Constancy, uniformity and symmetry of living systems: the computational functions of morphological invariance

Avshalom C. Elitzur *

The Seagram Center for Soil and Water Sciences, The Hebrew University, 76100 Rehovot, Israel

Abstract

Living systems, whether organs or entire organisms, display various forms of morphological invariance. Why? These phenomena are studied here from the Proto-Cognitive perspective, according to which evolution proceeds by processing information about the environment. The evolution of constancy, uniformity and symmetry is studied in detail. The study later focuses on the invariances of the plant's leaves and it is proposed that these invariances play a crucial role in the plant's development of individual form. Experiments are proposed to test these hypotheses. Morphological invariance is further examined in the light of thermodynamics and information theory. New thermodynamic restrictions are imposed on the processes of measurement and information recording. Uniformity and symmetry are shown to meet these restrictions. © 1997 Elsevier Science Ireland Ltd.

Keywords: Morphological invariance; Symmetry; Computation; Information; Thermodynamics

1. Introduction

Science-fiction movies depicting extra-terrestrial life often disappoint the biologist with their dull imagination. Nearly always, the alien in these movies appears highly anthropomorphic or resembling some other terrestrial organism. From the viewpoint of evolutionary theory, where chance plays such a cardinal role, the probability for such coincidences is much smaller than, say, the chance that two unrelated cultures, undergoing their independent histories, would raise two musicians who would compose identical symphonies.

One bet, however, seems to be safe when one tries to imagine how extra-terrestrial beings, if we ever encounter any, would look like: very probably, their bodies will demonstrate some form of symmetry. Whether their entire body or only parts of it would be symmetric, whether the sym-

* Present address: School of Physics and Astronomy, The Raymond and Beverly Sackler Faculty of Exact Sciences, Tel-Aviv University, Tel-Aviv 69978, Israel. E-mail: cfeli@weizmann.weizmann.ac.il

metry would be continuous (e.g. spherical or radial) or discrete (e.g. bilateral or threefold); dextrosinisteral (right-left), ventrodorsal (bottom-top) or anteroposterior (front-rear), is too risky to predict. But, based on all the known forms of living organisms on Earth, the general expectation of symmetry seems to be quite sound.

Why, then, do living organisms exhibit various forms of symmetry? Numerous discussions have addressed the biological *a*symmetries, while symmetry has been often taken for granted. However, the former only highlights the latter. Take, for example, the famous biomolecular asymmetry: all living forms possess proteins composed of 'left handed' amino acids while their nucleic acids, DNA or RNA, are made of 'right-handed' sugars. Various hypotheses have been proposed for the origins of this asymmetry, but nearly all of them agree that life could just as well exhibit the opposite handedness. Once primordial life has assumed left- or right-handedness, for whatever reason, the next generations simply had no choice but to adhere to it. But the initial preference is probably due to mere chance.

Symmetry, in contrast, has been dictated by evolution time and again, in independent lineages, even on the basis of previous asymmetries. It therefore reflects necessity rather than chance (Bérczi et al., 1993). In animals, for example, evolution has imposed somatic (external) symmetry upon the visceral (internal) asymmetry. Even in cases where topological constraints require asymmetry of the external structure, the initial symmetry is restored in another way. The left-right asymmetry of the conches of several snails is well-known, stemming from the unique difficulties posed by the task of magnifying a solid structure. Still, in those species who demonstrate a very high conch asymmetry, we witness a counterbalancing tendency of the conch to turn backwards rather than to the side. For example, in the *Cerithium*, whose conch is an elongated cone, the tip points straight backwards, thereby almost completely restoring the right-left symmetry. A peculiar example of symmetry (Neville, 1976) is seen in the eel *Leptocephalus diptychus*. During its post-larval stage, it has four spots on one side and three on the other. Asymmetry? No, because the body is transparent, thus displaying seven spots to both sides!

Why, then, does symmetry dominate the form of most organisms? And why, coming to think about that, should there be a common form to all members of the same species? And why, moreover, should organisms have constant forms in the first place? The search for explanations will carry us to domains as diverse as theoretical physics, morphology and epistemology. The issue is profound, prompting novel questions about the very nature of life.

2. The evolution of morphological invariance

Symmetry is only one example of morphological invariance, so let us first review the broader issue. I would like to show that, although the data looks inconsistent at first, overall morphological invariance increase with evolution.

We first notice that a few unicellular organisms, like *Amoeba*, do not have a constant form but ceaselessly change their form according to the varying circumstances. This plasticity enables the organism to respond to any change of the environment by an immediate change of its own body. This luxury, however, had to be given up by the multicellular organisms, who developed tissue specialization and constant form (in fact, even many unicellular organisms, such as the Class *Sarcodina* to which the *Amoeba* belongs, have constant form). In multicellular organisms, form constancy has developed gradually. The bodies of *Molusca* and *Annelida* exhibit a greater plasticity than *Arthropoda* and *Vertabrata*, who have a rigid skeleton. Also, *Vertabrata* are more rigid in that their growth does not involve metamorphosis but retains nearly the same form throughout the animal's life. Constancy of form is therefore the first step in the evolution of morphological invariance.

Once the constancy of form has been attained, the next stage was the development of uniformity. Two main trends have developed. Most sessile organisms, like plants and sponges, have a relatively constant form, yet it varies from one individual to another. In contrast, most mobile and locomotive organisms are uniform, with a typical bodily form shared by all members of the species.

