Chapter 7

Synthesis
Bibliography


Gestural communication in nonhuman primates (henceforth, primates) has been suggested to lie at the roots of human language, perhaps the most complex form of behaviour one encounters in the living world. Comparative studies, aimed at understanding shared features of language production and usage in phylogenetically related primate species, have revealed striking similarities in characteristics between primate gestures and human language, though with certain crucial dissimilarities. Gestures in apes, for instance, are used flexibly and intentionally, and develop ontogenetically during an individual’s lifetime, traits that typify human language. Gestures produced by wild apes, nevertheless, have rarely been reported to be referential, iconic or symbolic in nature, features that are hallmarks of human communication systems.

The understanding of gestural communication in our closest living phylogenetic kin is mostly derived from apes while other non-ape primate species have been largely ignored in this context. Earlier attempts to investigate gestures in a few monkey species revealed the use of flexible and intentional gestures in captivity but again, such studies have rarely been conducted in the wild. Moreover, previous research on monkey gestures had not implemented the definitions and methods standardised in ape gestural research. Thus, it has not been possible to achieve a common understanding of gestural communication in apes and non-apes, which, in turn, is indispensible for comparative and evolutionary studies. In my doctoral dissertation, I intended to address some of these unexplored areas in monkey gesture research, which would eventually contribute to a fundamental understanding of primate gestures across taxa.

I conducted my investigations in the Bandipur National Park in the state of Karnataka in southern India and attempted to explore the gestural communication system of bonnet macaques, an Old World cercopitheine primate endemic to peninsular India. Several free-ranging troops of the study species, particularly in the Bandipur population, have been continuously monitored over the past two decades, revealing the presence of extensive behavioural flexibility across individual members of these groups. Such characteristic lability in behavioural expression, displayed by this population of bonnet
macaques, made it highly suitable for a potential inquiry into their communication systems, especially that of gestures.

The first step towards an understanding of gestures in wild bonnet macaques necessitated, as outlined above, objective definitions of the gestural signals, adopted from the ape gesture literature. I followed the various criteria of flexibility and intentionality, postulated to distinguish gestures from other communicative signals during my study. The results of such an exercise revealed that bonnet macaques do indeed produce flexible and intentional gestures, manifest in the use of multiple gestures in a single context or a single gesture in multiple contexts and as persistent gesturing in the absence of an appropriate response from the audience until the signaller’s goals were achieved. My observations also indicated that some of the gestures might have been used by the macaques in a potentially referential, intentional manner, a hypothesis that demands further exploration in the future. In addition to the gestural repertoire of the study species, I also determined the functional meanings of each gesture, as revealed by the appropriateness of the recipient’s responses, aiding the signaller to achieve its original intended goal. Most of the gestures could be classified into distinct contextual categories, with the exception of a few, which were ubiquitously used across all several contexts, perhaps indicating their inherent flexibility.

In order to further characterise the gestural repertoire of the macaques, I compared the age- and sex-specific gestural repertoires across my study individuals. There appeared to be significant differences in the repertoire sizes of individuals across age classes, with the affiliative and agonistic gestural repertoires significantly increasing and the play repertoire decreasing with progressing age. These results were indicative of gradual developmental processes leading to the ultimate adult repertoire in the species. Moreover, each study troop had distinct patterns of gestural repertoires across age classes, suggesting the influence of immediate socio-ecological factors in shaping the final gestural repertoire of the study troops. There was also a distinct variability in the repertoire sizes of adult females and males, with affiliative gestures being significantly more represented in the female repertoire than in that of the males. This perhaps reflects the variable social roles that members of each sex have been independently selected for during the evolution of
the species. There were no significant influences of an individual’s social rank in the
dominance hierarchy on the size of their gestural repertoires. Individual repertoire sizes
did not vary significantly within an age-sex class and no idiosyncratic gestures could be
identified in any subject, evoking the possibility of processes other than ontogenetic
ritualisation to underlie the development of bonnet macaque gestural communication.
Finally, there were several gestures that were used in a single context as well as single
gestures deployed across contexts, confirming the flexible nature of gesture use by the
study bonnet macaques.

Similar analyses of age- and sex-based differences in the frequencies of gesture use
revealed that juveniles displayed the highest frequencies of gestures across contexts.
Affiliative gesturing was employed comparably across different age classes, agonistic
gestures were used at relatively higher frequencies by adults while play gestures were
more frequent among juveniles and infants. Amongst adult females and males, affiliative
and agonistic gesturing were both higher in the females, possibly reflective of a typically
female-bonded primate society. Play gestures, in contrast, were exhibited more by males,
possibly due to the presence of subadults, these levels significantly decreasing with
increasing age of the males. Gesture frequencies also varied amongst the age classes
across the study troops, which could be attributed to their immediate social environments
rather than their corresponding repertoire size. Affiliative gesturing was observed to be
highest among adult female-infant pairs and adult female-female pairs, perhaps emerging
from the close association of these two classes of individuals. Juveniles and infants
appeared to direct play gestures significantly more towards members of their own age
cohorts rather than towards one another. The social dominance ranks of signallers and
recipients did not influence levels of affiliative gesturing within adult females or within
adult males. Agonistic gestures, however, were more significantly directed down the
dominance hierarchy in both sexes of the study macaques. Rank differences between
adult individuals also did not affect the frequencies of gesturing towards one another in
same-sex pairs.

