"One should beware of mathematicians and all who make empty prophecies. The danger already exists that the mathematicians have made a covenant with the devil to darken the spirit and confine man in the bonds of Hell"

St Augustine, Bishop of Hippo, circa 400 A.D

"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 Sherington, 1924

Optimization Principles in Motor Control

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Outline

- Review of Muscle Contraction
  - From AP generation to contraction of fibers
  - Muscle proprioceptors (spindles and Golgi tendons)
  - Afferent and efferent axons
- The Muscle Simulink model
- Reflections on Models
- Optimization Principles in Motor Control
  - Understanding the fundamental question in biomechanics
  - Are all motor behavior optimal in some sense?
  - Kinematic versus dynamic objective functions
- Pre-Programmed Muscle Response During Downward Jumps

Muscles: Effectors of the Motor System

- The major output of the elaborate information processing that takes place in our brain is the generation of a contractile force in our skeletal muscles.

- Muscle fasciculus
  - Muscle fiber
    - Myofibril
      - Sarcomere

- Each muscle fiber is innervated by only one motor neuron, although each motor neuron innervates a number of muscle fibers

- The motor neuron and all the fibers it innervates is called a motor unit (the smallest functional unit controlled by the motor system)

Muscles: Effectors of the Motor System

- The number of muscle fibers innervated by one motor neuron is called the innervation ratio. The innervation ratio can vary between 10 and 2000
- A low innervation ratio indicates a greater capacity for finely grading the muscle total force

Muscles: Effectors of the Motor System

A simplified sequence from AP generation to muscular contraction

- Motor neuron fires an action potential
- It propagates down the motor axon until it reaches the neuro-muscular junction
- It triggers an AP in the muscle fiber
- This AP is propagated rapidly over the surface of the fiber and conducted into the myofibril by mean of the T-tubule system
- This in turn releases Ca^{++} from the Sarcoplasmic Reticulum (SR)-the SR serves as a store of Ca^{++}
- This in turn triggers the cyclic motion of Myosin heads, attaching and detaching on the Actin filaments, thus forming cross-bridges and generating the pulling force
- Ca^{++} are pumped back to the SR

Muscles: Effectors of the Motor System

- The force of contraction depends on the length of the muscle (length-tension relationship)
- The force of contraction also depends on the relative rates of movement of the Actin and Myosin filaments (tension-velocity relationship, Hill's curve)
- Motor units are recruited in a fixed order from the weakest to the strongest (Henneman size principle): The weakest inputs recruit the slow units which generate the smallest force and are most resistant to fatigue. The fast fatigue-resistant are recruited next, followed by the fast fatigable units which generate the strongest force.

Muscles: Effectors of the Motor System

- Muscle Proprioceptors (spindles and Golgi tendons)

  There are different types of receptors which respond to light, sound, odor, heat, touch, pain, etc. The receptors which lead to conscious sensations are called **exteroceptors**, those which are not responsible for conscious sensation are called- primary in motor functions- are called **proprioceptors**

  – Spindle organs

    Those are stretch receptors scattered deep within all muscles. They are usually attached in parallel with a muscle fiber, and therefore experience the same relative length change. Spindles give information about its length and rate of change of its length

  – Golgi tendon

    They are found very close to the junction between tendon and muscle fibers. They are placed in series with the muscle fibers and respond to the tendon stretch which accompanies a muscle tension. Thus they are **force transducers** for the muscle.

Muscles: Effectors of the Motor System

- The nerve axons which run out of the spinal cord are called **efferent**, the ones that carry information to the cord are **afferent**
- Group I afferent fibers have large diameters therefore relatively high conduction velocities. They bring information from the spindle (Ia) and the golgi (Ib) to the cord
- The efferent which innervate the main muscle mass are the α, and those that serve the intrafusal fibers within the spindles are called γ
- The stretch reflex, co-activation of α-mn and γ-mn

Muscles: Effectors of the Motor System

Stretch reflex stiffness

- Until recently, it was supposed that the tendon organ served as a sensor which turned off muscle activity (inhibited α-mn) when muscle force rose beyond safe levels

- Afferent activity from both spindles and Golgi tendons balance in such a way that neither muscle force nor muscle length should be considered as controlled quantity, rather their ratio (the stiffness or change in force per change in length) appears to be fixed by the stretch reflex

Muscles: Effectors of the Motor System

- **The sensorimotor cortex** is at the top of the chain of command in the sensorimotor area of the cerebral cortex. There is a specialized area in the cerebral cortex devoted to movement of the limbs (1691, the case of a knight with a fractured skull and paralysis of the left side of the body)
  - The fraction of the cerebral cortex controlling each part of the body is by no means proportional to the size of that part
  - If the cerebral cortex is removed, the animal continues to display all the locomotion reflexes, but cannot learn new skills

- **Basal ganglia** are a set of specialized nerve cells in the brain stem.