The distinction between mobile and locomotive organisms is important in this context. 'Mobile' denotes primitive organisms that are passively carried by water or air, whereas 'locomotive' refers to organisms that move voluntarily. We shall see that sessility, mobility and locomotion pose different morphological challenges.

The differences are more notable in respect to the next level of invariance, namely, symmetry. Whereas form constancy exhibits the organism's resemblance to itself over time and uniformity exhibits resemblance of various individuals to one another, symmetry is the resemblance of various parts of the same organism to one another.

All uniform organisms exhibit also some symmetry, but its degree varies[1]. Symmetry is maximal in some of the most primitive mobile organisms such as the above *Sarcodina*, some of which have a nearly perfect spherical symmetry. Upper on the evolutionary tree we encounter locomotive organisms, such as *Nematoda*, that have a biradial symmetry. *Echinodermata* basically have a fivefold symmetry. Symmetry declines further in animals like *Arthropoda* and *Vertabrata*, where it is usually only bilateral. Symmetry too, then, is related to evolution, although apparently showing a trend opposite to that of form constancy and uniformity.

To summarize, morphological invariances appear to be fundamental characteristics of the organism's structure, increasing or decreasing with evolution. Could they be telling us something important about the nature of life?

3. The proto-cognitive model: life is a computational process

Evolution presents a paradoxical form of 'wisdom', namely, ingenuity of solutions to the environment's challenges without there being a sentient mind devising these solutions. This riddle lies at the basis of the Proto-Cognitive Model (Elitzur, 1994, 1995, 1996, 1997), which I would like to apply to the present discussion. A brief introduction to the model follows.

Central to the model is the assertion that evolution is mainly a computational process. This assertion follows from the trivial fact that the living state is an *optimum* state. Change, for example, the glucose percentage in an animal's blood; interfere with the length of a tree's branches; or slightly alter the position of a bee-hive—organisms invariably react with manifest distress, trying to restore the upset optimum, or, when the change exceeds some limit, they just die. Now, these biological optima strictly depend on the environmental conditions to which the organism adapts. Hence, in order to achieve these optima and, moreover, to achieve many optima that together create a higher optimum, the genome needs precise *quantitative* information about the environment. The gravitational force, average temperature, pressure, chemical composition, etc.—only such quantitative data, encoded in the genome, allows the evolution of phenotypes optimally adapted to a particular environment. Like the cognitive mechanisms used by the individual organism during its ontogenetic development, the species as a whole employs proto-cognitive processes during its philogeny. The species, as it were, 'perceives' the environment, 'measures' its relevant variables and 'computes' the data for the purpose of increasing adaptation.

But how can such quantitative tasks as measurement and computation be carried out and recorded as genetic information? Evolution does it with a very efficient mechanism, namely, differential reproduction. Each genome grants the organism a certain life-time, determined by the genome's fitness to the environment. This life-time is eventually converted into the number of the organism's offsprings. Consequently, in each generation there are different percentages of genes in the population's gene-pool. In populations of rapidly-breeding organisms, even the slightest advantage can lead to considerable differences in the number of the mutant's offsprings, giving the mutation a boost for further development. When sexual reproduction also allows the assembly of new combinations between the surviving genomes, then the population as a whole is engaged, in

---

[1] Significantly, when domestication of animals and birds creates patterns of fur and feathers that deviate from the uniform pattern, the change is asymmetric as well.

effect, in a very efficient *computational* process, capable of gradually reaching optimal solutions to conflicting environmental challenges.

This proto-cognitive process is performed mainly by exploiting statistical rules. Consider, for example, the way by which a population 'detects' very subtle environmental factors. The fate of each individual organism is determined both by: (i) conditions that are inherent to that environment and prevail in space and time ('signal'); and (ii) local, random fluctuations ('noise'). The individual's fate is therefore subject to the whims of chance. However, the overall population is governed by more deterministic laws, due to the famous '$\sqrt{N}$ rule' (Schrödinger, 1945). This rule states that the random fluctuations that inflict a measurement have the magnitude of the square root of the number of atoms involved in the measured process. Evolution takes advantage of this rule by producing *multitudes* of individuals of the same species. When natural selection interferes with the population growth, the fraction of the population that eventually survives reflects mainly those environmental factors that repeatedly occur at various sites and times. The random factors 'cancel out', as it were, at the statistical level, enabling the environmental signal to outweigh noise (Elitzur, 1995).

Every organism, to summarize, constitutes a cognitive organ, whose fate adds to the information accumulated in the species' genome. At the same time, the organism is also a carrier of evolutionary information. This is similar to our sense organs that, while receiving information, already embed enormous information in their very structure. The structure of the eye, for example, is based on a very rich evolutionary knowledge about the nature of light. The same holds for the entire organism: It contains information that solicits further information. To use the illuminating expression of Lorenz (1973), every organism constitutes a *hypothesis* about the world, put to test by the struggle for survival. Life thus gains information about the world by the active strategy of constantly putting forward hypotheses, to be later proved or disproved by natural selection.

With these formulations in mind, we return to our initial question. Why is the form of so many living systems constant, uniform and symmetric?

4. Morphological invariance and the invariance of physical law

One basic clue comes from theoretical physics, where invariance plays an important role. Three elementary invariances of physical law are: (i) invariance under translation in time; (ii) invariance under translation in space; and (iii) invariance under reflection. Now (i) seems to be related to the living systems' above constancy of form, (ii) to their uniformity and (iii) to their symmetry[2]. Is this affinity between the physical and the biological invariances only coincidental or does it reflect a more profound relation? The Proto-Cognitive Model suggests an affirmative answer to the second option. Perhaps the organism's invariant form reflects cognizance of the environmental invariances. Let us systematically follow this affinity.

