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The Development of the Communication System of Chimpanzees during Ontogenesis

The objective of this study was to compare the communication processes of young and adult chimpanzees, to establish how the development of communication modes in the ontogenesis of these primates unfolds and to determine possible preconditions for the origin of hominid speech in the course of anthropogenesis.
Systems of communication were studied in 9 chimpanzees: 3 adult females, 3 adult males and 3 young chimpanzees. The chimpanzees were from the Saint Petersburg zoo and the laboratory for the physiology of primate behaviour at the Pavlov Institute of Physiology in the village of Koltushi in the Leningrad region.
Communicative behaviour was observed with the use of specially devised matrices that considered virtually all elements of communication (facial expressions, postures, gestures, tactile elements, acoustic signals etc.).
I discovered that communication in chimpanzees serves as a very important mechanism for increasing the sociability of group members. The most significant elements were those that belonged to friendly contexts, conveyed via acoustic and visual communication channels. Friendly gestures were accompanied by friendly sounds, connection between friendly visual and acoustic communication strengthened. In aggressive contexts, I noted harmonic sounds, and in friendly ones, mixed articulatory sounds like 'ah', 'oh', 'ooh'. The elements of communication complexes were not very variable and were used as established communication units. The communication process was quite labile and the communicative systems were characterized by great individual variability.

KEY WORDS: *communication complexes, chimpanzees, ontogenesis, communication systems*.

Introduction

The origin of human speech has always been, and still remains, one of the great puzzles in the theory of anthroposociogenesis. It has attracted the attention of scholars from various disciplines – linguistics, anthropology, psychology, ethnology (Bunak, 1951, 1966; Porshnev, 1973; Luriya, 1979; Faynberg, 1981; Vygotsky, 1982; Panov, 1983; Yakushin, 1985; Donskikh, 1988; Hamilton, 1974; Parker, Gibson, 1989; Walker, 1981; Campbell, 1982). In anthropology, the evolution of speech has traditionally been studied from a morphological point of view i.e., the structure of the larynx, brain, endocranium, mandible (Bunak, 1951, 1966; Khrisanfova, 1956; Voyno, 1964; Tobias, 1971). Recent decades have seen a considerable accumulation of material concerning the behaviour of

primates. There are two main approaches to studying primate communication: the experimental approach, and that based on observations in natural and artificial environments.

The experimental approach consists of training higher anthropoids in semiotic systems of human language (Gardner & Gardner, 1969, 1975; Premack, 1971; Savage-Rumbaugh, 1977; Patterson, 1978). These studies resulted in a reconsideration of several opinions on the capacities of hominids for complex forms of communication, as well as my own understanding and learning of the individual syntax rules of human language. They also threw new light on potential capabilities characteristic of the mentality of anthropoids (especially chimpanzees) (Gardner & Gardner, 1969, 1975).

The second approach was developed by ethnologists and consists of studying the spontaneous communication processes of apes in the wild and in laboratories and primatological centres (Schaller, 1968; Firsov, 1977; Fossey, 1990; Goodall, 1991; Goosen & Kortmulder, 1979). Moreover, scholars accumulated extensive material on the specific bioacoustic characteristics of various species of apes. This approach has turned out to be very fruitful for studying primate behaviour (Firsov & Plotnikov, 1981; Marler & Tenaza, 1977; Mori, 1983; Snowdon, 1986).

Present-day knowledge on primatology, paleoanthropology and neuromorphology has led to the necessity for a revision of hypotheses concerning the origin of hominid speech. Studying primate communication systems, especially those of higher anthropoids, will allow us to reconstruct the preconditions and main stages in the emergence of speech – a specifically human form of communication.

The objective of this study was to compare the communication processes of young and adult chimpanzees, to find specific features that are characteristic of the evolution of communication modes in the ontogenesis of these primates, and to determine possible preconditions for the emergence of hominid speech during the course of anthropogenesis.

