Studying primate cognition: from the wild to captivity and back

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Abstract

How do nonhuman primates process information about their social and physical world, and how do they make decisions? To address this question, research in the tradition of ethology and behavioral ecology aims to uncover how animals behave under ecological and evolutionarily valid conditions. By combining detailed observations of behavior in the wild with field experimentation, such studies have shed light on what primates know about predators, their home ranges and food sources, and their social environment. A second research stream takes non-naturalistic experiments into freely moving groups of wild or captive primates to test social learning, problem-solving skills, and motivation. Finally, captivity-based studies address a wide range of questions, using an array of different methodological approaches, often with the aim to explore the limits of the animals' abilities. This chapter compares the strengths and the limitations of the different research streams and proposes an integrative approach to developing a profound understanding of primate cognition.

Keywords: comparative cognition, developmental psychology, ethology, experimental psychology, field studies, playback, primate, social cognition

Background

What do we know about primate cognition today, and how do we know it? What are the kinds of questions we ask, and which methods do we employ to tackle nonhuman primates' (hereafter: primates) minds? Studies of primate cognition range from naturalistic observations and experiments in the wild to non-naturalistic experimentation with primates living in large enclosures (or the wild), and studies in captivity that stand in the tradition of developmental psychology. These three research streams are shaped by different conceptual frameworks and associated with different research practices.

Field studies are concerned with primate knowledge that is in one way or another relevant for their survival and reproduction. How do the animals process information about predators in the vicinity? What do they know about the food sources in their habitat? How do they respond to group members' signals or other animals in the area, and how do they integrate contextual information with information inferred from communicative signals? And, perhaps most prominently: what do they know about their social environment – the dispositions of their group members, the social and rank relationships between third parties, and the knowledge others around them may have. In sum, such field studies are concerned with what the animals know, what its adaptive value might be, and how the cognitive processes supporting the behavior in question evolved. A more recent development is the use of non-naturalistic experimentation in the wild. Such studies may have lower ecological validity, but they are necessary when experimental control over the amount of information made available is required – as in studies of learning, for example.

Captivity-based studies encompass an enormous variety of topics, ranging from perception to information processing and decision-making. Broadly, captivity-based studies fall into the categories of physical cognition and social cognition. Studies tapping into physical cognition investigate what the animals know about physical properties of objects, such as object permanence, connectedness, mass, quantities, etc., and about causal relationships or statistical patterns, to give just a few examples. The field of social cognition is concerned with questions such as what the animals know about social relationships, the knowledge states of others (and themselves), or other individuals' attributes, such as their skillfulness or propensity to help. Captivity-based studies are often guided by the question of how primates compare to humans. In the past two decades, a dominant approach was to run parallel tasks with primates and human children of different ages to uncover similarities and differences in cognitive performance between the different species.

Researchers in the different disciplines were not always interested in what the other respective camps had to offer. Field researchers may lament the lack of ecological validity of studies done in

captivity and may question whether it is acceptable to compare the cognitive performance of apes in captivity to that of children living in their family homes. Experimentalists working in captivity may point out that naturalistic observations are not suited to hone in on the cognitive processes underpinning behavior. They may also abhor the lack of control in field experimentation.

With this chapter, I aim to mend the rifts between disciplines. The way forward should be to think about how the different approaches can inform one another to produce better research ultimately. To promote an integrated perspective on primate cognition, I provide an overview of what the different research strands have to offer. This chapter does not aim to provide a comprehensive review of the state-of-the-art; I instead picked examples rather eclectically to make specific points.

Naturalistic studies

From behavioral observations to field experimentation

Intimate knowledge of the natural behavior of the study species constitutes the foundation of any ethological study. Targeted behavioral observations can be used to test whether the animals use signals strategically to regulate their interactions, how they choose their allies in agonistic interactions, or to which degree they intervene on behalf of others. Whenever feasible, hypotheses can (and should) be put to the test using an experimental approach. Whether a targeted observation or an experiment is inspired by observation or designed to test predictions from theory, it is essential to know how the animals behave to develop an appropriate and meaningful study protocol. Notably, acoustic recordings of the animals' vocalizations, combined with acoustic analyses (see Fischer et al., 2013, for an overview), are as foundational for understanding the animals' behaviour as observations of their social interactions or movement patterns.

Field experiments are the cornerstone of ethological research programs. In such experiments, information about food availability, presence of predators in the vicinity, or the group's social shenanigans may be manipulated. In particular, playback experiments have proven to be a powerful tool to probe how primates respond to information about predators and test what they know about their group members' relationships and knowledge states. Such experiments are possible because primate vocalizations are individually distinct, and group members recognize each other by voice characteristics (e.g., Rendall et al., 1996). The art of an ethological field experiment is to trick the animals into assuming that the information provided *could be real* – be it the growl of a leopard or the model of a snake presented to the animals. Therefore, utmost care is needed to avoid any hints to the experimental manipulation. Otherwise, one might run the danger of recording responses to situations that the animals deem to be 'unnormal.'

