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Chance and Purpose

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A comment on Sir Alister Hardy's Gifford lectures entitled "The Living Stream" (*Collins*, 1965) *with special reference to lecture VIII "Some Problems for Current Evolution Theory".*

Regularly over the years there appear books outside the main stream of publications on what we may call orthodox theory of the mechanism of evolution. Many such books contribute little, being based on little scholarship and much misunderstanding and provide evidence only about their authors. A few, like this one, suggest new syntheses, clarify issues that require investigation or add new ways of interpreting orthodox theory and showing its relevance in wider contexts than hitherto. All of them remind us of unsolved problems that have been shelved because of their intractability, but which by act of faith we believe will ultimately find solution in the expanding framework of orthodox theory.

In this book, Sir Alister Hardy proposes to raise beside orthodox theory, and to integrate with it, the concept that behaviour is a selective force which he believes to be a major and neglected component of the mechanism of evolution. He holds the view that behaviour may provide a major innovatory factor, the selection of the environment by the animal being as important as the selection of the animal by the environment.

Hardy sums up what he believes "to be the generally accepted view as to the mechanism of the process (of evolution): the action of natural selection upon the inherited variations which are found within any population of animals or plants and which appear to be due to the chance random changes in the chemical constitution of the nuclear material". This is a brief summary of orthodox theory, which holds that mutational production of new genes, random *with respect to need,* is the primary source of innovation and recombinational production of new combinations of genes its secondary source, but it is an incomplete summary. Contemporary theory does not hold that either mutation or recombination are alone sources of innovation. Neither of these will often produce innovation in a well adapted population since both are regularly recurrent phenomena, and hence most mutants and most of the recombinants that can be produced by existing gene complexes have been tried before, found wanting, and rejected by natural selection. It is only when an old, hitherto rejected, mutant finds itself in a new situation that innovation is likely. The mutant may then increase in frequency and as a consequence become involved through recombination in wholly new gene combinations and it is these that are the real innovations. In the orthodox theory then, though innovation may sometimes depend either on extremely rare mutational or recombinational events, it will normally depend on change in the conditions in which the population has to live, that is change in the environment. It is change of environment which is the true innovatory factor. A well adapted population must be put into a new situation if evolutionary change is to occur, and, of course, all populations that exist are sufficiently well adapted to do so. Neglect of this aspect of orthodox theory is at the root of much dissatisfaction with that body of theory.

Change in the environment, however, is a very complex concept. The environment of a population varies in space as well as changing in time, and the environment of a gene or an individual changes as it moves in space as well as in time. Further, environment changes with genetic change as well as with external change, the environment of a dwarf pea differing from that of a tall pea, of a colour-blind person from that of a fully colour perceptive person. The environment therefore changes with changes of genotype within the population, and the different members of the population meet different environments. It changes with time as a result of genetic change of all other species that interact with the members of the population whether by co-operation or competition in exploitation of environmental resources, or by preying on or being preyed upon by the members of the population. It changes also with space, most notably at the margins of the population, upon which the successful population is ever pressing, but beyond which the population must be ill adapted, and beyond which dispersal of one kind or other must always be exposing samples of the population to natural selection in, to them, new environmental conditions. Finally it changes in more subtle ways with changes of population size, for not only does the density of a population change its environment but also the chromosomes of an interbreeding population are regularly tested against one another, so that the good mixers are preserved by natural selection. The genetic environment of a chromosome and hence the relative probabilities of survival of a number of chromosomes, i.e. their relative fitnesses, change with the number as well as the quality of other chromosomes to which chromosome has to be adapted.

Anything that changes the environment of a well adapted population, whether its origin be extrinsic, or due to the action of, or change in, the population itself, by changing the environment of the population or of parts of it leads to evolutionary change of that population through natural selection, providing that appropriate genetic variance is available or arises by mutation. It is clearly in this context that behavioural variation may be relevant. Behavioural variation will bring certain members of a population into new environmental conditions and hence expose part of the population to new forces of natural selection in which the relative fitness of differing genotypes are altered.