Materials and methods

Key terms and concepts used in the work:

1. Communication is a process both conscious and unconscious between two variable entities which results in a reduction of uncertainty in behaviour. When observation of the behavioural characteristics of one of two interacting animals provides us with a basis for prediction concerning the behavioural characteristics of the other, then we are dealing with the process of communication.
2. A communication chain is a sequence of elements or complexes in the communicational exchange between two animals from the beginning of a particular contact to the end.
3. A communicative sequence is a system of the basic (most frequent) transitions from one communication element to another.

4. Communication pairs, based on signals and responses (a system of dialogues), represent a system of the basic (most frequent) transitions from the signals of one animal to the responses of another.
5. A communication complex represents simultaneous elements belonging to the different communication channels. There may be double, triple, quadruple, etc., complexes, depending on the number of elements involved.
6. I have distinguished four communication channels in the process of communication: visual, tactile, olfactory and acoustic. Visual forms of communication include facial expressions, postures and gestures.
7. Facial expressions represent expressive stereotypical responses by face and head muscles.
8. Posture represents static and dynamic movements of the head, body and hind limbs. There are also various spatial movements involved in the communication process.
9. Gestures are distant movements of the fore limbs.
10. Tactile elements refer to body contact movements of the fore limbs, head, body, etc.
11. Olfactory elements comprise sniffing and the marking of territory and other animals with special secretions.
12. Acoustic elements represent signaling with the use of vocal apparatus, where each sound has its own particular meaning and elicits changes in the behaviour or condition of the receiver.

The communicational processes of chimpanzees were observed from 2-6 hours per day for 7 months, both in the laboratory for the physiology of primate behaviour at the Pavlov Institute of Physiology in the village of Koltushi in the Leningrad Region, and at the Saint-Petersburg zoo. I studied the behaviour of six adult chimpanzees (3 males and 3 females) and three young chimpanzees (1 male and 2 females). In winter the chimpanzees were kept in specially equipped rooms, and in summer in outdoor aviaries equipped with crossbeams, seesaws and shelves. The young chimpanzees were sometimes observed at large, in the laboratory yard, where they could climb on trees and run on the grass. A brief summary of the chimpanzees studied is shown below.

TABLE 1. Information on the chimpanzees studied.

Name and sex	Birthplace	Age
1. Otto (male)	Germany	22
2. Genghis (male), Gamma's son	Koltushi	10
3. Lel (male)	Koltushi	10
4. Gamma (female)	Koltushi	20
5. Vega (female)	Saint-Petersburg zoo	19
6. Hippie (female), Otto's daughter	Saint-Petersburg zoo	14
7. Styopa (male), Gamma's son	Koltushi	2.5 and 3.5
8. Alpha (female)	Koltushi	3.5 and 4.5
9. Lesya (female)	Koltushi	2.5 and 3.5

Where the table indicates two ages, this is because the young chimpanzees were observed in August 1989 and again in September 1990.

In order to register the forms of communication observed, I adopted a method of integrated recording of the communication elements. Elements of visual, tactile and olfactory communication were recorded in a special matrix. At the same time, acoustic signals were recorded. After processing the matrices and recordings, I compiled a communication glossary (a list of elements). These elements were then arranged in groups according to the functional load and coded. The coding principle is shown in Table 2.

TABLE 2. Key for the coding of communication elements.

The frequency of these elements was calculated using the following formula:

Code	Elements or groups of elements with similar functions in the process of communication
I.	**FACIAL EXPRESSIONS**
I.1. I.1.a I.1.d	Glances Staring Scanning, neutral look
I.2.	Open mouth
I.3.	Lip movements
I.4.	Relaxed play face, smile
I.5.	Smacking, jaw popping
I.6.	Eyebrow, forehead, ear movements
II.	**POSTURES**
II.1. II.1.p II.1.o II.1.α	Coming closer and moving away, turning, nodding Coming closer Moving away Sitting side by side
II.2.	Exposure
II.3.	Demonstrations: swinging, thrusts, bouncing, stamping
II.4.	Erection, demonstration of genitals
III.	**GESTURES**
III.1.	Reaching, raising fore limbs
III.2.	Backing off, chopping with fore limbs
III.3.	Demonstrations: hitting substrate or body, targeted throwing of objects
III.4.	Handclapping
III.7.	Autogrooming
IV.	**TACTILE ELEMENTS**
IV.1.	Touching
IV.2.	Hugging, kissing
IV.3.	Grooming
IV.4.	Pushing, hitting, biting
IV.5.	Covering

