# Ritualization and Social Communication in Rhesus Monkeys

R. A. Hinde

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# Ritualization and social communication in Rhesus monkeys

By R. A. Hinde

*Sub-Department of Animal Behaviour, Department of Zoology, University of Cambridge,*
*High Street, Madingley, Cambridge*

## Introduction

The concept of ritualization, as used in the study of the signal movements of lower vertebrates, refers primarily to the evolutionary changes which such movements have undergone in adaptation to their function in communication. In this context, the term is thus used in reference only to movements which have such a function, and only when there is evidence that the resultant signal has undergone changes which make it more effective in that role. Many movements which influence the behaviour of others (e.g. penile erection, eating and drinking in rhesus monkeys, according to Altman 1962) have apparently not been ritualized, though homologous movements in other species may have been (e.g. penile erection in squirrel monkeys (Ploog & Maclean 1963)).

The changes involved have almost invariably been evolutionary ones, and thus reference to ritualization implies evidence that the properties of the signal have changed on an evolutionary time scale. This usually comes from the comparative study of contemporary closely related species. Just as the comparison, between related species, of morphological structures may suggest not only homologies but also views as to the evolutionary origins of the homologous structures, so also does comparison of patterns of behaviour. In addition, just as comparison within a species of related structures, such as the segmental limbs of a crustacean, or of different developmental stages of the same structure, can provide evidence of the course of evolution, so also can comparison of related movement patterns (e.g. Lorenz 1935, 1941; Tinbergen 1952, 1959, 1962).

Detailed comparative studies involving a number of groups of birds and fishes have suggested that many of the movements used in communication are derived from two sources. One of these is ‘intention’ movements, the incomplete or preparatory phases of activities. Thus the upright threat posture of the Herring Gull (*Larus argentatus*) consists largely of components which are intention movements of striking the adversary, such as a downward pointing bill and slightly raised wings, or of retreating (Tinbergen 1959). In some cases a display movement is derived from an intention movement which has been ‘redirected’ onto an object other than the individual which elicited the display. Thus Herring Gulls may peck into the ground when displaying against a rival: the movement is the same as pecking a rival, but is re-directed on to a new object (Tinbergen 1959). A second source is ‘displacement activities’: these are activities functional in one context which appear in a different functional context, involving conflicting behavioural tendencies, in which (before ritualization for a signal function) they appear to be functionally irrelevant. Thus during courtship many ducks make movements closely similar to those used in preening the wing feathers, but which in courtship are often incomplete and have no preening function (Lorenz 1941; Tinbergen 1952).

Ritualization can sometimes be inferred even when the evolutionary origin of the signal is quite unknown—for instance when comparative study indicates convergence in functionally related signals of different species (Marler 1957). But ritualization can be described only in terms of differences between a signal movement and its supposed primitive form. These differences are diverse, and it is difficult to catalogue them satisfactorily (but see Blest 1961). In general, however, they are such as to make the movement more suitable as a signal in the context in which it is used. They may thus involve changes in the coordination and relative intensities of the components of the whole—for instance in the neck, leg, wing and tail elements of the take-off movements of birds. These changes have often been accompanied by the development of structures which serve to make the movement more conspicuous or distinctive (Lorenz 1935). Another type of change which serves a related function is the development of 'typical intensity' (Morris 1957). Whereas the motivational factors which underlie the signal movements presumably fluctuate continuously, the signal movements themselves have more limited variability: this stereotypy presumably aids recognition.

Although the evolutionary origins of auditory signals are less well known than those of visual ones, inter-species comparison indicates that evolutionary changes in adaptation to a signal function have occurred similarly.

One final point requires mention here. Many, but not all, of the signal movements of lower vertebrates are given when the animal has conflicting tendencies to behave in incompatible ways. The upright threat of the Herring Gull, for instance, contains not only intention movements of attack (e.g. downward pointing beak and sometimes a forwardly inclined neck) but also components of retreat (e.g. the neck may be withdrawn somewhat and the beak inclined more horizontally). These conflicts may be described in terms of tendencies to attack, flee, behave sexually, nest-build, and so on (e.g. Tinbergen 1959) or in terms of more elementary activities (e.g. approach, retreat) (Andrew 1956). Of course this does not mean that all such signals are the result of conflict—bird song, or the calls made by birds in flight, for instance, have been ritualized but do not involve conflict.

