

Chapter 31 Social Learning, Traditions, and Culture

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HUMANITY'S CAPACITY for culture is one of the defining characteristics of our species. It has allowed humans to exploit and dominate the planet, and has created forms and levels of behavioral diversity to which no other species comes close. Accordingly, it's easy to think that human culture somehow divorces us from the biological world, releasing us to a large extent from the influence of Darwinian evolutionary forces that govern the rest of life on earth, and separating us qualitatively from even our closest relatives among the primates.

There is some essential truth in this. You need only look around you at the rich and multifarious manifestations of your culture to acknowledge the gulf between us and other primates. Nevertheless, one of the most exciting areas of primatology has increasingly suggested an equal truth: that our cultural nature did not make a sudden recent appearance, but instead evolved from origins about which compelling inferences can be made through comparative primatology. In the last decade or so, the literature describing these discoveries has mushroomed to proportions that no single scientist can encompass—a situation at once exhilarating and daunting. Surveying the high points of this body of work and supplying productive entry points to its deeper exploration are the central aims of this chapter.

To put this review in context, it is important to note that primatology does not stand alone in charting the evolutionary history of the phenomena of interest. Much has been discovered about the evolutionary roots of social learning and tradition through studies of broader swaths of the animal kingdom (Fragaszy & Perry 2003; Whiten et al. 2011),

especially fish (Brown & Laland 2003; Laland & Hoppitt 2003), birds (Lefebvre & Bouchard 2003; Zentall 2004) and nonprimate mammals (Laland & Galef 2009), as well as invertebrates such as insects (Leadbeater & Chittka 2007). However, studies of primates have been particularly influential in shaping our present understanding of social learning and culture.

Another reason not to divorce culture from the rest of biology is that once it is in place, culture can give rise to a new level of evolution: cultural evolution, in which traditions diversify progressively in ways that parallel Darwinian biogenetic evolution. A growing literature describes this, with an inevitable focus on the complexities of our own relatively recent past (Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985; Richerson & Boyd 2005; Mesoudi et al. 2006; Whiten et al. 2011, 2012). One can think of the evolutionary picture deriving from primatology as sitting, influentially, between the broader animal perspective and the narrower hominin-focused perspective, each of which has its own blossoming literature (Whiten et al. 2012).

This chapter is necessarily selective in its portrayal of this rapidly expanding field. Readers are urged to consult recent complementary works—including those of Subiaul (2007), Rapaport and Brown (2008), Laland and Galef (2009), and Caldwell and Whiten (2010)—which cover important topics that are absent or mentioned only briefly here.

Key Concepts and Terms

I begin by outlining the key “top-level” terms and concepts in this field. More finely distinguished terms are dealt with in relevant sections below.

Heyes (1994) defined social learning as “learning that is influenced by observation of, or interaction with, another animal (typically a conspecific) or its products” (p. 207). This can include such manifestations as copying others’ actions (imitation), but it also captures such things as learning from discarded tools or half-processed food items. Social learning is thus differentiated from individual learning, in which an animal learns through its own efforts alone. In social learning we always need to consider at least two individuals: the learner and the learned-from. The latter may possess skills or knowledge that the learner can benefit from assimilating, even if imperfectly. On the other hand, a social learner is vulnerable to picking up maladaptive behavior from others. It is important to recognize that “social learning” covers an enormous gamut of processes, from the entire content of a university education, in the case of some primates, to the experience of having one’s learning merely “socially biased” (Fragaszy & Visalberghi 2004) by, for example, following one’s mother and developing preferences for certain routes or food trees.

Social learning may be a relatively transitory phenomenon, as when a monkey learns from others’ foraging behavior that tree X is a good one to visit—information that is applicable only for a limited period. By contrast, social learning about more durable phenomena can give rise to traditions (fig. 31.1), defined by Frigaszy and Perry (2003, p. xiii) 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.” We shall look at some of the most interesting discoveries about primate traditions further below.

Defining “culture” is more contentious. Many researchers studying animal traditions treat culture and tradition (as defined above) as synonyms. Others, including many socio-cultural anthropologists, note that human cultures represent the products of complex systems of knowledge, belief, and values, and involve more than just the transmission of a set of traditions, so that the terms “culture” and “traditions” should not be conflated. Others worry that use of the term “culture” might be taken to imply that “culture” in animals is assumed to be *homologous* with human culture (sharing common evolutionary roots), as opposed to its possibly being only *analogous* (similar in some respects, but with no direct, ancestral evolutionary linkage; Galef 1992, 2009). Homology may exist, but it cannot be assumed a priori. Galef thus argues that the use of the term “culture” should

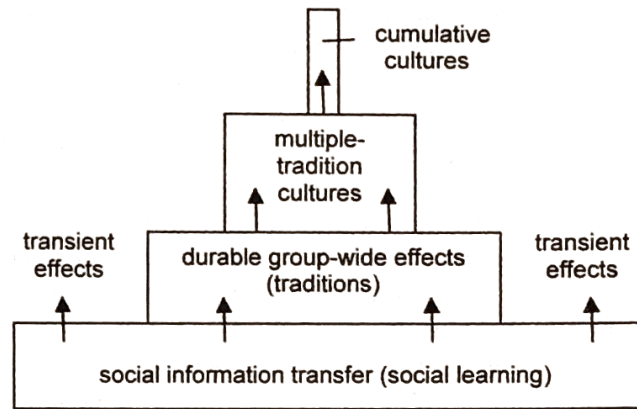


Fig. 31.1. Culture pyramid. The large base layer represents processes of social information transfer, which are increasingly demonstrated to be widespread among vertebrates and possibly invertebrates too (Danchin et al. 2004). Many of these have only transient effects such as focusing attention on a currently productive food source, but others may give rise to the sub-set of consequences that are traditions (level 2). “Cultures” have been distinguished from the existence of a tradition in several ways (see text), one of which focuses on the richness of phenomena associated with multiple traditions, so this is a third layer. Finally, a subset of cultures exhibit cumulative evolutionary changes, most notably in humans. The relative sizes of layers are notional. After Whiten & van Schaik 2007.

hinge on demonstrating humanlike forms of social transmission, such as imitation and teaching. Other researchers adopt different, principled criteria for describing some primate traditions as cultures, and we will look at these more closely later in this chapter (see also fig. 31.1).

A Century of Research

Inspired by the revelations of Darwin and Wallace, comparative psychology and primatology began to establish a fascinating scientific literature concerning social learning, based on experiments with captive animals, around the beginning of the twentieth century. The field has progressed ever since, creating a formidable reading list for anyone who aspires to master this field. Comprehensive listings and selective reviews of the achievements of the twentieth century are provided by Whiten and Ham (1992), Tomasello and Call (1997), and Subiaul (2007).

One can sympathize with the budding scholar of today who, in struggling to assimilate the burgeoning literature of the last decade or two, ignores the older literature in the process. However, this risks neglecting many wonderful pockets of early originality and discovery. To give just a single recent illustration of this, the new literature on culture-diffusion experiments (reviewed below; Whiten & Mesoudi 2008) for many years neglected to cite the earliest pioneering study on the topic, a gem “years before its time,” by E. Menzel et al. (1972).¹ Menzel and colleagues exposed

three young chimpanzees (*Pan troglodytes*) to novel objects, and then through repeated replacement of the most experienced chimp in the trio with a naïve one, demonstrated the buildup of consistent cultural attitudes of bravura and exploration of objects, an attitude that did not exist in the original trio.

