Computational Explorations in Cognitive Neuroscience
Chapter 7: Large-Scale Brain Area Functional Organization

7.1 Overview

This chapter aims to provide a framework for modeling cognitive phenomena based on the large-scale organization of the brain.

It proposes a functional organization of the brain composed of 3 main parts:

(1) posterior cortex
(2) frontal cortex
(3) hippocampal system

These 3 systems are proposed to interact to create different cognitive phenomena.
They represent a "cognitive architecture" – a high-level description of the neural processes underlying cognition.

4 major issues relating to learning, memory, and attention in the brain will be considered:

(1) the need for both slow integrative learning and fast separating learning

(2) the need for both active memory and overlapping distributed representation memory

(3) the need for both controlled processing and automatic processing

(4) the need for both declarative (explicit) memory and procedural (implicit) memory

Then 6 general problems will be discussed:

(1) how binding of distributed representations of multiple items occurs
(2) how multiple instances of the same item are represented
(3) how representations are compared
(4) how hierarchical relations are represented
(5) how recursive processing occurs
(6) how generalization, generativity, and abstraction occur

7.2 General Computational and Functional Principles

A useful distinction in the discussion of general properties of the implementation of cognition in the brain is between:
structure: the ways that information and processing are arranged within the brain, including patterns of connectivity and relations between different stages of processing.

and

dynamics: the temporal aspects of processing, including how activation flows through different stages and accomplishes goal-directed behavior.

7.2.1 Structural Principles

Here we consider 6 structural principles:

(1) hierarchical organization
(2) specialized pathways (streams)
(3) inter-pathway interactions
(4) large-scale distributed representations
(5) dedicated, content-specific processing and representation

Hierarchical Structure

Neurons are viewed as detectors of sets of conditions (features) in their inputs. Layers of neurons can perform transformations of input patterns that emphasize some distinctions between patterns and deemphasizes others. These transformations can be “shaped” by learning.

Properties of Neural Networks (Lecture 1): Computation as systematic mapping from input to output domain

The hierarchical structure of cognition is viewed as a sequence of layers.
These:

1. operate on sensory inputs
2. ultimately produce:
    a. motor output responses
    b. “interpretations” of the environment useful for subsequent behavior

These transformations operate under different constraints or objectives.
For example, an objective in visual object recognition is spatial invariance, i.e. an object must be recognized as the same regardless of size, location, or distance.
Hierarchical sequences of transformations operate at all levels of processing to achieve such objectives.

Specialized Pathways

Hierarchical sequences of transformation lead to progressive refinement of representation in different pathways. This means that the different pathways will be specialized for different types of representation.

In the primate visual system, the ventral processing system is specialized for visual form recognition and the dorsal processing system is specialized for visual spatial processing and visuomotor transformations.

General Principles of Neural Computation (Lecture 1): Division of Labor (#1)

Inter-Pathway Interactions

From a computational perspective, hierarchical processing structures benefit from communication between different specialized systems.

In the primate visual system, there are connections between the ventral and dorsal systems at every level. These connections “can mutually constrain or inform processing across different pathways to better deal with partial, noisy, novel, or particularly complex stimuli.”

General Principles of Neural Computation (Lecture 1): Weak Modularity (#2) and Constraint Satisfaction (#3)

At higher levels in the primate cerebral cortex, hierarchical organization gives way to heterarchical organization (interconnected areas at the same level).
[See J.M. Fuster, Cortex & Mind, Oxford U Press, 2003; M.-M. Mesulam, From sensation to cognition, Brain, 1998]

At these higher levels, we are forced to consider interactions between pathways because there is no basis for hierarchical transformations. Processing involves bidirectional interactions and mutual constraint satisfaction between areas.

Large-Scale Distributed Representation

These considerations lead to the idea that knowledge is distributed across widely distributed brain areas.

2 important implications of this idea:

(1) multiple areas participate in representing the same item of knowledge
(2) each area participates in representing multiple items

Dedicated, Content-Specific Processing and Representations

Processing consists of transformations of activity patterns. These transformations are shaped by knowledge accumulated through learning. Thus processing and memory occur in the same networks. This means that processing is "dedicated" and "content-specific". There is no general-purpose CPU.

Properties of Neural Networks (Lecture 1): a trained network functions as an associative memory

7.2.2 Dynamic Principles

The view of perception here is that it results when sensory inputs cause the propagation of activity through bidirectionally connected processing layers. The network tends to produce activation states that satisfy multiple constraints imposed upon it from the environmental inputs and the learned weights.

Internally maintained activation states carried over from prior processing (known as **internal context**) are critical in determining the response of the network to sensory input. These activation states provide additional constraints on processing.

