



Social learning and traditions in animals: evidence, definitions, and relationship to human culture

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The number of publications concerned with social learning in nonhuman animals has expanded dramatically in recent decades. In this article, recent literature addressing three issues that have been of particular concern to those with both an interest in social learning and a background in experimental psychology are reviewed: (1) the definition as well as (2) empirical investigation of the numerous behavioral processes that support social learning in animals, and (3) the relationship of the 'traditions' seen in animals to the 'culture' that is so important in shaping the development of behavioral repertoires in humans. © 2012 John Wiley & Sons, Ltd.

How to cite this article:

WIREs Cogn Sci 2012, 3:581–592. doi: 10.1002/wcs.1196

INTRODUCTION

As an animal engages in the myriad activities that facilitate its reproduction and survival, it often inadvertently provides information of potential use to others who either directly observe its actions or chance upon any changes in the physical environment that those actions have produced. Given the importance of such information extracted from the social environment to our own species, it is surprising that, until fairly recently, those interested in behavioral ontogeny in nonhuman animals (henceforth animals) largely ignored the possibility that social interactions played an important role in shaping animals' behavioral repertoires to meet environmental challenges. Indeed, it is only during the last 30 years that the contribution of socially acquired information to the development of the behavior of animals has become a focus of attention for researchers with backgrounds not only in Psychology, but also in Behavioral Ecology, Anthropology, Evolutionary Theory, Economics, and Robotics. The result has been a virtual explosion in both empirical and theoretical studies concerned with animals'

reliance on observation of the behavior of others when deciding how to respond to environmental challenges. Voluminous literatures now describe the role of social learning in animals from fruit flies^{1,2} to chimpanzees³ whether choosing among alternative: foods,⁴ mates,⁵ nest sites,⁶ oviposition sites,^{1,2} or migration routes⁷ or learning to recognize predators,^{8,9} exploit well-protected potential prey,^{10,11} use tools,^{12,13} or court effectively.¹⁴

In this article, three issues arising from the studies of animal social learning were selected because they have been of particular interest to psychologists: (1) empirical studies of the behavioral mechanisms supporting social learning leading to development of adaptive patterns of behavior in animals, (2) attempts to describe and define the various psychological processes that might support particular instances of social learning, and (3) discussions of the evolutionary relationship between animal traditions and human 'culture'. Unfortunately, a thorough review of the many hundreds of relevant publications relevant to even this limited number of topics is impossible in the space available here. The works cited both in the text and at the end of this article in *Further Reading* section provide entrees to recent literatures. Generally, these referenced materials will also have to be consulted for citations of the historical literature.

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THE ROLE OF SOCIAL LEARNING IN THE DEVELOPMENT OF ADAPTIVE PATTERNS OF BEHAVIOR

Both formal models¹⁵ and informal discussion¹⁶ provide insight into the circumstances in which reliance on social rather than individual learning should prove adaptive as well as the evolutionary consequences of engaging in social learning.¹⁷ Such theoretical analyses have demonstrated repeatedly that attending to the behavior of others can, at least in principle, lead a social learner to make maladaptive as well as adaptive decisions because a potential social model may have acquired some behavior in circumstances different from those that its observers face.^{16,18–20} However, in practice, assessment of the relative magnitude of rewards resulting from engaging in socially and individually learned alternative behaviors leads animals to rapidly abandon relatively less well-rewarded alternatives.^{21,22} Consequently, (1) knowledgeable models infrequently express maladaptive behaviors for naive individuals to copy, and (2) any relatively poorly rewarded socially learned behavioral alternatives are soon abandoned because of the relatively inferior rewards that they garner from the physical environment.

Paradoxically, humans, so heavily reliant on social learning to respond to environmental challenges, are more likely than animals to exhibit and transmit learned behaviors better suited to conditions other than those prevailing at the time and place where transmission occurs. Conformity to a human social group's established patterns of behavior is frequently rewarded with social acceptance and defection punished with anything from malicious gossip to execution. Rewards¹⁴ or punishments²³ for conformity to social norms are rare in animals. Consequently, humans are more likely than animals to have to reconcile competing reward systems and are therefore more likely than animals to continue to engage in socially learned behaviors that are poorly suited to their physical environments. The collapse of the Norse settlements in Greenland in mid-15th century, attributed at least in part to cultural conservatism and failure to acquire skills appropriate to a demanding environment,²⁴ provides a spectacular example of socially mediated, maladaptive behavior in humans. Less spectacular instances of apparent behavioral suboptimality in humans similarly often reflect compromises that animals rarely need make between rewards and punishments provided by their asocial and social environments.

