Monkeys and Prosimians: Social Learning

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Introduction

In this chapter, we highlight examples of social influences on learning observed in prosimians and monkeys and consider the role of socially mediated learning in the biology of these animals. Learning is always the outcome of interacting physical, social, and individual factors and takes place over time. Thus, we cannot parse learning, either as a process or as an outcome, into portions that are socially influenced and portions that are not. Instead, we can document how social processes affect behavior relevant to the learning process, and we can seek evidence for social contributions to learning outcomes.

To begin, we provide some background on the taxonomic groups of interest in this chapter: monkeys and prosimians. Primates are a remarkably diverse order. Body size alone spans three orders of magnitude, from tiny prosimians weighing a few hundred grams to massive apes weighing more than 100 kg. Diet, morphology, mating systems, locomotor style, life history, and every other aspect of the biology of these animals is as diverse as body size, and this diversity is important when considering the contributions of the social context to learning in particular species.

Phylogeny of Prosimians and Monkeys

As Fleagle (1999) discusses in greater detail, the order Primates includes two suborders: Prosimii, prosimians, and Anthropoidea, monkeys, apes, and humans (see **Figure 1**). The two suborders have evolved separately for at least 55 Million years. Two infraorders are classified within Anthropoidea: the platyrrhines (New World monkeys) and catarrhines (Old World monkeys, apes, and humans). New and Old World monkeys diverged approximately 40 Millions of years ago (Mya), and apes and hominids (hominids include modern humans and their ancestors; superfamily Hominoidea) diverged from the Old World monkeys (superfamily Cercopithecoidea) approximately 20 Mya. Given their lengthy independent evolution, variation in the life histories, body sizes, social organizations, etc., within each suborder, infraorder, and superfamily in the order Primates is to be expected.

The suborder Prosimii includes the infraorders Lemuriformes (the lemurs of Madagascar), Lorisiformes (the lorises of Africa and Asia and the galagos of Africa), and Tarsiiformes (tarsiers of Southeast Asia). All prosimians live in tropical habitats in Africa and Asia and the vast majority are arboreal and nocturnal. Prosimians are sometimes referred to as 'living fossils' because they appear to have some physical similarities to ancestral primates of approximately 50 Mya. In general, prosimians rely to a greater extent than other primates on olfaction. Some are solitary foragers; others travel and forage in groups ranging from small family units to larger social groups of as many as 27 individuals. We know less about the lifestyles and behavior of prosimians than of monkeys.

In comparison with prosimians, species in the suborder Anthropoidea are characterized by a relatively larger brain for their body mass, diurnal lifestyle, and a greater reliance on vision than on olfaction. Anthropoid species generally exhibit greater manual dexterity than prosimians, and anthropoids are more likely to live in groups. New World monkeys (infraorder Platyrrhini) are arboreal and relatively small-bodied, ranging in size from approximately 100 g (the pygmy marmoset [*Cebuella pygmaea*]) up to 10 kg (the muriqui [*Brachyteles arachnoides*] and spider monkey [Genus *Ateles*]). Many genera live in small family groups; others live in medium-to-large social groups (as many as 50–60 individuals). Within the New World monkeys are the subfamilies Callitrichinae (marmosets and tamarins), Atelinae (muriquis, woolly, howler, and spider monkeys), Pitheciinae (titis, sakis, bearded sakis, and uakaris), Cebinae (squirrel monkeys and capuchins), and Aotinae (owl monkeys, the only nocturnal anthropoid). During the platyrrhine radiation in the Americas, the genera adapted to distinct niches, making a living in different parts of the forest canopy and resulting in great diversity in social organization, reproductive strategy, diet, and locomotor style.

