Historically, much interest focused on the potential role of mammalian genitalia in promoting reproductive isolation of species. The ‘lock and key hypothesis’, for instance, proposed that genitalia are radically different between species in order to prevent interspecific mating and hybridization. A variant of this hypothesis is that bacula of different shapes elicit different responses from females during copulation, and that only species-specific stimulation will lead to successful reproduction.

How did the diverse bacula evolve then? Most recent attention has focused on the idea that rapid and divergent evolution of male genital morphology, including the baculum, is driven by sexual selection. This applies particularly to species where females mate with multiple males, as is very common among mammals. There are ways in which the baculum could influence sexual selection: for example, females might bias fertilisation in favour of males whose baculum (and penis) stimulates them most during copulation, a process known as ‘cryptic female choice’. Also, females may reliably assess male size or quality based on the baculum. Being able to assess male quality during copulation could be of particular benefit when opportunities for quality assessments before mating are limited, such as when copulation takes place underwater or underground. Baculum evolution could also be influenced by sperm competition. For example, the baculum might help deliver sperm optimally or displace the ejaculates of rival males. By supporting prolonged intromission after ejaculation, a baculum might also help males to reduce the risk that females will mate again with others.

Is there evidence for these ideas? There are some indications. For instance, if a larger baculum is advantageous in sperm competition, baculum size should be greater among species with more intense sperm competition. The correlation varies between groups, as might be expected if the baculum functions differently across taxa: more intense competition appears to favour a longer baculum among rodents and carnivores, but not among bats and primates. Also, sexually selected traits may show high phenotypic variance relative to non-sexual traits and scale positively in relation to body size. Indeed, in the muskrat (*Ondatra zibethicus*) large males have relatively larger bacula than small males and baculum traits (especially width) are particularly variable between males. However, high levels of variation and positive allometry are not necessarily a consequence of sexual selection. Baculum morphology has also been linked to male social status in the bank vole (*Myodes glareolus*). Dominant males have wider bacula than subordinates relative to their body size, which might at least partly explain the superior success of dominant males in sperm competition.

Do females have something similar to the baculum? Females do indeed have a homologous bone, the baubellum or *os clitoridis*, which is present in the clitoris of most if not all species with a baculum. It is usually a small bone with the appearance of an underdeveloped baculum, but it can sometimes be relatively large, as in the ring-tailed lemur (*Lemur catta*) where the baubellum is nearly half the length of the baculum. Unfortunately, even less is known about the baubellum than about the baculum…

Where can I find out more?

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Primer

Behavioral architecture of the cortical sheet

Rodney J. Douglas and Kevan A.C. Martin

The effortless ability of vertebrates to explore and exploit their environment is strongly correlated with the evolution of the most anterior part of their nervous system, the forebrain, where data from autonomic (visceral), limbic (emotive), and internal and peripheral sensors of the external world are combined to develop, decide, and deploy advantageous behaviors. The correlation of behavioral performance with forebrain expansion suggests that evolution has discovered the developmental means of building vertebrate brains to produce a scalable, special-purpose architecture for efficiently processing and expressing behavior. In mammals, the exuberant expansion of this forebrain is dominated by the growth of their cortex — the two-dimensional sheet that is the major source of their intelligent behavior, especially for primates.

The complexity of the brain is so overwhelming that at every level investigators have been forced to focus only on particular aspects of its evolution and development, or its structure and function, or the behavior it generates. However, over decades all these individual brushstrokes have accumulated to produce a surprisingly coherent and conceptually simple picture of the interrelationships of evolution, development, and brain organization to produce what we call here, the ‘behavioral architecture’ of the cortical sheet. In this primer we locate our current state of knowledge in a single conceptual framework that unifies these seemingly disparate fields of investigation. We show that while the relations between different parts of the sheet may be complex, they are not arbitrary, not least because the actual physical organisation of the cortical sheet itself defines a coherent logic by which effective

