Modèles mathématiques et corrélats anatomiques du mouvement

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OUTLINE

1. Cognition, action and movement

2. The organization of action

3. Computational motor control

4. Neural bases of motor control

COGNITION AND ACTION

What to move where

Cognitive science

vs.

Moving

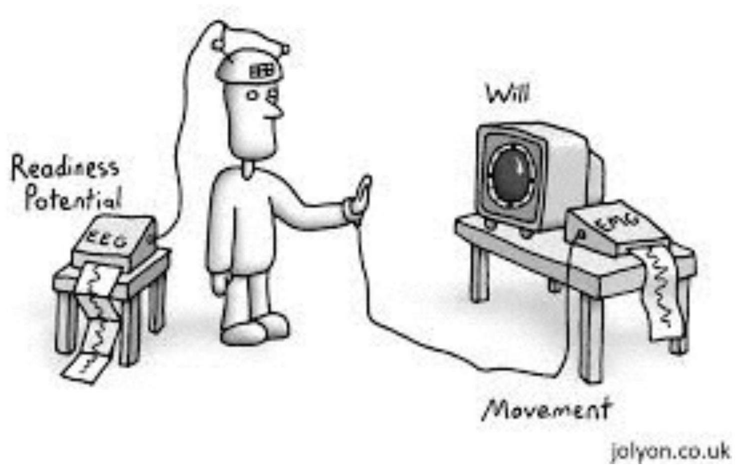
vs.

Motor control

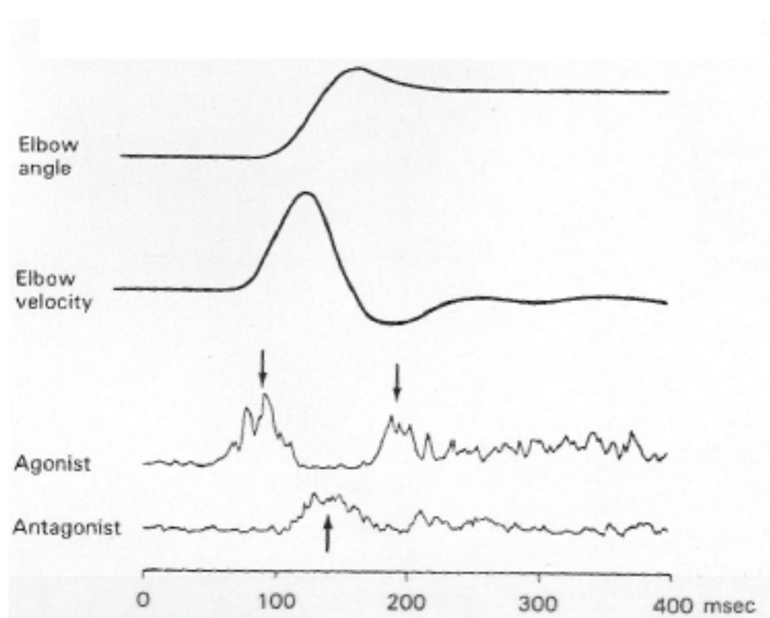
—Wolpert, 2007, *Hum Mov Sci* 26:511

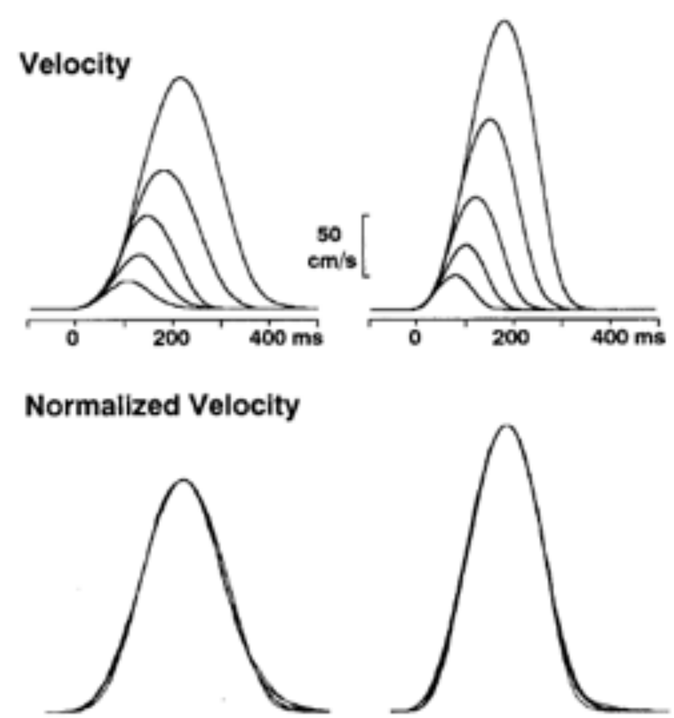
CONTENT OF ACTION

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

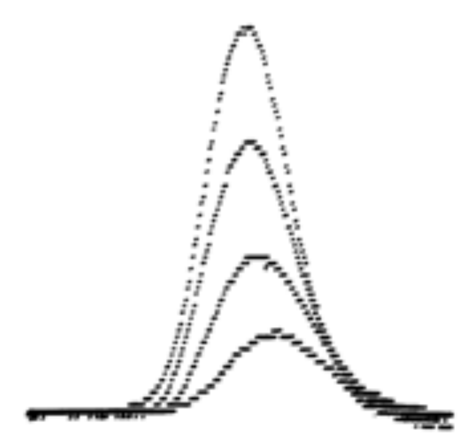


- Anticipatory electrical activities (EEG, EMG)
- Invariant profiles
- Scaling with task conditions





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

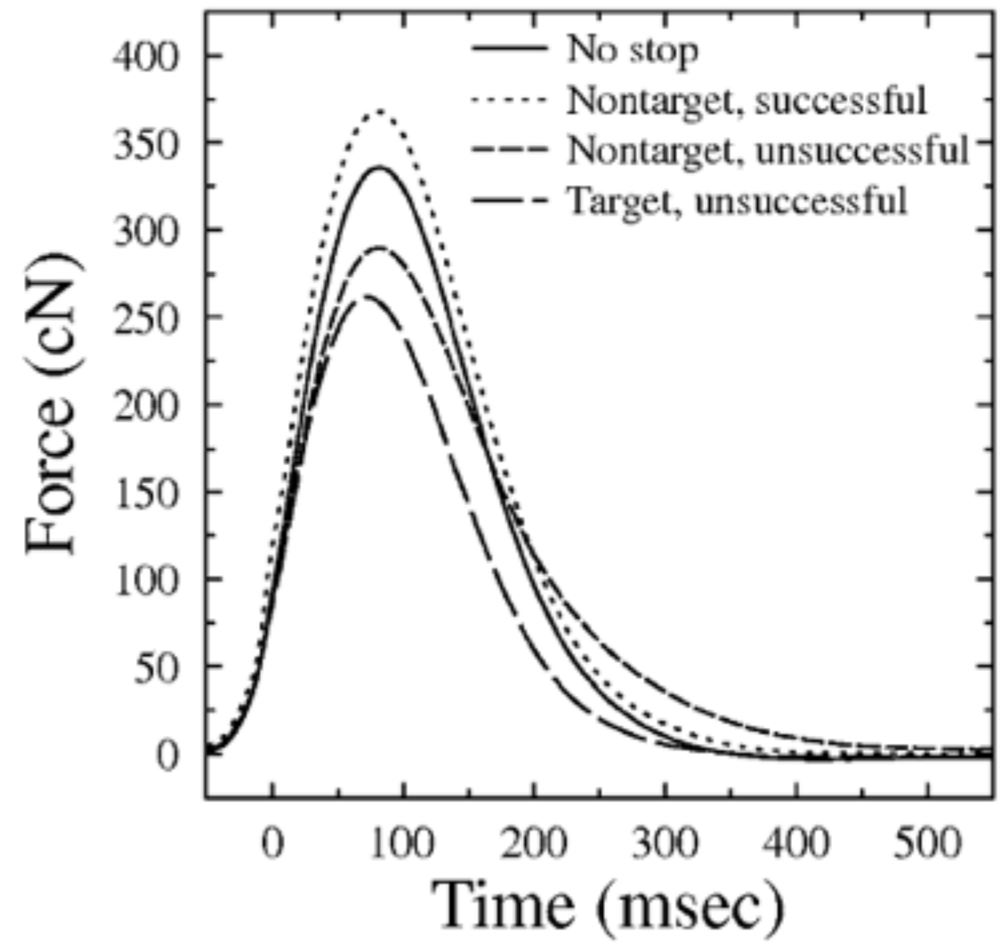


— Angel, 1973, *Q J Exp Psychol* 25:193

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)

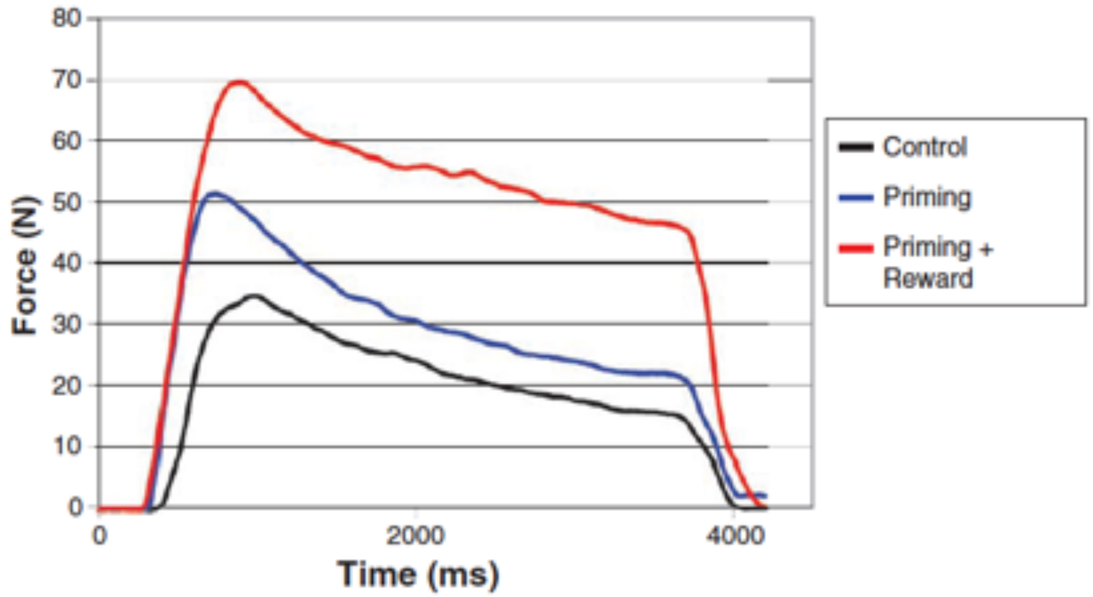


— Ko & Miller, 2011, *Psychon Bull Rev* 18:813

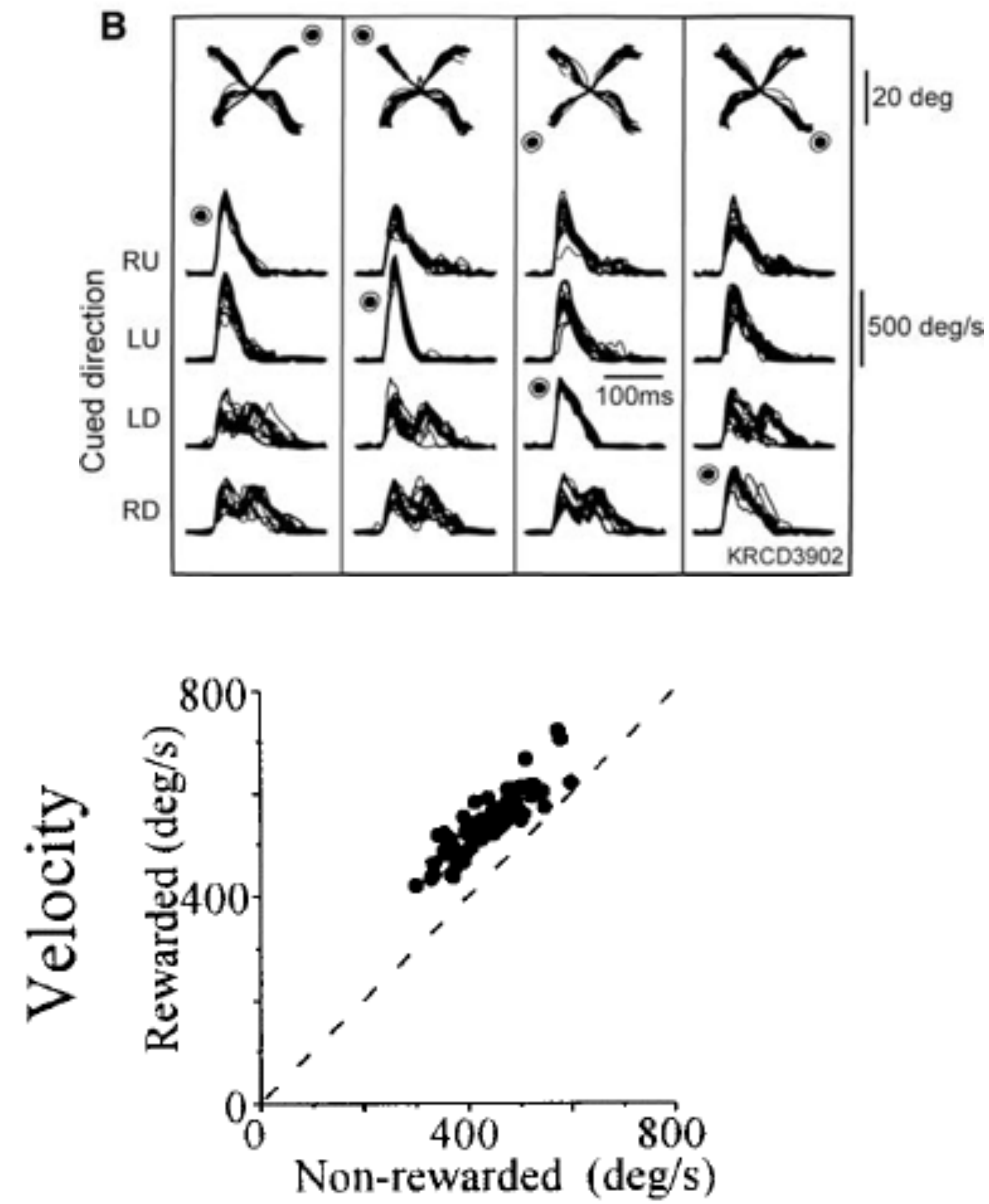
➞ Faster movements for words vs nonwords

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

ACTION REFLECTS MOTIVATION

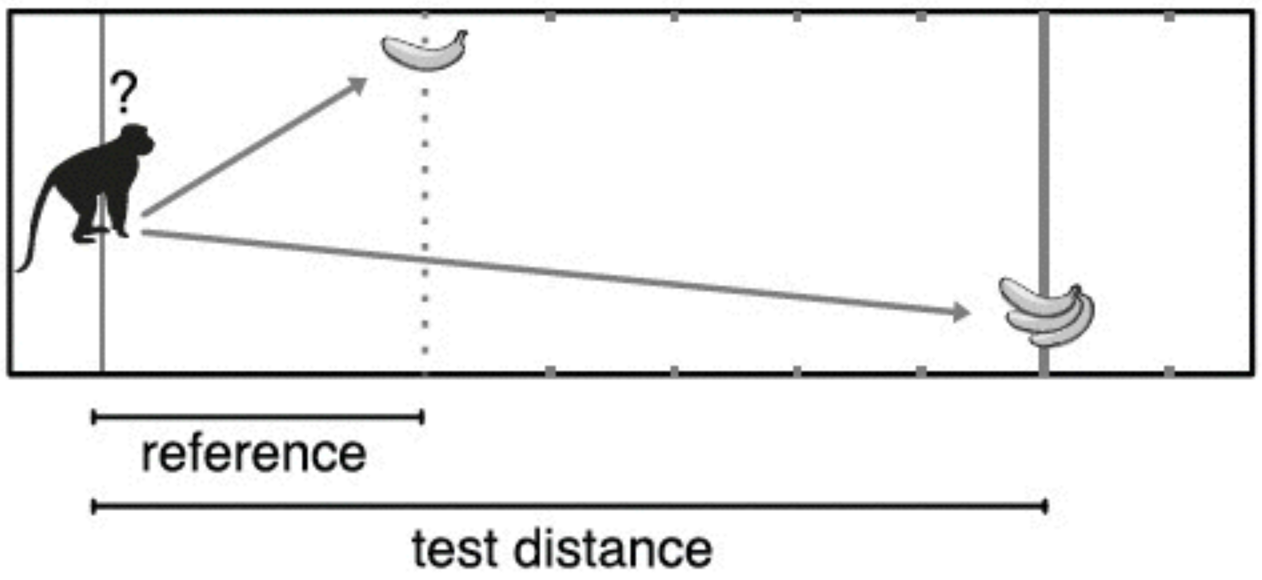


— Aarts et al., 2008, *Science* 19:1639

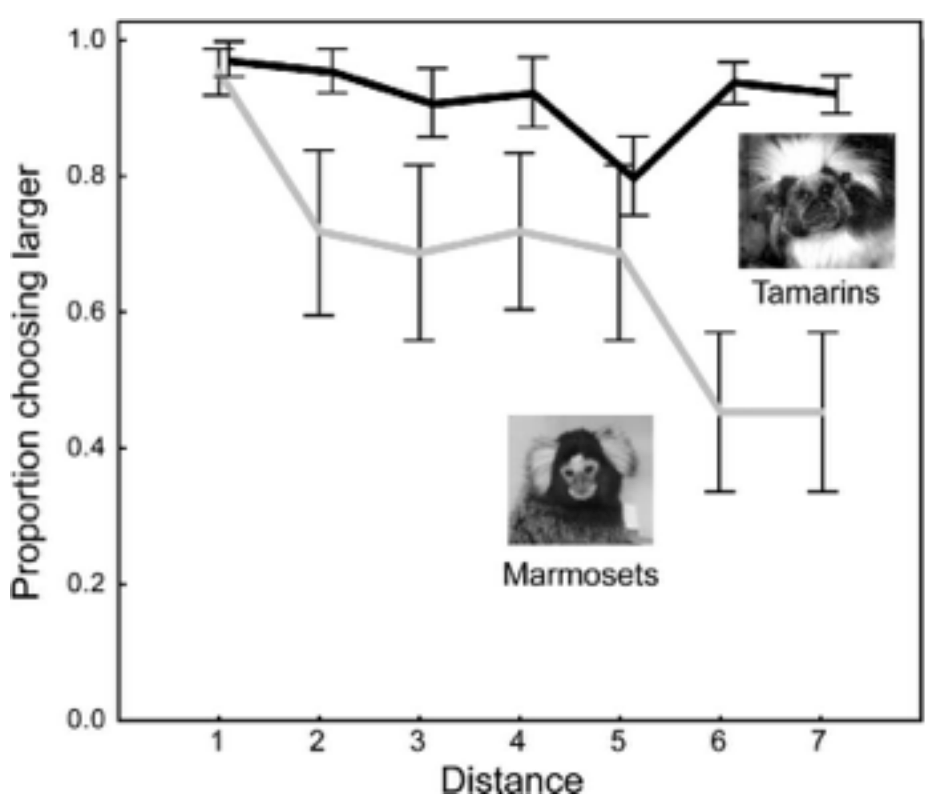


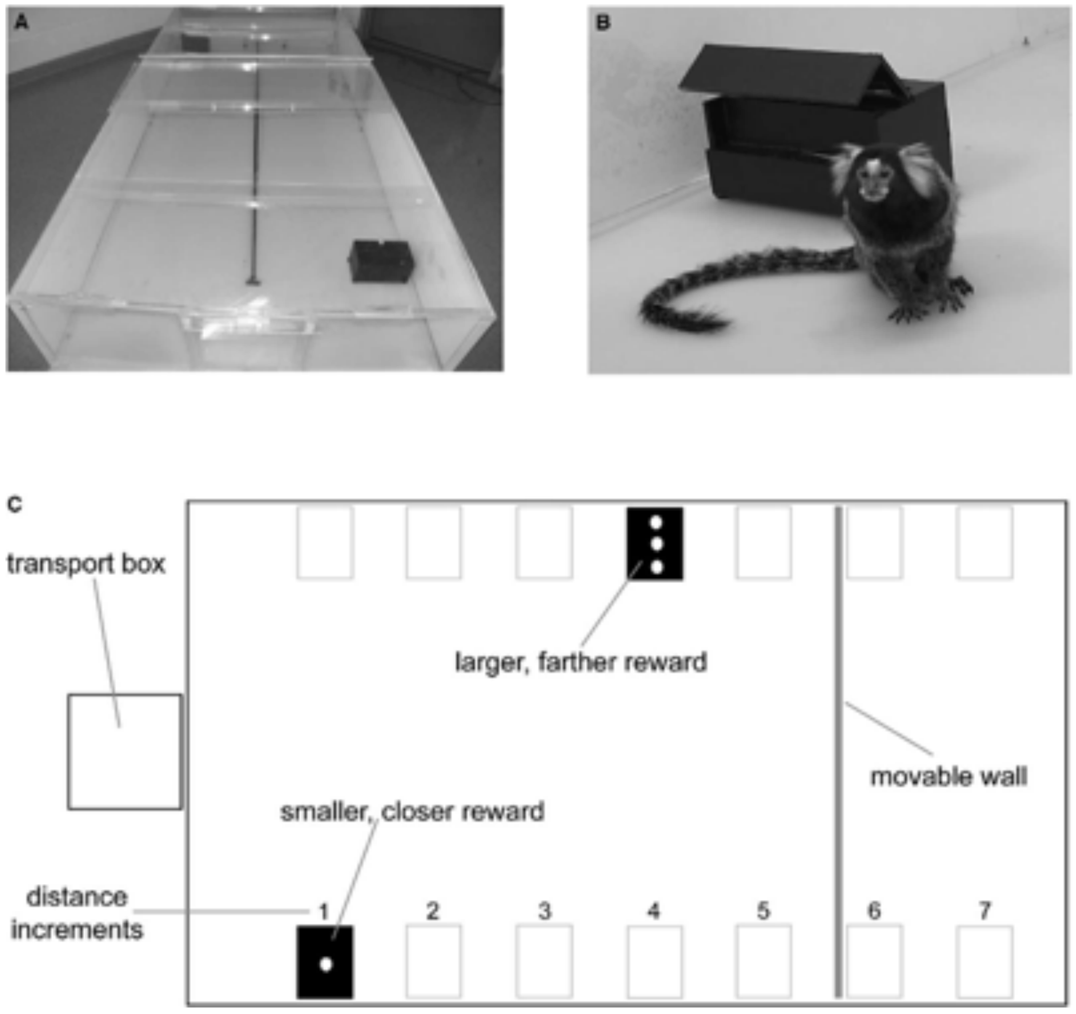
— Takikawa et al., 2002, *Exp Brain Res* 142:284

ACTION IS DECISION MAKING

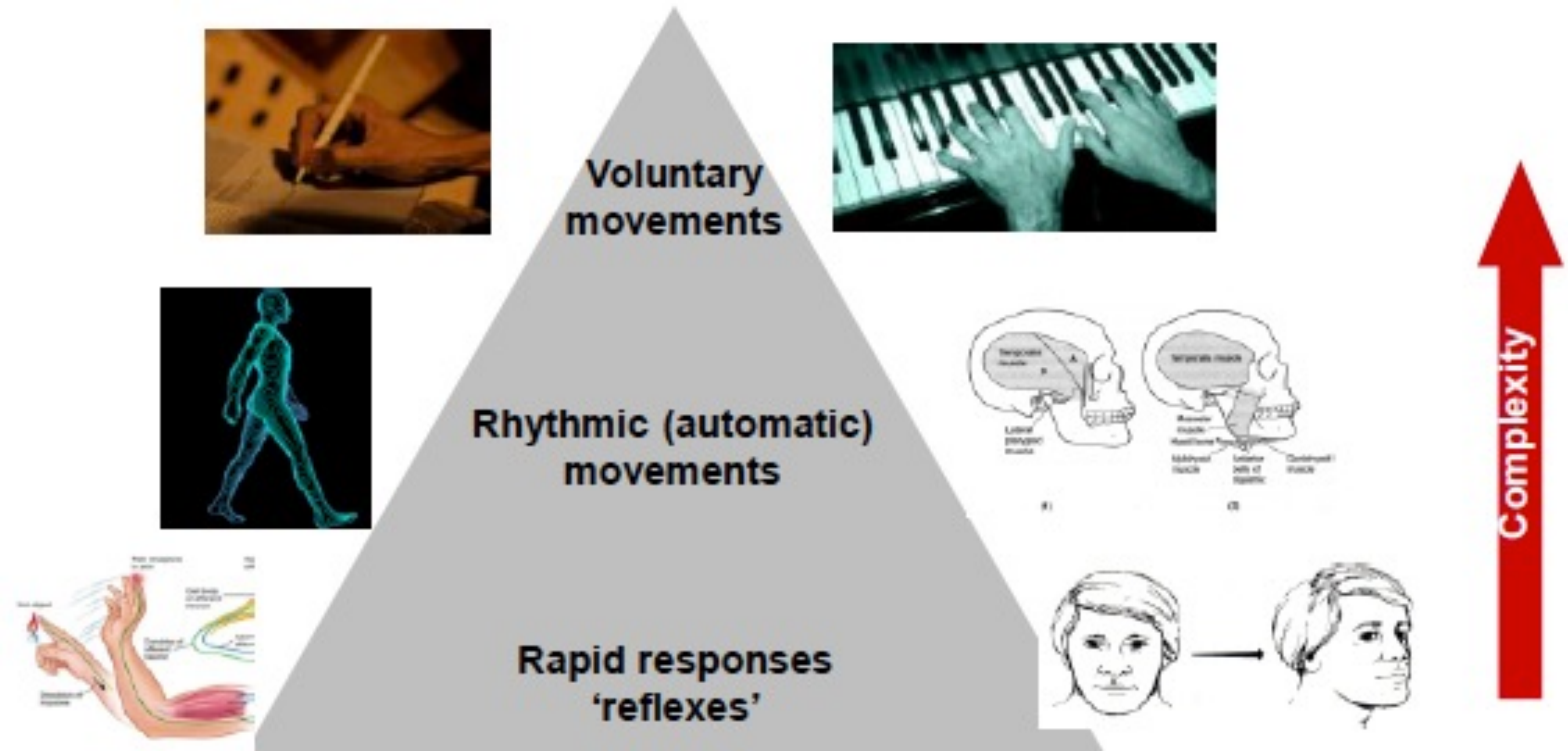


— Stevens et al., 2005, *Curr Biol* 15:1865





TYPES OF ACTION



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

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

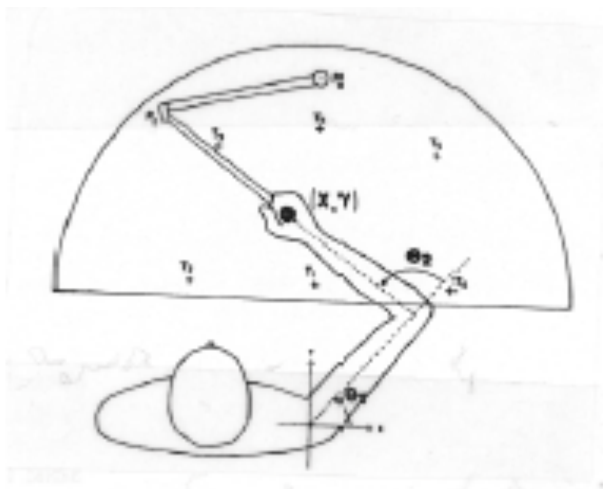
force/torque (Newton's law)

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

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

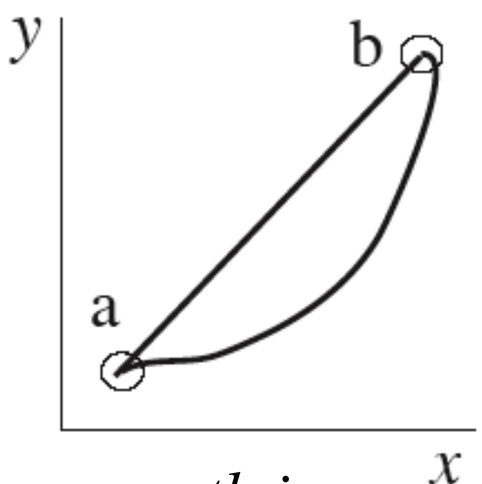


PROBLEMS

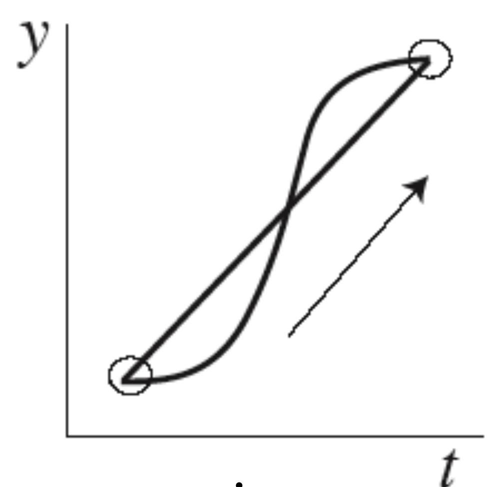
Redundancy

In task space, body space, muscle space, neural space
Problem of degrees of freedom (Bernstein's problem)
600 muscles, 200 joints