Examples of adaptive socially learned behaviors in animals now fill entire books and special issues

of journals (See *Further Reading* section). The two examples chosen for discussion here, one involving a vertebrate and the other an invertebrate, illustrate durable social influences on biologically important decisions. Each has been analyzed under controlled conditions in sufficient detail to permit at least preliminary discussion of: (1) the necessary and sufficient conditions for their social acquisition, (2) the interplay of social and asocial information in determining the duration of their expression, and (3) the potential of the social learning involved to result in a multigenerational tradition.

STUDIES OF THE ROLE OF SOCIAL INFORMATION IN THE DEVELOPMENT OF BEHAVIORAL REPERTOIRES

Social Influences on Food Choices of Norway Rats

Much empirical work on social learning in both mammals and birds has focussed on the role of social influences on various aspects of foraging behavior: locating feeding sites, evaluating the richness of feeding patches, deciding when to move from one feeding site to another, identifying safe foods, overcoming defenses of potential prey, etc.⁴ Studies under controlled conditions of the role of social information in shaping the food choices of Norway rats described below, motivated by reports of problems encountered in controlling pest populations of Norway rats living as human commensals, have proven particularly fruitful.²⁵

It was discovered many years ago that although placing a permanent poison-bait station in a rat-infested area results in considerable short-term decrease in the size of the target colony, this decline in number of rats is relatively brief, and the decimated colony eventually returns to its original size. Subsequent studies in both laboratory and field reveal that although most members of a target colony ingest a lethal dose of bait the first time that they eat it, almost invariably, a few individuals consume only a small amount of bait, become ill, but survive. Occurrence of illness following ingestion of unfamiliar bait results in survivors associating the bait with illness and subsequent refusal to consume it. Even more disappointing to the would-be rat exterminator, weaning young born to survivors of an initial encounter with a poison bait totally reject it. The young never even taste the bait the adults of their colony have learned to avoid, somehow learning from interacting with experienced elders to

avoid ingesting the poison present in their shared environment.

Subsequent laboratory studies²⁵ have shown that knowledgeable adult rats do not, in fact, dissuade their young from eating toxic baits. As elaborated below, weaning rat pups initially eat only when, where, and what adults of their colony are eating and are extremely hesitant to eat any food to which the adults of their colony have not introduced them. Consequently, following social introduction to the flavors of one or a few foods, young rats avoid all other foods, among them the toxic bait their colony's adults are avoiding.

Before birth and throughout later life, social information of various kinds biases rats to ingest foods eaten by conspecifics with whom they interact. For example: (1) Young rats gestated by a dam fed a distinctively flavored food during the last week of her pregnancy show an enhanced postnatal preference for the odor of that food. (2) Flavors of foods that a lactating rat eats can be incorporated into her milk, and at weaning, her pups prefer flavors that they have previously experienced in maternal milk. (3) Young rats frequently snatch food from feeding adults, and the young subsequently prefer foods that they have stolen from adults to foods picked up from the floor. (4) Young rats seeking food both use visual cues to locate adults near the nest and follow odor trails deposited by adults returning from distant feeding sites to find foraging sites that adults are exploiting.

Most thoroughly studied, after a naive 'observer rat', whether young or old, interacts with a 'demonstrator rat' that has recently eaten some distinctively flavored food, the observer shows a substantially enhanced preference for whatever food its demonstrator ate. Such relatively simple social learning can support multigenerational traditions of food preference (Figure 1).

The duration of such socially induced preferences is strongly influenced by both the time available to an observer rat to sample among alternatives and the relative reward experienced as a result of sampling the food for which an enhanced preference has been socially induced and any available alternatives.²⁷ Whether such sampling of alternatives occurs before or after social induction of enhanced preference for a food (Figure 2) profoundly affects the influence that sampling has on subsequent food choice. As can be seen in Figure 2, the opportunity to sample two foods before interacting with a demonstrator rat that has eaten one of them has little impact on the magnitude of social influence on observers' food choices. These data call into question a frequently suggested explanation for social influence on rats' food choices in terms