If the organism's form ought to adapt to those features of the environment that are not random, then sessile organisms on the one hand and mobile and locomotive organisms on the other hand, should indeed differ in this very respect. The sessile organism adapts its form to the *local* environmental conditions that sustain temporary fluctuations. An example of such an adaptation is given by the plant, whose individual form accords with the local slope of the ground, direction of light, etc. Hence the great individual variety in most plants' forms. Notice, however, that the plant's form is nevertheless constant: Unlike few, short lived unicellular organisms, the longevity of multicellular organism's necessitates a form that adapts to the *persisting* environmental conditions.

For the mobile and locomotive organisms, the task is much harder: They have to adapt to conditions that wildly fluctuate not only from one moment to another, but also from one site to another. Hence, their body is adapted to those features of the ground, water or air that prevail

---

[2] The basic laws of physics are also invariant under time reversal. This invariance, however, holds only at the microscopic level, while macroscopic processes exhibit the famous time asymmetry of entropy increase. Significantly, this exception too is reflected in the clear time-asymmetry of biological processes.

everywhere. The hydrodynamic or aerodynamic forms of fish and birds are only two examples for a structure that relies on the invariant characteristics of the medium in which the animal moves. For this reason, rabbits should resemble one another more than potatoes: The rabbit is adapted not only for eating a particular clover or escaping a particular fox, but rather for eating all kinds of grass and escaping all predators everywhere. Uniformity therefore represents a higher level of constancy, extending the constancy over time to constancy over space as well.

But then, if uniformity increases with the evolution of motility, why does symmetry not increase too? Well, as a matter of fact it does. Like uniformity, overall symmetry increases in *spacetime*. Let us follow its development in some detail.

Mobile organisms, i.e. those that lack independent modes of locomotion, often possess perfect symmetry. The reason is simple: They equally interact with the environment on all their sides, hence their form is spherically symmetric. Such a perfect spherical symmetry is found in many *Bacteria* and *Protista*, that passively flutter in water. Breaking of this perfect symmetry appears when a preferred posture and/or a preferred direction for locomotion develops. *Schypozoa*, for example, such as the medusas, have developed a specialized direction for swimming, giving rise to anteroposterior asymmetry while retaining radial symmetry in all perpendicular directions. *Echinodermata*, on the other hand, such as the sea urchin, have developed a preferred posture but not a preferred direction for locomotion. Here too, asymmetry has developed in the ventrodorsal axis while fivefold or even radial symmetry has been preserved in the other directions. If the echinoderm is approached from the side by a predator or food, it will not rotate; it has the same defensive measures and eating organs in all its sides. If however, it is turned upside down, it will rotate along this axis, in which it is not symmetric, in order to resume its specialized up-down position. Higher on the evolutionary scale we find animals like those belonging to *Phylum Arthropoda* (e.g. insects) and *Chordata* (e.g. vertebrates), who have developed both a preferred posture and a special direction for movement. They therefore present symmetry

breaking both in the ventrodorsal and the anteroposterior axes. Yet, in spite of this evolutionary reduction of morphological symmetry, the constant motion and rotation of these animals gives rise to increasing invariance at a more complex level. The locomotive animal remains far away from the predator and close to the prey; it always turns to the food its face while its predator gets its back. A new invariance thereby appears: *The animal faces the environmental challenge from similar distances and angles.*

To better comprehend this invariance it is instructive to consider a mammal that is capable of giving up its asymmetry and returning to an almost spherical symmetry, namely, the hedgehog when assuming the defensive posture. Significantly, it remains motionless while in this posture, since it does not have to rotate or move. It appears the same from all its sides (a sphere's projection from all sides is the same circle). Compare this with the behavior of the squirrel when approached by a predator: It keeps moving and turning, such that the predator never sees its back. Thus both animals, so different in their reaction to danger, nevertheless demonstrate the same basic invariance: Their form remains the same to predators from every side.

Other vertebrates that has regressed to the earlier, higher symmetry are the snakes. Here too, loss of the ventrodorsal asymmetry (and partly of the anteroposterior asymmetry) in favor of biradial symmetry parallels the loss of the specialized mode of walking on legs in favor of unspecialized crawling in which all sides of the elongated body are equally used[3].

A surprising support for this explanation of uniformity and symmetry comes from plants. The lack of uniformity in plants has an exception in the form of some trees that possess rigid, constant forms, such as the fir or the cypress. Now, like primitive mobile animals, all such trees also possess radial symmetry in addition to their uniformity. Significantly, all these trees also assume a

---

[3] Hydrodynamic and aerodynamic forms are, by definition, symmetric for this very reason. Their interaction with the medium in which they move is equal in the sides perpendicular to that of their motion.

precisely straight upright posture. The explanation for their symmetry is therefore simple: These trees, like mobile animals, have adapted their form to the one environmental condition that does not vary from one spot to another, namely, the gravitational field!

Morphological invariance is thus related to the organism's mode of interaction with the environment. Organisms that maintain an invariant position in respect to other objects have low morphological invariance, whereas organisms that cannot maintain a positional invariance have a high morphological invariance instead. In this respect, plants and locomotive animals are similar while mobile organisms are distinct. Both sessility and locomotion represent attempts to maintain constant position in respect to important agents in the environment, whereas passive mobility must be compensated by high symmetry, enabling equal adaptation of the all the organism's sides to all locations.

