(12/09/2012)

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Ideas that stand the [evolutionary] test of time

Published March 26th 2007 as part of a CNRS online conference and discussion on "Adaptation and Representation" see

HTTP://INTERDISCIPLINES.ORG/MEDIAS/CONFS/ARCHIVES/ARCHIVE 4.PDF

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ABSTRACT: Evolutionary psychology, memetics and models of cultural evolution focus on reproductive success. I will argue that fitness should in fact focus on differential persistence of entities instead of differential reproductive success of replicators. Understanding evolution as such shifts the nature of adaptation from reproduction to persistence, changing the means by which representational powers would be selected in biological systems.

1. Introduction

Evolutionary psychology, memetics and models of cultural evolution focus on adaptationist explanations and their appeal to replicators. This view fleshes out the notion that fitness should be understood in terms of differential reproductive success. I will argue that fitness should in fact focus on differential persistence of entities instead of differential reproductive success of replicators. Understanding evolution as such shifts the nature of adaptation from reproduction to persistence, changing the means by which representational powers would be selected for in biological systems.

After briefly explaining why replication is the Achilles' heel of evolutionary explanations of mind and culture, I will argue that a focus on replication in evolutionary thinking *in general* is the problem. I will do so by describing some experiments on artificial ecosystem selection where replicators are not an explicit part of the explanation of adaptations. By going beyond the focus on replicators, we will not only get novel predictions in biology, but also an understanding of adaptation that solves some difficulties for our understanding of the evolution of mind and culture. Because of the format, I can only provide a brief sketch of this view, but hopefully, the programmatic description offered here will be suggestive and thought-provoking.

2. Context

Gould and Lewontin (1979) famously argued against an exclusively adaptationist heuristics, showing how many biological traits and their current state could be better explained by appeal to other biological processes that are relatively independent of natural selection (e.g. developmental constraints). However, most attempts to give an evolutionary account of cognition adopt a strong adaptationist angle.

As Buller (2005) argues, evolutionary psychology refers both to a general broad research interest and a specific narrow research programme (defended among others by Buss, Pinker, Cosmides and Tooby¹) For Evolutionary Psychology (EP), as Pinker puts it (Pinker, 1997, p.21):

The mind is organized into modules or mental organs, each with a specialized design that makes it an expert in one arena of interaction with the world. The modules' basic logic is specified by our genetic program. Their operation was shaped by natural selection to solve the problems of the hunting and gathering life led by our ancestors in most of our evolutionary history.

If we adopt Gould and Lewontin's analysis we can see that Evolutionary Psychology is an extreme case of adaptationism.

Memetics, a distinct theory (Dawkins (1976)) geared towards explaining the evolution of cultural entities named memes (i.e. slogans, ads, songs, etc), adopts a similar adaptationist heuristics. Aside from arguments against adaptationism in general, the projects of EP and of memetics are unsavoury for distinct but related reasons.

- 1- The human experience of behaviour and culture seems to contradict the genetic hardwiring that is described by EP. The effects of learning on our behaviour weaken the appeal to an inneist framework. The means of inheritance (i.e. genetics) assumed by EP seem too rigid and too slow to account for the diversity, fluidity and apparent adaptiveness in response of human behaviour.
- 2- Memetics has an even more fundamental problem: the analogy between genes and memes breaks down when one tries to explain what actually reproduces and how it actually reproduces.

These two difficulties are serious flaws (or challenges for the more generous reader²) for two of the more credible evolutionary accounts of the mind and culture³. Examining these flaws highlights two major building of evolution by natural selection: heritability and differential reproductive success (Brandon 1990, reprising Lewontin 1978's articulation also adds of course variation). Evolutionary accounts of mind and culture wrestle with the difficulties of how heritable differences in behaviour could be passed on from one generation to the next and what would constitute the differential success that is necessary to obtain adaptation by natural selection. Difficulties in offering satisfactory explanations for this have hurt evolutionary accounts of mind and culture.

