Darwin's Legacy and the Study of Primate Visual Communication

FRANS B. M. DE WAAL

Living Links, Yerkes Primate Center, and Psychology Department, Emory University, Atlanta, Georgia 30322, USA

ABSTRACT: After Charles Darwin's *The Expression of the Emotions in Man and Animals,* published in 1872, we had to wait 60 years before the theme of animal expressions was picked up by another astute observer. In 1935, Nadezhda Ladygina-Kohts published a detailed comparison of the expressive behavior of a juvenile chimpanzee and of her own child. After Kohts, we had to wait until the 1960s for modern ethological analyses of primate facial and gestural communication. Again, the focus was on the chimpanzee, but ethograms on other primates appeared as well. Our understanding of the range of expressions in other primates is at present far more advanced than that in Darwin's time. A strong social component has been added: instead of focusing on the expressions per se, they are now often classified according to the social situations in which they typically occur. Initially, quantitative analyses were sequential (i.e., concerned with temporal associations between behavior patterns), and they avoided the language of emotions. I will discuss some of this early work, including my own on the communicative repertoire of the bonobo, a close relative of the chimpanzee (and ourselves). I will provide concrete examples to make the point that there is a much richer matrix of contexts possible than the common behavioral categories of aggression, sex, fear, play, and so on. Primate signaling is a form of negotiation, and previous classifications have ignored the specifics of what animals try to achieve with their exchanges. There is also increasing evidence for signal conventionalization in primates, especially the apes, in both captivity and the field. This process results in group-specific or "cultural" communication patterns.

KEYWORDS: primates; facial expressions; communication; culture; emotion

Address for correspondence: Dr. Frans B. M. de Waal, Living Links, Yerkes Primate Research Center, Emory University, 954 N. Gatewood Road, Atlanta, GA 30322. Voice: 404-727-3695 or 404-727-7898; fax: 404-727-3270.
dewaal@emory.edu

Ann. N.Y. Acad. Sci. 1000: 7–31 (2003).
doi: 10.1196/annals.1280.003

EARLY HISTORY

Charles Darwin was the first to look at human facial expressions the way, at the time, only a biologist would—namely, as a structural albeit dynamic feature of our species that can be described and catalogued in the same way as the morphology of a plant or animal. *The Expression of Emotions in Man and Animals,* which first appeared in 1872,[1] is a masterpiece of detailed analysis and insightful conjecture. One of Darwin's main objectives was to show how human facial expressions (a) constitute a shared heritage of our species; (b) have parallels with the expressions of other animals, such as dogs, cats, and primates; and hence (c) provide one more argument—a behavioral one—for evolutionary continuity. Humans may express happiness differently than dogs; but all humans do it one way, and all dogs another way, indicating that the expression of emotions is a species-typical trait.

I will not explore this argument here in relation to the human face (see Ekman[2] for a review of the debate surrounding the universality of human facial expressions), but I do wish to stress how Darwin was an ethologist before the name even existed, giving us in human facial expressions a powerful example of what German ethologists later came to call an *Erbkoordination*. In its English translation, this concept lost the *Erb* part (i.e., "inherited") and gained in rigidity as it became known as fixed action pattern, or FAP. The central idea of the FAP is that in the same way that each species is characterized by structural features (e.g., wings, ears, digestive system), each is also endowed with stereotypical motor patterns. The insight of ethologists was that the FAP, since it occurs in recognizable form in all members of a species, must have been subject to the same laws of natural selection as any other trait.[3,4] This means that we are permitted to apply the concept of *homology* to the FAP's of different species, hence that we can trace their evolutionary origin (see below). It also implies that we can look at FAP's as adaptations—that is, assume that they have been selected for a purpose. In the case of facial expressions the obvious assumed function is visual communication: the face is the most conspicuous part of the body during face-to-face interaction.

This went further than what Darwin had proposed,[1] but Darwin's strength was that he had picked the one feature of human behavior that seems to fit most or all of the above conceptualizations. In fact, facial expressions fit the mold of inborn behavior far better than many of the behaviors now discussed as such in evolutionary psychology, such as maternal care or rape—not that these patterns cannot have a genetic component; but they are highly flexible, and their occurrence varies with learning and environment. As such, they are far removed from the complex facial muscle coordination and vocalizations, such as laughing and crying, that appear early in life and are remarkably uniform across individual humans and cultures. But not only did Darwin pick a prime candidate of innate behavior, he also recognized and carefully documented the similarity of our own facial movements with those of other pri-

mates. He suggested that of all human facial displays only blushing may be unique.

After Darwin we had to wait a long time until another scientist took up the baton of primate facial expressions. The one who did, Nadezhda Ladygina-Kohts, is little known in the US due to her having written in German, French, and most of all her native Russian. Kohts's comparison between a juvenile chimpanzee and her own son, first published in 1935, has only recently been translated into English.[5] This richly illustrated book reveals a wealth of insight into the emotional significance of primate facial expressions along with modern-sounding cognitive reflections on imitation, self-awareness, tool use, and other topics that have become fashionable only over the last few decades. It was Robert Yerkes who first drew attention to Kohts's pioneering research by reproducing excerpts and illustrations from her work in *The Great Apes*.[6]

Comparative descriptions along the lines of Darwin, but conducted in far greater detail and with a wider range of species, first reappeared in the literature with the studies of Jan van Hooff.[7,8] To illustrate the depth to which van Hooff went in cataloguing displays in an objective fashion, here is a description of the pigtail monkey's "protruded-lips face." Note the purely descriptive terminology: as an ethologist, van Hooff was careful to describe first, before assessing the possible motivation and function of a particular display:

> When a female pigtail monkey is in heat, a male which has access to this female may frequently show a most peculiar response. During the period the male may repeatedly smell at the genital region of the female, which bears large swellings. It then shows a facial posture which is mainly characterized by a protrusion of the lips. The upper lip moreover is slightly curled upwards and the lower lip is pressed against it tightly. The smelling may last a few seconds; after the male lifts its head and with the face directed slightly upwards and the eyes gazing up in an undirected way, it maintains the facial posture for a short time. In a number of cases copulation follows [pp. 56,57].[8]

Van Hooff (1967) brought to bear the concepts of ethology on facial expressions by speculating about their causal underpinnings as deduced from concomitant behavior.[8] He also tried to trace their phylogeny from its distribution over the taxonomic tree. Thus, he speculated about the origin of facial displays (e.g., lip-smacking may derive from the consumption of particles picked up during grooming) and the conflicting tendencies underlying compound displays, such as teeth-chattering, which may reflect a mixture of lip-smacking (associated with forward tendencies) and teeth-baring (associated with withdrawal in many species). Van Hooff also posited that displays that grade into each other may nevertheless have separate evolutionary origins, such as the human laugh and smile. Van Hooff's work still stands as the most comprehensive and insightful comparative analysis of nonhuman and human primate facial displays since Darwin.

Van Hooff's study was followed by Goodall's fine ethogram of wild chimpanzee behavior[9] and several reviews of primate facial expressions.[10–12] Un-

fortunately, some of these publications employed a rather vague or interpretative terminology. Thus, one publication labeled a certain facial expression "the threat display," which ignored that primates show a great variety of threat faces and that even the macaques studied possess more than one such display (Section 3a).[12] This author also upheld the unfortunate common name of "grimace," or "fear grimace," for what had been termed the "silent bared-teeth display."[8] According to my dictionary, a grimace is a sharp contortion of the face, hence a term that does not even begin to define the facial configuration involved. Imprecise terminology obscures the morphology that is the staple of any phylogenetic approach.

The modern study of the human face, which was initiated at around the same time as the above work, adopted from van Hooff and other ethologists the sensible habit of a strictly neutral terminology. In terms of descriptive detail, the nonhuman primate studies, which had been ahead until the 1970s, were soon left behind, however. The facial action coding system (FACS)[13] provided a more systematic muscle-by-muscle evaluation of the face. In defense of primatologists, however, it must be added that FACS requires high-quality photography of facial movements, which in naturally behaving primates is quite a bit harder to obtain than in people, who can be asked to sit still and look into a camera.