TABLE 2. continued

V.	**OLFACTORY ELEMENTS**
V.1.	Naso – nasal sniffing
V.2.	Naso – anal sniffing
V.3.	Body sniffing
V.4.	Substrate sniffing, marking territory
VI.	**ACOUSTIC ELEMENTS**
VI.1.	Excitement, threat
VI.2.	Friendly, comfortable, contact sounds
VI.3.	Buffering sounds

F=K/N, where K is the number or amount of times this element was used during the whole time of observation and N is the number of 30-minute intervals, i.e., I obtained the frequency of elements displayed per 30 minutes. According to E.N. Panov (1983), the basic communication unit is a sequence of communication elements. Since one of the most important issues when studying animal communication is the question of the semantic and syntactic significance of communication chains, I made a point of recording and analyzing such sequences among primates. And I discovered that the communication process typical of apes was more sophisticated and represented not only sequences of elements but also sequences of communication complexes. With this end in view, I have specially coded all the matrices and then composed communication chains (Table 2).

An example of a chain is as follows: (I.1d – I.3) → III.7 → (I.1d – II.1p)* → (II.1L – IV.1)* → IV.3 → II.1o → III.7. Arrows indicate a transition from one communication element to another. Parentheses denote the more complex elements of a chain. Asterisks show elements of the animal that responded.

All communication chains were divided into three types: Type A - short ones, consisting of 2-3 sequential elements or complexes; Type B - average ones, consisting of 4-5 elements or complexes; Type C - long ones, with more than 6 elements or complexes. For the purposes of comparative analysis, I calculated percentage ratios for the different types of chains. In order to develop a model of the communication process, I devised schemata of communication sequences (see Figure 1). The principle for the development of these schemata was taken from A. Mori's works on the behavioral sequences of macaques (1982, 1984). This principle is based on comparing the frequency of particular elements used in communication. As a consequence, it allows us to distinguish the most frequent elements and the transitions from one element to another. I selected the basic transitions from one communication element to another that were repeated with a frequency of 0.1 per hour and used them for the development of the main schema.

While studying the communication processes, it was very interesting to examine not only the sequence of elements adopted by any given chimpanzee, but also the dialogues and interactions between two or more animals. While processing communication chains comprising elements adopted by two or more chimpanzees, I only made allowances for the transitions between elements that had been observed in the different chimpanzees. Thus, I obtained communication pairs based on signals and responses. The communication pairs were obtained by processing the communication chains. The responses elicited from animals receiving particular signals have been indicated with an asterisk. Basic transitions were those repeated with a frequency of no less than 0.1 per hour.

As a result, I constructed two schemata:

1) The sequence of communication elements characteristic of one animal, i.e. revealing the basic (most frequent) sequences.

2) The sequence of communication elements occurring in communication between two animals based on signals and responses, i.e., revealing of the most frequent responses from one animal to the signals of another.

For both schemata, I calculated stability factors showing a correlation between the basic transitions and all the other transitions in behaviour during the observation period. Stability factors are shown in various tables below. These factors represent a correlation between the number of basic transitions and the number of all other transitions. A communicative system with more basic transitions is more stable (i.e. less variable). Consequently, the stability factors of signals and responses represent a correlation between basic signals and responses and all other signals and responses. If an animal uses one signal frequently and receives almost the same response all of the time, then we can speak of the stability of this signal and its corresponding response.

