Economic Rationality and Explaining Human Behavior: An Adaptationist Program?

Jonathan Kaplan, Oregon State University, Oregon, UNITED STATES

Abstract: Attempts to explain human behavior that appeal to economic rationality share many of the same ontological assumptions and methodological practices that the so-called ‘adaptationist program’ in biology was criticized for. This program in biology was largely abandoned by biologists as poorly motivated, and replaced with the active testing of both adaptive and non-adaptive hypotheses regarding the spread and maintenance of traits in populations. This development was largely welcome by the biological community, despite having required the development of new tools, both conceptual and methodological. Many analysts of contemporary microeconomic practice criticize the assumptions and practices employed therein as similarly poorly motivated. Close attention to these criticisms reveal them to have more than superficial similarities to the critiques of adaptationism in biology. These similarities extend to some macroeconomics researchers recent suggestions of ways that hypotheses regarding the causes of people’s actions might be tested; as yet, however, these suggestions have not been embraced by the field as a whole. By attending to the ways in which biological practice has moved beyond the adaptationist program, similar changes in economic practice may be motivated.

Keywords: Adaptationism, Behavior, Biology, Microeconomics, Rational Choice Theory

Introduction

The use of the framework of economic rationality (through rational choice theory, game theory, and other formal models) to explain broad arenas of human behaviors (including some classic market oriented behaviors, see below) has been vigorously criticized. One way to think about these criticisms is to consider the assumptions they attack, assumptions involving the power and the scope of rational decision making in causing and explaining human actions. Taken together, these assumptions resemble in some key ways those assumptions that have been used to characterize certain attempts to explain the physical and behavioral features of organisms as biological adaptations, namely, to those attempts that are part of the so-called adaptationist program in biology. In biology, concerns about the legitimacy of the adaptationist program were largely ameliorated by the development of empirical techniques and by conceptual advances that have, in large part, made unnecessary the use of the assumptions which characterize the adaptationist program for understanding and explaining the history and development of traits, including adaptive traits. Instead of assuming that natural selection is a powerful and ubiquitous forger of adaptive traits (or, for that matter, assuming that biological “constraints” are so powerful and ubiquitous that non-adaptive hypotheses should be considered the “null”), biologists are now able to test particular adaptive and non-adaptive hypotheses, and compare the strength of models that posit different sets of causal mechanisms (see for example Sober 2008 for a summary of the logic of these tests). Insofar as the assumptions made in attempts to explain human behaviors by reference to models of economic rationality (such as rational choice theory) are similar to those that were criticized in biology as constituting an illegitimate adaptationist program, two questions present themselves: First, are the assumptions as they are used in attempts to explain human behavior illegitimate in the same way that the use of similar assumptions to explain biological adaptations was considered illegitimate? And second, if these assumptions are illegitimate in the case of explaining human behavior, can they be avoided, perhaps in a way similar to the way in which the assumptions that underlie adaptationism in the biological case can be and are (largely) avoided by contemporary research techniques?

I argue here that the similarities in the assumptions used by the adaptationist program in biology and those used in attempts to explain human behaviors in economics are illuminating of some of the serious problems with the latter. Further, I argue that the assumptions are largely necessary for the techniques as they are currently practiced, and that these assump-

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Economic Rationality and the many Roles of Rational Choice Theory

Rational Choice Theory (RCT) plays many different roles in economics. Rational choice theory can be meant to be a normative account of how people ought to behave, a descriptive account of how people actually behave, or a model of behavior meant to generate accurate but instrumental predictions of how people will behave (see Kaplan 2005). In the case of normative claims emerging from RCT, game theory (and other formalizations) are used to pick the courses of action most likely to lead to (some set of) desired outcomes. The failure to make choices consistent with one’s preferences, beliefs about the state of the world (including probabilities and outcome spaces), etc., is, on this view, a normative failure. But in other contexts, RCT is supposed to be a descriptive account of how people actually make decisions; the argument that people act in ways that are generally economically rational follows from the descriptive uses of RCT. Here, RCT is making a substantive claim about the actual causes of human actions, and an agent’s failure to make choices in that way (where “choices” are to be understood as including both conscious and unconscious reasoning) imply that RCT’s explanations are false in those cases; it is not a normative failure on the part of the agent but rather a failure of the theory to accurately describe the agent’s actual motivations for action. Closely related to RCT’s role in explaining the behavior of agents is its use in predicting the behavior of agents. The key distinction between the use of RTC in explaining behavior and its use in predicting behavior is that, as a model of human behavior, RCT could, in principle, provide good predictive accuracy despite being strictly speaking false (see Sober 2008 for discussion). Here, the failure of agents to act in ways consistent with the model would imply that the model is not adequate for predicting the behaviors of agents, and hence that the model is a poor one, not that the agents in question were themselves mistaken.

These different roles for RCT are not always properly distinguished either in work making use of RCT or in work critical of its uses (see Kaplan 2005). While the focus of this paper is the use of RCT as a description of the actions of agents, that is, on the use of economic rationality as a model of human behavior, the explanatory and predictive roles of RCT will not always be carefully separated, since the literature on the descriptive elements of RCT has not, for the most part, distinguished these positions. The reason for this is clear: the failure of a model of behavior to be adequately predictive (in arenas in which the model implies that it ought to be adequately predictive) is good evidence that the model is unexplanatory; however, that a model is predictively accurate is not good evidence that the model is in fact explanatory. Since many of the criticisms of RCT and economic rationality as a model of human behavior surround the failures of the models to make even minimally adequate predictions, the distinction is perhaps less important than it might be. If economic models of human behavior are eventually developed that have good predictive accuracy, distinguishing between the predictive power of the model and the actual causal structure of the world might become more important.

Economic Rationality and Human Behaviors

The application of economic models to human behavior in non-market arenas (and indeed, to individual decision-making in some markets) has long been criticized for both the assumptions these applications make about the causes of human behaviors and for the methodologies employed in the models’ attempts to explain human behaviors. Varoufakis, for example, has criticized these applications of economic rationality on the grounds that consistency between the explanation given by economic rationality and actual behaviors should not count as good grounds for assuming that those explanations are correct (1998); Rosenberg (1979) suggests a similar criticism, noting that the consistency between a formal theory and a particular data set is not evidence for the theory’s explanatory power if the theory was designed to fit that data set. Dupré has criticized these attempts to explain human behavior for their focus on individual behaviors and acts, as well as for the way in which any predictions that fail to be supported by empirical research can be (and often are) explained away by changing the assumptions made about, for example,

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2 Samuelson (2005) notes that one can also consider RCT to be a “philosophical exploration of the idea of rationality” and hence neither strictly speaking a normative claim nor a descriptive claim.
the preferences and beliefs of the actors (1987, 1998a). Sen has criticized the use of rational choice theory for both its assumption that a single utility function even could guide choices in many different arenas (1977) and for depending upon the idea that individual actions can be considered apart from the broader contexts in which they occur (1997). Green and Shapiro have argued that the application of rational choice theory to the political realm has been broadly unsuccessful, claiming (in part) that the reason these applications have been unsuccessful is that the explanations for behaviors are created post-hoc; they complain that it is assumed that actions are guided by rational choice, and the preference and reasoning required to fit the action to the model are then derived (1994, see also Shapiro 2000 for a popular account of this critique which extends it to other domains).

