Overview

Comparative cultural cognition

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Cultural learning is an adaptive mechanism which can lead to changes in behavior and cognition much faster than naturally selected genetic change. Although social learning is prevalent in many species, the capacity for significant cumulative culture remains restricted to humans. This capacity has been a driving force behind the evolution of complexity in our technologies and societies, and has allowed us to become the most widespread mammal on earth. The comparative study of cultural cognition assesses where important differences lie between species. A combination of observational studies in the wild, experimental studies in captivity, and field experiments together provide the most comprehensive methods with which to tackle the question. © 2009 John Wiley & Sons, Ltd. *WIREs Cogn Sci* 2010 1 23–31

The capacity for culture is integral to being human, and humans exhibit more complex cultural variants than any other species. Our cultural abilities have allowed us to populate a more diverse range of habitats, sustain more complex societies, and produce more intricate technologies than other animals.[1,2] Cultural variation is socially acquired and can bring about changes in cognition and behavior in a much shorter time than genetic or individually learned change.[3,4] Many nonhuman species exhibit social learning, but humans differ in generating an increasingly complex accumulation of changes across generations.[1] Exploring cultural cognition in other species can highlight important similarities or differences between humans and other animals. This is useful in tracing the evolution of distinctly human cognition,[5,6] and investigating how culture, as a nongenetic evolutionary process, interacts with biological evolution.[3,7]

The way in which we humans think about culture can have serious consequences for how we approach research with other animals. Different definitions of culture and its underlying processes can lead to significant differences in the perception of cultural abilities across species. Depending on which elements are deemed most important, very different conclusions emerge. Here we provide a general overview of recent advances in comparative cultural cognition, exploring evidence from free-ranging populations and new techniques in captive experiments used to trace culture in a wide range of species.

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DEFINING CULTURE

As Laland and Hoppitt state, 'culture is as rare or as common among animals as it is defined to be' (Ref 8, p. 151). Culture has been described as loosely as any behavioral patterns differing between groups, which cannot be explained by genetic differences[9] or as strictly as behavior patterns spread by teaching, language, or symbolism.[10,11] Depending on the precise definition, culture may thus be limited to humans or open to a whole range of species, even including some bacteria.[8,9,12] This is further complicated by a disagreement on how to label specific cultural processes. A distinction is often made between 'behavioral traditions' and 'culture'. For some, including many biologists, the terms 'tradition' and 'culture' are interchangeable.[8] Others prefer to say that nonhuman animals exhibit 'proto-cultures' and true culture is only found in humans.[13]

Definitions that are too strict and limit culture to humans do not allow for comparisons of the roots of culture across species. Alternatively, definitions that are too vague make it difficult to pinpoint and decipher particular mechanisms or differences between animals. Fragaszy offers a comprehensive definition of a tradition as 'a behavioral practice that is shared among members of a group; is performed repeatedly over a period of time (i.e., it is enduring); and depends to a measurable degree on social contributions to individual learning for its appearance in new practitioners' (Ref 14, p. 61). Regardless of whether

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this behavior is labeled as 'culture' or 'tradition', it usefully highlights several critical features that appear in most definitions. The first is that some degree of cohesion to a particular behavior must exist within a group. Secondly, behavioral patterns in one group should differ from those in another. Finally, this behavior should be socially acquired and sustained within the group, and differences between groups should not be explained by genetic or environmental processes. However, it may be that although many species exhibit culture or traditions, they do not necessarily exhibit similar forms. Animals may differ in terms of the type or quantity of information being socially transmitted, or in the social learning process itself. This in turn may affect how long behavioral variants survive across generations or how well the information spreads throughout a group, or between groups. Long-term observational studies of free-ranging populations help to identify differing behavior patterns and follow the spread of new innovations. Captive experiments can help decipher what particular social learning mechanisms are at play and how these may differ across species.

IDENTIFYING CULTURE IN FREE-RANGING POPULATIONS

Which Animals Are Cultural?