- **Cerebellum** is a major focus of incoming sensory information. The information reaching the cerebellum has to do with length, force, velocity of muscles and position of joints.

On Models and Other Demons

What do you think of the following quotes?

- "If a kinematic objective function can be found that leads to optimal trajectories that accurately reproduce the patterns of observed behavior, it implies that the brain ignores non-kinematic factors in selecting and reproducing that behavior"

- "If a dynamic objective function can be found that leads to optimal trajectories that accurately reproduce the patterns of observed behavior, it implies that the brain considers dynamic factors in selecting and reproducing that behavior"

Optimization Principles in Motor Control

Fundamental question in biomechanics

- The human limbs are involved in a prodigious variety of tasks. Movements tend to be graceful and usually involve many limb segments

- Different tasks typically require
  - different sequencing of muscle activation and limb motion
  - different information from sensors

- How are these movements organized? Fundamental question in biomechanics: Which muscles are used and in what pattern?

[Bernstein, *The Co-Ordination and Regulation of Movement*. Pergamon Press, 1967]

Optimization Principles in Motor Control

- One widely used mathematical tool is optimization theory
  Objective: to discover principles that guide goal-directed motor behavior

- Four components to an optimization problem:

  1. An objective function that quantifies what is to be regarded as optimum (also called performance function or cost function)
  2. A dynamic system that is to be controlled
  3. A set of controls that are available for modulation
  4. An algorithm capable of finding an analytical or numerical solution (tools of variational calculus)

- Given a model of musculo-skeletal dynamics, optimization theory re-maps Bernstein's problem of choosing among an infinity of possible patterns of muscle activation into an equivalent problem of choosing among an infinity of performance criteria

Optimization Principles in Motor Control

- Optimization-based models have been developed to address the "excess degrees of freedom" problem
- Recall Bernstein question: How does the motor system select the behavior it uses from the infinite number of possibilities open to it?
  - In mathematical parlance, this is an ill-posed problem in the sense that many solutions are possible
  - For example, most limb segments are moved by a larger number of muscles than appear to be necessary
  - To reach a cup of coffee, the hand may move along an infinity of paths
- Rephrasing the central question: How does the motor system chooses values for the large number of parameters that can be controlled in order to perform a goal-oriented movement?

Optimization Principles in Motor Control

- Need to make explicit and quantitative hypotheses about the goal of motor actions
- Are all motor behavior necessarily optimal in some sense? Maybe!
- One appealing possibility is that the nervous system has evolved to select “solutions” that are indeed “optimal”: the hypotheses is that in performing a motor task, the CNS produces coordinated actions that minimize some measure of performance (effort, smoothness, etc.)

Optimization Principles in Motor Control

- Kinematics versus dynamics objective functions?
  - Kinematics refers to the time course of an object (position, velocity, acceleration, etc.)
  - Dynamics refers to variables such as forces and torques

- Even single degree of freedom can be performed in a variety of ways:
  - Path is constraint
  - Speed along the path can vary (trajectory)

- Two different types of objective functions have been proposed, they reflect the two major competing theories of motor control:

Kinematic objective function   Dynamic objective function

Optimization Principles in Motor Control

Kinematic objective function, single-joint movements

- They are characterized by single-peaked, bell-shaped speed profiles. It was postulated (Hogan, 1984) that voluntary movements are made to be as smooth as possible
- A quantitative measure of smoothness is needed, one such measure is the squared magnitude of the jerk (rate of change of acceleration or third time derivative of position)

Optimization Principles in Motor Control

$$J = \int_{t_0}^{t_1} \left(\frac{d^3\theta}{dt^3} \right)^2 dt$$

$\theta(t)$ is the joint angle. Using variational calculus, the unique time history of joint positions that minimizes this performance measure may be derived analytically

$$\theta(t) = c_0 + c_1 t + c_2 t^2 + c_3 t^3 + c_4 t^4 + c_5 t^5$$

c_i are unspecified coefficients whose values are determined by the conditions at the beginning and end of movements (boundary conditions)

Optimization Principles in Motor Control

- When the movement is assumed to begin at rest in one position and end at rest in another, the "minimum jerk" or "maximum smoothness" movement turns out to have the smooth, uni-modal, bell-shaped velocity profile typical most experimental observations

- The maximum smoothness hypothesis is readily generalized to multi-joint motions.

