*The Spanish Journal of Psychology* (2017), **19**, e101, 1–7.
© Universidad Complutense de Madrid and Colegio Oficial de Psicólogos de Madrid
doi:10.1017/sjp.2016.102

CAMBRIDGE UNIVERSITY PRESS

# Cognition and Culture in Evolutionary Context

**Fernando Colmenares and María Victoria Hernández-Lloreda**

*Universidad Complutense (Spain)*

**Abstract.** In humans and other animals, the individuals' ability to adapt efficiently and effectively to the niches they have actively contributed to construct relies heavily on an evolved psychology which has been shaped by biological, social, and cultural processes over evolutionary time. As expected, although many of the behavioral and cognitive components of this evolved psychology are widely shared across species, many others are species-unique. Although many animal species are known to acquire group-specific traditions (or cultures) via social learning, human culture is unique in terms of its contents and characteristics (observable and unobservable products, cumulative effects, norm conformity, and norm enforcement) and of its cognitive underpinnings (imitation, instructed teaching, and language). Here we provide a brief overview of some of the issues that are currently tackled in the field. We also highlight some of the strengths of a biological, comparative, non-anthropocentric and evolutionarily grounded approach to the study of culture. The main contributions of this approach to the science of culture are its emphasis (a) on the integration of information on mechanisms, function, and evolution, and on mechanistic factors located at different levels of the biological hierarchy, and (b) on the search for general principles that account for commonalities and differences between species, both in the cultural products and in the processes of innovation, dissemination, and accumulation involved that operate during developmental and evolutionary timespans.

*Received 15 September 2016; Revised 9 November 2016; Accepted 11 November 2016*

**Keywords:** cognition, comparative approach, culture, evolutionary context, social learning.

This paper is meant to provide a short overview of some of the hot issues that are currently addressed in disciplines keen on searching for and identifying overarching explanatory principles that account for commonalities and differences across species in traditions or cultures and, more specifically, in its underlying behavioral and cognitive processes. Some of the topics briefly outlined here were actually reviewed in the lectures delivered by the invited speakers during the *Advanced International Seminar on Cognition and Culture and Evolutionary Context*, held in the Facultad de Psicología, Universidad Complutense de Madrid, 19–20 of October 2015. The speakers contributed papers (Boyd, Laland, van Schaik, & Whiten) or an arranged interview (Tomasello) that provide updated summaries of their main theoretical stances and supporting empirical evidence as leading experts in this subject. They are published in this issue.

## *What is this thing called culture?*

Would someone have trouble defining human culture? Hardly. Culture is all around us (for the example, the myriad artifacts and norms of the cultural niche we have constructed), over us (for example, the clothes and ornaments we wear), and inside us (for example, the friendly microbiota we host in our gut). We experience culture day and night, sometimes for good, sometimes for bad. Even laypeople would readily claim that culture is about the way we do things (for example, the way we dress, dance, play music, make films, write literary work, build houses, bridges and skyscrapers, drive, and cook our food), the way we behave in a huge variety of contexts (for example, at home, at school, at work, during rituals of birth, puberty, marriage, divorce, and death), and the way we run the multiple embedded layers of the societies we live in (for example, the family, the neighborhood, the city, the state, the UN). So, key components of culture include language, science, religion, politics, technology, and social institutions. In short, culture encompasses both observable artifacts and behaviors, as well as abstract symbols, values, beliefs and (civic and legal) norms.

Not surprisingly, the study of culture is the subject matter of a good number of scientific disciplines that fall within most of the major science divisions, including humanities, social sciences, health sciences and natural sciences. Of course, in each of these major fields and in its constituent specialized disciplines culture is defined differently as working definitions are typically tailored to the objectives and methods of the practicing scholars working in each particular specialty. Some of the disciplines that have traditionally tackled the study of

Correspondence concerning this article should be addressed to Fernando Colmenares. Facultad de Psicología. Universidad Complutense. Campus de Somosaguas. 28223. Pozuelo de Alarcón, Madrid (Spain). Phone +34–913943070.