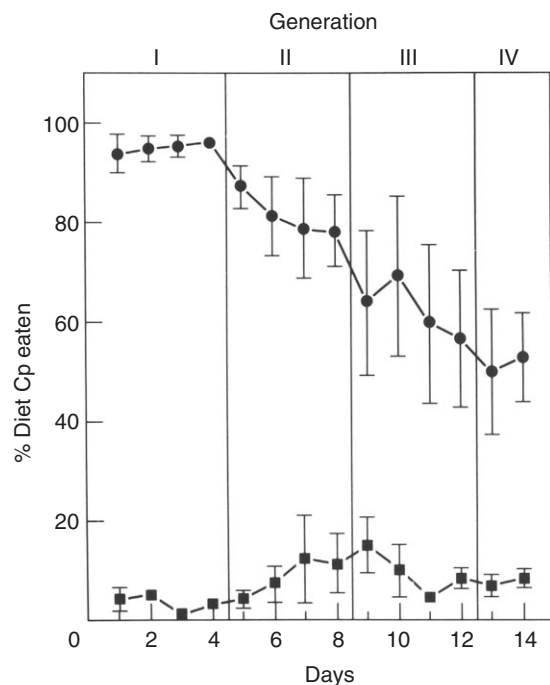


FIGURE 1 | Mean \pm SE amount of cayenne-pepper flavored diet (Diet CP) eaten by subjects housed in one of 10 enclosures each containing a founding colony of four rats. Members of each colony had been trained to eat either Diet CP or wasabi-flavored diet (Diet W) when offered both diets for 3 h/day. Immediately after the 3-h feeding period on each of days 2–5, one member of each founding colony was removed and replaced with a naive rat. On each of days 5–14, the rat that had been longest in each enclosure was removed and replaced. Day 1: enclosures contained only members of a founding colony; days 5–14: enclosures contained only replacement subjects. Generation IV contained replacements of replacements of replacements of replacements of founding colony members. (Reprinted with permission from Ref 26. Copyright 1995 Elsevier)

of a cognitively relatively sophisticated inference on the part of observers that foods others have eaten are "safe". Rather, social exposure to a food appears to change observers' affective response to that food, increasing its palatability.²⁸ The profound impact of sampling of diets after interacting with a demonstrator on food choice (also illustrated in Figure 2) provides strong evidence of the impact of personal experience on a socially induced food preference.

Transmission of food choice from a demonstrator rat to an observer rat depends on the observer experiencing the odor of a food at the same time that it experiences carbon disulfide (CS₂), a normal constituent of rat breath. Sensitivity to CS₂ is mediated by dedicated receptors in the rodent olfactory epithelium that express guanylyl cyclase (the GC-D olfactory subsystem). Gene-targeted 'observer' mice with disruptions of the GC-D olfactory subsystem show severe deficits in not only electrophysiological

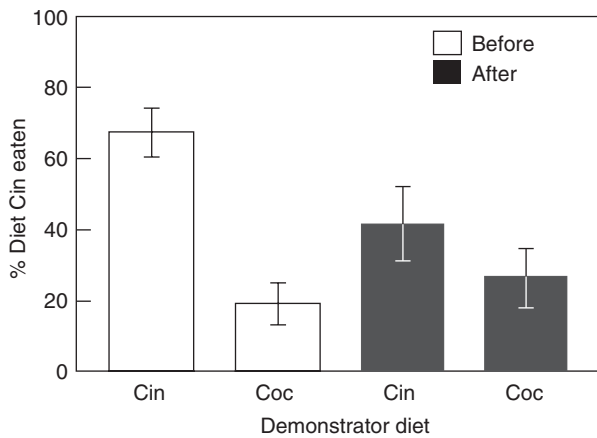


FIGURE 2 | Mean \pm SE amount of cinnamon-flavored diet eaten as a percentage of total amount eaten by observers choosing between cinnamon- and cocoa-flavored diets (Diet Cin and Diet Coc). Observers assigned to the 'Before' condition were maintained on both Diets Cin and Coc for 4 days before interacting with a demonstrator rat fed one of those diets. Observers in the 'After' condition were maintained on Diets Cin and Coc for 4 days after interacting with a demonstrator rat fed either Diet Cin or Coc. The data are from the 4th day after interaction. (Reprinted with permission from Ref 26. Copyright 1995 Elsevier)

and behavioral response to CS₂ but also in acquisition of enhanced preferences for foods that 'demonstrator mice' have eaten.²⁹

The anatomical and neuroendocrine substrates of social learning of food preferences in rodents has been examined in several laboratories, revealing involvement of many brain regions (e.g., hippocampus, subiculum, dentate gyrus, basal forebrain, and frontal cortex) as well as both neuropeptides (vasopressin, oxytocin) and gonadal hormones in the phenomenon.³⁰ Whether a hormone under investigation directly mediates social learning or influences social learning by affecting some aspect of social activity or sensory processing important for the naive to extract information from the knowledgeable is not always clear.

