

Opinion

# Socioconnectomics: Connectomics Should Be Extended to Societies to Better Understand Evolutionary Processes

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**Abstract:** Connectomics, which is the network study of connectomes or maps of the nervous system of an organism, should be applied and expanded to human and animal societies, resulting in the birth of the domain of socioconnectomics compared to neuroconnectomics. This new network study framework would open up new perspectives in evolutionary biology and add new elements to theories, such as the social and cultural brain hypotheses. Answering questions about network topology, specialization, and their connections with functionality at one level (i.e., neural or societal) may help in understanding the evolutionary trajectories of these patterns at the other level. Expanding connectomics to societies should be done in comparison and combination with multilevel network studies and the possibility of multiorganization selection processes. The study of neuroconnectomes and socioconnectomes in animals, from simpler to more advanced ones, could lead to a better understanding of social network evolution and the feedback between social complexity and brain complexity.

**Keywords:** social network; sociality; evolution; complexity; multilevel selection



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## 1. Introduction

Connectomics is the study of connectomes [1–4] or maps of the nervous system of an organism, mainly the brain in vertebrates and its analogous structure in invertebrates. Connectomics enables researchers to understand how information is treated and stored on microscopic (neuron basis) and macroscopic (brain module basis) scales. For example, how a disease affects brain structure and function or the variability in brain structure and how it changes with age. Connectomics is a set of network tools that helps researchers understand how the connective architecture of the brain is related to functional specialization. Recent computational advances have improved the measurement and storage of large datasets—those with thousands of connections between thousands of entities—analyzed primarily using graph theory or social network analyses (SNAs) [5,6]. These SNAs are used to assess how neural networks are structured regarding communities (i.e., modules), centralities (i.e., hubs and rich clubs), and efficiency (i.e., short communication paths), resulting in comparative and evolutionary applications concerning the function and selection of these neuronal architectures in different species [4]. Compared to neuroconnectomics, I propose that connectomics be applied and expanded to human and animal societies and social networks, leading to the birth of the domain of socioconnectomics. This involves transferring network analysis tools, applying natural selection concepts to social networks, and considering evolutionary processes (genetic selection, cultural selection, and multilevel selection [7,8]). This new study framework would open up new perspectives in evolutionary biology and add new components to theories such as the social brain [9] and cultural brain hypotheses [10]. According to the social brain hypothesis, brain size, particularly the neocortex, is related to group size. In contrast, the cultural brain hypothesis unifies more specific explanations centered on the environmental and social brain hypotheses, implying

that the brain was chosen for its ability to store and manage information acquired through asocial or social learning [10,11]. Therefore, the cultural brain hypothesis is a bit more complex and includes more parameters than the social brain hypothesis. Managing the complexity of social relationships—not just group size but identifying them, memorizing them, and identifying the social and cultural roles of group members according to environmental conditions—is challenging for animals, including humans. It should result in a link between social network complexity and brain complexity, indicating a link between neuroconnectomics and socioconnectomics.

