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

- cerebral cortex
  - pontine nuclei (mossy fibers)
  - convergence
  - divergence

- cerebellum – granule cells
  - vestibular and proprioceptive inputs
  - convergence = coordination across muscles of the body
  - divergence

- cerebellum – Purkinje cells
  - inferior olive (climbing fibers - ‘error’ signal induces learning)

- cerebellar nuclei (base of cerebellum – each contains homunculus)

- ventrolateral thalamus (and brainstem and spinal cord)

- motor/prefrontal cortex

convergence = coordination across muscles of the body

from the front... ...from the side
cerebellar function: the view from the cerebellar nuclei

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**cerebellum – Purkinje cells**

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

<table>
<thead>
<tr>
<th>fastigial nucleus</th>
<th>interpositus nucleus</th>
<th>dentate nucleus</th>
</tr>
</thead>
<tbody>
<tr>
<td>neuronal activity</td>
<td>eye mvmts. / walking</td>
<td>perturbation of limb/body from holding position</td>
</tr>
<tr>
<td>localized inactivation</td>
<td>posture and gait instability</td>
<td>tremor</td>
</tr>
<tr>
<td>function</td>
<td>postural adjustments</td>
<td>balance of agonist / antagonist muscles</td>
</tr>
<tr>
<td></td>
<td></td>
<td>timing / cross-muscle coordination</td>
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reaction time delays; poor endpoint control
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
convergence: all regions of cortex contribute to 2/3’s of output to prefrontal, premotor or motor cortex.
the direct and indirect pathways are modulated differentially by DA

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)

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

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

DA neuron firing rate

![Graph showing DA neuron firing rate vs. actual - predicted reward value](image-url)
convergence: all regions of cortex contribute

cortex → basal ganglia → cortex: direct, indirect, and hyperdirect pathways

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

'hyperdirect' pathway

GABA, enkephalin, D2

GABA, substance P, D1

Caudate/Putamen

excitation

inhibition

Dopamine modulation
entire neocortex: combined motor and sensory context

'motor' neocortex: implementation of decision

'direct' pathway - favored by high DA levels

strong excitation - weak excitation

weak inhibition - strong inhibition

'indirect' pathway - favored by low DA levels

strong inhibition - weak inhibition

weak excitation - strong excitation