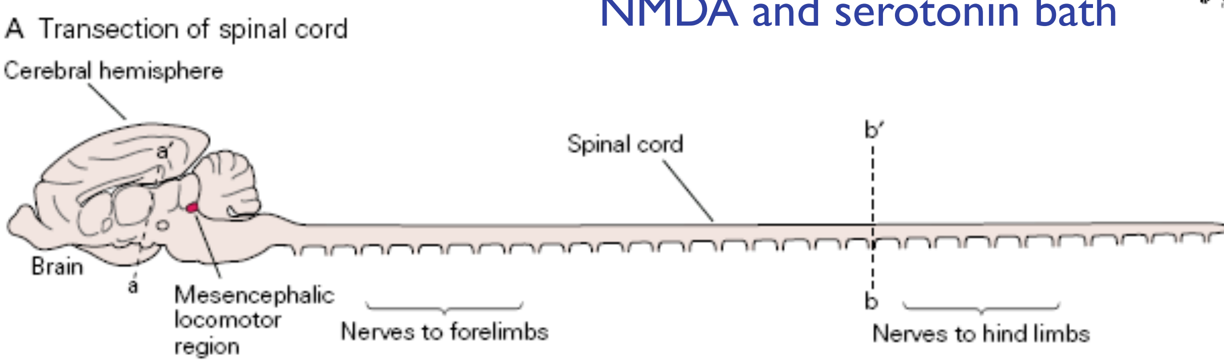
Oscillations in the spinal cord are activated by tonic brainstem activity

Spinal central pattern generator (CPG)

Neonatal rat spinal cord



NMDA and serotonin bath



Brainstem mesencephlic locomotor region (MLR) activates the CPG

- Increased stimulation intensity increases the frequency of oscillation
- Higher centers need not modulate fine details of movement

Principles of Neural Science, 4th ed. KS&J 37-1

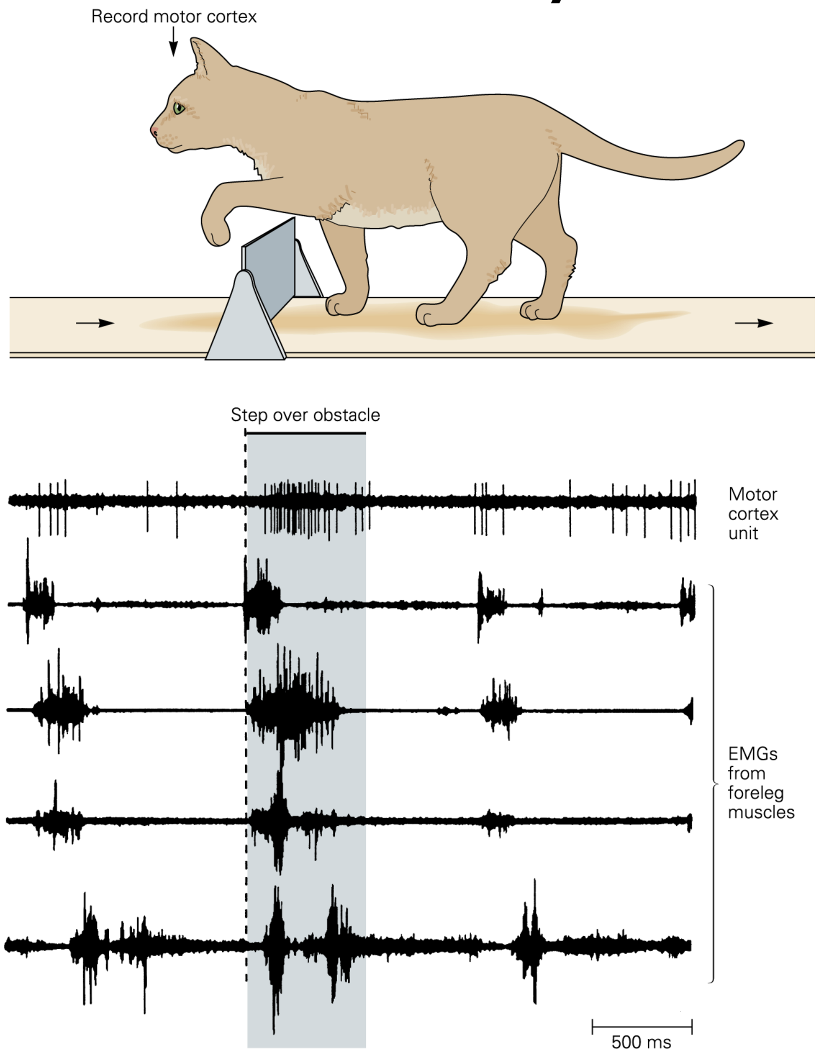
Gaits emerge from neuromechanical interactions

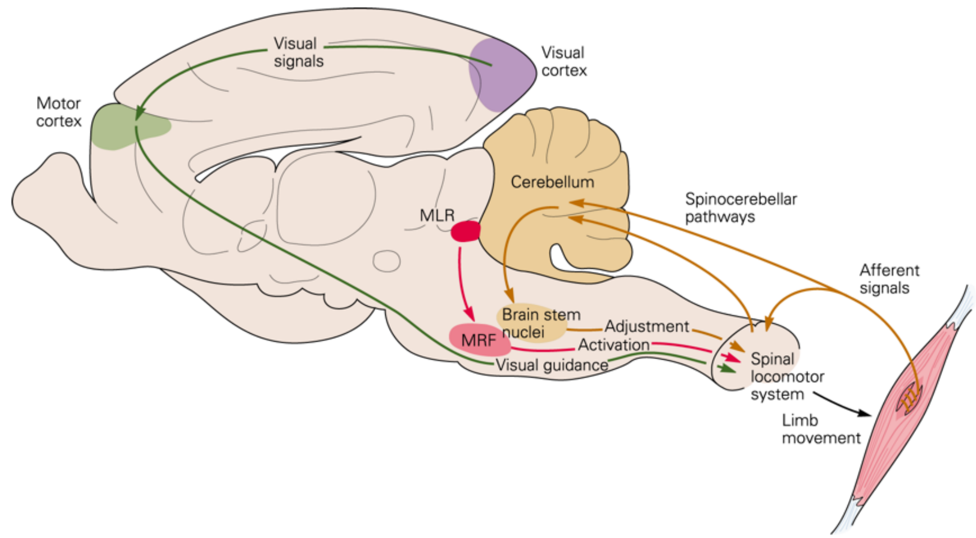
Decerebrate cat on treadmill
T. Graham Brown, ca 1920

From Swimming to Walking with a Salamander Robot Driven by a Spinal Cord Model Science 2007

Auke Jan Ijspeert,[1*] Alessandro Crespi,[1] Dimitri Ryczko,[2,3] Jean-Marie Cabelguen[2,3]

Descending signals from cortex initiate & modify the locomotor pattern





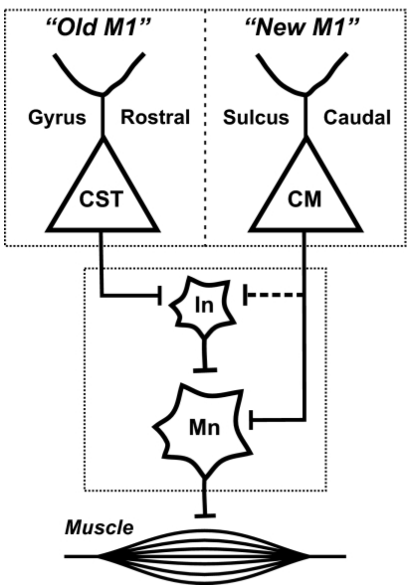
- Motor cortex is activated when stepping over obstacles
- Activity is additive to steady-state locomotor pattern

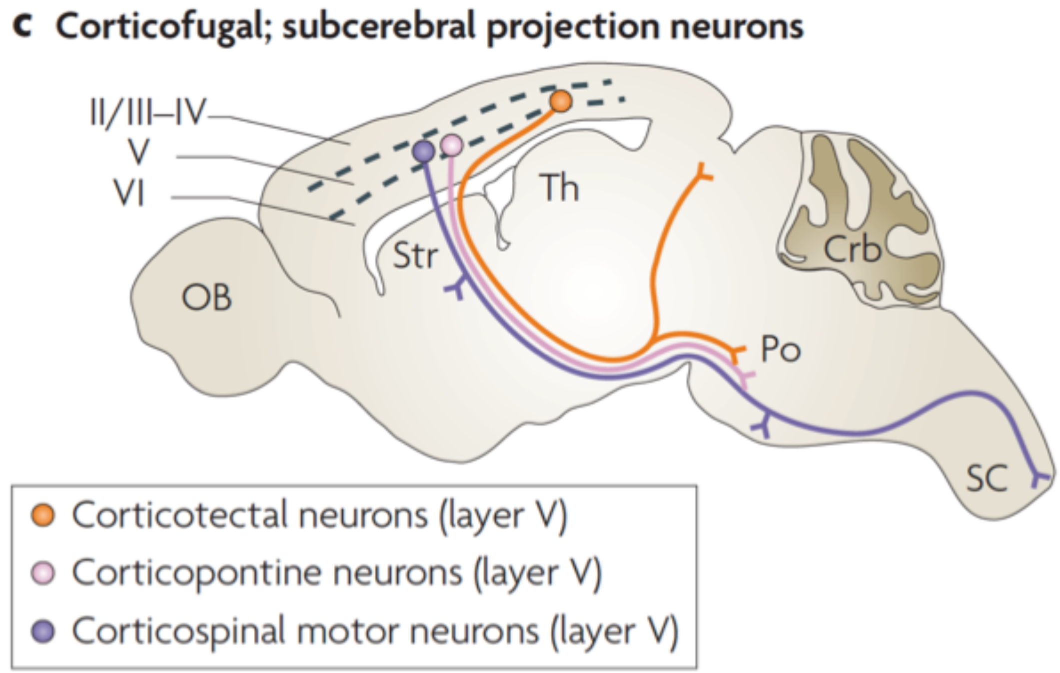
Trevor Drew UMontreal

Principles of Neural Science, 4th ed. KS&J 37-1

Corticospinal neurons project to multiple levels of the sensorimotor hierarchy

Corticospinal projections to motorneurons are mostly indirect and diffuse



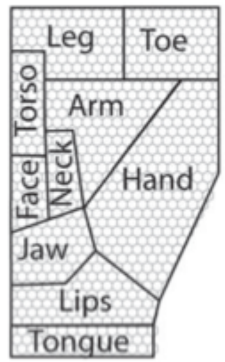


Corticospinal neurons have collaterals to striatum, red nucleus, caudal pons, medulla (these areas also have motor maps)

Rathelot and Strick PNAS 2009

Molyneaux et al Nature Reviews Neuroscience 2007

What is the function of the cortex in sensorimotor control?



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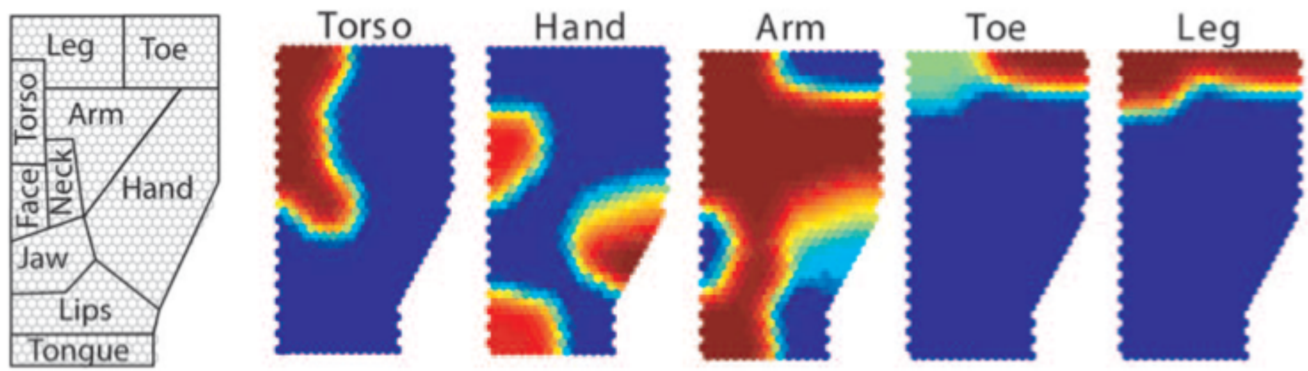

Kohonen network   Aflalo and Graziano, *J Neuroscience 2006*

Behaviorally-driven map for multijoint coordination?