We can therefore give a general formulation of the relation between the formal invariance of physical law and the morphological invariance of living systems. The macroscopic laws of physics are invariant under translation (in space and in time) and under rotation (in space). Statistically, this means that, in any given environment, most events are equally likely to occur to the organism at all sites, at all instances and from all angles. The organism's form, adapted to the invariant features of its environment, must therefore manifest similar invariances. And indeed, all organisms are invariant in one or more of the following senses:

1. organisms that ceaselessly change their form assume the same form in response to similar events;
2. organisms with a constant but individual form assume the same position at the same site throughout their lives;
3. organisms with a constant and uniform form that have no control on their position are highly symmetric, exhibiting the same projection to all sides;
4. organisms that are uniform but asymmetric along some axis assume the same relative position and relative angle to similar events.

5. Morphological invariance of sub-units

Morphological invariances are often more pronounced at the microscopic than at the macroscopic level. Even in non-uniform organisms, most cells of the same tissue are uniform. Many cells possess symmetry of their own. In fact, even the entire asymmetric organisms is cytologically symmetric in that the membranes in all its sides are composed of similar cells. Here too, it is not surprising to learn that neurons, whose function depends on their unique synaptic associations with the neighboring tissues, possess a very low uniformity and symmetry, whereas leucocytes, carried by the blood all over the body, are uniform and spherical.

Invariance of sub-units appears at the macroscopic level too. Such, for example, are plants, who usually have non-uniform and asymmetric forms, yet their leaves are fairly uniform and symmetric. In some plants, the number of leaves on each branch is constant, thereby creating appealing symmetry of the branches. In other plants, the branches themselves are arranged symmetrically. Many flowers possess threefold, fivefold, sixfold or even perfect radial symmetry. Many fruits have spherical symmetry.

In is in plant formation that I believe morphological invariance conceals some of the most profound biological insights. The plant's individual growth provides a fascinating subject for the student of morphogenesis because the plants' growing parts are, in effect, still embryos, continually growing new organs and yet accessible to direct observation. Leaves' uniformity and symmetry might prove instructive in the study of these processes.

6. Computational functions of leaf formation

Turning to the issue of plants' form, I hope I will be forgiven for beginning with a personal confession. Perhaps it does not merely reflect idiosyncratic taste; an interesting scientific problem seems to be involved too.

Of all civilized man's ways of interfering with nature in the name of aesthetics, nothing strikes

me as arrogant as the common practice of trimming trees. But why should such an innocent action offend me so much? It has to do with the feeling of awe and admiration that I, a dilettante biologist, feel when looking at an old wild tree. Erecting such a complex and stable structure only by molecular processes looks almost miraculous. Overcoming the gravitational force that threatens to break the tree branches and trunk, creating appropriate balance, avoiding branches' intersection with one another, the delicate distribution of leaves for an optimal exploitation of sunlight—all these difficult and even conflicting tasks, as well as many others, underlie the profound harmony and beauty of a mature tree's form. So, apart from its beauty, the tree's natural form presents a very elaborate solution to the environment's challenges.

Bearing in mind the central biological role of computation discussed above, surely the formation of a tree is a typical example of such a computation-based process. I would therefore like to call attention to the role of leaves in this computation. Our initial question is therefore posed in a new form: Why are the plant's leaves uniform and symmetric? In most plants the branches grow more intensively towards the more illuminated side of the plant, thus being non-uniform and asymmetric. Why then not the leaf itself? One possible answer is that symmetric and uniform leaves require shorter genetic programs for their production. However, bearing in mind the high complexity at the microscopic level that the genome has to create, leaf symmetry seems to make only little difference.

An intriguing explanation comes from the study of plant-parasite relations. Leaves are the main food resource of many insects and larvae. Luckily for the trees, many birds feed on these pests. It is thus desirable for the tree to inform the birds which of its leaves is harassed by the parasites. Could leaves' uniformity and symmetry enable the tree to do so? Heinrich (1979, 1992); Heinrich and Collins (1983) has provided three observations that support this hypothesis: (i) when the shapes of tree leaves were artificially damaged, the insect-eating birds frequented these trees or leaves more than undamaged leaves or trees; (ii) some caterpil-

lars carefully nibble the leaf margins in such a way that its symmetric form is maintained, thus making it harder for the birds to locate the damaged leaves; (iii) many oak species, whose leaves are neither uniform nor symmetric, seem to be immune to leaf-eating pests. Shmida (1992) has suggested a complementary hypothesis concerning flower symmetry, namely, that symmetry is positively correlated with high amounts of sugar in the flower. For this reason, so goes the hypothesis, pollinating insects prefer symmetric flowers. Symmetry, then, might enable the plant-beneficial animal to evaluate the plant's well-being, while asymmetry discloses the plant's illness.

Leaf uniformity and symmetry thus seem to provide efficient means of information transmission from the plant to other organisms. Could they also enhance the *reception* of information by the plant? The Proto-Cognitive Model seems to indicate an affirmative answer, supported by the following facts. The leaves of many plants change their angle throughout the day so as to get maximum sunlight. In order to best function as an 'antenna', for detecting the direction from which the light comes from, the leaf must be symmetric in relation to the direction that it faces. It is the comparison between the light absorbed by the leaf's right and left halves that enables precise location of the source's direction. Clearly, identical halves would perform this task most accurately[4].

