reduce intergroup cultural variation by rationally evaluating outgroup cultural information and adopting that which is deemed to be not only useful, but reliable. Second, the selective social learner is able to ensure accurate cultural transmission not only through imitative or conformist strategies, but also by evaluating various forms of cultural information on the bases of accuracy, logic, and internal coherence. Thus, when a 16-month-old corrects an informant who labels a shoe as a ball, upholding culturally specific labels, what may appear to be an early tendency toward conformity may involve critical appraisals of messages, along with epistemic inferences about the informant.

In sum, we suggest that Richerson and colleagues take into further consideration the role of the rational and selective social learner, who can critically evaluate cultural information and adjust their own learning accordingly.

Human cooperation shows the distinctive signatures of adaptations to small-scale social life

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John Tooby[a] and Leda Cosmides[b]

[a]*Center for Evolutionary Psychology, and Department of Anthropology, University of California, Santa Barbara, Santa Barbara, CA 93106;* [b]*Center for Evolutionary Psychology, and Department of Psychology and Brain Sciences, University of California, Santa Barbara, Santa Barbara, CA 93106.*

tooby@anth.ucsb.edu
cosmides@psych.ucsb.edu
www.cep.ucsb.edu

Abstract: The properties of individual carbon atoms allow them to chain into complex molecules of immense length. They are not limited to structures involving only a few atoms. The design features of our evolved neural adaptations appear similarly extensible. Individuals with forager brains can link themselves together into unprecedentedly large cooperative structures without the need for large group-beneficial modifications to evolved human design. Roles need only be intelligible to our social program logic, and judged better than alternatives.

The title of the target article advances the bold claim that: "Cultural group selection [CGS] plays an essential role in explaining human cooperation." By the end of the target article, the argument has been watered down: "evidence … [justifies] *taking the CGS hypothesis seriously* as [one] basic explanation" (sect. 7, para. 2, emphasis added). That is, vaguely characterized non-quantitative facts about humans do not prove the impossibility of CGS influencing the distribution of cooperative behavior, however minutely. We agree it is possible. Richerson et al. similarly retreat from CGS being an essential explanation for human cooperation, substituting the claim that it is an explanation for "our species' highly unusual ability *to create large societies with widespread cooperation*" (sect. 7, para. 2, emphasis added).

Because "large societies" are a recent evolutionary novelty, it follows that selection in ancestral small-scale societies was what predominantly forged the (genetically) evolved mechanisms that make cooperation in modern large-scale societies possible. Indeed, the context in which something evolves (e.g., cooperative mechanisms in foragers living in small-scale societies) does not predict its capacity to scale (e.g., cooperation in mass societies). Vision that evolved to see things closer than 3 miles can see for light-years; language capacities that evolved to allow our ancestors to speak to hundreds now allow us to speak to millions.

CGS proponents find the existence of cooperation in mass societies a self-evident evolutionary puzzle because the numbers involved evoke the impression that selection is not at equilibrium (which it need not be). In contrast, we think researchers need to carefully characterize the computational architectures of our evolved array of neural adaptations for exchange, delayed implicit reciprocity, risk-pooling, alliances, coalitions, coordination (such as theory of mind), bargaining, aggression, mateship, parenting, kin selection, partner choice, reputation, externality-management, social learning, and so on, together with their interactions. Only then can you know whether any puzzling residue of "group-beneficial behavior" in modern societies remains, requiring further explanation.

The dazzlingly extended forms of modern cooperation we see today (Adam Smith's division of labor supporting globe-spanning trade) appear differentially built out of adaptations for small-scale sociality that modularly scale, such as exchange – rather than the marginal benevolence of Smith's butcher, brewer, and baker. Evidence indicates that political attitudes toward welfare and redistribution reflect a specialized forager psychology of sharing for variance reduction (Petersen et al. 2012) and resource-conflict (Petersen et al. 2013). Societies that attempted to harness general benevolence to organize institutions and production – the USSR, East Germany, China, Cambodia, North Korea, Cuba – were spectacular cooperative failures. That they functioned at all depended on other scalable small-scale specializations – aggressive threats (conditional punishment), hierarchy, dominance, coalitions, and so forth.

