A Mind-Brain for Culture and Cultural Evolution

Peter J. Richerson
www.des.ucdavis.edu/faculty/Richerson/Richerson.htm
pjricherson@ucdavis.edu

Conference on *A Blank Slate? Brain Science and Cultures*
Fondazioni Intercultura
Firenze, April 4, 2019

Introduction

One of the important hallmarks of our species is our extreme dependence on complex cumulative culture for most of our adaptations (Boyd, Richerson, & Henrich, 2011). In this talk I reviewed what sort of demands culture places on the human mind or brain. I then review some of the cognitive neuroscience that produces a picture of the brain that is compatible with its being an organ that supports cultural adaptations.

Two Hypotheses

Two rather different arguments have been developed by evolutionary social scientists to explain how the human mind/brain is organized to make the human adaptation possible. Edward O. Wilson (1978) argued for a human nature theory in which selection on genetically coded “epigenetic rules” constrained learning and culture to conform to fitness enhancing ends. See also (Lumsden & Wilson, 2006). He argued that cultural evolution could not play any fundamental role in human evolution because culture only became important in the last few thousand years and because genes wired the human infant’s brain in “exquisite detail” before the child acquired any culture. The innatist Evolutionary Psychologists of the Santa Barbara school proposed a very similar theory according to which the brain is composed of hundreds or thousands of specialized, encapsulated modular elements that evolved in the Pleistocene to support our hunting and gathering life style (Frankenhuis & Ploeger, 2007; Tooby & Cosmides, 1992). These authors proposed that social scientists have greatly exaggerated the importance of transmitted culture relative to the innate information endowed to us by selection on genes in the Pleistocene (which they confusingly call “evoked culture”). Stephen Pinker (2002) is one of the most ardent defenders of this idea. In their introductory essay to the 25th anniversary edition of their 1981 book Lumdsen and Wilson (2006) discuss the relationship between their ideas and those of the Evolutionary Psychologists.

The second hypothesis stems from the evolutionary functional analysis of human culture (Boyd & Richerson, 1985; Richerson & Boyd, 2005). In this view, culture is an adaptation to spatially and temporally variable environments, especially environmental variation that occurs on relatively short time scales ranging from a generation out to perhaps a few hundred generations. Rapid variation within a generation mainly relies on individual level phenotypic flexibility, although rapid cultural diffusion among peers may spread useful innovations quite rapidly. Changes that are quite slow on the generational time scale are tracked well enough by selection acting on genes. The human brain is a metabolically expensive organ, prone to damage and a cause of obstetric difficulties for mothers and infants. The complexity of culture across primates correlates well with brain size (Reader, Hager, & Kevin, 2011) suggesting that our very large brain is necessary to support our extraordinarily complex cultures. Cultural evolution, in this view, simulates ordinary organic evolution by rather accurately transmitting a large volume of information by teaching and imitation from large social networks. Individuals select the information that they acquire and teach at least to some extent based on its utility. This selective teaching and imitation in turn makes causes cultural evolution to be faster than genetic evolution and hence capable of tracking rapidly changing environments in time and fine-scale changes in space (Perreault, 2012). It is perhaps no accident that human brains and the culture they support evolved in the hypervariable climates and ecologies of the Pleistocene.

