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SOCIAL COMMUNICATION IN THE CHIMPANZEE: A REVIEW

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Both organisms and automata can respond to small changes in energy with behaviors that are excessive from a thermodynamic point of view. This triggering phenomenon is what is meant here by *communication* [WIENER, 1950]. However, communication should not be restricted to the processes by which a single organism responds to inputs from its environment. Rather, an entire hierarchy of communicative processes, and the lower members of the hierarchy should be included within the definition as well. For example, activation of a retinal receptor by a single quantum of light is communicative just as much as an organism fleeing in response to a threat gesture by a specific. The reason for employing such a broad definition is that com-

munication ceases to be an aspect of complex systems and becomes instead almost synonymous with complex systems.

By *social* communication is meant the communication that mediates between organisms. Following this cybernetic perspective, social communication is not an aspect of social behavior but rather social behavior is an outgrowth of social communication, a point stressed recently by ALTMANN [1967] and BASTIAN [1968]. The change of perspective is not trivial, for it implies that the differences between societies are due to the kinds of information that reach the brain from other organisms and the kinds of processing that occur within the brain itself.

Another usage of the triggering concept of communication which is independent of the first is the definition of social communication as the process by which one organism triggers another. If by triggering another organism is meant a change in state in the brain of the recipient, then this usage is identical with social communication as used here. If, however, triggering implies alterations in overt behavior, on the order of response to ethological releasing stimuli, then the definition is too restrictive to be of much use in discussing communication in the chimpanzee.

BASTIAN [1968] has pointed out some limitations of the concept of information in animals. He notes that if our only evidence for information transfer by a signal is the response to it by another individual, then the supposed transfer of information cannot be distinguished from social behavior, and the terminology is purely gratuitous. This criticism does not invalidate the concept of information but only of information transfer. Information is a term that can only be defined in relation to cognitive process. Information theory provides a valuable insight by defining information in terms of the reduction of uncertainty. However, defining uncertainty on the basis of *a priori* probabilities of events restricts the definition to psychologically trivial situations. It is more useful to consider information to be whatever alters an organism's 'model' of the environment. A model, in the simplest sense, is an internal representation of external events, and the habituation of the orienting reaction and sensory encoding are obvious examples. THAYER's [1967, p. 87] definition of information as data that is meaningfully related to other data is similar to this usage. Whatever alters models will be informative, although not all information will be correct or true in a predictive sense. Since the alteration of models is due to the triggering effects already mentioned, it should be clear that there is no necessary contradiction between triggering and information. Looked at from internal perspective, we are informed by changes in our receptors. From an external perspective, these changes may be triggered by external events. The

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meant the communication that mediates cybernetic perspective, social communication is but rather social behavior is an outcome stressed recently by ALTMANN [1967]. This perspective is not trivial, for it implies that there is no simple relation between the kinds of information that reach the organism and the kinds of processing that occur within the organism.

concept of communication which is based on the idea of social communication as the process by which one individual triggers another. If by triggering another organism the response of the recipient, then this usage is trivial here. If, however, triggering implies a particular order of response to ethological relations, then this usage is restrictive to be of much use in discussing social communication.

Some limitations of the concept of information theory as the only evidence for information transfer between individuals, then the supposed distinction between social behavior and the rest of behavior, and the criticism does not invalidate the concept of information transfer. Information is a term that has a wide range of meanings. Information theory, in terms of the reduction of uncertainty on the basis of *a priori* probabilities, is a concept that is psychologically trivial situations. It is a concept that is used in the simplest sense, is an internal representation of the orienting reaction and is similar to the definition of information in AYER's [1967, p. 87] definition of information. Information related to other data is similar to the concept of information, although not all information is related to other data. Since the alteration of models is mentioned, it should be clear that there is a relation between triggering and information. Models are altered by changes in our receptors. Models may be triggered by external events. The

concept of information is of importance in discussing referential signs, and it will be encountered again in the last section of the paper, where some recent studies of referential signs in the chimpanzee are reviewed.

In discussing the communication of the chimpanzee¹, or of any animal, there are innumerable ways of organizing the data. Part of the difficulty in the scientific description of social behavior is that there is still no commonly accepted taxonomy of communicative process. Some authors have organized discussions around sensory modality, others around the structural properties of sign systems, others around behavioral complexes, and most have employed some combination of these approaches. These are not competing frameworks but all have a place in understanding the communication of the chimpanzee. However, the choice of descriptive framework is not arbitrary, since our classification of phenomena is part and parcel of our interpretation of them. If social communication is classified by channel, we must be careful not to create an organism that has more in common with Bell Telephone than with social beings: there is great emphasis on the differences between long distance and local calls, on variations in rate and cost, and on maps of lines and where they go². These cautionary remarks should be kept in mind, since the channel model is one of the frameworks used here. By *channel* is meant a functional relationship between a particular type of receptor and a particular type of effector. Following SENEOK's [1965] distinctions, diagrammed in figure 1, it is necessary that there be both a source and a destination for communication to occur. In social communication, the source and destination will be different individuals. The source-destination distinction is not equivalent to the effector-receptor distinction, since communication between two individuals may involve more than one channel. Technically, receptors and effectors are neurological concepts, and I make neurological distinctions where relevant.

Specialization is another useful concept. All sense organs are specialized for communication with the external or internal environment, but a sense organ is *specialized* for social communication when it is used primarily for receiving signals from other organisms. Receptors such as this are rare in higher organisms, but they are not uncommon elsewhere. For example, the olfactory receptors of the male silkworm moth respond only to the secretions of the female [MARLER and HAMILTON, 1966, p. 271]. In the chimpanzee, there

1 Commonly two species of chimpanzees are distinguished [NAPIER and NAPIER, 1967], but *Pan troglodytes* is best known behaviorally. Since there is little comparative data available, I consider all chimpanzees as equivalent.

2 This point has been forcefully made by RAY BIRDWHISTELL in a lecture [Stanford University, February, 1969], but I know of no references that make it equally well.

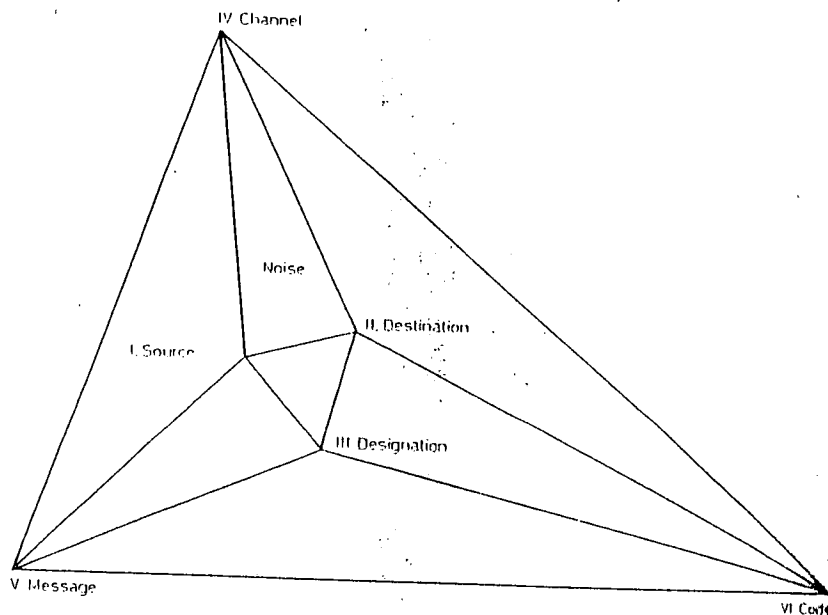
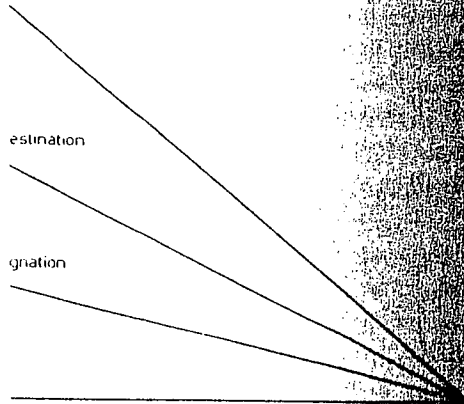


