

Culture in humans and other animals

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Abstract The study of animal culture is a flourishing field, with culture being recorded in a wide range of taxa, including non-human primates, birds, cetaceans, and rodents. In spite of this research, however, the concept of culture itself remains elusive. There is no universally assented to concept of culture, and there is debate over the connection between culture and related concepts like tradition and social learning. Furthermore, it is not clear whether culture in humans and culture in non-human animals is really the same thing, or merely loose analogues that go by the same name. The purpose of this paper is to explicate core desiderata for a concept of culture and then to construct a concept that meets these desiderata. The paper then applies this concept in both humans and non-human animals.

Keywords Behavior · Culture · Epigenetic · Evolution · Innovation · Social learning · Tradition

Introduction

The study of culture in animals¹ is a burgeoning area of research. Biologists, psychologists, and biological anthropologists are increasingly interested in the study of culture and are routinely describing the behavior of animals—from rats to sperm whales—in terms of culture (Laland and Galef 2009). Additionally, the field of

¹ To avoid repeated uses of ‘non-human’, I will use ‘animal’ in what follows, not as picking out the Anamalia, but as denoting all non-human animals.

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evolutionary-developmental biology is increasingly interested in understanding the modes of inheritance and the impact of non-genetic (epigenetic, behavioral, etc.) transmission on developmental systems (Gissis and Jablonka 2011). There is thus a need for a well-defined concept of culture that explicates the difference between culture and other forms of transmission—like epigenetics—and allows one to answer a host of empirical questions, for example: How widespread is culture among animal species? What impact does culture have on the evolution of animal intelligence or rates of encephalization? How is culture related to behavioral innovation? And what was required for human ancestors to make the transition from being acultural to being cultural? In order to answer these and related questions, there needs to be a general concept of culture that scientists can base their investigations upon. A concept of culture that, say, a priori excludes animals from possessing culture or that leaves culture only vaguely defined will be of little use. But in spite of this need, there has been no fully satisfactory account of what culture is (Laland and Galef 2009). Providing a concept of culture that can answer such questions and that can form a basis for the study of the origin and evolution of culture in animals is the task of this paper.

In developing a concept of culture, I will draw from the work of anthropologists, psychologists, and biologists—both attempts to characterize human culture as well as attempts to characterize animal culture. It might seem that the best way to define culture is to begin with the way in which the concept has been developed in humans and then simply apply it to animals. After all, the concept of culture was originally developed by and for humans. It is not even universally accepted that animals in fact possess—or are capable of possessing—culture (e.g., Galef 1992; Premack and Houser 2006). I counter that there are three reasons why an investigation into the concept of culture should incorporate animal culture from the start. First, as just mentioned, there has been recent intensive interest in animal culture and traditions. Because of this there has been much theoretical work on the concept of culture in animals. Second, there has been little recent work on the concept of culture by cultural anthropologists. In fact, some explicitly avoid using the term culture (Kuper 1999). Third, because of the comparative simplicity of animal culture, understanding it is a much more tractable problem. Once we have a handle on animal culture we can ask whether culture in humans is different in kind or only in degree from animal culture. Let's begin our attempt to construct a concept of culture with a brief survey of some past attempts at defining culture.

Culture concepts in historical context

Culture has been defined countless times over the past century and a half. Kroeber and Kluckhohn's (1952) survey of culture concepts lists 164 definitions, ranging from the catch-all definition of Tyler (1871)—“Culture, or civilization...is that complex whole which includes knowledge, belief, art, law, morals, custom, and any other capabilities and habits acquired by man as a member of society” (p. 1)—to the narrower, more specific definitions discussed below. Some of the definitions limit their scope to humans, while others are more inclusive. Despite the diversity of

definitions of culture, there are a few central properties or phenomena that many of the definitions take to be essential. I will discuss these here. (Note that this is not meant to be an exhaustive survey of how culture is defined in the various research traditions—this would require a monograph. Instead, this is an attempt to selectively highlight some of the central ways in which culture has been understood, which will help to motivate the definition proposed below.)

Culture as heredity

Many definitions of culture refer to an historical or heredity aspect of culture. For Linton (1936), “*culture* means the social heredity of mankind” (p. 78, italics in original). What kind of heredity is cultural heredity? One thing that culture is not is genetic inheritance. One might infer from this that culture is then best understood as being all non-genetic inheritance. This negative, residual category definition of culture has been promoted for many years—see Sapir (1924) for an early example—and the “geographic method” standardly used today in studying animal culture often assumes the view that if you eliminate genes and environment, what remains is culture. Such negative definitions are unsatisfying because it is not clear that all non-genetic inheritance should be considered culture, and it is questionable whether the category of non-genetic inheritance is sufficiently homogeneous to form a coherent category. If this does represent a homogeneous category, then it should be made explicit; one should articulate what culture is, not what it is not.

Culture as social learning

Social learning, like heredity, is another element common to many definitions of culture. Social transmission and heredity appear in early definitions—for example, “Culture includes all behavior patterns socially acquired and socially transmitted” (Hart and Pantzer 1925, p. 707)—and persist through contemporary definitions. Galef (1992) takes culture to consist in specific kinds of social learning: teaching and imitation. Social learning and hereditary conceptions of culture are closely related—social learning can be understood as a mechanism that allows for heredity.

Although social learning is a common central component in many definitions of culture, it remains uncertain whether the category of social learning is one that can readily be specified and demarcated from other forms of learning. Heyes (1994) classically defined social learning as “learning that is influenced by observation of, or interaction with, another animal (typically a conspecific) or its products” (p. 207). But as Sterelny (2009) notes, “it is far from clear that there is a distinctive and identifiable form of learning, social learning, that contrasts with (say) individual trial-and-error learning in response to ecological circumstances” (p. 295). Even if one were able to cleanly demarcate the category of social learning, it is not clear what relation it should bear to culture. McGrew (2009) argues that “[i]f culture equals social learning, then many creatures, e.g., octopus, guppy, and lizard, must be granted cultural status. If culture is more than social learning, then we must look elsewhere for essential criteria. On these grounds, it seems sensible to consider social learning as necessary but not sufficient for culture” (p. 50). Pace McGrew, it

is uncertain whether social learning is necessary or sufficient: If one includes phenomena such as the inheritance of food preferences in rats, which are transmitted across generations through non-genetic means, but which, under some restricted (“psychological” and not “physiological”) ways of understanding ‘learning’, would not count as transmission via social learning.

Culture as behavior patterns

Another way of defining culture is to base it on patterns of behavior: “A culture is a system of interrelated and interdependent habit patterns of response” (Willey 1929, p. 207). Many contemporary biologists and biological anthropologists identify culture with behavior patterns, specifically behaviors that are common or habitual in some groups but absent in others, where this difference cannot be accounted for by genetic or environmental differences. Jablonka and Lamb (2005), for example, “see culture as *a system of socially transmitted patterns of behavior, preferences, and products of animal activities that characterize a group of social animals*. The transmitted behaviors can be skills, practices, habits, beliefs, and so on” (p. 160, italics in original). Within anthropology, the identification of culture with patterns of behavior was common but received heavy criticism by Clifford Geertz. Geertz (1973) is very explicit that culture cannot consist in behavior: “culture is best seen not as complexes of concrete behavior patterns—customs, usages, traditions, habit clusters—as has, by and large, been the case up to now, but a set of control mechanisms—plans, recipes, rules, instructions (what computer engineers call “programs”)—for the governing of behavior” (p. 44). One major shortcoming of definitions based on behavior is that a behavior is a phenotype, and all phenotypic traits are in part build from genes and in part due to environment and (perhaps) culture. Thus, if culture is behavior, then culture cannot cause or explain behavior. The way to get around this problem is—as Geertz suggests—to understand culture as something that lies behind, or brings about, behavior.

