OBSERVATIONS AND THOUGHTS ON THE EVOLUTION OF FACIAL MIMIC

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Whenever animals live together they must be able to communicate their intentions, wishes or desires to one another; they must be able to make themselves understood. Various workers have, in the past, attempted to study the ways in which animals, as well as man communicate with one another and, in some fields, much progress has been made. This particularly applies to birds. In mammals much less is known, and attempts to find general rules or lines of evolution have so far yielded meagre results. There may be various reasons for this. Usually mammals lead a more retired life than, for example, birds, and in only a few places in the world are there opportunities equalling those offered by the South African National Parks to study the behaviour of larger animals in their natural surroundings. Most ethological studies of mammals have so far been carried out on captive animals, mainly domesticated forms, and rodents. There are also other reasons for the difficulties in the study of mammals. Contrary to birds, the majority of them rely much on their sense of smell and undoubtedly this sense plays an important part in their mode of communication. To man, with his very poorly developed olfactory sense, this mode of communication is very difficult to study. Without claiming to possess a very exhaustive knowledge of the existing literature (most of it is unobtainable in the Union), I shall summarise some of the trends as I understand them from my own experience and observations on mammals.

In the majority of mammals most visual communication is through postures and movement involving practically any part of the body. These are usually movements or postures of a body section, or a limb as a whole, not only part thereof. In carnivores and primates a new features, the facial expression, developes.

This is, however, only well developed in some of them.

To the vast majority of mammals the vision is of relatively little importance in their orientation and search for food. It is the scent that first of all guides them. Their nasal passages are large, giving room for highly developed turbinalia which carry the great areas of olfactory epithelium. This however

forces the eyes out towards the sides, making a bifocal vision almost impossible, but it increases the animal's visual field enormously. Hoofed animals such as cows, horses and pigs, as well as rhinoceros, anteaters, rodents, insectivores etc. all have their eyes widely separated by huge nasal cavities.

In carnivores, and particularly in primates, there is a marked tendency to reduce the olfactory cavity and with that the sense of smell. The eyes of these animals consequently move closer together which allows for them to be turned forward, thus permitting the development of a bifocal vision. An exception to this rule is the dog-headed monkey, such as the baboon, which have large nasal passages. These passages are, however, very narrow in their upper parts, thus making room for a pair of closely set, forwardly directed eyes. The following table which is taken from Prince (1956) gives the optic angles and visual fields of various animals:

Animals Examined	Angle Between eyes	Binocular Field	Combined Field
Man and simia	nil	140-160	180-190
Lemurs, cats	10-15	114-130	250-280
Dogs	30-52	78-116	250-290
Rabbit, hare, marmot	150-170	10-34	360
Squirrels	130-140	25-30	360
Cattle and horses ...	90-140	30-50	350-360
Guinea-pigs, goats ...	103-110	20-63	325-340

As will be seen from the table, the angles between the eyes as well as the visual fields are appreciably smaller in the primates and carnivores studied than they are in other mammals, while their binocular vision is correspondingly better.

Another feature which should be considered is the structure of the mammalian eye. Among diurnal animals we find a tendency to form a fixation area of the retina where the image seen is clearer than in other areas. This

area is termed a macula. In higher primates we find a depression, or fovea, of the retina with a greater concentration of sense cells. The fovea need not be situated in the optic axes but may be somewhat towards the side. Such temporal foveas will give a greater bifocal vision. In ungulates which have their eyes far apart, the macula tends to form a horizontal band across the retina, thus making a greater panoramic view possible. This ability to see objects clearly "all round the clock" without moving the head, is further facilitated by a horizontal pupilla.

As we see it, there are two trends amongst mammals: One is the increasing of the visual area to its maximum so that small movements in the landscape can be detected without the animal needing to move its head. This trend we find in the ungulates, which are preyed upon. The other tendency is the moving of the eyes forward, thus decreasing the angle between the optic and visual axes of the eyes, as well as diminishing the fixation area of the retina. In other words the animal is able to see only a small field clearly at a time, but due to its bifocal vision, it is now able to judge the distance to the object it views. This tendency is the one we find in primates and carnivores.

