

A measure for brain complexity: Relating functional segregation and integration in the nervous system

GIULIO TONONI, OLAF SPORNS, AND GERALD M. EDELMAN

The Neurosciences Institute, 3377 North Torrey Pines Court, La Jolla, CA 92037

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ABSTRACT In brains of higher vertebrates, the functional segregation of local areas that differ in their anatomy and physiology contrasts sharply with their global integration during perception and behavior. In this paper, we introduce a measure, called neural complexity (C_N), that captures the interplay between these two fundamental aspects of brain organization. We express functional segregation within a neural system in terms of the relative statistical independence of small subsets of the system and functional integration in terms of significant deviations from independence of large subsets. C_N is then obtained from estimates of the average deviation from statistical independence for subsets of increasing size. C_N is shown to be high when functional segregation coexists with integration and to be low when the components of a system are either completely independent (segregated) or completely dependent (integrated). We apply this complexity measure in computer simulations of cortical areas to examine how some basic principles of neuroanatomical organization constrain brain dynamics. We show that the connectivity patterns of the cerebral cortex, such as a high density of connections, strong local connectivity organizing cells into neuronal groups, patchiness in the connectivity among neuronal groups, and prevalent reciprocal connections, are associated with high values of C_N . The approach outlined here may prove useful in analyzing complexity in other biological domains such as gene regulation and embryogenesis.

A long-standing controversy in neuroscience has set localizationist views of brain function against holist views. The former emphasize the specificity and modularity of brain organization, whereas the latter stress global functions, mass action, and Gestalt phenomena (1). This controversy mirrors two contrasting properties that coexist in the brains of higher vertebrates: the functional segregation of different brain regions and their integration in perception and behavior. In this paper, we attempt to provide a measure that reflects their interaction. The understanding of these two aspects of brain organization is central to any theoretical description of brain function (2–4).

Evidence that the brain is functionally segregated at multiple levels of organization is overwhelming. Developmental events and activity-dependent selection result in the formation of neuronal groups—local collectives of strongly interconnected cells sharing inputs, outputs, and response properties (2). Each group tends to be connected to a specific subset of other groups and, directly or indirectly, to specific sensory afferents. Different groups within a given brain area (e.g., a primary visual area) can show preferential responses for different stimulus orientations or retinotopic positions. Moreover, at the level of areas or subdivisions of areas, there is functional segregation for different stimulus attributes such as color, motion, and form (5–7). Further evidence for functional segregation in a variety of systems is provided by

the analysis of the specific deficits produced by localized cortical lesions (8).

In contrast to such local specialization, brain activity is globally integrated at many levels ranging from the neuron to interareal interactions to overall behavioral output. The arrangement of cortical pathways guarantees that any two neurons, whatever their location, are separated from each other by a small number of synaptic steps. Furthermore, most of the pathways linking any two areas are reciprocal and, hence, provide a structural substrate for reentry—a process of ongoing recursive signaling among neuronal groups and areas across massively parallel paths (2, 3, 9–11). One of the dynamic consequences of reentry is the emergence of widespread patterns of correlations among neuronal groups (10–14). Accordingly, perceptual scenes appear unified and are globally coherent, a property essential for the unity of behavior. Disconnection of various cortical areas often leads to specific disruptions of these integrative processes (8).

We have shown (10, 11) that a balance between the functional segregation of specialized areas and their functional integration arises naturally through the constructive and correlative properties of reentry. Computer simulations of the connectivity and physiological characteristics of the visual system showed that neuronal activity in segregated areas simultaneously responding to different stimulus attributes can be integrated to achieve coherent perceptual performance and behavior even in the absence of a master area (10, 11). These models provide a parsimonious theoretical solution to the so-called “binding problem” (15).

In the present paper, we consider the relationship between functional segregation and integration in the brain from a more general theoretical perspective. By making certain simplifying assumptions, we show that these two organizational aspects can be formulated within a unified framework. We consider neural systems consisting of a number of elementary components that can be brain areas, groups of neurons, or individual cells. In this initial analysis, we choose the level of neuronal groups (2) and study their dynamic interactions as determined by the topology of their interconnections. We assume that the statistical properties of these interactions do not change with time (stationarity) and that the anatomical connectivity is fixed. Moreover, we concentrate on the intrinsic properties of a neural system and, hence, do not consider extrinsic inputs from the environment.

