

### 3 *The role of emotions in social relationships*

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#### **Introduction**

Differences in the quality of social relationships play a major role in the variation of social organization among gregarious animals. Understanding the differences between social relationships can be achieved by carefully studying the social interactions that group members exchange (Hinde, 1979). The same individual has different social relationships with two group members when it interacts in a different way with each of them. On a broader scale, groups or species differ in their social organization when relationships between group members display overall differences, i.e. when individuals interact with the average group member or distribute interactions among other group members in different ways.

In the case of macaques, the variation in dominance style (*sensu* de Waal, 1989a; Flack & de Waal, Chapter 8) among these closely related species is reflected at the interaction level by interspecific differences in the degree of tolerance toward the average group member (Thierry, 1985a, 2000; de Waal & Luttrell, 1989). Similarly, interspecific differences in the degree of kin bias in social interaction have been reported (Thierry, 1990a; Aureli *et al.*, 1997; Demaria & Thierry, 2001) and are likely to underlie much variation in macaque social organization. Understanding the mechanisms that bring about such differences would be an important contribution to the full comprehension of the relation between the social organization and the individual inputs and, in a broader sense, the relation between society and individual minds. In this chapter we attempt to contribute to such an understanding by exploring the role of emotions in explaining the variation in social interactions. Harlow's pioneering work has clearly shown the importance of the emotional bases of social exchanges starting from the mother–infant relationship (Harlow, 1958). The

differences in tolerance and kin bias across macaque species could be related to possible variations in other aspects such as the degree of impulsivity, anxiety, and the need for emotional support from others. Systematic research on interspecific variations in these aspects has not been carried out yet, although initial work has been promising (Clarke & Boinski, 1995).

We begin the chapter by reviewing the different positions on studying emotions in animals and define how we use the concept of emotion in the remaining part of the chapter. We then briefly present physiological and behavioral indicators of emotions that are particularly useful in animal studies. The indicators are used to review evidence of emotions in macaques. Particular attention is given to emotions as causes and consequences of social life and to their role in relationship assessment and mediation of social interactions. Finally, we propose a framework for future research in which we emphasize that the comparative study of emotional responses could provide insights into the selective pressures at the basis of the origin of social diversity across macaque species.

### **Animal emotions**

During the last two decades research on emotions has grown enormously but the majority of research has focused on humans (Cacioppo & Gardner, 1999; Aureli & Whiten, 2003). Terms with emotional connotations are still rarely to be found in studies of animal behavior. Although the recent development of the discipline of *affective neuroscience* (Davidson & Sutton, 1995; Panksepp, 1998) has produced a boost in research using animal models, relatively few studies have systematically investigated behavioral phenomena related to emotions in nonhuman animals.

The paucity of research on animal emotions is possibly mainly due to the fact that emotions have been traditionally described in terms of subjective experiences. For example, it is common to find in introductory psychology textbooks emotion being defined as an evaluative response of the organism involving physiological arousal, expressive behavior, and conscious experience. Most students of animal behavior have thus preferred to avoid terms related to emotions, seeing them as overly anthropomorphic. They have attempted instead to relate animal behavioral sequences to contextual contingencies and motivating factors (van Hooff & Aureli, 1994). The prevalent view has been that subjective experience, unlike behavior, cannot be observed, thus only behavior, and not emotion, can be scientifically studied.

There have been voices of dissent as to whether the impossibility of determining if nonhuman animals have subjective experiences should prevent the investigation of animal emotion (see Panksepp, 1989). The dissent has increased

in recent years and an alternative view has been put forward. The fact that scientists may never be able to investigate the subjective experience of other animals should not prevent the study of animal emotions (Aureli & Whiten, 2003). After all, we have difficulty in knowing whether our own subjective emotional experience is similar to that of other human beings, yet scientific research on human emotions has nonetheless progressed greatly. We certainly need to acknowledge that the degree of subjective feeling associated with emotion may vary, depending on the extent to which a species possesses the capacity of conscious awareness (LeDoux, 1995). In any case, subjective feeling, though important, is only one aspect of emotion (Öhman, 1993; Davidson & Sutton, 1995; LeDoux, 1995, 1996; see Damasio, 2000).

Following MacLean's (1952) evolutionary approach to brain anatomy, emotions cannot be assumed to be uniquely human traits because most of the brain structures involved in emotions are essentially the same in all mammals and perhaps in all vertebrates (LeDoux, 1996; Panksepp, 1998). MacLean's conceptual framework has been strongly supported by neurophysiological evidence (Panksepp, 1989, 1998; Brothers, 1990; Davidson & Sutton, 1995; LeDoux, 1996; Rolls, 1999). We can therefore use the term "emotion" without implying the conscious feeling that humans associate with it – other animals may experience it as well, but we may never be able to demonstrate this.

There is a growing consensus among scientists on the general function of emotions in terms of adaptive response to environmental demands, preparing the individual to cope with them and increasing survival (e.g. Ekman, 1984; Frijda, 1986; Lazarus, 1991; Öhman, 1993; LeDoux, 1996; Damasio, 2000). At the most basic level, emotions are part of the homeostatic regulation that assures the survival of the organism. This basic function is probably achieved by relying on a relatively simple evaluative system that differentiates between hostile and hospitable stimuli and allows rapid orienting responses of approach or withdrawal (Cacioppo & Gardner, 1999; see Davidson, 2000). This characteristic can explain why emotions are inseparable from the concepts of reward or punishment, of pleasure or pain, of advantage or disadvantage (Damasio, 2000) and why brain systems critical for reward–punishment evaluation are involved in emotional experience (Rolls, 1999). This conceptualization may explain why the dichotomous classification of "positive" and "negative" emotions, although potentially arbitrary, appears intuitively solid: it is actually based on very basic adaptive responses. It follows that the concept of positive and negative emotions, so pervasive in human psychology, can be confidently applied to the study of animal emotions.

A critical functional issue is the specific role of emotions in motivating organisms to act (Rolls, 1990; LeDoux, 1996). Emotions can be viewed as interfacing between sensory inputs and motor outputs in a way that allows *flexibility* in the response, in contrast to (genetically programmed or learned) fixed action

patterns as a reaction to a stimulus (Gray, 1975; Panksepp, 1989; Rolls, 1995). The essential function of emotions can therefore be summarized as gearing a particular type of motivational control to the perception of critical circumstances (Aureli & Whiten, 2003). This leads the individual to take a particular motivational stance, which severely constrains its further behavior, i.e. it constrains decision-making for some time appropriate for its referent (see Johnson-Laird & Oatley, 1992; Damasio, 1994). Although decision-making is constrained, this is only for an appropriate and temporary period. Overall flexibility of response is not hampered, but is achieved by changing the motivational stance elicited by different circumstances.