Two Challenges for a Theory of the Human Mind/Brain

The first challenge is cultural complexity and diversity. Human societies around the world today are highly variable, as documented by 19th and 20th Century anthropologists and sociologists (Johnson & Earle, 2000; Lenski & Lenski, 1982; Steward, 1955). Simpler hunting and gathering and small-scale farming societies differ substantially in their subsistence strategies and social organization. Complex societies have many social roles that take more advantage of the economic efficiencies of the division of labor, albeit at the expense of oft highly coercive and inegalitarian social systems. To support this diversity the brain has to have a large measure of flexibility. Take Stone Age watercraft as an example. The Austronesian navigators constructed fast-sailing outrigger canoes and large double-hulled voyaging ships that they used to people and exploit the remote tropical islands of the Pacific. Arctic North Americans built light, fast kayaks with a wooden frame and a watertight skin cover to hunt marine mammals in lethally cold waters in reasonable safety. These craft are triumphs of traditional boatbuilding, but many other types of serviceable watercraft were constructed to suit local conditions and raw materials. If humans have a boat-building module it would need to incorporate an improbably vast amount of highly specific knowledge, as if everyone was born with a PhD in marine architecture. Hunting equipment and skills, knowledge of plant foods and food processing techniques, farm crops and cultivation techniques, and languages and social institutions to manage large scale cooperation are other examples of cultural complexity and diversity. That humans are born with hundreds or thousands of innate equivalents of PhDs is not plausible. Ecologically, humans in the last 10,000 years constitute an adaptive radiation, as if we are thousands of species with distinctive socio-economic adaptations. Yet, biologically we remain a single species with rather modest genetic differences between us. Many of the genetic differences seem to be a result of culture driven gene-culture coevolution, such as the ability of adults from historically dairying populations to digest milk sugar (Henrich, 2016; Laland, 2017). It is also clear from archaeology and paleoanthropology that past human cultures were often very different contemporary ones and that many features of culture conform to patterns of descent with modification (Currie et al., 2016; Flannery & Marcus, 2012; Walker, Wichmann, Mailund, & Atkisson, 2012). Complex culture isn't built in a day, it evolves. Stone tools seem to go back in the hominin lineage even before the existence of our genus and the Oldowan stone tool tradition associated with the early members of our genus were rather sophisticated compared to chimpanzee tools (Toth & Schick, 2009). Durable tools already begin to have a modern cast around 100,000 years ago in Africa (Marean, 2015). So much for Wilson's (1978) claim that culture was a late part of human evolution! The human mind/brain must have a seriously "blank-slatey" character to accommodate the complexity and diversity of our behavior.

The second challenge is to account for why so much of the variation in human culture is adaptive in the sense of genetic fitness. The massive modularity hypothesis of the Evolutionary Psychologists suggests that humans should be adapted to the Pleistocene, not to the Holocene. But, it fact, humans have been much more successful in the Holocene than in the Pleistocene! Lumsden and Wilson's (2006) version of the human nature hypothesis suggests that selection for epigenetic rules should have proceeded apace in the aftermath of the transition to the Holocene but the evidence for major genetic changes to control culture are not in evidence. Rather cultural innovations seem to have acted to adapt genes to cultures rather than the other way around (Ross & Richerson, 2014). In the modeling analysis in Boyd and Richerson (1985) proposed that general purpose decision-making systems acting on cultural innovation, imitation, and teaching together with accurate social learning are sufficient to create the kind of cumulative adaptive evolution of culture that leads to kayaks and double-hulled voyaging ships. Even if the blank slateyness of culture, combined with relatively weak adaptive decision-making forces, leads often to cultural maladaptions, in principle it need only be true that cultural traits are on average adaptive enough to pay the total overhead of the costs of culture. Cultural maladaptations in fact don't seem to be rare (Paul, 2015; Richerson & Boyd, 2005).

The Cognitive Neuroscience of Culture

The cognitive revolution begun by Chomsky (1959) was a highly innatist alternative to the purportedly highly environmentalist behaviorism then dominant in psychology. Chomsky himself was not originally attracted to evolution ideas, but Wilson, Tooby and Cosmides, and Pinker did build a highly evolutionary version of his ideas based on the concept of human nature (Richerson, 2018). Pinker (1994), in particular argued for an evolutionary version of innatist linguistics. Ironically, in the meantime Chomsky did become interested in evolution but became minimalist regarding the innate elements of language (Chomsky, 1995; Hauser, Chomsky, & Fitch, 2002). Comparative linguists had come to the conclusion that in fact the principles incorporated into syntax were culturally very diverse and could not be accounted for by a relatively few innate principles (Christiansen & Chater, 2015; Newmeyer, 2004). Other basic tenets of linguistic innatism also suffered from empirical findings. For example, an innate Language Acquisition Device was said to be required because children received far too little information from their primary language teachers, typically their mothers, to infer syntactic rules. In fact, a careful analysis of a corpus of mother-infant speech interactions showed that language learning kids received a large amount of feedback regarding syntactic conventions (Moerk, 1983). By now, I believe that empirical cognitive neuroscience has circled back to a view of mind/brain development and function that is much closer to behaviorism than to the human nature theory. It also neatly solves the challenges of the complexity, diversity and general adaptiveness of culture. In what follows I review some of the most important contributions to this turn.