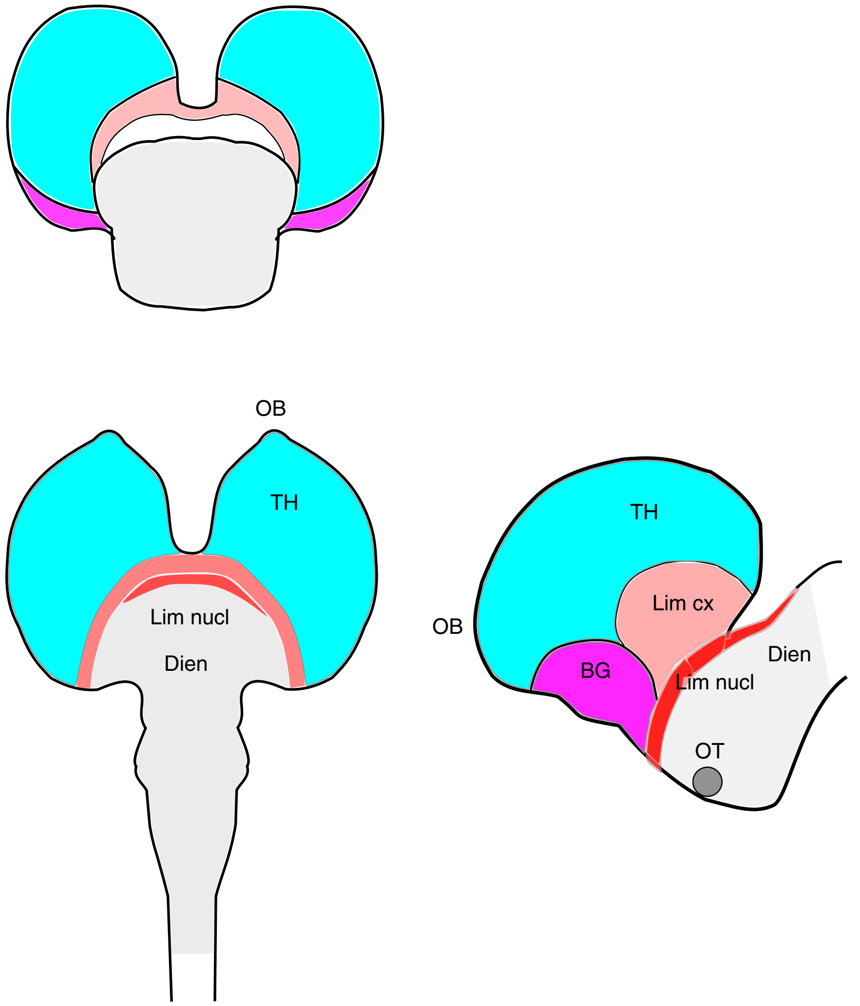

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Figure 1. Development of the forebrain in the mouse.
Schematic representation of the embryo at about embryonic day E13, showing the dramatic enlargement and elaboration of the anterior neural tube (adapted from Puelles, 2000). Top, transverse aspect; bottom left, dorsal aspect; bottom right, medial aspect. Cyan: pallial, presumptive cortical components of the telencephalon hemispheres (TH). Magenta: subpallial presumptive basal ganglionic components (BG). Light brown: limbic cortices (lim cx) and limbic nuclei (lim nucl). Grey: diencephalon (dien) and more caudal brainstem. OB: olfactory bulb. OT: optic tract.

behaviors can evolve and be expressed.

Development of a behavioural processor

The organization this behavioral processor can most easily be understood in terms of its development (Figure 1). The nervous system of vertebrates develops from a segmented axial neuroepithelial tube. The bilateral dorsal (alar) plates of this neural tube give rise to neuronal circuits that are predominantly sensory in the quality of their processing, whereas the bilateral ventral (basal) plates give rise to motor ones. The neural circuits of the more caudal segments of the tube are stereotyped on the spatial scale of segments, but their organization is profoundly modified in the rostral region where the tube gives rise to the forebrain. Here, the axially symmetric organization of the tube is replaced by a radial organization centered on the rostral end of the tube. This modified co-ordinate frame induces complex morphogenetic interactions between the segmental circuit organizers, and so yields the elaborate structure of the forebrain.

