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Evolutionary Transitions: how do levels of complexity emerge?

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It is a common observation that complex systems have a nested or hierarchical structure: they consist of subsystems, which themselves consist of subsystems, and so on, until the simplest components we know, elementary particles. It is also generally accepted that the simpler, smaller components appeared before the more complex, composite systems. Thus, **evolution tends to produce more complex systems, gradually adding more levels to the hierarchy**. For example, elementary particles evolved subsequently into atoms, molecules, cells, multicellular organisms, and societies of organisms. These discrete steps, characterized by the emergence of a higher level of complexity, may be called "evolutionary transitions". The logic behind this sequential complexification appears obvious: you can only build a higher order system from simpler systems after these building blocks have evolved themselves. The issue becomes more complicated when you start looking for the precise mechanisms behind these evolutionary transitions, and try to understand which levels have appeared at what moment, and why.

In recent years, several authors have tried to tackle this issue. As we will see, their approaches are diverse, and their results are concomitantly different. Part of the reason for this incoherence is that these researchers have worked mostly in isolation: they come from different traditions, and their works hardly make reference to each other. This is understandable, since the emergence of hierarchical levels is a pre-eminently multidisciplinary issue, involving at least physics, chemistry, biology and sociology. Another reason for the lack of coherent results is that the problem is intrinsically difficult, involving a host of phenomena (e.g. the origin of life) about which we know very little, spanning an enormous range of scales and domains, and being in essence ill-defined (e.g. most authors cannot even agree about which levels to include in their hierarchy). In spite of these difficulties, **some of the results are truly impressive**, and there is enough similarity in the different conceptual frameworks to express the hope that cross-fertilization may lead to an integrated theory in a not too far-away future.

Given the diversity of approaches, it is worth trying to classify them. One basic classication distinguishes quantitative from qualitative approaches, while another one distinguishes "structural" approaches, which focus on subsystems embedded in supersystems, from "functional" approaches, which focus on levels of information-processing or control (cf. Heylighen, 1999). The quantitative approaches are basically inductive: they gather numerical data about the different levels of complexity, such as the typical size, mass, or information content of a system at a given level and the time of its emergence; they then try to find regularities or "laws" that govern the relations between these parameters. A typical example of this approach is proposed by Max Pettersson in his book "Complexity and evolution".

In spite of this apparently scientific procedure, the limitations of the quantitative approach should be obvious. First, as Pettersson (1996) notes about his results, such "laws" can only be *descriptive,* not *predictive*, since you cannot create a new level at will, or even wait until one emerges. Second, the data from which these laws are induced are extremely limited: most authors distinguish about 9 levels, and it is very difficult to meaningfully state a "law" that applies to only 9 instances. Worse, these 9 cases are not objectively given, but to some degree dependent on the choice of the observer. Most observers would agree that particles, atoms, molecules, cells, and multicellular organisms constitute discrete levels of organization, but what about the other levels considered by Pettersson: "intermediate entities" (parts of a cell centred on one chromosome), "one-mother family societies", "multifamily societies", and "nation states"? Some of these give the impression that they have been introduced just to fill in an otherwise too large gap between the more clearly defined levels. If another observer, e.g., would distinguish only multicellular organisms and large scale societies, skipping Pettersson's two intermediate levels, then Pettersson's "laws" that relate the size of a system to the number of its level would no longer be valid.

To Pettersson's defense, it must be noted that he formulates two criteria to identify what he, following Joseph Needham, calls "integrative" levels. These criteria note that entities from a higher level must be primarily composed from entities of the lower level, but that some of these lower level entities should still exist independently of the higher level. For example, multicellular organisms are composed primarily from individual cells, but individual cells still exist as autonomous life forms. The problem with these criteria is that they allow for an indefinite number of intermediate levels. If I would argue that a nation state consists of the subsequent levels of households, neighborhood communities, cities, counties, and regions, then these levels would fulfil Pettersson's criteria, since a nation is obviously composed of several of these lower entities joined together, while each entity in the list could conceivably exist on its own, without being part of a system of the next level of complexity, as has happened during much of history. Such a more extensive list of levels would completely mess up the quantitative relations that Pettersson found.

Another problem with the quantitative approach is that the numbers involved range across an enormous width of scales, in Pettersson's case from about 10^{-27} gram (estimated mass of a particle) to 10^{12} gram (mass of a nation state). The obvious way to make such hugely divergent numbers comparable is to use logarithmic scales. This has the added advantage that it compresses error margins. For example, the largest and the smallest nation states differ in mass by a factor of about 10,000, but this reduces to a mere difference of 4 units on a logarithmic scale going from -27 to +12. Still, since all levels have such large error margins, it is not too difficult to choose a "typical" size for a system at a particular level, so that that you can draw a more or less straight line through your 9 data points. In conclusion, I would not be too impressed by the apparent regularities that Pettersson finds by playing with his logarithmic scales.

