Convergence and divergence are mostly reciprocated properties of the connections in the network of cortical areas

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Cognition is based on the integrated functioning of hierarchically organized cortical processing streams in a manner yet to be clarified. Because integration fundamentally depends on convergence and the complementary notion of divergence of the neuronal connections, we analysed integration by measuring the degree of convergence/divergence through the connections in the network of cortical areas. By introducing a new index, we explored the complementary convergent and divergent nature of connectional reciprocity and delineated the backward and forward cortical sub-networks for the first time. Integrative properties of the areas defined by the degree of convergence/divergence through their afferents and efferents exhibited distinctive characteristics at different levels of the cortical hierarchy. Areas previously identified as hubs exhibit information bottleneck properties. Cortical networks largely deviate from random graphs where convergence and divergence are balanced at low reciprocity level. In the cortex, which is dominated by reciprocal connections, balance appears only by further increasing the number of reciprocal connections. The results point to the decisive role of the optimal number and placement of reciprocal connections in large-scale cortical integration. Our findings also facilitate understanding of the functional interactions between the cortical areas and the information flow or its equivalents in highly recurrent natural and artificial networks.

Keywords: network analysis; edge property; random graph; reciprocity; information bottleneck; hub

1. INTRODUCTION

The cerebral cortex is parcelled into numerous functionally and structurally specific areas that are connected to each other via bundles of neuronal processes (Felleman & Van Essen 1991). This large-scale, directed, anatomical network of cortical areas serves as a blueprint for the understanding of cognitive operations (Passingham *et al.* 2002; Sporns *et al.* 2004; Kaiser 2007). The principles of cortical functional organization are integration and segregation, which ensure the integrated functioning of different specialized structures. It is assumed that integration depends crucially on convergence of neural connections (Tononi *et al.* 1998; Sporns *et al.* 2004; Friston 2005). However, in complex networks such as the cerebral cortex, network nodes (cortical areas) *per se* are subject to intense convergence/divergence via their multiple inputs and outputs. Furthermore, the relatively small size of the cortical network and the moderate variation in the number of connections formed by the areas do not allow the unambiguous and straightforward distinction of highly connected integrative centres (Barabási & Albert 1999; Sporns *et al.* 2007). In addition to convergence,

connectional reciprocity was suggested as the other important factor in cortical integration via supporting cooperation (Tononi *et al.* 1998). The high-level reciprocity characterizing the cortical networks (Felleman & Van Essen 1991) apparently interferes with convergence owing to the large overlap between the input and the target structures. The difficulty of identifying network properties relevant to cortical integration is illustrated by the fact that several different network measures, alone or in combination, were used to identify the role of areas in cortical integration, or analogously in large-scale information processing (Kötter & Stephan 2003; Costa & Sporns 2005; Sporns *et al.* 2007). Although these studies pinpointed various areas already known from the experimental observations as high-level integrative structures, there were also many discrepancies in regard to the role of different areas in cortical integration (Kötter & Stephan 2003; Costa & Sporns 2005; Sporns *et al.* 2007).

Previous analyses focused mostly on node properties, which evaluate the situation of a given node in the network (Wasserman & Faust 1994). In accordance with experimental observations, it was shown that the cortical areas known as higher order associational structures occupy a central position in the network (Kötter & Stephan 2003; Sporns *et al.* 2007). However, different indices rank the areas differently, which explains the need for their use in combination (Kötter & Stephan 2003;

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Costa & Sporns 2005; Sporns *et al.* 2007). In addition, node properties can be sensitive to variation in the dataset analysed (Kötter & Stephan 2003). In contrast to the node properties, edge properties evaluating the significance of connections in the network (Wasserman & Faust 1994; Kaiser & Hilgetag 2004) give the opportunity to include a specific relationship between the connected pairs of nodes in an objective way into the analysis. Our proposition is that additional information on edge properties helps to overcome the drawbacks of applying node properties alone in studying the topological characteristics underlying large-scale cortical integration. Notably, available information suggests that link properties, edge betweenness in particular, are sensitive measures in exploring biologically relevant characteristics of the cortical networks (Kaiser & Hilgetag 2004; Négyessy *et al.* 2006).