The forebrain has two major subdivisions: the more rostral telencephalon, and the more caudal diencephalon. The telencephalon gives rise to two bilaterally symmetrical fronto-lateral out-pouchings, the telencephalic hemispheres (Figure 1, below right). The dorsal telencephalic ‘pallium’ in mammals forms the three-to-six layered cortical structures, while a smaller, more ventral ‘subpallium’ forms various nuclei and structures like the basal ganglia. The diencephalon includes the thalamus, the nuclei of which form bidirectional connections with all regions of the neocortex, and which forms a crucial component in cortico-basal ganglia interactions.

In mammals, the forebrain’s expansion is dominated by the disproportionate increase in the pallium. The bulk of the pallium forms a cortical sheet of neurons that is the characteristic six-layered neocortex. It is ringed by various evolutionarily older three-to-six layer cortices that transition between the archaic nuclei located in the ventro-medial telencephalon and the more recent neocortex. There is continuing controversy over the roles and interactions of these older ‘limbic’ cortices and nuclei. For example, the various regions of this ancient ring have been implicated in emotion and evaluation (anterior cingulate); self-awareness (posterior cingulate); spatio-temporal episodic memory (hippocampus); emotional memory (amygdala), and even consciousness (insula). There is little doubt that these structures provide emotive and evaluative coloring of the forebrain’s input, cognitive processing and actions, and that they both motivate and constrain agent behavior. Rising as a great balloon from this discontinuous ring of limbic structures and paralimbic structures is the more regularly connected neocortical sheet with its systematic interactions with basal telencephalic and thalamic nuclei. It is on the organization of this sheet that we now focus.

A cortical sheet for computation

The forebrain is a striking example of a computing ‘technology’ in which organisation is tightly linked to function. The cortical cerebral hemispheres have evolved with increased processing capacity for the ‘teleceptor’ senses of olfaction, audition and vision, which permit the animal to interact with distal space, rather than reacting only to surface and internal stimuli. The ability to interact with distal space brings with it the need for long-range task and movement planning, as well as the requirement that these plans be executed economically in terms of resource accumulation versus cost. The growth in area of the rather uniform neocortex appears to support increasing sophistication of these functions. Although the cortex is folded in three dimensions, it can be unfolded in essentially a two-dimensional sheet surrounded by discontinuous 'patches' of limbic structures (Figure 2). The different functions of the cortical sheet must be distributed across its area rather than through its volume, and so there is large number and a great heterogeneity of functions, each of which is predominantly localized to some region of the sheet.

We suggest that these functions of sensory, motor and cognitive processing are organized across the computational sheet of cortex on two simple axes (Figure 2; Figure 3). The antero-posterior axis encodes the spatiotemporal scale of the agent's interaction with the environment, while on the orthogonal axis plans are composed laterally and evaluated medially. These planar axes are of course complicated by their structure in three dimensions. For example, the medio-lateral axis that begins at the cingulate cortex, wraps around the lateral aspect of the cerebral hemisphere towards the more medial parahippocampal gyrus. Also, there are many anatomical distortions that have occurred as the forebrain has expanded through evolution. For example, the greatly recurved outgrowth that is the temporal lobe of primates causes the evolutionarily more caudal nuclei of the pallium, such as the amygdala) to be swept forward in the rostral pole of the temporal lobe ('uncus', Figure 2).

A convenient origin of our antero-posterior axis is the central sulcus (horizontal red line, Figure 3). From there, the spatial scale of the animal's perception of the environment increases in a posterior direction, whereas the temporal scale of its action in those spaces increases anteriorly. Thus, the somatosensory areas, which lie immediately posterior to the central sulcus, process sense data arising from the current state of receptors in our skin, muscles, and joints. More posteriorly, the auditory cortex detects self-generated sounds and sounds originating from more distant sources. The most posterior regions of the cortical sheet process sensory data arising from the 'teleceptors' of the retina. The visual sense can detect objects and events that are the furthest distant from us (and which in terms of their impact on us, are also furthest removed in time).

