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Evolution and Cognition

Prometheus and Proteus: the creative, unpredictable individual in evolution

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> "On aime à deviner les autres, mais l'on n'aime pas à être deviné"
> (We relish seeing through others, but not being seen through)
> La Rochefoucauld, Maxim # 632

Summary. Evolutionary theory usually neglects two variables: the changes induced in the environment by the evolving organism, and individual uniqueness in sexually reproducing species. In order to fuel its maintenance and reproduction, an organism must average a positive net energy balance vis-a-vis its environment. It achieves this via aptations, which consist of information (i.e., the internalization of all that is predictable about the environment, including the machinery to take advantage of this information) and stored energy (to operate the machinery, including a safety margin to deal with events that are unpredictable in principle). Taking advantage of a prediction, however, interferes with what has been predicted; each adaptation by the organism therefore changes its environmental target. Today's organism is adapted to yesterday's environment, and today's predator inherits yesterday's prey image. This paper attempts to show that, over evolutionary time, the persistence of this asymmetric, time-lagged relationship is owed increasingly to genetically unique individuals.

Individual uniqueness as resulting from sexual reproduction is janus-faced. It endows an evolving population with both a forward-looking (promethean) and backward-looking (protean) feature. A population made up of genetically unique individuals is promethean (creative) in its ability to exploit non-homogeneous resources and respond serendipitously to environmental change via new genotypes; it is protean (elusive) in presenting a pursuer (predator or parasite) with a scattered target. Furthermore, because of the asymmetry between the winnowing of the target gene pool by the pursuer, and the genetic fixation in the pursuer of an outdated target image, the target keeps evolving away from the pursuer at a speed and in a direction that are a function of the pursuer's success. This mechanism ensures an evolutionary time lag between pursuer and target, which explains escalation, the stability of asymmetric coevolutionary systems such as the life/dinner principle, and the pervasiveness of the Red Queen effect. Individuality thus both promotes and retards the speed of evolution. Having probably originated simultaneously with predation, sex-generated individuality is a self-accelerating evolutionary process that may account for much of today's organismic and environmental complexity.

Key words. Evolution, adaptation, information, energy flow, individuality, complexity, sexual reproduction.

Introduction: Problems and hypotheses

Almost as a rule, evolutionary theory ignores or belittles two factors. One is the change that an organism, by the very process of evolving, may inflict on its living and non-living environment. The other is individual uniqueness as brought about by sexual reproduction, i.e., the fact that in a sexually reproducing population no two individuals (except identical twins) are identical in their genotypes, and even less so in their phenotypes. Both factors merge in the view that each organism is also environment to other organisms; it is both center and periphery, in ecological as much as in evolutionary time. Can evolutionary theory benefit from being restated in these terms?

Of the many possible reasons why the dialectic relationship between organism and environment, and the uniqueness of individual organisms have been neglected, the following come to mind:

1. Expediency in emphasizing what appears essential, at the expense of what appears incidental; i.e., a carry-over of idealistic-newtonian thinking that stresses equilibrium over non-equilibrium, symmetry over asymmetry, the probable over the improbable, the predictable over the non-predictable, the species over the individual. (Not unexpectedly, this human urge to press unique events into categories follows the very pattern of information gathering that is the central theme of this paper.)

2. A historical tendency to think of an organism's environment as exclusively or mostly physical, remotely controlled (e.g., by the sun) and therefore unresponsive; hence a tendency to ignore the short- or long-term feedback effects that an organism's behavior and evolution may have on the environment. Indeed, how could a shivering fox influence a winter day's coldness, or a cruising shark the ocean's currents? Does an improvement in the photosynthesizing ability of a plant change the sun's brightness?

3. Anthropocentricity, which arrogates both individual uniqueness and the ability to shape the environment to the human species alone.

First I shall examine the stated problem from the points of view of several biological disciplines of which some, in the words of H.J. Morowitz, may continue to be "on fast-moving trains going in opposite directions and not noticing what is happening across the tracks". I will then trace evolution as a process of escalating individuality, and describe organismic, ecological and evolutionary complexity as resulting from individuality, suggesting that the mechanisms of individuality may have far-reaching consequences for human existence. Throughout this paper I intend to present evidence in support of the following hypotheses:

1. Each adaptive step by an evolving organism brings about a complementary change in its environment. The environment invariably recedes from the organism adapting. *Today's organism is adapted to yesterday's environment.*

2. Interactions between organisms that are asymmetric in terms of energy flow (such as between predator and prey) are also asymmetric in information flow; as energy flows to the successful predator, information flows to the successful prey. *Today's predator inherits yesterday's prey image.*

3. Individuality as resulting from sexual reproduction mediates this asymmetric feedback and the ensuing time-lagged escalation; it is self-reinforcing and leads to increasing spatial and temporal complexity of organisms and environments through evolutionary time. Next to the basic drive of life itself, *individuality may be the most powerful motor in the shaping of the biosphere.*

The players and their fields

Organism-environment interaction

In order to fuel its maintenance and reproduction, an organism must average a positive net energy[1] balance vis-a-vis its environment[2]. It must know how to eat but not to be eaten before it has passed this know-how on to the next generation. The organism achieves this via aptations[3] (Gould and Vrba 1982), i.e., features that promote the flow of net energy from the environment to the organism. These features consist of information (i.e., the internalization by the organism of all that is predictable about its environment, including the machinery to take advantage of this information), and stored energy to operate the machinery, including a safety margin to deal with events that are unpredictable in principle.

Evolutionary theory usually describes the process of adapting as unilateral, i.e., the organism is influenced by the environment by means of selection and does all the changing whereas the environment changes independently (if at all). As Van Valen (1983) points out, this view is contained in "the common aphorism that evolution occurs by adaptation to the environment", and may be explained by the fact that "we then think of 'the environment' as mostly physical". The underlying assumption is that the physical environment does not respond to an organism's advances. Coming from an entirely different perspective, but with his eye firmly on the living side of the equation, Lorenz (1973) attempts to describe adaptations in information theory terms as

> an increase in the transinformation that exists between organism and environment...caused by processes within the organism without a concurrent noticeable change in the environment...an asymmetric correspondence brought about exclusively by changes in one of the two systems made to correspond.

This traditionally lopsided view has been rightly criticized by Lewontin (1982) who points out that "it is impossible to describe an environment except by reference to organisms that interact with it and define it"; we have neglected "to understand how much of what is 'out there' is the product of what is 'in here'". Levins and Lewontin (1985) make the strongest case yet for a dialectic relationship between an organism and its environment, in that "organisms select...modify...respond to...and transform the statistical structure of their environment...Organisms alter the external world as they interact with it" - plant roots alter the soil, grazers stimulate the production of forage, beavers shape entire landscapes by their dam building, phytoplankton influences global weather patterns (Lewis et al. 1990, Sathyendranath et al. 1991). Such changes extend into the internal environment as well so that "every part or activity of an organism acts as environment for other parts". Wuketits (1986) concludes that "we have, then, to recognize that organism and environment are *mutually* related, and to suppose that there is a flow of cause and effect in both directions". A number of recent papers (see, for instance, BioScience 38/11, 1988), including the Gaia model with its Daisyworld (Lovelock 1988), have stimulated interest in how organisms shape their ecosystems.

