A Cultural Species

Why a theory of culture required to build a science of human behavior

Abstract

Culture is thought by many social scientists, ranging from behavioral ecologists and evolutionary psychologists to economists and biologists, to be a mere "window-dressing" on human behavior, decision-making and psychology. Arguing to the contrary, this paper attempts to show three things. First, *culture* is required for understanding an enormous range of human psychology and behavior, including such things as foraging skills and technology, visual perception, prosocial behavior (cooperation, fairness and punishment) and economic decision-making. Second, because of the extended nature of human ontogeny and brain development, much of 'culture' is essentially built into the adult human mind. It's not just content; it's 'cognitive architecture' that is principally assembled between the ages of zero and twenty. Third, to understand the cultural nature of human psychology and behavior, we must focus on the learning/developmental processes that allow the brain to construct and program itself. I discuss how evolutionary theory can be used to generate productive hypotheses concerning the details of human cultural learning. To illustrate, I briefly summarize the work on prestige-biased and conformist transmission.

In contrast to other primate species, humans have successfully spread to nearly every corner of the globe in a relatively short period of time, from the dry savannahs and tropical forests of equatorial Africa to the frozen tundra of the Arctic and the humid swamps of New Guinea. Humans are unique in their range of environments and the nature and diversity of their behavioral adaptations. While many local genetic adaptations exist in our species, it seems certain that the same basic genetic endowment produces arctic foraging, tropical horticulture and desert pastoralism—a constellation of adaptive patterns that represents a greater range of subsistence behavior than the rest of the Primate Order combined. In terms of hunting tools, for example, some social groups use blowguns, others use bows and arrows and still others rely principally on boomerangs, clubs or atlatls. As for social organization, different human groups arrange themselves by clans, matrilines, moieties, symbolically-marked ethnic groups, phraties, and age-sets (just to name a few). Some social groups are segmentary, linking groups into larger and larger networks of relations; others recognize few relations beyond the immediate family. Similar lists marking the extraordinary range of human behavior—compared to all other species—could be constructed for religious beliefs, inheritance rules, sexual behavior, warfare, ritual practices, child-rearing, medicinal practices and many others.

If it were plausible that these variations were due to genetic differences and human evolutionary history was tens of millions of year deep, the story wouldn't be so complicated. Yet humans have *less* genetic diversity than most other primates (e.g. chimpanzees) and substantially *more* behavioral variation. Furthermore, the natural experiments resulting from migrations and contact periods demonstrate that many if not most of these differences are maintained by social learning, not simply exposure to different physical environments. This simple observation suggests that the immense success and diversity of the human species is rooted in capacities for social learning—i.e., our *cultural capacities*.

Below, I address the importance of human culture and our cultural capacities in two steps. In the first part, I argue through a series of case examples (drawing from history, ethnography and experiments) that 'culture', understood as learned information stored in brains, is essential for understanding an enormous range of human behavior, from foraging and hunting technology to visual perception and social behavior. The primary goal of this section is to suggest that human brains (in fact, our very 'cognitive architecture') are deeply affected by learning and developing in culturally-evolved environments. In describing this, and setting up the second portion of the paper, I will argue that much of this enculturation process occurs through an ongoing process of imitation and practice that, while it continues throughout the human lifespan, has a substantial influence during our extended ontogeny (ages 0 to 20). The second portion of the paper suggests a way to approach the essentially 'cultural nature' of humans by examining the psychological mechanisms of cultural learning that allow individuals to effectively extract adaptive behavior from the wash of information available in the social world. In closing the paper, I briefly highlight how, with some knowledge of these cultural learning mechanisms in hand, formal theoretical models that integrate these learning processes with various kinds of social structure and interaction, can illuminate a variety of sociological processes, such as the formation of ethnic groups, the evolution of societal complexity and large-scale cooperation, and the emergence of economic specialization and social classes.

Cultural learning is our primary mode of adaptation

In 1860, aiming to be the first Europeans to travel south to north across central Australia, Robert Burke led an extremely well-funded and equipped expedition of three men (King, Wills and Gray) from their base camp in Cooper's Creek in central Australia with five fully-loaded camels (specially-imported for the expedition) and one horse. Figuring on a maximum round trip travel time of three months, the foursome carried 12 weeks of supplies. Eight weeks later they reached the tidal swamps on the northern coast of Australia and began their return. After about ten weeks their supplies ran short and they began eating their pack animals. Two weeks later, Gray died of dysentery, illness and exhaustion, and the group jettisoned most of their supplies. A month later, they arrived back in their base camp, but found that their support crew had recently left, leaving only limited supplies. Still weak, the threesome packed the available supplies and headed to the nearest outpost of 'civilization' (a ranch at Mt. Hopeless, 240km to the south), following Cooper Creek. In less than a month, their clothing and boots were beyond repair, their supplies were again gone, and their sustenance consisted mostly of camel meat—their remaining camels starved to death. Faced with living entirely off the land, they began foraging efforts and tried to devise means to trap birds and rats. They also attempted to glean as much as they could from the aboriginals about nardoo, an aquatic fern whose spores they had observed the aboriginals using to make bread. Despite traveling along a creek, and receiving frequent gifts of fish from local aboriginals, they were unable to figure out how to catch fish the aboriginal way. Wills' journal, which he continued writing in up to his death, repeatedly expresses how impressed they were by the bountiful bread and fish available in aboriginal camps, in contrast to their own wretched condition. Two months after departing from their base camp, the threesome had become entirely dependent on nardoo bread and occasional gifts of fish from the locals. Despite consuming what seemed to be sufficient calories, all three became increasingly fatigued, and suffered from painful bowel movements. About a week later, Burke and Wills died, apparently poisoned and starved to death from eating improperly processed nardoo seeds. Unbeknownst to the trio, Nardoo seeds are toxic and highly indigestible if not processed correctly. Fatigued and delusional, King wandered off into the desert where he was rescued by an aboriginal group, the Yantruwanta. He recovered and lived with them for several months until a search party found him.

These men were not unprepared British schoolboys out on holiday, and the planning for this expedition could not have been more extensive. Yet, despite their big human brains, camels, specialized equipment, training and seven months of exposure to the desert environment prior to running out of supplies, these men failed to survive in the Australian desert—in contrast to the thriving native population. This story makes a simple point: Humans, unlike other animals, are heavily reliant on social learning to acquire large and important portions of their behavioral repertoire. No 'evolved cognitive modules' or rational calculation could alone deliver to these men the knowledge of how to detoxify *nardoo* spores, make rat traps, bird snares, or how to manufacture fishing nets from locally available materials.

Bow and arrow technology is culturally learned

The essentially cultural nature of human adaptation and behavior can be further made with a comparison of bow-and-arrow hunting technology from two groups of nomadic foragers—the Hadza of Tanzania and San of Botswana. Because both groups rely primary on bows and poisoned arrows for bringing down some of the same large game, these groups provide an interesting comparison. Table 1 lays out some of the details associated with Hadza and Kalahari (San) foragers hunting technologies.[1] First, note the substantial difference in the size of the bows made by the two groups. Hadza bows are at least twice as long as the bows of Kalahari foragers, and have a 'pull strength' at least 6 times greater. Second, the Hadza fletch their poisoned arrows with feathers from either Guinea fowl or vultures, while Kalahari foragers do not fletch at all. Third, while both groups use poison for big game, the Kalahari foragers manufacture their poison from chrysomelid beetle larva and casings found below ground around the corkwood bush. The Hadza, despite living around numerous corkwood bushes, predominantly use two kinds of poisons, one made from Shanjo seeds (*Strophanthus eminii,* a tree-bush), and the other (the preferred poison) from Panjube sap that is extracted by boiling the Panjube branches until a tarry black substance emerges. Finally, Kalahari foragers go through an extensive process to manufacture a quiver from the large lateral roots of an Acacia tree, while Hadza don't use a quiver at all.[2]

Clearly, all the skills, detailed knowledge and procedures that go into manufacturing this hunting equipment, which is essential to bringing down big game, is acquired predominately through some kind

[1] The data in Table 1 were compiled from Woodburn (1970), Lee (1979), Silberbauer (1981), Bartram (1997) and Liebenberg (1990).
[2] The Western Hadza in Sukumaland use hide quivers (Woodburn 1970: 31).

of imitative learning process. There is no way an individual can figure out all the details (such as where to find the beetle larva, or which branches to boil) that go into making a successful hunting kit, without learning extensively from others. In all the extensive ethnography on Kalahari foragers, we see no evidence that Kalahari hunters have experimented with longer (2+ meter) bows and fletched arrows (like the Hadza use), only to later reject these alterations. Woodburn (1970: 14) reports that enterprising Hadza have occasionally manufactured their bow staves from woods other than *mutateko* (*Dombeya kirkii*), but have always returned to *mutateko*—i.e., *most* Hadza have never experimented with alternative woods, they just use what everyone else is using. Kalahari foragers have *not* been observed to routinely test a range of beetles, seeds and branches for their poison-making possibilities, they just learn to gather and process chrysomelid beetles from other members of their group. If the acquisition of the adaptive repertoire were principally a product of individual learning, every individual would have to go through a trial and error process in which fletching, various potential poisons, and different size bows were tested. Ridden with errors, this stochastic process (based on a small number of trials) would generate massive within-group inter-individual variation, as some hunters would find different poisons and different sized bows most effective (depending on their physical size, luck, and whatever the search criteria are in their individual learning processes). Instead, while individual variation certainly exists, much of the variation is between groups. More importantly, detailed ethnographic observation corroborate this inference by showing that such manufacturing skills are acquired through a process of imitation and practice, not by free-ranging individual experimentation (Fiske, 1998). In our species, cultural learning is essential to even the most basic elements of foraging adaptations.

