



COMPLESSITÀ E RIDUZIONE

a cura di

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Riflettendo su complessità e riduzionismo

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Il volume raccoglie gli atti della XIII Scuola Estiva di Filosofia della Fisica, tenutasi a Cesena dal 13 al 18 settembre 2010. A partire dal 1998, il Centro Interuniversitario di ricerca in Filosofia e Fondamenti della Fisica (Urbino, Bologna, Salento e Insubria) organizza annualmente una scuola estiva in collaborazione con la Società Italiana di Logica e Filosofia delle Scienze (SILFS) e il Comune di Cesena. La scuola, diventata ormai punto di riferimento annuale per studenti, insegnanti e studiosi di varie discipline, affronta ogni anno un tema differente invitando i maggiori esperti italiani sull'argomento. Dedicata a "Complessità e Riduzionismo", l'edizione del 2010 si è avvalsa anche della collaborazione della Scuola di Dottorato in Antropologia ed Epistemologia della Complessità dell'Università degli

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Studi di Bergamo che, dal 2002, promuove in Italia e nel mondo la formazione e il perfezionamento di ricercatori esperti nella complessità storica, filosofica e antropologica delle scienze naturali e umane.

Come mostrano i contributi qui raccolti, durante i lavori della scuola, complessità e riduzionismo sono stati affrontati dai relatori a partire da prospettive diverse e sotto differenti punti di vista.

Gian-Italo Bischi, dopo aver brevemente delineato la storia della progressiva matematizzazione dell'economia, si è concentrato soprattutto sull'utilizzo di modelli dinamici non lineari. Sviluppati inizialmente in ambito fisico e basati su equazioni di evoluzione, tali modelli deterministici vengono utilizzati per prevedere – ed eventualmente controllare – l'evoluzione temporale di sistemi reali. Secondo Bischi, la scoperta che modelli dinamici non lineari (tipici dei sistemi sociali che presentano continue interazioni e meccanismi di feed-back) possono esibire comportamenti di caos deterministico, caratterizzato dalla proprietà di amplificare in modo difficilmente prevedibile perturbazioni arbitrariamente piccole, ha suscitato un certo imbarazzo e nel contempo creato nuove possibilità. Imbarazzo perché la presenza di caos deterministico rende insostenibile l'ipotesi dell'agente economico razionale, ovvero capace di prevedere correttamente; ma apre anche nuove possibilità, poiché tale scoperta mostra che quei sistemi economici e sociali caratterizzati da fluttuazioni in apparenza casuali potrebbero in realtà essere governati da leggi del moto deterministiche (anche se non lineari).

Se Bischi ha affrontato il tema della complessità in ambito economico, Salvo D'Agostino ha invece introdotto e approfondito il problema dei successi e dei fallimenti dell'assiomatizzazione in campo fisico. Uno degli aspetti più dibattuti della complessità sul versante scientifico e filosofico è infatti quello della supposta rinuncia a una generalizzazione dei procedimenti assiomatico-deduttivi come metodo generale della ricerca scientifica. A partire dalla considerazione che la fisica pre-relativistica è spesso stata considerata fondata prevalentemente sul trionfo di tale metodo, D'Agostino ha evidenziato la presenza di una posizione antagonista presente già in Newton e ripresa successivamente da Ampère e Maxwell. Alternativa al metodo assiomatico-deduttivo, tale prospettiva si fonda sul ricorso alla cosiddetta deduzione dai fenomeni. Una variazione sul tema, è stata individuata da D'Agostino anche nel contributo di Einstein in cui alla celebrazione del metodo assiomatico-deduttivo si contrappone una lode dell'osservazione dei fenomeni e della riflessione sugli esperimenti: è proprio ponendo il problema di una scelta o conciliazione fra le due che

Einstein avrebbe, secondo D'Agostino, il merito di aver aperto la via al pensiero scientifico moderno.

Sempre in ambito fisico, Arcangelo Rossi ha tracciato, da un punto di vista storico, il passaggio dai modelli riduzionistici che hanno caratterizzato lo studio delle realtà fisica nella scienza classica all'emergere della questione della complessità nella scienza contemporanea. In particolare, a partire dall'affermazione di Ernst Cassirer secondo cui la piena transizione da un'accezione sostantiva ed esplicativa dei modelli a una formale e funzionale sarebbe rintracciabile già alle origini della scienza moderna, Rossi ha mostrato come la visione della natura che emerge dalla scienza classica illuminista fosse comunque realista e riduzionista. Benché alcuni aspetti e alcune visioni non propriamente qualificabili come riduzioniste e meccaniciste siano già presenti all'interno della scienza classica, la tematica della complessità comincia a svilupparsi in fisica solo alla fine dell'Ottocento.

