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Adaptationism and the Power of Selection

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1. Adaptation, interaction and construction

Over the past 20 years, Richard Lewontin has written a justly famous series of papers about the concept of adaptation and its role in biology.[1] The most well known of these is "the spandrels paper," coauthored with Stephen Jay Gould (1979), but that oft-cited paper comprises just one piece of the argument.[2]

It is important not to overstate Lewontin's opposition to adaptationist ideas. He accepts that nature does contain some phenomena which can be described, with some adequacy, using the concepts favored by adaptationists, and which provide examplars for the adaptationist approach. He also holds that in the early development of evolutionary theory, a certain "alienated" picture of organisms' relations to their environments, which includes a focus on adaptation, was essential to theoretical progress (1983). But Lewontin certainly holds that adaptation is, at the present time, a *bad organizing concept* for biological research. The adaptationist's exemplars do not represent nature in general, and even in the paradigm cases (like industrial melanism) the adaptationist framework misdescribes, to some extent, the causal structure. Further, Lewontin does not just think that adaptation is a bad organizing concept for biology; he thinks the concept has a larger negative role, in reinforcing an erroneous general picture of the place of humans within our environment, both biological and cultural.

The perspective that adaptationist thinking exemplifies within biology is referred to by Lewontin as an "alienated" view. Organisms are treated by biological theory as the *objects* of external, autonomously generated forces in evolutionary processes. Individual development is explained in terms of the expression of coded instructions in DNA. Lewontin sees this developmental view as another in which the organism is cast as alienated from the forces governing its existence.

Lewontin holds that this picture of the general relationships that organisms have to external nature exists in a relation of mutual support with a more specific picture of the limitations associated with humans' power over their surroundings. The standard picture is thus both empirically inaccurate and politically harmful. As a consequence, Lewontin holds that we should replace the concept of adaptation, as an organizing concept in biology, with the concept of *construction*; organisms construct their environments, and are active subjects also in creating their own ontogeny (1983: p. 105).

In these respects, Lewontin has an interesting resemblance to John Dewey. Dewey also thought that an erroneous general view about living systems and organism/environment relations supports, and is supported by, a more specific, false picture about the scope and proper role for human powers in the world (1929). Dewey opposed theories of mind and knowledge which strictly separate subject and object, stress the gulf between them, and claim that the proper role of cognition is to attempt passive reflection of external reality. Dewey's views about the importance of practical action, guided by intelligence, as a transforming factor in nature are less overtly political than Lewontin's, but there is some similarity in their views about the relation between knowledge and action.

So Dewey and Lewontin agree to some extent about the errors to be avoided. They agree also that one way to improve our thinking about the human case is by correcting our view about the general biological issues. In particular, they think part of the answer is to give a new role in biological descriptions to relations, connections, interactions, mutual dependencies – to counteract the tendency in standard ways of thinking to assert false separations. A first step in such a rethinking is to understand "organism" and "environment" in general as only existing in the context of each party's relations to the other. The convergence between Dewey and Lewontin on this point, and on its significance, is striking; the reader is invited to guess which of these quotes come from which author:

1. The environment is not an autonomous process but a reflection of the biology of the species. Just as there is no organism without an environment, so there is no environment without an organism.
2. An environment is constituted by the interactions between things and a living creature.
3. [W]ith every differentiation of structure the environment expands. For a new organ provides a new way of interacting in which things in the world that were previously indifferent enter into life-functions.
4. There is, then, a genuine sense in which the evolution of life, the increase in diversity and interdependence of life functions, means an evolution of new environments, just as truly as of new organs.[3]

Lewontin, of course, discusses the biology in much more detail than Dewey ever did (and has the benefit of the best part of a century's improvements in biological knowledge). Dewey, on the other hand, discusses the epistemological significance of this connection-oriented view in much more detail than Lewontin. But in some ways they are remarkably complementary thinkers. This will come as a surprise to those who categorize Dewey simply as a liberal democratic theorist and think of Lewontin simply as a Marxist. But Dewey, like Marx, can be referred to as a "naturalistic left post-Hegelian." Dewey does not deploy the apparatus of dialectics when describing his metaphysical position (although he did go through an early stage of explicit Hegelianism), but his constant focus on the metaphysical role of relations owes a good deal to Hegel and the English-speaking Hegelian philosophies of the late 19th century.[4] Those philosophies were idealist in character; Dewey (after an idealist phase) came to a view that he saw as neither traditionally idealist nor materialist.[5] But like Marx, Dewey took with him Hegelian habits of thought when he turned towards a more scientific picture of the world, paying particular attention to Darwin. Lewontin and Dewey end up with somewhat similar "philosophies of nature."