Possible Origins of the Complex Topographic Organization of Motor Cortex: Reduction of a Multidimensional Space onto a Two-Dimensional Array

Review: Graziano The Neuroscientist *2007*

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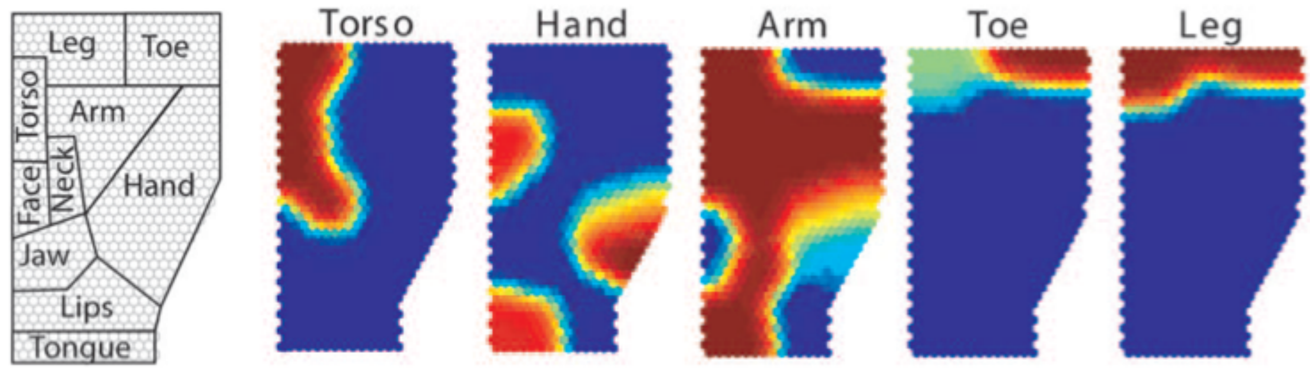

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Review: Graziano The Neuroscientist *2007*

Neuron 2015 Kawai, Markman…Olveczky

Motor Cortex Is Required for Learning but Not for Executing a Motor Skill

Tutor for learning new movements?

Corticospinal system sculpts and modulate subcortical excitability

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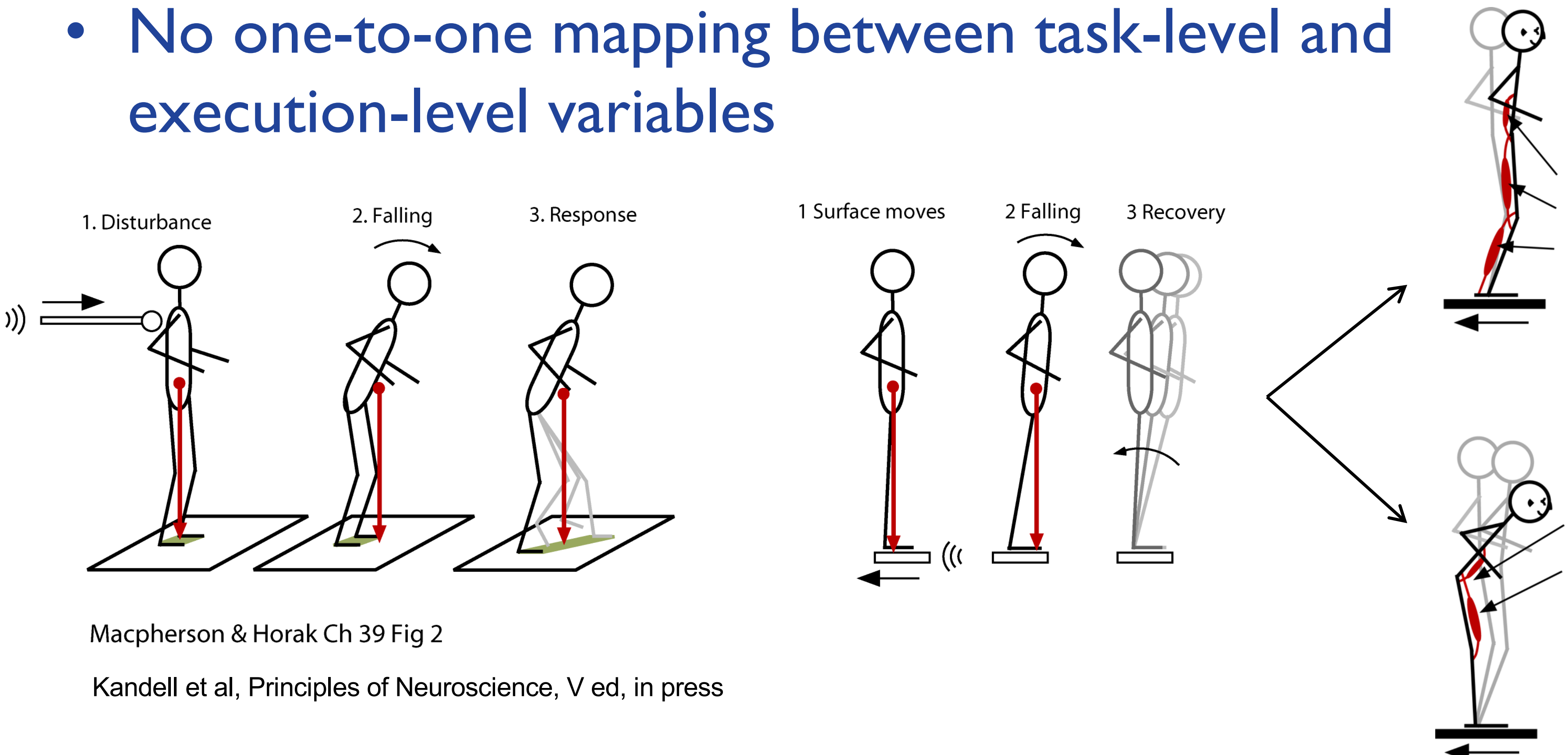
Balance control: intention versus implementation

Common goals, different execution strategies

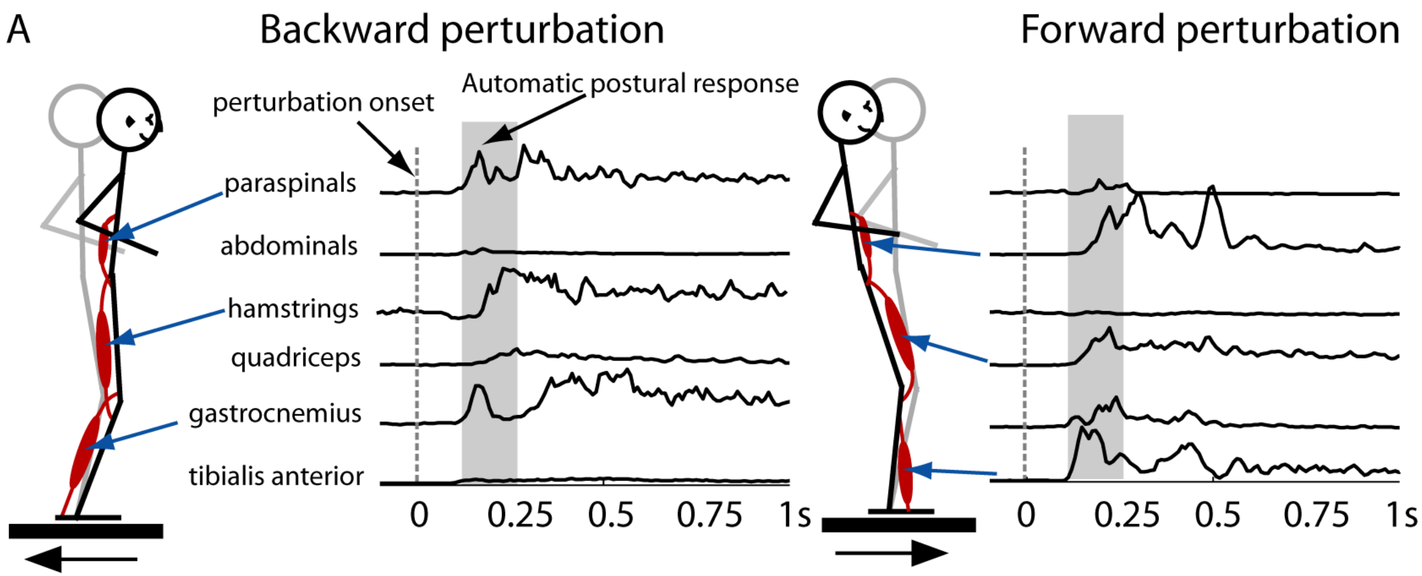
- Common goal: Maintain CoM over BoS
- Different implementation: EMG, biomechanics
- No one-to-one mapping between task-level and execution-level variables



Macpherson & Horak Ch 39 Fig 2

Kandell et al, Principles of Neuroscience, V ed, in press

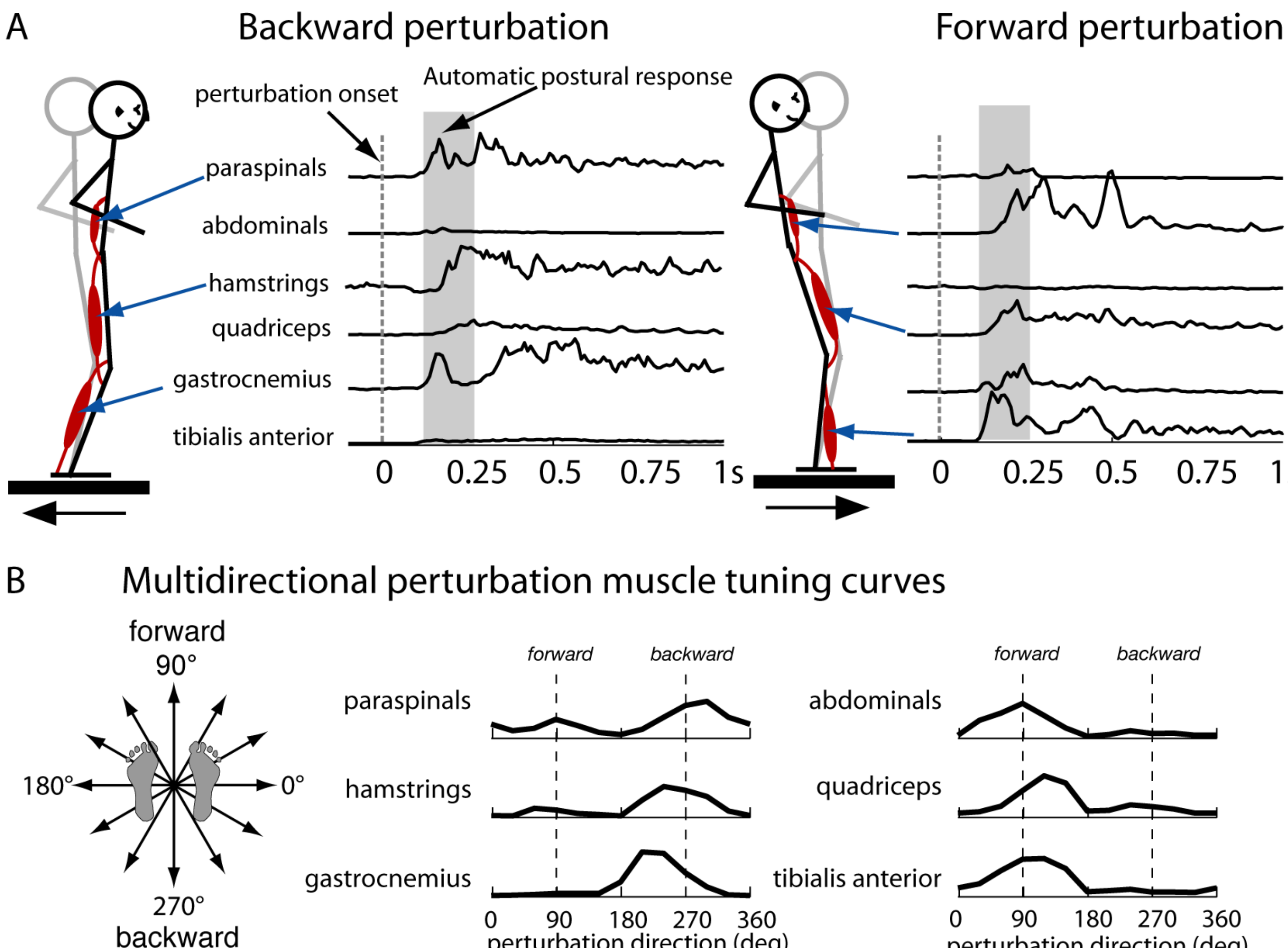
Reactive balance: activation of muscles is specific to direction of perturbation



- Different muscles activated for forward and backward perturbations
- Not co-contraction of all muscles
- Spinal response (50 ms), brainstem response (100 ms), voluntary response (>250 ms)

After Horak and Macpherson, *Handbook of Physiology* 1996

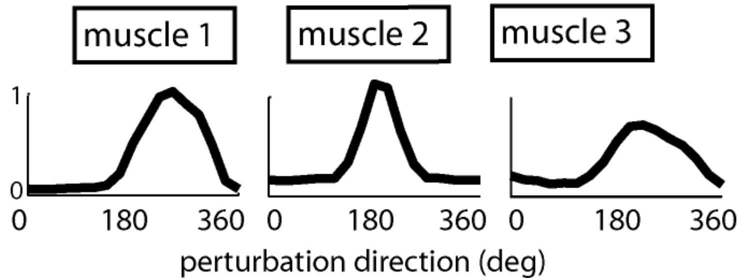
Muscle tuning curves illustrate complex spatial patterning at a single time point



After Horak and Macpherson, *Handbook of Physiology* 1996

Motor modules, a.k.a. muscle synergies, reveal structure in EMG patterns

Independent muscle activation?



