

## **Cognitive Ethology: A Behavioural Lens into the Primate Mind**

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**Lectures on Recent Trends in Ethology and Behavioural Sciences**

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## Introduction

Empirical studies on the cognitive abilities of nonhuman primates and their underlying mechanisms developed primarily because we assume that their intelligence and, if one may use the term, minds are most like our own. Through our understanding of them, we would possibly one day understand what it is like to be essentially human. However, this view that they are most like us also coexists in our minds with the equally pervasive idea that nonhuman primates differ fundamentally from us because they lack sophisticated language, and may, thus, also lack some of the capacities necessary for reasoning and abstract thought. Given the recent developments in our understanding of the cognitive abilities of many primates, including the possible existence of rudimentary semantic communication in some species, nevertheless, comparative studies on primate taxa may yet throw light on the nature and evolution of different human cognitive abilities, including that holy grail of current cognitive research – consciousness.

Why should we study the animal mind? In answering this question, it will be assumed that behaviour and all mental mechanisms in both animals and human beings result entirely from events that occur in their central nervous systems, and that there are no immaterial or supernatural processes underlying the workings of the mind – not even in the small fraction of human or animal brain events that result in conscious, subjective thoughts and feelings. And, as far as consciousness is concerned, it must be assumed, for the time being at least, that consciousness has an important function to play in our lives. These two important assumptions are enough to warrant an interest into how the various aspects of the mind, including consciousness, evolved as functional, operational processes to finally culminate in the magnificent complexity of the human mind. Where did it all begin? One very good reason for believing that it is indeed the animal mind that needs to be studied and therein lies the key to understanding our own wilful rationality is that the basic structure and functioning of neurons and synapses are quite similar in all animals with organised central nervous systems, including human beings. And so far, there is no convincing evidence that specific features of gross neuroanatomy are responsible for any particular operations of the mind that can clearly separate out humans from nonhuman animals.

One point that must be remembered, however, is that we are unaware of most of the events that occur in our brains. But that component of central nervous system activity that gives rise

to our conscious thoughts is of special significance because that is what binds us to a feeling of reality and makes us acutely aware of our existence. Animals possibly carry out much, or even most of their behaviour quite unconsciously, but insofar as they are conscious, their consciousness is an important attribute – from their own perspective and also from that of our own selfish one of trying to understand how we came to be what we are today.

This paper will attempt to briefly review some theoretical approaches that utilise observations of behaviour to examine the phenomenon of the animal mind. A few specific examples of primate social behaviour will particularly be examined in terms of the higher cognitive processes that may underlie the performance of these behaviours – in an effort to obtain some glimpses into the nonhuman primate mind.

### **The primate mind**

A feature that commonly characterises most primates including the great apes and humans is the presence of a complex society in which individuals spend most of their lives. Extensive social interactions between individuals of different ages, sexes, dominance ranks and kinship are typical of many of these societies. The development and maintenance of such complex social relationships – each different in its own way – is believed to have placed unusual demands and selected for enhanced cognitive abilities in individuals living in such societies. If this is true and if indeed there has been a general increase in social complexity – in at least some of its dimensions – during the course of primate evolution, does this provide at least indirect evidence that there has been a progressive evolution of the primate mind, culminating in the human mind, as well?

Although there is now increasing belief that primate minds can be rather complex, the question of whether nonhuman primates can be considered truly conscious continues to be a controversial one. Related to this problem is perhaps one of the most difficult aspects of studying consciousness – that of providing an objective scientific definition of the phenomenon. This definition obviously has to be functional in order that it can be dissected out analytically. And it becomes an even greater problem when studying nonhuman primates – because consciousness then has to manifest itself in behaviour – behaviour that can be unambiguously ascribed to being an effect of being conscious.