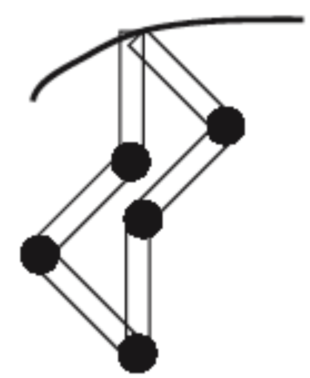
→ *Coordination*



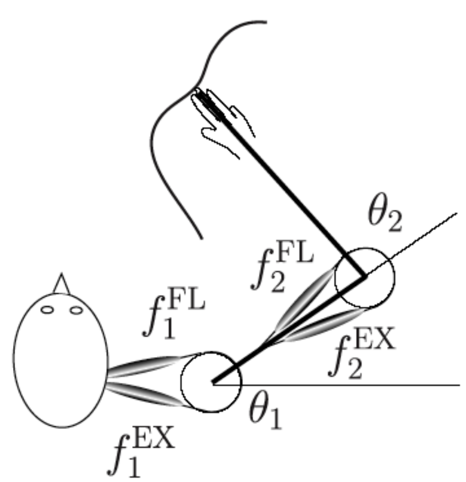
path in task space

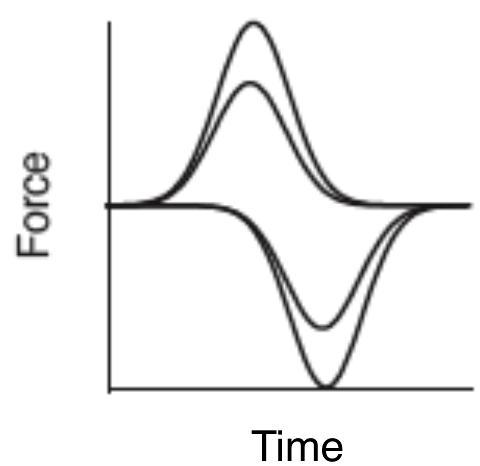


time course

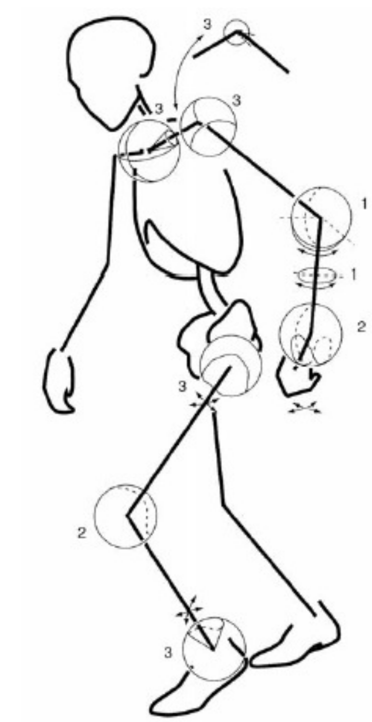


body space redundancy





muscle space redundancy

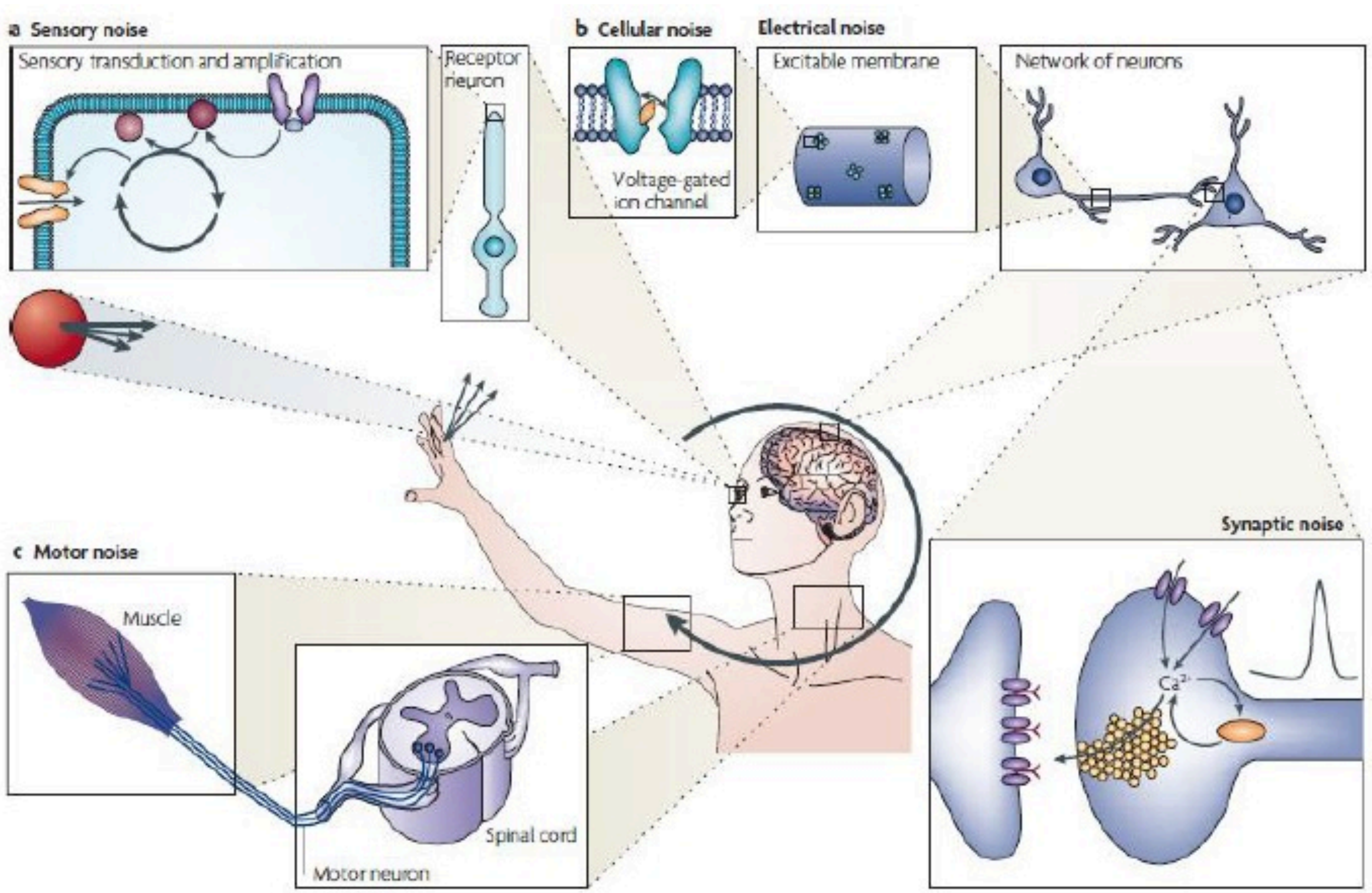


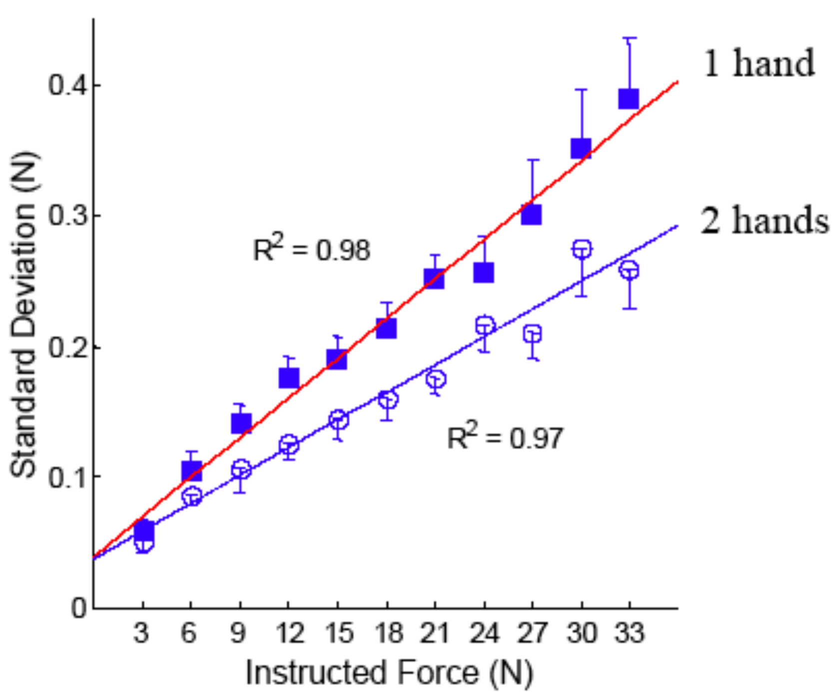
— Bernstein, 1967, *The Co-ordination and Regulation of Movement*, Pergamon

PROBLEMS

Noise

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





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

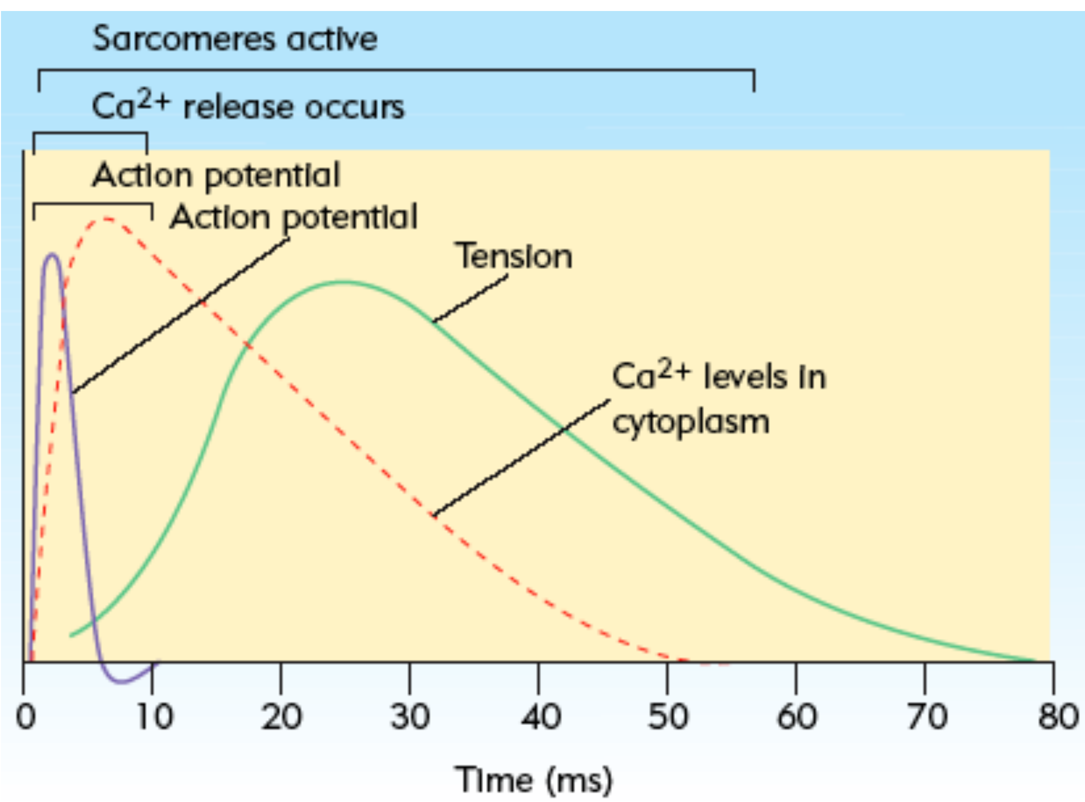
— Todorov, 2002, *Neural Comput* 14:1233

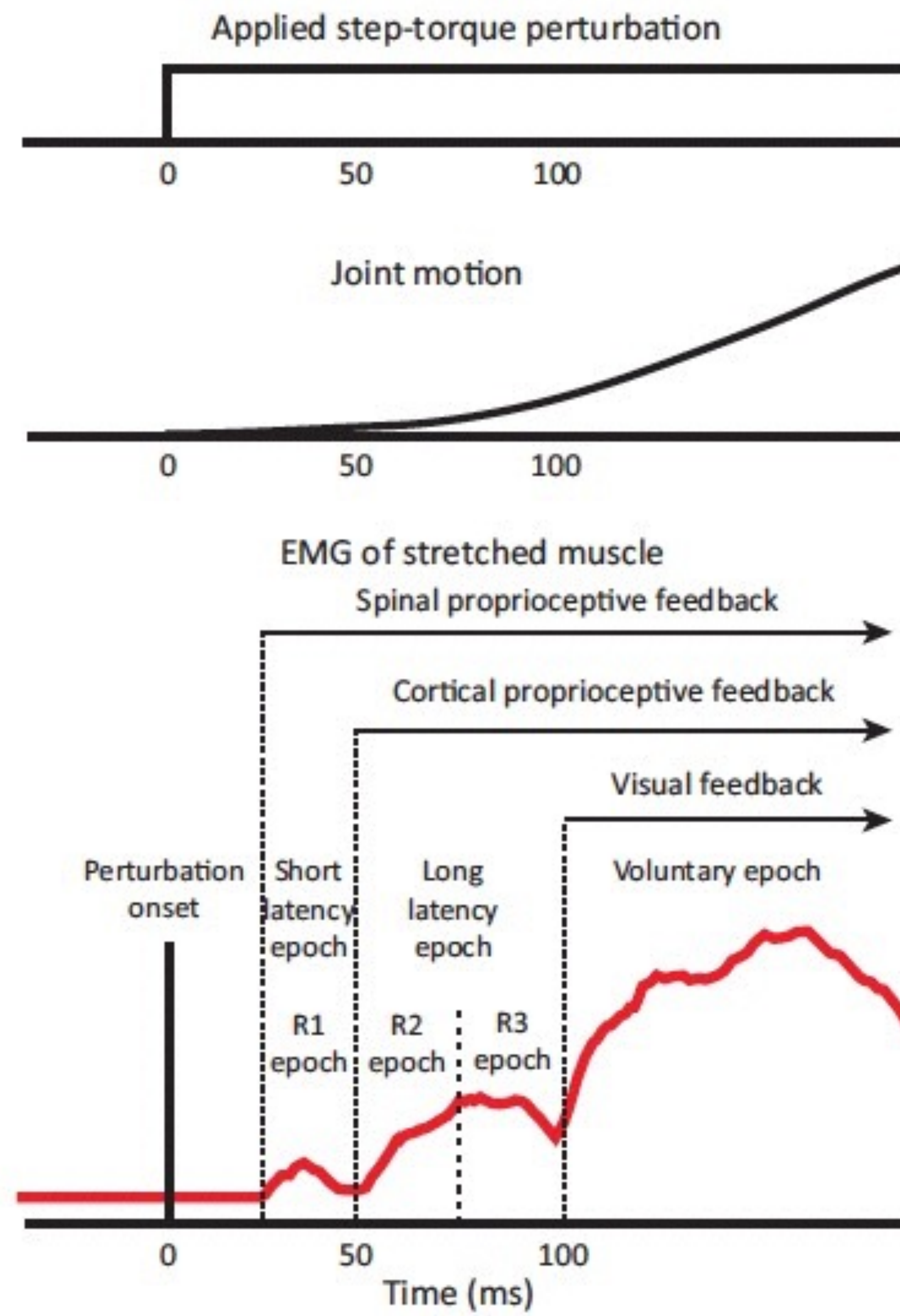
PROBLEMS

Delays

In afferent sensory information and efferent motor commands

→ *"We live in the past"*



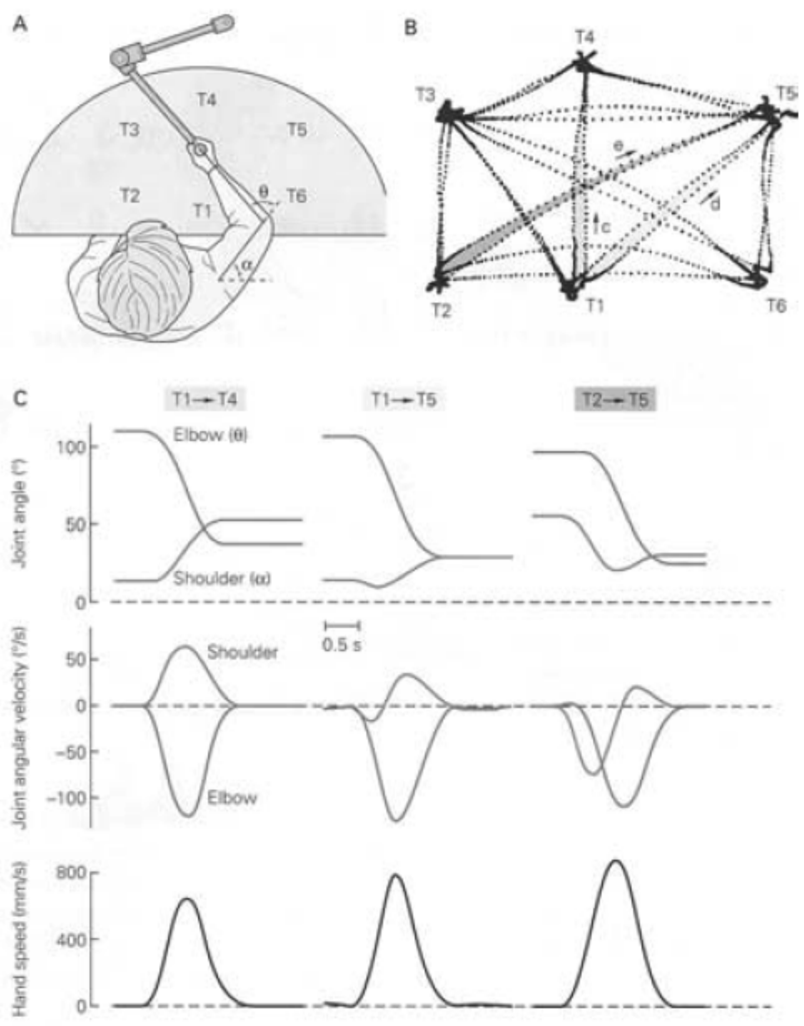


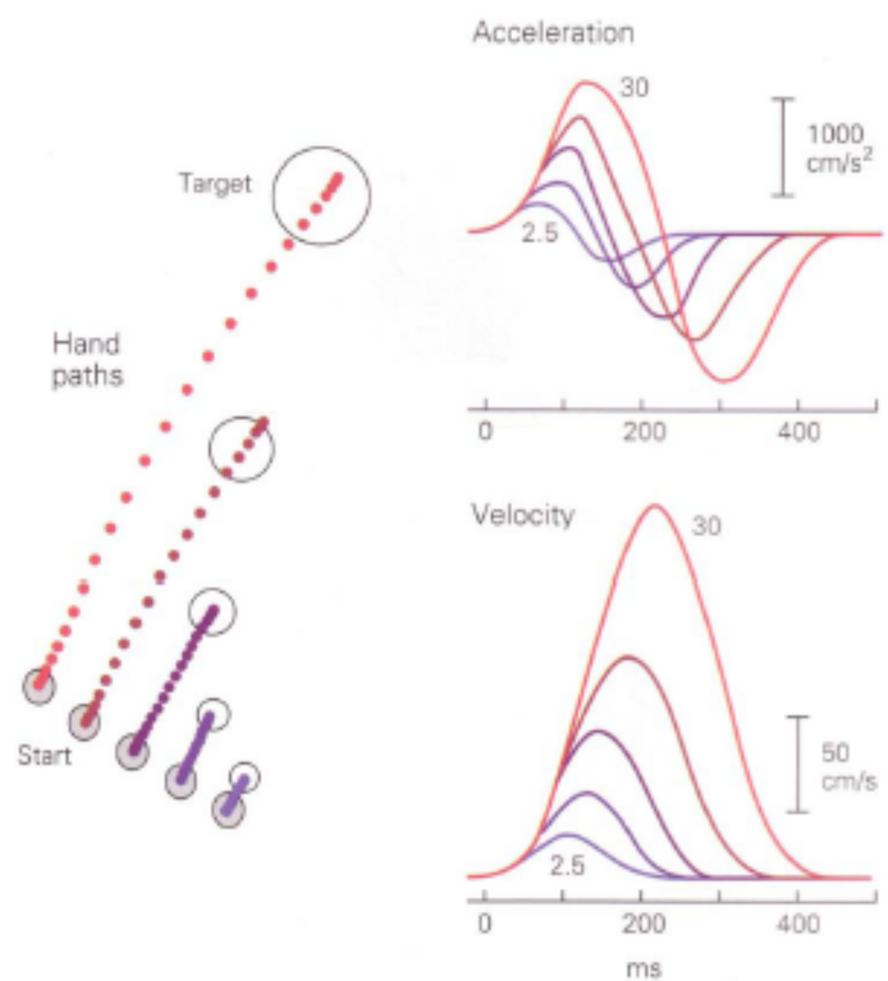
— Scott, 2012, *Trends Cogn Sci* 16:541

MOTOR INVARIANTS

Trajectories

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

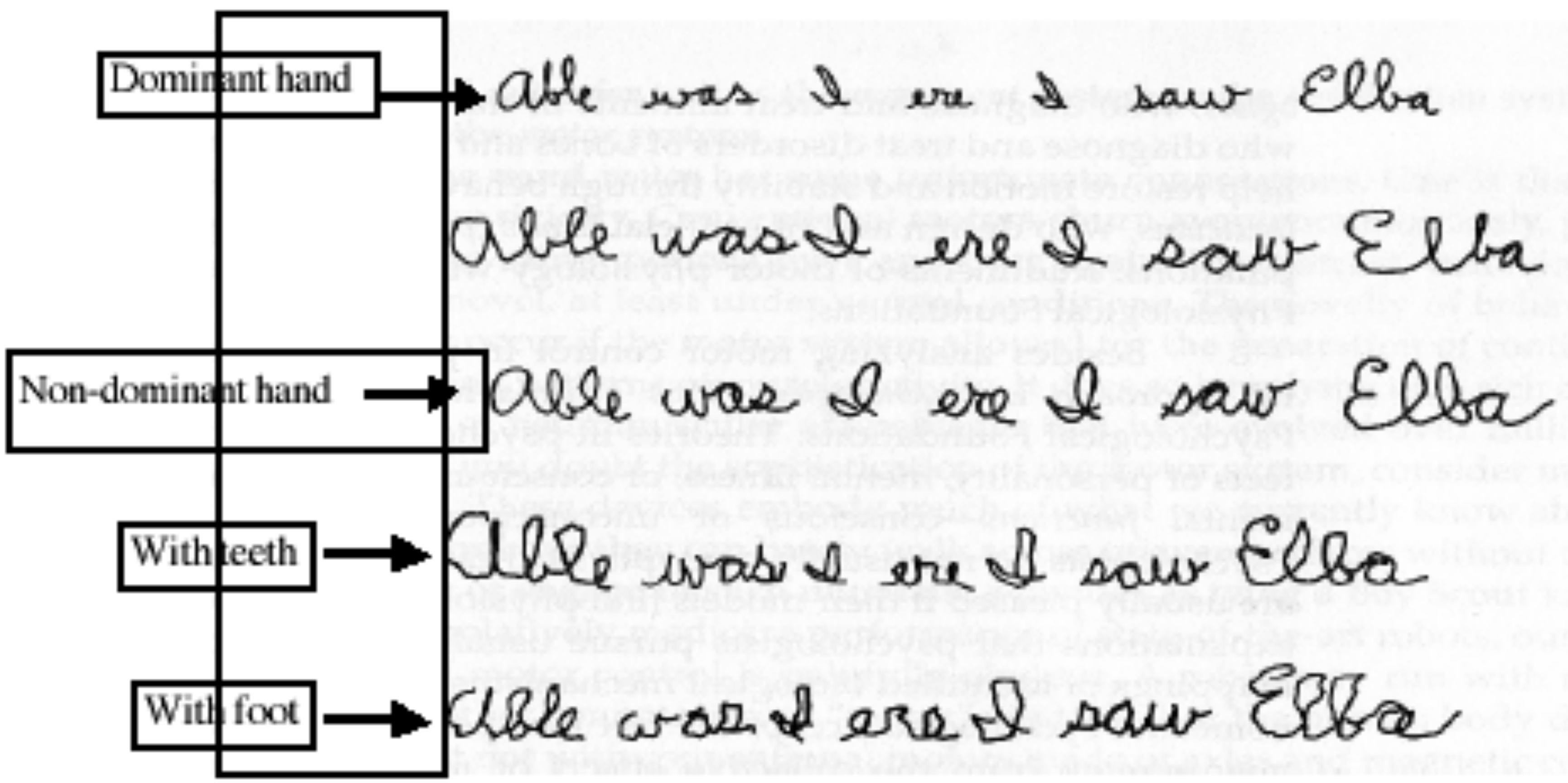




MOTOR INVARIANTS

Motor equivalence

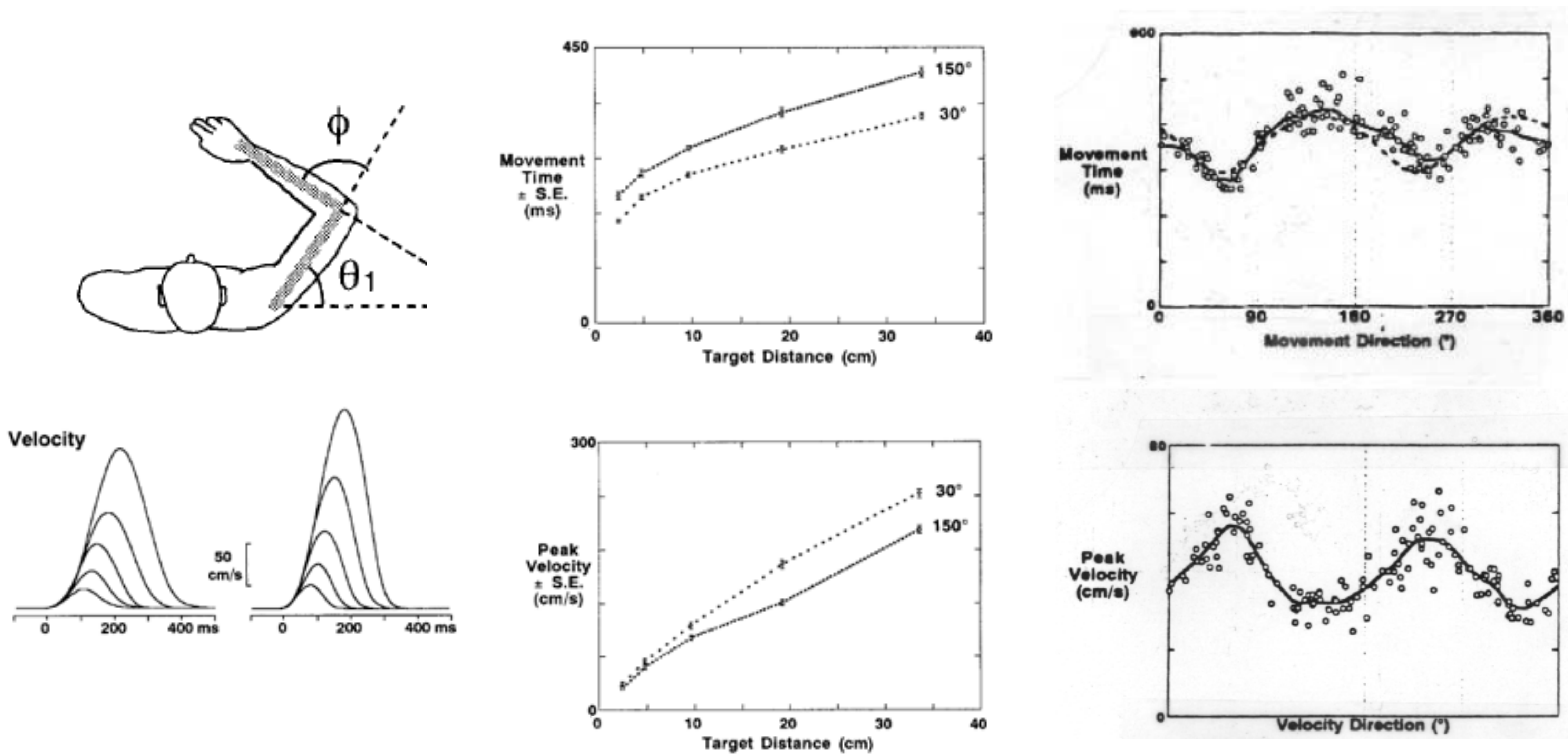
Actions are encoded in the central nervous system in terms that are more abstract than commands to specific muscles



MOTOR INVARIANTS

Scaling laws

Duration and velocity scale with amplitude and load

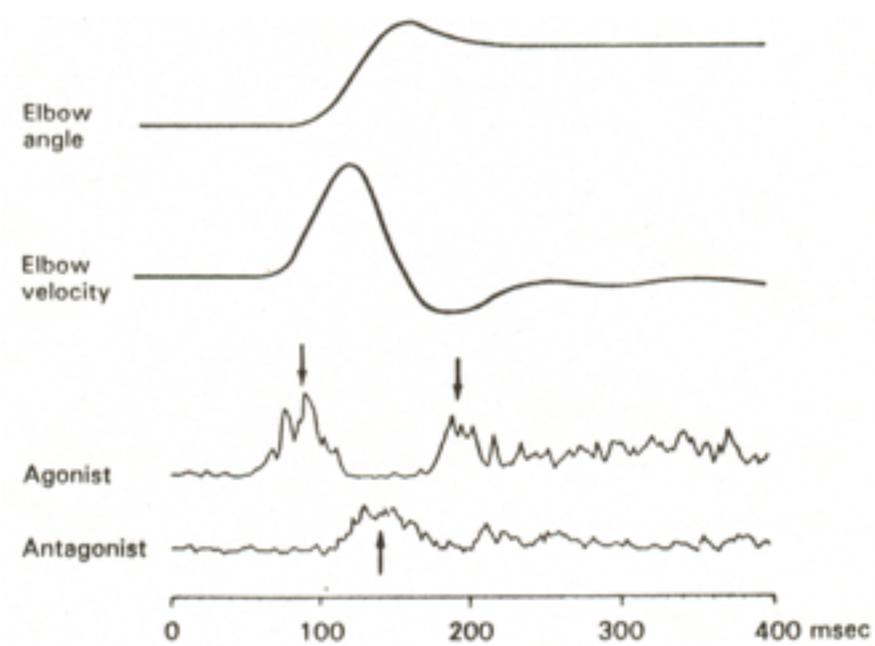


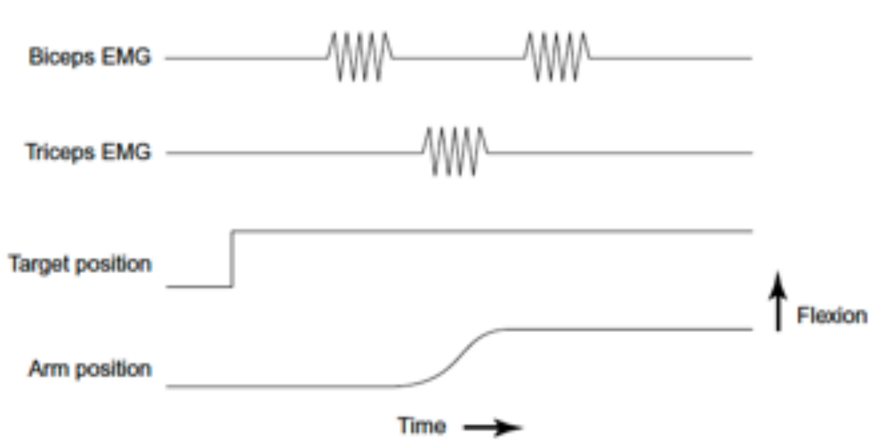
— Gordon et al., 1994, *Exp Brain Res* 99:112

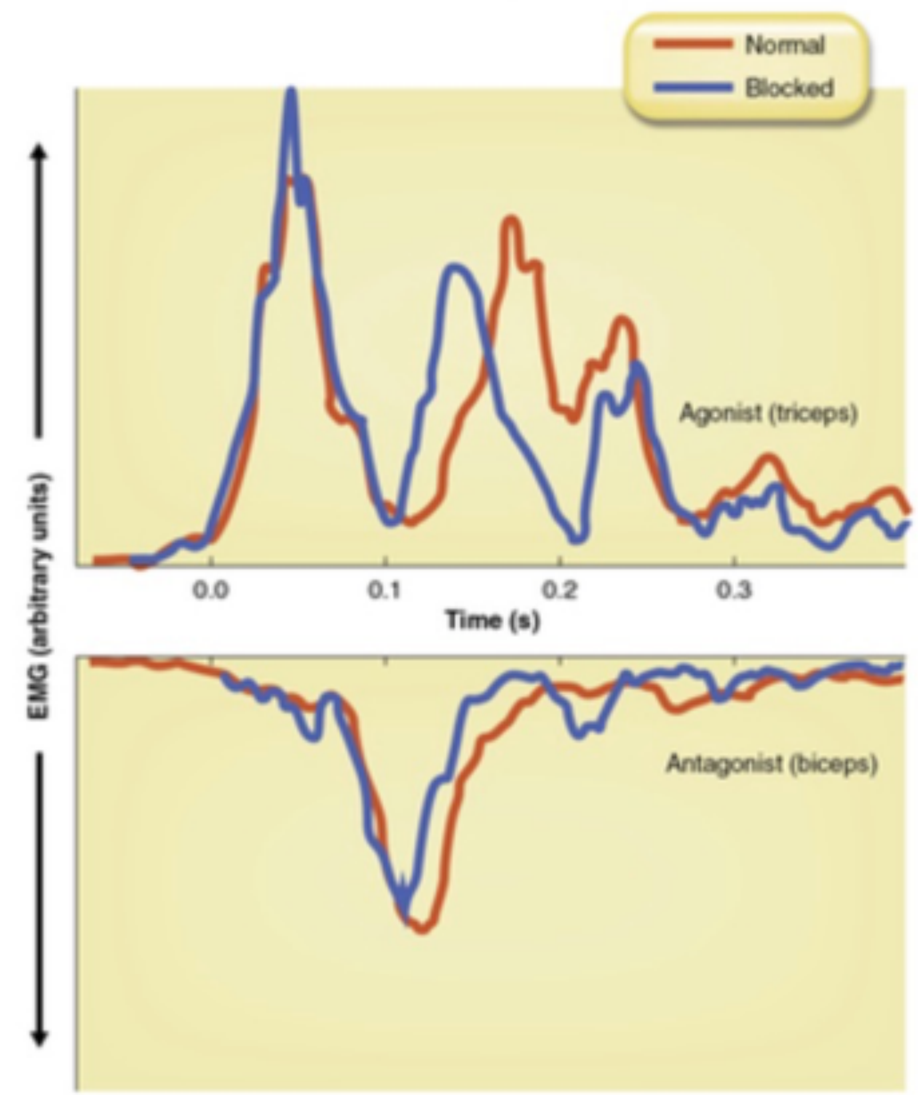
MOTOR INVARIANTS

EMG

Triphasic pattern during fast movements

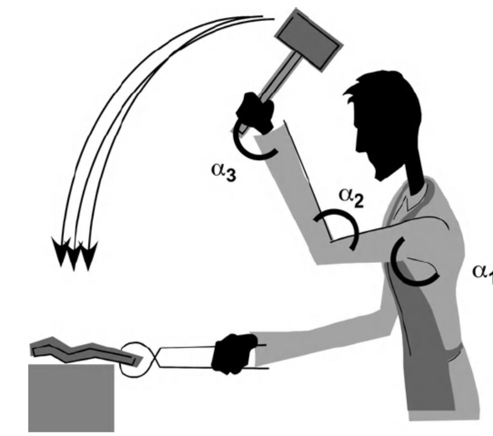






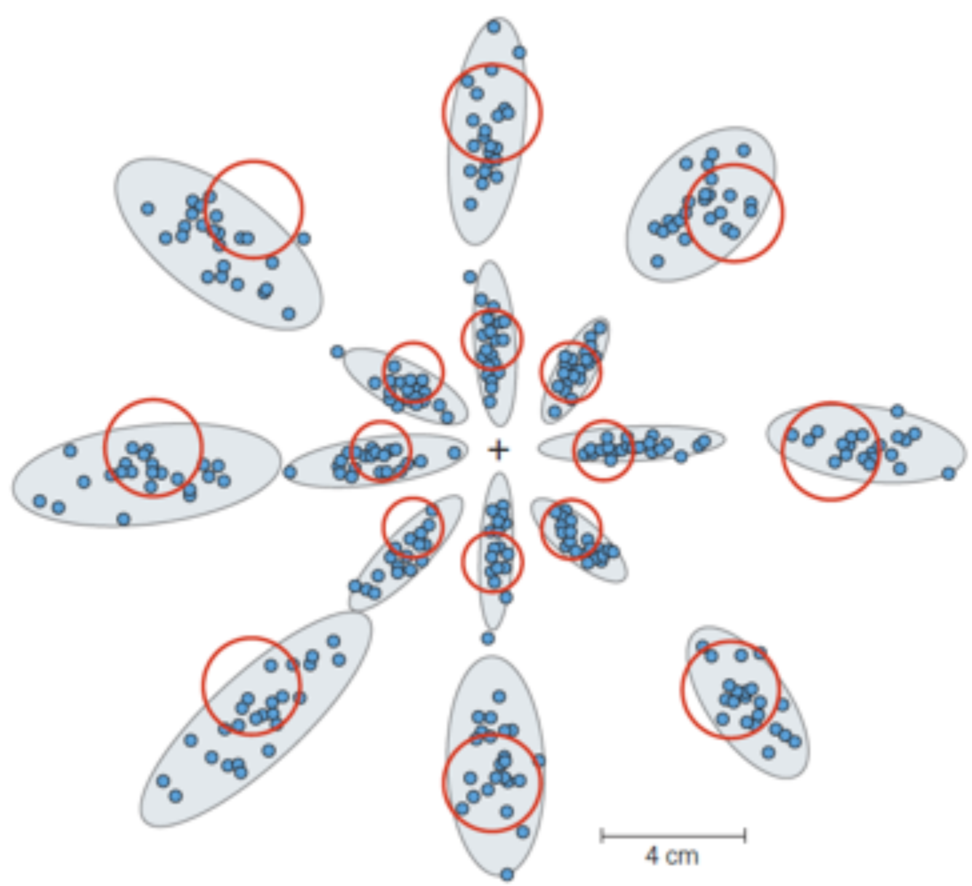
—Wadman et al., 1979, *J Hum Mov Stud* 5:3

