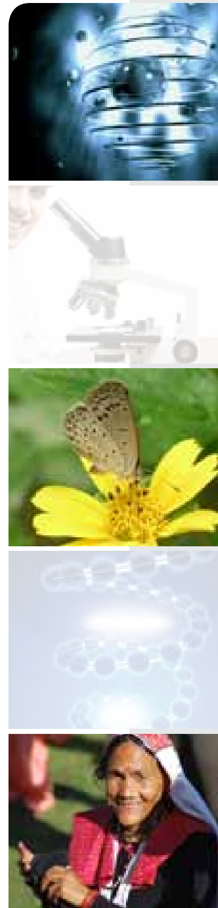
SYMMETRY AND BEAUTY IN THE LIVING WORLD



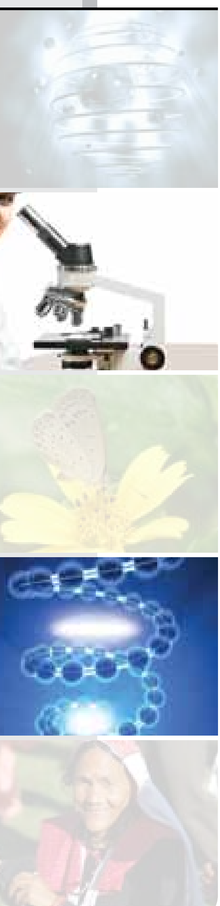
I thank the Governing Body and the Director of the G.B. Pant Institute of Himalayan Environment & Development for providing me this opportunity to deliver the 17th Govind Ballabh Pant Memorial Lecture. Pt. Pant, as I have understood, was amongst those who contributed in multiple ways to shape and nurture the nation in general and the Himalayan area in particular. Established to honour this great 'Son of the Mountains', the Institute carries enormous responsibilities and expectations from millions of people across the region and outside. Undoubtedly the multidisciplinary skills and interdisciplinary approach of the Institute and the zeal of its members to work in remote areas and harsh Himalayan conditions will succeed in achieving the long term vision of Pt. Pant for the overall development of the region.

My talk 'Symmetry and Beauty in the Living World' attempts to discuss aspects of symmetry and beauty in nature and their evolutionary explanations. I shall explain how these elements have helped developmental and evolutionary biologists to frame and answer research questions.

INTRODUCTION

Symmetry is an objective feature of the living world and also of some non-living entities. It forms an essential element of the laws of nature; it is often sought by human beings when they create artefacts. Beauty has to do with a subjective assessment of the extent to which something or someone has a pleasing appearance. It is something that people aspire to, whether in ideas, creations or people. Evolutionary biology tells us that it is useful to look for an evolutionary explanation of anything to do with life. When we try to do so, we discover that standards of beauty are related to the presence of symmetry, and both have an evolutionary underpinning.

Leaves, butterflies, fish and human bodies display approximate left-right symmetry; frog eggs show cylindrical symmetry; and adult sea urchins and starfish possess radial symmetry. Besides those, many embryos exhibit 'scale-invariance' to some degree: over a range of sizes, the relative proportions of the body parts (of the eventual adult) are more or less the same. How does symmetry originate in living systems? Related to the existence of symmetry,



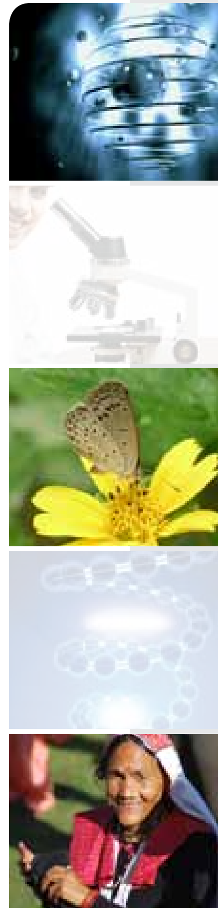
there is the concept of beauty. The concept is no doubt subjective. At the same time, it is culturally rooted. In common with cultural traits generally, it should be expected to have biological roots. What accounts for the fact that we have a notion of beauty at all? The 'ultimate' answer to both questions must be sought in evolutionary terms: according to a well-known saying of Dobzhansky, 'Nothing in biology makes sense except in the light of evolution'. Our sense of beauty has much to do with symmetry and is related to the way in which evolution works.

EVOLUTION

The Origin of Species marks a watershed in the history of science. This book by Charles Darwin established that life on earth was a product of organic evolution, namely a process of transformation based on natural law. Species were transformed via modification through descent; that was accompanied by their divergence into different species. The principle of evolution brought biology within the ambit of the physical sciences. Second, Darwin put forward, as Alfred Russel Wallace did independently, a means by which evolution could take place. He named it natural selection. Natural selection is a process in which certain traits (properties) spread within populations. They do so because an individual that possesses the trait does better in terms of survival or reproduction than an individual that does not possess it. Overall, the individual leaves behind more children (who propagate the trait in their turn) than the average member of the population. Such an individual is said to be more 'fit' than others. It is in this sense – and this sense only – that natural selection is also referred to as 'survival of the fittest'.

Sometimes the term 'Darwinism' is used for natural selection. This is unfortunate because the two stand for different things. Darwin made it clear that he believed natural selection to have been the most important, but not sole, means of effecting evolutionary change. Today, there is the growing realisation that other factors can constrain the scope of natural selection. They include environmental catastrophes, the 'interlocked' nature of early embryonic development, the fact that many creatures have a role in shaping their own environment, and principles of self-organisation.

