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The evolution of information in the major transitions

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Abstract

Maynard Smith and Szathmáry's analysis of the major transitions in evolution was based on changes in the way information is stored, transmitted and interpreted. With the exception of the transition to human linguistic societies, their discussion centred on changes in DNA and the genetic system. We argue that information transmitted by non-genetic means has played a key role in the major transitions, and that new and modified ways of transmitting non-DNA information resulted from them. We compare and attempt to categorise the major transitions, and suggest that the transition from RNA as both gene and enzyme to DNA as genetic material and proteins as enzymes may have been a double one. Unlike Maynard Smith and Szathmáry, we regard the emergence of the nervous system as a major transition. The evolution of a nervous system not only changed the way that information was transmitted between cells and profoundly altered the nature of the individuals in which it was present, it also led to a new type of heredity—social and cultural heredity—based on the transmission of behaviourally acquired information.

Keywords: Chemoton; Epigenetic inheritance; Neural organisms; Social learning; Species

1. Introduction

During the last 15 years of his rich and adventurous intellectual life, John Maynard Smith welded together within a single broad framework many of the most important themes in modern evolutionary theory. His book with Eörs Szathmáry, *The Major Transitions in Evolution* (1995), set the agenda for early 21st century evolutionary studies. This book focused on information (mainly genetic information), and explored its emergence in the ancient pre-DNA world, evolutionary modifications in its storage, the evolution of mechanisms of information transmission, and the new uses to which information was put during the history of life. The nature of biological information was also the subject of several of the papers Maynard Smith wrote in the later years of his life (Maynard Smith, 1999, 2000).

Our own interest in biological information stemmed from our studies of cellular epigenetic inheritance (Jablonka and Lamb, 1995), cultural inheritance in non-human animals (Avital and Jablonka, 2000), and human symbolic communication (Dor and Jablonka, 2000). Whereas Maynard Smith's discussions of information were centred around DNA and the genetic system, and he defended this focus in his conceptual work, we needed a notion of biological information that would encompass the inheritance of variations that are independent of variations in DNA. Our different views about the nature of the information that is important in evolution led to many fruitful exchanges and arguments with Maynard Smith, and in what follows we discuss some of these differences and develop some of our arguments further.

As a framework for our discussion, we will take the eight major transitions identified by Maynard Smith and Szathmáry (1995), which were: (1) from replicating molecules to populations of molecules in compartments (protocells); (2) from independent genes to chromosomes; (3) from RNA as both an information carrier and enzyme to DNA as the carrier of information and proteins as the enzymes; (4) from prokaryotes to eukaryotes; (5) from asexual clones to sexual populations; (6) from single-cell

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eukaryotes to multicellular organisms with differentiated cells; (7) from solitary individuals to colonies with non-reproductive castes; and (8) from primate societies to human societies with language. Maynard Smith and Szathmáry suggested that all of these transitions were associated with changes in the way that information is stored, transmitted or interpreted. They argued that higher-level entities could evolve through selection acting on lower-level units because the latter can benefit more by cooperating than by competing. Once an old entity became part of a higher level unit, it could no longer survive and reproduce independently because along with the emergence of the higher-level entity came mechanisms that ensured its stability and prevented it from disintegrating into its component parts.

The emergence of a new higher-level entity is not a criterion for all of the transitions Maynard Smith and Szathmáry enumerated. Whereas the majority led to an increase in complexity through the assembly of previously autonomously reproducing units, the third transition (which led to DNA as the hereditary material and proteins as enzymes) and the eighth transition (which led to linguistic societies) form a separate category. Neither of these transitions resulted in the emergence of a new, higher-level entity made of lower-level units. Rather, they led to the sophistication of the internal organization of an existing individual which enabled it to use and transmit a new type of information. The fifth transition, that which led to sexually reproducing organisms, is in a special category, because the types of entities that have emerged as a result of sex (i.e. sexual populations and species) are not individuals in the usual sense of the word—they are not cohesive, functionally integrated wholes that reproduce as a unit.

In our discussion of Maynard Smith and Szathmáry's transitions, we will use the categorization just suggested and focus on the inheritance of variations that are not based on differences in DNA sequences. We will argue that such variations and the systems underlying them coevolved with the genetic system, and were crucial in all eight transitions. We will also argue that because there was a serious omission in both our own and Maynard Smith and Szathmáry's analyses of the way changes in information transmission led to new levels of organization and new types of individuals, an additional major transition needs to be added to the list.

2. Types of information and the emergence of new evolving entities

Whereas Maynard Smith and Szathmáry (1995) see all evolution, from the emergence of the first DNA-based cells to the acquisition of language by hominids, in terms of changes in the genetic system, we have argued that new types of information and modifications of existing non-genetic information systems were fundamental to these transitions (Jablonka, 1994; Jablonka and Lamb, 1995, 2005). We believe that biological information should be seen in terms of the *interpretation* (or processing) of inputs, rather than as an inherent property of inputs, and is best defined in terms of the receiver system: a source becomes an informational input when an interpreting receiver can react to the form of the source (and variations in this form) in a functional manner (Jablonka, 2002; Jablonka and Lamb, 2005). According to this definition, the concept of information can be used only with reference to living (or designed-by-living) entities, yet it accommodates information stemming from non-living environmental cues as well as that from evolved signals. It recognizes and calls for a comparison between the processing and transmission systems associated with different types of informational inputs.