Sergio Chibarro, Lamberto Rondoni e Angelo Vulpiani hanno affrontato il ruolo del caos e l'emergenza di proprietà collettive all'interno della meccanica statistica. In particolare, hanno mostrato l'esistenza di due posizioni nettamente diverse: da una parte il punto di vista "tradizionale", risalente a Boltzmann e parzialmente formalizzato da Khinchin, secondo cui la meccanica statistica sarebbe caratterizzata in primo luogo dall'enorme numero di gradi di libertà; dall'altro la scuola "moderna" cresciuta intorno a Prigogine e ai suoi collaboratori, che considera il caos come l'ingrediente fondamentale. Anche attraverso alcune simulazioni numeriche, gli autori hanno mostrato come anche all'interno della meccanica statistica si faccia avanti il problema della complessità e del riduzionismo. Sebbene i risultati di Khinchin non siano in grado di rispondere in modo definitivo a tutti i problemi sollevati dalla relazione fra termodinamica e meccanica statistica, il numero estremamente grande di gradi di libertà che tale approccio prende in considerazione permette *l'emergere*, nei sistemi macroscopici, di proprietà del tutto assenti in sistemi piccoli.

Giorgio Turchetti ha introdotto il problema del passaggio dai modelli fisici ai sistemi complessi mostrando come i limiti che il disegno riduzionista incontra già per i sistemi fisici diventino decisamente più forti nel caso dei sistemi complessi. La grande differenza tra un sistema fisico e un sistema complesso risiederebbe infatti, secondo Turchetti, nel fatto che il primo, fissate le condizioni esterne, ha sempre le medesime proprietà, mentre il secondo cambia con il fluire del tempo, perché la sua organizzazione interna muta non solo al cambiare di fattori ambientali ma anche con il succedersi delle generazioni. È in tale prospettiva che egli

giunge a definire complessi non tanto i sistemi caratterizzati da proprietà emergenti e da interazioni non lineari tra i loro componenti (definibili come sistemi dinamici), ma piuttosto i sistemi viventi o quelli di vita artificiale che ne condividono le proprietà essenziali.

Il problema di complessità e riduzionismo in campo biologico è stato poi affrontato in maniera diretta da Luciano Boi e da Roberto Serra. Il primo ha mostrato come lo studio del comportamento dinamico delle strutture cellulari non possa essere descritto con sufficiente accuratezza né dalla convenzionale dinamica dell'equilibrio né da modelli statici e richieda quindi nuovi strumenti. In particolare, egli ha affrontato la necessità – per una comprensione del comportamento dei sistemi (dinamici) complessi – di un'adeguata conoscenza delle caratteristiche cinetiche e topologiche delle loro componenti. A differenza dello studio dei meccanismi molecolari, l'analisi del comportamento dinamico delle strutture cellulari non necessita tanto di una profonda e dettagliata conoscenza del comportamento di ogni singola molecola, ma piuttosto delle regole che governano il comportamento globale e collettivo dei sistemi.

In consonanza con il contributo di Boi, Serra ha spiegato come la scienza dei sistemi complessi abbia mostrato l'esistenza di "leggi" in gran parte indipendenti dalle specifiche caratteristiche delle entità microscopiche che tuttavia ne descrivono il comportamento e l'interazione. Se la ricerca di proprietà generali ha ormai assunto una grande rilevanza in ambito fisico, nelle scienze biologiche si trova ancora nei suoi primi stadi di vita. Attraverso una serie di esempi, Serra ha mostrato come tale approccio, da considerarsi non in opposizione alla biologia molecolare classica ma a essa complementare, sembra però portare anche in ambito biologico a importanti e promettenti risultati. Emblematico in questo senso è per Serra il lavoro di Kauffman che rivela come un sistema dinamico di geni che interagiscono fra loro mostri delle proprietà di auto-organizzazione che spiegano alcuni aspetti della vita, fra cui l'esistenza di un numero limitato di tipi cellulari in ogni organismo multicellulare.

