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## **Competition, Cooperation and Social Cognition in Nonhuman Primates**

*(Commentary to Jill Byrnit: Primate theory of mind: A state-of-the-art review)*

### *Discrimination, Motivation and Enculturation*

Jill Byrnit's article provides a valuable synthesis of research on the topic of theory of mind in nonhuman primates. In particular she identifies a number of problems which can strongly influence the performance of subjects in such experiments, creating difficulties of interpretation. The specific issues that she discusses are firstly, the difficulty of establishing that subjects' success is not purely down to discrimination learning; secondly, the difficulty of interpreting negative results, given the artificiality of the laboratory situation which may not elicit subjects' true abilities; and thirdly, possible differences in the actual cognitive abilities of different individuals, dependent on their level of experience with humans.

All three of these issues certainly merit attention, and each has no doubt caused numerous headaches for researchers, when designing their experimental methods, interpreting their results, and also when attempting to reconcile their own findings with the rest of the literature on the topic. However, the particular problem that I wish to discuss here is that of eliciting animals' true abilities through the use of "experiments in natural type settings", as Byrnit puts it (p29). The goal of running experiments in settings that are natural to the animal is undeniably an admirable one. But a problem remains in determining precisely what kind of experimental design might represent a natural situation to a given species (or even to a given individual).

### *Competitive Paradigms*

Recently, prominent researchers in the field of primate theory of mind (e.g. Hare et al., 2000; Hare et al., 2001; Hare, 2001) have proposed that two particular aspects of task design may be crucial to an individual's success, and Byrnit also draws attention to these factors in her review. Firstly, a large number of previous studies have required subjects to interact with human experimenters, whereas it may be the case that primates "possess a theory of conspecific minds, but not of human minds" (Byrnit, p28). Nonetheless, as Byrnit notes, when trained conspecifics have been used in place of human experimenters, little difference has been found in subjects' performances. However, it has also been suggested that typical

theory of mind experiments may seem unnatural to nonhuman primates in that subjects are expected to trust a cue provided by another individual, which indicates the presence of a food item. This kind of voluntary and honest communication about the presence of food may be extremely rare in the lives of many primates, since they are far more likely to be involved in competitive, rather than cooperative, exchanges over food items. Hare (e.g. 2001) in particular has argued that experiments should capitalise on this tendency to compete with conspecifics.

Experiments deemed to be "competitive", as opposed to cooperative, do indeed appear to have resulted in higher success rates for tests of social cognition in nonhuman primates. Hare et al. (2000) tested the behaviour of subordinate chimpanzees in the presence of dominant conspecifics. In both experiments subordinates were able to see two pieces of food, but should also be able to see that one of these was not visible to the dominant competitor. The subordinate chimpanzees typically preferentially headed towards the food that was not visible to the dominant individual. These findings do seem to contrast with those from experiments in which chimpanzees have been required to learn that a human experimenter will honestly indicate the presence of a food item for the chimpanzee's benefit (e.g. Povinelli et al., 1990). Vick and Anderson (2003) also report success using a competitive experimental paradigm with baboons. Subjects appeared to learn fairly readily that they should reach for one of two pieces of food which was *not* being gazed at by a human experimenter. This contrasted with their relatively poor performance using the standard object choice paradigm (which involves learning to reach for the item that *is* the focus of the experimenter's attention).

### *Primate Cooperation*

However, it is not necessarily the case that competitive experimental paradigms will facilitate the performance of every primate subject. It is important to bear in mind that there are large differences between primate species in terms of the degree of food sharing or food competition observed between conspecifics. Callitrichid primates, the marmosets and tamarins, are a taxonomic group renowned for their cooperative social systems. Callitrichid social groups typically constitute an alpha male and alpha female that breed, and their offspring, including adults, that contribute to the care of

infants born into the group. Relatively stable and highly inter-related extended family groups are therefore the norm (Digby et al., 2006). Within such family groups, the adults (including those other than the parents) initially provision infants with the majority of their solid food (Brown et al., 2004). Furthermore, in a number of callitrichid species, transfer of food is often accompanied by characteristic vocalisations by the adult (Snowdon, 2001).

