challenges to their ideas. We wish that our own critics would be so kind.

Extended evolutionary theory makes human culture more amenable to evolutionary analysis

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Abstract: Jablonka & Lamb's (J&L's) extended evolutionary theory is more amenable to being applied to human cultural change than standard neo-Darwinian evolutionary theory. However, the authors are too quick to dismiss past evolutionary approaches to human culture. They also overlook a potential parallel between evolved genetic mechanisms that enhance evolvability and learned cognitive mechanisms that enhance learnability.

In *Evolution in Four Dimensions* (Jablonka & Lamb 2005, henceforth J&L), the authors do an admirable job of outlining an extended, "four-dimensional" evolutionary theory, one in which inheritance can be non-genetic as well as genetic, organisms are active rather than passive, and variation may be directed as well as blind. Their effort can be placed alongside others, such as niche construction (Odling Smee et al. 2003), developmental systems theory (Oyama et al. 2001), and evo-devo (West-Eberhard 2003), that seek similar expansions, and point towards a new synthesis for not only the biological sciences, but also the behavioural and social sciences.

As J&L note, this extended evolutionary theory is much more amenable to being applied to human cultural change (their "fourth dimension") than the standard neo-Darwinian view. Social scientists who are critical of cultural evolution argue that human culture does not evolve because cultural change is guided or directed (Bryant 2004; Hallpike 1986), because cultural protagonists actively shape their environments (Ingold 2000; 2007), and because cultural inheritance is horizontal/blending (Moore 1994). Many of these objections derive from a lack of knowledge of such processes as epigenetic inheritance (Jablonka & Lamb 1995), niche construction (Odling Smee et al. 2003), horizontal genetic transmission (Rivera & Lake 2004), and adaptive mutation (Rosenberg 2001). Biological and cultural evolution are not as fundamentally different as these critics surmise. As J&L note, "Darwin's Darwinism" - the replicator-neutral, Lamarckian-inheritance version of evolution that Darwin outlined in The Origin of Species (Darwin 1859; henceforth The Origin) - is closer to their extended evolutionary theory than strict neo-Darwinism. Indeed, if we take "Darwin's Darwinism" as a benchmark, we find that broadly comparable evidence exists for cultural evolution as that which Darwin presented for biological evolution in The Origin (Mesoudi et al. 2004). Given these broad similarities between biological (genetic) and cultural evolution, we can profitably borrow tools, methods, theories, and concepts from evolutionary biology to analyse cultural change (Mesoudi et al. 2006), such as phylogenetic analyses (Lipo et al. 2005), population genetic models (Boyd & Richerson 2005), and experimental simulations (Mesoudi 2007).

This, however, leads me to a criticism of J&L's book – that they are too quick to dismiss past evolutionary approaches to human culture, and apply unfair double standards when judging the merits of cultural evolutionary analyses as compared to similar analyses in biology. They dismiss mathematical models of gene-culture coevolution and cultural evolution (Feldman & Laland 1996; Laland et al. 1995) as too heavily based on neo-Darwinian population genetics models and as ignoring

developmental/reconstructive aspects of culture (J&L, pp. 205–206), consequently arguing that such models "can provide only limited information about the spread of cultural variants" (J&L, p. 206). In fact, gene-culture coevolution models have significantly improved the understanding of some of the very issues that J&L discuss, such as the coevolution of lactose absorption and dairy farming (Feldman & Cavalli-Sforza 1989; see J&L, p. 293), the conditions under which social learning should be favoured over individual learning (Aoki et al. 2005; Boyd & Richerson 1995; see J&L, p. 158), the consequences of vertical versus horizontal cultural transmission (Cavalli-Sforza & Feldman 1981; see J&L, p. 188) and Lamarckian inheritance (Boyd & Richerson 1985; see J&L, pp. 228-29). That is not to say that such models might not be improved by taking into account factors such as development, as emphasised by J&L, but dismissing them in a single sentence is unjustified. After all, J&L would surely not also dismiss the vast body of population genetic models in biology, which use the same mathematics and simplifying assumptions as geneculture coevolution models, and which, despite also omitting factors such as development, have nevertheless proved enormously useful (Crow 2001).

J&L also dismiss the concept of the meme, arguing that "it is impossible to think about the transmission of memes in isolation from their development and function" (J&L, p. 209) and that "[in cultural evolution] there are no discrete unchanging units with unchanging boundaries that can be followed from one generation to the next" (J&L, pp. 211-12). Yet a large section of their book is devoted to making identical arguments for genes - that genes are not discrete units with unchanging boundaries, that genes cannot be thought of in isolation from their development and function, and that there is no simple one-to-one mapping between genes and characters. Yet, while the meme concept is dismissed as invalid, the gene concept, which was subject to the same criticisms as the meme, is not dismissed with the same conviction. Perhaps J&L would argue that the terms meme and memetics carry too much undesirable historical baggage (e.g., an association with "selfish genes"), yet they advocate keeping the term "Lamarckism" (J&L, pp. 360-62) despite similarly negative historical connotations. In my view, far more can be achieved by seeking to improve existing research traditions and concepts than by dismissing them entirely.

Finally, it might be instructive to draw further parallels between the different inheritance systems discussed by J&L. For example, there is a potential parallel between the genetic mechanisms that enhance evolvability (such as increased mutation during times of stress or in regions of the genome that deal with rapid environmental change) and cognitive heuristics that enhance creativity. The latter are learned strategies of learning that increase one's chances of making a useful discovery. These heuristics have been studied experimentally, such as Kaplan and Simon's (1990) "notice invariants" heuristic, in which focusing on aspects of a problem that change the least can increase the probability of a successful solution. Other heuristics have been identified using historical records. For example, Carlson (2000) identified, from Thomas Edison's notebooks, a small number of strategies that Edison repeatedly employed that increased his chances of inventing something successful, such as "simultaneously pursue multiple lines of investigation" or "repeat components in multiple inventions." These cognitive heuristics are the result of prior learning (individual and/or social) that guide future learning in directions that favour successful innovation, in the same way that the genetic mechanisms are the result of prior genetic evolution that guide future genetic evolution in directions that favour adaptive mutation. In addition to following fixed heuristics, however, humans can also actively and flexibly simulate the future, and this "mental time travel" does not appear to have any parallel in genetic evolution. That, however, is a story for another BBS article (Suddendorf & Corballis 2007).