Thus, as we move from the central sulcus towards the most posterior areas of the cortical sheet, we move from the processing sense data arising from the most proximal to the most distal regions of sensory space. The primary motor cortex, which provides the output for the skilled movements that are currently being executed, lies anterior to the central sulcus and adjacent to the primary somatosensory area. Lying anterior to primary motor cortex are the premotor areas that plan future movements. Yet more anteriorly are the areas of prefrontal cortex, which have expanded greatly in primates, especially man. These areas are crucial for key aspects of higher cognitive functions, such as planning,

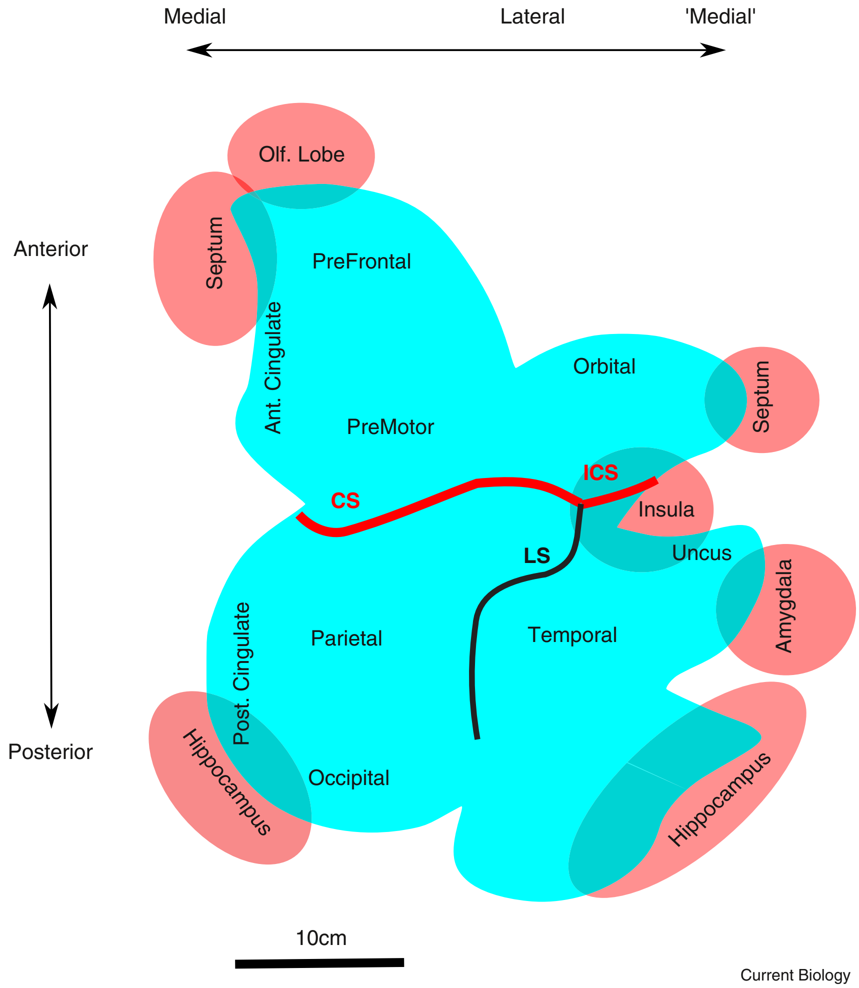

Figure 2. Adult human cortical sheet.
Schematic representation of the flattened cortical sheet of the right cerebral hemisphere and some of its related structures (adapted from van Essen and Drury, 1997). Cyan: cortical sheet; relevant limbic structures shown schematically as light brown blobs. The central sulcus (red, CS) and inferior-central sulcus (red, ICS) divide the sheet in the coronal plane. The highly convoluted and approximately hemispherical cortex has been flattened by making a few relieving cuts to preserve as far as possible the true relative sizes and major spatial relationships of cortical areas. The temporal cortex is separated from the more medial cortex by the prominent lateral sulcus (black, LS). In three dimensions, parts of the temporal and orbital cortex and the limbic components fold back under the cortical plate so that the divided septum and hippocampus in fact form continuous 'medial' structures.

