The Dynamic Manifestation of Cognitive Structures in the Cerebral Cortex

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Abstract

Cognitive structures are organized systems of information that embody the knowledge used to construct an individual's reality. Having phylogenetic and ontogenetic determinants, they reside latently in the connectional organization of the cerebral cortex, both within and between areas. Different cortical areas, containing separate classes of knowledge in their local associative memories, operate in conjunction with one another to instantiate cognitive structures in perceptuo-motor behavior. As multiple areas recursively interact in large-scale networks, their mutual constraint leads to the emergence of coordinated large-scale activity patterns. These patterns constitute a consistent construction of reality that fits the constraints imposed by the structures of the internal and external environments. This construction is the dynamic manifestation of cognitive structures in the cerebral cortex.

Introduction

Living things are embedded in a sea of chemical and energy flux. In order for individuals to perceive the external environment, their brains must obtain information from the neural activity that is transduced by sensory receptor arrays from environmental energy and chemicals. The fact that information about the environment is potentially available in receptor activity is clear, but the nature of the process by which it is obtained is not so obvious. The question of information processing is a problem because there is no independent source of instruction to the brain that reveals the correspondence between receptor activity and an external reality. In other words, although the environment may activate sensory receptors in various ways, it does not provide a direct representation of its true nature (Glasersfeld 1995). Knowledge of the environment cannot therefore simply be a passive encoding of predefined information. It must rather be actively constructed within a contextual framework provided by pre-existing neurocognitive structures.

Contextual effects have been shown to play an important role in both perceptual (McClelland & Rumelhart 1981) and motor processes (Houk & Wise 1995). These effects are not, contrary to conventional thought, simply a matter of constraint by the external environment. The brain itself must provide context, both for what it

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receives from without and what it processes within. One of the brain's functions is to create cognitive structures, which in their entirety embody the person's understanding of reality. A cognitive structure is an organized body of information that connects knowledge in a coherent framework (Rescher 1979). Cognitive structures are just as important in providing context for the processing of sensory information in the brain as the structure of the environment. In fact, perception may be viewed as a dynamic interaction between cognitive and environmental structures. This means, of course, that in this interaction cognitive structures are both active and actively created (Quartz & Sejnowski 1997).

Existing cognitive structures must be flexible in a way that allows the brain to rapidly adapt to changes in the external and internal milieus on a fraction-of-a-second basis. Yet their development occurs on a slower, ontogenetic time scale. An important neurocognitive question is how the brain can create and maintain stable cognitive structures while also retaining the ability to immediately adapt to environmental circumstances. That is, how can information that is stored in a stable form on a long-term basis be used adaptively to solve immediate processing demands placed on the system?

This paper describes a putative mechanism by which cognitive structure is manifested on a moment-by-moment basis as coordinated large-scale activity patterns in the cerebral cortex. An exposition of the neurophysiological details of this postulation is provided elsewhere (Bressler 1999). The idea derives from a body of research in humans and non-human primates demonstrating large-scale patterns of temporal coordination of cortical activity during cognitive task performance (Gevins et al. 1987; Bressler et al. 1993). The mechanism helps to explain how static knowledge stored in the structure of modified cortical synapses can be brought to bear dynamically for the processing of cognitive operations in real time. The background for this proposal comes from a perspective on cortical function that emphasizes a balance between local and large-scale interactions (Bressler 1994, 1995, 1996a,b; Tononi et al. 1994, 1996). Local interactions are conceived to take place in individual cortical area networks behaving in a fashion similar to the Hebbian Nerve Cell Assembly (Hebb 1949), while large-scale interactions occur among sets of multiple distributed local networks. Large-scale interactions are the basis for the mediation of context in cortical information processing. Context is built from the constraints that naturally arise as local networks undergo recursive interactions (Foerster 1984; Edelman 1989) with the other local networks to which they are connected.

The Formation of Cognitive Structure

The formation of cognitive structures in the brain is possible in large part because of the connectional anatomy of the cortex, which consists of at least three factors: (1) the large-scale topological structure of interconnected local networks; (2) the modified synaptic matrix within each local network; and (3) the modified synaptic connections between local networks. The large-scale anatomical architecture of the cortex is a mosaic of parcellated but interconnected areas (Kaas 1995). Individual areas have unique input sources and output targets, and projections between areas occur reciprocally in almost all cases that have been examined (Felleman & Van Essen 1991). Thus each area has a unique set of other areas with which it is reciprocally connected, and with which it thus can recursively interact. This architecture allows the creation of individual domains of knowledge in different areas (Humphreys & Riddoch 1987; Damasio et al. 1990; Martin et al. 1995), and also provides the substrate for functional interaction among those domains.

