Other Voices

Gestural Communication of Wild Bonnet Macaques *Macaca radiata* in the Bandipur National Park, Southern India

A Thesis
Submitted for the Degree of
Doctor of Philosophy

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Declaration

I hereby declare that the work presented in this thesis, entitled **Other Voices: Gestural Communication of Wild Bonnet Macaques *Macaca radiata* in the Bandipur National Park, Southern India**, has been carried out under the guidance of Prof Anindya Sinha and has not formed the basis for the award of any other degree, diploma or fellowship previously. The particulars given in this thesis are true to the best of my knowledge and belief.

Place: Bangalore
Date: 21.08.2015

Shreejata Gupta

Certificate

The research embodied in this thesis, entitled **Other Voices: Gestural Communication of Wild Bonnet Macaques *Macaca radiata* in the Bandipur National Park, Southern India**, was conducted by Shreejata Gupta in the School of Natural and Engineering Sciences, National Institute of Advanced Studies, Bangalore, India, under the supervision and guidance of the undersigned. It is certified that the thesis submitted is a bonafide record of research done by the candidate in partial fulfilment of the requirements for a doctoral degree and that the thesis has not previously formed the basis for the award of any other degree, diploma, associateship or fellowship or any other similar title of any other university or society.

Place: Bangalore
Date: 21.08.2015

Anindya Sinha
Guide

For my beloved *Didā* and *Dādubhāi*,

I think of you everyday

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Synopsis

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 cercopithecine 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.

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Chapter 1

Introduction

Human language is probably one of the most mysterious, as well as unparalleled, behaviours that one encounters in the biological world. With its inherent attributes of flexibility, intentional production, diversity, ontogenetic developmental roots and its symbolic nature, human language is unique and remains unchallenged by any other communication system in the animal world. In the quest for the evolutionary roots of language, intensive research has focussed on various communication modalities of nonhuman primates (henceforth, primates), the closest phylogenetic relatives of humans. The two major modalities that are included in primate communication systems are that of vocalisations and gestures, along with facial expressions used mostly in conjunction with the former two (reviewed in Slocombe et al. 2011). The theory of language evolution, thus, draws from comparative studies on vocal and gestural communication in primates, giving rise to binary views on a possible vocal-origin or a gestural-origin of human language (Hewes 1973; Seyfarth et al. 1980; Kudo 1987; Gouzoules 1995; Zuberbühler 2002; Arbib et al. 2008; Pika 2008; Slocombe et al. 2011).

1.1 Primate vocalisations and human language

Our efforts to understand human language had earlier focussed on primate vocalisations, particularly in monkeys (Seyfarth et al. 1980; Kudo 1987; Gouzoules 1995; Zuberbühler 2002) as well as in apes, including chimpanzees (Clark and Wrangham 1993; Mitani and Gros-Louis 1998; Crockford and Boesch 2003; Slocombe and Zuberbühler 2005) and bonobos (Clay et al. 2015). Although very nominal levels of flexibility exists in vocal production (reviewed in Hammerschmidt and Fischer 2008), the usage of primate vocalisations is characterised by higher levels of variability (Cheney and Seyfarth 1985; Mitani and Nishida 1993; Caine et al. 1995; Wilson et al. 2001; Tomasello and Zuberbühler 2002; Hopkins et al. 2007; Slocombe and Zuberbühler 2007). Some calls used in primate vocal communication have been known to be referential in nature, referring to external entities such as predators (Seyfarth et al. 1980; Zuberbühler 2000), although the intentionality behind such referential calls were not always clear (but see Schel et al. 2013). There have also been observations on call sequences and their modifications in monkeys, often to refer to various levels of threat (Ouattara et al. 2009a, 2009b), thus revealing, within them, a combinatorial capacity that has been considered a crucial component of human language. The development of primate vocalisations, however, seems to be non-flexible, without the general possibility of incorporation of novel calls into their inherent vocalisation repertoires. Moreover, their largely non-intentional usage made them fall short of meeting the basic characteristics of human language (see Tomasello and Zuberbühler 2002).

1.2 Primate facial expressions and human language

Primates use many facial expressions during communicative acts, which had been initially considered in efforts to understand their non-vocal modality (Ladygina-Kohts 1935; Van Hooff 1967; Van Lawick-Goodall 1968). During later years, however, scholars opined that facial expressions were probably associates of calls and other manual signals, being reflective of immediate emotional and motivational states of individuals (reviewed in Slocombe et al. 2011). Tanner and Byrne (1993) observed the spontaneous covering by hand of a play-face expression in a female gorilla, possibly illustrating the involuntary nature of facial expressions, as compared to manual gestures. Facial expressions, thus, appear to be uncontrolled actions and, in this respect, not important in our considerations of human language evolution. Researchers studying ape communication consider facial expressions as a separate category from those of gestures though both comprise non-verbal communication in the species concerned (Liebal et al. 2006). It has, nevertheless, been suggested that such expressions predominate gestural communication in monkeys (Zeller 1980; Maestripieri 1996, 1997, 2005; Ferrari et al. 2003; Hesler and Fischer 2007).

1.3 Primate gestures and human language

The other non-vocal modality, distinct from facial expressions, which primates employ in their communication—gestures—subsequently became the focus of our pursuit to unravel the roots of human language. Increasing evidence suggested that primate gestures are indeed closest to human language, more than any other communication system across taxa. The theory for a gestural origin of human language draws on the association of motor activities and mirror neurons in homologous regions of language production in the primate brain (Rizolatti and Arbib 1998; reviewed in Arbib et al. 2008). The characteristic behavioural similarities of primate gestures to those of language in its flexible production and use incline in the favour of this theory (Hewes 1973). Moreover, the onset of communication behaviour in pre-linguistic children occurs through gestures much earlier than spoken words develop, suggesting gestures probably being an older link to language formation (Werner and Kaplan 1972; Bates et al. 1975a, 1975b; Camaioni 1997). It has also been suggested that the symbolic nature of human language perhaps evolved from visual gestures in the evolutionary lineage of modern humans (Armstrong et al. 2007; Meir et al. 2013). Attempts at training apes to learn human language had also mostly been successful through gestures (Hayes 1951; Gardner and Gardner 1969; Patterson 1978; Greenfield and Savage-Rumbaugh 1990, 1991; Lyn et al. 2010), strongly nominating the gestural origins of human language to be of greater merit than that of primate vocalisations.

Adopting the established methodologies of human gestures studies, especially the Speech Acts Theory (Austin 1962; Bates et al. 1975b), the field of primate gesture studies, particularly those in apes, gained acceleration during the late 1970s (Plooij 1978, 1979). Following such attempts, several researchers have focussed on captive and wild populations of apes, reporting the flexible use of gestures, as manifest through the display of multiple gestures in the same context and of the same gesture in multiple contexts (Tomasello et al. 1994; Call and Tomasello 2007; Genty et al. 2009; Hobaiter and Byrne 2011), and their intentionality, as manifest in the signaller being aware of the attention state of the target recipient (Tanner and Byrne 1996; Pika et al. 2003; Liebal et al. 2004, 2006; Call and Tomasello 2007; Cartmill and Byrne 2007; Genty et al. 2009; Hobaiter and Byrne 2011). The intentionality behind primate gestures is further illustrated when apes persistently show the same gesture to elicit an expected outcome from recipients or when they sometimes form sequences of multiple gestures until the intended goal is achieved (Tomasello et al.1985; Leavens and Hopkins 1998; Leavens et al. 2004; Cartmill and Byrne 2007; Tomasello and Call 2007). Recent evidence also suggests that apes may be capable of even more sophisticated forms of referential gesturing, in which they refer to external entities during a dyadic interaction or even use iconic gestures in order to symbolise an intended communication (Pika and Mitani 2006; Pika 2012; Genty and Zuberbühler 2014).

Innovative gestures and individual variation in the use of such gestures have also been observed in chimpanzees (Tomasello et al. 1985; Goodall 1986), gorillas (Tanner and Byrne 1993, 1996), bonobos (Pika 2007) and orangutans (Cartmill and Byrne 2007), reiterating the inherent nature of flexibility in primate gesture production. Apes also express an ability to learn new gestures, as has been observed in human sign language-trained apes and more rarely, when individuals learn from conspecific individuals (Ladygina-Kohts 1935; Gardner and Gardner 1969; Rumbaugh et al. 1985; Fouts et al. 1989; Leavens et al. 1996). This indicates a capacity of ontogenetic learning of gestural structure and its effective use. In fact, the ontogenetic development of gestures in apes have been suggested to be ritualised over an individual's lifetime (Tomasello et al. 1994; see Call and Tomasello 2007), although other forms of social learning mechanisms might also be operative (see Genty et al. 2009 and Hobaiter and Byrne 2011). All these characteristics are similar to the basic tenets of human language, thus providing support for the gestural theory of language evolution.

Most of the results discussed here stem from research in ape gestural communication, which have then been generalised to primate gestural communication and its relation to human language hypothesised. There are, however, immense opportunities that remain unexplored in understanding gestural communication in other non-ape primate species, which may have the potential to further illuminate the processes underlying the evolution of primate gestures and, ultimately, human language. Moreover, the very few studies that have explored gestures in monkeys have mainly focussed on their gestural repertoires, an approach that is different from that adopted in ape studies. For instance, the methodologies proposed by Maestripieri (1996, 1997) or Hesler and Fischer (2007, adapted from van Hooff 1962, 1967) concentrate on the contexts of 'signals' and their prospective functions and that too, only in a few macaque species. However, these studies have not addressed the question of whether the signals were used intentionally, as were those in apes. It, therefore, remains an open question whether these macaque signals truly qualify as 'gestures', as has been defined in the ape gesture literature.

In this connection, it should be noted that gestures in Barbary macaques have been reported to show flexibility across contexts (Hesler and Fischer 2007) while Maestripieri (1997) suggests that gestures in pig-tailed macaques are more graded than discreet, thus postulating the possibility of flexible use across social situations. Although it has been proposed that monkeys lack individual variation, typical of apes, in gesture use (de Waal and Johanowicz 1993; Maestripieri 1998), innovative gestures have been reported in a range of species such as hamadryas baboons (Kummer 1995), bonnet macaques (Sinha 2005) and mandrills (Laidre 2008), indicating the potential ability of non-ape species to produce flexible gestures as well. Very recent experimental work on captive rhesus and Tonkean macaques also suggests that these species may be capable of gesturing intentionally (Canteloup et al. 2015a, 2015b), a phenomenon never reported earlier from non-ape primate species.

1.4 Research gaps identified in gestural communication

From the current state of the art of primate gesture research, it is evident that more explorations are necessary to understand gestural communication in non-ape species, particularly in order to facilitate comparative studies, especially in the light of evolution of human language. The few investigations on monkey gestures, although pioneering in the field, have not considered the fairly comprehensive methodologies that were standardised and used to understand ape gestures. It is, therefore, crucial that one pursues these methodologies in order to comparably understand gestural communication in other primate species, particularly to reveal the phylogenetic connections in the evolution of primate gestures. Such an exercise would provide invaluable information and construct a common platform for further comparative studies that may yet reveal novel insights into the evolution of human language.

1.5 Gestural communication in bonnet macaques: My thesis

My thesis, thus, aims to investigate what characterises and comprises true 'gestures' in the communication repertoire of bonnet macaques, an Old World cercopithecine primate endemic to peninsular India. I also intend to explore the flexibility and intentionality behind the use of such gestures by the study species, eventually to address the research gaps that currently exist in primate gestural research.

At the onset, I have categorised gestures in the bonnet macaque communication repertoire by following the definitional criteria established in ape gesture studies and referred to above (Chapter 2). Having identified the gestures in the study species, I investigated age differences in the gestural repertoire sizes as well as the frequencies of use of these gestures across age classes of adult, juvenile and infant macaques at different levels—those of the population, troop and the individual (Chapter 3). A similar exercise was conducted to understand gestural communication in adult females and males in order to determine sex differences in such communication, if any (Chapter 4). I then explored the various immediate factors that could potentially influence the development of gesture modalities as well as repertoire structure and the frequencies of gesture use by infant and juvenile bonnet macaques (Chapter 5). Finally, I aimed to understand the structure and functional meaning of gesture sequences displayed by the study species in order to detect the possible presence of syntax-like structures in the non-vocal communication system of bonnet macaques (Chapter 6).

This thesis is probably the first of its kind to explore gestural communication system in a macaque species in the wild. The results from this thesis would facilitate future in-depth studies on the communication behaviour of bonnet macaques and other non-ape species and pave the way forward in the adoption of comparative approaches to primate gesture studies.

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Chapter 2

Towards an Objective Definition of Gestures in Bonnet Macaques

2.1 Introduction

Investigations into primate gestures evolved by adopting methods that had traditionally been used in studying gestures in humans (Tomasello et al. 1985, 1994, 1997). Gestures in nonhuman primate communication, especially in those of apes, have been defined as "discrete, mechanically ineffective, physical movements of the body" (Hobaiter and Byrne 2011a; see also Genty et al. 2009, Cartmill and Byrne 2010) or "communicative signals produced by body postures or the movement of body parts, including the limbs, head and /or facial muscles to achieve an intended goal" (Tomasello and Call 2007). It had also been suggested that gestures should be signals always directed to a particular recipient and being mechanically ineffective, should elicit a voluntary response from the recipient (Pika 2008; Arbib et al. 2008; Schel et al. 2013). In previous studies on gestural communication of monkeys (Maestripieri 1996, 1997, 2005; Hesler and Fischer 2007), these established definitional criteria for gestures had, however, not been applied.

In this chapter, I have followed these standard definitions in my attempts to define gestures and evaluate the gestural communication system in my study troops of bonnet macaques. This is an essential exercise if one needs to facilitate comparative studies across taxa and more particularly, trace language-like markers, suggested to be antecedents of language in its currently extant form in modern humans, in the primate lineage.

2.1.1 *Defining gestures*

There are several criteria that have been laid down by previous studies on ape gestures (Tomasello and Call 2007; Hobaiter and Byrne 2011a), which need to be fulfilled by any communicative behaviour in order to be considered valid gestures. These criteria are discussed here.

I. Criterion of discreteness of behaviours

First, I considered only instantaneous behavioural events displayed by bonnet macaques to be potential gestures and not those that prevailed over longer durations of time. Thus, gestures are behavioural events rather than behavioural states (Altmann 1974); this is in accordance with the 'discreet' nature of gestures suggested by previous studies (Genty et al. 2009; Cartmill and Byrne 2010; Hobaiter and Byrne 2011a). It is but natural for gestures to be short and precise in order to represent immediately relevant information, which is the ultimate purpose of communication. If the act of communication is too spread over time, there is a potential risk of loss of information. There were several instances during my observations when a sender displayed multiple behaviours in quick succession towards a target individual. In defining gestures, however, I have considered only those instances where there was a single act displayed by the sender to initiate communication. This was done in order to avoid confusion in understanding the function of each potential gesture used by the macaques; consideration of gestural sequences would obscure our understanding of individual gestures. These behavioural sequences, however, have also been analysed independently later in my thesis (Chapter 6).

II. Criterion of joint attention between the sender and the receiver

Communication events that qualify as potential gestures are those that are directed towards target individuals while there is joint attention between the sender and the receiver (Tomasello et al. 1994). I considered, in this category, only those interactions in which a sender sent the signal when the recipient was attending to it, and a subsequent response was elicited. There were occasions when there was indeed joint attention between the sender and the receiver, but the response consisted of the receiver moving away or otherwise avoiding the signaller. I have not considered these interactions in the present analysis, as the motivations behind such responses were hard to interpret and did not reflect the communication context in which the sender initiated the interaction. Other circumstances, wherein there was an initiation of a potential communication event, involving at least two individuals, but the receiver did not attend to the act, have also not been considered in this analysis. Although such a strict criterion may have led to an underestimation of the actual number of gestures produced, it is evident that the display of an appropriate response must be considered essential to evaluate the effectiveness of a successful gesture and hence, this criterion was invariably included in my definition of bonnet macaque gestures.

III. Criterion of intentional goals

Intentionality is one of the necessary conditions for a communicative act to be considered a genuine gesture. Evidence for intentionality could be invoked, for example, when gaze alternations occur between the sender and the recipient during communication, when a recipient waits for an appropriate response from the receiver or displays persistence in communicating until a potential goal is achieved (Piaget 1954; Bates 1976; Bruner 1981; Tomasello et al. 1985; Tomasello et al. 1994; Pika et al. 2003). If any of these conditions was fulfilled, the relevant signal has been considered a gesture (Arbib et al. 2009). In my study, I considered a communication event to be intentional if

(a) The initiated behaviour elicits, always or at least in a significant number of instances, a response appropriate for the context. It should be noted that upon sending a signal, which allows the sender to establish a context of communication, there could be either a response in the same context or an inappropriate one. For example, if a sender sends a signal of affiliation, this could be reciprocated either by other affiliative responses (same-context response) or by agonistic / play / subordination / sexual signals (other-context responses). Same-context responses indicate that the initiated behaviour was displayed to a particular receiver with an expected outcome, favourable to the sender. Thus, the motivation behind the displayed behaviour could be considered fulfilled. Instances that elicit responses unexpected for that particular context, as, for example, an agonistic response to an initiated affiliative behaviour could represent decisions appropriate for other contexts but which cannot be evaluated in the light of the current discussions.

(b) In the absence of a response or in case of an inappropriate one in spite of a joint attention state, the sender persistently displays the same behaviour repeatedly or other related behaviours until a response is elicited. This indicates that the sender has an intended goal to achieve when the signal is sent, through which it attempts to alter the receiver's behaviour; the failure of eliciting a response motivates the sender to further pursue this communication until the goal is achieved.

To summarise, I explored the possible outcomes of interactions that involved the sending of a signal to an individual who was attentive towards the sender, the response elicited, and the subsequent behaviours displayed by the sender in the absence of an immediate response. The joint attention state of the sender and the receiver during such interactions indicated a communicative intention behind a signal, particular responses defined the function and context of the signal sent, and the persistent display of the same or of different behaviours, in cases when no appropriate response was received, suggested the sender's original goal-oriented intention. The fulfilment of all these requirements by a particular communicative behaviour, exhibited by the study species, allowed me to qualify it, according to the current definition prevailing in primate gestural studies, as a true gesture in its repertoire.

2.2 Methods

2.2.1 *Study area*

I conducted this study from February 2013 to July 2014 in the Bandipur National Park (11.66°N, 76.63°E) in the southern state of Karnataka, India (Figure 2.1). Spanning over c. 874 km^2, with an elevation ranging from 680 m to 1,454 m ASL, this Park experiences a typical tropical climate, prevailing across the region. The Park falls within the Nilgiri Biosphere Reserve, at the junction of the Deccan Plateau and the Western Ghats, and is characterised mostly by dry deciduous forests, interspersed with moist deciduous forest patches and shrublands. Bandipur is host to a rich ensemble of flora and fauna, including diverse trees, insects, amphibians, reptiles, birds, small and large mammal species (see Chatterjee 2012). The annual rainfall cycle allows us to demarcate a dry and a wet season, from December to May and June to November, respectively. The average rainfall in the area falls in the range of 141.44 ± 19 mm during the period from July to September (Chatterjee 2012). The most common primate species in this area is the bonnet macaque

Macaca radiata, the study species described below. The troops that I have studied belonged to a free-ranging population, though they led a highly provisioned life in the proximity of human habitations within the National Park.

2.2.2 *Study species*

The bonnet macaque is a cercopithecine primate extensively distributed across a wide range of habitats in southern India. The species is distributed rather commonly, possibly owing to its exceptional behavioural flexibility, as has been documented in earlier studies (Sinha 2001; Ram et al. 2003; Sinha et al. 2005). An elaborate behavioural repertoire and complex social interactions are both hallmarks of the species (A Sinha, pers. comm.). The ecological flexibility and behavioural lability reported for this species (Sinha et al. 2005) made it an ideal study subject for my proposed research. Moreover, the extensive phenotypic plasticity and behavioural traditions, displayed by certain populations of the taxon (Sinha 2005; Sinha et al. 2005), including in the context of communication (see Gupta et al. 2015), could potentially contribute significantly towards a comprehensive understanding of gestural communication in the species.

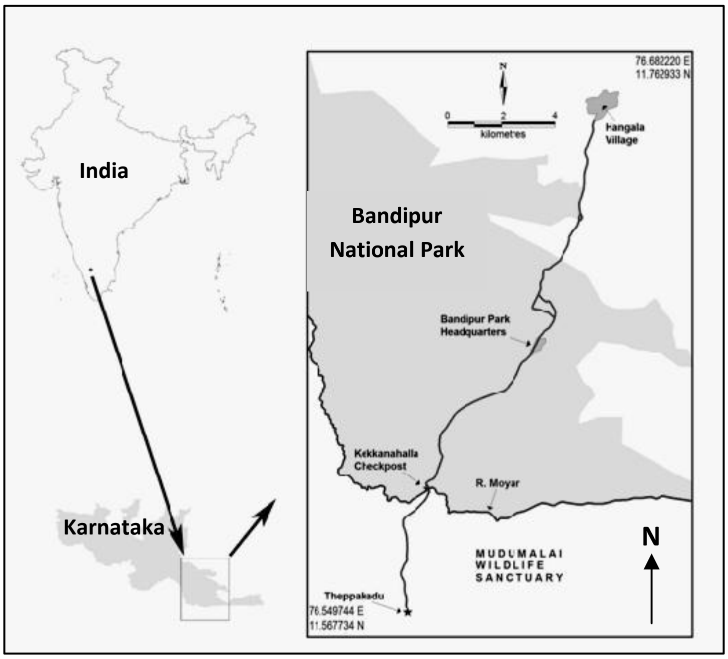

Figure 2.1 Location of the study site, the Bandipur National Park, southern India (adapted from Chatterjee 2012)

In bonnet macaque societies, females usually live in their natal troops throughout their life while males often emigrate to join other troops. Females form strong, linear, transitive dominance hierarchies when adult, with daughters of individual females occupying ranks just below those of their mothers. The dominance status of males is more fluid and determined mostly by aggressive interactions as well as the formation of successful coalitions.

I identified four study troops in and around the Bandipur National Park, three of which had a species-typical multimale-multifemale social organisation while one of them was a unimale-multifemale troop, an unusual, recently characterised form of organisation shown typically by this particular population (Datta-Roy and Sinha 2001; Sinha 2001; Sinha et al. 2003; Sinha et al. 2005). The study troops comprised a total of 29 adult females, 23 adult males, 31 juvenile and 26 infant individuals at the beginning of the study (Table 2.1). During the period of the study, two adults females of Troop HN2 were lost, one having been preyed upon by stray dogs while the other disappeared; two adult males from Troop HN2 and one from Troop C3 left their respective troops and joined neighbouring troops; in Troop HN2, two juveniles were killed in road accidents while one disappeared, and two juveniles of Troop TT1 were electrocuted on power-lines; one infant each of Troops HN2 and TT1 went missing, another one of HN2 disappeared at the same time as its mother while one infant each of Troops HN2 and C3 were run over by vehicles plying on the National Highway 17, that cuts through the National Park.

2.2.3 *Data collection*

The individuals of each study troop were identified on the basis of their morphological features and categorised into different age classes based on their body size and visually determined age-typical morphological characteristics. Following habituation and successful identification of all the individuals of a troop, I followed a standard 15-minute focal animal sampling of all troop members without replacement (Altmann 1974). Focal sampling was carried out from 09:00 to 17:30, six days a week. If the focal animal could not be followed after a certain time during observation, the observed data was discarded. I recorded all the individual and social behaviours displayed by the focal subject in the stipulated time. The data consists of 392.5 hours of observation over 109 individuals including infants, juveniles and adults (Table 2.1). The behaviours were coded on the basis of an ethogram (Appendix 2.1), prepared from observational accounts of the species spanning over 18 years (A Sinha, M Chatterjee and K Mukhopadhyay, pers. comm.) In addition to manual recording, I also video-recorded the behaviours using a Sony HD camera (Sony, Tokyo, Japan), which provided supporting evidence for the collected data.

Table 2.1 Composition of the four study troops and observation hours of bonnet macaques in the Bandipur National Park

Troop	**Social organisation**	**Adult females**	**Adult males**	**Juveniles**	**Infants**
TT1	Multimale-Multifemale	7	7	9	6
TT2	Unimale-Multifemale	6	1	4	4
HN2	Multimale-Multifemale	8	5	5	9
C3	Multimale-Multifemale	8	10	13	7
Observation hours:					
Total		131.75	85.75	100.00	87.50
Mean ± SE		4.54 ± 0.60	3.73 ± 0.53	3.23 ± 0.37	2.88 ± 0.44
Range		1.50 – 11.00	1.50 – 11.25	0.75 – 9.50	0.50 – 8.50

2.2.4 *Data analysis*

The conditions for any behaviour to qualify as gestures, as outlined above, were rather strict. There were, thus, several observed instances of communicative behaviour that I decided to exclude from the reported repertoire of gestures, given the rigorous definitional criteria for a gesture. It is noteworthy that this is a problem that has been faced by previous researchers studying ape gestures as well (Genty et al. 2009; Hobaiter and Byrne 2011a).

During my study, I recorded 5969 instances in which a potential gesture was used, which later reduced to 3349 after I eliminated the interactions in which multiple signals were used. Of these, 2655 interactions represented the use of a single potential gesture while only 2464 finally met the criterion of a joint attention state of the sender and receiver. These were then included as potentially true gestures in the present analysis.

The dominance hierarchy that prevailed in each troop was determined, independently for females and males, by an evaluation of dyadic and triadic interactions involving approach-retreat behaviour in the contexts of agonism, allogrooming and foraging. In all these interactions, the retreat of an individual from an approaching one, even in the absence of any agonistic behaviour, signalled the lower dominance rank of the former, relative to the latter. The dominance hierarchy for both sexes of bonnet macaques is linear and transitive.

Adult female and male bonnet macaques were categorised and ranked into five different age classes on the basis of their distinct age-related morphological characteristics. The age classes of the adult females were: 1 = Primiparous, 2 = Young, 3 = Mature, 4 = Old and 5 = Post-Menopausal, while those of the adult males were: 1 = Subadult, 2 = Young, 3 = Prime, 4 = Old, 5 = Very Old.

For defining gestures, behavioural events were recorded, along with the context of the response type that each elicited. Proportions of response types were tested with G-test of independence in order to find functions of each initiated gesture.

For the case study of potentially intentional referential gestures, I considered only those gestures displayed by adult females and males towards one another and towards juveniles and infants. We have excluded those displayed by juveniles and infants from the current analyses due to inadequate sample size. I calculated received allogrooming frequency per hour and frequency of gestures displayed per allogrooming-hour for each adult individual. A total of 328 such events of gesturing were recorded during a total of 24.68 allogrooming-hours, consisting of 874 initiated allogrooming events.

(i) The frequency of gestures displayed by each individual, expressed as events per allogrooming-hour received has been calculated using the following formula:

$$\frac{\Sigma\ RG_1}{\{\Sigma\ (t_1 + t_2) + (t_1 + t_3) + (t_1 + t_4) + \ldots\ldots + (t_1 + t_n)\}\ /\ n}$$

where,

RG_1 = number of possible referential gestures displayed by Individual 1

t_1 = total duration of observations on Individual 1 (in hours)

t_2 = total duration of observations on Individual 2 (in hours)

n = number of individuals that allogroomed Individual 1

(ii) The frequency of allogrooming received by each individual, expressed as events per allogrooming-hour, has been calculated using the following formula:

$$\frac{\Sigma\ [\{a_{1\text{-}2}\ /\ (t_1 + t_2)\} + \{a_{1\text{-}3}\ /\ (t_1 + t_3)\} + \ldots. + \{a_{1\text{-}n}\ /\ (t_1 + t_n)\}]}{n}$$

where,

$a_{1\text{-}2}$ = number of grooming events initiated by Individual 2 towards Individual 1

t_1 = total duration of observations on Individual 1 (in hours)

t_2 = total duration of observations on Individual 2 (in hours)

n = number of individuals that initiated allogrooming events towards Individual 1

Sex-differences and inter-troop variations of frequency of referential gesturing was analysed by Mann Whitney U-test, while rank and age correlations were performed by Spearman's rank correlation method, using the SPSS 17.0 and R 3.1.0, with input files tabulated in Excel spread-sheets.

2.3 Results

Following the above-mentioned criteria, I could identify 24 behaviours, displayed by bonnet macaques, which qualified as gestures used across different contexts, including those of affiliation, agonism and play (Table 2.2). Of these, 12 gestures were observed in the context of affiliation, seven in that of agonism and five in that of play. Moreover, these gestures could be categorised into tactile and visual, depending on the modalities involved.

2.3.1 *Responses and contexts*

I monitored the contexts in which specific responses were elicited when gestures were initiated by bonnet macaques and targetted to specific individuals (Appendix 2.2). There were invariably same-context responses to three of the 24 gestures: Biting Hard, Spot-Jumping and Hugging with Lip-Smacking (Figure 2.2). The first two gestures elicited agonistic and play responses, respectively, in all their instances of occurrence. Hugging with Lip-Smacking, on the other hand, elicited affiliative responses in 94.59% of the occasions, while the rest elicited either Moving Away or Avoiding, both being considered neutral responses; there were no other-context responses to this gesture. The percentage of affiliative responses to Hugging with Lip-Smacking was, however, significantly higher than that of the neutral responses (G-test of independence, df = 1, G = 317.60, $p < 0.001$, n = 37; Figure 2.2).

In case of the other 21 gestures, the responses elicited were in several contexts. I recorded the proportions of responses elicited by each of these gestures in different contexts. I tested, for each gesture, whether the highest proportion of responses in a particular context occurred significantly more than would be expected by chance alone and used this test to categorise the possible function of each gesture (Table 2.3). This enabled me to categorise the 21 gestures into 11 affiliative, six agonistic and four play gestures (Figure 2.3).

Table 2.2 Name, context and modality of gestures displayed by bonnet macaques

Code	Gesture	Context	Modality
LS	Lip-Smacking	Affiliation	Visual
SG	Soliciting Allogrooming	Affiliation	Visual
BG	Biting Gently	Affiliation	Tactile
CB	Pulling Close to Body	Affiliation	Tactile
HO	Holding Gently	Affiliation	Tactile
HS	Hugging with Lip-Smacking	Affiliation	Tactile
HU	Hugging	Affiliation	Tactile
MB	Mouth-to-Body Touching	Affiliation	Tactile
MT	Mouth-to-Mouth Touching	Affiliation	Tactile
NZ	Nuzzling	Affiliation	Tactile
PA	Patting	Affiliation	Tactile
TO	Touching	Affiliation	Tactile
HJ	Head-Jerking	Agonistic	Visual
LU	Lunging	Agonistic	Visual
OT	Open-Mouth Threatening	Agonistic	Visual
BH	Biting Hard	Agonistic	Tactile
EF	Eye Flashing	Agonistic	Tactile
HD	Holding Down Roughly	Agonistic	Tactile
SL	Slapping	Agonistic	Tactile
PL	Lunging in Play	Play	Visual
PO	Open-Mouth Threatening in Play	Play	Visual
SJ	Spot-Jumping	Play	Visual
PB	Biting in Play	Play	Tactile
PS	Slapping in Play	Play	Tactile

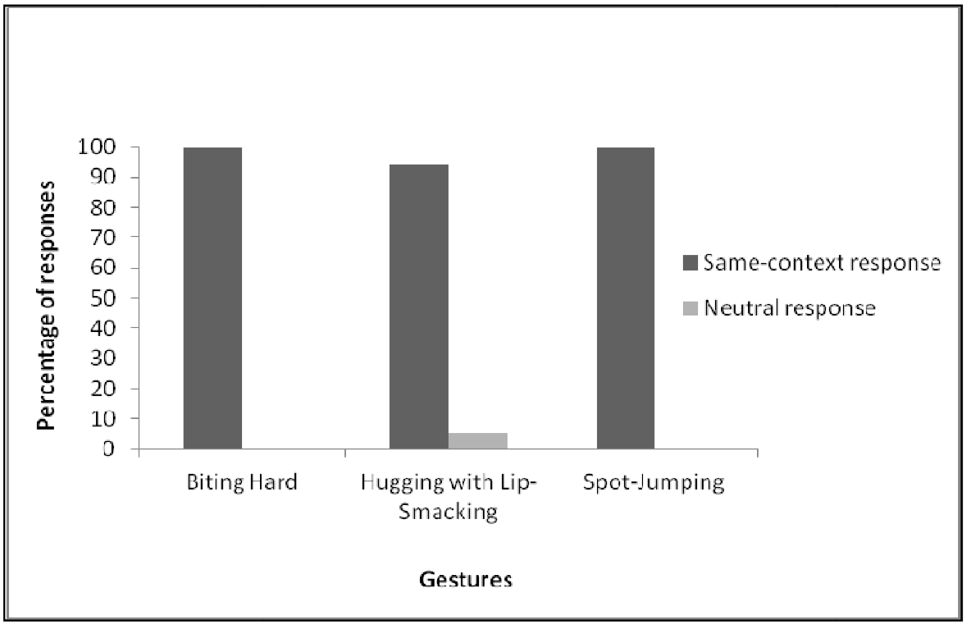

Figure 2.2 Gestures that invariably elicited same-context responses: Biting Hard (n = 2), Hugging with Lip-Smacking (n = 47) and Spot-Jumping (n = 6)

2.3.2 *Multifunctional gestures*

In addition to the 24 gestures reported above, the study individuals displayed eight other gestures, the responses to which did not allow me to identify a particular category to which they belonged (Table 2.4). It is possible that these gestures served specific functions in different contexts.

2.3.3 *Intentional use of gestures*

In 91 out of the 2464 instances in which a single gesture was initiated by a sender, the receiver did not respond in spite of their joint attention state. This led to the gesturing individuals wait for a response and eventually repeatedly displaying the same or different gestures; a positive response was evoked in 88 (96.70%) of these instances while on three occasions, there was finally no response from the receiver. An appropriate response in the same context was elicited in the majority of instances where a positive response was received (66 or 75% of 88 instances; G-test of independence, df = 1, G = 236.85, $p <$ 0.001). Of the 88 positive responses, 13 (14.77%) and 9 (10.23%) were in other contexts or constituted Neutral responses, respectively.