The explanation for the leaves' uniformity is similar. The formation of branches poses many demands to the plant: overcoming gravitational forces, optimal exploitation of light, avoidance of intersection between the branches, etc. In other words, reaching optimal form requires a great deal of computation to be carried by the plant. This task of branch formation consume much more resources than the formation of the small,

---

[4] The comparison between the light impinging on the leaf's two halves can be carried out in two ways. In many plants the leaf's two halves maintain an angle that is smaller than 180°. In these leaves the comparison can be made between the angle in which the light impinges on the leaves. In other plants, who have completely flat leaves, the comparison can be made between the mere amounts of light absorbed by the two halves.

short-lived leaves. Now leaves, besides fulfilling their known photosynthetic goal, are also capable of affecting the plant so as to grow towards those directions where light is abundant. For the plant to properly detect those directions in which light is abundant, it should rely on the overall sum of signals coming from a *multitude* of leaves. It is only with such a statistical averaging that random fluctuations 'cancel out.' Our question thus gets a new form: Would this statistical task be better performed with uniform leaves or with non-uniform ones? Clearly, have the leaves had different sizes and forms, the task would be much harder. Only with uniform and symmetric leaves can the plant compare and average all the environmental signals received by all of them (Elitzur and Shmida, 1995).

There is a zoological analogue to this presumed mechanism. Increasing evidence suggests that flocking behavior among social animals enables the herd to reach optimal decisions by averaging all the individual movements (Deneunbourg et al., 1991; Kerlinger, 1989). Here too, the entire herd might reach an optimal decision by a 'referendum' based on the sum of the individual decisions.

7. Empirical predictions and further questions

The above hypotheses concerning the proto-cognitive functions of morphological invariance yield a plenitude of predictions that are worth being tested by experiment or observation. They also prompt a host of new questions.

When a rule is conjectured, an important test of the rule's soundness is this: Exceptions from the rule should prove to disclose exceptions in other aspects as well. We have seen this when discussing the exceptions displayed by radially symmetric trees and the spherically and biradially symmetric vertebrates. Each case discloses non-trivial deviations in the organism's general biology. It is therefore instructive to discuss a few other organisms that deviate from the morphological rules we have formulated above; they should reveal other biological exceptions as well.

In animals and birds, deviations from uniformity and symmetry in the fur or feathers pattern are nearly always the result of domestication. Still, there are a few exceptions in the wild. The males of the ruff (*Philomachus pugnax*) display highly non-uniform patterns during the breeding season. In the African wild dog (*Lycaon pictus*) the fur pattern is not only individual but asymmetric as well. Significantly, both these species are exceptional among their fellow species of birds and mammals, respectively, in their social life and breeding habits. Greater exceptions are those displayed by locomotive animals that are asymmetric not only in their pattern but in their very body. Snails are the most notable example, but then they are also notable in their slowness, which makes them exempt from the need for the symmetry imposed on hydrodynamic or aerodynamic forms. The asymmetry of chelea (claws) in *Crustacea* presents other interesting examples. The hermit crab (*Coenobita*) is asymmetric, but for a good reason: It is adapted to the empty snail shell in which it lives. The heteroechely of other *Crustacea*, on the other hand, does not lend to this explanation as they do not dwell in shells. It is therefore worth studying these cases to see whether these deviations from the common symmetry are similarly related to special biological specializations. Interestingly, one of evolution's latest products, namely, *Homo sapiens* and the hominid apes, display an inborn bilateral asymmetry in terms of the functioning of the hands. This breaking of the bilateral symmetry, the last that has remained intact in most locomotive animals, seems easy to explain once we recall that when these animals perform manual work, the object is kept in an invariant position in relation to the two hands, and therefore the left and right hand can differentiate and specialize in their roles.

From these few examples we can derive a general prediction for all organisms that deviate from the morphological invariances characterizing their taxonomic groups: They should all disclose biological adaptations unique to those species.

An interesting phenomenon seems to occur in descendants of domesticated animals that have become wild again. The domestic pigeon, descendent of the rock dove (*Columba livia*), has lost its original wild pattern of feathers and acquired a wealth of patterns and colors. Large populations

of such pigeons became wild again, inhabiting cities all over the world. Having observed many such flocks, it seems to me that their average pattern gradually converges again, not to the original pattern but to a darker, less elaborate and much less beautiful form, but nonetheless considerably uniform and symmetric. A systematic study is therefore warranted to see whether selection pressure enforces again uniformity and symmetry on the new patterns of previously domesticated animals.

The hypothesis concerning the computational role of leaf formation can be tested in a number of ways. Similarly to Heinrich's experiment mentioned above, leaves could be artificially cut so as to have asymmetric forms. If the hypothesis is correct, this interference should affect the leaves' ability to follow the movement of the sun during the day. Similarly, it should affect the normal formation of the branch on which the leaves grow, in comparison to control branches. Plants that exhibit symmetry in the arrangement of leafs on the branch provide further opportunities for such experiments.

Another test is to look for proportions between leaf uniformity and symmetry on the one hand and the form of the entire tree on the other hand. As noted above, trees that have a uniform shape exhibit also radial symmetry, thereby disregarding local conditions in favor of environmental invariances. From our model it follows that such trees should have less uniform, less symmetric and/or less elaborate leaves. Indeed, a few symmetric trees that I have occasionally inspected do exhibit such a relation, but only a systematic study could yield a reliable correlation.