One obvious question arises from the observation that individuals acquire much of their behavioral repertoire (like how to process nardoo or make a hunting kit) from other individuals in their social group: If most people imitate, how did these intricately integrated cultural adaptations arise in the first place? This problem can be solved by understanding the psychology of human cultural learning and attention. If individuals, in the course of learning, pay particular attention to the most skillful or successful individuals in their groups (e.g., to the best hunters or arrow makers), and people make some errors in imitation—or even occasionally innovate something— culturally-learned repertoires will (under a wide range of conditions) become increasingly better adapted to local environments. Furthermore, this can occur without cost-benefit analysis, rationality, genetic change, or individual learning (Henrich, 2002, 2003). More generally, the cumulative nature of human knowledge, adaptive practices, and technology cannot be understood without examining cultural learning.

Table I. Comparison of Hadza and Kalahari foragers bow and arrow technology

ITEM OR PROCESS	KALAHARI FORAGERS	HADZA
Bow Size	1 meter or less	2.0-2.25 meters
Bow Pull	8kg – 10kg	60 kg
Bow shaft material	*Grewia flava*	*Dombeya kirkii*
Bow string material	Tendon of gemsbok, kudu or eland	Nuchal ligament of zebra, eland or buffalo, or the sinew of a giraffe
Bow string processing	Soaked and separated into fiber that are twined into a string 4m long, which is shortened by half four times via 'gravity twisting"	Fibers are chewed until soft and then rolled on the thigh
Securing and protective materials	Sinew bindings attached near end of bow to secure bowstring	Fresh skin from the tail or metapodials of impala, eland or giraffe are slipped over the end of the bow
Bow life span		1 year
Arrow shaft material and length	*Reeds and Grasses or sometimes Grewia flava; 35 to 45cm*	Light woods with a pith core
Tuning bow string to correct tension	Based on musical pitch	
Fletching	None	Feathers from Guinea fowl or vulture (poisoned arrows)
Fletching attachment	NA	Mastic and helically wound single fibers of sinew plus glue made from bulb
Arrow head	Fence wire (formally ostrich bone)	Metal with one or two barbs (two barbs for female game, one barb for males)
Arrow poison source	*Diamphidia* sp. (beetle larva and protective casings) often mixed with *Acacia* gum	2 types: Shanjo seeds (Strophanthus eminii) & Panjube sap (Adenium sp.) Panjube is preferred
Location of poison	20cm to 1 meter below ground near rare *Commiphora* bushes, typically harvested in late summer	
Processing of poison	Larval casing are rolled to homogenize them, and mixed with saliva and applied to arrow, then baked to a crust on the arrow shaft	*Panjube*: chopped up branches of Adenium are squeezed & slowly cooked into a tarry black substance
Poison application & protection	Poison is applied to upper shaft	Applied to head and wrapped in impala hides
Poison use	Almost always	Primarily for big game
Quiver size	75 cm	No quivers
Quiver materials	Outer bark of lateral roots of *Acaci luederitii* tree	NA
Quiver materials acquisition	Dug up and cut out of ground, avoiding section with emerging rootlets	NA
Quiver materials processing	Any rootlets must be drilled out; root length is roasted. Steam allows outing covering to be separated with pounding and twisting action	NA
Quiver assembly	Root sheath is bound w/wet sinew. One end is sealed with moist hide	NA

In response to my pointing out the cultural nature of the practices, many behavioral ecologists and perhaps some economists might be quick to suggest that each of these technologies could be explained as "optimal" given the details of the local ecology (prey distribution, tree cover, resource availability). While this may be true (it's impossible to say), it is largely irrelevant for deeming these practices and bodies of knowledge as cultural, and studying them as cultural evolutionary products that were produced and are maintained by the psychological processes that allow humans to acquire behavioral information by observation and imitation. Only the most devout behavioral ecologist would be unlikely to predict that if a band of Hadza were parachuted into the Kalahari, they would soon commence making small bows, drop the fetching from their arrows and start digging for beetle larva by corkwood bushes—unless they encountered and imitated the San.

Culturally-Constructed Cognitive Architecture

The danger in the above examples is that, while they illustrate both the culturally learned and adaptive nature of human practices and behavior, they run the risk of suggesting that the mind can be effectively divided into *structure* (the acquisition machinery) and *contents* (the knowledge and practices). However, a wide variety of evidence suggests that learning involves the construction of brain structures ('wiring'), which occurs throughout the human life course, but particularly during ontogeny (ages 0 to 20, Quartz, 1999; Quartz, 2002; Quartz & Sejnowski, 1997). Cortical gray matter continues increasing in the frontal and parietal lobes to age 12, in the temporal lobe until age 17 and in the occipital lobe through the first two decades of life. White matter increases in all areas to around age 22 (Giedd et al., 1999). This extended cerebral ontogeny, which allows human brains to construct and adapt themselves to their local social and physical environment (the 'EOA' = Environment of Ontogenetic Adaptiveness), may lead to a wide array of cross-cultural variation in people's susceptibility to visual illusions, hunting skills, memory, notions of fairness, and tastes for punishing. In short, people from different cultures—having experienced different social and physical environments while their brains were developing—likely possess different cognitive architectures.[3]

We will begin by considering the barn owl. Feldman and Knudsen (1997) compared the brain topography and circuitry of two sets of barn owls. The first group had prism goggles cemented to their heads soon after birth, while the second (control) group was left unadorned. After a period of weeks, the goggle-wearing owls adapted their ability to visually locate sounds in space to equal the sound-locating

[3] The criticality of ontogeny in adult performance is consistent with field data on the acquisition of foraging skills among extant hunter-gathers (Kaplan, Hill, Lancaster, & Hurtado, 2000). Among the Aché, foraging performance (skills and knowledge) take a long time to perfect, and depend critically on childhood environments.

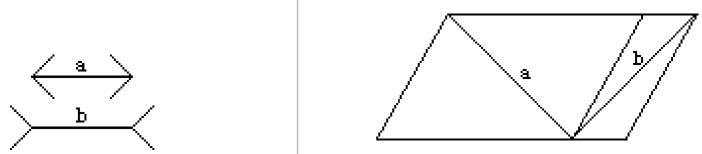
performance of their non-goggle-wearing brethren (the control group). After this period, the researchers compared the optic tectums—the portion of owl midbrain involved in audio-visual processing—of the two groups, and produced evidence consistent with a topographical reorganization and the formation of new anatomical axonal projections (DeBello, Feldman, & Knudsen, 2001; Hyde & Knudsen, 2002). That is, the goggles caused the juvenile owls' brains to adaptively rewire themselves (Quartz, 1999).

Culturally-constructed environments alter visual perception in humans

Like owls, human visual perception seems to respond to experience, and by conjectural inference from the owl data, human brains may rewire themselves via experience. Consistent with this hypothesis, cross-cultural experimental data demonstrates substantial differences in visual perception across populations. Building on W.H. R. Rivers' pioneering work, Segall, Campbell & Herskovits (1966) performed one of the few rigorously controlled cross-cultural experimental projects in the history of anthropology and psychology. Teaming up ethnographers with different expertise,[4] this interdisciplinary project gathered data on the susceptibility of both children and adults from a wide range of human societies to five 'standard illusions'. Their data and findings are numerous, so I will summarize only their hypotheses and findings for two of these visual stimuli, the Mueller-Lyer and Sander parallelogram illusions. Figures 1A and 1B show the two illusions. In their initial proposal, the authors predicted that groups with more experience/exposure to "carpentered environments" and "perspectival art" would be more susceptible to these two illusions.[5]

[4] The ethnographers were supplied with a 70-page "how-to" instruction booklet printed on washable paper. The book contained the experimental stimuli, detailed instructions on administering the experiments, sampling guidelines, and a set of questions about the environment and visual world of the society.
[5] Some subsequent findings have challenged these hypotheses (e.g., Jahoda, 1966), but these challenges have lacked the rigor and breadth to cast serious doubt on the major empirical patterns (Berry, 1968).

Figure 1: Two of the illusions used by Segall *et. al.* in their cross-cultural study of 'illusion susceptibility' in 17 societies. The lines labeled 'a' and 'b' in each figure are the same length, however typical Western subjects perceive line 'b' as longer than line 'a' in Figure 1A, and line 'a' as longer than line 'b' in Figure 1B.



(1A) Müller -Lyer Illusion

(1B) Sander Parallelogram

In the Mueller-Lyer illusion (Figure 1A), Western subjects typically perceive that the horizontal line segment marked 'b' is longer than the horizontal line segment marked 'a', when in fact 'a' and 'b' are the same length. By varying the lengths of lines 'a' and 'b' and asking subjects which of the two is longer, researchers can estimate the magnitude of the visual illusion for each subject—by determining the approximate point at which an individual perceives the two lines as being the same length.[6] For the Sander parallelogram (Figure 1B) subjects must again determine which line segment is longer, 'a' or 'b', and Western subjects typically perceive 'a' to be longer than 'b' even when they are the same length. Again, using a series of different figures that vary the relative lengths of 'a' and 'b', researchers can assess the illusion's strength by estimating the point at which subjects perceive the line segments as equal.