Pierluigi Graziani ha affrontato invece il problema della complessità computazionale in riferimento alla decidibilità della geometria elementare di Tarski. A partire soprattutto dai lavori di Fisher, Rabin e Meyers e in confronto con il lavoro di Tarski, Graziani ha analizzato come il problema della decisione si trasformi nella determinazione di quanto tempo e spazio di memoria impieghi un algoritmo di decisione per una teoria a determinare se un enunciato della teoria ne sia o meno un teorema. In teoria della complessità computazionale, infatti, si assume che siano computazionalmente intrattabili quei compiti che richiedono risorse di

tempo e spazio di memoria (le cosiddette risorse computazionali) che crescono esponenzialmente con la lunghezza dell'input; e che siano computazionalmente trattabili quelli che richiedono risorse che crescono al più in modo polinomiale con la lunghezza dell'input. In tale prospettiva, la complessità computazionale non concerne dunque quante risorse richiede lo svolgere un determinato compito, bensì quanto aumentano le risorse richieste al crescere delle dimensioni dei dati.

Claudio Calosi e Vincenzo Fano hanno mostrato come il problema della complessità e del riduzionismo riguardi anche il rapporto fra psicologia e fisica. In particolare, hanno proposto qui un nuovo esperimento mentale che hanno chiamato Shem-Shaun – dal nome dei due gemelli protagonisti del *Finnegan's Wake* di Joyce – e che solleva un problema per il Fisicalismo minimale in filosofia della mente. Il fisicalismo minimale viene infatti caratterizzato come quella tesi secondo cui le proprietà mentali sopravvengono nomologicamente sulla proprietà fisiche, una forma di riduzionismo per cui, stabilite le proprietà fisiche del mondo, quelle mentali sarebbero necessariamente determinate. Gli autori sostengono che, o il Fisicalismo minimale è incapace di dare un resoconto adeguato dell'esperimento Shem-Shaun o ne deve dare un resoconto che è in forte tensione con la nostra attuale immagine scientifica del mondo.

Nel loro insieme, i lavori presentati testimoniano da un lato la vivacità degli studi epistemologici sulla complessità e dall'altro l'importanza del concetto di complessità per la filosofia della scienza e, in particolare, della fisica.

Remarks on the Geometry of Complex Systems and Self-Organization

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1. Introductory remarks on the geometry of complexity

Let us start by some general definitions of the concept of complexity. We take a complex system to be one composed by a large number of parts, and whose properties are not fully explained by an understanding of its components parts. Studies of complex systems recognized the importance of “wholeness”, defined as problems of organization (and of regulation), phenomena non resolvable into local events, dynamics interactions in the difference of behaviour of parts when isolated or in higher configuration, etc., in short, systems of various orders (or levels) not understandable by investigation of their respective parts in isolation. In a complex system it is essential to distinguish between ‘global’ and ‘local’ properties. Theoretical physicists in the last two decades have discovered that the collective behaviour of a macro-system, i.e. a system composed of many objects, does not change qualitatively when the behaviour of single components are modified slightly. Conversely, it has been also found that the behaviour of single components does change when the overall behaviour of the system is modified.

There are many universal classes which describe the collective behaviour of the system, and each class has its own characteristics; the universal classes do not change when we perturb the system. The most interesting and rewarding work consists in finding these universal classes

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and in spelling out their properties. This conception has been followed in studies done in the last twenty years on second order phase transitions. The objective, which has been mostly achieved, was to classify all possible types of phase transitions in different universality classes and to compute the parameters that control the behaviour of the system near the transition (or critical or bifurcation) point as a function of the universality class.

This point of view is not very different from the one expressed by Thom in the introduction of *Structural Stability and Morphogenesis* (1975). It differs from Thom's program because there is no *a priori* idea of the mathematical framework which should be used. Indeed Thom considers only a restricted class of models (ordinary differential equations in low dimensional spaces) while we do not have any prejudice regarding which models should be accepted.

One of the most interesting and surprising results obtained by studying complex systems is the possibility of classifying the configurations of the system taxonomically. It is well-known that a well founded taxonomy is possible only if the objects we want to classify have some unique properties, i.e. species may be introduced in an objective way only if it is impossible to go continuously from one specie to another; in a more mathematical language, we say that objects must have the property of ultrametricity. More precisely, it was discovered that there are conditions under which a class of complex systems may only exist in configurations that have the ultrametricity property and consequently they can be classified in a hierarchical way. Indeed, it has been found that only this ultrametricity property is shared by the near-optimal solutions of many optimization problems of complex functions, i.e. corrugated landscapes in Kauffman's language. These results are derived from the study of spin glass model, but they have wider implications. It is possible that the kind of structures that arise in these cases is present in many other apparently unrelated problems.

