MOTOR CONTROL

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DISCLAIMER

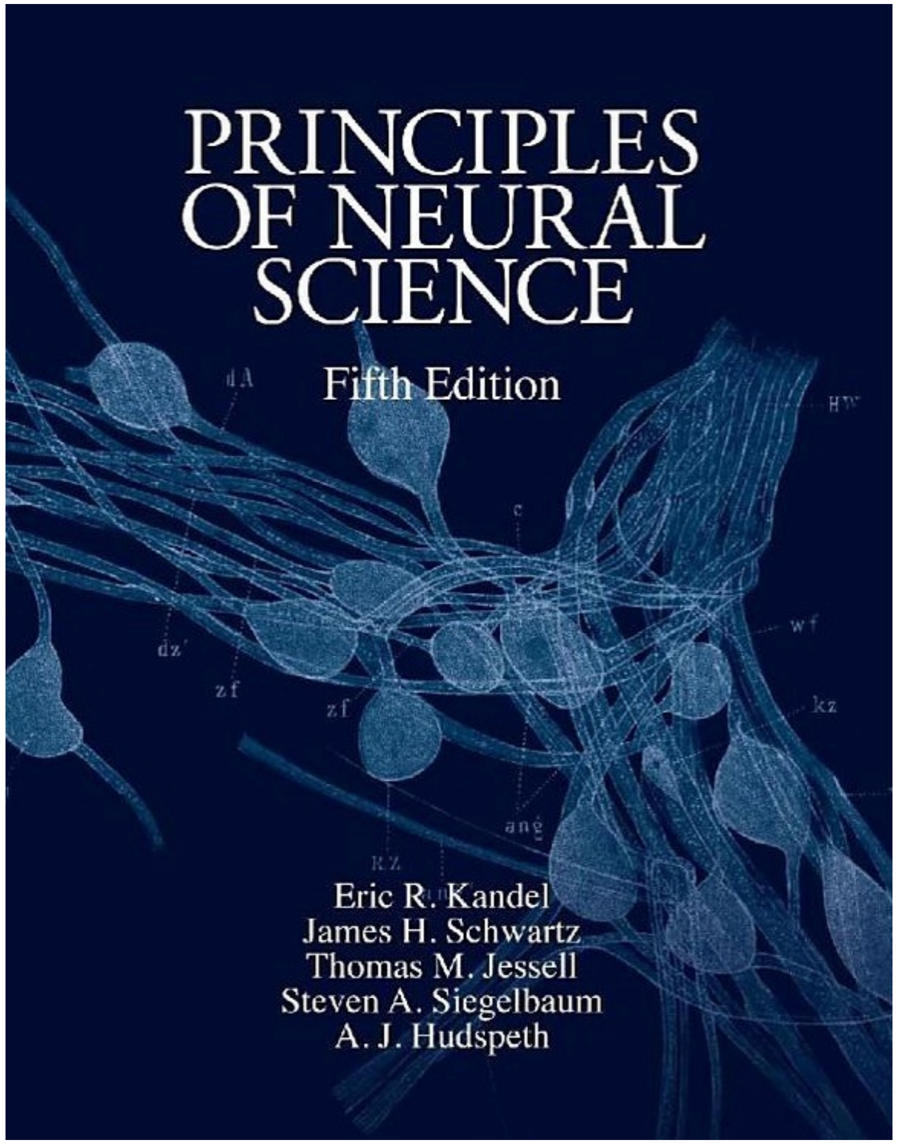
Nothing about

- Biomechanics
- Muscles
- Sensory receptors
- Motoneurons
- Reflexes
- Spinal cord
- Ascending/descending tracts
- Motor cortex

- Neurophysiology
- Neuropsychology
- Brain imaging

- Motor learning/skills
- Attention

- Posture, walking, writing, speaking



QUESTIONS

1. Why is ACTION an interesting object in the field of Cognitive Sciences?

2. Why robotic artifacts can be useful in the field of Cognitive Science?

ACTIONS

- Are driven by goals and they can reach these goals or fail to do so;

- Often involve some degree of volitional control;

- Require planning and decisions among alternatives;

- Involve prediction or anticipation of an intended outcome;

- Are often, albeit not always, associated with a sense of agency, that is, the agent's conscious awareness of carrying out the particular action and of its goals.

— Engel et al., 2013, *Trends Cogn Sci* 17:202

GOOD REASONS

"*To move things is all that Mankind can do … For such the sole executant is muscle, whether in whispering a syllable or in felling a forest.*"
— Charles Sherrington, 1924, *The Linacre Lecture*

"*The infinite diversity of external manifestation of cerebral activity can be reduced ultimately to a single phenomenon - muscular movement. Whether it's the child laughing at the sight of a toy, or Garibaldi smiling when persecuted for excessive love for his native country, or a girl trembling at the first thought of love, or Newton creating universal laws and inscribing them on paper - the ultimate fact in all cases is muscular movement.*"
"*Absolutely all the properties of external manifestations of brain activity described as animation, passion, mockery, sorrow, joy, etc., are merely results of a greater or lesser contraction of definite groups of muscles, which, as everyone knows, is a purely mechanical act.*"
— Ivan Sechenov, 1863, in *Reflexes of the Brain*

GOOD REASONS

"*For cognitions to be communicated, they must be physically enacted. It follows from this observation that a complete account of the cognitive system must explain how it transmits information to the environment as well as how it takes information in and retains and elaborates it.*"
— Jordan & Rosenbaum, 1989, in *Foundations of Cognitive Science*

"*The basic idea is that cognition should not be understood as a capacity for deriving world-models, which might then provide a database for thinking, planning, and problem-solving. Rather, it is emphasized that cognitive processes are so closely intertwined with action that cognition would best be understood as 'enactive', as the exercise of skillful know-how in situated and embodied action.*"
"*Cognition is not detached contemplation of the world, but a set of processes that determine possible actions. According to their view, the criterion for success of cognitive operations is not to recover pre-existing features or to construct a veridical representation of the environment. Instead, cognitive processes construct the world by bringing forth action-relevant structures in the environmental niche. In a nutshell, cognition should be understood as the capacity of generating structure by action, that is, of 'enacting' a world.*"
— Engel et al., 2013, *Trends Cogn Sci* 17:202

COGNITION AND ACTION

What to move where

Cognitive science

vs.

Moving

vs.

Motor control

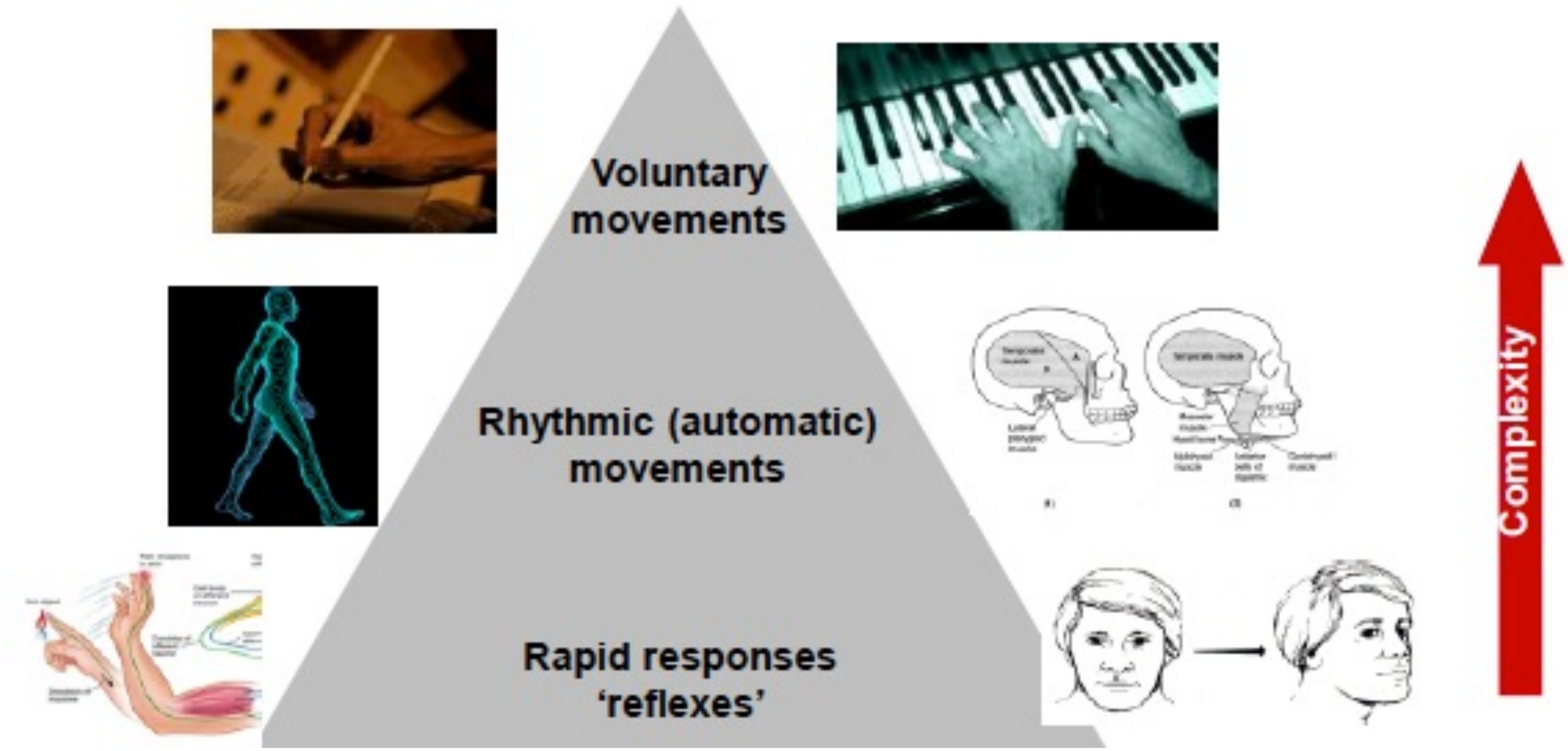
—Wolpert, 2007, *Hum Mov Sci* 26:511

« COGNITION IS ACTION »

« In cognitive science, we are currently witnessing a 'pragmatic turn', away from the *traditional representation-centered framework* towards a **paradigm that focuses on understanding cognition as 'enactive'**, **as skillful activity that involves ongoing interaction with the external world**. The key premise of this view is that **cognition should not be understood as providing models of the world**, but **as subserving action and being grounded in sensorimotor coupling**. Accordingly, cognitive processes and their underlying neural activity patterns should be studied primarily with respect to their role in action generation. »

— Engel et al., 2013, *Trends Cogn Sci* 17:202

TYPES OF ACTION

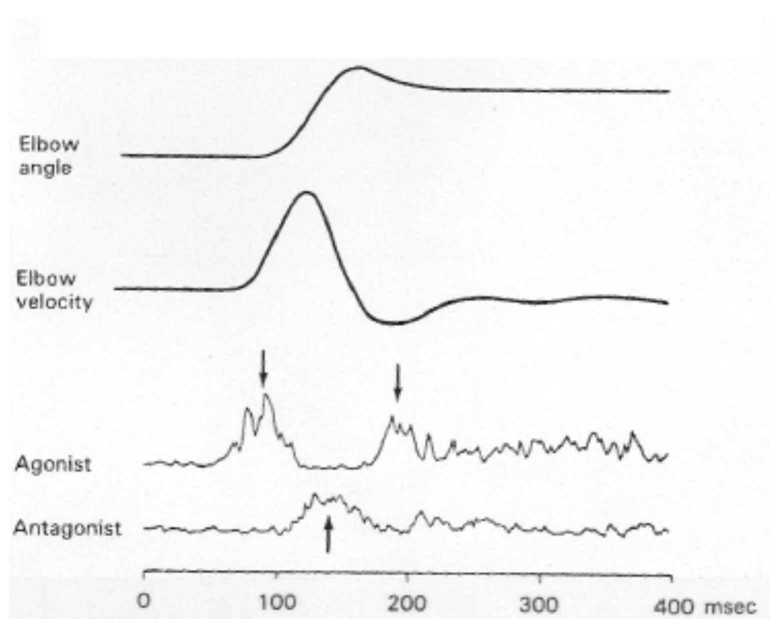


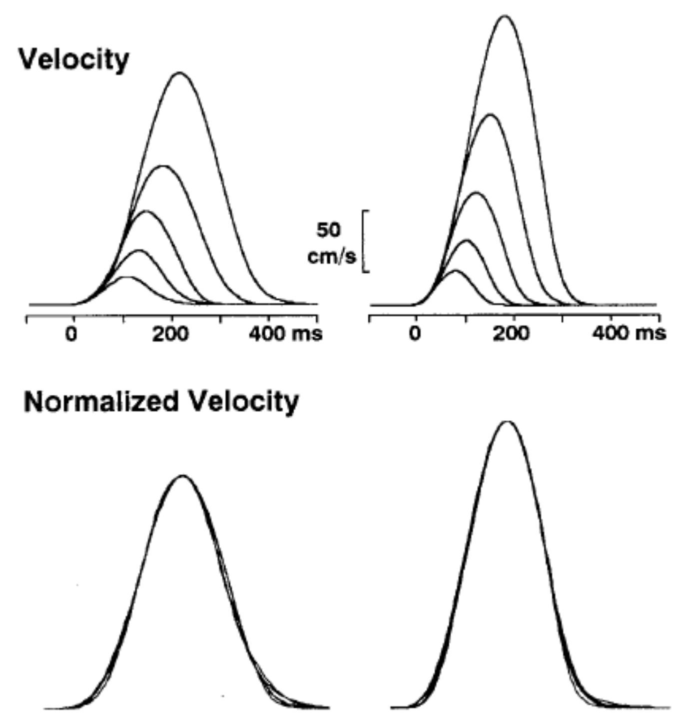
Walking, running, reaching, grasping, speaking, singing, writing, drawing, looking, smiling, keyboarding, …

CONTENT OF ACTION

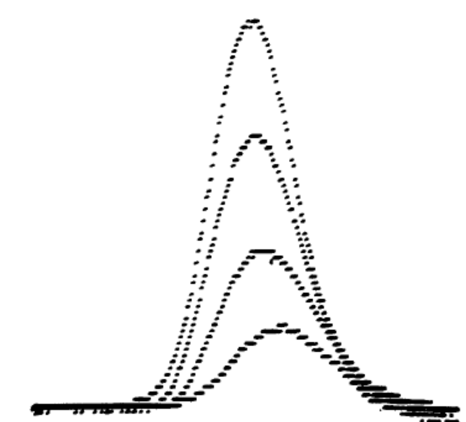
Every action has a specific direction (left/right, toward/away, …), and intensity (velocity, force, …)

- Anticipatory electrical activities (EEG, EMG)
- Invariant profiles
- Scaling with task conditions





— Gordon et al., 1994, *Exp Brain Res* 99:112

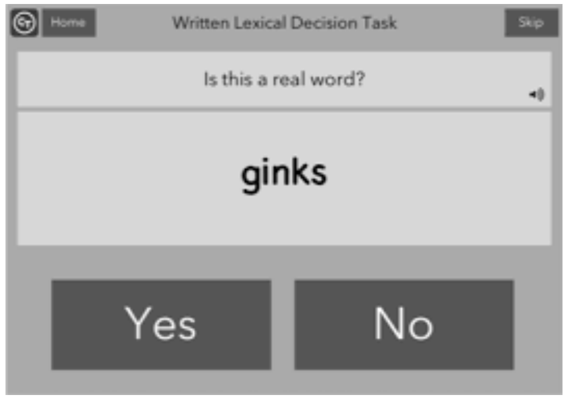


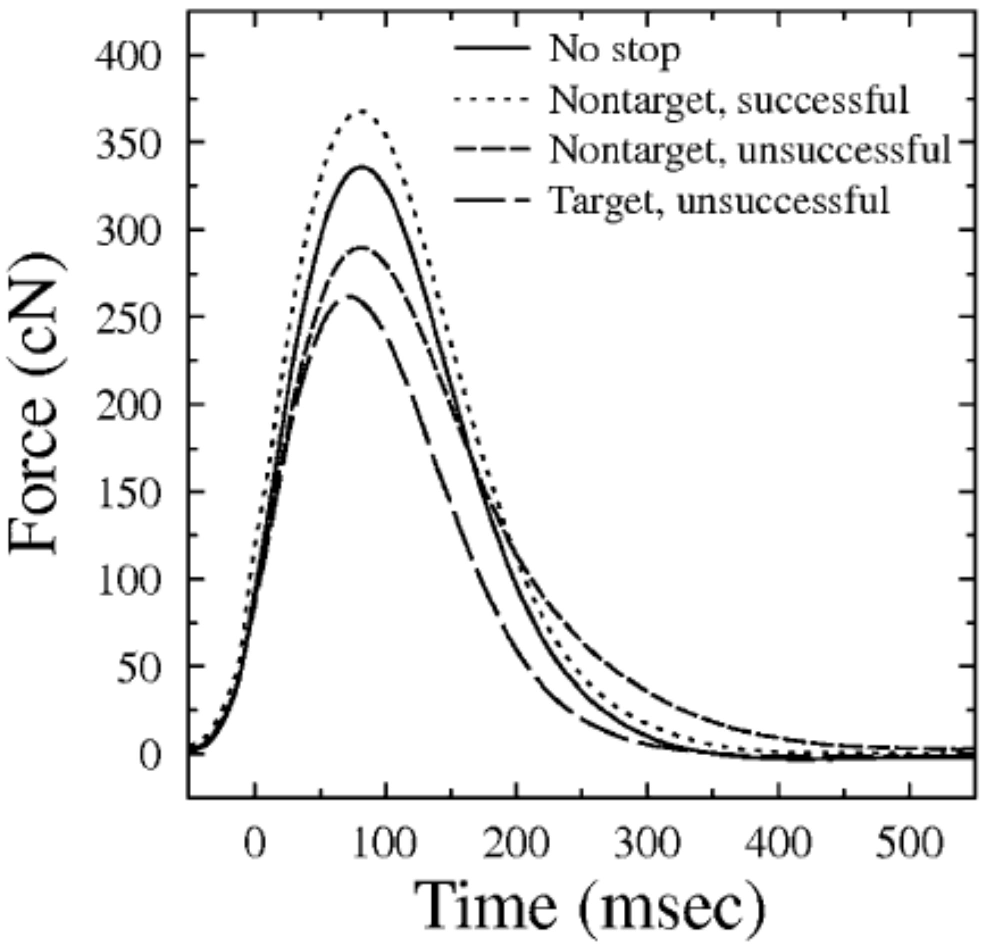
— Angel, 1973, *Q J Exp Psychol* 25:193

ACTION REFLECTS DECISION

Lexical decision task

Judge the lexical status (word/nonword) of a letter string, and indicate the decision by moving a handle in one direction (word) or in the other direction (nonword)



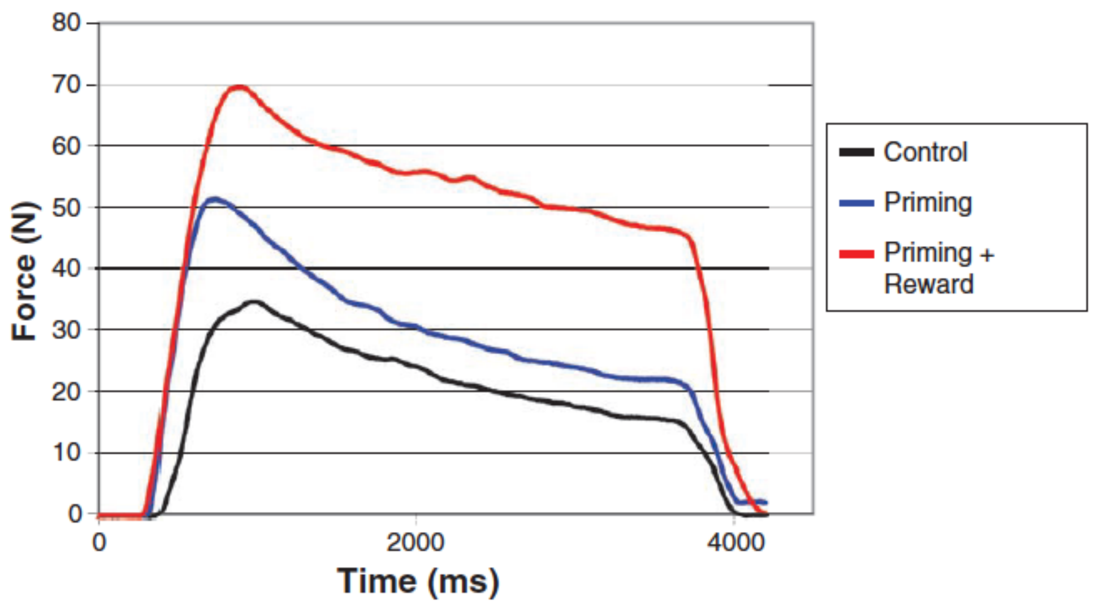


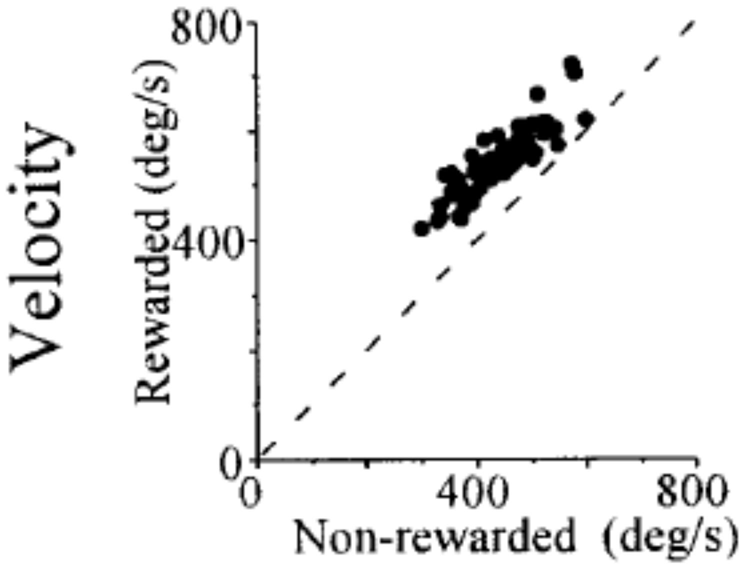
— Ko & Miller, 2011, *Psychon Bull Rev* 18:813

→ Faster movements for words vs nonwords

— Abrams & Balota, 1991, *Psychol Sci* 2:153

ACTION REFLECTS MOTIVATION

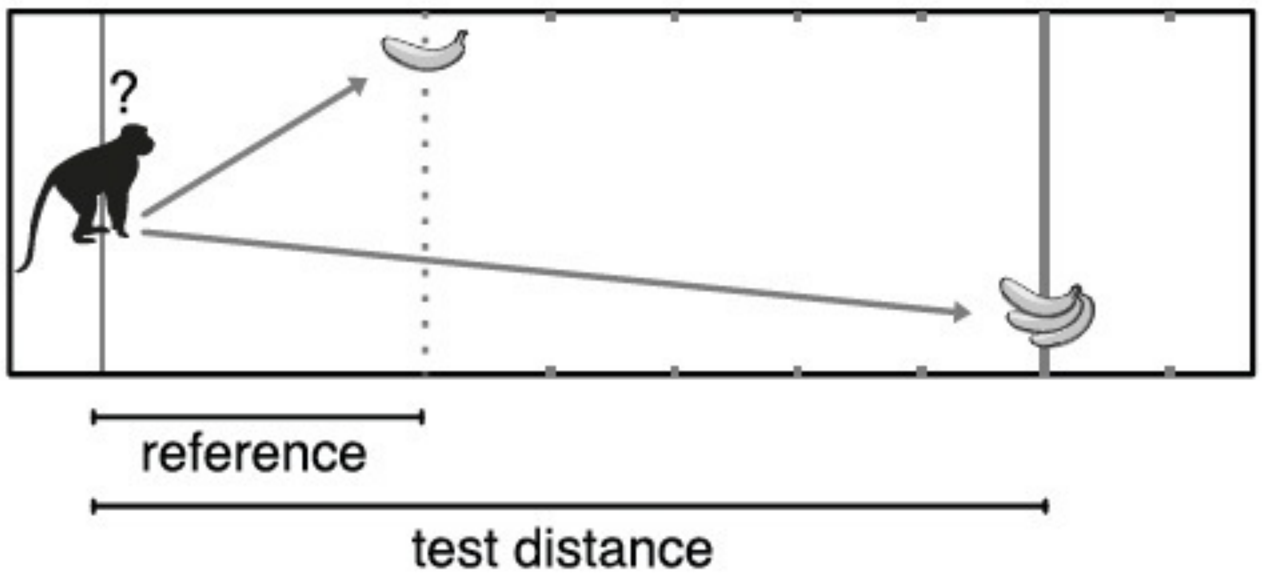




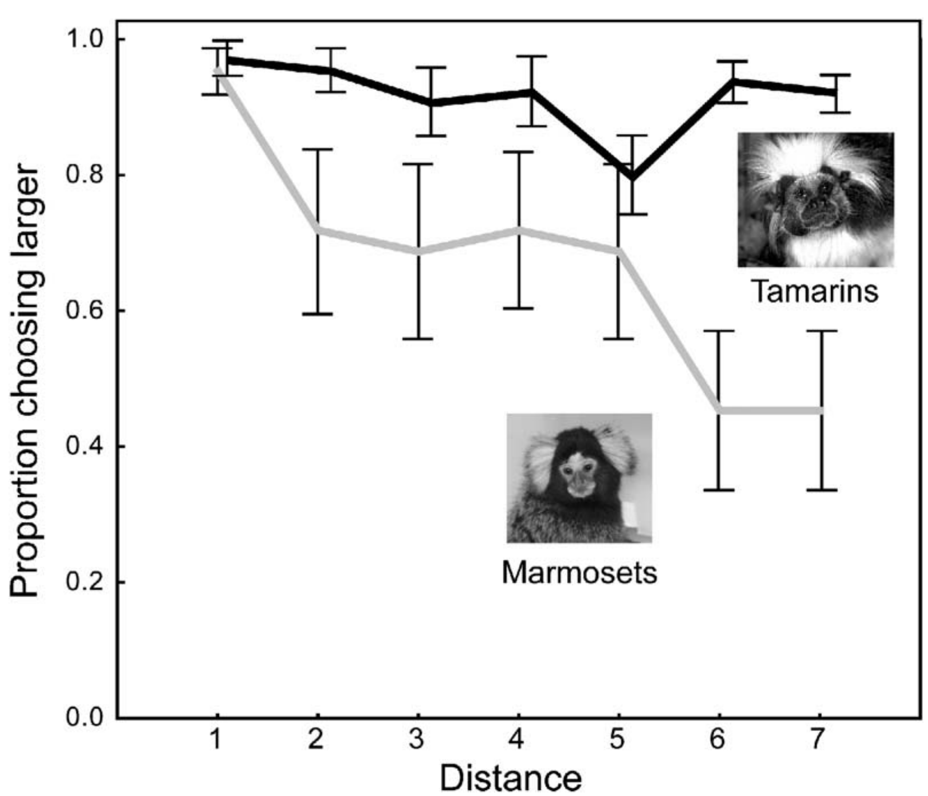
— Aarts et al., 2008, *Science* 319:1639

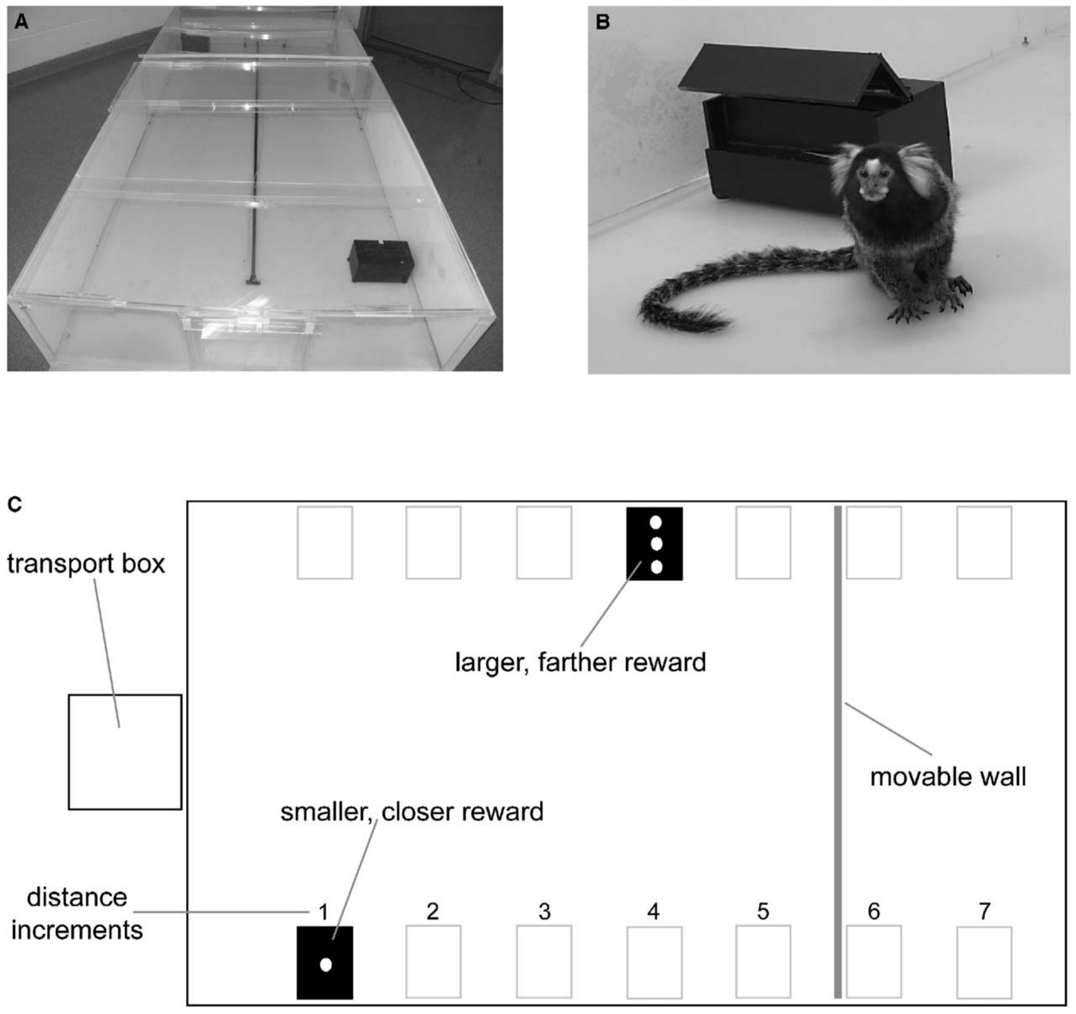
— Takikawa et al., 2002, *Exp Brain Res* 142:284

ACTION IS DECISION MAKING



— Stevens et al., 2005, *Curr Biol* 15:1865





THE ORGANIZATION OF ACTION

THE ORGANIZATION OF ACTION

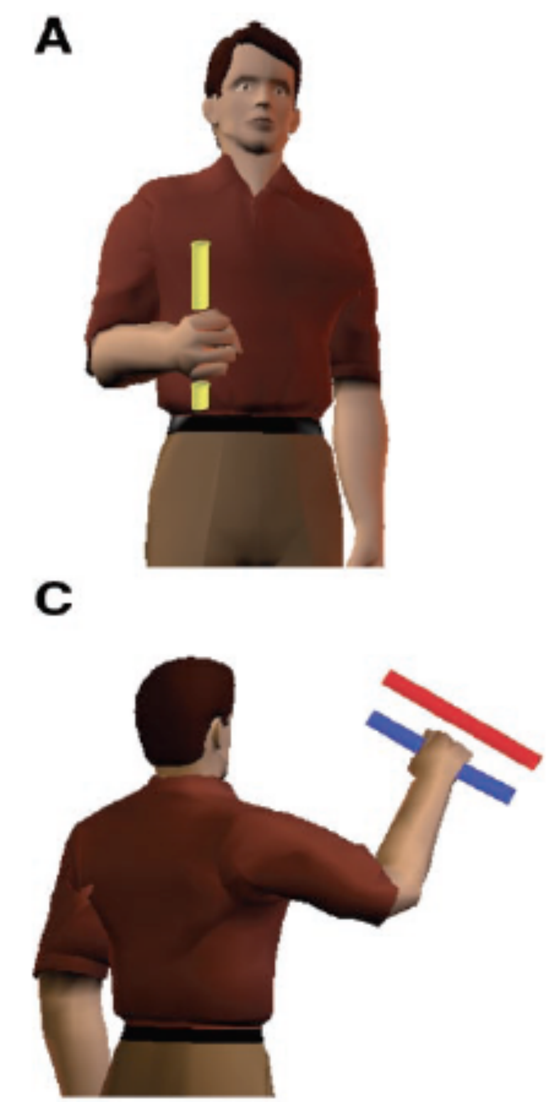
Idea, symbol, object

Space/time displacement/force in task space

Trajectory formation in body space

Joint/muscle force, activations

Neural commands



LEXICON

Kinematics

position, velocity, acceleration in task/body space

$$\begin{cases} x = L_1 \cos(\theta_1) + L_2 \cos(\theta_1 + \theta_2) \\ y = L_1 \sin(\theta_1) + L_2 \sin(\theta_1 + \theta_2) \end{cases}$$