Compared to New World monkeys, Old World monkeys (superfamily Cercopithecoidea) are mostly larger-bodied, ranging from around 1 kg to approximately 30 kg, and some are terrestrial. Old World monkeys include subfamilies Cercopithecinae (baboons, mandrills, drills, macaques, mangabeys, and guenons) and Colobinae (colobus monkeys and langurs), which differ particularly in their dietary adaptations (see Fleagle for details). Most cercopithecoid species live in large polygamous social groups with clear dominance hierarchies within and between matrilines (female kin groups), and some form multilevel societies during parts of the year. Of all primate superfamilies, cercopithecoids have the widest geographic range, greatest number of species, and form some of the largest groups and biomass

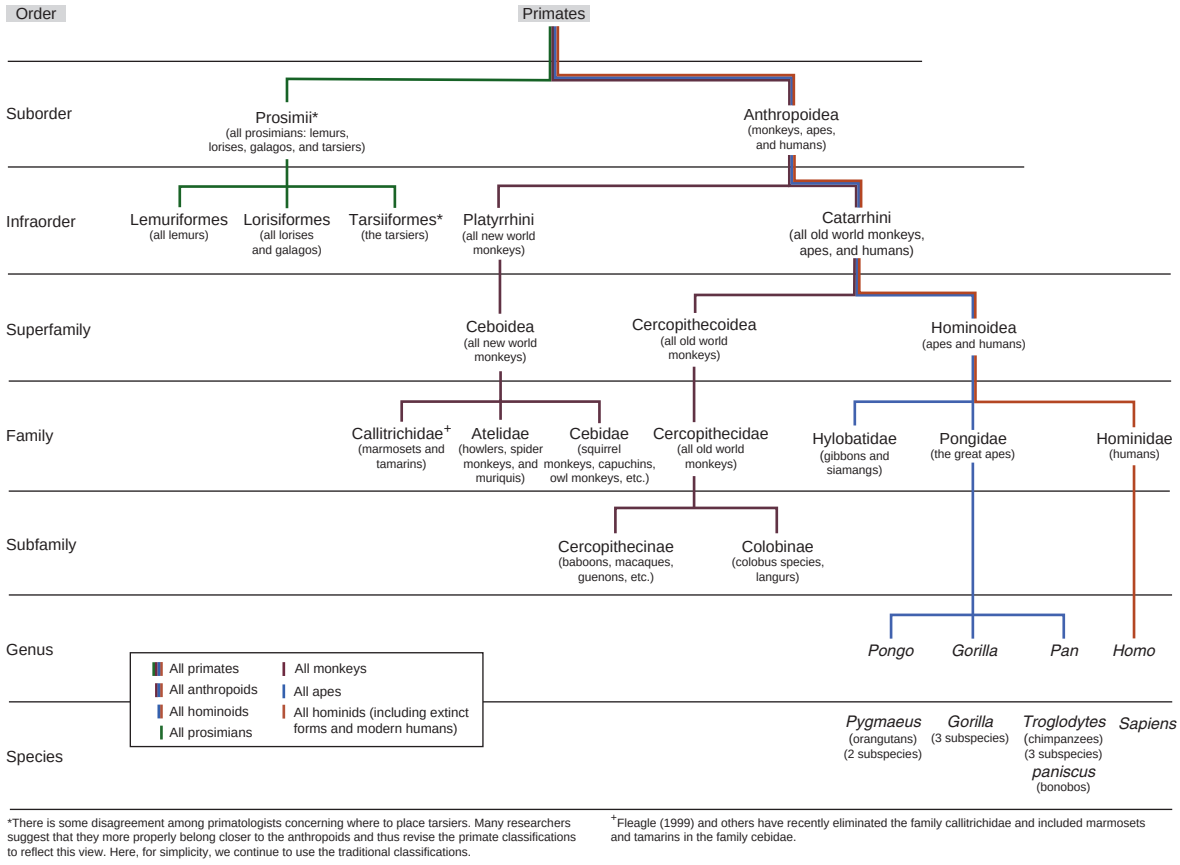

Figure 1 Primate taxonomic classification. This abbreviated taxonomy illustrates how primates are grouped into increasingly specific categories. Only the more general categories are shown, except for the great apes and humans. Reproduced from Turnbaugh WA, Nelson H, Jurmain R, and Kilgore L (2002) *Understanding Physical Anthropology and Archaeology*, 8th edn., with permission from Wadsworth.

densities in the primate order. Despite this, Old World monkeys have less diversity in diet and social organization than New World monkeys.

