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REVIEW ESSAY

Homunculi rule: Reflections on Darwinian populations and natural selection by Peter Godfrey Smith

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Down with essentialism

This is the best, most thought-provoking book in the philosophy of biology that I have read in a long time. It is rigorously argued, deeply informed, full of wonderful examples, and it has more novel ideas within its pages than any two other recent books in the field that I can think of. It has opened my mind on several key issues and changed my mind as well; it is also provoked me to come up with what I hope are better defenses of some of the points of my position criticized in the book.

One of the most important things we have learned from Darwin (but some philosophers, alas, still don't get it), is that essentialism is simply a mistake. There is no mystery about why many philosophers resist this verdict: their method, going back to Socrates, demands exceptionless definitions and self-evident axioms, from which deductive consequences can be made to flow. Philosophers are not alone in their weakness for essentialism. Even evolutionary theorists have often succumbed to the temptation to define the essence of Darwinism, the necessary and sufficient conditions for natural selection to occur. For one thing, this makes for effective pedagogy. But a good Darwinian should attempt to honor Darwinism about Darwinism itself—in Glenn Adelson's apt phrase—and Peter Godfrey Smith (henceforth PGS) shows us how to think about all the many marginal cases—the semi-Darwinian processes, proto-Darwinian phenomena, quasi-Darwinian relationships—without *marginalizing* them. Therapsids, after all, were just as real as their ancestor reptiles and their mammalian descendants, and the question of whether viruses are alive (or not—do we *have* to fish or cut bait?) is less important than seeing which Darwinian features viruses share with bacteria, with aspen groves, with us—and why. PGS sets out with a deliberately neutral, maximally latitudinarian, basic category, *Darwinian populations.* Literal populations of organisms are populations,

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of course, but so are all the cells in a multicellular organism, and the set of chromosomes in a cell, and (maybe) all the songs on the Hit Parade. Some populations are just more "Darwinian" than others, for a variety of reasons. The penumbral cases are just as real, and just as important to understanding biology, as the parade cases, the paradigms that unmistakably exhibit all the key features.

Two contributions

The most valuable contribution of the book, in my opinion, is PGS's introduction of a "spatial tool" (p8) a 3-d representation of one or another "Darwinian Space" (p. 63), in which Darwinian populations can be located, permitting us to see—at a glance—the relationships between key variables such as *fidelity of heredity* (*H*), *abundance of variation* (*V*), *competitive interaction with respect to reproduction (a), continuity, or smoothness of fitness landscape* (*C*) and *dependence of reproductive differences on intrinsic character* (*labeled S—for supervenience, roughly*). As Fig. 1 (p. 64) makes clear, we can comfortably represent only three variables at a time in a standard 3-d projection, but we can compose diagrams for any three other variables of interest *ad lib.*, and "In most cases, the way to think about Fig. 1 [for instance] is to assume that everything in the graph has high values on various unseen dimensions, so we can focus on the difference-making role of a few key factors" (p. 63). So if H is really low, for instance, (paradigmatic) evolution cannot occur because adaptations cannot accumulate faster than they dissipate due to mistaken transmissions, and we get the "error catastrophe" that must somehow be avoided in the early days of replication. If S is really low, selection is as good as random, not "for cause"—for any intrinsic merit, in effect, and you get drift. If C is really low, there are no traversable hill-climbing paths to the optimal arrangements, so populations will get stuck on inefficient or ineffective arrangements.

Another diagram, Fig. 2 (p. 95) plots *bottleneck* (*B*), *reproductive specialization* (*G, for germ/soma*) and *overall integration* (*I*). Note that we humans sit in the paradigm corner, sharing important affinities with oaks and Volvox that we don't share with aspens and buffalo herds. Such a visual display of the options "makes vivid the role of gradients and partial similarities between cases. Second, it gives us new ways of thinking about processes with a *non*-Darwinian character" (p. 65). Exactly. I expect to use these PGS Spaces a lot in the future. The basic schema is so powerful that it even extends beyond PGS's use of it, permitting us to notice omissions and biases in his own account. For instance, in spite of his salutary opposition to essentialist thinking, he gives short shrift to at least two dimensions which—I will argue—are just as important to a complete evolutionary account as the dimensions he discusses so illuminatingly: the gradient between "formal" and "material" replication, and the gradient between differential *replication* and differential *persistence*. It is not that he overlooks these entirely; he notes instances of purely "formal" parent-offspring relations (prions, retroviruses and LINE transposons) and he has careful discussions of the murky boundary between differential growth/persistence (aspen groves, tribal growth) and differential replication (oaks, Hutterite colonies (Sober and Wilson 1998)), but there are