The goal of the present study was to explore the network architecture responsible for large-scale cortical integration. To this end, we characterized the integrative properties of the areas of the cerebral cortex by quantifying the degree of convergence/divergence through their connections. Measuring link properties instead of node properties also has the advantage of investigating the role of reciprocal connections in cortical integration. Our study was rooted in the analysis of the shortest paths that represent global network characteristics, and is presumably less sensitive to variations in local network features expressed by the degree of nodal connections. To check the specificity of our findings on cortical graphs, the results were compared with those obtained on randomized counterparts. In sharp contrast to the cortex, organization of random graphs (where the network nodes are connected independently with equal probability) is very different from natural and artificial complex networks.

2. MATERIAL AND METHODS

(a) Connectivity data

We analysed the cortical networks that were subjects of previous studies including the macaque visuotactile cortex consisting of 45 nodes and 463 edges (Négyessy *et al.* 2006), the whole macaque cortex consisting of 71 nodes and 746 edges (Sporns 2002), as well as the cat cerebral cortex containing 55 nodes and 892 edges (Hilgetag *et al.* 2000a). Adjacency matrices contained unweighted connectivity data published originally in tract-tracing studies. For the macaque cerebral cortex, most of the data were derived from the CoCoMAC database (www.cocomac.org) and additional searches were made on PubMed (<http://www.ncbi.nlm.nih.gov/entrez/query.fcgi?db=PubMed>; Sporns 2002; Négyessy *et al.* 2006). Connectional data of the whole macaque cerebral cortex were downloaded from http://www.indiana.edu/~cortex/connectivity_toolbox.html (for further information, see Sporns 2002 and references therein).

(b) Data analysis

(i) Computing betweenness centralities

Betweenness centrality is computed using all the shortest paths in the network. First, we find all the shortest paths between all possible pairs of nodes s and t . For each s – t pair, we count the number of shortest paths between them that pass through a given node (node betweenness) or a given edge (edge betweenness) and divide them by the number

of all the shortest paths between s and t . Finally, we sum these ratios over all s – t pairs. Less formally, the betweenness centrality is the number of shortest paths in the network that pass through a given node or edge, but if there are k distinct shortest paths between nodes s and t , each of them weighs only $1/k$ in the final betweenness score.

(ii) Correlation of edge properties within cliques and loops

In each clique and loop, all convergence degrees (CDs, see definition in §3) of the same sign were summed. The sums of the opposite signs were correlated for all cliques and loops of the same size. Definitions of loops and cliques are as follows. Let us consider a sequence of nodes, $v_1, v_2, \dots, v_k$. This sequence is called a path if there exists an edge going from v_1 to v_2 , from v_2 to v_3 and so on. The sequence is a cycle if it is a path and if there also exists an edge going from v_k to v_1 . In this case, we call k the length of the cycle. From now on, we limit ourselves to cycles in which every node occurs only once. A cycle that is traversable both forward and backward along the edges is called a loop. A clique is a set of nodes, $v_1, v_2, \dots, v_k$, such that there exists an edge between any pair of nodes chosen from this set (note that this definition implies that all edges in a clique are reciprocal).

(iii) Rewiring and randomization

Two different kinds of rewiring procedures are presented. (i) Rewiring was performed by randomly moving the edges without changing the proportion of reciprocal edges (82%) in the macaque visuotactile network. Figure 6a shows the node-reduced CD values (see §3) of 100 rewired visuotactile networks. (ii) The level of reciprocity was varied by picking the edges or pairs of edges randomly and rewiring them appropriately until the desired reciprocity level was reached. Larger target reciprocity levels were achieved by choosing non-reciprocal pairs of edges and reconnecting one of them with the other in the opposite direction to form a reciprocal pair. Smaller target reciprocity levels were achieved by choosing an edge in a reciprocal pair and reconnecting it with a different, previously unconnected, pair of vertices. The averaged results of 100 iterations at each level of reciprocity are presented. During both rewiring procedures, creating multiple edges between two nodes with the same direction or violating the strong connectivity property of the network were forbidden. The Erdős-Rényi (ER)-like random graphs used for comparison had the same number of nodes and edges as the original visuotactile network. The randomized version of the whole macaque cerebral cortical network is freely available at http://www.indiana.edu/~cortex/connectivity_toolbox.html (for further information, see Sporns 2002).