Dynamic principles from Chapter 3 such as mutual support and inhibition are also important in determining the network response to sensory input.

Mutual Support and Active Memory

Mutual support of different representations by reciprocal excitation allows these representations to remain active even in the absence of input.

Internal excitation that persists over time is called **active memory**.

Active memory is typically of shorter duration than weight-based memory.
This is because the activity either fades out (e.g. because of fatigue) or is interrupted by other processes.

Although shorter acting, active memory provides internal context that can directly influence ongoing processing in other areas.

Weight-based memory can only directly affect units whose weights are changed.

Inhibition and Attention

Selective attention is viewed as an emergent property of processing that results from constraint satisfaction and inhibition.

Thus, rather than being a separate and independent system for selecting certain items for processing while excluding others, attention is seen as a natural result of processing in which the items for selection arise spontaneously from the operation of constraint satisfaction and inhibition under the influence of the external environment and the internal context.

7.3 General Functions of the Cortical Lobes and Subcortical Areas

7.3.1 Cortex

Visual processing streams originate in occipital lobe. Ventral pathway extends into temporal lobe; dorsal pathway goes to parietal lobe. Horizontal connections between the streams exist at each level of processing.

In general, posterior cortex has specialized sensory systems and frontal lobe is specialized for action, including at lower levels control of motor output and at higher levels interacting with posterior cortex in perception-action cycle.

7.3.2 Limbic System

Hippocampus: involved in rapid learning of new information

Cingulate cortex: involved in motor control, action selection, and decision making

Amygdala: involved in emotional processing

7.3.3 Thalamus

Subcortical structure with many subdivisions (nuclei). Serves as interface between cortex and external world.

Each cortical area is bidirectionally connected with a different thalamic subdivision. Some subdivisions are specialized to process information from sensory systems. Some are specialized for motor function. Some may be specialized for coordinating cortical function, including directing attention.

7.3.4 Basal Ganglia, Cerebellum, and Motor Control

The **basal ganglia** is a subcortical brain structure involved in motor control that may also play a role in cognition.

The authors propose a difference between the type of processing in the basal ganglia with processing in the cerebral cortex.

Cortical processing: continuous activity that shapes the flow and integration of information.
Basal ganglia processing: continuous sampling of accumulated evidence, but only discrete action is generated when high-threshold is exceeded.

In Parkinson's disease, which affects the basal ganglia, some patients have negative symptoms, including the lack of ability to initiate movements. These symptoms are consistent with an impairment of the basal ganglia's ability trigger actions.

It is possible that this same system has evolved to trigger more general "cognitive actions". That is, a function of the basal ganglia may be to control the updating and storage of activation-based memories in the frontal cortex.

7.4 Tripartite Functional Organization

Three brain systems:

Posterior cortex: occipital, temporal, parietal areas responsible for analyzing sensory inputs and forming associations that coordinate and integrate sensory processing.

Frontal cortex: active maintenance of information over time; used in controlled processing

Hippocampal system: medial temporal lobe areas (hippocampus, entorhinal cortex, subiculum, parahippocampal cortex, perirhinal cortex) responsible for rapid acquisition of novel information.

7.4.1 Slow Integrative versus Fast Separating Learning

Proposal: both posterior and frontal cortical areas use learning mechanisms described in Chapters 4-6. They develop representations of the important statistical characteristics of the sensory environments.

They process sensory inputs and produce motor action. The perception-action cycle requires interactions between posterior and frontal cortex.

To be effective, perceptual analysis and action production must be based on realistic knowledge of the world. Learning must be slow in order to integrate over many individual experiences and extract general underlying regularities of the environment.

Each experience is typically a fragmentary representation of the environment.

Slow learning is needed to blend the fragments (episodes) together smoothly. It allows weights to converge to the conditional probabilities of events in the environment. But the unique details of the individual fragments are lost.

Rapid learning is also necessary for successful behavior. Specific information, even if arbitrary, is often very important. For rapid learning to be useful, individual episodes must be kept separate, rather than integrated.

Slow and rapid learning are not compatible in the same learning system. It is proposed that *the hippocampal system provides a rapid learning system that is complementary to the slow learning system of the cortex.*

7.4.2 Active Memory versus Overlapping Distributed Representations

It is proposed that posterior and frontal cortical areas differ in the type of active memory that they employ.

In posterior cortex, active memory acts in conjunction with overlapping distributed representations to perform sensorimotor mappings.

Frontal (prefrontal) cortex has a more robust active memory maintenance system that acts in conjunction with more isolated representations.

7.5 Toward a Cognitive Architecture of the Brain

The neural basis of cognition (cognitive architecture) is proposed to depend on the interaction of three systems.