An important step in the quantitative measurement of symmetry is the method developed by Avnir et al. (Zabrodsky and Avnir, 1995 and references therein). The method, originally devised to measure molecular chirality, has been later extended to other domains. Rather than distinguishing between chiral and achiral objects, Avnir et al. have provided an exact quantitative measure that allows one to distinguish chiral objects from one another by their degree of shape chirality. The application of this method to our subject in order to measure the degrees of leaf symmetry in

various plants would provide further tests for the hypotheses proposed above.

Of course, the explanation proposed here for biological uniformity and symmetry as serving proto-cognitive purposes does not exclude the prevailing explanations (embryological, functional, etc.) but complement them. Indeed, in is by now commonly accepted that many biological systems, besides carrying out their main tasks, also constitute information-processing systems. The most notable example is the vertebrates' respiratory system, that has developed the additional function of vocal communication. To take another example, the blood system in the brain serves not only to transport nutrients and oxygen to the brain, but also enables the brain to measure the body's temperature, chemical balance, etc. Information abounds everywhere, especially in living systems. It is only natural to assume that evolution has learned how to use such sources of available information. More particularly, plant development has been shown to be directed by auxins, i.e., hormones secreted by growing branches and affecting other parts of the plant (Kagan et al., 1992; Sachs, 1991; Sachs et al., 1993). It has even been shown that leaves can distinguish between ordinary light and light that has passed through other leaves, thereby avoiding the branches intersecting one another (Novoplansky et al., 1990). Further research is very likely to reveal other 'sensory' functions of leaves and, consequently, other cognitive functions of the plant. We can therefore conclude that the introduction of information-theory concepts such as cognition and computation into biology is likely to provide many insights into the physical uniqueness of the living state.

The fertility of this approach is demonstrated by the two rival hypotheses concerning the biological role of body symmetry: (i) Möller (1992) argued that females' preference for symmetrical males, observed in swallows, reflects preference for healthier males, while (ii) Enquist and Arak (1994) and Johnstone (1994) argue that this preference stems from the fact that symmetrical forms, being invariant under rotation, are easier to recognize from various angles. In the Proto-Cognitive framework, the two hypotheses are

complementary: By the same reasoning that asserts that an organism's form has to be rotation-invariant in relation to observers, this form should be similarly invariant in relation to the *environment*. Adaptation poses equal demands to both right and left sides of the mobile organism. A symmetric form, therefore, both conveys information about the organism's well-being and is easier to be recognized by other animals. The above studies of leaf-symmetry (Heinrich, 1979, 1992; Heinrich and Collins, 1983) lend some support for (i), in that they show that asymmetry is an indication of sickness, yet they do not exclude (ii) (notice, by the way, that the latter hypothesis provides a very reasonable explanation for the high symmetry of most flowers and fruits: they should appear rotation invariant to the animals they have to attract!). Indeed, once the two hypotheses have yielded quantitative predictions, observations gave varying support for both of them in a few species (Ridley, 1992).

8. Symmetry, asymmetry and the physics of measurement

To reiterate, the Proto-Cognitive Model extends the notion of cognition from the ontogenetic to the phylogenetic level. Like the individual organism that perceives the environment through sense organs, so does the species 'perceive' the environment through the overall population of organisms. In both cases, quantitative data about the environment (e.g. distances, concentrations, temperatures, etc.) is recorded, whether in the nervous system or in the genome. Such recording of quantitative data constitutes, in fact, a fundamental action of information processing, namely, measurement. Now, a closer look into the physical principles underlying information recording and measurement shows that these processes are intimately related to symmetry. A discussion of this affinity might shed further light on the issue of biological symmetry.

Rosen (1995), in a surprising theorem against the prevailing cosmological theories of symmetry breaking, has proven that asymmetry is a more basic concept than symmetry, the latter being devoid of meaning in the absence of the former. In other words, asymmetry could not have originated in a perfectly symmetric universe, because there is no meaning to symmetry without there being something asymmetric to serve as a frame of reference for the invariance under rotation or reflection. This theorem's significance goes beyond theoretical physics. In the present context, it has an important bearing on the very notion of measurement.

Take, for example, a ruler. It is asymmetric in that its figures regularly differ from one another. Otherwise, had the figures been identical, the ruler would be invariant under translation and therefore incapable of measuring an object's position. However, the concept of information requires a somewhat surprising twist of Rosen's conclusion: For the measuring instrument to precisely measure a specific variable, other variables must not interfere with this measurement; they are 'noise' in relation to the specific variable to be measured. We can therefore extend this conclusion to a general requirement for the operation of measurement: *The measuring instrument's structure must be symmetric in relation to all irrelevant variables.*

This, for example, is the reason why the ruler must be straight: While assigning different values to the points along its edge, it assigns the same value to all points in the dimensions perpendicular to its edge. Had it not been so, that is, had the ruler not been straight, it would be measuring a mixture of two or more dimensions, losing its precision.

When the measuring device can also record the result, then, similarly to the above spatial combination of symmetry and asymmetry in the device's structure, a symmetry–asymmetry combination is needed in the time dimension as well. Prior to measurement there is a symmetry of probabilities, which, upon measurement, gives its place to the asymmetry of the actual result. In other words, prior to measurement the measuring device must be in an initial state S_0 that can evolve into any one out of the possible consequent states S_1, S_2, S_3, … All these subsequent states are, prior to the interaction with the measured object, equally likely to occur. Once, however, measurement has taken place, the consequent state is irreversible.