3. RESULTS

(a) Convergence degree of the connections

The degree of convergence and divergence was quantified by introducing a new edge-related index based on the analysis of the shortest paths (figure 1). The CD is defined as the normalized value of the difference between the number of input and target areas (Négyessy *et al.* 2006) connected via a particular link of a directed graph (figure 1). In exact terms, take the set comprising all the shortest paths in the network. If one chooses all the shortest paths containing the edge (i, j) , one may define two sets: $Input(i, j)$ containing all the nodes from which the shortest paths containing the edge (i, j) originate, and

Figure 1. Demonstration of the computation of CD. Input and target nodes connected via the shortest path through the directed edge between A and B (marked by thick arrow) are encircled by the grey areas. The actual CD value in this case is $(5-4)/(5+4) = +0.11$. Note that D and E are not included in the input field because the shortest paths from these nodes to B avoid the AB link. Note also that C has an alternative path to B via D and E, which has the same length as the one passing through the AB link.

$Output(i, j)$ containing all the nodes in which the shortest paths containing the edge (i, j) terminate. If $|Input(i, j)|$ denotes the number of elements in the $Input(i, j)$ set and $|Output(i, j)|$ denotes the number of elements in the $Output(i, j)$ set, then edge CD is defined as

$$CD(i, j) = \frac{|Input(i, j)| - |Output(i, j)|}{|Input(i, j)| + |Output(i, j)|}.$$

A positive value indicates convergent connection since the input field of the connection contains more nodes than the output field while the opposite is true for divergent edges characterized by negative CD values. The lack of correlation between CD and edge betweenness suggests that these values are independent (electronic supplementary material, table 1). Convergence (figure 2a; electronic supplementary material, figure 1a,c) and divergence (figure 2b; electronic supplementary material, figure 1b,d) are complementary, as shown by the largely reverse direction of the connections with the opposite sign of CD within the cortical networks. Convergent and divergent connections form two complementary sub-networks, which share the network nodes. Remarkably, the two sub-networks correspond to the backward (figure 2a; electronic supplementary material, figure 1a,c) and forward (figure 2b; electronic supplementary material, figure 1b,d) sub-networks along the cortical hierarchy (Felleman & Van Essen 1991; Scannell et al. 1995; Hilgetag et al. 2000b). Only a minority of the reciprocated connections breaks this symmetry by exhibiting the CD of the same sign in both directions (figure 3; electronic supplementary material, tables 2–4) and there were also edges with zero CD (electronic supplementary material, table 5). In addition, the magnitude of CD also tends to be symmetric in the case of reciprocal connections (figure 3; electronic supplementary material, figure 2). The balance of convergence and divergence was further tested on cliques and loops in the cortical network (figure 3; electronic supplementary material, figure 2). It is notable that balance increases steadily with the number of nodes included in the macaque, while there is a different tendency in the cat (figure 3; electronic supplementary material, figure 2). In contrast to cliques and loops, balance defined for randomly selected edges shows a definite positive correlation (figure 3).

