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The Growth of Structural and Functional Complexity during Evolution

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ABSTRACT. Although the growth of complexity during evolution seems obvious to most observers, it has recently been questioned whether such increase objectively exists. The present paper tries to clarify the issue by analysing the concept of complexity as a combination of variety and dependency. It is argued that variation and selection automatically produce differentiation (variety) and integration (dependency), for living as well as non-living systems. Structural complexification is produced by spatial differentiation and the selection of fit linkages between components. Functional complexification follows from the need to increase the variety of actions in order to cope with more diverse environmental perturbations, and the need to integrate actions into higher-order complexes in order to minimize the difficulty of decision-making. Both processes produce a hierarchy of nested supersystems or metasystems, and tend to be self-reinforcing. Though simplicity is a selective factor, it does not tend to arrest or reverse overall complexification. Increase in the absolute components of fitness, which is associated with complexification, defines a preferred direction for evolution, although the process remains wholly unpredictable.

Introduction

At least since the days of Darwin, the idea of evolution has been associated with the increase of complexity: if we go back in time we see originally only simple systems (elementary particles, atoms, molecules, unicellular organisms) while more and more complex systems (multicellular organisms, vertebrates, mammals, human beings) appear in later stages. Traditional evolutionary theory, however, had no methods for analysing complexity, and so this observation remained a purely intuitive impression. The last decades have seen a proliferation of theories offering new concepts and principles for modelling complex systems: information theory, general systems theory, cybernetics, non-equilibrium thermodynamics, catastrophe theory, deterministic chaos, complex adaptive systems, etc. These have led to the awareness that complexity is a much more important aspect of the world than classical, reductionist science would have assumed.

Paradoxically, this development has also been accompanied by a questioning of the idea that complexity necessarily grows during evolution. It turns out that complexity is itself a complex concept: difficult to define and to model, and easy to misinterpret. To a certain extent, complexity is in the eye of the beholder: what is complex for one observer, may be simple for another one. This awareness is reinforced by the wider intellectual climate, characterized by a "post-modern" philosophy, which stresses the subjectivity or culture-dependence of all scientific models. To this must be added the continuing trend away from anthropocentrism, which was started by Copernicus' insight that the Earth is not the center of the solar system, and Darwin's discovery that humans and animals have a common origin. The "growth of complexity" idea can be and has been used to argue that humanity, though it may no longer be at the center of the universe, is still at the top of the evolutionary ladder (Gould, 1994). The present relativistic ideology, which tends to put all people, theories, cultures and even species on an equal footing, shies away from the implied idea of a ladder or hierarchy of complexity, and therefore rejects the whole growth of complexity argument.

On the other hand, concrete observations in diverse domains seem to confirm in ever more detail the intuitive notion of increasing complexity. For example, the at present generally accepted "Big Bang" model of cosmogenesis and its extensions sees the evolution of the universe as one in which simple, homogeneous systems became more differentiated and integrated in subsequent stages: after several rounds of "symmetry breaking" caused by the cooling down of the universe, the primordial energy-matter field condensed into the 4 basic forces and the many families of elementary particles we know now. These particles got further integrated, first into nucleons, then into hydrogen atoms. About the same time, the more or less homogenous distribution of matter in space condensed locally, forming a heterogeneous distributions of stars, within galaxies, within clusters of galaxies. Hydrogen in stars, under the influence of heat and pressure, formed the different elements through nuclear reactions. Heavier elements that left the stellar core could then combine through chemical reactions to form a variety of molecules. Under the right conditions, these molecules would form dissipative cycles of reactions, that in a second stage would give rise to primitive life.

Once we enter the biological realm, things become more ambiguous, and examples can be found to illustrate both increase and decrease of complexity. Yet, the general picture is still one of more complex systems again and again evolving out of more simple ones, e.g. eukaryotes from prokaryotes, sexual reproduction from asexual reproduction, multicellular organisms from unicellular ones (see Maynard Smith & Szathmary, 1995). Once we reach the level of culture, the general growth of complexity again becomes more obvious. Perhaps with temporary exceptions, like the fall of the Roman empire, human history is characterized by an ever more quickly accumulating body of culture, science, technology, and socio-economic organization. Though the speed at which this happens may not have been noticeable in ancient civilisations, it has increased to such a degree that in our present "age of information" few people would dare to deny the observation that the world becomes more complex every year.

These two opposing forces, a philosophically motivated tendency to question the increase of complexity, and the recurrent observation of growing complexity at all stages of the evolutionary process, put the researchers on complex evolution in a strange predicament. Like Maynard Smith and Szathmary (1995), in their study of the major transitions in evolution, they feel obliged to pay lip service to the current ideology by noting the "fallacy" of believing that there is something like progress or advance towards increasing complexity, and then continue by describing in detail the instances of such increase they have studied.

The aim of the present paper is to clarify the issue, by arguing that there are theoretical grounds for concluding that complexity tends to increase, while noting that that increase is not as inexorable or straightforward as the evolutionists in the beginning of this century might have believed. This will be done by introducing a number of basic concepts and principles that can help us to conceptualize evolution and complexity. In a second stage, the main arguments used to criticize the view that complexity grows will be analyzed, and it will be shown how each of them can be countered in our more encompassing conceptual framework. This framework is an extension of the theory of metasystem transitions (Heylighen, Joslyn & Turchin, 1995), which is being developed in the context of the Principia Cybernetica Project.

What is complexity?

As noted, complexity has turned out to be very difficult to define. The dozens of definitions that have been offered all fall short in one respect or another, classifying something as complex which we intuitively would see as simple, or denying an obviously complex phenomenon the label of complexity. Moreover, these definitions are either only applicable to a very restricted domain, such as computer algorithms or genomes, or so vague as to be almost meaningless. Edmonds (1996, this volume) gives a good review of the different definitions and their shortcomings, concluding that complexity necessarily depends on the language that is used to model the system.

Still, I believe there is a common, “objective” core in the different concepts of complexity. Let us go back to the original Latin word *complexus*, which signifies "entwined", "twisted together". This may be interpreted in the following way: in order to have a complex you need two or more components, which are joined in such a way that it is difficult to separate them. Similarly, the Oxford Dictionary defines something as “complex” if it is “made of (usually several) closely connected parts”. Here we find the basic duality between parts which are at the same time *distinct* and *connected*. Intuitively then, a system would be more complex if more parts could be distinguished, and if more connections between them existed.

