# Evolution of Facial Expression

Many human expressions can be traced back to reflex responses of primitive primates and insectivores.

R. J. Andrew

When men are amused they draw back the corners of their mouth and emit a series of quavering grunts. Why should they make this quite arbitrary gesture, rather than some other one, to show friendliness and pleasure?

This sort of question, like so many others, was first seriously asked by Darwin. In *The Expression of the Emotions in Man and Animals* (*1*) he made a comparative survey of facial expression in primates and other mammals in an attempt to discover precursors from which human expressions might have evolved. Knowledge of the comparative anatomy of mammalian facial musculature, which was already well advanced at the time of Darwin (*2*), has continued steadily ever since (*3*). However, except for the monumental work of Ladygina-Kots on the chimpanzee (*4*), there has been little interest in continuing the comparative study of facial movements effected by these muscles until very recently (*5–7*), when a number of workers began to apply the methods first used by Lorenz (*8*) for studying the evolution of displays.

There is no doubt that the facial expressions of primates are excellent material for studying the evolution of behavior; an unusual advantage is the fact that the changes in anatomy which accompanied this evolution should make it possible to supplement the comparative study of living animals with paleontological material. However, the importance of the subject lies in the new approach it offers to some problems of human behavior and evolution.

By way of general introduction, it should be said that the living primates have evolved as six separate lines during most of the Tertiary. These are the tree shrews (Tupaioidea), the galagos and lorises of Africa and Asia (Lorisoidea), the lemurs of Madagascar (Lemuroidea), the monkeys of the New World (Ceboidea), the Old World monkeys and baboons (Cercopithecoidea), and apes and men (Hominoidea). The parallel evolution of displays which has occurred in these different lines is of much interest and is likely, with further study, to prove very revealing of the sort of selective pressures that are involved in such evolution. A monkey-like condition has been achieved in the Lemuroidea (*Lemur*), as well as in the Ceboidea, Cercopithecoidea, and Hominoidea (*9*).

The author is assistant professor of biology at Yale University, New Haven, Conn.

## Causation of Displays

Much of the confusion which has arisen in the study of the evolution of facial displays in human beings can be resolved by distinguishing firmly between their function and their causation. Facial expression has evolved, like other displays, to communicate information about the probable future behavior of the displaying animal. That it does so is attested both by observations of the responses of primates to human imitations of their facial displays or to slight changes in the faces of their fellows (see, for example, *10*), and by pioneering quantitative studies (*11*). However, the association of a particular expression with a high probability of attack, for example, does not mean that the expression is caused by a subjective feeling of anger or by the aggressive drive. As will be seen, some display components may be associated with a very fixed gaze, and others with vigorous expiration. Both the gaze and the expiration are responses evoked by characteristics of an opponent, but other objects which do not evoke aggressive responses may have these same characteristics and elicit these responses.

Landis (*12*) attacked the theory that, in man, specific emotions cause specific expressions, by showing that the expressions of subjects in certain very disturbing situations are quite variable. He pointed out that much of a human being's ability to interpret expressions (*13*) is due to the conventional meanings assigned to many of them. However, it was an over-reaction on Landis's part to dismiss all variation in expression as due to differing amounts of discharge along the facial nerve. Specific expressions can be elicited by specific stimulus situations; thus, the expression indicating "disgust" may be variable, but that made on biting a lemon is relatively standard.

The position taken here is basically that of Tinbergen (*14*), who showed that, in bird displays, the components which are derived from movements of attack or fleeing continue to vary appropriately in intensity as the likelihood of the displaying bird's attacking or fleeing changes. Clearly, attack and fleeing are not always the appropriate groupings of responses to consider when analyzing displays (*9*). But the thesis involved remains the same: display components tend to reflect much of the causation of the responses from which they derive.

Little is said here of the changes in causation that accompany the development of stereotyped patterns of display. Neither is the possibility that patterns of display become attached to specific stimuli from social fellows through conditioning considered at length, since the evolution of facial expression can only be discussed in broad outline here.

## Informative Responses

Before selection can begin to shape a response into a component of a display, the response must, on occasion, convey information to the animal's fellows about the future behavior of the animal which makes it. This is well exemplified by those components of facial expression which appear to have originated from protective responses which are evoked by startling, strange, or noxious stimulation. These components include flattening the ears and closing the eyes (movements whose protective function is clear) and withdrawal of the corners of the mouth (a movement whose functions are more complex, as is discussed later). In a full response, respiration is checked and the glottis is first closed and then suddenly opened with a vigorous expiration which clears air from the upper respiratory tract (*15*).

A relatively primitive condition, such as exists in many mammals (for instance, the domestic mouse), is exemplified in the primates by *Galago crassicaudatus* (Lorisoidea). A member of this species flattens its ears and narrows its eyes when any approximation of its face to a fellow animal or to some other potentially dangerous object seems imminent. In species with relatively mobile faces (for example, the domestic cat), the corners of the mouth are sometimes retracted. A confident animal will assume such an expression only when actually sniffing or grooming a fellow. The less confident the animal, the greater the distance from the object at which it will make these responses. Thus, in *Galago*, a male will show such responses when it is at some distance from a female, when approaching to attempt copulation. An inferior awaiting attack will make such responses when at a great distance from the object of fear, and for long periods. Protective responses of this type thus can convey information about social status and the likelihood of approach, before any evolution into displays has occurred.

## Ear Flattening, Scalp Retraction, and Eyebrow Movements

In the social Lorisoidea and Lemuroidea, ear flattening is a conspicuous protective response, occurring in social situations of the type just discussed. In such flattening, the medial part of the postauricular musculature somewhat retracts the posterior part of the scalp. In the Ceboidea and Cercopithecoidea, ear flattening also occurs, but scalp retraction tends to become the conspicuous part of the movement. With the participation of the frontalis muscle, the whole of the scalp forward to the eyebrows may be affected. This development is most marked in the macaques, mangabeys, and baboons, where conspicuously colored skin normally partly hidden by the eyebrow ridge may be drawn up over the ridge (as in the gelada baboon), or a topknot of long hairs may be flattened (as in *Cynopithecus niger*). Despite these developments, scalp retraction occurs in the same situations in which primitive ear flattening does. In confident play between equals, it occurs only when there is real danger that the animal's face will come in contact with the other animal. When an animal is making a threatening but not completely confident approach, or when it is approached by a superior animal, it may begin to display scalp retraction when the opponent is still at some distance. An interesting development is brief scalp retraction when an animal is greeting a superior at a considerable distance after a period of separation.

