

*Using comparative studies of primate and canid
social cognition to model our Miocene minds*

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Using comparative studies of primate and canid *social cognition to model our Miocene minds*

Thesis Advisors: Professors Richard Wrangham, Marc Hauser, and Michael Tomasello

Abstract

The greatest challenge facing anthropology is in explaining the evolution of human cognition. The evolution of unique social problem solving skills likely explain much of what is unique about our phenotype including language and culture. However, before we can test such hypotheses for the evolution of human cognition, we must first establish what cognitive abilities were derived during human evolution. Therefore, for my dissertation research I conducted experiments with chimpanzees to identifying which social cognitive traits our species inherited and which traits have arisen since our split with our last common ancestor with chimpanzees and bonobos. Contrary to previous research, the current results suggest that the earliest hominins already possessed an incipient mind, which at the very least allowed them to calculate how others perceived the world visually. Future work will continue to improve our ability to travel into our Miocene mind using increasingly sophisticated comparative methodology.

Acknowledgments

As with any other dissertation, mine is not the product of one individual's labor alone. Instead, this dissertation represents yet another example of how our species prospers largely as a result of our unique social cognition and temperament. My parents have always believed in me far more than I deserved, but I'm sure even they would have enjoyed the joke, especially after I almost failed out of second grade, if anyone had ever suggested I would finish a Ph.D. – much less from a school anyone had ever heard of. However, despite my inevitable future as a bus boy, countless people worked tirelessly and selflessly to educate and inspire me to be the best I could be. If it wasn't for their intolerance for anything but excellence my academic path, without question, would have been much abridged. I have a long way to go, but I can say with confidence, my dissertation, for better or worse, exists only because so many others have not only shared ideas and knowledge with me, but also because they did so with unbridled passion, persistence, and patience. I can only hope, therefore, the sincerity of my gratitude will not be in doubt as I *try* to thank the troop of steadfast family, friends, and teachers who never tire of pushing me up hill as I chase my own selfish dreams.

It is impossible for me to thank my parents in words. Without an understanding of evolutionary theory, I would question their sanity. Why would anyone forfeit so many of life's pleasures and comforts, as they always have, in favor of unmitigated investment in the education of four snot-nosed little brats – myself included? And invest they did, whether it was reading stories, coaching our sports teams, or discussing religion and politics, my parents always, always had time and energy for their kids. Of all the lessons learned from my parents so far, the most valuable are not the ones they taught but instead

the ones they infected me with. My mom never got tired of reminding me that it was the “lack of my own imagination” anytime I found myself bored. As a child, there was no defense from her inexhaustible imagination and insatiable desire to learn. How much fun we had finding out about bugs, frogs, bats and every other kind of creature moms do not normally tolerate, much less enjoy learning about. It cannot be anything but this that led me, a kid living in a sterile Atlanta suburb, to grow up wanting to learn everything about wildlife. What other mother would not only have allowed, but also encouraged her son to build his cockroach “farm”? Meanwhile, failure has never been an option for my Dad. Whenever I was frustrated and ready to throw up my hands, he was quick to remind me that, “Can’t never did anything!” My dad knows that winning is fun and his championship attitude assures that he has his fair share of victories. Having my padre as my coach, more than anything, showed me that success requires faith in one’s abilities even when they don’t seem to be up to the task. However, my education required more than my parent’s time and inspiration; it also required resources. My parents funded 18 years of private education. In deciding what college to attend, instead of pressuring me to accept scholarships at schools that did not offer the program of study I thought I might be of interest, they encouraged me to go to Emory so that I might be able to study primates – even if it meant they would scrimp and save to foot the bill. In no way am I the one who made the greatest sacrifices to see that this dissertation was completed. Thank you Mom and Dad for all your love! I know it wasn’t easy.

However my parents were not alone. My grandparents were right there beside them in helping to encourage and teach. I can remember Mimi being insistent that my old childhood dog’s plate had to be cleaned so that it looked shiny new – even if it was a

dawg dish. She told me animals deserve to be treated with dignity and respect just as much as people. Da was never put-off by the fact that we never caught anything when we went fishing every July. The only thing of import was to be outdoors, appreciate the beauty of nature, and eat a cold watermelon. Grandma was my biggest fan. It didn't matter that she hated my pet snakes (she always promised to get me a potbellied pig if I got rid of them, but unfortunately mom wouldn't let her!); she never failed to fully support my crazy interests. The summers my parents couldn't afford to send me to "nature camp", she made sure I got to go, and that I was buried in letters from Grandma and Da. Given that they were the first in their families to go to college, education was a serious matter to my grandparents. They made sure, using the most positive strategies possible, that I understood this also.

They may not believe it, but I'm thankful to my older siblings Burke and Alicia - especially for being the pioneers. I learned a lot about how to behave from watching them grow up. Much of my confidence came from the knowledge that they had succeeded. As for little my little brother Kevin, he might not remember, but we had a ton of fun together. Does blowing up stuff ever get old? Don't worry kido your gonna win your race.

My parents' willingness to invest so heavily in my education meant that during my lifetime as a student I have been taught by some unbelievably talented teachers. It started at *The Lovett School*: Helen Letts who somehow taught me how to read in third grade; Chatty White who made it cool to love nature; Lynn Eliot who tutored me on her own time at New York Pizza Exchange before my first middle school exams; Tom Bartelt with his vicious red pen finally taught me how to write a sentence and a paragraph

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Part I: Comparative studies of human cognitive evolution:

The future of anthropology?

The challenge of human cognitive evolution.

“The greatest difficulty which presents itself, when we are driven to the above conclusion on the origin of man, is the high standard of intellectual power and moral disposition which he has attained.”

Charles Darwin, The Descent of Man (1871, p. 390).

Darwin, of course, was correct. There can be no bigger challenge facing evolutionary theory than explaining the evolution of human cognition. The challenge originates from the fact that no evolutionary era in the history of life has resulted in more radical changes to any one species' phenotype than those that occurred during hominin evolution (Deacon, 1997, Tomasello, 1999; Klein, 1999). At the same time, no area of anthropological research promises to be richer with discoveries in the next decades than the research developing and testing hypotheses of human cognitive evolution (Corballis & Lea, 1999; Barkow et al., 1992). The promise for discovery has emerged with rapidly developing methods that might relax our paleoanthropological dependency, if only biological anthropologists resolve to invest more heavily in comparative cognitive studies of extant species.

What is so challenging about the evolution of human cognition? Again, Darwin himself expresses it best when he says,

“We have seen in the last chapter that man bears in his bodily structure clear traces of his descent from some lower form; but it may be urged that,

as man differs so greatly in his mental power from all other animals, there must be some error in this conclusion. No doubt the difference in this respect is enormous, even if we compare the mind of one of the lowest savages, who has no words to express any number higher than four, and who uses no abstract terms for the commonest object or affections, with that of the most highly organized ape. The difference would, no doubt still remain immense, even if one of the higher apes had been improved or civilized as much as a dog has been in comparison with its parent-form the wolf or jackal “ (Darwin, 1871, p. 34).

In no more than seven million years our lineage went from species whose few scattered members all independently built sleeping nests each night, to a single species of billions, organized into communities of millions, who together invent everything from baseball to rockets with which to fly to the moon. How is such dramatic evolution possible? Amidst the industrial revolution, Charles Darwin was well aware of the problem that human intelligence posed for his nascent theory of evolution. Yet before the birth of modern psychology at the turn of the 20th century, Darwin all but shied away from the problem, only dedicating a few dozen pages of The Descent of Man to an attempt at shrinking the great divide between human and nonhuman intelligence. His solution was to suggest that only quantitative differences exist between different species of animals including that of humans—an idea motivating Skinnerians for most of the 20th century—while only offering a collection of anecdotes as evidence for the plausibility of his case (later extended further by Romanes, 1882).

Although his anecdotes may have carried the day, Darwin clearly saw human cognitive evolution as one of the major challenges that evolutionary biology would have to tackle with intense and rigorous investigation. Clearly then, any field of inquiry that is serious about solving the mystery of human evolution *must* address the biggest mystery of all—that of the evolution of human cognition. Therefore, biological anthropology, the

only field solely dedicated to the study of human evolution, must overcome its historic apathy towards psychological research and dedicate significant resources toward identifying what our species' unique cognitive abilities are, and what evolutionary processes may have led to their evolution. In illustration of this apathy, a recent review lays out the future directions for studies of human evolution without mentioning the study of human cognitive evolution or the potential power of the cognitive sciences (including comparative and developmental psychology) in answering questions relevant to human cognitive evolution. Instead the author concludes that, "for all but the last 1-2% of the time span of an independent human lineage we are forced to rely on a third approach for the reconstruction of our evolutionary history, namely the location, recovery and analysis of any relevant fossil evidence (Wood, 2000)."

How are we, as modern biological anthropologists, going to move toward a viable theory of human cognitive evolution? One thing is certain: contrary to the supposition of Wood (2000), the staple of physical anthropology—primate fossils—will be relatively unhelpful in solving many of the mysteries of human cognitive evolution (Mithen, 1996; Tomasello, 1999). Although we can make some important inferences about human cognitive evolution from gross changes in morphology and technology, fossils studied in isolation can neither tell us what specific cognitive changes have taken place nor reveal what evolutionary processes might have led to those changes (although paleoecological reconstructions and paleoanthropological analysis are crucial for generating and testing hypotheses for selection pressures; Klein, 1999). For both these ends there is no other choice but to develop comparative methods that allow for the approximation of the problem solving behaviors of extinct hominoids from that of extant species. Ironically,

developmental psychologists have already realized the utility of using the comparative method for testing ontogenetic theories of human development (Wang & Spelke, 2002; Hauser, 2000). Hopefully in a similar way, anthropologists will also realize how powerful the comparative studies of animal cognition can be in producing and testing hypotheses relevant to resolving Darwin's greatest difficulty.

The comparative method

Together evolutionary biologists—including anthropologists and psychologists—have developed an extremely powerful tool for virtual time travel. Careful comparison between extant species can allow for conclusions about the phenotype of these species extinct ancestors (Harvey & Pagel, 1991). Inferences regarding ancestral phenotypes then can be used in accomplishing the ultimate goal of this time travel which is to understand what evolutionary mechanisms (i.e. natural selection) have caused the genotypic changes that result in the phenotypic variance we observe in extant species (Hauser & Fitch, 2002). There are surely different ways to describe the overall comparative method used across biology, but here I describe it as four sequential steps based on Tinbergen's four levels of analysis (Tinbergen, 1952). However, the sequential steps are only meant to aid in explaining the method and do not represent the reality of how comparative research is conducted. In fact, multiple research programs are typically carried out in parallel allowing researchers to adjust their own hypothesis and techniques based on the findings of researchers working on different "steps" of the same comparative problem.

The first step necessary for time travel is the identification of shared and derived traits across species. Traits can be classified as being shared or derived by applying simple rules of parsimony to comparisons between species of known phylogenetic relation (Harvey & Pagel, 1991; Klein, 1999). Shared traits (synapomorphs or plesiomorphs) are those traits present in close relatives that were inherited through common descent. For example, if four relatively closely related species all share a trait, one knows that this trait was 1) inherited by all species through common descent, and 2) the trait has existed since before the four species speciated (i.e. it is more parsimonious to assume the trait evolved only once instead of four times independently) (e.g. Tomasello et al, 1998). Derived traits (apomorphs) are those that were not inherited through common descent with other members of a clade. For instance, if only one of four closely related species possesses a trait, one knows that this trait 1) is derived since it evolved uniquely during this one species evolutionary history, and 2) the trait cannot be older than the species possessing it (i.e. it's more parsimonious to assume the trait evolved once instead of being lost three times independently) (e.g. Tomasello, 1999; Hauser et al, 2002).

The second step to successful time travel is identification of an ecological factor(s) correlated with the observed variance in a trait(s). Ecological factors correlated with variance in a trait can be exposed in two ways. First, comparisons between species can identify cases of convergence in a trait that correlate with an ecological factor. Convergences represent cases of analogous traits being derived multiple times, independently of one another and across a range of species (i.e. the possibility must be ruled out that similar traits are homologous). With the demonstration of convergence, an ecological factor(s) shared in common across the species with a homoplasy can be

nominated as a candidate selection pressure(s) responsible for the documented evolution (e.g. Kamil et al, 1994). Second, comparisons within species can reveal ecological factors that may contribute to evolution in a trait. An ecological factor can be nominated as a potential selection pressure in cases where variation within a species correlates with variation in an ecological factor (e.g. Boag & Grant, 1978; 1981)

The third step to successful time travel is the identification of an altered epigenetic pathway(s) responsible for a derived trait. Once a correlation has been established between an ecological factor and variance in problem solving behavior, it is then possible to search for an altered epigenetic pathway that may have been affected by pressure from the suspected ecological factor and is responsible for the observed variance in the trait. One way epigenetic pathways can be identified is by comparing individuals or species before and after they have been exposed to experience relevant to the development of the trait under study. For example, depriving or providing individuals of ecologically relevant experiences (i.e. interactions with conspecifics) can prevent or enhance physiological changes (i.e. testosterone levels) that are required for the development of morphological structures (i.e. neurogenesis) that control the expression of the trait under study (i.e. vocal learning in passerine birds, reviewed in Brainard & Doupe, 2002).

The fourth step to successful time travel is the demonstration that natural selection altered the implicated epigenetic pathway. Once an epigenetic pathway has been identified, in some cases it is possible to demonstrate that this pathway was a target of selection. Increasingly there will be opportunity to compare levels of nonsynonymous to synonymous changes in sequences of DNA involved in the expression of the

developmental pathway(s) in question (e.g. Iwama & Gojobori, 2002; Trut, 2001). If it can be demonstrated that the genetic architecture responsible for the development of these epigenetic pathway were subject to natural selection, then it can be inferred that the suspected ecological pressure acted as the selection pressure.

The comparative method for the study of human cognitive evolution

The comparative method can be powerfully applied to the study of human cognitive evolution (Wrangham et al, 1999; Tomasello, 1999; Wang & Spelke, 2002; Hauser et al, 2002). However, it is important to recognize from the outset that the questions we can answer with these methods are constrained by our fate as the sole surviving hominin species (Wood, 2000).

The resolution allowed for by the comparative method is completely determined by the extant species available for comparison. Unimpressively little can be concluded from the fossil remains of extinct hominins compared to what would be possible if comparative hominin psychologists had even one living individual to study. Therefore, during the period where, perhaps, the greatest changes in any species phenotype is observed (e.g. human culture and language, Tomasello, 1999; Hauser et al, 2002), we have the least amount of data to help in establishing when, how and why these changes occurred during the Plio-Pleistocene (Klein, 1999). Ironically, this means that the most difficult period of cognitive evolution to reconstruct, out of the entire history of cognitive evolution in animals, is the last seven million years of human cognitive evolution (Deacon, 1997). However, although the situation might seem bleak, it is far from

hopeless. There are three proven methods for attacking the problem of reconstructing human cognitive evolution based on the comparative method outlined above.

Hominin phylogenetic analysis

Although our species alone represents the hominin line, we are one among five extant species of hominoids (King & Wilson, 1975; Ruvolo, 1997). Therefore, there is plenty of opportunity to compare cognitive abilities among hominoids. What can we potentially learn from such comparisons? Most importantly, for those concerned with human evolution, careful comparisons between chimpanzees (*Pan troglodytes*), bonobos (*Pan paniscus*) and humans can allow for the identification of derived traits that have originated since our species split from our last common ancestor (LCA) with chimpanzees and bonobos. Chimpanzees and bonobos represent our species closest living relative with which we shared a common ancestor approximately five to seven million years ago (Ruvolo, 1997; Brunet et al, 2002; Wildman et al, 2003). Therefore, by comparing chimpanzee and bonobo cognition to that of our own, we can identify what aspects of human cognition 1) evolved before our species split with our last common ape ancestor, and 2) what cognitive traits were derived during hominin evolution (Deacon, 1997; Byrne, 1995).

How are such conclusions possible? First, if a trait is found to be present in all three species, it is most parsimonious to conclude that the existence of this trait in all three of these closely related species is not the result of three independent evolutionary events, but rather that the trait evolved once and is shared through common descent (Harvey & Pagel, 1991). Therefore, a comparative psychologist would conclude that a

cognitive trait shared by chimpanzees (and /or bonobos) with humans was most likely to have evolved before our two lineages split (e.g. gaze following and visual perspective-taking, Tomasello et al, 2003). Second, if a trait is found to be present in one of the three species, but not the other two, it is most parsimonious to conclude that this trait is present in the one species, because it evolved after the three species split (e.g. recursion and belief attribution, Hauser, 2002; Tomasello et al, 2003). However, study of the complete hominoid taxa would be necessary to verify with confidence that this was indeed the case. The derived origin hypothesis for a trait present in either humans, bonobos, or chimpanzees would be supported if that trait was also absent in gorillas and orangutans. However, if one or both of these extended relatives shared the trait then further research would be necessary to determine if the distribution of the trait represented a case of convergence or selection against the trait in those species without it (Miles & Dunham, 1993; Harvey & Pagel, 1991; Pilbeam, 1996).

In summary, a comparative psychologist can conclude that any cognitive trait that is present only in humans, but not chimpanzees and bonobos, is a derived trait produced during hominin evolution (this hypothesis would be substantially strengthened if such a trait was absent in orangutans and gorillas as well). Therefore comparing human cognition with that of chimpanzees and bonobos is an essential first step in identifying features of human cognition that are derived products of our unique evolutionary history (Premack, 1986; Deacon, 1997; Byrne, 1995; Tomasello, 1999; Povinelli, 2000; Preuss, 2000; Suddendorf & Whiten, 2001; Hauser et al, 2002).

Identifying evolutionary mechanisms

The first step to solving Darwin's greatest difficulty is identifying derived features of human cognition that are responsible for our species unique intelligences. Studies of nonhuman great ape cognition provide the only available method for revealing derived cognitive abilities that arose during hominin evolution. However, once these derived abilities have been identified, one is directly faced with the second puzzle presented by Darwin's greatest difficulty: how and why did these derived cognitive abilities evolve during hominin evolution? One way Darwin's greatest difficulty can potentially be addressed is by applying the four steps of the comparative method to studies of cognition across a wide range of animal taxa (including species of hominoids; Hauser & Fitch, 2002). Comparative psychologist can potentially identify derived cognitive abilities in nonhumans that converge with derived features of human cognition. Once a number of such homoplasies are identified, researchers can then work to explain how and why these derived traits evolved in the nonhuman species that possess them. With information about how and why apomorphies evolved in other species, inferences and testable hypotheses can be made regarding how and why derived cognitive traits evolved in humans.

One example of a derived cognitive trait that converges in interesting ways with a derived feature of human cognition (i.e. expansive long term memory relative to other hominoids, see Tomasello & Call, 1997 for a review) is the case of long-term spatial memory in some species of food hoarding birds (Shettleworth, 1998). A number of species of birds possess an unusual ability for remembering where they have hidden what type of food over extended periods of time. The presence of unusual memory in only a

few distantly related passerine species (and possibly paciforms) rules out the possibility that this trait has simply been inherited by those species possessing it. Instead, the evidence suggests a number of independent cases of convergence in memory ability in parids, sittids, and corvids (Healy & Krebs, 1992; Healy, 1994; Kamil et al, 1994; Clayton & Krebs, 1994; Clayton, 1995; Healy & Suhonen, 1996; Hampton & Shettleworth, 1996; McGregor & Healy, 1999). Comparative study of these species' behavioral ecology has revealed a potential ecological factor that is related to the variance across species in spatial memory. First, species that store food for later retrieval and consumption perform better in various spatial tasks than closely related species that do not store food (Kamil et al, 1994; Bednekoff et al, 1997). Second, among food storing species, those species or individuals within a species that rely most heavily on retrieving stored food perform the best on spatial memory tasks (Pravosudov & Clayton, 2002).

These findings suggest the functional hypothesis that unusual spatial memory abilities evolved due to the fitness advantage long term memory provided to food-caching species—especially those living in the harshest environments, where recovery errors could most easily result in death (Pravosudov & Grubb, 1998; Pravosudov & Lucas, 2001). Moreover, neuroethological research has begun to uncover aspects of the epigenetic pathway that was likely altered and may be responsible for the unusual spatial abilities in food storing species. A number of studies have found that adult members of food storing species possess enlarged hippocampi relative to closely related non-storing birds (Krebs et al, 1989) while hippocampal lesions reduce the accuracy of retrieval attempts in food storing species (Sherry & Vaccarino, 1989). In addition, developmental studies have shown that it is the experience of hiding and recovering food stores that

alters levels of hormones that then control levels of neurogenesis in the hippocampi of food storing birds (Clayton, 1996). Taken together, these findings suggest the hypothesis that 1) the enlarged hippocampus of food storing birds allows for their unusual memory capabilities, and 2) the genes that regulate the expression of hormones responsible for neurogenesis evolved in food storing species in response to directional selection. As a final step in understanding the evolution of the unusual spatial memory abilities in birds, evolutionary geneticists can potentially identify the gene complement involved in hippocampal neurogenesis and test for nonrandom genetic change (i.e. natural selection) by verifying whether a low ratio of nonsynonymous to synonymous changes exist in the identified gene(s). If completed, this comprehensive comparative research program on avian spatial memory will not only have revealed a cognitive adaptation, but also will have provided valuable insights into how we might explore the evolution of our own species' cognitive abilities.

The research program on spatial memory in nonhumans can reveal valuable information about human cognitive evolution from each level of the comparative research program. First, functional hypotheses for the evolution of human spatial memory can be refined and reevaluated in a manner that may lead to additional testable predictions (Sullivan & Eals, 1992). Second, because there is substantial evidence that the vertebrate genome is constrained in how it can change, it is likely that the evolution of derived memory systems in humans may be mediated by similar epigenetic systems as those identified in nonhumans (Hauser et al, 2002). With high quality information about cognitive evolution in nonhumans, anthropologists are in a strong position to make

inferences and develop testable hypotheses regarding derived features of human cognition as well.

Identifying the evolutionary mechanisms responsible for human cognition

Once the comparative method has allowed for the identification of 1) a cognitive trait(s) that was derived during hominid evolution, and 2) revealed how and why this analogous trait(s) evolved in distantly related species, we are most likely to make accurate inferences and develop testable hypotheses regarding how and why unique human intelligences evolved. First, although hominin species comparisons are impossible, an ecological factor(s) that is associated with a derived trait(s) of interest can potentially be identified using comparisons between modern humans. Just as in the case of the birds, an ecological factor can be nominated as a potential selection pressure in cases where variation within populations of our species correlates with variation in an ecological factor (Pravosudov & Clayton, 2002; Boag & Grant, 1978; 1981). However, in the search for an associated ecological factor, humans represent a special case. Because of rapid cultural evolution, unlike most nonhuman species, our modern environment does not present the ecological problems for which our derived cognitive abilities evolved to solve (Tooby & Cosmides, 1992). As a result, when attempting to uncover an ecological factor(s) associated with a derived human cognitive ability we must model the ancestral environment in which we spent the majority of our genetic evolutionary history (Bowlby, 1969; 1973; Symons, 1979; Irons, 1998).

This means our species cognitive evolution will be modeled best when cognitive differences within modern populations are interpreted upon consideration of ecological

pressures faced by modern hunter-gatherer groups who still live in environments that closely resemble our species ancestral environment (Tooby & Cosmides, 1992). For example, men outperform women on spatial rotation tasks while women outperform men on spatial memory tasks (e.g. Vanderburg & Kuse, 1978). This difference in performance has been hypothesized to be associated with sex specific ecological factors faced by modern hunter gatherers (e.g. hunting success in males is associated with skill at mental rotation while gathering efficiency in women is associated with spatial memory, Sullivan & Els, 1992). Such a hypothesized association between an ecological factor and a human cognitive trait can gain significant support if an analogous association is identified in nonhuman species as well. Indeed, sex differences in spatial abilities have been identified in association with sex specific ecological factors. The males of polygamous meadow voles, who must travel great distances during breeding season, also perform significantly better on spatial tasks than the relatively stationary female meadow vole. Meanwhile both sexes of the monogamous pine voles, neither of whom roam, perform equally on the spatial tasks (Gaulin & Hoffman, 1988). Once an ecological factor has been identified as being associated with variance in a derived human cognitive trait, then two techniques can be used to attempt to identify the epigenetic pathway that may have been effected by the nominated ecological pressure(s).

First, individuals with localized brain damage can be tested to reveal the importance of the damaged structure in either the development or processing of the derived cognitive trait under study (Damasio, 1994). Second, animals that possess cognitive traits analogous to the derived cognitive abilities identified in humans, can provide an experimental model for detailed study of the epigenetic pathway responsible

for the development of the ability in question. For example, recent studies have demonstrated that the hippocampal growth is regulated by corticosteroid levels in birds, primates and potentially humans as well (Gould, 2003). Finally, if an epigenetic pathway can be identified, in some cases it may also be possible to test whether this pathway was a target of selection. Techniques are under development for the identification of genes that may be responsible for the expression of derived cognitive traits in humans (e.g. Enard, et al, 2001; Iwama & Gojobori, 2002; Kitano et al, 2003; Caceres et al, 2003; Marcus & Fisher, 2003). Potentially, in the future a gene that is implicated in the expression of an epigenetic pathway responsible for the development of a derived human cognitive trait, might be tested for evidence of high levels of nonsynonymous to synonymous change. Overall then, if developed and used successfully, the comparative method has the potential to identify derived (and perhaps unique) human cognitive abilities while allowing for the determination of how and why such a unique trait evolved in humans.

Summary: How does the comparative method allow for time travel?

Although we are the only living hominin, the quality of the fossil and archeological record does not represent the boundary for studies of human evolution – including studies of human cognitive evolution (Mithen, 1996; Tomasello, 1999; Hauser et al, 2002). A myriad of answers to questions about our species unique evolutionary history can be uncovered using the comparative method (e.g. Hauser & Fitch, 2002). As described, the comparative method can allow for: 1) the identification of shared and derived traits and their distribution among species, 2) the identification of an ecological factor(s) correlated with trait variance, 3) the identification of an altered epigenetic

pathway(s) responsible for a derived trait(s), and 4) demonstrations that natural selection altered the implicated epigenetic pathway. All of these comparative steps can be pursued in parallel allowing researchers to refine their hypotheses and methods based on findings of researchers working on a different “step” of the same comparative problem.

Following the model for the comparative study of human cognitive evolution just described, evolutionary biologist interested in mastering Darwin’s greatest difficulty must pursue three research directions. These three areas of inquiry include:

Identifying derived hominin traits: Completing a cladistic analysis of hominoid

cognition for the identification of derived features of human cognition,

Identifying evolutionary mechanisms: Locating distantly related species possessing

convergent cognitive abilities with humans, while working to identify how and why such convergence occurred and

Identifying evolutionary mechanisms in hominins: Using methods and knowledge

from studies of nonhumans (areas 1 and 2) to make inferences and develop testable hypotheses regarding how and why derived human cognitive abilities evolved during the Plio-Pleistocene.

However, it must be acknowledged that investigations in all areas presents significant challenges. The foremost is the scope of interdisciplinary cooperation and expertise needed to address all four steps of the comparative method described above. Pursuing them all in concert requires the expertise of behavioral ecologists, behavioral neuroscientists, comparative psychologists, cognitive scientists, developmental psychologists, endocrinologists, embryologists, evolutionary geneticists, philosophers and more. With so many different disciplines involved, each with their own idiosyncratic

methods and languages, it may be unreasonable to expect a well-orchestrated research program encompassing all levels of inquiry. Instead, it seems it will be individuals who cross boundaries between neighboring disciplines that will provide the cross pollination necessary to assure progress. Not to be underestimated as well, are the methodological challenges presented by each the four comparative steps. The first two steps are dependent on the quality of interspecific measures of cognition, however little research has been designed to assess how one tests for and maximizes validity in comparative studies (e.g. is it better to keep the method the same between species or is it better to adjust the method while controlling for motivation between species? Hare, 2001). The second step requires detailed knowledge of a species ecology. Typically ecological hypotheses have not been based on thorough knowledge of behavioral ecology, but instead on indirect ecological indices (e.g. group size is used as a proxy of social complexity, Dunbar 1993).

The third step requires detailed knowledge of neuroanatomical development across species; however, such knowledge remains limited. In addition, detailed study of brain development typically requires highly invasive methods that are arguably not appropriate for many species that are most likely to demonstrate cases of convergence with humans (Hauser & Fitch, 2002). Finally, the fourth method requires finding functional stretches of the genome that are candidates for playing a role in the expression of the epigenetic pathway for a trait in question. Unfortunately, even when twin studies indicate a high level of heritability in a trait, the identification of candidate loci, much less genes, remains extremely difficult while maintaining a strong element of luck (Marcus & Fisher, 2003). Even when candidate genes are identified that might explain

the difference between cognitive ability in two closely related species, there is no guarantee these genes will be involved in the expression of the phenotypic trait under study (Kitano et al, 2003). As a result of these methodological challenges progress will remain slow, but will increase its momentum as the power of integrating the four comparative steps is more fully appreciated across disciplines.

Where to start? Studies of human social cognitive evolution

“It deserves notice that as soon as the progenitors of man became social (and this probably occurred at very early period), the advancement of the intellectual faculties will have been aided and modified in an important manner, of which we see only traces in the lower animals...”

Darwin (1871, p.161).

With the comparative method to aid us, where might we search for the derived cognitive trait(s) responsible the drastic changes observed in our species phenotype (e.g. cultural behavior)? Because of the current constraints on methodology, we clearly cannot conduct a phylogenetic analysis of the entirety of human “intelligence”. Instead we must concentrate our finite energies, and hope to find evidence for a little genotypic change that might have resulted in big difference in the human phenotype (Tomasello, 1999). Is there any evidence of where to start our search for the critical derived trait(s) produced during human evolution?

Although there is a panoply of hypotheses for what cognitive abilities may represent derived cognitive traits in humans (e.g. Povinelli & Cant, 1995; Byrne, 1995, Tomasello, 1999; Suddendorf & Whiten, 2001; Hauser et al, 2002; Berrett et al, 2003, etc), currently one of the most prevalent hypotheses for a derived cognitive trait that may explain much of what is unique about the human phenotype is the evolution of a suite of

social problem solving abilities that are commonly referred to as “Theory of Mind” or ToM (Cheney & Seyfarth, 1990a; Corballis & Lea, 1999; Tomasello, 1999). As illustrated in the quote above, Darwin himself alluded to the potential importance of human social problem solving abilities for human evolution, so he might not have been surprised that it is our human social cognition, more than any other cognitive domain, where we may qualitatively differ from all other animals.

What is Theory of Mind? Human social cognition is centered on our ability to think about the thoughts of others or ToM (Premack & Woodruff, 1978; Dennet, 1983). We are aware that others have perceptions, intentions and beliefs, and that these psychological states can differ from our own (Wellman, 1990; Perner, 1991). We are dependent on our ToM for navigating through our social world (Moore & Frye, 1991). For example while interacting with others you constantly use cues as subtle as the smallest movements of their eyes to make calculations about what they are thinking (i.e. if an old acquaintance gazes at your name tag, you know they don’t know your name) (Corkum & Moore, 1995). Based on what you are able to assess from such cues about the perceptions, intentions, and beliefs of others, you then adjust your own behavior in order to effectively communicate, teach or even deceive them (Baron-Cohen, 1999; Flavell, 1999). In fact, evidence suggest that children are largely dependent on their ability model the mental states of others in acquiring all types of cultural traditions unique to humans, including language (Tomasello, 1999; Tomasello, 2003). Therefore, it maybe our species’ ability to think about the thoughts of others that provides the ontogenetic foundation to much of what is considered unique to human cognition.

Because thinking about the thoughts of others, is thought to be absolutely crucial for our ability to function as normal adults in cultural world (Baron-Cohen, et al, 1985;

Tomasello, 1999), cognitive psychologists have concentrated on understanding the cognitive mechanisms underlying this ability. Psychologists have studied both how Theory of Mind develops in human children (for reviews see Flavell, 1999; Wellman et al, 2001) and more recently how and where the brain processes information about others thinking (for a recent review see Gallagher & Frith, 2003). The central finding of this research is the discovery that humans are not simply born with an adult-like Theory of Mind. In fact, the vast majority of children only become capable of thinking about epistemic states in others after their fourth birthday (Wimmer & Perner, 1983; Flavell, 1992). Meanwhile, those children that do not develop such an ability, typically suffer from debilitating cognitive disorders including Autism (Baron-Cohen, 1985; Leslie & Thiass, 1992; Baron-Cohen, 1995). However, although psychologists have begun to make progress in understanding the developmental and cognitive mechanisms underlying ToM, their almost exclusive focus on development in normal and abnormal children has left the most pressing questions regarding the evolutionary origin of ToM unanswered (Tomasello & Call, 1997; Povinelli, 2000).

Therefore, because of its potential importance to the evolution of human cognition my dissertation contains five series of experiments that use the comparative method to address the following questions:

Identifying derived hominin traits:

Chapters 2 and 3 - Is human ToM a derived product of hominin cognitive evolution or was ToM (or at least some ToM abilities) inherited by humans through common descent from a hominoid ancestor who also had ToM capabilities?

Identifying evolutionary mechanisms responsible for social cognitive evolution:

Chapter 4 - If we inherited ToM abilities from common descent, how deeply rooted are these ToM abilities phylogenetically within the primate order?

Chapter 5 – What evolutionary pressures may have driven social cognitive evolution in nonhuman primates? Is the performance of primates in cognitive tasks context specific?

Chapter 6 – Are there any nonprimate species that whose social cognition converge with derived features of human social cognition? What evolutionary pressures might have led to the convergence in social cognitive ability?

The future of comparative psychology as a tool for the study of human evolution:

Chapter 7 – How do we develop valid interspecific cognitive measures? What does the current research suggest about developing future comparative methods that maximize validity?

Chapter 8 – What do the most recent studies on nonhuman social cognition tell us about how and why unique human intelligences evolved? What do these new findings suggest as directions for future research?

Part II: Do chimpanzees know what conspecifics know?¹

Introduction

A recurrent theme in the study of primate cognition is the discrepancy between the cognitive skills that field researchers believe they see in the behavior of nonhuman primates in their natural habitats and those that can be rigorously demonstrated in more controlled experimental settings. A case in point are the skills of chimpanzees in understanding what conspecifics and humans do and do not see.

Observers of wild and captive chimpanzees have collected many anecdotes which seem consistent with the idea that chimpanzees have a sophisticated understanding about what others do and do not see (Whiten & Byrne, 1988). For example, one field worker has reported that a lone wild chimpanzee upon discovering hidden fruit distracted and led other group members away from the food before they themselves could discover it (Richard Wrangham, pers. comm.). In addition, chimpanzees have been seen to hide parts of their body (i.e. fear grimace) with their hands so that presumably other group mates would not be aware of their emotional state in tense situations (de Waal, 1982).

However, in two experimental paradigms used recently chimpanzees seemingly do not show a sophisticated understanding of what others can see in various experimental arrangements. First, in a series of experiments Povinelli and colleagues have shown that when chimpanzees are given the choice of begging from a human who can see them versus one who cannot, they choose indiscriminately in all but the simplest conditions

¹ Reprinted from *Animal Behaviour*, 61, Hare, B., Call, J. & Tomasello, M., Do chimpanzees know what conspecifics know?, pgs. 139-151, Copyright (2001), with permission from Elsevier.

(Povinelli & Eddy, 1996; Reaux et al., 1999). That is, although they choose appropriately when one human is facing them and the other has her back turned, they choose indiscriminately in a variety of other situations in which one human's view is occluded but the other's is not (e.g., when one human has a bucket over his head and the other does not). Second, when chimpanzees are given the task of finding food hidden somewhere in a row of opaque containers most individuals do not use human gaze as a cue for finding the hidden food (e.g., Tomasello, Call, & Gluckman, 1997; Call, Hare, & Tomasello, 1998; but see Itakura & Tanaka, 1998). Together, these studies would seem to indicate that the gaze following skills displayed by chimpanzees in semi-natural captive settings (e.g., Povinelli & Eddy, 1996; Tomasello, Call, & Hare, 1998; Tomasello, Hare, & Agnetta, 1999) do not reflect a rich social-cognitive understanding of the visual experience of others.

There are a number of alternative reasons for chimpanzees' inconsistent performance in these experimental paradigms, however. One hypothesis is that these paradigms are too unnatural, because in both a human communicates to a chimpanzee about a monopolizable food source. This setting is clearly a rare and strange situation for chimpanzees who almost exclusively compete with groupmates for monopolizable food resources (Hauser & Wrangham, 1987; Wrangham, 1980). Thus, it may be that chimpanzees do not understand the cooperative motive of the human communicator in these situations because it is so dissonant with both the selective pressures primate species have faced during their evolutionary history and with any individual's previous foraging experience. In a recent series of studies, therefore, Hare, Call, Agnetta, and Tomasello (in press) designed a new experimental paradigm to test what chimpanzees know about what

conspecifics can and cannot see. This new paradigm emphasizes competition between conspecifics rather than cooperation and communication with humans.

In each of five experiments a subordinate and a dominant individual were placed into rooms on opposite sides of a middle room. Each room had a guillotine door leading into the middle room. When this door was cracked (i.e. opened about 15cm) at the bottom, the subordinate subject could see into the middle cage and also see the dominant individual when her door was also cracked. Once the subjects door were cracked appropriately (depending on the study), two pieces of food were hidden behind barriers in various locations within the middle cage. After the food had been placed, an experimenter opened the doors for each individual and allowed both subjects to enter the middle room. As expected, when dominants had good visual and physical access to the two pieces of food they obtained them both on most occasions. However, in some cases the subordinate could see a piece of food that the dominant could not see. For example, the experimenter placed one of the pieces of food on the subordinate's side of a small barrier. The question in these cases, was whether the subordinates knew that the dominant could not see a particular piece of food, and that it was safe for them to go for it. This procedure is especially noteworthy relative to other experimental paradigms in that: (i) the chimpanzees interacted with conspecifics, not humans; (ii) no training was involved; and (iii) it involved competition, not cooperation, for food - which is arguably a more natural situation.

The central finding was that subordinates did indeed go for the food that only they could see much more often than they went for the food that both they and the dominant could see. A number of control conditions effectively ruled out the possibility that

subordinates were monitoring the behavior of the dominant or that they were responding to other aspects of the experimental situation. The findings of this study, therefore, suggest that chimpanzees do indeed know what conspecifics can and cannot see, and, further, that they use this knowledge to devise effective behavioral strategies in food competition situations. Thus, the overall methodological lesson is that when a more naturalistic experimental paradigm was found, chimpanzees demonstrated much more sophisticated social-cognitive skills.

An interesting possibility raised by this study is that this same procedure might be used to test chimpanzees' understanding of psychological states more complex than visual perception. Previous experimental approaches designed to explore what chimpanzees know about what others (humans in all cases) 'know' have mainly produced negative findings. For example, Povinelli, Nelson, and Boysen (1990) found that chimpanzees preferred to ask for food from a person who had witnessed its hiding over someone who had not witnessed its hiding - the inference being that they could discriminate a "knowledgeable" from an "ignorant" human. But the apes in this study only learned to do this over scores of trials with feedback on their accuracy after every trial (see Heyes, 1993, and Povinelli, 1994, for details). Moreover, Povinelli et al. (1994) failed to replicate these results with another group of chimpanzees, and Call, Agnetta, and Tomasello (in press) also failed to replicate them using a procedure designed to make the task easier for subjects.

The current studies therefore attempted to address the question of what chimpanzees know about what others 'know' - which in all cases in these studies reduces to what chimpanzees know about what others have and have not seen in the past - using

the basic methodology of the Hare et al (in press) paradigm where a subordinate competes for food against a dominant. In the first study of three there were two sets of baiting procedures in which one piece of food was always placed on the subordinate's side of one of two empty barriers. Each procedure had its own experimental and control condition that varied as a function of what the dominant witnessed during baiting. In one experimental condition the dominant was not allowed to see the food hidden, and so was uninformed of its location. In the other experimental condition the dominant saw a piece of food hidden in one location, but did not witness when it was moved to another location, and so was misinformed about the location of the hidden food. Both of these procedures had their own control condition in which the procedure was identical to its matching experimental condition except that in both controls dominants witnessed the entire baiting procedure and thus were informed of the food's hiding place. In all conditions the subordinate witnessed the entire baiting procedure and also could potentially monitor the dominant's visual access during the different procedures. Therefore, the subordinates could assess what the dominants had or had not seen before each competition began.