Before to go on with our considerations, we have to pick in mind two main complementary ideas about complexity. (i) According to the prevalent and usual point of view, the essence of complex systems lies in the emergence of complex structures from the non-linear interaction of many simple elements that obey simple rules. Typically, these rules consist of 0–1 alternatives selected in response to the input received, as in many prototypes like cellular automata, Boolean networks, spin systems, etc. Quite intricate patterns and structures can occur in such systems. However, what can be also said is that these are toy systems, and the systems occurring in reality rather consist of elements that individually are quite complex themselves. (ii) So, this bring a new aspect that seems essential and indispensable to the

emergence and functioning of complex systems, namely the coordination of individual agents or elements that themselves are complex at their own scale of operation. This coordination dramatically reduces the degree of freedom of those participating agents. Even the constituents of molecules, i.e. the atoms, are rather complicated conglomerations of subatomic particles, perhaps ultimately excitations of patterns of superstrings. Genes, the elementary biochemical coding units, are very complex macromolecular strings, as are the metabolic units, the proteins. Neurons, the basic elements of cognitive networks, themselves are cells.

In those mentioned and in other complex systems, it is an important feature that the potential complexity of the behaviour of the individual agents gets dramatically simplified through the global interactions within the system. The individual degrees of freedom are drastically reduced, or, in a more formal terminology, the factual space of the system is much smaller than the product of the state space of the individual elements. That is one key aspect. The other one is that on this basis, that is utilizing the coordination between the activities of its members, the system then becomes able to develop and express a coherent structure at a higher level, that is, an emergent behaviour (and emergent properties) that transcends what each element is individually capable of.

2. Complex systems

There are many different definitions of a complex system. It may range from the classical algorithmic complexity (Kolmogorov, Chaitin) to more recent and sophisticated definitions, such as: chemical definitions, statistical-physics definitions, topological-dynamic definitions, biological definition, etc. We already have given the most common and general definition in the literature of complex systems. It should be clear, however, that any given definition (especially a mathematical one) couldn't capture all the complex meaning we associate with the word complexity.

One interesting definition rest on the basic idea that the more complex the system, the more can be said about. I am excluding the factual description of the system, which may be very long. I refer only to the global characteristics. A few examples will help clarify this point. If I have a sequence of randomly tossed coins, 50% probability head, I have described the system. The only improvement would be the knowledge of the sequence itself. If on the contrary the sequence of bits represents a book, there is much more information, such as style, choice of words, the plot and so on.

If the book is really deep, complex, there are a very large number of things that can be said about it. Sometimes the complexity is related to the existence of different levels of description: one can describe an *Escherichia coli* at the molecular level, at the biochemical level, and at the functional level.

If we move towards a mathematical definition, we must realize that the concept of complexity, like entropy, is of probabilistic nature and it can be defined more precisely if we try to define the complexity of ensembles of objects of the same category. This is related to the notion of classification. The meaning of a complex classification is quite clear intuitively: a classification is very complex if there are many levels (i.e. orders, families, genera) and there are many elements in each level. Consequently a reasonable mathematical definition of the complexity of a classification should be possible.

3. External and internal complexity

Let's now introduce the notions of *external* and *internal* complexity of complex adaptive systems. These concepts are especially useful to analyze relations between an adaptive system and its environment. All open systems, let them be either thermodynamics, biological or cognitive, are chiefly concerned with this relation.

A *complex adaptive system* is situated in an environment. That environment is always more complex than the system itself, and therefore, it can never be completely predictable for the system, but the system depends on regularities of the environment for maintaining its energy supply needed to support its internal structure.

One important hypothesis one can suggest is that complex adaptive systems try to increase their external complexity and to reduce internal complexity. Each of two processes will operate on its own scale, but they are also intricately linked and mutually dependent upon each other.

The increase of internal complexity can for example occur through the creation of redundancy, e.g. duplication of some internal units or structures. The property of redundancy is very important in biological systems at the genetic level as well as at other more complex levels; for example, a same gene may realize different functions and, on the other hand, many genes may accomplish the same function. Upon this redundancy, a process of differentiation or specialization can operate, through controlled random mechanisms or internal selection, so that the system will become able to

handle more diverse input and thereby increase its external complexity. Once this happened, the system can then again try to represent this newly acquired input more efficiently and thus decrease its internal complexity. Conversely, for the decrease of internal complexity, the system can also find some of its input as irrelevant and meaningless for its purposes and thus decrease the external complexity.

As first definition, one can say that *external complexity* measures the amount of input, information, energy obtained from the environment that the system is capable of handling, processing. It is important that this can be measured as an entropy – and therefore, terms like “energy” need some qualification when employed in this context. In this sense, external complexity is data complexity.

Internal complexity can be defined as what that measures the complexity of the representation of this input by the system. In this sense, internal complexity is model complexity. The system will try to increase (or maximize) its external complexity, and to reduce (or minimize) its internal complexity.

