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EVOLUTIONARY TRANSITIONS AND ARTIFICIAL LIFE

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Abstract

A major challenge for artificial life is to synthesize the evolutionary transitions that have repeatedly formed differentiated higher-level entities from cooperative organizations of lower-level entities, producing the nested hierarchical structure of living processes. This article identifies the key elements and relationships that must be incorporated or synthesized in an artificial life system if these transitions are to emerge. The processes currently included in artificial life systems are unable to provide an adequate basis for the emergence of the complex cooperative organization that is essential to the transitions. A new theory of the evolution of cooperative organization is developed that points to the additional processes that must be included in artificial life systems to underpin the emergence of the transitions.

I Introduction

A distinctive feature of living entities is that they are organized as nested hierarchies: entities are composed of smaller units that are in turn composed of still smaller units, and so on. For example, human social systems are constituted by organisms that are in turn made up of cells that in turn comprise molecular processes.

From an evolutionary perspective, this familiar structure appears to result from the repeated formation of higher-level entities through the evolution of differentiated cooperative organizations of lower-level entities, for example, the formation of early cells from organizations of molecular processes, the eukaryote cell from complex symbiotic communities, multicellular organisms from organizations of cells, and social systems from organizations of metazoans. This evolution has been characterized by the establishment of an extensive cooperative division of labor within the organizations of lower-level entities that is associated with a high degree of cooperative differentiation and cooperative specialization.

A central objective of the artificial life approach is to synthesize from

artificial components key biological phenomena. If this objective is to be met, it will be necessary to synthesize entities that are organized as nested hierarchies, and to synthesize entities that undergo the critical evolutionary transitions to form differentiated higher-level entities. The importance of this challenge is widely recognized among artificial life researchers (e.g., see [17, 28, 32]).

In this article I set out (a) to demonstrate that the processes that are currently explicitly included in artificial life will not meet this challenge; and (b) to identify the specific features that need to be incorporated in an artificial life (alife) system to encourage the emergence of the transitions to higher levels of organization.

I begin in Section 2 by demonstrating that the processes that are currently proposed by theory to explain the evolution of cooperation are limited in their capacity to account for the formation of higher-level entities through the evolution of differentiated cooperative organizations of lower-level entities. Section 3 identifies a form of hierarchical organization that can comprehensively overcome these limitations and that has underpinned the transitions from molecular processes to cells, from cells to metazoans, and from metazoans to human societies. This is followed by consideration of the extent to which this form of organization has also been significant in the emergence of living from nonliving processes.

Section 4 notes that this form of hierarchical organization has not been synthesized in alife systems to date. To assist in identifying how this synthesis could be achieved, I analyze two illustrative examples of the evolution of hierarchical organization at different levels of organization. The article concludes in Section 5 by abstracting from the examples the key structures and relationships that would need to be incorporated or synthesized in an alife system for the hierarchical organization and transitions to emerge.

2 Horizontal Self-Organization

2.1 Cooperative Horizontal Organization

Under what circumstances will cooperative organizations arise within a population of living entities (e.g., a population of molecular processes, or cells, or multicellular organisms)? I will first consider the evolution of what will be referred to here as horizontal cooperative organization. This is organization in which entities are at the same level of organization and therefore do not have any capacity to control other entities within the organization--entities mutually influence each other in interactions and are unable to influence other entities unilaterally [29]. This contrasts with what I will refer to as vertical organization, in which a horizontal organization is controlled by one or more entities

that are in hierarchical relationship to the horizontal organization. The hierarchical relationship means that the entities are able to influence the horizontal organization without being influenced by it--this capacity to influence unilaterally constitutes the ability of the entities to control the horizontal organization [29]. The controlling entities collectively comprise what will be referred to in this article as the manager of the organization.

An organization of entities is constituted by a set of relationships between the entities. The relationships are in turn constituted by adaptations of entities. A cooperative organization will arise in a population where the cooperative adaptations that constitute the organization are selected and reproduced through time.

Adaptations that establish cooperative relationships between living entities at the same level of organization can be reproduced through time where the adaptations provide net advantage to the co-operators themselves. The advantage may accrue as a direct result of involvement in the cooperation itself (e.g., mutualism) or may depend on the initial co-operator gaining the benefit of a further cooperative act that is initiated by one or more other entities. In the case of reciprocal altruism, the further cooperative act is initiated by the beneficiary of the initial cooperation (e.g., see [3, 34]), and in the case of an autocatalytic set, by some other member(s) of the organization who may not have benefited directly from the initial cooperative act (e.g., see [11, 14]). At first glance, it may seem that kin selection and related mechanisms should also be treated as processes of horizontal self-organization. In general, these operate where the cooperation and its benefits are disproportionately directed to entities whose propensity to cooperate is similar to that of the initiator of the cooperation (e.g., due to relatedness, as in the genetic kinship theory of Hamilton [15]). However, on closer examination it is evident that these mechanisms involve vertical organization; as will be demonstrated in Section 3, kin selection operates where the horizontal organization of individuals is constrained and controlled by a lower-level manager comprising the genetic elements that are common across individuals due to relatedness.

Where the conditions necessary for the operation of these horizontal processes are appropriately met, cooperative organization will arise and persist in the population; the entities that comprise the cooperative organization and the organization itself are able to outcompete individuals within the population. Where the conditions are met, organizations can arise that exploit circumstances in which cooperation provides net benefits, for example, where individuals can provide benefits to others more efficiently than the others can produce the benefits themselves (e.g., specialization and cooperative division of labor); and where individuals refrain from actions that would otherwise benefit the individual but harm others in the organization (e.g., restraint of

competition that would otherwise degrade resources [16] or that would reduce overall profitability in an industry [25]).

Taken together with genetic kin selection, these horizontal processes may appear able to account for the evolution of relatively simple cooperative organizations such as most of those found among nonhuman metazoans.

2.2 Limitations of Horizontal Self-Organization

However, these processes alone are limited in their capacity to establish organizations that fully exploit the potential benefits of cooperation: The processes are unable to overcome fully the widely recognized impediments to the evolution of cooperation. These impediments arise because in most circumstances where selection operates at the level of individual entities, adaptations must compete primarily on the basis of their effects on the entity exhibiting the adaptation; the effects of an adaptation on other entities will not usually contribute to the success of the adaptation, no matter how beneficial its cooperative effects on others may be, and irrespective of whether the resultant cooperative arrangement is more competitive as a whole; and in most circumstances, selection will favor "free riders" or "cheats" that undermine cooperation by taking any benefits provided by other entities in the organization, without cooperating in return.

