

1 The Purpose of Primate Cognitive Studies

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Understanding the Origins of Human Cognition

Many contemporary primatologists and comparative cognition researchers will tell a similar story about how they knew where their path would lead them in their lives, often at quite a young age. It often starts with watching a documentary on National Geographic featuring Jane Goodall, George Schaller, or Dian Fossey, or seeing Kanzi the bonobo use symbols, Alex the parrot answering questions in his unique voice, or some species of ape/corvid using a tool in a fascinating way. We guess that most of the authors in this book can vividly describe the first time they watched the films of Jane Goodall interacting with the chimpanzees at Gombe or saw one of these other animals behaving in the intelligent manner they do. For one author (Schwartz), he first read *In the Shadow of Man* (Goodall, 1971) at the age of nine. For the other (Beran), it was reading about the lexigram use of chimpanzees Sherman and Austin (Savage-Rumbaugh, 1986). The human fascination with our fellow primates likely derives from both their obvious similarities to us as well as the huge gulf that divides us from other primates. Of course, once we get to graduate school, we must channel our fascination into suitable scientific questions. Thus, like many of the authors of the chapters in this book, we focus our scientific lens on three major questions – what nonhuman primate cognition (henceforth, primate cognition) tells us about our own human cognition, what comparing different primate species can tell us about the nature of cognition in general, and how cognition can inform our decisions to conserve species and improve the welfare of nonhuman primates. Once we address these laudable scientific goals, perhaps that returns us to our original adolescent fascination with apes and monkeys. As important as these scientific questions are, we also think that research on primate cognition links us to the natural world.

It is safe to say that there is no species that has exploited the cognitive niche more than human beings. How did it happen that our ability to reason, imagine, remember, create, and speak define who we are? Why did evolution take us down this path that allows us to fix engines, knit sweaters, and write scientific papers? Because cognitive processes and behaviors do not fossilize, one of the chief methods for addressing the question of human cognitive

evolution comes from comparative studies with primates. For example, for some time, developmental and cognitive psychologists have discussed the importance of a theory of mind, or our understanding of others' thinking, in the development of human intelligence. Given the mnemonic, attentional, and logical demands of theory of mind, there has been considerable speculation as to how and why such a system evolved. Partially because of these concerns, there is now an extensive literature (see Lewis & Krupenye, this volume) on the extent and underlying mechanisms of theory of mind in primates. Whereas early researchers thought of a theory of mind as a discrete step in which a small child transitions from not understanding to understanding, the comparative literature documents a host of transition states from no theory of mind to understanding lines of sight and who sees what to a full understanding of knowledge that another has been deceived (e.g., Kano et al., 2020; Lewis & Krupenye, this volume). Consider another well-researched and discussed area, namely communication and language. Language is a feature that seemingly is unique in defining humans and distinguishing us from other species. We know of no other species that has a full system of language, as we ourselves do. Many species have complex communication, but none that fulfills the criteria of language (Fitch, 2009). As a consequence, many scholars have puzzled over the potential biological evolution of language. This leads comparative researchers to look at communication systems in monkeys and apes (see Heesen et al., this volume; Heimbauer & Krause, this volume). Can such systems, for example, be considered as evolutionary analogs of human language or are their origins different? Similarly, the quest to instruct apes in human languages arises from the question of how our own language systems work and whether they require specific systems to learn or whether more generalized ones will suffice (Heimbauer et al., 2018). Thus, our understanding of our own cognition and where it comes from is predicated on an understanding of the systems of our primate cousins. The chapters here will elaborate on different aspects of primate cognition, which allows us to better understand our own.

At the same time, we, and many authors in this volume, want to remind the reader (and sometimes, ourselves) that focusing *solely on primate species* comes with its own pitfalls. Templer (this volume) and Vonk and Edge (this volume) remind us that a cross-species perspective on behavior and cognition is best accomplished through a truly comparative perspective that attempts to assess as many species as one can, guided by theoretical reasons more so than just logistical constraints. Of course, some species are easier to test, and primates may often provide the best starting point, or even the most ideal species with which to study some cognitive process, but comparative psychology needs to earn its name through vigilant efforts to be truly comparative. That this volume focuses on primates, and advocates for the need to study those species as crucial to understanding human cognition, does not mean that broader comparative programs of research are not equally relevant and illuminating. In fact, they are. Washburn and Walters (this volume) remind

us of the long history of primate cognition research but also of the need to situate that research in a broader comparative perspective (also see Beach, 1950; Beran et al., 2014; Bitterman, 1960; Dewsbury, 1984; Shettleworth, 2009; Wasserman, 1997).

