The motor system

To move things is all that mankind can do… whether in whispering a syllable or in felling a forest

C. Sherrington 1920
• Principles

• Components: Muscles, Spinal cord and spinal tracts, Subcortical areas, Cortical fields.

• Learning and plasticity
Three main types of movements

- Reflex
- Rhythmic
- Voluntary
• **Reflex**: *involuntary* coordinated patterns of muscle contraction and relaxation elicited by peripheral stimuli (~40ms)

Noxious stimuli excites ipsilateral flexor, and excites contralateral extensor

Stretch reflex: contraction of same and synergist and relaxation of antagonist
Rhythmic: Chewing, swallowing, and scratching, quadrupedal locomotion.

- The spinal cord and brain stem.
- Triggered by peripheral stimuli that activate the underlying circuits.
CPG: central pattern generators
Voluntary movements: principles

Goal directed

Reaching (~120 ms)
Feedback control (error correction)

A Feedback control: command specifies desired state

1. Gain
2. Delay (phase lag)
Feed-forward (open loop)

1. Very hard computationally
Feedback control (error correction)

Feedforward (open loop)

Notice onset of muscles
Improve with practice

• Co-contraction of muscles

• **Internal models**: a neural representation of the relationship between the hand and the environment (how the arm would respond to the neural command).
Inverse and forward internal models

An **internal model** is used either:

- to predict the movement consequences of a motor commands (**forward model**).

- to determine the motor commands needed to achieve a desired movement trajectory (**inverse model**).
Motor programs and Invariants

Motor equivalence

(Donald Hebb, 1950)
The motor program—trajectories and kinematics

Suggests planning in reference to the hand rather than joints and muscles (linear vs. nonlinear)
Pre-planning in vectors

Is there online visual feedback?
No - scaling of acceleration and speed

Invariant time (Isochrony)
**Kinematic** transformation: to transform a target position into a command to the skeletal system to move the hand i.e. to convert between coordinate systems;

**Dynamic** transformation: relate motor commands to the motion of the system; in the reaching task here considered, the forces applied changed the system without changing the kinematics.
Building blocks – segmentation - primitives

Isogony (equal angles)
Isochrony (duration independent of length)
2/3 power law: speed as a function of curvature

(A) Diagram showing a figure with a 10 cm measurement.
(B) Graph showing angle (rad) over time (s).
Designing a complex trajectory with limitations

- Antagonistic muscles
- Equilibrium point trajectory
Stable behavioral gestures
Reaction time and information

>= 40 ms for reflex
>= 120 ms for voluntary
100 ms for each bit of information
Speed – accuracy tradeoff (Woodsworth, 1890)

Less time for feedback corrections?
No, even without sensory feedback

Variability/noise of the components (neurons! much more than muscles)
Overcoming noise: optimization principles

• Minimum jerk (smooth acceleration)

• Minimum signal-dependent noise

• Optimal control: minimize only what is relevant, and ignore other variables.
Lateralization

- Wilder G. Penfield together with Herbert Jasper, treated epileptic patients by destroying neurons.
- Before that, he applied stimulation to different brain areas to probe the epileptic loci.
- One main finding was that each hemisphere controls (efferent nerves) and gets sensory inputs (afferent nerves) from the *contralateral* side of the body.
Decoupling can help, sometimes

- & Michael S. Gazzaniga
- Observed split-brain patients (removed corpus-callosum) and found that each hemisphere is a conscious system in its own right, even in conflicting mental processes.
- Object in the left visual field, will not be vocally named, but can be handled with the ______ hand

Franz et al. (1996), Psychol. Sci. 7:306-310
Hierarchical organization

- Cortex
- Basal-ganglia, cerebellum
- Brain stem
- Spinal tracts
- Spinal cord
- Muscles
Muscles

1. smooth muscles
2. cardiac muscles
3. skeletal muscles
Structure

Muscle fiber

myofibril

Sarcomere: functional unit

Terminal cistern
Transverse tubules
Sarcoplasmic reticulum
Sarcolemma (muscle fiber membrane)

Filaments
Mitochondrion

Z disk
Sarcomere

Thin filament (F-actin)
Tropomyosin
Tropinin
Actin

Thick filament (myosin)
The “engine”

Cross bridges →

Sacroplasmic reticulum

ADP → ATP
Force depends on length

Deformation + overlap
Force depends also on velocity
The force of a single muscle fiber is a function of:

- Stimulation rate
- Stimulation pattern
- The muscle length
- The velocity of contraction
- The fiber type
- The fiber organization
- The duration of exercise - fatigue
Motor unit:
motor neuron and the muscle fibers it innervates (one to many)
3 types of motor unit:

- **A Twitch**
  - Slow
  - Fast fatigue-resistant
  - Fast fatigable

- **B Unfused tetanic force**
  - 13 pps
  - 20 pps
  - 25 pps

- **C Fatigability**

Recruited by order of force (low to high)
Muscle proprioceptive organs

Spindle: length
Parallel

Golgi tendon: tension
Serial
The muscle spindles are sensitive to changes in length
Active range can be dynamically modulated
Golgi tendon organs are sensitive to the tension
Reflexes and actions