More parts to be represented means more extensive models, which require more time to be searched or computed. Since the components of a complex cannot be separated without destroying it, the method of analysis or decomposition into independent modules cannot be used to develop or simplify such models. This implies that complex entities will be difficult to model, that eventual models will be difficult to use for prediction or control, and that problems will be difficult to solve. This accounts for the connotation of *difficult*, which the word “complex” has received in later periods.

The aspects of distinction and connection determine two dimensions characterizing complexity. Distinction corresponds to variety, to heterogeneity, to the fact that different parts of the complex behave differently. Connection corresponds to constraint, to redundancy, to the fact that different parts are not independent, but that the knowledge of one part allows the determination of features of the other parts. Distinction leads in the limit to disorder, chaos or entropy, like in a gas, where the position of any gas molecule is completely independent of the position of the other molecules. Connection leads to order or negentropy, like in a perfect crystal, where the position of a molecule is completely determined by the positions of the neighbouring molecules to which it is bound. Complexity can only exist if both aspects are present: neither perfect disorder (which can be described statistically through the law of large numbers), nor perfect order (which can be described by traditional deterministic methods) are complex. It thus can be said to be situated in between order and disorder, or, using a recently fashionable expression, “on the edge of chaos” (Waldrop, 1992).

The simplest way to model order is through the concept of *symmetry*, i.e. invariance of a pattern under a group of transformations. In symmetric patterns one part of the pattern is sufficient to reconstruct the whole. For example, in order to reconstruct a mirror-symmetric pattern, like the human face, you need to know one half and then simply add its mirror image. The larger the group of symmetry transformations, the smaller the part needed to reconstruct the whole, and the more redundant or “ordered” the pattern. For example, a crystal structure is typically invariant under a discrete group of translations and rotations. A small assembly of connected molecules will be a sufficient “seed”, out of which the positions of all other molecules can be generated by applying the different transformations. Empty space is maximally symmetric or ordered: it is invariant under any possible transformation, and any part, however small, can be used to generate any other part.

It is interesting to note that maximal disorder too is characterized by symmetry, not of the actual positions of the components, but of the *probabilities* that a component will be found at a particular position. For example, a gas is statistically homogeneous: any position is as likely to contain a gas molecule as any other position. In actuality, the individual molecules will not be evenly spread. But if we look at averages, e.g. the centers of gravity of large assemblies of molecules, because of the law of large numbers the actual spread will again be symmetric or homogeneous. Similarly, a random process, like Brownian motion, can be defined by the fact that all possible transitions or movements are equally probable.

Complexity can then be characterized by lack of symmetry or “symmetry breaking”, by the fact that no part or aspect of a complex entitity can provide sufficient information to actually or statistically predict the properties of the others parts. This again connects to the difficulty of modelling associated with complex systems.

Edmonds (1996) notes that the definition of complexity as midpoint between order and disorder depends on the level of representation: what seems complex in one representation, may seem ordered or disordered in a representation at a different scale. For example, a pattern of cracks in dried mud may seem very complex. When we zoom out, and look at the mud plain as a whole, though, we may see just a flat, homogeneous surface. When we zoom in and look at the different clay particles forming the mud, we see a completely disordered array. The paradox can be elucidated by noting that scale is just another dimension characterizing space or time (Havel, 1995), and that invariance under geometrical transformations, like rotations or translations, can be similarly extended to scale transformations (homotheties).

Havel (1995) calls a system “scale-thin” if its distinguishable structure extends only over one or a few scales. For example, a perfect geometrical form, like a triangle or circle, is scale-thin: if we zoom out, the circle becomes a dot and disappears from view in the surrounding empty space; if we zoom in, the circle similarly disappears from view and only homogeneous space remains. A typical building seen from the outside has distinguishable structure on 2 or 3 scales: the building as a whole, the windows and doors, and perhaps the individual bricks. A fractal or self-similar shape, on the other hand, has infinite scale extension: however deeply we zoom in, we will always find the same recurrent structure. A fractal is invariant under a discrete group of scale transformations, and is as such orderly or symmetric on the scale dimension. The fractal is somewhat more complex than the triangle, in the same sense that a crystal is more complex than a single molecule: both consist of a multiplicity of parts or levels, but these parts are completely similar.

To find real complexity on the scale dimension, we may look at the human body: if we zoom in we encounter complex structures at least at the levels of complete organism, organs, tissues, cells, organelles, polymers, monomers, atoms, nucleons, and elementary particles. Though there may be superficial similarities between the levels, e.g. between organs and organelles, the relations and dependencies between the different levels are quite heterogeneous, characterized by both distinction and connection, and by symmetry breaking.

We may conclude that complexity increases when the variety (distinction), and dependency (connection) of parts or aspects increase, and this in several dimensions. These include at least the ordinary 3 dimensions of spatial, geometrical structure, the dimension of spatial scale, the dimension of time or dynamics, and the dimension of temporal or dynamical scale. In order to show that complexity has increased overall, it suffices to show, that—all other things being equal—variety and/or connection have increased in at least one dimension.

The process of increase of variety may be called *differentiation*, the process of increase in the number or strength of connections may be called *integration*. We will now show that evolution automatically produces differentiation and integration, and this at least along the dimensions of space, spatial scale, time and temporal scale. The complexity produced by differentiation and integration in the spatial dimension may be called “structural”, in the temporal dimension “functional”, in the spatial scale dimension “structural hierarchical”, and in the temporal scale dimension “functional hierarchical”.

It may still be objected that distinction and connection are in general not given, objective properties. Variety and constraint will depend upon what is distinguished by the observer, and in realistically complex systems determining what to distinguish is a far from trivial matter. What the observer does is picking up those distinctions which are somehow the most important, creating high-level classes of similar phenomena, and neglecting the differences which exist between the members of those classes (Heylighen, 1990). Depending on which distinctions the observer makes, he or she may see their variety and dependency (and thus the complexity of the model) to be larger or smaller, and this will also determine whether the complexity is seen to increase or decrease.