One of the major challenges of field experiments is that the animals are roaming freely; this is also true of non-naturalistic experimentation. The experimenter has no control over their movements, their interactions, or the appearance of real predators just when one is about to present a fake one. An unforeseen inter-group encounter may instantly upset a carefully staged playback experiment. Field experiments require patience, restraint, and an enormous amount of frustration tolerance. Yet, in my view, nothing beats the joy of a successful field experiment when one is allowed to peek into the monkeys' minds in their natural lives. Below, I outline different approaches to study primate cognition within an ethological framework, grouped by research area.

Observational studies of social knowledge

The ability to classify relationships between group members according to kinship, affiliation, and dominance is an essential adaptation to life in social groups (reviewed in Seyfarth & Cheney, 2015). Studies of social decision-making and partner choice provide insights into how animals evaluate other group members' abilities and skills and whether they factor in the quality of the relationship between themselves and the partner. One of the classic examples showing that nonhuman primates have rich representations of their relationships is the case of post-conflict interaction (PCI). From a cognitive perspective, PCIs are interesting because they can be conceived as a form of decision-making. The risk of renewed aggression is weighed against the motivation to restore the relationship. Wild chimpanzees (*Pan troglodytes verus)* living in the Taï Forest in Ivory Coast, for instance, engaged in PCIs predominantly with cooperative partners and frequent associates (i.e., "valuable partners"; (Wittig & Boesch, 2003). Other examples that demonstrate how careful observation can shed light on social information processing include the observation that vervet monkeys (*Chlorocebus pygerythrus*) selectively attack relatives of animals that previously had aggressed the subject's kin (Borgeaud et al., 2015; Cheney & Seyfarth, 1989). Similarly, in agonistic interactions, Japanese macaques (*Macaca fuscata*) and bonnet macaques (*Macaca radiata*) selectively solicit allies who rank higher than their opponent (Schino et al., 2006; Silk, 1999).

Another set of studies investigated how social partners use communicative signals to regulate interactions. In despotic species such as chacma baboons (*Papio ursinus*), a high-ranking female approaching a lower-ranking female will usually displace her, unless the higher-ranking female grunts. Approaches with grunts increased the likelihood of an affiliative interaction, including infant handling, and decreased the likelihood of displacement and aggression. Therefore, grunts have been conceived as a "signal of benign intent" (Cheney et al., 1995). Importantly, grunt usage was modulated by relationship strength and infant presence, indicating that females used the grunts strategically (for a species comparison see also Faraut et al., 2019; Silk et al., 2018). Similarly,

researchers have taken great interest in the question how the animals use non-vocal gestures in their social interactions (Hobaiter & Byrne, 2014; Pika & Mitani, 2006; Roberts et al., 2014).

Testing social knowledge using playback experiments

The first experimental evidence that animals represent the relationships between their group mates was gathered rather serendipitously in a playback study on mother-offspring vocal recognition in vervet monkeys. An infant's scream was played back to its mother from a well-hidden speaker to probe whether she would respond more strongly to her offspring's compared to another infant's vocalizations. Not only did the mother look longer at the speaker when her kid's screams were played, but more remarkably, other females in the vicinity looked at the mother, as if they knew that the screaming infant was indeed her offspring (Cheney & Seyfarth, 1980).

Wittig and colleagues (2007) tested experimentally whether an affiliative interaction between the aggressor's kin and the former victim might substitute for reconciliation in chacma baboons. To give an idea how tricky field experimentation can get, let me describe the contingencies of the experiment in more detail: The researchers had to wait until a higher-ranking female aggressed a lower-ranking female. They then needed to ensure that the aggressor had left, hide the speaker in the direction the aggressor had moved off, and check that none of the female's relatives were around. The second experimenter had to ensure that the subject did not interact with another animal and then needed to find the right angle to film its response. In the test condition, subjects heard 'friendly' grunts of a relative of the former aggressor; in the control condition, these grunts were from another high-ranking female unrelated to the former aggressor. Anyone who has ever worked with gregarious primates in the field will immediately understand how difficult it is to find a situation where all these conditions are met. There are simpler designs, but this example illustrates that field experiments can be extremely demanding – not only probing the animals' minds but also the experimenters' patience.

To investigate whether cooperative behavior is contingent on the quality of the previous interaction, Cheney and colleagues (2010) tested female chacma baboons in a playback experiment. The subject was played the partner's 'threat grunts' after the subject and partner had groomed or after the subject had threatened the partner (these threat grunts differ acoustically from the friendly grunts mentioned above). Subjects were more likely to approach the loudspeaker following the playback after grooming than after aggression, indicating that support was partly contingent upon the quality of the previous interaction (Cheney et al., 2010).

