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Social Learning and Culture in Child and Chimpanzee

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Annu. Rev. Psychol. 2017. 68:129–54

The *Annual Review of Psychology* is online at
psych.annualreviews.org

This article's doi:
[10.1146/annurev-psych-010416-044108](https://doi.org/10.1146/annurev-psych-010416-044108)

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Keywords

culture, tradition, social learning, imitation, chimpanzees, primates

Abstract

A few decades ago, we knew next to nothing about the behavior of our closest animal relative, the chimpanzee, but long-term field studies have since revealed an undreamed-of richness in the diversity of their cultural traditions across Africa. These discoveries have been complemented by a substantial suite of experimental studies, now bridging to the wild through field experiments. These field and experimental studies, particularly those in which direct chimpanzee–child comparisons have been made, delineate a growing set of commonalities between the phenomena of social learning and culture in the lives of chimpanzees and humans. These commonalities in social learning inform our understanding of the evolutionary roots of the cultural propensities the species share. At the same time, such comparisons throw into clearer relief the unique features of the distinctive human capacity for cumulative cultural evolution, and new research has begun to probe the key psychological attributes that may explain it.

Contents

INTRODUCTION	130
COMPLEMENTARY METHODOLOGICAL APPROACHES TO PRIMATE AND HUMAN CULTURE AND SOCIAL LEARNING	131
A FRAMEWORK FOR COMPARING CULTURE AND CULTURAL COGNITION ACROSS SPECIES	132
THE PATTERNING OF TRADITIONS IN TIME AND SPACE	134
Multiple and Diverse Traditions	134
Local Cultures Defined by Distinctive Arrays of Traditions	135
Linkage of Traditions Through Core Cultural Ideas	136
Cumulative Culture	136
SOCIAL LEARNING PROCESSES	137
Fidelity in Transmission: Cultural Diffusion Studies	138
Fidelity in Transmission: Imitation and Emulation	141
Overimitation	142
Selective and Rational Social Learning	143
Conformity	144
Cultural Ratcheting and Conservatism	145
Reflexive Recognition of Transmission Processes	146
Teaching	147
CULTURAL CONTENTS	147
CONCLUDING DISCUSSION	148

INTRODUCTION

Social learning is learning from others, as opposed to learning through one's own efforts, which is variously described as individual, personal, or asocial learning. Social learning can in turn give rise to traditions, or cultures, in which what is learned from others spreads to create enduring features of groups or populations. These cultures may be further transmitted from generation to generation.

The human propensity for social learning and culture pervades our lives. An enormous amount of the information encoded in our brains is assimilated from the culture in which we develop, ranging from our language to our social customs, technology, and other forms of material culture. Our species has developed a distinctive capacity for cumulative culture, such that over the generations, repeated cycles of innovation were incorporated into cultures that became progressively more sophisticated, underpinning the enormous evolutionary success of our species (Henrich 2015, Pagel 2012, Whiten et al. 2011). The achievements of our cumulative cultures have allowed human communities to spread across all major land masses around the world, whereas our nearest primate relatives, chimpanzees, have become restricted to pockets of their tropical forest niche in Africa.

Nevertheless, the remarkable human propensity for culture did not spring out of nowhere; research in recent decades has revealed much that it shares with the African apes and other species, providing unique insights into culture's evolutionary roots. An exponentially growing corpus of research has even documented the basic phenomena of social learning and culture across large swathes of the animal kingdom (Galef & Whiten 2017, Hoppitt & Laland 2013, Whiten et al. 2011). This research has largely focused on primates (Whiten 2012), particularly our closest living primate relative, the chimpanzee (Whiten 2010, 2011); hence the focus of the present comparative review.

The comparative study of social learning and culture is of considerable scientific importance for two main reasons. The first is anthropocentric, driven by our natural curiosity to uncover the evolutionary origins of our own distinctive human capacity for culture. Of course chimpanzees are not our ancestors, but features of social learning discovered to be shared between ourselves and our closest living relatives can be used to reconstruct the likely nature of social learning and culture in our shared ape ancestors. In the case of chimpanzees and their sister species bonobos, the combination of DNA, together with other molecular similarities between our species, and the fossil record suggests these ancestors lived in African forests 6 to 7 million years ago (Hara et al. 2012). The logic of this comparative approach to reconstructing the origins of our cultural cognition can be extended back through evolutionary time, from the origins of the great ape family that also includes gorillas and orangutans, around 14 or so million years ago (Hara et al. 2012), to ever more remote ancestries shared with all other mammals, all other vertebrates, and so on (Dawkins 2005). The other side of this coin is that comparative research simultaneously identifies those features unique to each species and so clarifies exactly what it is that evolved to make each distinctive since the time of common ancestry, such as the unique flowering of cumulative culture we witness in humans.

Another important scientific rationale for the comparative approach to cultural cognition lies in its broader implications for biology at large. Social learning and culture instantiate a “second inheritance system” (Whiten 2005, p. 52) built on the shoulders of the primary genetic inheritance system that provides the foundation of the evolutionary process. Inheritance via social learning has the potential for much more rapid behavioral adaptation than inheritance via genetic change, so our discoveries about such social inheritance across an increasing diversity of species transform our understanding of how the extended processes of evolution work (Mesoudi et al. 2006, Whiten et al. 2011). Chimpanzees remain particularly important from this perspective, because as reviewed below, much evidence suggests they display the most elaborate cultural profile among nonhuman animals.

COMPLEMENTARY METHODOLOGICAL APPROACHES TO PRIMATE AND HUMAN CULTURE AND SOCIAL LEARNING

Nonhuman primate (henceforth “primate”) research on social learning and culture has come from two main contexts: from the wild and from captive environments (the latter are sometimes tagged as “the lab” but often encompass large naturalistic enclosures, from research institutes to zoos and sanctuaries). The work conducted from these two differing perspectives has not uncommonly been presented as at loggerheads, with field studies argued to provide the only ecologically valid context for recording nonartifactual behavior (e.g., Boesch 2012) or the lab the only environment permitting tight control of the experiments deemed crucial in distinguishing the operation of social from individual learning (e.g., Galef 1990). Historically, most researchers have tended to fall into one camp or the other, but some have recognized the ideal complementarity the two contexts offer and have tackled questions about the nature of primate culture from these dual perspectives (Biro et al. 2003, Matsuzawa et al. 2001). Moreover, field experiments on the topic have begun to provide a productive bridge between the two approaches. In this review, I emphasize what I see as essential and complementary contributions that flow from these differing strands of research effort.

Field research on the great apes was long thought to be too dangerous or difficult to contemplate (one early adventurer sat in a cage in gorilla forests, and saw little!); thus, early research was mostly with captive apes. This research contributed important foundational findings. Of the 60 studies of primate social learning tabulated by Tomasello & Call (1997, table 9.2), 13 were conducted more than a century ago, and 4 of them were with chimpanzees [the most famous was pioneered by Yerkes (1916)]. Studies of home-raised chimpanzees, in particular by Hayes & Hayes (1952),


provided a wealth of observations of apparently spontaneous social learning (brushing one's teeth, applying lipstick) and experimental evidence of imitation (such as a trained "do this" request to—successfully—copy novel motor patterns) (Whiten & Ham 1992).

By contrast, 50 years ago we still knew virtually nothing of chimpanzee behavior in the wild. When multiple field sites across Africa at last began to generate long-term behavioral records, it became apparent that chimpanzees in different parts of Africa behaved in different ways. This finding culminated in international collaborative projects to systematically assess this variation and its potential cultural bases; these projects are summarized further below. This achievement might be thought to be more in the realm of anthropology than psychology, yet in my view it offers the most vital foundation to any psychological study of social learning, whatever the species. We need to begin with the nature of culture as it plays out and functions within a species' natural ecology and everyday life; more refined analyses can follow but make little sense unless we have an adequate picture of the cultural landscape of wild chimpanzees' everyday lives. In any case, research in the wild has extended to sophisticated statistical hypothesis testing and a handful of pioneering field experiments.