Dynamics

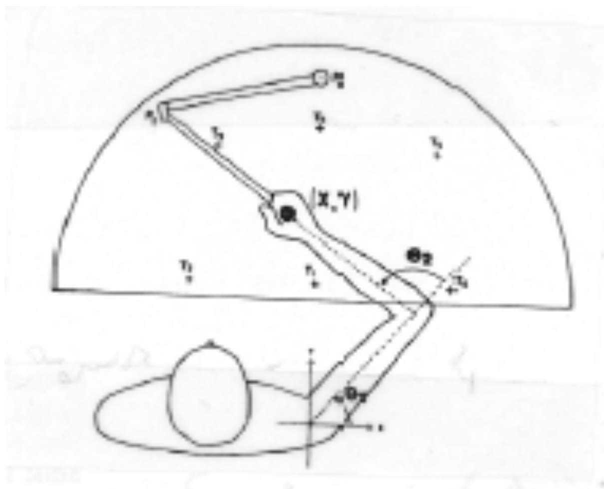
force/torque (Newton's law)

$$\begin{aligned} \tau_1 &= (I_1 + I_2 + m_2 l_1 l_2 \cos\theta_2 + \frac{m_1 l_1^2 + m_2 l_2^2}{4} + m_2 l_1^2)\ddot{\theta}_1 + \\ &\quad (I_2 + \frac{m_2 l_2^2}{4} + \frac{m_2 l_1 l_2}{2}\cos\theta_2)\ddot{\theta}_2 - \\ &\quad \frac{m_2 l_1 l_2}{2}\dot{\theta}_2^2 \sin\theta_2 - m_2 l_1 l_2 \dot{\theta}_1 \dot{\theta}_2 \sin\theta_2 \\ \tau_2 &= (I_2 + \frac{m_2 l_1 l_2}{2}\cos\theta_2 + \frac{m_2 l_2^2}{4})\ddot{\theta}_1 + \\ &\quad (I_2 + \frac{m_2 l_2^2}{4})\ddot{\theta}_2 + \frac{m_2 l_1 l_2}{2}\dot{\theta}_1^2 \sin\theta_2 \end{aligned}$$

Degrees of freedom

« the least number of independent coordinates required to specify the position of the system elements without violating any geometrical constraints »

— Saltzman, 1979, *J Math Psychol* 20:91



PROBLEMS

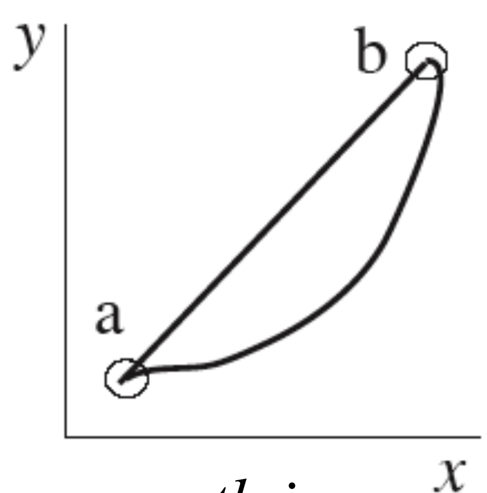
Redundancy

In task space, body space, muscle space, neural space

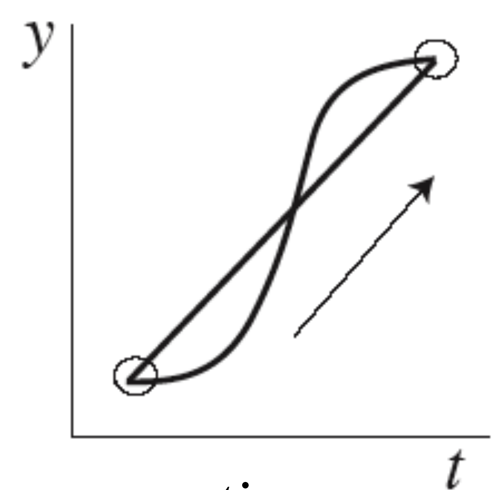
Problem of degrees of freedom (Bernstein's problem)

600 muscles, 200 joints

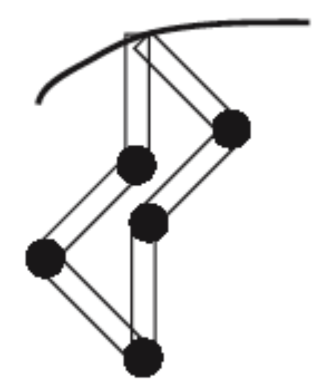
→ *Coordination*



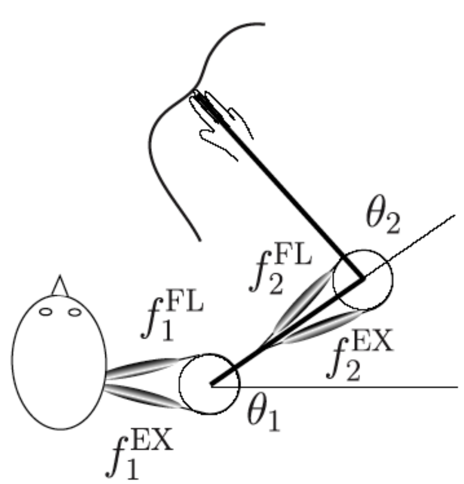
path in task space

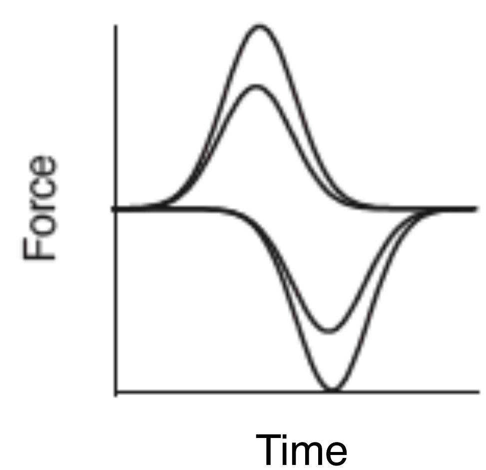


time course



body space redundancy





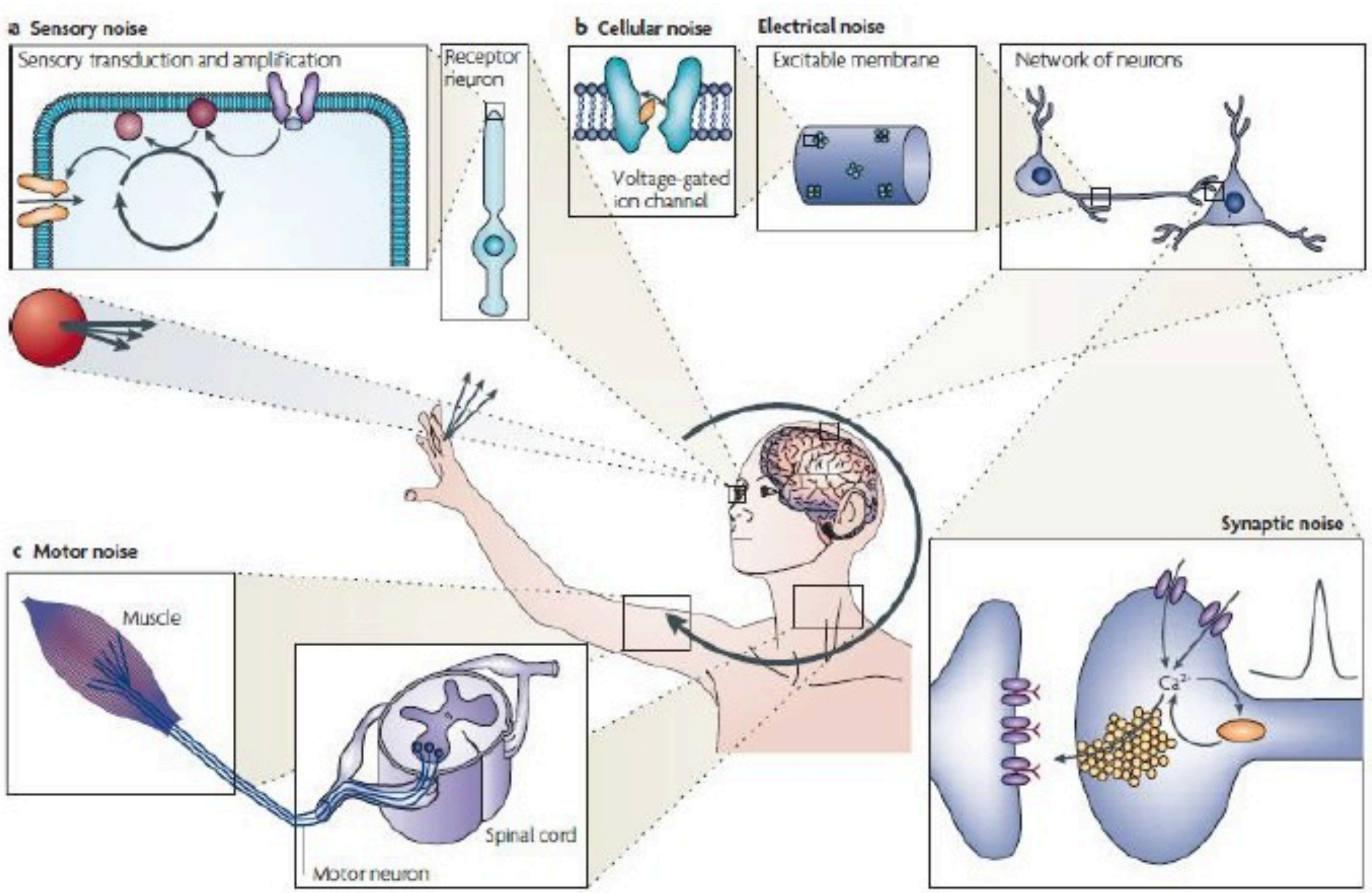
muscle space redundancy

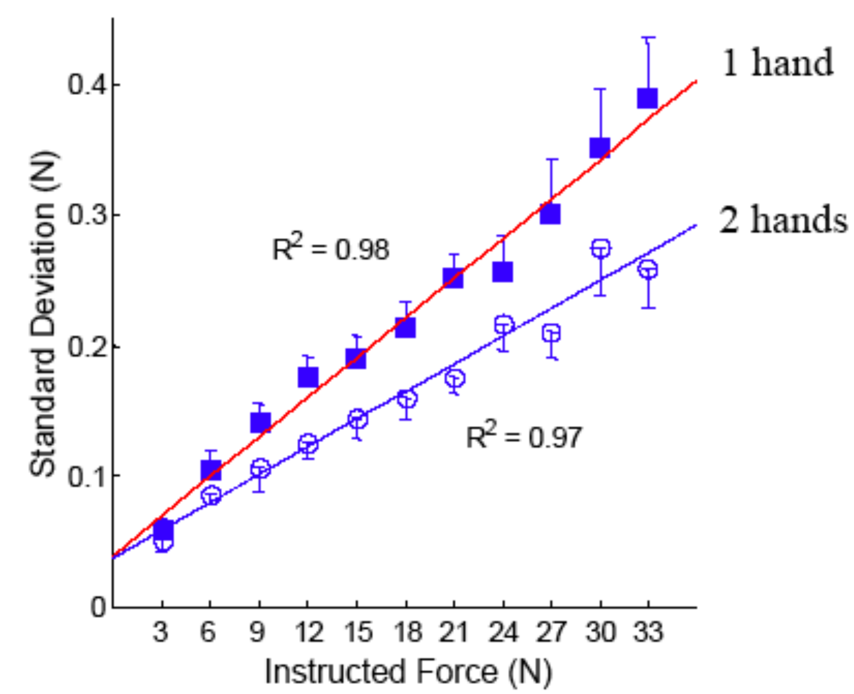
— Bernstein, 1967, *The Co-ordination and Regulation of Movement*, Pergamon

PROBLEMS

Noise

At all stages of sensorimotor processing (sensory, cellular, synaptic, motor)





— Faisal et al., 2008, *Nat Rev Neurosci* 9:292

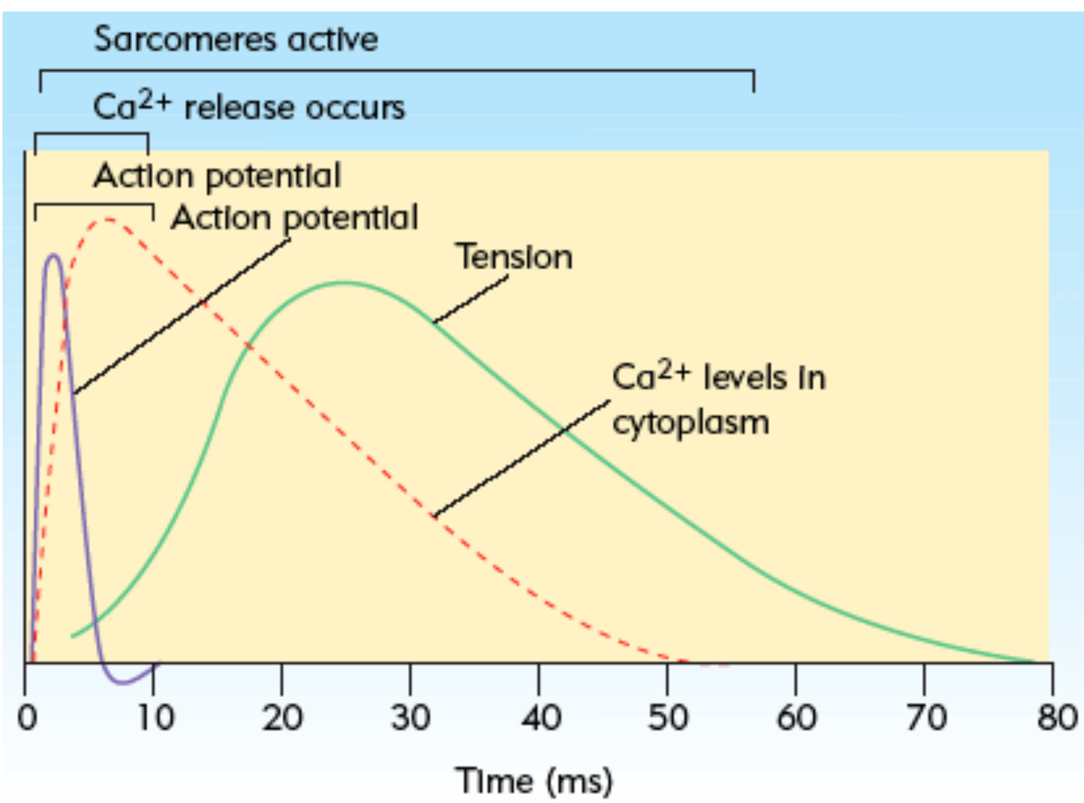
— Todorov, 2002, *Neural Comput* 14:1233

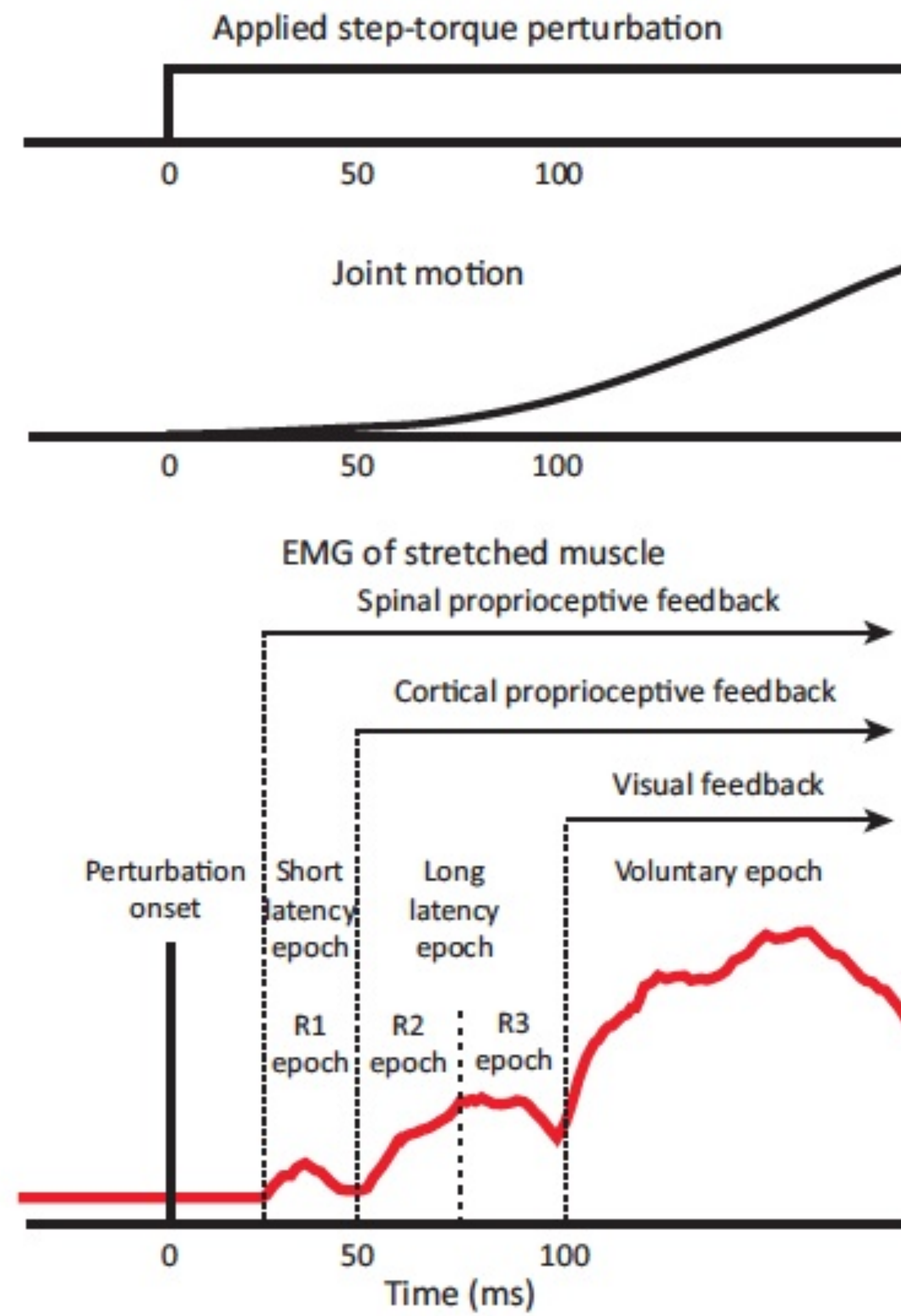
PROBLEMS

Delays

In afferent sensory information and efferent motor commands

→ *"We live in the past"*



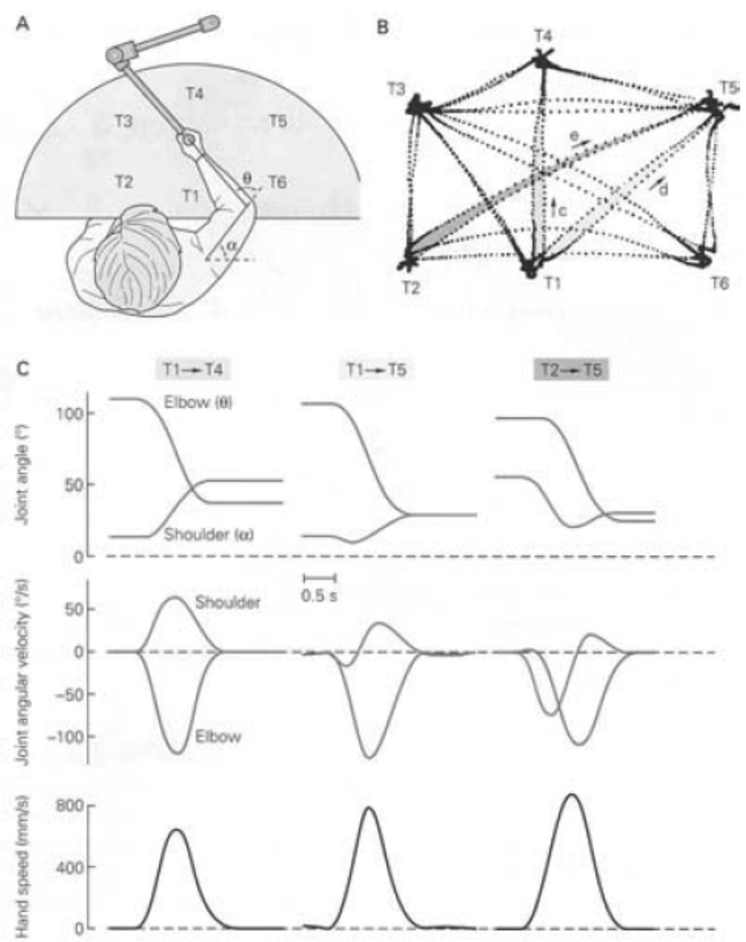


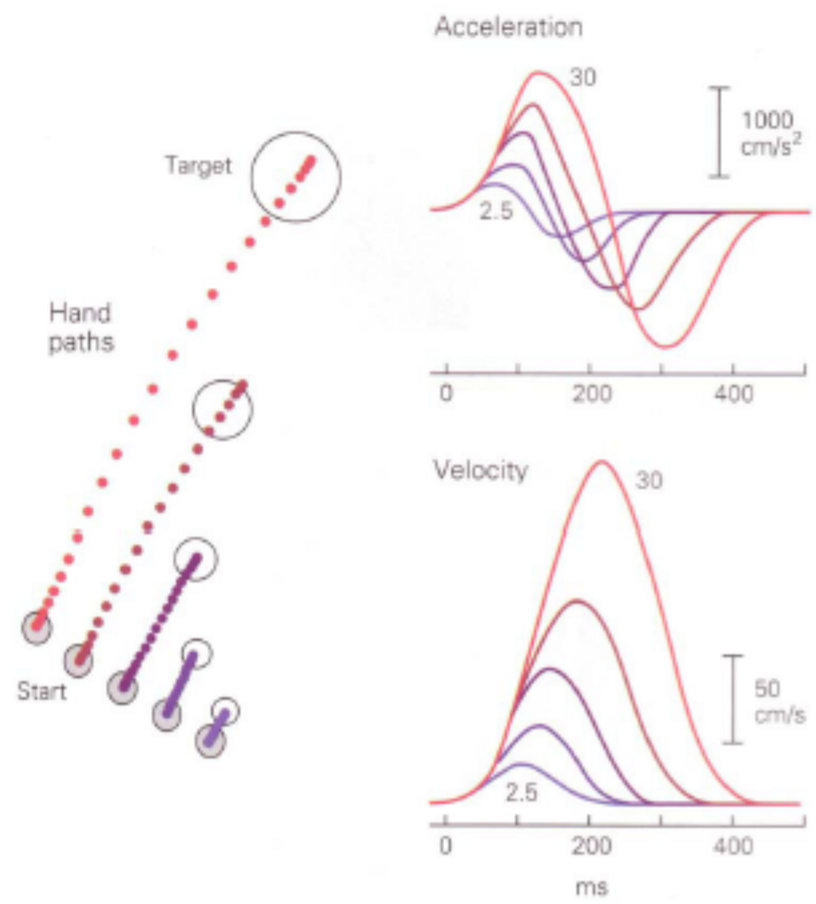
— Scott, 2012, *Trends Cogn Sci* 16:541

MOTOR INVARIANTS

Trajectories

Point-to-point movements are straight with bell-shaped velocity profiles

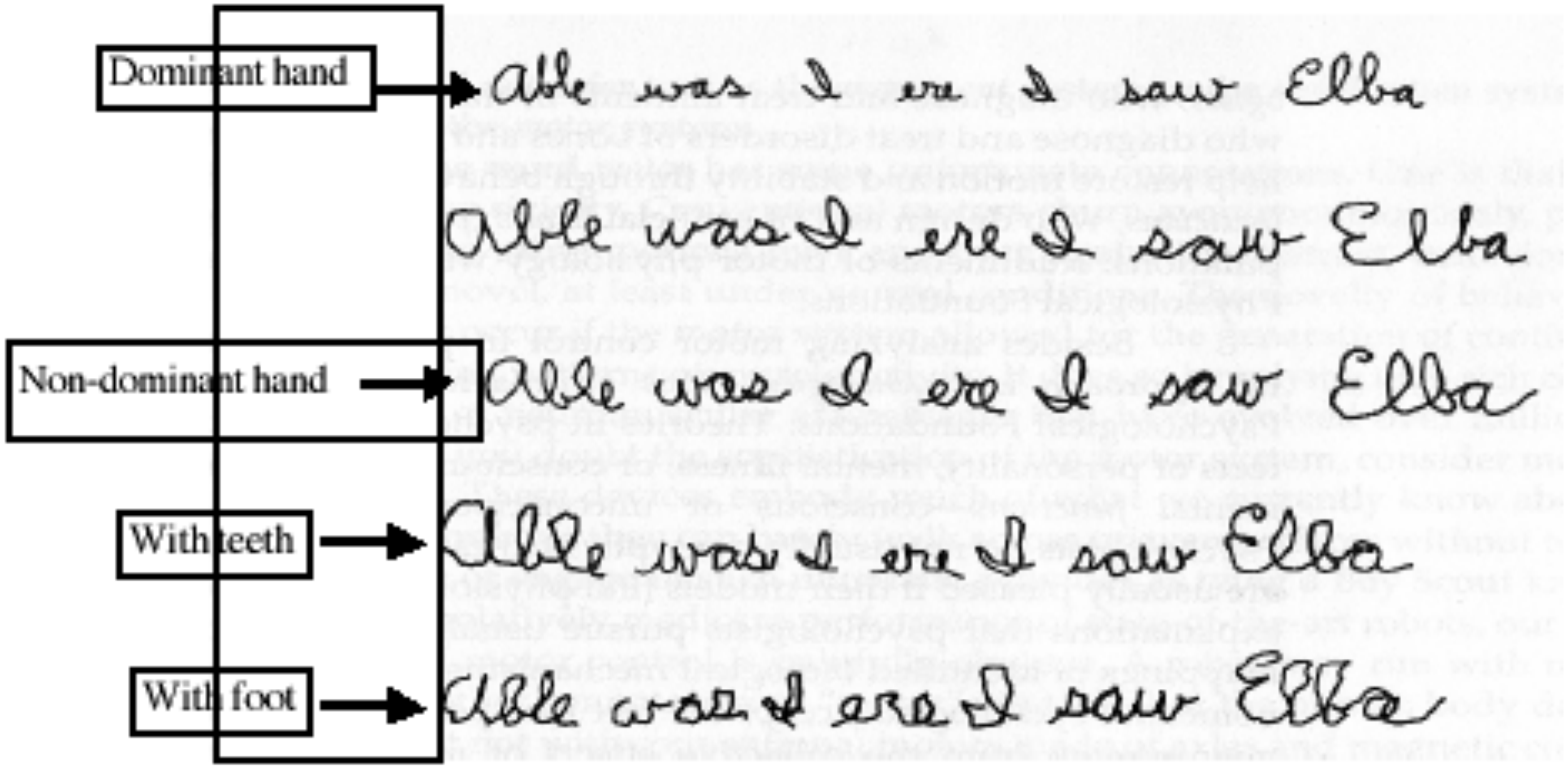




MOTOR INVARIANTS

Motor equivalence

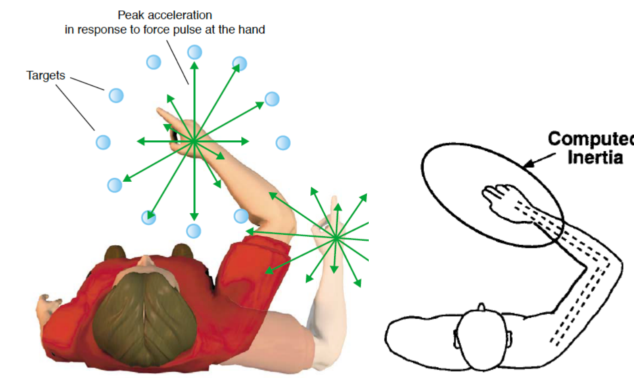
Actions are encoded in the central nervous system in terms that are more abstract than commands to specific muscles