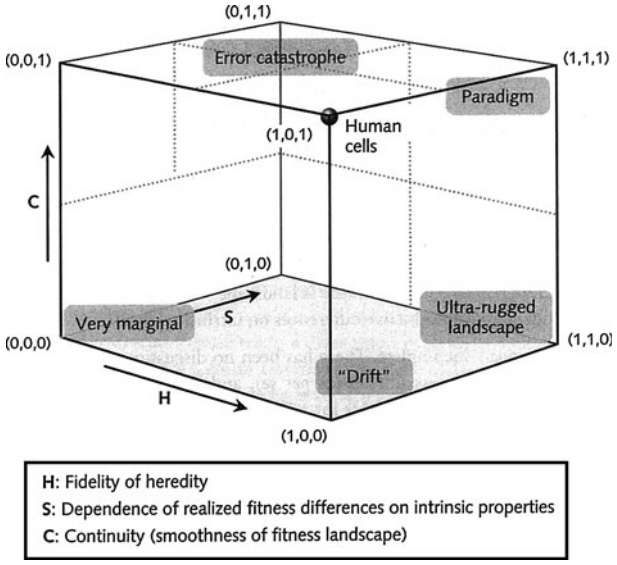


Fig. 1 Spatial representation.of.cases.in.terms of (H, S, C)

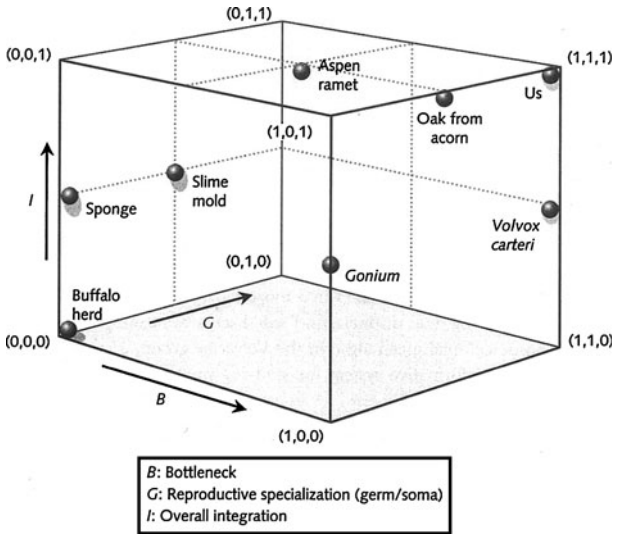


Fig. 2 A space using three reproduction-related dimensions (B, G, I)

candidate generalizations of these observations that are nicely revealed for our consideration when we plot these on PGS Spaces, generalizations that point to possible extensions of Darwinian thinking at two of its most notorious—and "opposite"—boundaries : the origin of life from pre-biotic phenomena at the early end and the origin of culture and language at the most recent end. More on this below.

Vying for the laurels of most valuable contribution is PGS's concept of *de-Darwinizing,* which can be visualized in a PGS Space as the *motion* of some

Darwinian populations, over evolutionary time, away from the far-upper-right paradigm corner to a more marginal position in the space. A vivid case is how the transition from unicellularity to multicellularity resulted in the partial de-Darwinizing of somatic-cell reproduction: these cells, a Darwinian population in their own right, are no longer in such competitive interaction (the *a* dimension) as their protist ancestors were, except when they get cancerous. Moreover, thanks to our high value on the G dimension (the germ/soma distinction) the difference in fitness between germ line and somatic cells is "location," not any intrinsic property, so our somatic cells are also Darwinian populations with low S, which is why their 'evolutionary activities' are not paradigmatically Darwinian (p. 56).

The concept of de-Darwinizing permits us to see clearly the similarities between eukaryotic cells, multi-cellularity and eusociality, for instance (p. 122). PGS stresses that this motion in the space of Darwinian possibilities is not itself purposive (e.g., p. 128), even though it responds to deep constraints.

Two problem themes

These two excellent ideas, PGS Spaces and de-Darwinizing motion within them, are in tension with two less valuable—indeed mildly obstructionist—themes in PGS's book:

1. His reluctance to characterize any Darwinian processes in terms of *information,* and
2. His disapproval of "agential" description and explanation.