The previous playback studies used the calls of just one animal, but there is also the possibility to fake an interaction between two subjects by pairing their calls. To test the social

knowledge of chacma baboons, Bergman and colleagues simulated an aggressive interaction between two animals. The call sequence consisted of a female's threat-call in conjunction with (submissive) screams given by another female. In the test condition, a lower-ranking animal's threat call was played, followed by the screams of a higher-ranking animal, thus violating rank relations. Apparent rank reversals either occurred between unrelated females or related females from the same matriline. The test subjects responded strongly to rank reversals, when they occurred between families. In contrast, they responded less strongly to within-family feuds, suggesting that they have both an understanding of the rank relations and the relatedness structure in their group (Bergman, 2003).

Presenting predator models

One of the pioneers studying chimpanzees in the wild was Adriaan Kortlandt, a Dutch primatologist. In 1960 – the same year that Jane Goodall traveled for the first time to Tanzania – he embarked on a trip to what was then known as Belgian Congo and watched a group of chimpanzees at the edge of their forest. Intrigued by the question of how early humans might have defended themselves against large predators, he presented the chimpanzees with an animated stuffed leopard that could even turn its head. When the chimpanzees spotted the leopard, they became extremely agitated and began clubbing the leopard model with sticks. Kortlandt distinguished between different techniques with which the apes attacked the model, including the „marital dish-smashing type" or the „police clubbing technique" (Kortlandt, 1975).

Predator models have by now been used in a wide range of studies probing different primate species' alarm call systems. For instance, Arnold and colleagues (2008) presented life-sized models of a stuffed leopard and a crowned eagle to free-ranging putty-nosed monkeys (*Cercopithecus nictitans martini*). The monkeys responded with sequences of calls, which differed in call type composition in relation to predator type. In this case, information about the predator type could not be inferred from the acoustic structure of single calls, but rather from the sequence of the calls. Cäsar and colleagues (2013) studied the alarm calls of black-fronted titi monkeys (*Callicebus nigrifrons*) given in response to models of a caracara (*Caracara plancus*) and an oncilla (*Leopardus tigrinus*). They placed both models on the ground and in the canopy to investigate the effect of predator type and location. The monkeys produced sequences of calls comprising two types of calls, and the composition of the sequences varied with both predator type and location (Cäsar et al., 2013).

Another popular method to simulate a predator's presence is to use an acoustic model – that is, to playback the sounds of the predator in question, such as a leopard growl or an eagle shriek. In their study of putty-nosed monkey alarm calls, Arnold and colleagues directly compared the monkeys' responses to the optic and acoustic models. Reactions to the optic models were somewhat

weaker than to playbacks (Arnold et al., 2008). In contrast, in Saki's monkeys, the animals responded more strongly towards the stuffed models than after playbacks (Adams & Kitchen, 2020).

Presenting a potential danger can also be used to probe what the animals know about each other's knowledge states. Crockford and colleagues (2012) placed a model snake near the traveling path of wild chimpanzees. They recorded whether a subject traveling ahead of the others would utter 'alert hoos' when other party members arrived. Receivers were categorized into three groups, having seen the snake and heard the alarm calls, having just heard the alarm call, or being ignorant. Signalers were more likely to produce alert hoos when receivers had not seen the snake (see also Girard-Buttoz et al., 2020; Schel et al., 2013). The interpretation of the results is not straightforward, as one needs to be able to distinguish whether subjects attend to the receiver's knowledge state or their behavior, and one needs to rule out a possible confound between signaler knowledge and receiver knowledge (see Crockford et al., 2017, for a follow-up study).

Playing back alarm calls

One of the most popular and successful approaches in experimental field research is the playback of alarm calls that had originally been uttered in response to different predators. These studies are often inspired by the motivation to understand the meaning of calls; they are also informative for understanding how animals classify events in their environment. One of the single most influential studies in primate communication investigated the meaning of vervet monkey alarm calls to the three major predator types the monkeys face: leopards, eagles, and snakes (Seyfarth et al., 1980). This study built on Tom Struhsaker's (1967) exquisite description of the vervet monkey vocal repertoire and consisted of playbacks of alarm calls given in response to these three main predator categories. Showing that the monkeys responded adaptively to the different alarm calls (Seyfarth et al., 1980), this study gave rise to a highly productive research program on the meaning of primate vocalizations (Fischer & Price, 2017; Seyfarth & Cheney, 2003; Zuberbühler, 2006).

A related question is how primates respond to the alarm calls of other species. In addition to behavioral observations, playback experiments are once more the method of choice. Not surprisingly, primates, as well as many other animal species (Magrath et al., 2015) attend to other species' alarm calls, as these are also suited to predict the appearance of a predator in the environment (e.g., Fichtel, 2004; Hauser, 1988). The reactions to hetero-specific alarm calls as well as studies of the ontogeny of responses to species-specific alarm calls point to the importance of learning in the comprehension of calls (Fischer & Price 2017).