For example, when I noted that a building has distinguishable structure down to the level of bricks, I implicitly ignored the molecular, atomic and particle structure of those bricks, since it seems irrelevant to how the building is constructed or used. This is possible because the structure of the bricks is independent of the particular molecules out of which they are built: it does not really matter whether they are made out of concrete, clay, plaster or even plastic. On the other hand, in the example of the human body, the functioning of the cells critically depends on which molecular structures are present, and that is why it is much more difficult to ignore the molecular level when building a useful model of the body. In the first case, we might say that the brick is a “closed” structure: its inside components do not really influence its outside appearance or behavior (Heylighen, 1990). In the case of cells, though, there is no pronounced closure, and that makes it difficult to abstract away the inside parts.

Although there will always be a subjective element involved in the observer’s choice of which aspects of a system are worth modelling, the reliability of models will critically depend on the degree of independence between the features included in the model and the ones that were not included. That degree of independence will be determined by the “objective” complexity of the system. Though we are in principle unable to build a *complete* model of a system, the introduction of the different dimensions discussed above helps us at least to get a better grasp of its intrinsic complexity, by reminding us to include at least distinctions on different scales and in different temporal and spatial domains.

Evolutionary mechanisms

Now that we have analysed complexity as a static property, we must turn to the concepts underlying dynamics and change. We will here try to describe evolution in the most general, most abstract way, so that it can be used to analyse the complete development from elementary particles to human culture. Every process of evolution can be conceptualized as an interplay between *variation* and *selection*. Although these concepts originated in biology, their domain of application is much wider, as illustrated by recent evolutionary approaches to computing, economics, design of molecules, or the development of scientific theories.

Variation is that aspect of a process that creates configurations different from the previous ones, in other words, that produces diversity or variety. Without variation there can be no change, so we will take variation as a primitive that does not need further explanation. Variation can be either *sequential*, a single system passing through a variety of subsequent configurations, or *parallel*, different systems independently diversifying into different configurations. Variation can be *internal*, as when the components of a system or their interrelation are changed, or *external* when a system is brought into contact or combined with different other systems (Heylighen, 1991a). The mutation of a chromosome is an example of internal variation, the recombination with another chromosome is an example of external variation. Variation on its own, without further constraints, produces entropy or disorder, by diffusion of existing constraints or dependencies. The equivalent for DNA is called “genetic drift”.

However, variation is generally held in check by selection. Selection is the elimination or reduction of part of the variety of configurations produced by variation. Selection decreases disorder or entropy, by reducing the number of possibilities (Heylighen, 1992). A system that undergoes selection is constrained: it is restricted in the number of variations it can maintain. The existence of selection follows from the fact that in general not all variants are equivalently stable or capable of (re)production: those that are more easy to maintain or generate will become more numerous relative to the others (Heylighen, 1992). If all possible configurations are equally likely to be produced or conserved, there is no selection, and the only possible outcome of the process is maximization of statistical entropy, as in the cloud of gas molecules that diffuses to homogeneously fill its container. Selection too can be *internal*, as when an unstable system (e.g. a radio-active atom) spontaneously annihilates, or *external*, as when a system is eliminated because it is not adapted to its environment (Heylighen, 1991a).

Although variation produces disorder, and selection produces order, it would be simplistic to conclude that their joint product must be complexity, as the midpoint between order and disorder. Variation and selection could simply annihilate each other’s effects, with the net result that nothing really new is created. (Simple mechanical motion can be interpreted as an instance of such a process, cf. Heylighen, 1991a). For a deeper analysis, we need to introduce the concept of “fitness”.

Fitness is an assumed property of a system that determines the probability that that system will be selected, i.e. that it will survive, reproduce or be produced. Technically, the fitness of a system can be defined as the average number of instances of that system that can be expected at the next time step or “generation”, divided by the present number of instances. Fitness larger than one means that the number of systems of that type can be expected to increase. Fitness smaller than one means that that type of system can eventually be expected to disappear, in other words that that type of system will be eliminated by selection. High fitness can be achieved if a system is very stable, so that it is unlikely to disappear, and/or if it is likely that many copies of that system will be produced, by replication or by independent generation of similar configurations (for example, though snow flakes are unstable and cannot reproduce, they are still likely to be recurrently produced under the right circumstances). The fitter a configuration, the more likely it is to be encountered on future occasions (Heylighen, 1994).

Although this technical interpretation may seem rather far removed from the intuitive notion, the English word “fit” is eminently suited for expressing the underlying dynamic. Its spectrum of meanings ranges between two poles: 1) “fit” as “strong”, “robust”, “in good condition”; 2) “fit” as “adapted to”, “suited for”, “fitting”. The first sense, which may be called “*absolute* fitness”, points to the capability to survive internal selection, i.e. intrinsic stability and capacity for (re)production. The second sense, which may be called “*relative* fitness”, refers to the capability to survive external selection, i.e. to cope with specific environmental perturbations or make use of external resources.

It must be noted that “internal” and “external” merely refer to complementary views of the same phenomenon. What is internal for a whole system, may be external for its subsystems or components. For example, the concentration of oxygen in the air is an external selective factor for animals, since in order to survive they need a respiratory system fit to extract oxygen. Similarly, the concentration of carbon dioxide is an external selective factor for plants. However, when we consider the global ecosystem consisting of plants and animals together, we see that the concentrations of both oxygen and carbon dioxide are internally determined, since oxygen is produced out of carbon dioxide by plants, and carbon dioxide out of oxygen by animals. Survival of the global system requires an internal “fit” of the two halves of the carbon dioxide - oxygen cycle: if more oxygen or carbon dioxide would be consumed than produced, the whole system would break down.

Similarly, when we look at a crystal as whole system, we see it as a stable structure that is unlikely to disintegrate, i.e. it is absolutely fit and survives internal selection. However, when we look at the molecules as the parts that make up the crystal, we see that they must have the right connections or bonds, i.e. fit relations, to form a stable whole. The exact configuration of each molecule is externally selected by the other molecules to which it must fit. In this way, every absolute or intrinsic fitness characterizing a whole can be analysed as the result of a network of interlocking relational fitnesses connecting the parts .

In summary, a system will be selected if: 1) its parts "fit together", i.e. form an intrinsically stable whole, 2) the whole "fits" its environment, i.e. it can resist external perturbations and profit from external resources to (re)produce.

The Growth of Structural Complexity

The above relational interpretation of fitness is sufficient to explain why variation and selection tend to produce complexity. As we said, variation produces differentiation, by creating a variety of distinct systems. Even if systems started from an initially similar configuration, independent variation processes will make their trajectories diverge, and make the resulting configurations increasingly diverse. The selection of fit relations will simultaneously produce integration, by producing stable bonds or linkages between distinct systems. Differentiation and integration together produce complexity.