In some regards, there is nothing wrong with this tension, and it is even to be welcomed. The best bandwagon should have a good set of brakes, and it is a good thing that PGS wants to limit his tolerance, lest his Darwinism about Darwinism dissolve into pluralistic mush. But the limits he sets need to be motivated and defended, and here I find some serious blind spots in his vision. His two pet peeves are related, of course, and can be found united, not surprisingly, in the work of Richard Dawkins (and John Maynard Smith, and George Williams, and David Haig, and myself, among others). The fact that most of the outrage expressed against Dawkins' talk of "selfish genes" is utterly benighted (e.g., Midgley 1979, 1983) should not lull us into thinking that there are no informed and sophisticated criticisms, and PGS sets out to distill the best objections to the widespread enthusiasm for thinking of genes as agents of sorts, with agendas, pursuing strategies, probing for weaknesses in their opponents, etc. What sets his critique apart from others is his uniting of this theme with a steadfast opposition to the position, most forcefully articulated by Williams (1992) that genes, like poems and recipes, are properly seen to be the *information carried* by one physical vehicle or another, translatable into different media, and properly (and unproblematically) abstract. Don't ask what a poem weighs, or what physical elements it is made of, and don't make the parallel mistake of thinking that genes *are* strands of nucleotides; they are the information carried by those sequences of codons. I had thought that this perspective was widely accepted as enlightened, but PGS will have

none of it, so I will deal with his mistrust of information first, and then turn to agents.

For PGS genes are "treated in a materialist way, as small parts of organisms" (p. 9). The language here is interesting. Those of us who view genes, like poems, as abstract, as informational items that depend on one physical vehicle or another, do not view ourselves as departing in the slightest from materialism any more than we regard our appreciation and use of the concept of *software* as a step towards a Cartesian view of computers. PGS, in contrast, does see something ominous, or at least untoward, in such abstractions. *But he never says why*. Or at least, so far as I can see, this is an unmotivated and misplaced abstemiousness in his brand of materialism. To check my own reading of his reluctance, I composed a thought experiment for him to consider:

Herb and Alice want to have a baby, but here's how they do it:

1. They both have their genomes sequenced.
2. Then they write a little computer program that does the meiosis algorithm on both their genomes, creating virtual sperm and eggs, which are then (randomly) united *in silico*, to create a new genome specification (which passes all bioinformatic tests for being the specification of the DNA of an offspring of Herb and Alice). (So far this is all done literally in terms of A, C, G. T, a purely computational process of string-rewriting.)
3. This specification is then used to construct, codon by codon, an actual DNA implementation of the entire genome
4. Which is then implanted in the nucleus of a human egg (if it matters to you whose egg this is, let me know), and becomes a "test tube baby" in one of the usual ways.

Now you might want to compare the resulting infant, Hal, with Swamp Infant, which is, thanks to Cosmic Coincidence (yuck) genetically identical to Hal. **Is either one of them the offspring of Herb and Alice?** I would say Hal is, and Swamp Infant is not (but Swamp Infant is impossible in every sense that matters—logical possibility is just not interesting here.) I'm not trying to pin any essentialism on you; I'm just trying to see how, given your antipathy to informational views, you would characterize this (quite possible) mode of…reproduction. It seems to me to be a case where Hal is very clearly the biological offspring of Herb and Alice, because what matters is information, and the causal transmission of information (in the form of ASCII code for "A", "C", "G" and "T", not in the form of molecules (codons). The causal link might, for instance, pass through telecommunication satellites, instead of taking the more direct, biochemical routes. (personal correspondence, 4/26/2010).

And here is the response from PGS:

> I accept that Hal is the offspring of Herb and Alice.
>
> I guess the closest real-world case of something like this would be reproduction by retroviruses, where the RNA in the virus gets transformed into DNA and then back into RNA in the new viral offspring. Your case is a grander case of the same sort of thing. There is structure in the parent, and by a

somewhat tortuous causal process we end up with similar structure in the offspring.