Fig. 1. A MORLEY triangle showing the relation between BÜHLER's model and an information-theoretical model of a communication network. MORLEY's theorem illustrates the relation between BÜHLER's model (the small equilateral triangle) and a more comprehensive information-theoretical model of a communication network. The encoder and decoder are often the same individual (after SEBEOK [1965]).

are no receptors specialized for social communication, although there are specialized sign systems³. A *sign system* is a system of signals specialized for social communication that employs normal input channels to the organism but whose structure is not reducible to the structure of the sensory channels that mediate it. For example, reading is not reducible to visual pattern recognition even though it presupposes the latter⁴. It is also possible to have specialized effectors. Some of the responses of the chimpanzees, such as piloerection

3 At low levels of organization, the distinction between sign systems and perception becomes meaningless. The releaser of classical ethology [HESS, 1962] might be considered to be a sign in organisms with well-developed distance receptors, but in animals with narrowly defined input and stereotypic response to it, there is little point in calling it one or the other. Even in lower vertebrates, the distinction between perception and signs is by no means obvious [LETTVIN, *et al.* 1959; BLAIR, 1968].

4 HOCKETT [1960] considered specialization to be a design-feature of sign systems, but I consider it to be a *sine-qua-non*.



relation between BÖHLER's model and an information network. MORLEY's theorem illustrates the small equilateral triangle and a more complex of a communication network. The encoder and after SEBEOK [1965]).

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distinction between sign systems and perception in classical ethology [HESS, 1962] might be possible. Well-developed distance receptors, but in a typical response to it, there is little point in calling it a sign. It illustrates the distinction between perception and sign systems [BLAIR, 1968].

and odor secretion, may belong in this category. The facial musculature has both specialized and unspecialized aspects which make it difficult to classify. The skeletal muscles are clear unspecialized effectors.

While good classifications of communication are possible using the concepts already mentioned, neurological studies indicate that different sign systems are mediated by different neural mechanisms, all of which may employ a given peripheral effector. This makes possible a new dimension of specialization – the case of specialized neural control over an effector that has remained a general-purpose device. This possibility is discussed in the last section of the paper. I will first introduce the various specialized sign systems of the chimpanzee.

THE NON-REFERENTIAL SIGN SYSTEMS

Specialized Effectors

The specialized effectors play a variable role in the total communicative world of the chimpanzee. Odors have been described for chimpanzees [VAN LAWICK-GOODALL, 1968; see also YERKES and YERKES, 1929, p. 322] that probably correspond to the odors emitted by the apocrine sweat glands of humans. In the distribution of apocrine sweat glands, chimpanzees are more similar to man than they are to lower primates [MONTAGNA and ELLIS, 1963], but little is known of their significance in either species. Specializations such as urine-marking that have been described for some other species of primates have not been reported.

Sweat glands receive autonomic innervation, and other autonomic effects have been given communicative significance by observers of chimpanzee behavior. Erection of the hair is a conspicuous feature of the emotional displays of the chimpanzees. VAN LAWICK-GOODALL [1968] notes that piloerection in feral animals occurs during courtship, aggression, in unfamiliar situations, or at meeting with other groups.

Another instance of a specialized effector is the tumescence of the sex skin. Like many Old World primates, the female chimpanzee possesses a sex skin contiguous with the external genitalia. The sex skin becomes tumescent in phase with the oestrous cycle, and it is a source of attraction to male chimpanzees. In the terminology of SCHEIN and HALE [1965], it is an *identification* sign that serves to establish that a conspecific is a suitable sexual partner. It is similar to the sexual signs of lower organisms in that it is a maturational phenomenon and highly dependent on hormone cycles, which in turn are con-

trolled by the autonomic nervous system. The tumescent female solicits sexual contact by presenting or assumes the posture in response to the advances of the male. The relationship between presenting and oestrous in the chimpanzee was first studied by YERKES and his colleagues. In one experimental design [YERKES, 1939], a male and a female chimpanzee were given access to each other for five-minute periods and their sexual behavior recorded. A total of 233 sessions were given, using three male and six female subjects. YERKES found that sexual receptivity in females occurred concurrently with genital swelling. Both male responsiveness and female receptivity were highest during maximal swelling. These data indicate that the sex skin is a good predictor of sexual receptivity, and it is not unlikely that the chimpanzee uses this information. It is of interest that inspection of a female's genitalia by a male is more likely to occur when swelling is minimal, both in captivity and the field [van LAWICK-GOODALL, 1968].

Related phenomena that cannot be classified as effectors except in a developmental sense are maturational characteristics and secondary sex characteristics. For example, juveniles have white hair in the anal regions and adults develop gray hairs. Baldness also occurs in the adults of both sexes [NAPIER and NAPIER, 1967]. While specialization of hair color and hair distribution are known to have communicative significance in other species of primates, there has been little attempt to investigate these phenomena in chimpanzees. VAN LAWICK-GOODALL [1968] notes that the white patch in infants develops about the time they begin to ride on their mother's back. Since mothers carrying their infants in this position are less likely to be attacked by males, she suggests that the white hair may serve to inhibit aggression. While the role of the specialized effectors deserves further study, the major communicative burden is borne by unspecialized effectors.

Unspecialized Effectors

The effectors in this category are the skeletal muscles, the vocal tract, and the facial musculature. The last two both have specialized aspects which must be discussed, but since they serve other functions besides communication, I have classified them as general-purpose structures. The facial musculature of the chimpanzee is well studied both anatomically and behaviorally. Anatomically, the chimpanzee is closer to man and the gorilla than to nonhominoid primates in regards to the superficial facial musculature [HUBER, 1931]. In all these species, the post-auricular musculature is reduced, leaving the ears largely

stem. The tumescent female solicits sexual posture in response to the advances of presenting and oestrous in the chimpanzee's colleagues. In one experimental design, five chimpanzees were given access to each other and their sexual behavior recorded. A total of five male and six female subjects. YERKUS males occurred concurrently with genital and female receptivity were highest during the time that the sex skin is a good predictor of the likelihood that the chimpanzee uses this information of a female's genitalia by a male is more minimal, both in captivity and the field (van

be classified as effectors except in a developmental characteristics and secondary sex characteristics: white hair in the anal regions and adult white hair occurs in the adults of both sexes [NAPIER]. The variation of hair color and hair distribution are of significance in other species of primates, therefore these phenomena in chimpanzees. VAN HOEFF the white patch in infants develops about the other's back. Since mothers carrying their infants to be attacked by males, she suggests that the major communicative burden is borne by

