

BOOKS BY JOHN BROCKMAN

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The **THIRD CULTURE**



by John Brockman

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Chapter 1

GEORGE C. WILLIAMS

"A Package of Information"

NILES ELDREDGE: I remember the English evolutionary geneticist John Maynard Smith remarking to me that he was astonished to find out that George Williams wasn't in our National Academy. Williams finally got elected in 1993. When I visited him in Stony Brook in the mid-1980s, he told me he was having a hard time getting grant support for his research, and I couldn't believe that. The two thoughts converged, because George really is the most important thinker in evolutionary biology in the United States since the 1959 Darwin centennial. It's astonishing that he hasn't gotten more credit and acclaim. He's a shy guy, but a very nice guy, and a very deep and a very careful thinker. I admire him tremendously, even though we've been arguing back and forth for years now.

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GEORGE C. WILLIAMS is an evolutionary biologist; professor emeritus of ecology and evolution at the State University of New York at Stony Brook; author of *Adaptation and Natural Selection: A Critique of Some Current Evolutionary Thought* (1966), *Sex and Evolution* (1975), *Natural Selection: Domains, Levels, and Challenges* (1992), and coauthor (with Randolph Nesse, M.D.) of *Why We Get Sick* (1995).

GEORGE C. WILLIAMS: Evolution, in the sense of long-term change in a sexually reproducing population, depends on the relative rates of survival of competing genes. Given that organisms may find themselves in an environment where there are close genealogical relatives, it follows that an organism is expected to react to cues of kinship in a certain way, so as to discriminate among the individuals it encounters on the basis of kinship, and be more benign and cooperative toward closer kin than more distant kin or nonrelatives.

My interest in evolution started in the summer of 1947, when I spent six weeks in the Painted Desert with a paleontologist named Sam Welles, who had a group of students there, officially in a summer course, but we spent most of the time swinging picks and shovels, digging fossils, as part of Welles' research project. He was a specialist in Triassic amphibians. Evenings were spent sitting around the campfire talking about things like evolution. For the first time in my life, people—real biologists, real scholars—were willing to sit and listen to my opinions. I was twenty-one years old. I certainly became interested in many aspects of evolution then, and shortly after that I signed up at the University of California at Berkeley for a course in evolution with Ledyard Stebbins, who at the time, and for quite a while thereafter, was the world's primary expert in evolution with respect to things botanical. Stebbins' course introduced me to Theodosius Dobzhansky's *Genetics and The Origin of Species*. Stebbins was great, but Dobzhansky's book was what got me interested in natural selection as a process.

At the University of Chicago, my job was strictly teaching. I was in their early-entrant undergraduate program—taught freshmen and

sophomores biology. They had a great-books approach. We read Darwin, Mendel, and others. Also I attended seminars by people such as Alfred Emerson, the termite specialist and recognized authority on things evolutionary. I found his ideas absolutely unacceptable. That motivated me to do something. If it was biology Emerson was discussing, I would be better off selling insurance.

I remember especially his lecture on the role of death in evolution. He was all in favor of death, and said that the reason we grow old and die is to make room for successors, so that they can have a chance. This seemed so totally impossible, given that evolution proceeds by natural selection. There was absolutely no logical way you could reconcile his ideas with Darwinism, even though he claimed to be a Darwinist.

This initiated my first theoretical obsession: the evolution of senescence—the decline in adaptive performance with age. You can't run as fast at sixty as you could at thirty. On the way home that evening, talking about the problem with my wife, I independently came up with an idea that Peter Medawar is chiefly responsible for and published in 1952, although he may have published something that foreshadowed it in the 1940s—and that is that the effectiveness of selection in maintaining adaptation is essentially the product of reproductive value and survival.

The survival factor is easier to appreciate. If you're more likely to be alive at thirty than at sixty, then selection will be more effective at maintaining adaptation at thirty than at sixty. At an age you'd be extremely unlikely to survive to, such as one hundred years old, adaptation would be a lost cause, and selection wouldn't be concerned with it.

As the effectiveness of selection declines, the effectiveness of its products declines. This explains the rising mortality rate that comes with age. It seemed to me at the time, and still does, that this is an inevitable conclusion, arising from just the simple fact of mortality. If there's any possibility of dying, at any age, then you're less likely to be alive at a later age than you are at an earlier age.