We now proceed to give formal definitions of our complexity notions based on the concept of entropy from statistical mechanics and information theory. Given a model θ , the system can model data as $X(\theta)$, with $X = (X_1, \dots, X_k)$, and we assume that $X(\theta)$ introduces an internal probability distribution $P(X(\theta))$ so that an entropy can be computed in (1) below. Our hypothesis then is that the system will try to maximize the external complexity,

$$-\sum_{i=1}^k P(X_i(\theta)) \log_2 P(X_i(\theta)). \quad (1)$$

The purpose of the probability distribution $P(X(\theta))$ is simply to qualify the information value of the data $X(\theta)$. In principle, this quantification is also possible through other means, for example, through the length of the representation of the data in the internal code of the system. If we assume optimal coding, however, which is a consequence of the minimization of internal complexity, then the length of the representation of a datum $X_i(\theta)$ behaves like $\log_2 P(X_i(\theta))$ (a code is good if frequent inputs are represented by short code words.)

The system can try to increase the amount of information $X(\theta)$ that is meaningful within the given model θ on a short time scale, or it can adapt the model θ on a larger time scale so as to be able to process more inputs as meaningful. When the input is given, however, for example when the

system has gathered input on a time scale when the distribution of input patterns \mathcal{E}^1 becomes stationary, then the model should be improved to handle that input as efficiently as possible, i.e. to decrease the internal complexity which we now define as follows

$$= - \sum_{i=1}^k P(\mathcal{E}_i(\theta)) \log_2 P(\mathcal{E}_i(\theta)) - \log_2 P(\theta). \quad (2)$$

The variation is given by

$$\min_{\theta} (- \log_2 P(\mathcal{E}/\theta) - \log_2 P(\theta)). \quad (3)$$

The expression to be minimized now consists of two terms, the first measuring how efficiently the data are encoded by the model, and the second one how complicated the model is. Of course the probability $P(\theta)$ assigned to a model depends on the internal structure of the system, and in principle, that internal structure then also became subject to optimization, in the sense that frequently used or otherwise important models get higher probabilities than obscure ones.

3.1. Pattern recognition in a neural network

We only mention the principle according to which a neural network can recognize patterns on the basis of a selective evaluation of inputs features via an internal feedback loop. (No detailed description will be presented here).

We assume that the network or system has stored or identified a collection of patterns labelled by $i = 1, \dots, n$. These patterns might correspond to faces, visual shapes or other geometric objects; for thinking about this example, it is probably useful to think about patterns to be recognized in visual scenes. Also, on its input, the system can evaluate certain features $\alpha = 1, \dots, m$, like edges, corners, or better, features of a somewhat higher level, like specific distribution of input pixels on some small sub-regions of the retina, or relative distances between certain conspicuous points of the scene. It is important for understanding the purpose of the network (the system) that we assume to in a situation where the network is not capable of evaluating all the possible features

¹ We use a different letter now to denote the inputs because we are now considering patterns on a different time scale.

simultaneously in its inputs, simply because there are typically far too many possibilities.

Rather the idea is that the network will selectively perform observations, that is, evaluate those features that have the highest potential for discriminating between these patterns that are probable candidates on the basis of the observations already performed. Thus, the basic design principle is a feedback loop between observations that affect the probability distribution in the space of patterns and the selection of further observations on the basis of that probability distribution.

We first need to implement the relationship between patterns and features. This can be done on the basis of supervised learning as is standard in neural networks. So, the observed values x^α of the features induces activations y^i of the patterns:

$$y^i : f(\sum_{\alpha} w_{i\alpha} x^\alpha), \quad (4)$$

where f might be a sigmoid function $f(s) = 1/(1+e^{-ks})$, where for our purpose a rather large value of the parameter k might be best so as to get a sharp threshold later on. Namely, we call a pattern i activated if $y^i > \theta$ is some threshold that we can turn to our convenience, perhaps again by supervised learning. The $w_{i\alpha}$ are weights that can likewise be learned through supervised Hebbian learning. The essential point is that they should be positive, and perhaps large, if feature α occurs in pattern i , and 0 or negative if not.

4. Examples of complex systems

Let us now give briefly some examples of complex systems took from different disciplines: chemistry, biology and physics. In all this examples, understanding how parts of a living system – genes or molecules – interacts is just as important as understanding the parts themselves.