Two functional definitions of consciousness that have been proposed are *perceptual consciousness*, the ability to possess certain mental states including emotions, thoughts, beliefs, desires, or memories, and *reflective consciousness*, the recognition by the thinking subject of its own perceptions and mental states. In other words, if an animal were perceptually conscious, it would be able to exist in certain mental states – it might, for example, be able to believe, think, or remember. If, in addition, it were reflectively conscious, it would be aware of its own mental states – whether they are beliefs, thoughts, or memories. Current thinking holds that some of the higher primates may indeed be perceptually conscious, but are extremely unlikely to be reflectively so. The principal reason for this bias against the belief that primates can reflect on their thoughts and actions may, however, largely be methodological: people can tell us what they are aware of, monkeys cannot.

### **Intentionality and attribution**

Functionally, an elegant theoretical framework to investigate higher cognitive processes in nonhuman primates in terms of mentalistic notions is that of the *intentional stance*, put forward by the cognitive scientist-philosopher, Daniel Dennett. If one assumes that animals are intentional systems capable of mental states like beliefs, desires and emotions, it is possible to consider them as beings with different levels of intentionality. Note that a particular individual of any species can be in different intentional states depending on the cognitive basis of the particular behaviour performed. Under this framework, however, each species has a unique position with regard to the order of intentionality that it can ever achieve, although lower-order behaviours can be exhibited as well.

To give an example, bonnet macaques typically give alarm calls to potential predators such as leopards or wild dogs. On hearing an alarm call given by a particular individual, the other troop members immediately run up trees and then scan for the predator. Theoretically, this behaviour could be considered under different orders of intentionality, as explained below, although cognitive psychology would aim to determine exactly which order it belongs to.

*Zero-order*: an individual has no beliefs or desires at all. All behavioural actions in this category are thus instinctive, invariably evoked in response to specific stimuli.

If the bonnet macaque alarm call truly belongs to this category, it must be hypothesised that bonnet macaques give alarm calls as a mere response to a stimulus – the sight of a predator – and no actual desires or beliefs are involved in this reaction.

*First-order:* an individual has beliefs or desires, but no beliefs about beliefs. Behavioural acts can thus be generated intentionally by the actor who, however, need not have any conception of the audience's mental states.

In this case, therefore, bonnet macaque alarm calls are given because the caller believes that there is a predator nearby although it may have no comprehension of the belief system of its troop members.

*Second-order:* Some conception exists about both one's own and other individuals' states of mind. An individual may thus behave in a particular way because it wants others to believe in something.

A bonnet macaque may thus give alarm calls because it wants its troop members to believe that there is a predator lurking nearby.

*Third-order:* At this level, an individual may want others to believe that it itself has a particular belief or is in a specific emotional state, or that it wants others to believe that it wants them to respond in a particular manner.

If bonnet macaques are truly third-order intentional systems, an alarm call may be given because the caller wants the other individuals to believe that it wants them to rush up the trees.

Human beings are typically third-order intentional systems exhibiting a wide variety of behaviours that can be classified under different orders of intentionality. When a human subject removes a finger from a pinprick or a flame involuntarily, for example, it is a zero-order intentional system, since there are no desires or beliefs associated with this behavioural act. Human linguistic communication, on the other hand, is a notable example of a system where the actor (or speaker) makes its own mental states apparent to the audience; this clearly requires third-order intentionality.

Higher-order intentionality (including second- and third-order levels) is interesting because it requires the ability to represent simultaneously two different states of mind – that of the actor and of the audience. To do this, an individual must recognise, for example, that it has knowledge, others have knowledge, and that there may be a discrepancy between them – or, for that matter, between any of the intentional states held by these two minds.

Unfortunately, very few studies – either in the wild or in captivity – have so far extensively tested for these alternative capacities of intentionality in primates.

A very important functional manifestation of higher order intentionality is *attribution*, whereby an individual is capable of attributing thoughts, emotions and desires to another individual. It is evident that primates are knowledgeable about each other's behaviour, to the extent that they can often predict and act upon this knowledge even before a behavioural interaction has occurred. But do primates know as much about each other's beliefs, emotions and intentions? To attribute beliefs, knowledge and emotions to both oneself and to others is to have a *theory of mind*, first outlined by Premack and Woodruff in 1978. And if indeed primates are able to attribute a mind – or more functionally, mental states – to each other, are they capable of recognising the similarity and differences between their own and others' states of mind as well?