(b) Convergence and divergence in cortical networks

There is a significant difference between the areas regarding the convergent and divergent nature of their input and output (figures 2 and 4; electronic supplementary material, figures 1 and 3). This is reflected by the markedly different distribution of the number of CD inputs and outputs with positive and negative CD values (electronic supplementary material, figures 4–6). Areas having exclusively, or almost exclusively, inputs or outputs in the backward (figure 2a; electronic supplementary material, figure 1a,c) and forward (figure 2b; electronic supplementary material, figure 1b,d) sub-graphs are at the two ends of this scale. To unfold the possible functional implication of the distribution of convergent and divergent connections in the cortical network, we summed and plotted the positive and negative CD values of the incoming and outgoing edges separately for each area (figure 5). The resulting plot, which we call a node-reduced CD representation of the network, has four quadrants (figure 5). The horizontal axis represents the area's total input CD, and the vertical axis represents the area's total output CD. The quadrants represent different functional properties in terms of integration in the cortex: the combination of divergent input and convergent output is, considering the information flow, equivalent to allocating information in the network. By contrast, convergent input and divergent output suggest that the area serves as a source of information in the network. Because afferents and efferents of an area typically have the opposite sign of CD, we discuss the biological relevance of the upper left and lower right quadrants (figure 5) throughout the study. The analysis includes the whole set of areas, which is repeatedly plotted in each quadrant. Figure 5 shows that there is a linear correlation between the sum of the incoming and outgoing CDs with the opposite sign in all the cortical networks analysed (electronic supplementary material, table 6). There is a gradual change between 'source' and 'allocating' properties through areas having both inputs and outputs in the two sub-graphs (figures 2, 4 and 5; electronic supplementary material, figures 1 and 3). The distance of the areas from the origin in the node-reduced CD representation (figure 5) corresponds to their ranking on the basis of the areas' average input and output CD (figure 4; electronic supplementary material, figure 3). Notably, with some deviation, CD-based ranking agrees well with the known hierarchical arrangement of the cortical areas in both the monkey and the cat (Felleman & Van Essen 1991; Scannell et al. 1995; Hilgetag et al. 2000b). It is particularly interesting that primary sensory and motor cortical areas show source characteristics, while allocating properties are exhibited by higher order associational structures (figure 4; electronic supplementary material, figure 3). It also appears that the gradual change between the allocating and source characteristics is present in all major clusters of the network (figures 2 and 4), which suggests the parallel existence of several hierarchically organized compartments in the cortex (Young 1992).

Notable exceptions were areas VIP and V4, which are thought as middle-range structures in the cortical hierarchy (Felleman & Van Essen 1991; Hilgetag et al. 2000b). However, these areas appeared as allocating in the

Figure 2. Convergence and divergence in the macaque visuotactile cortex. (a) Direction of convergent edges defined by positive CD values and (b) Divergent edges exhibiting negative CD values are drawn. Shades of the arrows are scaled to the magnitude of CD: dark grey shows large absolute CD values, and low CD values are represented by light grey. Note the different input and output characteristics of the areas, the central position of high-level associational areas and the marginal placement of primary sensory and motor structures. The bidirectional arrow between Id and 36 on (a) is a rare example of reciprocal connections with the same sign of CD. Also apparent is the clustered organization that corresponds to the dorsal visual cluster in the lower right, ventral visual cluster in the lower left and sensorimotor clusters in the upper part of the figures. Details of connectional data and cluster analysis are described in [Négyessy *et al.* \(2006\)](#). For the nomenclature and description of areas, see [Felleman & Van Essen \(1991\)](#). For the sake of better visibility, the name of some areas was shortened: MSTd/p to MSd, MSTl to MSI, PITd to PId, PITv to PIV, CITd to CId, CITv to CIv, AITd to AId, AITv to AIv, STPp to STp and STPa to STa. Area MSTd/p includes connections of both MSTd and MSTdp in the visuotactile network ([Négyessy *et al.* \(2006\)](#)).