Another one of Alfred Emerson's ideas was that evolution is much more concerned with cooperation than with competition. It seemed to me to be very much the other way around, and that there was something very special about the social insects which accounted for their extreme cooperativeness. That special thing was their kin-

ship—high levels of kinship within the colony. This was the focus of a theoretical paper I published in 1957. It was a model of natural selection between families; now I think that's a silly way to do it, but at the time I wasn't smart enough to think of the kin-selection idea, which was some years later worked out by William D. Hamilton. In extreme models, this kind of selection can lead to things like forgoing reproduction, if in so doing you can, for example, more than double the reproduction of a full sib. The full sib is half as good as you are genetically—that is, from the standpoint of getting your genes into future generations. In the social insects, of course, sisters may have a three-quarter relationship, because if they share a father then all the genes they get from the father are exactly the same.

These early experiences kindled an interest that has never gone away, and resulted in *Adaptation and Natural Selection*, my first book-length publication on this and related matters. By then I had worked on the problem of senescence and on cooperation between relatives, but I had a long list of other problems that interested me.

At that time, group selection was not explicit. V.C. Wynne-Edwards' big book on group selection—*Animal Dispersion in Relation to Social Behaviour*—came out in 1962, but I discovered it only after I was largely finished with *Adaptation and Natural Selection*. I submitted the manuscript in late 1963, and it referred to Wynne-Edwards' work, but I brought it in as a late revision of the manuscript.

There was some group-selection modeling prior to that, and explicit use of group-selection ideas by Alfred Emerson and A.H. Sturtevant, in a paper published in 1938. In 1945, Sewall Wright presented a group-selection model, in a book review of George Simpson's *Tempo and Mode in Evolution*. But the group-selection model wasn't easy to find if you didn't know about it already. Mostly, the group-selection idea was necessary to the way people were thinking about adaptation, although—and I find this extremely strange—they didn't realize it. They kept talking about things being for the good of the species. If it's for the good of something, and it's to arise by natural selection, it has to be produced by the natural selection of those somethings. In other words, one species survives as another one goes extinct. The basis of Wynne-Edwards' work on group selection was that you can't have things that work for the good of the group unless you have selection at the level of groups. What he was doing was looking for selection at the level of local breeding populations, and

whether they could be called separate species wasn't particularly relevant.

To most people's satisfaction, Wynne-Edwards has been proved wrong. Not that there's no selection at levels higher than the individual or the family, but simply that his particular formulation isn't likely to be a very strong force in evolution. It's now generally conceded that the phenomena he was explaining by this mode of thought are much better explained by other processes: by selection at lower levels, selection among individuals.

For instance, any reproductive restraint—anytime it looks as if individuals aren't reproducing at the maximum possible rate—is explainable simply on the basis of an individual optimal-resource-allocation model. You don't kill yourself trying to do something today if working at it a little bit more easily will enable you to try again tomorrow. Maybe you don't do it at *all* today, if conditions will be much better tomorrow. This kind of thinking explains the fact, for instance, that birds do not necessarily lay as many eggs in a breeding season as they demonstrably might. The allocation of their resources will be much more effective for reproduction with a lower-level expenditure on eggs, which will enable them later to spend more on feeding the young and later still, next year, having another breeding season.

There's a great conceptual deficiency in my earlier work, one that I shared with just about everybody else who was working at the time. I failed to realize what a tremendous problem the existence and prevalence of sexual reproduction is. I got interested in that in the early seventies, and I published a book in 1975 titled *Sex and Evolution*. There are a lot of complications that I didn't appreciate at the time, but John Maynard Smith and Bill Hamilton and many others have advanced our understanding tremendously in the last twenty years.

Richard Dawkins went in the right direction when he made the distinction between replicators and vehicles. David Hull's substitution of the term "interactor" for "vehicle" is a good idea, but that's a minor terminological matter. Dawkins didn't go nearly far enough in making that distinction, because he defines a replicator in a way that makes it a physical entity duplicating itself in a reproductive process. This is fine, but the important distinction lies at a still more basic level. He was misled by the fact that genes are always identified with DNA.

Evolutionary biologists have failed to realize that they work with two more or less incommensurable domains: that of information and that of matter. I address this problem in my 1992 book, *Natural Selection: Domains, Levels, and Challenges*. These two domains will never be brought together in any kind of the sense usually implied by the term "reductionism." You can speak of galaxies and particles of dust in the same terms, because they both have mass and charge and length and width. You can't do that with information and matter. Information doesn't have mass or charge or length in millimeters. Likewise, matter doesn't have bytes. You can't measure so much gold in so many bytes. It doesn't have redundancy, or fidelity, or any of the other descriptors we apply to information. This dearth of shared descriptors makes matter and information two separate domains of existence, which have to be discussed separately, in their own terms.