The lack of extensive use of scalp retraction in the Ceboidea is perhaps related to the incompatibility of this response with eyebrow lowering, which is an important response in this group. However, scalp retraction is often observed in capuchins—for example, in threat. The virtual absence of scalp retraction in man and the minor importance of this response in the apes can perhaps be similarly explained. It is not an inevitable consequence of lessened mobility of the ears, although this change may be a factor of some importance.

In all primates there is lowering of the eyebrows in connection with protective closing of the eyes. The primitive movement, which may be seen very clearly in the exaggerated protective responses of *Tarsius*, involves muscles that attach at the medial edge of the *orbicularis oculi*. The nasolabialis (Fig. 1) is involved in this movement, hence the upper lip is raised somewhat as the brows are lowered medially.

Eyebrow lowering that is almost certainly of this type occurs in many of the Ceboidea, from marmosets such as *Oedipomidas* to the advanced capuchins (Fig. 2), during friendly but hesitant approaches to a fellow and in similar situations. It is commonly accompanied at intervals by lateral head shaking and by eye closure. In capuchins, in particular, the resemblance of such a display to the full pattern of protective responses elicited by a nauseous taste, for example, is marked.

In mammals with very mobile brows (for example, the dog, some Ceboidea, and man), the eyebrows may be lowered during an intent stare at some object very close to the face. It is possible that this is a protective response comparable to the ear flattening and the narrowing of the eyes which occurs when an animal sniffs a strange object. However, man lowers his eyebrows not only in staring at nearby objects but also when trying to make out distant movements. Darwin (*1*) suggested that lowering the eyebrows may serve to exclude excessive lateral light. Another possibility is that it may help in achieving convergence of the optical axes when the head is held very close to an object (*7*).

As a result of this association, eyebrow lowering has come to be a means of emphasizing the fixed stare displayed in confident threat by many members of the Cercopithecoidea [for example, *Papio* (*10*) and *Cercopithecus*] and of the Hominoidea (and perhaps of the Ceboidea). In the Cercopithecoidea such eyebrow lowering is readily suppressed by scalp retraction in intense threat, whereas in the chimpanzee (*4*) and in man it persists and is accompanied by a drawing together of the eyebrows.

## Movements Associated with Respiration

One of the most important components of facial expression is the contraction of the sphincter muscle of the mouth (the orbicularis oris) during vocalization. Van Hooff (*6*) has suggested that such contraction may derive from suckling movements, since it occurs in advanced monkeys and apes in calls given when physical contact is desired.

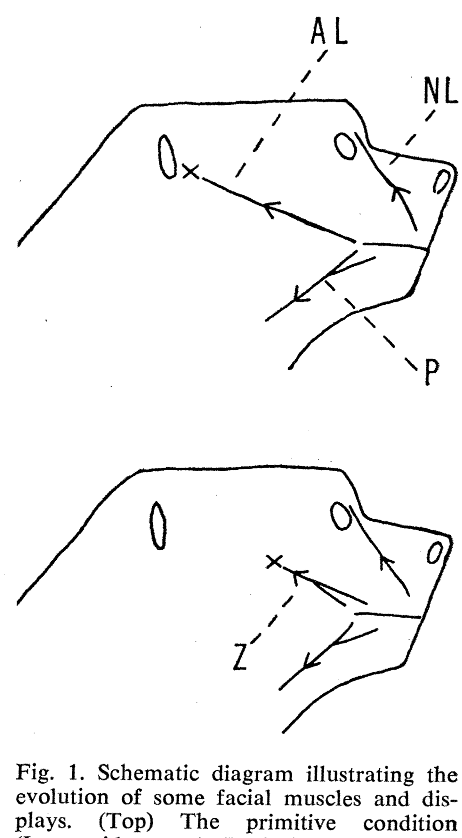


Fig. 1. Schematic diagram illustrating the evolution of some facial muscles and displays. (Top) The primitive condition (Lemuroidea and Lorisoidea): auriculolabialis (*AL*) only draws back the corners of the mouth. (Bottom) The advanced condition: zygomaticus (*Z*), the old auriculolabialis, now to a greater or lesser degree raises the upper lip as well as drawing back the corners of the mouth.

However, the orbicularis oris may in fact contract in any vocalization which involves vigorous expiration without marked tension of the glottis. This association is very widespread in the mammals: the contraction occurs in all the main lines of primates (except perhaps in *Tupaia*), including the primitive *Cheirogaleus* and *Galago*, and can be seen in a dog when it howls, in a lion when it roars, and in a deer when it lows. It probably originated from movements involved in dilation of the nostrils. In primitive mammals such dilation is effected by means of the maxillo-nasolabialis (Fig. 3), with which the orbicularis oris is closely associated. Myographic studies in *Tupaia* or *Lemur* are needed, to see whether, in primitive mammals, the orbicularis oris does indeed participate in the sustained dilation of the nostrils that accompanies vigorous inspiration and expiration. In capuchins, the area behind the nostrils is clearly seen to move posteriorly during marked contraction of the orbicularis oris in vocalization.

The contraction of the orbicularis oris during vocalization of the type discussed is a movement that has been retained in advanced primates probably because it has become a visual signal. Interaction between the orbicularis oris and retraction of the corners of the mouth, a combination which is associated with intense vocalization, becomes obvious in the calls of such lemuroids as *Lemur catta*. In the advanced Ceboidea and in the Cercopithecoidea and Hominoidea, this interaction results in very conspicuous changes in expression which sometimes precede the appropriate changes in intensity of vocalization. Contraction of the orbicularis oris may announce the onset of vocalization. In this connection, the protrusion of the lower lip which indicates that a child is likely to cry is of interest. Here, triangularis (Fig. 3), a derivative of orbicularis oris, is important.