visuotactile network (figures 2 and 4), by exhibiting very high absolute CD values in the upper left quadrant of figure 5. Both of these areas have central bridge-like position by connecting different clusters of the cortical network ([Felleman & Van Essen 1991](#); [Young 1992](#); [Jouve *et al.* 1998](#); [Négyessy *et al.* 2006](#); [Nepusz *et al.* 2008](#), figure 2; electronic supplementary material, figure 1). Position of the areas in the network can be quantified by centrality indices ([Wasserman & Faust 1994](#)). Both VIP and V4 exhibit high node betweenness centrality in the visuotactile network (electronic supplementary material, figure 7). Similar results were obtained for V4 in the macaque cortical network (electronic supplementary material, figures 1a,b and 3). However, VIP exhibited properties resembling lower order source areas in the whole macaque cortical network (electronic supplementary material, figures 1a,b and 3). This discrepancy is due to the lack of a substantial amount of connectional data in the case of VIP in the whole macaque cortical network, which has been only recently described ([Lewis & Van Essen 2000](#)) and included in the network analysis ([Négyessy *et al.* \(2006\)](#)).

Rank correlations computed to assess the interdependence of different node-related indices with node-reduced CD resulted in high correlations with node betweenness centrality (electronic supplementary material, table 7). By contrast, node-reduced CD weakly correlated with the transmission index ([Kötter & Stephan 2003](#)), which expresses convergence/divergence as the difference between the number of efferents and afferents. Moderate correlation appeared between the node-reduced CD and

Figure 3. Balance of convergence and divergence in the macaque visuotactile network. There is high negative correlation of CD in loops (circles) and cliques (squares) of the macaque visuotactile network. The number of areas in cliques and loops is shown on the x-axis, e.g. number 2 represents reciprocal connections between two areas. Numbers at the points indicate the number of instances found in the network. Note that computing loops with larger k values was computationally infeasible and is not shown. The inset shows the positive correlation for randomly selected edges (pluses). The number of randomly selected edges equals the number of edges in the cliques of the corresponding size (i.e. $n(n-1)$ for $n=2, 3, \dots, 7$).

the divergence measurement of [Costa & Sporns \(2005\)](#). However, this index could be computed and compared for each cortical area only at radius 1.

Figure 4. Average CD of the area's input (light grey bars) and output (dark grey bars) in the macaque visuotactile cortex. CD values computed in the total network are shown in different clusters separately: (a) dorsal visual, (b) ventral visual and (c) sensorimotor. Note the opposite characteristics of the bottom and top areas as indicated by the reverse sign of their average input and output CDs on the graphs. Note also the ranking of areas by the gradual reversion of the sign and magnitude of the average CD.

(c) *Contrasting characteristics of cortical and random graphs*

We tested the generality of our observations by rewiring and randomizing the cortical graphs. These data indicate that rewiring has no effect on the distribution of convergent and divergent connections (figure 6a). However, reciprocity plays an essential role: high linear correlation values between the sum of the incoming and outgoing CDs with the opposite sign appears only at high degree of reciprocity (figure 6b). When compared with the fully reciprocal case characterized by totally balanced

CD of the inputs and outputs, the fitting error changes slightly until reciprocity reaches a threshold from where it decreases steeply (figure 6b). Surprisingly, the reciprocity of the cortical networks is situated near this threshold value (figure 6b). Similarly to the cortical networks, the node-reduced CD values highly correlated with node betweenness centrality (Wasserman & Faust 1994) in the randomized test graphs (electronic supplementary material, table 7). Furthermore, when compared with random graphs with varying proportion of reciprocity, we observed major deviation from the

Figure 5. CD of the areas in the visuotactile (pluses), cat (crosses) and macaque (asterisks) cortices. There is strong negative correlation between the inputs and outputs of the areas as shown in the upper left and lower right quadrants. Note also the balanced magnitude indicated by the distribution of the values along the diagonal. The order of areas along the diagonal is practically reversed in the two quadrants. Note that all areas are plotted in each quadrant.

cortical-like networks. In contrast to the cortical graphs, linear correlation of node-reduced CD values was high, irrespective of the proportion of reciprocal edges in the random graphs (figure 6*b*).

