



Scio Ergo Sum: Knowledge of the Self in a Nonhuman Primate

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Abstract | The pressures of developing and maintaining intricate social relationships may have led to the evolution of enhanced cognitive abilities in many social nonhuman species, particularly primates. Knowledge of the dominance ranks and social relationships of other individuals, for example, is important in evaluating one's position in the prevailing affiliative and dominance networks within a primate society and could be acquired through direct or perceived experience. Our analysis of allogrooming supplants among wild bonnet macaques had revealed that individual females successfully evaluate social relationships among other group females and possess egotistical knowledge of their own positions, relative to those of others, in the social hierarchy. These individuals, therefore, appeared to have abstracted and mentally represented their own personal attributes as well as those of other members of the group. Bonnet macaques also seem to recognise that other individuals have beliefs that may be different from their own, manipulate another individual's actions and beliefs in a variety of social situations, and selectively reveal or withhold information from others—capabilities displayed by certain individuals that became evident in the course of our earlier studies on tactical deception in the species. In conclusion, the ability to develop belief systems and form mental representations, generated by direct personal experience, suggests a rather early evolutionary origin for fairly sophisticated cognitive capabilities, characterised by an objectified self with limited regulatory control over more subjective levels of self-awareness, in cercopithecine primates, pre-dating those of the great apes. We, therefore, argue, in this review, that bonnet macaques might represent an intermediate stage in the evolution of self-awareness, a process which began with the subjective awareness that characterises most, if not all, higher animal species and culminates in the most sophisticated form of symbolic self-awareness, apparently the hallmark of the human species alone.

Keywords: Bonnet macaque, Allogrooming, Tactical deception, Experience, Social cognition, Self awareness

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1 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^{1,4}. 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^{5,6}. Given our current understanding of the cognitive abilities of many primates, including the possible existence of rudimentary semantic communication in some species,^{7,8} however, it is possible that comparative studies on primate taxa may yet throw light on the nature and evolution of different human cognitive abilities, including consciousness.⁹

A feature that commonly characterises most primates, including monkeys, apes and humans, is the presence of a complex society in which individuals spend most of their lives. Extensive social interactions among individuals of different ages, sexes, dominance ranks and kinship are typical of many of these societies.^{10,11} The development and maintenance of such complex social relationships—each different in its own way—are believed to have placed unusual demands and selected for enhanced cognitive abilities in individuals living in such societies.^{12–14} An important component of such 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, amongst others, knowledge of the dominance ranks of other individuals and an awareness of the social bonds between other members of the group—both factors that seem to influence much of the social behaviour observed in primate societies. As such societies are typically characterised by both competition and cooperation, it becomes possibly even more important that individuals are able to consistently evaluate its own position in the prevailing rank hierarchy and social affiliative networks, and thus obtain knowledge of one's own self.

2 Social Knowledge in Nonhuman Primates

Several earlier observational and experimental studies have clearly shown that individual baboons,^{15–19} macaques²⁰; Datta,^{21–24} vervet monkeys^{25–27} and chimpanzees^{28,29} are knowledgeable about the relationships of their social companions; such knowledge seems to be usually acquired by observing the social interactions of other individuals. What is not entirely clear from the previous studies, however, is the nature of inferences that allows such knowledge to be acquired. Does an individual evaluate the social bonding between each of the interacting pairs of individuals relative to itself? Or, is it simply aware of the extent of the affiliative relationships enjoyed by another group member without specifically remembering each and every pair bond? At a more functional level, what is the relative importance of the frequency of affiliative interactions as opposed to the time spent in these interactions for such an assessment?

In an early experimental study that attempted to understand how nonhuman primates conceptualise social relationships, Bachmann and Kummer¹⁵ showed that a male hamadryas baboon (*Papio hamadryas*) was less likely to challenge a female possessed by another male, the stronger her affiliation with her companion. Hamadryas baboon males were thus apparently able to assess the social choice of females, but the experiment could not exclude the possibility that the entire relationship was read from the behaviour of only one of the group members. In other words, it is still not clear whether an individual can conceptualise the multiple relationships of a potential adversary, information that cannot obviously be obtained on the basis of the behaviour of a single individual alone. Extending this problem further, if knowledge about the social relationships of a number of group members can be simultaneously acquired, is an individual able to integrate information about all interactants when involved in a complex social interaction with more than one partner?

Yet another important functional aspect of knowledge acquisition and use involves the specific aspect of an attribute that an individual evaluates as it takes a particular decision. When a female macaque female acts on her knowledge of the dominance ranks of her social companions, for example, does she take into account their absolute ranks independent of her own, or

does she evaluate their respective positions in the dominance hierarchy relative to her own particular rank?

3 What Do Bonnet Macaques Know?

Our insights into the social knowledge, including knowledge of one's own self, in nonhuman primates come from behavioural observations on the adult females of a wild troop of bonnet macaques (*Macaca radiata*) inhabiting dry deciduous scrubland and mixed forests around Bangalore city in southern India.²⁴

We documented a particular kind of a competitive interaction for access to grooming partners between adult females—allogrooming supplants—in which a dominant female displaces one member of a pair of grooming females, both subordinate to her. There were 75 such observed triadic interactions and in 63 of these (84% of the cases, or the 'usual' cases), the more subordinate of the two individuals that were approached (henceforth referred to as 'subordinate') retreated even before the dominant female (the 'dominant') could reach them. In the remaining 12 instances (16% of the cases, or the 'exceptional' cases), however, the more dominant member of the dyad (the 'intermediate') moved away. As the majority of these supplants consisted of the subordinate individual retreating, it is plausible that such females prefer to avoid two higher-ranking individuals in such situations. Assuming that this is indeed true, what factors could have motivated the intermediate individual to retreat in the exceptional cases?