Dewey even wrote, in 1911, short articles on the topics of "adaptation" and "environment and organism" (among other topics) for an encyclopedia of education (1911a, 1911b. See chapters 1 and 2 of Levins and Lewontin (1985)). Lewontin would agree, I think, with much of the general thrust of what Dewey said there, although certainly they diverge on many details. Dewey was writing against the background of a strongly externalist picture of evolution made popular by Herbert Spencer, and trying to counter the asymmetric features of that view of organism/environment relations, a view in which evolution is seen as "the molding of pliable and passive organic beings into agreement with fixed and static environing conditions" (1911a: p. 265).[6] Spencer plays in Dewey's discussions a role similar to that played by standard "hard" versions of neo-Darwinism in Lewontin's writings.[7] One interesting difference is that Dewey's preference was to rehabilitate rather than ditch the concept of adaptation. Dewey thought it was possible to think of adaptation as a kind of mutual accommodation, rather than a one-sided relation in which the environment is in the driver's seat. This is possible because the environment itself necessarily changes when the organism changes (see the quotes above).

So Dewey and Lewontin both insist on redescribing basic organism/environment relationships in a language that stresses connection and interaction. Both do this in part to combat what they see as a prevailing tendency to impose an "alienated" (Lewontin) or "dualistic" (Dewey) set of distinctions upon a prior unity. Both hold that the project of coming to a better view of the

role of knowledge and action in human life is helped by improving the ways we describe these most basic organism/environment interactions.

Elsewhere I have criticized some parts of Lewontin's positive view, with its constant stress on relations of construction and interpenetration (1996, forthcoming b). I suggest that Lewontin (and also probably Dewey) counter the dualisms by going too far in the other direction, towards a holistic metaphysics in which connectedness is omnipresent.[8] To assert a view in which connectedness is ubiquitous is to risk losing all-important distinctions of degree. The relationships between organisms and environments feature a mixture of give-and-take, where the "give" and the "take" are quite different phenomena. If an insect species changes its color to match its surroundings, that is a very different phenomenon from what we would have if the insects started doing things that changed the color of the surroundings instead.

To *replace* adaptation with construction, as a guiding concept or central metaphor, is to risk going from one extreme to the other. So I disagree with Lewontin when he says that "organisms construct *every* aspect of their environment themselves" (1983: p. 104, my emphasis). A view that defines the organism and the environment entirely in terms of their relations to each other does enables us to make a claim like this (even about the first insect species described above) but that is not a conclusion we should welcome.

Dewey's insistence on connectedness has a similar tendency. He did make a great deal of the need to hang onto distinctions of degree: "while there is no isolated occurrence in nature, yet interaction and connection are not wholesale and homogeneous" (1929: p. 271). But it is possible for a reader to feel that these distinctions are lost in the constant stress on continuities and connections. I am sure that Lewontin would agree that Dewey's "interaction and connection are not wholesale and homogeneous" is an important principle for a dialectical philosophy also, and I think Lewontin would not want us to interpret his "organisms construct every aspect of their environment" in a way that conflicts with Dewey's point. But philosophies that place great stress on relations as determining the nature of the objects standing in these relations have a constant tendency to go too far towards a holistic picture. I believe it is better to not insist on the metaphysical primacy of either connectedness *or* separation, and to retain a conceptual framework with resources for recognizing real cases of both kinds.

2. A fly in the empirical ointment: explanatory adaptationism

Since the late 1970's a huge amount has been written about adaptationism, much of it prompted by the spandrels paper (1979), and by Gould's and Lewontin's other works. One recent literature has tried to separate a definite

empirical core from these disputes, and has tried to describe a test for the truth of the resulting adaptationist view. The main work I have in mind is Orzack and Sober (1994).[9] This literature makes use of a rather stripped-down conception of what adaptationism involves; basically, the adaptationist claim is seen as a claim about the power of selection to create near-optimal phenotypes. Consequently, this claim can be tested by trying to see how often a purely selectionist model of an evolutionary phenomenon predicts the data roughly as well as a richer, more "pluralist" model does.