### Emotions as intervening variables

Intervening variables are constructs used to explain complex webs of causation. For example, many different aspects of drinking behavior (e.g., effort to obtain drink, amount drunk) can be caused by many different factors (e.g., time since last drink, salt load). The causal linkage between a multiplicity of such factors and the many aspects they may influence can be explained most economically by hypothesizing a central intervening variable, in this case “thirst” (Miller, 1959). Although we may not be able to observe an animal’s state of thirst directly, we can infer it on the basis of observable phenomena and having done so we can well predict how the animal will behave in a variety of contexts. We can do so without having to decide whether thirst *feels* the same in ourselves and the animal of interest (Aureli & Whiten, 2003). This kind of approach to identifying phenomena that are not directly observable is normal and common scientific practice. A similar approach has been used for “states of mind,” such as thought and belief, of other individuals (Whiten, 1996; Call, 2001). The same logic can apply to the recognition of emotional states in animals (Hinde, 1972; Aureli & Whiten, 2003). The view of emotion as an intervening variable is highly compatible with the concept of flexible responses derived from emotional interfacing between sensory inputs and motor outputs, involving a process of canalization of motivational stance and decision-making (see above).

The understanding of the relationship between neurophysiological processes and the nature of emotions can benefit from viewing emotions as intervening variables (Fig. 3.1). On the one hand, neurophysiological phenomena may be incorporated into the web of causal links that justifies the attribution of a particular state of emotion, which has the explanatory power of an intervening variable. On the other hand, direct inferences from neurophysiological variables become more powerful when an inter-correlated array of them is identified, rather than a single one (Cacioppo *et al.*, 1993), and this indeed reflects the logic behind the concept of an intervening variable (Aureli & Whiten, 2003).

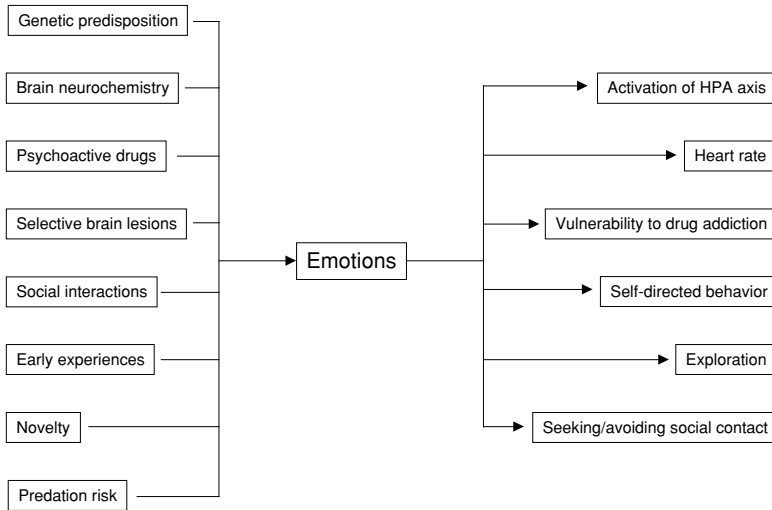


Fig. 3.1. Emotions as intervening variables relating causal factors to behavioral and physiological responses. (After Hinde, 1972; Aureli & Smucny, 2000.)

The integration of neurophysiological mechanisms with the perspective of emotions as intervening variables is also indicated from another theoretical position. Economical representations of events (such as intervening variables), although elegant, may not reflect reality if too simplistic. Biological solutions do not emerge *ex-novo* as the most parsimonious possibilities, but develop from pre-existing structures and therefore are constrained by their evolutionary past. Biologically relevant explanations of emotions as intervening variables should therefore aim to incorporate information about the underlying neurophysiological processes (Aureli & Whiten, 2003; see Zupanc & Lamprecht, 2000, for motivation as an intervening variable). In the remaining part of the chapter, we use the concept of emotion as an intervening variable involving neurophysiological processes but without implying subjective feeling.

### Indicators of emotions

In this section, we review research on emotional states and emotional expressions in human and nonhuman primates to illustrate various indicators of emotions. Given the recent growth of the field, the review cannot claim to be exhaustive. We especially focus on research that highlights indicators that have been used in studies on macaques. Here, however, we deliberately cover examples mainly from primates other than macaques because studies on macaques are

reviewed in detail in the next section. We start with the indicators of brain processes involved in emotions, and then we review indicators of peripheral physiological activity, followed by evidence of behavioral indicators.

### ***Indicators of brain processes***

Various methods have been used to explore the role of structures of the central nervous system and different neurotransmitters in the regulation of emotion. Traditionally these methods have been invasive (e.g., electrical stimulation, chemical manipulation, cerebrospinal fluid sampling, and lesions of specific brain areas). Through the use of these methods, much has been learned, for example, on the role of the amygdala in regulation of fear and other emotions (LeDoux, 1996; Aggleton & Young, 2000; Davis & Whalen, 2001; Amaral, 2002). More recently, noninvasive methods have been used, such as positron emission tomography (PET) and functional magnetic resonance imaging (fMRI). These techniques allow scientists to relate particular neuroanatomical areas and brain activity with emotional responses and emotional memory (Dolan & Morris, 2000; Reiman *et al.*, 2000; Davis & Whalen, 2001). Activity of specific brain areas and its possible asymmetric nature have been successfully investigated with electroencephalography (EEG) and other techniques (e.g., brain temperature). These findings suggest a lateralization of brain processing of emotions in human and nonhuman primates (Davidson, 1995; Canli *et al.*, 1998; Parr & Hopkins, 2000).

The plasticity underlying the flexibility of emotional states is achieved by the actions of neuromodulators. An important example of neuromodulators is provided by brain opioids. These are substances that produce pleasant sensations and that are usually released during “positive” emotions associated with rewarding situations (Dum & Herz, 1987; Panksepp *et al.*, 1997). For example, in talapoin monkeys the receipt of grooming increases the concentration of endogenous brain opioids (Keverne *et al.*, 1989).

### ***Physiological peripheral indicators***

Common techniques for the monitoring of peripheral physiological parameters include the measurement of functions such as heart rate, blood pressure, hand temperature, skin resistance, muscle tension, and hormonal levels (reviewed in Cacioppo & Tassinary, 1990; Bauer, 1998). Some studies use only one of these measures, whereas others monitor several physiological functions simultaneously. An example of a multi-measure study is the classical work by Ekman

and collaborators (1983) on human subjects while eliciting six emotions. Physiological changes depending on the quality of the elicited emotion have also been reported for nonhuman primates. For example, a study monitoring cardiac activity of infant chimpanzees differentiated their emotional responses to two conspecific vocalizations (Berntson *et al.*, 1989).