The proportion of retreats exhibited by the intermediate and subordinate individuals during these triadic interactions were not different from what would be expected on the basis of their behaviour during dyadic approaches, thus ruling out the simple hypothesis that retreats during grooming supplants could be guided by the outcome of simple one-to-one interactions that are much more frequent between pairs of adult females.²⁴ The outcome of behavioural interactions between adult female cercopithecine primates often depends on the respective positions that they occupy in the dominance hierarchy. In addition, inter-individual aggression is invariably directed down the hierarchy and usually serves to reinforce the dominance status of each female.¹¹ Could grooming females being supplanted decide to remain in place or retreat on the basis of their dominance ranks? Rank difference between the specific dominant, intermediate and subordinate individuals involved, considered in pairs, did

not differ significantly across the usual and the exceptional cases. Aggressive interactions initiated by the dominant females towards their intermediate and subordinate counterparts, examined across the entire observation period, also could not explain the behavioural difference of the supplanted females in the two situations.²⁴

Could the intermediate individual in the exceptional cases be avoiding the approaching dominant female since she is aware of a preference of the latter for the subordinate individual as a social partner? The dominant females did not appear to discriminate between the subordinate and the intermediate individuals as grooming partners with regard to time spent in grooming them, respectively, either in the usual or in the exceptional cases.²⁴ This would make it unlikely that, in the exceptional cases, the intermediates retreated because of a preference of the dominant females for the subordinates over them.

To summarise, the proportion of times that a subordinate female remains in place during an allogrooming supplant is not affected by her dominance rank, rank differences with the approaching female and her grooming companion, or the agonistic relationships between these individuals. Her response during these triadic allogrooming supplants also does not appear to be influenced by her corresponding behaviour when approached by dominant females during dyadic interactions.

4 Knowledge of Social Relationships

A different perspective to the decision-making process during triadic supplants could involve the act of not retreating performed by the subordinate female. When the identities of all the subordinate individuals involved in these 75 interactions were examined, a significant positive correlation was observed between their indices of social attractiveness (defined as the reciprocal of the coefficients of variation for allogrooming duration received from all other females in the troop) and their propensity not to retreat when approached, measured as the proportion of all approaches received (as the subordinate member of the triad) in which they were not supplanted.²⁴ The reciprocal of the coefficient of variation (mean/standard deviation) of the allogrooming that an adult female receives from other females can be maximised by increasing values of the mean, decreasing values of the standard deviation, or a combination of both factors. High values of this measure thus represent the consistency

with which an individual is preferred as a grooming partner by other females, and was, therefore, be used as an index of social attractiveness of that particular individual. Such indices were computed in terms of both, the frequency and the duration of allogrooming received by these individuals.

The above interpretation, therefore, implies that the subordinate member of a supplanted dyad was less likely to retreat, on being approached by a dominant female, when she was more socially attractive than her dominant grooming partner. This relationship, however, held only when social attractiveness was considered in terms of allogrooming time received by these individuals but not with respect to the frequency of grooming received by them. Moreover, no relationship could be discerned between the propensity to remain in place when approached and social attractiveness for the intermediate females of the triads, either for grooming time or frequency received.²⁴ Extensive bootstrapping simulations by random sampling of subordinate females from those involved in the 75 observed supplants confirmed that the observed correlation between the proportion of times that a subordinate female did not retreat when approached and her social attractiveness in terms of allogrooming duration was indeed significantly different from that expected by chance alone.²⁴ This, therefore, leads us to the conclusion that the intermediate female (that is, the dominant partner of the dyad) may actually be aware of the social attractiveness of the individual that she is currently with, and accordingly tend to retreat when approached by a still more dominant female.

It must be pointed out that the female macaques in our study troop did not appear to recognise and/or react to the social bonds that apparently exist between particular pairs of females (Sinha, unpublished observations). This is borne out by the fact that in the exceptional instances where the intermediate individuals retreated, the approaching dominant females did not appear to discriminate in directing grooming towards the subordinate and the intermediate individuals either with regard to the frequency of initiated events or the subsequent duration of grooming given to them. What is illuminating, however, is that these females nevertheless appeared to be responding to the social attractiveness of their partners as evaluated by the uniformity with which the latter received grooming from the other troop members. It is neither the mean grooming time received by the target individual nor the variation in the number of troop

members who groom her that are independently being taken into account, but a combination of both factors.

Bachmann and Kummer's¹⁵ classic study on the hamadryas baboon was one of the earliest attempts to demonstrate that primates may be aware of the social relationships of others and take decisions on the basis of such knowledge. Their experiments, however, could not distinguish whether it was indeed the social interactions that were providing cues to the observer, or simply the behavioural patterns of either of the two interacting individuals. Our study, however, showed that bonnet macaque females might be aware of the allogrooming that other individuals might be receiving from different members of the group. Knowledge of this kind, encompassing the multiple social relationships of target individuals, clearly needs to be acquired from observations of the actual social interactions of all the individuals involved in these relationships. It is very unlikely that the macaque females are simply reacting to the behavioural cues being provided by each observed individual in the troop.

To react to particular social relationships between pairs of group members, an individual would have to memorise the pattern of interactions among each pair. Observation and memorisation could suffice in small primate groups that are relatively stable over time but would obviously place increasingly difficult cognitive demands on an individual either as the group size increases or its composition changes (see also Ref. ²⁶). An alternative strategy that bonnet macaque females seem to have evolved is to obtain an impression of the social attractiveness of another individual with regard to its affinity to the other group members without specifically remembering each and every pairwise interaction. Such an ability would obviously appear to make the task of evaluating one's own position in the group's social network much less cognitively demanding.