Social learning is a widespread phenomenon in the wild. It can act as a shortcut or reduce the risks involved in individual learning. For example, animals can gain information about where and how to find food or mates, where to sleep, or how to avoid predators. The wealth of literature on the topic is immense.[15,16] Some of these are short-lived uses of socially acquired information, as in where to find the most plentiful food on a particular day, but others are less ephemeral and can lead to durable cultural behaviors. Long-term observations have led to the discovery of different behavioral patterns in the same species across populations with no apparent ecological explanation. These range from single variants to diverse collections of multiple traditions. The criteria set for culture determine which of these qualify. Under some definitions, a single variant between groups suffices. A large and diverse number of animals display single variants (e.g., vocal dialects in birds,[17] and cetaceans[18–20] and foraging techniques in monkeys,[21] rats,[22] and insects[23]).

In contrast, Whiten and van Schaik[24] urge that a population must be exhibiting an assemblage of traditions in order to be described as cultural. Chimpanzees, orangutans, and capuchin monkeys qualify under these criteria,[6,25,26] possibly some cetaceans[27] and perhaps one corvid species, the New Caledonian crow.[28] The difficulty with such field observations is determining whether or not variants are definitely socially transmitted. It is most commonly inferred that such behaviors are spread by social learning because they diffuse through the group too rapidly to be explained by genetic or ecological factors. The subject can be tackled in part by gathering data together across field sites for a given species, by careful analysis of the rate of spread of new behaviors throughout a group, by examination of the ontogeny of foraging techniques, or through experimental manipulation with free-ranging populations.

Behavioral Patterns Across Field Sites

In order to identify possible cultural variants, differences between groups of the same species living in similar habitats must first be established. Specific behaviors can then be identified as present or absent across different populations.[29–31] Recently researchers at nine long-term chimpanzee field study sites went one step further, pooling their data and identifying the frequency with which particular behaviors were performed within their groups. Those behaviors that were performed by at least several group members in at least one group but were absent from at least one other were identified as cultural variants. Researchers identified a total of 39 cultural variants spanning several domains, including foraging techniques, tool use, grooming, and social and courtship styles.[6,32] This process has since been repeated with orangutans, identifying 24 variants across technical and social domains.[25] In white-faced capuchins[26,33] and Japanese macaques,[34,35] some foraging techniques, social customs, and games were found in some groups and not in others. Such variation is not restricted to primates. Although the same approach has yet to be completed across sites, dolphins exhibit evidence of behavioral traditions across domains as well.[27,36] In addition, New Caledonian crows show evidence of complex, layered behavioral variations involving tool use that may be cultural.[28]

Such a rich and diverse range of variation across behavioral domains is highly suggestive of culture. In this way, each population is distinguished from others by its collection of traditions, rather than just one behavioral variant. It is particularly suggestive that some of these behaviors are purely social, so an environmental explanation is unlikely.[6,33] Phylogenetic analyses have also concluded that genetic explanations are not sufficient to explain behavioral differences between chimpanzee populations.[37,38] In

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addition, van Schaik[25] found a positive relationship between the number of cultural variants displayed and the opportunities to learn from others. This may not be a straightforward procedure, however, and has been criticized for not ruling out ecological explanations well enough.[8] For example, Whiten et al.[6] identified ant dipping as a cultural difference between groups of chimpanzees, with Gombe and Taï chimpanzees using different methods to fish for ants. Humle and Matsuzawa[39] studied this behavior in Bossou, where both forms are used, and found that the chosen technique depended on the species of prey, which varied in terms of aggressiveness (see Refs. 40,41 for more recent analyses that include both individual and social learning explanations). This work shows that ecological explanations cannot be ruled out completely, and caution should be exercised when cultural inferences are made.

Tracing the Spread of Variants: Individual Versus Social Learning

Modeling Diffusion Patterns

The diffusion of new behavioral traits can be investigated by modeling the expected rate at which a behavior would spread through social versus individual learning.[42] These models can then be compared against actual data from free-ranging animals. If the shape of the distribution curve differs significantly from the model, it might be the result of individual learning or other processes. It is generally assumed that social learning will occur at an accelerating rate: as more individuals learn the behavior and become potential demonstrators, there is a greater likelihood of naïve observers learning the behavior.[43] This approach can be used across a broad range of species. However, results should still be approached with caution. Distribution curves can overly simplify how animals behave, and many factors could potentially affect the distribution of learning. For example, levels of scrounging or identity-dependent social learning can easily affect the number of individuals learning a given behavior.[43] As the number of skilled individuals increases, the opportunity to scrounge increases, so some individuals may adopt this strategy instead.[44] Social tolerance can also play an important role in the spread of new behaviors.[45–48] Some individuals may only learn from specific group members (e.g., close kin), which can affect the rate at which individuals acquire new behaviors.

