the brain is not a strictly feed-forward system
rather, the connectivity of most brain regions is characterized by a combination of feed-forward and feed-back (or ‘re-entrant’) inputs
the basal ganglia, hippocampus, and cerebellum – shared properties

1. each system receives input from widespread regions of cortex
2. each system outputs back to cortex (as well as to other regions)
3. each system is composed of several sub-regions across which information input from cortex converges and output to cortex diverges
4. each system is implicated in learning and each exhibits a unique form of learning at the cellular level
5. neurons within each system exhibit firing patterns related to ‘contextual’ information (i.e., activity not related to a single sensory or motor variable)
the cortex-cerebellum-cortex loop: role in timing and adjustment of motor patterns

- inhibitory projection
- excitatory projection

1. **Cerebral Cortex**
   - Pontine nuclei (mossy fibers)
   - Vestibular and proprioceptive inputs

2. **Cerebellum**
   - Granule cells
   - Purkinje cells
   - Inferior olive (climbing fibers - ‘error’ signal induces learning)
   - Cerebellar nuclei (base of cerebellum – each contains homunculus)

3. **Ventrolateral Thalamus** (and brainstem and spinal cord)

4. **Motor Cortex**

**Convergence** = coordination across muscles of the body

**Divergence**
cerebellar function: the view from the cerebellar nuclei

......cerebellum – Purkinje cells

- cerebellar nuclei (high baseline rates modulated by Purkinje cell inhibition)......

<table>
<thead>
<tr>
<th></th>
<th>fastigial nucleus</th>
<th>interpositus nucleus</th>
<th>dentate nucleus</th>
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</thead>
<tbody>
<tr>
<td>Neuronal activity</td>
<td>eye mvmts. / walking</td>
<td>perturbation of limb/body from holding position</td>
<td>auditory and vision triggered mvmts.</td>
</tr>
<tr>
<td>Localized inactivation</td>
<td>posture and gait instability</td>
<td>tremor</td>
<td>reaction time delays; poor endpoint control</td>
</tr>
<tr>
<td>Function</td>
<td>postural adjustments</td>
<td>balance of agonist / antagonist muscles</td>
<td>timing / cross-muscle coordination</td>
</tr>
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</table>
basal ganglia: a complex of sub-regions damage to one or more of which is implicated in Parkinson’s disease, Huntington’s chorea, obsessive-compulsive disorder, Tourette’s syndrome, attention deficit disorder, and drug addiction.

substantia nigra has two sub-regions:
pars compacta = DA neurons
pars reticulata = GABA neurons (analogous to GPi)

globus pallidus has two sub-regions:
external segment = GPe
internal segment = GPi

the thalamic sub-region associated with the basal ganglia output is the ‘ventrolateral’ thalamus

together the caudate and putamen are called the ‘striatum’
cortex \rightarrow \textit{basal ganglia} \rightarrow \textit{cortex}: direct, indirect, and hyperdirect pathways

2/3's of output to, prefrontal, premotor or motor cortex

convergence: all regions of cortex contribute

'hyperdirect' pathway
the direct and indirect pathways are modulated differentially by DA

- **Direct path**
  - Cortex input (glutamate excitatory)
  - SNpc – DA input to D1 receptor enhances glutamate effect
  - GABA output to GPi

- **Indirect path**
  - Cortex input (glutamate excitatory)
  - SNpc – DA input to D2 receptor suppresses glutamate effect
  - GABA output to GPe

DA neuron activity is, at least in part, driven by positive errors in reward expectation (i.e., getting more value than expected given a specific condition)

DA neuron firing rate vs. actual – predicted reward value
entire neocortex: combined motor and sensory context

'motor' neocortex: implementation of decision

'indirect' pathway - favored by low DA levels

'direct' pathway - favored by high DA levels

strong inhibition weak inhibition
strong excitation weak excitation

striatum
GP internal
GP external
thalamus
basal ganglia also appears to determine the robustness of a response

reward expectation drives changes in latency to onset of a saccade following cue onset

antagonists of DA type D1 and D2 receptors differentially affect latency differences

different caudate neurons exhibit saccade related activity dependent on reward expectation (panel 1), on expectation of no reward (panel 2), or pre-saccade activity dependent on saccade type AND reward expectation (panel 3)
basal ganglia activity: mediation of individual response versus response sequence ‘chunks’

As rats learn the meaning of the tones, striatum activity ‘moves’ from concentration at the choice point to concentration at the start and end points.