Petersson's results become most interesting when they deviate from the simple, linear relation (on a semi-logarithmic scale; this means an exponential relation on a normal scale). Thus, he finds that, **since the origin of life, transitions towards higher levels seems to arrive much faster** than a purely exponential growth would warrant. This super-exponential increase is supported by some other data that he gathered, such as the growth in the human population and the explosion of new inventions, which show a similar pattern of acceleration. However, Pettersson does not offer any hypothesis to explain this apparent acceleration of evolution, and "forgets" to look at the earlier transitions that led to the emergence of particles, atoms, molecules, and life, where the trend seems to be slowing down rather than accelerating.

Another book, Richard Coren's "The Evolutionary Trajectory", looks in more detail at this acceleration of evolutionary transitions. It moreover proposes equations to model the process quantitatively (he calls this model "logistic escalation") and a beginning of a qualitative explanation, using the concept of growth of information. Not surprisingly, the major levels and corresponding transitions (13 in all) distinguished by Coren are different from the ones of Pettersson, and therefore the two models cannot really be compared. Coren focuses on transitions in the capacity for processing information ("functional complexity") rather than in the emergence of encompassing systems of systems ("structural complexity"). Thus, he is closer in his way of thinking to contemporary complexity theorists than Pettersson, who is interested in physical size rather than in information or entropy. Still, both authors largely ignore the ideas associated with the complex systems approach, in spite of their use of the word "complexity".

Also in other respects the two books are similar: they suffer from the same intrinsic weaknesses of the quantitative approach that I outlined above, they are both short, and in spite of their attempt at mathematical modelling they try to reach a very broad audience. The latter approach puts the two authors in a somewhat awkward situation, where they spend a lot of effort explaining elementary mathematical concepts, such as order of magnitude and logarithm, in a way reminiscent of high school text books. The effort seems rather wasted to me, since the people who would be interested to buy these books are likely to have at least a basic understanding of these concepts, and would rather skip these pages to go straight to the main results.

This brings me to the other main approach to studying evolutionary transitions: qualitative modelling. Here, the emphasis is on understanding how and why higher levels of complexity emerge, considering the evolutionary mechanisms of complexification rather than various measurements of size and information content. An excellent example of this approach can be found in the work of Maynard Smith and Szathmáry (MS&S). They have written two books on this subject, "The Major Transitions in Evolution" (1995), followed by "The Origins of Life" (1999), which discusses the same topics in a shorter and more accessible way. John Maynard Smith and Eörs Szathmáry are both biologists, the former with a long and distinguished career in evolutionary theory and the applications of game theory to behavior, the latter a specialist in molecular biology. Together, they span the whole range of biology, from molecules to societies, but their expertise unfortunately does not extend beyond the life sciences. Although they discuss one non-biological transition, the emergence of human language, they make it clear that this is not a domain they are really competent in, and they do not even mention other transitions, such as the origin of molecules or the origin of thought.

This lack of attention to the non-biological realm is compensated by their in-depth, detailed treatment of biological complexification. They define a "major transition" as an event in which entities that could replicate independently before the transition now get organized into an encompassing system that can only replicate as a whole. Basic examples are the origin of life, where molecules get arranged in an autocatalytic cycle where all components are needed to replicate one of them, genes that get arranged on a chromosome and thus lose their freedom to replicate independently, and cells that join to form a multicellular organism. Since these replicators all carry information, an evolutionary transition fundamentally changes the way in which information is stored, transmitted and translated. In that sense, their approach provides a bridge between

Pettersson's structural point of view and Coren's functional point of view, however, without really clarifying the connection between the two.

The originality of their approach is that they try to explain each of the eight transitions they distinguish through a purely Darwinian logic. This means that it should result from a series of small, undirected variations, each of which confers enough fitness to survive natural selection. This requirement is more difficult to satisfy than it may seem. It is obvious that systems at a given level (e.g. cells or multicellular organism) can be fit enough to survive, but there is a problem with the intermediate forms where components are to some degree constrained by an encompassing organization, but still capable of independent replication. Studies of the evolution of cooperation have highlighted the essential tension between "selfish" replicators and the collective to which they belong: although it is to the benefit of all members of the collective that its components would cooperate towards the common good, the greatest benefit accrues to the "defectors" or "free riders" that profit from the fruits of cooperation, while caring only for themselves. Thus, intermediate forms, where components can still replicate independently, are likely to be eroded from within: **the earnest cooperators who give up their own possibilities for selfish replication to benefit the collective will be outcompeted by the free riders**.