Serious field research relating to social learning and culture began only later in the twentieth century. First came the now-famous studies of the spread of innovations such as sweet-potato washing among Japanese macaques (*Macaca fuscata*) by Imanishi, Itani, Kawai, Kawamura, and their colleagues in the 1950s, well reviewed by Nishida (1987) and updated by Hirata et al. (2001). However, despite such behavioral innovations becoming routinely cited in textbooks as examples of imitation and tradition, the basis for concluding that their spread relied on social learning has more recently been debated. Some critics have noted that spread of the new habits was too slow to be consistent with imitation. Others have expressed worries that the behavior was shaped by the selective rewards given by caretaking staff. These controversies can be followed further through the pages of Galef (1991), de Waal (2001), Hirata et al. (2001), and Caldwell and Whiten (2010). Below I discuss newer, and I believe more compelling, findings from Japanese monkey studies.

The next major development came in the 1960s, when serious ape field research began. Following her discoveries about different forms of tool use, it was not long before Goodall (1973) was writing about the signs of “cultural elements in a chimpanzee community.” It is here that we begin to examine the subject in more depth.

Field Studies of Primate Cultures

A Regional “Cross-cultural” Perspective

As chimpanzee field studies proliferated across Africa, researchers began to realize that behavior patterns varied across the different sites, and some such differences were inferred to be likely local traditions (Nishida et al. 1983; Goodall 1986). Evidence from experimental studies with captive subjects has shown that apes readily learn different forms of tool use, so that consistent intersite variations are unlikely to be genetically based, and instead represent local traditions. The accumulating evidence was assembled by McGrew (1992) in a landmark volume boldly titled *Chimpanzee Material Culture*. Charts of variations across sites were later extended to include social and other forms of behavior as more studies accumulated (Boesch & Tomasello 1998).

However, these pioneering studies were based largely on what had been published for each site, so the growing cultural picture was likely incomplete. Primatologists do not necessarily publish full lists of the behavior patterns at their sites, and are particularly unlikely to publish accounts of those that are never seen locally, but are known elsewhere. To achieve a more complete picture, the leaders of the nine longest-term study sites pooled their data, which spanned a total of more than 150 years, extracting from it the behavior patterns that were common for at least one chimpanzee community yet absent at others, with no obvious genetic or environmental explanation for the difference (for example, absence of a given behavior was not of interest where the materials needed for it, such as nuts in the case of nut cracking with natural hammers, were unavailable). This procedure identified as many as 39 chimpanzee traditions across Africa, spanning a variety of types of behavior including foraging techniques, tool use, grooming, social styles, and courtship styles (Whiten et al. 1999, 2001; Lycett et al. 2009; see also chapter 11, this volume, fig. 11.4). For example, in “pestle pounding” a chimpanzee climbs into the top of a palm tree and uses a large frond to pound into the growing point and extract the nutritional pulp below—a striking behavior pattern customary at Bossou in West Africa yet absent a few hundred kilometers away in the Tai Forest. The existence of similar palm trees and the same subspecies of chimpanzee at these sites led the authors to exclude environmental or genetic explanations of the difference, and to identify the behavior as a local tradition at Bossou.

Identifying 39 such variants was remarkable because most reports of animal traditions identify only a single cultural variant, such as birdsong dialects or pine-cone stripping by black rats (Heyes & Galef 1996). The methodology used in the chimpanzee study was soon applied to orangutans (*Pongo* spp.), producing a remarkably similar picture, with two dozen traditions covering a variety of technical and social domains including food processing techniques, tool use, and communication patterns (fig. 31.2; van Schaik et al. 2003). The existence of such multiple-tradition cultures offers a further way in which the concept of “culture” can be interestingly differentiated from the case of a species displaying but a single specific tradition, such as the dialect of a songbird (fig. 31.1).

A certain degree of evolutionary convergence on such cultural complexity has since been identified in some New World primates. Researchers studying white-faced capuchins (*Cebus capucinus*) have pooled their data and identified putative intersite cultural variations in foraging behavior, such as in following army ants to catch the prey they flush out, which is habitual at one site but not at others



Fig. 31.2. Stick tools used to dislodge highly nutritious seeds from the dehiscent woody fruits of *Neesia* while avoiding contact with the stinging hairs lining the open valves. Shown are *Neesia* fruits, one with a tool still inserted, several used tools, and the remainder of a twig used to make a tool. These tools were used by an adult male Sumatran orangutan (*Pongo abelii*), but all individuals (except young infants) in the Suaq Balimbing population are known to use such tools (van Schaik 2004). Photo courtesy of Ellen Meulman.

(Panger et al. 2002; see also Ottoni et al. 2005; Perry 2009), as well as in interactions with other species (Rose et al. 2003). A groundbreaking analysis concerned variation in such strange “social conventions” as inserting fingers into the mouth, nostrils, and even eyes of group mates (fig. 31.3), and various “games” in which small objects such as hairs are put in one monkey’s mouth and extracted by another (Perry et al. 2003). These provide compelling evidence for traditions because (1) as the actions were purely social, environmental explanation was unlikely, and (2) in addition to identifying intersite differences, both the spread and the eventual decline of several of these behavior patterns were documented as existing in ways difficult to explain by processes other than social learning. The authors suspect that these peculiar conventions function to test social bonds.

An intriguing Old World counterpart to these discoveries comes from studies of the curious behavior of “stone handling” in Japanese macaques. This involves picking up a few stones and manipulating them in various ways, such as clacking them together or cuddling them. This has become a compelling example of a primate tradition, because its spread has been tracked from its earliest manifestation in just one or two animals to its customary performance across a group (Huffman 1996). Neither genetic nor environmental factors seem to offer plausible explanations for the spread of this apparently functionless activity. Most recently it has been discovered that each of 10 widely dispersed groups that developed this behavior show multiple variants that differentiate them culturally (Leca et al.

2007), echoing the patterning described above for the apes, but here restricted to just the one narrow domain of stone handling (fig. 31.4).

Sapolsky and Share (2004) have described a quite different kind of social convention spreading among olive baboons (*Papio anubis*). The origin of this lay in the deaths through food poisoning of the boldest and most aggressive members of a baboon troop, following their exploitation of human food waste at a tourist lodge. Lacking these males, the troop shifted to a more affiliative balance of social interactions, an “ethos” that was maintained over years when new males entered and which conformed to what Sapolsky and Share described as the new “pacific culture” of the troop.

It is difficult to directly compare these various monkey and ape studies, because only the chimpanzee and orangutan studies have attempted to quantify the variety of traditions in the same way. At present these chimpanzee and orangutan cultures, now described as displaying more than 40 and 30 different social and technical traditions respectively (van Schaik 2009; Whiten 2010) appear to remain unmatched in their scope and extent. The convergence on this pattern of multiple differences across sites in the case of Japanese macaque stone handling, by contrast, concerns variation in just one particular behavior pattern. The closest convergence with the ape picture is the one in capuchins, but here again the range of behavior patterns is relatively restricted, with most of the foraging variants listed by Panger et al. (2002) involving application of the same techniques, such as rubbing and pounding, to different target foodstuffs. Accordingly, Whiten and van Schaik (2007) tentatively concluded that the great apes display a distinctive cultural complexity, possibly associated with their relatively large brain size (the “cultural intelligence hypothesis”) and implying that the common great ape ancestor of around 14 million years ago is likely to have begun showing this complexity, continued and elaborated in different ways by its descendants.