By following these assumptions, functional segregation and integration are characterized in terms of deviations from statistical independence among the components of a neural system, measured using the concepts of statistical entropy and mutual information (16). Different neuronal groups are functionally segregated if their activities tend to be statistically independent when these groups are considered a few at a time. Conversely, groups are functionally integrated if they show a high degree of statistical dependence when considered many at a time. This leads to the formulation of a measure, called neural complexity (C_N), that reflects the interplay between functional segregation and integration within a neural system. In accord with recent attempts in

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physics and biology to provide rigorous definitions of complexity (17), we show that C_N is low for systems whose components are characterized either by total independence or total dependence and high for systems whose components show simultaneous evidence of independence in small subsets and increasing dependence in subsets of increasing size.

Using computer simulations, we then investigate the influence on C_N of certain fundamental properties of neuroanatomical organization. These include high connectivity, dense local connections that produce locally coherent neuronal groups, sparse but overlapping projective fields of neurons belonging to the same groups yielding axonal patches, and the prevalence of short reentrant circuits. We compare the computed values of C_N for simulated neural circuits that do or do not incorporate such properties and show that the connectivity patterns of the cerebral cortex are reflected in high C_N values.

Theory

Consider an isolated neural system X with n elementary components (neuronal groups). We assume that its activity is described by a stationary multidimensional stochastic process (16). The joint probability density function describing such a multivariate process can be characterized in terms of entropy and mutual information, used here purely in their statistical connotation (16, 18); i.e., no assumption is made about messages, codes, or noisy channels. If the components of the system are independent, entropy is maximal. If there are constraints intrinsic to the system, the components deviate from statistical independence and entropy is reduced. The deviation from independence can be measured in terms of mutual information. For instance, consider a bipartition of the system X into a j th subset X_j^k composed of k components and its complement $X - X_j^k$. The mutual information (MI) between X_j^k and $X - X_j^k$ is

$$MI(X_j^k; X - X_j^k) = H(X_j^k) + H(X - X_j^k) - H(X), \quad [1]$$

where $H(X_j^k)$ and $H(X - X_j^k)$ are the entropies of X_j^k and $X - X_j^k$ considered independently, and $H(X)$ is the entropy of the system considered as a whole (16). $MI = 0$ if X_j^k and $X - X_j^k$ are statistically independent and $MI > 0$ otherwise. Important properties of MI are symmetry [$MI(X_j^k; X - X_j^k) = MI(X - X_j^k; X_j^k)$] and invariance under a change of variables (16).

The concept of mutual information can be generalized to express the deviation from independence among the n components of a system X by means of a single measure, which we call its integration $I(X)$. $I(X)$ is defined as the difference between the sum of the entropies of all individual components $\{x_i\}$ considered independently and the entropy of X considered as a whole:

$$I(X) = \sum_{i=1}^n H(x_i) - H(X). \quad [2]$$

For a bipartition, rearranging Eqs. 1 and 2 leads to:

$$I(X) = I(X_j^k) + I(X - X_j^k) + MI(X_j^k; X - X_j^k). \quad [3]$$

Since $MI \geq 0$, $I(X) \geq I(X_j^k) + I(X - X_j^k)$, with equality in the case of independence. Note that, from Eq. 3, $I(X)$ is also equal to the sum of values of the mutual information between parts resulting from the recursive bipartition of X down to its elementary components. In particular, by eliminating one component at a time, $I(X) = \sum_{i=1}^{n-1} MI(\{x_i\}; \{x_{i+1}, \dots, x_n\})$.

Instead of considering the whole system X , we now consider subsets X^k composed of k -out-of- n components ($1 \leq k \leq n$; see ref. 19). The average integration for subsets of size k is denoted as $\langle I(X_j^k) \rangle$, where the index j indicates that the

average is taken over all $n!/(k!(n-k)!)$ combinations of k components. Note that $\langle I(X_j^1) \rangle = I(X)$, while $\langle I(X_j^0) \rangle = 0$. Given Eq. 3, $\langle I(X_j^{k+1}) \rangle \geq \langle I(X_j^k) \rangle$; i.e., $\langle I(X_j^k) \rangle$ increases monotonically with increasing k .

We now define the complexity $C_N(X)$ of a system X as the difference between the values of $\langle I(X_j^k) \rangle$ expected from a linear increase for increasing subset size k and the actual discrete values observed:

$$C_N(X) = \sum_{k=1}^n [(k/n)I(X) - \langle I(X_j^k) \rangle]. \quad [4]$$

Note that, like $I(X)$, $C_N(X) \geq 0$. According to Eq. 4, $C_N(X)$ is high when the integration of the system is high and at the same time the average integration for small subsets is lower than would be expected from a linear increase over increasing subset size.