Research on human culture has likewise applied a diversity of methodological approaches, ranging from immersive and participant explorations by some cultural anthropologists to a variety of more "scientific" methods of a stripe more familiar to readers of this journal. These include direct, quantitative observations of everyday life that parallel those referred to above for primates, arguably particularly important for peoples living hunter-gatherer modes of life, for these observations offer inferences about the major component of recent human evolution during which our ancestors lived only by such means (Hewlett et al. 2011). Field experiments have recently supplemented such observations (Berl & Hewlett 2015).

In the case of human culture, we additionally have archaeological remains that permit the direct reconstruction of the course of some elements of cumulative cultural evolution, back to the beginnings of the Stone Age 2 to 4 million years ago (Harmand et al. 2015, Stout 2011). Human cultures diversified regionally and began to display their own forms of evolution as cumulative cultures blossomed, and these phenomena have been studied by yet other methods that include the kinds of phylogenetic analysis invented by biologists to study the evolution of organisms (e.g., Atkinson 2011, Currie & Mace 2011).

The psychological processes underlying human social learning and cultural transmission have been studied for more than a century (Whiten & Ham 1992) and through a great diversity of approaches; most studies have focused on childhood as the period of greatest cultural uptake, but some also extend into adulthood. Productive cross-fertilization between the approaches and theories of comparative and developmental psychology has increased over the past 15 years (Nielsen & Haun 2016, Nielsen et al. 2012, Want & Harris 2002). Moreover, in a literature search for truly comparative studies of social learning applying similar methods to two or more species, Galef & Whiten (2017) found only a handful of examples across comparative psychology generally, yet as many as 24 covering direct and indirect chimpanzee/child comparisons [see **Table 1** and **Supplemental Table 1** (follow the **Supplemental Material link** in the online version of this article or at <http://www.annualreviews.org>)]. Accordingly, I visit and extend this corpus further below.

 **Supplemental Material**

A FRAMEWORK FOR COMPARING CULTURE AND CULTURAL COGNITION ACROSS SPECIES

Social learning and culture are complex phenomena, and any scientific comparison between species must accordingly dissect them to achieve any depth of analysis. A hierarchical analysis (illustrated in **Figure 1**) I recently developed as a comparative endeavor has also been embraced in a sister

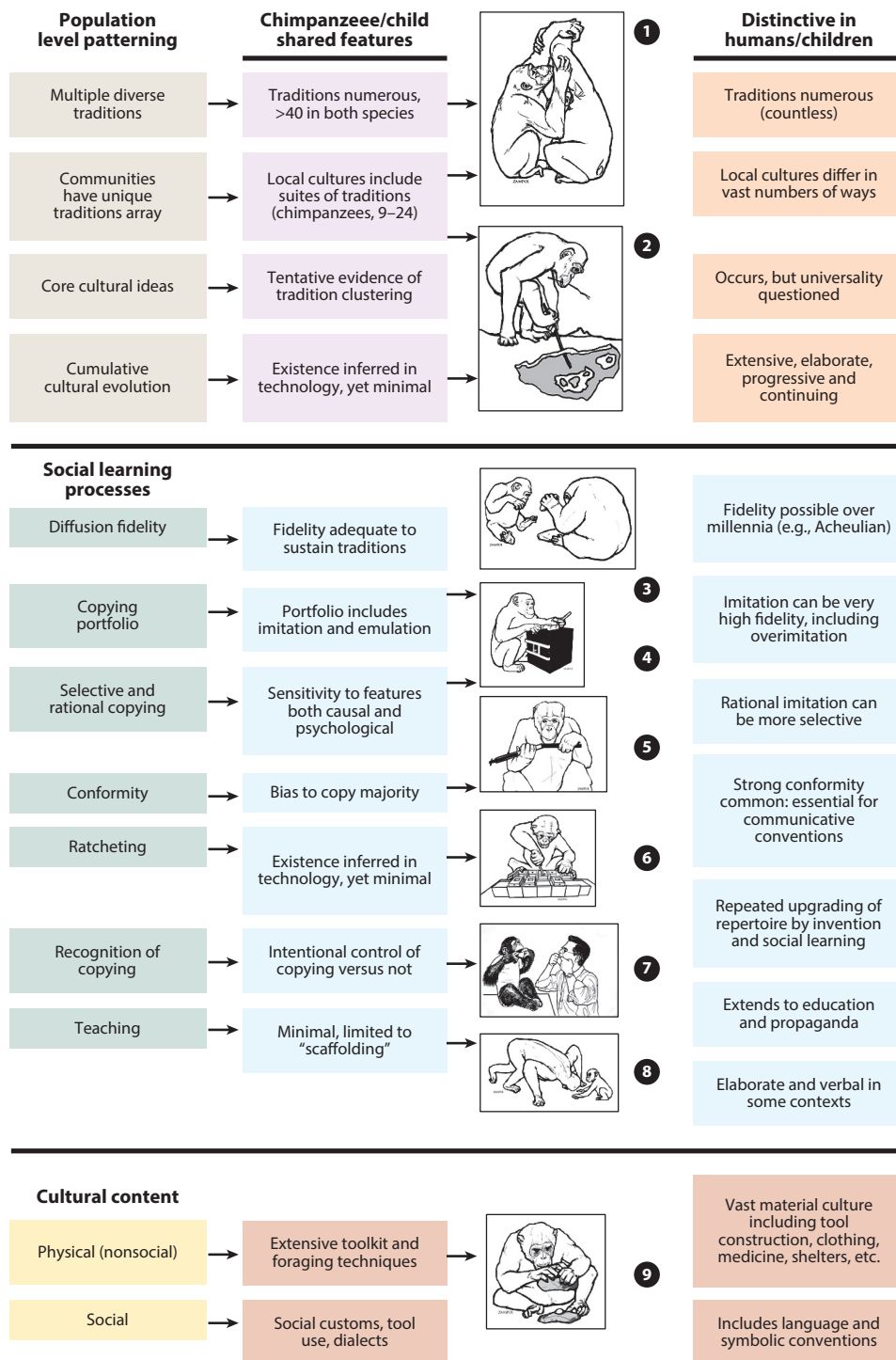



Figure 1

Features of culture shared by chimpanzees, humans including children, and (by inference) the common chimpanzee/human ancestor, and features of culture distinctive in humans. Features (rows) are nested under three main headings. Images represent examples discussed in detail in the text. For further explanation of each numbered image, see **Supplemental Text** (follow the **Supplemental Material link** in the online version of this article or at <http://www.annualreviews.org>). Adapted from Whiten (2011), with permission.

 **Supplemental Material**

discipline, cultural anthropology (Jordan 2015). The scheme initially identifies three dimensions along which species may be compared and contrasted (**Figure 1**). The first concerns the patterning of traditions over space (regional cultures) and time (historical change) and hence includes the topic of cumulative culture. Distinct animal taxa, such as humans, dolphins, and songbirds, show identifiable commonalities in such large-scale patterning despite great differences in the action patterns that populate the patterns. Such patterning could instead show interesting variation, as indeed it appears to do in the case of human cumulative culture.

Another feature concerns the content of culturally transmitted traditions. At different levels of analysis, species may either share or differ in such content, as in the significant repertoire of tool use inherited by chimpanzees as well as humans, or vocal dialects recorded in songbirds, whales, and humans.

The third division focuses on similarities and variations in the social learning processes involved, such as imitation and teaching. As for the other divisions, cross-species similarities can exist in social learning processes despite variation in the other two dimensions that concern the behavioral contents of traditions and their distributions over time and space. Social learning processes may strike the reader as the most clearly psychological of these three foci of analysis, but the relevance of the others should not be neglected; the particular content of a tradition (language, for example, or stone-tool knapping) also has a psychological dimension, and the larger-scale patterning of traditions in time and space incorporates both causes and consequences of cultural learning and content. In the following sections, I address each of the three divisions and key subcomponents in turn.