Indeed, one should expect the abiotic environment also to evolve, at least in the sense of mirroring organismic evolution. In terms of thermodynamics, each adaptive step of an organism (such as more efficient photosynthesis), at least at the time the step occurs, enhances the net energy flow to the organism from its environment, and must therefore be expected to bring about a complementary change in the latter. Some such feedback effects may seem negligible at first, and only emerge on closer inspection. Take the sun, that ultimate, faraway and seemingly inexhaustible resource, as an example: plants using sun energy may not make the sun itself less luminous at the source, but they affect the amount of sun energy available where it counts, at the point of harvest, which is the surface of our planet. More plants mean more shade, which means less sun energy for other plants, not to mention changes in evaporation, albedo etc., all of which influence the environments of other organisms. The difference in macroclimate between a rain forest and a desert caused by deforestation illustrates this point. "The activity of all living forms transforms the external world in ways that both promote and inhibit the life of organisms" (Levins and Lewontin 1985).

In view of this interdependence, an asymmetry between a given organism and its non-living environment exists insofar as the organism adapting acquires information and passes it on to the next generation, while the abiotic environment receives more diffused energy, which is inherited by the next generation of organisms.

Brooks and Wiley (1988: 29) allude to this time lag arguing that "most of the characteristics [of organisms] are inherited unchanged from their parents...(therefore) any active process of 'adaptation' is mostly adaptation to the past, not the present or future". But they then go on to claim that "organisms grow in environments, they are not molded by them". I rather propose that today's organisms have been molded by yesterday's environment, and tomorrow's environment will be shaped to a significant degree by today's organism - which explains the time-lagged, space-quilted diversity we see.

Adaptation and aptations

As the link between a successful organism and its environment, the process of adaptation and its result, aptations (Gould and Vrba 1982), are the key to understanding evolution. Of a bewildering array of definitions I cite only that of Vermeij (1987) who calls an aptation "any attribute that enables an individual organism to carry out a specific function and that therefore confers a selective advantage to that individual with respect to survival or propagation in a given environment". Since the many aptations an organism needs are under various constraints and may in fact neither be compatible nor energetically affordable in their most 'perfect' form, aptations are usually compromises - which means there is always room for improvement. Note that, like practically all other definitions, Vermeij's only addresses the organism side of the equation, treating the environment as unaffected.

Yet there can be no organismic adaptation without environmental cost. Adaptation by the organism, whether defined in structural or functional or whatever terms, brings about a temporary energy gain to the organism, and a corresponding energy loss to the organism's environment. In a thermodynamically more or less closed system (which a biologically mature earth approaches), any energy gain by one player must be balanced by an equivalent energy loss by another. Unchecked, 'runaway' adaptation should indeed only be expected in a utopian environment in which there is no feedback to the organism, i.e., where resources never diminish, wastes never accumulate, and enemies never materialize. Spiegelman's (1967) experiments showed what happens in such a case. He incubated viruses with an information content of 4500 nucleotides, stripped of their protein coats but provided with an inexhaustible supply of free nucleotide monomers and replicase. Under such conditions, the original strain was eventually replaced by a stable mutant with no more than 220 nucleotides, little more than the recognition site for the replicase that was vital for replication (Dyson 1985). The loss of flying ability in many island-colonizing bird species follows a similar pattern. (The structural simplicity of many parasites suggests the same, although I suspect that parasite life cycle complexity fairly compensates for it.) Spiegelman's results suggest that in a homogeneous, unchanging environment, i.e., in the presence of uncontested supplies and absence of threat - no competition nor escalation - evolution tends towards simplification rather than complexity. Yet as the paleontological record shows, real-life "evolution usually progresses by increases in complexity" (Bonner 1988), which suggests the forces in this direction must be powerful.

Within the framework of this paper I define an 'aptation' as any feature of an organism that, for whatever time period, enhances the organism's energy balance vis-a-vis its environment in view of reproduction, and 'adaptation' as the process that improves this energy balance.

Evolutionary epistemology

Based on seminal insights by Lorenz (1941), evolutionary epistemology (Wuketits 1986, 1990, Riedl and Wuketits 1987) describes life as a knowledge-gaining system,and evolution as a learning process. Via the Darwinian mechanism of mutation and selection, an organism gathers and refines information about its living and non-living environment and passes it on to its progeny. In this view an organism represents a hypothesis of its environment, continually tested by selection for its predictive value, and modified via adaptation for a better fit. Such a hypothesis consists of predictions, plus the machinery and energy to take advantage of what is being predicted. This is illustrated in Simpson's (1963) often quoted remark that "the monkey who did not have a realistic perception of the tree branch he jumped for was soon a dead monkey - and therefore did not become one of our ancestors". Each time a prediction regarding the occurrence of a coincidence or correlation, in time or space, between objects or events is confirmed, the hypothesis is strengthened (Riedl 1980). In other words, the repetitiveness of patterns is taken for predictability; via the process of evolution it then becomes part of the organism's own make-up, turning the organism quasi into a mirror image of all that is predictable in its environment.

Shields (1988: 265) characterizes aptation as consisting of "knowledge about those aspects of environmental features that are constant or vary within 'known' limits or both". What is constant is predictable; even a range of variability, provided it remains the same, is predictable and can therefore become part of the genetic endowment of the organism-as-a-hypothesis. Whether the adaptation to the predicted environmental feature is structural or functional, whether it is constitutional (inflexible) or inducible (Harvell 1990) or learnable is immaterial in this context. The main distinction is that an organism needs both: information about as much of its environment that is predictable (including the nature of events that are unpredictable in detail), and energy (including the wherewithal to deploy it), so as to make use of its predictions and decrease its susceptibility to all that is fundamentally unpredictable.

Events that, because of their uniqueness, contain a significant element of unpredictability, must be met largely by means of stored or embodied energy reserves that are deployed in generalized defensive structures, such as the shell of a mollusk, or tactics such as fight or flight. Increasingly with growing complexity of the organism-environment system, ontogenetic learning comes into play. Being both a reaction to and major driving force in creating structural (spatial) and functional (temporal) complexity (Pringle 1951), ontogenetic learning individualizes organism-environment interactions, thereby further increasing their unpredictability. Ontogenetic learning (as opposed to preprogrammed responses) is a step up in the self-reinforcing spiral of complexity.

In the case of a predator-prey[4] relationship the 'organism as predictor' means that a predator who catches a prey represents a successful 'prey catching hypothesis' whereas its unfortunate prey perishes as an unsuccessful 'predator avoidance hypothesis'. Each time a predator goes after its prey both hypotheses are put to the test. I intend to show that the asymmetry in information gain from such contests is a major ingredient in the evolution toward complexity.