EVOLUTION OF SIGNALS

Homology and Ritualization

Darwin wrote perceptively about the facial expressions of nonhuman primates.[1] For example, he noted that the bared-teeth expression, shown in FIGURE 1 by a black Sulawesi macaque, occurs when the animal is pleased to be caressed. Retraction of the lips to expose both rows of teeth is indeed a relaxed, friendly expression in this species as opposed to the same expression in most other macaques, in which it signifies submission. How do we know this? Quantitative analysis of natural social interaction sequences among Sulawesi macaques demonstrates that the bared-teeth display predicts the onset of affinitive contact between sender and addressee, hence that it likely is associated with a positive social attitude.[14] In these macaques, teeth-baring often occurs mutually between individuals. In the better known rhesus macaque, in contrast, teeth-baring is given exclusively by subordinate to dominant individuals—hence never mutually—and is a common response to threats and intimidations (FIG. 2).[15] The colloquial term "fear grimace" for all teeth-baring expressions derives from the familiarity of researchers with the rhesus monkey—the most common laboratory primate in the West—rather than from a comprehensive look at the primate order, in which this expression has a variety of meanings.

FIGURE 1. Darwin's *The Expression of the Emotions in Man and Animals*[1] included this gravure (p. 135) of a black Sulawesi macaque, a species in which the silent bared-teeth face indeed has the affectionate meaning claimed by Darwin's sources.

It should be pointed out that the fact that identical expressions in related species may carry different meanings is never an argument against evolutionary continuity. In evolution, motivational and functional "recasting" of traits is not unusual. We apply the concept of *homology* when similar traits of different species can be traced to their common ancestor (i.e., are present in both lineages going back all the way to the ancestral type). It is not at all unusual for homologous traits to vary in function, such as in the case of a bird's wing and the human arm. Both derive from the forelimb of the common ancestor between birds and mammals, yet wings and arms serve different functions. Shared ancestry is contrasted with analogy, or convergence, when similar traits (e.g., the fish-like shape of a dolphin) are considered independent products of similar evolutionary pressures. Preuschoft and van Hooff[16] provide guidelines for the distinction between homology and analogy in relation to facial expressions.

Ritualization is another common concept used in relation to the evolution of communication. This term refers to the "evolutionary transformation of

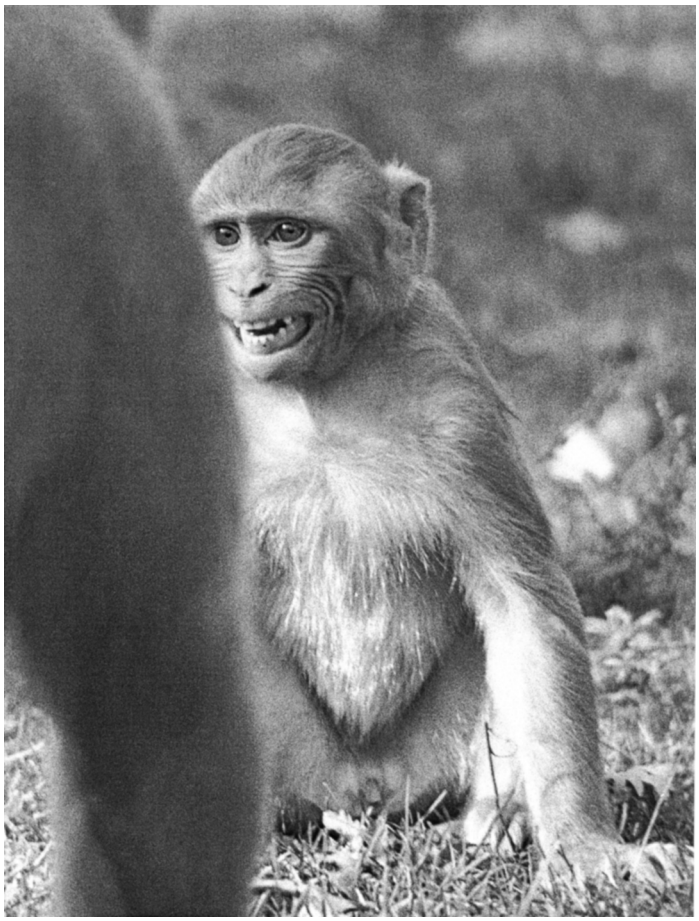

FIGURE 2. In contrast to the Sulawesi macaque (FIG. 1), rhesus monkeys employ the silent bared-teeth face as a signal of submission. Here a juvenile reacts with the display to an approaching dominant male. (Photograph by Frans de Waal.)

nondisplay behavior into display behavior."[17] This means that evolution "takes" a normal instrumental act, such as the wiping action against a branch with which many birds clean their bills, and turns this simple act into a signal by exaggerating the movement, giving it a typical form and intensity, and repeating or emphasizing it. All of this occurs, we presume, to enhance the signal value of the behavior by making it more conspicuous and recognizable. Ethology has documented numerous examples and applies the concept of ritualization to virtually every FAP related to communication. If, on the other hand, a recognizable signal develops during individual ontogeny rather than

in evolutionary time, we apply terms such as *formalization* and *conventionalization*. In humans, for example, hand-waving in greeting is often considered to be derived from times that people carried weapons and showed an empty hand before approaching a stranger. This act was turned into a signal used even when there were no weapons around. Conventionalization is a cultural process also known of nonhuman primates (discussed below in CULTURALLY LEARNED DISPLAYS).

Andrews was one of the first to speculate about the origin of ritualized facial displays, which, following in the footsteps of early of ethologists, he sought in instrumental acts termed "ancestral reflex actions."[18] Andrews speculated, for example, that frowning derives from intense attention to an object close to the face, because lowering of the eyebrows either focuses the eyes or protects them. The frown subsequently became integrated in threat displays. These first attempts at explanations of facial displays stand in contrast to Darwin's, which were often surprisingly devoid of adaptive assumptions.[19] In fact, Darwin did not always distinguish between signals as inherited characteristics or acquired habits.[1] Considering the frown, he followed an almost Lamarckian thought:

> As the effort of viewing with ease under a bright light a distant object is both difficult and irksome, and this effort has been habitually accompanied, during numberless generations, by the contraction of the eyebrows, the habit of frowning will thus have been much strengthened; although it was originally practiced during infancy from a quite different cause, namely as the first step in the protection of the eyes during screaming.[1]

Puckered eyebrows have been considered uniquely human ever since Darwin wrote that the frown may well be absent in apes.[1] He had tried to aggravate apes with an impossible, frustrating task, yet failed to get them to frown while concentrating. Only when he tickled a chimpanzee's nose with a straw did Darwin obtain a few vertical furrows between the eyebrows. Chimpanzees can and do frown at emotional moments, however; and bonobos—which have less pronounced eyebrow ridges, hence probably more flexible eyebrows—show an even stronger contraction of the *corrugators* in their so-called "tense mouth" face, in which the eyes are narrowed in a piercing expression.[20]

Laugh and Smile

Andrews also addressed the possible origin of the grin or smile, speculating that it derives from a reflex in which the teeth are bared in response to sudden, unpleasant, or noxious stimuli.[18] As an illustration, FIGURE 3 shows a baboon eating cactus with retracted lips. The spines are allowed to touch the teeth but not the vulnerable lips. This response to potentially harmful stimuli was, according to Andrews, turned into a signal by exaggerating the muscle

FIGURE 3. Ritualization refers to an evolutionary process that turns reflexes into communication signals by making them more stereotypical and conspicuous. This cactus-eating female baboon shows extreme lip retraction in reaction to noxious stimuli, the same reflex that evolution has turned into the bared-teeth display. (Photograph by Frans de Waal.)

movement and using it from a distance towards potentially harmful fellow group members. Reflexive teeth-baring thus evolved into a fearful or submissive expression.