The Ontogeny of Foraging Skills

Researchers can also trace the development of specific skills throughout ontogeny, looking for patterns of matching behavior between young and close associates. Lonsdorf and colleagues traced the development of termite fishing in female and male juvenile chimpanzees. They found that females observed their mothers performing the task longer than males and not only mastered the technique around 1 year earlier, but also adopted techniques like their mothers'.[49,50] Young male tufted capuchin monkeys also use significantly similar foraging techniques to males they are in close association with.[51] In dolphins, mothers and daughters have similarly sized behavioral repertoires, and display significantly correlated foraging techniques.[36]

Field Experiments

Many of the above methods have been criticized for not ruling out ecological or genetic explanations well enough.[8] In the case of chimpanzee tool-using behavior, for example, it may not only be a matter of checking that the appropriate tools are accessible across sites, but differences may be confounded by the availability of alternative resources which may lessen the necessity of a particular behavior.[52] Critics argue that the only way to truly rule out genetic or environmental causes is to engage in cross-fostering or translocation experiments. These involve moving individuals either out of their natal groups into new ones at a formative age, or swapping entire groups across environments.[8] Such tests have successfully shown that behaviors were socially transmitted in rats[53] and fish (French grunts[54]; Bluehead wrasse[55]). Unfortunately, such experiments have so far not been feasible with populations of larger free-ranging species, both logistically and from an ethical perspective.

Biro and colleagues provided a partial solution through a controlled field experiment. They followed the development of chimpanzee nut-cracking behavior at Bossou, Guinea, West Africa, for over 16 years, and then introduced novel nuts to the group and traced the acquisition of the behavior. This behavior subsequently spread after the use by one particularly skilled female who had experience with the nuts prior to her emigration.[56] In a recent study, Thornton and Malapert[57] trained demonstrators in meerkat groups to obtain rewards from different landmarks. They found that individuals tended to prefer the landmark chosen by their demonstrator, and those who had not seen a demonstrator were less likely to obtain rewards. This behavior suggests that foraging techniques were socially learned, although the effects were short-lived as individuals explored and discovered the nondemonstrated landmarks. To date, very few experiments of this type have been conducted and

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have produced mixed results.[58] Such field experiments provide more control in a free-ranging environment, by artificially introducing novel behaviors. While they cannot rule out the possibility of individual learning, they can be used in a larger range of species.

EXPLORING MECHANISMS OF CULTURAL TRANSMISSION IN CAPTIVITY

Critics of claims of culture in wild animals often emphasize that such claims are based on indirect inferences about how information is learned. Captive studies can help assess more rigorously whether or not a given species is capable of social learning. They also allow for direct comparisons across species on similar tasks. These tests can vary from simple two-action designs, through to more complex tests investigating artificially generated 'cultures'.

Investigating Social Learning Processes

Definitions

It is largely agreed upon that in order for a behavior to be deemed 'cultural' it must be acquired and maintained by social transmission processes.[13,59] Caldwell and Whiten provide a comprehensive definition of social learning that 'occurs when the behavior, or presence, or the products of the behavior, of one individual influence the learning of another' (Ref 60, p.193). Thus, social learning is an overarching category which can be subdivided into many different forms. The primary distinction lies between what aspects of what an observer witnesses are the most salient in determining their subsequent behavior.[59,61–64] When defining these mechanisms, a distinction is often made between 'imitative' and 'nonimitative' forms of social learning. Heyes defines nonimitative learning as occurring when 'observers learn about stimuli, objects or events in the environment, either to distinguish them from other classes of stimuli or to attach to them a positive or negative value by virtue of their relationships with other objects and events' (Ref 62, p. 100). Observing a particular behavior in a conspecific could simply trigger a behavior already existing in the natural repertoire of the observer, often referred to as contagion, priming, social or response facilitation.[61,63,64] Alternatively, the behavior of the model could facilitate interaction in a number of ways that lead to an increased possibility of the observer learning the specific solution through trial-and-error learning. Examples of this type of social learning are stimulus or local enhancement, where the attention of the observer is drawn to relevant objects or locations.[65,66] One distinction that might be particularly important in comparing humans and other animals is that between emulation and imitation. Imitation is said to occur when the observer learns about and copies the actions of the model, and emulation when the observer learns something about the environment, the objects involved in the demonstration, or the end result. Tomasello, Davis-Dsilva, Camak, and Bard[67] provided the first analysis of emulation after finding that chimpanzees would reproduce the final result of a modeled action, but not the exact technique used to achieve it.