- Charles S. Sherrington (1857-1952, Nobel, English Neurophysiologist)
  - Together with John Langley, supported the “localization of function” theory for the brain.
  -Mapped dorsal and ventral roots; opposing muscles, reciprocal innervations.
  -“reflexes are the simplest expressions of the interactive action of the nervous system”

  - Consists of only two neurons: a sensory neuron (the muscle spindle fiber) and the motor neuron. The sensory neuron synapses onto the motor neuron in the spinal cord. When Eccles passed a current into the sensory neuron in the quadriceps, the motor neuron innervating the quadriceps produced a small excitatory postsynaptic potential (EPSP). When he passed the same current through the hamstring, the opposing muscle to the quadriceps, he saw an inhibitory postsynaptic potential (IPSP) in the quadriceps motor neuron.

- Bernard Katz (1911-2003, Nobel): neurotransmitter release in synapses is quantal (Ach in motor nerve -> muscles)
Spinal cord, Brain stem and spinal tracts
Spinal cord

1. Local interneurons
2. Propriospinal (across segments)
3. Projection (to upper centers)
4. Motor neurons

**Motor nuclei:** cell bodies of motor neurons that innervate a muscle.

Medial nuclei are long across segments
Lateral are shorter
Brain stem pathways

**Medial** pathways (vestibulospinal, reticulospinal, tectospinal), terminates in ventromedial (axial) for postural control.  
**Lateral** pathways (rubrospinal) terminates in dorsolateral.
The corticospinal tract

A Ventral corticospinal tract

B Lateral corticospinal tract
Modulation by task and descending pathways
Cortex and control of voluntary movement
Somato-topical organization
Stimulation in M1

Electrical and magnetic stimulation

Lowest intensity

Twitch in single muscle/joint

Large (Betz) cells in lamina V

Many locations -> same muscle
Location - > several muscles
Cortical inputs

A Inputs to primary motor cortex

B Inputs to premotor areas
Coding of force in M1

Evarts, 68
Neurons can be context-dependent
Coding of external direction

\[ fr_i(MD) \approx b_i + k_i \cos(\theta_i - \theta_{MD}) \]

Georgopoulos 1982
Kinematics vs. dynamics

Extrinsic variables (end-point velocity/ position):
  Relative to torso
  Relative to eye
  Relative to shoulder

Intrinsic coordinates:
  Muscles shortening velocity
  Muscles tension

Joints’ velocity, torque, power.
The population vector

If:
- Many cells “care” about direction of movement
- Cells are tuned “cosine like” with a preferred direction
- Preferred directions are uniformly distributed

Then:

The actual movement can be estimated in Cartesian coordinates by a linear combination of weighting the preferred directions with the actual firing rate

$$MD \approx PV = \sum_{i=1}^{N} w_i \overline{C}_i$$
What can we do with it? Neural prostheses
Premotor areas

Premotor dorsal (PMd), premotor ventral (PMv), supplementary motor area (SMA), cingulate (CMA)

- Multi-joint representation
- Complex, meaningful
- Sensorimotor transformations
- Preparatory (set) activity
- Bimanual coordination (SMA)
- Sequence learning (SMA)
- Self-initiation (PMv, SMA) vs. cue-driven (PMd)
- Language, theory of mind
Preparatory (set) neurons are active before the movement.
Representation of plan and execution

Illusion task trajectories. Top row is five cycles from M1 units. Bottom row is from the PMv. The hand trajectory is blue, cursor trajectory is green, and neural trajectory is red. Each displayed trajectory is the mean across five repetitions.

Andy Schwartz
Cue-driven vs. self-initiated

Visual cue

Primary motor cortex

1st key touch

Premotor area

1st key touch

Supplementary motor area

1st key touch

Prior training

400 ms
Prehension: reaching and grasping

Neurons are context-specific (fire for a specific movement)
Learning and Plasticity

Maps: by lesions and skill learning
The basal Ganglia
Action - Selection

Direct pathway: facilitates movement.
Indirect pathway: inhibits movement.
Parkinson and Dopamine

Loss of dopaminergic input leads to increase in the indirect and decrease in the direct pathway => increase GPi => inhibition =? Hypokinesia
Treatment: pallidotomy or DBS
The cerebellum

- 10% of volume, >50% of neurons
- High regularity – a basic circuit module, but with different inputs and outputs
- Lesions result in damage of spatial accuracy and temporal coordination of movement
Error correction

• Evaluating disparities between action and intention (as perceived from sensory information).
Adaptation and motor learning via sensory feedback
Coordination and timing

• Timing: the ability to produce consistent intervals between movements based on an internal representation of time.

• Coordination: motor commands to one effector depend on the predicted state of another effector.
Thanks

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http://www.weizmann.ac.il/neurobiology/labs/rony/