The second study was similar to two conditions of the first study - the subordinate potentially could know whether her dominant competitor either had or had not seen the hiding - except that in this study the uninformed dominant was created in a different way. Instead of sometimes preventing the dominant from witnessing the baiting as in the previous study, in this study a dominant always saw the food hidden, but in one of the conditions this informed dominant was switched with a second uninformed dominant. It was this second naive dominant who the subordinate competed against. Therefore, this

study investigated subordinates' ability to keep track of what specific individuals had and had not seen (or potentially did or did not know). The third study had four conditions similar to those in the first study, but the paradigm was varied slightly so that the subordinate had to choose between two pieces of food, one of which the dominant had seen hidden and the other of which she had not.

The basic idea of the current studies, therefore, is that in all conditions the physical situation facing the subordinate was identical in the experimental and control conditions at the time of choice - either one or two pieces of food on its side of a barrier or barriers (out of sight of the competitor). The only difference between the conditions was that in the immediate past, the competitor either had or had not witnessed the food being placed or moved there. The current studies are therefore not concerned with what chimpanzees know about what their competitor does and does not see in the present, but rather what their competitor has and has not seen in the immediate past - or, in one possible description of this epistemological situation, what its competitor does and does not know about the current situation. These tests, thus, bear some resemblance to the almost exclusively verbal tests used by developmental psychologists to test children's understanding of: (i) seeing leads to knowing, and (ii) false belief (see Flavell, 1997, for a review). Whether these nonverbal versions should be interpreted in the same way is open to debate.

Study 1: Did she see it hidden or moved?

In this study a subordinate was faced with the choice of either going or not going for a piece of food during competition with a dominant. In some conditions she had witnessed the dominant witnessing the final placement of the food, whereas in others she

had witnessed that the dominant did not have visual access to the hiding procedures. Our hypothesis was that if the subordinates were sensitive to what others have or have not seen, they should approach and retrieve the food more often when the dominant was either uninformed or misinformed (as opposed to informed) about its location.

Methods

Subjects

Twelve adult and subadult (mean age = 21.6) chimpanzees (*Pan troglodytes*) housed in two social groups at the Yerkes Regional Primate Research Center Field Station participated in this study (see Table 2.1). Nine of the 12 subjects were subordinate to someone else in their social group and contributed to the data set, while the remaining three chimpanzees (Peony, Tai, and Ericka) were among the highest ranking in their respective groups and were only used in obtaining data from the other 9 subordinate subjects. All subjects were captive born except Peony, Phinneas, and Tai. When not being tested both groups had access to a number of indoor cages as well as a large outdoor enclosure. In addition, during testing all chimpanzees were fed twice daily, as usual, on a diet of fruit, vegetables, and chow. Water was available ad libitum. Subjects were tested in pairs consisting of a dominant and a subordinate individual (“dominant” and “subordinate” in all studies refers solely to dyadic food dominance). The dominance hierarchy used in the current studies (see Table 1) had previously been established for both groups by Hare, et al. (in press). All possible combinations of subordinate and dominant animals were tested except Rita-Georgia, Natasha-Borie, Tai-Ericka because they were assessed previously as being equally dominant (Rita and Natasha were subordinate to other females and were simply tested twice with the next highest-ranking female). These combinations produced a total of 33 dyads.

Subject	Age (years)	Sex	Birthplace	Participation in study #	Rearing history	Dominance rank
Group 1						
Bjorn	11	male	captivity	3	mother	1
Peony	31	female	wild	1-3	home-nursery	2
Borie	35	female	wild	1-3	mother	3
Georgia	19	female	captivity	1	mother	4
Rinette	12	female	captivity	1-3	mother	5
Natansha	12	female	captivity	1-3	mother	6
Anya	19	female	captivity	1-3	mother	7
Rita	12	female	captivity	1-3	mother	8
Kate	10	female	captivity	2	mother	9
Donna	9	female	captivity	1-3	mother	9
Group 2						
Erica	26	female	captivity	1-3	home-nursery	1
Tai	32	female	wild	1, 3	mother	1
Phineaus	33	male	wild	1-3	mother	2
Cynthia	19	female	captivity	1-3	nursery	3
Barbi	23	female	captivity	2	nursery	4

Table 2.1. Age, sex, birthplace, experiment participation, rearing history, and dominance rank of the subjects included in each of the experiments.

Procedure

Materials consisted of two opaque cloth bags (occluders) and small pieces of fruit (apples and bananas). A mechanical pincer mounted on a 3-meter pole was used from outside the cage by two human experimenters (E1 and E2) to place the fruit pieces behind occluders. Testing took place in a row of three adjacent cages (see Figure 2.1) - with one animal in each of the extreme cages and the food in the middle cage. All three of the cages consisted of three concrete walls, a concrete floor, and a wire mesh ceiling and fourth wall (facing a service hallway). There were guillotine doors between adjoining cages (0.6 square meters), and also a door to the outdoor enclosure (which remained closed during testing).

For testing, all extraneous objects and food were removed from the cages. For each trial one piece of fruit was placed on the subordinate's side of one of the occluders. The occluders were placed 2 meters apart, equidistant from the doors of each of the adjoining

cages. In order to make certain that the subordinate knew she was in a competitive situation, the occluders were placed closer to the dominant's than to the subordinate's door (2 meters from the subordinate's door and 1 meter from the dominant's door).

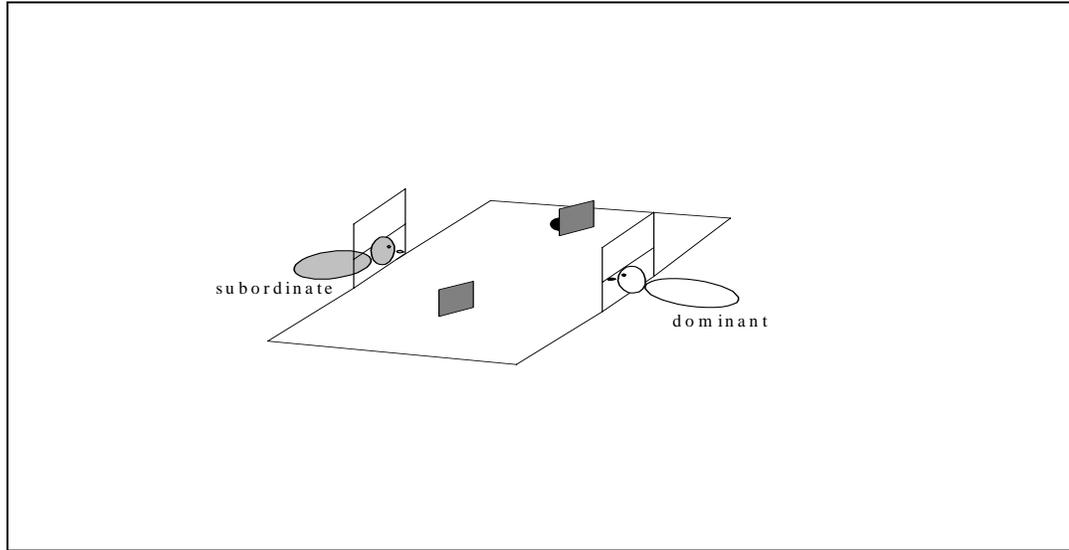


Figure 2.1. General experimental setup in Study 1-3.

There were two experimental conditions: Dominant Uninformed and Dominant Misinformed. Each of these had its own associated control condition in which the dominant was informed - which differed slightly from one another (see below). Each dyad was tested in four sessions (with all 33 dyads tested in Session 1 before moving on to Session 2). In each session each dyad participated in one trial in each of the four experimental conditions - for a total of 16 trials (4 per condition) for each dyad across sessions. Each session also included two probe trials (not of experimental interest but simply designed to counteract some possible learning effects; see below). Order of conditions was counterbalanced across dyads within each session separately. All testing was completed within approximately one month.

Since subordinate animals were allowed to watch the entire baiting process in all conditions, the experimental condition was determined by the dominant's experience in

the moments immediately preceding the competition. The four conditions were thus:

Competitor Uninformed: The dominant's door remained closed as one piece of food was placed on the subordinate's side of one of the two occluders.

Control Uni (competitor informed): The dominant's door was cracked as one piece of food was placed on the subordinate's side of one of the two occluders. (The subjects could thus see one another looking.)

Competitor Misinformed: The dominant's door was open as one piece of food was placed on the subordinate's side of one of the two occluders (subjects could thus see one another looking). Then the dominant's door was closed, and after 5-10 seconds, the food was moved to the subordinate's side of the second occluder.

Control Mis (competitor informed): The dominant's door was cracked as one piece of food was placed on the subordinate's side of one of the two occluders (subjects could thus see one another looking). Then, after 5-10 seconds and while the dominant watched (and subordinate could see this), the food was moved to the subordinate's side of the second occluder.

In each condition, the subordinate's door was open 15 cm. throughout the hiding process. In each condition, competition began with the subordinate's door being raised, giving her a small headstart and thus forcing her to make a choice before she could observe the dominant making her choice (as in Hare et al., in press, this was done to eliminate the possibility that the subordinate was simply reacting to the dominant's behavior in the middle cage). The dominant's door was raised at the moment the subordinate's hand first touched the floor of the middle cage. (If the subordinate had not entered the cage after 30 seconds, the dominant was allowed to enter.) In each condition, the dominant's door - regardless of whether it had been open before - was closed at the moment the competition began (as in Hare et al., in press, this was done to make sure that the subordinate was not influenced by seeing where the dominant was looking at the moment she made her choice).

In order to make certain that this procedure did not make the subordinates overconfident (i.e., assume they could go for the food indiscriminately since they had a headstart) two probe trials per session were included (randomly interspersed). In these probe trials the dominant's door was cracked and the piece of food was placed near (as opposed to on the subordinate's side of) one of the occluders, and both animals were released simultaneously.

Scoring and Data Analysis

In each trial E1 and E2 decided together which subject obtained the piece of food. As in Hare et al., (in press), this determination was completely unambiguous in every case, and so reliability assessments were deemed unnecessary. Analyses focused in all cases on the subordinate. Because different individuals were subordinate to different numbers of other individuals, different individuals participated as subjects in different numbers of trials. Consequently, each individual was given a single score in each condition by computing a proportion. For example, a given subject might be paired with three different dominants, giving her 12 trials in each condition. In this case she would receive a score out of 12 (e.g., 6/12 or .50) for each condition. Nonparametric statistical tests were used in all cases; tests were one-tailed unless indicated otherwise.

Results

Figure 2.2 presents the percentage of food pieces obtained by subordinate subjects in all four experimental conditions. Pairwise comparisons were made between the Uniformed condition and its control and the Misinformed condition and its control. As predicted, subordinate subjects retrieved a significantly larger percentage of food when dominants lacked accurate information regarding the location of food. The Wilcoxon test for Uninformed vs. Control was $T=36, N=8, P<.006$; for Misinformed vs. Control the Wilcoxon test was $T=36, N=8, P<.006$). In none of the experimental conditions was

there a difference across sessions - arguing against learning as a major factor. The Friedman tests were: Uninformed $\chi^2_2=2.1$, N=9, NS; Control Un $\chi^2_2=1.17$, N=9, NS; Misinformed $\chi^2_2=.83$, N=9, NS; Control Mis $\chi^2_2=3.9$, N=9, NS (all tests two tailed).

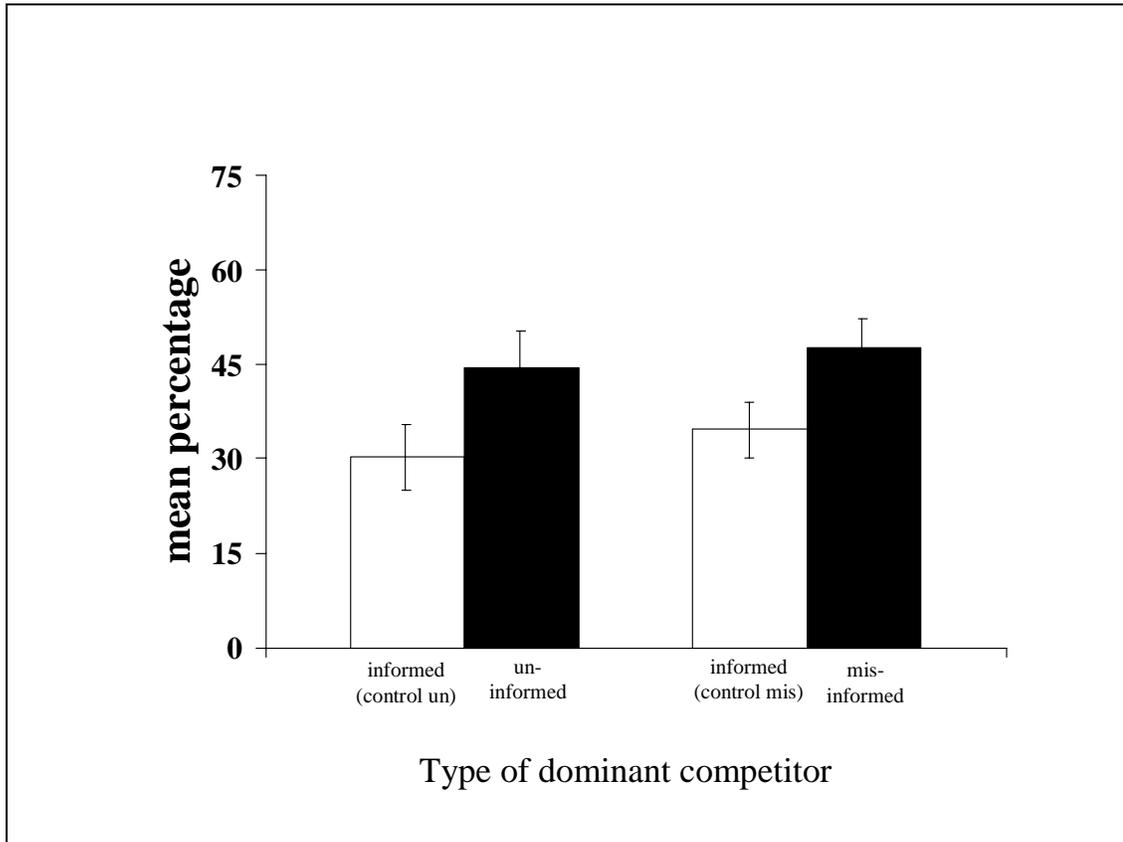


Figure 2.2. Mean percentage (\pm SEM) of pieces of food obtained by subordinate subjects in each of the four test conditions as a function of what the dominant competitor witnessed during baiting in Study 1.

The percentage of trials in which subordinates chose not to enter the baited cage was used as an additional measure to determine whether subjects' showed sensitivity to what their competitor had or had not seen during baiting. If subjects were sensitive to

their competitor's visual access, it would be expected that they would refrain from entering the cage more often during the two control conditions in which dominants knew the location of the food. Figure 2.3 presents the percentage of trials in which subjects chose not to approach in each test. Pairwise comparisons revealed that subordinate subjects chose to remain in their own cage significantly more often in the control conditions than in their respective experimental conditions (Wilcoxon test: Uninformed vs. Control Un $T=33.5$, $N=8$, $P<.015$; Misinformed vs. Control Mis $T=10$, $N=4$, $P<.034$).

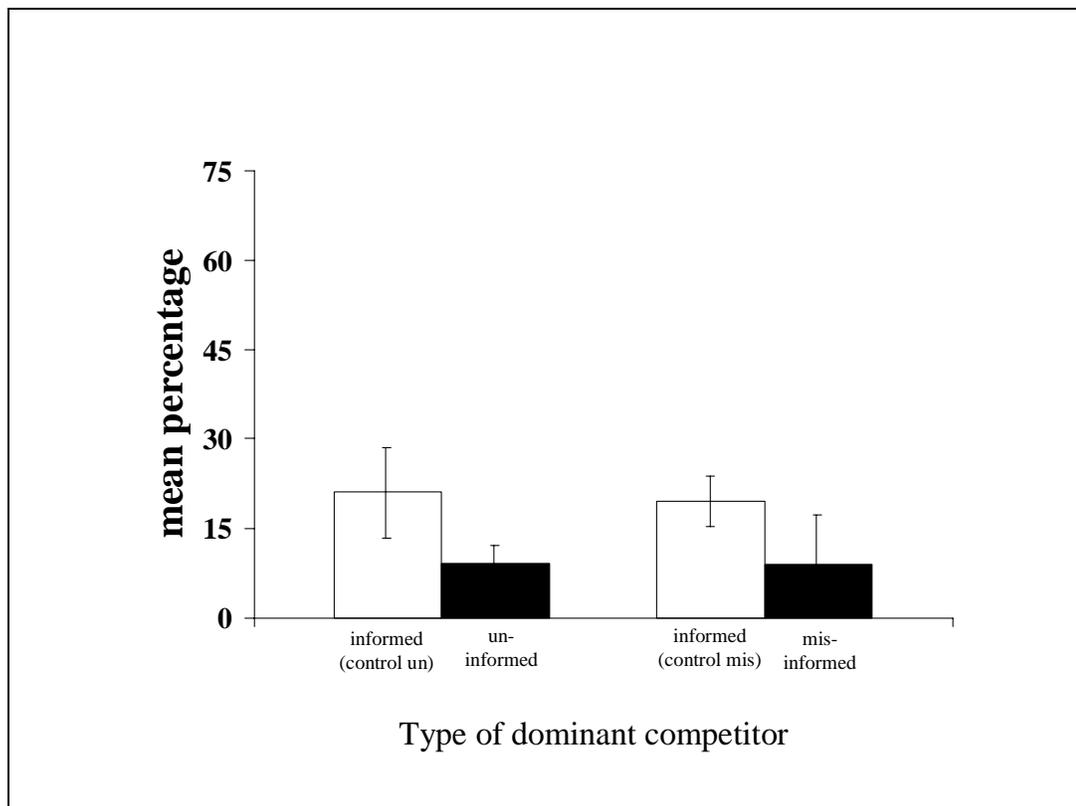


Figure 2.3. Mean percentage (\pm SEM) of trials subordinate subjects chose not to approach in each of the four test conditions as a function of what the dominant competitor witness during baiting in Study 1.

Finally, we assessed whether dominant competitors behaved differently depending on their experience, for instance, by approaching less when they had not seen food. There were no significant differences between experimental and control conditions in either the informed-uninformed (Wilcoxon test: $T=20.5$, $N=7$, NS, two tailed) or the informed-misinformed test (Wilcoxon test: $T=7$, $N=4$, NS, two tailed). Overall, dominants did not approach during 11% of the experimental trials compared to 7.6% in control trials.

Discussion

It is important to emphasize that in this study the perceptual situation facing the subordinate when she made her choice was exactly the same in all four experimental conditions: she could see two barriers, a piece of food on her side of one of them, and a closed door across the room. What was different was what she had experienced leading up to that moment of choice. In the two control conditions she had witnessed the dominant looking under the door as food was being either hidden or moved to a new location, whereas in the two experimental conditions she had witnessed only the dominant's closed door as food was either hidden or moved to a new location. What subordinates then chose to do was clear: they chose to go for the food more often, and they obtained it more often, when their dominant competitor had **not** seen it hidden or moved. The most obvious interpretation of this differential behavior is that the subordinate knew from its experience of the hiding process in each experimental condition whether or not her dominant competitor had seen, as she had seen, where the food had been placed.

These results are not easily explained by any kind of learning explanation since the subjects' performance did not change in any detectable way over the four sessions. This means that whatever information subordinates gained by watching the hiding process - and monitoring the dominant's visual access during the hiding process - involved something deeper than any kind of simple discriminative cue. These results also cannot be easily explained by any kind of behavioral cueing. At the time of the subordinate's choice the dominant's door was closed and so there were no behavioral cues to be seen - and the subordinate had to make her choice before the dominant's door was opened. Indeed, some subordinates on some trials in the control conditions (when the dominant had seen the hiding or moving) chose to stay in the cages for the entire 30 seconds, simply staring across at the dominant's closed door. Another possibility is that subordinates may have learned over trials that the dominant's behavior varied between conditions. For example, subordinates might have learned that dominants were less likely to approach if they had not seen the entire baiting. This hypothesis, however, was not supported by the data because dominants approached on a comparable number of trials in all conditions.

But there is one other hypothesis (and a corollary) that must be addressed. The hypothesis is that during the hiding process the dominant looked intimidating as the food was being hidden - in those conditions in which she saw food being hidden - which made the subordinate timid about going for the food at the time of choice. We may call this the intimidation hypothesis. This hypothesis has some plausibility for the comparison between the Uninformed condition and its associated control condition, since in the control condition the subordinate witnessed the dominant witnessing the hiding (and thus

had the opportunity to be intimidated) but this was not the case in the Uninformed condition (when the dominant's door was closed throughout). So, under the intimidation hypothesis, the subordinate should go for the food in the control condition but not in the Uninformed condition, and this is exactly what they did. The problem, however, is that this hypothesis cannot explain the difference between the Misinformed condition and its associated control condition. Subordinates witnessed dominants witnessing the hiding process in both of these conditions, and so they should have been equally intimidated in both. But this was not the case, as they went for the food more often in the Uninformed condition. So this alternative hypothesis will not work.

A corollary hypothesis is as follows: when the dominant witnesses the hiding she watches the food and then acts intimidating towards the place she saw it disappear; that is to say, by staring at it she marks it as 'mine'. On the surface, this hypothesis has some plausibility since subjects tended to avoid the food that the dominant saw hidden in the Mis Control, and they tended to go for the food in the new location after it had been moved in the Misinformed condition - a location that the dominant could not have looked at intimidatingly since no food was ever placed there while she was looking. The problem in this case is that Hare et al. (in press; Study 4b) were also concerned with this hypothesis and so ran a control study designed specifically to test it. They set up a situation in which the dominant could see the food but the subordinate could not (the food was on the dominant's side of one of the occluders), and they then released the subordinate into the middle cage to see if something in the dominant's behavior might serve to either attract or repel her to the location of the hidden food. The finding was that the subordinates chose randomly, apparently being neither intimidated nor attracted by

anything the dominant was doing in the direction of the food (see also Itakura et al., 1999).

Study 2: Who saw it hidden?

In the previous study subordinate chimpanzees behaved differently depending on what their dominant competitor had or had not seen during baiting. If their behavioral choices in that study were indeed a reflection of an underlying social-cognitive strategy, as opposed to some simple learned cue, then we would expect them to be able to use this strategy in a flexible manner in novel situations - and without taking numerous trials in the new situation to adapt. In this second study, therefore, we presented subordinates with a novel situation that required them to adjust their strategy. As in the two control (informed) conditions of the first study, food was placed on the subordinate's side of one of two occluders and the subordinate witnessed both the baiting procedure and her dominant competitor's witnessing of the baiting procedure. The critical manipulation was that on some trials, after the dominant had witnessed the baiting, she was switched for a new dominant individual. This new individual had been out of the experimental area completely when the baiting took place, and so could have no information about where the food was hidden. If chimpanzees have some understanding of what others have seen, as suggested by the previous study, then they should very quickly show a tendency to go for the food more often when they compete against a new (uninformed) dominant rather than the old (informed) dominant.

Methods

Subjects

Twelve adult and subadult chimpanzees (mean age = 20.1) participated in this study (see Table 1). Eight of the 12 subjects were used as subordinates and contributed to

the data set. Two of those eight subordinates had not participated in Study 1.

Procedure

In this study each of the eight subordinate individuals were tested with a pair of dominant competitors (i.e., not all combinations were used). Each subordinate participated in two sessions of four trials (for a total of 8 trials per subject). Within each session a subordinate competed against each of its two dominant competitors twice. In one condition (No Switch) the subordinate competed against the dominant who had witnessed the baiting, whereas in the other condition (Switch) she competed against the dominant who did not witness the baiting. Each subject alternated between experimental conditions, with the nature of the initial condition counterbalanced across subjects. All testing was completed within one week.

We used the same general food competition paradigm of Study 1 (Uninformed vs Un Control). In this case, however, there were two dominants (D1 & D2) who were housed separately in two adjoining cages on one side of the middle cage, with the subordinate in the cage on the other side of the middle cage. The layout of the occluders and placement of food were as in Study 1 (see Figure 2.1).

For each trial, a subordinate subject witnessed food being placed on her side of one of two occluders, and she witnessed a dominant witnessing this hiding also (as in the two control conditions of Study 1). After the food was hidden, the dominant's door was closed and there was a 90-second delay. What happened during this 90-second period depended on experimental condition:

Switched Competitor: During the 90-second period experimenters switched D1 for D2, the naive dominant who was in the adjoining cage. Then the dominant's door was cracked again 15 cm to show the subordinate that D1 was no longer present and that D2 (who did not witness the baiting) was now her competitor.

Same Competitor (control): D1 remained in her cage during the 90-second delay, and

then her door was cracked again 15 cm to show the subordinate that D1 (who had witnessed the baiting) was still her competitor.

After the subordinate had been shown her competitor, the dominant's door was closed and the subordinate was released while the dominant competitor's release was delayed until the subordinate began to enter the cage (as in Study 1). If the subordinate did not enter the cage within 30 seconds, the dominant was released (as in Study 1). Scoring and analysis were identical to those used in Study 1.

Results

Figure 4 presents the percentage of food pieces obtained by the subordinate subjects in each of the two conditions. As predicted, subordinate subjects retrieved a significantly larger percentage of food when they competed in the Switched condition, that is, with a competitor who they knew had not seen the baiting (Wilcoxon test: $T=36$, $N=7$, $P<.004$). Importantly, there were no significant differences in subject performance across the two sessions in either condition (Wilcoxon test: Same Competitor $T=18$, $N=6$, NS; Switched Competitor $T=8.5$, $N=5$, NS, two-tailed in both tests).

We also looked at subjects' tendency to approach the food in order to determine whether they were showing sensitivity to which dominant competitor they were facing. Due to the small number of trials involved, we scored as 'no approaches' those cases in which subjects entered the cage but did not cross the halfway line between the door and the occluders (there was a line drawn across the floor of the cage to help E's make this determination). Five subjects remained behind the halfway point more often in the Same Competitor condition while only one subject remained behind the line more often in the Switched Competitor condition (Wilcoxon test = NS). As was the case in the previous study, there were no significant differences in the dominants' approach behavior across conditions (Wilcoxon: $T=10$, $N=4$, NS, two tailed).

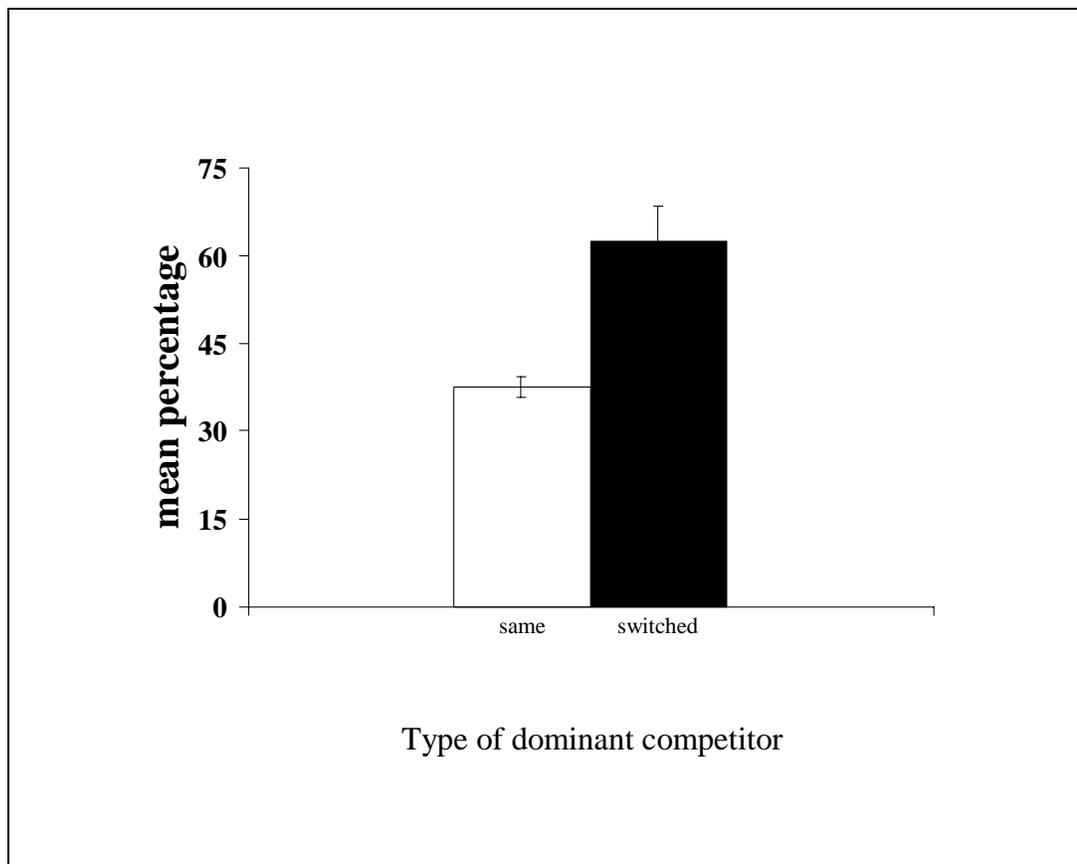


Figure 2.4. Mean percentage (\pm SEM) of pieces of food obtained by subordinate subjects in both of the conditions in Study 2 as a function of what the dominant competitor witnessed during baiting.

Discussion

The results of this study corroborate and extend those of Study 1. Again in this study subordinates were more likely to approach and retrieve food when their dominant competitor had not witnessed its placement. This finding is especially robust since all subjects showed the same response pattern immediately. Therefore, whatever subjects from Study 1 might have brought with them into this experiment, they quickly were able to adapt it to this completely novel situation (this study thus represents a case of successful triangulation in the terms of Heyes, 1993). In this regard, it is also important to note that both new subjects who did not participate in Study 1 also showed a

preference for retrieving food in the Switched Dominant condition. Again in this study, learning explanations cannot account for preferences since there were no differences between the two rounds for either condition. Also, the results of this study provide a kind of generalized control for the results of Study 1, since they in effect rule out the possibility that chimpanzees automatically responded to certain spatial and temporal arrangements of the baiting procedures in that study - since in this second study the exact same arrangements and procedures led to different results, the only difference being the personal identity of the competitor.

Perhaps most importantly, this study extended the results of the previous study by showing that chimpanzees can keep track of which individuals have witnessed a significant event and which individuals have not. It thus seems that chimpanzees have no trouble in combining their well-attested ability to recognize individuals (see Tomasello & Call, 1997, for a review) with their social cognitive skill of determining whether someone has or has not witnessed an important event. It is perhaps worth noting that apparently subordinates in our study did not think that the two dominants had exchanged information during the 90-second delay (initially suggested by Menzel, 1973), although this hypothesis might be better tested in a different experimental arrangement.

Study 3: Which piece did she see hidden?

The previous two studies are consistent with the hypothesis that chimpanzees are able to recognize and take advantage of what others have or have not seen. The current study was designed to further examine the flexibility of this ability. In the current study subordinates were required to remember what a dominant competitor had witnessed during the baiting of *two* pieces of food. In this study, subordinates always witnessed the baiting of both pieces of food, but dominants only saw one piece of food being hidden while she was either Uninformed or Misinformed about the location of the second piece of food. It was predicted that subordinates would preferentially retrieve those pieces of

food about whose location the dominant competitors were either Uninformed or Misinformed.

Method

Subjects

Twelve adult and subadult chimpanzees (mean age = 20.9) participated in this study (see Table 1). Nine of the 12 subjects were used as subordinates and contributed to the data set. The other four were only used as dominants to obtain data from the 9 subordinate subjects. All possible combinations of subordinate and dominant animals were tested except Natasha-Borie and Tai-Ericka because they were equally dominant (Natasha was a subordinate and was tested twice with the next highest ranking female instead). In addition, a new subject (Bjorn) was used as a dominant for Peony only (the highest ranking female in group 1 who had never played the role of subordinate in any experiment). These combinations created a total of 27 dyads.

Procedure

In this study, each dyad was tested in two sessions, each of which contained six experimental trials (a total of 12 trials per dyad), with 2 probe trials in each session as well. As in Study 1, order of conditions was counterbalanced across dyads within each session separately. All testing was completed within two weeks.

Subjects were tested in the same general food competition paradigm and the same general experimental conditions as in Study 1. The difference was that we used what we called 2-piece versions of each condition. That is to say, whereas in the first study the subject had to decide in each condition whether or not to go for the one piece of food, in this study we arranged it so that there were always two pieces of food and the dominant sometimes saw only one of them either hidden or moved. The subject then had to choose in every trial which of two pieces of food it should go for. As in Study 1, the

subordinate was able to witness all baiting procedures in all conditions. The four conditions were thus:

Competitor Uninformed: The dominant's door was cracked and the experimenter placed one piece of food on the subordinate's side of one of the two occluders. Then the dominant's door was closed and a second piece of food was placed on the subordinate's side of the other occluder.

Control Un (competitor informed): The dominant's door was cracked as first one piece of food was placed on the subordinate's side of one of the two occluders, and then a second piece of food was placed on the subordinate's side of the other occluder.

Competitor Misinformed: The dominant's door was cracked and both pieces of food were hidden on the subordinate's side of one of the two occluders (both behind same occluder). Then the dominant's door was closed. Then, after 5-10 seconds, one of the pieces of food was moved to the subordinate's side of the other occluder.

Control Mis (competitor informed). The dominant's door was cracked and both pieces of food were hidden on the subordinate's side of one of the two occluders (both behind same occluder). Then, after 5-10 seconds, one of the pieces of food was moved to the subordinate's side of the other occluder while both chimpanzees were watching.

All of the other procedures were as in Study 1, in particular the subordinate was always given a small headstart and the dominant's door was always closed at the time of her choice. Scoring and analysis were identical to those used in the previous studies. Again to guard against counterproductive learning strategies, we used probe trails (two per session, randomly interspersed). The probes were designed to solve the problem that was created by the fact that in all four experimental conditions both barriers were baited. If these were the only conditions, the baiting procedures could have become irrelevant for subjects since they could never choose incorrectly (unlike study 1 and 2). Therefore, two types of probe trials were used, one in which both subjects watched as only one piece of

food was hidden on the subordinate's side of a barrier and one in which both subjects watched as two pieces were hidden on the subordinate's side of one of the barriers.

Results

In this study, subordinates did not retrieve more food in the conditions in which the dominant had no knowledge of one piece's location (Wilcoxon test: Competitor Uninformed vs Control Un T=22, N=7, NS; Competitor Misinformed vs Control Mis T=14.5, N=7, NS, Figure 2.5). Of crucial importance was which piece of food subordinates retrieved within each of the two types of experimental conditions (i.e. the one the dominant had seen hidden or the one she had not seen hidden). Subordinates showed no preference in this regard in either the Uninformed (Wilcoxon test: T=18.5, N=7, NS, Figure 2.6) or the Misinformed condition (Wilcoxon test: T=11, N=5, NS, Figure 2.6), although the difference is in the predicted direction in both cases.

As in the other studies, we also analyzed subordinate approaches. The results were mixed. As predicted, subordinates chose not to approach significantly less often in the Misinformed condition (3.2%) as compared with the Control Mis (12.5%), Wilcoxon test: T=14, N=5. On the other hand, there were no significant differences between the Uninformed condition and the Un Control in how often subjects chose not to approach (Wilcoxon test: T=5, N=3, NS; Uninformed=2.5%, Control Un=7.4%,). We also assessed approaches using the 'halfway to the food' criterion of Study 2. No significant difference were found in subjects' tendency to approach pieces of food that their dominant competitor either had or had not seen.

In this study the approaches of dominants after release may be relevant to the behavior of subordinates. From the very beginning of the study we noticed that a number of dominants were using a completely new strategy against subordinates. Regardless of what they had seen during baiting, dominants began to approach the occluder that subordinates approached first (effectively "shadowing" the subordinates' movements).

Therefore, throughout this study we recorded in which trials dominants shadowed subordinates. Out of the 10 subjects who played the role of dominant 8 females frequently shadowed while 2 males never did. Dominants shadowed in 34% of trials, with the mean rate of shadowing by the 8 females being 43% of trials (ranging from 19% to 88% of trials).

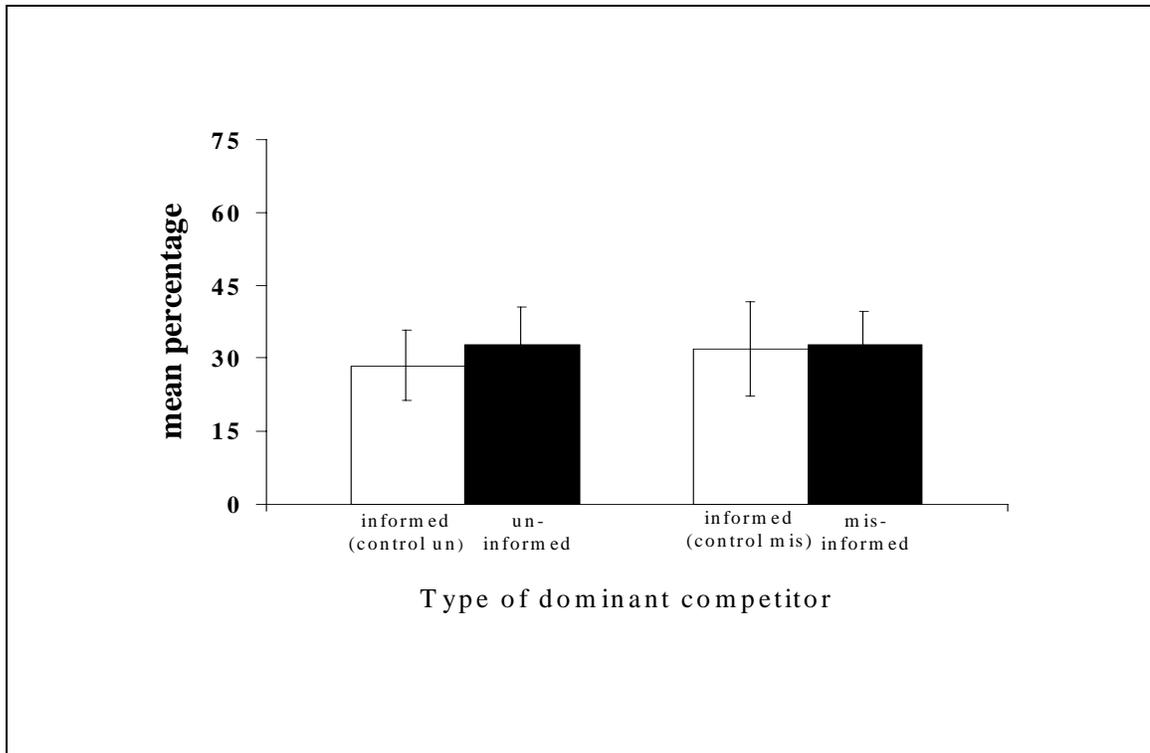


Figure 2.5. Mean percentage (\pm SEM) of pieces of food obtained by subordinate subjects in each of the four test conditions in Study 3 as a function of what the dominant competitor witnessed during baiting.