Considering the modes of living of primates and carnivores, it seems natural that such a tendency should evolve in these animals. Their whole life often depends on their ability to aim. The cat that jumps onto the mouse has its eyes more forward than the dog which pursues its prey. So also have the primates which jump from branch to branch in the tree tops.

Returning now to the question of the development of the facial mimic, we find that the primates and carnivores rely on their visual sense to a larger extent than do the other mammals. Their visual field is limited and they are unable to observe details of what is happening in more than a small limited area at the time. As already mentioned, any part of the animal body can be used as a means of expression, but only in some of the primates and carnivores is the face used to any appreciable extent. It seems as if the disability to observe all body sections of a fellow animal has facilitated the concentration of expressive movements and postures to the face.

There may, however, also be other reasons for this development. It is not all primates or all diurnal carnivores which possess an appreciable facial mimic. Bears, mongoose and meerkats among the carnivores, and lemurs among the primates, have very little facial expression. Owing to various mishaps with my suricates (*Suricata suricatta*) I have but few observations on these animals, which are the only lower carnivores I have had an opportunity to study, but they seem to make very little use of their face. They can draw

their lips and show their teeth but that seems to be about all. A study of their facial muscles confirms the impression that they are incapable of much facial mimic. There is a marked similarity in the development of the facial muscles of the suricate to those of the ring-tailed lemur (*Lemur catta*). In the lemur the only facial movements I have been able to detect have been confined to the surroundings of the eyes and on rare occasions to the drawing of the upper lip. Also a curious dropping of the upper lip has been noticed in the angry male. Thus in the primitive primate and in the primitive carnivore — so it seems — the face has not yet taken over the mimical function which it possesses in higher mammals.

In the suricate the body-postures as a whole, as well as the tone of voice, are very expressive and it leaves the observer little doubt about the mood of the animal. To what extent scent plays a role cannot be surmised until more observations have been carried out.

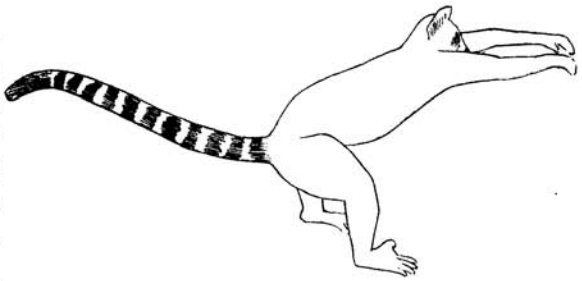
The lemur is far less vocal than the suricate, although it has a greater variety of sounds. A loud call similar to a cat's mew is an anxious, friendly call, a quick succession of doc-doc-doc is a warning of danger which when uttered loudly, makes the troupe flee to the nearest tree top. A twitter like that of a bird is a sign of fear. On occasions loud barks are emitted, similar to those of a dwarf pincher. Their function is identical to that of the warning barks of a baboon. The main communication seems however to be through postures involving the whole of the body, as well as by scent.

In the lemurs various parts of the body seem able to give off scent. The abovementioned hanging of the upper lip, of angry or upset males, seems connected with the production of scent. The lip looks swollen and moist. Moreover the great glandular areas on the fore arms become moist when the animal is greatly agitated, and on occasions, clear drops have even been seen to fall from the rams. This is particularly so during anger with an opponent whose strength the animal finds it difficult to assess. It is in this situation subject to two opposing drives, namely that to attack, and to flee, that these

glands become moist. A most characteristic ceremony may then be displayed. The animal grasps its tail between its arms and draws it between them so that the secretion from the glands is smeared onto it. This behaviour is visual and probably also olfactory to most animals with a better olfactory sense than man, and may act as a warning. When the animal has passed through this tail-embracing ceremony it may have gained enough courage to approach the opponent looking straight into its face.