Let us study this process in more detail by considering an individual system A. Internal variation and selection will have produced an intrinsically stable configuration. Suppose now that A is in contact with another system B. A will play the role of external environment towards B. The relative variation of B with respect to its environment A will undergo selection: some of the configurations through which it passes will be fit, i.e. stable, and therefore retained, others will remain unstable and therefore replaced by other configurations. If none of the configurations through which it varies is fit, nothing happens, and the overall configuration remains at the same level of complexity. However, if B's configuration fits its environment A, by definition, their mutual configuration will be retained, and a constraint will be imposed on their relative variation. B has "snapped into place", or "discovered a niche". Thus, a new, higher order system or *supersystem*, consisting of the subsystems A and B bound together by their relative constraint, is formed.

Note that although we saw A as the environment to which B may adapt, we might as well have reversed the roles and considered B as the environment or selector to which A tries to fit. Intrinsically, fit is a two way relation, although we do not need to assume that it is perfectly symmetric. For example, a parasite must fit its host strongly, since it is completely dependent on the host. On the other hand, the host would do better without the parasite. The host "fits" the parasite only in the very weak sense that it will survive the interaction. (if the host would die, the relation would be eliminated).

Further, more symmetric examples of the emergence of supersystems by the selection of fit relations are easily found. The more symmetric form of symbiotic fit is mutualism: organisms interacting in a way that benefits each partner. A classical example is the lichen, which looks like a single organism, but is in reality a symbiotic joining of two different organisms, an alga and a fungus, which support each other by producing substances the other partner is incapable of producing. It is now also generally accepted that eukaryotes, the complex, nucleated cells containing distinct organelles which form the basis of higher order animals and plants, evolved out of the symbiotic assembly of several simpler, prokaryotic cells (Margulis & Fester, 1991; Maynard Smith & Szathmary, 1995). Similarly, multicellular organisms result from the intricate co-adaptation or fit of individuals cells. On an even higher level, ecosystems are formed by the symbiotic coupling of a host of interdependent organisms.

The same principle pervades the lower levels of physics and chemistry. Particles, atoms or molecules that interact can form a physical or chemical *bond*, i.e. a collectively constrained configuration that has a lower potential energy than the unbounded configuration, and which is therefore more stable. Although bonds can be destroyed, this requires the (a priori not very likely) external input of the right amount of energy, whereas the creation of a bond can happen spontaneously by the emission of the surplus energy. In an environment that is not too rich in energy (i.e. that has a relatively low temperature), bound configurations are intrinsically more stable than configurations consisting of freely moving particles, and thus will be naturally selected. Since the second law of thermodynamics implies a natural tendency of energy to dissipate, it should not surprise us that the history of the physical universe since the Big Bang is characterized by the emergence of ever more numerous bonds between particles.

Some examples are the formation of a hydrogen atom by the electromagnetic bonding of a proton and an electron, of a helium atom by the strong nuclear bonding of different hydrogen atoms, and of the higher elements by different combinations of hydrogen, helium or other atoms with additional protons, electrons and neutrons. The weaker electromagnetic bonds formed between atoms produce a sheer infinite variety of molecules, and simple molecules (monomers) may combine to form complex chains or polymers. Different molecules may fit together to form crystals, which provide the underlying structure of rocks. In space, rocks tend to aggregate into asteroids, planets and planetary systems, held together by gravity. Again, the configuration where separate rocks have coalesced into a larger system has a lower gravitational energy, and is therefore more stable (and thus fit) than a configuration consisting of independently moving pieces.

These examples also illustrate the *hierarchical* architecture of structural complexity (Simon, 1962). Some types of relational fit are only tried out after others have been established. For example, electromagnetic bonds between atoms are only possible because the stronger nuclear forces have overcome the electrostatic repulsion between protons in order to form different types of atomic nuclei. This can be understood by noting that not all relations of fit have the same strength: some are more difficult to produce or to dislodge than others. For example, it requires much more energy to break up an atom than to break up a molecule, and it is easier to disperse a herd of animals than to separate the cells that make up their bodies. By definition, selection will prefer the relations with higher fitness to those with lower fitness (assuming that variation provides the opportunity to try out high fitness configurations). It is only after the available high fitness configurations have formed, that the remaining weakly fit linkages get a chance. Thus electromagnetic bonds will typically become important after the stronger nuclear bonds have stabilised, and before the weaker gravitational ones come into play.

The strong linkages will produce tightly bound assemblies or systems, in which internal variation has been strictly constrained. These systems will continue to undergo free external variation and appear in different combinations, until they discover a combination that is itself bound, i.e. in which the different components have established a set of (weakly) fit connections. This determines a less strongly bound higher order system, which has the more strongly bound systems as parts. This supersystem can now again undergo free recombination with other systems until a new, again less fit, type of linkage is discovered, producing a third order supersystem, which now has two levels of subsystems. Thus a nested hierarchy of systems is formed, where at each lower level smaller and fitter subsystems can be distinguished as components of the system at the level above.

This hierarchical structure illustrates our concept of differentiation along the scale dimension: zooming in will make us discover systems at ever smaller scales, which have different, stronger connections, that are typically less likely to disintegrate.

This greater stability of parts or subsystems, which seems to characterize the physical world, is not a universal rule, though. Remember that our definition of fitness included both difficulty of destruction (stability) *and* ease of production (“productivity”). In some systems (e.g. organisms), high (re)productive fitness is achieved in spite of low stability. For example, in ecosystems, relations between populations (e.g. predators and prey) are typically more stable than the individual organisms that make up the populations. Yet, the evolutionary time needed to develop a stable predator-prey relation is much longer than the time needed to produce an individual organism. Similarly, cells in the human body are typically more stable than the polymers that constitute them. However, the polymers are much more easy to produce than the cells.

Self-reinforcing Structural Complexification

Although the above mechanism explains the emergence of structural complexity in many different cases, it does not seem to guarantee the *continuation* of complexity growth. We could well imagine that variation might reach a point where it has discovered all fit configurations, and no further complexification occurs. However, it can be argued that not only structural complexification does not stop, but moreover that it has a tendency to accelerate. For example, it is well-documented by evolutionary biologists that ecosystems tend to become more complex: the number of different species increases, and the number of dependencies and other linkages between species increases. This has been observed as well over the geological history of the earth, as in specific cases such as island ecologies, which initially contained very few species, but where more and more species arose by immigration or by differentiation of a single species specializing on different niches (like the famous Darwin's finches on the Galapagos islands).