This literature, focusing on the power of selection, avoids something that Lewontin regards as essential to adaptationist thinking. It avoids commitment to a rich, "lock and key" picture of the structural "fit" between organism and environment. Lewontin argues that some such relation must be involved in adaptation, or it will not be possible to contrast the "before" and "after" states in an evolutionary process, and claim that selection has made the population *better adapted* to its niche or way of life. So Lewontin thinks there is more to the adaptationist picture of the world than is recognized in the Orzack/Sober test; there is more to adaptationism than a view about the causal power of selection. I won't discuss this (difficult) issue in the present paper.

Once the question is asked about the power of selection, however, it seems clear that Lewontin would bet that "adaptationism" as understood by Orzack and Sober is false. A good part of Lewontin's biological work has been on the role played in evolution by the peculiarities and contingent features of genetic systems (Lewontin 1974). And more generally, he has a skeptical view about the capacity of simple causal models to capture the behavior of biological systems. Such systems are subject, in virtue of their size and history, to a range of interacting forces with none dominating. This part of Lewontin's view is empirically testable in roughly the way Orzack and Sober have in mind.

In the rest of this paper, however, I will discuss another aspect of the issue of adaptationism, which tends to thwart attempts to cast adaptationism as a testable empirical claim. Orzack and Sober cast adaptationism as a view about the power of selection to create near-optimal phenotypes, and this has certainly been one part of what has been debated over the years. But there is also another way of asserting the "power of selection" – another, more elusive, claim which has always lurked around the discussions. In this sense, the power of selection is its ability to play a unique *explanatory* role, solving an otherwise insoluble problem.

In a more detailed discussion of the different forms of commitment to adaptationism (forthcoming a), I distinguish three adaptationist theses. I will reproduce all three here, for the sake of completeness, although only one will be discussed in detail.

> *Empirical Adaptationism*: Natural selection is a powerful and ubiquitous force, and there are few constraints on the biological variation that fuels it. To a large degree, it is possible to predict and explain the outcome of evolutionary processes by attending only to the role played by selection. No other evolutionary factor has this degree of causal importance.
>
> *Explanatory Adaptationism*: The apparent design of organisms, and the relations of adaptedness between organisms and their environments, are the *big questions*, the amazing facts in biology. Explaining these phenomena is the core intellectual mission of evolutionary theory. Natural selection is the key to solving these problems – selection is the *big answer*. Because it answers the biggest questions, selection has unique explanatory importance among evolutionary factors.
>
> *Methodological Adaptationism*: The best way for scientists to approach biological systems is to look for features of adaptation and good design.

"Empirical adaptationism" is my formulation of the empirical strand that I referred to above – the idea that Sober and Orzack hope to test via comparisons of models. "Explanatory adaptationism" is the view I will discuss below. "Methodological adaptationism" I understand as purely a policy recommendation. The methodological view can be argued for on the basis of empirical adaptationism, but there is also an argument for methodological adaptationism that some biologists accept which does not go via either of the other views. Some biologists claim they follow adaptationist methods simply because these methods have yielded what they take to be good results: "It worked for Darwin and Fisher!" Lewontin has an interesting historicist argument against such a view (1983). He does not deny that adaptationist thinking was essential to ideas that constituted a definite advance over earlier evolutionary theories. But this success was specific to an earlier theoretical context; progress from our current situation requires a different approach.

As we have three distinct adaptationist views, the denials of these three views comprise three distinct kinds of anti-adaptationism. Or speaking more formally, we could say there are three different dimensions here, and strongly adaptationist views, strongly anti-adaptationist views, and moderate views are possible for each dimension. It is possible to divide up the options further, in fact, as one could hold different views in different domains (e.g., molecular versus phenotypic evolution). But to keep the discussion simple I will usually just talk of arguments for and against the views outlined above.