Exactly what social learning mechanisms are necessary for the spread of cultural variants is still open to debate.[12,68,69] If social learning in any form is the only prerequisite, there is evidence of culture in a large range of species.[1,8,15,69] However, some argue that for behavioral variants to be truly cultural, they must be supported by imitation and even teaching.[70] Evidence of imitation and teaching is often difficult to trace in other species and may play only a limited role in behavioral development.[68] It may be that while any form of social learning can support culture in its simpler forms, a human propensity to imitate is what has led to our capacity for cumulative culture.

Experimental Techniques

The development of a 'two-action task' paradigm achieved great success at isolating social learning mechanisms.[71] In this approach, an animal can achieve the same reward in two different ways, either by using two different body parts (e.g., foot or beak) or by manipulating a device in one of two discrete ways. When the subject is interacting with the same part of the apparatus to achieve the reward, the behavior cannot be explained by stimulus enhancement. Research of this kind has been carried out successfully across a diverse range of taxa and supports claims that social learning is employed by many species (e.g., common marmosets,[72] chimpanzees,[73] rats,[74] Japanese quail,[75] and budgerigars[76]). Puzzle boxes called 'artificial fruits' were developed to look at the copying of sequences of behaviors, by simulating the removal of fruit defenses.[77,78] This investigation of hierarchical imitation not only replicates possible foraging strategies but also offers more concrete evidence of imitation[61] and has been used with several species.[77,79–81]

Diffusion Studies: Experimentally Manipulating 'Culture'

While dyadic methods are useful at deciphering what social learning mechanisms animals might employ, they do not directly test whether or not artificially introduced traditions can be sustained over time. Culture is also a group-level phenomenon, so it is instructive to test how such processes would work in a group setting. In a group diffusion study, a novel behavior pattern is artificially introduced into a group through an individual who has been trained to solve a task a particular way. This technique can be used most powerfully when combined with the two-action test paradigm. In this case, one solution would be seeded into one group, and a second solution into a second group. Ideally, a third group, which has been exposed to neither solution, would also be studied. All groups then have access to the given task and the spread of the solution techniques noted. Results using this technique vary, with behaviors spreading across groups (e.g., chimpanzees,[82,83] colobus monkeys,[84] guppies,[85] and chickens[86]), but in some cases not lasting long. Linear diffusion chains start with one model and one naïve observer; the latter then becomes the model for a second naïve observer and so on. Although this does not address the spread of behaviors in a group setting, it does allow researchers to pinpoint when corruption might occur. The replacement method combines these elements, by replacing one of a group of experienced individuals with a naïve observer. New recruits are thus exposed to a majority behavior, which makes the replacement method potentially useful to address questions concerning conformity effects. To date, just over 30 such experimental tests have been carried out in a variety of species including fish, birds, and primates.[58] They provide a useful complement to observational data from the wild and middle ground between dyadic social learning experiments and purely observational data.

CUMULATIVE CULTURE: THE DIVISION BETWEEN HUMANS AND OTHER ANIMALS?

