Contributions of Graph Theory and Algorithms to Animal Behaviour and Neuroscience

Nikolaos Smit
A0024

Examination committee:
Prof. Dr. Michael C. Dracopoulos, Department of Mathematics, NKUA.
Prof. Dr. Dimitrios Thilikos, Department of Mathematics, NKUA.
Dr. Dimitrios Zoros, Department of Informatics and Telecommunications, NKUA.

Supervisor:
Prof. Dr. Dimitrios M. Thilikos,
National and Kapodistrian University of Athens, Department of Mathematics.

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ABSTRACT

Graph theory and algorithms offer precious toolboxes for the modelling as well as the analysis of numerous phenomena in natural sciences. Here a review of the modern bibliography is presented, divided in four main chapters, giving some indications on how the concepts of these two disciplines can be used for the study of animal behaviour and neuroscience. As an exception the premier part of the first chapter provides a short discussion on the applications of graph theory on molecular biology. This choice made in order to make this work more complete and give to the readers from various backgrounds an, as much as possible, overall view of the future potential of such interdisciplinary approaches. The rest two sections of the first chapter deals with brain networks and central terms of graph theory, such as centrality, in their study. The second chapter introduces some concepts of animal sociality and refers to studies of animal cooperation, focusing on evolutionary graph and game theory. Moreover, in the last section of this chapter the collective motion of animal groups is discussed providing, into the bargain, an introduction of basic terms for the subsequent third chapter. Interdisciplinary research, aiming to unite methods from different fields, is vastly used in order to answer biological questions. Although, as it is presented below, both the fields of algorithms and biology can contribute to the elaboration of each other. Hence, the third chapter provides information about algorithms whose design has been inspired by the (collective) behaviour of animals in the nature. Finally, the fourth chapter deviates anew from the central focus of the previous chapters and makes a short introduction in the substantial controversial computational nature of cognition and by extension behaviour. Overall, one can observe that the cooperation of the above mentioned fields is extensive while the accomplished research opens new questions which can be studied only in the light of such collaborations.

ΣΎΝΟΨΗ

Η θεωρία γραφημάτων και οι αλγόριθμοι προσφέρουν πολύτιμες εργαλειοθήκες για τη μοντελοποίηση καθώς και την ανάλυση πολυάριθμων φαινομένων στις φυσικές επιστήμες. Εδώ παρουσιάζεται μια ανασκόπηση της σύγχρονης βιβλιογραφίας, χωρισμένη σε τέσσερα κύρια κεφάλαια, δίνοντας κάποιες ενδείξεις για το πώς οι έννοιες αυτών των δύο κλάδων μπορούν να χρησιμοποιηθούν για τη μελέτη της συμπεριφοράς των ζώων και της νευροεπιστήμης. Κατ ’εξαίρεση, το πρώτο μέρος του πρώτου κεφαλαίου παρέχει μια σύντομη συζήτηση σχετικά με τις εφαρμογές της θεωρίας γραφημάτων στη μοριακή βιολογία. Η επιλογή αυτή έγινε προκειμένου να καταστεί η εργασία αυτή πληρέστερη και να δοθεί στους αναγνώστες με διαφορετικό υπόβαθρο, όσο το δυνατόν περισσότερο, συνολική άποψη για τη δυνητική χρησιμότητα τέτοιων διεπιστημονικών προσεγγίσεων. Τα υπόλοιπα δύο τμήματα του πρώτου κεφαλαίου εστιάζουν σε δίκτυα του εγκεφάλου και σε κεντρικές έννοιες της θεωρίας γραφημάτων, όπως η κεντρικότητα, στη μελέτη τους. Το δεύτερο κεφάλαιο εισάγει μερικές έννοιες της κοινωνικότητας των ζώων και αναφέρεται σε μελέτες της συνεργασίας στο ζωικό βασίλειο, εστιάζοντας στην εξελικτική θεωρία γραφημάτων και παιγνίων. Επιπλέον, στη τελευταία ενότητα αυτού του κεφαλαίου συζητείται η συλλογική κίνηση ομάδων ζώων, παρέχοντας εκτός των άλλων, εισαγωγή βασικών όρων για το επόμενο τρίτο κεφάλαιο. Η διεπιστημονική έρευνα, με στόχο την ενοποίηση μεθόδων από διαφορετικούς τομείς, λαμβάνει χώρα ευρέως για να απαντήσει βιολογικά ερωτήματα. Εντούτοις, όπως παρουσιάζεται παρακάτω, η έρευνα στους αλγορίθμους και στη βιολογία μπορούν να συμβάλλουν στην ανάπτυξη η μια της άλλης. Ως εκ τούτου, το τρίτο κεφάλαιο παρέχει πληροφορίες σχετικά με αλγόριθμους των οποίων ο σχεδιασμός έχει εμπνευστεί από τη (συλλογική) συμπεριφορά των ζώων στο φυσικό περιβάλλον. Τέλος, το τέταρτο κεφάλαιο αποκλίνει εκ νέου από το επίκεντρο των προηγούμενων κεφαλαίων και κάνει μια σύντομη εισαγωγή στο σημαντικό, αλλά και αμφιλεγόμενο, υπολογιστικό χαρακτήρα της νόησης και κατ’ επέκταση της συμπεριφοράς. Συνολικά, μπορεί κανείς να παρατηρήσει ότι η συνεργασία των προαναφερθέντων πεδίων είναι εκτεταμένη ενώ η πραγματοποιημένη έρευνα ανοίγει νέα ερωτήματα που μπορούν να μελετηθούν μόνο υπό το φως τέτοιων διεπιστημονικών συνεργασιών.

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Provided that this section is the only one (likely) in which I can write irrelevant stuff, I want furthermore to thank several subjects that without knowing it, were inspiring the, sometimes almost literary, trajectory of the present thesis with helpful comments. I would like to sincerely thank these people, including my professors, who awkwardly smirked (and asked "what are you doing here?") when I said that I am attending this MSc, while being a graduate of a biology department. I almost believed that I am a biologist, during all this period that they were calling me 'ο βιολόγος'. I should not neglect to praise among them, mostly those who afterwards were replying to hundreds of questions due to my unawareness. Last, but most significantly, I want to salute all these people (of the supplementary set of the one formed by all the above mentioned subjects) who do (or did) not have the chance to study and those who chose not to, in order to fight for Freedom.

CONTENTS

INTRODUCTION

Almost in every field of natural sciences interacting agents play a significant role, forming complex interaction networks, while multiple scientific works have been published using ‘graph algorithms’ for handling such networks. Here we focus on ‘biological networks’ from an algorithmic and graph theoretical perspective. The present thesis aims to provide a balanced discussion, so that both readers with a background in biology and mathematics or computer science will be able to follow its content. The first and the fourth chapter act as prologue and epilogue respectively, giving some indications of further fundamental (biological) issues that can be examined in the light of graph theory or/and algorithms, apart from animal (social) behaviour which constitutes the central subject of the thesis. In particular, the first chapter deals with the use of graphs in the study of molecular and (nerve) cell biology, two fundamental fields of biology, while the fourth chapter contains a trial to approach the ‘mystery of cognition or consciousness’ and its translation into behaviour, from an algorithmic perspective.

In the present introduction, some basic preliminary knowledge of graph theory and biology is provided, for readers who are not aware of both fields. Afterwards, a broad view of what could be considered as a graph or network in biology as well as its potential extent is presented. The second and the third chapter, the core of this thesis, focus on the structure and the collective behaviour of animal groups. In particular, the second chapter contains subjects with regard to sociality and cooperation within animal groups by focusing on evolutionary graph and game theory as well as coordination of animal groups translated into collective movement such as flocking. Ultimately, in the third chapter algorithms inspired by the aforementioned animal behaviours are described.

0.1 Preliminaries I: Graph theory

Some fundamental concepts of graph theory are presented below, based on the book ‘Graph theory’ of Diestel [Diestel, 2018], unless noted otherwise. More specific terms referring to graphs or algorithms and used in later sections, are defined to the corresponding paragraphs. Approaches that explain techniques of handling big amounts of network data using graph theory can also be found in the increasing number of relative bibliography (e.g. [Eckman and Brown, 2006]).

A graph, denoted by the letter G, is an ordered pair of sets $G = (V(G), E(G))$, where the elements of $V(G)$ are the vertices and the elements of $E(G)$ are the edges of the graph G. More simple the set of vertices is denoted with the letter V and the set of edges with the letter E. The two basic features of a graph is the number of vertices $n = n(G) = |V(G)|$ and the number of edges $m = m(G) = |E(G)|$. The elements of E are two-element subsets of V, namely $E \subseteq [V]^2$ while V and E are disjoint ($V \cap E = \emptyset$). e is an edge at a vertex v, or equivalently a vertex v is incident with an edge e if $v \in e$. The two vertices joint with an edge are called the edge’s ends, whereas two vertices which are incident with a common edge or two edges which are incident with a common vertex are called adjacent. Two distinct adjacent vertices are called neighbours and the set of neighbours of a vertex v in G is denoted by $N_G(v)$. Pairwise non-adjacent vertices or edges are called independent, whereas whether all the vertices of G are pairwise adjacent, then G is called complete. If each edge e of G is associated with a real number $w(e)$, called its weight, then G is called a weighted graph [Bondy et al., 1976].

If $G = (V(G), E(G))$ and $G' = (V'(G), E'(G))$, while $V' \subseteq V$ and $E' \subseteq E$, then G' is a subgraph of G (and G a supergraph of G'). Two graphs G and G' are isomorphic if there is a bijection ϕ between the vertex sets of G and G' such that any two vertices u and v of G are adjacent in G if and only if $\phi(u)$ and $\phi(v)$ are adjacent in G'. If each vertex of G has the same degree (number of neighbours) k, then G is k-regular (or simply regular) graph. A cycle is a (2-regular) graph whose vertices can be arranged in a round sequence in order that two vertices are adjacent only if they are consecutive in the sequence [Bondy et al., 1976]. A path is a graph $P_k = (V, E)$ where $V = \{x_0, x_1, ..., x_k\}$, $E = \{x_0x_1, x_1x_2, ..., x_{k-1}x_k\}$ and x_i are all distinct. The distance $d_G(v, u)$ of two vertices v and u in the graph G is the length of a shortest $v - u$ path in G. The largest distance between two vertices of G is called diameter of G. If there is no path between two vertices v and u, it is setted $d_G(x, y) := \infty$. The Cartesian product $P_m \times P_n$ of two paths is the $(m \times n)$-grid or lattice (Fig. 1). When the set E of the edges, contains ordered pairs of vertices which are called directed edges (or arrows), the graph $D = (V(D), E(D))$ is called directed. The in-degree $d_D^-(v)$ and the out-degree $d_D^+(v)$ of a vertex v in D stand for the number of arrows heading to and from v respectively [Bondy et al., 1976].

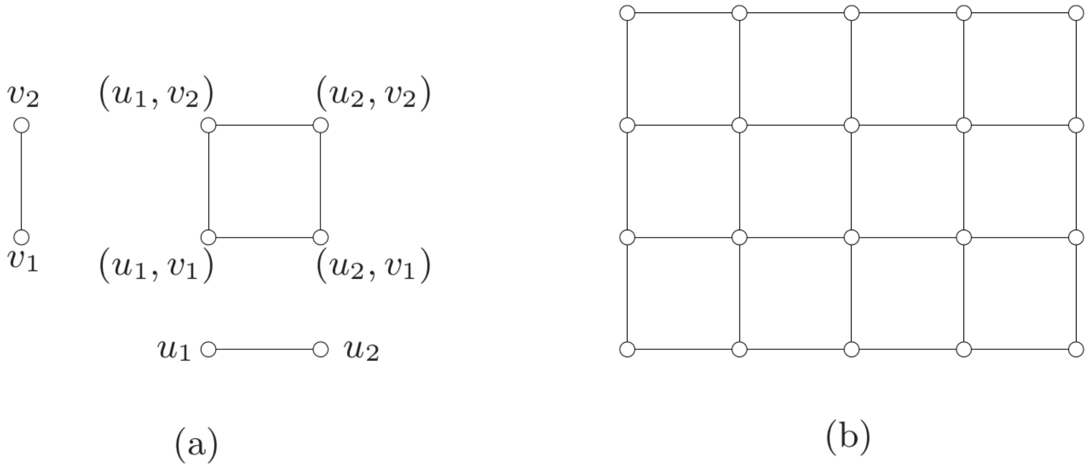


Figure 1: Lattices. (a) The Cartesian product $K_2 \times K_2$ and (b) the (5×4)-grid. Source: Adapted from [Bondy et al., 1976].

A graph is usually depicted by drawing a point for each vertex and joining two of them by a line if the two-element set of the corresponding two vertices are in E. Graphical representation of graphs helps in understanding their properties. Last but not least, provided that the subjects (or objects) that are represented as vertices in biology appear to have dynamic properties (destruction/death, alternation in behaviour etc.) the graphs have to follow the changes. In dynamic graphs some qualities such as set V, set E or the weights of the vertices and/or edges change over time [Harary and Gupta, 1997]. When a vertex is removed all its incident edges are removed as well.

0.2 Preliminaries II: Biology

0.2.1 Molecular and Cell biology

Each network-focused study is rooted in the mathematical discipline of graph theory. Such studies find application in a wide variety of biological networks, the structure of which has been shown to be non-random [Pavlopoulos et al., 2011]. The first sector of biology that one meets network structures is molecular biology which mainly refers to DNA and protein molecule interactions. Genes, proteins or even cells can represent vertices, and potential connection between these components (e.g. chemical reactions) can be regarded as edges. For instance, metabolic pathways constitute highly complicated networks, and their analysis lead us increasingly closer to the understanding of the chemical microcosm of the living organisms.

Therefore, in the premier part of the first chapter, concepts of molecular biology are discussed even if these are not directly related to neuroscience or animal behaviour.

As mentioned above, the vertices of the examined networks represent chemical molecules, where largely refer to DNA and proteins. A DNA molecule consists of a double helix of two coiled strands composed of four ‘structural units’, the nucleotides. Each nucleotide is characterised in relation to one of the following nitrogen-containing (nucleo)bases that embodies: thymine (T), adenine (A), cytosine (C) or guanine (G). Apart from the nucleo-bases each nucleotide is composed of a sugar (deoxyribose) and a phosphate group. The two strands are held together by hydrogen bonds existing only between pairs of complementary nucleobases, that is A-T and C-G. Provided that the two strands are complementary, knowing one of them, is enough for the reconstruction of the other one [Baker et al., 2003]. On the other hand, a protein molecule consists of one or more chains of organic compounds called amino acids. These chains result from the translation of DNA molecules and can fold into a specific three-dimensional structures that determines their activity [Branden et al., 1999]. The most enzymes are protein molecules.

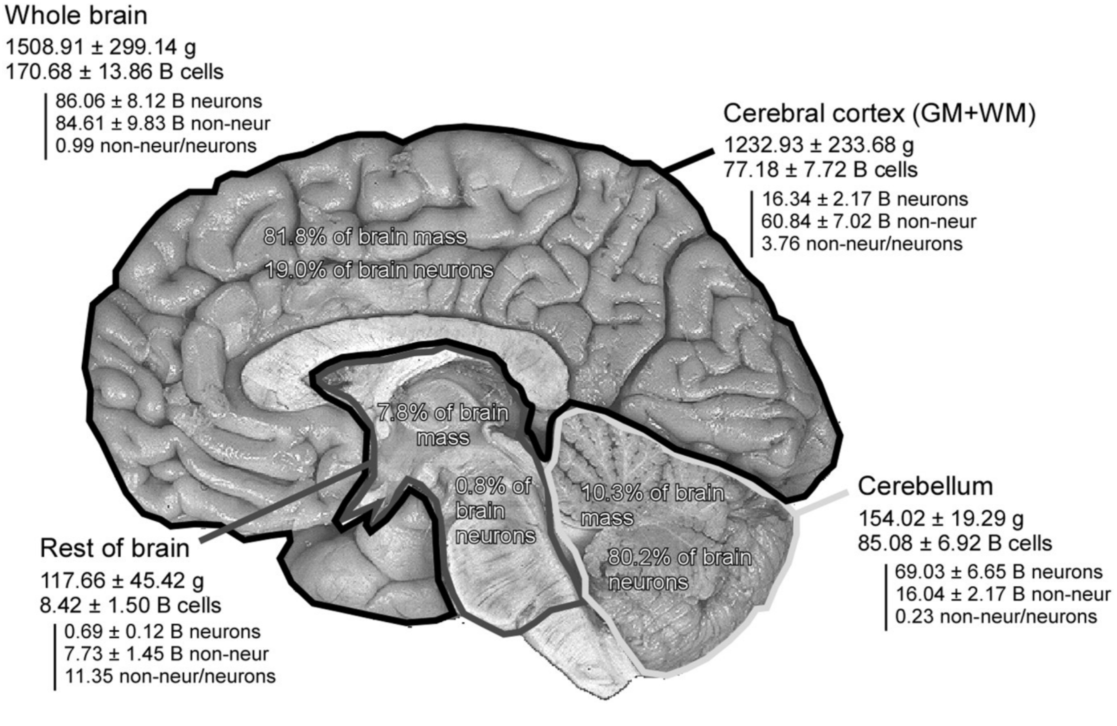


Figure 2: The human brain in numbers. Absolute mass, numbers of neurons, and numbers of non-neuronal cells in the entire adult human brain. Each value is the mean ± the standard deviation and refers to both hemispheres together. ‘B’ stands for billion. Source: Adapted from [Azevedo et al., 2009].

Neuroscience has also definitely taken advantage of network analysis. There are not many years that these disciplines cooperate but the results from their combination are already resonant. Graph theory has stimulated new research for the understanding of the brain as a intricate system of interacting components. Neurological and psychiatric disorders are nowadays studied in the light of network modifications, while the last years, there have been published several studies focused on brain connectivity using graph theory (e.g. [Sporns, 2003, Mason and Verwoerd, 2007]). One can find a wide range of fundamental graph theory constructs in these studies such as cut-vertices and bridges, centrality and density measures, in- and out-degree and so on. The human brain is believed to be bigger than expected for a mammal of this size. Adult male brain embodies an average of 86 billion neurons [Azevedo et al., 2009] without even mentioning the synaptic connections (Fig. 2). Therefore, we can likely imagine how complex are the networks that graph theory has take on to analyse.

0.2.2 Ecology - Behaviour - Sociality

The term of 'biological networks' may refer to networks of molecules, cells, individual organisms or even populations and species. This paragraph indicates the complexity that a network can have in the study of interspecific interactions. In natural communities, certain species are of high importance due to their links to many others. Each species plays a different role in the several ecosystems and their maintenance. This role may emerge from the interactions among species, which can be investigated in the light of network analysis. The most influential species are found to be located in central positions in networks of interspecific interactions. Jordán applied network analysis in food webs and suggested a simple method for describing the interaction structures in complex networks including three options (Fig. 3) [Jordán, 2009]. The first option refers to aggregation of several components of the networks in order to make the overall networks more manageable. This is not always an easy process, since the aggregation rules are not universal, although it has already used in ecosystems ecology [Christensen and Pauly, 1992]. The second option has to do with the isolation of only a part of the graph (subgraph), and examination of the interactions within it, where the main difficulty refers to the external effects from vertices out of the subgraph. The last option is to detect the central/critical vertices and to focus on them.