In Chemistry the word *complexity* present some ambiguity and it is highly dependent on context. In one characterization a complex system is: (i) one whose evolution is very sensitive to initial conditions or to small perturbations; (ii) one in which the number of independent interacting components is large; (iii) or, one in which there are multiple pathways by which the system can evolve. Analytical descriptions of such systems typically require nonlinear differential equations. In chemistry, almost every thing of interest is complex by one or both definitions.

We are here concerned with “tractable complexity”: a subset of complex problems (for example, oscillating reactions) provides classical examples of complex systems in the sense that they can be described analytically by relative simple sets of nonlinear differential equations. But, there are other complex problems of general importance for which there are no simple general solutions.

In the sequence of complexity – from static equilibrium, to dynamic steady state, to dynamic complexity, to chaos – there are chosen sets of chemical reactions whose properties make them appropriate as case studies in complexity. Oscillating reactions of the type represented by the Belousov-Zhabotinsky reaction are perhaps the best-known example. This class of chemical reactions has the characteristic that the simultaneous operation of two processes, reaction and diffusion, results in a system in which the concentration of reactants and products oscillate temporally and spatially and in which this oscillation can result in ordered patterns. In other words, coupled chemical reactions cause changes in concentration of the reagents that, in turn, cause local changes in the oxidation potential of the solution. These potentials can be visualized as oscillating travelling waves in such a reaction.

These reactions can be described mathematically by a system of nonlinear equations of greater or lesser complexity, but equations below represent a minimum set of two reaction-diffusion equations

$$\partial u / \partial t = F(u, v) + D_u \nabla^2 u \quad (5.1)$$

$$\partial v / \partial t = \epsilon G(u, v) + D_v \nabla^2 v \quad (5.2)$$

Here, u is the concentration of a species that catalyze reaction; v is the concentration of a species that inhibits reactions; $\partial u / \partial t$ and $\partial v / \partial t$ describe changes in concentration of u and v , respectively with time; $F(u, v)$ and $\epsilon G(u, v)$ characterize reactions between u and v , respectively; and D_u and D_v are the diffusion coefficients of u and v , respectively.

An important motivation in chemistry of studying complexity has been to learn about processes in living systems. One of the most striking characteristics of cells is the sheer complexity of metabolism. The human genome probably has on the order of 105 expressed gene products; many of these proteins are enzymes, receptors, and members of signalling sequences, that is, functional parts of metabolism. Understanding a system with this many interacting components is clearly out of the question. A more tractable problem is to examine discrete, relatively self-contained sections of metabolism. One metabolic cycle that has been studied in substantial detail

is glycolysis, that is, the conversion of glucose to pyruvate with the production of adenosine 5'-triphosphate and the reduced form of nicotinamide adenine dinucleotide (NAD)². This sequence of reactions involves 10 enzymes, with various levels of modulation of the catalytic activities of some of these enzymes by the products of others.

The second example of complexity I would like to mention concerns *biological signalling systems*. Biological signalling pathways interact with one another to form complex networks. Complexity arises from the large number of components, many with isomorphs that have partially overlapping functions; from the connections among components; and from the spatial relationship between components.

Signalling in biological systems occurs at multiple levels. Already compartmentalization introduces several levels of complexity. First, many signalling components and their substrates are anchored in the plasma membrane. The plasma membrane provides a milieu for biochemical reactions that is quite distinct from the cytoplasm in its properties. The lipid environment enables a new class of reactions involving hydrophobic interactions. Organelle formation leads to a further expansion of the possible cellular microenvironments, each with different biochemical properties and signalling capabilities. Second, the separation of reactions in space allows the same molecules in the same cell to carry entirely different signals. In other words, we already have signalling “wires” distinguished by the identity of the molecules in the pathways. Compartmentalization duplicates these existing wires and separates them in space. This multiplies the number of signals they can carry about.

In addition to sub-cellular compartmentalization recent research has highlighted the role of molecular scaffolds that provide regional organization by assembling signalling components into functional complexes. The cytoskeleton is a dynamic framework on which the cell builds this regional organization. The most dramatic example of its dynamism is cell division. In the quiescent cell, it is both the substrate and the scaffold for signalling processes.

² Nicotinamide adenine dinucleotide (NAD and its relative nicotinamide adenine dinucleotide phosphate (NADP) are two of the most important coenzymes in the cell. NADP is simply NAD with a third phosphate group attached. NAD participates in many redox reactions in cells, including those in glycolysis, and most of those in the citric acid cycle of cellular respiration. NADP is the reducing agent produced by the light reactions of photosynthesis, consumed in the Calvin cycle of photosynthesis, and used in many other anabolic reactions in both plants and animals.

