The brain and its relation to consciousness has long been a topic that appeared to be intractable. Indeed, this impression ultimately led Freud (1895) to abandon his highly regarded ‘Project for a Scientific Psychology.’ However, we believe that the problem of relating consciousness to brain processes is tractable, as have many other scientists and philosophers (e.g., Crick, 1994; Edelman, 1989).

It is our belief that consciousness is not a uniquely human property. By analogy, vision and perception are not uniquely human attributes; they are properties that are shared by all animals with the requisite neurological hardware. But each species is endowed with slightly different ‘hardware’. For example, the eyes and the (number of) identifiable cortical areas dedicated to visual processing differ from one species to another. Of course, the exact nature of the eye itself dictates the range and quality of information that can ever reach the cortex. The cortical areas dedicated to vision form a global network in which visual information is processed. To the extent that a certain
cortical area and its function do differ between species, or is missing altogether in a species, the network’s configuration will be altered. Thus, the network’s operation will be qualitatively changed, and the experience of seeing and perceiving must be different from animal to animal. Yet, they do perceive. Similarly, we believe that some animals possess the necessary hardware for consciousness. However, to expect animals to experience consciousness as humans do is equivalent to expecting them to see and perceive as we do.

From this perspective, consciousness is not something mystical and ethereal that defies attempts to relate it to the brain; it is a property of all brains with the necessary hardware. The question is, what is the fundamental process of consciousness, and what are the mechanisms that give rise to our unique experience of consciousness? We believe that being conscious reflects a preparatory and comparative process carried out by the brain in order to ready the organism for perception. This readiness for perception, coupled with environmental input, is consciousness. A more difficult aspect of consciousness is the phenomenological quality of being a person with a sense of individuality and historical place. Concern for this phenomenological aspect of human consciousness has lead some people to be dissatisfied with brain models of consciousness. However, there are certain aspects of brain evolution that may allow us to adequately account for the human phenomenological experience of consciousness as well.

We mentioned that we believe consciousness to be a process, and this point is worth elaborating. Pribram (1980) made an astute comparison between gravity and consciousness. Gravity is the result of an interaction between masses, and thus it cannot be found at a particular place in an object. Pribram defined consciousness in a similar way (i.e., as an interaction between the organism and the environment). Thus, we would not expect to find a particular brain region that is responsible for the feeling of consciousness.

Again, we turn to the process of vision for an analogy. Visual perception is not a “thing” that occurs at a particular region in the brain. Rather, it is a “constructive process” that involves both global views and access to the finer details, and it is achieved in a distributed network of brain regions. The visual object-recognition pathway is organized in a hierarchical fashion: cells in the primary visual cortex respond to simple parameters (such as orientation), whereas cells further along the pathway in the inferior temporal lobe respond to complex features, such as simple geometrical designs (Tanaka, 1993). The
distributed processing of object features means that there is no one place in the brain where we experience the object as a whole. Although some cells represent complex entities, such as hands and faces (Desimone, Albright, Gross & Bruce, 1984), scientists have not been able to find cells that respond exclusively to specific objects in the environment. Thus, "seeing" must involve a constructive process in which features are specified, combined, and ultimately experienced over a distributed network. To emphasize this point, it has been suggested that cognitive functions occur throughout our brain just as we live throughout our body (Herrick, 1948).

In the remaining sections of this chapter, we discuss how the process of consciousness is achieved. We also elaborate on how both cortical evolution and individual development contribute to the personal and subjective experience of consciousness. Our model contains two central ideas. First, consciousness depends upon the integration of affect and motivation with representations of sensory and motor information (i.e., sensorimotor patterns). This integration is necessary but not sufficient for consciousness. Emotions are believed to provide the guiding framework for cortical development and organization throughout the life span of the organism (Luu & Tucker, 1996; Trevarthen & Aitken, 1995; Tucker, 1992). Even in adulthood, consciousness must be mediated by brain mechanisms that have evolved to control primitive systems of affective regulation. These regulatory mechanisms are extensions of a vertical hierarchy of brain organization and development, and contribute directly to the character of what it feels like to be conscious. This regulation is the task of vertical integration (Tucker, 1993; Tucker & Derryberry, 1992) that will be discussed below. Without vertical integration, the content of our consciousness would be completely ephemeral — thoughts, images, and action plans would all pass fleetingly through our minds and would be easily displaced by the next capricious thought, image or action plan. This is not to say that the experience of consciousness is never ephemeral, such as when one is daydreaming. Rather, we want to emphasize that the forces that sustain cognition in a controlled manner are affective in nature and are represented at many levels in the neuraxis.

Our second central idea is that consciousness is fundamentally a preparatory and comparative process. It is preparatory in the sense that a frontal system dedicated to the processing of information according to internal motivational states prepares posterior, sensory regions so that they are more likely to register environmental stimuli that are congruent with the organism's
affective and motivational state. Consciousness is *comparative* in that the organism is constantly comparing its internal state with representations of the external environment so that inconsistencies or mismatches can be reconciled.

The cortical mantle can be divided, for explanatory purposes, into a posterior sensory system and an anterior response system (Jackson, 1931). This division is only a heuristic and should not be adhered to in the strictest sense because there are cells in the parietal lobe that are involved in movement, such as reaching and grasping (Jeannerod, Arbib, Rizzolatti, & Sakata, 1995). However, those areas contain neurons that seem to encode more global aspects of the action. Nevertheless, as we will show, the evolution of the posterior sensory system has increased the resolution and fidelity of the organism's environmental interface (Tucker, 1992). In contrast, the evolution of the anterior system has improved the representation of information regarding internal states and plans (i.e., improvements that have allowed information to be more flexibly reorganized, represented, acted upon, and perceived).