Figures 2 and 3 summarize the results for the Mueller-Lyer and Sander parallelogram illusions, respectively, for the 17 different societies studied by Segall *et. al.* Of these 17, there are 11 groups of African agriculturalists (some of whom also rely on foraging and pastoralism), one group of African foragers (San), one group of South African Europeans (Johannesburg), one group of Australian Aboriginal foragers (Yuendumu), 1 group of Philipino horticulturalists (Hanunóo), one mixed group of South African goldmine-laborers (Mineboy) and two groups of "Westerners" (Europeans and Americans). From 12 of these 17 societies, data was gathered from both adults (split equally into males and females,

[6] In the actual stimuli, the line segments and their accompanying 'heads' and 'tails' were laid out side-by-side, rather than vertically, as shown the Figure 1A. Also, the horizontal line segments were red, while the 'heads' and 'tails' were black. Coloring the lines facilitated communication.

ages 18 to 45) and children (ages 5 to 11). In Figures 2 and 3, the left-hand vertical axis gives the 'point of subjective equality' (PSE) and corresponds to the vertical bars for adults (white) and children (black). PSE is a measure of the strength of the illusion for each group. It represents how much longer segment 'a' must be than segment 'b' before people perceive them as equal (until there is a 50/50 chance that people from that group will choose either 'a' or 'b'). The right-hand vertical axis gives the difference between the PSE of the adults and children for each group and refers to the scatter of data points above the vertical bars. The names of the groups span the x-axis.

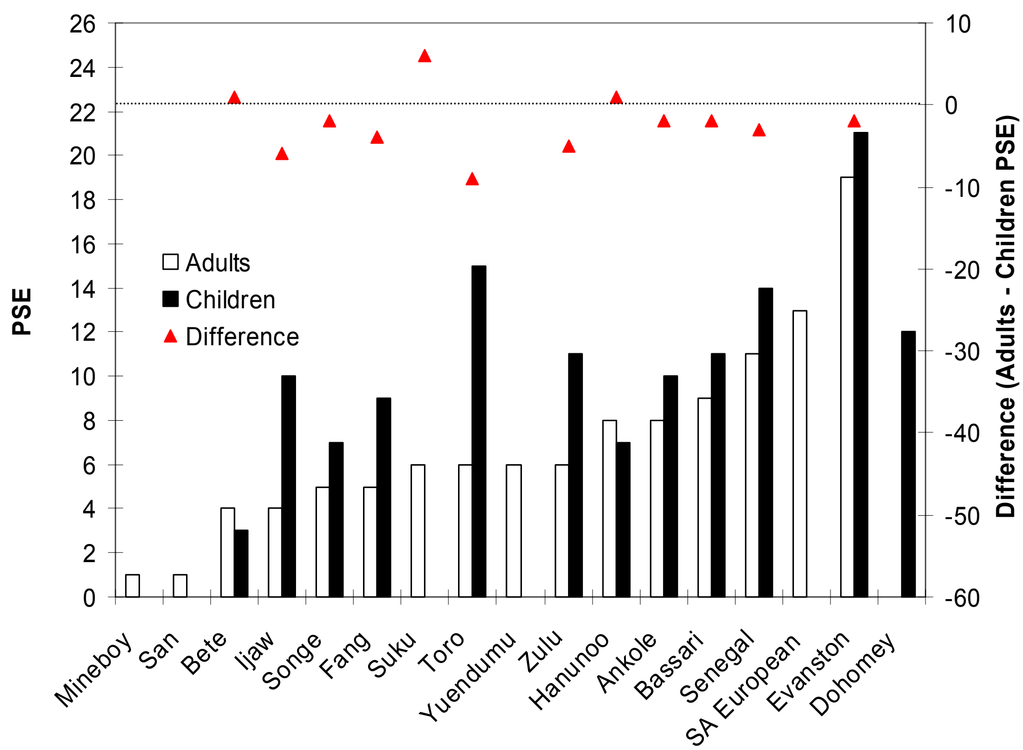


Figure 2: Mueller-Lyer Results for Segall *et. al.*'s cross-cultural project. PSE is the percentage that segment 'a' must be longer than 'b' before individuals perceive them as equal.

The results for the Mueller-Lyer stimuli show substantial differences among these social groups in their susceptibility to the illusion. American adults in Evanston (Chicago) are the most susceptible. On average, these adults require that segment 'a' be about a fifth longer than 'b' before they perceive them as equal (PSE = 19%). At the other end of the 'susceptibility spectrum', hunter-gathers from the Kalahari desert are virtually unaffected by this so called 'illusion' (they probably wouldn't call it an "illusion"), requiring that segment 'a' be only one percent longer than segment 'b' before seeing them as equal (PSE

= 1%). Looking across Figure 2, while there is significant variation across the range of social groups, there is a 'jump' between the rest of the world (mostly Africa) and Evanston.

Comparing across societies, children (ages 5 to 11) show a similar pattern to the adults on the Mueller-Lyer illusion. PSE scores range from over 20% among children in Evanston to 3% among Bete kids. The PSE scores for children correlate with their adult counterparts, $r = 0.81$—indicating that most of the cross-cultural effect is in place by age 11. Moreover, the amount of cross-group variation drops from a standard deviation of 5.5 among children to 4.5 for adults—that is, there is more cross-cultural variation in children than adults, so adolescence may act to reduce this cross-cultural variation. Developmentally, the scores show a fairly robust pattern: adults are consistently *less* susceptible to the illusion than children. This is illustrated by the scatter of triangles on the upper portion of Figure 2. The triangles (which refer to the right vertical axis) plot the difference between the PSE scores of the adults and children in each society. With three exceptions, the adults' scores are consistently less than the children of their society (in Figure 2, these are the triangles below the dotted zero-line). Of the 3 exceptions, only one is much above zero: Suku children were, on average, not susceptible to the illusion (and provided the lowest score of all the groups). These findings are consistent with more detailed developmental data from U.S. populations showing that adults are less susceptible to the illusion than children (Walters, 1942; Wohlwill, 1960). I will return to this developmental pattern below. Finally, note that while children were generally equal to or greater than adults *from their social group* in susceptibility, this pattern does not hold if we compare children and adults from different societies. Many child-samples are less susceptible to the illusion than adult-samples from other societies.

Figure 3 shows parallel findings for the Sander parallelogram. As above, susceptibility to the illusion varies from a high of 19% in Evanston to a low of around 10% for Mineboy (a mixed group of South African miners) and Bete (agriculturalists/foragers from the Guinea Coastal area). The PSE scores for children and adults show the same patterns discussed above. Children's scores correlate with adults at 0.60, and if we remove the aberrant Suku, the correlation jumps to 0.76. The variation between groups in PSE scores drops from children (std. dev. = 5.8) to adults (std. dev. = 3.47). As with the Mueller-Lyer illusion, children's susceptibility is greater than or equal to that of the adult members of their social group for all groups except the Suku (as illustrated by the scatter of triangles). Interestingly, there is a gradual decrease in the size of the adult adjustment with increasing children's PSE scores.[7] Thus, the same

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[7] One problem with these adult-child comparisons is that the EOA of the children in many of these small-scale societies may be very much different from the one experienced by the adults. Assuming children in societies like the Bete and Songe have experienced more 'carpentered environments' and 'perspectival art' than their parents did

general point is made: most of the ‘adult-level’ cross-cultural variation is in place by age 11, and ‘adolescence’ (age 11 to 20) acts only to reduce the size of the cross-cultural variation.

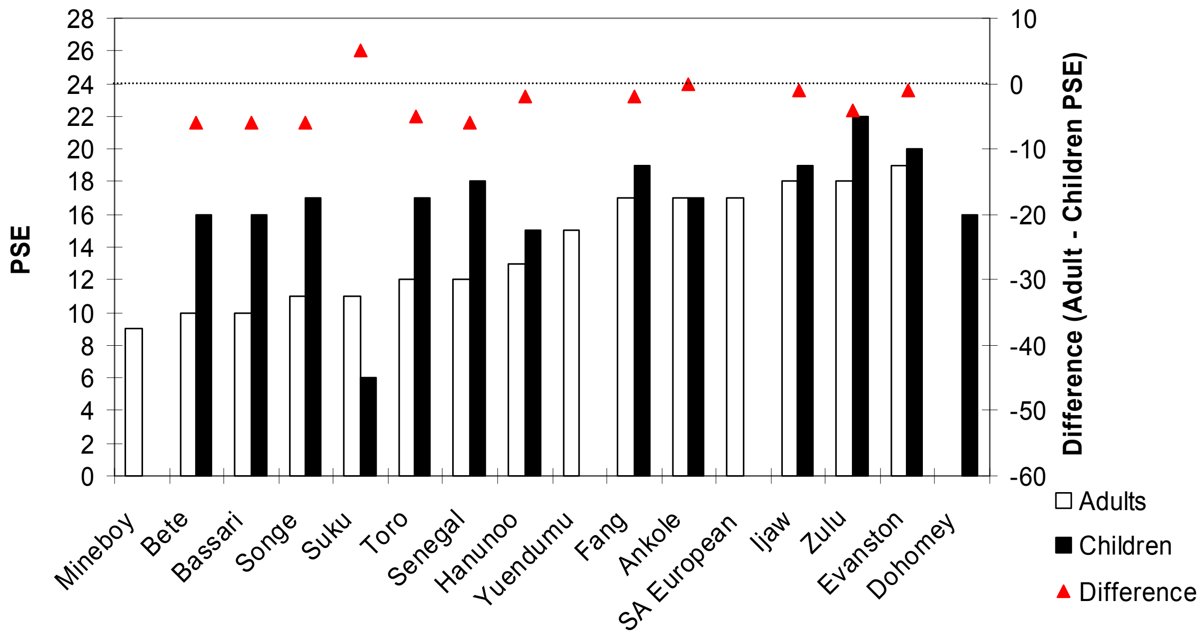

Figure 3. Sander Parallelogram Results from Segall et. al.'s Cross-Cultural Project

Detailed developmental data from several studies in the U.S. on the Mueller-Lyer illusion shows that susceptibility generally *decreases* from ages 5 to 12, reaching its lifetime low at the onset of adolescence, and then increases from 12 to 20. The decrease from five to 12 is larger than the subsequent increase in susceptibility, leaving adults less susceptible to the illusion than five year olds, but only because of the pre-adolescent decrease. Figure 4 shows this development trajectory for the Mueller-Lyer illusion using data from Wapner & Werner (1957)—the stimuli used here is slightly different from those used by Segall, so the PSE values indicate a stronger effect.[8] After 20, susceptibility to this illusion does not change again until old age (Porac & Coren, 1981; Wapner, Werner, & Comalli, 1960).