The initial state is not likely to be restored. Consider, for example, an unexposed film: All points must be equally capable of blackening, whereas after exposure the blackened points cannot become white again. Let us generalize this rule into the second requirement for the operation of measurement: *Any measuring instrument must begin with a dynamically-symmetric initial state, so as to end up in the appropriate asymmetric final state.*

Biological perception meets both the above requirements, the structural and the dynamic one, for carrying out efficient measurements. Most perceptions constitute, in essence, measurements of asymmetry: Perceiving an object's location gives information whether it is on the organism's right or left side, above or behind it, etc. Now, in order for the perceptual mechanism to be unbiased when performing such an asymmetry measurement, *the perceptual mechanism itself must be symmetric*, lest its own asymmetry interferes with the result. Hence the parity of eyes and ears, the symmetry of antennas, and, as proposed above, the symmetry of leaves.

This structural symmetry meets also the second requirement, namely, dynamical symmetry. Consider again the antenna, the pair of eyes and the symmetric leaf. In all these cases, the radiation impinges on two nearly identical halves of the apparatus. This is S_0 in the above notation. However, the two halves absorb the radiation differently, depending on the relative position of the light's source (S_1 or S_2). The structural symmetry ensures an unbiased operation of the asymmetric response, yielding accurate information about the source's relative position.

Biological symmetry thus seems to play a basic role of information recording. It provides the organism an unbiased background (symmetry of probabilities) upon which environmental information (asymmetry of the actual result) can be efficiently recorded and processed.

9. Symmetry, order and information: a thermodynamic perspective

If symmetry serves information processing, its function should accord with thermodynamic laws.

A brief discussion of this aspect will complement our discussion.

As stated above, any recording of information, such as measurement, requires a system to be in a state where the system has equal chance to end up in any one out of a number of possible outcomes. Let this state be called 'pre-set state'. Thermodynamically, this state is characterized by two seemingly-opposite conditions: low entropy and low information. Let us examine the reasons for this requirement.

First, the system has to be in low entropy, i.e. high order. An ordered state, by Boltzmann's classic definition, is compatible with only a few microscopic arrangements, while a disordered state can be one out of numerous microscopic states (put in common sense terms, there are only a few arrangements that make a room ordered, but numerous ways to make it disordered). Put dynamically, the ordered state is far from equilibrium. The second law of thermodynamics makes such states highly unstable. It is this instability of the pre-set state of the recording device that the incoming information upsets. The system then moves to one of the many states of higher entropy, closer to equilibnum. The new equilibrium that has been reached is more stable, giving an irreversible record of the result.

Second, in the pre-set state the recording or measuring system must contain no information, lest that information interferes with the incoming information. Previously recorded information might exist in the system's memory, but not in the recording part, where it would be nothing but 'noise'.

Such a pre-set state characterizes, for example, the unexposed photographic film or the clean writing paper. They manifest both low entropy and low information and record information by irreversible processes that increase both their entropy and information content.

The thermodynamic uniqueness of the pre-set state is illustrated by the resetting, or calibration, of a measuring instrument. Resetting erases all previous information and brings the instrument back to the unstable state of low equilibrium. Interestingly, Bennett's (Bennett, 1987) resolution of the paradox known as 'Maxwell's demon'

shows that the main thermodynamic cost of any measurement is paid during the *resetting* stage. Resetting, whereby previous information is erased yet the system's order is increased, returns the system to the pre-set state. Following Bennett, I have elsewhere (1994) pointed out constant resetting as one of the most basic characteristics of all living systems.

Clearly, symmetry provides an efficient basis for the pre-set state. A symmetric object is an ordered one, as it exhibits improbable correlations between its two or more sides. At the same time, symmetry represents lack of information (Ne'eman, 1990). A symmetric arrow cannot yield spatial information; only asymmetry provides the necessary signal. This is why measuring instruments, as noted above, possess initial symmetry, to be broken by the interaction with the measured object.

Let us now return to the Proto-Cognitive processes by which the genome records information about the environment. Do these processes employ pre-set states? Indeed, such are the three forms of morphological invariance considered in this paper: (i) the constancy of the organism's form; (ii) the resemblance of all individuals of the same species to one another; and (ii) the similarity of two or more sides of the organism's body. Consider constancy first. An organism that lives longer than a few hours exposes its phenotype to the challenges of the environment for a long enough period to survive various fluctuations. The orderliness of this state, namely, the endurance of the same structure over a long period, provides an efficient test of the organism's fitness to that environment, just like the film exposed for a few hours to get a satisfactory picture of a dim star. Uniformity is another example for a pre-set state, operating on the phylogenetic level. When a single genome asexually multiplies, it gives rise to a myriad of identical individuals that invade that environment. The initial population is highly ordered, yet it contains no specific information about the environment. Only after natural selection has played its role, destroying many organisms, does the number of surviving organisms reflect the genome's fitness to that environment. Here, in fact, a reliable *experiment* is performed,

testing the survival value of that genome. The result, i.e. the number of surviving individuals indicating the genome's fitness, is very reliable due to the numerous *replications* of the experiment. Uniformity thus plays in evolution a role similar to that of replication in scientific experiments. Now, in a realistic situation, where reproduction is sexual, the population as a whole contains not one genome but many. These genomes share certain genes and differ with other genes. Therefore, they constitute *control experiments* for each other. Uniformity thus constitutes an ideal pre-set state, enabling a reliable test of each genome's fitness. Finally, consider symmetry. A pair of sense organs, placed exactly on the opposite locations on the animal's head, exhibit an ordered state, yet the organs themselves give no information about the location of the object that they sense. It is their unequal response to external objects that gives that information.

