Modular Subdivisions of Dolphin Insular Cortex: Does Evolutionary History Repeat Itself?

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Abstract

■ The structural organization of the insular cortex in the bottlenose dolphin was investigated by examining Nissl- and myelin-stained tissue that was sectioned coronally and tangentially. An uneven distribution of cell clusters that coincided with myelin-light zones was observed in layer II. When the present observations were compared to descriptions of modules in other animals, we found that the range of module size is restricted, while the size of the brain, particularly the neocortex, varies dramatically. Indeed, despite the tremendous expansion of the cetacean neocortex, the size of the modules in the insular cortex is similar to that described for small-brained mammals like the mouse, suggesting that module size is evolutionarily stable across species. Selection for optimal-size processing units, in terms of the lengths of connections within and between them, is a likely source of this stability. ■

INTRODUCTION

The notion that the neocortex is divided into functional parts was popularized almost a century ago by Brodmann (1909). Architectonic analysis of cerebral cortex in a variety of mammals led Brodmann to divide the neocortex into separate fields, or areas. For decades the belief that these cortical areas are the building blocks of processing networks has persisted. Investigators have attempted to subdivide the cortex into major functional parts and to construct intricate networks involving feedforward and feedback connections between cortical fields (Kaas & Krubitzer, 1991; Van Essen, Anderson, & Felleman, 1992). Others have striven to understand how single neuron firing patterns in sensory, association, and motor areas of the cortex interface with these global networks and translate incoming sensory inputs into perceptions, cognition, memory, and learning. The difficulty of explaining psychological processes at a cellular or cortical network level suggests that analysis at an intermediate level of organization may be necessary.

Accumulating evidence indicates that within cortical fields, smaller units of construction are evident and are generally referred to as modules. Cortical columns or modules were first described by Mountcastle (1957) as an "elementary unit of organization of the somatic cortex made up of a vertical group of cells extending through all cellular layers." The module described by Mountcastle (1978) was not a fixed structure in the cortex, and he proposed that the cortex should "not be regarded as a collection of isolated units cemented together in a mosaic."

Recently, the term *module* has been used more variably to refer to a number of configurations of horizontal or tangential cell clusters that do not necessarily traverse all cortical layers, and even Mountcastle has proposed a modified rendition of his original thesis (1997). We define modules as small architectonic, neuroanatomical, and physiological territories that can be distinguished from other tissue within the classically defined cortical field. These types of tangentially distributed modules within a cortical field are exemplified by the barrels of the primary somatosensory area of rodents (Woolsey & Van der Loos, 1970) and by the blobs of the primary visual area of primates (Livingstone & Hubel, 1984).

Modules have been identified across species and across sensory systems (Krubitzer, 1995). Unlike cortical fields, they possess a uniformity in structure (Löwel, Freeman, & Singer, 1987; Purves, Riddle, & LaMantia, 1992), interconnections (e.g. Livingstone & Hubel, 1984; Krubitzer & Kaas, 1989), and neurophysiological properties (Hubel & Wiesel, 1963; Livingstone & Hubel, 1984; Sur, Wall, & Kass, 1984; Ts'o, Frostig, Lieke, & Grinvald, 1990). They can be induced to form in development (Constantine-Patton & Law, 1978), are susceptible, within limits, to environmental influences (Hubel & Wiesel,

1970; Durham & Woolsey, 1984; Löwel & Singer, 1992), are computationally predictable (Mitchison, 1991), and may better explain cortical evolution than the cortical field (Krubitzer, 1995). These structures contribute to the larger organization of functional divisions called cortical fields. Their ubiquity throughout the mammalian cortex leads us to question not only their function but also their evolutionary significance.

One way to address these questions is from a comparative perspective. By examining a variety of species we can ascertain similar features of organization, due to common ancestry (homology), and modifications in organization related to species specialization. More important, examining the products of the evolutionary process will allow us to understand how the mechanisms that generate change, which are governed by ontogenetic constraints, interact with selective pressures to shape the brain organization of extant mammals.

The goal of this study is to examine an animal that has a large neocortex that evolved independently from that of humans in an effort to determine if large brains are constructed in a similar fashion, independent of recent evolutionary history. The specific question we can begin to answer regarding animals with big brains, particularly humans, is how do the constraints imposed on nervous system construction affect cortical processing strategies and in turn the complex neural and morphological specializations associated with our species.

METHODS AND RESULTS

In the present investigation, the entire brains of two bottlenose dolphins (*Tursiops truncatus*) were removed and fixed, postmortem, in 10% formalin for approximately 2 years. These brains were cut into 1-cm slabs in either a frontal or a sagittal plane. From these slabs, the region of cortex termed the insula (Morgane & Jacobs, 1972) was dissected free from the remainder of the brain slab (Figure 1). The particular region investigated histologically was located at the anterior portion of the insula and termed the anterior insular area, or Ia (Jacobs, Galaburda, McFarland, & Morgane, 1984). This area was found to overlay the claustrum, as does the insula in primates. In the dolphin, however, this portion of cortex surrounds the lateral edge of the thalamus and the inferior portion of the basal ganglia, which resides just ventral to the ventral thalamus. It is not known whether the insular regions in dolphins and primates are homologous. These lineages are separated by over 85 million years of independent evolution (Archibald, 1996), and little is known about the insular cortex of sister groups. For both specimens, the insula of the left hemisphere was sectioned in the frontal plane, and the insula of the right hemisphere was sectioned tangential to the cortical surface. The insula was cut at a thickness of 50 μm and alternate sections were stained for Nissl substance or myelin (Gallyas, 1979).

Microscopic and macroscopic examination of the stained frontal sections revealed four architectonic subdivisions of the dolphin anterior insular cortex. The present study concerns the largest and most distinct of these architectonic fields, Ia, which has an area of approximately 900 mm^2 (60 mm mediolateral, 15 mm anteroposterior). Within Ia, an irregular clumping of cells in layer II was observed (Figures 2A and 3).[1] This clumping was markedly different from the laminar patterns observed in other regions of the insula (Figure 2B). The cell clusters in layer II ranged in size from 125 to 450 μm in diameter and had a mean diameter of 255 μm. The prominent cells within the layer II clusters were vertically oriented pyramidal cells, with somas approximately 10 to 12 μm wide. However, smaller cells were abundant in these clusters, the staining techniques used did not allow us to assign a particular classification to these remaining cells. Although not explicitly described, a similar clumping of cells can be observed in a previous study of the cytoarchitecture of the insular cortex of the dolphin (Jacobs et al., 1984).