The principal advantage that an animal enjoys if it is able to recognise that other individuals have beliefs which might be different from its own, is that it becomes capable of immensely more flexible and adaptive behaviour. It might then be able to manipulate another individual's actions and beliefs in a great variety of social situations. Furthermore, if it can recognise ignorance in others, it can selectively reveal and withhold information from them. Again, novel information can be transmitted across individuals by active teaching rather than by the relatively slow process of observational learning. However, there has almost been no such systematic studies of attribution of mental states in social animals, including non-human primates.

### **Predicting behaviour or predicting mental states?**

Perhaps the most difficult problem in understanding cognitive processes in primates is to determine whether an individual is simply reacting to the behaviour patterns of others or actually recognising their states of mind. It must be noted, however, that true mind-reading can also only be achieved through some form of observation and analysis of externally-manifested behaviour and can, therefore, perhaps be considered a sub-category of behaviour-reading. Responding to behaviour through associative learning paradigms and true mind-reading are, thus, perhaps, not mutually exclusive phenomena, but represent two extreme positions on a continuum. It becomes important, nevertheless, to distinguish between them when certain kinds of complex social behaviours are analysed, as described below, from the perspective of the cognitive processes that make such interactions possible.

One line of evidence that can potentially argue for mentalism as an underlying cognitive process rather than simple behaviour analysis, at least in certain situations, is that of projection of experience. This has stemmed from studies on role reversal in cooperative tasks in which an individual primate was first trained to perform a definite task to aid another individual in reaching a desired goal following which it was asked to take on the role of the other individual. These experiments have suggested that the great apes, notably chimpanzees, are able to master new roles with ease and perform novel tasks perhaps because they can attribute beliefs and desires to one another; their performance cannot be explained by simple learning of the behaviour of their partner before role reversal. Rhesus macaques, on the other hand, were observed to learn their new roles afresh when they perform cooperative tasks that they have only watched others carry out – and this has been attributed to a general lack of empathy.

In the remaining section of the paper, the possible cognitive mechanisms involved in two complex social processes displayed by wild bonnet macaques – social knowledge and tactical deception – will be analysed. Particular attempts will also be made to explore the conceptual contribution that attribution of mental states as well as orders of intentionality could offer towards an understanding of these mechanisms.

### **Bonnet macaques – the species and the troops**

The bonnet macaque (*Macaca radiata*), a cercopithecine primate found only in peninsular India, usually lives in large troops of 8 to 60 individuals; such multimale troops typically contain several adult males and females, as well as juveniles and infants of both sexes. Female bonnet macaques, like many other cercopithecines, usually remain in their natal group throughout their lives, and during adulthood, form strong, linear dominance hierarchies with daughters occupying dominance ranks just below those of their mothers. Adult females develop strong social bonds and display extensive allogrooming and other affiliative behaviour towards one another. Juvenile and adult males, on the other hand, usually emigrate from their natal troops, but bonnet macaque males appear to be unique in being rather unpredictable in this regard, some individuals even staying back to become the most dominant males in their respective natal troops. Adult males form unstable dominance hierarchies through direct aggression and coalitions, and, unusually for most cercopithecines, exhibit extensive affiliative interactions with one another.

Our insights into the social knowledge underlying decision-making processes in bonnet macaques come from a three-year study (from 1993 to 1996) on a wild troop inhabiting dry deciduous scrubland and mixed forests around Bangalore city. During the course of this study, the troop had 44–52 individuals, including 8–11 adult males, 11 adult females, and 22–30 juveniles and infants. Data on tactical deception are derived from observations on this troop as well as from a second troop, occupying an adjacent, partially overlapping home range during the same study period; this troop consisted of 30–35 individuals with 5–7 adult males, 10 adult females, and 15–20 juveniles and infants. In addition, tactical deception was also studied in a third troop inhabiting the Bannerghata National Park near Bangalore; this troop, consisting of 3–4 adult males, 6 adult females, 8 subadult males, and 8–14 juveniles and infants, was studied for a period of about 12 months during 1999–2000.