Specialized Effectors

skeletal muscles, the vocal tract, and the hands have specialized aspects which must be considered in their functions besides communication, I have considered their structures. The facial musculature of the chimpanzee is anatomically and behaviorally. Anatomically, the gorilla than to nonhominoid primates. The facial musculature [HUBER, 1931]. In all these cases, the musculature is reduced, leaving the ears largely

immobile. The loss of ear movements is more than compensated for by the greater refinement of the facial muscles proper, as indicated by their differentiation. DARWIN [1872] was of the opinion that some monkeys were more expressive than chimpanzees, but it is difficult to make comparisons of this kind. The fact that facial mobility evolved independently in several lines of primates [ANDREW, 1963a, 1963b] gives some support to this claim. While the facial muscles are striped muscles and under voluntary control, their association with visceral phenomena has always been close, and it is not surprising to find these muscles functioning in emotional displays. The various interactions of these muscles form points on a continuum that can be labeled as particular expressions. Several authors have attempted this for the chimpanzee, and I will briefly review their findings.

Facial Expression

VAN HOOFF [1962, 1967] has attempted a classification of facial expressions of Old World monkeys and apes on the basis of combined morphological and behavioral criteria. He has focused on the following structures: the position of the eyelids, whether the eyes are staring or looking away, whether the eyebrows are raised, lowered or neutral, whether the mouth is open or closed, whether or not the upper teeth are covered by the lips, whether the corners of the mouth are retracted vertically, horizontally, or not retracted at all, and whether the lips are protruded. To what extent these cues are 'psychologically real' for chimpanzees is still an unanswered question, but this line of investigation is a reasonable one for research to take. The work of MILLER [1967] on rhesus monkeys sets a precedent for the type of experimental design that will be needed, but the difficulties in analyzing the cues in visual communication in primates are formidable. As ALTMANN has noted, the best design is the Cheshire cat paradigm, in which the grin is presented without the cat. For these reasons, the described signs have been proved psychologically real only for human observers, but that should not be underestimated.

It is well known that eye contact is a means of initiating social encounters among all primates and staring among nonhuman primates is commonly a component of threat expressions⁵. The *staring open mouth face* as defined by VAN HOOFF [1967] is a common pattern among nonhuman primates. In macaques and baboons it is characterized by retraction of the scalp, flattening of

5 DIEBOLD [1968] presents an interesting discussion of eye contact and its implications.

the ears against the head, and raising of the eyebrows in addition to the stare and open mouth [see illustrations in ALTMANN, 1962, pp. 422-423]. The expression differs in chimpanzees by the fact that the eyebrows are often lowered in a frown and the ears are immobile. This difference illustrates one of the difficulties in the morphological classification of expression. Since eyebrow raising is done with the *frontalis* muscle and eyebrow lowering with the *depressor supercillii*, to what extent is the staring open mouth face the same expression in monkeys and apes? One solution to this problem is to use mixed criteria and employ a functional interpretation as an additional check. Since this expression is interpreted as a threat in macaques and baboons, one can ask whether it serves a similar function in chimpanzees. VAN HOOFF's [1967, pp. 23-24] remarks are worth quoting in full:

The opponent may react with different expressions, but frequently seen are fleeing and avoiding. This leads to the conclusion that this compound on the average expresses a probably dominant tendency to attack, thwarted by the tendency to flee. For this reason the compound was termed the *aggressive threat face* by VAN HOOFF [1962]. This does not mean that other tendencies may not be activated. Thus chimpanzees may show this display directed to a partner, while jumping on the spot on all fours; hands and feet beat the floor with force. This particular display, which has been observed especially during a number of introduction tests where it was directed towards the newcomer, might alternate with different behavior patterns: for instance, a fast run past the fellow, during which the animal is hit or kicked with force; flight or avoidance; smooth approach resulting in investigation, grooming, embrace, etc.; gnaw-wrestling accompanied by the *relaxed open-mouth face* (see below). Here, apart from the tendency to attack and to flee, a tendency to approach (smoothly), resulting in positive social behaviour patterns such as grooming, huddling, mating, or simply being close together (for short, termed '*social attraction*') may express itself.

VAN LAWICK-GOODALL [1968, p. 318] classifies the staring open mouth face under aggressive behavior but notes that the staring closed mouth face may occur prior to chase, attack, and copulation. The difficulties encountered by VAN HOOFF in classifying this particular facial expression in terms of function are not atypical, and it should be clear that morphological definitions of chimpanzee signs do not imply a one-to-one relationship between sign and response. For convenience of presentation the morphological framework is followed here as closely as possible, and in a later section I will try to remedy some of the distortion that this convenience introduces.

In expressions with baring of the teeth, different authors make different classifications. VAN HOOFF [1967] distinguishes between a frowning bared teeth face and a staring bared teeth face, both of which occur with screams. In the frowning version the eyes are closed or nearly so. In both the upper lips

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of the eyebrows in addition to the stare [ALTMANN, 1962, pp. 422-423]. The fact that the eyebrows are often lowered. This difference illustrates one of the functions of expression. Since eyebrow raising and eyebrow lowering with the depressing open mouth face the same expression, one solution to this problem is to use mixed criteria as an additional check. Since this expression is also found in macaques and baboons, one can ask if it is also found in chimpanzees. VAN HOOFF's [1967] answer is in full:

expressions, but frequently seen are fleeing expressions. This compound on the average expresses a thwarted by the tendency to flee. For this expressive threat face by VAN HOOFF [1962]. This expression is activated. Thus chimpanzees may be seen stamping on the spot on all fours; hands and feet display, which has been observed especially where it was directed towards the newcomer. Examples: for instance, a fast run past the fellow with force; flight or avoidance; smooth approach; embrace, etc.; gnaw-wrestling accompanied by. Here, apart from the tendency to attack and defend, resulting in positive social behaviour patterns, or simply being close together (for short).

classifies the staring open mouth face as a function. That the staring closed mouth face may be a function. The difficulties encountered by the author in facial expression in terms of function are clear. The fact that morphological definitions of a one-to-one relationship between sign and function and the morphological framework found in a later section I will try to remedy. The author's experience introduces.

teeth, different authors make different distinctions. One distinguishes between a frowning bare face and a frowning face, both of which occur with screams. The latter is used or nearly so. In both the upper lips

are retracted exposing the teeth. VAN HOOFF states that the staring expression occurs in attack or fight situations while the frowning expression occurs during submission to an attack. VAN LAWICK-GOODALL also distinguishes between two types of scream appropriate to the two situations. In both expressions the mouth is open, as would be expected with intense vocalization. Another expression, resembling a human smile, is given with the teeth close together. Sometimes it is accompanied by what VAN LAWICK [1968] terms 'squeak calls'. It is given by a subordinate to a dominant animal, and it is probably homologous to the fear grin described for rhesus monkeys [HINDE and ROWELL, 1962] and other primates.

The fear grin may appear as a smile to the naive observer, but enjoyment is conveyed in the chimpanzee by the relaxed open mouth face. Morphologically the latter is similar to the staring open mouth face, but the eyelids are more relaxed and the upper teeth are typically covered [VAN HOOFF, 1967]. LOIZOS [1967] in her review of play behavior in the chimpanzee notes that the most important structure for signaling play is the face. Postural and gestural factors also play a role, however, since play chases take place at a different tempo from real chases.