What has rarely been suggested however is that the problem is not with explaining the adaptation of behaviour but in how we understand the process of evolution of natural selection in general. The most plausible answers to our queries about mind and culture widen

¹Reprising Buller's distinction (2005, p.12), capitals will be used for the latter sense.

²See Blackmore 1998 for an informative discussion about how to limit the use of concept of meme to a more helpful context.

³In this paper I will treat the evolution of mind and culture as one and the same problem even though they are two distinct explananda (as the distinct projects of Evolutionary Psychology and memetics can attest). However, as I will show, a revised understanding of fitness may benefit both projects.

evolutionary theory to include some sort of genetic accommodation, or complex feedback interactions between organisms and their ecological niches (see for examples Boyd and Richerson 2005 and Odling-Smee et al. 2003 for an articulation of these promising ideas). I will now give a rough sketch of another alternative.

I will briefly describe why evolutionary theory needs to widen its approach in way that recasts differential success in terms of differential persistence (contra differential reproductive success). The example that I will use to show this will purposely not be a cognitive animal. Hopefully this will show that is not merely an ad-hoc argument to satisfy our desire to provide an evolutionary explanation of behaviour but rather a necessary change to explain actual cases of adaptation. The upshot for any evolutionary account of mind and culture will be that that the lack of credible replicators will not be seen as an absolute obstacle to have an explanation of the evolution of the mind and culture.

3. Fitness: population size mattered, but what do you do when you don't have populations?

Fitness since Darwin has been understood in terms of survival and reproduction. Because of population genetics and its centrality in contemporary evolutionary biology, fitness now refers to the frequency of alleles, but in more general fashion, fitness refers to the differential reproductive success of any entity be it a gene or an organism or even for some, groups or species. Dawkins (1976) translated this in terms of differential success of replicators. Dawkins makes the case that genes are the best replicators around. although he allows that other entities could act as replicators but this theoretical possibility is in fact only actualized by genes and (surprisingly) memes,. In any case, an entity with a higher probability of leaving more copies of itself than its competition is fitter than its competition. Although fitness has been understood in terms of survival and reproduction, the reproduction story has overshadowed the survival story. That is why EP and memetics focus their explanations on the replicators and how they lead to the phenotypes that we are interested about in this context (i.e. individual and social behaviours). But there are good reasons to believe that this replicator-centered story is not the only game in town.

Some biological systems (e.g. some clonal species, certain colonial organisms and symbiotic communities) appear to be evolving; by that I mean that they display adaptive change as a response to their selective environments and these changes accumulate and are fined tuned over time in order to increase the system's capacity to survive. This adaptive change occurs in response to selection on the parts of the system. However, I argue, these systems' evolution is not adequately captured by a concept of evolutionary fitness that is defined solely in terms of differential reproductive success or change in gene frequencies.

Let us briefly examine such a case and the insights it gives us into fitness. We will later see how a new definition to fitness might offer fertile ground for the evolutionary understanding of mind and culture.

The focus on persistence has been around for a long time in ecology (often under the guise of stability). Most advocates of the idea that whole ecosystems could evolve quickly realize that persistence, not reproduction, will be the way to go. Ecosystems obviously do not reproduce but they do persist some better than others. Theoretically the idea of ecosystem evolution is interesting but the problem has always been to identify real cases of ecosystem evolution. Ecosystem evolution had until very recently not been identified as a likely evolutionary process (although many believed it was at least a theoretical possibility). Most believed such evolution to be epiphenomenal (Hoffman 1979) or at least very unlikely (Hull 1980).

Aside of the theoretical difficulties with this hypothesis, an operational difficulty in testing the ecosystem evolution hypothesis was a problem of physical scale. How can one go about 'measuring' the evolutionary fate of a whole ecosystem? Ecosystems are relatively large and it will be very difficult to account for all the species constituting it and the interactions between them. But when one realizes that ecosystem or communities do not have to be 'large' relative to human scale, testing evolutionary hypothesis becomes much more manageable.