Hardy, following Thorpe and others whom he fully acknowledges, discusses this point of view most cogently. In the context of Darwin's Galapagos finches, which have evolved into a range of species with differing feeding habits and appropriate beak morphologies, Hardy asks, "Which is the more reasonable explanation of these adaptions: that chance mutations, first occurring in a few members of the population, caused these birds to alter their habits and seek new food supplies more suitable to their beak and so become a more successful and surviving race, or did the birds, forced by competition, adopt new feeding habits which spread in the population so that chance changes in beak form giving greater efficiency came gradually to be preserved by organic selection?" (p. 174). Hardy is here giving weight to the exploratory behaviour of animals. "The real initiating agent in the process is the new behaviour pattern, the *new habit*".

Thus far Hardy's view differs from the orthodox only in stress, for in effect he postulates that the exploratory behaviour of animals may take individuals beyond the margins of the existing environment and thus bring the population into a new environment. I see no reason to disagree, but would point out that, except in as much as the exploring animal may retreat from the new environment, it is formally in the same situation as that of animals or plants dispersed beyond the margins of the environment to which their parent population is adapted. If they survive they will come under new selective conditions. But genetic variants so dispersed must be adequately pre-adapted to the new environment if they are to survive, and it becomes a moot point whether it is the pre-adaptive variation, the dispersal, or the availability of the new environment that is the innovative factor. Likewise the individuals that adopt a new habit may well be a genetically appropriate and non-random sample pre-adapted to the new habitat the new habit opens up to them : behaviour genetics has not progressed far enough for us to know how often specific pre-adaptations must be relevant to the successful adoption of a new habit.

Hardy has certainly made a valuable contribution in stressing the role that behaviour must play in evolutionary innovation and tying it to the well established demonstration of genetic assimilation, and he is probably right in the view that most of us have underestimated its implications. As he points out, the change of selection with change of habit may sometimes be expected to have most complex consequences. "The importance of the activities and behaviour of the animal in determining its evolutionary fate is most obvious in cases where the animal is in a position to make direct use of a structure in a number of different ways—for example, to use its limbs for climbing, running, digging or swimming—but even physiological characters will also be affected. A change of diet will alter the selective value of digestive enzymes: a higher level of activity or a tendency to explore environments poor in oxygen will alter the selective value of changes in concentration or loading tension of blood pigments" (p. 186).

Further, in the special case where the species concerned has evolved to the level when social heredity is of importance so that the "new habit" discovered by one individual may be copied by its offspring or by less closely related individuals, as in the example of tits learning to open milk bottles, the behavioural innovation will be much more important for it may bring a substantial number of individuals very quickly into new selective conditions. Judgement of the importance of Hardy's point, therefore, depends in part upon judgement of the prevalence of learned behaviour generally. If we judge learned behaviour to be widely prevalent, we may judge behavioural innovation to be of great importance. Nobody will doubt that this has been so in the evolution of man, in fact it is the resulting origin of large scale social heredity and with it what I have elsewhere called evolution by "the inheritance of acquired environment" that has given man his special place on this planet.

Few, however, would raise this question for plants. Neither does Hardy. Nevertheless plants provide just as difficult problems as do animals when we wish to explain the origins of marvellously intricate examples of adaptation so that it is difficult to see how Hardy's postulates help to explain the origin of adaptations generally. Nevertheless Hardy does raise the question for all animals, and it is at this point that his book becomes controversial. His motive for doing so is clearly that he dislikes the chance component of evolution theory, and is searching for design, for final cause,[1] which he

[1] A "final cause" (not a proximal or last cause) is the teleological notion of a cause directing evolution to an intended result.

suggests may be maintained as a group-subconscious, holding the basic pattern of form within bounds consistent with the ultimate design.