4. DISCUSSION

(a) Studying convergence/divergence in complex networks

The present study examined large-scale cortical integration by introducing a new index to compute the degree of convergence in the network of areas. The most important novelty of present analyses is that CD measures the degree of convergence/divergence of the connections instead of the areas, which has two notable advantages compared to the previous analyses: (i) it characterizes the relationship of the neighbouring (directly connected) nodes in an objective manner by weighing the edges in a way that is characteristic of the topology, and (ii) node-reduced CD values define the integrative properties of the nodes within the network. Node-reduced CD derived from the shortest paths fundamentally depends on the network's global topology. This property may explain the lack of correlation between the node-reduced CD and the transmission index, which is a local network feature (Kötter & Stephan 2003). By contrast, node-reduced CD highly correlates with node betweenness centrality, which is also based on the computation of the shortest paths. Likewise, the moderate correlation with the divergence measurement of Costa & Sporns (2005), which is also based on the computation of the shortest paths, has been resulted probably by a limitation of their method, as this index can be computed for every cortical area at radius 1. A major achievement is that the present analyses defined both the pairwise relationships and the integrative properties of the nodes in the network unequivocally in a quantitative way. These distinctive properties of CD can make it preferable to other indices used in the network analyses. Because CD depends only on the network topology, the node-reduced CD

representation can be calculated for any kind of network. Important implications are that CD distinguishes the edges in reciprocal connections and delineates the information flow, or its equivalents, without *a priori* knowledge, even in the networks with high-level reciprocity. The great agreement of the results of our analyses with the neurobiological data supports the usefulness of CD in network analyses.

(b) Cortical reciprocity

Our results uncover the complementary properties of reciprocated connections in the cerebral cortex by showing that reciprocal connections have approximately equal magnitudes of convergence and divergence. The complementarity is consonant with the role of forward connections in transmitting highly specific information and with that of the backward connections, which convey contextual information (e.g. Angelucci *et al.* 2002). Interestingly, the actual level of cortical reciprocity is close to the value where balance of convergence and divergence appears; a further increase in the number of reciprocated connections abruptly results in the complete balance of the network. This suggests that in the cortical networks, reciprocity is maximized without reaching complete balance between convergence and divergence. In fact, some of the corticocortical connections were found to be non-reciprocal (Felleman & Van Essen 1991). Furthermore, approximately 80% of the known connections are bidirectional in the cortex (Felleman & Van Essen 1991), which is comparable to the level of reciprocity in the datasets used here (Hilgetag *et al.* 2000*a*; Sporns 2002; Négyessy *et al.* 2006). In addition, it seems unlikely to obtain highly consistent results due to missing data using datasets from different sources. Our results suggest that reciprocity is not the rule in forming cortical connections, but the function that constrains the proper placement of the reciprocated connections in the cortex, similar to what has been suggested for the thalamus (Deschenes *et al.* 1998). In contrast to the cortical networks, random graphs are balanced at the low level of reciprocity. As ER graphs have not been designed to perform specific functions at all, including information processing, this observation fits with the expectation of a negligible role of directedness in this class of graphs.

It is noteworthy that convergence and divergence are present and balanced not only in the case of reciprocal connections but also at larger scales in the sub-networks including cliques and loops in the macaque cortex. Cliques exhibited higher balance than loops, as cliques are the densest sub-structures in the networks. Moreover, the difference in the balance between the sub-structures is due to the fact that the input and output sets of all the edges in the cliques are similar, but this does not necessarily hold for the edges present only in the loops. On the other hand, the increase in the balance with the size of the sub-network suggests that in contrast to local interactions, integration becomes more pronounced and important at larger scales in the cortex. The positive correlation for the randomly selected edges provides indirect support for this suggestion. The cat cortex differed from that of the macaque cortex in this respect. Whether this is owing to the different cortical organization