Inter-individual interactions are essential for understanding the dependence of collective behaviours (BOX 2.2) on the individuals' actions. Animal groups such as herds of mammals, schools of fish, flocks of birds and swarms of insects exhibit a variety of behaviours including swarming about a food source or migrating over large distances in aligned groups. Group living and collective behaviours are often advantageous, regarding the efficiency of harvesting and foraging, the following of migration routes (and aerodynamic in avian systems), predation avoiding/defending and so on [Sumpter, 2010]. According to Sumpter, when someone studies collective animal behaviour, it is essential to determine the algorithmic principles which un-

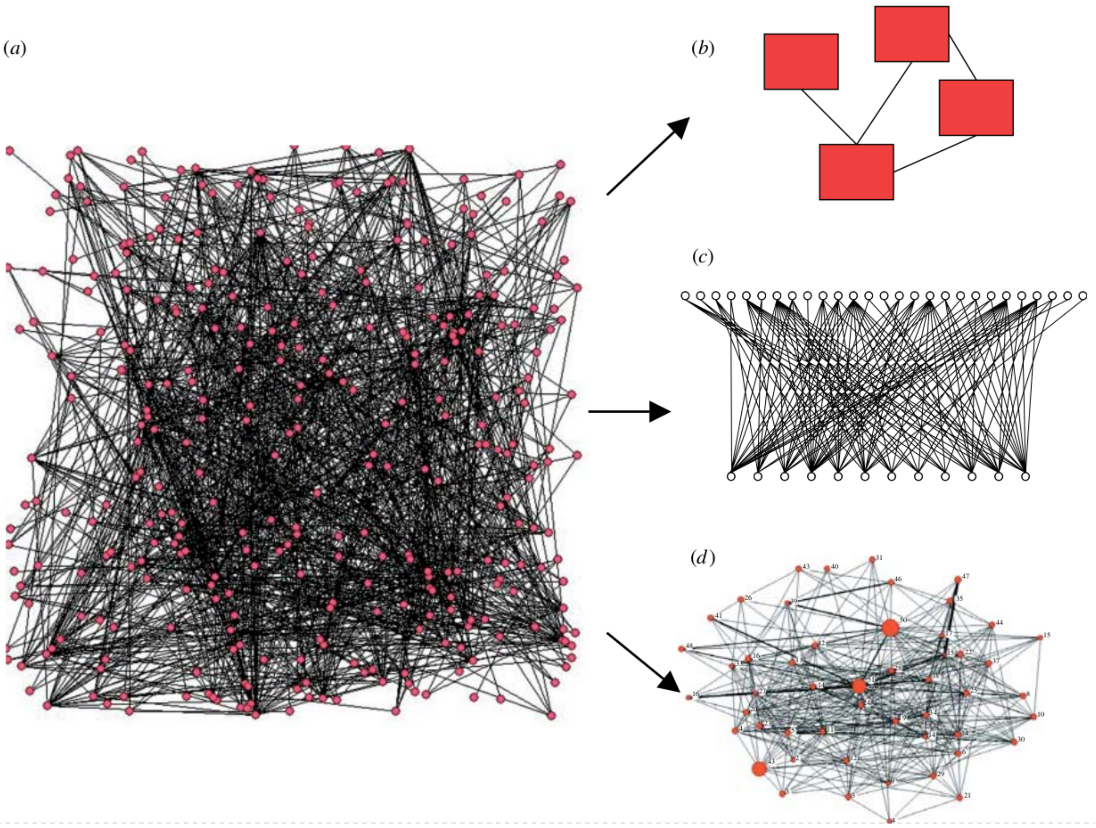


Figure 3: Three ways to efficiently study a complex network. (b) Aggregation to 'larger' vertices, (c) focus on a subgraph and (d) detect and focus on the most central vertices. Source: Adapted from [Jordán, 2009].

derpin these behaviours [Sumpter, 2006]. For the study of these algorithmic principles, one can make use of graph theory which has already monumentally contribute in the field of sociology. From a biological point of view, animal societies constitute highly useful study systems, providing better understanding of the social evolution, a fundamental sector of biology.

Individuals with different social roles in animal communities are examined often in the same way as in regular sociology and by extension the same 'tools' can be used in both fields. As an example, social insects (ants, bees etc) have been the subject for thousands of scientists around the world (see [Gordon, 2010]). Ants, a well studied organism, form extensive communication or trail networks. Experiments in the laboratory are commonly on the scale of centimetres, nonetheless in natural conditions such species create trail networks on the scale of kilometres [Hölldobler et al., 1990]. Deneubourg et al. examined the chemically mediated ant communication and suggested that simulation of

Figure 4: Foraging patterns of an army ant covering some 50x20m. Source: Adapted from [Deneubourg et al., 1989].

simple pheromone trail-laying and trail-following behaviour is sufficient for the creation of the ants' complex trail networks [Deneubourg et al., 1989]. Figure 4 depicts the foraging pattern of an army ant, indicating the extent which can be reached by a single individual. The foraging system includes thousands of individuals, which communicate with local chemical and tactile stimuli, and can cover $1000m^2$ per day. The resulting trail structure is created on a much larger scale than this of a single individual.

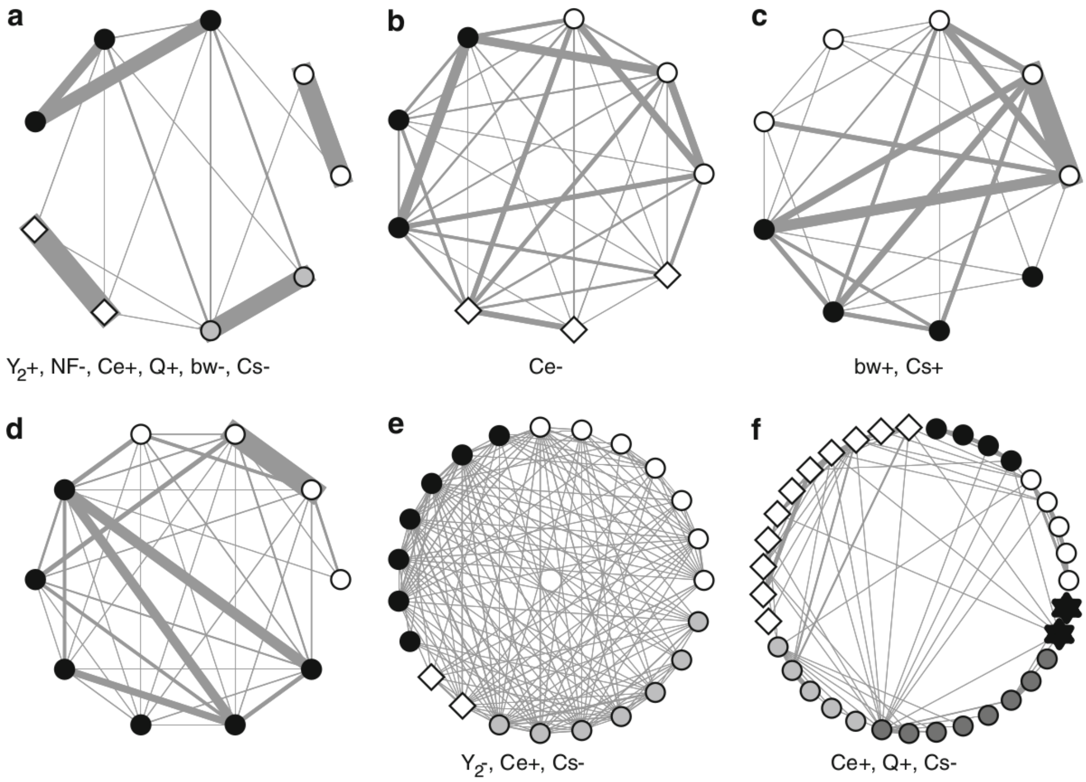


Figure 5: Edge (interaction) thickness represents edge's weight. Individuals (vertices) are represented by different symbols regarding the assignment to different subgroups. (a) Captive squirrel monkeys, (b) wild adult male chimpanzees, (c) wild wedge-capped capuchin monkeys, (d) captive long-tailed macaques, (e) wild bonnet macaques and (f) wild baboons are the six studied species. Symbols $+$ and $-$ stand for high or low values of the following metrics: edge weight disparity (Y_2), network flow (NF), eigenvector centrality (Ce), community modularity (Q), strength assortativity (bw), and vertex strength centralization (Cs). For explanation of the metrics, see below as well as the original publication: Source: Adapted from [Kasper and Voelkl, 2009]

Information flow is a concept that enhances our knowledge of collective behaviours of social animals. Using fundamental metrics of graph theory, social network analysis has been applied to the study of such inter-individual interactions and information flow in multiple organisms (e.g. fishes: [Jones et al., 2010]). Ilany and Akcay claimed that the emergence of social structure has been considered an outcome of social inheritance, for instance, offspring may have more chances to create ‘maternal contact’, that is to establish stronger bonds with individuals who interact with their parents [Ilany and Akcay, 2016]. Lusseau studied a network of dolphins and created a model of network’s responses to the removal of individual vertices [Lusseau, 2003]. As a result, the network’s diameter was slightly increased even after the removal of up to 30% of the group members. This suggested the resilience of the dolphin group to membership alteration. McCowan et al. investigated the utility of social network analysis for the study of primates [McCowan et al., 2008] whereas Kasper and Voelkl focused on primate groups with figure 5 effectually illustrating the interactions (edges) of individuals (vertices) in different groups as well as the examined metrics in their work [Kasper and Voelkl, 2009]. McCowan et al. supported that network stability influences the rhesus macaque individuals and the interactions among them [McCowan et al., 2011]. Overall, network analyses are essential for the investigation of animal communities, while these examples give only some first indications of the relevant research.

In 2009 four attributes of social network structure which concern behavioural ecologists were presented [Sih et al., 2009]. Firstly, within an animal group, differences in the social experiences and links of the members influence group as well as individual processes. Secondly, indirect links often play an important role. Thirdly, the significance of each animal in the network is dissimilar. Fourthly, and last, aspects of social networks can carry over across contexts. Graphs can represent relations referring to mate choice and sexual selection, predator-prey interactions, male-male competition, cooperation (e.g. anti-predator behaviour), reciprocal altruism, eavesdropping, space use (topological studies), kin selection, dominance ranks, social learning, information flow, foraging tactics, and grooming taking into account the four above mentioned attributes. Finally, provided that the studied networks depend on individual roles, one has to consider the interaction networks as series of dynamic events. For instance, death or removal of an important individual acting as a ‘social bridge’ and located by centrality measures, can likely result in group division [Flack et al., 2006].

CHAPTER 1

GRAPHS OF MOLECULES AND CELLS

Speaking about cells, maybe it is time to abolish them, or at least put only molecules inside and not beings.

1.1 Macromolecules

1.1.1 Some basic types of networks

Metabolic networks largely refer to biochemical reactions catalysed by enzymes. In terms of graph theory, enzymes or metabolites stand for vertices and an edge depicts either the connection of two enzymes that catalyse consecutive stages in a reaction chain, that is the product of the first reaction is the substrate for the second, or the connection of metabolites that participate in the same reaction. Metabolic networks, in general, include much more information as compared with other types of networks (e.g. cell-signalling and gene-regulatory networks). The above observations have been largely made in the bacterium *Escherichia coli* metabolic network [Edwards et al., 2001].

BOX 1.1

In **scale-free networks**, the number of edges k of a given vertex exhibits a power law distribution $P(k)\ k^{-\gamma}$, where $P(k)$ is the probability that a vertex has an edge in common with k other vertices. The probability of linking a given vertex i to a newly added one is proportional to the number of existing edges k_i adjacent to the vertex [Barabási and Albert, 1999].

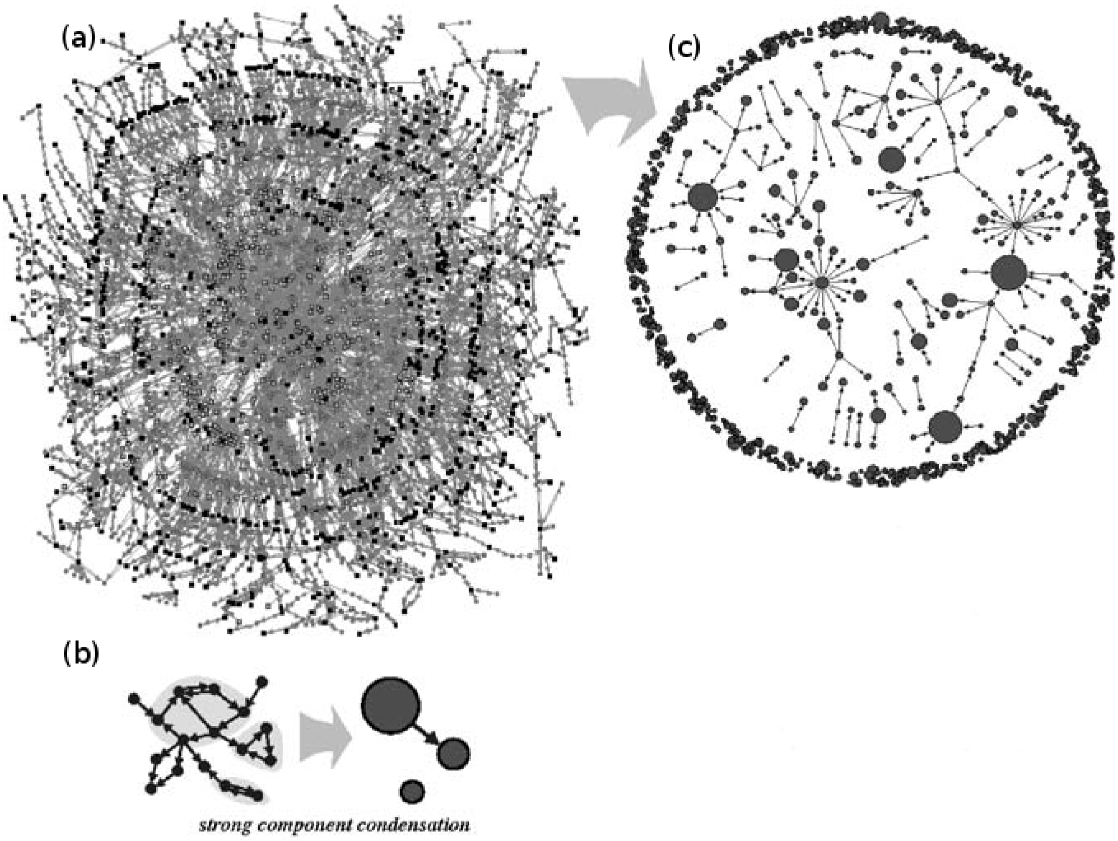


Figure 1.1: E. coli protein reaction network. (a) Illustration of the largest weak component (all vertices are connected by some path, ignoring direction) of a network, consisting of protein vertices (circles) and reaction vertices (squares). (b) The procedure of making the strong component graph. (c) The strong component graph in which, a directed edge (arrow) indicates the existence of a path connecting the two strong components in the original graph. Source: Adapted from [Ganguly et al., 2009]

Figure 1.1 illustrates the protein reaction network of *E. coli*, a common biological study organism. Its network can be depicted as a directed graph with 2846 vertices representing proteins and 2774 edges representing reactions. The graph consists of many relatively small strong components (a subgraph in which every vertex is reachable from any other), that is sub-graphs where there is a directed path between each pair of vertices. **Protein-protein interactions** (PPI) are essential for almost all cellular functions. Proteins usually operate through several interactions among them or with other biomolecules forming complex networks. The computational analysis of these networks is a major challenge. Protein-protein interaction (PPI) networks [Jeong et al., 2001] as well as metabolic networks [Jeong et al., 2000], part of the numerous biochemical networks in a living organism, often have the properties of scale-free networks (Box 1.1). In these networks, there are vertices of higher and lower significance, referring to the survival of the organism. Scott et al. introduced efficient (linear-time) algorithms for finding simple paths and rooted trees in graphs [Scott et al., 2006]. These algorithms were applied to protein interaction networks finding protein interaction pathways and are capable of reconstructing signalling pathways as well as of identifying functionally enriched trees.

Regulatory networks (GRNs) participate in the procedures of the central dogma of molecular biology (Fig.1.2) which refers to the flow of sequential information coded in the genetic material [Crick, 1970] and states that this information can not be transferred back once it has translated to protein. These networks include molecular regulators that interact with each other and the genetic material (that stores the genetic information of an organism and it is either DNA or RNA) and control the expression of the genes. The importance of these networks can become perceivable if one considers the accuracy of the molecule concentrations in an organism and that infinitesimal changes in the quantity of a protein can affect the cellular differentiation, which is the fundamental process in which a cell specialises in a cell type, e.g. gamete or nerve cell [Slack, 2009]. Overall, since every cell of an organism has the same genes, it depends on these networks, which genes will be translated to proteins. The network becomes more complex, if we consider that some genes may be linked either because their products participate in a common process or because they tend to be inherited together (e.g. They are located nearby, in the same chromosome).

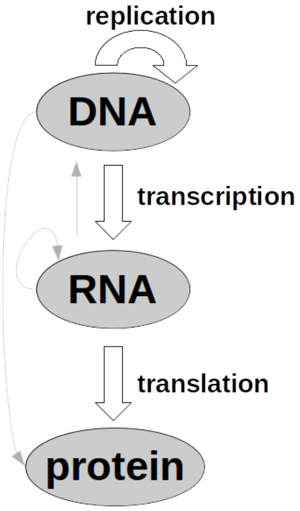


Figure 1.2: The central dogma of molecular biology. Black arrows show the general transfers and grey arrows special ones.

Gene-regulatory networks can be represented as directed graphs with activation/inhibition pathways. Transcription factors, usually proteins that have emerged by the translation of a gene, control the expression of genes which are translated into proteins that potentially act as transcription factors and so on. **Signal transduction networks**, that coordinate cellular responses, can be also represented as directed graphs and the individual paths could be distinguished in neutral, activating or inhibiting regarding their role. One example is the neural signals emerging from the nervous system, for the activation/inhibition of muscles. The complex interactions within these networks occur in the interior or the exterior of the cells among macro- or micro-molecules. Signalling pathways often include patterns, significant for the accomplishing of the transduction, such as feedback loops [Bhalla and Iyengar, 1999], which are overall common in biochemical networks and make them hard manipulable.

A rather lately examined network is that of **miRNAs**, which are short (~22 nucleotide) sequences of RNA that pair with mRNA molecules controlling their translation into proteins [Ruvkun, 2001]. mRNA is the usual mediate between a gene and the protein translated by the gene, namely it is the product of transcription that will be translated into protein. miRNAs are small non-protein biomolecules that participate in intracellular regulation and have mostly known sequence, therefore the identification of the interactions' network (miRNAs-expressed genome) it is (computationally) feasible [Shalgi et al., 2007]. Finally, the examination of the miRNAs' interactions may help to describe the complex regulatory mechanisms in the drug treatment [Cilek et al., 2017].

