The Evolution of Cognition in Primates, including Humans

David A. Leavens

University of Sussex

Accepted version of a chapter for

B. L. Schwartz & M. J. Beran (Eds), *Primate Cognitive Studies*, to be published by

Cambridge University Press.

*Please do not quote from this version. Citation:

Abstract

Cognition is the use of information to solve problems, and the evolution of cognition is the natural history of the application of problem-solving capacities to adaptive problems. The ecological contexts in which primates apply their cognitive capacities vary substantially, and therefore the specific problems pertaining to fitness—finding mates, finding food, predator avoidance, and so forth—elicit systematic patterns of comportment through these different environments. A central debate in comparative cognition concerns the degree to which cognitive abilities are shaped by natural selection: this is the question of whether any given problem-solving skill reflects the application of domain-general or domain-specific cognitive capacities. The debate over whether the demands of foraging or the complexity of the social environment exerts the greater force on brain evolution and behavior exemplifies that the kinds of questions that can be asked about cognitive evolution significantly depend on one’s prior commitment to the domain-specificity of adaptive behaviour. It remains a relatively open question whether there are cognitive specializations for navigating the physical world that are qualitatively distinct from specializations for navigating the social world. There is a panoply of investigative methods for eliciting problem-solving behavior in captive populations of primates, but there is also an emerging tension between proponents of ecological and internal validity, respectively. Here, I will argue that artificial, captive environments are, nevertheless, ecologically comprised and that the study of captive animals follows a long tradition of perturbation studies in ethology. I will finish with a number of case studies of primate cognition from both wild and captive environments.

Keywords: Primate cognition, experimental validity, embodied cognition, perturbation studies, physical cognition, social cognition, telementation.
Introduction

Cognition, in its most general formulation, is the use of information to solve problems. It includes, but is not limited to, learning processes—the development of context-appropriate responses to environmental circumstances. Entities that do not face problems (inanimate entities) are, typically, excluded from the category of cognizant beings, but otherwise there is a large range of systems that might be reasonably held to display cognition, and definitions of cognition in the contemporary literature reflect that variability. At the most exclusive end of the range of definitions, cognition is held to be a property of organisms with brains (most animals), whereas the most inclusive definitions extend to the biosphere, itself, and include a dizzying array of subsystems, including ecosystems, organism-environment contingencies, sub-organismal processes (such as immune system functioning, plant spacing, etc.). There is a restricted perspective from which cognition is a property of some neural systems bounded by a transductive envelope (i.e., where senses convert exosomatic energy and force to electrochemical signals), and this limits cognition to brain-bearing organisms (see Figure 1A). There is a wider perspective from which mentality is constructed not only of neural firing patterns in neural networks, but extends above this level of analysis to include organism-environment dependencies (e.g., a reasoned response to a particular task might involve not only the outcome of a neuronally based process, but also the interplay between elements outside an agent's body, and even including the prior experiences that foster response biases in the particular moment, both neural and behavioral; see Figure 1B). Thus, depending on one's a priori theoretical commitments, cognition might be something that happens in brains or it might be something that happens in complex systems that may or may not include organisms with brains, and there are a number of theoretical perspectives in between (see Shettleworth, 1998, Ch. 1, for a review of different approaches to cognition, and see Johnson, 2001, and Barrett & Henzi, 2005, for discussions of distributed cognition).
In relation to the evolution of cognition, the contemporary literature is generally focused on how organisms’ neural systems support adaptive changes across significant ecological and adaptive transitions. For example, both plants and animals have colonized terrestrial environments from oceanic origins, yet only the neural adaptations of animals to this new habitat are considered to be “cognitive adaptations” by many—that is, cognitive evolution is construed as an adaptive response in fitness-related problem-solving capabilities. Consider, for example, different honeybee communication systems (Figure 2): according to l’Anson-Price and Grüter (2015), there is an evolutionary progression in the complexity of honeybee dances from relatively simple waggle dances performed without reference to the gravitational field and associated with open nesting patterns (Apis florea) to complex, multimodal waggle dances that incorporate the gravitational field as a bearing marker (A. mellifera and others). One hypothesis to account for the evolution of the more complex waggle dances is that it increases the probability of finding richer food sources (l’Anson-Price & Grüter, 2015). Thus, the fitness-related problems faced by animals exert a shaping influence on their perceptions and use of environmental stimuli, including communicative cues from conspecifics.

Primates originated possibly as early as about 40-80 million years before the dinosaurs were driven to extinction at the Cretaceous-Tertiary boundary, about 65 million years ago (e.g., Heads, 2010), although most estimates are more recent than this (e.g., Fleagle, 2013). On balance, Cretaceous origins for the Primate order are likely, but it is hard to pin it down any more precisely than this, on present evidence. With the passing of the dinosaurs, other vertebrate species, including mammals, underwent an adaptive radiation, a relatively short-term explosion in diversity, as mammals began to exploit ecological niches formerly occupied by reptiles. The primate lineage grew in both diversity and range, so that primates are now found in tropical and sub-tropical regions around the world, and a few
species have extended into temperate regions. Humans, of course, have occupied and learned to survive in a large range of ecological contexts, through the use of technology. Primates today are a diverse branch of the mammalian order, displaying a remarkable range of foraging adaptations, anti-predator tactics, and social structures.

Animals (Metazoa) range in size about six orders of magnitude, from about 10 μM (parasitic cnidarians: Myxozoa) to nearly 30 M (blue whale: *Balaenoptera musculus*). The smallest Primate is the Pygmy mouse lemur (*Microcebus berthae*), in Madagascar, with a body plus tail length of about 22 cm, whereas the largest primate is the Eastern Lowland gorilla (*Gorilla beringei graueri*), which stands up to 1.85 M—primates, thus, vary in size about one order of magnitude. Physical features that distinguish nonhuman primates from other mammalian species include: five fingers, including opposable thumbs, the presence of nails at the ends of their digits (as opposed to claws), forward-facing eyes, and relatively large brains in relation to their body masses, with large visual cortices.

Primates display diverse locomotor patterns, ranging from quadrupedalism (walking on four limbs), to knucklewalking (a specialised locomotor pattern in the African great apes: chimpanzees, *Pan troglodytes* sspp., bonobos, *Pan paniscus*, and gorillas, *Gorilla* spp.), vertical clinging and leaping (some Malagasy lemurs and indri, as well as tarsiers), arboreal brachiation (swinging from branch to branch, as displayed by gibbons and siamangs, *Hylobatidae*), semi-brachiation (as in the New World spider monkeys and woolly spider monkeys, *Brachyteles* sspp.), and a number of species-unique locomotor specialisms, such as the human bipedalism (*Homo sapiens*) and the quadrumanualism (four-handed locomotion) that characterises orangutan movement through the forest canopy (*Pongo* sspp.).