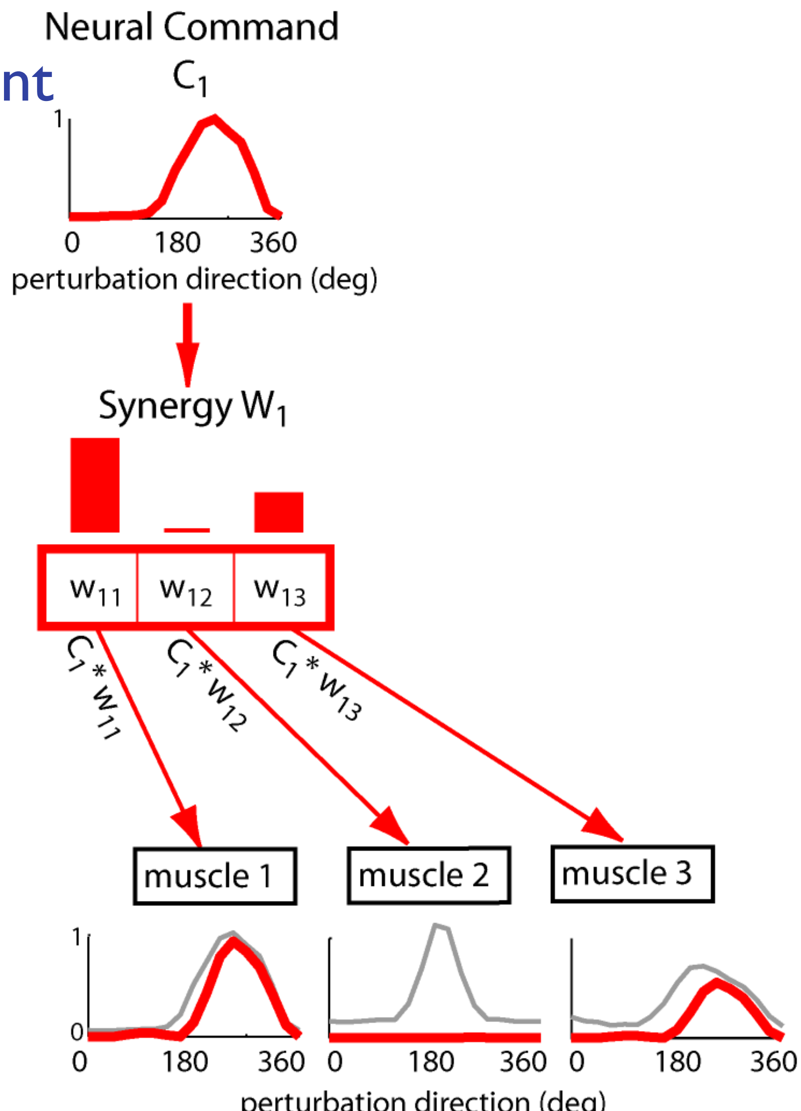
Ting, *Progress in Brain Research 2007,* Chvatal and Ting 2010

Motor modules define time synchronous co-activation of muscles

Direction-dependent command signal e.g. "push right"

Motor module: relative excitation of motor pool

Independent muscle activation?

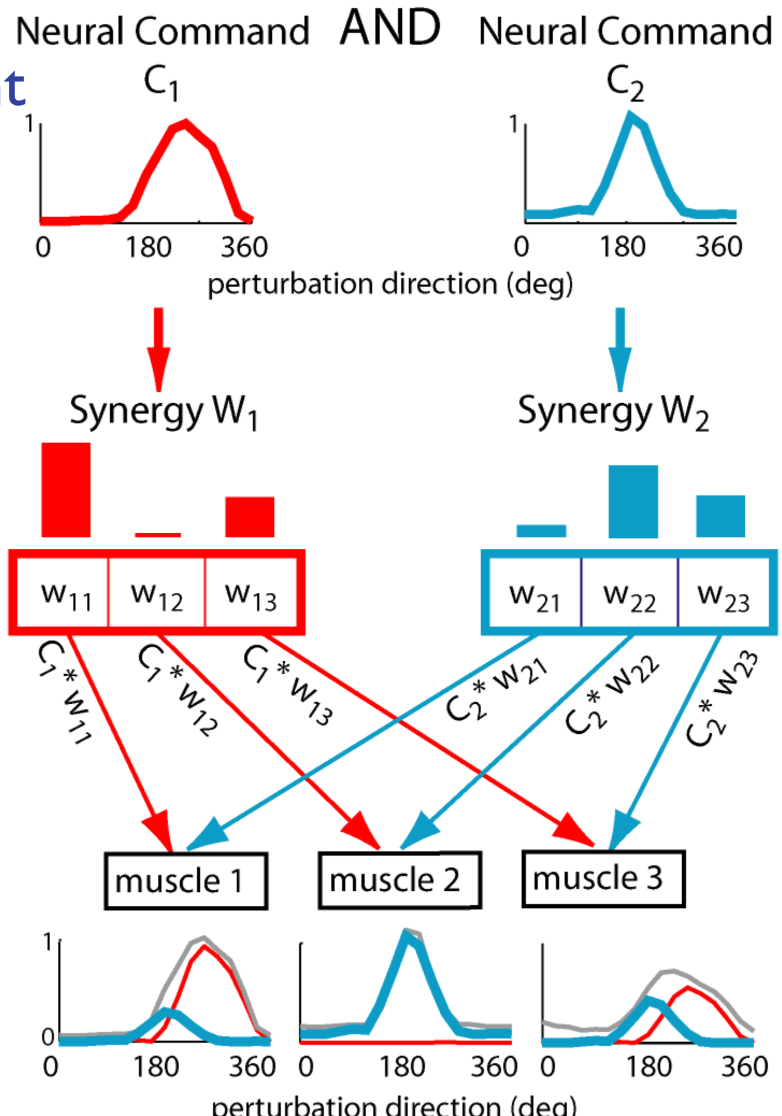


Ting, *Progress in Brain Research 2007,* Chvatal and Ting 2010

Muscles participate in multiple motor modules

Direction-dependent command signal e.g. "push right"

"push forward"



Motor module: relative excitation of motor pool

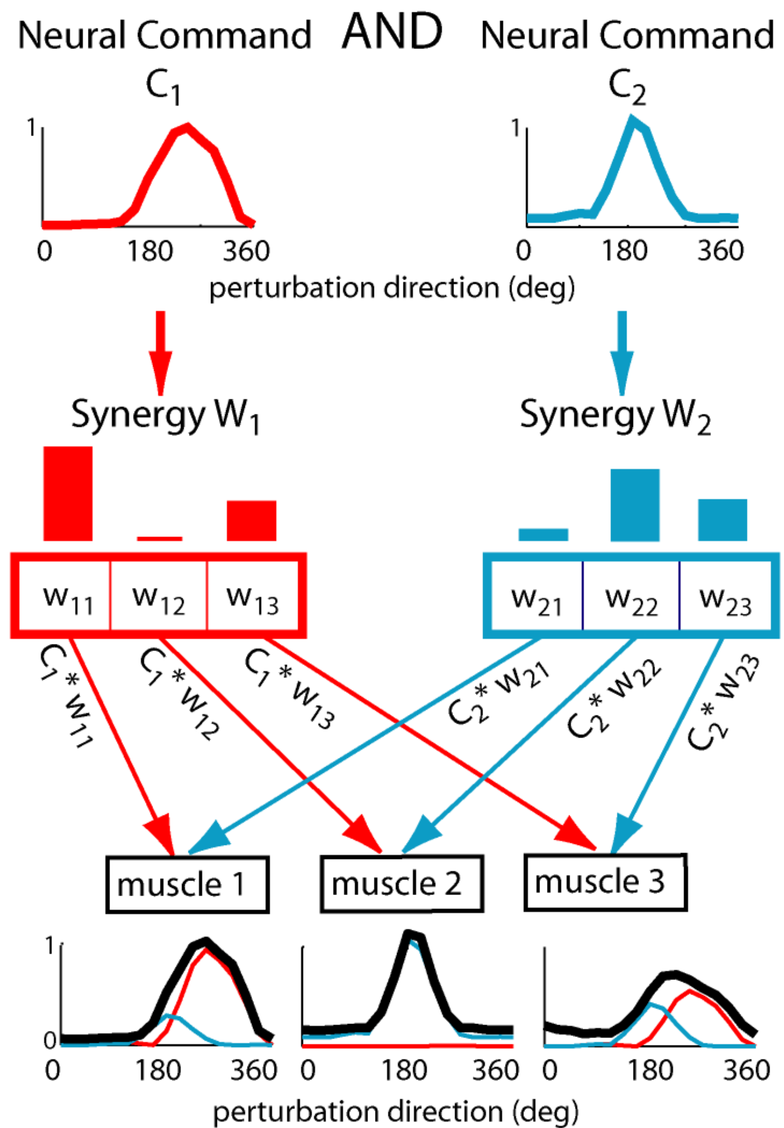
Independent muscle activation?

Ting, *Progress in Brain Research 2007,* Chvatal and Ting 2010

Motor modules reflect functional co-activation of muscles underlying variable motor patterns

"push right"

"push forward"



Motor modules "library of actions"

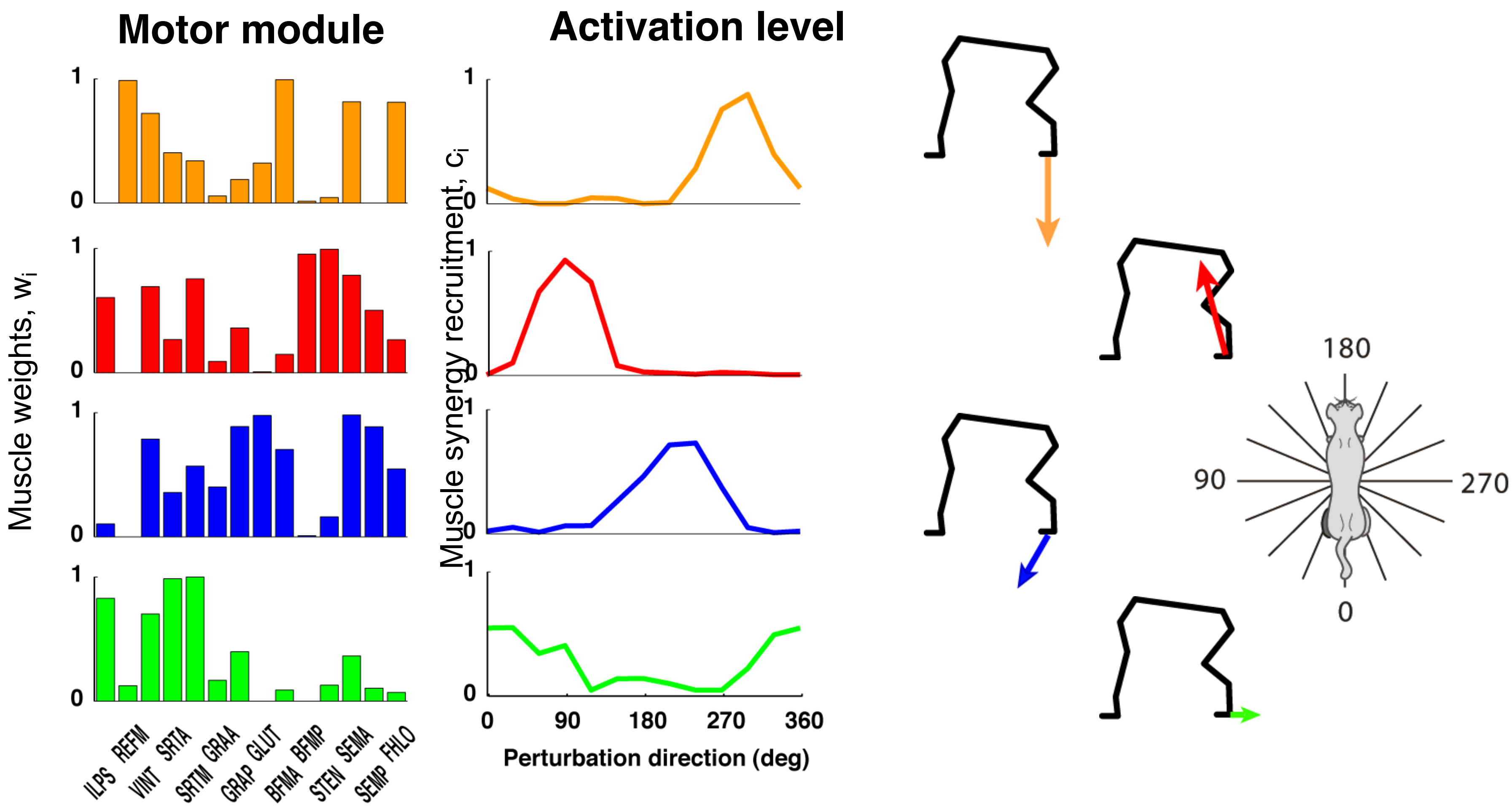
Non-negative matrix factorization (NMF):
Tresch et al. 1999
Lee and Seung 1999