Myelin stains of adjacent cortical sections also demonstrated an irregular staining. When the adjacent myelin and Nissl sections were aligned using blood vessels as a guide, it was found that the myelin-dense regions surrounded the cell clusters (Figure 4). Layer I of the region examined showed dense myelin staining. Within layer II, cortical fibers were seen to form fascicles that passed between the clumps of cells observed in Nissl-stained sections. Where there were cell-dense clumps, there was a distinct lack of staining for myelin. Fibers from layer I were observed to form bundles that passed through layer II and became less distinct in layer III. Fibers from these bundles could be seen to enter the regions where the layer II cell clusters were located (Figure 4B). Portions of the fiber bundles that passed through layer II appeared to be made up of fibers coming from deeper cortical layers.

In order to get an appreciation of the geometric arrangement of cell clusters and myelin-dense regions, the cortex sectioned tangential to the pial surface was similarly stained and examined. The extreme gyrification of the dolphin cortex and the prolonged fixation of the tissue prevented a manual flattening of the cortical sheet, as has been achieved in other mammals (Krubitzer, Clarey, Tweedale, Elston, & Calford, 1995). Some portions of the insular cortex, however, were flat enough to provide a good areal view of portions of this field. Nissl-stained sections showed that the cell clusters of layer II were patchy in their distribution and were reminiscent of the barrel cortex in primary somatosensory region (SI) of rodents (Woolsey & Van der Loos, 1970; Figures 5 and 6). The myelin pattern was similar in appearance to the myelin pattern reported for the primary visual area, VI, of some primates (Krubitzer & Kaas, 1989). In the bottlenose dolphin, myelin stains of tangentially sectioned cortex demonstrated a negative pattern to

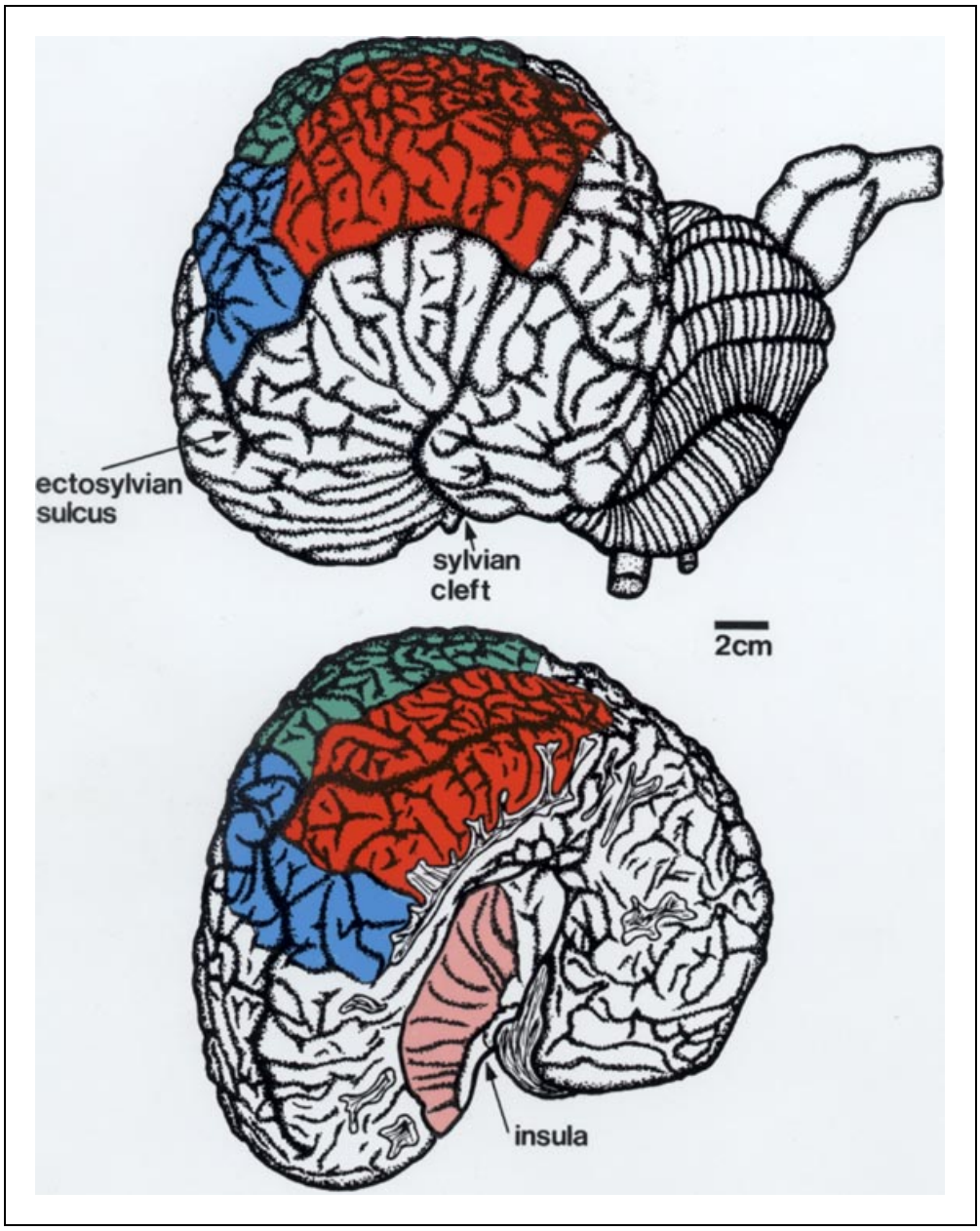

Figure 1. Lateral (top) view of the bottlenose dolphin cortex with visual (green), somatosensory (blue), and auditory (red) cortex indicated. The location of functional subdivisions relative to major sulci are taken from Bullock and Gurevich, 1979, and Lende and Welker, 1972). The insular cortex forms the floor of the sylvian fissure. In the bottom figure, the area of cortex overlying the insula has been removed, and the anterior insular region, Ia, examined in this study has been shaded in pink. In this figure dorsal is to the top and rostral is to the left.

that of the Nissl-stained cell clusters and formed a lattice-type arrangement located between the cell clusters (Figure 6). However, between one and four cell clusters were located in any particularly myelin-sparse region, rather than a perfect complementary relationship like that observed in rodent barrel cortex. This myelin lattice network in Ia had myelin-light regions with diameters on the order of 450 to 750 μm, whereas the cell clusters had diameters ranging between 125 and 450 μm.