THE PATTERNING OF TRADITIONS IN TIME AND SPACE

I first focus principally on chimpanzee findings because knowledge in the apes has been hard won only in recent decades and has often surprised us, in contrast with all we know about human culture from scientific research and from ourselves being immersed in the phenomena.

Multiple and Diverse Traditions

When the realization dawned that chimpanzee behavior may differ culturally across Africa, as human behavior is known to vary regionally, primatologists began to build charts of candidate regional traditions (Boesch & Tomasello 1998, Goodall 1986, McGrew 1992). These early explorations were eventually followed by a systematic analysis based on an explicit collaboration between the research groups responsible for the longest-term field studies (Whiten et al. 1999, 2001). The first of these focused on the six longest-running sites that together could collate 150 years of observations; the second analysis included three additional medium-term sites. Each of a long list of candidate traditions, consensually defined, was coded by the groups according to whether it was common at their site or absent without apparent ecological explanation. This process identified 39 putative cultural variants that were habitual or customary in at least one community yet absent in one or more other communities. This is an unprecedented number of variants for all but human societies; indeed, most studies identifying animal traditions have tended to report just a single one, such as the regional dialects of songbirds. The chimpanzee portfolio also widely spanned the species' behavioral repertoire, incorporating foraging techniques; tool use for feeding, comfort, hygiene and communication; and social and sexual gambits. Accordingly, the first commonality identified between humans and chimpanzees is that a substantial and diverse portion of the adult behavioral repertoire is derived from cultural inheritance. Such a state of affairs is thus inferred to have characterized our shared ancestry (Whiten 2011).

Local Cultures Defined by Distinctive Arrays of Traditions

A corollary to the discovery of numerous traditions is that each community is unique: Identifying a set of the relevant behavioral habits of any one individual chimpanzee can mean that its regional origin can be deduced, as can be done for a human being whose cultural attributes are scrutinized. This constitutes a second commonality.

Cultural complexity that comes close to matching both of these two features has been identified in studies of another great ape, the Asian orangutan (Krützen et al. 2011, van Schaik et al. 2003). The authors concluded that local cultures composed of diverse, multiple traditions constitute a characteristic that evolved 14 to 15 million years ago in the ancestors we share with all the great apes (Whiten & van Schaik 2007).

Concern exists about whether the behavioral differences among wild ape communities inferred to be cultural could instead be due to genetic variation across Africa or to environmental factors that are subtle and as yet undetected. Indeed, genetic differences between chimpanzee communities across Africa are correlated with differences in the putative cultural profile of the communities (Langergraber et al. 2011). However, this is a pattern we should expect because until recent times, when long-distance travel (e.g., by sea) made it possible for dispersing human groups to leapfrog past others, geographically and culturally distant communities were expected to be genetically more different, and thus the same would be predicted for apes. In addition, Lycett et al. (2010) examined the particular branching (phylogenetic) structure of putative cultural variants of chimpanzees distributed across study sites and found them incompatible with genetic species structure. Kamilar & Atkinson (2014) further extended these findings, revealing nested relationships between human communities' behavioral commonalities that apparently are diagnostic of cultural diffusion, and finding similar patterns in chimpanzees (but not in orangutans, perhaps because they have smaller networks).

Additional evidence that refutes genetic explanations comes from a variety of other sources. Such evidence includes one of the most striking regional variations: Across a large swath of far West Africa, natural stone and wooden hammers are customarily used to open hard-shelled fruits, but these tools are absent in other regions, despite availability of the needed raw materials. This variation clearly does not reflect genetic preparedness because experiments have shown that East African chimpanzees are perfectly capable of learning the technique if they witness another chimpanzee performing it (Fuhrmann et al. 2014, Marshall-Pescini & Whiten 2008a, Whiten 2015). Luncz & Boesch (2014) have further shown that despite their frequent gene exchange, the chimpanzees in neighboring communities display group-specific preferences in stone versus wooden tool selection, an intriguing finding given that females typically migrate as adults and so must conform to local customs for the group variants to be maintained.

Further evidence that chimpanzees can develop and sustain different traditions in different groups comes from studies incorporating multiple captive groups. For example, some but not all groups in an African sanctuary developed local traditions that included hammering hard-shelled fruits to break them (Rawlings et al. 2014), using a specific style of mutual grooming (handclasp; van Leeuwen et al. 2012), and most bizarre of all, poking a grass leaf into one ear and leaving it there, which serves no apparent function (van Leeuwen et al. 2014a,b). Neither genetic nor environmental differences can explain these variants. The spread of an incipient new tradition, using moss as a sponge to get water from a hole, has now also been documented (Hobaiter et al. 2014). Additional experimental evidence concerning the transmission of traditions is reviewed further below in a discussion of the underlying social learning abilities.

Linkage of Traditions Through Core Cultural Ideas

Cultural anthropologists have argued that elements of culture, such as ideas, memes, and traditions, are not particulate (the way traditions are treated in the discussion above, in which “39 putative cultural variants” are enumerated) but instead may be linked together through some core cultural cognitions (Levine 1984). Because the evidence for such phenomena in anthropology is typically linguistic, this issue is much more difficult to address for nonverbal creatures. However, the findings from recent experimental studies with wild chimpanzees may be relevant. In these studies, holes too small for chimpanzee fingers were drilled in fallen logs and filled with honey in two chimpanzee communities in different parts of Uganda. Chimpanzees in one of these communities (Kanyawara) habitually use stick tools to extract various resources, but stick tool use has long been known to be (unusually) absent in the repertoire of the second group (Budongo), although they use other tool materials, including masticated leaves as sponges to get water out of natural holes (Hobaiter et al. 2014, Whiten et al. 1999). When faced with the honey-filled holes, chimpanzees from each community responded differently (Gruber et al. 2009). Those at Kanyawara gathered sticks and quite efficiently dipped these into the holes so they could then lick off the honey. Budongo chimpanzees, by contrast, made and applied the kind of leaf sponges normally used to extract water, a much less efficient approach. The problem really required stick use, but the Budongo chimpanzees appeared to be “stuck” on their local, habitual technique. Indeed, when in a follow-up study leafy sticks were provided near the holes, Kanyawara chimpanzees promptly stripped the leaves off to make a stick tool, whereas the Budongo chimpanzees stripped the leaves off and used just the leaves for their habitual sponging approach (Gruber et al. 2011). The authors’ conclusion (and the title of their paper) was, accordingly, that “Wild chimpanzees rely on their cultural knowledge to solve an experimental honey acquisition task” (Gruber et al. 2009), an explanation that seems in accord with the notion that core cultural cognitions may pervade multiple contexts. This is, of course, a small-scale candidate for this effect in comparison with human examples, such as the contrast between an emphasis on independence and analytical thinking in Western cultures and an emphasis on collectivism and holism in the East (Nisbett et al. 2001).

Cumulative Culture

All authors working in the field of comparative cultural cognition now acknowledge that wild chimpanzees as a species have been shown to display numerous traditions together with unique multitrade local cultures, as outlined above, but conclusions about whether species other than humans display cumulative culture are more diverse. It is commonly stated that only humans have cumulative culture (e.g., Henrich 2015, Tennie et al. 2009). My own view is that this conclusion is premature and that chimpanzees do show some limited evidence of cumulative culture. The magnitude of the species differences in this respect is of course massive, but I suggest that we see initial significant signs of cumulation in chimpanzees, and it would have been from such beginnings that our special human capacities evolved.