Data on social knowledge and tactical deception were obtained by behavioural observations on all individually identified adult and subadult animals in the respective study troops; each sampling day usually consisted of 10 hours of observation, from 0800–1800 hours. The sampling methods used included focal animal sampling with samples of 15 minutes duration each on an individual chosen randomly without replacement and opportunistic sequence sampling of rare behavioural events and social interactions involving more than two individuals. The results reported here are based on approximately 1800 hours of observation on the three troops, sampling effort being comparable across all adult and subadult individuals in all these troops.

### **Social knowledge**

A very important component of social cognition is the social knowledge that individual primates might possess with regard to certain attributes of other individuals that they regularly interact with within their social group. In addition to the obvious recognition of each animal as a distinct individual, the possible attributes that such knowledge might encompass could include their dominance ranks and affiliative relationships – factors that seem to influence much of the social behaviour observed in primate societies.

In bonnet macaques, a frequent interaction between females is that of an allogrooming supplant, in which a dominant female displaces one member of a pair of grooming females, both subordinate to her. In the majority of these supplants (~80%), the most subordinate of the three individuals leaves her grooming partner as soon as she observes the dominant



female approaching them – such females are thus clearly aware of their own subordinate status relative to the other two individuals. On about 20% of these occasions, however, it is the other female (the more dominant of the two allogrooming individuals) that leaves – and the factor that most significantly appeared to influence this decision was the social attractiveness of her grooming partner, as defined by the amount and consistency of allogrooming that this individual received from all the other adult females in the troop. These dominant retreating females were thus clearly aware of the social relationships of their subordinate partners, in particular, and, by extension, of all the females in the troop.

That individual females might also know the relative dominance ranks of their troop members was revealed by the typical patterns of aggressive behaviour and allogrooming choices that followed such grooming supplants. Thus, in the instances when neither of the two allogrooming subordinate females retreated when the third dominant female approached them, the latter often displayed aggression preferentially towards the more subordinate of the two. Occasionally, however, she did not display any agonistic behaviour but proceeded to directly allogroom one of the two individuals – and, in the majority of these cases, she groomed the more dominant female. The approaching females thus appeared to be aware of the relative dominance ranks of the two approached females, both subordinate to her.

Logistic regression analysis of the decisions made by the grooming females to either remain behind or retreat during allogrooming supplants indicated that the two most important factors that were taken into consideration were knowledge of the subject's own dominance rank and her rank difference with the approaching dominant female. A model which incorporated only the absolute dominance rank of the latter failed to explain the observed behavioural patterns. Individuals, thus, clearly appear to be aware not only of their own positions in the rank hierarchy, but also of that of the other females in the troop. What is more interesting, however, is that this knowledge of another individual's dominance rank is egotistical in that it seems to be acquired only relative to one's own; a female knows of her rank difference with another female but does not appear to be aware of the absolute position of her adversary in the rank hierarchy.

Rank difference with the approaching dominant female and that with the grooming companion appeared to be important motivating factors when the more dominant member of an allogrooming dyad decided to retreat on being approached. Bonnet macaque females are thus clearly able to simultaneously process information about all their interacting

companions and then use this knowledge effectively during complex social interactions. The decisions made in this particular situation are, in reality, even more complex: the intermediate female in a grooming supplant chose to retreat as the approaching individual becomes relatively more dominant to her while her grooming companion became comparatively more socially attractive.