Nonhuman primates occupy diverse habitats in both the New and the Old Worlds, including island nations, such as Japan and Madagascar; however, there are no native primates in Australia. Primates tend to occupy tropical rainforests, but some species have
extended their ranges to habitats as diverse as high sub-tropical or temperate mountain regions, deserts and savannas, and even urban environments. Nonhuman primates range from fully diurnal to fully nocturnal species, with many strepsirrhines (includes Malagasy lemurs, African galagos, and Asian lorises) displaying a crepuscular (active around sunset and sunrise) or even cathemeral (active throughout various parts of the 24-hour daily cycle) lifestyle (Joffe et al., 2014; Tattersall, 2006). The dietary regimes of nonhuman primates are very diverse, with species specialising, variously, on leaf-eating (folivory), plant-eating (herbivore), fruit-eating (frugivory), gum-eating (gummivory), insect-eating (insectivory), and a number of omnivorous species, including those whose diet includes a variety of other vertebrates.

Similarly, the social structures of nonhuman primates are difficult to characterize in a few words, with striking differences across groups even within the same species (Fleagle, 2013). Some primates are primarily solitary, coming together only to breed, although they might maintain contact through communication with conspecifics in the vicinity. At the other extreme, some nonhuman primates live in large groups, and these can take a number of forms, from large aggregates of single-male harems to fission-fusion groups, in which sub-groups break off and forage and live separately for a time, then re-join the main group. Some nonhuman groups form monogamous dyads or polyamorous triads. In other species, the primary social unit comprises single adult males with multiple females. Social structure seems to be evolutionarily malleable, at least at the generic level: there are striking differences in dominance hierarchies, for example, between even closely related primates (contrast the alpha-male-dominated chimpanzees with the female-dominated, matriarchial bonobos; e.g., Boesch & Boesch-Acherman, 2000; Furuichi, 1997). Similarly, langurs (Presbytis spp.) display significant variation in their responses to human intruders (e.g., Nijman & Nekaris, 2012).
Theoretical Perspectives on Cognitive Adaptations

For much of the 20th Century, in accordance with principles of behaviorism, behavior was viewed as the result of domain-general learning mechanisms—from ants to aardvarks and Americans, organisms were viewed as the loci of associative processes, integrating environmental events and behavioral responses. Through classical conditioning, organisms learned environmental indices of reinforcement, and through operant conditioning, patterns of response were maintained in animals’ repertoires. Under the theoretical strictures of that time, any organism could substitute for any other in the study of animal behavior in the laboratory, and the field of comparative psychology became fixated on a few, easily managed captive species (Beach, 1950). Beach (1950) caricaturised the field with a figure depicting a Norway rat (*Rattus norvegicus*) leading a crowd of comparative psychologists to their doom (see his Figure 3, p. 118). By the 1960s, however, it had become clear that animals brought innate behavioral tendencies to the laboratory, that behavior was not infinitely malleable.

For one oft-cited example, Breland and Breland (1961) reported that they could not extinguish species-typical handling behaviors in animals they were training for their advertising business. Raccoons (*Procyon lotor*) would stop during routines and “wash” coins they were meant to transport, so they switched to pigs (*Sus scrofa domesticus*) and they would repeatedly stop and root the coins. This led the Brelands to conclude that animals were subject to prepotent instinctive behaviors, what they termed “instinctive drift.” Similarly, Bolles (1970), who was studying differences in the ease of acquisition of avoidance responses, noted that:

> survival is too urgent, the opportunity to learn is too limited, and the parameters of the situation make the necessary learning impossible. The animal which
survives is one which comes into its environment with defensive reactions already a prominent part of its repertoire (Bolles, 1970, p. 33).

These findings demonstrate that no complete account of animal behavior can fail to invoke their evolutionary histories, including the successions of ecological contexts in which they and their ancestors have lived, and they laid the groundwork for a psychology of animal behavior that has been increasingly integrated with biological perspectives on animal behavior.

In parallel with the discipline of comparative psychology, and largely associated with European scientists, the field of ethology was exploring the very kinds of behavioral adaptations that were challenging behaviorists in the United States. The Nobel laureate, Konrad Lorenz (1935), and many others, for example, demonstrated that many nidifugous (born feathered and leaving the nest early) species of bird will follow, essentially, the first conspicuous animate entity they can see, but only during a sensitive period of, typically, a few hours after hatching (reviewed by P. Bateson, 1966). The primary function of imprinting seems to be the formation of stable preferences for representatives of one’s own species, a preference that supports both early parenting and later sexual preferences.

Another prominent early area of ethological research was the deciphering of the honeybee (Apis spp.) waggle dance by the Nobel laureate, Karl von Frisch. In the waggle dance, bees rapidly walk in two adjacent ellipses—where the ellipses join, they adopt a waggling locomotor pattern (hence the name—see Figure 2). Distance to a nectar source is encoded by the amount of time the bee takes to accomplish the waggle portion of the dance, and the bearing to the nectar source is encoded by the angle between the axis defined by the coterminous boundaries of the ellipses and the vertical axis of the honeycomb, such that a vertically oriented dance indicates directly towards the sun (l’Anson Price & Grüter, 2015).
Food quality is also signaled by the rate of waggling. This sophisticated signaling system is an example of a complex signaling adaptation in a small-brained animal. These findings have fostered an ethological perspective on animal behavior that is, at times, biased towards interpretation of behavior in adaptationist terms.

Tinbergen (1959, 1963)—yet a third Nobel laureate—concisely highlighted the susceptibilities of comparative psychology and ethology to biased interpretation of animal behavior. Of comparative psychologists, he wrote of their tendency “to concentrate on a few phenomena observed in a handful of species which were kept in impoverished environments” (Tinbergen, 1963, p. 411; compare Beach, 1950). To fellow ethologists, he cautioned,

[t]here is no reason to suppose that behaviour characters have been subject to selection to a greater extent than any other character; the ethologist’s high regard for the influence of selection is due to his [or her] characteristics rather than to those of the material” (Tinbergen, 1959, p. 329).

Tinbergen (1963) was a towering figure in the study of animal behavior, and virtually all scientists can communicate their research questions and findings in terms of his “Four Questions” (P. Bateson & Laland, 2013):

- Mechanism: what biological or environmental factors cause the behavior?
- Development: where does the behavior fit in developmental sequences?
- Function: how does the behavior serve lifetime reproductive success?
- Evolution: what are the selective regimes that fostered the evolution of a behavior?

The first two of these questions are concerned with proximate causes (biological,
environmental, and developmental foundations) and the second two questions are concerned with ultimate causes (effects of evolutionary selective pressures on fitness).

