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The Frontal Feedback Model of the Evolution of the Human Mind: Part 1, The “Pre”-human Brain and the Perception–Action Cycle

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The frontal feedback model argues that the sudden appearance of art and advancing technologies around 40,000 years ago in the hominid archaeological record was the end result of recent fundamental change in the functional properties of the hominid brain, occurring late in its evolution. This change was marked by the switching of the driving mechanism behind the global, dynamic function of the brain from an “object-centered” bias, reflective of nonhuman primate and early hominid brains, to a “self-centered” bias, reflective of modern *Homo sapiens* and perhaps late *Homo erectus* brains. Such a transition in the global–functional properties of the brain was provided for by the progressive enlargement of the primate frontal lobe throughout its evolution. In late-developing hominids, this progressive enlargement effectively succeeded in reversing the preferred direction of information flow in the highest association areas of the neocortex from a caudo–rostral bias to a rostro–caudal bias. It was this reversal specifically that provided for the ability of humans to use symbolic thought in the creative expression of art, language, and the development of advancing technologies. Part 1 traces the hypothesized evolution of the primate brain from its early vertebrate beginnings through to the common ancestor of modern great apes and humans in order to set the stage for the proposed reversal, which is the subject of Part 2.

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The human brain is, of course, a remarkable organ. All one needs to do is look at the technological accomplishments and artistic achievements of

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humans to reach that conclusion. Too numerous to mention, these technological and artistic feats have literally transformed the planet we live on. What may be even more miraculous is that the human brain has achieved essentially all of these feats within a period of only 40,000 years or so, subsequent to the upper Paleolithic “explosion,” or as it is more popularly termed, the mind’s “big bang” (Calvin, 2004; Noack, 2006). No other mammal has achieved *even a hint* of technological or artistic progress in the last 40,000 years, or even in the last 40 million years.

What is it that happened to the human brain within such a short period of time to create such revolutionary abilities? The answer to that question, to be argued here, is a remarkably simple one: at some point during the evolution of the hominid brain (most likely around the time of *Homo erectus*), the preferred direction of information flow in the highest association areas of the neocortex began to *reverse* from a largely caudo–rostral bias to a largely rostral–caudal bias (Noack, 1995, 2004, 2006). This reversal was facilitated by the continuing expansion of the primate/hominid prefrontal motor cortex relative to posterior sensory-association areas throughout primate phylogeny, which, in late-developing hominids, began to shift the “balance of power” in cortical dynamics from one largely governed by the sensory systems to one largely governed by the motor systems. The end result of this shift was the effective replacement of the global functional mechanism governing non-human cortical behavior, the “perception–action cycle,” with a new mechanism unique to the human brain, the “frontal feedback system” (Noack, 1995, 2004, 2006). It was simply that fundamental shift, or “bifurcation,” as dynamists call it, in the global functional properties of the brain that signaled a revolution that was to result in the birth of the human mind. In fact, it will be argued here that the story of human evolution is, in essence, the story of this fundamental reversal taking place.

This first paper, Part 1, of a two-part series is intended to set the stage for the appearance of frontal feedback in the human brain by outlining a model for the evolution of the “pre”-human form of the primate brain just prior to frontal feedback taking effect. The main purpose in outlining this model is to identify what functional mechanisms that pre-human form of the brain utilized in the governance of intentional behavior in the animal and how those functional mechanisms were established during the course of vertebrate brain evolution up to that point. Part 2 will then describe how the appearance of frontal feedback in the late-developing hominid brain changed and utilized those earlier functional properties in order to create the panoply of mental faculties we have come to associate with the human mind.

The central theme that runs throughout both papers is that brain evolution is driven solely by the need for organisms to maintain homeostasis. Part 1 argues that the vertebrate line leading up to the pre-human primate brain met

that need largely by developing systems that “converted” sensory stimuli into successful motor behaviors in the presence of those stimuli. The ability of an organism to act quickly and successfully in the midst of a myriad of competing stimuli had a selective advantage in that it assisted the organism in finding food and mates and in avoiding predators. In pre-mammalian vertebrate species, it is suggested that this conversion task was accomplished largely by the development of brain systems that coupled species-typical, sensory feature-detecting systems with stereotyped behavioral “action patterns.” In mammals, the primary mechanism that emerged in order to accomplish this conversion task was the perception–action cycle, a cycle where the newly evolving sensory systems of the neocortex began to drive the newly evolving motor systems in a largely unidirectional feedforward fashion. This is the subject of Part 1.

Two Perspectives on Mammalian Brain Function

To begin, it will be helpful to outline the approach taken here in describing brain/cortical processes. Although most current theories of brain evolution and cortical dynamics do not acknowledge it, there are essentially two different ways of looking at how brains go about accomplishing the work that they do: the hierarchical or “information-processing” model and the dynamical-systems or “neurodynamic” model (Freeman, 2003a). Most of the currently popular “working-memory” (e.g., Chein, Ravizza, and Fiez, 2003) and “neural-correlates-of-consciousness” (Koch, 2004; Rees, Kreiman, and Koch, 2002) models employ only the standard hierarchical framework in their description of brain processes. However, it is the opinion of this author and others (Bressler and Kelso, 2001; Freeman, 2003a) that a synthesis of both perspectives is essential in describing the complex dynamics that occur between the collections of millions of neurons that characterize nervous system activity. Thus, in order to present as clear a picture as possible of the dynamical properties of the brain that changed throughout vertebrate evolution, a discussion of both perspectives will be presented, beginning with the standard hierarchical model.

The Hierarchical or “Information Processing” Perspective

The first stage in the representation of a sensory stimulus begins at the level of the sense organ, where raw energy from the environment is transduced into trains of action potentials, or “pulses,” that travel toward the central nervous system/brain (Freeman, 2003a). In vision, once information from the retinal stimulation reaches the cerebral cortex, various specialized regions in primary and secondary visual areas respond to characteristic features of the stimulus such as color, place, motion, etc. (Felleman and Van Essen, 1991). “Later” visual association areas further along the occipito–temporal sensory process-

ing stream have a similar function but respond, through hierarchical processing, to wider receptive fields characteristic of more complete representations of objects and their orientations in space (Tanaka, 2000; Tanaka, Saito, Fukada, and Moriya, 1990). The complete identification of a given stimulus is accounted for by the simultaneous activation of each of these spatially distinct areas of visual cortex (Konig, Engel, and Singer, 1995; Roelfsema, Engel, König, and Singer, 1997), collectively representing the varied properties of the stimulus. To put it more broadly, a given sensory stimulus excites a corresponding representative pattern, or "ensemble," of neurons in sensory cortices, which serves as the central representation of that stimulus (Mishkin, 1993; Noack, 1995).