Cortical Modules in Other Mammals

In the following section, we have compiled some of the previously published results on modular organization in other species (Table 1). We have measured these modules and generated a range of module size and a mean for a given species. We have also given the authors' measurements when they were provided (asterisk in Table 1). For example, the average size of ocular dominance columns in primates was taken directly from the studies that described them. The ranges and means for the other modules were calculated by scanning into a computer a traced line drawing of the modules from a particular study, and with the appropriate scale, the measurements of modules were obtained for 50 separate module axis using the NIH image program. In addition, where possible, we have obtained estimates of brain size and encephalization quotients (Jerison, 1982) in each species so that the size of the module relative to the total

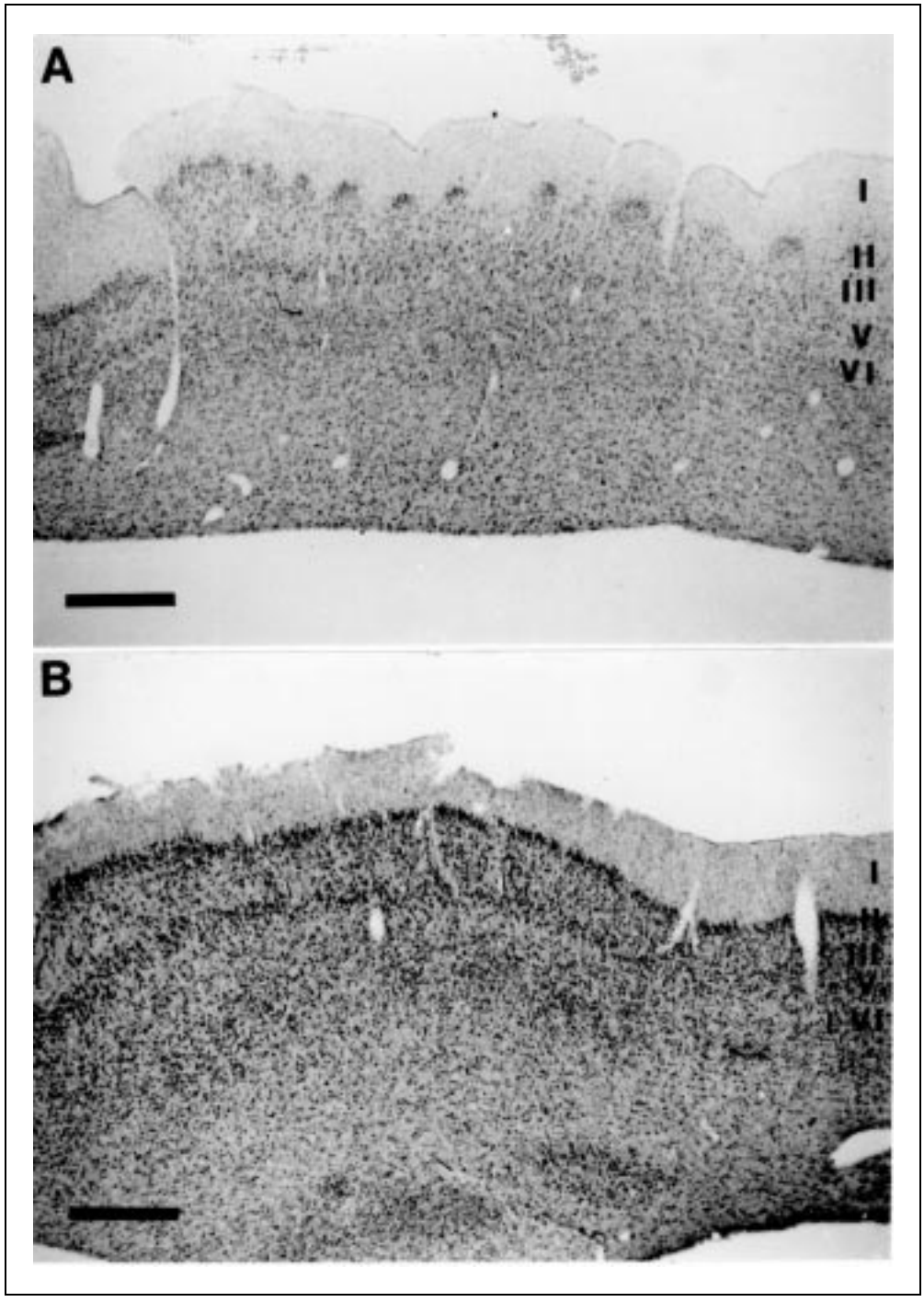

Figure 2. Light-field photomicrographs taken at low power from the dolphin anterior insular cortex (A) in which the clumping of cells in layer II is striking. In a neighboring region of insular cortex (B) the cell layers are distinct, but a conspicuous clumping of cells in layer II is absent (B). Cortical layers are marked at the right of each photograph and are taken from Jacobs et al., 1984. It should be noted that a distinct layer IV has not been identified, and it is still uncertain how the layers in the dolphin neocortex relate to the lamina in the neocortex of other mammals (e.g., see Revishchin & Garey, 1991). Scale bars equal 1 mm.

size of the brain could be appreciated. The measurements provided in Table 1 are for descriptive purposes only and were not subject to extensive statistical analysis. Our list is not exhaustive, but it provides a good survey of the information available on module and brain size.

Examination of the measurements from our own and other studies indicates that several similarities exist (Table 1). The most noteworthy of our observations is that the size of these cortical modules in the different species appears to vary less than the size of the brain. There is no obvious relationship between module size and brain size, and there appears to be no relationship between the encephalization quotient and module size. Thus, both the smallest and largest brains have modules that are of approximately the same size. For instance, the modules in the mouse barrel cortex (mean of 165 μm) and in the dolphin insular cortex (mean of 255 μm) vary by a factor of 1.6, whereas the size of their brains vary by a factor of over 3000 (Table 1 and Figure 7). Of course, this is an extreme example, but the uneven ratio of module size to brain size is clear from all examples listed in Table 1.

A second observation is that within a particular spe-

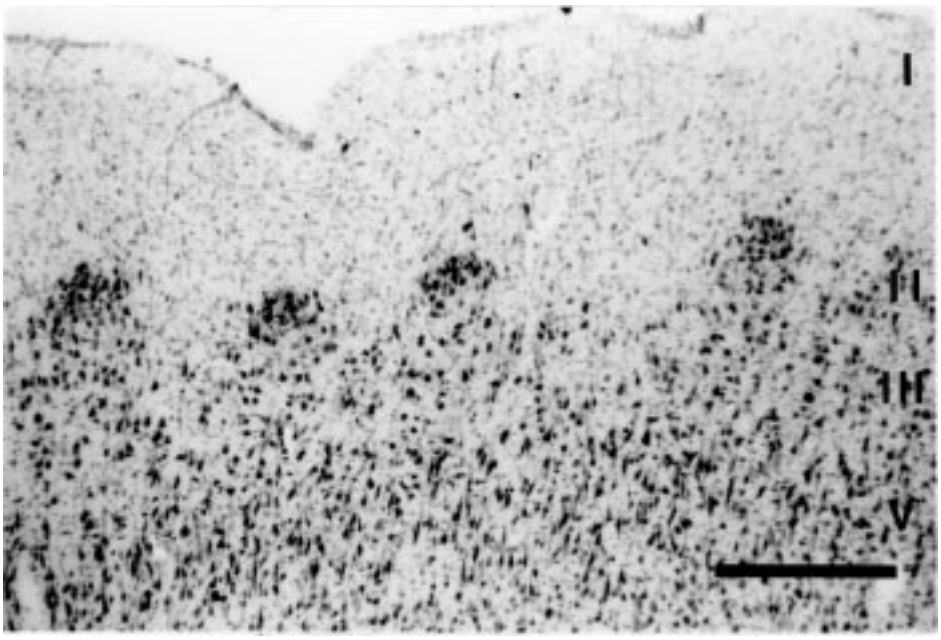

Figure 3. A light-field photomicrograph through layers I through V of the anterior insular cortex. The clumps in layer II contain a number of pyramidal cells. The layer immediately below layer II, the presumptive layer III, contains no clumps and is easily distinguished from the layer below it by a reduced cell density. Scale bar equals 500 μm.

cies, the size of a module within a unified functional collection of modules (e.g., mouse barrel cortex) has as much as a sixfold range in size.