The gene is a package of information, not an object. The pattern of base pairs in a DNA molecule specifies the gene. But the DNA molecule is the medium, it's not the message. Maintaining this distinction between the medium and the message is absolutely indispensable to clarity of thought about evolution.

Just the fact that fifteen years ago I started using a computer may have had something to do with my ideas here. The constant process of transferring information from one physical medium to another and then being able to recover that same information in the original medium brings home the separability of information and matter. In biology, when you're talking about things like genes and genotypes and gene pools, you're talking about information, not physical objective reality. They're patterns.

I was also influenced by Dawkins' "meme" concept, which refers to cultural information that influences people's behavior. Memes, unlike genes, don't have a single, archival kind of medium. Consider the book *Don Quixote*: a stack of paper with ink marks on the pages, but you could put it on a CD or a tape and turn it into sound waves for blind people. No matter what medium it's in, it's always the same book, the same information. This is true of everything else in the cultural realm. It can be recorded in many different media, but it's the same meme no matter what medium it's recorded in.

In cultural evolution, obviously, the idea of a coffee cup or a table is something that persists. The coffee cups and tables don't persist, they recur as a result of the persistence of the information that tells

people how to make coffee cups and tables. It's the same way in biology: hands and feet and noses and so on don't persist, they recur as a result of genetic instructions for making hands and feet and noses. It's the information that lasts and evolves. Obviously, it's because of the physical manifestations of the information that we know about the information. Dawkins has had trouble in convincing people, and this stems from his thinking of the gene as an object—of emphasizing the importance of replication rather than of proliferation of information.

Until you've made the distinction between information and matter, discussions of levels of selection will be muddled. Comparing a gene with an individual, for instance, in discussions of levels of selection, is inappropriate, if by "individual" you mean a material object and by "gene" you mean a package of information. It should be "gene" and "genotype." You have to look at levels of selection in both of these domains, and realize what you're doing. Comparisons of levels of selection should be within the same domain.

Having made the domain distinction, you then go to levels, and you find that in the two domains the levels do not correspond exactly. As a general rule, if we restrict our attention to sexually reproducing populations, there are only two possible levels of selection in the informational—or what I call the codical—domain: the gene and the gene pool. Selection can operate on alternative genes within a population; selection can act on alternative gene pools in a biota. Both of these are evolutionary factors that can produce interesting effects.

In the material domain, on the other hand, selection can operate at the level of alternative individuals, in the usual sense of "individual," or on groups of individuals—such things as insect colonies, or families whether they form elaborate colonies or not. These temporary groupings of individuals give rise to what the biologist David Sloan Wilson calls "trait-group selection," and also to selection between alternative populations. That's the physical basis for selection between gene pools. But the physical levels of selection below that level—for instance, between competing colonies of the same species of social insects—don't have a corresponding level in the codical domain. The events in the competition between insect colonies are recorded at the level of a gene. There are no sufficiently persistent genetic differences among colonies for effective selection in the codi-

cal domain. I believe David Wilson agrees with that. He's interested in selection among the interactors in the material domain.

The main messages of my 1966 book are now generally accepted. This would have been the case whether I wrote that book or not. The ideas would have prevailed by today, because people like Hamilton, Dawkins, Robert Trivers, and others were doing work at the same time, more or less, and if there hadn't been a single book in the mid-sixties to deal with the idea of levels of selection, I think one of those people probably would have written it. Dawkins' book *The Selfish Gene* is very much a case in point. It advanced things a lot further than mine did.

My lasting contribution will be for a clarification of the problems of the two domains and the levels of natural selection. I'll also be known as one of the people who first became interested in explaining why there is such a thing as sexual reproduction, and why it's so widespread.