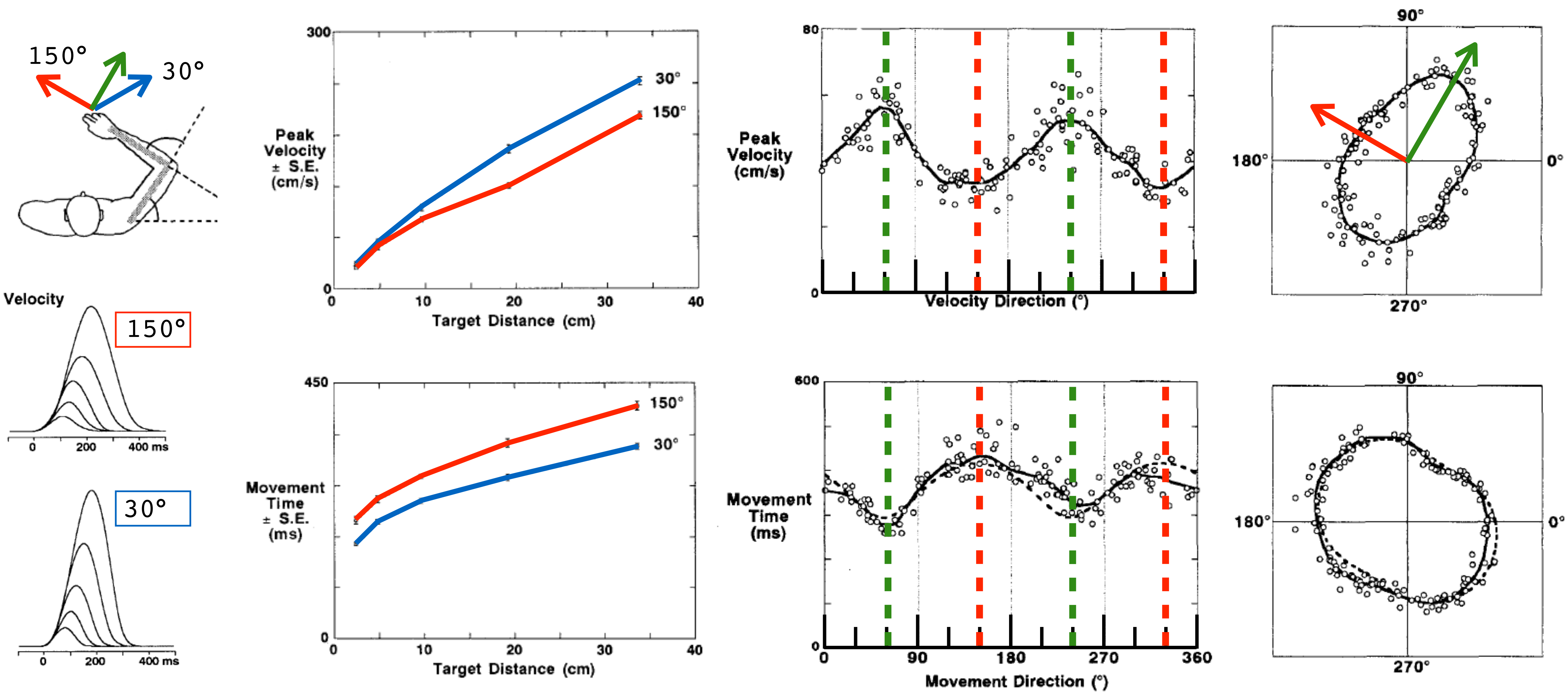


MOTOR INVARIANTS

Scaling laws

Duration and velocity scale with amplitude and load



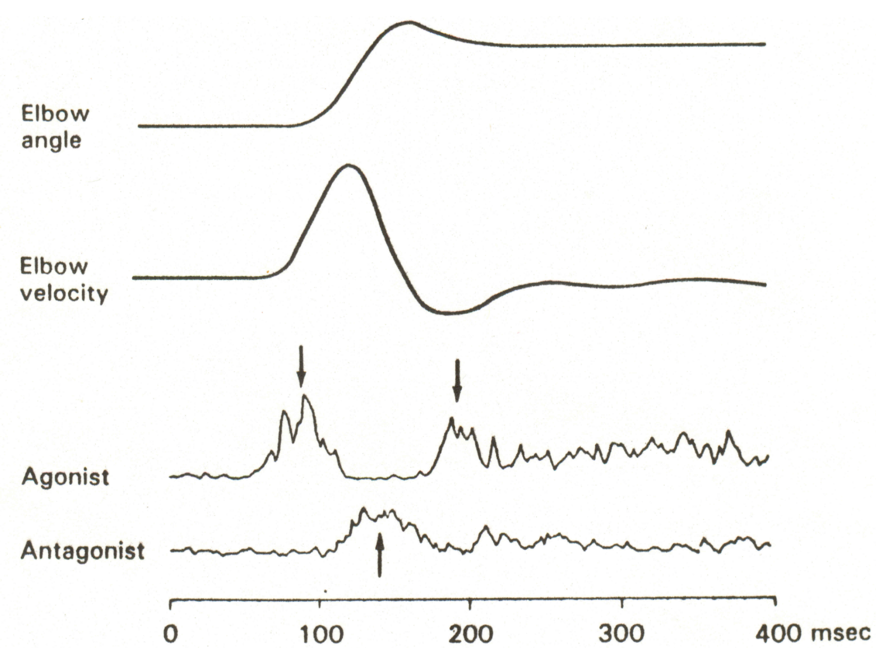


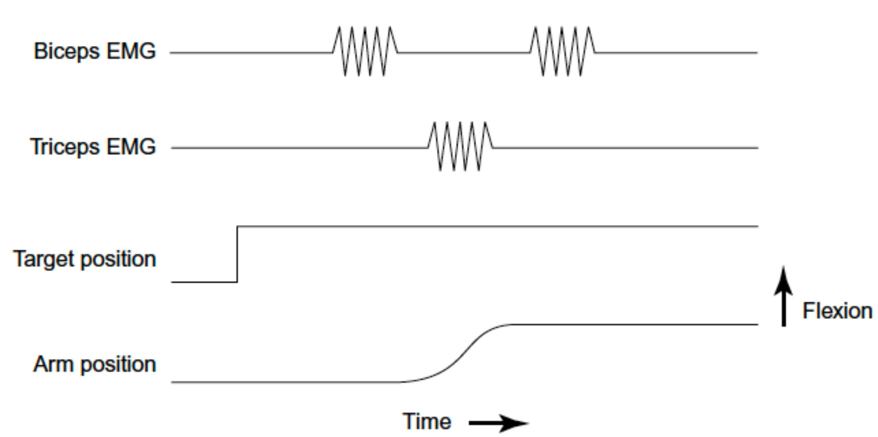
— Gordon et al., 1994, *Exp Brain Res* 99:112

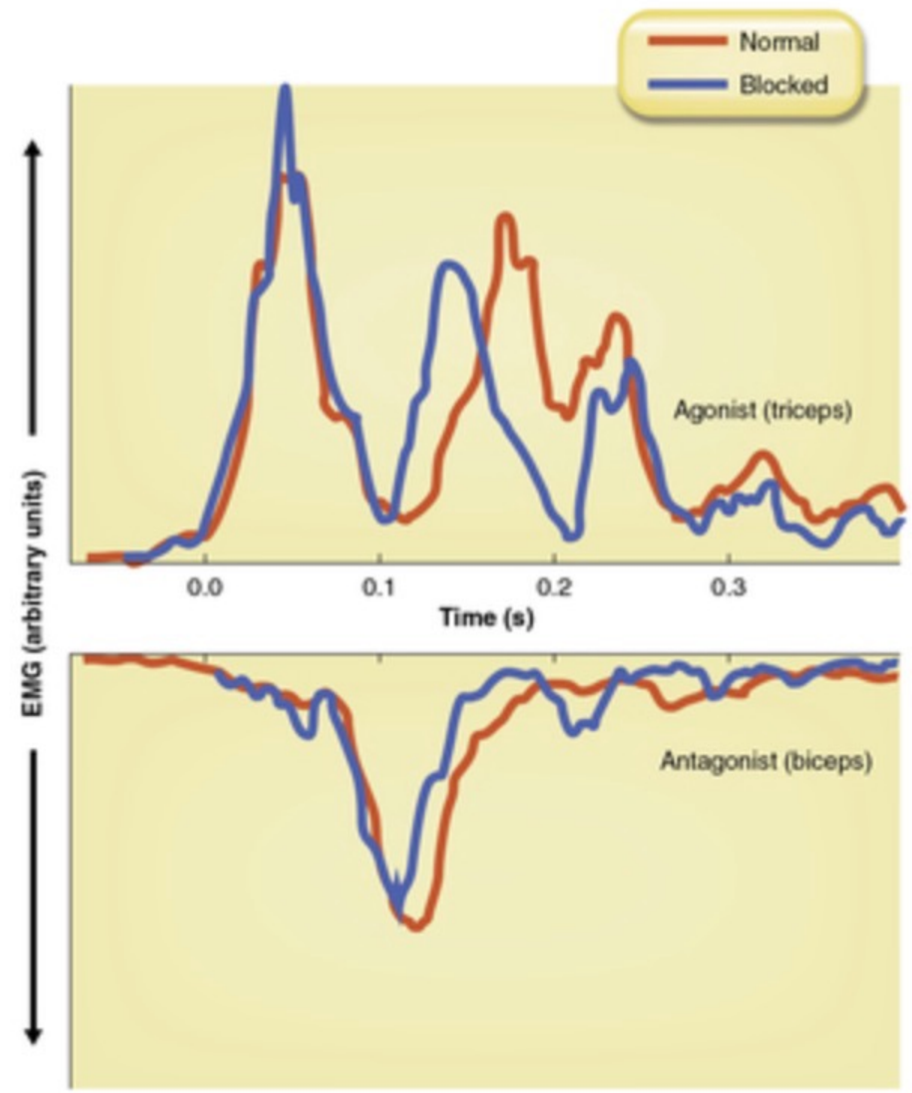
MOTOR INVARIANTS

EMG

Triphasic pattern during fast movements

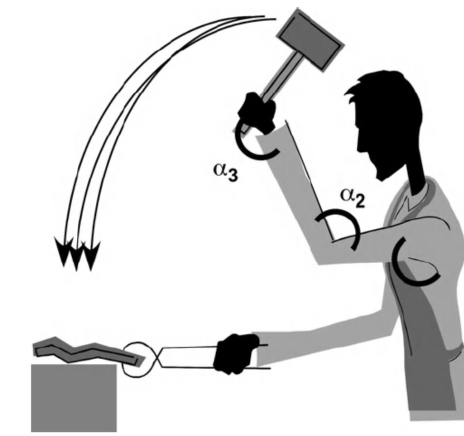






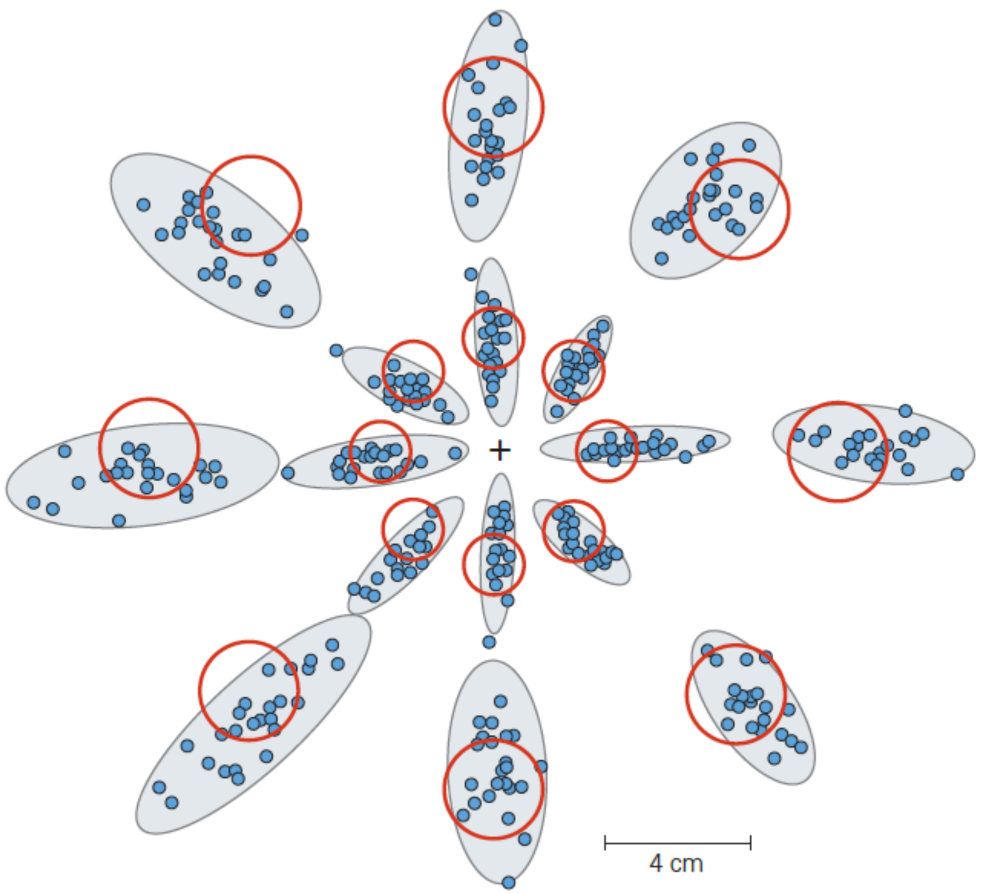
—Wadman et al., 1979, *J Hum Mov Stud* 5:3

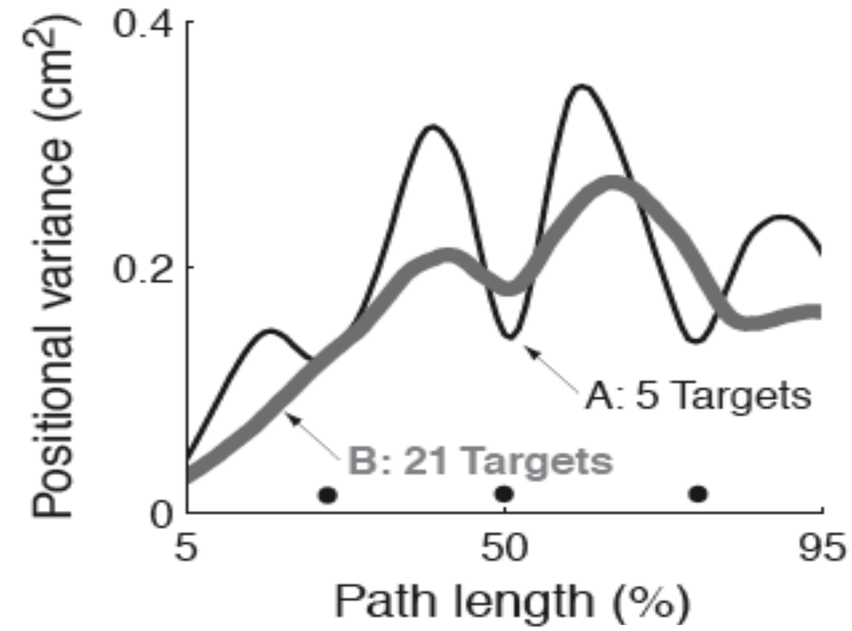
MOTOR VARIABILITY

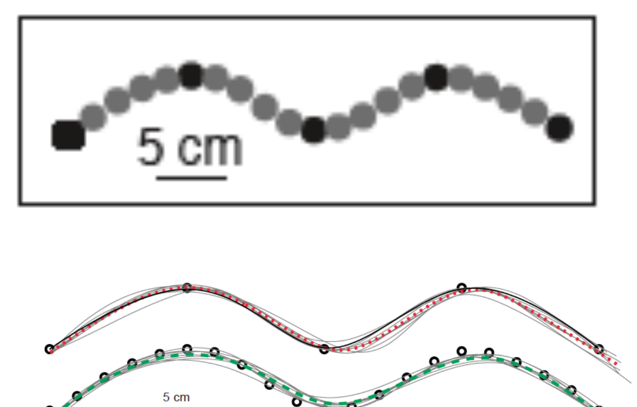


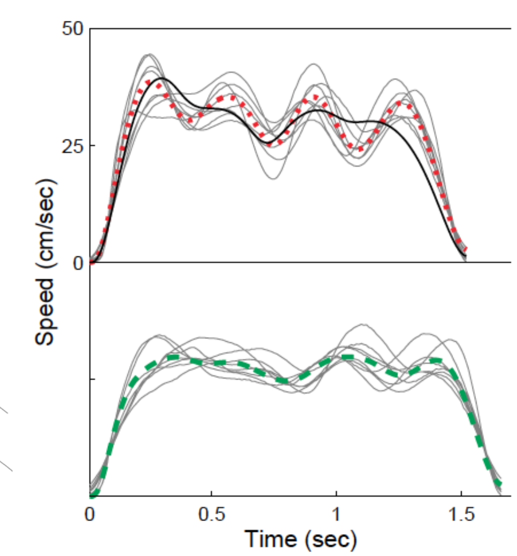
Uncontrolled manifold, structured variability

« Repetition without repetition » (Bernstein)









— Gordon et al., 1994, *Exp Brain Res* 99:97

— Todorov & Jordan, 2002, *Nat Neurosci* 5:1226

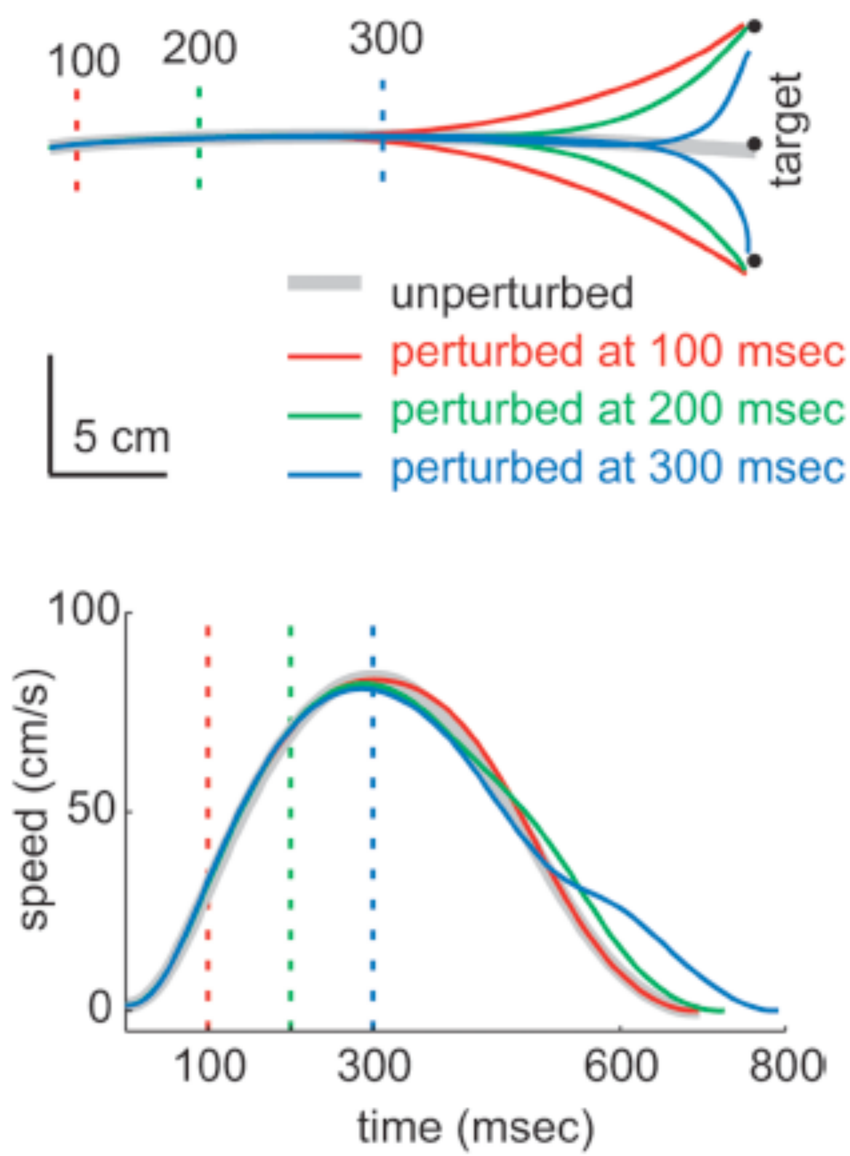
MOTOR INVARIANTS AND VARIABILITY

Are motor invariants are really invariants or simply by-products of control?

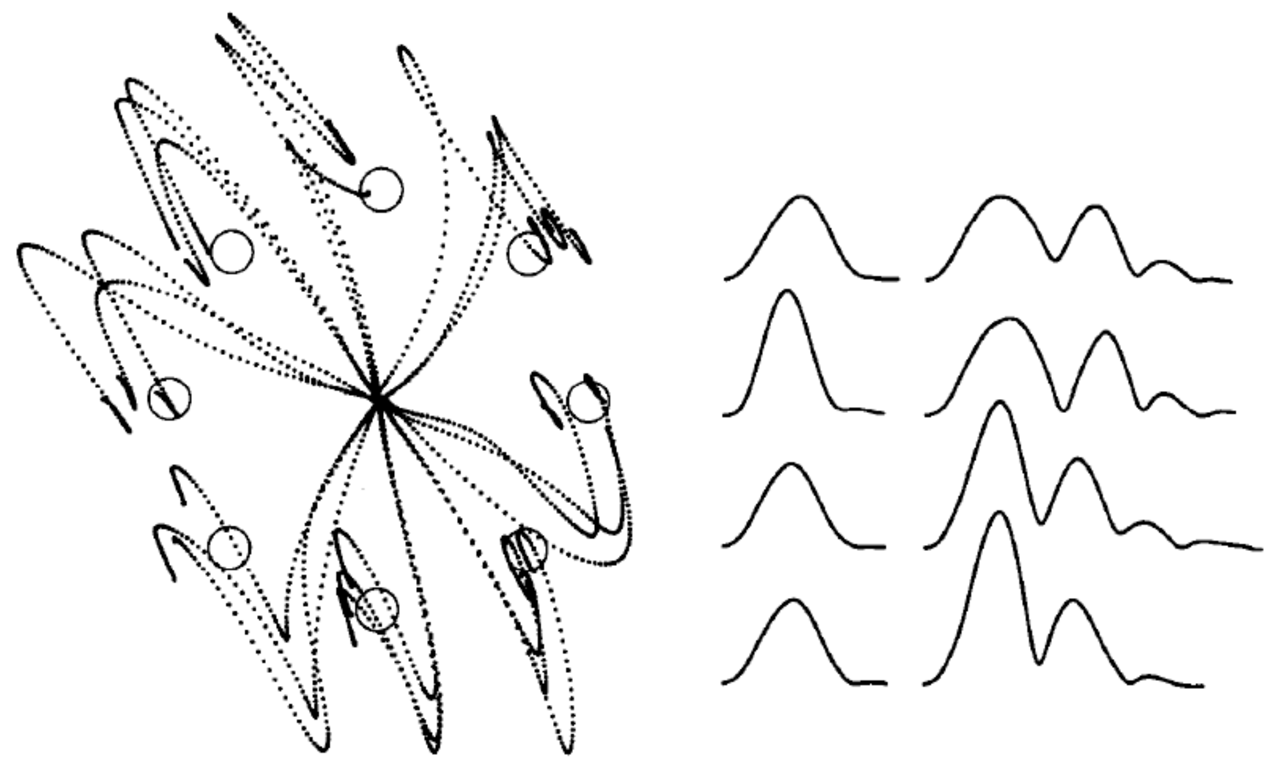
Motor variability is as important as motor invariants (structure of variability)

FLEXIBILITY

Motor control is highly flexible in space and time



— Liu & Todorov, 2007, *J Neurosci* 27:9354

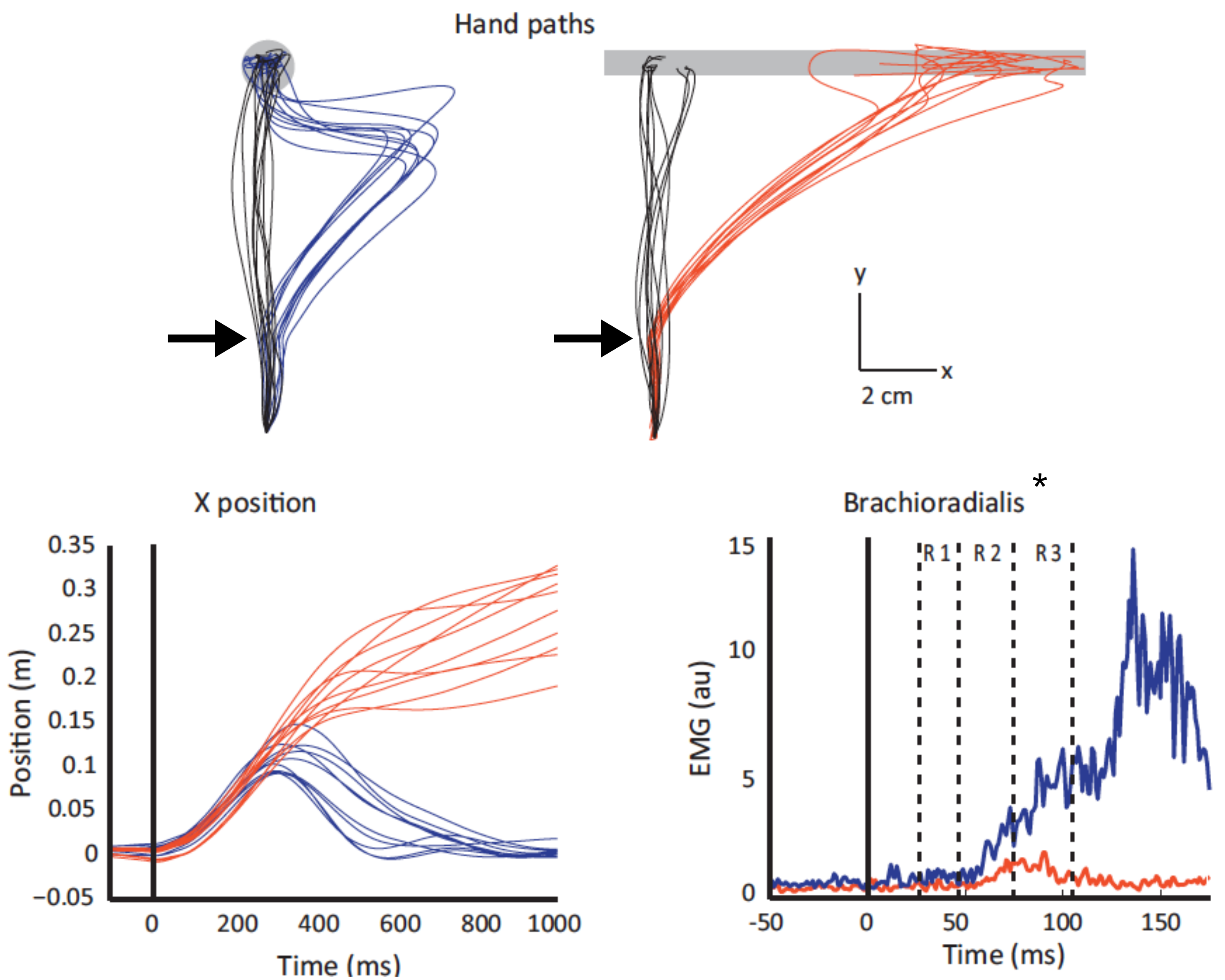


— Shadmehr & Mussa-Ivaldi, 1994, *J Neurosci* 14:3208

PERTURBATION — CORRECTION

Error corrections

only if perturbations affect the behavioral goal / ignored if they do not



Corrective responses are directed back to the circular target, whereas responses for the rectangular bar are redirected to a new location along the bar.

Corrective responses do not return to a desired trajectory

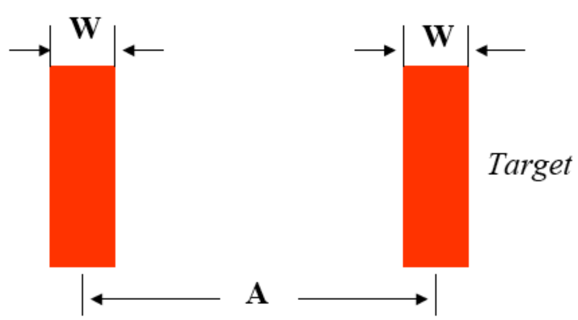
— Nashed et al., 2012, *J Neurophysiol* 109:999

(*) elbow flexor

LAWS OF MOVEMENT

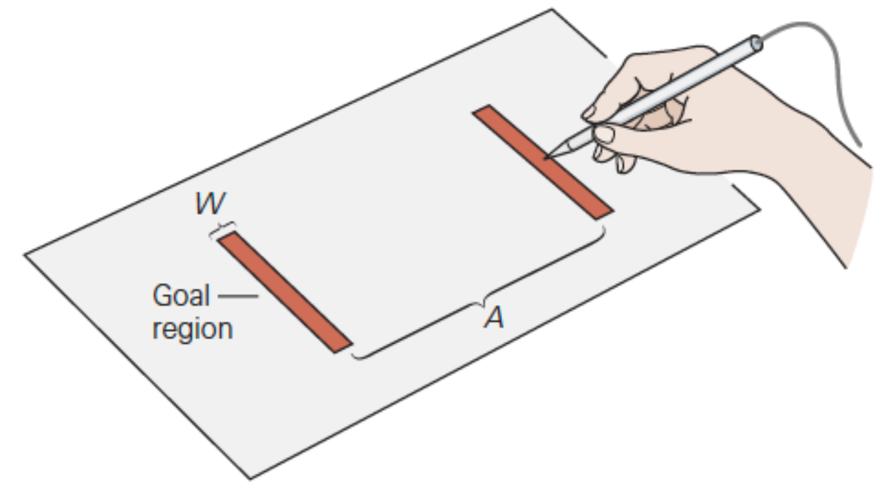
Fitts' law

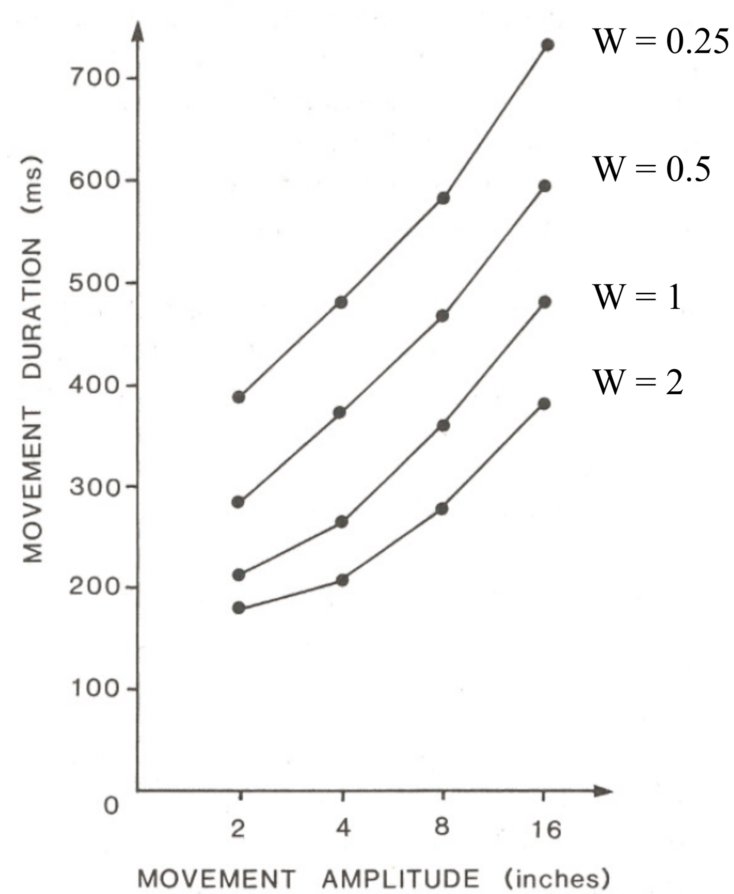
Speed/accuracy trade-off

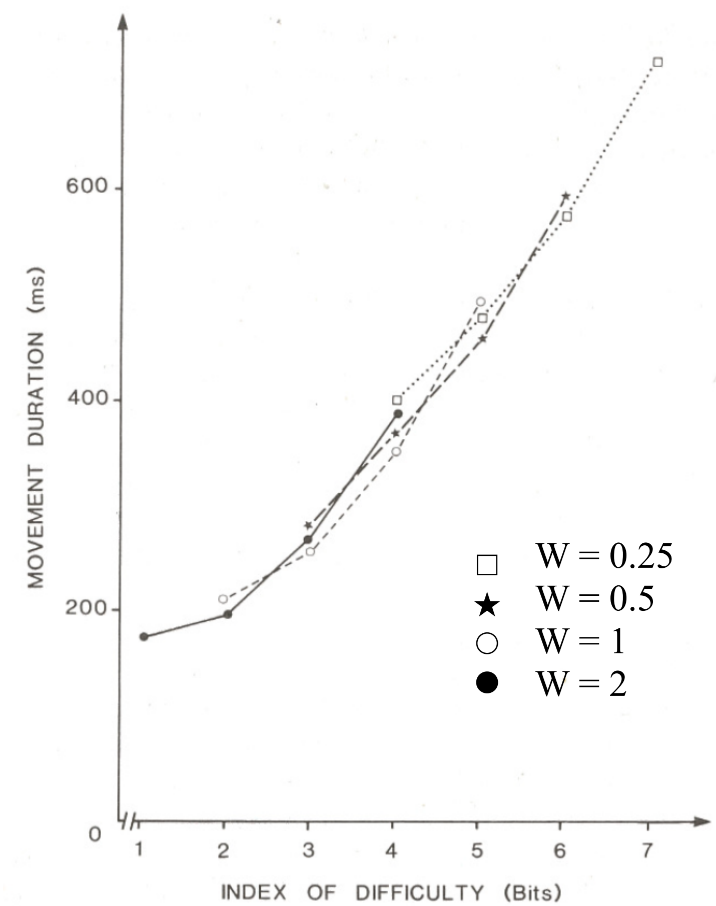


$$MT = a + b\,[\log_2 (2A/W)]$$

ID (index of Difficulty)