Weighted sum of Motor modules

Tutorial, code, and why I don't like PCA:
Ting and Chvatal 2010

Ting, *Progress in Brain Research 2007,* Chvatal and Ting 2010

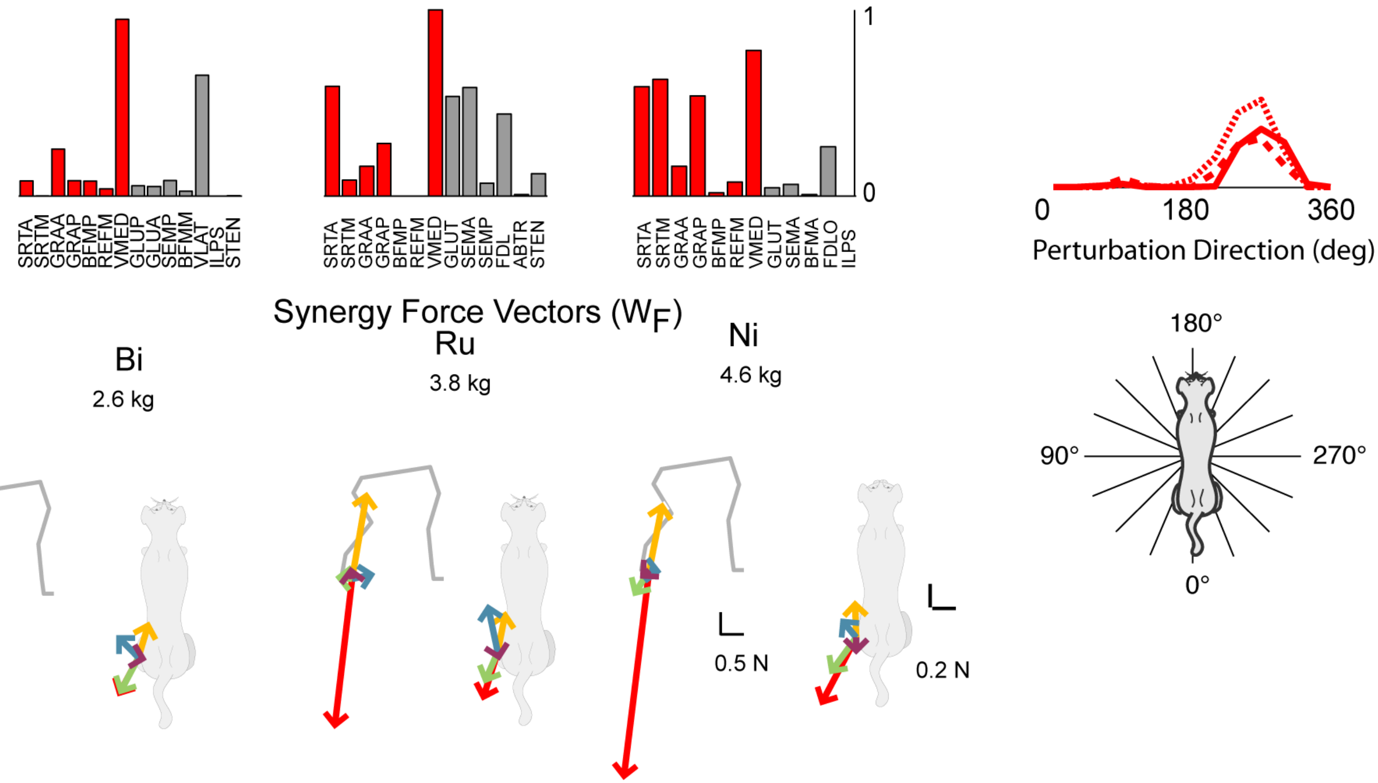
Structure: Motor module recruitment is correlated to an endpoint force vector



- Motor modules are predicted by energetic optimization
  Steele et al. 2013; deGroote et al. 2014; Todorov and Jordan 2002

Ting and Macpherson, *J Neurophysiology* 2005; Torres-Oviedo, Macpherson, Ting, *J Neurophysiology* 2006

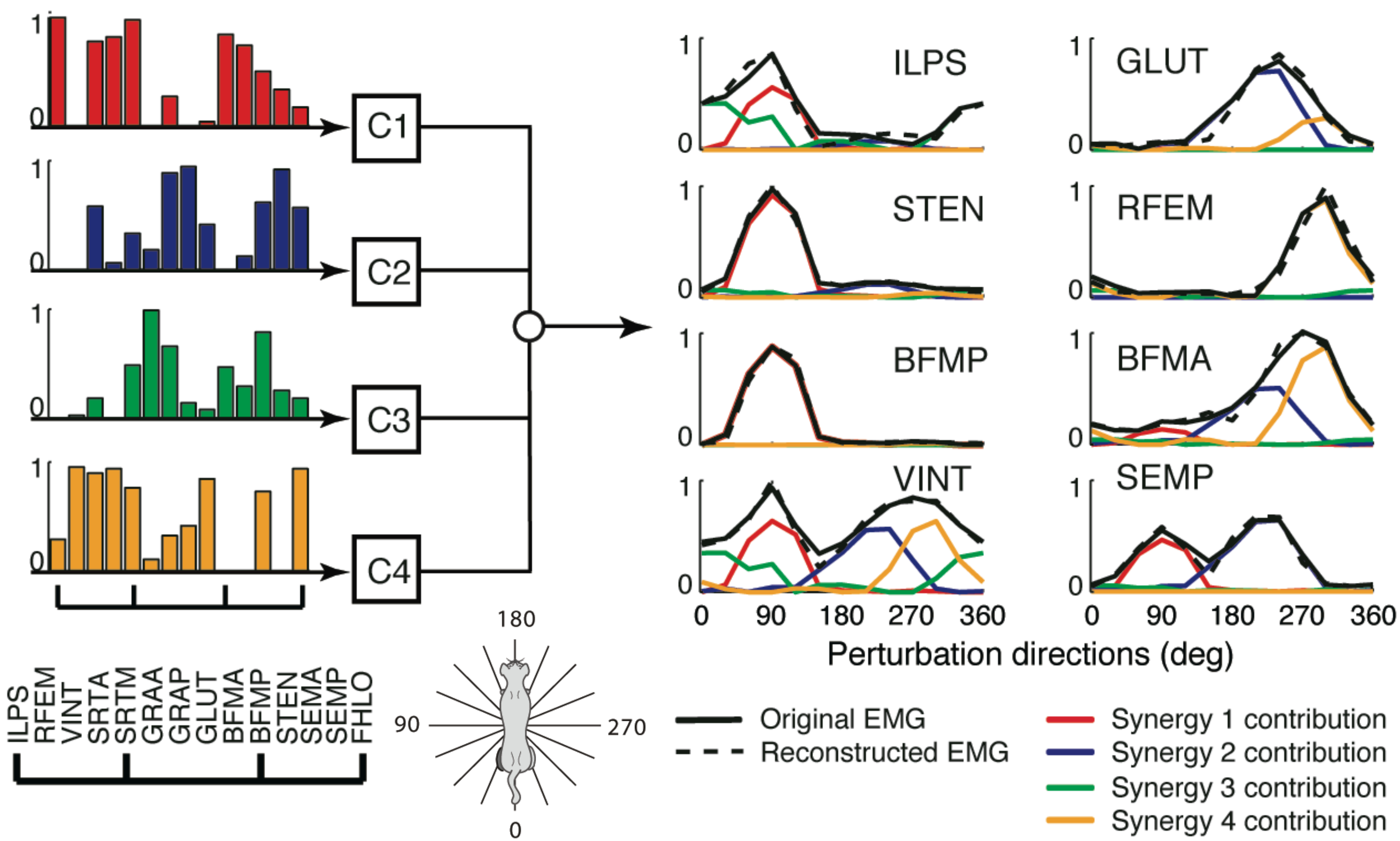
Individuality: each individual expresses a particular motor structure



- Motor modules are consistent across different biomechanical configurations and tasks in cats and humans
- People prefer habitual rather than optimal solutions De Rugy et al 2012, Ganesh et al 2010

Torres-Oviedo, Macpherson, Ting, *JNP* 2006; *humans*: Torres-Oveido and Ting *JNP* 2010; Chvatal and Ting 2013

Multifunctionality: Motor modules reveal hidden coordination between muscles

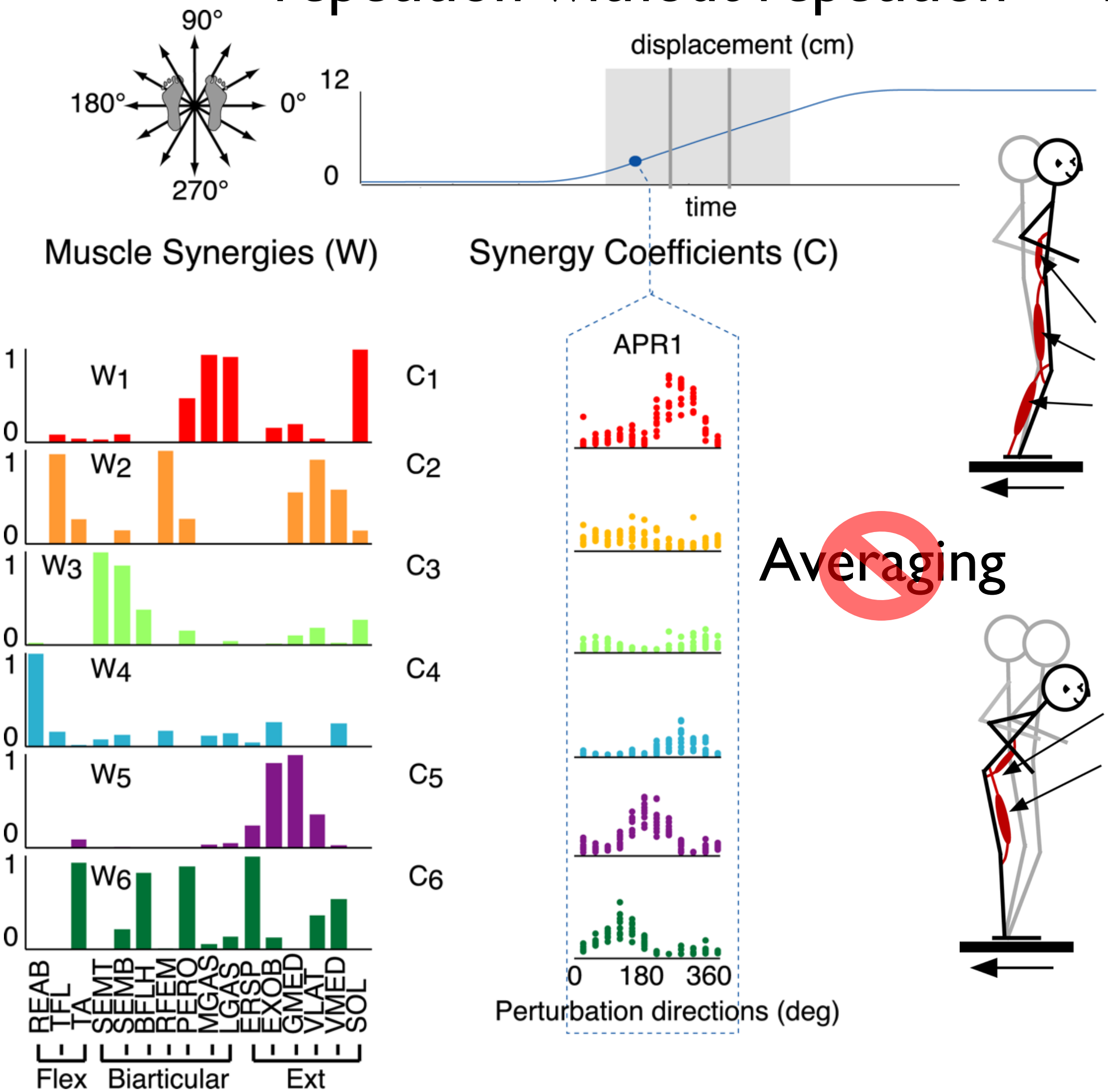


- Additive nature is a hard constraint on feasible coordination space

Ting and Macpherson, *J Neurophys 2005;* Torres-Oviedo et al. 2006;