But what do individuals actually observe and memorise? Whenever dominant females in the allogrooming dyad took a decision to move away, they appeared to do so primarily on the basis of the consistency with which the other females in the troop spent grooming time with her subordinate partner. It is interesting that the females seemed to be reacting more to the duration of grooming that the other individual received (as measured by the total time spent by her in this activity) than to the actual frequency of the initiated events. This would require that the observer simply scan the target individuals periodically

to note whether she is being groomed instead of remembering the actual number of times that an individual has been groomed. Again, this calls for a cognitively simpler mechanism to obtain the desired information. In addition, individuals also apparently need to remember whether different group members are uniformly grooming the target female during these scans.

5 Knowledge of Dominance Ranks

When all the 75 cases of competition for allogrooming partners were considered, there was a strong positive correlation between the frequency of approaches a female had received as the intermediate member of the triad and her social attractiveness in terms of grooming frequency received from all the other females in the group. This was in spite of the fact that the intermediate and subordinate individuals in the approached dyads did not differ in their social attractiveness in terms of grooming frequency or duration. In contrast, no relationship could be discerned at all between these parameters and the frequency of approaches received by the subordinate members of the allogrooming dyads. This clearly indicated that individuals who were more socially attractive as grooming companions for the females in the group were approached at comparatively greater rates by more dominant individuals. The important point here is that this did not hold true for the same females if they were the subordinate members in the supplanted dyad. The approaching dominant females, therefore, appeared to be well aware of the relative dominance ranks of the two approached females, both subordinate to her.

Support for the possibility that there could indeed be a preference for the intermediate females came also from the direct observations of 25 instances when a dominant female approached two allogrooming subordinates and proceeded to herself groom one of them. The dominant member of the dyad was preferentially groomed on a significant majority of 20 of these occasions; the subordinate received attention in only five instances. Consequently, these results would argue that the approaching female may be specifically attending to the more dominant member of the approached dyad, and therefore, she must be aware of the relative ranks of the two approached individuals.

The conclusion that an adult female bonnet macaque might indeed be aware of the dominance ranks of the other females in the group

was also supported by data from yet another kind of triadic interaction. On 17 occasions, a dominant female approached two of her grooming subordinates and supplanted one of them through aggressive interactions.²⁴ In 13 of these instances, the more subordinate of the two females was attacked while the intermediate individual received aggression on the remaining four occasions. Aggression was thus more significantly directed towards the subordinate individual than would be expected if the dominant female were to attack either of the females randomly.

An attempt was made to examine the factors that could motivate approaching females to preferentially exhibit aggression towards more subordinate females when supplanting a member of a grooming dyad.²⁴ The dominant females, involved in these 13 particular interactions, did not show any inherent preference in directing grooming (in terms of either frequency or duration) towards the intermediate individual over that towards the subordinate one over the entire observation period. The intermediate females were also not more socially attractive (in grooming frequency or duration) than were their subordinate companions. Finally, as compared to their intermediate counterparts, the subordinate females had not necessarily received more aggression from these particular dominant individuals in dyadic interactions over the observation period.

Is it nevertheless possible that the dominant female was aware of a differential response made by individuals of different ranks to aggression shown by her during dyadic interactions? The proportion of approaches received by females from more dominant individuals to which they retreated did not, however, correlate with their absolute ranks; dominant females may not thus be able to use such behavioural responses as cues to the relative ranks of their subordinates. There was also not a single instance during the entire observation period when any of the intermediate females, though often close in rank to the dominant individuals, had ever been observed to threaten or attack any of the latter (Sinha, unpublished data). On the other hand, a surprising result was that dominant females were significantly more likely to attack subordinates of higher rank than those of relatively lower ranks during dyadic interactions²⁴; this was in complete contrast to their behaviour during triadic interactions. Taken together, these results suggest that a dominant individual may be well aware of the ranks of two grooming females and may choose

to show aggression more towards the subordinate member of the dyad when she has a choice of supplanting one of them. These contrasting behavioural patterns also suggest that females may also choose different strategies depending on the prevailing situation; a more subordinate female is thus attacked only when another female is present.

How do macaque females assess individual ranks? Do they follow a brute force method by which individuals observe and remember dyadic interactions between each and every pair of troop members and then conclude a linear hierarchy? Alternatively, are bonnet macaques capable of inferring linear orders by associative transitivity³⁰? Such processing of serial information would be advantageous in allowing them to deduce individual ranks in the hierarchy from partial knowledge of agonistic relationships without having to observe interactions between every pair of individuals (for a discussion, see Ref. ⁷) Future studies under controlled conditions in the laboratory may provide an answer to this dichotomy.

6 Decision-Making During Allogrooming Supplants

Knowledge of dominance ranks and social attractiveness could thus be important factors that influence the probability that an individual will decide to either retreat or stay back during grooming supplants. It was, of course, clear that neither of these factors, by themselves, were of absolute importance since, in each case, it was not necessarily the dominant or the more attractive individual which failed to retreat. It thus became of interest to understand which of these aspects of an individual's social knowledge of her grooming companion correlate with the decision to retreat during a triadic interaction.