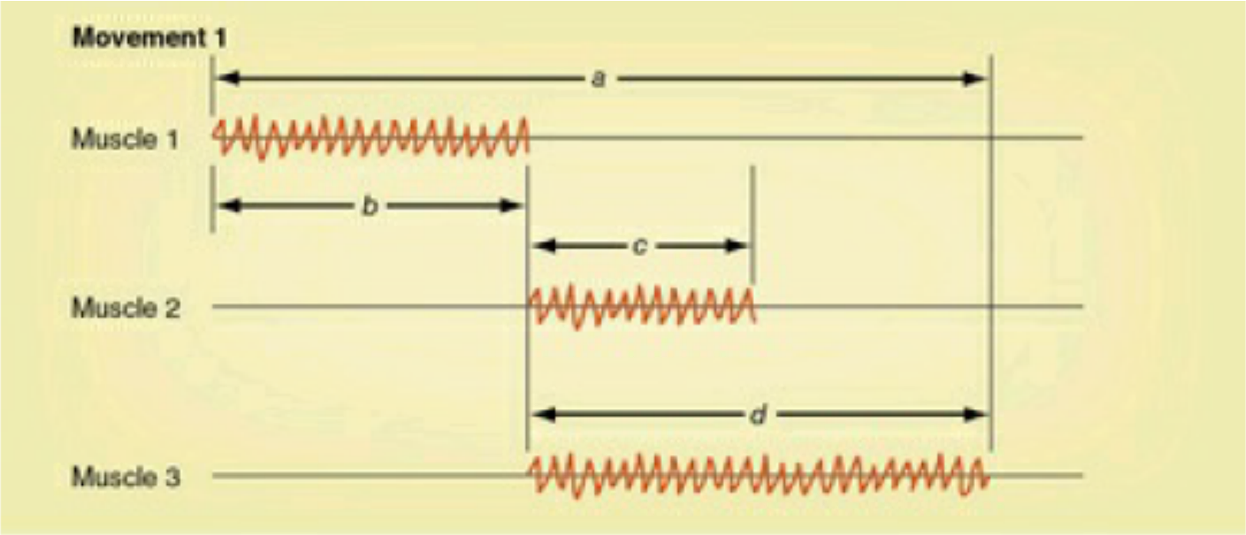


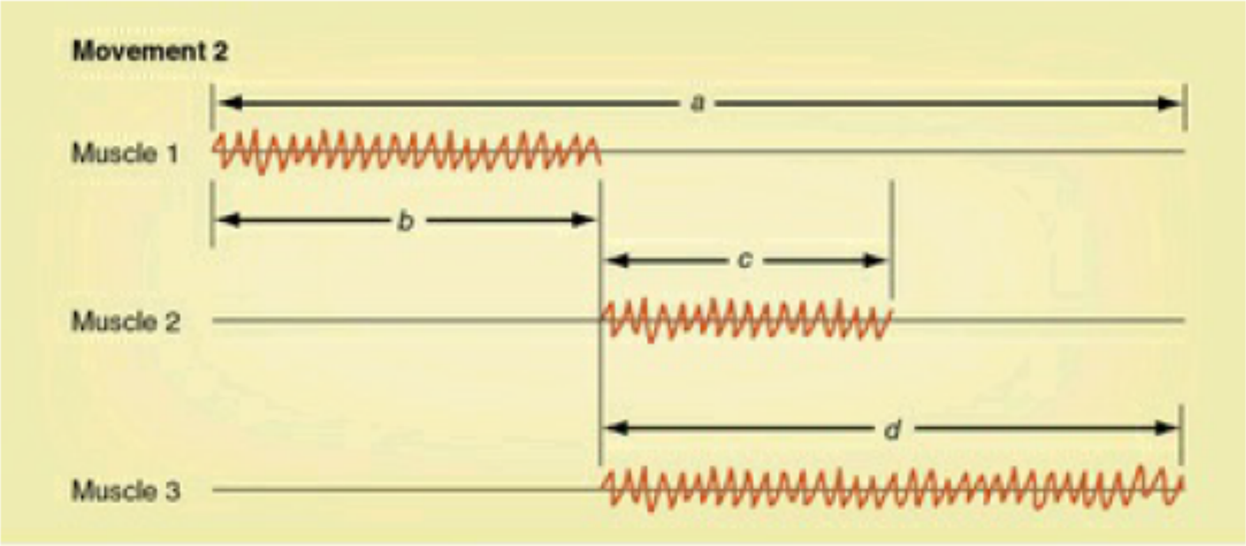
— Fitts, 1954, *J Exp Psychol* 47:381

— Jeannerod, 1988, *The Neural and Behavioural Organization of Goal-Directed Movements*, Clarendon Press

RELATIVE TIMING

Set of ratios of the durations of intervals
within a motor act





hypothetical relative timing of EMG traces

b/a = 0.4
c/a = 0.3
d/a = 0.6

— Schmidt & Lee, 2014, *Motor Learning and Performance,* Human Kinetics

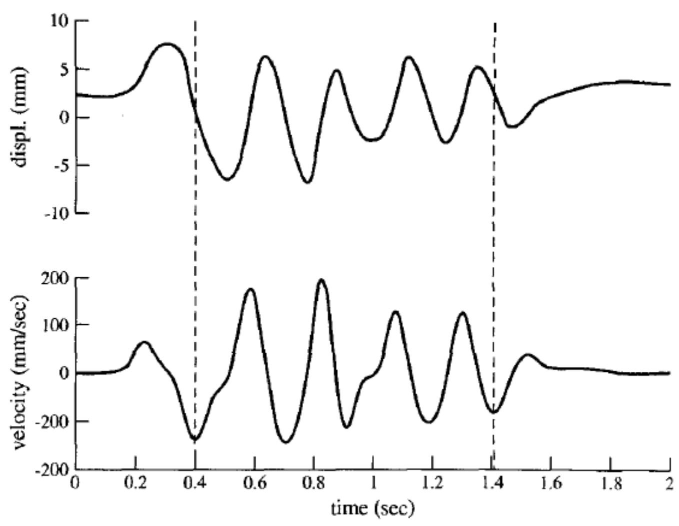
RELATIVE TIMING

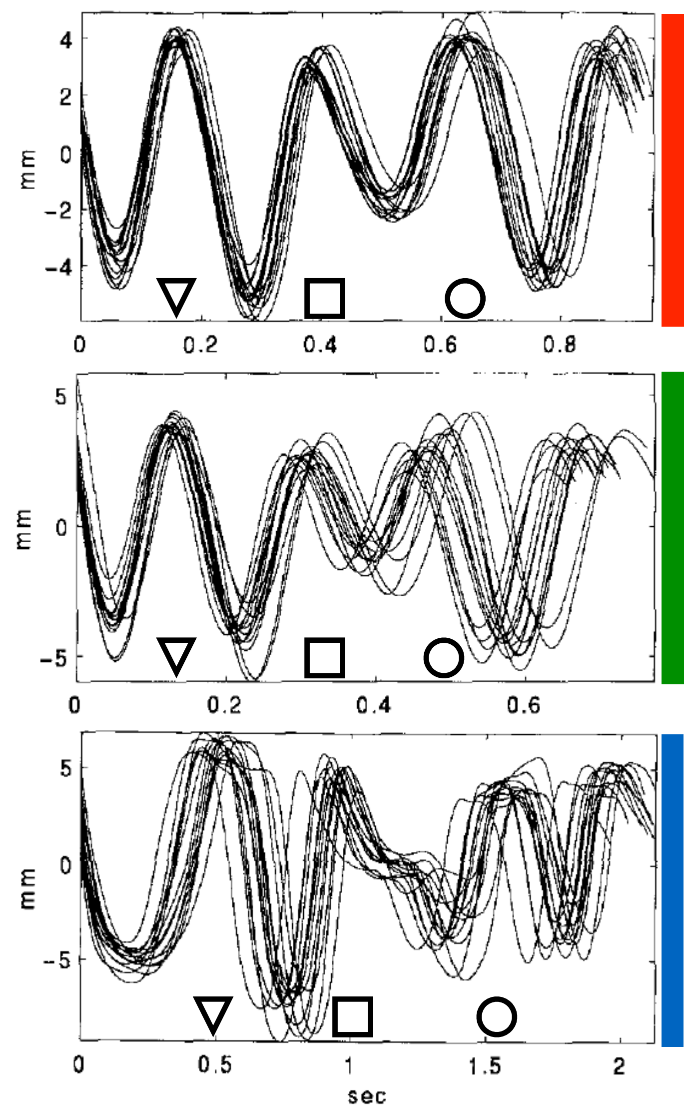
Speech

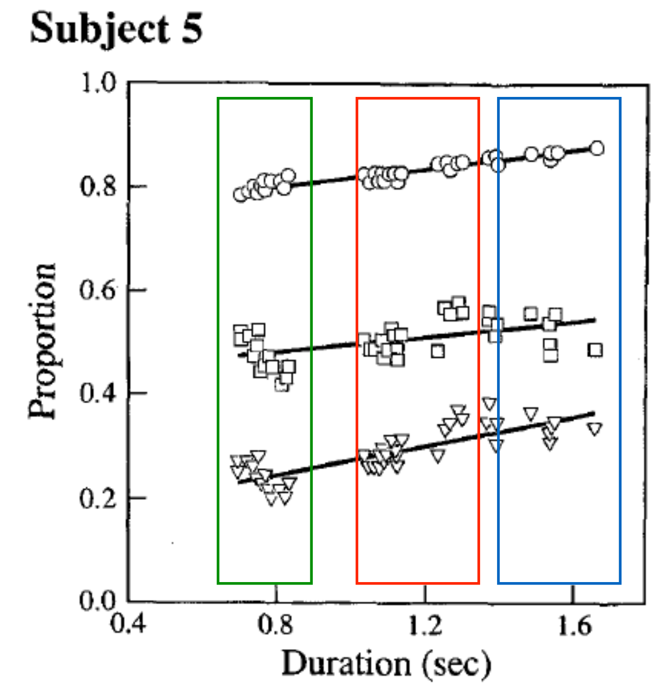
lower lip displacement during production of «buy Bobby a puppy» at different rates

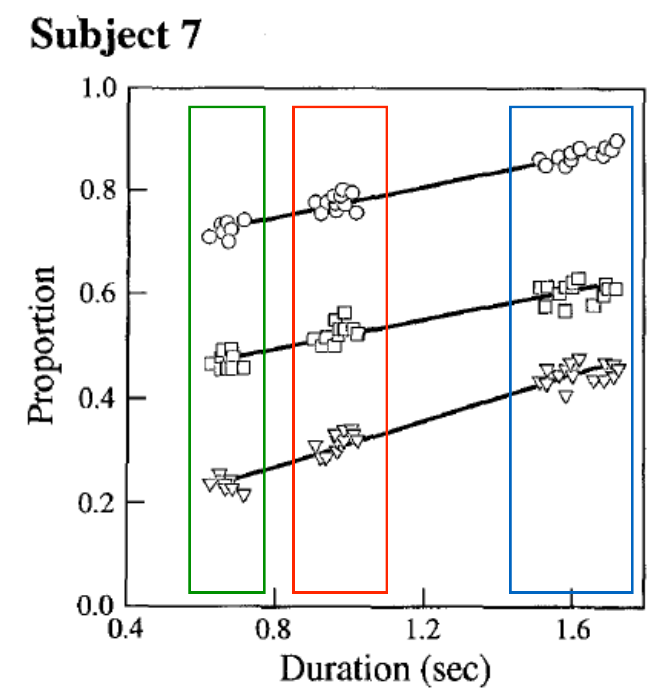
test of the *proportional duration* model

normal
fast
slow









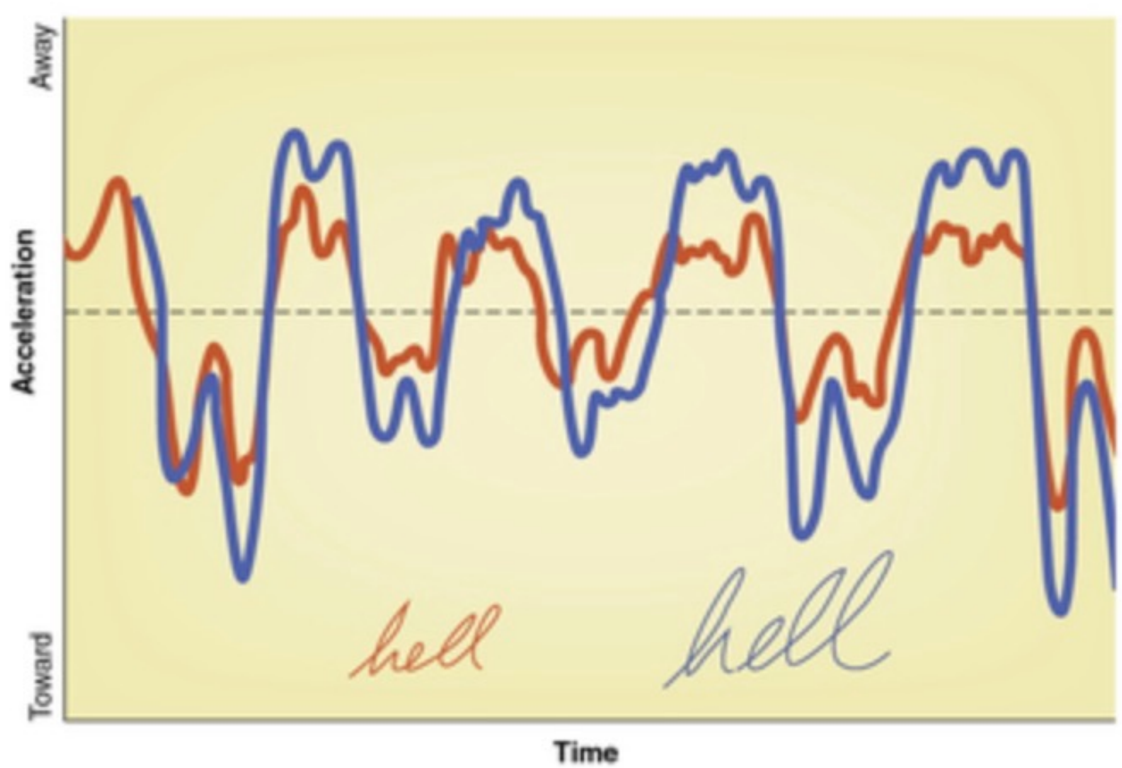
— Smith et al., 1995, *Exp Brain Res* 104:493

ISOCHRONY PRINCIPLE

Maintain constant duration

compensatory increase of speed with increasing amplitude

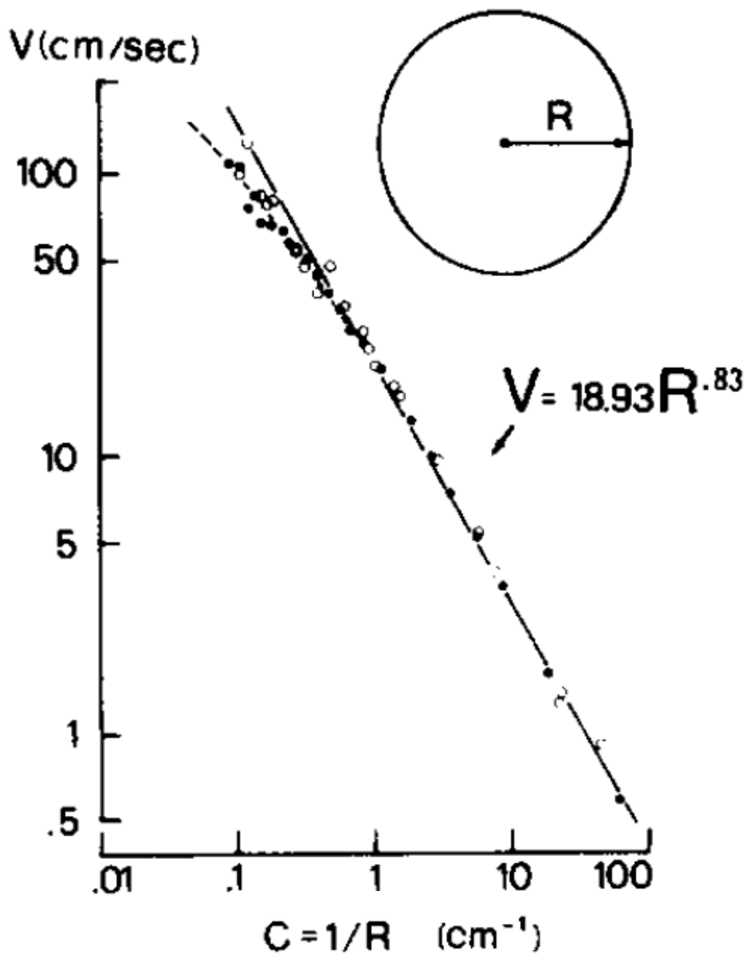
handwriting



— Hollerbach, 1978, *Doctoral Dissertation*, MIT

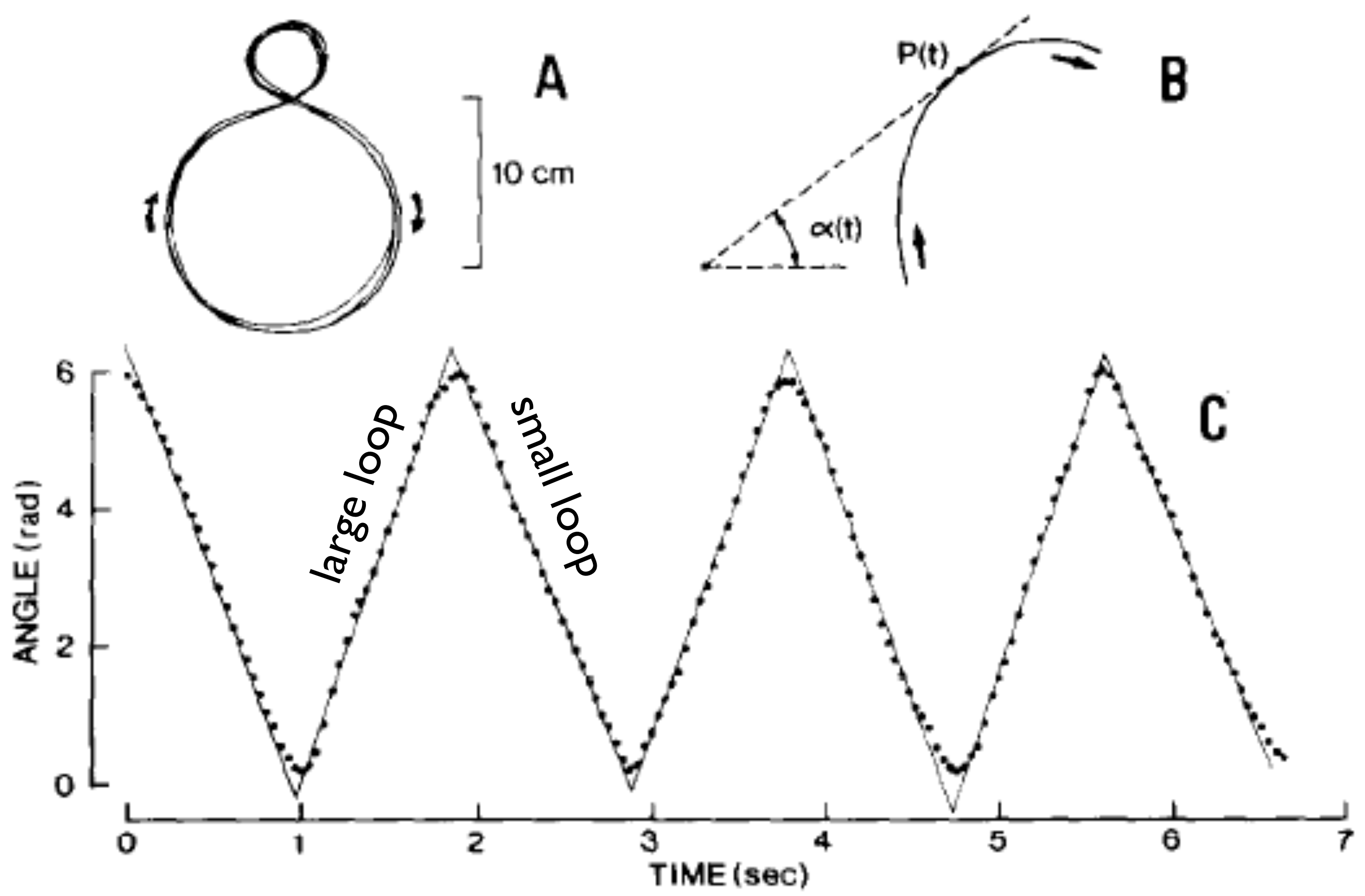
— Viviani & McCollum, 1983, *Neuroscience* 10:211

circle drawing



ISOGONY PRINCIPLE

Equal angles are described in equal time
in a drawing task



— Lacquaniti et al., 1983, *Acta Psychol* 54:115

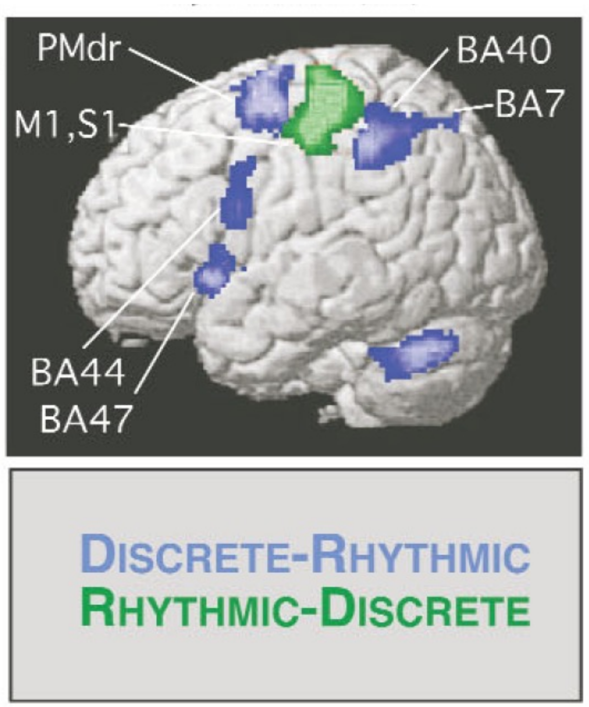
RHYTHMIC AND DISCRETE ACTIONS

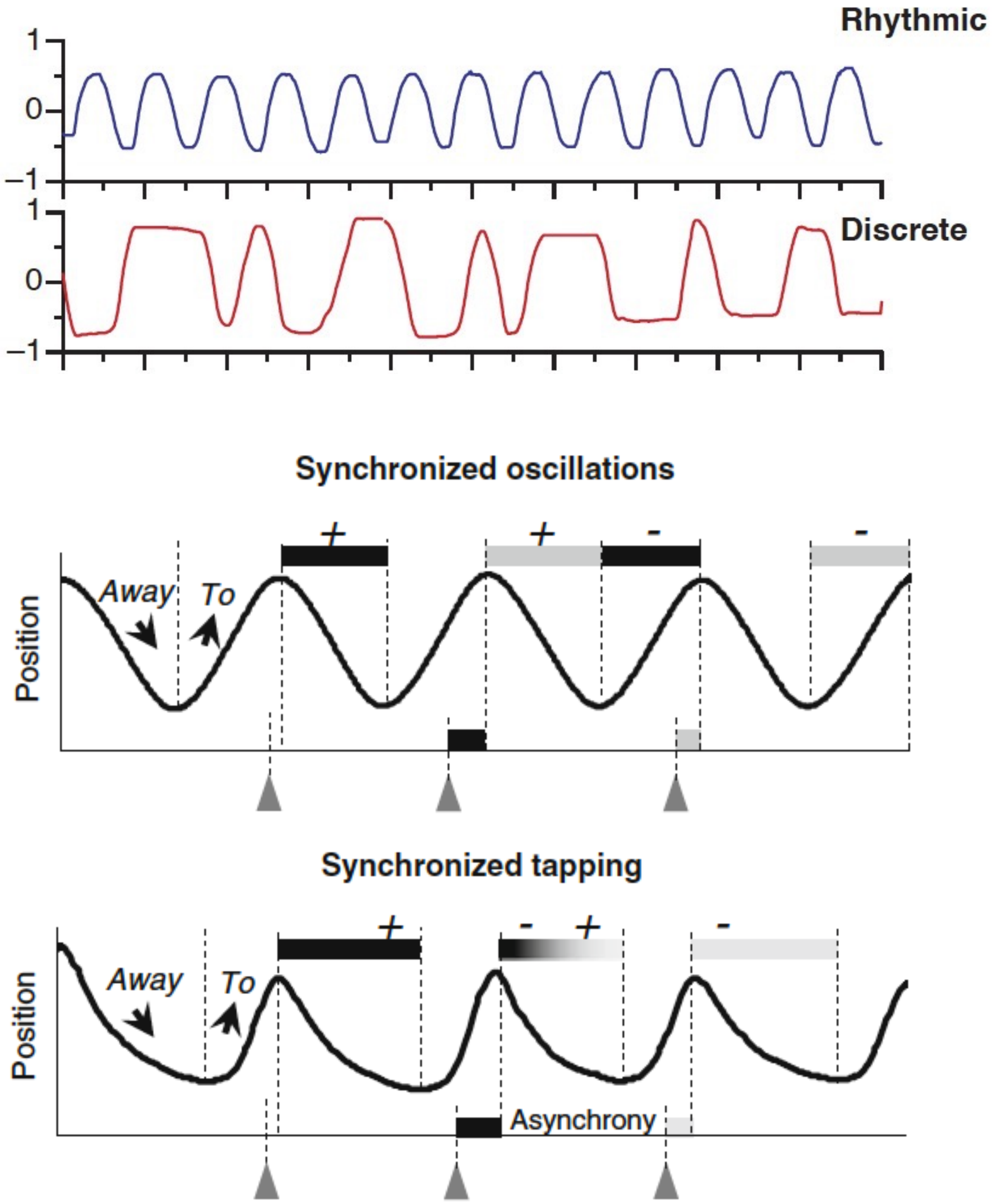
- **Rhythmic**

e.g. walking, chewing, scratching

- **Discrete**

e.g. reaching, grasping, kicking





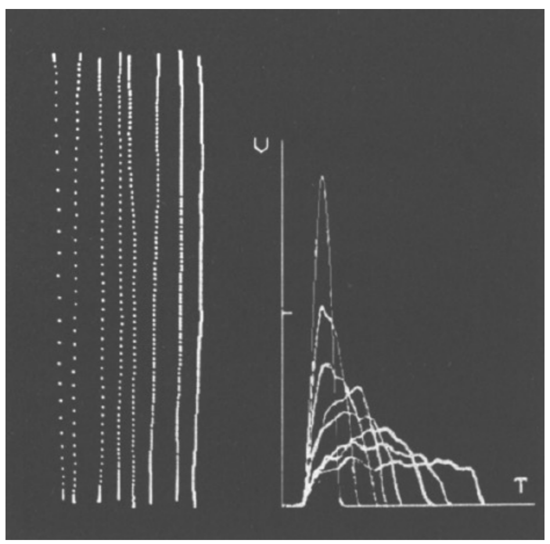
— Schaal et al., 2004, *Nat Neurosci* 7:1136

— Torre & Balasubramaniam, 2009, *Exp Brain Res* 199:157

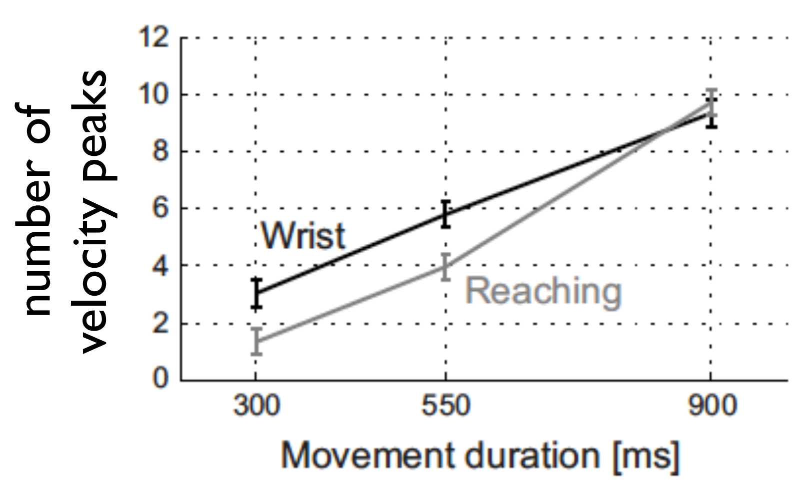
SLOW MOVEMENTS

Are not smooth

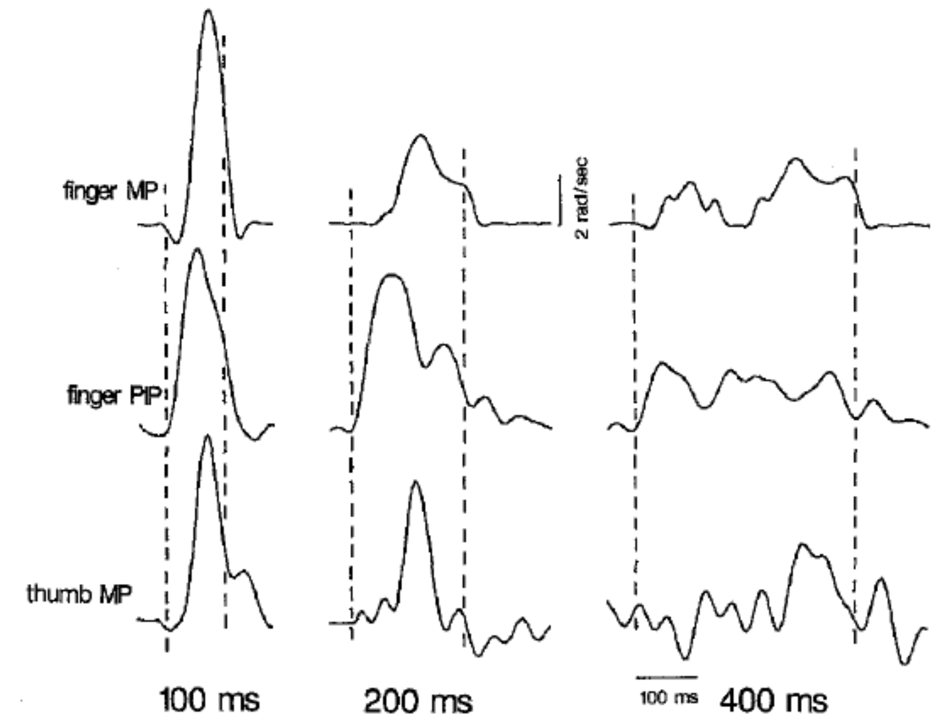
segmentation



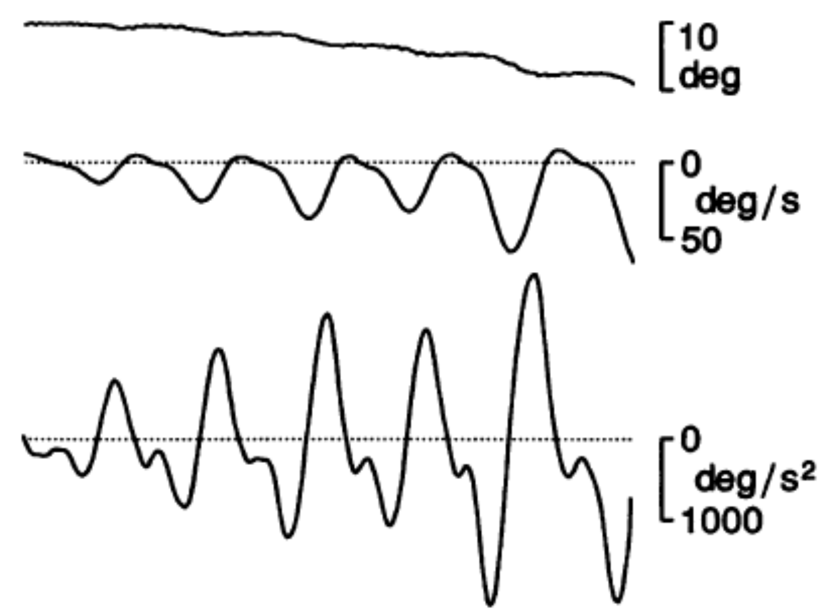
— Morasso et al., 1983, *Acta Psychol* 54:83



