Tyler Streeter
tylerstreeter@gmail.com

This text summarizes my knowledge of the anatomy and function of the components involved in biological intelligence. Note that it is full of speculations which attempt to connect brain functions with theoretical machine intelligence research.

Biological Components of Intelligence

General Principles

A sensory system neuron has a receptive fields, i.e. the set of receptors that affect its activity. A motor system neuron has a muscle field, i.e. the set of muscles that it can affect.

The motor hierarchy has the following principles:

- Somatotopic organization is retained at each level.
- Each level receives peripheral sensory info.
- Each level projects copies of motor commands to sensory relay nuclei, i.e. many systems receive copies of current actions.
- Relevant areas in the hierarchy have increased activation related to selective attention.

Attention is focused on a single area of the sensory hierarchy using a winner-take-all scheme (e.g. figure-ground recognition in visual perception, p. 494 of PoNS, 2000). Presumably, the "winner" is the area that generates the most novelty (or reduction in novelty), i.e. curiosity reward.

Visual System

Contains multiple submodalities/subhierarchies:

- motion (area MT, aka V5)
- depth (area MT, aka V5)
- form (various parts of the ventral stream)
- color (area V4)

Visual information separates into two major pathways:

- Dorsal stream (ends in PP cortex): depth, motion, spatial location; uses the fast, low-resolution, non-color magnocellular (M) cells
- Ventral stream (ends in IT cortex): form/outlines (edge detection), color, object recognition; uses magnocellular cells and the slow, high-resolution parvocellular (P) cells

The lateral geniculate nucleus (LGN) gets only 10-20% of its inputs from the retina; the rest are mostly feedback from higher areas.

The M and P pathways, starting in the retinal M and P ganglion cells, remain segregated from the retina to the cortex. V1 contains "blobs" and "interblobs," which both project to the ventral stream. V2 contains "stripes" (thick [dorsal] and thin [ventral]) and "interstripes" (ventral). See figures 25-12, p. 502, and 28-2, p. 550.

V2 responds to more abstract contours than V1. V4 responds to color and fine-grained form.

IT cortex responds to the most complex forms, like faces. Each cell's receptive field covers the entire fovea, and some cover the whole visual field. There is no clear retinotopic organization (position-invariance).

Area V1

V1 layered structure and connectivity: see figure 27-10, p. 533.

V1 contains three main types of cells:
- Simple cells: respond to bars of light at a specific orientation in a specific part of the visual field; built from the circular receptive fields of RGCs and LGN cells; basically, they perform edge detection
- Complex cells: also tuned to specific orientations, but independent of the location within the visual field (gets input from multiple simple cells with the same orientation); larger receptive fields than simple cells
- Blobs: respond to colors; not dependent on orientation

V1 contains "orientation columns" containing groups of simple cells that respond to similar orientations in the same part of the visual field (i.e. edge detection). These columns also contain complex cells that get input from the column's simple cells.

A "hypercolumn" is a computational unit that processes info from a small chunk of the visual field. It contains the full range of orientation columns (organized as a self-organizing map?) from both eyes. It also contains blobs. There are horizontal connections among different hypercolumns, usually within a radius of a few millimeters. It projects to higher cortical areas (e.g., V2, V3, V4, MT) and to subcortical areas (superior colliculus, pons, pulvinar, LGN, claustrum). It handles:
- orientation of bars of light/dark (edge detection)
- binocular interaction
- color
- motion

Area MT (middle temporal area)

Motion is detected when images move across the retina OR when the eyes/head move to track an object. MT cells, arranged in columns, are directionally sensitive; they are tuned to motion in specific directions. Their receptive fields are 10x that of V1 cells. Columns process motion in small chunks of the visual field. They respond to spots and bars via changes in luminance.

Depth is detected in various ways, including various monocular cues (e.g., parallax) and stereoscopic vision. Stereoscopic vision (mainly for distances less than 100 ft) uses binocular disparity, which is processed by disparity-sensitive cells that are tuned to specific amounts of disparity. These exist in V1, V2, V3, and MT.

Control of Gaze

The firing rate of extraocular motor neurons encodes eye position and velocity via bursts and tonic activity. This might actually be similar to the desired position and velocity of a servo/PD controller. There is no extraocular stretch reflex, even though the muscles are rich in spindles. All eye motor neurons participate in all types of eye movement.

The superior colliculus controls saccades. It uses a population code for direction and amplitude. The frontal eye fields and supplementary eye fields are also involved in saccades (supplementary eye fields encode target location). PP cortex is involved in visual attention; maybe the most unpredicted stimuli encoded in PP attract the most attention. Smooth pursuit system uses info from MT.

Spinal Cord

Lowest level of sensory and motor hierarchies. Contains motoneuron pools (aka motor nuclei) that innervate specific muscles.

Spindles - stretch and contract with intrafusal muscle fibers.

Alpha motor neurons:
- Receive input from spindles (Ia fibers)
- Firing causes extrafusal muscle contraction

Gamma motor neurons:
- Firing causes intrafusal muscle contraction

Alpha and gamma motor neurons both receive input from the motor cortex. Both systems can be used simultaneously.