Phylogeny and Socially Mediated Learning

This brief review of primate phylogeny suggests some reasons why we might expect socially mediated learning to vary across primate taxa. First, group demographics and social dynamics within groups define the social context, and thus influence socially mediated learning within a group. The number of groupmates, their age and sex, and the nature of social relationships within the group vary enormously across species, and may vary considerably within species as well. Groups of monkeys of the same species may live in smallish groups (4–7 individuals) or quite large groups (more than 40 individuals) depending on the local distribution of resources. Second, reliance on various sensory modalities (vision, olfaction, audition, and touch) in social interaction and in general activity varies across taxa. For example, species that are particularly attentive to smell (such as many prosimians) will be affected by social partners in a way different from that of species that are highly reliant on vision. Third, motor patterns and action proclivities vary considerably across species. For example, leaf-eating monkeys are generally less likely to manipulate objects spontaneously than species that feed on seeds and nuts. Finally, the variability in behavioral ecology across species means that individuals of different species are interested in different kinds of activities, locations, objects, and events. For example, leaf-eating monkeys may be less likely to attend to sequences of actions during feeding than are seed- or nut-eating species; omnivorous species are less likely to attend to the odor of leaves eaten by another than are dietary specialists. Behavioral priorities and proclivities of each species constrain what an individual is likely to learn in the first place, and thus the role of social context in learning.

The Sources of Social Context

Social Organization

The social organization (i.e., the size, demographic composition, and spatiotemporal coordination of individuals

within a group) and social relationships among individuals in a group provide the boundaries of the social context in which an individual can learn. As Coussi-Korbel and Fragaszy have proposed, conspecifics with which an individual has a long-term social relationship and that are frequently nearby are particularly important and enduring components of an individual's experience. In theory, the more closely individuals coordinate their activity in space and/or time, the more likely an individual's activity is to influence the activity of others. Individuals of species in which social partners spend more of their time apart than together are likely to experience less direct social influences on learning specific actions than species that spend most of their time in the company of conspecifics. For example, adults of many nocturnal prosimians form sleeping groups during the day but travel and forage alone at night (e.g., dwarf and mouse lemurs [Genus *Cheirogaleus* and *Microcebus*, respectively] and some galagos [Genus *Galago*] and tarsiers [Genus *Tarsius*]). These animals are therefore not often in the company of others that might influence their behavior. However, all monkeys and some prosimian species, such as lemurs, sifakas, and indris, remain in cohesive groups and are near conspecifics virtually all the time. This intensely social lifestyle affects every aspect of experience through every sensory modality. Interactions with conspecifics structure where and how an individual budgets the time that it devotes to different activities (e.g., travel vs. feeding), and conspecifics also influence how an individual responds to events that occur nearby. For example, as Cheney and Seyfarth have shown, monkeys attend to overt signals made by others concerning objects, events, or locations of affective value (i.e., desirable or objectionable) such as a recruitment call to a food site or an alarm call to a predator, even if out of sight or some distance away from the other group members.

Social Relationships

Individuals are more likely to be near others with which they share a mutually affiliative relationship (e.g., dependent offspring with a parent). If social influences on learning are maximized when individuals are near one another, then a potential learner will be more influenced by those with which it shares positive affiliations than by others: a phenomenon Coussi-Korbel and Fragaszy have labeled Directed Social Learning. Over time, uneven social influences on learning across individuals within a group can lead to the generation of behavioral variations among subgroups. For example, young Japanese macaques living in Koshima, a small island in Japan, first began to wash sweet potatoes in the sea when these were provided for them on a sandy beach on the island. Initially, only juveniles washed potatoes. In subsequent years, the juveniles' older siblings and mothers started to wash potatoes. Older individuals adopted the behavior more slowly than juveniles; adult males most slowly or not at all. If social influences contributed to the spread of the behavior, it did so unevenly across age and sex classes in accord with the predictions of the Directed Social Learning model. However, as Galef has indicated, a similar outcome could reflect accumulation of individual experience without any social influence, so we cannot definitively claim that social influence promoted the spread of the behavior. A similar caveat applies to several commonly cited examples of traditions in non-human primates. Observing the development of behaviors by new practitioners, with the requisite detail of social contexts and behavioral change over time, is necessary to make strong claims about the contributions of social context to learning a specific behavior. Such developmental studies are now underway with some species of monkeys.