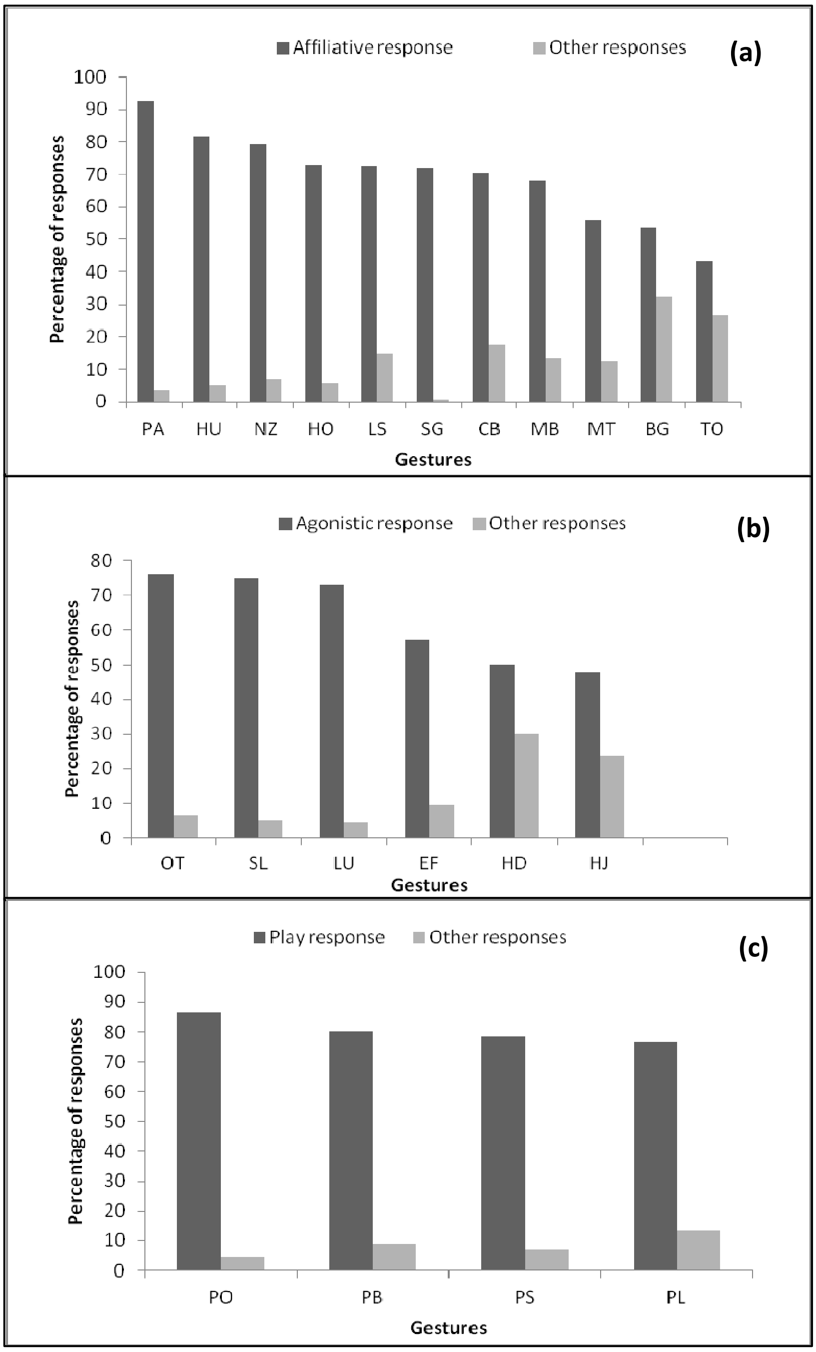

Figure 2.3. Percentage of responses in different contexts to (a) Affiliative, (b) Agonistic and (c) Play gestures. The codes for the gestures have been listed in Table 2.3

Table 2.3 Predominant responses to gestures in contexts of affiliation, agonism and play

Code	Gesture	Highest response (%)	Other responses (%)	Neutral response (%)	G	*p*	n
Affiliative gestures							
PA	Patting	92.59	3.70	3.70	674.84	< 0.001	27
HU	Hugging	81.88	5.00	13.13	386.11	< 0.001	158
NZ	Nuzzling	79.31	6.90	13.79	318.17	< 0.001	29
HO	Holding	72.86	5.71	21.43	284.82	< 0.001	70
LS	Lip-Smacking	72.73	14.69	12.59	202.65	< 0.001	143
SG	Soliciting Allogrooming	72.09	0.58	27.33	695.70	< 0.001	406
CB	Pulling Close to Body	70.59	17.65	11.76	185.47	< 0.001	17
MB	Mouth-to-Body Touching	68.18	13.64	18.18	156.84	< 0.001	24
MT	Mouth-to-Mouth Touching	56.25	12.5	31.25	104.42	< 0.001	16
BG	Biting Gently	53.57	32.14	14.29	81.80	< 0.001	28
TO	Touching	43.14	26.80	30.07	12.72	< 0.001	161
Agonistic gestures							
OT	Open-Mouth Threatening	76.09	6.52	17.39	291.40	< 0.001	46
SL	Slapping	75	5	20	319.40	< 0.001	20
LU	Lunging	73.13	4.48	22.39	323.84	< 0.001	67
EF	Eye-Flashing	57.14	9.52	33.33	142.79	< 0.001	21
HD	Holding Down Roughly	50	30	20	42.14	< 0.001	10
HJ	Head-Jerking	47.62	23.81	28.57	26.79	< 0.001	21

Play gestures							
PO	Open-Mouth Threatening in Play	86.36	4.55	9.09	467.77	< 0.001	22
PB	Biting in Play	80.26	9.21	10.53	311.98	< 0.001	75
PS	Slapping in Play	78.57	7.14	14.29	306.08	< 0.001	14
PL	Lunging in Play	76.38	13.57	10.05	253.70	< 0.001	199

Gestures were classified as affiliative, agonistic and play on the basis of the context of the highest proportion of responses. The proportions of responses were compared using the G-test of independence (df = 1)

Table 2.4 Multifunctional gestures that failed categorisation due to a lack of predominant responses in a particular category

Code	Gesture	Affiliative response (%)	Agonistic response (%)	Play response (%)	Dominance-subordination response (%)	Sexual response (%)	Neutral response (%)	n
MO	Mounting	38.46	7.69	7.69	15.38	0	30.77	13
PR	Presenting	1.01	2.02	0	38.38	32.32	26.26	99
PT	Pulling any Part of the Body	17.48	30.77	25.17	1.40	0.7	24.48	141
PU	Pushing	14.89	34.04	17.02	2.13	0	31.91	47
PN	Pinching	0	44.44	33.33	0	0	22.22	9
ST	Staring	0	23.08	3.85	15.38	0	57.69	15
RB	Raising Eyebrows	25	25	0	0	0	50	8
CS	Copulatory Lip-Smacking	22.73	36.36	0	9.09	4.55	27.27	22

It may be reiterated here that the persistent display of the same or other gestures on failure to elicit a response from the recipient in the first attempt and a significantly higher proportion of an eventual appropriate response indicate an intended goal behind the display of a gesture by the signaller. I investigated a particular gesture, Soliciting Allogrooming (SG), as a case study to illustrate the intentionality behind gestures displayed by bonnet macaques.

A noteworthy aspect of this gesture was that it had the potential of being self-referential in nature, thus enabling the signaller to refer to a particular body part, where it apparently intended to be groomed.

2.3.4 *Intentional referential gestures in bonnet macaques? A case study*

My study individuals used four distinct acts when they displayed the Soliciting Allogrooming gesture; these included Changing Position, Extending Head/Body, Showing Rear, and Holding Body Part (Table 2.5); all of these gesture acts allowed the individuals being groomed (groomees) to offer another part of their body to the groomer, different from the part being groomed earlier. A total of 328 such events of gesturing were recorded from the study troops. Of these events, 242 (73.78%) were exhibited by 23 of the 29 adult females (79.31%) and 86 (26.22%) by 16 of the 23 adult males (69.57%) during a total of 24.68 allogrooming-hours, consisting of 874 initiated grooming events.

In response to any of the four gesture types displayed by a particular groomee, the groomer immediately changed the original location of grooming and initiated this activity in the newly offered area or body part. These positive responses occurred following 308 of the 328 (93.90%) observed gestures. This was significantly greater than would be expected by chance, assuming that the groomer had an equal probability of changing or not changing the initial location of grooming, following the display of a gesture (G-test of independence, df = 1, G = 294.71, $p < 0.001$).

2.3.4.1 *Were these particular gestures referential?*

It is conceivable that these gestures may not have been indicative but could have occurred simply as a result of a change in the body posture of the groomee to a more comfortable position. This could also entail the groomer initiating allogrooming in a particular location in the groomee's body that was now closest to it. What was instructive, however, is that the grooming individual actually chose to groom only that particular part of the body that was referred to by the groomee. The success of such referential communication could also be gauged by the observation that the majority of these gestures elicited an immediate response. Moreover, evidence that these gestures could strongly influence the behavioural decisions of individuals came from three unique responses displayed by particular groomers, when the individuals being groomed had exhibited one of these gestures.

In the first instance, an adult female, ZG, of Troop HN2 was being groomed on her right shoulder by another adult female, KK, sitting next to her. When ZG performed a Head Extension gesture by tilting her head at a specific angle to the right, thus prominently displaying the left side of her neck, KK immediately extended both her arms across the groomee's body to allogroom the offered part of the neck, a rather distant and difficult part of the body for her to reach.

The second case involved an adult female, HC, in Troop C3, who held her tail out to a subadult male, MM, grooming her on her back; she thus displayed a Holding Body Part gesture. MM immediately stopped his grooming at the initial location and responded by initiating a fresh bout of grooming on the HC's tail.

In the third such instance, ZG of Troop HN2 exhibited a Showing Rear gesture, followed by a Holding Body Part, in which she held her right rump with her right hand in front of the alpha male, RS, who was grooming her on her upper back. RS removed ZG's hand from her rump and immediately started allogrooming her in that specific spot.

2.3.4.2 *Were these gestures intentionally produced?*

While the referential nature of the gestures used during allogrooming by the macaques could be inferred from the immediate positive responses shown by the groomers, the possible intentionality underlying these gestures could only be unravelled by monitoring the negative responses if any, to these gestures. In order to achieve any intended goal through the use of a gesture, the signaller should actively attempt to change the receiver's behaviour by repeatedly displaying the same or a related gesture, until the appropriate response is elicited. In our study, the groomee continued to actively solicit allogrooming from the same individual, on two different occasions, in spite of receiving a negative response to its initial solicitation.

In the first case, an adult female HS of Troop HN2 repeated the same gesture (Showing Rear) to RS, the alpha male of the troop, while, in the second instance, ZG of the same troop first solicited grooming from RS by displaying a Showing Rear gesture, followed by that of Extending Head, when the first gestural act failed to elicit a positive response. In both instances, the persistent gesturing ultimately led to successful allogrooming of the offered body parts and the groomees did not produce further gestures; this suggested that the solicitation of grooming at specific locations of the body may have been the intention of the gesturing individuals in the first place. The demonstrated use of multiple gestures by individual macaques to achieve the same goal thus testified to their capacity of means-end dissociation (Tomasello et al. 1994). Persistence and flexibility being the hallmarks of intentionality, the four referential gestures used by bonnet macaques in the context of allogrooming, thus, also appeared to be intentional in nature.

2.3.4.3 *Potentially referential gesturing: A general capacity in bonnet macaques*

In my study, approximately 6.78% (23 of the 339 events) of the total observed gestures received a negative response from the groomers, characterised by a cessation of grooming. In 21 of these 23 negative responses, the groomer ignored (by not responding in any way), avoided (by turning its body and looking away) or physically moved away from the groomee. What is noteworthy, however, is that in two instances, the groomee continued to actively solicit allogrooming from the same individual, ultimately eliciting grooming from the groomer.

The mean frequency of referential gesturing displayed per received allogrooming-hour by the 29 adult females (mean ± SE, 14.96 ± 2.76 events/h) was not significantly different from that by the 23 adult males (13.67 ± 3.85 events/h; Mann-Whitney U-test, two-tailed, U = 282, $p > 0.30$). The gestures Changing Position, Extending Head/Body and Holding Body Part were comparably displayed by both adult females and males, but the males exhibited a significantly higher frequency of Showing Rear ($p < 0.03$; Table 2.5).

Within each of the four study troops, the frequency of referential gestures displayed by the adult females and males did not correlate with their ranks in the dominancy hierarchy (Troop TT1: Females, Spearman's rho = -0.28, n = 7, $p > 0.50$; Males, Spearman's rho = -0.25, n = 7, $p > 0.50$; Troop TT2: Females: Spearman's rho = 0.27, n = 6, $p > 0.20$; Troop HN2: Females, Spearman's rho = -0.10, n = 8, $p > 0.80$; Males, Spearman's rho = 0.41, n = 5, $p > 0.40$; Troop C3: Females, Spearman's rho = 0.16, n = 8, $p > 0.60$; Males, Spearman's rho = 0.52, n = 10, $p > 0.10$; Figure 2.4) or their age classes (Females, Spearman's rho = -0.09, n = 23, $p > 0.60$; Males, Spearman's rho = 0.09, n = 23, $p > 0.60$; Figure 2.5).

An analysis of inter-troop variability in referential gesturing, however, indicated that the adult females of the unimale-multifemale Troop TT2 displayed significantly lower frequencies of gesturing per received allogrooming-hour (1.54 ± 0.98 events/h, n = 6) than those of the three multimale-multifemale troops (Troop HN2: 19.87 ± 5.70, n = 8; Mann-Whitney U-test, two-tailed, U = 4, $p < 0.01$; Troop C3: 25.26 ± 5.16, n = 8; U = 0, $p < 0.005$; Troop TT1: 9.08 ± 3.36, n = 7; U = 6, $p < 0.05$). An examination of a possible relationship between the observed frequencies of displayed gesturing and the levels of allogrooming received by these subjects revealed Troop TT2 females to have received higher frequencies of allogrooming from the other members of the troop (0.82 ± 0.11 events/h), as compared to that received by the females of two of the three multimale troops (Troop HN2: 0.40 ± 0.07, n = 8; U = 3, $p < 0.01$; Troop C3: 0.84 ± 0.13, n = 8; U = 24, $p > 0.90$; Troop TT1: 0.46 ± 0.07, n = 7; U = 7, $p < 0.01$).

Table 2.5 Types and frequencies of referential gestures displayed by adult bonnet macaques of the study troops during allogrooming

Referential gesture	Description	Frequency displayed by adult females (Mean ± SE)	Frequency displayed by adult males (Mean ± SE)	Comparison of frequencies displayed by adult females and males
Changing Position	Change of body orientation while being groomed	12.61 ± 2.29	14.10 ± 3.11	U = 315.5 $p > 0.70$
Extending Head/Body	Extending head, body or limbs towards the groomer while being groomed	1.92 ± 0.66	1.04 ± 0.44	U = 281 $p > 0.30$
Showing Rear	Stooping down in front of the groomer and displaying the rear	3.98 ± 1.21	4.40 ± 2.91	U = 226 $p < 0.03$
Holding Body Part	Holding a particular part of the body in front of the groomer	0.81 ± 0.55	0.62 ± 0.52	U = 327 $p > 0.80$

The frequencies of the different types of referential gestures displayed by females and males were compared using two-tailed Mann-Whitney U-tests (n = 29 females and 23 males)

Amongst the three multimale troops, only the females of Troop C3 exhibited higher frequencies of gesturing and also received higher frequencies of allogrooming than did those of Troop TT1 (referential gestures: U = 6, $p < 0.01$; allogrooming frequency: U = 10, $p < 0.05$). A similar comparison of the adult males of the three multimale troops (the single male of the Troop TT2 being excluded from the analysis), however, failed to reveal any significant difference in their frequencies of referential gesturing during the study

(Troop HN2 vs Troop C3: $n = 5, 10$; $U = 14$, $p > 0.2$; Troop HN2 vs Troop TT1: $n = 5, 7$; $U = 15$, $p > 0.70$; Troop TT1 vs Troop C3: $n = 7, 10$; $U = 16$, $p > 0.05$).

There was considerable individual variation, both among females and males, in the frequency with which they displayed referential gestures, with some individuals not exhibiting any of these gestures during the study period (see Figure 2.5). Again, could an explanation of this variation lie in the frequency with which they received allogrooming from the other troop members?

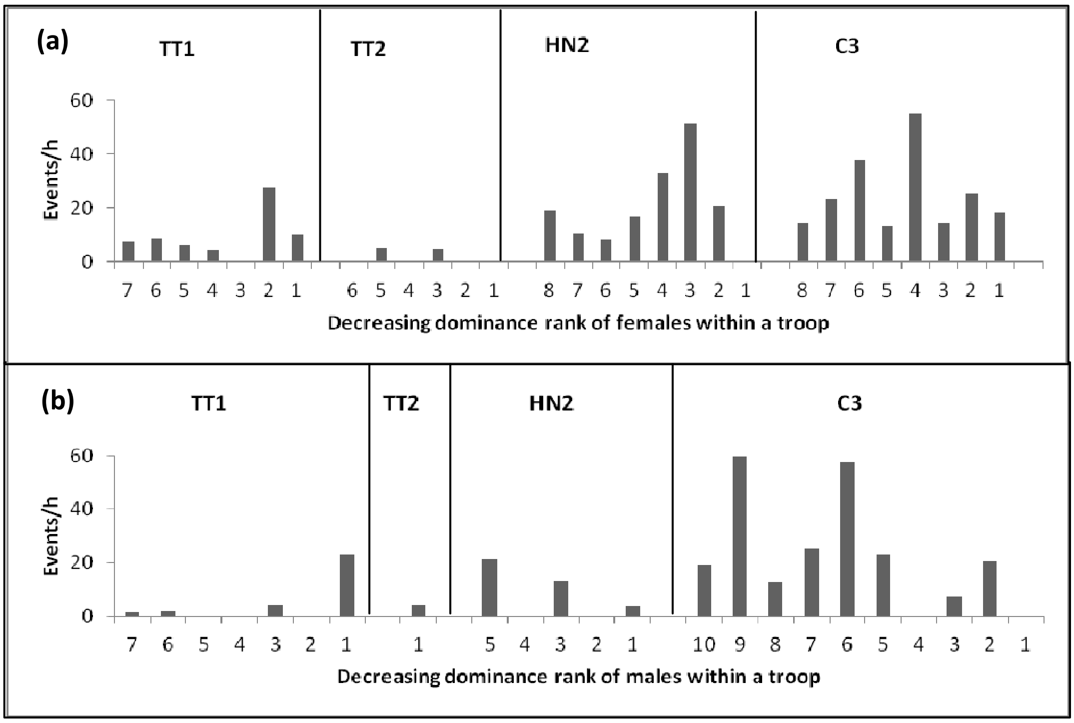

Figure 2.4 The relationship between the frequencies of referential gestures displayed by (a) adult females and (b) adult males and their respective dominance ranks within each of the four study troops, TT1, TT2, HN2 and C3

There was, in fact, a significant positive correlation between the frequency of referential gestures displayed by the males and the frequency with which they received initiated allogrooming (Spearman's rho = 0.65, $p < 0.001$). This relationship between referential gestures and the extent of grooming received was strengthened by my observation that the males, which exhibited referential gestures, received a significantly higher frequency of initiated allogrooming than those who did not (Mann-Whitney U-test, two-tailed, n = 16, 7; U = 20, $p < 0.02$). The study females, taken together, did not, however, display any such relationship between their grooming patterns and referential gesturing.

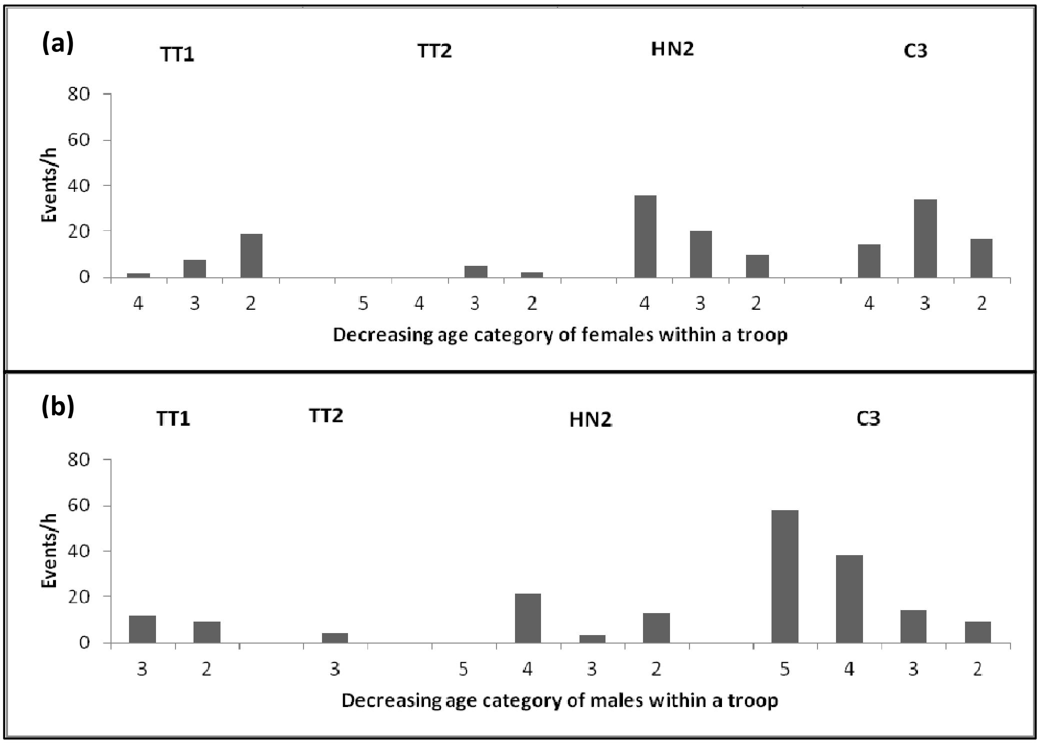

Figure 2.5. The relationship between the frequencies of referential gestures displayed by (a) adult females and (b) adult males and their respective age classes within each of the four study troops, TT1, TT2, HN2 and C3

2.4 Discussion

Bonnet macaques displayed a repertoire of 24 unique gestures, using visual and tactile modalities in the contexts of affiliation, agonism and play. Moreover, eight other gestures, the contexts of which could not be determined, also featured in the gestural repertoire of this species. All these 32 gestures fulfil the standard criteria of gestures as defined in extant primate communication literature (see Call and Tomasello 2007; Genty et al. 2009, Hobaiter and Byrne 2011a). Usually, in primate gestures, there is an additional category of auditory gestures that has been reported (Tomasello et al. 1994; Pika et al. 2003; Liebal et al. 2006; Call and Tomasello 2007; Genty et al. 2009, Hobaiter and Byrne 2011a). This category was, however, difficult to define in my study species, as the sound produced in some of these gestures was more a by-product of the actual behaviour displayed and did not appear to function as an auditory signal. For instance, gestures such as Lip-Smacking, Hugging with Lip-Smacking, Patting, Lunging, Slapping, Lunging in Play, and Slapping in Play often produced a sound in contact with other individuals or the substratum on which the behaviours were displayed (see also Hobaiter and Byrne 2011a).

There were other gesture-like behaviours, which occurred in sequences and evoked responses but it was not possible to determine the correspondence between these responses and the constituent behaviours in each sequence. These behaviours, therefore, could not be considered as single gestures in accordance with the strict definitional criteria that I have followed. These sequences, nevertheless, were crucial to understand the complete gestural repertoire of the species, which has never been reported previously, and have been analysed independently in Chapter 5 of this thesis. It should be noted that such gestural sequences have also been recorded earlier in apes and independently analysed as well (Tomasello et al. 1994; Liebal et al. 2004; Call and Tomasello 2007; Genty 2009; Genty and Byrne 2010; Hobaiter and Byrne 2011a, b).

2.4.1 *Responses and contexts*

The three gestures, Biting Hard, Spot-Jumping and Hugging with Lip-Smacking, which always received responses in the same contexts, revealed their functions unambiguously as agonistic, play and affiliative, respectively. The contexts of the other 21 gestures were similarly determined, but by the significantly higher proportions of responses elicited in particular contexts. The predominant response type indicated particular communicative functions of these gestures, similar to those observed in orangutan gestures, where typical gestures were associated with their contexts, representing the semantics of the signal (Cartmill and Byrne 2007). The responses evoked in other contexts could probably be attributed to the motivational states of particular recipients, preceding interactions previous to the observations, developmental factors and even the social history of the participants of the communicative events.

2.4.2 *Multifunctional gestures*

The functions of the additional eight gestures remain undecided owing to the absence of predominant response types. These gestures were indeed targetted to jointly attentive recipients and used intentionally, as evident from the persistent gesturing displayed by the sender. Mounting, for instance, elicited the highest percentage of affiliative responses but this was not significantly different from those elicited in the other contexts. It is possible that these gestures with undecided functions were more often used in association with other gestures, a hypothesis not tested in the present analysis. Additionally, these gestures could potentially be of an inherently flexible nature, thus making them ubiquitously applicable across contexts, as has been observed in apes (Tomasello et al. 1994, 1997; Tomasello and Call 2007; Genty et al. 2009; Hobaiter and Byrne 2011a).

It has been provocatively suggested that certain behaviours may be in the process of becoming established as ritualised signals in particular contexts (Daanje 1950; Tinbergen 1952; Morris 1957; Lorenz 1966; Zahavi 1980) and the function of such ritualisation being decreasing ambiguity over time in the history of a species (Cullen 1966). Is it then possible that these apparently multifunctional gestures have not yet assumed definitive roles but would become ritualised between the sender and the receiver by mutual understanding over evolutionary timescales in order to serve a certain function in particular contexts.

2.4.3 *Intentional use of gestures*

Bonnet macaques intentionally used gestures; this was evident when they persistently displayed the same gesture or other gestures on failure to elicit a response from the recipient in the first attempt, even though a joint-attention state prevailed between the sender and the recipient. A significantly higher proportion of such persistent gesturing ultimately evoked appropriate responses from the recipient, indicating a goal-oriented behaviour of the sender in the first place (see Tomasello and Call 2007). Occasionally, when neutral responses were elicited, however, it was not possible to understand the intentionality behind those particular gesturing events. In the present study, I have explored only awaiting a response and persistence behaviour as markers of intentionality underlying bonnet macaque gestures. There, thus, remains an extensive scope of investigating other criteria of intentionality, such as gaze alternation and adjustments made in response to the audience's attention state, in bonnet macaques, in order to evaluate and determine the various levels of intentionality underlying gestural communication in this species.

2.4.4 *Intentional referential gestures in bonnet macaques? A case study*

The four gestural acts, constituting the gesture of Soliciting Allogrooming in adult bonnet macaques—Changing Position, Extending Head/Body, Showing Rear and Holding Body Part—were used to display a particular part or area of the body that an individual probably sought grooming in and moreover, this was appropriately responded to by the groomer, always in the form of grooming behaviour. In the lack of an elicited grooming following any of these gestures, the persistence behaviour from the sender in two cases suggests there might be an underlying goal of the sender in the form of being groomed in the displayed body area. If such conditions are indeed met, these four gestures displayed by bonnet macaques qualify as referential gestures used intentionally in the context of grooming. Unlike the reports of referential gesturing by fish (Vail et al. 2013) and ravens (Pika and Bugnyar 2011) and referential calls by monkeys and chimpanzees (Cheney and Seyfarth 1990; Zuberbühler 2000; Cheney and Seyfarth 2007; Schel et al. 2013), wherein the referred entity were independent objects, these gestures by bonnet macaques appeared to exemplify self-referentiality, as has earlier observed in chimpanzees (Pika and Mitani 2006).

In the three individual case histories in which the groomers displayed rather specific responses to the potentially referential gestures shown by the groomees, it was evident that the grooming individual did not necessarily allogroom another individual on the most proximal and accessible locations of the body but chose to initiate a fresh bout of this activity on an area or part of the body that was referred to by the groomee by different indicative gestures. Moreover, the almost immediate response of the groomers in choosing to allogroom the body part being indicated suggested that they were able to comprehend and appropriately react to a referential gesture. Bonnet macaques, therefore, appear to be capable of referring to an external entity, here, a body part, thus drawing the attention of another individual to that entity and effectively altering the subsequent behaviour of the latter.

There, nevertheless, remain other possible explanations for the observed behaviour in bonnet macaques, including, for example, local enhancement (Thorpe 1956), according to which the extended body part or area simply acted as an additional stimulus for the groomer to start grooming in the new area. Under such considerations, the possible referential nature of the gestures, as postulated here, loses merit. Moreover, it is also possible that each allogrooming pair, for instance ZG and KK in the example provided, had ritualised the grooming pattern with effect to any change in body orientation such that the groomer began to groom the newly available area, suggesting non-referential gesturing on the groomee's part. My strong suggestions of intentionality underlying these particular bonnet macaque gestures, thus, remain to be robustly established, as also the persistent gesturing following an initial negative response was observed only in two instances. This part of the study, thus, opens up immense opportunity to explore the possible referential nature of certain gestures that are stably incorporated into the gestural repertoire of bonnet macaques. One possible way to test for referentiality of these gestures would be to conduct controlled naturalistic observations of the responses displayed by groomers to acts of autogrooming by the groomees. If, during an allogrooming act, for example, if the groomer changes its site of grooming following autogrooming by the groomee at that particular site, it would testify to this decision being driven by local enhancement rather than referentiality on the part of the groomee.

If indeed referential, the observed acts of gesturing appeared to be a general capacity of adult bonnet macaques, not influenced by either the social rank of individuals or their age-related experience. It thus seems possible that the frequency with which bonnet macaques displayed referential gesturing was driven, at least to a certain extent, by the frequency of allogrooming received by individuals, with the greater allogrooming received providing increased opportunities for such gesturing. While this was clearly evident in the case of the adult males, a similar relationship could be discerned only amongst the females of the two multimale troops that displayed a significant difference in their levels of gesturing. The contrasting relationship between gesturing and allogrooming displayed by the females of the unimale Troop TT2, however, may present a case of striking individual variation, which needs further investigation. It could lie in possible differences in the quality of allogrooming, of other social interactions or in individual behavioural patterns that may distinguish the unimale troops of bonnet macaques from those of the multimale troops, as has earlier been documented for the males in these two social organisations (Sinha et al. 2005). The marked individual variation in the frequency of referential gesturing observed across both sexes in all the troops could potentially reflect individual behavioural traits, driven by personality or other innate factors. Moreover, differences in such gesturing between troops could conceivably emerge from social behavioural traditions, as has been documented earlier for allogrooming patterns in the same population (Sinha 2005).

In conclusion, this report is possibly the first of its kind to document potential intentional referential gestural communication in any wild monkey. It appears from this study that wild bonnet macaques perhaps gesture to refer to particular body areas where they intend to be allogroomed, which elicits appropriate responses from their target groomers. These gestures were also possibly intentionally produced, as an absence of a response from the groomer induced either persistent gesturing or, rarely, the use of multiple gestures by the signaller, thus suggesting a goal-directed behaviour, wherein means could be dissociated from the end. Although these were not triadic referential signals as the signaller drew the receiver's attention to a part of themselves, a particular body part in this case, it surely illustrates a particular manifestation of mental state attribution in macaques, a phenomenon characteristic of higher levels of cognitive capacity (reviewed in Pika 2012; see also Sinha 2003, 2014). Such capacity of referential gesturing in intentional communication is quite rare in the animal world, only observed so far in chimpanzees (Leavens et al. 1996; Pika and Mitani 2006), bonobos (Genty and Zuberbühler 2014), Tonkean macaques (Canteloup et al. 2015), fish (Vail et al. 2013), ravens (Pika and Bygnyar 2011), dolphins (Xitco et al. 2004) and domestic horses (Wathan and McComb 2014). The ability to communicate intentionally while indicating external referents has been suggested to underlie the symbolic nature of human language, which apparently ontogenetically begins through gestures in pre-linguistic children (Werner and Kaplan 1972; Camaioni 1997). If future studies could systematically establish the suggested nature of intentional referentiality in these macaque gestures, a crucial link would be added to the already existing scholarship that enables us to strengthen our comparative understanding of language evolution.

A next step of investigation would also be to understand whether bonnet macaques use different types of gestural modalities, visual or tactile, depending on the receivers' attention state, as has been demonstrated in apes (Call and Tomasello 2007; Hobaiter and Byrne 2011a). It was not possible, during the present study, to record the preceding attention state of the receiver, as it was conducted on fairly large, open spaces in the wild, where the study subjects moved over long distances. It was, thus, impossible to video-record every movement, which could have revealed the attention state of the receivers during the initiation of gestural communication. Complementary studies, preferably in captivity, could address such issues, thus further clarifying the level of intentionality underlying the gestural system of this species.

Bonnet macaques, thus, have a gestural repertoire comprising a total of 32 gestures, which they use flexibly and intentionally across contexts of affiliation, agonism and play. The use of these gestures by different age-sex classes of the study troops, provide further insights into the functioning and development of this communication system in the species and will be addressed in the subsequent chapters.