1. Brain evolution and architecture

In this section, we lay the foundation for our model by giving a selective overview of theories of brain evolution. In addition, we describe some features of brain architecture that are relevant to our model.

1.1 Evolution and spherical organization

In 1948, Yakovlev proposed that the brain evolved along, and is organized as, a series of concentric spheres in which each sphere is successively and functionally linked to adjacent spheres (see Figure 9.1). At the core is the brainstem, with centers (such as the periventricular area) involved in the maintenance of homeostatic states (e.g., body temperature, blood sugar). Although this homeostatic core receives afferent signals from sensory receptors outside the brain, the core itself is also reactive to sensory stimuli. For example, heat applied to the anterior extremity of the third ventricle immediately produces changes in heat-regulating mechanisms, and \( \text{CO}_2 \) applied to the posterior brainstem produces changes in depth and rate of respiration. Moreover, these sensitive regions within the brain are modality-specific and tightly localized. From these observations Pribram (1960) argued that these homeostatic centers resemble sensory receptors.
The next sphere out is the reticular network which is involved in the control of arousal. The reticular network consists of a number of nuclei located in the medulla, pons, and midbrain. We will have more to say about arousal and activation later (see also Whitehead and Schliebner, this volume). Beyond the reticular network is the limbic system, located on the medial aspects of the cerebral hemispheres. Pribram (1960) argues that the limbic network links and regulates the multiple homeostatic functions of the brainstem with each other and with the arousal functions of the reticular activating network, thus, setting up biases that regulate behavior. The outermost shell is the neocortex.

The concentric organization of the brain reflects the organization of behavior (Yakovlev, 1948). Yakovlev argued that motility and other behavior, in relation to the world, is organized into three spheres. The simplest form of motility is that of visceration, such as respiration and blood circulation, in which changes in homeostatic states relate to the current physical environment. The next sphere of behavior involves the outward expression of internal states, that is, the expression of emotion. The final sphere involves behavior of effectuation which creates changes in the physical world. Just like the interdependence of the spheres in the cortical domain, Yakovlev states, "The behav-
ior of the organism is total; every heart beat, every twitch of a muscle, every movement and posture is an integral part of the total behavior which evolves and proceeds as a unity in time.” (p.315)

Vertical Integration. The large size of the cortical mantle (the outer most sphere) in both humans and nonhuman primates, relative to other animals, led early students of the brain to focus on its importance to behavior, and unfortunately, to overlook the importance of lower systems. Although it was known for some time that certain areas of the brainstem could be stimulated to produce alterations in the alert state, Moruzzi and Magoun (1949) were the first to systematically demonstrate that an ascending reticular activating system, arising from the brainstem, directly influenced the cortical state. Specifically, Moruzzi and Magoun found that stimulation of the brainstem reticular activating system produced changes both in the cat’s ongoing EEG and in its level of alertness. This important finding demonstrated that essential aspects of cortical functioning are regulated by subcortical structures. This led to the reconceptualization of the brain as being organized vertically (Luria, 1973; Pribram, 1960), which was implicit within Yakovlev’s (1948) formulation. John Hughlings Jackson (1931) proposed just such a vertical framework at the turn of the century, based on his observations of epileptic and brain-lesioned patients.

In his attempt to understand the principles underlying pathological conditions after brain damage, Jackson (1931) theorized that brain evolution has proceeded in an ascending fashion. In this theory, new structures grew outward from — and are superordinate to — older structures. The Jacksonian theory of brain evolution is that evolution moves from highly-determined and specialized brain areas to more flexible and generalized brain areas, and from a limited repertoire of automatic responses toward an increasing number of voluntary responses. In this framework, recently evolved brain structures regulate the more primitive structures which evolved earlier. Thus, the pathology observed after cerebral lesions can be understood in terms of the undamaged older structures being released from the control of the damaged, more recent structures; in this case, brain lesions lead to a dissolution (the opposite of evolution) of brain organization and function.

It is a principle of cortical organization that brain structures are reciprocally connected, with each area sending signals back to those structures from which it receives transmissions. Luria (1973) described a descending reticular activation network, originating in the prefrontal cortex (see Figure 9.1). In
fact, it has been known for some time that stimulation applied to the ventrolat-
dial surface of the prefrontal cortex can elicit visceral and autonomic re-
sponses such as respiratory arrest and changes in blood pressure in humans
and other animals (Kaada, Pribram & Epstein, 1949; Livingston, Chapman,
Livingston & Kraintz, 1947). These findings reveal connections between
prefrontal cortex and lower structures involved in the regulation of those
visceral and autonomic responses. Consistent with the Jacksonian principle,
this descending system recruits and regulates the ascending one so that
the prefrontal lobe can have broad influence over the rest of the cerebrum (Luria,
1973).

Because of the way the brain evolved and is organized, Tucker (1993)
pointed out that normal cerebral function and representation inevitably face
the task of vertical integration. That is, the task of integrating the multiple
representations of a function across the neural hierarchy (i.e., the different
concentric spheres) is to obtain coherent behavioral expression. For example,
in primate vocalization it has been shown that primitive organization of
phonation (e.g., respiration) takes place at the pons and medulla (Jürgens,
1979). Motivations are coupled to these elementary patterns at the level of the
caudal periaqueductal gray and tegmentum. The species-specific aspect of
vocalization involves contributions from the diencephalon (thalamus and
hypothalamus). The voluntary aspect of uttering a call is initiated at limbic
levels, and finally, voluntary call formation is organized at neocortical levels
(Ploog, 1992). Thus, the final product of coherent vocalization stems from the
coordination and integration of neural structures which separately compute all
aspects of the call, represented at various levels of the neuraxis. As is the case
for vocalization, temperature regulation (Satinoff, 1978), attention (Posner &
Dehaene, 1994), and human language (Brown, 1979) also involve multiple
levels of the neuraxis. For example, the superior colliculi, pulvinar, insula,
cingulate, and frontal and parietal cortices are all involved in various aspects
of attention.