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when they were kids, then the large differences between children and adults in these societies may reflect both development differences (which are relatively small in Evanston) and differences in the relevant EOA.

[8] Segall *et. al.* modified the more standard illusion to facilitate cross-cultural communication by adding colors and by separating the line segments slightly. These changes had the effect of reducing the strength of the illusion on typical Western subjects.

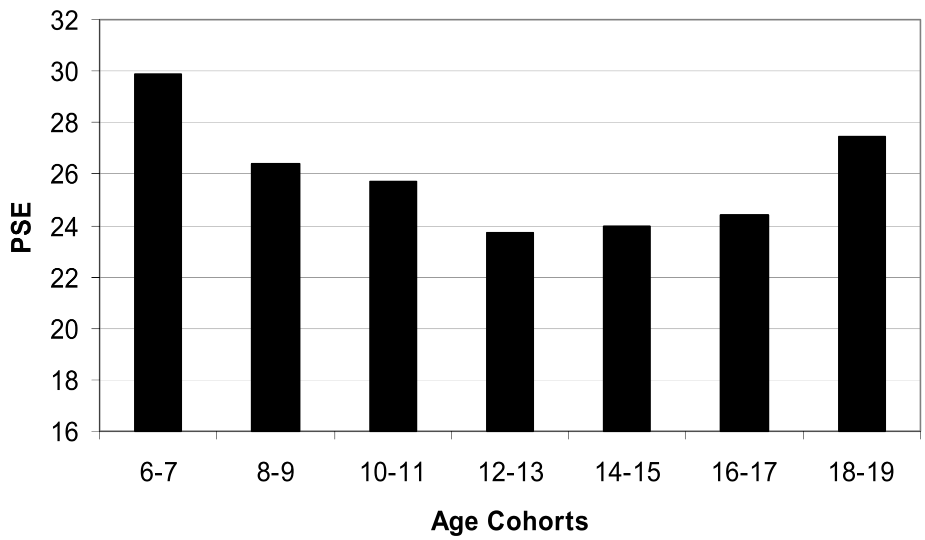

Figure 4. Developmental data for U.S. subjects using the Mueller-Lyer Illusion. Data is from Wapner and Werner (1957: Appendix 15).

These developmental data combined with the cross-cultural data suggest several important inferences. First, 'carpentered environments' and 'perceptival art', or whatever it is that accounts for the cross-group differences, likely has its effects between the ages of zero and 20, but not afterwards. Second, whatever causes the cross-cultural variation has much of its effect before age 11, otherwise children in the cross-cultural sample would not mirror the adult pattern. Third, these data suggest that variables like 'experience in a carpentered environment' can be misleading. What matters is not 'experience in carpentered environments' (or whatever the relevant variable), but 'experience in a carpentered environment *before* age 20'. This is relevant to critics of the 'carpentered environment' hypothesis who have suggested that the hypothesis fails because males and females in many of these societies have experienced substantially different amounts of contact with 'carpentered environments' (males spend much more time in seeking wage labor in cities), yet males and females consistently show little or no difference in illusion susceptibility. However, from the cultural developmental perspective, the observation confirms rather than contradicts the hypothesis, as females and males live in nearly identical visual environments between the ages of 0 and 12, when much of the effect seems to occur. Thus, males and females should be similar, and any experience differences after age 20 should have little impact.

While different visual experiences during ontogeny affect both owls and humans, there is an important difference: the human effect is the product of growing up in a culturally-evolved environment. As with foragers' bow and arrow technology, rectangular houses, 'carpentered corners', angular furniture and perspectival drawings, are products of particular cultural evolutionary trajectories. These environmental elements evolved non-genetically, through social learning, over centuries. There was surely a time in human history when—assuming Segall *et. al.*'s hypotheses are correct—the Mueller-Lyer illusion was not an illusion at all (or barely). Through an interaction between a particular line of cultural-technological evolution and the ontogenetic processes of brain development, these illusions were likely brought into existence. Thus, cultural evolution has likely generated changes in human brains without any changes in human genetics.[9]

Culturally-Evolved Social Behavior

As with their visual environments, human groups also experience different culturally-evolved *social* environments. It is within these culturally-evolved social environments that human brains continue their ontogenetic development. Through these ontogenetic processes, which deliver most of their effects between the ages 0 to 20, individuals acquire cultural rules, preferences, beliefs and the mental models of the social and physical world that propel their behavior. The learning process is fundamentally cultural: A combination of cross-cultural anthropological work (Fiske, 1998; Lancy, 1996), developmental psychology (Karmiloff-Smith, 1994; Meltzoff & Prinz, 2002; Tomasello, 1999b, 2000a, 2000b, 2000c) and neuroscience (Quartz & Sejnowski, 2000; Quartz, 1999; Quartz, 2002; Quartz & Sejnowski, 1997) suggest that children acquire their cultural understandings of the world though a process of imitation and practice that builds an increasingly hierarchical, integrated and abstracted understanding of the world. First, learners acquire the 'rules' of behavior by observation and direct imitation of the simplest components (a pattern that parallels language learning). Then, learners practice these bits of behavior in an ongoing process of rehearsal. As they master the bits, they gradually connect them through both higher-level forms of imitation (e.g., imitating strategies) and direct experience. Some developmental psychologists have increasingly characterized infants and children as 'imitation machines' (Tomasello, 1999a), with infants mimicking facial movements at birth (well, 42 minutes after birth, Meltzoff (2002)). These developmental patterns, which strongly differentiate humans and non-humans, suggest that 'imitation' is one of the essential developmental tools that natural selection has deployed to ratchet-up human cognitive abilities and adapt our cognitive architecture to the vast range of local social and physical environments (e.g., New Guinea swamps and moieties) that I mentioned at the outset of this paper. If true, one of the key tasks for explaining human adaptation, the success of the species, and our behavioral diversity will be to open the black box of 'imitation'. At the end of the paper I summarize some steps in that direction; first, however, I will attempt to persuade you that 'culture matters' in human social behavior.

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[9] However, these kinds of interactions surely set the evolutionary stage for the action of Baldwinian processes.

A combination of recent experimental work, deployed both cross-culturally and developmentally, suggests that growing up in a particular place has a substantial impact on an individual's social behavior. More specifically, experimental techniques designed to measure an individual's social preferences—e.g., their 'altruism', 'sense of fairness' and 'taste for punishing unfairness'—are consistent with three of the patterns discussed above. First, these social preferences are principally acquired over the first 20 years of life, although relatively smaller modifications may occur later. Second, growing up in different places results in quite different patterns of adult behavior, and these cultural patterns are likely largely in place *before* adolescence. Third, the learning sequence for social behavior is consistent with learning the 'rules' (or cultural models) first, and later integrating those rules with strategic considerations that operate within the context of the rules and associated expectations. Finally, as a corollary to these learning processes, having grown up in a particular place has a substantially larger impact on adult behavioral variation than individual-level variables like sex, age, income, wealth, education and wage labor experience. Thus, the substantial variation in social preferences (e.g., 'sense of fairness') that we observe across human social groups likely results from experience in different EOAs and the human propensity for cultural learning, not principally from differences in adult experiences (note the parallel with 'illusion susceptibility'). At this early stage of experimental research, cross-cultural and developmental work exists for three experiments of this type (called 'games'): the Public Goods Game, the Dictator Game and the Ultimatum Game. Because space is limited and the data are most extensive for the Ultimatum Game (hereafter 'UG'), I focus only on these experimental results for the remainder of the section.

The Ultimatum Game is a two-person bargaining experiment that has been extensively tested on undergraduate populations by experimental economists, psychologists and economic sociologists (see Camerer, 2003; and Roth, 1995 for reviews). In the base-line experimental setup, two 'players' are anonymously paired to divide a sum of real money (games are played with cash, which they players actually receive, and there is no deception). The first player, often called the 'proposer', must decide how much of the total sum ('the pot') to allocate to a second player, who is called the responder. Upon receiving an offer from the proposer, the responder must decide whether to "accept" the offer from the proposer, or "reject" it. If the responder accepts the offer, he/she receives the amount of the offer, and the proposer gets the remainder. If the responder rejects the offer, both players get zero (the pot vanishes). Both players are fully informed of the situation: they know the game is one-shot (will not be repeated) and that they will never know the identity of the other player. From the perspective of self-interested rational actors, this experiment leads to a straightforward prediction: responders should accept any non-zero offer, and proposers should realize this and offer the lowest non-zero amount possible. As you will see, this never happens, anywhere.