Taken together, these and similar sorts of critiques (which, of course, have themselves been attacked by supporters of economic rationality) point towards a number of questionable assumptions made and methodological practices employed when economic rationality is used in attempts to explain human behaviors. Critics accuse practitioners of making (at least) the following assumptions about human behaviors:

1. Human activities can be usefully considered to be assemblages of separate actions; these individual actions can be usefully considered to have been undertaken more or less independently of each other;
2. Human rationality is powerful enough, and the constraints on its action limited enough, that these actions can be assumed to be the result of agents rationally aiming towards some end; that is, it can be assumed that the actions are ‘utility-maximizing’ for the agent.

Critics further accuse attempts at using economic rationality to explain human behaviors of employing the following questionable methodological practices:

1. Consistency between an observed action (or pattern of actions) and a particular story which accounts for its rationality with respect to the agent’s preferences, beliefs, and goals is considered to be sufficient for accepting (at least preliminarily) the hypothesis that the behavior in question is in fact the result of a ‘rational decision’ (whether conscious or unconscious).
2. Any failure of a particular story about the rationality of a particular behavior (an observed inconsistency) leads immediately to the search for another account of the behavior which makes it out to be (economically) rational (rather than an exploration of alternate accounts of the behavior in question);
3. Any failure of a particular action to be optimal from the standpoint of the agent’s local preferences and utility is accounted for by evoking ‘trade-offs’ with other preferences; these claimed preferences are rarely subject to rigorous testing.

These assumptions and methodological practices resemble the assumptions and methodological practices that Gould and Lewontin criticized as constituting the “adaptationist program” in their classic “The Spandrels of San Marco and Panglossian Paradigm: A Critique of the Adaptationist Programme” (see Box 1). This should not, in one sense, be surprising; both ‘adaptationism’ and the above interpretation of “economic rationality” in microeconomic theory rely on ‘extremal’ principles – that is, in each case it is assumed that there is some (one) thing that is being maximized by the system described by that theory (see Rosenberg 1979). Adaptationists assumed that natural selection worked on the phenotypes of members of populations to maximize fitness, and that other influences on the average phenotypes of the populations in question were negligible; similarly, microeconomic theory supposes that people aim to maximize the satisfaction of their preferences (their utility) and that other influences on their actions are negligible.

In the case of microeconomic practice, the style of reasoning that these assumptions and methodological practices generate are most stark in works which attempt to apply rational choice theory to arenas of human behavior that are not traditionally thought of as market-oriented. However, these same assumptions and methodological practices can be seen used in more traditional accounts of market behavior, such as those found in basic text books in microeconomics, as well. Again, there is a striking parallel to adaptationist reasoning here. Adaptationism first came under sustained attack when its techniques were applied to human behaviors (see Pigliucci and Kaplan 2000, Lewontin 1979), but recognition of the problematic nature of the adaptationist assumptions in these less-traditional cases (human behaviors) led to the realization that those assumptions were wide-spread and too often ill-defended in more traditional cases (“ordinary” phenotypic traits). While the application of assumptions and techniques of economic rationality to human behaviors in non-market arenas has been controversial, the application of these assumptions to traditional market arenas has generally not been. However, as will become clear below, the problematic nature of the assumptions in non-market arenas has begun to inspire the re-evaluation of the models even in more traditional market arenas.
Turning first towards the kinds of assumptions that appear in traditional microeconomic texts, the introduction of Krebs’s *A Course in Microeconomic Theory* (1990) states that the “actor chooses from some specified set of options, selecting the option that maximizes some objective function,” that is, that “consumers have preferences that are represented by a utility function, and they choose in a way that maximizes their utility subject to a budget constraint” (Krebs 1990 4, emphasis in original). Krebs goes on to note that while consumers may not think in these terms, the models presuppose “that consumers act as if this is what they do” and that this leads to “testable restrictions of the models” used, in that some behaviors, if observed, would be inconsistent with the models; those models that “are not falsified by our observations” are “good positive models” (Krebs 1990 4). While Krebs is in fact somewhat skeptical about the robustness of these traditional models, he presents them along with the traditional model of preferences, in which the revealed preference theory can be used to generate (if all goes well) preferences consistent with observed behaviors (1990 42ff). It is worth attending here to the blurring of the explanatory and predictive roles; it is not clear whether Krebs is arguing that “good positive models” accurately model the causal structure of the world, or whether such models are able to achieve reasonable predictive accuracy despite not modeling the actual causes of human behaviors.

The assumption that other factors are negligible and can for the most part be ignored can be clearly seen in Asimakopulos’s summary of a chapter on consumer behavior. He writes that in the analysis presented the consumer

was assumed to be rational and to act on the basis of tastes that... change only slowly over time... The consumer was assumed to be very knowledgeable about the technical characteristics of the goods he was purchasing. The utility he expected to get from these goods was in fact what he obtained from them... (1978 133)

After noting that this leaves out many problems that a realistic analysis might have to account for, Asimakopulos notes that “the predictions obtained from such a theory do seem to have general applicability” (1978 133). Again, consistency between observed behaviors (changes in purchasing patterns, etc.) and the model are taken as good evidence that the model is descriptively and explanatorily useful.

With respect to trade-offs and the individual nature of actions, Blight and Shafto note that consumers are rational in the “very limited sense” that they “will seek to maximize utility” and that therefore the assumption that they will apportion their resources “between competing economic goods in such a way that the highest possible level of utility is achieved” (1989 63, 64). While they note that consumers fail to maximize their possible enjoyment of any particular good, this is to be explained by the ‘constraint’ of their not having unlimited resources (Blight and Shafto 1989 63). Varian explicitly defines utility as a description of preferences that are revealed through ‘choice behavior’ (Varian 1993 54-55), and argues that consumer preferences “are stable over the time period” that we are likely to observe them making choices (118). Further, Varian claims that consumer behavior can be best explained by attempts to ‘maximize utility’ with variations from expectations based on proxies for utility like money to be explained by the individuals preferences for e.g. risk-taking (1993, chapter 12).