Vertical integration is not a problem in an intact nervous system. How-
ever, when the integrity of the neuraxis is damaged, the failure of integration,
and thus cerebral functioning, becomes readily apparent. That is, symptoms
after a lesion to the hierarchy can be taken to reflect failures of integration and
as disruptions of a normally continuous process. For example, in human
language, lesions at limbic levels result in semantic errors, and lesions to
neocortical regions, such as Broca’s area, result in difficulties with phonemic
articulation, leaving semantics intact (Brown, 1979). The important point about vertical integration is that cortical functioning requires support from and continuity across the many levels of the vertical hierarchy.

1.2 Cortical evolution

Adaptive Pressure. Allman's (1990) theory of cortical evolution posits that the neocortex evolved as a consequence of emerging endothermic homeostasis in mammals (i.e., the need for warm-blooded animals to maintain their body temperatures within certain narrow limits). Internal regulation of body temperature allows the organism to function in a larger range of climates. The narrower range of internal temperature allows for finer tuning of biochemical functioning involved in metabolic processes, and thereby provides increased reliability in neuronal functioning. Unfortunately, the advantages afforded by internal regulation of thermal homeostasis are costly in terms of energy consumed. Therefore, Allman argued, the neocortex evolved to enable the animal to reliably map its food resources and plan strategies that would allow it to obtain those resources.

The environment of an organism is inherently noisy, and it is the task of the organism to extract the signal. In the mammalian brain vast regions of the neocortex are comprised of numerous topographically organized sensory maps. For example, Allman (1990) notes, through comparative studies, that in early marsupials approximately 75% of the neocortex consists of topographic sensory maps. In these topographic maps, the environmental stimuli transduced via receptor surfaces such as the retina, skin, or basilar membrane are represented at the cortical level in a spatial layout which mimics that of the receptor sheet. For example, the postcentral gyrus of each cerebral hemisphere has a map dedicated to somatosensory processing of the opposite half of the body. In this map, adjacent parts of the body surface are represented by neurons located in adjacent parts of the cortical map. It is through the correlated functioning of these sensory maps that noise is filtered and information extracted (Edelman, 1989). In other words, these sensory maps enable the recurrent images from the environment to be easily perceived.

Within this context, the evolution of the brain's sensory regions can be understood as increasing the resolution of the organism's environmental interface (Tucker, 1992). However, this enhanced representation of the external environment needs to be integrated with information from the motivational
core regarding the internal environment. In this way, behavior can be modified to prioritize the organism’s goals, and to achieve them in the most efficient manner possible. We will see that cortical evolution has emphasized this aspect as well.

_Trends and Growth Rings._ The cortex, through evolution, has substantially increased in size, accounting for more and more of the cerebral mass (Northcutt & Kaas, 1995). This expansion of the cortical surface has been argued to be a result of the extended period of cell division in the ventricular zone during neonatal development (Rakic, 1995). During embryonic development, cells created in this area migrate outwards to form columns or radial units that eventually give rise to cortical neurons. Thus, over the course of evolution, the increase in size of the cortex appears to have depended, at least in part, on the increases in the length of time that cells in the ventricular zone were allowed to divide and form cortical columns.

Along with the increase in cortical area, evolution introduced more cortical fields. For example, it is believed that most rodents have 5-8 areas dedicated to visual processing, whereas the macaque monkey, with more cortex, has approximately 30. Compare this with the belief that the _entire_ isocortex (six-layer cortex) of the first mammals contained only about 20 areas, including _all_ sensory modalities as well as motor areas (Northcutt & Kaas, 1995). The addition of new fields, which appears to be a hallmark of cortical evolution, has allowed for improved processing of the environmental stimuli encountered within the organism’s ecological niche. Although there are conflicting views regarding the process that controls the development of new cortical fields, evidence suggests that the new areas developed from older ones (Krubitzer, 1995).

Consistent with the current proposal of new cortical fields emerging from existing cortical areas, Sanides (1970) described cortical evolution as a process of differentiation out of two primitive moieties; the paleocortex (olfactory cortex) and the archicortex (hippocampal cortex). The paleocortex gave rise to cortices on the ventral and lateral surfaces, and the archicortex gave rise to cortices on the medial and dorsal surfaces.

The cortex is a laminated structure that varies in the number of layers throughout its extent. Each layer is dominated by a certain type of cell. For example, granular layer IV, the input layer, is predominantly occupied by small stellate cells which gives it a granular appearance. The infragranular layers (below layer IV) are output layers, whose neurons project to other
cortical areas and outside the cortex. The supragranular layers (above layer IV) are processing layers. Sanides (1970) used the pattern of variation in the number of layers and the cell distribution within these layers, to guide his theory of cortical evolution. He noted that, in comparison to more recently evolved tissue, primitive (i.e., limbic) cortex is characterized by sparse lamination and a laminar pattern that varies greatly between areas. With increasing differentiation from this primitive core, the cortex gained additional lamination, resulting in the six-layer isocortex. The evolutionary emphasis in cellular distribution shifted from the infragranular layers in primitive cortex to the supragranular layers in isocortex, suggesting that evolution has refined and extended the processing of sensory input. The evolutionary sequence of cortical differentiation is as follows: allocortex (two layers), proceeding to periallocortex (near allocortex — the laminar pattern resembles allocortex), to proisocortex (near isocortex — the laminar pattern resembles six-layer cortex), and finally to isocortex (6 layers — homogeneous). Figure 9.2 presents a schematic of this progression. Within this framework, all neocortical areas can be traced back to their roots in limbic cortex.