Culture as belief

One way to attempt to eschew the problem of defining culture in terms of behavior is to base it on beliefs possessed by and passed among individuals (as Geertz does above). This solution has some precedent. For example, for Wissler (1929) “a tribal culture is...the aggregate of standardized beliefs and procedures followed by the tribe” (p. 341). Schneider (1976) provides another example: “Culture constitutes a body of definitions, premises, postulates, presumptions, propositions, and perceptions about the nature of the universe and man’s place in it” (p. 203). Closely related definitions favored by many cultural anthropologists from the 1970s through the present focus on symbolism and meaning (e.g., Strauss & Quinn 1997). Does defining culture in terms of belief or meaning really avoid the problem that plagues the behavior-based definitions? Is not a (state of) belief also a phenotype? If so, it seems that this is no solution to the problem. Additionally, some varieties of cultural transmission do not require belief. Culture can be transmitted via imitation, but pure imitation does not seem to require beliefs. And there is the related epistemological

worry: If culture is a set of beliefs, then knowledge of culture requires knowledge of beliefs, but gaining such knowledge is a heavy burden, especially for the case of animals.

Culture as information

A further attempt to avoid the problem of culture as phenotype is to base culture on *information* instead of beliefs or behaviors. This is the solution favored by Richerson and Boyd (2005): “Culture is (mostly) information stored in human brains” (p. 61). This seems to provide symmetry between genes and culture: Something is genetic to the extent that it is brought about by genetic information, and something is cultural to the extent that it is brought about by cultural information. I agree with Richerson and Boyd about basing culture on information, but I do not fully agree with their characterization of culture. For one thing, why should we focus the concept of culture on the human nervous system and not define it more generically so that it becomes an empirical question which species are cultural? Another problem is that there is presumably a lot of information stored in human brains that is not cultural. Thus, there needs to be a way to demarcate the cultural information from the non-cultural information. Some other definitions of culture based on information avoid these restrictions (see discussion below), but they suffer from other difficulties.

Culture as environment

The relationship between the environment and culture has long been recognized: “[Culture is] that part of the environment which man has himself created and to which he must adjust himself” (Willey 1929, p. 500). Similarly, for Flinn and Alexander (1982), “[c]ulture can be regarded as an aspect of the environment into which each human is born and must succeed or fail, developed gradually by the succession of humans who have lived throughout history” (p. 397). And there has been recent emphasis on the way in which organisms (both human and non-human) structure their environments and how this affects their ecology and evolution (Odling-Smee et al. 2003). I agree that artifacts clearly can be cultural structures existing outside of the brain (the page that you are currently reading being an obvious example), but, as we will see below, I do not think that this means that we should *define* culture in terms of the environment.

Desiderata in a concept of culture

Now that we have some sense of the range of ways that culture has been conceptualized, it is time to turn to the task of this essay, which is to propose and defend a concept of culture. To begin, let’s ask what is desired in a concept of culture.

The first desideratum in defining culture is that such a definition should not be stipulative. It should instead be explicative—it should aim at capturing what we mean by culture. A stipulative definition is not illuminating and cannot be true or

false. Although it is sometimes useful to introduce a novel term and to stipulate its definition, merely stipulating what we ought to mean by ‘culture’ will not be insightful. If culture is a genuine thing in the world, then a concept of culture should aim at capturing it, not arbitrarily stipulating the meaning of the term. My intention is to produce a definition that does real theoretical work, that synthesizes the seemingly disparate phenomena that are considered cultural—and in so doing shows *why* we are justified in labeling the set of phenomena “culture.”

The very idea that such a synthesis is possible, however, has been called into question, with some suggesting that culture is not a single phenomenon, but a set of distinct components or conditions. McGrew and Tutin (1978) describe six conditions, “innovation, dissemination, standardization, durability, diffusion and tradition” that “form the beginnings of an operational definition” of culture (p. 245, italics in original). Similarly, Whiten et al. (2003) propose ten aspects of human culture and then ask the question of whether chimpanzees exhibit each of them. And Byrne et al. (2004) argue that a single unifying definition of culture should not be sought—that prior attempts to do so are incomplete. They instead offer six distinct “views of culture,” which they organize into three pairs of complementary views: bonus and inefficiency, pattern and sign of mind, and meaning and physical produce. I don’t have the space here to explicate each of these in detail, but I would like to argue that culture as I define it below underlies all of these views. Culture can (1) lead to beneficial (“bonus”) or “inefficient” behaviors, (2) causally explain behavioral patterns and can possess semantic content (“sign of mind”), and (3) lead to physical products and to systems of meaning. I agree that the three pairs described by Byrne et al. are indeed legitimate “views of culture,” and that McGrew and Tutin and Whiten et al. correctly point out distinct manifestations of culture. But it does not follow that this is how culture should be defined. In fact, the concept of culture that I will introduce below can be seen as connecting them, undermining the assertion that one should not seek a single, underlying definition of culture.

The second desideratum is that culture should be able to be used to explain differences between individuals or groups. If this is the case then—since the differences to be explained are phenotypes—culture cannot be identified with phenotypes. This is true because—as mentioned above—all phenotypes are a result of both genetics and environment (and perhaps also culture). Thus, while it is a mistake to hold that a gene or cultural variant is *the cause* of a particular phenotype, genes and cultural variants are legitimate causes of phenotypic differences in a population. Blue eyes are not caused by a particular gene, for example, but their being blue (as opposed to being brown, green, etc.) can be entirely due to a particular gene. For cultural variants to play analogous explanatory roles, they must also act as difference makers.

This desideratum does not, however, imply that for something to count as culture, that it cannot be universal across the species. Whether or not the entire world plays soccer does not answer the question of whether it is cultural. Instead, as we will see below, its being cultural has its basis in the sort of information responsible for the transmission and persistence of the behavior. Nevertheless, if soccer is cultural, then culture must explain the difference between populations that play soccer and other (actual or counterfactual) populations that do not.

Finally, as mentioned above, culture should not be a priori confined to the human species. For the concept of culture to be scientifically useful, it should not exclude animals from being contenders for exhibiting culture. As McGrew (2009) put it, “[d]efinitions are useful only if they clarify matters. All else is pedantry. Define culture as you must to tackle the question at hand; just make it clear, fair, and most of all, productive” (p. 56). A central part of being “productive,” is to leave open important empirical questions, like whether a particular species is cultural.

The definition of culture

I will begin the explication of the concept of culture by producing a concept that is far too broad, and then adding three restrictions that reduce the breadth sufficiently so that the right set of phenomena fall under the rubric of culture. I will then draw out some of the similarities and dissimilarities with existing concepts of culture based on information.

Culture defined

I will begin with this definition: *Culture is information transmitted between individuals or groups.* It is immediately clear that this is far too broad. If a snake bites me, information has been transferred between us. Minimally, the bite carries the information² that the snake is capable of biting humans. But such transmission of information is clearly not culture. To rein in this concept of culture, let’s begin to add our restrictions.

R1 *The information must bring about the reproduction of a behavioral trait.* This first restriction eliminates information that is passed from individual to individual but is nonetheless not culture. For example, the behavior of an alpha male might carry the information that it is an alpha male, but instead of making other males in the group disposed to behave like an alpha male, this information might merely increase their stress or even repress alpha male behavior. It is a central meaning of ‘culture’ that culture brings about the reproduction of behaviors, like those that form traditions. Because a tradition is a phenotypic pattern, it is a mistake to *identify* culture as a kind of tradition, as some have done (e.g., Boesch et al. 1994)—see below for a discussion of the culture-tradition relationship. Nevertheless, bringing about the reproduction of behavior seems to be a necessary condition for culture. While R1 refers to the reproduction of a behavioral trait, it does not specifically require *traditions*. The reason for this is that because traditions are generally taken to be transgenerational patterns, there is no reason that the behavioral trait needs to

² The concept of information has been used and often abused in the philosophy of biology (Moffatt 2011). I hope not to be committing these abuses in founding my account on information. Following Dretske (1983), the view here requires that individual signals are carriers of information. Thus, information in this context is not a mere measure of the average amount of uncertainty that is decreased by a communication channel, as in traditional mathematical accounts of information (Shannon 1948; Shannon and Weaver 1949).

persist across generational time—a short-lived fad is just as much cultural as a well-conserved tradition. This being said, although short-lived fads are culture, it has generally been the stable, long-term cultural patterns that have generated the most empirical interest and scrutiny.