An increase in heart rate has been shown to be associated with acute experience of anxiety in humans (Öhman, 1993; Berntson *et al.*, 1998) and is also produced by treatment of rhesus macaques with anxiety-eliciting drugs (Ninan *et al.*, 1982). Biotelemetry has been used to monitor physiological changes in free-moving nonhuman primates. In one such study, dominant male hamadryas baboons showed an anticipatory increase in heart rate in the seconds before starting an aggressive interaction (Smith *et al.*, 2000).

Various physiological events are characteristic of the “stress response” (von Holst, 1998) which results in the rapid mobilization of energy: heart rate, blood pressure, and breathing rate all increase to transport nutrients and oxygen where needed. The response is adaptive as it enables individuals to take immediate action in threatening situations. Measures of variation in hormones and neurotransmitters associated with the stress response (e.g., cortisol, norepinephrine) have provided biological support for individual differences in emotional profiles of children and olive baboons (Kagan *et al.*, 1988; Sapolsky, 2000).

### ***Behavioral indicators***

Since Darwin’s (1872) original emphasis, *facial expressions* have been among the emotional indicators primarily studied in humans (Ekman, 1993). There is evidence that facial expressions are also a means to convey emotions in nonhuman primates (Parr 2001; Preuschoft, Box 3). Darwin (1872) also pointed to vocal signals as primary carriers of emotional valence. There is substantial evidence that emotional experience produces changes in respiration, phonation, and articulation, which affect acoustic features, and that the acoustic features of *vocal emotional expression* are similar in human and nonhuman primates (Jürgens, 1998). Detailed acoustic analyses of human speech and primate vocalizations have revealed that vocal parameters not only index the degree of emotional intensity, but also differentiate emotional valence (Bachorowski & Owren, 1995; Fichtel *et al.*, 2001).

A less conventional set of behavioral indicators of emotional experience has been used recently in nonhuman primates. *Self-directed behaviors*, such as self-scratching and self-grooming, obviously have a hygienic function, but they have also been considered as displacement activities, i.e. activities which are apparently irrelevant to an individual’s ongoing behavior and which reflect

motivational ambivalence or frustration (Tinbergen, 1952; McFarland, 1966). Recent ethological studies on human and nonhuman primates have documented an increased frequency of these behaviors in situations of uncertainty, social tension, or impending danger (reviewed in Maestriperi *et al.*, 1992a; Troisi, 2002). Furthermore, pharmacological manipulations have demonstrated that self-directed behavior is strongly associated with anxiety in various primate species (Ninan *et al.*, 1982; Schino *et al.*, 1991, 1996; Maestriperi *et al.*, 1992b; Cilia & Piper, 1997; Barros *et al.*, 2000).

## **Emotions in macaques**

### *Neurobiological bases*

The neurobiological bases of emotional responses in macaques have been the subject of extensive investigations. “Positive” emotions associated with social contact appear to be mediated by brain opioids. Infant rhesus macaques separated from their mothers decrease their distress vocalizations (“coo” calls) when treated with low, non-sedative doses of morphine, while distress vocalizations increase in frequency after treatment with naloxone, an opioid antagonist (Kalin & Shelton, 1989). Interestingly, opioids appear to modulate both bonds between mothers and offspring and bonds between group mates: administration of naloxone to group-living juvenile longtailed macaques caused a generalized increase in the requests for affiliation directed to both the subject’s mother and to other groupmates (Schino & Troisi, 1992; see also Martel *et al.*, 1995).

“Negative” emotions such as fear of a staring human (probably perceived as a “predator”) appear to be modulated by the gamma aminobutyric acid (GABA)-benzodiazepine receptors. Diazepam decreased fearful responses to the human “predator” in isolated infant rhesus macaques (Kalin & Shelton, 1989). The amygdala seems to be the key brain structure involved in the mediation of acute fear and anxiety: in rhesus macaques, selective lesions of the amygdala caused a blunting of acute fear in response to the presentation of stimuli such as a snake or a threatening unfamiliar individual (Emery *et al.*, 2001; Kalin *et al.*, 2001).

There is suggestive evidence supporting the lateralization of emotions in rhesus macaques (Hauser, 1993). In the same species, fearful temperament is associated with asymmetric frontal brain activity (as assessed by electroencephalography) and to elevated concentrations of corticotropin-releasing hormone (CRH) in the cerebrospinal fluid (Kalin *et al.*, 1998, 2000). The genetic bases of interindividual differences in emotionality and brain monoamine functioning are just beginning to be investigated in both macaques (Champoux *et al.*, 1999; Bennett *et al.*, 2002) and baboons (Kaplan *et al.*, 2001; Rogers *et al.*,

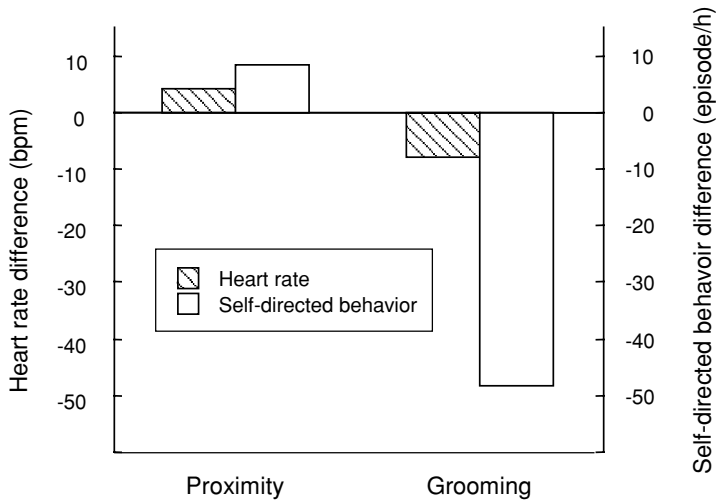


Fig. 3.2. Effects of social interactions on behavioral and physiological measures of emotions. Proximity to higher-ranking animals (within 0.5 or 1 m depending on the study) causes an increase, whereas receiving social grooming causes a decrease in both self-directed behavior and heart rate. Both measures are expressed as differences from control observations. The figure combines data from three separate studies on longtailed and rhesus macaques. Original results and methodological details can be found in Schino *et al.* (1988), Pavani *et al.* (1991) and Aureli *et al.* (1999). Note that self-directed behavior refers to scratching only in the study of the effect of proximity, and to the sum of scratching, self-grooming, body shaking, and yawning in the study of the effect of social grooming.