Variability: Trial by trial differences in muscle activity are not random

"repetition without repetition" – Bernstein 1969

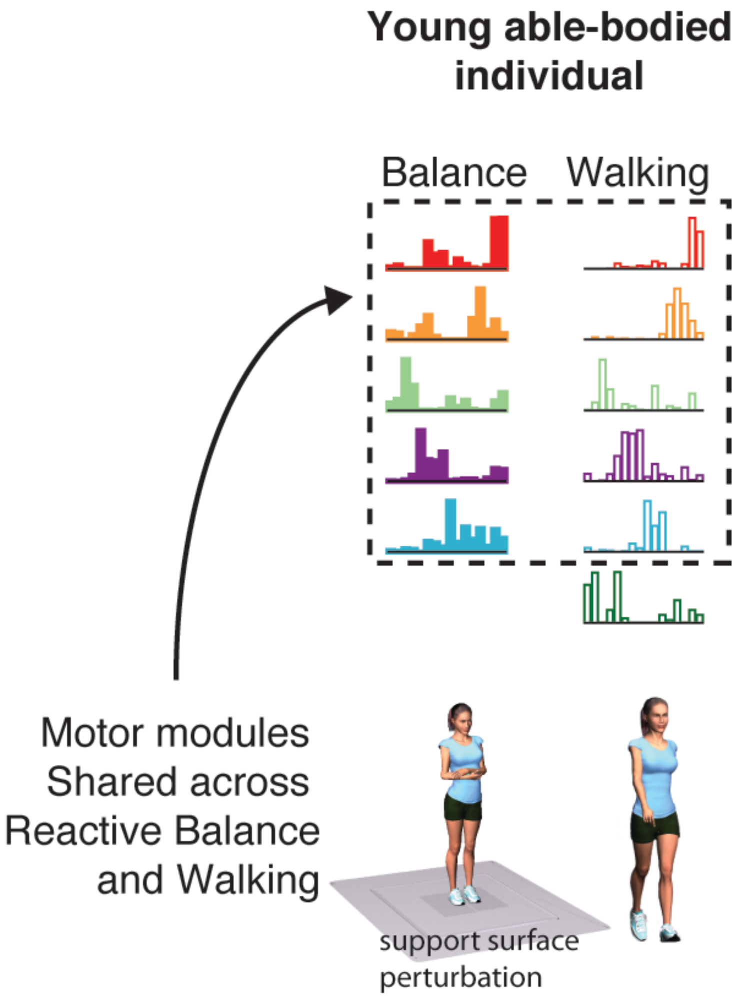


- Ankle and hip strategy are implemented by different motor modules
- Trial by trial variations reflect flexible recruitment of motor modules based on task demands and adaptation

Torres-Oviedo and Ting, *J Neurophysiology 2007*

Welch and Ting 2014

Generalization: common motor modules across motor tasks



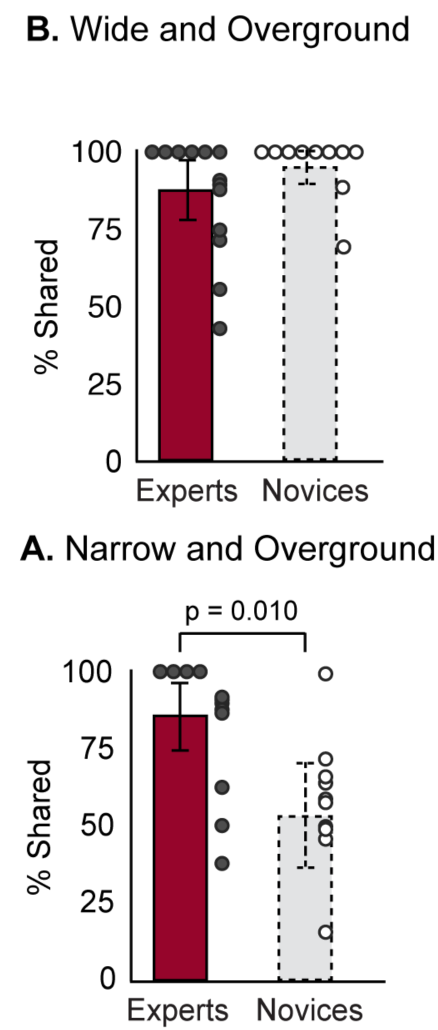
- Common modules for:
  - Walking, perturbation to walking, anticipatory stiffening of leg, reactive balance with feet in place, reactive stepping
- Motor modules may be the lowest level of motor organization and recruited by spinal, brainstem, and cortical mechanisms
- Motor module recruitment reflects desired CoM motion

Chvatal et al, *J Neurophysiology* 2011; Chvatal and Ting *J Neurosci* 2012; *Frontiers in Comp Neuro 2013*
Safavynia and Ting J Neurophysiology 2013 ab

Learning: Motor modules are shared across nominal and challenging tasks in dancers

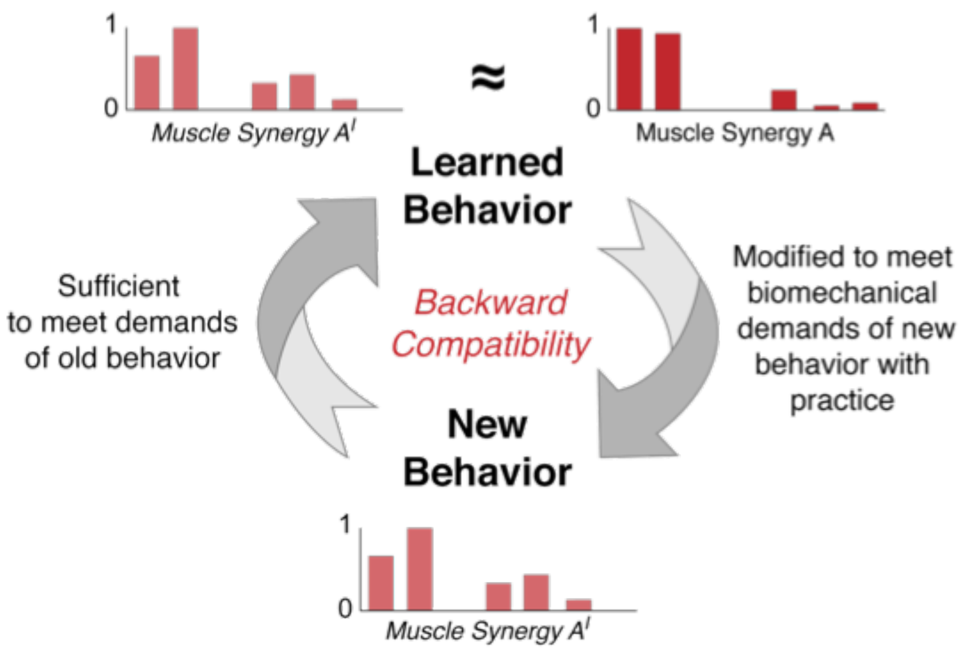
- We select "good enough" or "slop-timal" solutions to achieve multiple goals with adequate efficiency Latash 2012, Loeb 2012, Ting et al 2015
- Motor modules change with development and training Dominici et al 2011, Kargo and Giszter 2003
- Learning a more challenging task may involve refining existing motor modules Gentner et al 2010
- Training may expand the range of tasks performed with a set of modules, altering nominal task performance

Shared modules



Sawers, Allen, and Ting, *Journal of Neurophysiology 2015; Allen, Sawers Mckay Hackney, Ting, Journal of Neurophysiology 2017*

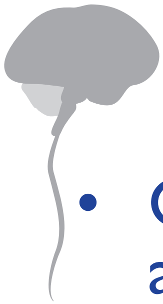
Versatility suggests a mechanism of backward-compatibility for learning new skills

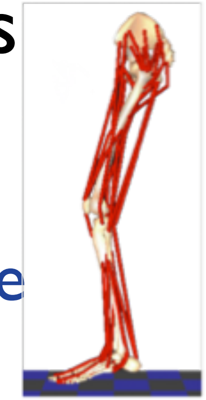


- Consistent with changes in early skill learning[1,2]
  - Modify existing rather than create new muscle patterns
- Consistent with Common Core Hypothesis[3,4]
  - Shared spinal circuits between behaviors
- Neural constraint on learning[5]
  - What can be learned and the rate at which it is learned
  - Basis for "The Natural"
- Differences in rehabilitation outcome

1. Kargo and Nitz, 2003 2. Nudo et al, 1996 3. Zehr 2005 4. Zehr et al, 2007 5. Sadtler et al., 2014

Motor modules: individual-specific solutions for similar movements

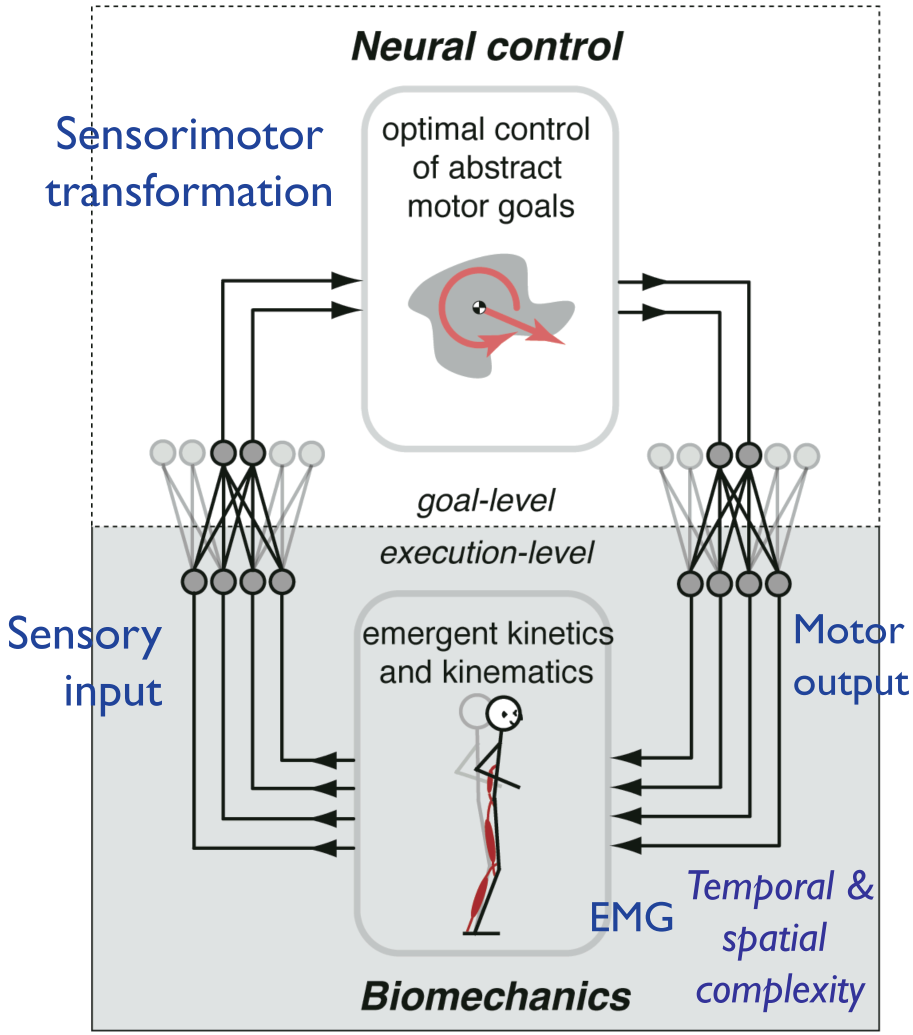




- Control points to transform motor goals into muscle activity throughout the nervous system
  - Re-re-representations of movements, "just as many chords, musical expressions. and tunes can be made out of a few notes" Hughlings-Jackson 1889
  - Motor cortex Overduin et al 2012, Rathelot and Strick 2009, Krouchev 2006, Kargo and Giszter 2003, Holdefer and Miller 2002
  - Brainstem Joshua and Lisberger 2014, Riddle and Baker 2010
  - Spinal cord Saltiel et al 1991, Hart and Giszter 2010
- A stored repertoire of available motor actions, facilitating rapid adaptation and flexible motor behavior without regard for low-level biomechanics
- A necessary concept for understanding motor variability and changes with development, evolution, training, and disease

