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REVIEW

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Can competitive paradigms increase the validity of experiments on primate social cognition?

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Abstract Experiments vary in their ability to distinguish between competing hypotheses. In tests on primate cognition the majority of this variation is due to an experimenter's ability to test primates in valid settings while providing the adequate amount of experimental control. While experimenters studying primate cognition can use methods of control perfected in captivity, it is still very unclear how to design and then objectively evaluate the external validity of new experimental paradigms. I recommend that more effort be allocated to specify how to create relevant test settings for primates. Primate social life is highly competitive. This means that all aspects of primates themselves, including their cognitive abilities, have likely been shaped by the need to out-compete conspecifics. Based on this hypothesis, sophisticated cognitive abilities of primates might best be demonstrated in competitive contexts. Thus, it is suggested that one possible measure of validity is whether investigators integrate a competitive component into their experimental designs. To evaluate this methodological prediction I review the literature on chimpanzee perspective-taking as a case study including several recent studies that include a competitive component in their experimental designs.

Keywords Chimpanzees · Perspective-taking · Ecological validity · Competitive paradigms · Social cognition

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, p. 265).

Any observed behavior can have multiple explanations as to 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 underlying behavior, and more specifically problem-solving behavior (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 and Zechmeister 1994). Cognitive ethologists strive to maximize experimental sensitivity. In addition, they wish to objectively evaluate the sensitivity of each other's experiments.

Unfortunately, as Koehler (1925) 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 often means that experiments vary in their ability to demonstrate that a behavioral strategy is guided by a sophisticated cognitive mechanism as opposed to 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

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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). Many methods of control have been developed and standardized, such as controlling for order effects, removing biases using blind experimenters, and counterbalancing. The merit of the different methods of control is that, when used appropriately and in concert, they are extremely powerful and can be applied to any species or paradigm allowing investigators 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, 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, p. 179). 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. This is why the primate cognitive literature is replete with examples of how methodological changes can dramatically change previously accepted results and interpretations (e.g., Oden et al. 1990; Boysen and Berntson 1995; Tomasello et al. 1998). Therefore, 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).

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 the results obtained are more likely to apply to situations outside the actual test. Even if negative results are obtained one can feel more confident that the results reflect the abilities of the animals and not simply the shortcoming of the experiment itself (although in the end negative results from any one experiment or approach remain difficult to interpret). In addition, experiments that consider validity should be more likely to yield positive results than experiments that are conducted in highly circumscribed or unfamiliar settings (e.g., Oden et al. 1990; Boysen and Berntson 1995; Tomasello et al. 1998). Therefore, in the case of cognitive tests on primates, ecological validity, defined as the degree to which an experiment is able to simulate a relevant aspect of subjects' individual ontogenies and/or their species evolutionary histories, is the measure that becomes most important for evaluating external validity (Hare et al. 2000, 2001). In summary, experimental control alone does not allow one to maximize the validity of experiments on primates. Instead, the combination of (1) proper control(s) and (2) an ecologically 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 and Call 1997; but see Cheney and 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 eliminated any 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, everyone 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, and chimpanzees (not to mention non-primates). 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, little 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 created valid test settings by taking the refined methods of control and adapting them for use in their subject's natural habitat (Cheney and 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 disrupting the lives of their subjects. Given the limits of field experimentation, is it possible to reverse the flow of information so that experimenters in captivity can learn how to improve their experiments from lessons learned by behavioral ecologists and ethologists studying animals in their natural habitat? In other words, by considering primate behavioral ecology will it be possible to generate 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 similar to methods of experimental control?

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. Next is suggested the first of what 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 so 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 will remain. This problem is 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 one’s 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 also pose serious threats to valuable resources and reproductive success. For example, in chimpanzees intergroup competition can often become lethal, with males raiding neighboring groups to kill lone males or the infants of unwary mothers (Wrangham and Peterson 1996; Wrangham 1999; Wilson et al., in press). Thus, it is clear that primates live their entire lives competing with conspecifics in order to maximize their reproductive success.