Turning to those authors who attempt to apply the methodology of economic rationality (via rational choice theory) to all human behavior, the use of these assumptions and methodological practices becomes more obvious. Posner argues that the “only way to assess the fruitfulness of extending economics into the nonmarket sphere is to make economic studies of nonmarket behavior and evaluate the results” (1981 2). How are these to be evaluated? Economic notions of rationality are applied to areas traditionally regarded as unlike traditional markets under the assumption that the actions taken will try to “maximize economic welfare” (1981 4). The test is whether the observed practices in the world are “consistent with the theory” (1981 7). In the context of a specific example, the effect that increased testing for HIV would have on the spread of the disease, Philipson and Posner argue that people’s economically rational behavior once tested for HIV “may increase the growth of the epidemic rather than retard it” (1993 12). Why? They write that:

The reason is that persons who test negative can use their test result to obtain risky sexual trades that they could not obtain otherwise, while nonaltruistic persons who test positive have a diminished incentive to choose safe sex. (1993 12)

That is, given that “risky” sex has a higher utility than “safe” sex, ceterus paribus, if an agent’s beliefs about the odds of contracting HIV are changed by testing such that, before testing, the additional utility of “risky” sex was outweighed by the dis-utility of contracting HIV given the agent’s beliefs about contracting HIV (without test results) but after testing, the additional utility of “risky” sex outweighed the dis-utility of contracting HIV, given the agent’s beliefs about contracting HIV (with test results). (See Box 2)

However, their prediction (that increased testing will, ceterus paribus, increase the rate at which HIV
is spread) is rather less bold than it might at first appear because once "the model is refined to take dynamic and other complicating factors into account, the clarity of its prediction concerning the effect of voluntary testing on the spread of the disease is diminished" (Philipson and Posner 1993 12). One such complicating factor is the number of altruistic persons and what their exact motivations are; once these are taken into account (Philipson and Posner 1993 55), the predictive value of the economic analysis is quite restricted. Any failures of the model can be accounted for by different preferences constraining the particular maximization of value from sex trades (or by agents holding different beliefs regarding e.g. the rate of HIV among potential sexual partners than originally assumed). For example, Philipson and Posner write that altruists (who they define as those who incorporate the utility function of another person into their own; see 1993 55) "are less likely to risk infecting" their sexual partners with HIV and are "therefore more likely to switch to safe sex rather than attempt to conceal" that they are infected or have engaged in risky sex with others (1993 56). On the other hand, an altruist "may be more willing to engage in risky sex if his or her partner derives utility from it" (Philipson and Posner 1993 55-56). The emergent picture is this: once someone thinks they might be infected, they are more likely to engage in risky sex with their partner, since risky sex is 'worth more' to them (is more enjoyable), and there is no longer a significant risk to themselves. If they fail to act this way, perhaps they are an altruist; that is, perhaps they have another confounding preference – not to infect their partner with a deadly disease. If an altruist then doesn’t behave quite as expected, they perhaps have yet another confounding preference – for example, not to disappoint their partner’s desire for unprotected anal sex. Given all these possible preferences, and the others that can be invented (or perhaps more charitably discovered), it is hard to conceive of any possible set of outcomes that can’t be accounted for. Clearly, consistency between the model and the observed behavior (if not predictive value) can be gotten by taking the observed behavior as evidence of e.g. a particular ratio of altruists with particular motivations existing in the population.  

So, the hypothesis that a decision about whether people’s willingness to engage in unsafe sex under a variety of conditions can be best understood by reference to what rational choice theory would predict, is given this analysis, untestable. The model depends on various factors that are difficult, if not impossible, to determine accurately enough for predictions to be reliably made. Aside from the obvious difficulties in determining the agent’s preferences, such models depend not on the actual state of the world, but on the agent’s beliefs about the state of the world (in this case, for example, the estimated chance of transmission of HIV given various sex acts, the probability, before testing, that one or one’s potential partner has HIV, etc); as these will not always be accurate (as Philipson and Posner themselves note, see 158ff), there is another area where the predictive power of the rational choice analysis is imperiled by its reliance on a difficult to discover subjective factor. Given these difficulties, the consistency of this model with (nearly) any actions on the part of the person choosing whether or not to seek unsafe sex can be assured by supposing that the preferences fall within certain bounds (see Philipson and Posner 1993 38 and 40 for some examples of the interactions of such bounds).

Of course, such models could be tested once ‘preferences’ and beliefs about ‘probabilities’ and the like have been determined and then assumed to be stable. But determining these preferences and beliefs is difficult, and generally the only way of doing so that results in their being consistent with models of the agent’s behavior is to infer the beliefs from that observed behavior (for some criticisms of the use of ‘revealed preference theory’, see for example Sen 1997, 1994, 1977). If these preferences and beliefs could be assumed to be stable, they might then be tested against future behaviors by making predictions based on the economic rationality model; however, this assumption would be unwarranted as preferences at least can be shown to not be stable, even over relatively short periods of time (see Froberg and Kane 1989a-d for a discussion of this in the case of medical preferences; but see Becker 1996 for an opposing interpretation of data usually taken to imply that preferences are unstable).

So, in the view that emerges from Philipson and Posner (1993) all the classic marks of an ‘adaptationist program’ are visible: “sex trades” are individual actions, taken more or less independently of other actions in one’s life; it is assumed that agents are attempting to maximize the utility gotten from these sexual encounters; a particular story that can account for the behaviors in terms of such maximization is taken as evidence that people really do attempt to maximize the utility gotten from sexual encounters; and variations between the predicted and observed behavior are accounted for by evoking trade-offs with other preferences, which are not (and probably cannot be) rigorously tested.

Becker takes a similar approach to explaining both why people marry the person they actually marry (as opposed to someone else) and why they marry when they do (as opposed to earlier, later, or not at all). An “efficient marriage market,” according to Becker, “assigns imputed incomes or ‘prices’ to all participants” (1981 66). While in general one expects “positive assortative mating, where high-quality men
are matched with high-quality women” it is true too that “some participants... choose to be matched with ‘inferior’ persons because they feel ‘superior’ persons are too expensive” (Becker 1981 66). However, another compounding factor is that “participants in marriage markets” have “imperfect information” about their potential spouses (Becker 1981 220). Since marriage increases the costs of searching for new potential partners “participants usually do not immediately marry the first reasonable prospect encountered, but try to learn about them and search for better prospects” (Becker 1981 220). But...

time, effort, and other costly resources must be spend on search, and the longer the search, the longer gains from marriage are delayed. A rational person would continue to search on both the ‘extensive margin’ of additional prospects and the ‘intensive margin’ of additional information about serious prospects until the marginal cost and marginal benefit on each margin are equal. In particular, rational persons marry even when certain of eventually finding better prospects with additional search, for the cost of additional search exceeds the expected benefits from better prospects. (Becker 1981 220)3

What then is the general explanation of marriage on this view? Well, marriage to the ‘right’ sort of person is utility-increasing. Even among the class of utility-increasing potential mates, though, some are better (will increase utility more) than others. Searches, both to find potential mates and to discover more about potential mates, have costs associated with them, so at some point the cost of continued searching outweighs the possible gains of continued searching, and one marries, even if one is sure that ‘better’ potential mates are available. Note that ‘mate searches’ are actions taken more or less independently of the rest of one’s life, on this view; at least, the way in which they could be integrated into one’s life is unclear. What kinds of gains does marriage bring? According to Becker, all kinds of gains, some obviously financial, some psychological, some involving time, etc. (see 1981 e.g. chapters 3, 4, 8). But again, people’s preferences are assumed to vary (recall that e.g. for some people, the high ‘cost’ of highly desirable mates encourages them to seek mates of a ‘lower’ quality than themselves) and so what one makes a potential ‘mate’ desirable is plainly at least in part subjective (although Becker 1981 argues that some measure of objective ‘quality’ is revealed by the ‘shadow pricing’ of potential mates in the ‘marriage market’).

