

A modest proposal: displacement activities as an indicator of emotions in primates

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Abstract. Displacement activities are behaviour patterns (mostly body care activities) characterized by their apparent irrelevance to the situation in which they appear. Scratching, autogrooming, yawning and body shaking are among the most commonly reported displacement activities in non-human primates. A review of the primate literature indicates that displacement activities tend to occur in situations of psychosocial stress and that their frequency of occurrence is affected by anxiogenic and anxiolytic drugs. In the light of this evidence, it is suggested that displacement activities can be used as indicators of emotional states arising in a variety of primate social interactions. Methodological problems associated with such a use are discussed. The hypothesis that displacement activities may also have a communicative function in non-human primates is not supported adequately by available data.

According to the usual definitions, displacement activities are behaviour patterns exhibited by an animal that are 'apparently irrelevant' to its ongoing activity (see Tinbergen 1952; Zeigler 1964). For example, in several sexual or agonistic contexts, passerine birds can clean their bills or feathers, eat or drink, or commit themselves to other activities that apparently do not have any obvious contextual relationship (Hinde 1953; Morris 1954; Rowell 1961). Similar examples have been reported in other animal groups such as arthropods, fish and mammals (e.g. Tinbergen & van Iersel 1947; Sevenster 1961; Duncan & Wood-Gush 1972; Hansen & Drake af Hagelsrum 1984; Roper 1984). Displacement activities are thought to occur in conflict situations (i.e. when two incompatible motivational tendencies are elicited simultaneously) or in situations in which an animal is prevented from attaining its goal (frustration; Tinbergen 1952; McFarland 1966). Different hypotheses concerning the emergence of displacement activities in these situations have been advanced. Some authors have taken the view that

tension builds up during conflict, and that this is in some way released by the performance of displacement activity (e.g. Tinbergen 1952). Others have suggested that the conflicting tendencies inhibit each other, allowing a third and irrelevant tendency to gain expression, so giving rise to displacement activity (e.g. van Iersel & Bol 1958). Another possibility is that conflict and thwarting situations are characterized by increased levels of arousal and that in this condition activities emerge 'which are prepotent in the animal's repertoire' (Bindra 1959).

In recent years displacement activities have been rather neglected as a topic of study. This may have resulted in part from a difficulty in recognizing these behaviour patterns. In fact, some of the features initially suggested as characterizing displacement activities (e.g. the absence of evident external stimulation, and morphological differences from the same behaviour patterns in their normal context) proved not to be entirely reliable. For example, it became apparent that (1) displacement activities can be strongly influenced by their normal causal factors (e.g. displacement grooming by state of the plumage: van Iersel & Bol 1958; displacement feeding by degree of prior food deprivation: McFarland 1965) and (2) under

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certain circumstances displacement activities need not be incomplete or imperfectly oriented but might be indistinguishable in form or orientation from the same behaviour patterns in normal contexts (Morris 1954; but see Roper 1984). The virtual absence of reliable morphological criteria to identify displacement activities has the consequence that their identification is based almost exclusively on a contextual analysis. Although the occurrence of one displacement activity rather than another in a given situation may be related to the ongoing activity of the animal (e.g. its posture; Tinbergen 1952), this behaviour usually has no obvious relationship with the presumed motivational state of the animal at that moment.

In several recent studies conducted on primates (Schino et al. 1988, 1990; Aureli & van Schaik 1991; Troisi et al. 1991), we have suggested that the analysis of the occurrence of displacement activities may provide insight into the emotional state of an animal and that, in spite of the problems of causal and functional analysis, this descriptive behavioural category could still provide a meaningful contribution to the general understanding of animal behaviour. The occurrence of displacement activities is associated with a state of internal conflict in animals and such a condition of motivational ambivalence is commonly believed to have an emotional counterpart (e.g. in the form of uncertainty or anxiety). It is well known that experimentally induced conflict situations (e.g. in traditional conflict tests such as punished drinking) are accompanied by a wide variety of autonomic responses including respiratory, circulatory and thermoregulatory changes (e.g. see Andrew 1956b). The physiological changes associated with autonomic activation can, in fact, provide a set of stimuli arising from the pelage or feathers, skin and blood vessels, which might be expected to elicit a variety of self-maintenance activities (among which displacement activities are most common; see Andrew 1956a, b). Without necessarily making inferences about the mechanisms underlying displacement activities, however, their consistent association with the activation of the autonomic nervous system would make them a powerful tool to identify and analyse such emotional states as uncertainty and anxiety, of which the activation of the autonomic nervous system is one of the more distinctive characteristics.