A third observation is that modules can be of two types. The first type is exemplified by the barrel cortex of rodents. In this type of module, distinct cellular clumps can be clearly identified in Nissl stains. This type of module is often identified in myelin-stained sections and with a variety of histochemical, immunohistochemical, and other anatomical techniques. Of the mammals surveyed, apart from rodent barrel cortex, the insular clusters of the dolphin described in the present study, the cluster cortex of manatees (Reep, Johnson, Switzer, & Welker, 1989), and the entorhinal clusters of humans, macaque monkeys, and rats also fall into this category. The dimensions of this type of cellular clump module range in size from 50 to 1000 μm. The second general type of module observed cannot be distinguished by Nissl-stained sections and does not show any hint of cellular clustering. However, even in the absence of morphological clustering, these cells appear to be anatomically and functionally cohesive units. This type of module is distinguished by the recruitment of nonclumped cells as evidenced by specific connectivity, and is most often delineated by histochemical staining for the metabolic enzyme cytochrome oxidase (CO). This type of CO module is observed for blobs of VI in primates, bands in VII of primates, bands in the SI bill representation of the platypus, and elongated clumps in the SI rhinarium representation of the star-nosed mole. The dimensions of this type of noncluster module range in size from 100 to 1000 μm.

A fourth observation is that cortical modules do not appear to be limited to a particular cortical layer. Some modules, such as those in the barrel cortex of rodents and ocular dominance columns in monkeys, are situated in layer IV, whereas other cortical modules are found in layers II, III, and VI. There is, however, a trend associated with the layer of cortex in which a module is found. Those in primary sensory areas, such as the barrels in rodents, ocular dominance columns in cats and primates, and CO stripes in the platypus, are mostly found in the thalamic recipient layer, IV, although this is not a general rule. For example the CO stripes in the platypus are also found in layer III, and CO blobs in primates are found in cortical layer III (Table 1). Other modules, not in primary sensory regions, like those reported for the dolphin insular cortex, manatee cluster cortex, and entorhinal clusters in humans, monkey, and rats, are found primarily in layer II but have also been reported in layers III and VI (Table 1). Thus, there does appear to be a distinction in cortical layers concerning modules; those in primary sensory areas are observed in the major thalamic recipient layers, and those not in primary sensory areas tend to be in other cortical layers. Further analysis of the dimensions of modules grouped into these two divisions do not show notable differences. Modules mainly associated with layer IV range in size from 50 to 1050 μm. For modules in other layers, the range in size is 125 to 1400 μm.

The fifth observation concerns the function of cortical modules. Many of the modules reported have been located in primary sensory areas, particularly visual and somatosensory areas. However, modules have been reported for nonprimary visual cortex (e.g., Krubitzer & Kaas, 1989), electrosensory cortex (Krubitzer, Manger,