What I am not so sure about is what role 'information' has in this case. You say:

> It seems to me to be a case where Hal is very clearly the biological offspring of Herb and Alice, **because what matters is information**, and the causal transmission of information (in the form of ASCII code for "A", "C", "G" and "T", not in the form of molecules (codons).
>
> What matters is the re-creation of structure in a new generation. Computers are information-processing devices, sure. And we use the computer to represent the genomes of Herb and Alice. I don't have any problem with the idea that somewhere in the memory of the machine there is a structure being used to represent Herb's genome. But that does not make inheritance an informational process. Forgetting genes, we could take a representation of Herb's facial features and a representation of Alice's facial features, and get the computer to do a meiosis-style mixing of them, and then build a robot with the blended face. Here we use an information-processing device to represent some structure in Herb and Alice, and also to create a new structure which is based in a particular way on the old structure.
>
> In your Hal case a form of artificial inheritance is devised, in which an information-processing device is used at some crucial steps. But that does not show that biological inheritance is a matter of transmission of information. It shows that information-processing *can* be used in the re-creation of structure across generations. Most of the time (in normal humans), something other than information-processing is used. (personal correspondence, 5/3/2010).

I am bemused by this response. The "recreation of structure" would seem to me to be close to a defining power of information. When a sender has a structure (a message) and succeeds in getting a receiver to recreate that structure, this just *is* successful information-transmission, however, it is accomplished. I think it is obvious that we want, or even need, a perspective that permits us to theorize, to make predictions and consider explanations, about phenomena that succeed in "recreating structure" via substrate-neutral paths. We learn that our enemy has somehow *obtained information* about the design of our new submarine. Did a spy copy the blueprints onto pieces of paper and smuggle them across the border, or encode a recipe for the design into patterns of dots and dashes that were sent by radio, or memorize the blueprints and walk across the border, or …? We might be able to discover that the information moved from Bethesda to Beirut to Bern to Bonn to Baghdad and still not know what physical medium or what code was involved in each leg of the journey. PGS grants that "artificial inheritance" can be accomplished by interposing an information-processing device (and nothing else) in the normal process. To me, that is as good as a proof that the normal process of reproduction is fundamentally an information-transmission process. In a similar vein you can replace the ropes and pulleys and drums connecting the helm to the rudder with radio links (together with the transducers and effectors needed to give

the skipper a sense of the resistance, and to actually move the rudder), showing that steering is fundamentally an information-transmission process or control process, as Norbert Wiener recognized when he created the term *cybernetics* from the Greek verb for *steering*.

A few days after this exchange, Craig Venter announced the creation of his novel bacterium with hand-crafted genome, inspiring PGS to send me another email message:

> Here is little Hal.
>
> http://news.bbc.co.uk/2/hi/science_and_environment/10132762.stm
>
> Though actually he has a formal parent and a material parent. (personal correspondence, 5/21/2010)

Just so; it is now possible to take the information and use it to construct a new vehicle for that information that can be read just fine by the organism that contains it.

"Darwinian paranoia"?

Now let me turn to his anti-agent theme, which is developed in much more detail, and is, in fact, as good as the punch line of his book.

According to PGS, "the agential perspective on evolution has always been an uneasy mix of the metaphorical and the literal…but all talk of benefits and agendas comes with a peculiar psychological power" (p. 10). The peculiar power is, of course, the power of the intentional stance (Dennett 1971, 1987), which enables us to think strategically about all manner of phenomena, from our fellow human beings and animals, to computers and even to evolutionary processes—evolutionary game theory, the tragedy of the commons, and the question I have claimed to be central to all evolutionary thinking, *cui bono*? (who or what is the beneficiary of this competition?). Let me note first that I agree with PGS that there is a variable mixture of the metaphorical and the literal here, but I view this as a feature, not a bug; it is just another instance of Darwinian anti-essentialism: drawing a "principled" dividing line between *genuine* belief-talk or agent-talk and mere *as if* belief-talk and agent-talk is the sort of task Jerry Fodor insists on, pounding his fist on the table, not a methodological maxim any Darwinian should have any truck with.

PGS cites David Haig as describing this as "a way for us to be smart when we think about evolutionary problems" but PGS doesn't "think that this is such a good thing." (p. 10) Why not? Because it leads to what Richard Francis (2004) has called "Darwinian paranoia", defined as "the tendency to think of all evolutionary outcomes in terms of reasons, plots, and strategies" (p. 10). And what is wrong with that? The coinage by Francis is a brilliant propaganda stroke—right up there with "Just So Story" (Gould and Lewontin 1979) and "Darwinian Fundamentalism" (Gould 1997)—but on closer inspection I find that, once again, rhetorical branding has taken the place of calm, objective criticism. I cannot recall a more mean-spirited