Usually another type of threat is now displayed. While looking into the enemy's eyes the lemur whips its tail over its back in the direction of the opponent (compare Schloeth, 1956). This action is now and again interrupted by a curious quivering of the upstretched tail. During the succeeding attack the animal stands on its hind legs with hunched shoulders, and bristling hairs. Its arms are spread as if in an attempt to impress its opponent and make it believe that it is bigger and stronger than actually is the case.

In this position the lemur lashes out with its sharp nails towards the enemy's eyes.



If the opponent is such that it causes no restraint on the lemur, all these ceremonies are left out and almost without warning it flies into its enemy's face, scratching and biting with its razor-sharp fangs.

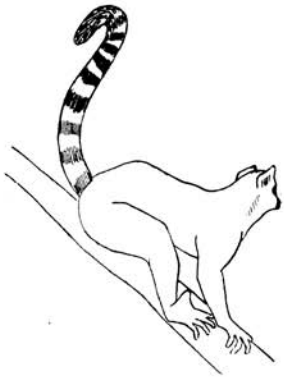
If, on the other hand, the lemur is inhibited from attacking, it starts yawning, and may look sideways with half closed eyes, until finally it probably decides to walk away.

Most of these various actions are primarily of an olfactory function. The embracing of the tail, the subsequent whipping and quivering of it, all serves to spread the odour, but because the movements are so easy to see they will also act as visible modes of expression.

Fiedler (1955) mentions a lemur male which regularly used its hand for squeezing secretion out of the glands on its fore-arms. The liberated secretion

was then deposited on the edge of a bucket. This action has never been observed in my private collection of lemurs.

Another form of behaviour frequently noticed among the ringtailed lemurs is the depositing of scent tracks. This action which has been described by Fiedler (1955) and others, is mainly performed by the female. She bends her tail forwards over her head and presses her genitalia against an upright object, usually a pole or a branch. Often she rubs her genitalia upwards by pushing with her arms thereby ending up in a curious hand stand.

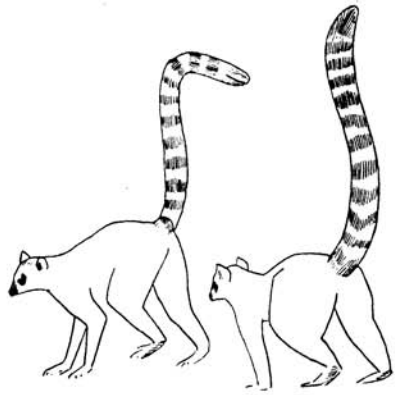


Shortly after the female has deposited her scent the male can be seen investigating the track with his nose. Now follows another peculiar ceremony. The male begins to pull the pole with his hands, first with both hands and thereafter alternating with the right and left hand, the free hand being lifted in a peculiar tense manner over the shoulder. The pulling is accompanied by a curious twisting of the body from side to side while the tip of the nose remains close to the track. Now and again this twisting of the body may also be performed without gripping the pole. Occasionally the male licks the track.

The animal appears to be in a state of exaltation and if interfered with, a swift attack may follow.

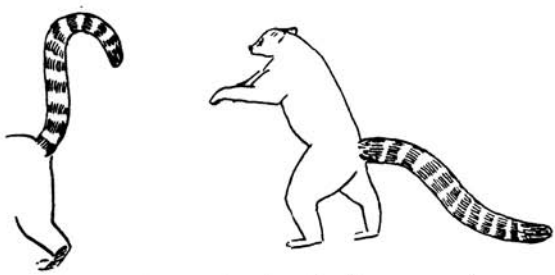
On rare occasions the male may mark objects in a manner similar to that of the female.

One more scent gland present in the ringtailed lemur should be mentioned, namely that on the front of each shoulder of the male. In which way these glands function in the communication between the animals is obscure, but they seem to be enlarged during the mating season and may act as an attractment to the female.