Each member of the 75 approached dyads either retreated or failed to do so; the dependent variable was thus a binary one and could be influenced by a number of independent variables. Logistic regression analysis^{31,32} was thus used to determine the factors that may critically influence the decision of a female in a grooming dyad to retreat when approached by a more dominant individual.²⁴ The independent variables that were considered in these analyses included the individual's own dominance rank, rank of the approaching dominant female, rank difference with the approaching female, rank of the grooming companion, rank difference with

the grooming companion, the individual's own social attractiveness in terms of the duration of grooming received by her from other females and the ranked difference in attractiveness with the grooming companion. Social attractiveness was considered only for duration of grooming received since this measure was found to be important for the macaques' knowledge of allogrooming relationships. Regression was carried out with all these variables taken one at a time as well as with all of them considered together.²⁴ The influence of the absolute dominance rank or social attractiveness was investigated by two slightly different approaches: once by including these variables directly as such, and once by including the difference in rank or attractiveness between the two individuals in the set of independent variables.

The first set of models examined the relative influence of the different variables on the probability that any female in an allogrooming dyad would retreat when approached by a more dominant individual.²⁴ Two regression coefficients, namely those associated with an individual's own dominance rank and with rank difference with the approaching female, were significant. According to this model, therefore, an individual had an increased probability of retreating as its position in the rank hierarchy fell, as it did when the approaching individual was relatively closer to it in rank. In contrast, an alternate model that incorporated the absolute dominance rank of the approaching female, instead of that for rank difference with her, failed to explain the observed patterns of retreats.²⁴ It is important to note here that as these models included decision-making by both the members of the grooming dyad as the dependent variable ($n = 150$, derived from 75 interactions), they would consistently fail to distinguish between the knowledge of one's own rank or attractiveness and that of the corresponding properties of the grooming companion. Knowledge about oneself was, however, preferentially incorporated into the tested models, as it is less cognitively demanding.

To examine more explicitly the combined influence of social attractiveness and dominance rank, the following alternate approach was also explored.²⁴ Models were constructed using, as the binary-dependent variable, either the decision of the dominant member of the grooming dyad or that of the more socially attractive one to retreat or not to do so, but maintaining the same independent variables as above. Absolute rank and attractiveness of the

grooming companion could also be now legitimately incorporated into these models as independent variables.

Rank difference with both, the approaching individual and the allogrooming companion, were found to significantly influence the probability of retreat of the more dominant member of the dyad in a particular model described in Sinha.²⁴ Such an individual was, therefore, more likely to retreat when the approaching female became relatively less dominant to her while the grooming companion became progressively more subordinate. An alternate model that incorporated knowledge of the absolute dominance ranks of the approaching individual and the grooming companion as well as the social attractiveness of the latter instead of their values relative to one's own, however, failed to reveal a significant influence by any of the independent variables.

Why would a dominant female retreat more often when she was with a relatively more subordinate individual? One solution to this problem possibly lies in the strong positive correlation that was observed between the rank difference of the dominant members of the dyads with their subordinate companions and their difference in social attractiveness in terms of grooming duration received.²⁴ Increasingly, more subordinate companions were, therefore, relatively more attractive as grooming partners to all the females in the group, and the retreating dominant females may have been aware of this relationship.

Regression models were also constructed to examine the influence of the different independent variables on the probability of the more socially attractive member of the grooming dyad retreating. Either of two alternative models, which surprisingly yielded identical estimates for the respective significant variables, could explain the observed behavioural patterns.²⁴ It was not possible, therefore, to determine which of the two variables—dominance rank of one's companion or rank difference with her—was more important in influencing the behaviour of these individuals. An alternative model that used these two variables alone yielded a good fit with the observed data but failed to assign priority to any of them.²⁴ Rank difference with the approaching female was, however, no longer a significant factor in these models. This last set of models, thus, clearly showed that the more socially attractive member of an allogrooming dyad was more likely to retreat (in spite of her popularity) as her companion became increasingly dominant to her.

To summarise, our logistic regression analysis indicated that the two most important factors that were taken into consideration for a decision to be made to move away or stay on during allogrooming supplants included knowledge of the subject's own dominance rank and her rank difference with the approaching dominant female. A model that incorporated the absolute rank of the latter failed to explain the observed behavioural patterns. Individuals, therefore, 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 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. This finding reinforces the view that social knowledge of primates might primarily be of an egotistical nature in that knowledge of another individual's attributes is best acquired and conceptualised in terms of the subject's own attributes. Knowledge of the absolute is also likely to be more cognitively demanding than knowledge of the relative, especially that based on the self. Relative knowledge of this kind can be easily obtained when the subject actively interacts with another individual; its acquisition does not necessarily require that she observe and memorise social interactions between other individuals and which do not involve her.

Rank difference with the approaching female and 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. Individuals are thus clearly able to simultaneously process information about all their interacting companions and then use this knowledge effectively during complex social interactions. The computations involved in this particular situation were further complicated by the fact that the intermediate female in a grooming supplant chose to retreat as the approaching individual became relatively less dominant to her while her grooming companion was comparatively more subordinate. Females in the study troop became increasingly socially attractive to others as they occupied progressively lower positions in the dominance hierarchy. A possible reason, therefore, for the intermediate female retreating in spite of being more dominant was the increasing attractiveness of her grooming companion. Again, the more socially attractive individual in the grooming dyad decided to leave only when her companion

became progressively more dominant to her. Taken together, it seems evident that high dominance ranks of individuals can compensate for their lower attractiveness and vice versa during grooming supplants.

Moreover, our findings suggest that individuals appear to be capable of not only integrating information about both their partners but seem to be simultaneously accessing different domains of their knowledge—those for dominance ranks and for social relationships—while making a decision; such knowledge is thus functionally integrative. Surprisingly, however, the logistic regression models failed to ascribe direct significance to knowledge of social attractiveness, either of one's own or of that of others, in the decision-making process.²⁴ Is it then possible that information about social bonds is acquired in terms of their correlated dominance ranks? If this is true, it would suggest that, as in humans, knowledge in this nonhuman species is hierarchically organised as well. Certain categories or domains of knowledge could thus be much more easily accessible than others to individuals, and these domains could be preferentially used for the storage of related information from other categories.