The motor neurons have multiple modes of operation:
- An external load, which causes stretching of the spindles, activates alpha neurons which compensates for the stretch. This maintains a desired joint angle via servo control.
- Gamma neuron signals (e.g., caused by cortical inputs) intentionally cause tension in the spindles, which contracts the extrafusal fibers; this allows gamma neuron signals to affect contraction "directly."

Brain Stem

Below cortex and above spinal cord in sensory and motor hierarchies. Combines spinal reflexes into higher-level automated movements.

Primary Sensory Cortices

These areas are some of the lowest levels of the sensory hierarchy for vision (occipital lobe), audition (temporal lobe), and somatosensation (parietal lobe).

Unimodal Sensory Association Areas

These areas are higher in the sensory hierarchy than the primary areas, but they are still segregated by modality; information from one modality does not combine with that of another modality. These include vision (occipitotemporal area), audition (temporal lobe), and somatosensation (parietal lobe).

Multimodal Sensory Association Areas

These areas are higher than the unimodal assication areas in the sensory hierarchy. They combine information across modalities. These include the following areas:

- Posterior multimodal sensory integration area (parietaltemporal area): integrates visuospatial localization, language
- Anterior multimodal sensory integration area (prefrontal cortex in front of premotor areas): possibly the primary site of planning; however, planning might occur at all levels of the sensory-motor hierarchies, in which case this area is concerned with very high-level planning; receives dopaminergic inputs
- Limbic (temporal, parietal, frontal areas, including the cingulate gyrus, hippocampus, amygdala): integrates emotion, memory

Primary Motor Cortex (MC1)

PP 5 -> MC1
somatosensory 1,2,3 -> MC1
all premotor areas (SMA/preSMA, premotor cortex, CMA) -> MC1
cingulate (prefrontal) -> MC1
MC1 -> premotor
MC1 -> prefrontal
MC1 -> cbm
MC1 -> red nucleus (rubrospinal tract)
Lowest level of cortical motor hierarchy. MC1 cells are active during movement. It is *not* a simple switchboard for individual muscles. It contains the building blocks of more complex movements. These building blocks are task-dependent, and they can be combined for different tasks. Each neuron has a "muscle field," a set of muscles it can affect, which may overlap that of neighboring neurons. In other words, there is divergence (areas in MC1 project to multiple muscles) and convergence (many MC1 areas project to the same muscles). For example, neurons that control specific digits are dispersed across the hand control area; moving a single digit requires excitation and inhibition of many muscles.

MC1 neurons have "receptive fields" corresponding to somatosensory inputs.

MC1 neurons are tuned for specific movement directions and force amplitudes (see Georgopoulos). Neuron activity varies with the force amplitude required (i.e. firing rate is linearly related to muscle force for a certain range of activity), not the displacement amplitude. An opposing load during movement increases MC1 cell activation because it requires more force; this probably requires a low-level feedback loop going through MC1. Direction and force amplitude are probably encoded with population coding (i.e. the sum of activity of a large population of cells).

The direct corticospinal tract affects motor neurons (affecting force directly) and spinal interneurons (modulating feedback).

Requires lower electrical activity to initiate movement than premotor areas.

Premotor Areas (SMA/preSMA, premotor cortex, CMA)

PP 5,7 -> premotor areas
prefrontal 46 -> premotor areas

premotor areas -> MC1
premotor areas -> spinal cord
BG -> thalamus -> premotor areas
CBM -> thalamus -> premotor areas

Requires higher electrical activity to initiate movement than MC1. Project to the same areas in the spinal cord as MC1, but with fewer overall connections. There are dense projections among the premotor areas themselves.

Mental rehearsal involves premotor areas and PP just like during actual performance.

Motor and premotor activity changes as actions become automatic (possibly moving to the cerebellum).

Supplementary Motor Area (SMA) and Pre-SMA

preSMA (only output) -> (main input) SMA
BG -> thalamus -> SMA
CBM (via thalamus?) -> SMA
prefrontal -> pre-SMA -> SMA
somatosensory (which parts?) -> SMA
visual cortex (which parts?) -> SMA
thalamus -> SMA
SMA -> corticospinal tract
SMA -> MC1
SMA -> red nucleus (rubrospinal tract)
SMA -> reticulospinal tract
Highest level of motor hierarchy. The pre-SMA is active only when learning new sequences, but not during well-learned sequences. The SMA is active when performing "mostly-"learned sequences, but its activity ceases as performance becomes automatic (possibly moving to the cerebellum). A "preparatory potential" is present immediately before movement initiation. Active during internally-guided (open-loop) movements? Involved in bilateral movements. The SMA is part of action initiation, especially for internally-triggered tasks.

Involved in several aspects of sequence learning (see Tanji, 2001):
1. Learning the initiate the beginning of the sequence.
2. Learning to link the end of one specific action to the beginning on another one
3. Learning to signal the end of the sequence.