These impediments are not restricted to the gene-based evolution of cooperation between multicellular organisms. They also manifest at all other levels of living processes: In relation to molecular processes see Maynard Smith [23] and Bresch et al. [71; in relation to the cellular level, see Buss [8]; and in relation to the human social level, see Olson [25] and Williamson [35].

The processes relied upon by reciprocity theory and by genetic kinship theory can overcome these impediments only to the extent that they can ensure that the effects of a cooperative adaptation on others are taken into account in determining the success of the adaptation: For example, kin selection is effective only to the extent that the effects of a cooperative adaptation benefit other individuals that also exhibit and reproduce the adaptation (e.g., related individuals), and reciprocity is effective only to the extent that the beneficial effects of a cooperative adaptation on others are returned through reciprocation to the individual exhibiting the adaptation. To the extent that the processes fail to ensure that the effects of an adaptation on others are not captured by the adaptation, cooperative arrangements that are more beneficial as a whole will nonetheless fail to evolve.

Of these processes, reciprocity might appear to have the greatest potential to account for the evolution of cooperation across the various levels of biological organization: Unlike genetic kin selection,

reciprocity is not limited to circumstances of genetic similarity, and unlike mutualism, it is not limited to cooperation that is intrinsically advantageous to all participants. However, reciprocity is susceptible to undermining by "cheats" (e.g., see [3]). This is particularly the case where cheats cannot be identified and excluded from the benefits of future exchanges. Cheating is especially undermining of reciprocal cooperation where the benefits of a cooperative act are not localized to a few identified recipients but instead spread to many others in the organization, making the identification and exclusion of cheats extremely difficult (e.g., "public goods" in the context of human systems of exchange relations). This difficulty severely limits the capacity of reciprocity to exploit fully the benefits of cooperation: Particularly in complex differentiated organizations, cooperation that benefits many other entities within the organization could be expected to play a significant role; and processes that are unable to establish cooperation of this type will be unable to achieve the evolution of such organizations.

Selection operating at the level of the group where each group is a horizontal organization is also limited in its capacity to overcome these impediments; within each group, the evolution of beneficial cooperation will be impeded as it is in all other horizontal organizations.

In summary, these horizontal processes clearly fall far short of the ideal of ensuring that all the effects of an adaptation on others (and ultimately on the organization as a whole) are appropriately and universally taken into account in determining the success of the adaptation. Horizontal processes are therefore unable to exploit fully the potential benefits of cooperative organization and are poor candidates to account for the evolution of the more complex forms of differentiated cooperative organizations that have characterized the major evolutionary transitions that have given rise to new levels of biological organization.

3 Vertical Self-Organization

3.1 The Governance of Living Processes

3.1.1 Management

What arrangements could arise that would overcome the limitations of horizontal organization and enable organizations to evolve the complex cooperative relationships that underpin the formation of new levels of biological organization?

From the analysis outlined above, it is evident that these limitations would be overcome by new arrangements within the organization that ensure that the success of cooperative adaptations is determined by the net effects of the adaptations on others in the organization (and ultimately their effects on the organization as a whole). To the extent that this

condition is met, cooperative arrangements that provide the greatest benefit to the organization would prevail.

Stewart [31] has suggested that this could be achieved by the inclusion within the organization of one or more entities that:

· are in hierarchical relationship with the entities that comprise the original horizontal organization and have the capacity to intervene in the organization to promote cooperation, for instance, by intervening to sustain or inhibit entities in the horizontal organization according to the extent to which their net effect on others either benefits or harms the organization; and

· are capable of evolving, and whose evolutionary success is dependent on the success of the organization as a whole. This coincidence of evolutionary interests between the intervening entities and the organization as a whole would ensure that the entities evolve interventions that realize their potential to promote beneficial cooperation.

These entities that are in hierarchical relationship to the original horizontal organization collectively constitute the manager of the organization.

In principle, the manager could intervene in a horizontal organization to support co-operators who provide benefits to others without benefit to themselves, and who would otherwise be outcompeted in the horizontal organization. Interventions of this kind could underpin the evolution of division of labor between entities in the organization, allowing the extensive cooperative specialization and differentiation that characterizes the major evolutionary transitions under consideration here. Interventions could also inhibit free riders who would otherwise undermine cooperation arising among other entities. The manager could also produce net benefits for the organization as a whole by supporting adaptations that produce only longer-term benefits and that would otherwise be outcompeted in the short term within the organization.

The manager could vary in the extent to which it overrides the adaptive capacity of entities in the horizontal organization. At one extreme, the manager would tightly control the horizontal organization, with all heritable adaptation originated by the manager (e.g., the genome's management of molecular processes within the eukaryote cell, and extreme examples of top-down management in human hierarchical organization). At the other, the manager would feedback general rewards and punishment to entities in the horizontal organization to reflect the effects of their adaptations on the organization as a whole, with the entities taking account of this feedback as they adapt (e.g., some modern, flexible forms of human organization). An ideal manager of this kind would cause entities

to adapt as if their effects on others were effects on self, enabling cooperative possibilities to be explored fully.

Significantly, this vertical organization would not have to rely on fortuitous synergy between the interests of the organization and the interests of its constituent entities for the interests of the organization to be maximized: Instead, an ideal manager would be able to construct whatever synergy of interests is needed to overcome any initial conflict between the interests of constituents and the interests of the organization to enable the organization to adapt optimally as a whole; the manager would do this by intervening to ensure that whatever adaptations of entities are needed to meet the interests of the organization are also in the interests of the entities. Under ideal arrangements, this would ensure that entities that are pursuing their own interests are also pursuing the interests of the organization. Once this synergy is achieved, cooperative relationships that maximize the interests of the organization would emerge as a consequence merely of the pursuit by entities of their own interests.