book on evolutionary thinking than Francis (2004)—spare yourself the experience and read Gintis (2004) accurate and critical review—and I hope that PGS will jettison Francis's term as unworthy to express his own critique in the future. My own experience discussing the term and the issues it raises with evolutionary biologists during the last year has shown that it gets in the way of serious communication. For instance, a biologist working on molecular evolution who sees the deep value of strategic formulations in considering the arms race between transposons and the genetic elements that combat them is likely to have the charitable reaction that "Darwinian paranoia" must refer to some pathological practice far removed from her bailiwick, and be frankly incredulous when told that she does indeed stand diagnosed as suffering from this disturbance. The plain fact is that agential talk is not at all restricted to the embattled terrain of evolutionary psychology—though this is where it is most often deplored by critics[1]—and is *literally* ubiquitous (that is, it can be found *everywhere* in evolutionary theorizing, from origin of life research and molecular genetics to cell biology, and yes, even evo-devo biology of the sort Francis champions as the alternative to it).

Ironically, PGS himself finds it irresistible to engage in agential talk when explaining and defending his own best ideas. Here are a few examples among many,[2] in PGS's discussion of de-Darwinizing: "Their independent evolutionary *activities* are c*urtailed, constrained*, or *suppressed* [my italics] by what is happening at the higher level" (p. 122), "Another way of dealing with this *problem* [my italics] would be for one member of the collective to *prevent* [my italics] reproduction altogether by other individuals…" "This can be put more explicitly in terms due to Calcott (2008). For a transition to occur there must somehow be both the *generation of benefit* and the *alignment of reproductive interests*" (p. 124). So Calcott is praised for putting it "more explicitly" instead of condemned for indulging in such metaphorical agential talk. A double standard is clearly visible, and PGS has not yet shown how to tell the good guys from the bad guys. (I am not asking, Fodor-like, for the *essence* of good—or bad –agential talk, but just some serious discussion of when and why it is good and bad.) PGS does say:

> …there is a style of selectionist thinking in biology that I think does not involve any form of paranoia. This is the kind of investigation where someone asks: suppose a population was like this, and such-and-such a mutation

[1] It is worth noting that evolutionary biologists confidently hypothesize historical events—horizontal gene transfers, for instance, that occurred billions of years ago, give or take a few hundred million years, or speciations and migrations that must have occurred at some point, ill-defined in space, time and causation—without fear of being chastised for indulging in Just So Stories. It is pretty much only hypotheses about human evolution that are held to a higher—conveniently unattainable—standard of evidence, by the critics of sociobiology or evolutionary psychology. Yes, there are egregious cases of hypotheses being defended solely on grounds of their plausibility, given the few facts available, but they shade into entirely reasonable cases—across biology, so far as I can see—with no clear boundaries. Much of the progress in evolutionary biology consists in the confirmation or disconfirmation of bold hypotheses that started out as plausible guesses—Just So Stories.

[2] See also, e.g., p. 133, on homing endonuclease genes, and p. 134: "The driving chromosome has a 'resistant' element at the place in the genome that the killer targets." See also PGS's reflections on why he doesn't accept the gene's-eye view as fundamental, pp. 134–5.

> appeared, what would happen to it? Thinking this way does not require the idea that genes are "ultimate beneficiaries" of anything (p. 145).

Of course it does not "require the idea"; one is entitled to theorize with both hands tied behind one's back. The question is whether couching this thinking in terms of the genes as ultimate beneficiaries is enlightening or leads to serious misdirection. Given PGS's expression of strong disapproval, I was expecting a parade of Bad Examples, shocking or embarrassing instances of agentialists led on a wild goose chase, or blinded to a simpler truth. But I found none in the book, and when I turned to Francis, I found the parade all right, but most if not all of the cases were instances of what I call *rathering*:

> A rathering is a rhetorical move much beloved by some of the other ideologues of biology, such as Steven Rose and the late Stephen Jay Gould. The general form of a rathering is "it is *not* the case that blahblahblah, as orthodoxy would have you believe; it is *rather* that suchandsuchandsuch–which is radically different." Some–not all–ratherings are little more than sleight-of-hand, since the word "rather" implies–without argument–that there is an important incompatibility between the claims flanking it. (Dennett forthcoming)

When encountering a rathering, one should always ask whether instead one can have one's cake and eat it too. In the case of Francis, the oft-implied claim is that one should be an evo-devo theorist *instead of* an adaptationist/selectionist/agentialist. Why not be both? Like PGS, Francis is quite content to help himself to doses of Darwinian paranoia when it is just too obvious that they are illuminating. (For the details, see the Gintis review.)