— Salmond et al., 2017, *J Neurophysiol* 117:1239



— Darling et al., 1988, *Exp Brain Res* 73:225

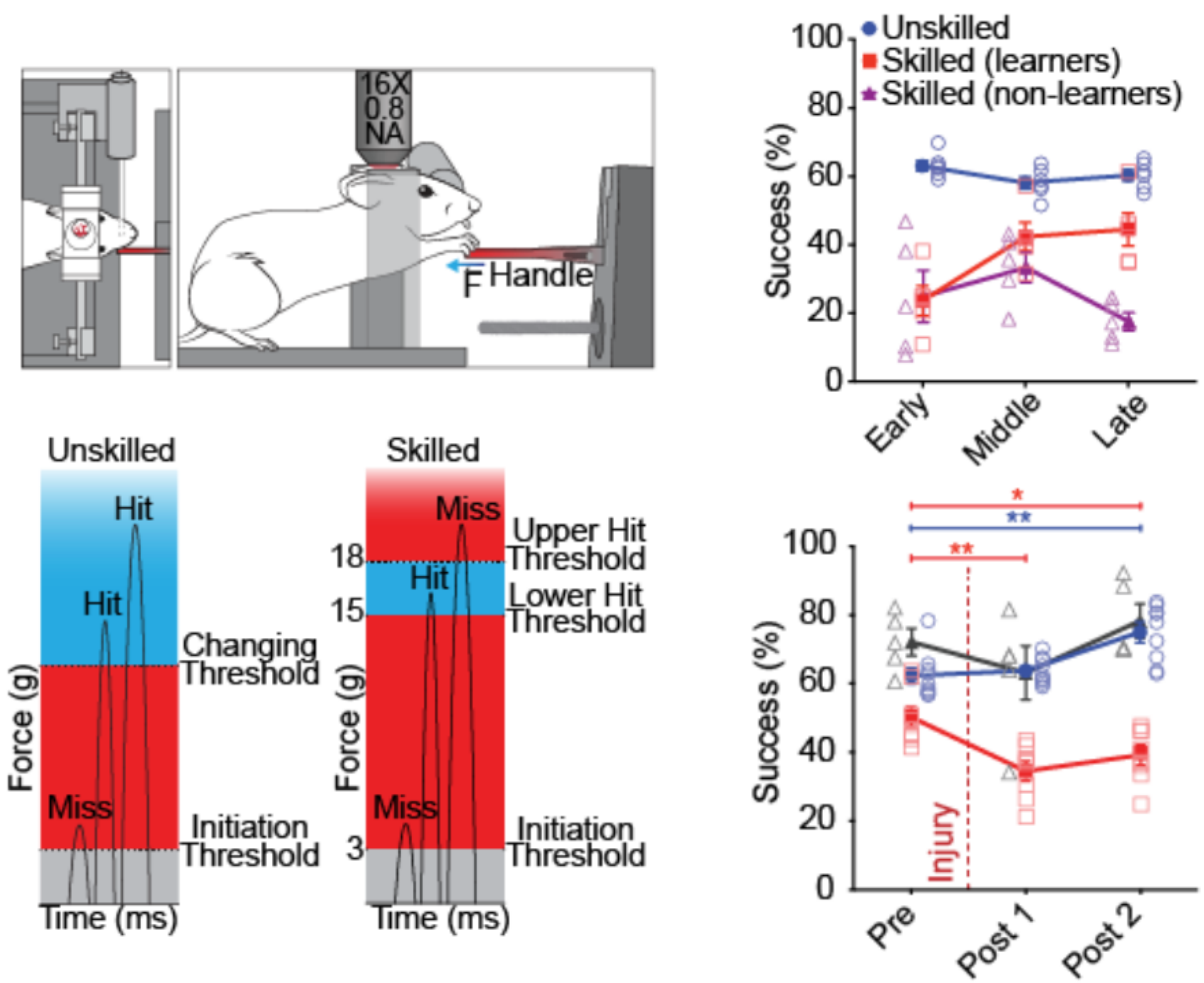


—Vallbo & Wessberg, 1993, *J Physiol (Lond)* 469:673

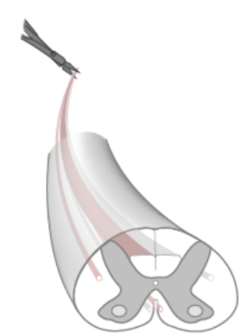
SKILLED/UNSKILLED ACTIONS

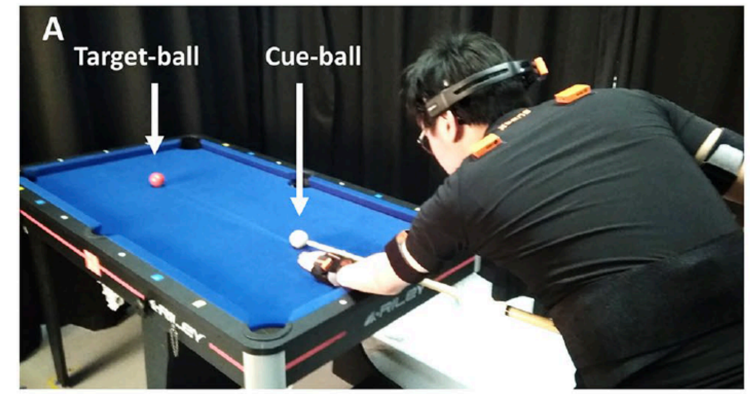
Training

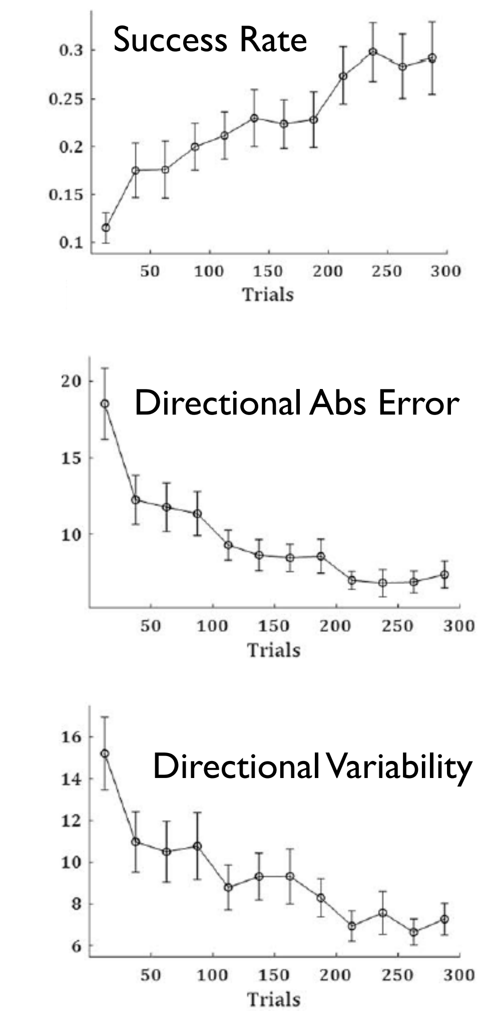
can decrease error/variability,
increase success/speed/accuracy
e.g. playing billiards (human)
e.g. lever pull (mouse)



pyramidotomy







— Serradj et al., 2021, *bioRxiv* 436415

— Haar et al., 2020, *Sci Rep* 10:20046

COMPUTATIONAL MOTOR CONTROL

COMPUTATIONAL MOTOR CONTROL

Descriptive (mechanistic) vs normative models

- Descriptive statements present an account of how the world is

↓

Action characteristics result from properties of synapses, neurons, neural networks, muscles, …

- Normative statements present an evaluative account, or an account of how the world should be

↓

Action characteristics result from principles, overarching goals, …

Problems: planning, control, estimation, learning

THEORETICAL BASES

Dynamical systems theory

Describes the behavior in space and time of complex, coupled systems.

$x[n]$ *state* $y[n]$ *output (observation)*

$u[n]$ *input (control)*

$x[n+1] = f(x[n], u[n])$ *state equation*

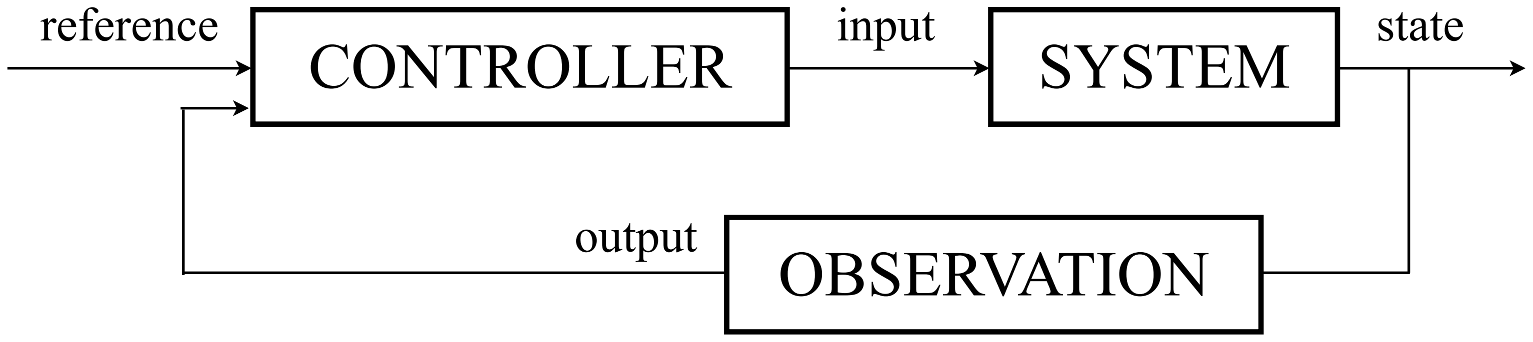
$y[n] = g(x[n])$ *output equation*

$y[n+1] = h(x[n], u[n])$

state: *« the smallest possible subset of system variables that can represent the entire state of the system at any given time »*

Control theory

Deals with the behavior of dynamical systems with inputs, and how their behavior is modified by feedback.



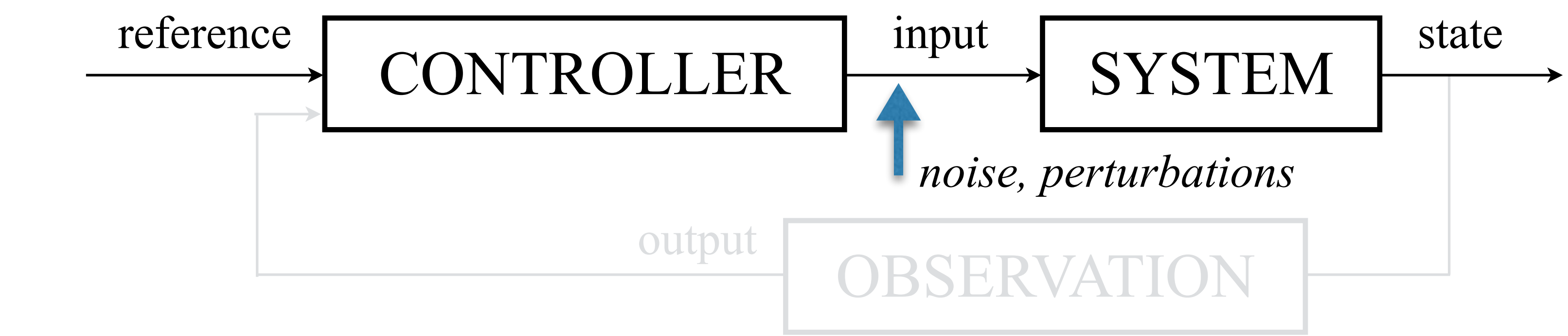
reference

- desired trajectory
- fixed point

TWO CONTROL PRINCIPLES

Open-loop (feedforward)

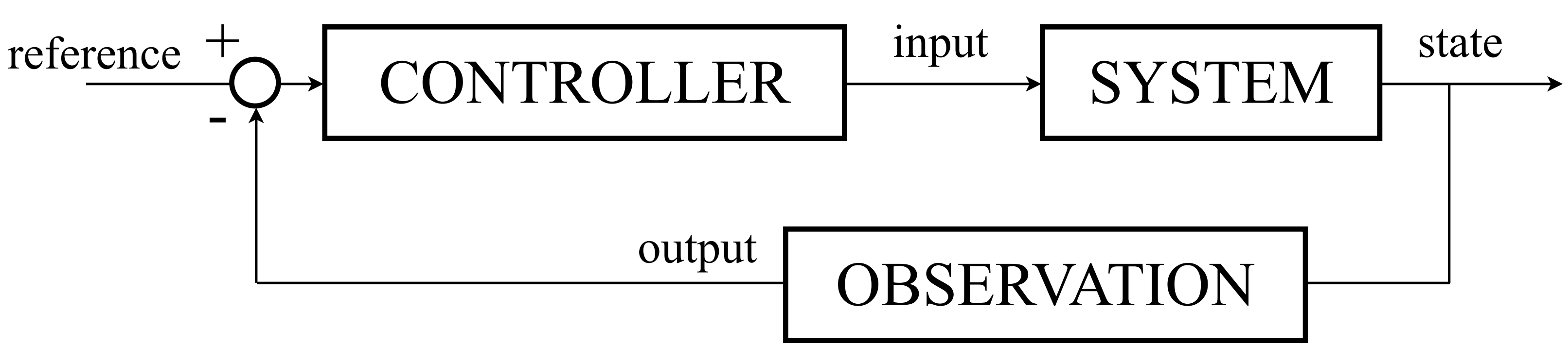
The controller is an ***inverse*** model of the system.



- Predictive control
- Model-based
- Sensitive to modeling uncertainty
- Sensitive to unexpected, unmodeled perturbations

Closed-loop (feedback)

The controller is a function of an error signal.

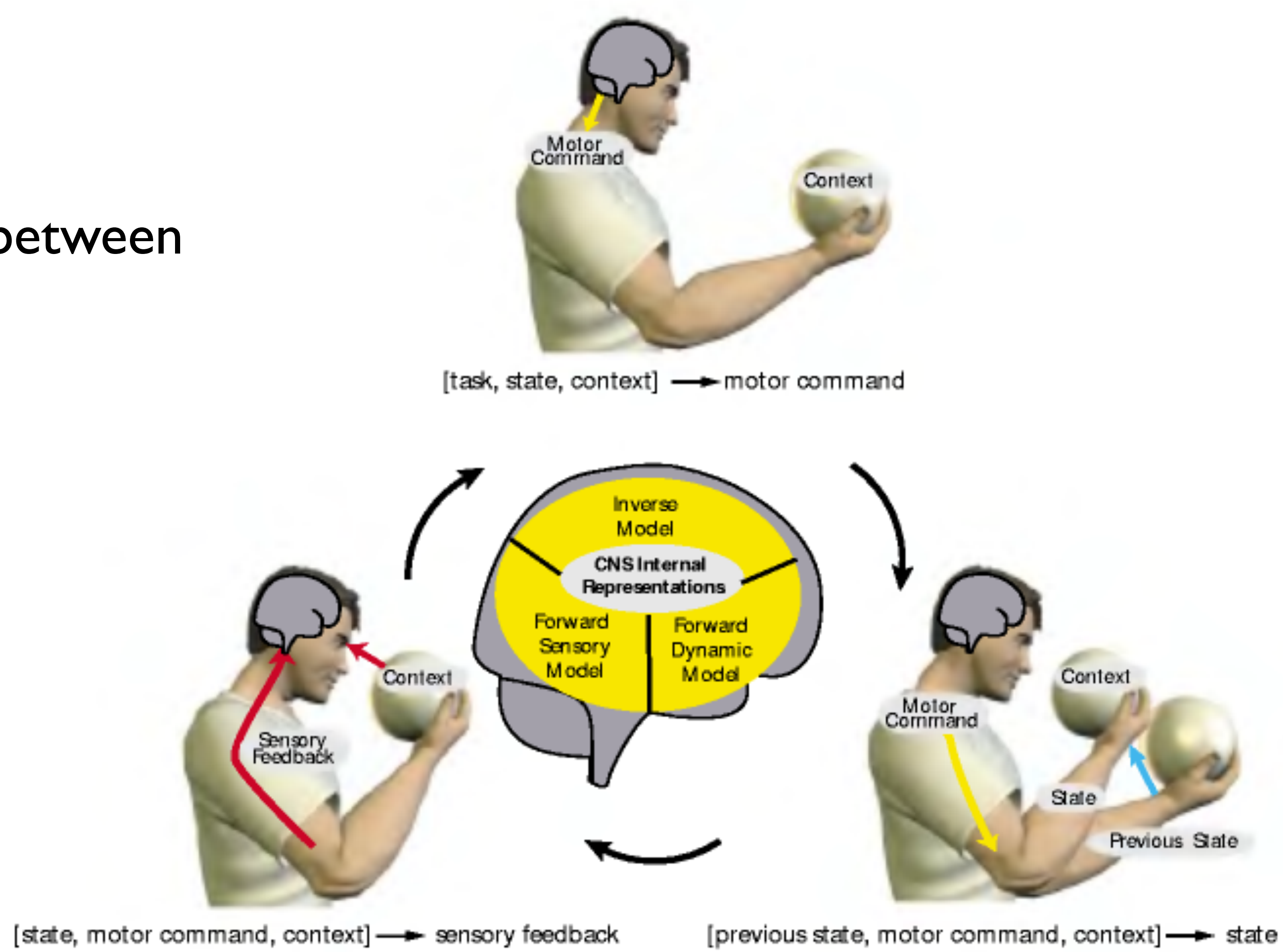


- Error correction
- No model
- Not sensitive to modeling uncertainty
- Robust to perturbations

INTERNAL MODELS

Direct (forward) model
Model of the causal relationship between inputs and their consequences (states, outputs).

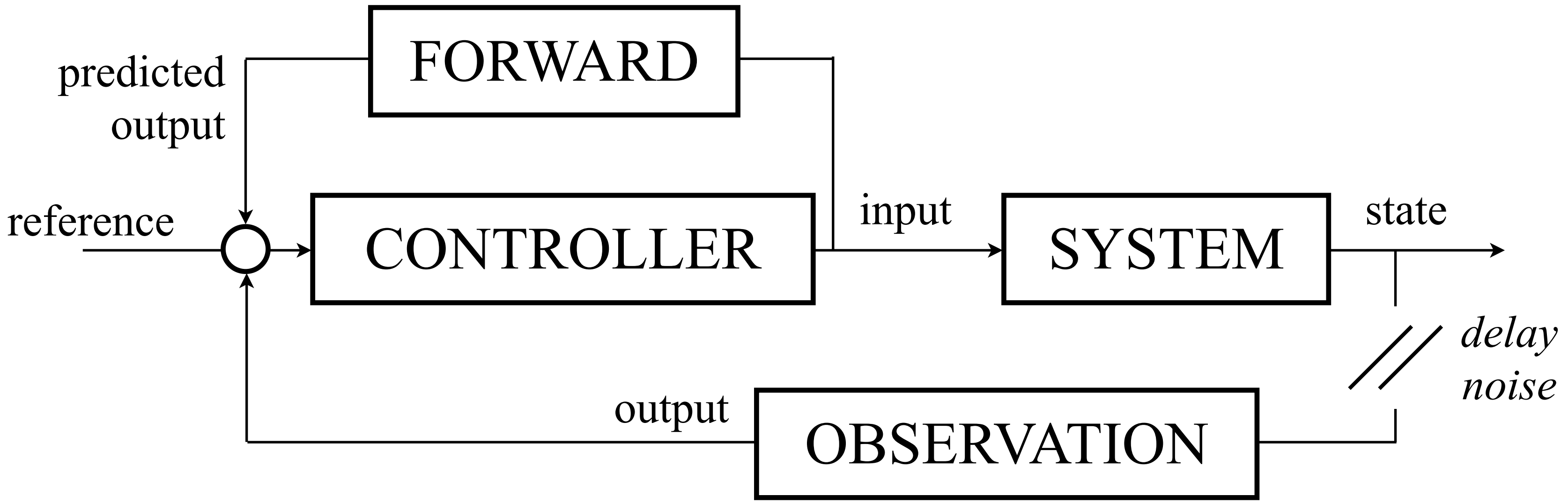
Inverse model
Model of the relationship between desired consequences and corresponding inputs.
! *Ill-defined model*



—Wolpert & Ghahramani, 2000, *Nat Neurosci* 3:1212

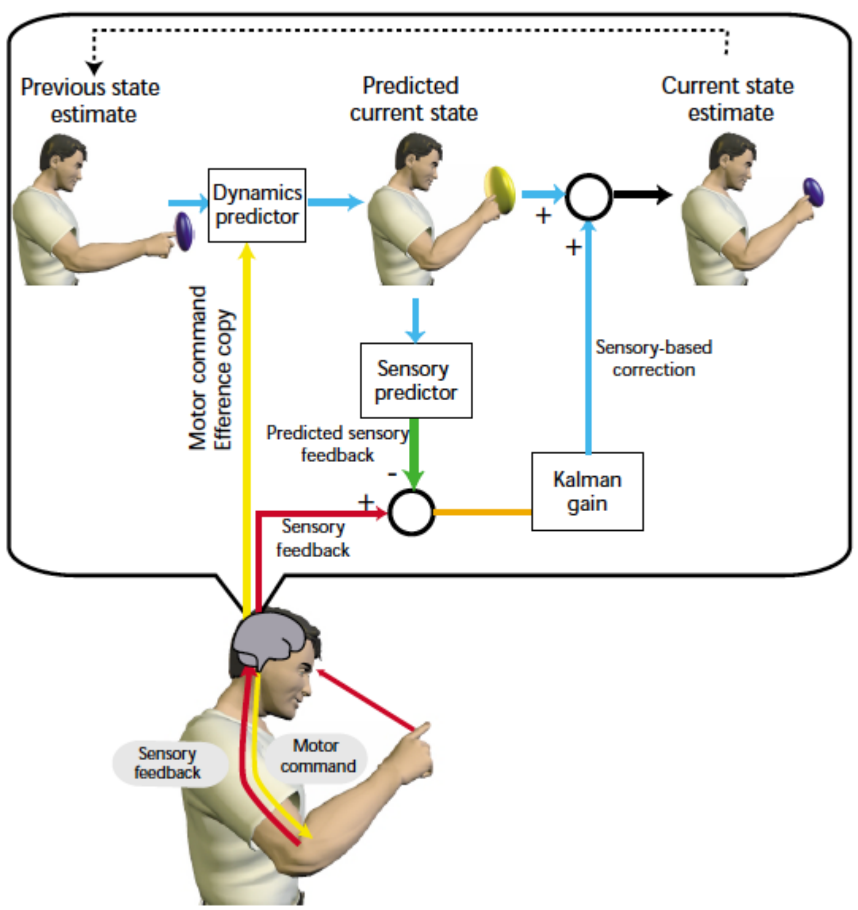
ROLE OF FORWARD MODELS

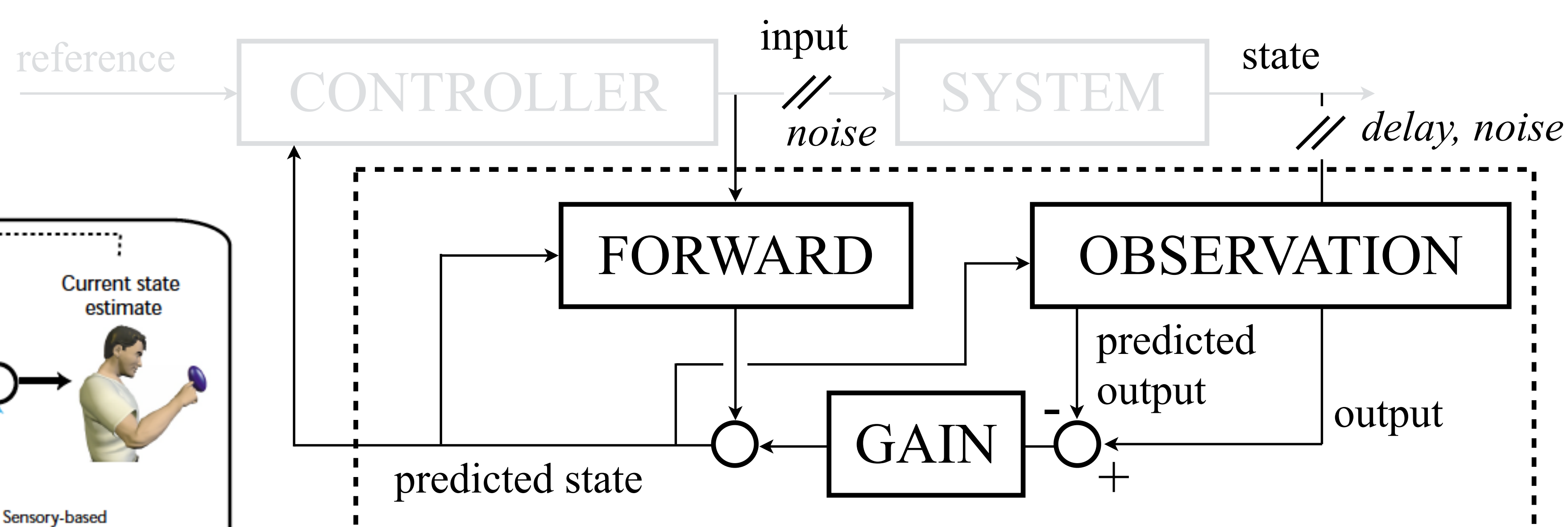
A system can use a direct model rather than an external feedfback to evaluate the effect of command and its associated error.
Avoid the instability due to delays in feedback loops.



THE KALMAN FILTER

Combines a forward model and a state observation to obtain the best state prediction in the presence of delays and noise





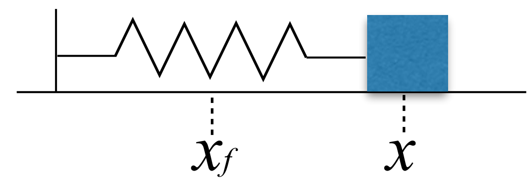
—Wolpert & Ghahramani, 2000, *Nat Neurosci* 3:1212

TWO MAIN THEORIES

Task-dynamics approach

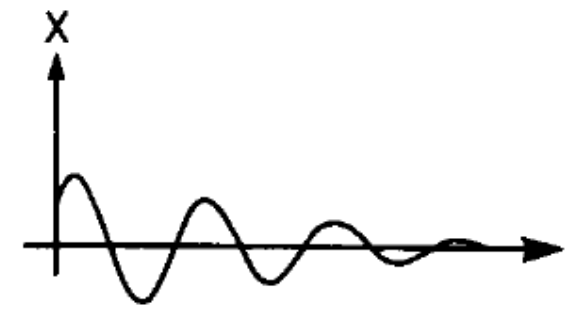
Generalized closed-loop systems. Movements result from convergence to attractors of a dynamical system.

Action systems approach
Dynamical systems
Ecological psychology



$$m\ddot{x}+b\dot{x}+k(x-x_f)=0$$

$$x=x(t,m,b,k)$$

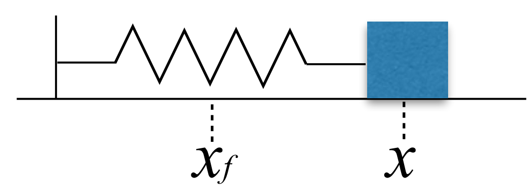


— Saltzman & Kelso, 1987, *Psychol Rev* 94:84

Internal model approach

Builds an inverse model of the system to follow a prescribed trajectory or match some constraints (e.g. optimization).

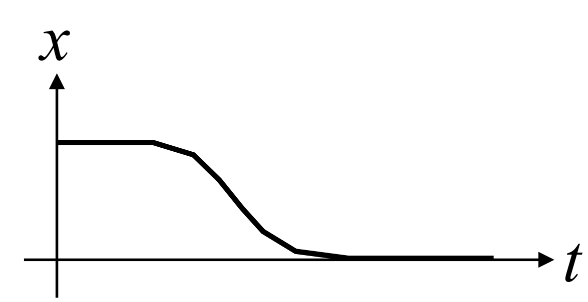
Information processing approach
Cognitive approach
Motor programs



$$m\ddot{x}+b\dot{x}+k(x-x_f)=u$$

$$u=u(t,m,b,k)$$

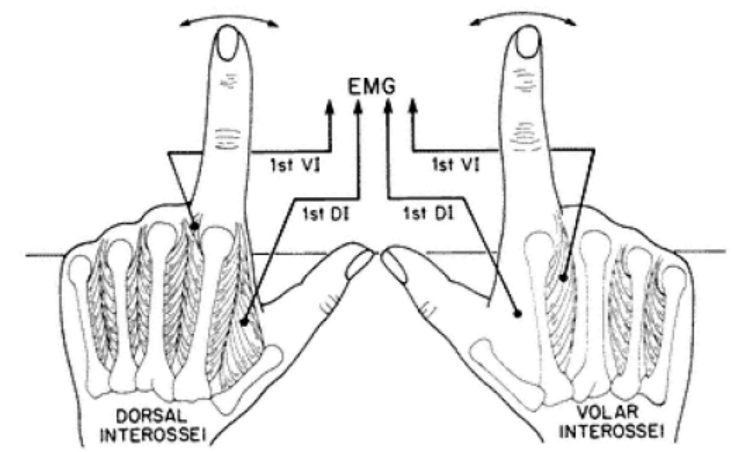
$$x=x(t,u)$$

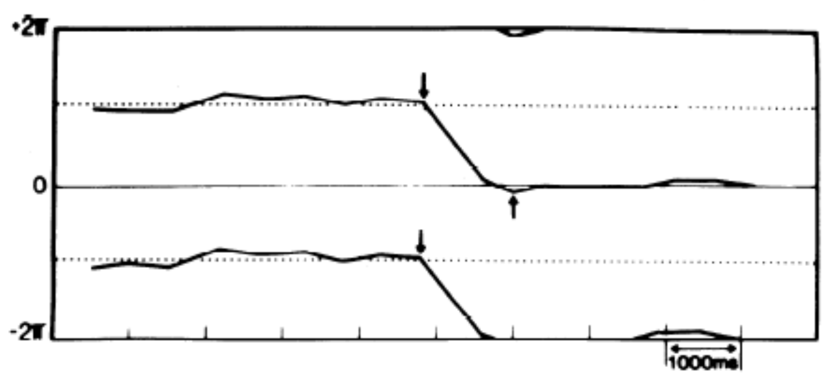


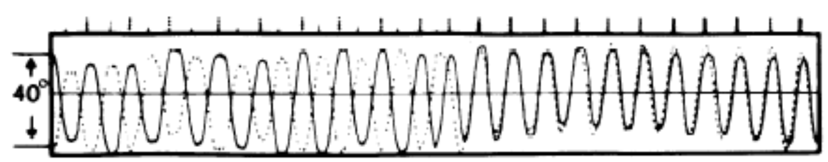
TASK DYNAMICS

Bimanual coordination

— start in opposition phase
— increasing frequency (1-5 Hz)



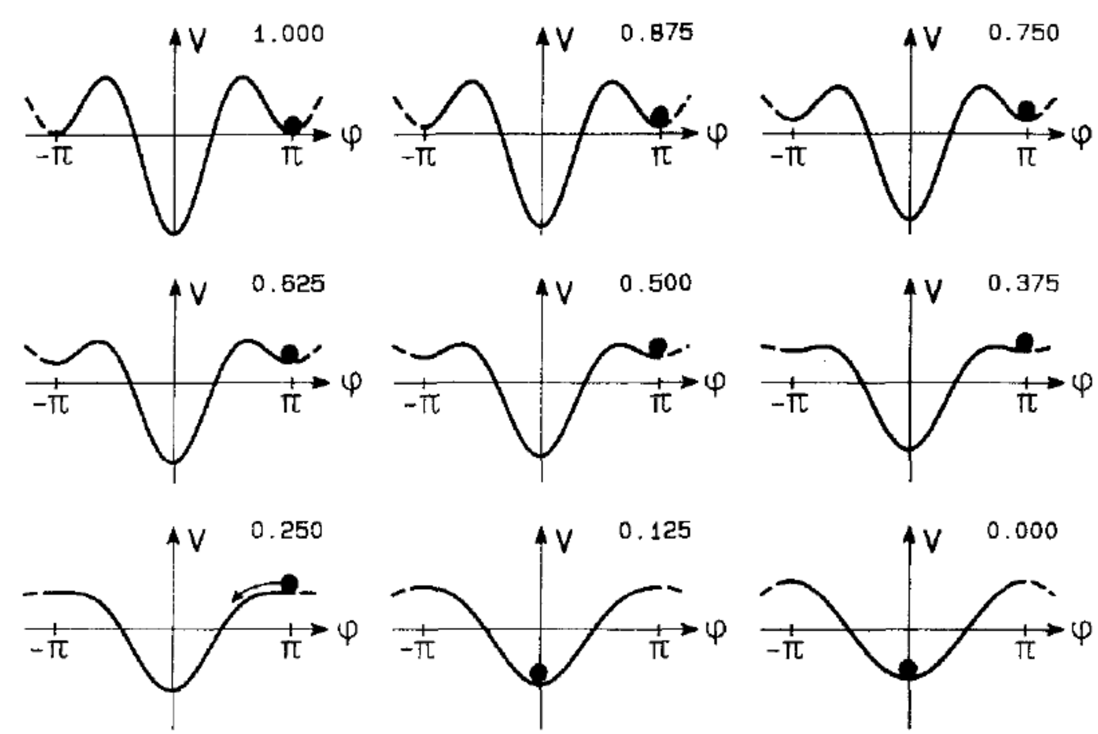




$$\dot{\phi} = -\frac{dV}{dt}$$

$$V = -a\cos\phi - b\cos 2\phi$$

phenomenological model



— Haken et al., 1985, *Biol Cybern* 51:347

OPTIMALITY PRINCIPLE*

The interaction between the behavior and the environment leads a better adaptation of the former to the latter. The tendency could lead to an optimal behavior, i.e. the best behavior corresponding to a goal, according to a given criterion.