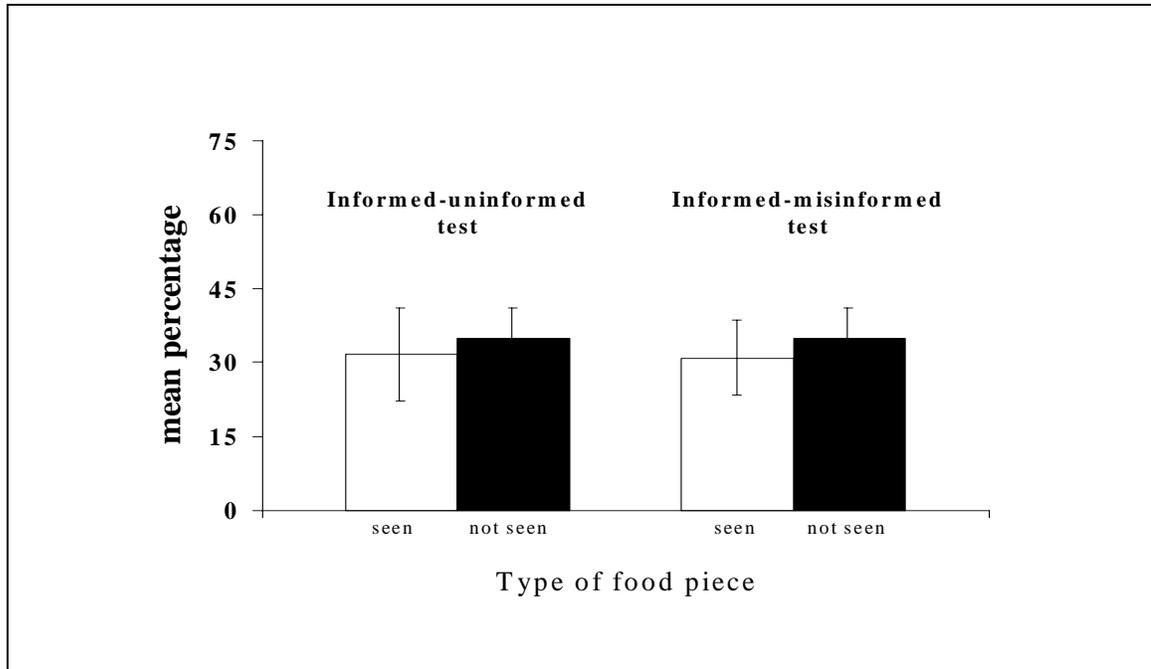


Figure 2.6. Mean percentage (\pm SEM) of pieces of food obtained by subordinate subjects in within both types of experimental trials in Study 3 as a function of what the dominant competitor witnessed during baiting.

Discussion

Unlike the previous two experiments, in this study there was little evidence to support the hypothesis that subordinates were sensitive to what dominants had seen during baiting. Only subordinates' tendencies to approach less in the Control Un condition (when dominants witnessed both pieces of food being hidden) were consistent with the previous findings. These inconsistent results might be explained in one of three ways.

First, it is possible that chimpanzees do not have the ability to know what others have and have not seen and to judge how this might affect their behavior, and this study simply reflects the lack of this skill. To maintain this hypothesis we would have to claim that the current study is somehow a better test of chimpanzee social-cognitive skills than the first two studies; we might base this judgement on the fact that in this study

chimpanzees had to make an active choice between two courses of action rather than simply deciding to go or not to go, as in the first two studies. It seems unlikely to us, however, that this study is the more valid one; rather, it is more likely that this study created additional problems for the chimpanzees unrelated to their social-cognitive skills - either procedural difficulties that required them to use other strategies or information processing demands that overloaded their non-social cognitive abilities.

The second possibility is thus that the addition of the second piece of food changed the incentive structure for the competitors. Since there was food behind each of the barriers on each experimental trial, it is possible that the competitive dimension of the situation was too greatly diminished. In anticipation of this problem, probe trials were used, but it is very possible that there were too few probes or that they did not work as planned. Some evidence for this possibility is the fact that subordinates retrieved the majority of food in both types of probe trials (54% overall) - presumably because they had learned over all the experiments to use their head start more effectively - and so it is possible that dominants may not have been rewarded enough in these probe trials for them to have an impact on their own retrieval behavior. A related problem was the shadowing strategy that many dominants developed. Although this strategy might also have been successfully used in the previous studies, in fact it was not (we did not code for it systematically in previous studies simply because it was not present); presumably it was learned over time by some individuals as an 'easy' way to get food. The problem shadowing creates, of course, is that if subordinates are going to be shadowed potentially every trial, it matters very little which occluder they go for when trying to avoid the dominant - what dominants did or did not see was, in effect, irrelevant since it did not affect their behavior.

Finally, chimpanzees' behavior in this study may reflect an inability to keep track of what others have seen with respect to two significant events; this may simply be an information overload that reflects a genuine cognitive limitation but not a limitation in

judging what others have and have not seen. In this regard, note that in the traditional 'change location' false belief tests commonly used with human children (Wimmer & Perner, 1983), subjects need only track another person's belief about a single object – the same as in Study 1 and 2. It is also possible that chimpanzees can track what their competitor has seen when two objects are hidden, but simply cannot organize this amount of information in a way that enables them to integrate it into their behavioral strategy.

It would clearly be a strong addition to the current findings to have a valid study in this general food competition paradigm in which the subject has to make an active choice between two pieces of food - one whose location she knows the competitor knows and one whose location she knows the competitor does not know. However, our conclusion for the moment is that this set-up in its current form is not a valid test - since it changes the incentive structure of the competition and may, in addition, place excessive information processing demands on subjects. Constructing a valid 2-piece choice version of this task thus remains a goal for future research.

General Discussion

The current results represent the clearest demonstration to date that chimpanzees know what their individual groupmates do and do not 'know', that is, what individual groupmates have and have not seen in the immediate past. Other experimental approaches have either found negative results or else have found positive results only after extensive training (e.g., Povinelli et al., 1990, 1994; Call et al., in press; Call & Tomasello, 1999). The reason that we were more successful than previous investigators is that we succeeded in finding an experimental situation that, unlike previous experimental situations, did not require chimpanzees to communicate with humans about the location of a monopolizable food resource (which is a very unnatural situation for them) or to be trained in how to behave in a novel task. With no training or human intervention, chimpanzees demonstrated their social-cognitive skills in a food

competition situation among themselves. Our failure to find positive results in Study 3 - requiring the subjects to compete over 2 pieces of food, only one of whose locations was mutually known - has a ready explanation in terms of the different behavioral strategies that this set-up engendered in the dominant competitor (and perhaps the extra information processing load it placed on the subordinate competitor).

The two tasks of Study 1 bear some resemblance to tasks that have been used with human children and considered as indicators that children understand that: (1) seeing leads to knowing, and (2) other persons can have false beliefs (Flavell, 1997). But ours are nonverbal tasks and so their interpretation is more difficult; we therefore prefer to remain cautious. From this cautious perspective, here is what we believe the current studies, in combination with other recent studies, demonstrate:

- Chimpanzees know what other individuals do and do not see. Thus, they reliably follow the gaze direction of others (Tomasello et al., 1998); they do this around barriers and past distractors (which suggests that they are doing much more than just using head direction as a discriminative cue; Tomasello et al., 1999); and they reliably use information about what conspecifics can and cannot see in a food competition situation (even involving knowledge that transparent barriers do not block the visual access of others; Hare et al., in press).
- Chimpanzees can recall what a conspecific has and has not seen in the immediate past (current Study 1), and this recall is associated with specific individuals (Study 2).
- Chimpanzees integrate this recall about what specific individuals have and have not seen into their behavioral decision making in competitive situations (Hare et al., in press, and current studies).

For some theorists, this profile is just another way of saying that chimpanzees know what others know. But the word 'know' is a multi-faceted word, and our view is that the current results demonstrate that chimpanzees know about some aspects of what others know, but perhaps not about other aspects. The problem is that in

many theoretical discussions of these issues, only two alternatives are presented: chimpanzees either have a 'theory of mind' like humans' (they engage in mental state attribution) or they simply learn by blind behavioristic conditioning (e.g., Byrne, 1995; Heyes, 1998). But we believe that there is a middle ground, what we have called 'an explanation of the third kind' (Tomasello & Call, 1997; Call & Tomasello, in press). This third way recognizes the widely accepted fact that chimpanzees do much more than associate experiences with one another blindly when they are interacting with the physical world, and then extends this recognition to their understanding of the social world. Just as chimpanzees have insight into some physical problems, which enables them to develop intelligent problem-solving strategies involving tool use and the like, so they have insight into some social problems, which enables them to develop intelligent problem-solving strategies in this domain as well. But this does not necessarily mean that chimpanzees have human-like social-cognitive skills ('theory of mind') in which they understand such things as: (i) others can have different perspectives on the same object I am now perceiving (e.g., from a different angle); (ii) I can simulate the visual experience of others by imagining how I would see things if I were in their place; and (iii) others have beliefs about things that may differ from my own and from reality. Indeed, chimpanzees show no evidence of such human-like, social-cognitive understanding in a variety of other studies of their social cognition (see Tomasello & Call, 1997, for a review).

One way of summarizing our third way hypothesis is to say that chimpanzees are able to engage in Level 1 perspective-taking (knowing that others can see things that I cannot and vice versa) but not Level 2 perspective-taking (knowing precisely what others see, including that they see the same thing I do but from a different perspective). In the current task, for example, they may simply employ a 'rewind strategy'. That is, they notice what their competitor sees and does not see as food is being hidden, and then, when the moment of decision comes, they 'rewind the tape' and act as if the competitor

were currently looking at the scene. In this view, chimpanzee social cognition is based on a representational understanding of the behavior of others, which permits them to do things like remember, foresee, and communicatively manipulate the behavior and social relationships of others. This cognitive machinery then enables them to react appropriately in social situations, and also to predict and influence their groupmates' behavior in novel situations. But these skills are not unlimited. Chimpanzees do not recognize certain kinds of intentional or mental states, and they may have trouble in developing strategies in situations in which they must use their knowledge to imagine what another might see in some totally novel situation. For example, in the current study it is unclear what subordinates would do if they were given the opportunity to manipulate a barrier so that it could either block the dominant's view or not (in a way reminiscent of some anecdotal reports of primate deception; Byrne & Whiten, 1988). The main point is that we should not be focused on the yes-no question (Do chimpanzees have a theory of mind?), but rather we should be focused on a whole panoply of more nuanced questions concerning precisely what chimpanzees do and do not know about the psychological functioning of others.

Although extremely informative, previous studies that have asked chimpanzees to demonstrate their social-cognitive skills by communicating with humans, often in a task that requires much training, are apparently asking too much of them. They require chimpanzees to comprehend the communicative intentions of others, and they are asking them to do this in a situation in which, for them, competition is a much more natural mode of interaction. Most chimpanzees probably go their whole lives without having anyone altruistically point out for them the location of a monopolizable piece of food right in front of the both of them (Hauser & Wrangham, 1987; Hauser et. al, 1993). Evolutionary theories of primate cognition stress the fact that primates exist within a complex social field and must constantly find new ways to compete against other individuals intent on reaching their own goals - or else they will not survive long enough

to pass on their genes (Humphrey, 1976, 1981; Krebs & Dawkins, 1984; Byrne & Whiten, 1988). It is therefore likely that primate social-cognitive abilities evolved to a large degree to allow individuals to outcompete competitors, and so it is in these kinds of settings that we are most likely to see these abilities expressed.

It is interesting to note in this regard that domestic dogs have been under a completely different regime of selective pressures, which may have encouraged more skills of cooperation and communication with others, especially humans. They thus perform very well - better than primates - in the Object Choice task in which they must learn to read human behavior as humans attempt to communicate to them about the location of a hidden, monopolizable food resource (Miklosi, et. al., 1998; Hare & Tomasello, 1999; Hare, Call, Tomasello, in press). In attempting to design ecologically valid experiments of primate cognition and social cognition, therefore, we (including ourselves) must always attempt to take into account not only their current behavioral skills and propensities but also the likely functional contexts within which their cognitive abilities have evolved.

*Part III: Do capuchin monkeys (Cebus apella) know what conspecifics do and do not see?*²

Introduction

A number of experimental studies have addressed the question of whether nonhuman animals have an understanding of how the visual perception of others works and affects behavior. In the hopes of drawing inference about human social cognitive evolution, the vast majority of these studies have focused on nonhuman primates (Tomasello & Call, 1997; Povinelli, 2000). For example, several experiments have examined whether apes understand that in order for another individual to see them the individual must maintain a certain posture (i.e. the other individual must be present, facing the subject with their eyes open, and oriented toward the subject) (Tomasello et al, 1994; Call & Tomasello, 1994; Povinelli & Eddy, 1996). In addition, following work on the development of visual perspective taking in children, experimentalists have also investigated whether any primate species has the ability to assess what another individual can and cannot see (so-called Level 1 understanding of another's visual perspective; Flavell, 1992).

It has been difficult to demonstrate something approaching Level 1 visual perspective taking in primates. For example, investigators have shown that a number of primate species follow the gaze of another individual, raising the possibility that primates

² Reprinted from *Animal Behaviour*, 65, Hare, B., Addessi, E., Call, J., Tomasello, M. & Visalberghi, E., Do capuchin monkeys (*Cebus apella*) know what conspecifics do and do not see?, 131-142, Copyright (2001), with permission from Elsevier.

understand that their groupmates see things that they do not (Povinelli & Eddy, 1996; Emery et al., 1997; Tomasello et al., 1998). However, studies have just begun specifying the mechanism underlying primate gaze following, making it unclear whether gaze following represents a case of visual perspective-taking (Povinelli & Eddy, 1996; Tomasello et al., 1999; 2001). There have been other paradigms designed to explore the visual perspective-taking abilities of primates as well, but studies that have produced positive results are potentially explained by simple learning hypotheses (Heyes, 1993; 1998) while experiments producing negative results have been criticized for lacking ecological validity (Gomez, 1996; Tomasello & Call, 1997; Matheson et al., 1998; Shettleworth, 1998; Hare, 2001).

Recently, Hare et al. (2000) devised a new test to examine whether chimpanzees know what other chimpanzees do and do not see. Two individuals, one dominant to the other, were placed in rooms on opposite sides of a test room where food was positioned in different ways. They were then released into the test room to retrieve the food. For example, two pieces of food were placed between the subjects so that one of the subjects could see both and the other could only see one of the food pieces (the food was hidden behind a small occluder). This paradigm was designed to help answer two questions: 1) are chimpanzees able to judge when another chimpanzee has visual access to food? 2) if they can assess when another individual cannot see food, can they use this information to develop a strategy for retrieving the food when competing against a conspecific? Initial results showed that if the food was placed so that one of the pieces of food was hidden from the dominant, subordinates preferentially retrieved the hidden food. In addition, if

the food was placed so that one of the pieces was hidden from the subordinate, dominants preferentially retrieved the at-risk visible piece first before retrieving the hidden piece.

Although these results were consistent with visual perspective-taking, it was possible that subjects were responding to behavioral cues given that the chimpanzees were released simultaneously. Therefore, in follow up studies subjects were released asynchronously with one subject given a slight head start over the other. This delay procedure forced subjects to decide which of the two pieces to approach before they saw where the competitor would go. Results were identical to the previous studies. Subordinates again preferred to approach and retrieve hidden food while dominants approached and retrieved at-risk visible food first. Moreover, several controls were run to rule out a number of other competing hypotheses. From these results, Hare et al. (2000) conclude that chimpanzees know what conspecifics do and do not see and that they can use this information to formulate effective social strategies. These findings and conclusion have since been corroborated by other studies using similar competitive paradigms (Hare et al., 2001; Hirata & Matsuzawa, 2001).

Although these results make it likely that our last common ape ancestor was able to assess what their conspecifics can see (at least in some situations) and use this knowledge to their advantage, further studies are needed to investigate the phylogenetic origins of this ability. For example, do the abilities of chimpanzees reflect general primate, or even mammalian, social cognitive abilities (i.e. potentially shared through common descent)? Alternatively, is the ability to assess what another individual can see a derived trait existing only within the hominoid clade?

The findings of a number of social cognitive studies in monkeys could be considered as consistent with the hypothesis that chimpanzees share the ability to assess what conspecifics can see with a number of monkey species (Byrne & Whiten, 1990; Coussi-Korbel 1994; Hauser, 1997; Kuroshima et al, 2002; Fujita et al, 2002) However, a number of studies are consistent with the hypothesis that monkeys do not understand how the visual perception of others works (Povinelli et al, 1991; Cheney & Seyfarth 1990b; Rendall et al, 2000; Kummer et al. 1996)

In light of previous research, the primary goal of the current investigation is to address the current discrepancy in the literature on primate visual perspective-taking. Although there is relatively little evidence to support the position that monkeys perform differently than apes in social cognitive tasks (Tomasello & Call, 1997), Hare et al., (2000) suggests that chimpanzees can assess what conspecifics can and cannot see, while there remains little compelling evidence that monkeys also have this capacity. Is the discrepancy due to the fact that monkeys, as with chimpanzees, are most likely to demonstrate their perspective-taking abilities when competing against conspecifics for food (as in Hauser, 1997 and Fujita et al., 2001), or is the difference between chimpanzees and monkeys real, and perhaps even an indication of different selective pressures on cognitive abilities?

To address these question, we attempted a replication of Hare et al (2000), using capuchin monkeys (*Cebus apella*), a species whose cognitive abilities are commonly compared with those of chimpanzees (Visalberghi & McGrew, 1997). Capuchin monkeys, as Platyrrhines, represent relatively distant relatives to the hominoids, with New World monkeys separating from Catarrhines approximately 40-45 million years ago

(Klein, 1999). Therefore, capuchin monkeys are an excellent test species for investigating both 1) the origins of visual perspective-taking in primates 2) the utility of the Hare et al. (2000) method for further comparative studies. If capuchin monkeys know what conspecifics do and do not see while competing for food, it is possible this ability evolved as early as 40 million years ago before the New-Old World split and that this form of visual perspective taking is common among many monkey species throughout the primate order. In addition, if the Hare et al. (2000) competitive paradigm can be used with capuchin monkeys successfully, it is likely it can be used with a number of other primate and nonprimate species in order to test further evolutionary hypotheses.

Experiment 1

Experiment 1 was designed to assess whether 1) capuchin monkeys have a strict enough foraging-hierarchy for our competitive test and 2) If capuchin monkeys readily compete over monopolizable food, are they strategic in their attempts to out compete competitors? We predicted, as subordinates, that capuchins would prefer to approach and retrieve hidden food that dominant competitors were unable to see. In addition, we predicted the capuchins, as dominants, would switch strategies and try to monopolize the food by first taking at-risk, visible food pieces before collecting pieces that were safely hidden behind a barrier.

Method

Subjects

Eleven adult and sub-adult capuchin monkeys (mean age 10 yrs.) participated in this experiment and all subsequent experiments (the same number of subjects participated in Hare et al. (2000) in order to provide equivalent statistical power). They were all born and raised in captivity and belong to two social groups at the Istituto di Psicologia. Capuchin monkey groups were housed in indoor-outdoor rooms (11-25 m³) which were furnished with perches and slides; a variety of plastic toys and wooden blocks were given on a daily basis. All cages were connected by means of sliding doors. Monkey chow, fresh fruits and vegetables were given once a day in the early afternoon. Three times a week monkeys received a mixture of cheese curd, vitamins, egg, bran, oats and sugar as was their normal routine. Water was available ad libitum and subjects were never deprived of food at any time. Nine of the capuchin monkeys were subordinate to someone else in their group while nine were dominant to someone else in their group (i.e. all individuals except the highest and lowest ranking individuals were both dominant and subordinate to other group members). When analyzing the behavior of the subordinates, we only include the nine subjects who were subordinate to someone in their group. Likewise, when analyzing the behavior of dominants, we only include the nine subjects who were dominant to someone in their group (this same procedure was used in all subsequent experiments as well).

Procedure

Subjects were tested in a row of three indoor rooms each measuring 1.7m x 3m and 2.6 m high which were accessed by a service hallway (see Fig. 3.1). The walls separating the rooms were concrete, as were the floors, while the ceilings and rear walls were wire mesh. Finally, the wall adjacent to the service hallway was glass so that experimenters could see and film the monkeys. The two outer cages each had sliding doors (50cm x 50cm and equidistant from each of side the walls) allowing animals to see either into the middle room when opened partially or to enter when opened fully.

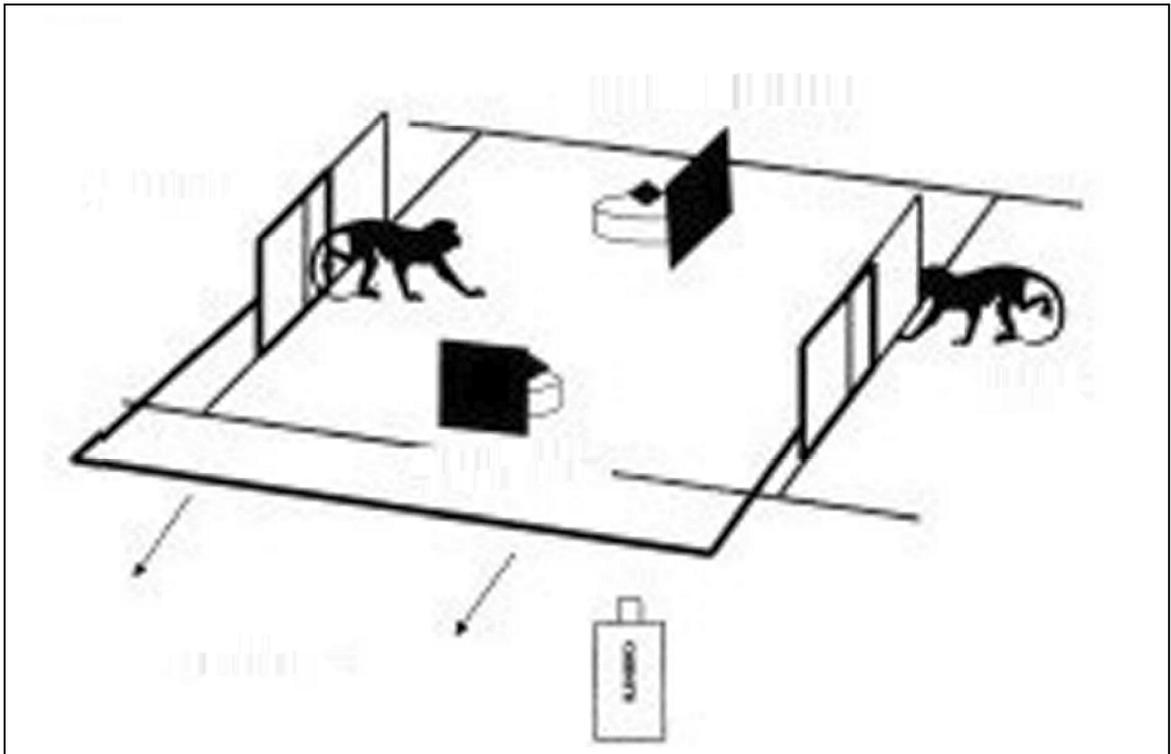


Figure 3.1. General experimental setup in Experiment 1-5.

Before testing began, each dyad in each of the two groups was assessed for dominance using food competition tests. One subject was placed into each of the outer

rooms and one piece of preferred food (a peanut) was placed on top of a small cylindrical platform (5 cm high and 12.4 cm in diameter) in the center of the floor of the middle room (equidistant between the two subjects). The door of each subject was then opened slightly allowing each subject to see a piece of food on the food platform and its competitor peaking through the other door. Then, both doors were opened simultaneously (the handles used to slide open the doors were connected so that experimenter 1 (E1) could open both doors simultaneously, see Fig. 1) and the animals were allowed to retrieve the piece of food. E1 scored which animal retrieved the food. This test was repeated four times for each dyad in a single session. In addition, in each session each dyad received a fifth trial in which an additional piece of food was placed on a second food platform. In this trial the two platforms were equidistant from both subjects (85 cm from each subject) and 80 cm from each other. Table 3.1 shows the results of the food dominance tests (which were further confirmed in the current experiment).

To assure that the subjects had a chance to learn that food could be found on either hiding platform, each subject was given three additional warm up trials. In these trials both food platforms were placed just as in the last trial of the dominance testing, but the dominant was not released and only watched through the doorway (which was opened approximately 10 cm).

The testing procedure was identical to the dominance testing except that two pieces of food were placed on food platforms equidistant between the two subjects (85 cm from each subject) with 80 cm between the platforms. In addition, a 14.2 x 20 cm piece of opaque, black plexiglass was attached to each of the platforms. The pieces of

plexiglass made it possible to hide one or both pieces of food from one of the competitors because the platform (and plexiglass) could be swiveled in place. Therefore, the platform could be turned so that the food placed on it was occluded by the barrier or it could be turned so that the food on the platform was visible to both subjects (see Fig. 3.1).

Subject	Age (years)	Sex	Rearing history	Dominance rank
Group 1				
Pepe	13	male	Human reared	1
Cognac	13	male	Mother	2
Robot	5	male	Mother	3
Paquita	10	female	Human reared	4
Roberta	14	female	Human reared	5
Robin H	3	male	Mother	6
Robiola	2	female	Mother	7
Group 2				
Gal	10	male	human reared	1
Rame	13	female	Mother	2
Paprica	11	female	human reared	3
Carlotta	16	female	human reared	4

Table 3.1. Age, sex, birthplace, experiment participation, rearing history, and dominance rank of the subjects included in each of the experiments.

Before each trial, the platforms were baited while one subject was waiting in each of the side cages. The sliding doors were closed so that neither subject could see the baiting. In each trial the middle room was baited in one of four ways.

Visible-Visible. The food platforms were turned so the plexiglass did not prevent either animal from seeing both pieces of food.

Hidden-Hidden. Both of the food platforms were turned so that the subordinate could see both pieces of food while the dominant could not see either.

Visible-Hidden. The food platforms were placed so that the subordinate could see both pieces of food but the dominant could only see one piece of food.

Visible-Hidden (S). The food platforms were turned so that the dominant could see both pieces of food but the subordinate could only see one.

After baiting, E1 left the middle cage and partially opened the subjects' doors to allow both animals to look into the middle room at the food platforms and at their competitor. Once both competitors had looked through their respective doors, both animals were released to retrieve the food. Once both pieces of food were removed from the platforms, the trial was over. All trials were videotaped.

All possible pairings of dominant-subordinate animals in both groups were tested once in each condition. Therefore, there were 27 dyads (27 dyads were also used in Hare et al., 2000) which each received one session of 4 trials for a total of 108 trials. Across subjects, the order of conditions was counterbalanced.

In addition, after the testing was completed, a non-social control test was conducted to see if any of the animals' preferences in the competitive experiment were produced by non-social factors such as a preference for food in front of barriers. Therefore, five of the subjects were given four trials in which they were released individually into the middle cage where both food platforms were baited. In each trial, one platform was turned so that the occluder was behind the food while the other was turned so that the occluder was to the side of the food (just like V-H test conditions). The two positions were both given twice on the right side and twice on the left for each subject.

Scoring and data analysis

In each trial, E1 recorded which subject(s) approached and who obtained which piece of food. A no approach was scored if an animal did not leave its cage before its competitor had retrieved both pieces of food. Determining who approached and retrieved the food was straightforward and unambiguous in every case (and this is true in all of the subsequent experiments as well), but as a precaution 20% of trials in the Visible-Hidden and Visible-Hidden (S) were randomly selected and the subordinates retrieval and approach behavior were scored again for reliability. Interobserver agreement on food retrieval and approach behavior were both 100% with a cohen's Kappa of 1.0.

The Visible-Hidden (S), Hidden-Hidden and Visible-Visible condition were used to assess the preferences of subjects as subordinates while the Visible-Hidden and Visible-Visible conditions were used to assess the preferences of subjects as dominants. Each individual received only one score for a given condition no matter how many trials it had received. To do this, we converted the scores of all individuals to "percentage success" scores. For example, a subject might be paired with four different animals on four different trials in the same condition and obtain two pieces of food. In this case, for this condition the subject would receive a score of 50%. We used this procedure to generate one number for each subject in each role (dominant or subordinate) for each condition. A Friedman test was used to test for overall effects of condition and post hoc comparisons were conducted. Therefore, Bonferroni corrections were used to control for multiple comparisons between conditions.

Results

The amount of food subjects retrieved as subordinates differed significantly between condition (29.3% V-H(S), 23.4% V-V, 34% V-H, and 77.9% H-H; Friedman test: $\chi^2_2 = 15.65$, $N=9$, $p < 0.001$). Pairwise comparisons (all tests are one tailed unless otherwise specified) between conditions reveal that as predicted subjects retrieved more food in the H-H condition than in the V-V condition (Wilcoxon test: $N=9$, $T=45$, $p=0.004$; significance level .017, Bonferroni correction) or the V-H conditions (Wilcoxon test: $N=9$, $T=45$, $p=0.004$). Although not significant, six subjects retrieved more food in the V-H condition and one retrieved more food in the V-V condition (Wilcoxon test: $N=7$, $T=23$, NS).

But the critical test is which piece of food subordinates preferred to retrieve within the V-H condition (see Fig. 3.2). As predicted, subordinates retrieved significantly more hidden food taking 76.3% while retrieving a mere 2.7% of the visible food ($N=8$, $T=36$, $p=0.006$).

We also recorded in which trial the subordinates chose not to approach, staying in their own room throughout the trial. Between conditions there was a significant difference in the approach behavior of subordinates (Friedman test: $\chi^2_2 = 11.842$, $N=9$, $p=0.004$).

Pairwise comparisons revealed that subordinates chose not to approach 36.7% of trials in the V-V condition while only 8.2% of trials in the H-H condition (Wilcoxon test: $N=5$, $T=15$, $p=0.023$).

In addition, we also coded when subjects used unusual strategies while retrieving food. In seven trials involving three individuals, subjects waited to approach the food

until the dominant entered and left the testing area or were distracted eating a piece of food. Also in one trial a subject approached only after the dominant's back was turned.

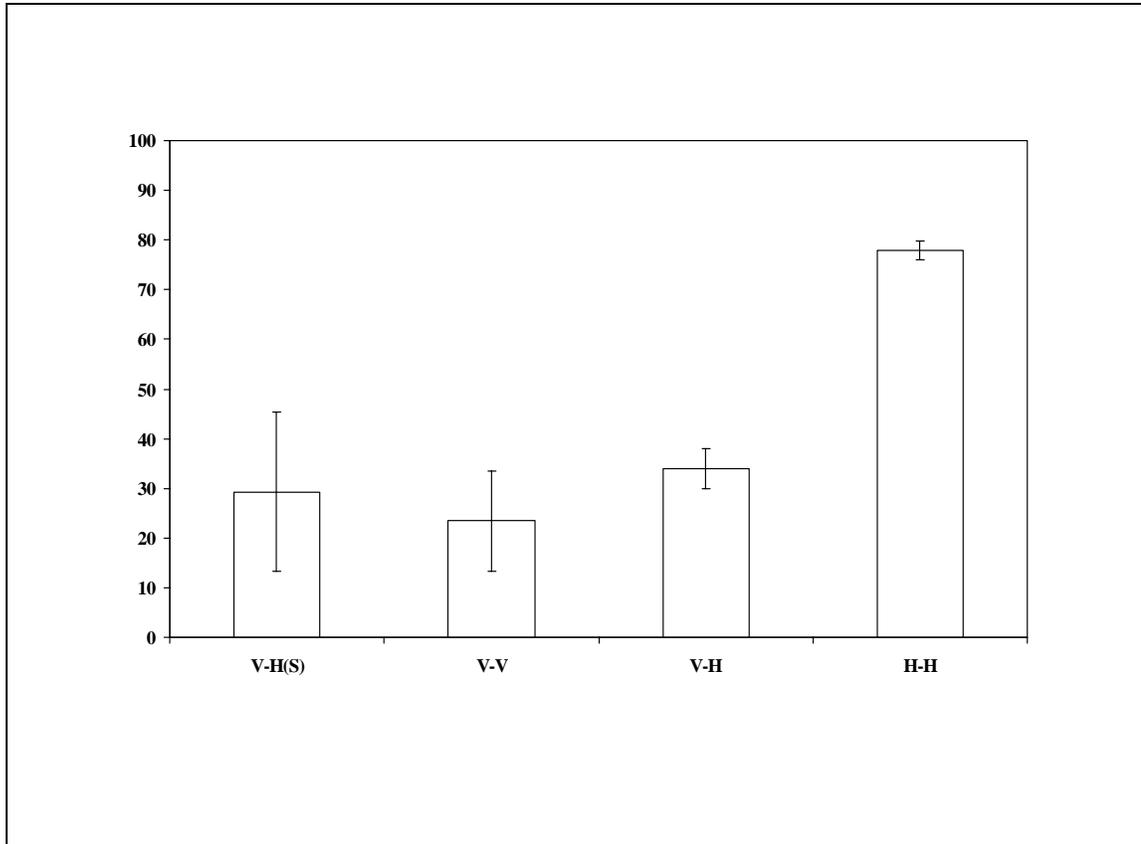


Figure 3.2. Mean percentage (\pm SEM) of pieces of food obtained by subordinates as a function of who had visible access to the food in Experiment 1.

We also coded subjects' food retrieval and approach behavior as dominants. Within the V-H(S) condition no preference for retrieving visible or hidden food was detected for dominants (Wilcoxon test: $N=4$, $T=7$, NS). Most important, when dominants retrieved both pieces of food in the V-H (S), condition they showed no preference for

retrieving either the visible or hidden food first (Wilcoxon test: $N=6$, $T=15$, NS).

Dominants approach behavior differed between conditions (Friedman test: $\chi^2_2 = 21$, $N=9$, $p<0.001$). Pairwise comparisons between conditions of dominants' approach behavior revealed that dominants chose not to approach significantly more in the H-H condition than in the V-V condition (Wilcoxon test: $N=7$, $T=28$, $p=0.009$). Finally, when tested in the non-social control conditions, subjects did not have a preference for food placed in front of a barrier (Paired sample t test: $t(4)=1$, NS)

Discussion

The results of this first experiment make it clear that the competitive paradigm is a viable test for assessing the visual perspective-taking abilities of capuchin monkeys. First, even though capuchins are considered a tolerant species, the subjects demonstrated that they had a strict enough food dominance hierarchy for the competitive test to work. Second, the results of the first experiment with capuchin monkeys look much like those of the chimpanzees, at least with respect to the subordinates. Between conditions, subordinates retrieved more food as the number of hidden pieces of food increased. In addition, subordinates retrieved more hidden than visible food within the V-H condition. Finally, subordinates approached significantly less when both pieces of food were visible to the dominant than when they were hidden. But in contrast, as dominants, the capuchin monkeys did not behave as the chimpanzees. Dominant capuchin monkeys did not preferentially retrieve the visible food first when both pieces were retrieved, even though, if one is trying to monopolize the food, it is best to take the at-risk visible piece first.

Overall, the performance of the capuchin monkeys, as subordinates, is consistent with the interpretation that they know what others do and do not see while, as dominants, their performance is not. Nonetheless, several alternative explanations are viable in both cases. The most obvious explanation is that subordinates are simply reacting to the dominant's behavior when deciding when to approach and which piece to retrieve. In favor of this interpretation is the fact that subordinates retrieved more food and approached more in the H-H condition, the condition in which the dominants approached significantly less. The fact that the dominants did not show a preference for visible food might be because they were very successful in attaining food without the use of a strategy.

Experiment 2

In experiment one, as subordinates, capuchin monkeys clearly showed a preference for the hidden food while as dominants they showed no preference. The purpose of the Experiment 2 is 1) to increase the potential for comparison between the performance of the capuchins and chimpanzees by assuring the capuchin monkeys had equal experience competing (i.e. the same number of trials in each of the test conditions) as the chimpanzees before the critical delay test (Experiment 3 and 4) and 2) to see if subjects, as dominants, will show more strategic behavior in their food retrieval if the situation is made more competitive by moving the food closer to the subordinate. Our predictions were the same as for Experiment 1.

Method

The same 11 subjects from Experiment 1 participated in this experiment (9 subjects played the role of subordinate and 9 the role of dominant). The testing procedure in this experiment was identical to the previous experiment with three exceptions: 1) the Hidden-Hidden condition was dropped and replaced by an additional Visible-Hidden trial. Therefore, in each session a dyad received one trial of the Visible-Visible condition, one trial of the Visible-Hidden (S), and two trials of Visible-Hidden for a total of four trials per session; 2) in the Visible-Hidden (S) condition the food platforms were both moved so that they were 45 cm from the subordinate and 125 cm from the dominant; 3) a new set of white, curved, plastic barriers (19.5 cm x 16 cm) were used as occluders.

Otherwise, as in Experiment 1, E1 placed one monkey in each of the outer cages and closed the sliding doors completely. Then E1 baited the middle cage in one of three ways (instead of four as in Experiment 1). Then, E1 partially opened both animals' sliding doors to allow both animals to view the food platforms and see its competitor. After both animals had peaked through their door, they were both released. E1 scored which animal(s) approach and who retrieved which piece of food.

All possible pairings of dominant-subordinate animals in both groups were tested in each condition once. As in Experiment 1, there were 27 dyads and 4 trials per session for a total of 108 trials. Across subjects, the order of conditions was counterbalanced. Scoring and analysis were the same as in Experiment 1. 20% of the Visible-Hidden and Visible-Hidden (S) trials were randomly chosen and the food retrieval and approach behavior of subordinates was recoded by a second coder for reliability. Interobserver

agreement for food retrieval was 94% with a Cohen's kappa of .92 while agreement was 97% with a Cohen's kappa of .87 for approach behavior. Finally, as with the previous experiment, a non-social test was conducted after this experiment with each of the nine subordinates receiving 4 trials to test for any potential non-social factors that might explain any of the observed preferences in the competitive test. A Friedman test was used to test for overall effects of condition and post hoc comparisons were conducted. Therefore, Bonferroni corrections were used to control for multiple comparisons between conditions.

Results

The amount of food that subordinates retrieved between conditions bordered on significance (10.5% V-V, 24.2% V-H, 27.6% V-H(S); Friedman test: $\chi^2_2 = 5.79$, $N=9$, $p=0.055$). Pairwise comparisons between conditions reveal that subordinates retrieved more food in the V-H condition than in the V-V condition (Wilcoxon test: $N=7$, $T=33$, $p=0.017$; significance level .017, Bonferroni correction). Although subjects did not retrieve more food in the V-H condition than in the V-H (S) condition this is undoubtedly due to the fact that in the V-H (S) condition the food platforms were placed much closer to them than to the dominant. In addition, within the V-H condition (see Fig. 3.3) subordinates preferred to retrieve hidden food taking 43.4% while only retrieving 5% of the visible food (Wilcoxon test: $N=8$, $T=36$, $p=0.008$).

Most importantly we also scored those trials in which the animals were released but the subordinates chose not to approach. Interestingly, subordinates chose not to approach in 54.7% of trials in the V-V condition when its competitor could see both

pieces of food and refused to approach in only 30.5% of the V-H condition when one piece was hidden from its competitor (Wilcoxon test: $N=8$, $T=34$, $p=0.012$).

In addition, we noted instances in which subordinate subjects seem to exhibit an unusual strategy while retrieving food. On two occasions (involving two individuals), subordinates waited until their competitor's back was turned before they attempted to retrieve food. In addition, on two occasions (involving two different individuals) subordinates took indirect routes when retrieving food.