Comparative psychologists, then, have historically been concerned with domain-general patterns of learning, in a few species, under well-controlled environmental conditions, to foster high internal validity. The early assumption of domain generality of learning used to bias this area of research towards environmental explanations and developmental progression was interpreted as a pattern of coherent consequences of learning experiences. In contrast, ethologists have tended more to focus on species-specific behavioral adaptations, usually in free-ranging animals living in their natural habitats in conditions of high ecological (external) validity. The interpretive bias was towards ultimate causes, such as function and evolutionary history, and even when researching mechanisms, explanations tended towards biologically inherited causes.

*Internal validity* speaks to the confidence with which a researcher can attribute a change in behavior to the experimental manipulation, whereas ecological validity is maximised when studying animals living and reproducing in the environments to which they are best adapted. With respect to internal validity, the aim of the experimental method is to attempt to hold everything constant except the factor being manipulated. If everything else is held constant and the dependent variable—here, behavior—changes in response to the experimental manipulation, then this is an example of high internal validity—the researchers can conclude with a high degree of confidence that the manipulation changed the behavior. In some physical and chemical systems, it is possible to achieve something close to this ideal, but when dealing with whole organisms—especially long-lived animals like primates—it is important to bear in mind that a perfectly controlled experiment is impracticable (Leavens & Bard, 2021); thus, experiments achieve different levels of strength, some designs are stronger than others, but no single experiment is ever going to be the last word on a research topic. In
between-subjects experimental designs, for example, the individual animals comprising each
group have been sampled from a population, and it is impossible to know how representative
of that population each group is. Because most experimental work with captive primates
involves opportunistic sampling of groups that have entered captive environments via
uncontrolled sampling methods, and because most captive primates have long and poorly
documented pre-experimental life experiences, then random sampling error of the subjects,
themselves, exists as an enduring lurking variable in captive primate studies (see, e.g.,
Leavens & Bard, 2021). Other pervasive lurking variables in studies of captive primate
cognition include the environmental effects of captive environments, themselves, on the
learning and development of primates. Captive primates, which are provisioned daily and
have little control over the compositions of their social groups, are not challenged to acquire
the kinds of foraging and social skills necessary for survival in the wild (e.g., Boesch, 2012a,
2021), and it is well-demonstrated that institutional rearing impedes cognitive development in
primates (e.g., Bard et al., 2014, and references cited therein).

As we will see, there are many extant claims that human cognition is unique among
primates (e.g., Tomasello & Call, 1997). Many of the more prominent claims of human
cognitive exceptionalism are based on direct comparisons between nonhuman primates and
humans, and it is therefore worth emphasising just how poorly controlled most of these
species comparisons are: representatives of these human vs. nonhuman primate comparisons
are routinely tested in different testing environments, with radically different levels of task-
relevant pre-experimental preparation, incommensurate sampling protocols, using markedly
different testing procedures administered to participants at different life history stages
(Leavens et al., 2019). As depicted in Figure 3, the contemporary industry standard of
multiply confounded experimental factors in human-nonhuman primate comparisons results
in a large array of possible interpretations, only one of which is that there might be a species
difference, attributable to the respective adaptive histories of the groups under comparison. Thus, over the last few decades, there has been a large number of claims for human cognitive adaptations based on overly optimistic interpretations of ape-human comparisons that are inherently uninterpretable—contrary to the ideal of the experimental method, direct ape-human comparisons are nowhere near capable of isolating the effects of evolutionary history from the effects of individual learning.

_Ecological validity_ is the degree to which results in artificial circumstances or captive animals can be generalised to animals living outside those artificial environments. What more ecologically valid practice, then, but to study wild animals living in their natural habitats, the environments to which, presumably, they are adapted by natural selection over many generations? From a fitness perspective, animals in the wild must successfully evade predators, find nourishment, and mate, and the daily complexities of survival pose an interminable chain of challenges over the lifetime of each individual. Numerous ethologists have pointed out that captive living conditions do not provide anything like the complexity of wild environments, and they argue that, therefore, only in the wild can the cognitive potential of animals be realized to its fullest capacity (e.g., Boesch, 2012a, 2021).

There is no question that captive environments are less complex than wild environments, but there are two caveats to this generalization: first, captive environments can pose problems not found in the wild, and therefore reveal behavioral capacities that would otherwise not be observed in any given species (e.g., Leavens et al., 2010; O’Malley & McGrew, 2000) and second, in many parts of the world primates live in longstanding sympathy with artificial human environments, for example, urban environments (e.g., Sinha & Vijayakrishnan, 2017). Thus, wild habitats will, in general, elicit only a partial subset of the full behavioral repertoires of primates. We can think of a space of latent adaptations that are triggered by certain environmental factors which might not exist in the environments of
free-ranging primates.

An example of environmental effects on communicative repertoires is discussed by Leavens et al. (2010, and Leavens, 2021): Wild chimpanzees only very rarely display manual pointing gestures (Hobaiter et al., 2014), institutionalized chimpanzees often point (e.g., Leavens & Hopkins, 1998), and pointing is ubiquitous among language-trained and other enculturated chimpanzees (e.g., Krause & Fouts, 1997; Savage-Rumbaugh, 1986). Among humans, pointing is a device for co-orienting two or more individuals to a particular locus and is considered a significant development milestone in human cognitive development. The near-absence of pointing among wild chimpanzees has been taken as evidence for a human-unique cognitive adaption for referential communication that is manifested in pointing of pre-verbal children (e.g., Povinelli et al., 2003; Tomasello, 2006). In contrast, Leavens (2021) argued that the relative paucity of pointing in wild chimpanzees, considered in relation to the ubiquity of pointing in enculturated chimpanzees, demonstrates that pointing is a species-typical gesture among chimpanzees, but it is not elicited very frequently in the daily lives of chimpanzees living in their natural habitats. The essential point, here, is that captivity does elicit behavioral competencies not seen, or seldomly seen in wild populations.

Internal validity and ecological validity exist in a state of tension: the more internal validity a researcher has, the less external or ecological validity they can claim, and the converse is also true, at least when dealing with most primate species. For small, short-lived organisms with small ranges, it is often possible to emulate wild environments in laboratory circumstances or to gain outstanding access to and control over natural habitats (e.g., honeybees). Among nonhuman primates, this kind of coalescence between internal validity and ecological validity is impracticable for most species, with the possible exception of the gummivorous callitrichids, whose home ranges in the wild can be as small as a single tree (Digby et al., 2010). Thus, studies of captive primates can reveal capacities not apparent
from observation of their comportment in wild habitats.