In humans, however, the homologous expression, known as the smile, has different connotations. Not that fear is never involved (e.g., someone who smiles too much is considered nervous), yet there is also an affectionate, even happy quality to the display. It has therefore been hypothesized that smiling evolved as an indicator of cooperativeness and altruism.[21,22] In a

---

FIGURE 4. Van Hooff's scheme showing the evolution of the smile and laugh. Starting with a primitive insectivore and progressing through the primates, the scheme illustrates the variety of ways in which the silent teeth-baring display **(left side)** and the relaxed open-mouth display or play face **(right side)** differ and resemble each other in monkeys, apes, and humans. The human laugh stems from the play face. It resembles the chimpanzee play face not only visually, but also in its accompanying breathy vocalizations. The human smile stems from the silent bared-teeth face. These homologies do not necessarily imply exact overlap in meaning of the displays, however. (Reprinted from J.A.R.A.M. van Hooff[23] with permission.)

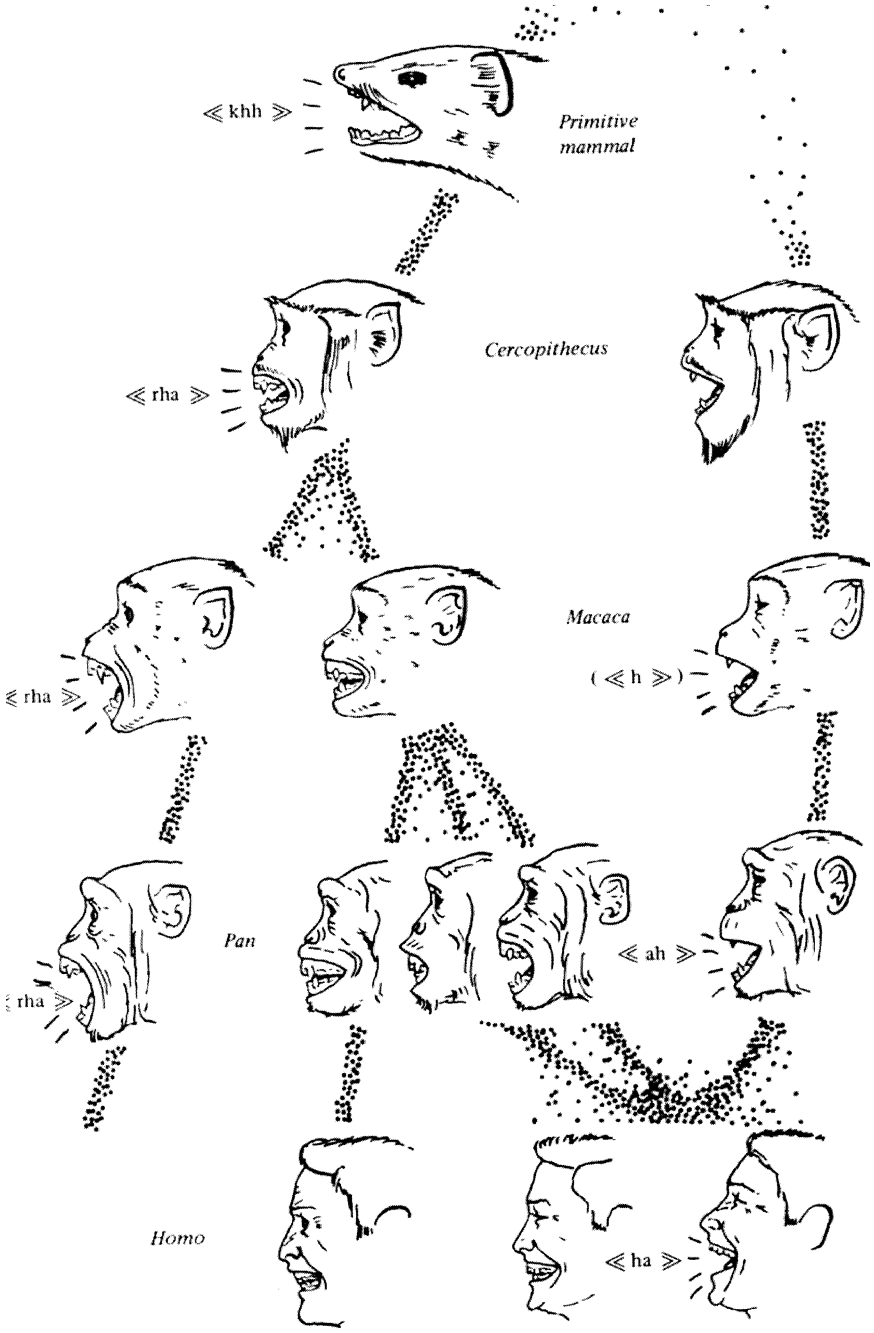

FIGURE 4. *See previous page for legend.*

phylogenetic analysis, van Hooff compared the way various primates employ the silent bared-teeth display and concluded that the appeasing and friendly qualities of the human smile are not unique.[23] In terms of appeasement. there is a clear connection with the bared-teeth display of a great variety of primates; and in terms of its friendly use, the human display connects with one of the chimpanzee's bared-teeth expressions (FIG.4). Van Hooff further proposed the "relaxed open-mouth display" of the chimpanzee and other primates as a homologue of human laughing. This expression, commonly known as the "play face," occurs especially during tickling matches and is often accompanied by sounds reminiscent of guttural, breathy human laughter.

At the time of these comparisons little was known about bonobos, inclusion of which makes an even stronger case for continuity. Bonobos—an ape species

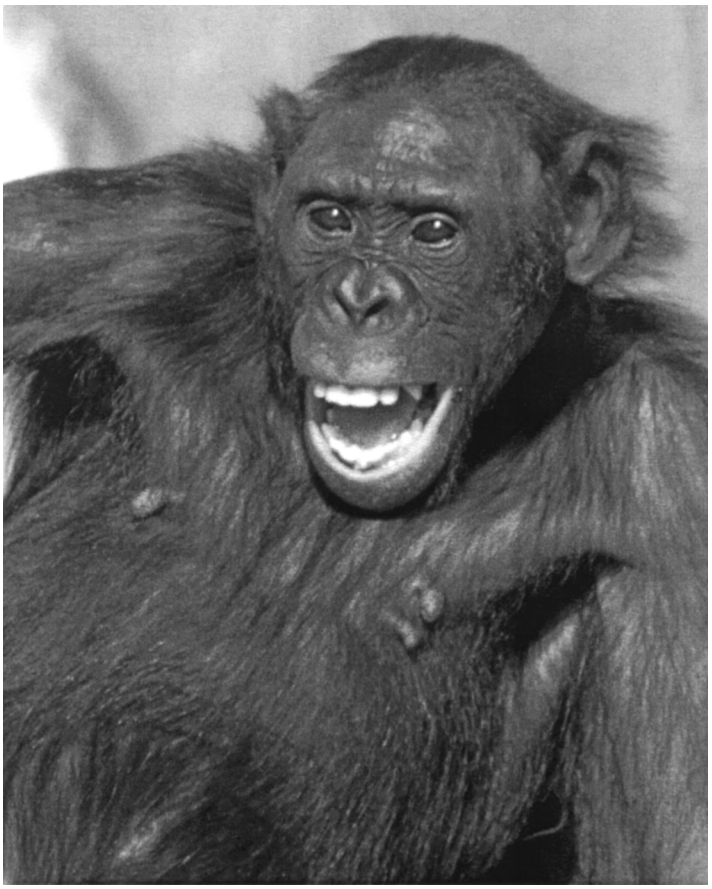

FIGURE 5. Since bonobos bare both rows of teeth in their play face, the resemblance with human laughing is even stronger than in chimpanzees, which generally bare the lower teeth only. (Photograph by Frans de Waal.)