But how quickly do the animals learn what a sound predicts? Wheeler and colleagues investigated how quickly wild black capuchin monkeys (*Sapajus nigritus*) learned to associate novel arbitrary sounds with predators (Wheeler et al., 2019). Animals living in three different social groups were confronted with a decoy ocelot paired with an arbitrary sound (a rooster's crow, the laugh of the Nelson Muntz character from the TV show 'The Simpsons', and a monotonous bell tone). Each group was exposed to the paired presentation on four occasions. In the subsequent playback test, the monkeys responded significantly more strongly to the sound paired with the predator than control sounds, providing experimental evidence that only a few pairings may be sufficient for associative learning to generate a new link between, in this case, a known scary stimulus (ocelot) and a completely novel one (the new sound) so that the new stimulus came to affect behavior.

Along similar lines, Wegdell and colleagues (2019) studied how quickly West African green monkeys (*Chlorocebus sabaeus*) associated the sound of a drone with the appearance of a drone. Strikingly, even after a single exposure, the monkeys were more vigilant and scanned the sky more frequently when confronted with the playback of the drone sound compared to a control sound. These studies show that rapid learning of what a sound predicts (and choosing the appropriate response) is possible; in stark contrast, primates in operant conditioning tasks using auditory stimuli in the lab often need hundreds, if not thousands, of trials. This discrepancy in performance is still not understood.

A powerful method in field experimentation is the experimental manipulation of contextual information and signal variation. In a series of studies with forest guenons, Zuberbühler and colleagues combined the presentation of a predator sound with the subsequent presentation of either a congruent or an incongruent species-specific alarm call (Zuberbühler et al., 1999). Such a design has become known as the 'prime-probe' method. It allows the researcher to experimentally modify the contextual information (presence of a predator) and the information conveyed in the call. Price and Fischer (2014) adapted this method to test how West African green monkeys integrate congruent and incongruent contextual and acoustic information. The monkeys were first shown a stuffed leopard or a model of a python and then exposed to either a leopard alarm call or a snake alarm call in a crossed design. The monkeys integrated both the contextual and acoustic information in their responses (Price & Fischer, 2014).

In summary, an array of different experimental approaches is available to probe how primates respond to predators and which signals and other tell-tale signs they can use to make predictions about events in their environment. All of the experiments that aim to tap into the animals' natural responses need to be conducted with utmost care. Above all, it is vital to consider the rate of presentation of the

stimuli. If the animals are frequently confronted with what turns out to be series of 'false alarms,' their responses might be diminished. Moreover, the trials need to be set up as inconspicuously as possible – otherwise, the subjects might learn that the experimenter has caused the disturbance (see Fischer et al., 2013).

Investigating primate ranging behavior

How do primates find their way to food sources? Do they plan their routes? And do they possess a 'cognitive map' of their home range? A combination of careful observation and smart field experimentation has shed light on the spatial cognition of primates, including their knowledge of food sources in their area. Noser and Byrne (2010), for instance, studied the ranging behavior of chacma baboons at the Blouberg Nature Reserve in South Africa. By analyzing the animals' routes during the day and factoring in the availability and location of different food sources and of neighboring groups, the authors concluded that the animals plan their routes and consider the value of various food sources when making their choices.

A significant challenge for understanding spatial cognition is to have full knowledge of what is available to the animals and then compare it to their choices. It is much easier to compile this information when the home ranges are small. Cunningham and Janson (2007) studied white-faced sakis (*Pithecia pithecia*), whose individual daily travel distances did not exceed 60 m. The analysis of the animals' travel routes indicated that the animals knew which of the fruit trees were presently productive and which water holes held water. A simple explanation would be that the monkeys regularly monitor the state of their home range. Yet, they may also be able to exploit indirect cues: Menzel (1991) tested the idea that primates may rely on indirect cues when selecting their travel routes in Japanese macaques (*Macaca fuscata*). In the late fall, the animals feast on persimmons. Menzel scattered some store-bought persimmons in the animals' territory in the spring. When the monkeys discovered the fruit, they went to the area of the persimmon trees, indicating that they possessed knowledge of where the fruits would usually be found.

In a study of collective decision-making in group movement in chacma baboons, King and colleagues (2008) placed an artificial clumped food source in the troop's home range. When the group arrived at the food source, the dominant male typically obtained the largest share of the resource, while the other group members often remained 'empty-handed.' In this way, the researchers induced an apparent conflict of interest between the group members. Nevertheless, the group's foraging decisions were consistently made by the dominant male. Subordinate group members followed the leader in the interest of staying together despite considerable costs ('unshared decision-making').

Under more natural foraging conditions, the leadership was more evenly distributed across the group ('shared decision-making'; King et al., 2008)

Technical advances are greatly influencing the study of group movement patterns in the wild. Strandburg-Peshkin and colleagues (2015) fitted 25 olive baboons with GPS collars that took positional fixes every second for 14 consecutive days. In this way, the authors were able to track all collared animals' movement patterns simultaneously. The baboons did not preferentially follow dominant individuals but were more likely to follow when multiple initiators went off in the same direction. While this study set a new standard in movement ecology, it is essential to note that it comes with the cost of having to trap and anesthetize all the animals. In many primate species, ethical concerns, conservation issues, or merely the animals' arboreal lifestyle will prevent the application of this method. Moreover, there is a trade-off between the sampling frequency and the run-time of the collars. A high temporal resolution is needed to get at the time-frame of individual decisions; a longer running-time is necessary to consider seasonal effects or changes in social relationships on group movement patterns.