There are many capacities that have been elicited in nonhuman primates in captive environments, including laboratories, that would be virtually impossible to observe in wild populations. The capacities of great apes to produce and comprehend linguistic symbols is a salient example of a cognitive capacity not yet witnessed among wild apes (e.g., Gardner & Gardner, 1969; Savage-Rumbaugh, 1986). Great apes have been demonstrated to comprehend and correctly use hundreds of symbols, to parse spoken English, and even to use symbols between themselves to effectively communicate (e.g., Fouts et al., 1989; Savage-Rumbaugh et al., 1993). Considered in relation to what we knew about the linguistic capabilities of nonhuman primates by mid-20th Century, these are astonishing demonstrations. There are many critics of these ape language studies, based on allegations of overly rich interpretations of the animals’ symbolic output; in truth, while some of these allegations of overly rich interpretation are plausible in some cases, much of the early ape language comprehension studies were conducted under double-blind conditions that far exceed the rigor of much more recent work in ape cognition (Krause & Beran, 2020). In addition, other criticisms of this body of work are based on some, perhaps unwarranted, assumptions that contemporary theorists make about language acquisition in humans—specifically, that almost every meaningful aspect of language acquisition is based on species-unique human biological and cognitive adaptations, and that nothing much about human language acquisition can be grounded in more domain-general associative processes. As Hixson (1998) put it:

because most language scholars believe that language is due to much more than a conditioning history, critics of the ape language research will readily point out whether such conditioning has occurred, and, therefore, claim the research has no
importance to human language (p. 37).

The capacities of nonhuman primates to produce and comprehend linguistic symbols has only been demonstrated in captive rearing circumstances. A growing number of researchers, including some former ape language researchers, now believe it is unethical to cross-foster great apes with humans; this is because cross-fostered apes live highly idiosyncratic lives—to return them to institutional settings is cruel, and they usually cannot be socialized to join other captive apes. Therefore, given the brevity of research grants, cross-fostered apes are often subjected to deeply tragic changes in their social fabrics and living circumstances, as research grants expire (e.g., Fouts & Mills, 1997). Nevertheless, one scientifically invaluable product of the ape language studies is the demonstration that nonhuman primates can, to a degree, express themselves with symbols and understand symbolic communication (Krause & Beran, 2020; Lyn, 2017).

“Prime Movers” in Primate Cognitive Evolution

In general, two classes of ecological factors are considered to be candidates for the evolutionary shaping of cognitive capacities in primates (e.g., Dunbar & Shultz, 2017): (a) social factors and (b) foraging factors. Interestingly, predation pressure is often considered in non-primate animals when considering the evolution of cognition (e.g., Brown & Braithwaite, 2005), but the literature on primate cognitive adaptations tends to consider anti-predator tactics only secondarily to its manifestation in, for example, large group sizes as anti-predator adaptations (Dunbar & Shultz, 2017). Different theorists emphasize aspects of one or the other class of “prime-mover” for the evolution of cognition (see Figure 4). But several features of primate lifeways have both feeding and social implications. For example, alloparenting, as displayed by several species of marmosets and tamarins (Callitrichidae), is
manifested by males carrying offspring (a social behavior) to permit the mother to forage (a feeding behavior; Digby et al., 2010). Similarly, the carcass-sharing of chimpanzees after a successful hunt has both social and feeding aspects (e.g., Boesch, 2012b; Goodall, 1986; Teleki, 1973).

Jolly (1966) was among the first to posit a relationship between social complexity and cognitive evolution; she argued that the high social intelligence of lemurs, coupled with their relatively poor performance in object manipulation tasks, indicated that social cognition was the evolutionary primitive, from which manipulative intelligence derives. Many others have since noted the complexities in social relationships, particularly in primates who live in large groups (e.g., Byrne & Whiten, 1988). Taking brain size measures (particularly relative neocortical volume) as a proxy of cognitive complexity, Dunbar has frequently noted the strong relationship between social group size and various measures of brain size in primates (e.g., Dunbar & Shultz, 2017). McComb and Semple (2005) reported that vocal repertoire size is positively correlated with social group size in primates. Thus, the fitness consequences of social aptitude are frequently heralded as a lifelong adaptive pressure on primates. Others have emphasized relationships between brain size and foraging patterns, finding, for example, that folivores (leaf-eaters), who feed on concentrated masses, generally have smaller brains than frugivores (fruit-eaters), who must navigate complex spatiotemporal distributions to find ripe fruit (e.g., DeCasien et al., 2017).

This dichotomous parsing of physical and social cognition reflects a theoretical commitment to the idea that there are domain-specific adaptations for learning in relation to animate and inanimate entities. A prominent textbook on primate cognition, for example, is organised separately around physical and social cognition (Tomasello & Call, 1997). As Shettleworth (1998) pointed out, in practice it is often difficult to sort out whether social animals are better domain-general learners, overall, or simply encounter social problems
more frequently than more solitary animals, or display domain-specific competencies as a result of selective pressures on learning processes (e.g., pp. 433ff). Byrne and Bates (2010) proposed that complex foraging contexts provide a social scaffold for parsing of sequences of manipulation of inanimate entities by animate social partners, and they speculated that this discriminative capacity—the ability to parse others’ behavioral sequences at crucial junctures in a program of food processing—might generalize to social problems, rendering a rigid physical/social cognition distinction “misleading” (p. 815). Orangutans, for example, are solitary foragers in the wild and, with a few exceptions (e.g., Fox et al., 1999) display little tool use in their natural habitats, but when brought into captivity or rehabilitation centers, they readily display a suite of imitative competencies (e.g., Russon & Andrews, 2011; Russon & Galdikas, 1993, 1995; Wich et al., 2009) and exceptional tool-using capabilities (e.g., Laumer et al., 2019). This uncertainty about the existence of specialized social learning adaptations is brought into particularly sharp relief when considering humans in comparison with other primate species. Humans are extraordinarily unusual animals by virtue of their reliance on technology and knowledge-based exploitative tactics across an immense range of environments (e.g., Heyes, 2018; Tomasello, 2019), yet it is this complex, distinctive, culture-based range of human rearing environments that renders comparisons between humans and other animals—which latter are raised in radically different environments, whether captive or wild—essentially uninformative on the question of human cognitive adaptations (see critiques by Boesch, 2007, 2012; Leavens, 2018; Leavens et al., 2019). That human children display an unusual propensity for vocal mimicry and are, in this characteristic, highly unusual primates, seems to be relatively uncontroversial, but vocal mimicry is hardly a uniquely human capacity (e.g., Pepperberg, 1999; Wich et al., 2009). At present, it remains an open question whether, among primates, social learning involves processes that are different from learning about physical properties or whether social
activities afford domain-specific suites of affordances that are exploited by domain-general learning processes.