An expression highly developed in the chimpanzee is the pout face. This is characterized by a puckering of the lips with the mouth slightly open. The animal is usually staring at another individual. This expression, similar to that seen in suckling behavior, is common among infants of many species, but in chimpanzees it is also common in adults. VAN LAWICK-GOODALL [1968] lists this under 'anxiety' and 'frustration' (quotation marks hers). It also occurs in situations that have a quality of anticipation. The KELLOGGS [KELLOGG and KELLOGG, 1933, p. 283] note that in Gua's use of this expression, the connotation was unpleasant but there was also a whimpering, pleading or imploring quality.

Some facial expressions are conspicuous by their absence. Lip-smacking, so common in macaques, is little used or absent. VAN HOOFF [1967] and others regard this gesture as a ritualization of an aspect of grooming behavior. The fact that grooming may occur less in chimpanzees than in macaques or baboons [SPARKS, 1967] may be related to this. Other facial expressions occur in the chimpanzee that can be conveniently taken as neutral points on the continuum of facial expressions - the relaxed face and the alert face. The crying face is self-explanatory.

While the facial expressions of the chimpanzee have been described as discrete entities, they are behaviorally continuous. Bearing in mind the reservations expressed above on psychological reality, it is possible that chimpanzees

segment this continuum into discrete expressions. This is a commonplace in human behavior, and the ability has been experimentally demonstrated in animals [LANE, 1967]. However, behavioral observation on chimpanzee response to the expressions of others does not contradict the continuous interpretation.

While the facial musculature of man and ape are similar, the extent to which chimpanzee expressions are recognizable to humans without special training is less than commonly believed. FOLEY [1935] gave 127 human subjects six of KOHT's⁶ pictures of chimpanzee expressions, which they were to match to the appropriate emotions drawn from a list of sixteen. Only one picture - crying - was correctly identified by a majority of respondents. However, it should be pointed out that neither humans nor chimpanzees will be normally exposed to facial expressions in isolation, and such expressions are doubtlessly a good deal more communicative when seen in context.

It is clear that facial expressions are closely associated with emotional states at the present time, but ANDREW [1963b] has attempted to show that their original functions were not expressive in character. This points up a difficulty with the concept of communicative specialization that is not easily resolved: when is a behavior pattern to be considered specialized for communication? The problem derives from the fact that anything that serves to predict anything else can function as a sign. Phylogenetically, most visual signs are derived from contingencies of this sort. MARLER [1961] has discussed the main types of responses operating in the specialization of visual signs. One is the intention movement, where an action that ordinarily precedes another type of action comes to stand for the subsequent action, as when baring the canines becomes a sign of attack. The second are the autonomic responses that accompany other behaviors. The third is the antithetical movement, where a certain behavior that is opposite to another behavior becomes a sign that its opposite is *not* likely to occur. For example, if erect hair, bipedal posture, and extended arms are predictive of aggressive behavior, then flattened hair, crouching, and tucked-under limbs are predictive of nonaggression. A fourth category is the displacement activity, a sort of residual category that is difficult to discuss without considering the various neural models that have been proposed to account for it, so I prefer not to deal with it here [MARLER and HAMILTON 1966, pp. 185-187]. Since these various behaviors are to some extent appropriate to the situations they indicate, there are many attributional elements in the sign repertoire of a species.

6 KOHT's [1935] monograph is not available to me as I write this. Many of her plates are reproduced in YERKES [1943].

crete expressions. This is a common place that has been experimentally demonstrated in behavioral observation on chimpanzee responses. It does not contradict the continuous interpretation of man and ape are similar; the extent to which they are recognizable to humans without special training is believed. FOLEY [1935] gave 127 human subjects chimpanzee expressions, which they were to match from a list of sixteen. Only one picture was chosen by a majority of respondents. However, neither humans nor chimpanzees will be normally isolated, and such expressions are doubtfully recognizable when seen in context.

Signs are closely associated with emotional states. SWANSON [1963 b] has attempted to show that their expressive in character. This points up a difficulty in the specialization that is not easily recognized. It is considered specialized for communication. The fact that anything that serves to predict anything is phylogenetically, most visual signs are derived from auditory. MARLER [1961] has discussed the main types of specialization of visual signs. One is the intention that ordinarily precedes another type of action, as when baring the canines becomes the autonomic responses that accompany the antithetical movement, where a certain behavior becomes a sign that its opposite is possible, if erect hair, bipedal posture, and extended arm behavior, then flattened hair, crouching, and a sign of nonaggression. A fourth category is the residual category that is difficult to discuss. It is neural models that have been proposed to deal with it here [MARLER and HAMMILL, 1964]. Various behaviors are to some extent applicable, there are many attributional elements in

not available to me as I write this. Many of her papers

EIBL-EIBESFELDT [1968] has attempted to show that facial expressions in man, similar to some that occur in the chimpanzee, qualify as innate releasing mechanisms [HESS, 1962]. In view of the fact that normal facial expressions occur in humans blind from birth [EIBL-EIBESFELDT, 1968; MANDLER, 1962], it is probable that there are innate motor patterns in higher primates. The question as to whether these constitute innate releasing mechanisms cannot be answered without analysis of the addressee's response to the expression and the way this response develops. Since a sign is neither the action of an effector nor the response of a receptor but a relationship between the two, the demonstration of innateness for one aspect of this relationship is not sufficient to establish an innate sign. At present, the type of experimentation needed has only been attempted for rhesus monkeys [SACKETT, 1966].

The Skeletal Musculature

The skeletal muscles are used as effectors in two different channels: for tactile communication and for visual displays. A visual display is a display monitored by the visual receptor. SMITH [1968, pp. 44-45] has defined *display* as 'an output of an organism which has been selected and modified in the course of evolution to function efficiently as a social signal', so that display is essentially equivalent to sign as used here, except that signs can arise from human invention as well as evolutionary process. For sheer exuberance, there are few organisms that can match the visual displays of the chimpanzee. Some of these displays, such as branch-shaking, are similar to those of some other species of nonhuman primates. Aggressive behavior in the chimpanzee can be manifested by charging, running, waving the arms, and the throwing of handy objects. One chimpanzee at Gombe Stream Reserve incorporated a discarded metal container into his displays with great effect [DAVID HAMBURG, lecture, Stanford University]. Numerous observers have reported on the role of object-throwing in chimpanzee displays, and the phenomenon is not uncommon [GOODALL, 1964; KORTLANDT and KOOLJ, 1963]. The throwing is often well-coordinated and aimed, which attests to the role of skilled movements in the emotional displays of this species - a phenomenon little studied but of great evolutionary importance.

The above behaviors may be accompanied by biting, scratching, hitting, hair-pulling, and slapping. These are logical consummatory behaviors of aggressive behavior, and while they are communicative, they are not signs by our definition. Of more interest is the fact that these behaviors are accom-

panied by vocalizations and autonomic effects, and in males, they may be preceded by the bipedal swagger. In the latter, the animal stands upright and shifts his weight from one foot to the other with arms extended horizontally. VAN LAWICK-GOODALL [1968] has observed it used as a threat or as a preliminary to mating.