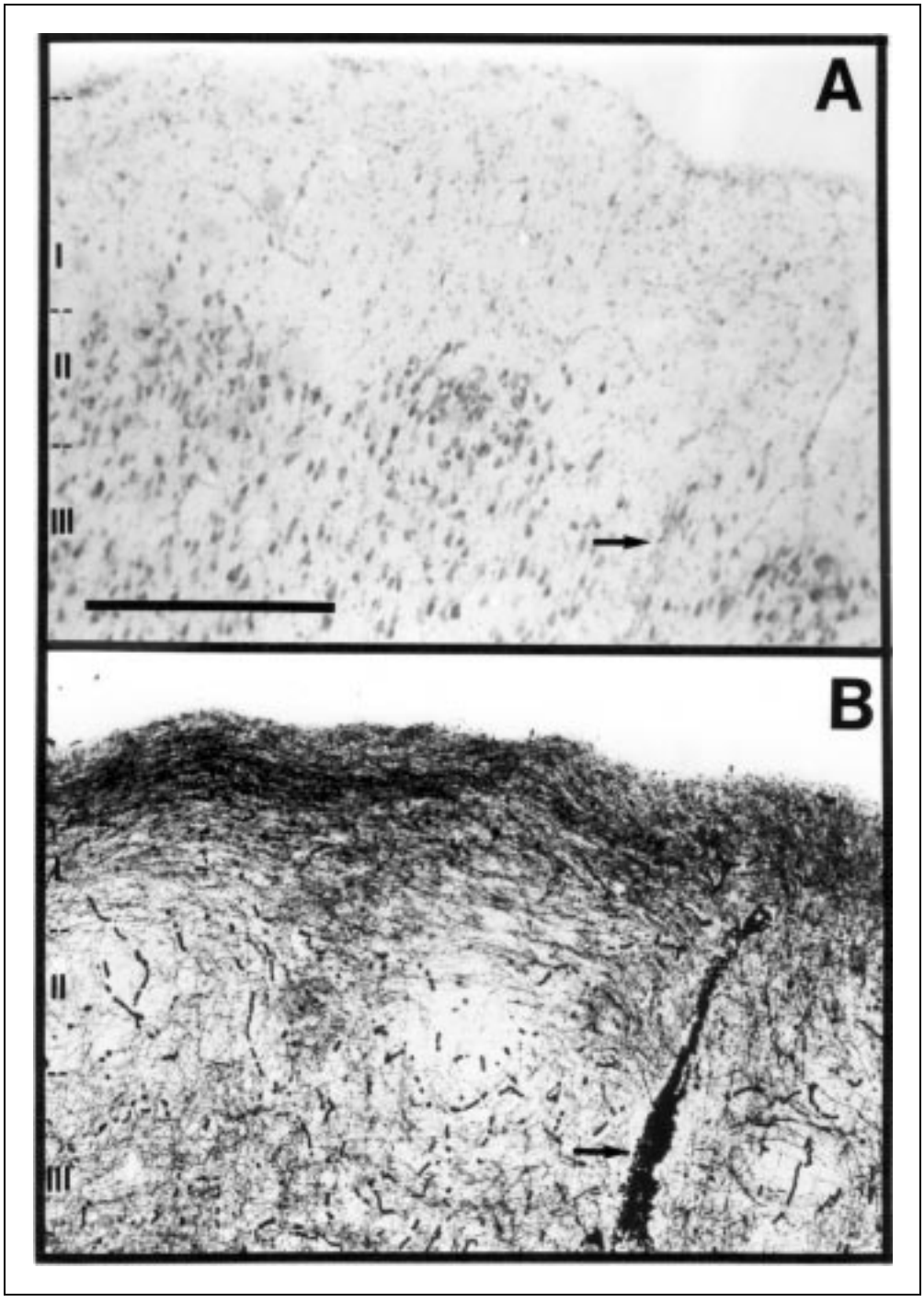

Figure 4. A high-power, light-field photomicrograph of a coronal section through the insula, in which the tissue has been stained for Nissl (A), and the adjacent section stained for myelin (B). Note the heterogeneous staining of cells in layer II. These clumps of cells are composed primarily of pyramidal cells, and they range from 125 to 450 μm in diameter. The myelin-stained section in B was photographed at the same magnification as the Nissl-stained section in A. When blood vessels and tissue artifacts (arrows) are aligned, it is found that the myelin forms a negative pattern of the cell clumps. Thus, the cell clusters are aligned with the myelin light regions. In A, layer I is cell sparse, and in B, layer I is myelin dense. Scale bar equals 500 μm.

Pettigrew, & Calford, 1995), auditory cortex (Middlebrooks et al., 1980), and entorhinal cortex (Hevner & Wong-Riley, 1992). Thus, modules are not restricted to a particular sensory system, and module size is not affected by the sensory system with which they are associated. For instance, the modules that subserve somatosensory functions range in size from 50 to 1000 μm, the modules that subserve visual functions range in size from 180 to 1400 μm, and the modules that subserve memory-related functions range in size from 150 to 800 μm.

In summary, cortical modules, regardless of the criterion used to define them (i.e., architecture, histochemistry, cortical layer, or function), do not show appreciable differences in size, despite the dramatic difference in brain size.

DISCUSSION

There are two important findings of the present investigation. First, although morphological and histochemical

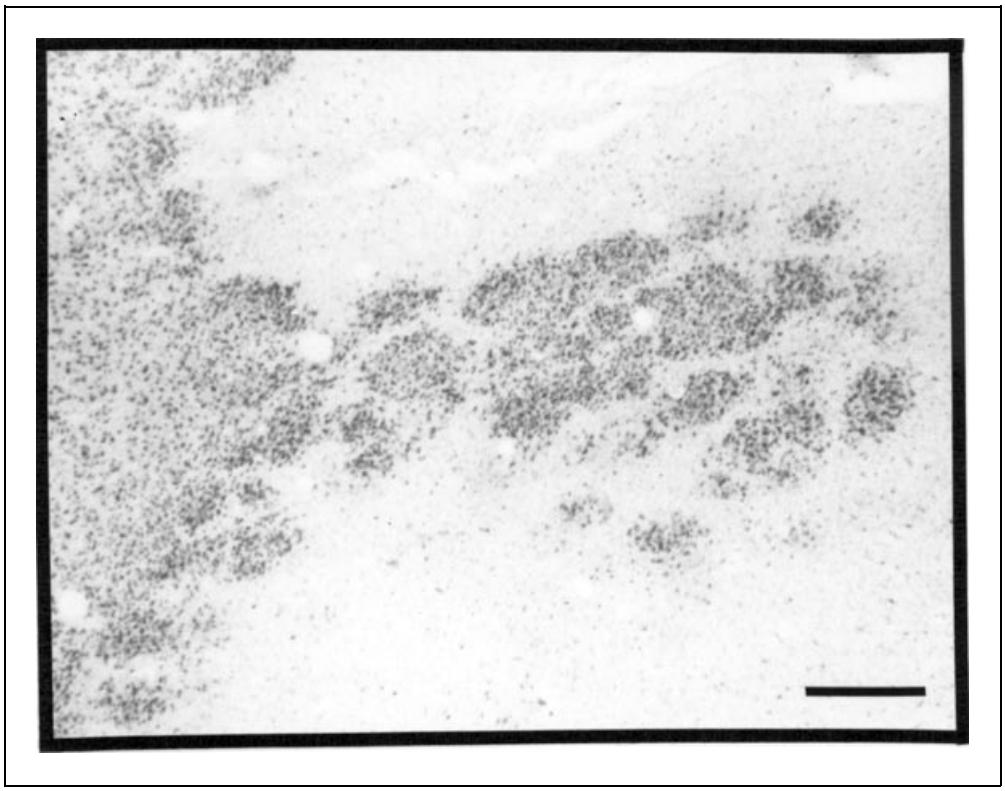

Figure 5. A light-field photomicrograph of the cortex cut tangential to the pial surface and stained for Nissl. The Nissl stain reveals cell-dense clumps in layer II that range in size from 125 to 450 μm. Scale bar equals 1 mm.

heterogeneity have been briefly described in the dolphin inferior colliculus (Glezer, Hof, & Morgane, 1995), this is the first description of structural heterogeneity, or modules, within a cortical field in cetaceans. Although there is no direct evidence pointing to the function of these specialized clusters, in our opinion it is likely that they are involved in auditory processing. The insular cortex is rostral to primary auditory areas in the flattened cortex, and the expansion of sensory cortex that occurs in mammals commonly involves an adjacent zone of cortex. For example, the visual extrastriate cortex, including VII, is contiguous with the primary visual area, VI, and occupies a large expanse of cortex of the temporal lobe in primates. Specialized visual areas are not found interspersed between auditory areas or between somatosensory areas. We suggest that in dolphins, the large expansion of cortex rostrolateral to known auditory cortex (Kesarev, Malofeyeva, & Trykova, 1977; Ladygina & Supin, 1978) is related to processing auditory inputs, and the modules observed in the present investigation are likely to be specializations of auditory cortex. Further, auditory and communication processing disorders in humans have been attributed to insular damage (Fifer, 1993; Habib et al., 1995), and PET studies have demonstrated insula activation to environmental sounds and sound movement (Griffiths, Bench, & Frackowiak, 1994; Engelien et al., 1995). Although not necessarily homologous, this region corresponds in location to Ia in dolphins.

The modules in dolphins were observed in layer II rather than in the presumed thalamic recipient layer IV, although the lack of granular cortex suggests that a layer other than IV may be the major thalamic recipient zone in these mammals (see Glezer, Hoff, & Morgane, 1992). Modules described in other sensory systems in other mammals have often been associated with layer IV (e.g., barrels in the mouse cortex; Woolsey & Van der Loos, 1970), however, there are a number of examples in which other layers show structural or metabolic heterogeneity (e.g., blobs in primary visual cortex of monkeys; Livingstone & Hubel, 1984; Krubitzer & Kaas, 1989, CO and acetylcholinesterase blobs associated with cell-dense regions in CL of manatees, Reep et al., 1989; for other examples see Purves et al., 1992). The presence of modules in the cerebral cortex in a variety of species suggests that they may be a universal feature of mammals (Purves et al., 1992; Krubitzer, 1995).