Gerald Edelman

Edelman's (1987) book *Neural Darwinism: A Theory of Neuronal Group Selection* made a number of important points. First, during early development of the neocortex of the brain, the best that genes can do is lay down a relatively coarse topography. In fact the topography of vertebrate brains is phylogenetically rather constrained such that brains are pretty much scale models of each other varying mainly in size (Krubitzer & Stolzenberg, 2014; Striedter, 2005). As the brain develops, many axons fail to establish useful connections with other neurons and are cannibalized. Those axons that do establish connections form an astronomical number of synapses, 150 trillion or so in the human brain. It is hard to imagine how many fewer genes can control the formation of synapses with the precision imagined by Wilson (1978). Developmental processes in fact shape the synapse by pruning those that are dysfunctional and strengthening ones that are useful. Even in adulthood the brain is a dynamic organ of phenotypic flexibility. Single cell recordings from the brains of macaques, one of whose digits was experimentally amputated, showed that the cortical resources devoted to the amputated digit were taken over by the resources devoted to other digits. The brain actively adapts to environmental contingencies. Klaus Immelmann (1975) reviewed the case of imprinting. How was it that Konrad Lorenz could cause a gosling to imprint on him? Immelmann supposed that genes could not code for a detailed picture of a goose, and that imprinting depended on taking the first nurturing animate thing it experienced to be Mom. The developing visual system could form a detailed picture of this caregiver, Mom proper or Lorenz as the case may be. In essence, the need to use developmental resources, including sensory inputs, to shape the wiring of the cortex generates phenotypic flexibility for free.

Michael Anderson

Edelman's picture of brain development and function was limited by a quite crude picture of brain development and function. In particular invasive experimental techniques were largely restricted to monkeys and "lower" animals. Apes and especially humans could be studied mainly via the effects of brain pathologies like stroke lesions. The advent of fMRI and other non-invasive imaging techniques offered a window into human brain development and function heretofore absent. The core of Michael Anderson's (2014) *After Phrenology: Neuronal Reuse and the Interactive Brain* is a large meta-analysis of fMRI data. Many tasks have been put to people when in the scanner and cognitive neuroscientists have built up a large corpus of images of what parts of the brain are active when performing these tasks. Anderson analyzed which small pieces of cortical tissue are active in many different tasks. It turns out that each task typically activates many localized areas across the cortex, but each small area participates in a number of tasks. The small areas seem to be specialized for different computational functions, but given tasks recruit of unique circuit of specialized modules. The specialized modules, rather than being dedicated to a particular task are recycled to participate in many different tasks. Anderson argues that these circuits are built during development. They can also be rebuilt for novel tasks. Reading is an example (Dehaene, 2009). The brain develops a general object recognition system that can be pressed into service to recognize letters and numerals. This reuse of cortical resources makes sense physiologically. Many dedicated modules would be inactive most of the time even as they generated overhead costs for their maintenance. Reuse keeps any given bit of cortical resource more or less constantly active making the overall overhead cost of the cortex as small as possible given the large variety of tasks it has to perform. The difficulty we have in "multi-tasking" may be due to reuse. If two tasks share any cortical resources, trying to do them both at once will lead to inference effects.