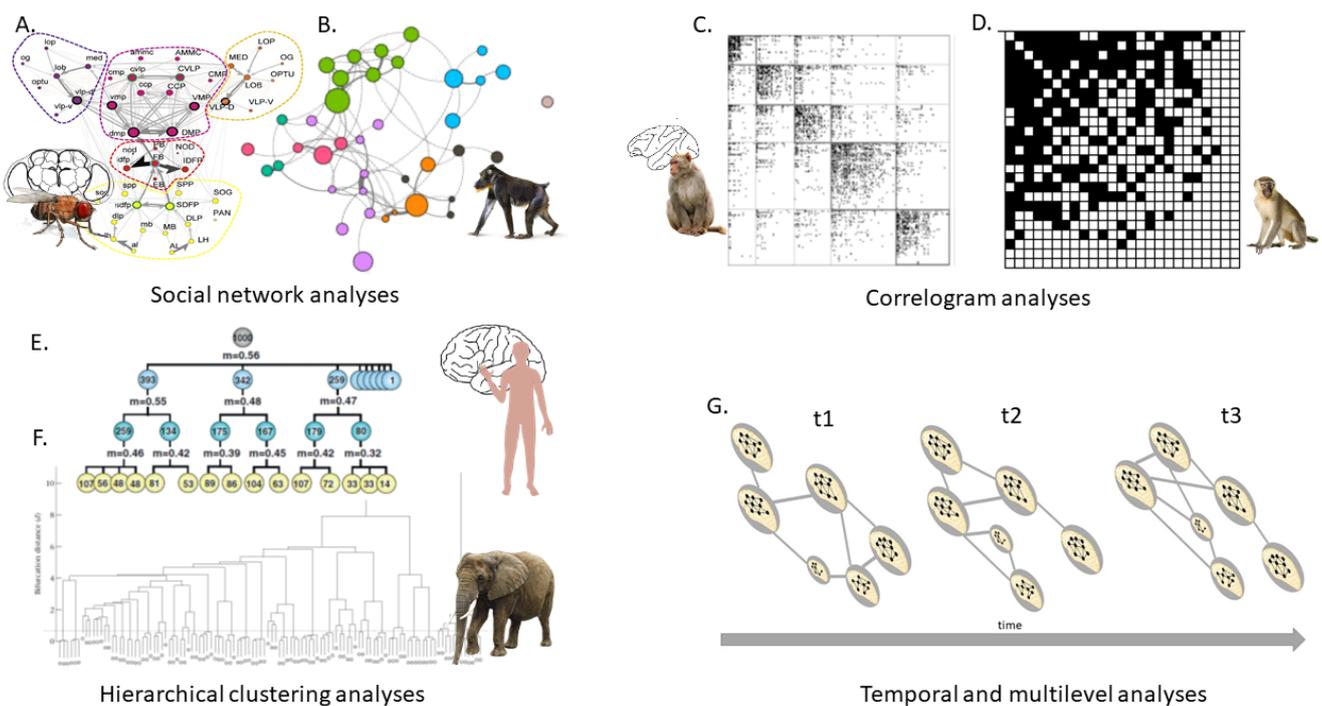
## 2. Universal Network Topological Properties

Based on the findings of Milo et al. [12], Oltvai and Barabási, in their study [13], proposed that the universal topological properties (e.g., scale-free connectivity, modularity, and hierarchy) observed from cellular to neural and ecosystem networks should be governed by similar principles. Other studies later proposed that such common features should reflect constraints imposed by selection forces and be shaped by evolutionary pressures [14,15]. Irrespective of the selection mechanism, we may wonder why networks—brain or society—“look the way they do and not any other way” [14]. Questions about neural networks are raised for human and animal societies, regarding how genetic and environmental interactions influence topology and its variability, how diseases affect structures, and how information is identified and shared [15]. Connectome architecture may follow general wiring principles that favor functionally important topological attributes that benefit efficient communication and global integration while minimizing biological resource expenditure. Many animals, including humans, live in societies because socialization improves fitness [16], allowing them to learn more about food, reproduction, and predators. However, proximity and social relationships increase the risk of disease. Individuals may become specialized to increase group efficiency, such as elders sharing information and leading, as societies face trade-offs of opposing forces increasing modularity [17,18]. Hence, answering questions about topology, specialization, and their links to functionality at one level (i.e., neural or societal) may help in understanding the evolutionary trajectories of these patterns at the other level. Henrich revealed that human evolutionary processes at the brain and social levels are always constant due to constant exchanges between these two structures [19]. Specific behavioral traits or personalities may be favored by genetic selection to a specific phenotypic composition of a group [20] and network topology [20,21]. For example, aggressive traits may be connected to modular networks. Similarly, cultural selection influences the transmission of adaptive behavior, and group members may choose to observe the best performers, modifying social network centralization [22,23]. Similar network “morphospaces” should be observed at these different levels if general selection principles apply to different levels of life organization [14]. Selection of network properties such as efficiency or modularity has been observed at the brain [24,25] and the group levels [26–28], implying that similar evolutionary processes may be responsible for these network topologies. For example, the network modularity of primate groups is higher than the modularity of theoretical networks with similar properties (e.g., size and density) [27], indicating a selection process supported by the fact that this network property and efficiency are linked to brain capacities in primates [26]. The same reasoning could be applied to ecosystems and their tropic and mutualistic networks [29].