$C_N(X)$ can also be expressed in terms of entropies or, like $I(X)$, as a sum of MI values. Following Eq. 2,

$$C_N(X) = \sum_{k=1}^n [(H(X_j^k) - (k/n)H(X))]. \quad [5]$$

Furthermore, following Eq. 3, $C_N(X)$ corresponds to the average mutual information between bipartitions of X , summed over all bipartition sizes:

$$C_N(X) = \sum_{k=1}^{n/2} \langle MI(X_j^k; X - X_j^k) \rangle. \quad [6]$$

Thus, according to Eq. 6, $C_N(X)$ is high when, on the average, the mutual information between any subset of the system and its complement is high. Note that, with respect to measurements of integration and complexity, it is meaningful to consider individual systems only. In such systems, no bipartition yields two statistically independent subsets (i.e., $MI(X_j^k; X - X_j^k) \neq 0$ for all j and k).

Computer Implementations

To examine the influence of various neuroanatomical patterns on C_N , we implemented different connectivity schemes in simulations of a visual cortical area, based on a previous model of perceptual grouping and figure-ground segregation (11). Neuronal activity was triggered by uncorrelated Gaussian noise rather than by patterned external input. Activity values of individual cells or average activities of neuronal groups were recorded and the resulting distributions were rendered approximately Gaussian. Simulations were carried out using the CORTICAL NETWORK SIMULATOR program run on an nCUBE (Foster City, CA) parallel supercomputer (11).

In addition, for the systematic testing of thousands of connectivity patterns, we instantiated them in simple linear systems that allowed us to derive their covariance matrices analytically. Each linear system X consisted of n components, each of which received connections from m other components ($1 \leq m \leq n-1$, no self-connections) resulting in a connection matrix $CON(X)$. $CON(X)$ was normalized so that the sum of the afferent synaptic weights per component was set to a constant value w . If we consider the vector A of random variables that represents the activity of the components of X , subject to uncorrelated Gaussian noise R , we have that, when the components settle under stationary conditions, $A = CON(X) * A + R$. By substituting $Q = [I - CON(X)]^{-1}$ and averaging over the states produced by successive values of R , we obtain the covariance matrix $COV(X) = \langle A^T * A \rangle = \langle Q^T * R^T * R * Q \rangle = Q^T * Q$.

In practice, various strategies can be used to calculate $I(X)$ and $C_N(X)$ from a set of data. Under the assumption that the multidimensional stationary stochastic process describing

the activity of the n components is Gaussian, all deviations from independence among the components are expressed by their covariances and the entropy can be obtained from the covariance matrix according to standard formulae (16). In particular, $I(X)$ can be derived from the covariance matrix $COV(X)$ or from the correlation matrix $CORR(X)$ or its eigenvalues λ_i according to the relationship: $I(X) = \sum_i \ln(2\pi e \nu_i)/2 - \ln[(2\pi e^n)|COV(X)|)] = -\ln(|CORR(X)|)/2 = -\sum_i \ln(\lambda_i)/2$, where ν_i is the univariate variance of component i and $|\cdot|$ indicates the determinant. Covariance matrices obtained from the simulations or from the analytic solution of linear systems were analyzed using MATLAB 4.1 (Mathworks, Natick, MA). $\langle I(X^k) \rangle$ was obtained from the eigenvalue spectrum of the correlation matrix by using all combinations for $k \leq 8$ or a small random sample for $k > 8$. Numerical analysis showed that this approximation consistently yielded highly accurate values for $C_N(X)$.

Results

We first illustrate some essential properties of neural complexity by calculating C_N for a set of covariance matrices used to exemplify its general behavior. We then show how C_N is affected by some key aspects of neuroanatomical organization.

Intuitively, complexity should be low if the components of a system are completely independent or uniformly dependent, and complexity should be high if there is evidence of various degrees of dependence and independence. C_N shows this characteristic behavior. As an example, in Fig. 1A, we plot the value of C_N for a series of Toeplitz covariance matrices (with constant coefficients along all subdiagonals) of Gaussian form having increasing correlation length σ ($n = 64$). As σ was varied from $10^{-0.5}$ (complete independence, all coefficients ≈ 0 ; Fig. 1B, case a) to 10^5 (complete dependence, all coefficients ≈ 1 ; Fig. 1B, case c), C_N was maximal (Fig. 1C) for intermediate values of σ , when the coefficients in the matrix spanned the entire range between 0 and 1 (Fig. 1B, case b). Fig. 1D shows that C_N increased with the integration I from 0 up to a maximum and then decreased to a low value.