In this way, vertical organization could comprehensively overcome the limitation in the capacity of group selection to evolve cooperative arrangements within groups that are each a horizontal organization: An ideal manager could, in principle, intervene in a horizontal organization to construct any possible set of relationships between entities and support any possible types of entities. Group selection operating on a population of ideal vertical organizations would therefore be unlimited in its capacity to search the space of possible organizations. It would not be restricted to searching that subset of the space of organizational types that contains only organizations limited to the restricted forms of cooperation that can arise and persist in horizontal organization.

3.1.2 The Hierarchical Relationship

The requirement that the intervenor(s) be in hierarchical relationship to the original horizontal organization is essential. It is not sufficient that there be entities within the horizontal organization that have the capacity to intervene in the way outlined to promote cooperation: An entity that is a typical member of the horizontal organization and that uses resources to sustain or inhibit other members of the organization without any benefit to itself is itself likely to be outcompeted in the organization (this is the "second-order problem" of Axelrod [1]).

How does the hierarchical relationship overcome the second-order problem? As we have seen, a hierarchical relationship exists between two sets of entities or processes when one set influences or constrains the other without being influenced by it [29]. This capacity to modify without in turn being modified constitutes the essence of the ability of one set of processes to regulate or manage another, by, for example, causing the

other set of processes to act or adapt in ways it would not in the absence of the regulation. The hierarchical relationship that constitutes vertical organization is fundamentally asymmetrical. This contrasts with purely horizontal organization in which entities interact dynamically, mutually influencing each other without dominance or control. n and manage a horizontal organization without in turn being influenced by it enables the manager to unilaterally appropriate for its own reproduction and maintenance resources and services from the horizontal organization. And it is able to obtain these benefits without having to participate in the competitive interactions and cooperative exchanges of the horizontal organization. This enables the manager to stand outside and act across the dynamical interactions of the horizontal organization, managing them for its own benefit.

This capacity to obtain resources and services unilaterally is critical because the capacity assists in ensuring that the evolutionary success of the manager is advanced by its ability to produce beneficial cooperative arrangements in the horizontal organization. The capacity to appropriate resources does this because it enables the manager to benefit from any beneficial cooperative arrangements supported by its interventions: It can harvest benefits and have them utilized for its own purposes. The coincidence of interests established in this way between the manager and the organization as a whole will be complete when the manager is fully dependent on the reproduction of the organization for its own reproduction and when the only way in which the manager can pursue its success is by enhancing the success of the organization as a whole.

This contrasts with the situation of a member of the horizontal organization that encounters the second-order problem: The member can sustainably engage in interactions that promote cooperation only to the extent that it benefits from these interactions; if the interactions themselves provide insufficient benefit to the member, then, unlike the manager, it has no capacity to sustain its involvement in the interactions by unilaterally harvesting from across the organization some of the wider benefits that may flow to the organization as a whole from its promotion of beneficial cooperation.

The manager that constrains the horizontal organization to produce beneficial cooperative arrangements may be either an upper-level manager that is external to the controlled entities, or a lower-level manager that is internal to the controlled entities.

3.1.3 Upper-Level Management

The constraints provided by an upper-level manager are termed boundary conditions by Salthe [29]. Key examples of an upper-level manager that manages a horizontal organization by producing boundary conditions that promote cooperation are an early cell that includes an RNA manager that

establishes beneficial cooperative arrangements in a protein-based autocatalytic set (the horizontal organization). It can do this by, for example, intervening to catalyze the formation of a protein that is beneficial to the autocatalytic set but that would not otherwise be reproduced within the set; and a human manager comprising a chieftain, ruler, government, or committee that promotes cooperation in a horizontal organization of humans by, for example, punishing individuals who undermine cooperation within the organization because they steal the products of cooperative arrangements or because they fail to reciprocate in exchange relations.

The evolution of these instances of upper-level management will be considered in detail in Section 4 to assist in identifying how the evolution of these forms of organization can be encouraged in artificial life systems.

3.1.4 Lower-Level Management

A lower-level manager comprises evolvable entities that are at lower levels in the nested hierarchies that constitute each of the entities of the horizontal organization; that is, a lower-level manager is composed of internal constituents of the entities of the horizontal organization, in contrast to an upper-level manager whose entities are external to the entities of the horizontal organization. Examples of these evolvable lower-level internal constituents include the genome in relation to a cell or a multicellular organism, and both the genome and clusters of socialized behavior patterns (e.g., norms) in relation to a human. These internal constituents influence the entities and organizations of which they are a part through lower-level constraints (termed initiating conditions by Salthe [29]). The constraints manifest in the entities of the horizontal organization as intrinsic properties of the entities that predispose them toward particular behaviors and other characteristics. It is worth noting here that genetic arrangements can comprise both an upper-level manager of molecular processes within a cell (the genetic elements are external to the processes being managed) and a lower-level manager of, for example, a society of organisms (in this case the genetic arrangements are internal constituents of the organisms being managed).

Identifying examples of lower-level managers, and understanding how they can control and constrain horizontal organization in ways that promote cooperation, is not so clear cut and intuitively obvious as it is for upper-level managers. It will be necessary to present a number of specific examples. The nature of lower-level management is probably best illustrated by the consideration of examples of human organization in which a horizontal organization can be controlled and constrained by both upper-level and lower-level management.

First, consider a level of organization in a hierarchical company or firm:

the behavior of individuals at this level can be controlled and managed both (a) by the establishment by a higher level in the hierarchy of an appropriate pattern of rewards and punishments (i.e., boundary conditions) for individuals; and (b) by assuring that these individuals have particular intrinsic properties, such as diligence, honesty, and conscientiousness. These intrinsic properties arise from lower-level constituents of the individual such as genes or socialized behavior patterns.

Second, consider a human family: The behavior of children can be constrained and managed by both (a) the establishment by parents (the upper-level manager) of appropriate patterns of rewards and punishments; and (b) by the inculcation in the children of particular behavior patterns (e.g., norms) that will form intrinsic, lower-level constituents of the children that constrain their behavior even in the absence of upper-level constraints such as the possibility of rewards and punishment.

Finally, consider a human social group such as a tribe: The group could be controlled to produce egalitarian behavior either (a) by a powerful ruler who rewards egalitarian behavior and punishes alternative behavior; or (b) by assuring that the group of individuals are constrained genetically to interact in an egalitarian way or are inculcated with behavior patterns that also constrain them to behave in this way.