One part of the motivation for opposing agentialism has always been the political hunch that it gives aid and comfort to the enemy, creationism. It is thought by many that talking about the design or purpose or teleology evident in the workings of nature is playing into their hands since, as they like to insist, there is no design without a designer. The alternative political hunch, which I share, is that it is much better to attack the supposed principle (no design without a designer) as a pre-Darwinian illusion, like the obsolete principle that atoms are, by definition, unsplittable. PGS addresses this division of opinion: "Sometimes Darwinism is seen as demolishing the last elements of a teleological outlook, but at other times Darwinism is seen as constructively domesticating these ideas, showing that they have a limited but real application to biological processes" (p. 12). I have always thought that the latter view is much more perspicuous, much more defensible, when explaining evolution to laypeople. It is just so obvious—to them, to everyone really—that organisms are breathtakingly cleverly designed, all the way down to the macromolecules. I was disconcerted to overhear some medical students talking in a bar recently. One exclaimed: "How could anybody believe in evolution after learning about the intricacies of the DNA replication machinery?" To the extent that well-meaning evolutionists had inadvertently convinced them that Darwinians are eager to gloss over or deny these facts, this is evidence that the political tactic of denying teleology root and branch is apt to be self-defeating. PGS goes so far as to

countenance a "very deflationary sense of 'supposed to'" (p. 13) and then draws back:

> But these [teleological] intuitions are part of a set of habits and ideas that steered us wrong for centuries, as far as theorizing is concerned, and had to be overcome to develop the Darwinian view. The *feeling* that some particular way of looking at things yields understanding should not always be taken at face value, is not the end of the matter (p. 13).

If he means that in the centuries before Darwin, they steered us wrong by convincing us that there was a Designer who created "all creatures great and small," he is right, of course, but if he means that Harvey was wrong about the function—the purpose—of the heart or the circulatory system, that naturalists were wrong about the purpose of male combat and display in competing for mates, or about the bargains made between plants and pollinators, he is distorting the history of science badly. It was after all Paley's mind-boggling catalogue of the teleological wonders of nature that inspired Darwin's curiosity in the first place. We can all be grateful that pre-Darwinian naturalists were not fanatically abstemious about postulating functional descriptions and explanations of the phenomena they observed, and were largely right to trust their "*feeling*" that they were encountering features with purposes.

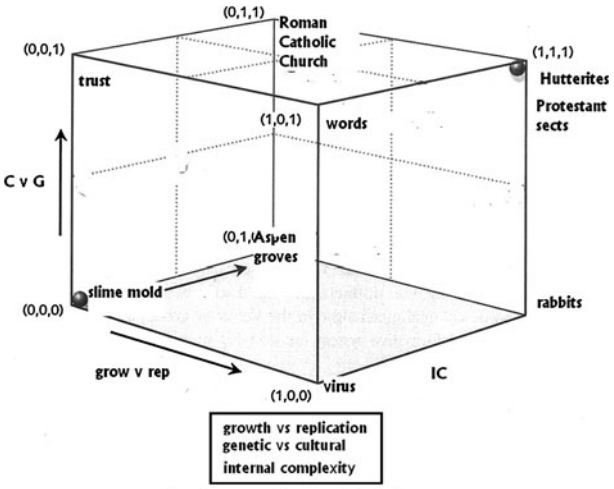
There is no doubt that there is an all too inviting slide from pre-Darwinian thinking via agential thinking into mistaken thinking about evolution, but it isn't obvious that agential thinking is the culprit. Exactly how is that supposed to work? PGS notes on p. 143 that Williams, Hamilton, and Maynard Smith developed the gene's eye point of view as an antidote to naïve group (and species) selectionism. But then, he says, it took on an illicit power of its own as a "special kind of agential narrative" (p. 144). Perhaps, but show us, please. He gives us a list of suspects: "demonic possession narratives, the sub-personal creatures of Freud's psychology (superego, ego, id), and selfish genes and memes" (p. 144). But you can't banish this whole flock of ideas with an epithet, lumping demonic possession with selfish genes, as if it were obvious that they were equally dubious ideas. You have to demonstrate that these are harmful ways of thinking, and that has not been done. Homuncular functionalism is alive and well in many guises, even in PGS's book: "The cells in a human are a bit like a parliament, or an orchestra—but one whose members reproduce as part of their orchestral activities" (p. 149).