Since an assessment of locomotor behaviour and vocal manifestations turned out to be incommensurable (Firsov & Plotnikov, 1981), I used bioacoustic analysis of sound signals. I have composed a list of acoustic signals with descriptions of signals and situations where they were used. This allowed me to denote main groups of sounds depending on the context of their usage (aggressive, buffering, friendly) and to characterize them with the use of bioacoustic data. The data were processed with sonography in the bioacoustic laboratory of the Chair of Vertebrate Zoology at the Department of Biology of Moscow State University (MSU).

Findings and discussion

Let us now examine the communication systems of adult and young chimpanzees.

Adult chimpanzees

Table 3 shows the communication elements of adult chimpanzees and the frequency the various elements were used by the individual animals.

TABLE 3. Communication elements and the frequency of their manifestation among adult chimpanzees

ELEMENTS	Genghis (lab)	Lel (lab)	Gamma (lab)	Otto (zoo)	Vega (zoo)	Hippie (zoo)
FACIAL EXPRESSIONS Neutral glance	1.86	1.83	3.48	4.79	6.33	6.67
Staring	0.21	0.13	0.12	0.50	0.33	0.61
Looking round	0.88	0.43	0.41	1.42	2.96	0.89
Open mouth	0.21	0.04	0.02	0.50	1.08	1.05
Open mouth with teeth	0.02	0.02	0.02	0.29	0.17	0.38
Half-grin	0.57	0.28	0.07	0.21	0.29	0.55
Half-grin with teeth	0.05	–	–	0.25	0.13	–
Grin	0.38	0.57	0.15	0.50	0.46	0.78
Oscitation	0.29	0.54	0.24	0.33	0.38	0.33
Bared teeth (closed grin)	0.05	0.09	0.02	–	0.04	–
Protruding lips	1.00	0.61	0.57	0.58	0.67	0.55
Pursed lips	–	0.02	0.02	0.04	–	–
Puckered lips	0.07	–	–	0.63	0.83	1.17
Puckered upper lip	0.07	0.02	0.02	–	–	–
Puckered lower lip	0.17	0.12	0.09	0.50	0.13	0.78
Turned-up lower lip	–	–	0.02	0.08	0.04	0.06
Turned-up upper lip	0.05	–	0.02	0.04	–	0.06
Both lips puckered and turned up	0.002	–	–	–	–	0.11
Saggy lower lip	0.76	0.35	–	0.08	–	–
Pouted lips	0.45	0.26	0.04	0.63	0.67	0.39
Pouted upper lip	0.19	0.02	–	0.17	0.29	0.06
Pouted lower lip	–	–	–	0.71	0.08	0.17
Compressed lips	0.05	–	–	0.13	0.13	–
Pursed lips	0.02	–	–	0.04	0.04	0.11
Bitten lower lip	0.02	–	–	0.08	0.04	–
Bitten upper lip	–	–	–	0.08	0.04	0.17