Studies of primates also serve an important role for conservation and welfare of species. Fieldwork, lab work, zoo research and education, and the push for funding support for sanctuaries and release programs for primates all benefit from, and contribute to, the appreciation and understanding of the general public for primates other than themselves. Conservation of primates in the wild is served by field studies, zoo studies, and research in laboratories that piques the interest of the taxpayer and donor who find themselves confronted with evidence that other species can communicate, cooperate, learn, remember, plan, scheme, reconcile, judge, and choose what they want. The tension between those working in the field, those working in the lab, and those working in zoos is unnecessary and counterproductive to the goal of convincing policy-makers, potential allies, and the general public that all primate species deserve protection of their natural habitat, and that all laboratory or zoo-housed primates deserve protection of basic and fundamental needs not just for their bodies, but also for their minds. Fischer (this volume) and Leavens (this volume) address this tension and present ideas for ways to allow studies of primates in different settings to complement each other and to keep the focus on the fascinating behavior and cognition of primate species in varied settings. This fascination occurs not just among those studying primates, but also for those who learn of the results of cognitive studies. This knowledge also provides members of *Homo sapiens* with a connection to the natural world. Although it is true that, in the ideal world, humans would protect the habitats of non-cute, non-mammal, non-“smart” species, in reality connectedness to nature often is felt best through an anthropomorphic lens. One can protect the scientific effort from such anthropomorphism while leveraging solid empirical results to engender in nonscientists a sense of connectedness because of psychological similarity, and if nothing else, *Homo sapiens* prides itself on how “sapiens” it thinks itself to be (we leave that question to authors of other books). At the same time, it is incumbent on those who study primates (and any nonhuman species) to consider the ethical implications of such studies. This is not always easy, but new technologies and forms of communication offer possibilities to learn maximally about primate cognition while interfering minimally with natural behaviors (see Ross et al., this volume).

Do Nonhuman Primates Do What Human Primates Do and What Do They Do Differently?

Contemporary cognitive psychology and neuroscience tells us that there is good evidence to support the idea of modularity of mind (Barrett &

Kurzban, 2006). That is, our traditional categories of cognition (e.g., learning, language, reasoning) seem to rely on separable neurocognitive systems. Although such statements are subject to debate, much cognitive psychology focuses on issues of whether cognitive processes can be dissociated from others and therefore determined by separable neurocognitive mechanisms. For example, one such area is whether language representation in bilinguals is achieved with two separable representations or whether a common semantic system maps onto two lexical systems (Altarriba & Robinson, 2018). For a second example, in research on long-term memory, decades of research has examined issues such as whether semantic memory (knowledge) and episodic memory (personal events) are separable neurocognitive systems (Addis et al., 2012; Tulving, 2002). As such, a logical question to ask of primate cognition is whether the nature of modularity is similar and whether, in any particular area, the systems are nearly identical across primate species, including humans. For example, there has been work investigating if primates have episodic memory systems similar to humans and whether episodic memory systems are dissociable from other memory systems (see Martin-Ordas, this volume). One of the current author's work (MJB) has examined if counting in primates is analogous to counting in young children (e.g., Beran, 2017). Jones and Roman (this volume) carefully consider this question as well as discuss the other forms of quantitative cognition that are shared across primate species.

This thinking can apply to relatively low-level processes and high-level processes. In primate metacognition research, there are two trajectories. One, the more low-level, investigates information-seeking studies (Call & Carpenter, 2001). These tasks consist of allowing an individual to either see food being deposited in a tube or being blocked from seeing if food is put in the tube. The dependent measure is then if the participant, when given a chance, looks down the tube before attempting to remove the food. Some primates and even some non-primate species will check when they have not actually seen the baiting event more often than when they have (e.g., Beran et al., 2013; Call, 2010). This broad finding of information-seeking suggests that this behavior, metacognitive or otherwise, is a shared mechanism and is likely to be found in other primate species, as of yet untested. However, the higher-order metacognitive processes, studied by asking primates to judge uncertainty or bet on their future performance, may arise from different mechanisms in different species (e.g., Kornell et al., 2007). There has not been adequate comparative work on higher-order metacognition in primates, but if researchers were to show, for example, that rhesus macaques display fluency-based illusions when making metamemory judgments (as has been documented by Ferrigno et al., 2017) but that capuchin monkeys showed no such illusions, one could argue that these higher-order metacognitive judgments arise from different processes in the two species. Templer (this volume) covers these issues in much greater detail, as well as outlining other informative future avenues of research to uncover the depths of primate (and non-primate) metacognition.