Throughout the mammals, sudden noisy expirations are commonly given in threat, often coincident with head thrusts or leaps forward. These expirations probably represent relatively unelaborated protective responses of the type already discussed. In the higher primates (and in *Lemur fulvus*), the expirations are usually quite audible and may even approach a bark, while the accompanying tensing of orbicularis oris causes the teeth to be covered by the lips (Fig. 4), despite wide opening of the mouth (an intentional movement of biting). In the hamadryas and gelada baboons the contraction is so marked that the lips are drawn in over the teeth. In human beings, lip rounding, often with a noisy expiration, in indignation ("confident threat") is a display of this type.

A final movement associated with violent expiration is a dorsalward tipping of the head. This is observed during the howls of a dog or of *Lemur catta* and probably helps to lower the epiglottis, so that the main current of air can flow through the mouth. It is probably from this movement that the head tilting observed in threat in *Macaca* and in some other cercopithecoids derives.

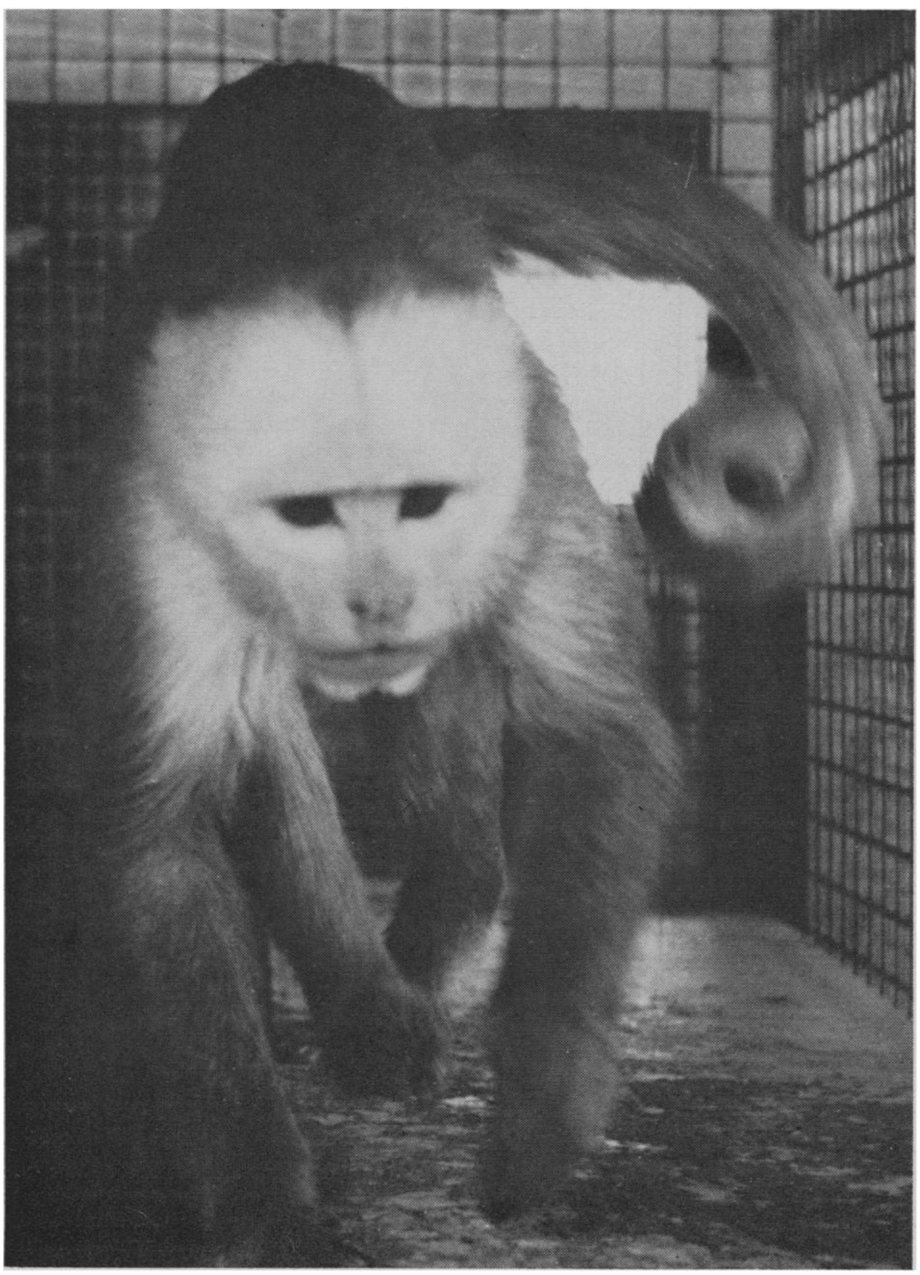

Fig. 2. *Cebus albifrons,* with eyebrows lowered in a hesitant approach to greet a fellow monkey.

**Whisker Movements**

Huber (*3*) maintained that the movement of tactile whiskers was a primary function of many facial muscles. This does not seem to be true in the insectivores and primates (*6*). In these animals, some whiskers (for example, those on the brows) are moved markedly, but the main function of the muscle contractions which move them is not tactile scanning of the environ-