As a result, almost everything about primates, including their morphology, behavioral repertoire, temperament, and 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 (Mitani et al. 1996). 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 and Whiten 1998). Also, as intraspecific competition becomes more intense across species, facial expressions, including those, which signal submission, become highly specialized to prevent costly miscommunications (Preuschoft 1995; Preuschoft and van Schaik 2000). In fact primates’ signals in general are designed for the purpose of manipulating and exploiting others so that their own selfish needs might be met (Krebs and Dawkins 1984). For example, primates are highly selective in the information they provide potential competitors about food resources (Dittus 1984; Hauser 1996, 2000). Thus, when chimpanzees discover a previously unknown food resource, they make species-specific food calls if they deem the food resource shareable while they remain silent if the food is monopolizable (Hauser and Wrangham 1987; Hauser et al. 1993). In addition, in experiments no informed individual spontaneously or overtly used communicative displays or signals to indicate to a conspecific the location of 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 and 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 persuade 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 absolutely refuse to move. If trying different foods or waiting for minutes (or in some cases hours!) fails, what is the quickest way to get a primate to move? Simply place a conspecific on the other side of the baited cage into which you want the subject to move. As soon as your subject realizes that another individual may get the food, it races into the cage and grabs the previously “undesirable” food!

Given that primates have evolved 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 and 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 the idea that when a competitive component is added to controlled experiments it leads to more sensitive paradigms? Next I discuss the difficulties of demonstrating perspective-taking and then review the chimpanzee perspective-taking literature as a case study for evaluating the utility of this first primate principle in designing more sensitive social cognitive experiments.

Problems with primate perspective-taking

Perspective-taking (more commonly referred to as mental attribution, theory of mind, mentalizing, or mindreading) allows one to understand that the actions of other individuals are not driven by the actual state of the world, but instead by each individual's own perceptions (i.e., visual or auditory) and or representations (i.e., desires and beliefs) of the world (Russon 1997; Flavell 1992). Or simply, an individual can put itself "in someone else's shoes," allowing it to consider and react to another individual's perceptions, desires, and beliefs as opposed to just their behavior (note that this definition of perspective-taking is much broader than the typical sense of the term which refers only to taking another individual's visual perspective).

Perspective-taking is considered an essential ingredient underlying what are considered some of the most human specific social cognitive abilities (Baron-Cohen 1999; Tomasello 1999). Coherent theories of the ontogeny and evolution of perspective-taking are therefore an important goal for better understanding human cognitive evolution (Corballis and 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 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 species 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 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), and (2) a way of having the subject demonstrate that it is aware of the differing perspective of the other individual. The task is complicated by the fact any individual's perspective (e.g., I see or believe there is danger) is usually highly correlated with its behavior (e.g., I scream and run) (Tomasello and Call 1997). Therefore, in order to demonstrate perspective-taking, experiments must show that subjects are making their decisions based not just on another individual's behavior, but instead by taking the perspective of another individual (i.e., being sensitive to someone's perceptions, desires, or beliefs about the world).

The success of developmental psychologists studying perspective-taking has been greatest when 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 (Edith), after which the toy is moved to a new hiding location. Finally the experimenters asks the child remaining in the room, "where will Edith look for the toy?" (Wimmer and Perner 1983). Sometime after his or her 4th birthday a child will answer that Edith will look in the original hiding spot, because they appreciate Edith's perspective: Edith could not know that the toy had been moved because she was not present when it was moved (i.e., she 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 and 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 her response on their own perspective or the behavior of the other individual. Unfortunately, those studying nonhuman primate perspective-taking must find behavioral measures 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, typically resulting in small sample sizes (<6 subjects is common). To compensate, experimenters must give subjects repeated exposures to treatments, making results vulnerable to simple learning hypotheses. Developmental psychologists on the other hand have an almost limitless supply of subjects. They can design experiments that administer single exposures to dozens of subjects. Second, the quality of small primate samples in 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, effectively reducing a sample by two. Third, many logistical constraints limit the possible designs of experiments on primates, such as the inability of experimenters to interact with their subjects physically, to test conspecifics together with other conspecifics, or to modify existing caging or housing structures to meet the needs of the experiment (i.e., the building belongs to a zoo or research center). Given the methodological demands and constraints on experiments of perspective-taking in nonhumans, it may come as no surprise that comparative psychologists lag far behind developmental psychologists working with human children. In addition, it also becomes evident that experiments on primate perspective-taking must maximize experimental validity.

