ON THE CHEMICAL NATURE AND ORIGIN OF TELEONOMY

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(Received 13 May 2004; accepted in revised form 10 June, 2004)

Abstract. The physico-chemical characterization of a teleonomic event and the nature of the physico-chemical process by which teleonomic systems could emerge from non-teleonomic systems are addressed in this paper. It is proposed that *teleonomic* events are those whose primary directive is discerned to be *non-thermodynamic*, while *regular* (non-teleonomic) events are those whose primary directive is the traditional *thermodynamic* one. For the archetypal *teleonomic* event, cell multiplication, the non-thermodynamic directive can be identified as being a *kinetic* directive. It is concluded, therefore, that the process of emergence, whereby non-teleonomic replicating chemical systems were transformed into teleonomic ones, involved a switch in the primacy of thermodynamic and kinetic directives. It is proposed that the step where that transformation took place was the one in which some pre-metabolic replicating system acquired an energy-gathering capability, thereby becoming metabolic. Such a transformation was itself kinetically directed given that metabolic replicators tend to be kinetically more stable than non-metabolic ones. The analysis builds on our previous work that considers living systems to be a *kinetic state of matter* as opposed to the traditional thermodynamic states that dominate the inanimate world.

Keywords: chemical evolution, kinetic state of matter, molecular replication, origin of life, replicative chemistry, replicator space, teleology, teleonomy

1. Introduction

One of the most striking aspects of living systems is their so-called "purposeful" character, evident in both their structural features and their behavior. As Dobzhansky et al. (1977) put it some years ago: "Purposefulness, or teleology, does not exist in nonliving nature. It is universal in the living world. It would make no sense to talk of the purpose or adaptation of stars, mountains, or the laws of physics. Adaptedness of living beings is too obvious to be overlooked." Given today's understanding of the material nature of life processes it would not be particularly controversial to claim that this purposeful, or teleonomic character, to use the term introduced by Pittendrigh (1958) several decades ago, has its roots within the chemical processes that constitute living systems. But to specify precisely how that teleonomic character is related to the chemical structure and dynamics of such systems is far from clear. Recent developments in complexity theory, while opening new avenues for understanding living systems (for recent reviews, see: Kauffman, 2000; Capra, 2002), do not seem as yet to have resolved the fundamental issues.

Several decades ago Monod (1972, pp. 21–22) pointed out that the very existence of this teleonomic character is highly problematical and leads to what he termed a "flagrant epistemological contradiction." On the one hand the laws of nature are *objective*—no purpose is ascribed to them. That realization was at the heart of the scientific revolution of the 17th century. Yet on the other hand biological systems are, as Monod put it, *projective*. All living systems are involved in carrying out a *project*, be it to hunt for food, to find a mate, to carry out research into the origin of life, or whatever. Enveloped as we are within a biotic world, we tend to take this projective character of living systems very much for granted. However, from a strictly chemical perspective this behavior of matter is actually quite remarkable. How is it at all possible for a chemical system to act purposefully, or, as Kauffman (2000) put it, to act on its own behalf? How could *projective* systems have emerged from an *objective* universe? Clearly troubled by this dilemma, Monod went so far as to state that this apparent contradiction constituted "the central problem of biology."

In this article we propose to explore the possible chemical basis of teleonomy (for an earlier view, see Lifson, 1987) and attempt to place that unique life characteristic within a more well-defined physico-chemical framework. The analysis comprises two stages. We first attempt to provide some physico-chemical characterization for an event we would define as teleonomic, and then, using that characterization, we attempt to specify the *category* of chemical systems from which teleonomic character could have emerged, as well as the particular physico-chemical principles that would make that transformation explicable.

Before commencing the analysis, we make two further comments. First, on the issue of teleology, the doctrine of final causes. Since that term is metaphysically charged and, therefore, highly controversial in scientific discourse, it is now generally replaced by the more scientifically correct "teleonomy." As a result of that change, much of the earlier resistance to the description of living systems as purposeful appears to have been eliminated. As Pittendrigh (1958) put it several decades ago, biologists are now comfortable in saying: "A turtle came ashore *to* lay her eggs," rather than "She came ashore *and* laid her eggs." Agreement, on this issue at least, appears general; an understanding of living systems cannot be achieved without first recognizing and accepting their teleonomic character.