Social influences within a group can be thought of as either vertical (across generations) or horizontal (within generations; among juveniles, for example). Vertical and horizontal social influences are common in primates. Vertical social influence is often discussed as promoting behavioral continuity between generations, while horizontal social influence is more likely to promote adaptive behavioral change; for example, in response to changing circumstances. Vertical social influence promotes continuity in commonplace and routine preferences and behaviors that young primates acquire gradually while traveling with adults, such as habitual travel routes and sleeping sites. Vertical social influence can also promote refinement of specific behaviors. For example, as Cheney and Seyfarth have shown, young vervet monkeys (*Cercopithecus aethiops*) gradually narrow the range of animals to which they give alarm vocalizations according to differential adult responsiveness to their calls. Adults respond to juveniles' calls in response to actual predators and ignore calls in response to benign animals.

Perry's studies of white-faced capuchins (*Cebus capucinus*) in Costa Rica provide examples of behaviors reflecting horizontal social influence. These monkeys sometimes develop idiosyncratic social behaviors ('games') that are played in pairs by close companions in a play context, but not between parent and offspring. One of the games identified by Perry and colleagues is the toy game, in which two monkeys take turns extracting an inanimate object, like a twig or leaf, from each other's mouth. In the toy game, one monkey holds the object tightly in its mouth without chewing it, and the other monkey attempts to pry open the first monkey's mouth and extract the item. Once retrieved, the monkeys then repeat the procedure or switch roles. Although initially one individual instigates a new game, eventually several different pairs in the group participate in the same game. Such behaviors are maintained by a particular social context and often disappear when that context disappears (e.g., when the key initiator of the behavior emigrates from the group).

For many species of primates, the most influential social partner from birth until independence is the mother, and in some species that share parental care, the mother and father (e.g., callitrichids, owl monkeys, and titi monkeys). Infants of most primate species are carried by the mother and thus are influenced by her activity as they travel together throughout the day. Even when able to travel independently, infants typically remain near their mother to nurse, rest, and feed, and this period of dependency is often considered important for skill learning by infants. Aye-ayes (*Daubentonia madagascariensis*), a nocturnal prosimian species, provide a striking example (see Figure 2). A significant part of the aye-aye's foraging activity involves extracting larvae from woody substrates, using a method called tap-foraging. In tap foraging, aye-ayes tap the substrate with a finger to locate a hollow cavity, gnaw the wood in the right place, and insert a specially adapted, long and skinny digit to probe the cavity and to extract the larva. Krakauer demonstrated several ways in which immature aye-ayes' proficiency in tap foraging is influenced by close proximity with their mother while she engages in the behavior. In general, the aye-aye mother allows her infant to remain nearby while she tap-forages. Over time, the infant begins to take over the site where the mother is working and extract the larvae itself. Infants of a naturally nontap-foraging mother attempted tap-foraging less often than other infants and never succeeded at extracting a larva.

Processes Mediating Learning in a Social Context

Facilitation and Enhancement

One common and powerful form of social influence on learning in primates is increased probability of performing a behavior when a conspecific is seen performing that behavior. Such socially facilitated behaviors are already in an individual's repertoire, for example, vocalizing or grooming. Another powerful social influence on behavior is increased interest in an object or in an area where another has recently been active or where others' previous activity has left artifacts (e.g., scents or physical alterations) (see Figure 3). Such increased interest in areas or objects where others have been active has been termed, respectively, local and stimulus enhancement; hereafter, enhancement. The bulk of empirical studies of social influences on learning in monkeys and prosimians have concerned these two phenomena.