E-mail: colmenares@psi.ucm.es

During writing, the authors' work was supported by project grant PSI2014–51890-C2–1-P from the Ministerio de Economía y Competitividad (MINECO), Spain (to FC).

https://doi.org/10.1017/sjp.2016.102 Published online by Cambridge University Press

culture and that are of particular interest in the present, inevitably more focused context, are behavioral biology (ethology), evolutionary anthropology, comparative psychology, developmental psychology, and evolutionary psychology. Even though their interests can and do at times overlap, and the boundaries between these disciplines are often fuzzy, however, as already advanced, they often address different issues, adopt different research strategies and, importantly, spell out different definitions of culture (Boyd & Richerson, 2005; Danchin & Wagner, 2008; Dugatkin, 2009; Dunbar & Barrett, 2007; Mesoudi, 2011; Richerson & Boyd, 2005; Tomasello, 2011; 2016a; van Schaik, 2016; Whiten, Hinde, Laland, & Stringer, 2011).

There are two core features of culture that can be laid down and that are largely uncontroversial and universal. First, its *group-linked specificity*, that is to say, wherever cultural processes are at work, groups will tend to develop their own idiosyncratic signatures which will, ultimately, lead to stronger both *within-group* cultural *identity* and *between-group* cultural *differences* over both developmental (i.e., within-generation) and evolutionary (i.e., across generations) timespans. This can then be seen as a functional and inevitable consequence of culture, one that is certainly likely to be adaptive (i.e., enhancing the individuals' biological fitness), even if it paves the way for the emergence of strong in-group versus out-group biases in overt behavior and its underlying psychological processes (for example, emotions, attitudes, and moral evaluations). Second, culture relies critically on a mode of *information transmission* that is *non-genetic,* involving both kin and non-kin, within the same and across generations. And this non-genetic mode of inheritance is social learning, that is, learning from conspecifics. This mode of acquiring information can potentially have extremely potent and lasting effects on behavioral variation within and across populations. Through social learning, individuals can acquire adaptive skills and knowledge far more quickly and efficiently than if they had to learn them individually, via trial-and-error. Such social learning is then a powerful device that narrows down within-group variation, and widens between-group differences. A further key consequence of culture is that it can drive gene evolution; thus, by regulating gene flow, culture can impact a population's genetic structure, and can drive speciation (Fisher & Ridley, 2013; Laland, Odling-Smee, & Myles, 2010; Richerson, Boyd, & Henrich, 2010; Whitehead & Rendell, 2015). As a matter of fact, it is widely agreed that much human behaviour has been driven by a process of gene-culture coevolution (Boyd & Richerson, 2005; Richerson & Boyd, 2005).

Now, if researchers from these different fields appear to basically agree upon these two core features of culture, then what's the fuss about? The fuss is about the kind of social learning processes that drive and sustain culture, especially when cross-species comparisons are undertaken (Galeff & Laland, 2009; Laland & Janik, 2006), and, in the case of human culture, about the nature of the transmission mechanism that ensures the fidelity and diffusion of cultural traits. The latter will not be pursued any further here (see, however, Acerbi & Mesoudi, 2015 for a recent review). Thus, what matters and makes a difference is not so much the biologically relevant functional consequences of learning the information socially, as the actual cognitive scaffold that underpins the emergence, the diffusion and the stability of cultural behavior and its variants. Even though uniqueness is not at all a unique characteristic of human evolution relative to the evolution of the other animals, the achievements of human culture are unparalleled in the animal kingdom, especially its cumulative nature over time (Dean, Vale, Laland, Flynn, & Kendal, 2014; Tomasello, 1994; 2011; 2015). This distinctive *cultural grade* attained only by humans suggests that perhaps it evolved in response to a largely unique combination of environmental pressures, including ecological and social, and of available raw material (enlarged brain size and advanced cognition). In fact, once the process got started, these various components were most probably engaged in a co-evolutionary process in which the brain, the social learning and other cognitive skills, the culture and the sociality and prosociality they produced were fitness-enhancing and exerted a positive feedback on one another. Before we come to grips with this, though, we shall briefly argue why the study of culture is relevant to psychology and why its framing in an evolutionary context can add much light on the phylogenetical and socio-ecological factors that shape culture and its commonalities and differences across species. Finally, as we will see, culture and its cognitive drivers develop and evolve in a socio-ecological niche that has selected for a suite of correlated traits, including sociality, cooperation, encephalization, and enlargement of neocortex.