As is well explained by E.O. Wilson (1992), not only do ecosystems contain typically lots of niches that will eventually be filled by new species, but there is a self-reinforcing tendency to create new niches. Indeed, a hypothetical new species (let's call them "bovers") occupying a hitherto empty niche, by its mere presence creates a set of new niches. Different other species can now specialize in somehow using the resources produced by that new species, e.g. as parasites that suck the bover's blood or live in its intestines, as predators that catch and eat bovers, as plants that grow on the bovers excrements, as furrowers that use abandoned bover holes, etc., etc. Each of those new species again creates new niches, that can give rise to even further species, and so on, ad infinitum. These species all depend on each other: take the bovers away and dozens of other species may go extinct.

This same idea can be generalized to other types of evolutionary systems: each new system that appears will become a new selector which provides opportunities for more new systems to “fit in”. A metaphor that may clarify this mechanism is that of an infinite jigsaw puzzle. Every system that is selected can be seen as a piece of the puzzle that has found a place where it fits, locking in with the neighbouring pieces. However, every newly added piece will add a segment to the puzzle’s outward border, where further pieces may find a place to fit. The more pieces are added to the puzzle, the larger the border becomes, and the more opportunities there are for further pieces to be added. Thus, every instance of “fit”, or niche filled, increases the number of available niches, leading to a run-away, positive feedback process of growing complexity.

Kauffman (1995) discusses a similar process for autocatalytic chemical networks, where every type of molecule can function as either a substrate or catalyst for a chemical reaction that produces further molecules types. He shows that randomly assembled sets of molecules will in general increase in diversity by such processes, and moreover argues that for larger initial diversities (variation) or higher probabilities of catalysis (selection or fit) diversity will increase more strongly, until a critical point is reached, where the system continuously generates new kinds of molecules that in turn catalyse the formation of still further molecules types, and so on, in an endless, accelerating explosion of novelty.

The Growth of Functional Complexity

Our previous arguments were limited to the development of structural complexity, i.e. the differentiation and integration, and associated symmetry breaking, of systems in the static, spatial dimensions. They did not take into account any complexity of the dynamics, behavior or functioning of these systems. It is the latter type of complexity that seems to distinguish human beings from similarly large and structurally complex systems, like cows, crocodiles or sharks. The question why functional complexity too appears to increase so quickly during evolution can be answered easily by combining the traditional cybernetic principle of the "Law of Requisite Variety" (Ashby, 1958) and a concept of co-evolution.

Until now we have seen “fit” basically as a static relation: either a system fits its environment, and then it remains in the same relation, or it does not, and then everything can change. However, when the environment itself changes in such a way as to affect the system, no static fitness relation is possible. However, an invariant configuration could stil be achieved if the system would continuously adapt to whatever environmental change impinges on it. The maintenance of an invariant configuration in spite of variable disturbances defines the problem of *homeostasis*.

As studied in cybernetics (Ashby, 1962), homeostasis can be achieved by control, i.e. the compensation of perturbations by the appropriate counteractions so that a desired goal is reached or maintained. The classical example is the thermostat which maintains a stable inside temperature in spite of external temperature changes by selectively switching a heating mechanism “on” or “off”. All living systems are control systems, actively maintaining a host of internal variables within a restricted domain by anticipating and reacting to all possible deviations from the preferred configuration. For example, when the level of sugar in the blood of an animal drops below a certain level, this will produce a feeling of hunger, which will make the animal search for and ingest food, which will again lead to the required increase in the sugar concentration.

Ashby's (1958, 1962) *Law of Requisite Variety* states that in order to achieve control, the variety of actions a control system is able to execute must be at least as great as the variety of environmental perturbations that need to be compensated. The larger the variety of available counteractions, the larger the set of disturbances that can be corrected, and the larger the domain of potential environmental situations in which the control system can survive. All other things being equal, greater control variety implies greater fitness. For example, an animal capable of finding and digesting more diverse types of food is likely to survive and thrive in a larger variety of circumstances. Therefore, evolution through natural selection will tend to increase control, and thus, because of Ashby’s law, internal variety. This can be interpreted as a functional differentiation, i.e. the appearance of more diverse activities or functions.

However, the larger the variety of available options, the more difficult it will become for the control system to select the most adequate one (cf. Heylighen, 1991b, 1994), and the longer it will take to decide which action to take. The resulting difficulty of decision-making becomes especially poignant if we take into account the fact that the solution of most problems (i.e. deviations from the desired situation) requires a series of actions. For example, reducing the feeling of hunger may require locating prey, stalking it, running after it, catching it, killing it, tearing apart the carcass, and swallowing the meat. Sequencing of elementary actions produces a combinatorial explosion in the number of possibilities to be considered. For example, the number of possible combinations consisting of a sequence of 10 actions selected from a repertoire of 100 available actions, is 100^{10}, an astronomical number that is absolutely unmanageable.

The most general way of coping with the complexity of decision-making consists in *factorizing* the decision problem, i.e. decomposing it into relatively independent subproblems, each characterized by its own subgoal (Simon, 1962). Each subproblem can be solved by a much smaller combination selected from a reduced set of actions. E.g. running requires a combination of different movements of the legs, whereas tearing requires a combination of movements of the jaws and neck. Each subgoal thus requires the coordination of a few closely related functions. The linkage between different subproblems is controlled at a higher level, where the goal of “hunting prey” activates a coordinated interplay of subgoals. This may again be controlled at a yet higher level, where the general problem of “reducing hunger” requires a balanced selection or division of labor between activities such as “hunting prey”, “gathering fruit”, and “digging up roots”.

Thus, different lower level activities are linked and integrated in the pursuit of higher order goals, which are themselves integrated at a yet higher level. This results in a functional hierarchy of control levels, which is in many way similar to, though not directly determined by, the structural hierarchy we discussed earlier. A detailed model of fundamental control hierarchies characterizing living systems can be found in Powers’ (1973, 1989) Perceptual Control Theory. The larger the variety of the environmental perturbations that need to be compensated, in general the larger the control hierarchy needed (cf. Aulin's (1979, 1982) *law of requisite hierarchy*). The emergence of a higher level of control, which may be called a *metasystem transition* (Turchin, 1977; Heylighen, Joslyn and Turchin, 1995), is a process different from, but to some degree analogous to, the emergence of a supersystem. Thus, the postulated evolutionary increase in control variety will necessarily be accompanied by a sequence of metasystem transitions (Heylighen, 1995).