Natural selection explains a striking feature of the living world: plants, animals and micro–organisms all give the impression of having been specially designed for whatever it is that they do. This is a property that they share with human artefacts: they appear to be products of design. They give every impression of being put together in a way that would make sense to an architect or engineer who had to design something for a pre-specified purpose. Keeping the purpose in mind, the designer or inventor makes an intelligent choice of the materials to be used and the means to be adopted so that not only is the goal achieved, but simultaneously, time and expense are minimised. In contrast, one cannot speak of a goal or a purpose of biological evolution. Rather, the outcome resembles a product of design, but there is no designer. Darwin and Wallace's discovery of natural selection was a big step towards the recognition that life is a property of matter.



SYMMETRY

'Symmetry' may be defined as follows: an object is symmetrical if it looks the same after it has been subjected to a transformation in space or time. The concept of symmetry can apply to abstract entities such as mathematical equations or physical laws; it can also refer to tangible objects. The transformations that one deals with usually are displacement (movement along a line), rotation and reflection. Symmetry is common in the living world. So is its opposite, asymmetry, or, more familiarly, 'handedness'. Therefore, one should expect that it has an evolutionary history. The type of symmetry seen in a particular plant or animal may reflect specific evolutionary pressures in the history of that lineage.

In principle, all but one of the 20 common amino acids that make up proteins can exist in one of two optically active isomeric forms. The two forms rotate the plane of polarised light in opposite senses: L, left-handed or 'laevo-rotatory' and D, right-handed or 'dextro-rotatory' (Fig.1). In practice, however, with minor exceptions, naturally occurring amino acids are always in the L form. D-amino acids are found in some opioid peptides,

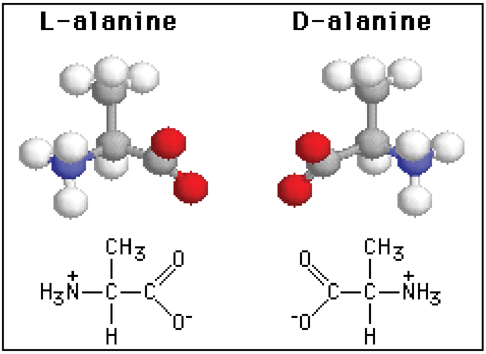
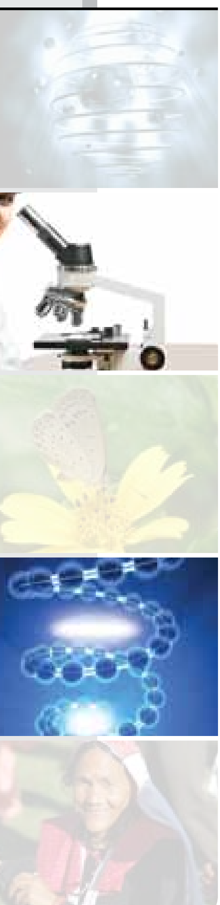


FIGURE 1: L-alanine and D-alanine (from http://www.phschool.com/science/biology_place/biocoach/images/bioprop/dlala.gif)

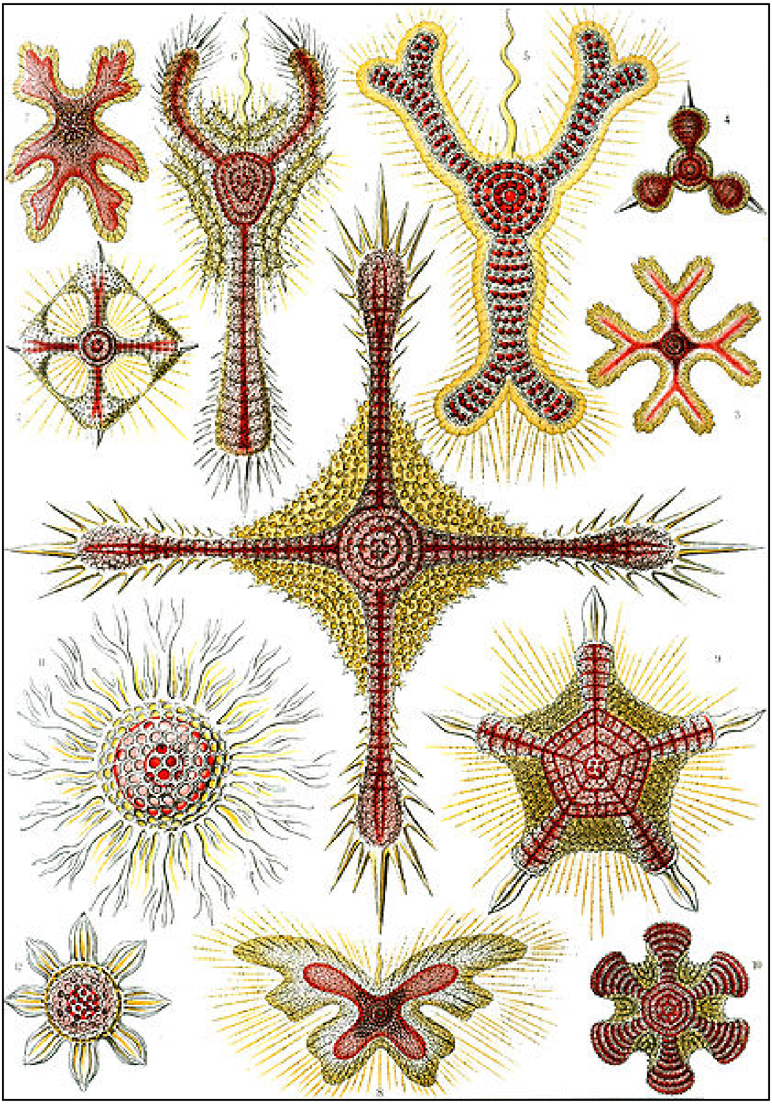


molecules with analgesic properties, and in snake venoms; also, they accumulate in the body with age.