In this paper we review current knowledge about displacement activities in primates and the information available to support the notion that they

may represent a useful behavioural tool to investigate the emotional status associated with social interaction in primates.

EMOTIONS IN PRIMATES

Inferring an animal's internal state from the observation of its behaviour is not a completely new procedure for ethologists. For example, ethologists have frequently assumed that the motivational state underlying a given posture can be assessed from the behaviour that accompanies or follows it, for example, the probability of a bird attacking or fleeing after posturing (Moynihan 1955; Hinde 1970). Although scientists routinely infer motivational states such as hunger and fear, they are considerably more reluctant to consider internal states associated with social interactions, such as affection or ambivalence, trust or jealousy. A growing number of studies have recognized that the cognitive capabilities of primates can be expressed at their best in the social environment, as opposed to the traditional experimental contexts in which animals are confronted with problem solving and tool use (Jolly 1966; Humphrey 1976; Kummer 1982; Byrne & Whiten 1988; Cheney & Seyfarth 1990). However, while awareness of social relationships by primates and their mental processes and intentionality are now openly discussed, references to feelings and emotions are conspicuously lacking (but see Cheney & Seyfarth 1990).

From studies on human subjects it is apparent that emotion and cognition are closely interwoven (see Hinde 1985). The elicitation of an emotional state often depends on similarities or discrepancies between aspects of the external situation as it is perceived and what is desired or expected. Complex social relationships are likely to have a strong emotional component, for the behaviour of a partner in an ongoing relationship often confirms or disrupts expectancies, interrupts behavioural sequences, or arouses conflicting motivations.

Social interactions of primates take place on a firm basis of recognition between individuals and imply awareness by individuals of the quality of relationships (e.g. in terms of dominance rank, kinship, or friendship) even between other individuals (Cheney & Seyfarth 1990). As such, they are likely to involve definite expectancies about any interactant's responses. Moreover, the term 'negotiation', recently used to describe the nature of a

large part of the social interactions of primates (e.g. see Dunbar 1988), emphasizes that much interaction involves attempts to control the partner or to adapt one's behaviour to that of the partner. On these grounds it is reasonable to believe that socially living monkeys frequently experience conflicting impulses, and that uncertainty and anxiety are a more or less inevitable aspect of social interaction. Since we cannot interview the animals and ask them for their subjective perceptions of certain situations and their emotional reactions to them, we can only look for physiological or behavioural indicators of emotional states. The evidence presented in the following sections strongly suggests that displacement activities may well be one of these behavioural indicators in primates.

DISPLACEMENT ACTIVITIES IN PRIMATES

Information on displacement activities in primates is scanty. First of all, there is no unequivocal agreement on which behaviour patterns in the primate repertoire can actually occur as displacement activities. Frequently primatologists allude to the 'displacement' nature of some behaviour patterns anecdotally reported to occur in particular circumstances. As in many other animal species, the behaviour patterns most frequently reported as displacement activities in primates include body care activities.

Scratching and autogrooming are easily observable body care activities in primates and are among the most commonly reported displacement activities (scratching: Kummer 1968; Bertrand 1969; Russell & Russell 1985; Diezinger & Anderson 1986; Easley et al. 1987; Schino et al. 1988, 1990; Aureli et al. 1989; Pavani et al. 1991; Aureli & van Schaik 1991; autogrooming: Bertrand 1969; Goosen 1974a, b; Russell & Russell 1985; Troisi & Schino 1987; Schino et al. 1988, 1990; Lopez-Vergara et al. 1989; Aureli & van Schaik, 1991). Displacement yawning has frequently been reported (Carpenter 1934, 1940; Hinde & Rowell 1962; Rowell & Hinde 1963; Kaufman & Rosenblum 1966; Kummer 1968; Bertrand 1969; Redican 1975; Hadidian 1980; Baenninger 1987; see also Easley et al. 1987; Schino et al. 1988, 1990; Troisi et al. 1990) and distinguished from normal yawning for its being frequently repeated and the teeth more clearly displayed (Bertrand 1969). In

this view, yawning acquires a threat meaning when the performer looks directly at the addressee (Bertrand 1969). Body shaking (a shaking movement of the body similar to that displayed by a wet dog) is referred to as a displacement activity by Rowell & Hinde (1963), Schino et al. (1988, 1990) and Aureli & van Schaik (1991). Displacement feeding has sometimes been reported (Schaller 1963; Bertrand 1969).