A prime example of its dual role is its synapse. Here the cytoskeleton, in particular the pre- and postsynaptic structures, are the anchors for a wide array of synaptic signalling molecules. Consequently, modifications of the synaptic cytoskeleton are a likely candidate for causing long-term changes in synaptic efficacy.

To conclude this section, we point out some theoretical remarks about characteristic properties of complex living systems. Let's start with some observations.

4.1. Network behaviours and emergent properties

1. Today, it is clear that the specificity of a complex biological activity does not arise from the specificity of the individual molecules that are involved, as these components frequently work in many different processes. For instance, genes that affect memory formation in the fruit fly encode proteins in the cyclic adenosine monophosphate (cAMP)³ signalling pathway that are not specific to memory. Biological specificity results from the way in which these components assemble and work together. Interactions between the parts, as well as influences from the environment, give rise to new features, such as network behaviour.

2. Consequently, “emergence” has appeared as a new concept that complements “reduction” when reduction fails. Emergent properties resist any attempt at being predicted or deduced by explicit calculation or any other means. In this regard, emergent properties differ from resultant properties, which usually can be predicted from lower-level information. For example the resultant mass of a multi-component protein assembly is simply equal to the sum of the masses of each individual component. However, the way in which we test the saltiness of sodium chloride is not reducible to the properties of sodium and chlorine gas.

An important aspect of emergent properties is that they have their own causal powers, which are not reducible to the powers of their constituents. For instance, the experience of pain can alter human behaviour, but the

³ Cyclic adenosine monophosphate (cAMP, cyclic AMP or 3'-5'-cyclic adenosine monophosphate) is a second messenger important in many biological processes. cAMP is derived from adenosine triphosphate (ATP) and used for intracellular signal transduction in many different organisms, conveying the cAMP-dependent pathway. One important intracellular signal transduction is the transferring of the effects of hormones like glucagon and adrenaline, which cannot pass through the cell membrane. It is involved in the activation of protein kinases and regulates the effects of adrenaline and glucagon. It also regulates the passage of Ca²⁺ through ion channels.

lower-level chemical reactions in the neurons that are involved in the perception of pain are not the cause of the altered behaviour as the pain itself has causal efficacy. It should be added that the concept of emergence implies “down-ward causation” by which higher-level systems influence lower-level configurations.

3. The constituents of complex systems interact in many ways, including negative feedback and feed-forward control, which lead to dynamic features (i.e., evolving in time and changing with time) that cannot be predicted satisfactorily by linear mathematical models that disregard cooperativity and non-additive effects.

4. Robustness is another essential property of biological systems. Understanding the mechanisms and principles underlying biological robustness is necessary for an in-depth understanding of biology at the system level. The phenomenological properties exhibited by robust systems can be classified into three areas: (i) *adaptation*, which denotes the ability to cope with environmental changes; (ii) *parameter insensitivity*, which indicate a system’s relative insensitivity to specific kinetic parameters; (iii) *graceful degradation*, which reflects the characteristic slow degradation of a system’s functions after damage, rather than catastrophic failure.

In other systems, such as fluid-mechanics systems, and also engineering systems, robustness is attained by using the following properties: (a) the capability to form a system control such as negative feedback and feed-forward control; (b) *redundancy*, whereby multiple components with equivalent functions are introduced for backup; (c) structural stability, where intrinsic mechanisms are built to promote stability; and (d) modularity, where sub-systems are physically or functionally insulated so that failure in one module does not spread to other parts and lead to system-wide catastrophe.

5. Remarks about the property of structural stability and on self-organization

It remains an open question whether the property of structural stability used in the biological context present some similar characteristics with respect to the concept of structural stability as it has been defined in differential topology in the 1960s by R. Thom and S. Smale.

Intuitively, a *phase portrait* (i.e. all the qualitatively different trajectories of the system) is structural stable if its topology cannot be changed by an arbitrarily small perturbation to the vector field. For instance,

the phase portrait of a saddle point is structurally stable, but that of a center is not: an arbitrarily small amount of damping converts the center to a spiral. Related to the concept of structural stability, we have the notions of *attractor* and *strange attractor*. The term attractor is difficult to define in a rigorous way. Loosely speaking, an attractor is a set to which all neighbouring trajectories converge. More precisely, we define an attractor to be a closed set A with the following properties: (i) A is an invariant set: any trajectory $x(t)$ that starts in A stays in A for all times; (ii) A attracts an open set of initial conditions: there is an open set U containing A such that if $x(0) \in U$, then the distance from $x(t)$ to A tends to zero as $t \rightarrow \infty$. This means that A attracts all trajectories that start sufficiently close to it. The largest such U is called the *basin of attraction of A* ; (iii) A is minimal: there is no proper subset of A that satisfies conditions (i) and (ii).