Symmetries in the living world almost never approach the degree of precision that is displayed by, for example, crystal structure: the construction of biological objects is not all that precise. Typically, when one says that the left and right parts of the body are symmetrical, it means that the asymmetry is no more than about 0.5-2.5%. In contrast, the spacing between planes in a crystal lattice can be accurate to within one part in a million. A measurement of the extent to which electromagnetic transitions in atoms do *not* conserve left-right reflection symmetry yielded a figure of 1 part in 10^{16}. Microscopic and sub-microscopic forms of life such as diatoms and viruses are exceptions to the general rule that 'biology is less precise than physics'. The reason, of course, is that the forms of such tiny creatures are determined by very similar principles to those that lie behind crystallisation (Fig. 2).

Molecular transport and dispersed chemical reactions become significant with an increase in size; the integration of the whole, moulded by natural selection, becomes of overwhelming importance at still larger scales. All these factors contribute to departures from ideal symmetry. To illustrate what this means, consider an object that consists of 10,000 components. Each of them is assembled independently and is accurate to within one part in a million. Then the whole object can be specified no

FIGURE 2: Haeckel's Radiolarians ("Kunstformen der Natur, 1904: Discoidea"; from http://en.wikipedia.org/wiki/File:Haeckel_Discoidea.jpg)



better than within one part in a hundred. A macroscopic physical structure consisting of very many microscopic sub-structures would be expected to show a comparable level of imprecision.

SYMMETRIES IN BIOLOGY

Prominent symmetries exhibited by living forms are mirror-image reflection (bilateral symmetry), rotation, and rotation combined with translation (helical or spiral symmetry). The second category includes cylindrical symmetry, that is, rotation about an axis through an arbitrary angle (Fig. 3), and 3-fold, 4-fold, 5-fold,

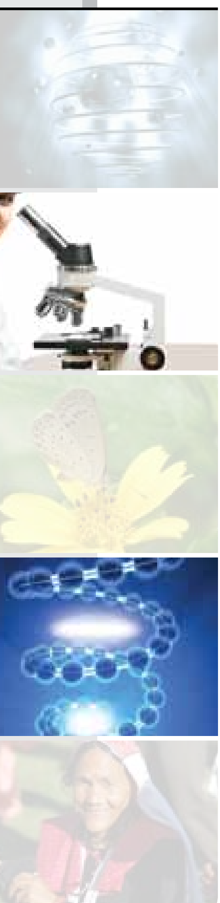
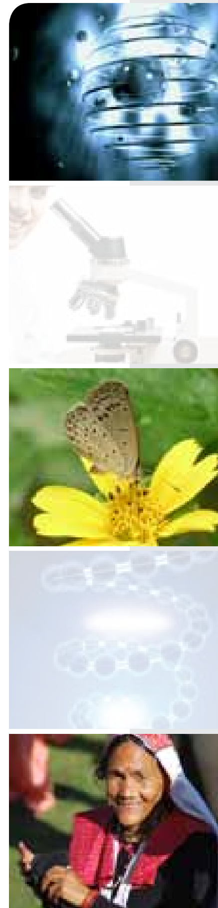


FIGURE 3: Haeckel, Sea Anemones ("Kunstformen der Natur", 1904; from http://en.wikipedia.org/wiki/File:Haeckel_Actiniae.jpg)

6-fold, 8-fold or higher rotational symmetry, going all the way to near-spherical symmetry (Fig. 4). A multi-protein structure, the proteasome, has been found to exhibit 7-fold symmetry; the presence of 5-fold symmetry (forbidden by crystallography) shows that we are dealing with biology, not physics.

FIGURE 4: Hollyhock pollen (from http://www.shelterpub.com/_symmetry_online/sym2_spherical.html)



There are unexpected features of symmetry in biology. First, the type of symmetry can change during the lifetime of an individual (e.g. a bilaterally symmetric sea urchin larva gives rise to a radially symmetric adult, see Fig.5; a bilaterally symmetric flatfish becomes asymmetric; a left-handed lobster can become right-handed following the loss of an appendage and regeneration). Second, an individual can exhibit more than one form of symmetry, sometimes in different parts (e.g. a plant can have both rotationally symmetric and bilaterally symmetric flowers,

FIGURE 5: Echinoderm (brittle star) changes from bilateral to radial symmetry during its life (from http://www.photomacrography.net/forum/viewtopic.php?t=652&sid=c5e1e08de879bc2977fa81e481c92563)

see Fig. 6; a fly larva that can display bilaterally symmetry as well as translational symmetry along its length). Third, symmetry may exist only at the level of the population, with each individual being either left- or right-handed (as in some flatfish).

A sub-category of population-level bilateral symmetry is known as *fluctuating asymmetry*. This means that although individuals are on the whole bilaterally symmetric, each of them is slight right- or left-handed. Sometimes the bias is hereditary, i.e. due to genetic factors; an instance of this is the handedness of shell coiling in some snails. In other cases it is an offshoot of the vagaries of development; the numbers of tail feathers on the left and right sides of the body in birds is an example.