Sex and reproduction

Referring to the noticeable recent increase in papers and books on the mechanism and evolution of sexual reproduction (Williams 1975, Maynard Smith 1978, Symons 1979, Daly and Wilson 1980, Halliday 1980, Bell 1982, Catton and Gray 1985, Eberhard 1985, Halvorson and Monroy 1985, Margulis and Sagan 1986, Michod and Levin 1988), Felsenstein (1988) wryly observes that "this year, the sex crisis seems to have returned". He concludes that, since this renewed interest was not brought about by any illuminating new data or hypotheses, "the problem has simply flared up again and will probably gutter out after a while". Crow (1988) counters that the identification of parasites as a particularly unpredictable and malevolent environmental variable by Hamilton (1980) and the renewed study of parthenogenesis by Maynard Smith (1986) represent, among others, important advances. The recent identification of the male sex-determining factor in mammals (Sinclair et al. 1990, Koopman et al. 1991), the recognition of segregation alone as an important mechanism in sexual reproduction (Kirkpatrick and Jenkins 1989), and the phenomena of chromosome imprinting and DNA methylation (Holliday 1989) can be added to this list. At the very least, therefore, the complex matter of sexual reproduction is now more open to inspection and integration with other disciplines.

What is sex[5]? Genetic recombination, as typically resulting from the reshuffling of DNA segments during crossing-over in the meiosis of diploid eukaryotes (i.e., most higher organisms), is now widely acknowledged as the central feature of sex. Outcrossing, i.e., the origin from different individuals of the DNA partner molecules in crossing-over, is a close second, whereas the differentiation of the reproductive cells into larger eggs and smaller sperm (anisogamy), and of the sexes into female and male, are related yet less critical phenomena (genital union being entirely incidental...). While recombination and reproduction do not have to follow each other they generally do, leading to a generation of new genotypes, hence to genetically non-identical, unique individuals[6].

Asexual reproduction in its simplest form, on the other hand, produces genetically identical units of offspring (clones). There are various intermediate modes of reproduction that result in intermediates between unique individuals and identical clones, just as there are many organisms that alternate sexual and asexual reproduction in their life cycles, often in response to differential environmental cues. As a general trend, the incidence of sexual reproduction increases whereas that of asexual reproduction decreases with increasing organismic complexity[7]. Consequently, mammals and birds reproduce only sexually, whereas most plants and lower invertebrates have asexual modes of reproduction occurring at least at some time of their life cycles. However, sexual reproduction is apparently so crucially wedded to the phenomenon of life that it pervades its entire realm (Crow 1988), the few known exceptions only waiting to be disproved or become extinct, whichever should happen first.

Because of their genetic uniformity, clonal organisms are 'categories' rather than individuals, and should therefore be predictable and vulnerable to a pursuer. In a world of clonal organisms, one favorable mutant in a predator species has the potential to extinguish an entire prey species, which in turn could result in the demise of the starving predator. The observation that "some of the most striking examples of specific, inducible defense responses occur in clonal and colonial animals" (Harvell 1990) suggests to me that inducible defenses are an asexual organism's short-term substitute for the protection from predation which individuality bestows on sexual populations.

But sex entails costs. In Maynard Smith's (1986) simple calculation, an all-female parthenogenetic population can reproduce twice as fast as one composed of half males, half females; in fact many species, from insects to lizards, have at least parthenogenetic phases in their life cycles. Other disadvantages of sex may be the breaking-up of proven genotypes, the energy costs and risks associated with meiosis and fertilization, etc. (Michod and Levin 1988). Since there is good evidence, however, that species which wholly abandon sex are short-lived on an evolutionary time scale, sex must convey a more than twofold advantage, at least in the long run. What is it?

Largely following Bell (1988), an eclectic list of the advantages of sex can be summarized as follows. Sex allows for mutations to be eliminated if and when they should become deleterious (a remedy for 'Muller's ratchet', i.e., the inevitable accumulation of mutations in an asexual population, see Chao 1990), but to be retained and recombined into new genotypes when currently neutral (Kimura 1983) or beneficial. The latter feature would increase individuality, and thus enhance the immediate exploitation of a heterogeneous environment as well as prepare at least some individuals, serendipitously, for survival in an unpredictably changing environment ('hopeful mini-monsters'). In addition, differential depletion of resources, particularly in antagonistic interactions between species, may lead to time-lagged genotype frequency dependence, as shown for parasite-host relationships (Seger and Hamilton 1988). Individuals interacting with spatial heterogeneity of the environment would account for a Tangled Bank hypothesis of diversity (Ghiselin 1988) whereas temporal heterogeneity (time lag) would form the basis of the Red Queen effect (Bell 1982). I suggest that the ability of sexually produced populations to balance opportunistic offense with rearguard defense is not only the core advantage of sex over asex but also a major force throughout evolution.

Individuality

It seems paradoxical that we should assign such great importance to human individuality (our own in particular), yet go to extremes to ignore individuality in other organisms. From the Bauplan of morphologists to group selection, the history of biology is replete with attempts to smooth over differences between individuals in order to arrive most expeditiously at the higher category. I do not intend to belittle the need for Bauplan nor higher categories, but simply point out that, as for instance in the study of the structure and stability of ecological systems,"individual variation seemed to be nothing more than an unimportant hindrance" (Lomnicki 1988). In a similar vein, Bell (1988) calls it "a withering comment on the ecological naivety of current population genetics that no [genotype-by-environment interaction] measurement is available from an undisturbed natural population, though large genotype-by-environment effects have often been reported in the agronomic literature". On the broader level of the philosophy of science it seems that much of the discussion (Crick 1966, as quoted in Beatty 1990) "whether the actual process of evolution is predictable" (and therefore science), or chance (and therefore history), could benefit from a distinction between the individual and its class. Much like the individual decaying atom vs. the half-life of its mass, the biological individual is unpredictable insofar as it is unique, but predictable insofar as it is a member of a population, species, or whatever category.

Individuality, in other words, continues to be either ignored or at best acknowledged as a quirky, irksome feature of living organisms that dilutes the lawful essence and distracts the student, rather than as a phenomenon worth investigating for its own evolutionary significance. I suggest that the more complex and less predictable an environment becomes as a consequence of individuality, the more individuality contributes to evolution, both as essence and dilution.

Protean behavior and unpredictability

Driver and Humphries (1988) give a fascinating account of what they call 'protean' [8] or unpredictable behavior in organisms. The 'jinking' in the 'single erratic display' of a fleeing rabbit, the scatter of a school of fry, the mobbing of a predator by a group of prey, injury-feigning and convulsoid displays are but a few examples of the many functional and structural devices that introduce unpredictability into an organism's repertoire. The immediate purpose of unpredictability is to deflect a pursuer's aim and to escape, whereas the longer-range purpose must be to prevent him from learning from his mistake. However, the tiniest shred of a pattern devaluates the protean display, as delightfully proven by L. Leakey (1969, quoted in Driver and Humphries 1988):

> As a boy I found that I could catch [hares] after observing that a fleeing hare always carries its ears at an angle until just before it jinks, when it lays them flat on its neck. By always sidestepping to the right at the moment a hare puts his ears down, I had a 50-50 chance that he would come straight into my hands and be caught!