The fact that the occurrence of these behaviour patterns is often irrelevant with respect to their obvious biological function, or to the stimuli that normally cause them, supports the view that they can occur as displacement activities. In the primate literature, however, other behaviour patterns have been considered as displacement activities without reference to these generally agreed standards of relevance. For example, male-male genital presentation and mount were categorized as displacement activities by Bertrand (1969) and Russell & Russell (1985) and included within tension behaviour by Easley et al. (1987), because they are said to occur out of their 'normal' context, i.e. a heterosexual interaction, and because they are 'incomplete' compared with true sexual mounts. Likewise, male monkeys carrying unrelated infants were considered to be performing 'pseudoparental acts' and the latter were considered as displacement activities because they did not occur in an 'appropriate' context (Russell & Russell 1985). Although the occurrence of the latter behaviour patterns (e.g. the male-male mount in baboons) may be related to an unstable social situation and risk of aggression (see Chadwick-Jones 1989), their inclusion in the category of displacement activities only on the grounds of their occurrence out of their most common context does not seem to be fully justified. In fact, many behaviour patterns can have different functions in different species and in different contexts. For example, yawning that occurs during an agonistic interaction may have a definite threat meaning in baboons, *Papio cynocephalus anubis* (Hall & De Vore 1965), inter-male mount may be an assertive behaviour (Chadwick-Jones 1989), and carrying an infant can be used by male monkeys as a buffer against other males' aggression (Deag & Crook 1971; Hrdy 1976). If irrelevance to the ongoing context is to be considered as one of the more reliable clues to identifying displacement activities, this seems not to be the case for such behaviour, for a clear function is evident in the context in which it is performed. Therefore, it should

not necessarily be argued that a motivational conflict underlies the exhibition of such behaviour.

DISPLACEMENT ACTIVITIES AS INDICATORS OF EMOTIONS

Behavioural Evidence

Evidence indicates that primate displacement activities are more frequent in stressful situations. Some reports consist only of anecdotal observations but in other cases quantitative data have been provided.

Increased proximity between individuals occurring at feeding sites or associated with direct social interactions (e.g. an approach for grooming), insofar as it brings about an increased probability of aggression, is presumably associated with behavioural ambivalence and anxiety. There are anecdotal reports of displacement activities occurring frequently in such circumstances, such as Smuts' (1985) description of a female olive baboon, *Papio anubis*, undecided over whom to feed near: 'she scratched herself several times, as baboons often do before making a decision'. Likewise, Hadidian (1980) observed that 'a low ranking adult male *Macaca nigra* yawned repeatedly after a dominant had approached and sat nearby' and Bertrand (1969) that 'when a macaque is approached by a dominant it may chew and even swallow things that it would not normally eat'. The increased occurrence of scratching and autogrooming by macaques in proximity to a higher-ranking individual has also been reported quantitatively. For example, Troisi & Schino (1987) found that, in group-living long-tailed macaques, *Macaca fascicularis*, female autogrooming is more frequent within 1 m of the alpha male than in the conditions of 'alone' or 'in passive contact'. Analogous results concerning scratching behaviour in long-tailed macaques were obtained by Pavani et al. (1991). The increased frequency of displacement activities in proximity to a dominant male may be explained by considering this situation as one in which two opposing social tendencies are in conflict: the one to approach the male further (e.g. in order to groom him or to sit in bodily contact with him) and the tendency to avoid the male lest he attacks (Troisi & Schino 1987). Diezinger & Anderson (1986), examining the occurrence of scratching by rhesus macaques, *Macaca mulatta*, at a feeding site, found that intermediate-ranking individuals are the ones who scratch themselves most: 'these individuals

appear to be more aroused or frustrated than dominants, who can easily monopolize the food, and than subordinates, who may stay clear of the feeding area and not even try to get access to the food'.

Displacement activities are also reported to occur frequently during or immediately after agonistic interactions. According to Poirer (1974), scratching is one of the most common displacement activities of male colobines during territorial conflicts. Among long-tailed macaques, intra-group aggression is followed by a dramatic increase in the rate of scratching, body shaking and autogrooming by the victim (Aureli et al. 1989; Aureli & van Schaik 1991). Among rhesus macaques as well, victims spend more time autogrooming after severe aggression (de Waal & Yoshihara 1983). One might argue that post-aggression body care activities are merely due to pelage dishevelment or tissue damage, especially if contact aggression has occurred. However, this explanation can be dismissed since reconciliation (also when the analysis is limited only to brief affiliative contacts) and redirection are effective in reducing the rate of these activities (Aureli & van Schaik 1991; see below). Displacement activities occurring after an aggressive episode, instead, might reflect the internal conflict between withdrawing, because of the fear of renewed attacks by the former aggressor, and approaching, in order to achieve reconciliation. Displacement activities might also reflect the arousal due to the uncertainty about the future social position, for victims are more likely to receive further attacks (Aureli & van Schaik 1991) and less likely to be tolerated around resources (Cords 1992).