Modular organization, as described and discussed in the present context, should not be confused with the vertical organization that has been repeatedly demonstrated in the cerebral cortex. A primary feature of tangential modularity, such as that described in this study, is physiological, architectonic, and histological discontinuity. Cortical columns, on the other hand, represent vertical continuity in terms of receptive field location for neurons in that column. Thalamocortical, interhemispheric, and ipsilateral cortical connections with a particular region of the cortex give the impression that cortical columns are discrete, and the actual size of these columns may be similar across mammals regardless of the size of the neocortex (Bugbee & Goldman-Rakic,

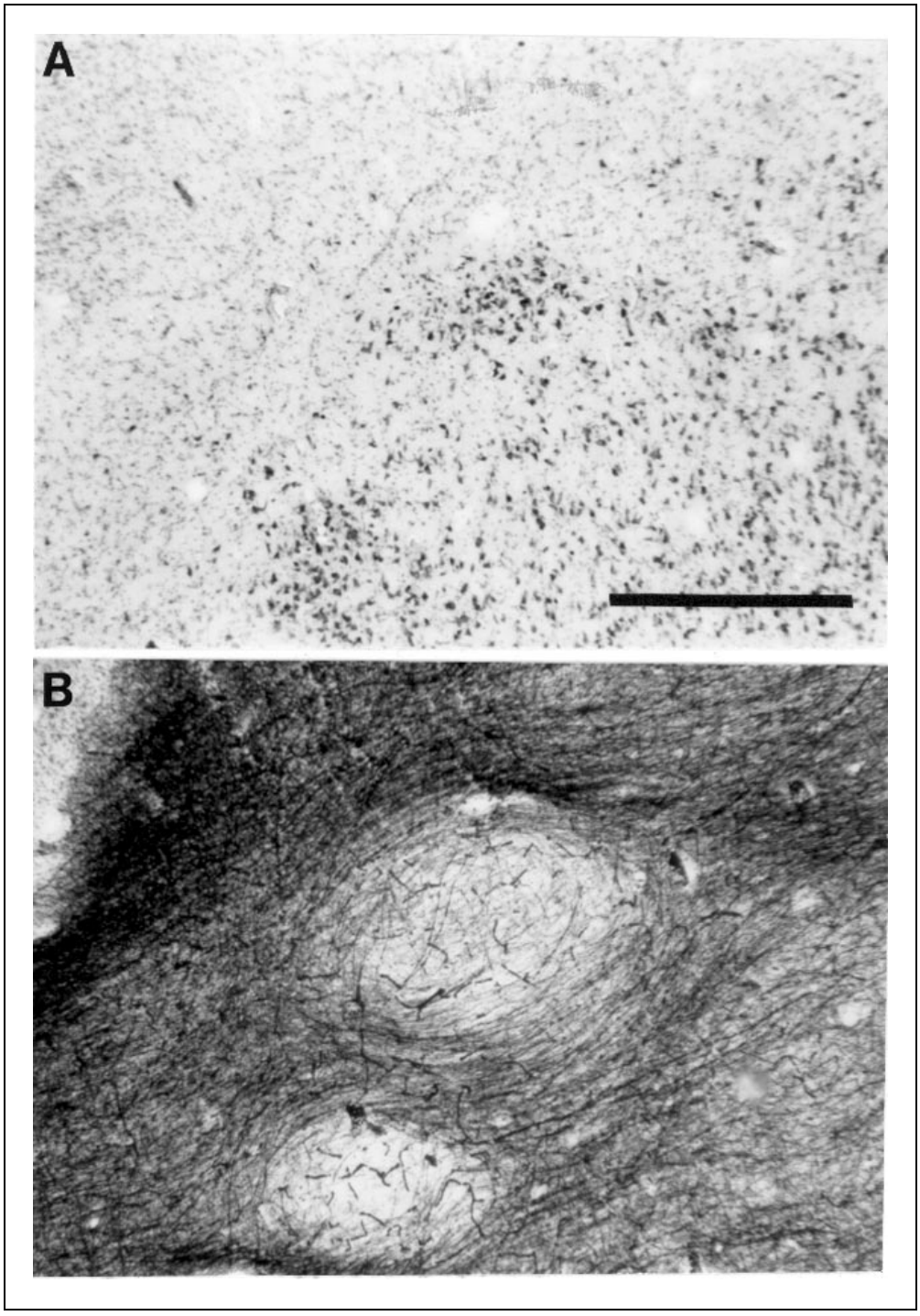

Figure 6. Light-field photomicrographs of cortex cut tangential to the pial surface and stained for Nissl (A) and myelin (B). These sections were photographed at the same magnification, and local blood vessels were matched so that the relationship of cell clusters to patterns of myelinated axons could be appreciated. The regions where neurons are clustered correspond to the myelin light zones. Scale bar equals 500 μm.

1983). However, columns demonstrated in this way could reflect locations along a continuum across a cortical field that has no inherent discontinuities. The horizontal boundaries of such vertical columns, when viewed using neuroanatomical tracing techniques, are set by the locations of the injections in the thalamus or cortex. An injection at a different, but adjacent, location could result in different but overlapping sets of labeled cells that appear in columns (see Mountcastle, 1978, for a review of cortical columns). This is in contrast to the module, whose horizontal boundaries are invariant. Modules as defined here may be columnar in that they might traverse the entire depth of the cortex, but they also may be only in some cortical layers.

The second important finding in this study is that although the brain size of neocortex from the smallest-brained mammal to mammals such as cetaceans varies by a factor of more than 3000 (Table 1), the size differences in cortical modules are disproportionate to the size differences in cortex (Figure 7). This suggests that

the microcircuitry of the cerebral cortex and the sizes of individual processing units within cortical fields are highly constrained.

An important question is why modules of a particular size are selected for in evolution. One possibility is that the size of thalamocortical afferents restricts the size of modules. This may be one factor that contributes to the size of modules in some regions of the cortex, but it is not the only factor because modules are found throughout the cortex in layers other than the thalamic recipient layer (see above comparisons). Another possibility, although not mutually exclusive from the first, is that the length of cortico-cortical connections plays a key role in determining module size. As brains increase in size, the internal organization changes in that very long connections are reduced, and more local processing occurs (Ringo, 1991).