With this restriction in place, we can now modify our original definition: *Culture is information transmitted between individuals or groups*³ *that brings about the reproduction of a behavioral trait.* The first thing to ask is whether this might be too restrictive, whether there can be culture without the reproduction of a behavioral trait. What about children who follow the rule of *not* doing whatever their parents do? Does this example provide a case of cultural transmission without the reproduction of a behavioral type? No it does not, and the reason for this will become clear when we examine how we ought to properly describe the behavior. In such a situation, is it true that there is no reproduction of a behavioral type? At one level the offspring are behaving exactly like their parents, i.e., they are following the same behavioral rule—do other than parents do (DOP). So if my parents wear leather shoes, I can follow this rule by wearing canvas shoes.⁴ What is being transmitted culturally here? One thing that may be transmitted is the rule to DOP. If this is what is culturally transmitted, then this rule is probably not passed simply from parent to offspring. Instead it could be that children observe what other parents and children are doing, note that what they are doing is negatively correlated and, because of this, produce behavior distinct from their own parents. The point is that there is a behavior that is reproduced and is culturally caused. And this is the behavior of doing whatever one's parents are not doing.

There are two ways to object to this move. One is to reply that the DOP rule need not be culturally transmitted. It could be that it is hard wired. Consider a very simple creature that pops into the world with the rule that it should forage differently than its parents. If they forage slowly, it will do so quickly. If they do so in the trees, it will do so on the ground. In these creatures with hardwired dispositions, is it the case that there is cultural transmission occurring? No, this does not fit the concept of culture. If a violent parent brings about submissive children, we do not label this “culture.” There is a culture—a culture of violence, in this case—only if the parents' violence precipitates violence in the children. Thus, not all effects that parents have on children are cultural.

The second way to object to the argument is to claim that the DOP rule is not properly considered a behavior: The behavior is the particular thing that the organism is doing, not some higher-level description of the behavior. DOP, then, is a higher-level behavior, a governing rule, or a metabeavior. One problem with this reply is that it is not obvious that there is a principled way to draw this behavior–metabeavior distinction. This is the case because any particular behavioral token can be subsumed under a number of different types. If described at a very fine grain of detail, every behavioral token represents a unique type. This is true because every

³ The addition of ‘or groups’ to this definition is to not exclude “collective cultures”—cultural variants that are only ascribable to groups, and not possessed (in whole) by any one of the individuals in the group.

⁴ An individual can follow DOP in some domains only. If the individual tries to follow this rule in all domains, it will quickly perish. (The parents eat and breathe, after all.).

performance of a behavior differs in some aspects from every other performance. Furthermore, behaviors are generally performed differently based on the circumstances of the organism, i.e., they incorporate environmental variables. Because of this, an argument against DOP being a behavior cannot be based on the fact that it incorporates a variable, namely, the behavior of the parent. Because of the multiplicity of descriptions of an organism's behavior—none of which is *the* correct description—what is required for there to be an instance of cultural transmission is that (1) there is a reproduction of behavior *at some level of description* and (2) this reproduction is an effect of information acquired from other individuals (or groups of individuals). Now that we have seen why this restriction is needed—and why it is not too restrictive—let's turn to the next restriction.

R2 *The information must flow through the behavior.* Jablonka and Lamb (2005) distinguish epigenetic from behavioral inheritance mechanisms, where culture falls exclusively under the domain of behavioral inheritance. Although this way of drawing the distinction works well for a variety of phenomena, it is not clear that culture and epigenetics can be so cleanly divided. This is because the behavior of an individual can bring about changes in the offspring through epigenetic mechanisms, such as the methylation of germline DNA (e.g., Anway et al. 2005). For example, some research suggests that the offspring (and grandoffspring) of male smokers die younger than they would have had their father (or grandfather) not smoked. Instead of being the result of breathing second-hand smoke (though this could exacerbate the effect), it is thought that the mechanism is epigenetic, where smoking causes the methylation of germline DNA, and these methylation patterns lead to shorter lives in the descendants (Pembrey et al. 2006). It is thus clear that the behavior of a parent can affect their offspring through epigenetic means.

In this example, the tendency of dying young is propagated from generation to generation. I would argue that what keeps this from being culture is not (as Jablonka and Lamb seem to hold) the fact that an epigenetic mechanism is involved in the propagation of the behavior (assuming, for the moment, that “dying young” is a behavior). Rather, it is the fact that dying young is an epiphenomenon: it is caused by the epigenetic methylation, but it does not in turn cause the methylation. Because of this, the pattern of many individuals in the lineage dying young is a pseudotradition. This behavior of the individuals in the parental generation does not precipitate this behavior in the young. If one were to intervene and make the parent live longer, the expected life span of the offspring would remain unchanged.⁵

Although I hold that the case of the smoker's offspring being disposed to die young is not a case of cultural tradition, I do not deny that some cases of cultural transmission can involve epigenetics. Consider the following example: A mother's grooming her pups causes an epigenetic effect in her pups. One of the results of this change is that the pups are in turn more likely to groom their pups once they eventually reproduce. Thus, the grooming behavior is propagated through the generations. This fits the above criteria since it involves information transfer from

⁵ Ignoring, of course, other possible effects of the parents on the life span of their offspring, such as parents who live longer being able to provide more resources for their young.

one individual to another (in this case from parent to offspring), and a behavioral trait is reproduced (in this case grooming). Such an example is not far fetched—new research is pointing to more and more cases in which epigenetic mechanisms can help propagate and sustain behavioral patterns. For example, DNA methylation of promoter elements can affect how genes are expressed and, consequently, behavior (Kaffman and Meaney 2007); and Weaver et al. (2004) found that maternal rat behaviors like licking and grooming could modify the epigenetic states of the offspring's genes.

The realization that there can be epigenetic transmission of cultural behaviors foregrounds an important distinction that is crucial to understanding culture and its relation to the various mechanisms by which culture can be transmitted. The distinction is that between the *channel* through which the information is flowing, and the *content* of the information. Sterelny (2009) perceptively notes that that in many discussions of animal behavior, researchers often shift between conceiving of social learning as learning with social information content and thinking of it as learning information through a social channel. Culture, as I am explicating it here, is information that flows through a channel from one organism (or group of organisms) to another, but it can take an indirect path. The information can flow through the environment (by walking on a particular path, a deer could bias the way that other deer walk, thus creating a traditional path), through the physiology of the organism (a mother rat's diet can be passed on to her pups via internal physiological pathways—in utero (Hepper 1988) or via milk (Galef and Sherry 1973)), or, as just mentioned, it can travel through an epigenetic pathway. Niche construction (Odling-Smee et al. 2003), like epigenetics, can thus serve as part of a cultural channel. The fact that the information flows through a rat's stomach or the ground does not determine whether it is culture. What makes it culture is the source, the recipient, and what effect it has on the recipient. We are now able to add the final restriction to the concept of culture.

R3 The information must have a lasting effect on the form or timing of the resultant behaviors. This restriction is to draw a distinction between mirroring and cultural transmission. Social organisms often mirror the behaviors of others in the population. One dog barking may set off a barking frenzy, but such frenzies do not necessarily change any of the dog's dispositions to bark—the barking merely triggers a preexisting disposition. Similarly, a zebra may begin to run because others in the group started to run. This zebra is led to run from information flowing from the behaviors of conspecifics, and its running brings about the reproduction of the behavior—thus, R1 and R2 are satisfied. But such behavior it is not cultural unless it sticks—unless, that is, the individual is modified in such a way that its behavior (its form or timing) has a lasting effect from the information.

With our three restrictions in place, we can produce our final definition of culture: *Culture is information transmitted between individuals or groups, where this information flows through and brings about the reproduction of, and a lasting change in, the behavioral trait.* Now that we have a concept of culture, let's see how it differs from past information-based definitions of culture and then turn to the question of whether it can make sense of culture in humans and animals.