The capacity of a lower-level manager to constrain and manage a horizontal organization gives it the potential to, for example, establish cooperative arrangements by constraining individuals to provide resources to specialists who would not otherwise be sustainable in the horizontal organization. And a lower-level manager has the same capacity as an upper-level manager to use its control of the horizontal organization to have the benefits of cooperation deployed to enhance the success of the manager, for instance, by directing resources to the reproduction of the genetic elements or behavioral patterns that collectively make up the manager. As is the case for an upper-level manager, if a lower-level manager is to realize fully its potential to promote cooperation, it must be evolvable, and its evolutionary success must be dependent on the success of the organization as a whole. If these conditions are met, the lower-level manager will evolve constraints that will produce beneficial cooperation in the horizontal organization.

Examples of organizations that are managed in this way by a lower-level manager composed of evolvable internal constituents of the entities in the horizontal organization are (a) a multicellular organism that is a horizontal organization of cells, with each cell constrained by a lower-level constituent, the genome. The genome is identical in all cells, and collectively these genomes across all cells constitute the lower-level manager that controls the organization of cells; (b) an insect society that is a horizontal organization of organisms managed by a genome that is

reproduced across the society as lower-level constituents of the organisms. Collectively the genomes constitute the lower-level manager; and (c) egalitarian groups of human hunter-gatherers that are composed of a horizontal organization of humans constrained by a cluster of socialized behavior patterns (e.g., norms) and probably also by some common genetic elements. The cluster of socialized behavior patterns is a lower-level constituent reproduced in individuals across the organization, which collectively constitute a lower-level manager. The cluster of behavior patterns can control the group to advance the interests of the manager by, for example, including behavior patterns that actuate individuals to reproduce the cluster by inculcating it in others, including in their progeny, and by actuating them to punish individuals (including by expulsion) in whom the cluster has not been reproduced.

3.1.5 Management Constituted by a Horizontal Organization

It has been implicit in the discussion to this point that the manager (whether upper or lower level) reproduces and responds to selection as a coherent unit. If this is the case, and if the success of the manager depends on the success of the organization as a whole, the management instituted by the manager will be in the interests of the organization. However, if the manager itself is composed of a number of entities, and is therefore itself a horizontal organization, competition among the entities will impede the ability of the manager to adapt optimally as a cooperative whole, in the same way that competition limits any other horizontal organization; and to the extent that the manager is unable to adapt optimally as a whole, it will fail to manage optimally the original horizontal organization in which it intervenes. Thus, for example, a management entity may establish hierarchical controls that serve its competitive interests at the expense of the interests of the manager as a whole, and a management entity that can establish a beneficial intervention in the initial horizontal organization may be outcompeted within the managing horizontal organization.

This is particularly a problem for lower-level management: A lower-level manager is necessarily composed of internal constituents within each of the entities of the original horizontal organization--the potential for competition among these numerous constituents is considerable. If the competition is not constrained in any way, a lower-level manager will not be constituted: The lower-level constituents will not reproduce or respond to selection as a coherent unit, and there will not be any capacity to modify outcomes across the horizontal organization at all. It will be an unmanaged horizontal organization. The establishment of arrangements that prevent differential success among its constituent entities have therefore been critical to the evolution of organizations managed by a lower-level manager.

This impediment to the evolution of the manager as a unit can be overcome

in the same way that it is for the original horizontal organization, that is, by the emergence of a new level of management that intervenes in the original managing horizontal organization to promote beneficial cooperation. In this way, multi-level management may evolve. However, if the new level of management is itself a horizontal organization, this is not a final solution: The impediment is simply exported to the new level.

Of course, the impediment will not arise when the manager is composed of a single entity, for instance, by a single RNA structure in the case of the molecular example of upper-level hierarchical control considered above, or by a chieftain in the example of human organization managed by an upper-level manager. This suggests that the impediment can also be overcome in relation to multi-level management by heading the management with a single entity that successfully controls lower levels of management. Many modern human hierarchical organizations are managed in this way.

However, arrangements of this sort can overcome the impediment only when the manager is composed of or headed by a single entity. The difficulty will resurface whenever the potential for competition among a number of entities arises, for instance, when a chieftain is to be replaced, or when the single RNA structure reproduces.

This problem is particularly significant when the manager is composed of an entity such as an RNA structure that discovers adaptations through a process that involves differential reproductive success between entities: In these circumstances, reproduction of the entity may result in competition between its progeny. This is less a problem in the case of a human ruler who tests alternative adaptations against internal models and against internal proxies for differential reproductive success, rather than by actual differential reproductive success among rulers.

3.1.6 Recursive Management of Competition

The difficulties that arise because of competition between entities that constitute the manager can, however, be overcome recursively without the emergence of new levels of management. These arrangements are recursive in the sense that they are established by adaptations of entities within the managing horizontal organization itself. Ideally, the arrangements will operate to suppress only competition that does not result in the success of heritable variation that maximizes the success of the organization ("heritable variation" is used broadly in this article to refer to all variation, genetic or otherwise, that can provide a basis for evolutionary change. It includes, for example, variation in ideas and beliefs that are transmittable between human individuals). Examples of organizations that can internally select heritable variation on the basis of its benefit to the organization (e.g., by testing the effects of alternatives on internal proxies for organizational success) are humans, and modern hierarchical organizations of humans. The advantage of internal testing is that it enables the organization to discover adaptations during its life, rather

than having to rely on differential reproductive success between organizations to test variation [31].

However, all competition involving heritable variation must be suppressed within organizations that do not have internal arrangements that can differentiate between variation that is likely to benefit the organization and variation that is not. These organizations must rely on a between-group selection process involving the differential reproductive success of organizations to select variation that maximizes the fitness of organizations. If selection operating at the level of the group is to be fully effective, competition between entities within the organization must be suppressed, thereby concentrating competition and natural selection at the between-organization level [36]. This ensures that there is no heritable differential success within the organisation, and that the only way in which entities can achieve heritable relative success is through their contribution to the differential success of organisations.

At first it may seem that a manager which is a horizontal organisation could have no greater capacity to recursively overcome internal competition than could the original horizontal organisation. Alternatively, it may be suggested that if the manager is able to recursively suppress competition, why couldn't the original horizontal organisation also do so, rendering the manager redundant and unnecessary?

