

Chapter 1

The Neurointeractive Paradigm: Dynamical Mechanics and the Emergence of Higher Cortical Function

Larry Cauller

1.1 Abstract

Recently established biological principles of neural connectionism promote a neuro-interactivist paradigm of brain and behavior which emphasizes interactivity between neurons within cortical areas, between areas of the cerebral cortex, and between the cortex and the environment. This paradigm recognizes the closed architecture of the behaving organism with respect to motor/sensory integration within a dynamic environment where the majority of sensory activity is the direct consequence of self-oriented motor actions. The top-down cortical inputs to primary sensory areas, which generate a signal that predicts discrimination behavior in monkeys (Cauller and Kulics, 1991), selectively activate the cortico-bulbar neurons that mediate directed movements. Unlike the widely distributed axons and long-lasting excitatory synaptic effects of the top-down projections, which generate the associative context for motor/sensory interactivity, the bottom-up sensory projections are spatially precise and activate a brief excitation followed by a long-lasting inhibition (Cauller and Connors, 1994). Therefore, the sensory consequences of a motor action are the major source of negative feedback, which completes an interactive cycle of associative hypothesis testing: a winner-take-all motor/sensory pattern initiates a behavioral action within a top-down associative context; the bottom-up sensory consequences of that action interfere with top-down sensory predictions and strengthen or refine the associative hypothesis; then the testing cycle repeats as the sensory negative feedback inhibits the motor/sensory pattern and releases the next winner-take-all action.

Given this neurointeractivity, perception is a proactive behavior rather than information processing, so there is no need to impose representationalism: neurons simply

respond to their inputs rather than encode sensory properties; neural activity patterns are self-organized dynamical attractors rather than sensory driven transformations; action is based upon a purely subjective model of the environment rather than a reconstruction. The associative hypothesis is the neurointeractive equivalent to awareness and hypothesis testing is the basis for attention. This neurointeractive process of action/prediction association explains early development: from self-organized cortical attractors in utero; to the emergence of self-identity in the newborn, who learns to predict the immediate effects of self-action (i.e. listening to its own speech sounds); to the discovery of ecological contingencies; to the emergence of speech by prediction of mother's responses to infant speech. Ultimately, our scientific paradigm likewise emerges by neurointeractivity as we learn to see the world in a way that explains more of the effects of our actions.

1.2 Introduction

A dominant trend in neuroscience research aims to characterize the sensory receptive field properties of cortical neurons. The success of this research is evident in the host of functional subdivisions across neocortex that have been defined this way. Much of this physiological research is based upon the method of transfer functions, a reverse engineering technique, which is used to characterize the output of an unknown device as a function of its inputs. This method correlates the neuronal activity observed in an area of cortex with respect to its sensory inputs or motor outputs. This correlation is used to define the function of each area with respect to the common field properties of its neurons as if that area is simply a transmission node in a communication pathway where its inputs are encoded and transformed into outputs.

Although highly productive, this analytical method implies an ill-founded "representation" paradigm, which views behavior as a reaction driven by inputs. This view has led to the predominance of the "neural code" concept and the idea that the function of a neuron (or cortical area) with a given receptive field (or class of fields) is to "represent" that characteristic of the input stimulus to the rest of the nervous system. The value of such a representation paradigm for an understanding of higher function is severely limited because it does not account for how the system must adapt to the representation and act upon unpredictable circumstances under the survival demands of dynamic environments. The representation paradigm is inherently open-ended as it defers the explanation of higher function to some sort of higher representation of representations without considering the path from output back to input that engages the environment. And it fails to explain how creative or autonomous behavior is generated without implying that a hidden supervisor or homunculus is responsible for interpreting and acting upon the representations.

In contrast, a comprehensive explanation of higher cortical function can be based upon a view of the cortex as part of a closed system, which engages environmental dynamics with the same interactive principles that govern its internal dynamics. Unlike the engineering approach, which must isolate a circuit element to determine

its transfer function, a comprehensive approach must deal with the dynamical interactivity generated collectively by reciprocally connected and mutually dependent circuits. Cortical outputs influence all sources of cortical inputs (e.g. motor movements cause sensory motion) and alternative methods are necessary to deal with the extreme complexity that arises from such interactivity. This pervasive feedback encloses the ecological system of the behaving organism within the functional architecture of interactivity between cortical areas and the environment.

The “neurointeractive paradigm” views the behaving system with respect to the interwoven levels of organization and multiple time scales embedded within the cortical architecture (Figure 1.1). Local neuron interactivity is embedded within the interactivity of more distant connections between a multitude of cortical areas. This intra-cortical interactivity is embedded within the interactivity between the motor/sensory structures at the bottom of the cortical architecture, and between the neocortex and autoassociative structures at the top (i.e. hippocampus and prefrontal areas). And the closed system architecture seamlessly fuses this cortical network with the motor/sensory interactivity between the organism and the environment (or between communicating organisms). From this neurointeractive perspective, higher function emerges from the system as a whole by the dynamical mechanics of self-organization over a lifetime of continuous development within a mutual ecology that integrates the complexity of the organism with the complexity of the environment.

The neurointeractive paradigm avoids the homuncular pitfalls of sensory coding, representation and attention by emphasizing proactive sensory behavior rather than passive sensory information processing: listening rather than hearing; touching rather than feeling; looking rather than seeing. By placing the emphasis upon action, all conscious sensory behaviors are based upon the act of attending. This perspective implicitly avoids the difficulty of defining an attention mechanism without implying a supervisor that somehow knows what is important and what may be dissected from the total sensory representation. Instead, each and every action attends to a subjective prediction by testing the current associative hypothesis about the sensory consequences of that action. Such sensory behavior is proactive because the motor action and its associated pattern of predictive cortical activity precedes the sensory consequences of that action and is modified post hoc by those consequences. From this perspective, the primary function of the sensory systems is to provide feedback in a form that guides the next action toward the next test of one’s subjective model of the world. This means that what one sees is largely determined by what one is looking for, rather than some sort of transformation of the objective world. The biological imperative of these interactive behaviors is to minimize uncertainty within a dynamic environment by learning to predict the sensory consequences of one’s actions and by continuously testing those predictions.

This chapter will identify the fundamental principles of cortical organization and motor/sensory interactivity, which subserve the development of these action/prediction associations. Nonlinear dynamical systems analysis is the most appropriate description of cortical complexity and the vocabulary of this analysis provides a heuristic explanation for the emergence of higher function when applied to cortical neurointeractivity. The neurointeractive cycle of give and take between the cortical

motor/sensory areas and the environment will be related to the dynamical mechanics of proactive exploratory behavior. By examining the process of early development with respect to the dynamical mechanics of cortical self-organization, the neurointeractive paradigm provides explanations for the emergence of higher functions such as self-identity, object recognition and speech communication.

