Cortex and Mind
Chapter 3

The underlying premises of this book are that:
1) All cognitive functions, e.g. perception, memory, attention, share the same representational substrate of neurons and their connections.
2) Different functions differ in the portion of that substrate used at any given time. No cognitive function has a fully dedicated cortical area or network.
3) A representational cortical network (cognit) may be used by any and all cognitive functions.

This chapter concerns the morphological features of cognits.
Structure of knowledge in connectionist models

*Connectionist models* of cognition explain the distributed nature of knowledge.

Common features of connectionist models:
1) they assume the distribution of knowledge in assemblies of units, neurons, or nodes that represent the component elements of knowledge.
2) the nodes are interconnected in networks by synapses.
3) the networks are layered.
4) some connections between layers are reciprocal, supporting *reentrant processing*.
5) layers are connected by parallel, convergent, and divergent connections.
6) networks learn by modification of synaptic weights.
7) in *unsupervised learning*, synapses are strengthened by temporal coincidence of pre- and post-synaptic activity.
Categories of knowledge

1) Cognitive function is based on the categorization of knowledge.

Knowledge can be categorized according to an astronomical number of criteria.

Perceptual categories are organized in cognitive hierarchies of progressive generality and abstraction.

Sensory percepts are at the low levels and symbolic percepts at the higher levels.

E.g. a picture of a terrier can be categorized as “dog”, “mammal”, “animal”, or “living thing”. It can also be categorized as “Rover”.

The picture can be categorized according to its elemental sensory properties, such as size, shape, color, texture, etc. Since the lowest levels of sensory categories appear to be hard-wired at birth, they may be considered to be a part of the phyletic memory of the species.

At any hierarchical level, an item can belong to more than one category. E.g. “dog” belongs to the category of “mammal” and the category of “four-legged animals”.
2) Perception is seen to consist in the classification of sensory items by the *binding* of features according to Gestalt grouping principles.

Examples of grouping principles:

a) common motion

Motion examples:
[http://www.biomotionlab.ca/Demos/BMLwalker.html](http://www.biomotionlab.ca/Demos/BMLwalker.html)

b) spatial contiguity (proximity)
c) temporal contiguity (proximity)

Temporal contiguity occurs when two or more stimuli are experienced close together in time and, as a result an association is formed.

Tone sequences, or “streams”

If the audio and video get even slightly out of sync, the viewer may hear an actor’s words before or after his lips move, which is easily detected and fairly annoying.
The strength of binding is affected by factors such as:
   a) repetition
   b) emotional or motivational connotation
   c) motor contingency

Once the hierarchical organization of perceptual categories is established by experience, *heterarchical* categorization of percepts also occurs through associations between higher level categories. E.g. associating “helicopters” and “pigeons” as “flying objects”.

Heterarchical categorization is necessary for concept formation and use.

3) Besides the hierarchy of perceptual knowledge, there exists a *hierarchy of action knowledge*.

The basic motor elements of actions are at the bottom. Above them are progressively higher action categories relating to:
   a) movement patterns
   b) goal-directed actions
   c) plans, syntax, etc.

As in perceptual categorization, action categories are organized by principles of spatial and temporal proximity.
Cortical modularity

Cortical areas differ in:
   a) local cytoarchitecture
   b) sources of their connections
   c) targets of their connections

These structural differences are thought to be the basis for the specialized functions of different cortical areas.
Horizontal organization:

6 layered sheet with common laminar pattern throughout:
I: plexiform layer
II: small pyramidal cells that project to ipsilateral cortical areas
III: small pyramidal cells that project to contralateral cortical areas
IV: stellate cells that receive thalamic input & input from hierarchically lower cortical areas (striking appearance in primary visual cortex; absent in primary motor cortex)
V, VI: large pyramidal cells that project to subcortical structures, including thalamus, basal ganglia, midbrain, spinal cord
**Vertical organization:**
1) Apical dendrites & primary axons of pyramidal cells are arranged vertically
2) Vertical *minicolumns* span cortical width – considered to be smallest processing unit of neocortex
3) Connectivity and cell density are dense within columns & sparse between columns
4) Columnar width in range of 30-50 microns
5) Columns originate in primordial matrix of proliferative layer
6) Each column results from upward migration and superposition of ~100 neurons
7) Functional macrocolumns in primary sensory and motor areas are 50-500 microns wide; unified by common extrinsic connections

In association cortex, functional modularity is not obvious. Minicolumns are still seen, and interareal connections terminate in vertical patches 200-500 microns wide.
Visual cortical hierarchy:
1) functional columns in primary visual cortex (V1) are well-organized and contain cells selectively responsive to low-level visual features, e.g. line orientation, color; receptive fields are small and visuotopic map is precise
2) at progressively higher levels, modularity becomes less well-organized and cells are selectively responsive to more complex visual features; receptive fields are progressively larger and visuotopic map becomes less precise and disappears
3) inferotemporal cortex is high in the visual hierarchy – it is part of visual unimodal association cortex, representing a transitional stage between lower-level visual analysis and higher-level polymodal analysis
Sensorimotor cortical hierarchy:
1) primary somatosensory and motor cortices are symmetrically arranged around central sulcus
2) each is somatotopically organized & each lies at the base of a cortical hierarchy
Cortical hierarchy of perceptual networks

1) *Primary cortical areas* in each sensory modality send fiber projections (by pyramidal cell axons) to higher-order areas that are specialized for processing more complex information in the same modality.
2) Successive areas within each modality are linked by reciprocal fiber pathways.
3) Higher-order areas comprise *unimodal association cortex* within each modality.