## Ritualization in primates

To what extend do these principles apply to the signal movements of primates? Like lower vertebrates, each primate species has a repertoire of postures, gestures and calls used in social communication. It is not possible to give a precise estimate of the number of signals used by any one species because of their variability (see below), but it is of the order of 20 visual signals and 20 auditory ones. This is not so very different from the number possessed by many birds (e.g. Marler 1959; Thorpe 1961). But few primate species have yet been studied in detail, and comparative studies of related species, though suggestive (e.g. van Hooff 1962; Andrew 1963), have so far reached only a preliminary stage.

As with lower vertebrates, many of the expressive movements of primates have been evolved from intention movements. The threat postures of the Rhesus monkey, for instance, may combine intention movements of both locomotion towards and away from the adversary with intention movements of biting: often the threatening animal remains on one spot jerking alternately forwards and backwards (figures 1, 2; see also Hinde &

Rowell 1962). The biting sequence is carried further in the 'symbolic' biting often used for instance by males in stopping a fight between females, and in the 'play' biting of juveniles: here the bite is complete except for the closing of the teeth (see also Hall 1962).

Andrew (e.g. 1963) has suggested that many primate expressive movements have been evolved from the intention movements of self-protective responses—i.e. responses which serve to protect the major sense organs and other sensitive areas against possible noxious effects from the source of stimulation. A man exposed to such a stimulus may shake his head, draw back his lips, protrude his tongue, close his eyes, lower his eyebrows, flatten his ears and close his glottis. These all have a protective function against either attack or against noxious chemical substances. The closure of the glottis, accompanied by expiration, may lead to coughing. Many primate expressive movements seem to have evolved from components of such protective responses. Thus in fear-evoking situations Rhesus monkeys and many other species withdraw their lips in a 'fear grin', exposing the teeth (figure 3); and the ears are lowered in threat (figure 1).

FIGURE 1. Mild threat by a Rhesus monkey from sitting position. This position is likely to be followed by a jerk towards the opponent.

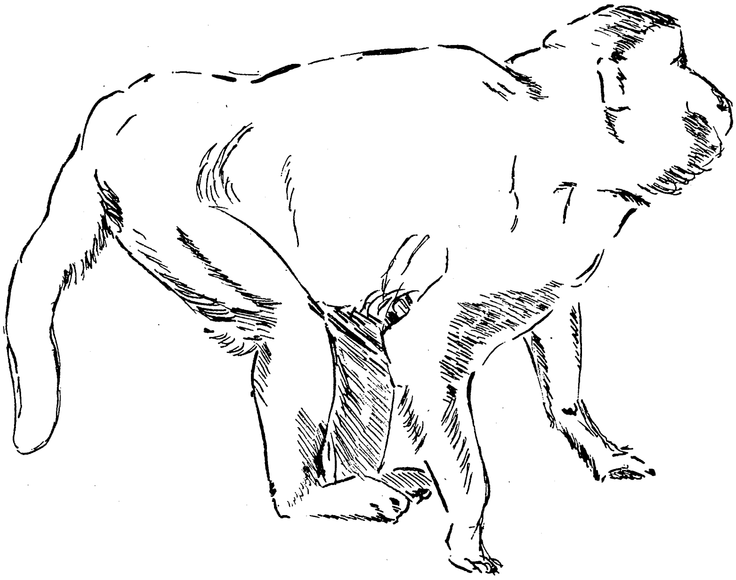

FIGURE 2. 'Threat' which may be followed by either approach to or withdrawal from the rival. Note the ambivalent leg posture.

We have seen that some display movements of lower vertebrates are derived from 'redirected' intention movements (see p. 285). It is possible that some of those expressive movements of primates which involve the production of mechanical sounds by branch-shaking or ground-slapping have been derived similarly (see, for example, Emlen 1962), the aggressive movement being re-directed onto an inanimate object (figures 4, 5).

Few of the expressive movements of primates can be regarded as derived from displacement activities. One example, however, is the female's soliciting posture. This is often used in non-sexual contexts, and appears to reduce the aggressiveness of a more dominant individual of either sex. Although it may lead to the animal being mounted, this is usually not accompanied by intromission.