Pandya and associates (Pandya, Seltzer & Barbas, 1988; Pandya & Yeterian, 1990) have meticulously illustrated Sanides’ theory of evolution for the frontal lobe (see Figure 9.3). The paleocortical trend begins in the temporal pole and orbitofrontal regions, and gives rise to three ventrolateral sectors in the frontal lobe: the precentral, premotor and prefrontal. In contrast, the mediodorsal aspect of the frontal cortex stems from the archicortex. The periallocortex of the anterior cingulate is the first step in the sequence away from the allocortex within this trend. It then differentiated into areas such as the premotor (including the supplementary motor area) and primary motor cortex. In the prefrontal cortex, it differentiated into cingulate areas in front of the corpus callosum, and then into areas on the dorsal surface. The principal sulcus and the inferior frontal sulcus demarcate the boundary on the dorsolateral surface of the two trends in monkeys and humans, respectively (Pandya et al., 1988; Pandya & Yeterian, 1990; Sanides, 1970). Again, this sequential differentiation has entailed an increase in the number of cells in layers III and IV.

Sanides (1970) further proposed that the evolutionary pattern of cortical differentiation proceeds in a ring-like manner — new areas form the core and contain denser thalamic input, whereas the originating cortex forms the outer ring. Sanides found that even in Brodmann’s architectonic map, the ring of
Figure 9.2, A-D. Schematic diagrams to show the progressive development of cortical areas from the two primordial moieties (archi and paleo) through successive steps: periallocortex (Pall) to proisocortex (PRO) to isocortex. (from Pandya et al., 1988; reprinted with permission).
differentiation can be seen — area 18 forms a ring around area 17 and area 19 encircles area 18. In this manner, the intermediate cortex retains its connections with the other older area as it forms new connections with the newly formed field. Newly developed areas, however, retain few connections with older areas, other than with the one from which they emerged. The development of the new areas from previously existing cortex may result from new, correlated inputs invading an extant area with subsequent aggregation of similar types of inputs (Krubitzer, 1995). In other words, new inputs to an existing area grow to form modules within these extant fields. If there are modules with similar inputs they might aggregate to form a new field. This process of new field formation can then produce an island within the existing area. Thus, the evolution of the environmental sensory interface, (i.e., cortical fields involved in the processing of sensory information) can be regarded as a process of cortical differentiation into specialized new fields with an increasing emphasis on supragranular, processing layers.
1.3 Cortical circuits organized according to evolutionary progression

Although a variety of cortical projection patterns had been recognized for some time, it was Sanides’ (1970) theory of cortical evolution that provided a truly elegant framework in which to conceptualize the organizational principle of cortical projections. Pandya and associates (Pandya et al., 1988) applied this theory to the pattern of cortical projections and found that they could be explained by the sequential stages of cortical evolution.

Pandya et al. (1988) noted that early studies of cortical projections tended to focus only on the efferents of primary areas, and that back-going projections were not given the attention that they merit. Projections from primary areas to downstream fields originate in infragranular layers and terminate in layer IV; the reciprocating back-projections from association areas to sensory and primary sensory areas originate in infragranular layers and terminate in layer I.

The forward-projections are arranged consistently with the notion of sequential processing of information, such that more abstract aspects of the information are represented and processed in areas downstream. For example, neurons in 'downstream' visual areas have larger receptive fields and respond to more complex features than neurons earlier in the system (Tanaka, 1993; Zeki & Ship, 1988). It was originally believed that the back-going projections served only to produce feedback regarding receipt of forward transmission. We now know that they do much more, and that back-going projections serve to link areas of progressive lamination (Pandya et al., 1988). Also, they may have a direct influence on the processing and representation of information in the areas upstream (Zeki & Ship, 1988). It has been suggested that cortical layer I serves as a short-term buffer, akin to short-term memory, in which sensory information is held for subsequent corticocortical integration (Vogt, 1991). If this is the case, then it can be seen that back-projections terminate in a layer that can potentially affect the processing of incoming information.

Within each cortical trend (i.e., archicortical and paleocortical), cells within a given area send axons to both a less and a more differentiated area, mainly to their evolutionary neighbors; a given area’s projections to areas of distant evolutionary age is rare. Using visual cortex as an example, area 18 has many connections to areas 17 and 19, but areas 17 and 19 have fewer direct connections to each other. Presumably, these areas evolved in sequence from 19 to 17, demonstrating that projections from one area to other areas of distant
evolutionary age are rare. Across the two trends, this pattern of projection indicates a similar preservation of evolutionary rank, and this pattern holds across sensory modalities as well (Pandya et al., 1988). Logically, from Sanides’ (1970) growth-ring theory, this pattern of cortical projections would be expected — as more recent areas evolved, they became separated from older fields. Thus, evolution of the sensory cortex also can be regarded as a gradual transition towards sensory segregation.