Turning an Observational Spotlight onto Social Learning

The relatively “macro” levels of field study outlined above are complemented by “micro” studies examining the development of putative cultural behaviors. For example, Lonsdorf (2005; Lonsdorf et al. 2003) found that young female chimpanzees, who spent significantly more time than young males watching and participating alongside their termite-fishing mothers, mastered the technique more than a year earlier than their male peers, and that unlike the males they also tended to follow their mothers’ technique in the length of their fishing tools and depths of their probing—behavior consistent with learning by observation. Similar kinds of

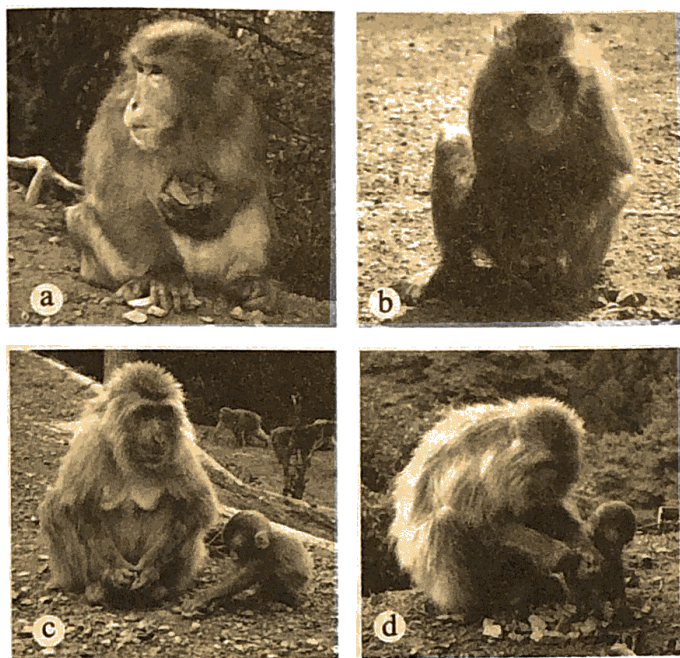


Fig. 31.3. Social conventions in capuchins. Here a male, “Fonz” has his finger in the eye of a female, “Rumor,” while she has her finger in his nostril. For further explanation, see text. Photo courtesy of Susan Perry and the Lomas Barbudal Monkey Project.

correlations consistent with social learning have been identified by Agostini and Visalberghi (2005) in black-horned capuchin monkeys (*Cebus nigrinus*), where the profile of foraging techniques and preferences of young males corresponded significantly with that of the adult males they most closely associated with.

At the broadest levels of social learning, young primates' common association first with their mother and then with a wider group, over the long period of immaturity that characterizes the order, provides many opportunities to learn such basic but crucial things as “what, where, and how to eat” (Rapaport & Brown 2008). In many primates, immatures begin their foraging career by taking scraps from adults who are feeding, and then progressing to “cofeeding” simultaneously with them on the same food source. Both of these behaviors are likely to shape the developing individual's knowledge of what to eat and where to find

it, as is shown in the Agostini and Visalberghi study noted above. Figs. 31.4c and 31.4d illustrate this kind of context in the parallel case of stone handling. One step beyond this is provisioning by adults in response to juveniles' begging. This has been commonly documented in the great apes and in New World callitrichines (marmosets and tamarins) and capuchins, but has been little described in Old World monkeys (Rapaport & Brown 2008, table 4). Where such provisioning does occur, the interactions often focus on items that the juvenile needs to learn about, like resources that are hard to find and process (Silk 1978). That this is likely to function in social information transfer as well as straightforward nutrition is supported by a number of studies that show how the behavior becomes more common for items relatively novel to the young, who appear to be “begging for knowledge,” in the title of one such study concerning Bornean orangutans (*Pongo pygmaeus*, Jaeggi et al. 2008).



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		Captive troops					Free-ranging troops				
Category	SH pattern	Ara.A	Wak.A	Takh.	JMC	Kosh.	Ara.E	Sho.A	Sho.B	Tak.B	Tak.C
Investigative activities	Lick							-	-		
	Move inside mouth							-	-		
	Pick							-	-		
	Put in mouth							-	-		
Locomotion activities	Carry							-	-		
	Carry in mouth							-	-		
	Move and push/pull							-	-		
	Toss walk							-	-		
Collection activities	Pick and drop							-	-		
	Pick up small stone(s)							-	-		
Percussive or rubbing sound producing activities	Clack							-	-		
	Combine with object							-	-		
	Flint							-	-		
	Flint in mouth							-	-		
	Pound on surface							-	-		
	Rub in mouth							-	-		
	Rub stones together							-	-		
	Rub with mouth							-	-		
	Shake in hands							-	-		
	Slap							-	-		
	Swipe							-	-		
	Tap in mouth							-	-		
Other complex manipulative activities	Flip							-	-		
	Put in water							-	-		
	Rub/put on fur							-	-		
	Spin							-	-		
	Stone groom							-	-		
	Throw							-	-		
	Throw and jump							-	-		
	Throw and run							-	-		
	Throw and sway							-	-		
	Wash							-	-		
	Wrap in leaf							-	-		
No. pattern occurrence		5	20	32	19	4	20	11	10	15	19

Fig. 31.4. Stone handling (SH) traditions among Japanese macaques. (a) cuddle; (b) roll in hands; (c) infant beginning to manipulate mother's stones; (d) infant manipulating "own" stones; (e) chart showing frequency of occurrence of the 33 SH patterns that are absent in some studied troops. Black: customary (exhibited by at least 90% of the sampled individuals in at least one age class, or at least 70% of the sampled individuals in at least two age classes). Hatched: habitual (observed at least three times in several individuals, consistent with some degree of social transmission). Spotted: present (observed at least once). White: absent (not observed despite at least 90 hours of observation). White with dash: unknown. Two troops at each of Shodoshima (Sho.A and Sho.B) and Takasakyama (Tak.B and Tak.C) are neighboring troops that share the same feeding site.

Adults of some species go further, calling juveniles to discovered food items or even actively offering them the food (see also chapter 29, this volume). The latter again appears to be common in great apes and in callitrichines (Rapaport & Brown 2008), two distantly related groups at opposite ends of a spectrum of body size and encephalization. In a study of wild golden lion tamarins (*Leontopithecus rosalia*), adults were observed to avoid eating the insect prey they had discovered and to instead make food-offer calls, after which youngsters approached, investigated, and tackled the prey themselves. This echoes the parental behavior of other predatory mammals such as cats (Caro & Hauser 1980; Thornton & Raihani 2008), thus raising the prospect of a functional level of “teaching”—an issue we return to later.

One of the greatest challenges faced by the field studies reviewed above is to provide robust evidence that the documented phenomena truly rely on social learning. Social learning can be identified unambiguously with the simplest kind of experiment, contrasting a group of subjects who see a model perform a novel behavior pattern and a control group who see no such model. Unfortunately, such an experiment is very difficult to engineer in the wild, as is experimentally translocating a primate skilled in some behavior from their natal group into a naïve one to discover whether their skill spreads (this might also be considered unethical). At the time of writing, field experiments have been completed for only a handful of nonprimate species (reviewed by Whiten & Mesoudi 2008), such as meerkats (Thornton & Malapert 2009), and have only recently begun for primates (Gruber et al. 2009;² van de Waal et al. 2010). Given the dearth of field experiments, debates have erupted about just how strong the evidence is for social learning in the field studies (Galef 1991; Laland & Galef 2009). For example, it is difficult or impossible to be sure that some subtle, unrecognized environmental factor has not shaped a local behavior variant through individual learning.