Using adult participants (age 22+) from industrialized societies, the UG show robust results. The strong modal offer is a 50/50 division. Offers above 50% of the total pot, and below 30% are rare, and low offers are often rejected.[10] Among undergraduates, for whom we have by far the largest database, the overall patterns are similar, although offers tend to be slightly lower. This research also shows that 'stake size' (the amount of money in the pot), 'sex' and adult 'age' (for those over 22) do not significantly influence game behavior (Camerer, 2003; Camerer & Hogarth, 1999).[11]

Recently, Harbaugh and associates (2002) have begun administering these kinds of experiments to children (ages 7 to 18) in rural Oregon in order to explore the developmental trajectories of social preferences. As an additional point of comparison, I have included data from a sample of graduate students from UCLA that provide a point of reference for 'adults' (ages 22+). Interestingly, the youngest children (age 7, 2nd grade) conformed most closely to the economists' model of rational self-interest—they made smaller UG offers than older children (and adults), and were more likely to accept lower offers. Figure 5 provides a comparative plot for these data. Each age cohort is labeled along the vertical axis such that the distributions of offers for each age cohort can be examined by reading horizontally across the possible offer amount, which label the x-axis. The relative sizes of the bubbles graphically show the proportion of the samples for each cohort that made the corresponding offer. In the 50% offer bubbles I have included the actual percentage. The plot illustrates a gradual movement from higher variance and a greater proportion of low ('selfish') offers among 7 year olds to lower variance and a higher proportion of 50/50 and near 50/50 offers among older individuals. This trajectory is, however, not linear. By age 9 (4th and 5th grades), 68% offer 50% and only 18% are making offers of 20% and below. However, by age 18 (12th grade), the lower offers have entirely disappeared, yet the fraction of 50/50 has also dropped to 43%, reflecting a shift from 50% to 40% offers (which now account for 45% of all offers)—as we'll see, this may reflect an interest in strategic thinking. In total, 88% of the 18-year old cohort makes either 50/50 or 60/40 offers. Considering these data in light of the previous work on moral development (e.g., Kohlberg, 1976) suggests that by age 9 (5th grade) most children have learned the

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[10] I base these claims on six data sets: (1) ULCA graduate students with a mean age of 26 (Henrich, 2000), (2) Chaldeans from Metro Detroit with a mean age 34.5 (Smith, 2001b), (3) Rural Missourians with a mean age of 40 (Ensminger, unpublished), (4) Swiss adults from a rural town outside of Zurich (Falk, unpublished), (5) employees from a distribution center for a large publishing company in Kansas City with a mean age of 37 (Carpenter, Burks, & Verhoogen, 2002), and (6) older students from Kansas City Community College with a mean age of 27.

[11] There is a smattering of studies suggesting that 'sex' matters; however the overall pattern of results is inconclusive and restricted to undergraduate populations (Camerer, 2003).

'cultural rules' or 'cultural models' that govern behavior in the UG situation, and, lacking a higher level integration, they stick close to these rules.[12] After age 12, we observe an increasing amount of 'strategic reasoning' within the context of these cultural rules (note, the growth of the 40% offers).

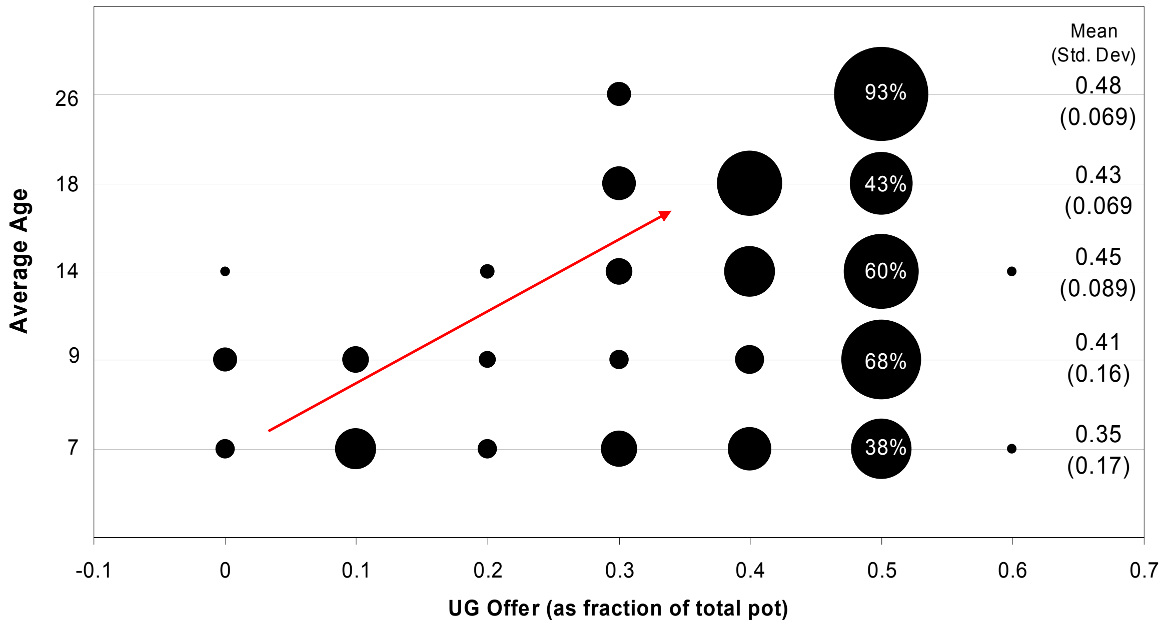

Figure 5. The distribution of Ultimatum Game offers for 5 different age groups. The distribution should be read horizontally, with the size of the bubble illustrating the proportion of the sample making the corresponding offer.

Figure 6 allows us to examine both the learning trajectory of the 'taste for punishment' (as measured by responder's behavior) and the amount of strategic behavior on the part of proposers in different age cohorts. On this plot I have added data from adults in rural Missouri and from an ethnic group from Metro Detroit (the Chaldeans[13]) to provide an 'adult' point of reference—I couldn't use the UCLA data because there weren't any rejections. The black bars on Figure 6 give the 'income maximizing offer' (IMO) for each age group. The IMO is the amount a proposer would offer if he wanted to maximize only his income from the game, and he had full knowledge of the probability of rejection at each possible offer amount. Thus, a group's IMO captures the strength or willingness of its responders to punish offers they deem 'unfair'. The black bars in Figure 6 show the development of an increasing taste for punishment. The

[12] This may not be unlike a novice arrow-maker, who must stick closely to the rule of manufacture because he lacks the knowledge and skill to innovate and experiment.
[13] The Chaldeans are Catholic immigrants from Iraq. Ethnographic and experimental details can be found in Smith (2001a; 2001b).

black and white bars together (stacked) reach to the mean offer for each group; thus, the white bars visually express the difference between what the proposers give, and what the responders demand. In the rural Missouri case, the IMO (50%) is *higher* than the mean offer (48%), and thus I've used a 'top-down' black to white shading.[14]

It is worth noting that the 'sense of fairness' (the UG offer) evolves to near its adult value by age 9 (in terms of the modal offer), and is lagged by the acquisition of a 'taste for punishment'. This sequence is interesting, since some economists have supposed that the 'taste for punishment' drives the apparent fair-mindedness of proposers among university populations. Developmentally, this is not the case, as fairness precedes punishment---children first learn the normative behavior (give half, or thereabouts), and then develop a taste for punishing norm violators at a cost to themselves.

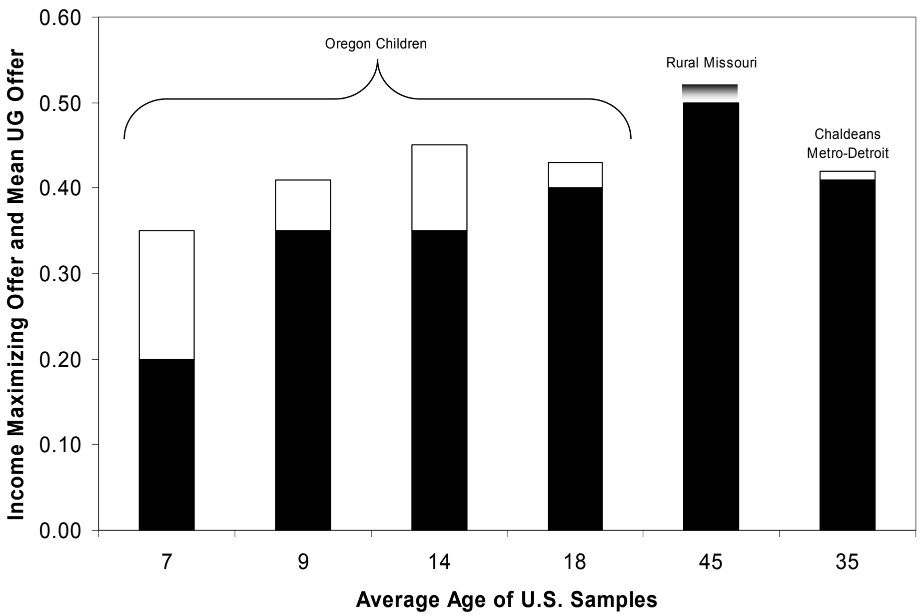

Figure 6. IMO and Mean UG Offers compared for a range of age cohorts in the U.S.