TABLE 3. continued

Chewing with lips	0.33	0.30	0.09	0.38	1.33	0.17
Protruding tongue	0.05	0.07	0.02	–	0.21	0.06
Licking lips	0.10	0.02	0.02	0.04	0.17	0.11
Smacking lips	0.24	0.17	0.02	0.04	0.08	0.17
Chattering of teeth	0.02	–	–	–	–	0.17
Flush	0.17	0.07	0.04	0.33	0.25	0.78
Eyebrow movements	–	–	–	0.13	0.04	0.33
Ear movements	–	–	–	–	0.13	–
Wrinkled forehead (horizontal folds)	0.07	–	0.04	0.08	0.55	0.55
Play face (smile, half-open and upward-sloping mouth)	0.21	0.46	0.02	–	0.21	0.55
MOVING AND POSTURES Coming closer	0.38	0.22	0.67	1.33	0.67	0.83
Moving away	0.10	0.33	0.11	1.38	0.54	0.50
Sitting alone	0.88	2.12	1.02	2.46	1.83	1.39
Sitting side by side	1.17	0.48	0.81	1.83	1.33	1.38
Walking after someone	–	–	–	0.21	0.08	0.22
Walking side by side	–	0.02	0.02	0.08	–	–
Hanging and swinging	0.38	0.13	0.04	–	–	–
Swaying when seated	0.26	0.35	–	0.17	0.04	–
Swaying when standing up	0.21	0.52	0.02	0.29	0.08	–
Walking and swaying	0.02	0.39	–	0.08	–	–
Thrust (body throw)	–	0.09	–	0.08	–	–
Bouncing	0.19	0.07	0.02	0.13	0.04	–
Turning	0.02	–	0.02	0.04	–	0.11
Turning away	0.02	0.02	0.11	0.13	0.08	0.11
Exposing	0.05	0.04	0.57	–	0.04	0.06
Lifting up head	–	–	–	0.13	0.13	0.06
Waggling head	–	0.04	0.04	0.04	0.04	0.06
Nodding	–	0.04	–	0.17	0.21	–
Head thrust	–	0.02	–	0.08	–	–

TABLE 3. continued

Lying	0.71	1.54	0.43	1.13	1.25	1.00
Standing	0.31	0.35	0.20	0.38	–	0.17
Hanging	0.36	0.41	0.93	0.17	0.08	0.11
Climbing	1.19	0.93	0.35	0.21	0.17	0.22
Walking	0.64	1.26	0.22	1.08	0.25	0.44
Running	0.12	0.20	0.20	–	–	–
Jumping	0.36	1.17	0.02	0.04	–	–
Standing on hind limbs	–	–	–	0.08	0.21	0.06
Demonstration of genitals	–	–	0.09	–	–	–
Penis erection	0.05	0.02	–	0.08	–	–
Raised hackles	–	–	–	0.29	–	–
GESTURES Autogrooming	1.36	1.41	2.61	3.04	1.54	2.33
Slapping hands	0.05	1.00	0.04	–	0.08	–
Knocking on surface with hands	0.69	0.37	–	0.38	–	0.22
Knocking on surface with objects	–	0.04	–	–	–	–
Shaking bars	0.10	–	0.02	0.08	–	–
Targeted throwing	0.19	0.20	–	0.13	0.29	0.11
Offering supine hand	0.12	0.04	0.02	0.38	0.29	0.89
Offering prone hand	0.02	0.04	0.20	0.08	–	–
Waving hand	0.29	0.02	0.04	0.08	0.08	–
Chopping with hand	0.07	–	0.02	0.04	–	–
Waving hand with object	0.19	–	–	–	0.08	–
Offering hand with object	0.10	0.07	–	–	0.04	–
Shaking hands bent at elbows	0.05	0.02	–	–	0.04	–
Shaking palm in front of face	–	0.07	0.02	–	–	–
Raising hand	0.05	–	–	–	–	–
Covering face with palm	0.05	0.02	–	–	0.08	–
Waving aside	–	–	0.07	–	0.21	0.06

TABLE 3. continued

Pointing hand	–	–	–	–	–	–
Hand thrust	0.17	0.07	0.002	0.08	–	0.17
TACTILE ELEMENTS Touching with hand	0.40	0.11	0.33	0.17	0.25	1.10
Pushing with hand	0.05	0.02	0.07	–	–	0.17
Grasping with hand	0.07	–	0.04	–	0.04	0.28
Dash with hand	0.19	0.07	–	0.08	–	0.06
Active grooming	1.33	0.70	1.63	0.58	0.25	0.72
Pulling with hand	0.02	–	0.04	–	–	0.06
Touching with hand	0.07	0.08	0.11	–	–	0.17
Licking body	0.17	0.09	0.11	–	–	–
Kissing	0.10	0.07	0.15	0.08	–	0.06
Hugging	0.10	0.07	0.02	0.13	0.04	0.11
Touching partner's body with own body	0.07	0.02	0.04	0.04	–	0.17
Cuddling	–	0.04	–	0.17	0.17	0.17
Placing hand on anal-genital region	0.02	0.02	–	–	–	–
Mass fight	–	–	–	0.04	0.04	0.06
Touching with object	–	–	–	0.04	–	–
Hit with body, foot, head	–	–	–	–	–	–
Hit with object	–	–	–	–	–	–
Covering with hand	–	–	–	–	–	–
Climbing and hanging	–	–	–	–	–	–
Biting	–	–	–	–	–	–
Wrestling	–	–	–	–	–	–
Tickling	–	–	–	–	–	–
Holding with hand	–	–	–	–	–	–
OLFACTORY COMMUNICATION Naso-nasal	–	–	0.04	0.38	0.21	0.28
Naso-anal	0.02	0.02	–	0.29	0.13	0.17
Naso-corporal	–	–	0.07	0.33	0.13	–