Optimization Principles in Motor Control

Kinematic objective function, multi-joint movements

- The objective function can be written as follows in the Cartesian coordinate frame of the hand:

$$J = \int_{t_0}^{t_1} \left[\left(\frac{d^3 x}{dt^3} \right)^2 + \left(\frac{d^3 y}{dt^3} \right)^2 \right] \times dt$$

- Assuming the movement start and end at zero velocity from (x_0, y_0) to (x_f, y_f) at time t_f ($\tau = t/t_f$)

$$x(\tau) = x_0 + (x_0 - x_f)(15\tau^4 - 6\tau^5 - 10\tau^3)$$
$$y(\tau) = y_0 + (y_0 - y_f)(15\tau^4 - 6\tau^5 - 10\tau^3)$$

Optimization Principles in Motor Control

- The maximum smoothness theory yields in the multi-joint movement several explicit predictions:

1. Trajectories of the limbs are straight line paths
2. The tangential velocity along that path is smooth and uni-modal
3. The shape of the limb trajectories are invariant under translation, rotation, and amplitude scaling

- These predictions are in agreement with experimental observations

Optimization Principles in Motor Control

Limitations of the kinematic objective functions

- A troubling aspect of this theory is that it implies that at higher levels in the motor system, the brain does not take into account any dynamic considerations such as energy required, the loads on the limb segments or the force and fatigue limitations of the neuromuscular system

- In other words, it implies that the brain determines the "optimal" trajectory independently of the physical system that will generate the movement, i.e., the limb!

> "It seems very strange that the optimal trajectory of our movement is determined perfectly independent of the dynamic quantities such as arm length, payload, motor command, torque or external force, etc."

Y. Uno and M. Kawato, 1989

Optimization Principles in Motor Control

Limitations of the kinematic objective functions (suite)

- The trajectories derived for the minimum jerk model are invariant with respect to the region of the work-space and independent of external forces
- The minimum jerk model determines trajectories irrespective of gravity
- To circumvent this problem within the framework of optimization theory, a second type of objective functions was formulated based on dynamic variables (joint torques, muscle forces, etc.)

Optimization Principles in Motor Control

Dynamic objective function

- Models using a dynamic objective function in movements assume that the CNS solves the three following computational problems at different levels:

1. Determination of a desire trajectory
2. Transformation of visual coordinates of the desired trajectory to body coordinate
3. Generation of motor commands (forces and torques) to realize the desired trajectory

Optimization Principles in Motor Control

Dynamic objective function, multi-joint movements

- One dynamic objective function proposed is the following:

$$J = \int_{t_0}^{t_f} \sum_{i}^{n} \left(\frac{dz_i}{dt} \right)^2 dt$$

- z_i is the motor command fed to the i-th actuator (muscle) out of n actuators

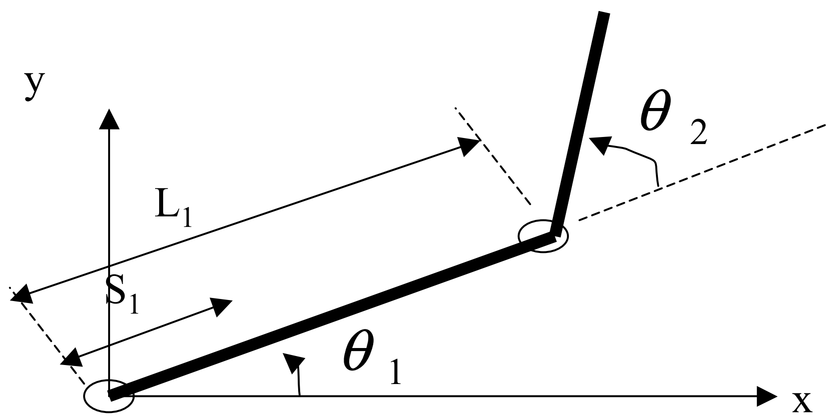
- In order to compute optimal trajectories predicted by this minimum torque change model, the dynamics equations of the musculo-skeletal system must first be specified because *J* depends on the dynamics of the controlled object

Optimization Principles in Motor Control

- Problem: it is difficult to describe the the musculo-skeletal system exactly because it is a complex system.