2. Brain maturation

Partially paralleling the phylogenetic, vertical evolution of the brain, ontogenetic cerebral maturation proceeds in a similar manner from the central core out, at least up to the level of the cortex. Myelination and metabolism studies have shown that brainstem structures, with the exception of the reticular system, mature earlier than the striatum, and that the striatum, in turn, matures earlier than most cortical areas (Brody, Kinney, Kloman & Gilles, 1987; Chugani & Phelps, 1986; Yakovlev & Lecours, 1967). Surprisingly, at the level of the cortex, the progression reverses. That is, the most recently evolved sensory areas are the first to mature (Brody et al., 1987; Chugani & Phelps, 1986; Gibson, 1991). The primary sensory areas are the first to myelinate and are the ones associated with the highest level of glucose metabolism at this stage of development. The maturation then proceeds outwards from the precentral and postcentral gyri towards the frontal pole and parietal/occipital association cortices (Kinney, Brody, Kloman & Gilles, 1988). The frontal and forebrain limbic cortices mature later than the posterior half of the brain and, in general, are the last cerebral structures to mature (taking up to 8 years or more to develop mature levels of myelination).

Yakovlev and Lecours (1967) observed that both progressions of maturation, from subcortical to cortical, and from primary sensory to association and limbic cortex, seem to coincide. For example, subcortical fibers mediating somatic experience myelinate before those fibers that mediate more integrative experience. This is the same pattern observed at the cortical level. Moreover, myelination of thalamic projections to association areas of the cortex is synchronized with myelination of fibers leaving these cortical areas. This overall pattern of brain maturation has been described as a gradient of central convergence onto the prefrontal cortex and the related limbic forebrain (Luu & Tucker, 1996).
2.1 An epicritic organizational system

Based upon these evolutionary and maturational progressions, it is possible to describe an organizational system that is specialized for the processing and representation of sensory information. As we have explained, the evolutionary trend is toward increasing differentiation and segregation. For the different sensory modalities, this trend directly influences the topographic organization, and thus representation, of sensory information. As mentioned earlier, to the extent that an organism’s brain contains additional cortical fields dedicated to processing and representing information within a specific sensory modality, the more refined and accurate will be that organism’s experience and representation of its environment within that modality.

The evolution of highly differentiated and articulated topographic maps has yielded posterior sensory systems equipped with highly refined localization properties. Derived from neurology, the term “epicritic,” coined by Henry Head (Pribram, 1981), refers to local signs of sensation, signs that can be localized in space and time. For example, the pain system, as it enters the thalamus from the spinal cord, splits into two pathways. One of these two pain pathways leads from the ventral posterior nucleus of the thalamus and terminates in the somatosensory cortex (Vogt, Sikes, & Vogt, 1993). These cells have small receptive fields for noxious stimuli; a prick on the hand induces a sensation that is of limited duration and that can be localized to the hand. With their exquisitely precise topographic maps, the posterior sensory systems provide representation of information with high spatial and temporal resolution ideal for the extraction, processing and storage of environmental stimulus features (Damasio, 1989; Edelman, 1989). This can be contrasted with the other, more diffuse and non-localized pain pathway to be described later.

The nature of representations within this epicritic system is not only determined by the cortical fields that have evolved over the history of the species, and of the type of information that these fields receive, but it is also determined by maturationally dependent, developmental processes. Sculpting of cortical circuitry in early-maturing cortices is a result of a form of development known as “experience-expectant development” (Greenough & Black, 1992). This form of development, seen most often in posterior sensory systems (e.g., the formation of ocular dominance columns), involves an overproduction of synapses in anticipation of environmental events. Environmental stimuli then provide the input necessary for neuronal activity, and each
synapse is either strengthened or eliminated depending upon its activity level and that of its neighbors. Experience-expectant development occurs only within a narrowly defined window of time (i.e., a critical period).

Greenough and Black (1992) argued that experience-expectant development mechanisms evolved under three conditions. First, information that guides the retention and elimination of synapses is common to all young members of the species. Second, the events that provide this information must occur reliably for all members of the species and must have done so throughout the evolution of the cerebral system under question. Finally, the maturational time window in which the information is provided is critical.

To summarize, the posterior epicritic system can be regarded as a sensory system that is influenced by early developmental mechanisms and that it is affected by species-specific information. Moreover, this system emphasizes temporal and spatial resolution. This system can be generally regarded as containing specialized mechanisms for the processing and representation of the environment. The epicritic system, through the correlated activity of neurons arranged in topographic maps, extracts invariances from an environment that is inherently noisy and unorganized (Edelman, 1989; Pribram, 1960). Through reentrant connections, patterns of activity in different cortical maps can become correlated so that environmental inputs become categorically grouped. Because of these properties, the structure of the categories formed and represented within the epicritic system is based upon physical stimulus features such as shape, and is analogous to basic-level and subordinate-level categories (for example, chairs and rocking-chairs, respectively). Thus, an abstraction (i.e., an average) of a category within the epicritic system still reflects the shape of individual members of the category (Rosch & Mervis, 1975; Rosch, Mervis, Gray, Johnson & Boyes-Braem, 1976).

2.2 A protocritic recategorical system

As noted previously, the human brain has grown in size, most notably the prefrontal lobe (Benson, 1993). During this evolution, the prefrontal lobe has also increased in its intrinsic and extrinsic connectivity (Altman, 1995; Fuster, 1989; Nauta, 1964). This suggests that the trend in prefrontal-lobe evolution is toward increasing its processing capacity and ability to organize the information provided by improved sensory systems. However, the prefrontal lobe’s functions are fundamentally different from the specialized functions of the epicritic system.
The prefrontal lobe appears to be involved in learning general tasks (not limited to a single processing domain) that are not supported by specialized circuits (Gaffan, 1994). For example, learning to associate reward with a visual stimulus involves circuits connecting visual cortex with the amygdala. Lesions to these areas or to their underlying connections produce failures to overtly learn the association. Learning the association of instructional cues with an appropriate choice does not have a specialized mechanism and thus depends upon prefrontal functioning (Gaffan, 1994). Prefrontal lesions or damage to its connections with the visual cortex impair learning of these tasks. More than likely, learning to successfully navigate through a complex social world is also a task that lacks specialized mechanisms.