The anatomical foundation for cognitive structure begins forming during prenatal development. The most important developmental process during this period is most likely the creation of phylogenetically determined topological order in corticocortical connectivity. After birth, the topological individuality of cortical areas allows them to develop as semi-autonomous information processing domains. As the infant begins producing coordinated motor patterns, such as limb movements and coordination of gaze, patterned inputs are received by sensory receptor arrays. Spatial activity patterns are produced in primary sensory areas of cortex, which transmit patterned activity to multiple secondary areas. These transmit not only to tertiary areas, but also back to the primary areas, and to each other. Complex large-scale patterns of recursive interaction are created in the cortex among areas within sensory modalities, between sensory modalities, between sensory and motor areas, and among sensory, motor and association areas.

The cortex is changed by these recursive interactions in at least two ways that are significant for the formation of cognitive structure. First, the coordinated activity of pyramidal cells within an area strengthens the synaptic connections among them (Hebb 1949; Singer & Gray 1995). Activity patterns that are statistically significant over time produce patterns of strengthened connections within the synaptic matrix of each cortical area. A repertoire of strengthened connection patterns is established over time conforming to the statistical structure of the activity patterns that the area has expressed (Tononi et al. 1996). However, patterns in the various cortical areas are not strengthened in isolation, but rather in conjunction with one another. A second type of modification with experience is the strengthening of synapses between pyramidal cells in connected cortical areas (Callaway & Katz 1991; Singer & Gray 1995). This occurs when activity patterns in connected areas repeatedly appear as part of large-scale interareal conjunctive patterns.

These three factors, topological order, local synaptic modification, and interareal synaptic modification, underlie the formation of cognitive structure during development. Local areas are considered to serve as associative memories for specific elementary types of information. But each local associative memory is coupled with a number of others according to the topological ordering of cortical interareal connectivity. Cognitive structure depends not only on local stores of information, but also on heightened probabilities of conjunction among domains of knowledge stored in separate cortical areas. The range of possible states of a local network is determined by its past history, but the particular state that it manifests at any time is determined by its recursive interactions with other local networks. Context for processing in each network, thus, is provided by constraints imposed by the states of the other networks with which it interacts.

Interareal Pattern Constraint and Large-Scale Relaxation

The formation of multiple distributed local networks having unique repertoires of stored patterns, and the linking together of these local associative memories by long-range connections, have profound consequences for the dynamic manifestation of large-scale neurocognitive activity patterns in the cerebral cortex. The local network expresses information at any instant by exhibiting one particular functional state out of all the states that are possible (Jackendoff 1993), and this state is instantiated as a spatial pattern of activity over its surface (Barrie et al. 1996). Each local network has a range of possible states that it can enter, each manifesting a different spatial pattern of activity. The range of variability of these spatial patterns is in large part determined by the structure of the local synaptic matrix. That is, the instantaneous local activity pattern is always attracted by previously learned patterns. But the pattern that appears in the local network is not solely determined on a local basis. Local networks are in constant two-way communication with multiple other local networks. The pattern that appears in any one network depends on its interactions with the others to which it is connected (Mumford 1994). Because the connections between cortical areas are almost universally bi-directional, the situation is not that of one area imposing its pattern on another, but rather of multiple areas acting to *constrain* the pattern in each other.

Pattern constraint is a potentially powerful mechanism for the formation of novel dynamic coordination patterns in large-scale networks. These patterns are expressions of the cognitive structure existing in the local and long-range patterns of modified synapses in the cortex. Conjunctive pattern constraint among local areas is hypothesized to involve a relaxation process (Rumelhart & McClelland 1986; Churchland & Sejnowski 1994) whereby distributed collections of local area networks, connected in large-scale networks, transiently converge to mutually consistent sets of quasi-stable activity patterns (Mesulam 1994). In this process, some local networks in the large-scale network become temporarily coordinated, while others are temporarily excluded from participation in the coordination state. Furthermore, the spatial activity pattern within each coordinated local network, representing its contribution to the large-scale pattern, is temporarily stabilized. The ability to make a coherent movement or form a coherent percept may derive from this transitory large-scale pattern stabilization, since the mutual satisfaction of multiple constraints can act as a powerful determinant of system behavior.

Relaxation does not lead to a fixed, permanent stable state for a number of reasons, including the recursive character of interareal interactions, the continuously changing patterns of input to the cortex, and the intrinsic instability of neuronal activity. Large-scale relaxation is not therefore a simple response to an externally imposed stimulus, but rather an ongoing dynamic process. After each epoch of activity pattern stabilization in a set of local networks, the system is capable of reorganization through the engagement and disengagement of different local networks. The large-scale coordination state of the cortex is able to evolve in time, with the potential for different sets of local networks to relax into mutually consistent states at each instant.