Risk of aggression associated with assessment of social status may also bring about high levels of displacement activities. When two unfamiliar female macaques are paired in a relatively small cage, the delayed establishment of clearcut dominance relationships brings about a sharp increase in the frequency of scratching, autogrooming and yawning over time (Schino et al. 1990; see also Rowell & Hinde 1963). In contrast, when unfamiliar macaques rapidly display a formal indicator of status differences such as the bared-teeth display, displacement activities are much less frequent. The pairing of familiar individuals, whose dominance relationships have already been established, results in the exhibition of displacement activities with a frequency comparable to that of the unfamiliar macaques of the latter group. Thus, regardless of

familiarity with the partner, the uncertainty about assessment of social status is associated with high levels of body care patterns (Schino et al. 1990). The relation between dominance rank and the occurrence of displacement activities, however, is not clear. High-ranking individuals tend to yawn more often than low-ranking ones in Celebes macaques, *Macaca nigra* (Hadidian 1980), in long-tailed macaques (Troisi et al. 1990) and in chimpanzees, *Pan troglodytes* (te Boekhorst et al. 1991). This difference fits well with the hypothesis that yawning is also a mild form of threat. However, no such difference is found among Japanese macaques, *Macaca fuscata* (Troisi et al. 1990). Very inconsistent results have been found for scratching. Subordinate long-tailed macaques scratch themselves at higher rates than dominant ones (Pavani et al. 1991). On the other hand, in baboons and chimpanzees, dominant individuals scratch more frequently (Easley et al. 1987; te Boekhorst et al. 1991). The relation between dominance rank and scratching is likely to be context-dependent. In fact, there is no difference relative to dominance rank in the baseline rate of scratching among rhesus monkeys; however, in a feeding context, scratching increases in intermediate-ranking individuals (Diezinger & Anderson 1986). Similarly, subordinate Japanese macaque females scratch themselves more often than dominant ones during pregnancy but not after giving birth (Troisi et al. 1991).

The occurrence of displacement activities has been reported to be more generally associated with a decision-making process. Kummer (1968) noticed high rates of scratching by male hamadryas baboons, *Papio hamadryas*, during the initial phases of group coordination for movement. Before determining the final direction to be taken, the male leader appears to be pulled in various directions by the centripetal tendency of the females and the behaviour of the male neighbours. As a possible consequence of these conflicting impulses, the males scratch frequently before shifting position (Kummer 1968). Similarly, Diezinger & Anderson (1986) reported that scratching occurs at a high frequency in close temporal association with a change in behaviour and interpreted it in terms of a moderate indecision on behalf of the performer.

In the cases explored so far, displacement activities emerged in situations involving uncertainty about how to behave and about other individuals' intentions. In other cases, an increase in the frequency of displacement activities has been reported

in situations where a motivational conflict was not immediately identifiable. This seems to be the case with Scucchi et al. (1991), who reported that, in oppositely sexed pairs of long-tailed macaques under laboratory conditions, male displacement activities increase during the periovulatory phase of the female menstrual cycle, suggesting that the presence of an ovulating female brings about a generalized increase in male arousal.

Physiological and Pharmacological Evidence

The hypothesis that primate displacement activities are a behavioural manifestation of uncertainty and anxiety requires physiological and pharmacological validation. In the first case, it should be demonstrated that the exhibition of these behaviour patterns is consistently accompanied by physiological changes typical of these states such as increased heart rate, blood pressure and plasma levels of catecholamines and corticosteroids (e.g. Axelrod & Reisine 1984). In the second case, it should be shown that drugs that are effective in eliciting or reducing clinical anxiety (i.e. anxiogenics and anxiolytics) would be capable of, respectively, increasing and reducing the rate of displacement activities. However, since there are no unequivocal physiological indicators of anxiety (e.g. see Morrow & Labrum 1978) whereas effective anxiolytic and anxiogenic drugs are currently available, the pharmacological validation would probably be more convincing.