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Appendix 2.1

Ethogram of individual and initiated social behaviours displayed by bonnet macaques in the study troops

Individual behaviours

Serial Number	**Behaviour**	**Codes**	**Notes**
1	Alarm Calling	AC	
2	Cough-Like Calling	IC	Only produced by infants
3	Movement-Calling	MC	
4	Lost-Calling	LO	
5	Feeding on Naturally Available Food	FE	
6	Feeding on Provisioned Food	FR	
7	Foraging on Naturally Available Food	FO	
8	Foraging on Provisioned Food	FP	
9	Autogrooming	GR	
10	Bipedal Watching	BW	
11	Coughing	CI	
12	Looking	LK	
13	Lying Down	LD	
14	Moving	MV	
15	Playing	PY	
16	Resting	RS	
17	Sitting	SN	
18	Sitting Alertly	SA	
19	Sneezing	SZ	
20	Urinating	UR	
21	Tooth-Picking	TP	
22	Regurgitating with Subsequent Ingestion	VM	
23	Watching Out for Other Troops	WT	

24	Yawning	YW	
25	Sleeping	ZZ	
26	Shaking Branches	SB	
27	Tasting Own Oestrous Material	TE	
28	Rubbing Genitals with Hands	RG	
29	Eating Own Ejaculate	EJ	
30	Missing from the Troop	XX	

Initiated social behaviours

Serial Number	**Behaviour**	**Codes**	**Notes**
Affiliative behaviours			
1	Allogrooming	AG	
2	Allogrooming with Lip-Smacking	AS	
3	Biting Gently	BG	
4	Biting Another Individual's Infant	BI	
5	Pulling Close to Oneself	CB	
6	Approaching, Followed by an Affiliative Interaction	CM	
7	Cheek-Touching	CT	
8	Raising Eyebrows at Another Individual's Infant	EN	
9	Following	FW	
10	Fur-Stroking	FT	
11	Greeting-Grunting	GG	
12	Affiliative-Grunting	GU	
13	Allogrooming Another Individual's Infant	GI	
14	Grappling	GP	
15	Huddling	HE	
16	Handling Another Individual's Infant	HI	

17	Handling Another Individual's Infant with Lip-Smacking	HL	
18	Holding any Part of the Body Gently	HO	
19	Hugging with Lip-Smacking	HS	
20	Hugging without Lip-Smacking	HU	
21	Hugging Another Individual's Infant	UI	
22	Jumping on Another Individual's Back	JB	Only produced by infants and juveniles; sometimes used in the context of play
23	Licking	LI	
24	Lip-Smacking	LS	
25	Mouth-to-Body Touching	MB	
26	Mouth-Sniffing	MF	
27	Mouth-to-Mouth Touching	MT	
28	Nibbling	NB	
29	Nuzzling	NZ	
30	Nuzzling Another Individual's Infant	NI	
31	Smelling / Sniffing	SO	
32	Smelling Another Individual's Infant	OI	
33	Patting	PA	
34	Pulling Another Individual's Infant	PI	
35	Raising Eyebrows	RB	
36	Soliciting Allogrooming with Positive Response	SG	
37	Soliciting Grooming with Negative Response	SR	
38	Touching	TO	
Agonistic behaviours			
1	Aggressive Screaming	AM	
2	Approaching, Followed by an Aggressive Interaction	AP	
3	Biting Hard	BH	
4	Displaying a Bared-Teeth Threat	BT	

5	Chasing	CH	
6	Eye-Flashing	EF	
7	Fleeing	FL	
8	Fear-Screaming	FS	
9	Fear-Grimacing	GM	
10	Ground-Slapping	GS	
11	Threat-Growling	GT	
12	Holding Down Roughly	HD	
13	Head-Jerking	HJ	
14	Head-Jerking at Another Individual's Infant	JI	
15	Lunging	LU	
16	Leaping Away from Another Individual	LW	
17	Displaying an Open-Mouth Threat	OT	
18	Punishing Own Infant with Head-Jerks and Bite	PH	
19	Punishing Own Infant with Head-Jerks and Slap	PP	
20	Pinching	PN	
21	Pushing Away	PU	
22	Pushing Away Another Individual's Infant	EI	
23	Pulling Another Individual's Body or any Part of it Roughly	PT	
24	Rushing at Another Individual Aggressively	RA	
25	Screeching	SE	Usually produced by infants
26	Slapping	SL	
27	Slapping Another Individual's Infant	SI	
28	Spot-Jumping	SJ	Also produced in the context of play
29	Soliciting Agonistic Support with Positive Response	SS	
30	Soliciting Agonistic Support with	SU	

	Negative Response		
31	Staring	ST	
32	Wagging Tail	WT	
33	Showing Aggression to Humans	AH	
Dominance-subordination behaviours			
1	Approaching with the Other Retreating	AR	
2	Genital Fondling	GF	Also produced in the context of affiliation
3	Mounting	MO	
4	Mounting with Lip-Smacking	MS	
5	Presenting with Positive Response	PR	
6	Presenting with Negative Response	PG	
7	Presenting with Lip-Smacking, with Positive Response	PM	
8	Presenting with Lip-Smacking, with Negative Response	PX	
9	Retreating	RE	
Sexual behaviour			
1	Copulating with Ejaculation	CJ	
2	Copulating without Ejaculation	CO	
3	Copulating with Lip-Smacking with Ejaculation	CE	
4	Copulating with Lip-Smacking without Ejaculation	CK	
5	Copulatory Lip-Smacking	CS	
6	Saw-Like Vocalisation During the Last Phase of Copulation or After Copulation	CV	
7	Gazing	GZ	
8	Herding	HE	
9	Inspecting by Tasting Oestrous Material	IE	Also produced in the context of dominance-subordination

10	Inspecting by Smelling	IO	Also produced in the context of dominance-subordination
11	Inspecting Visually	IS	Also produced in the context of dominance-subordination
12	Inspecting by Touching	IT	Also produced in the context of dominance-subordination
13	Copulatory-Bobbing Laterally	LB	
14	Copulatory-Bobbing Vertically	UB	
15	Consorting	SX	
Play behaviours			
1	Biting in Play	PB	
2	Chasing in Play	PC	
3	Retreating in Play	PE	
4	Lunging in Play	PL	
5	Displaying an Open-Mouth Threat in Play	PO	
6	Slapping in Play	PS	
7	Wrestling in Play	PW	
8	Rushing at Another Individual in Play	RP	
9	Leaping Away from Another Individual in Play	LY	
Neutral behaviours			
1	Avoiding	AV	
2	Moving Away	MA	
3	Ignoring	IG	
4	Coo-Calling	CC	
5	Lifting Arms to Free Nipples	LF	Only infants produced this behaviour towards their respective mothers

6	Nipple-Fondling	NF	Only infants produced this behaviour towards their respective mothers
7	Suckling	SK	Only infants produced this behaviour towards their respective mothers
8	Observing Intently	OB	
9	Sleeping Together	SP	
10	Sitting in Contact or within Half-Metre	SW	
11	Retreating from Another Individual's Infant	RI	
12	Touching Nipples	TN	Only infants produced this behaviour towards their respective mothers
Total number of behaviours = 116			

Appendix 2.2

Ethogram of responses elicited by gestures displayed by bonnet macaques in the study troops

Serial Number	**Behaviour**	**Codes**	**Notes**
Affiliative responses			
1	Allogrooming	AG	
2	Allogrooming with Lip-Smacking	AS	
3	Biting Gently	BG	
4	Biting Another Individual's Infant	BI	
5	Pulling Close to Oneself	CB	
6	Approaching, Followed by an Affiliative Interaction	CM	
7	Raising Eyebrows at Another Individual's Infant	EN	
8	Following	FW	
9	Greeting-Grunting	GG	
10	Affiliative-Grunting	GU	
11	Allogrooming Another Individual's Infant	GI	
12	Huddling	HE	
13	Handling Another Individual's Infant	HI	
14	Holding any Part of the Body Gently	HO	
15	Hugging with Lip-Smacking	HS	
16	Hugging without Lip-Smacking	HU	
17	Hugging Another Individual's Infant	UI	

18	Jumping on Another Individual's Back	JB	Only produced by infants and juveniles; sometimes used in the context of play
19	Licking	LI	
20	Lip-Smacking	LS	
21	Mouth-to-Body Touching	MB	
22	Mouth-Sniffing	MF	
23	Mouth-to-Mouth Touching	MT	
24	Nibbling	NB	
25	Nuzzling	NZ	
26	Nuzzling Another Individual's Infant	NI	
27	Smelling / Sniffing	SO	
28	Smelling Another Individual's Infant	OI	
29	Patting	PA	
30	Pulling Another Individual's Infant	PI	
31	Soliciting Allogrooming with Positive Response	SG	
32	Touching	TO	
Agonistic responses			
1	Aggressive Screaming	AM	
2	Approaching, Followed by an Aggressive Interaction	AP	
3	Biting Hard	BH	
4	Displaying a Bared-Teeth Threat	BT	
5	Chasing	CH	
6	Eye-Flashing	EF	
7	Fleeing	FL	
8	Fear-Screaming	FS	
9	Fear-Grimacing	GM	
10	Ground-Slapping	GS	

11	Threat-Growling	GT	
12	Holding Down Roughly	HD	
13	Head-Jerking	HJ	
14	Head-Jerking at Another Individual's Infant	JI	
15	Lunging	LU	
16	Leaping Away from Another Individual	LW	
17	Displaying an Open-Mouth Threat	OT	
18	Pinching	PN	
19	Pushing Away	PU	
20	Pulling Another Individual's Body or any Part of it Roughly	PT	
21	Rushing at Another Individual Aggressively	RA	
22	Screeching	SE	Usually produced by infants
23	Slapping	SL	
24	Slapping Another Individual's Infant	SI	
25	Spot-Jumping	SJ	Also produced in the context of play
26	Staring	ST	
Dominance-subordination responses			
1	Genital Fondling	GF	Also produced in the context of affiliation
2	Mounting	MO	
3	Mounting with Lip-Smacking	MS	
4	Presenting with Positive Response	PR	
5	Presenting with Negative Response	PG	
6	Retreating	RE	

Sexual responses			
1	Copulating with Ejaculation	CJ	
2	Copulating without Ejaculation	CO	
3	Copulating with Lip-Smacking with Ejaculation	CE	
4	Copulatory Lip-Smacking	CS	
5	Gazing	GZ	
6	Inspecting by Tasting Oestrous Material	IE	Also produced in the context of dominance-subordination
7	Inspecting by Smelling	IO	Also produced in the context of dominance-subordination
8	Inspecting Visually	IS	Also produced in the context of dominance-subordination
9	Inspecting by Touching	IT	Also produced in the context of dominance-subordination
Play responses			
1	Biting in Play	PB	
2	Chasing in Play	PC	
3	Retreating in Play	PE	
4	Lunging in Play	PL	
5	Displaying an Open-Mouth Threat in Play	PO	
6	Slapping in Play	PS	
7	Wrestling in Play	PW	
8	Leaping Away from Another Individual in Play	LY	
Neutral responses			
1	Avoiding	AV	
2	Moving Away	MA	
3	Ignoring	IG	

4	Suckling	SK	Only infants produced this behaviour towards their respective mothers
5	Observing Intently	OB	
6	Sleeping Together	SP	
7	Sitting in Contact or within Half-Metre	SW	
8	Lying Down	LD	
9	Retreating from Another Individual's Infant	RI	
10	No Response	NR	
Total number of responses = 91			

Chapter 3

The Gestural Repertoire Size of Bonnet Macaques:

Differences between Age- and Sex Classes, and Flexibility in the Use of Gestures

3.1 Introduction

The communication repertoire of a species is usually defined by the compilation of signals shown by individuals of different age classes (Pika et al. 2003; Hesler and Fischer 2007; Liebal 2007a, b; Pika 2007; Genty et al. 2009; Hobaiter and Byrne 2011). Most of these studies have concentrated on comparing juvenile and infant gestures to those of adults in order to understand differences between repertoire structure and use between age classes. Such an exercise is, of course, crucial for the understanding of the underlying developmental processes that ultimately give rise to the species-specific gestural communication system. As a result of such endeavours, we have also gathered insights into the evolution of human and nonhuman primate gestural communication, especially in the light of human language development (reviewed in Tomasello and Zuberbühler 2002, Tomasello and Call 2007).

Longitudinal studies, such as the pioneering one by Tomasello et al. (1994) that explored gestures of young chimpanzees across generations, illustrate the importance of comparative analyses of gesture structure and function across individuals of different age classes in the elucidation of characteristic features of primate gestural communication, including intentionality, flexibility and ritualised learning processes. Differences in the repertoire and use of gestures among young individuals and with those of adults may be attributed to developmental processes such as social learning or ontogenetic ritualisation, as in the case of chimpanzees (Tomasello et al. 1994; Call and Tomasello 2007a, b), in which the species-typical repertoire is distributed among individuals spanning different age classes. It has also been suggested that the entire gestural repertoire could potentially be present at birth but the proper usage of particular gestures is learnt over time, as proposed by the gradual-learning model for vocalisations in vervet monkeys (Seyfarth and Cheney 1997; Pika et al. 2003). Irrespective of the exact mechanisms that lead to age-based differences in gestural repertoire and use, it is evident that such comparative studies do reveal the resemblances in developmental processes that underlie primate gestures and human language, thus providing insights into the evolutionary continuity of communication systems in the primate lineage.

Apart from age differences being an important consideration, it is also necessary to investigate the gestural repertoire of different individuals in the same age cohort, both within and across the two sexes. Once individuals in a primate society attain adulthood, they acquire specific rank positions in the social dominance hierarchy, which may, in turn, influence their gestural repertoires, depending on the variable social experiences that they have undergone. The two sexes of the same species may have evolved under different biological and social selection pressures, and this could have potentially shaped their communication systems differently. Indeed, such sexual differences have been reported for olfactory communication (Heymann 1998), vocal communication (Cheney and Seyfarth 1990; Locke and Hauser 1999; Tomaszycki et al. 2001; Greeno and Semple 2009; Bouchet et al. 2010) as well as gestural communication (Hopkins and Leavens 1998; Hesler and Fischer 2007; Liebal 2007a, b; Slater et el. 2009; Hobaiter and Byrne 2012). A recent study on chimpanzee gestural communication by Scott (2013), for example, has systematically addressed questions regarding sex differences in gestures used during intra-sex and inter-sex communication, possibly for the first time. The structure and organisation of each primate society and the resulting roles of females and males therein may lead to distinct life-histories, which may eventually reflect their communication modalities and patterns. Thus, it becomes crucial to understand differences in adult communication structure and function in order to trace the evolutionary history of the sexes that have evolved in different primate social regimes.

Although attempts have been made to understand age- and sex-based differences in gestural communication in several primate species (Pika et al. 2003; Liebal 2007a, b; Pika 2007; Genty et al. 2009; Hobaiter and Byrne 2011), systematic efforts in this regard are almost non-existent in macaques (but see Maestripieri 1996, 1997, 2005 and Hesler and Fischer 2007). Macaque gestures, in general, have been less studied and there are virtually no detailed investigations of the influence of biological and social factors such as age, sex, and the social positions of individuals in this evolutionarily successful primate taxon.

Bonnet macaque societies offer an excellent opportunity to understand such biological and social influences on the social behaviour of the species, especially the prevailing communication structure. Like most macaques, the female social rank hierarchy of bonnet macaques hardly intersects with that of the males and there exist different mechanisms for the establishment of dominance hierarchies across the two sexes (Sinha 2005). The females are often closely related kin and the female rank hierarchy is matrilineal with high-ranking matrilines often retaining their dominant positions throughout their lives (Sinha 2001). Male dominance relationships, however, are usually individual-based, with physical abilities and occasionally male associations, coalitions and alliances contribution to individual rank positions, sometimes irrespective of kinship.

The relationship of infant and juvenile bonnet macaques to adult females is also distinct from that with males. Infants, until weaned, usually get more opportunities to interact with the females of the troop, other than their mothers, due to the close female association that characterise bonnet macaque society. Independent juveniles, on the other hand, associate both with their mothers, especially during foraging, resting or alliance formation during agonistic interactions, as also with the adult males of the troop (pers. obs.; A. Sinha, pers. comm.). From such observations, it may be hypothesised that this species would be characterised by significant differences in the nature and patterns of gestural communication within each sex. The gestures exchanged between males could, thus, conceivably convey more information regarding dominance-subordination associations while those between females would possibly preferentially reflect affiliative relationships. Juveniles and infants, in contrast, could potentially have a preponderance of play gestures in their repertoires, as has been reported for chimpanzees, gorillas and orangutans (Liebal 2007; Genty et al 2009; Hobaiter and Byrne 2011).

The aim of this study was, thus, to understand the differential repertoire size and types of gestures displayed by adult individuals of both sexes, as well as juvenile and infant bonnet macaques in the four study troops at the population-, troop- and individual level. In addition, I also investigated the flexibility of gesture types, if any, as defined by their variable use in different contexts by the study individuals of different age classes.

3.2 Methods

3.2.1 *Study area and study troops*

I conducted this study in the Bandipur National Park, Karnataka, southern India on four troops, namely TT1, TT2, HN2 and C3, exactly as described in Chapter 2 (see also Table 2.1 and Figure 2.1 of Chapter 2). Behavioural data were collected on 29 adult females, 23 adult males, 31 juveniles and 26 infants, again as described in Chapter 2.

3.2.2 *Data collection and analysis*

I conducted 15-min focal animal sampling on randomly chosen individuals without replacement (Altmann 1974) and recorded all gestures (described in Tables 2.2 and 2.4 of Chapter 2) displayed by individuals of different age classes. The possible functions of the gestures were determined on the basis of the response received, again as described in Chapter 2, and accordingly incorporated into the affiliative, agonistic or play repertoires that were constructed for the study troops. The repertoires included only those gestures that were observed at least twice in each individual, in an effort to exclude idiosyncratic gestures, if any (Hobaiter and Byrne 2011).

My observations, which totalled 392.5 h, were carried out daily from 09:00 to 17:30, during the period from February 2013 to July 2014. The total hours of observation on individuals of the different age classes have been shown in Table 2.1 of Chapter 2. Video recordings were conducted to substantiate my observations, whenever necessary.

In this chapter, I have considered only those gestures that were displayed in the contexts of affiliation, agonism and play by the study individuals of different age classes. Three gestures, Copulatory Lip-Smacking (CS; used in a sexual context), Presenting (PR; used in sexual and dominance-subordination contexts) and Mounting (MO; used in affiliative, agonistic, play and dominance-subordination contexts) that met the strict criteria of the definition of gestures, described in Chapter 2 (see also Table 2.4 of Chapter 2) were, however, excluded from the present analysis due to insufficient sample size.

The dominance hierarchies that prevailed within the adult females and males in each study troop was determined as described in Chapter 2. The independent categorisation and ranking of the adult female and male individuals into five different age classes, on the basis of their distinct age-related morphological characteristics, have also been described in Chapter 2 of this thesis.

Individual repertoire size for the study troop members were estimated by including all the gesture types displayed in the respective contexts of affiliation, agonism and play. The differences between mean repertoire size across the different age classes were evaluated by the Mann-Whitney U-test while Spearman's rank correlation was applied to determine the relationship of the age class and rank of individuals to their respective repertoire size. Statistical analyses were conducted with the help of the software R, version 3.1.0 (R Core Team 2014) and SPSS Statistics 17.0 (SPSS Inc. 2008).

3.3 Results

3.3.1 *Age differences in gestural repertoire size*

3.3.1.1 *Repertoire size: Population-level*

The adult bonnet macaques of both sexes in the four study troops displayed a total gestural repertoire, including those exhibited in affiliative, agonistic and play contexts (Table 3.1, Figure 3.1), the size of which was comparable to and not significantly different from those exhibited by the juveniles and infants in these troops (Table 3.2, Column 6). Moreover, there was no correlation between the total gestural repertoire size and age class across all the study individuals (Spearman's rank correlation, rho = 0.08, n = 109, $p > 0.40$; Figure 3.2, Panel 1).

Table 3.1 Total and contextual gestural repertoire size displayed by individual bonnet macaques of different age classes

Repertoire	**Adult** **n = 52**	**Juvenile** **n = 31**	**Infant** **n = 26**
Affiliative			
Mean ± SE	11.58 ± 0.63	10.00 ± 0.83	9.27 ± 0.84
Range	7 – 19	1 – 18	3 – 17
Agonistic			
Mean ± SE	4.87 ± 0.40	2.97 ± 0.44	1.43 ± 0.32
Range	0 – 12	0 – 9	0 – 5
Play			
Mean ± SE	1.08 ± 0.30	5.16 ± 0.49	4.65 ± 0.32
Range	0 – 10	0 – 11	2 – 8
Total			
Mean ± SE	17.12 ± 0.96	18.13 ± 1.37	15.19 ± 1.29
Range	6 – 35	3 – 36	4 – 28

The affiliative gestural repertoire size of adults and juveniles, and those of juveniles and infants, taken together across all troops (Table 3.1), were not significantly different from one another (Table 3.2, Column 3). The adults, however, employed a larger affiliative repertoire than did the infants. There was also a significantly positive correlation between the repertoire size of affiliative gestures and age class, ranging from infants to adults (Spearman's rho = 0.25, n = 109, $p = 0.01$; Figure 3.2, Panel 2).

In agonistic contexts, adults bonnet macaques used a significantly larger number of gestures than did juveniles or infants (Table 3.2, Column 4) while the juveniles had a greater repertoire size than did the infants in this context. The agonistic gesture repertoire size was also observed to increase with the age class of individuals (Spearman's rho = 0.46, n = 109, $p < 0.0001$; Figure 3.2, Panel 3), akin to that of the affiliative repertoire.

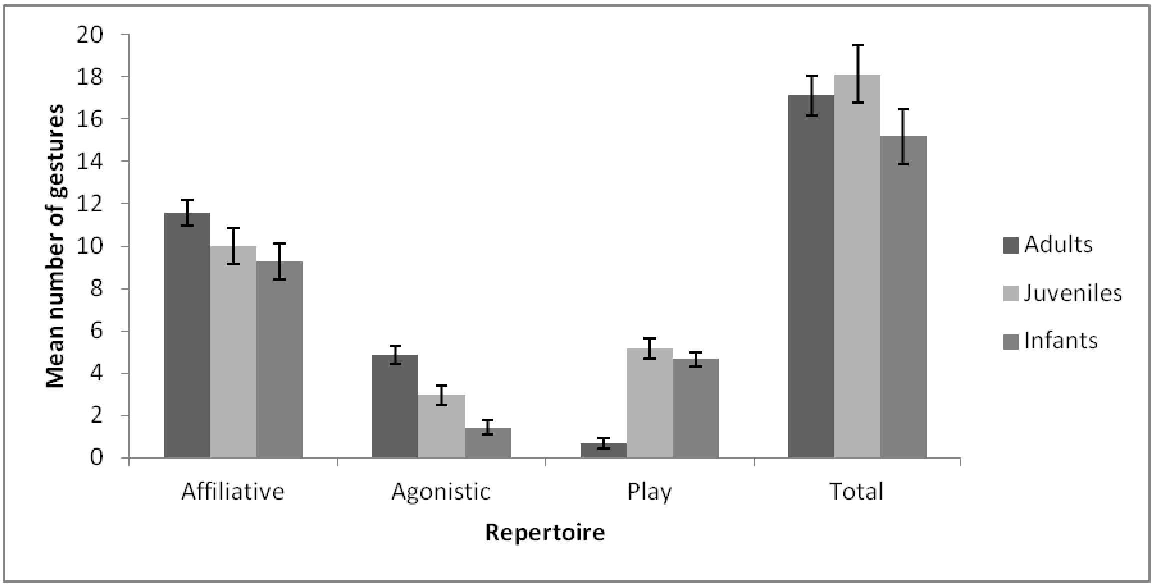

Figure 3.1 **Total and contextual gestural repertoire size of adult, juvenile and infant bonnet macaques during the study period**

Table 3.2 **Comparison of the total and contextual gestural repertoire size displayed by individual bonnet macaques of different age classes**

Age class		**Affiliative** **U, *p***	**Agonistic** **U, *p***	**Play** **U, *p***	**Total** **U, *p***
Adult n = 52	**Juvenile** n = 31	U = 641 $p > 0.10$	**U = 495** **$p < 0.002$**	**U = 163** **$p < 0.001$**	U = 741 $p > 0.50$
Adult n = 52	**Infant** n = 26	**U = 475** **$p < 0.04$**	**U = 196** **$p < 0.001$**	**U = 78.50** **$p < 0.001$**	U = 567.50 $p > 0.20$
Juvenile n = 31	**Infant** n = 26	U = 353 $p > 0.40$	**U = 231.50** **$p = 0.005$**	U = 344.50 $p > 0.30$	U = 305.50 $p > 0.10$

The repertoire size was compared using two-tailed Mann-Whitney U-tests. The statistically significant differences have been highlighted in bold

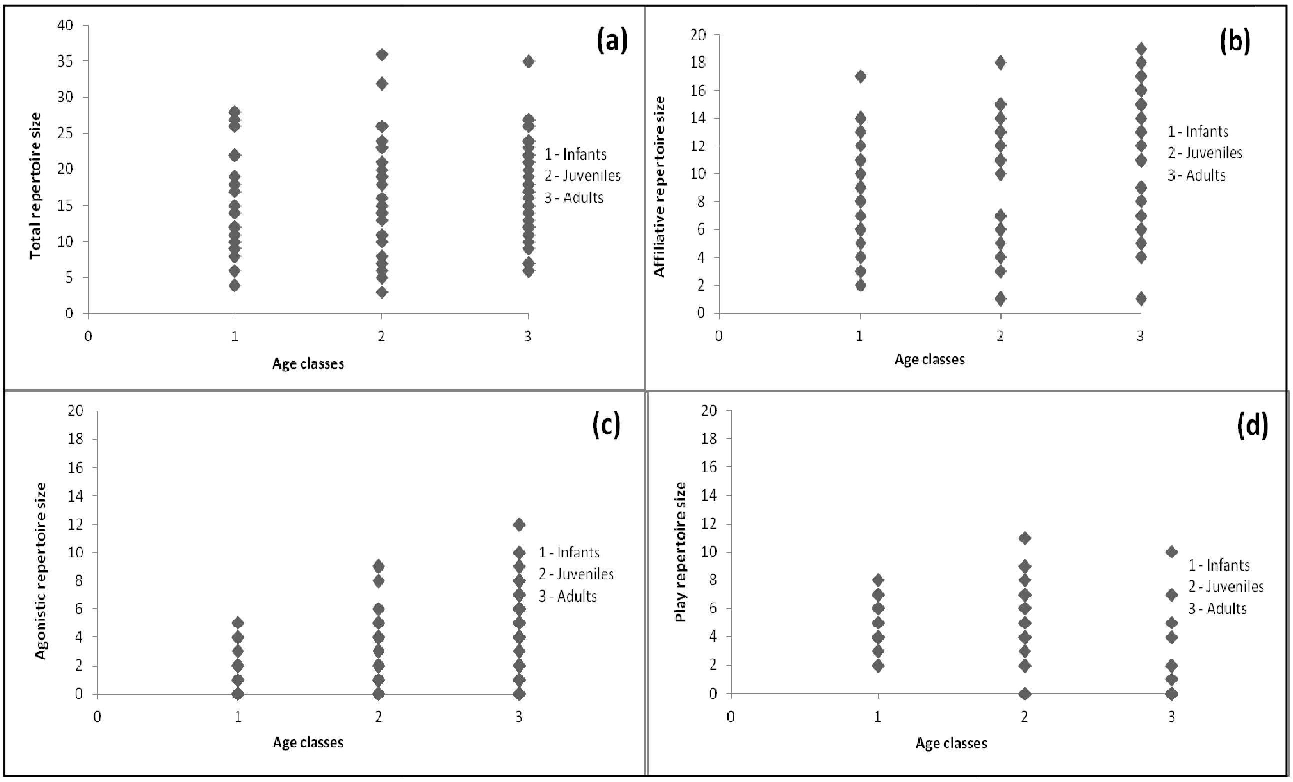

Figure 3.2 Correlation between gestural repertoire size and age class in the study troops: (a) Total, (b) Affiliative, (c) Agonistic and (d) Play repertoires

Finally, both, the infants and the juveniles of the study troops displayed a larger gestural repertoire size than did the adults in the context of play behaviour (Table 3.2, Column 5). The play gestural repertoire size, however, did not differ between that of the juveniles and the infants. The size of the play gestural repertoire, in contrast to those of affiliative and agonostic contexts, however, decreased significantly with age class (Spearman's rho = -0.67, n = 109, $p < 0.0001$; Figure 3.2, Panel 4).

3.3.1.2 *Repertoire size: Troop-level*

The total and contextual gestural repertoire size displayed by individuals of different age classes in each of the four study troops have been depicted in Figure 3.3 and Table 3.3.

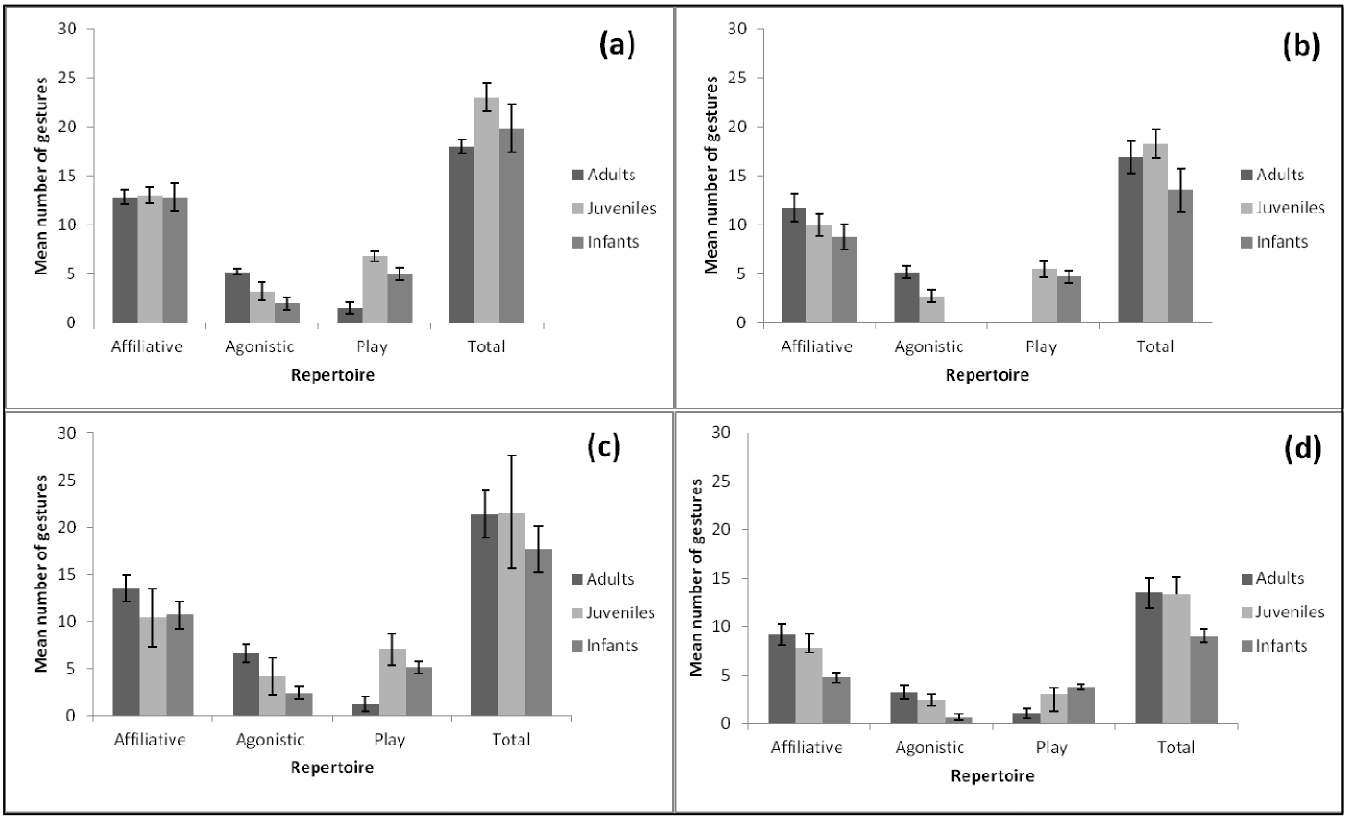

Figure 3.3 Total gestural repertoire size of adult, juvenile and infant bonnet macaques in the four study troops and repertoire size in the contexts of affiliation, agonism and play: (a) Troop TT1, (b) Troop TT2, (c) Troop HN2 and (d) Troop C3

A comparison of their size, the results of which have been shown in Table 3.4, indicate that, amongst adults, the total repertoire size of the multimale-multifemale Troop HN2 was significantly larger than that of the other two multimale troops TT1 and C3, with the former, in turn, being larger than the latter. These three troops, however, had a comparable number of adults (Table 3.3). The agonistic repertoire size of these troops showed an identical pattern but the affiliative repertoire size was significantly higher in the troops TT1 and HN2 than that of Troop C3 (Table 3.4).

Table 3.3 Total and contextual gestural repertoire size displayed by individual bonnet macaques of different age classes in the four study troops

Troop and age class	**Affiliative** Mean ± SE Range	**Agonistic** Mean ± SE Range	**Play** Mean ± SE Range	**Total** Mean ± SE Range
Troop TT1				
Adult n = 14	12.79 ± 0.70 9 – 17	5.21 ± 0.35 3 – 7	1.5 ± 0.61 0 – 7	18.00 ± 0.73 14 – 22
Juvenile n = 9	13.00 ± 0.87 7 – 15	3.22 ± 0.95 0 – 8	6.78 ± 0.52 4 – 9	23.00 ± 1.39 13 – 26
Infant n = 6	12.83 ± 1.35 7 – 17	2.00 ± 0.58 0 – 4	5.00 ± 0.63 3 – 7	19.83 ± 2.18 11 – 27
Troop TT2				
Adult n = 7	11.71 ± 1.41 6 – 15	5.14 ± 0.63 3 – 8	0	16.86 ± 1.64 10 – 22
Juvenile n = 4	10 ± 1.08 7 – 12	2.75 ± 0.63 1 – 4	5.50 ± 0.87 0 – 7	18.25 ± 1.44 14 – 20
Infant n = 4	8.75 ± 0.48 8 – 10	0	4.75 ± 1.11 2 – 7	13.50 ± 1.55 10 – 17
Troop HN2				
Adult n = 13	13.53 ± 1.42 5 – 19	6.62 ± 1.02 0 – 12	1.23 ± 0.76 0 – 10	21.38 ± 2.50 6 – 35
Juvenile n = 5	10.40 ± 3.08 1 – 18	4.20 ± 1.98 0 – 9	7.00 ± 1.70 2 – 11	21.60 ± 5.95 5 – 36
Infant n = 9	10.67 ± 1.43 2 – 14	2.43 ± 0.65 0 – 4	5.11 ± 0.63 2 – 8	17.67 ± 2.44 4 – 28
Troop C3				
Adult n = 18	9.17 ± 1.13 1 – 16	3.22 ± 0.67 0 – 10	1.06 ± 0.49 0 – 7	13.44 ± 1.56 7 – 27
Juvenile n = 13	7.83 ± 1.43 1 – 14	2.50 ± 0.48 0 – 5	3.00 ± 0.65 0 – 7	13.33 ± 1.77 3 – 20
Infant n = 7	4.71 ± 0.52 3 – 6	0.67 ± 0.33 0 – 2	3.71 ± 0.29 3 – 5	9.00 ± 0.69 6 – 12

It is noteworthy that the unimale-multifemale troop TT2, even with a smaller number of adults, had total and contextual repertoire sizes not significantly different from that of the three multimale troops. Play gestures were not considered in these comparisons due to their insufficient sample size.

The juveniles of Troop C3 exhibited the smallest total gestural repertoire size amongst the multimale troops. The juveniles of the unimale Troop TT2 displayed a comparable total repertoire size to that of the troops HN2 and C3 but one smaller than that of Troop TT1. The affiliative repertoire size was greater for the juveniles of Troop TT1 than those of both the troops TT2 and C3 while the play repertoire size was greater amongst the juveniles of TT1 than that of C3. The agonistic repertoire was comparable across the juveniles of all the four study troops.

The infants of Troop C3 had significantly higher total and affiliative repertoire sizes, as compared to those of TT1, HN2 and TT2, while the Troop TT2 infants displayed a larger agonistic gestural repertoire size than those of Troop TT1 (Table 3.4). It is illuminating that the infant play gestural repertoire size remained similar across the study troops.

Table 3.4 Comparison of the total and contextual gestural repertoire size displayed by individual bonnet macaques of different age classes in the four study troops

Age class	**Comparison**	**Affiliative repertoire U, *p***	**Agonistic repertoire U, *p***	**Play repertoire U, *p***	**Total repertoire U, *p***
Adult	TT1 vs TT2 (n = 14, 7)	U = 43 *p* > 0.60	U = 46.50 *p* > 0.80	-	U = 45 *p* > 0.70
	TT1 vs HN2 (n = 14, 13)	U = 68 *p* > 0.20	**U = 48.50** ***p* < 0.04**	-	**U = 45** ***p* < 0.03**
	TT1 vs C3 (n = 14, 18)	**U = 71.50** ***p* < 0.04**	**U = 62.50** ***p* < 0.02**	-	**U = 58.50** ***p* < 0.01**
	TT2 vs HN2	U = 27.50	U = 26	-	U = 22

	(n = 7, 13)	$p > 0.10$	$p > 0.10$		$p > 0.05$
	TT2 vs C3 (n = 7, 18)	U = 43.50 $p > 0.20$	U = 31.50 $p > 0.05$	-	U = 39.50 $p > 0.10$
	HN2 vs C3 (n = 13, 18)	**U = 52** **$p < 0.01$**	**U = 57.50** **$p < 0.02$**	-	**U = 60** **$p < 0.03$**
Juvenile	TT1 vs TT2 (n = 9, 4)	**U = 5** **$p = 0.05$**	U = 16 $p > 0.80$	U = 9.50 $p > 0.10$	**U = 4** **$p < 0.03$**
	TT1 vs HN2 (n = 9, 5)	U = 18.50 $p > 0.60$	U = 19 $p > 0.60$	U = 18.50 $p > 0.60$	U = 22 $p > 0.90$
	TT1 vs C3 (n = 9, 13)	**U = 16.50** **$p < 0.004$**	U = 50 $p > 0.60$	**U = 11.50** **$p = 0.001$**	**U = 8** **$p < 0.001$**
	TT2 vs HN2 (n = 4, 5)	U = 8.50 $p > 0.70$	U = 9.50 $p > 0.90$	U = 7 $p > 0.50$	U = 8 $p > 0.70$
	TT2 vs C3 (n = 4, 13)	U = 21 $p > 0.60$	U = 21.50 $p > 0.60$	U = 11 $p > 0.10$	U = 11 $p > 0.10$
	HN2 vs C3 (n = 5, 13)	U = 23 $p > 0.30$	U = 29.50 $p > 0.70$	U = 14.50 $p > 0.07$	**U = 20** **$p < 0.04$**
Infant	TT1 vs TT2 (n = 6, 4)	U = 4 $p > 0.10$	**U = 2** **$p < 0.04$**	U = 11.50 $p > 0.90$	U = 3 $p > 0.06$
	TT1 vs HN2 (n = 6, 9)	U = 18.50 $p > 0.30$	U = 25 $p > 0.80$	U = 26 $p > 0.90$	U = 21 $p > 0.50$
	TT1 vs C3 (n = 6, 7)	**U = 0** **$p = 0.001$**	U = 8 $p > 0.70$	U = 10.50 $p > 0.10$	**U = 1** **$p < 0.004$**
	TT2 vs HN2 (n = 4, 9)	U = 9 $p > 0.10$	U = 6 $p > 0.07$	U = 16.50 $p > 0.80$	U = 9 $p > 0.10$
	TT2 vs C3 (n = 4, 7)	**U = 0** **$p < 0.007$**	U = 8 $p > 0.30$	U = 9.50 $p > 0.40$	**U = 2** **$p < 0.03$**
	HN2 vs C3 (n = 6, 7)	**U = 7** **$p < 0.009$**	U = 18 $p > 0.10$	U = 16 $p > 0.10$	**U = 7.50** **$p < 0.009$**

Repertoire size was compared using two-tailed Mann-Whitney U-tests. The statistically significant differences have been highlighted in bold

3.3.1.3 *Repertoire size: Individual level*

The study individuals in the bonnet macaque troops did not display comparable frequencies of gestures in the contexts of affiliation, agonism and play within each age class. There was also considerable individual variation in the use of each gesture within and between age classes. The gesture Lip-Smacking (LS), for example, was shown by all the adult females and males but only 80.65% of the juveniles and 80.77% of the infants displayed this gesture. Similarly, all females displayed the gesture Hugging (HU), while 69.57% adult males, 77.42% juveniles and 92.31% infants exhibited this behaviour. The individual gestural profiles of the study macaques of different age classes across contexts and the percentage of individuals that deployed these contextual gestures have been tabulated in Tables 3.5, 3.6, 3.7 and 3.8.