### *Culture and psychology*

The mutualistic relation existing between the various psychological disciplines and the science of culture is ancient and beyond doubt as testified by the many reviews where its status has been assessed (Han et al., 2013; Heine & Buchtel, 2009; Kim & Sasaki, 2014; Kitayama & Uskul, 2011; Lehman, Chiu, & Schaller, 2007). Recently, *Current Opinion in Psychology* published a themed issue entitled Culture: Advances in the Science of Culture and Psychology. In the overview provided by their editors (Gelfand & Kashima, 2016), they noted how essential is culture to human psychology

https://doi.org/10.1017/sjp.2016.102 Published online by Cambridge University Press

and went on to highlight some key issues reviewed by the contributors that cover such topics as, for example, culture and the brain, culture and genetics, cultural diffusion in animals and humans, cultural learning, culture and attachment, culture and motivation, culture and emotion, culture and cognition, culture and personality, culture, norms, and morality, culture, mental health, and wellbeing, culture and psychopathology, culture-gene coevolution, culture and language evolution, and niche construction in human culture. Paraphrasing the words of one of the architects of the Modern Synthesis of post-Darwinian evolutionary theory, Theodosius Dobzhansky, who stated "nothing in biology makes sense except in the light of evolution (Dobzhansky, 1964, p. 449), some culture researchers have claimed that "nothing in human behavior makes sense except in the light of culture" (Morgan, Cross, & Rendell, 2015, p. 215).

There are at least three major areas in which researchers in this interdisciplinary field can engage to produce fertile work of interest to psychologists of various persuasions. First, given the reliance of culture on variously complex cognitive processes, continuing work aimed to scrutinize the nature of such processes is warranted. More specifically, we need much more experimental research on the precise social learning mechanisms that are required for deploying different forms of culture. In this context, more studies of the processes of innovation (asocial learning), faithful dissemination (social learning), and accumulation (ratcheting effect) that drive group-specific cultures are highly needed. Second, we should continue research aimed to assess how the cultural niche that individuals actively construct impacts their own wellbeing and biological fitness. This work would contribute to elucidate the role of culture as producer, not simply product, of cognitive and social skills that enhance the individuals' welfare and fitness. In this regard, much work still remains to be done on the effect of optimal (or suboptimal) cultural niches on the psychological and biological functioning of individuals. Lastly, a broad cross-species comparative analysis of culture, its psychological foundations, and the processes that preserve, accumulate and innovate cultural traits, on the one hand, and of the psychological and biological consequences of culture, on the other hand, would further our understanding of the evolutionary tree of commonalities and differences across species in culture-cognition relations and of the niches (ecological, social, cognitive, and cultural) that have contributed to shape them.

## *Culture in evolutionary context*

Although ethologists and comparative psychologists have long been interested in the study of the *four whys* of behavior and mental processes (Shettleworth, 2010), including, of course, both proximate as well as evolutionary (ultimate) causes, it has been only recently that evolutionary theory has made its way into the territory of psychological disciplines (and other health sciences) that have traditionally been concerned only with the study of the proximate factors driving normal and impaired human behavior and psychological function (Brüne, 2008; Nesse et al., 2010). In contrast to the anthropocentric flavor of these traditional psychological disciplines and their lack of interest in the study of ultimate causes, an integrative biological approach to the study of culture aims to cross and re-cross levels of biological organization (for example, genome, brain, behavior, and cognition), to integrate information from all four whys, and to identify explanatory principles that, based on history (evolutionary and individual) and ecology (physical and social), account for commonalities and differences between the cultural achievements deployed by different species. This truly biological approach relies heavily on the comparative method; and the processes themselves (cultural traits, social learning mechanisms) rather than any particular (privileged) species turn out to be the primary focus of interest. However, as expected, there are different ways in which evolutionary theory can inform research on culture and cognition. Here we will briefly comment on three problems that can arise in the comparative study of culture in humans and nonhumans (the other animals). (Actually, these problems are commonplace in animal-human comparisons of behavior and cognition in general).