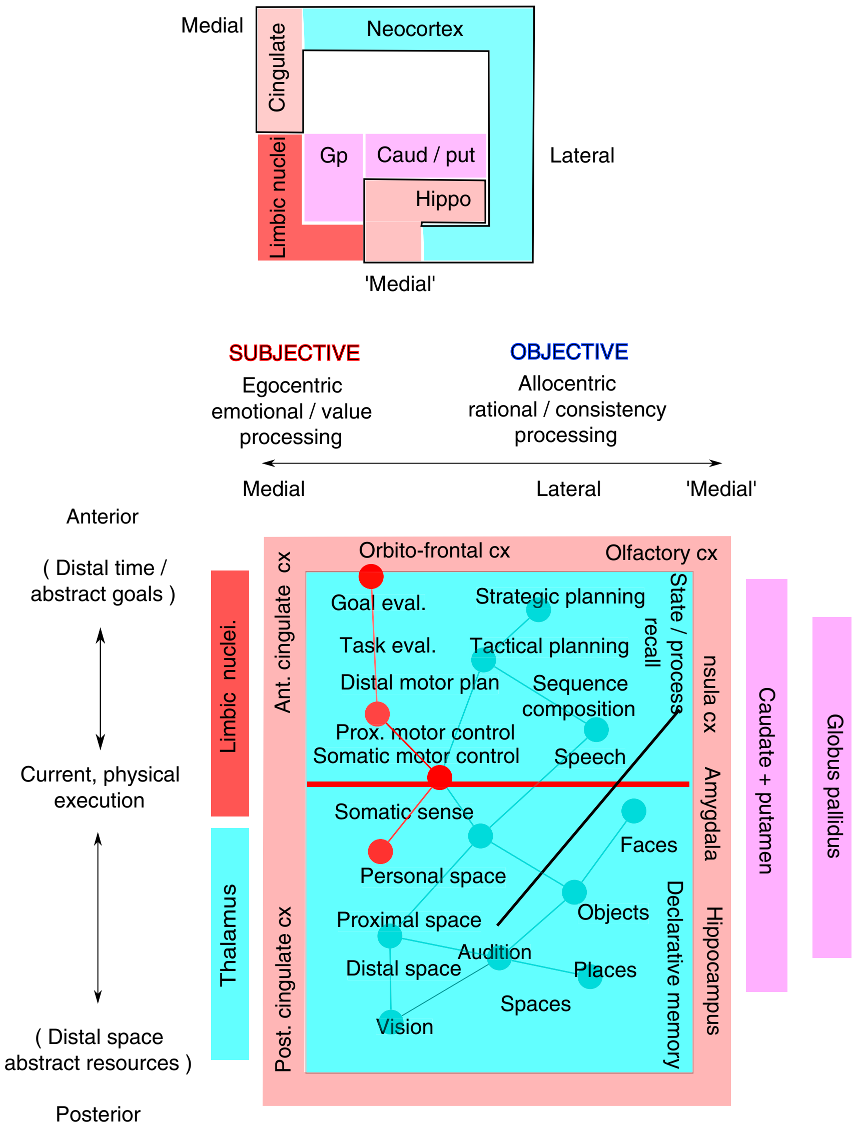

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Figure 3. Functional organisation of cortical sheet.
Schematic showing functional organization of cortical sheet of the right hemisphere and some of its related structures, Above: transverse section shows how the sheet folds in three dimensions, so that limbic nuclei, basal ganglia (gp, globus pallidus; caud/put, caudate and putamen), and hippocampus (hippo), come to occupy more 'medial' positions, interposed between the neocortex and the medial telencephalon and diencephalon beneath (not shown). Below: unfolded in plan view, the cortical sheet (cyan) is surrounded by limbic cortices (brown, e.g. cingulate cortex, insula) and their associated nuclei (red, e.g. septal nuclei, amygdala). The concept presented here is that the components of behavior are systematically distributed across this regular sheet. Around the central sulcus (thick red horizontal line) processing relates to the direct and immediate engagement of the agent with its environment. The more anterior cortex processes potential action repertoires, plans and goals that extend forward in time, whereas the more posterior cortex processes space, which extends progressively further from the agent (and so also further into future planning time). The temporal lobe encodes objective structures such as places, objects, and faces. This lobe is greatly enlarged in primates, including humans, and is intimately related to the declarative memory functions involving the hippocampus. The emotive subjective signals of the limbic cortices color/bias the processing of the evolving plans of the more medial areas. More lateral cortical areas are relatively isolated from these colorings and process alternative action sequences and spatial structure in a more semantically and syntactically objective manner. Dynamically evolving behaviors are represented schematically as graphical structures composed of 'nodes', the regions of active processing, and 'edges', which represent the axonal communication channels between active nodes. The channels act directly through cortico-cortical connections, or indirectly via thalamus and basal ganglia. Multiple behaviors may evolve simultaneously (green graph, see text), while the red graph represents the various functional relations of the behavior currently being executed.

evaluation of future actions, selective attention and decisions.

In this analysis, the central areas of the cortical sheet are largely concerned with events and objects appearing in present time, while the anterior areas are concerned with events over much longer time scales, ranging from the immediate present to the distant past and possible future. In this way, the spatio-temporal organization of the perceptions and actions that support behavior are systematically distributed across the cortical surface. Consequently, the 'hierarchical' nature of behavioral scale from future planning down to the details of the current implementation is directly encoded as locations in the space of the cortical sheet.

