

How do the abstract patterns of behavior resist being broken up by selfish behavior?

Richerson et al. posit that group-variable culturally transmitted social norms with group-level functionality are evidence of CGS. Teaching and following norms and rules are practices that function to overcome selfish and impulsive behavior. We have rules such as “brush your teeth twice a day” to ensure that our offspring act in a self-controlled manner and to maximize their fitness in the long run, and we have rules such as “help others” to ensure the coherence of the group.

In different environmental situations, natural selection occurring within groups and between groups may have different relative strengths. Even if cooperation, defined as “working together toward a shared aim” (Wehmeier and Hornby 2000), was selected because it commonly enhanced the individual’s long-term fitness, it neither follows that cooperation enhances all cooperators’ fitness, nor that all acts that we classify as parts of cooperative behavior do so. A truly self-sacrificing act can come about because it is generally advantageous to cooperate, and making decisions on a case-by-case basis is costly. Just as a single drink in a pattern of abstinence does not significantly change the correlation between that pattern and PIEs (e.g., good health), a single fitness-reducing act of an individual will not significantly change the correlation of cooperative behavior and its fitness-enhancing effect resulting from the group’s collaboration.

Richerson et al. offer a coherent framework which is supported, complemented, and potentially slightly modified by the proposed considerations of behavioral patterns and their consequences in different time frames.

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## Self-interested agents create, maintain, and modify group-functional culture

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**Abstract:** We agree that institutions and rules are crucial for explaining human sociality, but we question the claim of there not being “alternatives to CGS [that] can easily account for the institutionalized cooperation that characterizes human societies” (target article, sect. 7). Hypothesizing that self-interested individuals coercively and collaboratively create rules, we propose that agent-based hypotheses offer viable alternatives to cultural group selection (CGS).

Richerson et al. argue that cultural systems, such as prosocial religion and institutions that maintain social order, play a vital role in enabling the cooperation of both small- and large-scale human societies. We agree. But we are unconvinced that cultural group selection (CGS) is the only hypothesis able to account for the existence of such phenomena. CGS leads to group-functional culture by selecting on cultural variation (Boyd & Richerson 2010), but such selection presupposes that group-functional equilibria exist already, suggesting that other processes, including within-group dynamics, contribute to the emergence of group-functional culture. Since researchers have long recognized that individuals with the requisite power coercively and consensually create rules, we propose a complementary “rule-making

hypothesis” for group-adaptive institutions. Understanding the contribution of such agent-based social processes is essential for evaluating the value and limits of CGS theory.

Focusing specifically on rules and institutions that control social deviance (one of Richerson et al.’s three examples of group-adaptive culture; see sect. 6.2), we describe two manifestations of this rule-making hypothesis. The first emerges when asymmetries in power or influence allow parties to create and impose rules that satisfy their own interests. Depending on whether the interests of these coercive authorities coincide with those of the group, these individuals will sometimes but not always create and maintain rules with group-level benefits. An alternative form of this hypothesis develops when power is more evenly distributed. In these cases, coordinated groups of individuals can consensually create, modify, and enforce rules that control defection.

Individuals can have key roles in producing group-functional rules if they have sufficient power or influence to institute cultural changes and enforce new rules. Schapera (1970) observed that Tswana tribal chiefs drove cultural change by introducing innovations ranging from single rules, such as the banning of beer, to infrastructural changes, like the establishment of a police system. The chiefs’ objectives in creating rules included quelling social disturbance, reducing poverty, and collectivizing otherwise divergent interests – goals with explicit group-level benefits. Functional rules can also stem from leaders dealing with novel forms of conflict. Llewellyn and Hoebel (1941), in their ethnography of the Cheyenne legal system, described how tensions arose after one man borrowed another individual’s horse without permission. The military chiefs eased the friction between the parties and then established a rule: “Now we shall make a new rule. There shall be no more borrowing of horses without asking ... [If] the taker tries to keep them, we will give him a whipping” (p. 128). Considering the role of coercive rule-makers offers an alternative explanation not only for the origin of group-functional culture, but also for its maintenance, because powerful rule-makers should continue to enforce group-functional rules as long as the rules satisfy their own perceived self-interest. Moreover, the coercive authority dynamic accounts for the ubiquity of institutions that asymmetrically benefit the powerful, spanning etiquette norms (e.g., Trobriand Islanders: Malinowski 1926) and food taboos (e.g., the Etoro: Kelly 1980; the Aranda: Spencer & Gillen 1927; and the Sanumá: Taylor 1981).

Coercive rule-makers who have the power to change rules should create group-functional culture when their own interests coincide with those of their groups. In some cases, these overlapping interests stem from coercive rule-makers preferring groups with cooperative, compliant individuals. Elders of the Kurnai of Australia demanded that young boys “listen to, and obey the old men” and “live peaceably with their friends” (Howitt 1885, p. 316), rules that improve the welfare of the elders while also creating group-level benefits. Studies of punishment in animal societies show that CGS is not necessary for the coercive enforcement of group-adaptive behavior (Singh and Boomsma 2015). Reeve (1992) found that naked mole rat queens harass lazy subordinates, while Flack et al. (2005; 2006) noted that dominant macaques police conflicts among subordinates, stabilizing their own high status while reducing within-group conflict.