One classic in the comparative study of culture is the question of animal culture: Do animals have culture? The answer has generated heated and recurrent debates, but the issue is still far from settled (Galeff & Laland, 2009; Laland & Janik, 2006). In practice, the answer depends on how we define culture. On the one hand, if we define it in terms of cultural characteristics (for example, the ratchet effect), high-level cognitive processes (for example, imitation and intentional teaching), and advanced behavioral mechanisms (for example, cooperation and norm enforcement) that are known to be largely unique to humans, then there is little possibility of exploiting the many potential insights that can be gained from animal-human comparisons. On the other hand, however, relaxing too much the criteria to calling something culture can also blind or at least distort our view of cultural phenomena that may well be species-unique. All of this has to do with the way we envisage evolution. If we all endorse the Darwinian (and contemporarily dominant) view of evolution as a tree, rather than a ladder, then we should be as comfortable (and unsurprised) with finding evolutionarily unique innovations (discontinuities) as with

https://doi.org/10.1017/sjp.2016.102 Published online by Cambridge University Press

encountering similar traits that still can be due to shared ancestry (homologies) or shared ecology (homoplasies). Most culture researchers acknowledge the uniqueness of human culture, but many still appear to be reluctant to accept some of its implications, for example, that it may be discontinuous with nonhuman culture, as if doing so were unevolutionary.

Comparative studies of culture (and other behavioral and cognitive processes) make researchers particularly prone to be haunted by two ghosts: the ghost of the evolutionary ladder and the ghost of the recapitulation principle. The evolutionary ladder, a descendant from the concepts of *Scala Naturae* (or *natural* ladder) and the Great Chain of Being, sees evolution as progressive. Although this model of upward evolution has long been rejected, the idea is so appealing and intuitive that even highly experienced and sophisticated evolutionary biologists may fall into the trap (Rigato & Minelli, 2013). Some culture researchers claim that animals, particularly those most closely related to humans, might possess a version of culture which is continuous, albeit less advanced, with human culture. In this context, the temptation to see human culture as just a scaled-up version of animal culture is strong, as is the temptation to "ladderize" the cultural characteristics of different animals (for example, traditions versus cultures) and enlarge the elite club of privileged species, located at the apex of the evolutionary ladder, made up of humans and animals that arguably most closely resemble humans (e.g., chimpanzees). A version of the recapitulation principle would claim that adult stages can be seen as scaled-up versions of juvenile stages and the latter can be seen as resembling the adult stages of ancestral species that are believed to have departed less from their common ancestor (e.g., human infants versus adult chimpanzees). The implications of this view of evolution and development are far reaching and need to be scrutinized more closely.

*Social learning as the scaffolding of culture*

Although the ladder view of evolution encourages scientists to regard human culture (and many other traits) as simply more complex (higher in the ladder) than chimpanzee culture, or the latter as more complex than, say, capuchin culture (traditions), a genuinely tree thinker might also contend that the unquestionably profound differences existing between the cultures of humans and chimpanzees perhaps reflect the operation of equally deep differences in the cognitive scaffolds that sustain them. And this would not necessarily challenge orthodox evolutionary theory. It is true that any evolutionary (or developmental) species-unique innovation will always be built to some extent upon building blocks already available in the ancestral precursors, however, it is equally true that the history of life is replete with examples of life forms that have evolved revolutionarily novel functions that cannot be detected in a rudimentary or incipient way in their ancestors, especially if they are distant. Sometimes these new, discontinuous functions evolve (or develop) when separate precursor ingredients are assembled in an innovative way.

Social learning is the key non-genetic information transmission mechanism involved in any form of culture; however, there are very many different ways in which individuals can acquire not-yet-known information from others (Heyes, 1994; Hopper, 2010). And this is crucially important in order to assess the extent that different species deploy similar or unique cultures and, if they are found to be different, the extent that such differences are of degree or in kind. Some forms of social learning are cognitively more demanding and many culture researchers posit that imitation and, especially, intentional teaching are largely uniquely human (Fogarty, Strimling, & Laland, 2011; Tomasello, 2016b). A number of studies have reported that when exposed to an imitation task, children are more concerned than are other great apes to copy the demonstrator's actions. Unless they are enculturated, chimpanzees are more likely to engage in emulation learning in that their efforts are more organized towards matching the outcome or result attained by the demonstrator, but not her actions. In fact, this species-unique tendency to exhibit imitative learning is remarkable as children have been found to even copy irrelevant or arbitrary (nonfunctional) actions, a tendency that is exacerbated when the goal of the demonstrator's action is unclear.