2001). Significant interactions between genetic predisposition and early rearing experiences seem to characterize the development of emotionality in macaques (see Suomi, 1999; Chapter 2).

### *Emotions as consequences of social interactions and relationships*

Social interactions have been shown to cause short-term emotional reactions. Proximity to dominant individuals, insofar as it is related to an increased uncertainty and risk of aggression, is associated in longtailed macaques with increases in self-directed behavior such as scratching and self-grooming (Troisi & Schino, 1987; Pavani *et al.*, 1991; see also Castles *et al.*, 1999, for similar data on olive baboons). Similarly, in a biotelemetry study of emotional responses of rhesus macaques during social interactions, Aureli and collaborators (1999) monitored the heart rate of free-moving individuals, recording their response to being approached by different group members, while controlling for movement. The approach of a dominant individual caused an increase in heart rate (Fig. 3.2),

whereas the approach of a subordinate or kin did not cause consistent heart rate changes. The increases in self-directed behavior and heart rate as a consequence of potentially threatening interactions are mirrored by the decreases observed during and following friendly interactions, possibly associated with positive emotions. Receiving social grooming reduces both self-directed behavior and heart rate (Fig. 3.2) (Schino *et al.*, 1988; Boccia *et al.*, 1989; Aureli *et al.*, 1999). Similarly, heart rate and self-directed behavior increase during the post-conflict period and are reduced following reconciliation, i.e., the friendly reunion of former opponents that may occur after conflict (Fig. 3.3) (Aureli & van Schaik, 1991; Smucny *et al.*, 1997; Aureli & Smucny, 2000).

Other evidence of emotional responses to social interactions is provided by studies investigating dominance effects. Different changes in heart rate are found between dominant and subordinate longtailed macaques in response to varying proximity with group members during the initial phases of group formation (Manuck *et al.*, 1986). Furthermore, intermediate-ranking rhesus macaques scratch themselves more than others at feeding time probably because they experience higher uncertainty about how to behave than do dominant individuals, who easily monopolize the food, and subordinate individuals, who wait for access to the food (Diezinger & Anderson, 1986).

Evidence that facial displays are perceived as expressions of emotional states is provided by an elegant (although problematic for animal welfare) series of experiments involving pairs of rhesus macaques in the role of 'informer' and 'responder'. Miller (1971) reported that the view of a silent bared-teeth display exhibited by the informer was sufficient for the responder to press a lever and avoid an electric shock. The informer responded with this facial display when seeing a warning signal indicating the upcoming electric shock, but the warning signal was not visible to the responder who had to base its response only on the fear conveyed by the display of the partner.

Over a longer time span, social relationships can modulate the emotional responsiveness of macaques to stressful events. Schino & Troisi (2001; see also DeVinney *et al.*, 2001) described how yearling Japanese macaques often respond to the birth of a sibling (and to the associated abrupt reduction in maternal availability) with depression and emotional withdrawal, as evidenced by greatly reduced social play. The likelihood of a depressive response in the yearling macaques was predicted by the quality of the mother-yearling relationship *before* the sibling birth: yearlings having a warmer relationship with their mother were less likely to become depressed following the birth of a sibling.

Social relationships can also induce changes in brain functioning and neurochemistry, possibly influencing emotional responsiveness. For example, social dominance has been shown to alter brain dopaminergic functionality as assessed by PET. After becoming dominant, longtailed macaques showed an increase in

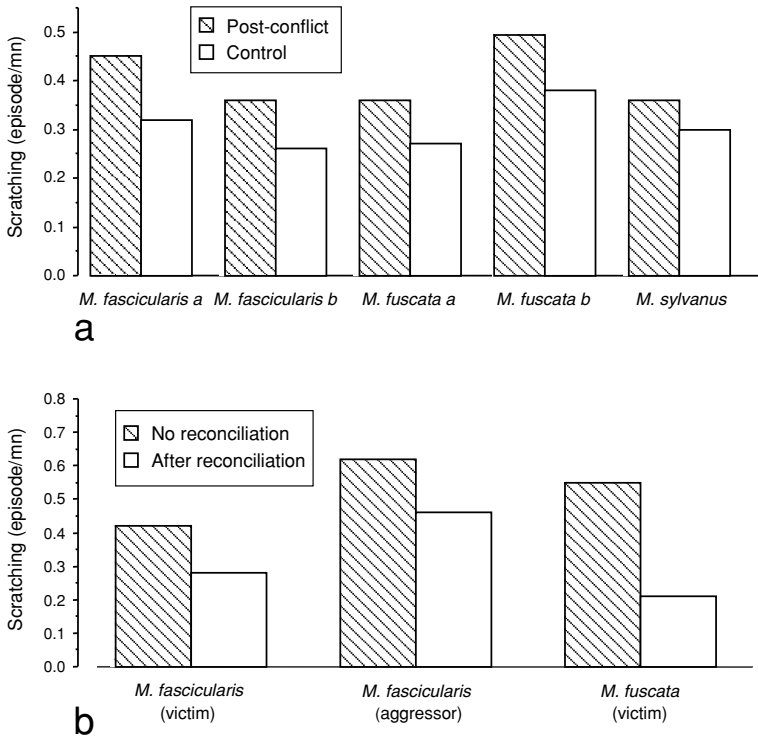


Fig. 3.3. Effects of aggression and reconciliation on rates of scratching shown by macaques. (a) Scratching displayed by victims of aggression during post-conflict and control periods in five populations of macaques (rates of the two periods are significantly different in all comparisons). Sources of data: *Macaca fascicularis a* from Aureli & van Schaik, 1991; *M. fascicularis b*, from Aureli, 1992; *M. fuscata a*, from F. Aureli, H. Veenema & C. van Panthaleon van Eck (unpub. data); *M. fuscata b*, from Rosati, 1996; *M. sylvanus* from Aureli, 1997. (b) Scratching displayed by former opponents during post-conflict periods with no reconciliation and during post-conflict periods following reconciliation in three populations of macaques. Sources of data: *M. fascicularis* (victim) from Aureli & van Schaik, 1991; *M. fascicularis* (aggressor) from Das *et al.*, 1998; *M. fuscata* (victim) from Kutsukake & Castles, 2001.

indices of brain dopaminergic activity and a consequent decrease in the reinforcing properties of cocaine (Morgan *et al.*, 2002). The experience of social dominance and the associated higher degree of perceived control over environmental and social events may modify emotional responses mediated by brain dopaminergic activity.