Many evolutionary and economically-oriented researchers might seek to view the above trajectories as a more or less fixed pattern of 'moral development' that is part of a reliably developing complex of species-specific cognitive architecture (please excuse the excessive jargon). For example, the robust results of the UG among university students was initially interpreted by some as the operation of evolved cognitive

[14] The Missouri experiment used a somewhat different version of the Ultimatum Game in which responders had to commit themselves—prior to seeing the actual offer amount—to what they would do at each of the possible offer amounts (which were limited to 10% increments).

modules for social interaction (Hoffman, McCabe, & Smith, 1998; Nowak, Page, & Sigmund, 2000) that arose in the human lineage via natural selection operating through the logic of repeated interaction (Axelrod, 1984; Trivers, 1971). This evolved piece of cognitive machinery, which would have allowed humans to take advantage of cooperation in small groups of repeated interactants, is assumed to 'misfire' in the context of the one-shot UG, thereby causing people to behave fairly and punishment unfairness.[15] However, UG data gleaned from 15 small-scale societies as part of a unified inquiry into human social behavior makes this position increasingly difficult to maintain (Bowles & Gintis, this volume). The results show substantially more variation across the human spectrum than is observed in comparing U.S. samples ranging in age from 7 to 70, and much of the cultural variation is likely present by age 9.

Because Bowles and Gintis (this volume) summarize our study of UG behavior in 15 small-scale societies, I will only briefly lay out the results vis-à-vis the goals of the present paper. Figure 7 presents the UG offer distributions in the same format as with the developmental data (Figure 5). The social groups represented include three groups of hunter-gathers (Lamalera, Ache and Hadza), 4 groups of pastoralists (Orma, Sangu herders, Kazakhs, Torguuds), 6 groups of horticulturalists (Quichua, Machiguenga, Gnau, Au, Achuar and Tsimane) and 3 groups of small-scale agriculturists (Shona, Mapuche, Sangu farmers). Both socio-political complexity and market integration vary substantially across this sample of groups (see Henrich et. al. forthcoming and Bowles & Gintis this volume for details).

Focusing on proposers' offers, the results show substantial variation, both within and across groups. The mean offers range from 25% among the Quichua of the Ecuadorian Amazon to 58% among the whale hunters of Lamalera (Indonesia). The modes span the range from 15% among the Machiguenga of the Peruvian Amazon to 50% among a wide range of groups. However, while the range of mean offers is large, they cover less than 50% of the possible spectrum. 80% of all offers fall between 10% and 50% (inclusive). Analyzing individual offers using multivariate linear regressions involving age, sex, income, education, wealth and social group (group-level dummies), shows that only 'social group' captures any significant portion of the variance.

[15] While this argument has often been passively accepted, it has severe empirical and theoretical problems (Fehr & Henrich, forthcoming).

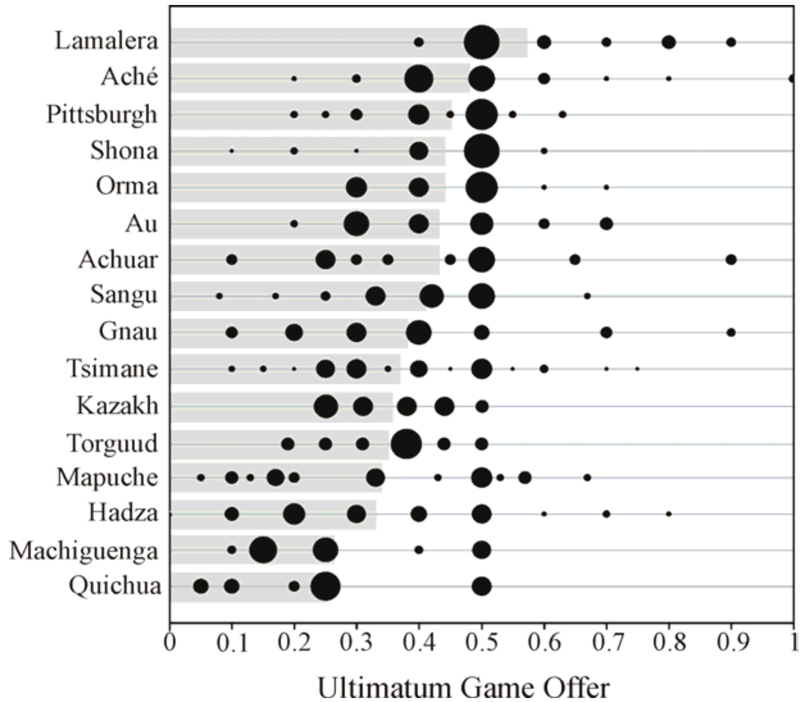

Figure 7. Bubble size represents the proportion of offers made at each amount for each group. The right edge of the lightly shaded horizontal gray bar is the mean offer for that group.

Comparing adult behavior from several of the societies to 7 year-olds and 9 year-olds from Oregon (compare Figures 5 and 7) shows that the adults in some societies express quite different notions of fairness than U.S. children, often favoring lower offers than the 7 year-olds, and showing less preference for the 50/50 offers. Thus, the developmental and learning trajectories that produce adult social behavior among Machiguenga, Quichua, Hadza, Tsimane and Mapuche likely follow quite different paths than that observed in Oregon, and the divergence is likely evident by age 7, and firmly in place by age 9.

As with the proposers, the behavior found among responders shows substantial cross-group variation. Some groups, like the Tsimane and Machiguenga in the Amazon, have few or no rejections at all despite a large number of low offers. Thus, the hypothesis that humans will reliably develop a 'taste' for punishing unfairness (or inequity), and that this taste will be extended to include individuals in one-shot, anonymous transactions, is not supported. Yet, by age 7, children in Oregon have already acquired some 'taste' for punishing anonymous others. The combination of these results suggests that the cultural differences in 'tastes for punishment' are emerging by age 7, and substantial by age 9. At the other end of the spectrum, groups like the Hadza, Gnau and Au, show rejection rates as high, or higher, than those found for university students for comparable size offers. Interestingly, the two New Guinea groups (the Au and Gnau) both show a willingness to reject offers above 50%. Although this curious pattern is not observed in U.S. samples, it makes sense in the ethnographic context of many New Guinea societies (Tracer, forthcoming).

For groups with some rejections (>2), we estimated their IMO's and plotted them on Figure 8 using the same approach as with the kids. Note that IMO's could not be estimated for several groups because of a lack of rejections (despite low offers); thus, the societies plotted on Figure 8 likely represent the 'high end' of the IMO spectrum (not the low end!).[16] As above, the black-to-white shading used on the Sangu farmers' bar indicates that their IMO was higher than their mean UG offer. These cross-cultural results show that IMO's vary in the adult populations from below that found among 7 year olds in the U.S. to roughly the same as that found among U.S. adults. The agreement between UG means and IMO's (the white section) also varies substantially from near zero for Hadza foragers and Sangu farmers to large values among the whale-hunters of Lamalera and the Achuar.

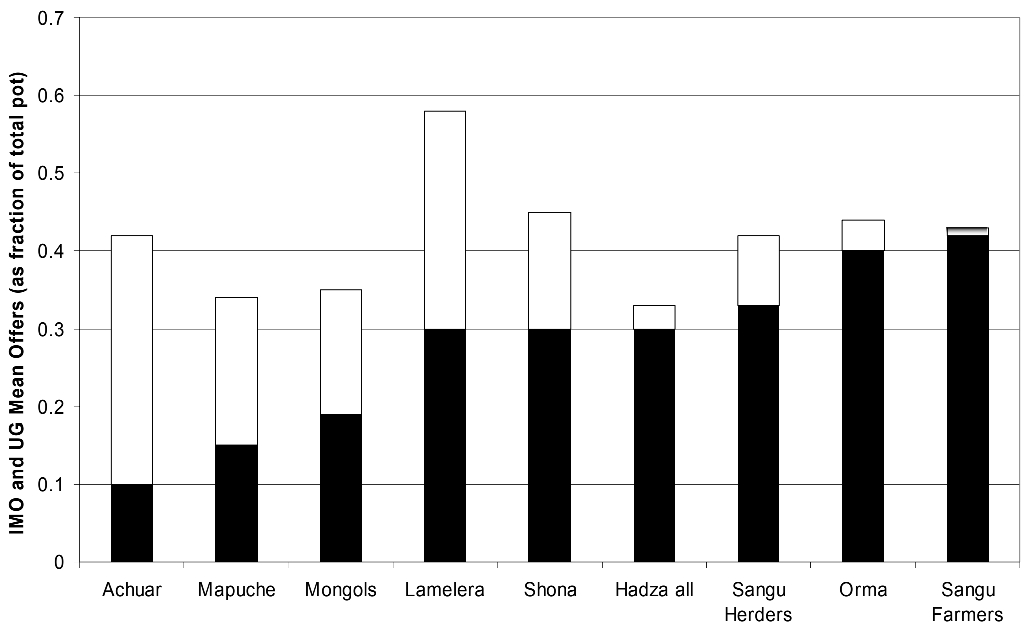

Figure 8. IMO and UG Mean Offers for several societies. The black bars give the IMO and the stacked black-white combination reaches the mean UG for each group. Because the Sangu farmers had a higher IMO than mean UG, I used the shaded cap (see text)

[16] IMO's also could not be estimated for the Au and the Gnau of New Guinea because of the non-monotonic nature of their rejections. A description of the numerical procedure for estimating IMO's can be found in McElreath and Camerer (forthcoming).