Other definitions of culture as information

There is a long tradition of defining culture in terms of information, and it is thus not this part of the above definition that is novel. Instead, what I have done is to refine and to make explicit just what role information must play in order for it to be cultural. Other authors that define culture in terms of information often define culture in an overly permissive way, with all information transferred between individuals being cultural. Take Bonner's (1980) definition of culture as "the transfer of information by behavioral means, most particularly by the process of teaching and learning" (p. 9). Such a definition of culture includes any transmission of information via behavior, thus of the three restrictions proposed above, only R2 is required. I hope that the above discussion of R1 and R3 persuasively show that without these, the domain of culture becomes far too broad. Most other definitions are similarly broad. Durham (1991) argues that "[t]o qualify as cultural, a given unit of information must be learned from other individuals [...], not transmitted genetically [...] or acquired from isolated experience" (p. 5). Although this is similarly too expansive (if one reads his criterion as both necessary and sufficient), Durham perceptively notes that "there were fundamental problems in my conceptualization of culture as socially transmitted behaviors or 'traits' rather than the socially conveyed information behind them" (p. 167). He thus rightly identifies culture with the information, not the effects of the information. Others, who may resist providing a complete articulation of the necessary and sufficient conditions for culture, nevertheless hold that information transmission is a necessary condition: "Fidelity of information transmission is required for culture, however it is defined" (Heyes 1993, p. 1004; for further papers on culture as information, see, e.g., Flinn 1997 and Alvard 2003).

In defending culture as information, Cronk (1999) suggests that "[s]ome of the confusion over the value of the idea that we should use the term 'culture' to refer only to socially transmitted information lies in a failure to understand that while culture is indeed not directly observable, it is nonetheless real. Real things that are not directly observable are routine things in many sciences [...] We can observe it only through its effects on behavior, not directly, inferring its presence when behavior forms certain patterns and its absence when those patterns are not present" (p. 13). This, too, is a position I hold. Thus, while many others have argued for culture being based on information, there has not been adequate work describing the precise role that this information must play in order for it to be culture.

As we saw above, however, information-based definitions are not the only ones with contemporary currency. Boesch and Tomasello (1998) point to very different approaches coming from different disciplinary backgrounds, especially evolutionary biology and comparative psychology: "The basic dichotomy is between biological approaches, in which all information that is transmitted nongenetically among members of a group is of interest (e.g., Bonner 1980; Boyd and Richerson 1985; Dawkins 1976; Cavalli-Sforza and Feldman 1981; Munding 1980), and more psychological approaches, in which the main concern is the cognitive and learning mechanisms by means of which such information is transmitted (e.g., Galef 1992, 1996; Tomasello 1990, 1996)" (p. 591). In this essay, I am siding with the

information-based definition. The reason for this is that I think that these should be open empirical questions: Which behavioral/observational/cognitive mechanisms allow for cultural transmission? How do distinct manifestations of these various mechanisms lead to particular manifestations of culture, such as cumulative culture? By defining culture in terms of specific mechanisms, the first, and possibly also the second, questions become determined a priori.

This does not, however, mean that studying mechanisms is not a central part of studying culture, it is merely that culture should not be defined in terms of mechanisms. Studying these mechanisms and the way in which they convey information is vitally important. Call and Carpenter (2002), for example, argue that we may partition the information flowing from the performance of a goal-directed action into three kinds, information about goals, actions (motor patterns), and results. A population-level propagation of a particular kind of result could be due to the transmission of information about goals, actions, results, or some combination thereof. The combination of information transmission that is realized in a particular instance will determine whether the behavior should be considered imitation, emulation, mimicry, etc. (see Figure 9.2 in Call and Carpenter 2002 for a full taxonomy). This partitioning of information is important in understanding cultural dynamics and the differences across species in how traditions are propagated, though they are not necessary for the definition of culture. Any of the three sources can bring about cultural transmission. (For more on the forms of socially transmitted information and their consequences, see also Acerbi et al. 2011; Caldwell et al. 2012; Mersmann et al. 2011; Hopper et al. 2007, 2012).

I will now explore in a little more depth some of the mechanisms associated with cultural transmission and will show how the definition of culture proposed above is able to make sense of both culture in humans and animals.

The scope and mechanisms of cultural transmission

In testing this concept of culture, in seeing whether it includes the right set of phenomena and excludes all that we would exclude from the realm of culture, there are a few key questions we should ask: Is all of what we call culture in humans captured by this concept? Do animals exhibit culture? If so, which ones and in what ways? What are the mechanisms by which culture is transmitted in humans and animals? Let's begin with the general question of the relationship between tradition and culture.

Culture versus tradition

It has been noted that those who study animal culture fall into two camps, those who take 'culture' and 'tradition' to be synonymous and those who do not (Whiten 2009). Those who do not claim synonymy generally reserve 'culture' for a subset of traditions: all culture is traditional but not all traditions are cultural (Whiten and van Schaik 2007). As an example of this later camp, Galef (1992) argues that culture consists in a specific kind of mechanism, namely imitation: no imitation, no culture.

He holds that while animals exhibit traditions, because they do not imitate, they do not exhibit culture.

The definition of culture explicated above also leads me to distinguish culture from tradition, but implies a very different relationship between culture and tradition than that argued for by Whiten and van Schaik. Instead of culture being a kind of tradition, culture is best seen as what *engenders* tradition. Traditions are patterns of behavior, similarities between individuals or groups over generational time, that are caused by culture. This is a view held by, for example, Fragaszy and Perry (2003), when they define tradition as “a distinctive behavior pattern shared by two or more individuals in a social unit, which persists over time and that new practitioners acquire in part through socially aided learning” (p. xiii). Thus, all traditions are cultural (in the sense that what makes a tradition a tradition is culture). Can there be cultural transmission that is not traditional? This depends, of course, on how we understand the notion of a tradition. If traditions require culturally-caused *transgenerational* behavioral similarities, then there can be non-traditional cultural transmission. This would include the kind of transmission that occurs within a generation but that does not persist long enough to cause similarities over generational time. Cultural transmission of this kind certainly occurs in humans—fads, for example—and (animal culture being more conservative) probably occurs less frequently in animals. This thus represents a reversal of Whiten and van Schaik’s (2007) claim that culture is a subset of tradition. Instead, tradition is a subset of cultural behavior.

Because those who study animal behavior generally either equate tradition and culture or see culture as a subset of tradition, this might make one question whether the above explication of culture has gotten things right. Because of this, I will say a few words in defense of this view of culture and point out some problems with the more standard definitions of animal culture. First, take the equation of culture and tradition: There are two reasons, one minor and one major, why culture and tradition should not be equated. The minor reason is that by understanding the terms synonymously, we lose the possibility of maintaining a more nuanced view of culture and tradition—by sharing a definition, it is not an empirical question what the relationship is between culture and tradition. The major problem with this view is that because it is clear that a tradition is a kind of behavior pattern, if culture is tradition then culture is also merely a behavior pattern. As discussed in the [Culture concepts in historical context](#) section, this then leaves us in need of a term for what *explains* this pattern of behavior.

One might counter that it is social learning that plays this role: Social learning is the mechanism and culture/tradition is the effect. But arguing that social learning plays the role of explaining culture/tradition is like arguing that (for a species without culture and in a homogeneous environment) the phenotypic differences between groups of individuals are explained by the mechanism of reproduction. The reason that this is wrong is that it is not reproduction per se that explains parent-offspring similarities—or the differences between different individuals or groups. Instead, it is the informational content of what is passed on—in this case genes—in the act of reproduction that is important. And just as genes have a role to play in such explanations, so cultural has an analogous role to play.

The two ways that scientists understand the relationship between tradition and culture—either as synonymous or as culture as a kind of tradition—make it clear that culture is often seen as a pattern of behavior. In the major papers documenting culture in great apes (Whiten et al. 1999, van Schaik et al. 2003) culture is identified with differences in behavior that are not explained by environmental or genetic differences. How does the concept of culture developed in this paper make sense of the claims of animal culture in these and similar studies? The behavior patterns identified in these studies, instead of being culture, are culturally caused. Thus there is no problem with the class of phenomena that the scientists classify as culture being labeled ‘culture’. It should just be recognized that such patterns, instead of being culture itself, are evidence for culture. This is analogous to the genetic case: A parent-offspring similarity in, say, eye color is not itself genetic, but is evidence for a genetic cause.