In fearful-submissive contexts, a number of gestures can occur. One display which chimpanzees share with other nonhuman primates is the presenting posture. In this, the subordinate animal presents its hindquarters to the dominant, and the posture may vary from slight flexion of the limbs to a true crouch. WICKLER [1967] has suggested that presenting displays are derived from sexual posturing and serve to inhibit aggression through their sexual association. In frightening situations the presenting posture may be replaced by a crouching posture, in which the animal's body rests on the ground and all limbs are flexed. This may be manifesting both self-protective and anti-theft qualities. A less extreme crouching posture, termed bowing by VAN LAWICK-GOODALL [1968], is sometimes seen when a subordinate approaches a dominant animal that has shown aggressiveness.

One of the most interesting gestures to be seen in the chimpanzee is the extended hand gesture. The arm is extended toward another individual with the palm turned upwards. This often occurs in food-sharing contexts [NISSEN and CRAWFORD, 1936], and it may be derived phylogenetically from the intention movement of taking food. The animal with food frequently hands some to the gesturing animal.

Chimpanzees are capable of spectacular displays quite early in life. A common display among chimpanzee infants is the temper tantrum. YERKES [1943, p. 30] has given the following description:

The temper tantrum is a good example of resentful behavior. It is a violent expression of protest, although not necessarily of anger. I have seen a youngster in the midst of a tantrum glance furtively at its mother or caretaker as if to discover whether its action is attracting attention. It flings itself on the ground or against objects as if indifferent to personal injury or actually seeking it, rolls or writhes, beats its head or body with its arms, throws its limbs and head about, scratches its skin and pulls or plucks its hair, and almost invariably cries, screams, or yells. The vocalization especially gives one the impression of extreme anger. Only a sound film can do justice to a temper tantrum.

Parental response varies. Some mothers ignore this behavior [VAN LAWICK-GOODALL, 1968], but other mothers respond by giving the child what it desires [VAN LAWICK-GOODALL, 1967].

There are a number of behavior patterns that are mediated by the skeletal muscles that function in the tactile channel, or more accurately, the skeletal

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onomic effects, and in males, they may be. In the latter, the animal stands upright and to the other with arms extended horizontally, as observed it used as a threat or as a protest.

... a number of gestures can occur. One display other nonhuman primates is the presenting animal presents its hindquarters to the domy from slight flexion of the limbs to a suggested that presenting displays are derived to inhibit aggression through their sexual tions the presenting posture may be replaced the animal's body rests on the ground and be manifesting both self-protective and anti- re crouching posture, termed bowing by VAN metimes seen when a subordinate approaches own aggressiveness.

... gestures to be seen in the chimpanzee is the m is extended toward another individual with often occurs in food-sharing contexts [NISSEN] may be derived phylogenetically from the mian. The animal with food frequently hands some

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... example of resentful behavior. It is a violent expres- ssarily of anger. I have seen a youngster in the wild- its mother or caretaker as if to discover whether he flings itself on the ground or against objects as if he- actually seeking it, rolls or writhes, beats its head w- limbs and head about, scratches its skin and pulls ably cries, screams, or yells. The vocalization especially me anger. Only a sound film can do justice to a scene

... me mothers ignore this behavior [VAN LAWICK-GOODALL] mothers respond by giving the child what it desires [7].

... havior patterns that are mediated by the skeletal tactile channel, or more accurately, the skeletal

muscle effector-tactile receptor channel. While a given behavior pattern may function in two or more channels simultaneously, behavior involving bodily contact can be classified as tactile communication to distinguish it from the purely visual signs. This distinction is justified empirically. As MARLER [1965] has pointed out, it is important to distinguish the locus of stimulation in tactile communication, and there are two sorts of distinctions that should be made: the particular part of the body that is stimulated and the kinds of receptors that are activated. There are specialized receptors for touch and receptors that function to communicate pain. While the latter are probably not receptors at all, neurologically speaking, but rather free nerve endings, they can be considered as receptors from the communicative point of view. These two channels of tactile communication - no matter how many other channels may also be involved - are the primary communicative inputs for sexual behavior (copulation) and aggression (biting, scratching, etc.).

The tactile channels are employed intensively from the moment of birth on, when the grasp reflex and the sucking reflex bring the infant into tactile contact with its mother. Experiments with isolation-reared monkeys indicate that physical contact with even inanimate mother-surrogates can have anxiety-reducing effects in infants [HARLOW and HARLOW, 1965]. Experiments with infant chimpanzees indicate that their threshold to pain is raised when they are being held [MASON and BERKSON, 1962]. In isolation-reared primates, the tactile communication is among the most severely disrupted behavior. Chimpanzees isolated for their first twenty-one months show very little normal tactile behavior with conspecifics, even after years of social contact [MASON, DAVENPORT and MENZEL, 1968]. This is not surprising in view of the importance of tactile communication in mother-infant relationships.

In the chimpanzee, the grasp reflex is less well-developed at birth than in lower primates, and the infant's position on the mother's belly demands the active cooperation of the mother. VAN LAWICK-GOODALL [1967] records how mothers would cradle young infants by walking on three legs or with a haunched gait. As the infant gets old enough to crawl, it will rejoin its mother in response to a light touch to its back, a sign that has been observed in other species as well. After about five months of age, infants will ride on their mother's back. This change of position is initiated by the mother, who places the infant on her back. Later, this active participation is replaced by a postural cue from the mother. This transition reflects a more general sequence of events: the supplementation ontogenetically of communication via contact receptors by communication mediated by the distance receptors. This seems to hold for auditory communication as well, and the KELLOGGS note that their chimpan-

zee Gua was more responsive at first to tactile than to auditory commands. The importance of the distance receptors begins about the twenty-second week, when the infant first ventures away from its mother.

MASON [1965] has noted the effects of various types of contact on the distress vocalization of infant chimpanzees (fig. 2), and the evidence is consistent with the interpretation that in the early stages of childhood, nontactile communication is used primarily to regain contact with the mother and that tactile communication has a stress-reducing quality of its own. As the child matures, the facial expressions already discussed will assume more communicative significance. The pout face, for example, may be used by infants in begging for food. When juveniles become separated from their mothers, a behavioral sequence ranging from the pout face, through whimpering, to crying may occur [VAN LAWICK-GOODALL, 1968]. Infants also have a distinctive scream which leads to immediate retrieval by the mother.

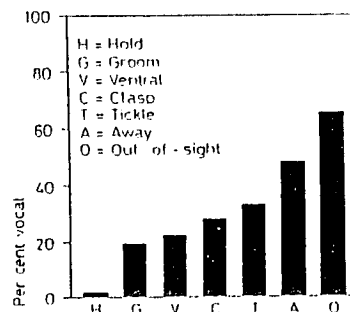


Fig. 2. Effects of various forms of social stimulation on distress vocalizations in an unfamiliar situation (after MASON [1965]).

One form of tactile communication, grooming, becomes more developed as the child grows older. Mutual grooming does not usually appear in the laboratory chimpanzee before four years of age [MASON, DAVENPORT and MENZEL, 1968]. VAN LAWICK-GOODALL [1967] reports instances of grooming behavior by infants as young as twenty-six weeks, but the behavior does not become common until about three and a half years of age. Infants are at first an object of attention to their mothers, and reciprocal grooming is a later phenomenon. Generally, infants are not groomed until at least three months of age. As the infant grows, his mother grooms him for longer periods and reciprocation is attempted. As adolescence is reached, both the length of grooming bouts and the frequency of mutual grooming between mother and child also increase.