The higher level processes in a control hierarchy will necessarily extend over longer time intervals, since they require the preliminary completion of lower level subprocesses. For example, the process of hunting prey will take place at a much slower pace than the subprocess of moving a leg in order to sustain running. The higher the level at which a goal is situated, the longer term the planning involved. For example, human activities may be planned for years ahead, whereas the most complex activities of bacteria are likely to be completed in seconds. Thus, the functional hierarchy produces differentiation and integration in the temporal scale dimension, similar to the differentiation and integration in the spatial scale dimension characterizing the structural hierarchy.

Self-reinforcing Functional Complexification

Again, we must ask whether functional complexification can continue indefinitely. Since we may assume that the environment as a whole has always more variety than the system itself, the evolving system will never be able to achieve complete control (i.e. be capable to thrive under all possible circumstances). Yet we may assume that it will at least be able to gather sufficient variety to more or less control its most direct neighbourhood. We might imagine a continuing process where the variety of an evolving system slowly increases towards but never actually matches the infinite variety of the environment.

On the other hand, as internal variety increases, decision-making becomes more difficult (even if we assume that decision-making difficulty can be strongly reduced by hierarchical factorization), and so it becomes less and less advantageous to further increase functional variety. The evolving system will asymptotically reach a trade-off level, depending on the variety of perturbations in its environment, where requisite variety is in balance with difficulty of decision-making and perhaps other limiting factors on complexity. For example, for viruses the balance point will be characterised by a very low functional variety, for human beings by a very high one.

This analysis assumes that the environment is stable and a priori given. However, the environment of a system A itself consists of evolving systems (say B, C, D...), which are in general undergoing the same asymptotic increase of variety towards their trade-off points. Since B is in the environment of A, and A in the environment of B, the increase in variety in the one will create a higher need (trade-off point) in variety for the other, since it will now need to control a more complex environment. Thus, instead of an increase in complexity characterised by an asymptotic slowing down, we get a positive feedback process, where the increase in variety in one system creates a stronger need for variety increase in the other (cf. Waddington, 1969). This self-reinforcing interaction is an illustration of the “Red Queen Principle” (Van Valen, 1973), which says that a system must continuously develop in order to merely *maintain* its fitness relative to the systems it co-evolves with. The net result is that many evolutionary systems that are in direct interaction with each other will tend to grow more complex, and this with an increasing speed.

As an example, in our present society individuals and organizations tend to gather more knowledge and more resources, increasing the range of actions they can take, since this will allow them to cope better with the possible problems appearing in their environment. However, if the people you cooperate or compete with (e.g. colleagues) become more knowledgeable and resourceful, you too will have to become more knowledgeable and resourceful in order to keep up with them. The result is an ever faster race towards more knowledge and better tools, creating the "information explosion" we all know so well.

The present argument does not imply that all evolutionary systems will increase in complexity: those (like viruses, snails or mosses) that have reached a good trade-off point and are not confronted by an environment putting more complex demands on them will maintain their present level of complexity. But it suffices that some systems in the larger ecosystem are involved in the complexity race to see an overall increase of available complexity.

Selection for Simplicity

As mentioned in the introduction, many researchers have criticized the idea that complexity grows during evolution. We will now review some of the main arguments proposed by these critics, and show how they can be replied to in our framework.

The most obvious counterargument to growing complexity is that there are evolutionary *costs* to complexity: if the same purpose can be achieved by a simpler design, this design is in general preferable to the complex one. We have already discussed the costs in more difficult decision-making and co-ordination connected to functional complexity. For structural complexity, it can similarly be noted that more complex designs bear the cost of the production and maintenance of more diverse material components. The more parts a system has, the more likely it is that one of the parts would malfunction because of an error or because of lacking resources.

This can to some extent be overcome by redundancy or the building up of reserves, but it seems obvious that if a simpler design is proposed by variation, this will in general be preferred by selection. Sometimes, a totally new, much simpler method to achieve the same purposes is discovered. Examples of such a revolution from the history of science would be the heliocentric model of Copernicus replacing the hopelessly complicated Ptolemaic model for the trajectories of the planets, or the replacement of the multi-part propeller mechanism for planes by the much simpler jet engine (Arthur, 1993).

Yet, outside the realm of science such revolutionary simplifications seem extremely rare. To start, if a simple solution was readily available, it is likely that that solution would already have been found, since normally evolution starts with simple configurations before it explores the more complex ones. By definition there are much less simple configurations than complex ones, and therefore it should be easier to first discover the simple ones. Second, the fact that a simpler solution exists does not make it likely that that solution will be found by blind variation starting from a very different initial configuration. For a new configuration to evolve, it must not only be fit, but moreover all configurations intermediate between the present one and the new one must be fit (a requirement that does not apply to scientific speculation). For radically new designs, it is not very likely that sufficiently fit intermediate configurations for all transitional steps would be discovered by variation.

This general principle may apply with particular strength to changes in complexity, if we believe the argument advanced by Saunders and Ho (1976). They argue that for evolution it is in general much easier to add a component, which is not likely to do much harm, than to take away a component, which is likely to disturb a complex network of interdependencies. This seems to be confirmed by the observation of vestigial organs, like the appendix, which are conserved by evolution even though they are no longer needed. Thus, even though a radically simplified design with much less components may exist, it is unlikely that this configuration can evolve by taking away components one by one. For example, imagine a jet engine “evolving” out of a propeller engine by the gradual elimination of unnecessary parts.

This also fits in with our general view of structural complexification, where selection first builds up the smaller and fitter subsystems (which are unlikely to disappear in a later stage) as a foundation and then merely experiments with adding less strongly bound systems here or there. When considered from this angle, the selective force of simplicity is likely to only play a part in *minimizing the increase of complexity*: from different, otherwise equivalent ways to increase fitness, which by the above reasoning all tend to add complexity, the one will be preferred which adds the least. In that sense, simplicity basically functions to “streamline” designs, not to radically alter them.