Connectivity. As indicated in Fig. 1, a necessary although not sufficient condition for high complexity is high integration. In neuroanatomical terms, this means that a complex neural system must be highly interconnected. Fig. 2 shows results obtained from simulations of a primary visual area (11). In Fig. 2A, cases a and b represent a pattern of connectivity that, as implemented in the model, closely resembles neuroanatomical data. This pattern (11) is characterized by (i) strong local connections between neurons of similar specificity forming neuronal groups, (ii) weaker local connections between groups belonging to different functional subdomains (orientation preferences), (iii) preferential horizontal connections between groups belonging to the same functional subdomain, and (iv) a limited spatial extent of axonal arborizations, characterized by a marked fall-off of connection density with distance. Such a specific connectivity scheme results in "axonal patches" as seen in the visual cortex—i.e., axon terminals originating from neurons within a given group are concentrated in a few discrete clusters. If the connection density among the neuronal groups is significantly reduced with respect to the original model (Fig. 2A, case a), the groups behave quite independently and do not synchronize (Fig. 2B, case a). The corresponding covariance matrix contains uniformly low values (Fig. 2C, case a), the system is only minimally integrated, and $C_N(X)$ is very low (Fig. 2D, case a). At the connection density of the original model (Fig. 2A, case b), neuronal groups synchronize in ever changing combinations (Fig. 2B, case b). The corresponding covariance matrix (Fig. 2C, case b) shows

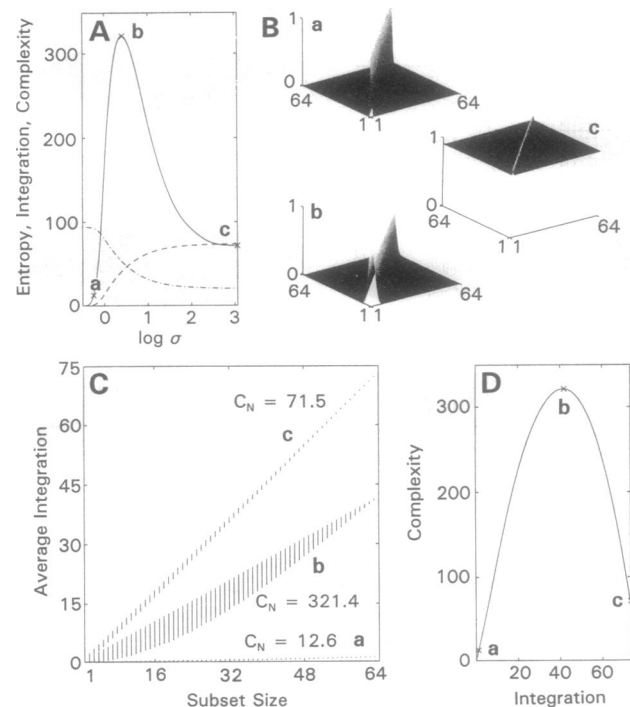


FIG. 1. Complexity C_N obtained from Gaussian Toeplitz covariance matrices ($n = 64$) with constant mean and varying σ . Uncorrelated noise (10%) was added to the matrix diagonal. (A) C_N (solid line), I (dashed), and H (dash-dotted line) as a function of $\log \sigma$. (B) Covariance matrices for cases a, b, and c as marked in A and D. (C) Average integration for increasing subset size for cases a, b, and c. Complexity is the area (shaded) between the linear increase of integration and the curve linking discrete values of average integration for increasing subset size. (D) C_N as a function of I . In case a, for very low values of I , C_N is very low; the components are independent. In case b, for intermediate values of I , C_N is high; the components are correlated in a heterogeneous way. In case c, for very high values of I , C_N is low; the components are completely and uniformly correlated.

significant correlations distributed in a heterogeneous pattern and both $C_N(X)$ and $I(X)$ are high (Fig. 2D, case b).