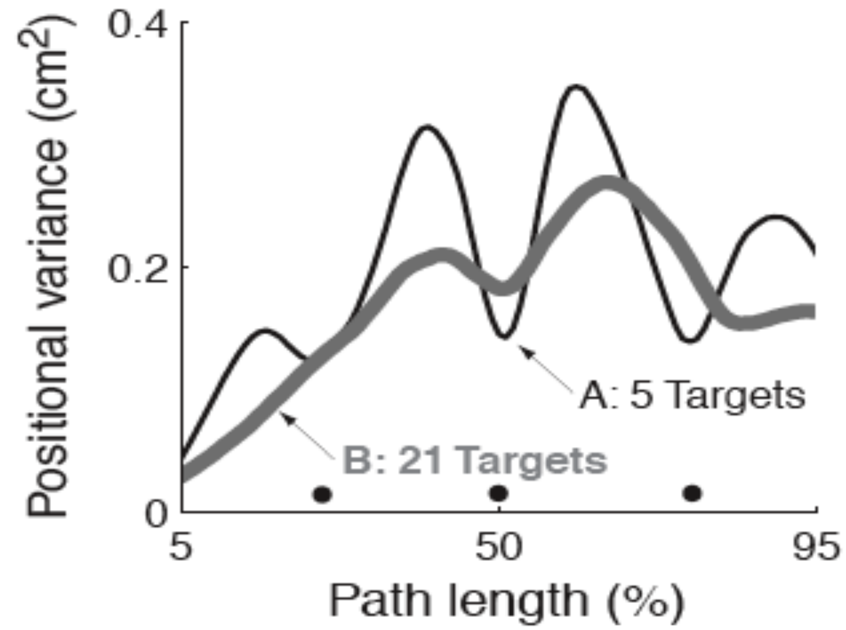
MOTOR VARIABILITY

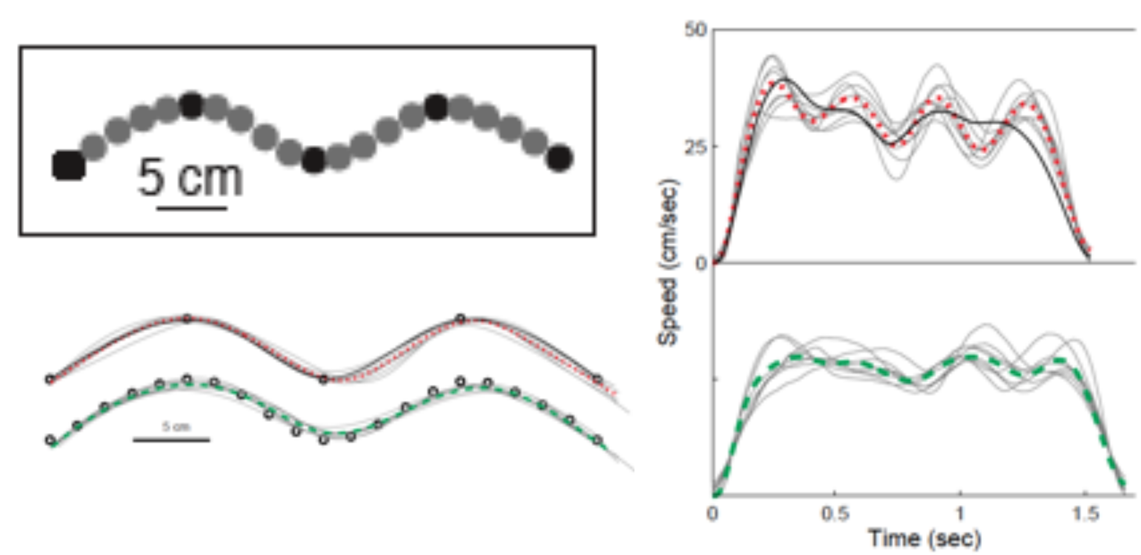


Uncontrolled manifold, structured variability

« Repetition without repetition » (Bernstein)





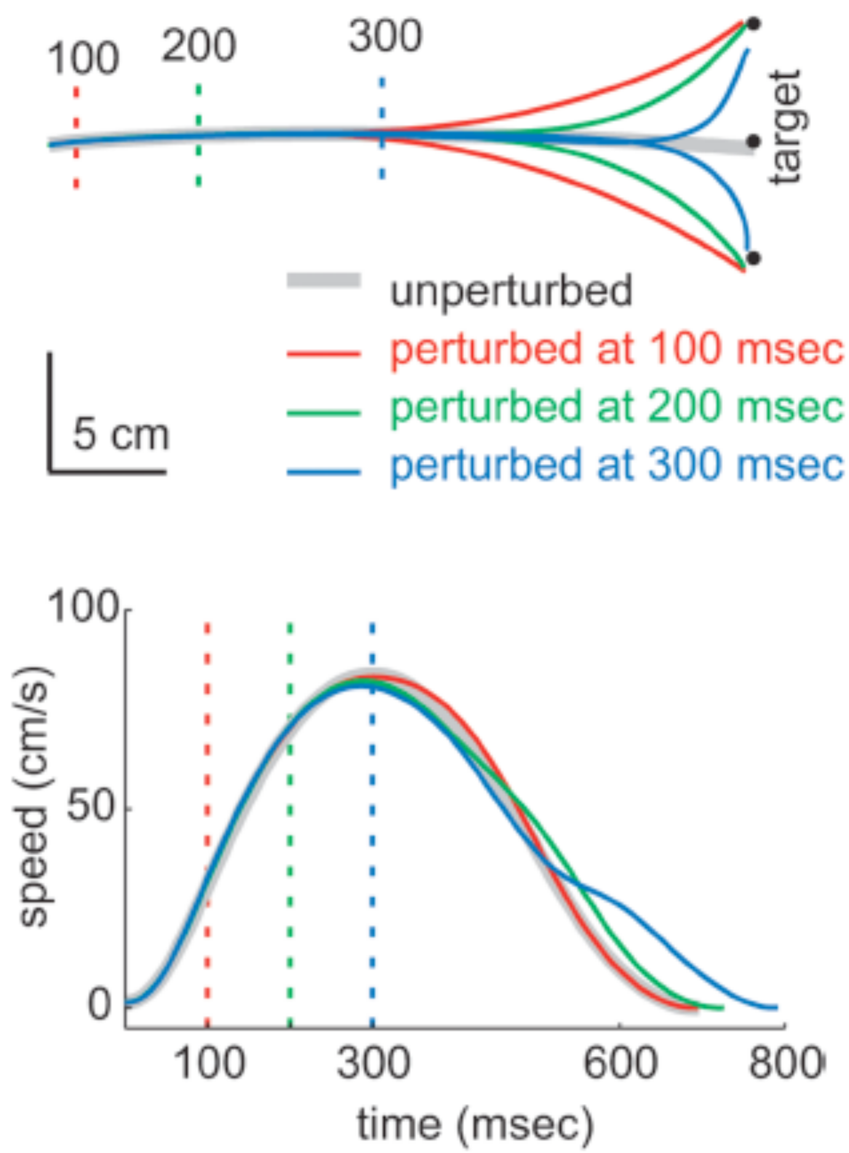


— Gordon et al., 1994, *Exp Brain Res* 99:97

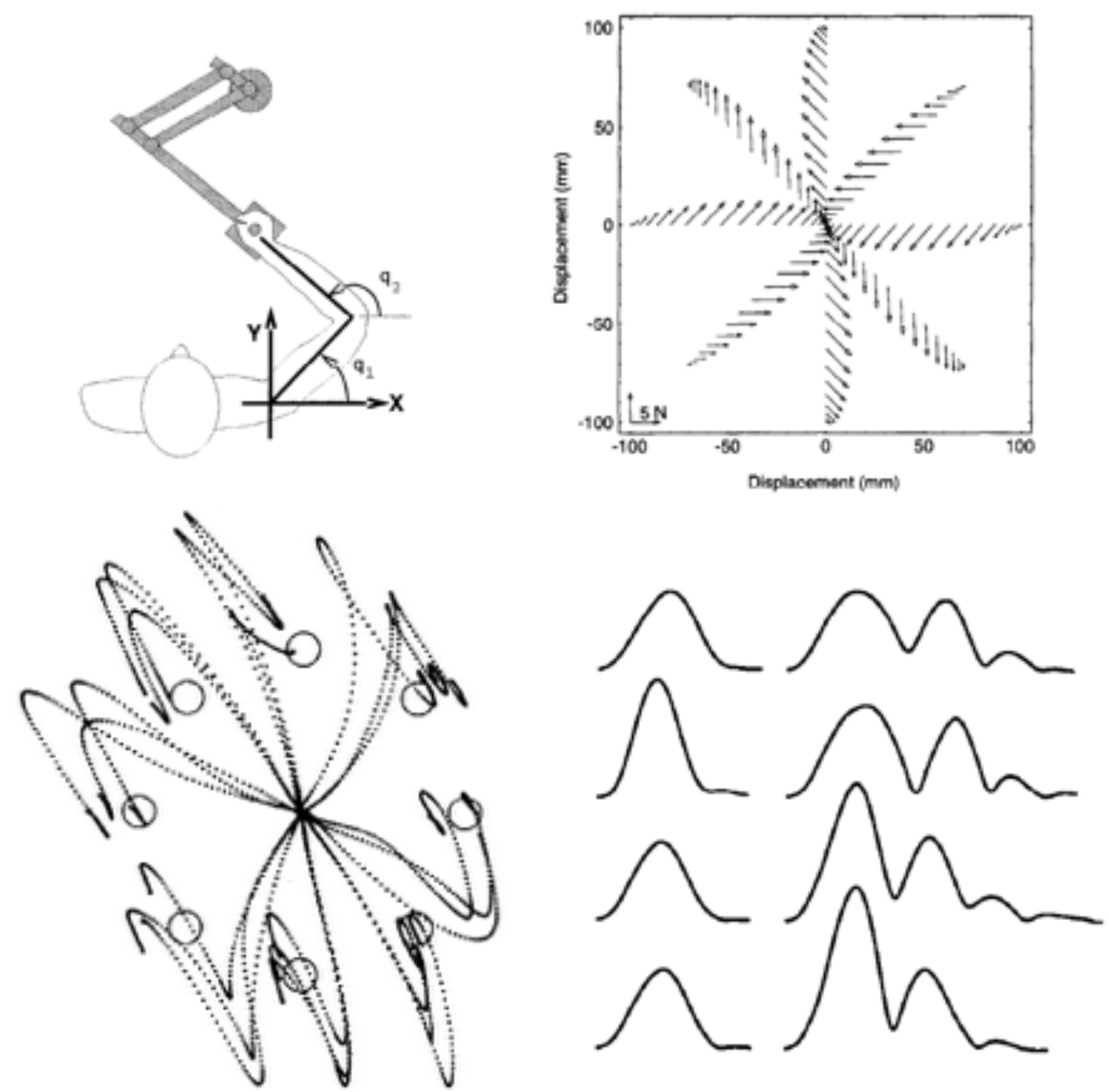
— Todorov & Jordan, 2002, *Nat Neurosci* 5:1226

FLEXIBILITY

Motor control is highly flexible in space and time



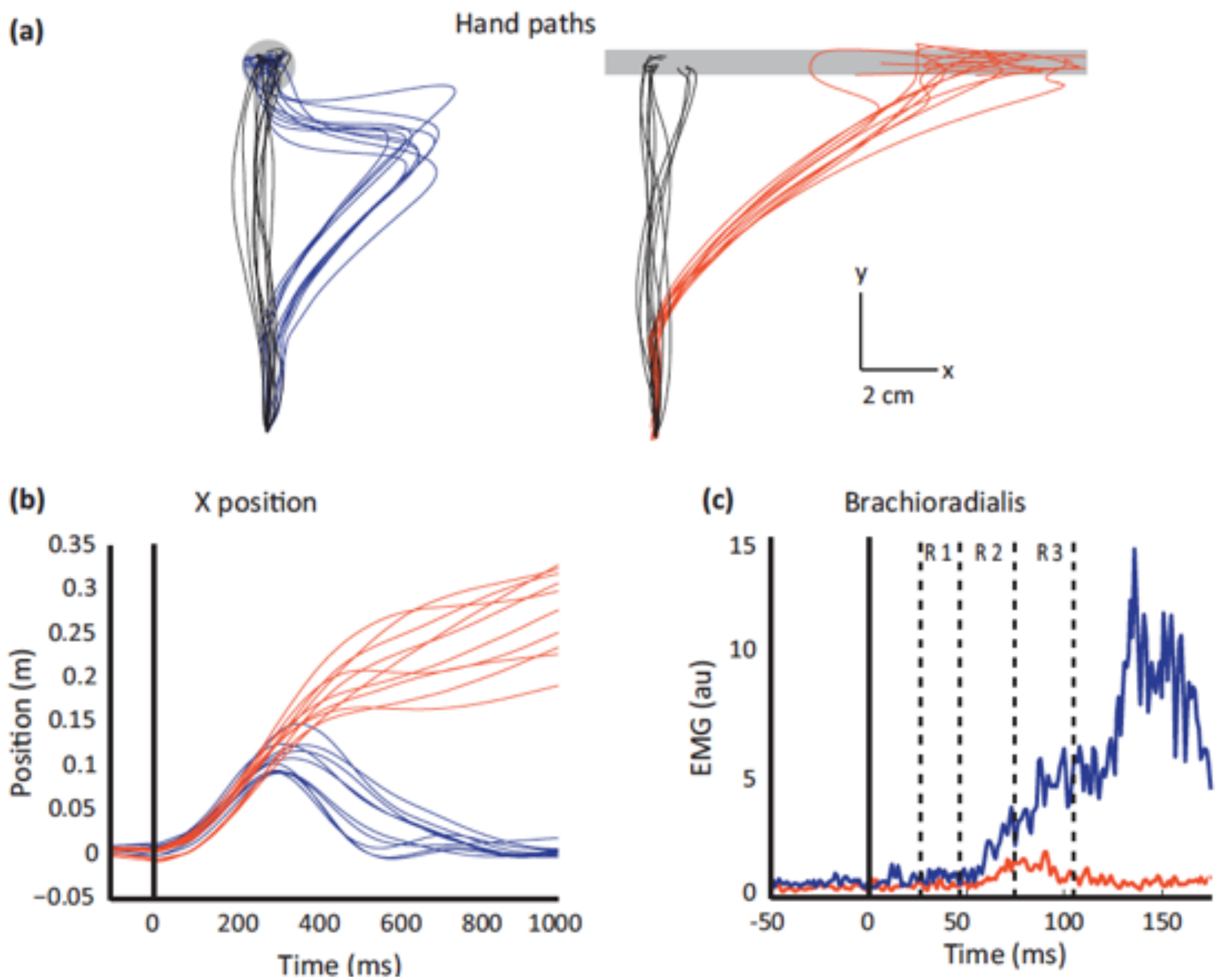
— Liu & Todorov, 2007, *J Neurosci* 27:9354



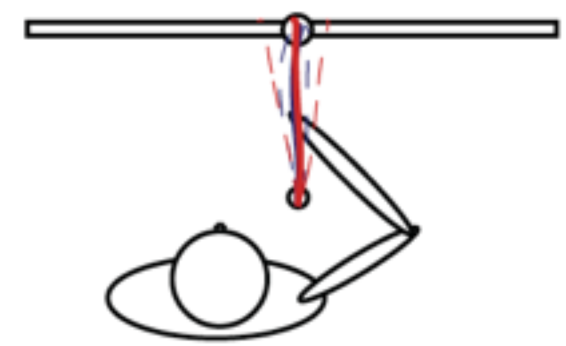
— Shadmehr & Mussa-Ivaldi, 1994, *J Neurosci* 14:3208

FLEXIBILITY

Errors are only corrected if they affect the behavioral goal and are ignored if they do not



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



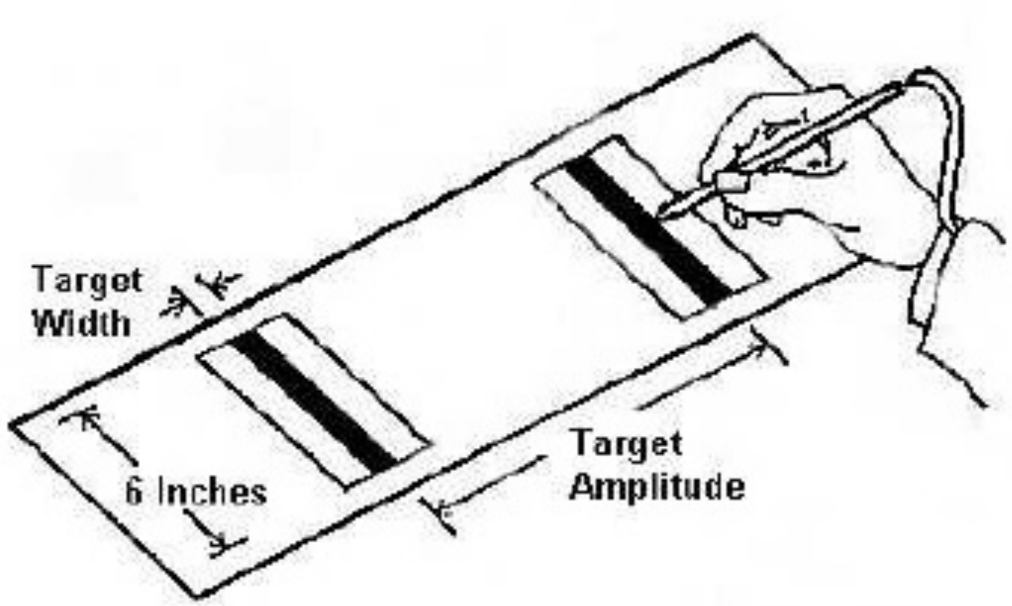
Corrective responses are directed back to the circular target, whereas responses for the rectangular bar are redirected to a new location along the bar.

→ **Corrective responses do not return to a desired trajectory**

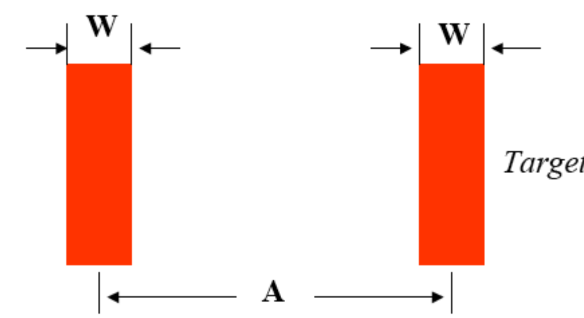
LAWS OF MOVEMENT

Fitts’ law

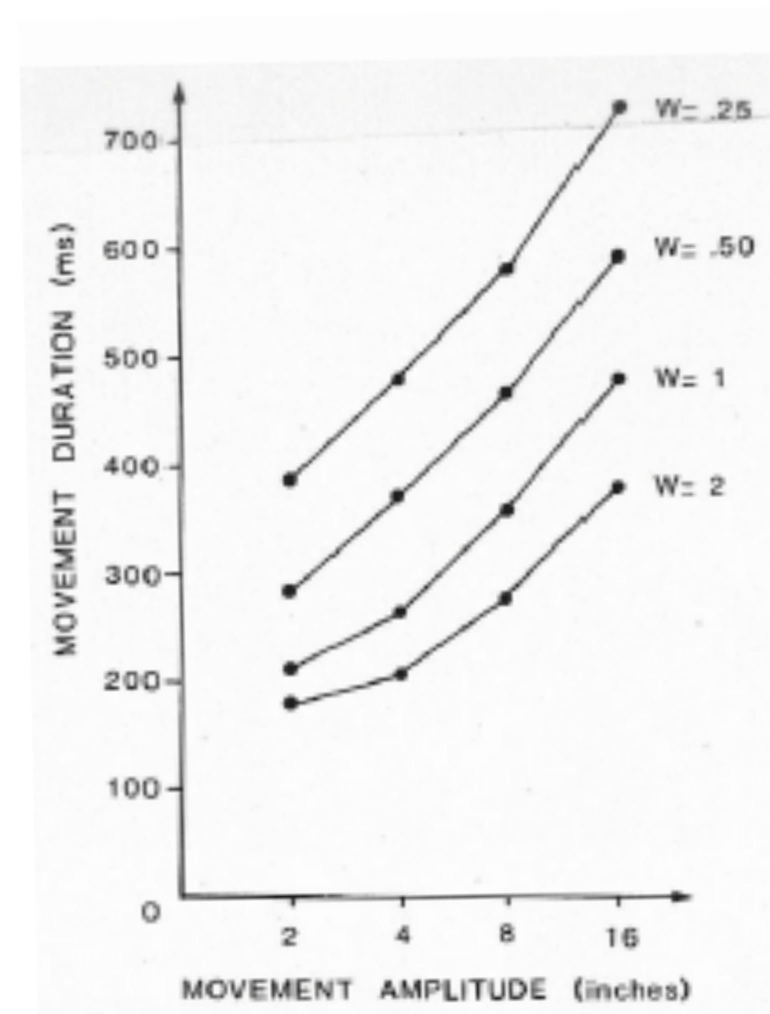
Speed/accuracy trade-off



— Fitts, 1954, *J Exp Psychol* 47:381



$$MT = a + b\,\underbrace{[\mathrm{Log}_2\,(2A/W)]}_{\text{ID (index of Difficulty)}}$$



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*

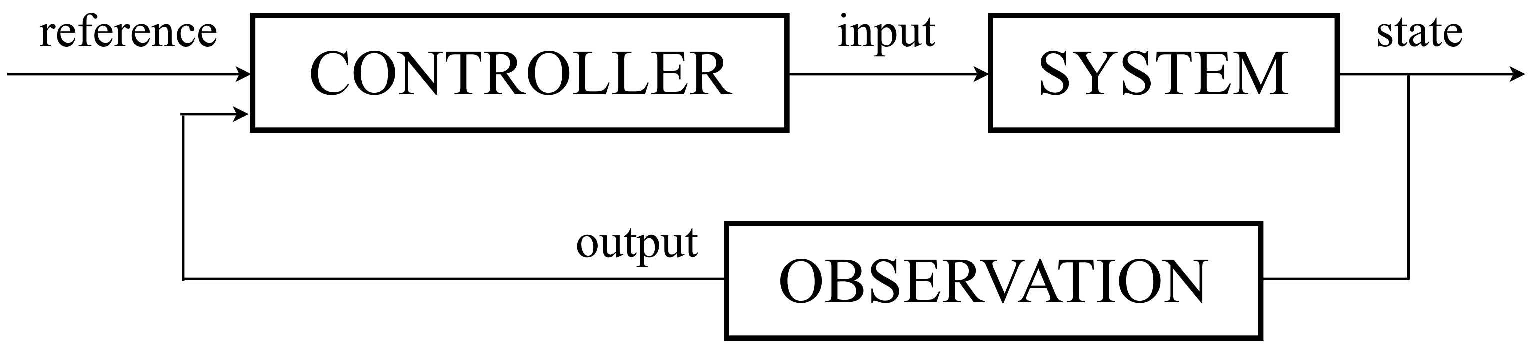
$y[n] = g(x[n])$ *output equation*

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

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

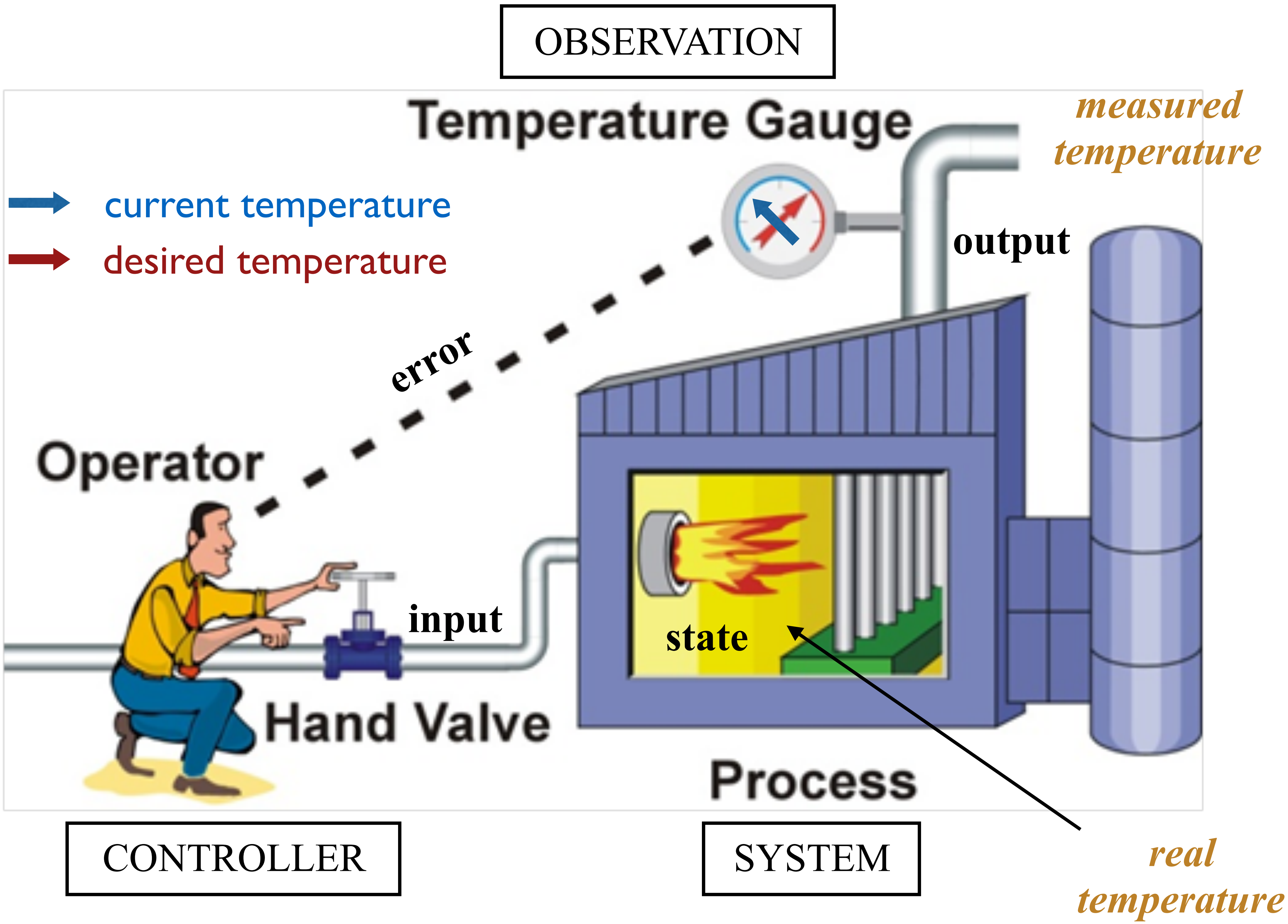
Control theory

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

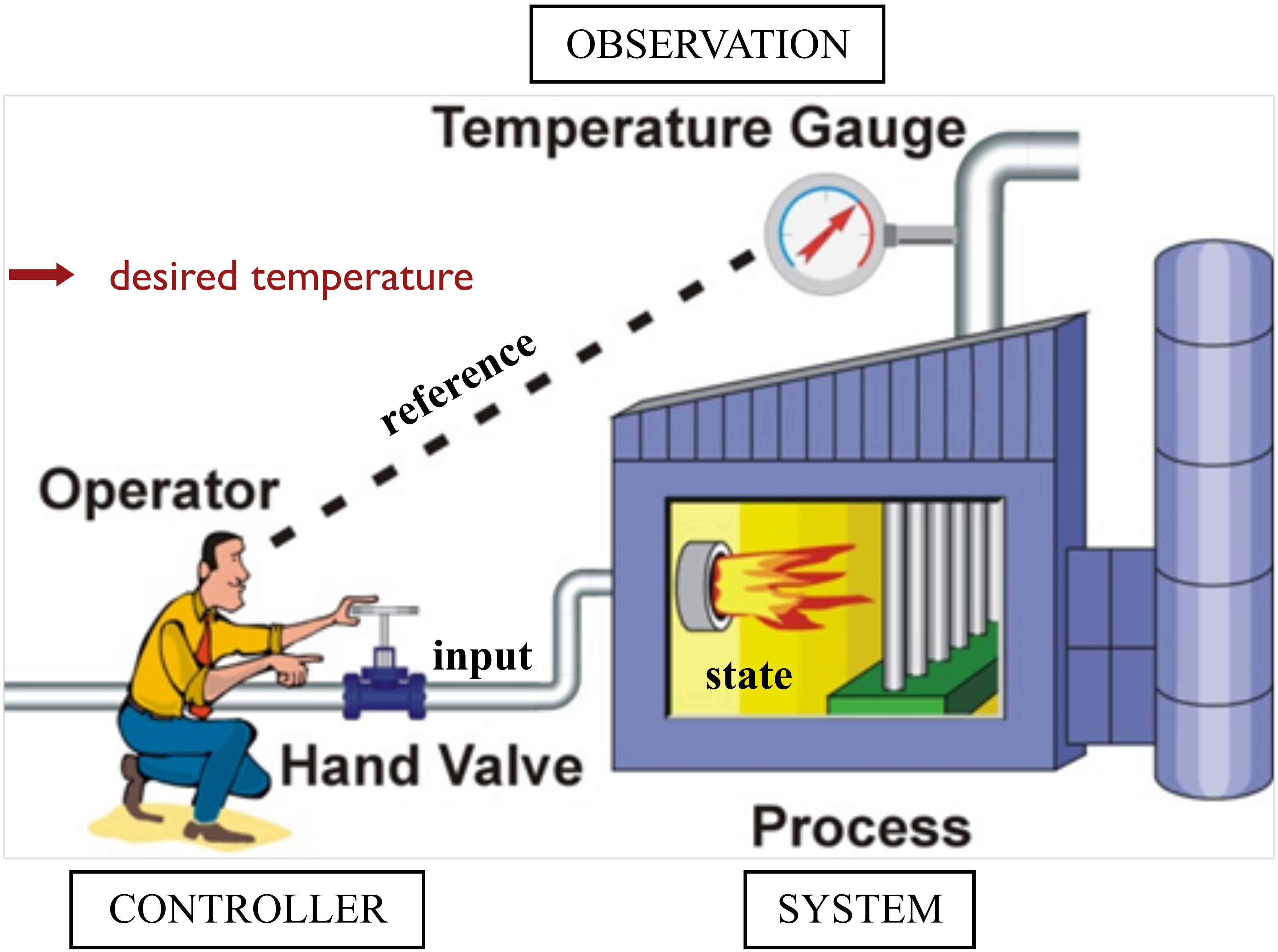


reference
- desired trajectory
- fixed point

TWO CONTROL PRINCIPLES — CLOSED LOOP



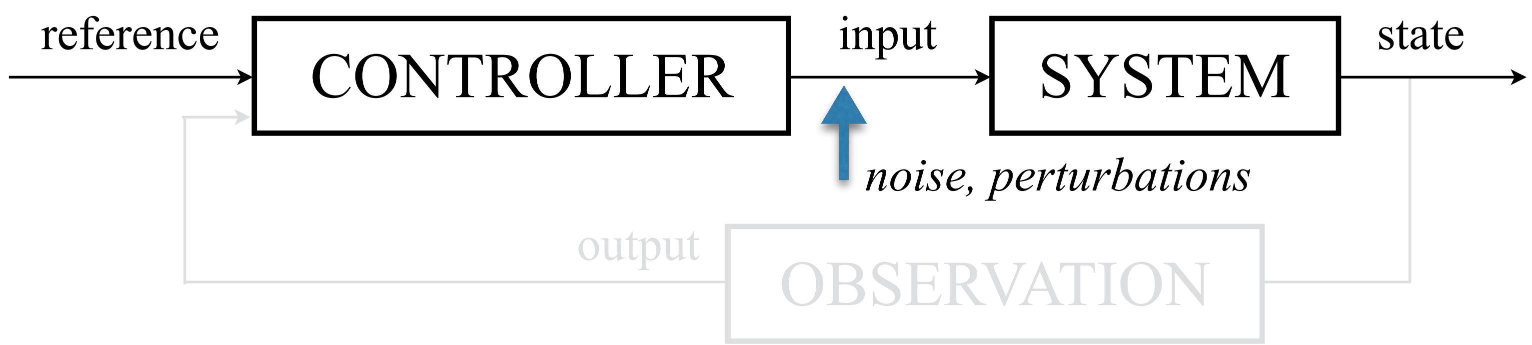
TWO CONTROL PRINCIPLES — OPEN LOOP



TWO CONTROL PRINCIPLES

Open-loop (feedforward)

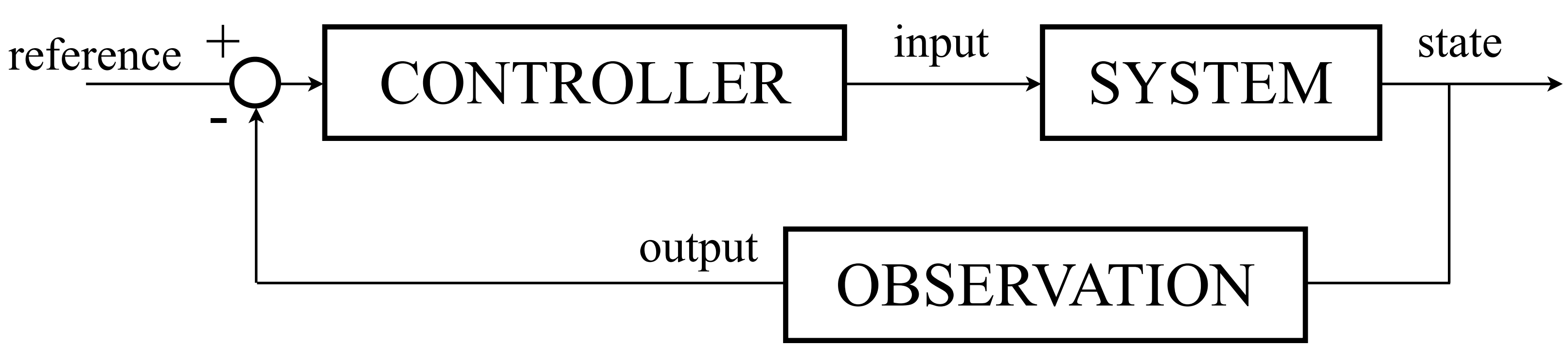
The controller is an *inverse* model of the system.



