sense of "become part of mainstream science") much of sociocultural anthropology and related fields.

The "rescue" involves applying the compatibility test. This task is possible and worth doing but not necessarily easy, given the often vague vocabulary and ever-changing buzzwords of the disciplines involved. The goal is to salvage the bulk of existing sociocultural anthropology – all those studies of that change-in-scale phenomenon now labeled "globalization," all those multi-sited ethnographies, all those moral mission ethnographies seeking to expose social injustice – all of this simply wonderful, even if humanities-rather-than-science-oriented – anthropology. The material now becomes ore to mine and then to refine by passage through the compatibility sieve. Wherever a sociological assumption (e.g., the "glass ceiling" is socially constructed rather than a reflection of different male/female fitness interests) rings the incompatibility bell, there is a problem to be addressed. Perhaps one discipline is right and the other wrong, perhaps both are wrong – let us seek a grant to study the issue.

Academic disciplines are fairly autonomous, and it is very doubtful that most sociocultural anthropologists will pay attention either to the authors' call for biology or to my own for vertical/compatible integration. Instead, humanities-oriented anthropologists will probably simply lose the turf war as policy-makers and the educated public turn to the hypothesis testers, the data gatherers, the mathematical model builders for their understanding of human societies. But I think that vertical/compatible integration represents a way of salvaging much of the existing discipline. Both the efforts advocated by the authors and the approach for which I am here spreading propaganda, are entirely compatible, and I would like to see both proceed.

Why we need memetics

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Abstract: Memes are not best understood as semantic information stored in brains, but rather, as whatever is imitated or copied in culture. Whereas other theories treat culture as an adaptation, for memetics it is a parasite turned symbiont that evolves for its own sake. Memetics is essential for understanding today's information explosion and the future evolution of culture.

Mesoudi et al. have helpfully situated memetics within the framework of theories of cultural evolution. I disagree with parts of their formulation and suggest some further reasons why memetics is essential for understanding cultural evolution.

First, Mesoudi et al. claim that "A common assumption of memetics is that cultural knowledge is stored in brains as discrete packages of semantic information" (target article, sect. 3.5.2, para. 1). I disagree. This was not assumed by Dawkins (1976) when he invented the term "meme" thirty years ago this year, nor by Dennett (1991; 1995), nor by me (Blackmore 1999; 2001). Aunger (2002) does take this view, but otherwise it is mostly the critics of memetics who do so – aiding their attempts to demolish memetics.

There are at least three issues here: whether memes must be stored in brains, whether they are discrete, and whether they consist of semantic information. The discreteness issue is clearly dealt with by the authors, so I shall comment on the other two. Like others, I have argued that memes need not exist in brains, and this follows directly from Dawkins's original formulation. He derived the term "meme" from the Greek *mimeme*, meaning "that which is imitated," giving as examples "tunes, ideas, catch-phrases, clothes fashions, ways of making pots or of building arches." Ideas (if such a vague term can be pinned down) may arguably be thought of as semantic information in brains – depending on one's definition of "idea" – but what about skills and fashions? A new skill copied from someone else undoubtedly involves changes in the brain, but these changes are not "semantic information" and in any case they are not what is copied; somehow, through the complexities of the human capacity for imitation, a second person ends up acquiring a new skill from having observed the first. By definition, whatever is copied in that process is the meme. This may be a hard concept to pin down and to build theories upon, but we miss the point if we think of memes as little bullets of information inside heads.

Mesoudi et al. also claim that "cultural information is represented primarily in the brain" (sect. 3.5.3). Since it is hard to measure quantities of cultural information, I cannot dispute this, but I would like to point out that as every day passes, more and more cultural information is being stored in computers and digital media of various kinds. Just as we can reconstruct a little of ancient Greek philosophy from the memes left behind by its proponents, so a future civilisation might reconstruct a great deal of our culture from the far more extensive memetic debris left behind. Memetics can handle this far better than other theories of cultural evolution, including the possibility that memes might continue to thrive and evolve even if all humans died.