An important observation in our study on social knowledge was 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 pairwise affiliative relationships.²⁴ As mentioned earlier, they also appear to know the relative dominance rank of each adult female in the troop—a clear example of recognition and knowledge of the individual attributes of one's group members. What is most relevant and significant for this review, however, is that the decision to retreat or remain behind during allogrooming supplants depended on the absolute position of the actor in the dominance hierarchy—the more subordinate an individual the more likely she was to retreat. Clearly then, each female bonnet macaque has knowledge of some of her own individual attributes—knowledge that she has acquired through her own direct interactions with her group members.

7 Intentional Tactical Deception in Bonnet Macaques

Human-like deception requires that an individual who signals information create a false belief in another individual, the audience. The signaller thus recognises that the mind of the audience can

be in a state of knowledge different from one's own and that it is possible to alter and hence, control mental states of others 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.^{33,34} All such acts of tactical deception are thus functional, and most cases of deception documented in primates have been included in this category.³³

But is primate deception truly intentional and moreover, attributable to a theory of mind (see Ref. ³⁵ for a theoretical discussion)? Does the deceiver actually attempt to alter the beliefs of another individual when it actively suppresses some information from it or signals false information to the other? Intentional communication, as postulated in humans, thus requires an understanding of the mental states of articulators, which, in turn, requires complex cognitive capacities.^{36,37} Subsequently, intentionality in nonhuman communication systems was operationalised through different orders of intentionality^{38–40}; see also Ref. ⁴¹ Zero-order intentionality, for example, is a merely reflexive communication, not involving any sophisticated cognitive process. Higher orders of intentionality, on the other hand, involves some recognition of the one's own mental states as well as those of the audience, culminating in the capacity of the actor to successfully communicate its own intentions and goals to the audience, the characteristic feature of third-order intentionality.^{38,40,42,43}

Given the difficulty of empirically establishing the presence and recognition of mental states in both human infants and non-verbal animals, however, various general behavioural criteria have been suggested to qualify a behavioural signal to be intentional.^{44–48} These criteria include (1) the social use of the behavioural act, as indicated by it being directed to particular recipients, modified by various factors, such as the presence or composition of the attendant audience; (2) sensitivity of the signaller to the attentional states of the recipients; (3) manipulation of the attentional states of recipients to attract attention, particularly when a mutual attention state between the signaller and recipient is absent, such as the actor moving itself into the line of view of a recipient; (4) monitoring the responses of the audience and (5) persistence in the production and/or elaboration of the behavioural signal until a desired communicative goal is met.

Our analysis of 128 events of social interactions of a potentially deceptive nature, which we observed in three different study bonnet macaque troops,⁴¹ provide evidence for the majority of these constituting intentional acts of tactical deception, at least in terms of the behavioural criteria listed above. The troops, however, differed widely with regard to the social situations in which tactical deception was displayed—competition for food (effectively obtaining food from another individual), sexual encounters (avoiding sexual advances from other individuals, successfully pursuing one's own sexual interests and disrupting the sexual pursuits of other individuals), aggressive interactions (avoid aggression directed at oneself, effectuate aggression towards a target individual or redirect received aggression towards a third party) and affiliative interactions (effectively disrupt the affiliative interactions of other individuals). Moreover, there were striking differences in the distribution of deceptive acts across the seven functional behavioural categories of deception commonly used by the individuals in each of these troops; these included affiliative behaviour, threat behaviour, non-responsive behaviour, inhibition of interest, non-contextual behaviour and calls, neutral behaviour and diversion of aggression (see also Ref. ⁴¹)

8 Is Macaque Tactical Deception Mentalistic?

What was more critical, however, was to determine whether the acts of intentional deception displayed by the macaques actually involved, additionally, an effective reading of the audience's mental states. The hallmarks of a cognitive behaviour, which could potentially rule out the possibility that it was generated simply by associative learning paradigms, are generalisation, variability and flexibility.⁸

A notable feature of the deception displayed by certain individual macaques in the study troops, in accordance with these requirements, was their ability to generalise the use of more than one kind of functional behavioural category to achieve the same goal. All seven behavioural categories, listed above, could thus be employed to avoid aggression directed at oneself. One particular adult male in one of the study troops, for instance, employed affiliative, threat- or non-responsive behaviour on different occasions to avoid aggression directed at himself. Some individuals were also capable of the converse generalisation, using one behavioural category to deceive in a number

of different contexts. One of the study subadult males, for example, used affiliative behaviour to deceive in three different contexts, including, in this particular case, avoiding aggression directed to oneself, effectuating aggression towards another individual or disrupting the sexual pursuit of an individual competing with itself for a potential mate. In general, affiliative behaviour was employed to deceive in all the seven contexts, described above, by individuals in the three study troops. Such generalisability of the use of different behavioural acts by wild bonnet macaques to deceive in different social contexts thus bear testimony to the essentially cognitive nature of tactical deception in this species.

Not only is tactical deception in bonnet macaques highly generalisable, there was striking individual variation in the performance of deceptive acts by individuals across the three study troops. Certain individuals thus exhibited deceptive acts with very high frequency 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 ability to deceive being independent of other individual attributes, including age, indicate that many of these acts could involve mentalism on the part of the actor rather than simple behaviour analysis, as the latter would usually imply that rates of deception would increase with age and/or social experience.