(Fortunately for hares, foxes apparently aren't as clever as Leakey was, or otherwise hares might either have become extinct - and so might foxes for that matter, - or only jink to the left...).

Although they refer to mutations as "the ultimate protean phenomena", Driver and Humphries (1988) deal with unpredictability mainly from an ontogenetic point of view. However, they suggest that "protean defense displays may require considerable escalation of an opponent's armaments, if they are to be overcome". I propose that a population composed of unique individuals is itself protean, and that the degree of protean unpredictability increases with individual uniqueness. Phylogenetic and ontogenetic learning are attempts by one opponent to catch up with the other's unpredictability, but to the degree that this learning itself occurs in individuals, it contributes to further complexity.

Competition

Darwin (1859) already emphasized competition as the editor of the raw copy provided by individual variability resulting from mutations and recombination. According to Van Valen (1983), organisms compete for the free energy potentially available which, in almost all cases, on the ecological and evolutionary time scales, is both limited and potentially available to other organisms. He goes on to say that "in this view, a predator competes with its prey for use of free energy in the prey". While this may be appealing from the predator's point of view, I see at least three ways in which 'free', i.e., as yet un-owned (e.g., sunlight) or voluntarily shed (e.g., leaf litter) energy should be different from energy that is already embodied in an organism. The first is that free energy is usually less concentrated, and therefore less desirable, than embodied energy. The second is that the owner of embodied energy, having spent energy in the effort of collecting it, can be expected to defend it up to the point where the defense expenditure approaches the combined values of the store plus the effort of collecting it. The third reason is that, in non-human organisms, energy is almost invariably stored within the body, which means that the involuntary loss even of 'surplus' energy is tantamount to fitness loss, injury or death.

In an attempt to distinguish the gathering of free energy from the robbing of owned energy I suggest the terms 'horizontal' and 'vertical' competition. In horizontal competition, two organisms compare their ability to tap an outside source of energy (which may be abiotic such as sunlight or water, or biotic such as food or a mate). Such comparison may happen anonymously, or shoulder-on-shoulder or with horns locked. In 'vertical' competition, on the other hand, one organism attempts to take the energy that another has already incorporated (as in predation and parasitism); the other in turn tries to protect itself from such robbery or murder. The fact that predation and parasitism are a form of 'contact sport', i.e., cannot be carried out without the contestants meeting and gaining knowledge about each other, leads to arms races and escalation.

Horizontal and vertical competition often run concurrently, as in all heterotrophs competing with each other for the energy contained in a food organism, but the difference between the two types lies in the directions of the flow of energy and information. As Vermeij (1987) points out, losers in (horizontal) competition "are often prevented from acquiring or retaining some resource... but usually survive", whereas the losers in predation do not. In other words, horizontal competition results in losses or gains by degree whereas vertical competition, in the case of predation, has an all-or-nothing outcome (parasitism and grazing are somewhat intermediate in that the loss to the host is by degree, yet parasite and host, grazer and plant acquire knowledge about each other). Historically, horizontal competition has been assigned vastly more significance in evolution than vertical competition. I want to help redress this imbalance by showing that, with increasing ecosystem complexity, vertical competition, and with it arms races (Dawkins and Krebs 1979) and escalation, take on a growing share of competitive interactions, with individuality as the linchpin.

Coevolution and escalation

Once defined as "the direct or indirect interaction of two or more evolving units [that] produces an evolutionary response in each", coevolution (Ehrlich and Raven 1964, Gilbert and Raven 1980, Nitecki 1983) may in fact be so pervasive as to comprise most of evolution (Van Valen 1983). More recently, Vermeij (1987) has correctly proposed to restrict the term to cases of 'adaptive reciprocity' (such as the evolutionary interactions between plants and pollinators), and to apply the term 'escalation' to cases of arms races between exploiters and their resources.

In reaffirming earlier views by Darwin (1872), R. A. Fisher (1958) and others that enemies are the most important agencies of selection, Vermeij (1987) puts forward three hypotheses for the evolution of plants and animals during the Phanerozoic eon:

> 1. traits that enhance the competitive and antipredatory capacities of individual organisms have increased in incidence and in degree of expression...2. more recently evolved individuals are better adapted to their biological surroundings than ancient ones were to theirs..., and 3. biological hazards due to competitors and predators have become more severe, ... that is, the capacities of enemies have increased, as have the risks they pose to potential victims. This is the hypothesis of escalation.

Escalation, and arms races in general, clearly offer a historical explication for the observed increase in complexity (Bonner 1988). They provide at least a partial answer to the puzzle of 'anamorphosis', i.e., the overall evolutionary phenomenon to proceed from simple to complex organisms that baffled, among others, Bertalanffy (quoted by Davidson 1983). Vermeij develops his hypothesis expressly under the premise that "selection at the level of the individual is more important in the history of aptations than are processes at higher levels"; this offers a handle for showing that the genetic mechanism for such selection and escalation can be found in the Red Queen effect (Hamilton 1980, Bell 1982).

Arms races and the life/dinner principle

Ever since the replacement of the soft, good-of-the-species-oriented view of selection (which Darwin never promoted; see Ghiselin 1988) with the hard, 'selfish gene' view (Dawkins 1976), many interactions between organisms, even between the sexes and generations of the same species, have been interpreted as 'arms races' in which the aggressive partner's advance (adaptation) triggers a corresponding defensive or evasive move (counter-adaptation) in the other. Arms races may lead to complex interdependencies in which the manipulative influence of a genome reaches far beyond the organism in which it resides, giving rise to the notion of the 'extended phenotype' (Dawkins 1982). It is important to remember, though, that all arms races are energetically asymmetric in that one partner always benefits whereas the other always loses; only the degree of net energy transfer changes with each adaptation and counteradaptation.

Dawkins and Krebs (1979) coined the term 'life/dinner principle' for the type of sustained asymmetric arms race that exists for instance between the rabbit and the fox. Named after the fable of Aesop it proposes that " the rabbit runs faster than the fox, because the rabbit is running for his life while the fox is only running for his dinner". Both are spending energy in running, but the race (and thus the energy flow) becomes radically asymmetric if and when the fox catches up with the rabbit. So why haven't rabbits become extinct? Dawkins (1982) suggests that because of the asymmetry, mutations for fast running are more strongly selected for in the rabbit than in the fox. I intend to show that genetic individuality is the mechanism by which asymmetric arms races (that is: any relationship in which one organism unilaterally draws energy from another) can be maintained over evolutionary time periods.