Second, it should also be pointed out that a discussion on teleonomic systems and how they emerged cannot be entirely separated from the physico-chemical process by which life itself emerged. As already noted, life's teleonomic nature is one of its most defining characteristics. However, rather than asking the traditional question: how could living systems have emerged from inanimate matter? we ask: how could teleonomic character as a physico-chemical phenomenon have emerged from non-teleonomic systems? Hopefully insight into how teleonomic systems could have emerged will shed additional light on the general problem of how life itself emerged.

2. Discussion

Keeping in mind that causal explanation generally and biological ones in particular, can never be absolute (Mayr, 1988), let us begin our analysis by attempting to characterize in physico-chemical terms what we would classify as a teleonomic event. After all, any attempt to seek a physico-chemical understanding of teleonomic behavior must, in the first instance, base itself on some physico-chemical characterization of what constitutes a teleonomic event, as opposed to a regular event.

2.1. Physico-chemical characterization of a teleonomic event

The physical process in which a hot cup of coffee cools, or the chemical process in which a piece of iron rusts when exposed to the elements, are considered natural processes and devoid of teleonomic character. The global explanation for why such processes take place is the one provided by the Second Law of Thermodynamics: all irreversible processes lead to a global increase in entropy. In fact the general explanation as to why any chemical reaction proceeds is grounded in these same terms, though the precise thermodynamic description can be expressed in a number of different, though equivalent ways. Thus, when we ask what is the directive responsible for the cooling of a cup of coffee, or the rusting of a piece of iron, the answer is the thermodynamic one; the *only* necessary consequence of such irreversible processes is a global increase in entropy. Hot coffee cools and iron rusts because these two systems are responding to the effects of the thermodynamic directive. All the physical and chemical changes that take place (for example, the rusting piece of iron changes its mass and its color) emanate from the action of that thermodynamic directive. We can, therefore, summarize by saying that for a macroscopic physicochemical system, all irreversible physico-chemical transformations considered to be non-teleonomic are attributed solely to the thermodynamic directive.

Let us now consider processes that are generally regarded as teleonomic, for example, a predator stalking its prey, a bacterium swimming upstream in a glucose solution gradient, or the process that epitomizes teleonomic behavior at the chemical level—cell division. For all the above processes the Second Law is of course fully applicable. All of these teleonomic actions by "autonomous agents" (Kauffman, 2000) have been brought about through a complex set of chemical reactions that have led to a global increase in entropy, primarily through the conversion of high-energy molecules such as ATP into lower energy ones, such as ADP. Yet despite the fact that precisely the same thermodynamic consequence, i.e., a global increase in entropy, derives from both teleonomic and non-teleonomic processes, we recognize a clear distinction between the two types of events, a distinction that would benefit from explicit physico-chemical characterization. Accordingly, we propose the following definition for a teleonomic event: For a macroscopic event to be classified as teleonomic we must be able to discern some *primary non-thermodynamic* directive

for that event. The thermodynamic directive, though necessarily operative, appears to play a subsidiary role.

At first sight the definition may seem somewhat vague given the infinite number of possible non-thermodynamic directives that could be imagined, though, as we will subsequently see, for single-cell life forms the non-thermodynamic directive can actually be characterized in explicit physico-chemical terms, but we put this point aside for the moment. So what do we mean by a non-thermodynamic directive, and how can such a directive be recognized? Since directives of any kind often can not be discerned directly, only indirectly by the consequences of their action, we can state that we discern a non-thermodynamic directive when we discern an interrelated pattern of non-thermodynamic consequences, i.e., a consistent pattern of behavior that does not appear to be directly associated with the thermodynamic directive, though it must, of course, be consistent with it. Let us illustrate this idea with Monod's prime example of a purposeful event—the process of cell division.