Finally, quality of early mother–infant relationships has repeatedly been shown to have long-term effects on juvenile and adult emotionality in a variety of



Fig. 3.4. A Japanese macaque infant approaches a playmate while its mother watches and scratches herself (Rome Zoological Park, Italy). (Photograph by G. Schino.)

macaque and other primate species (Hinde & Spencer-Booth, 1970; Andrews & Rosenblum, 1994; Schino *et al.*, 2001, for data on macaques; see Fairbanks & McGuire, 1988, 1993; Dettling *et al.*, 1998, for data on other primates). Both correlational and experimental studies concur in documenting an association between maternal style experienced as infants and later emotionality as juveniles/adults. Interestingly, behavior under baseline, non-stressful conditions is not affected by early experiences, while they potently affect responses to mildly stressful situations such as interactions with unfamiliar conspecifics or objects, response to aggression and to the proximity of dominant individuals. Emotional responses investigated in these studies ranged from self-directed behavior to urinary cortisol, to latency to approach unfamiliar objects or locations.

### *Emotions as causes of social interactions and relationships*

Anxiety has long been suggested as a proximate factor underlying interindividual differences in macaque maternal style (e.g., Hooley, 1983). Empirical support for this hypothesis has been provided by the significant correlations that have been demonstrated to exist between behavioral indicators of anxiety, such as scratching and visual monitoring (Fig. 3.4), and protective maternal styles (Troisi *et al.*, 1991; Maestripieri, 1993).

A more direct test of the role of anxiety in modulating macaque social behavior derives from ethopharmacological studies that investigated the effects of psychoactive drugs on animals living in social groups. Maestripieri and collaborators (1992b) found that administration of an anxiogenic drug (beta-CCE) to infant rhesus macaques increased their contact seeking behavior toward their mothers, while anxiolytic drug treatment (with midazolam) facilitated

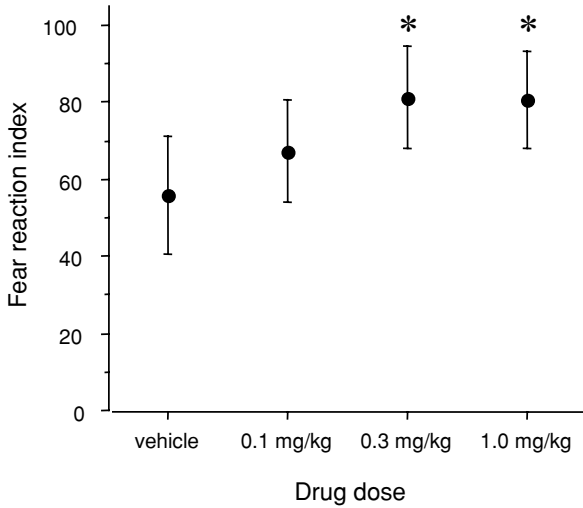


Fig. 3.5. Effect of various doses of an anxiogenic drug (FG 7142, a benzodiazepine inverse agonist) on the fear reaction shown by mature male longtailed macaques to the approach of the dominant male. The asterisks indicate significant differences from the vehicle control. The fear reaction index is calculated as the percentage of received approaches to which the subject responds with bared-teeth or an immediate leave. (After Schino *et al.*, 1996.)

playful interactions with group mates, especially with older individuals. An anxiolytic drug (diazepam) increased the rate of friendly exchanges during reunion of familiar juvenile rhesus macaques, whereas an anxiogenic drug (d-amphetamine) had the opposite effect and increased submissive behavior (Thierry *et al.*, 1984). Schino and collaborators (1996; see also Bellarosa *et al.*, 1980; Knobbout *et al.*, 1996) observed increased fear reactions to the approach of a dominant individual as a consequence of anxiogenic treatment (with FG 7142) in mature male longtailed macaques (Fig. 3.5).

Interindividual differences in emotionality (and here we move very close to issues relevant to personality/temperament: see Chapter 2) as assessed by basal plasma cortisol were shown to be linked to differences in the styles of dominance among high-ranking wild olive baboons (Sapolsky & Ray, 1989; Sapolsky, 2000). No comparable data are available for macaques, but consistent interindividual differences in cortisol concentrations and heart rates have been reported for adolescent rhesus macaques (Rasmussen & Suomi, 1989). Similarly, among infant rhesus macaques consistent interindividual differences in reactivity to mildly stressful stimuli have been described (Suomi, 1999). Highly-reactive infants share behavioral and physiological characteristics with “shy” children (Kagan *et al.*, 1988).

Furthermore, interindividual differences in impulsivity seem to underlie much variation in primate social behavior and even life history. In male vervet monkeys impulsivity, as measured by means of an intruder challenge test, showed large interindividual variation and peaked at age 4 years, the typical age of emigration in this species. High-ranking males showed moderate levels of impulsivity while low-ranking males were either extremely or very slightly impulsive (Fairbanks, 2001). In rhesus macaques, heart rate was lower in males who had recently emigrated than in males of comparable age who were still in the natal group (Rasmussen *et al.*, 1988).

Primate impulsivity has also been linked to the functionality of the serotonergic system. Low serotonergic activity is correlated with severe aggression, excessive mortality and early emigration in rhesus and longtailed macaques (Botchin *et al.*, 1993; Mehlman *et al.*, 1994, 1995; Kaplan *et al.*, 1995; Higley *et al.*, 1996a,b,c; Chapter 2) and with high impulsive scores in male vervets during the intruder challenge test (Fairbanks, 2001). Pharmacological manipulation provided experimental confirmation of some of these correlational results (Fairbanks, 2001). Recently, it has even been suggested that the interspecific differences in the tendency to emigrate observed in male hamadryas and olive baboons may be linked to differences in serotonergic activity (Kaplan *et al.*, 1999). No comparative data of this kind for interspecific differences are available for macaques.

### **The mediating role of emotions**

From the examples presented in the previous two sections a clear picture emerges in which emotions can be viewed both as causes and consequences of social interactions. In this respect, emotions may play an important part in linking social interactions and therefore may have a mediating role in social exchanges between individuals. Such a mediating role is implicit in the “intervening variable” concept illustrated in Fig. 3.1.

There has been growing attention to the mediating role of emotions in the human literature (Frijda, 1986; Panksepp, 1989; Rolls, 1995) and in research on other animals (Crook, 1989; Lott, 1991; Pryce, 1996; Owren & Rendall, 1997; Aureli & Whiten, 2003). The emotional experience (without implying subjective feeling) of an individual is certainly affected by the frequency and quality of previous interactions with group members (see above). Emotional states may express a crucial integration of the information contained in the various interactions between two partners and may change over time depending on the interactions exchanged. The emotional experience can then be functionally equivalent to the processes of bookkeeping of the various interactions

with a partner, computation of their relative frequencies, and conversion of their quality and associated information into a common currency, all needed for relationship assessment (Aureli & Schaffner, 2002). The resulting emotional experience is partner-dependent. Thus, emotional differences can be at the core of the observed variation in social interactions reflecting the variation in relationship quality across partners.