A compelling theory to account for the length of observed connection patterns in the nervous system has been proposed by Cherniak (1994). The premise of this theory, termed component placement optimization (CPO), is that the spatial layout of the brain is the result of a minimization of total connection costs (i.e., length of connections). Long neural connections would require a large volume of metabolically active tissue, and such connections would have increased conduction times, resulting in signal-propagation delays (Ringo, 1991; Szymanski, Bain, & Henry, 1995). For the evolution of biological life, rapid reaction time to sensory input is crucial. The present study supports this theory by describing modules of a limited size in an animal whose neocortex has undergone a huge expansion. Because the efficiency of processing that shorter connections confer is increased, and the metabolic requirements are decreased, the range of module size and long-range connections between fields in both large and small brains, respectively, is evolutionarily stable. The inference of course is that other mammals with large brains, like humans, elephants, and whales, are subject to similar selective pressures. Although there is only sparse data on cortical architecture and connections in other mammals with larger brains, accumulating evidence in humans indicates that modules of a restricted size are present (e.g., Horton & Hedley-Whyte, 1984; Tootell, Dale, Sereno, & Malach, 1996) (see Table 1).

Another question is why are modules generated in the first place? One hypothesis is that correlated activity during neural development generates both physiological and structural heterogeneity in neural tissue. For instance, the stripes induced in the optic tectum of frogs are a compromise between the requisite of retinotectal ganglion cells to map onto a particular target and the correlated activity of developing axons from each eye (Constantine-Patton & Law, 1978). Similarly, observations in a number of mammals led Purves and colleagues (1992) to propose that heterogeneity observed in the cerebral cortex is the result of synapse formation during development. More importantly, these investigators point to the epiphenomenal nature of these "iterated patterns of brain circuitry." Although we agree that the presence of these heterogeneities is likely to reflect developmental constraints, we propose that modular evolution has led to functional optimization. Of course a brain need not be designed in its present form to perform the tasks that extant mammalian brains are capable of generating, but selection of particular developmental processes has led to their present construction, and this same process of selection appears to have restricted their size.

Although there is still dispute over the mechanisms involved in cortical field development, the present results allow us to infer the time frame in development in which module formation occurs. In a recent review by Rakic (1995), it was proposed that the expansion in cortical surface area could be accounted for simply by a prolongation of horizontal proliferation of progenitor cells in the ventricular zone during development. If this is indeed what occurs in evolution, cells destined to form the cerebral cortex must be multipotential, with differentiation of functional subunits occurring after the horizontal proliferation. If module formation occurred before or during cell proliferation and cortical expansion, one would expect to see modules change in size by the same factor by which cortex increases in size. The present results and results from other investigators demonstrate that this is not the case (Table 1).

Whatever the mechanism of module generation and maintenance may be, it is clear that constraints have been imposed on the cascade of developmental events necessary to generate a viable nervous system, which restricts the possibilities for cortical evolution. Indeed, the major lineages listed in Table 1 (rodents, primates, cetaceans, and carnivores) are separated by as much as 130 million years of independent evolution (e.g., monotreme ancestors diverged in the early Cretaceous; Clemens, 1989; Flannery, 1989; Westerman & Edwards, 1992). The observation of modules of a such a restricted size, given the changes in brain size and the time frame in which changes occurred, requires explanation. We propose that the ubiquity of modules and the apparent convergent evolution of module size indicate that there may be underlying homologous rules of cortical development that cause initial segregations, and that there is independent evolution of a restricted size of module, possibly due to selection for an optimal connection length. Of course the evolution of human cortex is enslaved by similar developmental events and subject to the same selective pressures.

Kaas (1995) has proposed that large brains are redesigned in such a way as to group neurons that interact very closely and thereby reduce connectional complexity. Of course modules have been observed in both large- and small-brained mammals. However, modular organization may have been exploited to a greater extent in larger-brained mammals, such as humans, because long-

:, neurochemistry, and location across a range of mammalian species compare
n EQ for some of the species, the areal dimensions of the modules are remark
: does vary within the same species by up to 5 times.

Table 1. Variations of module size, architecture (EQ) of each species. Despite huge disparities i important to note that occasionally module size

:st	*Smallest axis*	*Mean size (μm)*	*Cortical layers*	*Architecture*	*Histochemistry and other*	*Module type*	*Animal*	*Large axis*
)0	120		IV	Nissl, fiber	Various	SI barrels	Brush-tailed possum[1]	50
)0	190	290	IV	Nissl, fiber	Various	SI barrels	Rabbit[1]	50
)0	260	760	IV	Nissl, fiber		SI barrels	African porcupine[1]	100
)0	135	225	IV	Nissl, fiber	Various	SI barrels	Grey squirrel[1]	40
5	135	230	IV	Nissl, fiber		SI barrels	Prairie dog[1]	33
'5	100	145	IV	Nissl, fiber		SI barrels	Chipmunk[1]	17
)0	75	180	IV	Nissl, fiber	Various	SI barrels	Ground squirrel[1]	30
'0	110	265	IV	Nissl, fiber	Various	SI barrels	Guinea pig[1]	47
0	75	165	IV	Nissl, fiber		SI barrels	Chinchilla[1]	30
0	75	155	IV	Nissl, fiber		SI barrels	Gerbil[1]	25
0	100	205	IV	Nissl, fiber		SI barrels	Muskrat[1]	40
0	50	165	IV	Nissl, fiber	Various	SI barrels	Mouse[1]	32
5	115	210	IV	Nissl, fiber	Various	SI barrels	Rat[1]	38
5	65	170	IV	Nissl, fiber	Various	SI barrels	Hamster[1]	28
0	600	850	III, IV	Fiber	Cytochrome oxidase	SI stripes	Platypus[2]	100
0*	100*	350			Cytochrome oxidase	SI stripes	Star-nosed mole[3]	50

)	110	210	II, III		Cytochrome oxidase	Area 17 blobs	Owl monkey[4]	27(
)	195	280	II, III		Cytochrome oxidase	Area 17 blobs	Macaque monkey[5]	38(
)	250	345	VI		Cytochrome oxidase	Area 17 blobs	Humans[6]	40(
)	1000		II, III		Cytochrome oxidase	Area 18 bands*	Squirrel monkey[7] Thick	137(
)	400		II, III		Cytochrome oxidase		Thin	89(
)	400	900	II, III		Cytochrome oxidase	Area 18 bands	Squirrel monkey[8]	140(
)	205	240	II, III		Cytochrome oxidase	Area 18 bands	Marmoset monkey[8]	37(
5	140	335	II, III		Cytochrome oxidase	Area 18 bands	Owl monkey[8]	55'
)	140	415			Cytochrome oxidase	Area MT clusters	Owl monkey[4]	50(
)*	200*	290*	IV		Cytochrome oxidase	Ocular dominance columns	Talapoin monkey[9]	40(
)*	280*	350*	IV		Cytochrome oxidase	Ocular dominance columns	Cebus monkey[10]	45(
5*	180*	370*	IV		Radiography	Ocular dominance columns	Spider monkey[11]	41'
)*	250*	425*	IV	Fiber	Various	Ocular dominance columns	Macaque monkey[9]	50(
)*	400*	490*	IV	Neither	Radiography	Ocular dominance columns	Chimpanzee[12]	60(
)*	685*	680*	IV	Fiber	Cytochrome oxidase	Ocular dominance columns	Human[13]	105(
		330–435*				Ocular dominance columns	Cats[14]	
)	200	315	II	Nissl	Cytochrome oxidase	Cluster cortex	Manatee[15]	40(
)	125	255	II	Nissl, fiber		Insular clusters	Dolphin[16]	45(
)	200	620	II, III	Nissl	Cytochrome oxidase	Entorhinal clusters	Human[17,18]	80(
)	200	310	II, III	Nissl	Cytochrome oxidase	Entorhinal clusters	Macaque monkey[17]	40(
)	150	245	II	Nissl	Cytochrome oxidase	Entorhinal clusters	Rat[17]	30(