equally close to us as the chimpanzee—frequently bare their teeth in friendly and apparently pleasurable contexts, such as in the midst of sexual intercourse.[20] One German investigator of bonobos even spoke of an *Orgasmusgesicht* (or "orgasm face").[24] The bonobo's play face, too, bears a striking resemblance to the human laugh. Whereas the chimpanzee's play face is characterized by covered upper teeth, the bonobo's often includes full teeth-baring in which the upper teeth tend to be exposed (FIG. 5). This makes the bonobo laugh look very human-like indeed, especially if it is combined with the relatively loud laughing sounds of this species.[20]

The laughing expression of apes is clearly homologous with that of our own species: the laugh derives from a widespread mammalian play expression.[25] As we have seen, however, homology does not necessarily imply that the expression functions in the same way in all hominoids (i.e., humans and apes). In bonobos and chimpanzees laughing is closely tied to play, whereas in our own species it occurs under a much wider range of circumstances. Playful interaction is obviously included and can be considered the original laughing context, but we use the same expression also in bonding (i.e., "laughing with") and, sometimes, as a hostile signal (i.e., "laughing at"). Corresponding with this functional differentiation, laughing sounds are more variable in our species than in apes (Bachorowski, this volume).[26]

Hominoid Specialties: Grading and Gesturing

Ever since Ladygina-Kohts,[5] the chimpanzee has been the standard for comparisons between human and nonhuman facial expressions. TABLE I pro-

TABLE 1. A review of chimpanzee facial expressions and vocalizations, cross-referenced to previous descriptions in the literature[27]

Expression	Other names
Bulging-lips face	glare or compressed lips face;[9] attack face[7]
Relaxed open-mouth display	play face;[9, 30–33] relaxed open-mouth display[23]
Silent bared-teeth display	grin;[7,9,12] horizontal bared-teeth expression;[8,30] bared-teeth yelp face; silent bared-teeth display[23]
Staring bared-teeth scream face	rough scream;[34] roar, growl, scream;[35] double-tone scream[36]
Stretched pout-whimper	stretch pout-whimper;[7,8,37] whimper face, hoo-whimper, pout-moan[9]
Silent pout	pout[30]
Pant-hoot	pant-hoot;[9,37] rising hoot[30]
Pant-grunt	pant-grunts;[37] panting, bobbing pants;[9] rapid oh-oh[30]
Teeth-clacking	lip smack and teeth clack;[37] lip-smacking[30]
Splutter	splutter[30]

vides a review of the 10 main facial/vocal displays of this ape and the various labels used for these in the literature.[27] These labels do not convey the richness of context in which chimpanzees communicate, the possible meaning of their signals, and how these are combined with gestures and vocalizations. For example, there is the issue of the gradedness of signals.[28,29] What is meant by gradedness is that instead of having only signal types A and B, one also observes many types in between, such as AB and BA mixtures. Whereas this certainly is relevant to primate vocalizations, I find grading even more striking in the facial expressions of the great apes. It is easy to characterize the typical "silent pout" versus a "stretched pout whimper," but we also know that these expressions frequently grade into each other. Smooth transitions between expressions are common in apes, probably reflecting underlying shifts in emotions. Grading and intensity variations in facial expressions seem more typical of apes than monkeys, such as macaques, in which the face more often seems to freeze in a mask-like display. In the hominoids the face is continuously in motion at emotionally charged moments. It should be noted, however, that the gradedness versus discreteness of facial expressions in various species has never been the subject of systematic analysis.

It is also rarely noted in the literature that free hand gestures are limited to the hominoids. This is not a mere quantitative difference with monkeys, as with respect to the grading of signals, but a qualitative one. Facial expressions and vocalizations are common means of communication in all of the primates and beyond, but, with the exception of a single gesture to be treated below, monkeys lack ritualized hand gestures. Macaques may slap the ground with a hand when threatening another or reach back to their partner during a sexual mount, but these are the limits of their manual communication.[38] Contacts with a substrate or partner do serve a signal function but involve more than the hand. Bonobos, in contrast, wave at each other, shake their wrists when impatient, beg for food with open hand held out, flex their fingers towards themselves when inviting contact, move an arm over a subordinate in a dominance-gesture, and so on (FIG. 6). They even gesture with their feet.[20]

Like facial expressions, the free hand gestures of apes are ritualized—that is, they are stereotypical, exaggerated, and tied to specific contexts. The begging gesture, which is also universal in humans, most likely derives from a cupped hand held under the mouth of a food possessor. The origin of this gesture is visible in the only ritualized monkey gesture known to me, which is hand-cupping by capuchin monkeys. If one monkey possesses food, another will reach out a hand and hold it under the possessor's chin so as to catch dropping morsels. This seems an instrumental act, but the same gesture can also be given from a distance—for example, when two capuchin monkeys are separated by mesh and one is consuming food, as in our food-sharing experiments.[39] In those instances, the gesture is used as a distant signal, divorced from its instrumental function, similar to the way all of the great apes use it. An important difference remains, however, in that apes have generalized the

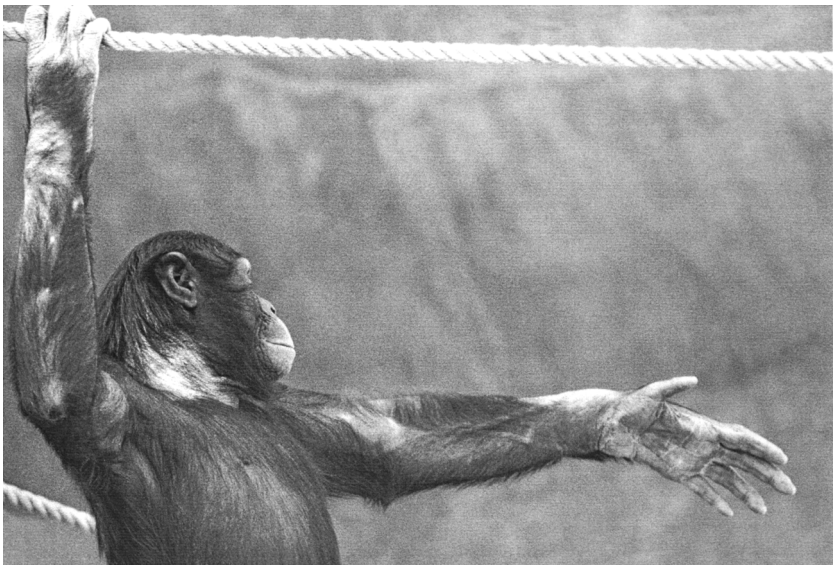

FIGURE 6. Hand gesture by a bonobo male inviting a female for sexual contact. Free hand gestures are a unique feature of ape and human communication; they are not found in the monkeys. (Photograph by Frans de Waal.)

meaning of the begging gesture to a variety of situations, whereas in capuchins the gesture is food-specific. Apes use the same begging gesture also to obtain support and help, so that in their case the precise referent needs to be read from the social context (see SIGNALS IN CONTEXT below).

Apes gesture more with the right than the left hand.[40,41] Since the right hand is left-brain controlled, this means that ape gestures share the same lateralization as human language. The highly flexible use of ritualized hand gestures, their recent appearance on the evolutionary scene (compared with other means of communication), and their culture-dependency in both humans and apes (see CULTURALLY LEARNED DISPLAYS below) should provide food for thought for any consideration of the role that gestural communication may have played in the evolution of human language.[42]

SIGNAL INTERPRETATION

Macaque Appeal-Aggression

A facial expression by itself cannot tell us if it is aggressive, fearful, or friendly. Such judgments are derived from concomitant behavior, a technique

going back to classical analyses of fish and bird behavior. To give a simple illustration of such an analysis, in an earlier study we considered the agonistic displays of longtail macaques.[43] We documented the temporal associations among 31 behavior elements, ranging from the staring open-mouth face to lip-smacking and from chasing to crouching. The reasoning behind this study was that if patterns cluster together in time, the underlying motivation and functional context will be the same. Spontaneous action sequences were analyzed to arrive at a 31×31 matrix indicating the frequency with which each behavior element occurred with every other. The observed matrix was then statistically compared with one based on random association.