Ting and McKay, *Current Opinion in Neurobiology 2007;* Ting, *et al. Neuron 2015*

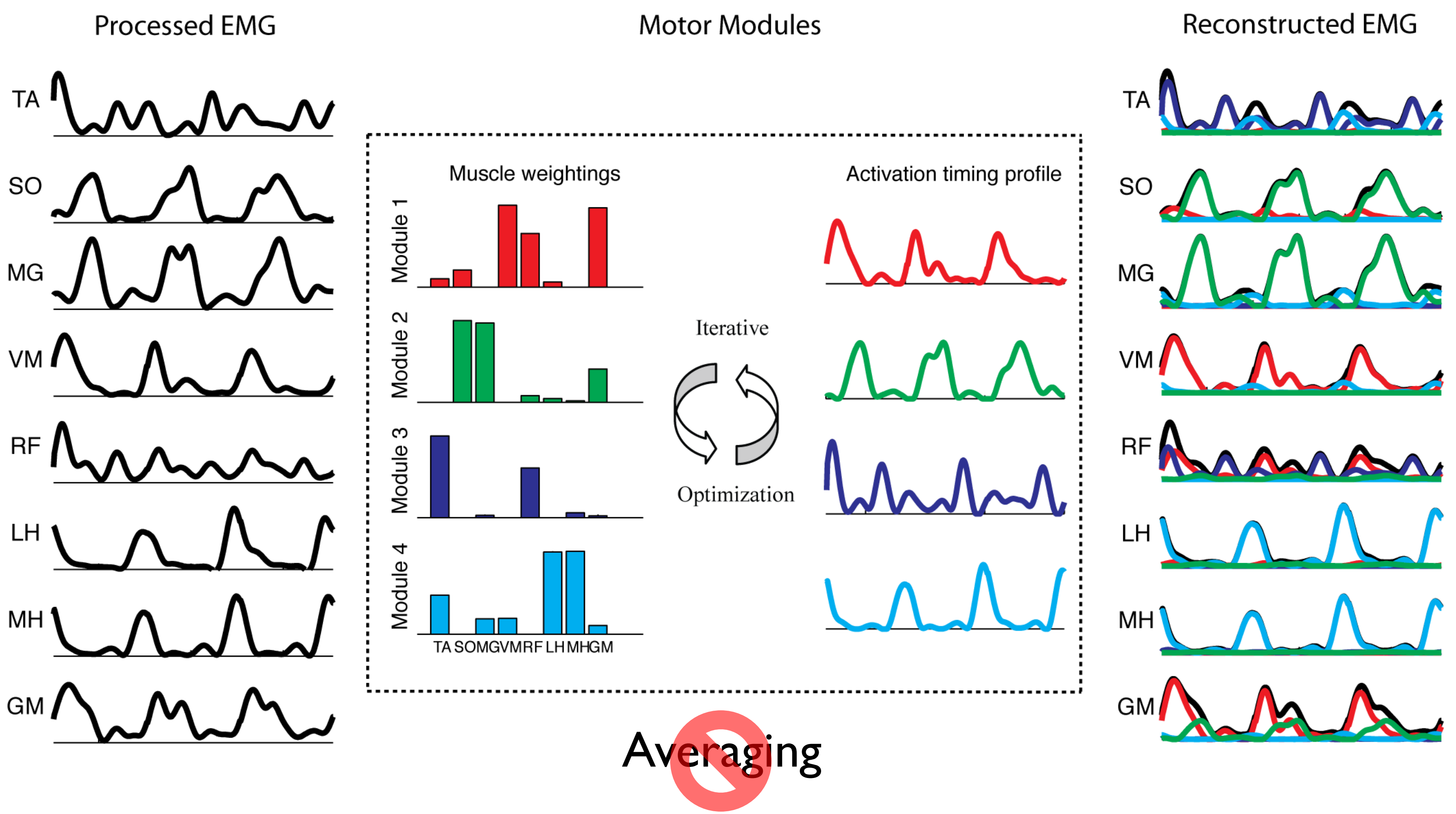
Structure of muscle coordination pattern reflect neural sensorimotor processes



- Hierarchical arrangement of temporal and spatial structure similar to locomotion McCrea and Rybak 2008
- Temporal structure reflects goal-level control
- Spatial structure for muscle and multi-joint coordination

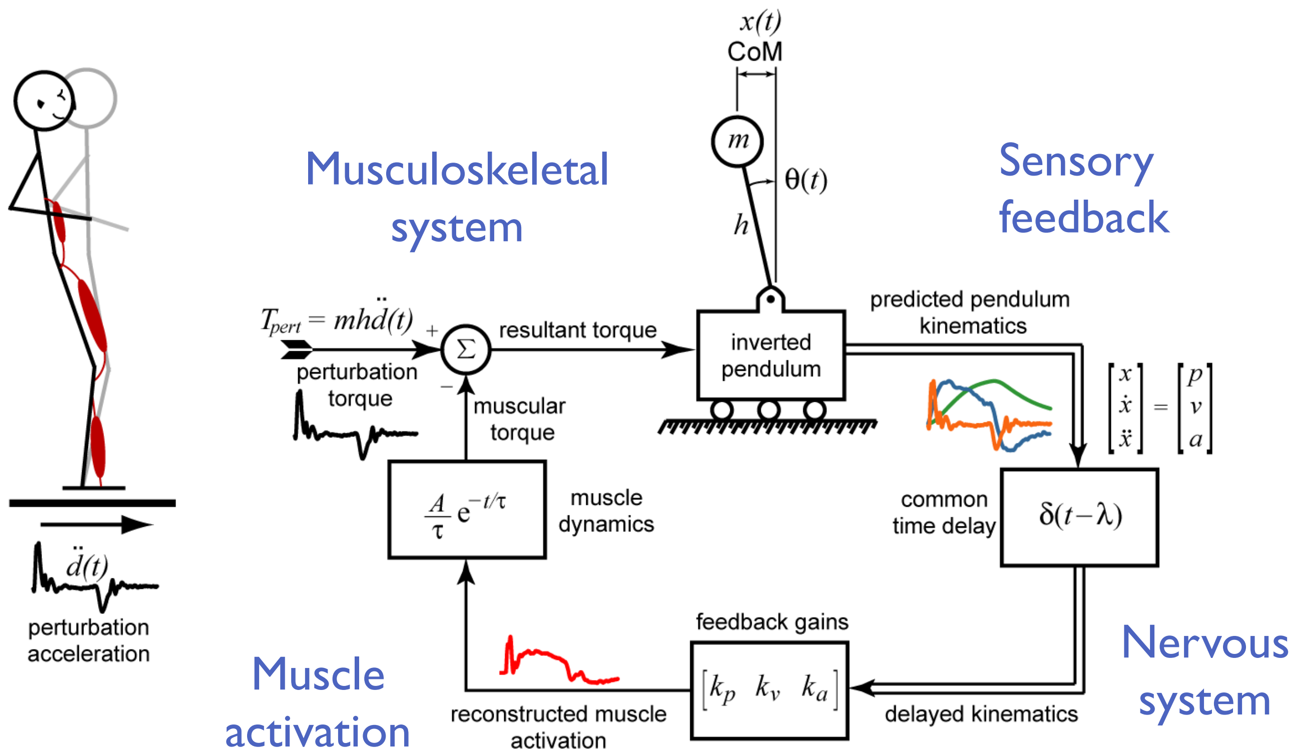
Ting and McKay, *Curr Op in Neurobiol 2007; Chiel et al. J Neuorsci 2009 ;Ting et al.* Int J Numer Method Biomed Eng 2012

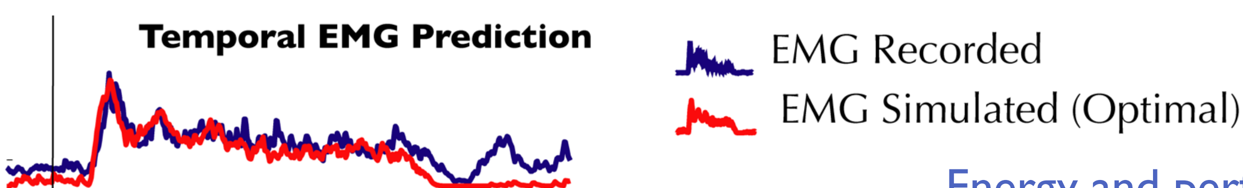
Variations in recruitment of motor modules account for cycle-by-cycle variations in walking



Clark, Ting, Neptune, Zajac, Kautz *J Neurophysiology*, 2010 McGowan, Neptune, Clark, Kautz, *J Biomechanics* , 2010

Delayed sensorimotor feedback of CoM acceleration, velocity, and displacement



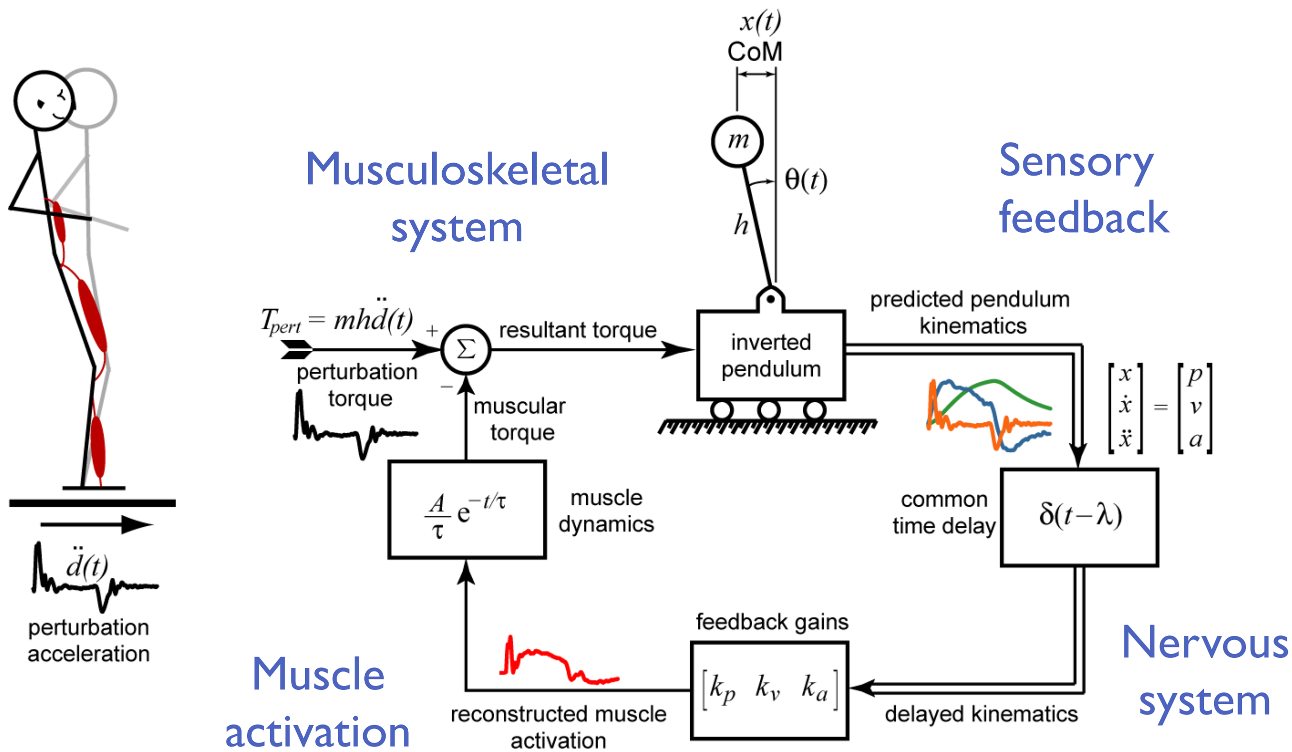


$$\min_{k_p,k_v,k_a} \left[J = \int_0^T (x^T Q x + \rho u^2)\, dt + \Omega \cdot x(T) \right]$$