All the adult females and males that were observed in the four study troops displayed gestures in both modalities—tactile and visual. This was, however, not necessarily true for the study juveniles and infants, as individuals belonging to both these age classes exhibited tactile gestures but visual gestures appeared to follow a developmental profile with most of these gestures being shown by relatively older juveniles. This aspect of gestural development in the two modalities has been analysed in Chapter 5.

Table 3.5 Percentage of adult females in the four study troops that displayed different types of contextual gestures

Individual	EM	ES	HC	MO	NF	PF	PG	SS	HN	HS	KK	LK	PM	SR	YD	ZG	BK	DK	DN	EK	PE	WH	WS	AJ	BU	CK	RF	SC	SE	n	%
Affiliative gestures																															
BG	x	x					x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x			x	x	x		21	72.41
CB	x	x	x	x			x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x			x	x	x	x	24	82.76
HO	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	28	96.55
HS	x	x	x	x			x		x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x		x	x	x	24	82.76
HU	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	29	100.00
LS	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	29	100.00
MB	x	x	x	x	x		x	x	x	x	x	x	x	x		x		x	x	x	x	x	x	x	x	x		x	x	25	86.21
MT		x							x	x		x	x	x		x	x	x		x	x									11	37.93
NZ	x		x	x	x		x		x	x	x	x		x	x	x				x		x	x					x	x	17	58.62
PA	x		x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x			x		x	24	82.76
PT	x	x	x	x	x	x		x	x	x	x	x	x	x		x	x	x	x	x		x	x	x	x	x	x	x	x	26	89.66
PU	x	x		x					x	x						x		x	x	x			x			x	x		x	13	44.83
RB	x	x	x				x	x	x	x	x	x	x	x		x			x					x						14	48.28
SG	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	x	x	28	96.55
TO	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	28	96.55

Agonistic gestures																														
BH	x	x								x	x			x		x			x		x						x			9	31.03
EF	x	x	x	x					x	x	x	x	x	x		x		x	x	x	x		x		x	x	x		x	20	68.97
HD		x	x							x			x	x					x	x	x	x						x		10	34.48
HJ	x	x	x	x					x	x	x	x	x	x		x	x		x	x				x	x	x	x	x	x	20	68.97
LU	x	x	x	x	x				x	x	x	x	x	x		x	x	x	x	x		x	x	x	x		x		x	22	75.86
OT	x	x	x	x	x				x	x	x	x	x	x		x	x		x	x	x	x	x	x	x			x	x	22	75.86
PN	x	x								x	x		x	x										x	x					8	27.59
PT		x							x			x		x												x			x	6	20..69
PU	x	x	x	x					x	x		x	x	x			x		x	x	x	x		x	x	x	x		x	19	65.52
SL	x	x		x		x	x		x	x	x	x	x	x		x		x								x				14	48.28
Play gestures																														
HD																															
HJ																															
PB		x											x									x								3	10.34
PL																							x							1	3.45
PN																															
PO	x												x									x								3	10.34
PS									x																					1	3.45
PU	x																													1	3.45
PT																															

The troop membership of the individuals has been depicted according to the following colour scheme:

Troop C3	Troop HN2	Troop TT1	Troop TT2

Table 3.6 Percentage of adult males in the four study troops that displayed different types of contextual gestures

Individuals	AN	BD	BL	EL	FM	KC	M2	MM 1	NM 1	SM	BT	NM 2	NT	RI	RS	DT	KF	KJ	LT	PD	PK	SB	MM 2	n	%
Affiliative gestures																									
BG									x	x	x	x	x			x	x			x	x	x	x	11	47.83
CB				x			x			x	x				x	x	x		x	x	x			10	43.48
HO	x	x		x				x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	18	78.26
HS								x			x	x	x		x		x		x					7	30.43
HU	x		x	x							x	x	x	x	x	x	x	x	x	x	x	x	x	16	69.57
LS	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	23	100.00
MB			x	x	x					x	x				x	x	x	x	x		x			11	47.83
MT											x													1	4.35
NZ											x					x	x		x					4	17.39
PA		x		x						x	x		x		x									6	26.09
PT	x						x				x				x	x	x	x			x	x		10	43.48
PU	x									x					x	x			x					5	21.74
RB	x	x	x	x	x				x	x	x			x	x	x	x	x	x	x	x	x	x	18	78.26
SG	x			x	x		x	x	x	x	x		x		x	x		x		x	x	x		17	73.91
TO	x	x		x			x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	19	82.61

Agonistic gestures																									
BH									x	x	x		x									x		5	21.74
EF	x		x	x			x	x	x	x	x		x		x	x	x		x	x		x		15	65.22
HD					x					x	x		x						x	x	x	x	x	9	39.13
HJ												x	x		x		x	x		x		x	x	8	34.78
LU	x		x		x	x				x	x		x		x	x	x	x	x	x	x	x	x	16	69.57
OT	x		x	x		x				x	x		x		x	x	x	x	x	x	x	x	x	16	69.57
PN															x									1	4.35
PT			x	x							x		x		x			x			x	x		8	34.78
PU											x		x		x			x			x		x	6	26.09
SL										x	x		x		x	x			x	x	x	x		9	39.13
Play gestures																									
HD											x													1	4.35
HJ											x													1	4.35
PB		x	x			x					x				x	x				x	x			8	34.78
PL		x	x								x					x	x			x	x			7	30.43
PN											x													1	4.35
PO		x	x			x					x				x	x			x		x			8	34.78
PS		x	x			x					x		x			x			x		x			8	34.78
PU		x									x					x					x			4	17.39
PT		x	x			x					x					x					x			6	26.09
SJ		x									x					x								3	13.04

The troop membership of the individuals has been depicted according to the following colour scheme:

Troop C3	Troop HN2	Troop TT1	Troop TT2

Table 3.7 Percentage of juveniles from the four study troops that displayed different types of contextual gestures

Individuals	BC	CP	CC	DF	DL	DW	EB 1	FN	MJ	PM	RJ	SJ	YY	AC	BC	HJ	NF	NL	AB	BD	BL	BS	EB 2	LE	PN	SL	SP	CH	HB	PL	VV	n	%
Affiliative gestures																																	
BG		x				x			x	x	x			x		x		x	x	x	x	x	x	x	x	x	x	x		x		19	61.29
CB			x						x	x		x		x		x		x		x		x	x		x	x	x	x	x			15	48.39
HO		x		x	x	x	x		x	x	x	x	x	x		x		x	x	x	x	x	x	x	x	x	x	x	x	x		25	80.65
HS					x					x	x			x		x		x		x		x		x					x		x	11	35.48
HU		x			x				x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	24	77.42
LS		x	x	x	x				x	x	x	x	x	x		x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	25	80.65
MB		x			x				x	x	x	x	x	x		x		x		x	x	x	x		x	x	x	x		x		19	61.29
MT		x			x							x				x		x	x	x		x	x	x	x	x	x	x		x		15	48.39
NZ	x	x								x						x	x	x		x	x	x					x	x	x		x	13	41.94
PA					x				x			x	x			x					x	x	x									8	25.81
PT		x			x	x			x	x	x	x	x			x		x		x	x		x	x	x	x	x		x			22	70.97
PU										x						x		x		x	x					x	x					7	22.58
RB			x		x	x	x	x	x	x	x	x	x	x		x					x	x	x	x		x	x					18	58.06
SG		x	x	x	x	x	x		x	x	x	x		x		x		x	x					x	x		x		x	x	x	21	67.74
TO		x	x		x				x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	25	80.65

Agonistic gestures																																
BH									x					x		x				x					x	x						6	19.35
EF		x		x	x				x		x			x	x	x														x		9	29.03
HD						x						x		x		x				x				x		x	x					8	25.81
HJ								x	x		x				x	x	x						x				x	x				9	29.03
LU	x				x	x			x			x	x	x		x				x				x	x	x	x		x			14	45.16
OT	x								x	x	x			x		x				x				x	x		x	x		x		12	38.71
PN																											x					1	3.23
PT					x	x						x		x		x								x	x	x	x	x		x	x	12	38.71
PU		x			x			x		x				x		x						x			x		x		x			10	32.26
SL		x			x			x			x				x									x	x	x		x				9	29.03
Play gestures																																
HD			x											x					x		x		x	x	x	x			x			9	29.03
HJ														x																		1	3.23
PB		x	x	x	x	x	x				x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	27	87.10
PL	x	x		x	x	x	x				x		x	x		x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	24	77.42
PN														x		x	x	x			x		x	x	x					x		9	29.03
PO	x	x		x	x	x	x				x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	26	83.87
PS	x			x		x	x						x	x		x		x	x	x	x		x	x	x		x		x	x	x	18	58.06
PU						x								x		x		x		x	x	x				x				x	x	10	32.26
PT		x		x	x	x	x				x		x	x	x	x	x	x		x	x	x	x	x	x	x			x	x	x	22	70.97
SJ						x							x	x		x		x	x	x			x	x		x						10	32.26

The troop membership of the individuals has been depicted according to the following colour scheme:

Troop C3	Troop HN2	Troop TT1	Troop TT2

Table 3.8 Percentage of infants from the four study troops that displayed different types of contextual gestures

Individuals	E1	E2	EV	H1	NI	P1	MI	HI	IH	KI	LI	PI 1	SI	YI	Z2	ZI	BI	DI	EI	ID	PI 2	WI	AI	CI	IS	SI	n	%
Affiliative gestures																												
BG				x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	22	84.62
CB								x			x		x			x	x	x	x		x						8	30.77
HO				x				x	x	x	x	x	x		x	x	x	x	x		x	x	x	x	x	x	18	69.23
HS									x						x	x	x	x				x					6	23.08
HU	x	x		x	x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	24	92.31
LS			x	x			x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	21	80.77
MB		x						x	x	x	x		x		x	x	x	x	x	x	x	x			x	x	16	61.54
MT				x	x				x	x			x		x	x		x	x		x		x				11	42.31
NZ	x	x	x		x			x	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	22	84.62
PA										x						x											2	7.69
PT	x				x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x				20	76.92
PU							x	x					x			x	x	x			x	x		x			9	34.62
RB								x																			1	3.85
SG																x		x									2	7.69
TO		x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x		x	x	23	88.46

Agonistic gestures																												
BH																					x					1	3.85
EF																	x									1	3.85
HD																										0	0.00
HJ	x															x											2	7.69
LU		x														x	x	x				x					5	19.23
OT								x		x			x			x		x			x						6	23.08
PN												x	x			x						x					4	15.38
PT				x				x		x					x	x	x										6	23.08
PU				x				x		x					x												4	15.38
SL								x											x		x	x					4	15.38
Play gestures																												
HD																							x			x	2	7.69
HJ																											0	0.00
PB	x	x	x	x	x		x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	x	25	96.15
PL	x	x	x	x	x	x	x	x	x	x		x	x		x	x	x	x	x	x	x	x	x	x		x	23	88.46
PN								x																			1	3.85
PO	x	x	x	x		x	x	x	x		x	x	x			x	x	x		x	x	x	x			x	19	73.08
PS	x						x	x	x				x		x	x		x				x					9	34.62
PU									x	x	x	x				x	x					x	x	x	x	x	11	42.31
PT		x		x		x	x	x	x	x		x	x	x	x	x	x	x	x	x		x	x				18	69.23
SJ								x										x									2	7.69

The troop membership of the individuals has been depicted according to the following colour scheme:

Troop C3	Troop HN2	Troop TT1	Troop TT2

3.3.2 *Sex differences in gestural repertoire size*

3.3.2.1 *Repertoire size: Population level*

The adult females across the troops displayed a mean total repertoire size (± SE) of 17.11 ± 1.44 gestures, which was significantly larger than the 13.83 ± 0.96 gestures shown by the adult males (Mann-Whitney U-test, two-tailed, U = 148.50, n = 29 and 23, $p = 0.001$; Figure 3.4). The adult female repertoire of affiliative gestures (11.58 ± 0.81) was larger than that of the adult males (8.30 ± 0.63; U = 83, $p < 0.0001$), while the agonistic repertoire was not different in size between the two sexes (U = 252.50, $p = 0.13$). A similar comparison was not conducted for play gestures due to insufficient sample size, with only six of the 29 females and eleven of the 23 males exhibiting play gestures during the entire study period (Figure 3.4).

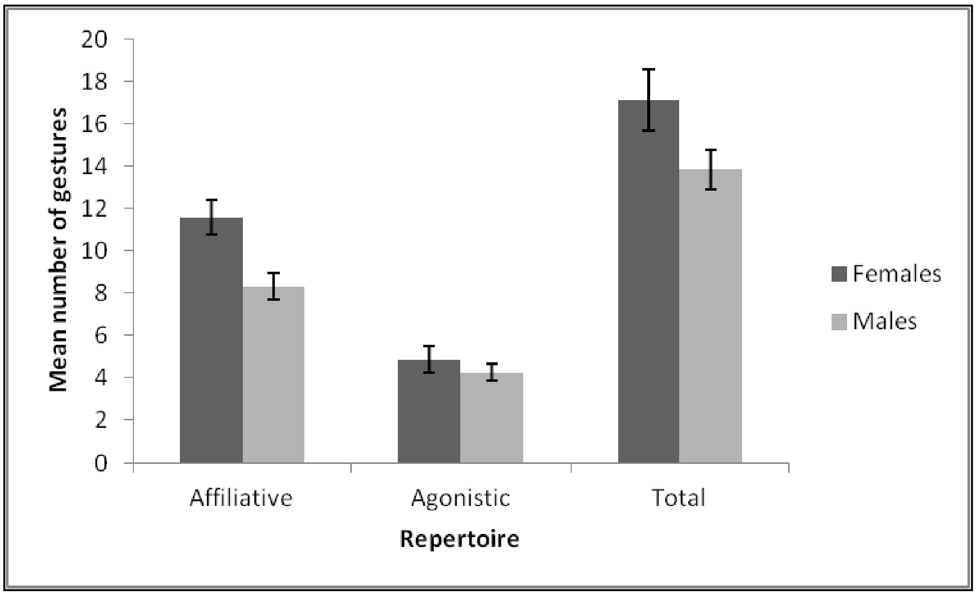

Figure 3.4 Total and contextual gestural repertoire size of adult female and male bonnet macaques across the four study troops

3.3.2.2 *Repertoire size: Troop level*

I compared the repertoire size of the adult females and males across the four study troops (Table 3.9).

Table 3.9 Total and contextual gestural repertoire size displayed by adult females and males in the four study troops

Troop and adult sex class	**Affiliative repertoire** Mean ± SE Range	**Agonistic repertoire** Mean ± SE Range	**Total repertoire** Mean ± SE Range
Troop TT1			
Female n = 7	14.57 ± 0.65 13 – 17	5.00 ± 0.49 3 – 7	19.57 ± 1.02 14 – 22
Male n = 7	11.00 ± 0.79 9 – 14	5.43 ± 0.53 4 – 8	16.43 ± 0.65 14 – 18
Troop TT2			
Female n = 6	12.67 ± 1.23 7 – 15	5.00 ± 0.73 3 – 8	17.67 ± 1.69 10 – 22
Male n = 1	6.00	6.00	12.00
Troop HN2			
Female n = 8	15.88 ± 1.32 7 – 19	7.00 ± 1.07 0 – 10	23.25 ± 2.37 7 – 27
Male n = 5	9.80 ± 2.27 5 – 17	6.00 ± 2.19 0 – 12	18.40 ± 5.42 6 – 35
Troop C3			
Female n = 8	13.25 ± 1.15 7 – 16	4.25 ± 1.32 0 – 10	17.88 ± 2.44 9 – 27
Male n = 10	5.90 ± 0.92 1 – 11	6.00 ± 2.40 0 – 4	17.00 ± 9.90 6 – 13

The total repertoire size of females of Troop HN2 was significantly larger than those of the troops TT1 and TT2. The females of this troop had larger affiliative repertoires than did the females of troops C3 and TT2. The agonistic repertoire size was greater among the HN2 females, in comparison to those of TT1 (Table 3.10). The adult males of Troop TT1 exhibited larger affilative repertoire than that of Troop C3, however, the C3 males showed a greater total and agonistic repertoires than did those of Troop TT1. The only male of the unimale troop TT2 was excluded from this analysis as were play gestures, as before, due to insufficient sample size.

Table 3.10 Comparison of the total and contextual gestural repertoire size displayed by adult female and male bonnet macaques in each troop

Adult sex class	**Comparison**	**Affiliative repertoire U, *p***	**Agonistic repertoire U, *p***	**Total repertoire U, *p***
Adult female	TT1 vs TT2 (n = 7, 6)	U = 12.50 $p > 0.20$	U = 19.50 $p > 0.80$	U = 15 $p > 0.40$
	TT1 vs HN2 (n = 7, 8)	U = 11.50 $p > 0.50$	**U = 8.50** $\mathbf{p < 0.03}$	**U = 7** $\mathbf{p < 0.02}$
	TT1 vs C3 (n = 7, 8)	U = 23 $p > 0.60$	U = 25 $p > 0.70$	U = 23 $p > 0.60$
	TT2 vs HN2 (n =6, 8)	**U =5.50** $\mathbf{p < 0.02}$	U = 10 $p > 0.08$	**U = 6** $\mathbf{p < 0.03}$
	TT2 vs C3 (n = 7, 18)	U = 18.50 $p > 0.40$	U = 20.50 $p > 0.60$	U = 23 $p > 0.90$
	HN2 vs C3 (n = 13, 18)	**U = 9.50** $\mathbf{p < 0.02}$	U = 18 $p > 0.10$	U = 17 $p > 0.10$
Adult male	TT1 vs HN2 (n = 7, 5)	U = 12.50 $p > 0.40$	U = 15 $p > 0.70$	U = 14 $p > 0.60$
	TT1 vs C3 (n = 7, 10)	**U = 6.50** $\mathbf{p < 0.004}$	**U = 6** $\mathbf{p < 0.004}$	**U = 3.5** $\mathbf{p = 0.001}$
	HN2 vs C3 (n = 5, 10)	U = 11.50 $p > 0.09$	U = 15 $p > 0.20$	U = 15.50 $p > 0.20$

The repertoire size was compared using two-tailed Mann-Whitney U-tests. The statistically significant differences have been highlighted in bold

3.3.2.3 *Repertoire size: Individual level*

The gestural repertoire size of adult females and males in each of the study troops did not, in general, appear to be significantly influenced by their respective ranks in the social dominance hierarchy (Table 3.11).

Table 3.11 Correlation of the total and contextual gestural repertoire size of adult female and male bonnet macaques to their dominance ranks within their respective troops

Troop	**Adult sex category**	**Affiliative repertoire** **ρ, *p***	**Agonistic repertoire** **ρ, *p***	**Total repertoire** **ρ, *p***
C3	Adult female (n = 8)	ρ = 0.66 *p* = 0.78	ρ = 0.63 *p* = 0.1	**ρ = 0.76** ***p* = 0.03**
	Adult male (n = 10)	ρ = 0.55 *p* = 0.09	ρ = 0.56 *p* = 0.09	ρ = 0.53 *p* = 0.12
HN2	Adult female (n = 8)	ρ = 0.33 *p* = 0.42	ρ = 0.09 *p* = 0.84	ρ = 0.45 *p* = 0.26
	Adult male (n = 5)	ρ = 0.60 *p* = 0.29	ρ = -0.15 *p* = 0.81	ρ = 0.50 *p* = 0.39
TT1	Adult female (n = 7)	ρ = 0.36 *p* = 0.43	ρ = 0.7 *p* = 0.08	ρ = 0.58 *p* = 0.17
	Adult male (n = 7)	ρ = -0.45 *p* = 0.32	ρ = 0.02 *p* = 0.97	ρ = 0.47 *p* = 0.29
TT2	Adult female (n = 6)	ρ = 0.41 *p* = 0.43	ρ = 0.09 *p* = 0.09	ρ = 0.09 *p* = 0.87
	Adult male (n = 1)	-	-	-

The correlations were evaluated using Spearman's rank correlation test. The statistically significant differences have been highlighted in bold

The only exception to this pattern was the adult females of the multimale troop C3, who exhibited a positive correlation of their total repertoire size to their dominance ranks. It is also worth pointing out that there appeared to be a strong trend of both agonistic and affiliative repertoire size of the males of this troop being positive correlated to their social rank (Table 3.11). A similar tendency was also observed among the females of Troops C3, TT1 and TT2 in terms of their agonistic gestural repertoire size. The total and contextual gestural repertoire size of the study adult individuals, taken together, did not, however, show any significant correlation or a trend thereof, with their age class (Table 3.12).

Table 3.12 Correlation of the total and contextual gestural repertoire size of adult female and male bonnet macaques to their age class across the study troops

Adult sex category	Affiliative ρ, *p*	Agonistic ρ, *p*	Total ρ, *p*
Adult female (n = 29)	ρ = 0.05 *p* = 0.80	ρ = 0.16 *p* = 0.40	ρ = -0.06 *p* = 0.75
Adult male (n = 23)	ρ = 0.20 *p* = 0.38	ρ = 0.10 *p* = 0.66	ρ = -0.03 *p* = 0.91

The correlations were evaluated using Spearman's rank correlation test

3.3.3 *Flexibility in gesture use*

Following Call and Tomasello (2007a, b), we analysed the contexts of use of gestures by our study individuals to ascertain whether multiple gestures were used in a particular context or whether the same gesture was employed in different contexts. Such variability, along with the influence of the audience's attention state on the choice of gestures exhibited in particular contexts, has been considered hallmarks of behavioural flexibility and intentionality in primate gestural communication.

The study macaques deployed 13 unique gestures (41.94% of the gestural repertoire) in the context of affiliation and five each (16.13%) for agonism and for play. Thus, a total of

23 (74.19%) gestures were displayed in specific contexts alone, exemplifying the use of multiple gestures in single contexts (Figure 3.5). There were three gestures (9.68% of the total repertoire)—Pinching (PN), Holding Down Roughly (HD) and Head-Jerking (HJ)—which were displayed in two contexts each, agonism and play. About 38.48% of all adult females, 39.13% adult males and 25.81% juveniles used HD in agonistic contexts, while none of the study infants did. Approximately 13.04% adult males, 29.03% juveniles and 7.69% of the infants used HD in play. HJ was used by individuals of all age classes (65.52% adult females, 26.09% adult males, 25.81% juveniles and 3.85% infants) in agonistic contexts while only adult males and juveniles displayed HJ (4.34% adult males, 3.23% juveniles) during play. Finally, there were two gestures (6.45% of the repertoire), Pulling (PT) and Pushing (PU), which were used in all the three contexts (Figure 3.5).

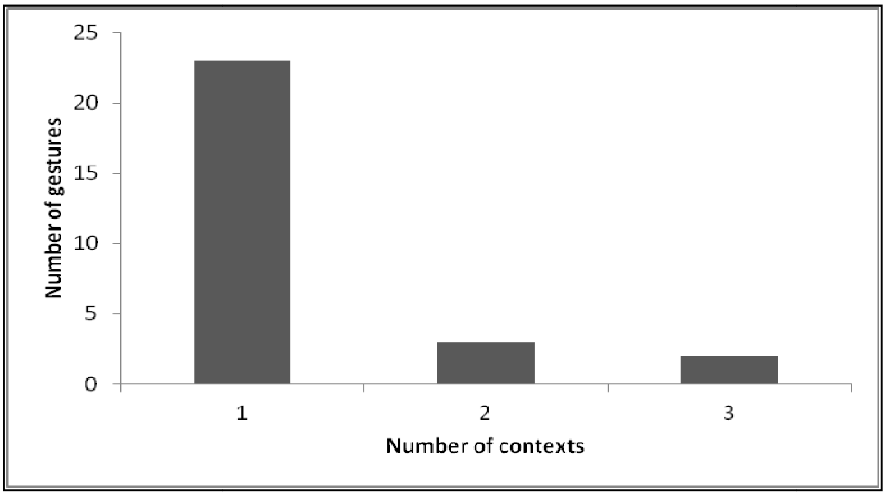

Figure 3.5 **Variability in the number of gestures employed by the study bonnet macaques of all age classes in different contexts**

I was, however, unable to analyse the variability in gesture choice shown by the study individuals in response to the audience's attention state as only 22.56% of the displayed gestures were visual in nature, a modality that alone can be investigated to detect any such variation and that too by using video frame-by-frame analysis, a method not adopted in this particular study.

3.4. Discussion

3.4.1 *Age differences in gestural repertoire size*

3.4.1.1 *Repertoire size: Population level*

The complete gestural repertoire size of adult, juvenile and infant bonnet macaques were not significantly different from one other, unlike in chimpanzees (Tomasello et al. 1997; Hobaiter and Byrne 2011), bonobos (Pika et al. 2003), gorillas (Genty et al. 2009), orangutans (Liebal et al. 2006; Liebal 2007a), siamangs (Liebal et al. 2004) and Barbary macaques (Hesler and Fischer 2007). The juvenile repertoire of bonnet macaques consisted of a few gesture types more than those of the adults, but was not significantly larger in size. The gestural repertoire size of Barbary macaques, in contrast, has been reported to be largest for adults (Hesler and Fischer 2007).

Interestingly, when the complete repertoire of the study species was categorised on the basis of the different contexts of gesture production, the affiliative and agonistic gesture repertoires showed a significant increase in size with age, the adults having larger repertoires than either the juveniles or infants. In case of the play gestural repertoire, however, repertoire size significantly decreased with age, with infants having the highest number of play gestures that gradually reduced in number in juveniles and adults. Juvenile apes are known to have the largest repertoire amongst all age classes, which results from a significantly varied play repertoire in the respective species (chimpanzees: Tomasello et al. 1997, Hobaiter and Byrne 2011; bonobos: Pika et al. 2003; gorillas: Genty et al. 2009; orangutans: Liebal et al. 2006, Liebal 2007a). It is important to note here is that although each age class of bonnet macaques had a comparable total gestural repertoire size, the contextual repertoire size varied with age. It is obvious that the contexts of social interactions change with progressing age and this is likely to have given rise to the differential nature of the gestural repertoires displayed by each age class. Thus, the lower number of affiliative and agonistic gestures in infant and juvenile bonnet macaques is replaced by a greater number of play gestures, an activity in which they spent most of their observed time.

3.4.1.2 *Repertoire size: Troop level*

There was a marked variability in the repertoire sizes exhibited by the different age classes of macaques across the study troops. The agonistic and affiliative gestural repertoires of the adults of Troops HN2 and TT1, for example, were larger than that in Troop C3, which was similarly reflected in their total repertoire size. The troops HN2 and TT1 were located alongside the national highway, which runs through the study area within the Bandipur National Park, and a populated village respectively and thus, both depended heavily on human-provisioned food. Troop C3, on the other hand, resided in a comparatively open space in the tourist zone of the Park, where it had ample opportunities of feeding on natural resources and thus avoiding high levels of intra-troop aggression (see, for example, Ram et al. 2003), although they were occasionally provisioned by visiting tourists. This could reflect in the relatively lower levels of agonistic communication in this troop, as compared to that in the other two troops that were more prone to intra-troop aggression. The decreased levels of affiliative gesturing, however, may not be explained with this argument. It is conceivable that human interventions in the form of food provisioning could have changed the communication repertoire of the species, as similar observations of behavioural alterations have been made earlier for other troops in the same population (Ram et al. 2003; Sinha et al. 2005).

The juveniles of TT1 also exhibited larger repertoires of affiliation than those of C3 and TT2 and of play than those in C3, perhaps owing to the greater number of similar aged juveniles in TT1. Moreover, it is possible that the relatively predator-free habitat of Troop TT1 in the village bordering the Park may have facilitated more communication amongst the juveniles, in comparison to those of Troop C3.

The infants of Troop C3, on the other hand, exhibited a larger total repertoire than those of all the other troops. This difference may have stemmed from the fact that in Troop C3, which had the most number of matrilines amongst all the study troops, mothers spent more time with their kin, along with their infants, thus providing increased opportunities of communication amongst the infants. This may have also, in turn, been facilitated by the greater ease of communicating, through both tactile and visual modalities, in their larger, relatively open, home range.

3.4.1.3 *Repertoire size: Individual level*

Individual variation in the use of each gesture type in different contexts was not particularly pronounced among the different age classes, with neither idiosyncratic gestures displayed by individuals of any troop nor group-specific unique gestures being evident. Idiosyncratic gestures are believed to be one of the indicators of the process of ontogenetic ritualisation, through which ape gestures have been suggested to develop during an individual's lifetime (chimpanzees: Tomasello et al. 1994, Call and Tomasello 2007b, but see Hobaiter and Byrne 2011; gorillas: Pika et al. 2003, but see Genty et al. 2009; orangutans: Liebal et al. 2006). However, there could be other developmental processes underlying gesture development, which could eventually give rise to flexible intentional usage of genetically pre-disposed signals (Redshaw and Locke 1976; Berdecio and Nash 1981; Pika et al. 2003; Genty et al. 2009; Hobaiter and Byrne 2011). In bonnet macaques, the set of infant gestures appeared to be gradually replaced by those of juveniles and finally, by the set of gestures that adults used more regularly. Nevertheless, it could also be a result of an ongoing process of observational learning of the proper use of certain gestures by younger individuals, as has been hypothesised for gestures in chimpanzees and gorillas (Pika et al. 2003; Genty et al 2009; Hobaiter and Byrne 2011) and for vocalisations in vervet monkeys (Cheney and Seyfarth 1990).

3.4.2 ***Sex differences in gestural repertoire size***

3.4.2.1 *Repertoire size: Population level*

Sex differences in communication systems of primates have only rarely been reported earlier. Olfactory communication in primates, for instance, often involve sexually distinct repertoires, in which scent-marking behaviour in females is different in intensity and use from those of males while the identification of scents by sniffing in males has evolved differently than in females (Heymann 1998). Tomaszycki et al. (2001) report similar observations of differential vocalisations—call types as well as call use—among infant and juvenile rhesus macaques belonging to the two sexes. It has also been observed that affiliative social vocalisations are predominant among the females of certain species than in their male counterparts (Seyfarth 1990); female savannah monkeys, for example, vocalise more, directing their calls towards other females than towards males (Locke and Hauser 1999; Greeno and Semple 2009). In red-capped mangabeys, the vocal repertoire size and call usage differ among the two sexes, suggesting separate social roles that may have possibly evolved for the respective sexes (Bouchet et al. 2010).

In the gestural communication system of primates too, there are repertoire differences among the two sexes as well as category preferences, as has been reported in several species. Pro-social signalling, for example, is more common in male spider monkeys than in females (Slater et al. 2009). Specific gestures, as, for instance, in sexual contexts, are typically displayed only by male siamangs and Barbary macaques (Hesler and Fischer 2007; Liebal 2007a). Female orangutans also display more visual gestures than do males (Liebal 2007b) while male orangutans as well as siamangs produced relatively more tactile gestures (Liebal 2007a, b). Gestural studies in chimpanzees have rarely investigated such issues except for certain observations on sex differences in sexual signalling (Hobaiter and Byrne 2012) or signalling to humans under captive conditions (Hopkins and Leavens 1998). A recent study by Scott (2013) focussed systematically on sexual differences in gesture use by chimpanzees and illustrate how evolutionarily distinct pressures could have potentially shaped isolated repertoires for each sex. I made similar observations in bonnet macaques, wherein females, in general, had larger repertoires than did males, possibly contributed to by the larger inventory of affiliative gestures that they typically exhibited. This strongly supports the hypothesis put forward by Scott (2013) that social pressures may be acting differently on the two sexes, resulting in distinct communication strategies in female and male individuals. Bonnet macaques, typically forming female-bonded societies, are likely to consist of females who would display a greater diversity of affiliative gestures than would males. The social hierarchies of the study troops or the age differences among the adults in them, however, did not appear to influence the gestural repertoire size, unlike that reported in other macaques (Maestrepieri 2005).

3.4.2.2 *Repertoire size: Troop level*

The adult females of Troop HN2 displayed a larger total repertoire size than did those in the troops TT1 and TT2 and HN2 females exhibited a greater number of affiliative gestures than those of TT2 and C3, as well as more agonistic gestures than those of Troop TT1. The more extensive affiliative repertoire among the HN2 females could be due to the presence of distinct matrilines, marked by strong social bonds, a finding not so evident among the TT2 females. Although the number of matrilines in C3 was larger than in HN2, all the dominant females of HN2 belonged to a single matriline, perhaps making the affiliative relationships stronger in this troop. The significantly higher levels of agonistic behaviour displayed by the females of Troop HN2, in comparison to that among the females in the other study troops, could once again possibly be attributed to their location next to a busy highway, thus potentially increasing stress levels among the troop members during provisioned feeding (Ram et al. 2003). The total and agonistic gestural repertoires of the adult males of Troop C3 were larger than that of Troop TT1. In C3, the males often migrated to neighbouring troops during the study period and occasionally rejoined their original troops (pers. obs.), which perhaps required them to display more agonism in order to continuously establish and retain their ever-changing social positions. Troop TT1 males, on the other hand, showed more affiliative gestures than did those in C3, probably because they were similar in their age and belonged to the same age cohorts. Although it is difficult to discern particular patterns in the gestural repertoires of adult females and males across the study troops, the observed variation could have resulted from several factors driven by their immediate environment, personality traits of individuals, and other social factors such as individual developmental histories.