Cell division, from the physico-chemical viewpoint, is nothing more than a highly complex chemical process. During cell division an elaborate chemical machine is activated whose directive appears to be the multiplication of cells such that every aspect of cellular structure and function seems to be directly or indirectly related to that process of multiplication, rather than to the general thermodynamic directive. Any individual reaction within the dividing cell of course obeys the Second Law and in that sense appears to be driven by the thermodynamic directive. But inspection of the system as a whole reveals a global pattern of behavior that is not simply explained by just the thermodynamic directive. To illustrate, if an essential element for cell metabolism is absent from the growth medium of a dividing bacterium (e.g., the amino acid tryptophan), then complex control and regulation mechanisms are activated that lead to the synthesis of the enzymatic system required to synthesize that essential amino acid. Similarly, if glucose, a cell's primary energy source, is replaced by lactose, a less direct source, then a complex multi-step process that produces the enzyme that breaks down the lactose to glucose and galactose, is initiated (Freifelder, 1983). These are just two examples out of the multitude of control and regulation factors within all living systems, which together point unambiguously to a clear pattern of behavior: cell structure and dynamics, physical and chemical, are addressed toward one goal—cell multiplication. It is that overall pattern that identifies the *non-thermodynamic* directive, which at this stage of the discussion we will only identify as the cell multiplication directive. Before continuing, let us be quite clear that in stating that cell structure and dynamics are addressed toward the goal of cell multiplication, we are not implying the existence of global teleology in any way. Rather, we are conforming to modern biological thinking in accepting that the teleonomic character of living systems is empirically irrefutable, and thereby serves as a fundamental organizing principle in biology, in particular functional biology (Mayr, 1988).

It is at this point in our analysis that we are confronted by the Monod paradox, which can now be rephrased in more traditional physico-chemical terminology.

Given our earlier statement that it is the thermodynamic directive that ultimately drives *all* chemical reactions, simple and complex, the question now arises how can a *non-thermodynamic* directive, whatever its nature, emerge from what is in fact nothing more than just a complex chemical system. How can we explain in physico-chemical terms the process of emergence, whereby some chemical system whose primary directive was thermodynamic, has become transformed into one with a discernible *non-thermodynamic* directive? In order to answer this question we first need to enquire whether *simple* chemical processes can exhibit a non-thermodynamic directive.

2.2. KINETIC AND THERMODYNAMIC DIRECTIVES IN SIMPLE CHEMICAL PROCESSES

Consider a general reaction in which some substance A can react by two competing pathways—a kinetically preferred one leading to a thermodynamically *less* stable product, X, or an alternative higher free energy pathway leading to a thermodynamically *more* stable product, Y (Figure 1). For such a system the preferred product will depend on the reaction conditions that are applied. When the system is under conditions of so-called kinetic control the kinetically preferred product X is favored. However under conditions where the reaction barrier is readily overcome and significant equilibration is achieved, the thermodynamically preferred product Y is favored. Thus, product formation is governed by a combination of thermodynamic and kinetic factors, where the thermodynamic directive is the *primary* one, without which neither X nor Y can form, while the kinetic directive is the *secondary* one—secondary in that it can only influence *which* of the available thermodynamically allowed reaction pathways will be followed. This conclusion is important in that it indicates that for a simple chemical process both kinetic *and* thermodynamic directives are operative, though *kinetic directives are secondary*

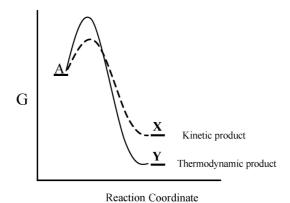


Figure 1.

to thermodynamic ones. Kinetic directives only operate within thermodynamically allowed constraints.

2.3. KINETIC AND THERMODYNAMIC DIRECTIVES IN CELL REPLICATION

Let us now return to the process of bacterial cell multiplication, our model purposeful event, and remind ourselves what takes place from a chemical point of view. When a sample of Escherichia coli bacteria is placed in a growth medium of glucose solution and essential mineral salts, the chemical reaction that has taken place is one in which some of the glucose, about 40%, is converted to (living) cellular material, the kinetically preferred product, while the remaining 60% is oxidized to carbon dioxide and water, the thermodynamically preferred products (Monod, 1972, p. 19). At first sight there seems to be a competition between kinetically and thermodynamically controlled pathways, in that both kinetic and thermodynamic products are formed. In reality, however, the process is under strict kinetic control. These two pathways are *not* in competition with one another as one frequently observes for regular chemical systems. The energy-producing metabolic process of glucose oxidation is coupled to the energy-consuming process of cellular material production enabling that latter process to take place. The process of emergence has led to a chemical system in which just sufficient oxidation of glucose to carbon dioxide occurs to cover the free energy requirements of the complex process of cell multiplication. So, within a biological system, the thermodynamic component of the reaction pathway is present and appears to have evolved for one reason alone to power the energetic requirements of the kinetic (replicative) pathway. Thus the complex chemical process of cell multiplication is primarily kinetically directed, though of course the thermodynamic requirements of the kinetically directed process are fully met through the utilization of an accessible energy source—glucose chemical energy.