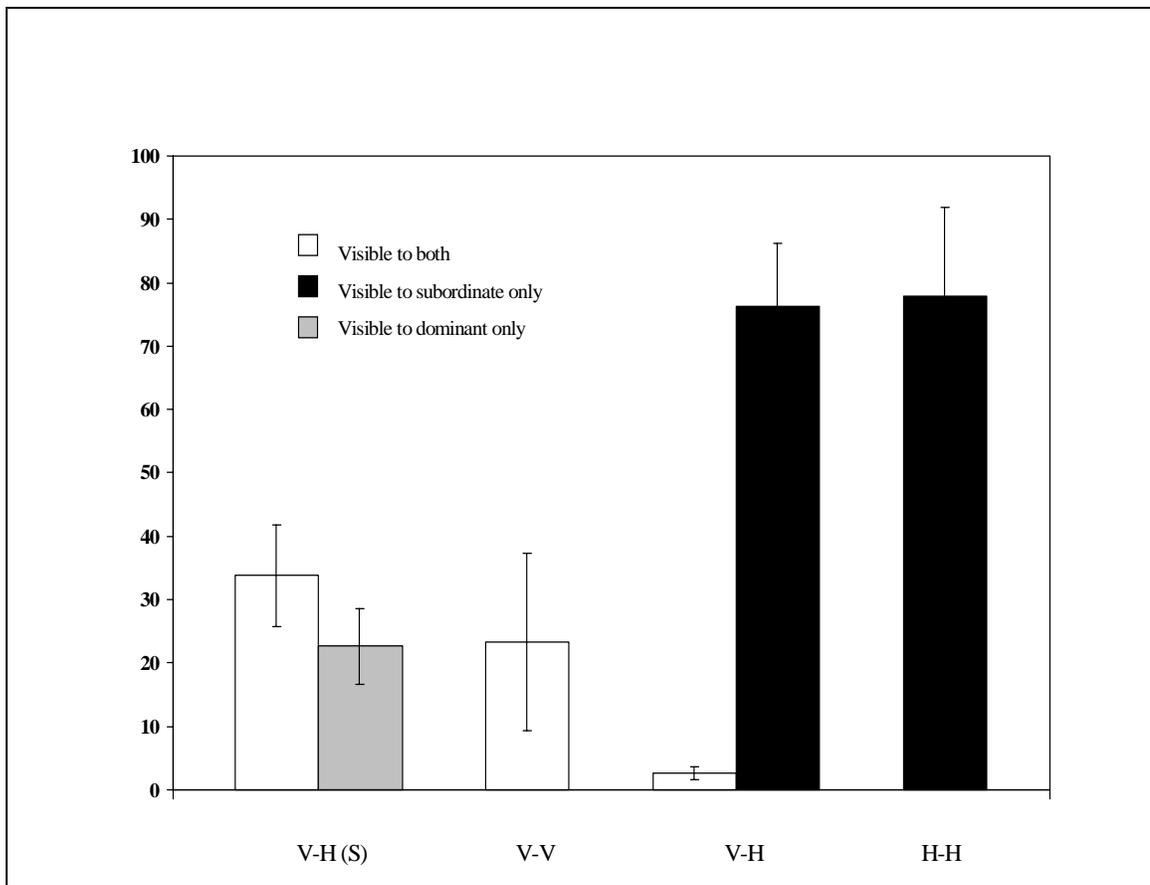


Figure 3.3. Mean percentage (\pm SEM) of pieces of food obtained by subordinates as a function of who had visible access to the food in Experiment 2.

We also analyzed the retrieval pattern and approach behavior of the dominants. The most important comparison is within the V-H (S) condition in which the food platforms were placed closer to the subordinate than the dominant. In this condition, dominants retrieved the visible food (Wilcoxon test: $N=6$, $T=21$, $p=0.013$), but when they retrieved both pieces of food they showed no preference to first retrieve the at-risk visible piece (Wilcoxon test: $N=5$, $T=14$, $p=0.078$, two tailed). In addition, in all conditions and in all but one trial, dominants approached the food resulting in no difference between conditions (Friedman test: $\chi^2_2 = 2$, $N=9$, NS).

Finally, when tested nonsocially, subordinates showed no preference for food placed in front of a barrier nor did they exhibit a side bias; they did have a strong bias for the food platform in the rear of the testing room (Paired sample t test: $t(8)=4.619$, $p=0.002$).

Discussion

Experiment 2 corroborated the findings of Experiment 1. Capuchin monkeys, as subordinates, preferentially retrieve hidden over visible food within and between conditions. In addition, and perhaps most interestingly, they approach less often when both pieces of food are visible to a dominant competitor than when one piece is hidden. One possible explanation for this approach behavior is that when both pieces of food were visible subordinates decided not to approach before they even saw the dominant approach. This interpretation is supported by the fact that the preference of subordinates for approaching more in the V-H condition cannot be explained as a function of

subordinate interest, given more food was available in the V-V condition. In addition, this finding cannot result from decreased interest by dominants in the V-H condition, because dominants approached in every trial but one across all conditions. It is possible, however, that when dominants see two pieces of food they are more excited or intimidating than when they only see one piece of food and the subordinates detect this before the trial or as the dominant approaches. Therefore, subordinates would preferentially approach when a piece of food is hidden. In addition, it is possible that once the dominants entered taking the visible piece of food they were less likely to then motion toward the second piece of food in the V-H condition. Therefore, subjects would be more likely to approach in the V-H condition. Either of these “intimidation hypotheses” (Hare et al., 2000) would explain the observed difference. Experiment 3 and 4 are designed to address these hypotheses.

Again in Experiment 2, the dominants behave as if they were using information about what their competitor could see. The critical finding is that when dominant subjects retrieved both pieces of food they do not first retrieve the at-risk visible piece of food. Dominants showed no preference, although the food in the V-H (S) condition was placed much closer to the subordinate making it more difficult for the dominant to retrieve both pieces of food. Therefore, as dominants, capuchins are either more tolerant of subordinates or are less strategic in their retrieval behavior than chimpanzees. The former hypothesis seems implausible given that subordinates are clearly intimidated by the dominants approaching often refusing to even approach (over half the trials in the V-V condition). Given dominants show little strategic retrieval behavior, further investigations will focus solely on whether subordinates are taking the visual perspective

of dominants. Finally, although in the nonsocial test subordinates showed a preference for the food platform in the rear of the testing room; this preference apparently did not interfere with their food retrieval strategies.

Experiment 3

In completing the previous two experiments, the capuchins have had a similar experience to the chimpanzees before their delay test. Specifically, they received the same number of trials in each of the conditions, although the types of barriers and the order they received the conditions were slightly different. Therefore, in Experiment 3 we replicated the occluder experiment from Hare et al. (2000). This delay test is critical because it eliminates the possibility that the subordinate capuchin monkeys preference for hidden food is due to monitoring the dominant's approach behavior. In Experiment 3, we released the subordinate with a slight head start and noted which piece of food it first approached and which piece of food it retrieved. This allowed us to determine whether subordinates were using the dominant's behavior when retrieving food or whether they possibly based their decision on what the dominant was able to see. If subordinate capuchins know what others do and do not see they should approach and retrieve more hidden food. If subordinates react to the behavior of their competitor they should approach randomly while preferring to retrieve hidden food.

Method

The subjects were the same 11 as in the first two experiments (9 played the role of subordinate). New occluders were used for this experiment made of grey, opaque, plastic

(triangular in shape: 17.2 cm x 36 cm). The food platforms were baited in three different ways by E1:

Visible-Visible. The food platforms were turned so that both pieces of food were visible to both animals.

Hidden-Hidden. Both of the food platforms were turned so that the subordinate could see both pieces of food while the dominant could not see either.

Visible-Hidden. The food platforms were placed so that the subordinate could see both pieces of food but the dominant could only see one piece of food.

After baiting, E1 partially opened the dominants door while E2 partially opened the subordinates door (the bar connecting the two door bars was removed allowing the two doors to be opened at different times) so that the animals could see the food platforms and each other. Once they were both peeking through their respective doors the experimenters released the animals giving the subordinate a slight head start. E2 opened the door of the subordinate first. E1 then opened the door of the dominant as the subordinate approached a line drawn on the floor half way between its own door and the platforms. E1 then scored the initial direction of approach for the subordinate and which animal retrieved which piece of food. All trials were videotaped. If the subordinate chose not to approach for 30 seconds the trial was ended and a no approach was scored.

Each dyad received one trial of the Visible-Visible condition and the Hidden-Hidden condition while receiving four trials of the Visible-Hidden per session. All possible pairings of dominant-subordinate animals in both groups were tested. Therefore, there were 27 dyads and 6 trials per session for a total of 162 trials. Across subjects, the order of conditions was counterbalanced. Scoring and analysis were the same as in

Experiment 1. 20% of the Visible-Hidden trials were randomly chosen and the food retrieval and approach behavior of subordinates was coded by a second coder for reliability. This coder was blind to the location of the occluder when coding the direction of the subordinates first approached. Interobserver agreement for food retrieval was 95.7% with a Cohen's kappa of .94 while agreement was 95.7% with a Cohen's kappa of .92 for the direction of first approach. Finally, as with all the previous experiments, a non-social test was conducted after the experiment with each subordinate receiving 4 trials to test for any potential non-social factors that might account for the observed preferences in the competitive test. A Friedman test was used to test for overall effects of condition and post hoc comparisons were conducted. Therefore, Bonferroni corrections were used to control for multiple comparisons between conditions.

Results

Unlike previous experiments there was no difference in the amount of food that subordinates retrieved between conditions (30% V-V, 45% V-H, 50% H-H; Friedman test: $\chi^2_2 = .56$, N=9, NS). Although there was no significant differences between conditions, within the V-H condition (see Fig. 3.4) the subordinates did retrieve more hidden food (Wilcoxon test: N=9, T=43.4, p=0.007).

As for the approach behavior, because the door of the dominant was not opened until the subordinate began to approach, subordinates approached in all but eight trials and there was no difference between conditions (Friedman test: $\chi^2_2 = .2$, N=9, NS). Therefore, the critical test in this delay experiment is the direction of first approach that the subordinates took before the dominant was released within the V-H condition.

Subordinates did not preferentially approach the hidden food (Wilcoxon test: $N=7$, $T=17.5$, NS). Dominants approached in all but eight trials resulting in no difference in their approach behavior between conditions (Friedman test: $\chi^2_2 = 2.93$, $N=9$, NS). Finally, as in the previous experiments, the nonsocial control test revealed that subjects did not have a preference for food hidden behind barriers nor a side bias, but they did prefer to retrieve food on the rear food platform first (Paired sample t test: $t(8)=4.619$, $p=0.002$).

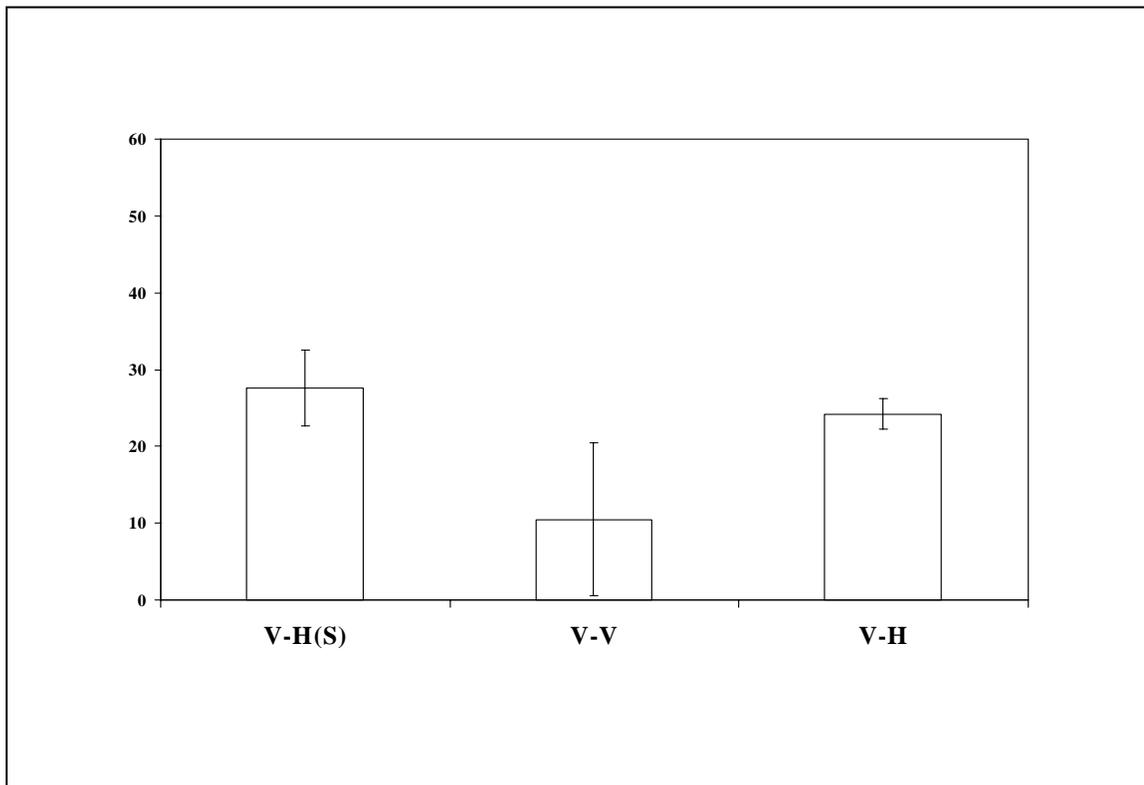


Figure 3.4. Mean percentage (\pm SEM) of pieces of food obtained by subordinates as a function of who had visible access to the food in Experiment 3.

Discussion

The results of this experiment are very different from those of the previous two experiments. Much of this difference is likely attributable to the fact that subordinates were released with a slight head start over the dominant. Subordinate subjects no longer retrieved more food between the different conditions and there was no difference in their approach behavior between conditions. But the critical test is within the V-H condition. If subordinates retrieved and approached hidden food more often in the previous experiments because the dominant is unable to see if, they should approach hidden food first and retrieve more of it within this condition. Although subjects did retrieve more hidden food, they did not preferentially approach the hidden pieces of food. Therefore, we are unable to rule out the likelihood that subordinates are basing their retrieval decision on the behavior of the dominant.

There are two additional reasons why subordinates might not have shown a preference to approach hidden food: 1) the non-social control tests between each experiment show that while subjects do not have a preference for food hidden behind barriers they do have a strong preference for food placed on the rear platform near the back wall of the testing room. It is possible that this bias is somehow interfering with their decision making. However, this seems unlikely given that subjects did have a preference for hidden food in Experiment 2 while showing the same preference in the non-social test 2) because subjects retrieved about 50% of the food in each of the three conditions (on average a piece per trial), it is possible there was no motivation for strategic behavior. In the next experiment we address both of these possibilities.

Experiment 4

It is possible that this preference for the rear food platform somehow interfered with their decision making. Therefore, we moved the food platforms to eliminate or reduce subjects preference for the back platform. Second, it is possible that the subordinate subjects did not need to be strategic about which piece of food to approach first since with their head-start they retrieved almost half of the food in Experiment 3. To address this second problem we also moved the two food platforms closer to the dominant individual to make the situation even more competitive. In this way it would be more difficult for the subordinates to obtain food. Therefore, to continue to be successful in retrieving food subordinates might be forced to be more strategic about which piece of food to approach and retrieve first. Our predictions were the same as for Experiment 3.

Method

The 11 subjects (9 subjects played the role of subordinate), opaque occluders, and procedure were identical to Experiment 3. The food platforms were both shifted 8 cm toward the rear wall of the cage and 40 cm closer to the dominants door. Therefore the food platforms were 45 cm from the dominant and 125 cm from the subordinate before the trial started (the two barriers were still 80 cm apart from each other).

Each dyad, again, received one trial of the Visible-Visible condition and the Hidden-Hidden condition while receiving four trials of the Visible-Hidden condition per session. All possible pairings of dominant-subordinate animals in both groups were tested once. Therefore, there were 27 dyads and 6 trials per session for a total of 162 trials. Across subjects the order of conditions was counterbalanced. Scoring and analysis were

the same as in Experiment 1. 20% of the Visible-Hidden trials were randomly chosen and the food retrieval and approach behavior of subordinates was coded by a second coder for reliability. This coder was blind to the location of the occluder when coding the direction the subordinates first approached. Interobserver agreement for food retrieval was 95% with a Cohen's kappa of .93 while agreement was 95% with a Cohen's kappa of .91 for the direction of first approach. Finally, as with all the previous experiments, a non-social test was conducted after this experiment with each subordinate receiving 4 trials to test for any potential non-social factors that might explain any of the observed preferences in the competitive test. A Friedman test was used to test for overall effects of condition and post hoc comparisons were conducted. Therefore, Bonferroni corrections were used to control for multiple comparisons between conditions.

Results

There was a difference between conditions in the amount of food that subordinates obtained (30% V-V, 45% V-H, 50% H-H; Friedman test: $\chi^2_2 = 6.89$, $N=9$, $p=0.032$). Between conditions pairwise comparisons reveal that subordinates retrieve more food in the H-H condition than the V-V condition (Wilcoxon test: $N=7$, $T=28$, $p=0.009$; significance level .017, Bonferroni correction). In addition, subjects retrieved more hidden food than visible (see Fig. 3.5) within the V-H condition (Wilcoxon test: $N=7$, $T=27$, $p=0.014$).

Although the subordinates' food retrieval changed from the previous experiment the approach behavior did not. Subordinates refused to approach in only three trials making it impossible to test between conditions. The most critical result, though, is which

piece of food subordinates chose to approach first with their head start. Subjects did not preferentially approach the hidden piece of food first (Wilcoxon test: $N=6$, $T=12.5$, NS). As in the previous experiment, dominants approached in almost every trial and there was no difference between conditions (Friedman test: $\chi^2_2 = 3.85$, $N=9$, NS). Finally, in the nonsocial control subjects did not prefer food in front of barriers, have a side bias or a bias for one of the food platforms over the other.

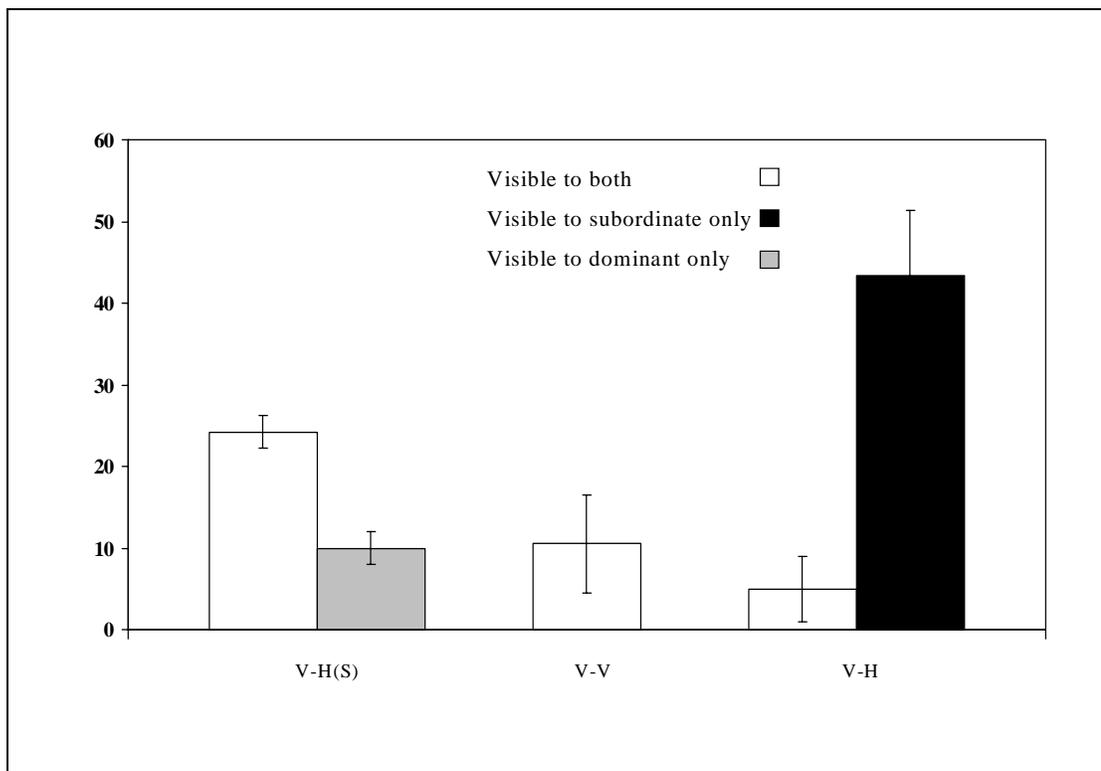


Figure 3.5. Mean percentage (\pm SEM) of pieces of food obtained by subordinates as a function of who had visible access to the food in Experiment 4.

Discussion

The results of Experiment 4 do not support the hypothesis that the subordinates are sensitive to what the dominant is able to see. Although subordinates retrieved more hidden food within and between conditions they did not prefer to approach the hidden food first when they were released with a slight head-start over their dominant competitor. In addition, because the food platforms were shifted from their position in the previous experiments, this result cannot be a product of subjects' preference for one of the food platforms or the fact that the situation was not competitive enough. First, subjects previous preference for the rear platform disappeared in the nonsocial control test. Second, unlike the previous experiment, subordinates retrieved different amounts of food between conditions. Although these results do not add support that subordinates assess what dominants can see, it is possible that there was simply too much social and non-social information to be encoded and processed before a social strategy could be implemented. The next experiment attempts to make the task simpler for the subordinates to test for this possibility.

Experiment 5

To reduce the burden of nonsocial information in this experiment the capuchin monkeys only had to make a decision of whether to approach and retrieve one piece of food. Sometimes this piece of food was visible to a dominant and sometimes it was hidden. If subordinates know what the dominant cannot see, they should approach and retrieve food more often or faster when it is hidden. If while competing over food

subordinates rely on their competitor's behavior, they should show no preference in their approach and retrieval behavior between conditions.

Method

The 11 subjects (9 subjects played the role of subordinate) and procedure were identical to that of Experiment 3 and 4. The exceptions to this are that only one piece of food was hidden on the two food platforms in one of two ways and trials did not end after 30 seconds. The two ways the food was hidden were:

Food Hidden. One platform was turned so that the subordinate could see the piece of food but the dominant could not. The second platform was turned so that both animals could see that it was empty.

Food Visible. One platform was turned so that the subordinate could see that the platform was empty but the dominant could not. The second occluder was turned so that both animals could see the food.

As before, subordinate subjects were released with a head start. The dominant's door was not opened until the subordinate approached the line halfway to the food. Unlike previous experiments, a trial did not end after thirty seconds. The experimenter waited until the subject approach and the food was gone before the trial was over. Each dyad received 2 trials of each condition per session and each of the 27 dyads were tested in one session for a total of 108 trials. E2 recorded who approached which food platform, and who retrieved the food. In addition, from the videotape the latency to approach was scored for the subordinate in each trial.

Results

Subjects retrieved almost equal number of food pieces between conditions taking 38.7% of food in the Food Hidden condition and 40.3% in the Food Visible condition. In addition, subordinates mean latency to approach between conditions was identical (63.1 seconds in the Food Hidden condition and 63.3 seconds in the Food Visible condition). We also looked at the approach and food retrieval behavior of subjects within the first 30 seconds (the length of a trial in Experiment 1-4). In the first 30 seconds subjects retrieved 11% of the hidden food and only 2% of the visible food but this is not a significant difference (Wilcoxon test: $N=3$, $T=6$, NS). In addition, subjects chose not to approach in the first 30 seconds equally often between conditions (68.7% of Food Hidden trials and 68.7% of Food Visible trials).

Discussion

Even with less non-social information to deal with subjects still had no preference for retrieving or approaching the food hidden from the dominant. In addition, when only considering the first thirty seconds of trials, there is not a significant difference in the amount of food that subjects retrieved or approached between the two conditions. Therefore, it seems that reducing the amount of nonsocial information did not lead to more strategic behavior. This negative finding was not due to the situation becoming less competitive given that only one piece of food was under contest. To the contrary, subjects within the first 30 seconds chose not to approach in almost 70% of trials and retrieved little food. It seems this experimental situation was competitive and there was need for an effective social strategy.

General Discussion

This series of experiments has demonstrated that when competing for food capuchin monkeys excel at reading the behavior of conspecifics, but they do not use information about what others do and do not see. The competitive test worked well because, although capuchins are characterized as a socially tolerant species (Mendres & de Waal, 2000), when competing over monopolizable food they show a clear foraging hierarchy. Every dyad within a group competed for food and the same individual consistently approached and retrieved more food than the other.

This initial result was confirmed by the first two experiments with subordinates consistently retrieving hidden food to avoid the dominant that was released simultaneously. In addition, subordinates' preference for hidden food demonstrated that subjects were at least sensitive to the behavior of the dominant and possibly could judge to which piece of food their competitor had visual access. In Experiment 2, the dominants also demonstrated sensitivity to the behavior of others in retrieving more food visible to the subordinate. However, there is little evidence for visual perspective-taking while playing the role of dominant, given that dominants did not prefer to retrieve at-risk visible pieces of food first when taking both pieces of food. Given the preference of subordinates, for hidden food, the final three studies were designed to test between the predictions of the visual perspective-taking and behavior reading hypotheses. In these delay studies the subordinate was released first only knowing that the dominant would soon approach, but did not see her behavior when initially deciding which food piece to retrieve. If subordinates' preferences in previous studies were a result of knowing what the dominant could and could not see, within the Visible-Hidden condition they should

have continued to approach and retrieve hidden food even when they did not see the dominant approach. In contrast, if their preferences were a product of reading the behavior of the dominant (i.e. to avoid the dominant), then subjects should have initially approached randomly, but with the entrance of the dominant avoid her by retrieving the hidden food.

In all three of these critical delay experiments without the approach behavior of the dominants to rely upon, subjects approach and retrieval patterns were consistent with the predictions of the behavior reading hypothesis and not with the visual perspective-taking hypothesis. The subordinates' initial direction of approach within the Visible-Hidden condition in Experiment 3 and 4 showed that they did not have a preference for approaching hidden food. At the same time, the subjects still retrieved more hidden food. Therefore, subordinates initially approached randomly, and then upon the entrance of the dominant, adjusted their own approach (to avoid the dominant) and took the hidden piece of food. Finally, even in Experiment 5, when the amount of non-social information was reduced, there was no evidence that subjects were taking into account what their competitor was able to see. Subordinates did not approach the hidden food quicker or more often than the visible food. Importantly, because less food was available in this experiment, the situation became more competitive. Within the first thirty seconds (the duration of trials in experiment 1-4) subordinates approached in less than half of trials and overall retrieved little food. Therefore, it seems there was great need for an effective social strategy.

Although this competitive task was unable to demonstrate any evidence of visual perspective-taking in capuchin monkeys, the capuchins were impressive in the way that

they read the behavior of their competitor and used strategies to avoid dominants and retrieve food similar to that reported by Coussi-Korbel (1994) in mangabeys. In fact, their behavior reading strategies were extremely effective in almost every context. Subordinates retrieved a large proportion of the food in almost every test.

Although our results show that capuchins perform differently than chimpanzees on this task, given that absence of evidence is not necessarily evidence of absence, it would be premature to conclude that capuchin monkeys have no ability for visual perspective-taking. It is only after dozens of experiments and dozens of different approaches have been utilized that one can feel confident that null results might accurately reflect the ability of a test species (Heyes, 1998). For example, future tests could be designed so that behavior reading has little or no payoff in a similar competitive situation while assessing what others do and do not see has a high payoff. In this way, one would maximize the likelihood that the subjects might demonstrate any visual perspective-taking abilities they might possess. For example in the first four experiments, reading your competitors behavior may simply have been too effective to warrant assessing what another individual could see. In contrast in Experiment 5, it is possible that dominants were simply too intimidating keeping the subordinates from approaching at all. Perhaps designing a experiment similar to Experiment 5 which limited the amount of nonsocial information needed while also reducing the competitiveness of the situation might yield more promising results. In addition, it might be fruitful to replicate and extend other paradigms such as the one developed by Fujita et al. (2002).

Although a negative finding from a single investigation does not typically allow for straightforward interpretations, we must reemphasize that the original impetus of this

experiment was to compare the visual perspective-taking abilities of capuchin monkeys to that of chimpanzees using the same experimental methodology. For this purpose, the current experiments represent an adequate test. As chimpanzees, capuchin monkeys have a clear foraging-hierarchy, which allows for the competitive food tests. In addition, subordinates of both species demonstrated that they were intimidated by the dominants in attempting to avoid them by retrieving more hidden food. Yet unlike chimpanzees, when capuchins do not have the approach behavior of the dominants to use, they do not initially approach the hidden food.

In conclusion, capuchin monkeys perform differently from chimpanzees when competing for food. While subordinate capuchin monkeys are extremely sensitive to the behavior of dominants, there was little evidence that they assess what conspecifics do and do not see when approaching and retrieving food. In contrast, Hare et al. (2000) found that chimpanzees were sensitive to the behavior of their competitor, but also individuals changed retrieval strategies depending on the identity of their competitor and the visibility of the food. Further investigations will be needed with a number of species to test whether visual perspective-taking abilities pre-date the hominoid clade, but from this experiment there is no evidence that visual perspective-taking abilities evolved before the New World-Old World split 40-45 million years ago. Finally, it seems that the food competition paradigm will be a useful comparative tool in any future investigation into the evolution of perspective-taking in primates and other nonhumans.

Part IV: Chimpanzees deceive a human competitor by hiding

Introduction

Humans are skillful at deceiving one another because they understand the causal link between an individual's psychological states (perceptions, desires and beliefs) and their subsequent behaviour. When it is to their advantage, therefore, humans can withhold, conceal, or falsify information about the world or themselves in order to manipulate other people's psychological states. This ability is sometimes called intentional deception—to distinguish it from related non-cognitive phenomena such as bodily camouflage—and it is hypothesized by some theorists to be a crucially important hominid cognitive specialization (Baron-Cohen, 1999; Cheney and Seyfarth, 1990a; Heyes, 1998; Tomasello, 1999; Whiten and Byrne, 1988).

While many species possess morphological or behavioural adaptations that function to deceive predators, prey, or conspecifics, there is little, if any, experimental evidence that any nonhuman species is capable of intentional deception (Cheney and Seyfarth, 1990a; Gyax, 2000; Hauser, 1997; Hauser et al., 1993; Jackson et al., 2002; Ristau, 1991; Whiten and Byrne, 1988). While there are examples of animals using various behavioral strategies that function to deceive others (Dielenberg, 1999; Emery and Clayton, 2001), in each case there is a more parsimonious explanation that does not require imputing intentional deception as the mechanism underlying the behavior (Cheney and Seyfarth, 1990a; Heyes, 1998). For example, subordinates of some primate species refrain from giving food calls that might attract dominants, and they sometimes

even actively lead approaching dominants away from the location of hidden food (Coussi-Korbel, 1994; Goodall, 1986; Hirata, 2001; Menzel, 1974). Although suggestive, in each of these cases it is possible that subordinates had simply learned that they were more likely to obtain food if they refrained from behaving towards it while a dominant was also present and not behaving towards it³ (Anderson et al., 2001; Cheney and Seyfarth, 1990a; Fujita et al., 2002; Heyes, 1998; Mitchell and Anderson, 1997; Woodruff and Premack, 1979).

Recent studies have suggested that one of humans' two closest primate relatives, the chimpanzee, understands what other individuals can and cannot see – and in certain situations what they have and have not seen in the immediate past (Hare et al., 2000; Hare et al., 2001; Tomasello, 1999). Thus, in the right context chimpanzees might also be able to manipulate actively and flexibly what others can and cannot see when it is to their benefit. In the current study, therefore, we tested whether chimpanzees are able to assess when a competitor can and cannot see them and then manipulate that individual's visual information by concealing their approach toward contested food.

We introduced 8 chimpanzees (6 mother-reared, 2 nursery reared) to a food table and a competitive human experimenter (E) before being tested. The rectangular table sat in the middle of a rectangular booth comprised of 3 Plexiglas sides. Subjects began trials facing E and could attempt to approach and obtain food placed on both sides of the table

3 Support for this interpretation comes from experimental studies in which primates were trained to indicate the location of hidden food for a human, who would then find it and give it to them. Over many dozens or even hundreds of trials, these primates (including chimpanzees) learned to refrain from using the indicating behavior (and in some cases even occasionally indicated the wrong location) when an individual who did not share food was present (17-19). Because it takes primates so long to master this skill and it does not easily generalize to new settings, it is likely that individuals only learned to predict what different individuals will do in one specific situation and adjusted their behavior accordingly. There is thus currently no solid experimental evidence that nonhuman primates, or other animals, can intentionally deceive others.

before E removed it (Fig. 4.1). After the introduction, we tested chimpanzees in 3 different experimental set-ups. In the first, subjects could choose to either approach food that was being watched or food that was not being watched by E. In the second, they could choose to approach food from behind a transparent barrier or an opaque occluder as E watched. In the third, subjects could choose to approach from behind a barrier that occluded their approach either partially or fully as E watched. Because chimpanzees can assess what others can or cannot see (Hare et al., 2000; Hare et al., 2001; Tomasello, 1999) we predicted that in these conditions subjects would spontaneously conceal their approach from their competitor by 1) preferring to approach food not being watched over food being watched 2) preferring to approach behind visual occluders over nonoccluding barriers and 3) varying the directness of their approach depending on whether a more indirect route to the food might better conceal their intent to approach.

Each experimental set-up included three different conditions, which were all run in a single session for a given subject (ten trials per condition with the order administered counterbalanced within and across subjects). In each session two of these conditions were experimental tests in which subjects could potentially attempt to deceive E by hiding their approach, while the third condition was a non-social control in which E left the room (to test for any biases that subjects might have in the experimental set up⁴). In

4 Because of subject's unexpected preference for the transparent barrier in the Non-social control we ran additional analysis to test if subjects used the occluder to hide. First, a two-way ANOVA (condition x barrier type) was used to compare subjects' approach behaviour in the Occluder test to the Non-social control. There was a significant effect of condition [$F(1,7)=16.66$, $p=0.005$] and a significant condition x barrier type interaction [$F(2,21)=15.234$, $p=0.006$] with subjects avoiding approaching the transparent barrier significantly more in the Occluder test than in the Non-social control. Second, we also examined the first trials within the Occluder test and Non-social control conditions. Subjects had a significant preference for approaching behind the occluder in the first trial they approached in the Occluder test but not in the Non-social control [Sign Test, $p<0.05$]. Finally, after removing two subjects who had significant preferences for the transparent barrier in the Non-social control (both individuals approached behind the transparent barrier in all 10 trials, $p<0.002$, binomial probability), we found that the remaining

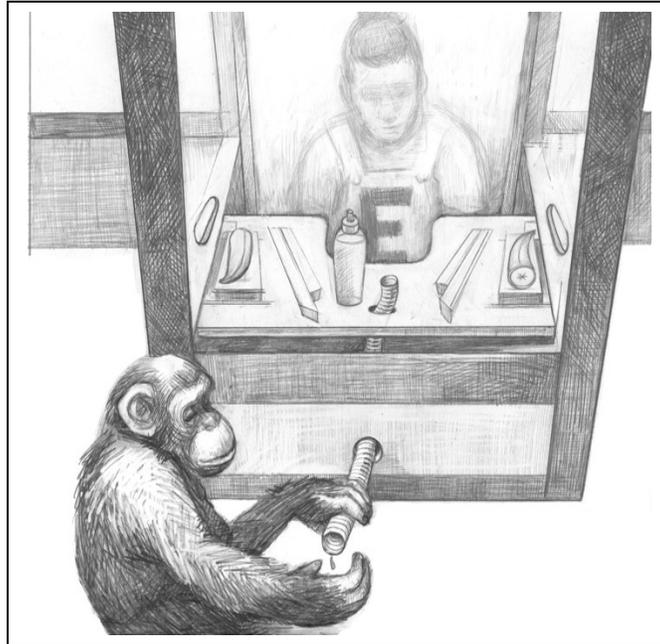


Figure 4.1. The experimental apparatus showing the experimental room, the testing booth, experimenter, and subject (in addition, the placement of the food table, the sliding food trays, the hand holes in the two Plexiglas windows for the subject to reach through, and the juice tube are also visible.) E sat behind the table in a 3 sided Plexiglas booth and poured juice through a tube so that the subjects sat opposite him across the table while drinking the juice with their mouth. Food was then placed in a dish on sliding tracks on either side of the table. E then simultaneously pushed the two pieces of food (banana) within reach of oval hand holes in the Plexiglas test windows on either end of the table. Subjects had to chose between approaching one of the food pieces which could

six subjects did have an overall preference for hiding behind the occluder in the Occluder test (T=19, N=6, $p < 0.045$, Wilcoxon Sign Rank test).

be obtained if they reached through one of the oval hand holes and grabbed the food before E removed it by pulling it back out of reach⁵.

In Session 2, the two experimental tests were: 1) the Face and Chest test: a replication of the condition by the same name in Session 1; and 2) the Occluder test: one of the two transparent choice windows was covered with a large opaque occluder while E stared directly ahead. The Non-social control had the same set up as the Occluder test except E left the room⁵. Subjects again had a preference for avoiding the food E was watching in the Face and Chest test [$t(7)=3.38$, $p=0.006$], replicating the results from the first session. In the Occluder test subjects did not have a reliable preference for approaching behind either the opaque occluder or the transparent barrier. But this result is explained by the fact that some subjects had a strong aversion to the occluder regardless of whether E was present or not - as revealed in the Non-social control in which overall subjects preferred to approach behind the transparent barrier [$t(7) = 2.86$, $p=0.012$] (Table 4.1). When the two subjects having a significant aversion to the opaque occluder are removed from the analysis (both individuals avoided it in all 10 trials in the Non-social control), the remaining six subjects preferred hiding behind the occluder in the Occluder test ($T=19$, $N=6$, $p<0.045$, Wilcoxon Test).

In Session 3 (Fig. 4.2) the two experimental tests were: 1) the Double Occluder test: two occluders were placed on the same side of the table, occluding E's view of one of the food pieces (E looked straight ahead), while the food on the other side was visible

⁵ Further information on material and methods is available at Science online.

Session 1		<u>Approach Direction</u>	
<u>Experimental Tests</u>		<u>hidden from E</u>	<u>visible to E</u>
Face and Chest		5.87 (\pm 1.06)	1.25 (\pm 0.37)
Face versus Chest		3.75 (\pm 0.65)	1.75 (\pm 0.36)
<u>Control</u>		<u>left side</u>	<u>right side</u>
Non-social		6.13 (\pm 1.34)	3.9 (\pm 1.34)
Session 2		<u>Approach Direction</u>	
<u>Experimental Tests</u>		<u>hidden from E</u>	<u>visible to E</u>
Face and Chest		5.75 (\pm 1.26)	1.37 (\pm 0.37)
Occluder		3.5 (\pm 0.93)	1.88 (\pm 0.74)
<u>Control</u>		<u>side with occluder</u>	<u>side without occluder</u>
Non-social		2.9 (\pm 0.74)	7.1 (\pm 0.74)
Session 3		<u>Approach Direction</u>	
<u>Experimental Tests</u>		<u>hidden from E</u>	<u>visible to E</u>
Double Occluder		6.5 (\pm 1.38)	0.88 (\pm 0.35)
Split Occluder		4.6 (\pm 0.94)	2 (\pm 0.6)
<u>Control</u>		<u>side with occluder</u>	<u>side with split occluder</u>
Non-social		4.5 (\pm 0.33)	5.5 (\pm 0.33)

Table 4.1. Subjects' mean number of approaches (\pm SEM) for both possible approach directions in each condition of session 1-3.

to E and 2) the Split Occluder test: E looked straight ahead while the subject chose to approach food either behind an opaque barrier that obstructed E's view of the food or a split barrier (each part half the size of the occluder on the other side) that could occlude

the subject and E from one another at eye level and also at lower body level - but with a gap in between the two allowing E to see the subject's body approaching⁶. In the Non-social control the barriers were positioned as in the Split Occluder test but E left the testing room. Subjects preferred to approach behind the visual occluder both in the Double Occluder test [$t(7) = 3.56, p = 0.005$], and in the Split Occluder test [$t(7) = 3.59, p = 0.005$], thus successfully hiding from E in both cases. Subjects had no preference for either of the different types of barriers within the Non-social control (Table 4.1).



Figure 4.2. A picture of the experimental manipulations used in the Session 3. From left to right: the Double Occluder, Split Occluder, and Non-Social control. See supplemental online material for movies and pictures of all the conditions in all three sessions.

In order to see if subjects came to the experiment with an understanding of how to hide from E's view, or if they learned to do so during the experiment, we conducted two tests of learning. First, within each session we looked to see if subjects' approach

⁶ Further information on material and methods is available at Science online.

behavior changed across the session. This was done by comparing the first ten trials to the last ten trials of all the experimental test trials within each session. There was no evidence from any of the 3 sessions that subjects increased their frequency of hiding in the last ten experimental test trials as compared with the first ten [all three paired t tests $p > 0.55$]. Second, within each of the sessions we also tested whether subjects had a preference for spontaneously hiding from E in the very first trials in which they approached. Subjects had a preference for hiding in both of their first trials in the experimental conditions in all three sessions [Session 1: $T=17.5$, $N= 6$, $p<0.051$; Session 2: $T=10$, $N= 4$, $p<0.023$; Session 3: $T=15$, $N= 5$, $p<0.013$; Wilcoxon Sign Rank test].