The logic of this research program can be extended to comparisons across primate species. For example, much has been made of the similarities and differences between tool use in capuchin monkeys, chimpanzees, and humans (Boesch et al., 2017; Fragaszy et al., 2010) and between metacognitive judgments and control between capuchin monkeys and rhesus monkeys (Beran & Smith, 2011; Smith et al., 2009). Given the gulf of evolutionary time that separates capuchin monkeys from their Old World counterparts, evidence for common mechanisms suggests an old system that predates the break of New World monkeys from other primates. If such is the case, then advanced cognitive systems are likely to have been lost across the evolution of other New World monkeys, while retained in capuchin monkeys. However, evidence suggesting different mechanisms for tool use in capuchin monkeys and Old World primates would imply that tool use evolved separately and may be served by different underlying cognitive mechanisms. In this case, the cognitive mechanisms that allow for tool use in capuchin monkeys may have evolved separately, allowing capuchin monkeys to fill a niche in the neotropics that other primate species could not. Thus, looking comparatively across primate species can tell us both about our own origins and the potential means by which a species occupies a cognitive niche. This research has been very successful in the comparative psychology of tool use (see Sanz et al., this volume). We recommend this approach to other areas of primate cognition.

The Nonhuman Primate Brain as a “Simple” Version of the Human Brain

In many areas of neuroscience, the brains of monkeys, particularly the brains of rhesus macaques, have stood in as models of the human brain. For example, the groundbreaking Nobel Prize–winning work of David Hubel and Torsten Wiesel on the organization of the visual cortex is based on the brains of rhesus macaques (and cats) but generally is considered a suitable model for the organization of our own human visual cortices. Research shows remarkable correspondence to specific regions in the brains of rhesus macaques and in the brains of humans with respect to the organization of visual processing (Hubel & Wiesel, 2005). We speculate that common mechanisms with respect to basic vision between rhesus macaques and humans will also be largely shared across Old World monkeys and apes. However, of interest is what differences exist in the neural systems of vision across primates and whether the commonalities in vision across primate species extend to cognitive systems, such as memory and reasoning (Livingstone & Hubel, 1984) and even basic aspects of perception and misperception of the physical world (see Parrish & Agrillo, this volume). To give an example, owl monkeys (*Aotus trivirgatus*) are nocturnal monkeys who presumably evolved from other day-dwelling New World primates (Jacobs, 1977). Thus, one might anticipate that the neural

mechanisms that control their dark adaptation are different from nocturnal prosimians (e.g., galagos) that emerged much earlier in evolution.

Our thesis here is that, like with cognition, we can expect to find both the similarities across primate brains and the differences between them to be revealing. Until recently, most neuroscience on primates has been through invasive means, such as single-cell recording. But recent advances in neuroimaging (see Hopkins, this volume) and the use of techniques such as eye-tracking to study social cognition (Howard & Lonsdorf, this volume) allow for more direct comparisons using common techniques or intuitive measures of behavior. We suspect that future research will clearly demonstrate that primate brains are not simplified human brains and that even for issues such as visual perception, there will be great differences in addition to commonalities (Parrish & Agrillo, this volume). Understanding the comparative differences between the relation of anatomy and physiology to function across species will be an important area in the field going forward.

Ecological Approaches to Primate Cognition

Traditionally, comparative cognition takes place in the lab – a place where researchers can do actual experiments with maximum control. Thus, for example, a rhesus macaque and a capuchin monkey can be put in the same apparatus with the same stimuli and do the same task. Given that all variables are identical across conditions, any differences in behavior will be attributed to structural differences between the two species. We assert that this tradition has been very successful at giving us important results (e.g., Parrish et al., 2019), and our goal in this section is not to criticize, just to expand on it. As can be seen in the chapters represented here (e.g., Koops & Sanz, this volume; Vonk & Edge, this volume), such lab work is only one path toward understanding comparative cognition. Cognition can and should be studied in naturalistic environments. In particular, in the chapters on cooperation, empathy, communication, and theory of mind (Brooker et al., this volume; Heesen et al., this volume; Mayerhoff et al., this volume), it becomes clear that it is possible to address issues of cognitive processes in field studies. Moreover, it is necessary, as placing primates in their ecological homes allows us to infer the function of their cognitive processes as well as their structure (Clay et al., 2016).