While frequently interacting is important in communication, the choice of posture of the body

Other animal movements: surprise communication. Good communication through movement.

When signs, posture, aggression, well-tight for education, performance are coordinated.

Chimpanzee

than to auditory commands. It begins about the twenty-second day of its mother. Various types of contact on the face (see Table 2), and the evidence is consistent with the mother and infant's ability of its own. As the child will assume more communicable, may be used by infants separated from their mothers, as well as through whimpering, to cry. Infants also have a distinctive sound when they are with the mother.

Effects of various forms of stimulation on distress vocalizations in a familiar situation (after MASON [1963]).

Grooming, becomes more developed and does not usually appear in the infant until the age of 18 months. MASON, DAVENPORT and others reports instances of grooming between mothers and infants as early as 10 weeks, but the behavior does not become reciprocal until at least three months of age. Infants are at first groomed by their mothers for longer periods and reciprocally, both the length of grooming and the frequency of grooming between mother and child also

While SPARKS [1967] suggests that grooming behavior occurs most frequently in baboons and macaques, grooming is nonetheless important in the interactions of chimpanzees. As with rhesus monkeys [SADE, 1965], grooming is important in maintaining mother-child bonds into adulthood. Moreover, it is common in friendly contexts, in meetings between dominant and subordinate animals, after copulation, and between animals that are anticipating choice tidbits of food. VAN LAWICK-GOODALL [1968] records gestures and postures involved in the solicitation of grooming, such as presenting the part of the body to be groomed to another individual.

Other types of contact behavior also occur in adult chimpanzees. Dominant animals may respond to presenting by touching the subordinate. Patting movements also occur in this context. Mutual embracing occurs in fearful, tense, or surprising situations, or when animals meet after an absence. Kissing is a common response by a subordinate animal to a dominant. VAN LAWICK-GOODALL [1968], following a suggestion by MASON, concludes that the tactile communication of adult chimpanzees is derived from the tactile communication that occurs between mother and infant. If this is correct, then tactile communication not only becomes supplemented by distance channels as development proceeds but also expands its original domain.

While I have considered presenting behavior under the rubric of visual signs, this classification is somewhat inaccurate. It seems reasonable to suppose, as WICKLER [1967] suggests, that presenting can function to reduce aggression because of its association with sexuality. Since the important modality in sexual behavior is tactile, presenting can be termed a tactile sign as well as visual, especially when the addressee responds with mounting. The tight-beam transmission of tactile communication makes it an ideal channel for communication between particular individuals. Since social communication is essentially the control of one brain by another, tight-beam channels permit differential control over individuals and as such permit the development of social systems with high differentiation. For this reason, tactile signs are extremely important in the functioning and maintenance of groups and coalitions. A more conventional statement of this is to say that tactile signs express positive affect.

Vocal Effectors

Chimpanzees, like many species of higher primates, have air sacs contiguous with the vocal tract [ANDREW, 1963a; KELEMEN, 1949]. These have been interpreted as anatomical specializations functioning in vocal-auditory communi-

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cation. There has been little attempt, however, to evaluate their significance. More attention has been focused on behavioral and morphological analysis of chimpanzee vocalizations. ANDREW [1963] and REYNOLDS and REYNOLDS [1965] have published sonagrams of the calls, and a number of observers have described such calls with musical notation [YERKES and LEARNED, 1925] or onomatopoeic English names.

Most of the vocalizations constitute a graded series, varying in frequency, intensity, and duration. In aggressive behavior, vocalization may range from a short low-pitched bark to a loud drawn-out roar, termed, by VAN LAWICK-GOODALL [1968] a 'wraah' call. When an element of fear is present, the vocalization becomes more high-pitched. When a subordinate animal is being attacked, the fearful calls are transformed into a scream. In relaxed situations, such as grooming, chimpanzees may emit soft grunts or groans. A vocalization usually interpreted as laughing often accompanies the play face. It consists of a series of grunts. In young chimpanzees, as with human children, it can be readily elicited by tickling [KELLOGG and KELLOGG, 1933]. When feeding or approaching food, several different calls may be given: a loud barking sound, short high-pitched squeaks, and soft or loud grunts [VAN LAWICK-GOODALL, 1968; YERKES and LEARNED, 1925]. YERKES and LEARNED record a double-tone call when the cage containing their two chimpanzees was entered each morning by the keeper, or more generally, before the animals were fed. The call began with the upper tone alone, but the lower tone appeared as the call became louder, a succession that is due to the structure of the chimpanzee larynx [KELEMEN, 1949]. Both loud barks and screams also occur in the presence of food, and YERKES and LEARNED single out one call as occurring predominantly when fruit was presented. A common vocalization is the 'oo' call or 'hoo' whimper. It frequently accompanies the pout face, and it is very common in young animals. It appears to be the vocal equivalent of that facial expression.

One of the remarkable vocal displays of the chimpanzee is the class of calls termed panting hoots. The calls in this class often grade into screams, roars and other indications of high arousal. They occur with a slight pout to the lips, and the mouth is slightly or completely open. They are a common occurrence in the excited visual displays described earlier, such as drumming, stamping, and branch-shaking. Typical contexts are the approach of another group, as a response to distant calls, and on seeing the observer. Vocalization by one animal frequently leads to a chorus of calls by all members of the group. Ordinarily, the excitement subsides after a few minutes, but REYNOLDS and REYNOLDS [1965] record occasions when vocalization lasted for hours. They write as follows [p. 409]:

le attempt, however, to evaluate their significance based on behavioral and morphological analysis of the calls, and a number of observers have used musical notation [YERKES and LEARNED, 1921] to describe them.

These calls constitute a graded series, varying in frequency and intensity. In the context of aggressive behavior, vocalization may range from a loud drawn-out roar, termed, by VAN LAWICK-GOODALL [1968], as a 'roar'. When an element of fear is present, the vocalization is high-pitched. When a subordinate animal is being attacked, the vocalization is transformed into a scream. In relaxed situations, chimpanzees may emit soft grunts or groans. A vocalization of a high-pitched note often accompanies the play face. It consists of a series of short notes, as with human children, it can be described as 'chattering' [KELLOGG and KELLOGG, 1933]. When feeding or playing, different calls may be given: a loud barking sound, a high-pitched note, and soft or loud grunts [VAN LAWICK-GOODALL, 1968]. YERKES and LEARNED record a double-toned call when their two chimpanzees were entered each morning into a cage, before the animals were fed. The call began with a high note but the lower tone appeared as the call became more prolonged. Due to the structure of the chimpanzee larynx, barks and screams also occur in the presence of a high-pitched note. Single out one call as occurring predominantly in a particular context. A common vocalization is the 'oo' call or 'howl', which accompanies the pout face, and it is very common in the context of the vocal equivalent of that facial expression. The vocal displays of the chimpanzee is the class of call, which often grade into screams, roars, and howls. They occur with a slight pout to the lips, which are completely open. They are a common occurrence in the context of the approach of another group, as described earlier, such as drumming, stamping, and howling. In contexts are the approach of another group, as described earlier, such as drumming, stamping, and howling. In contexts are the approach of another group, as described earlier, such as drumming, stamping, and howling. In contexts are the approach of another group, as described earlier, such as drumming, stamping, and howling.