The size reached by an adult is among the defining features of living systems. It is surprising, therefore, that many biological patterns can be indifferent to overall size. This is referred to as size invariance or scale invariance. One example is known to all of us, because the outcome is a pair of 'identical' twins (properly referred to as monozygotic twins; Fig.7). Such twins are the result when a single fertilised egg splits into two and each half goes on to develop into an embryo. Sometimes such twins

FIGURE 6: Digitalis (foxglove): Radially symmetric (top) and bilaterally symmetric (bottom) flowers in the same plant (from http://en.wikipedia.org/wiki/Floral_symmetry)

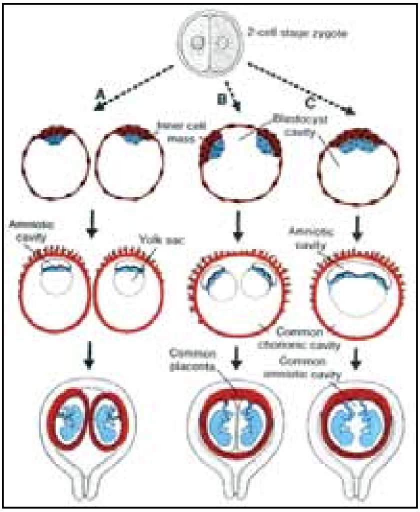
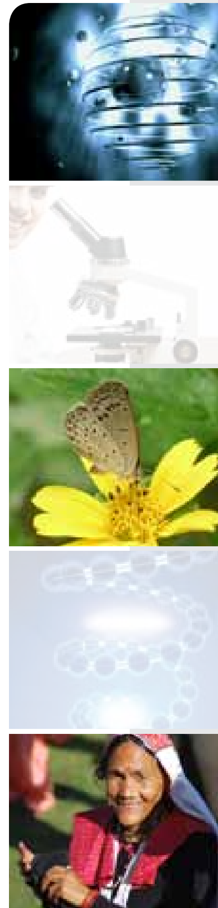


FIGURE 7: Monozygotic twins (from http://www.med.yale.edu/obgyn/kliman/placenta/twins/twinsdiagrams.html)



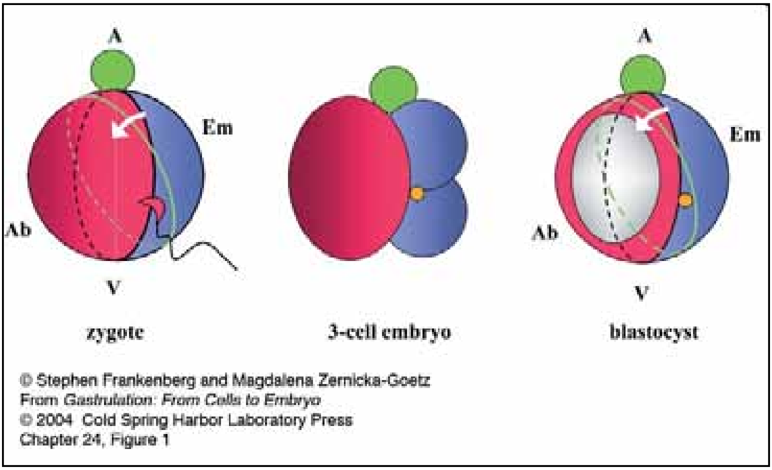
have opposite handedness. More spectacular cases involve the production of identical quadruplets or octuplets; this happens frequently in armadillos. In contrast to scale-invariance, there are many examples of *allometric* development. If we denote the linear dimensions of two body parts by x and y, scale invariance implies that x is proportional to y. In allometry, x is proportional to some power of y.

Interestingly, living creatures also exhibit *temporal* symmetries or symmetries in time. The early cell division cycles that follow the fertilisation of the egg resemble each other. It is as if a 'daughter' cell mimics the mother that gave rise to it. Also, oscillatory phenomena at the level of cells, tissues or whole organisms - are common in biology.

DEVELOPMENT OF SYMMETRY

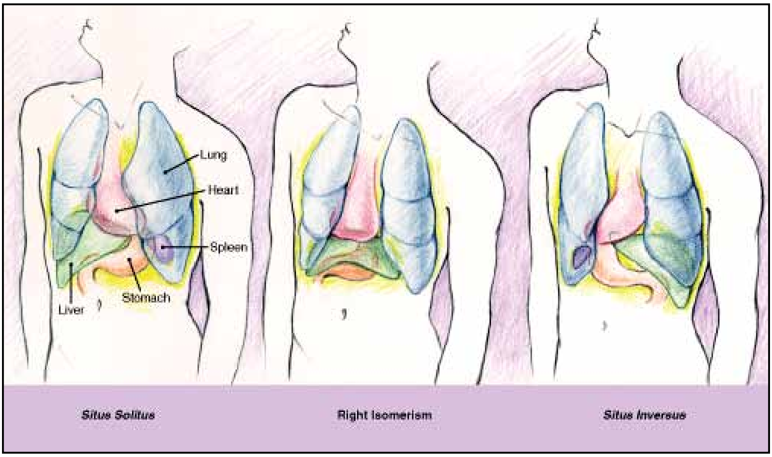
How does the symmetry of the living state develop? Many symmetric forms can be traced back to the symmetry of the unfertilised egg. But the egg is itself a highly differentiated product of the mother. This illustrates an important point. The conventional picture of a living organism as a static entity is misleading; we are all four-dimensional entities, changing with time. The end coincides with the beginning. This is expressed in the saying that the hen is an egg's way of making another egg. If an egg is cylindrically symmetrical, the point where the sperm fertilises the egg, with the cylindrical axis, defines a plane of bilateral symmetry. Then the egg can develop into a bilaterally symmetric adult (Fig. 8).