A case study that illustrates this, but also shows how follow-up research can nevertheless spiral up to more sophisticated and compelling conclusions, concerns ant dipping in chimpanzees. Whiten et al. (1999) had noted regional differences in which chimpanzees in some communities used only a short stick to harvest several ants and transfer them to the mouth, whereas those in other communities used a long wand to gather a ball of ants, and swept them into the mouth using a more complex bimanual swiping movement. The difference was inferred to be cultural because similar raw materials were available at both locations. However, both of these techniques were later found to occur also at a third site, where the long-wand technique was shown to be more common for a species of ant that had a particularly vicious bite and was more likely to be found near the

nest hole (Humle & Matsuzawa 2002). Thus, it was possible that the difference in behavior across sites was due to differences in the prey. These findings led to a suite of impressively detailed quantitative studies of both chimpanzees and ants at several sites, permitting a more rigorous and sophisticated analysis that identified both individually and socially learned elements (Humle 2006; Möbius et al. 2008; Shöning et al. 2008). These authors concluded that in addition to the aspects of tool use that have been shaped environmentally by the distribution of different ants, there are cultural differences in whether ants are eaten at different sites, and in some of the ways chimpanzees eat them, including the contrast between the nibble-from-short-stick method used at Tai and the more complex techniques employed elsewhere.

Experimental Tests of Cultural Transmission: Diffusion Experiments

Contrasting with the dearth of social learning experiments in the wild, scores of such experiments with captive primates have been conducted through the past century (Tomasello & Call 1997; Subiaul 2007). These have much illuminated the mechanisms whereby one individual learns from another: the subject of the next section. In such studies, a single observer typically watches a single model. This neat dyadic scenario is useful for distinguishing between learning processes, but is less well suited for investigating traditions and cultures, which by their nature go beyond a pair of individuals. One cannot simply extrapolate from dyadic tests to gauge the capacity of animals to sustain the multiple transmissions required to sustain traditions, so a different design is needed.

A “diffusion experiment” fits this bill. In the simplest design, a novel behavior pattern is “seeded” by training an initial individual, then the extent to which this pattern will spread across a population of conspecifics is examined, in contrast to a control group lacking a model. Ideally this will be done with multiple experimental and control groups. Over the last 30 years a corpus of such studies has built up, but quite haltingly until recent times, with just 33 experiments, covering a variety of animals from fish to apes, identified and reviewed by Whiten and Mesoudi (2008).³ Aside from the Menzel et al. (1972) study mentioned earlier, this approach has been applied to primates with adequate controls only in the last few years, all such studies being conducted in captivity.

The first of these (Whiten et al. 2005) involved a three-group design. A high-ranking female from each of two separate groups of chimpanzees was taken aside and trained to

use a stick tool to extract a grape from an artificial foraging problem (the “panpipes”) outside her enclosure mesh, using just one of two different techniques. In one technique, “lift,” the stick was hooked through the top of the obstacle and used to lift it up so the food would roll toward the chimp. In the second technique, “poke,” the stick was poked through a hidden flap so that it pushed the obstacle backwards until the grape fell and rolled toward the chimp through a lower pipe. Each newly created “expert” was then reunited with her group, where she displayed her new skill. Each of the two techniques was found to spread preferentially in the seeded group, thus providing the first experimental evidence that chimpanzees can sustain such traditions. However, fidelity of transmission was not high for all the chimpanzees, with some in one group discovering and adopting the technique more common in the other group (the “poke”—perhaps the more natural approach for chimpanzees). Nevertheless, the overall difference in traditions remained in place at two- and nine-month retests. A third, control, group that saw no seeded model failed to discover either technique, confirming these were novel routines for the chimps in the experimental conditions.

Such experiments as these and the field studies reviewed in the earlier section thus provide complementary evidence defining the scope of cultural phenomena in the species of interest. The field studies crucially map the scope of putative traditions in the wild and their functional significance, yet are limited in their capacity to show that social learning is definitely responsible, rather than genetics or individual learning. Diffusion experiments in captivity can rigorously test the capacity of the species to learn such inferred traditions.

To date, only a small number of such experiments have been published for primates. These include six with chimpanzees (collated in Whiten et al. 2007), one with guerezas (*Colobus guereza*, Price and Caldwell 2007), one with macaques (stump-tailed macaques, *Macaca arctoides*, and rhesus macaques, *Macaca mulatta*, deWaal and Johanson 1993) and two with tufted capuchin monkeys (*Cebus apella*, Dindo et al. 2008, 2009). The latter study and one on chimpanzees (Horner et al. 2006; incorporating human child subjects also) are the first to apply to primates a specialized “transmission chain” design. In this, just one naive primate watches the initial model; upon later mastering the task, that individual becomes the model for another, and so on along a potential chain of transmission. Here one knows exactly who is learning what, and from whom, at each step in the spread of a tradition. For both the chimpanzees and capuchins, each of two different ways of opening an “artificial fruit” (fig. 31.5) were transmitted with high fidelity along chains of individuals, simulating the passing of tradi-

tions through a series of generations. For these species, at least, the capacity to sustain different cultural variants in these ways has at last been clearly demonstrated (figs. 31.6 and 31.7). Consistency between such results and those from the wild is beginning to build a fuller and more compelling picture of the scope of traditions in primates than was possible even a decade ago.

The Mechanisms of Social Learning

The term “social learning” covers a very broad gamut of processes, some relatively simple and widely distributed, others more cognitively sophisticated and, it appears, more restricted in their distribution. As social learning research has developed through over a century of work, more and more distinctions have been made, and full taxonomies of social learning processes have become elaborate (see Whiten et al. 2004). The picture is made more complex because many different authors have offered what they see as improved distinctions, thus promoting either new concepts or new definitions of old ones. “Imitation” offers an illustration of this. Whiten and Ham (1992) defined imitation simply as observationally “learning the form of an act,” but dozens of other definitions abound in the literature, typically adding various other criteria, such as the imitator also understanding and copying the goals of the act (Tomasello et al. 1993). Some authors insist on high fidelity matching to the model, others require only that some matching is detectable. Still others split imitation into different kinds. All in all, the field has become notorious for being somewhat treacherous and often bewildering to the uninitiated reader. The more positive side of this is that the rich variety of kinds of social learning is at last being grasped scientifically. In evaluating any one study, the reader is advised to scrutinize the author’s definition of the terms at stake and strive to appreciate how they may relate to the wider literature.

Unlike language acquisition in humans, vocal learning in nonhuman primates plays a less important role (Snowdon & Hausberger 1997) than observational learning in the visual mode. Here, given space limitations, we focus on three main classes of observational learning that are most frequently distinguished. More wide-ranging analyses can be consulted elsewhere (Call & Carpenter 2002; Whiten et al. 2004; Hurley & Chater 2005; Hoppitt & Laland 2008; Heyes et al. 2009).