3.4.2.3 *Repertoire size: Individual level*

Although there was no strong correlation between the social rank of individuals or their age to the gestural repertoire sizes displayed by both adult female and male bonnet macaques, it is interesting to note that there were certain tendencies of agonistic gestures being performed at higher levels by higher ranking individuals, which could be considered intuitively obvious. The lack of a relationship between the increasing age of adults and their repertoires, however, appeared to indicate that social experience among these adults did not markedly influence already established gestural repertoires.

3.4.3 ***Flexibility in gesture use***

The flexibility of gestures displayed by bonnet macaques seemed to be similar to those observed in other apes and in Barbary macaques, which exhibit the capacity of means-end dissociation by using similar gestures in different contexts and multiple gestures in the same context (Tomasello et al. 1994, 1997; Pika et al. 2003; Liebal et al. 2004; Liebal et al. 2006; Hesler and Fischer 2007; Liebal 2007b; Genty et al. 2009; Hobaiter and Byrne 2011). The effect of the audience's attention state on gesture choice, another important factor that reflects the intentionality and flexibility underlying gesture use (see Tomasello et al. 1994) could not be precisely ascertained in my study. The modalities of the gestures of bonnet macaques were not too diverse, with most gestures being tactile in nature. Moreover, the study site presented mostly open, large areas, making it difficult to videotape all the movements displayed by the free-ranging individuals in the macaque troops. While it was not problematic to observe and manually document most of the behaviours displayed by the study individuals, it was not always possible to track the attention state of the receiver when the sender initiated a particular communicative event, which could have facilitated by detailed frame-by-frame video analysis. The intentional nature of bonnet macaque gestures was, however, evident from the persistent gestural communicative attempts displayed by many signallers on failure to elicit a response from the receiver (discussed in Chapter 2). Future studies could potentially focus on audience effects, which are likely to reveal other interesting characteristics of the gestures used by this species.

This study is possibly one of the first to systematically investigate the age-sex differences in the gestural repertoires of any macaque species in the wild. My study also suggests that genetically acquired gestural repertoires can develop through processes, such as observational learning of gesture usage, other than ontogenetic ritualisation, in a non-ape species. It is noteworthy that primate gestural systems, in general, thus appear to be both flexible and intentional in nature and reflect common processes underlying gestural development across both non-apes and apes, perhaps culminating in the most complex form of primate communication known—human language. In the following chapters, I explore differences in the functionality of gesture use displayed by different age-sex classes of bonnet macaques in the study troops.

3.5 References

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Chapter 4

Frequency and Use of Gestures by Bonnet Macaques:

Differences between Age- and Sex Classes

4.1 Introduction

The gestural repertoire of bonnet macaques is similar in size across age classes, from infants to juveniles and ultimately, adults. However, the types of gestures in this repertoire vary from age to age, with play gestures dominating the infant repertoire, and these being gradually replaced by affiliative and agonistic gestures in the adult repertoires. In addition to these age-differences, bonnet macaques also display sex differences in gesture repertoire size, females having a larger repertoire, especially consisting of affiliative gestures, than the males. These observations, which have been discussed in the previous chapter, indicate the presence of developmental processes underlying the ontogenetic acquisition of the gestural repertoire by individuals. It is however, important to investigate the differences in performance of such gestures in terms of their frequency of use by individuals belonging to various age class and sex categories, in order to understand the functionality of such gestures and the processes of gradual change with age, if present.

In humans, the effects of social rank on gesture deployment has been reported in children till the age of four to ten years, wherein particular gestures, especially aggressive ones, were directed down the hierarchy towards socially adjacent individuals (Hold 1976). There also seemed to have been a gradual change in facial gestures in young children with varying social positions (Zivin 1977). It has also been reported that there are perhaps sex-differences in the types of gestures used by humans, with aggressive gestures typically displayed at higher frequencies by males than by females (Maccoby and Jacklin 1980; Buss and Shackelford 1997). Such observations suggest a subtle role for social ranks, sender-receiver social positions and sex differences in the use of human gestures.

In some species of nonhuman primates, especially apes, the frequency of gesture use is the highest in juveniles, mostly in the context of play, but which eventually decreases in adults (Tomasello et al. 1994; Tomasello et al. 1997; Pika et al. 2003; Liebal et al. 2006; Genty et al. 2009; Hobaiter and Byrne 2011). In other primate species, such as rhesus macaques, the dominance ranks of individuals play a crucial role in determining the frequency of use of certain gestures (Maestripieri and Wallen 1997). Although not particularly in the context of gestural communication, Seyfarth (1976, 1977) and Fairbanks (1980) did observe that positive social behaviour such as allogrooming was always received at higher proportions by dominant vervet monkey individuals. Such allogrooming behaviour was exchanged mostly among individuals of adjacent social ranks. In general, sex differences do appear to exist in gesture use across many species, where particular gestures are used either by males or females at high proportions (Maestripieri 1996; Maestripieri and Wallen 1997; Maestripieri 2005; Hobaiter and Byrne 2012).

Most studies in nonhuman primates that have explored the influence of age or sex on the performance of gestures, as revealed by the frequency of their use, have been carried out on great apes. Among non-ape species, gestural communication in rhesus macaques, pigtailed macaques and stumptailed macaques have been investigated in some detail, particularly with respect to the functional use of such gestures by individuals of different social ranks. However, these studies followed a rather broad definition of gestures, which included facial expressions, body postures and limb movements, irrespective of the intentionality behind such signals, thus not complying with the strict definition of gestural communication in ape studies (see, for example, Call and Tomasello 2007). Moreover, the influence of the nature of the sender-receiver combination involved in gestural communication was not addressed in these studies. I, however, feel that it is imperative to follow the definitions of gestures, that have been standardised for ape and human studies, for other primate species as well, in order to facilitate comparative studies across taxa and to arrive at a more comprehensive understanding of the evolution of gestural communication in the primate lineage, including humans.

In this chapter, I investigate the frequencies of gestures used across different contexts by bonnet macaques belonging to varying age and sex classes, and determine the possible differences between them, as has been established for apes (Tomasello et al. 1994, 1997; Pika et al. 2003; Liebal et al. 2006; Genty et al. 2009; Hobaiter and Byrne 2011). I also intended to understand the pairwise interactions, and their variation, in the frequency of gestures deployed towards recipients of varying age and sexes, in order to understand whether particular sender-receiver pairs influenced the frequency of certain types of gesturing (see also Maestripieri 1996 and Liebal et al. 2006). Finally, I attempted to understand the direction of gesture use along the dominance hierarchy, separately in males and in females, as well as the influence of rank differences between individuals on the frequency of gesturing towards one another; this would facilitate a comparison of such patterns, if any, with those that have been observed in the case of other social behaviours such as allogrooming in other primate species (Seyfarth 1976, 1977; Fairbanks 1980; Maestripieri and Wallen 1997; Schino and Aureli 2008; Tiddi et al. 2012; Macdonald et al. 2013).

4.2 Methods

4.2.1 *Data Collection and Analysis*

This study was conducted on the study bonnet macaque troops TT1, HN2, TT2, C3 (described in Table 2.1, Chapter 2) in the Bandipur National Park of Karnataka state in southern India. Data on the frequency of different types of gestures used (Tables 2.2 and 2.4, Chapter 2) were collected from 29 adult females, 23 adult males, 31 juveniles and 26 infants through 15-min focal animal sampling on randomly chosen individuals without replacement (Altmann 1974). Video recordings were conducted to substantiate the observations whenever necessary.

The frequency of gestures displayed by each individual was calculated as follows:

$$\text{Gesture frequency} = \frac{\Sigma\ [\{b_{1\text{-}2} / (t_1 + t_2)\} + \{b_{1\text{-}3} / (t_1 + t_3)\} + ... + \{b_{1\text{-}n} / (t_1 + t_n)\}]}{n}$$

where,

$b_{1\text{-}2}$ = number of gestures displayed by Individual 1 towards Individual 2

t_1 = total duration of observation on Individual 1 (h)

t_2 = total duration of observation on Individual 2 (h)

n = total number of individuals that received gestures from Individual 1

The dominance hierarchy and age classes of individuals in each troop were determined following the methods described in Chapter 2 of this thesis.

Observations, which totalled 392.5 h, were carried out daily from 09:00 to 17:30, during the period from February 2013 to July 2014. In this chapter, I have only considered those gestures displayed in the contexts of affiliation, agonism and play by all individuals, as in Chapter 2. Descriptive, non-parametric, statistical tests, including Mann-Whitney U-test and Spearman's rank correlation were conducted with the help of the software R, version 3.1.0 (R Core Team 2014) and SPSS Statistics 17.0 (SPSS Inc. 2008).

4.3 Results

4.3.1 *Age differences in frequency of gesture use*

4.3.1.1 *Frequency of gesture use: Population level*

The juveniles of the study troops displayed significantly higher frequencies of all gestures, as compared to the adults, while the adults used a higher frequency of gestures than did the infants (Tables 4.1 and 4.2, Figure 4.1). Moreover, the frequency of all gesture types displayed by individuals of all age classes significantly decreased with increasing age (Spearman's rank correlation, rho = -0.27, n = 109, p = 0.005; Figure 4.2, Panel 1).

The contextual frequencies of affiliative gestures exhibited by adults, juveniles and infants, taken together across all troops (Table 4.1), were not significantly different from one another (Table 4.2, Column 3). Affiliative gesture frequencies, however, positively correlated with increasing age (Spearman's rho = 0.19, n = 109, p = 0.05; Figure 4.2, Panel 2).

Table 4.1 Total and contextual gesture frequencies displayed by individual bonnet macaques of different age classes

Context of gestures	**Frequency of gestures (act/h)**		
	Adults **n = 52**	**Juveniles** **n = 31**	**Infants** **n = 26**
Affiliation			
Mean ± SE	0.77 ± 0.06	0.65 ± 0.05	0.64 ± 0.06
Range	0.26 – 2.08	0.19 – 1.49	0.32 – 1.31
Agonism			
Mean ± SE	0.30 ± 0.03	0.23 ± 0.05	0.11 ± 0.03
Range	0 – 0.83	0 – 1.07	0 – 0.57
Play			
Mean ± SE	0.18 ± 0.05	0.78 ± 0.11	0.91 ± 0.13
Range	0 – 1.81	0 – 2.52	0.22 – 2.45
Total			
Mean ± SE	1.25 ± 0.09	1.73 ± 0.12	1.66 ± 0.17
Range	0.44 – 3.48	0.74 – 3.64	0.65 – 3.60

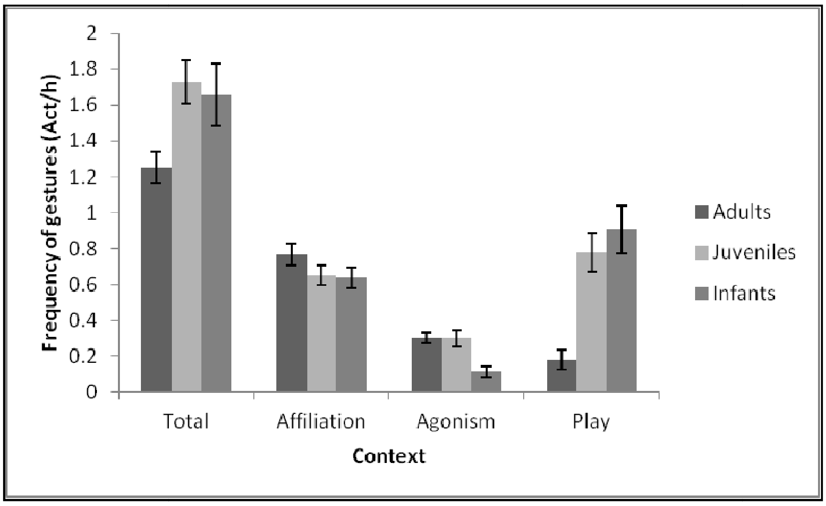

Figure 4.1 Mean frequencies of gestures displayed by adults, juveniles and infants of the four study troops in different contexts. The error bars represent standard error of the mean

Adult bonnet macaque individuals, across all the troops, on the other hand, displayed the highest frequency of agonistic gestures, as compared to both the juveniles and infants (Table 4.2, Column 4). Agonistic gesture frequency, similar to that of affiliation, increased significantly with age (Spearman's rho = 0.43, n = 109, $p < 0.001$; Figure 4.2, Panel 3).

Table 4.2 Comparison of the gesture frequencies displayed by individual bonnet macaques of different age classes across contexts

Age class		**Affiliation** **U, *p***	**Agonism** **U, *p***	**Play** **U, *p***	**Total** **U, *p***
Adult n = 52	**Juvenile** n = 31	U = 715.50 *p* > 0.30	U = 742.50 *p* > 0.50	**U = 252** ***p* < 0.001**	**U = 441** ***p* < 0.01**
Adult n = 52	**Infant** n = 26	U = 585 *p* > 0.30	**U = 252** ***p* < 0.001**	**U = 144** ***p* < 0.001**	**U = 481** ***p* < 0.04**
Juvenile n = 31	**Infant** n = 26	U = 374 *p* > 0.60	**U = 186** ***p* < 0.001**	U = 374 *p* > 0.60	U = 305.50 *p* > 0.20

The frequencies were compared using two-tailed Mann-Whitney U-tests. The statistically significant differences have been highlighted in bold

In the context of play, however, juveniles and infants displayed significantly higher frequencies of gestures than did the adults, while being comparable to one another (Table 4.2, Column 5). The displayed frequency of play gestures was negatively correlated to age (Spearman's rho = -0.18, n = 127, $p < 0.05$; Figure 4.2, Panel 4).

4.3.1.2 *Frequency of gesture use: Troop level*

The frequencies of all gestures and those displayed in the contexts of affiliation, agonism and play, by individuals of different age classes in each of the four study troops have been presented in Figure 4.3 and Table 4.3.

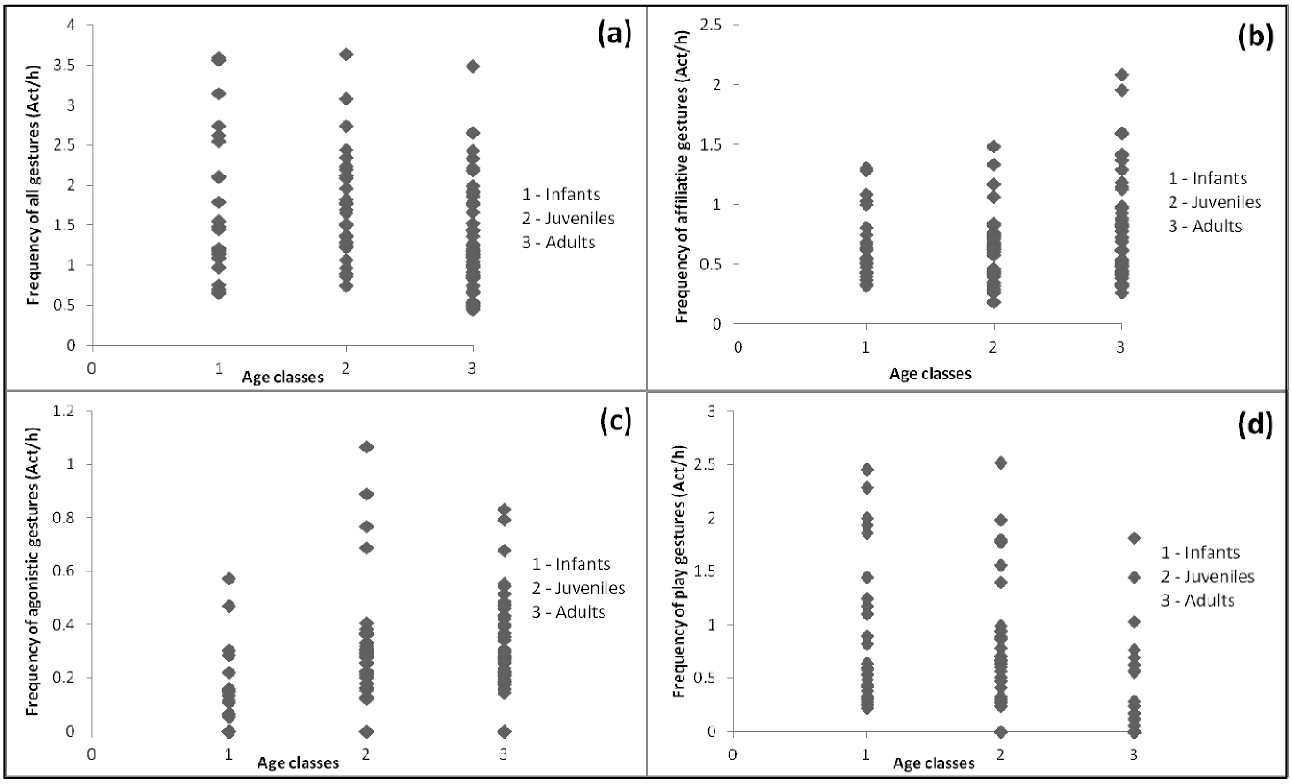

Figure 4.2 Correlation between total and contextual gesture frequencies and age class in the study troops: (a) Total, (b) Affiliative, (c) Agonistic and (d) Play gestures

The frequency of all gestures displayed by the adults were comparable across troops (Table 4.3), with no significant differences between one another, except for Troop TT2, in which the adults showed a higher frequency of gestures than did those in Troop TT1 (Table 4.4). The affiliative gesture frequency displayed by the adults of TT2 and C3 was significantly higher than those in TT1 and TT2 respectively (Table 4.4). The affiliative and agonistic gesture frequencies of the TT2 adults were higher than those of HN2. Play gesture frequency amongst the adults were not compared due to insufficient sample size.

Amongst the juveniles, the total gesture frequency displayed was significantly higher in Troop TT2 as compared to those in all the other troops (Table 4.3, Table 4.4); the total frequency was also significantly higher amongst C3 juveniles than those in either Troop TT1 or in HN2 (Tables 4.3 and 4.4). The affiliative and play gesture frequencies were higher amongst the Troop TT2 juveniles than those in Troops HN2 and C3; juveniles of Troop C3 displayed significantly more affiliative gestures than those in HN2. The displayed agonistic gesture frequency was higher in C3 juveniles than those in TT2. Play gesture frequency in Troop TT2 juveniles was higher than those in Troop TT1 (Table 4.3, Table 4.4).

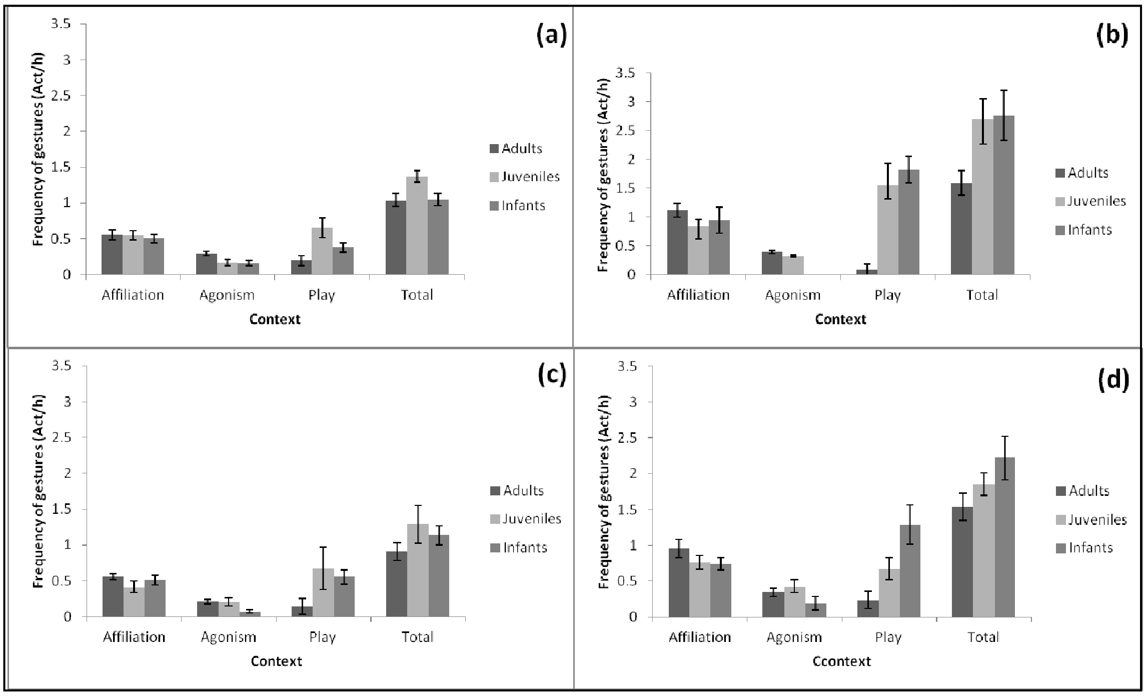

Figure 4.3 **Total and contextual gesture frequencies of adult, juvenile and infant bonnet macaques in the four study troops: (a) Troop TT1, (b) Troop TT2, (c) Troop HN2 and (d) Troop C3. The error bars represent standard error of the mean**

The infants of Troops TT2 and C3 exhibited significantly higher levels of total gesture frequency than those in Troops TT1 and HN2 respectively. The play gesture frequency had similar patterns in all the troops. The affiliative gesture frequency of Troop C3 infants was higher than those in HN2 while the frequency of agonistic gestures was greater in Troop TT1 infants than those in TT2 (Table 4.3, Table 4.4).

Table 4.3 Total and contextual gesture frequencies displayed by individual bonnet macaques of different age classes in the four study troops

Troop and age class	**Frequency of gestures (act/h) in different contexts**			
	Affiliation Mean ± SE Range	**Agonism** Mean ± SE Range	**Play** Mean ± SE Range	**Total** Mean ± SE Range
Troop TT1				
Adult n = 14	0.55 ± 0.07 0.32 – 1.15	0.29 ± 0.03 0.18 – 0.55	0.19 ± 0.07 0.11 – 0.77	1.04 ± 0.09 0.52 – 1.44
Juvenile n = 9	0.55 ± 0.07 0.26 – 0.84	0.17 ± 0.04 0.12 – 0.41	0.65 ± 0.14 0.27 – 1.56	1.37 ± 0.08 1.82 – 1.36
Infant n = 6	0.50 ± 0.06 0.33 – 0.75	0.16 ± 0.04 0.13 – 0.31	0.38 ± 0.06 0.22 – 0.58	1.04 ± 0.09 0.64 – 1.21
Troop TT2				
Adult n = 7	1.11 ± 0.12 0.81 – 1.59	0.39 ± 0.03 0.28 – 0.51	0.63 ± 0.00	1.59 ± 0.21 1.18 – 2.65
Juvenile n = 4	0.84 ± 0.12 0.62 – 1.17	0.31 ± 0.03 0.22 – 0.39	1.54 ± 0.38 0.88 – 2.52	2.70 ± 0.35 1.96 – 3.64
Infant n = 4	0.94 ± 0.22 0.37 – 1.31	0.00	1.82 ± 0.23 1.18 – 2.29	2.76 ± 0.44 1.55 – 3.60
Troop HN2				
Adult n = 13	0.56 ± 0.04 0.26 – 0.78	0.21 ± 0.03 0.14 – 0.43	0.14 ± 0.11 0.05 – 1.44	0.90 ± 0.13 0.44 – 2.19
Juvenile n = 5	0.41 ± 0.08 0.19 – 0.67	0.20 ± 0.06 0.16 – 0.36	0.67 ± 0.30 0.24 – 1.80	1.29 ± 0.26 0.74 – 2.12
Infant n = 9	0.51± 0.07 0.32 – 1.03	0.07 ± 0.02 0.05 – 0.15	0.55 ± 0.10 0.30 – 1.24	1.14 ± 0.13 0.67 – 1.79
Troop C3				
Adult n = 18	0.95 ± 0.13 0.31 – 2.08	0.34 ± 0.06 0.19 – 0.83	0.24 ± 0.06 0.17 – 1.81	1.54 ± 0.19 0.49 – 3.49
Juvenile n = 13	0.76 ± 0.10 0.35 – 1.49	0.43 ± 0.09 0.18 – 1.07	0.67 ± 0.15 0.47 – 1.99	1.85 ± 0.67 0.89 – 3.09
Infant n = 7	0.74 ± 0.08 0.50 – 1.09	0.19 ± 0.09 0.29 – 0.57	1.29 ± 0.09 0.48 – 2.45	2.22 ± 0.30 1.14 – 3.56

Table 4.4 Comparison of the total and contextual gesture frequencies displayed by individual bonnet macaques of different age classes in the four study troops

Age class	Comparison	Affiliation U, p	Agonism U, p	Play U, p	Total U, p
Adult	TT1 vs TT2 (n = 14, 7)	**U = 8** **$p = 0.001$**	U = 24 $p > 0.06$	-	**U = 17** **$p < 0.02$**
	TT1 vs HN2 (n = 14, 13)	U = 80 $p > 0.60$	U = 69 $p > 0.30$	-	U = 62 $p > 0.10$
	TT1 vs C3 (n = 14, 18)	**U = 66** **$p < 0.03$**	U = 108 $p > 0.50$	-	U = 84 $p > 0.10$
	TT2 vs HN2 (n = 7, 13)	**U = 0** **$p < 0.001$**	**U = 7** **$p = 0.001$**	-	**U = 6** **$p = 0.001$**
	TT2 vs C3 (n = 7, 18)	U = 48 $p > 0.30$	U = 47 $p > 0.30$	-	U = 51 $p > 0.40$
	HN2 vs C3 (n = 13, 18)	U = 75 $p > 0.09$	U = 81 $p > 0.10$	-	**U = 54** **$p < 0.02$**
Juvenile	TT1 vs TT2 (n = 9, 4)	U = 7 $p > 0.10$	U = 6 $p > 0.07$	**U = 3** **$p < 0.03$**	**U = 0** **$p < 0.01$**
	TT1 vs HN2 (n = 9, 5)	U = 14 $p > 0.20$	U = 18 $p > 0.60$	U = 17 $p > 0.50$	U = 18 $p > 0.60$
	TT1 vs C3 (n = 9, 13)	U = 38 $p > 0.10$	**U = 26** **$p < 0.04$**	U = 55 $p > 0.80$	**U = 8** **$p < 0.001$**
	TT2 vs HN2 (n = 4, 5)	**U = 1** **$p < 0.04$**	U = 4 $p > 0.10$	U = 3 $p > 0.10$	**U = 28** **$p < 0.05$**
	TT2 vs C3 (n = 4, 13)	U = 18 $p > 0.40$	U = 23 $p > 0.70$	**U = 6** **$p < 0.03$**	**U = 1** **$p < 0.04$**
	HN2 vs C3 (n = 5, 13)	**U = 11** **$p < 0.04$**	U = 16.50 $p > 0.10$	U = 31 $p > 0.90$	**U = 8** **$p < 0.05$**
Infant	TT1 vs TT2 (n = 6, 4)	U = 5 $p > 0.10$	**U = 2** **$p < 0.04$**	**U = 0** **$p = 0.01$**	**U = 0** **$p = 0.01$**
	TT1 vs HN2 (n = 6, 9)	U = 26 $p > 0.90$	U = 11.50 $p > 0.06$	U = 15 $p > 0.10$	U = 24 $p > 0.70$

	TT1 vs C3 (n = 6, 7)	U = 7 $p > 0.05$	U = 19 $p > 0.80$	**U = 2** **$p = 0.005$**	**U = 2** **$p = 0.005$**
	TT2 vs HN2 (n = 4, 9)	U = 8 $p > 0.10$	U = 6 $p > 0.07$	**U = 1** **$p < 0.005$**	**U = 2** **$p < 0.02$**
	TT2 vs C3 (n = 4, 7)	U = 9 $p > 0.40$	U = 8 $p > 0.30$	U = 8 $p > 0.30$	U = 7 $p > 0.20$
	HN2 vs C3 (n = 6, 7)	**U = 9** **$p < 0.02$**	U = 30 $p > 0.90$	**U = 8** **$p < 0.02$**	**U = 7** **$p < 0.009$**

Frequencies were compared using two-tailed Mann-Whitney U-tests. The statistically significant differences have been highlighted in bold

4.3.2 *Sex differences in frequency of gesture use*

4.3.2.1 *Frequency of gesture use: Population level*

The adult females across the four study troops displayed a mean (± SE) frequency of all gestures of 1.25 ± 0.12 act/h, while the adult males exhibited a frequency of 1.03 ± 0.12 act/h, the total gesture frequencies across the two sexes being comparable (Mann Whitney U-test, two-tailed, U = 235, n = 29 and 23, $p > 0.05$). However, the gesture frequencies for each context varied significantly across the two sexes. Affiliative and agonistic gestures were, thus, displayed more by adult females (Affiliative: 0.87 ± 0.08 act/h, Agonistic: 0.32 ± 0.03 act/h) than by the adult males (Affiliative: 0.48 ± 0.07 act/h, U = 103, n = 29 and 23, $p < 0.0001$; Agonistic: 0.22 ± 0.03, U = 226, n = 29 and 23, $p < 0.05$); play gestures were, however, more frequent amongst the adult males (0.33 ± 0.09 act/h) than amongst the females (0.06 ± 0.02 act/h, U = 239, n = 29 and 23, $p < 0.05$; Figure 4.4).

4.3.2.2 *Frequency of gesture use: Troop level*

The gestural frequencies displayed by the adult females and males were compared across the study troops (Table 4.5).

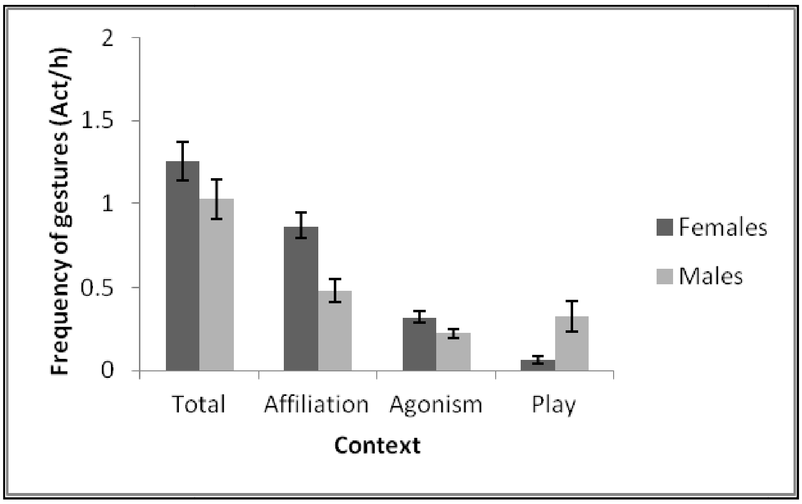

Figure 4.4 **Mean frequencies of total and contextual gestures displayed by the adult females and males of the four study troops. The error bars represent standard error of the mean**

The adult females of Troop TT2 displayed a significantly higher frequency of total and affiliative gestures as compared to those of both Troops TT1 and HN2 (Tables 4.5 and 4.6). The adult females of Troop C3 exhibited a higher frequency of affiliative gestures than did those of Troops TT1 and HN2 while the Troop TT2 females displayed a higher frequency of agonistic gestures than did the Troop HN2 females.

Adult males, on the other hand, displayed comparable total gestural frequencies across troops (Tables 4.5 and 4.6). In the Troop TT1, however, the adult males exhibited a higher frequency of affiliative and agonistic gesture frequencies than did those in Troop C3 and Troop HN2 respectively. Play gestures were, once again, not considered in this analysis due to insufficient sample size.

4.3.2.3 *Frequency of gesture use: Individual level*

Among adult females, the frequency of gesture use was not influenced by increasing age, except for play gestures, which were negatively correlated to the age category within adults (Table 4.7). In case of adult males, the frequencies of performance of all gestures decreased with increasing age category. Affiliative and agonistic gesture frequencies did not depend on age, however, while play gesture frequencies were negatively correlated with increasing age (Table 4.7). Data for these analyses were pooled across all individuals in the four study troops in order to incorporate representatives of all the adult age categories present in the study population.

Table 4.5 Total and contextual gesture frequencies displayed by adult females and males in the four study troops

Troop and adult sex class	**Frequency of gestures (act/h) in different contexts**		
	Affiliation Mean ± SE Range	**Agonism** Mean ± SE Range	**Total** Mean ± SE Range
Troop TT1			
Female n = 7	0.73 ± 0.10 0.33 – 1.15	0.29 ± 0.06 0.18 – 0.55	1.08 ± 0.12 0.52 – 1.44
Male n = 7	0.37 ± 0.02 0.32 – 0.49	0.29 ± 0.04 0.19 – 0.48	1.00 ± 0.14 0.54 – 1.52
Troop TT2			
Female n = 6	1.16 ± 1.13 0.81 – 1.59	0.39 ± 0.03 0.28 – 0.51	1.66± 0.23 1.20 – 2.66
Male n = 1	0.83	0.36	1.18
Troop HN2			
Female n = 8	0.65 ± 0.03 0.50 – 0.78	0.2 ± 0.03 0.23 – 0.43	0.93 ± 0.07 0.50 – 1.16
Male n = 5	0.40 ± 0.05 0.26 – 0.54	0.18 ± 0.02 0.14 – 0.21	0.86 ± 0.34 0.44 – 2.19
Troop C3			
Female n = 8	1.27 ± 0.17 0.48 – 2.08	0.52 ± 0.09 0.21 – 0.83	1.83 ± 0.30 0.75 – 3.49
Male n = 10	0.70 ± 0.15 0.31 – 1.96	0.32 ± 0.05 0.19 – 0.55	1.30 ± 0.22 0.50 – 2.43

Table 4.6 Comparison of the total and contextual gesture frequencies displayed by adult female and male bonnet macaques in each of the study troops

Adult sex class	Comparison	Affiliation U, *p*	Agonism U, *p*	Total U, *p*
Female	TT1 vs TT2 (n = 7, 6)	**U = 6** $\boldsymbol{p < 0.04}$	U = 12 $p > 0.20$	**U = 6** $\boldsymbol{p < 0.04}$
	TT1 vs HN2 (n = 7, 8)	U = 23 $p > 0.60$	U = 26 $p > 0.80$	U = 18 $p > 0.20$
	TT1 vs C3 (n = 7, 8)	**U = 9** $\boldsymbol{p < 0.03}$	U = 16 $p > 0.10$	U = 14 $p > 0.10$
	TT2 vs HN2 (n = 6, 8)	**U = 0** $\boldsymbol{p = 0.001}$	**U = 6** $\boldsymbol{p < 0.03}$	**U = 0** $\boldsymbol{p = 0.01}$
	TT2 vs C3 (n = 7, 18)	U = 19 $p > 0.50$	U = 22 $p > 0.80$	U = 24 $p = 1.00$
	HN2 vs C3 (n = 13, 18)	**U = 8** $\boldsymbol{p = 0.01}$	U = 19.50 $p > 0.10$	**U = 9** $\boldsymbol{p < 0.02}$
Male	TT1 vs HN2 (n = 7, 5)	U = 16 $p > 0.80$	**U = 2** $\boldsymbol{p = 0.01}$	U = 8 $p > 0.10$
	TT1 vs C3 (n = 7, 10)	**U = 12** $\boldsymbol{p < 0.03}$	U = 30 $p > 0.60$	U = 28 $p > 0.50$
	HN2 vs C3 (n = 5, 10)	U = 15 $p > 0.20$	U = 13 $p > 0.10$	U = 10 $p > 0.07$

The frequencies were compared using two-tailed Mann-Whitney U-tests. The statistically significant differences have been highlighted in bold

The influence of the social dominance rank of the adult individuals on their frequencies of use of different gestures was investigated separately for females and males for each study troop. The frequencies of total and contextual gestures, except those of play, were not dependent on the dominance ranks of both female and male individuals in Troops TT2 and C3. However, in Troop TT1, while female social rank did not influence gesture frequencies, there was a significant negative correlation between the rank hierarchy of males and their frequencies of overall gesturing in this troop (Table 4.8). In Troop C3, in contrast, the frequencies of exhibited affiliative and agonistic gestures increased with dominance rank amongst females (Table 4.8). Play gestures were analysed only when at least 50% of the adult individuals displayed at least one play gesture in each troop. There was a significant negative correlation between the frequencies of play gestures and dominance ranks only amongst the males of Troop TT1 (Table 4.8).