If teaching is simply defined as a form of social learning whereby an individual (i.e., the tutor) modifies its behavior in a way that results in a naïve individual (i.e., the pupil) learning a new skill more quickly or more efficiently (Thornton & Raihani, 2010), and attention is only paid to the functional consequences in terms of immediate benefits obtained only by the pupil and immediate costs incurred only by the tutor, then a number of animal species, including humans, are considered to exhibit teaching (Hoppitt et al., 2008; Thornton & Raihani, 2010). However, teaching in humans is unique (Tomasello, 2011; 2016b), even among the great apes, in that human tutors intentionally and pedagogically instruct their pupils not only about observable facts (the earth is rounded), but also about abstract concepts and theoretical principles (why the earth and many other entities of its kind are expected to also be rounded). Thus, different species can share superficially analogous teaching behaviors that enhance their fitness; however, these behaviors can be based on very different cognitive processes that would be a shame not to charter carefully.

https://doi.org/10.1017/sjp.2016.102 Published online by Cambridge University Press

*Culture, norm conformity and norm enforcement*

Human culture also stands out for two other largely distinctively or even uniquely evolved features: *norm conformity* and *norm enforcement* (Tomasello, 2016b). Humans tend to be strong conformists, that is, individuals are highly inclined to conform to the behavior that is most common in a group (group normativity) (Claidière & Whiten, 2012; Morgan & Laland, 2012). This has important theoretical and applied implications that deserve to be analyzed in depth. Norm conformity contributes to strengthen in-group cultural homogeneity and to stabilize it over time and, at the same time, it exacerbates between-group cultural differences. This scenario can be rather frightening, for example, if the group's norm favors high levels of both in-group and out-group antisocial behavior. The evolutionary approach to the study of norm conformity in humans has started to chart the conditions under which different levels of conformity are more likely to be favored (see Claidiere & Whiten, 2012, for a recent review). Also, experimental studies of cultural norms of tool use in chimpanzees have provided evidence of conformity bias in this species, although this bias was found only in a subset of individuals (Whiten, Horner, & de Waal, 2005; see also van Schaik, 2012).

The reliance of human culture on cooperation is another of its standout features (Boyd & Richerson, 2009; Tomasello, 2011). It is not only that the large-scale cooperation of humans is unprecedented in the animal kingdom, it is that even from an early age on humans actively engage in norm enforcement, also called third-party punishment, directed against individuals who deviate from the norm (Tomasello, 2016b). Thus, humans are not only positively prosocial towards others, but they also punish norm transgressors (negative prosociality) (Boyd, Gintis, & Bowles, 2010). Interestingly, and rather paradoxically, third-party punishment enforces group normativity by discouraging the behavior of two classes of deviants, defectors and above-the-average (hyper)cooperators (Hermann, Thöni, & Gächter, 2008).

*Innovation, dissemination, and stability*

A hallmark feature of human culture is that it is cumulative (Dean et al., 2014; Tomasello, 2011); although some researchers have claimed, on the basis of experimental work, that other species might also be able to accumulate information, albeit in a much more rudimentary way (Davis, Vale, Schapiro, Lambeth, & Whiten, 2016). For culture to accumulate over time, groups need a mix of innovators (responsible for increasing the group's repertoire of cultural behaviors) and conformists (responsible for keeping and spreading the behaviors that are already in place). In recent years this field of study has flourished and made important contributions, as several workers have sharpened the theoretical framework, have designed various experimental paradigms (for example, diffusion chains, open diffusion, and replacement designs), have carried experiments in captivity, in more naturalistic contexts, and even in the wild, and have adopted an explicitly comparative and evolutionary approach (see Whiten, Caldwell, & Mesoudi, 2016 for a recent review).

Some researchers have also articulated theoretical frameworks aimed to understand the evolution of the many processes that make the melting pot of culture and that can generate positive feedback loops between them. These include brain evolution (amount of neural tissue available to support variously cognitively demanding skills), life history (tradeoffs of various kinds, for example, growth versus reproduction), innovativeness (asocial or individual learning), intelligence (problem-solving ability), different forms of social learning (imitation, emulation, teaching), and behavioral disposition (social tolerance), among others. One virtue of these models is that they take into account what is known about the biological context and natural history of the species compared and use it to devise nuanced empirical tests that allow identify the ecological, social or cultural conditions under which natural selection can favor similar or alternative (sometimes condition-dependent) adaptive strategies. It has been found, for example, that brain size, asocial learning skills, intelligence, and social learning capacities are correlated (Reader & Laland, 2002; Reader, Hager, & Laland, 2011). This lends support to a central prediction of the cultural intelligence hypothesis that posits that sociality does increase the opportunity for acquiring information via social learning and this also selects for increased asocial learning skills (van Schaik & Burkart, 2011; van Schaik, 2016; Whiten & van Schaik, 2007).