The relevance of the spatial organization on the cortical sheet is that anatomical constraints on local and remote connectivity of neurons now have a direct interpretation in terms of the structure and dynamics of evolving and competing covert and overt behaviors. This is an extraordinarily important insight, because it implies that the world semantics are systematically encoded in cortical space, and this in turn raises deep questions about the structural and functional architecture of the processing sheet. It is important to note, however, that because there is a simple spatial organization of function it does not mean that a behavior is localized to a single region on the sheet. Instead, the various aspects of a coherent behavior can be seen as the functional co-ordination of several or many different regions of relatively localized processing.

Evidence for such co-ordination is seen, for example, in the motor cortex, which was once thought to implement a homunculus-like organization in which activation of micro-regions lead to the activation of specific muscle groups. More recently it has become clear that appropriate stimulation of micro-regions of the motor cortex can elicit individual complex action sequences drawn from a repertoire of behaviorally relevant sequences that involve multiple muscles. On a larger scale, the areas of motor cortex are interconnected with parietal and prefrontal areas. In this way the evolving motor sequence is constrained by a larger context that involves matching actions to objects (for example in grasping) by the parietal cortex, and sequencing the actions of a planned task by the prefrontal cortex. Further dynamics arise through the interactions with subcortical structures such as the basal ganglia, which steer, reinforce, or veto behaviors.

The prefrontal cortex (PFC; Figure 2) plays an important role in cognitive evaluation, decision-making and task control in relation to abstract goals. The more medial PFC is closely associated with the limbic anterior cingulate cortex, which expresses affect and motivation, while the more rostral orbito-frontal cortex is engaged in selecting large-scale behaviors under the constraints of appetitive and aversive social, emotional, and material stimuli. By contrast, the more dorsal regions of PFC are engaged in resolving constraints on less emotive cognitive dimensions such as form, location, order, and pattern. The inferolateral PFC, either alone or in concert with the hippocampus, may provide a repertoire of partial solutions that supports the dorsal PFC.