Because the maturation of the prefrontal and limbic cortices is protracted, their cortical wiring is subjected to a different form of cortical development than earlier maturing cortical areas. The protracted maturation of the prefrontal and limbic cortices allow for more ‘experience-dependent’ developmental mechanisms to sculpt their cortical wiring (Greenough & Black, 1992). This form of cortical sculpting refers to synaptic pruning that occurs later in cortical maturation. In contrast to experience-expectant mechanisms, experience-dependent development is characterized by a lack of a critical time window during maturation in which information must be present in order for functional cortical sculpting to occur. Because of this lack of a critical period, the organization of cortical circuitry through experience-dependent mechanisms is more greatly influenced by the individual experiences of the organism than on experiences that are anticipated as a result of their consistent appearance throughout the evolution of the species. For example, the location of food, warmth, shelter, and potential mates, and recognizing one’s position within a social hierarchy are things in flux for a good part of (if not throughout) the life of an animal and would not benefit from predetermined cortical encoding within narrow time intervals. The synaptic changes occurring with this form of development involve massive sprouting of dendritic fields (see Greenough & Black, 1992).

The findings of experience-dependent development (Greenough & Black, 1992) and self-regulating functions of the prefrontal lobe (Tucker, Luu, & Pribram, 1995) combine to form a useful theoretical framework. From this perspective, the evidence of central convergence in cerebral maturation suggests that the representations within prefrontal and limbic networks are based upon abstractions of environmental stimuli guided by internal states (Luu &
That is, sculpting of late-maturing cortical areas comes under the influence of early-maturing cortical sensory areas and subcortical structures. Early-developing sensory areas provide environmental information, and subcortical structures involved in affective self-regulation provide information about internal states.

Recordings from neuronal populations in the prefrontal cortex of the behaving monkey have revealed that neuronal groups undergo quick, functional reorganization as a result of stimulus context and the behavior of the animal (Aertsen et al., 1991). Although Aertsen and colleagues did not investigate the role of limbic and subcortical structures in this functional reorganization, the fact that the reorganization was dependent upon the behavior of the monkey is compelling. Similarly, single-cell recording studies have demonstrated that the correlated firing between two cells depends upon the animal attending to the stimulus (Ahissar et al., 1992). Furthermore, it has been shown that the catecholamine brainstem systems (Mattson, 1988), which have been suggested to be primitive affective/attention control systems (Tucker & Williamson, 1984), can potentially suppress or facilitate synaptic development. The information provided by internal states allows this generalized system to recategorize and represent the information extracted by the posterior sensory areas.

Thus, this generalized, recategorical system prioritizes and filters the torrent of exquisitely detailed sensory information emanating from the epipetic system, according to the relevance of the sensory information to the organism’s goals. We would expect that its representations would emphasize the function and ideals of things-in-the-world: these are the features of things that are most closely linked to our motivational states and goals. These representations are extracted invariances related to the social history of the organism. Just as there are species-specific encodings of perceptual invariances, this generalized, recategorical system may be in a position to encode invariances of a personal nature. For example, in some individuals their social history has sculpted a system in which threats to the self are, more often than not, readily extracted from social situations. These representations can be regarded as personal affordances (Luu & Tucker, 1996). That is, information that is represented in this generalized, recategorical system bears a personal viewpoint upon the experience and processing of new information.

The structure of representations in this generalized, recategorical system may be similar to the structures of superordinate-level categories (e.g., tools,
furniture, Rosch & Mervis, 1975), theory categories (Medin, 1989), and goal-driven categories (e.g., things to keep us warm, Barsalou, 1985). In contrast to representations in the epicritic system, in which membership in a category depends upon physical features, membership in these types of categories is defined by function, theories, and ideals. Moreover, unlike basic and subordinate categories, and in keeping with the general nature of the system, an abstraction of the members does not reflect correlation among physical features of the members.

In contrast to the local signs supported by epicritic representations, the prefrontal network’s representations are non-local, being diffusely distributed across both space and time. For example, a second pain pathway (mentioned briefly above) leads from spinal cord to the medial nuclei of the thalamus and terminates in the anterior cingulate (Vogt, et al., 1993). Cells within the anterior cingulate have broad receptive fields; a single cell’s receptive field for noxious stimuli can be the entire body surface. This pain pathway appears to be responding to the valence of the noxious stimuli. Pribram (1981) has designated the term “protocritic” to describe a brain system that processes and represents these non-local signs.

3. The process of consciousness

“Emotion is assumed to be always present in ordinary consciousness, giving it a particular experiential quality and maintaining its purposeful flow.” (Izard, 1980) (p. 193).