Social Learning of Oviposition Site Preferences in Fruit Flies

A female fly's decision as to where to lay her eggs can have important effects on the development and viability of her young, and therefore, on her fitness. Adult female fruit flies' choice of egg-laying medium is influenced profoundly by social interaction with conspecific demonstrators that have been trained to use only one of two distinctively flavored media that are subsequently made available to an observer fruit fly as oviposition sites.¹

As in rats' learning socially about foods, naive observer flies learn from social interaction not which

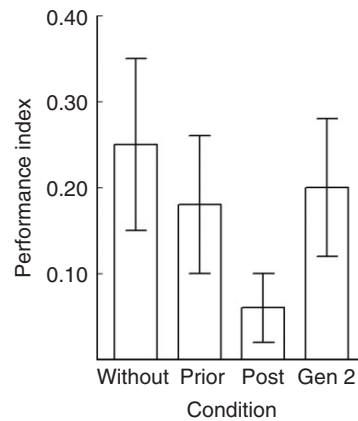


FIGURE 3 | Demonstrator flies trained to lay eggs on either banana flavored medium (B) or strawberry flavored medium (S) interacted with naive demonstrators that subsequently chose between B and S. A performance index (PI) of 1.0 would indicate complete copying of demonstrators' choices by their respective observers and a PI of 0, no influence of demonstrators' choices on those of observers. Without = observers with no experience of S or B before demonstration; Prior = 12 h of experience of both B and S before demonstration; After = 4 h of exposure to B and S after demonstration and before testing; Generation 2 = observers of demonstrators that had learned socially to prefer one medium to the other. (Reprinted with permission from Ref 1. Copyright 2012 Elsevier)

medium to avoid, but which medium to exploit. Also as in rats social learning about foods, observer flies learn socially to prefer their respective demonstrator's medium for oviposition even if the media present when the demonstrator was trained are not present when demonstrator and observer interact. And again as in rats, preference induction in fruit flies depends not on simple exposure of an observer to the flavor of the medium that its demonstrators has exploited, but on exposure to that flavor in the context provided by cues emitted by a demonstrator fly.

In fruit flies, as in rats, exposing observers to the media they are to choose between before they interact with a demonstrator has relatively little effect on subsequent social transmission compared with sampling media after interacting with a demonstrator. As in rats, sampling after social learning greatly attenuates demonstrators' influence on observer fruit flies subsequent choices of oviposition medium (Figure 3). Again, as in Norway rats, observers fruit flies that have learned socially to prefer one medium to another can serve as demonstrators for a new generation of observers transmitting a socially acquired preference to this second generation (Figure 3).

The striking parallels between the features of social learning of preferences for flavored media seen in Norway rats and other mammals from bats³¹ to

hyenas³² and in fruit flies suggest that similar forms of social learning may be widely distributed across the animal kingdom. Further, the convergence of the ways in which social and asocial information are integrated in two such phylogenetically distant species suggests that similar forms of integration may be widely adaptive. Perhaps most important for the future, demonstration of socially induced preferences in fruit flies provides a model system suitable for molecular analyses of the bases of both social and asocial learning.³³

DEFINITION OF SOCIAL LEARNING: FROM LOCAL ENHANCEMENT TO TEACHING

As is evident in the preceding section, the behavioral mechanisms involved in diverse instances of social learning often have features in common. Consequently, considerable effort has been devoted to creating a vocabulary useful in discussing the various ways in which social interaction of two animals can increase the similarity of their behavior. Indeed, by late twentieth century, the language used to describe the various psychological processes presumed to support instances of social learning in animals had become not only excessively complex but also contradictory, interfering with rather than facilitating discussion of relevant phenomena.

In the past 30 years, a number of authors^{34–39} have proposed definitions and taxonomies of social learning processes that, even if not resolving all disagreement, have gone a considerable way toward bringing order out of prior chaos. Gradually emerging consensus as to how to dissect social learning into distinctive elements (if not as to what words to use in referring to the elements that dissection produces) provides a useful advance, despite the difficulty in deciding precisely what sort of observation or experiment suffices to distinguish one element from another.^{35,36}

The most recent effort to provide a comprehensive vocabulary, that of Hoppitt and Laland,³⁶ provides a set of definitions consistent with Heyes's³⁵ emphasis on using characteristics of the social learning situation (i.e., the stimuli or stimuli and responses being associated) rather than behavioral processes internal to the organism (e.g., attention or motivation) when differentiating types of social learning. In practice, Hoppitt and Laland's³⁶ approach does not result in definitions very different from those found in earlier taxonomies based on processes internal to the animal, for example that of Whiten and Ham (Ref 37, Figure 1) a portion of which is reproduced

here (Figure 4). The figure provides a succinct summary of the types of distinction that have proved important over the decades.