Thus, in the prefrontal association areas the medial-lateral axis of the cortical sheet links limbic evaluation (“WHY?) to appropriate behavioral procedure (HOW?). In the post-central parietal association areas it is the constraints on actions in space (WHERE?) that are at issue. More laterally down the extent of the temporal lobe, the domain is of objects in that space (WHAT/WHO?), while a long-term repertoire of their partial relations is established as episodic memories by the hippocampus.

Composing behaviours

The neural correlates of a given ‘behaviour’ can be seen as an evolving assembly, composed of the relevant regions on the cortical sheet. For example, a behaviour playing out on the cortical sheet may be composed of distant stimuli perceived by vision and hearing, which are resolved by multisensory integration in higher-order processing regions in sensory cortex to be a familiar object located in a certain region of external space. This goal-specific spatial information in turn combines synergistically with the development in the premotor cortex of a motor tactic for acquiring the object. These tactics, however, are themselves constrained by values computed on the anterior cingulate cortex, and by strategic goals being processed in the orbitofrontal cortex. Thus, the different aspects of the same behaviour are distributed across the sheet. The processing in regions distant from the sensorimotor areas at the middle regions of the sheet (located around the central sulcus) are in planning space, for unlike the central regions, they do not control current actions. Consequently, different potential behaviours, possibly with conflicting requirements and outcomes, can be processed concurrently in those more distant regions of the sheet. As the implications of these different potential behaviours approach the more central regions, they must be resolved by competition. Finally, it is only at the central regions of the sheet that the motor actions of the ‘winning’ behaviour must be exclusive and consistent.

In our view, the pattern — or graph, for example the linked green dots in Figure 3 — of interacting regional activities across the sheet has a direct interpretation in terms of the composition of behavior. This distributed, concurrent view of cortical behavioral processing runs counter to the more localized models promoted by the thresholding analysis methods of functional magnetic resonance imaging (fMRI). It also runs counter to psychological and philosophical models of human (and animal) behavior that attribute intelligent action to a single sentient agent — a ‘homunculus’. Such models neglect how brain computation must inevitably be a physical process, occurring in real time and cohering across physical space. Brain computation is carried out in the face of strong constraints: on the information transformations available in its processors, on how state is stored, errors corrected, messages communicated, and bandwidth requirements satisfied. In the context of these constraints, biology has found in the forebrain a self-evidently excellent solution for capturing relevant knowledge and performing approximate inference in real time at a performance level far beyond current technologies. The solutions indicate a number of key strategies and constraints underlie the organization and function of the cortical sheet.

Although the forebrain may be responsible for generating the impression of unity of self and purpose by its generation of coherent external actions, this apparent unity is at variance with its complex structural and functional organization. Neuronal processing in the forebrain is at any moment widely and inhomogenously distributed across fields of neurons that are only sparsely connected to one another. Therefore, our model of observed and experienced behavior is of concurrently active and competing agents dynamically composing their various agendas, while yielding to the dominant agent only in the short spatiotemporal scale of the actual physical execution.

Constraints of connections

The exact axial organization of the various functional fields of neurons on the cortical sheet appears crucial to the generation of coherent behavior, because the organization of the forebrain is highly conserved and scales up across higher mammals to primates to provide increased cognitive performance. This elegant relationship between organization and function might be considered only a biological nicety, were it not for the fact that the biological forebrain provides substantially more intelligence than the most advanced computing technology. Currently two very different strategies are being applied to explain brain function. One school favors detailed ‘bottom-up’ reconstruction and simulation of neuronal circuits, the other school favours ‘top-down’ abstract mathematical models of reasoning such as Bayesian inference, with little regard for the details of brain circuits. The concept of the cortical sheet offers instead a ‘middle-out’ approach that relates anatomical structure and neuronal function to actual performance — the key links that lead directly to the principles and technology of ‘neural engineering’. Because the architecture of the neuronal circuits must satisfy the physical constraints necessary for coherent (behavioral/cognitive) processing, we need to understand how the permissible patterns of activation on the sheet are constrained by the actual spatial organization of the sheet.