Social facilitation is particularly common in primates in the context of feeding. For example, individuals are likely to begin eating, even if satiated, if nearby group members are eating. Social facilitation can lead to exposure to a new food item, or support exploratory activities that indirectly aid learning a foraging skill, as when young monkeys learn to locate hidden prey through repeated bouts of searching begun while or shortly after seeing others forage for hidden prey. This simple mechanism can support individuals developing the same dietary preferences as their groupmates, as individuals eating at the same time usually eat in the same place, and therefore often eat the same things. More generally, social facilitation results in temporal coordination of group activity.

Enhancement may occur through multiple senses and over an extended time period. For example, an individual's attention may be drawn to a foraging site through observation of another feeding, hearing the other's actions (such as breaking a stick), eating food items derived from

Figure 2 Mother and infant aye-aye foraging jointly. Aye-ayes (*Daubentonia madagascariensis*, lemurids) locate hidden prey by tapping on woody substrates. Infants begin to practice this technique at the same sites as their mothers. Photo by David Haring/Duke Lemur Center.

Figure 3 Infant Japanese macaques (*Macaca fuscata*, cercopithecines) attend closely to their mother's activity with stones. In groups of Japanese macaques provisioned with food, many individuals engage in stone-handling, and this behavior has been characterized as a tradition. Photo by Jean-Baptiste Leca/Primate Research Institute, Kyoto University and Iwatayama Monkey Park.

another's activity at the site, smelling another's mouth, and encountering artifacts (including scents) of past foraging activity, as well as through joint contact with materials another is handling. Any and all of these experiences increase the probability that an individual will investigate the site that another is exploiting or has exploited. Typically, young primates show strong interest in sites where others, especially adults, are foraging (see **Figure 4**). To the extent to which juveniles' proximity is tolerated by adults, young primates may approach and eat dropped food or even take bits of food from another's hand or mouth. However, even when young monkeys do not acquire food as a result of approaching, they are still intensely interested in sites where others forage.

Although most adult monkeys and prosimians do not overtly share food, enhancement of interest in foraging sites appears to be actively promoted in callitrichids. For example, Rapaport and Brown have found that adult golden lion tamarins (*Leontopithecus rosalia*; see **Figure 5**), which live in cohesive family groups that are led by a cooperatively breeding pair, emit food-offering vocalizations that draw their dependent offspring to a site containing live prey or large/tough-skinned fruit. Instead of taking the food for themselves, an adult waits until a juvenile reaches the site and allows the juvenile to extract the food item. This form of provisioning (or, as Rapaport and Brown refer to it, opportunity teaching) peaks around weaning (3–4 months) and continues untill infants are about a year old. Adults selectively provision infants with items that are difficult to process.

Callitrichids rely to varying degrees on extractive foraging for hidden foods, and participating in foraging with adults apparently helps youngsters learn to search in appropriate places and to perform appropriate actions. Research has shown more overt instances of adults actively providing social supports for youngsters learning to forage in callitrichids than in other monkeys, such as cercopithecines and colobines, which live in larger groups and show less shared parental care. Brown and Rapaport suggest that the degree of parental assistance in foraging seen in callitrichids is matched only by apes.

Motor Imitation

Motor imitation (i.e., performing a specific action after observing another perform the same action) is thought to contribute importantly to learning in humans. Currently, we have no evidence that prosimians or monkeys imitate novel actions spontaneously, as do humans. Nevertheless, recent experimental evidence indicates that marmosets and tamarins (callitrichids) will use the same part of the body to move an object that they have witnessed a conspecific use to solve a foraging problem. Currently, callitrichids provide the best evidence of imitation of familiar actions in monkeys. It is interesting that callitrichids have aptitude in this domain (as well as in opportunity teaching), whereas cercopithecoid monkeys do not, because callitrichids are phylogenetically more distant from hominids than cercopithecoid monkeys (see **Figure 1**), while true imitation is present in hominids.