The transmission of information between generations, whether through reproduction or through communication, requires that a receiver interprets (or processes) an informational input from a sender who was previously a receiver. When the processing by the receiver leads to the reconstruction of the same or a slightly modified organization-state as that in the sender, and when variations in the sender's state lead to similar variations in the receiver, we can talk about the hereditary transmission of information. This typically occurs through reproduction, but it can also occur through communication if communication leads to a trait of one individual being reconstructed in another. Clearly, if the hereditary transmission of information is seen in this way, there is no need to assume that all hereditary variations and all evolution depend on DNA changes (see also Griesemer, 2000).

3. Multiple types of heredity in the pre-DNA world and the first transition

The Major Transitions begins with a pre-DNA world and its first self-reproducing entities. As is evident from Maynard Smith and Szathmáry's discussion of the information generated and embodied in these ancient reproducers, transmissible non-DNA information not only existed, but was a prerequisite for the stages that followed later and culminated in the evolution of a DNA-based genetic system. The nature of this non-DNA information and its transmission is particularly clear in their discussion of Gánti's chemoton, a theoretical protocell (Gánti, 2003).

Gánti's chemoton (Fig. 1) is made up of three autocatalytic subsystems, which are integrated in a way that makes a stable, functional entity with all the properties of life. It uses substances from the external environment, transforms them into the material of which it is composed, and exudes by-products; in other words, it metabolizes. It also grows and reproduces. At the core of the chemoton is the metabolic engine—an autocatalytic metabolic cycle that transforms nutrients into the substances needed in the other two subsystems and for its own reproduction. The second autocatalytic subsystem is a membrane system, in which products from the metabolic cycle are converted into

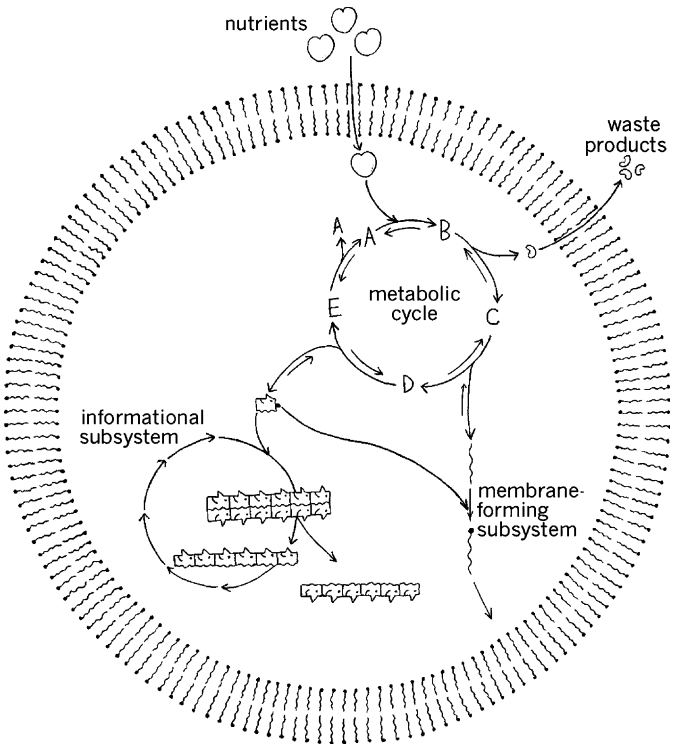

Fig. 1. Gánti's chemoton (based on Gánti, 2003, Fig. 1.1, p. 4). The autocatalytic metabolic cycle is a subsystem that uses nutrients to reproduce A, and in so doing produces waste products and the basic raw materials for both informational and membrane-forming subsystems. The links between the three autocatalytic subsystems mean that they grow and reproduce in a regulated, coordinated manner.

units that are spontaneously incorporated into the membrane that forms the boundary between the chemoton and its milieu. The third autocatalytic subsystem is one that carries information relevant to the whole system. It is a linear double-strand polymer made of molecular units that are another product of the core autocatalytic cycle. It grows and reproduces by the template-based addition (through a polycondensation reaction) of these units to the single 'strands' of the initially double-strand structure, thus forming two double-strand polymers. This template-based polymerization occurs only when the units that are components of the polymer reach a critical concentration. When this happens, the original polymer separates into two single structures, and the polymer components are consumed as they join to form the new double structures. The membrane system and the linear polymer are functionally linked because growth of the membrane depends on a by-product formed as the linear molecule polymerises. Eventually, when the membrane reaches a critical size, for physical reasons it becomes deformed, and this leads to fission.

The three autocatalytic subsystems of the chemoton form a unified system that displays heredity. The hereditary properties of the whole are affected by the linear polymer, because its length controls the number of turns of the metabolic cycle that are needed to produce the units necessary for its own reproduction and the production of the by-product needed for forming membrane units. Chemotons can vary: they can have different chemical cycles leading to different rates of production of components, or to chemically different membrane components that affect when fission occurs, or to different-length linear polymers. All such chemotons would breed true, so natural selection between them could occur. However, the most important (although highly constrained) source of hereditary variation is the length of the linear polymer, because this is the only subsystem in which variation need not involve a change in the chemical nature of the components, only a change in their organization. Variation in the length of the polymer would allow several hereditary variants in growth rates, whereas variations in the chemical cycle and membrane components would be more constrained by the special functions of these subsystems. Gánti showed that the constraints that limit heritable variability in the model shown in Fig. 1 are overcome if the linear polymer is made up of two types of unit rather than one, and hence its sequence, rather than its length, controls reproduction.