Another reason why culture should not be identified with patterns of behavior is that there can be culture in the absence of behavioral heterogeneity. If it were the case that all humans ate mammals, it would not follow that eating mammals is not cultural. It could be that all individuals were culturally identical with respect to this trait. And just as complete behavioral homogeneity causes problems for accounts of culture, the requirement of intra-group homogeneity combined with inter-group heterogeneity also causes problems. Consider again Jablonka and Lamb’s (2005) definition of culture: “a *system of socially transmitted patterns of behavior, preferences, and products of animal activities that characterize a group of social animals*” (p. 160, italics in original), Caldwell and Whiten’s (2011) assertion that “[c]ultural behaviors are those which are (1) specific to members of a group [...] and (2) transmitted via some form of social learning” (p. 653), or Shweder’s (2001) definition of culture as “community-specific ideas about what is true, good, beautiful, and efficient” (p. 437). This understanding of cultural behaviors as ones that *characterize a group* is too restrictive. Instead, the extent to which culture homogenizes groups should be an empirical question, not one of definition. Sargeant and Mann (2009), for example, argue that “many putative cultural behaviors of bottlenose dolphins, particularly foraging behaviors, are not common to an entire population” (p. 154). I agree with Sargeant and Mann that such behaviors should not be considered acultural just because they represent intra-population heterogeneity. (Also see Aunger (1999) for a cutting critique of identifying culture as *shared*.)

Animal culture

Do animals have culture? There are two main ways to deny animal culture. One, as was mentioned above, is to link culture to a particular mechanism. Culture is realized if and only if the mechanism is realized. The second strategy for excluding culture from animals is to exclude animals based not on mechanisms, but on the significance or function of the putative cultural behavior. Let’s begin by considering the first strategy.

It is true that humans are in many ways unique in their forms and capabilities of cultural transmission. Humans appear to have a unique adaptation for pedagogy

(Gergely and Csibra 2006; Csibra and Gergely 2006, 2011) and pedagogy has in turn played a profound role in human evolution (Sterelny 2012). Humans have complex discriminative abilities, giving them high fidelity and selectivity (Over and Carpenter 2012; Nielsen 2012; Gergely and Csibra 2005), and we appear to be uniquely motivated to share psychological states with others (Tomasello et al. 2005), and are uniquely able to successfully navigate complex social arenas (Herrmann et al. 2007) and to conceive of beliefs as motivators for action, independently of their truth values (Call and Tomasello 2008). Human imitative abilities have been offered as a requirement for culture (Galef 1992), and imitation has been shown to be automatic in humans (Lyons et al. 2011) and important in shaping human behavioral repertoires from a very young age (Meltzoff 1988). It is argued that while humans can imitate, animals, even our closest relatives, can merely emulate (Call et al. 2005). Others, however, have suggested animals can imitate (Whiten et al. 2009), or that imitation is not necessary or even unimportant for culture (Heyes 1993).

Mechanisms like imitation, proposed by some as a bar for true culture, certainly have significant consequences for how culture can be manifested. Cumulative culture, for example, is ubiquitous in humans, though all but absent in animals—and it is debated which mechanisms and capacities explain this (Caldwell and Millen 2009, 2010; Laland 2004; Marshall-Pescini and Whiten 2008). These are important debates about the origins and evolution of culture—why even if animals exhibit culture, their cultural variants undergo little evolution (Hopper et al. 2011; Ramsey 2007). But in order to not decide a priori what role culture has and what capacities and mechanisms are necessary for it, the definition of culture must not be tied to specific mechanisms or abilities. It is for this reason that the definition of culture articulated above is as free as possible from requiring particular mechanisms, capacities, abilities, etc.

Let's now consider one more way to resist animal culture. Premack and Houser (2006) take the second strategy mentioned above, taking a particular sort of function to be a necessary condition for something to count as culture. They argue that “the function of human culture is to clarify what people value, what they take seriously in their daily lives, what they will fight for and use to exclude or include others in their groups [...] Based on [this] point [...], we argue that nothing in animal behavior comes remotely close to this aspect of human culture” (p. 275). Using the case of “H-day,” when Sweden switched from driving on the left to driving on the right, they suggest that “[w]hen on a given date and hour, Sweden changed its driving practice, Swedish culture did not change, and neither did the accident rate” (p. 276). I hold that Premack and Houser are wrong, the Swedish change was a cultural change. They were wrong about the accident rate—it precipitously declined with the “H-day” switch, with not a single fatal accident the 2 days following.⁶ But this is not why I think that it should be considered culture. Instead, it is that if we have to assess the values of the putative cultural variants in order for them to count as culture, this provides a severe burden on researchers. They now have to establish not only how these behaviors came about, they must also establish how the animals

⁶ <http://www.time.com/time/magazine/article/0,9171,941144,00.html>.

regard the behaviors. Such a valuation metric is all but impossible to produce as an objective, quantifiable standard. For a trait to be cultural, neither the way it is regarded, nor the fitness significance (Enquist and Ghirlanda 2007; Ehn and Laland 2012), should serve as necessary conditions for traits counting as cultural.

The arguments against animals having culture thus seem weak on conceptual grounds, but they also do not seem to be in line with the thrust of contemporary research. As Laland and Hoppitt (2003) argue, the bar for animals having culture is often higher than that for humans. To be fair, a concept of culture that bridges humans and animals without a priori eliminating any of the taxa from being considered cultural, will set a universal bar for being considered cultural. Furthermore, the evidence for animal culture has recently progressed from captive experiments and observations of geographic trait variations to genuine field experiments (Gruber et al. 2009). It is time, not to artificially exclude animals from possessing culture, but to embrace the exciting contemporary work on animal culture and to produce just the sort of bar that Laland and Hoppitt call for. The above definition is an attempt to help provide this bar. It provides clear and precise criteria for what it takes for information to be cultural, and it does so without artificially excluding particular taxa. Furthermore, the cases of what scientists have judged to be animal culture are, for the most part, culture according to the definition above. And the mechanisms associated with culture—emulation, stimulus enhancement, etc. (see Whiten and Ham's 1992 Fig. 1 for a full taxonomy)—are all mechanisms allowing for the flow of culture under this definition. The definition, then, does a good job articulating animal culture, but can it make sense of the complex and contested domain of human culture?

Human culture

Ironically, in recent decades cultural anthropology has offered a number of criticisms of the use of the term 'culture', with some anthropologists suggesting that one should refrain from its use altogether (Appadurai 1996; Friedman 1994; Keesing 1994; Kuper 1999; Fox 1999), with Clifford (1988) arguing that, "[i]t may be true that the culture concept has served its time" (p. 274). While some have attempted to counter this anti-culture trend (e.g., Brumann 1999), contemporary anthropology retains a strong skepticism about the usefulness (or coherency) of the concept. There are a number of reasons that culture seems problematic to anthropologists. One reason is that some feel that culture is too polysemic, and that, as Kuper (1999) put it, "the more one considers the best modern work on culture by anthropologists, the more advisable it must appear to avoid the hyper-referential word altogether, and to talk more precisely of knowledge, or belief, or art, or technology, or tradition, or even ideology" (p. x). Another objection traces back to *colere*—the Latin root of the word 'culture' meaning, inter alia, *to cultivate*. Just as a field can be in a natural state, fully cultivated, or any state in between, so, it was thought, a people can exist in a spectrum from natural (or "savage") to cultured (or "civilized"). Anthropologists now generally reject this way of thinking about culture—although in common parlance one still hears of one group being more or less cultured than another—and hold that all peoples have a unique culture, not

capable of being placed on a graduated scale. This is analogous to the shift from viewing species as existing on a *scala natura* from the “lower” animals to the “higher” animals to Darwin’s (1859) insight that each species is just as much a product of evolution as any other, and that—contra Lamarck (1809)—the “lower” species are not evolving toward the higher.