Even ancestral foragers had institutions (enduring coordination with different roles). We do not understand why individually selected psychological adaptations for cooperation, coordination, coalitions, theory of mind, metarepresentations (i.e., x is a rule), intelligent instrumental reasoning (that allows locally contingent tailoring of actions to goals), social learning, a social psychology that understands and deploys incentives, hierarchies (and so on) are considered inadequate to explain institutions, then or now. It is puzzling why the authors believe that modern institutions cannot be far better explained without recourse to CGS, by the combined operation of these neural adaptations in dense, persisting social networks of intelligent, cultural agents (Boyer & Petersen 2011). When the interlinked cognitive niche adaptations (Tooby & DeVore 1987; see also, Pinker 2010) such as intelligence, language, and culture are added, it is difficult to see any obvious cooperative anomalies.

Gene-culture coevolution proponents claim to see overwhelming evidence of group-beneficial, individually costly behaviors in large societies that cannot be explained by (their computationally impoverished models of) reciprocity. For example, many results are interpreted as showing prosocial, other-regarding preferences purportedly inconsistent with individual selection, including a taste for fairness, excess generosity, and a failure to uniformly act with short-run selfishness. These preferences, together with a taste for altruistically punishing fairness norm-violators, are believed to work together to make people sacrifice their individual interests for the benefit of the group – which then helps groups in intergroup competition. However, the supporting experimental findings typically involve constrained choices that conflate hypotheses, rather than test them cleanly. When these defects are removed from experimental designs, supporting results collapse. For example, when subjects have the added choice of taking from others as well as giving, they no longer give in dictator games (List 2007). Young children, purportedly averse to unfair divisions, will choose to pay a cost to reduce the welfare of others when given the chance (Sheskin et al. 2014). In previous experimental designs testing for third-party punishment of unfair dividers, the only choices available were to punish or not. When this demand-characteristic is removed by adding the option of rewarding unfairness, average "altruistic" punishment approaches zero (Pedersen et al. 2013). Where partners can defect on both the subject and third parties, subjects punish those who defect on them personally (Krasnow et al. 2012). Moreover, they only punish those they subsequently choose to interact with, not those who could only harm others. This indicates that punishment is a tool of negotiation, and not primarily designed to altruistically uphold group norms.

Finally, the models typically used to represent individually selected strategies of social interaction ("reciprocity") are strikingly impoverished (e.g., Cooperate, Defect), are largely free of social ecology and computation, and rest on many implausible assumptions. They need to be replaced with an adaptationist game theory. For example, to determine whether to cooperate, agents need to know whether an interaction is one-shot or repeated. When this aspect of real-world cooperation is added to simulations of reciprocity, then "excess" generosity reliably coevolves with reciprocity, eliminating observed generosity as an evolutionary puzzle (Delton et al. 2011). The rapid cultural dynamics of moral norms (think French Revolution) seem far better explained by rivalrous agents opportunistically seeking allies to jockey for self-advantageous norms (Tooby & Cosmides 2010), than by the slow accumulation of group-benefiting norms through some groups doing better than others. In 1789, institutions that developed over a thousand years were swept away in a thousand days. Thus, we may find that the code and open parameters of evolved programs underlie the combinatorial rules and building blocks of institutional cooperation.

Cultural group selection is plausible, but the *predictions* of its hypotheses should be tested with real-world data

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Peter Turchin[a] and Thomas E. Currie[b]

[a]*Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, CT 06269;* [b]*Centre for Ecology & Conservation, College of Life and Environmental Sciences, University of Exeter, Penryn Campus, Cornwall, TR10 9FE, United Kingdom.*

peter.turchin@uconn.edu **T.Currie@exeter.ac.uk**
http://cliodynamics.info
http://biosciences.exeter.ac.uk/staff/index.php?web_id=Thomas_Currie

Abstract: The evidence compiled in the target article demonstrates that the assumptions of cultural group selection (CGS) theory are often met, and it is therefore a useful framework for generating plausible hypotheses. However, more can be said about how we can test the predictions of CGS hypotheses against competing explanations using historical, archaeological, and anthropological data.