Boesch (2012) proposes several candidate cases of small-scale cumulation in chimpanzees. In an example I judge to be currently the most impressive, chimpanzees in the central Congo region have been filmed approaching clearings where they will fish not horizontally in termite mounds as is seen in several communities, but instead extract termites from nests several feet beneath the surface (Sanz et al. 2009). To do this, the chimpanzees first push a stout stick downward into the earth, doing so forcefully and often using their foot to assist in a manner similar to digging with a spade. Having thus created a subterranean tunnel, they prepare fresh, slim stems, which

they brought to the site in anticipation, by stripping one end through their teeth to make a comb that will better elicit biting by the termites. The chimpanzees then carefully insert the prepared stem down the long tunnel and withdraw it to nibble off the termites that are biting the brush end. We have no documentation of the history of this elaborate sequence, just as for most of those sequences used in weapon and trap making by human hunter-gatherers, but the cumulative history of the latter is not in doubt, and it likewise seems unimaginable that chimpanzees could have built up this sequential fishing procedure in a single generation. It seems quite miraculous that the chimpanzees know a technique that will extract these termites from deep in the earth; it seems highly plausible that the technique started with termites close to the surface and has evolved over generations into the more elaborate form we see today.

Such candidate cases pale in comparison to the pace and scope of cumulation we have witnessed in recent phases of human history, but they are important to recognize if we are to properly understand the underlying cultural cognition of both species. Moreover, cumulative culture of any significant magnitude is a relatively recent phenomenon along the evolutionary line from the time of our shared ancestor up to the emergence of modern humans. For a long time, the first archaeological evidence for the beginnings of the stone age came at 2.6 million years (Semaw et al. 2003), but new evidence appears to push this back to perhaps 3.3 million years (Harmand et al. 2015); nevertheless, the cumulative step from flaked cobbles to discriminably more advanced, symmetrically shaped Acheulean blades did not come until around 1.8 million years. That procedure then endured, with only minimal progressive change, for another million years or so before the next noticeable cumulative steps took place (Stout 2011), despite hominid brain sizes already being midway between those of chimpanzees and modern humans. Although chimpanzee cumulative culture appears minimal, it is relevantly comparable to perhaps the greater part of the six to seven million years or so of our unique hominin evolutionary pathway. I review potential explanations for the contrast between chimpanzees and modern humans in the capacity for cumulative culture in the social learning section below.

SOCIAL LEARNING PROCESSES

Chimpanzees are both our closest living relatives, with whom we shared our last nonhuman ancestor, and the species that, along with humans, has been the subject of the greatest number of studies of social learning; such studies have often led the way in comparative psychology's exploration of new dimensions in the nature and scope of animal culture. These two observations are not unrelated. This corpus of research probes the psychological mechanisms and processes that make possible the scope of culture in the two species that was outlined in the sections above. Relevant studies include those concerned with fidelity of cultural transmission, different grades of social learning, selective factors modulating what is copied and from whom, conformist copying, teaching, and capacities underwriting cumulative cultural evolution.

The intrinsic interest in chimpanzees is one reason why chimpanzees are represented in an unusually high proportion of studies in which one species is closely compared with another; these comparisons are centered mainly on humans, although in some cases other great ape species are included. **Supplemental Table 1** summarizes 24 such studies, including a set collated in Galef & Whiten's (2017) chapter (see **Table 1** for comparative studies published from 1993 to 2015). The following discussion draws on these as well as other studies that do not offer direct comparisons between species in the same paper. Interested readers may also find it helpful to consult Whiten et al. (2004) for a similar summary of the 31 articles on great ape social learning published since those listed in Tomasello & Call's (1997) book, which covered all such papers up to 1996.


 **Supplemental Material**

Table 1 Comparative social learning studies with children and (other) apes, 1993–2015. Studies are listed chronologically by publication date. (See Supplemental Table 1 for further details.)

Direct comparisons of child and ape social learning studies		
Reference	Title	
Nagell et al. 1993	Processes of social learning in the tool use of chimpanzees (<i>Pan troglodytes</i>) and human children (<i>Homo sapiens</i>)	
Tomasello et al. 1993b	Imitative learning of actions on objects by children, chimpanzees and enculturated chimpanzees	
Call & Tomasello 1995	The use of social information in the problem-solving of orangutans (<i>Pongo pygmaeus</i>) and human children (<i>Homo sapiens</i>)	
Carpenter et al. 1995	Joint attention and imitative learning in children, chimpanzees and enculturated chimpanzees	
Whiten et al. 1996	Imitative learning of artificial fruit processing in children (<i>Homo sapiens</i>) and chimpanzees (<i>Pan troglodytes</i>)	
Call et al. 2005	Copying results and copying actions in the process of social learning: chimpanzees (<i>Pan troglodytes</i>) and human children (<i>Homo sapiens</i>)	
Horner & Whiten 2005	Causal knowledge and imitation/emulation switching in chimpanzees (<i>Pan troglodytes</i>) and children (<i>Homo sapiens</i>)	
Tennie et al. 2006	Push or pull: imitation versus emulation in great apes and human children	
Horner et al. 2006	Faithful replication of foraging techniques along cultural transmission chains by chimpanzees and children	
Herrmann et al. 2007	Humans have evolved specialized skills of social cognition: the cultural intelligence hypothesis	
Horner & Whiten 2007	Learning from others’ mistakes? Limits on understanding of a trap-tube task by young chimpanzees and children	
Hopper et al. 2008	Observational learning in chimpanzees and children studied through “ghost” conditions	
Buttelmann et al. 2008	Rational tool use and tool choice in human infants and great apes	
Tennie et al. 2009	Ratcheting up the ratchet: on the evolution of cumulative culture	
Haun et al. 2012	Majority-biased transmission in chimpanzees and human children, but not orangutans	
Dean et al. 2012	Identification of social and cognitive processes underlying human cumulative culture	
van Leeuwen et al. 2014a	Human children rely more on social information than chimpanzees do	
Haun et al. 2014	Children conform to the behavior of peers; other great apes stick with what they know	
Vale et al. 2014	Public information use in chimpanzees (<i>Pan troglodytes</i>) and children (<i>Homo sapiens</i>)	
Claidière et al. 2015	Selective and contagious prosocial resource donation in capuchin monkeys, chimpanzees and humans	
Ape experiments with earlier (or later) child studies explicitly compared to them		
Ape reference	Child studies compared	Title
Call & Tomasello 1994	Nagell et al. 1993	The social learning of tool use by orangutans
Whiten et al. 2005a	Flynn & Whiten 2012, Hopper et al. 2010, Whiten & Flynn 2010	Conformity to cultural norms of tool use in chimpanzees
Tomasello & Carpenter 2005	Bellagamba & Tomasello 1999, Carpenter et al. 1998, Meltzoff 1995	The emergence of social cognition in three young chimpanzees
Marshall-Pescini & Whiten 2008b	Whiten et al. 2009	Chimpanzees (<i>Pan troglodytes</i>) and the question of cumulative culture: an experimental approach
Buttelmann et al. 2007	Gergely et al. 2002	Enculturated chimpanzees imitate rationally

 Supplemental Material

Fidelity in Transmission: Cultural Diffusion Studies

One of the most commonly cited explanations for the gulf between the cultural achievements of humans and chimpanzees concerns the relative copying fidelity of the two species. One prominent version of this explanation was promoted by Tomasello and colleagues in a series of publications

[from Tomasello et al. (1993a,b) to Tennie et al. (2009)]. A dichotomy was initially drawn between two social learning processes that have driven much comparative research, especially concerning apes. One learning process was imitation, defined as the copying of others' actions. Imitation had already been studied in comparative and developmental psychology for much of the prior century. The other process, emulation, was newer and highlighted by Tomasello (1990) following a study in which chimpanzees had failed to imitatively copy a tool-use sequence displayed by a conspecific retrieving food, yet showed they had learned something of the function of the stick tool by the way they directed it at the target (Tomasello et al. 1987). Tomasello described this as emulation: recreating the desirable results of another's actions rather than their form. Emulation could thus be considered to lie between imitation and the simple and widespread forms of social learning known as stimulus (with regard to objects) and local (with regard to locations) enhancement, in which all that is socially acquired is the locus of attention displayed by others.