In the chemoton model, interactions between three chemical subsystems with autocatalytic self-sustaining and self-reproducing properties lead to the emergence of a biological system. How such a biological entity could have evolved has been the subject of much speculation. According to some schemes, the RNA-first models, an autocatalytic system based on template replication was the primary component, with RNA molecules acting as both replicators and enzymes; protein metabolic networks and membrane systems evolved later. Other models suggest that metabolic protein networks with surrounding membranes came first, and RNA-like systems evolved within them. These and other theories are well reviewed by Fry (2000). For our purposes, it is unimportant which of the theories is most likely to be correct, because it is what they have in common that we find most interesting. In almost all models it is assumed that at some point an RNA-based system took control, and the independent transmission of variations in metabolic functions and membrane structure was no longer possible. This assumption is rarely articulated or examined, and its validity can certainly be questioned. It is true that modern organisms could not exist without the genetic system, and all cell systems ultimately depend on DNA, but cellular elements such as membranes, prions, self-sustaining metabolic cycles, modified DNA bases, and various molecular marks attached to DNA all show heritable variation that is independent of variation in DNA base sequences. Whether the hereditary properties of these extant elements reflect an ancient origin, or whether they all evolved from scratch in the context of modern cells is an interesting but largely unexplored question. Whatever the answer, it seems clear that the evolution of the DNA sequences that now control the production of the components of these inherited cellular elements must have been guided by the functional requirements of the ancient

metabolic and membrane systems that existed before nucleic acids took overall control.

As we see it, both theoretical and empirical studies suggest that from the very beginning of life there were different types of self-producing systems, each with the potential to vary. It was the integration and coevolution of such systems that underlay the first transition and eventually led to life based on nucleic acids. Subsequently, changes in nucleic-acid-based heredity were always accompanied by and coevolved with other elements and functions that displayed variation and hereditary continuity. In other words, not only did the nucleic acid system of information transmission evolve, so too did other, epigenetic, inheritance systems, and all contributed to the major transitions.

4. Transitions to new levels of organization: the evolution of chromosomes, eukaryotic cells, multicellular organisms, and social groups

In each of these transitions, entities that reproduced autonomously before the transition became part of an assembly of similar entities that formed a new functioning whole. The original entities lost their ability to reproduce independently, and the new whole, the higher-level entity, became the unit of reproduction. Its stability was assured by the division of labour that led to the obligatory interdependence of the component units, and by the evolution of various policing mechanisms that prevented them from behaving autonomously. We believe that in all of these transitions, the transmission of non-DNA information played a key role, particularly in ensuring the evolutionary stability of the new entity.

4.1. From genes to chromosomes: genetic and epigenetic coevolution

Maynard Smith and Szathmáry provided a convincing explanation of why, during the evolution of protocells, selection favoured independent genes becoming linked together. They argued that the higher-level unit, the chromosome, was selected because it eliminated intracellular competition between the component genes by synchronizing their replication; it also ensured the complementation of genes that enhanced fitness in daughter cells. However, although satisfying, this explanation does not go far towards explaining the evolution of the type of chromosomes found in cells today. In these, very long DNA molecules are closely associated with many kinds of protein and RNA.

We have previously argued that in early evolution, as DNA sequences were linked together or were added by duplication, there would have been selection for organizing and packaging the lengthening molecules in ways that protected them, allowed them to be replicated, and left sequences available for transcription. As a result of this selection, various proteins that provided support, protection, and anchoring systems became closely associated with DNA. Critically, we believe, the selection of these elements was such as to enable existing states of gene activity to be rapidly re-established after cell division and allow continuous functioning (Jablonka and Lamb, 2005). Theoretical models have shown that, in the conditions likely to have been experienced by early unicells, it would have been an advantage for daughter cells to inherit the phenotype of their parent (Lachmann and Jablonka, 1996). Selection would therefore have favoured chromatin-marking systems, i.e. inherited non-DNA components of chromosomes that would enable the rapid reconstruction of the existing states of gene activity following DNA replication and cell division.

Nothing much is known about this aspect of chromosome evolution. In eukaryotes, whose nuclear DNA is associated with histones and a whole battery of other proteins and RNA molecules, it is fairly obvious that DNA sequences and the non-DNA chromatin components must have coevolved. It is equally clear that heritable chromatin marks (e.g. transmitted DNA methylation patterns and histone modifications) have been important in this evolution. However, although it is now generally recognized that DNA sequences are not the only source of information in chromosomes, how chromatin and chromatin marking evolved has been a neglected aspect of chromosome evolution. The only chromatin marking system that has received attention from evolutionary biologists is that involving DNA methylation, which has been variously interpreted as a modification of a system that originally defended cells against genomic parasites (Bestor, 1990; Bird, 1995), or as an early regulator of gene expression that in some organisms assumed a role in cell memory (Jablonka and Lamb, 1995; Regev et al., 1998).