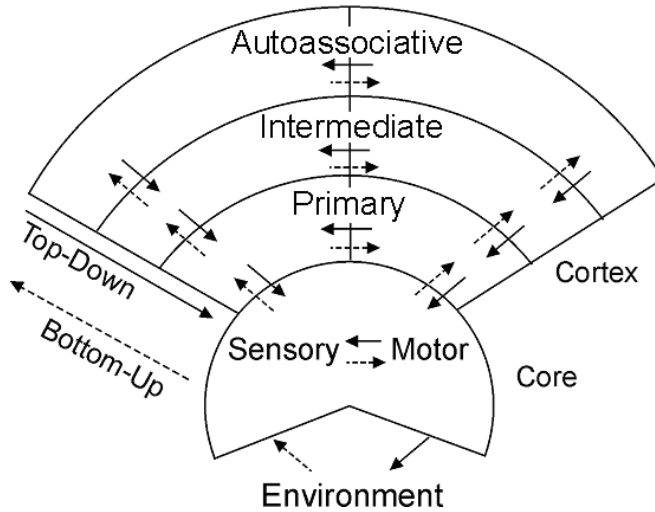


Figure 1.1. Closed hierarchical architecture of cortical interactivity. This highly simplified diagram represents the general organization of reciprocal bottom-up and top-down interconnections between the three essential shells of the cortical hierarchy. Areas within lower shells (i.e. Primary and Intermediate) provide bottom-up projections to the areas within higher shells (i.e. Intermediate and Autoassociative, respectively). Simultaneously, the higher areas provide top-down projections to areas in shells just below them. While a minimum of three such hierarchical shells are characteristic of neocortex, there are many areas within each of these shells and sub-shells may be distinguished, especially in primates. The entire cortical system may be subdivided into sensory and motor halves based upon the direct connections of the areas in the Primary shell to sub-cortical structures in the Sensory-Motor core. But interconnections between areas within each shell diffuse the sensory or motor identity of cortical areas throughout higher shells of the hierarchy. The self-sustaining cortical interactivity generated by this system of reciprocal interconnections reaches out to the environment through the motor and sensory structures in the sub-cortical core of the central nervous system for interactivity with selected elements of the Environment. Such extreme simplification is required to appreciate the closed nature of the system, and thereby eliminate the implication that some unidentified influence from outside the system is responsible for its complex behavior.

1.3 Principles of Cortical Neurointeractivity

The conceptual framework for this neurointeractive explanation of emergent higher function should be based upon the functional architecture of cortex where lesions have the most direct effects upon higher function. Beyond the enormous associative

capacity of such extensively connected neural networks, at least five relatively unappreciated characteristics of cortex are essential for the dynamical neurointeractivity that subserves the emergence of higher function:

1. All areas of the cortex are always active. Although cortical states may be associated with fundamentally different modes of activity (i.e. slow-wave sleep versus alert desynchronization), neurons throughout cortex are always active.
2. The great majority of inputs to cortical neurons originate within the cortex itself. Almost all of the remaining inputs are from the thalamus, but the cortex is the major source of inputs to the thalamus. Therefore, with respect to the cerebral cortical system, which should be considered a network of interacting cortico-thalamic circuits, almost all connections in cortex provide cortical feedback.¹
3. Outputs from a wide expanse of cortex, including the motor areas and the primary and higher order sensory areas, project directly to the subcortical structures responsible for the directed head, eye and finger movements that generate sensory inputs (e.g. cortico-tectal, cortico-pontine, cortico-spinal). Indeed, most sensory systems require movements or some other form of stimulus dynamics for the generation of receptor or primary afferent activity. This top-down control over the generation of bottom-up inputs is directly responsible for the proactive motor/sensory behavior that leads to the neurointeractive emergence of higher function. In addition, sensory cortex directly influences the earliest sensory nuclei in the central pathways (e.g. cortical projections to the dorsal horns or dorsal column nuclei directly influence somatosensory inputs where they enter the central nervous system). By all accounts, all sensory inputs that reach the cortex are influenced by top-down projections from the cortex itself.
4. All cortical connections are reciprocal. These reciprocal connections are the anatomical basis for cortical neurointeractivity. For instance, the primary sensory areas send “bottom-up” projections to secondary sensory areas (e.g. from visual area 17 to areas 18 and 19). These bottom-up projections are reciprocated by “top-down” projections from the secondary areas to the primary areas (e.g. from areas 18 and 19 to area 17). This directionality of the sensory path defines the cortical hierarchy from the primary areas,

¹ These two characteristics lead to the conclusion that cortical activity is self-sustained by pervasive endogenous feedback, especially in utero or during sensory deprivation or sleep. The term cortical “neurointeractivity” refers to this self-sustaining ensemble of collective neural behavior. Furthermore, given the plasticity of cortical synapses, cortical circuits and the neurointeractivity they sustain are in a continuous state of modification and self-organization.

which are direct targets of sensory inputs, to the higher order areas which receive indirect sensory inputs through the primary areas. In both directions, these cortical projections are always excitatory and it is likely that all areas may be activated by either bottom-up or top-down inputs. However, this top-down influence over cortical activity has not been thoroughly studied because the conventional transfer function approach would require careful manipulation of the top-down inputs, which are nearly inaccessible. The potential significance of this top-down activation of primary sensory areas is indicated by the finding that the primary visual areas may be activated in humans during mental imagery when the eyes are closed (Kosslyn et al., 2001). It is not useful to refer to either bottom-up or top-down projections as “the feedback” pathway because they are both sources of feedback with respect to the other. The dynamical complexity of cortical neurointeractivity is generated by this pervasive reciprocity, which extends across all areas of the cortex, creating a richly embedded system of multiple time-scales and interwoven levels of organization (i.e. interactivity between reciprocally connected primary sensory and motor areas is embedded within the interactivity between primary and secondary shells). The complexity of this collective neurointeractivity rises above the sum of all the embedded activities.

5. The reciprocal connections between cortical areas are structurally and functionally asymmetric with respect to the spatial distribution of the axon projections, and with respect to the synaptic physiology of the connections (Figure 1.2).

Structurally, bottom-up projections from lower areas preserve the sensory topography with dense ($<0.5 \text{ mm}^2$), point-to-point terminal axon clusters in the higher areas. In contrast, top-down projections from higher areas are distributed widely across the lower areas with top-down axons extending horizontally ($> 2 \text{ mm}$) in all directions across the sensory topography in the lower areas (Rockland and Virga, 1989; Felleman and Van Essen, 1991; Cauller, 1995; Cauller et al., 1998). In addition, while the bottom-up cortical projections target a specialized population of local circuit neurons in middle layers, the top-down projections excite the subset of cortical neurons with layer I dendrites, which includes the large pyramidal cells that project to the brainstem nuclei for the top-down control of sensory-oriented movements.

Functionally, bottom-up projections activate a strong, but brief excitatory response ($< 10 \text{ ms}$) which is abruptly terminated by a strong, long-lasting inhibition which may last longer than 50 ms (Douglas and Martin, 1991; Borg-Graham et al., 1998; Amitai, 2001). In contrast, the top-down projections activate a strong, relatively long-lasting excitation ($> 30 \text{ ms}$) without inhibition (Cauller and Connors,

1994). Figure 1.3 relates the cortical microcircuit (Douglas and Martin, 1991) to the functional asymmetry of reciprocal cortical connections in the context of cortical neurointeractivity.