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 test species 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 20 years ago (Premack and Woodruff 1978) there still remain only a handful of experiments on chimpanzees that are relevant to evaluating perspective-taking. In addition, after 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 (Heyes 1993, 1998; Povinelli 1996; Tomasello and Call 1997).

Information relevant to chimpanzee perspective-taking began to be collected over 30 years ago with 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). Such observations provide extremely valuable informative 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 and Whiten 1992). In addition, no matter how frequently behaviors such as those observed by Goodall (1971) are witnessed, it is impossible to determine if the animal is trying to manipulate the perspective of its 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 and Whiten 1992).

Menzel (1974) reports the first set of experiments that are relevant to chimpanzee perspective-taking. Food was hidden while 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 Coussi-Korbel 1994 for a similar finding with monkeys). Although many of the strategies used by the chimpanzees were consistent with perspective-taking, and unlike previous anecdotes are highly replicable (Hirata and Matsuzawa, in press), it is still unclear whether the chimpanzees were reacting to the behavior of their competitors or their perspective.

The first experiments explicitly designed to test for perspective-taking were carried out by Premack and colleagues (Premack and Woodruff 1978; Woodruff and Premack 1979; Premack 1988). In spite of some ingenious designs, all of these 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 full of treats on the wall (see Premack 1988; Tomasello and Call 1997 for reviews). 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 similar to that of Premack (1988) that has since become the most widely known study of chimpanzee perspective-taking. Povinelli et al. (1990) first trained four chimpanzees to discriminate between an ignorant and a knowledgeable human experimenter while trying to obtain 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). During baiting, a second experimenter remained outside of the room and therefore was ignorant of 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. The chimpanzees were allowed to choose a cup. 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 pointed.

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.

Heyes (1993) argued against the claim that the chimpanzees successfully transferred to the new test situation, and Povinelli (1994) acknowledged that, indeed, it was possible that subjects had simply learned to use some discriminative cue to perform successfully in the second study. 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 a simple cue when successful.

Call and Tomasello (1999) conducted the first nonverbal test for perspective-taking that simulates the traditional false-belief tests developed for use with children. First, behind an occluder a human experimenter would place 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 1993, 1998; Povinelli 1996; Tomasello and 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

Retreat!

Based on the idea that previous studies were consistent with a "low-level model of behavior reading", recent research efforts have been channeled into what are considered simpler tests which investigate abilities thought of as elementary 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 do chimpanzees understand about the visual experience of other individuals. But it is important to realize that these paradigms represent starting points; even if the chimpanzees mastered them all, the abilities tested are neither necessary nor sufficient to demonstrate perspective-taking (Heyes 1998; Call et al. 2000).

Tomasello et al. (2001) 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 and 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 demonstrated for human infants (Butterworth and Jarret 1991; Corkum and Moore 1995).

These findings stand in stark contrast to the results of two other paradigms. Povinelli and Eddy (1996b, 1996c) 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 experimenters assumed one of two postures. For example, one individual faced the subject while the other stood with their back turned. In another condition both experimenters faced the subject but one would either have their eyes closed or head turned away from the subject. In all of the studies the subjects were rewarded for placing 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 avoided experimenters with their back turned, preferring those facing them, they needed dozens of exposures to improve on any of the other discriminations (i.e., they reached toward the person facing them as often as the one whose head was turned away). Although there are many possible interpretations, 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 and Povinelli 1999).