But even this shift from the *scala natura* view to a more egalitarian view is taken to be problematic. One reason for this is that many anthropologists feel that to discuss, say, “the Machiguenga culture” implies that the Machiguenga are homogeneous, unchanging, and (prior to contact) pure. The critics hold that the implication is invalid because peoples like the Machiguenga are temporally and spatially heterogeneous and often lack clear boundaries. While I agree with many of these critiques, I feel that the critics have gone too far. Although—as is the case quite generally in the sciences—there is a cost to making generalizations (information is always lost), it is only through generalizations and models that understanding is gained. The same is true of cultures. Speaking of the dispositions of the Machiguenga has its place in understanding the Machiguenga, even though the dispositions may not be shared by all of the individuals. The thick descriptions and tendencies to avoid generalization of contemporary cultural anthropology is not unlike the natural historian, who represents the habits of species and characteristics of places in rich detail. But in addition to natural history one can practice ecology, which often deals with the same phenomena, but at a more general level and with a heavier reliance on abstract models. And just as to condone natural history does not constitute an attack on ecology, to condone ethnography is not to attack more general conceptions of culture. Natural historians and ecologists are simply asking different questions and applying appropriately distinct techniques to try to answer the questions.

Furthermore, even those anthropologists who hold that one should eschew the term ‘culture’ have difficulty ridding themselves of the concept. In some cases this has resulted in simply swapping the word culture for another, less familiar word or phrase. Take the example of Bourdieu’s (1990) concept *habitus*. ‘Habitus’ is defined as “a system of acquired dispositions functioning on the practical level as categories of perception and assessment...as well as being the organizing principles of action” (p. 13). This definition, instead of being an alternative to culture, is simply one among many attempts to define culture.

Given both the necessity and the diversity of the concepts of culture, let’s now examine several of the roles that ‘culture’ plays in discussions of humans and see the degree to which the concept developed above captures these roles. In humans, the concept of culture is used variously. We speak of such things as cultural behaviors, events, or artifacts, pop culture and high culture, and we hold that cultures sometimes go extinct or hybridize with other cultures. Often when ‘culture’ is used in such ways, it is not culture itself that is being referred to, but instead actual behaviors or objects. Let’s examine some of these uses of ‘culture’ in more detail.

Individual behavior

An individual’s behavior is sometimes taken to be “cultural.” Culture in this sense is related to—or even synonymous with—tradition: a behavior is cultural just in

case it is part of some tradition. This use of ‘culture’ is fully compatible with the concept developed above: traditional behaviors are cultural because they are culturally caused.

Group behavior

It is common to refer to the culture of specific groups, e.g., American culture, Southern culture, Quaker culture. This use is tied to both tradition (Quaker culture, e.g., is in part constituted by a group-level tradition) as well as the group-level distinctiveness (Quakers behave differently than other folks). This use of ‘culture’ is also fully compatible with the concept developed above: Quaker culture is culture because the distinctive Quaker behaviors are culturally caused and the distinctiveness consists in a set of distinctive cultural variants.

High/Low culture

Some events are classified as *high culture* and others as *low culture*. Sometimes high culture events are simply referred to as cultural events, whereas low culture is not culture. How can we make sense of this distinction in light of the concept of culture developed above? While it is desirable to try to capture the variety of ways that the term culture is used, one should not expect a single concept of culture to capture all of the diverse uses of the term. In this case, there is a normative component to the term culture: Cultural (or high cultural) events are taken to be better (in one way or another) than acultural (or low cultural) events. This normative component of the culture is not part of the concept developed above.

Cultural artifacts

Some human creations are taken to be cultural objects. A cultural object can be understood as an artifact resulting from cultural behavior. Since not all human behaviors are cultural, not all artifacts are cultural. The more innovative a behavior is, the less it is cultural (though such an innovation can become socially transmitted and thus become cultural). See Ramsey et al. (2007) for a discussion of innovation and its connection to culture.

Is human and animal culture “the same”?

We have seen that the concept of culture developed above applies to both humans and animals. But does it therefore follow that animal and human culture is *the same*? First, let’s consider what this question means. Sameness in science is a heterogeneous category; it includes sameness of form, function, composition, and the more illusive sameness concept known as homology, which is purported to hold in the absence of sameness of form, function, and composition (Ramsey and Peterson 2012). Sameness of function is often termed “analogy” and analogous traits are generally contrasted with homologous ones. This distinction is an

important one in assessing the controversies over whether animal behavior can legitimately be considered “cultural.” Consider Galef’s (1992) argument that it “can be misleading to speak of an evolution of culture in animals (e.g., Bonner 1980); this usage suggests homology when there is evidence only of analogy” (p. 172). He goes on to concede that one can legitimately refer to analogous parts by the same name, but that one must be careful not to infer a common evolutionary origin from a mere analogy:

It might be argued that it is no more misleading to talk about “culture” in mammals and humans than it is to discuss the “wings” of birds and bats or the “eyes” of vertebrates and insects. All three cases involve using the same label for analogous features rather than for homologous ones. There is no problem with using the labels “wings” or “eyes” to refer to analogous structures, however, because no one suggests that bat wings evolved from bird wings or that vertebrate eyes evolved from invertebrate ones. (p. 172)

In response to Galef’s argument, I agree that culture, as the concept is explicated above, in no way implies a relation of homology. Culture is based on the transmission of information, and sameness of information does not imply sameness of evolutionary origin, i.e., homologousness. Thus, the above concept of culture does not imply any claims about homology relations among cultural species. Instead, as de Waal and Bonnie (2009) point out, culture is like respiration: “In the same way that the definition of respiration does not specify whether the process takes place through lungs or gills...the concept of cultural propagation does not need to specify how organisms acquire behavior from each other” (p. 21).

Thus the question to ask of a cultural species is (1) what mechanisms/abilities/dispositions (MAD) underlie the cultural behavior? and (2) are any of these MADs homologous across species? If the latter question is answered in the affirmative, then the third question to ask is whether (3) these MADs were the basis of culture in the most recent common ancestor of these species. If it turns out that some of the MADs that underlie culture are the same across species, but that (3) is false, then it follows that culture may not be homologous, but may instead represent a deep homology (Shubin et al. 2009). This is analogous to the situation with vertebrate and invertebrate eyes: both lineages have eyes, their most recent common ancestor lacked eyes, but there is overlap in the role of specific genes in building eyes. The PAX6 gene, for example, not only plays an important role in the development of the eye, but mutations in the gene can have similar effects across taxa, such as *Aniridia* in humans, *Small eye* in mice, and *ey* in *Drosophila* (Quiring et al. 1994). Such mutations point to a deep homology across eyes, not a relation of homology.

The question of whether culture in humans and animals is homologous is thus dependent not only on the homologous character of the underlying cultural capacities, but also on the relationship of culture to these capacities over evolutionary time. This question is very difficult to answer not only because the relation to culture over time of these capacities is not well known, but the question of whether the capacities themselves are homologous is also not well known. As de Waal and Bonnie (2009) notes “the question whether human and ape cognition are homologous will remain unanswerable until we have far more precise definitions

and tests of the underlying capacities” (p. 21). The most probable answer is that while some human mechanisms for cultural transmission are homologous with those underlying cultural transmission in other species, humans have some unique mechanisms as well (Tennie et al. 2009).

The question of the homology of cultural capacities is therefore one that is very difficult to answer, but it is also not a question that needs to be answered before we can discuss and study culture in animals.

Conclusions

Although it is impossible to capture all of the various meanings of ‘culture’ with a single concept, there is a need for a well-defined, fully explicated concept of culture that biologists, anthropologists, and psychologists can help themselves to. In this paper I have attempted to provide such a concept. Culture is defined as information transmitted between individuals or groups, where this information flows through and brings about the reproduction of, and a lasting change in, the behavioral trait. Instead of merely stipulating a definition of culture, in creating this definition I have tried to be sensitive to the way in which the concept is used by scientists and others to describe culture in both human and animals.