In general, whether theorists emphasize social or foraging factors in cognitive evolution--with their privileging of proxy measures for cognition such as brain size, group size, or food dispersion--these “prime mover” approaches to the evolution of cognition stem from a priori commitments to neurocentric models of cognition, the idea that cognition happens in individual brains. Arguing from a more embodied and distributed theoretical perspective on cognition, Barrett and her colleagues (e.g., Barrett et al., 2007) have criticised the social complexity approach to cognitive evolution, essentially arguing that because humans have a propensity for creating narratives about abstract social relationships in accounting for our own social behavior, that we fall prey to anthropomorphizing the social behavior of our close kin. In other words, that we find evidence for relationship maintenance in nonhuman primates—in grooming patterns, in reconciliation behavior, and so forth—and that we describe these patterns in terms of familiar terms such as “coalitions” does not establish parity in psychological processes between animals and humans. They suggested “that apparent cognitive complexity may emerge from the interaction of brain, body and world, and is not merely due to the level of internal complexity the animal itself possesses” (Barrett et al., 2007, p. 568). Thus, one criticism of “prime mover” accounts is that the core assumption that complexity in social engagements or in foraging behavior is, in some way, entirely constituted by the putative cognitive processes occurring in the brains of the organisms under scrutiny, which is—at least under current technological capabilities—not warranted by the nature of the evidence.

Cognitive Capabilities in Primates Previously Considered to be Uniquely Human
The last century has seen a boatload of discoveries into the heretofore unanticipated
capabilities of nonhuman primates. A representative list of cognitive abilities previously held
to be uniquely human appears in Table 1. These discoveries support Darwin’s (1871) claim
that “the difference in mind between man [i.e., humankind] and the higher animals, great as it
is, certainly is one of degree and not of kind” (p. 85). Here, I will turn to a consideration of
some of these competencies. There are additional extant and emerging areas of inquiry that
warrant discussion (e.g., mirror self-recognition, neonatal imitation, discrimination learning,
spatial memory, etc.), but space limitations prohibit an exhaustive review.

Insight Learning

    W. Köhler (1925) reported a series of experiments with a group of captive
chimpanzees. A banana was tied to a rope and lifted out of reach. Presented with wooden
crates and two sticks that were each too short to reach the banana, Sultan and Chica worked
out putting the two poles together and stacking the crates to get high enough to retrieve the
banana. Köhler interpreted these acts as examples of insight learning. At about the same
time that Köhler was working with chimpanzees and other animals in the Canary Islands,
Yerkes (1916) reported that an orangutan displayed a discontinuity in its learning curve. In
that study, two monkeys and an orangutan were challenged to find treats in one of a number
of boxes. To succeed, the animals had to work out an arbitrary pattern of baiting. The two
monkeys displayed slow, monotonic increases in their performance, but the orangutan
persisted at chance levels for a large number of trials and then, essentially overnight, attained
a protracted and near-perfect performance level. This shape in the performance curve—a
rapid and large-magnitude increase in performance—constituted evidence for insight
learning, as opposed to trial-and-error learning, an operationalization of an “Aha!” moment.

Tool Use
Although tool use by great apes in captivity had been well-demonstrated, it was not until the middle of the 20th Century that reports of tool use in the wild by chimpanzees began to appear in the scientific literature. Beatty (1951) was the first to report the use of stone hammers and anvils in Liberia. Goodall (1968) reported the use of thin probes for termite “fishing” from termite mounds and for retrieval of ants by chimpanzees in Tanzania. In Senegal, the manufacture and use of spears to kill and retrieve bushbabies has been reported by Pruetz and Bertolani (2007). The use of rock hammers has also been reported in New World capuchin monkeys (*Cebus apella libidinosus*, e.g., de A. Moura & Lee, 2004; Fragaszy et al., 2004). Because there are many observations of primates gathering and preparing materials in advance of their use, transporting them to the sites of their use, this constitutes evidence of planning.

**Use of Symbols**

Gardner and Gardner (1969) reported the correct use of modified American Sign Language signs by a chimpanzee named Washoe, tested under double-blind conditions. Later, Rumbaugh (1977) reported the use of symbols from an artificially constructed language (“Yerkish”) by a chimpanzee named Lana. It is now well-demonstrated that great apes can be trained to recognize and use arbitrary symbols to communicate both with their trainers and with each other (e.g., Savage-Rumbaugh et al., 1978). The symbolic repertoires of these apes are modest, in comparison with humans—to date, repertoires of several hundred symbols have been reported, compared with the lexicons of humans in the tens of thousands. Still, that apes can use and comprehend symbols is indisputable, and this word-learning capacity entails that great apes are capable of joint attention (the acquisition of a symbol with shared meaning requires that symbol users can coordinate their attention with others about specific entities; e.g., Krause & Beran, 2020).
Theory of Mind

Theory of mind is an alleged capacity to represent another’s mental contents. In practice, it is evidenced in humans by responses to verbal prompts, and appears in Western populations at about four-and-a-half years of age (e.g., François & Rossetti, 2020). There is a body of literature that claims false-belief understanding in younger children, primarily based on their looking behavior in certain experimental situations, typically involving violations of expectations, but as Barone and Gomila (2020) noted, these “indirect false belief” experiments do not necessarily entail that young children represent others’ false beliefs, and their remarks also pertain to studies of nonhuman primates’ false-belief understanding that rely on the “anticipatory looking” of the animals (e.g., Krupenye et al., 2016). However, the first alleged scientific demonstration of theory of mind by a chimpanzee was made by Premack and Woodruff (1978a,b): in their study, Sarah, a chimpanzee, demonstrated the ability to select a photograph corresponding to the correct solution to a series of videotaped problem vignettes involving human actors attempting to complete some task (e.g., selecting a photograph of a key after seeing someone attempting to escape a room, selecting a photograph of an electrical cable plugged into a wall socket after seeing something attempting to use a phonograph, etc.). Premack and Woodruff argued that Sarah must have been able to represent the desires of the actors in these vignettes, although Premack later rejected this interpretation, arguing that chimpanzees and monkeys “attribute only two mental states, goal-seeking and perception” (2007, p. 13865). Later, Call and Tomasello (1999) presented a bait-and-switch paradigm to great apes and human children, finding that human children, but not great apes discriminated ignorance in an interlocuter, although that conclusion is hampered by significant procedural differences in how the humans and the apes were treated (e.g., Thomas et al., 2008). In a remarkable field experiment, Crockford and her
colleagues (2012, 2017) found that chimpanzees in Uganda preferentially informed other chimpanzees that were ignorant of the presence of a snake model hidden in the underbrush. At a minimum, this study shows that chimpanzees can discriminate between others’ differential perceptual access to potential dangers in their signalling behavior. On balance, however, it is open to reasonable debate whether theory of mind is a conceptual capacity, a verbal skill, or, perhaps, a conceptual skill afforded by verbal facility, because no unambiguous demonstration of the representation of mental states in others has been conducted with nonverbal or preverbal participants.