4.2. From prokaryotes to eukaryotic cells: how important was epigenetic inheritance?

The evolution of eukaryotic cells from prokaryotic ancestors involved the loss of a rigid cell wall and the acquisition of a cytoskeleton, organelles, a nucleus, and a set of internal and external membranes. The way genetic information was stored and transmitted was transformed: in eukaryotes most DNA is located in nuclear chromosomes, which have multiple replication origins, and are distributed to daughter cells through the elaborate process of mitosis by means of which each cell receives an identical set of genes. According to Maynard Smith and Szathmáry (1995), the events involved in the transition may have been initiated by the loss of the prokaryote's rigid cell wall, and almost certainly involved a symbiotic association between such a proto-eukaryote and several formerly independent prokaryotic cells, which in time became the mitochondria, chloroplasts, and possibly other organelles.

We believe that epigenetic inheritance, particularly that based on structural–templating mechanisms, was essential for this transition. Many years ago, work on the inheritance of cortical variations in ciliates led some people

to suggest that many supramolecular cell structures are reproduced by three-dimensional templating mechanisms based on some kind of topological complementarity (reviewed by Nanney, 1968). This type of reconstruction was termed 'guided assembly' by Grimes and Aufderheide (1991), who discussed the generality of the process and its importance in cell heredity (see also Jablonka and Lamb, 1995). Guided assembly seems to underlie not only the reconstruction of the cortical structures of ciliates, but also, in all cells, the reconstruction of the cytoskeleton and centrosomes, which play a central role in the formation of the mitotic spindle. Although centrosomes seem to be able to form spontaneously, usually their assembly is guided by existing centrosomes. This means that variations in the size, number and nucleation capacity of centrosomes can be inherited in cell lineages (Salisbury, 2001).

Centrosomes are not the only variable cell structures that show hereditary continuity: cell membranes form only in association with pre-existing membranes of the same kind (Cavalier-Smith, 2004). As a membrane grows, proteins that mark the identity of the membrane-type ensure that it is the target for the incorporation of similar membrane proteins, so the membrane 'breeds true'. Cavalier-Smith has identified 18 such hereditary membranes, and argued convincingly that their loss and gain were rare but crucial events in cell evolution. The incorporation of the prokaryotic cells that became the organelles of eukaryotic cells probably depended on the ability of the organelles-to-be to preserve the structure of their particular membrane systems through guided assembly.

There seems to be little doubt that during the transition to eukaryotic cells, as cell architecture and cell division became more complex, mechanisms that provided structural continuity assumed greater importance and coevolved with the genetic system. Without reliable structural inheritance, the transition would not have been possible: the internal skeleton that was necessary after the prokaryotic cell wall was lost, the structural elements necessary for mitosis, and the construction of the membranes of the cell and its organelles, all depend on information transmitted through guided assembly.

4.3. The evolution of multicellularity: the epigenetic view of the transition

The transition to multicellularity occurred several times (Bonner, 1988), but the most interesting of the transitions are those that led to present-day plants, animals and fungi. In these, a division of labour between genetically identical component cells has resulted in many interdependent, phenotypically different cell-types. Because the determined and differentiated states of these are inherited in cell lineages, the importance of non-DNA information transmission (epigenetic inheritance or 'cell memory') in the evolution of complex multicellular organisms has been widely recognized (e.g. see Jablonka, 1994; Jablonka and Lamb, 1995; Maynard Smith and Szathmáry, 1995; Wolpert, 1990).

There is good evidence (reviewed in Jablonka and Lamb, 1995) that unicells transmit non-DNA information about their structure and state of activity to daughter cells, so it can be assumed that during the evolution of multicellular organisms, transmission mechanisms that existed in ancient unicells were recruited and selectively modified in ways that improved their efficiency and fidelity. Without efficient transmission of epigenetic information, the component cells of new multicellular organisms would have switched to inappropriate states that would have compromised the success of the individual as a whole. Epigenetic inheritance is thus one of the reasons why multicellular plants and animals retained their coherence in spite of the turnover of their component cells, and the evolution of many aspects of their development makes more sense when the role of epigenetic inheritance is recognized.

The integrity of multicellular organisms depends on their cells cooperating rather than competing. Often the division of labour between them means that most cells forgo the opportunity to contribute to the next generation of organisms, leaving this to sister-cells in the germ line. Yet, potentially, since almost all cells have the same genetic information, any cell could compete for germ line status. One reason why many of them cannot do so successfully is that their determination and differentiation have given them inappropriate *epigenetic* information. This has to be erased before they can be effective as germ cells, and as we know from the attempts to clone mammals, removing developmental legacies and restoring cells to an uncommitted state is not easy: even on the rare occasions when cloning is successful, the animals produced are often abnormal (Solter, 2000). The difficulty in restoring totipotency may be a consequence of the complexity of mammalian development, because as the number of specialized cell-types increased during evolution, the number of epigenetic switches required to produce them increased too. Although in simple organisms with few cell-types and few developmental switches it might be easy to reverse epigenetic changes and restore cells to an uncommitted state, reversing or removing all traces of the whole sequence of events that gave rise to the differentiated cells of complex metazoans is likely to be much more difficult and error-prone. Mistakes would jeopardize the development of any organism that was produced from a former somatic cell. Consequently, there would be strong selection for mechanisms that prevent somatic cells from changing roles and becoming germ cells. Such selection may be one of the reasons why the de-differentiation of most specialized cells is effectively impossible.