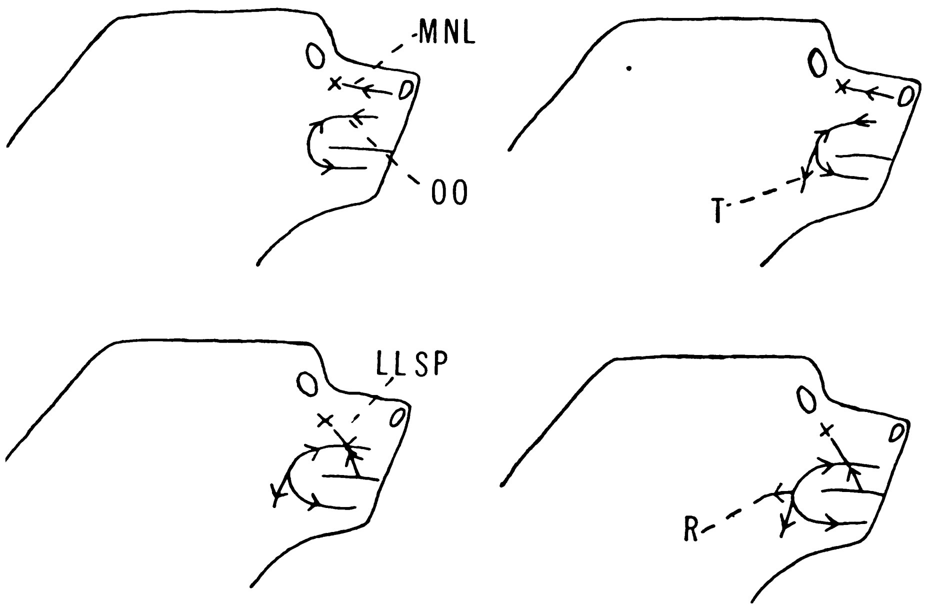


Fig. 3. Schematic diagrams illustrating the evolution of some facial muscles and displays. (Top left) The primitive condition (Lemuroidea and Lorisoidea): maxillo-nasolabialis (*MNL*) dilates the nostril, probably helped somewhat by orbicularis oris (*OO*), with which it is closely associated. (Top right) The development in Ceboidea and the gibbons of triangularis (*T*), which tends to depress the corners of the mouth. (Bottom left) In Cercopithecoidea and advanced apes the early maxillo-nasolabialis has become the levator labii superioris proprius (*LLSP*). (Bottom right) In man, the risorius (*R*), a branch of orbicularis oris, has become a retractor of the corner of the mouth. [After Ruge (*2*) and Huber (*3*)]

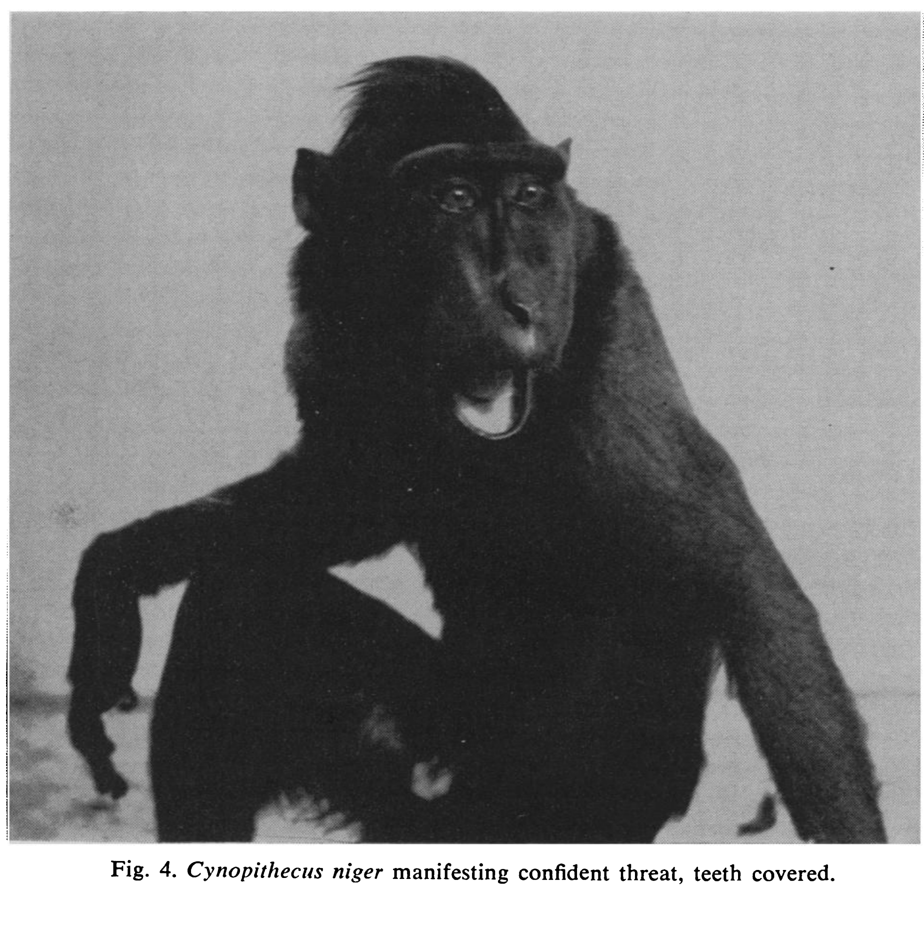

Fig. 4. *Cynopithecus niger* manifesting confident threat, teeth covered.

ment but the protection of sense organs.

Movement of the whiskers on the sides of the muzzle was originally probably slight and incidental to the contraction (*16*) of the maxo-nasolabialis (the nostril dilator) and the nasolabialis (which turns the tip of the nose from side to side). In a number of rodents, and in isolated members of the Insectivora, such as the elephant shrew, the association between these muscles and movement of the whiskers has been increased, so that the whiskers scan the environment with a regular and rapid sweep, as a part of sniffing in olfactory exploration. This development did not occur in any of the primates that have been studied, including such mouse-like forms as *Microcebus*, or in such insectivores as the hedgehogs. A second elaboration is widespread in the carnivores (for example, in the cat, the dog, and the civet). Here these whiskers are erected during any sudden approximation of the face to a possibly damaging object. The movement is probably related to contraction of the maxillo-nasolabialis in vigorous expiration. It is observed in some lemuroids, but in these it is slight and may be a purely respiratory movement. It is possible, though unlikely, that this movement of vibrissae may have had some effect on the early evolution of lip rounding in primates.