Premotor Cortex (Lateral Premotor Areas)

BG -> thalamus -> premotor
cbm -> thalamus -> premotor
PP areas 5 and 7 (secondary somatosensory) -> premotor
area 46 (prefrontal) -> premotor
visual cortex (which parts?) -> premotor
premotor -> MC1
premotor -> spinal cord
Below SMA in cortical motor hierarchy. Active during preparation. Active during complex movements, planning, mental rehearsal, etc. Active during sensory-triggered, sensory-guided (closed-loop) movements. Neuron populations represent mappings from stimulus to response (i.e. policies).

Cingulate Motor Area (CMA)

Basal Ganglia (BG)

==

cortex -> BG -> brain stem
cortex -> BG -> thalamus -> [prefrontal, premotor, MC1, SMA] (reentrant loop)

A central component of reinforcement learning, i.e. learning the value of situations, action selection. Only active during action selection. Active during the early stages of learning a particular task (i.e. before it becomes a well-learned "chunk"). The BG plus the midbrain dopamine neurons (substantia nigra pars compacta, or SNc) form the basic components of reinforcement learning.

All areas of cortex send excitatory projections to the striatum. Direct and indirect pathways in the BG focus activity on specific areas and inhibit the rest (action selections via winner-take-all?). Each area of the motor hierarchy is joined to the BG, allowing reinforcement learning at specific parts of the hierarchy (one at a time, guided by attention). The sensory hierarchy might only be connected at its highest levels (maybe only in sensory-motor association areas), so "value function learning" would only operate at high levels.

Dopamine activity increases during unexpected rewards and decreases during the absence of expected rewards. This activity is precisely timed, indicating the presence of a "state representation" with precise temporal activity. (This might include a short history of previously experience states.)

4 Main Nuclei (see chapter 43 of PoNS, 2000 for diagrams):
1. Striatum - The major input part of the BG. Includes the caudate nucleus (more cognitive), putamen (more motor), and the ventral striatum (which includes the nucleus accumbens). Comprised of two components: matrices/matriosomes and striosomes/patches. Receives major inputs from cortex, thalamus, and brain stem. Projects to GP and SNc.
2. Globus Pallidus (GP), (aka Pallidum) - Includes internal (GPi) and external (GPe) components. This forms the major outputs from the BG.
3. Substantia Nigra - Includes the pars compacts (SNc) and pars reticulata (SNr). The ventral tegmental area (VTA) is part of SNc.
4. Subthalamic Nucleus (STN) - ?

5 Main Circuits:
* Note: Each loop starts and ends in the same region of cortex. Each circuit is very topographic with little convergence between circuits, see Figure 43-5, p. 859, in PoNS, 2000.
1. Skeletal-Motor - Connects to MC1, premotor, SMA, and primary somatosensory cortex. Motor and somatosensory areas project in an overlapping manner to the putamen. This might represent the policy.
2. Oculomotor - Involves the frontal and supplementary eye fields.
3. Dorsolateral Prefrontal - Connects to prefrontal cortex. Involved in "executive functions" and problem solving.
4. Lateral Orbitofrontal - Connects to the lateral prefrontal cortex. Involved in empathetic and socially-appropriate responses. This might be part of the value function.
5. Limbic/Anterior Cingulate - Involved in "motivated behavior." Might send reinforcing stimuli diffusely to the BG and cortex via the VTA and SNc. This might be part of the value function.

Cerebellum (cbm)

==

spinal cord -> cbm
cbm -> thalamus -> MC1
cbm -> thalamus -> premotor
cbm -> thalamus -> prefrontal
cbm -> magnocellular red nucleus
cbm -> parvocellular red nucleus
cortex -> cbm (via the brainstem) -> thalamus -> cortex (reentrant loop) (which parts of cortex???)
PP -> cbm -> premotor

A general purpose timing/sequencing device that helps to automate tasks. Involved in perception, motor control/motor learning, and planning/mental rehearsal. Involved in well-learned open-loop actions; closed-loop during learning. Evaluates disparities between intention and action, and trains itself based on these errors. Has 40x more inputs than outputs. Mossy fibers bring in sensory info. Climbing fibers fire "complex spikes" during unexpected events; these are teaching signals. Purkinje cells send outputs. Damage disrupts spatial accuracy, temporal coordination, and motor learning. The premotor -> cebellular -> rubro cerebellar loop might be part of mental rehearsal.

The cerebellum might maintain a short-term history of recent states. The combination of the current state with a short history of states would provide an augmented state representation. This would be useful for learning temporal relationships among events. If this hypothesis is accurate, the cerebellum would function as a general-purpose short-term memory device.

Maybe it stores well-learned policies; this is supported by the facts that: 1) it contains so many neurons, making it able to store a lot of policies, and 2) it receives copies of information passing between the cerebral cortex and spinal cord, giving it a chance to learn certain regular patterns and possibly take them over.

Hippocampus

==

Essential for forming new long-term declarative memories. It could maintain "starting points" for planning trajectories. Without it, planning trajectories might not proceed. Evidence: place cells in rat hippocampus fire rapidly in (reverse) order when resting after a maze task. It is connected to the top of the sensory-motor hierarchy.

Anterior Cingulate Gyrus

==

Region of the cingulate cortex which surrounds the corpus collosum. Possibly involved in reward processing and action selection. Activity is negatively correlated with visual task performance.