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Sex differences in vocal communication among adult rhesus macaques☆

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Abstract

In female-bonded primate species, females invest more time in grooming than males, and the majority of this grooming occurs in intra- rather than intersexual interactions. These clear sex differences in sociability reflect females' need to forge and maintain complex networks of social relationships with other females in the group. Increasing evidence indicates that vocal signals can have a similar function to grooming in mediating social interactions and relationships, and sex differences in patterns of use of vocal communication comparable to those seen for grooming might therefore be expected to occur. In this study of free-ranging adult rhesus macaques, we tested for such patterns, focusing on the frequency of utterance of three types of vocalisations given during close-range social interactions: coos, grunts, and girneys. As predicted, we found that females gave such calls significantly more frequently than males and also directed more of these vocalisations towards other females than to males; males' rate of vocalising towards the two sexes was not significantly different. To our knowledge, these results provide the first evidence for a sex difference in the rate of production of social vocalisations among adult nonhuman primates. The finding that increased sociability is associated with increased reliance on vocal communication may have important implications for theories of language evolution.

Keywords: Volubility; Vocal communication; Rhesus macaque; Sex differences

1. Introduction

In female-bonded primate species, adult females spend significantly more time involved in grooming than adult males and also devote a much higher proportion of their time to same-sex rather than mixed-sex grooming interactions (e.g., Cooper & Bernstein, 2000; Kaplan & Zucker, 1980; Sugiyama, 1971). These differences reflect the fact that in such social systems, females need to spend more time in servicing networks of social relationships and do so particularly with animals of their own sex (Seyfarth, 1977). These social networks are the fundamental constituents of the social system (Dunbar, 1988); understanding the way they are maintained is therefore essential for understanding the evolution of primate sociality. While studies of primate social networks have typically focussed very strongly on grooming as the key social bonding mechanism, grooming is not the only means by which primates may regulate their social interactions (Seyfarth & Cheney, 1993). Indeed, an increasing body of work indicates that primate vocal signals can fill a very similar niche to grooming in mediating social exchanges and relationships (Silk, 2002).

Bauers and de Waal (1991), for example, found evidence that the coo vocalisations of female stumptailed macaques (*Macaca arctoides*) facilitate positive social interactions; approaches preceded by coos were significantly more likely to lead to friendly contact than if no such call had been given. Similarly, observational studies of rhesus macaques (*Macaca mulatta*) by Silk, Kaldor, and Boyd (2000) suggest that the grunts and girneys given by females when approaching others signal benign intent, with calling during approaches associated with both a lower likelihood of aggression from the approaching animal and reduced numbers of submissive gestures by the animal being approached. A study by

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Cheney, Seyfarth, and Silk (1995) indicated that the post-conflict grunts of female chacma baboons (*Papio hamadryas ursinus*) play a role in reconciling opponents after aggression. Female subjects who had recently been attacked by a more dominant female responded less strongly to playback of the scream of the attacker if that female had grunted to them following the attack, indicating that these post-aggression grunts serve to mollify defeated opponents. These studies, along with many others of a similar nature (e.g., Mori, 1975; Palombit, Cheney, & Seyfarth, 1999), highlight the importance of vocalisations—in addition to grooming—in mediating primates' social interactions and, ultimately, their relationships.

If vocal communication is important in supporting social networks and supplements grooming in this respect, it would be predicted that we should see patterns of intersexual variation in the use of vocal signals similar to those seen for grooming. In the case of female-bonded species, adult females should not only vocalise more than adult males but also vocalise more often towards members of their own than the opposite sex. To our knowledge, no study has yet tested for these patterns of variation in vocal communication. A sex difference in overall rate of vocalisation (also known as volubility) was identified in infant vervet monkeys by Locke and Hauser (1999), who found that females vocalised significantly more often than males. In their study, however, most vocalisations were care elicitation calls directed at mothers; whether the sex difference in infant volubility translates into a similar bias in adulthood, when social networks are fully established, is unknown.

Data on sex differences in patterns of vocal communication are also relevant to current ideas relating to language evolution. Dunbar (1993) has argued that the pressure to maintain social networks as group size increased during human evolutionary history may ultimately have driven the evolution of language as a novel social bonding mechanism. According to this theory, when group size reached a point where the time demands of grooming became unmanageable, language evolved as a more time-efficient 'vocal grooming' mechanism (Dunbar, 1993). Extending this line of logic, it has been proposed that the selective pressures driving language evolution would have acted more strongly on the nondispersing sex, the members of which needed to establish and service a larger and more complex network of long-term relationships (Dunbar, 1996). This latter hypothesis would be supported by evidence from nonhuman primates indicating that even in the absence of language, vocal communication is more important for the philopatric sex, members of which form the core of the group.

In this study, we set out to investigate whether sex differences in primate social communication, well documented in relation to grooming, extend also to vocal communication. The overall rate of production of three types of vocalisations given during close-range social interactions—coos, grunts, and girneys—was examined among free-ranging adult rhesus macaques (*M. mulatta*). This rate was compared between males and females. Then, for each sex separately, the rate of vocalisation towards the two sexes was compared.

2. Methods

2.1. Study site and subjects

This study was carried out in a population of free-ranging rhesus macaques on the island of Cayo Santiago, Puerto Rico. This population is provisioned daily with monkey chow placed in one of three large feeding corrals, and water is available *ad libitum* from a number of drinking troughs around the island. Rhesus macaques live in multi-male, multi-female groups. Females are philopatric and consequently form the core of the social group with established social relationships and networks. Males, particularly sexually mature males, assume a more peripheral position in the social structure.

Data for this study were collected during observations of one group of rhesus macaques (Group S). Study subjects were 16 adult females and 7 adult males. Data were only collected from adult animals in this study as it is only in adulthood that social networks are fully established (Datta, 1988).

2.2. Data collection

Data were collected during 15 min focal follows from March 27 to June 12, 2006, between 0700 and 1430 h. A total of 182 and 46 h of data were collected for females and males, respectively. Throughout the study period, focal individuals (except oestrous females) were sampled at least once every 2 days. The order in which focal animals were followed was randomised each day, and focal observations of the chosen animal began on locating them, unless the subject was sleeping, in oestrus or in the feeding corral. The daily provision of food on Cayo Santiago meant that monkeys' vocalisation rates were significantly elevated during this time. Feeding in the corral was also highly competitive due to the nature in which it was carried out, making morning feeding time highly artificial, not resembling a natural setting. Animals were therefore not followed while in the feeding corral. Data were not collected from females while they were in oestrus, due to their unusual behaviour during this period (Sahi, 2003). If the subject was lost at any point during the focal watch, the observation was suspended until the animal was found again. The focal watch was abandoned if the subject was not found after 30 min.

Recordings of vocal bouts were made using a Marantz PMD670 solid-state recorder and Sennheiser MKH416 microphone to allow quantification of the rate of production of vocalisations. As this study relates to social communication, only grunts, coos, and girneys were recorded; these three types of calls are given in close-range—generally affiliative—social contexts (Erwin, 1975; Hauser, Evans, & Marler, 1993; Rowell & Hinde, 1962; Silk et al., 2000) and