The Red Queen effect

Drawing on the paleontological record, Van Valen (1973) proposed that the rate at which species become extinct is more or less constant because their environment is continually changing. He called this the 'Red Queen effect', in reference to an episode in "Through the Looking-Glass" in which, after much running, Alice and the Red Queen find themselves exactly at the same spot from which they had started. Questioned by a panting, incredulous Alice, the Red

Queen says: "Now, *here*, you see, it takes all the runnig *you* can do, to keep in the same place". By analogy, Bell (1982) called 'Red Queen' the time-lagged frequency dependence in the genotypes of antagonists such as parasites and hosts, as first described by Hamilton (1980), and suggests that "the coevolution of antagonists continually reverses the direction of selection acting on combinations of genes" (Bell 1988).

Seger and Hamilton (1988) expand on this model for the "sweeping back and forth of host and parasite on the coevolutionary 'dance floor'":

> As one host genotype increases in frequency it favors the increase in the parasite genotype best able to exploit it, whose subsequent increase lowers the fitness of that host genotype, allowing a different host genotype to increase, which favors a different parasite genotype, and so on... Thus any genotype that was common in the recent past is likely to suffer relatively low fitness at present, because of the evolutionary change that its commonness induced in the other species. In effect, the current position of each species is a "memory" of the recent history of the other, and so the fitnesses of the genotypes of each species appear to exhibit negative frequency dependence with a time delay, even though there is no *explicit* intraspecific frequency dependence in the model.

Ideas put forward by Haldane (1949) and others (see Clarke 1979: 463) propose that "the host's best defense may be based on genotypic diversity, which, if recombined each generation, can present to the parasites what amounts to a continually moving target" (Seger and Hamilton 1988). On the basis of a scheme first introduced by Jaenike (1978), Hutson and Law (1981) and Bell (1982) proved that "non-zero rates of recombination will evolve in explicit genetic models under time-lagged frequency dependence... The most plausible candidate for a source of time-lagged frequency dependence is the coevolution of two mutually antagonistic species, especially parasites and hosts" (Bell 1988). Based on the assumption that coevolved biological enemies will disproportionately attack the most common phenotype, the advantage of sex under this hypothesis stems from the production of rare phenotypes which are more likely to escape such attack (for exceptions see Clarke 1979: 462). Bell and Maynard Smith (1987) developed a model to show how the mutual antagonism between two species can lead to a cyclical game of time-lagged frequency-dependent selection that tends to destabilize both genotype frequencies and linkage disequilibrium. In such cycling, high-recombination alleles can have a large short-term selective advantage. They conclude that "negative species interactions may be central to the evolution of phenomena such as sexuality, recombination and outcrossing, which ensure that a previously successful strategy is systematically abandoned" (Bell and Maynard Smith 1987).

I would expect that the addition of an occasional constructive mutation to the sweeping back and forth of the partners should 'punctuate the equilibrium' and transport one partner, then the other to the next higher 'dance floor', in a process called escalation. While the Red Queen effect has been increasingly accepted for parasite-host relationships (Lively et al. 1990) it should, in theory, also hold for predators and prey, grazers and host plant; i.e., all encounters between Darwinian individuals in which energy flows in one direction and information in the opposite.

Evolution as escalating individuality

To live means to maintain a positive energy balance

Thermodynamically a living organism is an open system that exchanges matter and energy with its surroundings (Bernal 1951, Prigogine and Stengers 1984, Wieser 1986). It keeps itself in a dynamic equilibrium by taking energy from its environment, storing it or putting it to work for its metabolism and reproduction, and returning degraded energy to its environment. Net energy flow must play a central role in life's ability to build, maintain and pass on order amidst growing disorder.

Adaptation is a net energy gain to the organism...

As a process in evolution, adaptation can be seen as the (albeit temporary) shift in net energy flow between an organism and its environment in the organism's favor. Competition favors that organism which by means of adaptation is able to improve its net energy balance so as to invest more of it in its progeny than its competitors. If "adaptations enhance the fitness and contribute ... to the survival of the individual" (Sluys 1988), then an aptation is a channel for net energy flow from the environment to the organism, and the process of adaptation improves this channel.

...but an energy loss to its environment

Yet each adaptive step in an organism's evolution must bring about a simultaneous, complementary shift in its environment, which means that the latter, living or non-living, is losing energy, at least at that moment. Such influence may range from minor and short-lived (such as oxygen depletion in a pond due to respiration), to major and lasting (such as carbon dioxide accumulation in the atmosphere due to combustion), but is never zero; it is added to those changes of the environment that can be assumed as happening independently of the biosphere (such as the sun's luminosity over eons).

To predict means to avoid energy surprises

The successful organism uses its energy surplus for maintenance and reproduction. Keeping the energy balance positive requires information regarding energy sources (such as the sun, or prey) as well as energy sinks (such as predators, parasites), and energy reserves (such as body fat) to be invested in seeking sources and avoiding sinks. Predicting the environment guards against energy surprises. The necessary information is acquired through the process of evolution, such that an organism internalizes from its environment all that is predictable regarding energy sources and sinks.

An organism is a hypothesis of its environment

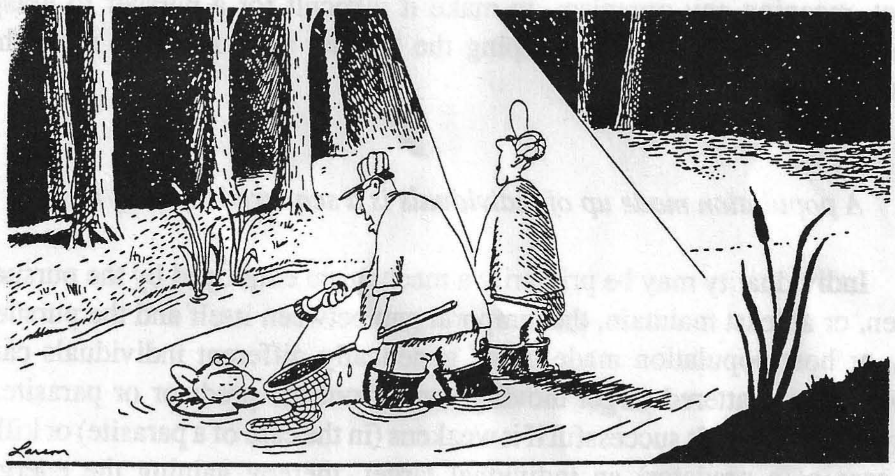
An organism thus consists of information (that is, internalized environmental predictability), and embodied energy; it is a hypothesis of its environment designed to deal with the latter so as to secure net energy. Consisting of a set of nested subhypotheses, i.e., aptations, an individual-as-hypothesis is tested in each energy interaction with its environment. Validated hypotheses replicate, invalid hypotheses fall by the wayside.