That relatively few people will search forever for the ‘perfect’ mate and that most people will marry people from roughly the same (social and economic) background is not seriously doubted by anyone; these are not surprising predictions of the theory but rather well established sociological facts. Given this, one might reasonably doubt that the mere consistency of Becker’s mathematical treatment and these observations with is good evidence that the economic model of marriage given by Becker provides valuable insights. Given the number of assumptions that must be made, both about the motivations of people getting married (their ‘preferences’), the amount of information that they have, the costs they associate with spending more time searching, etc., it would, as usual, be hard to find any behavior that cannot be accounted for on the basis of some decision-theoretic argument or other. Untestable trade-offs are evoked at every staged: if some people search longer, then they had a preference for a ‘higher quality’ mate; if some people don’t search for so long, well, perhaps the high ‘cost’ of ‘high quality’ mates put them off, and they ‘settled’ for the first utility-increasing partner they found.

What is lacking, as usual with adaptationist-style reasoning, is the ability to rigorously test the hypothesis, or to make startling, or for that matter even consistently accurate, predictions (and not just in non-market realms, see Box 3). As a result, the failure of any predictions made (that HIV testing will increase, rather than decrease, the spread of HIV, etc.) tends to be regarded as evidence that the subjective preferences and interpretations of probability ascribed to the agents were incorrect, but not as evidence that the rational choice model might be inappropriate in these cases. Again, this move, criticized by Lewontin and Gould in the biological case of adaptationism, permits keeping the basic ‘adaptive’ (in this case, utility maximizing) hypothesis despite its failure given a particular story (in this case, a story about the agent’s attempt to maximize utility based on particular preferences and beliefs). Since it is assumed that the agents are acting on the basis of rational self-interest, any failure of the model is accounted for not by re-considering that assumption, but rather by inventing new constraints, preference rankings, or beliefs, which, again, are not subject to rigorous testing.

Similar kinds of arguments could be compiled ad nauseam. Becker uses an economic model not only

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3 There is currently an active debate in the evolutionary psychology and economics of human behavior communities about what the ‘best’ search strategy for mates really is. Suggested techniques range from sampling some 37% of the number of potential mates you expect to ever meet, then pick the next potential mate that is even better than the best of that lot, to sampling perhaps only 5% or even fewer potential mates, then picking the next potential mate that is even better. See the discussion following Miller’s “Mate Choice: from sexual cues to cognitive adaptations” (1997) and citations therein.
to explain why individual marriages take place, but why the institution of marriage takes the general form that it does within particular cultures (e.g. the ease of divorce, monogamous versus polygamous traditions, etc. see 1981 chapter 2). Posner argues that the criminal justice system is best understood in economic terms (and would work even better if such reasoning was explicit) (see for example Posner 1981; Wilson and Herrnstein do some similar work in their 1985). Becker extends rational choice theory to understanding addictive behavior, including styles of quitting (Becker 1996). And again, similar styles of reasoning can be found in many basic economic texts, both in the context of decisions between consumer goods, and in other contexts, such as how agents value ‘leisure’ time versus the money to be gained from working longer hours. The basic assumptions – that the actions are undertaken to optimize a particular outcome, undertaken by the agent more or less independently of other actions in their lives, that the actions do maximize the outcomes (at least overall), and that discrepancies between predicted actions and the actions actually taken are best explained by other preferences the agent may have which constrain maximization on the current axis – can be found in much microeconomic reasoning, and especially in that reasoning which tries to explain broader (rather than narrower) aspects of human life.

Back to Biology: The End of Adaptationism?

Gould and Lewontin suggested that adaptationism (as they described it – see Box 1, above) was a poor approach to understanding the history and biological meaning of biological traits, largely because it conflated the ability to tell a good adaptive story with having gathered evidence that the story was true (or at least likely to be true). The move from “it is possible that this trait y is an adaptation (was the result of natural selection) for performing function x” to “y is an adaptation for doing x and was selected for its ability to do x” was too often made, they claimed, based merely on the trait (y) happening to do something like x now and a story about the adaptive significance of doing x seeming plausible. At the time, Gould and Lewontin were clear that they believed adaptation by natural selection to be a supremely important – indeed, in many ways the most important – evolutionary mechanism (1979 155); however, they argued that in order to understand how specific traits arose and were maintained in a population required more than telling a good story, and that explicit attention to non-adaptive possibilities would often be valuable (1979 156ff).

It has been argued that the characterization of the adaptationist program given by Gould and Lewontin, and followed here, is too strong, and represents something of a straw-man in the debates surrounding adaptation (see e.g. Dennett 1995 and cites therein). This view is unfortunate, because it obscures the enormous (and for most part welcome) changes in the way evolutionary biology deals with adaptation that have occurred since the 1970s, changes that Gould and Lewontin’s writings were centrally involved with bringing about. They were not the first, and certainly not the only, biologists to criticize the poor reasoning too often used in thinking about adaptation in the 1950s through 1970s; well before the “Spandrels” paper, many of the same points had been made by, for example, Williams (1966). In any event, Rose and Lauder, in their discussion of the history of ‘adaptationism,’ argue that by the early 1980s the sort of facile reasoning about adaptations criticized by Gould and Lewontin (and Williams) was in sharp decline, at least in part because of the influence of Gould and Lewontin’s critiques (Rose and Lauder 1996 1-2).

But of course, “the demise of the old adaptationism,” to use Rose and Lauder’s phrase (1996 3), did not mean the end of hypotheses involving adaptation in evolutionary biology – far from it! Indeed, Rose and Lauder’s edited collection Adaptation is primarily an exploration of the many advances in formulating and testing adaptive and non-adaptive hypotheses regarding the origin and maintenance of traits in populations that had occurred since the “Spandrels” paper was published (Rose and Lauder, eds. 1996). In the almost three decades since the “Spandrels” paper was published, empirical techniques have been developed, and conceptual advances made, that permit the assumptions and methodological practices that defined the adaptationist program to be, for the most part, dispensed with (see Pigliucci and Kaplan 2000 and cites therein).