## Grins and Snarls

There are three different situations in which the corners of the mouth are retracted (in a "grin") in primitive mammals such as the opossum, the tree shrew, and *Microcebus*. (i) Grinning occurs when the animal is about to make a hard bite, with the back teeth, at food or in defense. (ii) Grinning is evoked as a protective response by startling stimuli or by close approximation of the animal's face to an unknown or dangerous object. This is observed especially in animals with mobile faces, such as man (*17*), the cat, or the monkey. (iii) Grins accompanying vocalization that involves closure or high tension of the glottis, even when there is no nearby potential danger (examples of such vocalization are the intense clicks made by *Microcebus* and the lorisoids during exploration or on loss of contact with their fellows, and the high-pitched calls of cats, mongooses,

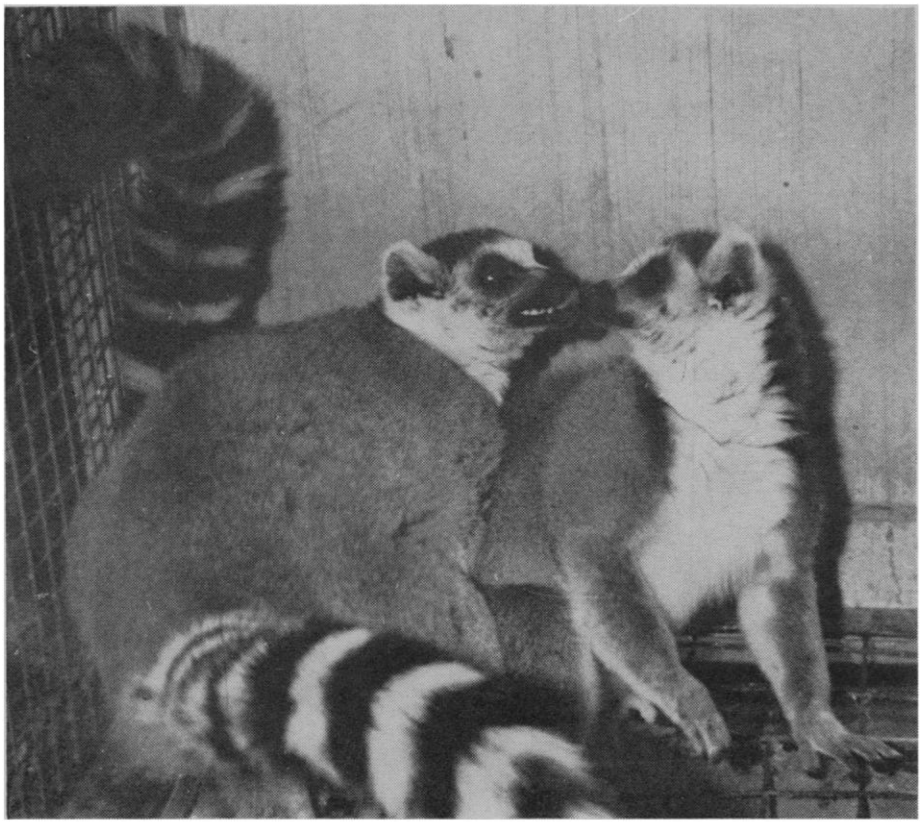

Fig. 5. *Lemur catta* manifesting grin, with grooming tongue movement, at a sudden movement of a superior fellow.

and equids). This association suggests an origin of vocalization from the closure or narrowing of the glottis, followed by vigorous expiration, which is elicited, together with other protective responses, by startling stimuli (*7*). The present function of this type of grin in primitive mammals is not certain. It may already have acquired a signalling function in some cases, and in others, contraction of the platysma may strengthen the neck during intense vocalization. Since vocalization and protective responses are often induced by the same stimuli, it is often impossible to decide what type of grin is involved (for example, in defensive shrieks); indeed, the question may be meaningless in such cases.

In primitive mammals, grins elicited by startling stimuli probably have at least two functions: preparation for a defensive bite or preparation for ejecting material from the mouth. Similarly, the head shaking which may accompany them may be a means of injuring opponents or prey or of shaking objects out of the mouth. It is thus probable that the suggestion that the human grin derives from a biting movement (*6, 18*) is in part valid; however, the history of the grin is too complex for so simple an explanation to be adequate.

In the advanced Lemuroidea, grins may occur in connection with calls given on loss of social contact (an example is the wail of *Lemur catta*), or with calls given in defense (Fig. 5) or in frustration. The Lorisoidea differ from the Lemuroidea chiefly in that they emit intense clicks or crackling sounds in situations in which *Lemur*, for example, might grunt or bark. As a result, a male galago may grin while making crackling sounds when approaching a female to attempt copulation, as well as during shrieks made in defense or in frustration.

In *Cercopithecus* the situation is not very different from that in the advanced Lemuroidea. Grins occur not only during defensive shrieks but in primary association with some vocalizations (such as the trill of *C. mitis*). (Shrieks made in frustration are examples of such primary association in *Macaca, Papio*, and *Theropithecus.*) In more advanced forms, grins are evoked more and more easily and may be made in new situations and in association with low-intensity vocalization or in silence. Thus, rhesus will sometimes grin in silence when greatly frightened by a fellow. This trend is complicated by the increasing importance of lip retraction. This increase in lip retraction is in part due to the shift in attachment of the zygomaticus and platysma muscles from the corner of the mouth to include the lips, in primates other than Lemuroidea and Lorisoidea (*2*) (Fig. 1). It is also partly due, in the Cercopithecoidea, to the fact that the maxillo-nasolabialis, a nostril dilator, has developed into a lip elevator, levator labii superioris proprius. Since nostril dilation was originally easier to elicit than grinning, this development may have been associated with a drop in the threshold of lip elevation; unfortunately, the nature of the interaction between the original elevator (the nasolabialis) and the new one is not yet clear in the advanced Cercopithecoidea. The combination of grin and retraction of the upper lip ("high grin") occurs in the hamadryas and gelada baboons when an animal greets a fellow after separation, and sometimes in play fighting between equals (Fig. 6). [In most Cercopithecoidea, and frequently in the hamadryas and gelada baboons, the mouth is simply held wide open in play fighting; Bolwig (*19*) has, on occasion, observed some slight tensing of the corners of the mouth in *Cercopithecus* at play.] The high grin also occurs readily, particularly in *Cynopithecus niger* and *Mandrillus* spp., during relatively aggressive approaches to a stranger (see Fig. 7). The expression suggests that of a snarling dog, but it is likely that the dog's snarl has a different history, deriving from a baring of the canines to bite. Such a movement, in an unelaborated form, is seen in primates when they are eating.