The final series of studies tested the ability of chimpanzees to find food 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 chimpanzee knows food is being hidden, but does not know where), then the experimenter typically waits until the subject is looking at him before providing a cue (e.g., eye direction, head direction, pointing, tapping the correct container) 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 it chooses the correct cup). 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 and Eddy 1996c; Povinelli et al. 1997, 1999; Tomasello et al. 1997; Call et al. 1998, 2000; Itakura et al. 1999; but see Itakura and Tanaka 1998). Again these results have been interpreted as being inconsistent with an appreciation of the visual experience of others. So even, after pursuing these "simpler" approaches 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.

More control

Heyes (1993, 1998) reiterates the weakness of anecdotes as evidence for perspective-taking and makes a compelling case that no perspective-taking experiment with primates thus far has sufficient controls to rule out more parsimonious interpretations of the results. She concludes that until experiments that use appropriate controls are designed and implemented no convincing evidence for perspective-taking in primates (or nonhumans) will ever be generated. Heyes proposes 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 invites her *Behavioral and Brain Sciences* commentators to assess her new paradigm and suggest how it might be improved or replaced.

Heyes' proposed study is derived from the procedure of Povinelli et al. (1990). First, the chimpanzees would be trained to discriminate between two 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 reward 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 then it would be predicted that in the transfer test the subjects would immediately generalize the skills they learned in the first training stage to 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 many of the problems of previous experiments and for inciting a number of constructive responses, her suggested approach would without doubt produce a null result. Although she briefly acknowledges the need for, "knowledge of the habits and natural history of primates" (p. 113) her suggested paradigm has no external validity. In no review of the habits or natural history of chimpanzees will one find the word goggle or a discussion of cooperative interactions over food between chimpanzees and different species.

Perhaps much more surprising than the exclusive focus on control are the 23 responses by the commentators. While 13 responses evaluated or made suggestions to further improve the controls proposed, only 3 mention the fact that the new paradigm seems "unnatural", with only Matheson et al. (1998) suggesting a more naturalistic alternative. Furthermore, all nine of Heyes' revisions to her experiments in response to the commentators again dealt with issues of control. So, in summary, although critical issues of control are discussed (i.e., avoiding differential reinforcement and using methods of triangulation), only a small minority of individuals consider the ecological validity of the testing situation when designing tests of primate perspective-taking.

A chimpanzee perspective

The final suggestion is based on the intuition felt by some that previous experiments on perspective-taking have seemed contrived or somehow lacking in ecological validity (Shettleworth 1998; Matheson et al. 1998; Tomasello and Call 1997). For example, Gomez (1996, 1998) argues that chimpanzees have evolved to solve problems about chimpanzee minds, and therefore tests of perspective-taking should be designed to test if chimpanzees understand the perspective of other chimpanzees instead of humans. But Gomez does not specify how this goal should be achieved, and he outlines an experiment which involves apes communicating with humans about a hidden key that opens boxes containing food (see also Whiten 2000).

Unfortunately, no one has specified the aspect of conspecifics might improve the performance of chimpanzees in tests of perspective-taking. This has made it easy to 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 and Seyfarth 1990b; Hauser 1997; Rendall et al. 2000 for examples with monkeys).

A competitive perspective

What is needed are experiments that provide ecologically valid test settings and also have the flexibility to permit critical controls (such as triangulation and no differential rewarding) discussed in Heyes (1993, 1998). Might the competitive primate principle be part of the answer?