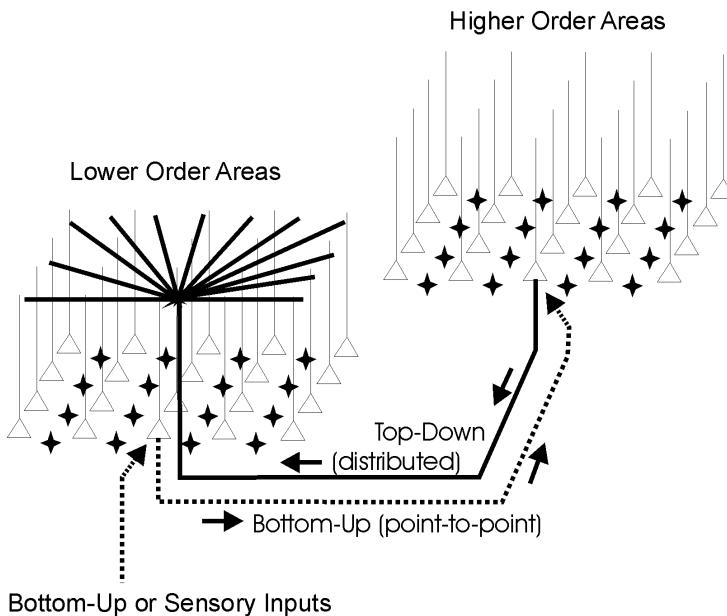


Figure 1.2. Asymmetric reciprocal connections between cortical shells. Areas within subjacent shells of the cortical hierarchy are represented as single layers of inhibitory (solid stellates) and excitatory (open pyramids) neurons. Figure 1.3 presents the more complex, multi-layered view of cortex. Bottom-up projections from lower shells of the hierarchy (i.e. sensory inputs or projections from primary areas to higher areas) excite both inhibitory and excitatory neurons within a relatively small locus of the higher cortical area. In contrast, the top-down projections from areas in higher shells ascend through the cortical layers to contact specialized dendrites of the excitatory neurons that extend to the surface, out of the reach of the inhibitory neurons. While each point in a lower area sends bottom-up projections to corresponding points in higher areas, the top-down projections from a point in a higher area extend horizontally across the surface of the lower area, which effectively distributes the higher influence to all points of the lower topography.

This reciprocal asymmetry has important functional consequences for cortical interactivity. This asymmetry superimposes topographic precision with widespread associativity throughout the cortical system. The distributed and long-lasting top-down projections generate an associative context throughout the cortical architecture which is sustained by the neurointeractivity generated by the higher order autoassociative areas. In contrast, the bottom-up pathway rapidly projects intense, spatially and temporally precise sensory patterns, which are immediately followed by equally precise and much longer lasting inhibitory after-patterns. This secondary bottom-up inhibition is the important source of sensory negative feedback, which resets the

cycle of motor/sensory interactivity and propels the system toward an orthogonal attractor state. This process of motor/sensory interactivity interferes (positively and negatively) with the associative context that cascades over the cortical hierarchy from the top-down. Throughout the cortical architecture, this process of asymmetric interference drives the cycle of neurointeractivity that is the basis for autonomous self-organization and the emergence of higher function in dynamic environments.

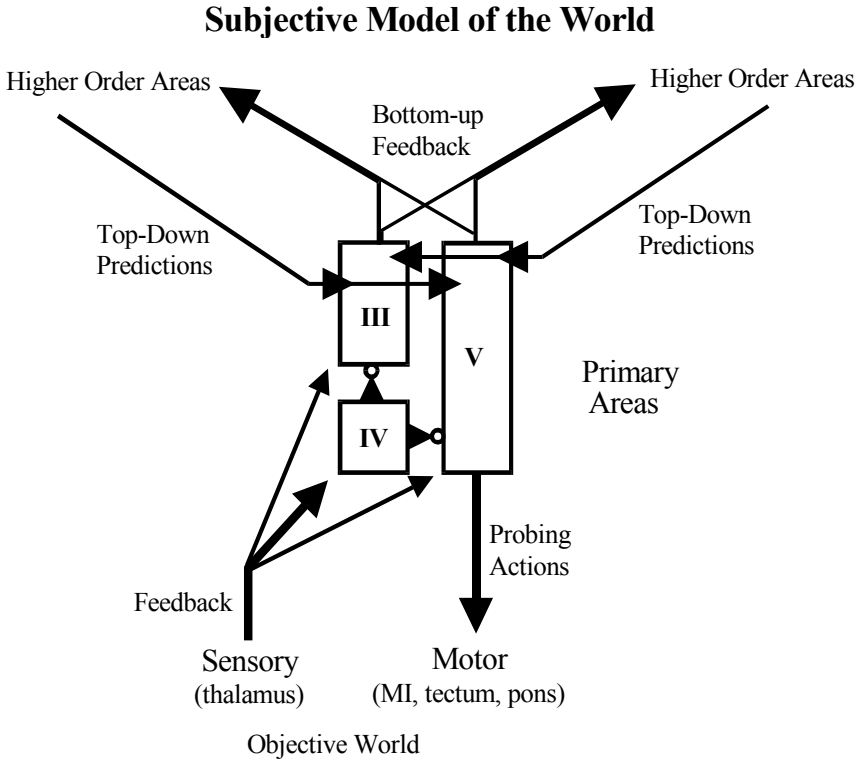


Figure 1.3. Canonical microcircuit for cortical neurointeractivity. The principal targets of the excitatory bottom-up projections from the sensory systems to the primary areas, and from lower to higher cortical areas, are the excitatory and inhibitory neurons found in the middle cortical layers. This initial bottom-up excitation spreads across cortical layers, but is abruptly terminated by the secondary inhibition generated by the response of the middle layer (IV) inhibitory neurons. Both the bottom-up and top-down projections between cortical areas originate primarily from the neurons in upper cortical layers (III), while the projections out of the cortex to motor and other sub-cortical structures originate from the neurons in lower cortical layers (V). In contrast to the middle layer neurons, which are most sensitive to bottom-up inputs, the projection neurons in upper or lower layers have specialized dendritic branches that extend to the surface of the cortex where the excitatory top-down projections from higher areas terminate. These top-down projections to the most superficial layers avoid the inhibitory neurons of the middle layers, such that top-down excitation is terminated primarily by the secondary inhibition generated by the middle layer response to bottom-up inputs.

1.4 Dynamical Mechanics

Nonlinear dynamical² systems analysis provides a comprehensive description of the neural mechanisms that mediate neurointeractivity and leads to a heuristic explanation for the emergence of higher function by cortical self-organization. Dynamical systems analysis identifies hidden deterministic structure in the midst of hyperdimensional complexity. We have found that even the simplest reciprocal networks of model neurons, based upon biologically realistic neural mechanisms, can generate dynamical interactivity with fractal chaotic structure or impose that structure upon a background of random inputs (Jackson et al., 1996). We have coined the term “chaoscillator” to characterize such a minimal network of two reciprocally connected excitatory/inhibitory neuron pairs because, following small changes in connection strengths or input intensity, their self-sustained behavior suddenly switches from periodic to chaotic. It should not be surprising that the behavior of cortex, which consists of enormous numbers of interacting chaoscillators embedded within a closed architecture of interwoven levels of organization and multiple time scales, also generates the unpredictability and rich spectral content of chaotic complexity.