To this point, we have illustrated the ability of powerful individuals to create group-adaptive rules. However, the development of group-functional culture does not require that novelty originate with coercive authorities. Parties of similarly powerful individuals can also establish and maintain rules to control each other’s behavior. Systems of rules that emerged across camps during the California Gold Rush represent a well-studied example of self-interested individuals coordinating to create and enforce novel institutions of social order. Despite the absence of organized state law, miners residing at promising digs convened and instituted majority-approved rules to protect mining rights and safety (McDowell 2004). Violations of those rules spurred injured parties to seek redress through the support of the community, who used coordi-

nated punishment to enforce rules. Ostrom's (1990) review of small-scale institutions that manage common pool resources similarly exemplifies how the coordination of self-interested agents can produce group-functional culture. Fishermen in Alanya, Turkey, for example, took 10 years to perfect an institution to control overharvesting and conflict, with a built-in means of motivating individuals to monitor and enforce violations of mutually recognized rules. Last, group consent can interact with authorities to produce group-functional culture. Among the Enga of New Guinea, leaders presented cultural innovations to their groups, though group consensus ultimately governed adoption. As Wiessner (2002) summarized, "The innovations promoted were ones that leaders felt could be played to their own advantage; the innovations that stuck were those that worked for the individual and the group" (p. 251).

Here we briefly reviewed evidence that individuals motivated by self-interest can create group-functional culture through coercion, consensus, or both. Although our discussion is largely restricted to rules controlling deviance, these arguments apply to the development of other domains of group-functional culture as well, such as institutions that reward otherwise costly behaviors (Glowacki & Wrangham 2013) and prosocial religion (Norenzayan et al. 2016). Only after recognizing complementary and alternative hypotheses for group-functional culture, as well as the criteria for testing among them, will we be able to assess Richerson et al.'s claim that CGS is uniquely important in generating the cultural systems underlying human cooperation.

## The selective social learner as an agent of cultural group selection

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**Abstract:** Developmental research characterizes even the youngest learners as critical and selective, capable of preserving or culling cultural information on the bases of informant accuracy, reasoning, or coherence. We suggest that Richerson et al. adjust their account of social learning in cultural group selection (CGS) by taking into consideration the role of the selective learner in the cultural inheritance system.

Richerson et al.'s discussion rightly characterizes social learning as one of the key facilitators of cultural group selection (CGS). While we agree with the idea that social learning is essential for cultural inheritance, and serves as a source of cultural variation and selection, we believe that the authors' discussion has underspecified the significant role of the rational, critical, and selective social learner in these evolutionary processes.

We would first like to note that behavioral imitation, which the authors focus on, is not the only form of social learning that could reduce intergroup cultural variation. Cultural variation between groups is a starting point not only for the spread of group-beneficial behaviors but also for group-beneficial beliefs, ideas, or concepts. Contact with out-group scientific knowledge, for example, could result in the adoption of this cultural information by less successful groups. In such cases, learning would not be primarily imitative in nature – one could not describe cross-cultural learning about microbes, for example, as primarily imitative in nature, and yet this has reduced between-group variation in cultural beliefs about the unseen causes of disease.

That said, the selective social learner is influenced by factors beyond those cited by Richerson et al. (those being a penchant for conformity, the sway of prestige, affinity for cultural norms, or

group membership biases). A growing body of developmental research characterizes even the youngest social learners as active participants in the learning process, whose selectivity can act to preserve or cull testimonial information on the basis of its accuracy, support, and coherence with other beliefs (Stephens et al. 2015). These belief-formation processes are supported by children's rapid assessments of others' competence, expertise and trustworthiness. Monitoring the content and coherence of messages protects learners against misinformation, alerting them to conflicts between incoming messages and their already established knowledge and beliefs (Mercier & Sperber 2011). For example, infants detect overt labeling errors and anomalous referential actions (Gliga & Csibra 2009). They expect humans with appropriate information to speak truthfully, and actively correct inaccurate labelers (Koenig & Echols 2003). In imitation research, children have been found to give priority to the approach taken by a successful individual over an unsuccessful group, showing that in learning actions, successful outcomes often trump conventional means (Scotfield et al. 2013; Seston & Kelemen 2014; Wilks et al. 2015). Further research suggests that the detection of inaccuracy might lead to enhanced memory for incompetent sources and poor memory for the information they present (Corriveau & Harris 2009; Koenig & Woodward 2010; Sabbagh & Shafman 2009).