Cecelia Heyes

Heyes' (2018) book *Cognitive Gadgets: The Cultural Evolution of Thinking* proposes that the innate part of the mind consists mainly of a few powerful domain general self-organizing tools. The most important of these is associative learning. Brains are very good at picking out patterns in sense data and actions related to the patterns are reinforced or punished, causing some associations to become stable parts of behavior and others to be extinguished. In the human case, associative learning is powerfully assisted by teaching and imitation. Other authors (Carey, 2009; Csibra & Gergely, 2011; Tomasello, Carpenter, Call, Behne, & Moll, 2005) argue that imitation and teaching are innate early developing core cognitive capacities especially well developed in humans, but Heyes insists that infants use their domain general learning systems of learning and social learning to build even these basic capacities. It seems to me that the innate core capacities hypothesis leaves plenty of room to explain cultural diversity, but Heyes even more radical rejection of innatist explanations is certainly interesting. It is easy to see how reinforcement acting on learned and social learned behaviors could act to keep culture adaptive in the genetic sense, and Heyes reviews evidence that innate attentional biases and emotions play roles in this regard.

Jaak Panksepp

Panksepp and Biven's (2012) *The Archaeology of the Mind: Neuroevolutionary Origins of Human Emotions* reviews Panksepp's career-long work on the brain's emotional circuitry. He discusses seven emotions SEEKING, RAGE, FEAR, LUST, CARE, PANIC and PLAY. These terms are mostly close to our folk understanding of the emotions but some are not so familiar. SEEKING is generally pleasant motivating emotion we feel when on a motivated quest to fulfill some goal. Thus, some people scale mountains or sail across a sea just for the fun of it. PANIC is the aversive emotion infant mammals feel when separated from their mother. In humans, the general mammalian attachment of mothers to offspring has been extended to generate emotional attachments to other kin, friends, and even groups. Solitary confinement is a harsh punishment for humans because it deprives us of exercising these pleasure producing bonds. Panksepp's and colleagues core research involved mapping the circuits in the brain stem and adjacent regions that generate these emotions and their neuromodulator chemistry. This is done using common laboratory animals like rats, but the evidence suggests that these circuits are highly conserved in mammals. The mapping techniques are far too invasive to use on humans but the evidence is that the basic circuitry is the same in our species. For example, recreational drugs often light up one circuit and the ensuing behaviors in rats and humans are similar. For example, cocaine stimulates the SEEKING circuit in rats and produces behaviors in that species that are quite parallel to its effects on humans. The four emotions in red above are experienced as reinforcing and those in black as aversive. Together with the appetitive emotions like hunger and thirst, Panksepp's seven emotions are a low level neurological account of how associative learning works. Panksepp notes that projections from the emotion centers run into the cortex so pathways exist by which the emotions can act to shape circuits there. But the cortex receives projections from the cortex as well, so that learning and culture can modulate the emotions. For example, Nisbett and Cohen (1996) show how a culture of honor that is common in the American South upregulates cortisol (FEAR) and testosterone (RAGE) in Southern males.

William Baum

Baum's (2017) third edition of his book *Understanding Behaviorism: Behavior, Culture, and Evolution* reminds us that behaviorism never really died. A certain Cognitive Revolution triumphalism made it seem so in some quarters. Pinker (2002) wrote "strict behaviorism in pretty much dead in psychology" when in fact its American adherents alone hold annual meetings with thousands of participants. They are responsible for major advancements in the treatment of psychiatric illnesses like autism. I am known among Brazilian psychologists mainly because I've coauthored with Baum! Pinker (2002) also remarks "Behaviorists believed that behavior could be understood independently of the rest of biology, without special attention to the genetic makeup of the animal or the evolutionary history of the species." This is arrant nonsense! The very subtitle of Baum's book points to just such factors and the text enlarges on them. Obviously, what acts as reinforcement is specific to each species, at least in detail. Wolves would not be reinforced by being fed pond weeds and moose would not be reinforced by being fed wolf meat. Innatist cognitivists like Pinker completely ignore associative learning. Certainly that was to neglect an obviously important process in shaping behavior. What is more surprising to me is the extent to which cognitive neuroscientists have come full circle back to pretty strict (very strict in Heyes' case) behaviorism! It is not entirely clear to me just where the issue will settle in the end, but it seems like the innatist human nature picture of cognition is badly, if not completely, flawed. Genes are important in the sense that the conserved emotional and appetitive regions generate reinforcement that tends to keep culture adaptive even as processes like cultural group selection generate cooperation on a scale larger than can be explained by selection on genes (Richerson et al., 2016).