From the perspective of the neurointeractive paradigm, the dynamical system of self-organized attractors that results from adaptive cortical reciprocity is the new functional equivalent to Hebbian cell assemblies. Indeed, the notion of the “phase sequence” (Hebb, 1949) or the “synfire chain” (Abeles, 1991) is literally equivalent to a dynamical attractor. Such attractors are patterns of activity that follow a deterministic path through the space of all possible activity patterns. The advantage of the attractor description is that it relates on-going spatiotemporal activity to the hyperdimensional structure of the system’s history in the same way that planetary motion is related to the solar system of orbits within the galaxy of solar systems. This dynamical approach provides a higher dimensional perspective that helps to explain system behavior by identifying the geometry and the limits of its complexity.

There are several neural mechanisms that determine the path and cohesion of cortical attractors:

1. Neurons are nonlinearly sensitive to coincident inputs (i.e. Abeles’ synchronous gain). This nonlinearity turns each neuron into a coincidence or synchronicity detector such that the collective pattern of cortical activity is directly related to the pattern of correlation within the antecedent state of cortex.
2. Synaptic feedback mediates both positive correlation by mutual excitation and negative correlation by mutual inhibition, both of which participate in the self-organization of the attractor structure by the nonlinear sensitivity of neurons to correlated inputs.

² The term “dynamical systems” is used to distinguish the specific case of dynamics that leads to temporal chaos and fractal geometry much like the term “classical” refers to the specific case in classical mechanics or classical music.

3. Winner-take-all domains, such as cortical columns, are local attractors, which may be generated by local cooperativity (i.e. mutual excitation or common inputs) embedded within a field of lateral inhibitory competition. The winner-take-all attractor phenomenon may also result from simple physical constraints. For instance, it is only possible to move the eyes or the arm in one direction at a time. Any such winner-take-all phenomenon constrains a specific subset of correlated activities.
4. Long-term synaptic plasticity strengthens attractors by associativity, both by enhancing the connections between coactive neurons (i.e. Hebb's postulate), and by depressing the connections between neurons whose activity is uncorrelated (i.e. anti-Hebbian). Such associative neurophysiological mechanisms may result in nearly permanent changes in connection strength and are widely believed to be responsible for memory. These associative mechanisms tend to stabilize the system-wide attractor structure because they lead to repetition, and repetition further strengthens the attractor structure. This plasticity is synergetic with the other attractor mechanisms, which also depend upon neural correlation.

All such attractor mechanisms carve out and strengthen the specific path that the system behavior travels through the state space of all possible behaviors. In general, these neural attractor mechanisms are excitatory. But the ubiquitous inhibition that keeps check against runaway excitation plays an equally important role for attractor formation by inhibiting states (e.g. "losers") that are incompatible with the attractor. These attractor mechanisms are the gravity and glue that hold together the dynamical structure of neurointeractivity by pulling the system behavior toward quasi-stable fixed-points or periodic limit cycles.

The unpredictable richness of deterministic chaos can be described in terms of a "strange attractor" that temporally escapes a quasi-periodic orbit and re-enters with different initial conditions, travels through a higher or lower orbit, and then escapes again, re-enters, and so on. The escape is mediated by "repeller" mechanisms, which create a saddle point in the orbit that destabilizes the system away from the attractor. By contrapuntal interplay, such coupled attractor/repeller mechanisms propel the system to autonomously explore its state space and self-organize a system-wide, associative hyper-structure of quasi-stable attractor sequences (Figure 1.4).

Several neural mechanisms mediate the repeller dynamics of neurointeractivity:

1. Intrinsic neuronal outward currents such as the voltage-sensitive IA or calcium-dependent IK(Ca) mediate frequency adaptation, after-hyperpolarization or other types of intrinsic inhibition that are secondary to strong, sustained activation.

2. Short-term synaptic depression decreases the strength of connections from neurons that remain highly active (Markram, Chapter 5, this volume).
3. Local inhibitory feedback is greatest for those neurons that are most active because they are at the central focus of all the surrounding inhibitory neurons excited by that activity. This mechanism is a ubiquitous characteristic of neural systems. While its role in controlling runaway excitation is usually emphasized, this repeller function of recurrent inhibition employs the same mechanism to propel the system behavior from one action to the next.
4. The long-range feedback inhibition mediated by the secondary component of the cortical response to bottom-up sensory inputs imposes a negative after-image with the same, high spatial resolution of the bottom-up sensory topography. This repeller corresponds to the negative sensory feedback that terminates the current action and guides the attractor sequences for exploratory behavior.

All such repeller mechanisms are secondary to the activation generated by an attractor. They grow in strength during that activation until they shut down that particular attractor and allow the system to escape to another attractor. The persisting repeller effects generated in response to an attractor create an anti-attractor (like a negative after-image) that drives the system away from that particular attractor toward the specific subspace of pseudo-orthogonal attractors that are normally inhibited by the attractor.

This coupling between attractor and repeller mechanisms constrains the sequential order of quasi-stable attractor states and segments a hyper-space of potential attractor sequences. The complexity of a particular attractor sequence (i.e. series of eye movements) is a neurointeractive product of the environmental consequences of that sequence on the one hand (i.e. series of visual signals generated by looking at an object), and of the hyper-structure of the system-wide associative context on the other (i.e. what one thinks they are looking at). Depending upon the bottom-up sensory consequences of each action, the top-down influences of the associative context bias the primary motor/sensory areas toward a specific next attractor action within the space of all orthogonal attractors. In this way, the positive (or negative) interference between the associative context and the motor/sensory interactivity with the environment simultaneously guides the attractor sequence and strengthens (or weakens) the associative hyper-structure by correlation (or decorrelation).

The associative context ties together the action/prediction associations in the form of motor/sensory attractors related to a specific set of environmental contingencies such as those encountered while interacting with an object or while communicating with a person. Over the unique course of development, a subjective model of the world grows as a strange attractor hyper-structure of associative contexts. An associative context, which is self-sustained by the auto-associative neurointeractivity at the