And dispensing with those assumptions and methodological practices turns out to be a good idea, because many of the adaptive hypotheses generated

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1 Kitcher has argued that Lewontin has since become less willing to accept traditional accounts of natural selection and adaptation in general (Kitcher, 2000), and Godfrey-Smith makes a similar point about Lewontin’s resistance to adaptation as a “bad organizing concept for biological research” (Godfrey-Smith 1999 181). Dennett has argued that Gould later became less enthusiastic about the role played by natural selection and adaptation than a reasonable reading of the “Spandrels” piece or other work published by Gould in the 1970s would imply (Dennett 1995, esp. chapter 10). While these claims are debatable, they are besides the point here; as I will argue below, the difficulties with the adaptationist program as described above can be (and for the most part have been) solved within evolutionary biology. Insofar as these solutions still leave some researchers uncomfortable, it is not the adaptationist program as traditionally defined that they are uncomfortable with, but rather, for example, with uses of the concept of adaptation more generally or the limitations of the so-called “modern synthesis” as it is usually understood.
with the adaptationist program turned out to be at best misleading (see Williams 1966, Lewontin 1978, various in Rose and Lauder, eds. 1996 and cites therein). The more we learn about the complexities of developmental and evolutionary biology, and especially about the relationship between changes at the genotype level and phenotypic evolution, the less likely it appears that simplistic adaptive hypotheses, based on little more than observing the trait as it exists now and thinking about how that could have been useful to the organism in the past, will generate adaptive stories that can stand up to empirical testing (see Futuyma 1997, Schlichting and Pigliucci 1998). Of course, this shouldn’t be taken to mean that these hypotheses will not point in some interesting directions for further research; one can reject the adaptationist program without rejecting the thesis that understanding adaptation by natural selection is central to understanding evolution. Indeed, Godfrey-Smith points out that one can support what he calls “Methodological Adaptationism,” the position that biological systems are best approached by looking “for features of adaptation and good design,” without thinking that adaptive hypothesis are either particularly special or particularly likely to be the whole story (Godfrey-Smith, 2001; see also 1999).

Nor does rejecting an adaptive hypothesis mean rejecting the thesis that the trait in question is functional in the way implied; as Gould and Lewontin themselves pointed out, many organisms make good use of traits that arose (and, indeed, are currently maintained by natural selection) for other reasons entirely. Griffiths (following Gould and Vrba 1982) notes that traits which were formed by natural selection working on one aspect of their use may be used in a new functional way, and that this way can either result in the trait being actively maintained by natural selection on that new use (an exadaptation in his terminology) or simply be used in the new way but not actively maintained because of that use (an exaptation in his terminology) (Griffiths 1992).

What has become obvious in the biological case is that in order to make a case for a trait being an adaptation, especially an adaptation for performing a particular function or functions for the organism, one has to do rather more than be able to tell a good story. Fortunately, at least in the case of some plants and animals, techniques have been developed that permit biologists to actually test particular adaptive and non-adaptive hypotheses (see Pigliucci and Kaplan 2000 and cites therein, various in Rose and Lauder eds. 1996 and cites therein). Making a case for a particular hypothesis regarding the origin, spread, and maintenance of a trait in a population usually involves gathering several different kinds of evidence, as generally speaking no single kind of evidence is sufficient to exclude important alternate possibilities (see Box 4). Rarely will it be possible to gather all the kinds of evidence that one might wish to have in order to test various models that include adaptive and non-adaptive causes; however, with enough different kinds of evidence one can achieve a reasonable degree of confidence in a particular adaptive (or, for that matter, a particular non-adaptive) hypothesis (of course, just what constitutes ‘enough’ here is often hotly debated; see for example the exchanges between Dennett and Gould, e.g. Dennett 1995 and Gould 1997).

Lessons for Economics: Moving Beyond Rational Choice Theory & Economic Rationality

In the biological case, the alternatives to adaptationist-style reasoning about adaptive hypotheses are now well-known. Models that include constraints of various sorts (often the result of pleiotropy, allometry, etc.), selection for the ability to take on many different (adaptive) traits rather than for a particular trait simpliciter (e.g. regulatory phenotypic plasticity), and the like, serve as alternatives for simple-minded adaptive stories. Testing specific articulations of these alternate hypotheses in individual cases is often, as noted above, difficult and time-consuming. But the pay-off of going through the process of rigorously testing both adaptive and non-adaptive hypotheses in individual cases is more than just not making mistakes; the pay-off is often a better understanding of the process by which particular traits came to be associated with particular (suites of) genes and way(s) in which the structure of the organism has been shaped by its phylogenetic and developmental history (see for example Schlichting and Pigliucci 1998; Rose and Lauder 1996).

Gould and Lewontin argued that organisms are “so integrated and so replete with constraints upon adaptation... that conventional styles of selective arguments can explain little of interest about them” (1979 594). While this kind of claim probably represents an over-selling of constraints (see for example Schlichting and Pigliucci 1998 158, 166 and cites therein, and Pigliucci and Kaplan 2000 and cites therein), the basic idea, that organisms must remain integrated wholes if they are to be successful (be reasonably fit) and therefore that natural selection on particular uses of particular traits to produce ‘adaptations’ is unlikely in the extreme to be the whole story of phenotypic evolution, is surely sound (Schlichting and Pigliucci 1998, see especially 162-166; Pigliucci 2001, especially chapters 4 and 5; West-Eberhard 2003). Indeed, it isn’t clear what it would mean for natural selection to be the “whole story” – natural selection, after all, can only work on populations consisting of entities with particular (instanti-
ated) systems of development and heredity (the “substrate,” to use the terminology of Matthan and Ariew 2002).

So rather than approaching the question of testing hypotheses through for example something like the list of alternative hypotheses that Gould and Lewontin argued should be considered (and, ideally, tested) before accepting an adaptive hypothesis regarding a particular putatively adaptive trait (1979 591-593, see Box 5), we would do better to attend to their more general point, namely, that claims that particular traits were adaptations needed to be explicitly formulated and tested aggressively against reasonable competitors. This is one of the key points made by Sober in Evidence and Evolution – hypotheses are best tested against other hypotheses, and hence we should think in terms of selecting among alternative models, models that incorporate different causes (and different numbers of kinds of causes), by finding ways to test the models against each other (Sober 2008; see also Shipley 2000).

The point that assessing the etiology of particular phenotypic traits in a population is, in the biological case, not best considered independently of the rest of the organism, its ontogeny, and its phylogenetic history has an obvious counterpart in the economic case. Human actions do not, for the most part, occur in a void. Indeed, some authors have suggested that our ability to undertake ‘utility-maximizing’ actions in the world is so constrained by our need to live at least marginally coherent lives within rich and complex social systems that the latter represents a far more important and interesting place to look for explanations of our behavior than the former (see Dupré 1998a, 1998b, also various remarks in Sen 1999, e.g. 8-10, 199-203, 263-281, etc.). And the causes embedded in models of our behavior that constitute the explanations in these cases will not be of any one kind, or indeed, any few kinds. Rather, these authors have suggested that the kinds of causes needed by the models are likely to be at least as diverse as the explanations we use to explain our actions in everyday life (few of which, of course, involve explicit references to utility-maximization).