#### *Mental representation of individual attributes*

What is noteworthy here is that individual macaques seem to be knowledgeable about the general social attractiveness of particular females in terms of the allogrooming that they receive from other individuals, rather than remember specific pair-wise affiliative relationships. Since, as mentioned earlier, they also know the relative dominance rank of each adult female in the troop, this seems to constitute a clear example of recognition of individuality and individual attributes by these animals. Furthermore, the decision to retreat or remain behind during allogrooming supplants also depends on the absolute position of the actor in the dominance hierarchy – the more subordinate an individual the more likely she is to retreat. Clearly then, each bonnet macaque female has knowledge of some of her own individual attributes as well.

Although all of these abilities must obviously call for some form of fairly sophisticated mental representation of particular individuals associated with their specific properties, including themselves, what remains unclear is how exactly such information is categorised and coded for in the non-verbal cognitive architecture of the macaque mind. It is also important to note that the bonnet macaque's knowledge system is integrative in nature – each female takes into consideration attributes of the two individuals that she is simultaneously interacting with and behaves appropriately given the relative strengths of these properties. Whatever, therefore, may be the stored imagery of the individual attributes of the two females she is interacting with, it is possible for her to access both these sources and integrate them when making a decision.

#### *Attribution of motives*

Since during allogrooming supplants, the dominant member of the grooming dyad is more likely to retreat if her grooming partner is very socially attractive, these females behave as if they 'believe' that the approaching individual is targeting their subordinate, but usually more

socially attractive, companion. Bonnet macaques thus seem to be capable of attributing motives to other individuals within their social matrix, suggesting that they may be able to develop beliefs about such motives.

The hypothesis that these particular females acted on the basis of a valid belief system comes from supporting observations of other triadic interactions when a grooming supplant did not actually occur. During certain such incidents, as described above, the approaching individuals were most likely to display aggression and chase away the more subordinate of the two individuals, while on other occasions, if they did not demonstrate any aggression, they almost invariably preferred to groom the more dominant member of the dyad. Why then occasionally did the more dominant member of the allogrooming dyad retreat?

It would appear that this decision was taken on the basis of a belief that a highly socially attractive individual is more likely, in general, to be the preferred target for affiliative interactions, even if she holds a relatively low position in the dominance hierarchy. The nature of this belief and the attribution of a corresponding motive to the approaching individual also seem to be rather natural since bonnet macaque females evaluate social attractiveness of an individual on the basis of the levels of allogrooming received and the consistency with which such grooming is received from other females in the troop.

#### *Projection of experience?*

It should be noted that this particular belief system is, in some sense, erroneous – given the actual choices that the troop females made in their display of aggression and grooming preferences. In other words, since the approaching females usually chose the dominant member of the allogrooming dyad as a grooming companion, it is surprising why, in other instances, it were these same females that retreated when they were with a socially attractive subordinate.

What is noteworthy here is that individual females seem to exhibit this erroneous behaviour even though on several occasions they themselves had preferentially allogroomed the dominant member of a grooming pair after approaching such dyads. Could this be considered a failure, in some sense, to project their own past experiences, and thus to adopt different, but suitable, behavioural strategies under changing situations? Thus, is it possible that a bonnet macaque female, as the dominant member of a grooming pair, is unable to

attribute the correct motive to an approaching individual although she herself has experienced that particular motive earlier as an approaching individual? If this is indeed true, bonnet macaques are similar to rhesus macaques, which were unable to empathise with and understand the motivations of their partners in a laboratory cooperative task although they themselves had taken up similar roles earlier; as mentioned earlier, successful role reversal in these experiments was necessarily accompanied by fresh trial-and-error learning.

### **Tactical deception**

Human-like deception requires that an individual who signals information create a false belief in another individual, the audience. The signaller thus needs to recognise that the audience's mind can be in a state of knowledge that is different from one's own and that it is possible to alter and hence, control others' mental states without necessarily changing one's own. Such manipulations are usually tactical in that they involve the use of acts from the normal repertoire of the actor in situations where they are likely to be misinterpreted by the audience – leading to some tangible benefit for the actor with or without some corresponding cost to the audience.