As indicated above, the labels used to describe various processes of social learning vary from one taxonomic scheme to the next, but the distinctions being made remain relatively constant. For example, both Whiten and Ham³⁷ and Hoppitt and Laland³⁶ distinguish cases in which social attraction leads only to exposure to an aspect of the environment and contributes only indirectly to social learning. The latter authors refer to such instances as 'local enhancement' and the former as 'exposure', but both make the same distinction. Similarly, 'response facilitation' in Hoppitt and Laland's³⁶ terminology and 'contagion' in Whiten and Ham's³⁷ seem to refer to identical phenomena. The important point is that the dissection of social learning from different points of view seems to result in rather similar categories, suggesting convergence concerning meaningful distinctions.

Both sets of definitions of social learning processes discussed in the preceding paragraphs are similar in that they are concerned with processes that might be confused with imitation of either of two sorts: (1) 'contextual imitation' (as a consequence of observation of a demonstrator's behavior a naive observer becomes more likely to perform a behavior already in its repertoire in a new context^{36,40} or (2) 'production imitation' (as a consequence of observing a demonstrator perform a behavior not in an observer's repertoire, the observer becomes more likely to perform that behavior).^{36,40}

Discovery of instances of imitation in animals ('from an act witnessed learn to do an act;' (Ref 41, p. 79)) has historically been considered particularly important for two reasons. First, difficulties in explaining imitative acts as products of the usual sort of associative learning and in understanding how perception of another performing an act is transformed into performance of that act (i.e., resolving the 'correspondence problem') suggest that imitation may be more cognitively demanding than other sorts of social learning.^{42,43} In the case of perceptually transparent imitation of a demonstrator's movement (e.g., imitating a demonstrator grasping an object), stimulus matching involving mirror neurons that respond to both seeing an action and engaging in that action may be involved,^{44,45} although whether mirror neurons are a cause or effect of imitation has yet to be determined. In perceptually opaque imitation, when an observer cannot see her own behavior (e.g., imitating the facial expression of another) either cross-modal matching of a visual input with proprioceptive