But using a prediction changes what has been predicted

Yet by predicting that energy will flow from A to B at time X, and stepping into the energy flow so as to divert it to its advantage, an organism changes the very energy flow it had predicted. Such interference can never be zero. If even the act of measuring brings about changes in what is being measured, regardless of how much the energy flow involved is kept to a minimum, then an act whose main intent is not information gain but energy gain must be expected to interfere even more. In general one should assume that the interference of a prediction with the predicted event will be the greater, the more precise the prediction is and the more limited the resource is in comparison with the rate at which it is being exploited. As an example (Bell 1988), a plant genotype conveying a rapid growth rate at high nitrogen levels will be selected over its low-nitrogen, slower-growing competitor until it has depleted the available nitrogen resource, at which time its competitor will be favoured. This time-delayed feedback loop results in a shift in gene frequency in the exploiter, and the shift itself, hence the time delay, increases with the very efficiency of the exploitation. Yet the interaction between organism and abiotic environment does not induce teleonomy in the latter; the abiotic environment simply moves 'away' from the organism's advances (e.g., towards a more depleted state), but there is no mechanism for the abiotic environment to seek a direction or determine the speed of receding. Such teleonomy is the reserve of the biotic environment.

Information is proprietory and saves energy

The accumulation of information should be favoured over the accumulation of energy in the course of evolution, for two reasons. The first is that the more information an organism has about sources and sinks the less energy it needs to spend on seeking/avoiding them. Information is a long-term investment. The second reason is that information, whether coded in genes or neurons, is proprietory to the organism that owns it and is destroyed when digested by the predator. Energy stored as body tissue or fat, on the other hand, is not only vulnerable to general catastrophic destruction (such as a forest fire, or anoxia; Ott 1981) but it also invites robbery.



"See, Frank? Keep the light in their eyes and you can bag them without any trouble at all."

Each organism is both hunter and target

Being more concentrated than its sources such as sunlight or prey, the embodied energy of an organism thus becomes itself the target of energy-seekers, i.e., predators and parasites. Energy seekers will benefit from internalizing as much as possible of the target organism's predictability; by acquiring information they reduce the need to store energy, and thereby reduce their own attractiveness as a target. (As a consequence, the 'ultimate' organism should be expected to consist almost exclusively of information, with virtually no energy store/structure to present a target. Viruses approach this state. Conversely, there is no organism that consists of mostly energy but little information - it would be sitting duck. Did dinosaurs fall in this category, with their lopsided energy/information ratio?)

Each organism, therefore, is both pursuer and pursued. As a pursuer it must be forward-looking, and strive to internalize all that is predictable about its environment regarding energy sources and sinks. As a pursued it must cover its rear, and avoid becoming someone else's energy source. It must try to avoid becoming predictable in its weaknesses. (Being predictable in one's strength may convey an albeit temporary advantage). The organism's dilemma as a pursuer is thus to make its environment as predictable as possible in order to take advantage of energy sources and avoid energy sinks, but as a pursued to remain itself as unpredictable as possible so as not to fall prey to someone else's prediction. Being a hypothesis of what is predictable in its environment, however, an organism is itself predictable, and therefore vulnerable to being predicted by a pursuer. The more homogeneous a population or species is, the more predictable it is in its characteristics, and the more quickly one should expect a pursuer to home in by internalizing the target's predictability. It must be in the interest of any potential target, meaning any organism, to make it difficult for a pursuer to grasp its essential predictability, thus keeping the pursuer from catching up with the pursued.

A population made up of individuals is a scattered, moving target

Individuality may be primarily a mechanism employed by the pursued to widen, or at least maintain, the temporal gap between itself and the pursuer. A prey or host population made up of genetically different individuals can be viewed as a scattered target moving away from the predator or parasite. An individual pursuer is successful if it weakens (in the case of a parasite) or kills (in the case of a predator) an individual target, thereby gaining the energy to reproduce; whereas an individual pursued is successful if it escapes such action and hence goes on to reproduce.

It is the statistical predictability of groups of biological individuals that constitutes what taxonomists call a species, and what a species calls prey, predator, parasite or host - a defined source or drain of energy. (A predator that feeds on two or more congeneric species would thus have something akin to a 'genus concept'...) The confusing element in individuality is that each individual not only differs from the mean in an unpredictable way, but the mean can only be known if all individuals are known. Assuming that prey individuals occur in a normal distribution it should be in the interest of a predator to 'aim' for the mean, since this is where most individuals can be expected. Yet the only phylogenetic mechanism for a predator to learn about his prey is to kill it. (The principal difference between predation and parasitism here is not that the parasite does not kill its host, but that their life spans are reversed: parasites are usually shorter-lived than their hosts whereas predators are longer-lived than their prey. In addition, parasites are generally more specialized to one host than predators are to one prey. I would expect both of these factors to influence the speed and magnitude at which the time lag oscillates; parasites should be faster learners than predators.)

Today's hunter aims at yesterday's target

Today's generation of both prey and predator is descended from yesterday's successful parents - at first a seemingly symmetric relationship. Yet for predators, success meant catching prey whereas for prey it meant avoiding predators. The gene pool of today's prey generation is shaped by yesterday's loss of those individuals that succumbed to the predator, either because they were the least fit or because together they made up the commonest genotype (which, in this model, amounts to the same). The gene pool of today's predator generation, on the other hand, is shaped by those individuals that were successful in catching prey (under the assumption that unsuccessful predators do not reproduce). This results in an asymmetry regarding the 'fit' between predator and prey. Today's prey gene pool (1-x) is made up of yesterday's (1) minus yesterday's losses (x) to the predator, whereas today's predator gene pool is made up of those who caused the losses (x). In other words, the prey's gene pool has been sharpened or redefined by its losses whereas the predator's gene pool is focused on the losses (x), not the survivors (1-x). *By definition, today's predator inherits yesterday's prey image; the prey remains a step ahead.* The attention of today's predator is aimed at a vacuum; both aim and vacuum were created yesterday by his parents' successes. In the terms of evolutionary epistemology, each prey individual caught strengthens the prey's 'predator avoidance hypothesis' but weakens the predator's 'prey catching hypothesis'.

Energy flows to the successful predator, and information to the successful prey

There is complementarity between the pursuer and its target inasmuch as energy (and 'misinformation') flows to the successful pursuer while information flows to the missed target. Phylogenetic learning, therefore, is not symmetric between pursuer and target. The target learns exclusively from its losses whereas the pursuer gets misinformation from its gains. In both, though, the individual mediates such learning. The prey's learning is focussed, through the elimination from its gene pool of those genotypes that don't make it. The predator's learning is diffused by the capture of those very individuals that, by his action, are eliminated from shaping the prey's gene pool. Individuality, from the target's point of view, is a deliberate spreading of misinformation about the composition of its gene pool. The cost of such misinformation can be chalked up to sex.

Prey 'escapes' as a function of the predator's success

In consequence, a prey population made up of genetically different individuals constitutes a scattered target that is moving away from the predator, as a function of its interaction with the predator, both in ecological and in evolutionary time. The direction and speed of the target's movement away from the pursuer is largely determined by feedback from the predator's success. Both scatter and movement are made possible by individuality, itself a result of recombination.