The idea is to describe a movement not in terms of its characteristics (kinematics, dynamics), but in an abstract way, using a global value to be maximized or minimized.

E.g. smoothness, energy, variability, …

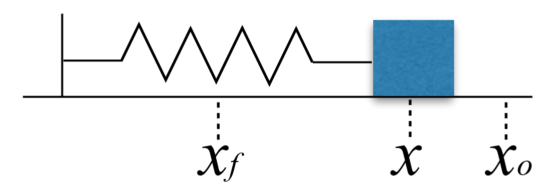
***Debated issue (e.g. — Schoemaker, 1991, *Behav Brain Sci* 14:205)**

OPTIMAL MOTOR CONTROL

Extension of the internal model approach

control theory → optimal control theory

Define an « *objective* function »: minimization/maximization of task and action related quantities (*cost*, *utility*)

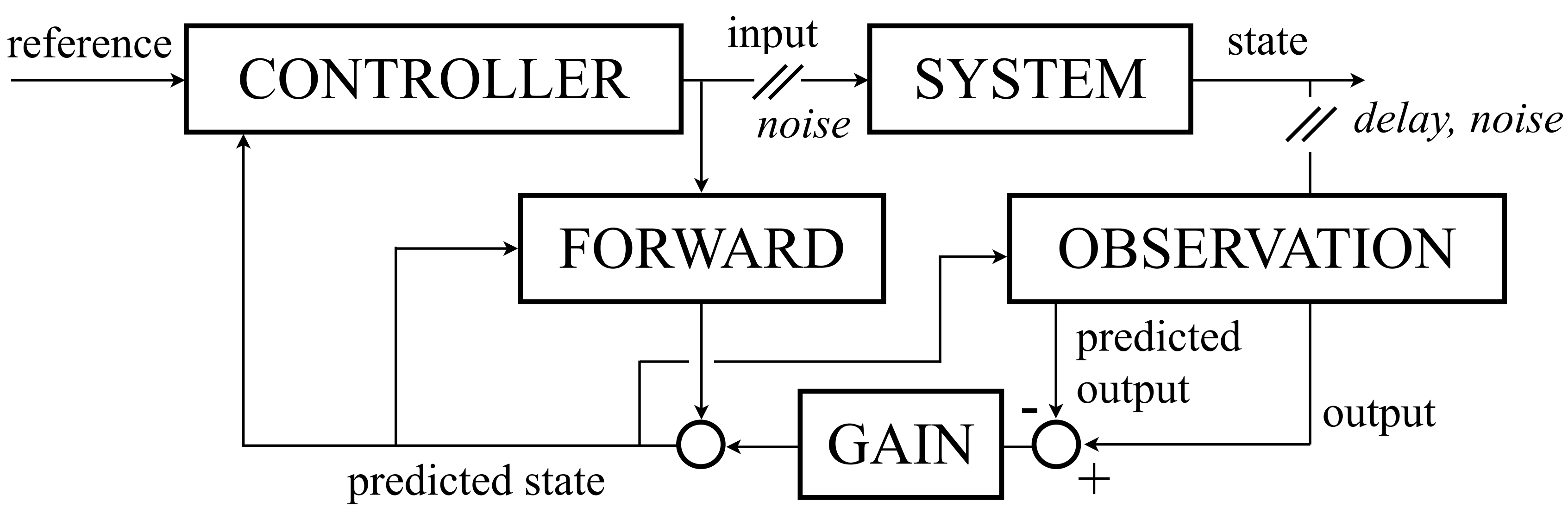


Find the smallest $u(t)$ (t in $[t_o;t_f]$) such that

$$x(t_o) = x_o,\ x(t_f) = x_f$$

and

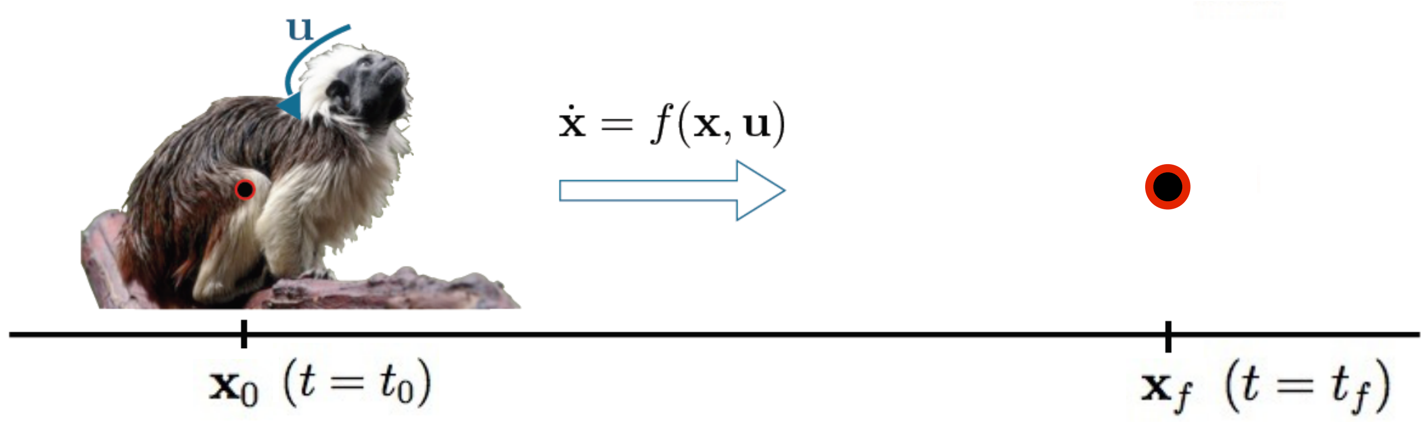
$$m\ddot{x}+b\dot{x}+k(x-x_f)=u$$



—Todorov, 2004, *Nat Neurosci* 7:907

FROM MOVEMENT TO ACTION

Movement

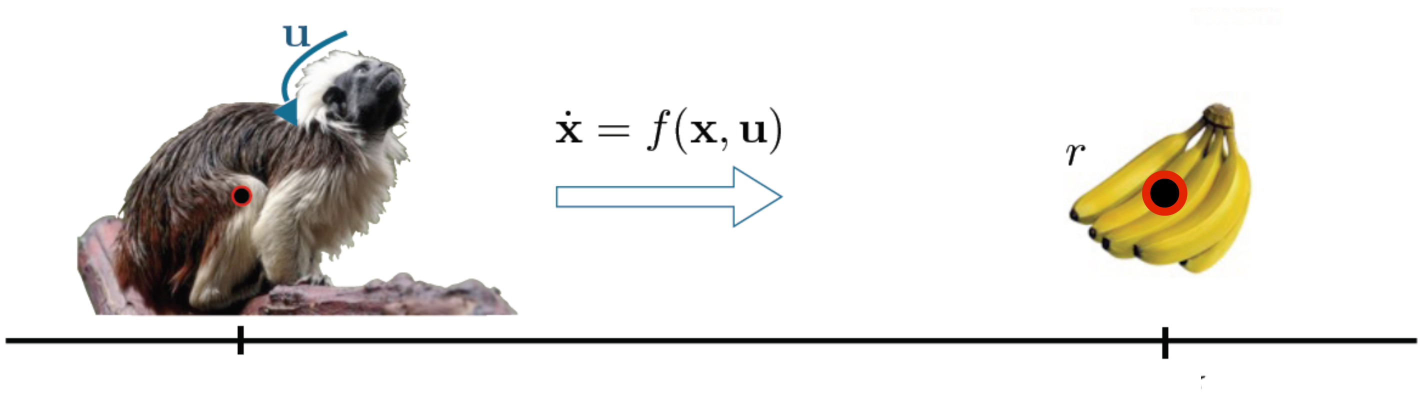


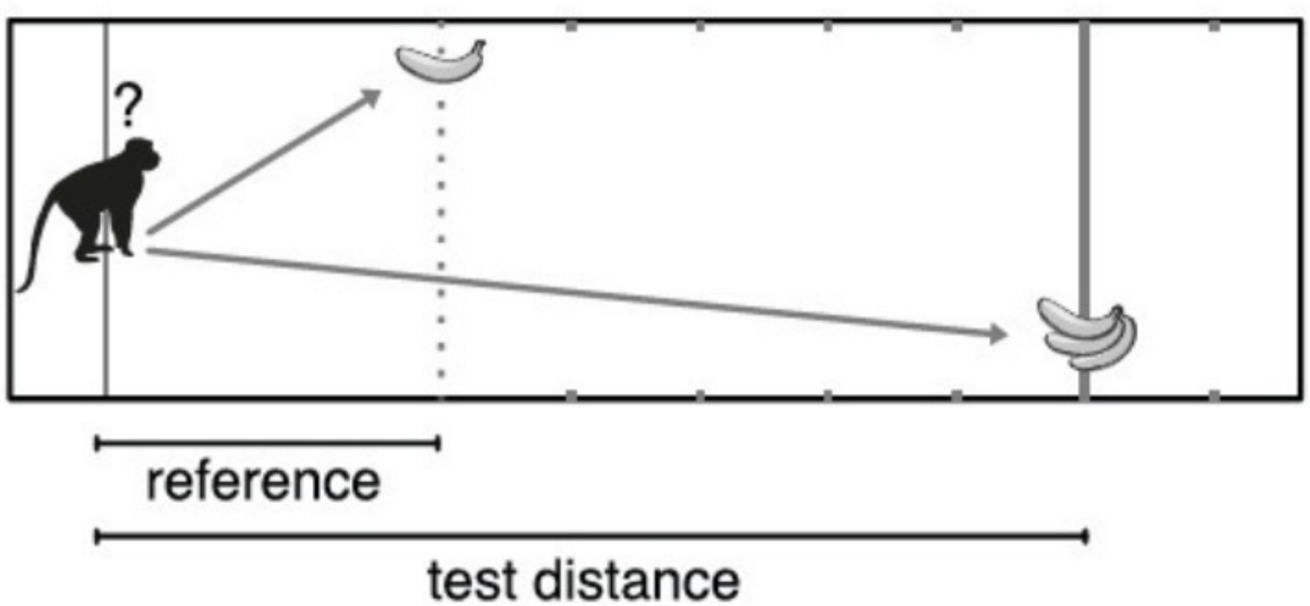
$$J^* = \min_{\mathbf{u}} \int_{t_0}^{t_f} ||\mathbf{u}(t)||^2 \ dt$$

Minimizing costs, fixed time

FROM MOVEMENT TO ACTION

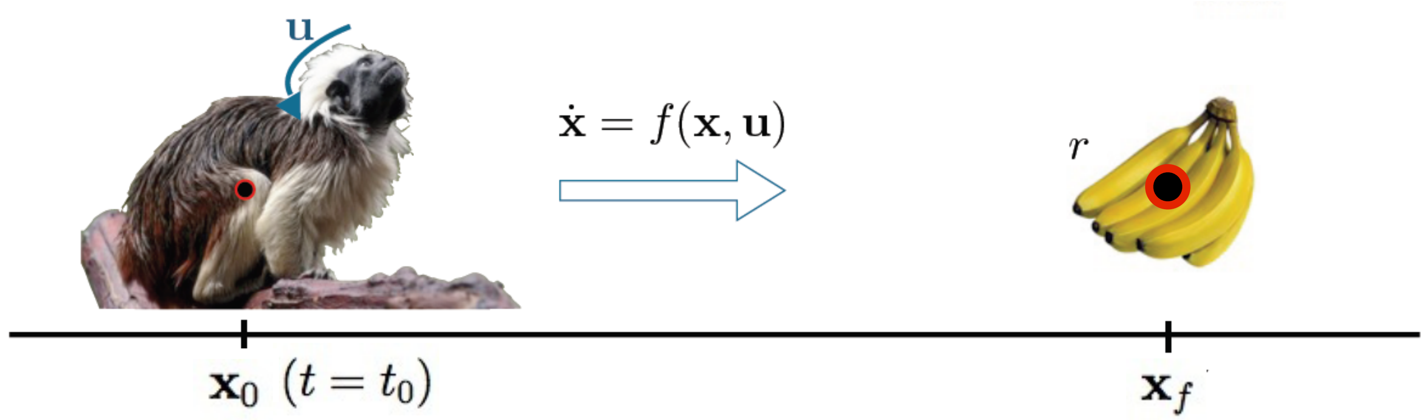
Action



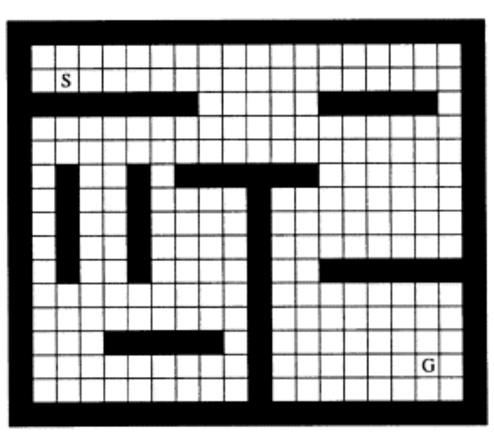


FROM MOVEMENT TO ACTION

Reinforcement learning



$$V(\mathbf{x}_t) = E[r_t + \gamma r_{t+1} + \gamma^2 r_{t+2} + \ldots | \mathbf{x}_t]$$

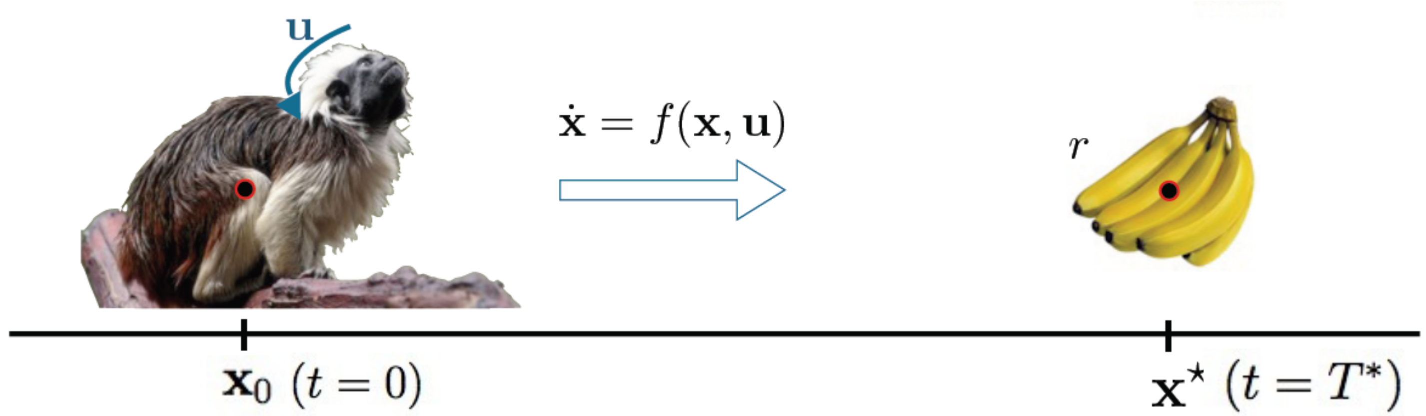


Maximizing benefits, open time

— Sutton & Barto, 1998, *Reinforcement Learning*, MIT Press

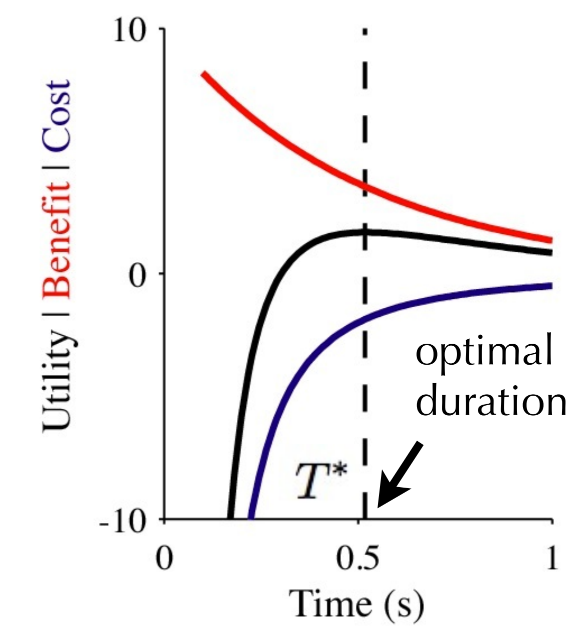
FROM MOVEMENT TO ACTION

Reward/effort trade-off



$\mathbf{x}$	state
$\mathbf{u}$	control
r	reward
γ	discount factor
ρ	benefit scaling
ε	cost scaling
$\mathbf{x}^*$	target state

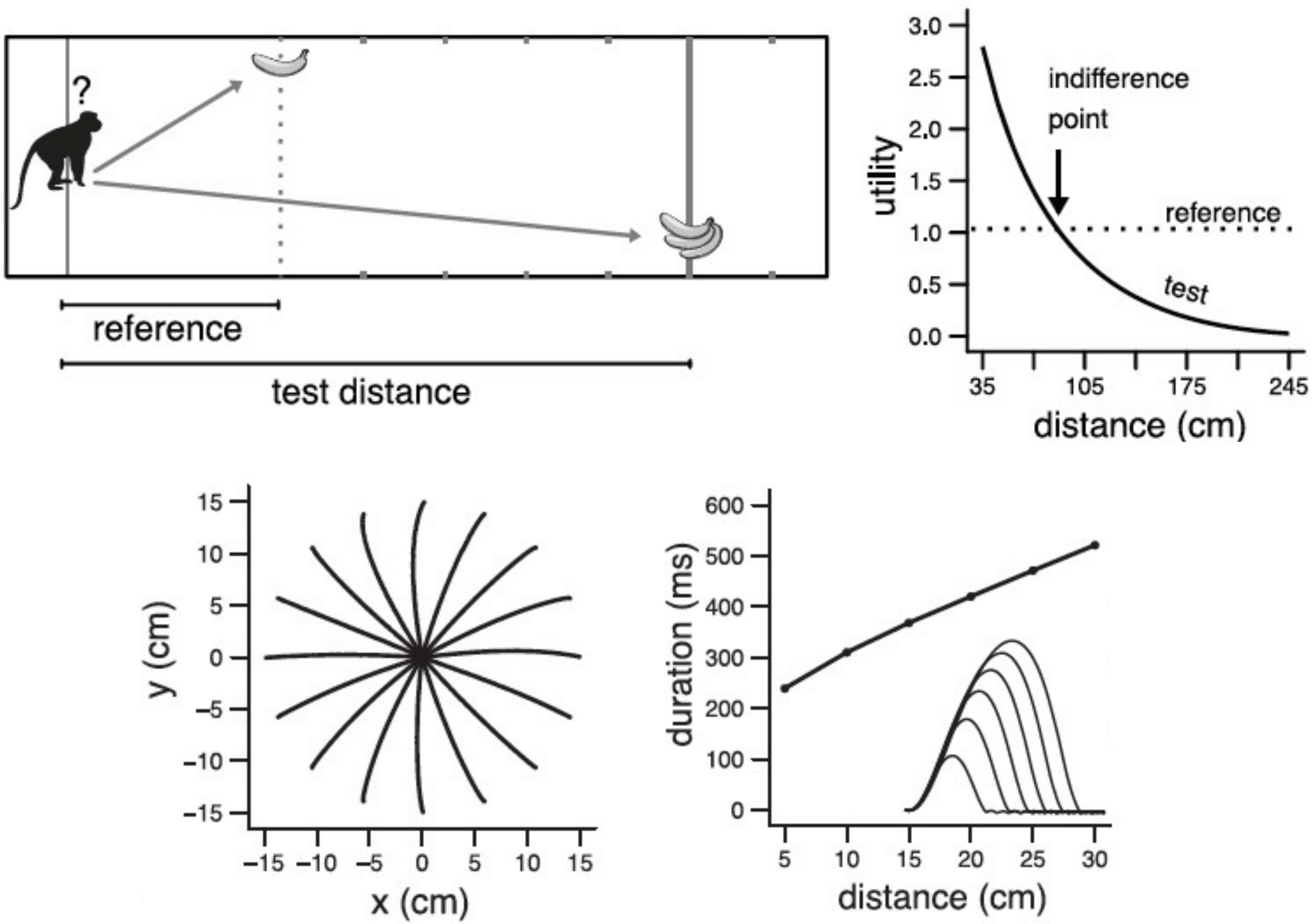
$$J^* = \max_{\mathbf{u}} \int_0^\infty e^{-t/\gamma} \left[\rho r \delta(||\mathbf{x}^* - \mathbf{x}(t)||) - \varepsilon \, ||\mathbf{u}(t)||^2 \right] \, dt$$



— Rigoux & Guigon, 2012, *PLoS Comput Biol* 8:e1002716

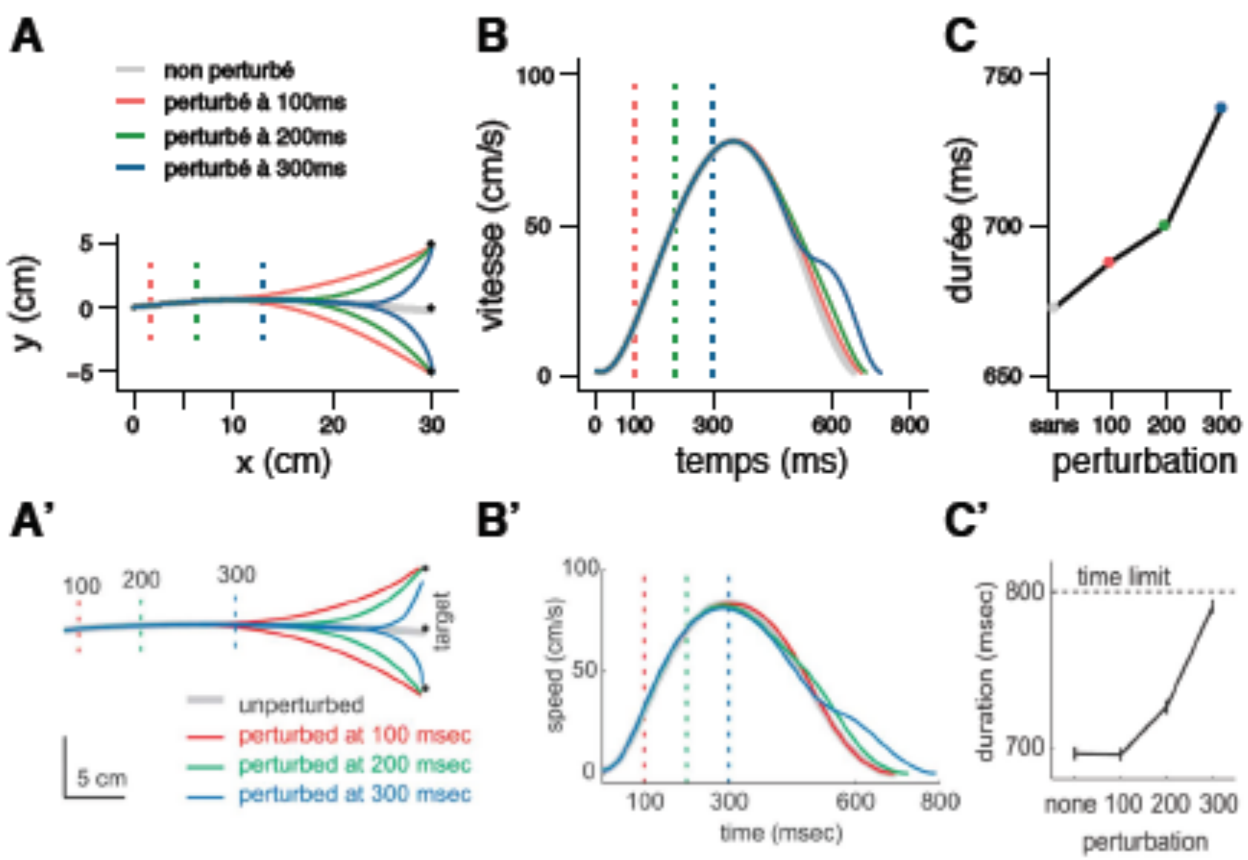
FROM MOVEMENT TO ACTION

Reward/effort trade-off

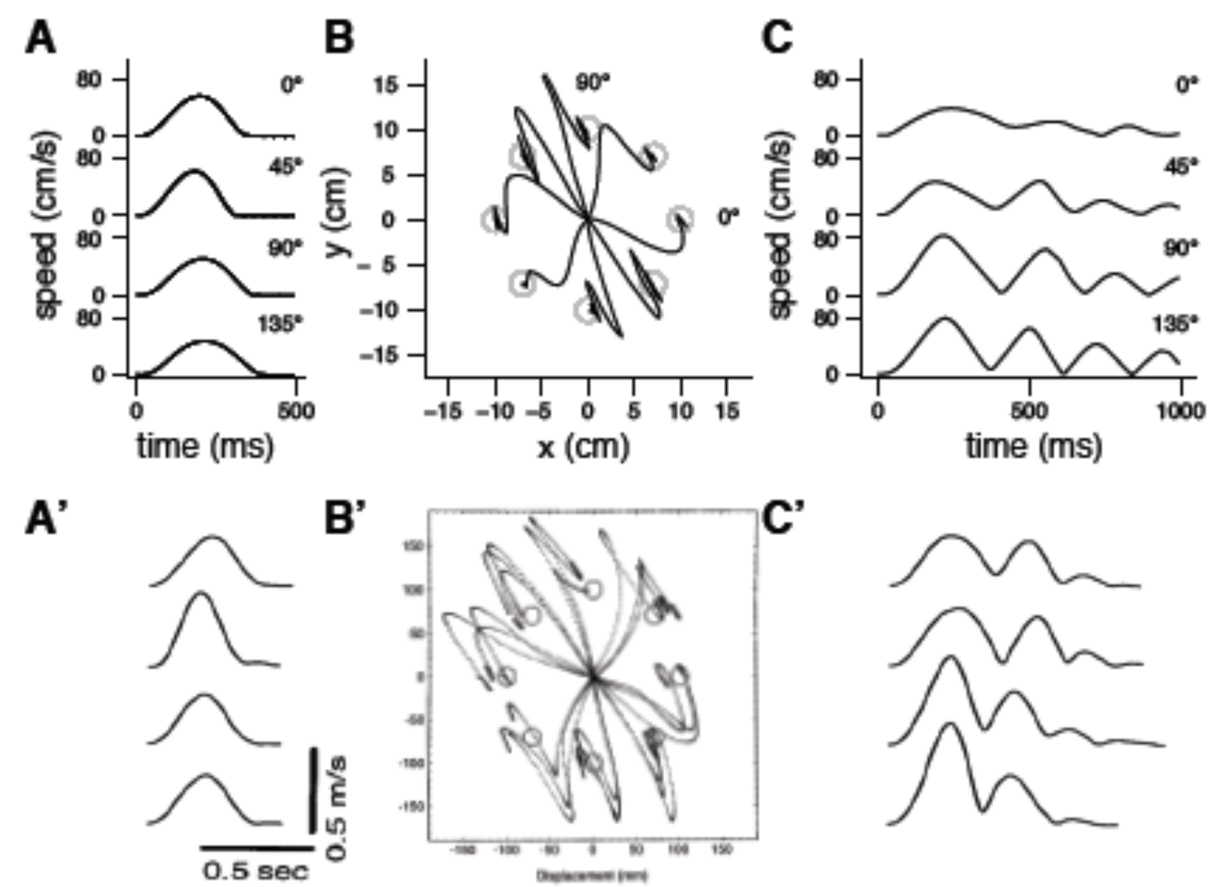


FROM MOVEMENT TO ACTION

Reward/effort trade-off



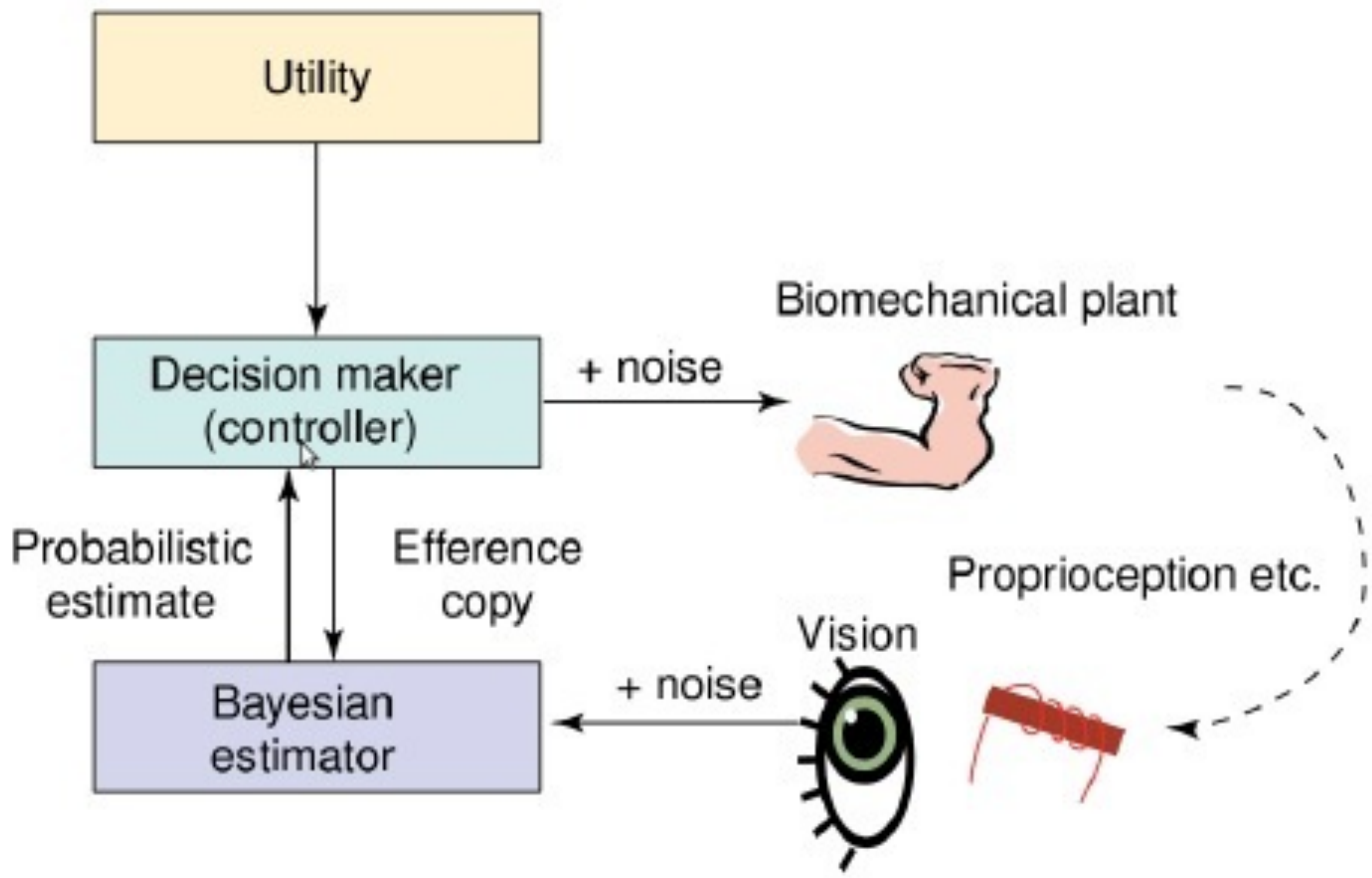
— Liu & Todorov, 2007, *J Neurosci* 27:9354