We have argued previously that there are other features of development that are probably outcomes of selection against allowing cells with inappropriate epigenetic marks to become germ cells (Jablonka and Lamb, 1995). For example, it may be the evolutionary reason why, in many animals, the germ cell lineage is segregated very early in

embryogenesis and remains quiescent, dividing infrequently, throughout the rest of development. The advantage of this early segregation is that the future germ cells have very little epigenetic memory to erase, and there is little chance of them acquiring new heritable epigenetic variants (epimutations). Physical segregation of the germ line also makes it less likely that errant somatic cells will be in a position to contribute to the next generation.

Recently, Lachmann and Sella (2003) have suggested that the evolution of a distinct germ line could itself have occurred through an epigenetically mediated route. They have presented models that show how the transmission of epigenetic information between generations of simple multicellular organisms can lead to a division of labour in which some cells make no contribution to the progeny, i.e. it can lead to a germ line–soma distinction. In their simplest model, a multicellular organism in which all cells are genetically identical is made up of two types of cell, A and B, which are epigenetically different. Organisms with these two cell-types function well as a whole, and when reproduction occurs, both types A and B can act as single-cell spores. Each can recreate the whole A + B organism, because as well as giving rise to cells of its own epigenotype, a daughter cell can differentiate into the other epigenotype. Occasionally, Lachmann and Sella suggest, a new epimutation, A′, arises. This epimutation improves the functioning of the whole organism (A′ + B). However, although A′ cells can form both A′ and B cells, A′ cannot itself be recreated from B spores, which therefore continue to recreate A + B organisms. In these circumstances, selection will lead to either (i) the loss of A′ and the restoration the original situation, or (ii) the invasion of a mutation or epimutation that is able to enable both A′ and B spores to differentiate into A′ + B, or (iii) the transfer of resources from B cells, which cannot recreate the whole A′ + B organism, to A′ cells, which can. If the third path is taken, not only will the A′ + B organism take over, but the evolution of germ line–soma differentiation will have taken place.

Even if the origin of the germ line–soma distinction was not by the type of epigenetic path that Lachmann and Sella suggest, we have no doubt that the emergence of stable, complex multicellular organisms and the evolutionary shaping of their development was strongly influenced by epigenetic inheritance. The efficiency of cell memory, the stability of the differentiated state, the extent of selection and cell death among somatic cells, the segregation between soma and germ line, and the massive restructuring of chromatin that occurs during the production of gametes were all shaped partly by the effects of epigenetic inheritance, and epigenetic inheritance systems were shaped by the evolution of development (Jablonka and Lamb, 1995). We believe it is impossible to understand the emergence and the evolution of multicellular organisms without taking epigenetic inheritance and the genetics of epigenetics into account.

4.4. The evolution of social groups: the integrating role of social learning

The origin of the social groups in which there is a division of labour that involves some individuals giving up reproduction is seen by Maynard Smith and Szathmáry (1995) as one of the major transitions in evolution. Certainly, how the seemingly altruistic behaviour seen in these societies evolved and why it is maintained have been prominent and controversial issues in evolutionary biology, and in his own theoretical work Maynard Smith made many important contributions to the debate. In *The Major Transitions*, he and Szathmáry discussed explanations of altruism that are based on kinship, on enforcement, and on reciprocity. The models they considered are all essentially gene based: this is explicit with kinship and enforcement models, and even though explanations in terms of game theory do not demand a genetic basis for the various behavioural strategies they incorporate, they are assumed to have genetic underpinnings.

The transition to a social way of life in which group members cooperate rather than compete has happened many times, but, for reasons that are easy to understand, evolutionary biologists have focused their theorizing mainly on the extreme, eusocial groups, in which some individuals do not breed at all. For the origins and stability of these societies, gene-based theories have provided plausible, albeit incomplete, explanations. There have been other, less dramatic, transitions to a social way of life, however. In many social groups, socially learned cooperative behaviours increase the productivity of the individuals in the group relative to that of animals that are not group members, yet the evolutionary effects of such behaviourally transmitted information have rarely been explored. In general, it has been assumed that information transmission through social learning cannot lead to the establishment of group properties that are robust enough to lead to effective selection among groups.

This assumption has been challenged by Avital and Jablonka (2000). Although their arguments were based mainly on data from birds and mammals, they believe they may also be valid for other groups, including social insects. They argued that there are many ways in which social learning can lead to the functional cohesion of a group of animals, and that in birds and mammals the survival of social groups is completely dependent upon the ability of their members to learn from others and transmit socially learned information. When these information transmission mechanisms collapse, the groups disintegrate and ‘social death’ occurs (Calhoun, 1973). Without social learning, it is very unlikely that social groups of birds and mammals could have evolved at all.

Avital and Jablonka maintain that social learning often leads to the establishment of group traditions, and these traditions are not always as ephemeral as is commonly supposed. They suggested that they persist because mutually supporting feedback loops between different

learned behaviours can stabilize the whole behavioural repertoire and life-style of the group. When different traditions lead to differences in group productivity and proliferation, or alter the chances of extinction, group selection and evolution based on socially learned traditions occurs. Hence, social learning has two main effects: it is a precondition for the evolution of the complex social groups found in mammals and birds, and it allows cultural evolution within the groups that can be the basis for selection between them. Cultural evolution may lead to traditions that result in even more effective communication within the group, and even more interdependence and altruism among group members.