Visual elements of communication

Facial expressions. Having observed adult chimpanzees miming, I distinguished 36 elements, 18 connected with lip expressions. Chimpanzees are characterized by the frequent use of grinning, protruding lips, pouting, chewing with lips. Expressions connected with eyebrow movements are rarer. I found certain differences between the miming of chimpanzees from the zoo and those from the laboratory in Koltushi (Table 3). For example, the following elements were more significant in animals from the zoo: neutral glance, staring, scanning, open mouth, open mouth with teeth, eyebrow and ear movements. I also found some differences in the adoption of elements related to lip expressions. All in all, animals from the zoo had a richer repertoire of mimes with a higher frequency of expression of the various elements.

Postures. I noted 40 types of posture, movement and locomotion related to communication. Predominantly, chimpanzees perform knuckle-walking and climbing. In general, the animals at Koltushi were more active – partly due to larger aviaries. I also found some resemblances in the posture behaviour of two couples of chimpanzees. The first couple, Vega and Hippie (both from the zoo) moved closer to other chimpanzees more frequently than they moved away; they also moved and got onto their hind limbs less frequently than the others. The second couple, Genghis and Gamma, (from the laboratory) moved away less frequently, though they moved around their aviary much more. The remaining couple of chimpanzees – Otto and Lel (from the zoo and from the lab, respectively) moved closer and moved away with the same frequency but lay down a lot. Lel had the habit of jumping frequently during aggressive demonstrations**.**

Gestures. I distinguished 18 elements associated with gestural communication. In general, gestures in communication were more significant for the chimpanzees from the laboratory. In most cases, they had a more diverse range of gestures with higher average frequencies. I observed similarities between: Vega and Hippie, who offered supine hands most often, threw objects at certain targets, and waved aside; Gamma and Otto, who frequently performed autogrooming, shaking bars, and offering prone hands; and finally, Genghis and Lel, who rarely carried out autogrooming, though more frequently hit surfaces with their hand, performed waving aside, hand thrusts, and offered hands with objects.

Tactile elements. I identified 15 tactile elements in communication (Table 3). Most often, the chimpanzees touched with fore limbs in various ways. At the same time, Genghis and Gamma actively groomed, kissed and touched with hands more often than the others. Lel and Otto touched with their hands less often, demonstrated less active grooming and hugged each other quite frequently. Vega and Hippie touched and snatched frequently with their hands and cuddled with their bodies. Vega groomed the other chimpanzees more rarely than the others. Some of the elements of tactile communication in Table 3 do not have any digital values. These are elements that were only found in the behaviour of young chimpanzees and are presented in the table only for comparison, i.e., to see which elements of tactile communication disappeared in the behaviour of adults.

Olfactory elements. Naso-nasal sniffing was performed more often by females and naso-anal sniffing by males. The chimpanzees at the zoo used olfactory elements of communication more actively than the chimpanzees from the laboratory (Table 3).

Acoustic signals. 7 classes of acoustic elements were distinguished. Variants of signals and their functional loads are shown in Table 4. This is the first time such a description of chimpanzee acoustics has been provided in scientific literature.