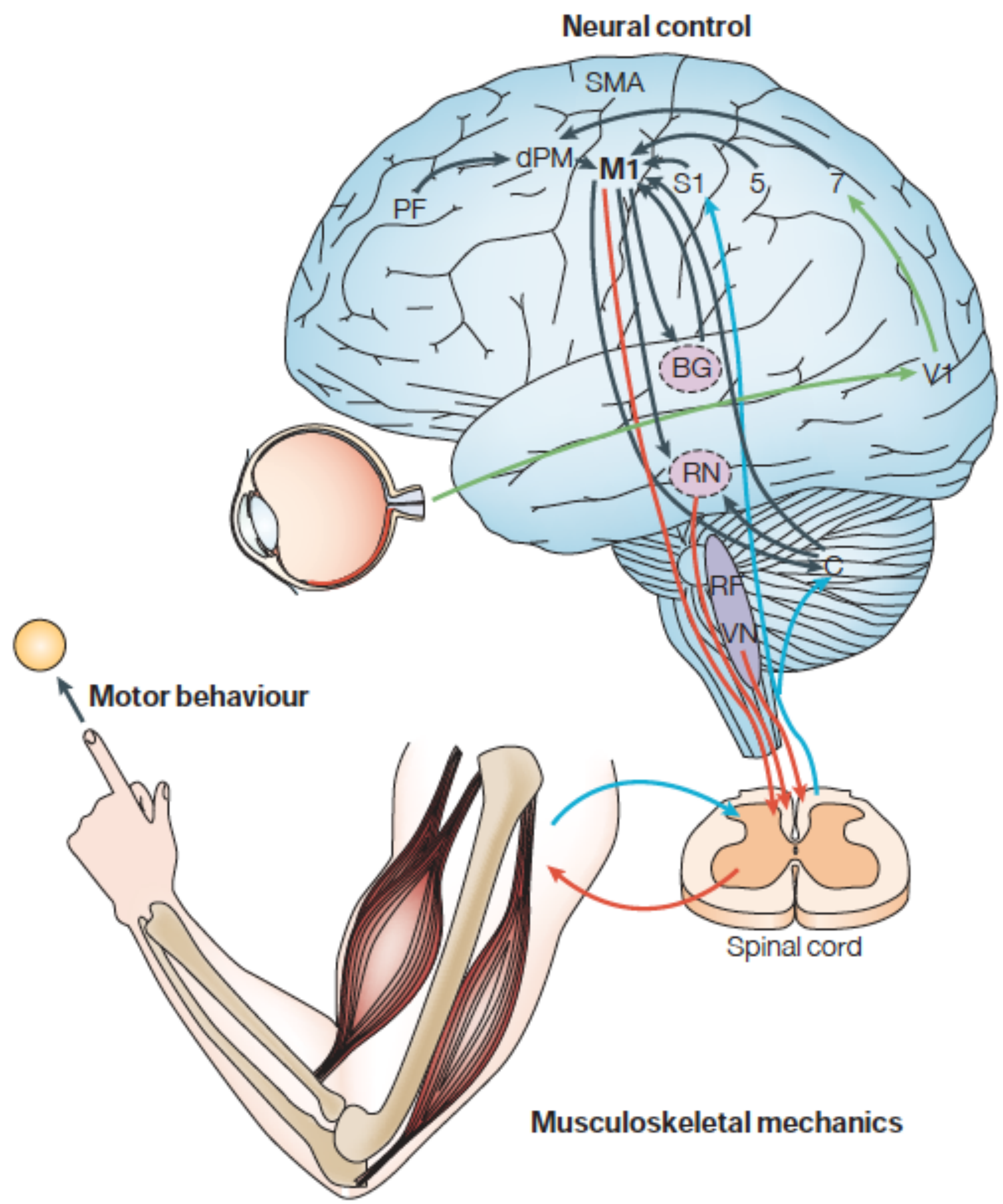
— Shadmehr & Mussa-Ivaldi, 1994, *J Neurosci* 14:3208

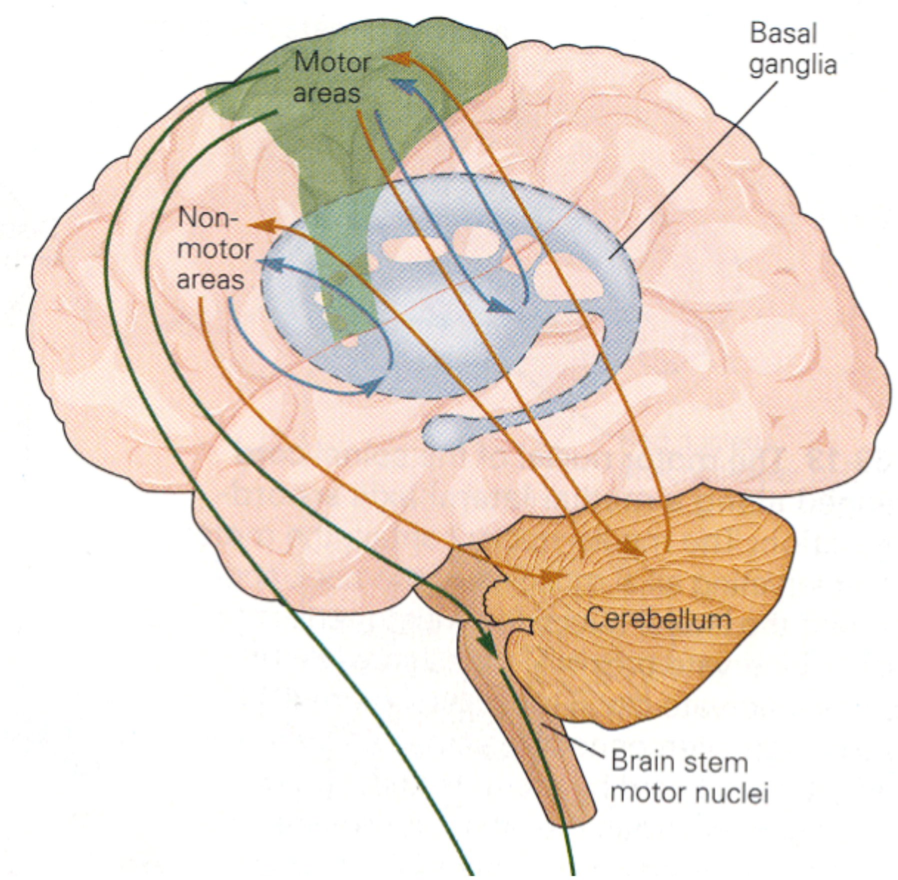
EXTENSION

Bayesian inference



ANATOMICAL ARCHITECTURE

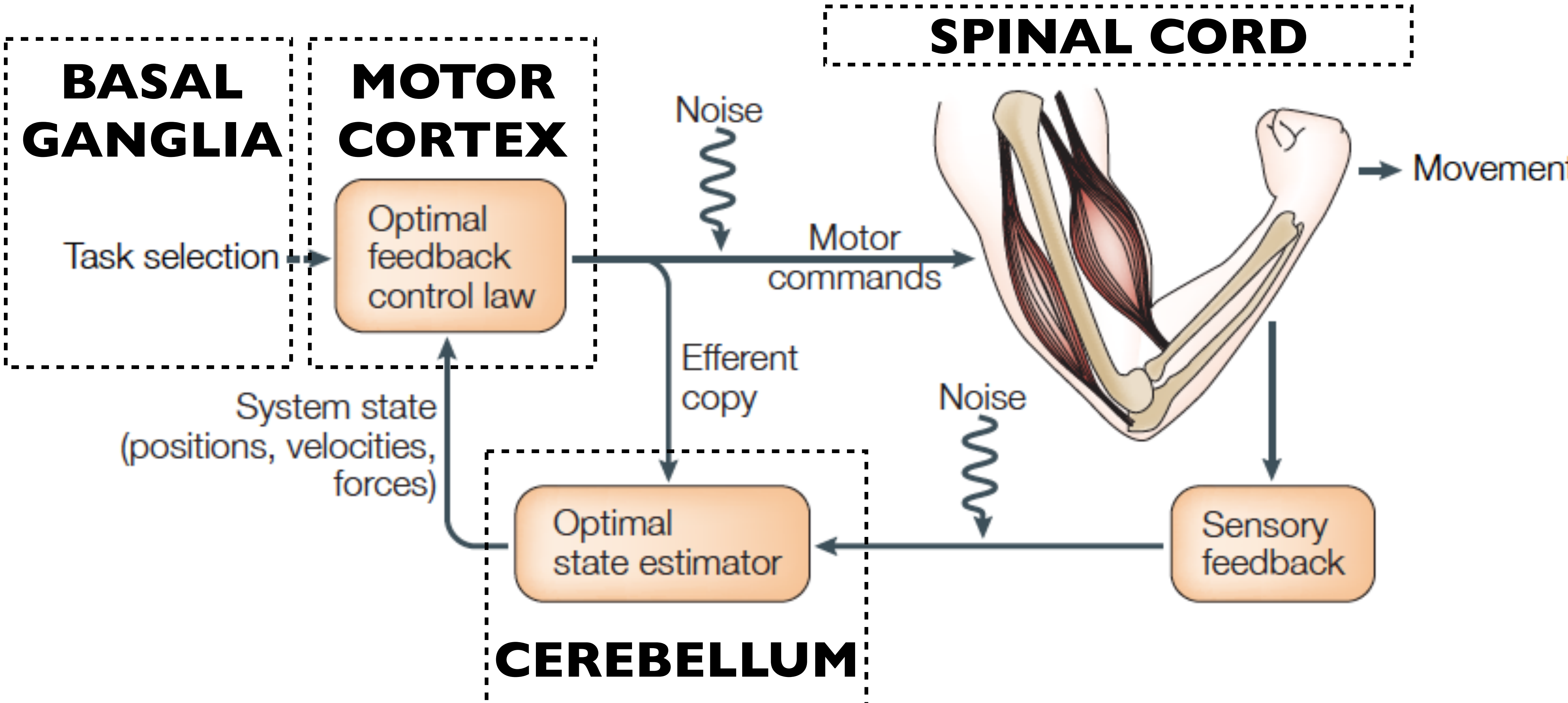




— Scott, 2004, *Nat Rev Neurosci* 5:534

COMPUTATIONAL NEUROANATOMY

COMPUTATIONAL NEUROANATOMY



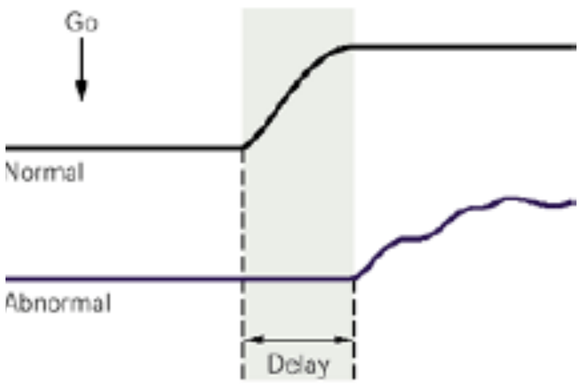
— Scott, 2004, *Nat Rev Neurosci* 5:534

— Guigon et al., 2007, *Eur J Neurosci* 26:250

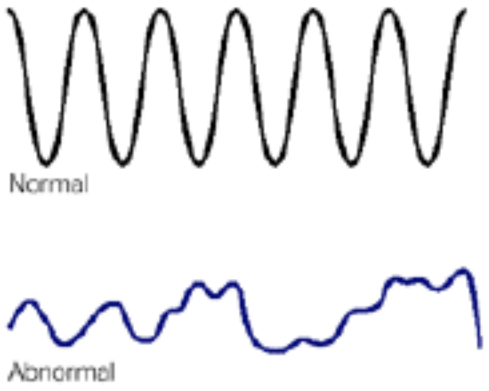
— Shadmehr & Krakauer, 2008, *Exp Brain Res* 185:359

CEREBELLAR DEFICITS

Ataxia



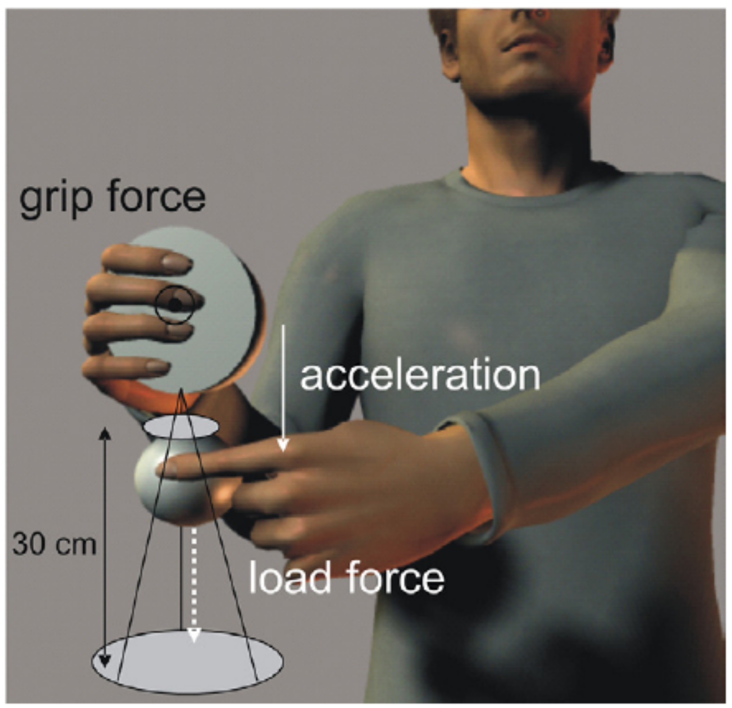
dysmetria



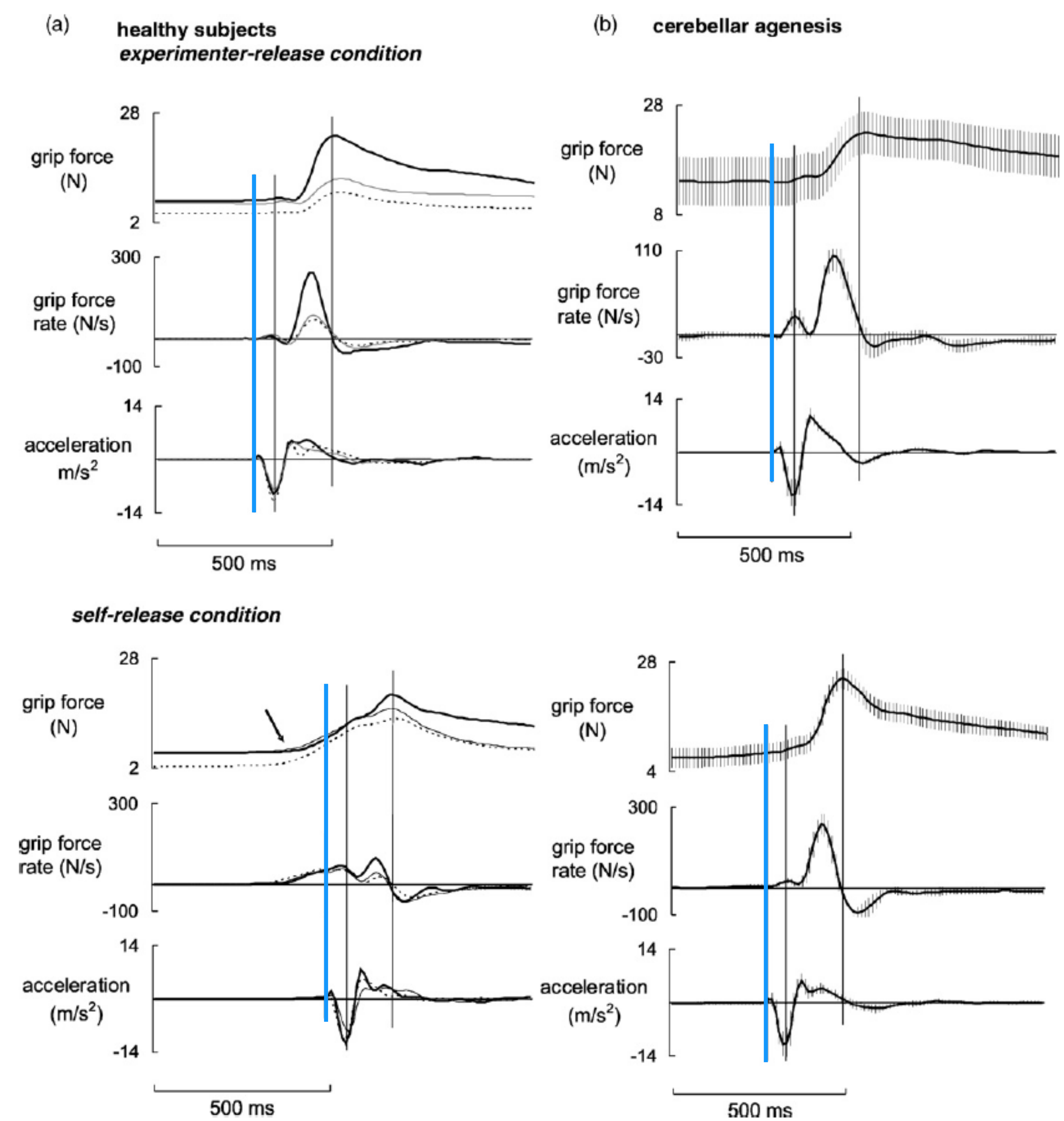
dysdiadochokinesia

CEREBELLAR DEFICIT

Deficit in predictive grip force control

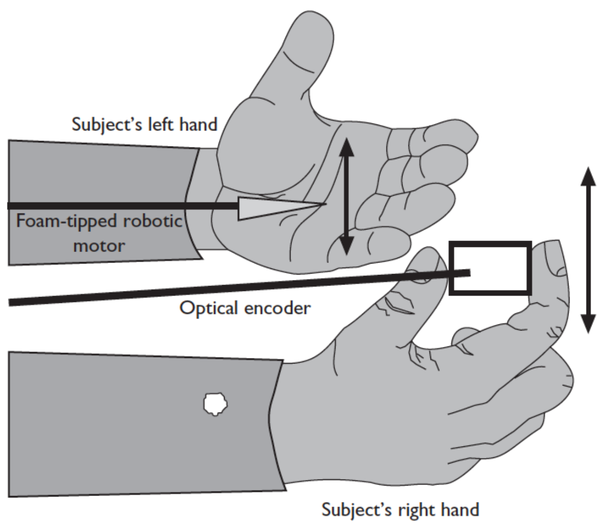


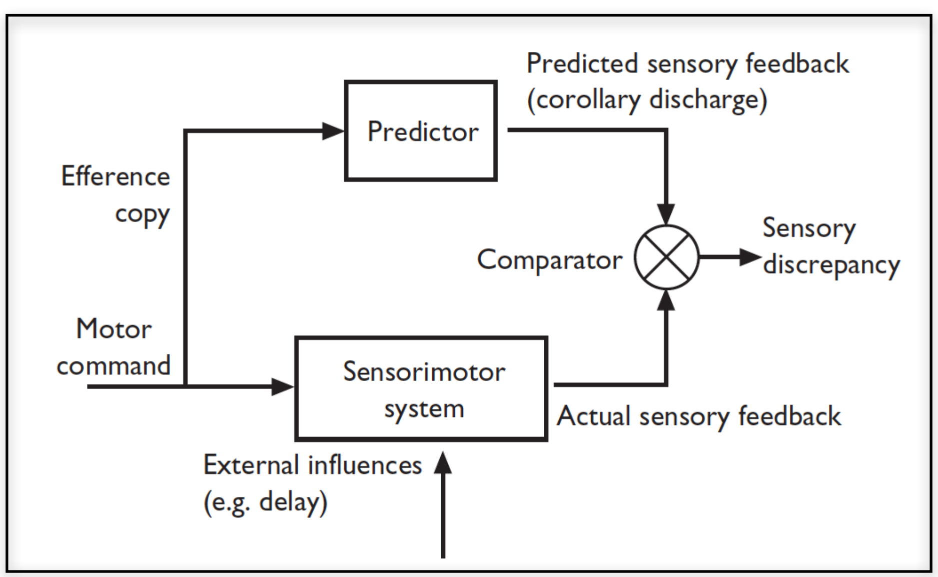
— Nowak et al., 2007, *Neuropsychologia* 45:696

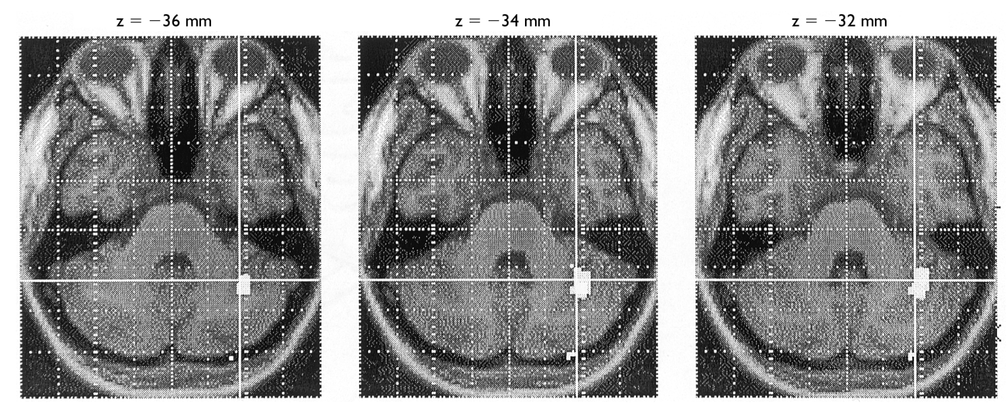


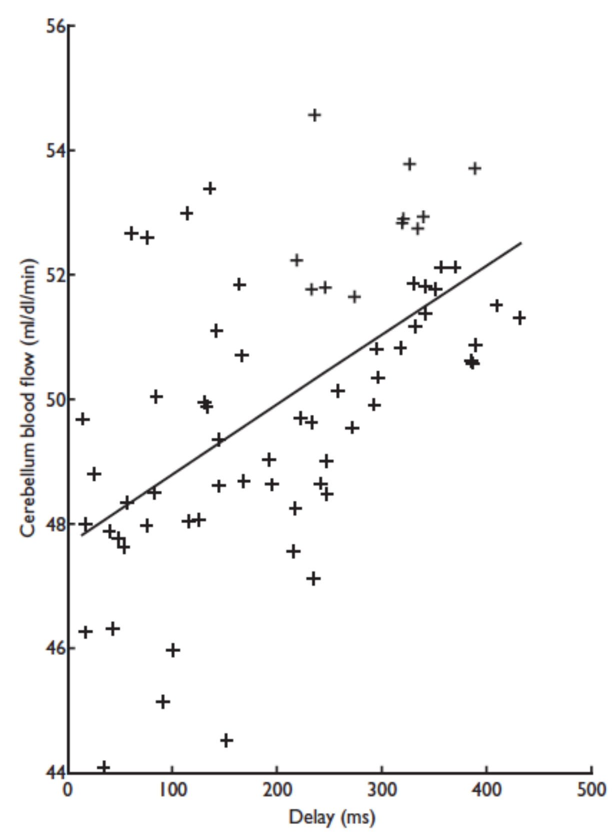
PREDICTING SENSORY CONSEQUENCES

The cerebellum is involved in predicting the sensory consequences of action









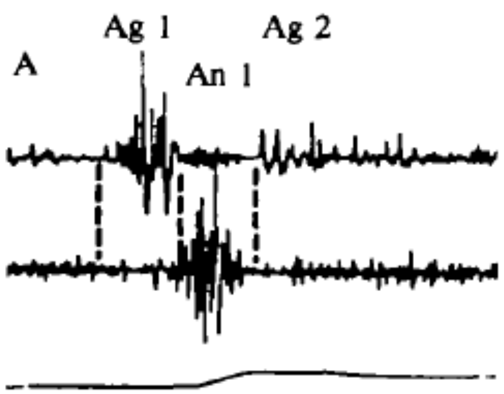
Activity in the right lateral cerebellar cortex shows a positive correlation with delay.

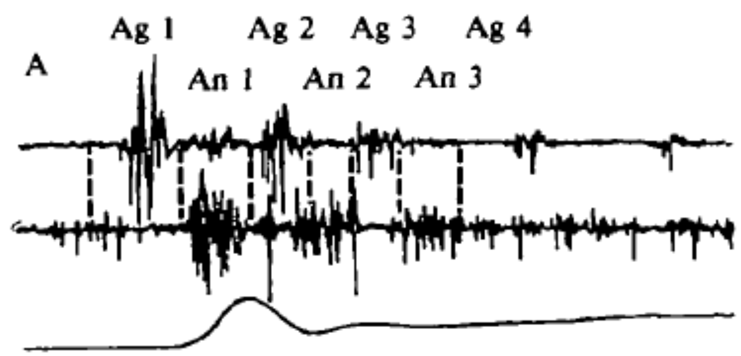
The cerebellum is involved in signalling the sensory discrepancy between the predicted and actual sensory consequences of movements

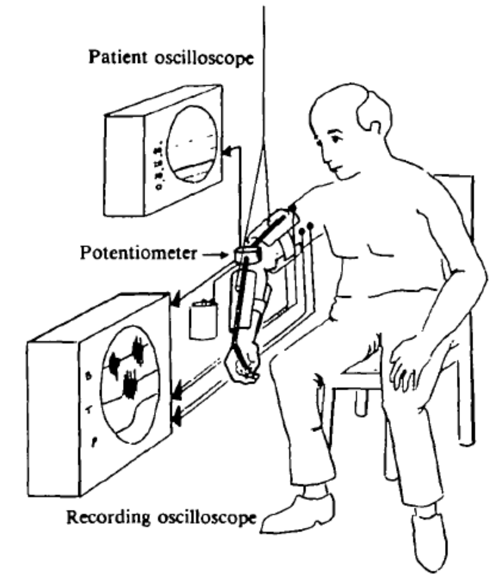
— Blakemore et al., 2001, *NeuroReport* 12:1879

BASAL GANGLIA DEFICITS

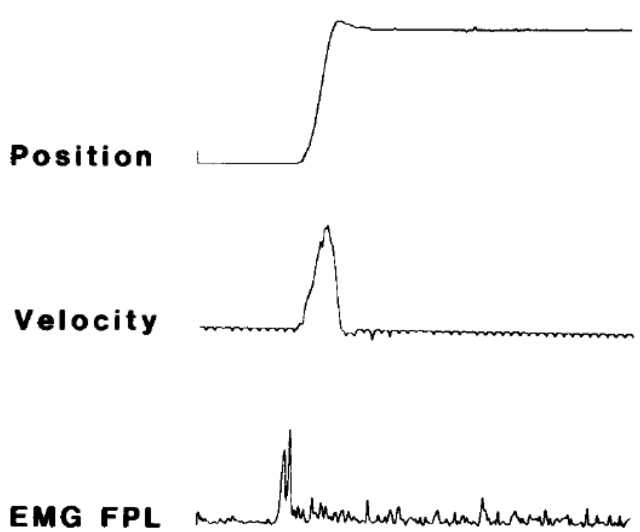
Movements and EMG are segmented

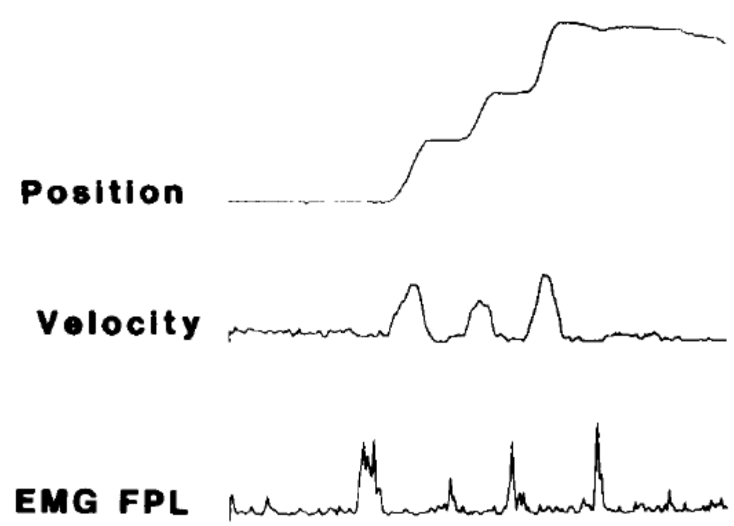






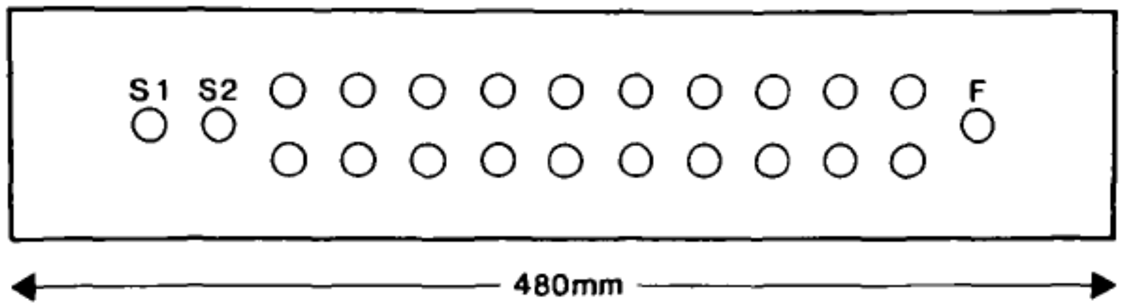
— Hallett & Khoshbin, 1980, *Brain* 103:301