An example of the mediating role of emotions in macaques can be extracted from the study of conflict resolution. Aggression causes an increase in post-conflict anxiety in both the victim and the aggressor as indexed by self-directed behavior and heart rate (Aureli *et al.*, 1989; Aureli & van Schaik, 1991; Aureli, 1992; Smucny *et al.*, 1997; Das *et al.*, 1998). The post-conflict anxiety appears to be due both to the risk of renewed aggression incurred by the victim (Aureli & van Schaik, 1991; Aureli, 1992) and to the disturbance of the (valuable) social relationship between victim and aggressor (Aureli, 1997; Katsukake & Castles, 2001). Anxiety seems to be a proximate factor facilitating reconciliation which, in turn, reduces the risk of renewed aggression (Aureli *et al.*, 1989; Aureli & van Schaik, 1991; Cords, 1992; Katsukake & Castles, 2001), restores the social relationship (Cords, 1992) and thus causes a reduction in anxiety (Aureli *et al.*, 1989; Aureli & van Schaik, 1991; Smucny *et al.*, 1997; Das *et al.*, 1998; Katsukake & Castles, 2001). Post-conflict anxiety and reconciliation appear therefore to be part of a homeostatic mechanism, which regulates and stabilizes macaque social relationships threatened by aggression. In particular, post-conflict anxiety may mediate the occurrence of reconciliation by motivating opponents to exchange friendly behavior in the aftermath of aggressive interactions (Aureli & Smucny, 2000).

Since reconciliation appears to repair the relationship between former opponents disturbed by the previous conflict, it makes sense that reconciliation occurs more often between individuals with more valuable relationships (de Waal & Aureli, 1997; Aureli *et al.*, 2002). The same individual therefore engages in friendly post-conflict reunions depending on the quality of the relationship with the former opponent. This requires great flexibility in the frequency of interaction with various group members and with the same individual over time. Differential post-conflict anxiety could generate flexible responses to conflicts as shown in studies of longtailed and Japanese macaques. Rates of post-conflict scratching by the recipient of aggression were higher after conflicts between likely valuable partners (without being associated with higher rates of renewed attacks: Aureli, 1997; Katsukake & Castles, 2001) and reunions occurred more often following conflicts between such partners (Aureli *et al.*, 1989; Katsukake & Castles, 2001). Differential post-conflict anxiety may therefore reflect relationship assessment and mediate the effect of relationship quality

on conflict resolution. The assessment could be based on the relative loss of benefits due to relationship disturbance: more valuable relationships provide greater benefits and their disturbance would produce greater loss and higher levels of anxiety. Anxiety may mediate not only post-conflict resolution, but could also play an important role in the flexible occurrence of other forms of conflict management (e.g., forms to prevent aggressive escalation: Aureli & Smucny, 2000).

A less detailed example derives from the study of the relationship between the establishment of dominance relations and the occurrence of affiliation (see Kummer, 1975, for pioneering work on this subject in gelada baboons). Schino and collaborators (1990) showed that when unfamiliar longtailed macaque females are paired, the lack of established dominance relations causes tension and anxiety in the form of high self-directed behavior. If dominance relations are not defined in the first minutes of interaction, affiliation is prevented and anxiety increases progressively. The increased anxiety may in turn be instrumental in promoting the definition of dominance relations thus allowing affiliative interactions (e.g., grooming) to take place. Grooming in turn reduces anxiety and tension (Schino *et al.*, 1988). Again, emotions appear to be part of a homeostatic mechanism that mediates macaque social interactions.

The above study can also be interpreted from the relationship assessment point of view. The nature of the relationship of each pair was reflected in the rate of self-directed behavior. When the unfamiliar females delayed the establishment of dominance relationships, the rate of self-directed behavior was much higher than when dominance relationships were quickly established. The level of uncertainty about the relationship influences the degree of anxiety that individuals experienced. Thus, the assessment of dominance relationships with partners may be mediated by the level of anxiety experienced when in proximity with them and this in turn may affect the subsequent interactions. In fact, pairs with established dominance relationships engaged in social grooming sooner than pairs with undecided dominance relationships (Schino *et al.*, 1990).

## Conclusion

Their role in mediating social interactions and providing a means for relationship assessment makes emotions good candidates as proximate mechanisms underlying the variation in social organization across macaques. Differences in tolerance and kin bias (Chapais, Chapter 9; Thierry, Chapter 12), and possibly in other aspects of social life across macaque species could be related to potential interspecific variation in emotional experiences, which in turn trigger

different social behavior. To test this hypothesis, systematic research on interspecific differences and similarities in emotional responses to a variety of social and non-social stimuli is needed. The degree of impulsivity, anxiety levels under various circumstances and the need for emotional support from others would be among the critical aspects that should be investigated with a comparative approach. The comparative research carried out so far on some of these aspects is limited but promising (Clarke & Boinski, 1995; Capitanio, Chapter 2). Future research needs especially to compare directly interspecific (and intergroup) differences in emotionality variables with interspecific (and intergroup) differences in social variables taking into account possible sex differences (i.e., males and females of the same species may differ in such variables) and examine whether variations in the two sets of variables are meaningfully interlinked. Interspecific (and intergroup) comparisons between emotional responses and multiple social variables could elucidate whether the diversity of social interactions across macaque species (and groups) is due to different causes or to one major underlying principle of covariation.

One way of systematically gathering information on the possible emotional causes of social variation is to expand the comparative study of brain neurochemistry and monoamine functioning. The first step could be genus-wide correlations between overall patterns of social interaction (e.g., tolerance, kin bias) or life history (e.g., dispersal, lifelong rank trajectory) and various measures of brain metabolism (e.g., cerebrospinal fluid monoamine metabolite concentrations, pharmacological challenges). Furthermore, interspecific (and intergroup) differences in emotional responses could be investigated through pharmacological manipulation. The development of comparative psychopharmacology could provide the opportunity, for example, to study the effects of anxiolytic and anxiogenic drugs or of opioid antagonists on the modulation of interspecific differences in tolerance or kin bias (see Schino & Troisi, 1992, for a successful case of intraspecific manipulation).