One might think that in macaques the two main agonistic clusters would be aggression (e.g., forward tendencies, physical attack) on the one hand and fear or submission (e.g., withdrawal, self-protection) on the other. A third cluster was found, however, which consisted of noisy threat displays combined with behavior directed at bystanders. To distinguish such behavior from exchanges with the opponent itself, de Waal spoke of side-directed behavior.

A self-confident dominant individual will give a simple stare with gaping mouth, sometimes with a few soft grunts, which is the most common form of threat in macaques. In doing so, the dominant will concentrate its attention entirely on the opponent. This pattern was labeled *straight-aggression*. A less confident individual, on the other hand, will draw attention to its confrontations with others by grunting loudly, pointing with its chin towards the opponent, presenting its behind to potential allies, such as dominant males, and "show looking" for support from bystanders with exaggerated jerky turns of the head. This was termed *appeal-aggression*, since it could be demonstrated that this form of threat (a) increases the probability of third-party support for the performer and (b) is typical of social climbers.[44] In a dramatic illustration, an alpha male who temporarily lost his position showed appeal-aggression, which he had *never* done before, during the period in which he regained his position.[45]

Macaques thus have two distinct ways of threatening an opponent: one way serves to underline existing rank positions, whereas the other serves to claim or reclaim a certain rank by recruiting third-party support. These threat displays seem adapted for their respective purposes, given that the first type is almost silent and the second type conspicuous and noisy.

Signals in Context

As opposed to a recent claim that nonhuman primates have no parallel to positively toned human expressions and generally "lack unabashedly positive facial or vocal responses"(Ref. 22, p. 154), it should be pointed out that all of the primates have a great variety of affiliative signals, ranging from contact-

calls and lip-smacking in monkeys to copulation squeals, pouting, play faces, and laughing vocalizations in the apes. Well-documented examples of affiliative vocalizations are the chuck-calls of squirrel monkeys[46] and girney grunts of macaques.[47] Moreover, the teeth-baring expressions of some primates, such as Sulawesi macaques and bonobos, are similar both morphologically and functionally to the human smile (see LAUGH AND SMILE above). The ethograms of Goodall,[9] van Hooff,[30] and de Waal[20] should leave no doubt that expressions of affection, reassurance, and reconciliation are among the most common forms of communication in apes.

The interpretation of these signals derives from detailed sequential analyses. The first to apply such an analysis to great ape behavior was van Hooff,[30] who distinguished 60 behavior elements in the repertoire of chimpanzees. Fifty-three of these elements were analyzed so as to determine the frequency with which they occurred together. By feeding thousands of transitions into a cluster and factor analysis, the investigator arrived at a classification into what could be called seven motivational systems, such as play, excitement, affinitive, and aggressive systems. The analysis showed how extremely integrated the chimpanzee's behavioral repertoire is in that some behavior patterns occurred in a great variety of contexts. The interpretation of a behavioral system was given by behavior with extremely high loadings on the factor in question (e.g., grooming on the affinitive system).

A variant on the same analytical technique was applied in an analysis of the behavioral repertoire of the bonobo.[20] Forty-four behavior patterns were classified as to the behavioral context in which they occurred. The analysis compared the distribution over forty nonexclusive context types (e.g., object competition, play invitation, alarm) with the frequencies of these contexts in order to determine which associations significantly exceeded chance level. In this way, each behavior pattern could be contextually placed. As in the chimpanzee study,[30] the focus was on the most recognizable communication displays, thus ignoring variations and subtle gradations.

Whereas it is useful to assign behavior patterns to general motivational categories and contexts, to determine their exact meaning requires additional work. To return to the earlier example of macaque aggression, we are justified in calling both types of display "aggressive," but in fact the two distinct types are more accurately characterized as "assertive" versus "challenging." Thus, the highest ranking dominant rarely challenges anybody: he needs only to raise an eyebrow to get them to move away. Young social climbers, on the other hand, can successfully defeat others only if they have the backing of their family, which they actively recruit while challenging their opponent. Such distinctions in the meaning of facial/vocal displays are lost if we distinguish only aggression and fear. Fear responses, too, need to be broken down into a number of types, such as withdrawal and submission. These are entirely different modes of dealing with dominants. Submission may occur without any withdrawal or flight responses at all: some animals, such as chimpanzees

and wolves, commonly express submission during actual approaches by subordinates to the dominant in a greeting ceremony.[48]

Analyses of the specific meaning of communication signals are rare, perhaps because there is no single method that can address all possible meanings. Each specific behavior requires a different approach. For example, monkey alarm calls require one methodology (Seyfarth & Cheney, this volume), recruitment screams another,[49] and contact calls yet another.[50] Different approaches are required because alarm calls deal with predators, recruitment screams are sensitive to immediate social context, and contact calls vary with the presence or absence of kin and other associates. One cannot apply a single paradigm to all of these vocalizations. Facial expresssion research is different, again, in that it requires visual presentation: one cannot do a play-back experiment as is done with calls from concealed speakers. The most controlled studies on the perception of facial stimuli and their emotional evaluation is the work by Parr (this volume).

The situation becomes even more complex if one particular signal may have multiple meanings dependent on the context. For example, a monkey may present its anogenital region so as to attract a sexual partner, but it may do the same during a reconciliation, leading to a hold-bottom or mount with the former opponent.[51] The same gesture may also be used to secure support, as with baboons, in which a female appeases a dominant male while threatening her opponent.[52] Context dependency is even more striking in the gestural communication of apes. The begging gesture, for example, has absolutely no meaning unless one can deduce its referent from the context. Obviously, if the gesture is directed at a food possessor, we assume that it relates to food; but chimpanzees also use the begging gesture as a side-directed behavior (i.e., directed at bystanders during a confrontation with another). Here the begging seems to serve recruitment of support. In a detailed video analysis of agonistic encounters, most side-directed behavior was aimed at individuals likely to support the performer, yet a few kinds are specifically directed at likely allies and protectors of the opponent. These patterns, such as kissing and embracing, probably are appeasement attempts serving to prevent disadvantageous interventions.[53]

To conclusively prove such functions is a difficult task, but I hope that the above makes it clear that the meaning of signals is incompletely captured by the general labels common in the literature, such as "aggressive" or "affinitive." Communication is a complex interplay between senders and receivers, each with their own goals and agendas. The early ethologists employed a rather mechanistic terminology that never captured this interplay and the flexible usage of sometimes-conflicting strategies. Monkeys and apes operate within a larger social context, staying in tune with multiple partners at once. To view communication as negotiation between sender and receiver about potential outcomes may prove to be a more fruitful framework than to view it in terms of general motivations and functions.[54–56]

Deictic Signals: Pointing

With regards to intentional signaling, a special place is often assigned to pointing, defined as the drawing of attention of another party to a distant object by locating it for the other in space. Given that there is no point to pointing unless one understands that the other has not seen what you have seen, "deictic" gestures, as they are known, are customarily linked to intersubjectivity and theory of mind. As a result, such gestures are sometimes considered uniquely human.[57,58]

In considering the evidence for ape pointing, the first step is to move away from anthropocentric definitions, such as the one requiring an outstretched index finger. The fact that some animals don't have arms and hands, let alone fingers, is no reason to declare a priori that pointing is beyond their abilities. We should take a broad view, one that includes whole-body points as noted in a classic study with juvenile chimpanzees.[59] The investigator would take one of the juveniles with him to hide food or a frightening object, such as a toy snake, in the grass of a large outdoor area. When the entire group was released, the others quickly understood the nature of the hidden object (attractive versus aversive) and its approximate location by watching the "knower's" body language, such as, visual orientation and posture.

A number of experiments support the view that our closest relatives, the great apes, have mastered referential signaling. For this, the hand-point has been investigated, not because it is the most natural way for apes to point, but because apes readily learn that this gesture activates humans. Investigators tested captive chimpanzees who had extensive experience with people walking, making it natural for the apes to have learned how to draw attention to items they want, such as a piece of fruit that has dropped out of their cage. Do the apes spontaneously attract attention to out-of-reach food?[60,61]

It turns out that the majority of chimpanzees will gesture to the human experimenter. They will point with the whole hand at the banana outside of their cage, and a few even point with an index finger. No one ever explicitly trained these apes to do so, and there are clear signs that they monitor the effect in exactly the same way that has been used to define intentional pointing in children. The ape first makes eye contact with the human, then points while alternating its gaze between the food and the human. One chimpanzee pointed manually at the banana and then with a finger at her mouth!