The notion that information transmitted through socially learned behaviour has been important in the evolution of some animal societies leads to a broader and more inclusive view of the transition to sociality, because it makes it possible to see the origin and stability of all types of social groups in similar terms. The essence of many explanations of the transition to a stable social group is that it was possible because genetic relatedness meant that individuals all had copies of the genes that resulted in some behaving altruistically. The explanation offered by Avital and Jablonka suggests that in some cases it is the behavioural relatedness that is important—that groups evolve and retain their coherence when, through social learning, their members possess the same behavioural information. In general, it seems that the transition to a stable social group requires that the individuals that form it have to inherit the same behavioural information, but this information need not be transmitted through DNA; it can also be transmitted through social learning.

5. The unique status of the transition to sex

Cellular epigenetic inheritance may have been important in the evolution of genetic recombination and meiosis (De la Casa-Espéron and Sapienza, 2003; Holliday, 1984; Jablonka and Lamb, 1995), and hence in the origin of sex, but this is not the aspect of the transition that we want to discuss here. Instead we want to look at how the transition to sexual reproduction affected information transmission, and what the consequences of the changes it made were.

Sexual reproduction makes the gene, rather than the whole genotype, the unit of transmission, and changes the probability that a particular parental gene will be present in a particular offspring from nearly 100% to 50%. Importantly, as a result of sex, organisms from different lineages can communicate genetically—they can exchange genetic information. Whereas before the transition genetic information was transmitted only (or mainly) vertically within lineages, after the transition the whole population, made up of multiple lineages, becomes the unit in which information is exchanged and transmitted. Communication between individuals becomes obligatory in sexual reproduction.

The result of the transition to sexual reproduction is the emergence of two new entities – the sexual population, which is defined by the ability of its members to engage in genetic exchange, and the species, which is the population of populations that can potentially engage is such exchange. The emergence of these new entities is a transition to a higher level of organization, in the sense that individuals within a population can no longer reproduce independently, but depend on others. However, the outcome of the transition is not a new level of individuality, because this would require that the population is a cohesive, functionally integrated whole that reproduces as a unit and is systematically a target of selection. It is not. Nevertheless, a new unit of evolution, the sexual species, does emerge from the transition.

The formation of a new unit involves, by definition, the creation of new boundaries, which in the present case are the boundaries of genetic information exchange. Populations that do not share genetic information evolve independently and in time may diverge. Reproductive isolation—the absence of genetic exchange—is a criterion for sexual species distinction. It may be the outcome of pre-zygotic features that prevent members of two populations mating, or of post-zygotic problems that lead to abnormal development or sterility in the offspring of any matings that do occur. However, whether it is pre-zygotic or post-zygotic, reproductive isolation is a result of the *phenotypic* properties of individuals, and differences in phenotypes are not always caused by differences in genotype. This means that the boundaries to gene exchange need not themselves be based on genetic differences. The inability of individuals from different populations to interbreed can also be the result of incompatibilities in their epigenetic or behavioural heritage: differences in chromatin marks can lead to hybrid sterility or inviability, and behaviourally transmitted information (e.g. about courtship sites or songs) can prevent would-be mates meeting and mating (Avital and Jablonka, 2000; Jablonka and Lamb, 1995, 2005). Consequently, even though sexual species are defined in terms of genetic information exchange, the creation of the barriers that prevent gene exchange and lead to the formation of new species may be initiated by heritable epigenetic and behavioural variations.

6. Transitions to new types of individuals with novel systems of information transmission: the evolution of DNA and its translation, and of symbolic language

This type of transition has not led to a new higher level of organization: the cell that is DNA-based and has a translation machinery is still a single cell, and the linguistic community is still a social group. However, in both transitions, a new type of information and associated processing system evolved, and altered the activities of existing entities in ways that had profound effects on their development and evolution.

6.1. The evolution of DNA and of translation: a double transition?

The transition to cells in which DNA transmits information and proteins act as enzymes involved the evolution of a complicated set of interrelated processes. The most difficult to envisage is the origin of the genetic code and translation, and Maynard Smith and Szathmáry focused on this aspect of the transition. They suggested that short runs of amino acids became associated with RNA enzymes (ribozymes) and initially acted as cofactors, enhancing the catalytic efficiency and chemical range of the ribozymes. Gradually, with the assistance of other ribozymes with amino acid cofactors, longer RNA–oligopeptide complexes were formed. Eventually, the enzymatic activity of these oligopeptides became spatially and functionally independent of their RNA, and the RNAs that assisted in their formation evolved to have their present tRNA, mRNA, and rRNA functions.

The details of the scenario just outlined suggest a plausible evolutionary route to coding and translation, but there is no indication of how, why or when DNA replaced RNA as the genetic material. The replacement was probably associated with DNA's greater stability, which may have become increasingly important as genes were linked together and nucleic acid molecules got longer, but at what stage in the transition did it occur? It seems to us that the best way to view the transition to cells with DNA as the genetic material and proteins as enzymes is as double one. Either the evolution of the genetic code and translation followed an earlier transition from RNA to DNA as the genetic material, or, as is more commonly assumed, coding evolved first and was followed by the transition to DNA as information carrier (Poole et al., 1999; Szathmáry, 1993).