- Consider the following two-joint system:

Optimization Principles in Motor Control



$$z_1 = \left(I_1 + I_2 + 2M_2L_1S_1\cos(\theta_2) + M_2L_1^2\right)\times\ddot{\theta}_1 + b_1\ddot{\theta}_1$$
$$+\left(I_2 + M_2L_1S_2\cos(\theta_2)\right)\times\ddot{\theta}_2 - M_2L_1S_2\left(2\dot{\theta}_1 + \dot{\theta}_2\right)\times\dot{\theta}_2\sin(\theta_2)$$

$$z_2 = \left(I_2 + M_2L_1S_2\cos(\theta_2)\right)\times\ddot{\theta}_1 + I_2\ddot{\theta}_2 + b_2\ddot{\theta}_2$$
$$+ M_2L_1S_2\left(\dot{\theta}_1\right)^2\sin(\theta_2)$$

Optimization Principles in Motor Control

- Since the dynamics of the multi-joint system is nonlinear, the problem of finding the unique trajectory that minimizes J is a nonlinear optimization problem.

- Consequently, it seems impossible to obtain analytical expression of the solution of this problem, unlike the case with the minimum jerk problem

- Predictions vs experiment
  - Trajectory depends on arm posture and external forces
  - Not always straight paths

- The minimum torque change model succeeded in reproducing observed trajectories under various conditions

Optimization Principles in Motor Control

- Physiological advantage of each model: Why would the CNS want to minimize
  - torque change?
  - Jerk?

Pre-Programmed Muscle Response During Downward Jumps

- Literature review
  - Engberg and Lundberg (1969)

    EMG activity during walking in cat limbs

    "EMG was triggered 5 to 10 ms prior to impact", sort of feedforward activation "a centrally programmed event anticipating stance"

  - Melvill-Jones and Watt (1971)

    Tested the above conclusion on humans during sudden falls. Found consistent EMG burst activity beginning 75ms after drop. Concluded that "deceleration resulted from a timed burst of pre-programmed muscle activity". Problem with this study: dropped subjects from heights up to 20cm! Activity triggered by vestibular input?

  - Greenwood and Hopkins (1976)

    Studied EMG activity during voluntary and unexpected jumps, heights up to 120cm. Findings: Two peaks of activity: 80ms after release only in unexpected jumps + consistent time before landing (related to the voluntary control of landing)

Pre-Programmed Muscle Response During Downward Jumps

– Dyhre-Poulsen and Laursen (1980, 1983, 1985)

Analyzed landing mechanisms and EMG activity in monkeys during downward jumps. Onset of EMG activity started occurred with great precision 80ms before landing. Still an argument against pre-programming: visual monitoring of distance during jump? Lights turned off, same activation pattern, locked to the time of expected impact

– McKinley and Smith (1983)

Performed similar experiments on blindfolded and labyrinthectomized cats.

– Watt *et* al. (1986) plus numerous other studies

It is widely acknowledged that microgravity exposure causes profound changes in human balance, posture control and locomotion. Watt et al. tested astronauts subjected to sudden drops. All subjects are “unsteady postflight”. Reaons for decrement in performance?

Astronauts stated the floor coming up to meet them, and is there before they were ready for it

Pre-Programmed Muscle Response During Downward Jumps

- The missing link: A proposed model to account for the above observations
  - The previous experiments suggest that the "flying object" has an estimate of the time of impact $\widehat{T}_{impact}$ why?
  - Prior to jump, a visual estimate of the height is performed $\widehat{H}_0$
  - What is needed to go from estimated height to estimated time of impact?

A representation of the gravity field in the sensorimotor system, or an internal g-model

$$\widehat{T}_{impact} = \sqrt{\frac{2\widehat{H}_0}{g_{CNS}}}$$

Pre-Programmed Muscle Response During Downward Jumps

- When astronauts perform postflight jumps, one hypotheses regarding the performance decrement (other than muscle atrophy) is that internal representation of the gravity field is altered:

$$g_{CNS} < g_{true} \Rightarrow \widehat{T}_{impact} > T_{true}$$

- Hence the floor is “there before [they are] ready for it”!