The reader is cautioned that, while these IMO data are completely consistent with previous data and the theoretical lines in this paper, they are by far the least reliable results presented herein. There are several reasons for this: (1) several of the IMO estimates are based on small samples and few rejections, (2) ethnography suggests that some individuals in some field sites imagined 'punishment' taking place outside the game (Achuar), or by supernatural forces (Mapuche), and (3) the Lamalera result derives from rejection data based on sham offers that were all below 50%, so we don't know if people in Lamalera would have accepted the hyper-fair (over-50%) offers that characterized the actual Lamalera proposer data (as I noted, both the Au and Gnau rejected hyper-fair offers, so this concern isn't outlandish). Thus, while I don't think this data should be ignored, I do think it must be weighted accordingly.

Consistent with the proposer findings, the responder data also show that age, sex, income, education and wealth do not significantly predict the likelihood of a rejection. Examining the data across all groups, only 'social group' and 'amount offered by proposers' are important predictors of responder behavior. The likelihood of a rejection increases as the proposer's offer decreases. Controlling for this, the likelihood of rejection still varies significantly across our 15 groups. The combination of these developmental and cross-cultural results suggests that a 'taste for punishment,' like 'fairness,' is—at least partially—an acquired taste, whose flavor and intensity strongly depend on the cultural environment one grows up in.

In this section, I have highlighted two age trends in UG behavior. Among Oregon children, we observe that both a 'sense of fairness' (i.e., a preference for equitable distributions) and a 'taste for punishment' increase with age, between ages 7 and 26 (and I've commented on the non-linear nature of this development). However, among adults from both industrialized societies and a wide range of small-scale societies, no 'age effects' have been observed. In fact, individual-level variables like income, education and wealth are notoriously non-predictive. In light of the above data, I argue that the first effect (cultural learning during ontogeny) explains the second observation (little importance of 'adult' individual level variables). If individuals acquire their 'taste for punishment' and 'sense of fairness' principally during ontogeny, as Harbaugh et. al.'s data suggest, then adult variables such as adult age, income and wage labor participation, that may vary over an individual's *adult life course*, will show a relatively small effects vis-à-vis the cultural environment of ontogeny—because the social preference is mostly constructed during our extended ontogeny.

This explains another pattern in the cross-cultural UG data: the presence of group-level effects of market integration in the absence of any significant individual-level effects of market participation (Henrich et al., forthcoming).[17] Our analysis shows that a *group's* market integration is a significant predictor of its mean UG offer: higher levels of market integration predict higher UG offers. However, looking at the within group analyses across the field sites, individual-level measures of market exposure (like wage labor participation or cash cropping) consistently fail to reveal predictive effects. This is an apparent refutation for those (like evolutionary psychologists and economists) who don't consider the cultural learning and the ontogeny of cultural models and preferences. Typically, the argument about the effects of markets runs like this: the experience of working or operating in markets and market institutions alters an individual's beliefs or preferences vis-à-vis the kinds of anonymous transactions that characterize the UG, thereby leading to higher offers (i.e., more 50/50 offers). Thus, market exposure affects individuals directly as adults, and group-level differences merely represent the aggregate effects of the adults' market exposure. From such theoretical premises, while our group-level effects of market integration stand as a partial confirmation of the hypothesis, the failure of individual-level measures presents a prickly puzzle.

However, now consider such a theoretical proposal from the perspective of the 9-yearolds in rural Oregon, 77% of whom offered 40% or 50% of the total pot in the UG, and achieved a mean offer of 41% (equal to or greater than most of the adult samples in our small-scale societies). It seems likely that if we were to measure the 'market integration' of these kids using variables like wage labor or commercial selling, we would find them to be one the least market integrated groups in our 15-socieity sample, yet they have one of the highest mean UG offers and a substantial IMO compared to many of our social groups. However, while not actually participating in any wage labor themselves (or very little), they have grown up in one of the most market-integrated societies in the world. As a consequence, they are indirectly acquiring the cultural models, preferences, habits, and beliefs that will allow them to function effectively as adults in their society. Thus, this combination of cross-cultural and developmental data suggests that having grown-up in a more market integrated society may make one more likely to make offers at or near 50% in the UG as an adolescent or adult, but subsequent market experience may not substantially alter behavioral patterns acquired while growing up. This approach predicts that group-level measures, to the degree that they reflect and correlate with the EOA's of the experimental participants, will predict the mean behavior of the group. At the same, this cultural learning approach predicts that post-adolescent adult variations in income, age, and wealth will not substantially predict game behavior, although small effects should be anticipated, as adults continue learning throughout their lives.

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[17] Market integration is the degree to which an individual or group has experience or interaction in market transactions.

Along the same lines that I discussed with regard to the Mueller-Lyer illusion, the market integration hypothesis, at least in its standard form, should predict that we observe numerous sex differences between males and females in UG behavior. Because males in many of the societies we studied spend more time than women in wage labor and market transactions, males should make higher UG offers and be more willing to punish inequitable offers. As noted, this is not the case. Yet, if we consider the EOA of our subjects and recognize that this environment makes the predominant contribution to adult social preferences, then the similarity between males and females should be expected, rather than puzzling.

Repose

Above, through a series of examples, I have attempted to argue the following two points:

1) Humans, compared to other animals, are heavily reliant on culturally learned information for survival. Human ontogeny occurs in a culturally-evolved world that is replete with culturally-learned 'solutions' to local environmental and social situations/problems that have been honed over generations. These 'solutions' must be learned from other individuals.
2) Because of humanity's extended juvenile period and the associated cognitive plasticity, the culturally-constructed environments of human ontogeny likely affect how we think and perceive the world in fairly deep ways. This means that our 'cognitive architecture' will evolve non-genetically through an interaction between culturally-evolving environments and our ontogenetic learning processes that allow, at least in part, our brain's cognitive architecture to adapt to the circumstances of the current generation. This also implies that people who experience different cultures will have different brains.

Unfortunately, these observations alone do not get us very far: People learn their culture by growing up in a particular place, and this learned 'culture' affects their decisions and behavior. These observations, despite being essentially ignored by Economics, Biology, Political Science and most of Psychology, have been at the foundation of Anthropology since early in the 20th century, and have provided the unquestioned point of departure for much of anthropological inquiry in the last 80 years. Yet, while likely being true in the broadest sense, they have not proved particularly useful in my view. Below, I attempt to show how evolutionary theory can be applied to the ontogenetic dilemma faced by individuals growing up in a particular place, to understand the psychological learning processes that individuals use to adaptively acquire their behaviors, skills, preferences, tastes, knowledge and mental models of how the world works. For a more extensive introduction into how a 'cultural learning approach' represents the natural extension and application of evolutionary theory to the human species, the reader might begin with Henrich & McElreath (forthcoming).

Programmed for adaptive cultural learning

The claim here is that understanding culture and cultural learning requires understanding the psychological processes that construct our minds, making them 'self-programmable' (Pulliam & Dunford, 1980). From this point of departure an immense variety of questions can be posed. One question that allows theorists to address a variety of more anthropological issues related to cultural adaptation, diversity and history focuses on how individuals 'figure out' who, what and when to imitate. An evolutionary approach suggests that natural selection will favor cognitive mechanisms that allow individuals to more effectively extract adaptive information, strategies, practices, heuristics and beliefs from other members of their social group at a lower cost than that demanded by random imitation or individual learning (experimentation, etc.). Below, I summarize research on two types of cultural learning processes that are derived from formal theoretical underpinnings and empirically-grounded in both laboratory and field evidence.

Prestige- and Rank-biased Transmission

If individuals vary in skills (e.g., tool making), strategies (e.g., tracking techniques), and/or preferences (e.g., for foods) in ways that affect fitness, and at least some components of these differences can be acquired via cultural learning, then natural selection may favor cognitive capacities (or biases) that cause individuals to preferentially learn from the more skilled or knowledgeable individuals. The greater the variation in acquirable skills among individuals, and the more difficult those skills are too learn via individual learning (trial and error), the greater the pressure to preferentially focus one's attention on, and imitate, the most skilled individuals. In laying out this evolutionary process, Henrich & Gil-White (2001) have called this capacity "rank-biased transmission": Individuals rank potential 'cultural models' (i.e., individuals they may learn from) along dimensions associated with underlying skills (e.g., hunting returns), and focus their social learning attention on the most highly ranked (those most likely to possess acquirable skills, practices, etc.). Interestingly, while ability to rank individuals by foraging success is widely observed in non-humans (Stammbach, 1988), these animals show little or no ability to acquire skills or knowledge from successful foragers. With the rise of cultural capacities in the human lineage, natural selection needed only to connect these learning abilities with pre-existing ranking capacities. As a side effect of its individual-level adaptiveness, rank-biased transmission can lead to faster rates of cumulative cultural adaptation compared to vertical transmission, and produces cumulative cultural adaptation even in the complete absence of individual learning, as long as people make learning errors and the population is sufficiently large enough (Henrich, 2003).

This theory suggests that because underlying traits like 'skill' and 'knowledge' are often difficult to observe, success and achievement measures are used as proxies. This explains the widespread observation that people copy successful individuals. Further, because the world is a noisy, uncertain place, and it's often not entirely clear which of an individual's many traits have led to their great success, this approach suggests that humans have evolved the propensity to copy a wide-range of cultural traits from successful individuals, only some of which may actually relate to the individuals' success. If information is costly, this strategy will be favored by natural selection even though it may allow neutral and somewhat maladaptive traits to hitch-hike along with adaptive ones. In a world of costly information, cognitive adaptations don't always produce adaptive behavior (even in ancestral environments), but dual inheritance theory allows one to systematically predict the circumstances of maladaptation.