## 3. Network Analyses at Different Life Organizations

Neural and social networks share a theoretical foundation, and they also share network analysis tools. This is not new, as social network analyses have been used in both domains for approximately 20 years. However, this statement contributes to a more solid understanding of socioconnectomics as neuroconnectomics. Measuring the connection or activity of an entity—whether a neuron or an individual—differs from neuroconnectomics, which is based on magnetic resonance imaging, electron microscopy, and histological techniques [1]. In contrast, socioconnectomics is based on ethological observations or

loggers [30]. However, the same network analyses are used to work on connectomes when these connections are measured (Figure 1). The generalized mathematical language of graph theory is now used in many scientific disciplines, allowing possible comparisons of connectomes at different levels. SNAs are a set of measures used at different levels of the network [6]: the entity level (a neuron or an individual), the intermediate level with the presence of clusters and their relationships, and the network level to assess global properties such as efficiency, diameter, density, or modularity [6,31]. When it comes to understanding the role of certain neurons or brain areas in linking others and explaining brain asymmetry, efficiency, or robustness (i.e., the ability to withstand failures and perturbations, mainly alternative pathways between two entities), betweenness centrality is also a popular and useful measure in animal social networks to understand the roles of individuals. For example, individuals with a high betweenness link different communities, allowing the transfer of information and leadership in dolphins [32] and dominance and policing characteristics in macaques (Figure 1A,B) [33]. Correlograms, which are used to show the existence of modules in the brain, are also used to determine communities in primates and how these communities are nested based on dominance (Figure 1C,D) [34,35]. Dendrograms and hierarchical clustering analyses can also be used to assess communities (Figure 1E,F). This has been demonstrated in elephants, where units fuse and split depending on the dryness of the season [36].



**Figure 1.** Instances of analyses used in neural and social networks study. (A,B) Common social network analyses used to assess individual (e.g., neuron or group member) and global properties, respectively, in the *Drosophila* brain and a group of mandrills. (C,D) Correlogram analyses measuring the existence of modules and nestedness [35] in the macaque brain and a group of vervet monkeys. (E,F) Analyses measuring clusterization in the human brain [37] and an African elephant population [36]. (G) Framework to study and compare socioconnectomes with neuroconnectomes over time. Figures are used with permission.

#### 4. Same Challenges to Understanding Evolution

The fact that the same toolkit can be used for neuroconnectomics and socioconnectomics is significant because this implies that the results can be compared between these two levels, allowing for comparative connectomics not only between brains [4] or societies [38] of different species but also between brains and societies. However, trials comparing

different levels of life organization in network topologies are extremely rare [12,13,35,39,40] because of a lack of exchange between scientific communities and different ways of considering evolutionary processes driving network topology. The same challenges arise when combining connectomics with comparative ethology and comparative neuroscience to discover common organizational plans while accounting for species diversity. However, scientists in both domains are concerned with the same methodological issues in obtaining, storing, and analyzing large datasets [2], necessitating the development of new tools. Both neuroscientists and behavioral ecologists would benefit from sharing technologies in this context. Beyond this technological comparison, the field of “comparative network analysis” [4] is used to examine similarities and differences across a range of network classes. It provides a powerful approach to answering the question of which topological network attributes are specific to nervous structures and which represent more universal network organization properties as human and animal societies. Therefore, it offers a unique tool for determining which network properties are unique to brain networks and which are shared with social networks.

## 5. Future Research and Challenges

Expanding connectomics to societies should be done in comparison and combination with multilevel studies and the possibility of multiorganization selection processes [7]. Evolutionary processes may favor the phenotypic composition of a group [41], implying that individuals with different personalities and, thus, social traits in a group may favor different network topologies. This is known as “collective social niche construction” [7]. This type of multilevel connectomics could be envisioned in two ways: first, as a multi-species comparison, and second, as a lifespan comparison, allowing researchers to assess the selection processes (genetic versus cultural) leading to specific network topologies.

*Multilevel selection:* There is no argument that the brain network is subject to selection pressures and evolves to reach a certain level of optimality [24,25,42,43]. However, it is more difficult to propose the same evolutionary theory for social network topology [44–49]. Hence, it is challenging to apply connectomics to societies in the same way it is applied to the brain. However, the social network topology is governed by the group behaviors of group members [8,50], whereas individual behavior is governed by genetic [51–53] and cultural selection [54,55] ([7] for a review of mechanisms). Pressures such as predation, access to information, pathogens, access to food, and mating may favor certain behaviors of individuals to increase their fitness by making them more central in their networks, closer to relatives, and so on. Therefore, it is possible to observe the selection of some network properties that may eventually favor the fitness of both some and all group members, even if the benefit is not distributed equally. Hence, rather than considering selection on a group level, I consider it on multiple levels [8,45]. Multilevel selection typically favors phenotypic benefits that can be shared by all group members [56]. The coding of a group phenotypic composition [41] for network topology may be favored by evolutionary processes and could be referred to as “collective social niche construction” [7]. This consideration makes it possible to apply connectomics to societies.