Direct evidence that, in non-human primates, displacement activities are associated with autonomic activation is lacking, even though circumstantial evidence suggests that this may be the case. Among macaques, separate studies have reported that both heart rate and frequency of scratching increase following an episode of aggression and both are reduced after the individual is groomed (Schino et al. 1988; Aureli et al. 1989; Boccia et al. 1989). However, no study has investigated directly the relation between physiological and behavioural measures.

More information is available as far as the effects of drugs on displacement activities are concerned. Among non-human primates, there is evidence that following some anxiogenic treatments, together with the physiological reactions typical of an autonomic activation, behavioural expressions appear that are very similar to displacement activities. For example, treatment of chair-restrained rhesus

monkeys with the anxiogenic compound β -CCE elicits a wide range of physiological (increased heart rate, blood pressure and circulating cortisol) and behavioural changes such as increased vigilance and scratching (Ninan et al. 1982; Insel et al. 1984; Crawley et al. 1985), yawning and chewing (Lagarde et al. 1990). In the stump-tailed macaque, *Macaca arctoides*, electrical and pharmacological activation of the locus coeruleus, a major brain noradrenergic nucleus which has often been implicated in anxiety, elicits scratching and yawning (Redmond & Huang 1979). In group-living adult female long-tailed macaques, the acute administration of the anxiolytic drug lorazepam causes a selective reduction in the frequency of scratching (Schino et al. 1991), this being especially marked in low-ranking animals. Lorazepam has similar effects on autogrooming (A. Troisi & G. Schino, unpublished data). Similarly, midazolam tends to reduce scratching behaviour in 30-week old rhesus monkey infants, while treatment of the same infants with β -CCE tends to increase the frequency of scratching and is associated with a marked increase in the infant's contact-seeking and maintaining behaviour with the mother (Maestripieri et al. 1992).

Although a physiological validation would be helpful, both the behavioural and the pharmacological evidence support the intuitive belief that displacement activities may be a behavioural expression of a state of anxiety. As such, they could constitute an effective tool for quantifying the monkeys' emotional reactivity to social or environmental stressors with a non-invasive, purely observational method.

Applications of Behavioural Indicators of Emotions

What could the usefulness of a behavioural measure of an emotional state be? In what way could it help to improve the general understanding of primate behaviour? As previously observed, many aspects of the complex social environment of primates can be considered as tension-producing. Accordingly, mechanisms for social adaptation are likely to have evolved. The notion that allogrooming can serve as a tension-reduction mechanism is an old one (e.g. Terry 1970) but, probably for the lack of an operational definition of tension, it has scarcely been supported quantitatively. By using displacement activities (scratching, autogrooming, yawning and body shaking) as a measure of tension, Schino et al. (1988) found that, in caged hetero-

sexual pairs of long-tailed macaques, female allogrooming significantly reduces the frequency of male displacement activities both during the course of allogrooming and after it, this being proportional to the amount of grooming received. These observations concur with Boccia et al.'s (1989) finding of a heart rate reduction in an individual being groomed, in providing quantitative support for the tension-reduction hypothesis. A similar use of displacement activities was made by Aureli et al. (1989) and Aureli & van Schaik (1991) to gather quantitative evidence that, among group-living long-tailed macaques, reconciliation after agonistic encounters or redirection of aggression against a third individual reduce the victim's level of tension. When reconciliation between former opponents takes place, scratching, body shaking and autogrooming occurring after an attack decline much more rapidly to baseline levels than when no reconciliation occurs. A similar reduction in the scratching rate (but not in body shaking and autogrooming) occurs after the redirection of aggression. These findings allowed the authors to suggest that the function traditionally attributed to reconciliation, that is to repair the social relationship between the two opponents, may also involve the immediate effect of reducing the victim's anxiety and tension (Aureli et al. 1989). Interestingly, the reoccurrence of aggression against the victim, which is one of the possible causes of the victim's anxiety, is also reduced by both reconciliation and redirection (Aureli & van Schaik 1991).

In the examples mentioned above, displacement activities were used to assess the function of another behaviour pattern. They served to provide quantitative evidence that affiliative interactions can be intimately related to the emotional states of the animals and, specifically, that they are effective in reducing the social tension associated with certain behavioural interactions. However, since the emotional reactions to external stimuli are largely dependent on the subjective perception of such stimuli, displacement activities can also represent a means to reveal and evaluate quantitatively differences between individuals in how they react to stressful situations. A large part of the variability in behavioural strategies adopted by animals in a variety of circumstances is related to the different perception of their social environment as potentially threatening for themselves. Measuring the emotional reactivity of individuals to various

kinds of social confrontations may allow one to understand how individuals perceive the quality of the relationships between themselves or to explore the extent to which they are able to cope with an unfavourable external environment.