GPS tracks of researchers following their study species will remain indispensable for studying decision-making and spatial cognition in the wild. Green and colleagues (2020), for instance, conducted nest-to-nest follows on male chimpanzees living in the Nyungwe National Park, Rwanda. While pursuing an individual male, GPS fixes were taken every 5 m, from which the authors were able to reconstruct the males' travel paths. The authors then applied least-cost modeling, which determines the most efficient route assuming full knowledge of the environment. The least-cost model explained the travel paths better than an agent-based model based on local knowledge. With their combination of high-resolution spatial data, a detailed representation of the terrain, and modeling, the authors concluded that the chimpanzees have a spatial memory of their home range landscape.

It should be noted that in recent years, ethical concerns regarding field research have been raised more loudly. For instance, the presentation of predator models may be stressful to the animals or the repeated presentation of alarm calls may lead to habituation of the animals to "false alarms." The use of GPS collars requires trapping and in larger animals the need to anaesthetize the animals. But even beyond such research practices that may be deemed 'invasive' by some, the presence of field researcher may affect the animals' survival: while the frequent presence of researchers may deter poachers, the habituation of the animals to humans makes the animals more vulnerable. Further discussion of the ethical aspects of field research clearly seems warranted.

Summary and conclusions – naturalistic studies

The strength of field research lies in its focus on questions that are immediately relevant for the animals, which puts these studies into a firm evolutionary and ecological framework. With a combination of careful observation and field experimentation, it is possible to illuminate the animals' ecological knowledge, discern their social and communicative strategies, and tap into their social knowledge. Yet, there is also a range of questions that remain elusive – specifically when it comes to the acquisition of knowledge. We may know now that chimpanzees follow a least-cost model when navigating their environment (Green et al., 2020). But why? Do they have a mental representation of their environment that allows them to calculate the most efficient route to the goal at any point in time, or have they simply experienced that specific routes are the least demanding ones, and now the group generally operates on procedural knowledge? Distinguishing habits from goal-directed behavior is central in comparative psychology (de Wit & Dickinson, 2009), but it is challenging to get at these questions in animals that already established their routines. In naturalistic studies, we cannot control the experience the animals already had with the stimulus material. Indeed, the two studies reported above on learning mechanisms (Wegdell et al., 2019; Wheeler et al., 2019) used non-naturalistic stimuli (the presentation of a drone or the signature laughter of Nelson Muntz).

The question of prior experience is particularly pertinent in social learning: how specifically do the animals learn from one another? Do primates mainly pay attention to *which kinds* of food others are handling or *where* they are doing it, or are they also paying attention to *how* they are processing the food? What is the role of individual (trial-and-error) learning? How long does it take a monkey or an ape to figure out a problem? To get a grip on the animals' learning mechanisms, we need to confront them with novel problems. Here, non-naturalistic experimentation can provide crucial insights.

Non-naturalistic experimentation 'in the wild'

Getting the animals engaged

Wouldn't it be great to set up a giant gambling parlor in the wild to explore the cognitive mechanisms wild primates employ experimentally? I have personally witnessed two attempts to provide chacma baboons with experimental apparatuses in the wild: Klaus Zuberbühler explored the possibility of setting up a trap-tube experiment in the wild. The reward was a marula nut, and only one juvenile male could be bothered to play around with the device, while everyone else opted for the marula nuts that were simply scattered on the ground. The other attempt involved a carefully constructed apparatus with three large and colorful buttons. Pressing the buttons started the playbacks of different baboons' grunts, and the aim was to check whether subjects would show any preferences for specific

individuals' grunting. The animals could not care less (see Fischer, 2017, for details). It is tough to engage primates who have to look out for predators, search for food, or keep track of who is hanging out with whom to engage with some problem-solving device when there is no appreciable reward.

Non-naturalistic experiments often involve some form of food reward, to motivate the animals to engage in the task. 'Novel object' tests aimed to assess the subjects' boldness/neophobia are an exception to the rule (e.g., Almeling et al., 2016). In many field sites, food provisioning is not allowed. Even if it were allowed, it might not be desirable because food provisioning may alter the animals' natural ranging and social behavior. Thus, this kind of research takes place only at a few select field sites willing to tolerate the disturbance such experimentation creates. The vast bulk of non-naturalistic experiments have been conducted with animals living in monkey parks, sanctuaries, or breeding grounds like the island of Cayo Santiago. An advantage of working in outdoor enclosures and sanctuaries is that there are often many subjects available. Yet, the living conditions are fundamentally different from the wild: the animals are provisioned with food and do not experience predation, group structures and sizes may differ considerably, and in the case of sanctuaries, one might want to consider the animals' previous traumatic experience. All of these factors have the potential to impact the motivational dispositions of the animals, which in turn needs to be considered when interpreting the data.