## Concluding Comment

The science of culture is a burgeoning interdisciplinary field. Here we have highlighted some of the strengths of a biological, comparative, non-anthropocentric and evolutionarily grounded approach to the study of culture. This integrated approach has stimulated a wealth of theoretical and empirical studies that have already produced a rich body of knowledge on the evolved psychology that underpins human and animal cultures. We have also emphasized that evolutionary studies should be prepared to come across (and look for) continuities and discontinuities in the processes that make culture possible in the first place, in the cultural variants that emerge in different biological and ecological contexts, and in the feedback loops that arise between

https://doi.org/10.1017/sjp.2016.102 Published online by Cambridge University Press

the various processes and outcomes, both during development and evolution. There is no doubt that the human niche is strongly cognitive, social, and cultural (Boyd, Richerson, & Henrich, 2011; Tomasello, 2011, 2015; Whiten & Erdal, 2012). Getting to know the way in which an individual's shapes its cultural niche and the way in which the cultural niche's echo fashions the individual's psychology, its wellbeing, and its biological fitness is of the greatest relevance. The road ahead is full of intriguing questions, testable hypotheses, and ingenious experimental protocols… and waiting to be walked. The subject is intellectually appealing and worth pursuing.

## References


**Acerbi A., & Mesoudi A**. (2015). If we are all cultural Darwinians what's the fuss about? Clarifying recent disagreements in the field of cultural evolution, *Biology & Philosophy*, *30*, 481–503. https://doi.org/10.1007/s10539-015-9490-2

**Boyd R., & Richerson P. J**. (2005). *The origin and evolution of cultures*. Oxford, UK: Oxford University Press.

**Boyd R., & Richerson P. J**. (2009). Culture and the evolution of human cooperation. *Philosophical Transactions of the Royal Society of London B*, *364*, 3281–3288. https://doi.org/10.1098/rstb.2009.0134

**Boyd R., Gintis H., & Bowles S**. (2010). Coordinated punishment of defectors sustains cooperation and can proliferate when rare. *Science*, *328*, 617–620. https://doi.org/10.1126/science.1183665

**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*, 10918–10925. https://doi.org/10.1073/pnas.1100290108

**Brüne M**. (2008). *Textbook of evolutionary psychiatry: The origins of psychopathology*. Oxford, UK: Oxford University Press.

**Claidière N., & Whiten A**. (2012). Integrating the study of conformity and culture in humans and nonhuman animals. *Psychological Bulletin*, *138*, 126–145. https://doi.org/10.1037/a0025868

**Danchin É., & Wagner R**. (2008). Cultural evolution. In É. Danchin, L.-A. Giraldeau, & F. Cézidy (Eds.), *Behavioural ecology* (pp. 693–725). Oxford, UK: Oxford University Press.

**Davis S. J., Vale G. L., Schapiro S. J., Lambeth S. P., & Whiten A**. (2016). Foundations of cumulative culture in apes: Improved foraging efficiency through relinquishing and combining witnessed behaviours in chimpanzees (*Pan troglodytes*). *Scientific Reports*, *6*, 35953. https://doi.org/10.1038/srep35953

**Dean L. G., Vale G. L., Laland K. N., Flynn E., & Kendal R. L**. (2014). Human cumulative culture: A comparative perspective. *Biological Reviews*, *89*, 284–301. https://doi.org/10.1111/brv.12053

**Dobzhansky T**. (1964). Biology, molecular and organismic. *American Zoologist*, *4*, 443–452. https://doi.org/10.1093/icb/4.4.443

**Dugatkin L. A**. (2009). *Principles of animal behavior* (2nd Ed.). New York, NY: Norton.

**Dunbar R. I. M., & Barrett L**. (Eds.). (2007). *The Oxford handbook of evolutionary psychology*. Oxford, UK: Oxford University Press.