As the reader can see, PGS has not made a dent in my unrepentant enthusiasm for the design stance in biology, for seeing biology as reverse engineering at every level. Indeed, I emerge from his critical review more confident than ever that this is the best way of thinking biologically, largely because his persistent and eloquent resistance to the idea comes up with so little that perplexes or discomfits me.

What about memes?

When PGS turns to cultural evolution, his discussion, as usual, is more open-minded, nuanced, and imaginative than one generally finds (among meme-skeptics, in particular) and he makes some valuable original points. He proposes, contra

Sperber, for instance, that the focus should be on "how various mechanisms that might be found in human culture relate to the Darwinian framework in principle, rather than to say which mechanisms are the most empirically important ones" (p. 147). And he sees that the rejection of an evolutionary approach to culture by Fracchia and Lewontin (1999) is not conclusive: 'an initial populational mode of interaction (which would be Darwinian in various regards) may give rise to something else" (p. 149). Indeed it may; citing Reisman (2005), he suggests that cultural items are less like a population when the society becomes more structured, where power relations are more asymmetrical. This is—though he doesn't note this—a good place in the discussion for another PGS space, along these lines:



A space using three reproduction-related dimensions

Here we see de-Darwinizing that parallels the multicellular organism case, in which the structure of relations between the elements (one is tempted to say the *organic* structure) render large "memeplexes" (Blackmore 1999), such as theories and religions, less amenable to (most) Darwinian perspectives.

He even notes the limited applicability of dual pathway (genetic and cultural) inheritance, where the fitness in question is always considered to be the fitness of the humans. There is a second way of being a Darwinian about culture, the memes way: "cultural variants as making up their *own* Darwinian population" (p. 150). This however,

> does not, in principle, require replicators. Here, as before, I understand replicators as members of a Darwinian population that reproduce asexually with high fidelity, "preserving structure" over many generations of copying (p. 151).

PGS does not like the replicator concept, and offers, in addition to the (inconclusive) objection that it is "agential," an uncharacteristically opaque argument against it. He says that the replicator concept isn't necessary and, more important,

doesn't handle all cases. The argument he gives for this is a thought experiment about an imaginary possibility of evolution occurring in the absence of any replicators at the lower level (p. 33). But such a mere "conceptual" possibility, methinks, may depend, like so many philosophical thought experiments about what is possible or impossible in principle, on not looking deeper at the causal structure of this imagined heritability. What PGS needs to offer is a positive sketch (it can be equally imaginary) of a mechanism in which there is *clearly* no replicator lurking, but in which the molar effects (tall breeds tall, etc.) are more or less guaranteed.

He also notes that the replicator concept typically breaks things into "types" (alleles at a locus, really) and that this type-casting is "not necessary." He "in contrast, will make much of the simple phenomenon described above: the possibility of evolution in a situation where *everything is unique*." He ties this to 'epigenetic' inheritance (Jablonka and Lamb, 1995) (p. 34). What is curious about this objection is that it threatens to violate his own anti-essentialism. How is it an *objection* that there are (or, really, *might* be) cases in which no clear replicator is found but which still count as (marginal) cases of evolution? Can't the replicator folks say "Yes, there are these marginal phenomena in which replicatorhood is close to zero"? PGS notes this possibility (p. 39) but I don't see that his later discussion dismisses it. (I think I may well be misunderstanding PGS on this point; on my reading, his arguments fall clearly short of meeting their burden.)