The model above can be generalized to all sensory modalities, with characteristic stimulation in each respective sensory organ being represented by a characteristic neuronal ensemble in its respective sensory cortice. One notable and important feature of such sensory processing is that the majority of cortical sensory processing areas are located in the posterior and temporal regions of most mammalian brains, posterior to the central sulcus in larger brains. The entire region of cortex anterior to the central sulcus is involved primarily in the representation of motor behaviors. As we will see later, this sharp geographical division between sensory and motor areas has important implications for human brain function.

Hierarchical processing is a universal property of mammalian neocortical function (Bond, 2004). That is, elemental features of a sensory stimulus are represented in primary sensory cortices, and these elemental features are combined in a "bottom-up" fashion to represent more complex and complete representations of the stimulus in sensory association areas (Felleman and Van Essen, 1991; Simons and Spiers, 2003; Tanaka et al., 1990). This hierarchical processing is also witnessed in motor areas of cortex, although in the reverse direction. That is, complex motor behaviors in mammals are organized in a hierarchical "top-down" fashion beginning in prefrontal areas, proceeding through supplementary and premotor areas, continuing through primary motor cortex, and finally moving through subcortical and spinal nuclei to arrive at motor effectors in the musculature (Fuster, 1989). A given motor behavior, then, can be viewed as possessing its own unique neuronal ensemble in prefrontal motor cortex. That particular ensemble represents the hierarchical coordination, or sequencing, of movements involved in the production of that particular behavior.

For example, the behavior of reaching out, grabbing a banana, peeling the banana, and consuming the banana would have its most abstract representation in the prefrontal area of the cortex. Activation of a prefrontal neuronal ensemble representative of this behavior would be actualized through the prefrontal cortex's coordination of the execution of components or subroutines of

that behavior in more primary motor cortices (Fuster, 1989, 1999; Greenfield, 1991). These subroutines may reflect the act of reaching the hand out, the act of grasping, the act of peeling, and the act of chewing and swallowing respectively. As we will see in Part 2, this hierarchical organization of motor function has important implications for the production of human cognition (Case, 1985; Piaget, 1971) and language (Greenfield, 1991, 2002; Reilly, 2002).

As mentioned, a given sensory stimulus transduced in the retina excites a corresponding "neuronal ensemble" in primary sensory cortex. This ensemble is composed of cortical neurons characteristically excited by each unique pattern of retinal stimulation coming from the environment. That sensory stimulus becomes stored in the brain under conditions of reinforcement when that particular ensemble of neurons becomes connected together into an enduring interconnected network of neurons (Harris, 2005; Skarda and Freeman, 1987). This network is commonly referred to as a "cell assembly," after Hebb (1949). A cell assembly is formed via the selective strengthening of the synaptic connections between the neurons (or a critical portion thereof) involved in the given neuronal ensemble. The exact mechanism of the formation of a cell assembly has still not been determined (Freeman, 1995; Llinas, 2001; Mishkin, 1993; Rolls, 1999), but is generally thought to be constructed in the following manner: the excitation of a characteristic neuronal ensemble causes its constituent neurons to fire synchronously. Under conditions of reinforcement, certain biochemical neuromodulators, such as acetylcholine and/or norepinephrine (Freeman, 1995; Mishkin, 1993), are released into the cortex from subcortical limbic structures and serve to strengthen the synaptic connections between the simultaneously active neurons. The result is a strongly interconnected "cell assembly," which serves as the *stored* central representation of the stimulus.

The cell assembly allows for the re-creation of the cortical neuronal ensemble in the absence of the actual sensory stimulus.¹ For example, if only a small portion of the original stimulus is present, the strongly interconnected cell assembly will use the partial information to "complete" the ensemble through facilitated synaptic interconnections (Skarda and Freeman, 1987). Thus, the sight of a partially covered banana, say, where just the stem and a small portion of the body are exposed, can internally re-create the image of an entire banana that the animal had an earlier encounter with through "triggering" the release of its representative cell assembly.

¹It is important to note that the neuronal ensemble representative of a given sensory stimulus changes over time (i.e., it is not invariant to an invariant stimulus) since the microanatomical structure of the cortex changes due to the ongoing formation of cell assemblies there (Freeman, 1995). Therefore, it is better to think of the ensemble more specifically as the manner in which the brain *currently* represents any particular given stimulus rather than thinking of it as a static entity within the brain.

Cell assemblies can be chained together to represent a temporal sequence of events, or "scenario," much like the individual frames in a movie reel are chained together to compose a scene (Freeman, 2005). Hebb (1949; see also Harris, 2005) referred to such chaining as the "phase sequence." Freeman (2003b) and Tsuda (2001) refer to such chaining as "chaotic itinerancy." The mechanism by which these cell assemblies are chained together and reactivated via chaotic itinerancy will be discussed later.

In a fashion similar to the storage of a sensory stimulus, the representation of a motor routine is stored as a sequence of chained cell assemblies in the mammalian frontal cortex (Fuster, 1989). Piaget (1971) labeled these complex motor routines "action schemes." In an action scheme, the cell assemblies represent the "frames" of the action sequence and are representative of the specific sequences of movements involved in the behavior as organized by neuron pools in the prefrontal cortex. These sequences are organized in a hierarchical fashion (Fuster, 1989; Greenfield, 1991), which, as we will see in Part 2, has important implications for the organization of human language and cognition.

One plausible model of animal behavior emerges that views information flow in the cortex as moving from posterior sensory areas to frontal motor areas in a largely unidirectional "feedforward" fashion (Noack, 1995). That is, stimuli coming from the environment trigger the excitation, or "release," of a chain of cortical cell assemblies in posterior sensory regions representative of an associated previous sensory experience. The release of these sensory cell assemblies, in turn, triggers the release of a corresponding chain of cell assemblies in frontal cortices representative of a behavior that in a previous encounter led to reward via the stimulus (e.g., consummation) or led to the removal of the stimulus if it was punishing.

Consider a simple example. Imagine a monkey exploring a banana and a stick. Upon exploring the banana manually, the monkey may remove some of the banana's peel. If the monkey then attempts to consume the banana, it will receive food reward, which will excite reward areas in subcortical limbic structures in the animal's brain. The excitation of these structures will, in turn, trigger the release of certain critical biochemicals globally into the cortex. The presence of these "consolidatory" biochemicals in the cortex would then serve to store the experience by strengthening the synaptic interconnections between simultaneously active neurons. These simultaneously active neurons represent, respectively, the neuronal ensembles of the sensory experience in posterior sensory cortices and the action scheme in frontal motor cortices.

If, on the other hand, the monkey attempts to consume the stick, no food reward will be had, and therefore no association will be made. In fact, the bitter taste of the stick may condition its sensory representation to a behavior of avoidance through punishment, which works counteractively to the reward

mechanism (Noack, 1995; Rolls, 1999; Stein, 1964; Valenstein, 1964, and see below). The consequence of either case is that, in a future encounter with a banana and a stick, the behavior of grabbing, peeling, and consuming the banana will be greatly facilitated while the stick will be largely ignored. Over time, the monkey comes to make a large number of such associations with a large number of stimuli in its natural environment. This process of "learning" which stimuli to approach and which to avoid, along with having a facilitated behavior to negotiate either, greatly aids in the animal's survival.