*Multilevel connectomics:* The study of neuroconnectomes and socioconnectomes in animals, from simpler to more advanced ones, could lead to a better understanding of social evolution and the feedback between social and brain complexity. It would be specific about how social structures influence individual fitness and, consequently, the selection of heritable social traits. The cultural brain hypothesis states that brain complexity in humans is not only due to our social complexity but also to the ability of our brain to store, manage, and share information [10,11]. Directly comparing neuroconnectomes with socioconnectomes of different individuals in different species, as with the cultural brain hypothesis, by comparing different ethnic groups could add more elements to confirm or deny the social brain hypothesis. A similarity index could be measured between indices (e.g., efficiency, modularity) of the neuroconnectome and the socioconnectome of an individual, human, or animal, and the similarity index could be compared across species, environmental condi-

tions, and other variables. One important question is how the brain and social complexity are linked. Several studies have found a positive correlation between the two connectomes in mammals [9,57], giving rise to the social brain hypothesis and, later, the cultural brain hypothesis. However, these hypotheses are still being debated [58–61]. The link is not obvious in other animal taxa and may even be inverted, as in eusocial insects, whose brain structures may be simpler than in vertebrates. Nevertheless, societies remain highly complex [42,62]. Moreover, it would be critical to show how certain neural connectomes underpin specific social behaviors. We already know that certain brain parts are linked with some behaviors, such as language, emotions, and other capacities. Apart from the connection between different parts of the brain allowing the emergence of consciousness, which is linked to the theory of mind and social complexity, we do not know how neuroconnectomes may influence socioconnectomes. Beyond simple correlation studies, one could consider selecting specific neuroconnectomes in species such as *Drosophila* and assess how they are linked to the social behavior of the species and the emergent social network.

*Aging connectomics:* Several studies have found a link between social complexity and brain size based on the social brain hypothesis [9]. However, developing social interaction capability in vertebrates and their corresponding neural networks involves a critical temporal dimension (Figure 1G) [63]. Nonetheless, this longitudinal aspect is just gaining momentum. Animal brain size, structures, and social relationships take time to develop, and may take several years [64–66]. This implies that there is a temporal dimension to investigate in developing these two structures. This hypothesis has recently been tested intraspecifically with some individual brain structures linked to several social partners [67]. However, very few studies have been conducted to investigate how some brain structures are linked to social centralities of group members and, more generally, network topologies, and how age affects neuroconnectomes and socioconnectomes. Measuring the two parameters at different ages or life stages of individuals would reveal processes that link sociality to longevity and brain aging. Multilevel connectomics, which means linking the neuroconnectome to the socioconnectome, could also be envisaged across the lifespan [3] of an individual, from birth to death, as both sociality and the brain change with age. The social network of an individual specifically is flexible throughout their life and appears to be partly independent of chronological age, with regulatory processes and bidirectional effects on individual senescence and fitness [63]. The question of the directionality of the effect between changes in the brain and social network remains unanswered, and a detailed longitudinal study of connectomes spanning the lives of individuals could provide an answer to the causality issue. It could also lead to direct applications in brain diseases linked to sociality. It is difficult to study this developmental covariation between neuroconnectomes and socioconnectomes because it requires measuring. For example, the brain structure of all group members undergoes changes throughout their lives. Technologies such as fMRIs exist only for animals of a certain size and are still expensive for large and long-term studies.

## 6. Conclusions

To better understand how our brain and social world are structured, we can use network analysis tools to connect two disparate domains while answering similar questions about network properties and functionalities. In the same way we study brain structure (neuroconnectomics), we should study the evolution of social structures (connectomics). This way of thinking, which incorporates multilevel selection, could lead to a better understanding of the back and forth between different levels of organizations. Further, it advances our understanding of brain complexity concerning sociality, adding elements to the social and cultural brain hypotheses. Hence, as neuroconnectomics is the study of brain structures and the evolutionary processes underlying them, socioconnectomics should become the study of social networks and the evolutionary processes underlying them. This framework could also be extended to other types of networks, potentially resolving one of the most important scientific questions concerning the universality and evolution of

some physical and biological rules. Further, supposed selection and evolution were found to apply to many levels of living organizations [12,14]. In that case, there is no reason why they should not also apply to all of them, particularly to animal and human social networks [7,68,69].

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