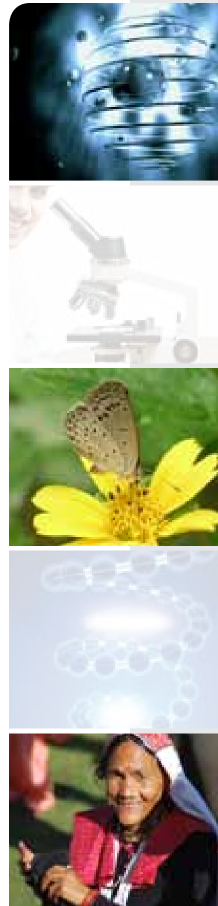
FIGURE 8: A cylindrically symmetrical egg becomes bilaterally symmetrical after fertilisation



However, an external appearance of bilateral symmetry can mask internal handedness. For example, the human heart is almost always on the left side of the body (Fig.9). There are theories that try to explain asymmetry as the result of a polarised spatial distribution of molecules inside the developing embryo. Two aspects of asymmetry are peculiar to human beings. One involves handedness - in the conventional sense that for performing a whole set of activities we prefer one hand over the other. The other aspect is related to a 'handedness' in the brain. Either the left or the right side of the brain is specialised in respect of certain tasks (e.g. the left side for language). The handedness of the hands and the brain are more or less independent of each other. On the whole the left hemisphere is dominant for language in left-handed people. But the right-hemisphere is dominant for language in a higher proportion of left-handers than right-handers.

FIGURE 9: Distribution of internal organs in the body showing *Situs inversus* (from http://www.rndsystems.com/mini_review_detail_objectname_MR03_TGF-betaLigands.aspx)

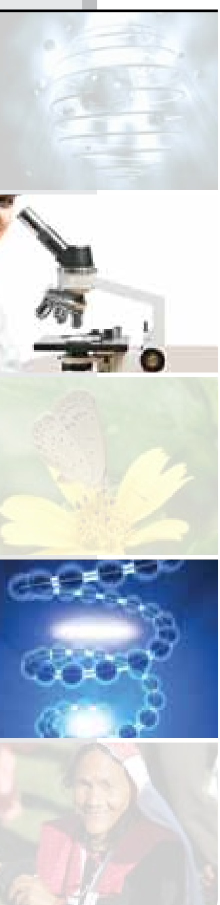




Discussions of how symmetry comes about during development often lean on a model that the pioneer computer scientist Alan Turing put forward in 1952. Turing's scheme explains how a perfectly homogeneous, and therefore symmetrical, system can spontaneously develop circular or bilateral symmetry, or periodic patterns (stripes, spots), or asymmetry, if the right sorts of chemical reactions take place. There can also be patterns that vary with time and resemble oscillations or travelling waves. The underlying cause is that molecular diffusion and chemical reactions are intrinsically 'noisy'. Such models have been used to explain the origin of periodic stripes on the skin of certain fish and for the symmetrical positioning of the plane of cell division in bacteria.

The genetic basis of biological symmetry is on the whole unknown. It may happen that the number of genes and gene products involved is so large that theorising about a genetic basis becomes uninteresting to. *Situs inversus,* an extremely rare condition in human beings, results in a mirror-image transposition of the heart and other internal organs., may be an exception to the rule. Such people are symptom-less and tend to remain undetected until their condition is picked up during routine medical examination. It may have a genetics-based explanation: there is a known genetic mutation in the mouse that gives rise to the same outcome. That apart, alterations in genetic states can affect symmetries in striking ways.

When a mutation that results in loss of gene function affects symmetry, it tends to do so by raising the symmetry, not lowering it. Normal (wild-type) fruit fly larvae are segmented along their body length. Superficially, many of the segments look the same. But they display differences on closer examination; these differences are lessened in mutant larvae. Along similar lines, the fruit fly *Drosophila melanogaster* has one pair of wings attached to a thoracic segment and a pair of balancers attached to the next posterior segment. A mutant can be four-winged; the balancers are converted to a second pair of wings. Here is an example of temporal symmetry. A certain round of cell division in the nematode worm *Caenorhabditis elegans* is asymmetric. The two daughters that result are both different from the mother. In a mutant worm the same cell division yields just one differentiated daughter; the other daughter resembles the mother. Therefore the mother-like daughter reiterates her pattern of cell division.

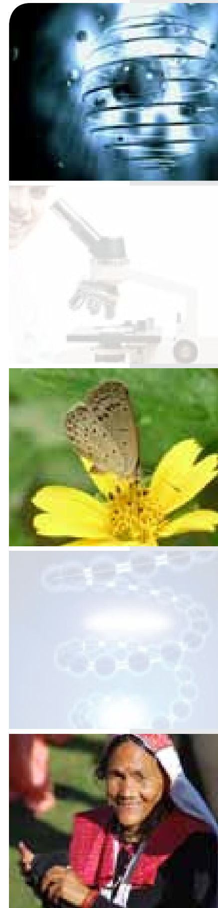


Reiterations like this are significant from an evolutionary viewpoint, because they indicate a return to a higher symmetry in the mutant form. Modern flies (dipterans) are believed to have evolved from four-winged insects, and insects are believed to have derived from animals like millipedes - or perhaps crustaceans. Both possible ancestral forms have body segments that are much less different than those in flies. In these cases the mutants just described resemble atavisms: they seem to hearken back to an ancestral state. Evolution involves the coming into play of new genetic capabilities. This suggests that behind the evolution of novel forms there may have been genetic functions that fostered symmetry-breaking transformations.