In "recent" artificial selection experiments, a good case for artificial ecosystem selection was provided. Swenson and others⁴ (2000a, 2000b) describe three experiments where artificial selection is used to shape the phenotype of whole ecosystems. Let me briefly describe one of their experiments:

They take 2ml of sediment (dirt, bacteria, etc) and 28 ml of water from a pond for each of 72 test tubes; they are then incubated. Each tube is then measured for pH level (which was the arbitrary trait they decided to select on, but a good trait to measure phenotypic change in ecosystems since the pH level is a feature of the physical substrate, the dirt, and the water, and not only the micro-organisms living in the dirt). They then take the 6 test tubes with the highest pH. From each test tube they take 5 ml of mud and add 25 ml of autoclaved pond mixture. And repeat. They did observe an increase in Ph level in the "winning test tubes". As strange as it seems the mud samples produced the phenotype that enabled them to "survive" in this artificial selective environment. And more importantly they were stable enough so that the increase in pH level actually was retained across "generations"⁵ and amplified across time.

By showing how small malleable ecosystems could be artificially selected to "get" a desired trait they show that at least in theory, we could observe the same thing in nature.

To make sense of ecosystem evolution, defining fitness in terms of offspring numbers will only take us so far. Microsystems with higher pH persisted better than microsystems with lower pH. The pH level is a trait of the whole ecosystem.

The only way for the "mud" to persist is if it changes its pH. It does so without reproducing. But its phenotype changes thanks to environmental pressures, and this change persists and increases

⁴Note that David Sloan Wilson was the senior researcher on these studies. He has worked extensively on issues surrounding complex biological organisation such as groups and multi-level selection.

⁵The quote signs are used here since we do not get real generations, but only forced selective events on separate test tubes.

over time. There are no populations of ecosystems...

Again I am not claiming that reproduction is not involved at all here, but I am claiming that it is not the salient feature to explain the transformation of the phenotype of the ecosystem as a whole. Extend the experiments above in a thought experiment. Let's say that a higher pH lead to slower erosion. The patches of mud with a higher pH would persist whereas the ones with lower pH would erode. There is natural selection here. But is there evolution? If the patch only gets smaller and smaller there is just natural selection. Van Valen (1989) makes a similar point: erosion may be seen a selective process without there being adaptation: one must not confuse selection and response to selection (see Brandon 1990 for a detailed analysis of this). The latter is what we need to have adaptations. As Van Valen argued as well, in purely abiotic cases there is likely no response to selection (and therefore no adaptation or evolution). But our thought experiment here is not like this. If the patch eventually stabilizes, and moreover may grow thanks in part to reproductive success of some of its micro-organisms but also possibly the chemical reactions of the physical substrates, AND if the pH increases (leading to less erosion) then it seems we have evolution by natural selection even though offspring contribution might not be the best way to describe the evolutionary change. To understand the fitness of the ecosystem one will have to understand how components of that ecosystem (and selection on these components) contribute to the capacity of the system to persist⁶.

Thoday in 1953 suggested that to be fitter is to have a higher propensity to leave even only one offspring in 10 to the 8 years. But why should we talk about offspring at all? If we wish to examine two ecosystems, couldn't we compare their relative fitness in terms of their capacity to still be there in x number of years? Couldn't we say that *if* this propensity (which will fluctuate over time) is the result of environmental pressures then what we have is evolution by natural selection? Ecologists have been suggesting concepts like differential persistence for ecosystems for many years, but actually, many cases of evolution below this level of organisation demand such view. Elsewhere (Bouchard 2004, Bouchard in preparation) I argue that many clonal species (e.g. Quaking aspen), colonial organisms (termite colonies) and many cases of symbioses show responses to selection that can only be explained by appeal to differential persistence, not differential reproduction. This doesn't mean that there are no replicators, but rather that at least in some cases of evolution, replication is but a means to increased persistence not the sine qua non condition for adaptation to selective pressures.