Each unimodal sensory system sends (at different stages) long-distance projections to *transmodal areas.*
The main transmodal areas:
  a) lateral frontal cortex for sensory-motor associations
  b) limbic & paralimbic cortex for emotional associations & memory consolidation
  c) parietal & temporal multimodal cortical convergence areas for cross-modal associations

Connections between unimodal and transmodal areas are also reciprocal.

The connectional hierarchy serves as a structural basis for the hierarchical representation of perceptual knowledge.

The hierarchy of perceptual knowledge corresponds to categories of progressively higher abstraction:
  a) The lowest levels are elementary unimodal sensory feature categories.
  b) Higher levels are more complex unimodal perceptual feature categories.
  c) At the highest levels are transmodal semantic and symbolic categories.
## Organizational principles of perceptual knowledge in the neocortex

<table>
<thead>
<tr>
<th></th>
<th>Primary</th>
<th>Unimodal Association</th>
<th>Transmodal</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Hierarchical level</strong></td>
<td>low</td>
<td>middle</td>
<td>high</td>
</tr>
<tr>
<td><strong>Anatomical organization</strong></td>
<td>single areas</td>
<td>multiple distributed areas</td>
<td>convergence regions</td>
</tr>
<tr>
<td><strong>Module size</strong></td>
<td>small</td>
<td>intermediate</td>
<td>large</td>
</tr>
<tr>
<td><strong>Receptive field size</strong></td>
<td>small</td>
<td>large</td>
<td>none(?)</td>
</tr>
<tr>
<td><strong>Perceptual representation</strong></td>
<td>elementary sensory features</td>
<td>complex sensory features</td>
<td>word meaning</td>
</tr>
<tr>
<td><strong>Categorical example</strong></td>
<td>edges</td>
<td>faces</td>
<td>names</td>
</tr>
</tbody>
</table>
Lesions at progressively higher anatomical levels leads to deficits at progressively higher categorical information processing.

**Examples of lesion effects:**

a) primary sensory cortex (V1): *anopsia* (focal loss of vision)

b) unimodal association cortex:
   i. (extrastriate cortex): *cortical achromatopsia* (loss of ability to detect color)
   ii. (IT): *visual object agnosia* (inability to name a visual object)

c) transmodal association cortex (posterior superior temporal gyrus): *semantic aphasia* (loss of the ability to comprehend words)
Cortical hierarchy of executive networks

The *perception-action cycle* refers to the recurring sequence of perception and action that repeats as the organism interacts with the environment. Each action sets the stage for a new perception, which in turn enables a new action.

This cycle depends on the functional linkage between posterior cortical areas for perception and frontal areas for action, each organized hierarchically.
The frontal lobe action hierarchy:

a) primary motor cortex (Brodmann area 4) is at lowest level
b) the premotor cortex (Brodmann area 6) is one level up
c) prefrontal cortex (Brodmann areas 8,9,10,46) is at the next level up
d) hierarchical arrangement is based on ascending order of generality of action and temporal dimension
e) frontal areas receive projections from and send them to posterior sensory areas – long connections link corresponding levels in action and perceptual hierarchies
f) prefrontal cortex also has reciprocal connections with limbic structures
   i) dorsolateral prefrontal cortex is connected with cingulate cortex, hippocampus & parahippocampal cortex – related to formation of motor memory
   ii) orbital prefrontal cortex is connected with amygdala – related to evaluation of motivational significance of external stimuli
Functions of action hierarchy:
1) The primary motor cortex (M1) networks represent distinct movements involving specific muscle groups. Muscles are grouped by intended action as well as by somatic location.

2) The premotor cortex contains networks representing motor trajectories and goals. Movement representations are more distributed than in M1.
   
i) lateral premotor cortex (area 6b): cells tuned to kinematic properties of movement; also contains mirror units that are activated by the observation of movements made by others.
   
ii) medial premotor cortex (area 6a or supplementary motor area – SMA): neurons are active before & during the execution of movement sequences: representations are thus defined by temporal order as well as spatial position. SMA is also the source of the readiness potential, a slow ERP wave that precedes self-initiated movements.
3) The prefrontal cortex contains networks representing plans of action. Lesion impairs functions that depend on temporal integration of sensory and motor information, including spoken language. Prefrontal cells show sustained activity in the delay interval of delay tasks; related to contingent negative variation (CNV), a slow ERP wave preceding the S2 in a S1-S2 paradigm. These neural signals at the cellular and population levels result from a widely distributed executive cognit.
Heterarchical representation in association cortex

1. Most memories are represented in cognitive networks (cognits) that span levels within hierarchies and across different hierarchies (i.e. are heterarchical).
2. Sensory events are integrated into the structure of pre-existing knowledge.
3. Integration of sensory events with pre-existing knowledge occurs at higher levels than primary sensory cortex.
4. Integration of experience in more than one modality involves transmodal association cortex.
5. Integration of sensory events with action involves prefrontal cortex.
6. High-level cognits represent abstract concepts; they are represented in association cortex; they are connected to lower-level cognits with which they are associated.