The simplest of the three main processes is *stimulus enhancement*, in which an observer’s attention is merely focused on some stimulus through the actions of another individual. This process can include the results of the latter’s actions, such as leaving a termite-fishing tool at a termite

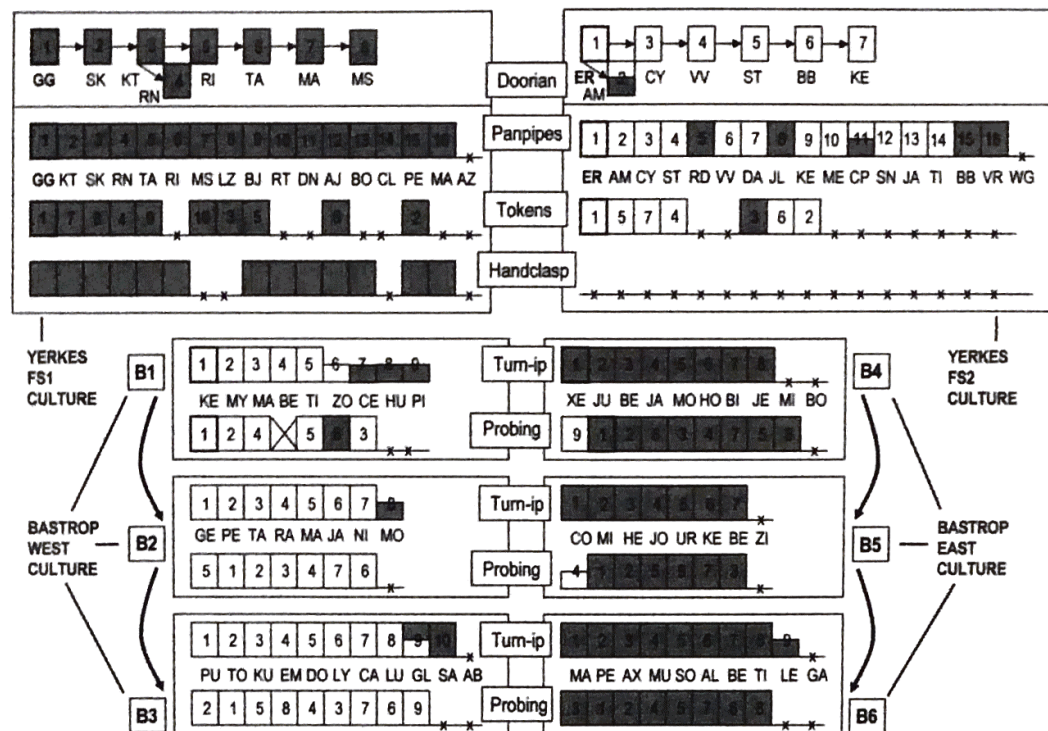


Fig. 31.6. The results of diffusion experiments in captive chimpanzees. Each rectangle represents a chimpanzee, with a two-character ID code. Different tasks, named in the center, were available in both local populations named on either side, but different techniques (cf. fig. 31.4), coded here as dark versus light, were seeded in one individual, marked here as no. 1, in each population. The “Doorian” experiment, in which one model slid open a door and the other model opened a hatch set into the slide, was run as a “transmission chain” in which each learner later became the model for the next chimpanzee in the chain, as indicated by the arrows; all other experiments involved “open diffusion,” with no predetermination of potential order of transmission. At Bastrop, transmission extended from groups B1 to B2 and B3, and from B4 to B5 and B6. Handclasp grooming spread spontaneously in the FS1 population only. Numbers represent order of acquisition for each task. For further explanation, see text and Whiten et al. (2007). These studies demonstrate the capacity of chimpanzees to sustain multiple-traditions cultures, consistent with the interpretation of regional variations among wild chimpanzees.

ground. Learning by *imitation*, by contrast, involves copying some novel aspects of another individual’s actions, as explained above. The third process is *emulation*, in which the observer learns from the environmental results of what the other individual does, rather than from imitating their actions. Emulation goes beyond stimulus enhancement to learning such information as the properties or functional significance of what is being manipulated, such that the observer is then more likely to succeed in the task. This might involve the observer choosing a quite different approach (thus contrasting markedly with imitation), but alternatively it might result in an action similar to the original, which might thus look superficially like imitation. A closer look reveals several quite different types of emulation (Whiten et al. 2004).

Observational Learning in Apes

In the study of social learning in apes, particularly chimpanzees, a prime focus has been on whether they truly “ape” in the sense of imitating, or whether this supposition has been



Fig. 31.5. Recording a young chimpanzee working on an “artificial fruit,” Ngamba Island, Uganda, 2001. Artificial fruits have been designed to study the observational learning of foraging techniques. They are designed to incorporate “defenses” that need twisting, poking, peeling and the like, simulating the routines required of challenging natural food resources. Once these are removed, the participant gains access to the edible fraction inside. Defenses are typically designed so that they can be dealt with in either of two quite different ways (e.g., “pulling and twisting” versus “poking through”); participants witness only one of these, so the information they acquire can later be precisely measured. See Whiten (1998) and text for more details. Photo courtesy Andrew Whiten.

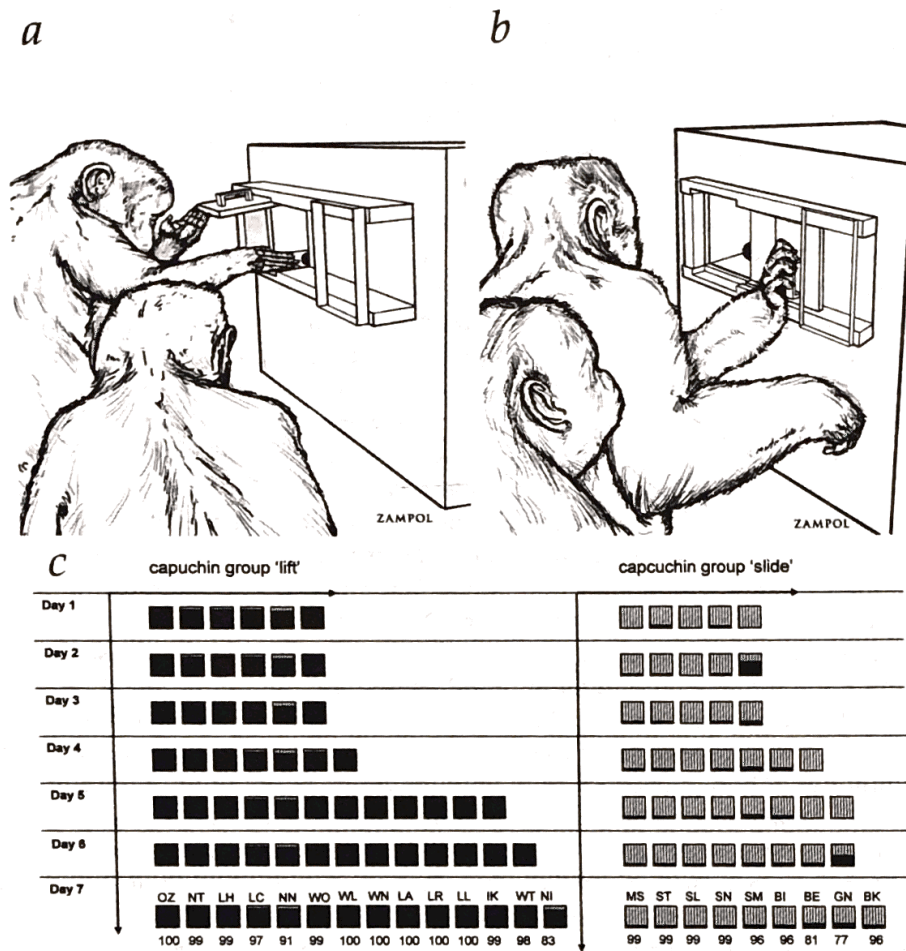


Fig. 31.7. An "open diffusion" study with capuchin monkeys: (a) capuchin performing "lift" technique on artificial doorian fruit; (b) capuchin performing alternative "slide" technique to gain reward; (c) spread of each technique in groups where one male was first taught to use either the lift or slide technique (after Dindo et al. 2009). Each symbol represents the proportion of each technique performed by each individual on consecutive days. Dark = slide, light = lift. Numbers indicate the percentage of actions performed on day 7, corresponding to that seeded in the group on day 1.

based on a failure to recognize alternatives, particularly emulation. The concept of emulation came to prominence following a study in which Tomasello et al. (1987) found chimpanzees failing to copy the trick used by one chimpanzee who used a stick tool to extract food from a foraging device. Since control chimps who saw no model nevertheless handled the stick (even though not copying what the model did with it), the authors concluded that something more than stimulus enhancement was involved. The observers appeared to be learning something about the raking functions afforded by the stick—and this kind of learning has been distinguished as "emulation" (Tomasello 1990).