Not surprisingly, the architecture of the mammalian neocortex is consistent with the mechanics behind the model of animal behavior described above. Primary sensory areas and polymodal sensory association areas neatly converge in the posterior regions of cortex and have vast forward connections to frontal motor cortices (Pandya and Yeterian, 1985). Furthermore, these posterior sensory areas are generally much larger than frontal motor areas in the great majority of mammals (Kaas, 1987). As we will see, such an architecture suggests a feedforward flow of information in the cortex from the environment to the posterior sensory areas, through to the frontal motor areas, and finally back into the environment through the musculature. The subsequent changes in the environment produced by the resulting behavior present new stimuli to the posterior sensory cortices guiding the ongoing behavior of the animal toward some goal in a closed-loop fashion. This process is referred to by Freeman (2003a) as the "action-perception cycle" and by Fuster (1989, 1999, 2003) as the "perception-action cycle," but both describe the same basic process. Fuster (1989) states:

In all forms of behavior, from the simplest and most automatic to the most elaborate and deliberate, motor action is not only initiated or triggered by sensory signals, but also regulated in the course of time by sensory feedback generated by changes that action itself induces on the environment. Thus, a semblance of a circular pattern of influences is at work in motor behavior: from the environment upon the organism through sensory receptors, from the organism upon the environment through motor effectors, from the environment back upon the organism again through sensory receptors, and so on. This pattern of interactions between the organism and the world around it . . . establishes the principle of the indissoluble union of perception and movement. (pp. 175-176)

The concept of the perception-action cycle is important because it describes how an animal interacts with its environment for the purposes of attaining a goal, usually the satiety of a biological need or the removal of a punishing stimulus. However, the language that the hierarchical model uses to describe the perception-action cycle is conceptually insufficient to precisely understand and explain how the brain actually accomplishes these tasks. A whole new science and language of "brain talk" was required in order to do this.

The Neurodynamic Perspective

The hierarchical models have difficulty describing global brain processes because these models deal with discrete elements: neurons. Although it is recognized that neurons are embedded in networks and do not function alone, research is still targeted at the level of the individual neuron and at how the activity of the neuron changes in response to some stimulus input or changes in relation to some behavioral output. Most commonly, it is assumed that if a neuron changes its behavior in some significant way during a controlled event, then that neuron is related to that event or function in some fashion. While this is not necessarily an erroneous assumption, it is severely limited in its explanatory power. The experience of a sensory event or production of a motor behavior involves the collective activity of hundreds of millions of neurons and is reflective of the relative activity between each one of those neurons. Measurement of a significant change in the activity of only one or a few of those neurons is informative, but an accurate description of the perceptual event would require the simultaneous measurement of each of the millions of neurons involved in the perception. This is impossible using the current techniques and language of the information processing perspective and thus most neural correlates of consciousness models.

The neurodynamic perspective, however, offers relief from such limitations. Arising largely out of the pioneering work of Freeman (2000), a new language and vocabulary has emerged that views complex interactions in the brain as a global dynamic process instead of as discrete interactions between individual neurons.² In the neurodynamic perspective, it is the collective activity of large groups of neurons that is the focus of analysis, not the individual neuron (Bressler and Kelso, 2001). This collective activity is identified in EEG tracings, which can be used to construct "phase portraits" of the behavior of millions, even billions, of interacting neurons, yielding a window into brain function opaque to other techniques (Freeman, 2000; Han and Postnov, 2003; Kozma, 2003). It is important to note, however, that the neurodynamic perspective is not intended to act as a substitute for the concepts of the hierarchical model, only to embellish it and provide a language that is more suitable for describing how the brain works.

The most important concept in the neurodynamic model is that of the "chaotic attractor." The attractor represents the collective behavior of a given area of cortex during a given event and can be represented pictorially via a phase portrait, which highlights how this behavior changes over time. This phase portrait reveals a "shape" to the attractor, which is represented *generally*

²Considering that neurodynamic terms and concepts have not been standardized, this paper will closely follow Freeman's (1995, 2000) formulation and terminology.

by the oscillatory activity between populations of excitatory and inhibitory neurons in cortical neuropil and *specifically* by the modulation of such oscillatory activity via sensory, motor, or limbic influences (Freeman, 2000).³ The attractor is intimately associated with the cell assembly in that excitation of the cell assembly defines the shape of the attractor over that area of cortex (Skarda and Freeman, 1987). More specifically, the triggering of a given cell assembly constrains its particular area of cortex into phase-coherent oscillatory activity whose shape is revealed in the spatial voltage amplitude modulations about that cortex (these amplitude modulations reveal a "spatial signature" to the cell assembly, which can be represented pictorially via a contour-map sketching [see Freeman, 1991; Skarda and Freeman, 1987]). Thus, the cell assembly represents the physical substrate of a specific sensory experience or a motor behavior, and the attractor represents the dynamic expression of that cell assembly through the cortical activity that emerges when that cell assembly is triggered.

Accordingly, attractors are "built" when a cell assembly is formed through the selective strengthening of synapses (Skarda and Freeman, 1987). During this process, the behavior of the cortical areas in which the attractor is being built exhibits little synchrony and is said to be "high dimensional." This high dimensionality results from chaotic effects in the cortex, which may be due in part to multiple competing internal influences in the cortex (described below) or to the presentation of a novel stimulus. Once the attractor is built, however, the re-excitation of its corresponding cell assembly causes the activity in that entire area of cortex to behave in a highly cooperative, or synchronous, fashion. Such an attractor is known to be "low dimensional," or a "near limit-cycle," attractor (Skarda and Freeman, 1987).

These neurodynamic processes describe how the excitation of a cell assembly can constrain the activity of a large number of neurons, or large area of cortex. The actual cell assembly that achieves this effect need only occupy a small percentage (>5%) of total cortical area affected (Skarda and Freeman, 1987). In fact, the excitation of a cell assembly can constrain the activity of an entire neocortical hemisphere, allowing the effects of a small stimulus input to direct the behavior of virtually the entire brain. The next sections will discuss more specifically how that may happen.

³Neuropil is a general term that refers to the tissue that is formed by interconnecting neurons (Freeman, 1995).

Metastability and the Preparation for Chaotic Itinerancy

The Background Attractor

In order to investigate how a stimulus triggers a cell assembly and how that cell assembly directs the actions of the entire cortex to produce an associated behavior, it is first necessary to look at how the cortex behaves in the absence of such activity. When a cell assembly is not active in the cortex, the cortex manifests what is known as a “background attractor.” The background attractor represents an unstructured state of affairs in the cortex due to multiple competing influences there (Freeman, 1995). These influences can come from several sources, among them (1) ambient sensory stimulation, (2) impinging subcortical limbic activity, and (3) cortico-cortical activity. Each of these influences can be viewed as competing to trigger some form of global cell assembly in sensory cortex. If they do not agree on the triggering of a particular, or “common,” cell assembly, the activity remains high dimensional, like “choppy surf” due to turbulent winds.