Surprisingly enough, in lecture V, "The creative powers of selection", Hardy takes an orthodox view of the evolution of animal colouration, though colour pattern and behaviour must function in relation to one another. Yet he cannot take it when it comes to the question of the basic morphological pattern of a group or the complex examples of organization he treats as problems. He does not consider the point that we know most about the evolution of colour pattern and know very little about morphogenesis at all even at the embryological level so that speculation is freer in the latter context.

One has to ask therefore to what extent Hardy's problems are not created by his need for a final cause rather than merely by our present ignorance. In fact if we look at his lecture VIII "Some problems for current theory" we may legitimately question whether they are real problems in a general sense. The first is "the problem of homology". Only the most naive geneticist could after 1906 have believed, as Hardy said he believed in 1932, that "The same homologous structures must clearly be due to the same hereditary factors handed on generation after generation from the early ancestors with occasional changes by mutation". It was in 1906 that Bateson and his colleagues explained the Emily Henderson, Blanche Burpee sweet pea cross, showing both varieties were white for genetically different reasons. Hardy cannot believe that "the only explanation of homology . . . is that *selection by the environment* is governing the maintenance of all the internal spatial relationships of the animal", but I cannot really see his difficulty. "Selection by the environment" only means that the animal that works in that environment survives and the one that does not does not. And of course any change of one part can only make the animal work better in that environment (or any other) if that change leaves the animal organized. In other words change to be viable must conform to existing organization (which I might call "Empedocles' principle" [see below], and which another recent book *Internal factors of evolution* by Lancelot Whyte tried to raise into a "new principle" of evolution). Organization must be continuous, so that evolution is a historical process that can only build upon the past. It is an open ended process but every evolutionary stage limits the number of possible futures and homology is a logical consequence of this, especially since natural selection is more regularly conservative than creative, a point Hardy seems to have missed. Again, in discussing the transposition of segmental position of limbs or change in relative growth rate, Hardy seems to forget that individual development is, as it has to be, an organized process, and that mutational changes affecting one component of the developing organism must have consonant consequences on the development of other parts. Here is a point on which many commentators have gone astray, and thus found difficulty in believing that "random" mutations may produce organized effects. A mutation directly affecting one organ cannot be considered as affecting that organ only, because the different parts of an animal interact in development, so that the different parts develop in co-ordinated ways. An extreme mutant may affect the development of an organ to such an extent that this co-ordination breaks down: if so it will be rejected by conservative selection. Only organized organisms can exist so that their organization is no different reason for surprise than their existence.

Now the organization of development is little understood. But we do know that embryonic tissues have wider potentialities than are actually realized in development. The different parts of an embryo inhibit neighbouring parts from developing the "wrong" way and promote their development in the right way, and the result is that changes in one part produce co-ordinated changes in others. Many mutants are known which alter such control in drastic ways, such as producing a leg-like organ instead of an antenna. Environmental or experimental manipulation can have similar effects showing the multipotency of the parts when the control is altered. If a child breaks a bone in the upper arm and it is displaced, provided the arm is kept hung right so that the weight stresses are suitably placed, new bone will form in the non-bone tissue, and the displaced bone will dissolve away. One can see the new bone as fibrous looking lines on X-ray photographs within a week. In the face of such facts, I find no difficulty in the fact that the leg may be produced by segments 25 to 30 in one vertebrate and 8 to 10 in another, or in regarding the resulting legs as homologous, for surely it is the processes of development that are homologous, rather than the end results. There seems to me no need to postulate a final cause or archetypal design to explain these problems of homology that Hardy raises.