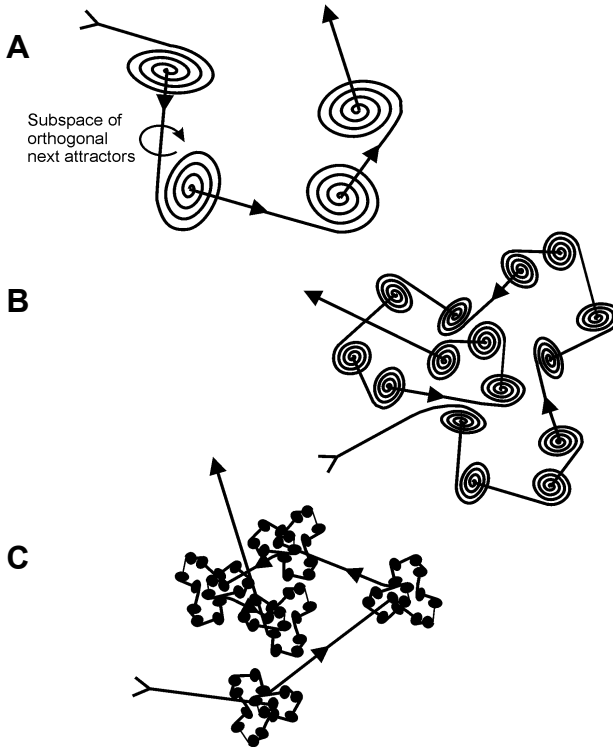


Figure 1.4. Self-similar hyper-structure of cortical attractor/repeller saddle points. (A) The path of cortical activity through state space falls toward attractors represented here as spirals approaching fixed points to provide a specific locus for the saddle point where the repeller overcomes the attractor. But such saddle points may occur as the state approaches limit cycles or more complex attractors as well, which may themselves appear as fixed points from another hyper-dimensional perspective. As repeller mechanisms take over, the activity state is propelled from the saddle point toward an orthogonal set of attractors represented here as a trajectory that is perpendicular to the plane of the spiral. Such saddle points liberate the activity state to move from one elementary action attractor (e.g. sensory/motor movement) to an orthogonal set of next actions thereby maintaining a structure that links together action sequences. (B) At a larger scale in hyper-dimensional state space, represented here in only three dimensions, sequences of elementary actions (as in A) are linked together into a similar hyper-attractor represented here as a spiral of spiral sequences. An example of such a hyper-attractor is an associative structure (e.g. for interaction with a complex object such as a tennis ball) that extends beyond the primary areas to tie together sensory/motor movement sequences that are reinforced by successful sensory predictions. The saddle points of such associative hyper-attractors propel the activity state from one associative context to the next depending upon the higher order consequences of the actions (e.g. this is probably a squash ball because it doesn't bounce well). (C) This hyper-structural process is extended here in the form of a spiral of spirals of spiral sequences to illustrate that saddle points may exist across the scales of associative structures from elementary movements to complex conceptual frameworks. This hyper-structure can tie together all activity states throughout the cortex in a way that is guided by interactive experience.

top of the cortical hierarchy, imposes relative stability for the immediate motor/sensory actions in a dynamic environment. This higher order neurointeractivity changes relatively slowly because it is indirectly coupled to the rapid neurointeractivity in the motor/sensory areas during behavior. The long-lasting excitation and widespread distribution of these top-down associative influences impose a contextual background of structured activity. This context serves as a reference with which the immediate motor/sensory attractors become associated by the covariance rules of synaptic plasticity mechanisms. As a result, the associative context gains the power to bias the attractor sequence and promote a context-based series of actions, depending upon the sensory experiences that occur when that context is present.

These dynamical mechanics of cortical neurointeractivity generate a rich diversity of adaptive behavioral patterns and provide the necessary flexibility to cope with the survival demands of dynamic environments. These mechanisms propel behavior through the system-wide, associative hyper-structure of attractor sequences guided by experience and the environmental consequences of one's actions. Self-organization during environmental interactions reinforces action sequences whose sensory consequences stabilize the cortical neurointeractivity between motor and sensory areas within the hyper-structure of associative contexts that extends throughout. The embedded cortical system of interwoven levels of organization and multiple time-scales generates rapid motor/sensory interactivity with dynamic environmental contingencies under the relative stability imposed from the top-down by the higher order associative context. This dynamical systems description of cortical neurointeractivity provides a comprehensive account of extreme complexity from a geometric perspective that helps to explain the hyper-dimensional emergence of higher function.

1.5 The Neurointeractive Cycle

The “neurointeractive cycle” (Figure 1.5) describes the dynamical cortical process that subserves exploratory behavior in terms of the attractor/repeller mechanics that generate adaptive sequences of quasi-stable attractors. While analogous cycles may describe the dynamical interactivity throughout the network of reciprocally connected cortical areas, the following description refers to the actions mediated by the motor and sensory areas of cerebral neocortex because these can be related most directly to observable behavior. The associative context guides this neurointeractive cycle, which generates specific actions and, in turn, the sensory consequences of those actions modify the associative context. The neurointeractive cycle drives the continuous process of dynamical self-organization and the immediate give and take of proactive behavior as it revolves around four functional phases:

1. *Top-Down Prediction.* The widely distributed top-down influence of the associative context biases the neurointeractivity between the motor and sensory areas toward a specific winner-take-all attractor. Prior to the cortical generation of any movement or other action, this cortical motor/sensory attractor associates activ-

ity in the sensory areas with the activity in the motor areas that generates the action. This cortical sensory component becomes predictive because it is modified by the sensory consequences of the motor action. The next time this motor/sensory attractor is activated, the sensory component will predict the consequences of the motor action. In this way, the quasi-stable dynamics of the attractor create a temporally inverted association between an intended action and its consequences.

2. *Probing Action.* The pattern of corticofugal activity within the motor component of the motor/sensory attractor generates a specific winner-take-all action or movement. This action pattern is a small facet of a hyper-dimensional complex associative structure. Any given action may be generated under a wide range of associative contexts, but each action probes the environment and tests a specific, top-down sensory prediction that is consistent with the current associative context.
3. *Bottom-Up Feedback.* The environmental consequences of the motor action generate a pattern of bottom-up sensory inputs. This bottom-up pattern rapidly ascends through the cortical hierarchy with characteristically high precision with respect to both the spatial topography of the sensory input and the timing of the excitatory sensory signal. Collision of this bottom-up signal with the top-down context triggers associative mechanisms throughout the cortex and deflects or reinforces the attractor path that generated the probing action. Secondly, the inhibitory phase of this bottom-up sensory projection generates a negative after-image that repels the system away from the current motor/sensory attractor toward a new action that is associated with different sensory predictions of the same associative context. To the extent that the bottom-up sensory input pattern corresponds with the cortical sensory component of this motor/sensory attractor, the secondary bottom-up repeller mechanism enhances the intrinsic repeller of recurrent inhibition that follows all attractors and propels behavior to the next action/prediction.
4. *Associative Interference.* There are several effects of the bottom-up sensory feedback that guide the short-term evolution of the attractor sequence and the long-term self-organization of the associative hyper-structure. As the bottom-up sensory pattern ascends through the cortical hierarchy, it interferes with the endogenous pattern of activity sustained by the higher order associative context. To the extent that the cortical sensory pattern associated with the motor action predicts the pattern of sensory inputs generated by that action, associative correlation or “positive interference”

occurs. Nonlinear excitation (i.e. synchronous versus asynchronous coactivation) is generated at points of positive interference, which reinforces the motor/sensory attractor as well as the secondary repeller generated by that attractor. Similarly, at points where the sensory input pattern is correlated or uncorrelated with the cortical action/prediction attractor, the higher order predictive success of the top-down associative context is strengthened or weakened, respectively, by the associative mechanisms of synaptic plasticity.