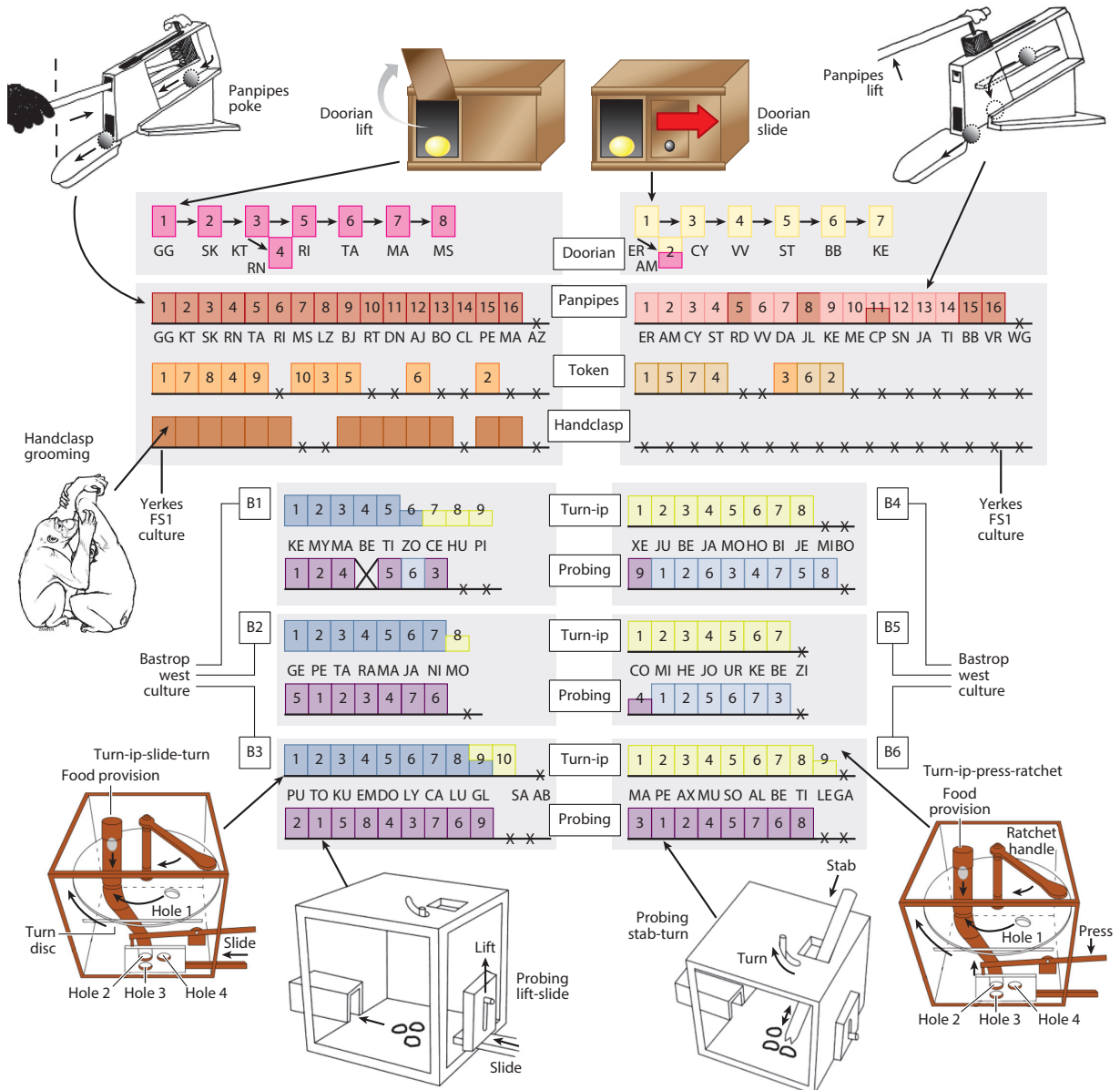
It has been suggested that the often high-fidelity action copying of which children are capable is what permits cumulative culture, because this is what is needed to maintain each progressive step up the cultural ratchet, whereas in the case of emulation the learners have to generate an action sequence of their own to achieve the desirable results they learned about. A considerable corpus of studies has offered support for this hypothesis (e.g., Call et al. 2005, Nagell et al. 1993), and much of it has been reviewed (and debated) by Tennie et al. (2009) and Whiten et al. (2009). For example, Herrmann et al. (2007) presented young children, chimpanzees, and orangutans with modeled behavior patterns and reported that in contrast to the results of other tests revealing often quite similar levels of physical cognition, only the children showed significant evidence of imitating the model.

However, Herrmann et al. (2007) employed only human models, such that the apes faced a model of a different species, whereas children could copy a human adult. Other types of studies have come to different conclusions regarding fidelity of transmission; these are broadly classed as diffusion or transmission studies and have been reviewed up to 2008 for human subjects by Mesoudi & Whiten (2008), for other species by Whiten & Mesoudi (2008), and for both categories in the period since by Whiten et al. (2016). These studies go beyond the classic social learning experimental design that asks, "What does B learn from model A?" to a design that is more appropriate for investigating cultural transmission because whole micropopulations are involved. In the first controlled experiment of this kind with chimpanzees, Whiten et al. (2005a,b) trained one chimpanzee how to use a stick tool to extract food from a foraging box (termed panpipes) using one method (termed lift) and then reunited her with her group; similarly, a model trained to use an alternative method (termed poke) was seeded back into her own group. It was found that these alternative techniques spread differentially in the groups in which they were seeded and became incipient, recognizably different traditions (**Figure 2**). Indeed, although some corruption occurred, with some individuals discovering the alternative technique, it was found that two months later these individuals had tended to reconverge on the technique most common in their group. This experimental design does not discriminate between imitation and emulation but rather suggests that chimpanzees have the capacity to transmit and sustain with adequate fidelity the kinds of alternative tradition inferred from the observations in the wild outlined above.

This design has been labeled open diffusion because it leaves open who will watch the models and who will (or will not) copy what they do. In a more controlled alternative, the diffusion chain, just one observer witnesses the model, then after mastering the task (however they do it) the observer becomes the model for the next observer, and so on along a chain. Horner et al. (2006) applied this approach to both children and chimpanzees and found fidelity along the chains for both (along chains of 10 children; chains of just 6 chimpanzees were used because of the challenging pragmatics of such maneuvering with captive apes). Other variants on these experiments at two

different sites confirmed that chimpanzees can express adequate fidelity in sustaining multiple-tradition cultures (Whiten et al. 2007) (**Figure 2**).

The panpipes open-diffusion chimpanzee experiment outlined above has also been repeated with young children in small nursery groups (Flynn & Whiten 2012, Whiten & Flynn 2010). This generated more complex results, with both similarities to and differences from the chimpanzee findings. Initially there was similarity in that two recognizably different incipient traditions were established already on day 1 of the study, as tool-use skills spread across the groups. However, children were quicker than chimpanzees to discover the alternative technique and also invented a third intermediate one. These innovations could in turn be shown to spread by social learning, with



a majority of children being social learners and a minority the innovators who either modified what they learned from others or, more rarely, invented a technique quite different from the one they had learned. This particular child/chimpanzee comparison is thus sobering in that it shows greater fidelity in the chimpanzees than in the children; however, this was surely not because children are inherently less able to faithfully copy but rather that they could independently master the task better and were more ready to innovate. One lesson is thus that in making such comparisons, the level of challenge in the task for each species can be a critical factor in the resulting picture of fidelity of transmission that each presents.

Fidelity in Transmission: Imitation and Emulation

These findings leave unanswered the question of the imitation and emulation profile that truly characterizes each of the two species. Hopper et al. (2007) tackled this issue in the panpipes studies with chimpanzees through a ghost experiment. In this approach, the usual results of a model's actions are recreated without any model present, so the conditions for emulation are available but do not permit imitation. In the ghost experiment, the lift technique, which involves lifting up a blockage to release the food reward, was performed by surreptitious operation of fishing line above the device. No chimpanzees learned from this ghost experiment, in marked contrast with how well chimpanzees had acquired the behavior from seeing it modeled in the earlier diffusion study. This suggests that chimpanzees are limited in their ability to learn merely from object movements [Tomasello (1998) had once suggested such emulation might occur if the wind blew an object instead of the mother moving it] and instead need to watch the actions of a model, consistent with imitative social learning (Hopper et al. 2015).