His discussion of Sober and Wilson's treatment of the Nuer and Dinka notes that in this instance, in place of tribal *reproduction* (with daughter tribes spawned somehow) tribal *growth* is the analogue or stand-in, and this is marginal in PGS's terms, but he goes on to observe: "A group that persists does have the opportunity to transform itself into another kind of group—in that sense persistence is linked to novelty" (p. 152). Yes, and here is where PGS might have looked at the other end of the biological spectrum, the pre-biotic world, and seen that much the same applies there. Before there were replicators in a strong sense, there was differential persistence and differential growth (of metabolic cycles or networks, of proto-membranes, etc.), and these provide an arguably stable (stable enough) framework for the development and maintenance of novel features. As he says, in discussing the origin of novelty early in the book, "Natural selection can reshape a population in a way that makes a given variant *more likely to be produced* via the immediate sources of variation than it otherwise would be" (p. 43). This is the key to the Baldwin Effect, of course, but also can be seen to be critical in some prebiotic processes: they raise the probability of certain otherwise extremely improbable combinations coming into existence—without requiring full-blown replicators to set the stage. Just as the Tufts undergraduate *student body* of 2006 becomes the student body of 2007 and then 2008, with departures and arrivals as well as returning students, preserving some characteristics while transforming, gaining and losing others, so the pre-biotic world could contain phenomena that explored the space of possible characteristics in a way that improved the prospects for the rise of novel adaptations. PGS acknowledges that persistence can substitute for replication, and then adds: "But it is a weaker link than the one seen when there is differential reproduction" (p. 152). Perhaps, but he gives no grounds for this. Is it true? And even if it is, he has shown us how to embrace marginal, weak cases of Darwinian

phenomena, and almost certainly such proto-Darwinian processes paved the way for the paradigm processes that took over so fecundly.

PGS finds the memes approach "strange" and adds "It *is* a strange idea, though this fact can be obscured by patterns of description that reify cultural traits and make things like 'ideas' sound more concrete than they are" (p. 152). What is this problem of concreteness? He has already cited prions as bona fide cases of parent-offspring that are entirely "formal" not material, and adds: "So formal reproduction can be a basis for Darwinian evolution." Right there he is granting the main point of Dawkins' discussion of memes. (See Szathmary 1999, for more on the parallel between prions and memes.)

Now we just have to look at the details, seeing how memes are like and unlike other Darwinian populations. PGS offers a nice example of using a turntable as a musical instrument.

> A few people see or hear you, and do the same thing. The behavior spreads. It is not quite accurate to say that your individual behavior was the parent of theirs, but something close to this is true (p. 152).

As he says, they acquire a "disposition." How concrete is that? The induction of change (e.g., prion protein refolding) will do for formal reproduction (p. 153), so the induction of disposition acquisition should count as well. We could make good use of another PGS space with abstract-concrete on one of the dimensions. Another dimension could be number of parents. As PGS observes (p. 153), having a single parent is not essential. Words, for instance, are spread from person to person by the joint action of a variable number of "parent" utterances. The first time a new token is perceived by a child, it is, perhaps, just a distinctive sound; the second time, it is a rather familiar distinctive sound; the third time, it is a sound plus some recognizable context, and perhaps the accumulated effect of those three parent tokens is enough to install a copy in the brain of the child, where it will either soon die without offspring of its own, or else provoke its own rehearsal, yielding offspring and grand-offspring of its own. Usage and pronunciation—and, of course, meaning—can then be pruned and shaped by further encounters with conspecifics. Not the replication system of bacteria or bears, but still recognizably a process in which structure (characterized at a very abstract level!) is recreated by a causal process that depends on the structure of the "parents" (so that mutations—of meaning or pronunciation, for instance) get transmitted).

There are a bounty of other thought-provoking claims and suggestions in the book. One highlight: there are three varieties of reproduction: basic or simple, collective, and scaffolded. The asexual replication by fission of single cells is the paradigm of simple reproduction; our variety is actually an instance of collective reproduction, and viruses, chromosomes, mitochondria and (for those who take them seriously) memes are instances of scaffolded reproduction. Another is the very interesting discussion of Haig and Grafen, and the idea that "Genes, roughly speaking, are late-comers" (p. 140). The idea is that (re-)identifiable sequences of genetic material that can have "an evolutionary role" arose as a product of the evolution of crossing-over; "And the evolution of crossing-over is what set small genetic elements free as evolutionary players" (p. 141). There are many others.

So PGS has enlightened me, and clarified my thinking on these topics. We are close to harmony on the question of the potential role of memes: not all of cultural evolution (in the broadest sense of the term) is illuminated by being considered a Darwinian process taking one Darwinian population (of memes) to a successor population, but there is plenty of room for such a perspective, and work for it to do, particularly in the earliest days of culture, and in the evolution of the simplest units of cultural transmission (e.g., words, the paradigm memes). What discord remains is largely due to PGS's continuing streak of puritanism about the use of the intentional stance in biology, and a concomitant reluctance to talk in informational terms. I view the resulting tension as another one of nature's salutary opponent processes: I tug in my favored direction and he tugs in the opposite, and we tend to correct each other's overstatements.

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