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

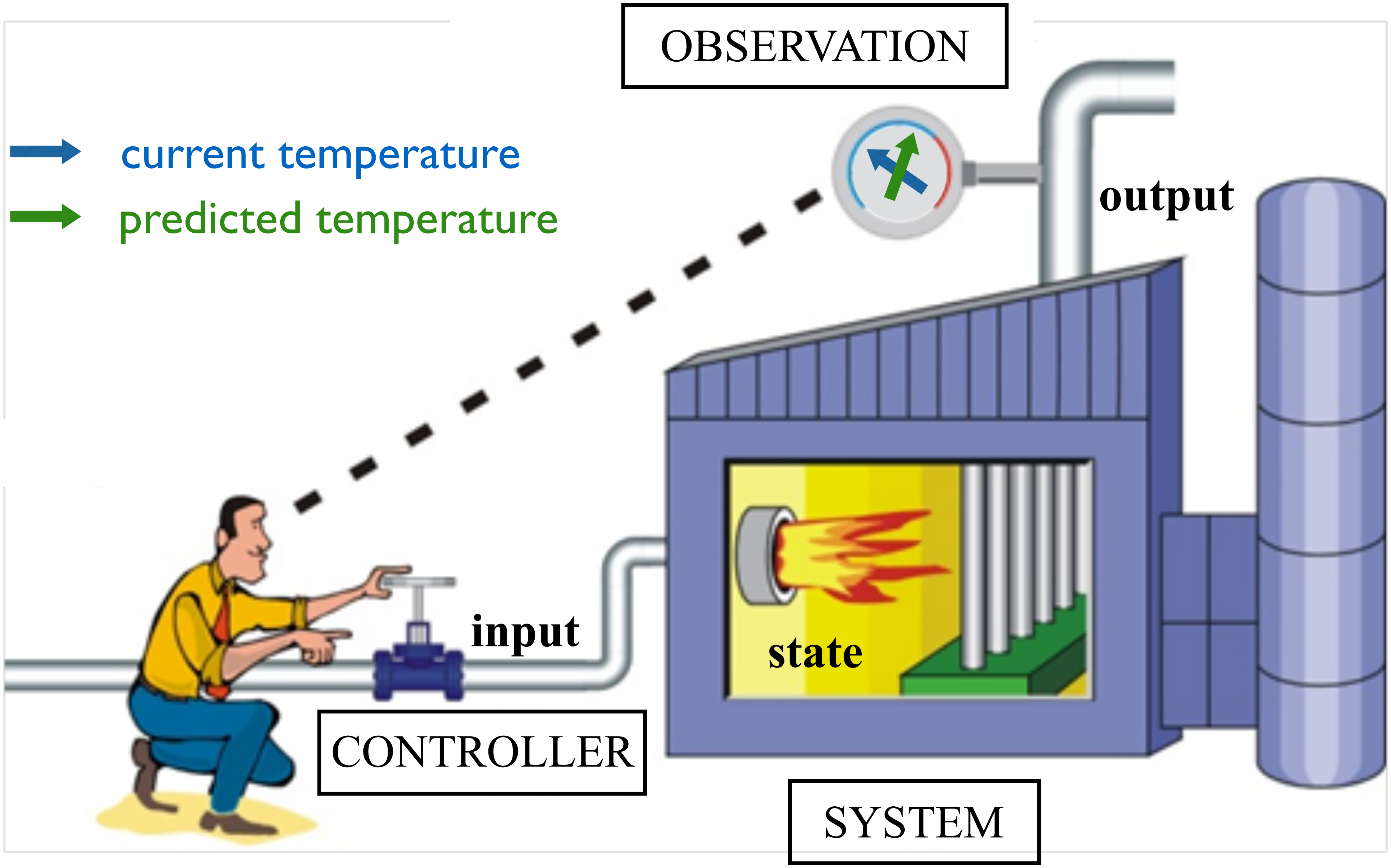
Closed-loop (feedback)

The controller is a function of an error signal.



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

FORWARD MODEL

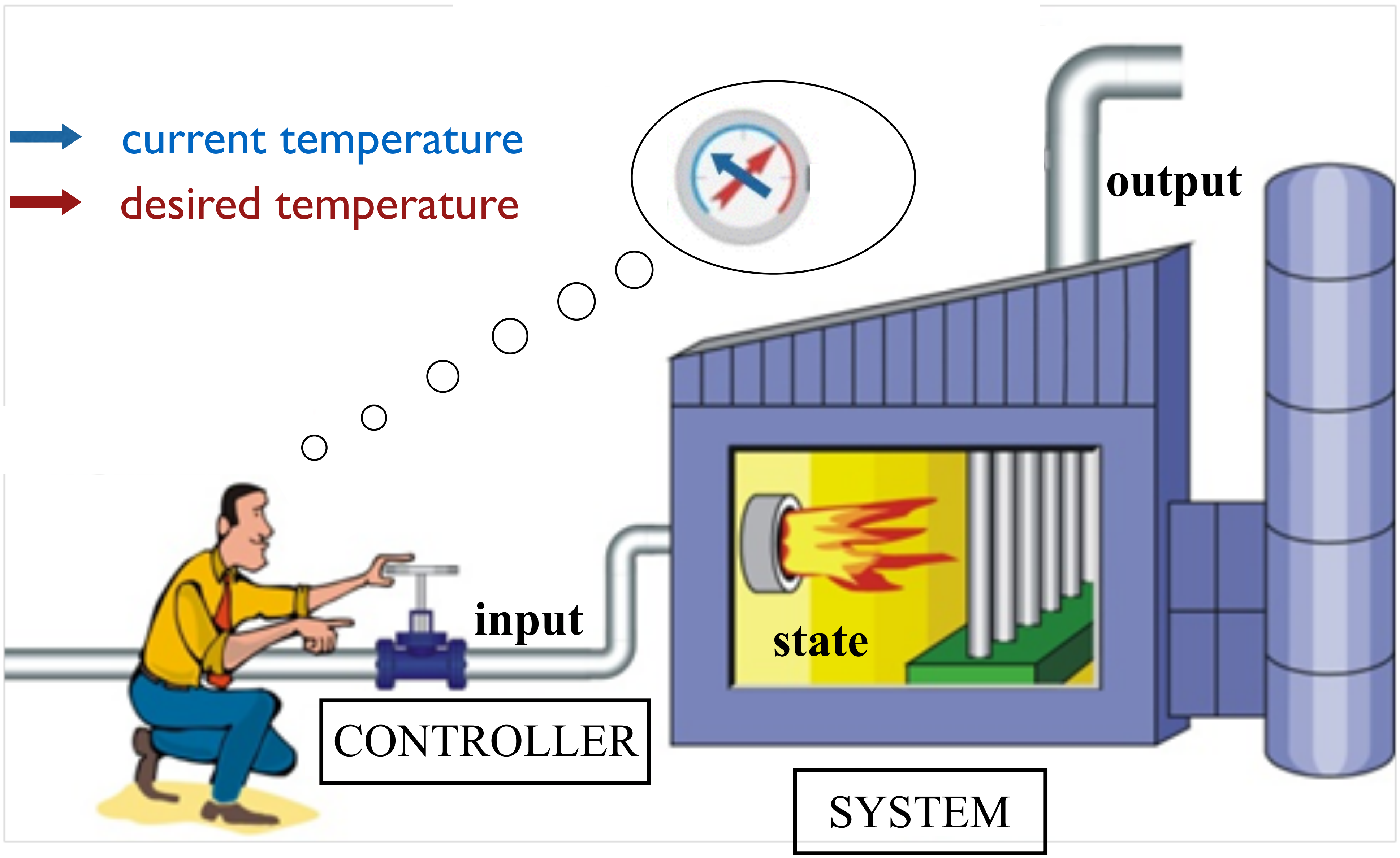


Model of the causal relationship between inputs and their consequences (states, outputs)

input → predicted output

input → predicted state

INVERSE MODEL



Model of the relationship between desired consequences (outputs, states) and corresponding inputs

desired state → **input**

desired output → **input**

OPTIMALITY PRINCIPLE

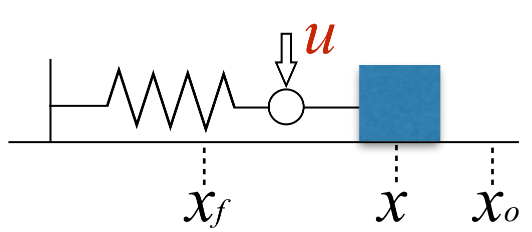
Definition

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.

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*)



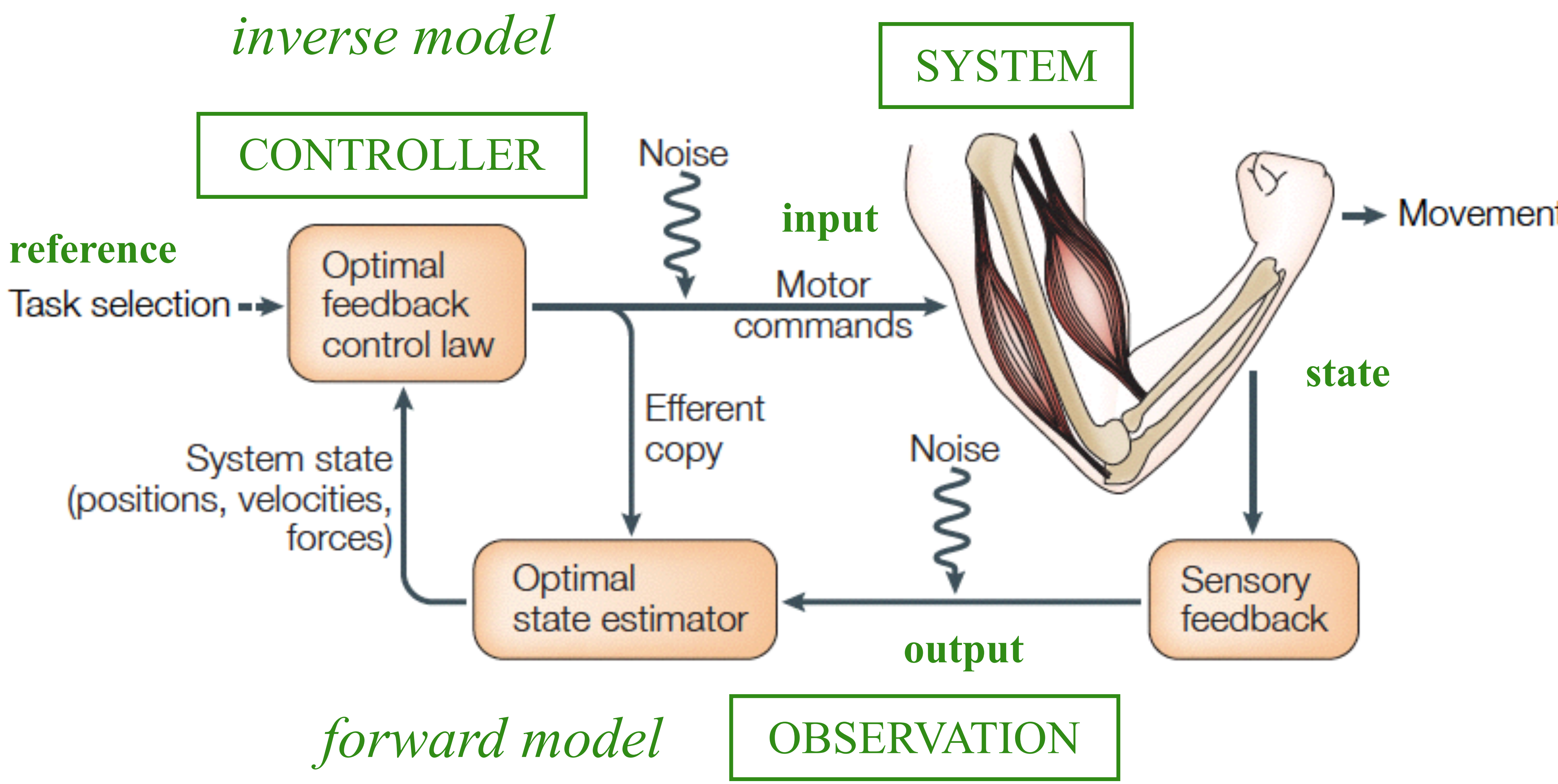
Find the smallest $u(t)$ (t in $[t_o;t_f]$) such that

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

and

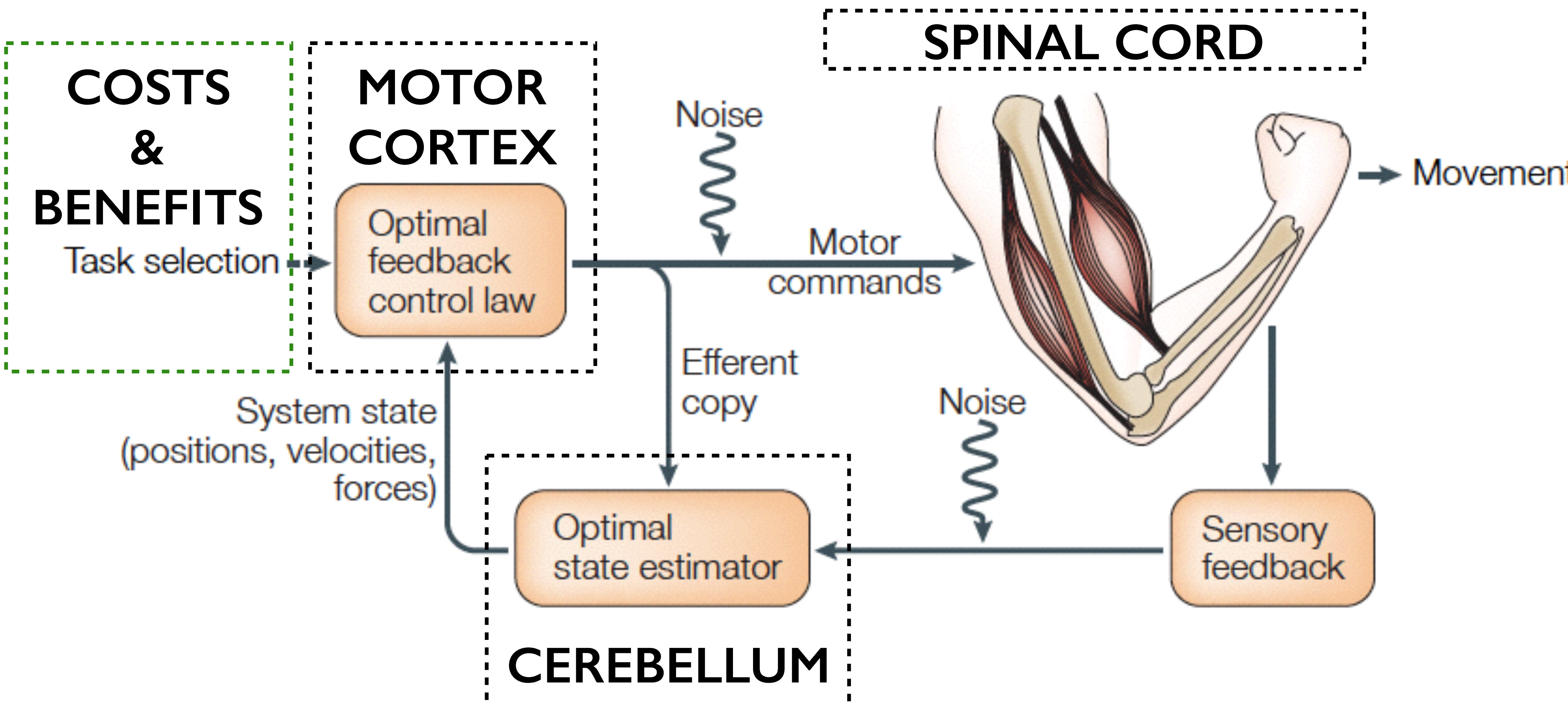
$$m\ddot{x} + b\dot{x} + k(x - x_f) = u$$