Nonhuman animal cultures and human cultures differ drastically in terms of both the quantity and quality of behavioral variants. Human cultures are made up of numerous layered behavioral variants across a diverse range of domains, from religious practices, music, and language to constructive technology. Differences between populations of nonhuman animals do not vary to the same degree, or across so many different domains. There is little evidence of animals exhibiting cumulative culture—the accumulation of modifications over time resulting in innovation that no individual could have discovered on his or her own.[1]

As previously noted, many argue that the quality of social learning is the major factor dividing human cultural processes from those of other animals. It is thought that humans are inherently imitators, replicating behaviors to a high level of fidelity, whereas other animals copy aspects of behavior, rather than every specific detail.[4] As such, behaviors are liable to be lost during transmission in nonhuman animals so that subtle modifications are not replicated. Many studies have addressed this by directly comparing human children and chimpanzees on similar tasks. Until recently, it was thought that children imitate on such tasks, whereas chimpanzees emulate, thereby not copying the exact actions of the demonstrator.[67,87] However, there is some evidence that captive chimpanzees can imitate, although they may only do so under certain conditions and not as consistently as humans do. It may be that the difference between humans and other animals is quantitative rather than qualitative in some cases.[1] For example, when presented with an artificial fruit with two defenses, one relevant and one irrelevant, chimpanzees copied the irrelevant action when the task was perceptually opaque, but not when it was transparent.[88] Human children are very adept imitators and will even imitate irrational or unnecessary behaviors.[89,90] However, this pattern tends to emerge around the time children reach 3 years of age. Prior to this, they seem to adopt similarly flexible strategies as chimpanzees, only copying actions when it is rational to do so.[91,92] This coincides with the ability to share intentions, or the development of theory of mind in children, which might play an important role in the ability to culturally learn.[93]

Experimentally Investigating Cumulative Culture

To date, very few studies have directly investigated cumulative culture experimentally in different species. These tests are useful to determine if captive animals might display artificially induced cumulative culture, and if not, what might be impeding the accumulation of modifications. Additionally, they help to determine if human cumulative culture relies on imitation rather than other social learning mechanisms. In one such task, juvenile chimpanzees first learned how to access honey using a simple method after watching a human demonstrator. They were then presented with a more complex but more efficient method (allowing for

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access to both honey and nuts). Chimpanzees tended to stick to the first method, thereby gaining access to limited honey, rather than adopting the upgraded method.[94] In contrast, in a recent follow-up study, 8 out of 12 children did learn to use the upgraded method.[95] It is possible that chimpanzees are limited by a 'copy if dissatisfied' strategy, whereby if they are already attaining food they are not sufficiently motivated to move onto more complex methods.[96,97] Conversely, children may be more motivated socially to do as the model is doing, regardless of the reward.

Caldwell and Millen recently completed a series of studies investigating cumulative culture in adults.[98] Participants were given the task of building paper airplanes designed to fly as far as possible, with new participants entering the group every 2 min 30 s to simulate new 'generations'. The researchers later varied the amount of information available in each group, so that some naïve group members had access to varying combinations of teaching, actions, or end results only.[99] Each of these methods resulted in superior products in the later generations than early generations, suggesting that emulation (seeing end results only) was sufficient for the transmission of cumulative culture. This is a particularly striking result, and suggests that differences in the quality of social learning mechanisms may not be the key distinction driving cumulative culture in humans.

CONCLUSION

There are clearly major differences in cultural learning between humans and other animals. The best way to quantify these differences is still open to debate, and the problem is often muddled by disagreements as to what constitutes 'culture' in other species. Definitions that are too strict limit culture to humans and impede the study of culture across species. Conversely, definitions that are too loose make it difficult to pinpoint specific differences. We have discussed methods used in the field to discover evidence of possible culture in other species. Further, we have reviewed techniques of exploring cultural learning processes in captivity.

Fieldworkers observe animals in their natural environments, so their findings are the most ecologically valid. However, they typically rely on circumstantial evidence of social learning.[8] Captive experiments can help pinpoint the learning mechanisms involved and can work to artificially introduce behavioral patterns and trace their diffusion. However, they do not provide a natural environment and species may be displaying behaviors they would not in the wild. In the case of enculturated animals, they might be displaying a more diverse range of behaviors, or conversely, their abilities might be impaired as compared to their wild counterparts.[27,100] Field experiments provide an excellent opportunity to combine ecological validity with a degree of experimental control. In addition, the experimental study of the mechanisms underlying cumulative culture in both humans and other animals remains under-researched. Recent advances in this area are very promising, and further research with a wider range of species is needed.

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