A long-standing view is that the cortex is composed of a hierarchy of interconnected areas each providing some specific processing, with increasing complexity of responses as one moves up the hierarchy. In vision, the discovery that some neurons in the temporal cortex of humans respond selectively to famous faces — for example, the ‘Jennifer Aniston Cells’ — provided strong encouragement for this view. But the hierarchical model ignores the actual nature of the connections between cortical areas. Very recent data from the primate brain now offer a radically different view of the rules whereby the cortical sheet connects. The cortical sheet in macaque monkey is over 60 mm in diameter, whereas the distribution of axonal lengths of the neurons that connect different cortical areas has a spatial decay constant of only about 12 mm, indicating that most broadband cortical connections are rather local, and that high bandwidth long-range connections are improbable.

The surprising restriction of broadband direct cortical connections to short distances suggests that these distance-density relations are key to understanding diverse aspects of cortical architecture, including area formation and cortical folding. Moreover, they raise fundamental questions about the localization of processing on the cortical sheet. Is the restricted range of direct broadband connections on the cortical sheet required for richer processing by virtue of permitting more independence between cortical regions? If so, what is the computational trade-off between locally coupled and the more remote uncoupled processing? This raises further questions of why more intelligent animals, which generally have the largest cortices, may also have the most independent regional processing.

Constraints of brain size

It is often said on good evidence that the brain has a scalable architecture. Within taxons brain size can vary over a factor of 100, and even the size of the human brain can vary over a factor of four. The neocortical sheet occupies a larger and larger fraction of the brain as we move from carnivores (40%), to monkeys (53%), apes (76%), and humans (80%). Although the evolutionary antecedents of the mammalian neocortex are the subject of current debates, it is clear that mammals, especially humans, have been particularly advantaged by the flexibility the neocortex offers. The fossil record shows that the size of the hominim brain has increased three-fold in three million years, so that modern humans now possess a brain that is three times bigger than it should be if scaled for a primate of our body weight. Comparative studies also show that primate brains are not simply inflated versions of rodent brains, but show differential increases in key regions, especially neocortex. Human brains show significant differences even compared to our closest hominid relations, the chimpanzees.

Because brain size scales with body weight, the area of the cortical sheet can vary enormously simply due to an animal’s absolute size. The change in the size of the sheet poses the question whether an exponential distance rule is scalable for different brain sizes? Recent evidence suggests that interconnectivity across the cortical sheet in primates *decreases* with increasing brain size, although these studies have been limited to how cortical grey and white matter scale with size. The measurements show that the white matter volume reduces relative to grey matter as the brain enlarges. Hence, long-distance connections apparently decrease in number in the larger brains, or are lost altogether. This scaling effect has important consequences for a wide range of theories concerning organizational principles of the cortex, ranging from areal specialization to wire minimization and cortical folding. As a decrease in the effects of long-distance pathways in the large brain could degrade the network performance, this may be one explanation of the vulnerability of the human brain to degenerative diseases.

Conclusion

Our view is that the rapid evolutionary expansion of neocortex has been made possible by building an ‘isocortex’ — a structure that uses repeats of the same basic local circuits throughout a single sheet. The connections between these local cortical and their subcortical partners determines the overall computational architecture of a particular cortical sheet of a given species. This strategy allows both the conservation of the basic functional architecture and computational principles on the cortical sheet as it changes size and provides a ready means of expanding old cortical areas or intercalating new cortical areas as animals evolve and adapt in new environments. While current research efforts are devoted to developing ‘high-throughput’ methods to reconstruct tiny volumes of brain at synaptic resolution, there is the equally great challenge of synthesising the huge amounts of data arising from structural, physiological, and behavioral studies that altogether sample the brain at many different levels of resolution. The concept of the cortical sheet provides a unifying framework and a clear logic for connecting these different levels of expression of structure, function and behavior.

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