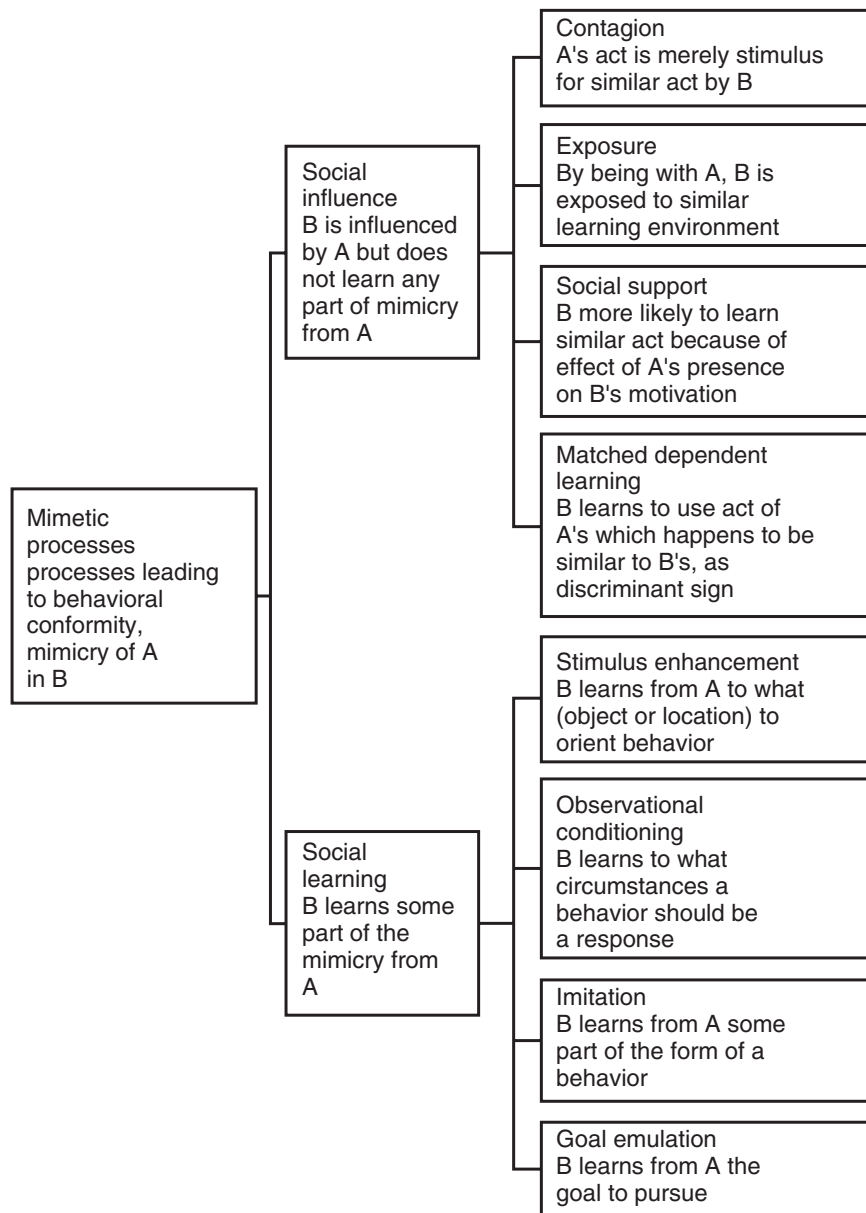


FIGURE 4 | Detail from a taxonomy of asocial- and social-learning processes. The latter, pictured, here, can lead to nongenetic spread of behavior either through a population or across generations. (Reprinted with permission from Ref 37. Copyright 1992 Elsevier)

output, perhaps based on prior associative learning,⁴³ or an hypothesized ability to imagine oneself in the place of another ('perspective taking'^{38,39}) may be involved.

Second, as will be considered further in the final section of this article, an ability to imitate precisely has been proposed as important for the emergence of 'cumulative culture.' Consequently, the question of whether animals imitate may prove important for understanding the greater complexity of the products of human than of animal social learning⁴⁴⁻⁴⁶ (but see Ref 43).

Teaching

Both Whiten and Ham's³⁷ and Hoppitt and Laland's³⁶ sets of definitions of social learning processes are limited to cases in which the behavior of knowledgeable individuals only inadvertently provides information that is exploited by the naive; knowledgeable, potential 'demonstrators' play an essentially passive role in information dissemination. Like imitation, 'teaching', in which knowledgeable individuals play an active role in behavioral propagation is relevant to the discussion of animal and human 'culture' in the last section of this article.

Caro and Hauser⁴⁷ define teaching as occurring when a knowledgeable individual engages in some behavior that is not only costly and without immediate benefit to itself but also causes a naive individual to acquire some skill more rapidly than it otherwise would. Such definition treats teaching as an ‘altruistic’ behavior in the neo-Darwinian sense of that word, placing the phenomenon firmly within a contemporary evolutionary framework. Teaching has only recently found a place in taxonomies of animal social learning, probably for two reasons. First, historical emphasis in such taxonomies on processes that might be confused with learning by imitation⁴² made discussion of teaching unnecessary. Second, until quite recently there have been no generally accepted examples of teaching in animals. Although the waggle dance of honeybees,⁴⁸ known for decades, clearly fulfills Caro and Hauser’s⁴⁷ criteria for teaching, historically, bee behavior has been largely ignored in the social-learning literature possibly because interest has focussed on evolutionary precursors of human social learning, surely less likely to be found in insects than in vertebrates in general and apes in particular.

Some have suggested that teaching may be uncommon in preliterate human societies,^{49–51} possibly because of inappropriate focus in the anthropological literature on explicit linguistic instruction of the type common in modern nation states. However, recent review of archeological and ethnographic evidence of teaching, adopting a definition of teaching similar to that proposed by Caro and Hauser,⁴⁷ and therefore incorporating nonverbal costly behaviors of potential teachers that facilitate behavioral acquisition by observers⁵² indicates that ‘...the gradual scaffolding of skills in a novice through demonstration, intervention and collaboration...has played an essential role in securing the faithful transmission of skills across generations...’ (Ref 53, p. 316).

Although common even in preliterate human populations,⁵⁴ costly behavior that facilitates transmission of knowledge or skills to others (‘teaching’) appears to be rare in nonhuman animals.⁵⁵ Only dancing in honeybees, tandem running in ants, food recognition in babblers, and handling of dangerous prey in meerkat are generally accepted as meeting Caro and Hauser’s criteria.^{23,47,56,57} The domain specificity of teaching in nonhumans, (2) the unusual phylogenetic distribution of known cases, and (3) the absence of confirmed cases of teaching in any nonhuman primate suggest that available examples of teaching in animals are analogous to rather than homologous with human teaching and can therefore provide insight into

functions of teaching not the phylogenetic development of the human ability to teach.