Non-naturalistic experiments vary concerning the presence of the experimenter. In some cases, one simply deploys some device. In others, the experimenter is actively presenting the 'problem' to the animals. With the latter approach, the experimenter becomes 'part of the game,' something that one keenly wishes to avoid in naturalistic field experiments. In the following, I will discuss a small number of exemplary studies to provide an idea of the range of approaches used.

Manipulating foodstuffs

Manipulated foodstuffs were used to investigate the role of social learning in foraging decisions in four groups of wild vervet monkeys (van de Waal et al., 2013). The monkeys were provided with two adjacent containers, one filled with soaked corn dyed pink and the other blue. Corn dyed with one of these colors (pink in two groups, blue in two others) was treated with aloe vera leaves, rendering the corn bitter and distasteful. After three monthly training sessions, the monkey only ate the corn of the color not treated with aloe; thus, feeding preferences were firmly established. Months later, the researchers again offered corn of the two colors, but now both were palatable. Infants all adopted their mothers' preferences. More critical was the question of whether males that had transferred between groups with different food preferences would maintain their color preference or switch to the local

'custom'. Most of the males changed to the new group's color, providing evidence that social learning may override individually acquired preferences (van de Waal et al., 2013).

In a recent study, van Leeuwen and colleagues installed a 'juice fountain' in a sanctuary for chimpanzees to investigate prosocial tendencies (van Leeuwen et al., 2021). The fountain could (seemingly) be operated by the chimpanzees from some distance by pushing a button (actually, the experimenter controlled the fountain). Animals who were pushing the button could not access the juice themselves. In the three groups of chimpanzees, button-pushing frequency and duration increased over time, but there was considerable variation between different social groups. This finding was taken as evidence that prosocial behavior can spread in different groups with different dynamics (van Leeuwen et al., 2021).

Puzzle boxes

Puzzle boxes, also known as 'artificial fruits,' had long been employed in captivity to study social learning and the formation of social norms in a large number of primate species (Whiten, 2000). Derivatives of such puzzle boxes have also made it into the wild. For instance, to explore social learning in lemurs, Schnoell and Fichtel (2012) conducted a social diffusion experiment with four groups of wild red-fronted lemurs (*Eulemur rufifrons*). In two of the four groups, the animals were presented with a 'two-option' feeding box, where the animals could either pull or push a door to get access to a food reward. In the initial phase, two groups were presented with boxes in which one opening option was blocked, whereas two groups were presented with unblocked boxes. In the test phase, all four groups were shown unblocked boxes. In the test phase with both opening options available, lemurs that had previously learned that only one technique worked also discovered the other method but generally preferred the original method (Schnoell & Fichtel, 2012). One problem with such kinds of experiments in rather despotic animals is that high-ranking individuals may monopolize the food source. To avoid such monopolization, Schnoell and Fichtel (2012) presented two to three boxes at a time.

To test age-related variation in inhibitory control, cognitive flexibility, and persistence, we presented Barbary macaques (*Macaca sylvanus*) living in the outdoor enclosure La Forêt des Singes with three problem-solving tasks (Rathke & Fischer, 2020). The apparatus for the cognitive flexibility task consisted of a transparent compartment with two sliding doors; the compartment was fixed in a half-open wooden box. During testing, one of the doors was blocked, and a peanut was placed behind the blocked door. We wanted to measure how long it took the monkeys to figure out that they had to open the other door and reach around to obtain the nut in relation to age. We presented the box to 99 monkeys between 2 and 29 years of age. Twenty (mostly older) subjects never approached the box.

Of the 79 subjects that engaged in the task, only 21 tried to use the other door, and of these, only nine opened it and obtained the peanut (Rathke & Fischer, 2020).

Interactive experimentation

An example of interactive experimentation was a study on number representation in rhesus monkeys (Hauser et al., 1996). The paradigm rested on the successive addition of items into a box and then presenting the outcome, which would either conform to the number of items placed into the box or be smaller or larger. This paradigm had been used previously with human infants. Once a suitable subject was located, the experimenter set up a display box 3 to 5 m away from the subject. At the front of the box was a screen that could be slid up and down; at the back was a cloth pouch. The pouch could be used to hide or add items. In two familiarization trials, the screen was closed, and the subject saw how first one and then another eggplant was put into the box. The screen was then opened, and the monkeys were shown the two eggplants. In the subsequent test trial, a third eggplant was taken from the pouch and added to the set. Monkeys looked longer at the box when the expectation of how many items should be in the box did not match how many were seen after screen removal than in the control trials where it matched.