The role of individuality in time-lagged asymmetries provides a phylogenetic explanation for frequency-dependent selection (Lewontin 1974), which has been held responsible for the maintenance, within natural populations, of unexpectedly high levels of variation and polymorphism (Ghiselin 1988). It may also shed light on certain forms of apparent altruism, such as the 'survival of the imperfect exploiter' (Ott 1981), i.e., the observation that some predators are less efficient exploiters of prey than expected, thereby contributing to ecosystem stability.

Teleonomy focuses on the past

In reality, the picture is enormously more complicated. Analyses of food webs (May 1988) reveal that most species interact not with two but with 3-5 other species on average; the number of interactants is consistently higher (4.6) in relatively constant environments than in fluctuating ones (3.2). In British food webs consisting of green plants, insect herbivores and insect parasitoids, each herbivorous insect species was found to be typically attacked by 5 to 10 different species of parasitoids alone. Furthermore, mutations and migrations continually change the makeup of both hunter and target populations, and there are countless more intrinsic and extrinsic factors that influence survival and reproductive success of all partners.

Yet unless one assumes that all asymmetries stemming from individuality add up to symmetry, which is rather improbable, a biosystem emerges whose information content does not match its actual environmental target. The 'a priori' of evolutionary information contained in organisms, which has come about as an 'a posteriori' of their experience in evolution (Lorenz 1941), lags constitutionally behind the world which it addresses - teleonomy with an incurably myopic focus.

The trajectory of any organism-environment system must thus be chaotic (and the sum total of all trajectories through evolution may make up a state space bounded by the materially closed nature of the earth; Barlow and Volk 1990). Strangely akin to the behavior of a non-linear equation it is "like walking through a maze whose walls rearrange themselves with each step you take" (Gleick 1987: 24). In chaos terminology, biosphere complexity may be the sensitive dependence on and amplification of the small initial disturbances that individuality brings about.

Complexity arose from individuality

Life's history as growing complexity

Tracing the increase of complexity during the course of evolution by means of the increase in the upper limit of the size of plants and animals, Bonner (1988) proposes that "a selection for size increase has meant new worlds to conquer, either to avoid predation and competition or to be especially successful as a predator or competitor". The overall increase in diversity (as measured, for instance, by the number of plant and animal species, genera, orders, etc.) over the past 400 million years is well documented (Bonner 1988); it means, among others, vastly more organism-organism interactions and thus a higher degree of environmental definition by bioticy variables. The frequency of organism-organism interactions grew with the stability and the complexity of an ecosystem (e.g., tropical rain forests and coral reefs) as well as with the size and longevity of organisms. Individuality continues to be both the cause of and the buffer in this increasing complexity, caught between the impossible tasks of fending off a growing number of potential pursuers and predicting an increasingly fragmented and unpredictable environment.

Complexity increases with individuality

Complexity describes the number of and connections between the elements of a system, within and across levels of hierarchy. To the degree that the elements and their connections are identical in space and time, complexity poses only a quantitative problem for predictability. Genetic individuality, however, implies non-identity of these elements, which results in non-identity in time and space of their interactions with each other and with the rest of their environment. Both the parts and their intercations thus exist in diluted, mixed states (the genotypes of individuals) that share properties to varying degrees. It becomes the task of the predictor to distill the essence - i.e., the category, the lawful, the largest common denominator - from the contingent, incidental, non-repetitive, ephemeral features. The difficulty to predict a system, therefore, can be expected to increase with the degree to which its parts and their interactions are individualized . The more complex a system becomes, the more information a predictor needs to process and internalize it - which itself contributes to making the system more complex. But how did it all begin?

Life internalizes energy and information

Life is the ability to maintain itself far from energy equilibrium with its environment (Eigen and Schuster 1979). From the very beginning, the motor of evolution was the differential in energy and information between a heterogeneous (by mutation) proto-organism on one side, and a spatially and temporally heterogeneous physical world on the other. Each serendipitous fit (proto-adaptation) between a variant of one with a variant of the other, in terms of higher propensity for energy flow from environment to organism, led to a proto-aptation loosely fitting a proto-niche. Proto-aptations, or hypotheses, were passed on to the next generation and were subjected to competition and selection. Such internalized environmental predictability would have originally consisted of the physical-chemical properties of matter, including a differentiation between energy sources (such as hydrogen sulfide, or sunlight) and sinks (such as temperatures unfavorable to metabolism). It may then have progressed to include time and geological constants (solar and lunar rhythms such as diel, tidal, monthly, seasonal), and spatial dimensions and cues (magnetic, stellar and other orientation devices). With the advent of predation the need to predict would have broadened to include biosphere variables such as the properties of food and foes, both preferably to be detected early in time, over an increasing distance in space and at decreasing concentrations. Sense organs and their use, from the close-up-and-now variety such as touch and taste to the long-distance-and-ahead-of-time instruments of smell, hearing and seeing, are one set; effector organs such as for locomotion, defense, food catching, digestion and reproduction are another such set of sub-hypotheses that together make up the overall predictor which a successful organism must be.

Yet the asymmetry of the very energy flow facilitated by each successful prediction changed both organism and environment. The spatial asymmetry of energy flow was accompanied by a temporal asymmetry in information flow; as today's net energy flowed one way, tomorrow's information flowed the other. The result is that the energy source, i.e., the organism's environment, invariably comes out ahead of the energy recipient's predictions. As long as the energy source is non-living, both the magnitude of its lead and the direction in which it recedes from an organism's advances are governed by the degree to which it is depleted or otherwise influenced by the latter. But neither lead nor direction are inheritably linked to the organism's advances; a non-living environment is changed by, but does not defend itself against energy losses, nor does it pass on organized information about such - in contrast to the living environment.

Regardless of whether one agrees that life began in the form of information-biased nucleic acids or as metabolism-biased proteins, or the former parasitizing the latter (Dyson 1985), the energy differential between living matter (proto-organisms) and non-living matter (proto-resources) must have been rather small at first. One should assume, therefore, that competition was horizontal, between living organisms for non-living resources (including free organic molecules), rather than vertical, between living organisms for each other's substance. In other words, competition was mainly for resources outside organisms rather than for resources that had already been embodied as energy and information.

As proto-organisms grew in complexity they presumably also grew in bulk (be it one molecule at a time), and hence in energy content. The 'realization' by one proto-organism that another proto-organism was a more concentrated potential source of energy than the current source of both, led to vertical competition, i.e., predation/parasitism, and hence escalation.

Sex is extinction insurance

The prototype of sex, in the form of gene shuffling, may have originated with life itself, possibly as a molecular sloppiness during gene replication (Devoret 1988). It may then have been retained as a repair mechanism, both endogenous and exogenous, to substitute and/or weed out deleterious mutations (Bernstein et al. 1988). Genetic individuality, first a byproduct of sex, became its main purpose with the invention of vertical competition, i.e., the involuntary loss of energy by one organism to another. Because of the asymmetry in information gain between exploiter and exploited, species that operated as populations of unique individuals maintained a time lag between themselves and both their predators and their prey, and were therefore less prone to extinction. However, as predator and prey are linked in this energy flow quandary, every advance (adaptation) by the exploiter brought about a complementary withdrawal (counteradaptation) by the exploited. In genetically polymorphic species this would have resulted in time-lagged cycles (hence in no complexity increase), but each beneficial new mutant entering the game would have transported the players successively onto other levels of complexity. Together with the known mechanisms of sympatric and allopatric speciation, and keeping in mind that each adaptive step of an organism changes both its living and non-living environment, this mechanism can account for much of the complexity of today's biosphere.