TABLE 4. Sound signals of adult chimpanzees

Signal	Frequency of use			Bioacoustic characterization	Situation
	males	females	all		
1. Hooting (sometimes ending with a screaming cry).	0.34	0.18	0.26	Mixed sound. Basic formant – 150-600 Hz. Maximum frequency – 6-8 kHz. Sound duration – about 110 ms. Series, intervals – 100-500 ms.	When males get excited before aggressive actions. Intervals become shorter towards the end of the series and sound intensity increases.
2. Cries (all types) a) Male cry.	0.06	–	0.03	Mixed or harmonic sound (2-5 harmonics). Basic formant – 1-1.75 kHz. Max. frequency – 6-7.5 kHz. Sound duration – 900-1100 ms. The spectrum frequency is constant.	Used with agonistic thrusts (sometimes after hooting).
b) Female cry (similar to squealing).	–	0.03	0.015	Mixed or harmonic sound (3-4 harmonics). Two formants are more intense: 1) 1-1.5 kHz 2) 2.25-2.75 kHz. Maximum frequency – 4 kHz. Frequency-modulated. Sound duration – 655-800 ms.	To express fright during an attack by an alpha animal; during a rumpus.
3. Barking (all types).	0.08	0.06	0.07	Mixed sound. 3-4 harmonics. The central part is more intense. Basic formant – 500-1000 Hz. Amplitude- and frequency-modulated. Basic formant modulation depth – 300-1500 Hz. Maximum frequency – 5-7 kHz, generally at the beginning of sound. Sound duration – 820-920 ms.	Emitted by excited chimpanzees at the end of a common rumpus, after aggression and subsequent to cries. An element of a male threat in the case of swaying.

TABLE 4. continued

4. Howling.	–	0.05	0.03	Harmonic sound, up to 9 harmonics. Weak frequency-modulated. Two formants are more intense: 1)300-600 Hz, 2) 2.5-2.9 kHz. Amplitude-modulated. The first formant is the loudest in the middle of the sound. Maximum frequency – 5.3 kHz, sound duration – 2290 ms	Seems to have a calming effect after a skirmish or rumpus.
5. Calm sighing, hooting	0.15	0.11	0.13	Noisy sound. The interval of 200-1200 Hz is more intense. Max. frequency –7 kHz. A series, individual sounds are hardly distinguished.	First contact, when meeting other animals; when asking for something; when an excited male is becoming calmer.
6. A series of guttural 'oh' sounds.	0.08	0.10	0.09	Sounds of weak intensity – could not be processed with sonography.	An eating sound made before feeding or while eating.
7. Play sounds: squeaking, creaking, whining, a series of 'ah' sounds with aspirations.	0.13	–	0.06	Whining. Mixed sound. Basic formant – 2.3-2.6 kHz. Max. frequency – 8 kHz. Duration – 530 ms. Squeaking. Harmonic sounds. 3 harmonics. Basic formant – 700-1200 Hz. Frequency-modulated. Maximum frequency – 6 kHz. Sound duration – 520 ms. Frequent aspiration with groan. Noisy sound. Maximum frequency – 7 kHz. A series of sounds. Sound duration – about 160 ms.	When a chimpanzee is willing to make contact with someone; during wrestling and grooming; to express pleasure while eating.

The chimpanzees from the laboratory at Koltushi hooted, emitted play sounds and cried more often. The zoo animals were characterized by frequent eating sounds.