Even more relevant to CGS, research in this field suggests that children make rational learning decisions on the basis of whether or not the messages they receive from informants violate their existing understanding of the world (Sobel & Kushmir 2013). Preschoolers, for example, have been known to preferentially learn from more expert (Koenig & Harris 2005; Koenig & Jaswal 2011), more grammatically proficient (Corriveau et al. 2011; Sobel & Macris 2013), and logically consistent informants (Doebel et al. 2011). They also flexibly adjust their trust in informants' testimony based on their understanding of what is improbable and impossible (Corriveau et al. 2014; Shtulman & Carey 2007; Woolley & Ghossainy 2013). Young learners' reliance on their own understanding of what is correct, true, or possible should not be underestimated: Their preferences for native-accented speakers (Corriveau et al. 2013), adults (Jaswal & Neely 2006), and familiar speakers (Corriveau & Harris 2009) are reversed if they learn that such sources have proven inaccurate. This is not to say that children are always critical in the face of message conflicts: Preschoolers have been found to trust a deceptive adult who provides inaccurate information about an object's location (Jaswal 2010; Jaswal et al. 2010). Interestingly, this may be because preschoolers are more sensitive to violations of commonly held cultural knowledge (Stephens & Koenig 2015; Koenig & Stephens 2014).

As children develop, they incorporate their growing knowledge and experience about speakers and the world to evaluate new information. Considerations about message coherence and plausibility are taken into account along with other factors – including, as Richerson et al. mention, informant prestige, cultural conventions, conformity, normativity, group membership, and so on. We suspect that children appraise social learning situations based on their recognition of both cultural and epistemic norms, with priority afforded to each based on the situation (Hodges 2014), type of testimony or information being exchanged (Stephens & Koenig 2015), and the values endorsed in their environment (Reifen Tagar et al. 2014).

How exactly does this selective learner play a role in CGS? Richerson et al. describe three forms of social learning that help maintain or reduce group-level cultural variation: (1) accurate, rapid social learning; (2) conformist social learning, described as mechanisms that maintain intergroup variation of cultural norms and behaviors; and (3) selective imitation of cultural behaviors, described as a process by which intergroup variation is reduced. Along these lines, we would argue that the selective learner's ability to critically evaluate cultural information on the basis of its accuracy, support, and coherence contributes to CGS in two main ways. First, as previously described, the social learner can

In this regard, we enthusiastically endorse the path forward painted by **Turchin & Currie**. The gold standard in empirical inference has become fitting competing models to data using techniques such as Markov Chain Monte Carlo simulations and testing the goodness of fit of these models to data using Bayesian and information theoretic measures (e.g., Gerbault et al. 2014). Advances in genomics have furnished huge amounts of historical data on the course of evolution. Human languages, living and dead, have long been mined for human historical information, and to some extant non-linguistic data have been used as well (see sect. 3.2). As Turchin & Currie suggest, archaeological and historical data can surely be assembled into databases that can support model-fitting and model-comparison approaches.

## R15. Conclusion

Our commentators made many useful addenda to the main argument in the target article but also introduced a number of caveats. They retained varying degrees of skepticism about the reality of the CGS processes. However, none of the skeptics addressed the empirical foundations for applying the Darwinian syllogism to human groups, except in special cases. In the target article we presented evidence that:

1. Human groups often differ culturally.
2. Cultural variation is transmitted from generation to generation by social learning.
3. Success in intergroup competition is frequently determined by cultural differences.

We included only a small proportion of the vast amount of evidence that exists to support these statements. We attempted to select the best and admit that the quality of this evidence varies. However, consider the possibility of applying the CGS framework to non-human species, even the other great apes. Chimpanzee groups have appreciable amounts of cultural variation, including traditional differences in social customs like grooming (Whiten et al. 1999). Chimpanzees are comparatively good social learners, as judged by the standards of other non-human animals, albeit much less adept than human children (Dean et al. 2012; Whiten et al. 2009). Chimpanzee communities certainly compete vigorously. But so far as we are aware, there is no evidence that success in competition is influenced by a cultural trait. Some whale and dolphin species also have significant cultural traditions. Some group selection on them is conceivable and the current evidence is suggestive (Whitehead & Rendell 2015). Most nonhuman social learning systems are considerably less sophisticated than those of chimpanzees and dolphins. No other vertebrate species has societies that compare to those of humans in size and organizational complexity. Certainly, skeptics about the importance of CGS processes in other species can raise strong doubts about their role. Only in humans is there abundant, if not always unassailable, evidence for all of the legs of the Darwinian syllogism operating at the group level.

## NOTE

1. Krasnow & Delton represent a particular, highly controversial brand of evolutionary psychology developed by Tooby & Cosmides. It has become conventional to use capitals to distinguish the particular brand from the

generic field. Accordingly, whenever “Evolutionary Psychology” appears capitalized in our text, we are referring to this term in Tooby & Cosmides’ sense.

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[The letters “a” and “r” before author’s initials stand for target article and response references, respectively]

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