Only twice, however, did this happen at night; the four other times it lasted for a few hours during the daytime. The 'carnivals' consisted of prolonged noise for periods of hours, whereas ordinary outbursts of calling and drumming lasted a few minutes only. Although it was not possible to know the reason for this unusual behavior, twice (see below) it seemed to be associated with the meeting at a common food source of bands that may have been relatively unfamiliar to each other. At the time of one of these six 'carnivals' we were inside the forest close to the chimpanzees, while a third observer, a visiting European, was on a hill overlooking the area and reporting on all vocalizations and drummings and their directions. Inside the forests we were attempting to locate the chimpanzees to observe, if possible, the behavior associated with the tremendous outburst. Unfortunately, this proved impossible. Calls were coming from all directions at once and all groups concerned seemed to be moving about rapidly. As we oriented toward the source of one outburst, another came from another direction. Stamping and fast-running feet were heard sometimes behind, sometimes in front, and howling outbursts and prolonged rolls of drums (as many as 13 rapid beats) shaking the ground surprised us every few yards.

NISSEN [1931] notes that these calls are audible for a mile or more. It is clear that the prolonged and energetic visual displays also have an auditory counterpart. In fact, all of the signs discussed earlier have vocal counterparts or accompaniments, and for this reason the channel concept is likely to distort chimpanzee communication if applied too narrowly. As was pointed out several years ago by MARLER [1965], only rarely does a primate monitor his environment through a single channel, and even more rarely is he dependent upon specialized communication for his information. The modality most likely to function in single channel communication is audition, since auditory signs may mediate between individuals obscured by foliage, but the typical communicative situation in the chimpanzee is a complex of posture, gesture, facial expression, vocalization, autonomic response, and purposive behavior. As MARLER [1965] suggests, multichannel monitoring will increase the redundancy (and hence the reliability) of the information transmission and make the animal sensitive to subtle differences in the behavior of others.

Neural Mediation

It is clear from this brief review that the non-referential signs of the chimpanzee do not differ greatly in form from those of other species of nonhuman primates. There is reason to believe that their neural mediation is also similar. The sign systems of nonhuman primates are intimately involved in what PRIBRAM has termed the Four F's: feeding, fleeing, fighting, and sex. It is commonly agreed that the neural mechanisms that execute the behavioral se-

quences appropriate to these functions are mediated by the limbic system [MACLEAN, 1949], as defined by PRIBRAM and KRUGER [1954]. Among the structures included within this complex are the phylogenetically older cortex on the medial surface of the hemispheres and various subcortical nuclei such as the amygdala, septum, and the anterior nucleus of the thalamus. In addition, there are important connections with the autonomic structures of the midbrain and diencephalon and with the reticular activation system. The importance of these structures for what is commonly termed 'emotional behavior' is well attested to by studies too numerous to summarize here [ADEY and TOKIZANE, 1967; GLASS, 1967; PRIBRAM, 1961, 1969; ZANCHETTI, 1967]. It is of interest that the few studies on the neurology of primate sign systems show that they are mediated by the limbic system. ROBINSON [1967] was able to evoke normal vocalizations from numerous locations within the limbic system of rhesus monkeys but none from neocortical sites. Limbic mediation has also been found for the penile erection displays of squirrel monkeys [PLOOG, 1967; PLOOG and MACLEAN, 1963]. The vocalization of nonhuman primates and the nonlinguistic vocal signs of humans are similarly mediated [BRAZIER, 1967]. While there is little evidence bearing directly on the chimpanzee, the anatomical similarity of these structures in higher primates makes the conclusion of limbic system mediation readily applicable to the chimpanzee.

Functional Interpretations

The behaviors involved with the Four F's, as MACLEAN [1949 and elsewhere] has argued, constitute the mechanisms that serve to maintain the individual and the species. Behavioral studies have demonstrated a close relationship between animal social communication and the limbic system functions in a wide variety of taxa. The functions listed by SMITH [1968] for the social communication of New World fly-catchers of the genus *Tyrannus* are also appropriate to the chimpanzee: attraction and repulsion of conspecifics, individual recognition, appeasement and reassurance, threat, providing environmental monitoring information to conspecifics, alerting, and the associating of adults and dependent offspring. A perusal of the functions listed by other authors for other species [COLLIAS, 1960; HINDE, 1966] shows that these functions are typical ones in animal communication systems. MARLER [1968] has recently interpreted the communication of nonhuman primates in terms of aggregation and dispersal. It is suggested that the data on nonhuman primate social systems are not incompatible with the idea that these systems function to maintain

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ctions are mediated by the limbic system (PRIBRAM and KRUGER [1954]). Among the complex are the phylogenetically older cerebral cortex and various subcortical nuclei such as the anterior nucleus of the thalamus. In addition with the autonomic structures of the brain with the reticular activation system. The limbic system is commonly termed 'emotional behavior' and is numerous to summarize here (ABRY and PRIBRAM, 1961, 1969; ZANCHETTI, 1967). The neurology of primate sign systems shows the limbic system. ROBINSON (1967) was able to find numerous locations within the limbic system and neocortical sites. Limbic mediation has also been displayed of squirrel monkeys (FRIDLAND, 1967), localization of nonhuman primates and the signs are similarly mediated (BRAZIER, 1967). Applying directly on the chimpanzee, the anatomy of higher primates makes the conclusion of applicability to the chimpanzee.

Functional Interpretations

Our F's, as MACLEAN [1949 and elsewhere] has demonstrated a close relationship between the limbic system functions in the genus *Tyrannus* are also appropriate and repulsion of conspecifics, individual assurance, threat, providing environmental information, alerting, and the associating of individuals of the functions listed by other authors (FRIDLAND, 1966) shows that these functions are similar in nonhuman primates in terms of aggression. MARLER [1968] has recently shown data on nonhuman primate social systems that these systems function to maintain

populations in ecological equilibrium. Given the close relationship between animal communication and limbic system functions and given our definition of a social system as an outgrowth of social communication, it is to be expected that animal societies will be interpretable largely in terms of the regulation of the social aspects of sex, hunger, and aggression⁷. While the non-referential signs of the chimpanzee can be dealt with in this general framework, there are several factors that militate against applying these concepts too narrowly.

The field studies of GOODALL [1965] and REYNOLDS and REYNOLDS [1965] indicate that if chimpanzee societies are well-defined homeostatic systems, they are more subtle ones than the cohesive groups of terrestrial monkeys. Since the signs of the chimpanzee are not particularly distinctive, the explanation of these differences probably lies in the way in which the signs are used and the extent to which they are supplemented by observational learning and intelligent decision-making. It is likely that detailed examination of the way in which chimpanzees interact will reveal that the specialized sign systems constitute only one part of their communicative activity, and that for this species there is no good dividing line between social communication and cognitive process.