Energy and performance tradeoff

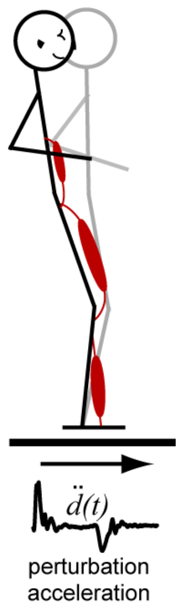
Lockhart and Ting, *Nature Neuroscience* 2007, Welch and Ting, *J Neurophysiology 2008, 2009, Safavynia and Ting 2011, 2013*

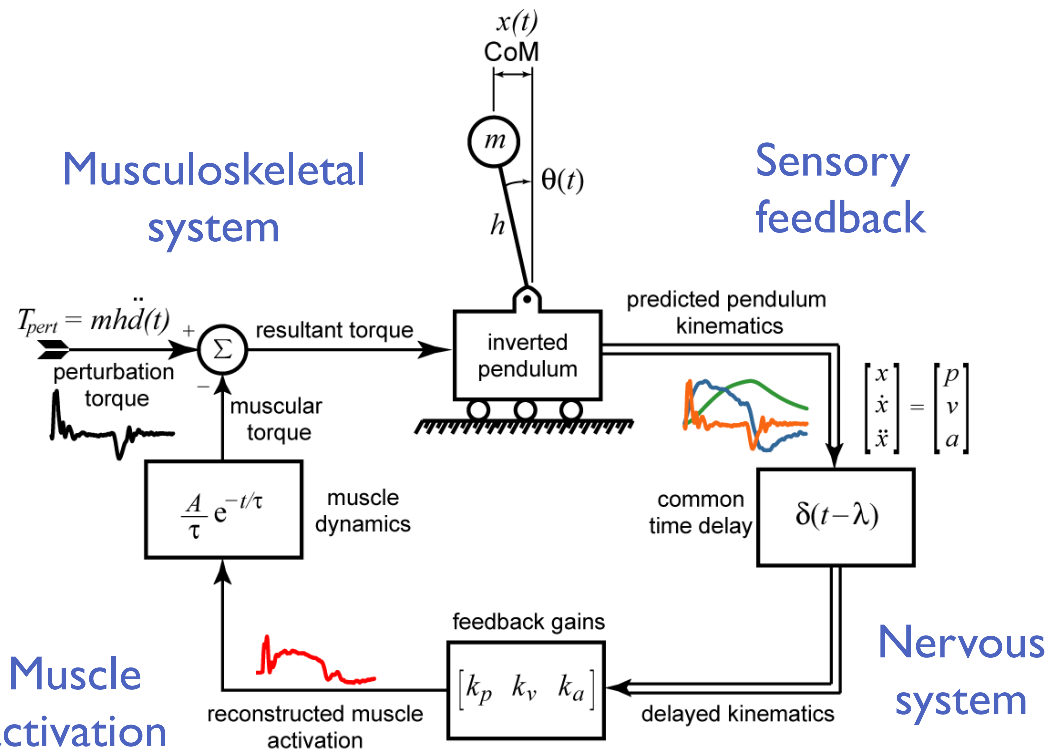
Delayed sensorimotor feedback of CoM acceleration, velocity, and displacement

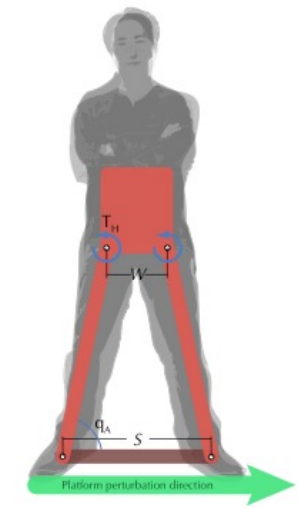


Lockhart and Ting, *Nature Neuroscience* 2007, Welch and Ting, *J Neurophysiology 2008, 2009, Safavynia and Ting 2011, 2013*

Delayed sensorimotor feedback of CoM acceleration, velocity, and displacement

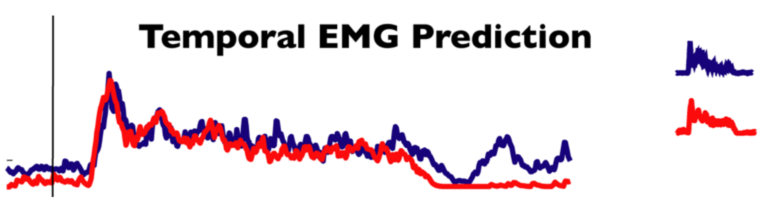






Bingham, Choi, Ting *J Neurophysiology* 2011

Bingham and Ting 2013 IEEE TNRSE



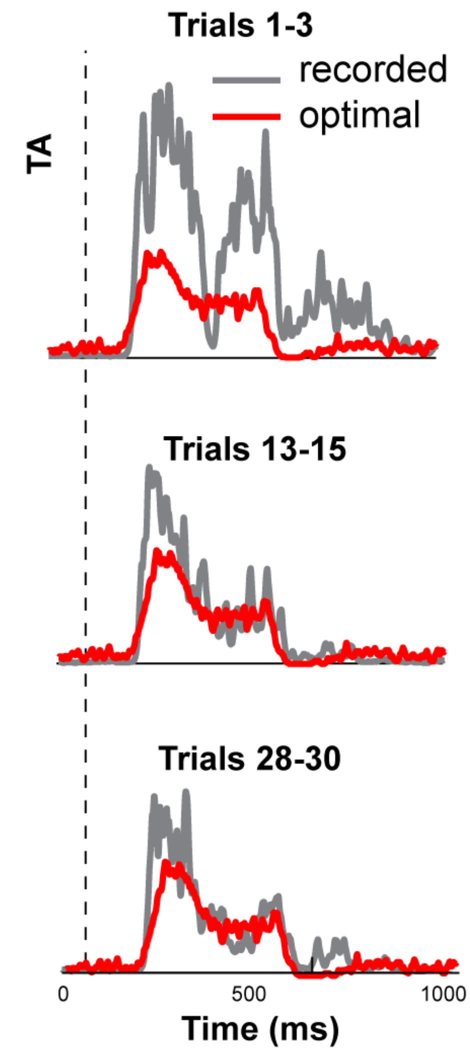
$$\min_{k_p, k_v, k_a} \left[J = \int_0^T (x^T Q x + \rho u^2) dt + \Omega \cdot x(T) \right]$$

Energy and performance tradeoff

Lockhart and Ting, *Nature Neuroscience* 2007, Welch and Ting, *J Neurophysiology 2008, 2009, Safavynia and Ting 2011, 2013*

Variations in feedback gains can characterize changes in adaptation and individual differences

- Reduction in feedback gains over repeated perturbations
- Similar CoM displacement
- Tradeoff between performance and effort
- Parameter variation within a low dimensional space may speed adaptation