A. Posterior cortex:
1. Learns slowly
2. Forms integrated, distributed, overlapping representations
3. Exhibits short term active memory that is easily interrupted by new stimuli

B. Prefrontal cortex:
1. Learns slowly
2. Has more isolated representations
3. Has dynamic regulation mechanisms that allow it to maintain active memories over longer delays and that are less easily interrupted by new stimuli

C. Hippocampal system:
1. Learns rapidly
2. Forms separate representations that minimize interference between memory representations
3. Role of active memory unclear

7.5.1 Controlled versus Automatic Processing

Controlled processing refers to the ability to flexibly adapt behavior to different task demands. It is usually contrasted with *automatic processing*, which refers to the simpler, more direct stimulus-response association.

Remember our discussion of the differences between *Serial Symbol Processing* (SSP) and *Parallel Distributed Processing* (PDP) models in artificial intelligence, and the difference between *top-down* and *bottom-up* approaches to identifying networks in the brain.

Historically, SSP models have tended to take a top-down approach and focus on controlled processing, which includes high-level cognitive functions such as problem solving and logical reasoning.

PDP models have tended to take a bottom-up approach and focus on automatic processing, which includes low-level cognitive functions such as sensory perception and stimulus-response mapping.

SSP models are usually based on centralized control agents (executives) that direct peripheral automatic processing systems. The use of control agents may be effective for some types of problem: witness the CPU in the modern serial processing digital computer.

PDP models are based on distributed knowledge and processing. They do not distinguish between central and peripheral systems. In general, controlled processing is viewed as an emergent network property in PDP models.

The challenge for PDP modeling is to answer the question of *how controlled processing can be modeled as an emergent property*. The attempt by the authors is based on the proposed tripartite cognitive architecture.

7.5.2 Declarative/Procedural and Explicit/Implicit Distinctions

Declarative (explicit) memory is related to controlled processing. It refers to the ability for intentional verbal recall of knowledge. The term “explicit” implies that such recall is conscious.

Procedural (implicit) memory is related to automatic processing. It refers to the ability to recall knowledge by action rather than verbal recall. The term “implicit” implies a lack of conscious access.

It has been suggested that consciousness is related to representations in the brain that are extended in time and can have widespread influences. In terms of neural networks, the authors propose that “*we are aware of those things that are playing a prominent role in constraining the global constraint satisfaction settling process within the brain*.”

Of the three systems in the cognitive architecture, the prefrontal cortex and hippocampal systems are thought to be more involved in constraining processing in goal-directed behavior than the posterior cortex. Thus, it could be said that the prefrontal cortex and hippocampus are responsible for the control of processes that enter consciousness, whereas the role of the posterior cortex is to provide the content of consciousness.

7.6 General Problems

A set of basic principles has been developed and implemented in Leabra. These have been shown to work in training networks to perform low-level automatic processes. The authors claim that these same principles, alone, can be used to achieve high-level controlled processing.

Others have proposed models that use a *dynamic temporal binding* mechanism to implement symbolic representations in neural networks.
The authors reject such models as going beyond the standard integration of weighted activation signals on which their principles are based.
They claim that problems in object recognition and sentence-level processing can be better solved by the Leabra approach.

7.6.1 The Binding Problem for Distributed Representations of Multiple Items

The binding “problem” arises whenever:

1) different features of a given object are represented separately
2) multiple objects must be represented

The “problem” is to understand how the system binds together the separate features representing an object.

The authors argue that object information is NOT represented separately, but that representations incorporate aspects of all features of the object. In other words, the representations are *conjunctive*. They claim that this scheme is practical if individual units are allowed to represent *multiple combinations of conjunctions*.

An alternative solution is to use processing dynamics to establish binding between different features without using dedicated content-specific representations that encode conjunctive information. One proposed implementation of this solution is that binding is performed by the synchronization of oscillations representing different features.

An unresolved issue is whether synchronized oscillations in the nervous system play a functional role or are merely an epiphenomenon.

The weight of accumulated evidence suggests that they <u>do</u> play a functional role.

The authors claim that a problem “with the synchrony-based binding idea is that it requires entirely new mechanisms for processing the bound information”.
They ask how information can “become associated with a representation that only exists as a relatively fleeting temporal synchronization”.

Synchronized Oscillations in Learning and Memory

However, oscillations arise spontaneously in the nervous system.
See:
I of the Vortex: From Neurons to Self, R. Llinas, 2001.
Rhythms of the Brain, G. Buzsaki, 2006.

Synchronized oscillations may be used for both:

a) *encoding* information in long-term memory, i.e. changing weights, and
b) *retrieval* of information from long-term memory

There is evidence that synaptic plasticity in the hippocampus depends on ongoing *theta oscillations*. Furthermore, LTP occurs when stimulation is delivered at the peak of the theta rhythm and LTD occurs when it is delivered to the trough.