For DNA to become the main genetic material, there had to be mechanisms for replicating it and transcribing it into RNA, but both of these processes probably evolved through relatively straightforward modifications of the existing mechanisms of RNA replication. The advantage of these modifications would be that whereas, before the evolution of DNA replication and transcription, RNA was both the genetic material and had an enzyme role, after it there could be a division of labour, with DNA assuming the major hereditary role and RNA specializing in enzymatic and regulatory functions. If we adopt the scenario in which DNA evolved before coding, then we can assume that as RNA abandoned its role in heredity and acquired more extensive enzymatic and regulatory functions, it recruited various other molecules, such as amino acids and peptides, for better performance of these functions. This would then have been the starting point of the transition to the genetic code and translation. It may be significant that in present-day eukaryotic genomes only a very small fraction of the DNA codes for proteins, although a lot is transcribed into RNA. More and more functions—enzymatic as well as regulatory—are being attributed to these RNA molecules. Moreover, it seems increasingly likely that the replication of RNAs is ubiquitous in eukaryotes, and the main DNA inheritance system exists sides by side with a complementary RNA system, in which RNA retains a dual role as hereditary material and enzyme/regulator. It begins to look as if we, the eukaryotes, are still living in a largely RNA world!

There are many tempting speculations one can make about what we have described as a double transition. For example, are the small RNAs associated with the RNAi systems, which in present-day cells constitute epigenetic inheritance and cellular immune systems, a relict of the ancient RNA world? What was the nature of the first protein enzymes? Were they selected to have self templating, prion-like, properties, because that would have given them greater structural and functional stability in a cellular world in which the specificity of translation was still low? Whatever the answer to these questions, it seems that the transition to cells with DNA as the genetic material and proteins as enzymes went through two stages: first the division of labour between DNA (hereditary material) and RNA (enzymes and regulators), and then the evolution of coding and translation. Each of these stages was fundamental, and we believe that the relicts of the first part of the transition are to be seen in the roles RNA molecules now have in enzymatic and regulatory functions in present-day cells.

6.2. The evolution of language

The transition to human societies with linguistic communication required changes in anatomy and sensorimotor systems and an increase in cognitive ability, but the part of the transition that is most difficult to explain is how humans acquired the capacity to quickly master the complex rules of grammar when young. We have suggested previously how this competence for language could have emerged through the coevolution of genes and culture (Dor and Jablonka, 2000; Jablonka and Lamb, 2005). Initially, we suggested, all of the elements that hominids used to communicate with each other had to be learnt, i.e. all 'language' information was transmitted through social learning. However, as communication acquired greater significance for the group, there was strong selection for the ability to learn elements of the language quickly and accurately. The result was partial genetic assimilation of the basis of these elements. We do not want to go into all the details of the evolutionary process we have suggested, because the point we want to make here is a very simple and obvious one. It is that, as with all the other transitions, it is impossible to understand the evolution of the new type of individual (the community of linguistically endowed humans) without accepting that non-genetic information transmission (in this case cultural transmission) played a significant role.

7. Neural information: the big omission

We have argued that in two of the major transitions—the evolution of social groups and the evolution of linguistic communities—learning through and from others had a key role. Such social learning, like most forms of learning, requires a nervous system, so the evolution of the nervous system and the processing of neural information were preconditions for the transitions that depended on behavioural transmission. However, neither in Maynard Smith and Szathmáry's analysis nor in our own was much attention given to the nervous system. This is strange, because if the hallmark of a transition is a change in the way information is stored, transmitted and processed, then the emergence of the nervous system, a system that transmits a new type of information (neural information), should surely be seen as one of the most important transitions in evolution. Since the nervous system is a key distinguishing feature of metazoans, failing to recognize its evolution as a major transition is even more surprising.

The reason why the authors of this paper overlooked the nervous system is because the transmission and processing of neural information occurs *within* an individual, and our focus has been on the types of transmission that occur *between* individuals. However, this is not a very good reason. Neural processing, which started with nerve nets in simple diploblastic animals like *Hydra*, was certainly a new way of transmitting information among cells, with far-reaching evolutionary consequences. Its specificity and speed, and its potential for integration and memory storage, were far greater than that of intercellular communication systems based on hormones.

In the nervous system, information is encoded and transmitted as electrical signals that are fired along neurons which interact with various receptor and effector cells. Firing (sender) neurons release chemical neurotransmitters, of which there are several kinds, and each target (receiver) cell can combine and interpret the signals relayed by the neurotransmitters in a way that allows them to have different meanings in different places. The flexibility of many of the interactions and interconnections between neurons allows variant local neural circuits to be formed; with even a small number of interlinked elements (nerve cells) and a small number of potential connector sites (terminal branches and dendrites), the number of possible circuits is enormous. Circuits can be embedded within circuits, and circuits can communicate laterally, with both negative and positive feedback relations within and between them. Hence, through the construction of the circuits that link them, there can be a very rich mapping between inputs and responses. The structure of the system also allows partially active circuits, which may represent latent memory states that later can readily be made fully active.