So are chimpanzees emulators or imitators? If we first ask, "Can apes imitate?," then a positive, if qualified "yes" is offered by "do-as-I-do" experiments, in which chimpanzees (Custance et al. 1995) and a Sumatran orangutan (*Pongo abelii*, Call 2001) were first exposed to a training set

of actions (e.g., "touch chin") meant to convey the idea that when asked to "do this," they would attempt it. The apes were then tested with a battery of 48 different and, as far as possible, novel kinds of facial, postural, and manual actions (e.g., "touch nose"). In the cases of both the orangutan and the chimpanzees, independent judges viewing videotapes of the experiments could identify matches significantly over chance expectations. The orangutan performed best, fully imitating 58% and partially imitating 36% of the 48 target actions. The fidelity of their imitation was, however, still poor compared to what a child is typically capable of.

Thus, apes *can* achieve bodily imitation, if only at crude levels by human standards. Whether they typically *do* imitate is another question. Answers to this question have been pursued principally by allowing experimental subjects to observe a model solving a novel foraging task, such as opening an "artificial fruit" (fig. 31.5), and comparing their later tendency

to duplicate the model's performance with that of a control sample of chimpanzees who have seen no model, and/or who have witnessed a model using a different technique.

The working hypothesis of Tomasello et al. (1993), in a much cited classic overview of the field, is that apes typically emulate rather than imitate. This was supported by a series of experiments, reviewed by Tomasello and Call (1997) and Call et al. (2005), that showed chimpanzees and orangutans failing to imitate in ways that children in the same tests did, and instead acting more in line with emulation. In the latter study, for example, where a conspecific model extracted a reward from a tube in either of two ways (cracking it open or pulling caps off the ends), children typically copied the technique they had seen, even when the model acted merely as if *trying* a technique without success. By contrast, chimpanzees did not show significant matching and, unlike the children, tended to try a method *different* from the one they had seen being attempted without success.

These chimpanzees might be seen as acting more adaptively than the children in this situation, opting for an alternative to the approach they had seen fail. Indeed, more recent research has suggested that chimpanzees may be more *selective* than children in their approach to social learning. In a study by Horner and Whiten (2005), some subjects watched a familiar model first vigorously poke a stick tool into the top of an opaque box, then use it to extract a reward from a lower hole. Other subjects saw the same thing, but with a transparent box where one could now see that the operation in the top hole actually had no causal connection with the lower one. Chimpanzees in this study behaved selectively, tending toward emulation with the transparent box, by omitting the action at the top; but they swung toward a more imitative response in that they ran off the whole sequence, starting at the top, with the opaque box where causal irrelevance could not be detected. Human children, by contrast, tended to copy everything, even with the transparent box—a startling level of conformity I shall return to later.

This developing image of chimpanzees, not so much as “either/or” emulators or imitators but as selective social learners, was reinforced in a different context by Buttelmann et al. (2007), who found that chimpanzees were more likely to copy the body part used to perform an act (e.g., butting with the head) when the model's hands were free, than when the hands were occupied. This evidenced a power of discrimination that developmental psychologists have described as “rational imitation”—the chimpanzee chooses whether or not to copy according to whether the model is rationally choosing to act as they do, as opposed to merely having to act in that way (e.g., using one's head because the hands are unavailable; see also chapter 30, this volume).

The characterization of apes primarily as emulators is also complicated by recent experiments taking a quite different approach. In “ghost conditions,” the movements of objects normally manipulated by a model are instead made to happen with no model present (for example, by surreptitiously moving them using fine fishing line), thus offering only the information that emulation focuses on (Tennie et al. 2006; Hopper et al. 2007, 2008). The latter two studies contrasted a complex and challenging task (the “panpipes” described above) with a simpler one (sliding a door to one side to gain access to food behind it). Only in the latter task was there initial evidence of subjects matching their behavior to what they had seen happen, and even then it was fleeting. With the panpipes the chimpanzees failed to learn from the ghost condition, whereas the diffusion studies had shown that they learn much from the normal full demonstration in which a live model performs the actions (Whiten et al. 2005), consistent with “imitation” in the broad sense.⁴

Byrne and Russon (1998) suggested that apes might indeed copy actions, but that they do so at the level of the overarching structure of a complex routine (“program-level-imitation”), without necessarily imitating all the details—in which case their copying might neglect picky details, yet count as imitation in an interesting way. Byrne and Russon offered examples from their studies of wild gorillas (*Gorilla gorilla*) and sanctuary-living Bornean orangutans (Russon & Galdikas 1993). These case studies were not generally viewed as compelling in the peer commentary on Byrne and Russon's (1998) article, and indeed the first attempts to experimentally investigate one of the key gorilla behaviors (manual processing of nettles before ingestion), failed to yield supportive evidence (Tennie et al. 2008). However, if we restrict the idea to action *sequence* learning rather than to the hierarchical organization Byrne and Russon emphasized (Whiten et al. 2006), the Horner and Whiten (2005) study outlined above fits the bill, for chimpanzees showed that they could split the sequence in the case of the transparent box, yet copied both elements in sequence with the opaque box (probing in the top hole, and then in the lower hole). Note that alternative *sequences* of quite different actions were also transmitted with high fidelity in the groups they were seeded in, in diffusion experiments (Whiten et al. 2007).

Apes reared intimately with humans, rather than with conspecifics, have been described as “enculturated,” particularly when the relationship converges on that which normally exists between a human child and a parent. Some of the most impressive instances of imitation have been recorded for such apes, stimulating debates about whether these outcomes reflect latent capacities in the apes

or whether their minds have been fundamentally reshaped and enhanced by their experiences. Readers are encouraged to consult Bering (2004) and Tomasello and Call (2004) to engage with these debates, which have occupied students of apes more than those researching other species (but see Fredman & Whiten 2008).

Observational Learning in Monkeys

Just as apes have long been assumed to “ape,” the expression “monkey see, monkey do” has suggested similar expectations for monkeys that were seemingly reinforced by the studies of Japanese monkey traditions cited earlier.