So while an action may be ‘useful’ to us in various ways, our reasons for undertaking that action may or may not have much to do with that usefulness. Our lives are filled with ‘constraints’ upon the choices we make, and even constraints upon what areas of our lives are subject to rational deliberation at all (see Sen 1997, esp 747-751). To claim that we never make decisions to act with particular aims in mind, or that none of our habitual actions were originally undertaken because they are useful to us in one way or another, would be foolish (or insane). But rejecting the adequacy of economic models of human behavior with a single parameter – utility maximization for the agent – is eminently reasonable. As noted above, attempts to explain all of human behavior, even all of human economic or market behavior, through the single lens of utility-maximizing economic rationality has come under serious attack from within economics (see for example Sen 1977 for one of the classic statements of this objection, and Varoufakis 1998 and Sen 1999, especially pages 76-77 and 250ff, for more recent articulations of such objections).

In considering the range of possible motivations for human actions, it is perhaps worthwhile to draw a few more explicit parallels between the etiology of human actions and etiology of biological traits. In the biological case, for example, some traits are possessed by organisms not because of the traits’ current functional role, but rather simply because of phylogenetic inertia; these traits may once have been ‘useful’ and the explanation for how they reached their current form in the first place may make essential reference to that ‘use,’ yet the reason they continue to exist now might have nothing to do with the original causes of their existence. Similarly, it seems likely that some of the actions taken by agents are the result of inertia. Whatever the initial reason for adopting a habit was (if any such reason there was), it may have long since ceased to be important, and yet the action (the habit) may continue on unabated; this might be true both of relatively idiosyncratic actions and, perhaps more obviously, of customs and rituals. Other parallels might include kinds of actions that were originally undertaken for one kind of reason, but turn out to serve other purposes in the lives of the agents in question as well. These would be, depending on the details, the equivalent of what have been called “exaptations” or “exadaptations” in the biological case (see above and Griffiths 1992). And some of our actions may well be necessary by-products of other actions (which themselves may or may not have been taken for ‘rational’ purposes); this would be the equivalent of biological traits that emerge from selection on other traits, due to the contingencies of development or the need for the organism to maintain a certain level of integration.

While it would be possible to explore any of these parallels in great detail, for the sake of brevity I will consider only one detailed example. Sen argues that there are a number of situations in which we find ourselves unable to choose options that would maximize utility (see Sen 1997, 1999 261-281). Social norms, for example, constrain our ability to act in utility maximizing ways; the fact that we live within a particular social milieu influences our decision-making in both obvious and more subtle ways (see 1999,1997, 1994, 1977). In effect, Sen argues that social commitments and moral imperatives cannot be successfully reduced to a single utility function,
nor can conventional rule following (1997 748, see also 1999 76-77, and 1977). Further, these are all different kinds of reasons and cases, and cannot be reduced to each other, nor to a any more fundamental desire or reason. On Sen’s analysis, what “underlying forces” cause particular behaviors is an empirical matter, albeit one that is difficult to determine satisfactorily given contemporary empirical and conceptual tools (see Sen 1999 261-281, 1997 748-750).

As Sen put it in “Rational Fools” (1977) a person with “no use for these distinctions between quite different concepts... must be a bit of a fool” (1977 102). Sen’s later work suggest that a theory which attempts to make every individual action out to have the same causal structure (rational deliberation, either conscious or unconscious) and over-all end (utility maximization), should, likewise, seem a bit foolish (see Sen 1999, 1997).

But simply pointing out the limitations on the current ability of economists to deal with the difficult empirical matter of determining what set of factors (rational deliberation, personal habits, conventional rule following, etc) went into determining the actions of particular agents is not yet doing the work of reformulating particular hypotheses into forms that could be subjected to rigorous testing. Thaler, for example, has explicit called for microeconomic analyses to take explicit account of the fact that people act in ways which are not fully rational and not fully captured by models that assume rational decision making (see Thaler 2000 and cites therein).

In his programmatic “From Homo Economicus to Homo Sapiens” Thaler argues for taking proper account of a number of different confounding factors in microeconomic modeling. These include the sorts of biases to which Tversky et al have drawn attention to (Thaler 2000 133-6; see various in Kahneman, Slovic, and Tversky 1982 and Bell, Raiffa, and Tversky 1988), the recognition that not all economic actors will act in their rational best interests (Thaler 2000 136-7), the recognition that human cognition is complex and that these complexities need to be taken account of in any theory which attempts to model human behavior (137-8) and the recognition that ‘emotional’ reasons for acting can be powerful but hard to model using theories that assume agents to be motivated by rational self-interest (139-140).

The task of developing and testing more complex economic models of behavior is simplest in those arenas in which the number of potentially interacting causes is limited, either artificially (as in experimental settings) or by limitations on the relevant preferences (as in traditional financial markets). And in these arenas, “behavioral” economics is in fact making some headway; simpler models of utility maximization are being replaced with models that take a number of confounding causal factors into account (see Mullainathan and Thaler 2001 and cites therein). Thaler suggests that by testing particular hypotheses about why agents perform the actions they actually perform, including hypotheses that make at least some of the agents out to be performing actions that are in some deep sense non-rational, one can sometimes determine the actual ‘mix’ of (mostly) rational and less-rational actors, and the ways in which the less-rational actors actually make decisions, and from there begin to develop more reasonable (and hence more predictively accurate) models of market behavior, especially in financial markets (2000 136-7, 140). But this makes clear that testing models of human that include various sorts of causes (both rational and non-rational) demands more than just creating models that are consistent with observed behavior; it involves finding ways to independently test the parameters used in the various models, and ways to test the predictive accuracy of the models so-developed.

Thaler claims that the reason economic models could not begin to include such information until recently is that economists lacked both the conceptual and empirical tools for incorporating such complex information into their models, and indeed for determining the empirical results themselves (Thaler 2000 140). Advances over the last few decades, Thaler suggests, have made building models of human behavior which use empirically grounded assessments of the actual reasons that particular agents perform particular actions possible, albeit still very difficult. And Thaler suggests that some of this work has in fact already been done, and that some of the better models of e.g. stock market behavior take account of at least some of the factors that these difficulties point towards (Thaler 2000 136; see also ).

More broadly, “experimental economics” attempts to both discover behaviors in need of explanation and to test particular models of behavior (see for example Samuelson 2005). Thaler argues that these two projects are closely related, in that it is difficult to determine what kinds of motivations for behaviors regularly occur, and, even once those are known, it remains difficult to incorporate those kinds of empirical results into the models (Thaler 2000 140). As difficult as such a project is in “traditional” market arenas, extending such models into non-market arenas is likely to be very much more complex and difficult indeed. But perhaps in non-market areas such modeling will prove to be less fruitful in any event; Ostrom’s work for example points towards the possibility that qualitative models may be more useful for guiding policy than more formal models (see e.g. Ostrom 2002). If one is interested in designing a stable resource-sharing regime, the lessons from the qualitative models may be sufficient, and these models do not require that the causal influ-
ences of particular emotional (or other non-economically rational motivations) be accurately discovered or formally incorporated.