To give an example, marked differences in mothering styles (e.g. in terms of the role played in maintaining contact with the infant and of the frequency of restraint of the infant) among primiparous and multiparous macaque mothers have often been ascribed to a higher anxiety in the former, possibly related to their inexperience in evaluating the potential threats to the infant (Mitchell & Stevens 1969; Hooley & Simpson 1981). In fact, Troisi et al. (1991) provided quantitative support for this hypothesis by finding positive correlations between rates of scratching and maternal possessiveness and warmth, two composite measures of quality of relationship that reflect a possessive maternal style. Furthermore, only the frequency of scratching recorded after parturition was correlated with a possessive maternal style. In contrast, scratching recorded before parturition was not correlated either with postpartum scratching or with maternal style. These results emphasize that females may react differently to motherhood. In other words, maternal possessiveness could not be predicted on the basis of differences between individuals in baseline emotionality (prepartum scratching), but actually reflected an emotional condition triggered by the presence of the infant.

The characterization of the emotional response of an animal to a particular social or environmental confrontation may help to explain why that animal performs one particular behaviour instead of another and why in similar situations different individuals adopt different behavioural strategies. Being paired with an unfamiliar individual in a cage of limited dimension may be considered a stressful situation. The distance between individuals is considerably reduced and the animals do not have any opportunity to escape or to obtain assistance from third parties to settle their disputes. Schino et al. (1990) showed that, in several caged pairs of unfamiliar female long-tailed macaques, the unresolved establishment of dominance relationships, possibly because asymmetries in perceived relative power (see Datta 1983) were not clearcut, did not allow affiliative interactions to take place and resulted in a rise in tension. Conversely, in other pairs, when asymmetries in perceived relative power were likely

to be substantial, dominance relationships were rapidly established and the individual who perceived the situation as more threatening (as suggested by its higher frequencies of displacement activities) was the one to take the initiative for affiliative interactions (unpublished data). As suggested by these examples, displacement activities can provide a valuable tool to highlight the differential perception of a stressful situation by individuals and to predict the direction in which their interaction will evolve. The investigation of emotionality underlying individual differences in behavioural strategies is likely to be one of the areas in which the study of displacement activities can be more fruitful. Nevertheless, in this area much work is still to be done.

Methodological Problems

The use of displacement activities as indicators of emotions in primates is complicated by a number of methodological problems. One of them is the difficulty of distinguishing conflict-related behaviour patterns from their normal counterparts, that is from the same behaviour patterns displayed as comfort activities. The criteria of functional or causal irrelevance are difficult to apply when body care patterns are at issue because it is easy to overlook the causal stimuli or the functional consequences of comfort activities. Some authors have suggested that the behavioural morphology (i.e. the intensity and/or duration) of primate displacement activities may be a distinguishing feature (Diezinger & Anderson 1986). Others have expressed the same idea in more categorical terms: 'a displacement activity is always fragmentary and incomplete when compared with the same activity carried out in its normal mood and context' (Russell & Russell 1985). Studies testing this hypothesis (e.g. by correlating differences in morphology with other behavioural or physiological changes occurring in a stressful situation) are needed. The few available data are conflicting. On the one hand, among captive chimpanzees rough scratching (i.e. when the action performed includes the movement of the arm) performed by the dominant male is more likely to be associated with agonistic conflicts and bluff displays than gentle scratching (i.e. when scratching takes place only through movement of the hand or fingers; te Boekhorst et al. 1991). On the other hand, in long-tailed macaques, anxiolytic treatment decreases not

only the frequency but also the mean duration of autogrooming (A. Troisi & G. Schino, unpublished data). This finding suggests that displacement autogrooming is not necessarily shorter than 'hygienic' autogrooming and that morphological differences between displacement activities and their normal counterparts need not necessarily be expected.