All such acts of tactical deception are thus functional, and most cases of deception documented in primates can be included in this category. But is primate deception truly intentional, attributable to a theory of mind? Does the deceiver actually attempt to alter the beliefs of another individual when it actively suppresses some information or signals false information to the other? Or, has experience simply taught the deceiver the use of certain behavioural strategies in particular situations, leading to predictable responses from the audience and thus allowing the actor to achieve a desired goal?

#### *Mind-reading or behaviour-reading?*

The overwhelming majority of the 128 records of social interactions that could be potentially considered deceptive, obtained from the three study troops of bonnet macaques provide clear evidence for tactical deception over other competing explanations. It is also noteworthy that although individuals in all the troops exhibited comparable levels of deception overall, the three troops differed widely with regard to the social situations – competition for food, mates and grooming partners, as well as aggressive interactions – during which tactical

deception was displayed. There were also striking differences in which of the 15 categories of deceptive acts were commonly used by the resident individuals in each of these troops.

A striking feature of the deception displayed by bonnet macaques is the remarkable individual variation in the performance of these acts. Certain individuals thus exhibited deceptive acts with very high frequency and at levels significantly greater than that shown by other individuals within the troop; moreover, such deceptive abilities appeared to be independent of age categories and dominance ranks of the actors. The fact that certain individuals are more adept at deception than are others and that the ability to deceive is independent of other individual attributes is an indication that many of these acts could involve mentalism on the part of the actor rather than simple behaviour analysis. An alternative explanation could, of course, be that these particular individuals are good social learners and, therefore, more efficient behaviour analysts. This seems unlikely since it would require complex behavioural contingencies (of the kind displayed during tactical deception) to occur with high probabilities for individuals to learn their associations successfully; such contingencies, however, appeared to be relatively rare.

If, on the one hand, macaques are indeed better social learners than mentalists while, on the other, complex social situations where deceptive behaviour could be learnt are rare, it might be predicted that individuals who exhibit high levels of deception should perform the same acts repeatedly. However, in all the troops, there was a significant positive correlation between the frequency of deceptive acts and the functional categories to which these acts belonged; in other words, individuals who deceived more did so in many more different ways! This is an indication that these individuals may indeed be better cheaters with perhaps greater insights into the power of manipulative behaviour than other individuals.

Moreover, certain rare acts of tactical deception displayed by the study individuals were extremely complex and involved several simple categories of deceptive acts juxtaposed together and performed in rapid succession to achieve one particular desired goal. It is extremely improbable that these individuals had experienced an earlier identical behavioural contingency for them to learn all the constituent deceptive acts.

Another characteristic feature of the tactical deception exhibited by bonnet macaques was that individuals did not invariably use deceptive strategies in apparently identical situations, a result not expected if these acts were being performed in response to certain behavioural

contingencies. What could not be easily ruled out, of course, is that there were subtle differences in these apparently identical situations – and these may have triggered off the deceptive acts in some of them but not in others.

A related finding to this form of volitional control of deception was that of some individual adult males who changed their repertoire of deceptive acts following changes in the social environment. This happened when two particular males emigrated out of one troop and joined a neighbouring one; following this movement, they exhibited very different categories of deceptive acts. A major difference that these individuals faced in the two situations was that of their dominance ranks, which fell drastically once they had joined the new troop. It is, therefore, entirely possible that the perception of their specific positions in the rank hierarchy in the respective troops as well as the changing demands of the new social milieu may have triggered on a completely different repertoire of deceptive acts in the two males.

If the argument put forward regarding the involvement of the mind in at least some of the acts of tactical deception practised by bonnet macaques can be accepted, it would seem logical that such manipulation must necessarily involve at least second-order intentionality. This would mean, in simple terms, that an individual performs a deceptive act in order to change the belief system of the audience – and then takes advantage of the false belief, which has been generated, to achieve a particular personal goal.