Based on the above description, two points can now be made. First, the cell replication reaction, like all other chemical processes, is governed by both kinetic and thermodynamic directives. But in contrast to what one finds for regular (non-teleonomic) chemical reactions, the relative importance of the kinetic and thermodynamic directives appears to have *inverted*. In some manner that we will subsequently discuss, the process of emergence that led from some simple prebiotic chemical process to the complex chemical process of cell multiplication *has inverted the relative importance of the two physico-chemical directives—kinetic and thermodynamic*. Whereas in regular chemical processes the thermodynamic directive is the primary one with kinetic directives taking on a secondary role, for cell replication it is the *kinetic* directive that is primary, with the thermodynamic directive now playing the secondary and supportive role.

Second, we stated earlier that the teleonomic behavior expressed by some entity reflects a non-thermodynamic directive that is operative on that entity. For cell multiplication, that archetypal purposeful process, we have now identified that

non-thermodynamic directive to be the *kinetic* directive, a directive that we noted is present in *all* chemical reactions, but which in biological systems has replaced the thermodynamic directive as the *primary* driving force. As we have discussed in a previous publication (Pross, 2003), the powerful kinetic directive associated with all living systems derives from the special kinetic characteristics of the replication reaction, a character that derives from its autocatalytic nature. Let us now, therefore, consider for what kinds of chemical systems and by what means can the primary directive be transformed from being thermodynamic to being kinetic. Answering this question is pivotal since it would in effect indicate how so-called *projective* systems could, though following established laws of nature, emerge from an *objective* universe. In the next section we point out that it is the special kinetic characteristics of the replication reaction that enable a chemical system under the primary control of the thermodynamic directive to be transformed into some alternative chemical system whose primary directive is kinetic.

2.4. Transformation of non-teleonomic chemical systems into teleonomic ones

We now attempt to provide some general mechanism by which non-teleonomic systems directed by thermodynamic forces, can be transformed into teleonomic systems directed by non-thermodynamic forces (i.e., kinetic forces). Note that the somewhat metaphysically tainted question: how could purposeful processes emerge from an objective world? can now be expressed in purely physico-chemical terminology: how could a chemical process whose primary directive is thermodynamic, become transformed into one whose primary directive is kinetic?

Building on the seminal work of Eigen (1971, 1992) we have recently characterized the process of biological complexification as beginning with the emergence of some replicating molecule and its subsequent exploration of replicator space (Pross, 2004a; Pross and Khodorkovsky, 2004). We have suggested that the selection rule within replicator space—the space that incorporates all systems capable of self replication—is different to the selection rule in regular chemical space, the space that contains within it all "regular" chemical systems. Whereas within regular chemical space the transformation of one chemical system into another is fundamentally thermodynamically directed, within replicator space the corresponding transformation is in many cases kinetically directed. Within replicator space it is kinetic stability rather than thermodynamic stability that reflects the replicating system's ability to maintain its presence. The transformation of one replicating system into another tends to be from kinetically less stable to kinetically more stable (Pross and Khodorkovsky, 2004). Given the above statements we can now address the question: what is the primary directive that drives the replication reaction kinetic or thermodynamic, bearing in mind that the answer to this question may help explain how "purposeful" processes could have emerged from an "objective" universe.