The best way to envision the background attractor is to imagine an enormous number of individual cell assemblies superimposed on the same area of cortex, let's say sensory cortex. The neurons in that area of cortex are “redundant” in that any given neuron may be involved in many separate cell assemblies. The identity of any given cell assembly is housed in the complex pattern of synaptic interconnections among these redundant neurons. The triggering of a cell assembly ordinarily begins at a “site of nucleation” (Freeman, 1995, 2003b), where one of the three critical influences described above excites some critical subportion of the neurons involved in the assembly. The effects generated from the excitation of this subportion spread out radially, through facilitated synaptic connections, recruiting more and more neurons involved in the specific assembly until some critical threshold is reached. At this point, the represented region of cortex jumps into what is known as a “burst pattern” (Freeman, 1991), whereby the activity in that region becomes constrained into the identity of that cell assembly, thus manifesting its representative attractor.

The background attractor results from the activity that occurs prior to this burst taking effect. In order for a burst to take effect, a “consensus” is needed among these multiple competing influences in order to trigger a common global cell assembly. In the absence of such a consensus, cortical activity reflects instead a large number of separate, “nascent” chaotic attractors competing to cause such an effect. The activity of each of these nascent attractors begins at a separate, spatially distinct site of nucleation in the cortex, and, spreading radially, the activity of these attractors *collide* at multiple regions about the cortex much like the wavefronts that would appear if you threw a

handful of pebbles into a still pond (these radially symmetric wavefronts appear as “phase cones” in cortical activity [Freeman, 2003b]). A consensus is reached when one of these nascent attractors overpowers all the others to create the burst or when common activity among a few of the nascent attractors overpowers all the others to create the burst. However, until that happens, cortical dynamics remain in a high-dimensional chaotic state reflective of these colliding nascent chaotic attractors, manifesting the background attractor.

The background attractor is not a useless artifact of cortical activity. On the contrary, it plays a very important role. The unstructured nature of the background attractor keeps the cortex in a “ready” state, ready to respond immediately to the smallest of inputs in order to direct the cortex into a global burst state. This property of the cortex is known as “metastability” (Bressler and Kelso, 2001). Metastability, or “metastable dynamics,” is an important property of cortical function because the high-dimensional chaotic behavior of the background attractor prevents cortical activity from becoming entrained into a stable periodic orbit such as is witnessed in slow-wave sleep or epileptic seizures (Bressler, 2002a, 2002b). Such periodic activity renders the cortex relatively insensitive to sensory stimulation since its signals are averaged out, or “masked,” by the deep periodic entrainment and, thus, disables the stimulus’ ability to trigger a cell assembly.

Chaotic Itinerancy, Frame Rates, and the Phase Sequence

Again, the functional utility of the background attractor is that it “primes” the cortex to receive sensory input by rendering cortical activity sensitive to that input. Once a stimulus is identified through the triggering of an associated cell assembly, which locks the cortex into a stable and “learned” attractor, the cortex is set to become engaged in what Tsuda (2001) refers to as “chaotic itinerancy.” Chaotic itinerancy essentially refers to the manner in which individual cell assemblies representing static images become chained together into a temporal sequence of events in sensory cortices and into a complex, hierarchically organized sequential action scheme in motor cortex. Hebb (1949; see also Harris, 2005) referred to such chaining of cell assemblies as the “phase sequence,” but did not have a neurodynamic framework with which to explain how it works. Now we do.

Chaotic itinerancy most likely begins through the native timing of the oscillations in cortical neuropil, which are ongoing and regular in the mammalian (40 Hz in humans [Llinas, 2001]) brain during the waking state of the organism. These regular oscillations are interrupted every so often as ambient sensory stimulation triggers cell assemblies as described in the previous section. Specifically, the triggering of a cell assembly upsets or “resets” (Freeman, Burke, and Holmes, 2003) the phase of global cortical oscillation as the influ-

ence of its subsequent burst spreads throughout the cortex. It is at this point that the process of chaotic itinerancy is initiated. For example, each cell assembly that represents some stimulus object, say that of a banana, can be thought of as a static "frame" in a movie film reel (Freeman, 2005). Once a cell assembly is triggered, the process of chaotic itinerancy serves to trigger temporally associated cell assemblies, or frames of the movie, in successive order, which is like putting that movie into motion. Each of these frames is slightly different, reflecting any transformation of that stimulus, such as the banana being moved or peeled. Thus, each frame is unique and technically possesses its own unique cell assembly. The entire collection of frames as a whole, however, are so closely related to each other that the *gross shape* of the global attractor representative of the scene can remain relatively unchanged throughout the event, with minor changes in the shape of the attractor reflecting successive frames of the scene (Freeman [1995] refers to these minor changes as "wings" about the global attractor).

In neurodynamic language, the process whereby these frames transition from one to another in orderly succession is modeled as a process whereby successive chaotic states of the cortex pass through a "trajectory" (Tsuda, 2001). The particular states and the trajectories between them are said to define the "phase space" or the "state space" of the global attractor (Tsuda, 2001). The transition between these states is assumed to occur biologically in the cortex through changes in neuronal activity reflective of the triggering and "dying" of individual chaotic states representative of the static frames. Such activity is embodied by spreading waves of cortical activity, which reflect the dynamical orbits between successive attractors in a given sensory scenario, or "remembered event."

Accordingly, a given sensorimotor scenario would be re-triggered in a fashion similar to that by which it was stored because the spreading of neuronal activity is assumed to flow, through facilitated synaptic connections, along the same orbits or dynamical paths that occurred when the sensory scenario was originally stored (Tsuda, 2001). Although it is tempting to associate the frame rate of chaotic itinerancy with the global 40 Hz (γ) cortical oscillations, recent evidence suggests that the actual frame rate may be more in the alpha–theta range (Freeman, 2003a; Freeman et al., 2003), identified via "phase resetting" with each successive frame. These studies underscore the notion that the global 40 Hz rhythms and chaotic itinerancy reflect two complementary systems, with chaotic itinerancy in the cortex "riding on top of," or superposed on, the thalamocortical oscillations. In a perceptual sense, the regular 40 Hz oscillations may be viewed as the background, or "ground," of a scene and the global attractor emerging from chaotic itinerancy as the foreground, or "figure." The particular shape of that global attractor embodies the content of the perceptual figure and is synonymous with our "focus of atten-

tion." For example, when a stimulus catches our eye and becomes the focus of our attention, the surrounding world doesn't just *disappear*. There is a cohesion, a unity, to our entire experience, that can be accounted for by the spatio-temporal superposition of these two systems.