Table 4.7 Correlation of the total and contextual gesture frequencies displayed by the adult female and male bonnet macaques to their age class in the four study troops

Adult sex category	**Affiliation** **ρ, *p***	**Agonism** **ρ, *p***	**Play** **ρ, *p***	**Total** **ρ, *p***
Female n = 29	ρ = 0.16 *p* = 0.42	ρ = 0.15 *p* = 0.44	**ρ = -0.40** **$p < 0.04$**	ρ = 0.09 *p* = 0.61
Male n = 23	ρ = -0.15 *p* = 0.49	ρ = 0.16 *p* = 0.45	**ρ = -0.57** **$p < 0.01$**	**ρ = -0.48** **$p < 0.03$**

The correlations were evaluated using Spearman's rank correlation test. The statistically significant differences have been highlighted in bold

4.3.3 *Gesture frequency: Sender-recipient pairs*

4.3.3.1 *Age-sex pairs*

In pairwise interactions, I aimed to determine the possible differences in the mean frequency of gestures displayed in each context by individuals belonging to various age-sex categories towards the other members of each study troop (Table 4.9). The highest number of interactions was observed in juvenile – juvenile pairs (44.76% of play, 35.24% of affiliative and 20% of agonistic gestures), followed by adult female – infant pairs (66.17% of affiliative, 31.34% of agonistic and 2.49% of play gestures) and adult female – adult female pairs (79.35% of affiliative and 20.65% of agonistic gestures).

Table 4.8 Correlation of the total and contextual gesture frequencies displayed by adult female and male bonnet macaques with their social dominance ranks within their respective troops

Troop	Adult sex category	Affiliation ρ, *p*	Agonism ρ, *p*	Play ρ, *p*	Total ρ, *p*
TT1	Female (n = 7)	ρ = -0.25 *p* = 0.59	ρ = -0.16 *p* = 0.78	-	ρ = -0.03 *p* = 0.94
	Male (n = 7)	ρ = - 0.49 *p* = 0.27	ρ = -0.45 *p* = 0.31	**ρ = -0.93** ***p* < 0.01**	**ρ = -0.85** ***p* < 0.03**
TT2	Female (n = 6)	ρ = 0.86 *p* = 0.87	ρ = -0.60 *p* = 0.21	-	ρ = -0.37 *p* = 0.47
	Male (n = 1)	-	-	-	-
HN2	Female (n = 8)	ρ = 0.36 *p* = 0.39	**ρ = 0.71** ***p* = 0.05**	-	**ρ = 0.76** ***p* < 0.04**
	Male (n = 5)	ρ = 0.10 *p* = 0.87	ρ = - 0.10 *p* = 0.87	ρ = -0.21 *p* = 0.74	ρ = -0.10 *p* = 0.87
C3	Female (n = 8)	ρ = 0.48 *p* = 0.23	ρ = 0.64 *p* = 0.09	-	ρ = 0.55 *p* = 0.16
	Male (n = 10)	ρ = 0.10 *p* = 0.77	ρ = 0.50 *p* = 0.14	-	ρ = 0.12 *p* = 0.75

The correlations were evaluated using Spearman's rank correlation test. The statistically significant differences have been highlighted in bold

Adult females exhibited significantly higher frequencies of affiliative gestures towards infants than they did towards juveniles or adult males (Table 4.10, Column 2). Affiliative gestures displayed by adult females towards one another were significantly higher than those towards juveniles and adult males (Table 4.10, Column 2). Agonistic gesture frequencies displayed by adult females were preferentially directed towards other adult females, juveniles and infants, as compared to those towards adult males (Table 4.10, Column 3). Play gestures displayed by adult females were not analysed due to insufficient sample size.

Adult males, in general, did not show any significant differences between the frequencies of affiliative gestures that they directed towards individuals of any age-sex class. Agonistic gestures from males were directed at highest frequencies towards infants, followed by towards other adult males and juveniles (Table 4.9). None of these were, however, significantly different from one another. Agonistic gestures displayed by adult males towards adult females were, in contrast, significantly lower than those directed towards other members of the troop (Table 4.10, Column 3). Play gestures displayed by adult males were not significantly different towards any of the particular age-sex categories observed (Table 4.10, Column 4).

Juvenile individuals showed the highest frequency of affiliative gestures towards infants, as compared towards other juveniles, adult females or adult males (Table 4.9 and Table 4.10, Column 2). Juveniles displayed most of their agonistic gestures towards other juveniles and infants, both at significantly higher levels than those shown towards adult females (Table 4.10, Column 3). Juveniles hardly interacted agonistically with adult males (only five instances). During play behaviour, juveniles directed play gestures significantly more towards other juveniles than towards infants (Table 4.10, Column 4). Play gestures were rarely directed by them towards adult females (only three instances) or adult males (only 13 instances).

Table 4.9 Total and contextual gesture frequencies displayed by different age-pairs of bonnet macaques in the four study troops

Age-sex pair	Frequency of gestures (act/h) in different contexts		
	Affiliation Mean ± SE Range	**Agonism** Mean ± SE Range	**Play** Mean ± SE Range
Adult female – Adult female	n = 146 0.90 ± 0.07 0.06 – 11.14	n = 38 0.27 ± 0.04 0.08 – 2.85	-
Adult female – Adult male	n = 42 0.33 ± 0.05 0.06 – 2.74	n = 6 0.14 ± 0.04 0.12 – 0.27	-

Adult female – Juvenile	n = 85 0.63 ± 0.08 0.05 – 3.71	n = 70 0.35 ± 0.04 0.05 – 2.00	-
Adult female – Infant	n = 133 1.26 ± 0.12 0.06 – 5.33	n = 63 0.44 ± 0.06 0.05 – 1.11	-
Adult male – Adult female	n = 64 0.39 ± 0.04 0 – 3.20	n = 33 0.16 ± 0.01 0.05 – 1.06	n = 1 1.44± 0.00
Adult male – Adult male	n = 62 0.40 ± 0.04 0.07 – 1.39	n = 25 0.29 ± 0.05 0.02 – 1.06	n = 7 0.77 ± 0.30 0.05 – 1.33
Adult male – Juvenile	n = 62 0.46 ± 0.06 0 – 1.79	n = 50 0.29 ± 0.03 0.01 – 0.70	n = 15 0.96 ± 0.34 0.05 – 2.65
Adult male – Infant	n = 39 0.75 ± 0.18 0.07 – 1.22	n = 19 0.37 ± 0.07 0.08 – 1.28	n = 5 0.15± 0.03 0.11 – 4.35
Juvenile – Adult female	n = 95 0.52 ± 0.05 0.05 – 5.23	n = 13 0.14 ± 0.03 0.04 – 0.39	n = 3 0.22 ± 0.10 0.04 – 5.25
Juvenile – Adult male	n = 55 0.35 ± 0.04 0.09 – 3.39	n = 5 0.16 ± 0.03 0.10 – 0.55	n = 13 0.85 ± 0.20 0.23 – 1.11
Juvenile – Juvenile	n = 74 0.47 ± 0.07 0.35 – 3.60	n = 43 0.27 ± 0.03 0.05 – 0.88	n = 94 1.06 ± 0.13 0.05 – 6.29
Juvenile – Infant	n = 101 1.14 ± 0.12 0.05 – 7.75	n = 27 0.39 ± 0.06 0.06 – 0.66	n = 24 0.46 ± 0.07 0.09 – 6.71
Infant – Adult female	n = 78 0.67 ± 0.10 0.05 – 5.18	n = 11 0.19 ± 0.04 0.06 – 0.57	n = 2 0.83 ± 0.26 0.15 – 1.45
Infant – Adult male	n = 33 0.24 ± 0.05 0.06 – 3.50	-	n = 3 0.14 ± 0.03 0.45 – 0.97

Infant – Juvenile	n = 41 0.34 ± 0.04 0.05 – 1.87	n = 5 0.16 ± 0.07 0.06 – 0.28	n = 31 0.45 ± 0.08 0.07 – 2.62
Infant – Infant	n = 84 0.78 ± 0.07 0.05 – 3.03	n = 12 0.14 ± 0.02 0.05 – 0.43	n = 70 0.95 ± 0.12 0.06 – 4.89

Infants showed affiliative gestures at significantly higher frequencies towards other infants as compared to those towards juveniles, adult females or adult males (Table 4.10, Column 2). Infants directed affiliative gestures more frequently towards adult females than they did towards adult males (Table 4.10, Column 2). They displayed no agonistic gestures towards adult males while those exhibited towards adult females, juveniles or other infants did not significantly vary from one another. In play gestures, infants showed the highest frequencies towards other infants than they did towards juveniles (Table 4.10, Column 4). They, however, rarely displayed play gestures towards adult females (only two instances) or towards adult males (only three instances).

Table 4.10 Comparison of the contextual gesture frequencies initiated in pairwise interactions by bonnet macaques towards individuals of different age-sex categories

Category	**Affiliation** **n, U, *p***	**Agonism** **n, U, *p***	**Play** **n, U, *p***
F–F vs F–M	**n = 146, 42** **U = 1363** **p < 0.001**	**n = 38, 6** **U = 53.50** **p < 0.04**	-
F–F vs F–J	**n = 146, 85** **U = 4325.50** **p < 0.001**	n = 38, 70 U = 1144.50 p > 0.20	-
F–F vs F–I	n = 146, 133 U = 8688 p > 0.10	n = 38, 63 U = 1003.50 p > 0.10	-

F–M vs F–J	**n = 42, 85** **U = 1345** **$p < 0.03$**	**n = 6, 70** **U = 77.50** **$p < 0.02$**	-
F–M vs F–I	**n = 42, 133** **U = 1142** **$p < 0.001$**	**n = 6, 63** **U = 80.50** **$p < 0.001$**	-
F–J vs F–I	**n = 85, 133** **U = 3567** **$p < 0.001$**	n = 70, 63 U = 2102 $p > 0.60$	-
M–F vs M–M	n = 64, 62 U = 1925 $p > 0.70$	**n = 32, 24** **U = 252** **$p < 0.03$**	-
M–F vs M–J	n = 64, 61 U = 1933 $p > 0.90$	**n = 32, 50** **U = 502** **$p = 0.005$**	-
M–F vs M–I	n = 64, 39 U = 984.50 $p > 0.07$	**n = 32, 19** **U = 129.50** **$p = 0.001$**	-
M–M vs M–J	n = 62, 61 U = 1848 $p > 0.80$	n = 24, 50 U = 591 $p > 0.90$	-
M–M vs M–I	n = 62, 39 U = 984 $p > 0.10$	n = 24, 19 U = 175 $p > 0.10$	-
M–J vs M–I	n = 61, 39 U = 970 $p > 0.10$	n = 50, 19 U = 373.50 $p > 0.10$	-
J–F vs J–M	**n = 94, 55** **U = 2019** **$p < 0.03$**	n = 12, 4 U = 16 $p > 0.30$	n = 4, 9 U = 6 $p > 0.10$
J–F vs J–J	n = 94, 74 U = 3004 $p > 0.10$	**n = 12, 42** **U = 98** **$p = 0.001$**	**n = 3, 94** **U = 47** **$p < 0.05$**
J–F vs J–I	**n = 94, 101** **U = 3115.50** **$p < 0.001$**	**n = 12, 27** **U = 64** **$p < 0.01$**	n = 3, 24 U = 17.50 $p > 0.10$

J–M vs J–J	n = 55, 74 U = 1854.50 $p > 0.30$	n = 4, 42 U = 39 $p > 0.08$	n = 12, 94 U = 556.50 $p > 0.90$
J–M vs J–I	**n = 55, 101** **U = 1288** **$p < 0.001$**	n = 4, 27 U = 28 $p > 0.10$	n = 12, 24 U = 91 $p > 0.70$
J–J vs J–I	**n = 74, 101** **U = 2080.50** **$p < 0.001$**	n = 42, 27 U = 970 $p > 0.30$	**n = 94, 24** **U = 790** **$p < 0.03$**
I–F vs I–M	**n = 78, 33** **U = 881.50** **$p < 0.01$**	-	n = 2, 3 U = 0 $p > 1.00$
I–F vs I–J	n = 78, 41 U = 1539 $p > 0.70$	n = 11, 5 U = 21 $p > 0.50$	n = 2, 30 U = 9 $p > 0.10$
I–F vs I–I	**n = 78, 84** **U = 2320** **$p = 0.001$**	n = 11, 12 U = 58 $p > 0.60$	n = 2, 70 U = 51.50 $p > 0.50$
I–M vs I–J	**n = 33, 41** **U = 425.50** **$p < 0.01$**	-	n = 3, 30 U = 18 $p = 0.10$
I–M vs I–I	**n = 33, 84** **U = 450.50** **$p < 0.001$**	-	**n = 3, 70** **U = 21** **$p < 0.02$**
I–J vs I–I	**n = 41, 84** **U = 889** **$p < 0.001$**	n = 5, 12 U = 27.50 $p > 0.70$	**n = 30, 70** **U = 678** **$p = 0.005$**

The frequencies were compared using two-tailed Mann-Whitney U-tests. The statistically significant differences have been highlighted in bold. F = Adult females, M = Adult male, J = Juvenile, I = Infant

4.3.3.2 *Rank differences in pairs*

Adult females and adult males of the study population displayed pairwise affiliative gestures towards other adult females and males respectively independently of their dominance ranks within each pair (Female-female pairs: Subordinate – Dominant vs Dominant – Subordinate, Mann-Whitney U-test, two-tailed, U = 2406.5, n = 69 and 73, $p > 0.60$; Male-male pairs: Subordinate – Dominant vs Dominant – Subordinate, U = 396, n = 37 and 25, $p > 0.30$). Agonistic gestures, however, were directed down the hierarchy at significantly higher frequencies, both amongst adult female and male pairs (Female-female pairs: Subordinate – Dominant vs Dominant – Subordinate, U = 16.50, n = 3 and 35, $p < 0.05$; Male-male pairs: Subordinate – Dominant vs Dominant – Subordinate, U = 25, n = 6 and 18, $p < 0.06$; Figure 4.5).

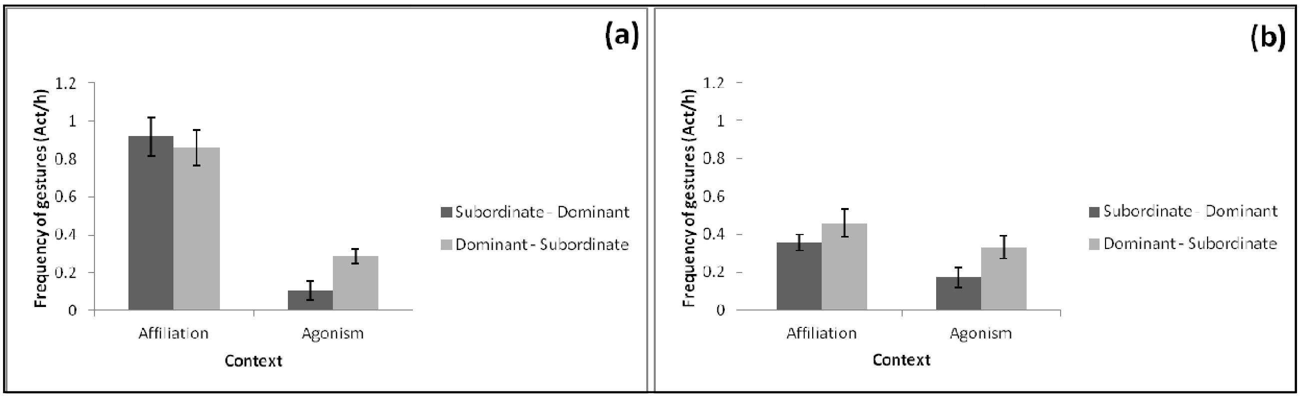

Figure 4.5 Frequencies of gestures displayed by dominant and subordinate (a) adult females and (b) adult males in pairwise interactions with other adult females and males respectively. The error bars represent standard error of the mean

I also investigated whether the rank difference between individuals in pairwise interactions influenced the frequency of gesturing by the species. Increasing or decreasing rank differences across individuals were not correlated with the frequency of affiliative gestures, particularly in females, although there was a strong trend towards a greater frequency of gesturing by the subordinate partner in pairs of males of increasing rank difference (Female-female pairs: Spearman's rank correlation, rho = -0.026, n = 142, $p = 0.76$; Male-male pairs: Spearman's rho = 0.24, n = 62, $p = 0.06$). There was no significant pattern in agonistic gesturing by both the sexes as well (Female-female pairs: Spearman's rho = 0.15, n = 38, $p = 0.37$; Male-male pairs: Spearman's rho = 0.27, n = 24, $p = 0.20$).

4.4 Discussion

4.4.1 *Age differences in frequency of gesture use*

4.4.1.1 *Frequency of gesture use: Population level*

The use of gestures by bonnet macaques varies with their age class, with juveniles displaying the highest frequency of total gesture use. Such an observation has been reported for several ape species as well (chimpanzees: Tomasello et al. 1994, Tomasello et al. 1997, Pika et al. 2003, Hobaiter and Byrne 2011; gorillas: Genty et al. 2009; orangutans: Liebal et al. 2006), wherein the frequencies of gesture use also declined after the juvenile stage. Contextual gestures, or those displayed in the contexts of affiliation, agonism and play, were also used variably by bonnet macaque individuals of various age classes. Affiliative gestures were uniformly frequent in every age class, while adults and juveniles displayed more frequent agonistic gestures in their repertoire than did infants. Infants, on the other hand, exhibited the highest frequency of play gestures, followed by juveniles, with their levels significantly declining in the adults.

When the total frequency of gesture use was considered, infants were observed to mostly have play and affiliative gestures in their communication repertoire, which were gradually joined by agonistic gestures at the juvenile stage while, finally, the adult repertoire predominantly came to consist of affiliative and agonistic gestures. Thus, the juvenile stage appeared to be the age at which bonnet macaques used most of the gesture categories at comparable levels in their repertoire, possibly leading to the highest frequency of total gesture use amongst the three age classes studied. The overall frequency of gestures was negatively correlated with age in bonnet macaques, with affiliative and agonistic gestures significantly increasing with age, while play gesture frequencies decreased comparably. Similar conclusions could be drawn about the gestural repertoire size of the individuals of the four study troops, wherein play gestures dominated the infant and juvenile gestural repertoires while affiliative and agonistic gesture types primarily constituted the adult repertoire structure (Chapter 3).

4.4.1.2 *Frequency of gesture use: Troop level*

The frequency of gesture use by individual macaques across age classes revealed distinct patterns within each of the study troops. Individuals of Troops TT2 and C3, in general, displayed higher frequencies of gestures in all contexts, particularly when compared to those exhibited by individuals of the troops TT1 and HN2. Although a comparison of the respective repertoire sizes of individuals across troops did not suggest members of TT2 to be significantly distinct from the rest of the study population, they definitely stood out with respect to their gesture usage. Similarly, C3 members had a significantly smaller repertoire size than those of Troops HN2 or TT1 although they displayed higher frequencies of gestures in all contexts in comparison to individuals of the other troops. Is it possible that it was imperative for the individuals of the unimale-multifemale troop TT2 to communicate with each other relatively more frequently in order to maintain group cohesion and avoid predators, given their smaller troop size, as compared to the other study troops? Troop C3 individuals, residing in a relatively larger, more open habitat, could potentially require more gestures than those in Troops HN2 and TT1, which occupied restricted home ranges in predominantly human-dominated areas. It is, thus, conceivable that the frequency of use of gestures was probably more influenced by the immediate socio-environmental conditions of each study troop rather than the structure or richness of the repertoire per se.

4.4.2 ***Sex differences in frequency of gesture use***

4.4.2.1 *Frequency of gesture use: Population level*

Sex differences in the use of gestures were also prominent in case of adult bonnet macaques, similar to the observations made for their respective repertoire sizes as well (Chapter 2). The frequency of use of all gestures across contexts was not significantly different amongst adult females and males; however, females displayed higher frequencies of both affiliative and agonistic gestures than did males. These high levels of gestural display were possibly compensated by the relatively high frequency of play gestures displayed by adult males, thus yielding comparable levels of total gestural frequencies by the two sexes. The use of play gestures by male bonnet macaques possibly owed much to the subadult males, who were included in this category and who often engaged in high levels of play behaviour. Sexual differences in gesture use have also been reported in other primates such as the pigtailed macaque, wherein the frequency of certain gestures, as, for instance mounting or headstands, were relatively more displayed by males than by females (Maestripieri 1996, 1997) or in chimpanzees, where males exhibited higher frequencies of consortship gestures than did females (Hobaiter and Byrne 2012). This is perhaps in concordance with the hypothesis proposed by Scott (2013) that differential selective pressures on females and males may have resulted in the differential use of gestures by the two sexes in primates, and the bonnet macaque may be no exception.

4.4.2.2 *Frequency of gesture use: Troop level*

The adult females of Troops TT2 and C3 displayed relatively higher frequencies of gestures than did those in the troops HN2 or TT1, a similar trend to that observed across age classes. The adult males of Troop TT1, however, exhibited higher affiliative and agonistic gestures, as compared to those displayed by the males of Troops HN2 and C3 respectively. This could result from the fact that, during the study period, there was a change in the alpha, or the most dominant, male in this troop, which may have necessitated increased communication between the males of this group, across contexts, in order to negotiate their newly forming social roles. It is noteworthy that in this case too, it be reiterated that the variability in such gesture use across troops did not necessarily match the observed variability in the respective gestural repertoire sizes of the study troops.

4.4.2.3 *Frequency of gestures: Individual level*

The frequency of display of affiliative and agonistic gestures did not appear to be influenced by the different age categories of adult female and male bonnet macaques. However, the exhibition of play gestures was negatively correlated with adult age, which was probably influenced by the higher frequency of play gestures displayed by subadult males, the levels of which eventually decreased once they became prime adults.

The dominance hierarchy also did not have any influence on the frequency of gestures used by both adult females and males, similar to the general trend observed earlier in pigtailed macaques (Maestripieri 1996); however, further investigations focussing on particular gestures of other macaque species have reported a prominent effect of rank on frequency of gesture use in case of rhesus macaques, stumptailed macaque and even in pigtailed macaques (Maestripieri 2005). The observed negative correlation of play gesture frequencies with increasing age of the adult males in one of my study troops of bonnet macaques, however, suggests that the social dominance hierarchy could potentially affect gesture use in some cases, as, for example, play gestures by subadult males in this particular study.

4.4.3 *Gesture frequency: Sender-recipient pairs*

4.4.3.1 *Age-sex pairs*

The most number of interactions involving gestural communication occurred amongst juveniles with one another, followed by adult females towards infants and between the adult females themselves. Juveniles engaged in play behaviour during most part of their interactions and used play gestures at relatively high frequencies. Similar observations have been made in orangutans, where juveniles and subadults engaged in most part of gestural communications events (Liebal et al. 2006). Infant bonnet macaques displayed the highest frequency of affiliative and play behaviour towards other infants. Between adult females and males, infants directed higher frequencies of affiliative behaviour towards the former, possibly because infants generally interact with their mothers and their female associates most of the time in this typically female-bonded society. There was hardly any agonistic behaviour displayed by infants. Juveniles, on the other hand, displayed the highest frequencies of affiliative and agonistic gestures towards infants, while they preferred to direct their play gestures towards other juveniles more frequently than towards infants. Thus, it seems, both infants and juveniles tend to engage in play behaviour with members of their own age cohort, rather than playing with one another.

In the case of adult females, affiliative gestures were most frequently displayed towards infants, followed by towards juveniles and the least towards adult males. This is also probably driven by the fact that adult females always tended to associate most with their own infants and juveniles, with whom they engaged in most affiliative interactions. Amongst adults, females showed significantly higher frequency of both affiliative as well as agonistic gestures towards other females, rather than towards males, another hallmark of a female-bonded society, such as that of bonnet macaques, wherein adult females need to maintain their respective social positions, both through appropriately applied affiliative and agonistic interactions (Smuts et al. 1987). Adult males, in contrast, displayed no significant differences in the frequencies of gestures that they exhibited towards receivers of any age class or sex. However, their frequencies of agonistic gestures were significantly directed towards infants and juveniles, as compared to those towards adult females. Thus, it seems that the communication interactions of both sexes of bonnet macaques follow distinct patterns, possibly driven by their particular ecological roles and social compunctions (Scott 2013).

4.4.3.2 *Rank differences in pairs*

Finally, when the directionality of gestures with respect to dominance ranks of senders and receivers was explored, no particular relationship could be discerned between affiliative gestures and the dominance hierarchy, both amongst adult females and males, unlike that suggested for allogrooming behaviour (Seyfarth 1976; Seyfarth 1977; Fairbanks 1980). However, frequencies of agonistic gestures were significantly directed down the hierarchy in both sexes, as has been seen earlier in the case of submissive gestures in rhesus macaques (Maestripieri and Wallen 1997). I also attempted to determine whether rank differences between individuals affected the frequency of gesturing towards one another, but this revealed no significant patterns in case of either affiliative or agonistic gestures, both in females and in males. Thus, my observations do not match those on adult female vervet monkeys wherein individuals received more allogrooming from individuals of adjacent rank (Fairbanks 1980). There was, however, a strong trend in affiliative gestures being displayed by the subordinate individual at higher frequencies in pairwise interactions between males of increasing rank difference.

Similar to the gestural repertoire size in the species, the frequency of use of contextual gestures by bonnet macaques appears to be characterised by distinct developmental patterns, with variable frequencies of gestures used at various ages. Individuals perhaps possess the capacity to produce most gestures from birth but, nevertheless, use certain gestures more than others at a particular age, this repertoire gradually changing with time. It is important to note here that I could not detect any idiosyncratic use of particular gestures by my study individuals and thus, did not find any evidence for ontogenetic ritualisation processes, as has been reported earlier in chimpanzees (Tomasello et al. 1994; Pika et al. 2003; Call and Tomasello 2007). It, however, appears possible that other processes similar to that postulated in the gradual-learning model (Seyfarth and Cheney 1997) for the use of vocal communication in vervet monkeys could underlie the development of gestural communication in bonnet macaques. In order to further investigate such processes, the next chapter will explore the gestural repertoire and frequency of gestural use by infant and juvenile bonnet macaques, with a particular focus on their social interactions, their mothers' social positions and their own individual tendencies—a consideration of the plausible causes influencing the gradual development of gestural communication in the species.

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Chapter 5

Factors influencing development of gestural repertoires and their use in immature bonnet macaques

5.1 Introduction

The gestural profile of bonnet macaques, constructed on the basis of signals that are displayed towards particular individuals in flexible and intentional ways, has been described in Chapter 2. The results presented in Chapters 3 and 4 suggest that the contextual gestural repertoires as well as their frequency of use possibly undergo developmental processes during the lifetime of individuals. The affiliative and agonistic repertoire sizes significantly grow with age while the play repertoire reduces; frequencies of agonistic gestures also increase with age and again, the degree of use of play gestures decreases with time. The appearance of such age-specific gesture assemblages and specific patterns of their usage could be influenced by several possible developmental factors. In ape gestures, for example, it has been suggested that the predominant process underlying the development of gestural communication is that of 'direct conventionalization' or 'ontogenetic ritualisation', by dint of which a signal becomes a gesture by individualistic learning of the sender and its receiver (Tomasello et al. 1985, 1989, 1994, 1997; reviewed in Call and Tomasello 2007; see also Bekoff 1972).

Some reports of gestural communication in wild chimpanzees (Hobaiter and Byrne 2011) and gorillas (Genty et al. 2009), however, suggested processes other than that of ontogenetic ritualisation behind gestural development in apes. Genetically inherited signals were postulated to be used in flexible intentional ways, meeting the definitional criteria of gestures that had already been laid down (see Call and Tomasello 2007). In my study, the apparent lack of individual idiosyncratic gestures and the existence of variability in gestural repertoire size and gesture use within specific age classes in bonnet macaques (discussed in Chapter 3) largely suggest factors that potentially influence the development of gestures in this species, distinct from those that result in individualistic ritualisation. Amongst the several factors that could be responsible for the appearance of such patterns in the gestural repertoire of bonnet macaques, a crucial factor could be gradual motor development in the production of gestures; this factor has also been suggested to be important in gestural onset and early use of gestures in several ape species (Schneider et al. 2011). Even in human children, it has been suggested that the beginning of locomotory activities has significant effect on their cognitive development (reviewed in Campos et al. 2000). Maturation of motor capacities has also been considered crucial for the production of calls in primates (Seyfarth and Cheney 1997). Additionally, inherent genetic and neural factors have been hypothesised to be instrumental in affecting the development of emotional as well as cognitive processes, eventually leading to particular primate communication profiles (Adolphs 2001). It has also been reported that sudden changes in the genetic environment of individuals could significantly influence vocal behaviour in avian and mammalian species (Janik and Slater 2000). It is also conceivable that the development of gestures in primates could be similarly influenced by such factors though such detailed studies are lacking in these taxa.

Apart from such physical and physiological factors, the importance of the surrounding social environment in influencing the developmental patterns of gestural communication cannot be ignored. Although not directly investigated in communicative behaviours, such influences have been explored in related contexts, as, for example, the development of social behaviour. It has, thus, been reported that female and male rhesus macaque individuals, reared in the absence of their mothers, grew to be more submissive and aggressive respectively in their social interactions (Wallen 1996). Bekoff (1972) has similarly suggested that the relationships of infants to all other age-sex categories of individuals within the social group should be considered in our attempts to understand social influences on communication development, particularly in mammals.

It is, therefore, important to directly explore the contributions of the immediate social environment, particularly the social interactions that an individual undergoes in the course of development, and the role of the mother and other close kin on the ontogeny of communication patterns, including those of gestures. It should be noted, however, that bonobo and chimpanzee infants did not appear to be influenced by their respective mother's gestures, as evident from a lack of gesture sharing between the respective individuals (Schneider et al. 2012). It is conceivable, nevertheless, that the differential positions of mothers in the prevailing social dominance hierarchy could expose their offspring to variable communication environments, in turn, affecting developmental processes. Human speech development, for instance, has been known to depend to the levels of social exposure in the form of acquaintance with adult talk and enhanced motivations to verbally communicate with others (Locke and Snow 1997). The vocal behaviour of birds and nonhuman mammals has also been suggested to be affected considerably by such environmental factors (Janik and Slater 2000). Schneider et al. (2011) also speculate that the weaning of infants may have an important role in the possible increase of their gesturing levels, as this is the phase when they attain independent identities as social components of the group, as they emerge from their mother's protective care (also see van Lawick-Goodall 1968).

The observations of the onset of gestures in the four ape species (Schneider et al. 2011) indicated differential trajectories of development of gesture modalities, visual gestures being predominant during the initial phases of gesturing, possibly as a result of the various evolutionary pressures that these species are subject to. In monkeys, however, the onset of tactile gestures appeared to take precedence over those of visual gestures during the initial stages of life, gradually being complemented with the latter with increasing age (Grigor'eva and Deryagina 1987). Could this modality specificity also be a fall out of the specific social environments that individuals of a particular species finds itself in? Or, is it more a species-typical, genetically modulated phenomenon?

There have been several studies in ape gestures that attempted to understand the ongoing developmental processes underlying gestural communication, by investigating specific gestures in young individuals alone (Plooij 1978, 1984; Tomasello et al. 1985; Bard 1988; Tomasello et al. 1989, 1994; Pika et al. 2003; Schneider et al. 2011). I attempted to similarly explore, in this chapter, the factors that may influence the age-specific appearance and usage of gestural communication by bonnet macaques. As Tinbergen (1951) and Welker (1961) had very aptly suggested, that the ontogeny of any behaviour during younger stages is important to understand the adult behaviour of a species, I have further classified my study infant and juvenile individuals into more specific age categories, differing by one year each, and investigated the differences in gesture repertoire size and frequency of their use with every year of progress. I have also considered age and repertoire size as proxies for individual factors potentially acting as predictor variables of the frequency of gesture use. In addition, the mother's rank and frequency of gestures received by an individual from all the other members of the troop have been considered as social factors possibly influencing the repertoire size and gesture use of these infants and juveniles. Although this study is not as exhaustive as earlier attempted by Schneider et al. (2011), wherein they had tracked the gestural trajectory of captive individual apes in each month of their early life, I reiterate here that my study is a preliminary endeavour to unravel and understand the potential biological and social influences on gesture development in bonnet macaques in the wild.

5.2 Methods

5.2.1 *Data collection and analysis*

This study was conducted on four troops of free-ranging bonnet macaques in the Bandipur National Park in the state of Karnataka in southern India, during February 2013 to July 2015. The description of the troops has been provided in Table 2.1 of Chapter 2. Behavioural data were collected through 15-minute focal animal sampling on randomly chosen individuals without replacement (Altmann 1974), and the gestures used by individuals considered on the basis of the list tabulated in Chapter 2 (Tables 2.2 and 2.4). Gesture frequencies were calculated using the same formula described in Chapter 4 (Section 4.2.1). The 26 individuals in the study troops that belonged to the infant age class were further classified into age categories of 0-1 year and 1-2 year of age while the 31 individuals belonging to the juvenile age class were classified into the age categories of 2-3 year, 3-4 year and >4 year of age. Data were based on a total of 175 hours of observation, with a mean (± SE) of 3.07 ± 0.28 h for each individual, ranging from a total of 0.5 to 9.5 h. The descriptive analysis of the data was conducted using SPSS Statistics 17.0 (SPSS Inc. 2008).

I also used generalised linear modelling to understand the influence of individual and social factors on the gestures displayed by these individuals. The predictor variables for a particular response variable— frequency of gestures displayed by an individual—were repertoire size, age category of the individual, frequencies of received gestures and the mother's rank in the dominance hierarchy (for known mother-infant pairs). For another response variable—individual gestural repertoire size—the predictor variables considered were age category of the individual, frequency of gesture received and the mother's rank. I ran multiple models with the factors in isolation as well as in various combinations to determine the best-fit models using second-order Akaike's Information Criterion (AICc). I then considered the averaged best-fit models to comprehend the influence of the significant predictors tested on the gestural repertoire size and the frequency of gesture use by the infant and juvenile study individuals. For this purpose, I used the package MuMIn in the statistical software R, version 3.1.0 (R Core Team 2014).