1.1.2 Motifs

Biological functions such as gene transcription or translation are regulated by intricate networks of proteins (PPI), transcription factors, cells and more. Some motifs, that is, repeatedly occurring patterns are over-represented in these networks as it has been proved after comparisons with random networks. Furthermore, comparisons of regulatory networks of different organisms could probably unveil interesting evolutionary information referring to conserved patterns. Motifs can be considered as one more characteristic in (applied) graph theory along with clustering coefficient (cliquishness) and so on. Nevertheless, it has been shown that tracking down a motif is not essentially significant [Lesne, 2006]. *In vivo* analyses that examine the role of motifs as a part of large networks are still challenging. It would be a reasonable conjecture that each motif has its particular importance. Interestingly, in 2005 it was published a work claiming that the plethora of the motifs does not have any immediate functional or evolutionary counterpart [Mazurie et al., 2005]. The authors proposed as an explanation the presence of the motifs inside a variety of network formations, or more simple, that they share vertices or edges with the rest of the network.

BOX 1.2

Graph Alignment: Find an one-to-one mapping across the vertices of two (or more) graphs such that, if two vertices are connected in the first graph, their images are connected in the other graph(s) [Feizi et al., 2016]. We can observe the similarity of the problem to this of Graph Isomorphism (BOX 1.4). That being said, a reduction is pointless, considering that Graph Alignment aims to find the superior (maximum overlap) mapping with the minimum error if an exact alignment is not feasible (optimization of a cost function).

In the context of 'motif studying' there was developed a noteworthy algorithmic procedure, relevant to this of sequence alignment, described as Graph Alignment (Box 1.2) [Berg and

Lässig, 2004]. We know that sequence alignment is well studied and there are platforms, such as BLAST (Box 1.3), dealing with it adequately (polynomial-time algorithms). Hence, graph alignment seems to be more challenging as a computational problem, since we do not still know any suitable polynomial-time algorithm. The above mentioned procedure was using a scoring function, emerging from a stochastic model, that measures the statistical significance of motifs. Another innovative question that the same study was dealing with, is the consideration of network evolution as a stochastic process.

BOX 1.3

Basic Local Alignment Search Tool (**BLAST**) is a bioinformatic tool, based on an algorithm which compares primary biological sequence information, that is amino-acid sequences (proteins) and nucleotide sequences (DNA and/or RNA). It can compare a query sequence with one or more sequences' databases and identify these which resemble the query sequence above a specified threshold. The most common comparison are these of a protein query to a database of proteins or both strands of a DNA query against a DNA database, however there are many versions combining different features [Pevsner, 2015].

Detecting network motifs by exhaustively enumerating all subgraphs needs runtime strongly increasing in relation to the network size. As a response, Kashtan et al. have introduced a 'random sampling' algorithm for estimating subgraph concentration/detection with runtime asymptotically independent of the overall size of the network [Kashtan et al., 2004]. This approach, according to the authors, makes possible the estimation of subgraphs' concentrations in larger networks in a higher extent than before. It has further been showed that machine-learning algorithms along with motif search algorithms perform very well in predicting interacting proteins [Albert and Albert, 2004]. Using the conserved properties of a protein-protein interaction network, they can succeed rates of 20-40% for predicting the correct interaction partner of a protein.

The detection of modules, motifs or clusters, in interaction networks, has been concurrently achieved on multiple graphs. Koyutürk et al. presented an efficient (computational tractability) algorithm for detecting frequently occurring patterns and modules in metabolic pathways and other biological networks [Koyutürk et al., 2004]. For more details about motifs in graphs and networks in biology, see [Mason and Verwoerd, 2007].

1.1.3 DNA and sequencing

The most non-biologists relate DNA with any research in biology, hence a more detailed discussion about it could not be excluded from the present thesis. There are plenty examples of graph models, helping the mathematically characterization of DNA sequences. Qi et al. introduced a method that creates a directed graph for each DNA sequence, and aims to the determination of sequence similarity, a typical task that biologists face on a daily basis [Qi et al., 2011]. The credibility of this methods was verified by comparing the results to previous studies, while the time complexity was shown to be low in comparison to other alignment-free methods. One further example is the parallel graph decomposition algorithm participating in DNA sequencing published in 2004 [Bokhari and Sauer, 2004], which was using the output from a nanopore sequencing device and an Eulerian path (BOX 1.4) approach. In nanopore sequencing devices, an ionic current passes through a nano-scale hole along with biological molecules and the differentiations of the currents are measured. This information can lead to the identification of the molecules. For further detail on DNA sequencing with nanopores see [Branton et al., 2010] and [Schneider and Dekker, 2012].

BOX 1.4

NP (nondeterministic polynomial time) is a complexity class of decision problems. NP is defined as the class of decision problems which can be solved in polynomial time on a non-deterministic Turing machine. Equivalently, the solutions of problems in this class can be verified in polynomial time. A decision problem Π is **NP-complete** if Π is in NP and every problem in NP is reducible to Π in polynomial time.

HAMILTONIAN PATH: Is it possible to construct a path that visits every vertex exactly once? (NP-complete)

TRAVELING SALESMAN: Is it possible to find a cycle shorter than k (total weight) which visits every vertex exactly once? (Decision version. NP-complete)

EULERIAN PATH: Is it possible to construct a path which visits every edge exactly once? (not NP-complete)

GRAPH ISOMORPHISM: Are two finite graphs isomorphic? (not known to be NP-complete)

[Arora and Barak, 2009, Diestel, 2018, Papadimitriou, 2003]

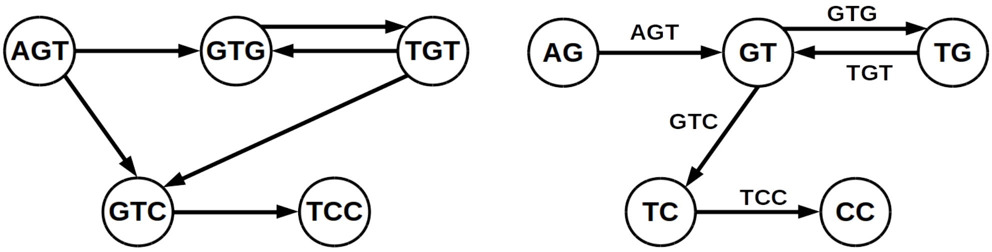
One common methodology for the recognition of the primary DNA structure is sequencing by hybridization, when oligonucleotides are used as complementaries of the given strand of length n. The oligonucleotides of length l that hybridize with our strand can be used for the creation of the (supplementary of this) strand. For this last part, back in 1988, there was introduced a method utilizing graph theory, in which the researchers related the problem with the NP-complete problem of finding a HAMILTONIAN PATH [IuP et al., 1988]. This was realised by turning each oligonucleotide of the set into a vertex and connecting (with an arc) two vertices if the l−1 rightmost nucleotides of the first vertex/oligonucleotide complement the l−1 leftmost nucleotides of the second one. If one manages to find a HAMILTONIAN PATH in the created directed graph, then a possible solution has been found. Provided that HAMILTONIAN PATH is a NP-complete problem, there will not be an polynomial time algorithm (BOX 1.4).

'DNA graphs' labelled with different values of label length and alphabet's size α, in which the label is written, can be compared. Recognition algorithms can look for Hamiltonian or Eulerian paths which correspond to large DNA sequences (e.g. genes) [Blazewicz et al., 1999]. In figure 1.3 there is an example illustrated. The relevant problem of (DNA) sequence similarity is a typical in the field of computational phylogeny (BOX 1.5). In 2011 a novel and accurate approach was proposed that induces a weighted directed graph for every DNA sequence [Qi et al., 2011]. A representative vector is created by the adjacency matrix (A $n \times n$ matrix A, where $A_{i,j} = 1$ if $ij \in E$ or $A_{i,j} = 0$ otherwise) of this graph in $O(n^2)$ time, for a specific DNA sequence of length n. The similarity matrix can be obtained in time $O(sl^2)$, where s is the number of the sequences and l the maximum length. This method uses large amount of information as long as investigates rearrangements (e.g. mutations), taking into account the frequency as well as the order of the nucleotides.

BOX 1.5

A typical way to consider evolution is the examination of the conserved features of the living organisms. Comparisons of different species can possibly lead to reliable phylogenetic trees , that can be modelled with the assistance of graph theory (e.g. [David, 1982] and [Brandes and Cornelsen, 2009]). A **phylogenetic tree** is a ramified diagram depicting the evolutionary relationships among biological species and it commonly relies on genotypic (genetic material (see GRN)) or phenotypic ('appearance') characteristics, representing branching evolutionary histories [Baum and Smith, 2013]. In terms of graph theory a phylogenetic tree can be modelled as a tree, usually rooted and connected.

One more work, published in 2016, was focusing on the sequencing and sequence comparison from a graph-theoretic perspective [Jafarzadeh and Iranmanesh, 2016]. The researchers, firstly, studied the problem of 'Fragment Assembly', that is: *Given a multiset of fragments (substrings), construct the best string (superstring) that contains each of the strings in the multiset.* The



(a) The graph G (b) The graph G'

Figure 1.3: An example with the initial sequence AGTGTCC of length $n = 7$ is illustrated [Blazewicz et al., 1999]. (a) If the oligonucleotides are of length $l = 3$, after the hybridization, we have the set {AGT, GTG, GTC, TGT, TCC}. In the graph G we observe that the only Hamiltonian path is $AGT \rightarrow GTG \rightarrow TGT \rightarrow GTC \rightarrow TCC$ from which the initial sequence can be read. (b): Since Hamiltonian Path is NP-complete problem, we need a way to transform it to a problem solvable in polynomial time [Pevzner, 1989]. This can happen by matching each vertex of graph G to an edge of a new graph G', that is, the set of edges in G' corresponds to the set of vertices in G. An edge connects two vertices labelled with the l−1 leftmost and rightmost nucleotides respectively, of the oligonucleotide of the edge. We can now look for a Eulerian Path in G', which is $AG \rightarrow GT \rightarrow TG \rightarrow GT \rightarrow TC \rightarrow CC$ and leads to the initial sequence as well.

desired superstring has to be of minimal length (shortest common superstring), whereas the fragments are parts of a given DNA sequence and are used for its reconstruction. There was a trial to achieve an overlap graph for which the finding of superstring of minimal length is not NP-complete. The problem can be represented as an overlap graph that contains a vertex for each string in the multiset and it is identical to Hamiltonian Path. In particular, we have an instance of the NP complete problem Traveling Salesman Problem. However, the problem can be efficiently solved by using Eulerian Path (fragments are represented by edges) in an overlap graph. Therefore, a new graph has to be constructed, by using strong product (Box 1.6) of graphs, for comparing and analysing DNA sequences.

BOX 1.6

For the **strong product** of the graphs G and H, $G \boxtimes H$ [Bondy et al., 1976], applies:

- the vertex set of $G \boxtimes H$ is the Cartesian product $V(G)\times V(H)$; and
- any two distinct vertices (u, u') and (v, v') are adjacent in $G \boxtimes H$ iff:
  - u is adjacent to v and $u' = v'$, or
  - $u = v$ and u' is adjacent to v', or
  - u is adjacent to v and u' is adjacent to v'

1.2 The Brain

The nervous system's structures of organisms such as primates or lower-scale mammals consist of complex networks, organised and mediated by extended interconnections among the brain regions. The continuous study of the brain, has examined its functioning during a wide variety of tasks. Graph theoretical analysis has been applied even to the study of fetal brain connectivity [Thomason et al., 2014], summarizing observations about development of brain networks prior to birth, or to the analysis of functional brain networks and signals during motor learning tasks [Huang et al., 2016]

The connectivity in the brain can be discerned in anatomical, functional and effective. The first one, refers to the structural links, called synapses, between neuronal units. These 'real' networks can certainly be dynamic (e.g. Learning tasks may stimulate the creation of new synapses) albeit at long time scales such as hours to days [Sporns et al., 2004]. The spatial scales can further vary depending on the contextually function of the connection, which can possibly demand extensive long-distance connections. Functional connectivity refers to temporal correlations between, often spatially remote, neuronal units [Friston et al., 1993]. This kind of connectivity is time-dependent, since neurophysiological measurements made in different brain areas at distinct moments can indicate different correlations. Ultimately, effective connectivity refers to the effect of a neural system over another, including structural parameters [Friston et al., 1993]. This is also time-dependent as long as pathways and regions' interactions in the brain are frequently modified. Functional and effective connectivity are practically different: The notion of effective connectivity contains the causal influences that neural units exert over another. For further details, see [Friston et al., 1993].

Graph theory can be applied in the study of complex brain networks, which are either of structural or of functional importance. These networks, either inter-neuronal or inter-regional, are considerably complex with peculiar topological features and reveal small-world network (Box 1.7) properties [Bassett and Bullmore, 2006, Achard et al., 2006]. Firstly, the neural elements consisting the vertices have to be determined, for instance as anatomically defined regions or electroencephalography/MEA (Box 1.8) electrodes. Secondly, a continuous measure of association among them has to be estimated, for instance based on the connection probability

BOX 1.7

A **small-world network** is a graph, with low average path length, where the distance (l) between two vertices randomly chosen grows proportionally to the logarithm of the number of vertices in the network ($l = O(logn)$ as $n \to \infty$)

among the regions (the axonal projections and synapses act as edges). Consequently, there has to be created an adjacency matrix and estimated the convenient features always in contrast to these of random graphs. The matrix relies on the connectivity among the vertices, while the generated graph is de facto directed.

BOX 1.8

A Multi-Electrode Array (**MEA**) is an array of electrodes used for recording electrical signals of neurons in vitro or in vivo. The recorded electrical activity provides a macroscopic view of neuronal networks [Spira and Hai, 2013].

Even if specific characteristics are observed in distinct points of a network, these occur on account of the whole network's function. Hence, it is not always easy to come to a conclusion regarding the functional networks based on a structure. One way to investigate whether (or how much) a functional network is based on the structural one, is by examining the brain's resting state [Greicius et al., 2009]. In such a state, the brain does not perform any explicit task, nevertheless remains watchful. Here has to be noted that 'indirect connections' of a functional nature are presumably hidden in the structural connectivity.

Computational studies have been accomplished looking into the association of dynamic patterns and structural properties [Honey et al., 2007, Galán, 2008]. The general indication is that the topology of the two categories of networks is highly similar. Nonetheless, the research results give a complete perception only in the one direction, that is, how functional brain networks depend on the structural ones. The opposite direction, regarding the shaping of structure after functional neuroplasticity (Box 1.9) modifications, is less considered.

BOX 1.9

Neural plasticity can be defined as the ability of the nervous system to adopt a new functional or structural state in response to alterations in the environment [Ganguly and Poo, 2013]. A neuron can possibly alternate its functional role in a circuit by altering how it responds to inputs or influences other neurons. This is may happen by strengthen or weaken the synapses, changes depended on experience.

Synchronization of an organism's biological procedures is a cardinal point. The more complex an organism is, its networks has to be more precisely adjusted. Mason and Verwoerd suggested that brain's network failure of synchronisation correlates with pathological situations such as schizophrenia and described the application of Kuramoto model (BOX 1.10) to the nervous system [Mason and Verwoerd, 2007]. The properties of a brain network, can lead to draw a conclusion about pathological situation. This way of diagnosis indicates another field of application for graph theory, that of medicine and curative strategies. Differences between patients' and healthy individuals' networks, pointed out, for instance, by fMRI or structural MRI experiments, have been shown in situations like traumatic brain injury [Sharp et al., 2014], schizophrenia [Liu et al., 2008], depression [Gong and He, 2015], epilepsy [Bernhardt et al., 2015], Parkinson's disease [Olde Dubbelink et al., 2013], dementia (Alzheimer) [Stam et al., 2006] and others. The, ultimately cited, work of Stam et al. at 2006, was innovative in correlating graph theory with disease-related differences in brain network topology.

BOX 1.10

Kuramoto model is a fundamental mathematical model used for the description of synchronization phenomena [Kuramoto, 2012]. The model portrays the coordinated behaviour of chemical and biological oscillators systems and it has been applied on a large scale in neuroscience. Usage of Kuramoto model for the study of neuronal synchronisation in the brain has also been accomplished in former studies (e.g. [Cumin and Unsworth, 2007]), focusing on the adaptive nature of neurons in the brain.

Except of studies which approach brain as a whole, there are attempts to come to conclusions about specific regions of the brain. Mears and Pollard have recently published a review focusing, through graph theory, on amygdala [Mears and Pollard, 2016], a brain region essential for the processing of memory, decision-making and emotional responses [Amunts et al., 2005]. Their conclusions support the importance of this region in normal brain function, mental illness and emotional processing tasks. Moreover, seems that depression correlates with 'an enhanced influence of the amygdala in resting brain networks'. Neural networks that are functionally connected during brain resting state and the alternations to these connections due to experience reveal fundamental questions that can be investigated in the light of graph theory.

One more technique that takes advantage of the computational analyses in neural networks, applies intervention. As an example, deleting of a vertex can help in understanding the way that a specific network carries out its tasks. The intervention can be either targeted or random whereas by collation of the two networks' behaviour, before and after the intervention, helpful conclusions may be extracted [Honey and Sporns, 2008]. It has been recently developed a MatLab-based software called BRAPH (BRain Analysis using graPH theory) that analyses the connectivity of brain networks. The software uses information collected with techniques as the above mentioned and has the potential of visualizing the results. It can give output in form of undirected binary and weighted brain connectivity graphs. Assessments or comparisons of the brain graphs are also possible with the aid of further algorithms [Mijalkov et al., 2017]. Some additional (graph) programs or tools designed for the study of brain networks are the Brain Connectivity Toolbox, the Graph Theory GLM (GTG) MATLAB Toolbox and the GraphVar.

The idea of *matching index* is another concept of graph theory used for the inspection of similarity of vertices in brain networks [Pavlopoulos et al., 2011], and depends on the common neighbours of the examined vertices. Let i and j be the two vertices of our interest, then their *matching index*, as defined by [Pavlopoulos et al., 2011], is

$$M_{ij} = \frac{\sum \text{CommonNeighbours}}{\sum \text{TotalNeighbours}}$$

One example of *matching index* application is in the prediction of the connectivity of cerebral cortical networks [Costa et al., 2007]. The cerebral cortex is a region of the brain that plays a central role in cognition, memory, attention, perception, awareness, consciousness and so forth. It is divided into left and right cerebral hemispheres while contains an amount of the gray matter [Kandel et al., 2000].

1.3 Centrality measures

As in many types of networks, in biological ones, there are vertices of higher importance playing a central role, for example as mediators, and they are often fundamental for the network's topology. It has to be noted that a 'biological network' or part of it can participate in more than one functions, hence, the role of a vertex could probably change depending on the contextually action. Moreover, it has been shown as a standard that the intracellular networks form modules [Rives and Galitski, 2003] and a popular methodology for their identification uses network clustering algorithms [Emmons et al., 2016]. Network clustering includes simple methods, including the shortest path length and the number of shared neighbours as distance measures [Rives and Galitski, 2003] or more complicated such as betweenness centrality clustering [Girvan and Newman, 2002]. In this last section of the first chapter, a short discussion referring to the idea of centrality in (brain) networks is presented.