The reason why the original horizontal organization and the manager have fundamentally different capacities in this respect is that the manager controls a horizontal organization, and it can use this control to construct structures and processes that can act across the organization to suppress competition. Only a manager has the capacity to control and constrain the organization on a sufficient scale to suppress competition across the organization.

However, this raises a further issue: How can adaptations that suppress competition become established within the manager so that they can achieve the necessary hierarchical control across the organization? how will they overcome competition from alternatives within the manager that don't invest resources in the suppression of competition? This further instance of the second-order problem can be overcome in the following way: Suppressors will not be outcompeted if the competition they suppress within the organization also includes the competition they would otherwise encounter from alternatives. That is, successful suppressors must also suppress competition from alternatives who do not suppress.

A series of examples will illustrate how a manager is able to suppress competition by using its capacity to control a horizontal organization and how the controls can escape the second-order problem and avoid being outcompeted within the manager. Consider a horizontal organization of organisms that is managed by a lower-level manager that is composed of

genetic arrangements: Genetic elements that arise in the manager may actuate individuals to direct their cooperation preferentially toward closer relatives who are more likely to include and to reproduce the manager, and who are also more likely to include and reproduce these particular genetic elements (i.e., the kin selection processes of Hamilton [15]); genetic elements that arise in such a manager also may actuate individuals to punish other individuals who do not exhibit the actions of individuals controlled by the manager as well as individuals who do not act as if they include the particular genetic elements that actuate punishers; that is, non-punishers are also punished (this example is explored in detail by Boyd and Richerson [6], but without the hierarchical perspective developed here); and finally, genetic elements may arise that actuate individuals to direct their cooperation toward supporting the reproduction of only a single individual within the horizontal organization, thereby preventing the reproduction of individuals that might not include the manager and that also might not include these particular genetic elements (e.g., some eusocial insect colonies).

Arrangements that suppress competition at various levels of organization and that have been studied in some detail are surveyed by Jablonka [19]. Additional examples to those already considered above, described from the hierarchical perspective, include the organization of genes on single chromosomes, which reduces competition among genes within the upper-level manager that manages molecular processes within cells [9]; meiosis, which also limits competition among genes and chromosomes within the upper-level manager of cells [13, 24]; and sequestration of the germ line together with reproduction through a single cell, which reduces competition between the genomes that constitute the lower-level manager controlling organizations of cells [8].

3.1.7 The Significance of Vertical Organization

However, the successful suppression of competition within the organization and its concentration at the between-group level is not sufficient in itself to ensure that group selection will be able to establish the extensive level of cooperative differentiation that characterizes the key evolutionary transitions. For this to be achieved, the variation that arises between organizations must include the production of organizations within which the necessary division of labor is able to be sustained--selection will be unable to select these forms of organization if the variation presented for selection does not include them. The vertical arrangements discussed here are therefore essential to the key evolutionary transitions not only because they allow the comprehensive management of competition, but also because, as we have seen, they can control horizontal organization to produce a wide range of alternative organizations that would not otherwise be available for selection. For instance, a manager can underpin comprehensive differentiation by intervening to redirect resources to support specialists that could not

otherwise reproduce or even persist in a horizontal organization.

The significance of vertical organization is somewhat obscured in the instances of the evolution of cooperative organization commonly studied by biologists. This is because these instances involve organizations of entities that already include evolvable lower-level constituents (i.e., genetic arrangements), and a manager can be readily constituted merely through the suppression of competition between these pre-existing lower-level constituents across the organization. The significant role of vertical organization is more clearly seen by studying evolutionary sequences in which the evolvable lower-or higher-level entities are initially absent or poorly developed, as in the sequences discussed in Section 4.

In summary, the process of vertical self-organization described here is essential for the evolutionary transitions in which higher-level entities have been formed through the evolution of highly differentiated cooperative organizations of lower-level entities. The familiar nested hierarchies of living processes arise through the repeated formation of organizations of entities that are managed by hierarchical arrangements that ensure the entities adapt and act to serve the interests of the organization as a whole.

3.2 The Governance of Matter

3.2.1 The Hierarchical Perspective

To what extent can the concepts and processes that underpin this account of horizontal and vertical self-organization in living processes also provide an understanding of the emergence of living processes from inanimate matter?

Horizontal organization among nonliving entities is widespread: It is evident that interactions among entities at the same level of organization can give rise to organizations of entities. Such organizations form and persist to the extent that the relationships between entities that constitute the organizations are reproduced to some extent through time, because, for instance, the relationships represent stable or dynamic equilibria. However, in contrast to horizontal organization among living processes, mere physical persistence is a sufficient condition for nonliving processes: In the case of living processes, the adaptations that underpin relationships must be not only physically realizable, but also competitive, for instance, by maximizing the fitness of participants. As for vertical organization in living processes, hierarchical relationships among nonliving entities will be constituted where one set of processes or entities is able to influence another set without in turn being influenced.

It is evident from consideration of the material world that the asymmetrical functional relationships that characterize hierarchical separation can arise when there is a difference in scale between interacting entities or processes: For example, where entities differ sufficiently in scale, a larger-scale entity may influence the dynamical behavior of a set of smaller-scale entities without itself being influenced by the interactions; because of its larger scale, the hierarchical entity does not participate in the lower-level processes dynamically: It stands outside and acts across the dynamic of smaller-scale entities.

The difference in scale is often reflected in the duration of time of phenomena (longer for higher-scale entities) or of the length of periods between events (longer for events coming out of processes of larger scale). When an asymmetrical functional relationship is constituted in this way, processes that constitute boundary conditions would operate on a much slower time scale than the dynamical interactions of the level below; from the perspective of an entity participating in the lower-level dynamic, boundary conditions of this type are typically seen as relatively unchanging features that are not influenced by the individual entity and the interactions in which it is involved [29].