Moreover, male bonnet macaques, which exhibited tactical deception at high levels, employed a relatively greater number of behavioural categories to effectively deceive their target individuals.⁴¹ Given this remarkable variability in deceptive abilities and that complex social situations where deceptive behaviour could potentially be learnt are rare, it has been argued that certain individuals may have indeed been better deceivers, with perhaps greater insights into the power of manipulative behaviour than other individuals in the same troop.⁴¹

Certain individual bonnet macaques also displayed noteworthy flexibility within their repertoire of deceptive behaviour. To cite a striking example, nine of the sixteen acts of deception observed among the eight resident males of one particular study troop were performed by a single young subadult male within a period of 8 months from the time he had emigrated into the group.⁴¹ Remarkably, these nine acts belonged to all seven different

behavioural categories of deception. Additionally, some events of tactical deception, shown by a few male macaques, were also extremely complex and involved several simple categories of deceptive acts juxtaposed together and performed in rapid succession to achieve a particular desired goal.⁴¹ These deceptive behavioural sequences indicate the ability of particular actors to innovatively combine behavioural acts in a definite sequence—the syntax of such sequences demand further investigation.

If the arguments put forward regarding the mentalistic nature of at least some of the acts of tactical deception displayed by wild 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 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.

It is important to note that tactical deception in bonnet macaques may be under a certain degree of volitional control. Certain individual adult males, for example, were observed to change their repertoire of deceptive acts and significantly increase their frequency of deception following changes in their social environment, brought about by emigration into a foreign troop.⁴¹ 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 as well as increased rates of tactical deception in these individuals.

Finally, deceiving individual macaques occasionally exhibited behavioural components of a deceptive strategy that did not appear to be compatible with the ‘belief’ system that the actor appeared to communicate to the target individuals as its own.⁴¹ In these instances, the actor seemed incapable of recognising the internal consistency with which the different behavioural components of its deceptive strategy must be presented to its potential targets. 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, in these cases, the target individuals also did not appear to have read the internal

inconsistency of the actor’s deceptive strategy; this may have been due to their own theory of mind being similarly incomplete.⁴¹

9 Experiential Knowledge of the Self in Primates

What does the acquisition and application of experientially acquired knowledge of oneself suggest of self-awareness and the concept of the self in nonhuman species such as bonnet macaques? Although traditionally considered an exclusive domain of humans, the nature of the self in other species and its appearance in our species has, more recently, begun to attract serious academic attention.^{49–51} These psychologists have clearly recognised an essential biological continuity of the self across species and its natural history over evolutionary time scales. In their comprehensive treatise on the evolution of the symbolic self, defined as the ability to both consider oneself as an object of one’s own reflection and to store the products of such reflections, abstract and/or language-based, in memory,⁵¹ Sedikides and Skowronski⁵² distinguish between three aspects of the self: subjective self-awareness, objective self-awareness and symbolic self-awareness.

Subjective self-awareness, the cognitive capacity of an organism to differentiate between itself and its socioecological environment, allows an individual to engage in some form of self-regulation (a process where systemic parts coordinate the action of one another⁵³) as well as perceive, interpret and change its environment through self-initiated action. It is crucial to note here that subjective self-awareness does not imply that cognitive representations of the individual’s attributes are constructed and stored in memory⁵²; there is only a ‘crude’ differentiation between the organism and its environment. This differentiation is, however, essential for survival and, along with self-regulation and response to environmental stimuli, has been considered to be implicit or non-conscious.⁵⁴ The processing of complex visual and auditory stimuli, cognitive representation of the physical and social environment, counting, remembering, categorisation, communication—both with one another and with predators, use and manufacture of tools, and the development of effective problem-solving strategies^{55–57} have all been considered attributes of subjective self-awareness. These cognitive abilities do not, however, assume a cognitive representation of self and can be successfully executed in the absence of such a representation.⁵²

Objective self-awareness, in contrast, has been variously defined (reviewed in Ref. ⁵² as an individual's cognitive capacity to "become the object of its own attention" (Gallup, ⁵⁸ to be aware of its "own state of mind"; ⁵⁹ and "to know it knows, to remember it remembers".⁶⁰ The presence of objective self-awareness implies the presence of a primitive cognitive representation of the self, also referred to as the 'objectified self'.⁵² Consequently, objective self-awareness allows for self-referential behaviour, enabling individuals to use their own knowledge to model the knowledge of other individuals, anticipate what other individuals might do in certain situations by attributing motives or intentions to them, and influence other individuals by intervening in their behaviour. It has been explicitly suggested that species without objective self-awareness should not exhibit such abilities and only the great apes, particularly orangutans, chimpanzees, bonobos and humans, amongst primates are objectively self-aware.⁵² Finally, the reflective capacity afforded by objective self-awareness is believed to occur at an explicit or conscious level, and is able to regulate and variously control subjective self-awareness.^{52,54,60,61}

Symbolic self-awareness, a unique capacity of adult humans alone, refers to both the language-mediated and abstract representation of certain attributes of the self and the use of this representation to function effectively in affective, motivational and behavioural domains.^{51,52} A close examination of the psychological basis of the human self suggests three closely related and occasionally functionally inter-related capacities: representational, executive and reflexive.⁵¹ The representational capacity is able to acquire, maintain and organise self-relevant information, both concrete and abstract, and which can depict the past, present or future. These representations can also include meta-cognition (a comprehension of how others perceive one's behaviour), information about dyadic relationships, one's position within the group, or about intragroup dynamics and intergroup relations.⁵¹ The executive ability allows the symbolic self to regulate its relationship with its socioecological environment, primarily through the processes of valuation (protecting and enhancing the self), learning (improving the skills and abilities of the self) and homeostasis (seeking and endorsing information consistent with the self⁵¹); The third, reflexive, capacity of the self enables it to respond flexibly and dynamically to environmental changes by accessing and activating or deactivating different components of the stored self-knowledge. Furthermore, Sedikides and Skowronski⁵¹ note that

an interaction between the above three capacities of the self allows an individual to "process information in a way that is detached from the immediate environment, travel mentally in time, imagine and contemplate the future, simulate the consequences of one's own actions, and take preparatory steps for what might come as well as reparative measures for what has come".