My topic from here will be explanatory adaptationism, because it is the least well understood of the three. Explanatory adaptationism constitutes a reply to some of the empirical arguments in the spandrels paper, and other arguments from the multiplicity of evolutionary factors operating in natural

populations. Explanatory adaptationism does not claim that selection is omnipresent or omnipotent; selection can be seen as rare and highly constrained. But, the explanatory adaptationist holds, selection is uniquely important as it provides a solution to the central problem faced by biology. This, it is claimed, gives selection pre-eminence among evolutionary factors.

Richard Dawkins (1986) and Daniel Dennett (1995) are the great publicists for explanatory adaptationism. The view also has an ally in Robert Brandon (forthcoming) and receives a 50% endorsement in Sterelny and Griffiths (forthcoming).

Empirical and explanatory adaptationism are both views that can be said to asset the power of selection. But "power" is understood here in two different ways. Empirical adaptationism sees natural selection as a powerful causal force, as the creator of most of what we find in the biological world. For explanatory adaptationism, selection is uniquely "powerful," but not in the sense associated with empirical adaptationism. Instead, natural selection has a unique *explanatory* power.

So there is a pure form of explanatory adaptationism which scrupulously tries to avoid any commitment to empirical adaptationism. Such a view concedes that selection might only explain 1% of evolution, but insists that this is the 1% that counts.[10] Such a view need not confront some of the problems raised by the complexities of population genetics, and the role of developmental factors and the like. However, it is only a very pure form of explanatory adaptationism that avoids these problems. Both Dawkins and Dennett do not stay pure; they both stray into stronger positions including extra empirical and methodological commitments. (Dennett, I think, strays more than Dawkins.)

Further, although the explanatory adaptationist avoids some hard empirical problems, the view does not avoid all. The explanatory adaptationist has to hold that natural selection *is* the key to solving the problem of apparent design. Such a claim might seem uncontroversial – many evolutionists of a "pluralist" cast of mind will accept such a claim. However, some are likely to dissent, claiming that for evolution to be creative, it must involve more than a simple combination of mutation and selection. Some may see this as part of the message of Wright's shifting balance theory (1932), and his disputes with Fisher. Wright argued, on this interpretation, that the creative aspect of evolution requires a more complex machine than mutation and selection in an undifferentiated large population.

I will not discuss this problem here; instead I will accept the second half of explanatory adaptationism, for the sake of argument, and will focus on the first part, the part which makes a claim about the "biggest questions" for biology.

In my formulation of explanatory adaptationism, two components of the big problem are distinguished. These are (i) the apparent design of organisms, and (ii) their relations of adaptedness to their environments. I distinguish these two in order to avoid controversy. Some might think that these are the same issue, or that one of the two is primary, while others might recognize two distinct questions. I mention both issues, to be sure to capture both.

Also, while some say that adaptedness is *the* central question, it is also quite common to hold that there are two central questions for biology: adaptedness and diversity. That position is close enough to explanatory adaptationism for my present purposes.

A first objection to explanatory adaptationism is as follows: although many might agree that we find apparent design in nature interesting, this is apparently just a fact about our psychology. As onlookers, we are puzzled by some things and untroubled by others, but why should we take this to reflect differences between objectively puzzling and objectively unpuzzling states of affairs in nature itself? Why should we infer that the phenomena that we happen to find puzzling are "the most important" phenomena? For an explanatory adaptationist like Dawkins or Dennett, the human eye is in the class of uniquely important phenomena for biology. The human toenail, probably, is not in that class. But toenails are just as real as eyes, and toenails have an evolutionary history as well. Rhaposodies about eyes might have a place in popular books and in public relations exercises, where rhapsodies about toenails might be less effective. But should the dispassionate biologist pay any attention to this? The "special status" of apparent design appears, in this light, to be analogous to the special status of cute and appealing animals in the conservation movement. Pictures of endangered koalas are more likely to elicit big donations than pictures of endangered spiders, but this fact has little scientific importance.

If this objection is correct, explanatory adaptationism is revealed to be nothing more than the personal preference of some biologists and philosophers; they find selection important because it answers questions that they happen to find interesting. Earlier I claimed that a pure explanatory adaptationist is able to avoid some of the difficult problems that beset empirical adaptationism. But if the objection I am discussing is correct, it turns out that explanatory adaptationism avoided those scientific problems because it is not a scientific position at all, but just a set of preferences that some people happen to hold.