Axonal Patches and Neuronal Groups. Despite the large number of cortical connections, the overall connectivity of cortex is sparse as compared to a complete matrix of n^2 connections among n neurons. It is instructive to compare cortical connectivity patterns with other equally sparse but differently arranged patterns. The pattern of connectivity modeled after the organization of a primary visual area characterized by the presence of specific axonal patches yielded high $C_N(X)$ (Fig. 2, case b). In case c, the same number and strength of connections as in case b were present but intergroup connectivity was arranged in a completely uniform (i.e., random) way (Fig. 2A, case c). Dynamically, all neuronal groups were found to be locked in a globally synchronized state (Fig. 2B, case c); accordingly, their covariances were uniformly high (Fig. 2C, case c). In this case, although $I(X)$ was higher than that obtained with the more specific "patchy" connectivity, $C_N(X)$ was considerably lower (Fig. 2D, case c).

For a more systematic test of the influence of "patchiness" on $C_N(X)$, we implemented thousands of different connectivities as linear systems. Each system consisted of $n = 8$ components that received a fixed amount w of synaptic weights distributed over m connections per component. This connectivity could be distributed uniformly across all components ($m \rightarrow 7$) or restricted to progressively more specific sets of components ($m \rightarrow 1$). Fig. 3A shows that the evenly distributed connectivities (e.g., Left Inset) gave rise to con-