A stronger case for simplicity might be made in situations where the demands of the environment become less complex. A classic example is that of cave fish, which started to live in a completely dark environment and thereby became blind. When we look in more detail, though, we see that the material infrastructure of the fish’s eye is still mostly there, it just does not work anymore. The function was lost, not because of selection for simplicity, but because of the lack of selection for sight. It is likely that sight was destroyed by a sequence of undirected, deleterious mutations, which in a different environment would have been eliminated by selection. This is rather an instance of the spontaneous increase of statistical entropy in the absence of selection than of the evolution of simplicity.

A better example is proposed by McShea (1991): he observed that in several mammals (whales, seals, otters, ...) that started to live in the water, the complexity of the vertebral column has diminished over evolution. This can be explained by the fact that the forces acting on a body suspended in water are much more homogeneous than the forces acting on a body that is supported by legs. Adaptation to the aquatic environment necessitated a more symmetric, more homogeneous vertebral column. This change in complexity is quite small, though, as the number of components (vertebrae) and their connections has actually remained the same: only the differentiation in shapes has somewhat diminished. Thus the Ho and Saunders (1976) argument has not been contradicted.

More extreme examples of simplification can be found in *parasites*. Viruses, which can exist only as parasites, are the simplest forms of “organisms” known. Also different types of parasitic organisms (e.g. worms) seem in a number of aspects more simple than their free-living relatives. First, we must note that it is not obvious that the shift to a parasitic way of live has led to the evolutionary simplification of a more complex form. Though it was previously assumed that viruses are degenerated forms of initially more complex organisms, it now has been suggested that they have in fact developed from segments of the host’s DNA that have turned independent (“selfish DNA”, cf. Dawkins, 1976).

Even if we assume that loss of complexity has occurred in parasites, this does not imply that overall complexity has decreased. The parasite can afford to be functionally simple, because the host provides a very stable environment. This is achieved by the high functional complexity of the host, needed (because of the law of requisite variety) to counteract all outside perturbations. The higher the host’s functional variety of counteractions, the lower the variety of perturbations remaining inside the host’s organism, and the lower the variety needed by the parasite to survive in the inner milieu. Thus, the simplicity of the parasite is possible only because of the complexity of the host!

But things do not remain that clear-cut: the presence of the parasite will be experienced by the host as a new perturbation, which will trigger the evolution of yet another set of counteractions, increasing the host's functional complexity. The parasite in turn will need to adapt to the host's new defenses, increasing its functional complexity. This will trigger another round of counter-defenses, and engender the classical "arms race" type of escalation between host and parasite, leading to a continuing growth of complexity in both parties. In conclusion, parasitism tends to increase overall complexity.

As an illustration, it has recently been suggested that the success of the HIV virus in overcoming the body's defenses may be due to the very high mutation rate of the virus. The presence of an increasing variety of mutated variants strains the capacity of the immune system to develop the appropriate antibodies. Once the variety of mutants has become too large, the requisite variety of counteractions (antibodies) needed to maintain control becomes larger than the variety the immune system is capable of providing, and the immune system breaks down, leading to the full outbreak of AIDS. Although each HIV virus on its own is quite simple, the army of mutant forms has a much larger complexity than a population of non-mutated viruses.

The Direction of Evolution

A more fundamental criticism of the idea of increasing complexity, formulated among others by Stephen Jay Gould (1994), is that such an increase implies a preferred direction for evolution, a continuing "progress" or advance towards more sophisticated forms. Recent advances in evolutionary theory (such as the theory of punctuated equilibrium) and observation of evolutionary phenomena seem to indicate that evolution is a largely unpredictable, chaotic and contingent series of events, where small fluctuations may lead to major catastrophes that change the future course of development. At first sight, this seems inconsistent with any constant "direction". Yet, an example will show that there is no necessary contradiction.

Consider a rock that rolls down from the top of a steep mountain. Given that the slightest irregularity in the terrain may be sufficient to make the rock fall either into the one or the other of a host of downward slopes or valleys, the exact path of the rock will be virtually impossible to predict. Repeated experiments are likely to produce final resting positions that are miles apart. Yet, one thing will be certain: the final position will be lower than the initial position at the top. Although we cannot know the direction of movement in the horizontal dimensions, we do know that there is only one possible sense in which it can move along the vertical dimension: downward.

To apply this metaphor to evolution, we need to discover the equivalent of the "vertical" dimension, in other words we need to define a variable that can only increase during evolution (like vertical distance from the top). Entropy plays the role of such a variable for thermodynamic systems, but this seems hardly useful to describe complexification. Fisher's (1930) fundamental theorem of natural selection has shown that another such variable exists for populations of living systems: average fitness. This follows straightforwardly from the fact that fit individuals by definition will become more numerous, while the proportion of less fit individuals will decrease. This reasoning can be generalized to cover non-biological systems too.

It might be objected that fitness is a relative notion: what is fit in one type of environment may no longer be fit in another environment. Thus, the inexorable increase of fitness only holds in invariant environments (which seem wholly atypical if one takes into account co-evolution). Gould proposes the following example: the evolution from hairless elephant to woolly mammoth is due merely to a cooling down of the climate. If the climate becomes warmer again the woolly variant will lose its fitness relative to the hairless one, and the trend will be reversed.

Yet, we have discussed ways to increase “absolute” fitness. First, the system may increase its internal or intrinsic fitness, by adding or strenghtening bonds or linkages between its components. This, as discussed earlier, is typically accompanied by the increase of structural complexity. Second, the system may increase its fitness relative to its environment by increasing the variety of environmental perturbations that it can cope with, and thus its functional complexity.

This may be illustrated through the climate change example: though the warm-blooded, woolly mammoth is only relatively fitter than its hairless cousin, it is absolutely fitter than a cold-blooded reptile, which would never have been able to adapt to a cold climate, with or without hair. Warm-bloodedness means temperature control, i.e. the capacity to internally compensate a variety of fluctuations in outside temperature.

All other things being equal, a system that can survive situations A, B and C, is *absolutely* fitter than a system that can only survive A and B. Such an increase in absolute fitness is necessarily accompanied by an increase in functional complexity. Thus, evolution will tend to irreversibly produce increases of functional complexity.