One possible criticism is that without a single exception these apes are familiar with human behavior. Would they ever have developed pointing in the absence of a species that itself points all the time and responds to it? There are two pertinent reports. One concerns my own multiple observations of more than two decades ago about how female chimpanzees may enlist the support of a male against a rival if the male has not been involved from the start, hence does not know who the opponent is in the melee of a confronta-

tion. On such occasions, the aggressor may indicate her opponent by pointing her out to her male ally.[62]

The other report is the only one on wild apes. It concerns bonobos in dense forest that alerted their mates to hidden scientists (Ref. 63, p. 289):

> February 24th, 1989, 13:09 h. Noises are heard coming from the vegetation. A young male swings from a branch and leaps into a tree which is some 5 m away. He sits in a fork of the tree 10 m off the ground. He emits sharp calls, which are answered by other individuals who are not visible. He points—with his right arm stretched out and his hand half closed except for his index and ring fingers —to the position of the two groups of camouflaged observers who are in the undergrowth (30 m apart). At the same time he screams and turns his head to where the other members of the group are.
>
> 13:12 h. The same individual repeats the pointing and calling sequence twice. Other neighboring members of the group approach. They look towards the observers. The young male joins them.

The context of these instances of pointing strongly suggests awareness of the lack of knowledge of others (the apes pointed at objects hidden from view or hard to discern), and the behavior was accompanied by visual checking of its effects. Also, the pointing disappeared once the recipient had looked or walked in the indicated direction. Many of the same elements are present in the best controlled study of ape referential pointing with a female chimpanzee, who spontaneously and after long time intervals pointed out hidden food to humans with access to the hiding locations outside of the ape's cage. The humans did not know where the food was—they often were not even aware that food had been hidden—hence had to follow the ape's detailed instructions.[64]

CULTURALLY LEARNED DISPLAYS

Expressions of emotions appear in every member of a species in similar or identical form even if opportunities for learning have been scant. As a parallel to deaf and blind children who, despite a lack of or very limited learning opportunities, exhibit all the human facial expressions in emotionally appropriate contexts,[65] a deaf female chimpanzee at the Arnhem Zoo seemed to utter all of the varied calls of her species in the right context.[62]

It is often assumed, therefore, that the production of communication signals is little affected by learning (but see Ref. 66). The correct reading and interpretation of signals, on the other hand, seems open to many environmental influences. For example, responsiveness to communication signals varies with exposure to species-typical stimuli and opportunities for associative learning;[67] the appropriate response to vervet monkey alarm calls by juveniles of the species increases with age and experience.[68]

To the general rule that the production of communication displays is less influenced by learning than their appraisal, one important exception exists, however: the culturally transmitted communication displays of the great apes—that is, displays that individuals learn from each other. Whereas Tomasello *et al.* have argued against this possibility—"… imitative learning is not a major factor in the acquisition of new behaviors by chimpanzees" (Ref. 69, p. 153)—the same chimpanzee colony studied by these authors has yielded a prime example of a culturally transmitted gesture. The spread of hand-clasp grooming was followed among the chimpanzees at the Yerkes Primate Center Field Station, starting with interactions that invariably involved the same adult female.[70] Hand-clasp grooming, which is also known of a few wild chimpanzee communities,[71] occurs when two chimpanzees mutually groom each other, while one of the two takes the hand of another, lifting both of their hands high into the air. They thus sit in a perfectly symmetrical A-frame posture, each with its free hand grooming the pit of the other's lifted arm. This remarkable gesture may promote grooming reciprocity. At Yerkes, it took about one decade for the grooming hand-clasp to spread from the one female who originated it to all of the adults in the colony. The behavior ended up being commonly performed without this female's involvement, including after her temporary removal from the group.

The result of transmission through learning is that a group may develop a set of communication displays shared by all of its members but distinct from displays common in other groups. Thus, hand-clasp grooming has never been reported for any captive chimpanzee group other than the one at Yerkes. The same applies to a ritual typical of the bonobos at the San Diego Zoo, which during grooming customarily clap their hands or feet together, or tap their chests with their hands. One bonobo will sit down in front of another, clap her hands a couple of times, then start grooming the other's face in alternation with more hand-clapping. This makes the San Diego Zoo the only place in the world where one can actually *hear* apes groom. When new individuals were introduced, they picked up the habit in about two years.[72]

The same bonobos show a facial expression that may be unique for this group—it has never been reported for any other group, captive or wild, making it perhaps the only documented case of a learned facial expression in nonhuman primates. The bonobos' "duck face" is described as follows: "The lips are flattened at the mouth-corners over a greater length than in the pout face, creating a semblance to a duck bill. At the front the lips are not curled outward to the extent as in the pout face, leaving a smaller opening. No vocalizations occur with the display" (Ref. 20, p. 196). The duck face typically occurs during grooming bouts, in both groomers and groomees (FIG. 7).

Other examples of group-specific communication derive from a comparison of vocalizations across several zoo groups of chimpanzees[73] as well as from field studies on chimpanzees across Africa.[74] The latter report, while emphasizing tool use, includes several communication displays such as leaf-

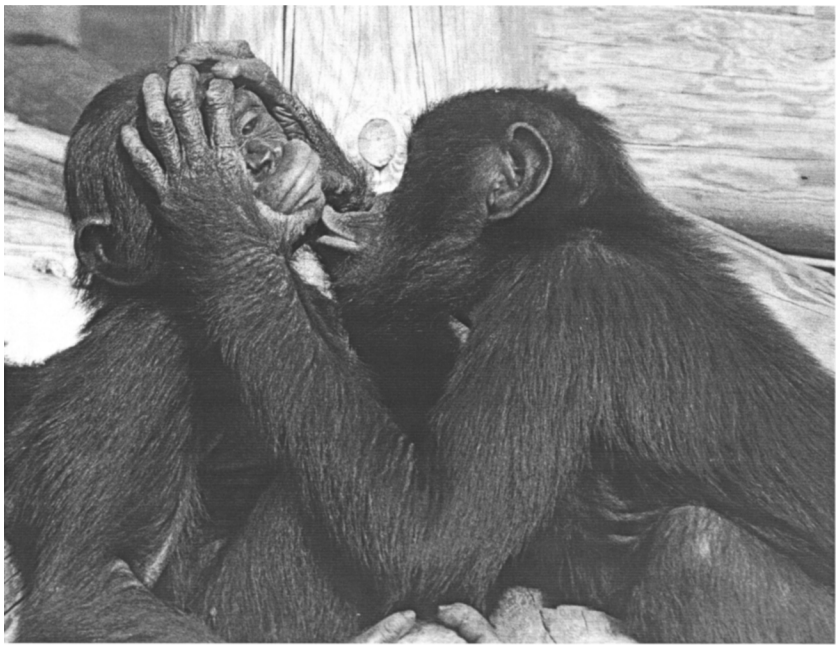

FIGURE 7. One bonobo grooming another shows the duck face, an expression known only of the colony at the San Diego Zoo. This facial expression is conventionalized, meaning that it is socially transmitted, hence a cultural feature of this one group of apes. The duck face has never been reported for any other bonobos, captive or wild. Conventionalization is prominent in ape communication. (Photograph by Frans de Waal.)

clipping in courtship, the rain dance, and the aforementioned hand-clasp grooming. Recently, yet another custom was reported for wild chimpanzees, the so-called "social scratch." In this gesture, one individual rakes the hand back and forth across the body of another, usually scratching the other with the nails. It seems the typical "you scratch my back, I'll scratch yours" gesture; yet however familiar this sounds, in wild chimpanzees the social scratch is limited to a single community.[75]