We would also like to suggest that the comparative study of emotional responses can provide a framework to identify which of the possible selective pressures (e.g., predation risk, between-group competition, infanticide risk) is at the basis of the original diversity in macaque dominance style. For example, experiments with predator models in different species can provide systematic evidence of differential behavioral and emotional responses to them and therefore indirect information on the relative attitude to such external threats and the relative need of forming tight bonds with group members for cohesiveness and possible cooperative actions. As previously proposed by Lott (1991), differential predation risk is likely to lead to differential anxiety, which would in turn promote differential group cohesiveness to cope with such a risk. The fact that a drastic reduction in the number of potential primate predators is among the

first negative consequences of transformations imposed on the natural habitats of most macaque species by human actions leaves extrapolations from such experiments to be one of the few options we have to obtain insights into the role of predation as one of the original selective pressures. Similarly, the systematic investigation of behavioral and emotional responses to the exposure to same-sex or opposite-sex unfamiliar individuals (both experimentally in captive settings and opportunistically in the wild) in different macaque species can provide insights into the role of between-group competition and infanticide or sexual harassment in promoting differential intragroup tolerance and thus shaping social organization.

The comparative study of emotional responses to social and nonsocial factors can also be useful in order to acquire information on current patterns of social organization where data are difficult to gather in the wild (again often because there is no pristine natural macaque habitat left). An example of such investigations is the comparative study on responses to all-male group formation carried out by Clarke and collaborators (1995). Liontailed macaque males showed a much higher stress response than longtailed macaque males and the group formation had to be aborted. This outcome suggests high levels of male–male intolerance in liontailed macaques, a characteristic that certainly contributes to the higher proportion of one-male groups in wild populations of this species (Singh *et al.*, 2002).

Scientists need to make the most of the unique body of knowledge currently available on macaque societies and develop integrated approaches that combine socioecological variables with individual characteristics. The framework presented here is just one example of these approaches. Viewing emotions as causes and consequences of social life leads us to focus on their role in relationship assessment and mediation of social interactions. This is a bottom–up approach that integrates individual characteristics (e.g. emotional responses and personalities) with social interactions and relationships and that can reveal the building blocks of social organizations. We are still at the early stages of the integrative effort and more focused comparative research needs to be carried out to obtain a comprehensive picture of the development and evolution of macaque societies. The macaque model needs to be tested in other taxa so as to obtain unifying principles that could be at the root of human sociality.

### **Box 3 Power and communication**

Signe Preuschoft

Primate facial expressions represent an evolutionary legacy. Old World monkeys use about seven facial displays in the context of bonding alone. The

facial expressions used in the context of assertion are less well studied, but include approximately six additional displays (van Hooff, 1967; Redican, 1975; Preuschoft & van Hooff, 1995a). These displays are defined by their appearance, and fulfill different social functions in different species. While phylogeny cannot explain these differences in function, they coincide with differences in power asymmetry between the species.

Many facial displays are ancestral homologies of all the macaques, and also shared in common with other Old World monkeys, with apes and sometimes even New World monkeys (Preuschoft & van Hooff, 1995a,b, 1997). Among these widespread displays are the homologues to human laughter and smiling, the relaxed open-mouth display (ROM) and the silent bared-teeth display (SBT) (van Hooff, 1972; Preuschoft, 1995a; van Hooff & Preuschoft, 2003). However, the function of smiling (SBT) and laughter (ROM) displays varies between species, ranging from formal subordination, over submission and appeasement, reconciliation, to affiliation, reassurance, and even to playfulness (Preuschoft, 1992, 1995a; Preuschoft & van Hooff, 1997). Along with the functional differences, the extent to which the ROM and the SBT displays overlap morphologically differs as well (Fig. 3.6). When used in an overlapping range of functions the SBT and ROM displays tend to merge in appearance as well, producing an open-mouthed bared-teeth laughter face that is accompanied by the typical panting play vocalization.

Such functional variability is not limited to the genus *Macaca*. Importantly, even within the genus *Macaca*, the variation in the function of laughter and smile homologues is not predicted by phylogeny (but see Thierry, Chapter 12). Phylogeny would predict the functions of SBT and ROM in pig-tailed macaques should resemble those in Tonkean and liontailed macaques. Barbary macaques, the most conservative macaque, should resemble gelada baboons – but this is not the case (Dücker 1996). The situation in common chimpanzees is similar to that in Barbary macaques, whereas bonobos and humans resemble Tonkean macaques with respect to the function of laughter and smile (van Hooff, 1972; Lockard *et al.*, 1977; Preuschoft & van Hooff, 1997; S. Preuschoft personal observation). The differences within the great apes as well as the similarity between some great ape species and some macaque species is impossible to reconcile with the idea that phylogeny predicts the function and form of smile and laughter homologues.

On the other hand, the functional differences between species of macaques do correspond to characteristic differences in power asymmetry (Fig. 3.6). Power asymmetries are evident in a set of covarying social traits, including both dominance and sociopositive interactions (Thierry, 1985a, Chapter 12; de Waal, 1989a; de Waal & Luttrell, 1989; Preuschoft & van Schaik, 2000).