In this view the only crucial steps in evolution were predation and sexuality; they seem inseparable like Siamese Twins. Predation arose as the realization by proto-organism A that proto-organism B had a higher energy content than B's (and A's) resource. Individuality arose as B's defense response, then became universal (except for brief opportunistic asex interludes when food was plentiful and predators scarce) as the best compromise between offense and defense. All other advances in the history of organisms, whether described in structural or functional terms, follow from this first compromise.

It is tempting to think that the long slumber of prokaryotes and early eukaryotes - which, based on the fossil record, may have lasted 2.5 billion years - was broken by genetic individuality taking on a prominent role as a self-accelerating mechanism for evolution towards complexity.

Individuality - Janus with promethean and protean features

In conclusion I see individuality, the product of sexual reproduction, as a janus-like[9] feature with a forward- as well as a backward-looking function. The forward-looking, promethean[10] function is fairly well appreciated; it is the ability to shed deleterious mutational ballast, take optimum advantage of heterogeneous resources, spread the costs and risks of aptations, and respond serendipitously to environmental change by creating new genotypes. The backward-looking, protean function, however, consists in laying a smokescreen that not only confuses pursuers but actually intensifies with the pursuer's success. This internal conflict between the two faces of Janus leads to the successive replacement of embodied energy with information, in response to the imperative 'be a great hunter but a small target'. Individuality can thus be expected to speed up the evolution of the pursued but check the evolution of the pursuer.

Individuality is the most cost-effective and flexible compromise between the conflicting needs of the organism-as-pursuer to home in quickly on a point target yet avoid, as organism-pursued, becoming a point target oneself. This aspect may be the main reason for the relative stability, over co-evolutionary time spans, of asymmetric organism-organism relationships such as epitomized in the life/dinner principle. Ontogenetic learning (i.e., the internalization of experience by the phenotype) gains increasing importance with growing organismic complexity, as an even-handed promise to the pursuer for faster response time, and to the pursued for better defense via greater individuality. Organism-organism interactions increase in proportion with the age, stability and complexity of environments as well as with the longevity, size and complexity of organisms; they increased over the history of life.

If life can be described as 'the drive to internalize energy and information so as to make more energy available for replication', then individuality introduces a second drive, which is directed 'away from the first'. Individuality balances both drives in a precarious compromise between 'eating but not be eaten'. The evolving emancipation of the soma, from mere vehicle for replicators (Dawkins 1976, 1982) to a body with a fair extension in time and space, is itself the outcome of individuality trying to accommodate these conflicting mandates. By encompassing the opposed needs of 'running towards' and 'running away from', the self-reinforcing Janus effect of individuality fuels the growing complexity in the evolution of the biosphere. In an analogy with the roles of mutation and selection one might credit 'life' with providing the raw material, and 'individuality' with molding it into complex shapes.

Janus-faced individuality therefore answers Bertalanffy's question why 'survival of the fittest', in a real world (as opposed to Spiegelman's sheltered petri-dish world), does not result in microbes only; it illuminates if not the meaning so at least the mechanics of an evolutionary drama in which "life spirals laboriously upwards to higher and even higher levels, paying for every step" with the introduction, at ascending levels, of death, pain, anxiety... (quoted by Davidson 1983).

It remains to be explored, though, to what extent some of the principles here outlined are applicable, as analogies or homologies, to the human condition. Is the drive to internalize energy and information, throughout evolution, at the root of human acquisitiveness and inquisitiveness? Is this why we relish ordering the world around us, including fellow humans, in categories yet strongly resent being categorized ourselves? Finally, is the time lag between an adapting organism and its receding environment the equivalent of the eternal gap between having and wanting, and therefore the ever self-renewing obstacle to the human conquest of happiness?

Notes

1. For simplicity's sake I follow Odum's (1983) lead in using 'energy' to stand for both matter and energy, in the sense of Miller's (1978) 'matter-energy'. 'Net energy' then stands for 'useful work extracted by an organism from free energy-matter that passes through the organism before it is excreted as degraded energy-matter and entropy'. This definition explicitly allows for time delays caused by energy-matter embodied and stored in the organism. The underlying assumption is that the major part of this 'useful work' will go towards reproduction, the balance towards somatic maintenance.

2. I define 'environment' here in the sense of 'what is relevant to a given organism' (Levins and Lewontin 1985), i.e., only what the organism interacts with energetically. The remainder of the non-living and living world that surrounds an organism *may* become environment in the same way an exaptation may turn into an aptation.

3. Following Gould and Vrba (1982) and Vermeij (1987) I am using 'adaptation' to mean

the evolutionary process that results in 'aptations', i.e., heritable features that promote an organism's fitness (=net energy balance in view of reproduction).

4. I am using 'predator', 'parasite', 'pursuer' and 'hunter' somewhat loosely and interchangeably as meaning 'exploiter of someone else's embodied energy'; and 'prey', 'host', 'pursued' and 'target' in the complementary sense of 'exploited'. The former, therefore, include herbivores as well as disease agents, whereas the latter include whatever is food to the former. I am aware that I am lumping a wide range of organism types and degrees of exploitation, but I believe that this simplification is justified in view of the shared asymmetry in energy and information flow.

Some of this vocabulary (including arms races, escalation, strategy, etc.) may sound uncomfortably anthropomorphic and bellicose; it is, however, the standard set of metaphors used in some biological disciplines (particularly sociobiology, but also immunology) to describe the changing fortunes of a resource and its user. My occasional use of 'he' and 'him', finally, when referring to a predator in cases where 'it' would be ambiguous does not imply a chauvinist belief that all predators are male.

5. For a broader treatment see especially Michod and Levin (1988).

6. I use 'individual' here in the sense of 'a genetically unique entity derived from sexual reproduction' rather than, like Buss (1987), as the opposite of colonial.

7. Notable exceptions are, among others, the absence of asex in many aschelminth taxa, and its presence in Tunicata (esp. Salpida), Reptilia (parthenogenetic lizards), and even Mammalia (i.e., polyembryony producing identical siblings in the armadillo).

8. In reference to the Greek god Proteus who was in great demand because he saw into the future and spoke the truth - but had to be caught in order to part with his oracle. Trying to escape he would turn himself into a lion, a dragon, a tree, water, fire... but concede defeat and talk provided one was not put off by his metamorphoses.

9. The Roman god Janus was usually depicted with a backward- and forward-looking face so he could watch over both the comings and goings at the gate over which he presided.

10. In Greek mythology, Prometheus foresees, and is credited with creating mankind out of earth and water.

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