Homeostasis and the Production of Intentional Behavior

To restate, according to the standard hierarchical model, a sensory stimulus excites a representative cell assembly in posterior cortices, which, in turn, excites a representative cell assembly in frontal motor cortices, resulting in an associated behavior. Although this hierarchical model of animal behavior is conceptually simple and essentially accurate, it masks the underlying complexities of actual cortical function and consequently has little explanatory power when it comes to understanding just how it is that the brain accomplishes such a task. In reality there are many more variables involved. These variables relate specifically to how the behavior of the animal serves to sate its current "needs" and, therefore, to how the brain regulates the expression of neocortical sensorimotor couplings toward that end.

The first consideration involves Freeman's (1995, 2000) concept of "intentionality." According to Freeman, the ongoing behavior of an animal can be viewed as the continuous succession of "intentional acts." The concept of intentionality is not unlike that of the perception-action cycle (Fuster, 1989, 1999, 2003) in that it describes how an animal interacts with objects in its environment and how it comes to "know" those objects or associate them with "meaning." It is this association of an object with meaning that determines how that object is manipulated or used in order to satisfy the needs of the animal.

An intentional act can begin in a variety of ways. One way is through the presentation of a significant stimulus to the animal. For example, the sight of a charging lion is likely to put our monkey into the intentional action of *flight* regardless of whatever else is happening in its brain at the time. More commonly, though, intentional acts are initiated and maintained through the biological needs of the animal (e.g., Rolls, 1999). A need can be defined generally as *the biasing of brain function in some characteristic manner in response to some change in the organism's internal state, or "internal milieu"* (author's definition).⁴

The concept of the internal milieu underscores the most important and fundamental property of all brain function in general, that of maintaining homeostasis. The body of any organism is enclosed within a "boundary" (Damasio,

⁴The *internal milieu* is defined generally as the collection of the internal chemical and physiological processes within an organism that make up its "internal environment" (see Damasio, 1999, p. 138).

1999). That boundary, in turn, encloses a complex chemistry that must be maintained at all times within set narrow ranges in order to keep the organism alive. In fact, it can be asserted that *everything the brain does is only for the purpose of maintaining homeostasis*. The observed behavior of any animal is a complex symphony of neuroactivity trying to maintain the multitude of biological states of the organism within such set levels. These states are largely reflective of the concentration of various substances and hormones in the blood, as well as of the condition of the viscera (Parvizi and Damasio, 2001). Each of these states can be viewed as having some characteristic affect on an associated brainstem cell population, or “thermostat,” sensitive to changes in that particular state, with dozens of such thermostats distributed about the brainstem and limbic system (Damasio, 1999; Swanson, 2003). Swanson (2005) has labeled this collection of brainstem thermostats the “behavioral control column.”

When a brainstem thermostat goes out of an “acceptable” range, its cell population reacts by issuing a signal. That signal likely comes in the form of a neuronal burst that excites brainstem and subcortical limbic (including basal ganglia) structures in some characteristic manner (Redgrave, Prescott, and Gurney, 1999). The principal effect of this neuronal burst is to initiate an exploratory behavior designed to put the animal in the presence of stimuli that may serve to sate the need. Subsequent activity in that cell population then serves to “gate” the expression of behaviors that may help to sate that need. Activity in the cell population accomplishes this gating by facilitating or inhibiting the expression of currently active sensorimotor couplings present throughout the forebrain. For example, the excitation of a behavioral-control-column “hunger” thermostat may serve initially to mobilize a sedentary animal and then subsequently to gate the expression of a consummatory behavior once the animal comes across an adequate food stimulus.

In pre-mammalian vertebrate species (typified by extant reptiles) these gated behaviors and the sensory stimuli that elicited them were highly stereotyped and species-typical (Rolls, 1999; Tinbergen, 1951), which is likely due to the highly conserved and crude topographic properties of sensory and motor maps in pre-mammalian forebrain sensorimotor structures (Manger, Slutsky, and Molnar, 2002; Striedter, 2005). Thus, while learning by simple associations was possible in these pre-mammalian species, the plasticity of expression of that learning was severely limited by the crudeness of those sensorimotor mappings. Even so, such stereotypy played one selective advantage: it fit many different vertebrate species within certain ecological niches where crude sensorimotor transformations sufficed to maintain homeostasis in those organisms. Undoubtedly, this maintenance relied on a large collection of brainstem thermostats issuing signals of varying intensity simultaneously, with the more intense signals receiving priority over the weaker ones, thus guiding the selection of behaviors accordingly (Rolls, 1999).

The Mammalian Perception–Action Cycle

The homeostatic control mechanisms driving behavior described in the previous section are a property of every vertebrate brain as every vertebrate brain from fish to reptiles to mammals contains a brainstem behavioral control column (Striedter, 2005; Swanson, 2005). However, while these primitive homeostatic thermostats have a relatively direct influence over gating the expression of behavior in pre-mammalian vertebrate species, it will be argued in this section that their influence over behavioral expression in mammals is more indirect and is manifested through their regulation of a completely new behavioral control system unique to the mammalian brain: the neocortical perception–action cycle. The appearance of the perception–action cycle in mammals and subsequently the “perception–action cycle conversion hypothesis” forwarded here is characterized by two events, (1) the evolution of the neocortex as the primary sensorimotor processing structure in the mammalian forebrain and (2) the “reassignment” of the more archaic “subcortical” forebrain structures into a “limbic system” which served to regulate the dynamical properties of the neocortex. Each of those events will be discussed in turn.

Evolution of the Neocortex

The six-layered neocortex is perhaps the most distinguishing anatomical feature of the mammalian forebrain (Rakic and Kornack, 2001). The manner in which it evolved from putative homologous forebrain structures in lower vertebrates has long been a mystery and continues to remain the subject of heated debate (Aboitiz, Morales, and Montiel, 2004; Allman, 1999; Karten, 1997; Rakic and Kornack, 2001; Striedter, 2005). Theories about the origins of the mammalian neocortex fall mainly into one of two camps. The first camp argues that the neocortex was derived from the ventral portion of an archaic vertebrate olfactory-related structure, the “pallium,” and is at least partially homologous to its putative counterpart in reptiles, the “dorsal ventricular ridge” (Karten, 1991, 1997). The second camp argues that the neocortex developed independently from the *dorsal* portion of the pallium, leaving the ventral portion to develop into limbic system related structures such as the amygdala (Aboitiz et al., 2004; Striedter, 2005). Although the debate between these two camps has raged for decades, recent developmental embryological and genetic evidence seem to support the latter explanation — that the neocortex was derived from a generalized “dorsalizing” of the archaic pallium whereas the reptilian dorsal ventricular ridge was derived from a generalized “ventralizing” of the pallium (Aboitiz et al., 2004; Smith–Fernandez, Pieau, Reperant, Boncinelli, and Wassef, 1998; Striedter, 2005).