In graph theory the term of centrality refers to the identification of vertices with the 'higher significance', for instance influential individuals in social networks, species in food-webs or hubs in the brain. There are plenty mathematical measures of centrality, whereas the most common of them can be found below. *Betweenness centrality* is based on shortest paths and it is computed for each vertex as the number of the shortest paths in the graph that pass through the vertex [Freeman, 1977]. This method can also assist in the discovery of clusters by detecting their links. *Degree Centrality*, corresponds to the number of the edges connected to a vertex and shows the number of interactions the vertex is involved in [Freeman, 1978]. Considering that all the neighbours of a vertex are not equivalent, led to the definition of *Eigenvector Centrality*, that shows a vertex importance according to the importance of its neighbours [Freeman, 1978]. *Closeness Centrality* ranks as more significant vertices those with low mean distance to all others [Joyce et al., 2010]. Finally, one not so common centrality measure is *Subgraph Centrality* [Estrada and Rodriguez-Velazquez, 2005] that characterizes the vertices being depended on the number of subgraphs of network in which they participate. There is paid more attention to small subgraphs, making this method suitable for studying network motifs. It has been additionally shown that in protein interaction networks, subgraph centrality is more related with the lethality (when individual proteins are removed), than the number of edges per vertex [Estrada and Rodriguez-Velazquez, 2005].

In 2010, there was defined a new centrality metric called *Leverage Centrality* which, in order to evaluate the role of individual vertex in a brain network, takes into account the connectivity of its immediate neighbours and the information exchange among them [Joyce et al., 2010]. This metric was used in the analysis of functional magnetic resonance imaging (fMRI) data but it has also been applied later to real-world networks [Li et al., 2015]. The concept of leverage centrality may seem similar to this of eigenvector centrality but the authors compared all the degree, betweenness, eigenvector and leverage centrality on functional (healthy) brain networks generated, and underlined their differences. The distinction of leverage and eigenvector centrality was proven experimentally by the fact that one group of vertices of high values of eigenvector centrality had lower leverage, while another group with lower values of eigenvector had higher leverage centrality. Moreover, as compared to betweenness or eigenvector, leverage centrality was proved to be more accurate at locating vertices of high degree. It was proposed that this metric could possibly detect with precision vertices of high importance within the network, since it was showed that uses information not included in the concepts of degree, betweenness or eigenvector centrality. The four centrality metrics were shown to be positively correlated, while leverage and eigenvector both contained information not apparent from the other two metrics. The uniqueness of leverage in comparison to existing centrality methods consists of the allowing of parallel (and no serial) processing, as this is accomplished in the brain. More formally, leverage centrality measures the relationship between the degree of a given vertex (v) and the degree of each of its neighbours (v_j), averaged over all neighbours (N_v), and is defined as:

$$l_v = \frac{1}{deg(v)} \sum_{v_i \in N_v} \frac{deg(v) - deg(v_i)}{deg(v) + deg(v_i)}$$

Some years afterwards the publication of the aforementioned study, Vargas et al. investigated the leverage centrality from a mathematical perspective [Vargas Jr et al., 2017] and it is worth to mention some of their interesting results.

Proposition. *For any graph* $G, \sum_{v\in G} l_v \leq 0$

Proof. For a regular graph G, there is $l_v = 0, \forall v \in G$ and thus $\sum_{v\in G} l_v = 0$. For a non-regular graph G, there will be two connected vertices v and u such that $deg(u) > deg(v)$ and the contribution of each edge vu to the sum of leverage centralities is $\frac{1}{deg(v)}\left(\frac{deg(v)-deg(u)}{deg(v)+deg(u)}\right) + \frac{1}{deg(u)}\left(\frac{deg(u)-deg(v)}{deg(v)+deg(u)}\right) < 0$. Concluding, we have that the sum of leverage centralities is $\sum_{v\in G} l_v = \sum_{(u,v)\in G} \frac{1}{deg(v)}\left(\frac{deg(u)-deg(v)}{deg(v)+deg(u)}\right) - \frac{1}{deg(u)}\left(\frac{deg(u)-deg(v)}{deg(v)+deg(u)}\right)$. □

The fact that leverage centrality is negative comes to light by considering that each edge between two vertices of different degrees contributes a negative amount to the sum of the leverage centralities. It is further proved that the maximum number of vertices with positive leverage centrality is $n-1$, while there are graphs with $n-1$ vertices of negative leverage centrality (eg. the star graph $K_{1,n-1}$). A proved bound for any vertex v is $|l_v| \leq 1-\frac{2}{n}$. Ultimately, there exist graphs where the leverage centrality of all vertices is distinct (Fig. 1.4). Further details, including the connection between the number of distinct leverage centralities in the Cartesian product of paths and the triangle numbers, can be found in the original paper [Vargas Jr et al., 2017].

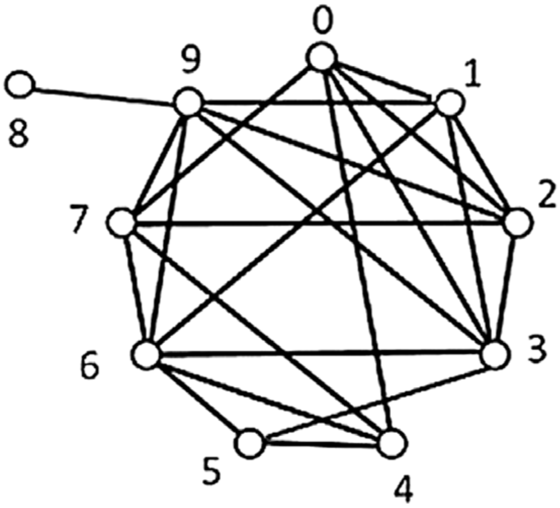


Figure 1.4: Graph G with distinct leverage centrality of each vertex. Source: Adapted from [Vargas Jr et al., 2017].

Apart from brain networks, the study of more of the above and below mentioned categories of 'biological networks' makes use of the idea of centrality. For instance, as we have already seen, centrality measures can be used for clustering purposes and a recent automated method finds clusters of interconnected proteins in PPIs. The proposed algorithm divides the network into clusters by subtracting the edges of uppermost betweenness centrality, then recalculating and repeating until a fixed number of edges have been subtracted [Dunn et al., 2005]. The term of centrality is also shortly included in the next chapter referring to social animal networks. Ultimately, for formal definitions, further details and extra centrality measures (e.g. Katz centrality), the book of Newman is an excellent manual [Newman, 2018].

CHAPTER 2

ANIMAL BEHAVIOUR

I tried to exclude human behaviour, even if it is an animal, because I do not like its behaviour.

2.1 An introduction to Animal Sociality

Mutual aid, mutual support and sociability in animal kingdom has been suggested to be a feature of utmost importance for the maintenance of life, the preservation of each species and its further evolution [Kropotkin, 1922]. Social organization indicates how community features are influenced by individual patterns of social interaction. Alternation in the social structures or the effect of environmental factors can possibly predicted, diverse social networks can be compared and individuals with key roles in information flow can be detected [Makagon et al., 2012]. Below there are presented the five major principles of social network analysis as they were described by Makagon et al., from which the first three are essential for animal behaviourists:

- Prominence (dominance) - Centrality measures
- Individual's network range - Number of vertices within a specified distance (diameter)
- Cohesion (group internal strong relationships) - Clustering coefficient and Assortativity
- Structural equivalence (similarity to the social environment)
- Brokerage (bridging)

Social behaviour of animals, including humans, is a well studied field nowadays. The concept of animal social networks was firstly introduced by Wilson in 1975 [Wilson, 2000] and since then animal sociality is attracting the attention of hundreds of scientists. From social insects, such as ants, to highly evolved mammals, such as primates or dolphins, the social structures form excellent study systems which eventually resemble primitive human societies. Information flow regarding simple communication for mating, disease vulnerability, resources access, social stability and social learning (BOX 2.1) can be modelled using the precious toolbox of graph theory.

Social interactions is a broad term describing a wide range of processes, from dyad communication to collective behaviour (BOX 2.2) of whole groups. In social animals, learning [Coussi-Korbel and Fragaszy, 1995], predator recognition [Vilhunen et al., 2005], mate choice [Amy et al., 2008] and many more processes are 'transmitted' through social interactions and highly affected by group dynamics which change through time while the members of the groups carry different services. Inter-individual interactions may shape the phenotype of the interacting sides and Montiglio et al. suggested that social structure has an impact on social plasticity regarding the mean phenotype expressed in a group, the extent of phenotypic variation available for selection and the group potential to respond to selective pressures [Montiglio et al., 2018].

BOX 2.1

Social learning is a cognitive process accomplished in a social context and suggests that new social behaviour can be acquired by observing and imitating others [Bandura and Walters, 1963].

BOX 2.2

Collective behaviour refers to a form of social coordinated behaviour of groups. These phenomena are often spontaneous and do not reflect existing social structure (laws and conventions). Animal groups such as shoal of fish and bird flocks navigate without leaders but they are still coordinated [Blumer, 1951].

Provided that we deal with real animal societies, some characteristics may vary due to migration or births/deaths. Even small changes could seriously affect the function of the network always depending on the social role of the 'removed' individuals. One relevant social organisation, studied in the light of behavioural ecology, is the fission-fusion society. The term 'fission-fusion' was introduced to describe the social system of some species, such as elephants, dolphins or primates, that change the size of their groups according to the availability or distribution of resources as well as their activity. In particular, fission-fusion dynamics refer to the variation in inter-individual dispersion and animal subgroup size or/and composition [Aureli et al., 2008]. These group dynamics influence subgroup size, dispersion and composition, while they are advantageous in exploiting food resources. One relevant example of the importance and complexity of the animal social structures is the 'cohabitation' of the dolphins in the gulf of Corinth (Greece, Mediterranean Sea), where three species of dolphins into the gulf form permanent mixed associations [Frantzis and Herzing, 2002]. The cohabitation of these species can be compared, according to Frantzis, to the coexisting of humans, gorillas and chimpanzees, which show similar genetic differences. Other unusual social systems, include cooperatively breeding traits, where group members help to rear offspring which are not their own. This is rather challenging for the evolutionary theory because of its contrast with the expected selfish behaviour, often promoted by natural selection. Overall, we can see that sociality in animal kingdom shows features that are not (currently) present in human societies and thus the study of these systems is essential, inter alia, for the understanding of human social evolution. For this purpose, graph/network theory constitutes a significant toolbox.

Graph theory metrics have been widely used in the recent behavioural literature [Wey et al., 2008]. The network modelling of animal communities can, except of the identifying of structural patterns, detect the flow of information. The pathways that this flow follows can be studied further for the understanding of other incidents such as pathogen transmission [Krause et al., 2007], which has already been studied in the light of graph theory [Ganguly et al., 2009]. Studying the role of each individual of the community can lead to conclusions about its influence in the transfer of pathological conditions and studies of such context have repeatedly materialized in mammals (e.g. [Corner et al., 2003] and [Guimarães Jr et al., 2007]). It has been long since proposed that some individuals in animal networks may be prominent in the access to resources and information [Coussi-Korbel and Fragaszy, 1995]. Vital and Martins used computer simulation in order to distinguish the significance of several graph/network metrics in the study of 'central' individuals in social animal groups [Vital and Martins, 2009]. As a result, they concluded that the most metrics are highly related to the amount of sampling and the group size. They further confirmed that these metrics can be used for dealing with small social groups typical in behavioural studies. The study was focused on the 'Gatekeepers', which are individuals with powerful influence on the behaviour of the group as a whole, due to the fact that they control the access to certain resources. One can imagine examples of such individuals considering that many social animals follow tiered structures leaded by dominants [Flack et al., 2006], while other individuals, located at the boundaries between communities, undertake to carry out communication among groups of the same species [Lusseau and Newman, 2004]. Figure 2.1 depicts a schematic representation of a network with four communities, in which, the vertices adjacent to red edges could be regarded as 'individuals in the boundaries'. The authors proposed that different social roles, affected by both strain and sex, influence the process of group learning. In conclusion, some individuals transfer information, to others in a community, more efficiently and in this way, they play central role, for instance in foraging [Reebs, 2000].

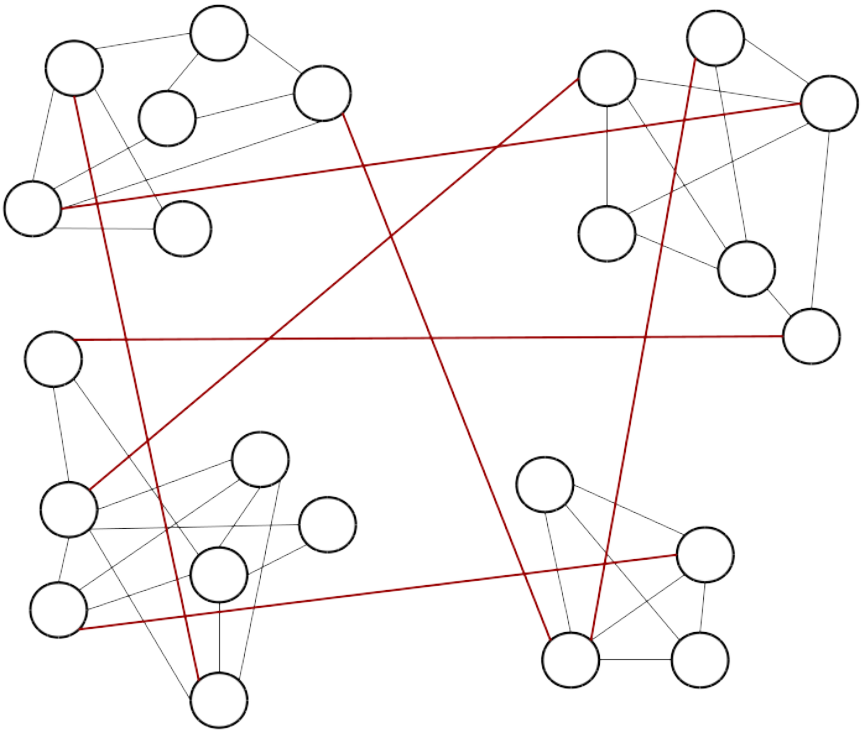


Figure 2.1: Network community structure. Four communities of densely connected, with black edges, vertices. Red edges represent connections among individuals of different communities.

In respect to centrality measures, Freeman has, in early times, shown that betweenness performs better than degree and closeness centrality in identifying important individuals in a social group [Freeman, 1978]. Lusseau and Newman used two graph theory metrics, betweenness centrality and assortativity, in the study of animal social groups to identify individual roles [Lusseau and Newman, 2004]. Both of these metrics provide information about the structure of the network as well as its dynamic behaviour. Broadly speaking, *assortativity* represents to what extent a vertex is linked to neighbours of 'similar' properties with itself. This 'similarity' was firstly referring to the vertices' degree (number of neighbours), although it has been further correlated with other vertices' features such as weight, k^{th} level vertex degree (number of vertices that are in distance no more than k) and more, as well as with non-topological features (in social networks), such as language, race, sex and age [Quayle et al., 2006]. The formal (original) definition of this graph metric was given by Newman for unweighted, undirected networks and needs multiple pre-definitions [Newman, 2002]. Lastly, a network is called assortative when vertices of high degree are, on average, connected to other vertices of high degree and vice versa.

The idea of clustering coefficient has further been used for the analysis of patterns of social interactions in animal populations [Pike et al., 2008]. Clustering coefficient measures the tendency of a graph's vertices to cluster together [Saramäki et al., 2007]. When Flack et al. removed 'conciliator' (individuals who were intervening in the conflicts) subjects from a group of macaques, there was a reduction in clustering coefficient and more aggressive encounters were risking society consistency [Flack et al., 2006]. A relative network property to clustering, is the 'community structure'. Communities can be considered as subsets of vertices with dense connections (edges) within the subsets and relatively sparse connections among the subsets (Fig. 2.1). Girvan and Newman introduced a new methodology for locating communities, focusing on the edges among the communities instead of the 'central' ones [Girvan and Newman, 2002]. In their study, the proposed algorithm was not applied in animal social networks but in several food webs and social networks. The term of betweenness centrality was generalised to edges, so that the edge betweenness refers to the number of shortest paths between vertices in which this edge participates. For a network $G = (V, E)$, the betweennesses is calculated for all m edges in time $O(mn)$. One simplified version of the proposed algorithm is the following:

Algorithm COMMUNITY TRACKING

```
Calculate the betweenness of all the edges of the network
Remove the edge with the highest betweenness
Recalculate betweennesses for all edges affected by the removal
Repeat from step 2 until no edges remain
```

Provided that the algorithm proceeds to a calculation after each edge removal, the total running time is $O(m^2n)$. Notwithstanding, this time is a worst case scenario, as long as only some paths/edges (at most these in the same component) are affected in each step, and therefore the algorithm usually runs faster. The iterations of edge removal are essential for the efficacy of the algorithm, because in the case of multiple edges among pairs of communities, the betweenness of all these are not necessarily high.

Social network analysis and graph theory can, furthermore, provide a deeper view on social relationships of animals and contribute to their husbandry and welfare [Rose and Croft, 2015]. Coleing used social network analysis as a tool in the management of captive animals whose social lives may differ from the social (widespread) structures found in the wild [Coleing, 2009]. For this study the simultaneous monitoring, via video camera, of all individuals in the examined group, including their interactions was essential. There was studied a group of ten elephants at Chester Zoo and in particular social interactions of playing (mostly juvenile individuals), dominance, greeting body contact etc. An innovative characteristic of this study was the combination of all the aforementioned aspects in a single network. Complex attributes of the social behaviour can further be investigated with a combination of social networks. With various operations using matrix arithmetic, different matrices can be combined [Aldous and Wilson, 2003]. If A is a set representing 'aggressive encounters' and B represents family bonds, the operation $A \setminus (A \cap B)$ represents the aggressive encounters among individuals from diverse families. As an example, figure 2.2 presents a directed graph including information for every prosocial behaviour (benefits other individuals [Eisenberg et al., 2015]) of the group of ten elephants (greeting body contact, close proximity and following networks) [Coleing, 2009].

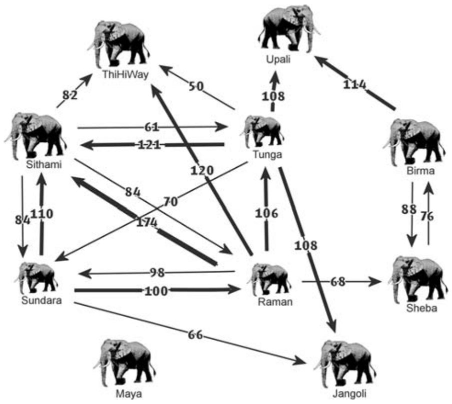


Figure 2.2: Directed graph with information of a combination of prosocial behaviour. Source: Adapted from [Coleing, 2009].

Coleing moreover explained the term of two-step relationships, where the interactions among some individuals influence the relationships among different ones [Coleing, 2009]. According to that study, two-step effects can be assessed with the tools of matrix algebra. By squaring the matrix of the direct interactions, we obtain the incidents among individuals of distance two. Indirect links play in important role in many networks and certainly in social ones as well. The metrics of the central individual's (CI) reach (vertices of distance two) and the clustering coefficient are useful in that direction. Along with these two, Sih et al. introduced 'exclusivity', an indirect social network metric which characterises the relationships of a CI with its partners, whereas it is equal to the reverse of their degree [Sih et al., 2009]. In particular, if the CI has a link with individual i who has n more neighbours, then it has an exclusivity value $\frac{1}{n+1}$ for this relationship. An example of what application this term can have is found in sexual selection (BOX 2.3). If a male individual mates with female individuals who mate as well with many partners (low exclusivity), has decreased mating success.

BOX 2.3

Sexual selection is a form of natural selection which refers to reproductive success. Some individuals have better success because of their sexual attractiveness or the selection of 'efficient' partners. Hence sexual selection is divided to intersexual where members of the one sex select their partners, and intrasexual where members of the one sex compete among them for access to partners of *a* different sex [Andersson, 1994].