In expressing this objection I call the preference "personal," though clearly it is often not an individual-level matter. As Kuhn (1970) argued, perceptions of which problems are important and compelling are a key component in traditions of normal science (or "paradigms," in one of Kuhn's senses). So a

scientific community will contain mechanisms for directing students towards a certain class of problems as worthy of research. But if the "importance" of the problem of design is only a matter of this kind of Kuhnian embedding, that is not a vindication of explanatory adaptationism.

The objection I am describing need not claim that no question is ever "more important" than another. Questions and problems can differ in practical importance, of course. And one question can be "bigger" than another in a logical or informational sense; questions about all trees are bigger than corresponding questions that are just about oak trees. But the objection claims there is no sense in which one question can be objectively "bigger" than another which will support explanatory adaptationism. Even if a problem is or was particularly troubling to the scientific community, the scientists' states of perplexity are not to be confused with aspects of the world they study.

Explanatory adaptationists do have a reply available to this first objection. Dawkins and Dennett make strong claims about the role of biological explanations of design within the scientific world view as a whole. Dawkins (1986) claims that apparent design in nature was the one thing which, prior to Darwin, could motivate a traditionally religious outlook on the natural world. Darwin, by destroying the "Argument from Design," transformed not only biology but the entire intellectual landscape. And the idea of natural selection was the key to this transformation. If this is true, then natural selection becomes more than just another evolutionary factor, and more than a great biological idea; it becomes integral to the entire project of anti-theological, naturalistic explanation of the world.

Dennett's conception of the role of Darwinism in intellectual life is, if anything, even more ambitious. For Dennett, selective explanation is the only antidote to an erroneous pattern of thinking that is so widespread that traditional religious thinking is only one instance of it. Darwinism enables us to do without "skyhooks," miraculous interventions in nature that explain the occurrence of design, purpose and meaning.

One can agree with much of what Dawkins and Dennett say about the role of the problem of design in intellectual history, without agreeing with the conclusions they draw about biology. The role that Darwinism plays in the entire scientific project is extrinsic to the scientific work done by biologists themselves. The job of describing the significance of biological theories for questions about religion, purpose, meaning and so on belongs primarily to *philosophy* of science. So when a philosopher looks on at biology (or a biologist dons a philosophical hat), natural selection might shine out like a beacon, in a way that no other evolutionary factor does. But that does not give natural selection any more causal power within evolving systems themselves. An accurate biological description of how selection interacts with other factors

should not be affected by these extrinsic considerations. So, according to this objection, the role of natural selection in dealing with religion, and so on, should not affect how biologists organize their work. Biologists should set up their work in a way that is responsive to the best current information about which sorts of research will enable us to understand biological phenomena – not in a way that complements a philosophical campaign.

So that is one reply to the explanatory adaptationist's claims about the importance of selection in holding the secular viewpoint together. But I suspect that Lewontin would think this reply concedes too much to explanatory adaptationism. It is also possible to oppose the view in a more head-on way.

3. Rejecting natural theology

The reply given to explanatory adaptationism above, which accepts the problem of design but claims that the problem is only "central" in a sense irrelevant to biological work, accepts at face value a certain set of questions and problems. These questions have been handed down to us from a pre-scientific world view. But there is no reason why we should take our questions from world views that have been adandoned, any more than we should take our answers or methods.

The context in which the "problem of design" was originally posed was a religious context. The problem was elaborated in a way aimed at showing to maximum effect the power and plausibility of the religious solution. So another possible reply to explanatory adaptationism rejects the idea that the traditional problem of apparent design is a well-posed and well-motivated question, in the light of current knowledge. Rather than being a problem that has turned out to be visible and challenging from both theological and naturalistic points of view, the "problem" of design and adaptedness is itself a product of a theological view of the world. So on this view, explanatory adaptationism wrongly accepts the terms of debate favored by theological views of the world; it is the *tradition of natural theology continued*.