Welch and Ting, *in review*

Common neural principles and mechanisms for interacting with the environment

Tradeoffs in performance and energetics

Sparse representation

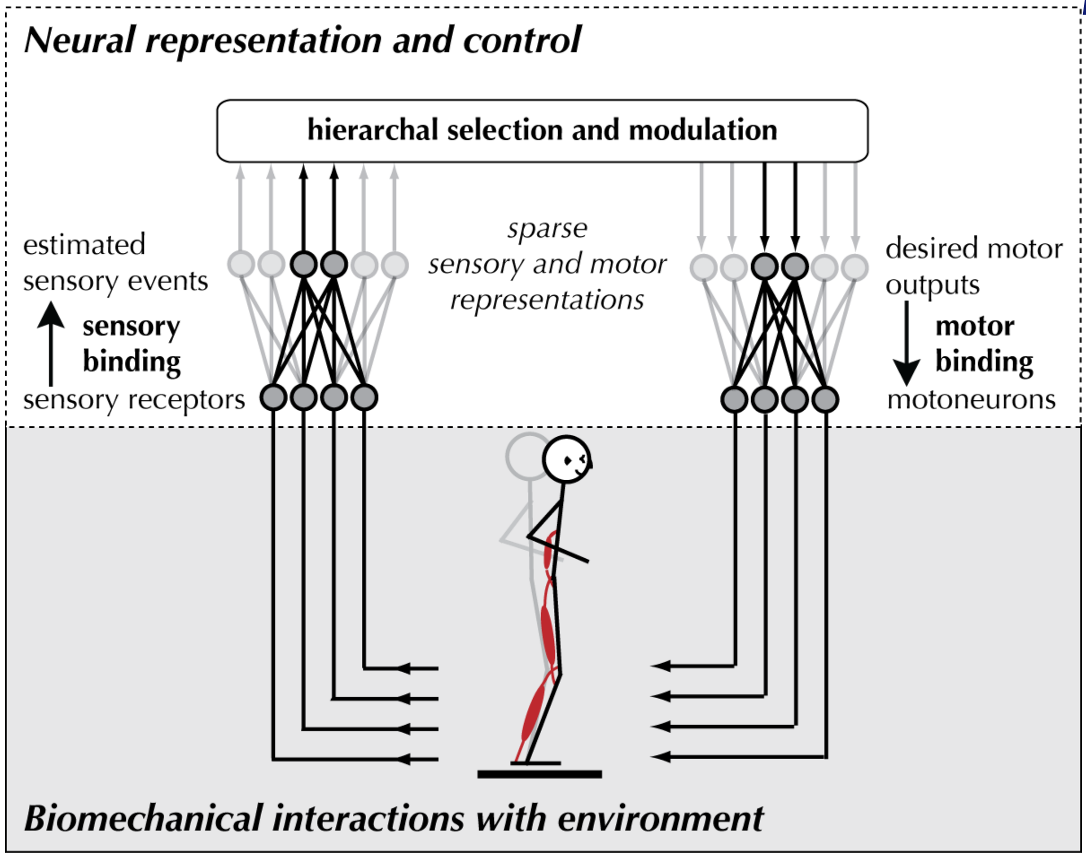
Tradeoffs in performance and energetics

convergence

divergence

correlated inputs

correlated outputs



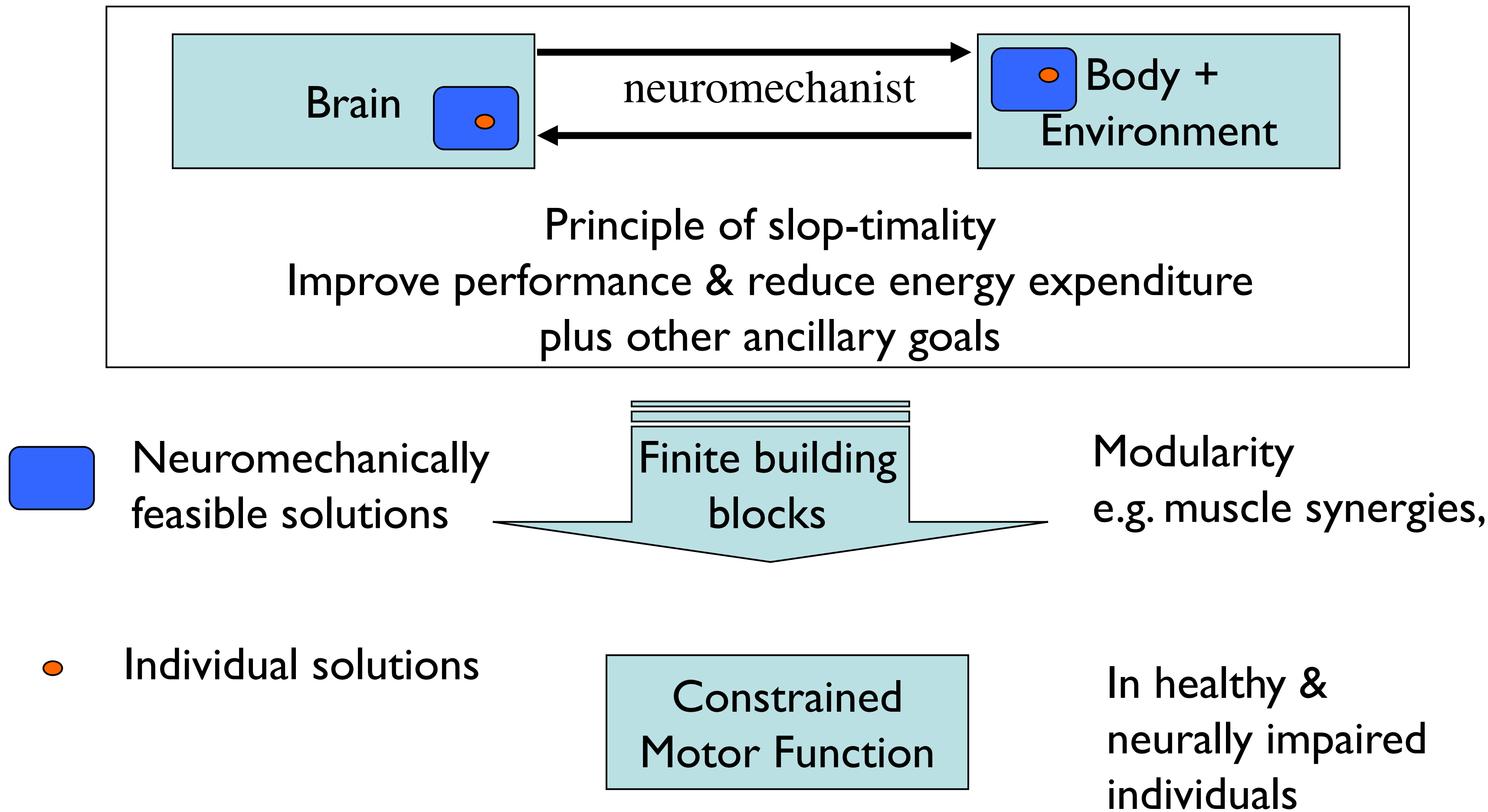
Environmental interactions

Ting and McKay, *Current Opinion in Neurobiology 2007; Chiel et al. J Neuorsci 2009 ;Ting et al. IJNMBME 2012*

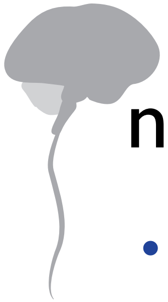
Muscle synergies specify **meaningful *relationships*** between muscles

- The same muscles are reconfigured to produce actions
- The number of meaningful actions that we can make exceed the number of muscles
- 2^n combination of muscles considering only binary state
- Muscle synergies are like a musical chords
  - there are more possible chords than notes
  - classes of chords that convey certain emotions
  - each composition uses a limited number of chords
  - combinations of chords might have meaning
  - there are atonal or “discordant” chords
  - each composer tends to choose certain chords and chord combinations over others, creating an individualized signature

Characteristic and constrained motions in individuals emerge from neuromechanical interactions



Ting and McKay *Current Op. in Neurobiology 2007;* Tresch and Jarc *Current Op. in Neurobiology 2009;Ting* et al. Neuron 2015



Need for motor modularity emerge from neuromechanical redundancy and complexity

- **Motor structure** – effect of biomechanics
  - Almost no biomechanical bounds on muscle activity in walking

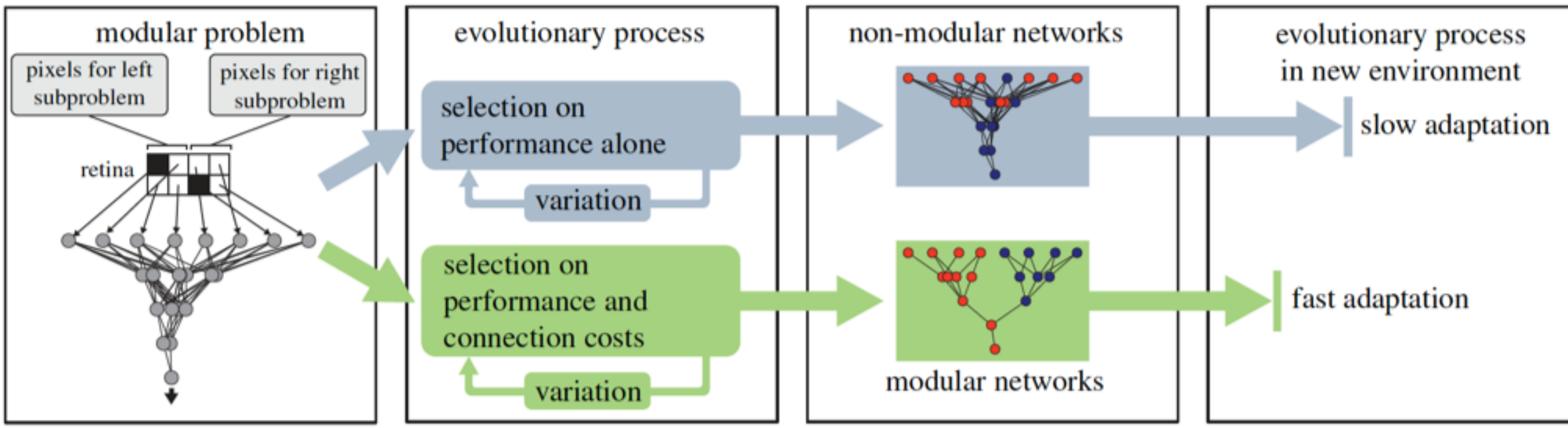
    Simpson et al. 2015, Sartori et al. 2013; 2015
- **Motor abundance** – many solutions to the same task
  - Different motor modules have equivalent function
- **Motor variability** – repetition without repetition
  - Variations at the level of motor module recruitment
- **Multifunctionality** – the same muscles are reconfigured to create the whole motor repertoire
  - There must be more motor modules than muscles
- **Motor individuality** –Individual-specific motor modules may be shaped by evolution, development, and experience
  - You say "to-may-to" and I say "to-mah-to"

    De Rugy et al 2012, Ganesh et al 2010, Kuhl 2004

Slop-timal, not optimal

Ting et al. *Neuron 86:38-54* 2015

Hierarchy and modularity facilitate fast and robust adaptation and learning



PROCEEDINGS OF THE ROYAL SOCIETY B

2013

The evolutionary origins of modularity

Jeff Clune[1,2,†], Jean-Baptiste Mouret[3,†] and Hod Lipson[1]

Generalization in vision and motor control

Tomaso Poggio[1] & Emilio Bizzi[1,2]

Nature 2004

- Includes performance and connection costs
- Applicable over multiple timescales

Individual “slop-timal” biases in decision-making

CellPress

Neuron

Perspective

2017

Neuroscience Needs Behavior: Correcting a Reductionist Bias

John W. Krakauer,[1,*] Asif A. Ghazanfar,[2] Alex Gomez-Marin,[3] Malcolm A. MacIver,[4] and David Poeppel[5,6]

	LEVELS	
Computation	1	why (problem)
Algorithm	2	what (rules)
Implementation	3	how (physical)

- A set of rules or algorithms that allows goals to be achieved with different implementations
- Requires that the systems we study are redundant and complex
- Allows for adaptation, learning, creativity, and rehabilitation

Brain and computation bootcamp: Why movement matters

- Sensorimotor control as the canonical decision-making process
  - How to rapidly and robustly achieve behavioral goals by coordinating the same motor apparatus in different ways?
- Hierarchichal and distributed mechanisms for sensorimotor control
  - Parallel reflex, automatic, and voluntary control allow computation on increasingly abstract goals
- Neuromechanical principles for movement
  - Modularity to deal with redundancy, facilitate robustness, flexibility, and learning, leading to individual differences

My brain and computation wish list

- Improved non-negative pattern identification for recorded muscle and neural patterns:
  - more modules than muscles
  - Include temporal correlations
- Unsupervised learning of recorded movement dynamics across individuals, populations, diseases
  - Subtle differences that our brains see easily
- Hierarchical reinforcement learning for movement
  - Different learning rate, time delays, connection cost, reconnection cost, variability and randomness
- Control-theoretic approaches to understand changes in neural *and* biomechanical dynamics

More food for thought

Motor variability is not noise, but grist for the learning mill

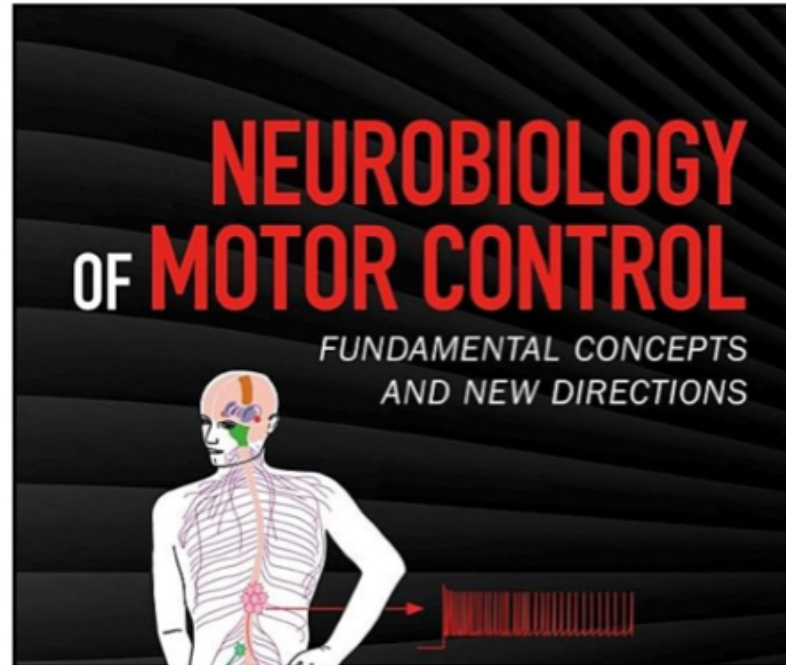
Nature Neuroscience 2014

David J Herzfeld & Reza Shadmehr

A study demonstrates that variability in how people perform a movement can predict the rate of motor learning on an individual basis. This suggests that motor 'noise' is a central component of motor learning.

Temporal structure of motor variability is dynamically regulated and predicts motor learning ability

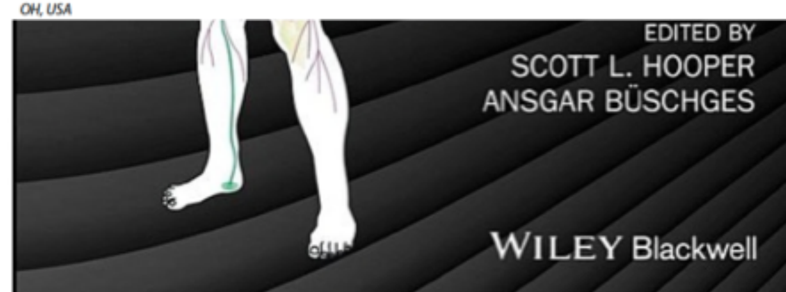
Howard G Wu[1,4], Yohsuke R Miyamoto[1,4], Luis Nicolas Gonzalez Castro[1], Bence P Ölveczky[2,3] & Maurice A Smith[1,3]



Muscle, Biomechanics, and Implications for Neural Control

Lena H. Ting[1,2] and Hillel J. Chiel[3]

[1] Department of Biomedical Engineering, Emory University and Georgia Institute of Technology, Atlanta, GA, USA
[2] Department of Rehabilitation Medicine, Division of Physical Therapy, Emory University, Atlanta, GA, USA
[3] Departments of Biology, Neurosciences, and Biomedical Engineering, Case Western Reserve University, Cleveland, OH, USA

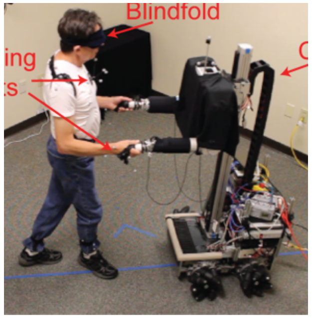


CellPress

Neuron
Perspective

Neuromechanical Principles Underlying Movement Modularity and Their Implications for Rehabilitation

Lena H. Ting,[1,2,*] Hillel J. Chiel,[3,4,5] Randy D. Trumbower,[1,2] Jessica L. Allen,[1] J. Lucas McKay,[1] Madeleine E. Hackney,[6,7] and Trisha M. Kesar[1,2]



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NSF EFRI 1137229
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