principle of the week: the population code

“they’ll fix you…they fix everything” - Robocop
motor neurons and muscle fibers: one motor neuron → one muscle, but to many fibers (but all of the same type)

- slow-twitch: 50 ms to peak force, relatively small force, non-fatiguing (aerobic), useful for tonic movements as in maintaining posture, innervated by type S motor neurons

- fast-twitch: 25 ms to peak force, large force, fatigue easily (glycolysis), useful for quick powerful movements. (jerk), innervated by type F motor neurons capable of high firing rates
common, repeatedly utilized behaviors such as walking, chewing, withdrawal (e.g., a finger from a hot stove) imply the workings of central pattern generators - these are, in turn, formed of muscle ‘synergies’ that evolve over time.

activation / inactivation patterns of muscles at any given time are ‘synergies’ (e.g., knee and hip extensor muscles contract while ankle and knee flexors relax at time given by red arrow)

Kargo and Nitz, JNS, 2003
a second look at the knee-jerk reflex (versus normal muscle activation)—spinal cord interneuron networks coordinate different muscle activation / inactivation patterns

the knee-jerk reflex – dorsal root ganglion cells responding to muscle spindle afferents activate the ‘agonist’ muscle (quadriceps) while inactivating an ‘antagonist’ muscle (hamstring) through an inhibitory interneuron

but…..activation of the hamstring will stretch the patellar tendon connecting the quadriceps to the tibia (and activate the golgi tendon organ)…..so what about situations where activation of the hamstring is required?

answer: inputs from, for instance, motor cortex which drive hamstring contraction through motor neurons also inhibit dorsal root ganglion cell inputs to the quadriceps muscle by hyperpolarizing the presynaptic terminal (thereby preventing transmitter release)
motor control involves the selection of muscle synergies by several different systems

corticospinal (motor cortex output)
vestibulospinal
reticulospinal (mesencephalic locomotor region)
rubrospinal (receives output from cerebellum)

spinal cord interneurons:
1. can be excitatory (green) or inhibitory (red)
2. are interconnected with themselves and motorneurons
3. may have axons which cross the commissure and/or extend into other segments
4. are recipients of both converging and diverging motor cortex inputs
convergence AND divergence of corticospinal axons

single motor cortex neurons projecting to the spinal cord exhibit divergence of their axon terminals to motor neurons of the ventral spinal cord that, in turn, innervate different muscles (i.e., a single motor cortex neuron can activate several different muscles)

spike-triggered recordings of six muscles of the forearm

eighboring regions of motor cortex (e.g., thumb and forefinger)

projections of motor cortex neurons converge onto single spinal cord motor neurons (e.g., ‘thumb’ and ‘forefinger’ regions of the motor homonculus may form synapses on the same motor neuron)
defining the patterns produced by population firing rate vectors

action potential rasters (tic marks) for a single neuron during 5 separate reaches to eight different directions from the center point – this neuron fires the greatest number of action potentials for the south and southeast reaches (red line indicates preferred direction)

across a population of motor cortex neurons, each will have a different preferred direction – by considering the firing rate of all recorded neurons at any given time (i.e., the population rate vector), the associated direction of movement can be predicted

Georgopoulos, 1988
Moran and Schwartz, 1999
robo-monkey: interfacing the activity patterns of monkey motor cortex neurons with a robot arm – monkeys learn to generate activity patterns that will control a robot arm

robot arm & ‘fingers’ pinching a piece of food – monkey subsequently moves food to mouth
controlling the controller: premotor cortex drives activity patterns in motor cortex and is, in turn, driven by both prefrontal and parietal cortices
dissociating the premotor and motor cortex I: premotor cortex in navigating rats exhibits more abstract relationships to action – mapping of action, sequence-dependence of action mapping, and mapping of action plans

sequence-dependent action mapping: this neuron fires after the last turn if it’s a right

route 1 - LRL  route 2 - LRR  route 3 - RLL  route 4 - RLR

action planning: this neuron fires during forward locomotion preceding right turns

route 1 - LRL  route 2 - LRR  route 3 - RLL  route 4 - RLR

action mapping: this neuron fires during the execution of any right turn

route 1 - LRL  route 2 - LRR  route 3 - RLL  route 4 - RLR
dissociating the premotor and motor cortex II: activity may reflect the position of an action in an action sequence

Activity of a single premotor neuron which fires over the final segment / action irrespective of the direction of movement

Activity of single premotor neuron which fires over the first segment / action irrespective of the direction of movement
dissociating the premotor and motor cortex III: ‘mirror neurons’ of the premotor cortex – activity maps actual as well as witnessed behaviors of the same type

right: a neuron in premotor cortex fire during grasping AND as the monkey watches someone else do the same thing

below: a neuron in premotor cortex fires when the monkey breaks a peanut (M), when he sees and hears someone else do the same (V+S), when he only sees it (V), and when he only hears it (S)

below-right: a neuron in premotor cortex fires when an object is grasped even if the object is hidden by a screen (but known to be in place)