Maynard Smith and Szathmáry do not propose a general solution to this fundamental probem. They rather consider each transition on its own and examine mechanisms that may have suppressed the tendency to defect. They find clear examples of such mechanisms in existing systems, but because of lacking data usually have to make an educated guess about how such an enforcing mechanism may have evolved. For example, it is well-known that mitochondria—organelles that are part of our (eukaryotic) cells but that originally descend from free-living (prokaryotic) bacteria—are inherited only from the mother. In fact, it has recently been observed that the few mitochondria from the father that accompany the sperm into the egg cell during fertilization are not just diluted into the much larger mass of egg mitochondria, but actively seeked out and destroyed. MS&S argue that this is necessary to prevent competition between different mitochondrial strains, which might otherwise be won by those best at replicating themselves, rather than at supporting the encompassing cell. Yet, they offer no explanation of how this control on mitochondria has evolved.

To be fair, the organization of biological organisms is so complex, and we still know so little about how it functions and even less about its history, that you cannot expect anybody to understand the details of its evolution. MS&S do an excellent job in bringing together everything that is known in an integrated theoretical framework, which tries to fill as many of the gaps as possible. The strength of their work is that they combine a detailed knowledge of specific mechanisms with a long range, encompassing view. If you are interested in all the technical details with specific references to the literature, you should read their "Major Transitions". If you only want the wider view, with just enough detail to illlustrate how the abstract mechanisms have played their part in specific transitions, read "The origins of life". The first book is addressed specifically to biologists, and I must admit that although my knowledge of the matter is quite extensive for a non-biologist, I had to skip a number of sections in the book because they got too technical. I did not have the problem with the second book, which was precisely at my level of understanding: simply and elegantly explained, but with enough depth and detail that I constantly had the feeling that I was learning important new insights. In spite of the clarity of writing, the absence of mathematics, and the shortness of the book, it is not really intended for the kind of "high school" public that Pettersson and Coren have in mind. Apart from the origin of life, most of the topics discussed (e.g.

the origin of chromosomes, of eukaryotes and of insect societies) are unlikely to attract the interest of a broad audience, and the constant use of specialized biological terms and examples (ribozyme, oligonucleotide, lysosome, phagocytosis, ...), even though most of them are explained in the text, would tire all but the limited public that are genuinely interested in the origin of biological organization. But for the latter public I can only recommend the book for its clarity and depth.

As I already indicated, the only weakness of the MS&S approach is that their focus on specific cases sometimes makes you lose sight of the wider picture of the emergence of levels of complexity. Another book, Valentin Turchin's "The Phenomenon of Science" (1977) discusses the process in the most general possible terms. Turchin introduces the concept of a "metasystem transition" which he defines as the evolutionary emergence of a higher order system, *controlling* the subsystems of the level below. **He sees a metasystem transition as a "quantum" of evolution**, a discrete, progressive step towards more complex organization. Like the other authors, he uses the example of the emergence of multicellular organisms, in which individual cells are not only joined in a supersystem, but controlled by a metasystem which makes different cells perform different functions at different moments. The originality of this approach is its foundation in the cybernetic concept of regulation or control, which naturally leads to hierarchical organization, differentiation, and increased functionality. (A more up-to-date discussion and application of Turchin's theory of metasystem transitions can be found in the volume edited by Heylighen, Joslyn and Turchin (1995)).

As a cyberneticist, Turchin's knowledge of biological mechanisms is limited, and he focuses instead, like Coren, on information processing. Unlike Coren, he does not treat information merely as an abstract quantity, but as the raw material for an increasingly complex cognitive system. In parallel with the mainly "structural" transition to multicellularity, Turchin's main sequence of "functional" transitions details the increasingly sophisticated capability of the nervous system to control the environment, from movement to simple reflexes, nerve nets, learning, and thought, to human culture. He goes into more detail about the latter development, examining a number of smaller scale transitions in humanity's capacity for reasoning, with an extensive review of the history of science and mathematics. He concludes by predicting that the next large scale metasystem transition will produce a "super-being", an integrated system that encompasses the whole of humanity.

Like the other books, Turchin's is addressed to a broad, non-specialist audience. It is clearly written and its mathematics does not go beyond high school level, although Turchin, unlike Pettersson and Coren, does not spend much time in pain-staking explanation of elementary concepts such as logarithms and powers of ten. Although the book is nearly a quarter of a century old, it is actually more relevant to present-day complexity research than the ones of Pettersson and Coren, for example by providing an elementary introduction to neural nets. What it lacks are the up-to-date, detailed observations of biological systems and the solid grounding into recent evolutionary models that are the main strength of Maynard Smith and Szathmáry. MS&S, on the other hand, lack the simple, unifying concept of the metasystem transition that forms the backbone of Turchin's approach.