3.1 The importance of vertical integration to the conscious process

Tucker and Williamson (Tucker & Williamson, 1984) suggested that a unidimensional construct of arousal cannot account for an organism’s complex attentional control and self-regulatory functions. They proposed that the brain has two systems pertaining to arousal, each regulated by a different brainstem neuromodulator system. These systems are believed to be inherently affective in nature, and they influence attentional, engagement, and cognitive styles. That is, these brainstem systems are not affectively neutral, but rather their activity also engenders changes in emotion, engagement tendencies, and modes of cognition.
On one hand, the activation system is centered upon the dopamine cells of the tegmentum and substantia nigra. Its activity produces a redundancy bias that maintains focused attention and routinizes action. It produces an analytic cognitive mode. The activation system is believed to be central to the experience of negative affect, such as anxiety. On the other hand, the arousal system is regulated by norepinephrine cells of the locus ceruleus. This system produces a habituation bias so that novel events capture attention. The cognitive mode of this system is holistic. Its activity is believed to be central to the experience of positive affect, such as elation (for a detailed description see Tucker and Williamson, 1984).

Psychometric studies on the structure of mood have similarly revealed that attention, engagement, and cognition are intimately entwined (Tellegen, 1985; Watson & Tellegen 1985). Traditionally, mood space has been described as consisting of a pleasant-unpleasant dimension and an engagement-disengagement dimension. However, based upon their factor analytic studies of mood descriptors, Tellegen and Watson argued that mood space can also be validly described by the dimensions of positive and negative affect. This alternative description is just a 45 degree rotation of the axes that describe the pleasant-unpleasant and engagement-disengagement dimensions. However, Watson and Tellegen argued that their rotation is preferable because their two axes conform to the natural clustering of the mood descriptors. High positive affect is characterized by words such as active, elated, and excited. High negative affect is characterized by descriptors such as nervous, jittery, and fearful. Tellegen and Watson argued that these dimensions are more than just dimensions of arousal or affective. Rather, the descriptors suggest that they are dimensions that describe mood, arousal, engagement styles, and cognitive mode. For example, high positive affect is characterized as pleasurable engagement with an orienting cognitive mode. Thus, we can argue that the association between attention, affect, engagement, and cognition as described by the activation and arousal systems and the two dimensions of affect reflect a vertical integration of cerebral functioning.

Vertical integration of valenced arousal systems serves to affectively motivate, sustain, and integrate sensorimotor patterns. Without affective and motivational input from the brainstem, sensorimotor patterns in the neocortex lose their immediacy and quickly fade (Tucker, 1992). This principle may underlie certain symptoms displayed by patients with frontal lobe and limbic lesions. For instance, Pribram (1950, 1991) argued that limbic lesions disturb
complex action plans because the states and action of the homeostatic centers are no longer coordinated. In addition, it is possible to observe abnormal influences of emotion on cognition in persons with relatively intact brains. Patients with a right temporal lobe epileptic focus display exaggerated emotionality, whereas those with a left temporal lobe focus exhibit obsessive thoughts or ruminations and a catastrophic response in their self-evaluations (Bear & Fedio, 1977). Tucker (1981, 1992) suggests that the symptoms experienced by temporal-lobe epileptics reflect the exaggerated constraints applied on cognition by emotions. From this perspective, the content of the left temporal-lobe epileptic’s consciousness is filled with ideational and intellectual themes (such as philosophical and religious ruminations), whereas the content of the right temporal-lobe epileptic’s consciousness is affectively colored with feelings of elation. Thus, emotion, through vertical integration, is inextricably bound up with consciousness.

3.2 The process

A complex organism, through evolution, becomes endowed with cerebral mechanisms that allow it to go beyond simple, reflexive responses to the environment. These mechanisms allow the organism not only to respond to the environment, but also to be aware of it. However, the reflex-arc, a simpler conceptualization, did dominate the way in which the functioning of the nervous system was earlier construed (see Pribram, 1960). The concept of a reflex-arc in its simplest form describes a loop in which a reflex (response) is elicted by a stimulus. This loop is a closed circuit and does not account for how information picked up by sensory receptors can be internally influenced. Decades ago, Pribram noted that the available evidence suggested that such one-way construals of the function of the nervous system are missing something. The problem that must be faced in studying the functioning of the brain is to specify how efferent (back) projections influence receptor mechanisms.

Attempting to go beyond the reflex-arc to account for internal influences on information processing, Pribram (1960) proposed a cybernetic model of cortical functioning. In this model, the protocritic and epicritic systems detect discrepancies between their respective representations of the incoming information and adjust behavior accordingly so that the perturbations are reduced. In this way, the normal functioning of these systems requires a comparative process. From this perspective, the organism is no longer seen as a passive
processor of information; rather, the organism is viewed as having control over the information that it receives. These systems, however, are not seen as isolated — they must function together to produce adaptive behavior.

In studying the symptoms of frontal lobe lesions, Teuber (1964) and Nauta (1971) proposed theories of cortical functioning that also emphasized the ability of the brain, especially the frontal lobe, to affect its own reception of peripheral stimuli. These theorists suggested that projections from one cortical area to another can alter the functioning of the receiving areas either by producing a corollary discharge, or by producing set-points at which ongoing actions are compared against somatic states. For Teuber (1964), the frontal lobe sends a corollary discharge to the posterior areas of the brain to prepare the sensory systems to receive information based upon the executed action. Extending this concept, Nauta (1971) proposed that the prefrontal cortex instantiates set-points that assist the organism in anticipating and integrating action patterns across time (a form of working memory for action plans).

More recently, the possible effects of back-projections on sensory processing upstream has been extended beyond the frontal cortex (see Edelman, 1989; Zeki & Ship, 1988). For example, it has been shown that projections from primary visual cortex (V1) back to the lateral geniculate nucleus (LGN) can alter the firing of cells within the LGN (Sillito, Jones, Gerstein & West, 1994). They do so by altering the firing threshold of the LGN cells.