The idea that monkeys would go beyond learning by stimulus enhancement to exhibiting imitation was endorsed by several of the first wave of experimental studies in the first half of the twentieth century (Whiten & Ham 1992). However, critical scrutiny of these studies later stressed that the experimental designs were weak in discriminating imitation from stimulus enhancement (Galef 1988; Whiten & Ham 1992). Moreover, an extensive series of well controlled experiments by Visalberghi and Frigaszy on tufted capuchins, for which expectations were high because of these monkeys’ high brain-to-body ratio and busy manipulateness, was evaluated in the authors’ influential review paper “Do monkeys ape?” (1990) with an essentially negative verdict. For example, capuchins did not copy the actions of a conspecific that used a stick to push food items out of a tube; indeed, they showed better success at this task after additional individual experience with the objects than through opportunities for social learning. After a further decade of studies performed by themselves and others on capuchins and other species of monkeys, Visalberghi and Frigaszy (2002) held essentially to this verdict.

Additional studies have increasingly suggested relatively sophisticated processes of social learning, including imitation. These include studies by other workers on tufted capuchins. Cusance et al. (1999) found evidence consistent with emulation or low-fidelity imitation in capuchins’ matching of whichever of two ways of opening an artificial fruit they had witnessed. Fredman and Whiten (2008) found evidence of their imitating either of two forms of tool use (prying a lid off a foraging device versus stabbing through it), and Dindo et al. (2008, 2009) demonstrated marked fidelity of matching in diffusion experiments of the kind described earlier in this chapter (fig. 31.7).

At the other end of the scale of brain-to-body ratios, common marmosets (*Callithrix jacchus*) have shown evidence of bodily imitation in matching a model’s use of either mouth or hand to open a box (Voelkl & Huber 2000; see also Bugynar & Huber 1997). These workers have also pio-

neered a very precise measurement system to show a very close match between model and observer, consistent with bodily imitation, in the bodily trajectory used in a foraging task (Voelkl & Huber 2007). Kumsashiro et al. (2009) claimed to have “trained” Japanese monkeys to imitate, such that the learned ability transferred to a novel context.

From a quite different perspective, Subiaul et al. (2004) described what they dubbed “cognitive imitation” in rhesus macaques. Subiaul et al. allowed one naive monkey to watch another who was skilled in pressing, in the correct order, four images that lit up in different places in a 4×4 grid—a task that had minimal manipulative content yet tested the subjects’ grasp of sequencing. The observer monkey mastered the task faster after this experience, implying assimilation of the sequence required in the task. The term “cognitive imitation” is perhaps unfortunate insofar as it suggests that other forms of imitation are not cognitive, but the phenomenon is impressive and it suggests that monkeys are capable of learning much more by observation than was thought just a decade ago.

The discovery of “mirror neurons” in monkeys has raised the prospect of understanding the neural underpinnings of action imitation. Mirror neurons are distinctive in firing both when a monkey performs a certain action (such as picking up a nut) and when it merely sees another individual do the same thing (Rizzolatti 2005). Earlier doubts about the imitative prowess of monkeys, however, led such researchers to attribute other functions to them, such as understanding goal-directed actions in others. The identification of imitation-related mirror neuron activity in humans (Iacoboni 2005), however, coupled with the newer evidence of imitation in monkeys, suggests that a potential linkage between mirror neurons and social learning in non-human primates may yet repay further study (Ferrari et al. 2009).

Teaching

When Galef (1992) argued that the term “culture” should be applied only to cases in which the transmission mechanisms in animals are akin to those of humans, he made reference to teaching as well as imitation. Is teaching part of the social learning process in primates?

If intentional teaching requires some level of “theory of mind,” in which the teacher recognizes a state of ignorance in the learner that can be rectified by intervening, one might expect to see teaching in the great apes, for whom the most evidence for such insights has accumulated (Whiten 1999, and see chapter 30, this volume). However, such teaching has been claimed only in the case of the particularly challenging task of nut cracking using natural hammers by chimpanzees (Boesch 1991). Just two cases of demonstra-

tion were described, the bulk of the mother's contribution being at the level of stimulating and facilitating her offspring's efforts by tolerating theft of nuts and hammers and sometimes actively providing them. Ape mothers have also occasionally been observed to confiscate nonfood plants from their offspring and cast such items aside (Rapaport & Brown 2008).

Aside from such uncommon cases as these, there is scant evidence of teaching in apes and Old World monkeys. By contrast, recent reviews document more extensive evidence of teaching in other animal taxa, particularly in animals that have to make the transition from weaning to foraging on difficult foods, the most obvious cases of which concern predation (Hoppitt et al. 2008; Thornton & Raihani 2008). Such analyses rest on a conception of teaching that does not require intent but is instead focused on functional criteria, notably supporting such effects as skill development at personal cost (Caro & Hauser 1992). Teaching in this sense has been well demonstrated by experimental studies in meerkats, which provide disabled prey to their young and otherwise adjust their behavior to facilitate the development of hunting skill (Thornton & McAuliffe 2006). Rapaport and Brown (2008) suggest that there is no similar pressure for this kind of social learning in most primates, who can instead negotiate a more gradual acquisition of the adult diet (in which animal prey constitutes only a minor part), relying on the kinds of observational learning outlined above during a typically long, drawn-out period of immaturity and parental dependence.

Perhaps the primate behavior closest to the kind of teaching seen in meerkats occurs in callitrichines. In these species it has been shown that parents are more disposed to offer their young novel foods than to offer them foods they are already familiar with, a possible case of "opportunity teaching" in that parents shape what the young may then learn by their own efforts (Rapaport 1999). Further, as noted earlier, golden lion tamarins have been observed to give food calls upon finding large insect prey, but then inhibit their own capture of the prey so that the young are attracted to it and then deal with it themselves (Rapaport & Ruiz-Miranda 2002).

Interdisciplinary Fertilization and Applications

Before moving to a concluding overview of what this corpus of studies of primate social learning has to tell us about the evolution of culture within primate societies, we should pause for a moment to note the links between this body of work and its sister disciplines. These links often represent

two-way streets in which primatology offers information of great interest to other disciplines and also learns from them (Claidière & Whiten 2012).

One long-standing link is with developmental psychology. Reference has already been made to studies that systematically compare social learning in apes and children, to which we return below. There is much more scope for fruitful exchange of methodologies and concepts between the disciplines. For example, in reviewing the child social learning literature, Want and Harris (2002) borrowed from the conceptual framework and methodologies developed in comparative psychology, as did Horowitz (2003) in extending similar studies to adults. Other cross-fertilizations extend to the study of social learning in autism (Whiten 2006). The reciprocal flow from developmental to comparative psychology is also considerable, and is nicely illustrated by the adoption of concepts and methods from child psychology to great effect in the studies of Buttelmann et al. (2007, 2008), described earlier.

A further link is with robotics, where workers in artificial intelligence are striving to create imitative robots and are keen to learn from our growing understanding of social learning in a variety of organisms (Dautenhahn & Nehaniv 2002). It is to be hoped that knowledge transfer will become a two-way street here also.

A quite different link is with the growing areas of phylogenetic and paleoanthropological study of human cultural evolution, which increasingly use sophisticated numerical methods to reconstruct cumulative cultural diversification (Mace & Holden 2005; Whiten et al. 2012). Lycett et al. (2009) have now extended this approach to apes and paleoanthropologists are incorporating primatological discoveries into models of the past (Whiten et al. 2009).

Among more practical applications, two areas can be highlighted. The first is conservation, in which a limited role has been established for the reintroduction of primates into selected habitats. As might be predicted from the work reviewed in this chapter, many primates need to acquire much of the information they need to survive and breed through social learning, whether it is provided by knowledgeable conspecifics or by human caretakers simulating that role (Custance et al. 2002; Stoinski et al. 2003).