While the non-referential signs fall under the rubric of emotional expression, there are likely to be phylogenetic differences in the significance of this phenomenon. Rather than being the primitive mechanisms that they have been long considered, the emotions are well developed in higher primates. Recent developments in the psychology of emotion [GLASS, 1967; MANDLER, 1962; SCHACHTER, 1967] have emphasized the role of cognitive factors in emotional experience, and it is also likely that cognitive factors will prove equally important in emotional expression. That emotional behavior in the chimpanzee is variable, idiosyncratic, and given in response to complex categories of stimuli has been known for many years [HEBB, 1961], and this suggests that the limbic system signs of this species function in close conjunction with intelligence and learning. Other support for this conclusion can be drawn from neurological data. The anatomical components of the limbic system, with the exception of the olfactory bulb, either retain their proportionate size or expand in size in the course of primate phylogeny [STEPHEN and ANDY, 1964]. Secondly, there is a growing belief that the frontal cortex, which is

7 ROWELL [1962] and ROWELL and HINDE [1962] have described the vocalizations of the rhesus monkey in terms of an analogic system. Behaviorally, this seems to be true for the chimpanzee as well. Analogic signs would be particularly useful in the functioning of homeostats.

anatomically defined as the projection area of the dorsomedial nucleus of the thalamus [NAUTA, 1964; PRIBRAM, 1960], constitutes the intrinsic cortex of the limbic system, giving these structures increasing neocortical representation in the course of primate phylogeny. While the limbic system is more than a visceral brain and has important memory functions, for example, it is not unlikely that these new neural mechanisms are also involved in the mediation of emotional expression in the chimpanzee, and indirectly, in its social organization.

In addition to the specialized communication already discussed, the chimpanzee has a capacity to learn sign systems whose specialization was created by human tutors. While this communication uses the visual-gestural channel employed in some limbic system signs, the neural control is likely to be very different. For this reason it may be necessary to take neurological criteria into account in future definitions of channel.

THE REFERENTIAL SIGNS

Recent work by R. A. and B. T. GARDNER⁸ with the young chimpanzee Washoe [KELLOGG, 1968] indicates that chimpanzees can learn signs having similarity to aspects of human language⁹. HOCKETT [1960] has discussed codes used in social communication in terms of their design features – that is, structural differences useful in comparative study. Two of HOCKETT's design features are displacement (the ability to talk about things removed in space and time) and semanticity, which includes reference and denotation. Codes that possess these properties are here defined as *referential* or *symbolic*. Washoe's performance qualifies as an example of the referential use of signs.

The GARDNER's are raising a young chimpanzee in a human social environment. However, unlike previous experiments [HAYES, 1951; KELLOGG and KELLOGG, 1933], no language is spoken in the presence of the ape, and all communication between the humans involved and between humans and animal is conducted in American Sign Language gestures. Washoe has learned about fifty signs and uses them intelligently. When presented with a gesture she can respond appropriately, such as choosing the correct object from among an array or performing the appropriate activity. When presented with an object, she can respond with the correct sign. The signs are used instrumentally

8 Reference added in proof: R. A. GARDNER and B. T. GARDNER: Teaching sign language to a chimpanzee. *Science* 165: 664-672 (1969).

9 DAVID PREMACK of the University of California, Santa Barbara, is doing research along similar lines, but as far as I know, his findings have not yet been published.

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SOCIAL COMMUNICATION

region area of the dorsomedial nucleus of the thalamus (Gardner, 1960), constitutes the intrinsic cortex of the thalamus. The thalamus is increasing neocortical representation in the thalamus. While the limbic system is more than a visuo-motor system, for example, it is not unlikely that it is also involved in the mediation of emotion. The limbic system, and indirectly, in its social organization: communication already discussed, the chimpanzee communication uses the visual-gestural channel. For referential signs, the neural control is likely to be very similar. It is necessary to take neurological criteria into account in this channel.

REFERENTIAL SIGNS

GARDNER⁸ with the young chimpanzee Washoe. Chimpanzees can learn signs having similarity to referential signs. HOCKETT [1960] has discussed codes used in the study of their design features – that is, structural features about things removed in space and time) and denotation. Codes that possess a referential or symbolic use. Washoe's performance: the referential use of signs.

young chimpanzee in a human social environment. Washoe's experiments [HAYES, 1951; KELLOGG and GARDNER, 1969] are spoken in the presence of the ape, and all signs involve humans and between humans and animals. Washoe has learned sign language gestures. Washoe has learned sign language intelligently. When presented with a gesture, she chooses the correct object from among the appropriate activity. When presented with an object, she performs the appropriate activity. The signs are used instrumentally.

GARDNER and B. T. GARDNER: Teaching sign language to a chimpanzee. *Science*, 163: 664-672 (1969).
University of California, Santa Barbara, is doing research now. His findings have not yet been published.

also, so that the animal will make a sign to elicit responses in her human keepers, such as obtaining a glass of water. While none of these activities alone is unique, when they are combined into a functional system of sign, referent, and response, it is meaningful to speak of referential signs, that is, symbols. In this referential communication the original functions of animal communication are not necessarily lost. When an animal says 'Give banana', this expression informs us of hunger in much the same way (although perhaps not as reliably) as a food call. However, it also informs us in another way, in that it also calls attention to bananas. It is this second kind of informativeness that referential signs make possible.

Washoe can use combinations of signs, on the order of the sentence given above. While this is a clear example of co-occurrence of signs, it is not yet syntactic in a human sense of the term. To consider a sign system as syntactic, the relations between the signs must function as semantic markers. By this criterion, Washoe's sign system is combinational rather than syntactic. Also, the application of other linguistic categories to the codes taught to animals must be done cautiously. Washoe can throw a ball to the persons indicated by the ASL signs for *him* and *me*. The GARDNERS [lecture, Stanford University, 1969] have interpreted this usage as an example of pronouns in Washoe's sign system. While pronouns can be used in a Tarzan style of discourse, it is better to consider such usages as pointers and restrict the term 'pronoun' to signs that can also function metalinguistically. In spite of these reservations, Washoe's accomplishments indicate that living apes are capable of communicative behavior whose nearest analog is linguistic communication in man. While the attempts to teach apes vocal-auditory symbols [HAYES, 1951, KELLOGG and KELLOGG, 1933] are not directly comparable, it is not unlikely that this symbolic faculty is more highly developed in the visual than in the auditory modality. In the light of these recent experimental findings, it will be interesting to examine the behavior of feral chimpanzees for any evidence of untutored animals using these abilities in a natural habitat.

SUMMARY

Social communication is defined as communication that mediates between organisms. While any kind of sensory channel may function in social communication, the discussion was restricted to inputs that have become specialized for this function. Such specialized codes are termed sign systems. The signs of the chimpanzee are described on the basis of the channel that mediates them, where channel is defined as a relationship between a particular effector and a particular receptor. It is pointed out that while

the channel concept is convenient for discussion purposes, chimpanzees actually receive input through a number of channels simultaneously; and because of this, attempts to deal with signs in isolation will not yield very good predictions. A review of the signs of this species indicates that they are morphologically similar to the signs of other species of nonhuman primates, that they serve functions similar to those described for other animals, and that they are mediated by similar neural mechanisms. However, it is suggested that some reappraisal of our concept of emotional expression may be needed for higher primates, on the basis of behavioral and psychological data, and that a more rigorous examination of the way in which chimpanzees employ their signs may yield significant differences. Lastly, some recent attempts to teach chimpanzees referential signs are described. The results indicate that there are two kinds of specialized signs systems employing the same peripheral channel, and that eventually our concept of channel must be described in terms of differing neural mechanisms.

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