2.2 Cooperation, competition and a view of game theory

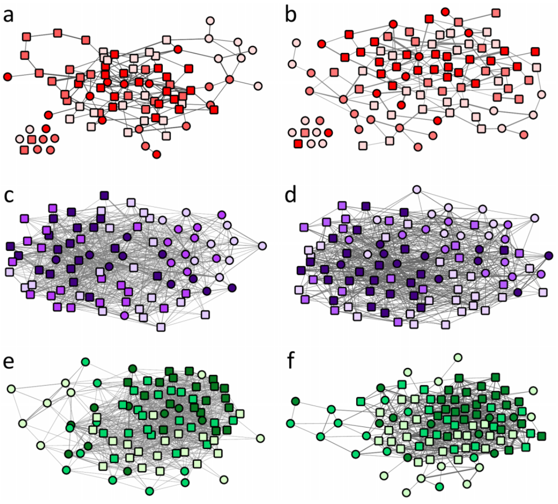


Figure 2.3: Social networks of adult rhesus macaques interactions. Grooming (a, b), aggression (c, d), and spatial proximity (e, f). 2010 (a, c, e) and 2011 (b, d, f). Squares stand for females and circles for males. Colour intensity represent dominance rank, with darker colors representing higher rank. Edge width represents the interaction's frequency. Source: Adapted from [Brent et al., 2013].

Graph theory constitutes a considerably convenient framework for the investigation of social structures influenced by the evolution of cooperation and competition. Along with evolutionary game theory can help in the design of realistic simulations in heterogeneous populations [Santos and Pacheco, 2005]. Evolutionary game theory (EGT) pertains to the application of game theory (BOX 2.5) to the theory of evolution and the 'survival of the fittest'. It applies, in big timescales, to organisms that interact repeatedly and offers the opportunity to examine reward and punishment evolutionary strategies. In the same context, one can observe evolutionary stable strategies (ESS) which refer to situations that all the individuals of a population adopt the same strategy, whereas different strategies (mutant phenotypes) do not invade and substitute the ESS [Cowden, 2012]. Moreover, animal social interactions including cooperation, altruism and competition, have been studied in the genetic basis of sociality. Brent et al. suggested the heritability of sociality in macaques [Brent et al., 2013], where the tendency to aggressive or friendly behaviours was found to have a heritable component. In figure 2.3 there are presented six graphs, part of the analysis from this study. Overall we can infer that the application of graph along with game theory is essential for the modelling of animal cooperation.

2.2.1 'Coopetition'

In natural or artificial systems, competition and cooperation may coexist. Brandenburger and Nalebuff conceived the term 'coopetition' in order to describe this coexistence in the strategic management [Brandenburger and Nalebuff, 1997]. Through such interactions, agents form subgroups with cooperating individuals within and opposing between the subgroups. Hu and Zheng, in order to describe coopetition networks, used directed signed graphs (Box 2.4), in which the positive and negative labels on the edges were representing cooperation and competition respectively (Fig. 2.4) [Hu and Zheng, 2014].

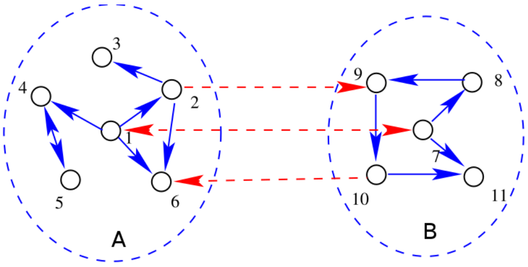


Figure 2.4: Coopetition network G. Network G is a signed graph with solid blue edges represent positive and dashed red edges represent negative interactions. The edges are positive within and negative between the two subgraphs A and B of G. Source: Adapted form [Hu and Zheng, 2014].

Hu and Zheng proposed a neighbour-based multi-agent system in which each agent interacts only with its neighbours for the decision-making referring to its next action. The structural balance (Box 2.4) was essential for this study, since a structurally unbalanced network can not be split into fractions. Furthermore it is considered an assumption according to which, coopetition networks have a subgraph that has at least one root vertex which influences directly or indirectly all the others. It has to be clarified that the interactions among the individuals in these networks may be more complicated. Depending on the circumstances, two individuals could be cooperators and opponents respectively. Therefore, it could be more appropriate each edge to be weighted with a vector (w_a, w_b) where $w_a < 0$ and $w_b > 0$ referring to competition and cooperation respectively, though in (signed) graph theory an edge's weight has to be a real number. Lastly, two more disciplines that could contribute to the study of the aforementioned collective dynamics, are game theory as well as overlay networking.

BOX 2.4

Directed signed graph is a directed graph $\mathcal{G}^s = (V, E, A)$ where A is an adjacency matrix describing the edge information of a positive or negative sign [Hu and Zheng, 2014].

A signed graph is **balanced** if the product of edge signs around every cycle is positive (all its cycles are positive) [Harary et al., 1953].

2.2.2 Game theory

Social interactions can be perceived as games among players who fight for their survival and prosperity, hence game theory is a fitting discipline for their modelling. Suzuki and Akiyama examined the evolution of cooperation in social dilemmas played in sizeable groups [Suzuki and Akiyama, 2005]. In their proposed model, each individual had its own strategy of decision-making depended on the group members' reputations which are determined by previous behaviours. An image score that ranges from -5 to 5 and changes by one unit upwards and downwards if the player cooperates or not respectively, represents reputation which is initialised to zero. A number $k \in (-5, 6)$ stands for the strategy, whereas the individual cooperates if the average image score of other members of the group is at least k. The algorithm of the simulation is illustrated below:

Algorithm Basic Game

```
1: An initial population of n individuals is created
2: Their strategies are distributed randomly from $-5$ to 6
3: g individuals are chosen randomly from the population
4: These g individuals play a game
5: Steps (2) and (3) are repeated m times
6: Individuals leave offspring depending on their fitness
7: Image scores are reset to zero
8: Repeat steps (2)-(6)
```

In evolutionary biology, costs and benefits are measured in terms of fitness. This game was simulated as a selection/reproduction process that increases good performing strategies. In each round g ($g \geq 2$) out of the n group members are randomly chosen to play the game. Each individual either contributes c or declines to do it and has a relative payoff. The payoff matrix corresponds to the 'g-person Prisoner's Dilemma game' (BOX 2.5), where $g \geq 2$. At the end of each generation, the individuals leave offspring according to their fitness that is determined by all the m rounds. For the selection of the individuals there was used a 'binary tournament selection' procedure as follows:

1. Two candidates are selected randomly as parents
2. The one with higher fitness is picked to be the parent with probability 0.9
3. A copy of the parent is added to the population for the next generation
4. The selection process is repeated n times

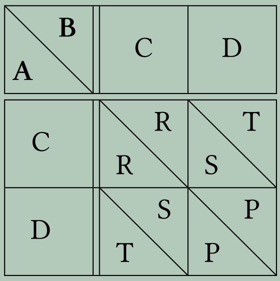
The overall conclusion of multiple studies was that the evolution of cooperation is more difficult as the group size increases even if the 'reputation effect' is included [Joshi, 1987, Boyd and Richerson, 1988, Suzuki and Akiyama, 2005]. Further details follow in the BOX 2.5.

BOX 2.5

Game theory is the study of mathematical models of strategic interaction between rational decision-makers [Myerson, 2013]. In other words, a mathematical approach dealing with strategic interactions, regarding costs and benefits, among individuals [Myerson, 1991].

One example of a game analysed in its terms is the Prisoner's Dilemma which appears in multiple forms. Its name derives from the story Albert W. Tucker told to illustrate it, which was representing the players of the game as two prisoners [Poundstone, 1993]. An 'original' form and some generalisations are described below [Kreps et al., 1982]:

Prisoner's Dilemma: Let there be two players A and B, and each of them chooses either to 'Cooperate' or to 'Defect'. If both A and B cooperate, they receive a reward R and if both defect, they receive a punishment P. If B defects while A cooperates, then B receives a temptation T whereas A receives a sucker's payoff S, and vice versa. The condition $T > R > P > S$ must hold for the payoffs, that is mutual cooperation is superior to mutual defection as well as defection is the dominant strategy for both players. Alternatively, there are four possible combinations of the choices, that is CC, CD, DC and DD.



B **A**	C	D
C	R R	T S
D	S T	P P

Payoff matrix of the original Prisoner's Dilemma.

Social dilemmas in natural communities may involve more than two enmeshed individuals which furthermore take into account previous behaviours of their partner(s) in the game. Therefore, it follows the description of a generalised version, the 'g-person iterated Prisoner's Dilemma', where $g \geq 2$ [Joshi, 1987]:

If the game is played more than once in succession and the players remember previous actions in order to change their strategy accordingly, the game is called 'iterated prisoner's dilemma'. This version demands also the condition $2R > S + T$, to prevent alternating cooperation and defection giving a greater reward than mutual cooperation. If furthermore, the game is played by n individuals, each participant faces $n - 1$ others and its payoffs depend on the strategies of all of them. Let k of the partners of a player choose C (and the rest, $n-1-k$, choose D), the payoffs depending on the players choice are given by the function:

$$f(C) = \frac{nCC + (n-1-k)CD}{n-1}, \qquad f(D) = \frac{nDC + (n-1-k)DD}{n-1}$$

Finally, the total payoff is the average payoff which would have been collected from two-person games played with each partner separately. The 'g-person prisoner's dilemma' demands also that [Boyd and Richerson, 1988]:

1. Defecting is the 'dominant strategy' for each player (no matter how the player's partners may play), that is altruistic behaviour is costly[a].
2. Switching of an individual from D to C benefits its partners.
3. The average payoff of the group members increases if someone switches from D to C, that is the benefit from cooperation to the group as a whole exceeds the individuals' costs of cooperating.
4. If all players choose D, the outcome is worse than if each player had chosen C.

---

[a] If the individuals are chosen randomly and interact only once, this 'rule' guarantees that cooperative behaviour can not thrive [Nunney, 1985].

		What you do	
		C	**D**
What I do	**C**	**REWARD** I get blood on my unlucky nights, which saves me from starving. I have to give blood on my lucky nights, which doesn't cost me too much	**SUCKER'S PAYOFF** I pay the cost of saving your life on my good night. But on my bad night you don't feed me and I run a real risk of starving to death.
	D	**TEMPTATION** You save my life on my poor night. But then I get the added benefit of not having to pay the slight cost of feeding you on my good night.	**PUNISHMENT** I don't have to pay the slight costs of feeding you on my good nights. But I run a real risk of starving on my poor nights.

Figure 2.6: Vampire bat blood-donor scheme. CC-Reward: Fairly good, DC-Temptation: Very good, CD-Sucker's Payoff: Very bad, DD-Punishment: Fairly bad. Source: Adapted from [Dawkins, 1976].

Abramson and Kuperman studied an evolutionary version of Prisoner's Dilemma, where players were placed in a small-world network while they were able to modify their strategy in order to imitate the one of the most accomplished neighbour [Abramson and Kuperman, 2001]. The topology of the community, from regular lattices to random graphs, appeared to lead to diverse behaviours. In terms of the Prisoner's Dilemma, as this is described above, we can perceive the cooperative behaviour of many animals, while its iterated version is likely more suitable for the study of such behaviour since animals often engage in long term partnerships. Dawkins presented some relevant examples and two of them are mentioned below [Dawkins, 1976]. The first example refers to the bird behaviour of removing ticks from each other's feathers. It is essential for a bird to pull off the ticks from itself, although it is not able to reach the top of its head alone and if a companion assists, this means that it will spend time and energy. The idea of the iterated Prisoner's Dilemma game is that the bird has to help its companion too (or maybe not?). The second example pertains to reciprocal food exchange of vampire bats (Fig. 2.6). The blood/food exchange rate depends upon how starved is the bat [Wilkinson, 1984]. The blood that the donor bat provides is less valuable to it than to the starving companion, while when a bat is starving it is a great profit to get fed by its companions (who were previously fed by it [Wilkinson, 1990]). When one is 'full of blood', the benefit from refusing to share is relatively insignificant.

2.2.3 Evolutionary graph theory

Evolutionary graph theory studies how topology affects evolutionary dynamics and it has applications in many fields of biology, such as ecology (or multi-cellular organization [Lieberman et al., 2005]). Once more, vertices stand for individuals while the edge's weight w_{ij} denotes the probability that individual/vertex i places its offspring into vertex j, that is weighted edges denote reproductive rates. If $w_{ij} = w_{ji} = 0$ then there is no edge between the two vertices. An example of the adjacency matrix $W = [w_{ij}]$ which determines the graph's structure is illustrated in figure 2.7. Graph structure can highly affect the fixation probability of a mutant, that is the suppression/amplification of selection or random drift (BOX 2.6). A wide variety of graphs, determined by the isothermal theorem, show a balance between selection and drift [Lieberman et al., 2005]. In its terms, the vertex's temperature is equal to the sum of the weights of all incoming edges, indicating the frequency of the vertex's replacement, where the hottest the vertex is, the more often is replaced. Isothermality can be alternatively expressed as a requirement that W is doubly stochastic, that is each row and column sums to one.

BOX 2.6

Genetic drift is a mechanism of evolution in which the frequency of an existing gene variant (allele) of a population changes due to random sampling of organisms over generations [Masel, 2011].

Additionally, in a homogeneous population of size n, consisting of residents and mutants, which corresponds to a fully connected graph, the dynamics of selection and random drift is traditionally studied by the Moran process. At each step of this process, an individual is chosen to leave an offspring (duplicated) depending on its fitness and a randomly chosen individual is replaced by the offspring. Moran process describes the stochastic evolution in a finite population and it follows that the population size is preserved [Moran, 1958].

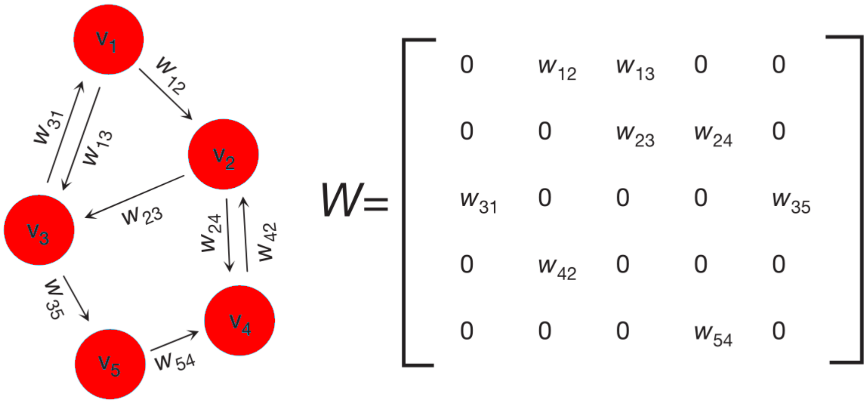


Figure 2.7: Model of evolution in evolutionary graph theory. In the stochastic matrix W, w_{ij} stands for the probability the vertex j to be replaced by the offspring of i. Alternatively, a generalisation would select an edge ij depending on its weight and the fitness of its ends. If the weights are identical and the graph is complete, the Moran process is obtained. Source: Adapted from [Lieberman et al., 2005].

A fundamental raising question refers to the fixation probability of a randomly placed mutant or alternatively the probability for a single mutant to take over the whole population. The natural selection is more powerful if the mutant's fitness is highly correlated with its probability of fixation. If all residents are identical with fitness 1 and the newly introduced mutant has fitness r, the fixation probability of the mutant is $\rho = \left(1 - \frac{1}{r}\right) / \left(1 - \frac{1}{r^n}\right)$. The isothermal theorem dictates that isothermal graphs (e.g. all regular lattices) have fixation probability ρ if and only if all vertices have the same temperature.

It is moreover feasible to create graphs (population structures) which amplify selection and avoid random drift. Figure 2.8 depicts a super-star which along with related structures have the property that for large n, the fixation probability of any advantageous mutant tends to one, whereas if the mutant is disadvantageous the probability tends to zero. Therefore, the fixation of the advantageous mutants is independent of the selective advantage. Nevertheless, this amplification is 'costly' since as it increases, the average fixation time goes to infinity. Finally, it has been proven that if k stands for the maximum path between any two vertices and n is large enough, then there is $\rho = \left(1 - \frac{1}{r}\right) / \left(1 - \frac{1}{r^{kn}}\right)$.

As it is mentioned above, in unstructured populations, where the members do not have permanent interactions, natural selection seems to favour defectors over cooperators. Ohtsuki et al. suggested the simple rule that evolutionary dynamics (natural selection) on graphs favours cooperation only if the benefit b that brings upon, divided by the induced cost c, exceeds the average number of neighbours (connectivity) k in the network [Ohtsuki et al., 2006]. In several animal societies the social structures are complicated and possibly affect the level of cooperation in a way that according to the researchers, the fewer the connections, the easier it is the promotion of cooperation. In the proposed model of an evolutionary game, the vertices of a graph stand for the players and edges for links in terms of game dynamical interaction and biological reproduction.

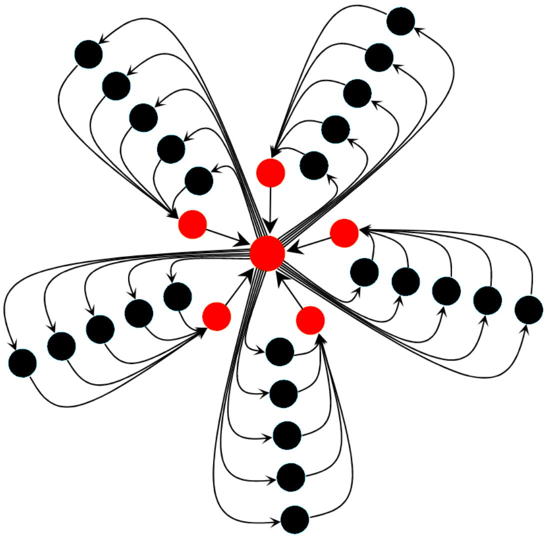


Figure 2.8: The super-star. Its symmetric properties imply that as the number of 'flower petals' and the number of vertices in each flower petal increases, its role as a 'selection amplifier' raises the fitness of advantageous mutants. On an amplifier of parameter k a mutant of fitness r bears up as one of fitness r^k in the Moran process. Here $k = 3$ but it can be extended in arbitrarily large values. Source: Adapted from [Lieberman et al., 2005].

Let n individuals form a population where cooperators help all their neighbours. Whether for the neighbours of the cooperator A there is $N_A = k$ and i of them are also cooperators, the payoff for A is $bi - ck$ (b: benefit, c: cost), whereas if the defector B has j adjacent cooperators, its payoff is bj. The overall fitness of a player is the sum of its baseline fitness (constant value) increased by the total payoff from the game. When the payoff is small in comparison to the baseline fitness the selection is weak, otherwise the selection is strong. Hence, the game is one of the several factors that affect the overall fitness.

Firstly there was examined a concept where in each step an individual was dying randomly, and its former neighbours in relation to their fitness were competing for the evacuated site (Fig. 2.9). The idea behind this concept is that when a group member is dying, its position is occupied by the offspring of the fittest neighbour ("death-birth' updating'). The question if cooperation can be favoured on certain graphs was translated into the probability the whole population to turn into cooperators by a single cooperator. The cooperation was found to be favoured if this probability is over $\frac{1}{n}$.