In the courtship I have observed, the male follows the female, nose to tail, in a manner similar to that of baboons. If she is ready she will probably stop and allow the male to mount. Unfortunately the final stages have not been observed and a film showing various examples of earlier stages was sent for processing and got lost. A more careful analysis of the events has therefore not been possible.

It will be seen from the above that although the ringtailed lemur has its eyes directed forwards and decreased visual field with a bifocal sight, the facial mimic has not yet developed. This may partly be due to the presence of a large macular area in the eyes of these animals, so that they can concentrate their attention to a wider field than the higher primates, which have a fovea; but undoubtedly the prevalence of scent communication is the prime factor which has made the facial mimic superfluous. Schloeth (1956) has pointed out that primitive animals approach one another with the nose to the ano-genital region.



In higher forms there is a preference for a nose to nose approach. In the highest forms again there is a tendency for the animals to reduce the nose to nose approach and in monkeys for example there is a transfer back to the nose to ano-genital approach. Schloeth points out that by liberating the face from the olfactory contact it becomes free to develop visible elements of expression; in other words a facial mimic.

In the ringtailed lemur the first approach is nose to nose. My own observations show that this applies not only when one lemur approaches another, as described by Schloeth, but also when an approach is made to other animals, such as dogs, and even humans. Afterwards they turn their attention to the genital region.

In monkeys the nose to nose approach has been much depressed and almost completely replaced by the nose to genitalia or anus approach. In smaller monkeys such as *Macaca mulatta* (Chance, 1956) and *Cercopithecus aethiops*, the inferior animal usually presents its hindquarters to its superior.

In baboons this behaviour has become much ritualized and I have often observed, in the wild that a female passing in front of a male presents to him even when far out of his reach. Although the presenting in these animals is very much a visual act, its olfactory function has not been lost and the way in which monkeys examine, smell and lick each other's ano-genital region, is familiar to every observer. In gorilla (Schloeth, 1956) the visual impression is of paramount importance, but the first visual examination of the other individual is always followed by touch as well as an olfactory examination of faeces, picked up in the fingers.

Among the carnivores (Schloeth, 1956) most forms seem to have a nose to nose approach to one another, but in hyaenas and dogs the prevalent first approach is nose to ano-genital region. Before their approach usually goes a visual examination of the counterpart. Cats may also approach one another with nose to ano-genital region but of more importance, besides the visual recognition, is an examination of scent tracks. It is interesting in this connection to notice that hyaenas, dogs and cats are the only carnivores which to my knowledge, have developed a facial mimic and it seems to me that the dog is the animal in which this facial mimic has reached its highest development. Curiously enough it shows features similar to the facial mimic of man.

In monkeys and apes most communication is visual and the facial mimic is of supreme importance. Too little is however known about the rules governing the facial mimic and some of the interpretations would appear directly to contradict each other. This is mainly due to the animals' swiftly changing mood; swinging from confidence to fear, and from a wish to attack to that of fleeing. Also the rhythm in which facial and other movements is performed may be significant. As the movements are extremely quick and difficult to follow and to photograph, it is understandable that wrong interpretations and contradictions will occur.

Wörner (1940) has tried to record on cine-film the various facial movements of the Rhesus monkeys and found that the movement up and down of the eyebrows follow a regular sinuous curve in the friendly animals. In cases where they are angry the lowering of the eyebrows is sudden and quicker than the raising. He therefore concludes that it is primarily the rhythm of their movements which convey to other monkeys, whether a monkey is angry or friendly. He points out, however, that also a slight frowning is noticeable in the angry monkey.

The main difficulty in accepting Wörner's theory uncritically is that he has not ensured that his angry monkey did not suffer from fear besides anger, nor is it quite clear to what extent the animal was under influence of other emotions and drives such as that to attack. In most cases animals will be under the influence of various emotions which may very well be conflicting.