While it is likely, then, that each structure was derived independently from a separate portion of the pallium, the functional role of the neocortex and dorsal ventricular ridge were similar insofar as each essentially represented the "addition" of a new sensory-related processing structure "on top" of the existing vertebrate brain plan (typified by the bony fish). In both reptiles and mammals, the dorsal ventricular ridge and neocortex are, respectively, the largest and most prominent of the forebrain structures. What makes the mammalian neocortex "special" relative to the reptilian dorsal ventricular ridge, however, is the location in which it developed. Thus, whereas the development of the dorsal ventricular ridge was *interior* to the pallium, the development of the neocortex was *exterior* to the pallium, developing essentially as a new sensory structure "stacked" on top of the archaic reptilian dorsal cortex/pallium (Swanson, 2003). The end result is that the size of the dorsal ventricular ridge became essentially limited to the space it could occupy within the lateral ventricle whereas the neocortex could grow to an enormous size through a progressive tangential expansion and gyrification of its surface. This tangential expansion of the neocortex was accompanied by a novel radial (Rakic and Kornack, 2001), or "columnar" (Mountcastle, 1997), organization of thalamocortical afferents running from the ventricle to the pial surface, which allowed the neocortex to produce "high-resolution" topographic maps of the environment as opposed to the crude topographic representations found in the more "nuclear" organization of the dorsal ventricular ridge (Manger et al., 2002; Striedter, 2005).

In regard to the functional properties of these two structures, the early neocortex paralleled that of the dorsal ventricular ridge as each were primarily sensory processing structures whose output was targeted mainly at the basal ganglia, the principle motor-related forebrain structure in these early species (Aboitiz et al, 2004). However, with the appearance of a dedicated motor cortex in the eutherian (placental) line of mammals (Kaas, 2005), the primary output of the existing sensory neocortex began to shift away from the basal ganglia and toward these nascent motor cortices (Granger, 2006). Such a shift was not a trivial occurrence as it was accompanied by two other major structural changes in the eutherian brain. Those two other structural changes were (1) a redirection of the output of the basal ganglia away from brainstem action-pattern "initiator" pools (Swanson, 2003) back toward the neocortex via the dorsal thalamus, completing a large, cortico-striatal-thalamocortical loop of information flow, and (2) the appearance of a distinctly mammalian cortico-spinal (pyramidal) tract, which served to carry information from the nascent motor cortex directly out of the forebrain and into the spinal column, completely bypassing the "old" basal ganglia motor apparatus (Aboitiz et al., 2004; Granger, 2006).

Collectively, the structural changes that occurred with the appearance of eutherian mammals suggest a major reorganization in the functional properties of the brain. This reorganization is identified as the progressive shift away from a sensorimotor processing architecture targeted largely on the basal ganglia and brainstem motor pools and toward a sensorimotor processing architecture targeted on the motor cortex and cortico-spinal tract. The radial, columnar organization of processing elements in this new cortically based system allowed for (1) an extremely detailed and sophisticated representation of the sensory environment and (2) an extremely sophisticated and plastic construction of action scheme sequences followed by the subsequent finely detailed expression of those sequences through the cortico-spinal tract. This new cortically based system was such an advance over the previous subcortical system that the story of the evolution of the mammalian brain is essentially the story of the progressive autonomizing of this system through the progressive reorganization of the forebrain described in the previous paragraph. All that was left to be done at this point was to find a role in this conversion process for the now subcortical structures of the brain whose functional properties the new system had usurped. It will be argued in the next section that the mammalian brain accomplished this task by essentially turning the entire subcortical architecture into an extended behavioral control column known as the "limbic system." The job of the limbic system was to regulate the dynamics of this new cortical perception-action cycle through the "binary management" of the expression of motor behaviors active in frontal motor cortex. It did so through converting the large variety of stereotyped sensorimotor action-pattern pathways inherent in the pre-mammalian brain into generalized reward and punishment "systems."

Evolution of Reward and Punishment Systems

According to the perception-action cycle conversion hypothesis, the functional role of the "pre-mammalian" sensorimotor processing architecture and hence the primitive behavioral action patterns of which it was composed changed with the appearance of the neocortex. These now subcortical "limbic action patterns" changed from acting as a direct interface between the environment and behavior to acting more generally to regulate the dynamics of the perception-action cycle.⁵ This transition was accomplished via an

⁵In this paper and in Part 2, the terms "action pattern" and "limbic action pattern" will be used interchangeably and will refer to behavioral movement sequences organized by non-cortical structures such as the basal ganglia and brainstem motoneuron pools (Swanson, 2003). By contrast, the term "action scheme" will be used to denote behavioral movement sequences organized within the motor areas of the neocortex.

anatomical and functional consolidation of the multitudes of these limbic action patterns into generalized reward and punishment systems (Glickman and Schiff, 1967). These reward and punishment systems then served to regulate the dynamics of neocortical activity through binary management of the expression of motor behaviors in the musculature. In short, the cortical representations of behaviors that are conditioned to the reward system become facilitated as expressed behaviors, whereas cortical representations of behaviors that are conditioned to the punishment system become inhibited. The dynamic “push–pull” of this binary arrangement defines the functional utility of the perception–action cycle in the production of intentional behavior in mammals.

The first step in tracing the emergence of the perception–action cycle comes from looking at the constitution of limbic action patterns in the vertebrate brain. Evolving over millions of years, the variety and complexity of these action patterns can be quite great in reptiles *and* in mammals, and can vary significantly from species to species (Llinas, 2001). In general, though, the primal limbic action patterns can be viewed as falling into one of two categories: (1) those that are involved in approaching a given sensory stimulus (e.g., consummation, sexual contact, aggression) and (2) those that are involved in avoiding a given sensory stimulus (e.g., aversion, withdrawal, defensive posturing) [Damasio, 2003; Glickman and Schiff, 1967]. Because of their functional similarities, it has been suggested that the collection of limbic action patterns involved in approach behavior may have become consolidated into an anatomical *brain reward system* while those action patterns involved in avoidance behavior became consolidated into a *brain punishment system* (Glickman and Schiff, 1967). Anatomically, such a consolidation would be a natural effect considering the commonality of motor pathways used to execute approach and consummation behaviors versus those used to execute withdrawal behaviors. Functionally, such a consolidation would be a natural effect considering that approach behaviors (e.g., consummation) tend to be associated with stimuli that normalize an out-of-range brain thermostat (e.g., food), whereas avoidance behaviors (e.g., withdrawal) tend to be associated with stimuli that push these thermostats out of range (e.g., an excessively “hot” object).