Finally, and strikingly, on many trials subjects avoided approaching the food directly in favor of a more indirect approach, immediately distancing themselves from the food by one to three meters from the starting position before attempting to approach it. In the introduction, one subject approached indirectly once (i.e., $<1\%$ of trials). In the experimental tests of Session 1, 6 of 8 subjects approached indirectly in one or more trials (15% of all trials), whereas no subject approached indirectly in the Non-social control. The conditions thus differed from one another in number of indirect approaches [$F(2,21)=3.63$, $p=0.044$], with both of the experimental tests in Session 1 having more indirect approaches than the Non-social control ($p < .05$ in both cases, Fischer LSD). In Session 2, 5 of 8 subjects approached indirectly in one or more trials of the Experimental tests (16% of all trials), whereas no subject approached indirectly in the Non-social control. This difference in approaches was marginally significant [$F(2, 21)= 2.65$, $p=0.094$], with the Occluder test being higher than the Non-social control ($p<0.05$, Fischer LSD). As expected, subjects never used an indirect approach in Session 3 (since

an indirect approach could not be seen by E given the positioning of the occluders in the experimental tests).

The results of these experiments demonstrate that chimpanzees can flexibly use knowledge of a competitor's psychological state (in this case what a competitor can or cannot see) to develop deceptive approach strategies that will conceal their attempt to obtain contested food. They avoided approaching food that the experimenter was watching in favour of approaching food that was not being watched; they preferred to approach food behind various visual occluders while refraining from approaching food behind nonoccluding transparent or opaque barriers; and they used indirect approaches when these could potentially aid in concealing their intent to obtain the contested food. Subjects almost exclusively approached indirectly if their departure would be visible but their return would be hidden.

Taken together with other recent findings on chimpanzee cognition (Kulhmeier and Boysen, 2001; Hare et al., 2000; Hare et al., 2001; Tomasello, 1999), these findings provide further evidence that chimpanzees understand some of the psychological states of others (Povinelli and Eddy, 1996; Call et al., 2000). Given previous findings that in situations similar to the current experiment some monkey species are not able to use occluders to hide from a human, it is possible that this ability is not a hominid specialization but instead a hominoid specialization (Kummer et al., 1996). But, importantly, chimpanzees show such understanding only, or at least most naturally, in situations involving competition not cooperation - suggesting that many human cognitive differences derive from our ability to cooperate with one another culturally and linguistically (Tomasello, 1999). And of course there are still types of deception - for

example, active falsification and deception involving language (i.e., lying) - that may prove to be the sole province of human beings.

*Part V: Chimpanzees are more skillful in competitive
than in cooperative cognitive tasks*

Introduction

There is currently a very large discrepancy in the findings of different studies of chimpanzee social cognition. On the one hand, recent research has shown that chimpanzees know what other individuals can and cannot see, and even what others have and have not seen in the immediate past (Hare et al., 2000; 2001). Moreover, in some situations they can also formulate behavioral strategies to actively manipulate what others can and cannot see by hiding their own approach to contested food (Hare et al., submitted). In all of these studies chimpanzees display their understanding and skills from the very first trials of testing, with no training from humans required. On the basis of these studies, therefore, we might conclude that chimpanzees understand some of the psychological states of others, and they can even take measures to actively manipulate those states when it is to their own advantage.

On the other hand, in a different experimental paradigm chimpanzees show surprisingly weak social-cognitive skills. Of special importance is the so-called Object Choice paradigm. In this paradigm subjects are presented with two opaque containers, only one of which contains food (and they know this - and also that they can choose only one). A human experimenter then looks or points continuously at the container with food hidden inside. In the study of Call, Hare, and Tomasello (1998) not one of six chimpanzees used this cue to find the food. Tomasello, Call, and Gluckman (1997) and

Call, Agnetta, and Tomasello (1999) provided chimpanzees with several other types of visual-gestural cues in this same paradigm and also found mostly negative results. Povinelli, Bierschwale, and Cech (1999) found that some chimpanzees could learn to use similar cues after several dozen trials, but they also showed in various ways that this was for them only a learned behavioral cue, not an indicator of the visual experience of others; for example, when the experimenter turned his head in the direction of the baited container but looked to the ceiling, subjects chose the correct container just as often as if the experimenter looked directly at it. Itakura, Agnetta, Hare, and Tomasello (1999) used a trained chimpanzee conspecific to give the gaze direction cue, but still found mostly negative results. Other primate species also take dozens or scores of trials to learn to use human social cues in the object choice paradigm (Anderson et al, 1995; Vick & Anderson, 2001; Neiworth et al, 2002). In addition, once primates learn to use one social cue to find hidden food in this task, they do not readily generalize to either a new social cue or a slight change in procedure using the same cue (Tomasello, Call, Gluckman, 1998; Povinelli et al, 1997). And it is not the case that the object choice paradigm is simply confusing for animals. Many studies show that domestic dogs are very skillful in this task, successfully using a variety of different social cues produced by both humans and other dogs - with no training from humans in this context (e.g., Hare et al., 1998, 1999; Miklosi et al., 1999). Indeed, in the one study in which chimpanzees and dogs were directly compared, the dogs were much more skillful - and this included puppies with very little human experience (Hare et al., 2002).

Chimpanzees' struggles in the object choice paradigm are thus surprising, given their skills in some other experimental paradigms. Their struggles are also surprising

given that many evolutionary theorists have noted that primates have an unusually complex socioecology that should result in strong selection for social-cognitive skills in general (e.g., Byrne & Whiten, 1988). One hypothesis for explaining this puzzle comes from considering more precisely the kinds of social problems that group living primates have faced over evolutionary history and in daily life. For example, primates avoid giving food calls when they discover monopolizable food, but instead are more likely to call when food is sharable (Dittus, 1984; Hauser et al, 1993; Hauser, 1997). In addition, primates have never been observed to indicate the location of hidden food to conspecifics overtly by gesturing towards it (Menzel, 1975; Coussi-Korbel, 1994; Hirata & Matsuzawa, 2001). These observations highlight the fact that group living primates are constantly competing against conspecifics for access to food and mates - so much so that it has been difficult to explain why primates live in social groups at all (Wrangham, 1980; Sterk et al, 1997). It thus follows that selection has favoured individuals capable of outcompeting conspecifics.

Based on this line of reasoning, Hare (2001) proposed the Competitive Cognition Hypothesis to explain the seemingly inconsistent pattern of results in experimental studies of chimpanzee (and perhaps other primate) cognition. The hypothesis predicts that chimpanzees will demonstrate the greatest skill and/or motivation in competitive, rather than in cooperative, cognitive tasks (see also Tomasello et al, 2003). The fact is that the paradigms in which chimpanzee social-cognitive skills have been most impressively displayed all are basically competitive in nature (Hare et al., 200; 2001; submitted). In contrast, in standard object choice tasks a cooperative human altruistically communicates to subjects the location of a monopolizable food resource - a situation

unlike those for which primate cognition is naturally adapted. Following this line of evolutionary reasoning, it is also not surprising that domestic dogs, who have been selected for cooperating and communicating with humans, perform best in cooperative-communicative cognitive paradigms such as the traditional object choice task.

Although such comparisons across studies are suggestive of a difference in chimpanzees' performance in cooperative and competitive tasks, what is needed is a single task setting within which chimpanzees experience social cues in either a cooperative or a competitive context. In the current study, therefore, chimpanzees were tested in the object choice paradigm in one of two ways. First, in some cases a human first established a cooperative relationship with a chimpanzee subject (e.g., by encouraging them in a friendly manner), and then later, in test trials, provided the cooperative-communicative cue of pointing to indicate the hidden food's location - all as in the standard object choice task. Second, in other cases a human first established a competitive relationship with a chimpanzee subject (e.g., by obtaining contested food whenever he could and protesting when the subject got food), and then later, in test trials, tried unsuccessfully to reach one of the two opaque test containers in an attempt to obtain it before the subject. The actual physical movements of the human in these two cases were actually highly similar: in both cases he extended his arm toward the hidden food's location. However, in one case he was doing this in an attempt to help the subject locate the food - in which case the subject had to read his communicative intentions - whereas in the other case he was doing it in an attempt to get the food for himself - in which case the subject only had to infer the target of his reaching action. To try to establish in more detail some of the specific parameters affecting chimpanzees' performance in this new

version of the object choice paradigm, we also tested them in a similar but different task involving simple discrimination (location) learning - also in both a competitive and a cooperative mode. Finally, in both the communication task and the discrimination-location task, subjects competed both against a human and a conspecific - to see if the nature of the competitor made a difference.

Experiment 1

In this study we tested whether subjects would be more successful at finding food when they could exploit unintentional cues from a human competitor or when a human cooperator intentionally provided communicative cues. We predicted that the subjects who were introduced to the competitor would be more successful in using a social cue to locate hidden food than those who were introduced to a cooperator - even though both groups were provided with an almost identical cue (extended arm) to the location of the hidden food. Perhaps importantly, the subjects for this study had previously been tested for their ability to use the social cues of a cooperative-communicative human in a standard object-choice task. There was no evidence from individual or group analyses that these subjects were capable of spontaneously finding hidden food when a human experimenter gazed at (oriented his eyes), looked at (oriented his face), or pointed to the hiding location containing the food (Barth et al, in prep).

Method

Subjects

12 chimpanzees participated in this study (Table 5.1 shows each subject's sex, age, rearing and testing history). All the chimpanzees tested live at the Wolfgang Köhler Primate Research Center in the Leipzig Zoo, Germany. Animals were not food deprived for testing, and water was available at all times throughout this and all subsequent experiments. All subjects were tested in a familiar testing room. Subjects could choose to stop participating at any time.

Name	Sex	Age	Rearing History	Testing History
Robert	Male	27	Nursery	2
Riet	Female	25	Nursery	1, 2
Fraukja	Female	26	Nursery	1, 2
Natasha	Female	22	Nursery	1, 2
Corey	Female	26	Nursery	2
Ulla	Female	25	Nursery	1
Frodo	Male	9	Mother	1, 2
Fifi	Female	9	Mother	1, 2
Sandra	Female	9	Mother	1, 2
Jahaga	Female	9	Mother	1, 2
Truddy	Female	9	Mother	1, 2
Patrick	Male	5	Mother	1, 2

Table 5.1. Subject's sex, age, rearing and previous experience in object choice studies who participated (1 indicates subject participated in Barth et al, in prep; 2 indicates subjects participated in Hare et al, 2002).

Apparatus

See Figure 5.1 for a picture of the experimental set up. A table (91x80cm) with a sliding food platform was placed inside a testing booth which included two Plexiglas testing

windows (71 x 60cm) with two oval hand holes. The sliding food platform (1 x .1 m) rolled in tracks cut into the top of a wooden table and could slide across the table between the two testing windows (90 cm). Two cups were attached to the sliding platform with hinges and were 50 cm apart. Two oval hand holes (10 cm x 3 cm) were cut into the subject's Plexiglas testing window and allowed subjects to reach their fingers out so that they could retrieve food from one of the testing cups when the sliding platform was pushed forward. Experimenter 1 (E1) could sit across from the subject on one side of the testing apparatus while experimenter two (E2) could slide the food platform b/w the subject and the experimenter.

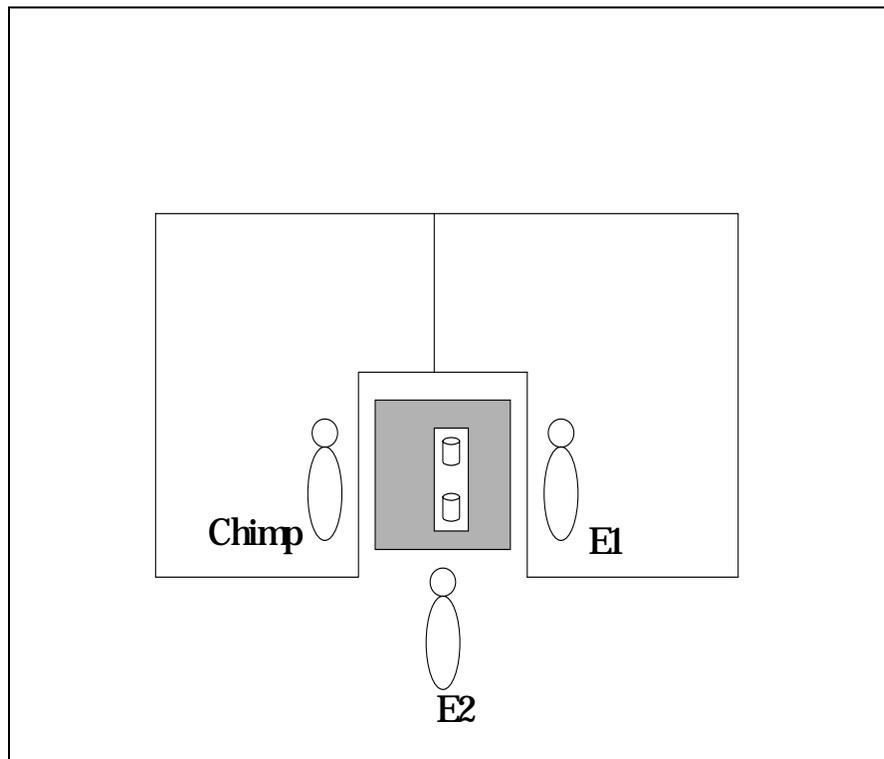


Figure 5.1. The experimental apparatus and the position of the subjects , social partner (competitive or non-competitive) and experimenter.

Procedure

Warm-up

First all subjects were introduced to the apparatus. Once the subjects were seated in front of the testing window with the two oval hand holes, E2 repeatedly placed food in one of the two cups and moved the food platform within reach of the subjects until they learned that they could reach through one of the two oval hand holes and retrieve the food reward by opening one of the cups. If the subject chose the cup in which the food was hidden first, they were allowed to retrieve the food. If the subject chose the incorrect cup first, E2 pulled the sliding platform out of reach, showed the subject that the food was in the other cup, but did not give the food to the subject. The food was hidden half of the time on the left and half the time on the right.

Introduction

After subjects knew how to use the apparatus, they were introduced to their informant (E1) who would provide a cue to the location of hidden food in the subsequent test. Half of the subjects received the introduction with a competitive informant and half of the subjects received an introduction with a cooperative informant. The informant sat across the booth and testing table from the subject so that both were looking directly at each other. As in the warm-up, the session began when the subject was seated or standing in front of the testing window. E2 then placed an opaque barrier (70cm x 40cm) between the food platform and the subject, showed the subject that they were holding food, and baited one of the cups with food. Therefore, the subjects knew that food was hidden, but did not know in which cup it was hidden. Then E2 removed the opaque barrier and

pushed the food platform within reach of the subject so that they could choose one of the cups. Meanwhile, E1 remained still while staring at a point slightly above the subject.

Once the subject chose to search in one of cups, E1 behaved in different ways depending on whether they would be a competitive or cooperative informant during the test session.

Competitor: E1 sat behind a Plexiglas window panel like the subject (except E1's

Plexiglas window had a large hole (10 cm x 8 cm) in the center of the window. This hole allowed E1 to reach his entire forearm out of the window, but not within reach of the food. If the subject chose the correct cup, as the subject retrieved the food, E1 banged on his Plexiglas window while rocking and staring at the subject. Meanwhile, if the subject chose the incorrect cup, E2 immediately slid the food platform within reach of E1 who opened the correct cup and ate the food (occasionally making food grunts) in view of the subject.

Cooperator: E1 did not sit behind a Plexiglas panel. Instead, the window frame was

empty. Therefore, E1 could have reached through the window at any time to grab the hidden food, but did not. If the subject chose the correct cup, E1 loudly encouraged the subject by repeatedly shouting things such as "good job" in a positive tone and occasionally clapping while the subject retrieved the food. Meanwhile, if the subject chose the incorrect cup E2 immediately slid the food platform within reach of E1 but E2 removed the food placing it in a food bucket while E1 apologetically shouted things such as "oh, sorry" to the subject.

Test

Immediately after the introduction session, subjects participated in the test session. The procedure of the test session was identical to the introduction except that during the test, once the food was hidden E1 gave a cue to the location of the hidden food.

Reaching cue: If E1 was a competitive informant, once the food was hidden, he reached out of the hole in the Plexiglas window (30 cm) extending effortfully toward the cup where the food was hidden (using his cross lateral arm). The hand was extend palm down and all fingers extended while the experimenter stared at the correct hiding location.

Pointing cue: If E1 was a cooperative informant, once the food was hidden, he extended his arm (30 cm) and pointed at the correct hiding location (cross lateral arm with only index finger extended) while gaze alternating between the correct hiding location and the subject.

Design

Half of the subjects were introduced and tested with the competitive informant and half with the cooperative informant. The warm-up, introduction, and test were given in one session to each subject. Subjects were given between 4-8 trials in the warm-up. In addition, subjects were given four warm-up trials before and half-way through both the introduction and test. For both the introduction and test sessions subjects were given 18 experimental trials. Therefore, subjects participated in a total 52 trials in the introduction and test session. Food placement was counter balanced within a session and across

subjects with half of the subjects having food hidden in the right cup first and half on the left first. Food was never hidden in the same cup on more than two consecutive trials.

Scoring & Analysis

E2 scored live which of the two cups was chosen first by each subject (first cup touched). All trials were videotaped by two video cameras. Each subjects performance in the test session was compared to chance (within the experimental trials of the test session subjects needed to make thirteen correct choices out of eighteen: binomial probability, one tailed) while the performances of the two groups with the different type of informant were compared to chance using one-sample t test and to each other with independent t tests. Given our prediction that subjects would find more food when competing against an informant, all tests are one tailed unless indicated otherwise (as they are in all subsequent experiments). Finally, effects of experience on the subjects performance within test sessions was assessed by comparing the number of correct choices within the first nine trials to the last nine trials within each group using paired t tests (two tailed).

Results

Table 5.2 presents the number of correct responses for each of the subjects in the test session. Three of the six subjects who were tested with a human competitor used the reaching cue above chance levels to find the hidden food ($p < 0.05$, binomial probability, in each case). Meanwhile, none of the subjects tested with a human cooperator used the pointing cue to find the hidden food. Figure 5.2 presents the mean number of correct

responses for both groups of subjects. As a group, the subjects who were tested with a competitive informant used the reaching cue above chance [$t(5)=3.67$, $p=.008$] while the

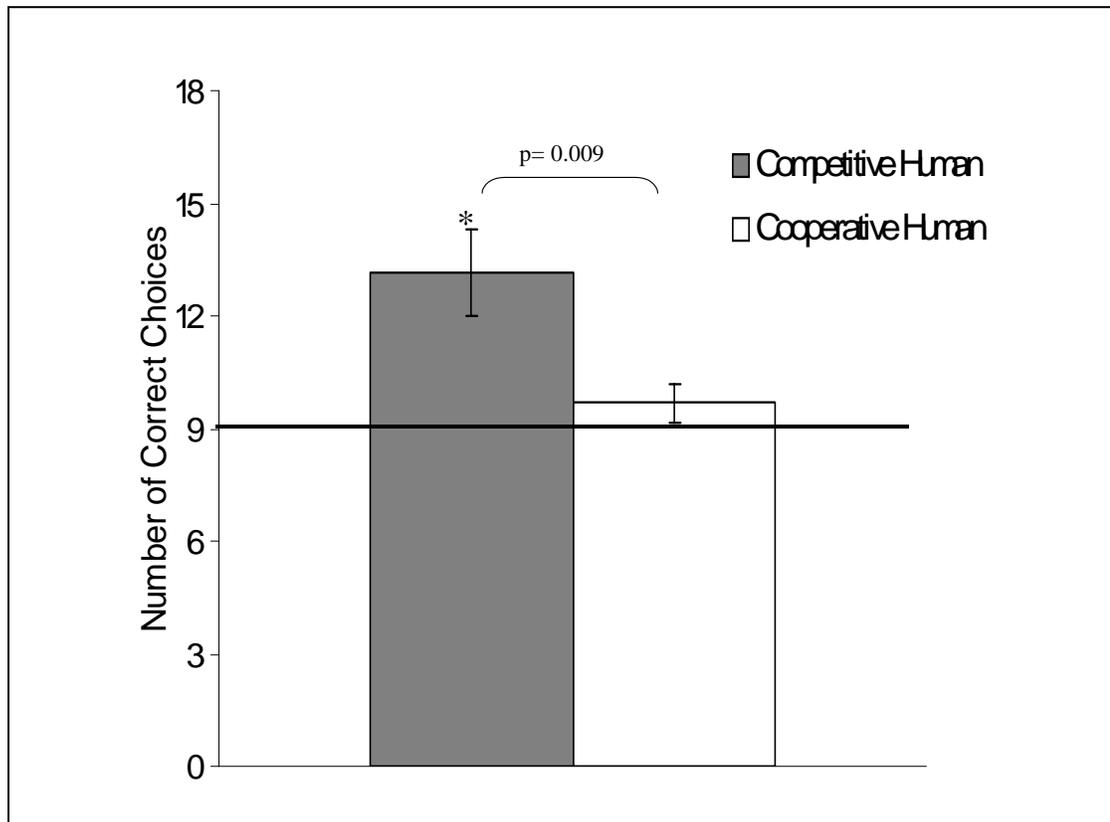


Figure 5.2. Mean number of correct choices (\pm SEM) by subjects tested with a competitive and cooperative-communicative experimenter in Experiment 1.

group performance of subjects tested with a cooperative informant did not use the pointing cue at above chance levels ($t(5)=1.38$, $p= NS$). In addition, when the performance of the two groups is compared, the group exposed to a competitor's reaching cue found significantly more food than the group exposed to a cooperator's pointing cue [$t(10)=2.82$, $p=.009$]. Finally, when the first and last half of the test trials within each

group are compared, there was no effect of experience - either when the groups are considered together or separately. Subjects thus came to the experiment with the skills they display; they did not learn them in the experiment.

subject	Experiment 1		Experiment 2		Experiment 3		Experiment 4	
	Human Reach	Human Point	Human Competes	Human Cooperates	Conspecific Reach	Human Point	Conspecific Competes	Human Cooperates
Robert	13	-	-	12	9	12	9	9
Reit	12	-	8	-	15	9	15	9
Jahaga	17	-	-	8	17	11	12	11
Sandra	16	-	11	-	14	16	11	9
Fifi	11	-	-	10	15	14	15	11
Truddy	10	-	11	-	17	16	13	9
Natasha	-	8	-	9	11	9	8	16
Fraukja	-	10	7	-	9	9	12	10
Cory	-	9	-	11	11	9	9	9
Ulla	-	11	9	-	10	8	15	10
Frodo	-	9	-	9	16	15	10	5
Patrick	-	11	9	-	10	9	10	7
MEAN S	13.17	9.67	9.17	9.83	12.83	11.42	11.58	9.67

Table 5.2. Number of correct choices in the test session by each subject in each experiment. Scores in bold are significantly above chance (binomial probability, $p < .05$).

Discussion

Chimpanzee subjects who were introduced to and tested with a human competitor performed better in an object choice task than those who were introduced to and tested with a human cooperator-communicator. Whereas more than half of the subjects tested with a competitor were above chance (as individuals) in using the reaching cue to find the hidden food, none of the subjects tested with the cooperator was above chance (as an individual) in using the pointing cue to find the hidden food - which led to a significant group difference in favor of competition as well.

It is important to emphasize that during testing the behavior and social cues provided by the human were highly similar in the two conditions: the experimenter reached or pointed toward the food with an outstretched arm and hand. What differed across conditions was only the context set up before the testing - competitive or cooperative - and the facts that: (1) in the cooperative test trials the cooperator alternated gaze between food location and subject, as is typical in intentional communication (see Tomasello et al., 1985, for observations of gaze alternation in chimpanzees during natural gestural communication); and (2) in the competitive testing condition the competitor obtained and ate the food reward after trials in which the subject chose incorrectly. It is also noteworthy that chimpanzees' poor performance in the cooperative condition was despite the fact that they had received, in a previous experiment, 50 differentially rewarded trials with a cooperative-communicative experimenter in the object choice task (Barth et al., in prep), and so could potentially have learned the direction of the hand (or some such) as a simple discriminative cue indicating food location.

These results thus provide the first direct support for the Competitive Cognition Hypothesis, in the sense that chimpanzees performed better in the exact same task under conditions of competition than they did under conditions of cooperation. Further support is also provided by informal comparisons of different studies, using different experimental paradigms, in which chimpanzees seem to show their most complex social-cognitive skills in competitive settings - which suggested the hypothesis in the first place (Hare, 2001). But precisely how and why competition should activate or facilitate chimpanzees' social-cognitive skills, in a way that cooperation seemingly does not, remains to be determined. As a first step in this direction, in Experiment 2 we tested whether the observed effect in Study 1 is limited to situations in which subjects can exploit the behavior of others when competing with them, and so employ their social-cognitive skills, or whether competing for food improves chimpanzees' performance even in a simple discrimination task in which the individual simply needs to learn that the food is always to be found at the same location (with one shift to the other location in the middle of the trials).

Experiment 2

Experiment 1 established a basic phenomenon, but the two experimental conditions differed from one another in a number of ways. In a second study, therefore, we changed one key parameter: the cognitive task to be solved (i.e., the nature of the information available for locating the hidden food). In this study subjects had to find hidden food based on where they had seen it hidden in previous trials (it was hidden in the same cup for 9 consecutive trials and then in the opposite cup for the last 9 trials of a

test session) with no social cue given at all. They did this, as in Experiment 1, either with a competitive experimenter - who established a competitive relationship before testing and who obtained and ate the food during testing on trials in which the subject was incorrect - or with a non-competitive experimenter - who established a cooperative relationship before testing and who never obtained or ate the food during testing. The question being asked is thus whether performing in a competitive versus cooperative environment affects chimpanzees' performance in a very simple cognitive task in which the competitor and cooperator provide no social cues - and in fact are mainly incidental to the task at hand.

Method

The subjects and apparatus were the same as in Experiment 1 (see Table 5.2 for the subjects in each test group). The introduction procedure establishing a competitive or cooperative relationship between experimenter and subject, before testing, was also identical. The test procedure was also identical except that no cue to the location of the hidden food was provided in either condition (i.e. the experimenter did not reach or point toward the correct cup before the subject made their choice). The only information about the food's location available to subjects during testing was the fact that in the first 9 trials the food was hidden in the same cup, and then it was hidden in the opposite cup for the last 9 trials of the session. There were 3 sessions so that subjects had a total of 44 trials. Half of subjects in each group had food hidden in the right cup for the first 9 trials and left cup for the next 9 trials - and vice versa for the other group of subjects. Scoring and analysis were the same as in Experiment 1.

Results

Table 5.2 presents the number of correct choices for each of the subjects. No individual in either group found the hidden food at above chance levels ($p > .05$, binomial probability, in all cases). Figure 5.3 presents the mean number of correct responses for

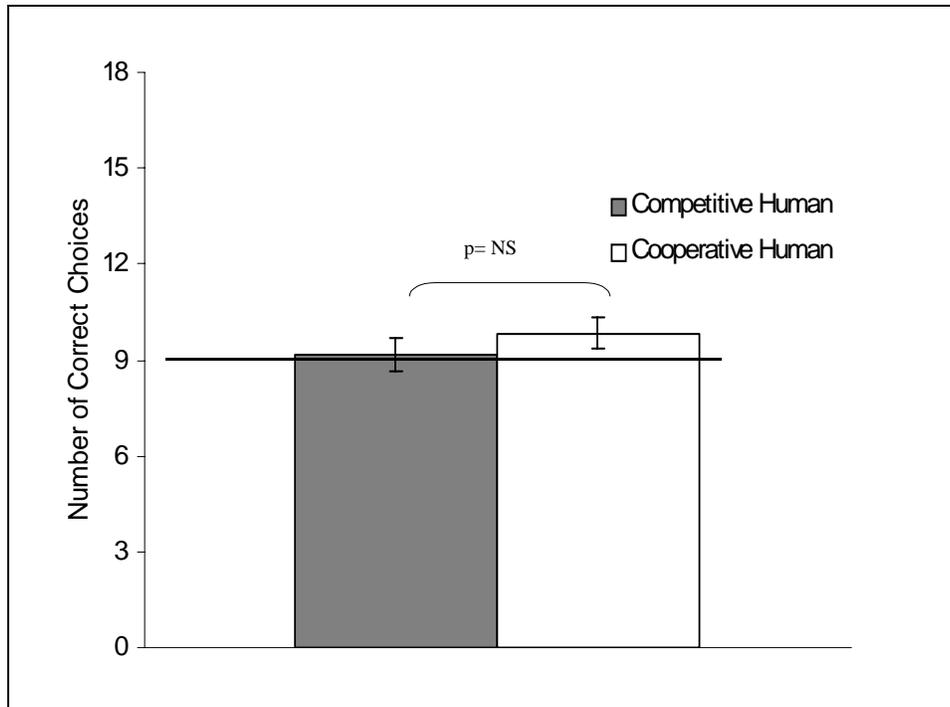


Figure 5.3. Mean number of correct choices (\pm SEM) by subjects tested with a competitive and non-competitive human in Experiment 2.

both groups of subjects. Neither group found food at above chance levels, and there was no difference between the performance of subjects between the two. Finally, when the first 9 test trials are compared to the last 9 trials within each group there was no evidence for learning overall - although subjects found significantly less food in the last 9 trials than in their first 9 trials with a non-competitive experimenter [$t(5) = 6.51$, $p = 0.002$].

Interestingly, all but one subject had a significant preference (14 or more trials, $p < .05$, binomial probability, two tailed) for only choosing one of the two cups throughout the entire test session. Side biases are most often observed when subjects are not able to use any other information provided.

Discussion

The competitive context did not make a difference to chimpanzees' performance in this simple discrimination task in which the location of hidden food was best predicted by its location on the previous trial. In this task, the cooperator and competitor were essentially nothing more than onlookers, unlike in Experiment 1 where they gave the essential cue to the food's location. One interpretation of this result is that the kind of cue provided in Experiment 1 was a crucial part of the experimental manipulation.

Specifically, it may be that subjects perceived the reaching as one instance of trying to accomplish something, since in other studies chimpanzees have shown the ability to distinguish trying from not trying (Call et al., submitted). On the other hand, they did not know what to make of the pointing gesture, which did not look like trying because the human's reach was not blocked and she alternated gaze (whereas in trying the human stays focused on the goal).

Alternatively, it is possible that this task was simply too difficult, given that no individual or group found food at above chance levels. In the object choice tasks in which these same subjects have previously been tested (Barth et al, in prep), food was not hidden in the same hiding location for more than two trials in a row (including in the introduction of the current experiment). When subjects cannot find food reliably, they

frequently develop an optimizing strategy in which they exclusively choose the same cup (Itakura et al, 1999). By repeatedly choosing the same cup they are assured of 1) going no more than two trials without finding food 2) finding food in half of trials (assuming side is counterbalanced). Indeed, an examination of subject errors shows that all but one subject had a significant side bias for one cup. This suggest that in this first exposure to the new baiting regime subjects were overly committed to their optimizing strategy regardless of their social partner - given that they did not find the information provided very salient.

Finally, it is interesting to note that it was only when subjects were tested with a non-competitive human that they found significantly less food in their last nine trials than in their first nine trials. While only suggestive, it may have been that subjects maintained their level of performance because they were more motivated when competing. If true, perhaps subjects will be even more motivated and find more food if they are tested on the same task again, but this time with a conspecific competitor replacing the human competitor. In order to test the effect of a conspecific competitor on the performance of subjects, we again tested subjects using the same two cognitive tasks in Experiments 1 and 2, except in both of our follow-up experiments a conspecific competitor was substituted for a human competitor.

Experiment 3

The current study was a replication of Experiment 1 with the exception that the competitive informant in this task was a conspecific. In addition, unlike the first two experiments all subjects were tested with this conspecific first. It was only after all

subjects had competed against a conspecific that they were again tested with a cooperative-communicative human informant. The prediction is that even though all subjects will have more exposure to the social cue being provided (extended arm and hand) when tested with a cooperative human, they will still find less food than they did when previously tested with a competitive conspecific who provided the same cue.

Method

Subjects

Subjects were the same as in Study 1 and 2. Two of the 12 subjects played the role of competitor in place of E1 (competitive informant). These conspecific-competitive informants were chosen based on their size, motivation, and rank within the group. After experiment 2 was completed and before the current experiment, 11 of 12 of our subjects (Ulla was not tested) participated in Hare et al. (2002) in which a cooperative-communicative human indicated the location of hidden food to subjects by gazing at, reaching toward, touching, and leaving a wooden block on top of the baited cup. Only 2 (Truddy & Patrick) of the 11 subjects tested used these conspicuous social cues to find the hidden food at above chance levels (meanwhile 9 of 11 dogs used the same cues to find the hidden food). Note that all three subjects who used the cues of the competitor in Experiment 1 again failed to use a similar cue when it was again provided by a cooperative-communicative human informant.

Apparatus

Again, a table was placed in the testing booth between two Plexiglas testing windows. A few modifications were made to the table and the Plexiglas window on the side of the informant to make it possible to have either a conspecific or human informant (see Figure 5.4). For both informants the window frame was partially occluded by pieces of plastic (60 x 25 cm) so that it was only possible for the subject to see the informant when their body and head were equidistant between the two testing cups. In addition, when a conspecific was the informant an additional piece of plastic could be placed over



Figure 5.4. The social cue provided by the competitive conspecific and the non-competitive human in experiment 3.

the hole (10 x 8 cm) in their Plexiglas window that created a smaller vertical oval (7 x 3 cm). Finally, a piece of Plexiglas (65 x 10 cm) was attached on the subjects side of the food platform via a metal slide (allowing it to slide 14 cm). Therefore, to choose and

open one of the two cups on the food platform subjects first needed to push the Plexiglas out of the way.

Procedure

Before testing a conspecific informant was identified that would reliably reach out toward a cup of food when placed just out of reach on the food platform while another chimpanzee was across the table. Food (half a banana) was placed on the food platform and once both subjects were at the testing window the food platform was moved toward the conspecific informant until the food was just out of reach. The informant (Truddy) was tested dyadically (6 pilot trials) with the most dominant female (Riet) and she reliably reached for the out of reach food (Patrick was Truddy's informant). Once the informant was identified all the subjects were briefly (4-8 trials) reintroduced to the apparatus to make sure that the subjects were acquainted with the modifications to the apparatus. The subjects were shown that food they had seen hidden could be retrieved by 1) sliding the Plexiglas attached to the food platform to one side and 2) pushing open one of the two cups (attached with hinges) to the sliding food platform.

Introduction

As in the first two studies, the subjects were introduced to their informant before the test session. After the subject approached the testing window and the informant was ready, an opaque occluder (1 x .5 m) was placed in front of the informant's window so she was not visible to the subject. Then an opaque occluder (70 x 40 cm) was positioned between the food containers and the subject while food was hidden in one of the two

cups. Therefore, subjects knew that food was hidden but did not know in which cup it was hidden. Once the food was hidden, E2 removed the opaque occluder hiding the cups, pushed the food platform toward the subject, and allowed them to reach through one of the choice holes. If the subject chose the correct cup, they were allowed to retrieve the food and 1) the human informant loudly praised the subject or 2) the conspecific competitor often showed signs of frustration (screaming, shaking hands vigorously, rocking, or pacing). Meanwhile, if the subject chose the incorrect cup the occluder in front of the informant was removed, the food platform was moved out of reach and 1) E2 removed the food while E1 said “so sorry!” or 2) the conspecific competitor was allowed to retrieve the food.

Test

The procedure was the same as that in the introduction with the exception that 1) an opaque barrier was not placed in front of the informants so that they could watch the baiting 2) Once the food was hidden the food platform was first pushed in the direction of the informant so that they could provide a cue to the food location (see Figure 4) and 3) during all test session there were a number of motivational trials included in which the food was hidden, as in a test trial, but the conspecific competitor was allowed to retrieve the hidden food while E2 retrieved the food from the cups once it was pushed toward the cooperative-communicative human.

Design

All subjects were tested with the conspecific informant first and then the human informant second. In each introduction and test subjects were given four warm-up trials and 18 experimental trials. In addition, within the test session nine motivational trials were conducted (to maintain the informant's motivation for reaching). Therefore, subjects participated in a total of 53 trials. Food placement was counter balanced within sessions and across subjects with half of subjects having food hidden in the right cup first and half on the left first. Food was never hidden in the same cup on more than two consecutive trials. Scoring was the same as the previous experiments.

Results

Table 5.2 presents the number of correct responses for each of the subjects in the test session. Six of twelve subjects who were tested with a conspecific competitor used the reaching cue above chance levels to find the hidden food; four of twelve subjects tested with the human informant used the pointing cue to find the hidden food ($p < 0.05$, binomial probability, in each case). Figure 5.5 presents the mean number of correct responses for both groups of subjects. As a group, the subjects found the food at above chance levels when being cued by a conspecific competitor and a human informant (conspecific competitor: $t(11) = 4.24$, $p < 0.001$; human informant: $t(11) = 2.74$, $p = 0.02$). However, when the two groups are directly compared, subjects found significantly more food when they were competing against a conspecific competitor than when they were cooperating with a human [$t(11) = 1.85$, $p = .045$]. Finally, when the first nine trials are compared to the last nine trials in each session there was no effect of experience.

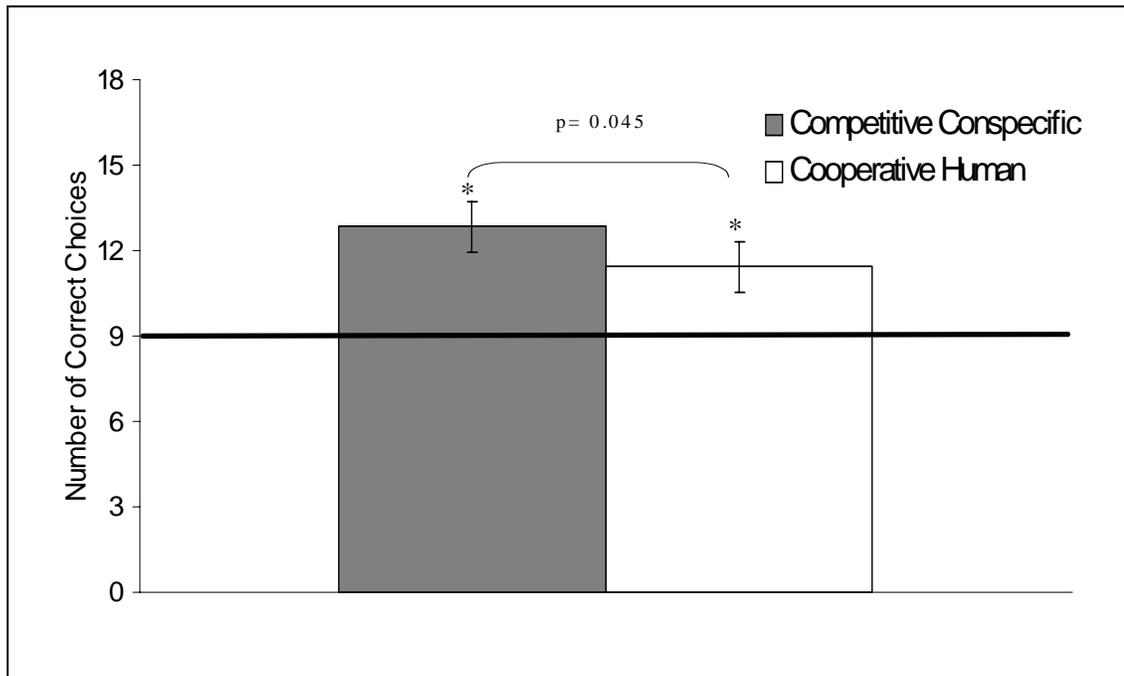


Figure 5.5. Mean number of correct choices (\pm SEM) by each subject when tested with a competitive conspecific and a cooperative-communicative human in Experiment 3.

Discussion

As in Experiment 1, chimpanzees in this study were more successful at using a social cue to find hidden food when they were competing than when they were cooperating. The difference was that in this case the other individual they were competing against was a conspecific (the cooperator, of course, had to be a human again). This was true even though subjects had less experience when tested with the competitor (all subjects were tested with a conspecific competitor first). Interestingly, however, subjects were better in the cooperation condition of this study than they were in

Experiment 1, even though the conditions were basically identical. The most plausible explanation is that chimpanzees can learn to exploit a pointing cue with some experience - as established by previous research (see Povinelli et al, 1997 and Call et al, 1998; 2000) - and so by the time they engaged in this condition they had learned to use arm extension as a discriminative cue to the food's location. Evidence for this interpretation is the fact that all of the individuals who used the cues of a cooperative-communicative human successfully in this study had already been successful using the social cue when competing either in Experiment 1 or the first session of the current study.