Cultural communication patterns tend to be nonfacial and nonvocal. This is perhaps due to the apes' limited control over face and voice. Not that apes have absolutely no control over their facial musculature. I have documented games in bonobos that involve the repeated pulling of novel, strange faces, and described a range of deceptive tactics in chimpanzees.[62,72,76] These cases include giving false expressions or suppressing expressions when they certainly would be expected (Ekman, this volume, discusses human examples). A recent comparison of anecdotes of deception confirms that the examples are more numerous and more striking for apes than for monkeys.[77] Control over the face seems present, therefore; yet is probably incomplete at emotion-

TABLE 2. Domains of visual communication in which our closest relatives, the anthropoid apes, may differ from monkeys, suggesting that these characteristics developed recently in the primate order or only in the hominoid lineage

Domain	Apes	Monkeys
Graded signals	expressions A and B grade into each other through intermediates; the face is continuously in motion	expressions are relatively discrete
Free-hand gestures	ritualized manual gestures with free hand are common	absent
Deictic communication	intentionally directing the attention of another to the environment while monitoring the effect on the other (e.g., pointing)	absent
Conventionalized signals	certain signals spread socially; hence these signals vary across groups of the same species	rare or absent
Contextually defined meaning	the meaning of signals needs to be extracted from their specific context	less common
Emotional control	ability to suppress, modify, or call forth visual displays, such as for deceptive purposes	rare or absent

ally charged moments. This may explain why in both humans' and apes' facial expressions are less culturally variable than manual gestures.

It is perhaps due to this bias that no good examples of culturally transmitted communication exists for monkeys: one of the absolute differences between monkey and ape visual communication is the absence of free-hand gestures in monkeys (see HOMINOID SPECIALTIES: GRADING AND GESTURING above). Such differences need to be explored further, since patterns unique to apes likely tell us something about what set the visual communication of our ancestors apart. Hypothetical differences between monkey and ape communication are summarized in TABLE 2. Characteristics that we share with apes but not monkeys likely evolved recently; hence they may have provided a basis for the development of even more unique patterns, found only in humans, such as symbolic signaling.

REFERENCES

1. DARWIN, C. 1998. The Expression of the Emotions in Man and Animals, 3rd edit. P. Ekman, Ed. Oxford University Press. New York.
2. EKMAN, P. 1998. Afterword: universality of emotional expression? A personal history of the dispute. *In* The Expression of the Emotions in Man and Animals, 3rd edit. P. Ekman, Ed.: 363–393. Oxford University Press. New York.

3. TINBERGEN, N. 1953. Social Behavior in Animals. Chapman & Hall. London.
4. LORENZ, K.Z. 1981. The Foundations of Ethology. Touchstone. New York.
5. LADYGINA-KOHTS, N.N. 2002. Comparative study of ape emotions and intelligence. *In* Infant Chimpanzee and Human Child: A Classic. F.B.M. de Waal, Ed. Oxford University Press. Oxford.
6. YERKES, R.M. & A.W. YERKES. 1929. The Great Apes: A Study of Anthropoid Life. Yale University Press. New Haven, CT.
7. VAN HOOFF, J.A.R.A.M. 1962. Facial expressions in higher primates. Symp. Zool. Soc. London **8:** 97–125.
8. VAN HOOFF, J.A.R.A.M. 1967. The facial displays of the Catarrhine monkeys and apes. *In* Primate Ethology. D. Morris, Ed.: 7–68. Aldine. Chicago.
9. GOODALL, J. & H. VAN LAWICK. 1968. The behaviour of free-living chimpanzees in the Gombe Stream Reserve. Anim. Behav. Monogr. **1:** 161–311.
10. CHEVALIER-SKOLNIKOFF, S. 1973. Facial expression of emotion in nonhuman primates. *In* Darwin and Facial Expressions. P. Ekman, Ed.: 11–90. Academic Press. New York.
11. REDICAN, W.K. 1975. Facial expressions in nonhuman primates. *In* Primate Behavior. L.A. Rosenblum, Ed.: 103–194. Academic Press. New York.
12. REDICAN, W.K. 1982. An evolutionary perspective on human facial displays. *In* Emotion in the Human Face. P. Ekman, Ed.: 212–280. Cambridge University Press. Cambridge.
13. EKMAN, P. & W.V. FRIESEN. 1978. The Facial Action Coding System. Consulting Psychologists Press. Palo Alto, CA.
14. PREUSCHOFT, S. 1995. 'Laughter' and 'Smiling' in Macaques: An Evolutionary Approach. Unpublished Thesis of the University of Utrecht. Utrecht.
15. DE WAAL, F.B.M. & L.M. LUTTRELL. 1985. The formal hierarchy of rhesus monkeys: an investigation of the bared-teeth display. Am. J. Primatol. **9:** 73–85.
16. PREUSCHOFT, S. & J.A.R.A.M. VAN HOOFF. 1995. Homologizing primate facial displays: a critical review of methods. Folia Primatol. **65:** 121–137.
17. IMMELMANN, K. & C. BEER. 1989. A Dictionary of Ethology. Harvard University Press. Cambridge, MA.
18. ANDREW, R.J. 1965. The origins of facial expressions. Sci. Am. **213:** 88–94.
19. FRIDLUND, A.J. 1994. Human Facial Expressions: An Evolutionary View. Academic Press. San Diego, CA.
20. DE WAAL, F.B.M. 1988. The communicative repertoire of captive bonobos (Pan paniscus), compared to that of chimpanzees. Behaviour **106:** 183–251.
21. SCHMIDT, K.L. & J.F. COHN. 2001. Human facial expressions as adaptations: evolutionary questions in facial expression research. Yearb. Phys. Anthropol. **44:** 3–24.
22. OWREN, M.J. & J.-A. BACHOROWSKI. 2001. The evolution of emotional expression: a "selfish gene" account of smiling and laughter in early hominids and humans. *In* Emotions: Current Issues and Future Directions. T.J. Mayne & G.A. Bonanno, Eds.: 152–191. Guilford Press. New York.
23. VAN HOOFF, J.A.R.A.M. 1972. A comparative approach to the phylogeny of laughter and smiling. *In* Non-verbal Communication. R. Hinde, Ed.: 209–241. Cambridge University Press. Cambridge.
24. BECKER, C. 1984. Orang-Utans und Bonobos im Spiel. Profil Verlag. Munich.
25. FAGAN, R. 1981. Animal Play Behavior. Oxford University Press. New York.