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References

- Acerbi A, Tennie C, Nunn CL (2011) Modeling imitation and emulation in constrained search spaces. *Learn Behav* 39(2):104–114
- Alvard MS (2003) The adaptive nature of culture. *Evol Anthropol Issues News Rev* 12(3):136–149
- Anway MD, Cupp AS, Uzumcu M, Skinner MK (2005) Epigenetic transgenerational actions of endocrine disruptors and male fertility. *Science* 308:1466–1469
- Appadurai A (1996) *Modernity at large: cultural dimensions of globalization*, vol 1. University of Minnesota Press, Minneapolis
- Aunger R (1999) Culture as consensus: against idealism/contra consensus; cultural consensus as a statistical model. *Curr Anthropol* 40(S1):93–101
- Boesch C, Tomasello M (1998) Chimpanzee and human cultures. *Curr Anthropol* 39(5):591–614
- Boesch C, Marchesi P, Marchesi N, Fruth B, Joulain F (1994) Is nutcracking in wild chimpanzees a cultural behaviour? *J Hum Evol* 26:325–338
- Bonner JT (1980) *The evolution of culture in animals*. Princeton University Press, Princeton, NJ
- Bourdieu P (1990) *In other words: essays towards a reflexive sociology*. Stanford University Press, Palo Alto, CA
- Boyd R, Richerson PJ (1985) *Culture and the evolutionary process*. The University of Chicago Press, Chicago
- Boyd R, Richerson PJ (2005) *The origin and evolution of cultures*. Oxford University Press, Oxford
- Brumann C (1999) Writing for culture. *Curr Anthropol* 40(S1):1–27
- Byrne RW, Barnard PJ, Davidson I, Janik VM, McGrew WC, Miklósi A, Wiessner P (2004) Understanding culture across species. *Trends Cogn Sci* 8(8):341–346
- Caldwell CA, Millen AE (2009) Social learning mechanisms and cumulative cultural evolution is imitation necessary? *Psychol Sci* 20(12):1478–1483

- Caldwell CA, Millen AE (2010) Human cumulative culture in the laboratory: effects of (Micro) population size. *Learn Behav* 38(3):310–318
- Caldwell CA, Whiten A (2011) Social learning in monkeys and apes: cultural animals? In: Campbell CJ, Fuentes A, MacKinnon KC, Panger M (eds) *Primates in perspective*. Oxford University Press, Oxford, pp 652–662
- Caldwell CA, Schillinger K, Evans CL, Hopper LM (2012) End state copying by Humans (*Homo Sapiens*): implications for a comparative perspective on cumulative culture. *J Comp Psychol* 126(2):161
- Call J, Carpenter M (2002) Three sources of information in social learning. In: Dautenhahn K, Nehaniv CL (eds) *Imitation in animals and artifacts*. MIT Press, Cambridge, MA, pp 211–228
- Call J, Tomasello M (2008) Does the chimpanzee have a theory of mind? 30 Years later. *Trends Cogn Sci* 12(5):187–192
- Call J, Carpenter M, Tomasello M (2005) Copying results and copying actions in the process of social learning: chimpanzees (*pan troglodytes*) and human children (*Homo Sapiens*). *Animal Cogn* 8(3):151–163
- Cavalli-Sforza LL, Feldman MW (1981) *Cultural transmission and evolution*. Princeton University Press, Princeton
- Clifford J (1988) *The predicament of culture: twentieth-century ethnography, literature, and art*. Harvard University Press, Cambridge
- Cronk L (1999) *That complex whole*. Westview Press, Boulder
- Csibra G, Gergely G (2006) Social learning and social cognition: the case for pedagogy. *Process Change Brain Cogn Dev Atten Perform XXI*:249–274
- Csibra G, Gergely G (2011) Natural pedagogy as evolutionary adaptation. *Philos Trans R Soc B Biol Sci* 366(1567):1149–1157
- Darwin Charles (1859) *On the origin of species by means of natural selection*. Murray, London
- Dawkins R (1976) *The selfish gene*. Oxford University Press, Oxford
- de Waal FBM, Bonnie KE (2009) In tune with others: the social side of primate culture. In: Laland KN, Galef BG (eds) *The question of animal culture*. Harvard University Press, Cambridge, pp 19–40
- Dretske F (1983) *Knowledge and the flow of information*. MIT Press, Cambridge
- Durham WH (1991) *Coevolution*. Stanford University Press, Palo Alto, CA
- Ehn M, Laland K (2012) Adaptive strategies for cumulative cultural learning. *J Theor Biol* 301:103–111
- Enquist M, Ghirlanda S (2007) Evolution of social learning does not explain the origin of human cumulative culture. *J Theor Biol* 246(1):129–135
- Flinn MV (1997) Culture and the evolution of social learning. *Evol Human Behav* 18(1):23–67
- Flinn MV, Alexander RD (1982) Culture theory: the developing synthesis from biology. *Human Ecol* 10(3):383–400
- Fox RG (1999) Culture—a second chance? *Curr Anthropol* 40(S1):Si–Sii
- Fragaszy DM, Perry S (2003) *The biology of traditions: models and evidence*. Cambridge University Press, Cambridge
- Friedman J (1994) *Cultural identity and global process*, vol 31. Sage Publications Ltd, Thousand Oaks
- Galef BG (1992) The question of animal culture. *Human Nat* 3:157–178
- Galef BG Jr (1996) Social enhancement of food preferences in Norway rats: a brief review. In: Heyes C, Galef BG Jr (eds) *Social learning in animals: the roots of culture*. Academic Press, New York, pp 49–64
- Galef BG, Sherry DF (1973) Mother's milk: a medium for transmission of cues reflecting the flavor of mother's diet. *J Comp Physiol Psychol* 83:374–378
- Geertz C (1973) *The interpretation of cultures*. Basic Books, New York
- Gergely G, Csibra G (2005) The social construction of the cultural mind: imitative learning as a mechanism of human pedagogy. *Interact Stud* 6(3):463–481
- Gergely G, Csibra G (2006) Sylvia's recipe: the role of imitation and pedagogy in the transmission of cultural knowledge. In: Enfield NJ, Levenson SC (eds) *Roots of human sociality: culture, cognition, and human interaction*. Berg Publishers, Oxford, pp 229–255
- Gissis SB, Jablonka E (2011) *Transformations of lamarckism: from subtle fluids to molecular biology*. The MIT Press, Cambridge
- Gruber T, Muller MN, Strimling P, Wrangham R, Zuberbuhler K (2009) Wild chimpanzees rely on cultural knowledge to solve an experimental honey acquisition task. *Curr Biol* 19(21):1806–1810
- Hart H, Pantzer A (1925) Have subhuman animals culture? *Am J Sociol* 30:703–709