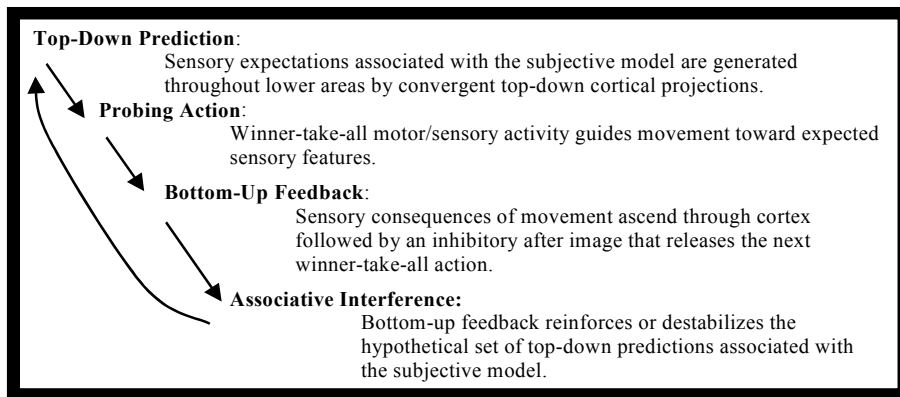


Figure 1.5. Interactive cortical cycle of active sensory hypothesis testing. The dynamical interactivity generated by these reciprocal projections between cortical areas generates a cycle of self-organization that is propelled by the mechanisms of the cortical circuit. These neural mechanisms support a regenerative, but non-repetitive cycle of cortical activity: the top-down influence of distributed cortical activity generates activity in lower areas, some of which produce motor actions; the consequences of this top-down activation and the motor actions it generates results in negative sensory feedback and other bottom-up inhibition; in turn, this bottom-up inhibition at specific cortical loci releases the next top-down motor action generated at other cortical loci under the continuing top-down influence of the more slowly evolving pattern of distributed cortical activity. This figure relates equivalent functions to each phase of this interactive neural cycle which emerge in the context of sensory/motor interactivity with the objective world to give meaning to both the structure of the distributed cortical activity and the overt actions associated with that structure. To the extent that this associative structure successfully predicts the bottom-up or sensory consequences of these actions, the structure is reinforced by reactivation of predicted cortical loci, or it is destabilized by bottom-up activation of unpredicted loci which moves the system toward a new associative structure.

This cycle is the driving force at the core of the neurointeractive process distributed throughout the cortical system. The cortex employs the same neurointeractive cycle that generates a variable repertoire of flexible behavior to explore environmental complexity, and simultaneously construct and refine the cortical associative hyper-structure that guides this exploratory behavior. As the cortex adapts and the sensory prediction improves, positive interference also strengthens the secondary

repeller effect of the bottom-up sensory negative feedback by improving the coupling between the sensory input and the sensory prediction component of the action/prediction attractor. This drives the system away from the action/prediction attractor more effectively, prevents repetition, and propels the system toward a more distinct orthogonal subspace of attractors that emit a new probing action to explore a distinct set of predictions.

The top-down associative context simultaneously guides the sequence of action/prediction attractors, is modified by the bottom-up sensory consequences, and serves as a relatively stable associative reference for the action/prediction sequence as a whole (Figure 1.5). The neurointeractive cycle supports repetitive actions until the sensory component of the cortical action/prediction attractor adapts to predict the sensory consequences of these actions. As the prediction improves, the secondary bottom-up inhibition of the sensory consequences becomes aligned with the cortical sensory activity and strengthens the repeller to propel the system toward the next action, and then on to the next associative context. A sign of this adaptive process should be a transition from repetitive, highly stereotyped actions to more variable and experimental behaviors. Conversely, if the associative context does not account for the sensory consequences of its exploratory actions, the repeller remains too weak to propel the system through its dynamical structure. In this case, the neurointeractive cycle generates repetitive, persistent exploratory actions until the system learns to predict the sensory consequences or the associative context destabilizes in the absence of correlative support and another context takes over and is tested for its ability to account for its actions. In this way, the exploratory behavior of neurointeractivity steadily makes better predictions, probes more effectively, and naturally discovers the rules of environmental contingencies.

Another way of looking at this neurointeractive cycle is in terms of experimental hypothesis testing. The neurointeractive cycle solves the inverse problem of coping with extreme environmental complexity using severely limited sensory and motor abilities by a process that is analogous to the scientific method: Theory leads to specific hypothetical predictions, experimental actions, and comparison of predictions with measured observations, which, in turn, leads to confirmation, refinement or modification of theory, further experimentation, and so on. The top-down associative influence over the motor/sensory areas generates an elementary hypothesis about the nature of the environment, which predicts the specific sensory consequences that should follow a specific motor action. Then the interference between the top-down sensory prediction and the bottom-up sensory consequences of that action test the suitability of the hypothesis in a form that directly modifies the associative structure, or thesis, that generated the hypothesis. In an analogous way, our scientific view of the objective world is modified by experimentation. Indeed, our subjective experience of the world around us may be drastically changed by scientific discovery. Accordingly, scientific method may be considered a formalization of the neurointeractive process that generates conscious behavior.

Other theories have also emphasized the basic process of hypothesis testing. Most of these have described sensory processing in terms of a prediction generated from the top-down in the primary sensory cortex (e.g. Mumford, 1994; Ullman, 1994).

However, such predictions are typically in the form of a static, complete image that is compared to the bottom-up sensory pattern without considering the movements or other sensory-oriented actions that are essential for dynamical neurointeractivity and exploratory behavior. Although such models also view the cortical process in terms of a solution to the inverse problem of sensory perception, they remain basically representational because their goal is to reconstruct an accurate image of the sensory pattern, usually without specifying how such a representation is interpreted or related to behavior.

There is no need to reconstruct the structure of the environment in the form of a complete sensory image. Most objective details, such as the texture of wood or the color of water, are not essential to behavior and they may be re-observed directly, in all their complexity for fascination at some other time. Indeed, the fleeting sensory images generated during conscious behavior are sparse and incompletely processed (Quartz and Sejnowski, 1997, *ibid*). Instead, it is only necessary to predict the elementary sensory consequences of a specific subjective action that are critical tests of the current associative hypothesis (e.g. rightward eye movement across a hypothetical flat square should encounter two equal parallel edges, which fade before the next, probably perpendicular movement). The neurointeractive process emphasizes these simple predictions of sensory elements in direct relation to elementary actions, rather than the reconstruction of an accurate representation of the sensory image. Such a process of experimentation is highly robust with respect to generalization from specific experiences to other perspectives and variable conditions, because it actively searches for pieces of supporting evidence. When such hypothesis testing models are extended to describe the multitude of reciprocal interactions throughout the closed cortical system, an extremely powerful associative process is combined with the ability for autonomous exploratory behavior.

The “hierarchical clustering” model developed by Ambros-Ingerson et al., (1990) provides a more neurointeractive form of hypothesis testing which also provides a solution to the inverse problem of perception. Their model categorizes complex sensory patterns by generating a sequence of increasingly specific subcategories through a reiterative cycle that removes the features of the less specific categories from the input pattern. With respect to dynamical mechanics, neurointeractivity within this network generates a specific sequence of pseudo-orthogonal, local winner-take-all attractors, propelled by top-down inhibitory repellers that are coupled to the attractors. In many ways, the neural basis of this categorization process is analogous to the neurointeractive cycle.