ANIMAL TRADITIONS AND HUMAN CULTURE

The current controversy concerning the relationship between animal traditions and human culture reflects in part the diverse vocabularies, analytical tools, and interests that researchers with backgrounds in different disciplines bring to the study of social learning. As we have seen, some researchers focus attention on analyzing and defining the behavioral processes that can support social learning, while others are more interested in exploring the functions of social learning. Some conduct observational studies of social learning in natural settings, others work in the laboratory under controlled conditions. Yet others use formal models as a tool for dissecting phenomena of interest⁵⁸ and sophisticated statistical techniques to both trace the flow of social information through populations and distinguish among various behavioral processes supporting the social transmission of behavior.⁵⁹

Unfortunately, few investigators are adept at integrating the many approaches currently available to the modern investigator. A result is frequent disagreement about both the use of language and the implications of data. Some see chimpanzee culture, for example, as homologous to human culture, arguing, first, that ape and human culture share a defining characteristic (variation in group-specific behavioral repertoires resulting from social learning), and second, that it is no coincidence that the closest phylogenetic relatives of *Homo sapiens* exhibit the most human-like culture.^{60,61} Others, are less convinced, viewing human culture as both dependent on psychological processes that are either absent or severely limited in apes and possessing characteristics that animal culture lacks. On the latter view, ape ‘culture’ is analogous to rather than homologous with that of humans.^{44–46,62}

Difficulties inherent in studying the behavior of natural populations of apes^{63,64} and cetaceans,^{22,65} the animals most often proposed as bearers of culture, result in evidence of culture resting largely on observational and circumstantial, rather than experimental, evidence. Relevance of experiments in the laboratory to understanding of the development of behavioral repertoires in free-living animals will always be open to challenge.⁶⁶ Consequently, controversy as to the relationship of animal culture to human culture is not likely to be fully resolved any time soon.

The notion that animals are bearers of culture gained prominence following publication in *Nature* and *Science* of syntheses of many decades of field observation of the behavioral repertoires of geographically distinct populations of chimpanzees and orangutans.^{63,64} These reviews, as well as studies of capuchin monkeys⁶⁷ and bottlenose dolphins,⁶⁵ provided compelling evidence of unique clusters of social behaviors and/or foraging technologies that differentiated each group examined from others of its species. The divergence between groups in behavioral repertoire without apparent ecological or genetic cause led to the assertion that great apes, like humans, exhibit 'culture', a view reinforced by laboratory demonstrations of chimpanzees both imitating complex patterns of behavior⁶⁸ and maintaining traditions of simple behaviors across laboratory 'generations'.^{3,60}

Generally, those most familiar with the behavior of free-living primates^{61,69} and cetaceans⁷⁰ are most likely to express the view that the intergroup differences in the behavioral repertoires of the species that they study are 'cultural'. Indeed, the diversity in social behaviors and means of exploiting materials⁶¹ seen in apes in particular, is obviously similar in many ways to the culture of humans and possibly different in at least some important ways from the traditions of other animals (See Ref 71 for an interesting possible parallel to ape culture in a nonprimate). The choice of whether to focus on similarities or differences in the nature of human and animal traditions seems to depend at least in part on whether function or mechanism are treated as more important in defining culture, with those focussed on function tending to regard human and animal culture as more similar than those focused on mechanism.

Further, while all agree that animal tradition and human culture provide naive individuals with a means of acquiring adaptive behavioral innovations at relatively low cost, some argue that human culture serves functions never seen in animal traditions. For example, Perry⁷² and Hill,⁷³ who take an anthropological perspective on the definition of culture, emphasize the apparently unique human attribute of clustering socially learned traits into integrated units that act as indicators of shared group membership and result in communal understanding of appropriate behavior. Such idiosyncratic social norms (rituals, socially learned laws, etc.) that define group membership are characteristic of all human cultures, but seem to be absent in the 'culture' even of great apes.

Those who call attention to differences in the processes supporting the social transmission of

behavior in animals and humans focus on those processes that appear to have the potential to affect the complexity and efficacy of social transmission of information.^{46,62,73} For example, maintenance of the social norms that concern Perry⁷² and Hill⁷³ may often require enforcement of sanctions for noncompliance, and few animals and no primate has been shown to punish transgressors.²³ Naive young humans are both able and apparently highly motivated to imitate closely the behavior of proficient demonstrators.⁷⁴ Although apes and cetaceans tend to copy simple behaviors of those they observe,^{3,65} their imitation is both less precise and less frequent than that seen in human children.⁷⁵ Even quite young human children engage in explicit pedagogy; apes do not.⁷⁶ Humans use language to communicate social information; no animal does. Such differences in the processes involved in human and animal social learning may have profound consequences for the effectiveness of behavioral transmission across generations.