Besides 'skill' and 'success', natural selection should favor any reliable cues that allow imitators to more effectively focus their attention on models that are likely to possess behaviors and strategies that are both readily learnable and adaptive for the imitator. For example, assuming the sexual division of labor is relatively old in the human lineage, imitators should preferentially focus their attention on successful members of *their own sex* because these individuals are likely to have skills and knowledge that will be useful to learners in their roles in later life. Further, children should not only preferentially copy members of their own sex, but should pay particular attention to children who are somewhat older than themselves. By preferentially imitating individuals who are skilled, older and of their same sex, imitators increase their likelihood of acquiring adaptive behaviors and strategies, and can effectively scaffold themselves up to increasingly more complex skills: If you are an 8-year old, you would be wise to first master the skills of the most successful 11-year old before aspiring to imitate the most successful 16 year old. Once you've mastered the skills of the 16-year old, perhaps you will focus your attention on learning from the most skilled adults in your village. Other criteria like 'self-similarity' and shared ethnic markings can also facilitate more adaptive cultural learning (McElreath, Boyd, & Richerson, 2003). All of these evolutionary hypotheses find substantial support in both laboratory experiments and ethnographic observation (Henrich & Gil-White 2001).

Following this line of evolutionary thinking suggests that once rank-biased transmission (as an innate cognitive ability) has spread through the population, highly skilled individuals will be at a premium, and social learners will need to compete for access to the most skilled models. This creates a new selection pressure on rank-biased learners to pay deference to those they assess as highly skilled (those judged most likely to possess useful information) in exchange for preferred access (and perhaps assistance, hints, etc.). Deference benefits may take many forms including coalitional supports, general assistance (chores), caring for the offspring of the skilled, gifts, etc. Such deference patterns provide a costly signal of whom other individuals believe is highly successful or skilled because deference is 'paid' to such individuals in exchange for copying opportunities—faking the signal would require paying deference benefits to unskilled individuals.

With the spread of deference for high skilled individuals, yet another opportunity is presented for natural selection to save on information costs. Naïve entrants (say immigrants or children), who lack detailed information about the relative skills and successes for potential cultural models, may take advantage of the existing pattern of deference to knowledgeable individuals, and use 'received deference' as a cue of underlying skill. Assessing differences in deference patterns provides a 'best guess' of the skill ranking until more information can be accumulated over time. This also means skilled individuals will prefer deference displays that are easily recognized by others (in public). Thus, along with the ethological patterns dictated by the requirements for high fidelity social learning (proximity & attention), deference displays also includes diminutive body positions and socio-linguistic cues. The end point of this process gives us the psychology, sociology and ethology of 'prestige', which must be distinguished from those associated with phylogenetically older 'dominance' processes (see Henrich & Gil-White, 2001 for details).

From this theory, Henrich & Gil-White (2001) derived and tested 12 predictions about the interrelationships between preferential imitation and influence with prestige deference, age, sex, memory, and ethological patterns (e.g. gaze and skill). Specifically regarding imitation and influence, these findings show (1) unlike other animals, human infants come out of the womb imitating and by 9-months are copying both goals and actions (Meltzoff, 2002; Tomasello, 2000a), (2) both adults and children preferentially imitate more skilled and prestigious individuals, usually unconsciously, (3) this imitation occurs even when the 'thing being imitated' is not clearly connected to the imitatee's domain of skill or prestige, (4) children preferentially imitate older, same-sex models across a wide behavioral domain, and (5) people remember what prestigious individual say more than same-status individuals and unconsciously align their opinions with prestigious individuals, even when the individual's opinion is not related to their domain of prestige (e.g., people care about Tiger Woods' political views). Combined with numerous related findings, this work indicates prestige and rank-biased transmission are part of our cultural learning processes that build and adapt our brains to local social and environmental circumstances.

Conformity bias

What should an imitator do when his own information is ambiguous, and any observable differences in success/prestige among individuals do not covary with the observable differences in behavior? For example, suppose everyone in your village uses blowguns for hunting, except one guy who uses a bow and arrow, and obtains fairly average hunting returns—and you have no experience with either one. Do you begin investing in learning to manufacture and use the bow or the blowgun?

Theoretical work (Boyd & Richerson, 1985; Henrich & Boyd, 1998; Henrich & Boyd, 2002) suggests that, to deal with such information-poor dilemmas, natural selection will favor psychological machinery designed to copy the ideas, behaviors, beliefs, strategies and practices of the majority. Termed, c*onformist transmission,* this mechanism allows individuals to aggregate over the behavior of many individuals. Because behavior implicitly contains the effects of each individual's experience and learning efforts, conformist transmission can be the best route to adaptation in information-poor environments. To see this, suppose every individual is given a noisy signal (a piece of information) from the environment about what the best practice is in the current circumstances. This information, for any one individual, might give them a 60% chance of noticing that hunters who use blowguns bring back slightly larger returns than those who use bows in this local environment. Thus, using individual learning alone, individuals will adopt the more efficient hunting practice with probability 0.60. If people only did individual learning, 60% of the adult population would end up using blowguns and 40% bows. But, if an individual imitator samples the behavior of 10 other experienced individuals, and adopts the majority behavior, his chances of adopting the superior blowgun technology increases to 75%—this is because under conformist transmission individuals give substantial weight the majoritarian behavior according to its frequency in deciding what practice to pursue. Furthermore, consider this: if learners only use their environmental information (perhaps acquired by experimentation) when it is unambiguous and use conformist transmission the rest of the time (which is most of the time), then this combination of learning processes will eventually lead the entire group to adopt the slightly superior blowgun technology, even though most people get ambiguous information and thus imitate most of the time. In contrast, if individuals relied only on their information and did not use imitation, 40% of the population (on-average) would adopt the inferior technology every generation. Now, recall Woodburn's ethnography: all Hadza use a quite similar complex of hunting technology, most Hadza never experiment with using a different wood for their bows, and the occasional Hadza experimenters always seem to return to the commonly used *mutateko* wood.

Building on this conformist logic and extending Boyd & Richerson's (1985) original work, Henrich and Boyd (1998) used simulations to investigate the interaction and coevolution of vertical transmission (parent-offspring transmission), individual learning and conformist transmission in spatially and temporally varying environments. These results confirm that conformist transmission is likely to evolve under a wide range of conditions. In fact, these results show that the range of conditions that favor conformist transmission are wider than those for vertical transmission alone—suggesting that if imitation (via vertical transmission) evolves at all, we should also expect to observe a substantial reliance on conformist transmission. Several other predictions about human social learning were derived, but here there is only space to mention two. First, individuals will prefer conformist transmission over vertical transmission, assuming it is possible to access a wider range of cultural models at low cost (which is often, but not always, the case). Second, as the accuracy of environmental information decreases, reliance of conformist transmission (over individual observation/learning) will increase. Laboratory evidence clearly indicates both a conformist effect in learning and problem solving (that is not related to concern about how one will appear to peers), and that these effects increase as the uncertainty of environmental information increases. Henrich (2001) provides evidence consistent with the effect of conformist transmission by analyzing the temporal dynamics of the diffusion of innovations.

Cobbling up from Cultural Learning to Sociological Phenomena

Cultural learning mechanisms not only provide cognitively realistic and developmentally plausible mechanisms for acquiring adaptive behaviors and strategies in complex, variable environments, they also provide a foundation for building a higher level set of theories that target population-level phenomena. Using formal modeling techniques, cultural learning mechanisms that are both theoretically and empirically grounded—like conformist and prestige-biased transmission—can be combined with population structure, environmental and ecological factors and social interaction to rigorously study a wide range of population-level phenomena. To illustrate, I will mention a few of the phenomena that my coauthors and I are investigating.

1) Combining social interactions in coordination dilemmas (such as whether to adopt beliefs and practices for brideprice or dowry) with prestige-biased transmission, McElreath et. al. (forthcoming) have shown that symbolically-marked social groups ('ethnic groups') will spontaneously arise under a wide range of conditions. They also show that an 'in-group learning bias' (a bias to learn from and interact with people who share your symbolic markings) can genetically coevolve through this process, as natural selection acting on genes takes advantage of the changed social environments left in the wake of cultural evolution.
2) Integrating demographic considerations with prestige-biased transmission, I've shown that larger populations of social learners will generate faster rates of adaptive cultural evolution (e.g., in technology and practices), and that under some conditions a sudden drop in population size can

result in a gradual process of maladaptive cultural losses. Predictions derived from this model are consistent with the maladaptive losses observed in the Tasmanian archaeological record (Henrich, 2003).

3) A combination of conformist transmission and prestige-bias transmission can stabilize cooperative strategies in large social groups in a manner not possible in an a-cultural species (Henrich & Boyd, 2001). This can lead to a process of cultural group selection and culture-gene coevolution that will generate increasingly complex social, political and economic institutions on time-scales of 100's and 1000's of years (Boyd & Richerson, 2002; Henrich, forthcoming; Richerson & Boyd, 1998, 2000; Soltis, Boyd, & Richerson, 1995).
4) Cultural learning processes, certain kinds of social interaction, and increasing productive capacities (associated with technological evolution) can lead to the evolution of economic specialization and class inequality under a wide range of conditions (Henrich & Boyd, n.d.).
5) A combination of conformist transmission and prestige-bias can explain the S-curves, initially slow diffusion and 'takeoff points' that characterize much of the diffusion of technology, practices and novel beliefs (Henrich, 2001).

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