Because the nonliving world is separated into components and processes that differ widely in scale and that often are also organized as nested hierarchies (e.g., quarks, protons, atoms, molecules, oceans, planets, galaxies, etc.), hierarchical interactions are pervasive. As a consequence, the provision of an adequate account of processes at any particular focal level of nonliving processes will usually require the inclusion of relevant processes at both lower and higher levels of hierarchy that influence and constrain the focal level but do not participate in the interactions of the focal level dynamic [29]. For example, chemical systems with identical initiating conditions and identical focal-level processes can unfold into entirely different systems under different boundary conditions (e.g., under differences in temperature, pressure, and the location and form of any structures of greater scale and stability that interact with the system, such as any structure that contains the system); and processes at the quantum level may unfold as waves or particles depending on the boundary conditions they encounter. The hierarchical perspective is essential to provide an adequate account of the evolution of physical systems in the material world where boundary conditions vary in space and time.

3.2.2 Management that Produces New Organizations

This capacity for boundary conditions to influence the nature of the organizations of entities that will form and persist in an interacting dynamic of entities is critical to our discussion here: Just as living entities that are in a hierarchical relationship with a dynamic of

interacting living entities may produce forms of organization that would not have arisen otherwise, nonliving entities may similarly constrain a material dynamic.

Thus at a given focal level of nonliving organization, an interacting dynamic of entities may give rise to horizontal organizations of entities that themselves form entities of larger scale. These larger-scale entities may interact in hierarchical fashion with the parent dynamic of smaller-scale entities, providing new boundary conditions that constrain the dynamic to produce new forms of organizations of entities that would not have arisen otherwise in the dynamic.

For example, at the molecular level, an interacting dynamic of smaller-scale atoms and molecules may give rise to molecules of larger scale (formed as horizontal organizations of smaller-scale atoms and molecules) that in turn provide new boundary conditions for the dynamic of smaller-scale entities; the larger scale enables the molecules to stand outside and act across the dynamical interactions of the smaller-scale entities to produce outcomes that would be improbable in the unconstrained dynamic. Thus a larger-scale molecule could cause the formation of molecules that are unlikely to arise in the unconstrained dynamic because their formation requires, for example, a coming together and particular positioning of a number of smaller-scale molecules that is highly unlikely to occur spontaneously in the interactions of the dynamic: The capacity of the larger-scale molecule to stand outside and act across the dynamic in both space and time enables it to collect together over time the outcomes of a number of different events that are highly unlikely to occur simultaneously but that are likely to occur sequentially over time, and to put together particular spatial arrangements and positionings of smaller-scale entities that would otherwise be improbable. This process is, of course, from another perspective, chemical catalysis. The new organizations formed in this way may themselves constitute higher-scale entities that in turn provide new boundary conditions for the dynamic, resulting in the formation of further organizations that would not arise spontaneously in the unconstrained dynamic, and so on.

In this way, a new space of possible arrangements of matter can be opened up for exploration. Organization is no longer limited to what can come together fortuitously through the unconstrained interactions of entities in a horizontal dynamic; vertical organization opens the way to the formation of more complex organizations by a process of construction.

However, the search of this new space will generally be undirected: There will not necessarily be any pattern to the organizations produced. On the basis outlined, vertical organization can manage matter to form organizations that would not otherwise arise, but this management would not necessarily have any particular objective or direction; it does not include any overriding mechanism that, for example, would ensure that only

management that achieved particular outcomes would persist.

3.2.3 Self-Replicating Management

Such an overriding mechanism may arise, however, if and when these processes of horizontal and vertical self-organization produce self-replicating management, for instance, through the production of larger-scale entities that manage the parental dynamic to produce copies of themselves. These entities may be self-replicating as individuals, or as a collection of entities (e.g., the autocatalytic sets of Eigen and Schuster [11]; and Farmer et al. [14]).

A key feature of self-replicating management is that away from equilibrium it produces a larger-scale organization (the population) whose growth, until it is otherwise limited, is subject to positive feedback--every increase in population size in turn increases the capacity of the population to grow. When the population encounters resource limits, the result is competition between members of the population, which drives the familiar process of natural selection. Natural selection in turn gives the management of matter direction and pattern--only the most competitive management will persist. In contrast, the population growth of managing entities that are produced by other types of managing entities is not driven in this way by positive feedback: An increase in the population of one type of manager does not in turn have any effect on the extent to which additional managers of that type are produced.

Although populations of self-replicating managers may achieve substantially higher scales than individual managing entities, initially this does not mean that management will be organized or that matter will be managed on these larger scales--as we have seen, without vertical organization there is limited capacity to evolve large-scale cooperative adaptations that coordinate the activities of individuals across the greater scales: Selection founded on competition precludes the less fit, irrespective of whether they are participating in a beneficial cooperative arrangement that is more competitive as a whole.

3.2.4 Management of Management

As we have also seen, this limitation can be overcome through the formation of horizontal organizations of self-replicating managers that are in turn managed by arrangements in hierarchical relationship to the managers. Repetition of this process will produce living processes organized as nested hierarchies and will progressively extend the management of living processes across space and time. In this way, as managed living processes increase in scale, they gain the capacity to manage the material world at greater and greater scales to reproduce themselves. Whatever level of nonliving organization living processes originate in, life will tend to become organized at, and manage matter at,

increasingly larger scales.

When applied at the molecular level of organization, this account parallels in many respects the standard theories of the origin of life through the evolution of self-replicating molecular systems (e.g., see [21]). However, these accounts have not identified the essential hierarchical relationship between the self-replicating entities and the dynamic they manage, and they have not recognized that this vertical organization arises for similar reasons to the emergence of vertical organization in living processes: The capacity to influence without in turn being influenced enables a manager to govern the level below to produce advantageous forms of organization that would not arise spontaneously in that level.

4 The Emergence of Evolutionary Transitions in Artificial Life

4.1 Cooperation in Artificial Life

It will be necessary for artificial life to include the processes of horizontal and vertical self-organization if it is to synthesize living processes that are organized as nested hierarchies, and if it is to synthesize the evolutionary transitions that give rise to them. There are numerous examples of alife systems that have successfully included instances of the processes of horizontal self-organization dealt with in Section 2, such as mutualism and reciprocity (e.g., [2, 17, 18, 22, 27, 33]). Not only have these alife systems evolved cooperation when cooperative adaptations are initially incorporated in the system and set in competition with non-cooperators, but some systems have also discovered cooperative adaptations not explicit in the initial system (e.g. Ray [27]; and Lindgren and Nordahl [22])

However, if artificial life is to synthesise the evolutionary transitions that give rise to new levels of organisation, the processes of horizontal self-organisation need to be complemented by vertical self-organisation. To date, artificial life has not been synthesised explicitly to encourage the emergence of vertical organisation, and the synthesis of entities that undergo an evolutionary transition to form higher level entities is seen as an important challenge for the future (e.g., see [28, 32]). Furthermore, when alife practitioners have recognized the importance of the synthesis of evolutionary transitions they have tended to focus on the transition from the cellular to the multicellular level where the vertical system is initially constituted by lower-level management, rather than the transition to cells and to modern human social systems where the vertical system constituted by upper-level management is more significant. To point the way to how this synthesis can be initiated, it is necessary to develop and to operationalize the concept of hierarchical relationship, identifying the critical features of the relationship so that they can be incorporated in alife systems.