In natural communities, cooperators and defectors may coexist and the authors represented such a population with a complete graph. In terms of evolutionary game theory, the ones who benefit from these circumstances are the defectors. However, this is just an occasion and below

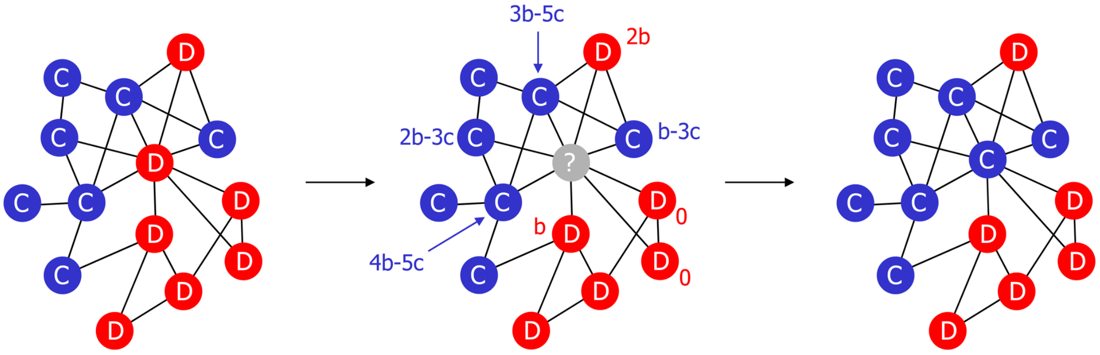


Figure 2.9: The rules of the game. Each cooperator (blue) pays a cost c per neighbour to provide it with a benefit b, whereas defectors only receive benefits. The individual's fitness is equal to $1 - w + wP$, where w is a measure of the selection's intensity and $w = 1$ stands for strong whereas $w << 1$ stands for weak selection. Here the vertex marked with the question-mark will change from a defector to a cooperator with a probability $\frac{F_C}{F_C + F_D}$, while the total fitness of all the neighbouring cooperators and defectors is respectively $F_C = 4(1 - w) + (10b - 16c)w$ and $F_D = 4(1 - w) + 3bw$. Source: Adapted from [Ohtsuki et al., 2006]

there are some more mentioned. Cycle: The group of defectors which turned into cooperators from the same 'root-cooperator' form an uninterrupted cluster. It was found that, if the population's size is large and the selection is weak, selection favours cooperation if $\frac{b}{c} > 2$. Regular graphs: (cycles, spatial lattices, random regular graphs) The calculation of a fixed probability is impossible, since pretty complicated patterns may occur with the interference of a defector.

In another examined update mechanisms, at each step a randomly chosen individual update its strategy. Either carries on with the former one or espouses one of its neighbours' (depending on their fitness). It was found that cooperators are favoured if $\frac{b}{c} > k + 2$. This way of updating appears if loops to every vertex, in the first update mechanism, are included. If the connectivity k of any vertex stands for its adjacent edges (loop counts twice), the rule $\frac{b}{c} > 2$ applies in both updating rules. Furthermore, depending on the update mechanisms, cooperation may be never favoured. If at each step an individual in relation to its fitness is leaving an offspring who takes the place of a randomly chosen neighbour, it is taken into account only the payoff of individuals at the boundary between cooperators and defectors, where cooperators are at a disadvantage.

Regarding the initial invasion of cooperators, in the model of Van Baalen and Rand there was introduced another condition under which (provided that migration events do not occur) a few cooperators can invade a population of defectors effectively, if $\frac{b}{c} > \frac{k^2}{k-1}$ [Van Baalen and Rand, 1998]. Altruism can be favoured if groups with many cooperators become essentially larger than groups with few. In natural conditions, an individual may have plenty links although only certain are significant. Therefore, the 'significant link' average degree k' is smaller than the degree k used in the above described studies where all edges were weighted equally. In conclusion, the favouring of cooperation might remain potent.

The results of the aforementioned study [Ohtsuki et al., 2006] are in accordance with Hamilton's rule [Hamilton, 1964, Grafen, 2007] which is one of the most commonly accepted explanation of the evolution of altruism and collates the benefit (b) with the cost (c) of the assisting behaviour. The rule suggests that the altruists will reinforce their assisting behaviour if $ab - c > 0$ where a stands for the frequency to which the benefits of altruism accrue to fellow altruists rather than to other group members. When interactions are determined by the social (network) structure, natural selection may favour cooperation and it, finally, follows that increased benefits of altruism in a given structure (cycles, spatial lattices, other regular graphs, random and scale-free networks) will favour the prosperity of cooperators [Ohtsuki et al., 2006].

BOX 2.7

Inclusive fitness theory suggests that an individual's success depends on the cooperative and altruistic behaviour while combines the individual's survival and reproduction (direct fitness) with the effect of the individual's behaviour on the survival and reproduction of its relatives (indirect fitness). **Kin selection** theory is based on the concept of inclusive fitness and describes an evolutionary strategy which favours the success of an individual's relatives, even at a cost to it's own success [Hamilton, 1964].

Lehmann et al. suggested that evolutionary graph theory models can be translated into classical kin selection models (BOX 2.7), emphasizing the importance of the spatial subdivision of populations [Lehmann et al., 2007]. They created (isothermal regular) graphs with vertices containing more than one individual and allowed interactions to vary with the distance between vertices. Therefore, the evolution of further assisting as well as harmful behaviours on graphs examined based on a broader inclusive fitness (BOX 2.7) model.

2.3 Collective motion

Collective behaviours help animal groups move harmoniously and abruptly change direction synchronised. A rather representative example is the swirling of the schools of fishes, shaping a vortex, under the pressure of a predator. A consequent question is how the common decision is reached and scientists have tried to answer by categorizing the emergent collective motions as functions of the system's parameters [Couzin et al., 2002]. The research of collective behaviour has made use of several tools of modern science from technological to theoretical such as algorithms and theoretical mathematics. For instance, Nikodem introduced an approach of modelling the collective animal behaviour based on set theory and relations [Nikodem, 2013]. It was suggested that simple behavioural rules can potentially lead to complex behavioural patterns depended on set cardinality. Using relations, allows the researcher to consider distance as a topological property and the proposed relational model approaches sufficiently well the collective behaviours of many animal groups/species, but not all.

Bode et al. described a model of collective animal motion, considering preferential social interactions of the individuals, and presented the potential influence of the social network on it [Bode et al., 2011]. The social structure was shown to affect three aspects of the animal groups, the cohesion, the individual spatial position and the hierarchical dynamics. In particular, three hypotheses were examined. The first hypothesis was referring to the correlation of strong social preferences of the group members with the enhancement of the group cohesion. Secondly it was tested if group members with multiple strong connections within the social network tend to be nearby to the centre of the group contrary to members with fewer strong connections. The third and last hypothesis was pertaining to the hierarchical dynamics and their exclusive derivation from the social network.

According to the above mentioned model, collective behaviour relies on local alignment, repulsion and attraction between individuals. The assumption that the response to the environmental changes of every group member is under an identical stochastic rate, is essential. In the proposed approach, each group member receive information only from the individuals within a zone of radius r_A around it, which is called sensory zone. The researchers generated the following five different social network structures of 100 individuals, in order to investigate the potential influence of network structure on group cohesion and alignment: A fully connected network (no structure) where all connections were equal (Fig. 2.10a), a network with two (Fig. 2.10b) and a network with three (Fig. 2.10d) components respectively, a network with a key individual (hub) strongly connected to all others (Fig. 2.10e) and a network with randomly created strong connections (Fig. 2.10c) based on Erdős-Rényi model for generating random graphs (BOX 2.8).

The hypothesis referring to the group cohesion is the one more relevant to the present study. The results from its examination indicated that strong pairwise social preferences between group members do not always improve group cohesion, while social networks consisting of two components (Fig. 2.10d), do not lead in higher cohesion in comparison to the control case (without social structure). It was additionally tested, by three different network structures (with two, one or no ‘key individuals’), which features of the network affect group fragmentation. The group cohesion and alignment appeared to increase after the removal of key individ-

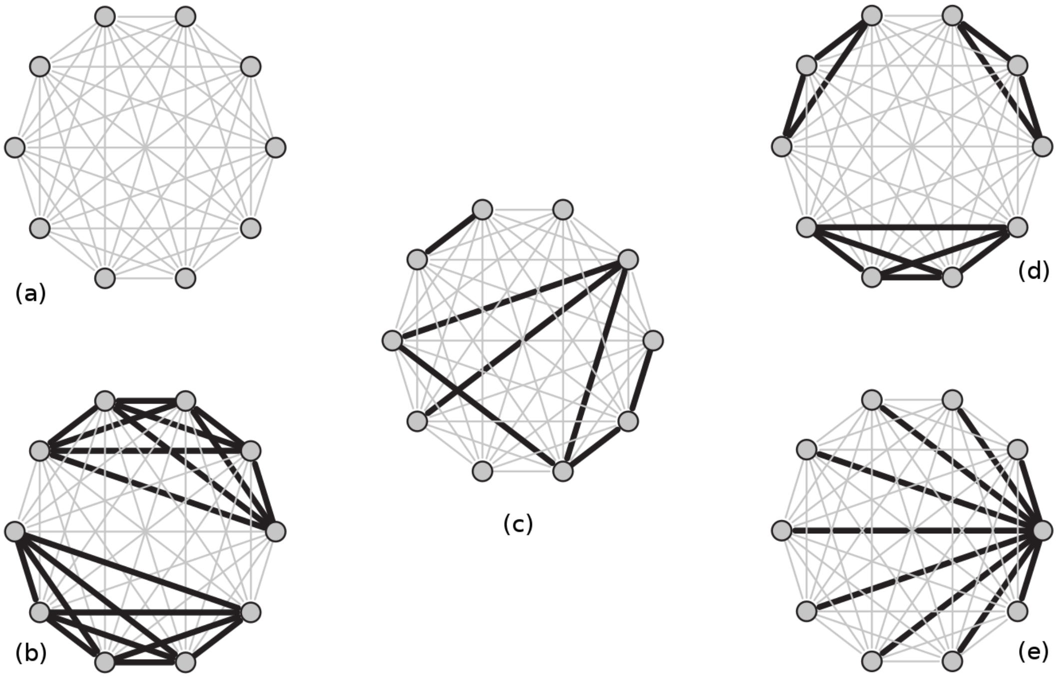


Figure 2.10: Five different social networks referring to collective motion. Each network consists of $N = 10$ vertices/individuals, whereas in the accomplished simulations the networks were scaled up to $N = 100$. The weak connections are represented by grey edges and the strong connections with black. (a) Control case: all connections are equal (either weak or strong). (b) Two separate components. (c) Random network with edge probability 0.1. (d) Three separate components. (e) A key individual, with strong connections to all the others. Source: Adapted from [Bode et al., 2011]

uals and hence, one can draw the conclusion that strong preferences may be disadvantageous to group cohesion while homogeneous networks favours it. Regarding the second hypothesis, it was predicted that animals with many social links are located nearby to the centre of the moving group, that is the position within the social network can be associated with the spatial position. Last but not least, purely social preferences can lead to hierarchical group dynamics, although these may not be translated into the expected social structure.

BOX 2.8

A **random graph** is created by successively placing edges at random within a set of n isolated vertices. One common question using these graphs is whether a particular graph property is likely to emerge [Bollobás, 1998]. In a mathematical context, a random graph usually pertains to the **Erdős-Rényi model** in which strong edges are independently added to the graph from the set of all potential edges with a fixed probability [Erdos and Rényi, 1960].

2.3.1 Flocking

“Flocking is a form of collective behaviour of large number of interacting agents with a common group objective” [Olfati-Saber, 2006]. A flock of collectively moving organisms (or dynamic systems etc.) can be represented by a dynamic network, in which the interaction between two unites/vertices of the network correspondents to an edge. In this design, two units which are topologically closer have more possibilities to affect the motion of each other. Provided that the flock is moving, the positions and the environmental factors change, therefore the network is modified relatively. There are many studies focusing on flocking and make use of graph theory for its analyses (e.g. [Ben-Asher et al., 2008]). Williams and Sukhatme described a spatial model in a proximity-limited system, subject to network non-local topology constraints, which could be formalized by a representation as a dynamic graph [Williams and Sukhatme, 2013]. Some further relative studies are presented below.

In 1987, there was published the first work using flocking computer simulation [Reynolds, 1987]. The flock’s members were represented by particles, forming a particle system-flock while the approach was simulating the behaviour of each member independently. The individuals were trying to remain united and simultaneously to avoid collisions with each other or other obstacles. The author described the following three heuristic (behaviour) rules, in order to build a simulated flock:

1. Collision Avoidance: avoid collisions with nearby flockmates
2. Velocity Matching: attempt to match velocity with nearby flockmates
3. Flock Centering: attempt to stay close to nearby flockmates

Flocks in the nature have not been observed to get overloaded depending on the number of the participating members, but function equally regardless the cardinality of the set-flock. An individual might stay on the lookout for itself and its two or three nearest neighbours, while pays only a little attention on the rest of the flock. Therefore, individuals in the nature can flock in constant time. However, the described ‘flocking algorithm’ appeared to have complexity $O(n^2)$, where n is the flock’s size. This problem partially originates from the fact that the simulation is running on a single computer, whereas in the natural flocks the processing is distributed to the flock members.

Based on field studies, Ballerini et al. suggested that the interactions among the individuals within a flock do not depend on metric distances, but rather on the topological distance [Ballerini et al., 2008]. Each bird appeared not to interact with all its neighbours within a metric distance but only with a fixed number of them, while Nagy et al. claimed that the place of the individual in the hierarchy is related to its spatial position within the flock [Nagy et al., 2010].

In 2006, there was introduced an approach for the determination of interaction rules that result in collective behaviour development [Olfati-Saber, 2006]. In particular, there were described three flocking algorithms, two for free-flocking and one for constrained flocking, related to network structures. The 'problem' could be described as a process in which a set of agents 'reach of a common decision' about a quantity of interest, such as turning direction. The information exchange among the agents was depending on an interaction rule which was characterized as 'consensus algorithm'. The design can be considered as a graph $G = (V, E)$, where $V = \{1, 2, 3, ..., n\}$ are the vertices/agents and (the set of) a pair of them belongs to E if and only if the two corresponding agents interact with each other. The common decision is reached when $\alpha_1 = \alpha_2 = \alpha_3 = \cdots = \alpha_n$, where α_i is the state of the i^{th} agent that refers to the specific quantity.

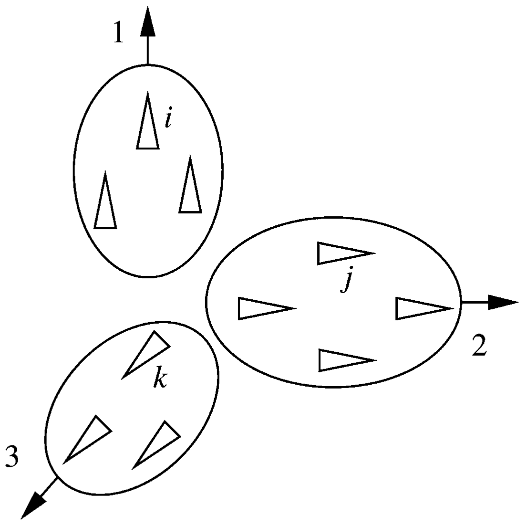
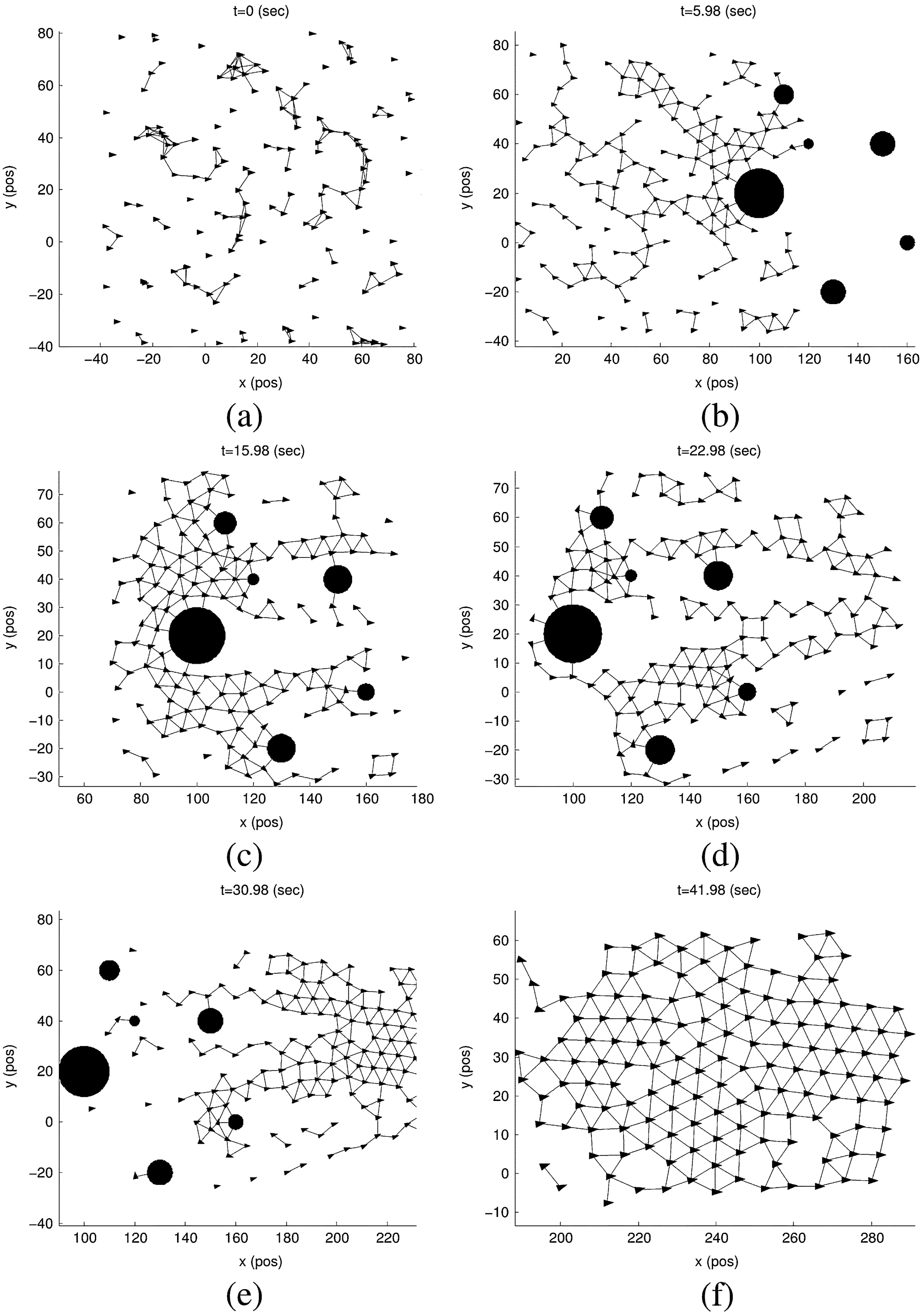


Figure 2.11: Fragmentation phenomenon. Source: Adapted from [Olfati-Saber, 2006]

The researchers, furthermore took into account the existence of obstacles, that could possibly imitate predators. They studied limited obstacles such as (infinite) rectangles and spheres, formally described as connected convex areas in $\mathbb{R}^m$ with smooth manifolds for borders. Overall, they presented consecutive snapshots of the proximity structure during 2-D or 3-D flocking in free or constrained space. Depending on the initial states and the number of the agents, the first algorithm failed to produce flocking behaviour, as it is demonstrated in figure 2.11, along with the consequential regular fragmentation. However, the other two algorithms resulted in flocking, with the third one having obstacle avoidance capabilities through 'transitional fragmentation' (splitting), essential for predator evasion. When obstacles-predators are presented among the initial and the (intended) final flock position, the agents need to split in subgroups in order to avoid the obstacles and to rejoin afterwards. Similarly, the squeezing maneuver, for moving through narrow spaces between nearby placed obstacles, was examined. Figure 2.12 illustrates the consecutive snapshots of the split/rejoin maneuver of $n = 150$ agents avoiding $o = 6$ predators-obstacles. The initial velocities were set to zero and the initial states were chosen randomly, from a Gaussian distribution, in $\mathbb{R}^2$ for 2-D and in $\mathbb{R}^3$ for 3-D flocking. There was shown that after some (finite) time, the agents form and preserve connected a flock.