EVOLUTION OF SYMMETRY

Why is biological symmetry an almost universal feature of life? We can look for answers that are based on physics and chemistry alone. On the other hand, experience shows that it is useful to speculate on whether natural selection might provide an answer. One is made to think of the possible advantages of symmetry in terms of heritable components of reproductive fitness.

How might symmetry have originated during evolution and what might be responsible for its persistence? If cellular life began in the ocean, as is generally believed, the first question may have a straightforward non-evolutionary answer. Minimum energy considerations involving surface tension and fluid pressure would have led the very oldest cells to adopt spherical shapes.



The real issue concerns whatever might have lead to deviations from spherical symmetry. The evolution of sexual dimorphism may have played a role. One of the two sexes, the female, produces a large egg cell and endowed it with nutrients. If the nutrients are made of macromolecules, as in yolk, they will separate from the rest of the egg on account of their differential buoyancy: the egg acquires cylindrical symmetry. There is a plausible argument for the origin of bilateral symmetry too. Given that it is of advantage to cover the distance between two points in the shortest time, moving in a straight line would be favoured over moving in an arc. A bilaterally symmetric arrangement of the organs of motility would be economical. By providing equal motive forces on two sides of the body, it would allow for rectilinear motion. It would favour the reception of sensory inputs from as wide an angle as possible too. Amoeboid cells move randomly, but they can home in towards targets (e.g. food). Like them, many animals that make use of flotation (e.g. jellyfish) have retained cylindrical symmetry.

There can be symmetry in the population as a whole but every individual can be asymmetric. In some flatfish, a free-swimming adult drops to the ocean floor and begins a largely sessile life. Whether it chooses to rest on its left or right side is a matter of accident. The (new) lower eye and mouth move around to the

top after the choice has been made. At the end, about 50% of the population is 'right-handed' and about 50% is 'left handed'.

In lobsters and fiddler crabs one of the two anterior-most claws - it does not matter which one - grows to an enormous size and serves as a signal for sexual attraction. When the large claw is also used as an organ of combat, it may help individuals to develop it on the same side of the body as the prevailing majority; in that case one would get entire populations of left - or right-handed individuals.

The most intriguing, if also most controversial, evolutionary speculations involving symmetry revolve around fluctuating asymmetry. The term refers to the commonly seen deviation from perfect bilateral symmetry in individuals (e.g. the human face). Fluctuating asymmetry is ascribed to the fact that a host of chance factors influence the course of development. As a result the precision with which any feature develops is invariably less than 100%. Turning the reasoning the other way around, one can argue that individuals who show relatively low levels of fluctuating asymmetry must have incorporated a high level of quality control.

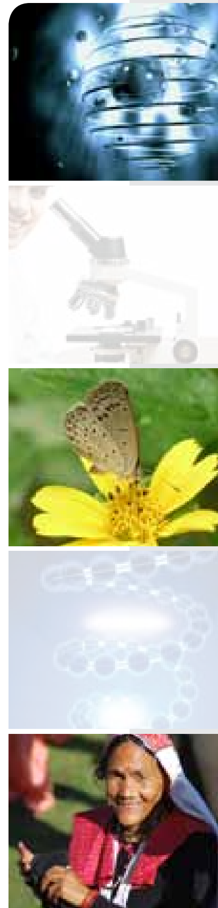
If so, their symmetry could be a signal of fitness, because they are showing that they are capable of investing the resources required to fine-tune developmental processes. The ability to detect and respond to the signal would be advantageous to potential mates as well as potential competitors. Some experiments show that such is indeed the case; females prefer males of higher symmetry. A similar tendency is said to exist in human beings too.

Yellow dung flies of the species *Scatophaga starcoraria* tend to congregate around fresh cattle droppings; males outnumber females 4 to 1. Measurements were made on three classes of males: those on a dropping that had paired with a female, those on the dropping that remained unpaired and solitary males from the surrounding grass. Males belonging to the first, successful, group had markedly similar left and right halves, but the males in the other two groups were quite asymmetrical. This was true of two structures that were monitored, the wing and the tibia (a segment of the foreleg).

What do these findings mean? Females obviously are choosing the most symmetrical males, but why? A possibility is that the more symmetrical a male, the larger it is: one can plausibly argue that a large male has "better" genes than a small one. But measurements did not bear this out: there was no correlation between degree of symmetry and body size. In fact, the largest males of the lot were those that were unsuccessful.