I will begin by briefly examining a range of illustrative examples of the evolution of management at various levels of organization to develop a more concrete understanding of the evolution of essential elements of the hierarchical relationship in living processes. I will conclude by abstracting from the examples the relationships and processes that are

common to the various instances of the evolution of vertical self-organization and that need to be included or synthesized in an alife system if vertical organization is to emerge.

4.2 Evolution of Modern Human Organization

I will commence with an illustrative example of the evolution of human organization. However, it should be noted that this example concerns the evolution of modern, hierarchical human organizations, which have arisen during the 12,000 years to the present, and which have largely replaced the more egalitarian hunter-gatherer societies that preceded them (the evolution of the hunter-gatherer phase is dealt with by, for example, Knauft [20], Boehm [5], and Wilson and Sober [37]). It also should be noted that, as aptly pointed out by Erdal and Whiten [12], these modern human hierarchical organizations "are not merely reborn ape hierarchies, but uniquely human in both their behavioural detail and their cultural recognition" (p. 178). It is this form of organization that is responsible for the extraordinary level of cooperative differentiation in modern human societies, which matches that found in the other major evolutionary transitions that are the focus of this article.

Consider a small, stand-alone horizontal organization--a tribe or an agricultural community. An individual or alliance of individuals that has the ability to coerce other members of the organization (due to physical strength or superior weapons) may be able to extract a disproportionate share of the resources and services produced in the organization (e.g., food and reproductive opportunities). Critically, these hierarchical individuals do not have to participate in the competitive interactions or mutually advantageous exchange relations of the horizontal organization to obtain these resources. This manager may emerge from within the human group or may itself be a free-living band that moves from group to group plundering resources.

A distinction can be drawn between interventions made by the manager in the horizontal organization that simply appropriate resources, and those that actually cause the production of benefits that provide direct and immediate benefits to the manager (e.g., the coercion of individuals to make weapons or grow food for the manager). The latter class of intervention is a short step away from interventions that increase the resources available to the manager by promoting the efficiency of the organization as a whole. For example, the manager may punish cheats who would otherwise undermine beneficial cooperation in the horizontal organization by not reciprocating in exchanges of goods; and it may provide resources to individuals to promote the performance of actions that are beneficial to the organization but that would otherwise not be sustained because they would not produce sufficient direct benefit for the individual (e.g., group defence).

These distinctions suggest an evolutionary sequence that begins with a manager whose relationship with the group is largely limited to appropriating benefits, moves through a phase in which the manager also intervenes in the group to cause the production of benefits that directly benefit the manager (but without improving the overall productive capacity of the group), and then moves to a relationship where the manager manages the group to increase its overall capacity to produce benefits, some of which are appropriated by the manager for its maintenance (e.g., taxation). The end result of this evolutionary sequence is a manager that has the capacity to improve substantially the competitive capacity of the organization at the intergroup level, whose success and continued existence is dependent on the organization of which it is an obligate part, and whose interests lie to a significant extent in using this capacity to promote the success of the organization as a whole, particularly when the group is in competition with other groups.

To the extent that the interests of the organization and the interests of a ruler who heads the manager coincide, the ruler's adaptation of its management of the organization will tend to maximize the success of both the organization and the ruler--through the adaptation of the ruler, the organization is able to adapt continually to changing internal and external events. In these circumstances, heritable adaptation at the level of the group does not have to rely on a between-group selection process, and all heritable variation is not suppressed within the manager or within the horizontal organization.

This contrasts with forms of organization in which the human group is primarily managed by a lower-level manager composed of genetic elements and/or of clusters of socialized behavior patterns--in these organizations the potential for competition within the manager is considerable, and it must be tightly controlled. Consequently, adaptation of the manager has to rely on differential success between groups, except in the limited circumstances when some variation within the lower-level manager can be successfully managed. (Rappaport [26] and Boehm [5] identify some arrangements within small human groups that could maintain the necessary control over competition while allowing some flexibility during the life of a group.) This difference in adaptive capacity is likely to have been a significant factor in the competitive superiority of human organization managed by an upper-level manager [29].

In this illustrative example, the hierarchical relationship is founded upon the capacity of the manager to use coercion to influence and constrain the horizontal organization without in turn being influenced by it. This hierarchical relationship is advantageous to the manager because it gives the manager the capacity to appropriate resources and services unilaterally that would otherwise be available to the horizontal organization. Significantly, this capacity to appropriate benefits also creates the potential for the manager to benefit from advantageous

cooperative arrangements, which it establishes by appropriate interventions: The capacity enables the manager to harvest benefits flowing from the cooperative arrangements. However, this potential will not be realized until interventions are discovered that enable the manager to promote cooperation, and unless the manager's association with the horizontal organization is sufficiently prolonged to enable it to harvest the benefits produced. The capacity of the manager to influence the horizontal organization unilaterally forms a basis for the development of these interventions that may, for example, entail selective punishment and the differential redistribution of appropriated resources.

As is necessary if this proposed evolutionary sequence is to be considered plausible and is to avoid the second-order problem, the individuals that participate in the sequence are not required to act other than in their direct individual interests at any phase of the sequence. In particular, the sequence envisages that the manager intervenes in the horizontal organization to promote cooperation only when the interventions produce net benefits to the manager. The second-order problem is avoided through the capacity of the manager to appropriate the wider benefits that flow to the organization from the cooperation that its interventions promote--unlike members of the horizontal organization that are limited by the second-order problem, the manager is not dependent on having to obtain net benefits from the interventions themselves.