To return to our discovery of the ability of bonnet macaques to represent some of their own attributes, including their respective positions in the dominance hierarchy prevailing in the group, it could be speculated whether such representation characterises subjective or objective self-awareness in this species. Although, as mentioned above, objective self-awareness has been hypothesised to exist only in the great apes, two lines of evidence from our results^{24,41} could argue for the development of an objectified self in these macaques (*sensu strictu*⁵²)

First, the integrative nature of the knowledge acquired and organised by individual macaques allows them to simultaneously access information on the dominance ranks of more than one interacting individual and use these representations to aid social decision-making, as shown above for allogrooming supplants. The sophistication that characterises the nature of such knowledge, rarely documented earlier in nonhuman primates, surely provides a convincing case for objective self-awareness in this species, far beyond what has been postulated to define subjective self-awareness.⁵²

Second, our observations of certain behavioural decisions made by bonnet macaques, as, for example, the retreat by dominant members of grooming dyads when their grooming partners were more socially attractive lead to the argument that the dominant females behaved as if they were guided by a 'belief' that the approaching individual was targeting their subordinate, but more socially attractive, companion.^{24,41} In other words, it would appear that this decision to retreat was taken on the basis of a belief that a highly socially attractive individual was more likely, in general, to be the preferred target for affiliative interactions, even if she held a relatively low position in the dominance hierarchy. That such a belief might indeed be valid is supported by our earlier observation that there was a strong positive correlation between the number of approaches that the dominant female of the allogrooming dyad received from other females and her social attractiveness.²⁴ The nature of this belief and the attribution of a corresponding motive to the approaching individual also seem to

be rather pragmatic, as female bonnet macaques 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.

The display of intentional, and often innovative, tactical deception by certain individuals, with the underlying possibility that these behavioural strategies involve second-order intentionality also provides support to the idea that these deceiving individuals acted as if they intended to change the belief system of the targets of their deception. 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.

What is important to point out here is that the attribution of such motives or intentions to other individuals is a definitive hallmark of objective self-awareness, which usually enables organisms to model the behaviour of other organisms on the basis of their own knowledge and, in the process, anticipate how these individuals might act in certain situations by attributing intentions to them.⁵²

10 Mental Representation of Individual Attributes

Although the egotistical, integrative and hierarchical nature of the knowledge acquired, organised, memorised and applied during social decision-making by individual bonnet macaques must obviously call for some form of fairly sophisticated mental representation of particular individuals, including themselves, in association with certain specific properties, what remains unclear is how such information is exactly categorised and coded for in the non-verbal cognitive architecture of the macaque mind. Although there have been extensive studies on category formation and some of its underlying cognitive mechanisms with respect to physical objects or features (reviewed, for example, in,⁶²) the formation of social categories, particularly with regard to conspecific individuals, remains largely unstudied in nonhuman species.

In general, there are two kinds of social categorisations that social species such as bonnet macaques may have achieved: recognition of conspecific individuals with identification of particular individuals and the representation of transitivity in social hierarchies.

An essential cognitive requirement for any individual would be to differentiate between

members of different species, especially between conspecific and heterospecific individuals, and often between different categories of conspecifics such as dominant and subordinate members of its own social group or between related kin and non-related members of the group. In a classic study on two captive longtailed macaque individuals, Verena Dasser showed that the subject individuals were able to distinguish photographic slides of familiar individuals from their own social group from those of unfamiliar members of another group and between slides of familiar individuals dominant or subordinate to other group members and, presumably, to themselves as well.⁶³ Remarkably, she further showed that these individuals were capable of distinguishing between mother–infant pairs and other unrelated adult female–infant pairs in their social group as also differentiate between adult sister and non-sister pairs in the group.⁶⁴ This study on social recognition thus clearly demonstrates the capacity of macaques to abstract certain general classes of social relationships (mother–offspring or sisters) within their social group although, admittedly, it is not evident whether they were able to form a social concept of these relationships in general, that is, beyond their own familiar social group. Thus, do macaques form conceptual categories of the social bonds that exist between conspecific individuals in general, including dominant–subordinate relationships? Our study individuals appeared to distinguish between different classes of dominant and subordinate individuals, relative to their own social rank, within their group. But were they able to form abstract categories of dominance and subordination that would allow them to recognise such individuals when they observed unfamiliar social groups? Neither Dasser's studies on captive longtailed macaques nor ours on wild bonnet macaques have tested for such a capacity—and this is a crucial step that needs to be taken in the future before we can conclusively argue for the ability of these species to form truly abstract concepts of social relationships as we do.