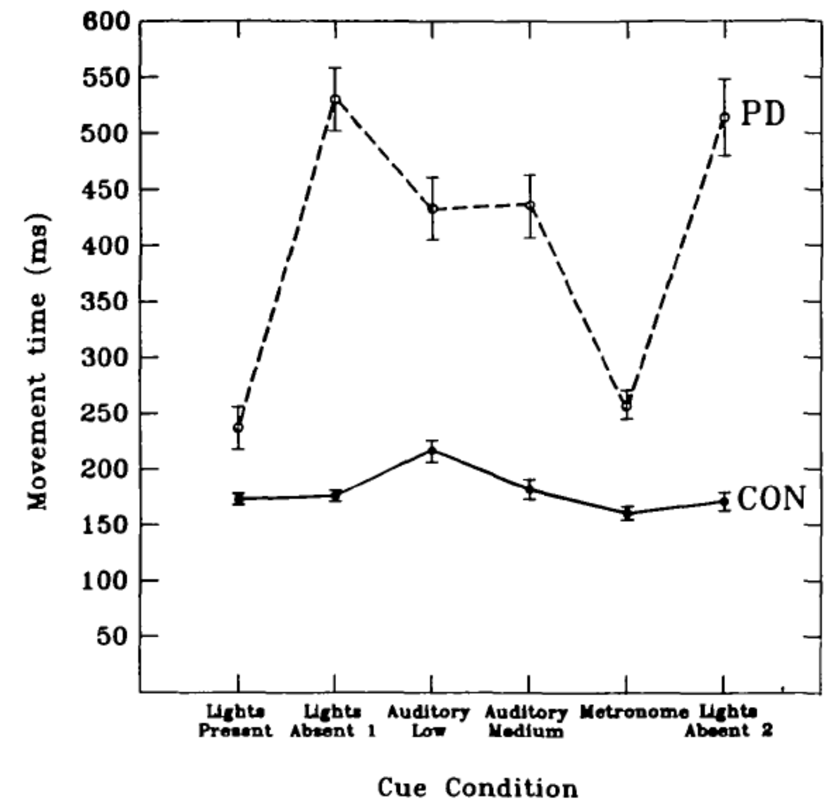


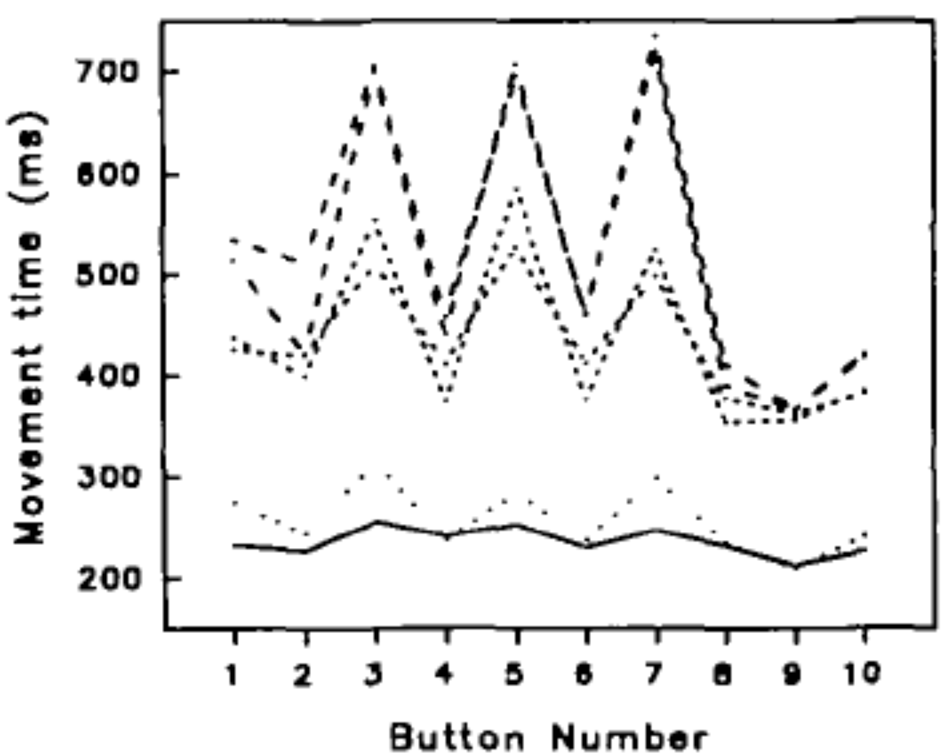
— Berardelli et al., 1984, *Neurosci Lett* 47:47

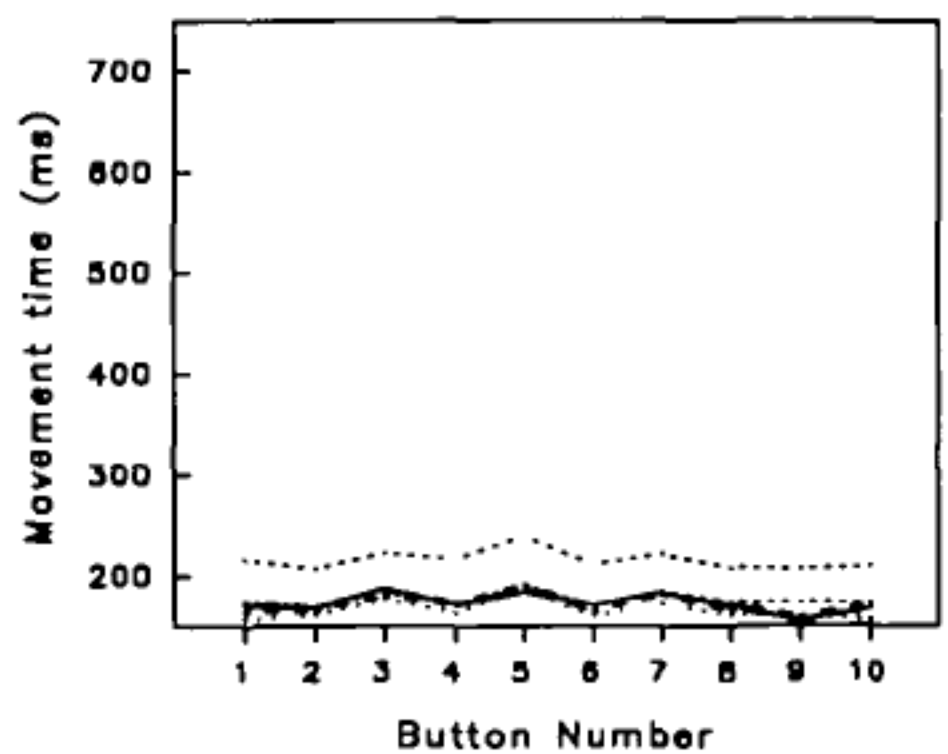
BASAL GANGLIA DEFICITS



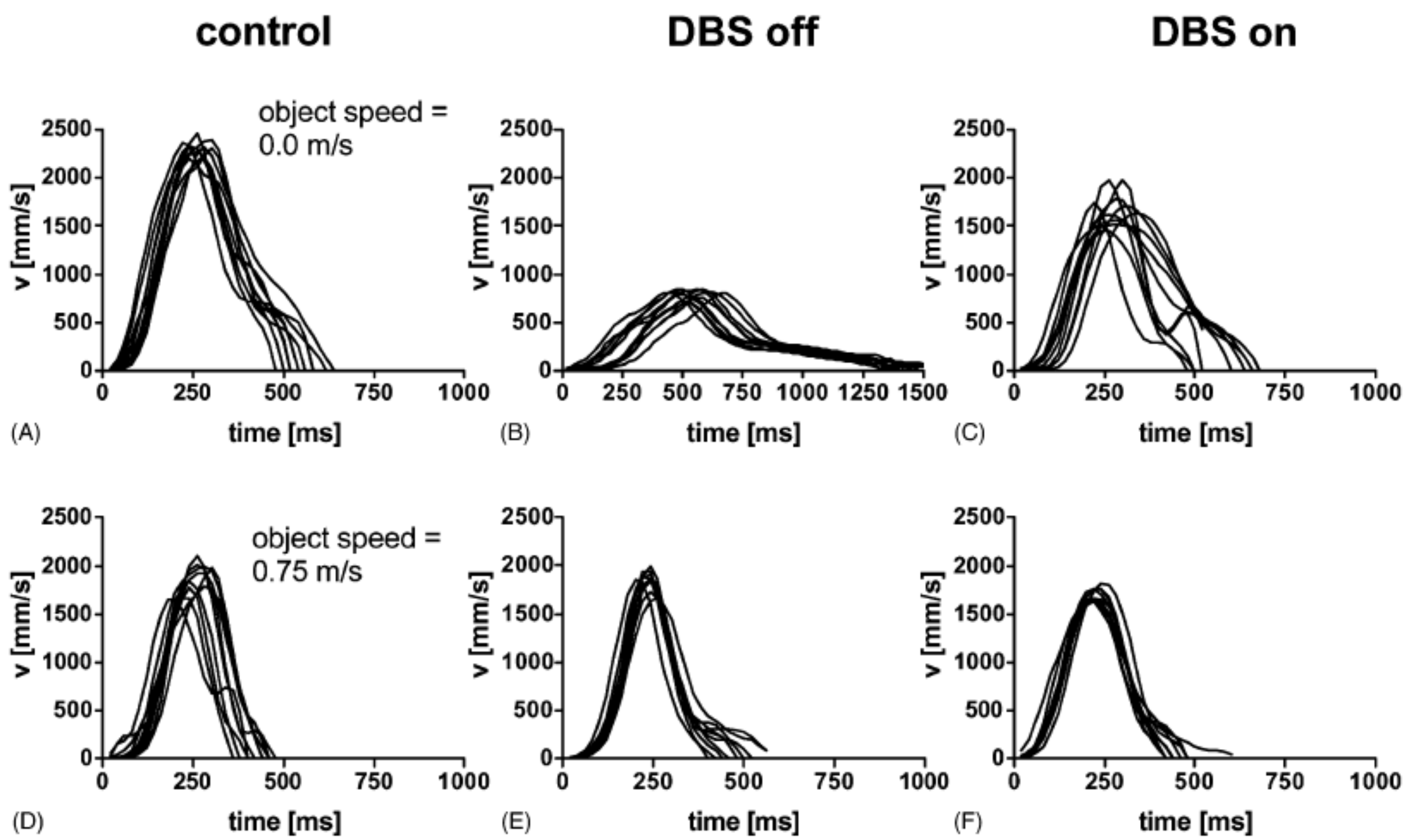
— Georgiou et al., 1993, *Brain* 116:1575







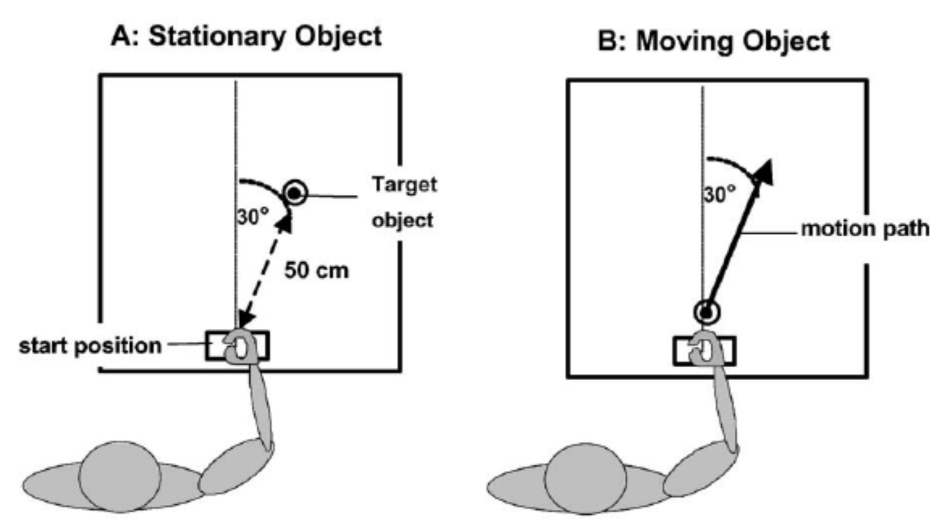
BASAL GANGLIA DEFICITS



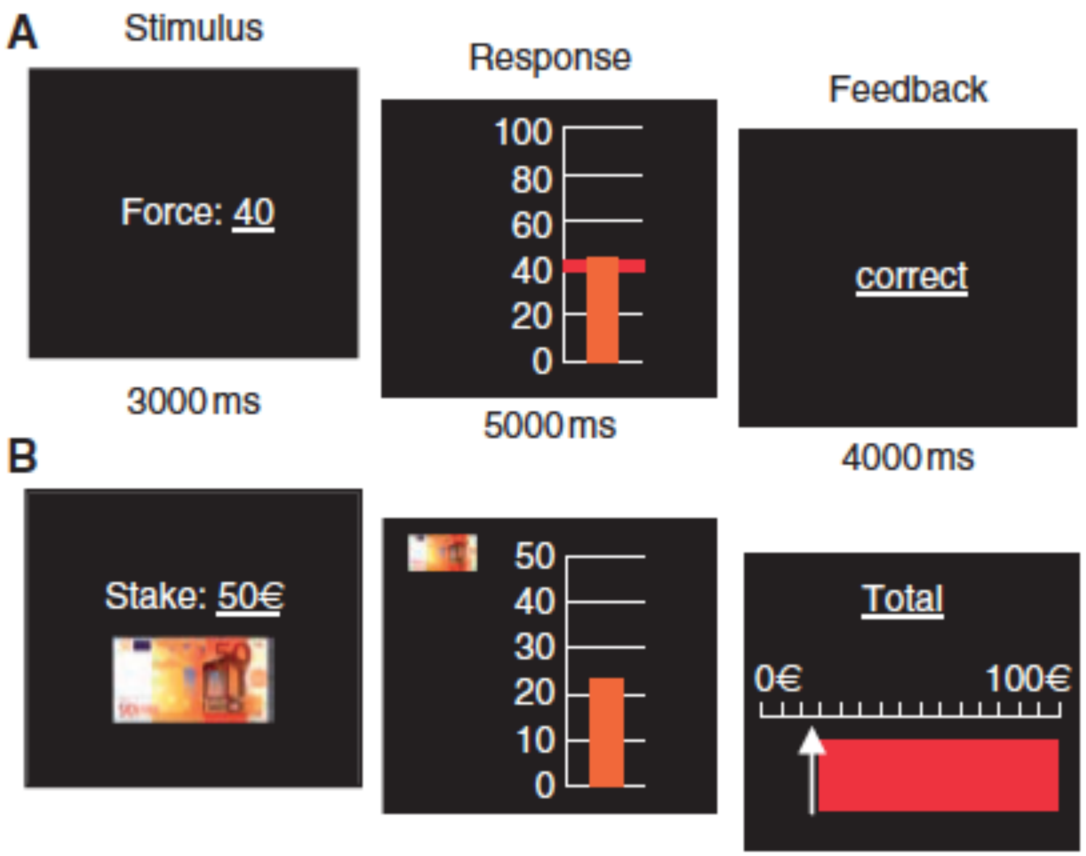
Reaching to
moving targets

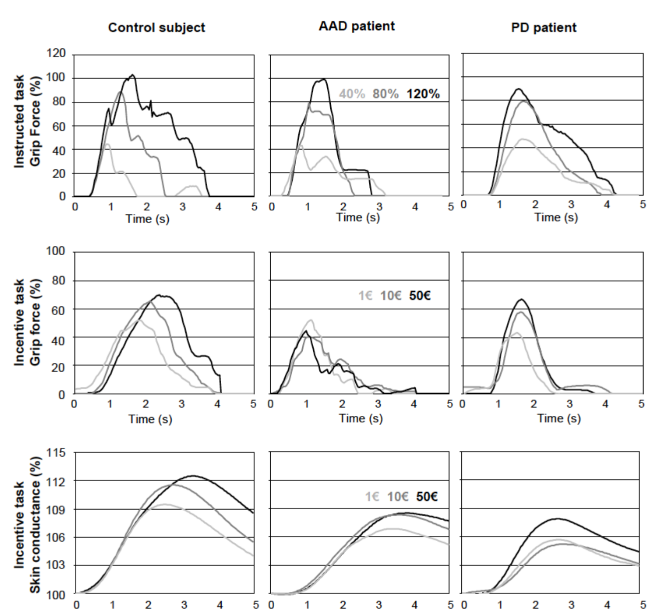
Paradoxical
kinesia in PwPD

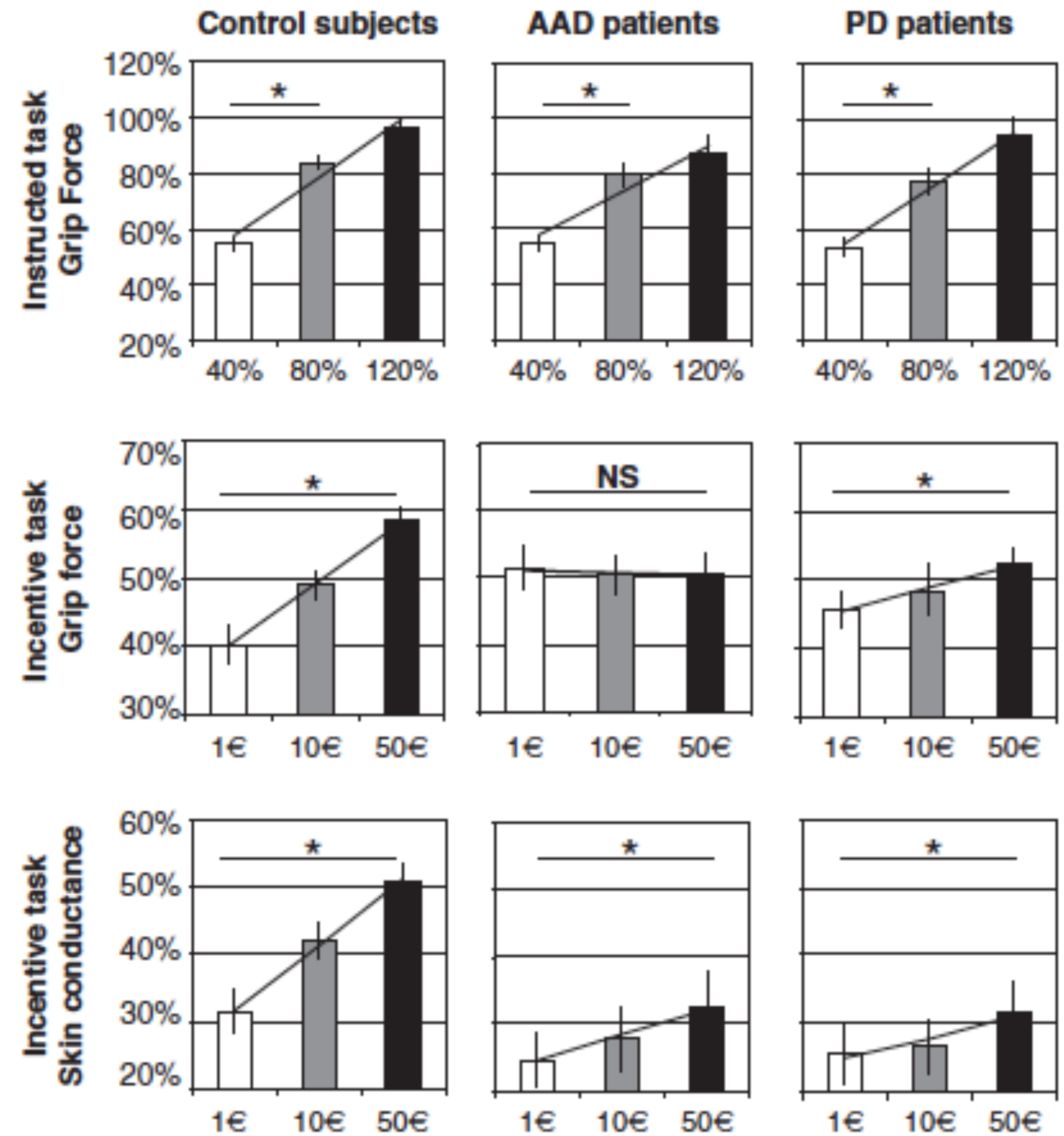
— Schenk et al., 2003,
Neuropsychologia 41:783



PARKINSON'S DISEASE AND MOTIVATION







— Schmidt et al., 2008, *Brain* 131:1303

DISCLAIMER

The computational model is « wrong »
does not explain: discrete/rhythmic actions, skilled/unskilled actions, isochrony, slow movements, …

— Guigon, 2021, *Psychol Rev* in press

The computational neuroanatomy is « wrong »
does not explain: the role of the motor cortex, the contribution of the basal ganglia to motor control, how the cerebellum can implement a state estimator, where motor memories are stored, …

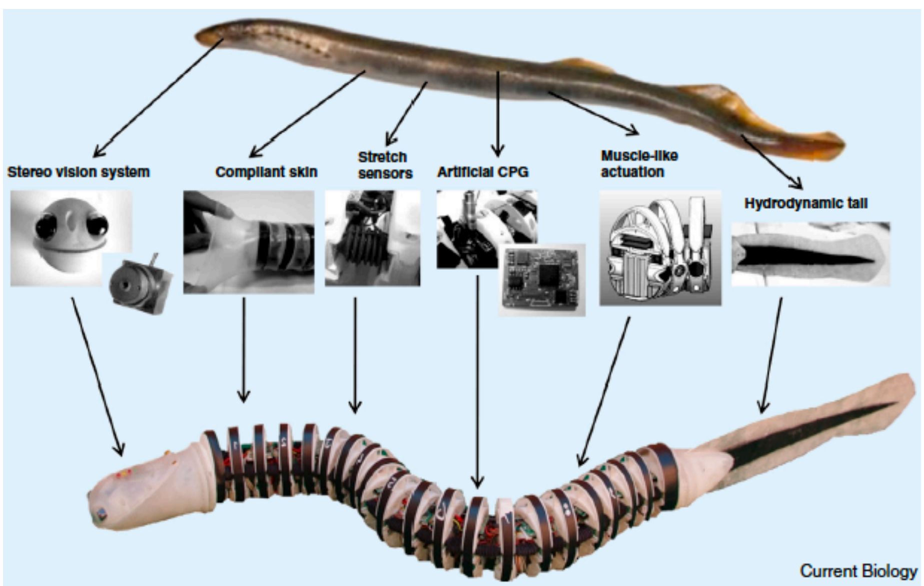
— Serradj et al., 2021, *bioRxiv* 436415

— Dhawale et al., 2021, *Nat Neurosci* 24:1256

ROBOTICS AND NEUROSCIENCE

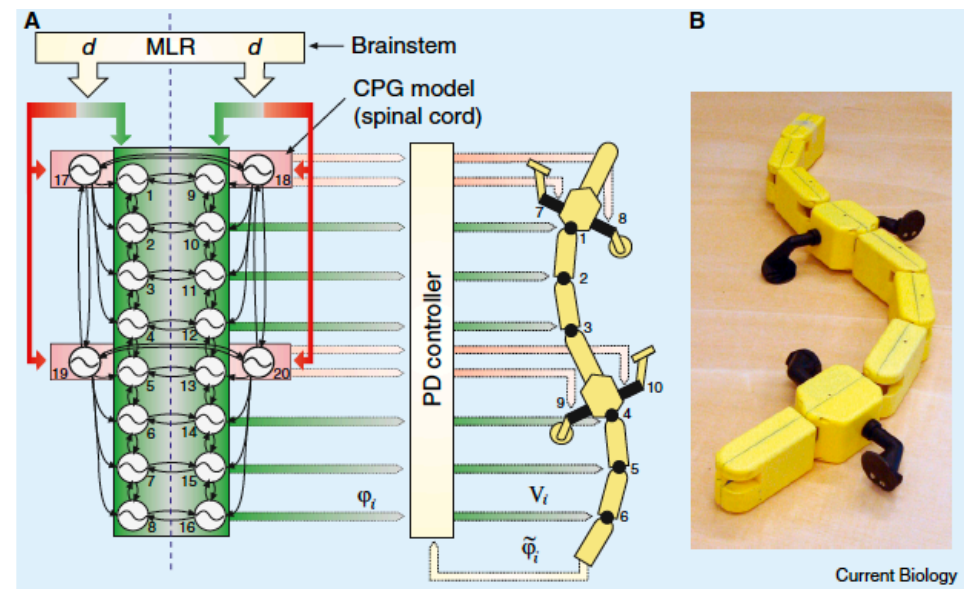
lamprey-like swimming robot

to explore the mechanisms of visually-guided swimming in the lamprey



salamander robot driven by a spinal cord model

replicates the typical swimming and walking gaits of the salamander



— Floreano et al., 2014, *Curr Biol* 24:R910

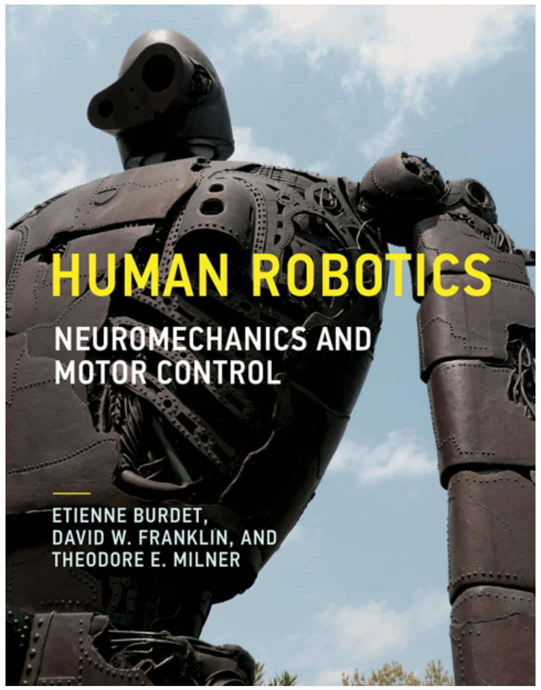
ROBOTICS AND COGNITIVE SCIENCE

The field of robotics is heavily inspired by biology; a clearer understanding of how nature accomplishes efficient and precise motor control is critical to the development of advanced robotic systems.

As human interaction with technology continues to expand, ergonomic design and intuitive control based on the principles of human movement and motor control will also become increasingly important.

Chihira Aico

REFERENCES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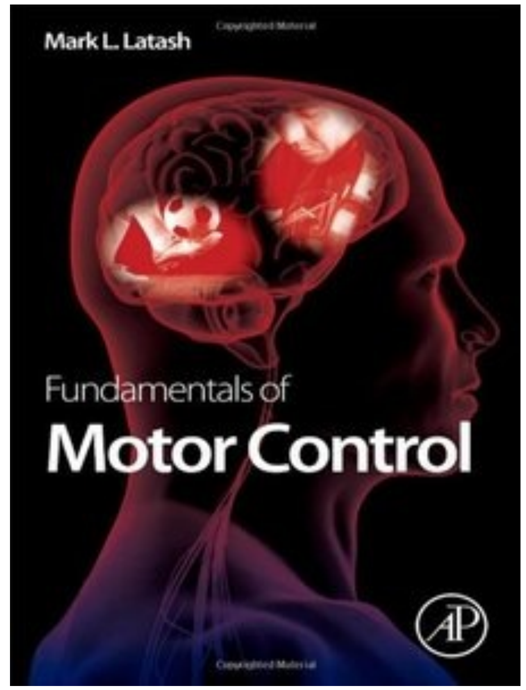
NEUROMECHANICS AND MOTOR CONTROL
ETIENNE BURDET, DAVID W. FRANKLIN, AND THEODORE E. MILNER


Mark L. Latash
Fundamentals of
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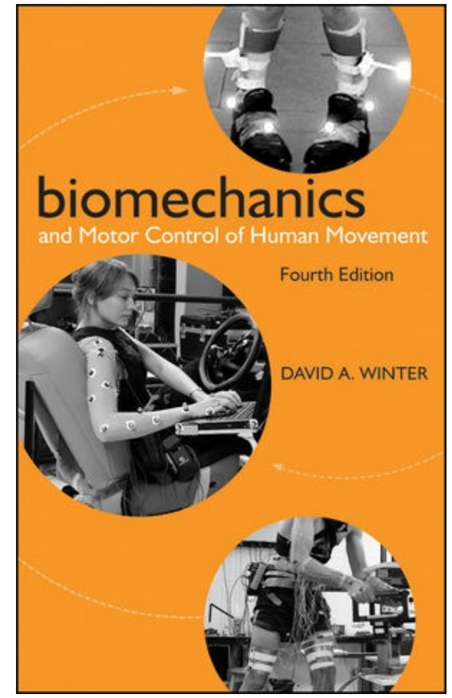
biomechanics
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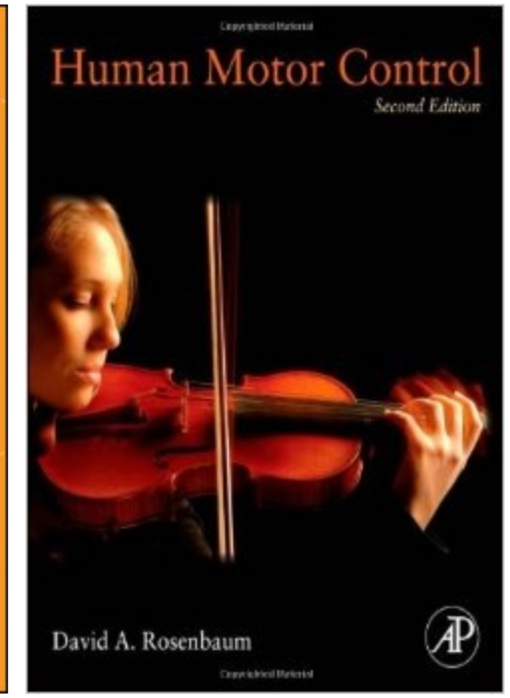
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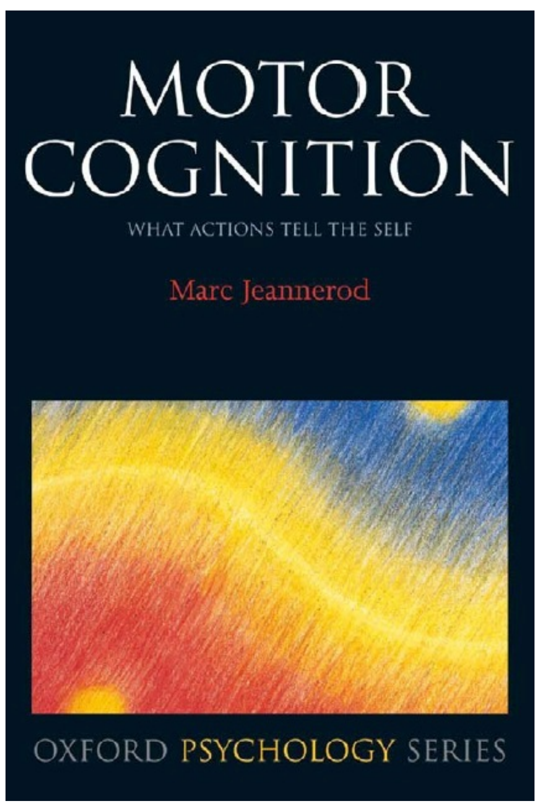
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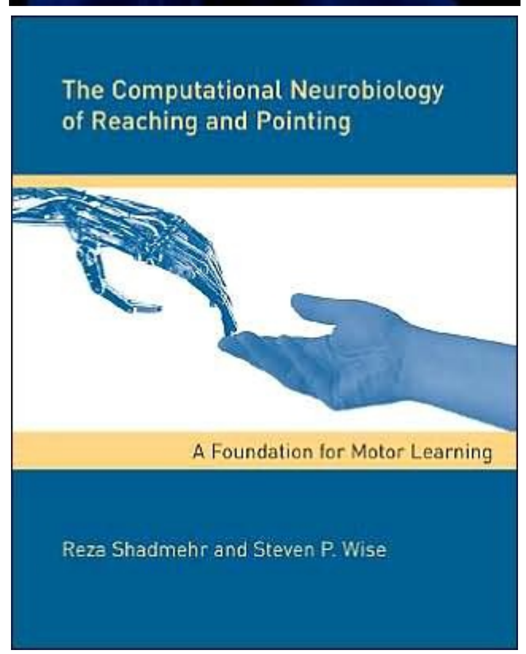
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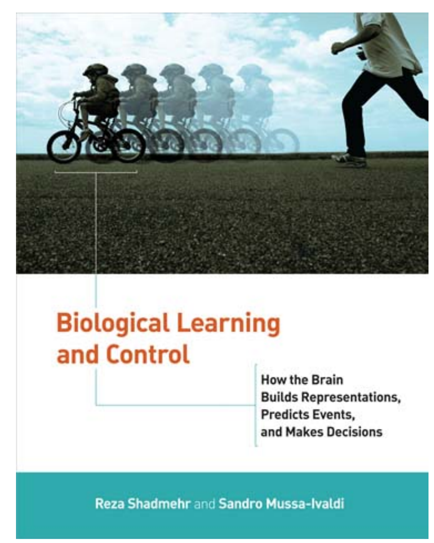
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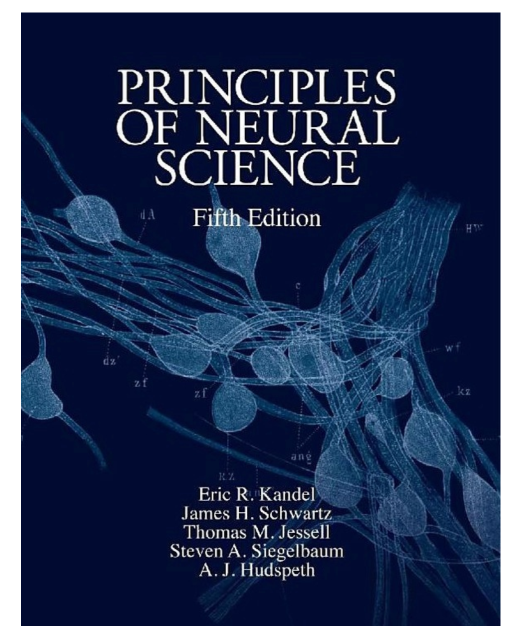
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