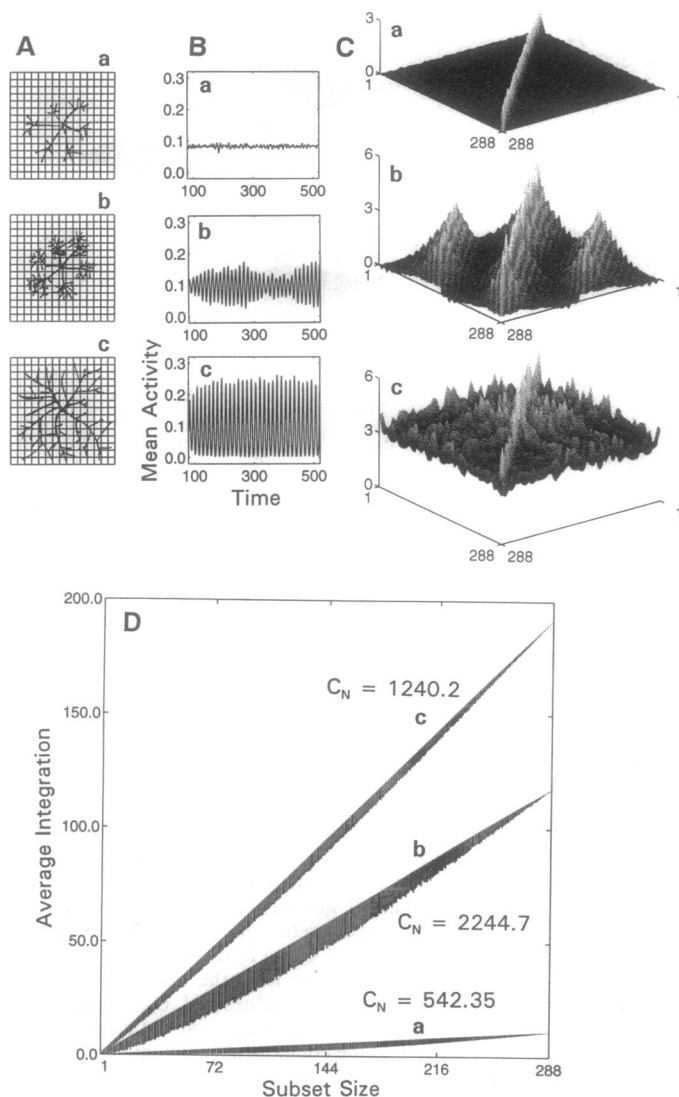


FIG. 2. Integration and complexity obtained from simulations of a primary visual area for different patterns of connectivity. All cases shown contain 512 neuronal groups in two arrays (16×16) and were modeled as collections of 40 excitatory and 20 inhibitory neurons that are mutually interconnected (11). No external input is provided to the network; neuronal group activity is triggered by intrinsic Gaussian noise. The groups tend to discharge in an oscillatory fashion. To compute C_N , we sampled the mean activity traces of groups forming the central 12×12 portion of the two arrays (one for each orientation preference) for 10,000 time steps (discarding an initial transient) and derived the covariance matrix. (A) Schematic connectivity patterns. (B) Mean activity traces of the entire array for the first 400 time steps after the initial transient. Large amplitude is an indicator of coherent activity within the array. (C) Covariance matrices. (D) Average integration and complexity derived from the covariance matrices. Cases a, b, and c (compare Fig. 1) explore the variation of $C_N(X)$ with different patterns of intergroup connections. In case b, intergroup connections are clustered in local patches around the group of origin (details in ref. 11); connections are spread within a 5×5 region for the same orientation domain, and within a 3×3 region for a different orientation domain. Case a is identical to b, but the connection density is reduced 2-fold. In case c, the same amount of intergroup connections as in case b are distributed uniformly within the array. While $I(X)$ increases from case a to b to c, $C_N(X)$ is highest for case b and lower for cases a and c.

siderably lower $C_N(X)$ than patchy connectivities (e.g., *Right Inset*), even after normalizing the complexity measure to take account of $I(X)$.

These models demonstrate that, under constraints of sparsity, higher values of $C_N(X)$ are obtained when neuronal

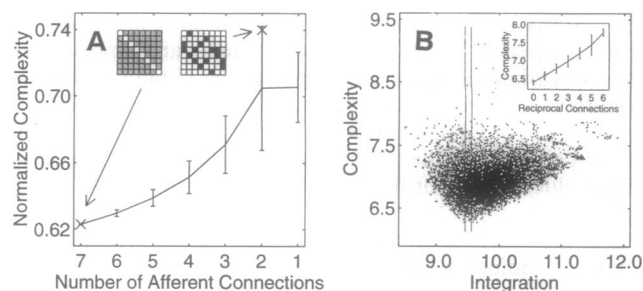


FIG. 3. (A) Normalized complexity $C_N(X)/I(X)$ for linear systems composed of eight components (groups) and a varying number m of connections (axonal patches). Total amount of connectivity is constant ($w = 0.9$). Each point gives the mean \pm SD for 1000 randomly generated networks, each representing an individual system. Normalized complexity increases as connectivity patterns go from uniform to patchy. (*Insets*) Connection matrices (open squares, no connection; shaded squares, low synaptic weight; solid squares, high synaptic weight), corresponding to a uniform (*Left*) and a patchy (*Right*) connectivity. (B) Distribution of $C_N(X)$ and $I(X)$ for 10,000 randomly generated linear networks of eight components with $m = 2$ ($w = 0-9$). Both $C_N(X)$ and $I(X)$ vary over broad numerical ranges. Vertical lines indicate the subpopulation of networks at constant $I(X)$ that was analyzed for the presence of reciprocal connections between pairs of components. (*Inset*) $C_N(X)$ of these networks grows on average with the number of such reciprocal connections.

groups have specific anatomical projective fields, as opposed to uniformly distributed projections. Many studies suggest that such "patchiness" is a general property of the neuroanatomical organization of intraareal connections. For instance, intrinsic connectivity within visual cortical areas is characterized by preferential connectivity between groups sharing similar functional properties and by limited spatial extent of arborizations. Synaptic contacts are concentrated in patches of relatively constant size (see e.g., ref. 20). Patchiness and specificity seem to be equally characteristic of many thalamocortical, commissural, and long corticocortical connections (especially "forward" connections; see ref. 7).

A prominent "patch" of axon terminals is due to axon collaterals branching in the immediate vicinity of the cell body (20). Such strong local connectivity contributes to the organization of neurons into neuronal groups (2). To examine the influence of group structure on C_N , we sampled single neurons from two or more groups. For many sets of parameters, dissolving the group structure (e.g., by taking local collaterals within a group and redistributing them uniformly among all other groups) resulted in a marked decrease of C_N (data not shown). Thus, it appears that the organization of a brain region into neuronal groups will, through local cooperative effects, contribute to higher levels of C_N .

Reciprocal Connectivity. Most intra- and interareal neuronal pathways are reciprocal, thus allowing for the process of reentry (2-4). It is therefore informative to investigate the impact of reciprocal connectivity on $C_N(X)$. In linear models we noticed that, for constant n , m , and w , different connectivity patterns produced a wide range of values for $C_N(X)$ (Fig. 3A). There were many cases for which the values of $C_N(X)$ and $I(X)$ were dissociated. For example, Fig. 3B shows a population distribution of 10,000 randomly generated and sparsely interconnected linear systems with $n = 8$, $m = 2$, and $w = 0.9$. Closer analysis of this population revealed that, for constant values of $I(X)$, an increase in $C_N(X)$ tended to correlate (Fig. 3B *Inset*) with the number of reciprocal connections between pairs of components; it is notable that such connections are a key structural substrate for reentry. $I(X)$ did not show this tendency. At lower values of w , both $I(X)$ and $C_N(X)$ tended to increase (data not shown) with the number of reentrant circuits.