Almost without exception (the exception being studies of gaze following) studies of perspective-taking 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, 1994, 1997; Povinelli and Eddy 1996c; Tomasello et al. 1997; Call et al. 1998, 2000; Itakura and Tanaka 1998; Call and Tomasello 1999; Itakura et al. 1999) 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 and Eddy 1996b, 1996c; Reaux et al. 1999; Theall and Povinelli 1999). In fact only one experiment has included any competitive component at all (Woodruff and Premack 1979). But the competitive nature of primate social life means that these types of cooperative-communicative settings are highly artificial for chimpanzees. Recall that evolutionary theories emphasize the manipulative function of animal signals (Krebs and Dawkins 1984) while experiments with chimpanzees have even demonstrated their natural tendency to avoid communicating about monopolizable food resources (Hauser and Wrangham 1987; 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, having experienced selective pressures that have encouraged cooperative-communicative interactions with humans (Serpell 1995), outperform primates in the cooperative-communicative object choice task described above (Hare et al. 1998; Miklosi et al. 1998; Hare and Tomasello 1999; McKinley and Sambrook 2000; Agnetta et al. 2000). 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. 2000). Thus, comparison of the abilities of domestic dogs to those of primates in the object-choice task shows how important it can be to consider a species' evolutionary history in designing experimental methodologies. Experiments on chimpanzee perspective-taking should clearly avoid communication or cooperation especially when monopolizable food is at stake.

With this insight Hare et al. (2000, 2001) designed a new paradigm which emphasized competition between conspecifics, rather than cooperation and communication with humans in order to test whether chimpanzees could take the perspective of another individual.

Hare et al. (2000) tested members of two large socially housed groups of chimpanzees in pairs, allowing them to compete 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. Thus, for each pair one of the chimpanzees was always dominant and the other subordinate, but any one subject frequently switched between the two roles during testing depending on whom they competed against (only the highest- and lowest-ranking individuals did not play both roles). For each trial a subordinate and a dominant chimpanzee were placed in 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 they could do to prevent the dominant competitor from taking all the food, but when this same individual was the dominant competitor she tried to assure she obtained both pieces of food. Indeed, in all the conditions 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 one subject could see a piece of food that the other could not see. 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.

When individuals were subordinate and the dominant competitor could only see one of the pieces of food, the subordinates retrieved more hidden food that the dominant could not see. In addition, when these same individuals switched to the role of dominant, they no longer preferred to retrieve hidden food first, but instead retrieved the piece of food that its competitor could see first (consequently dominants were almost always able to obtain both pieces of food). Control studies were also run to rule out the possibility that the observed preferences were due to behavioral cueing or 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's door remained completely shut until after the subordinate committed to approaching a piece of food. 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 on 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 the subordinates' preference for food behind barriers from the previous four studies suddenly disappeared. Together, these findings 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.

Hare et al. (2001) 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 experimental 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.

Chimpanzees were tested in four pseudo-randomized conditions in the first study. 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 placed on her side of one of two barriers. In addition, she could also monitor what her dominant competitor witnessed during baiting.

In the uninformed control condition the dominant could 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 could not watch as the food was hidden 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 second 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. After baiting, as in Hare et al. (2000), subordinates were always released first to ensure that their retrieval decisions were not simply in reaction to the behavior of the dominant. In addition, if the subordinate chose not to approach for almost half a minute after her door was opened, the dominant was released to retrieve the food.

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 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 of learning across four sessions of testing.

A second transfer study tested whether the subjects would generalize their preferences to a novel pair of conditions without needing numerous trials to do so. 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, naive dominant that had not witnessed the baiting (in the control condition the original dominant remained). Although each subordinate only received four trials in each of the two types of conditions, subjects immediately preferred to approach and retrieve food against the competitors that had not seen the baiting (including two subjects who did not participate in the first study). In addition, 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 that study to this new test setting. Taken together the results of this series of studies demonstrate that chimpanzees have sophisticated perspective-taking capabilities and may even be sensitive to the knowledge of other individuals.

This new "competitive conspecific" paradigm has many advantages over previous methods:

1. Chimpanzees were tested in a competitive food paradigm among conspecifics in a way that simulates a setting that is relevant to each individual's ontogeny and the species evolutionary history. No cooperation, communication, or training was required.
2. Without the need for training, a larger sample of animals were used in these two studies (mean of 14.5) than in all perspective-taking studies (mean of 4.6), allowing a more sensitive test that can detect smaller effects using group statistics (which means that anyone attempting to replicate these findings will need more than the 6 or 7 individuals commonly used in tests on chimpanzees).
3. It is difficult to make parsimonious learning arguments because
   A. The chimpanzees were never differentially rewarded only needing to demonstrate their spontaneous preferences.
   B. Some subjects did not participate in every study.
   C. Subjects participated in few trials per study while switching between two different roles.
   D. Methods were developed to eliminate the possibility for behavioral cueing.
   E. A number of novel transfer test were conducted and the subject's performance remain consistent across tests.
4. Finally, this paradigm can be used to test for perspective-taking in other species of primates.