Such sensory categorization models have primarily been applied to the analysis of a static sensory input pattern without consideration of the interactive behavior that is essential for most conscious sensation. The hierarchical clustering model emphasizes neurointeractivity between the cortex and the peripheral olfactory structures, and such models in general are well suited for olfaction where a static sensory pattern may be assumed.³ Like the “sparse coding” model of primary sensory processing

³ However, it is probably significant that in rodents where this hierarchical model has been applied most specifically, sniffing movements are synchronized with whisking movements that probe the somatosensory domain at the same time.

developed by Olshausen and Field (1997), such categorization models demonstrate how associative correlation may generate a statistical components analysis of complex input patterns. The sparse coding model emphasizes neurointeractivity between primary and secondary cortical visual areas, but like other categorization models, it does not deal with behavioral interactivity or environmental dynamics. In many ways, the neurointeractive process of exploration and discovery is analogous to an extended version of these categorization models. For instance, it may be possible to demonstrate that the neurointeractive cycle generates a dynamical sequence of action/prediction attractors during exploration in natural environments that progresses hierarchically from general impressions to critical tests of specific hypotheses generated by the associative context. Such a comprehensive model of hierarchical neurointeractivity would provide robust flexibility because it shifts the center of immediate action outward to directly engage the dynamics of environmental complexity.

From the neurointeractive perspective, action/prediction attractor sequences related to specific experiences are tied together by an associative context, and the dynamical interdependence of these contexts as a whole forms a system-wide associative hyper-structure which adapts to environmental complexity. This hyper-structure becomes a uniquely subjective theoretical framework or paradigm or model of the world, which ties together all the associations between specific motor actions and sensory expectations. These associations define the meaning of behavioral actions in terms of the subjective experiences that stabilize the action/prediction attractors. Similarly, the neurointeractive system's model of the world is purely subjective. It is built upon the associative structure that was self-organized from the beginning of development, for a large part in the absence of structured sensory inputs, from the unique perspective and history of the organism. This subjective model of the world is the neurointeractive alternative to the sensory transformation of the objective world that characterizes the representational paradigm. By dynamical self-organization, the neurointeractive cycle incrementally constructs this subjective model out of the same unique patterns of cortical activity that mediate the continuous flow of conscious exploratory behavior.

1.6 Developmental Emergence

Given the self-sustaining predominance of cortical feedback and ubiquitous synaptic plasticity, the associative structure of cortical activity continues to self-organize from the first moments of cortical development in utero. Throughout the closed cortical system, the dynamical mechanics of cortical neurointeractivity pull this associative structure up by the bootstraps. The prenatal development of lateral inhibition and other attractor mechanisms provides the anatomical basis for local winner-take-all domains and the greater complexity of interwoven functional columns. Even in the absence of sensory inputs, the development of cortical attractors associates patterns of activity in the motor areas with patterns in the sensory areas, which directly inter-

connect with those motor areas. The newborn infant spends most of its time in rapid eye movement (REM) sleep and many have wondered about the sensory content of a newborn's dream. From the neurointeractive perspective, this REM sleep corresponds to the process of dynamical self-organization that prepares the infant to explore environmental complexity.

From the first moments following birth, environmental sensory consequences become contingent upon motor actions (e.g. hearing oneself cry, seeing the visual motion generated by head and eye movements, or feeling the texture of cloth when the limbs are moved). This newborn behavioral/environmental interactivity joins the cortical motor/sensory interactivity embedded within the self-organized complexity of the newborn's associative structure.

As associative neural mechanisms depend upon input correlation, attractors that associate the most reliable sensory consequences with movements or other actions will develop first. By far, the most reliable sensory consequences are those that are directly generated by one's own actions in a static environment (e.g. rightward visual motion with leftward eye movements, or varying sounds with modulated vocal action). As the newborn continues to interact with the environment, these fundamental action/prediction attractors will strengthen and form a durable, subjective framework for the associative hyper-structure that grows with the system throughout its lifetime. All higher action/prediction attractors are built upon this framework of "self" complexity. And the neurointeractive process that constructs the subjective model of "self identity" leads to the emergence of higher function as the self becomes distinguished from other, and then grows to include one's influence upon objects and those significant others who respond reliably to our actions.

This emergence of self identity may be specifically related to the dynamical mechanics of the neurointeractive cycle. As the cortex gains influence over the actions of the newborn, the pattern of motor activity that effects movements is already associated with internally consistent patterns of cortical activity in the sensory areas, which have developed without the correlative influence of the sensory input systems. But once the cortical motor activity generates reliable sensory consequences, the associative interference phase of the neurointeractive cycle aligns the sensory component of the cortical motor/sensory attractor with these highly predictable input patterns. Soon, given the reliability of these predictions in nurturing environments, the sensory component of the motor/sensory attractor predicts the sensory consequences of the motor action. The next time a pattern of cortical motor activity generates a probing action, it is associated with a pattern of cortical sensory activity that predicts the sensory consequences of that action, even before the action is emitted. In this way, the cortical attractor that generates rightward eye-movements simultaneously predicts leftward visual motion and vertical edges as part of its self-consistent associative structure. Similarly, the auditory cortical pattern for high pitched sounds becomes an integral component of the motor/sensory attractor that tightens vocal tension. These motor/sensory attractors are the first to stabilize in the newborn under the reliable feedback from the sensory system, and they are reinforced throughout a lifetime of interacting with the environment.

The same neurointeractive process gradually aligns the higher order associative hyper-structure with these stable motor/sensory attractors and creates a subjective model of self identity, which ties together the set of all attractors that predict the self-consistent sensory consequences of probing actions (e.g. rightward sensory consequences of leftward action). By providing a widely distributed, top-down referential background for feature analysis, self identity provides a stable framework for object identification and the construction of a subjective model of the objective world. As the infant probes objects in the environment, the physical characteristics of those objects generate consistent sensory features that are highly correlated with the probing actions. For instance, horizontal eye movements across a square generate a parallel pair of equal length edges out of all the possible vertical edges that are self-consistent with that action. The square object is further identified by subsequent vertical eye movements that generate a correlated subset of horizontal edges. In the presence of a specific object, the neurointeractive cycle modifies the top-down predictions of those probing actions by the associative interference between elements of the self-consistent framework and the highly correlated set of sensory consequences generated by the object. In this way, the associative context related to a specific object is created out of the structure of self-identity as it guides a sequence of probing actions, which, in turn, become associated with a subset of self-consistent predictions. By generating probing actions that critically test hypotheses about the unique identity of the object, the associative context distinguishes the object from the background of self.

Speech and other vocal communication are very special cases of neurointeractivity. The development of speech in humans is perhaps the most carefully studied form of cognitive development and has already been described in terms of dynamical systems analysis (Elman et al., 1997). Although characteristically variable in the specific timing of developmental stages, the sequential growth of infant speech complexity is well established. In particular, with respect to the neurointeractive cycle, infant babbling progresses from reduplicated to variegated sequences of elementary speech action (i.e. babababa to baba-dada) before it progresses to referential word formation. Accordingly, the neurointeractive cycle would generate repetitive speech actions until the cortical sensory component of the motor/sensory attractor adapts to match the sensory consequences of those actions. As this prediction improves, the secondary inhibition generated by the bottom-up sensory inputs becomes aligned with the action/prediction attractor, thereby strengthening the repeller and propelling the system toward a new action/prediction attractor. This cortical neurointeractivity generates the variable sequences of speech sounds observed in variegated babbling. And the development of babbling behavior provides a revealing demonstration of the neurointeractive formation of self identity as the infant learns to predict the sounds of its own speech.