The transition from the primal limbic action pattern mechanics of behavioral response to the mechanics governing the perception–action cycle was undoubtedly a long and gradual one. Early in this transitional phase, it is likely that each specific action pattern worked in *cooperation* with the newly evolving neocortex in the production of behavior. In this scheme, the role of the early neocortex would have been simply to provide a more general display of the larger sensorimotor context within which a specific action pattern operated. For example, as biologically significant “sign” stimuli triggered narrowly tuned feature detector cells in subcortical areas, the larger *polymodal*

sensory context of the event would have been simultaneously constructed into a representational map in sensory neocortex. Similarly, as sign stimuli triggered specific, stereotyped action patterns in subcortical motor areas, the *actual* sequencing of movements that accompanied the presentation of that stimulus, reflective of perhaps competing action patterns and other environmental effects, would have been constructed into a novel action scheme in frontal motor cortices. Therefore, cortical and subcortical processes *worked together* to produce a more plastic interaction with the environment. This cooperation was manifested in a bottom-up fashion in that (1) cortical sensory maps were only constructed upon the presentation of a genetically predetermined sign stimulus (at least initially), and (2) frontal cortical action schemes were only constructed upon the successful execution of an associated limbic action pattern in the maintenance of homeostasis. Conversely, this cooperation was manifested in a top-down fashion in that (1) sensory neocortex provided a rich source of cross-modal sensory associations built upon experience through which to trigger a specific limbic action pattern, as opposed to that action pattern relying simply on genetically pre-wired sensitivities to select stimuli, and (2) frontal motor cortex provided for a greater plasticity in behavioral expression through embellishing the execution of a given limbic action pattern(s) [Arshavsky et al., 1997; Hikosaka, 1998]. Both these bottom-up and top-down effects were facilitated through the formation of bidirectional cortico-limbic cell assemblies, which tied the cortical and subcortical systems together by means of the processes discussed earlier.

While the arrangement described above may have existed as such in primitive mammalian species during the early phylogenetic growth of the neocortex, a new functional property emerged as the greater expansion of the cortex began to effectively mask the apparent participation of stereotyped behaviors. At this point, the main functional utility of these limbic action patterns was not in the specific behaviors they produced, but rather in the contribution they made to the activation of the larger reward or punishment *systems* that they composed. This change is marked by an important functional property being assigned to each system in the production of *expressed* behavior. In a nutshell, (1) activation of reward areas, composed of approach-related limbic action patterns, served to facilitate the expression of motor routines currently active in frontal motor cortex, while (2) activation of the punishment system, composed of withdrawal-related limbic action patterns, served to inhibit that expression. Evidence for this arrangement is found in the intimacy of reward pathways with basal ganglia structures, frontal motor cortices, and the dopaminergic system, each of which are related to the expression of behavior (Graybiel, 1995; Redgrave et al., 1999; Rolls, 1999). Punishment areas of the brain do not share this same intimacy and, in fact, appear to reciprocally inhibit activation of the reward system (Stein, 1964; Valenstein, 1964). The "push-pull" inhibition of

these two systems may then account for the means by which activation of the punishment system inhibits the expression of behavior, an effect that is evidenced in part from studies of the stimulation of punishment areas of the brain, which frequently produces "freezing" reactions in mammals (Scieli, Petrovich, Swanson, and Thompson, 2004; Valenstein, 1964). Whatever the case, the survival advantage of such an interaction is clear: the act of consuming a food product would be facilitated since that same behavior was conditioned to the reward system in a previous encounter while the act of touching a hot stove would be inhibited since in a previous experience that behavior was conditioned to the punishment system. In this way, the ongoing operant behavior of the animal becomes largely "shaped" through the facilitation of rewarded behaviors and the inhibition of punished behaviors.

As far as the perception–action cycle is concerned, the importance of this intimate association between cortical representations of stimuli and their associated reward and punishment systems cannot be overstated. One reason this relationship is important is that it is responsible for determining which cortically represented behaviors are executed and which are inhibited, governing the ongoing operant behavior of the animal. This is again an example of top–down control, whereby a biologically significant cortical map directs the behavior of subcortical limbic structures in the production of behavior. Another reason this relationship is important is the reverse: bottom–up modulation of cortical activity from limbic structures. Again, the cortico–limbic cell assembly is a two-way street, and cortical cell assemblies can be triggered by limbic activity just as easily as the reverse. The effect this bottom–up modulation has is significant because it allows emotional states (limbic action patterns) elicited purely from changes in the internal milieu to direct the content of cortical activity through its release of cell assemblies there. For example, the absence of food in the gut of an animal may cause a hunger-related thermostat to start issuing a signal. This signal, in turn, has two effects: (1) it triggers an exploratory action pattern designed to put the animal into a region where food may be found (more specifically, it mobilizes the animal out of an area where there is no food), and (2) it sensitizes the cortex to respond selectively to food-related stimuli. It does the latter by creating an "environment of attractors" associated with that need (hunger) in the cortex. In other words, the need of hunger would release a myriad of previous experiences in the cortex related to food products. An animal mobilized due to hunger is most likely to find itself interacting with and consuming food objects in this instance because the presentation of a food stimulus is most likely to create polymodal "consensus" in the cortex, resulting in the triggering of a global sensorimotor cell assembly and, thus, an associated consummatory behavior.

Reafferance and the Guidance of Intentional Behavior

This process whereby an internal state such as hunger can bias the sensory cortex to react selectively to stimuli has been investigated empirically by Rolls (1999; see also O'Doherty, Rolls, Francis, Bowtell, McGlone, Kobal, Renner, and Ahne, 2000) and is referred to as "reafferance" by Freeman (1995). Reafferance refers to brain dynamics involved in the "expectation" of a stimulus, and it serves to *guide* the animal through the perception-action cycle by orienting its sense organs into optimal positions in order to best receive crucial sensory information at each step in the cycle. According to the present discussion, such an effect is created by the limbic system's release of previously stored sensory scenarios in the cortex related to the current need.

In order to demonstrate reafferance in action, let us return once again to our example of the monkey and banana. Initially, a change in the internal milieu of the monkey due to hunger excites a corresponding "hunger" pattern of activation in limbic structures. Such activation, in turn, mobilizes the animal by triggering a general exploratory behavior (limbic action pattern) designed to move it out of its present location and into a location where food may be found. In addition, concomitant limbic activation of the cortex triggers sensory cell assemblies, and thus sensory scenarios in the cortex that in the past have been associated with food reward. The triggering of these assemblies is general at first, encompassing a wide array of food-related items and their associated environmental contexts, but becomes more specific as *actual* sensory stimuli force the sensory cortex into more specific, previously learned attractors. Such an effect serves to gradually guide the animal toward the satiety of the need. For example, if food is usually found in vegetation zones and the monkey happens to be in a non-vegetative zone, the sight of a nearby vegetation zone may orient the monkey in that direction. As the monkey moves into a region where bananas are usually found, activity in its sensory cortices start triggering cell assemblies associated with bananas. This action sets up the process of reafferance, whereby limbic triggering of previously stored cell assemblies prime sensory cortex for the actual or expected input (in this case, the banana).⁶ When that input arrives, the cortex accommodates it naturally and adjusts the shape of its global attractor according to the specific properties of the actual stimulus, such as its actual shape and orientation in space (McCrone, 1999). Such an event would reflect the monkey actually encountering the banana.