Corroborating the findings of Hare et al. (2000, 2001) is the study of Hirata and Matsuzawa (in press) which modifies the competitive food paradigm of Menzel (1974) to explicitly test for perspective-taking. In this experiment pairs of chimpanzees competed for food that experimenters hid in one of several locations in 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 several days the subordinate individual in each pair is allowed to watch as the experimenter hides the food and after baiting the subjects are released simultaneously to retrieve the food. Gradually, individuals developed strategies for out-competing each other for the food. As in Menzel (1974), subordinates continually produced novel strategies for out competing the dominant (i.e., by leading him the wrong way), while simultaneously the dominant devised its own strategies for outwitting the subordinate (i.e., by following her everywhere). But the critical manipulation came when one day the experimenters hid 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. Taken together with Hare et al. (2000, 2001) these studies strongly suggests that chimpanzees employ perspective-taking capabilities. In addition, these studies clearly demonstrate the utility of the competitive primate principle for designing 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 evolved and are used daily.

A competitive future?

But how useful is the competitive primate principle really? Is it of limited use or can it really help provide insight into designing experiments investigating other domains of social cognition? For example, can the competitive primate principle help in the study of cooperation? Most observed cases of primates cooperating involve two individuals working together to defeat a third in a social conflict (Harcourt and de Waal 1992), yet all previous attempts to investigate whether primates can solve problems by coordinated cooperation have presented only two individuals a physical task that requires working together to obtain a monopolizable piece of food (for a review see Tomasello and Call 1997). Perhaps the reason animals have shown little coordination in these paradigms is because they did not interpret them as cooperative situations at all, but instead as competitive situations over the food (e.g., Chalmeau 1994)

Would two primates be more likely to show coordinated cooperation in problem solving tasks if they were competing in an alliance against another individual for shareable food(s)? One possible design might be as follows: pairs of individuals are housed in two separate rooms. In one of the rooms is an apparatus, which consists of a long PVC pipe tilted towards the ground that empties into the cage next door. Inside the pipe is food (oranges) which can be launched down the pipe by one subject using a simple pinball like trigger. Toward the end of the pipe (before it empties into the cage next door) is an opening where an individual can grab the food rewards. The problem facing the subjects is that one individual cannot trigger and grab food before it all goes into the cage next door where the second pair of subjects is waiting. Will the cage mates interpret their neighbors as competitors and work together in a coordinated fashion? Do they reverse roles and share food reciprocally? Does the presence or identity of the neighbors matter? What happens if you move the apparatus into the neighboring cage? Does the new pair learn to cooperate faster after seeing the first pair? From this one paradigm the possibilities seem exciting and limitless.

Conclusion

Just as in humans (Barkow et al. 1992; Burnham and 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 and Call 1997). Although there is an entire field dedicated to understanding the evolutionary pressures that shape the behavior and cognition of primates, experimentalists 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 observations and ideas of others, is that the first of these principles is the simple but profound fact that all primates have evolved 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, the validity of experiments would be substantially increased in other domains of inquiry as well.

One important concluding point: just as with powerful statistics, increasing the sensitivity of experiments is a probabilistic endeavor. First, because a sensitive experiment is conducted, of course, does not necessarily lead to the demonstration of 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 like powerful statistics, increase the probability of being able to reject a null hypothesis or distinguish between competing hypotheses (Gottsdanker 1978). So again, it seems critical to consider the sensitivity of an experiment when investigating the limits of the test species or subjects' cognitive abilities (i.e., previous attempts have been unsuccessful). In the case of studies on primate social cognition this may mean incorporating a competitive component into future experimental designs.

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