5.3 Results

5.3.1 *Gestural repertoire size and frequency of gesture use by different age categories*

Tactile gestures were represented in the gestural repertoire of every study individual in all the age categories observed. In contrast, visual gestures were displayed by 27.27% of the infants belonging the 0-1 year age category (n = 11) and 12.5% of the 1-2 year-old age category (n = 8). All the juveniles in the 2-3 year-old category (n = 16), 88.24% in the 3-4 year-old category (n = 17) and all juveniles of the >4 year-old category (n = 5) exhibited the use of visual gestures. The gestural repertoire size and the frequency of gesture use, however, varied across these age categories. Among infants, only two visual gestures—Lip-Smacking and Open-Mouth Threat in Play—were displayed by more than 50% of all individuals (listed in Table 3.8 of Chapter 3). However, all the other six visual gestures—Soliciting Allogrooming, Head-Jerking, Lunging, Lunging in Play, Open-Mouth Threatening in Play and Spot-Jumping (listed in Table 2.2 of Chapter 2)—were displayed by more than 50% of the juveniles in the study troops.

The mean frequencies of use of tactile and visual gestures by the study infant and juvenile macaques (Table 5.1; Figure 5.1) were compared across the age categories (Table 5.2). Tactile gestures were used comparably by these immature individuals belonging to all the observed age categories. The frequencies of tactile gestures displayed by the study individuals were also not significantly correlated to their increasing age (Spearman's rank correlation, rho = -0.057, n = 57, *p* > 0.60).

Table 5.1 Frequencies of tactile and visual gestures displayed by the study infant and juvenile bonnet macaques

Age category	**Frequency of gestures (act/h) in different modalities**	
	Tactile Mean ± SE Range	**Visual** Mean ± SE Range
0-1 year-old infants n = 11	15.78 ± 2.01 8 – 28.62	3.01 ± 0.63 2 – 7.43
1-2 year-old infants n = 8	18.96 ± 2.80 11.53 – 31.10	5.59 ± 2.21 0 – 20.52
2-3 year-old juveniles n = 16	18.95 ± 3.07 3 – 55.56	8.19 ± 1.47 2.29 – 26.67
3-4 year-old juveniles n = 17	14.47 ± 2.07 2 – 29.11	8.32 ± 1.16 1.5 – 18.67
>4 year-old juveniles n = 5	14.67 ± 2.75 8.33 – 20.94	8.75 ± 0.86 6 – 10.35

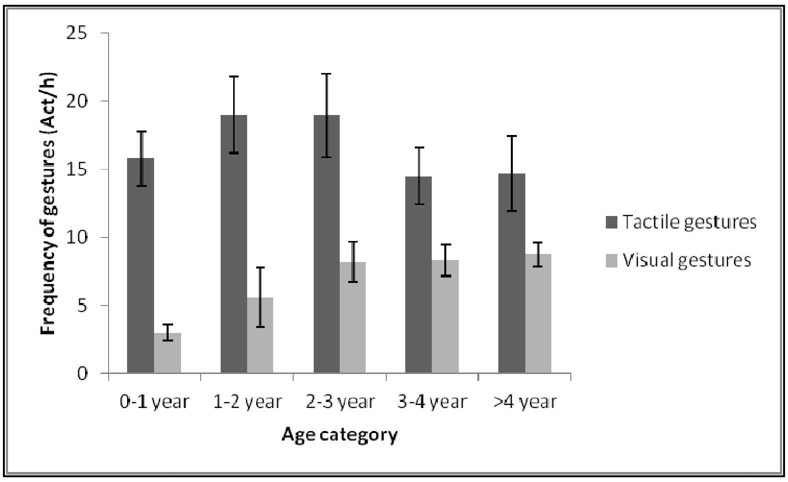

Figure 5.1 Frequencies of tactile and visual gestures displayed by the study infant and juvenile bonnet macaques

The frequencies of visual gesture use by infants in the 0-1 year age category, however, were significantly less than those by juveniles in the 2-3 year, 3-4 year and >4 year age categories. It is informative that the 1-2 year-old infants displayed significantly lower frequencies of visual gestures than did the oldest juveniles in the >4 year old age category.

Table 5.2 Comparison of the frequencies of tactile and visual gestures displayed by the study infant and juvenile bonnet macaques

Age category	**Tactile** **(U, *p*)**	**Visual** **(U, *p*)**
0-1 year vs 1-2 year n = 11, 8	U = 33.50 *p* > 0.30	U = 28 *p* > 0.20
0-1 year vs 2-3 year n = 11, 16	U = 74.50 *p* > 0.50	**U = 22.50** ***p* = 0.001**
0-1 year vs 3-4 year n = 11, 17	U = 89 *p* > 0.80	**U = 31** ***p* < 0.01**
0-1 year vs >4 year n = 11, 5	U = 27 *p* > 90	**U = 1.5** ***p* = 0.001**
1-2 year vs 2-3 year n = 8, 16	U = 62.50 *p* > 0.90	U = 35 *p* > 0.80
1-2 year vs 3-4 year n = 8, 17	U = 56 *p* > 0.50	U = 36 *p* > 0.06
1-2 year vs >4 year n = 8, 5	U = 15 *p* > 0.50	**U = 5** ***p* < 0.04**
2-3 year vs 3-4 year n = 16, 17	U = 111 *p* > 0.30	U = 123.50 *p* > 0.60
2-3 year vs >4 year n = 16, 5	U = 34 *p* > 0.60	U = 28 *p* > 0.30
3-4 year vs >4 year n = 17, 5	U = 42 *p* > 0.90	U = 38 *p* > 0.70

The frequencies of gestures displayed were compared using two-tailed Mann-Whitney U-tests. The statistically significant differences have been highlighted in bold

There was, however, neither any significant difference in the usage of visual gestures by the more proximate-aged 0-1 and 1-2 year-old infants nor by the older infants and the younger juveniles of the 2-3 year and 3-4 year age categories (Figure 5.1). The display of visual gestures also increased significantly with increasing age category of the study individuals (rho = 0.51, n = 57, $p < 0.001$).

The mean gestural repertoire size of the study infants and juveniles have been presented in Table 5.3 and Figure 5.2, while their contextual frequencies of affiliative, agonistic and play gestures are depicted in Table 5.4 and Figure 5.3.

Table 5.3 The contextual gestural repertoire size of the study infant and juvenile bonnet macaques belonging to different age categories

Age category	**Affiliative** Mean ± SE Range	**Agonistic** Mean ± SE Range	**Play** Mean ± SE Range
0-1 year-old infants n = 11	7.09 ± 1.08 1 – 14	0.82 ± 0.33 0 – 3	4 ± 0.38 2 – 7
1-2 year-old infants n = 8	9.38 ± 1.41 2 – 14	1.5 ± 0.60 0 – 4	4.62 ± 0.71 2 – 8
2-3 year-old juveniles n = 16	10.00 ± 1.31 1 – 17	1.86 ± 0.47 0 – 5	5.31 ± 0.46 2 – 9
3-4 year-old juveniles n = 17	9.12 ± 5.76 1 – 18	3.06 ± 0.67 0 – 9	5.76 ± 0.75 0 – 11
>4 year-old juveniles n = 5	13 ± 0.55 11 – 14	4.4 ± 1.03 2 – 8	3.4 ± 1.17 0 – 7

The results of a comparison of such gesture use by the study individuals belonging to the different age categories have been provided in Table 5.5. The affiliative repertoire size remained comparable across all the age categories observed, except that the juveniles of the >4 year category displayed a significantly larger repertoire size than did the youngest infants, belonging to 0-1 year category (Table 5.5, Column 2).

Table 5.4 **Frequencies of contextual gesture use by the study infant and juvenile bonnet macaques belonging to different age categories**

Age category	**Frequency of gestures (act/h) in different contexts**		
	Affiliation Mean ± SE Range	**Agonism** Mean ± SE Range	**Play** Mean ± SE Range
0-1 year-old infants n = 11	0.61 ± 0.09 0.31 – 1.28	0.10 ± 0.05 0 – 0.57	0.89 ± 0.22 0.22 – 2.45
1-2 year-old infants n = 8	0.60 ± 0.08 0.33 – 1.03	0.10 ± 0.04 0 – 0.22	0.95 ± 0.25 0.28 – 2.00
2-3 year-old juvenile n = 16	0.68 ± 0.08 0.26 – 1.30	0.24 ± 0.06 0 – 0.77	0.93 ± 0.15 0.24 – 2.29
3-4 year-old juveniles n = 17	0.61 ± 0.80 0.08 – 1.48	0.26 ± 0.05 0 – 0.89	0.80 ± 0.17 0 – 2.52
>4 year-old juveniles n = 5	0.81 ± 0.13 0.07 – 1.33	0.43 ± 0.16 0.18 – 1.07	0.38 ± 0.10 0 – 0.57

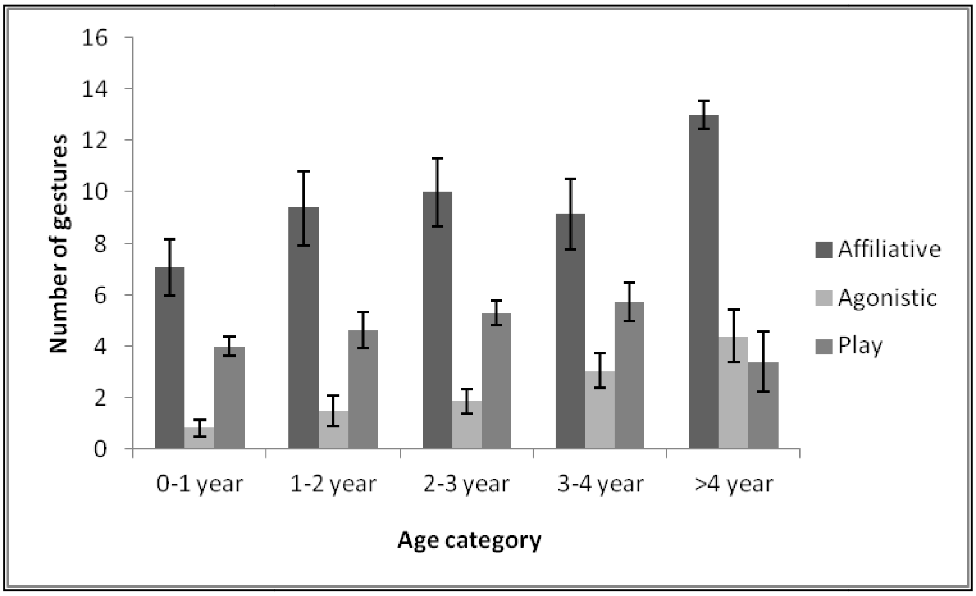

Figure 5.2 **Contextual gestural repertoire size of the study infant and juvenile bonnet macaques belonging to different age categories**

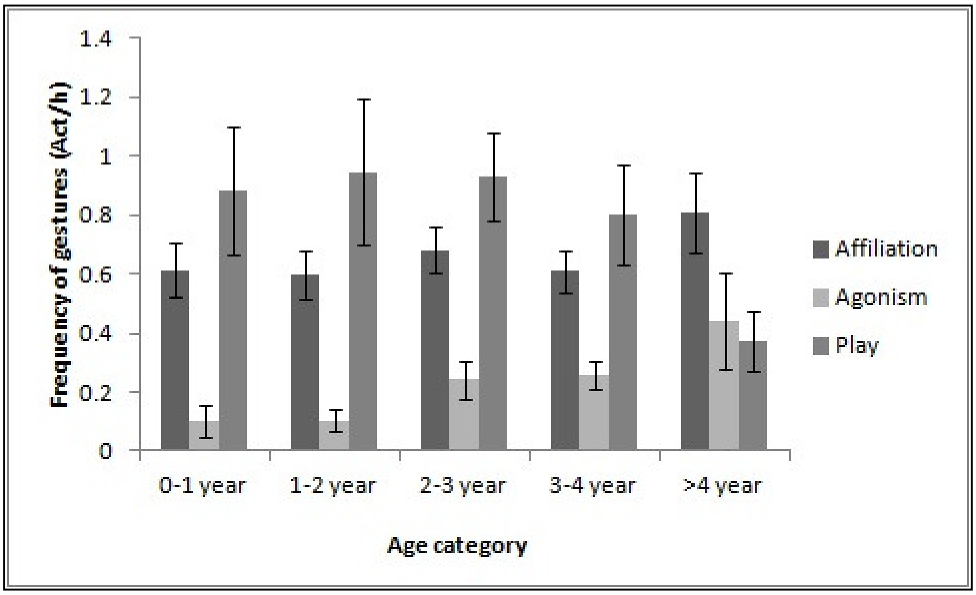

Figure 5.3 **Frequencies of contextual gesture use by the study infant and juvenile bonnet macaques belonging to different age categories**

The frequencies of affiliative gesture use, however, remained comparable across the age categories. The contextual agonistic repertoire size was significantly larger in the >4 year-old juveniles in comparison to the infants in the 0-1 year and the 1-2 year categories or the 2-3 year-old juveniles; moreover, the 3-4 year-old juveniles exhibited a larger agonistic repertoire than did the infants in the 0-1 year category (Table 5.5, Column 2). The frequencies of agonistic gestures was also significantly higher amongst individuals in the 3-4 year category than those in the 0-1 and 1-2 year categories while the oldest >4 year-old juveniles displayed significantly greater frequencies of such gestures than did the 0-1 year-old and 1-2 year-old infants. The play gestural repertoire, in contrast, was larger in 0-1 year-old infants, as compared the juveniles in 3-4 year category while the frequencies of play gesture use was higher among the 2-3 year-old juveniles than those in >4 year category (Table 5.5, Columns 2 and 3).

5.3.2 *Factors influencing the gestural repertoire size and frequencies of gestures displayed*

I considered six generalised linear models to test for the factors that could potentially influence the gestural repertoire sizes and thirteen models to examine those possibly influencing the frequencies of contextual gesture use by infant and juvenile bonnet macaques in each of the contexts of affiliation, agonism and play.

Table 5.5 Comparison of the gestural repertoire size and frequencies of contextual gesture use by the study infant and juvenile bonnet macaques belonging to different age categories

Context and age category	**Repertoire size (U, p)**	**Frequency of use (U, p)**
Affiliation		
0-1 year vs 1-2 year n = 11, 8	U = 27.50 $p > 0.10$	U = 42 $p > 0.90$
0-1 year vs 2-3 year n = 11, 16	U = 60 $p > 0.10$	U = 68 $p > 0.30$
0-1 year vs 3-4 year n = 11, 17	U = 71 $p > 0.30$	U = 87 $p > 0.70$
0-1 year vs >4 year n = 11, 5	**U = 4.5** **$p = 0.005$**	U = 13 $p > 0.10$
1-2 year vs 2-3 year n = 8, 16	U = 57 $p > 0.60$	U = 58 $p > 0.70$
1-2 year vs 3-4 year n = 8, 17	U = 67.50 $p > 0.90$	U = 66 $p > 0.90$
1-2 year vs >4 year n = 8, 5	U = 7.50 $p > 0.06$	U = 10 $p > 0.10$
2-3 year vs 3-4 year n = 16, 17	U = 120 $p > 0.50$	U = 115 $p > 0.40$
2-3 year vs >4 year n = 16, 5	U = 30.50 $p > 0.40$	U = 26 $p > 0.20$
3-4 year vs >4 year n = 17, 5	U = 25 $p > 0.10$	U = 26 $p > 0.20$
Agonism		
0-1 year vs 1-2 year n = 11, 8	U = 42 $p > 0.60$	U = 42.50 $p > 0.60$

0-1 year vs 2-3 year n = 11, 16	U = 75.50 $p > 0.40$	U = 51 $p > 0.09$
0-1 year vs 3-4 year n = 11, 17	**U = 53** **$p < 0.04$**	**U = 43** **$p < 0.01$**
0-1 year vs >4 year n = 11, 5	**U = 6** **$p < 0.01$**	**U = 6** **$p < 0.01$**
1-2 year vs 2-3 year n = 8, 16	U = 58 $p > 0.90$	U = 37 $p > 0.20$
1-2 year vs 3-4 year n = 8, 17	U = 43.50 $p > 0.10$	**U = 30** **$p < 0.03$**
1-2 year vs >4 year n = 8, 5	**U = 5.50** **$p < 0.04$**	**U = 3** **$p = 0.01$**
2-3 year vs 3-4 year n = 16, 17	U = 88.50 $p > 0.10$	U = 109 $p > 0.70$
2-3 year vs >4 year n = 16, 5	**U = 12.50** **$p < 0.03$**	U = 20 $p > 0.10$
3-4 year vs >4 year n = 17, 5	U = 26 $p > 0.20$	U = 26 $p > 0.20$
Play		
0-1 year vs 1-2 year n = 11, 8	U = 37 $p > 0.60$	U = 40 $p > 0.70$
0-1 year vs 2-3 year n = 11, 16	U = 51.50 $p > 0.07$	U = 76 $p >0.50$
0-1 year vs 3-4 year n = 11, 17	**U = 49.5** **$p < 0.04$**	U = 84 $p > 0.60$
0-1 year vs >4 year n = 11, 5	U = 23 $p > 0.60$	U = 18 $p > 0.30$
1-2 year vs 2-3 year n = 8, 16	U = 49.50 $p > 0.30$	U = 60 $p > 0.80$
1-2 year vs 3-4 year n = 8, 17	U = 48 $p > 0.20$	U = 58 $p > 50$

1-2 year vs >4 year n = 8, 5	U = 14.50 $p > 0.40$	U = 11 $p > 0.20$
2-3 year vs 3-4 year n = 16, 17	U = 113.50 $p > 0.40$	U = 118 $p > 0.50$
2-3 year vs >4 year n = 16, 5	U = 23 $p > 0.10$	**U = 11** **$p < 0.02$**
3-4 year vs >4 year n = 17, 5	U = 22 $p > 0.10$	U = 28 $p > 0.20$

The gestural repertoire size and frequencies of gestures displayed were compared using two-tailed Mann-Whitney U-tests. The statistically significant differences have been highlighted in bold

The selected models that tested for affiliative repertoire size as well as displayed frequencies of affiliative gestures did not yield any significant result (Tables 5.6a, 5.6b, 5.7a and 5.7b).

Table 5.6a Component models showing significant predictor variables for the contextual gestural repertoire sizes of the study bonnet macaques

Predictor variable	Degree of freedom	Log likelihood	Akaike Information Criterion (AIC)	Delta AIC	Weight
Affiliative					
Frequencies of gestures received	3	-169.24	344.9	0.00	0.73
Age category	6	-166.62	346.9	1.99	0.27
Agonistic					
Age category	6	-121.27	256.20	0.00	1
Play					
Frequencies of gestures received	3	-127.55	261.50	0.00	1

Table 5.6b Model coefficients for significant predictors of the contextual gestural repertoire sizes of the study bonnet macaques

	Estimate	**Standard error**	**Z value**	***p***
Affiliative				
Intercept	9.37	1.84	5.03	< 0.001
Frequencies of gestures received	-0.77	1.08	0.70	0.49
1-2 year	0.62	1.52	0.40	0.69
2-3 year	0.78	1.61	0.48	0.63
3-4 year	0.55	1.31	0.41	0.68
>4 year	1.59	2.94	0.54	0.59
Agonistic				
Intercept	1.17	0.61	1.90	0.06
1-2 year	0.33	0.97	0.34	0.73
2-3 year	0.50	0.82	0.61	0.55
3-4 year	1.89	0.80	2.36	< 0.03
>4 year	3.23	1.13	2.86	< 0.01
Play				
Intercept	4.13	0.53	7.83	< 0.0001
Frequencies of gestures received	0.94	0.50	1.87	0.07

The agonistic repertoire size, on the other hand, was significantly predicted by age category, wherein these repertoire sizes were positively influenced by the 3-4 year-old and >4 year-old juveniles (Tables 5.6a and 5.6b); the agonistic repertoire size, in turn, positively influenced the frequencies with which the study infants and juveniles displayed agonistic gestures (Tables 5.7a and 5.7b).

None of the factors significantly influenced the play repertoire size of the study infant and juvenile macaques although the frequencies with which these individuals displayed play gestures were significantly influenced by the received frequencies of the same play gestures (Tables 5.6a, 5.6b, 5.7a and 5.7b).

A subset of this data, consisting of 26 infants (age categories of 0-1 year and 1-2 year) and juveniles (only the age category of 2-3 year) whose mothers were known, was analysed with an additional predictor variable, mother's rank, to determine its effects on the gestural repertoire size as well as the frequencies of gesture use by these immature bonnet macaques. The models did not, however, yield mother's rank to be a significant variable that could explain the observed contextual gestural repertoires or the frequencies of usage of such gestures by the select infant and juvenile bonnet macaques (Tables 5.8a, 5.8b, 5.9a and 5.9b).

Table 5.7a Component models showing significant predictor variables for the frequencies of gesture use in different contexts displayed by the study bonnet macaques

Predictor variable	Degree of freedom	Log likelihood	Akaike Information Criterion (AIC)	Delta AIC	Weight
Affiliation					
Frequencies of gestures received	3	-8.73	23.9	0.00	0.73
Frequencies of gestures received, Repertoire size	4	-8.55	25.9	1.96	0.27
Agonism					
Repertoire size	3	6.55	-6.6	0.00	1
Play					
Frequencies of gestures received	3	-28.07	62.6	0.00	0.67
Repertoire size, Frequencies of gestures received	4	-27.61	64	1.40	0.33

Table 5.7b Model coefficients for significant predictors of the frequencies of gesture use in different contexts displayed by the study bonnet macaques

	Estimate	Standard error	Z value	*p*
Affiliation				
Intercept	0.54	0.08	6.38	< 0.001
Frequencies of gestures received	0.11	0.07	1.56	0.12
Repertoire size	0.001	0.004	0.27	0.79
Agonism				
Intercept	0.14	0.04	3.41	< 0.002
Repertoire size	0.03	0.01	2.72	< 0.01
Play				
Intercept	0.10	0.12	0.84	0.40
Frequencies of gestures received	0.82	0.09	9.00	< 0.0001
Repertoire size	0.02	0.02	0.92	0.36

Table 5.8a Component models showing significant predictor variables for the contextual gestural repertoire sizes of a subset of the study infant and juvenile bonnet macaques

Predictor variable	Degree of freedom	Log likelihood	Akaike Information Criterion (AIC)	Delta AIC	Weight
Affiliative					
Frequencies of gestures received	3	-75.63	158.3	0.00	1
Agonistic					
Frequencies of gestures received	3	-46.32	99.7	0.00	1
Play					
Age category	4	-46.70	103.3	0.00	1

Table 5.8b Model coefficients for significant predictors of the contextual gestural repertoire sizes of a subset of the study infant and juvenile bonnet macaques

	Estimate	Standard error	Z value	*p*
Affiliative				
Intercept	11.97	2.09	5.72	< 0.001
Frequencies of gestures received	-3.11	1.73	-1.80	0.09
Agonistic				
Intercept	1.69	0.45	3.79	< 0.001
Frequencies of gestures received	-0.83	0.67	-1.24	0.23
Play				
Intercept	4.00	0.47	8.56	< 0.0001
1-2 year	0.63	0.72	0.87	0.39
2-3 year	1.71	0.75	2.29	< 0.04

5.4 Discussion

The study infant and juvenile bonnet macaques, belonging to all the observed age categories, used tactile gestures comparably; there was, however, a pronounced variability in the use of visual gestures. The frequencies of use of these gestures were, in general, comparatively lower in infants than in the juveniles. Moreover, the frequencies of visual gesture use significantly positively correlated to increasing age while those of tactile gestures remained relatively unaffected. I, thus, observed gestures in the visual modality to undergo significant development during the early years of bonnet macaque individuals, ultimately being represented ubiquitously in the gestural repertoire of all the study adults. It is striking that very similar developmental profiles for gestures in these two modalities have been reported earlier for immature stump-tailed macaques and hamadryas baboons (Grigor'eva and Deryagina 1987). This pattern, common across the monkey taxa observed, is, however, not in accordance with that in apes, which were found to use relatively more visual gestures at younger ages. As Schneider et al. (2011) have speculated, this noticeable difference could be due to differential selective pressures acting on the different species, now with their distinct phylogenetic histories.

Table 5.9a Component models showing significant predictor variables for the frequencies of gesture use in different contexts displayed by a subset of the study infant and juvenile bonnet macaques

Predictor variable	Degree of freedom	Log likelihood	Akaike Information Criterion (AIC)	Delta AIC	Weight
Affiliation					
Frequency of gestures received	3	-1.98	11.05	0.00	0.54
Repertoire size	3	-2.70	12.49	1.43	0.26
Frequency of gestures received, Repertoire size	4	-1.56	13.03	1.97	0.20
Agonism					
Frequency of gestures received	3	13.35	-19.62	0.00	0.67
Repertoire size	3	12.65	-18.21	1.41	0.33
Play					
Frequency of gestures received	3	-13.57	34.23	0.00	0.56
Age	5	-11.55	36.11	1.87	0.22
Repertoire size	4	-13.12	36.14	1.91	0.22

5.4.1 *Gestural repertoire size and frequency of gesture use by different age categories*

The affiliative and play gestural repertoire sizes as well as the respective frequencies of use of these contextual gestures remained largely comparable across the infants and juveniles observed, suggesting little influence of age on these two communicative functions. In the case of agonistic gestures, however, the repertoire size and the frequencies of their usage varied significantly between the youngest infants and the oldest juveniles, indicating perhaps a distinctive developmental trajectory. This is in contrast to the earlier findings from ape gesture studies, wherein affiliation-related gestures were observed to be less frequent among older apes during the development of gestural communication while play gestures gradually increased in their usage (Schneider et al. 2011); agonistic gesture development, unfortunately, has never been reported for apes.

Table 5.9b Model coefficients for significant predictors of the frequencies of gesture use in different contexts displayed by a subset of the study infant and juvenile bonnet macaques

	Estimate	**Standard error**	**Z value**	***p***
Affiliation				
Intercept	0.55	0.20	2.65	0.008
Frequencies of gestures received	0.13	0.12	1.08	0.280
Repertoire size	-0.01	0.01	0.58	0.563
Agonism				
Intercept	0.09	0.04	1.94	0.05
Repertoire size	0.03	0.02	1.20	0.23
Frequencies of gestures received	0.03	0.07	0.45	0.63
Play				
Intercept	0.03	0.22	0.13	0.90
Frequencies of	0.87	0.13	0.12	< 0.0001

gestures received				
1-2 year	0.08	0.18	0.45	0.65
2-3 year	0.04	0.12	0.32	0.74
Repertoire size	0.01	0.03	0.32	0.75

5.4.2 *Factors influencing the gestural repertoire size and frequency of gestures displayed*

The affiliative gestural repertoire or the frequencies of usage of these contextual gestures were not correlated to any of the factors that I employed in the generalised linear models. The agonistic gestural repertoire, however, appeared to be significantly developed in relatively mature juvenile bonnet macaques, belonging to the 3-4 year and >4 year age categories, indicating a possible age-related developmental trajectory of these particular contextual gestures. The frequencies of use of agonistic gestures, in turn, appeared to be significantly influenced by the agonistic repertoire sizes of individuals, indicating the presence of relatively greater number of these contextual gestures translating into higher frequencies of their use. Play gestures displayed by immature macaques, in contrast, seemed to be influenced only by the frequencies of similar gestures received from other troops members, suggesting that the immediate social environment may, in certain situations, shape the nature of gesture use in this macaque species.

In the quest for factors influencing gestural development in immature bonnet macaques, my observations indicate that various factors could differentially influence gestures used in functionally distinct contexts. It is noteworthy, for instance, that in the apparent absence of ontogenetic ritualisation as a process underlying gestural development in monkeys (and perhaps in wild apes; see Genty at al. 2009, Hobaiter and Byrne 2011), there could be an amalgamation of certain inherent biological factors, such as age and gestural repertoire size, as well as some immediate social factors, including, for example, the frequencies of gestures received during individual interactions, which might be instrumental in the gradual shaping of a species-specific adult gestural repertoire, in a species such as the bonnet macaque. It is imperative that further, more directed, studies are designed to understand the role of motor development as well as other genetically determined variables in determining the trajectories of gesture development in this species, akin to what has been conducted in the course of other behavioural and communication studies (see, for example, Wallen 1996; Locke and Snow 1997; Janik and Slater 2000; Adolphs 2001).

Although an in-depth, month-by-month, analysis of the progression of gesture development, similar to what had been attempted earlier by Schneider et al. (2011) in captive apes, was not possible during the course of this study on wild bonnet macaques, subsequent investigations focussing on immature bonnet macaques alone would clearly be instructive in teasing apart the factors that crucially affect and influence the ontogeny of gestures and the complete development of contextual gestural repertoires in this species.

5.5 References

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Chapter 6

Display of sequences of gestures and other signals by bonnet macaques

6.1 Introduction

Communication through gestures in primates is now well established, especially in apes as well as in a few macaque species (Maestripieri 1996, 1997; see Call and Tomasello 2007). In the previous chapters of this thesis, the gestural repertoire of bonnet macaques, the study species, has been defined and the age- and sex differences in the use of those gestures documented. In all the previous analyses of gestures in bonnet macaques, I have considered single gesture use in any communicative act, in order to unambiguously understand the meaning of and the corresponding responses to each gesture. There were, however, several gestural communicative acts, composed of different gestures strung together or sometimes gestures combined with other signals. The latter have been considered as signals alone as they were not used singly frequently enough to be analysed by the standard definitional criteria that could potentially qualify them as true gestures (discussed in Chapter 2). In the current chapter, I have analysed all the observed gesture and signal sequences in order to determine their functions in the bonnet macaque communication system.

Combinations of gestures forming sequences have been observed in a few language-trained bonobos and chimpanzees (Greenfield and Savage-Rumbaugh 1990, 1991; Brakke and Savage-Rumbaugh 1995, 1996; Leavens et al. 2004; Lyn et al. 2010). These sequences appeared to be comparable to semiotic combinations produced by human children and were suggested to potentially provide insights into the evolutionary roots of human language. Such gesture combination abilities have also been sporadically reported from wild and zoo-living chimpanzees (Plooij 1978; Tomasello et al. 1994; Tomasello and Camaioni 1997), indicating that the capability to combine signals may be typical of these species rather than being specially acquired characteristics of human-raised individuals alone. It is crucial to ascertain the additional functions of such combinations of gestures in comparison to single uses of each of their component parts. Tomasello et al. (1994) hypothesised that the gesture sequences are probably constructed syntactically using meaningful gestures that follow an initial 'attention-getter' gesture. When this hypothesis was tested on a captive chimpanzee group (Liebal et al. 2004), there was no evidence for the presence of such syntax in the gesture combinations; they were, however, capable of altering the meaning of an act, as compared to when the component gestures were used singly. Such findings indicate that the observed gesture sequences may not entirely be used randomly but perhaps serve particular functions during certain communication acts.

Following this first systematic study of gesture sequences by Liebal et al. (2004), there has only been two other such investigations conducted on wild gorillas and chimpanzees (Genty and Byrne 2010; Hobaiter and Byrne 2011). The gorilla gesture sequences appeared to functionally different from what had been found in the captive chimpanzees (Liebal et al. 2004). Wild gorillas, thus, neither seemed to use the sequences as attention-getters nor did they alter the semantics of communication from that served by the single gestures alone, except in a few instances. The structure of these sequences, however, was not random, as revealed by Markov transition analysis (Genty and Byrne 2010). In the study on wild chimpanzees (Hobaiter and Byrne 2011), a noteworthy discovery was made. The age-specific use of combinatorial gesture appeared to gradually decrease with age, thus, perhaps suggesting a process of 'repertoire-tuning' after which the proper usage of gestures was achieved. Although these three systematic studies vary in their conclusions, probably owing to subtle differences in the methods followed in defining a gesture sequence, a combination of their results does raise important questions regarding the potential functions of such serial gesturing in nonhuman primates. Even if the structure of their communicatory sequences fails to reflect the syntactic properties of human language, the phenomenon, by itself, may be worth investigating, given our interests in effectively understanding the communication systems of our closest phylogenetic kin.

Investigations of gesture sequences, following the studies in apes, have never been conducted on monkeys. In this chapter, I have attempted to determine the possible presence of a gesture combinatorial capacity, akin to that in apes, in bonnet macaques and, if found, examine their possible functional meanings. This study, thus, represents a first step towards an understanding of the structure of monkey gestures beyond an analysis of isolated gestural units alone. Such an endeavour is crucial in building up the rather meagre existing database on combinatorial signal use by nonhuman primates, a potential candidate in the comparative understanding of human language evolution.

6.2 Methods

6.2.1 *Data collection*

I adopted the methods that have been applied to analyse gesture sequences of gorillas by Genty and Byrne (2010). The data were collected by 15-minute focal animal sampling on randomly chosen individuals, without replacement, across the four study troops of bonnet macaques, described in Section 2.2 of Chapter 2. The gesture components of the sequences were determined on the basis of the definitional criteria provided earlier in this thesis (Tables 2.2, 2.3 and 2.4 of Chapter 2). A gesture sequence was defined as a series of gestural acts, displayed one after the other with a separation time of one second or less between successive gestures. Gestures that were separated from one another by more than a second were considered as single gestures and analysed independently. These results have been discussed in the preceding chapters of this thesis. There were also several sequences, which have been analysed separately, wherein the component gestures were associated with other signals, which could not themselves be analysed and identified as true gestures due to their low levels of performance by the study macaques. Henceforth, I refer to the sequences consisting of gestures and/or signals as gesture sequences and the gestures or signals themselves as gestures, except in certain specific situations that have been clarified, as and when required.

6.2.2 *Data analysis*

The gesture sequence lengths and their frequencies of usage in various contexts were compared to those of the single gestures displayed by the study macaques (see also Liebal et al. 2004 and Genty and Byrne 2010). I also examined the probability of certain gestures being used more often singly or as components of sequences.

In order to understand the structure of the sequences and determine the transition probabilities of one gesture to the subsequent one, I applied Markov transition analyses following the methods described in Genty and Byrne (2010). A matrix of pairwise transition probabilities was constructed for all the observed component gestures and signals (Fabricius and Jansson 1963) and particular transitions that occurred at least four times during the entire study duration were considered for further analysis (Genty and Byrne 2010). The probabilities of these associations between any two gestures were then tested for their significance of association using the binomial test in R 3.1.0 (R Core Team 2014). I also investigated whether there were certain gestures that initiated or ended a sequence at significantly higher probabilities than did others.

In addition, I explored functional properties of gesture sequences through the following analyses (see also Genty and Byrne 2010):

1. A comparison of the relative success of gesture sequences in which a particular gesture is repeated a variable number of times and that of this gesture used singly;
2. Whether particular gesture sequences were more successful in eliciting appropriate responses than were the combined effect of the component gestures when performed alone;
3. The possibility that individuals preferred to display persistence by subsequently using gesture sequences in the initial absence of a response to the use of a single gesture alone.

In these three sets of analyses, I evaluated the success or efficiency of the test gestures or sequences by measuring the proportion of times appropriate responses were evoked in relation to those in which they were not ('no-response situations').

My analysis of the second functional property of gesture sequences, listed immediately above, involved a set of two-component-long gesture sequences. I first calculated the probability of elicitation of no-responses for each of the two component gestures or signals of these sequences, when performed in isolation [say, for example, p(A) and p(B) of two particular components A and B respectively] and then computed the expected combined probability of no-response when both were displayed independently by multiplying their individual probabilities [p(A) × p(B)]. This value was then compared with the observed probability of no-response when these gestures or signals were performed together as a gesture sequence [p(A-B)]. It can be hypothesised that if p(A) × p(B) is greater in value than p(A-B) or, in other words, if the probability of no-response is less when the two components are performed in a gesture sequence, the sequence, as a whole, is more effective in evoking a response than when the two components are exhibited in isolation (see also Genty and Byrne 2012).