Mesoudi et al. comment that there is no clear equivalent of the genotype/phenotype distinction in culture, an issue bearing on the vexed question of whether cultural inheritance is "Darwinian" or "Lamarckian." I agree with them that without further advances the distinction is speculative, but I would like to go further.

Memes are relatively new on this planet, and their replication and storage has not yet settled down to anything like the efficient system adopted by genes. If evolutionary systems themselves evolve, then we should expect improvements in their copying and storage systems over time. The process of separating the genotype and phenotype protects against information loss and is an obvious improvement (more generally conceptualised as a shift from "copy-the-product" to "copy-the-instructions"; Blackmore 1999).

We can see that this shift has happened in memetic evolution in the past and it is still going on today. Unaided human imitation is crude and unreliable, entailing huge information loss, but human meme machines were only a first step in the coevolution between memes and their copying machinery. The evolution of language improved fidelity, and writing and printing presses improved fecundity and longevity, but more recently new processes have appeared that have a clear distinction analogous to Weismann's barrier. An example is the program with which this commentary is being written – Microsoft Word. All over the planet there are millions of copies of this program that are all identical, or very nearly so. Yet each copy of Word leads to completely different documents, and it is the success of these documents that prompts people to buy copies of Word and the factories to turn out more of them. Copying the instructions for making documents leads to much faster evolution than copying the documents themselves.

So do we need memetics? Yes, because of the fundamental difference between memetics and all other theories of cultural evolution. This is best illustrated by Dennett's (1995) powerful question "Who benefits?" According to other theories, culture is an adaptation, and (in spite of occasional maladaptive cultural traits) the genes will always, as Wilson puts it, "keep culture on a leash" (Lumsden & Wilson 1981). In this view humans or their genes are the ultimate beneficiaries. Until recently Boyd and Richerson's theorising appeared to be close to memetics, but they have now made it clear that they do not consider memes to be replicators that evolve for their own sake (Richerson & Boyd 2005). So for them, too, culture is an adaptation.

According to memetics, culture is not and never was an adaptation. It began as a by-product of the evolved capacity for imitation that then took off on its own evolutionary trajectory, using us

humans to grow and evolve for its own benefit. It is more like a parasite turned symbiont than an adaptation.

This makes a big difference not only to how we understand human evolution but to our predictions for the future. Memetic evolution constructed human brains and is now building better, higher fidelity meme machines, including computers, the Internet, and digital media. For the moment we humans are essential to the further evolution of the memosphere, but there are already many memes created that never have contact with a human being, and there will be more. Memetics alone makes sense of this and will help us understand what is happening.

Analogies are powerful and dangerous things

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Abstract: The analogy between biological and cultural evolution is not perfect. Yet, as Mesoudi et al. show, many of the vaunted differences between cultural and genetic evolution (for example, an absence of discrete particles of cultural inheritance, and the blurred distinction between cultural replicators and cultural phenotypes) are, on closer inspection, either illusory or peripheral to the validity of the analogy. But what about horizontal transmission? We strongly agree with the authors that the potential for horizontal transmission of cultural traits does not invalidate an evolutionary approach to culture. We suggest, however, that it does require a different evolutionary treatment.

Here, not to admonish the authors for oversight but to emphasize potential pitfalls in conceiving of the culture–biology analogy too narrowly, we list some common misconceptions about transmission modes.

1. First, any trait can be fed into a software program to produce, or map, a phylogeny. This does not mean that the phylogeny is the most accurate depiction of the trait's history, nor that vertical transmission best accounts for its distribution. This may seem obvious, but a number of studies cited in the target article are founded on such erroneous logic.

The absolute value of a goodness-of-fit measure, such as RI or CI or even the familiar R^2, is rarely informative. Rather, the same data must be analyzed with multiple models to make sense of measures of fit. Statistical measures developed to test for "treeness" are also of little help. They are based on strong assumptions about evolutionary process that cannot be casually applied to data produced by any evolutionary process. Indeed, all existing phylogenetic methods make strong assumptions about independence of lineages, rates of evolution, and other important aspects of descent, and biologists rarely employ any such method without first exploring its sensitivity to violations of these assumptions with simulated data. We fail to see how, without explicit models of cultural evolution and simulation studies, we can infer from published work that phylogeny provides the most accurate depiction of a trait's history.