Conclusions and Directions for Future Work

What ought to be clear from the above discussion is that we cannot consider the reasons that individual actions were undertaken without considering the structure of our lives more generally and the actual causal pathways which resulted in the actions. Being able to tell good stories about our actions being attempts to ‘maximize utility’ given our beliefs and preferences does not guarantee that the actions were actually undertaken for that purpose. In the biological case, the assumptions and methodological practices associated with adaptationism (in the strong sense outlined above) have come to be rejected by most biologists (see Rose and Lauder 1996). I have argued that the assumptions and methodological practices used in microeconomic practice (and especially in attempts to use economic analyses to explain human behavior more broadly) share much in common with those of the adaptationist program in biology, including some of the faults. Currently, however, with respect to abandoning ‘adaptationist’ assumptions in favor of actively testing alternative hypotheses, microeconomic practice seems to be lagging behind biological practice.

There are, no doubt, a number of reasons for this gap. One of them is likely that determining the reasons that particular human behaviors were undertaken is arguably a more complex undertaking than determining the causal pathways through which a particular biological trait acquired the particular form it has. A related problem is that where a trait performs a large number of useful functions, it is notoriously difficult to apply such techniques as optimization analyzes, and very difficult to determine which relevant selective pressures (if any) were responsible for the trait’s current form (see Niklas 1994, 1997; Schlichting and Pigliucci 1998, especially those sections dealing with the evolution of constraints, and cites therein). It is prima facie plausible that most human behaviors are of this sort; think for example of the myriad of different functions ‘going to work’ serves, ranging from the instrumentally valuable earning of income to the intrinsically valuable social interactions (on this topic, see Sen 1999 92-94). Another reason for the current gap between economic practice and biological practice is likely related to the difficulties often encountered when attempts are made to test biological hypotheses involving possible human adaptations; these difficulties often result from ethical constraints which limit our ability to generate certain kinds of empirical evidence about human traits, both physical and behavioral.

Yet another difficulty is likely related to the persistent confusion (noted above) of the normative and descriptive aspects of economic models, including microeconomic models; indeed one of the improvements in economic modeling Thaler recommends is to more sharply distinguish these two roles (2000 138-9). The only similar confusion in evolutionary biology was between ‘how possibly’ and ‘how actually’ stories, but even so, the historical nature of the adaptive stories in evolutionary biology has always been fairly clear (see Griffiths 1996).

In the end, if economic models relying solely or mostly upon agents making rational choice are rejected, it will not be only because the assumptions underlying such models are poorly motivated; until better ways of modeling behavior that do not rely on such assumptions and methodological practices are developed, such models remain the only game in town. Similarly, until it became possible to actually test particular hypotheses about how particular traits arose and were maintained in the biological case, the calls demanding that these hypotheses be aggressively tested were largely ignored (Gould and Lewontin 1979, Rose and Lauder 1996, Pigliucci and Kaplan 2000).

While techniques for testing hypotheses about why particular agents undertook particular actions are in fact being developed, this development has been slow and unsteady, and so the sort of storytelling activities engaged in by, for example, Posner and Becker may well remain popular for some time to come. However, the recognition that there is a better way, one which takes account of the actual process that leads people engage in some activities rather than others, strongly suggests that such stories should be rejected as inadequate for the acceptance of the hypotheses they argue for. And if these stories have other (e.g. normative rather than descriptive) roles, that role must be separately defended.

References


Text Boxes

**Box 1: Gould and Lewontin’s Characterization of Adaptationism**

Gould and Lewontin characterized the adaptationist program as making the following assumptions and engaging in the following methodological practices (1979 151-153):

**Ontological Assumptions**

1. Organisms can be usefully considered as assemblages of traits, the adaptive nature of each of which can be considered independently of the others.
2. Natural selection is powerful enough, and the constraints on its power limited enough, that traits should generally be assumed to be optimally suited for the tasks they are currently performing.

**Methodological Practices**

1. Consistency between the observed trait and an explanatory story told in terms of natural selection is sufficient for the preliminary acceptance of the hypothesis that the trait is adaptive and evolved in the way that the story suggests.
2. The failure of one adaptive story leads immediately to the search for another adaptive story, rather than the exploration of non-adaptive alternatives.
3. Any failure of particular traits to be optimal is accounted for by invoking ‘trade-offs’ with other adaptive traits; these ‘trade-offs’ are rarely subject to rigorous testing.

**Box 2: A Formal Model of “risky” Sex Decisions**

Consider an agent considering whether to have “risky” or “safe” sex.

Let:

- $u(\alpha x)$ be the utility that agent $\alpha$ expects to derive from an outcome $(x)$
- $P(\alpha x|a)$ be the agent’s beliefs about the probability of outcome $(x)$ occurring, given action $a$
- $R$ be engaging in a “risky” sex act
- $S$ be engaging in a “safe” sex act
H be the acquisition of HIV

Philipson and Posner claim that HIV may spread more rapidly if testing is available if an agent, A's, beliefs and preferences are such that:

1. \( u(AR) + P(AH|R&notest\text{ available})(uAH) < u(AS) + P(AH|S&notest\text{ available}) \) but
2. \( u(AR) + P(AH|R&text{ available})(uAH) > u(AS) + P(AH|S&text{ available}) \).

Philipson and Posner suggest that this will likely be the case when one believes that if one's partner has tested negative for HIV, the risk is relatively low, or when one believes that once one has tested positive for HIV, the risk of additional sex with HIV infected partners is very low.

However, consider an agent A who is an “altruist” (that is, they incorporate the utility function of their partner into their own), and who believes that if they are HIV+, then their chance of passing the HIV infection on to their partner during a “risky” sex act is such that their partner, A’’s, preferences are:

3) \( u(A'R) + P(A'H|R)(uA'H) < u(A'S) + P(A'H|S) \)

Then, it is entirely possible that the availability of testing may decrease the spread of the disease, if:

4) \( u(AR) + P(AH|R&no test\text{ available})(uAH) + u(A'R) + P(A'H|R&no test\text{ available})(uA'H) > u(AS) + P(AH|S&no test\text{ available}) + u(A'S) + P(A'H|S&no test\text{ available}) \) but
5) \( u(AR) + u(A'R) + P(A'H|R)(uA'H) < u(AS) + u(A'S) + P(A'H|S) \)

That agent A may not in fact know either the preferences of agent A’ or the probabilities that agent A’ believes attach to various outcomes additionally complicates matters.

**Box 3: Predictions and Rational Choice Theory**

Predictions made using decision-theoretic models under the assumption that the agent’s preferences and beliefs have been uncovered, are stable, and are broadly aimed at maximizing the agent’s individual welfare are rarely accurate (see Sen 1977, 1994). As noted in the main text, the failure of these predictions in non-market arenas tends to be regarded as evidence that the subjective preferences and interpretations of probability ascribed to the agent were incorrect. The problem is that there is growing evidence that the predictions of rational choice theory fail even where there are good – indeed, superb – reasons to believe that the subjective preferences ascribed to the agents cannot in any real way be inaccurate, and that the probabilities the agents are working with at least ought to be reasonably accurate and consistent.