Some Cognitive Properties of Interareal Pattern Conjunction

The proposed mechanism of interareal pattern conjunction endows cortical information processing with certain unique advantages. First is the property of *associativity*, by which the activation of a particular pattern in one local network coactivates linked patterns in other local networks (Rauschecker 1995). This capacity is essential for joining together related information from different knowledge domains, such as in the association of names and visual images. However, this association is not merely a conditioning of one pattern by another, since it occurs within the overall framework of cognitive structures (Deese 1970). The coactivation of patterns in different cortical areas is constrained by the patterns of connectivity formed between those areas. Constraint comes about both from the specific areas that are interconnected and from the particular patterns of synaptic modification between interconnected areas. The association of patterns in two local networks is not therefore a simple stimulus-response affair, with one pattern evoking another indirect unconditional fashion. Pattern association occurs under the influence of constraints imposed by multiple interacting local networks. And because these networks are interconnected with specific topological order, the constraints operate within a structured framework. In short, association always occurs within the context of cognitive structure.

This view of cortical information processing may be helpful for understanding the neural basis of linguistic processing. Jackendoff (1994) has proposed that complementary structures, embodying syntactic, semantic, and phonological information are necessary for language comprehension and articulation. But the individual structures are not solely capable of resolving ambiguities at their own levels, and so are interdependent. Each structure constrains the form of the various linguistic components that emerge in comprehension or articulation concurrently and interactively with the other structures. In terms of the present discussion, each linguistic structure may be viewed as being incorporated in a distributed set of interconnected local cortical networks. Auditory and motor networks may be interconnected with all three linguistic networks. In this scenario, linguistic constraints are instantiated by the constraints that interconnected local area networks naturally impose on one another as they mutually resolve their states. The construction of each comprehended or articulated speech component represents the emergence of a large-scale linguistic coordination state, concurrently satisfying the constraints of the different linguistic structures.

Another advantage of pattern conjunction is the property of *dispositionality*, a characteristic of cortical function that has been extensively discussed by Damasio (1994). What this means in the present context is that the activity patterns of some local cortical networks serve a dispositional role in directing the coordination of other local networks. Local dispositional networks interact in the same way as local sensory or motor networks, but the information they provide serves to specify the composition of the large-scale coordination pattern. The recruitment of a dispositional network into a coordination pattern can thus serve to recruit additional sets of specific local networks. Each recruited set may contain other dispositional networks with the potential for recruiting even further sets. In this way the cortex may evolve through a series of large-scale coordination states. Thus, dispositional networks may significantly contribute to the ability of the cortex to manifest a temporal progression of logically connected states.

Dispositional networks in the cortex may exist at different hierarchical levels above the primary sensory and motor areas, and different areas may potentially contribute to the orderly evolution of the cortical state. The dorsolateral prefrontal cortex has been shown to play a particularly pivotal role in the mediation of cross-temporal contingencies while at the same time providing for anticipatory set (Fuster 1989). Prefrontal function may be interpreted in the present context as that of guiding the cortex through orderly progressions of large-scale coordination states. The importance of this area in regulating the temporal ordering of connected behaviors may derive from its ability to store and express dispositional patterns representing large-scale coordination of both cortical and subcortical structures. It may be optimized for this ability by its connections with several other areas, themselves having similar ability. Thus in addition to being reciprocally connected with other cortical areas, the prefrontal cortex is also connected with the hippocampus, basal ganglia, cerebellum, and pulvinar, subcortical structures which may each contribute in different ways to the evolution of the cortex through successive large-scale coordination states (Edelman 1989). Local networks within the prefrontal cortex itself may be recruited by other dispositional networks, either cortical or subcortical. Successions of prefrontal dispositional patterns may be linked in time, their manifestation coordinating the participation of large numbers of cortical and subcortical areas in the execution of specific goal-directed behaviors.

Conclusions

Activity in sensory receptor arrays has a statistical structure that must be learned by the brain by repeated sampling (Riedl 1984; Tononi et al. 1996). The synaptic matrix of the cortex accommodates this structure within itself through modification at the local level in cortical area networks and at the global level between local networks. As the cortical synaptic matrix develops and adapts to the environment, it also accommodates the structure of the internal milieu (Damasio 1994), so the external environment is never its sole determinant. Furthermore, because its own components constantly shape the activity in each other, the cortex, in a very direct way, accommodates its own structure within itself. The cognitive structures that develop in this process thus embody structure from the outside world, the body, and other cognitive structures. This means that the organism's behavior, both perceptual and motor, can never simply be a matter of responding to an external stimulus.

The interpretation of external stimuli, and the accompanying motor acts, depend on the intrinsic context provided by a cortical system of interacting local networks. Each local network may make a contribution to the larger system based on its own associative memory and its interactions with other local networks to which it is connected. The interactions lead the cortex to configure itself in particular coordination states that are mutually consistent among its component local networks. These large-scale coordination states are the dynamic manifestation of cognitive structures in the cortex. As such, they are not the representation of a reality that is separate from the individual, but rather constitute the construction of the individual's own reality.

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