Another complicating factor is the necessity of defining accurately the emotional state associated with the occurrence of displacement activities. In the primate literature, the term 'tension' has often been used to describe the inferred subjective experience of the individual exhibiting a displacement activity. We believe that the use of the term 'tension' should be limited to the description of social situations involving latent hostility or opposition between individuals. Referring to the subjective experience of the animal, the term 'anxiety' seems to be more appropriate for several reasons. First, in the clinical literature, anxiety is defined as a state of apprehension or uneasiness that stems from the anticipation of danger (American Psychiatric Association 1987), and primate displacement activities are commonly observed under circumstances where an individual is confronting a potential source of danger. Second, motivational conflict, which is thought to be a possible mechanism responsible for displacement activities, is the paradigm used in experimental psychopharmacological research for modelling anxiety. Third, anti-anxiety drugs have been shown to decrease the frequency of occurrence of displacement activities (see above). In a previous paper, Troisi et al. (1991) have pointed out, however, that conflict and anxiety are not necessarily overlapping emotional states: an extremely anxious individual is unlikely to experience uncertainty between alternative courses of action (i.e. conflict) because of its marked tendency towards escaping the stressful situation. If so, displacement activities should only reflect moderate levels of anxiety. Alternatively, if autonomic activation independent of conflict is the mechanism responsible for displacement activities, it is plausible to assume that these behaviour patterns would also occur in states of intense anxiety or fear. Our current knowledge does not allow us to give a definite answer to the question what are the emotional states associated with primate displacement activities? Studies based on behavioural, physiological and pharmacological data are needed to clarify this crucial issue.

CONSEQUENCES AND FUNCTIONS OF DISPLACEMENT ACTIVITIES

Considering the amount of time and energy invested by non-human primates in displacement activities, it is reasonable to pose the question whether these behaviour patterns serve some adaptive function(s). Displacement activities might serve as a means of limiting the costs related to an internal conflict and act as re-regulating activities that in some way keep the animal within optimal physiological or psychological limits (this hypothesis has been advanced for stereotyped behaviour in general, see Mason 1991). For example, one could speculate that displacement activities reduce distress by focusing the animal's attention away from noxious stimuli or by causing physiological changes. In this latter regard, it is interesting to note that behaviour involving body contact such as allogrooming has been shown to release endogenous opioids in monkeys (Keverne et al. 1989).

Another possible function of displacement activities is social communication. Social animals are continuously faced with choosing between different behavioural options whose consequences and success will depend crucially on the internal motivational state and probable future behaviour of other animals. As a consequence, natural selection will favour animals that become sensitive to every spontaneous emergence of behaviour in others that could represent possible clues from which their future responses may be predicted (Krebs & Dawkins 1984). The exhibition of displacement activities might convey information about an animal's mood and motivational state and be relevant in all kinds of social interactions in which the assessment of the other's intentions is crucial (e.g. contests). Classical ethological studies have demonstrated that, in a variety of species, displacement activities have become incorporated into a definite display through the process of ritualization (see Tinbergen 1952). In non-human primates, there is no evidence that conflict behaviour has evolved into display behaviour. A notable exception is 'symbolic feeding' in mountain gorillas, *Gorilla gorilla beringei*. About 5–10% of the chest-beating displays by silverbacked gorilla males are preceded by ritualized feeding: vines or herbs are gently placed between the lips but are not ingested. Members of the group recognize symbolic feeding and generally move away from the actor, thus escaping the subsequent violent parts of the display (Schaller 1963).

However, ritualization is not a prerequisite for social communication through displacement activities to occur and two other possibilities remain: (1) the exhibition of displacement activities by an animal may convey information and produce behavioural changes in others because animals may have learned from past experience some behavioural contingencies (e.g. that a repeated sequence of scratching bouts by a dominant male is likely to be followed by aggression); and (2) individuals are capable of generalizing the relationship between the exhibition of displacement activities and the subsequent behavioural responses of the performer. Primates recognize that they have emotions and that others have emotions and use the attribution of emotions to others as a means to predict and explain their behaviour: in other words, they have what has been termed 'a theory of mind' (Premack & Woodruff 1978; Premack 1988; for discussion about the levels of intentionality see Dennett 1988; Cheney & Seyfarth 1990; Kummer et al. 1990).

As far as non-human primates are concerned, if systematic evidence for awareness of knowledge and attribution to others is scanty (see Cheney & Seyfarth 1990), evidence referring to emotions is virtually non-existent. Speculations about whether primates use displacement activities to make inferences about emotional states or intentions should first be preceded by experiments in which these behaviour patterns are examined in terms of the responses they evoke in others. Goodall (1986) put forward the hypothesis that displacement activities in chimpanzees can 'reflect emotional states and convey information to others regarding the mood and the intentions of the individual concerned'. She observed that, in the context of group travelling, scratching on behalf of the leader 'can be a clear-cut signal, indicating that he is about to go'. Similarly, 'a mother, having moved to a low branch prior to descending a tree, stops, glances at her infant, and gives slow but vigorous scratches down her side. An obedient infant responds rapidly, hurrying to cling to her for the descent' (Goodall 1986). In captive chimpanzees, scratching by the dominant male is frequently followed by appeasement displays ('pant grunt') by other individuals (Cervi & van Hooff 1990; te Boekhorst et al. 1991). Since scratching is also frequently associated with bluff displays, it has been suggested that other individuals may predict through scratching when the male is about to display or to attack and to prevent it with appeasement behaviour (Cervi & van Hooff 1990;