As a number of writers have stressed, the category of displacement activities is neither causally homogeneous nor clearly defined. In the present instance, the soliciting posture is perhaps not wholly irrelevant, since it contains elements of intention movements of moving away combined with a static posture. It is, however, the posture as ritualized for use in a sexual context which appears in agonistic ones. Little further change in its form seems to have occurred. It is at least possible that it has come to appear in this context because the intention movements of running away, coupled with actually staying, produced a static posture similar to sexual soliciting, which was thus more likely to occur because of the consequent postural facilitation (Lind 1959). Since it reduced aggression, the adoption of the soliciting posture would have adaptive value and be selected.

FIGURE 3. The fear grin.

Many primate expressive movements, however, are derived neither from intention movements nor from displacement activities. An obvious example is social grooming: this occupies a large part of the time in most primate groups, and its importance as a means of communication seems to outweigh any role it may have in removing parasites. An indication of this is provided by evidence showing that the direction of grooming between sex partners varies with the stage of the menstrual cycle (Michael & Herbert 1963): although this could be related to concomitant changes in skin sensitivity, an influence of changes in relative dominance status seems more probable. The influence of such motivational factors supports the view that the grooming complex has been ritualized for

FIGURE 4. Branch shaking by a male Rhesus whose technique was to grasp the branch on which he was standing and shake it up and down.

FIGURE 5. Branch shaking by a male Rhesus whose technique was to shake the top wire of the cage.

communication rather than serving merely in care of the body surface. Indeed the grooming movements are sometimes incomplete and clearly ineffective in cleaning the fur. Although social grooming resembles displacement behaviour in utilizing motor patterns evolved for a different functional end from that which it now serves, it differs in the virtual absence of any indications of conflict. The movements used by many lower primates in leaving scent marks on branches similarly seem not to depend on conflict (but see Moynihan 1964).

It must be stressed that the evolutionary origin of the movements involved in many primate social signals are still obscure. The movements used by many prosimians to distribute the secretions of scent glands, urine or faeces on branches (e.g. Ilse 1955); or the movements of embracing and 'friendly' stroking and touching used by baboons (Hall 1962) and chimpanzees (Goodall, personal communication) have a quite unknown evolutionary origin.

We must next consider the changes which primate expressive movements have undergone in adaptation to their signal function. In many cases these are similar to those seen in lower primates—an accentuation or elaboration of the movement to suit it to its signal function. We have already seen the exaggerated lip withdrawal in the fear grin, and the elaborate but incipient intention movements of attack in some threat postures. Such elaboration does not necessarily involve an increase in amplitude of the movement: the evolution of some expressive movements involves a reduction in signals which might elicit a response inappropriate to the individual concerned. For instance the cringing and turning away seen in submissive animals involve a reduction in stimuli which might elicit attack (figures 6, 7). The development of conspicuous structures concomitant with the elaboration of the movement has occurred to a much smaller extent in primates than in, say, birds, but many species of monkeys have developed conspicuous structures which appear to be important in species recognition and are no doubt shown off by displays. Furthermore, many prosimians have specialized glands whose secretions are deposited by stereotyped movements and presumably function in territorial marking (e.g. Ilse 1955).

Often, however, elaboration of the movement is difficult to detect in primates because of the almost total lack of development of 'typical intensity'. The components of the movement may occur at all stages of intensity, and slight movements may be more common than exaggerated ones. The threat movements used by Rhesus monkeys are a case in point. Although they can for convenience be divided into categories which have differing probabilities of leading to attack or flight, all intermediates occur (e.g. Hinde & Rowell 1962; Altmann 1962). The same is true of the noises made by this species in agonistic situations. Rowell (1962; see also Rowell & Hinde 1962) arranged them in order of decreasing likelihood of their being accompanied by attack, and found it worthwhile to give nine names to points on this continuum. She found, however, that intermediates were frequent not only between successive points on this sequence, but also even between the most aggressive 'roar' and the least aggressive 'screech'; and that the 'pant-threat' had intermediates with three other calls. Similar variability is found in the vocalizations of baboons (Bolwig 1959) and many other species (Andrew 1963). Furthermore, the different components of any of the conventionally named display movements may vary independently—a threatening Rhesus monkey may have its ears raised or lowered, its fur up or down. Comparable variability has been found in birds (Stokes 1962), and its importance in avian displays has probably been underestimated, but it would appear to be more common in higher mammals (e.g. cats, Leyhausen 1956; elephants, Kühme 1961, 1963) and primates. Amongst the primates the extent to which the more frequent types of vocalizations are linked by intermediates varies between species: Moynihan (1964) suggests that the intermediates may be less common in nocturnal forms, in which auditory communication is of primary importance, than in ones with an extensive repertoire of visual expressive movements. Lack of 'typical intensity' and variability in the combinations of the components of display movements may make a signal more difficult to recognize, but it does of course permit the communication of a wide range of shades of internal state.