The V1 inputs to the LGN are not strong enough to drive the LGN cells by themselves — in order for the LGN cells to depolarize they need additional retinal input. As a group, those LGN cells which receive a common input via projections from V1 will be synchronized in their firing when the appropriate stimulus is provided. Crick and Koch (1990) have argued that synchronization of neuronal function across separate areas of visual cortex provides a form of short-term memory that leads to visual awareness. In the study by Sillito et al., it is unlikely that visual awareness can occur in the LGN. We believe that awareness involves synchronization at a more global-network level, and that projections from the protocritic networks are required.

As explained previously, the prefrontal cortex mediates the process of recategorization and the representation of personal affordances. This protocritic system, by way of its connections to the posterior, epicritic system, facilitates the synchronization of different sensory maps within the epicritic system to form coherent percepts. However, recall the observation that cells receiving inputs from the back-projections will not depolarize, i.e., be syn-
chronized in their functioning, without environmental input. As a result a percept is not fully achieved until environmental information provides the confirming signals. The synchronization of activity in the epicritic system as mediated by protocritic networks gives consciousness a flavor that is beyond mere stimulus awareness.

The influence of the protocritic recategorical system allows for the individual history of the organism to influence cortical binding and the experience of consciousness. Bruner (1957) has long argued for the concept of readiness during perception. That is, the act of perceiving involves the process of categorization, and the categories which are developed influence the organism's readiness and ability to perceive stimuli. To the extent that incoming information violates the expectations inherent in a preconfigured system, either the organism will attempt to correct the discrepancy (Pribram, 1960), or the information will be incorrectly perceived or not perceived at all (Bruner, 1957).

Within this framework of consciousness, the interaction between the protocritic and epicritic systems explains the personal and idiosyncratic nature of human conscious experience. The abstraction of invariances, or personal affordances, by the protocritic system preconfigures sensory systems to receive, extract, and be aware of information in idiosyncratic ways (e.g., the tendency to perceive threat in social situations). In addition, it is through the workings of this system that ongoing events may be left out of consciousness. Bruner (1957) coined the term "perceptual defense" to describe events that occur in the environment but are left out of perceptual awareness, and he suggested that this is a result of interference caused by currently active categories (for our purposes categories represented in the protocritic system). These categories distort or exclude, by way of the protocritic system's projections to the epicritic sensory system, poor-fitting environmental events such that these events are either misperceived or are not perceived at all. Thus, actual ongoing events may be left out of consciousness altogether by interference from representations in the protocritic system.

4. Summary

Cortical binding through synchronized neural firing across sensory maps has been proposed to be a mechanism for consciousness. We believe that it is a key to understanding only one aspect of consciousness and that aspect is
sensory awareness. The process of consciousness that we have described extends awareness within specific sensory modalities to a global sense of awareness of the environment based upon individual experiences. This is accomplished by suggesting that consciousness is a process of preparation and comparison.

The process depends on integration of cerebral functioning across the vertical hierarchy, and also upon the interaction of two systems: the frontal protocritic system and the posterior epicritic system. Evolution has elaborated each of these two systems. The epicritic system became more differentiated and has progressed toward increasingly refined sensory processing and segregation. In following its own course of differentiation, the protocritic system has increased both in size and in the density of its intrinsic and extrinsic connections. In organisms alive today, each system differs in the rate at which it matures, and as a result each is under the influence of different developmental processes. These developmental processes determine, in part, the nature of the representations within each system.

There are certainly aspects of human consciousness that cannot be accounted for in our model. For example, cortical circuits supporting human language certainly contribute to and alter the conscious experience (see Edelman, 1989). At the present time, we do not have a clear notion of how to fit these circuits and their functions into our model. However, this should not serve as a deterrent to the claim that consciousness can be related to the brain. After all, human language is a product of the brain and its influence and contribution to consciousness must be through cerebral means.

Finally, because our model is highly influenced by theories of brain and cortical evolution, we feel obligated to take a moment to entertain the question of which non-human animals experience consciousness. It is likely that animals with a reasonably developed cortex that is able to carry out this comparative process probably do experience consciousness. But certainly the quality of their experience must be different from what we humans experience, because each neural mechanism involved in the process differs to some degree between species.
Notes

Phan Luu was supported by NIMH grants MH42129 and MH42669 awarded to Don M. Tucker and the James S. McDonnell Foundation to support the Center for the Cognitive Neuroscience of Attention. Daniel J. Levitin was supported by a National Defense Science and Engineering Graduate Fellowship. John M. Kelley was supported by NIMH Training Grant #5T32MH18935. The authors are indebted to the following for their helpful discussions: Gerald S. Russell, Michael I. Posner, and Don M. Tucker. We are especially grateful to Peter Grossenbacher for his extensive feedback and suggestions.

Address correspondence to Phan Luu, Electrical Geodesics, Inc., Riverfront Research Park, 1850 Millrace Drive, Eugene, OR 97403, or send electronic mail to pluu@EGI.com

1. By 'primitive,' we mean cortex with heterogeneous laminated patterns (i.e., allocortex and periallocortex, as compared to isocortex, which is homogeneous in its laminar pattern). In comparative studies of the brain, the term 'primitive' is reserved for structures and areas that are apparent between species and are thus assumed to be present in their common ancestor.

2. The term isocortex means homogeneous cortex but this is a misnomer; isocortex (neocortex) is highly heterogeneous. It was probably thought to be homogeneous in comparison to the allocortex because the term allocortex originally applied to all other cortices that were not isocortex, including cortices now referred to as periallocortex and proisocortex.

References