Discussion

Traditionally, localizationist and holist views of brain function (1) have exclusively emphasized evidence for either functional segregation or for functional integration among components of the nervous system. Neither of these views alone adequately accounts for the multiple levels at which interactions occur during brain activity (2). Previously, we illustrated the interplay of functional segregation and integration in a series of computer simulations of the visual system (10, 11). In this paper, we introduce a general measure, called neural complexity C_N , that encompasses these two fundamental aspects of brain organization and at the same time resolves many issues raised by conflicting views on local vs. global functions.

C_N measures how much the increase of integration with increasing subset size deviates from linearity—i.e., roughly speaking, how much more integrated the whole is than its parts (see Eq. 4). Equivalently, C_N can be seen as a measure of the mutual information between each part of a neural system and the rest, summed over all possible bipartitions (see Eq. 6). Consistent with intuitive notions and with current attempts in physics and biology to conceptualize complex systems, C_N is high for systems such as the vertebrate brain that conjoin local specialization with global integration. On the other hand, C_N is low for systems that are composed either of completely independent parts (e.g., in physics, dilute gases) or of parts that show completely homogeneous behavior (e.g., crystals).

A major aim of this paper was to make use of C_N to analyze some principles of neuroanatomical organization. This analysis pointed to certain structural characteristics of the brain associated with high values of C_N . These include a high density of connections, strong local connectivity helping to organize cells into neuronal groups, patchiness in the connectivity among neuronal groups, and a large number of reentrant circuits. A broader exploration of this arena of theoretical neuroanatomy will require the extension of the present analysis to other important characteristics not considered here—for example, the diffuse terminations of back-projections and the distribution of inhibitory connections.

In these initial attempts to characterize functional segregation and integration within the unified framework of neural complexity, we have not confronted many issues raised by the richness of brain organization and function. For example, the present measure of complexity does not explicitly consider the heterogeneity of the actual components of a neural system. Moreover, to measure their deviation from statistical independence in terms of the statistical notions of entropy and mutual information, we have considered neural systems under stationary conditions only. It is not yet apparent to what degree the present measure can usefully be extended to nonstationary conditions. If this extension proved feasible, the hypothesis that the brain is uniquely organized in such a fashion as to achieve the integration of functionally specialized areas and neuronal groups within the few hundreds of milliseconds needed for conscious perception and behavior (3, 10) could be rigorously tested.

In the present work, our conclusions were drawn on the basis of various computer simulations. A full validation of the measures introduced here requires their application to data obtained directly from brains *in vivo*. Preliminary investigations seem to bear out the prediction that the covariance matrices provided by functional neuroimaging in human subjects are associated with high values of C_N (K. J. Friston, G.T., O.S., and G.M.E., unpublished data). We also expect that C_N should be strongly altered under different neural states: for example, we predict that, during conscious awareness (3), heterogeneous patterns of short-term correlations within the corticothalamic system will result in high values of

C_N , and during globally synchronized states, such as slow-wave sleep, C_N will have lower values.

A number of other biological systems exhibit complexity and appear to be susceptible to the kind of analysis described here. The circuits of gene regulation in prokaryotes and eukaryotes, various endocrine loops, and the coordinative events observed during embryological development are significant examples. It remains to be seen whether our approach will also prove useful in more widespread applications such as the analysis of parallel computation and communication networks. It is also an open question whether our measure of complexity might be extended to a consideration of temporal patterns, particularly since complex dynamical systems have time evolutions that, especially near phase transitions, are in between the two extremes of complete randomness (e.g., a coin flip) and complete regularity (e.g., a clock; references in ref. 17).

Finally, it should be stressed that in the present work we have examined only the intrinsic characteristics of complex neural systems, without considering the influence of extrinsic inputs or the question of how those characteristics arose during evolution, development, and experience. Viewed more broadly from a selectionist perspective, however, the main reason why the brain of a higher organism is complex is that the environment it samples is complex. It remains to be seen how neural complexity is altered by a succession of diverse signals from the world to yield adaptive behavior.

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