Behaviorists' skepticism about mentalistic explanations led them to consider explanations for behavior that outside the brain. As I have emphasized, associative learning adapts behavior to the environment by reinforcement and punishment. The rest of the body also plays a role. We have a hand well adapted to grasping things and our world is full of handles, many of them attached to artifacts but some of them attached to natural objects—a "handy" rock is a makeshift hammer. Behaviorists are interested in an integrated approach to behavior combining bodies, genes, culture, and individual learning into evolved whole organisms living in dynamic environments. Brains/minds are just one organ without which you are dead. It ought not to be fetishized any more than the liver. The cognitive neuroscientists I have reviewed speak to many of these themes as well.

Conclusions

The rigidity of the highly innatist accounts of the mind/brain given by the cognitive revolutionaries and by the human nature theorists cannot account for the complexity and diversity of human cultures. A good argument can be made that they can't do justice to the behavioral diversity of many species with appreciable capacities for learning, social learning, and other forms of adaptation via phenotypic flexibility (Levis & Pfennig, 2016).

As important as culture and other modes of phenotypic flexibility are, especially in our species, genes have an important role to play if we are to explain the general adaptiveness of behavior. The lesson from the cognitive neuroscience I have reviewed strongly suggests that the influence of genes is not mainly through direct construction of cortical circuits, but in their construction of the senses, post-cranial anatomy and physiology, and the ancient emotional and appetitive circuits in the brain. The role of genes in the development of cortical circuits is indirect, operating through general purpose mechanisms like associative learning. There may be some direct genetic role for core cognition elements like an early developing capacity of imitation. The cultural-evolutionary constraints imposed by the complexity and diversity of cultures and their adaptiveness cannot speak to such proximate details.

The cognitive neuroscience I have review suggests that the neocortical parts of the brain should be thought of as an organ much like the adaptive immune system. The massive size of the human neocortex reflects that complexity of our cultural adaptations, other species with large and medium sized brains, also seem to be using this organ as a means of phenotypic flexibility. It is interesting that over the last 65 million years, brain size has been increasing in many mammalian lineages (Jerison, 1973) while environmental variability has been increasing (Zachos, Shackleton, Revenaugh, Palike, & Flower, 2001). This is probably not an accident!

Genes and culture coevolve. Our large brain is costly, and only so long as the behavior generated by learning and culture could pay the large metabolic bill the brain generates could it go on expanding. Humans have used our free hands to build technology and our ability to craft and obey social rules to solve collective action problems. The size of our brain and the sophistication of our culture seem to parallel each other and the rising drumbeat of high frequency climate variation as the Pleistocene climate evolved (Richerson & Boyd, 2013). One unfortunate result of fetishizing the role of the brain in behavioral evolution has been a tendency to think that changes in the brain drove our evolution. From the whole-body-in-the-environment perspective, preadaptations like hands and advanced ape sociality, confronted with an increasingly variable environment, might have been the prime drivers of human evolution and large brains a consequence not a cause.

References

Anderson, M. L. (2014). *After Phrenology: Neural Reuse and the Interactive Brain*. Cambridge MA: MIT Press.

Baum, W. M. (2017). *Understanding Behaviorism: Behavior, Culture, and Evolution* (Third ed.). Malden, MA: John Wiley.

Boyd, R., & Richerson, P. J. (1985). *Culture and the Evolutionary Process*. Chicago: University of Chicago Press.

Boyd, R., Richerson, P. J., & Henrich, J. (2011). The cultural niche: Why social learning is essential for human adaptation. *Proceedings of the National Academy of Sciences, 108*(Supplement 2), 10918-10925. doi:10.1073/pnas.1100290108

Carey, S. (2009). *The Origin of Concepts*. New York: Oxford University Press.

Chomsky, N. (1959). A Review of Skinner's *Verbal Behavior*. *Language, 35*(1), 26-58.