Consider a general replicative system autocatalytic in X depicted in

$$A + B + C \xrightarrow{X} X + Z, \tag{1}$$

where X might be a polynucleotide, A, B and C activated nucleotides, and Z pyrophosphate ion, or X could be a pair of rabbits, A, B and C, carrots, water, and oxygen, and Z, rabbit waste and carbon dioxide. Whatever the identity of X and its building blocks A, B, C, etc, the system constitutes an element in replicator space. So what drives this reaction? For molecular replication the directive for the reaction, as for any other individual chemical reaction, is thermodynamic. The replicative process by which the replicating molecule acts as a template and assists in the linking of its building blocks to form a second molecular copy only proceeds if the reaction conditions are such that the equilibrium concentration of molecular replicator has yet to be achieved. The reaction proceeds till the equilibrium state is reached—when the free energy of the system is at its minimum value. Once equilibrium concentrations of template and monomeric components are reached, the reaction stops. Thus, according to our physico-chemical classification of purposeful events, we would have to characterize that process of molecular replication as objective—a non-teleonomic reaction. While that molecular replication process is undeniably under kinetic control such that the reaction products are kinetically rather than thermodynamically preferred (as for product X in Figure 1), the driving force for this chemical reaction (as for all other regular chemical reactions) is thermodynamic.

Let us now return to that archetypal teleonomic event—the kinetically driven process of bacterial cell multiplication. It is the emergence of an energy-gathering capability during the evolutionary process that enables the bacterial cell system to follow the kinetically directed pathway of cell multiplication thereby satisfying the thermodynamic demands on the one hand, while at the same time relegating those thermodynamic requirements to a secondary role. The conclusion that one is led to, therefore, is that the transition from a pre-metabolic replicating system to one with an energy-gathering metabolic capability was the point at which teleonomic behavior emerged, at least as defined in this paper. It is the incorporation of a metabolic capability into the replicating system that transforms the primary directive from being thermodynamic (i.e., reflecting an objective process) to being kinetic (i.e., reflecting a teleonomic process). The question now arises: how could the transition from a pre-metabolic replicator to a metabolic replicator occur? Or to phrase the question differently, why would a pre-metabolic replicator tend to acquire metabolic capability? An answer to this question would in effect help explain why an *objective* replicator would be transformed into a *projective* (teleonomic) one (see also, Pross, 2004b).

We have recently argued that the process of complexification in replicator space is kinetically directed, that incremental increases in replicator kinetic stability, at least during the emergence stage of evolution, are often associated with an increase in complexity (Pross, 2004a). Indeed, complex replicators are undeniably kinetically (though *not* thermodynamically) more stable than simple ones, as revealed by even a superficial comparison of the two groups. Replicating molecules—simple replicators by definition, required precise reaction conditions and the guiding hand of a skilled chemist in order to undergo successful replication (Orgel, 1995; von Kiedrowski, 1986). On the other hand, bacterial cells, complex replicators by comparison, manage to replicate prodigiously under remarkably variable conditions with no human assistance whatever (often despite human effort to stop such replicative processes). It would appear, therefore, that the conversion of a non-metabolic replicator into a metabolic one would lead to an increase in kinetic stability because it would be through the process that thermodynamic impediments on replicative capability would be largely circumvented. In fact, once a replicating entity would have incorporated an energy-gathering capability of any kind, the door to an entire new region of replicator space would have opened up. Given that the far-from-equilibrium regime of replicator space is where the kinetically most stable replicators happen to be located, access to that region of replicator space would lead to an enormously wide range of successful replicators. Indeed, inspection of the biotic world makes it clear that with few exceptions (specifically viruses and phages), successful replicators are all metabolic (though of course, even viruses and phages depend upon metabolic energy but obtain it indirectly from the host cell). Thus, the exploration of replicator space uncovers a myriad of paths all leading toward enhanced replicator kinetic stability. However, it is the incorporation of a metabolic capability at some point along that path that constitutes one of the most significant milestones on the road toward highly kinetically stable replicators.

So what was the first chemical event that would have transformed an *objective pre-metabolic* replicator into a *purposeful metabolic* one? Being a historic question, the answer may never be known. Such questions can only be answered, if at all, by accessing the historic record. But a model process that would illustrate the *kinds* of processes that could have led to this transition can be outlined (Pross, 2004a). Consider a molecular replicator X, whose structure co-catalyses the formation of some other molecular entity exhibiting photo acceptor properties PA, and capable of self-assembly with the molecular replicator to yield a molecular assembly, X//PA (Equation (2)), that is itself capable of self-replication.

$$X + PA \rightarrow X//PA$$
. (2)