However, in these ghost studies, there is no active model, even in a refinement of the method in which a passive conspecific is included in the scenario (Hopper et al. 2008). An ingenious alternative accordingly offered by Tennie et al. (2010) involved first showing participant chimpanzees that pouring water from a bottle into a cylinder could make a peanut inside rise to the top of the cylinder so it could be retrieved. However, no bottle was provided for the chimpanzees. Some chimpanzees responded by fetching water from their drinker in their mouths and spitting it into the cylinder, which when repeated delivered the peanut. This action is true emulation because it involves the chimpanzee recreating a desirable result by using a means different from that shown by a model. It does not show that chimpanzees are limited to emulation, but it does identify one context in which they can take this approach, contrasting with the negative results from the ghost experiments.

Horner & Whiten (2005) challenged the dichotomy of child-imitators and chimpanzee-emulators in a different way. These investigators conceptualized the distinction as more of a

Figure 2

Spread of experimentally seeded, multiple traditions generating four chimpanzee “cultures.” At each location [Yerkes (*a*) and Bastrop (*b*)], alternative techniques were experimentally seeded in a single individual, and all spread locally. Each two-letter code represents a single chimpanzee, and color-coding corresponds to the technique seeded in the first individual in each case. (*a*) At Yerkes, lift versus slide methods (first row) were seeded to open a door for access to “doorian” fruit; these techniques spread as a diffusion chain (Horner et al. 2006). In the second row, poke versus lift panpipes techniques spread in an open (unconstrained) diffusion (Whiten et al. 2005a,b). The third row illustrates a bucket versus a pipe posting option for tokens in an open diffusion (Bonnie et al. 2007). Handclasp grooming (fourth row) arose and spread spontaneously only in the Yerkes FS1 community. (*b*) At Bastrop, techniques included (first row) actions termed turn-ip-slide-turn versus turn-ip-press-ratchet and (second row) probe lift-slide versus probe stab-turn used to extract food from two different devices; each technique spread to a second group (third and fourth rows; groups B2 and B5) and then to a third group (fifth and sixth rows; B3 and B6) (Whiten et al. 2007). Numbers indicate order of acquisition. Figure based on data in, and adapted with permission from, Whiten et al. (2007).

continuum, and to test this notion they structured an experiment in which young chimpanzees and children watched a familiar model extract a reward from either an opaque or a transparent box. In the case of the opaque box, the model first used a stick tool to open a hole in the top, rammed the tool in several times, then opened a second hole on the side and inserted the stick to bring out the reward and share it. The transparent box was identical, but when the stick was rammed in the top, it was perfectly visible that it merely tapped on a horizontal partition and could not affect what happened on later insertion of the tool into the lower hole. Accordingly, it was predicted that an intelligent imitator like a child would likely imitate the whole sequence in the opaque condition but would prefer a more emulative response with the transparent box, omitting the actions directed at the top hole.

In the experiment, the chimpanzees made this distinction and produced much more complete copies of what they had seen, including ramming the stick in the top hole, in the opaque condition than in the transparent condition. Thus, rather than producing only emulation (omitting actions on the top hole) or mindlessly “aping” all of the actions (not discriminating between the two conditions), the chimpanzees showed flexibility of social learning, switching between emulative responses and those in which they imitated the sequence with the opaque box. An interesting and surprising finding was that the children tended to copy all actions faithfully in both conditions, a response now known as overimitation.

Overimitation

Lyons et al. (2007) coined the term overimitation after having amply replicated the effect with a transparent puzzle box and other manipulable artifacts and failing in several efforts to encourage 3- to 5-year-old children to behave “more sensibly.” For example, Lyons and colleagues offered training episodes in which children were encouraged to identify visibly, causally unnecessary action components, such as stroking a feather on a jar before unscrewing the top, and advised children, “Remember, don’t do anything silly and extra. Only do the things you have to do, okay?”—all to no avail. Whiten et al. (2005b; see also Horner & Whiten 2005) suggested that the effect might represent a rule of thumb (“copy all, correct later”) that was typically productive for children when learning from competent adults and others. Lyons et al. (2007) went further to posit an “automatic encoding mechanism” whereby young children automatically interpret adult actions on unfamiliar objects as causally effective, a functional disposition given that the child is surrounded by a vast array of mysterious objects, the causal workings of which are at least initially quite opaque.

Overimitation has since been confirmed and further explored in numerous studies that have identified the phenomenon in several quite different cultures (Berl & Hewlett 2015, Nielsen et al. 2014) and also extended its age range. The foundational studies were with preschool children, and it was initially anticipated that the effect would dissipate as children matured in their cognition. In fact, the reverse was found, with adolescents (Nielsen & Tomaselli 2010) and then adults (McGuigan et al. 2011; **Figure 3**) displaying an even more pronounced effect. Lyons et al. (2011) have provided further evidence in support of the operation of a causal encoding function, but other studies have suggested that in many contexts a social function may be served through building bonds by being more like others; complying with others’ assumed wishes; or acquiring cultural conventions, norms, and ritual procedures (Hoehl et al. 2014, Kenward et al. 2011, Keupp et al. 2013, Nielsen et al. 2008).

It is customarily stated that overimitation is a distinctive human property that is not seen in apes, but this statement hinges only on the original findings of Horner & Whiten (2005) and one other study (Nielsen & Widjojo 2011) that clearly begs for more replication and elaboration. An effect perhaps akin to overimitation was reported by Price et al. (2009), who completed a

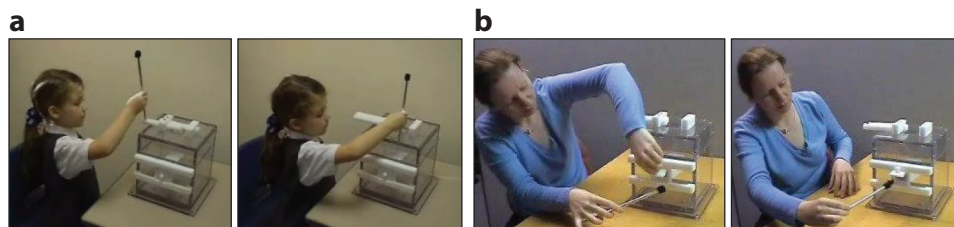


Figure 3

Sequence of models' actions in an overimitation study. Photos illustrate (a) a child model performing the causally irrelevant actions of shifting a bolt to access the top hole and then inserting a stick tool, and (b) an adult model performing subsequent causally necessary actions to reveal the lower hole and then inserting a stick tool to retrieve a reward. Stills from video presentations used with permission from McGuigan et al. (2011).

study showing that chimpanzees exposed to a model joining two sticks to make a long rake to pull in food were more likely than nonobserving individuals to learn this technique. A handful of these controls did, however, work out the stick-joining option themselves. Testing the cognitive flexibility of successful chimpanzees later by offering closer food items that did not require use of the long rake tool, Price et al. (2009) discovered that the social learners were more likely than the individual learners to persist in the stick-joining technique they had acquired by observation. Arguably, this is at least “overcopying” and indicates some of the potency of social learning we see in the case of overimitation.

Selective and Rational Social Learning

Although copying others can be a productive and safe way to learn, it can also lead one astray if what is copied happens to be maladaptive. Accordingly, we may predict that evolutionary and developmental processes will refine selective biases about when, from whom, and even how best to copy, depending on context. One example of chimpanzees' selectivity was demonstrated in the transparent box experiment of Horner & Whiten (2005), although in that case it contrasted with lack of selectivity in children. However, other studies have demonstrated a range of forms of selectivity in children's social learning (Price et al. 2016, Wood et al. 2013). Many investigators have examined this selectivity in the realm of language, revealing the bases over which children learn to trust (or not trust) the verbal testimonies they hear (Harris 2012), so direct comparisons with apes do not apply. However, comparisons are feasible in other domains.