(a) (b)

(c) (d)

(e) (f)

Figure 2.12: Split/rejoin maneuver. $n = 150$ agents form flocking after the evasion of $o = 6$ predators-obstacles. It was proven that no agent passed from the obstacles' positions during its course, while one can observe the switching topology of the network. Source: Adapted from [Olfati-Saber, 2006].

BOX 2.9

A **Voronoi partition** is a partitioning of a plane into regions (Voronoi cells), based on the distance of each plane's point from previously specified points called seeds. Each cell corresponds to a seed and consists of all the plane's points closer to that seed than to any other [Aurenhammer, 1991].

Ultimately, Lindhé et al. introduced a flocking algorithm, based on Voronoi partitions (BOX 2.9), leading to collision-free flocking in environments with obstacles of general shape [Lindhé et al., 2005]. The algorithm was distributed and each agent's actions were based only on the position of its neighbouring ones. Relative distance and orientation information were used at each time-step, while collision avoidance was always guaranteed. If the given optimisation problem is feasible, the agents will tend to the goal and if the above mentioned criteria are met the agents will form a flock.

CHAPTER 3

ALGORITHMS INSPIRED BY ANIMAL BEHAVIOUR: FOUR EXAMPLES

Every algorithm is inspired by animal behaviour, since algorithms are products of thinking and thinking is a behaviour.

One would expect that the synergy of animal behaviour along with algorithms would stand for the application of algorithms on the analysis of animal behaviour. Nevertheless, the linking of the two disciplines is ‘undirected’, that is there are approaches in the field of algorithms, inspired by animal behaviour. In the following paragraphs, some (optimization) techniques inspired by animal behaviour are presented.

3.1 Particle Swarm Optimization

Particle Swarm Optimization (PSO) algorithm [Kennedy and Eberhart, 1995] is a method that is iteratively improving a prospective solution with regard to a given measure. It moves the particles (prospective solutions) in the search-space according to mathematical operations over the particle’s position and velocity. The movements depend on the best known positions of the particles, and aim to the best known positions in the search-space. In each round the positions are updated as better ones are found by other particles. This is expected to move the ‘swarm of particles’ towards the best solutions. The idea behind the algorithm lies in the social behaviour of bird flocking or fish schooling. The collective motion of such organisms is coordinated by interactions among neighbouring individuals [Vicsek and Zafeiris, 2012]. PSO has been shown to be a flourishing metaheuristic technique (BOX 3.1) with hundreds of papers investigating its application. Poli aimed to categorise a large number of publications referring to PSO applications in metallurgy, biomedical, robotics, communication, entertainment and others [Poli, 2007].

BOX 3.1

In computer science and mathematical optimization, a **heuristic** technique trades optimality, completeness, accuracy or precision for speed. It is designed for (approximately) solving a problem more quickly when other methods are too slow or fail to find any exact solution. A **metaheuristic** is an approximate algorithm aiming to provide a sufficiently good solution to an optimization problem, combining heuristic methods for exploring a search space [Blum and Roli, 2003].

3.2 Collective Animal Behaviour

BOX 3.2

Global optimization refers to a collection of algorithms used to statistically sample a space of parameters or variables to optimize a system, though it is further often used to sample a huge space for information [Ingber, 2009]. More simple, it is an attempt to find a global optimum of an objective function defined in a given search space.

A second algorithm inspired by animal behaviour is the metaheuristic algorithm Collective Animal Behaviour (CAB) for global optimization (Box 3.2) [Cuevas et al., 2012]. As it has formerly been mentioned, a wide range of (gregarious) animals from swarms of locusts to herds of mammals such as wildebeests, exhibit collective behaviours including migrating, swarming etc in orderly arranged groups. The cooperation offers multiple advantages to the group members regarding the defending effectiveness (predation avoidance), improvement of aerodynamics and others. In CAB, the searcher agents emulate an animal group, in which the interactions among the individuals depend on simple behavioural regulations, modelled as mathematical operators. The concept of CAB is, by simulating the behaviour of the animals, to 'remember' and store the best solutions. The memory is divided into one part for storing the best locations at each generation and another one for the best overall positions during the complete evolutionary process. After the comparison to other known optimization algorithms, CAB has shown high performance. It firstly considers a set of operations that represent the rules of the interaction. Each solution of the search space corresponds to an animal position and each animal is characterised by a ‘fitness value’ that is its ascendancy in the group. When two animals confront each other, the most ‘mighty’ prevails. CAB is an iterative process:

Algorithm CAB

```
Initialise random solutions (positions)
Keep the position of the best individuals
Move from or to nearby neighbours (local attraction and repulsion)
Move randomly
Compete for the space within a determined distance (update according to the ascendancy)
```

3.3 Ant Colony Optimization and Artificial Bee Colony

Another well-known algorithm has been inspired by the ant colony behaviour. During their exploration for a path between their colony and a source of food, ants lay down pheromone trails in order to direct the other members of the colony to resources that they have possibly located. If an ant finds such a trail, instead of randomly wander, follows the trail, whereas reinforce it with additional pheromone in case of successful resource locating. Ant Colony Optimization (ACO) algorithm [Dorigo et al., 1991] refers to a probabilistic technique which can be reduced in finding paths in graphs. The ants are represented by simulation-agents which locate optimal solutions by moving through a parameter space representing all possible solutions. The agents record their positions and the quality of their solutions, so that in the next iteration more individuals will find better solutions. The algorithm is based on greedy search, positive feedback as well as distributed computation.

Algorithm BEES ALGORITHM

```
Initialise population with random solutions
Evaluate fitness of the population
while stopping criterion not met do
    Form new population
    Select sites for neighbourhood search
    Recruit bees for selected sites and evaluate fitnesses
    Select the fittest bee from each patch
    Assign remaining bees to search randomly and evaluate their fitnesses
end while
```

One variation of the aforementioned technique relates to the behaviour of another social insect, the bee. Inspired by honey bees' foraging behaviour, Pham et al. introduced an optimisation method called the Bees Algorithm. The basic steps of this algorithm can be found above and a similar algorithm that helps in the comprehension of the steps of the Bees Algorithm [Pham et al., 2006] is described below.

The honey bee swarm foraging behaviour has been also simulated by the Artificial Bee Colony (ABC) algorithm which solves optimisation problems [Karaboga, 2005]. The bees colony is partitioned in three groups who carry out the two major processes/behaviours of the recruitment to a nectar source and its abandonment: the employed bees, the onlookers and scouts. The employed bees are associated with a specific food source which they are currently exploiting, whereas they transfer and share, with a certain probability, information about its efficiency, direction or distance from the hive. Scouts are looking for food sources in the surrounding environment of the hive, while onlookers are anticipating in the hive until they get information from the employed bees in order to establish a food source. One employed bee corresponds to each food source, and when the food source of an employed bee is depleted, it turns into a scout. The following are the principal steps of the algorithm.

Algorithm ABC

```
Send the scouts onto the initial food sources
while stopping criterion not met do
    Send the employed bees to determine the food sources' nectar amounts
    Calculate the probability value with which sources are preferred by the onlookers
    Stop the exploitation process of the sources abandoned by the bees
    Send the scouts in the search area for discovering new sources, randomly
    Memorize the best food source found so far
end while
```

The positions of the food sources correspond to possible solutions of the optimisation problem, whereas the nectar amount represents the quality of the solution. As the nectar amount increases, the probability for the onlookers to select the corresponding food source increases as well. The recruitment rate refers to how promptly the colony locates the new food. This process can be translated into the swiftness with which the optimal or feasible solutions can be discovered. ABC is very simple and it is shown to be robust, applied for solving numerical optimization problems.

3.4 Hunting Search

The Hunting Search (HuS) algorithm [Oftadeh et al., 2010] refers to one more metaheuristic approach inspired by the group hunting of predators such as wolves or dolphins. The algorithm simulates hunters as search positions and preys as potential solutions. In natural conditions, hunters act as below: Encircle the prey and gradually tighten their ring until at least one of the predators catch the prey. The individual predators adjust their positions in accordance with the position of other members. In case that the prey escapes, the predators rearrange the group in order to attack anew. Following this method, predators can catch preys that possibly move (run or swim) faster than them. Terrestrial hunters are also taking into account further factors, such as avoiding to have the wind on their back (Direction from the predator to the prey) in order not to be detected (smelled). HuS relates this with the 'forbidden areas' of the search space, while each predator stands for a solution and the prey for the optimum point in our work. Particularly, in constrained optimization problems, 'solution-hunters' can be orientated in the design space (movement toward leader), avoiding the forbidden areas and locating the feasible ones. The leader is the hunter with the best position at the current stage, that is the optimum solution. If any hunter finds a better 'place' than the one of the current leader, it becomes leader in the next stage. Figure 3.1 displays the procedure.

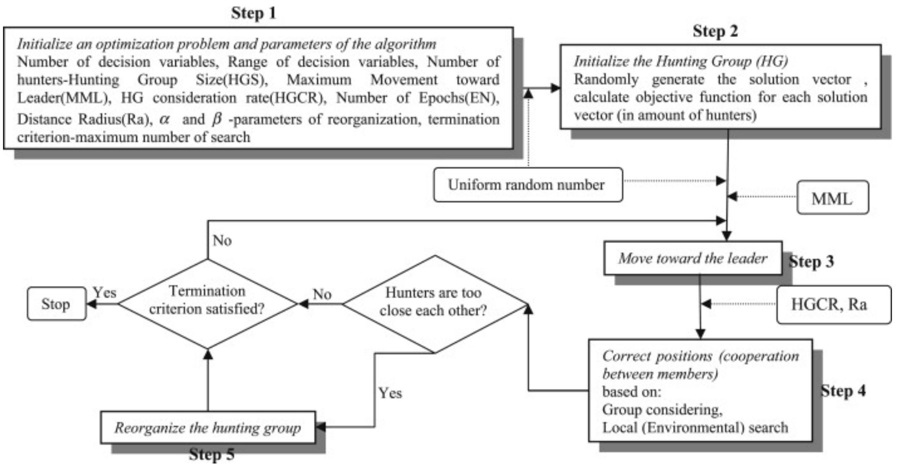


Figure 3.1: Optimization procedure of HuS algorithm. MML stands for maximum movement toward the leader and HGCR for hunting group consideration rate. Both parameters are used to improvise the hunter position defined in the third and forth step. Source: Adapted from [Oftadeh et al., 2010].

Depending on the prey's position, there is a possibility for each hunter to catch it. In HuS, the value of the objective function depends on the value of each decision variable. Last but not least, HuS is a metaheuristic algorithm using stochastic searches and does not demand initial value settings of the decision variables, while addresses continuous optimization problems (Box 3.3). It has been shown that a generalisation of this algorithm can be used in some combinatorial optimization problems such as the TRAVELLING SALESMAN. The steps of the algorithm are presented below.

Algorithm HUS

```
1: Specify the optimization problem and parameters of the algorithm
2: Initialize the hunting group (HG)
3: Move toward the leader
4: Correct the positions (cooperation between members)
5: Reorganize the hunting group
6: Repeat Steps 3, 4 and 5 until the termination criterion is satisfied
```

BOX 3.3

Continuous optimization problems: A solution's assessment is accomplished by placing the values of specific decision variables into an objective function. The assessment of the function value, may include errors, costs, efficiency and so on [Oftadeh et al., 2010].

Definition. *A model of a continuous optimization problem, generally shown as* $Q = (S, \Omega, f)$, *has the following features.*

- *A search space defined over a finite set of continuous decision variables* (S).
- *A set of constraints among the variables* (Ω).
- *An objective function to be minimized* $(f : S \to R_0^+)$.

CHAPTER 4

CAN COGNITION AND BEHAVIOUR BE (PARTIALLY) PERCEIVED AS ALGORITHMIC PROCEDURES?

If algorithmic procedures are a result of cognition but cognition is an algorithmic procedure, seems like... If algorithmic procedures are a result of cognition but cognition is an algorithmic procedure, seems like... If algorithmic procedures are a result of cognition but cognition is an algorithmic procedure, seems like...↻

While examining the link between the brain and behaviour, Krakauer et al. suggested a more pluralistic notion of neuroscience [Krakauer et al., 2017]. The behavioural research aims at understanding, while neural activity shows the causality. Comparing the brain-behaviour relationship with a computer science analogy, they considered the example of software (what?) and hardware (how?). The investigation of behaviour helps discovering component processes and their underlying algorithms. In this chapter, algorithms are roughly non-symbolic and consist of explicit series of steps or/and rules for answering some question, solving a problem or performing a task. They provide instructions prescribing how to proceed at each step. These algorithms could be innate, learned or even complex, that is, combining both categories. Furthermore, given that the brain mainly participates in information processing, Ruffini approached consciousness, based on neurophysiological or neuroimaging data, from an algorithmic information theory perspective, that is a combination of information and computation theory [Ruffini, 2017]. The mystery of the mind's function has led to hypotheses which link it to computational/algorithmic processes and in this chapter the potential computational nature of thought and behaviour from different perspectives is discussed.

4.1 A mathematical perspective

In 1961, Lucas introduced an argument, claiming that Gödel's first incompleteness theorem is opposed to the idea that human mind is a computer (or equivalently a Turing machine) [Lucas, 1961]. This argument found many rivals who supported the Computational Theory of Mind (CTM) and Artificial General Intelligence (Box 4.1), stating that the mind is an information processing system where consciousness and cognition represent computation. Three decades later, Roger Penrose with his two books, [Penrose and Mermin, 1990, Penrose, 1994] argued that Gödel's incompleteness theorem poses problems for the aspect that the mind is a computer. There has been extensive debate on the aforementioned arguments, and several objections have been expressed. In any case, these discussions deviate and exceed the purviews of the present thesis, getting involved in disciplines such as quantum physics.

BOX 4.1

Artificial General Intelligence is the stance that it is possible to create a machine capable of successfully perform any cognitive task of the human mind. As an example, we can refer to the famous 'Turing Test' [Turing, 2009] that is: "write a computer program that can simulate a human in a text-based conversational interchange" [Goertzel and Pennachin, 2007].

BOX 4.2

"A system that consists of only finitely many states and transitions among them is called a finite-state transition system. We model these abstractly by a mathematical model called a finite **automaton**" [Kozen, 2012].

Plentiful lines have been written about the computational features of the mind (e.g. [Jackendoff, 1987]) and many conjectures have been done, including the aforementioned. Multiple physical and biological processes can be likened to algorithmic procedures in a rather abstract way, although there are evidences to believe that some problems that human's mind can consider and possibly 'solve', are not formally computable. However, until the mystery of cognition is completely clarified, such comparisons will not be avoided. In the next paragraph a study that aimed to practically investigate the brain from mathematical point of view is presented.

Research on the brain areas involved in a specific cognitive task is quite advanced, locating these which respond to distinct stimulus. However, the processed information in each cognitive function is not easy to detect. Having this in mind, one wonders what information is transferred and distributed throughout the different brain areas. Schyns et al. tried to translate brain activity to a set of particular information processing states [Schyns et al., 2009]. Brain's cognitive states, being responses to specific stimulations, are coordinated by an information processing system. The transitions among information processing states were correlated, by the researchers, to the operation of a finite automaton (Box 4.2), which suppose to be (generally a Turing machine) competent of computing any 'intuitively computable function'. In terms of the 'Church's thesis' (Church-Turing thesis [Enderton, 2001]), the cognitive procedures were speculated to be cognitive algorithms, specifically a finite set of information processing states and a transition table. This table, acting as a transition function [Sipser, 2006] with a sensory input, defines the rules for proceeding from one state to the next one in order, ultimately, to result in behavioural responses. The identification of the information used or processed in each state and the transition among the states are the two essential parts of the cognitive algorithm.

4.2 A philosophical point of view

Many decades now, there is an ongoing debate on how cognition relates to the brain, from a particular philosophical perspective. A mechanistic explanation of behaviour is provided by computationalism, a family of theories about the mechanisms of cognition, supporting that 'cognition is computation'. In 2009 there was published an enlightening review making the distinction among different approaches in the context of computationalism [Piccinini, 2009]. There has been supported that computationalism is rooted in Church-Turing thesis (e.g. [Baum, 2004]), however, these arguments seem not to take into account that Church-Turing thesis pertains to what can be computed by algorithms. The link with cognition could be likely accepted provided the conjecture that all cognitive processes are algorithmic procedures.

One former theory was perceiving cognition as the manipulation of linguistic, or sentence-like structures, while the brain function (how it works) and computationalism are at 'different levels'. In this context is essential to mention two basic concepts, the classicism ('cognition is computation over linguistic structures') and connectionism ('cognition is what neural networks do'). The original connectionism supports that behaviour can be explained by the connections among neurons which are translated into stimulus-responses relations [Hebb, 1949] and a similar idea is the associationism, which though do not include the biological mechanism in order to explain the associations. Contemporary connectionism suggests that behaviour is a translation of neural network activity, however, provided that brain is the organism's component which underlies cognition, and the networks formed by brain cells perform the cognitive functions, this view is trivial. In conclusion, the study of the organisation of nervous system could likely provide us with more knowledge supporting the one theory over the other (Fig. 4.1).