Cumulative Culture

Researchers interested in the behavioral processes that support purported examples of tradition or culture in animals have called attention to the near ubiquity in human social groups of cumulative culture (the widespread accretion of knowledge over generations) and the apparent absence of cumulative culture in even our closest primate relatives.^{19,46} Although there is some evidence consistent with the view that species other than our own exhibit cumulative culture,^{76,77} such evidence is not convincing to most,^{78,79} and even if accepted as demonstrating cumulative culture, leaves open the question of why, if great apes for example are capable of developing cumulative culture, they have made such sparing use of that ability.

The importance of cumulative culture to the success of *Homo sapiens* in extending the species range to exploit a vast range of habitat suggests that cumulative culture provides considerable adaptive advantages. The absence of cumulative culture in animals despite the numerous social learning processes that humans and animals share suggests that there is something unique about human social learning that limits accumulation of knowledge over generations, the 'ratcheting' of behavioral innovation⁷⁹ to human populations.

There is no shortage of hypotheses as to the causes of the divergence in the ability of humans and apes to develop cumulative culture. Laland¹⁵ has proposed that an ability to evaluate the utility of behavioral alternatives may be both necessary for cumulative culture and lacking in nonhumans. Galef⁶²

has suggested that imitation (see also Ref 19) and teaching are both necessary for cumulative culture and far more developed in humans than in other species. Tomasello⁴⁶ has proposed that to be effective both imitation and teaching require the ability to take the perspective of a model or pupil, a capacity that like imitation is presumed by many to be far more fully developed in humans than in other animals. Gergely and Csibra⁸⁰ have provided experimental evidence that children will copy the behavior of a human demonstrator more faithfully when provided with explicit pedagogical cues, and suggest that the human capacity for culture co-evolved with the ability to learn and transfer knowledge through teaching, a process which they argue is independent from, and possibly preceded, language or a capacity to adopt the perspective of others.

Castro and Toro⁸¹ argue that both increased efficiency in imitation and the ability to reward or punish the behavior of others (which they treat as simple forms of teaching) are both necessary for cumulative culture to emerge and lacking in animals. Vaesen⁸² attributes the greater sophistication of tool use and manufacture in humans than in apes to apes' deficiencies in eight cognitive abilities that may make it extremely difficult if not impossible, for apes to achieve human levels of performance: (1) better hand-eye coordination, (2) a unique system for causal thought, (3) a unique system for representing functional knowledge, (4) remarkable inhibitory control and foresight, (5) a suite of sophisticated social learning strategies, (6) a unique disposition for teaching, (7) increased social intelligence, and (8) all the fruits of language (easing social learning and teaching, knowledge preservation, cooperation, innovation, and the like.) Many are relevant to the potential for cumulative culture.

The vast majority of analyzed instances of social learning in animals appear to be the result of either local enhancement or emulation. In either case, naive individuals have independently to develop rewarding behavior to direct toward whatever aspect of the

environment their attention has been directed by the behavior of others. There is no precise copying of the behavior of proficient individuals and, therefore, no possibility of cumulative improvement in performance. Only precise copying of the behavior of a succession of proficient demonstrators repeated over 'generations' can support the cumulative improvement that results from repeated grafting of adaptive innovations onto socially transmitted behaviors. Precise imitation, teaching, language, etc. each has the potential to promote precise copying and the consequent emergence of cumulative culture.

CONCLUSION

George Romanes,⁸³ Darwin's protégé and heir in matters behavioral, proposed that field mice learned by watching the activities of human boatmen to provision and launch rafts made of cow dung and to cross streams steering their improvised vessels with their tails. In the intervening decades, we have come a very long way in our understanding of the facts of animal social learning. Progress in analysis of the behavioral mechanisms that support the acquisition and use of information acquired by observing the behavior of others has been at least as great as the increase in the accuracy of behavioral observations that provide the basic facts for scientific study of social learning.

Advance in our comprehension of both the role of social information in the development of behavioral repertoires of animals and the processes supporting social learning in animals seems unlikely to slow. Exploitation of recently developed mathematical tools,⁸⁴ experimental methods,⁸⁵ and neuroanatomical, genetic, and molecular techniques to analyze instances of animal social learning^{29,33,44,45} will surely lead to new insights. Consequently, exploration of the development, evolution, function, and physical substrate of animals' ability to exploit social information promises to be at least as exciting in the 21st century as it has been in the 20th century.

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