When the gestural profiles of infant and juvenile bonnet macaques were closely
examined, I observed the frequencies of tactile gesture use to be comparable across all
individuals while there was a gradual development of visual gestures from young infants to the older juveniles. Agonistic gestural repertoire size and the frequencies of use of such gestures were found to be significantly higher in older juveniles whereas affiliative and play gestures were comparable across these age categories. I then investigated the influence of certain innate factors such as individual age and repertoire size as well as certain social factors such as the mother’s social rank and frequencies of received contextual gestures on the processes underlying the development of gestures across my study infants and juveniles. Generalised linear modelling of these factors and their combinations indicated repertoire size and progressive age to significantly influence gesture use, particularly in the context of agonism. The levels of display of play gestures, in contrast, depended directly on the frequency of similar gestures received, indicating the importance of the surrounding social environment in the expression of such gesturing. These results indicate that processes other than ontogenetic ritualisation, which has been postulated to underlie the appearance of ape gestures, may be responsible for the development of gesturing in this macaque species.

Finally, my study on bonnet macaques revealed the use of gesture sequences—gestures combined with other gestures or other signals—by individual subjects during their communicative acts. I investigated such sequences to unravel their conventional structures, if any, through Markov transition analyses and also attempted to understand the possible meanings of such sequences. My analyses revealed significant structural components in such sequences, with certain gestures invariably used either at the beginning or at the end of a particular sequence, with the former perhaps fulfilling the function of attracting the attention of target recipients. Certain gestures also had significantly higher probabilities of being associated with other particular gestures or signals, resulting in independent communicative networks constituted by affiliative-play or agonistic gestures. Although the functional meaning of such gesture sequences were not very apparent in every situation they were used in, they seemed to be significantly more effective in eliciting responses from targetted recipients, than were the same gestures repeatedly performed singly or other, functionally similar, single gestures, during persistent gesturing by signallers following an initial failure to evoke an appropriate response. What is clear, however, is that these gesture sequences, though an intrinsic
component of the communication repertoire of bonnet macaques, do not appear to be functionally similar to the syntax of human language; their presence in the gestural repertoire of the species, nonetheless, should motivate us to design further studies in order to precisely determine their functions in the communication system of this macaque.

In conclusion, my research is probably the first of its kind to explore the gestural communication of any non-ape species in its natural environment, systematically employing the standardised protocols of gesture research established in ape communication studies. This, I hope, will be a fundamental contribution to the scholarship of primate communication studies and in the process, open up exciting avenues in our endeavour to understand the evolution of primate gesturing, in general and the origins of human language, in particular.
My thesis aimed towards an understanding of the gestural communication system in a population of wild bonnet macaques in the Bandipur National Park in the state of Karnataka, southern India. It was important initially to define a gestural repertoire for the study species, as this was the first study to have systematically addressed their nonvocal communication. The various criteria, adopted from earlier ape gesture studies (Tomasello et al. 1994; Liebal et al. 2006; Call and Tomasello 2007; Pika 2008; Genty et al. 2009; Hobaiter and Byrne 2011a), were considered necessary conditions to be fulfilled by the signals displayed by bonnet macaques in order for them to qualify as true gestures. At the onset, the signals had to be discreet and targeted towards particular recipients and being mechanically ineffective, had to elicit a voluntary response from the receivers—a condition that I could clearly identify in the free-ranging study troops. The responses evoked as a result of the display of such signals, in turn, defined their functional meaning as well as determined the contexts in which they were employed (see Cartmill and Byrne 2010).

The more challenging aspect of gestures—to determine their underlying intentionality—was, however, difficult to ascertain, on occasion, in the free ranging study individuals. There are several behavioural manifestations that potentially illustrate the intentionality of signals, of which I investigated response waiting and persistence in gesturing until an appropriate response was elicited from the recipient (see Call and Tomasello 2007). Bonnet macaques displayed consistent gesturing in the absence of an initial response and ceased to gesture after the recipient finally responded, suggesting a predetermined goal of the signaller’s display of gestural communication. The other two characteristics of intentionality—audience checking and gaze alternation—could not, however, be tested in the present study. It was not possible to monitor, during my observations, the recipients’ reactions before and after a potential gesture was displayed by the signaller, particularly given the dispersed nature of the troop members in the study site. This deficiency could also not be compensated for by video analyses of the data due to logistic problems. There, thus, remains a further scope, in the future, to investigate the various additional aspects of intentional production of gestures in this species in to determine the various levels of flexibility that probably underlie their gestural communication system.
During my study, I also observed the subjects to display a gesture, Soliciting for Allogrooming, in a manner that was suggestive of a potential referential and intentional nature of this particular gesture. During an act of allogrooming, for instance, the groomee would change its body orientation or hold a specific part of its body to perhaps indicate particular areas on their body where they intended to be groomed. The groomer, in response to such an action from the signaller, immediately shifted to the newly displayed body area and continued its grooming there. Although potentially self-referential in nature, such an observation is extremely exciting to encounter in a wild macaque species, as such observations are very rare, even in wild apes (Pika 2012). This particular gesture displayed by bonnet macaques is in urgent need of systematic studies in the future, with proper control situations, in order to confirm the true nature of referentiality that might exist in such gestures displayed by a non-ape primate species.