4. From mud to mind

How does this muddying the water help us understand the evolution of mind and culture? What were the two difficulties of evolutionary accounts of mind and culture highlighted in the introduction? Heritability and replication. Evolutionary accounts of mind and culture have given explanations that were tied to the arguably implausible efficacy of specific replicators (genes for EP and memes for memetics). In the context of the case we have just briefly examined here we

⁶Van Valen 1989, 1991 suggests that biotas do evolve but that their fitness is to be understood in terms of energy control. I will not go through this account here but elsewhere I describe some of the limitations of that account (see Bouchard 2004 for a detailed analysis of his views).

can see that we may not have to identify replicators at all to identify adaptations.

I am obviously not providing a full story here, but one may see this possibility in light of its possible advantages. Let's apply the persistence model to our question of interest.

- How could memetics benefit from a persistence model?

One of the difficulties with the memetics project was in explaining the process of replication of memes. Imitation is often invoked but one does not get a convincing story as to what is actually being copied and how. Even if we charitably let go of this shortcoming, one who would still need a metric to compare the relative success of various memes⁷. A population of meme would be composed of what? In a replication-based view of adaptation, their numbers become the salient feature, but it seems perverse (and unhelpful) to compare the "wazzup" meme with the 'swoosh' logo on a running shoe based on their numbers. Using probability to persist as a metric, we could compare the fitness of these very different memes without having to identify population sizes. The number of occurrences is of course linked to increased persistence, but it's not a necessary condition for it (just as in nature, the number of individuals is only weakly inversely related to the risk of extinction). It may be better to be a rare meme than to be a very numerous meme to persist for a long time (think of a super-luxury item like a Fabergé egg). This hints at why reproductive success may not be the best way to understand evolution in all cases.

- How could Evolutionary Psychology benefit from a persistence model?

The short answer is that in a strict sense, it cannot: as mentioned previously Buller 2005 distinguished between a narrow view of evolutionary psychology (EP) and a broader view. EP as based exclusively on genes to pass on adaptive behavioural capacities is not obviously compatible with a persistence model of fitness and adaptation. But again, one should realise that reproductive success is a good means for a lineage to persist. Certain human behaviours increase the likelihood that homo sapiens will be around for some time. These behaviours are passed on in the lineage hypothetically genetically and probably culturally as well. If EP can extend its research program to include these non-genetic means of inheritance (to include aspects of memetics or other theories of cultural evolution), it will become more a more plausible theory of the evolution of mind and culture. If it accomplishes this openness, a persistence story will become useful for reasons highlighted above.

Much (much) more needs to be said to flesh out this suggestion, but the idea remains: evolutionary psychology and memetics pin their explanatory hopes on finding plausible replicators for the explananda they are interested in, namely human capacities for behaviours and the apparent evolution of culture. I have argued here that the relative failure of these two projects should not be surprising since evolution by natural selection may not necessarily

⁷Is it 'better' (fitness-wise) to be a meme in as many heads as possible or in fewer heads filled with less memes? Is it better to be a visual meme or an audio meme?

exclusively rely on replicators to create evolution by natural selection. As long as you have parts of a system that react differentially to pressures from the environment and that the 'winners' (the ones still around) are there (retained, inherited, etc.) for future selection events, one gets evolution by natural selection. Most of the time in nature these 'parts' are organisms (or genes depending on your point of view) and the 'systems' are the species. Most of the time species persist by producing more offspring than less. But for many biological systems, success is in the persisting not the reproducing. In many cases of evolution by natural selection, there are no actual populations. This is potentially positive news for evolutionary accounts of mind and culture. Persistence is an intuitive notion when thinking about culture (think of traditions for instance) and culture is an important aspect of our behaviours. What I am hinting here is that persistence may be necessary to understand the adapted nature of our minds.

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