'Picture book' studies

In the last decade, several studies have presented photographs of conspecifics to animals to address the distinction between in-group and out-group (Schell et al., 2011), the preference for bond partners (Almeling et al., 2016), and socio-emotional biases across age (Rosati et al., 2018). Trials may involve the simultaneous presentation of two photos of conspecifics and use looking preference; i.e., whether subjects spend more time looking at one of the stimuli than the other. Alternatively, just one photo is presented in a given trial and the looking time duration is compared across different conditions. The advantage of the choice paradigm lies in the direct assessment of an individual's preference – a drawback, however, is that the experimental set-up is clumsier and potentially disturbing to the animals.

Summary and conclusions – non-naturalistic studies

Non-naturalistic experiments provide a valuable approach to investigating social learning, cognitive performance, and even social information processing. Using more or less elaborate experimental devices, researchers can address a broader array of questions than in naturalistic studies. The ecological validity is often less clear, however. If valuable food rewards are used, one may need to develop strategies to keep high-ranking subjects at bay, and disturbances can be frequent. Moreover,

offering food will clearly impact the animals ranging patterns and activity budgets. Despite these limitations, non-naturalistic studies are an essential component in the study of primate cognition.

Studies in captivity

The major advantage of work in captivity, be it in research centers or zoos, is the control these setting afford. We can manipulate the timing, amount, and type of information made available to a specific individual. We can separate test subjects from the groups or have specific individuals engage in cooperative or competitive tasks. In terms of the apparatuses, the sky, or rather the researcher's ingenuity (and budget), is the limit. A bonus is that most of the animals living in captivity are bored stiff, and thus, cognitive testing can be viewed as an enrichment program for the animals. The use of food or liquid rewards allows us "to push the animals to the limits", as it were, and understand what they can and cannot do. Yet, we may learn little about whether the problems presented matter to them. Simultaneously, many approaches involve extensive training, and it is not always clear how the training and familiarization phases bias the subjects in one way or another during the test trials. A full review of all of the different experimental approaches applied in primate cognition studies in captivity would be clearly beyond the scope of this chapter. I here review only a few methods to give an idea about the variety of things that are possible. I have discussed puzzle boxes, artificial fruits, and picture studies above; these have all been used in lab studies.

Interacting with the experimenter

A relatively simple set-up involves the face-to-face presentation of different types of problems to the animals, where the test subject is separated from the experimenter by a barrier. The primate cognition test battery (Fichtel et al., 2020; Herrmann et al., 2007; Schmitt et al., 2012) heavily relied on such interactive testing. Interactive set-ups have been used in a wide range of other studies, including studies of delay-of-gratification (Beran et al., 2014), representational formats (Evans et al., 2012; Schmitt & Fischer, 2011) or inequity aversion (Brosnan & de Waal, 2003; Massen et al., 2012).

A typical example is the 'transposition task,' where three opaque cups are placed on a sliding table, still pulled back from the barrier. The experimenter puts a food reward in full view of the subject under one of the cups and then shuffles the location of the cups in a predetermined fashion. Then, the table is pushed towards the subject, which indicates its choice by pointing at the desired cup. If the subject points at the correct one, it receives the food reward. One of the great strengths of the interactive design is that it is simple and comparatively cheap. Therefore, such simple tasks are well suited for collaborative work, as in the ManyPrimates project (ManyPrimates et al., 2019).

Two individuals competing/cooperating

Social cognitive testing of primates by an experimenter has been met with some criticism, as the animals are faced with a human instead of a conspecific. Therefore, more and more studies involve two or more subjects engaged in a competitive or cooperative task. Brian Hare and colleagues conducted one of the foundational studies in this context, which was designed to test whether chimpanzees consider what others can and cannot see (Hare et al., 2000). For such experiments, one needs a series of rooms or test cages where doors can be opened and closed. In this particular study, the two test subjects were in their rooms connected by the testing room. Sliding doors separated the three rooms. Two plates with food rewards were placed in the testing room, and the experimenters manipulated the visual access of the dominant animal to the food rewards. Subordinate chimpanzees were more likely to choose the food reward that the dominant could not have seen, indicating that they understood what others see and know (see Kaminski et al., 2008, for a follow-up study).

Studies using different spatial arrangements have investigated whether chimpanzees choose the best cooperator (Melis et al., 2006), whether they trust (Engelmann & Herrmann, 2016) or help each other (Engelmann et al., 2019). We tested whether long-tailed macaques (*Macaca fascicularis*) compared themselves to others. The performance was only affected when the animals were competing for the same resource, but not when they worked side by side (Keupp et al., 2019; Schmitt et al., 2016). In summary, researchers have multiple ways of probing how the animals assess each other and how their assessment affects their social choices. This area is highly active, and further methodological developments are likely just around the corner.