My investigations into age- and sex differences in the gestural repertoire sizes as well as frequencies of gesture use by bonnet macaques revealed interesting developmental patterns, wherein there was an increase in affiliative and agonistic gestures with age while play gestures declined; adult females too gestured differentially than did adult males. The development of gestural communication in my study species did not appear to follow the processes of ontogenetic ritualisation, as has been generally suggested for ape gestures (Tomasello et al. 1985, 1994, 1997). There could perhaps be other innate or social factors that influence the gradual course of gesture development in this macaque, as has also been suggested for gorillas and chimpanzees in certain wild populations (Genty et al. 2009; Hobaiter and Byrne 2011).

A unique feature of gesture use by bonnet macaques, which emerged from my study, concerns the observation that the immediate social environment of each troop induced differential use of gestures amongst troop members that belonged to particular age-sex classes, suggesting that each troop may be unique in their behavioural expression within a larger world of population- or species-typical gestures. This raises the very important question of whether, in the future, our efforts at understanding behaviour should shift its focus even more from the species- or population level to those of groups or even individuals, each with its unique immediate physical and social environments.
During my study, I attempted to explore the influence of certain inherent factors, for example, the age of an individual or its expressed repertoire size as well as certain social factors, for example, the mother’s social rank or frequencies of contextual gestures received by an individual on the processes underlying the development of gestures in immature bonnet macaques. An intriguing observation that I made was the ubiquitous use of tactile gestures by infants and juveniles alike although gestures in the visual modality gradually developed in older juveniles. This pattern appears to be a characteristic feature of gestures in monkeys, as it has also been reported earlier from young stump-tailed macaques and hamadryas baboons (Grigor’eva and Deryagina 1987); this is in direct contrast to the developmental trajectories of gesture modalities in apes, wherein tactile gestures gradually develop with age while visual gestures are uniformly present in all immature individuals. I also observed that individual age, gestural repertoire sizes and the nature of the communicative environment that an individual was exposed to directly contributed to the levels of gesturing in immature macaques, indicating factors other than individual learning that may drive gesture ontogeny. The next step would be to conduct more detailed investigations, adopting methods from the earlier, important study by Schneider et al. (2011), that would trace, in greater detail, the progression in different aspects of gesture development displayed by individual infant and juvenile macaques.

Finally, when I studied the gesture sequences used by bonnet macaques during communicative events, I observed that there was indeed a concrete structure of such sequences that the study individuals exhibited. Certain gestures were combined with other gestures or signals to form distinct communication networks, independently in contexts of affiliation and agonism. The beginning and end of a sequence was also significantly composed of certain gestures alone, a possible indication that such formations had definite functional meanings, as, for example, the beginning gestures could act as ‘attention-getters’ (Tomasello et al. 1994). It was evident that the sequences were not preferred by bonnet macaques over single gestures in order to increase the efficiency of communication, an observation akin to what has been reported earlier from gorilla gesture sequences (Genty and Byrne 2010, but see Liebal et al. 2004 in chimpanzees). The discovery that gesture sequences were functionally more effective
than were single gestures, sometimes used repeatedly, in eliciting appropriate responses from the recipients during persistent gesturing indicates one functional use of gesture sequences in the gestural communication system of the study bonnet macaques. In the future, such investigations should, however, compare gesture sequences between different age classes of individuals in order to test the ‘repertoire tuning’ hypothesis proposed by Hobaiter and Byrne (2011b), which suggests that gestures sequences used by immature apes are finally attenuated to form the adult gestural repertoire. I could not, unfortunately, address this proposed important function of gesture sequences—an exercise that demands further investigation—due to insufficient data on gesture sequences exhibited by my study individuals in each age class.

This thesis is the first step in comprehensively unravelling the various characteristics of gestural communication in bonnet macaques, an effort that has rarely been attempted in any wild monkey species before. By defining the gestures in a non-ape species, following the standard methods established in ape gesture studies, my thesis, I hope, will fundamentally contribute to the scholarship of primate gesture research by providing a shared ground of understanding, facilitating further comparative studies across the primate lineage. I also believe that it is imperative to consider multimodal communication systems in primates, as, for example, functional combinations of vocalisations and gestures, in order to understand the holistic flexibility and intentionality that is then imparted to such a system (see, for instance, Slocombe et al. 2011). It is also possible that we will acquire greater insights into the structure and function of primate gesture sequences if such a multimodal approach is adopted, paving the way towards a unified theory of language evolution, rather than the current binary postulates of the independent vocal-origin or gestural-origin of human language.
7.1 References


