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Title: A Framework for Modeling Human Evolution
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Abstract

Culture-led gene-culture coevolution is a *framework* within which substantive explanations of human evolution must be located. It is not itself an explanation. Explanations depend on such concrete historical evolutionary factors such as the control of fire, collective child-rearing, lethal weapon technology, altruistic cooperation and punishment, and the mastery of complex collaboration protocols leading to an effective division of social labor.

The target article nicely elaborates the strong relationship between cultural group selection and gene-culture coevolution. The authors correctly observe that gene-culture coevolution significantly strengthens genetic group selection models. However, there really are no purely genetic group selection models in the literature. All such models employ the *phenotypic gambit* (Grafen 1984), in which complex transmission processes are treated as though they were the product of a single allele of the genome. Such models represent equally any transmission process, cultural, genetic, or interaction between the two, that depend only on vertical transmission from parents to offspring (Gintis 2014).

The paper's contention that cultural group selection is "a basic explanation for our species' highly unusual ability to create large societies with widespread cooperation between non-relatives," is incorrect. Cultural group selection is not an explanation of anything. Rather, it is a *framework* within which such an explanation can fruitfully be developed. The main features of human cooperation, which include collective child-rearing without a reproductive division of labor (Hrdy 2000, Wilson 2012), hunting large game with lethal weapons (Wrangham and Carmody 2010), altruistic cooperation and punishment (Bowles and Gintis 2011), as well as collaborative skills depending on a *theory of mind* (Tomasello 2008), follow from the particular evolutionary history of our species.

Curiously, the authors suggest that there is evidence for culture-led gene-culture coevolution only "for a few simple genetic traits." In fact there is overwhelming evidence for this process as central to the constitution of *Homo sapiens*, a few pieces of which I will cite here.

- **Human Self-domestication:** Darwin noticed that selective breeding of mammals for tameness entailed a pattern of similar side-effects of domestication to human society in distinct species. Darwin even suggested that man himself "may be compared with those animals which have been long domesticated" (Darwin 1871, Ch. 7). Belyaev (1979) corroborated this insight, studying captive silver foxes bred for tameness. These animals developed humanly-attractive faces with short snouts, floppy ears, patches of white fur on their heads, and curly tails (Gibbons 2014). More recently, Cieri, Churchill, Franciscus, Tan and Hare (2014) documented domesticated syndrome changes in human evolution since the Middle Stone Age and Upper Paleolithic, and Wilkins, Wrangham and Fitch (2014) have proposed a general genetic model explaining the domestication phenomenon.

  This is evidence for a very straightforward culture-led group selection mechanism in which an increasingly complex division of labor and social norms that rewarded cooperation (Tomasello 2014) favored genetic changes that produced a more domesticated and prosocial human disposition.

- **Control of Fire and the Reorganization of the Human Upper Torso:** Prior to the control of fire, hominins inhabited trees at night as a defense against predators. Because predators have an instinctive fear of fire, the control of fire permitted hominins, who were already bipedal, to abandon climbing almost completely (Wrangham and Carmody 2010). The lack of need for brachiation freed the hand, arms, and shoulders of proto-humans to evolve for other purposes (Gintis, van Schaik and Boehm 2015).

- **Lethal Weapons and the Physiology of Throwing:** Hominins developed the use of long-range projectile weaponry, and such techniques were central to human social life (Bingham 1999, Wilkins, Schoville, Brown and Chazan 2012). Humans are unique in possessing the neural machinery for rapid manual-brachial movements that allows for precision stone-throwing, which depends on the brain's capacity to orchestrate a series of rapidly changing muscle movements (Calvin 1983). Roach, Venkadesan, Rainbow and Lieberman (2013) showed that *Homo erectus* had already evolved this capacity for accurate overhead throwing. Humans are unique in possessing a torso musculature optimized for the powerful and accurate throwing of projectile weapons.

- **Language and the Physiology of Communication:** The increased social importance of communication in human society rewarded genetic changes that facilitate speech. Regions in the motor cortex expanded in early humans to facilitate speech production. Concurrently, nerves and muscles to the mouth, larynx and tongue became more numerous to handle the complexities of speech (Jurmain, Nelson, Kilgore and Travathan 1997). Parts of the cerebral cortex, Broca's and Wernicke's areas, which do not exist or are relatively small in other primates, are large in humans and permit grammatical speech and comprehension (Belin, Zatorre, Lafaille, Ahad and Pike 2000, Binder, Frost, Hammeke, Cox, Rao and Prieto 1997) .

  Modern humans have a larynx low in the throat, a position that allows the throat to serve as a resonating chamber capable of a great number of sounds (Relethford 2007). The first hominids that have skeletal structures supporting this laryngeal placement are the Homo heidelbergensis, who lived from 800,000 to 100,000 years ago. In addition, the production of consonants requires a short oral cavity, in whereas our nearest primate relatives have much too long an oral cavity for this purpose. The position of the hyoid bone, which is a point of attachment for a tongue muscle, developed in Homo sapiens in a manner permitting highly precise and flexible tongue movements.

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