26. BACHOROWSKI, J.-A., M. J. SMOSKI & M. J. OWREN. The acoustic features of human laughter. J. Acoust. Soc. Am. In press.
27. PARR, L.A., S. PREUSCHOFT & F.B.M. DE WAAL. 2002. Afterword: research on facial emotion in chimpanzees, 75 years since Kohts. *In* Infant Chimpanzee and Human Child. F.B.M. de Waal, Ed.: 411–452. Oxford University Press. Oxford.
28. ROWELL, T.E. 1962. Agonistic noises of the rhesus monkey. Symp. Zool. Soc. London **8:** 91–96.
29. MARLER, P. 1976. Social organization, communication and graded signals: the chimpanzee and the gorilla. *In* Growing Points in Ethology. P.P. Bateson & R. A. Hinde, Eds.: 239–279. Cambridge University Press. London.
30. VAN HOOFF, J.A.R.A.M. 1973. A structural analysis of the social behaviour of a semi-captive group of chimpanzees. In Expressive Movement and Non-verbal Communication. M. von Cranach & I. Vine, Eds.: 75–162. Academic Press. London.
31. ANDREW, R.J. 1963. The origin and evolution of the calls and facial expressions of the primates. Behaviour **20:** 1–109.
32. ANDREW, R.J. 1963. Evolution of facial expression. Science **142:** 1034–1041.
33. BOLWIG, N. 1962. Facial expression in primates with remarks on a parallel development in certain carnivores. Behaviour **22:** 167–192.
34. MARLER, P. 1969. Vocalizations of wild chimpanzees: an introduction. *In* Proceedings of the Second International Congress of Primatology. C.R. Carpenter, Ed.: 94–100. Karger. Basel.
35. REYNOLDS, V. & F. REYNOLDS. 1965. Chimpanzees of the Budongo Forest. *In* Primate Behavior. I. De Vore, Ed.: 368–424. Holt, Rhinehart, & Winston. New York.
36. YERKES, R.M. & B. LEARNED. 1925. Chimpanzee Intelligence and Its Vocal Expressions. Williams & Wilkins. Baltimore, MD.
37. MARLER, P. & R. TENAZA. 1976. Signaling behavior of apes with special reference to vocalization. *In* How Animals Communicate. T. Sebeok, Ed.: 965–1033. Indiana University Press. Bloomington, IN.
38. ALTMANN, S.A. 1962. A field study of the sociobiology of rhesus monkeys, *Macaca mulatta*. Ann. N.Y. Acad. Sci. **102:** 338–435.
39. DE WAAL, F.B.M. 1997. Food-transfers through mesh in brown capuchins. J. Comp. Psychol. **111:** 370–378.
40. HOPKINS, W.D. & F.B.M. DE WAAL. 1995. Behavioral laterality in captive bonobos (Pan paniscus): replication and extension. Int. J. Primatol. **16:** 261–276.
41. HOPKINS, W.D. & R.D. MORRIS. 1993. Handedness in great apes: a review of findings. Int. J. Primatol. **14:** 1–25.
42. CORBALLIS, M.C. 2002. From Hand to Mouth: The Origins of Language. Princeton University Press. Princeton, NJ.
43. DE WAAL, F.B.M. 1976. Straight-aggression and appeal-aggression in Macaca fascicularis. Experientia **32:** 1268–1270.
44. DE WAAL, F.B.M. 1977. The organization of agonistic relations within two captive groups of Java-monkeys (Macaca fascicularis). Z. Tierpsychol. **44:** 225–282.
45. DE WAAL, F.B.M. 1975. The wounded leader: a spontaneous temporary change in the structure of agonistic relations among captive Java-monkeys (Macaca fascicularis). Neth. J. Zool. **25:** 529–549.

46. SMITH, H.J., J.D. NEWMAN & D. SYMMES. 1982. Vocal concomitants of affiliative behavior in squirrel monkeys. *In* Primate Communication. C.T. Snowdon, C.H. Brown & M.R. Peterson, Eds.: 30–49. Cambridge University Press. Cambridge.
47. GREEN, S. 1975. Variation of vocal pattern with social situation in the Japanese monkey (Macaca fuscata): a field study. *In* Primate Behavior: Developments in Field and Laboratory Research, Vol. 4. L.A. Rosenblum, Ed.: 1–102. Academic Press. New York.
48. DE WAAL, F.B.M. 1986. Integration of dominance and social bonding in primates. Q. Rev. Biol. **61:** 459–479.
49. GOUZOULES, S., H. GOUZOULES & P. MARLER. 1984. Rhesus monkey (Macaca mulatta) screams: representational signaling in the recruitment of agonistic aid. Anim. Behav. **37:** 182–193.
50. BAUERS, K.A. & F.B.M. DE WAAL. 1991."Coo" vocalizations in stumptailed macaques: a controlled functional analysis. Behaviour **119:** 143–160.
51. DE WAAL, F.B.M. & R. REN. 1988. Comparison of the reconciliation behavior of stumptail and rhesus macaques. Ethology **78:** 129–142.
52. KUMMER, H. 1957. Soziales Verhalten einer Mantelpavian-gruppe. Huber. Bern.
53. DE WAAL, F.B.M. & J.A.R.A.M. VAN HOOFF. 1981. Side-directed communication and agonistic interactions in chimpanzees. Behaviour **77:** 164–198.
54. HINDE, R.A. 1985. Expression and negotiation. *In* The Development of Expressive Behavior: Biology-Environment Interactions. G. Zivin, Ed.: 103–116. Academic Press. Orlando, FL.
55. CHADWICK-JONES, J.K. 1991. The social contingency model and olive baboons. Int. J. Primatol. **12:** 145–161.
56. DE WAAL, F.B.M. 1996. Conflict as negotiation. *In* Great Ape Societies. W.C. McGrew, L.F. Marchant & T. Nishida, Eds.: 59–172. Cambridge University Press. Cambridge.
57. BUTTERSWORTH, G. & L. GROVER. 1988. The origins of referential communication in human infancy. *In* Thought without Language. L. Weiskrantz, Ed.: 5–24. Clarendon Press. Oxford.
58. POVINELLI, D.J. 2000. Folk Physics for Apes: The Chimpanzee's Theory of How the World Works. Oxford University Press. Oxford.
59. MENZEL, E.W. 1973. Leadership and communication in young chimpanzees. *In* Precultural Primate Behavior. E.W. Menzel, Ed.: 192–225. Karger. Basel.
60. LEAVENS, D.A. & W.D. HOPKINS. 1998. Intentional communication by chimpanzees: a cross-sectional study of the use of referential gestures. Dev. Psychol. **34:** 813–822.
61. LEAVENS, D.A. & W.D. HOPKINS. 1999. The whole-hand point: The structure and function of pointing from a comparative perspective. J. Comp. Psychol. **113:** 417–425.
62. DE WAAL, F.B.M. 1998 [1982]. Chimpanzee Politics: Power and Sex among Apes. Johns Hopkins University Press. Baltimore, MD.
63. VEÀ, J.J. & J. SABATER-PI. 1998. Spontaneous pointing behaviour in the wild pygmy chimpanzee (Pan paniscus). Folia Primatol. **69:** 289–290.
64. MENZEL, C.R. 1999. Unprompted recall and reporting of hidden objects by a chimpanzee (Pan troglodytes) after extended delays. J. Comp. Psychol. **113:** 426–434.
65. EIBL-EIBESFELDT, I. 1989. Human Ethology. Aldine. New York.

66. TAGLIALATELA, J.P., S. SAVAGE-RUMBAUGH & L.A. BAKER. 2003. Vocal production by a language-competent *Pan paniscus*. Int. J. Primatol. **24:** 1–17.
67. MASON, W.A. 1985. Experiential influences on the development of expressive behaviors in rhesus monkeys. *In* The Development of Expressive Behavior: Biology-Environment Interactions. G. Zivin, Ed.: 117–152. Academic Press. Orlando, FL.
68. CHENEY, D.L. & R.M. SEYFARTH. 1990. How Monkeys See the World. University of Chicago Press. Chicago.
69. TOMASELLO, M., J. CALL, K. NAGELL, *et al*. 1994. The learning and use of gestural signals by young chimpanzees: a trans-generational study. Primates **35:** 137–154.
70. DE WAAL, F.B.M. & M. SERES. 1997. Propagation of handclasp grooming among captive chimpanzees. Am. J. Primatol. **43:** 339–346.
71. MCGREW, W.C. & C.E.G. TUTIN. 1978. Evidence for a social custom in wild chimpanzees? Man **13:** 243–251.
72. DE WAAL, F.B.M. 1989. Peacemaking among Primates. Harvard University Press. Cambridge, MA.
73. MARSHALL, A.J., R.W. WRANGHAM & A.C. ARCADI. 1999. Does learning affect the structure of vocalizations in chimpanzees? Anim. Behav. **58:** 825–830.
74. WHITEN, A., J. GOODALL, W.C. MCGREW, *et al*. 1999. Cultures in chimpanzees. Nature **399:** 682–685.
75. NAKAMURA, M., W.C. MCGREW, L.F. MARCHANT & T. NISHIDA. 2000. Social scratch: Another custom in wild chimpanzees? Primates **41:** 237–248.
76. DE WAAL, F.B.M. 1992. Intentional deception in primates. Evol. Anthropol. 1: 86–92.
77. BYRNE, R.W. & A. WHITEN. 1990. Tactical deception in primates: the 1990 data-base. Primate Rep. **27:** 1–101.