Chomsky, N. (1995). *The Minimalist Program* (iv + 420 ed.). Cambridge MA: MIT Press.

Christiansen, M., & Chater, N. (2015). The language faculty that wasn't: a usage-based account of natural language recursion. *Frontiers in Psychology, 6*(1182). doi:10.3389/fpsyg.2015.01182

Csibra, G., & Gergely, G. (2011). Natural pedagogy as an evolutionary adaptation. *Philosophical Transactions of the Royal Society B, 366*, 1149-1157.

Currie, T. E., Turchin, P., Bednar, J., Richerson, P. J., Schwesinger, G., Steinmo, S., . . . Wallis, J. J. (2016). Evolution of institutions and organizations. In D. S. Wilson & A. Kirman (Eds.), *Complexity and Evolution: toward a New Synthesis for Economics* (Vol. Strungmann Reports, vol. 19, pp. 201-236). Cambridge MA: MIT Press.

Dehaene, S. (2009). *Reading in the Brain: The Science and Evolution of a Human Invention*. New York: Viking.

Edelman, G. M. (1987). *Neural Darwinism: The Theory of Neuronal Group Selection*. New York: Basic Books.

Flannery, K., & Marcus, J. (2012). *The Creation of Inequality: How Our Prehistoric Ancestors Set the Stage for Monarchy, Slavery, and Empire*. Cambridge, MA: Harvard University Press.

Frankenhuis, W. E., & Ploeger, A. (2007). Evolutionary Psychology versus Fodor: Arguments for and against the massive modularity hypothesis. *Philosophical Psychology, 20*(6), 687-710. doi:10.1080/09515080701665904

Hauser, M. D., Chomsky, N., & Fitch, W. T. (2002). The faculty of language: What is it, who has it, and how did it evolve? *Science, 298*(5598), 1569-1579.

Henrich, J. (2016). *The Secret of Our Success: How Culture Is Driving Human Evolution, Domesticating Our Species, and Making Us Smarter.* Princeton: Princeton University Press.

Heyes, C. (2018). *Cognitive Gadgets: The Cultural Evolution of Thinking*. Cambridge MA: Harvard University Press.

Immelmann, K. (1975). Ecological significance of imprinting and early learning. *Annual Review of Ecology and Systematics, 6*(1), 15-37.

Jerison, H. J. (1973). *Evolution of the Brain and Intelligence*. New York: Academic Press.

Johnson, A. W., & Earle, T. K. (2000). *The Evolution of Human Societies: From Foraging Group to Agrarian State* (2nd ed.). Stanford, Calif.: Stanford University Press.

Krubitzer, L., & Stolzenberg, D. S. (2014). The evolutionary masquerade: Genetic and epigenetic contributions to the neocortex. *Current Opinion in Neurobiology, 24*(0), 157-165. doi:http://dx.doi.org/10.1016/j.conb.2013.11.010

Laland, K. N. (2017). *Darwin's Unfinished Symphony: How Culture Made the Human Mind*. Princeton: Princeton University Press.

Lenski, G. E., & Lenski, J. (1982). *Human Societies: An Introduction to Macrosociology* (4th ed. Vol. McGraw-Hill). New York.

Levis, N. A., & Pfennig, D. W. (2016). Evaluating ‘plasticity-first’ evolution in nature: Key criteria and empirical approaches. *Trends in Ecology & Evolution, 31*(7), 563-574. doi:http://dx.doi.org/10.1016/j.tree.2016.03.012

Lumsden, C., & Wilson, E. O. (2006). *Genes, Mind, and Culture: The Coevolutionary Process. 25th Anniversary Edition*. New Jersey: World Scientific.