This preferred direction must not be mistaken for a preordained course that evolution has to follow. Though systems can be absolutely ordered by their functional complexity, the resulting relation is not a linear order but a *partial order*: in general, it is not possible to determine which of two arbitrarily chosen systems is most functionally complex. For example, there is no absolute way in which one can decide whether a system that can survive situations A, B and C is more or less complex or fit than a system that can survive C, D and E. Yet, one can state that both systems are absolutely less fit than a system that can survive all A, B, C, D and E. Mathematically, such a partial order can be defined by the inclusion relation operating on the set of all sets of situations or perturbations that the system can survive. This also implies that there are many, mutually incomparable ways in which a system can increase its absolute fitness. For example, the first mentioned system might add either D or E to the set of situations it can cope with. The number of possibilities is infinite. This leaves evolution wholly unpredictable and open-ended.

For example, though humans are in all likeliness absolutely more functionally complex than snails or frogs, evolution might well have produced a species that is very different from humans, yet is similarly at a much higher functional complexity level compared to the other species. In perhaps slightly different circumstances, the Earth might have seen the emergence of a civilisation of intelligent dogs, dolphins or octopuses. It is likely that analogous evolutions are taking place or have taken place on other planets. Though humanity seems to have reached the highest level of functional complexity in the part of evolution that we know, more intelligent and complex species may well exist elsewhere in the universe, or may appear after us on Earth. The conclusion is that a preferred direction for evolution in the present, generalized sense does not in any way support the ideology of anthropocentrism.

A final criticism raised by Gould (1994) is that the appearance of more complex systems during evolution does not imply that complexity growth is a general trend for all evolving systems. Like Maynard Smith (1970) and Fisher (1986) suggested, complexity may be the trivial result of the fact that evolution started with relatively simple configurations and afterwards randomly explored the surrounding space of possible configurations, as well in the direction of more complex as in the direction of more simple configurations. If this general diffusion in all possible directions continues, it is normal that ever more complex configurations will continue to be discovered here or there. Yet, the average complexity of systems may well remain practically the same.

Gould (1994) supports this interpretation by the observation that since the beginning of life on Earth simple as well as complex organisms have continued to proliferate. In fact, the most numerous organisms, bacteria, are also among the most simple. If we would calculate some kind of average complexity for every living organism on Earth, the astronomical number of bacteria would dwarf the number of more complex organisms, including humans, and thus virtually annihilate their contribution to overall complexity.

The fallacy with this reasoning is that it presupposes a somewhat arbitrary cut-off point for the lowest level complexity, starting with the simplest living organisms. If we had started with molecules rather than organisms, the increase in the number of bacteria would certainly have been seen as an increase in overall complexity. Yet, one might again have objected that there are innumerably more molecules being formed than bacteria, and therefore on average nothing much would change for complexity. The same reasoning can be repeated down to the level of elementary particles. Yet, if we look at the whole sequence of formation of more complex entities, the general trend is clear, though on average the effect would be “diluted” by the higher frequency of simpler forms.

This higher frequency is simply a side-effect of the process of structural complexification that we have discussed. Indeed, more complex forms can only be developed on the basis of already existing simpler forms. Therefore, there is always a time lag between the appearances of simpler and subsequent, more complex forms. At any moment in time, simpler forms will generally have had much more time, and more resources to develop and spread. Moreover, structurally simpler forms by definition are smaller and therefore many more can be built with the same amount of building blocks. The “averaging” simply obscures the fact that on all levels there is a trend for the more complex forms to increase in number.

Conclusion

We have tried to clarify why complexity appears to grow during evolution. Although increasing complexity seems intuitively obvious to most observers (cf. McShea, 1991), it has recently been questioned whether there effectively is an inexorable growth of complexity. By defining complexity as the combination of distinction (variety) and connection (dependency) in at least the spatial, temporal and scale dimensions, we were able to redefine complexification as the combination of differentiation and integration in these dimensions.

The fundamental mechanisms of evolution are variation, which produces spatial differentiation of systems, and selection on the basis of (relative) fitness, which produces structural integration by creating more and stronger linkages between different systems. Together they produce the growth of structural complexity, characterized by the development of nested hierarchies of subsystems and supersystems. This complexification process tends to be self-reinforcing, because the filling of a niche by an additional system (i.e. the creation of a link) creates further niches (i.e. opportunities for additional linkages).

Complexification in the temporal dimension corresponds to an increase in the variety and linkage of a system’s activities or functions. Selection for functional differentiation is entailed by the law of requisite variety, according to which a larger repertoire of possible actions allows the system to survive in a larger variety of situations, and therefore to be absolutely fitter. The need to minimize the difficulty of decision-making and co-ordination between an increasing number of activities leads to the integration of groups of related activities into higher-order functions. The resulting functional complexification produces control hierarchies consisting of object systems and metasystems. This process too is self-reinforcing, since it engenders a complexity arms race between co-evolving systems.

The two mechanisms of structural and functional complexification are moreover likely to reinforce each other: a structurally more complex environment requires a more complex set of functions to cope with it. Similarly, functional complexification seems to require a richer set of structural components and connections to implement it, although this latter issue has not been discussed in this paper. A more in-depth analysis of the subtle interaction between structural and functional complexity seems necessary (see also Heylighen, 1995).

The proposed mechanisms are not intended to show that evolution follows a preordained course towards some kind of Omega Point of maximal complexity. Rather, it is assumed that evolution is largely unpredictable and contingent on a host of uncontrollable factors, which may steer its course in any of an infinite number of directions. However, it is noted that directions in which complexity increases are generally preferred. This follows from the more fundamental result that evolutionary transitions are asymmetric with respect to time (cf. Heylighen, 1992), since they tend to monotonously increase fitness. Though fitness is relative to the environment, it has two components that can increase in an absolute sense, internal fitness (strength of linkages between components) and number of environmental perturbations that can be counteracted. Increases in these two components tend to be accompanied by respective increases in structural and functional complexity, although selection for simplicity is likely to minimize complexification.

Still, it can happen that systems evolve towards a simpler organization, although this seems rare. It is most likely to occur when the system enters a simpler environment, as when an organism becomes an internal parasite or moves back from the land to the water, but these are obviously unusual examples which go against the general trend of environments becoming more complex. The net effect will tend to be that the new ecosystem, formed by environment together with the newly added system (parasite, cave fish, aquatic mammal, etc.) will become more complex than it was before the appearance of the simplified system.

As advocated by McShea (1991), we need elaborate studies of instances of evolution characterized by apparent increase or decrease of complexity for a further clarification of these trends and for a determination of the exact conditions under which complexity is most likely to increase or decrease.

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