2. Most cultures are of course made up of multiple traits, each of which may have a different phylogeny. Untangling the distinct phylogenies of separate traits is complicated (McElreath 1997), but assuming that all traits have the same tree simply avoids the issue. Using a narrow range of conserved vocabulary to construct language classifications yields a narrow view of language evolution – other aspects of language typically have different histories (Thomason & Kaufman 1988). Even among well-behaved biological species, different loci sometimes have different phylogenies (Enard & Pääbo 2004). Indeed, few geneticists would even attempt to construct a single phylogeny for the entire genome. The bulk of what we know about human history suggests strong mixing at many scales. Hence, assuming populations evolve independently, as typical maximum likelihood does, for example, is something few biologists are now willing to assume (Relethford 1998).

3. The authors support the use of a phylogenetic approach in comparative analyses to deal with Galton's problem, claiming (sect. 4, para. 2) that "evolutionary methods . . . (e.g., the phylogenetic analyses) work equally well for both biological and cultural evolution." Unfortunately, this is not true. A recent simulation study shows that as the prevalence of horizontal transmission of cultural traits between populations increases, so do Type I errors (rejection of a true null hypothesis) (Nunn et al. 2006). Importantly, a tiny amount of horizontal transmission is sufficient to cause serious problems. This parallels recent empirical work in biology which shows that trying to correct for phylogeny when working with rapidly evolving traits such as bird song can introduce serious error (Rheindt et al. 2004). More to the point, how can we claim that methods developed for analyzing genetical evolution work "equally well" for culture when we know, for example, how sensitive phylogenetic contrast analyses are to topological inaccuracies (Symonds 2002)?

4. The authors scrupulously differentiate macroevolutionary from microevolutionary questions, but others they cite have been less careful. Cavalli-Sforza and Feldman (1981) adopted the terms vertical and horizontal transmission from the field of epidemiology to denote, respectively, parent-offspring transmission and transmission between any two (usually unrelated) people. Soon these terms were adopted for use at the intergroup level, referring to traits that were spread from parent to daughter populations and between neighboring populations. Is an extrapolation from micro- to macroevolutionary processes legitimate? For example, from a study of Aka pygmies showing vertical transmission (parent-to-child) to account for a large majority of skills learned by children (80% of skills studied), is it appropriate to infer that Aka culture *as a whole* is highly conservative (Hewlett & Cavalli-Sforza 1986, p. 933)? The unstated assumption here is that the transmission patterns that occur within populations are the same as those that occur between populations. This, however, is untested because we have no measure of the extent of horizontal transmission between different populations, for example, between Aka and other pygmy populations, or between Aka and non-pygmy populations. Furthermore, even if all transmission is vertical, if there is any intermarriage between groups (or other kinds of immigration), vertical transmission within groups will not preserve variation between groups. A particularly clear example of the mismatch between transmission modes within and between populations, specifically inferring micro from macro patterns, comes from language. There is good reason to believe that portions of language are highly conserved within cultural lineages (Cavalli-Sforza et al. 1992), and yet we know that parents have limited influence on the language of their children after an early age; immigrant children do not speak their new national languages with their parents' accents.

To be clear, we are not arguing that cultural evolution, because of horizontal transmission, invalidates an evolutionary approach, only that it requires novel treatment within a general evolutionary framework. More specifically, we think that some tree-based approaches are highly flawed (Borgerhoff Mulder et al. 2006) and need more thought (Eerkens et al. 2006). Analogies are powerful things. But returning to first principles and considering how cultural evolution functions in its own right are, in the long run, more powerful yet.

More generally, we think that this is a fabulous article – a wide-ranging and truly creative review, bristling with insight