Scientific theories such as cultural group selection (CGS) must be assessed in two ways. First, the basic underlying *assumptions* on which an idea rests should be shown to be coherent and realistic. Second, the theory should generate hypotheses with testable *predictions* about phenomena in the real world that we should observe if the theory is correct. In the target article, Richerson et al. do an excellent job of demonstrating that, indeed, the assumptions of CGS theory are often met, and it is therefore a useful framework for generating plausible hypotheses. In particular, the properties of cultural inheritance, processes such as conformity and frequency dependence, and the ubiquity and importance of institutions enable the maintenance of variation between groups upon which selection can act even in the face of physical migration between groups (a large hurdle facing genetic group selection models). The importance of this should not be underestimated, given the somewhat controversial and divisive history of this subject.

However, we feel there is more that can be said about how we can test the predictions of CGS hypotheses as explanations of human cooperation, specifically with respect to testing them against competing explanations. CGS is an overarching framework that can generate more specific hypotheses that can be tested against alternatives. Let's consider the following: over the last 10,000 years, the scale of human cooperation has increased by several orders of magnitude: from small-scale groups of some hundreds of foragers to large modern states with populations of hundreds of millions. Social scientists have advanced a multitude of theories explaining this "major evolutionary transition" (*sensu* Maynard Smith & Szathmáry 1995). Such theories tend to come in several flavors (Carballo et al. 2014). "Functionalist" (or "voluntaristic") explanations emphasize benefits of cooperation to all: buffering environmental risk, managing competition and efficient allocation of resources, producing public goods such as an irrigation system, and capturing returns to scale in, for example, economic production (Johnson & Earle 2000). In contrast, "conflict" explanations focus on the dark side of large-scale sociality: class struggle and exploitation, warfare and conquest (e.g., Carneiro 1970). CGS theory can combine these functionalist and conflict elements, but in a highly specific way: Cooperation within societies evolves as a result of conflict and competition between societies.

It is possible (indeed likely) that the best explanatory model will combine more than one mechanism, with different factors, perhaps, interacting in nonlinear, synergistic ways. Evaluation of such complex quantitative explanations is not a problem for modern methods of analysis, especially when combined with a program of building mathematical models that explicitly incorporate such interactions. In our own research we have made a number of steps in this direction. In a recent paper (Turchin et al. 2013) we examined whether increased competition between groups due to the development of horse-based forms of warfare (i.e., involving chariots, cavalry, etc.) was an important force in the historical emergence of very large-scale human societies ("empires"). Following the logic of CGS (or multi-level selection more generally), we constructed an agent-based computer simulation in which "cooperative" cultural traits were only selected for due to the beneficial effects they had in competition between groups (without between-group competition, there was a heavy bias against developing such traits). We were able to test the predictions of this model against historical data about the spatial distribution of empires over a 3,000-year period. Encouragingly, the predictions of the model showed a good match to the real data. Furthermore, turning off some of the important parameters in the models produced a large drop-off in the match between simulations and data. This indicates that our hypothesis is at least a plausible explanation for the evolution of socio-political complexity. This model is admittedly a gross simplification of the actual historical process, and these results are still somewhat preliminary; however, this work does demonstrate the ability to quantitatively test the predictions of hypotheses informed by CGS, using the empirical record of past human societies.

The next step is to test this hypothesis more explicitly against other alternative explanations, including those not motivated by CGS. An important point here is that different theories make very different predictions as to where, when, and under what circumstances we should see the rise of large-scale societies in the archaeological and historical record, and such things as the order in which different aspects of societies emerge. So far the progress in testing such theories has been slow. Yet the huge corpus of historical and archaeological information provides us with a remarkable empirical resource for testing theories and rejecting empirically inadequate explanations. The key is transforming the wealth of information into a systematic form that facilitates the kinds of analyses we described above. Currently, we are collaborating with colleagues from across multiple disciplines and around the world to develop a databank of coded and quantitative historical and archaeological information about past societies (Seshat: Global History Databank: http://seshatdatabank.info/), with which hypotheses about cultural evolution and human history can be tested, including those informed by CGS theory (Turchin et al. 2015). For example, in one project we are assessing the idea that competition between groups led to increased egalitarianism in human groups, particularly beginning with developments of several "axial-age" religions (Bellah 2011). Importantly, this idea will be rigorously tested against other competing explanations, for example, the idea that religion is the "opiate of the masses," by which elites keep the majority of the population