Figure 6. Effect of rewiring on the areas' CD in the cortical networks. (a) Rewiring the visuotactile network without changing the proportion of reciprocal connections has little influence. (b) Comparisons to full reverse correlation of the incoming and outgoing CDs (i.e. $y = -x$) characterizing the total reciprocity. Mean square error of linear fit was normalized by the number of vertices in the corresponding networks and plotted to show the essential role of the reciprocity level on the balance of the areas' CD in the cortical-like networks (solid lines, macaque visuotactile; dotted lines, macaque; dashed lines, cat). Note the low level of error and the lack of effect when rewiring the random graphs (circles, randomized version of the visuotactile network; pluses, randomized version of the macaque cortex). The two lines corresponding to the randomized version of the visuotactile network practically coincide; there is no difference related to rewiring between the two quadrants. Note also that the reciprocity level shown by the vertical lines is close to the point where complete balance starts to emerge in the cortical networks, i.e. where the sum of the CDs of a given sign terminating on an area starts to approach the sum of the CDs of the opposite sign originating from that area and vice versa. Thick lines and symbols represent average error of the linear fit in the upper right quadrant, and thin lines and symbols in the lower right quadrant (as shown in a).

in the two species or owing to insufficient data about the cat cortical connectivity remains to be tested. Considering the rudimentary knowledge of the cat cortical connectivity when compared with that of the macaque, our findings regarding the balance of networks, in general, favour the latter case.

(c) Cortical hierarchy as division of labour

Node-reduced CD exhibiting gradual transition between opposite source and allocating characteristics largely corresponds to the known cortical hierarchy in all the networks analysed (Felleman & Van Essen 1991; Scannell et al. 1995; Hilgetag et al. 2000b). This observation shows that cortical areas at different levels of hierarchy exhibit a characteristic role in cortical integration. Primary sensory cortices (e.g. V1, 3b), the most representative examples of 'source areas', have adaptive, isomorphic representations of receptor surfaces (Kaas 2000). On the other hand, 'allocating areas' receiving divergent connections and emitting convergent links could be important in preventing congestion in the network. We found area 46 of the prefrontal cortex as one of the typical examples of the allocating areas. This observation is consistent with the role of the prefrontal cortex (especially area 46) in executive functions via controlling the information flow in the cortical network (Goldman-Rakic 1987; Fuster 1997; Miller & Cohen 2001; Constantinidis & Procyk 2004; Marois & Ivanoff 2005; Miller & D'Esposito 2005). Remarkably, our observation is also in full agreement with human studies identifying homologous regions of the prefrontal cortex as the central bottleneck of information processing in dual-task decision making (Dux et al. 2006). Furthermore, the areas bridging the clusters (e.g. VIP, V4), and are in a key position to regulate cluster interactions, also exhibit allocating properties. This finding predicts bottleneck effects in exchanging information between clusters, which identify cortical processing streams (Goodale & Milner 1992; Young

1992; Jouve et al. 1998; Hilgetag et al. 2000a; Négyessy et al. 2006), during the performance of demanding tasks. It is important to note that both in cat and macaque, the areas exhibiting bottleneck properties correspond to the hubs identified by Sporns et al. (2007), who argued that these cortical structures play pivotal role in the coordination of the information flow. Considering the mid-level structures such as MT, V3 and area 2, the mixed convergent and divergent input and output connectivities suggest an intense interplay between top-down and bottom-up processes, which may explain the strong attentional effects shown within some of these areas (Kastner & Ungerleider 2000; Boynton 2005).

In conclusion, we presented evidence for the specialization of the cortical areas according to their role in cortical integration based on the degree of convergence through their connections and have identified two functionally complementary cortical sub-networks. This finding suggests that coordination of the information flow presents an evolutionary constraint in complex networks such as the cerebral cortex, in which information processing plays a primary role. Whether these findings are applicable to other complex networks remains to be tested. In cortex, the network architecture, as shown here, could be largely responsible for the structured organization of ongoing spontaneous activity (Raichle & Mintun 2006; Mantini et al. 2007), which was suggested as the main functional activity of the brain (Fiser et al. 2004; Raichle & Mintun 2006). These findings could be important when constructing and applying brain prosthetic devices and interfaces in the future.

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