Experiment 4

The current study was a replication of Experiment 2 (discrimination-location task), with the exception that the competitive informant in this task was a conspecific. In addition, like Experiment 3 using a conspecific competitor, it was only after all subjects had competed against the conspecific that they were again tested with a non-competitive human. Although in Experiment 2 subjects did not find more food in this simple task when competing against a human, it may be that they will perform more skillfully in this study when they are competing against a groupmate with whom they compete on a daily basis.

Method

The subjects and apparatus were the same as in Experiment 3 (conspecific competitor). The procedure was basically the same as in Experiment 2 (discrimination-location task). The subjects were given 4 warm-up trials (as well as the conspecific

competitors) and 18 introduction trials in which food was hidden in one of the two cups for no more than two consecutive trials and placement was counterbalance within and between subjects. After the introduction, subjects again received four warm-up trials (as did the conspecific competitor), and then in the test session food was hidden in one of the cups for blocks of 9 trials (the placement on the first trial was counterbalanced across subjects). Therefore, subjects received a total of 44 trials. Scoring and analysis were the same as in the previous experiments. One small difference in procedure is that in this study the conspecific's/human's Plexiglas window was covered throughout the trial (in both the introduction and test) until the subject chose to search one of the cups (therefore informants provided no social cues at the time of choice).

Results

Table 5.1 presents the number of correct responses for each of the subjects in each condition. Four of 12 subjects who were tested with a competitive conspecific found the food at above chance levels; only one of 12 subjects found the hidden food at above chance levels when tested with the non-competitive human ($p < .05$, binomial probability, in each case). Figure 5.6 presents the mean number of correct responses for both conditions. As a group, subjects found food at above chance levels when competing against a conspecific [$t(11) = 3.58$, $p = .002$], but not with the non-competitive human [$t(11) = .86$, $p = \text{NS}$]. In addition, subjects found significantly more food when competing against a conspecific than when interacting with a non-competitive human [$t(11) = 1.86$, $p = 0.044$]. Finally, when the first nine trials are compared to the last nine trials in both test sessions there was no effect of experience within either session.

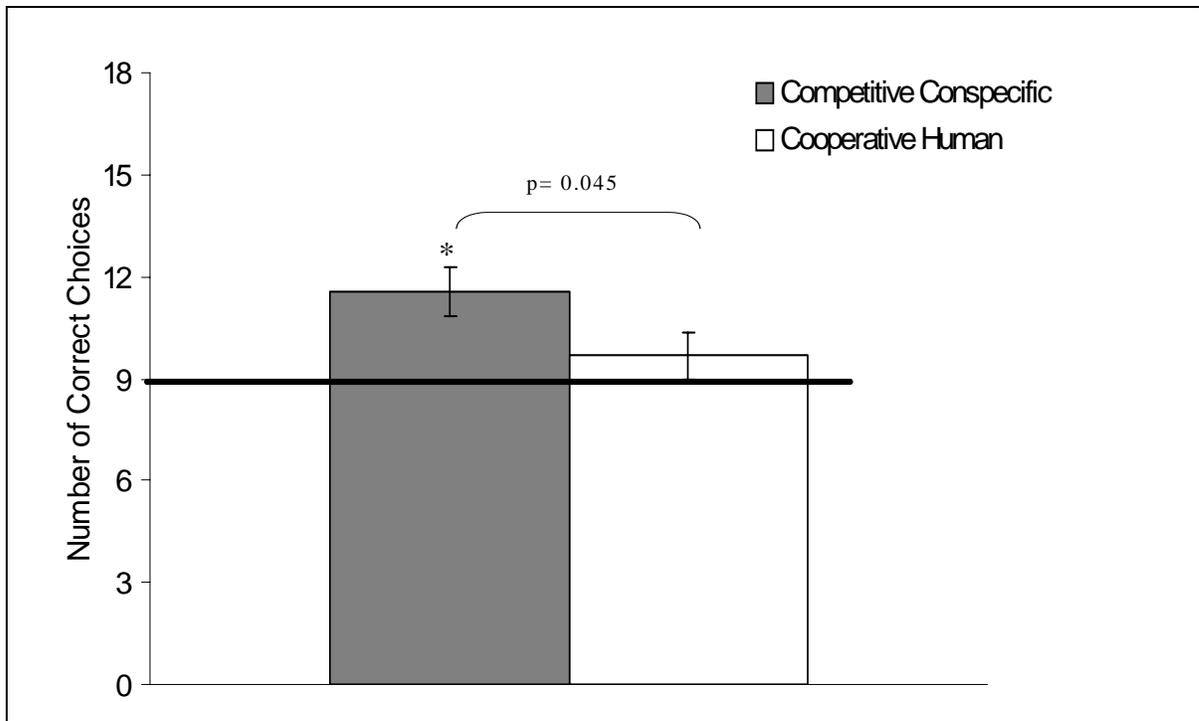


Figure 5.6. Mean number of correct choices (\pm SEM) by each subject when tested with a competitive conspecific and a non-competitive human in Experiment 4.

Discussion

In Experiment 2, chimpanzees did not learn reliably to find food in the location they last found it regardless of whether they were paired with a cooperative or competitive human. In this study, they finally learned to do this, but only when competing against a conspecific (not in the presence of a non-competitive human). Again, as in Experiment 3, it is important to note that this difference was found even though subjects had more experience with this task when they were tested with a non-competitive human than when they were tested with a competitive conspecific. Because

the information available to subjects in the two conditions of this experiment was identical, the most likely explanation for the results is that subjects were simply more motivated when competing. The results of this study thus suggest that chimpanzees are more skilled at finding food when competing across a wide range of tasks. The negative results of Experiment 2 are most likely the result of the difficulty of the task; it took them many trials to learn it, and they learned it first only in this fourth study. They did this only with the conspecific competitor; whether they would have learned it just as well with human competitor in the fourth study is at this point an open question.

General Discussion

In the current study chimpanzees performed better in two different tasks when competing than when cooperating. In the standard object choice task, this finding was robust regardless of whether the competitor was a human or another chimpanzee. In a simple discrimination-location task in which food was repeatedly found at the same location (with one switch), chimpanzees did not at first become skillful whether competing or cooperating with a human, but in a later study they did become skillful - but only when competing (not cooperating) with a conspecific. Whereas comparison across other studies had previously suggested that chimpanzees display their most sophisticated cognitive skills in competition rather than in cooperation, this is the first study to demonstrate this directly in a single experimental paradigm.

Experiments 1 and 3 were designed to replicate the standard object choice procedure that has become increasingly popular in testing the ability of animals to exploit the social cues of others. The majority of research with chimpanzees using the object

choice paradigm has found that subjects typically require considerable experience before they reliably use human social cues to find hidden food. Experiments 1 and 3 demonstrate that it is possible to improve subjects' spontaneous performance with social cues in this same task by simply having them compete. Critically, in both experiments what varied between the types of interactants was not the available social cue - an outstretched arm and hand in both cases - but instead the social context in which the cue was provided. The context was differentiated by introducing the subjects to two types of interactants who reacted to their success and failure in completely opposite ways. While the competitor protested the subjects' success and ate the reward when they were wrong, the cooperative-communicator was supportive of the subject in success and failure and never ate the food reward. It was only after subjects were introduced to their social partner that the competitor unintentionally informed the subject as they reached for the out-of-reach food while the cooperative-communicator intentionally communicated to the subject by pointing to the food within his reach. In support of the Competitive Cognition Hypothesis, the main finding was that subjects found more food when their social partner was a competitor. Therefore, from these results it seems that chimpanzees maybe more skilled and/or motivated to exploit social cues when they are competing over the food rewards.

Experiments 2 and 4 found that this effect is not confined to the object choice task involving the reading of a social cue at the time of choice, but it also extended to a simple discrimination task in which there were no social cues. In these studies subjects were again introduced and tested either with a competitive or non-competitive social partner, but in a task where food location on the previous trial was the only cue. Specifically,

subjects could only reliably find the food by remembering where they had either found or seen food hidden at the end of the previous trial. In Experiment 2 subjects were unsuccessful regardless of the social context. However, in Experiment 4 subjects found more food when they were competing against a conspecific than when they were interacting with a non-competitive human. This suggests that the Competitive Cognition Hypothesis applies to a range of cognitive tasks. Because the second study was run before the fourth study, is not totally clear if the conspecific competitor is a crucial part of the competition effect in this task.

The findings of Experiments 1 and 3 are consistent with the hypothesis that chimpanzees do not understand the communicative intentions of humans. The critical test for this hypothesis is each subjects' first encounter with the pointing cue before they can simply learn a contingency between the cue and the food location. In the first experiment, six subjects were given the pointing cue by a human who had demonstrated no interest in the food reward during the introduction. All of these subjects were unable to find the food with the pointing cue. Subsequently in Experiment 3, only subjects who had previously been successful using a competitor's reaching cue were also successful when in their next session a human pointed. Perhaps most striking are the performances of two subjects, Riet and Jahaga, who were both successful using the cues of a competitor, but then were unable to use the same social cue to find food when the cue was provided by a cooperative-communicative human. Conversely, there was no subject who was able to use the social cue of a cooperative-communicative human but not that of a competitor. Therefore, these results support the hypothesis that chimpanzees do not understand the communicative intent of a cooperative-communicative experimenter.

However, at the same time that the results of Experiments 1 and 3 support the communicative intent hypothesis they are also consistent with a motivational hypothesis. Subjects may have also found more hidden food when competing in these Experiments because they were more motivated to succeed and paid more attention when competing. The strongest evidence for this hypothesis comes from Experiments 2 and 4 where subjects could not base their decision on an available social cue at the time of choice. Subjects only were successful at finding hidden food when competing against a conspecific – arguably the most motivating social partner given that this competitor was an individual that subjects compete with daily. However, this explanation must account for subjects success in Experiment 1 and failure in Experiment 2 with a human competitor. One plausible explanation is that the task used in Experiment 2 and 4 was simply more difficult given that there were no cues to the food’s location at the time of choice. Therefore, success in this uncued task required a more motivating social partner – a conspecific competitor. Alternatively, subjects’ performances in Experiment 2 and 4 may not be due to differences in motivational levels, but instead a simple learning explanation. For example, subjects may have performed better in Experiment 4 since they had the benefit of participating in Experiment 2. However, this learning hypothesis cannot be the only factor explaining the subjects' performance in Experiment 4, since they fell back to chance when tested with a non-competitive human. Therefore, if there was learning, it was specific to the competitive social context.

Although there may be various ways to explain the effect of competition on chimpanzees performance in cognitive tasks, the current investigation has demonstrated with quantitative comparisons that there is a phenomenon that needs explanation. This

phenomenon highlights the importance of an ecological approach to theories of cognitive evolution and to the design of cognitive Experiments. There are few Experiments designed specifically to investigate the socio-ecology of primate social cognition (though see Drea & Wallen, 2002, for an exception), and there are no agreed-upon conventions for how to maximize the ecological validity of cognitive tasks for use with chimpanzees (e.g., Would being tested in a social group make a difference? Should males and females be tested in the same way?) Cognitive skills evolve to solve ecological problems relevant to maximizing survival and reproduction, and so to understand the process of cognitive evolution in any species we must identify the types of ecological problems that have driven their cognitive evolution. And we must also attempt to understand how cognitive skills are integrated with and possibly constrained by other psychological systems (e.g. emotional/motivational) that have also evolved to maximize survival and reproduction.

*Part VI: The domestication of social cognition in dogs*⁷

Introduction

It is predicted that primates, especially great apes and humans, should excel at social cognitive problem solving (theory of mind, broadly defined) (Byrne and Whiten, 1988; Humphrey, 1976). Indeed, recent research has shown that primates possess impressive social cognitive abilities. For example, many species of nonhuman primate follow the gaze direction of conspecifics and humans to outside objects – an adaptive social-cognitive skill for detecting food, predators, and social interactions among groupmates (Tomasello et al., 1998). Chimpanzees even follow the gaze direction of humans past distracting stimuli and behind barriers to a specific target, and they also understand that another individual cannot see something if its perspective is occluded by a barrier - thus demonstrating a fairly sophisticated understanding of how the visual perception of others works (Hare et al., 2000; Hat et al., 2001; Tomasello et al., 1999).

Curiously, however, there is one task involving gaze following in which chimpanzees and other primates perform poorly. In the so-called object choice task, an experimenter hides a piece of food in one of two opaque containers, and the subject, who did not see where the food was hidden, is allowed to choose only one. Before presenting the subject with the choice, the experimenter gives a communicative cue indicating the food's location, for example, looking at, pointing to, tapping on, or placing a marker on the correct container. The large majority of primates choose randomly in this task, no

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matter the cue, and those who eventually perform well typically take hundreds of trials to learn (Anderson et al., 1995; Call et al., 2000; Povinelli et al., 1997).

In contrast, domestic dogs (*Canis familiaris*) are skilled in the object choice task. Dogs use many different visual cues presented by humans (e.g., looking at, pointing to, or touching the correct container), including novel cues such as the placing of an arbitrary marker on the correct container. They even are successful if the human moves toward the incorrect choice while giving the cue, or when the cues are presented statically (e.g., the dog enters the room to see the human already looking or pointing). Many dogs are skilful from the first trial, with no learning effects observed during the experiment. Importantly, controls have ruled out the possibility that dogs use olfactory cues to find the hidden food (Agnetta et al., 2001; Hare and Tomasello, 1999; Hare et al., 1998; Soproni et al., 2001).

An obvious question is how domestic dogs have acquired these skills. One hypothesis is that canids in general are unusually flexible in the types of social information they are capable of exploiting. For example, wolves, the closest relative of dogs (Vila et al., 1997), permanently live in cooperatively hunting social groups, making it likely that they need to exploit the behavior of conspecifics and quarry alike - and this ability may then generalize to humans (Povinelli et al., 1997). This hypothesis predicts that many canids (and especially wolves) should show similar skills as dogs. Another hypothesis is that domestic dogs have much more experience with humans than most primates, and so they have learned their skills during their individual ontogenies. This hypothesis predicts that variation in individual dogs' experience with humans will be associated with variation in task performance – and, as a corollary, young dogs should have relatively poor skills. Finally, a third hypothesis suggests that there has been

selection pressure on dogs during domestication for specific skills of social cognition and communication with humans. This hypothesis predicts both that dogs should be more skilful than wolves and that variations in human experience should not effect the performance of either species, and past a certain age dog puppies should be as skilful as older dogs. In the current studies we tested among these three hypotheses by comparing the performance of (1) adult dogs and wolves who were both reared by humans and (2) puppies of various ages and amounts of exposure to humans.

In a first experiment 7 adult wolves and 7 adult dogs⁸ were administered a series of object choice tasks⁹ in which they had to choose one of two opaque containers, whose contents they did not know (and only one of which contained food)¹⁰, based on the following communicative cues: 1) Gaze+Point+Tap Cue (GPT): The experimenter looked toward the baited bowl while extending their cross-lateral arm and tapping on it

8 Seven wolves (mean 6.14 years) and seven dogs (mean 3.5 years) participated. The wolves lived together at the Wolf Hollow Sanctuary, Ipswich Massachusetts, USA in large outdoor enclosures (.6 hectare). The wolves were raised by humans for the first three months of their life and subsequently interacted with their caretakers daily. In addition, the 3rd author is a caretaker and collected the majority of the wolf data. Testing did not interfere with the wolves' daily activity or feeding schedule. Water was available ad libitum. The seven dogs were recruited from families living in the Boston, MA area.

9 Each wolf was tested individually in a familiar holding enclosure (40 m²). Each dog was tested individually in a familiar room. The test apparatus consisted of a plastic container (.6x.5x.4m) with a wooden board (1m long) placed on top which could be pushed forward with ease. Food was hidden underneath one of the two plastic bowls (10 cm diameter) placed at opposite ends of the board. Therefore, the experimenter could slide the bowls towards the waiting subject. The subjects indicated their choice of bowls by approaching and touching a plastic doorstop protruding from each bowl 10 cm.

10 An experimental session began after the subject could reliably find food they saw hidden in one of the bowls. This typically took 6-10 warm-up trials. For each experimental trial the subject was positioned in front of the apparatus and food was hidden under one of the bowls, but the subject did not see where. After checking that the subject was equidistant between the two hiding locations, the experimenter would gain the attention of the subject (by calling their name or showing them food) and give one of the cues. The experimenter then returned to their resting posture, and pushed the bowls forward to allow the subjects to choose. The subjects were only rewarded if they touched the correct bowl first.

for 3-5 seconds making a small noise. 2) Gaze+Point Cue (GP): identical to GPT except the tapping was replaced with pointing at the baited bowl (index finger 10-15 cm from the bowl). 3) Point Cue (P) identical to GP except no gaze cue given (the experimenter looked at the subject) 4) Control Cue (C): the experimenter gave no cue (looked straight ahead)¹¹.

Dogs found more food than the wolves with all three visual cues, but not in the control (Fig 6.1): GPT, $t(9.77)= 7$, $p < 0.001$, GP, $t(7.14)= 2.54$, $p= 0.038$, P, $t(7.33)= 2.2.78$, $p= 0.026$ (Welch independent two sample t-test). As a group, the dogs were significantly above chance on each of the cues: for GPT cue, $t(6)= 8.44$, $p < .001$; for GP cue, $t(6)= 3.413$, $p= 0.014$; and for P cue, $t(6)=3.7$, $p= 0.01$ (one sample t-test); however, they were not above chance in the control condition. As a group the wolves were above chance for one cue: GP cue, $t(6)= 2.45$, $p= 0.05$ (and not above chance for GPT cue, the P cue, or in the control condition). No effect of learning across trials was detected in either species.¹² Individually, all dogs were above chance on at least one cue while no wolf was above chance on any cue. No subject was above chance in the control condition. Seven dogs used the GPT cue, 5 used the GP cue, and 4 used the P cue to find the food above chance ($p < .05$, binomial test, one tailed). Three dogs used all three cues, 3 dogs used two cues (2 used GPT and GP and one GPT and P), and one dog only used one cue (GPT).

11 All subjects received cues 1-4 in order. A subject received no more than 18 trials per session. Therefore subjects were tested on at least eight days, receiving 36 trials in each of the four conditions for a total of 144 trials per subject (108 experimental trials followed by 36 control trials). Half of the trials were videotaped.

12 Learning within sessions was assessed by comparing 1) the first and second half of trials and 2) the first 5 and last 5 trials for each species by cue using paired t tests.

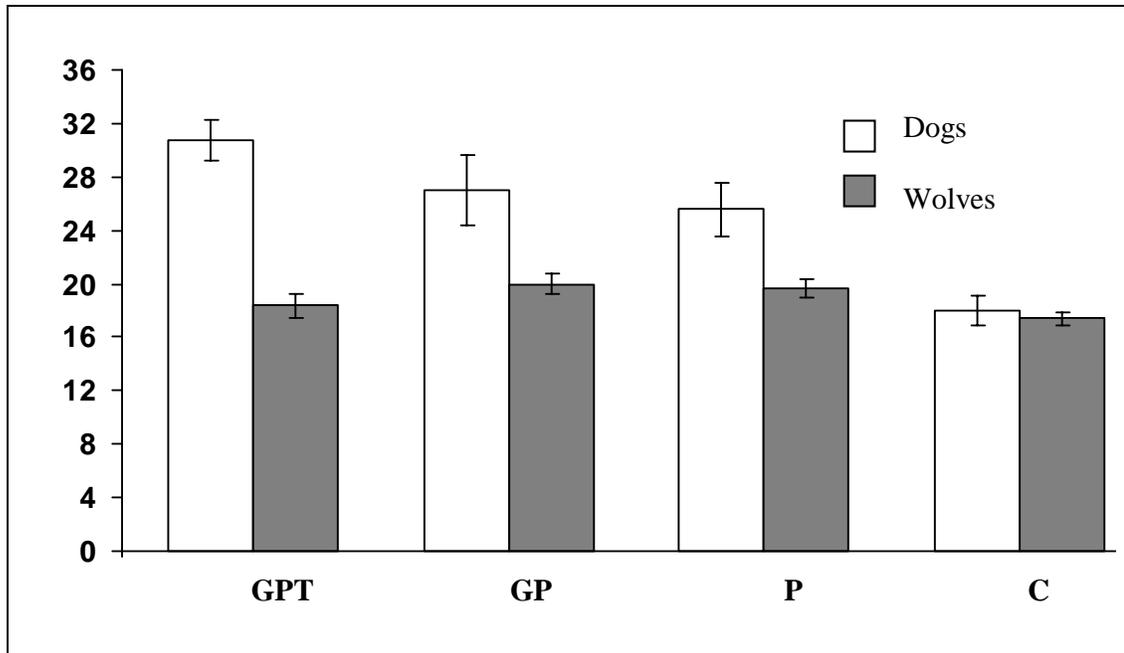


Figure 6.1. Mean number (\pm SEM) of correct responses by the seven dogs and wolves in each condition. Chance performance equals 18 correct choices.

In a second experiment, the same basic methodology was used¹³ with a set of 32 dog puppies varying in age from 9 to 26 weeks. The puppies were tested with two cues: 1) Gaze + Point (GP): same as for adults in experiment 1 and 2) Gaze (G): The experimenter turned his head in the direction of and stared at the bowl where the food was hidden.

Some puppies had lived with human families (adopted between birth and 8 weeks of life) throughout their lives (family-reared), whereas others had lived for their entire

¹³ The only changes were that the bowls were spread 1.5 m apart on the ground and a second experimenter held the subject until experimenter 1 gave a cue while lying on the ground (to assure the subjects saw the cue). In addition, experimenter 1 continued giving the cue while Experimenter 2 released the subject to find the food.

lives with littermates in a kennel and so had been exposed to humans for only a few minutes each day for husbandry purposes (litter-reared)¹⁴.

There was no difference between the rearing groups in their use of either cue (independent t-tests). Individually, 3 of 6 family-reared and 5 of 6 litter-reared puppies used the GP cue to find food, and 1 family-reared puppy used the G cue ($p < .05$, binomial test, one tailed). No effect of learning across trials was detected in either group (Fig 6.2). To test the effect of age on performance a cross-sectional analysis was conducted in which subjects were separated into three age groups (9-12 weeks, 13-16 weeks, 17-24 weeks).¹⁵

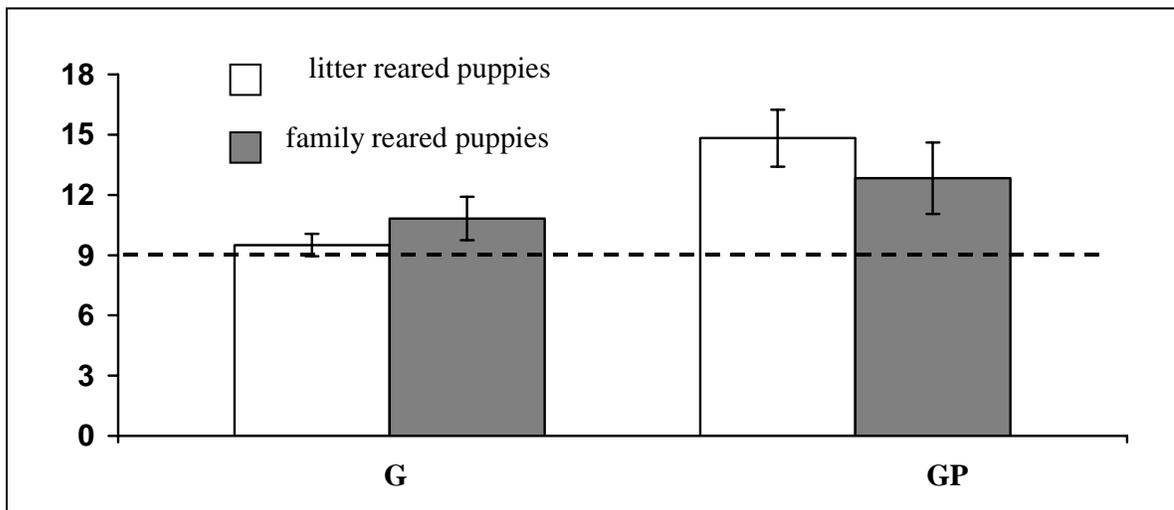


Figure 6.2. Mean number (\pm SEM) of correct responses by both rearing groups. Chance performance equals 9 correct choices.

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- 14 Twenty four puppies were recruited from puppy classes in Boston, MA. 8 puppies lived their entire lives with littermates awaiting adoption at Pik a Pup Kennel Holliston, MA. These puppies interacted with humans only briefly for a few minutes each day and only for husbandry purposes.
- 15 To test for the effect of rearing history 6 family reared puppies and 6 litter-reared puppies received 18 trials with both cues. The remaining dogs were only included in the cross-sectional analysis of age and performance receiving 18 trials with one cue. All trials were videotaped.

Using a two-way ANOVA with age and cue as factors, no effect of age was detected (Fig 6.3), but there was a group difference between the GP cue and G cue $F(1, 26)=16.15, p< 0.001$, with puppies finding more food when the GP cue was available than the G cue alone. However, as a group, puppies used both cues to find the food at above chance levels: GP cue, $t(14)=6.1, p<0.001$; G cue, $t(16)=3.26, p=0.005$ (one sample t-test). No effect of learning across trials was detected for either cue or age group.

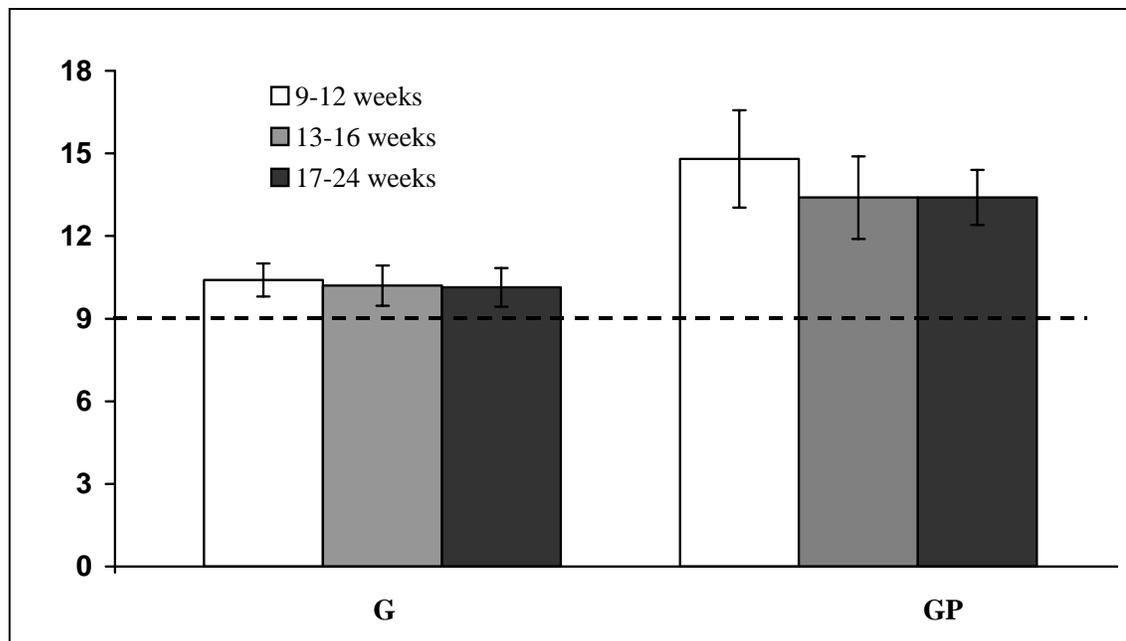


Figure 6.3. Mean number (\pm SEM) of correct responses for each age group of puppies with both cue. Chance performance equals 9 correct choices.

A number of studies have established that, unlike nonhuman primates, dogs are experts at using human communicative cues to find hidden food. The findings of our two studies replicate this result, and also provide strong support for the hypothesis that this

superior performance is due to the fact that dogs have undergone relatively extensive social-cognitive evolution during domestication. This hypothesis is suggested by the facts that: (1) the performance of the wolves in our study was relatively poor, resembling that of nonhuman primates; whereas (2) the performance of the dog puppies was much better - and this did not depend either on their age or on the amount of experience they had had with humans (which was, in all cases, less than that of the wolves who were family reared and as adults interacted with humans daily). It is thus likely that during the process of domestication, individual dogs that were able to use social cues to predict the behavior of humans were at a selective advantage. As a result, some aspects of the social cognitive abilities of dogs have converged, within the phylogenetic constraints of the species, with those of humans through a phylogenetic process of enculturation. In conclusion, our findings demonstrate a significant social cognitive difference among closely related nonhuman species while providing strong evidence for the adaptive context – in this case a unique context - in which this difference evolved.

*Part VII: Can competitive paradigms increase the validity
of experiments on primate social cognition?*¹⁶

Introduction

"...the success of the intelligence tests in general will be more likely endangered by the person making the experiment than by the animal. One must learn and, if necessary, establish by preliminary observation, within what limits of difficulty and in what functions chimpanzee can possibly show insight: negative or confused results from complicated and accidentally-chosen test-material, have obviously no bearing upon the fundamental question, and, in general, the experimenter should recognize that every intelligence test is a test, not only of the creature examined but also of the experimenter himself. I have said that to myself quite often, and yet I have remained uncertain whether the experiments I performed may be considered "satisfactory" in this respect: without theoretical foundations, and in unknown territory, methodological mistakes may quite well have occurred; anyone who continues this work will be able to prevent them more easily" –Koehler, 1925, pg 265.

Any observed behavior can have multiple explanations for how and why it might have occurred (Hauser, 2000). Therefore, cognitive ethologists design and conduct experiments for the purpose of distinguishing between different possible mechanisms which may be underlying the behavior(s), and more specifically problem solving behavior(s), of animals (Shettleworth 1998). The validity of an experiment (also referred to as experimental sensitivity) is the measure of an experiment's probability of being able to reject a null hypothesis or distinguish between competing hypotheses (Gottsdanker 1978; Shaughnessy & Zechmeister 1994). Investigators interested in animal cognition strive to maximize experimental sensitivity. In addition, they wish to objectively

16 Reprinted with permission from Hare, B. 2001. Can competitive paradigms increase the validity of experiments on primate social cognition? *Animal Cognition*, 4, 269-280.

evaluate the sensitivity of the experiments of others as well as their own.

Unfortunately, as Koehler (1925) so eloquently pointed out, depending on the quality of design, experiments vary in their ability to distinguish between competing hypotheses. In experiments on animal cognition this means that experiments vary in their ability to demonstrate that a behavioral strategy is guided by a sophisticated cognitive mechanism as opposed to various more parsimonious ones. Two components of design account for much of this variation 1) the proper use of experimental control (internal validity) and 2) the appropriateness of setting or situation in which the experimenter poses her experimental question to her test subjects (external validity) (Gottsdanker, 1978; Shaughnessy and Zechmeister, 1994). Therefore, experimenters interested in either designing or evaluating the validity of an experiment must take into account both the controls and setting of a paradigm.

Historically psychologists have placed a major emphasis on the utility of experimental control for the purpose of increasing the sensitivity of experiments (Shettleworth, 1998). Experimental control refers to the ability to produce a setting(s) in which one can isolate and manipulate a variable(s) relevant to deciding between two (or more) competing hypotheses (Martin and Bateson, 1993). There are many methods of control which have been developed and standardized such as controlling for order effects, removing biases using blind experimenters, and counterbalancing. The merits of the different methods of control are maximized when used appropriately and in concert; they are extremely powerful and can be applied to any species or paradigm allowing experimenters to objectively evaluate each other's experiments. In addition, if an experiment is controlled well, a positive result (rejection of the null hypothesis) reflects

the ability of the test subjects and should be replicable.

Less emphasis has been given to the limitations of experimental control. First, control can not make the results of an experiment generalizable to situations outside the test situation itself (Gottsdanker, 1978). Second, absolutely no amount of experimental control can help interpret negative results (i.e., an animal is unable to perform a task or performs in a way that is consistent with the null hypothesis) “which seldom lend themselves to diagnosis” (Premack, 1988: p179). No matter how well an experiment has been counterbalanced or randomized, it is impossible to hypothesize whether a null result was obtained because of the animal or because of the experiment. It is only after dozens of experiments and dozens of different approaches have been used that one can feel confident that null results might accurately reflect the ability of a test species (Heyes, 1998).

To illustrate the two limitations of control consider the following examples. Premack (1983) investigated the ability of chimpanzees to discriminate and match the relationships between different categories of objects. In this study he first presented subjects with a picture of either matched objects (AA) or mismatched objects (AB). Then he showed the chimpanzees two other pairs of pictures, one with a matched pair and the other with a mismatched pair of objects. It was the chimpanzee's task to choose the one that had the same relation as the original sample. For example, if the sample was AA and the choice was between CC and CD the chimpanzee was to choose CC. Premack (1983) found that language-trained chimpanzees successfully solved the task, while chimpanzees who had never learned any type of symbolic code failed. It was concluded that the different performances were due to the language capabilities of the successful

chimpanzees and that any chimpanzee without similar training would be unable to solve the task. But Oden et al. (1990) subsequently found that four infant chimpanzees (around 1 year old) with no prior training demonstrated an appreciation of the relationships that the chimpanzees of Premack (1983) did not. Why the discrepancy? Oden et al. (1990) used a procedure with the infants that simply allowed them to interact with different pairs of objects during a natural play bout. First they were allowed to play with one of two types of samples (AA or AB). Then they were given two pairs of objects (one CC the other CD) and were allowed to play with them, as they liked. Oden et al. (1990) found, when the new set of objects were handed to the subjects, they chose to play with the objects that was different from the one they had played with originally. This clearly demonstrated that they spontaneously recognized and could match the relationships of different objects.

Anderson et al. (1995) conducted the first experiment on gaze following (assessed by head movement) with two capuchin monkeys. In the experiment, a human turned his head in the direction of hidden food and stared. Anderson et al (1995) found no evidence that either monkey was able to use the human gaze to help in finding the hidden food. Subsequently, using a different method Itakura (1996) completed an exploratory study investigating the ability of 11 species of primates to follow the gaze of a human experimenter (the experimenter turned his head to the left or right). Again, from this study there was little evidence to suggest that any of the species of primates followed the gaze of the human experimenter. With this evidence it seemed that the gaze following skills of most primates and particularly monkeys was very limited. But Tomasello et al. (1998) hypothesized that these studies might have been affected by the fact that the

primates were required to follow a human gaze. Therefore, they designed an experiment that tested the ability of several species of primates (including four species of monkeys) to follow the gaze of conspecifics. All five species tested followed the gaze (head movement) of their conspecifics.

Oden et al. (1990), and Tomasello et al. (1998) were able to design more sensitive experiments because they realized that the original poor performance may not apply to all situations, and that the animal's difficulty in solving the task might be due to some aspect of the experiment that was irrelevant to the skill under investigation (also see Boysen and Bernston, 1995). Therefore, they designed new paradigms only after thought into which experimental setting would be most likely to allow animals to show their most sophisticated cognitive abilities. It was only after the appropriate setting was chosen that the methods of controls were developed.

Although methods of experimental control cannot help null results become more generalizable or interpretable, the second major component of validity potentially can. Assessing the external validity of an experiment, one puts test subjects in experimental situations that somehow simulate aspects of the real world that are relevant to the individual or species (Gottsdanker, 1978). If subjects are tested in settings with high amounts of external validity (such as during play or when animals are among conspecifics as in the examples above), the results obtained are more likely to apply to situations outside the actual test. In addition, even if negative results are obtained one can feel more confident that the results reflect the abilities of the animals and not simply the short coming of the experiment itself (although in the end negative results from any one experiment or approach remain difficult to interpret). In addition, as in the examples

above, experiments that consider validity should be more likely to yield positive results than experiments that are conducted in highly circumscribed or unfamiliar settings. Therefore, in the case of cognitive tests on primates, ecological validity, which I define as the degree to which an experiment is able to simulate a relevant aspect of test subjects' individual ontogenies and/or the evolutionary histories of their species, is the measure that becomes most important for evaluating external validity (Hare et al 2000, in press). In summary, experimental control alone does not allow one to maximize the validity of experiments on primates. Instead, the combination of using 1) control in 2) an ecological valid setting, allows one to maximize the validity of cognitive experiments on primates.

Captive Experimenters

Most studies of primate cognition are experiments, which are conducted in captivity (Tomasello & Call 1997; but see Cheney & Seyfarth 1990a). Captivity affords comparative psychologists the control which is essential for isolating and manipulating variable(s). For example, the beauty of the Skinner box in the eyes of the behaviorist is that the researcher has gone to the extreme to eliminate competing variables that might contaminate results.

Unfortunately, creating a valid test situation in captivity that is relevant to either the individual ontogeny or evolutionary history of a test species is much more difficult. For example, anyone can agree that regardless of species or paradigm the number of pieces of food hidden left or right must be counterbalanced. At the same time it is extremely difficult to generate a set of objective principles which might help distinguish between experiments with high and low amounts of ecological validity for species as

diverse as aye-ayes, cotton top tamarins, or chimpanzees (not to mention nonprimates). The challenge is only magnified when one considers the multitude of questions that experimenters wish to ask using an infinite number of paradigms. In addition, the problem may be exacerbated by the likelihood that the majority of comparative psychologists studying primates never get the opportunity to observe their test(s) species in their natural habitat. As a result of these difficulties, relative to the effort that has gone into developing methods of experimental control, much less attention has been focused onto the specifics of how to maximize or even objectively evaluate the ecological validity of captive experiments on primate cognition. In fact, some of the most intrepid and successful cognitive experimentalist studying primates have sometimes resigned to meet the challenge of creating valid test settings by taking the refined methods of control and adapting them for use in their test subject's natural habitat (Cheney & Seyfarth 1990a; Hauser 1996).

But is conducting experiments on wild animals the only way to produce ecologically valid experiments? Clearly not everyone can study animals in their natural habitat and more importantly not all experimental questions can be answered by studying wild animals. In the field it is exceedingly difficult for experimenters to consistently and repeatedly produce controlled conditions in a timely manner without completely disrupting the lives of their test subjects. Given the limits of taking experiments into the field, is it possible to reverse the flow of information so that now experimenters in captivity can learn how to improve their captive experiments from lessons learned by behavioral ecologists and ethologists studying animals in their natural habitat? In addition and perhaps most importantly, using primate behavioral ecology will it be

possible to generate a number of generalizable principles of primate ecology which can help in not only inspiring the creation of novel paradigms, but also may allow experimentalist to more objectively assess the validity of captive paradigms in a similar way that is possible for methods of experimental control?

I believe experiments on primate cognition can be improved by attending to primate behavioral ecology. In addition, I think with much effort and debate, it should be possible to make progress in developing principles of primate ecology that can help in developing and assessing the external validity of new paradigms. In the next section I suggest the first of what I hope might become a number of “primate principles” that can help experimenters design and evaluate experiments on primate social cognition.

A primate principle: Primates are competitors

The lives of all primates are dominated by intense competition with conspecifics. All environments have finite supplies of resources on which survival and reproduction are dependent. Typically species evolve as to minimize the amount of direct competition they experience in obtaining resources by developing their own unique niches. For example, a species may become highly specialized at eating a certain food that no other species utilizes. But even when niche partitioning allows an individual to escape interspecific competition, competition with conspecifics, who of course rely on the same resources, will remain. This problem is only intensified for group living primates. In species as diverse as ring tailed lemurs, squirrel monkeys, and chimpanzees the majority of the day is spent in the company of ones most intense competitors: conspecifics. In fact the competition within groups is so intense and potentially costly to reproductive success

that it has been a challenge for behavioral ecologists to develop theories of why primates might live in groups at all (Wrangham 1980; Van Schaik 1989). In addition to intragroup pressures, conspecifics from other groups pose serious threats to valuable resources and reproductive success as well. For example, in chimpanzees intergroup competition can often become lethal with male chimpanzees raiding neighboring groups to kill lone males or the infants of unwary mothers (Wrangham & Peterson 1996). Thus, it is clear that primates live their entire life competing with conspecifics in order to maximize their reproductive success.