A second capability that needs to be investigated is whether individual macaques can conceptualise a linear, transitive, hierarchical order as exemplified by a social dominance hierarchy that typically prevails within their social group. Dasser showed that her longtailed macaque subjects correctly recognised the dominance–subordination relationships that existed in the group and the identity of the various group members, the slides of which were presented to them (⁶³ unpublished; summarised in Ref. ^{65,66}). The

macaques had thus formed and had access to an empirical concept of the asymmetry that characterises a dominance hierarchy. It is also apparent that such a mental representation went beyond the simple memory of pairwise interactions of the group members, a salient finding of our own study on bonnet macaques as well.²⁴ There is, however, no evidence, in either study, of the macaques having formed an abstract concept of asymmetric dominance relationships that could be generalised even across unfamiliar individuals, as discussed above with regard to the conceptualisation of social relationships as well. There is also no support from Dasser's studies of individuals being able to generate a social transitive order or to represent social transitivity as a conceptual category that would generally apply to dominance–subordination relationships. It is instructive that in our study too, logistic regression analyses clearly failed to provide any evidence of bonnet macaques knowing the absolute dominance ranks of their group members—a possible correlate of being able to assign all interacting individuals to specific positions in a dominance rank order. They were able to assign ranks to these individuals in relation to themselves and knew the dominant–subordinate positions of interacting pairs of females. It has been argued that a cognitive process that underlies a truly perceptive inference of social transitivity should be able to anticipate the most likely outcome of a third dominance–subordination contest on the basis of visually acquired, remembered information on the status of two conspecifics in combination with the observer's own dominance or subordination experience with at least one of the conspecifics.⁶² The authors also suggest that short-term recognition of the visually and/or socially familiar individuals too must be involved in the prediction of the transitive outcome while long-term individual recognition should strengthen the stability of the knowledge of linear dominance in groups of socially interacting individuals.

An alternate cognitive mechanism has been put forward by Cheney and Seyfarth,⁷ who suggest that, instead of transitive inference, individual primates may have the capacity of associative transitivity, by virtue of which they may be able to internally represent the sequential order among a series of individuals; the ordering would require a simple prior association between two particular individuals, say A and C, which become related but not according to a relational rule common to the antecedent pairs of stimuli, here A–B and B–C. Individuals could thus consistently form representations of the relationships between

individuals that interact relatively frequently. For example, if an individual Z is dominated at very high rates by all the individuals in the group while an individual A dominates all these individuals, the ability to deduce associative transitivity would recognise the clear prevailing asymmetry between individuals A and Z, and spontaneously conclude that A would most probably dominate Z. No true deductive inference is necessary to represent such a transitive link. Unfortunately, there has not been any clear demonstration yet of nonhuman species being able to mentally construct and categorise a linear dominance hierarchy on a perceptive basis or on a purely conceptual one.

It is nevertheless important to reiterate here that our study individuals appeared to be able to conceptualise the dominant–subordinate relationships of their group members relative to themselves but it remains unclear how they were able to achieve this mechanistically. Was there a form of visual behaviour matching that they were able to accomplish and generalise, at least within their own group? Moreover, during triadic interactions, the integrative property of the bonnet macaque's knowledge system allowed her to respond appropriately to the relative dominance ranks of the two other interacting individuals. It is striking, therefore, that whatever may have been the stored imagery of the individual attributes of the two females she was interacting with, it was possible for her, as discussed above, to access both these stored resources and integrate them when finally making a socially complex decision.

11 Experiential Knowledge in the Socioecological World

It is noteworthy that an elaborate example of tool manufacture and use by a wild female bonnet macaque from the same study troop, that we had documented earlier, indicated the possibility that the individual was able to perceive the underlying causality of her actions and also form a mental model of the tool to which she could repeatedly refer.⁶⁷ In the course of our long-term study on the ecology, demography and behaviour of wild bonnet macaques in the Mudumalai Wildlife Sanctuary (see Sinha et al. 2005 for details), we later observed yet another complex behaviour on the banks of the River Moyar in June 2004. Two young adult males (from a group of five bachelor males) systematically collected and washed wild mangoes that floated down the river, prior to consuming them. On one such occasion, one of these males misplaced a mango that he was washing and conducted a very directed search for

it by feeling the shallow river floor close to the bank with his left hand. In addition to providing evidence for a planned, goal-driven action, this observation suggests that individual macaques appear to know the shape, feel or texture of a food item such as a mango, once again strong evidence for a capacity to characterise the physical properties of objects and remember them through subjective self-awareness.

In conclusion, the ability to form mental representations, generated by direct personal experience, appears to underlie the bonnet macaque's interactions with both the mechanical as well as the social components of her immediate environment. This suggests a rather early evolutionary origin for fairly sophisticated cognitive capabilities, characterised by an objectified self with limited regulatory control over more subjective levels of self-awareness, in cercopithecine primates, predating those of the great apes. The nature of the objective self-awareness displayed by bonnet macaque, however, appears to be unusual in terms of the features believed to typify this kind of self-awareness.⁶² While individual macaques seem to be remarkably adept at acquiring fairly comprehensive and exact knowledge of the positions of different individuals in the dominance hierarchy relative to themselves, they may not be able to rank them in a linear transitive order or form abstractions of such a hierarchy. Individuals may also be able to attribute motives or intentions to the group members they interact with although they may occasionally hold erroneous beliefs and fail to project their experiences while predicting the behavioural motivations of other individuals (see also.⁴¹ Finally, female bonnet macaques may be capable of accessing and integrating information on the dominance ranks of two (and more?) individuals while making a social decision during interactions with these individuals while certain individual macaques may be capable of attributing and manipulating the belief systems of other individuals. These are major advancements over simple one-on-one decision-making driven by associative learning paradigms, which have long been considered typical of most nonhuman species, including non-ape primates. We must, therefore, conclude this essay with the speculation that bonnet macaques might represent an intermediate stage in the evolution of self-awareness in animals, a process that began with the subjective awareness that characterises most, if not all, species and culminated in the most sophisticated form of symbolic self-awareness, which appears to be the hallmark of the human species alone.

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