The second of Hardy's problems or puzzles is provided by what Medawar described as class B adaptations, all characteristics which could be acquired by use but are laid on in advance by development. Both Hardy and Medawar find most difficulty with the fact that "at birth a baby has a complete pattern of dermal flexure lines". Hardy states (p. 224) that "I must refer the reader to his full discussion of these interesting problems: I mention them here because the class B adaptations are in general those which are most likely to have been formed by the method of organic selection (or genetic assimilation if you prefer it); *however*, Medawar points out a difficulty which has to be faced. As he says:

> '... the selective forces are *sometimes* relatively obvious: if it is advantageous to have thickened feet at all, it will be advantageous to have them ready made when the foot is first put to ground. With other adaptations the selective advantage is much less obvious. What can be the value of genetically prefabricated flexure lines of the hand?'

What indeed? I borrow this question as another in my list of the difficult problems evolutionary theory has to meet".

I need only stress that one does not have to experience pregnancy to know that an unborn baby may be very active! In fact this activity is surely part of the developmental process. The developing attachment of muscle to bone, the developing relation of bone end to bone socket are kept under control by movement. The stretching of tendons controls the direction of elongation of cells and so on. Perhaps the dermal flexures of the new born baby's hands *are* a consequence of use.

Again I find his examples of flatworms acquiring weapons from the hydra they eat no different from other examples of the intricacy of biological organization (p. 229). "*Technitella legumen* constructs a long cylindrical case entirely of sponge-spicules it has picked up from the sea-bed (Fig. 69); Heron-Allen and Earland described it as follows:

> 'The shell wall consists of two distinct layers of spicules: an outer layer, in which the spicules are all laid with their long axes parallel to the long axis of the test; and an inner layer of spicules laid with their long axes at right angles to the outer layer. We thus get as close an approximation to 'woof and warp' as is possible with a rigid, non-flexible material, and it is obvious that the strength of the test must be enormously increased by the crossing of the two layers, as resistance to tensile strain is given in two directions instead of one'."

This I find if anything less remarkable than the fact that unicellular plants can manufacture their own cellulose fibres and lay them down in just the same way as warp and woof in making their cell walls, and I see no need for fundamentally different explanations of the two even though one does involve what is conventionally called "behaviour" and the other does not.

All these would seem to be examples of the organization of organisms which must be organized if they are to exist. Because they must be organized if we are to observe them, it seems to me that the fact that they are organized can tell us nothing of how they came to be organized.

I would say the same of each of Hardy's problems except the last. This latter, an example of the beautiful and complex patterning of male birds, Hardy clearly misinterprets, because, I think, of his behavioural bias, when he says (p. 232) "Such colour patterns and behaviour, we now realize, are mainly concerned with stimulating the female to co-operate in the sexual act and to maintaining the bond of partnership between the pair till the family are reared". Hence his puzzle that "with the great variability of the gene complex . . . I remain surprised that the design, the *plan* of its layout, is indeed so constant". He has missed the primary function of such patterns. Their origin, and their contemporary stability, must relate to their other function, not as stimulants, but as discriminators. They surely originated as part of the isolation mechanism that keeps the species separate from other species. Conservative selection will continually function to keep the pattern constant despite the genetic variation available, for it must preserve both functions so that the species will remain isolated and continue to reproduce. If either failed the species as such would cease to exist.

Once this is understood this becomes but another example like all Hardy has raised, as have many before him, where the problem is to explain the co-ordination of behaviour and morphology, of the development of one organ and another functionally related to it. His problems are all examples of the old problem : the evolution of organization, marvellously intricate and appropriate organization in manifold variety. And so the influence of Paley's argument from design comes in. Can such design originate by the selection of random chance mutations or must we invoke some teleological principle, some final cause?

But, and with this *but* the cogency of such arguments must fall, I repeat that if organisms were not organized they would not exist. Back to Empedocles who postulated that life originated as a collection of spontaneously generated limbs and bodies and heads, which combined at random to form animals. Of these only those which functioned survived, hence the origin of organisms (and a rational explanation of a few mythological monsters into the bargain). Empedocles was at least clear that organisms must be organized if they are to be. That they are can provide no evidence as to how they came to be so. The selection of chance mutations must produce design just as much as direction by deity, *élan vital,* or anything else, and in a heterogeneous changing environment presenting manifold potential habitats it will produce design in manifold variety.