ARCHITECTURE



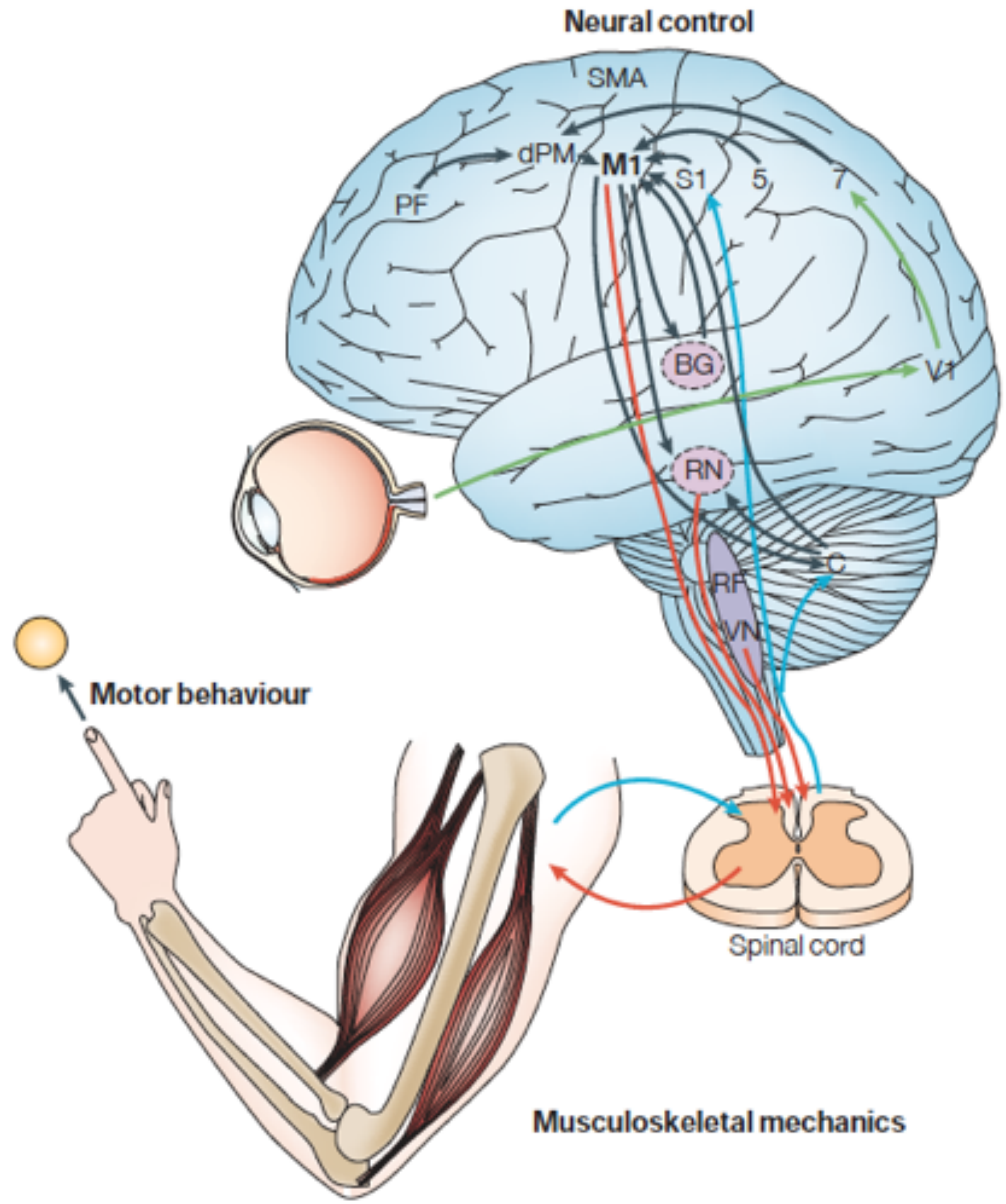
— Scott, 2004, *Nat Rev Neurosci* 5:534

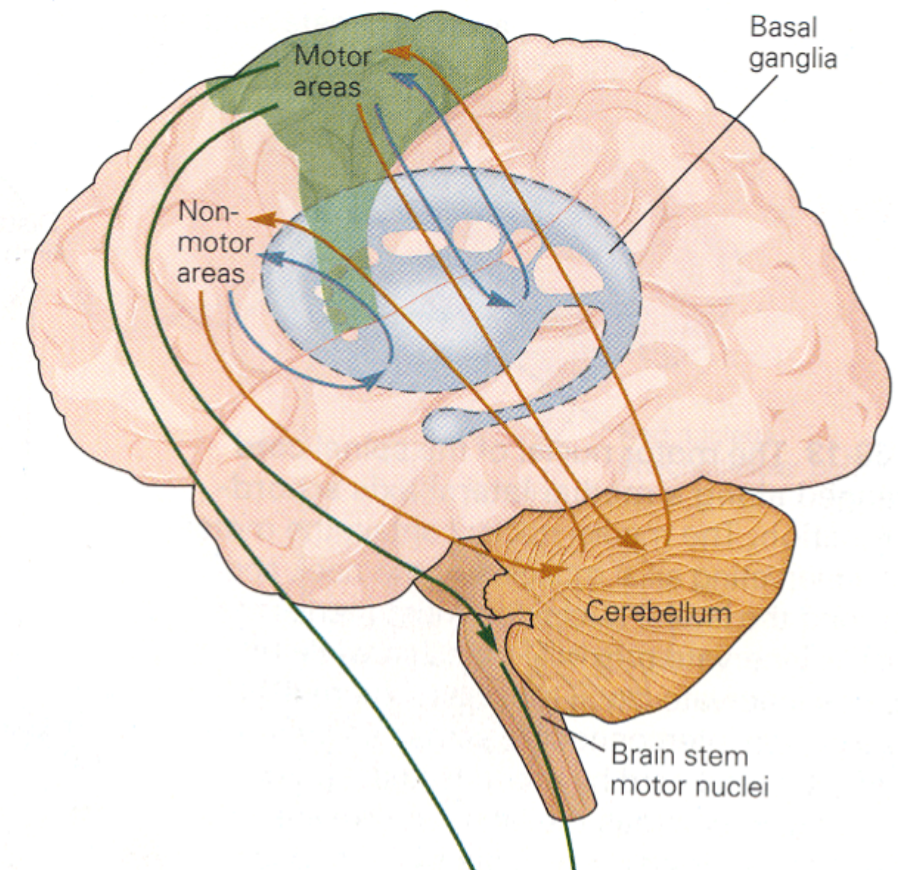
ARCHITECTURE



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

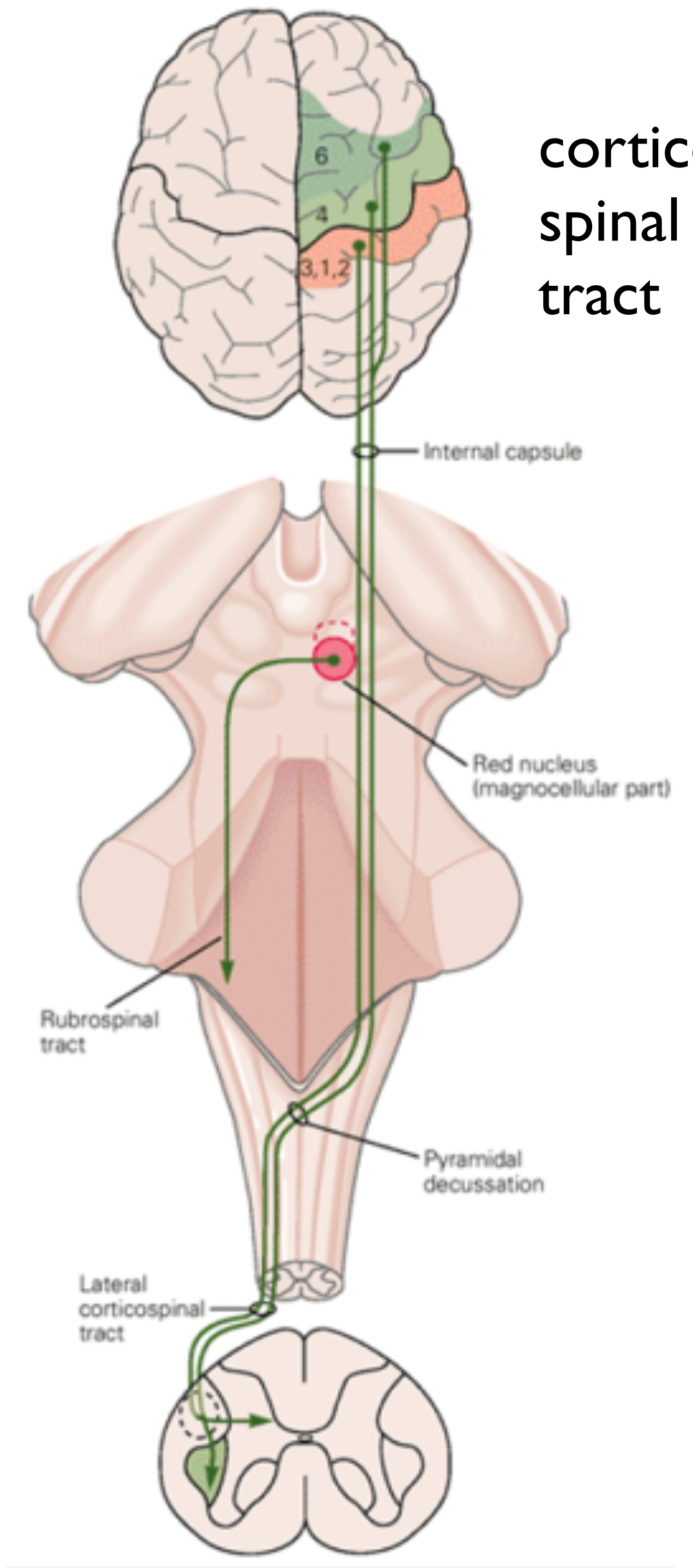
ANATOMY



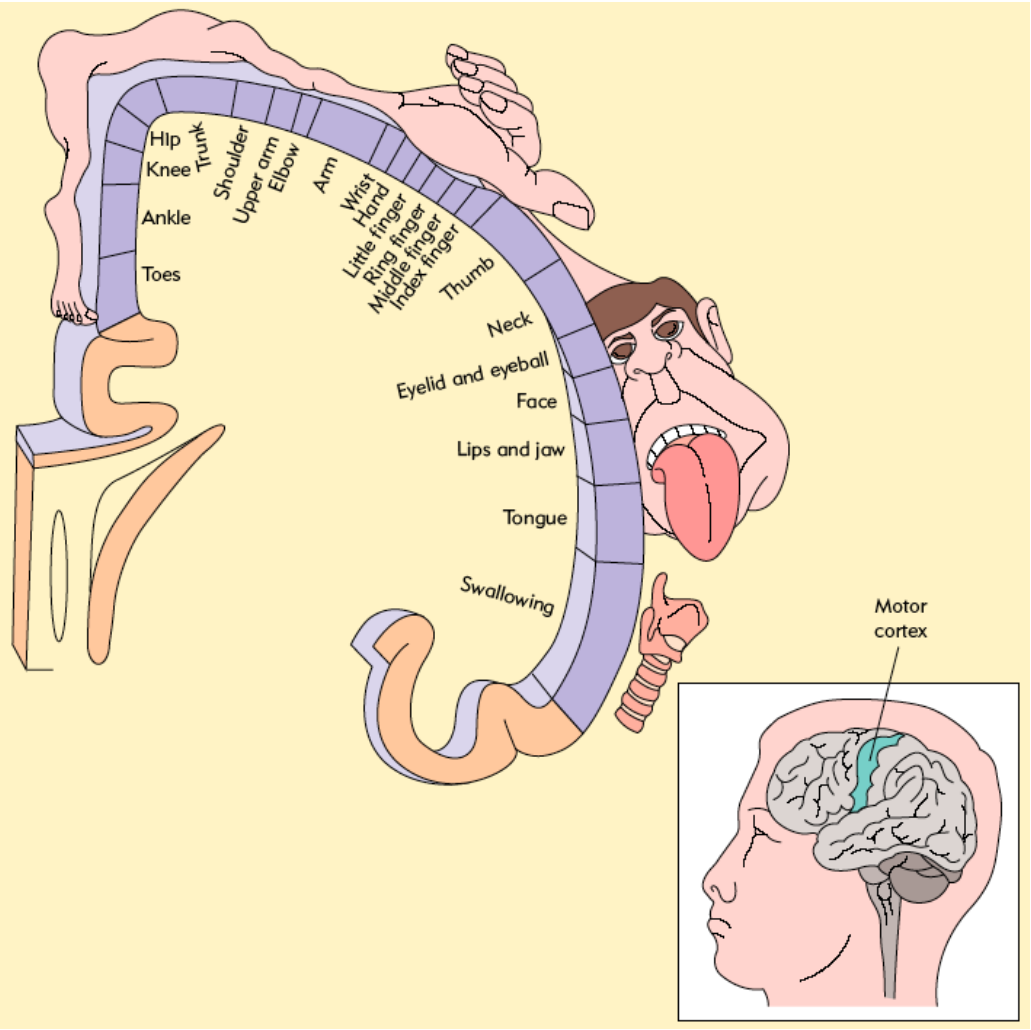


— Scott, 2004, *Nat Rev Neurosci* 5:534

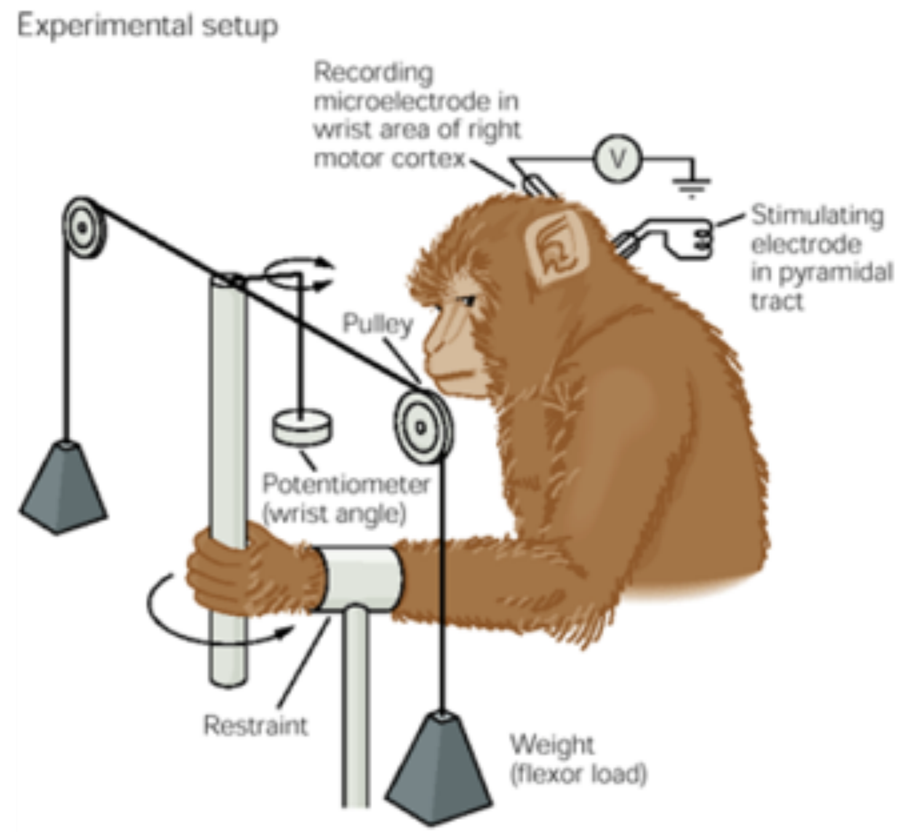
MOTOR CORTEX

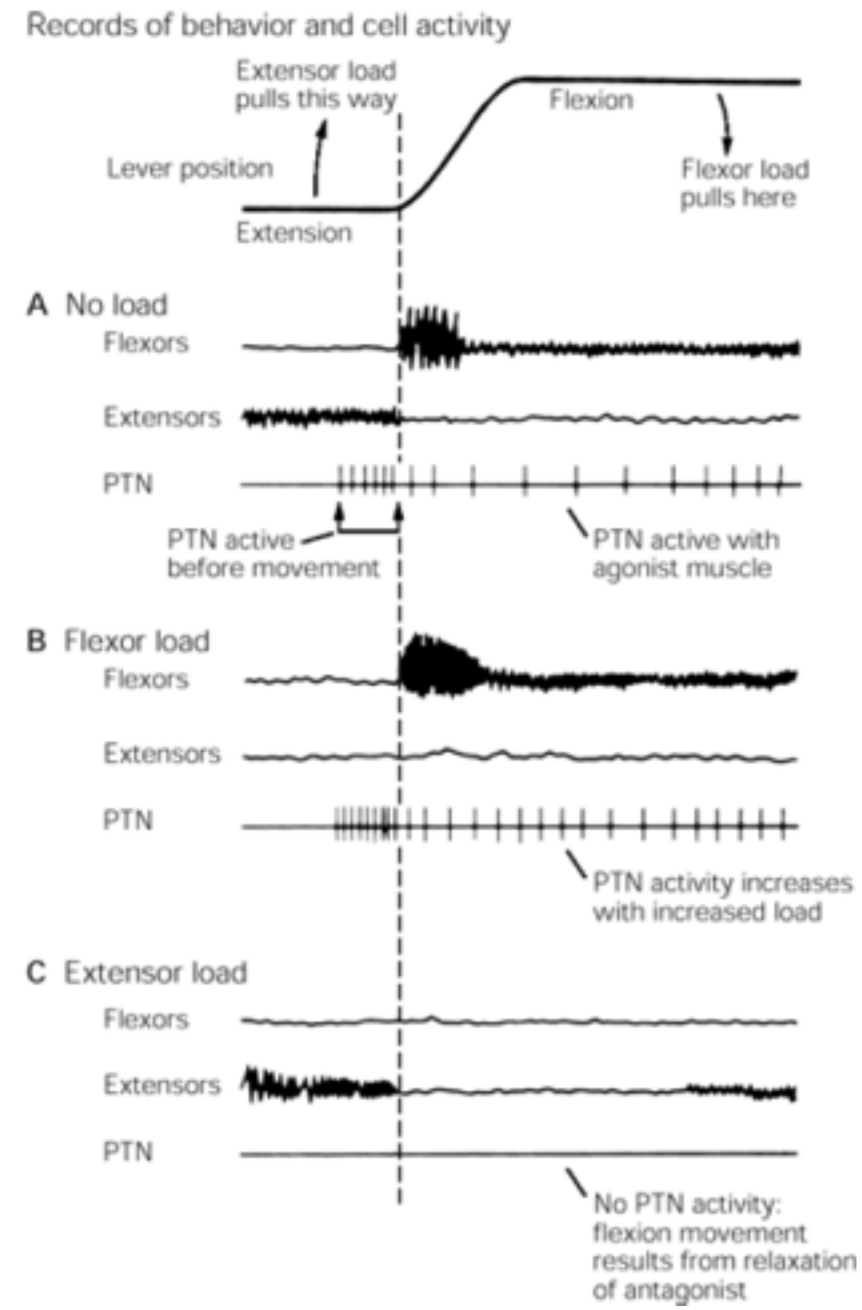


cortico-
spinal
tract



MOTOR CORTEX — PHYSIOLOGY



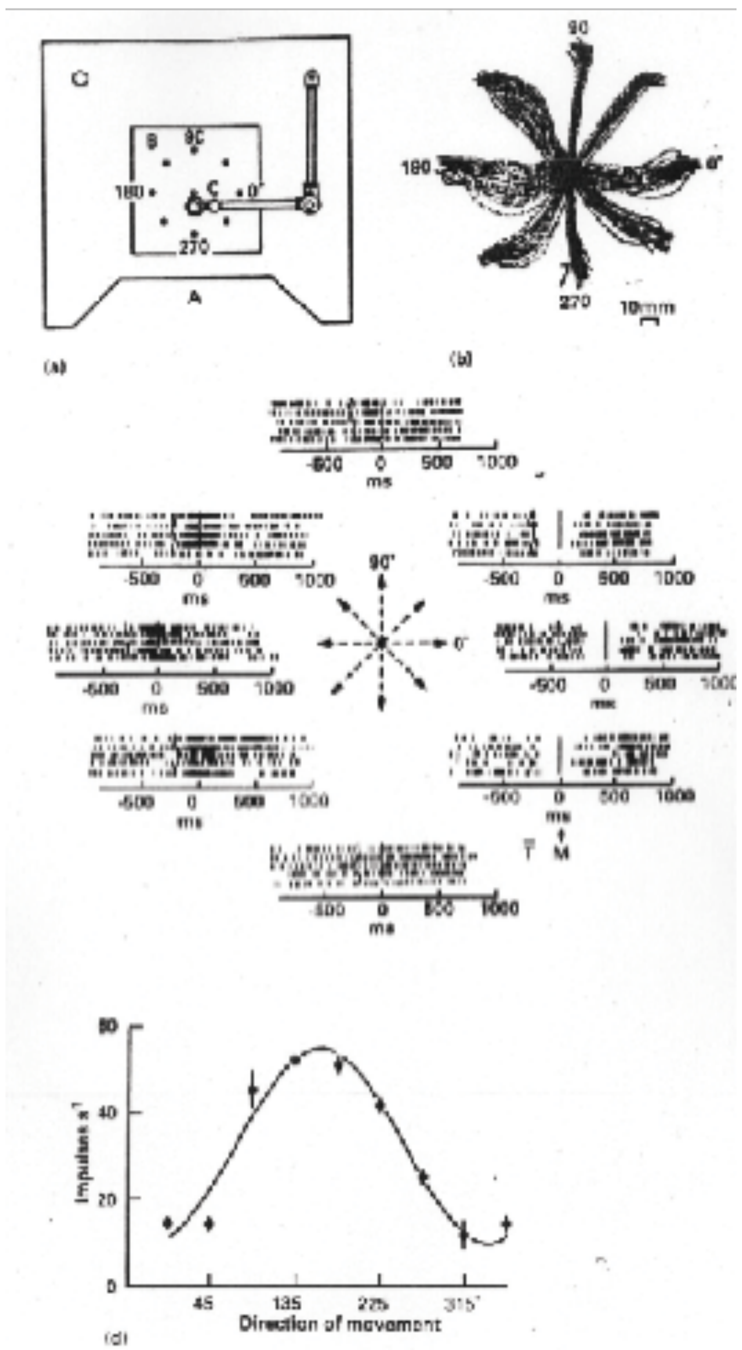


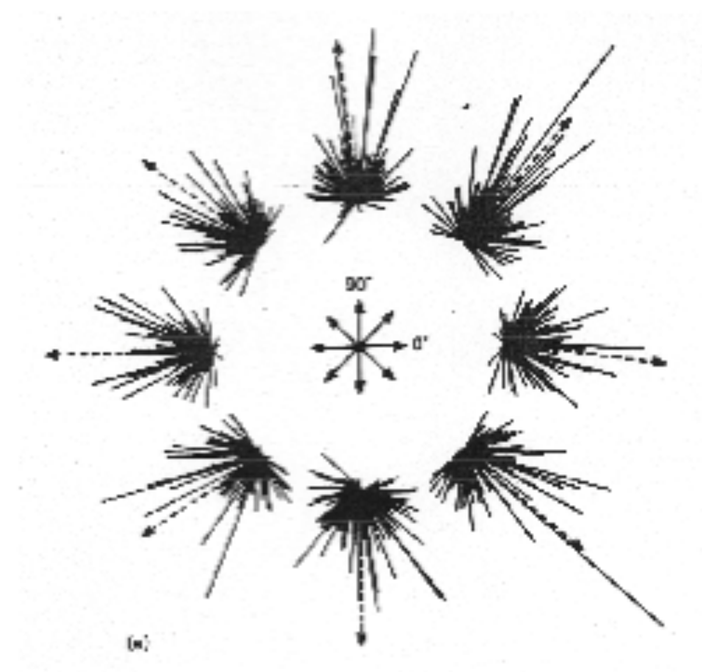
For the majority of PTNs discharge frequency was related primarily to the force (F) and dF/dt and was only secondarily related to the direction of displacement.

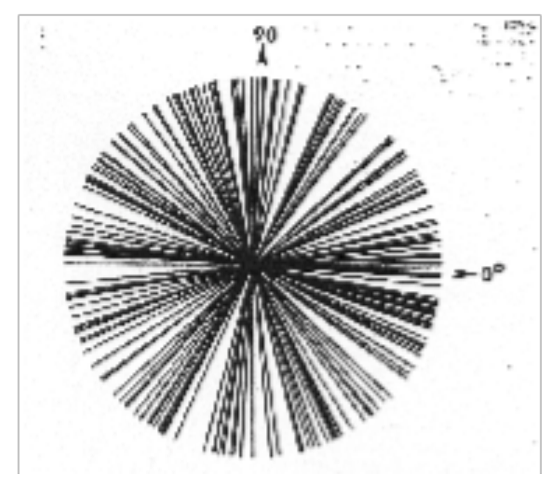
Some PTNs which were unrelated to force were related to the direction of displacement, but not to the fine details of the displacement in the way that numerous other PTNs were related to the fine details of applied force.

— Evarts, 1968, *J Neurophysiol* 31:14

MOTOR CORTEX — PHYSIOLOGY



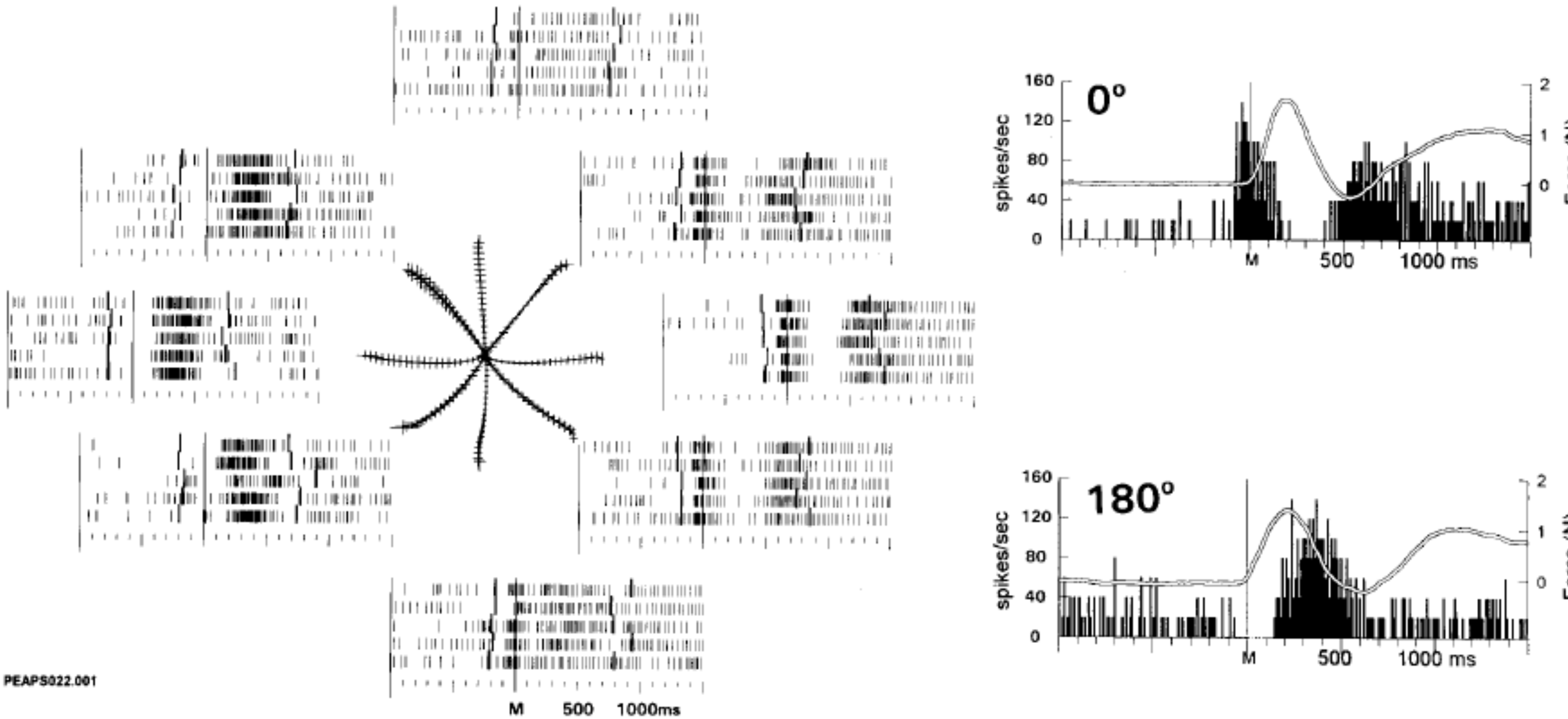




— Georgopoulos et al., 1982, *J Neurosci* 2:1527

MOTOR CORTEX — PHYSIOLOGY

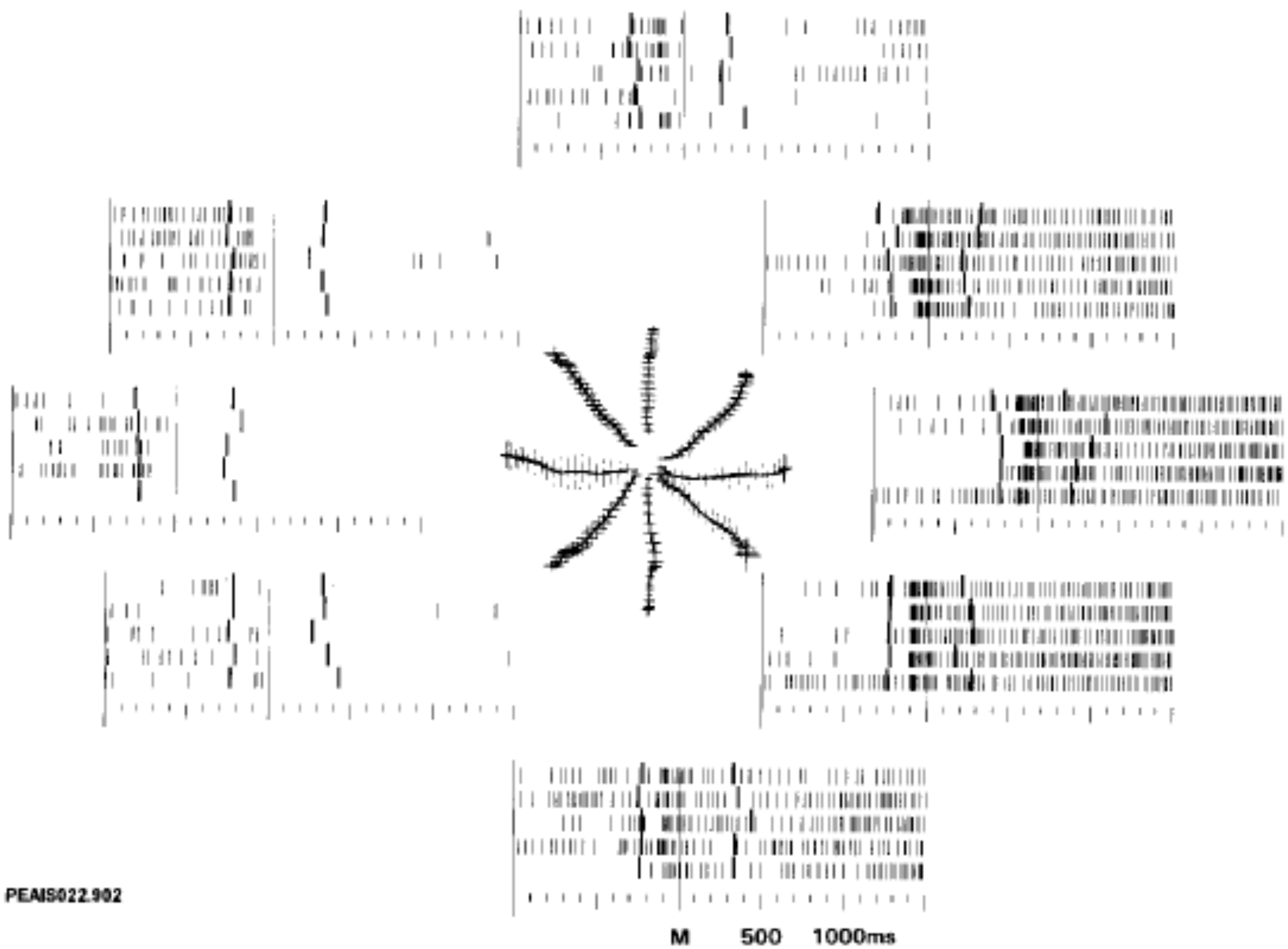
Movement task

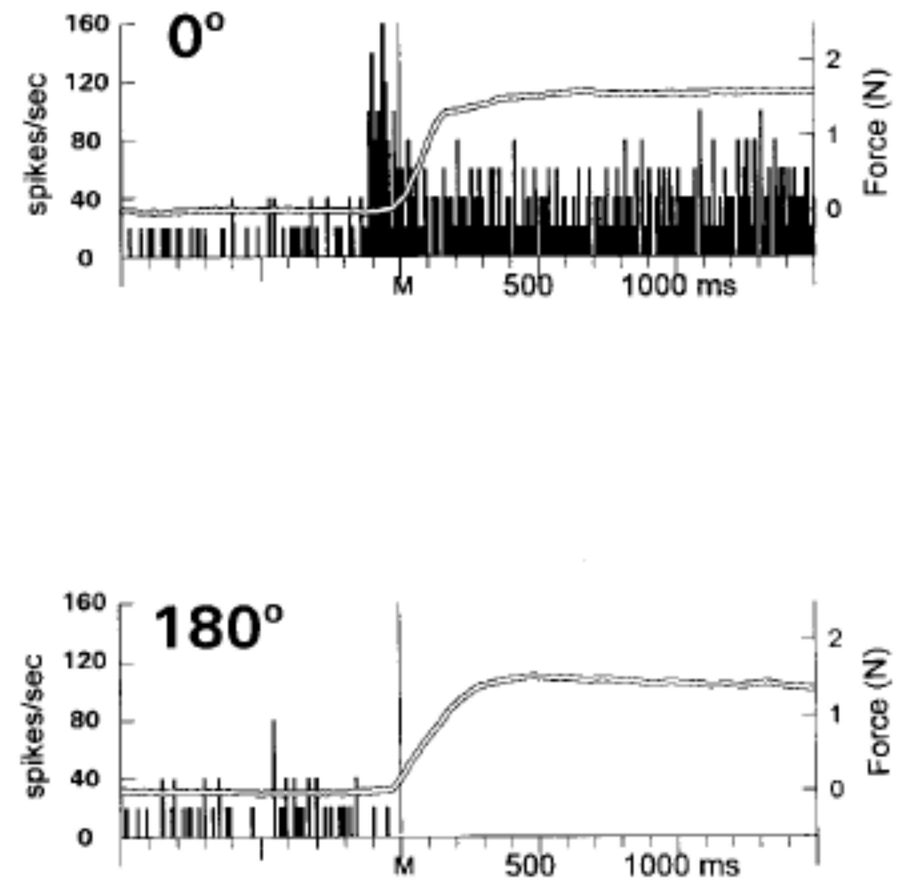


— Sergio & Kalaska, 1998, *J Neurophysiol* 580:1577

MOTOR CORTEX — PHYSIOLOGY

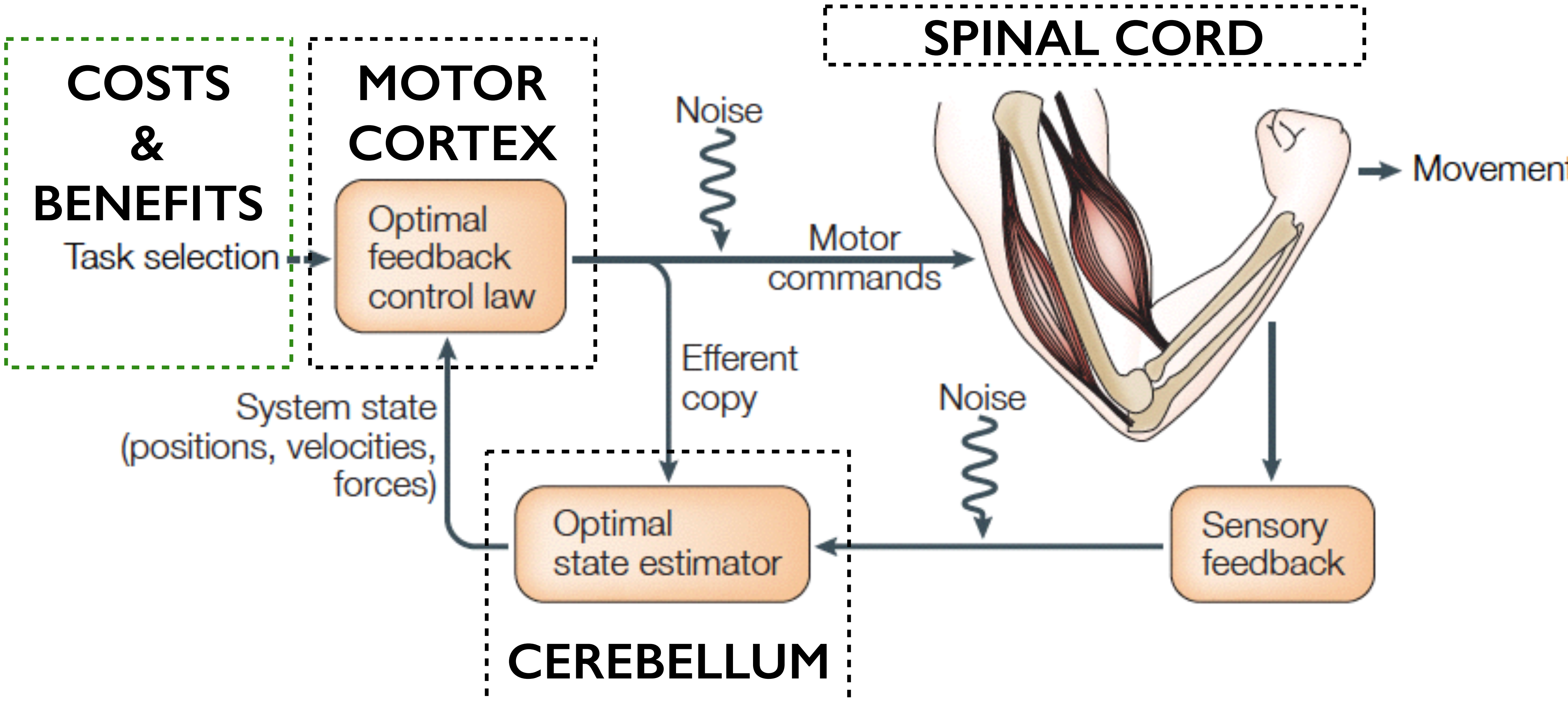
Isometric task





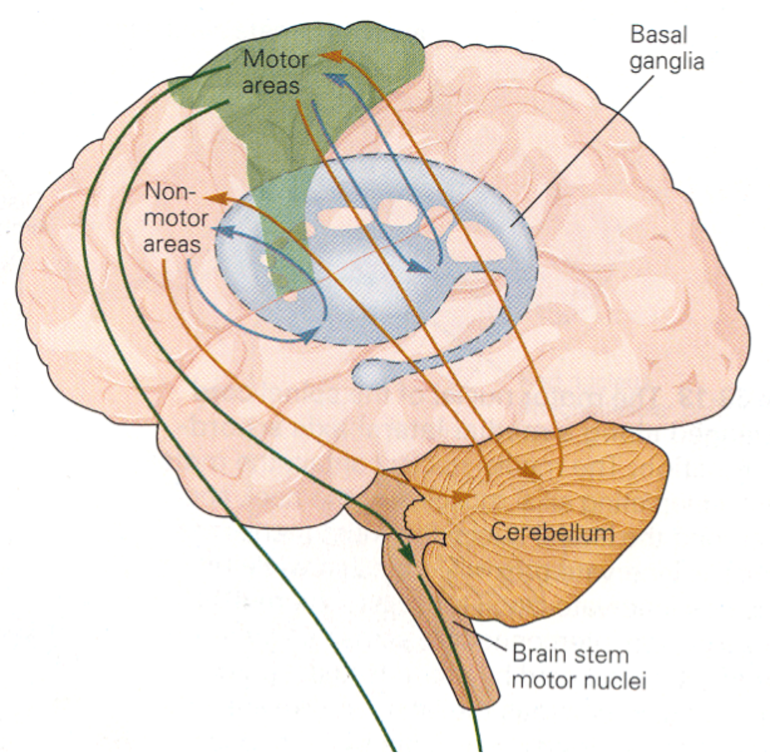
— Sergio & Kalaska, 1998, *J Neurophysiol* 580:1577

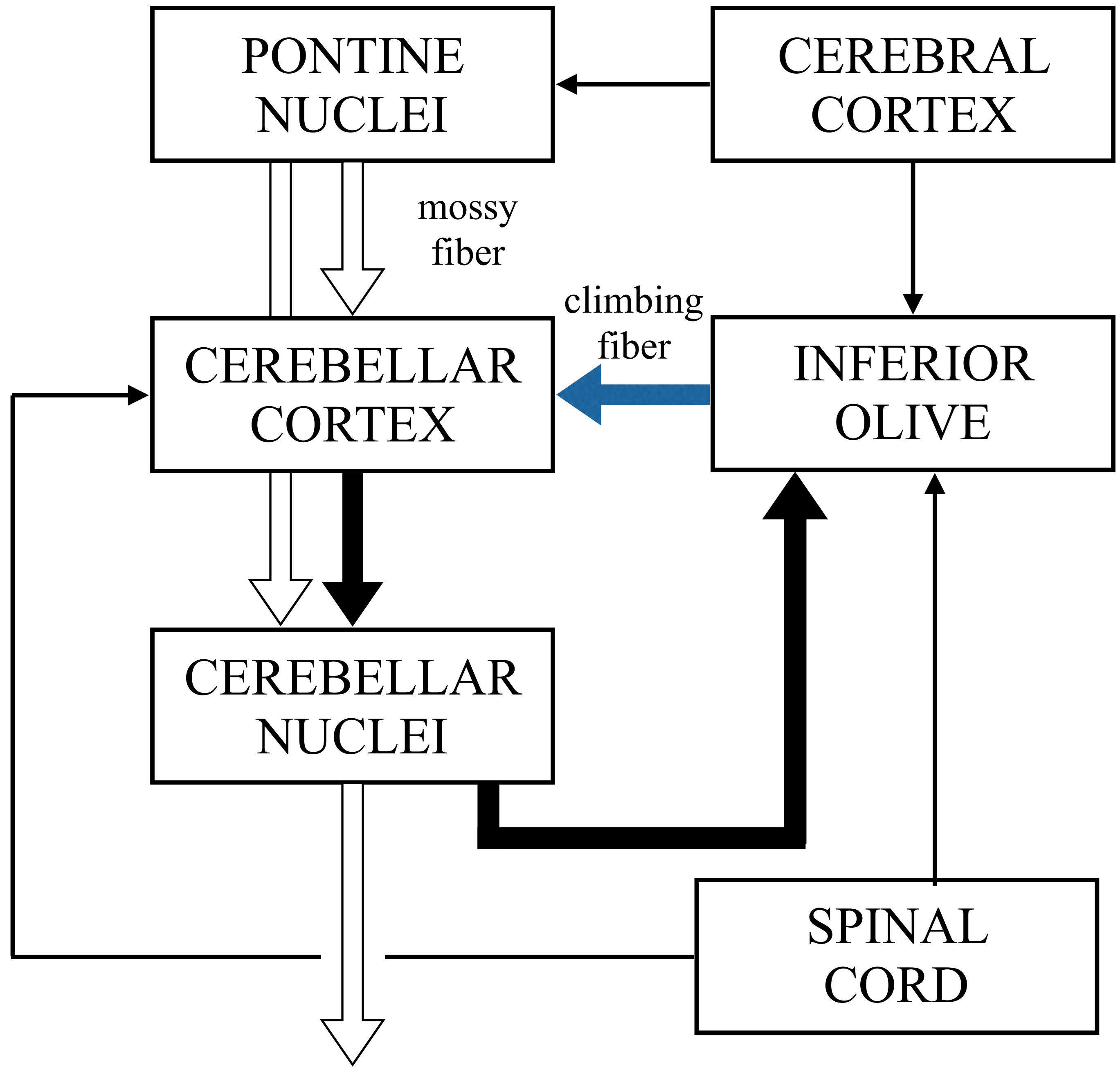
ARCHITECTURE



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

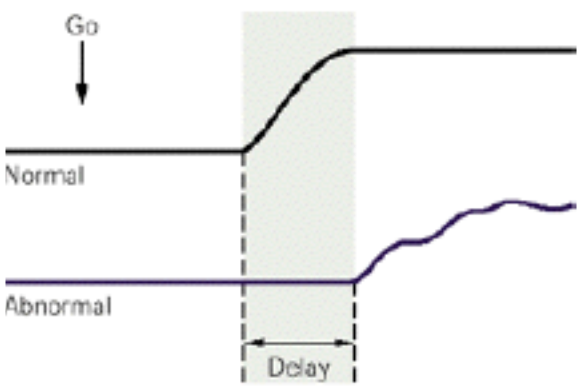
CEREBELLUM


Motor areas
Basal ganglia
Non-motor areas
Cerebellum
Brain stem motor nuclei

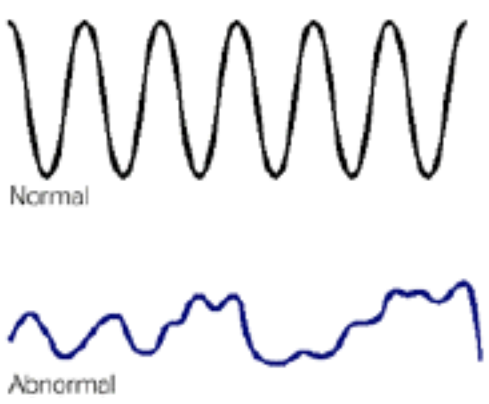

PONTINE NUCLEI
CEREBRAL CORTEX
mossy fiber
climbing fiber
CEREBELLAR CORTEX
INFERIOR OLIVE
CEREBELLAR NUCLEI
SPINAL CORD