Krubitzer et al. (1995b)[2], Catania & Kaas (1995)[3], Krubitzer & Kaas (1990b)[4], Purves & L
a)[8], Florence & Kaas (1992)[9], Rosa et al. (1988)[10], Florence et al. (1986)[11], Tigges & Tigge
evner & Wong-Riley (1992)[17], Beall & Lewis (1992)[18], Stephan et al. (1988)[19], Hofman (1
cats, we obtained the range of mean interband distance and divided by 2. The encepha
eight (Jerison, 1973). All EQs are from Eisenberg (1981). Asterisks mark measurements t

Note: Results are derived from Woolsey et al. (1975)[1], I
Wong-Riley & Carroll (1984)[7], Krubitzer & Kaas (1990
(1987)[14], Marshall & Reep (1995)[15], present study[16], H
(1981)[22]. For the size of ocular dominance columns in
expected brain size for animals of a particular body w

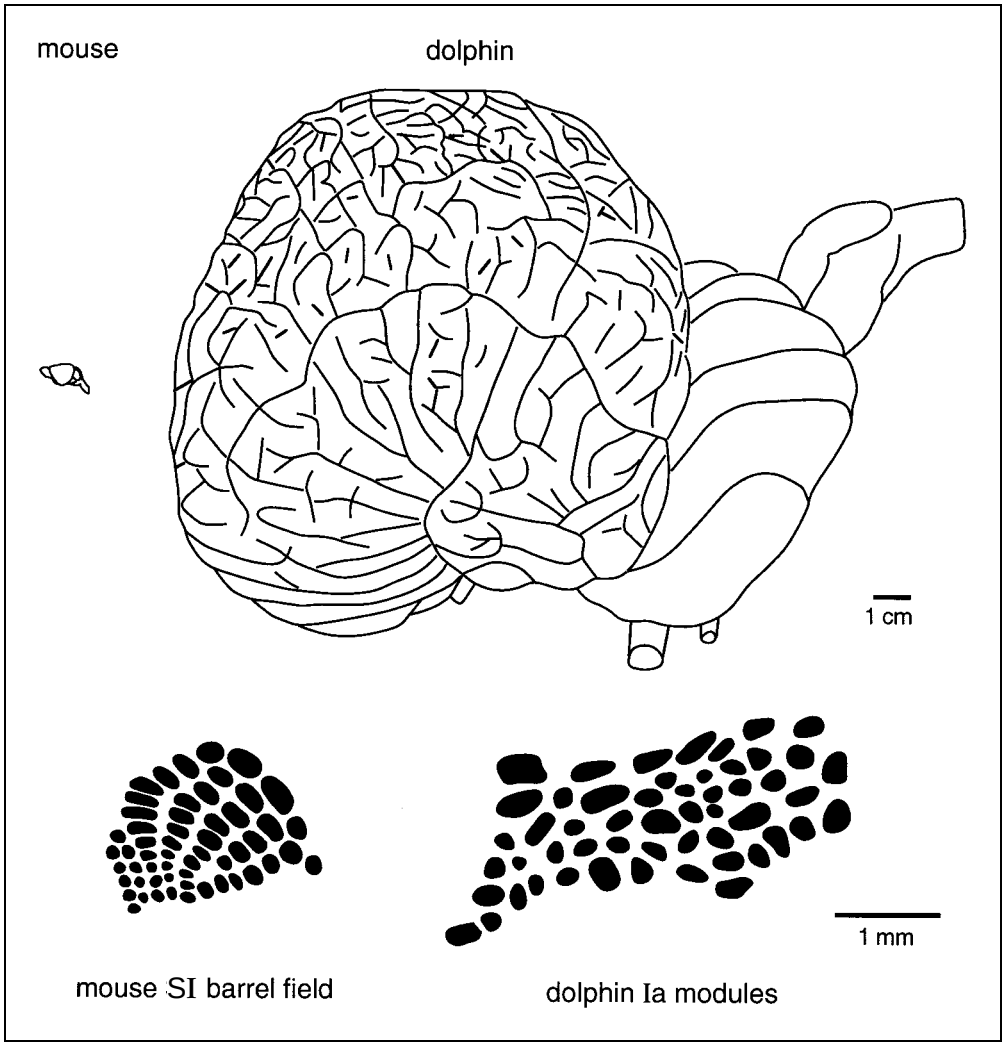

Figure 7. The size of the brain of a dolphin (top right) and a mouse (top left). Despite the enormous difference in the overall size of the brain and amount of neocortex, the modules described in the insular cortex in the present investigation (bottom right) and the modules described in mice for the vibrissae representation in SI (bottom left) are very similar in size.

range corticocortical connections appear to be selected against. Similarly, it has been postulated that lateralization of function in the large human brain is due to the selection for short intrahemispheric connections necessary for high-resolution, time-critical tasks such as language. Such short connections would circumvent the problem of extremely slow processing across the corpus callosum (Ringo, Doty, Demeter, & Simard, 1994). These investigators postulate that other large-brained mammals, such as elephants and cetaceans, will be subject to similar constraints and thus possess similar types of brain organization.

Although evolution has been likened to a tinkerer (Jacob, 1977), examination of the products that evolution constructs indicates that there is a limited collection of tools, or underlying mechanisms, that are accessed to build brains. Thus, in the course of evolutionary history, repetition of similar structural elements occurs. To understand cortical function and evolution, then, it may be equally profitable to focus attention on these anatomically, physiologically, and structurally cohesive cell assemblies (Singer, Engel, Kreiter, & Munk, 1997), in addition to higher levels of organization, such as the cortical field, and smaller units of organization, such as individual neurons.

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Note

1. The laminar distribution of cells in the dolphin neocortex appears to be quite different from that of other mammals, and the relationship between dolphin neocortex and that of other mammals is still a matter of conjecture (e.g., see Jacobs et al.,

1984; Revishchin & Garey, 1991). A conspicuous layer IV appears to be absent. In the present study, we have used the laminar assignations of Jacobs et al., 1984.

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