The Ceboidea show a similar trend toward facilitation of the grin. Marmosets grin during intense vocalization in defense or in friendly greeting. (Like the Lorisoidea, the Ceboidea emit high-pitched, intense vocalization more often, and in more kinds of situations, than other primates do.) In spider monkeys and woolly monkeys a relatively advanced display has been observed: these monkeys grin and make crackling noises when getting slightly the worst of it in rough play.

Among the Anthropoidea, the gibbons show clear association of grin and vocalization in that they grin whenever their grunting develops into intense squeaking. In man, chimpanzee, and gorilla, grins, with marked retraction of the lips, occur in association with shrieks from fear, frustration, or general excitement. A similar expression occurs in "moderate anger" (*4*) in the chimpanzee, perhaps because of a tendency to shriek. The exact motivation of the animal at such times is not fully clear. In man, confident attacks are accompanied by rounding of the lips, and shrieks occur during aggressive tantrums. Men may grin silently while fighting, but they grin in a similar way during purely physical exertion. Related responses (for example, raising the lip and closing the eyes, in *Cynopithecus niger*) are observed in other primates working hard to overcome a physical obstacle. It is likely that these are protective responses, related to the concentration of attention on the obstacle and the lack of precaution against possible injury when it yields. Most important of all is the facilitation of the smile in social interaction in man. [This may have, in part, an anatomical basis, since a muscle derived from the orbicularis oris, the risorius, is added to the other retractors in man (*2*).] Such smiles grade into purely protective grins. Thus, the fixed smile sustained during verbal or other attack by a superior has much in common with the grin which is often assumed during periods when some undesirable event seems likely to occur suddenly (for example, when one is making adjustments to a delicate mechanism which it would be easy to damage). Similarly, the evocation of a grin in the startle response (*17*) resembles in some ways the very ready evocation of smiling in infants by "peek-a-boo" games. On the other hand, smiles are clearly associated with vocalization, not only in the ready development of laughter, as smiles grow more intense, but even in smiles made in silence (in infants smiling often involves closure of the glottis) and followed by noisy expiration. The condition in human beings, like the comparative data on the grin, thus suggests that it may be wrong to try to separate the grin as pure protective response from the grin of vocalization.

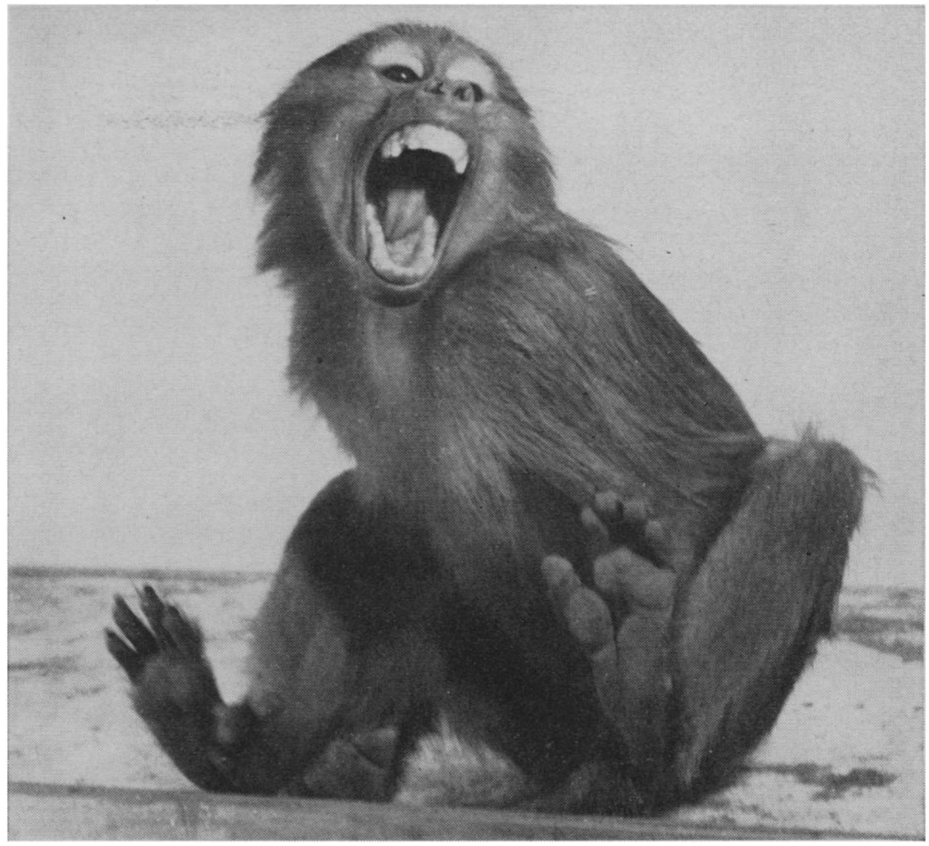

Fig. 6. Hamadryas baboon, manifesting a high grin when preparing to pounce in play.

## Grins and Pleasure

A great deal remains to be said about the causation of the human smile. The early attachment of the smile response to fellow human beings may be compared to the attachment to a mother object of a variety of responses (for example, that of seeking for bodily contact) during imprinting in nidifugous birds, and it is as little understood. Most important, however, is the relation between smiles and feelings of pleasure. McClelland and his school have shown that human subjects judge small changes in stimulation to be pleasant and large changes to be unpleasant (*20*). One of the main stimulus situations evocative of protective responses is a sudden large change in stimulation. Progressive facilitation of a protective response such as the