CEREBELLAR DEFICITS

Ataxia



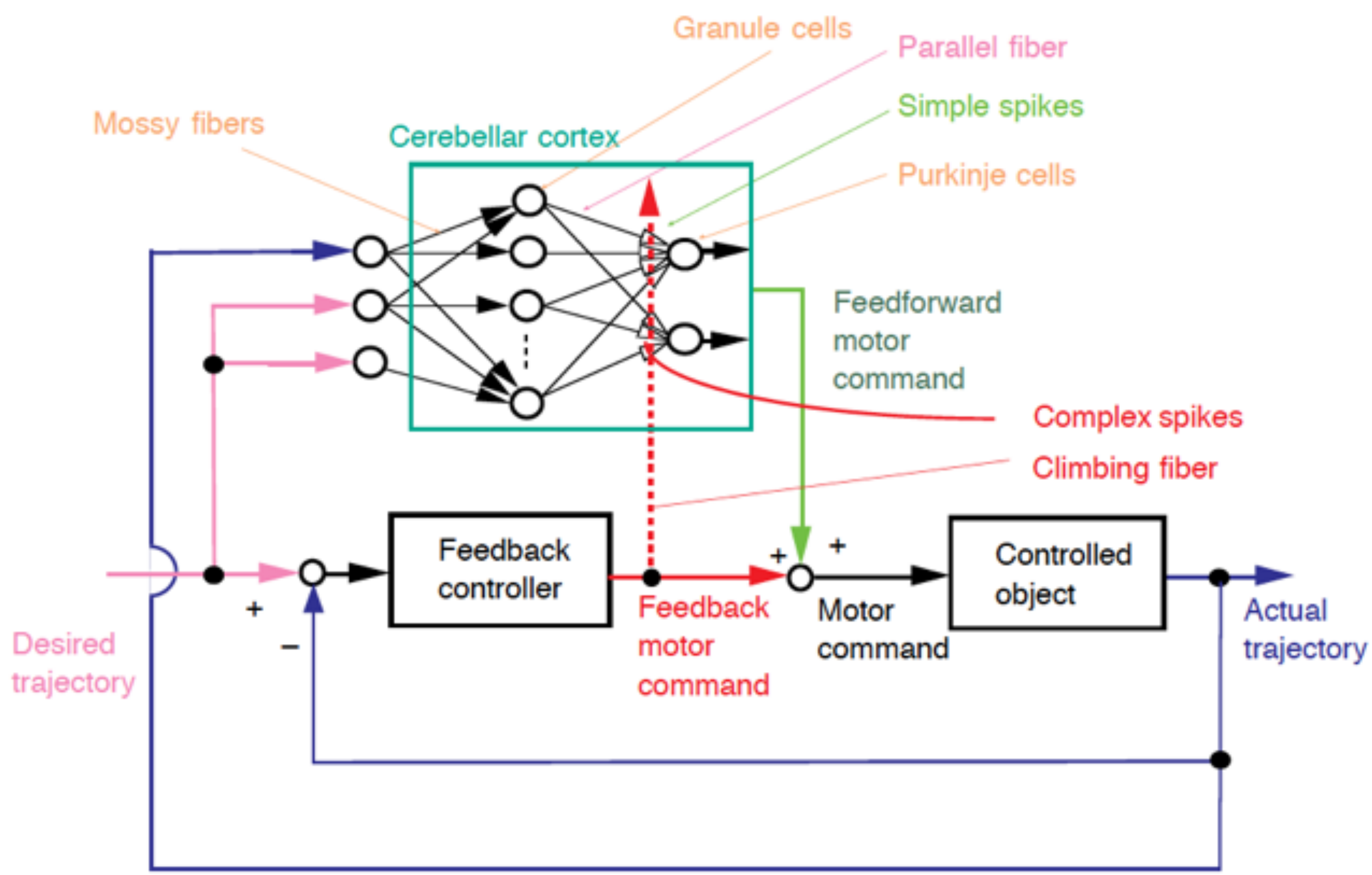
dysmetria



dysdiadochokinesia

CEREBELLUM — MOTOR THEORY

The cerebellar circuitry computes some function that directly creates or modifies the patterns of muscle activations and synergies that underlie coordinated movement



—Wolpert et al., 1998, *Trends Cogn Sci* 2:338

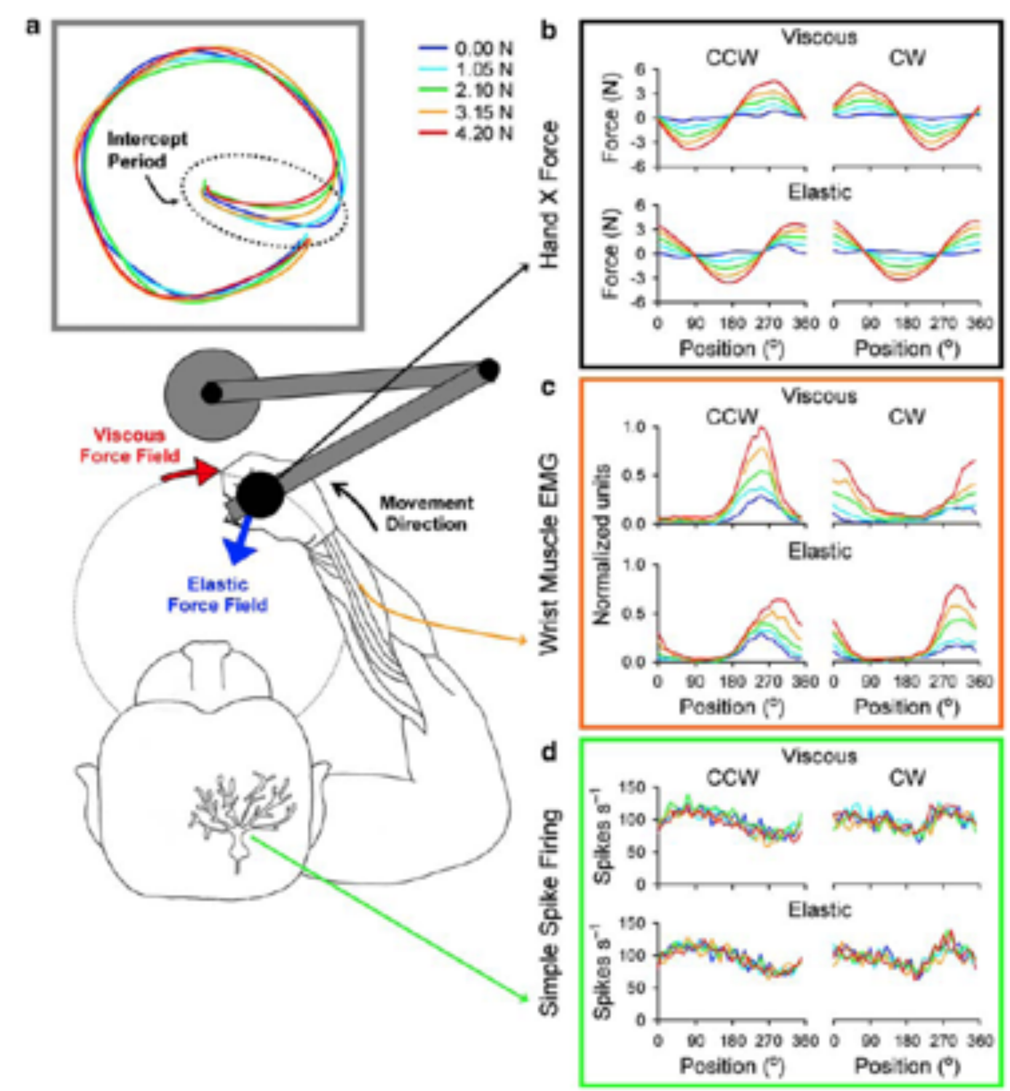
CEREBELLUM — AGAINST THE MOTOR THEORY

Strong parallelism in the phylogeny between the size of the cerebellum and the complexity of sensory systems

— Paulin, 1993, *Brain Behav Evol* 41:39

The discharge pattern of Purkinje cells is not modulated by forces applied during movement execution

— Pasalar et al., 2006, *Nat Neurosci* 9:1404



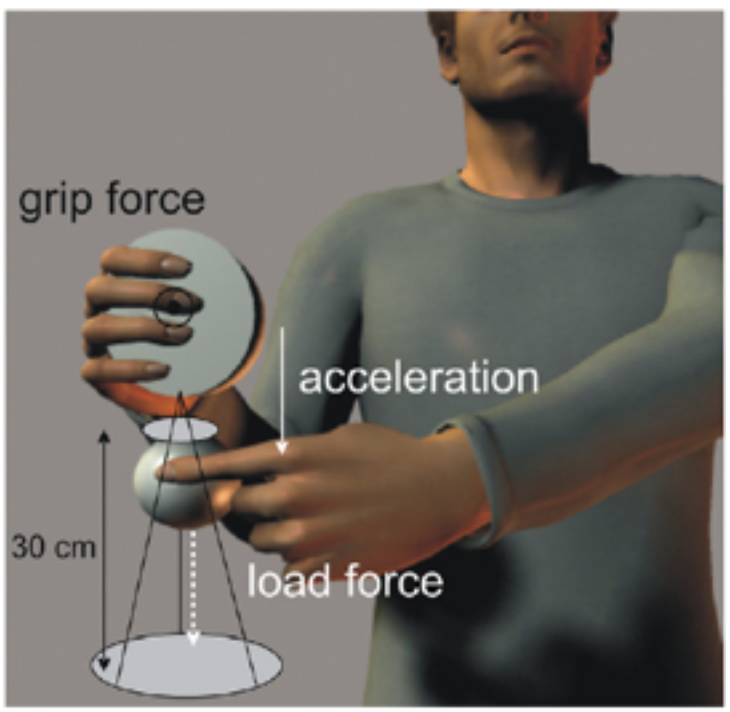
Also true for thalamic neurons

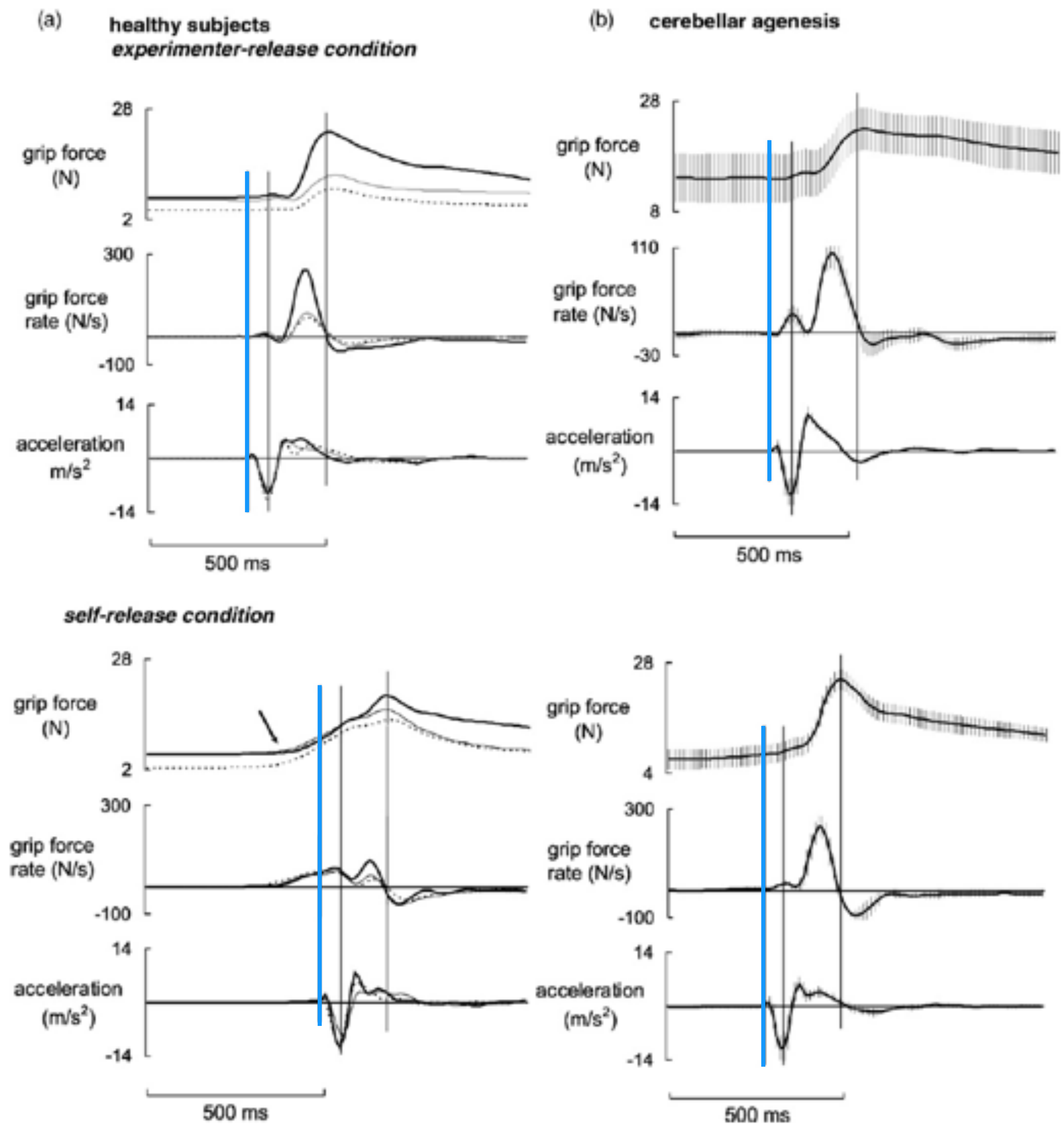
— Ivanusic et al., 2006, *Brain Res* 104:181

➤ **Incompatible with a representation of an internal inverse model**

CEREBELLAR DEFICIT

Deficit in predictive grip force control

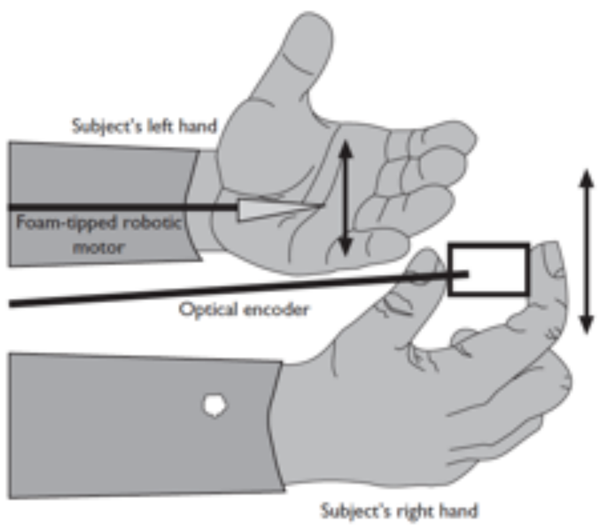


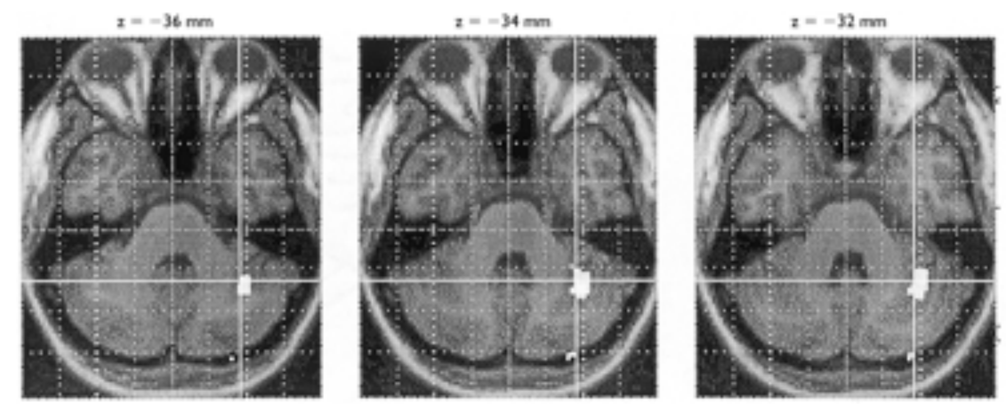


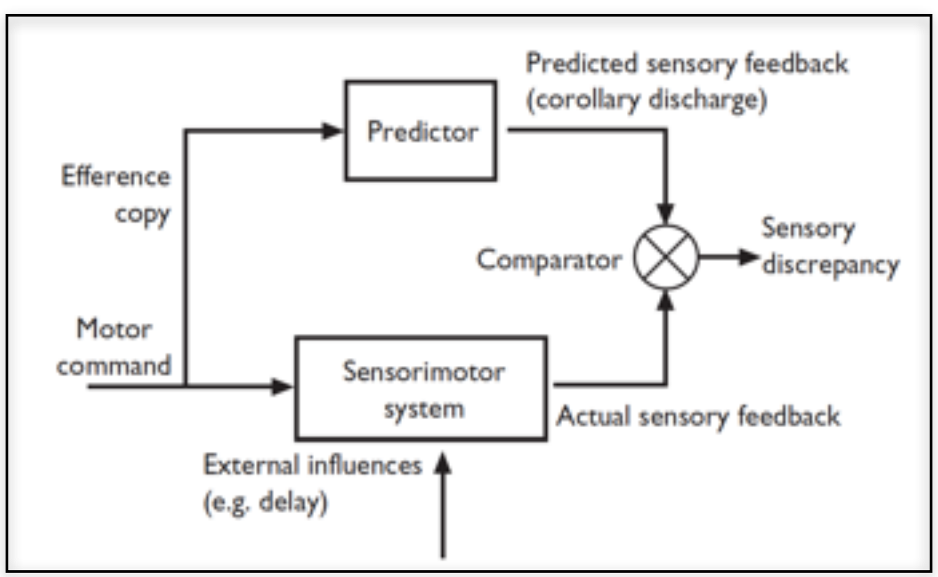
— Nowak et al., 2007, *Neuropsychologia* 45:696

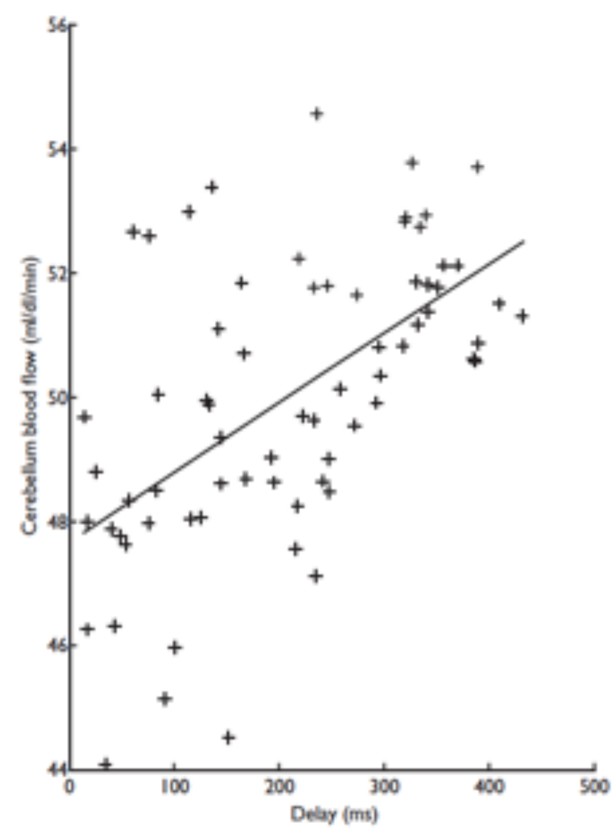
PREDICTING SENSORY CONSEQUENCES

The cerebellum is involved in predicting the sensory consequences of action







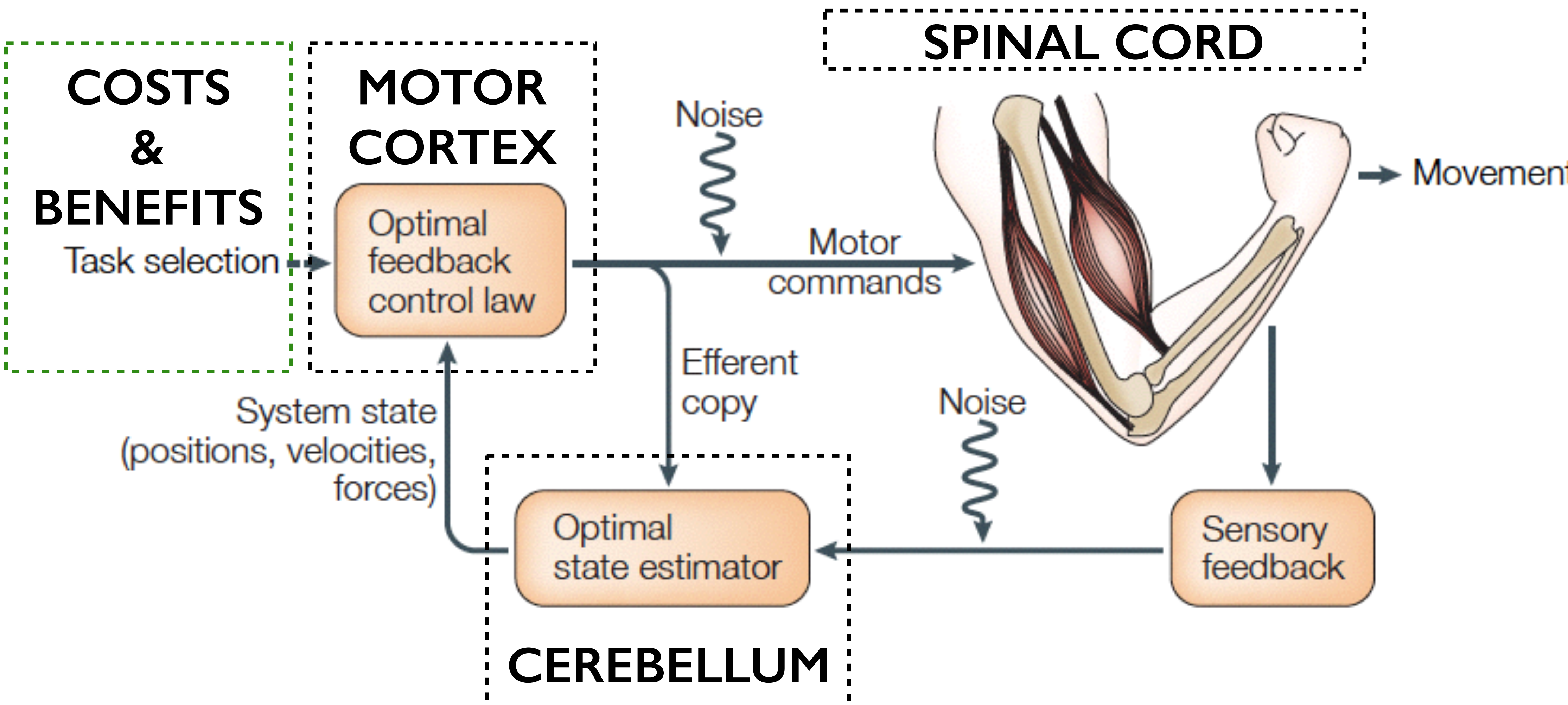


Activity in the right lateral cerebellar cortex shows a positive correlation with delay.

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

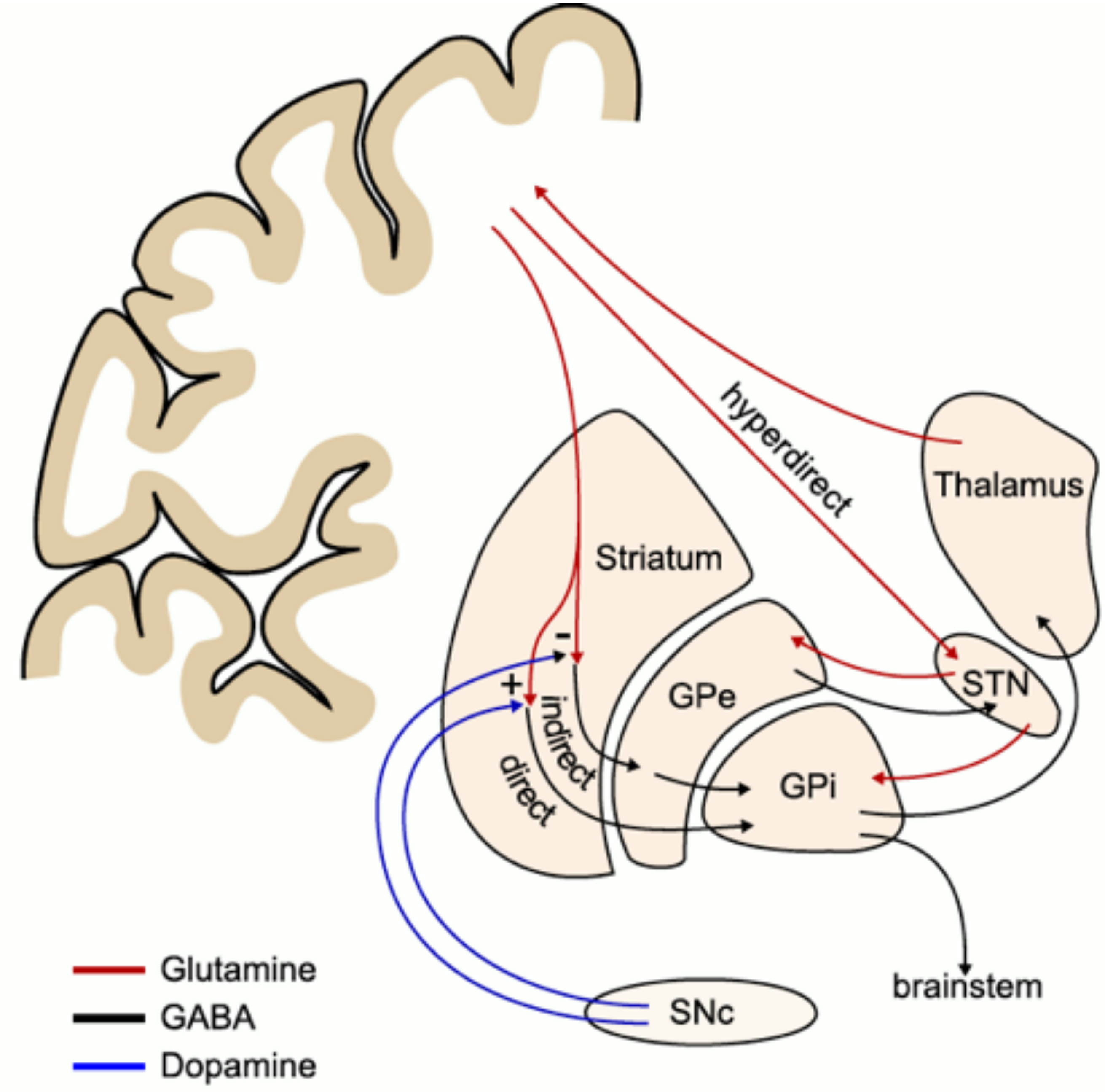
— Blakemore et al., 2001, *NeuroReport* 12:1879