6.3 Results

My observations revealed that there were two kinds of associations that formed gesture sequences—gesture-gesture associations and gesture-signal associations; both of these associations were analysed independently. All the 32 gestures that comprised the bonnet macaque gestural repertoire occurred in the observed sequences (Appendix 6.1) while there were 16 non-gesture signals—Bared-Teeth Displaying, Branch-Shaking, Copulatory-Bobbing Vertically, Fear-Grimacing, Gazing, Ground-Slapping, Inspecting by Smelling, Inspecting by Tasting Oestrous Material, Inspecting by Touching, Inspecting Visually, Leaping Away, Licking, Mounting, Mounting with Lip-Smacking, Sniffing and Touching Nipples—that featured in the gesture-signal associations (Appendix 6.2).

6.3.1 *Length of sequences and their contexts of usage*

The frequencies of occurrence of all the observed sequences were compared with that of single gestures or signals (henceforth, gestures unless otherwise specified), some of which were also components of the sequences. Single gestures were displayed more frequently by the study individuals than were the gesture sequences (Table 6.1). There were, thus, 2368 instances of single gesture use while gesture sequences occurred 915 times, constituting 72.13% and 27.87% of the 3283 cases of observed use of single gestures and gesture sequences respectively. Of these, 812 sequences were composed of gestures alone while there were 64 2-length (sequences consisting of two components), 23 3-length and 16 4-length gesture-signal associations. A comparison of the contexts of usage revealed significantly greater use of single gestures in during affiliation and play (Affiliation: G-test of independence, $G = 372.73$, $df = 1$, $n = 1446$, $p < 0.001$; Play: $G = 75.45$, $df = 1$, $n = 403$, $p < 0.001$; Figure 6.1) while no such differences could be detected in the context of agonism ($G = 2.71$, $df = 1$, $n = 296$, $p > 0.09$).

Table 6.1 Number of gesture sequences of various lengths displayed by bonnet macaques in the four study troops

Number of components	**Total**
2	722
3	130
4	46
5	11
> 5	6
Total number of sequences	915

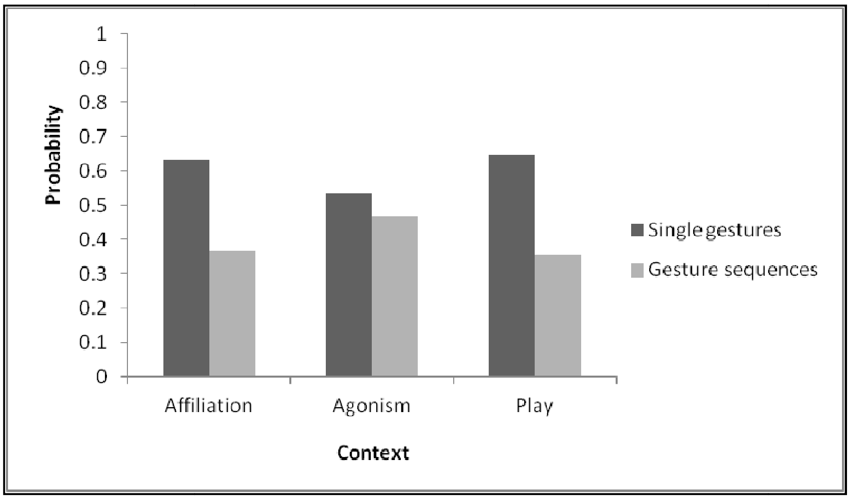

Figure 6.1 Probability of single gestures and gesture sequences being displayed in different contexts by the study bonnet macaques

I evaluated whether all the 32 gestures and 14 of the 16 non-gesture signals were comparably used by the study macaques as independent units or as components of sequences (Figure 6.2). Two signals—Bared-Teeth Displaying and Copulatory-Bobbing Vertically—were never used singly and hence, removed from this analysis. The results revealed 12 gestures and 3 signals to be significantly preferentially used in as sequence components while 13 gestures and one signal were more likely to be used as independent units during gestural communication by the study bonnet macaques (Table 6.2).

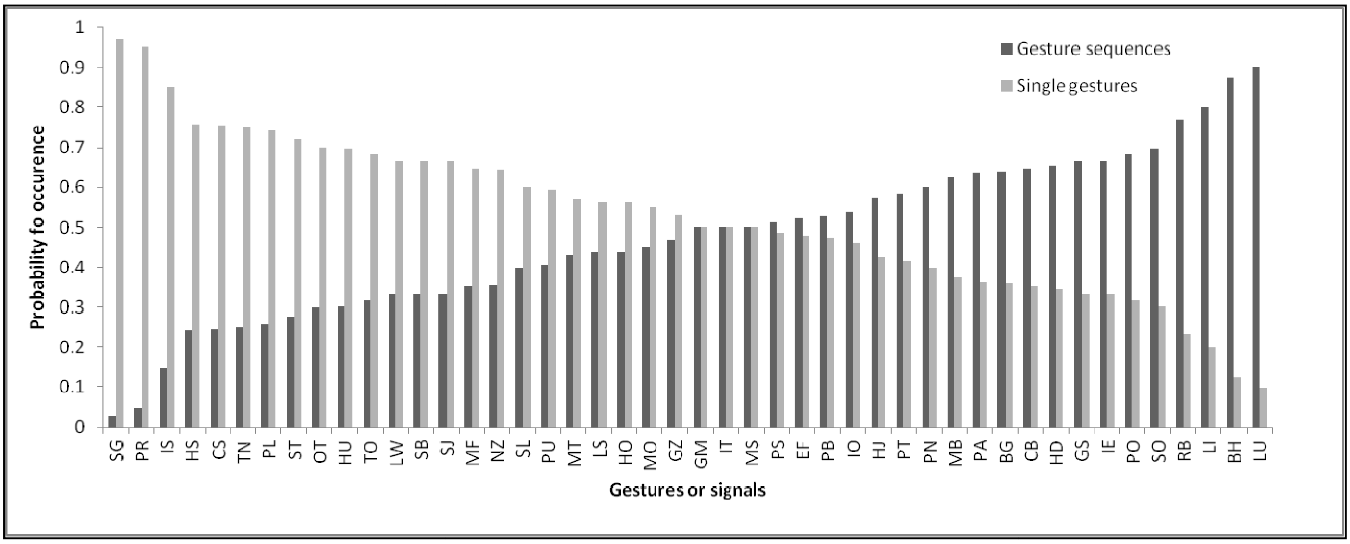

Figure 6.2 **Proportional use of gestures and signals either as components of sequences or independently as single units by the study bonnet macaques**

Table 6.2 **Gestures and signals that were significantly used either as components of sequences or independently as single units by the study bonnet macaques**

Gesture or signal	**G**	***p***	**Significant occurrence**
BG	21.43	< 0.001	Sequence component
BH	26.45	< 0.001	Sequence component
CB	19.15	< 0.001	Sequence component
HD	5.87	< 0.03	Sequence component
LU	106.00	< 0.001	Sequence component
MB	22.06	< 0.001	Sequence component
PA	9.18	< 0.01	Sequence component
PO	18.02	< 0.001	Sequence component
PT	20.00	< 0.001	Sequence component
RB	57.97	< 0.001	Sequence component
SO	36.21	< 0.001	Sequence component
ST	7.92	< 0.01	Sequence component
IE	4.95	< 0.03	Sequence component
LI	4.46	< 0.04	Sequence component

CS	31.85	< 0.001	Single unit
HO	10.17	< 0.01	Single unit
HS	22.65	< 0.001	Single unit
HU	143.35	< 0.001	Single unit
LS	13.04	< 0.001	Single unit
MF	17.76	< 0.001	Single unit
NZ	10.23	< 0.01	Single unit
OT	27.23	< 0.001	Single unit
PL	146.09	< 0.001	Single unit
PR	342.62	< 0.001	Single unit
PU	6.87	< 0.01	Single unit
SG	1039.17	< 0.001	Single unit
TO	141.40	< 0.001	Single unit
IS	63.85	< 0.001	Single unit
EF	0.26	> 0.60	Not significant
HJ	2.40	> 0.10	Not significant
MT	1.94	> 0.10	Not significant
PB	0.97	> 0.30	Not significant
PN	0.06	> 0.80	Not significant
PS	0.06	> 0.80	Not significant
SJ	2.12	> 0.10	Not significant
SL	2.85	> 0.09	Not significant
GM	0.00	1.00	Not significant
GS	0.71	> 0.40	Not significant
GZ	0.11	> 0.70	Not significant
IO	0.15	> 0.60	Not significant
IT	0.00	1.00	Not significant
LW	0.71	> 0.40	Not significant
MO	0.40	> 0.50	Not significant
MS	0.00	1.00	Not significant
SB	0.71	> 0.40	Not significant
TN	2.30	> 0.10	Not significant

Gestures and signals have been depicted according to the following scheme:

Gesture	Signal

Proportions were compared using the G-test of independence

6.3.2 *Structure of the gesture sequences*

The structure of the gesture sequences was analysed by the Markov transition method in order to evaluate the probability of association between any two gestures. There were 372 such gesture-gesture and gesture-signal associations, of which only 99 of them occurred at least four times during the observation period. Of these 99 dyads, 33 gesture-gesture associations occurred significantly more than others and four gesture-signal dyads were significantly paired. Among the 33 gesture dyads, seven were repetitions of the same gesture. The remaining 26 gesture-gesture associations formed two main clusters, one with affiliative and play gestures (Figure 6.3a) and the other with agonistic gestures (Figure 6.3b). The four gesture-signal associations have been depicted independently in Figure 6.3c. The seven repeated-gesture associations were composed of the following gestures: Biting Gently, Head-Jerking, Mouth-to-Mouth Sniffing, Patting, Pulling, Raising Eyebrows and Touching.

There were nine particular gestures that were used at the beginning of a sequence and ten at the end of a sequence with significantly higher probabilities than were other gestures in the same positions (Tables 6.3 and 6.4)

Table 6.3 Gestures used significantly more at the beginning of a sequence than others, evaluated by the binomial test

Codes	**Gestures**	**n**	***p***
CB	Pulling Close to Body	33	< 0.04
HO	Holding	77	< 0.001
HU	Hugging	64	< 0.001
LS	Lip-Smacking	62	< 0.001
MB	Mouth-to-Body Touching	54	< 0.001
PL	Lunging in Play	56	< 0.001
PT	Pulling any Part of the Body	104	< 0.001
RB	Raising Eyebrows	34	< 0.05
TO	Touching	124	< 0.001

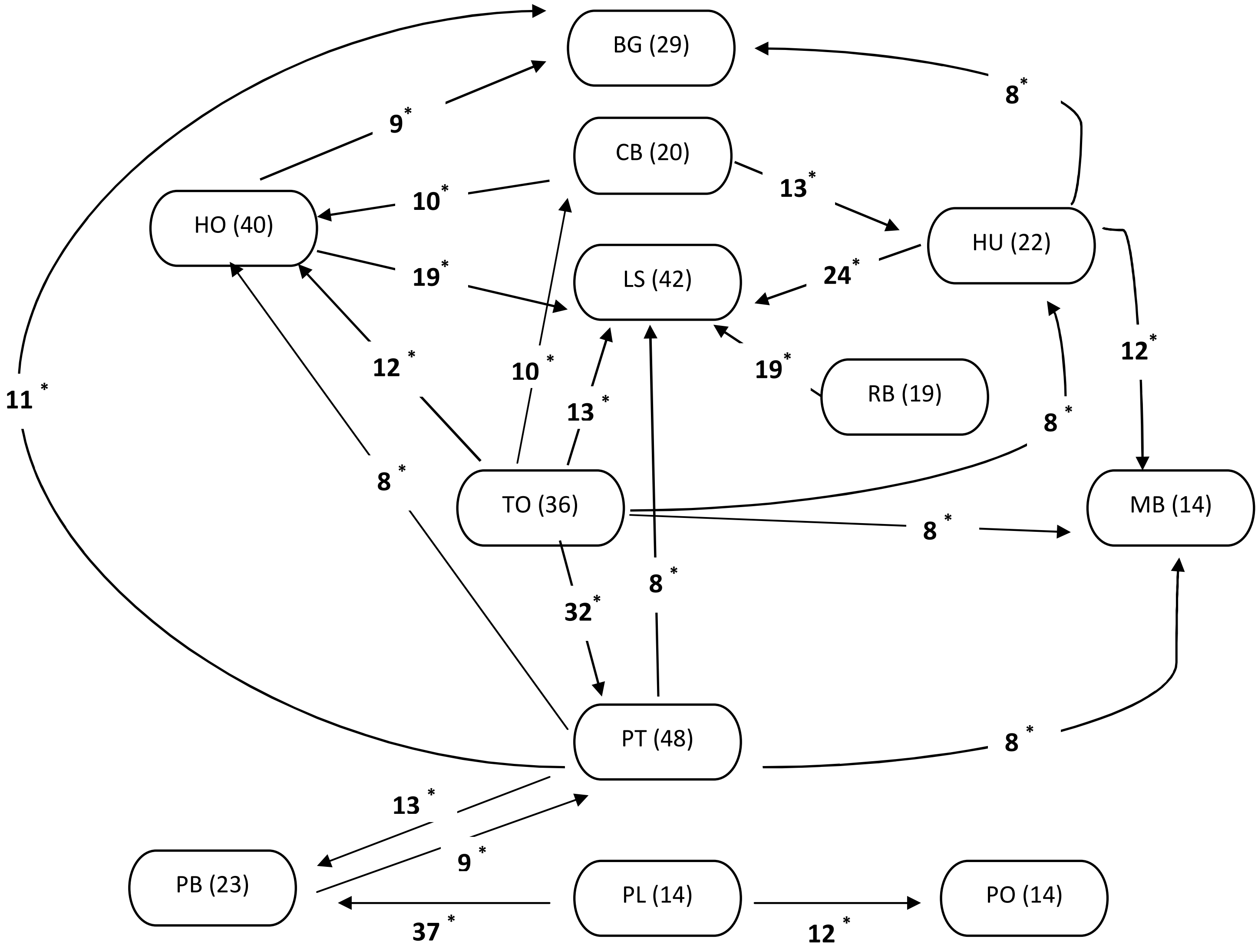

Figure 6.3a **Network of affiliative and play gesture-gesture associations displayed by the study bonnet macaques. Each box represents the gestures (listed in Table 6.2) along with the number of sequences each occurred in. The arrows indicate the gesture significantly associated with the preceding one. The numbers next to the arrows signify the occurrence frequency of each gesture-gesture pair. The asterices depict significant associations of the components, as evaluated by the binomial test. For the behaviour codes, see Appendices 6.1 and 6.2**

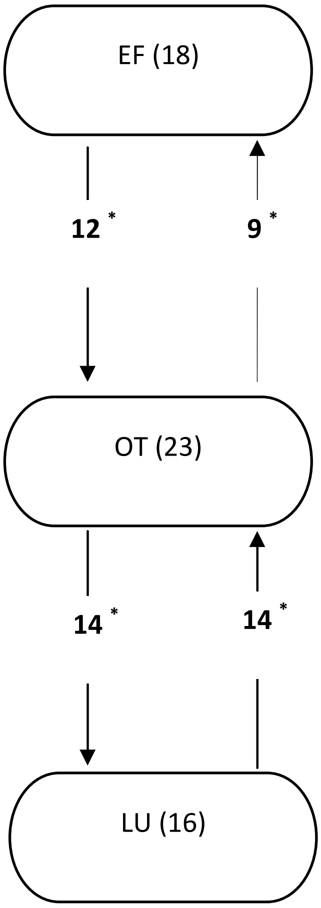

Figure 6.3b **Network of agonistic gesture-gesture associations displayed by the study bonnet macaques. Each box represents the gestures (listed in Table 6.2) along with the number of sequences each occurred in. The arrows indicate the gesture significantly associated with the preceding one. The numbers next to the arrows signify the occurrence frequency of each gesture-gesture pair. The asterices depict significant associations of the components, as evaluated by the binomial test. For the behaviour codes, see Appendices 6.1 and 6.2**

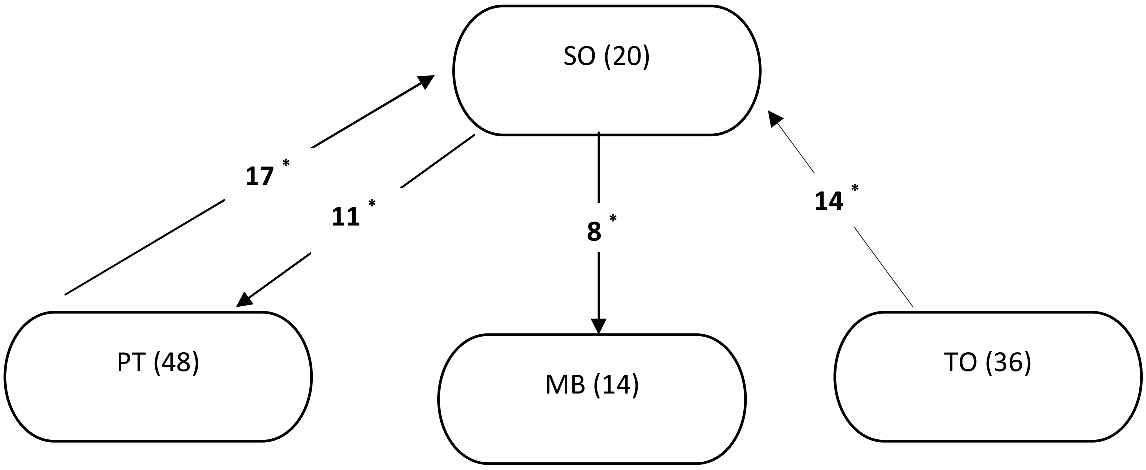

Figure 6.3c Network of gesture-signal associations displayed by the study bonnet macaques. Each box represents the gestures (listed in Table 6.2) and the signal, Sniffing (SO) along with the number of sequences they occurred in. The arrows indicate the gestures or signal significantly associated with the preceding one. The numbers next to the arrows signify the occurrence frequency of each component pair. The asterices depict significant associations of the components, as evaluated by the binomial test. For the behaviour codes, see Appendices 6.1 and 6.2

Table 6.4 Gestures or signals used significantly more at the end of a sequence than others, evaluated by the binomial test

Codes	Gestures or Signals	n	*p*
BG	Biting Gently	64	< 0.001
HO	Holding	60	< 0.001
HU	Hugging	58	< 0.001
LS	Lip-Smacking	106	< 0.001
MB	Mouth-to-Body Touching	62	< 0.001
OT	Open-Mouth Threatening	41	< 0.001
EB	Biting in Play	69	< 0.001
PT	Pulling any Part of the Body	95	< 0.001
TO	Touching	37	< 0.001
SO	Sniffing *	33	< 0.01

*** Sniffing is a non-gesture signal**

6.3.3 *Gesture repetitions and sequences: Advantages over single gestures?*

I first compared the relative success of gesture sequences, in which a particular gesture was repeated a variable number of times, with that of the same gesture used singly; success or efficiency of a gesture or a sequence was measured in terms of the proportion of times either of them evoked an appropriate response from the receiver, as compared to those that did not (‘no-response situations’). The proportions of appropriate responses elicited by the repeat sequences (23 of 48 events) and their component gestures used singly (345 of 659 events) were comparable (Figure 6.4) and did not differ significantly from one another (G = 0.63, df = 1, $p > 0.40$).

I next examined the relative efficacy with which repeated-gesture sequences were able to induce the receivers to produce responses, appropriate to a particular context. For seven unique gesture sequences, in which a particular gesture was produced repeatedly to yield sequence lengths of one to three components, there appeared to be no significant relationship between sequence length and the probability of that sequence evoking a positive response (Spearman's rank correlation, rho = -0.26, n = 17, $p > 0.20$; Figure 6.5). This indicated that the repetition of a particular gesture, displayed in a sequence, was possibly not an alternative strategy adopted by the study macaques to increase the probability of evoking an appropriate response from the target audience.

Figure 6.4 Probability of appropriate or no responses being elicited by single gestures and repeated-gesture sequences displayed by the study bonnet macaques

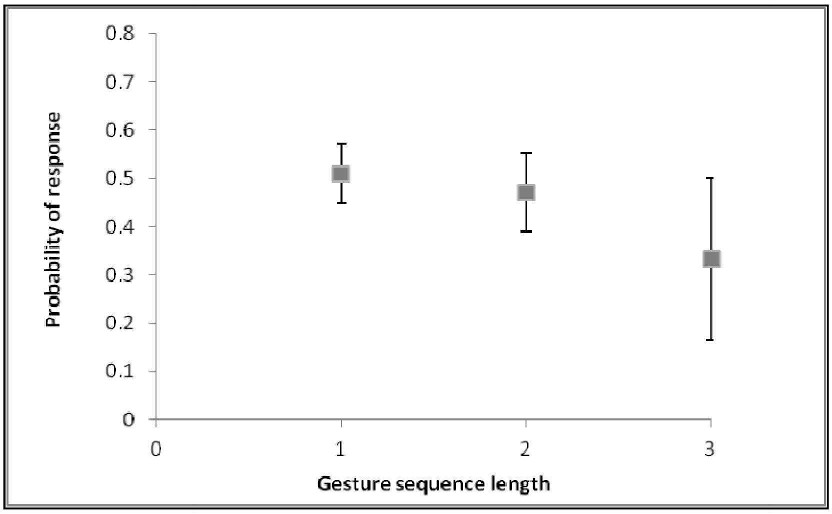

Figure 6.5 The probability of appropriate responses being elicited by repeated-gesture sequences of increasing lengths displayed by the study bonnet macaques

I also investigated whether gesture sequences, consisting of two distinct components, were relatively more effective in eliciting responses from recipients than were each of these two components, performed singly. The 33 gesture-gesture sequences and the four gesture-signal sequences that had significantly greater probabilities of association were considered in this analysis. The observed probabilities of no-response were found to be higher for 26 of the 29 two-component gesture sequences (Table 6.5), indicating that these sequences were not necessarily more effective in eliciting a response than were their components, when performed independently.

6.3.4 *Strategies of persistent gesturing: Gesture sequences and single gestures*

In this analysis, I evaluated the possibility that individuals preferred to display persistence by subsequently using gesture sequences in the initial absence of a response to the use of a single gesture alone. In other words, were the macaques deploying gesture sequences as alternatives to single gestures on receipt of a non-response from the recipient?

Single gestures were displayed 2368 times during the observation period, of which 899 instances (37.96%) constituted no-response situations. In these situations, the signalling individual terminated the communication process in 807 instances (89.77%) while in the remaining 92 events (10.23%), the signaller persisted until the intended goal was achieved. I then investigated whether, during persistence, the use of gesture sequences were preferred over the repetition of the same gesture, which was not originally responded to, or the use of other functionally similar gestures. On the observed 92 occasions of persistent gesturing, the study individuals used gesture sequences on 23 occasions, including 22 gesture sequences and one repeated-gesture sequence (26.44% of the total instances), the same gesture repeated singly on 42 (48.28%) and alternative, but functionally similar, gestures displayed singly on 27 (25.29%) occasions. Assuming that the study individuals were equally likely to use any of these strategies to persistently communicate with the recipient, they appeared to prefer to repeat the initial gesture singly, following the failure of the recipient to respond in the first instance (G-test of independence, $G = 18.50$, $df = 2$, $p < 0.001$).

Table 6.5 Comparison of the calculated expected and observed probabilities of no-responses elicited by two gestures or signals, displayed independently and in two-component gesture sequences respectively

Sequence	n	Expected probability	Observed probability
CB-HO	10	0.17	0.43
CB-HU	13	0.09	0.22
EF-OT	12	0.14	0.44
HO-BG	9	0.25	0.83
HO-LS	19	0.21	0.4
HU-LS	**24**	**0.11**	**0.10**
HU-BG	8	0.13	0.43
HU-MB	12	0.19	0.67
LU-OT	**14**	**0.05**	**0.00**
OT-EF	9	0.14	0.5
OT-LU	**14**	**0.05**	**0.00**
PB-PT	9	0.09	0.33
PL-PB	37	0.04	0.29
PL-PO	12	0.03	0.57
PT-HO	8	0.25	0.50
PT-LS	8	0.18	1.00
PT-BG	11	0.21	0.60
PT-PB	13	0.09	0.50
PT-MB	8	0.31	1.00
PT-SO	17	0.31	0.67
RB-LS	19	0.34	0.75
SO-PT	11	0.31	0.80
TO-HO	12	0.25	0.78
TO-LS	13	0.18	0.50
TO-PT	32	0.21	0.76
TO-HU	8	0.13	0.50
TO-CB	10	0.15	0.33
TO-MB	8	0.31	0.50
TO-SO	14	0.31	0.50

Cases where the observed probability was less than that of the expected probability have been highlighted in bold

But were the persistent displays of the same gesture, performed singly, effective in evoking an appropriate response from the targetted recipients? Table 6.6 depicts the frequencies of appropriate and no responses elicited from the recipients when the signallers used the three strategies—same gestures repeated singly, gesture sequences and alternative, functionally similar, single gestures—during occasions of persistent gesturing. A comparison of the effectiveness of these three strategies made it clearly evident that the performance of both gesture sequences and alternative, functionally similar, single gestures were more successful than the same gestures repeated singly in evoking greater proportion of appropriate responses (Gesture sequences and same gestures: $G = 11.84$, $df = 1$, $p < 0.001$; Alternative gestures and same gestures: $G = 5.65$, $df = 1$, $p < 0.02$). Gesture sequences were, however, even more effective than the alternative single gestures in this regard (Gesture sequences and alternative gestures: $G = 8.75$, $df = 1$, $p < 0.01$).

Table 6.6 Frequencies of appropriate and no responses received in response to different strategies during occasions of persistent gesturing by the study bonnet macaques

Strategy	Appropriate response	No response
Gesture sequence	17	6
Same gesture, repeated singly	22	20
Alternative, functionally similar, single gesture	17	10

6.4 Discussion

The study bonnet macaques used gesture sequences of two kinds, those with gesture-gesture combinations and with gesture-signal combinations and they were of varying lengths. The gesture-gesture combinations were composed of signals that were independently considered as true gestures, as they met the criteria laid down for the definition of gestures (see Chapter 2). The gesture-signal sequences, on the other hand, were combinations of true gestures and other signals that could not be established to be true gestures for two principal reasons. First, there was an absence of a sufficient number of single-use occurrences adequate for the testing of the criteria laid down for the definition of true gestures in the case of three signals—Bared-Teeth Displaying, Copulatory-Bobbing Vertically and Gazing. Second, in the case of 13 other signals—Branch-Shaking, Fear-Grimacing, Ground-Slapping, Inspecting by Smelling, Inspecting by Tasting Oestrous Material, Inspecting by Touching, Inspecting Visually, Leaping Away, Licking, Mounting, Mounting with Lip-Smacking, Sniffing and Touching Nipples—the joint attention state between the signaller and recipient did not prevail in most of the events when the signaller displayed these particular signals and they could not, therefore, be defined as true gestures. It is, however, noteworthy that these signals were used in conjunction with other gestures, incorporated into gestural sequences and, thus, formed an integrative communication system with other true gestures. It is also entirely possible that these signals would ultimately qualify to be true gestures as larger gesture datasets are build up in the course of future, long-term studies.

6.4.1 *Length of sequences and their contexts of usage*

The lengths of the different gesture sequences produced by the study macaques varied from two to five gestural components, which were comparable to those observed in gorillas and chimpanzees, and were also less frequently produced than were single gestures, again as found in the apes (Genty and Byrne 2010; Hobaiter and Byrne 2011). Affiliative and play gestures were displayed singly significantly more than in sequences by the macaques, contrasting to what has been observed in chimpanzees and gorillas, wherein the most frequent sequences consisted of play gestures (Liebal et al. 2004; Genty and Byrne 2010; Hobaiter and Byrne 2011). It, thus, appears that bonnet macaques prefer to communicate through single gestures although a certain proportion of their communication events is indeed represented by complex combinations of gestures and signals to form gestural sequences.

In the bonnet macaque gestural repertoires, there were certain gestures that were significantly more used as components of gestural sequences than as single communicative units and vice versa. This could be an indication that certain gestures possibly have an inherent capacity to be executed singly while others are more likely to be effective in transmitting their communicative content only when combined with other gestures.

6.4.2 *Structure of the gesture sequences*

The Markov transition analysis revealed that the gestural sequences used by bonnet macaques did indeed have typical structures, with some gestures preferentially associated with certain other gestures or signals while others had high probabilities of being repeated a variable number of times to form distinctive repeated-gesture sequences. More remarkably, certain gestures were very likely to be incorporated at the beginning or at the end of a sequence than were other gestures or signals. Similar observations have been made earlier for gorillas, wherein certain gestures formed a network with other gestures, at probabilities higher than would be expected by chance (Genty and Byrne 2010).

In my study bonnet macaques, there were two structural clusters that were formed with significantly associated gestures in each cluster. It is illuminating that one of these networks consisted of affiliative and play gestures while agonistic gestures alone constituted the other cluster. What must be noted here is that these two structural clusters of closely associated gestures appeared to be functionally distinctive and, therefore, possibly served very different roles in the gestural communication networks of the macaques. I could also detect a third network consisting of a few gestures and other signals, including Pulling any Part of the Body (PT), Sniffing (SO), Touching (TO) and Mouth-to-Body Touching (MB), the functional role of which was not very evident but which could serve either as an affiliative or a curiosity-driven sequence of behavioural interactions, occasionally leading to sexual inspection.

It may be relevant to mention here that the gestures—Pulling any Part of the Body (PT) and Touching (TO)—were preferentially associated with several other gestures and signals, which subsequently followed these gestures with very high probabilities of occurrence. These two gestures were also often positioned by the macaques at the beginning of many gesture sequences. In Chapter 2, both these gestures were shown to have multiple functions in the bonnet macaque gestural repertoire, and I hypothesised that these and several other gestures were inherently flexible in their usage across contexts, especially in conjunction with other behaviours. It is, thus, conceivable, from both these sets of evidence, that certain tactile gestures like PT and TO could act as "attention-getters" (Tomasello et al. 1994) and could invariably be performed before other gestures, which actually conveyed the true intention of the communication event once the attention of the recipients were secured.

I also speculate that another possible function of the observed structural network of gestural sequences in bonnet macaques could be to constantly manipulate the communication event as it proceeds and leave opportunities open to carry out sudden, but appropriate, modifications of the sequence in response to the signals received from the targetted audience, similar in principle to what has also been suggested by Genty and Byrne (2010). Future, more detailed, studies focussing on these particular gestures may reveal their true functions, either as a flexible gesture that could potentially serve different functions in different contexts or as an attention-attracting signal, which ensures the attention of the recipient individual before a complex, potentially costly, communication event is executed.

6.4.3 *Gesture repetitions and sequences: Advantages over single gestures?*

The gesture sequences used by the study bonnet macaques were, as noted above, of two types—the same gesture repeated in a sequence (repeated-gesture sequences) and sequences composed of heterogeneous gestures and/or signals (gesture sequences). The length of the repeated-gesture sequences did not appear to significantly increase the efficacy of communication, especially as compared to the single use of the gestures that composed the particular sequences. Moreover, for the overwhelming majority of two-component gesture sequences, the sequences themselves did not seem to elicit significantly elevated levels of positive responses from the audience, as compared to the combined effect of the same two gestures performed singly. Thus, although there were three such sequences that did appear to increase the probability of the recipient responding than to their individual component gestures, the overall function of such gesture sequences in the communication repertoire of my study species continues to remain obscure, similar to what has been concluded earlier for the gesture sequences produced by wild gorilla populations (Genty and Byrne 2010).

6.4.4 *Strategies of persistent gesturing: Gesture sequences and single gestures*

In situations when an initial single gesture failed to evoke any response from the targetted recipient and the signaller exhibited persistence in gesturing, individual macaques of all the four study troops preferred to repeat the same gesture singly rather than employ gesture sequences or alternative, functionally similar, single gestures. The same gestures repeated singly during such persistent signalling attempts were, however, not as successful in evoking an ultimate response from the audience as were gesture sequences, which were the most effective, or other functionally similar gestures, again performed singly. The gesture sequences, thus, clearly had a significantly functional role in successfully evoking positive responses during persistent gesturing exercises.

Another possible reason of repeating the same single gestures during persistence gesturing could be to maintain an uninterrupted flow of the communication process or to manipulate this process in anticipation of responses, as mentioned above and also discussed by Genty and Byrne (2010). It is also possible that the display of such serial gesturing depends on individual temperaments, which react variably to immediate socio-environmental factors, but the testing of these ideas awaits future research.

From the perspective of gesture sequence structure, the potential changes in the modality of the components of gestural sequences could not be explored as most of the bonnet macaque gestures were tactile in nature. It would also be worthwhile to study the effects of the temporal variation between the sequence components on the functional use of such gestural sequences. Moreover, the dependence of the performed gestures on the attention state of the recipients could not be ascertained given the constraints of my observational studies. Finally, further studies on bonnet macaque gestural sequences should adopt a developmental perspective and explore the age-dependent development and expression of such sequences, again as pointed out by Hobaiter and Byrne (2011).

6.5 References

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Appendix 6.1

Component gestures of gesture sequences displayed by bonnet macaques

Code	Gesture	Context
BG	Biting Gently	Affiliation
CB	Pulling Close to Body	Affiliation
HO	Holding Gently	Affiliation
HS	Hugging with Lip-Smacking	Affiliation
HU	Hugging	Affiliation
LS	Lip-Smacking	Affiliation
MB	Mouth-to-Body Touching	Affiliation
MT	Mouth-to-Mouth Touching	Affiliation
NZ	Nuzzling	Affiliation
PA	Patting	Affiliation
SG	Soliciting Allogrooming	Affiliation
TO	Touching	Affiliation
BH	Biting Hard	Agonism
EF	Eye Flashing	Agonism
HD	Holding Down Roughly	Agonism
HJ	Head-Jerking	Agonism
LU	Lunging	Agonism
OT	Open-Mouth Threatening	Agonism
SL	Slapping	Agonism
PB	Biting in Play	Play
PL	Lunging in Play	Play
PO	Open-Mouth Threatening in Play	Play
PS	Slapping in Play	Play
SJ	Spot-Jumping	Play
CS	Copulatory Lip-Smacking	Multifunctional
MO	Mounting	Multifunctional
PN	Pinching	Multifunctional
PR	Presenting	Multifunctional
PT	Pulling any Part of the Body	Multifunctional

PU	Pushing	Multifunctional
RB	Raising Eyebrows	Multifunctional
ST	Staring	Multifunctional
Total number of gestures = 32		

Appendix 6.2

Component signals of gesture-signal sequences displayed by bonnet macaques

Code	**Gesture**	**Context**
BT	Bared-Teeth Displaying	Agonism
GM	Fear-Grimacing	Agonism
GS	Ground-Slapping	Agonism
GZ	Gazing	Sexual
IS	Inspecting by Smelling	Sexual
IE	Inspecting by Tasting Oestrous Material	Sexual
IT	Inspecting by Touching	Sexual
IO	Inspecting Visually	Sexual
LW	Leaping Away	Affiliation
LI	Licking	Affiliation
MO	Mounting	Dominance-subordination
MS	Mounting with Lip-Smacking	Dominance-subordination
SB	Branch-Shaking	Affiliation
SO	Sniffing	Agonistic
TN	Touching Nipples	Neutral
UB	Copulatory-Bobbing Vertically	Sexual
Total number of signals = 16		

Chapter 7

Synthesis

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

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