The definition of the pre-set state as a combination of low entropy and low information might seem contradictory to readers who are used to the common definition of information as the opposite of entropy. A deplorable confusion still prevails in the literature concerning the relation between entropy, order, information and complexity, especially in the context of life sciences (Elitzur, 1996). Equally, I believe, a correct application of these notions provides one of the most fruitful paradigms for modern biology. A thorough analysis of these terms and their applications is carried out elsewhere (1997).

10. Concluding comments

Three types of morphological invariance, namely, constancy, uniformity and symmetry, turn out to offer penetrating insights into the nature of life. In the framework of the Proto-Cognitive model employed here, constancy, uniformity and symmetry appear to be simple means by which life records and processes information about the environment, on both ontogenetic and phylogenetic levels. Morphological invariances exhibit high degrees of order, creating a blank, unbiased background for the recording of infor-

mation. They are thus akin to the basic scientific requirement of replicability. For the purpose of ruling out local, random artifacts, the replicated experiment or measurement should use identical, calibrated and unbiased instruments.

This framework has been shown to provide a wealth of testable hypotheses that warrant further research, as well as a new way of asking questions. The enormous variety of structures displayed by living systems, especially the highly accessible plants, is very appealing in this respect.

The precise relation between order, information, complexity and other relevant terms, especially in the biological context, warrants further study, now in progress (Elitzur, 1997). Needless to say that the preceding discussion has dealt only with a few of the fascinating questions posed by morphology and morphogenesis.

References

Bennett, C.H., 1987, Demons, engines, and the second law. Sci. Am. 257(5), 88–96.

Bérczi, S., Béla, L. and Molnar, I., 1993, On symmetry and topology of organisms in macroevolution. Symmetry Culture Sci., 2, 123–137.

Deneunbourg, J.L., Gross, S., Becker, S. and Sandini, G., 1991, Collectively self- solving problems, in: Self Organization, Emerging Properties, and Learning, A. Babloyantz (ed.) NATO-ASI series B-260, (Plenum, New York).

Elitzur, A.C., 1994, Let there be life: Thermodynamic reflections on biogenesis and evolution. J. Theor. Biol. 168, 429–459.

Elitzur, A.C., 1995, Life and mind, past and future: Schrbdinger' 5 vision fifty years later. Perspect. Biol. Med. 38, 433–458.

Elitzur, A.C., 1996, Life's emergence is not an axiom: A reply to Yockey. J. Theor. Biol. 180, 175–180.

Elitzur, A.C., 1997, Information, complexity, and the physical uniqueness of the living state. Preprint WIS-CP-96bc.

Elitzur, A.C. and Shmida, A., 1995, Biological symmetry and information processing. Symmetry 6, 178–181.

Enquist, M. and Arak, 1994, Symmetry, beauty and evolution. Nature 372, 169–172.

Heinrich, B., 1979, Foraging strategies in caterpillars: Leaf damage and possible predator avoidance strategies. Oecologia 42, 325–337.

Heinrich, B., 1992, Avian predation constraints on caterpillar foraging, in: Caterpillars: Ecological and Evolutionary Consfraints on Foraging, N.E. Stamps and T.M. Casey (eds.) (Chapman and Hall, New York).

Heinrich, B. and Collins, S.L., 1983, Caterpillar leaf damage and the game of hide-and seek with birds. Ecology 64, 592–602.

Johnstone, R.A., 1994, Female preference for symmetrical males as a by-product of selection for male recognition. Nature 372, 172–175.

Kagan, M., Novoplansky, N. and Sachs, T., 1992, Variable cell lineages during the development of somatal patterns. Ann. Bot. 69, 303–312.

Kerlinger, P., 1989, Flight Strategies of Migrating Hawks (University of Chicago Press, Chicago).

Lorenz, K., 1973, The Other Side of the Mirror (Hartcourt, New York).

Möller, A.P., 1992, Female swallow preference for symmetrical male sexual ornaments. Nature 357, 238–240.

Ne'eman, Y., 1990, The interplay of symmetry, order and information in physics and the impact of gauge symmetry on algebraic topology. Symmetry Culture Sci. 1, 229–255.

Neville, A.C., 1976, Animal Asymmetry (Edward Arnold, London).

Novoplansky, A., Cohen, D. and Sachs, T., 1990, How Portulaca seedlings avoid their neighbors. Oecologia 82, 490–493.

Ridley, M., 1992, Swallows and scorpionflies find symmetry is beautiful. Science 257, 327–328.

Rosen, J., 1995, Symmetry in Science: An Introduction to the General Theory (Springer, New York).

Sachs, T., Novoplansky, A. and Cohen, D., 1993, Plants as competing populations of redundant organs. Plant Cell Environ. 16, 765–770.

Sachs, T., 1991, Pattern Formation in Plant Tissues (Cambridge University Press, Cambridge).

Shmida, A., 1992, The ecology and evolution of the beauty of flowers. Preprint, The Hebrew University of Jerusalem.

Schrödinger, E., 1945, What is Life? (Cambridge University Press, Cambridge).

Zabrodsky, H. and Avnir, D., 1995, Continuous symmetry measures. 4: Chirality. J. Am. Chem. Soc. 117, 462–473.