Deception

Woodruff and Premack (1979) presented four chimpanzees with a series of interactions with two human trainers. A person baited one of two containers outside the cages and in full view of the chimpanzees, then departed. After a short interval, either (a) a cooperative trainer or (b) a competitive trainer (signified by wearing a bandana across the face, like a bandit) entered the room. The trainers awaited a deictic signal from the chimpanzees, before approaching the indicated container. The competitive trainer took the treat from the container and departed the room, whereas the cooperative trainer delivered the treat to the chimpanzees. Over time, two of the chimpanzees stopped responding in the presence of the competitive trainer, and the other two began indicating the unbaited container in the presence of the competitive trainer! Thus, deceptive communication has been elicited from chimpanzees in controlled, experimental conditions, lending support to ethological observations of apparently deceptive behavior in a range of primates and other animals (e.g., Mitchell & Thompson, 1986).

Comprehension of Speech
Savage-Rumbaugh and her colleagues (1993) compared the speech comprehension of a two-year-old child and an eight-year-old bonobo (*Pan paniscus*), finding that the two individuals displayed comparable levels of understanding spoken instructions. This demonstrates that, whatever cognitive or neural adaptations might support speech comprehension in humans, nevertheless there is a significant latent capacity for speech perception in bonobos; as noted above, this is a finding that would not have been possible from observation of wild bonobos living in their natural habitats.

**Mental Rotation**

Shephard and Metzler (1971) reported that humans who are asked to imagine rotating shapes in their minds display reaction times that are highly correlated with the amount of imagined rotation. Vauclair et al. (1993) later reported that baboons (*Papio papio*) displayed a similar phenomenon, albeit only when stimuli were presented to their left cerebral hemispheres (right visual fields). Similar findings have been reported for one rhesus monkey (*Macaca mulatta*), but not in two others by C. Köhler et al. (2005). Thus, response patterns consistent with a capacity for mental rotation has been demonstrated in nonhuman primates.

**Metacognition**

Defined as knowing that one knows, metacognition is operationalized in monkeys by providing an opt-out option (an “uncertainty response”) that animals can use in conditions of high uncertainty (e.g., Smith, 2009; Smith et al., 1997). Typically, this line of research challenges subjects to classify stimuli into superordinate classes—e.g., sparse distributions versus dense distributions. As distributions become middling dense, it becomes difficult to classify them, and monkeys, for example, will select an option to abort such uncertain trials, if that option is provided to them. Smith (2009) interprets this as an expression of an inability
to classify a stimulus into a stimulus class; if he is correct, then this provides a broad metaphor for human uncertainty: particularly the reluctance to admit ignorance.

Imitation

Currently a topic of some considerable debate, anecdotes of imitation by nonhuman primates have persisted for well over a century. Kearton (1925), for example, reported that his companion, a juvenile chimpanzee named Toto, adopted the habit of smoking tobacco in a pipe from observing Kearton smoke—a photograph in that book depicts Toto with a pipe’s stem held in his lips. In a systematic observational study, Russon and Galdikas (1993) reported numerous instances of rehabilitant orangutans imitating human actions, such as siphoning of liquids and toothbrushing. Custance et al. (1995) argued that if imitation was so widely observed in great apes, then “we should be able to demonstrate this fact in controlled experiments” (p. 839), and they went on to describe their application of the “do as I do” training protocol, first developed by Hayes and Hayes (1952). Hayes and Hayes used this demonstration protocol to foster the acquisition of arbitrary actions by their home-raised chimpanzee, Viki. Custance and her colleagues (1995) trained two institutionalized chimpanzees to imitate 15 arbitrary actions and then tested them on 48 novel actions. Two coders were able to reliably identify the actions imitated from video footage of the animals without the demonstrations. From the standpoint of cognition, some theorists suggest that imitation, as humans do it, requires the ability to mentally represent the intentions of the modeller (e.g., Tomasello et al., 1993), but because these were arbitrary actions, Custance et al. argued that their work demonstrated a generalized imitation response. Tomasello et al. (1993) presented the example of children’s acquisition and use of conventional symbols as exemplary of the kind of imitation that they believed was uniquely human: “the appropriate use of a conventional symbol can only be learned imitatively; it is unlikely to the point of
impossible that infants will discover for themselves the same arbitrary connection between
sound and referent that adults have conventionalized” (p. 498). Yet, the evidence for symbol
mastery by great apes, discussed above, surely establishes that great apes can establish
appropriate sign-referent connections (e.g., Krause & Beran, 2020), suggesting that any
cognitive difference must be of degree (and, perhaps, modality), rather than kind. Froese and
Leavens (2014) have speculated that imitation is a response to uncertainty in interpreting the
objectives of agents involved in goal-directed activities, where conventionalization is
ubiquitous, as in human cultures, uncertainty is high and imitation frequent. Still, this view
does not account for the extraordinary human capacity for vocal mimicry, which seems to be
unparalleled among primates (e.g., Fitch, 2000). Some researchers discriminate “true”
imitation from emulation, and posit that the former is cognitively more complex, because an
imitator must closely mimic both the observed behavior and grasp the functional relevance of
an act, but, as Hobaiter and Byrne (2010) pointed out, emulation appears later in development
than “true” imitation (Want & Harris, 2002; and see Horowitz, 2003)—more mature humans
are more likely to adopt the apparent goal of a demonstrator than copy their exact behavioral
sequences, which argues against the idea that slavish mimicry is an index of advanced
cognitive processing. Thus, currently, there is intense debate over the question of whether
imitation requires the cognitive ability to model other minds.

Pantomime

Pantomime is the re-enactment, for communicative purposes, of particular action
sequences. As with imitation, there are many anecdotal reports of pantomimic behavior
among nonhuman primates (e.g., W. Köhler, 1925; Savage-Rumbaugh et al., 1986). Some
great ape gestures are inherently iconic, such as the begging gesture that is displayed by great
apes and humans, where the hand is held out in a supinated, often slightly cupped posture
(e.g., Leavens & Hopkins, 1998; Teleki, 1973). Prima facie, the begging gesture seems to serve as an embodied, iconic representation of receipt. Similarly, rump presents, where the signaller turns their backside to the recipient seem to embody the expression of subordination (e.g., Goodall, 1968). Beckoning, that involves the hand and arm making apparently referential representations of a path through space is another example (Genty & Zuberbühler, 2015). In systematic observational studies, Tanner and Byrne (1996) described a number of iconic gestures displayed by a male gorilla, and Russon and Andrews (2011) described 18 iconic gestures by orangutans, including a re-enactment of a past event. Yet, some hold that the ability to pantomime is uniquely human: Arbib (2018), in particular, views pantomime as a phase of evolutionary development, after our split with the other great apes, on the path to protolanguage and thence to language (see Russon, 2018, for an alternative view).