It has been proposed that the theta rhythm allows the hippocampus to alternate rapidly between conditions that promote memory encoding and memory retrieval.

Oscillations at other frequencies have also been linked to memory processes.
See:
Memory and Brain Dynamics, E. Basar, 2004.

Memory processes in the neocortex have been linked to oscillatory activity in the theta, alpha, beta, and gamma frequency ranges.

Binding by synchronized oscillations may not be as contrary to the Leabra principles as the authors suggest. Attractor dynamics do not necessarily require *point attractors*; they may also rely on *limit cycle attractors*.

Synchronization of oscillations allows an additional level of binding between different parts of an evoked representation than is possible with simple activations. Synchronized oscillatory activity may allow the association of different parts of overlapping, distributed representations whose association might be ambiguous if just based on activation level.

7.6.2 Representing Multiple Instances of the Same Thing

2 ways are proposed for recognizing multiple instances of the same object

1. An attentional mechanism may be directed at each instance of the object sequentially. As the attentional mechanism move from one instance to the next, another mechanism must detect that each instance is unique and count the number of instances. This way assumes that the object representations persist long enough for the attentional mechanism to visit each instance.
2. Spatial location representations may be stored separately from object identity representations, and used to distinguish one instance of the object from multiple instances. [This still requires a binding mechanism to link spatial and identity representations.]

7.6.3 Comparing Representations

Sequential activation is not feasible in the case of comparing two different items because both must be represented at the same time.

3 possible mechanisms are suggested for comparing 2 different items:

1. The network dynamics produce a representation of what the two items have in common. This “commonality” representation is then used as the basis for a comparison judgment.
2. A stimulus representation is compared with a stored representation of a different stimulus by assessing how well the stimulus activity pattern corresponds with the pattern of weight values of the store stimulus.
3. The same stimulus may be represented in different brain regions, e.g. frontal and posterior. A comparison could then be made between the two representations based on some goodness of fit measure.

7.6.4 Representing Hierarchical Relationships

A problem in hierarchical representations is that a given item is both higher than (consists of) some other items and lower than (is a component of) some other items.
How can the structural relationship information of an item as a component of a higher entity be reconciled with its invariant representations as a unique object?
Are there "relationship" representations that bind together component representations with a higher entity representation?

See:
Time-locked multiregional retroactivation: a systems-level proposal for the neural substrates of recall and recognition. A. R. Damasio, Cognition 1989 Nov;33(1-2):25-62.

The multiple distributed representations answer is that there are many invariant representations active at higher levels. That is, the same object may be represented in different ways a higher levels, i.e. as a unique object and also as a component of a higher entity.

It is also possible that a sequential attentional mechanism focuses on different aspects of hierarchically structured objects.

7.6.5 Recursion and Subroutine-like Processing

A primary process may depend on other subsidiary processes for its completion. It may be necessary for the results of the primary process at a certain stage to be given as input to a subsidiary process whose output is then fed back as input to the primary process. The authors distinguish two types of subsidiary process: *recursion* (involving the same type of processing as the primary process) and *subroutine* (involving a different type of processing).

This may be how sentences are processed, with the primary processing of the sentence being composed of subsidiary clause processes.

The authors admit that this type of processing is difficult for a system that processes in the same networks where data are stored. However, they claim that the brain does not rely on this type of processing most of the time. They further claim that, when it does occur, it depends on specialized memory systems to maintain information about prior states of the system.

7.6.6 Generalization, Generativity, and Abstraction

The authors propose that *generalization* results from the *abstraction* that occurs in hierarchical representation. That is, activation of a categorical representation at a higher hierarchical level will allow generalization over all the specific-instance activations of that categorical class that occur at lower levels.

Generativity refers to the novel creation of new combinations of known representations.

The authors do not propose a mechanism for generativity. However, it might also depend on abstraction. A categorical representation could be combined with novel feature activations at lower levels to produce novel constructs. For example, imaging a green horse.

7.6.7 Summary of General Problems

Most of these "problems" result from limited knowledge about the representations involved.

<u>Overall conclusion</u>: it is important to question the representational assumptions that give rise to the problem in the first place.

The authors mean this argument as a defense against critics of the neural network approach to cognition. However, it also applies to their assumptions.

For example, they state that the "binding problem" is "not as much of a problem if there is some element of conjunctivity in the representations".

Synchronized oscillations may be a fundamental aspect of representation in the brain. If so, then a mechanism based on synchronized oscillations could provide the conjunctivity that the authors desire. Thus, their assumption that oscillations are an epiphenomenon must be questioned.