In addition to the importance of balancing lab work with field work, even within studies that are exclusively lab-based (or completely field-based), it is important to consider the natural ecology of any species when considering their cognition (Schwartz, 2019). Ecological considerations as simple as whether an animal can or cannot use its fingers to press icons on a touchscreen can impact the possible outcomes for a study. In more practical terms, animals bring their natural tendencies into our lab, and we ought to be aware of them. In a broader sense, ecological considerations should influence what hypotheses

are made and how species might differ. For example, such consideration of natural ecology has been highly successful in predicting the memory performance of corvid birds. Thus, Balda et al. (1995) found that foraging ecology – that is, what foods are eaten and whether the birds stored food – predicted performance on memory tests. Food-storing birds outperformed those that did not store food on spatial memory tests, but did not on nonspatial memory tests. Similarly, knowing that scrub jays store food that perishes quickly and food that lasts longer led to the hypothesis that scrub jays would show episodic-like memory. Indeed, Clayton and Dickinson (1999) showed a pattern of memory not seen in other birds that demonstrated that they could retrieve what occurred where and when that occurred. We have argued elsewhere how important it is to apply principles of foraging ecology to primate cognition (see Platt et al., 1996, for such an example; Schwartz, 2019). We also think that such principles would also be useful in studying human cognition (see Tooby & Cosmides, 2016, but also see Hampton, 2019).

Some Thoughts for Readers of This Volume

One of the patterns one will see while reading the chapters in this volume as well as throughout primate comparative cognition is an attempt to make generalizations about a given species based on a small sample of animals. That is, many of the conclusions of these chapters are statements like, “these studies show that chimpanzees have knowledge of what other chimpanzees are seeing,” or “red-ruffed lemurs showed rudimentary concepts of numbers.” This is a typical goal in cognitive science – to be able to make generalizations about a species, whether our own or another. This is a worthy goal, but we think it will be increasingly important to consider another approach to psychology, one that focuses on individual differences. Those who live with dogs and cats know that there is much individuality within these species, and similarly, zookeepers, for example, know that individual lemurs, spider monkeys, and orangutans have their own individual personalities that distinguish them from their peers. Thus, we think one future direction in primate cognition is to consider individual differences in nonhuman primates. We do not disagree with the logic of the proof-of-concept approach to comparative psychology (e.g., that if one bonobo can pass the false-belief test, then the species has the capacity). But seldom do we really consider what it means when one of our test animals successfully learns a task but another does not.

This introduces a companion concern. The replication “crisis” in all areas of science has been particularly evident in psychological science. As noted by Farrar et al. (this volume), this crisis will come to comparative psychology and will impact studies of primate cognition. Efforts at replication are essential, but difficult. However, there are approaches that can aid with concerns about how reliable the results of primate cognition studies are. These include

preregistration, collaborative data collection to increase sample sizes (e.g., ManyPrimates et al., this volume; ManyPrimates et al., 2019), and other analytic and modeling techniques that can provide greater confidence in the results that are reported from such studies (e.g., Beran, 2018; Farrar, Altschul, et al., 2020; Farrar, Boeckle, et al., 2020; Stevens, 2017). We hope that this discussion motivates primate research teams around the world to consider these important issues.

Another topic that is important is distinguishing instinctual behavior from consciously cognitive behavior. One of the constant themes in these chapters is the adaptability and cognitive capability of primates. However, in many situations, primates may rely on innate mechanisms or associatively learned behaviors first before cognitive resources are brought to bear. Such is the case in our own species. Humans rely on innate mechanisms for many behaviors. For example, infant exploration of novelty and patellar reflexes, among other behaviors, qualify as such. In nonhuman primates, innate mechanisms may cover more aspects of behavior. For example, whereas in humans, damage to V1 causes devastating blindness, in rhesus macaques, regardless of what may happen to visual consciousness, the monkeys seem to be able to act based on vision in a seemingly normal manner (Humphrey & Weiskrantz, 1967). Similarly, wild green monkeys in Barbados flee up trees in response to recorded leopard sounds, even though there are no leopards in Barbados, and the monkeys have been living on Barbados for 350 years in the absence of those leopards (Burns-Cusato et al., 2013). Thus, it is likely that at least some component of these calls is grounded in an innate response, though in Barbados, leopard alarm calls are made in response to dogs (Burns-Cusato, personal communication, 2019). Even as comparative cognition emerges from the stern conservatism of behaviorism, we still must be aware that in some cases innate responses may be involved in the flexible cognitive mechanisms that we wish to explore.

Returning to our original theme of the fascination many of us have with nonhuman primates, it is our sincere wish that this volume kindles or rekindles your fascination with our biological relatives. This book was largely conceived and written during the COVID-19 pandemic, which, among other things, prevented many of the authors from being able to interact with their primate participants in their labs or visit research sites in countries where primates live in their natural habitat. This break from being able to interact with nonhuman primates was often reported as the most distressing in a time when many of us might have been more concerned with our own health. Thus, our intention with this volume is to indulge people's interest in primates and provide them with an up-to-date compendium on the state of the science in primate comparative cognition. We hope this volume inspires its readers to consider the inherent value of all primate species, and to perhaps engender a strengthened connection to our primate relatives with whom we share our one and only planet.

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