Intentional Communication

There are two primary strands of connotation in contemporary use of the term “intentional” to describe communication: (a) it can mean “voluntary”—a signaller can choose not to display a signal (e.g., Hopkins et al., 2007, 2011; Liebal, 2018; Tanner & Byrne, 1993) and (b) it can mean “aboutness”—the signal refers to something external to the communicators (e.g., Bard, 1992; Gómez, 1990). While the scientific literature is slightly muddled by the ongoing, parallel invocation of these two different senses of intentionality, nevertheless, from the standpoint of measurement, several laboratories have adapted operational criteria for intentional communication that were originally developed in the study of human communicative development (Bates et al., 1975). In general, human children, around the first year of life, begin to tailor their signals for the attentional status of an interlocutor—using visual signals when interlocutors are facing them, and using auditory signals when interlocutors are facing away. They look, alternately, between interlocutors and
referents in triadic contexts. They will persist and elaborate their signaling in the face of communicative failures (Golinkoff, 1986). These features also characterize the gestural communication of great apes (e.g., Call & Tomasello, 2007; Leavens et al., 2005; Liebal, 2018) and more recent work is demonstrating similar capabilities in the communication of monkeys (e.g., Bourjade et al., 2014, 2015, 2019; Kumashiro et al., 2002; Hattori et al., 2007, 2010). On the balance of evidence, and contrary to a large number of claims published throughout the 20th Century, intentional communication seems to be a primitive, shared capacity of humans and other primates.

Pointing Production

Although long considered a uniquely human gesture that indexes a human species-unique cognitive capacity for referential communication (e.g., Butterworth, 2003; Tomasello et al., 2007), anecdotal reports of pointing by apes have existed in the scientific literature for more than a century (e.g., Furness, 1916; Witmer, 1909). Systematic observational studies have established that captive chimpanzees point, even when there is no human present (Savage-Rumbaugh, 1986), and there are a handful of observations of pointing in, respectively, wild bonobos (Veà & Sabater-Pi, 1998; Douglas & Muscovice, 2015) and chimpanzees (Hobaiter et al., 2014). Systematic experimental studies have established that captive great apes do point to out-of-reach entities under controlled, laboratory conditions (e.g., Call & Tomasello, 1994; Leavens & Hopkins, 1998; Leavens et al., 1996, 2015). As noted by Leavens (e.g., 2021), pointing by apes is commonplace in captivity, yet vanishingly rare in the wild, which he argues implies that captive environments pose communicative challenges that are only very rarely experienced by wild apes: these circumstances include barriers to direct action coupled with a reliance on others to act on the world on behalf of the signaler. Pointing has now been reported in numerous vertebrate species (reviewed by...
Krause et al., 2018; Leavens, 2021), including great apes and monkeys (e.g., Blaschke & Ettlinger, 1987; Kumashiro et al., 2002; Meunier et al., 2013; Mitchell & Anderson, 1997). While most researchers now accept that animals do point, there are persistent claims that human pointing is cognitively unique, produced with a desire to manipulate interlocutors’ states of mind (e.g., Tomasello et al., 2007, among many others). As Leavens et al. (2019) have noted, it is not possible to objectively confirm this communicative motivation in either nonverbal animals or preverbal humans; therefore, whether humans have unique motivations for pointing remains an open question.

Comprehension of Pointing

It has been widely claimed that humans have a unique capacity to comprehend the deictic cues (including pointing and gaze direction) of others, and that this is because humans have unique cognitive capacities for discerning the communicative intent of the signaler (e.g., Hare & Tomasello, 2005; Tomasello et al., 2007). In fact, there are at least three significant interpretive challenges in the empirical record cited to support this conclusion of human cognitive exceptionalism. First, nonhuman primates are systematically tested with different protocols, relative to humans and other animals, such as domestic dogs (Clark et al., 2019; Krause et al., 2018; Leavens et al., 2019; Lyn, 2010; Mulcahy & Hedge, 2012). Most saliently, nonhuman primates tend to be tested in cages, which tend to suppress performance when this manipulation is applied to representatives of other species, such as domestic dogs (*Canis lupus familiaris*: e.g., Clark & Leavens, 2019, 2021; Kirchhofer et al., 2012). Second, great apes are routinely tested on their comprehension of deictic cues with insufficient pre-experimental exposure to such cues to form a generalized response to these deictic cues (e.g., Leavens, 2014; Leavens et al., 2019; Lyn, 2010); indeed, when tested on comprehension of deictic cues, great apes who have been richly exposed to daily interactions with humans
display no apparent difficulty in their comprehension of these deictic cues (e.g., Itakura et al., 1999; Leavens & Clark, 2017; Lyn et al., 2010; Russell et al., 2011). Thus, although nonhuman primates do seem to suffer from the global effects of institutionalization (e.g., Bard & Leavens, 2014), when they are provided comparable opportunities to engage with humans as the groups with which they are being compared, there is no apparent incapacity in comprehending pointing and other deictic cues. Finally, even monkeys pass these kinds of experimental tasks, given a modicum of relevant experience (e.g., Anderson et al., 1995; Blaschke & Ettlinger, 1987; see review by Krause et al., 2018).

Conclusions

Consideration of the range of facts and theoretical approaches summarized briefly in this chapter renders a number of conclusions relevant to the ambition of understanding the evolution of primate cognition. First, the nature of this area of inquiry warrants investigation beyond the natural habitats of nonhuman primates; this is because no single ecological context can elicit the full range of competencies that are latent in any given primate. Second, some experimental studies of primate cognition in laboratory conditions have been, to a degree, over-sold: in practice, researchers usually lack sufficient experimental control over the lifetime experiences of captive nonhuman primates to control for a large number of confounding or lurking factors. In the most egregious practices, rhetoric is used to misdirect readers’ attention away from these lurking and confounded variables. Third, many observational studies have been, to a degree, undersold: a disciplinary obsession with statistical measures of central tendency and the use of inferential statistics in hypothesis-testing analytical procedures have, arguably, misdirected disciplinary attention away from essential foundations in observation and natural history of animals in both natural and captive environments. Fourth, selective pressures manifest at the fulcrum sites of reproductive
fitness and feeding or mating tactics are not necessarily disjunct categories of activity, particularly in social-living animals. Even where we find high correlations between neural measures and broad measures of sociality or of foraging complexity, such findings do not discriminate between potential prime movers, because foraging success does not apportion independently of social interactions among social primates. Fifth, many cognitive capabilities once thought to implicate uniquely human selective pressures are now seen to be shared, primitive traits with the other primates (Table 1). One putative human-unique capability that has withstood the onslaught of evidence is, of course, language.