As a result, almost everything about primates including their morphology, behavioral repertoire, temperament, and potentially even cognitive abilities has been molded by the need for a competitive design. Morphologically, for example, many species of primate are sexually dimorphic, typically with males being larger than females. Sexual dimorphism is highly correlated with the intensity of male-male competition over females. Behaviorally there is great need for methods of reconciliation and appeasement, so that after a stressful competitive interactions social relationships can be repaired and maintained (Castles & Whiten 1998). Also, as intraspecific competition becomes more intense across species, facial expressions, which signal submission, become highly specialized to prevent costly miscommunications (Preuschoft 1995). In fact primate signals in general are designed for the purpose of manipulating and exploiting others so that their own selfish needs might be met (Krebs & Dawkins 1984). For example, primates are highly selective in the information they provide potential competitors about food resources (Dittus 1984; Hauser 1996; Hauser 2000). Thus, when chimpanzees discover a previously unknown food resource, they make species specific food calls if

they deem the food resource sharable while they remain silent if the food is monopolizable (Hauser & Wrangham 1987; Hauser et al 1993). In addition, it has never been observed in experiments where primates have competed for hidden food that an informed individual overtly uses communicative displays or signals to indicate to a conspecific the location of the hidden food (Menzel 1974; Coussi-Korbel 1994).

Finally, the temperaments of primates also reflect their competitiveness. In social settings primates are typically extremely persistent in trying to obtain what they desire. For example, primates have many different types of strategies to obtain what they desire from others including incessant and ear piercing temper tantrums, grooming alliance partners for days, or weeks of displaying and intimidation (Harcourt & de Waal 1992). Anyone who has worked with captive primates will have experienced first hand their "must win" attitude. For instance, for my own experiments it is necessary to constantly shuffle subjects between cages. Typically one can convince a subject to move to a new cage by placing food inside, but very frequently whether it be a capuchin monkey or chimpanzee the subject will still absolutely refuse to move. When trying different foods or waiting for minutes (or in some cases hours!) does not work, what is generally the quickest way to get any primate subject to move? Simply place a conspecific on the other side of the baited cage in which you want the subject to move. As soon as your subject realizes that another individual may get the food, they race into the cage, grab the food and eat it.

Given that primates are designed to compete with conspecifics, it has also been hypothesized that the most sophisticated cognitive abilities of primates were selected because of their value in out-competing one's competitors (Jolly 1966; Humphrey 1976;

Byrne & Whiten 1988). If this hypothesis is correct, one would predict that it is in these competitive situations that one is most likely to see sophisticated cognitive abilities expressed. It then follows that experiments that integrate a competitive component into their design may be more likely to demonstrate the most sophisticated cognitive abilities of primates (Povinelli, 1996). But now that we have this candidate principle, is there any evidence that might support that when a competitive component is added to controlled experiments it leads to more sensitive paradigms?

Problems with primate perspective taking

Perspective taking (more commonly referred to as mindreading, mental attribution, theory of mind, or mentalizing) is an essential ingredient underlying what are considered some of the most human specific social cognitive abilities (Tomasello 1999). Coherent theories of the ontogeny and evolution of perspective taking are therefore an important goal of cognitive ethology (Corballis & Lea 1999; Heyes 1998). Great effort has accordingly been focused on operationalizing and specifying how various types of perspective taking develop in human children, and whether any of these same abilities might be present in any nonhuman primates.

While developmental psychologists have made great strides in charting the development of perspective taking in humans, comparative psychologists have struggled to even demonstrate that any nonhuman primate species (or any nonhuman for that matter) has any ability to take the perspective of another individual (Heyes 1998). Perspective taking is difficult to demonstrate, because the experimenter must find 1) a situation in which the test subject's perspective does not correspond with the perspective

of another individual (otherwise it is always possible that the subject is behaving in terms of its own perspective), 2) a way of having the subject demonstrate that it is aware of the differing perspective of the other individual. The major problem in accomplishing these two goals is the fact that any individuals' perspective (e.g. I see danger) is usually highly correlated with its behavior (e.g. I scream and run) (Tomasello & Call 1997). Therefore, in order to demonstrate perspective taking, experiments must be able to show that subjects are making their decisions base not just on another individuals behavior, but instead by taking the perspective of another individual (i.e. being sensitive to someones perceptions, desires or beliefs about the world).

Subsequently, the success of developmental psychologists studying perspective taking has been dependent on studying human children after their language skills have begun to develop. For example, in the traditional "false belief" task two children witness a toy being hidden. One of the children is then escorted outside of the room (Bill). The toy is moved to a new hiding location. Finally the experimenters asks the child remaining in the room, "where will Bill look for the toy?" (Wimmer & Perner 1983). Sometime after their fourth birthday a child will answer in various ways that Bill will look in the original hiding spot, because they understand Bill's perspective: Bill could not know that the toy had been moved (i.e. he has a false belief). The use of language has been absolutely critical to this and almost all subsequent methods used to test perspective taking in children (but see Call & Tomasello 1999). By using linguistic responses one can clearly demonstrate that a child is sensitive to the information to which another individual has access and not simply basing their response on their own perspective or the behavior of the other individual.

Those studying nonhuman primate perspective taking do not have the advantage of using linguistic responses as dependent measures of perspective taking. Therefore, behavioral measures are required that emulate the ability of language to eliminate competing hypotheses.

But there are a whole host of other problems. First, primates are difficult to maintain, resulting in small sample sizes. To compensate experimenters must typically give subjects repeated exposures to treatments making any result vulnerable to parsimonious learning hypotheses. Developmental psychologists on the other hand have an almost limitless supply of subjects. Therefore, if they wish, they can design experiments that administered single exposures to each of dozens of subjects. Second, the quality of a primate sample to be used for cognitive experiments is not assured. If within and across tasks two subjects (maybe not always the same two) have wavering attention or motivation, they may appear unsuccessful while a sample is effectively reduced to two. Whereas, if an experimenter detects that a child is problematic for any reason, it can be replaced. Third, there are many logistical constraints that limit the possible designs of experiments on primates such as the inability of experimenters to interact with their subjects physically, test conspecifics together with other conspecifics, or modify existing caging or housing structures to meet the needs of the experiment (i.e. the building belongs to a zoo or research center). All of these problems severely constrain the potential for designs of experiments on captive primates.

Given the extreme methodological demands and constraints placed on experiments of perspective taking in nonhumans, it may come as no surprise that comparative psychologists seem to lag far behind developmental psychologist working

with human children. In addition, it also becomes evident that experimenters interested in investigating perspective taking must design and conduct experiments after great thought into how to maximize experimental validity. In the next sections I review how experimental methods for testing perspective taking in chimpanzees have evolved over time and some of the current schools of thought on how to improve experiments on perspective taking. Finally, I offer my own suggestion of how to improve perspective taking experiments based the proposed primate principle outlined above.

Perspective taking in chimpanzees

Partially because of their genetic relation to humans (Ruvolo 1997) and their availability, but mostly as a result of their seductive morphological and behavioral similarities to our own species, chimpanzees became the most popular battle ground for investigators interested in gaining insights from nonhumans about the development and evolution of perspective taking (while the other apes have remained virtually ignored). Although research into chimpanzee perspective taking was initiated over twenty years ago (Premack & Woodruff 1978) there still remain only a handful of experiments on chimpanzees that are relevant to evaluating perspective taking. In addition, after these studies have been subjected to years of intense scrutiny, none are considered to have produced any compelling positive evidence that chimpanzees have the capacity to take the perspective of another individual in any form (Heyes 1993; 1998).

Information relevant to chimpanzee perspective taking began to be collected over thirty years ago with the advent of the first chimpanzee field studies. Goodall (1971) made several intriguing observations of individuals discovering previously unknown food

resources and then proactively using strategies to assure that this resource remained unknown to other conspecifics (i.e. leading conspecifics away from the food). These observations and others like them provide extremely valuable information about the cognitive potential of a species and when they might be deployed, but, as is always the case with anecdotes, it is unclear how replicable they might be (Byrne & Whiten 1992). In addition, no matter how frequently you observe behavior such as those observed by Goodall (1971) there is no way to determine if the animals are actually trying to manipulate the perspective of its conspecific competitor (i.e. preventing it from seeing the food) or trying to affect its behavior only (i.e. preventing it from retrieving the food) (Heyes 1993, 1998; Byrne & Whiten 1992).

Menzel (1974) reports the first set of experiments that are relevant to chimpanzee perspective taking. In one of many manipulations performed with his subjects food was hidden as a subordinate member of a group of young chimpanzees watched and the others did not. Then all of the chimpanzees were released to find the hidden food. Menzel found that over time the knowledgeable subordinate developed strategies to prevent the naïve dominants from finding the food and in return the dominants developed their own strategies to counter those of the subordinate. In some cases the subordinate would even “lead” the dominant away from the food before attempting to obtain it (see Cousi-Korbel 1994 for a similar finding with monkeys). Although many of the strategies used by the chimpanzees were consistent with perspective taking, it was still unclear whether the chimpanzees were reacting to the behavior of its competitor and not its perspective.

The first experiments explicitly designed to test for perspective taking were carried out by Premack and colleagues (Premack & Woodruff 1978; Woodruff &

Premack 1979; Premack 1988). Although they came up with many ingenious designs, all of their experiments were extremely artificial. For example, many experimental procedures involved humans doing complex sets of actions on human objects (i.e. heaters and record players), required subjects to watch TV, realize that a masked experimenter with a crowbar was a “villain”, or push a button that magically opened a cabinet on the wall full of treats (see Premack 1998 or Tomasello & Call for a review). In addition, all these clever but contrived experiments were susceptible to simple behavioral cueing and learning hypotheses making it difficult to demonstrate perspective taking (Heyes 1998).

Povinelli et al. (1990) conducted an experiment with striking similarities to an experiment briefly reported by Premack (1988) that has since become the most recognized study of chimpanzee perspective taking. Povinelli et al. first trained four chimpanzees to discriminate between an ignorant and knowledgeable human experimenter while trying to find hidden food. The chimpanzees first watched as a human experimenter baited one of several cups behind an occluder (so that the chimpanzees knew food was hidden, but did not know in which cup). Meanwhile during baiting, a second experimenter remained outside of the room and therefore was ignorant to the location of the hidden food. After baiting, the second experimenter entered the room and both experimenters pointed to one of the cups with the knowledgeable experimenter always pointing to the cup with food and the ignorant experimenter always pointing to an empty cup. Then the chimpanzees were allowed to choose in which of the cups they believed the food was hidden. If they chose the cup with the food, they were rewarded. If they chose the incorrect cup, they did not receive the food. After hundreds of trials the chimpanzees became proficient at choosing the cup to which the

knowledgeable experimenter was pointing while avoiding the cup which the ignorant experimenter indicated.

After all subjects were experts in this first task, a second and critical transfer test began. This test was identical to the first study except that this time the ignorant experimenter remained inside the experimental room with a paper bag over his head (therefore, even though he did not leave the room as before, he was still ignorant to location of the hidden food). The question was whether the chimpanzees would be able to generalize the skills they learned in the original study to this new situation (i.e. the subjects should trust the experimenter who witnessed the hiding immediately without any need for additional learning). Povinelli et al. (1990) concluded that the chimpanzees successfully transferred their previous understanding to this new situation and that therefore, chimpanzees can take the perspective of another individual.

However, in response to the critique of Heyes (1993), who refuted the claim that the chimpanzees successfully transferred to the new test situation, Povinelli (1994) reported that, indeed, it was possible that subjects had simply learned to use some discriminative cue to perform successfully in the second study. In addition, both Povinelli et al. (1994) and Call et al. (2000) have since replicated Povinelli et al. (1990), but again were unable to rule out the possibility that subjects who were performing well had simply learned to use some type of cue when successful.

Call & Tomasello (1999) represents the first nonverbal test for mental perspective taking that successfully simulates the traditional false belief tests developed for use with children. First, behind an occluder a human experimenter would hide food in one of two hiding locations (i.e. so the apes knew food was hidden, but did not know where) as a

second experimenter (the communicator) watched the baiting. After the baiting, the communicator then left the room. While the communicator was gone the baiting experimenter switched the locations of both the containers. Finally, the communicator returned and indicated the location in which they had originally seen the food hidden (which was incorrect) after which the chimpanzee was allowed to choose a container. For the apes to demonstrate perspective taking they had to realize that the communicator had not seen the containers switch locations after baiting. Therefore, the chimpanzees should ignore the human's signal and choose the container that was not indicated. Most importantly, unlike all previous experiments, before testing began potential subjects were screened during a pre-training phase. Potential subjects were required to demonstrate that they understood many of the logistics of the task before they participated in actual test of perspective taking. Therefore, each subject had to be able to track both the location of hidden food if its location was switched with another empty hiding location and ignore the signal of an experimenter if she was incorrect about where food was hidden. Although seven apes (5 chimpanzees and 2 orangutans) succeeded in the pretests, none of them demonstrated that they were able to take the perspective of the human experimenter in the false belief test.

Mainly based on this set of studies a number of authors have concluded that thus far there remains no compelling evidence for perspective taking in chimpanzees (Heyes 1998; Tomasello & Call 1997). In response to these and other results there have been a number of approaches that have been pursued for the purpose of improving experiments on chimpanzee perspective taking.

Different perspectives

I. Retreat!

Based on the belief that previous studies were consistent with a “low level model of behavior reading”, recent research efforts have been channeled into what have been characterized as simpler tests which investigate abilities that are considered rudimentary to perspective taking (Povinelli 1996; Hare et al 2000). Research has focused on the ability of chimpanzees to 1) follow the gaze of a human into space 2) discriminate between the attentive posture of two experiments to obtain food, and 3) use social cues provided by an experimenter to find hidden food. The question that all these approaches attempt to address is what chimpanzees understand about the visual experience of other individuals. But it is important to realize that all these paradigms represent starting points. Even if the chimpanzees were completely successful in them all, none of these approaches can provide conclusive evidence for or against perspective taking in chimpanzees (Heyes 1998; Call et al. 2000).

Tomasello et al. (in press) have demonstrated that chimpanzees begin to follow gaze in late infancy and as adults rapidly habituate to the gaze of a human who repeatedly looks at nothing. Povinelli & Eddy (1996a) and Tomasello et al. (1999) have also demonstrated that chimpanzees can follow human gaze around physical barriers and past a distracting object. Taken together these studies clearly show that chimpanzees gaze following skills are at least as sophisticated as those that have been demonstrated for human infants (Jarret & Butterworth 1991; Corkum & Moore 1995).

These findings stand in stark contrast to the results of two other paradigms. Povinelli & Eddy (1996b, c) trained seven chimpanzees to put their hands through one of

two holes in a plexiglass wall. Then while standing in front of a lone chimpanzee two human experimenters assumed one of two postures. For example, one individual faced the subject while the other stood with their back turned. Or in another condition both experimenters faced the subject but one of the two experimenters either closed their eyes or turned their head away from the subject. In all of the studies the subjects were rewarded for putting their hand through the hole in front of the experimenter that a human adult would judge as being able to see the subject. Although the chimpanzees immediately chose the experimenter that was facing them in the first condition, it took them dozens of exposures to improve on any of the other discriminations (i.e. they stuck their hand through the hole in front of the person facing them as often as the one whose head was turned away from the chimp). Although there are many possible interpretations (as is the case for humans who commonly use visual gestures and facial expressions while talking on the telephone to someone on a different continent), it has been concluded from this and other similar studies that chimpanzees do not have a sophisticated understanding of others' attention (see also Reaux et al. 1999; Theall & Povinelli 1999).

The final series of studies tested the ability of dozens of chimpanzees to find food that is hidden in one of two containers using social cues provided by a human. The procedure of this so-called object choice paradigm is as follows: behind a small occluder a human hides food in one of two cups (so that the chimpanzees know food is being hidden, but do not know where), then the experimenter typically waits until the subject is looking at him and then provides a cue (eye direction, head direction, pointing, tapping the correct container, etc.) that always accurately communicates the location of the

hidden food, and finally the subject is given the opportunity to choose one of the containers (and are rewarded when choosing the correct container). Chimpanzees have shown very little ability and/or inclination to use any of the cues that the humans provide about the location of the hidden food (Povinelli & Eddy 1996c; Povinelli et al. 1997; Tomasello et al. 1997; Call et al. 1998; Povinelli et al. 1999; Itakura et al. 1999; Call et al., 2000 but see Itakura & Tanaka 1998). Again these results have been interpreted as being inconsistent with any appreciation of the visual experience of others. Unfortunately, after pursuing this “easier” approach we are again left with mixed results that are difficult to interpret. Although chimpanzees clearly have sophisticated understanding of the gaze of others, it may take more sensitive experiments to investigate their understanding of the visual experience of others in different situations.

II. More control

Heyes (1993, 1998) reiterates the weakness of anecdotes as evidence for perspective taking and then makes a compelling case that no perspective taking experiment with primates thus far has used the appropriate amount of controls to rule out the most parsimonious interpretations of their results. She concludes that until experiments are designed and implemented that use controls properly no evidence for perspective taking in primates (or nonhumans) will ever be generated. Based on the merits and problems of the experiments she reviews in her target article, much to her credit she bravely suggests a new experiment which she feels has all the necessary controls for a successful nonverbal test of perspective taking. In the hope of sparking a healthy debate she then invites her *Behavioral and Brain Sciences* commentators to assess her new paradigm and

suggest how it might be improved or replaced.

Her proposed study is based on the general procedure of Povinelli et al. (1990) and is guided by the goal of providing appropriate controls for the purpose of ruling out parsimonious hypotheses. First, the chimpanzees would be trained to discriminate between two human experimenters based on what the experimenters had seen in the past when food was hidden (i.e. one leaves the room and the other stays and witnesses the baiting). Second, is a critical transfer stage where human experimenters are now both present during baiting, but one of the experimenters wears a pair of opaque goggles while the other wears translucent goggles. In this critical transfer test there is no differential rewarding so that it is difficult for subjects performance to be affected by learning. As in Povinelli et al. (1990), if chimpanzees can take the perspective of a human than it would be predicted that in the transfer test the subjects would immediately generalize the skills they learned in the first training stage into the transfer test. This hypothetical result would represent a successful case of triangulation (Heyes 1993).

Unfortunately, although Heyes (1998) should be commended for suggesting a potential solution to the many problems she cites in previous experiments and for inciting a number of constructive responses, her suggested approach would without doubt produce a null result. Although she briefly acknowledges in one sentence of her fifteen page review the need for, “knowledge of the habits and natural history of primates” (p113) her suggested paradigm has no obvious external validity. Clearly in no review of the habits or natural history of chimpanzees will one ever find the word goggle or a discussion of cooperative interactions over food between chimpanzees and different species.

Perhaps what is much more surprising than exclusive focus on control, is the twenty-three responses by the commentators. While thirteen responses evaluated and/or made suggestions to further improve the controls used in the proposed experiment, only three mention the fact that the new paradigm seems “unnatural”. Only Matheson et al. (1998) suggested an alternative that they felt was more natural. The emphasis on control is reflected again in the fact that all nine of Heyes’ revisions to her experiments in response to the commenters dealt with issues of control. So in summary although some very important issues of control are discussed (i.e. avoiding differential reinforcement and using methods of triangulation), it also becomes apparent that only a small minority of individuals consider the relevance of the testing situation when designing tests of primate perspective taking.

III. A chimpanzee perspective

The final suggestion is based on what amounts to a strong intuition felt by many that previous experiments of perspective taking have seemed contrived or somehow lacking in ecological validity (Shettleworth 1998; Matheson et al. 1998; Tomasello & Call 1997). For example, Gomez (1996, 1998) argues that chimpanzees are designed to solve problems about chimpanzee minds, and therefore tests of perspective taking need to be designed to test if chimpanzees understand the perspective of other chimpanzees instead of humans as all earlier test have done. But within both articles he does not specify how this goal should be achieved and then outlines an experiment, which involves apes communicating with humans about a hidden key, that opens boxes with food (see also Whiten, 1999).

Unfortunately, no one has previously specified what exactly it is about conspecifics that might improve the performance of chimpanzees in tests of perspective taking. This has made it easy for anyone to quickly dismiss the importance of this methodological point, “A charge is sometimes made that chimpanzees have a theory of mind, but it is a theory of chimpanzee mind, not of the human one. Although it has an appealing biological ring upon close inspection if this idea is intended to be distinct from the notion examined above, it becomes very difficult to define (Povinelli 1996, p 323).” It may be because it has been difficult to define what a chimpanzee perspective might be like that until very recently no one had ever tested for chimpanzee perspective-taking using conspecifics as others (but see Cheney & Seyfarth 1990b for an example with monkeys).

IV. A competitive perspective

I agree both that previous tests of perspective taking have been highly contrived and artificial and I agree with Heyes (1993; 1998) that serious attention must be given to the amount of experimental controls in future tests. Therefore, what is needed are experiments that can provide ecologically valid test settings which also have the flexibility to allow for many of the controls suggested (such as triangulation and no differential rewarding). Is the competitive primate principle part of the answer?

Almost without exception (the exception being studies of gaze following) tests of perspective taking (many reviewed above) have tested chimpanzees in cooperative-communicative paradigms in which either a human experimenter altruistically shares information with a subject about the hidden location of a monopolizable food resource

(Premack 1988; Povinelli et al. 1990; Povinelli et al. 1994; Call & Tomasello 1999; Call et al. 2000; Povinelli & Eddy 1996c; Povinelli et al. 1997; Tomasello et al. 1997; Call et al. 1998; Itakura & Tanaka 1998; Itakura et al. 1999; Call et al. 2000) or a chimpanzee is required to signal to humans in some way in order to acquire a monopolizable piece of food (Premack 1988; Povinelli et al. 1992; Povinelli & Eddy 1996b,c; Reaux et al. 1999; Theall & Povinelli 1999). In fact only one previous experiment has included any competitive component at all (Woodruff & Premack 1979). After one reflects upon the competitive nature of primate social life (see above), it becomes apparent why these types of cooperative-communicative settings are highly anthropomorphic for a species such as chimpanzees. Recall that evolutionary theories emphasize the manipulative design of animal signals (Krebs & Dawkins 1984) while experiments with chimpanzees have even demonstrated their natural tendency to avoid communicating about monopolizable food resources (Hauser et al. 1993).

In strong support of the hypothesis that cooperative-communicative paradigms are highly unnatural for primates is the fact that domestic dogs, who have been under a completely different regime of selective pressures that have, indeed, encouraged cooperative-communicative interactions with humans (Serpell et al. 1997), out perform primates in the cooperative-communicative object choice task described above (Hare et al. 1998; Miklosi et al. 1998; Hare & Tomasello 1999; Mckiney & Sambrook, 2000; Agnetta et al, submitted). Meanwhile wolves, the direct ancestors of dogs, who have not been artificially selected to engage in cooperative-communicative interactions, do not use social cues provided by humans as with the chimpanzees (Agnetta et al. in press). Therefore, after considering the abilities of domestic dogs relative to primates in the

object choice task it becomes very apparent how important it can be to consider a species evolutionary history in designing experimental methodologies. Thus, experiments on chimpanzee perspective taking should clearly avoid any form of communication or cooperation when monopolizable food is at stake.

With this insight Hare et al. (2000) designed a new experimental paradigm to test for visual perspective taking in chimpanzees. This new paradigm emphasized competition between conspecifics, rather than cooperation and communication with humans. Members of two large socially housed groups of chimpanzees were tested in pairs and competed over two pieces of food. Before testing the food dominance hierarchy was established for each group so that all combinations of individuals could be tested together. This meant that in each test one of the chimpanzees was always dominant and the other subordinate, but that almost all of the subjects frequently switched between both roles during testing (i.e. only the highest and lowest ranking individuals did not play both roles). For each trial a subordinate and a dominant chimpanzees were placed into rooms on opposite sides of a middle room which was baited with two pieces of food. Each cage had a guillotine door leading into the middle room which, when partially opened, allowed the subjects to observe where two pieces of food had been placed at various locations within that room. In addition, they could see their competitor looking under her door as well. After the competitors had seen where the food was placed, the doors for both individuals were opened, allowing both subjects to enter the middle room and retrieve the hidden food.

When a subject was subordinate there was little that they could do to prevent their dominant competitors from taking all the food while when this same individual was the

dominant competitor she did everything possible to assure she obtained both pieces of food. Indeed, in all the studies in which dominants had visual and physical access to both pieces of food they retrieved the majority of them undisputed. However, many times opaque occluders were arranged in front of a piece of food so that either the subordinate could see a piece of food that the dominant could not see or vice versa. The question in these cases was whether the subjects were sensitive to what their competitor could or could not see, and whether they adjusted their retrieval pattern based on the position of the occluders and the identity of their competitor.

The results showed that when individuals were subordinate and their dominant competitor could only see one of the pieces of food, the subordinates targeted the hidden piece of food that the dominant could not see. In addition, when these same individuals switched to the role of dominant, and their subordinate competitor could only see one of the pieces of food they immediately changed strategies. Now instead of the hidden piece of food, they targeted the piece of food that their competitor could see.

Several control studies were then run to rule out alternative explanations such as behavioral cueing and various forms of learning by testing the chimpanzees in several novel situations. For example, in a critical experiment subordinates were released slightly before the dominant and the dominant door remained completely shut until after the subordinate committed to approaching a piece of food hidden from the dominant or one that was not. Therefore, in choosing which piece of food to retrieve the subordinates only knew that the dominant would be released, but never had any cues available from the dominant from which to base their retrieval decision. As before, the subordinates preferred to retrieve the hidden piece of food. In addition, when the opaque occluder was

replaced with a completely novel transparent barrier (these animals had very little previous exposure to transparent materials) the subordinates' preference for food behind barriers from the previous four studies suddenly disappeared. Together the findings of these studies represent strong evidence that chimpanzees know what conspecifics can and cannot see, and further, that they use this knowledge to devise effective behavioral strategies in food competition situations.

Following this study Hare et al. (in press) adapted the same "competitive food paradigm" to allow for more challenging tests of perspective taking. These studies were designed to test what chimpanzees know about what others have and have not seen in the immediate past and whether they can use this knowledge to develop effective social strategies. In the new design the same procedures of Hare et al., (2000) were followed, with two exceptions. First, only one piece of food was always hidden on the subordinates' side of one of two barriers (i.e. hidden from the dominant) in the middle cage. Second, what the dominant competitors witnessed while the food was been hidden varied by condition.

First, chimpanzees were tested in four pseudo-randomized conditions. In all four of these conditions the subordinate subject always witnessed through her partially opened door the entire baiting procedure as one piece of food was place on her side of one of two barriers. In addition, she could also monitor what her dominant competitor witnessed during baiting as well. In the uninformed control condition the dominant was allowed to witness the baiting through her partially opened door as the piece of food was placed behind one of the two hiding locations. In the uninformed condition the dominant was not allowed to watch as the food was hidden behind one of the two hiding places because her

door remained closed during baiting. In the misinformed control condition the dominant watched through her partially opened door as food was hidden behind one occluder and then subsequently moved behind the other occluder. While in the misinformed condition the dominant watched as food was hidden behind one of two hiding locations, but then her door was shut and the food was moved to the other hiding location. As in the critical study reported for Hare et al. (2000), after baiting the subordinate was always released first to ensure that they were not simply basing their retrieval decisions on the behavior of the dominant. In addition, if the subordinates chose not to approach for thirty seconds after her door was opened, the dominant was released to retrieve the food. Indeed, subordinates had a strong preference for retrieving food in the uninformed and misinformed conditions when their dominant competitors had not seen the entire baiting sequence. Even more impressive was the fact that subordinates in the control conditions refused to even approach the food more often than in the other two conditions. This result showed that before the trial had started the subordinates had already decided not to attempt to retrieve the food that their competitor had seen hidden. In addition, there was no evidence for learning across sessions.

If chimpanzees truly were taking the perspective of their competitors in the first study, as opposed to reacting to some unspecified cue, one would expect that they would be able to use this sophisticated social cognitive ability in a flexible manner in novel situations. In addition, they should be able to adapt to this new situation without needing numerous trials to do so. The two conditions in the second experiment of Hare et al. (in press) were designed to test for this possibility. In both conditions food was placed on the subordinate's side of one of two occluders as both competitors watched through their

partially opened doors. The critical manipulation was that in one of the conditions, after the dominant had witnessed the baiting, she was switched for a new dominant individual that had not witnessed the baiting. This new naïve individual had been out of the experimental area when the baiting took place, and so could have no information about where the food was hidden. Although each subordinate only received four trials in each of the two types of conditions, it was found that subjects preferred to retrieve food when their competitor was naïve to its location. In addition, subjects tended to be less likely to approach as far when competing against the original dominant who had seen the food hidden. Both of these results support the idea that chimpanzees may even assign knowledge to certain individuals. In addition, not only did the two subjects that had not participated in the first study also prefer to retrieve food when their competitor was naïve, but again there was no evidence for learning. In replicating the results of the first study it seems that the chimpanzees successfully triangulated the abilities they demonstrated in "study one" to this new test setting. Taken together these two studies allow us to reject the null hypothesis while supporting the interpretation that chimpanzees have quite sophisticated perspective taking abilities.

In summary in this new approach, 1) Chimpanzees were tested in a competitive food paradigm that simulates a setting that is relevant to each individual's ontogeny and the species evolutionary history. 2) Chimpanzees were asked to take the perspective of other chimpanzees instead of human experimenters 3) Absolutely no cooperation, communication, or training were required. 4) Because there was no need for time consuming training a larger sample of animals were used in these two studies (mean of 14.5) than in all perspective taking studies reviewed above (mean of 4.6). This larger

sample also allowed for the use of group statistics (which means anyone attempting to replicate these findings will need more than 6 or 7 individuals frequently used in tests on chimpanzees). 5) Also because of the relatively large sample every subject did not have to participate in every study. 6) It is difficult to make parsimonious learning arguments, because the chimpanzees were never differentially rewarded and were only asked to demonstrate their spontaneous preferences. Also methods were developed to eliminate the possibility for behavioral cueing. Finally, in each study subjects participated in few trials while also having to constantly switch between two different roles (dominant and subordinate). 7) The paradigm was also flexible enough to allow a number of novel studies in attempts to triangulate. 8) Finally, this paradigm can also be used to test for perspective taking in other species of primates (or nonhumans).

Corroborating the findings of Hare et al. (2000; in press) is the study of Hirata & Matsuzawa (submitted) which modifies the competitive food paradigm of Menzel (1974) to explicitly test for perspective taking. In this experiment pairs of subjects competed for food that experimenters hid in one of several locations all over a large enclosure. While the food is hidden the subjects can see each other, but are kept in separate cages that can be opened to either show or release them into the large enclosure. Over a number of days the subordinate individual in each pair of animals is allowed to watch as the experimenter hides the food and after baiting the subjects are released simultaneously to retrieve the food. Over a number of days individuals developed strategies for out competing each other for the food. As in Menzel (1974) subordinates continually produce novel strategies for out competing the dominant (i.e. by leading him the wrong way), while simultaneously the dominant devised their own strategies for outwitting the subordinate

(i.e. by following them everywhere). But the critical manipulation came when one day the experimenters hide the food in the large enclosure without showing the subordinate where it was located and the dominant potentially saw that the subordinate had not witnessed the baiting. In this completely novel situation when released simultaneously in contrast to all previous trials some dominants suddenly ignored the behavior of the subordinate when searching for the food. Although it would be interesting to see how the chimpanzees behaved in a number of other novel situations, this study taken together with Hare et al. (2000, in press) strongly suggest that chimpanzees do indeed have perspective taking capabilities. In addition, these studies clearly demonstrate the potential utility of the competitive primate principle in designing more sensitive experiments of social cognition. Finally (and perhaps most importantly), these studies support the idea that primates and other animals are most likely to demonstrate their most sophisticated cognitive abilities in the situation for which they were designed and are used daily.

Conclusion

Just as in humans (Barkow et al. 1992; Burnham & Phelan, 2000), when the cognitive abilities of animals are pushed to their absolute limit, they are most likely to demonstrate their most sophisticated cognitive abilities in the situations for which they evolved and are used daily (Shettleworth 1998; Tomasello & Call 1997). Although there is an entire field dedicated to understanding the evolutionary pressures that shape the behavior and cognition of primates, experimentalist are still without any explicitly stated principles of primate ecology or evolution which might help in designing and objectively evaluating

the validity of experiments on primate cognition. What I have suggested, based on many of the observations and ideas of others, is that the first of these principles is the simple fact that all primates have been designed to compete with conspecifics. By reviewing the work on chimpanzee perspective taking I have attempted to demonstrate how this principle might be put into practice to increase the sensitivity of experiments on social cognition. If this and other primate principles can be developed and utilized in experiments on primate cognition, I would predict that experimenters would be able to substantially increase the sensitivity of experiments in other domains of inquiry as well.

One important concluding point: just as when powerful statistics are used, increasing the sensitivity of experiments is a probabilistic endeavor. First, because a sensitive experiment is conducted, of course, does not mean that it will be able to demonstrate the skill under study. Second, it is clearly not always necessary to have the most sensitive experiments to investigate certain cognitive abilities. For example, chimpanzee gaze following skills are so robust it has been easy to investigate them using human experimenters. The point is that sensitive experiments, just as with powerful statistics, increase the probability of being able to reject a null hypothesis or distinguish between competing hypotheses (Gottsdanker, 1978). So again, where it seems critical to consider the sensitivity of an experiment is when you are aware that you are pushing the limits of your test species or subjects cognitive abilities (i.e. you or they have been unsuccessful in previous attempts). In the case of studies on primate social cognition this may mean including a competitive component in any future experimental designs.

*Part VIII: Tempering Darwin's greatest difficulty:
How, when, and why did derived features of human
social cognition evolve?*

Introduction

This dissertation was designed to aid in resolving Darwin's greatest difficulty (Darwin, 1871). In doing so, this series of investigation had two goals 1) use the tools of modern psychology to identify aspects of human cognition that might account for our species unique intelligences and 2) reveal how and why these unique cognitive abilities may have evolved during hominin evolution (Chapter 1). Therefore, within this conclusion I will review the findings presented in the previous chapters both in relation to how they contribute to our understanding of human cognitive evolution and what avenues they suggest for future investigation. More specifically, I first propose what aspects of our social cognition are shared and derived since our species split from our LCA. Second, based on the observed species differences in the use of human social cues, I propose a potential selection pressure that may explain many species differences in social problem solving ability. Third, I hypothesize that this same selection pressure is likely to have played a role in the evolution of the observed changes in human social problem solving.

Identifying Derived Hominin Traits

What aspects of our social cognition did we inherit through common descent from our LCA? This investigation was largely inspired by the social intelligence hypothesis which suggest it is elements of human social cognition that are largely responsible for much of what is unique to the human phenotype (Humphrey, 1976; Byrne & Whiten, 1988; Dunbar, 1992; Tomasello, 1999). Cognitive and developmental psychologists have hypothesized that it is our species ability to think about the thoughts of others, or Theory of Mind (ToM), that provides the ontogenetic foundation to much of what is considered unique to human cognition (Dennet, 1983; Perner, 1991; Baron-Cohen, 1995; Carruthers & Smith, 1996; Tomasello, 1999; Sperber, 2000) This hypothesis predicts that our last common ape ancestor with chimpanzees (*Pan troglodytes*) and bonobos (*Pan paniscus*) or LCA did not possess any ability to think about the thoughts of others and that our ToM is a product of hominin evolution. All previous investigations studying chimpanzee ToM have failed to reject this null prediction either producing null results or results that are readily explained by learning, behavior reading or egocentric explanations of the observed problem solving behavior (Savage-Rumbaugh, et al 1979; Premack, 1986; Cheney & Seyfarth, 1990a; Povinelli et al, 1990; 1994; Heyes, 1993; 1998; Baron-Cohen, 1995; Carruthers & Smith, 1996; Povinelli & Eddy, 1996; Hauser, 1997; Call & Tomasello, 1999; Call et al, 2000; Povinelli, 2000). Therefore, until very recently, the overwhelming consensus has been that Theory of Mind is unique to *Homo sapiens* with Tomasello & Call (1997) concluding in their comprehensive review of research on primate cognition,

“...with regard to understanding the less observable aspects of behavioral functioning, there is no solid evidence that nonhuman primates understand the intentionality or mental states of others”

(Tomasello & Call, 1997; p. 340).

Subsequently, it has also been concluded that ToM in humans represents a completely derived feature of our cognition that arose during the Plio-Pleistocene (although, see Byrne, 1995 or Russon et al, 1996).

However, this dissertation directly challenges this consensus. Taken together, recent findings and those of the current investigation contradict the view that chimpanzees have no understanding of the psychological states of others. Instead, it seems that chimpanzees do make social decisions based on the unobservable psychological states of others although it is now unclear exactly which psychological states they understand and to what extent. These findings do not contest the hypothesis that there are derived (and perhaps unique) aspects of human Theory of Mind, but they do suggest aspects of human ToM were inherited through our LCA while emphasizing the difficulty of successfully identifying derived features of human ToM.

Visual perspective- taking is not a derived hominin trait

Largely because of the primacy of visual information in our own lives and that of other primates (Klein, 1999), the majority of research on mentalizing in chimpanzees has focused on their understanding of how visual perception in others works. Together with the current findings, many convergent lines of evidence now support the hypothesis that chimpanzees are capable of level 1 visual perspective-taking (Flavell, 1986; 1992) – at least in some contexts (Tomasello et al, 2003).

Gaze following studies have shown that chimpanzees are capable of assessing when others see something that they are not capable of seeing. Several studies have ruled out a number of nonmentalistic explanations for chimpanzee gaze following. For example, chimpanzees gaze following cannot only be explained as a case of reflexive co-orienting. When chimpanzees gaze follow (Povinelli & Eddy, 1996; Tomasello et al, 1998), but do not see anything of interest, they will look back to their social partner before continuing to search, as if to make sure they are looking in the correct direction (Call et al, 1998). If a chimpanzee is subsequently unable to detect anything of interest, they do not slowly habituate to a human who continues to gaze alternate, but instead immediately ignore this unreliable social cue (Tomasello et al, 2001). If a visual barrier prevents a chimpanzee from matching their line of sight with that of another individual who is gazing intently, chimpanzees do not simply gaze at the barrier, but instead move so as to match their own line of site with that of the other individual (Povinelli & Eddy, 1996; Tomasello et al, 1999). In addition, after turning their head in the direction of another's gaze, chimpanzees do not simply attend to the first interesting object encountered, but instead ignore distracting objects in favor of matching their line of sight to that of their social partner (Tomasello et al, 1999). These findings support the hypothesis that chimpanzees know when they can or cannot see what someone else can see.

Systematic study of the retrieval strategies used by chimpanzees during food competition has revealed that chimpanzees are capable of assessing what others can see in the present, remembering what others have seen in the past, and predicting what others will be able to see in the future. Hare et al (2000) demonstrated that chimpanzees know

what others can and cannot see. Before seeing the behavior of their competitor, subordinate chimpanzees—in order to avoid their competitor—prefer to retrieve hidden food over food that is visible. However, this preference for hidden food disappears if the opaque barriers used to hide the food are replaced with transparent barriers. Meanwhile, dominant individuals—again before they see the behavior of their competitor - prefer to retrieve “at-risk” visible food first while obtaining food hidden in “safety” second (Hare et al, 2000).

This initial finding was followed by two studies that tested whether chimpanzees also can remember and predict what others can see. Hare et al (2001; chapter 2) found that the same chimpanzees tested in Hare et al (2000) were also capable of remembering what others had seen in the recent past. Subordinate chimpanzees preferred to approach food if the dominant was not present while the food was being hidden. Subordinates also preferred to retrieve food if the food’s location was changed when the dominant was not present. In addition, Subordinates preferred to approach the food if the dominant who was present during baiting was replaced with a new dominant who was not present during the baiting. Therefore, Hare et al (2001; Chapter 2) conclude that chimpanzees know what others have and have not seen in the immediate past. Finally, Hare et al (submitted; Chapter 3) tested an entirely new group of chimpanzees and found that these individuals were capable of assessing what others would or would not see in the future. When competing versus a human over contested food, chimpanzees were more likely to avoid approaching food via a route that the human would be able to see. Instead the chimpanzees approached food that their competitor was not facing or they used various

visual barriers to occlude their approach to the food – even if this required taking an indirect route to the food.