te Boekhorst et al. 1991). On the whole, however, the evidence of a communicative function of chimpanzee scratching is far from being compelling and the possibility that, in the above-mentioned cases, the individuals reacted to other elements (e.g. piloerection) which preceded an attack cannot be ruled out. Possible support for the hypothesis that primate displacement activities can be used as signals comes from the finding that scratching and yawning are sensitive to some kind of voluntary control because they increase following food reinforcement (Louboungou & Anderson 1987; Anderson & Wunderlich 1988; Anderson et al. 1990). Because displacement activities can be conditioned, these authors suggested that these acts are not rigid and reflex but instead they can be used as a communicative gesture.

In the analysis of the possible functional significance of displacement activities, it should be mentioned that a communicative function that is unrelated to their being an expression of an emotional state has also been postulated. Some authors have taken for granted that the exhibition of displacement activities in contests has the immediate function of distracting the partner or the opponent from certain physical features of the performer (that, for example, might elicit its aggressiveness) or concealing the performer's real intentions about the prosecution of the interaction. Trivers (1985), considering the appearance of displacement activities during animal contests, hypothesized that they '... may, in fact, serve to distract attention from salient features of the interaction'. Similarly, De Waal (1986) observed that 'when chimpanzees try to ignore each other's intimidation displays or when two adversaries are waiting for the first conciliatory overture to occur, they may turn their attention to something unimportant or carefully inspect details of their own body as a way of hiding apparent embarrassment or disappointment', and discussed displacement activities within the general framework of deception among primates. On this view, displacement activities are not regarded as a behavioural expression of an emotional state, but rather, their exhibition would be aimed at concealing the animal's real emotions and intentions. They would be part of that particular kind of deception termed 'distraction' (Whiten & Byrne 1988) in which the agent manipulates the attention of another individual by shifting it from one locus in the environment to a second locus (e.g. from one part of the body to

another one). However, this presumed function of displacement activities relies entirely on a subjective impression of the human observer and no evidence exists to support the claim that the performer is actually attempting to manipulate the other's attention.

GENERAL CONCLUSIONS

Displacement activities are among the easiest behaviour patterns to observe in the primate repertoire. However, while other aspects of primate behaviour are currently being analysed in great detail, these behaviour patterns receive little attention from primatologists. In this paper we have reviewed current knowledge about primate displacement activities by pointing to their potential values as a behavioural indicator of emotional states associated with social interactions.

Even though the use of displacement activities as behavioural indicators of primate emotions is currently complicated by a number of methodological problems, this seems to be a promising area of research for two different reasons. First, findings emerging from this kind of study are likely to improve our general understanding of the causal mechanisms and functional consequences of displacement activities, which is important considering that our knowledge of these aspects has not progressed in the last two decades. Second, the use of displacement activities as simple behavioural measures of emotionality can favour the adoption of the ethological approach by those researchers such as physiologists or psychopharmacologists who are less familiar with the recording of spontaneous behaviour in freely interacting primate subjects.

In addition to these general contributions, the use of displacement activities as behavioural indicators of primate emotions may have important implications for specific areas of primate research. Information on the emotional reactivity of animals to social and environmental stimuli may shed light on how certain behavioural profiles are determined as well as on how predispositions to pathologies may arise. A wide range of genetic-environmental influences may give rise to differences between individuals in emotional reactivity to stressors. This, in turn, will affect the general pattern of interaction between the individuals and their environment. A particularly strict relationship

between emotions and behaviour may be argued for primates whose social life entails a high degree of cognitive capabilities. In these animals, social behaviour may have evolved functional characteristics aimed at coping specifically with emotional states, and in particular at reducing anxiety associated with social interactions. However, this hypothesis, as well as the fact that different behavioural responses of individuals confronted with similar conditions (e.g. motherhood) might reflect differences in emotionality, has so far only been a matter for speculation. Measuring reliable physiological and behavioural indicators of these emotional states (and displacement activities may well be included among the latter) allows one to turn these speculations into testable hypotheses.

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