Through the evolution of a nervous system, the extent and scope of information transmission, processing, and storage was greatly increased, and the result was the emergence of a new type of individual, the neural individual, with a high level of internal integration and the ability to make rapid adaptive responses. However, the emergence of the neural individual meant more than a change in the nature and speed of adaptation. Neural processing led to behaviour based on sensory perception, and this in turn led to a form of communication between individuals that did not require contact or the transmission of physical material from one to the other. This mode of information transmission had interesting consequences, one of which was the ability of animals to learn from others through perceiving their behaviour or the outcomes of their behaviour, i.e. it led to social learning. When the process of learning from others continues across generations, a form of behavioural inheritance emerges. In other words, the evolution of neural information led to a new type of communication between individuals, and to a new way of transmitting information from one generation to the next. Both the transition to social groups and the transition to linguistic communities are based on the evolution of neural individuals.

8. Summary and conclusions

In Table 1 we have summarized our view of how different types of information are involved in Maynard Smith and Szathmáry's (1995) 'major transitions'. For reasons given earlier, we have subdivided the transition that led to the genetic code and translation. However, we have not divided the first transition, which led to the emergence of protocells, because although its complexity suggests that several different types of change occurred, exactly how it should be split is unclear. The table includes the transition to organisms with a nervous system, which was not on Maynard Smith and Szathmáry's list, because the nervous system had such profound effects on information transmission both within and between organisms that we believe it must rank as a major transition. There are interesting similarities, which can be seen in the table, between the outcomes of the emergence of the nervous system and the transition to DNA and translation, in both of which the interpretation of information involves decoding processes.

The table shows that although the transitions share some features, each has a combination that makes it unique. Two broad categories were identified earlier—the transitions that led to a new type of individual made up of units that previously reproduced autonomously, and those that led to the sophistication of the internal organization and information processing of an individual. There are differences within each of these categories, however, and the transition to sexually reproducing organisms does not fit comfortably in either. Because of sex, individuals become dependent on each other, so there is a new level of organization, but the result of the transition is not a new type of unit that functions as a whole. It is also difficult to categorize the first transition, which resulted in protocells. In a sense it

Table 1
Information changes and the major transitions

Transition	New unit made up of previously autonomous units?	Additional type of hereditary information?	Change in transmission between generations?	New type of information storage?	New type of functioning whole?	Types of coevolving inheritance systems
From replicating molecules to molecules in compartments	Yes (protocell)	Possibly (as different autocatalytic systems are integrated)	Yes (replicating molecules transmitted as groups)	Yes (in protocells)	Yes (protocell)	Different autocatalytic systems
From independent genes to chromosomes[a]	Yes (chromosome)	No	Yes (genes transmitted synchronously in linked groups)	Yes (in chromosomes)	Yes (chromosome)	Genetic + epigenetic
From RNA to DNA + RNA (no proteins)	No (but increased internal division of labour)	Yes (DNA)	Yes (DNA replication)	Yes (in DNA)	Yes (cell with DNA)	Genetic + epigenetic
From DNA + RNA to the genetic code and proteins	No (but increased internal division of labour)	No	No	Yes (as a code)	Yes (cell with translation)	Genetic + epigenetic
From prokaryotes to eukaryotes	Yes (eukaryotic cell)	No	Yes (coordinated reproduction of the new unit)	No	Yes (eukaryotic cell)	Genetic + epigenetic
From asexual clones to sexual populations	Yes (population and species)	No	Yes (segregation and recombination)	Yes (in populations)	No	Genetic + epigenetic
From single-cells to complex multicellular organisms	Yes (multicellular organism)	No	No (but chemical communication among cells and sometimes among individuals)	Yes (in differentiated gametes)	Yes (multicellular organism)	Genetic + epigenetic
From a chemically integrated to neurally integrated individuals	No (but increased internal division of labour)	No (but hereditary potential greater)	No (but neural communication among cells, and eventually among individuals)	Yes (encoded in neural impulses and circuits)	Yes (animal with a nervous system)	Genetic + epigenetic (+ sometimes behavioural)
From solitary individuals to colonies and social groups	Yes (integrated group)	Yes (socially acquired and transmitted information)	Yes (through social learning)	Yes (in social networks)	Yes (social group)	Genetic + epigenetic + behavioural
From primate groups to human linguistic communities	No (but increased internal division of labour)	Yes (symbolic information)	Yes (through linguistic communication)	Yes (in symbolic networks)	Yes (linguistic society)	Genetic + epigenetic + behavioural + symbolic

[a]The initial stages of the transition from unlinked genes to chromosomes probably occurred before the evolution of DNA as the genetic material; however, since later evolution involved DNA-containing chromosomes, this part of the transition should really follow rather than precede the transition to DNA.

was a transition to a higher level of organization through the integration of component units, but unlike the transitions to chromosomes, eukaryotic cells, multicellular organisms, and social groups, the components were not all of the same type. The transition that led to the protocell involved the integration of fundamentally different autocatalytic systems. This makes it very different from all other transitions.

In the final column of the table we have indicated the types of coevolving inheritance system that were involved in each transition. As we have argued throughout this paper, non-genetic information contributed to, and was changed by, all of the transitions, so seeing them solely in terms of what happened to and through DNA leaves out too much. In particular, a DNA-centred view of information transmission means that there is no role for instructive processes in evolutionary theorising, other than in the evolution of human societies. Our view, which incorporates information transmitted through epigenetic inheritance and by behavioural means, makes developmental, instructive mechanisms part of all evolutionary changes, including those that resulted in transitions to new types of entities with new ways of storing, transmitting and using information.

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