Human language is, as far as we know, unique in the animal kingdom. There are numerous hypotheses of the adaptive function of language and even one prominent hypothesis of the absence of adaptive function of language. Language permits planning of resource exploitation at significant temporal and spatial distances, perhaps evocative of our savannah origins. Language permits sophisticated kin networks extending over many generations. Language permits contractual arrangements of unparalleled detail. Language permits poetry, wooing, rhetoric, persuasion, damnation, and justice. Did language evolve “for” any of these capabilities, or are these activities afforded by language? There are numerous, impressive, elegant arguments in support of a variety of mutually inconsistent views, but for present purposes, I simply note that consideration of the evolution of cognition in primates is exemplary of the conundrum: it seems most unlikely that the ultimate cause of the human language facility is the elucidation of the evolution of primate minds. Indeed, these considerations would seem to have virtually no fitness consequences, whatsoever. Human cognition, then, is exemplified by the use of information to solve problems that can only be perceived with the mediation of human language.

References


10.1016/j.neuron.2010.03.010


[https://doi.org/10.1017/CBO9780511542305.005](https://doi.org/10.1017/CBO9780511542305.005)


[https://doi.org/10.1177/17456916198966](https://doi.org/10.1177/17456916198966)

[https://doi.org/10.3389/fpsyg.2014.00065](https://doi.org/10.3389/fpsyg.2014.00065)


[https://doi.org/10.1007/bf02382747](https://doi.org/10.1007/bf02382747)


[https://doi.org/10.4161/19420889.2014.992742](https://doi.org/10.4161/19420889.2014.992742)


between a Japanese monkey and a human through eye gaze and pointing. 


https://doi.org/10.1371/journal.pone.0211031


doi_10.1073_pnas.0706147104

Premack, D., & Woodruff, G. (1978a). Does the chimpanzee have a theory of mind? The
Behavioral and Brain Sciences, 4, 515-526.


Academic Press.

communicative rearing environments in the development of social and physical
https://doi.org/10.1111/j.1467-7687.2011.01090.x

https://doi.org/10.1075/is.17028.rus

Biology Letters, 7, 627-630. doi: 10.1098/rsbl.2010.0564

(Pongo pygmaeus). Journal of Comparative Psychology, 107, 147-161.
https://doi.org/10.1037/0735-7036.107.2.147

action selectivity in rehabilitant orangutan (Pongo pygmaeus) imitation. Journal of
Comparative Psychology, 109, 5-17. https://doi.org/10.1037/0735-7036.109.1.5

http://dx.doi.org/10.1037/0096-3445.115.3.211


https://doi.org/10.1016/s0010-0277(96)00726-3


[https://doi.org/10.1073/pnas.2.11.639](https://doi.org/10.1073/pnas.2.11.639)
Table 1. A representative list of allegedly human-unique cognitive capacities and their demonstrations in nonhuman primates.

<table>
<thead>
<tr>
<th>Capability</th>
<th>Representative Sources</th>
</tr>
</thead>
<tbody>
<tr>
<td>Insight learning</td>
<td>Yerkes (1916), Köhler (1925)</td>
</tr>
<tr>
<td>Tool use</td>
<td>Köhler (1925); Goodall (1968)</td>
</tr>
<tr>
<td>Use of symbols</td>
<td>Gardner &amp; Gardner (1969); Rumbaugh (1975)</td>
</tr>
<tr>
<td>Theory of mind</td>
<td>Premack &amp; Woodruff (1978); Krupenye et al. (2016)</td>
</tr>
<tr>
<td>Deception</td>
<td>Woodruff &amp; Premack (1979)</td>
</tr>
<tr>
<td>Comprehension of speech</td>
<td>Savage-Rumbaugh et al. (1993)</td>
</tr>
<tr>
<td>Mental rotation</td>
<td>Vauclair et al. (1993)</td>
</tr>
<tr>
<td>Metacognition</td>
<td>Smith (1997, 2009)</td>
</tr>
<tr>
<td>Imitation</td>
<td>Custance et al. (1995); Hobaiter and Byrne (2010)</td>
</tr>
<tr>
<td>Pantomime</td>
<td>Russon and Andrews (2011)</td>
</tr>
<tr>
<td>Intentional Comm</td>
<td>Woodruff &amp; Premack (1979); Leavens &amp; Hopkins (1998)</td>
</tr>
<tr>
<td>Pointing production</td>
<td>Call &amp; Tomasello (1994); Leavens et al. (1996)</td>
</tr>
<tr>
<td>Pointing comprehension</td>
<td>Anderson et al. (1995); Blaschke &amp; Ettlinger (1987)</td>
</tr>
</tbody>
</table>
Figure Captions

Figure 1. **Schematic representations of two views on the locus of cognition.** (A) A neurocentric view of cognition, in which the locus of cognitive processes is the brain. (B) A distributed view of cognition, in which cognitive processes are seen as located in the interactions of event-related entities related by episodic relevance.

Figure 2. **The increasing sophistication of the dance language with phylogenetic development of the dance.** (A) Dwarf honeybees perform dances on horizontal surface in the direction of the food source. (B) Giant honeybees perform dances on vertical surface and orient dances with gravity and celestial cues. *Apis dorsata* also has auditory cues when dancing. (C) Cavity-nesting honeybees perform dances in darkness on a vertical surface. Dances are oriented with gravity and celestial cues. All species produce auditory cue when dancing. Bees in (B,C) are both dancing directly upwards, indicating that the food source is in the direction of the sun. Areas of the comb on which bees dance are colored red. (Figure and caption from l’Anson Price & Grüter, 2015, their Figure 1).

Figure 3. **Direct human vs. nonhuman primate comparisons are ambiguous.** Most allegedly human-unique cognitive adaptations are based on poorly controlled experimental comparisons between human and nonhuman primates. The large number of uncontrolled, confounding variables cannot isolate evolutionary history as a causal factor, when differences are reported. In this figure, six systematically confounded variables (top row) lead to 63 possible explanations for a group difference—only one of these 63 viable explanations is that humans have a species-unique cognitive adaptation.
Figure 4. “Prime movers” in the evolution of primate cognition. Factors, with examples, of fitness-relevant adaptive pressures in primates.
Figure 1

A.

B.
Figure 3

<table>
<thead>
<tr>
<th>6 Confounded Factors</th>
<th>Test Environment</th>
<th>Task Preparation</th>
<th>Sampling Regimen</th>
<th>Test Procedure</th>
<th>Age</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>15 two-way interactions</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>20 three-way interactions</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>15 four-way interactions</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6 five-way interactions</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1 six-way Interaction</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

= 63 Explanatory regimes, of which only one is a simple species difference.
Figure 4