In the future, breakthroughs in evolutionary biology may come in the field of paleontology. Fieldwork now going on will be recognized several decades from now as having provided extremely important information. People I've never heard of are out there digging, looking for pollen grains in lake sediments, or dusting off trilobites from Paleozoic shales. Other important insights will come from people working in traditionally unrelated fields—for instance, on things like conflict between genomes. The most immediately enlightening and convincing work that's going on now is in explanations being advanced for things like genetic imprinting—that is, the fact that in early development the activity of the gene depends upon whether it came from the mother or the father. I'm most involved in a recent publication by the biologist David Haig on genetic conflict in human pregnancy. This may not in fact be the clearest example of genetic imprinting, and certainly it isn't going to be the one most easy to work with, but it's work of this nature that's likely to get people thinking seriously about levels and domains of selection.

My recent work concerns what I call Darwinian medicine—the general applicability of evolutionary ideas in medical research, practice, and education. It arose in conversations with Randolph Nesse, a medical doctor and professor at Ann Arbor. Another important factor for me was a paper by Paul Ewald in 1980.

Ewald started life as an ornithologist and got interested in medi-

cine one day when he got sick. It was an intestinal pathogen that got him—not quite as dramatic as Alfred Russel Wallace getting his inspirations during an attack of malaria. Paul started thinking about the evolutionary interaction between hosts and parasites. That led to his paper on how to use evolutionary ideas to interpret the observations one makes in infectious diseases—the symptoms and signs seen in the host. It struck me that these were extremely important ideas, which should be tremendously useful in medicine.

I had already been thinking about senescence and life histories in general, and certainly senescence is a medical problem. From general population genetics I knew something about inherited disorders. These are quite different kinds of medical problems, but all of them are susceptible to evolutionary interpretations, in ways that it seems to me would benefit the practice of medicine. The more I got to thinking about it, and talking to Randy Nesse about it, the more I realized that there is no kind of medical problem for which the theory of natural selection will not be relevant, for curing or preventing a disease.

One of Paul's most important insights is that AIDS is probably not a new disease, in the sense of HIV being a new pathogen. What we're dealing with is a pathogen that has rapidly evolved a much higher level of virulence because of its environmental circumstances. It may have been an organism that, prior to two or three decades ago, was transmitted primarily from parent to offspring—and maybe rarely between sex partners—and therefore the evolutionary factors acting on its virulence necessarily kept it very nonvirulent. Individuals with this virus had to survive long enough to reproduce, or the virus wouldn't be transmitted.

Now, take people with this virus and move them into a completely different social situation, in which families are disrupted and men are being served mainly by prostitutes who are dealing with hundreds of men per year. You now have a situation in which the opportunity for the transmission of the disease to another individual no longer depends upon the long-term survival of the individual that has it. Therefore the restraints on its virulence are removed. Within an individual, the more virulent the strain, the better it will do, because the more virulent the strain the more of that particular virus there will be for transmission to the next individual. We've shifted the balance of selection on this virus from mainly between individuals—be-

tween hosts—to within hosts. Within hosts, there's normally selection for increased virulence. Suddenly the virulence of the HIV went way up. This is just one example. There are many, many examples of human activities that influence the evolution of virulence in our pathogens.

There are many other ways in which evolutionary ideas can be brought to bear on medicine—for instance, in dealing with the mismatch between our evolved adaptations and the environment in which we now find ourselves. This mismatch is probably the main source of medical problems today.

In twenty or thirty years, medical students will be learning about natural selection, about things like balance between unfavorable mutations and selection. They will be learning about the evolution of virulence, of resistance to antibiotics by microorganisms, they will be learning about human archaeology, about Stone Age life, and the conditions in the Stone Age that essentially put the finishing touches on human nature as we now have it. These same ideas then will be informing the work of practitioners of medicine, and the interactions between doctor and patient. They'll be guiding the medical research establishment in a fundamental way, which isn't true today. At the rate things are going, this is inevitable. These ideas ought to reach the people who are in charge—the doctors and the medical researchers—but it's even more important that they reach college students, especially future medical students, and patients who go to the doctor. They'll have questions to ask that doctor, who will have to have answers. I hope this set of ideas produces a certain amount of bottom-up influence on the medical community, via students and patients. But I hope also that there's some top-down influence—that it will be influencing the faculties in medical schools and the researchers on human disease.

STEPHEN JAY GOULD: George Williams is a very important man. He's a quiet, gentle man who has had enormous influence on evolutionary theory since the 1960s, particularly through *Adaptation and Natural Selection*, in 1966, which was largely a critique of the false logic in forms of group selectionism then current and a defense of a fairly hard-edged strict Darwinian view based on individual selection. It was a methodological argument; he didn't say that group selection is impossible in principle, he just said that the arguments heretofore