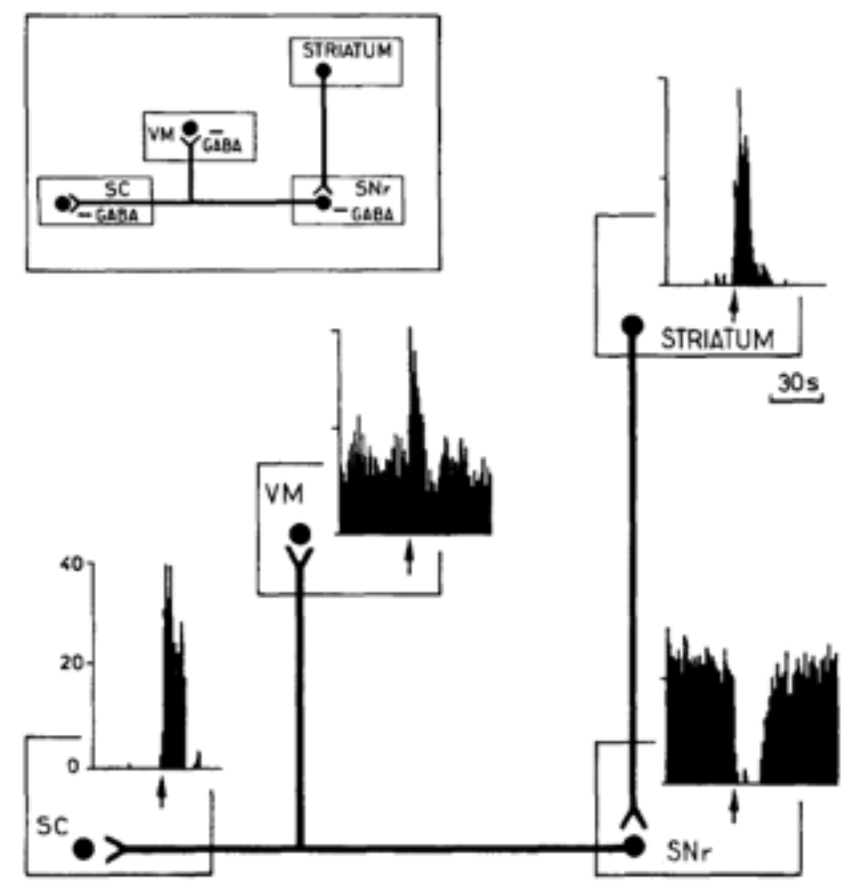
ARCHITECTURE



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

BASAL GANGLIA



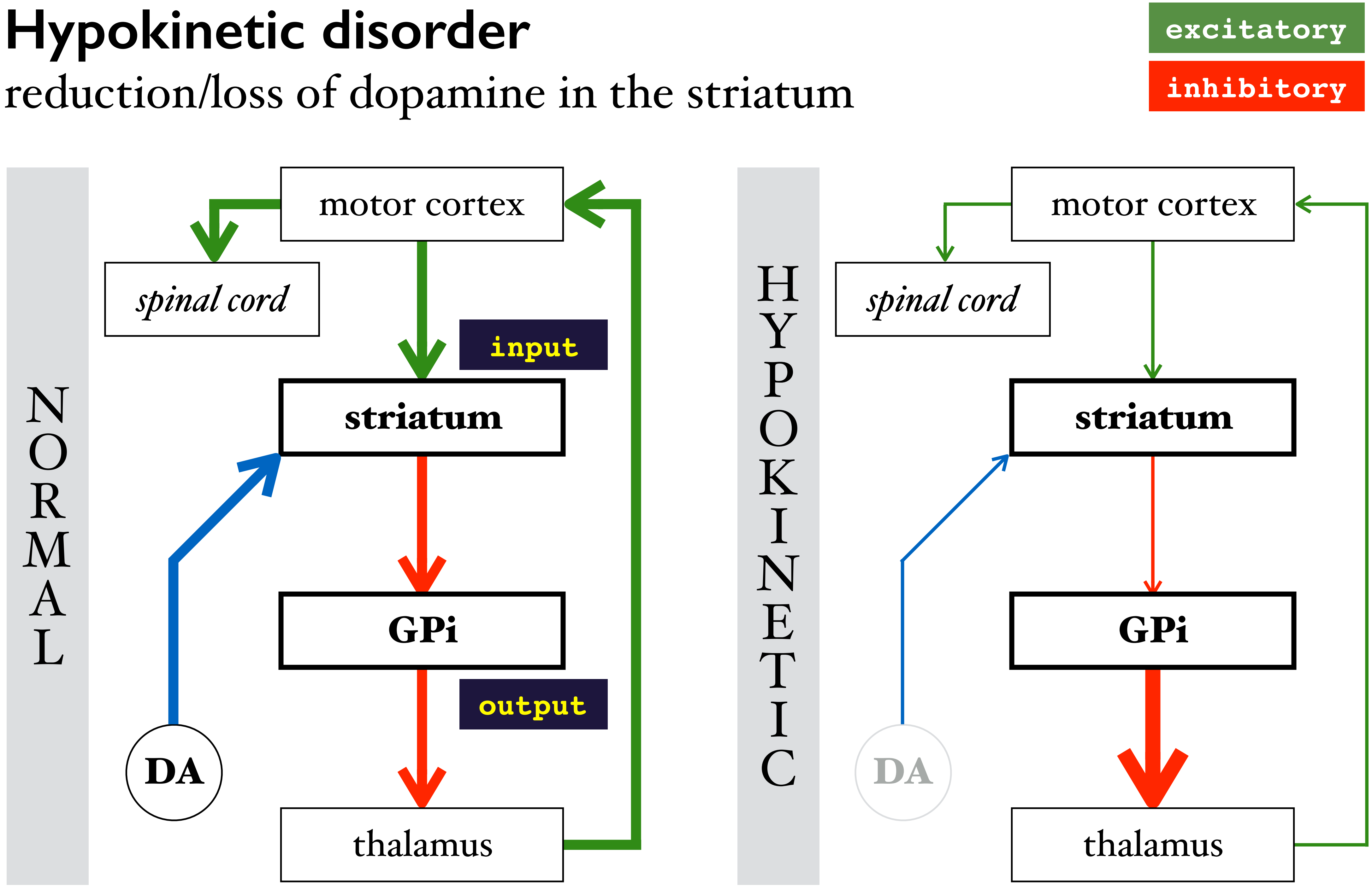


— Chevalier & Deniau, 1990, *Trends Neurosci* 13:277

PARKINSON'S DISEASE

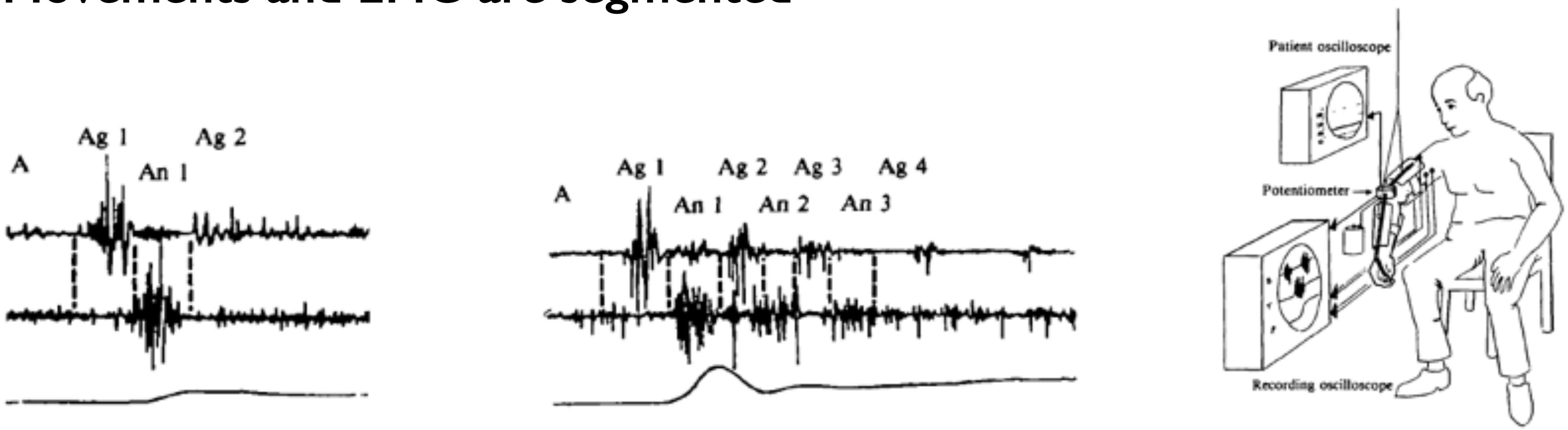
Hypokinetic disorder

reduction/loss of dopamine in the striatum

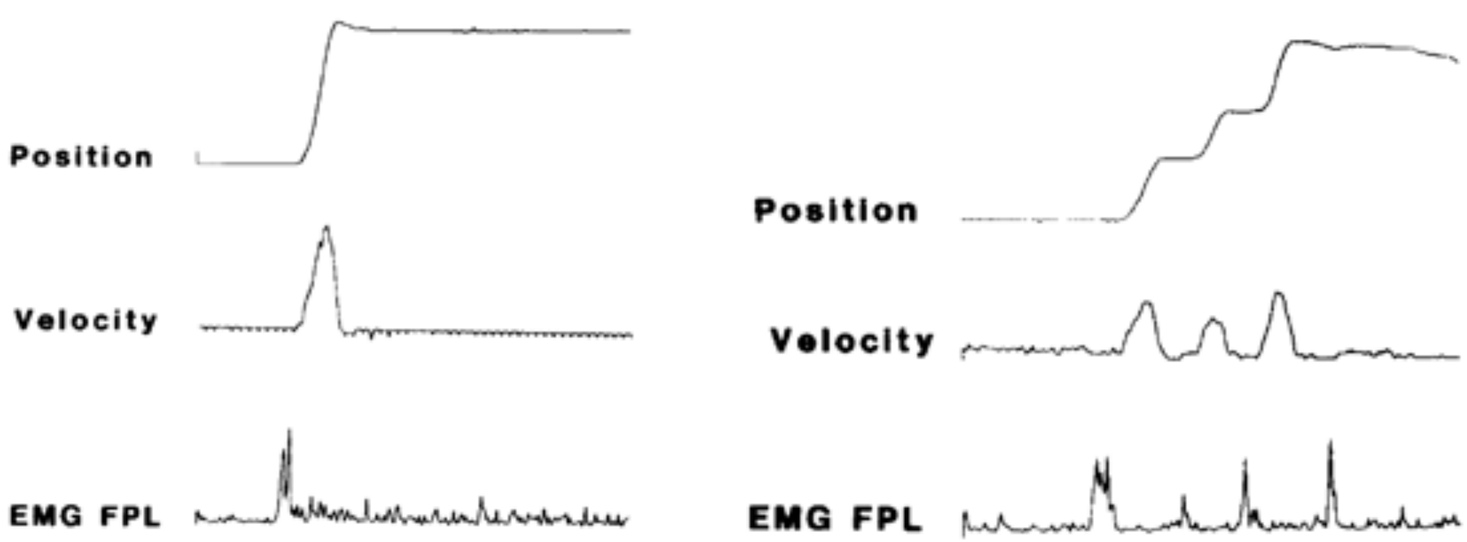


BASAL GANGLIA — MOTOR DEFICITS

Movements and EMG are segmented

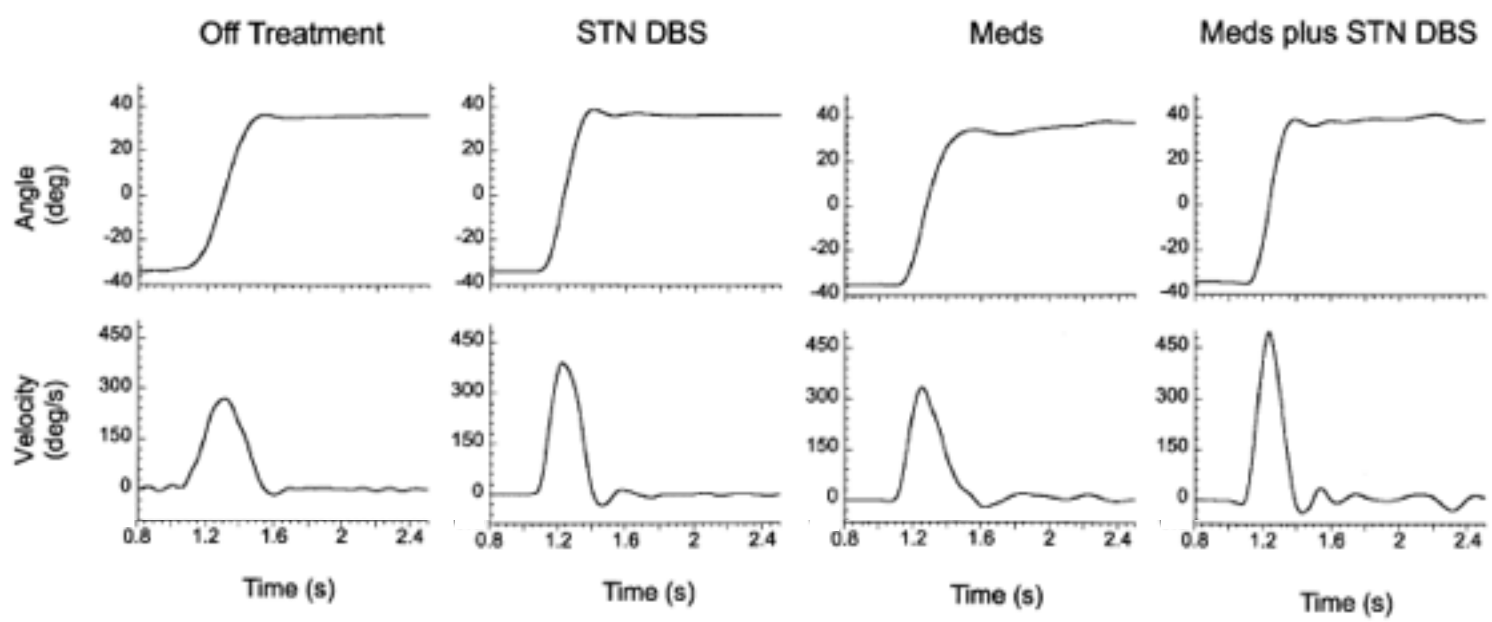


— Hallett & Khoshbin, 1980, *Brain* 103:301



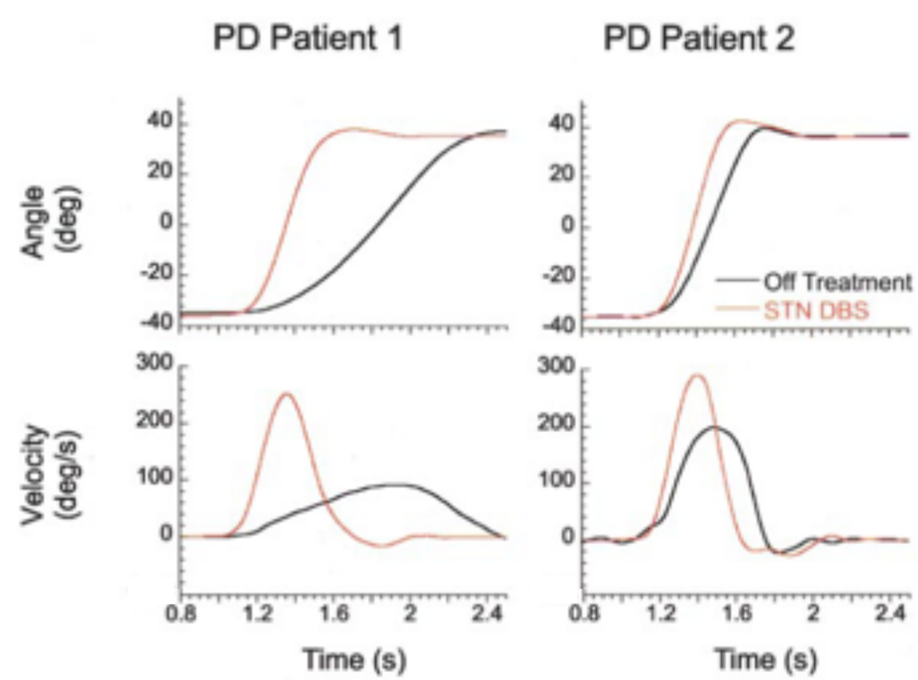
— Berardelli et al., 1984, *Neurosci Lett* 47:47

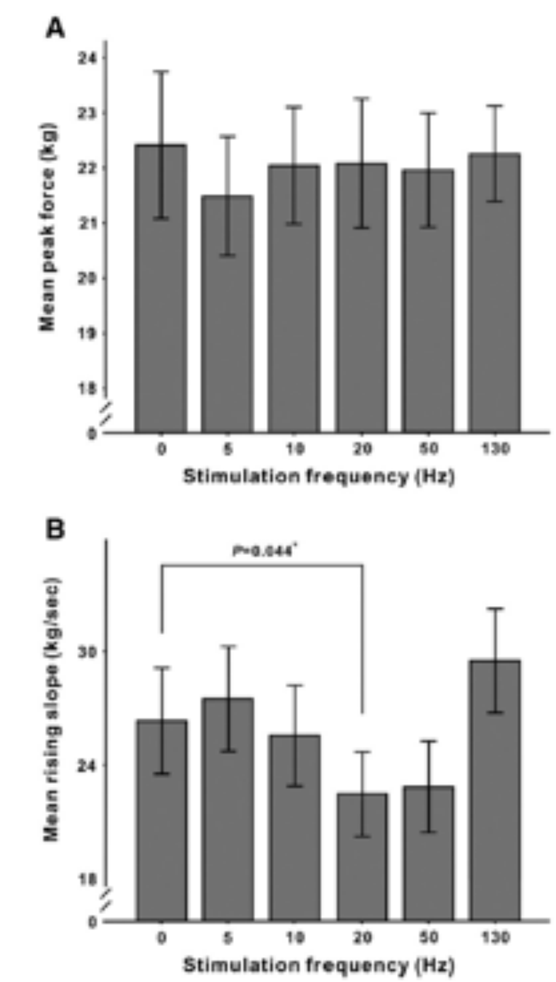
BASAL GANGLIA — MOTOR DEFICITS



Single joint elbow movements in PwPD

Effect of medication and deep brain stimulation

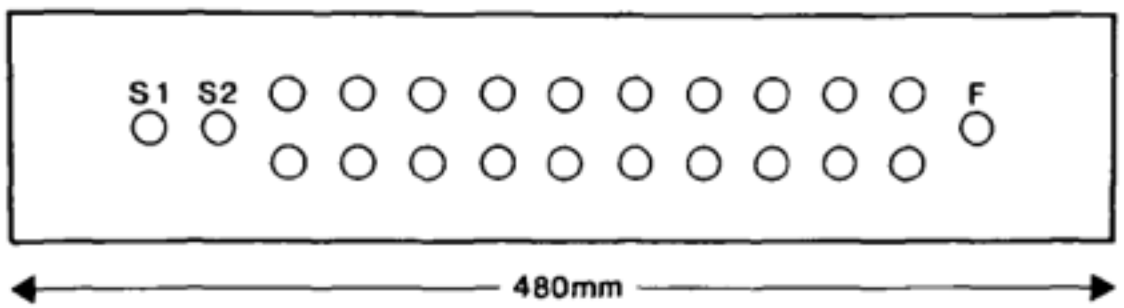


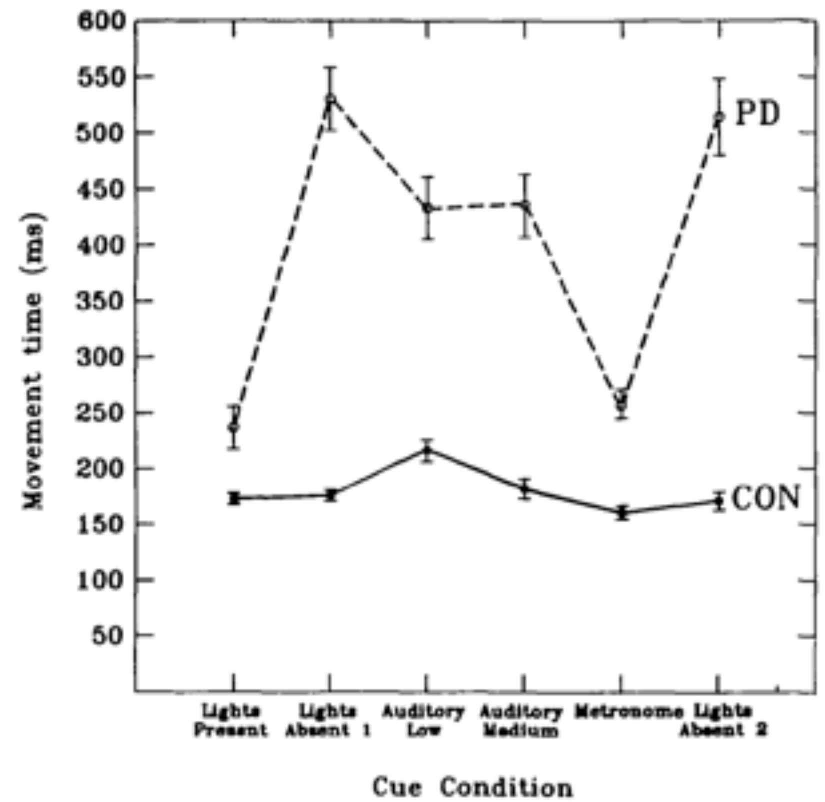


— Vaillancourt et al., 2004, *Brain* 127:491

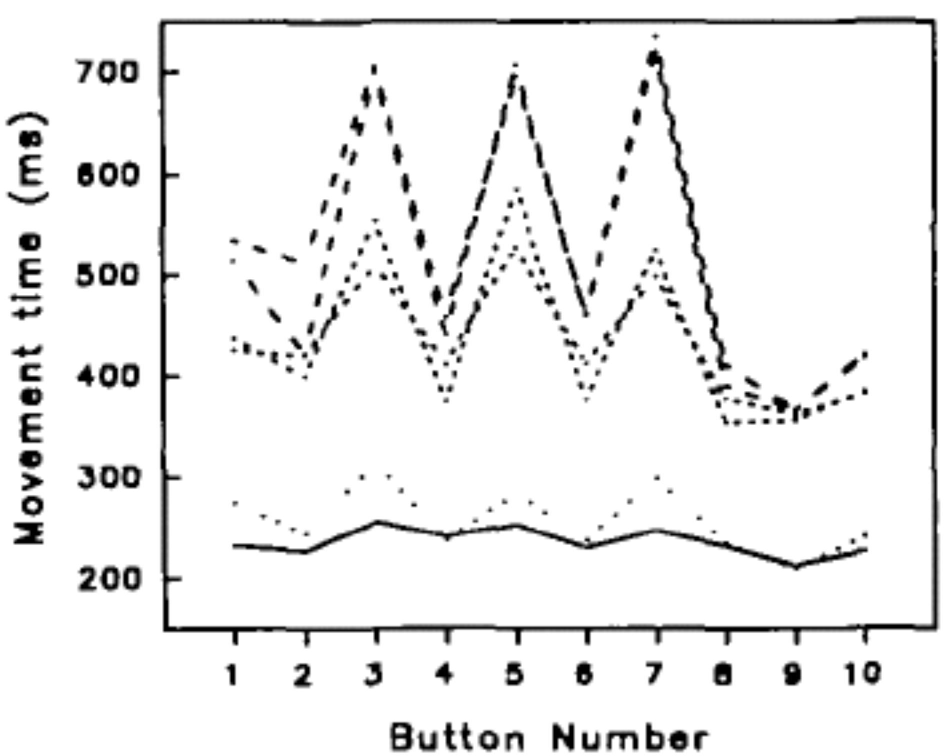
— Chen et al., 2011, *Exp Neurol* 231:91

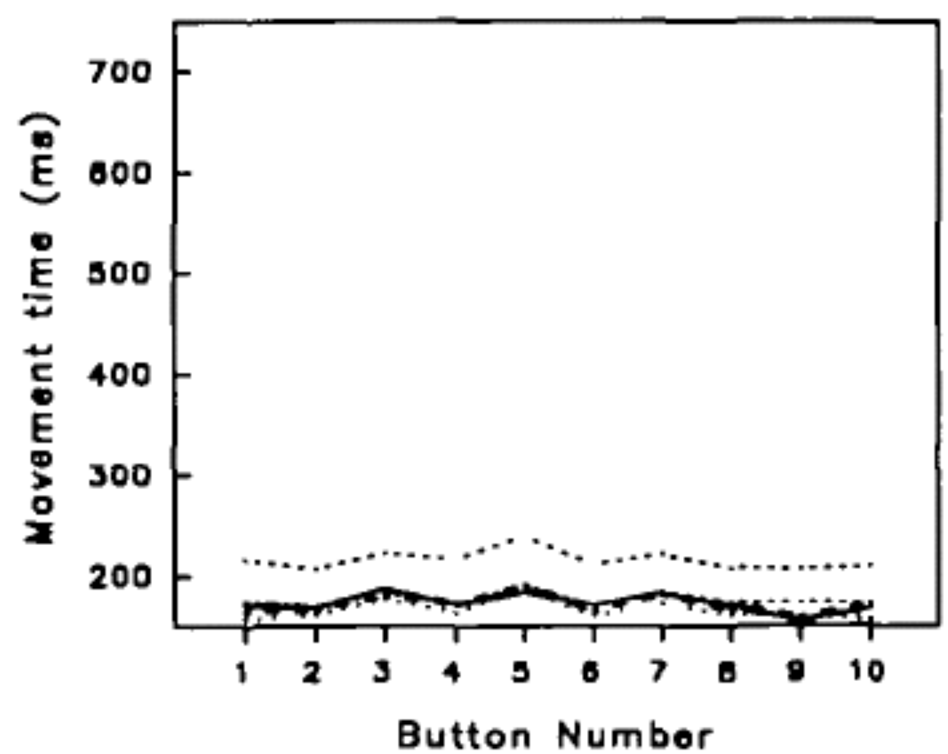
BASAL GANGLIA — MOTOR DEFICITS



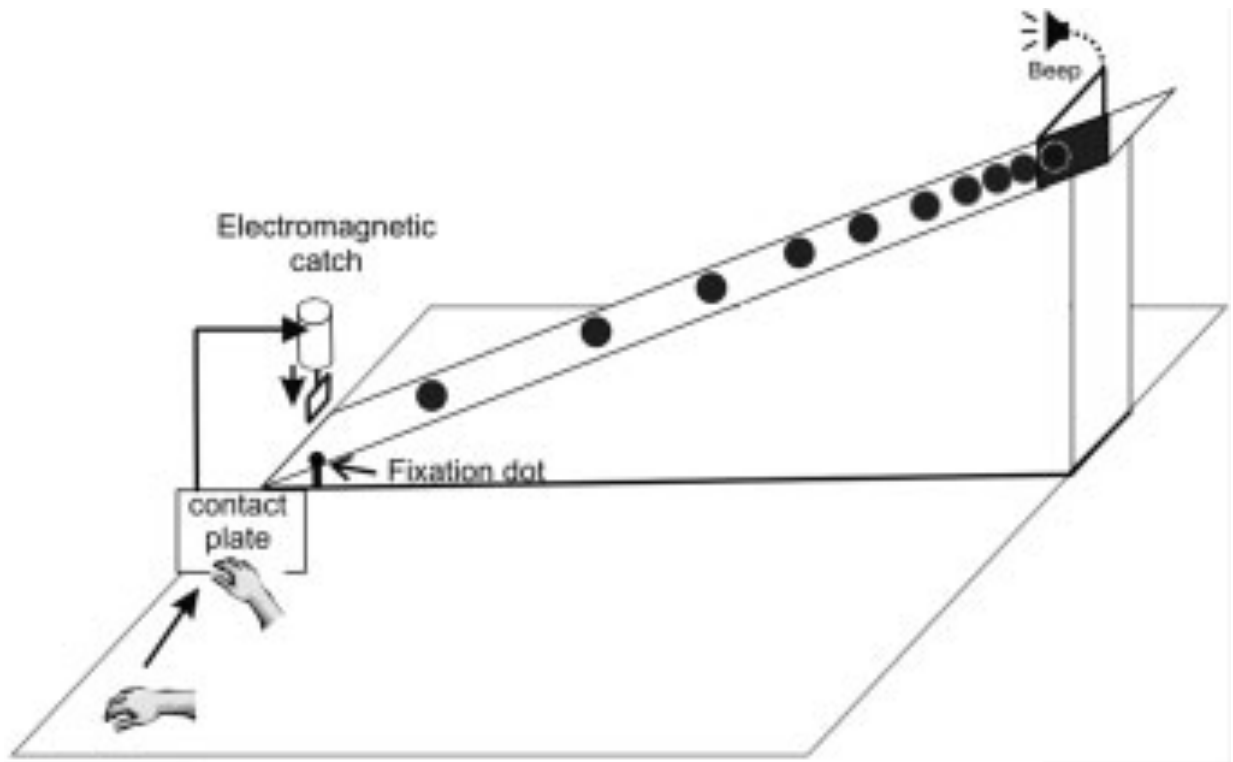


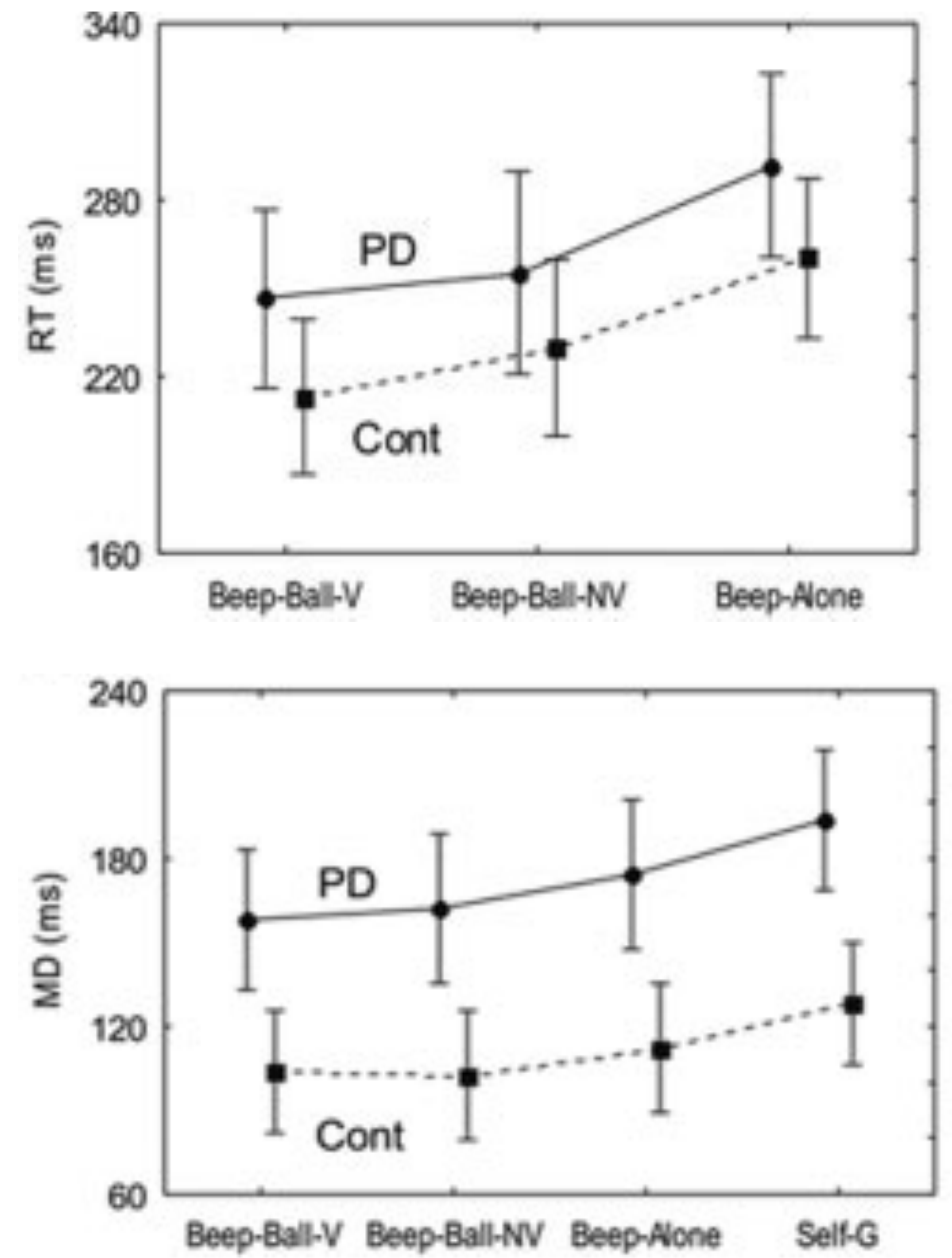
— Georgiou et al., 1993, *Brain* 116:1575