Nobody doubts the importance of natural theology to the history of evolutionary theory. It was an powerful part of the intellectual context in which British biology developed, especially in the 19th century. Darwin was much influenced by this tradition, and its stress on adaptation. He thought that a satisfactory theory of evolution had to account for the "the innumerable cases in which organisms of every kind are beautifully adapted to their habits of life" (Darwin 1969: p. 119). This is very much the way the natural theologians saw the phenomena: "[T]here is an adaptation, an established and universal relation between the instincts, organization, and instruments of animals on

the one hand, and the element in which they are to live, the position which they are to hold, and their means of obtaining food on the other . . . "[11] Richard Dawkins (1986) self-consciously presents his account of the problem posed by apparent design in the same terms used by Paley and the natural theology tradition. He accepts the question exactly as they wanted it posed.

So some, probably including Lewontin, might reply that we should not accept natural theology's questions; we should reject them as well as the answers. They are part of a discredited world view that it has taken much time and agony to get over.

A reply of this kind could be given with various degrees of strength. It seems likely that Lewontin would regard the problem of design as overrated; that he would see Dawkins as deeply mistaken to accept the problem in the natural theologian's terms. But it would be a very strong claim to say that the *entire appearence* of a problem here comes only from having a theological view of the world. For my part, I think the design problem has been oversold in recent discussions, but I don't think it vanishes altogether if we look at the world through wholly secular spectacles.

So, adaptationism is not one view but at least three distinct positions. With respect to both empirical and methodological adaptationism, it is not up to a philosophical discussion to decide these issues, but only to describe them. The third view, explanatory adaptationism, is itself partly philosophical in character. Although I think the "problem of design" has been somewhat oversold, I do accept its importance. This importance, however, is probably not of a kind that gives support to adaptationism as a program of scientific research.

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Notes

[1] For a small sample of discussions of adaptationism, see Maynard Smith (1978), Kitcher (1987) and other essays in Dupre (1987), Dennett (1995), and the essays in Orzack and Sober (forthcoming).

[2] Much of the key material is collected in Levins and Lewontin (1985); noteable exceptions include Lewontin (1982), and the spandels paper (1979).

[3] Quote 1: Lewontin (1983), p. 99, Quote 2: Dewey (1938), p. 152, Quote 3: Dewey (1938), p. 32, Quote 4: Dewey (1911b), p. 438. Dewey's use of "life-functions" is a giveaway perhaps. Also, compare 3 and 4 with this (more historically specific) quote from Lewontin: " An organism's genes, to the extent that they influence what the organism does in its behavior, physiology and morphology, are at the same time helping to construct an environment. So, if genes change in evolution, the environment of the organism will change too." (1991: p. 112)

In case it is not completely obvious from the text, I stress that I am not suggesting any borrowing from Dewey by Lewontin when I juxtapose these quotes; the aim is to show a convergence, which has an explanation in larger intellectual and political projects, and in the history of Hegel-influenced philosophies.

[4] Westbrook (1991) has an interesting treatment of both Dewey's early relationship to absolute idealist philosophies, and his relationship later in life to Marxism. Dewey found Marxism too quasi-religious and kept it very much at arm's length, though he was aware of some convergences.

[5] Dewey became willing to accept the label "emergent" for his theory of mind and its physical basis (1929: p. 271).

[6] I have discussed the relation between Dewey and Spencer, and links between Dewey and Lewontin, in more detail in Godfrey-Smith (1996).

[7] "Hardened" in the sense of Gould (1980).

[8] I worry, like others, that the "developmental systems theory" of Oyama (1985), Griffiths and Gray (1994) and others is tending the same way. Many of these authors acknowledge Lewontin (especially Lewontin 1983) as an influence, but they develop a distinctive view of their own. Sterelny, Smith and Dickison (1996) share these suspicions about holism and developmental systems theory; Griffiths and Gray (1997) is a rather forceful reply.

[9] See also Brandon and Rausher (1996), Orzack and Sober's reply in the same issue, and the various papers in Orzack and Sober (forthcoming).

[10] See Dawkins (1986: pp. 271–272, 303–304). "[L]arge quantities of evolutionary change may be non-adaptive, in which case these alternative theories may well be important in parts of evolution, but only in the boring parts of evolution, not the parts concerned with what is special about life as opposed to non-life." (p. 303)

[11] This quote is from Charles Bell, given by Coleman (1977), pp. 59–61 without a detailed reference.

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