A second practical area concerns welfare and management of captive primates, where care staff often informally report that animals have learned such things as being compliant in receiving injections, mothering infants, or mating by watching experienced conspecifics live or on video. There appears to be only minimal systematic testing of such procedures (Lambeth et al. 2008), but this seems to be an area in which it would be extremely worthwhile to do so.

Conclusions: The Evolution of Social Learning in Primate Societies

Have we learned enough yet to attempt to construct an evolutionary scenario for the phenomena discussed in this chapter? Barely. The evidence for traditions and cultures in the wild comes from long-term studies of multiple groups, and so it still remains to be reported for most primates, with just a handful of species focused on to date. There is a dearth of such information even for such a well-studied group as the baboons. Even where species are well studied, as is the case with chimpanzees, controversy still surrounds the true nature and scope of their cultural repertoire. However, we may have reached an opportune point to start building a set of working hypotheses. This may help clarify where gaps in our knowledge exist and what is most needed in the next phase of research in this exciting area.

A first hypothesis is that the most basic social learning processes of stimulus enhancement and observational conditioning are available to all primates. Such processes have been identified in much broader groups of animals, extending to both vertebrates and invertebrates (e.g., Curio et al. 1978; Galef & Whiskin 2008). In conjunction with what we know about specific primate life histories and societies reviewed elsewhere in this volume, we may predict that young primates, during their typically long periods of immaturity, will learn to discriminate among such crucial things as foods, foraging sites, and predators, most commonly first through the mother, and later from whatever wider society they are exposed to (chapters, 7, 8, 10, and 11, this volume). The latter process may be moderated significantly by the levels of social tolerance that prevail (van Schaik et al. 1999).

In Old World monkeys there is surprisingly little compelling evidence for more structured modes of social learning (Tomasello and Call 1997, table 9.2: but see Subiaul et al. 2004; Subiaul 2007). By contrast, there is more to social learning in the relatively distantly related New World monkeys and apes (great apes, at least; we still know all too little of social learning in gibbons).

Consider New World monkeys first. As detailed earlier, there is much evidence across several taxa for both provisioning, in response to begging and active giving—in both cases, with a focus on foods that are difficult to harvest and/or process. In the callitrichines there is even evidence of dedicated food calls used in ways that are consistent with “teaching” (encouraging the skills associated with locating and dealing with invertebrate prey). The prevalence of these interactions concerning novel items suggests that the func-

tion is not restricted to nutrition directly, but extends to information transfer (Rapaport & Brown 2008). There is also evidence of both marmosets (Voelkl & Huber 2000, 2007) and capuchins (Dindo et al. 2008, 2009) copying the foraging techniques of others. Finally, in capuchins there is evidence of regional variation in multiple traditions involving social conventions, foraging techniques, and possibly tool use (e.g., Perry et al. 2003).

Turning to apes, we see several of these features too: provisioning in response to begging, active food offering, confiscation of problem items, and facility in copying the techniques of others (Whiten et al. 2004; Rapaport & Brown 2008). The copying is relatively sophisticated in extending to the sequential and perhaps hierarchical structure of actions, and the very nature of imitation is understood by apes well enough for them to learn the “do-as-I-do” game and actively test others who appear to be imitating them (Nielsen 2005; Haun & Call 2008), thus going beyond monkeys’ recognition of being imitated (Paukner et al. 2005, 2009). Consistent with these capacities, great apes (orangutans and chimpanzees, at least) appear to exhibit the richest multiple-tradition cultures among nonhuman animals, incorporating a diversity of behavior types including social behavior, courtship gambits, foraging techniques, and tool use. The fact that all these features are shared with humans promotes the inference that they also would have been shared with our common ancestor of around 14 million years ago (Whiten 2011).

A thorough analysis of the evolutionary changes involved in the giant leap human culture took from the platform provided by those ancestral features is a substantial task (see Klein & Edgar 2002; Boyd & Silk 2006; chapter 32, this volume). Here we can only note that there have been changes in three principal aspects of culture (Whiten 2005, 2009a). The first concerns the large scale spatiotemporal patterning of culture. As we have seen, ape culture can extend to multiple regional differences in traditions, as occurs in humans. But human culture goes further to display extensive evolutionary change in its own right: the culture of each generation builds on what went before, often leading to what Tomasello (1999) has described as a progressive “ratcheting” of cultural diversity and achievement. In this, culture echoes Darwinian biological evolution (Mesoudi et al. 2006). Examples are to be found in every aspect of human culture, from language (Gray et al. 2009) to religion and technology (Shennan 2002). The second set of changes concerns the contents of culture: the types of behavior that are culturally transmitted. Some such contents are shared with apes, such as tool use, but major new ones have emerged, particularly in the social domain, on

the scale of such examples as spoken language and religion (Whiten 2009b).

The third set of changes is in transmission mechanisms. In some societies these mechanisms have become as elaborate as those involved in formal education extending into adulthood, and such conduits as books and the Internet. However, just what forms transmission takes in hunter-gatherer societies, which are more representative of much of our history over the last million years or so, remains frustratingly unclear. Some reports appear to imply that teaching is rare and that observational learning predominates—a situation much more akin to what we see in nonhuman primates (Whiten et al. 2003). But even observational learning takes different forms. There is debate over the nature of such differences (Herrmann et al. 2007; de Waal et al. 2008; Tennie et al. 2009; Whiten et al. 2009), with some researchers concluding that true imitation is limited to human children and is not shared by other apes, and other researchers disagreeing with the contention that the contrast between children and apes is so stark, as has been discussed above. Nevertheless, there is much consensus that children attain unique levels of imitative fidelity. Indeed, recent work has focused on the discovery of what has been dubbed “over-imitation,” in which children are so ready to copy that they become unable to inhibit themselves from blindly imitating the actions of others even when perceptual cues should tell them the actions are wildly ineffective (Lyons et al. 2007; Whiten et al. 2009; see Nagell et al. 1993 for an early example).

Whatever the features of social learning and culture that separate humans from other primates, it has become clear that extensive foundations for these behaviors must have existed in the various ancestors we share most recently with other apes and further in the past with other primate taxa. Such inferences appear increasingly substantial as aspects of social learning, traditions, and cultures are identified in other primates that exhibit manifest commonalities with human counterparts.

However, this human-centered perspective, while reflecting a common motivation for interest in the topics of this chapter, is but one among many. Social learning and traditions have evolved into their present forms across all of the hundreds of living species “tips” of the primate family tree. A comprehensive analysis of the evolution of these cultural phenomena across the whole primate order is a perfectly valid, nonanthropocentric aspiration for the discipline. At present, the kinds of data required for this have been collected for only a small subset of primates, particularly those highlighted in this chapter—but it is to be hoped that these data will provide a future inspiration for other primatologists to help fill in the gaps.

Notes

1. I am grateful to Josep Call for earlier drawing my attention to the pioneering diffusion experiment of Menzel et al. (1972).
2. Gruber et al. (2009) have shown that wild chimpanzees presented with the same novel honey-dipping problem at one site, where they habitually use sticks for probing, and at a second, where instead leaf sponges are used, go on to apply their local technique, which the authors attribute to their “cultural knowledge.” This suggests the feasibility of related diffusion experiments in the field.
3. Whiten and Mesoudi (2008) review 33 diffusion experiments conducted with fish, birds, and mammals.
4. Tennie et al. (2010) further enrich the picture by using a different approach, showing evidence of emulation in chimpanzees when the context does not allow imitation of a technique used by a model.

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