I therefore feel that Hardy has failed to show that there is any necessity to add any substantial new principle to orthodox evolution theory. He leaves me with the quotation from Simpson that he uses early in the book (p. 14) still perfectly acceptable. "It would be brash, indeed, to claim complete understanding of this extraordinarily intricate process, but it does seem that the problem is now essentially solved and that the mechanism of adaptation is known. It turns out to be basically materialistic, with no sign of purpose as a working variable in life history, and with any possible Purposer pushed back to the incomprehensible position of First Cause".

But I would take issue not only with Hardy, who is searching for justification for his thesis, but also with Simpson who concludes that "Man is a result of a purposeless and materialistic process that did not have him in mind". Both fail to realize that unpredictability may be perfectly compatible with design and purpose in the Universe, and Simpson seems to miss the possibility that the Universe might have purpose even though the purposer did not have man in mind.

First let us consider what the prerequisite of continued life on this planet is. It is that living things once originated must be able to survive contemporary conditions and leave, over the long term, descendants capable of surviving future different conditions. Now, unless we suppose that primitive early life on this planet was always *able to predict* future conditions, something that we ourselves are pretty incompetent at, then the prerequisite of continued survival is ability to adapt to an *unpredictable* future. The only way to do this is to generate variance at random in sufficient (but not excessive) quantity, which, as I have discussed elsewhere, is exactly what the genetic systems of successful organisms do. Most such random variations are undesirable and are eliminated by stabilizing selection which I have here called conservative selection. But the continued production of such variation is a prerequisite of survival in the unpredictable future. In other words the need for a random chance component in evolution is built in to the design of the Universe if indeed the Universe is designed. Chance therefore is a component of design. Indeed I would maintain that it is the key to understanding the design, or purpose of the Universe.

It is only if one is prepared to accept that in some at present unknown, hence mystic, way organisms have always been aware of the needs that the future may impose upon their descendants that we can escape this conclusion.

Hardy accepts this and his position is self consistent. He does so because he seeks design and seeks it as a final cause. I cannot accept it because the whole notion of final cause is antithetic to me. It makes the whole of evolution past and future predictable, closes all the open-ended questions, negates all freedom, requires that every quantum jump, every mutation, every genetic recombination, every act of choice, be wholly determined in time and place, and makes nonsense of my sense of responsibility.

Further I find it impossible to make sense of a creator who could gain anything from the creation of a wholly predictable Universe. Contemplating one's own image provides limited satisfactions. Man made in the image of God seems to me a lesser purpose than Man, or rather something better, that is self-created. If therefore we were to postulate a Creator, would we not be forced to suggest that for the creation to have purpose its consequences must be unpredictable? A random element must be built in and left to function without interference so that there shall be interest in the outcome. A wholly predictable Universe makes no sense to me. But it might make sense to suppose that the purpose of the Universe is that it should create something unpredictable with whom community could prove worthwhile.

This argument is I am aware, naive. But I think it less so than Paley's argument and all those related to it. Evolution on this planet is a historical process in which chance plays its part and as such is not in detail predictable. Every event, whether "caused" or not, limits the infinite number of possible futures to those including that event in their past. There may remain an infinite number of possible futures, for at the beginning there were doubtless an infinite number of infinite numbers of possible futures (most of them leading to an early extinction of life here but perhaps to more interesting creations elsewhere!). Chance played its part at many places, but the surviving organisms must appear designed. If the Universe itself was designed for a purpose, chance is part of that design and there can be no finality in arguments that attempt to evade it.

This book is sincere, self-consistent, well argued, and worth much study. It has done much to aid me to clarify my thoughts on design and chance and hence I have found it a book of great value even though, as I have tried to make clear, I think much of it is fundamentally wrong.