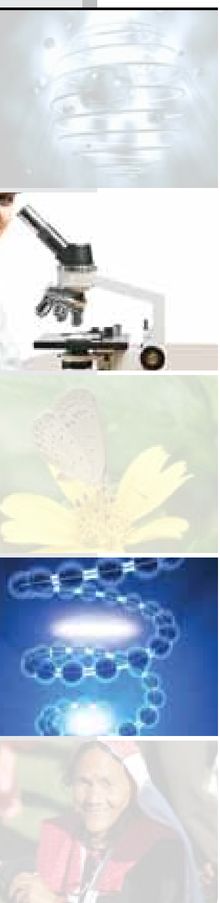
Two answers have been offered as solutions to the puzzle. One, suggested by the Liverpool scientists, is that symmetrical males are better at executing the complex manoeuvres associated with flying that are so essential for a fly successfully to complete for access to a female. For example, what aeronautical engineers call the wing load turns out to be smallest for the successful males, slightly higher for unsuccessful males on the dropping and highest of all for males that are just hanging around in the neighbourhood. The differences appear to be significant, as much as, 25 per cent of the average.

An entirely different argument, that we will come across again, has been advanced by the Israeli evolutionary biologist A Zahavi. Each may contribute part of the solution. Zahavi thinks that form and visual appearance act as powerful signals in themselves. They convey to an observer an accurate indication of one's real worth, which in the ultimate analysis means one's genetic quality. It is important for signals to be intrinsically reliable, because otherwise it becomes easy to manipulate others by sending misleading signals. In other words the signals that evolve are such that only honest signallers can afford it: Cheating is a prohibitively expensive option. When a weight-lifter lifts her weights we knew for sure that she has powerful muscles, just as we know for sure that a five-star hotel wedding means that someone is very rich. So a high degree of symmetry implies that the plant or animal is built with precision tools that have low error tolerances in terms of their genetic makeup – with 'good' genes.



BEAUTY

Human beings are products of evolution. Evolution takes place at two levels, biological and cultural. Culture is a reflection of organised patterns of behaviour. The possession of culture depends on a host of physical and mental abilities that depend, ultimately, on muscles and brains. But the engines of cultural evolution, namely nerve and muscle cells, are themselves the products of biological evolution This means that what we think of as culture, including values that reflect our idea of beauty, may have biological roots. Irrespective of whether the word 'beauty' reflects a cultural value-system or is the outcome of successful manipulation of our sensory and analytical capabilities, the biological question remains legitimate: *why* do we think of something as beautiful? Is it possible that what we think of as 'beautiful' may reflect an underlying component of fitness?



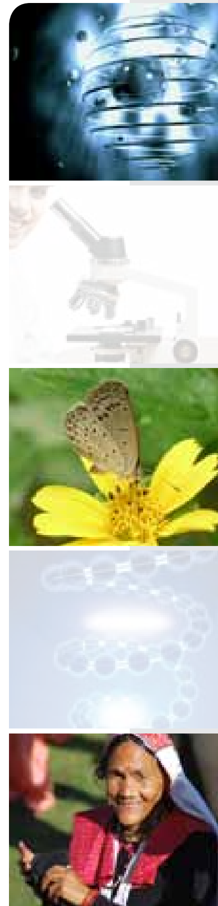
In attempting to answer this question, we should be aware of the possibility that the notion of beauty may not be uniquely human. Three quotations from Darwin point to this. The first is ".. when we behold male birds elaborately displaying their plumes and splendid colours before the females, .. it is impossible to doubt that the females admire the beauty of their male partners" *(The Descent of Man and Selection in Relation to Sex, vol. I, p 63, 1871*; see Fig.10*)*. The second quotation goes "In most, but not all parts of the world, the men are more highly ornamented than the women, and often in a different manner; sometimes, though rarely, the women are hardly at all ornamented (ibid, vol. II, p. 343; see Fig.11). Finally, ". each race has its own style of beauty, and we know that it is natural to man to admire each characteristic point in his domestic animals, dress, ornaments, and personal appearance, when carried a little beyond the common standard" (ibid, vol. II, p.369).

Sexual selection

Darwin developed a whole theory of what he called sexual selection to explain the evolution of exaggerated body ornamentation in individuals of one sex – usually the male. The ornaments are

FIGURE 10: Decorated tribesmen from Papua New Guinea (from www. caesartort.blogspot.com)

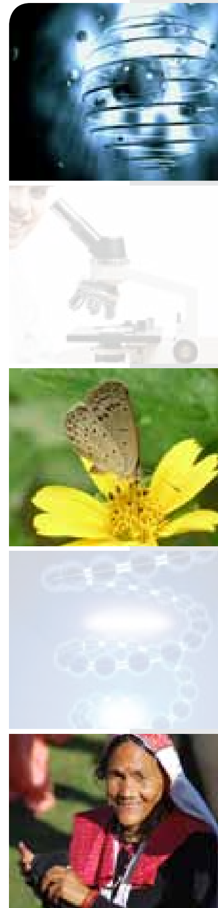
FIGURE 11: Bird of paradise (from http://returntotheoutdoors.wordpress.com/2009/10/12/the-whirlwind/blue-bird-of-paradise/)



often not just exaggerated, they are also attractive. The feathers of peacocks (see Fig.12), the tusks of elephants and body patterns on mating animals are examples. The reason why it is difficult to account for such exaggerations in a conventional manner is that they seem to harm, not help, their bearer. Peacocks with long tails have problems with flying, deer with large antlers can get trapped by tree branches and anything that is loud or vivid is an invitation to a predator. Sexual selection is a special case of natural selection in the sense that it favours the elaboration of differences between the sexes (whereas the simplest form of natural selection would lead to a reduction of differences between one individual and another).