## Callitrichid Social Cognition

It has been argued that the cooperative social system of the callitrichid monkeys may be associated with peculiarities (amongst nonhuman primates at least) of communication and cognition (Snowdon, 2001; Frigaszy & Visalberghi, 2004). To take social learning as an example, common marmosets are to date the only monkey species for which a claim of “true imitation” has been made (Voelkl & Huber, 2000). The tolerant callitrichid social structure may allow for improved opportunities to learn skills from conspecifics. Caldwell & Whiten (2003) investigated the performance of common marmosets on an artificial foraging task, comparing those that had been allowed to interact closely with (and share the food rewards produced by) a trained familiar conspecific, with those that had observed a similar demonstration through wire mesh. Those that were able to interact and share food rewards were subsequently more likely to perform the food-finding skill themselves when tested alone, compared with those that simply observed the demonstration. Frigaszy and Visalberghi (2004) note that marmosets’ tolerance of group members during feeding facilitates learning opportunities, and that such close-up learning situations may be considerably less common in capuchin monkeys.

Little is currently known regarding the performance of callitrichids on tests such as the object choice paradigm, but a recent experiment by Burkart and Heschl (in press) provides intriguing insights. They found that common marmosets (like the baboons studied by Vick & Anderson, 2003) were actually quicker to learn to preferentially reach for one of two food items that was not being stared at, compared with learning to reach for the one that was being stared at. Given the cooperative social system of callitrichids, this may seem counter-intuitive. But in fact, Burkart and Heschl (in press) argue that the effect may be general to primates, and may represent subjects’ expectations about possession. Primates, they argue, expect others to reach for objects at which they are looking (e.g. Santos & Hauser, 1999).

## Competition or Caution?

However, further alternative explanations also seem consistent with the data. As research by Byrnie and others has shown, primates appear to be able to learn fairly readily to reach for an object which another individual is either standing next to, or reaching towards with a pointing gesture (e.g. Byrnie, 2004;

Itakura et al., 1999). However this seems wholly inconsistent with the notion that the subjects view the experimental situation as a competitive one, or even one in which they simply avoid taking another individual’s “possession”. It may be the case, however, that primates do have a tendency to avoid particular objects or areas, if another individual is intently fixated there, and yet not making any kind of approach. The apparent difficulty of learning to approach gazed-at objects may therefore have less to do with competition, and more to do with caution. This interpretation would also be consistent with findings which indicate that primates may learn a gaze cue more readily if some other aspect of the situation suggests a foraging context (e.g. food call vocalisation, Itakura et al., 1999), as presumably this disambiguates the valence of the gaze cue.

## Hylobatid Social Cognition?

There is another primate group whose data might prove to be informative, from the point of view of the naturalness or otherwise of competitive experimental paradigms, and the reasons for their success. This is the family Hylobatidae, the gibbons. Gibbons form stable heterosexual pairbonds, evidenced by characteristic affiliative behaviours, such as vocal duetting and joint defence of territory (Bartlett, 2006). It is the hylobatids, along with the callitrichids, that Whiten and Byrne (1988) have drawn particular attention to in their review of tactical deception in primates, noting that the low levels of such behaviour observed in these groups may have more to do with their social structure than their cognitive capacities: “Callitrichids and hylobatids ... are typically observed in monogamous family groupings which encourage a high degree of cooperation; hence deception, if it is indeed an available option, would seldom be beneficial.” (Whiten and Byrne, 1988, p242).

Gibbons, like the majority of primates tested, have been found to engage in visual co-orientation (at least in one study, Horton & Caldwell, 2006, with *Hylobates pileatus*). Furthermore, the gibbons tested by Horton and Caldwell (2006) also appeared to have expectations about the focus of another individual’s attention. It appears therefore that further tests of social cognition in these species, such as the standard object choice paradigm, and its variants, would certainly be justified and could potentially prove enlightening.

## Conclusion: “Natural” Experimental Settings

In conclusion, it is relatively difficult to establish with any great certainty that the recent success of “competitive” paradigms in tests of primate social cognition has truly been attributable to the inherent intuitiveness of competition for the subjects. Some other factor (or factors) may well account for the success of these particular paradigms. This view is

somewhat supported by the performance of callitrichids on these particular tasks, which appears comparable to that of chimpanzees and baboons (see Burkart & Heschl, in press, for a replication of Hare et al., 2000, with common marmosets, as well as the object choice experiment described above).

In my opinion it is almost impossible, *a priori*, to predict what kind of experimental set-up will bring out the best in our subjects. At the moment we are restricted to making fairly post-hoc justifications of the success or otherwise of various paradigms, and those justifications may not necessarily be accurate. So, although I am in full agreement with Jill Byrmit's suggestion that experiments investigating primate social cognition should move more towards natural situations that have relevance to the subjects, I suspect that in practice we will continue to make numerous false starts, and learn which paradigms work best from our own successes and failures.

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