**Fisher S. E., & Riddley M**. (2013). Culture, genes, and the human revolution. *Science*, *340*, 929–930. https://doi.org/10.1126/science.1236171

**Fogarty L., Strimling P., & Laland K. N**. (2011). The evolution of teaching. *Evolution*, *65*, 2760–2770. https://doi.org/10.1111/j.1558-5646.2011.01370.x

**Galef B. G., & Laland K. N**. (Eds.). (2009). *The question of animal culture*. Cambridge, MA: Harvard University Press.

**Gelfand M. J., & Kashima Y.** (2016). Editorial overview: Culture: Advances in the science of culture and psychology. *Current Opinion in Psychology*, *8*, iv-x. https://doi.org/10.1016/j.copsyc.2015.12.011

**Han S., Northoff G., Vogeley K., Wexler B. E., Kitayama S., & Varnum M. E. W**. (2013). A cultural neuroscience approach to the biosocial nature of the human brain. *Annual Review of Psychology*, *64*, 335–359. https://doi.org/10.1146/annurev-psych-071112-054629

**Heine S. J., & Buchtel E. E**. (2009). Personality: The universal and the culturally specific. *Annual Review of Psychology*, *60*, 369–394. https://doi.org/10.1146/annurev.psych.60.110707.163655

**Herrmann B., Thöni C., & Gächter S**. (2008). Antisocial punishment across societies. *Science*, *319*, 1362–1367. https://doi.org/10.1126/science.1153808

**Heyes C. M**. (1994). Social learning in animals: Categories and mechanisms. *Biological Review*, *69*, 207–231. https://doi.org/10.1111/j.1469-185X.1994.tb01506.x

**Hopper L. M**. (2010). 'Ghost' experiments and the dissection of social learning in humans and animals. *Biological Reviews*, *85*, 685–701. https://doi.org/10.1111/j.1469-185X.2010.00120.x

**Hoppitt W. J. E., Brown G. R., Kendal R., Rendell L., Thornton A., Webster M. M., & Laland K. N**. (2008). Lessons from animal teaching. *Trends in Ecology and Evolution*, *23*, 486–493. https://doi.org/10.1016/j.tree.2008.05.008

**Kim H. S., & Sasaki J. Y**. (2014). Cultural neuroscience: Biology of the mind in cultural contexts. *Annual Review of Psychology*, *65*, 487–514. https://doi.org/10.1146/annurev-psych-010213-115040

**Kitayama S., & Uskul A. K**. (2011). Culture, mind, and the brain: Current evidence and future directions. *Annual Review of Psychology*, *62*, 419–449. https://doi.org/10.1146/annurev-psych-120709-145357

**Laland K. N., & Janik V. M**. (2006). The animal cultures debate. *Trends in Ecology & Evolution*, *21*, 542–547. https://doi.org/10.1016/j.tree.2006.06.005

**Laland K. N., Odling-Smee J., & Myles S**. (2010). How culture shaped the human genome: Bringing genetics and the human sciences together. *Nature Reviews Genetics*, *11*, 137–148.

**Lehman D. R., Chiu C., & Schaller M**. (2004). Psychology and culture. *Annual Review of Psychology*, *55*, 689–714. https://doi.org/10.1146/annurev.psych.55.090902.141927

**Mesoudi A**. (2011). *Cultural evolution: How Darwinian Theory can explain human culture and synthesize the social sciences*. Chicago, IL: University of Chicago Press.


https://doi.org/10.1017/sjp.2016.102 Published online by Cambridge University Press

**Morgan T. J. H., & Laland K. N**. (2012). The biological basis of conformity. *Frontiers in Neuroscience*, *6*, 87. https://doi.org/10.3389/fnins.2012.00087

**Morgan T. J. H., Cross C. P., & Rendell L. E**. (2015). Nothing in human behavior makes sense except in the light of culture: Shared interests of social psychology and cultural evolution. In V. Zeigler-Hill, L. L. M. Welling, & T. K. Shackelford (Eds.), *Evolutionary perspectives on social psychology, evolutionary psychology* (pp. 215–228). New York, NY: Springer International Publishing. https://doi.org/10.1007/978-3-319-12697-5_17

**Nesse R. M., Bergstrom C. T., Ellison P. T., Flier J. S., Gluckman P., Govindaraju D. R., … Valle D**. (2010). Making evolutionary biology a basic science for medicine. *Proceedings of the National Academy of Sciences*, *107*, 1800–1807. https://doi.org/10.1073/pnas.0906224106