According to Darwin, sexual selection depended on the fact that because one male could fertilise many females, the number of children fathered by males could vary a lot. On the other hand, whether a female mated with one male or many, the number of children born to her would be the same. Therefore there would be a strong premium in favour of males that could monopolise mating to the extent possible. Thus sexual selection was supposed

FIGURE 12: The elaborate tail feathers of the peacock (from http://library.thinkquest.org/05aug/01006/Peacock.jpg)



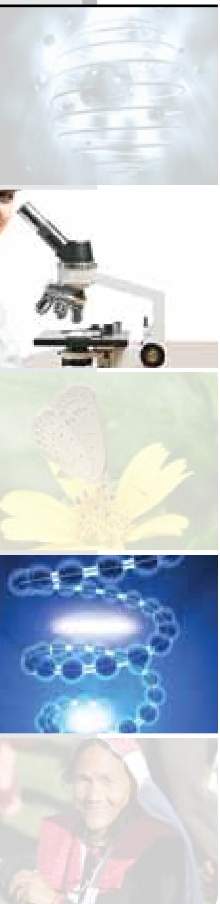
to be driven by two factors. First, males would compete with one another to get access to as many mates as possible. This favoured an increase in the size of males and also a development of their organs of combat (e.g. horns and tusks). Second, females would be choosy about which males they mated with. On what basis would they exercise their choice? Darwin thought that an aesthetic sense in females could make them prefer males with exaggerated ornamentation.

Sexual selection and symmetry

A number of studies show that the males that are more successful at mating are also more symmetrical. This has been found in many animals. In the case of plants, flowers that are more successful at eliciting pollinator visits are also more symmetrical. However, symmetry may not be the only factor involved. Zebra finch male chicks that have high levels of the steroid hormone testosterone are aggressive in begging for food and generally more dominant. Females prefer mating with attractive males, where the attractiveness can be manipulated by the experimenter by providing a red band around the legs. It appears that the female interprets (what we call) attractiveness as a sign of relatively high fitness and favours the eggs laid after such matings with an extra-large dose of testosterone. There is something similar to this in barn swallows. These birds are frequently infected by parasites. When that happens their fitness drops; for example, they do not grow as much as they would have otherwise. Sexual ornamentation in the male – as reflected by the length of the tail feathers – reflects the extent to which the male carries parasites. A heavy parasite load is correlated with shorter length. Finally, females prefer to mate with highly ornamented *and* symmetrical males. This suggests that just as a long tail indicates the relative absence of parasites, so also a high degree of symmetry may indicate a higher quality individual.

Sexual selection and beauty

Curiously, the tendency of the female to favour males that display exaggerated traits may depend on features of their sensory and behavioural makeup that predate the appearance of the traits. For example, male frogs of the species *Physalaemus pustulosus* have a special 'chucking' element in their calls, a feature that is attractive to females. Males of the related species *P. coloradorum* do not have this element in their calls. However, *P. coloradorum* females show a preference for artificial calls that have the chucks added on. In other words, what might be compared to an 'aesthetic sense' that assesses beauty may exist prior to and independently of the beautiful object.



On what basis might females exercise their choice? Darwin's guess was that the basis of the choice was entirely arbitrary, and that certain male traits just became more 'popular' - in a way similar to the spread of fashion among humans.('fashion', runaway selection) This guess was reinforced mathematically by R A Fisher, who showed that once the fashion began, it would rapidly lead to the fashionable element becoming exaggerated. Contemporary hypotheses of the basis of female choice are more rooted in conventional natural selection. W D Hamilton and M Zuk proposed that body ornamentation was in fact a signal of 'good genes' – for example, as in the barn swallow example, a highly ornamented male showed that it had the capacity to keep itself free of parasites. Therefore females were choosing males that would father children with similar good genes.

A third hypothesis seems strange at first but makes sense when one thinks about it. Proposed by A Zahavi, it says that the first impression one has of exaggerated body ornaments, namely that they are harmful, is in fact correct. The ornaments are indeed handicaps. However, a male that carries the handicap is advertising the fact that it can live with the handicap; in fact that it can overcome the handicap. It does so, because the handicap is costly. A male that lacked the necessary inner resources of stored nutrition would be unable to develop a comparable handicap. If it tried to do so, it would become so feeble in every other respect that it would not survive for long. In Zahavi's language, the handicap is an honest signal of the male's quality. The handicap principle has turned Darwin's theory of sexual selection on its head and has provoked a great deal of experimentation.

SUMMARY

Few things are as pleasing to the eye or ear as symmetry. Whether it is a flower, a bird or another human being, almost nothing excites our attention and quickens our interest as much as a symmetrical appearance. The opposite is true as well. Blatant lack of symmetry can be jarring, which is why Picasso's paintings are an acquired taste. Unlike mathematical symmetries, those in real life are approximate. Our left and right halves are not exactly identical, each petal on a flower does not match the others perfectly and the segments of an earthworm can be told apart (with some effort). Developmental biologists have been engaged on the question of what brings about a symmetric form in an animal or plant; evolutionary biologists want to know why symmetry should be there at all. It appears that symmetries are good for us…in an evolutionary sense. The pleasing quality of symmetrical objects, and our aesthetic preference for beauty, may have distant evolutionary antecedents.

ACKNOWLEDGEMENTS

Much of the present text has been reproduced from the following three sources: an article that appeared in the Economic Times of 29 April 1995, the Preface to a volume containing talks given at a symposium on evolution organised as part of the mid-year meeting of the Indian Academy of Sciences in July 2009 and finally, an article entitled "Symmetry in the Living World: How and Why", based on a talk given at the Indian Institute of Science Education and Research, Mohali, in February 2010. The last two are in the process of being published.

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