Observations I have made on the Chacma baboon (*Papio ursinus*) shows that a lifted head, forward bent ears, lowered frowning eyebrows and a stiff gaze at the opponent, is a definite and "Uncontaminated" threat. Jenny, my female baboon, who is the dominant animal, needs only to look this way at Joe, the male, to cause him to yell with fear and seek shelter. The posture is invariably followed by attack unless I interfere. In my Vervet monkeys (*Cercopithecus aethiops*) a similar posture in Jack, the male, also precedes an unrestrained attack. Intermixed with the drive to attack is normally the emotion of anger which primarily is indicated by the raised hairs on the animal's neck and shoulder. The impulse to flee which invariably is paired with the emotion of fear, is indicated by lowering of the head, lifting of the eyebrows and backward pressing of the ears. In between these two extremes namely the uninhibited angry attack and the fearful retreat, are various grades of conflicting behaviour in which both drives play a part. In baboons jerky movements with a lowered head and front quarter, lashing out with the hands in the direction of the opponent, rubbing the ground with the hands, lifting and lowering of the eyebrows, moving the ears forwards and backwards, raising of the hand on the shoulder, and gazing straight at the opponent, are all actions which are combined. It can be difficult, when viewing such combined activities and postures, clearly to decide which factors are submissive and which are aggressive. Movements and postures similar to those described in baboons, occur in my vervets, although I have a much smaller number of observations on them and they are much more timid than the baboons. For these reasons observations of pure aggression or retreat are difficult, but it seems to me that the postures and movements of aggression and submission are very similar, and that the quick movements of eyebrows and ears are a result of rapid fluctuations in the mood of the animal, alternating between aggression and retreat. It is like the rope dancer shifting his centre of gravity from one side to another in order to keep his balance. If this interpretation is correct, then Wörner's recordings are not recordings of the pure expression of one emotion, but of certain features expressing a balance between various emotions. Until many more observations on the mode of expression are made on a far greater number of primate species, it is not possible to say for certain which interpretation is the correct one. However, having found, and also demonstrated that I can predict action sequences in my baboons, I feel inclined to adhere to my own interpretation as described here and elsewhere (Bolwig, 1957, 1959). It is obvious that there must be great variations in the mode of expression even within the same group of animals, (such as the primates) and that these variations run parallel to the anatomical and physiological variations. *Sercopithecus* for example cannot produce a visible snarl, while the baboon, which has a well developed canine muscle, can. In spite of such variations there appear to be certain general rules governing the mode of expression in the old world monkeys,

apes and man. Frowning, for example, always indicates anger and aggression, lifting of the eyebrows fear and submission. Forward-bent ears, indicate confidence, but when pressed against the back-head, it means fear and/or submission is shown. A stiff gaze towards the counterpart is a sign of aggression. An evasive look is a sign of submission. Raising of hairs shows anger. Added to these expressive postures are a number of other postures which multiply as the animal ascends the evolutionary ladder. Thus the baboon, for example, has a grimace which can be interpreted as laughter and which is also present in the chimpanzee. This animal in turn possesses a much greater variety of facial expression than the primates which are less evolved.

Finally it is worth noticing that there are similarities in the facial expression of higher old world primates and higher carnivores. Frowning, snarling, hair raising, staring and ear-raising in these animals (with the possible exception of cats) all express the same emotions. No reason for this simliarity can be offered at the moment, but the explanation might be found in the common ancestry of carnivores and primates. Should this be so, it is interesting to speculate that there might have been a certain organisation of the innervation of the muscles which has facilitated one particular line of evolution in their use as instruments for the expression of emotions. It is too early to say whether a comparative anatomical and physiological study of insectivores, primates and carnivores may reveal anything in this direction, but it is a problem which should be kept in mind by facial anatomists. Moreover, a study of emotional expressions of the new world monkeys might lead to an understanding of the evolutionary trend.

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