If economic rationality applies anywhere, the reasoning goes, it ought to apply to financial markets; there is no excuse for not attempting to maximize the expected financial gain in these cases and markets are large enough that “mistakes” on the part of individual agents ought to be “washed out” by the general pattern. The problem is that the predictions that emerge from the assumption that market behavior is predictable from the model of human behavior given by rational choice theory are too often verifiably and obviously false.

For example, where stock in a single company is available as if it were two different stocks (e.g., trading in different markets), the prices of the two stocks ought to reflect the (single) value of the underlying company, and hence ought to be stable with respect to each other; indeed, their prices ought to reflect the proportion of ownership, etc., that the stocks assign. But this is often not the case: stocks associated with the same underlying companies will change value independently of one another (see Mullainathan and Thaler 2001). More generally, Mullainathan and Thaler (2001) note that in an efficient market with rational investors, there ought to be very little trading; the high levels of trading on stock exchanges therefore suggests that investors are not, in general, acting according to traditional models of markets that assume rationality.

The failures of RCT to predict human behavior in experimental contexts where there is some attempt to minimize the relevance of non-monetary preferences are legion, with the one-shot, anonymous “Ultimatum Game” perhaps the most famous case. In this game, one player makes a proposal for splitting a resource neither player has any prior claim to, and the other player can “accept” or “reject” the proposal. If the offer is accepted, both players get the amounts suggested by the split; if it is rejected, neither player gets anything. Given the anonymity and one-shot nature of the game, for the player “accepting” or “rejecting” the decision to reject
any non-zero offer is for them to turn down “free money,” with no obvious benefit, as the only other person they are harming by doing so (the “proposer”) is not known to them & will very likely not be interacting with them again. And yet, in most cultures tested, players will reject offers viewed as “unfair” even at substantial costs to themselves (rejecting, for example, offers that would leave them with money equivalent to several hours of wage labor at the rates they are usually paid). Further, attempts to explain the variation that exists between cultures has not yet been successful (see Chibnik 2005).

Given these kinds of failures, a rethinking of the basic assumptions that go into explaining human actions as the result of people making rational decisions to maximize their expected utility would seem to be in order.

**Box 4: Evidence Relevant for Comparing Models Involving Adaptive and Non-adaptive Causes**

Sober, in *Evidence and Evolution*, argues compellingly that neither adaptive nor non-adaptive hypotheses should be considered *a priori* more likely in evolutionary biology (neither models with or without natural selection as a cause constitute a reasonable “null” hypothesis) (Sober 2008). Rather, the strength of models with various causal parameters (various kinds of selection, and various sorts of non-selective causes) should be explicitly compared on the basis of the available evidence.

The following chart sketches the kinds of evidence that particular techniques can generate:

<table>
<thead>
<tr>
<th>Technique(s)</th>
<th>Kind(s) of Evidence Generated</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phenotypic manipulation (laboratory or field)</td>
<td>Fitness consequences of the traits in question, causal mechanisms associated with traits and fitness consequences</td>
</tr>
<tr>
<td>Transplant studies</td>
<td>Fitness consequences, hypotheses re: selective pressures, hypotheses re: local adaptations</td>
</tr>
<tr>
<td>Laboratory evolution</td>
<td>Robustness of pathways, strength of constraints</td>
</tr>
<tr>
<td>Optimization analyses</td>
<td>Qualitative assessments (for quantitative plausibility), sensitivity, path-dependence</td>
</tr>
<tr>
<td>Phylogenetic analyses</td>
<td>History of trait, homology (shared derived) vrs homoplasy (independent derivation)</td>
</tr>
<tr>
<td>Regression analyses / Comparative Method</td>
<td>Relationship between trait and environmental variables, strength of relationship, relationship between trait and fitness</td>
</tr>
</tbody>
</table>

These kinds of evidence include evidence about the history of the trait within in the populations of interest (phylogenetic histories, molecular systematics), evidence about the fitness consequences of the trait (ecological field studies, laboratory evolution studies, experimental phenotypic manipulations, etc.), optimization analyses (often stressing the possible constraints on optimization), and such methods as regression analyses of the trait(s) of interest to test whether natural selection has been a major force in shaping them (Lande-Arnold analyses and the contemporary extensions of them) (again, see Rose and Lauder eds. 1996 and cites therein for discussions of these methods, Pigliucci and Kaplan 2000 for a brief summary of some of them).

**Box 5: Gould and Lewontin’s “Partial Typology of Alternatives”**

Gould and Lewontin argued that the following kinds of causal hypotheses regarding the origin, spread, and maintenance of traits in populations should be considered when testing adaptive hypotheses:

1. No adaptation and no selection: the trait in question may be the result of e.g. genetic drift or phylogenetic inertia.
2. Indirect selection: the trait in question was not the subject of selection – its features are the result of its association with another trait (which itself may or may not itself have been the subject of natural selection).
3. Selection without adaptation: a trait may increase in frequency due to natural selection but not be ‘adaptive’ as generally understood. Lewontin’s example involves a resource-limited species and a genetic mutation which doubles fecundity: this does not increase the population’s mean fitness, it only alters the population dynamics.
4. Adaptation without selection: the trait may be adaptive but not itself the product of selection. Phenotypic plasticity of the “developmental accommodation” form may be one example of this; although the ability of development to “accommodate” new environments or genetic backgrounds and produce useful phenotypes may be an ability that was selected for, the phenotype itself might be adaptive but entirely novel, and hence could not itself be the result of selection. Another example: while hermit crabs usually end up well camouflaged, this adaptive feature is the result of their using whatever shells happen to be around them; since in general the cast-off shells they find have been left by organisms that have adapted (by natural selection) to the local environment, the crab’s shells end up adapted, as well.

5. Adaptation and selection, but no basis for distinguishing between alternative adaptations: while the trait may be adaptive and have been selected for, there may be no way of distinguishing between different forms of a trait on the basis of their adaptive significance (the problem of multiple adaptive peaks). While it is likely that the rhino’s horn is the result of natural selection, it is plausible that the difference between one- and two-horned rhino’s is the result not of different selective regimes, but rather an accident of history.

6. Adaptation and selection, but the particular adaptation represents a ‘secondary’ use of a trait already present in the population for other (generally historical, but often also adaptive) reasons. This is the case to which Gould and Vrba later referred to as ‘exaptation’.

About the Author

Jonathan Kaplan
Dr. Jonathan Kaplan earned his Ph.D. in Philosophy from the Stanford Philosophy Department in 1996. He currently specializes in the Philosophy of Biology, Philosophy of Science (including the social sciences), and Political Philosophy. Prior to his current position as an Associate Professor of Philosophy at Oregon State University and Chair of the OSU Philosophy Department, he served as an Assistant Professor of Philosophy at the University of Tennessee in Knoxville, a Lecturer in Philosophy at Stanford University, and was a post-doctoral fellow with the Stanford University Biomedical Ethics Center’s Program in Genomics, Ethics and Society. His most recent book, Making Sense of Evolution co-authored with evolutionary biologist Massimo Pigliucci, was recently published by the Chicago University Press.