- Hepper PG (1988) Adaptive fetal learning: prenatal exposure to garlic affects postnatal preferences. *Anim Behav* 36(3):935–936
- Herrmann E, Call J, Hernández-Lloreda MV, Hare B, Tomasello M (2007) Humans have evolved specialized skills of social cognition: the cultural intelligence hypothesis. *Science* 317(5843):1360–1366
- Heyes CM (1993) Imitation, culture and cognition. *Animal Behav* 46(5):999–1010
- Heyes CM (1994) Social learning in animals: categories and mechanisms. *Biol Rev* 69(2):207–231
- Hopper LM, Spiteri A, Lambeth SP, Schapiro SJ, Horner V, Whiten A (2007) Experimental studies of traditions and underlying transmission processes in chimpanzees. *Anim Behav* 73(6):1021–1032
- Hopper LM, Schapiro SJ, Lambeth SP, Brosnan SF (2011) Chimpanzees' socially maintained food preferences indicate both conservatism and conformity. *Animal Behav* 81(6):1195–1202
- Hopper LM, Marshall-Pescini S, Whiten A (2012) Social learning and culture in child and chimpanzee. In: De Waal FBM, Ferrari PF (eds) *The primate mind: built to connect with other minds*. Harvard University Press, Cambridge, 99–118
- Jablonka E, Lamb M (2005) *Evolution in four dimensions—genetic, epigenetic, behavioral, and symbolic variation in the history of life*. MIT Press, Cambridge
- Kaffman A, Meaney MJ (2007) Neurodevelopmental sequelae of postnatal maternal care in rodents: clinical and research implications of molecular insights. *J Child Psychol Psychiatry* 48:224–244
- Keesing RM (1994) Theories of culture revisited. In: Borofsky R (ed) *Assessing cultural anthropology*. McGraw-Hill Inc, New York, pp 301–310
- Kroeber AL, Kluckhohn C (1952) *Culture: a critical review of concepts and definitions*. The Museum, Cambridge
- Kuper A (1999) *Culture: an anthropologists' account*. Harvard University Press, Cambridge
- Laland KN (2004) Social learning strategies. *Learn Behav* 32(1):4–14
- Laland KN, Galef BG (2009) *The question of animal culture*. Harvard University Press, Cambridge
- Laland KN, Hoppitt W (2003) Do animals have culture? *Evol Anthropol Issues News Rev* 12(3):150–159
- Lamarck JB (1809) *Philosophie zoologique*. C. Martins, Paris
- Linton R (1936) *The study of man*. Appleton-Century Crofts, New York
- Lyons DE, Damrosch DH, Lin JK, Macris DM, Keil FC (2011) The scope and limits of overimitation in the transmission of artefact culture. *Philos Trans R Soc B Biol Sci* 366(1567):1158–1167
- Marshall-Pescini S, Whiten A (2008) Chimpanzees (*Pan Troglodytes*) and the question of cumulative culture: an experimental approach. *Animal Cogn* 11(3):449–456
- McGrew WC (2009) Ten dispatches from the chimpanzee culture wars, plus postscript (revisiting the battlefronts). In: Laland KN, Galef BG (eds) *The question of animal culture*. Harvard University Press, Cambridge, pp 41–69
- McGrew WC, Tutin CEG (1978) Evidence for a social custom in wild chimpanzees? *Man* 13(2):234–251
- Meltzoff AN (1988) Infant imitation after a 1-week delay: long-term memory for novel acts and multiple stimuli. *Dev Psychol* 24(4):470
- Mersmann D, Tomasello M, Call J, Kaminski J, Taborsky M (2011) Simple mechanisms can explain social learning in domestic dogs (*Canis Familiaris*). *Ethology* 117:1–16
- Moffatt B (2011) Conflations in the causal account of information undermine the parity thesis. *Philos Sci* 78:284–302
- Mundinger PC (1980) Animal cultures and a general theory of cultural evolution. *Ethol Sociobiol* 1(3):183–223
- Nielsen M (2012) Imitation, pretend play, and childhood: essential elements in the evolution of human culture? *J Comp Psychol* 126(2):170–181
- Odling-Smee FJ, Laland KN, Feldman MW (2003) *Niche construction: the neglected process in evolution*. Princeton University Press, Princeton
- Over H, Carpenter M (2012) Putting the social into social learning: explaining both selectivity and fidelity in children's copying behavior. *J Comp Psychol* 126(2):182–192
- Pembrey ME, Bygren LO, Kaati G, Edvinsson S, Northstone K, Sjöström M, Golding J, The ALSPAC Study Team (2006) Sex-specific, male-line transgenerational responses in humans. *Eur J Human Genet* 14:159–166
- Premack D, Houser MD (2006) Why animals do not have culture. In: Levinson SC, Jaisson P (eds) *Evolution and culture*. MIT Press, Cambridge
- Quiring R, Walldorf U, Klöter U, Gehring WJ (1994) Homology of the eyeless gene of *Drosophila* to the small eye gene in mice and *Aniridia* in humans. *Science* 265:785–789
- Ramsey G (2007) The fundamental constraint on the evolution of culture. *Biol Philos* 22:401–414

- Ramsey G, Peterson AS (2012) Sameness in biology. *Philos Sci* 79(2):255–275
- Ramsey G, Bastian ML, van Schaik C (2007) Animal innovation defined and operationalized. *Behav Brain Sci* 30:393–437
- Richerson PJ, Boyd R (2005) Not by genes alone: how culture transformed human evolution. The University of Chicago Press, Chicago
- Sapir E (1924) Culture, genuine and spurious. *Am J Sociol* 29:401–429
- Sargeant BL, Mann J (2009) From social learning to culture: Intrapopulation variation in bottlenose dolphins. In: Laland KN, Galef BG (eds) *The question of animal culture*. Harvard University Press, Cambridge, pp 152–173
- Schneider D (1976) Notes toward a theory of culture. In: Basso KH, Selby HA (eds) *Meaning and anthropology*. University of New Mexico Press, Albuquerque, 197–220
- Shannon CE (1948) A mathematical theory of communication. *Bell Syst Tech J* 27:379–423
- Shannon CE, Weaver W (1949) *The mathematical theory of communication*. University of Illinois Press, Urbana
- Shubin Neil, Tabin Cliff, Carroll Sean (2009) Deep homology and the origins of evolutionary novelty. *Nature* 457:818–823
- Shweder RA (2001) Rethinking the object of anthropology and ending up where Kroeber and Kluckhohn began. *Am Anthropol* 103(2):437–440
- Sterelny K (2009) Peacekeeping in the culture wars. In: Laland KN, Galef BG (eds) *The question of animal culture*. Harvard University Press, Cambridge, pp 288–304
- Sterelny K (2012) *The evolved apprentice*. MIT Press, Cambridge, MA
- Strauss C, Quinn N (1997) *A cognitive theory of cultural meaning*. Cambridge University Press, Cambridge
- Tennie C, Call J, Tomasello M (2009) Ratcheting up the ratchet: on the evolution of cumulative culture. *Philos Trans R Soc B Biol Sci* 364(1528):2405–2415
- Tomasello M (1990) Cultural transmission in the tool use and communicatory signaling of chimpanzees? In: Parker S, Gibson K (eds) *‘Language’ and intelligence in monkeys and apes: comparative developmental perspectives*. Cambridge University Press, Cambridge, pp 274–311
- Tomasello M (1996) Do apes ape? In: Heyes CM, Galef BG Jr (eds) *Social learning in animals: the roots of culture*. Academic Press, San Diego, CA, USA, pp 319–346
- Tomasello M, Carpenter M, Call J, Behne T, Moll H (2005) Understanding and sharing intentions: the origins of cultural cognition. *Behav Brain Sci* 28(5):675–690
- Tyler EB (1871) *Primitive culture*. Brentano’s, New York
- van Schaik CP, Ancrenaz M, Borgen G, Galdikas B, Knott CD, Singleton I, Suzuki A, Utami SS, Merrill MY (2003) Orangutan cultures and the evolution of material culture. *Science* 299:102–105
- Weaver ICG, Cervoni N, Champagne FA, D’Alessio AC, Sharma S, Seckl JR, Dymov S, Szyf M, Meaney MJ (2004) Epigenetic programming by maternal behavior. *Nat Neurosci* 7:847–854
- Whiten A (2009) The identification and differentiation of culture in chimpanzees and other animals: from natural history to diffusion experiments. In: Laland KN, Galef BG (eds) *The question of animal culture*. Harvard University Press, Cambridge, pp 99–124
- Whiten A, Ham R (1992) On the nature and evolution of imitation in the animal kingdom: reappraisal of a century of research. *Adv Study Behav* 21:239–283
- Whiten A, van Schaik CP (2007) The evolution of animal ‘cultures’ and social intelligence. *Phil Trans R Soc B* 362(1480):603–620
- Whiten A, Goodall J, McGrew WC, Nishida T, Reynolds V, Sugiyama Y, Tutin CEG, Wrangham RW, Boesch C (1999) Cultures in chimpanzees. *Nature* 399:682–685
- Whiten A, Horner V, Marshall-Pescini S (2003) Cultural panthropology. *Evol Anthropol Issues News Rev* 12(2):92–105
- Whiten A, McGuigan N, Marshall-Pescini S, Hopper LM (2009) Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. *Philos Trans R Soc B Biol Sci* 364(1528):2417–2428
- Willy EE (1929) The validity of the culture concept. *Am J Sociol* 35:204–219
- Wissler C (1929) *Introduction to social anthropology*. Henry Holt and Co, New York