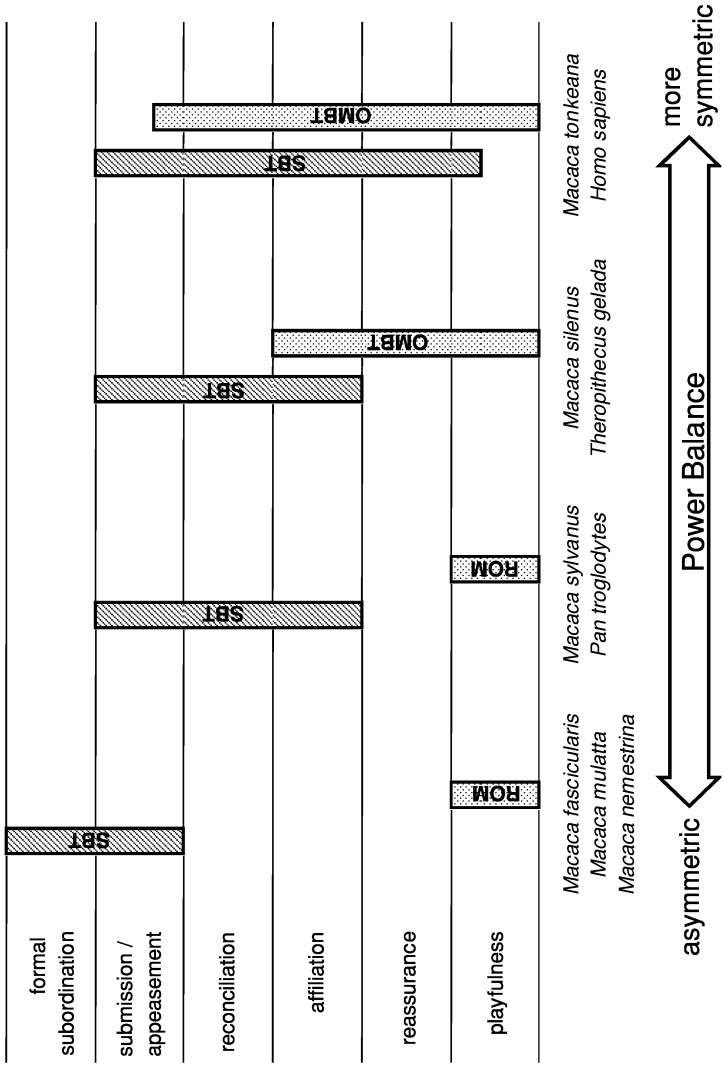


Fig. 3.6. The social functions of silent bared-teeth (SBT) and relaxed or open-mouth bared-teeth displays (ROM and OMBT respectively) coincide with characteristic differences in power balance but not with phylogeny (*M. fascicularis*: Preuschoft *et al.*, 1995; *M. nemestrina*: S. Preuschoft, J. Flack, and M. L. Gong, unpub. data; *Theropithecus gelada*: Dücker, 1996; *M. silenus*: Preuschoft & Beckmann, 1995; Beckmann, 1997; *M. tonkeana*: Preuschoft 1995b; see reviews in Preuschoft & van Hooff, 1997; Preuschoft & van Schaik, 2000; Thierry, 2000).

In obligatory social species the need for sociopositive interactions can profoundly alter the power dynamics in dyads, since it results in leverage power on the side of the needed individual (Hand, 1986; Lewis, 2002). Species-typical power asymmetries were established in independent studies (Thierry, 1985a, 2000; de Waal & Luttrell, 1989). On this basis macaque species can be arranged on a continuum from very asymmetric to more balanced power relations (Thierry, 2000, Chapter 12; Preuschoft & van Schaik, 2000).

The “Power Asymmetry Hypothesis” of functional changes predicts the greatest functional overlap of the SBT and the ROM display for species with the most symmetric power relations (Preuschoft & van Hooff, 1995b, 1997). The SBT functions as a genuine expression of friendly attraction, and may serve to appease or reassure an interaction partner and may even accompany a play invitation. Shading in with the SBT, the play face becomes a open-mouthed bared-teeth laughter face which not only expresses skittish playfulness but is also used in reconciliation and even appeasement (Thierry *et al.*, 1989; Preuschoft, 1995b). The species with the most asymmetric power relations, on the other hand, show the opposite pattern. As an indicator of formal subordination, silent-baring of the teeth is restricted to the communication of submission and appeasement. Confined to the play context, the morphologically wholly distinct relaxed open-mouth display earmarks playful transgression of rules.

The situation in pigtailed macaques is particularly interesting. While generally considered a member of the *silenus*-group (Delson, 1980; Fooden, 1980; Morales & Melnick, 1998) pigtailed power relations resemble those of the more distantly related longtailed macaques, and are clearly more asymmetric than those of their closer relatives, Tonkean or liontailed macaques (Castles *et al.*, 1996; Thierry, 2000; J. C. Flack, unpublished data). Pigtailed communication turns out to be exactly in line with the power asymmetry hypothesis: like other “despotic” macaque species, pigtailed macaques use only a ROM display, and not the open-mouth bared-teeth display that is typical of those with more balanced power relationships. The ROM is restricted to the context of play, and the SBT is used as an appeasement signal and expresses formal subordination (Fig. 9.2) (S. Preuschoft, J. C. Flack & M. L. Gong, unpublished data).

In species with strictly asymmetric power relations we find signals that are only performed by the subordinate member of a dyad and express a readiness to yield (de Waal & Luttrell, 1985; Preuschoft, 1999). Such indicators of formal subordination exist because conflicts of interest are consistently won by the dominant. Formal status indicators communicate a

sender's perception of the power relationship between itself and the receiver (Preuschoft, 1999; Preuschoft & van Schaik, 2000). It is therefore expected that, contingent upon differences in power asymmetry, macaque species should also vary in the use of formal status indicators. This is indeed the case: species with rather balanced power relationships, such as Tonkean or lion-tailed macaques do not use any status indicators. Species with reduced power asymmetries, like Barbary or stumptailed macaques, do not use indicators of subordination but of dominance. Dominance indicators express a dominant's assertive tendency (Reichler, 1996). In these species the subordinate does not volunteer to yield without solicitation but waits until precedence is claimed by the dominant. Barbary macaques and geladas use a rounded-mouth stare as dominance indicator (Reichler, 1996; Preuschoft *et al.*, 1998). In stumptailed macaques formal biting is documented to function as a dominance indicator (Chevalier-Skolnikoff, 1974; Demaria & Thierry, 1990).

It also appears that the variation in power asymmetries is not limited to the genus *Macaca*. Similar variation also exists among great apes, and data indicate corresponding differences in communication patterns (van Schaik *et al.*, 2004). Among platyrrhines, tufted capuchin monkeys have been likened to chimpanzees in their potential for food sharing, hunting and tool use, and there is research linking these behaviors with social tolerance and cooperation (Coussi-Korbel & Frigaszy, 1995; de Waal, 2000). It is therefore interesting that we found tufted capuchins to use a SBT in both courtship and play, but not as a response to aggression (D. R. Valenzano, E. Visalberghi & S. Preuschoft, unpublished data).

The selection pressures that influence a display's social function arise from the receivers. The social relationship between sender and receiver, that is whether emphasis is more on competition or on cooperation, is critical to how the receiver will respond to a display, and when it will suit a sender to publicize private motivational states (Dawkins & Krebs, 1978). When the relationship is mainly cooperative we expect displays to be rich in meaning, because misunderstandings are not dangerous, and receivers to exhibit little "sales-resistance", i.e., to respond to even subtle cues. On the other hand, when relationships are predominantly competitive, displays should be highly salient and unambiguous, while the skeptical receivers respond only where necessary (Krebs & Dawkins, 1984). Clearly, such differences in power balance will also produce differences in emotional dispositions (Aureli & Schino, this Chapter).

Such interpretations rely on a functional link between communication patterns and the power asymmetry characteristic for a macaque society. There

is not always a close match between social variables established in field studies as opposed to those found in studies of provisioned or captive groups (e.g., Kawamura, 1958; Hill & Okayasu, 1996). The covariation between dominance styles and communication patterns, which are inherited, therefore provides strong evidence that dominance styles, or power asymmetries, should be interpreted as evolved, rather than ephemeral, context-induced variability.