A final book on this topic, "Evolution's Arrow" by John Stewart (2000), makes a first step towards bridging Turchin's cybernetic approach and MS&S's biological approach. Like Turchin, **Stewart argues that evolution is fundamentally progressive**, producing ever more complex and more adaptive systems. For Stewart, the basic force driving this emergence of higher levels is cooperation: if a number of systems manage to find a pattern of interaction that is to their mutual benefit, the resulting synergy will produce an integrated supersystem. A group of such supersystems may again enter into a cooperative assembly, determining a supersystem of a yet higher level. Thus, **cooperation extends over increasingly large spans of space and time**, from the cooperation between molecules in a primitive cell, to the cooperation between countries in a globalized economy. Like MS&S, Stewart discusses in detail the evolutionary obstacles to the emergence of cooperation among intrinsically selfish systems. Unlike MS&S, however, he proposes a general solution to the "free rider" problem.

This solution fits in with Turchin's model: the appearance of a control system (a "manager" in Stewart's terminology), that keeps selfish abuses in check. Although Turchin's book, which was written before the great sociobiological debates, skips the issue of how cooperation can evolve, I have myself shown how his approach can be extended to help resolve the issue (Heylighen & Campbell, 1995). Whereas I viewed control basically as an abstract, functional concept, the originality of Stewart's approach is that he conceives of a very concrete kind of "manager" that takes control of a group for purely selfish purpose, but ends up promoting cooperation that is to everybody's benefit. Perhaps the simplest illustration of this idea is a shepherd "managing" a group of sheep, or a farmer "managing" a group of crops. The farmer takes control over the crops purely for his own benefit, to be able to consume more of them. Yet, because of his care to plant the crops at equal distances, keep them free from weeds, and prune them into the most efficient shape, the crops actually grow and reproduce more efficiently, being freed from the destructive competition for sunlight, water and nutrients with each other and other plants. Thus, management increases the fitness of both the farmer and the crops.

Some examples of managers producing evolutionary transitions are DNA taking control of the autocatalytic cycle that led to the first living cells, and chieftains or tribal heads that get to dominate a small band of people by sheer force, but gradually turn into managers of an efficient cooperative organization. Like MS&S, Stewart also discusses the example of mitochondria able to reproduce only through the mother, but now with an emphasis on the different controls exerted by the cell to keep the mitochondria from free riding. These examples of managers are all external to the system they control, but managers can also be internal, like the genes that make social insects behave altruistically towards their nest members, or the internalized restraints inculcated by morals and religion that predispose people towards honesty in their interactions with others (cf. Heylighen & Campbell, 1995).

Although Stewart's initial focus, like MS&S, is on biology and the evolution of cooperation, he continues, like Turchin, with the emergence of higher levels of control in information processing, leading to systems that are ever more intelligent and thus better able to meet evolutionary challenges. He in particular notes that systems increase their evolvability, e.g. by evolving sexual recombination to more efficiently explore the space of possible genomes. He ends up discussing the future of human society, with a special focus on the strengths and limitations of market mechanisms. Given his background in social systems, his views on society are more explicit than Turchin's, but his analysis of cognitive mechanisms is less detailed, albeit infused with the same kind of "cybernetic" thinking. All in all, given that the two authors came to their conclusions independently, from quite different backgrounds, the parallelism between the two theories is remarkable.

Like the others, Stewart's book is easy to read and directed at a wide audience. Its writing style is perhaps a little less elegant than the one of MS&S, with a tendency towards redundancy, repeating the same phrases in many different places. The absence of mathematics and of dense biological terminology makes it generally accessible, although the book tackles a lot of intrinsically complex issues often at a high level of abstraction. This means that the book is likely to be appreciated only by the people genuinely interested in understanding the evolution of complexity across levels.

In conclusion, after Turchin's 1977 book, which was largely ignored, the last five years have witnessed a flurry of wide-ranging, non-technical books discussing evolutionary transitions towards greater complexity. A review of these books makes it clear that the domain is still in its infancy, with little consensus about terminology, methodology, mechanisms or even the definition of organizational levels. Yet, the deeper parallelisms, especially between the approaches of Turchin, Steward, and Maynard Smith and Szathmáry, hold out the hope that an integrated theory is on the horizon. Even some of the quantitative results of Pettersson and especially Coren may find their place in such a theory. For example, Coren's logistic escalation curve looks remarkably similar to the "qualitative" curve that I drew to illustrate Turchin's "law of the branching growth of the penultimate level" (Heylighen, 1995), while the acceleration of evolution measured by both Coren and Pettersson might back up Stewart's observation that evolution itself evolves so as to become more efficient. A first step towards constructing such a theory might be for the different researchers in this domain to simply study each others' work, instead of continuing to work in virtual isolation.

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