BASAL GANGLIA — MOTOR DEFICITS

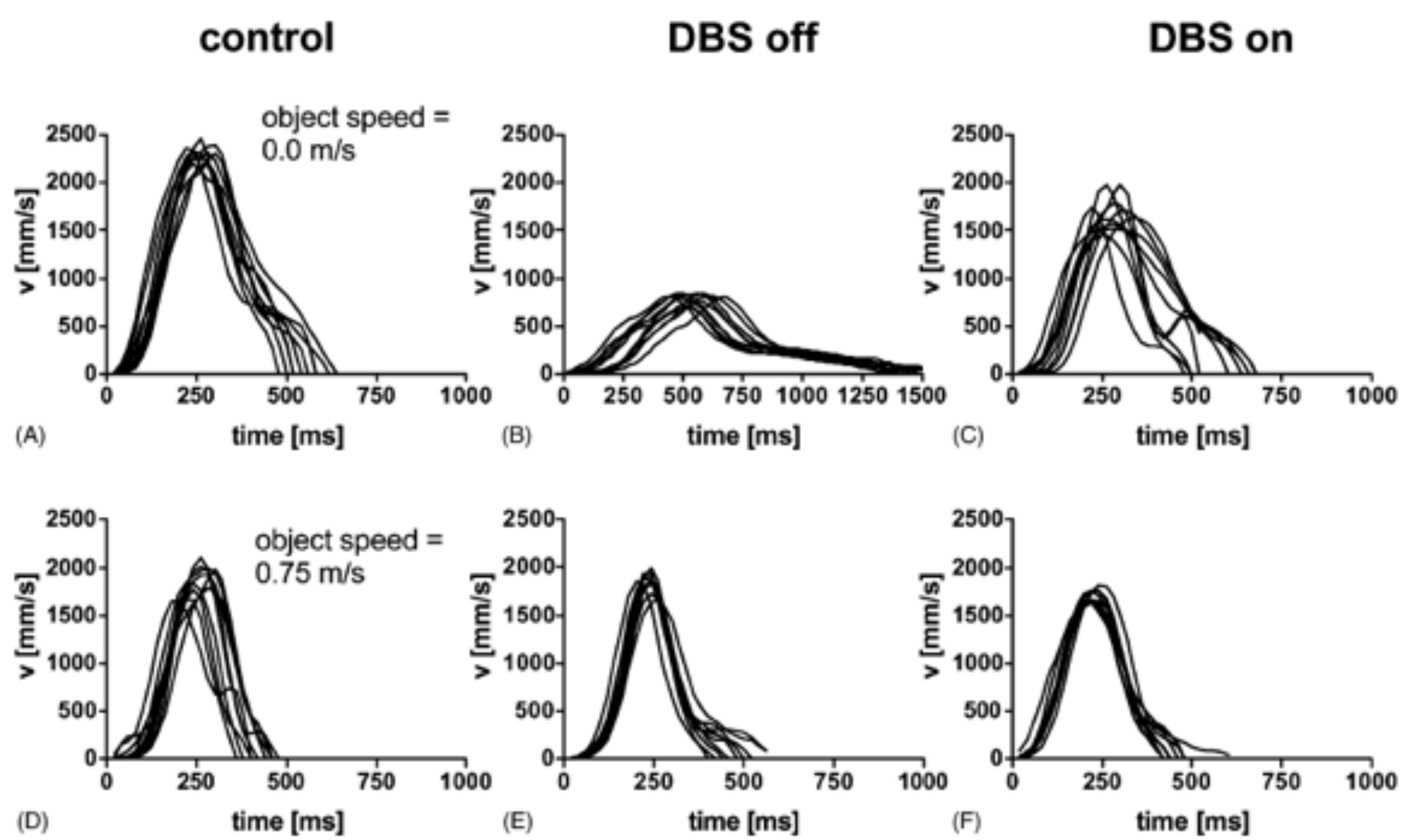




Paradoxical kinesia in PwPD

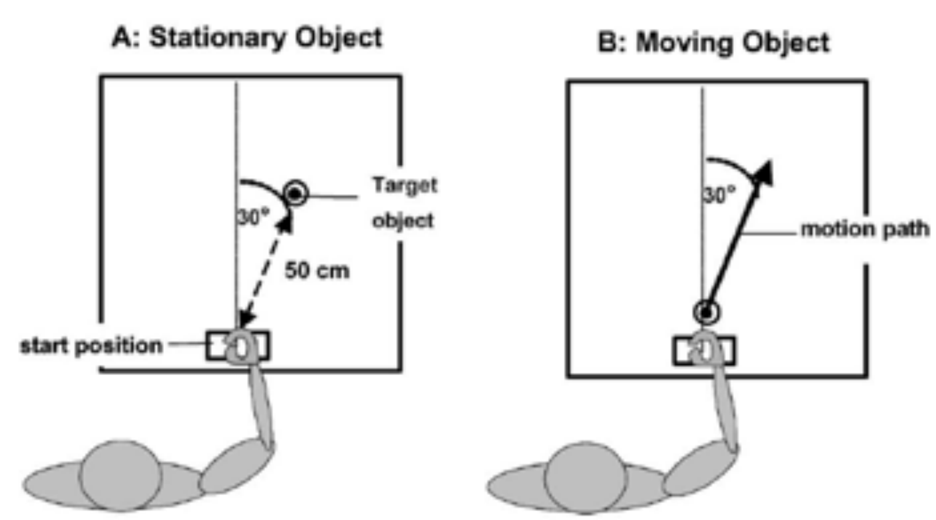
— Ballanger et al., 2006, *Mov Disorders* 21:1490

BASAL GANGLIA — MOTOR DEFICITS



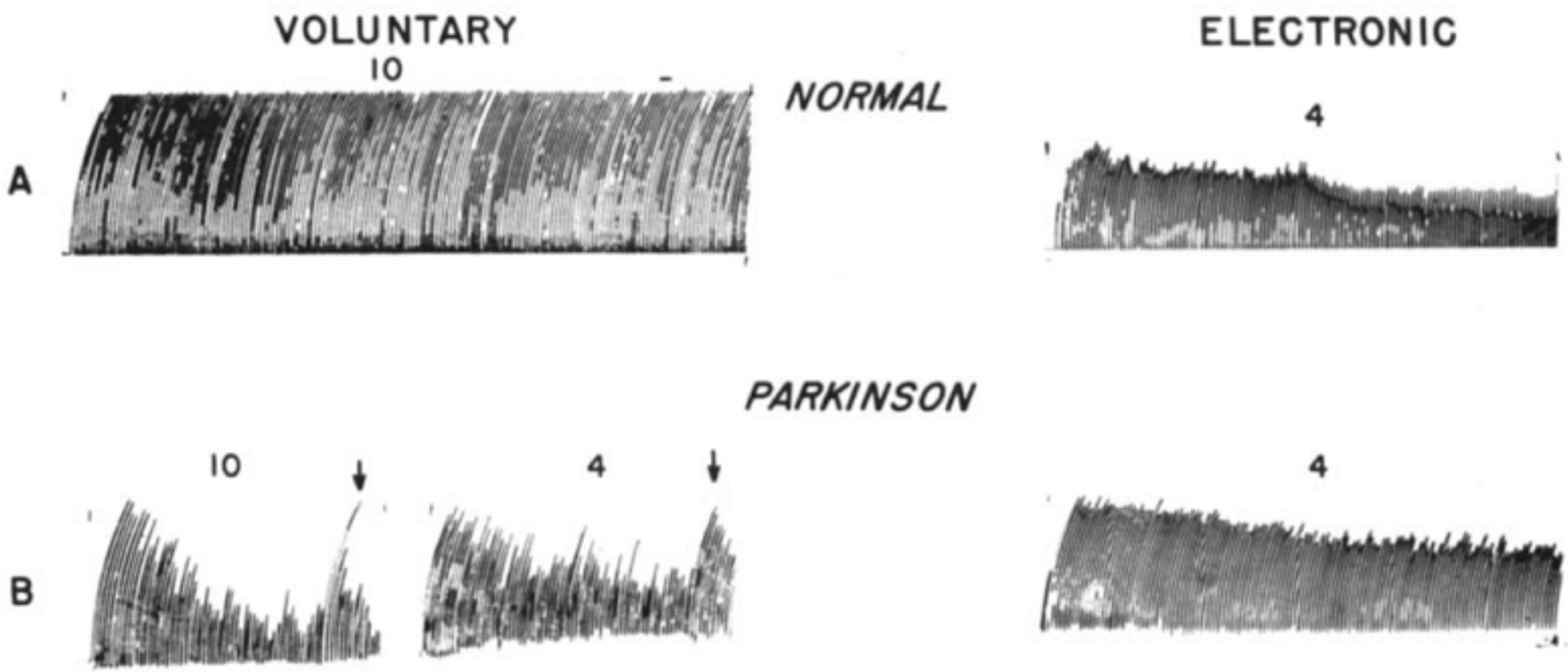
Reaching to moving targets

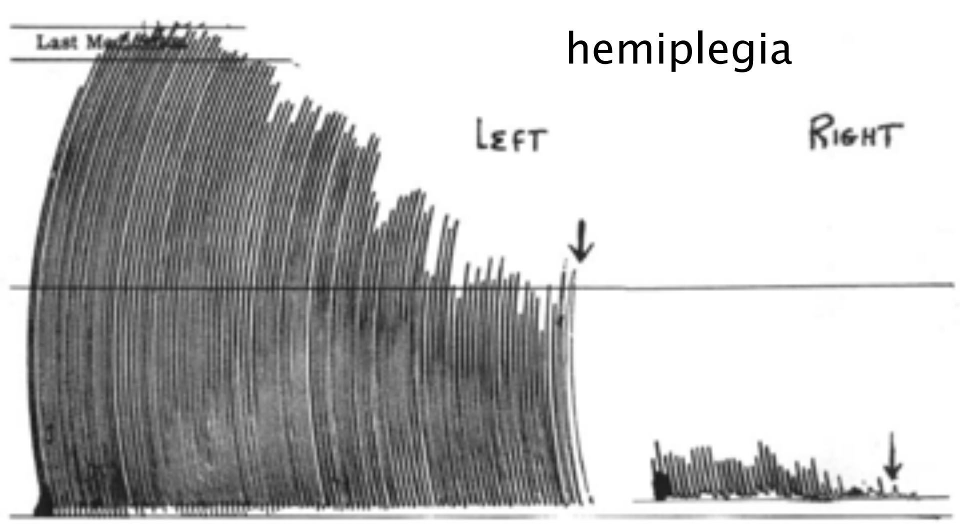
Paradoxical kinesia in PwPD



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

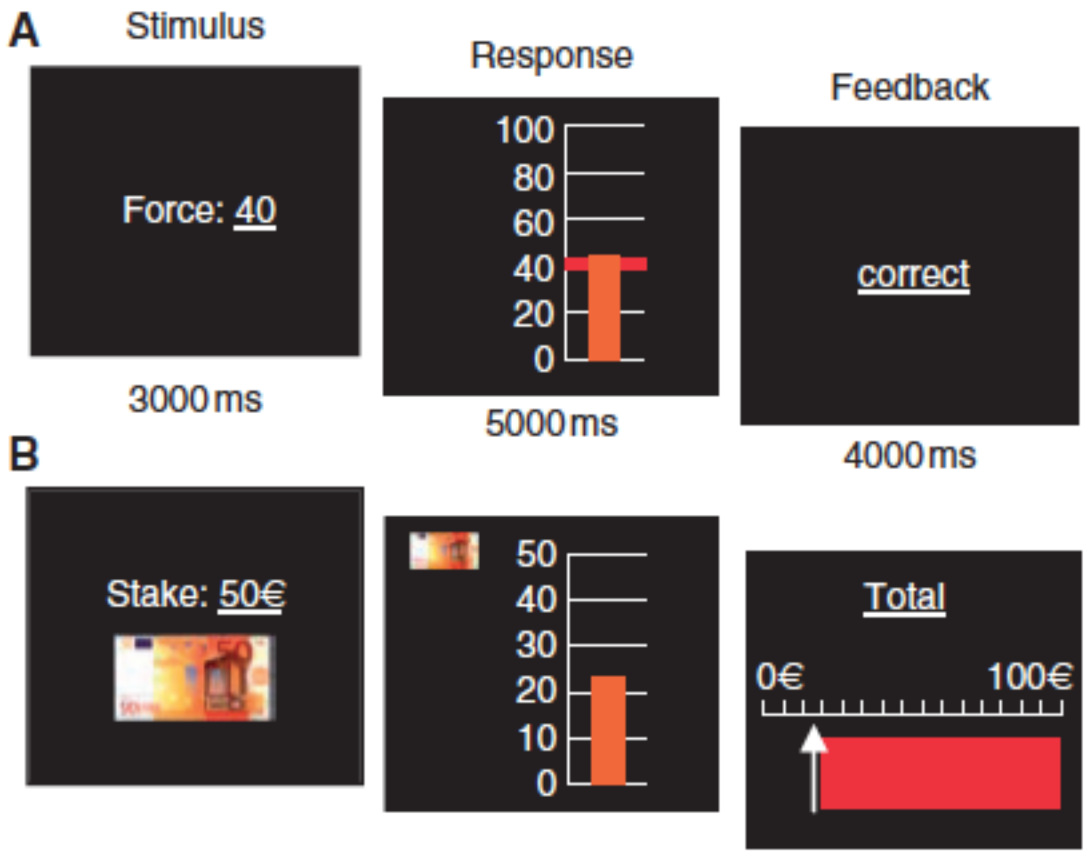
PARKINSON'S DISEASE AND MOTIVATION

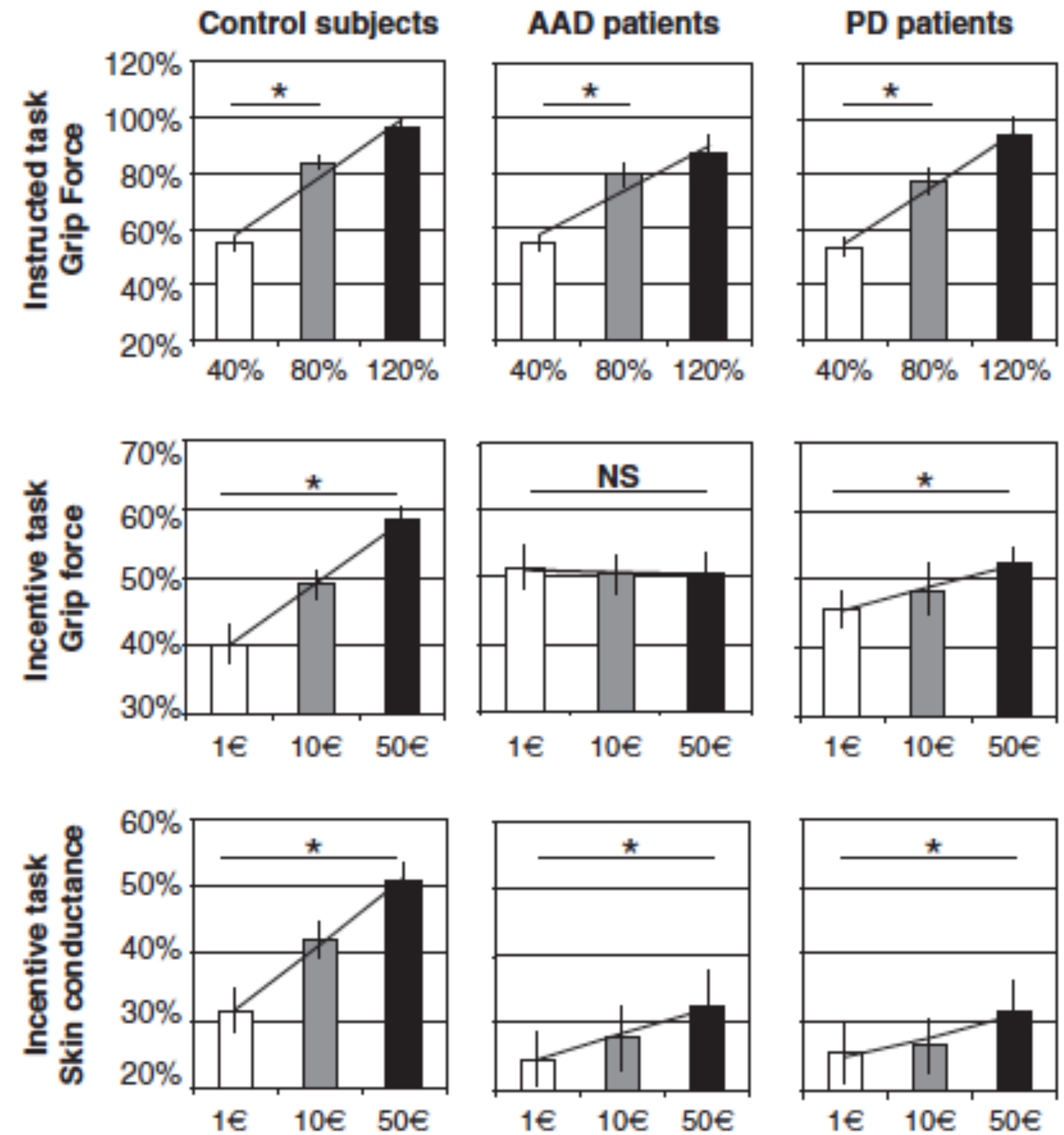


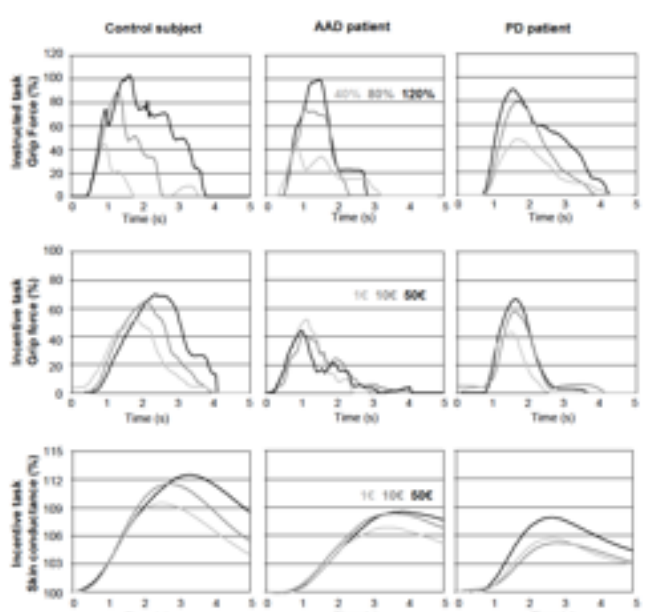


— Schwab et al., 1959, *Neurology* 9:65

PARKINSON'S DISEASE AND MOTIVATION

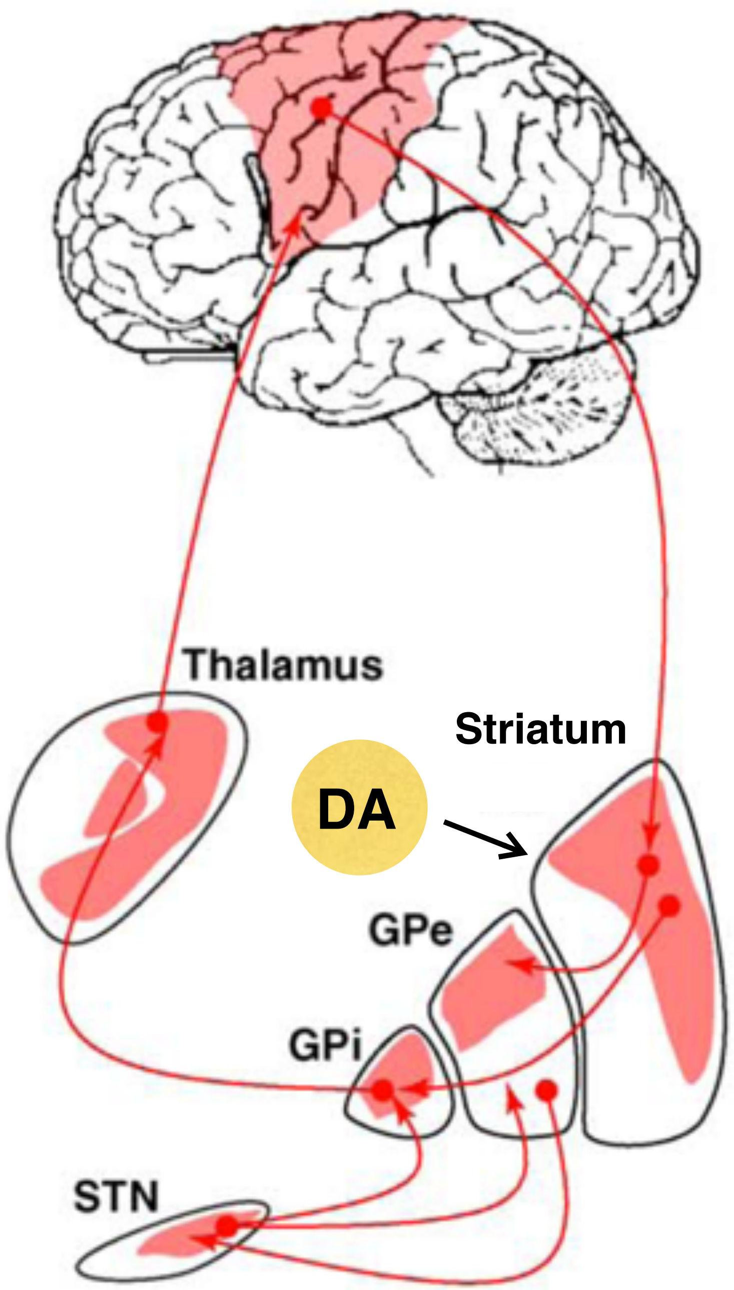




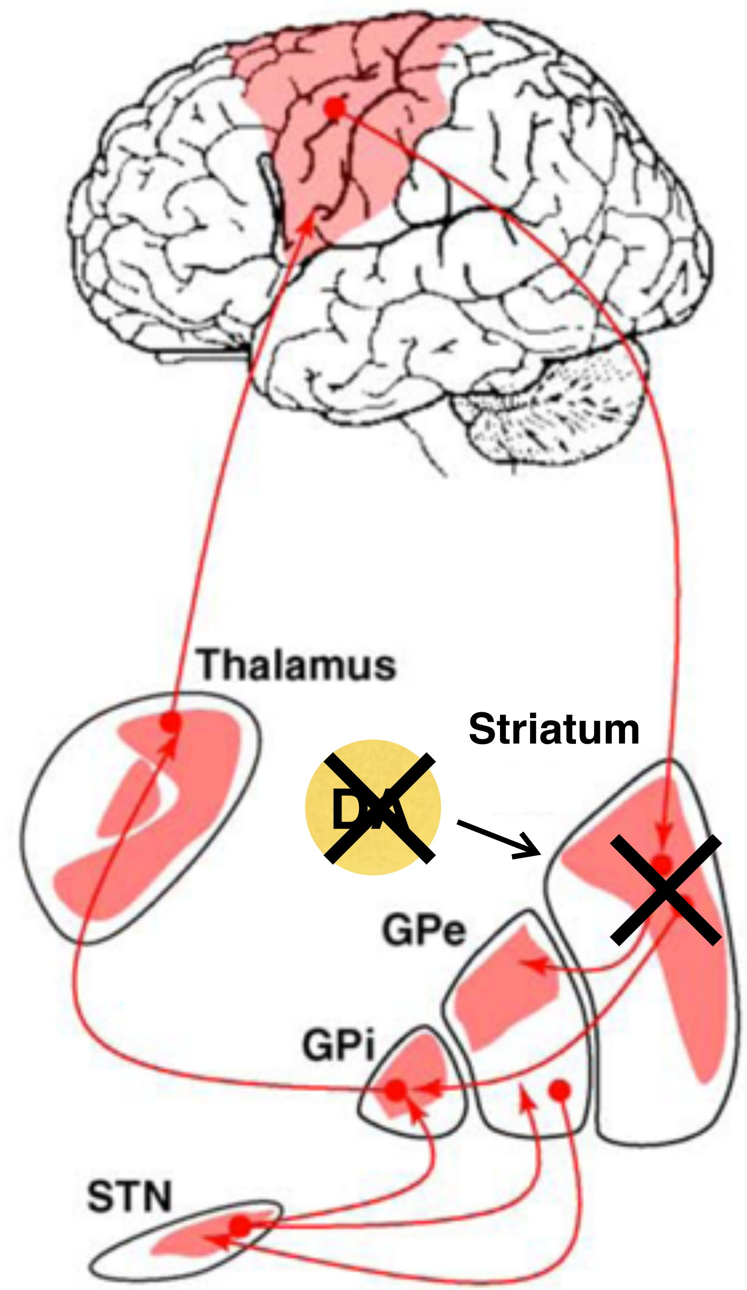


— Schmidt et al., 2008, *Brain* 131:1303

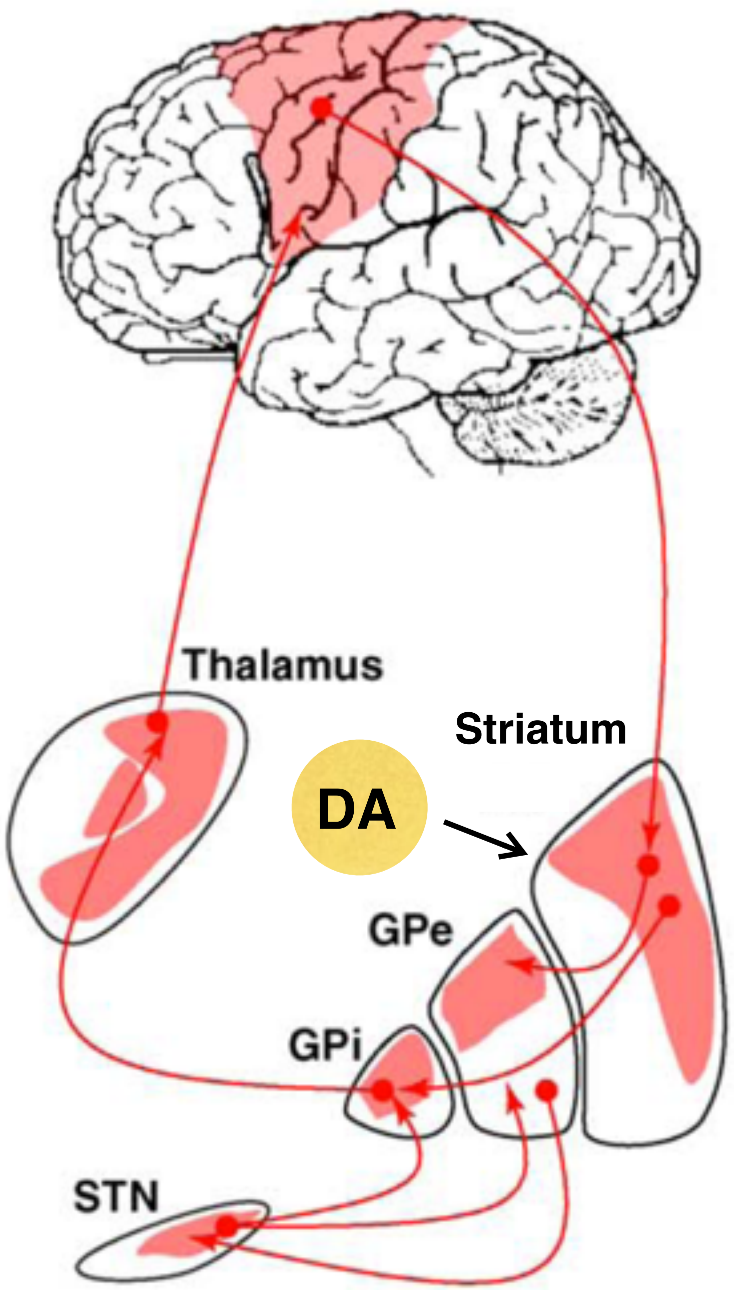
BASAL GANGLIA — INPUT/OUTPUT



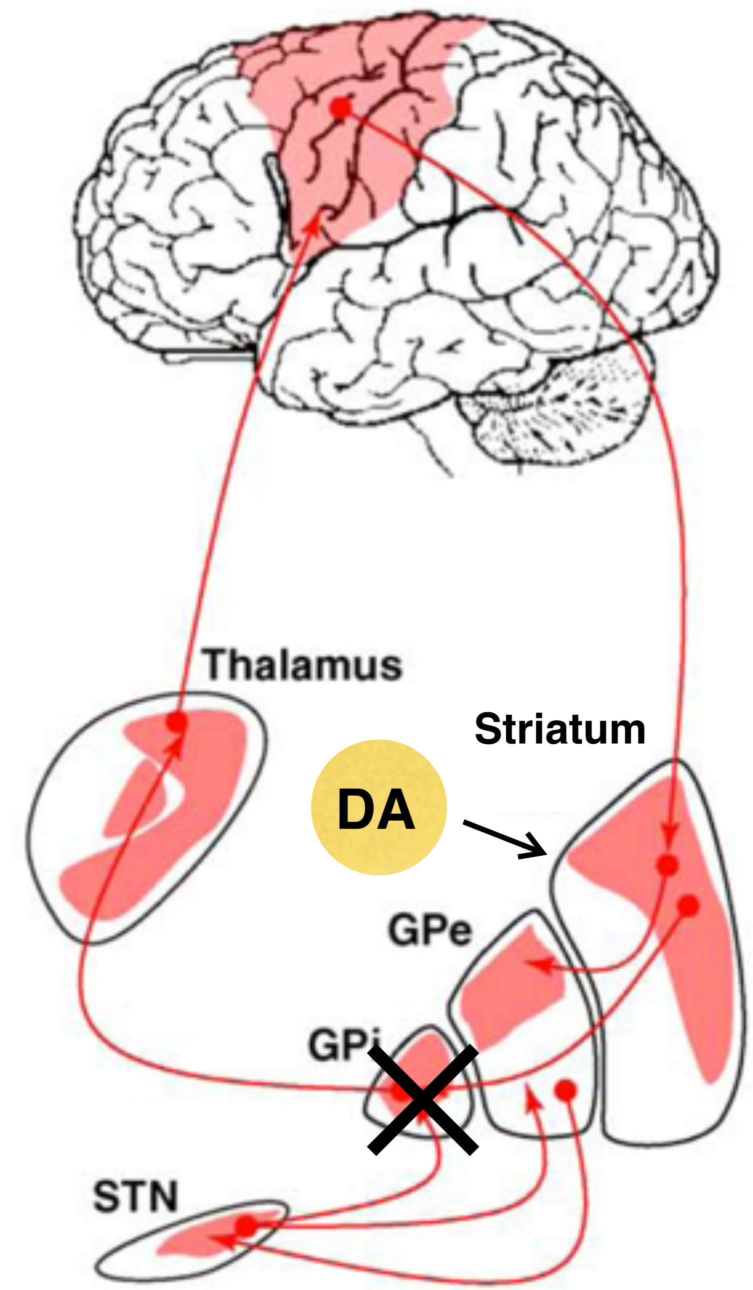
Neurologic and psychiatric disorders (Parkinson's, Huntington's disease, Dystonia, Tourette) when the principal INPUT nucleus (striatum) is affected or DA innervation is modified



BASAL GANGLIA — INPUT/OUTPUT

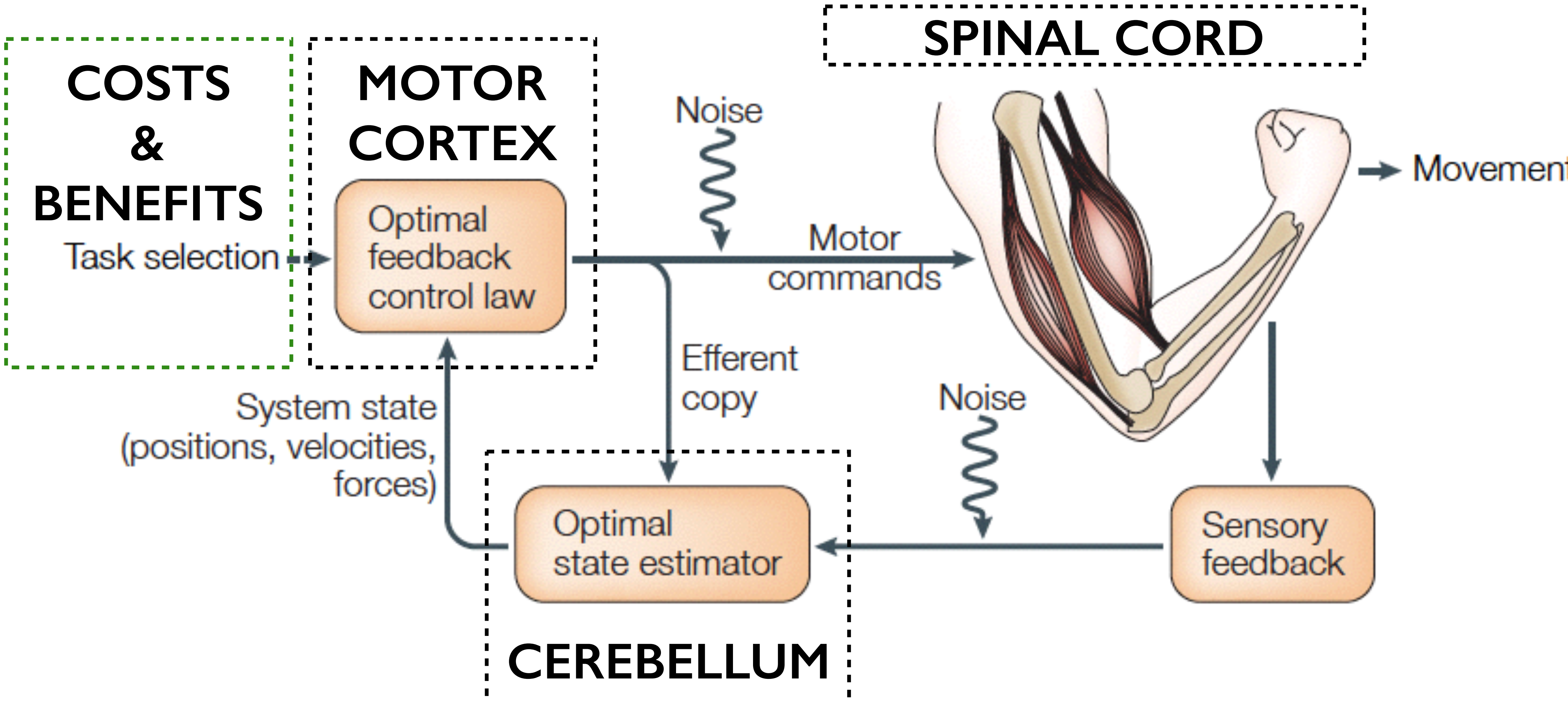


Very different outcome following discrete lesions of main OUTPUT regions of the BG (GPi, SNr): subtle or imperceptible effects



Pallidotomy: effective treatment for striatal associated disorders. Better to block BG output completely than allow faulty signals from BG to pervert the normal operation of the system

ARCHITECTURE



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