Figure 6. The cringing position of a subordinate female. Contrast with figure 7.

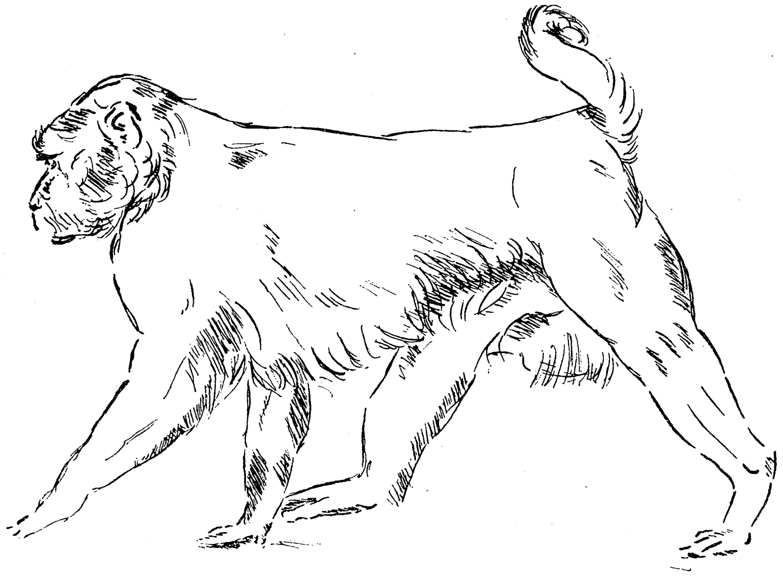

Figure 7. A dominant male pacing the cage. Note the straight back and the tail position.

In a number of displays the ritualization seems to have involved little change in the movement pattern itself, but considerable quantitative change in the motivational factors underlying it. Thus the observation that yawning occurs especially in mildly aggressive situations (figure 8, see also Hinde & Rowell 1962), or that the direction of social grooming varies with the menstrual cycle (Michael & Herbert 1963) strongly suggests the operation of selective forces to promote a relationship between a movement and a particular motivational state even though the movement pattern itself is unchanged.*

FIGURE 8. Yawning.

With a few notable exceptions, such as the song of some birds (e.g. Thorpe 1961), the signal movements of lower vertebrates are little affected by individual learning. This is also true of primates, but learning does play a role in those movements which lead to the production of mechanical noises, such as the 'branch-shaking' of Rhesus monkeys. In captive groups of this species each male has a limited repertoire of such techniques which, though stereotyped in individuals, differ between them (figures 4, 5). Furthermore, learning may well play a larger role in the interpretation of expressive movements by other individuals in primates than it does in other vertebrates.

In conclusion, then, the occurrence of ritualization in the expressive movements of primates seems generally similar to that in lower vertebrates. It must be stressed, however, that in both there are many cases in which the evolutionary origin of the signal movement, and thus the nature of its ritualization is, obscure.

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* Andrew (1963) believes that many vocalizations and associated facial movements had a common origin in a group of protective reflexes evoked by sudden intense 'stimulus contrast'. His definition of 'stimulus contrast' is however unsatisfactory in that it remains unclear whether stimuli are regarded as possessing the characteristics of 'contrast' because they elicit particular types of responses, or whether responses are grouped together because they are elicited by such stimuli. Thus Andrew's consequent suggestion that there has been no fundamental change in the causation of these vocalizations during their early evolution remains unsubstantiated.

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