From this series of studies it is now clear that chimpanzees are quite flexible in their ability to determine when others can see things that they cannot and conversely when others cannot see something that they can see. When determining what others can see, chimpanzees are even capable of assessing when others have not seen something they have seen in the recent past and when others will and will not be able to see something in the future. Based on this profile, it is most parsimonious to conclude that chimpanzees at least share with humans level 1 visual perspective-taking abilities (although see D'Archi & Povinelli, 2002 and Povinelli & Vonk, 2003). Moreover, if this conclusion is correct, then it can also be inferred that level 1 visual perspective-taking is not a unique evolutionary product of hominin evolution and was instead inherited by both chimpanzees and humans through their last common ancestor (i.e. the ability did not evolve twice independently since the two sister species split).

Understanding cooperative-communicative intent is a derived hominin trait

Recent research, including the current investigation, support the hypothesis that chimpanzees do not comprehend (or attend to) the cooperative-communicative intent of others. The same subjects who show an appreciation for what other can see perform poorly in any task that requires them to use social cues provided by a cooperative-communicative human (Hare & Tomasello, in press; chapter 5). For example, in the so-called object choice task, an experimenter hides a piece of food in one of two opaque containers, and the subject, who did not see where the food was hidden, is allowed to

choose only one. Before presenting the subject with the choice, the experimenter gives a communicative cue indicating the food's location, for example, looking at, pointing to, tapping on, or placing a marker on the correct container. The majority of individuals, regardless of whether they are chimpanzees or other primates, do not spontaneously perform above chance levels in these tasks no matter the cue. Those individuals who eventually perform well typically take dozens of trials or more to learn any one cue (Povinelli et al, 1997; Tomasello et al, 1997; Call et al; 1998; 2000; Itakura et al, 1999; Hare et al, 2002; Hare & Tomasello, in press). In addition, when primates have been tested in more difficult tests that require them to show flexible use of social cues (i.e. use an old cue in a new way or use a novel or arbitrary social cue in the same way as a previous cue was used previously) without exception they fail to generalize their previous skills to any kind of new setting or social cue (Povinelli et al, 1997; Tomasello et al, 1997) Therefore, it has been hypothesized that, unlike young human children, chimpanzees are not capable of assessing the cooperative-communicative intent of another individual (Tomasello 1999; 2003). If true, then it is likely that the ability to assess cooperative-communicative intent is a derived trait in humans that evolved during hominin evolution.

Future research

The current research only represents a starting point. Vast amounts of research will be necessary before we can feel confident that derived features of human social cognition have been identified. Fortunately, the current findings suggest a number of avenues to work toward accurately identifying derived features of human cognition.

One extension of the current work is research into chimpanzees' understanding of other's perspective across different perceptual modalities. For example, there has yet to be an explicit investigation of whether chimpanzees know when another individual can hear them. While there is evidence that chimpanzees are more likely to use communicative gestures that involve auditory or tactile cues in some context when visual gesture cannot be seen (Tomasello et al, 1994; 1997; Hostetter et al, 2001) and that they are more likely to communicate the discovery of food if it is sharable (Hauser & Wrangham, 1987; Hauser et al, 1993), the appropriate controls have not been possible to allow for strong conclusions regarding whether chimpanzees are making such judgments based on unobservable psychological states. One approach to testing for auditory perspective taking would be to slightly modify the various competitive paradigms and controls used in Hare et al (2000; 2001; submitted) to test if chimpanzees make efforts to minimize the noise they make when obtaining contested food from others. For example, will a subordinate chimpanzee avoid food that requires noisy processing in favor of less desirable food that can be eaten in silence, if a hungry dominant is within earshot?

A second important extension of recent work will be further exploration of chimpanzees' abilities at attributing intentions and beliefs to others. While there is overwhelming evidence that chimpanzees do not understand cooperative-communicative intent, this does not preclude the possibility that chimpanzees have some ability to assess others intentions in some other form or context. Supporting this idea are recent demonstrations that chimpanzees discriminate between 1) an intentional and accidental communicative act and 2) an individual who is unwilling versus one that is unable to share food (Call & Tomasello, 1998; Call et al, in press). Given the centrality of

intentionality to theories of cognitive development and evolution in humans (e.g. Wellman, 1990; Meltzoff, 1995; Gergely et al, 1995; Tomasello, 1999; 2003), these recent findings call for further research testing the limits of chimpanzee use of unobservable goals and desires in making social decisions (Tomasello et al, 2003).

Finally, resolution in the matter of whether chimpanzees attribute epistemic states will play a central role in assessing the relationship between the evolution and development of language and metarepresentation (Astington, 2001). A number of authors suggest there can be no metacognition in nonlinguistic species (Smith, 1996; Segal, 1998; Nelson, 1996; Suddendorf & Whiten, 2001). In support of this hypothesis, early language development predicts later skill on theory of mind tasks but not vice versa (Astington & Jenkins, 1999). In addition, deaf children whose language acquisition is delayed, frequently fail false belief tasks until their communicatory skills reach age-normal levels – and these failures include failures on nonverbal tasks (Gale et al, 1996; Peterson & Siegal, 1995). This hypothesis, for the dependence of metacognition on language, would be refuted if it were found that a nonverbal species attributed belief states. Therefore, work on chimpanzee mental attribution could play a central role in testing this hypothesis further. Perhaps surprisingly, there has been almost no research designed to assess whether chimpanzees attribute epistemic states to others. Only two non-verbal tasks have been designed that resemble verbal false belief tasks used with children. One of these studies with chimpanzees found results inconsistent with belief attribution in a conventional cooperative-communicative paradigm (Call & Tomasello, 1999) while the other result was consistent with belief attribution using a competitive paradigm (Hare et al, 2001). Given recent findings suggesting that a wide range of

species, including chimpanzees, can skillfully recognize and act appropriately depending on their level of uncertainty (Smith, 1995; Sheilds et al, 1997; Call & Carpenter, 2001; Hampton, 2001;), perhaps future competitive paradigms will also reveal that the machinery is present in animals for simulating or theorizing about similar epistemic states in others (Gopnik, 1992;1993). Therefore, it remains an open question as to whether chimpanzees attribute belief states to others (Tomasello et al, 2003).

In summary, recent research including the current investigation have demonstrated that understanding psychological states is not completely unique to humans, but instead was in some part inherited from our LCA. If this conclusion continues to gain empirical support from research with great apes, we will be charged with developing methods that are capable of identifying more precisely what it is that is unique about human metacognition (Tomasello et al, 2003). This research is central to tempering Darwin's greatest difficulty, since it is only when we know with some certainty what changed during human evolution that we can design the means for determining how those changes occurred.

Identifying Evolutionary Mechanisms

What variation exist across species in visual-perspective taking abilities and understanding others cooperative-communicative intent? What mechanism(s) for change might account for how and why the observed variation in problem solving ability evolved?

Just as with any other biological system - be it morphological, physiological or behavioral - there must be documentation of heritable variation across species before

attempts can be made to understand how and why evolution occurred in a trait(s) (Gould, 2002). The most powerful way to study how and why evolution in a trait occurs is to document cases of convergent evolution (chapter 1). This requires demonstrating differences between closely related species followed by similarity between distantly related species in the trait under study (Losos & Miles, 1994). Once a case of convergence is identified, it is possible to study the closely related, but divergent species in order to identify the changed system(s) that is responsible for the differences in problem solving behavior (i.e. increases in hippocampus volume lead to increases in spatial memory). Meanwhile, it is also possible to develop testable ecological hypotheses that might explain the presence of analogous traits between more distantly related species (birds most dependent on food caching evolve the largest hippocampus and spatial memory).

Unfortunately, although this type of cladistic analysis can be developed into a powerful form of time travel, unlike behavioral ecologists (Krebs & Davies, 1993) and paleoanthropologists (Losos & Miles, 1994; Klein, 1999), the potential of this type of phylogenetic analysis has gone largely unrecognized in the field of animal cognition (Shettleworth, 1998). As a result, in Sara Shettleworth's comprehensive review of evolutionary studies of animal cognition she concludes,

“By contrast, there is little systematic data relevant to cognitive evolution at the level of detail required to draw conclusions on the issues touched on here. One way forward is comparisons of close relatives with divergent ecologies (Shettleworth, 1998, p. 571).”

Theoretical and logistical reasons are likely responsible for the absence of evidence for convergence in cognitive abilities across kingdom *Animalia* (Wundt, 1894;

Hodos & Campbell, 1969; Wasserman, 1997). Historically, comparative psychologists have tested few species and when choosing species for study have relied largely on issues related to convenience (Beach, 1950; Dewsbury, 1998) instead of sound evolutionary considerations – such as the species potential for detecting meaningful convergence in cognition (Shettleworth, 1998). Such theoretical and logistical constraints leave comparative psychologists with an impoverished set of methods that are incapable of reliably detecting cognitive difference responsible for species differences in problem solving behavior (e.g. Tryon, 1940; Searle, 1949; Premack, 1983; Oden et al, 1990; Hare & Tomasello, in press; Hare et al, in prep). As a result, the biggest challenge that remains for comparative psychology is to develop systematic methods for comparing cognitive abilities across species who vary dramatically in non-cognitive systems be it morphology, physiology, or even emotional reactivity (e.g. Breland & Breland, 1961; Bitterman, 1965; Hare & Tomasello, in press; Chapter 5). Until such methods are developed and implemented studies of comparative cognition will remain a backwater of evolutionary research.

Because the majority of testing has concentrated on so few species and used such varied methods, currently meta-analyses are only feasible using gross qualitative comparisons across the widest spectrum of taxa. Such comparisons have only allowed for conclusions about general evolutionary trends across orders and classes while lacking the resolution necessary to detect cases of convergence within orders. For example, Iwaniuk et al (2001) found that larger brained mammalian orders, or those assumed to be better problem solvers, showed the highest level of play, or behaviors assumed to facilitate the development of problem solving abilities, yet this same relationship was

absent when comparisons were made within any one order. Moreover, it has been so difficult to identify any qualitative differences in cognitive ability within the primate order that in the most comprehensive review of work on primate cognition to date the authors conclude, “There is no evidence that apes and monkeys perceive or cognitively represent their physical or social worlds in qualitatively different ways.” (Tomasello & Call, 1997, p. 399-400).

Unfortunately even when qualitative comparisons across different orders and classes are reportedly identified, poorly sampled species, wildly differing methods and conflicting theoretical approaches all prevent any clear consensus about the validity of the findings from developing or surviving scrutiny (Hodos & Campbell, 1969). A review of reviews on animal social learning provides a recent example of the difficulty in interpreting purported differences in problem solving behavior. Caldwell & Whiten (2002) recently completed a second order meta-analysis of studies on social learning in animals (one of the most intensely studied areas in animal cognition) in an attempt answer the question “is a comparative psychology of social learning possible?” They examine the conclusions of nine contemporary review articles and find that there is no agreement between any two of the nine authors about the imitative capacities of animals. As evidence of this level of dissent, even with only a few species under consideration, each review article differed in both the number of species they were willing to accept as capable of imitation (ranging from 1-5) and those that were not (ranging from 1-7).

The specter of ever developing a comparative psychology of any cognitive system seems ever more dim given that even the very best cases for convergence in cognitive ability remain controversial (i.e. spatial memory and song learning in birds, Hauser,

1996). A number of researchers have found that birds that rely heavily on food-caching for survival also have the largest hippocampus while performing unusually well on spatial memory tasks relative to closely related non-caching species (Balda & Kamil, 1989; Sherry & Vaccarino, 1989; Krebs et al, 1989; Kamil et al, 1994; Provosudov & Clayton, 2002). These initial findings have led these behavioral neuroscientists to hypothesize that birds who rely most heavily on food storage have been under strong directional selection for improved spatial memory. As predicted by this “adaptive specialization hypothesis”, a number of species have been tested and found to fit this general pattern (Provosudov & Clayton, 2002).

However, although seemingly an exquisite case of convergent evolution where a clear selection pressure has been identified, this adaptive hypothesis does not survive uncontested (Bolhuis & Macphail, 2001; Macphail & Bulhuis, 2001; Heyes, 2003). Macphail & Bulhuis (2001) refute evidence for the adaptive specialization hypothesis arguing that when the six best studied species are compared in a meta-analysis the species that rely most heavily on caching 1) do not perform best on all spatial task and are many times outperformed by non-caching species while 2) only developing enlarged hippocampus if they have had sufficient experience with caching (i.e. calling into question the heritability of enlarged hippocampi and enhanced spatial abilities in these species). Meanwhile, Heyes (2003) does not deny the existence of enhanced performance in spatial memory tasks in caching species, but does suggest that this improved performance is due to higher resolution in non-cognitive input processes (i.e. sensory and motor) and not because of a qualitative change to the mechanism underlying their spatial memory - the caching species have higher levels of high quality spatial

information to remember which results in quantitatively larger memory systems not qualitatively different types of representations or organizations within the memory system (a similar argument cannot be ruled out in the case of learning and memory in bird song given that variance in song learning is largely hormonally mediated, Brainard & Doupe, 2002). Such arguments lead these skeptics to assert,

“The failure to find solid support for the ecological view supports the view that there are no qualitative differences in cognition between animal species in the processes of learning and memory.”

Macphail & Bolhuis (2001; p. 341).

Therefore, previous to this dissertation there were few, if any, experimental demonstrations of convergent evolution in cognition between distantly related species and no examples of convergent evolution in social cognition (perhaps, with the possible exception of mirror “recognition” in apes but not monkeys, Macphail, 1987; Tomasello & Call, 1997; Macphail & Bolhuis, 2001).

As a result of this difficulty and historical apathy toward uncovering cases of convergent cognitive evolution in animals (Hodos & Campbell, 1969; Shettleworth, 1998), it is currently impossible to test even the most appealing hypotheses for how and why cognitive changes occur across species. For example, the social intelligence hypothesis is perhaps the most frequently invoked functional explanation for variations in social cognition across species (Humphrey, 1976; Byrne & Whiten, 1988; Cheney & Seyfarth, 1990a; Harcourt & deWaal, 1992; Tomasello & Call, 1997; Dunbar, 1998). The social intelligence hypothesis posits that much of what makes primates and even human cognition unique evolved in the social domain (Cheney & Seyfarth, 1990a). At some point during primate evolution an evolutionary arms race was initiated which created directional selection pressure for increases in social cognitive ability that were only

tempered by physiological and genomic constraints (Byrne & Whiten, 1988; Dunbar, 1993). This hypothesis predicts that modern species identified as having more complex social systems will also demonstrate more sophisticated social cognitive abilities. Indeed, indirect support for this hypothesis is garnered from the finding that various measures of group size, a proxy for social complexity, and various measures of brain size, a proxy for intelligence, are correlated within the primate order (Dunbar, 1992; 1993; Kudo & Dunbar, 2001). Although compelling, such correlations cannot demonstrate a causal relation between social complexity and social cognition. This requires experimental evidence of convergence in social cognitive ability in distantly related species that live in similarly complex social fields. Unfortunately, this type of evidence does not exist currently. In fact, there has yet to be even one demonstration of convergent evolution in any social cognitive ability across nonhumans (although see Byrne, 1993 for a positive correlation between the levels of anecdotal reporting of deception in primates and group size). Therefore, although correlational tests support the predictions of the social intelligence hypothesis, even the strongest proponents concede the need for valid experimental comparisons of social cognitive abilities across species (Barret et al, 2003). Until methods are available that allow for these types of comparisons and patterns in convergence emerge that can be studied in detail, all such functional hypotheses will remain largely speculative.

Visual perspective taking may be unique to hominoids

The current research along with the research of others provides no evidence that non-hominoid primates are capable of visual perspective-taking. This is particularly striking

given that the majority of the work on visual perspective-taking in monkeys has been carried out by ecologically minded cognitive ethologists. Almost all studies examining the ability of monkeys to take the visual perspective of others can be characterized as having a high degree of ecological validity – in some cases this work has even been carried out in the field (e.g. Rendell et al, 2000). For example, Cheney & Seyfarth (1990a) found that when Japanese and rhesus macaque mothers saw a “predator” (a veterinarian) approach their offspring, they were no more likely to give an alarm call if their offspring were unable to see the approaching predator than if the offspring were able to see the approaching predator. In a study resembling that carried out with chimpanzees in Hare et al (submitted; chapter 4), Kummer et al., (1996) found that when long tailed macaques were given the opportunity to hide from a “predator” (a human with a hose) behind an opaque barrier or a transparent barrier, it took them many trials to learn to avoid the predator by staying behind the opaque barrier (also see Hauser, 1997; Kuroshima et al, 2002; Fujita et al, 2002).

Hare et al (2003; chapter 4) corroborates these previous findings in providing no evidence to support the hypothesis that monkeys are capable of visual perspective-taking. Hare et al (2003; chapter 4) found that, unlike chimpanzees, subordinate capuchin monkeys (*Cebus apella*) prefer to retrieve hidden food, but only in reaction to the approach behavior of a dominant. At the same time, dominants had no preference for approaching visible or hidden food, regardless if they could observe the subordinate’s approach behavior or not.

This finding, together with many previous studies, suggests the possibility that there is a difference in problem solving ability between monkeys and apes. If correct it

may be that visual perspective-taking evolved during hominoid evolution. However, such a conclusion is tenuous until further research is carried out with a number of monkey species. Fortunately, as demonstrated by successfully testing capuchin monkeys (a relatively distant relative of hominoids), the new competitive food retrieval paradigm of Hare et al (2000) will allow for quantitative comparison between a diverse range of primate species.

Convergent cognition in humans and canids is due to temperament evolution

The current research provides the strongest evidence to date for convergent evolution in social problem solving abilities across distantly related species. Domestic dogs use human social cues to locate hidden food (Miklosi et al, 1998; Hare et al, 1998). The abilities of dogs have appeared superior to that of chimpanzees when qualitative comparisons have been made between the two species (Hare & Tomasello, 1999). Dogs are capable of using static cues, novel and arbitrary cues, and ignore misleading directional cues – all of which represent social problems for which primates including chimpanzee show little skill in solving (Hare et al, 2002; Chapter 6). Critically, controls for olfactory cues rules out the possibility that dogs are skilful because they can smell the hidden food. Hare et al (2002) confirmed the previous qualitative comparisons between primates and dogs in finding that on the identical object choice tasks dogs found significantly more food than chimpanzees when a human placed a novel and arbitrary marker on top of the baited cup.

The identification of this unusual ability in dogs led to an investigation into its origin (Hare et al, 2002). First, comparisons revealed that dogs did not inherit their

unusual ability for using human social cues through common descent with wolves. When dogs and wolves were compared for their ability to use three different human social cues in finding hidden food, all of the dogs tested were skilled at using the cues while none of the wolves used the cues to find the food. Second, it was found that tremendous exposure to humans is not necessary for dogs to develop the ability to use human social cues skillfully. Puppies differing in age and levels of exposure to humans during ontogeny were equally skilful at using human social cues to find hidden food. Taken together, these findings suggest that during domestication dogs were exposed to selective pressures that improved their social problem solving abilities resulting in convergent abilities with humans (relative to that of primates) in their ability to use social cues (Hare et al, 2002).

Once this suspected case of convergence in social problem solving ability between humans and dogs was identified, the question became how and why this convergence occurred. What heritable psychological system(s) was effected by what type of selection pressure(s) resulting in the modern dog phenotype with its expression of an enhanced ability to read social cues? Although neuroanatomical and physiological comparison between closely related species can potentially allow for inferences about psychological systems responsible for convergence and the selection pressures that led to the changes (Provosudov & Clayton, 2002; Brainard & Doupe, 2002), it is rare even in the case of non-cognitive systems to make inferences about selection pressures with confidence without direct experimental manipulation (e.g. Boag & Grant, 1978; 1981; Grant & Grant, in press). Therefore, in order to understand how and why changes in problem solving ability occurred in dogs, the comparisons on social tasks was extended to include a canid species for which both the psychological system and selection

pressures that differ between two experimental populations are known. Hare et al (in prep) compared the ability of Balyeav's experimentally domesticated foxes to those of controls in using human social cues. The experimental foxes were selected for breeding over 45 years based on the criteria of whether they approached or retreated at the sight of a human experimenter. Based on this criteria a number of morphological, physiological, and behavioral changes associated with domestication occurred at higher levels in the selected than in the unselected populations of foxes (Trut, 2001). Most relevant to understanding the evolution of problem solving behavior are the observed changes in neuroanatomy that are associated with changes in emotional reactivity. The selected foxes have drastically smaller adrenal cortex as well as other associated limbic areas (no gross changes to nonlimbic areas have been observed) while their circulating levels of serotonin are five times higher than that of the control foxes (Trut, 2001). These changes are directly related to changes in temperament with selected foxes being less emotionally reactive (fearful or aggressive) in novel situations or while humans are present (Trut, 2001). Hare et al (in prep) found that the experimentally domesticated foxes were more skillful at using human social cues than control foxes. Given the substantial changes to the limbic and endocrine systems of the selected foxes, these findings suggest that the domestic dog also possess their unusual ability for using human social cues as a result of selection against emotional reactivity which led to changes in noncognitive systems.

The results of Hare & Tomasello (in press; Chapter 5) provide further support for hypothesis that variance in emotional reactivity can explain differences across species in social problem solving behavior. Hare & Tomasello (in press) find evidence that chimpanzees are more skilful in competitive than in cooperative cognitive tasks

regardless of whether they are social or nonsocial problems (also see Vick & Anderson, 2003 who find that baboons show enhanced performance in the object choice paradigm when competing against an experimenter). Because the competitive effect is present across social and nonsocial domains, it seems unlikely that chimpanzees difficulty in cooperative-communicative social tasks can simply be explained with cognitive deficit hypotheses alone. Instead, the improved performance of chimpanzees across cognitive domains when competing suggests the possibility that chimpanzees are more emotionally aroused and attentive when they are forced to compete for a food reward. This emotional arousal and attention may then be responsible for the improved performance in the different problem solving tasks. If correct, such findings draw into question the validity of many of the previously used cooperative-communicative paradigms as tests of “cognitive ability” while suggesting that differences between chimpanzees and humans in using social cues may be explained as much by differences in temperament as by differences in cognition.

Future Research

Research will be required to further test the hypothesis that visual perspective-taking is a derived and unique trait in hominoids. In order to test this hypothesis research will be necessary with other species of monkeys. However, given constraints on resources species should be chosen for comparison that will provide the most powerful test of the prediction of phylogenetic and functional hypotheses. One species that would provide an interesting test of the hominoid specialization hypothesis and the social intelligence hypothesis is the savanna baboon (*Papio anubis*). The hominoid

specialization hypothesis predicts that baboons, as cercopithecines, will not be capable of visual perspective-taking while the social intelligence hypothesis predicts that baboons, with their complex social field, will be likely to have experienced selection for sophisticated social problem solving skills – perhaps resulting in the evolution of perspective-taking skills. Indeed, baboons do seem to have an impressive mastery over many aspects of group living (Kummer, 1971; 1995; Noe, 1992; Bergman et al, 2003). In addition, the dominance style of savanna baboons is typically characterized as far more despotic than egalitarian (Kummer, 1995) – assuring that subordinates will have incentive during testing to use the most effective strategy possible in retrieving food while competing against a dominant competitor. Therefore, such an investigation should be possible without requiring significant modification to the same competitive food retrieval paradigm used by Hare et al, (2000; 2003). It is only after the distribution of visual perspective-taking skills across primates and non-primates are understood that possible scenarios for its evolution in hominoids can be suggested and tested.

Significant amounts of research will be required to fully understand the effect of emotional reactivity on the social problem solving ability of animals. Currently, comparative psychologists allocate little theoretical or empirical attention to the interdependence of emotional and cognitive systems in determining problem solving skills. Instead a myopic focus on cognition inevitably leads to the conclusion that variation in problem solving behavior is a product of variation in cognitive ability. However, repeatedly it has been difficult to demonstrate that selection for increases in problem solving ability has focused on cognitive systems alone (e.g. Tryon, 1940; Searle, 1949; Hare et al, 2002; Hare et al, in prep). Therefore, it seems that instead of ignoring

or superficially controlling for the influence of temperament on problem solving behavior, future research should be dedicated to understanding how emotional and cognitive systems are integrated and many times constrain each other (Hare & Tomasello, in press). In addition, the possibility that most inter and intraspecific differences in problem solving behavior are a result of temperament evolution and not cognitive evolution must be taken seriously. It is possible that the mammalian genome is most amenable to changes in the functioning of neuroanatomical and endocrine systems responsible for levels of emotional reactivity. Therefore, improvement in problem solving ability is most readily accomplished through selection on noncognitive systems. If correct, this may suggest the somewhat radical hypothesis that truly qualitative differences in cognition maybe relatively rare across species.

Evolutionary mechanisms in hominins

If humans inherited some features of our Theory of Mind while others represent derived cognitive features unique to humans, what mechanism(s) for change (i.e. selection pressures and evolutionary pathways) might account for how and why the observed unique features of the human Theory of Mind evolved?

Research on human cognition is primarily conducted by cognitive psychologists who concentrate on understanding mechanisms involved in perception, memory, computation, and inferential abilities in developing and adult humans (Piaget, 1952; Miller, 2003). A fledgling subset of cognitive psychologist study adult cognition from an adaptive perspective (e.g. Symons, 1979; Daly & Wilson, 1981; 1982; Barkow et al, 1992; Girgerenzer & Hug, 1992; Pinker, 1994). However, these evolutionary

psychologists concentrate exclusively on demonstrating the utility of adaptationist models for explaining the behavior of modern adult humans. Therefore, the majority of this research focuses on demonstrating that adaptive predictions based on knowledge of selection pressures during the environment of evolutionary adaptedness (Bolby, 1969; 1973; Symons, 1979; Irons, 1998), mainly inferred from research on modern humans living lifestyles similar to Plio-Pleistocene hunter-gathers (e.g. Kaplan & Hill, 1985; Chagnon, 1988), provide a powerful theoretical framework for explaining all types of anomalies in modern human behavior (Tooby & Cosmides, 1990). The main method available to evolutionary psychologists is the identification of context or content dependent processing. It is inferred that low variance in success within a discrete cognitive domain is indicative of canalization in a system crucial for solving ecologically relevant problems faced by Plio-Pleistocene hunter-gathers. For example, humans are better at detecting violations in social contracts than they are at detecting logically identical violations in more abstract and artificial algebraic relations when presented in the Wason selection task (Cosmides, 1989). This context dependent processing is interpreted as a case of domain specificity that suggests selection for the ability to detect cheaters in the Plio-Pleistocene (Tooby & Cosmides, 1992). Therefore, evolutionary psychologists can potentially either predict and explain anomalies in human behavior that social scientists cannot by taking a functional perspective or they can identify cases of domain specificity that nominate selection pressures which may have previously shaped hominin cognition.

With promises to revolutionize studies of human psychology, evolutionary psychology has proliferated into diverse domains of research including studies of mate

choice, incest avoidance, human sexuality, intergroup conflict, foraging adaptations, communicative function of facial expressions, functional design of emotions, social cognitive modules, cooperation and more. However, with all its diversity the research program of “evolutionary psychology” is not designed to contribute broadly to studies of human cognitive phylogeny. Instead, researchers are narrowly focused on combating the so called “Standard Social Science Model” which has arguably dominated studies of human psychology (Tooby & Cosmides, 1992). Unfortunately, this means that while evolutionary psychology has begun demonstrating the utility of adaptive thinking in explaining human behavior, as has been done for animals, at the same time evolutionary psychology has contributed little that might help identify and explain the evolution of derived features of human cognition. Therefore, the researchers with the greatest appreciation for the power of evolutionary theory in explaining human behavior do not seem to have an equal appreciation for the problem that Darwin himself saw as the “greatest difficulty” for his incipient theory (Darwin, 1871).

Thus, evolutionary psychologists must realize, when comparative psychologists are successful in identifying derived aspects of human cognition and can demonstrate how and why such cases of cognitive evolution occur in others species, it is also possible for them to use comparative data to develop tests with humans designed to reveal how and why unique cognitive abilities evolved in our own species. For example, just as the demonstration of domain specificity in detecting cheaters can reveal the signature of selection pressures on logical reasoning, so can the identification of domain specificity lead to testable hypotheses for how and why humans evolved aspects of ToM identified as being derived – such as an understanding cooperative-communicative intent in others.

Moreover, knowledge of how and why cognitive evolution occurs across animal species can help in refining hypotheses of selective pressures that led to changes in problem solving abilities during the Plio-Pleistocene. This latter approach, could prove especially useful in answering critics who point out that phylogenetic accounts of variance in human cognitive ability have yet to specify genetic mechanism effected by proposed selection pressures (Richardson, 1996; Davies, 1999; Heyes, 2003). Animal models potentially allow for the identification of evolutionary pathways that may have been effected by selection pressures in animals and humans alike. For example, work with animals suggest that change in noncognitive systems may be responsible for context and content dependent processing within the social domain (e.g. Hare & Tomasello, in press; Hare et al in prep). Future research with such animals may allow for the identification of the genetic architecture whose modification is responsible for the observed changes in noncognitive systems that produce canalization in social problem solving behavior (e.g. Enard et al, 2002). Such research with animals then makes it far more plausible to attribute similar cases of context or content dependent processing in humans to a similar set of genetic changes while suggesting paths to verify such hypotheses. It is this type of hybridization of research programs that will not only help in resolving Darwin's greatest difficulty, but also will represent a field deserving the title of evolutionary psychology.

Hominoid comparisons reveal derived hominin traits

It is only through research on nonhumans that we can identify derived features of human cognition that evolved since our species split with our LCA (Hauser et al, 2002). Currently, based on comparisons with chimpanzees, it seems plausible that aspects of our

human ToM are derived traits (Tomasello et al, 2003; Povinelli & Vonk, 2003). This finding adds support to the hypotheses that it is aspects of our human ToM that allows for much of our unique human intelligences (Dennet, 1983; Perner, 1991; Baron-Cohen, 1995; Carruthers & Smith, 1996; Tomasello, 1999; Sperber, 2000). Therefore, if a coherent theory of human cognitive evolution is to become a reality, it will be crucial for evolutionary psychologists to determine how and why human ToM evolved.

Identifying convergence reveals selection pressures

Research on social cognition in primates and canids now suggests that variation in social problem solving in these species is largely explained by variance in non-cognitive systems that play a role in motivating attention and prosocial behavior (Hare & Tomasello, in press; Hare et al, in prep). While chimpanzees, who presumably have been under intense selection for competitive ability, are sophisticated in solving a number of social tasks while competing (Byrne & Whiten, 1988; Hare & Tomasello, in press), at the same time, they are poor at solving similar tasks that require cooperation and communication with others (Tomasello et al, 2003). Meanwhile, dogs, who evolved to live sympatrically with humans (Coppinger & Coppinger, 2001), are skilled in many of the exact same cooperative-communicative tasks that chimpanzees and other primates universally fail (Soprani et al, 2001; Hare et al, 2002) due to changes in levels of emotional reactivity (Hare et al, in prep). Taken together, these findings suggest the hypothesis that selection on temperament during human evolution may have played a critical role in either increasing our species potential for social problem solving or at least

facilitating directional change by lifting a constraint(s) that might otherwise have prevented any benefit from increases in cognitive ability.

As an example of how temperament evolution may have played a central role in the evolution of derived social problem solving abilities in humans, consider recent findings on chimpanzee cooperation. Chimpanzees show little capability for spontaneous cooperation in instrumental tasks (Crawford, 1937; 1941; Chalmeau, 1994; Povinelli & O'Neil, 2000), yet Perez et al (underway) found that a chimpanzee's cooperative skill in a novel, instrumental task is best predicted by her level of tolerance with her potential collaborator (i.e. partners who can sit next to each other and share food without fighting can spontaneously solve an instrumental task requiring cooperation). This suggests that levels of emotional reactivity can act as a prohibitive constraint on collaborative behavior in chimpanzees. Chimpanzees may be limited in their ability to coordinate and collaborate in activities largely because they are too emotionally volatile in the presence of conspecifics and food (i.e. even if chimpanzees can cognize about cooperation they would still seem inflexible due to constraints on their temperament). If true, this would also suggest that many unique problem solving behaviors in humans are not only a result of cognitive evolution but also temperament evolution, while also making it likely that changes in emotional reactivity may have preceded cognitive evolution in many cases. This level of evolutionary analysis is not possible with exclusive focus on either humans or nonhuman primates alone. Therefore, a comprehensive theory of human evolution will depend on the ability of evolutionary psychologists to integrate their findings on domain specificity in adult humans with demonstrations of selection pressures and evolutionary pathways in nonhumans by comparative psychologists.

Future Research

Determining how and why unique aspects of human cognition evolved is the greatest difficulty Darwin willed to us, yet we still know little of what the unique features of human cognition are and how and why they evolved. While work comparing chimpanzee and human social cognition have begun to uncover derived features of human ToM, currently there is little we can do but speculate on how and why these features evolved. If we are to truly test the limits of evolutionary theory, effort must be concentrated on identifying selection pressures and their targets during human cognitive evolution. Because some derived features of ToM have been identified with some certainty, studies working to identify context and content dependent processing in the development and utilization of adult theory of mind will be central to such a research program.

While comparative psychologists are working to identify derived aspects of human social cognition, developmental and cognitive psychologists have largely left unexplored ToM in humans past early childhood (see Keysar et al, 2003). Therefore, it is unclear exactly in what context ToM capabilities are actually relied upon, when ToM mistakes are most likely to occur, and what level of variance exist in adult ToM capabilities. However, there is good reason to believe in this case that the absence of evidence is not evidence of absence. First, from the sparse research on adult ToM there is evidence that adult humans rely on simple associative learning strategies in settings in which it is predicted ToM would be exclusively implemented (Galgiardi et al, 1995) while adults also repeatedly make ToM mistakes in attempts to solve seemingly simple communicative problems (Keysar et al, 2003). Second, there is evidence for extreme

variance in ToM capabilities across cultures (Lillard, 1998) and within cultures (Ekman et al, 1999). Given its potential importance to many unique human intelligences, it will be critical for evolutionary psychologists to probe the limits of adult ToM. As it is discussed by most developmental psychologists, it would seem ToM is infinitely flexible and domain general cognitive mechanism (Wellman, 1990; Moore & Frye, 1991; Povinelli & Vonk, 2003). However, future research is likely to uncover context and content dependent variation in human social problem solving – including in adult humans with a normally functioning ToM (e.g. Nickerson, 1999; Keysar et al, 2003).

In addition to neglecting ToM in adult humans, cognitive scientists tend to ignore variance in problem solving behavior that is caused by non-cognitive systems. While it is essential to control for non-cognitive variance in problem solving when attempting to gain an understanding of a cognitive mechanisms, it can be extremely misleading when studying how and why evolution in problem solving ability occurred in humans and other species. Undoubtedly, many cognitive and non-cognitive systems are inextricably intertwined for the purpose of solving ecologically relevant problems. Many social cognitive decisions are not only effected by, but are dependent on emotional centers of the brain assigning affective valiance to social input (Damasio, 1994; Haxby et al, 2000). For example, Kawashima et al, (1999) found evidence for specific activation of the amygdala during human gaze monitoring task while Stone et al (2003) found that human patients with bilateral damage to their amygdala had specific deficits in assessing another individual's visual perspective (see Emery, 2000 for a review of similar cases in animals). Having implicated the limbic system's involvement in human ToM decisions, it becomes likely that variance in emotional reactivity will play a role in explaining

variance in performance on tasks typically considered strictly cognitive or ToM tasks. A growing literature is revealing heritable categories of human emotional reactivity that remain stable across an individual's lifetime (Robinson et al, 1992; Kagan, 1997; 1998) while recent research suggests a relationship between certain temperamental profiles and variance in behaviors related to the expression of ToM in children. For instance, DiBiase & Lewis (1997) found that children with high reactive temperaments were more likely to show embarrassment upon developing self-recognition abilities than children with low reactive temperaments (see also Kochanska et al, 1997). Meanwhile, Morales et al (2000) found a correlation between temperament profiles in infants under the age of one and levels of joint attention and subsequent speed of word learning during initial phases of language acquisition. Finally, Rice et al (1997) found that during a competitive and presumably emotionally evocative task 3 year olds, "...can grasp the distinction between appearance and reality when their goal is to trick someone." If Rice et al (1997) are correct, the success of children in this competitive task would occur a full year earlier than is typically documented in standard appearance-reality tasks (i.e. Flavell, 1986; 1992). Therefore, future research with human children and adults must develop methods capable of describing in detail the relationship between emotional and ToM centers of the brain while exploring context and content dependent processing in social cognitive tasks. Uncovering how cognitive and emotional systems are integrated and constrain each other will likely play an important role generating and testing hypotheses for how and why derived features of ToM evolved in humans.

Summary of conclusions

- 1) Darwin saw explaining the evolution of human cognition as the “greatest difficulty” for his incipient theory of evolution through natural selection. Therefore, studies of human cognitive evolution must become more central to the field of Anthropology and Evolutionary Psychology.

- 2) Investigations of human cognitive evolution are possible through virtual time travel. First, unique or derived human cognitive traits must be identified by comparing human cognition with that of chimpanzees and other hominoids. Second, cases of convergent cognitive evolution must be identified so that plausible hypotheses can be developed for how and why cognitive evolution takes place. Third, using knowledge from comparative research, human psychologists can test hypotheses for how and why unique cognitive abilities evolved by studying cognitive development and cases of domain specificity. It is only by integrating all three approaches that it will be possible to assess what is unique about human cognition and how and why it evolved since our lineage split from our last common ancestor with chimpanzees and bonobos.

- 3) Chimpanzees are capable of understanding some psychological states in others – the question now is which ones and to what extent. The current investigation challenges the previously held consensus that chimpanzees have no capabilities to model the psychological states of others. There is now sufficient evidence to show that chimpanzees know what others can and cannot see and that this knowledge extends

both into the past and future. At the same time, there is evidence that chimpanzees are not as flexible as humans in assessing the cooperative-communicative intent of others. It is possible this increase in flexibility in reading other's cooperative-communicative intent plays a role in allowing for many of our species unique intelligences (i.e. including aspects of language acquisition). Powerful new comparative methods now exist that allow for the necessary ecological validity and controls so that future study should reveal in detail exactly how similar the chimpanzee ToM is to that of humans.

- 4) Although comparisons between species can reveal how and why cognition evolves, there has yet to be an uncontested demonstration of convergent evolution in cognitive ability across species. Little research effort has been invested in perfecting the steps of developing valid cross species comparisons in cognition. As an example, it was previously concluded that chimpanzees failure to use social cues was a result of a cognitive deficit. The current results support the hypothesis that non-cognitive factors may play as large or larger role in effecting a species ability to flexibly utilize social cues as variance in cognitive ability. Chimpanzees were found to be more skillful in competitive than in cooperative cognitive tasks, supporting the hypothesis that chimpanzees are most emotionally aroused and attentive in competitive social contexts. Further support for this temperament hypothesis is the fact that domestic dogs, who have evolved to cooperate and communicate with humans, are far more skillful at reading human social cues than chimpanzees in cooperative-communicative social context, yet this increase in skill is likely due to temperament evolution alone –

not cognitive evolution. The current results highlight the fact that variance in problem solving behavior does not correlate with cognitive abilities one to one. In addition, these findings point to the need to develop techniques for detecting species differences in cognitive ability while at the same time demonstrating the essential role of temperament evolution in the evolution of social problem solving abilities – including during human evolution.

- 5) Lessons learned from comparative studies of animal cognition can be applied to research on human cognition. Human psychologists interested in understanding how and why humans are unique can use comparisons between humans and other hominoids to help direct their research efforts. For example, through research on our closest relatives we know it is likely that humans are unusual in their ability to assess cooperative-communicative intent and possibly even belief states in others. Therefore, human researchers can investigate how such abilities develop and function to understand how such abilities might account for unique human intelligences. In addition, study of convergence in problem solving behavior across species produces testable hypotheses for how and why problem solving abilities evolve in animals - including humans. Therefore, human researchers can use the lessons learned from such studies and investigate whether such hypotheses may help explain how and why unique human intelligences evolved. For example, the current results demonstrate the effect of temperament evolution on social problem solving abilities. In a similar way it may be that humans unique social intelligences are largely a result of temperament evolution during the Plio-Pleistocene. This hypothesis can be tested by examining

temperament's effect on the development of problem solving behavior in children while also examining how well temperament hypotheses can predict and account for cases of domain specificity in adult humans. Thus, to have a full understanding of human evolutionary psychology, it will be necessary for evolutionary psychologists to embrace the methods and results of comparative psychologist who are equally interested in understanding human evolution.

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