One example lies in what has been called rational imitation. Gergely et al. (2002) repeated Meltzoff's (1998) dramatic demonstration that human infants can be so imitative as to copy an adult bizarrely bowing down his head instead of using his hand to switch on a light, and they included a new condition in which a model wrapped a blanket round herself, preventing use of her hands. Imitation was more rare in this condition. The conclusion drawn was that even by age one, infants' theory of action is sufficiently sophisticated to recognize that the blanket means using one's head would make sense, whereas without the blanket, using one's head must be intentional and worth copying.

Buttelmann et al. (2007, 2008) have since adapted this paradigm for apes and have expanded it such that the unusual actions are done not only with the head but also with the foot or by sitting on objects to make them light up or make a sound, again either in hands-free or hands-occupied (e.g., wrapped by a blanket or holding a box) conditions. In their work with enculturated chimpanzees

(i.e., intimately reared by humans), these authors found rational biases in apes that were similar to those identified in children.

Other biases concern from whom it is best to learn. Incidental observations that chimpanzees might be attending and learning from higher-ranked individuals led Horner et al. (2010) to have high- and low-ranked models post tokens in different receptacles to obtain rewards; they showed that the higher-ranked model's choice was preferentially copied by others. The adaptive benefit of such a bias is likely to be that high rank is a marker of having access to the best resources as well as being correlated with overall biological fitness, so such an individual is a good one to copy—an effect akin to copying prestigious individuals in the case of humans (Henrich & Gil-White 2001). Kendal et al. (2015) have provided complementary evidence, from social learning dynamics in chimpanzee groups, of biases to copy both dominant and already-knowledgeable individuals.

Effects similar to the latter have also been documented in experiments with children [reviewed by Wood et al. (2013) and Price et al. (2016)]. For example, Zmyj et al. (2010) showed that even in infancy, the more competent of two models will be preferentially copied. Age appears to be a cue to this factor, with a number of experiments showing that adults are more likely to be copied than child peers (McGuigan et al. 2011, Rakoczy et al. 2010); however, in play contexts this bias may be reversed (Zmyj et al. 2012), which is an additional measure of the subtlety of selective learning rules in play. Such subtleties suggest a somewhat paradoxical contrast with the lack of selectivity that is the hallmark of overimitation and, at least at first sight, the phenomenon of conformity (Whiten 2013), which is discussed in the next section.

Conformity

Conformity was first made famous by work in social psychology, notably that by Asch (1956), who arranged that a visibly incorrect choice would be given by all but one adult (the subject) in a group of individuals asked in turn to make a simple perceptual judgment about relative line length. Approximately 30% of the participants conformed to the expressed group judgment by stating the same preference as others in the face of quite clearly visible evidence to the contrary. The effect was later investigated in children, with Walker & Andrade (1996) reporting as many as 85% of 3- to 5-year-olds conforming in an Asch-like scenario, which reduced steadily with age to only 9% in 12- to 14-year-olds; by contrast, approximately 20% of 3- to 4-year-olds in a more recent study by Corriveau & Harris (2010) did so, but here the other children were shown only on video.

As noted above, in the panpipes study of Whiten et al. (2005a,b), chimpanzees that discovered the nonseeded solution tended to return later to the group norm—the seeded method—which thus suggested an effect akin to that demonstrated in the Asch paradigm, insofar as the chimpanzees knew of both options and appeared to veer to the norm just because it was the most commonly seen. However, van Leeuwen & Haun (2014) note that this does not exclude a tendency to return to one's first-learned technique, and these authors are skeptical of the existing evidence for this kind of conformity adduced for primates or indeed any nonhuman animals.

The panpipes study had not set out to test for conformity. The first study to do so for the lower-level question of whether naïve chimpanzees (i.e., individuals not needing to overturn existing personal preferences) would favor copying a majority was conducted by Haun et al. (2012), who arranged that subjects saw three conspecifics posting tokens in one of three receptacles, whereas just one conspecific did so three times in a different receptacle. Like children in the same experiment, when chimpanzees decided which receptacle to post their token in to gain reward, they tended to prefer the receptacle chosen by three different chimpanzees. However, this did not require any switching of preference. Haun et al. (2014) did present this dilemma, with individuals first learning a reward location preference, then witnessing three conspecifics choosing a different

location. Here, just over half of the 2-year-old children switched to conform to this location, whereas only 1 of 12 chimpanzees tested did so.

In the wild, however, there is different evidence suggesting conformity. Luncz & Boesch (2014) and Luncz et al. (2015) identified subtle but significant differences in the seasonal preference in adjacent communities for different tool materials for cracking nuts. The authors argue that both genetic and ecological explanations for these differences can be discounted, leaving cultural transmission as the inferred cause. The local preferences were also shown by females, who have immigrated from neighboring communities and hence are inferred to have conformed to the new local norms they have experienced, a tendency documented as one female migrated and gradually converged on local patterns (Luncz & Boesch 2014). It is possible that such biases are brought into play when individuals face uncertainty, as is the case in immigrating to a new community and home range, and other cases of conformity recently reported in other primates (van de Waal et al. 2013) and birds (Aplin et al. 2015a,b) fit this pattern.

A somewhat different notion of conformity has been thought important by other researchers who focus on human cultural dynamics. Boyd & Richerson (1985) have defined conformity as an exaggerated tendency to copy the majority. If 80% of individuals in a community express a preference for option A over option B, then immigrants would show this level of conformist transmission if the probability of their opting for A was significantly greater than 0.8, an important effect because, as the authors' modeling has shown, such a tendency would reinforce in-group cultural homogeneity and intergroup cultural diversity. Evidence that humans behave in this way is mixed (Claidière & Whiten 2012), but Morgan et al. (2015) have demonstrated such behavior in young children—again, interestingly, especially in contexts of uncertainty. The use of a large population of marked individuals recently provided evidence of such a conformist effect in birds (Aplin et al. 2015a,b), but to my knowledge there is no primate literature as yet, possibly in part because of the large sample sizes needed.

Cultural Ratcheting and Conservatism

The gulf between the minimal evidence for cumulative culture in primates and the vast cumulative cultural achievements of humans was acknowledged previously in this review. Can this difference be explained at the level of the social learning processes available? Just a handful of studies have so far sought to examine chimpanzee responses in experimental scenarios that offer some opportunities for cumulative cultural change. In the first exploration, Marshall-Pescini & Whiten (2008b) presented young chimpanzees with boxes containing nuts and honey and modeled opening a small hatch in each box, dipping in a small stick, and then licking the honey off it. This action was shown to be socially learned through contrasts with an asocial control sample. Participants were then shown a more complex option that involved inserting the tool into a space to release the lid so that all of the honey and nuts inside became available. Chimpanzee subjects did not learn the complex option once they had acquired the simpler dipping method, whereas two control individuals who had not acquired the dipping method did manage, by exploration, to arrive at the more complex technique. Young children presented with the same scenarios (but gaining prizes other than honey and nuts) did tend to show cultural ratcheting, first learning the simple probing technique and then building on this knowledge to master the levering method of opening the lid (Whiten et al. 2009). Thus what appeared to be limiting the chimpanzees was a marked conservatism, which also has been described in studies in which chimpanzees stuck to inefficient methods despite the presence of models displaying more efficient ones (Hrubesch et al. 2008).