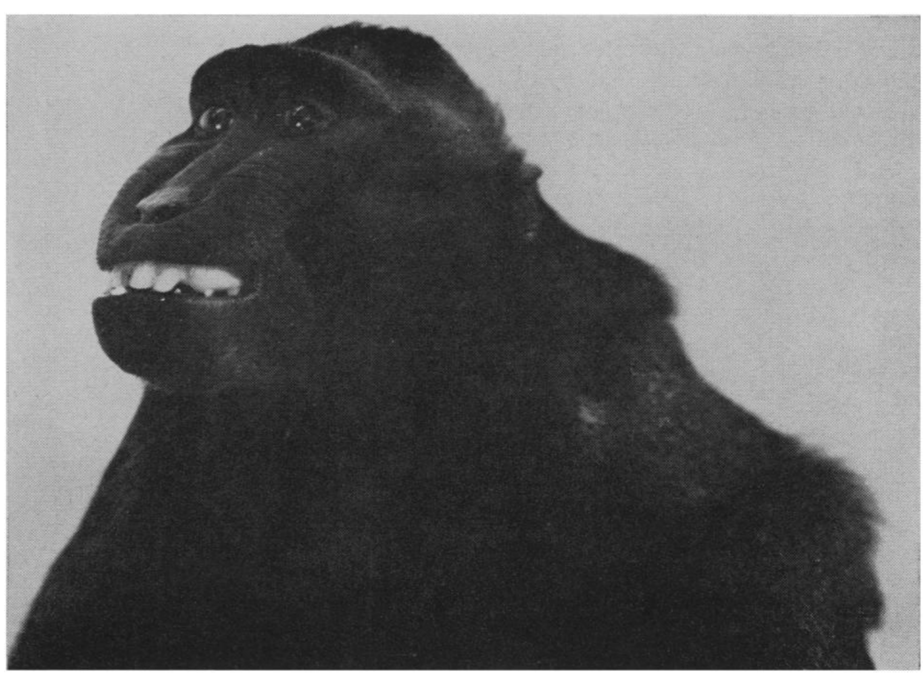

Fig. 7. *Cynopithecus niger* lifting its upper lip before sneezing. A similar movement is made in greeting and in great exertion. Its occurrence before sneezing (as in man) may be related to the evolution, from the early nostril dilator maxillo-nasolabialis, which one would expect to be active before sneezing, of levator labii superioris proprius.

grin could thus reasonably be expected to lead to a condition in which the response could be evoked by changes in stimulation small enough to be judged pleasant (that is, "interesting" or "amusing"). A comparable situation appears to exist in the domestic chicken, where vocalizations are evoked by changes in stimulation, or by stimuli conspicuous for some other reason. Calls of the lowest intensity are evoked by stimulus changes which attract the chick toward the stimulus (*21*). In accord with an assumed origin of this type for smiles of pleasure or amusement is the evocation of smiles and laughter by jokes, since the essence of a joke is the right degree of discrepancy between the real ending and that anticipated.

## Tongue Movements and Facial Mobility

In all the fully social primates there is a certain amount of grooming of social fellows. A superior will approach a fellow without hesitation to groom him, but an inferior may pause at a little distance and repeatedly part the lips and allow the tongue to protrude in movements of incipient grooming. Such movements thus indicate the friendly intentions of an inferior or an equal. Protrusion of the tongue occurs in the Ceboidea but shows little development into a display even in such advanced forms as spider monkeys. In the Lemuroidea, *Lemur fulvus* and associated species show pronounced and very rapidly repeated protrusion of the tongue. The resulting conspicuous display is so readily evoked that an animal sometimes makes it even on meeting inferiors, particularly when they also make the display. A similar condition has evolved in the Cercopithecoidea, where the mobility of the lips has made lip movement the most conspicuous part of the display. Lip smacking is greatly facilitated in young macaques and baboons during periods when they have a special tendency to seek physical contact with their social fellows. Lip smacking in greeting a fellow after separation is probably also related to the establishment of contact; it, too, readily develops into true grooming behavior. The Cercopithecoidea smack their lips in certain of the same situations in which human beings smile, although the two displays have very different histories. The parallel is strengthened by the fact that lip smacking very readily evokes the same display in a fellow.

No such display has been elaborated in the apes and man, although protrusion of the lips to grasp an object may take its place to some extent. This movement occurs both as a preliminary to grooming and during investigation of a strange (sometimes distant) stimulus, and it may have some signalling function in both contexts.

The tongue movements of grooming so modulate the grunts of the baboons as to make them very like sounds made by human beings. Such modulation is effected by changes in the resonances associated with the subdivisions of the vocal tract as their dimensions change. The type of sound that reveals such changes most clearly is a "humanoid grunt," since this provides a uniform and relatively complete coverage of the pitches at which resonances may occur, thanks to the very small gaps which separate overtones (*22*). Among the primates so far studied, such calls are given commonly in a wide range of social situations only by baboons. In the hamadryas it can be shown that, as in man (*23*), the two main "formants" (resonances) are associated with the front and back cavities of the mouth, which are separated by the tongue. In most calls the back cavity is mainly responsible for the lowest formant.

Grunts are modified by changes in the mouth aperture, but the sensitivity to tongue movements is the more impressive. During greeting or just before lip smacking, movements of the tongue within the closed mouth, which are quite invisible, can readily be detected, both by ear and on spectrograms, if the animal grunts. It is possible that the importance of tongue movements in display in the Cercopithecoidea has played some part in the evolution of humanoid grunts, since it is only in *Lemur fulvus* and its associated species that deep grunts have developed as greeting displays in the Lemuroidea, and these are also the only Lemuroids with a marked tongue-protrusion display (which serves to modulate the grunt). It seems likely that an important early function of vocalization in the prelanguage stage of human evolution was to carry information about invisible positions of the tongue in facial displays. Analogy with *Lemur fulvus* and the baboons suggests that the ancestors of man may have evolved a more exaggerated use of grooming movements of the lip and tongue in display than is usual in the Hominoidea.

The trend in primate evolution, as Huber emphasized (*3*), has been toward increased facial mobility. Clearly, however, it is wrong to present this trend, as Huber did, as being purely a development toward the human condition. Facial mobility has increased independently in the Lemuroidea (compare *Lemur* with *Microcebus*), the Ceboidea (compare *Cebus* with *Aotes*), the Cercopithecoidea (compare *Cercopithecus* with the baboons), and Hominoidea (compare the gibbons with man), and different components have sometimes been emphasized in different lines. The elaboration of scalp retraction, lip smacking, and grinning in advanced cercopithecoids is as effective in producing conspicuous and elaborate systems of displays as is that of frowning, lip protrusion, and grinning in the Hominoidea.