#### *Visual perspective-taking*

Several events of deception by three individuals in two different troops involved acts of physical concealment in which the actor either simply hid from the target behind some physical object or performed a behaviour surreptitiously behind a barrier, occasionally leaning out to inspect whether the target individual was still present. Since all these individuals repeatedly performed this exercise – in different contexts and using different objects or barriers to hide behind – these acts would appear to represent a genuine tactic and were possibly not simply events coincident by chance.

This kind of visual perspective-taking, estimating what would be visible from another individual's point of view, has earlier been seen in other primates, notably chimpanzees and baboons. Such an ability to recognise and utilise the geometric perspective of another individual has been equated to being able to represent correctly another individual's mental

representation in one's own mind, although there have also been dissenting views on such an identity.

#### *An incomplete theory of mind?*

Subordinate adult bonnet macaque males often give out loud predator alarm calls when they are chased by more dominant males – even if there are no predators in the vicinity. An extremely intriguing variant of this deceptive act was observed in one of the study troops. A victim of aggression emitted a false predator alarm call on being chased, but continued to give this call even as he descended from the tree and continued to walk on the ground – behaviour that would never have been performed if there was truly a predator around.

Deceiving individuals thus occasionally exhibit behavioural components that are not compatible with their own apparent 'belief' system, as communicated to others. An important point here is that notwithstanding its incompleteness, such a belief system must have been generated to alter the belief state of the audience – a return to second-order intentionality. What is also noteworthy is that the aggressor did not appear to have read the internal inconsistency of the deceptive act; this may have been due to his own theory of mind being similarly incomplete.

#### **Summary**

Cercopithecine or Old World monkey societies are typically characterised by social relationships established between individuals belonging to different age cohorts, dominance ranks and kinship groups. Given the unique nature of each and every relationship that individuals need to develop and maintain, it is perhaps not surprising that bonnet macaques may be inherently capable of solving many complex social problems. These monkeys may, for example, observe the social interactions of other individuals in the troop and acquire knowledge of different attributes of these individuals, thus aiding their own decision-making during social interactions. Many individuals are also potentially capable of developing strategies of tactical deception; these strategies not only encompass different categories of deceptive acts but are also employed in a variety of social situations, including agonistic interactions and competition over food, allogrooming companions and sexual partners.

Underlying these complex social strategies may be the ability of individual macaques to form rudimentary mental representations of their social interactants and their various attributes, including their relative dominance ranks and social attractiveness. Interestingly, an elaborate example of tool manufacture and use by a bonnet macaque, documented earlier, indicated the possibility that the individual was able to perceive the underlying causality of its actions and also form a mental model of the tool to which it could repeatedly refer. The cognitive ability to form mental representations could thus underlie the bonnet macaque's interactions with both the mechanical as well as the social components of its immediate environment.

Analyses of the decision-making processes that bonnet macaques employ during social interactions indicate that individuals appear to attribute distinct motives to other individuals, a clear example of second-order intentionality. Moreover, several acts of tactical deception provide evidence that the macaques are capable of attributing visual perspectives to another individual, thus being able to perceive what would be visible from that particular individual's point of view. This arguably constitutes another way in which a monkey is able to comprehend another monkey's mental representation of the world – again a prime cognitive candidate for second-order intentionality.

Bonnet macaques, it can be argued, may thus have some degree of comprehension of the mental world of other individuals and are able to attribute distinct individuality to each other, including themselves. But does this imply that they have a theory of mind? It has been discussed above that, during social interactions, individuals may fail to project their own experiences onto others and are thus often unable to correctly predict the true motives of other individuals. Moreover, even in instances of tactical deception where the macaques communicate their apparent 'beliefs' to others, they exhibit behavioural components incompatible with their own beliefs. Extensive observational studies on the study troops have also so far failed to turn up any clear evidence for unambiguous third-order intentionality, which could be considered evidence for a true theory of mind. In conclusion, therefore, even if bonnet macaques do have a rudimentary theory of mind, it is a construct incomplete in many ways, some of which have been outlined here and some that still remain to be discovered.



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