A neurointeractive explanation for the development of speech communication is especially interesting because the cortical activity in the sensory areas, which adapts to predict the sensory consequences of one's own speech actions, is simultaneously prepared to predict those similar sensory patterns generated by the speech of others. Such communication is extremely effective because it is directly constructed from

the subjective framework of self-consistent action/prediction associations. The caregiver guides the development of this communication by nurturing a bridge from the babbling speech of the infant, to the complexity of language. This “motherese” approximates the infant’s speech with an exaggerated prosody that segments and emphasizes the language elements such as subject, action, object (e.g. mama loves baby). Motherese interacts with the same action/prediction attractors that are self-organized during babbling and creates an associative context that biases the speech attractor sequence toward the language structure. This establishes an almost direct, intimate link between the cortical neurointeractivities of the speaker and the listener.

The neurointeractive cycle continues to build upon the associative hyper-structure by learning to predict the consequences of one’s actions upon objects and others by the same process that self-organizes the framework of self identity. Manipulative actions upon objects generate sensory consequences that create cortical predictions. The structure of these action/prediction associations adapts to the complexity of the environmental physics. Similarly, the associative hyper-structure adapts to predict the influence of one’s speech upon the behavior of others, and the structure of these action/prediction associations adapts to the complexity of the language. In this way, the framework of self grows by incorporating one’s predictable influence upon the environment.

1.7 Explaining Emergence

A direct, explicit explanation, like the explanation of planetary movements or the explanation of chemical reactions, is not possible for the explanation of emergent properties such as the hydrodynamics of H_2O or the economics of the market place or the autonomy of conscious behavior. In contrast to systems that are driven by global external forces such as gravity or thermodynamics, emergence arises from complex systems whose dynamics are dominated by the local interactivity between extremely large numbers of elements. Given this pervasive interdependence, an explicit account of the behavior of any single element would require a recursive accounting of all the elements. This complexity and enormity is beyond the capacity for a comprehensive understanding even though the individual elements and interactive physics may be relatively simple. Although it may be impossible to map direct causal relations for a specific emergent phenomenon, scientific methods may determine the relations between emergent properties that apply to the higher order physics (i.e. the thermodynamics of chemical reactions or the psychology of neural systems). At some point, the explanation of emergence depends upon a quantal leap in understanding from the structure and dynamics of the elements, to the functions and interrelations of the collective properties.

Computer modeling techniques that make it possible for the first time in history to realistically simulate the collective behavior of enormous numbers of simple elements (i.e. weather patterns or brain activity) offer the best tool for the analysis of complex systems. The growing field of dynamical nonlinear systems analysis pro-

vides the most appropriate description of this complex behavior. However, methods for demonstrating the emergence of higher function using such computational or mathematical models face obstacles that are not generally appreciated. Functionality is not pre-programmed, so a long period of autonomous interactivity in a complex environment is required for the dynamical self-organization of adaptive behavioral patterns (e.g. infants take years to develop speech). Particular functions (e.g. speech or visual recognition) emerge from dynamical system properties (e.g. communication and exploration) by real-time interactivity with the specific environmental contingencies that nurture those functions. Therefore, to demonstrate emergence using computational models, the nurturing environment, either real or virtual, must be included in the model for the higher function to be recognized. Unfortunately, a comprehensive simulation of the nurturing environment may be more difficult to construct than an artificial nervous system. And an artificial nervous system capable of real-time interactions with real environments requires extremely advanced computer and robotic hardware. These technical breakthroughs are imminent, but a major shift toward the neurointeractive paradigm is necessary before such tools may help us explain the emergence of higher function.

References

- Abeles, M. (1991) *Corticronics: Neural Circuits of the Cerebral Cortex*. Cambridge, UK: Cambridge University Press.
- Ambros-Ingerson, J., Granger, R., Lynch, G. (1990) Simulation of paleocortex performs hierarchical clustering. *Science* 247: 1344–1348.
- Amitai, Y. (2001) Thalamocortical synaptic connections: Efficacy, modulation, inhibition and plasticity. *Rev Neurosci*. 12 (2): 159–173.
- Borg-Graham, L.J., Monier, C., Fregnac, Y. (1998) Visual input evokes transient and strong shunting inhibition in visual cortical neurons. *Nature* 393: 369–373.
- Cauler, L.J. (1995) Layer I of primary sensory neocortex: Where top-down converges upon bottom-up. *Behavioural Brain Research* 71: 163–170.
- Cauler, L.J., Clancy, B., Connors, B.W. (1998) Backward cortical projections to primary somatosensory cortex in rats extend long horizontal axons in layer I. *J. Comp. Neurol.* 390: 297–310.
- Cauler, L.J., Connors, B.W. (1994) Synaptic physiology of horizontal afferents to layer I in slices of rat SI neocortex. *J. Neuroscience* 14: 751–762.
- Cauler, L.J., Kulics, A.T. (1991) The neural basis of the behaviorally relevant N1 component of the somatosensory evoked potential in SI cortex of awake monkeys: Evidence that backward cortical projections signal conscious touch sensation. *Exp. Brain Res.* 84: 607–619.
- Douglas, R.J., Martin, K.A. (1991) A functional microcircuit for cat visual cortex. *J. Physiol.* 440: 735–769.

- Elman, J.L., Parisi, D., Bates, E.A., Johnson, M.H., Karmiloff-Smith, A. (1997) Rethinking Innateness: A connectionist perspective on development. Boston: MIT Press.
- Felleman, D.J., Van Essen, D.C. (1991) Distributed hierarchical processing in the primate cerebral cortex. *Cereb. Cortex* 1 (1): 1–47.
- Hebb, D.O. (1949) *The Organization of Behavior*. New York: John Wiley.
- Jackson, M.E., Patterson, J., Cauller, L.J. (1996) Dynamical analysis of spike trains in a simulation of reciprocally connected “chaoscillators”: Dependence of spike pattern fractal dimension on strength of feedback connections. In: J.M. Bower (Ed.) *Computational Neuroscience: Trends in Research*. San Diego: Academic Press.
- Kosslyn, S.M., Ganis, G., Thompson, W.L. (2001) Neural foundations of imagery. *Nat. Rev. Neurosci.* 2 (9): 635–642.
- Mumford, D. (1994) Neuronal architectures for pattern-theoretic problems. In: C. Koch, J.L. Davis (Eds.) *Large-Scale Neuronal Theories of the Brain*. Cambridge, MA: MIT Press, pp. 125–152.
- Olshausen, B.A., Field, D.J. (1997) Sparse coding with an overcomplete basis set: A strategy employed by V1?. *Vision Res.* 37: 3311–3325.
- Quartz, S.R., Sejnowski, T.J. (1997) The neural basis of cognitive development: A constructivist manifesto. *Behav. Brain Sci.* 20: 537–596.
- Rockland, K.S., Virga, A. (1989) Terminal arbors of individual “feedback” axons projecting from area V2 to V1 in the macaque monkey: A study using immunohistochemistry of anterogradely transported Phaseolus vulgaris-leucoagglutinin. *J. Comp. Neurol.* 285 (1): 54–72.
- Ullman, S. (1994) Sequence seeking and counterstreams: A model for bidirectional information flow in the cortex. In: C. Koch, J.L. Davis (Eds.) *Large-Scale Neuronal Theories of the Brain*. Cambridge, MA: MIT Press, pp. 257–270.