The interpretation of such changes is complicated by the fact that the movements involved retain functions other than display. *Tarsius* has very exaggerated face-protecting responses, which are very readily elicited by such mild stimuli as a strange taste. In this it differs markedly from such lorisoids as *Galago senegalensis,* whose way of life seems to be very similar. The condition in *Tarsius* is probably related to the extreme reduction of the muzzle, in an animal which takes relatively large prey. Similar exaggerated responses are observed in the cats, and in cats the exaggerated protective responses are also conspicuous in social encounters.

However, it is almost certain that an increased need for conspicuous displays, capable of carrying an increased amount of information about probable future behavior, has been of great importance in the evolution of facial mobility. In general, for example, it is the highly social mammals which have exaggerated facial displays. This is clear when we compare wolves with the expressionless and solitary bears, for example, or such a social form as *Lemur catta* of the Lemuroidea with *Microcebus.* It is thus reasonable to look for some difference in social structure to explain the progressive increase in facial mobility within the

Cercopithecoidea that is found when *Cercopithecus* is compared with "typical" macaques like the rhesus, and when the rhesus is compared with the gelada baboon, for example. I have suggested (*22*) that the necessity, in terrestrial baboons, for sexually mature but subadult males to remain closely associated with the troop, since this serves as the refuge from danger (see *24*), may have increased the need for expressive displays in these species, as compared with species such as rhesus and the Japanese macaques (*25*), in which subadult males can leave the troop for long periods of time. The demonstration by Kummer (*26*) that in the hamadryas baboon the troop is divided into stable subgroups (consisting of one male with a harem of females), with which subadult males are only loosely associated, emphasizes the need for more comparative studies, in the field, of social structure and of the use of displays.

The detailed study of human facial displays promises to be the most difficult, as well as the most important, area of this field of investigation. Cross-cultural studies by anthropologists will be essential, since it is often difficult to decide what features of human facial expressions are conventional expressions learned during infancy. Developmental data will be needed as a part of such studies, since it is already clear that such conventional expressions are usually exaggerations or imitations of inborn movements.

It has been seen that man's basic repertoire of facial displays is similar to that of the apes. The reasons for the differences between the Hominoidea and the Cercopithecoidea, and the possible effects these differences may have had on evolution, once they were established, offer a fascinating field for future research. A number of other differences between man and other hominoids will probably prove equally revealing. Man's use of tears, for example, may relate to a greater selection, in our line, for displays evoking defense and assistance.

## Conclusion

Facial expressions in primates are caused neither by specific conditions or drives nor by pleasure or unpleasant feelings, although they do convey information about the motivation of the animal which shows them. They appear to have evolved from such sources as responses through which vulnerable areas are protected, responses associated with vigorous respiration, and grooming responses, and they retain something of the causation of the early responses from which they stem.

Similar facial displays have evolved in the four lines of primates in which monkey-like forms have developed. The resemblances and the differences between the displays of our own line and those of the others offer new sources of information concerning the evolution of human behavior (*27*).

### References and Notes


1. C. Darwin, *The Expression of the Emotions in Man and Animals* (Murray, London, 1872).
2. G. Ruge, *Morphol. Jahrb.* **11**, 243 (1886); *Untersuchungen über die Gesichtsmuskulatur der Primaten* (Engelmann, Leipzig, 1887).
3. E. Huber, *Evolution of Facial Musculature and Facial Expression* (Johns Hopkins Press, Baltimore, 1931).
4. N. N. Ladygina-Kots, "Ditia shimpanze i ditia cheloveka," *Sci. Mem. Museum Darwinianum Moscow* (1935).
5. N. Bolwig, *Koedoe* **2**, 60 (1959).
6. J. A. R. M. Van Hooff, *Symp. Zool. Soc. London* **8**, 97 (1962).
7. R. J. Andrew, *Behaviour* **20**, 1, (1963).
8. K. Lorenz, *J. Ornithol.* **89**, 137 (1935).
9. R. J. Andrew, in *Evolutionary and Genetic Biology of the Primates*. J. Buettner-Janusch, Ed. (Academic Press, New York, in press).
10. N. Bolwig, *Behaviour* **14**, 136 (1959).
11. R. E. Miller, J. H. Banks, N. Ogawa, *J. Abnormal Social Psychol.* **64**, 343 (1962).
12. C. Landis, *J. Comp. Psychol.* **4**, 447 (1924).
13. T. Engen, N. Levy, H. Schlosberg, *J. Exptl. Psychol.* **55**, 454 (1958).
14. N. Tinbergen, *Quart. Rev. Biol.* **27**, 1 (1952).
15. The observational data described in this article are either taken from R. J. Andrew (*7*) or published here for the first time.
16. E. Huber, *Quart. Rev. Biol.* **5**, 133, 389 (1930).
17. C. Landis and W. A. Hunt, *J. Psychol.* **2**, 215 (1936).
18. N. Tinbergen, *Z. Tierpsychol.* **16**, 651 (1959).
19. N. Bolwig in preparation.
20. D. C. McClelland, J. W. Atkinson, R. A. Clark, E. A. Lowell, *The Achievement Motive* (Appleton-Century-Crofts, New York, 1935); R. N. Haber, *J. Exptl. Psychol.* **56**, 370 (1958).
21. R. J. Andrew, *Animal Behaviour*, in press.
22. ———, in *Symp. Zool. Soc. London*, in press.
23. H. K. Dunn, *J. Acoust. Soc. Am.* **22**, 740 (1950).
24. S. L. Washburn and I. De Vore, *Viking Fund Publ. Anthropol.* **31**, 91 (1961).
25. C. R. Carpenter, *J. Comp. Psychol.* **33**, 113 (1942); K. Imanishi, *Psychologia* **1**, 47 (1957).
26. H. Kummer and F. Kurt, *Folia Primatol.* **1**, 4 (1963).


27. The work discussed here was supported by the National Institutes of Health (grant MH G5137). I am grateful to Professor D. F. Poulson for the generous facilities afforded by the Yale department of biology, and to Mrs. R. Peck for her help in observation, and for taking the photographs of Figs. 2, 4, 5, and 6. I am indebted to Dr. R. B. Klopman for Fig. 7.