Consideration of other forms of hierarchical human organization indicates that the required capacity of the manager to influence the horizontal organization can be initially established other than by coercion: Examples can be readily found where it is established by informed consent arising from common interests within the relevant horizontal organization (e.g., voluntary associations), or by manipulated consent of the horizontal organization (e.g., religious cults), or by combinations of informed consent, manipulation, and force. However, irrespective of its initial basis, if the manager is to be capable of optimally managing the horizontal organization in the interests of the organization as a whole, the manager must have sufficient power, scale, and scope to act across the organization to influence the interests of its members in the domain covered by the organization: To the extent that it is unable to deter cheating across the organization (e.g., by fines, imprisonment, or execution) or to promote beneficial cooperation across the organization (e.g., by paying employees, providing awards, or conferring status), the interests of the organization will not be maximized. Beneficial management will also be impaired to the extent that the access of the manager to benefits is not dependent on the manager managing in the interests of the organization as a whole: For example, policing will tend to fail to the extent that police can obtain benefits (e.g., bribes) from the horizontal organization they manage; an executive may get too close to his or her staff (i.e., may value the esteem of staff more than some incentives offered by the organization); and a bureaucrat may be able to avoid

accountability to the organization as a whole.

It should also be noted that in modern huma organization, lower-level management as well as upper-level management is often operative in creating the conditions for the emergence of cooperative organization: For example, it has long been recognized that socialized behavior patterns (lower-level management) that produce trust and honesty in individuals participating in economic exchange relations can reduce the incidence of cheating and lessen the need for its control by upper-level management (e.g., see [35]).

4.3 The Evolution of RNA Management of Molecular Processes

As a further illustrative example, consider a horizontal organization at the molecular level that comprises an autocatalytic set of proteins. Single self-replicating RNA molecules or small groups of RNA molecules that are autocatalytic in combination may be able to manage (appropriate) some of the metabolic constituents of the protein-based autocatalytic set to maintain themselves and reproduce. The RNA may also discover the capacity to catalyze particular processes within the autocatalytic set that directly assist the maintenance or reproduction of the RNA. In this way, an RNA upper-level manager of sufficient size and stability would stand outside the competitive interactions and exchange relations of the horizontal organization, managing them for its own benefit. The RNA could move from organization to organization, draining them of resources and services.

As for the example of human organization, the capacity of the RNA upper-level manager to manage the horizontal organization also creates the potential for it to intervene in a way that promotes beneficial cooperative arrangements and to harvest the benefit of any cooperative arrangements that are promoted in this way. For example, the RNA might catalyze a protein that provides benefits to other members of the autocatalytic set, but which itself receives no benefits in return, and which would be an altruist in the absence of support from the RNA; and the RNA might catalyze a process that inhibits the reproduction within the autocatalytic set of a cheat or freeloader that takes benefits from the set without providing any benefits in return (the capacity for cheating and competition to prevent optimal cooperation in autocatalytic organization in the same way as in other horizontal organization is dealt with in detail by Maynard Smith [23], Bresch et al. [7], and Bagley and Farmer [4]). Once this potential is realized, the RNA manager would find advantage not only in harvesting the horizontal organization, but also in managing and intervening in the horizontal organization to make available greater benefits for harvesting. The discovery of such arrangements is more likely when the manager and horizontal organization live in close association: The manager is more likely to be able to capture the benefits of any cooperation promoted by it the more prolonged its association with

the horizontal organization.

Again, the end result of this evolutionary sequence is a manager that has the capacity to enhance the competitive ability of the organization at the intergroup level, whose success and continued existence is dependent on the organization of which it is an obligate part, and whose evolutionary interests lie to a significant extent in using this capacity to promote the success of the organization as a whole. Once again we have an evolutionary sequence in which selection operating on the manager is progressively brought into alignment with selection operating at the level of the organization. However, in contrast to modern human organization, RNA does not have any internal capacity to adapt heritably, variation must be suppressed within the organization, and heritable adaptation must rely on between-group selection. Dyson [10] has proposed a similar evolutionary sequence for early cells, but without the general and unifying hierarchical perspective developed here.

5 Conclusion

If artificial life is to meet its central objective of synthesizing key biological phenomena, it must be able to synthesize entities that are organized as nested hierarchies and synthesize evolutionary transitions in which differentiated higher-level entities are formed from cooperative organizations of lower-level entities. This will necessitate the inclusion in alife systems of the processes of vertical self-organization to complement the processes of horizontal self-organization that have already been synthesized in some systems.

The particular way in which vertical organization is actually constituted in any specific case differs both within and between the various levels of organization, depending in each instance on contingencies such as what it is that determines the success of entities, and how entities can influence each other's success.

However, at a higher level of abstraction it is possible to identify the key structures and relationships that are common to the various instances of vertical organization that have been discussed above, and which would need to be incorporated or synthesized in an alife system for vertical organization to emerge. These are:

1. Horizontal organizations of adaptive agents (i.e., evolvable entities), with each organization constituted by relationships that arise and persist due to the capacity of the adaptive agents to engage in cooperative interactions within the organization in which the success of each agent participating in the interaction is increased (e.g., cooperation that is mutually or reciprocally beneficial);

2. Within each horizontal organization, the possibility of adaptive agents

arising that have the capacity either to:

(a) engage in interactions with other adaptive agents within the organization in which the success of the other agents is increased, but their own success is decreased (e.g., altruists); or

(b) engage in cooperative interactions with other adaptive agents within the organization without making any contribution to the interactions (e.g., cheats that do not reciprocate or do not contribute to mutualistic cooperation);

3. Managing adaptive agents associated with each horizontal organization, with each agent having the capacity to:

(a) engage in interactions with the agents of the horizontal organization in which the success of the managing agents is increased and the success of the agents of the horizontal organization is decreased (e.g., the unilateral appropriation of resources by the manager from across the horizontal organization); and

(b) engage in interactions differentially with agents of the horizontal organization in which the success of the agents of the horizontal organization is either increased or decreased, and the success of the managing agents is decreased (e.g., the capacity of the manager to intervene across the organization to support altruists or inhibit cheats); and

(c) exhibit adaptations that suppress differential success among the managing adaptive agents within the organization (e.g., recursive suppression of competition within the manager).

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