Marshall-Pescini & Whiten (2008b) suggested that this conservatism might have been associated with a readiness to accept a satisficing payoff from the dipping technique. However, this

hypothesis was not supported in a later study by Dean et al. (2012) in which chimpanzees and children (and capuchins) were presented with a puzzle box that offered scope for cumulative cultural progress through three levels, at each of which improved rewards could be gained by implementing progressively more challenging manipulations. Children typically progressed through more levels than did the other primates, and in particular, the primates did not benefit by learning from the rare conspecifics that succeeded at the higher levels; thus, the primates failed to display cumulation. In this respect the results concur with earlier ones documenting conservatism (outlined above). However, Dean et al. (2012) also implemented a condition in which participants could no longer obtain rewards at the lowest level. This condition clearly prevented any satisficing operations, yet most of the chimpanzees still failed to show cumulative progress despite occasional modeling of the higher-level techniques by other members of their group.

Dean et al. (2012) compared behavioral profiles of the species and found that children showed a number of behavioral differences to which superior achievements in cumulative progress might be attributed. These differences included spontaneous teaching, prosocial sharing of rewards, and a greater likelihood of matching the behavioral methods they saw successful children already using. It is not possible to discriminate which, if any, of these play a causal role; it may be that all act in concert to make the behavioral difference. To complicate the picture, some studies have experimentally manipulated these variables to test their importance. Caldwell & Millen (2009), for example, ran experiments in which small groups of young adults attempted to make paper planes that flew as far as possible, with potential cumulative cultural progress afforded by removing and adding new members to create chains of overlapping memberships. Information transfer was constrained in different conditions to allow only teaching, only imitative copying, or only emulation (because only the results of groups' actions were witnessed). It was found that chains operating under the latter constraint did as well as those in which teaching was offered or imitation of models was allowed. Similar results have been reported using a different paradigm (Zwinner & Thornton 2016). However, Wasieleski (2014) has argued that different results are to be expected with significantly more complex and challenging activities, and she has explored approaches that may confirm this hypothesis.

Reflexive Recognition of Transmission Processes

A distinctive way in which imitation has been studied in apes is the “Do-as-I-do” approach pioneered by Hayes & Hayes (1952). In this method, the ape first learns to attempt to copy what a trainer does via a set of training actions, upon a request such as “Do this,” and is then tested with a battery of relatively novel actions. Custance et al. (1995) replicated the Hayes & Hayes (1952) study in a more rigorous, objectively coded fashion using a battery of 48 novel acts with two young chimpanzees; Call (2001) did likewise with an enculturated orangutan, recording 58% full imitations and 32% partial imitations of this substantial battery. What I emphasize here is that these apes could “learn the game,” which required them to recognize what it is to imitate. Interestingly, several intensive efforts to train monkeys to do this have failed (see Whiten et al. 2004), suggesting that achievement of this reflexive recognition of the imitation process may be distinctive to the great ape mind. Young children do this, of course, in playing the “Simon says” game, which is effectively a “Do-as-I-do” procedure.

In the case of children, teaching perhaps comes into this general category. Whiten & Flynn (2010) and Dean et al. (2012) have noted that in the course of their experiments on social learning in groups of children, some children spontaneously began to teach other children what they had learned. Children thus not only come to benefit from imitating and being taught, but also explicitly

recognize these processes and what they can achieve, and they apply the processes prosocially to other children. Chimpanzees can come to recognize at least the imitation side of this process.

Teaching

In countries with well-articulated educational systems, teaching looms large in conceptions of the processes whereby culture is transmitted. Informal teaching is often to be observed in the home and other segments of children's lives. However, over past decades anthropologists have often remarked on the lack of explicit teaching in hunter-gatherer societies, in which there are constant daily opportunities to learn simply by direct observation (reviewed in Whiten et al. 2003). It remains possible that the lack of explicit teaching may reflect a lack of systematic observation and quantification, and Hewlett et al. (2011) have argued as much in the context of their pioneering observations of the natural history of cultural transmission in the hunter-gatherers of the African Congo Basin. A broader conception of teaching converges with this newer picture (Kline 2015, Kline et al. 2013).

However, little comparable teaching has been described in wild chimpanzees, beyond an often patchy tolerance of youngsters as they become involved in activities such as nut cracking and are allowed to take and use their mother's hammer materials and nuts (Boesch 2012). This finding contrasts with the fact that evidence of teaching, in the functional sense of incurring a cost to support some aspects of development, exists among certain other animal taxa (Thornton & Raihani 2008), as illustrated in the structured ways that adult meerkat caretakers bring scorpions for pups to practice with, disabling and recovering the scorpions in ways adapted to the different stages of handling competence in the pups (Thornton & McAuliffe 2006). It may be that there is particular pressure on this kind of support for predatory species, such as felines and meerkats, whose young have to make a major developmental leap from being fed by their mothers to succeeding in the challenging pursuit of prey capture and killing. Hoppitt et al. (2008) suggest that by contrast, apes have well-articulated observational learning mechanisms and a long period of immaturity in which to learn skills that can be mastered in a more gradual stepwise fashion, such as opening difficult foods and fishing for invertebrate prey with tools.

CULTURAL CONTENTS

Much of the discussion of what makes human culture special focuses on the phenomenon of cumulative culture and the social learning processes that make it possible. However, a large part of what makes human and chimpanzee cultures look so different is surely the particular behavioral and material content of those cultures, which may profoundly affect the psychological nature of the cultural transmission processes themselves. For example, in language acquisition a child assimilates material with its own unique recursive and syntactic structure, semantics, and pragmatics; there is no direct counterpart in what a young chimpanzee assimilates. The material cultures of even those nomadic hunter-gatherers who can carry all their possessions on their back include such categories as medicines, multicomponent constructed tools, weapons and traps, clothing, fire, musical instruments, and jewelry and other adornments, together with all of the know-how that allows items to be made and their functions served. Aside from language, social customs may include nonverbal gestures and rituals, dance, music and song, religion, social customs and rules, and institutions such as marriage.

This is not to say that no overlaps in content exist between humans and other apes, but comparisons must be at an appropriate level of abstraction. Thus, at a very broad level, one can recognize

a commonality between humans and chimpanzees in the possession of a material culture involving both a diversity of types of tool materials and a diversity of related technological functions. Within these functions one can further recognize more particular commonalities at the level of tool use for foraging, for comfort (e.g., leaf mats), and for hygiene (e.g., wipes for body fluids).

CONCLUDING DISCUSSION

Despite the millennia of human history over which we have shared the planet with our closest animal relative, until only a few decades ago we had scarcely any inkling that chimpanzees had the richness of cultural traditions that recent sustained fieldwork, coupled with scientific collaboration, has uncovered. Newly discovered putative traditions are regularly reported. Discoveries in Africa have been complemented by cultural diffusion experiments that have confirmed the social transmission capacities suggested by the field research, and in both these lines of research the chimpanzee studies have repeatedly pioneered approaches later followed by studies of other primate and nonprimate species, including a significant number with human children. Together, these studies have shown that chimpanzees and other apes have extensive, multiple-tradition cultures that shape significant parts of their lives and profoundly affect the nature of development, phenomena shared with our own species and thus pointing to an ancient ancestry. The same is true for numerous aspects of the underlying social learning processes outlined above and summarized in **Figure 1**.

However, I end by pointing out that developmental and comparative research has discovered that this is all part of a larger picture, one that delineates a cluster of sociocognitive features that underwrite humanity's remarkable evolutionary success, yet as for culture and social learning, foundations have been uncovered by primate research. The other pillars of this sociocognitive complex include mind reading (aka theory of mind), language, and egalitarian dispositions coupled with forms of cooperation, unprecedented in primates, that are crucial adaptations in the hunter-gatherer way of life (Whiten & Erdal 2012). Human cumulative culture supports each of these and is in turn facilitated by them. Roots of each can be discerned through recent primate research, but it is likely that it is the way in which the positive feedbacks among them create a uniquely deep social mind that has made our species such a formidable presence on the planet.

DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

The author is grateful for the support of grant ID40128, "Exploring the Evolutionary Foundations of Cultural Complexity, Creativity and Trust," from the John Templeton Foundation during the writing of this review.

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