Marean, C. W. (2015). An evolutionary anthropological perspective on modern human origins. *Annual Review of Anthropology, 44*(1), 533-556. doi:10.1146/annurev-anthro-102313-025954

Moerk, E. L. (1983). *The Mother of Eve--As a First Language Teacher*. Norwood, NJ: Ablex.
Newmeyer, F. J. (2004). Against a parameter-setting approach to typological variation. *Linguistic Variation Yearbook, 4*(1), 181-234. doi:10.1075/livy.4.06new
Nisbett, R. E., & Cohen, D. (1996). *Culture of Honor: The Psychology of Violence in the South*. Boulder, CO: Westview Press.
Panksepp, J., & Biven, L. (2012). *The Archaeology of Mind: Neuroevolutionary Origins of Human Emotions* WW Norton & Company.
Paul, R. A. (2015). *Mixed messages: Cultural and genetic inheritance in the constitution of human society*: University of Chicago Press.
Perreault, C. (2012). The pace of cultural evolution. *PLoS ONE, 7*(9), e45150. doi:10.1371/journal.pone.0045150
Pinker, S. (1994). *The Language Instinct: How the Mind Creates Language* (1st ed.). New York: W. Morrow and Co.
Pinker, S. (2002). *The Blank Slate: The Modern Denial of Human Nature*: Allen Lane (Penguin) / Viking.
Reader, S. M., Hager, Y., & Laland Kevin, N. (2011). The evolution of primate general and cultural intelligence. *Philosophical Transactions of the Royal Society B: Biological Sciences, 366*(1567), 1017-1027. doi:10.1098/rstb.2010.0342
Richerson, P., Baldini, R., Bell, A., Demps, K., Frost, K., Hillis, V., . . . Zefferman, M. (2016). Cultural group selection plays an essential role in explaining human cooperation: A sketch of the evidence, together with commentaries and authors' response. *Behavioral and Brain Sciences, 39*(e 30), 1-68. doi:doi:10.1017/S0140525X1400106X
Richerson, P. J. (2018). The use and non-use of the human nature concept by evolutionary biologists. In E. Hannon & T. Lewens (Eds.), *Why We Disagree About Human Nature* (pp. 145-169).
Richerson, P. J., & Boyd, R. (2005). *Not By Genes Alone: How Culture Transformed Human Evolution*. Chicago: University of Chicago Press.
Richerson, P. J., & Boyd, R. (2013). Rethinking paleoanthropology: A world queerer than we supposed In G. Hatfield & H. Pittman (Eds.), *Evolution of Mind, Brain, and Culture* (pp. 263-302). Philadelphia: University of Pennsylvania Museum of Archaeology and Anthropology.
Ross, C. T., & Richerson, P. J. (2014). New frontiers in the study of cultural and genetic evolution. *Current Opinion in Genetics and Development, 29*, 103-109.
Steward, J. H. (1955). *Theory of Culture Change: the Methodology of Multilinear Evolution*. Urbana: University of Illinois Press.
Striedter, G. F. (2005). *Principles of Brain Evolution*. Sunderland MA: Sinauer.
Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005). Understanding and sharing intentions: the origins of cultural cognition. *Behavioral and Brain Sciences, 28*(5), 675-691. doi:10.1017/S0140525X05000129
Tooby, J., & Cosmides, L. (1992). The psychological foundations of culture. In J. Barkow, L. Cosmides, & J. Tooby (Eds.), *The Adapted Mind: Evolutionary Psychology and the Generation of Culture* (pp. 19-136). New York: Oxford University Press.
Toth, N., & Schick, K. (2009). The Oldowan: The tool making of early hominins and chimpanzees compared. *Annual Review of Anthropology, 38*(1), 289-305. doi:10.1146/annurev-anthro-091908-164521
Walker, R. S., Wichmann, S., Mailund, T., & Atkisson, C. J. (2012). Cultural phylogenetics of the Tupi language family in lowland South America. *PLoS ONE, 7*(4), e35025. doi:10.1371/journal.pone.0035025
Wilson, E. O. (1978). *On Human Nature*. Cambridge MA: Harvard University Press.

Zachos, J. C., Shackleton, N. J., Revenaugh, J. S., Palike, H., & Flower, B. P. (2001). Climate response to orbital forcing across the Oligocene-Miocene boundary. *Science, 292*(5515), 274-278. Retrieved from http://www.sciencemag.org/cgi/content/full/292/5515/274