⁶Anyone who has taken a drink out of the "wrong cup" is likely to have experienced reafferance in action. Most of us can recall a time when we confidently took a drink out of a container we thought was, say, *milk* and it turned out to be *orange juice*. The startled reaction that ensues comes from the turmoil that results when an orange juice stimulus is introduced into a sensory cortex filled with "milk related" attractors. The cortex must make adjustments in order to accommodate the unexpected stimulus

It is important to note that the smooth and efficient execution of each of the behavioral steps involved in finding and consuming a banana is contingent on the reinforced execution of the previous step in the sequence. This reinforcement serves to continually “propel” the animal toward the attainment of the goal. Thus, a previously rewarded behavior such as that of moving toward a vegetative zone when hunger sets in serves to reinforce its own expression through (1) facilitative feedback of the action scheme’s activity through the cortico–striatal thalamocortical loop and (2) the continued presence of the image of the vegetative zone in visual sensory cortices. The combination of these two factors facilitates “consensus” in the sensorimotor networks of the neocortical perception–action cycle, which, in turn, serves to lock in a low-dimensional chaotic itinerant “intentional state” in the animal as it moves toward the vegetative zone. If the animal were to stray from the path, the visual image of the vegetative zone would vanish, facilitating the punishment system and breaking the itinerant cycle, thus serving to inhibit the further expression of the errant behavior. Accordingly, consensus in neocortical sensorimotor networks would be broken along with the low-dimensional chaotic itinerant state, creating a high-dimensional state of activity in the neocortex representing a “search mode” (Harter and Kozma, 2005). This search mode is characterized by the animal maneuvering its sensory apparatus in an attempt to once again find a reinforced stimulus in order to reinstate the perception–action cycle. This process of the successive reinforcing of behaviors occurs again as the monkey enters the vegetative zone and the reinforcing stimulus becomes the banana itself.

Once the monkey encounters an actual banana, it is tempting to think that the animal simply grabs it and manipulates it according to a previously learned sensorimotor association. The reality, however, is a bit more complicated. Every encounter a monkey has with a banana is unique. Different circumstances and variables come into play every time a monkey finds, peels, and consumes a banana, even if those differences are only slight. Each of the specific sensory scenarios is stored as a *unique* sensorimotor representation, complete with unique motor subroutines and associated sensory representations. Each scenario is similar enough to the others, though, that they are all tightly associated into what can be referred to as a general “task-oriented” global attractor for the manipulation and consummation of a banana. As described earlier, the best way to envision a task-oriented global attractor is as a large collection of superimposed cell assemblies with a large number of “common” redundant neurons in each cell assembly. In the frontal cortex, this collection of cell assemblies represents the action schemes for a particular class of behavior (in this case, that of the manipulation of a banana). In posterior cortex, the corresponding tightly associated collection of specific sensory scenarios involved with the interaction with a banana represents what can

be referred to as a “category” attractor (evidence for the existence of these “class related” attractors comes from the findings that cortical association areas [Caramazza and Mahon, 2003] and even some earlier regions [Ohl, Scheich, and Freeman, 2001] seem to respond more to the categorical relationships of stimuli rather than to specific stimulus features). Thus, the task-oriented global attractor involves the animal’s entire collection of stored sensory events and motor behaviors associated with a given class of stimuli.

Getting back to our example, once the “banana” task-oriented global attractor is activated through the presentation of an appropriate stimulus (a banana), the actual behavior that is realized will depend on the specific details of the current environmental situation. In that situation, the multitude of the animal’s previously stored sensorimotor experiences with a banana are brought to bear on that specific encounter in order to negotiate the immediate act. That act may combine previously learned motor sub-routines in a subtly distinct manner. The newly constructed sensorimotor representation is then added to the body of representations existing in its task-oriented global attractor. Thus, the more experiences the monkey has with a banana, the more specific subroutines or behaviors it will have at its disposal in order to more “skillfully” negotiate the specific act. As with the perceptual “frames” in the movie reel discussed earlier, these specific variations on the common theme can be viewed as “wings” about the global attractor, the task-oriented global attractor being the general act of finding, peeling, and consuming a banana and the multitude of specific and individual sensory experiences and manual subroutines associated with that global attractor constituting the wings.

Summary

We have arrived at a general model for animal behavior that explains how the animal maintains homeostasis through interaction with its environment. Such homeostatic maintenance is achieved initially through the mobilization of the animal due to a biological need and then by the satiety of that need through the process of reafferance, chaotic itinerancy, and the production of intentional acts. The production and maintenance of such intentional acts is accomplished through the perception–action cycle, a closed-loop system whereby sensory systems drive motor systems in a largely unidirectional, posterior-to-frontal feedforward fashion.

It is precisely this “closed-loop” feature of the perception–action cycle that makes the perception–action cycle such a remarkably efficient system. The rigid control of the motor cortices by the sensory cortices serves to lock the animal into tight interaction with its surroundings by continuously converting the bewildering array of complex environmental energies that impinge upon it into quick and successful behaviors within that environment. This

“conversion” of sensory information into motor behaviors occurs largely within the neocortex, where complex environmental energies rapidly reduce to generalized classes of represented objects in the form of category attractors. These category attractors, which are representative of real objects in the animal’s environment, are then acted upon in the real environment by the animal. The result is that the world of the nonhuman animal is mostly “object-centered,” a world driven largely by the continuous appearance of these object-entities and the subsequent responses of the animal to these object-entities. In short, there is no room for what we may call “thought” or “reflection” in a brain governed by the perception-action cycle. The perception-action cycle is much too efficient for such distractions; it runs in one direction only.

In the human brain, however, the situation is quite different. There, the closed-loop tyranny of the nonhuman perception-action cycle was broken, decisively. The breaking of that cycle was accomplished by the progressive expansion of the prefrontal cortex throughout primate phylogeny, which continued to lessen the controlling influence that the posterior sensory systems had on driving motor behaviors. At some point in the late evolution of hominids, probably around the time of *Homo erectus*, the prefrontal cortex grew to such an extent that it was no longer controlled or driven by posterior sensory cortices; that is, the motor behaviors of these late hominids was no longer enslaved by the current environmental circumstance. The reason for placing this event around the time of *Homo erectus* is simply that *Homo erectus* is believed to be the first mammal ever known to *not* flee from fire when it encountered it. This suggests that the tyranny of the perception-action cycle had been broken in this species. From there, the further expansion of the prefrontal cortex effectively *reversed* the direction of the flow of information in the hominid neocortex to a rostro-caudal bias, pushing the influence of the prefrontal cortex further and further back toward primary sensory cortices as *Homo erectus* evolved into *Homo sapiens*. The story of that reversal and the effect that it had upon the emergence of the human mind is the subject of Part 2.

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