Finally, we define a strange attractor to be an attractor that exhibits sensitive dependence on initial conditions. Examples of strange attractors are fractal sets and also chaotic attractors. Just to conclude this section, let us remark that the four properties listed above are also found in biological systems. Bacterial chemotaxis⁴ is an example of negative feedback that attains all three aspects of robustness. Redundancy is seen at the gene level, where it functions in control of the cell cycle and circadian rhythms, and at the circuit level, where it operates in alternative metabolic pathways in *E. coli*. Structural stability provides insensitivity to parameter changes in the network responsible for segment formation in *Drosophila*. And modularity is exploited at various scales, from the cell itself to compartmentalized yet interacting signal-transduction cascades.

Lastly, the concept of self-organization in cellular architecture is linked to the complexity of biological systems. A central question in modern cell biology is how large, macroscopic cellular structures are formed and maintained. It is unknown what determines the different shapes and sizes of cellular organelles, why specific structures form in particular places, and how cellular architecture is affected by function and vice-versa.

⁴ *Chemotaxis* is the phenomenon in which somatic cells, bacteria, and other single-cell or multicellular organisms direct their movements according to certain chemicals in their environment. This is important for bacteria to find food (for example, glucose) by swimming towards the highest concentration of food molecules, or to flee from poisons (for example, phenol). In multicellular organisms, chemotaxis is critical to early development (e.g. movement of sperm towards the egg during fertilization) and subsequent phases of development (e.g. migration of neurons or lymphocytes) as well as in normal functions. In addition, it has been recognized that mechanisms that allows chemotaxis in animals can be subverted during cancer metastasis.

Two fundamentally different mechanisms exist to generate macromolecular structures: *self-assembly* and *self-organization*. Whereas self-assembly involves the physical association of molecules into an equilibrium structure, self-organization involves the physical interaction of molecules in a steady-state structure. For example, virus and phage proteins self-assemble to true equilibrium and form stable, static structures. In contrast, most cellular structures (i.e., the cytoskeleton, nuclear compartments, or endocytic compartments) are open for exchange of energy and matter and are governed by steady-state dynamics.

The concept of self-organization is based on observations of chemical reactions far from equilibrium, and it is well established in chemistry, physics and ecology. Self-organization in the context of cell biology can be defined as the capacity of a macromolecular complex or organelle to determine its own structure based on the functional interactions of its components. In a self-organized system, the interactions of its molecular parts (and not the molecular parts themselves) determine its architectural and functional features. The processes that occur within a self-organized structure are not underpinned by a rigid architectural framework; rather, they determine its organization.

For self-organization to act on macroscopic cellular structures, three requirements must be fulfilled: (i) a cellular structure must be dynamic; (ii) matter and energy must be continuously exchanged; (iii) overall stable configuration must be generated from dynamic components.

Recent studies indicate that many cellular structures fulfil the requirements for self-organization. Particularly, self-organization seems to play an important role in the construction and dynamics of three major macroscopic cellular structures: namely the cytoskeleton, the cell nucleus, and the Golgi complex.

Why self-organization? And why self-organization is related to complexity? To answer these questions, consider the followings facts. Macroscopic cellular structures are characterized by two apparently contradictory properties. On one hand, they must be architecturally stable; on the other hand, they must be flexible and prepared for change. Self-organization ensures structural stability without loss of plasticity. Fluctuations in the interactions properties of its components do not have deleterious effects on the structure as a whole. However, global and persistent changes rapidly result in morphological transformations. The basis for the responsiveness of self-organized structures is the transient nature of the interactions among their components.

The dynamic interplay of components generates frequent windows of opportunity during which proteins can change their interaction partners or be modified. The effective availability of components is controlled by posttranslational modifications via signal transduction pathways.

Self-organization is an elegant, efficient way to organize complex structures. The properties that determine the organization are the intrinsic properties of the structure's components. In protein polymers, the protein-protein interaction properties determine the architecture; in membrane structures the flow of membranes determines the architecture. Thus, self-organization is a simple but effective way to optimally organize cellular structures.

The study of complex dynamic behaviour of cellular structures requires new tools. The behaviour of dynamic cellular structures cannot be described accurately by conventional equilibrium dynamics or by static models. To understand the behaviour of complex (dynamic) systems, the kinetic and topological characteristics of their components must be known. In contrast to the study of molecular mechanisms, isn't must sufficient to understand in detail the behaviour of single molecules; rather, the rules that govern the global and collective behaviour of systems must be uncovered.

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