Such an entity being both replicative and possessing an energy gathering capability would be less bound by thermodynamic constraints than X alone. To the extent that the replication reaction of such an entity would require energy input, its structure (one we can now classify as teleonomic) would enable the necessary energy to be gathered, leading to a replicating assembly of enhanced kinetic stability. In other words, given that X/PA could be expected to be kinetically more stable than X alone due to its energy gathering capability, the transition from a pre-metabolic

X to a metabolic X//PA could be expected to be kinetically selected—a favorable transition in replicator space leading to the emergence of a teleonomic system (i.e., kinetically directed) from an objective, thermodynamically directed world. Interestingly, the utilization of solar energy to power living systems can be traced back to some of the earliest photosynthetic prokaryote life forms, giving credence to the kinetic benefits of this kind of molecular association. Moreover, such kinetically directed association can be viewed as a molecular precursor to the more complex biological association process described in the endosymbiotic theory (Margulis, 1981), in which eukaryotic cells are thought to have emerged through the association of bacterial cells.

3. Concluding Remarks

We have attempted to demonstrate that once a physico-chemical definition of an event that we would characterize as teleonomic is set down, the emergence of teleonomic systems from an objective world can be rationalized in physico-chemical terms. It is chemical orthodoxy to state that chemical processes are governed by the combined effects of kinetic and thermodynamic directives, but when comparing a regular chemical reaction, e.g., the combustion of hydrocarbon to carbon dioxide and water, with the archetypal *teleonomic* chemical process (cell multiplication), we see that a key distinction is just in the identity of the primary directive. For "regular" chemical reactions it is the *thermodynamic* directive that predominates, while for metabolic replicative reactions it is the *kinetic* directive that predominates. Thus, the process of emergence was one that led to a switch in the primary directive from being *thermodynamic* to being *kinetic*.

How could such a fundamental change in the primary directive of a chemical system have come about? Within replicator space—the space that incorporates all replicating systems—we have proposed that the selection rule that governs likely transitions is a kinetic one, i.e., there is a tendency for kinetically less stable replicators to be replaced by kinetically more stable ones. We have demonstrated that this process leads to a process of complexification, so that the acquiring of an energy-gathering capability is just part of that kinetically stabilizing complexification process. In other words the conversion of pre-metabolic (thermodynamically driven) replicators into metabolic (kinetically driven) replicators would itself have been a kinetically favored process, and would have led to the transition from *objective* to *projective*. Simply put, *teleonomic* (i.e., metabolic) replicators tend to be kinetically more stable than *regular* (i.e., non-metabolic) ones, and therefore could be expected to emerge through the ongoing exploration of replicator space.

Is our definition of a purposeful event unique? Possibly not. It does not attempt to characterize teleonomic behavior in complex multi-cell replicators other than in the very broadest of terms, and it does not attempt to relate teleonomic character in multi-cell replicators to that observed in single-cell replicators. However, the

intention of this article has been to demonstrate that, based on a workable and consistent definition of such an event at the cellular level, the transition from objective to projective can be seen to be an understandable physico-chemical phenomenon. Thus, the idea that has been offered from time to time, that the emergence of life necessitates some as yet undiscovered physico-chemical principles (e.g., Kauffman, 2000), seems to us unjustified. In the parallel kinetic world of replicating entities the emergence of teleonomy simply reflected the drive toward greater stability, but a stability that is kinetic rather than thermodynamic. In earlier papers we attempted to show that two of living systems' most striking characteristics, their extraordinary complexity and far-from-equilibrium character, can be attributed to our description of life as a kinetic state of matter (Pross, 2004a; Pross and Khodorkovsky, 2004). In this paper we have attempted to demonstrate that life's other most striking characteristic—its teleonomic character—also fits in comfortably with this kinetic perspective. We, therefore, reaffirm the view that all living systems can be usefully classified as a manifestation of replicative chemistry—a discrete branch of chemistry whose detailed working principles at the chemical level (as opposed to the biological level) are only beginning to be uncovered (Sievers and von Kiedrowski, 1994; Orgel, 1995; Pieters et al., 1994, 1995; Lee et al., 1996, 1997; Yao et al., 1998).

Acknowledgements

The author is indebted to Professors Avshalom Elitzur, Vladimir Khodorkovsky and Leo Radom for helpful comments on an earlier draft of this paper.

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