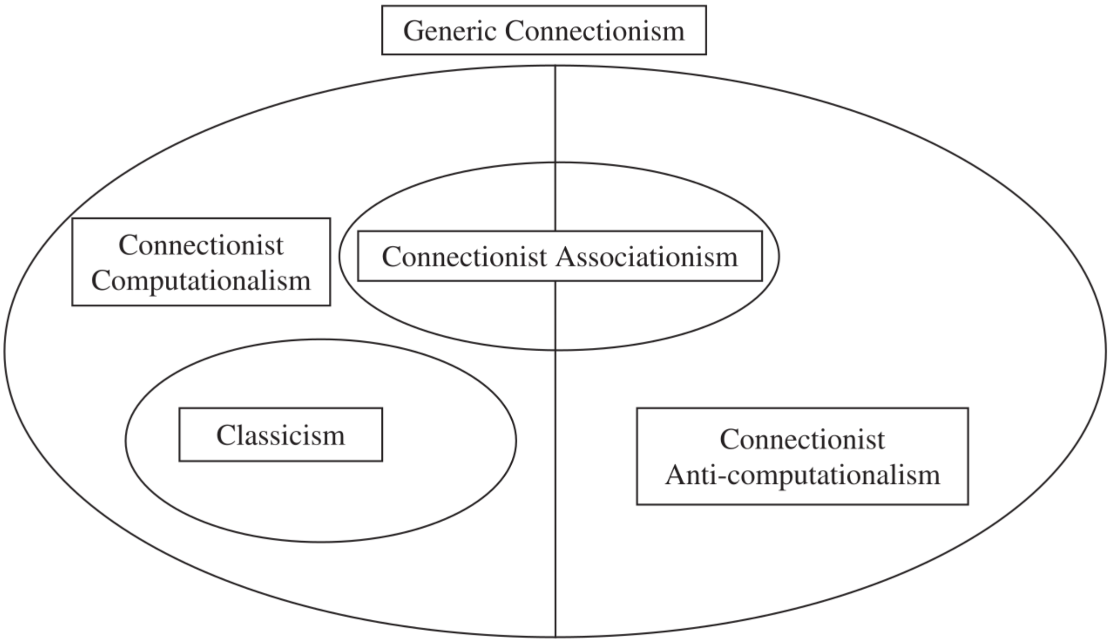


Figure 4.1: Theories about cognition. *Classicists* support that cognition depends on neural networks which act as manipulators of linguistic structures. *Non-classicist connectionists* support that cognition depends on non-classical neural network computation. *Anti-computationalist connectionists* support that cognition depends on neural networks which do not refer to computation. Source: Adapted from [Piccinini, 2009]

Here a short discussion of the already expressed arguments in the aforementioned context is included. The idea that cognition involves something beyond computation is further developed (possibly by a version of computationalism) in the idea that involves (hyper-)computations more powerful than what a Turing machine can accomplish [Bringsjord and Arkoudas, 2006]. However there is no evidence indicating that a genuinely Turing-uncomputable problem (such as Halting Problem [Sipser, 2006]) can be solved by human cognition. Moreover, computation is lacking the aspect of consciousness, which is (controversially) involved in cognition and there are various approaches trying to describe consciousness in computational terms (e.g. [Dennett, 1993]) and determine whether cognition indeed involves consciousness. Although, even if consciousness involves something beyond computation, there is still possible to play an important role in the cognition procedures. Additionally, Van Gelder supported that cognition is not computation since cognition does not manipulates representations as computationalism presupposes [Van Gelder, 1995]. Thompson proposed that cognition is not computation because in comparison to cognition, the computation is disembodied and unembedded (uncoupled with body and environment) [Thompson, 2010], although computation needs not be disembodied and unembedded. Last but not least, cognitive states refer to certain issues, or in other words involves intentionality, whereas computation does not involve such feature and thus one wonders how it could simulate cognition [Searle, 1980].

4.3 Primates

In this section by means of some examples of the contemporary literature, there is presented, how primate, including human, cognition has been linked to algorithmic procedures. In 2005, Cantlon and Brannon trained monkeys (*Macaca mulatta*) to sort arrays in relation to the number of their elements and be able to pick the 'bigger' or 'smaller' array depending on a color mark [Cantlon and Brannon, 2005]. The goal of the study was to investigate if monkeys show a semantic congruity effect (BOX 4.3) during numerical comparisons as well as if they use the same comparison algorithm for their decision-making. In that case, the semantic congruity effect could not be attributed to linguistic processes. Monkeys revealed an analogous semantic congruity effect to the human one, influencing decision time. This result of qualitative similarity in response patterns, supports the idea of an evolutionarily primitive size-comparison algorithm shared to primates, including human.

BOX 4.3

Semantic congruity effect: Appears when comparing two stimuli and you have to decide which is smaller (or larger), in relation to a specific dimension. When the stimuli are both large, humans tend to pick the larger one faster, whereas when both stimuli are small, they tend to pick faster the smaller one. Therefore, the direction ('choose larger' or 'choose smaller') of the comparison is crucial for this congruity effect [Shaki and Algom, 2002].

Jordan and Brannon showed that human infants (7 months old) are capable to discriminate visual (faces they see) and auditory (voices they hear) stimuli exclusively depended on numerical representations [Jordan and Brannon, 2006]. In particular, the infants pay attention preferably to visualisation of adults which include the same number of voices and talking individuals. This finding suggests a common cognitive process, regarding numerical representations, in nonverbal animals and preverbal humans. In 2006 it was proposed that the above mentioned decision process represents an 'If-Then rule' that could form, along with other aspects, the steps of an algorithm [Yildirim and Beachell, 2006]. The researchers of this last study, further presented an example of summing two multi-digit numbers, supporting that sum calculation (of large numbers) is a steps' sequence, similar to those of a computational approach. The process is explained in text as follows:

Algorithm Primates

```
1: Read the numbers
2: Add their appropriate digit and any carry
3: Save the result as the appropriate digit of the sum
4: If there is a carry for the possible summation of the next digit, save it
5: If there are more digits to add, go to Step 2
6: Save the carry as the most significant digit of the sum
```

4.4 Ants: The social insects

Sumpter suggested that when studying collective behaviour one has to identify the 'behavioural algorithms' of each individual and the way that information flow follows among them [Sumpter, 2006]. It is well known that artificial intelligence (AI) and cognitive science aim to design algorithms which model or represent the processes of the mind. On the other hand, as shown in the previous chapter, the behavioural algorithms could possibly contribute to the design of mathematical models for broader problem solving. The study of social insects and particularly ants has provided the scientists with plentiful insights on all the above mentioned fields.

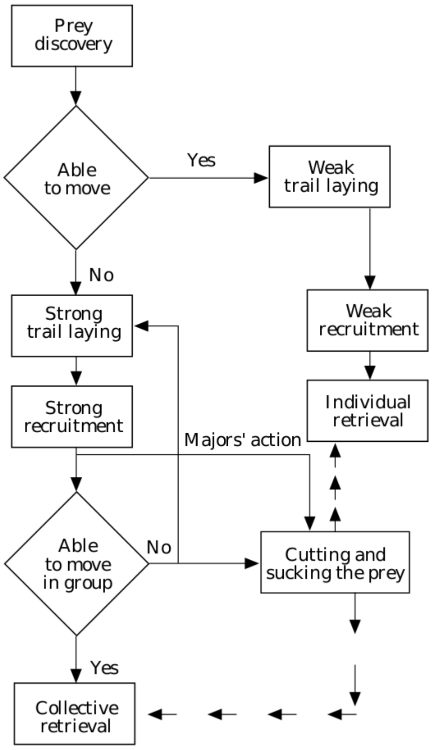


Figure 4.2: Algorithm I of foraging. Decision-making process of ants while forage for prey. Source: Adapted from [Detrain and Deneubourg, 1997]

Detrain and Deneubourg studied the problem solving and information processing of social insects, in a complex environment [Detrain and Deneubourg, 2002]. Different conditions often influence the same decision rule to lead to diversified behaviours and foraging patterns. Each member of an ant colony who acts as foraging scouter is crucial for the behaviour of the whole colony. It is responsible to decide whether to create or reinforce a pheromone trail which leads to a food source [Hölldobler et al., 1990]. Figure 4.2 illustrates the decisions made during foraging process, in relation to the prey size. Different foraging patterns emerge both of individual (when the prey is small enough) and cooperative (when the prey is larger) revisit of the food source. The second situation is characterised by a well-defined foraging trail which depends on the pheromone trail-laying. The traction resistance of the prey, was shown to affect the forager's decision to 'ask' (or not) the help of the other members of the colony. When the researchers prevented the transfer of the prey, the trail pheromone concentration was increased to a value such the one observed in large prey collecting. Weak or intense trail-laying depends on the success in prey carrying, while weak but frequent pheromone laying is accomplished when small food objects are abundant and can be carried by the explorer solely. If the carrying of the prey remains ineffective, even after the assembly of more colony members, the next step is the dissection and sucking of the prey's hemolymph.

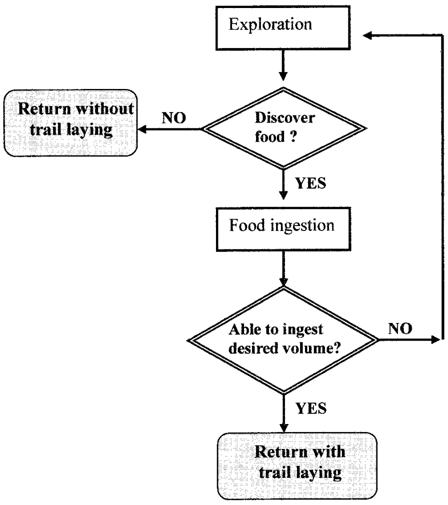


Figure 4.3: Algorithm II of foraging. Decision-making process of ants while make use of a liquid food source. Drawn from results of [Mailleux et al., 2000]. Source: Adapted from [Detrain and Deneubourg, 2002]

Figure 4.3 represents the actions of the foragers when exploiting liquid sources [Mailleux et al., 2000]. When the source's volume exceeds the amount that the present foragers can carry, the 90% of them reinforce the trail with pheromone. Contrarily, plenty individuals return 'empty-handed' when the volume is small. The number of trail-layers depends on the source's volume, but the pheromone deposition of each trail-layer is consistent. Each individual, in order to decide if it will reinforce the trail, relies on its ability to ingest a intended food volume - threshold (not fixed for each forager). If the subject is not able to ingest as much as it intends to, as a result of crowding, low source volume or running out of the source, it will carry on foraging and possibly return empty-handed. The above threshold decision rule helps further the determination of individuals which participate in honeydew production of aphid colonies. Therefore, the food source volume influences the colony as a whole, by means of the fraction of trail-laying individuals over the number of the members return.

Two more examples from social insect behaviour, which resemble algorithmic procedures are displayed. Figure 4.4 depicts an ant colony's selection of a new nest as an algorithmic form of

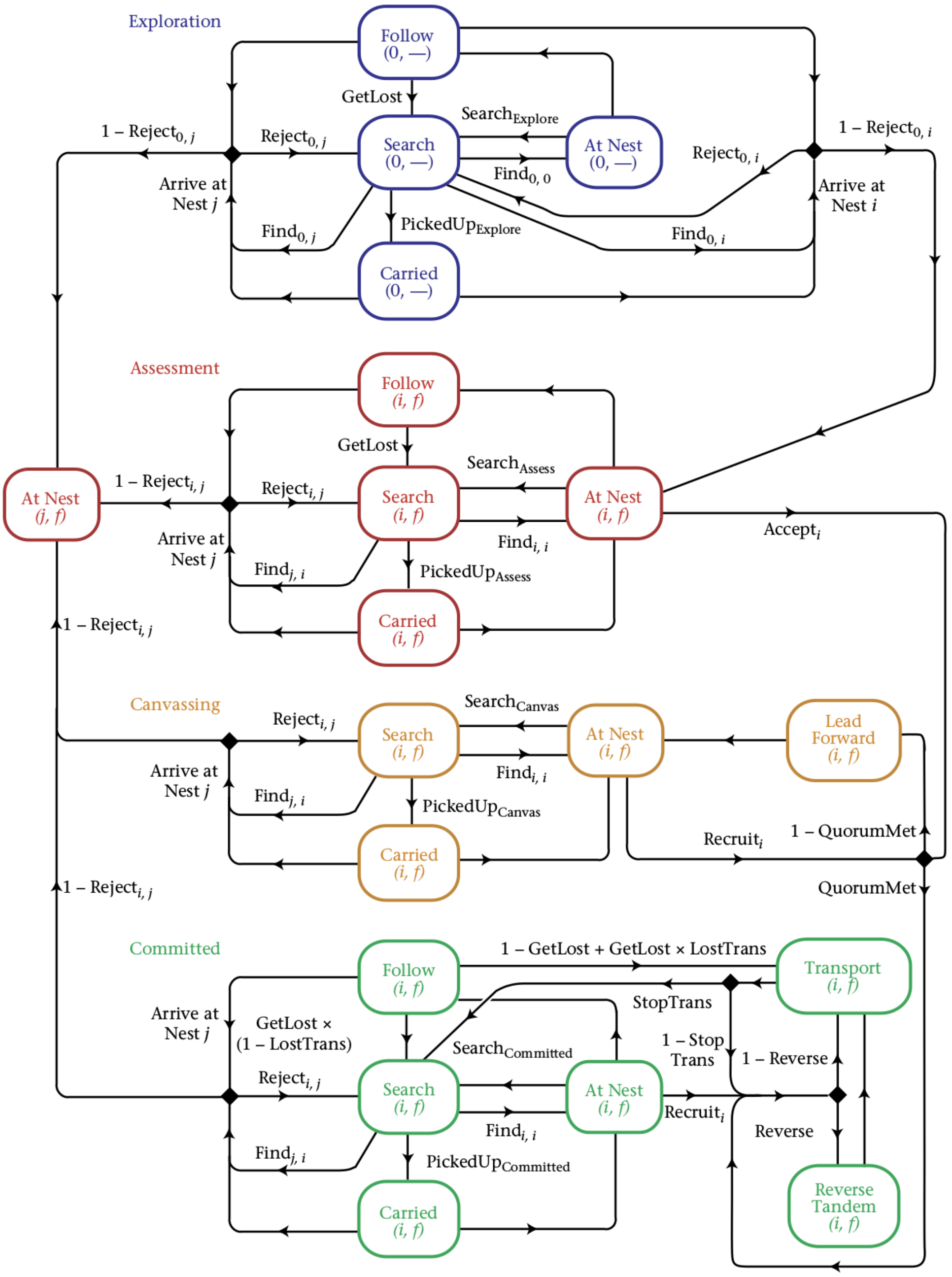


Figure 4.4: Emigration behaviour of *Temnothorax* ants. If one considers the depiction as a graph, the vertices/boxes represent behavioural states and the edges/arrows transitions among them. The labels indicate measured probabilities for each transition. Each individual begins at the exploration level (blue), searching for potential nest location. When it locates a promising site continues in the assessment phase (red), evaluating this site. Afterwards, in canvassing phase (yellow), accepts the site temporarily and leads collective runs along with other nest-mates who further assess the site. Ultimately, the individual completely commits the site by promptly transporting passive adults and broods, in the committed phase (green). Subscript i declares the location that is currently being assessed by the ant, whereas subscript f declares the initial nest from which ants are recruited. Source: Adapted from [Pratt et al., 2005]

the collective decision-making mechanism. Each ant corresponds to a distinct agent and their behaviour is represented as a states' network connected by transition probabilities. Overall, it is shown how the individual data lead to the determination of an algorithmic form for the emigration. Figure 4.5 depicts the 'life history of a (bee) forager'. For further details on information processing in social insects, foraging strategies of ants and so on, see [Detrain et al., 1999]. Additionally, an interesting consideration of the 'neuron-like' behaviour of ants can be found in 'Box 2' of [Couzin, 2009]. Ant colonies, similarly to neuronal systems, can be regarded as systems of parallel information-processing which perform complex collective decision-making pertain to moving, foraging and other behaviours.

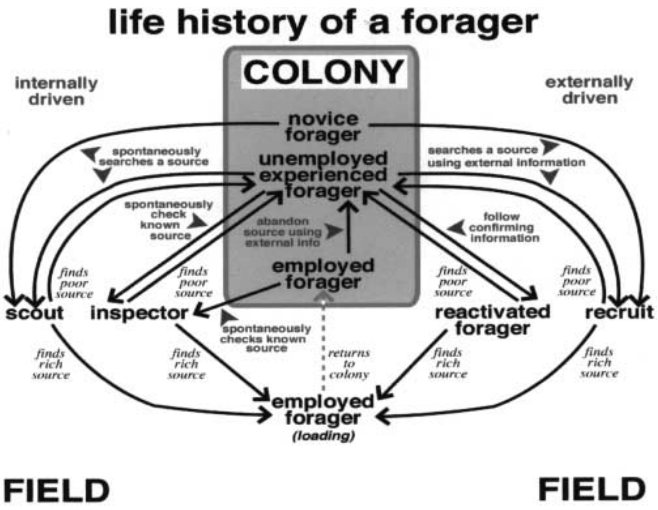


Figure 4.5: Behaviour control structure of a bee forager. Seven behavioural categories are observed, on the left internally driven and on the right externally driven. The transitions among the categories and the information on which these transitions are based are also illustrated. When/if a rich source is located the searching forager turns into an employed but if the source is poor or absent turns into unemployed by its returning to the hive. Source: Adapted from [Biesmeijer and de Vries, 2001]

CONCLUSIONS AND FUTURE PROSPECTS

This thesis provides a review of the collaboration between biology and concepts of algorithms as well as graph theory, focusing on animal behaviour and neuroscience. Apart from the presented, in these terms, further mathematical applications can be developed. Graph theory is the mathematical discipline which underpins the study of complex biological networks whose structure seems to be linked to function and not to randomness. In the first chapter a discussion of molecular and cell biology is included. The analysis of cellular and (bio-)molecular processes needs the design of highly dynamic models due to their switching network topology, while it is essential to identify the genetic and environmental factors which influence network features. Moreover, plentiful measures of graph theory are applied to the study of complex networks in the brain. They can be used in order to explain the structure-function relationships in the context of anatomical and neurophysiological studies, that is to investigate the functional role of brain network connectivity in the information processing. Synchronization processes, network comparisons and responses to stimuli, including damage, as well as the plasticity of brain networks can be possibly modelled with graph theory. In the future, the optimal way of combining data from diverse sources (e.g. fMRI or MEA) and converting to graphs for expression of the microstructure has to be verified, whereas the properties of the graphs which indicate or predict cognitive disturbances have to be determined.

A range of examples for the use of graph theory and algorithms in the study of networks in the behavioural sciences was also provided. Such approaches can help us identify patterns of social organisation and by extension to compare social structures of different populations or species. Social network analysis based on graph theory is capable to identify vertices of individuals or subgroups whose role is crucial to the network function and stability. Analysis of collected representative data provides an excellent framework for testing hypotheses about social behaviour, following the information flow through groups and evaluating the significance of indirect social links as well as the effects of social structure on the group and individual welfare.

Observational studies could reveal how network structure affects the level of cooperation, while graphs with vertices of coexisting competition and cooperation relationships have to be developed for the modelling of more general coopetition networks. Future studies have to explain how collective decision-making emerge from interactions among (selfish) individuals in these graphs and how well mathematical models can describe the dynamics of collective behaviour in nature. Furthermore, game theory models along with the methods of neuroscience can enrich the study of social decision-making by exploring adaptive partner choices which may depend on features such as cooperativeness, health, aggressiveness, sex and more. Lastly, the determination of the algorithms that produce the collective animal behaviour can elucidate the way that natural selection has promoted their evolutionary origin. On the contrary, coordinated animal behaviour can inspire the design of (optimisation) algorithms.

The adaptive collective behaviours in self-organized systems based on environmental parameters and simple decision rules shape the dynamics of information transfer in the nature and can contribute to the modelling of problem-solving. Algorithms inspired by animal behaviour include metaheuristic, optimisation and further techniques. Compared to other well-known methods, these algorithms have been shown to perform efficiently for dealing with optimization problems while they may impose fewer mathematical requirements. Future development of similar techniques is still needed to solve more complex and real optimization problems.

Approaches which aim to explain functions of cognition with algorithms have been published in the course of the last decades. Algorithmic and computational perspectives of neuroscience explore the neural circuits and causal manipulation in order to determine what information is computed and how. For the understanding of the brain as a (Turing) machine which processes information, we have to relate stimulus to behaviour through the dynamics and transitions of information processing states.

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