**Reader S. M., & Laland K. N**. (2002). Social intelligence, innovation, and enhanced brain size in primates. *Proceedings of the National Academy of Sciences*, *99*, 4436–4441. https://doi.org/10.1073/pnas.062041299

**Reader S. M., Hager Y., & Laland K. N**. (2011). The evolution of primate general and cultural intelligence. *Philosophical Transactions of the Royal Society of London B*, *366*, 1017–1027. https://doi.org/10.1098/rstb.2010.0342

**Richerson P. J., & Boyd R**. (2005). *Not by genes alone: How culture transformed human evolution*. Chicago, IL: University of Chicago Press.

**Richerson P. J., Boyd R., & Henrich J**. (2010). Gene-culture coevolution in the age of genomics. *Proceedings of the National Academy*, *107*, 8985–8992. https://doi.org/10.1073/pnas.0914631107

**Rigato E., & Minelli A**. (2013). The great chain of being is still here. *Evolution: Education and Outreach*, *6*, 18. https://doi.org/10.1186/1936-6434-6-18

**Shettleworth S. J**. (2010). *Cognition, evolution, and behavior*. Oxford, UK: Oxford University Press.

**Thornton A., & Raihani N. J**. (2010). Identifying teaching in wild animals. *Learning & Behavior*, *38*, 297–309. https://doi.org/10.3758/LB.38.3.297

**Tomasello M**. (1994). The question of chimpanzee culture. In R. W. Wrangham, W. C. McGrew, F. B. M. de Waal, & P. G. Heltne (Eds.), *Chimpanzee cultures* (pp. 301–377). Cambridge, MA: Harvard University Press.

**Tomasello M**. (2011). Human culture in evolutionary perspective. In M. Gelfand (Ed.), *Advances in culture and psychology* (pp. 1–34). Oxford, UK: Oxford University Press.

**Tomasello M**. (2015). *A natural history of human thinking*. Cambridge, MA: Harvard University Press.

**Tomasello M**. (2016a). *A natural history of human morality*. Cambridge, MA: Harvard University Press.

**Tomasello M**. (2016b). The ontogeny of cultural learning. *Current Opinion in Psychology*, *8*, 1–4. https://doi.org/10.1016/j.copsyc.2015.09.008

**Van Schaik C. P**. (2012). Animal culture: Chimpanzee conformity? *Current Biology*, *22*, R402–R404. https://doi.org/10.1016/j.cub.2012.04.001

**Van Schaik C. P**. (2016). *The primate origins of human nature*. New Jersey, NJ: Wiley.

**Van Schaik C. P., & Burkart J. M**. (2011). Social learning and evolution: The cultural intelligence hypothesis. *Philosophical Transactions of the Royal Society of London B*, *366*, 1088–1016. https://doi.org/10.1098/rstb.2010.0304

**Whitehead H., & Rendell L**. (2015). *The cultural lives of whales and dolphins*. Chicago, IL: University of Chicago Press.

**Whiten A., & Erdal D**. (2012). The human socio-cognitive niche and its evolutionary origins. *Philosophical Transactions of the Royal Society of London B*, *367*, 2119–2129. https://doi.org/10.1098/rstb.2012.0114

**Whiten A., & van Schaik C. P**. (2007). The evolution of animal 'cultures' and social intelligence. *Philosophical Transactions of the Royal Society of London B*, *362*, 603–620. https://doi.org/10.1098/rstb.2006.1998

**Whiten A., Caldwell C. A., & Mesoudi A**. (2016). Cultural diffusion in humans and other animals. *Current Opinion in Psychology*, *8*, 15–21. https://doi.org/10.1016/j.copsyc.2015.09.002

**Whiten A., Horner V., & de Waal F. B. M**. (2005). Conformity to cultural norms of tool use in chimpanzees. *Nature*, *437*, 737–740. https://doi.org/10.1038/nature04047

**Whiten A., Hinde R. A., Laland K. N., & Stringer C. B**. (2011). Culture evolves. *Philosophical Transactions of the Royal Society of London*, *366*, 938–948. https://doi.org/10.1098/rstb.2010.0372

https://doi.org/10.1017/sjp.2016.102 Published online by Cambridge University Press