Touch-screens

A powerful method to present primates with different problems is the use of touch-screens (e.g., Inoue & Matsuzawa, 2007). Touch-screens are also widely used in primate neuroscience, as they allow exquisite control over the stimulus material presented. Correct choices are rewarded with food or liquid. It may require extensive training until the animals understand how to operate the touch-screen. One advantage of touch-screen based research is that the influence of the experimenter is minimized. Touch-screen tasks can be used to study basic perceptual processes and learning mechanisms (e.g., Joly et al., 2014). More important, touch-screens allow the presentation of very sophisticated problems that would be difficult to implement in real life. For instance, animals can be trained to wager before or after choosing, to test metacognition (Ferrigno et al., 2017; Morgan et al., 2014).

A remarkable set-up involving touch-screens is the automated learning device (ALDM) established in the primate station in Rousset, France, where a group of Guinea baboons (*Papio papio*) has free access to an array of containers, each equipped with a touch-screen. The animals are tagged

with RFID-chips in their forearms, and when they reach through the holes in a plexiglass screen to operate the touch-screen, the system recognizes the animals' IDs and automatically uploads their task. The animals are free to engage in the tasks and typically work in many but relatively short bouts. Ultimately, the trial number generally is much higher than in set-ups where the animals have to be separated from the rest of the group (Fagot, 2009). Other researchers have also begun to introduce freely accessible touch-screens (Calapai et al., 2017; Paxton Gazes et al., 2013).

Dyadic Interactive Platform

A novel development is the 'dyadic interaction platform' that allows two agents to engage in a joint competitive or cooperative task on a vertical touch-sensitive transparent display set up between the two players. In this way, the animals not only act on the same visual objects, but they also can monitor and respond to each other's actions in real-time. Such a set-up comes closer to naturalistic interactions while maintaining controlled laboratory conditions. 'Transparent games' allow the study of social decision-making while maintaining face-to-face action visibility. Moeller and colleagues (2020) studied how rhesus monkey pairs performed in a transparent version of the 'Bach or Stravinsky' (formerly 'Battle of the Sexes') coordination game, in which the dyad needs to settle on one of two options. The macaque pairs ultimately converged on coordination, but in a relatively simple way: They persistently selected either one of the two coordinated options or one of the two display sides. The dyadic interactive platform opens up new possibilities for testing what the animals are paying attention to, how they plan their actions, adjust them on short notice, and develop coordinated or competitive strategies viz-a-viz a conspecific social partner (Moeller et al., 2020; Voinov et al., 2020).

Summary and conclusions – captivity studies

Studies in captivity offer unprecedented control over the experimental situation, and there has been an avalanche of ever more ingenious experimental designs (Engelmann & Herrmann, 2016; Haux et al., 2021; Keupp et al., 2019). Technological advances, such as the development of avatars (Wilson et al., 2020), facial and body movement capture and recognition as part of the interaction with a touchscreen-task will open up new avenues of research. At the same time, work in captivity (as in the wild) is often hampered by small sample sizes (but see Herrmann et al., 2007). More important is the question to which degree training and familiarization procedures shape the animals' performance in a given study, when rewards are involved in the experiment. Moreover, the animals typically pass from one study to the next, which works both for and against the experimenter: on the one hand, the animals already expect to be confronted with some problem to solve; on the other, there may be carry-

over effects where choices may be affected by experience in previous studies. To which degree such carry-over effects affect performance has rarely been studied to date (Okamoto-Barth et al., 2011).

Concluding remarks

The overview of different research paradigms and traditions has shown that they all have their respective strengths and weaknesses. Field research boasts high ecological and evolutionary validity. Still, it is often difficult (or impossible) to hone in on the cognitive mechanisms. At the same time, studies in captivity enable researchers to develop precisely controlled experiments that allow us to distinguish between different hypotheses. A difference between field-based and captivity research concerns the attention and motivation of the animals – wild animals have other things to attend to do. In a more restricted environment, the animals will be more motivated to engage in a problem. Since performance is dependent on both motivation and ability, we need to be careful when drawing inferences from variation in primates' behavior in different settings (e.g., compare Almeling et al., 2016; Bliss-Moreau & Baxter, 2019).

In the last decades, many of us have seen situations where researchers from one camp or another met each other with disdain. The sometimes outright dismissive stance did not do the field a favor – instead, I believe that we should rather aim to learn from each other. This is particularly true for the topic of social cognition, which transcends field and captive research. A thorough understanding of what is relevant to individual primates in the wild is essential to devise experimental designs that tap into the cognitive processes employed when animals solve problems in a complex social setting. The growing field of social neuroscience has also taken an interest in the question how primates behave in their real lives, and it is here where much can be gained from joining forces across the different approaches. The increasing use of wireless electrophysiology enables researchers to put subjects into social settings and ever more complex planning and decision-making scenarios (Berger et al., 2020), while studying the neural substrate involved in the animals' decision. Field research should thus be conceived as a source for ideas for experimentation in captivity, while research on captive animals can provide field researchers with necessary information regarding the animals' cognitive mechanisms. Perhaps our increasing ability to take our communication online (even from the field, I note with a certain pang of regret) will help to break down the barriers between the different research areas and foster exchange.

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