Figure 4 Infant and juvenile bearded capuchins (*Cebus libidinosus,* cebids) watch an adult crack a palm nut using a stone hammer, a common behavior in many wild groups of this species. Young monkeys regularly attend closely to proficient crackers and collect bits of broken nut from sites where adults crack. This tolerant social context is thought to promote investigation of appropriate sites and materials by the youngsters, and thus to aid them in learning to crack nuts. Photo by Barth Wright/EthoCebus Project.

Figure 5 Adult golden lion tamarin (*Leontopithecus rosalia,* callitrichids), carrying twins. Parents in this species call their dependent offspring to places where a hidden food item can be procured, a phenomenon called 'opportunity teaching'. Photo by Jessie Cohen/National Zoo, Smithsonian Institution.

Learning a Decision Rule through Observation

Psychologists have long been interested in whether individuals can learn arbitrary decision rules from watching others select objects from a set. Typically, a subject observes a skilled partner and a short time later works on an identical problem. Monkeys have considerably greater success on this kind of task than in reproducing novel actions after watching others perform them. For example, Subiaul trained two rhesus macaques (*Macaca mulatta*, cercopithecines) to touch in fixed order each of four pictures appearing simultaneously on a touch-screen monitor. Each monkey trained alone and became an expert at a particular sequence of four pictures, and then each monkey learned the other monkeys' sequences as well as other new sequences. Both the monkeys more quickly learned the series that they had watched their social partner perform than series that they had not watched the other monkey perform. As each monkey was already skilled at touching pictures in a particular sequence, what each monkey learned from watching the other was the order in which to touch a new set of pictures. Subiaul labels this type of learning 'cognitive imitation,' because the observer adopts a rule demonstrated by another, rather than a particular action. Subiaul argues that monkeys can adopt novel decision rules, but not match novel actions, from watching others because matching novel actions depends upon 'derived neural specializations mediating the planning and coordination of fine and gross motor movements' that some hominids (see Whiten, this volume), but not monkeys and prosimians, possess.

Biological Significance of Socially Mediated Learning

Socially mediated learning probably serves biological functions in primates similar to those it serves in other taxa. Social partners provide a context for learning in non-human primates, both highlighting relevant features of the environment through enhancement and promoting behaviors that are generally appropriate for a particular place and time through social facilitation. In the short term, social mediation of learning reduces risk during the acquisition of useful skills and knowledge, and social mediation may be especially beneficial to acquiring certain foraging skills. Differentiated relationships with specific others produce a mosaic of learning opportunities across individuals within a group, thus promoting behavioral variation within a group.

Social mediation of learning can also have longer-term consequences when it results in traditions (i.e., relatively enduring behaviors acquired in part by socially mediated learning and practiced by at least two members of a group). Behavioral traditions hold strong interest for evolutionary biologists because traditions generate and maintain behavioral variation over time outside of, or perhaps even ahead of, changes in the genetics of a population. In this indirect manner, socially mediated learning contributes to evolution, and social learning becomes central to the contemporary debate about the relationship between traditions in non-human animals and the phenomenon of culture (for discussion see Perry, this volume, or Caldwell and Whiten, 2007).

Summary

Monkeys and prosimians have varied social lives, which influence how and what individuals learn. In general, monkeys and prosimians are interested in conspecifics and attend to what they are doing. The motivation to synchronize behavior with others (social facilitation) promotes behavioral coordination within a group. Interest in where another is acting (enhancement) draws attention to both places and objects. Such processes channel an individual's activity sufficiently that monkeys and prosimians tend to acquire preferences and behavioral patterns similar to those of their groupmates. Monkeys match the specific actions of others only in very limited circumstances. The influence of older on younger individuals promotes the maintenance of behaviors across generations (traditions), and enduring traditions may have an impact on natural selection.

See also: Apes: Social Learning; Culture; Imitation: Cognitive Implications.

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