Communication complexes. The chimpanzees used double complexes i.e., complexes comprising at least 2 elements from Table 2 more often – from 60% to 100%, while triple complexes represented 15.8% to 32.5%. Quadruple complexes were demonstrated even more rarely - from 5.3% to 9.4%, and the most sophisticated quintuple communication complexes were noted in only 2% of cases. Sex differences in the use of

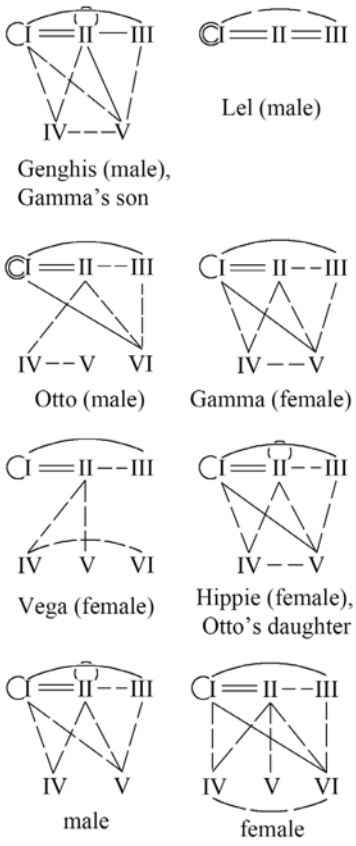
complexes were not detected (see Table 5).

An analysis of the connection between elements in complexes showed that females had a more rigid connection between facial expressions, tactile elements and acoustic signals. The female complexes included some elements of olfactory communication. Sometimes the females used complexes with several elements of postures (Figure 1).

However, if one examines the individual characteristics of complexes, one can see some variations. The complexes of Gamma and Hippie were very similar. Olfactory elements were found only in the complexes of Otto and Vega. Lel used quite simple complexes consisting of facial expressions, postures and gestures. Lel and Vega did not demonstrate any connections between gestures and sounds. Otto, Hippie and Gamma demonstrated close connections between facial expressions and acoustic signals. Genghis and Hippie used some posture complexes (Figure 1).

Table 5. Percentage ratios of the various communication complexes and chains among adult chimpanzees (%)

Usage	Genghis	Lel	Otto	Gamma	Vega	Hippie	*Males*	*Females*
Double complexes	64.0	100	70.3	78.9	81.3	60.0	70.9	71.3
Triple complexes	28.0	–	20.3	15.8	18.7	32.5	21.3	23.4
Quadruple complexes	6.0	–	9.4	5.3	–	7.5	7.1	5.3
Quintuple complexes and more	2.0	–	–	–	–	–	0.7	–
CHAINS Type A	40.9	58.6	31.9	35.9	18.2	41.2	41.7	33.7
Type B	34.1	37.9	38.3	33.3	54.5	38.2	36.7	40.0
Type C	25.0	3.5	29.8	30.8	27.3	20.6	21.6	26.3
Contact initiation								
	88.6	89.7	85.1	95.0	68.2	70.6	87.5	80.0



I. Facial expressions
II. Postures
III. Gestures
IV. Tactile elements
V. Olfactory elements
VI. Acoustic elements. (See Table 2)

I have identified a number of communication complexes and found the connection between elements expressed as percentage ratios:

- - - - - - - - - from 1 to 9.99%
---------- - from 10 to 19.99%
========== - from 20% and more.

Figure 1. Connections between elements in the communication complexes of adult chimpanzees

Communication chains. This study has demonstrated that females make short contacts much less frequently than males. The minimum percentage of such contacts was demonstrated by Vega (18.2%) and the maximum by Lel (58.6%). Long-lasting contacts were more characteristic of females and especially Gamma (30.8%). At the same time, males and females had an almost equal number of contacts of medium duration (33-39%) and only Vega showed a greater percentage (54.5%).

Contacts were generally initiated by males, though the highest value for this type of behaviour was shown by Gamma (95%) (Table 5).

Communicative sequences. The communication processes of males and females, and the species as a whole, are shown in the form of a diagram in Figure 2, i.e., it shows certain regularity in behaviour – a sequence of adopting particular communication channels while communicating with group members. For example, when becoming closer, if the communication takes place between two chimpanzees, then they generally sit side by side and start to groom their partner. Males sometimes sniff the body and anal-genital region, while females offer hands or emit contact sounds. After moving away, chimpanzees usually start autogrooming.

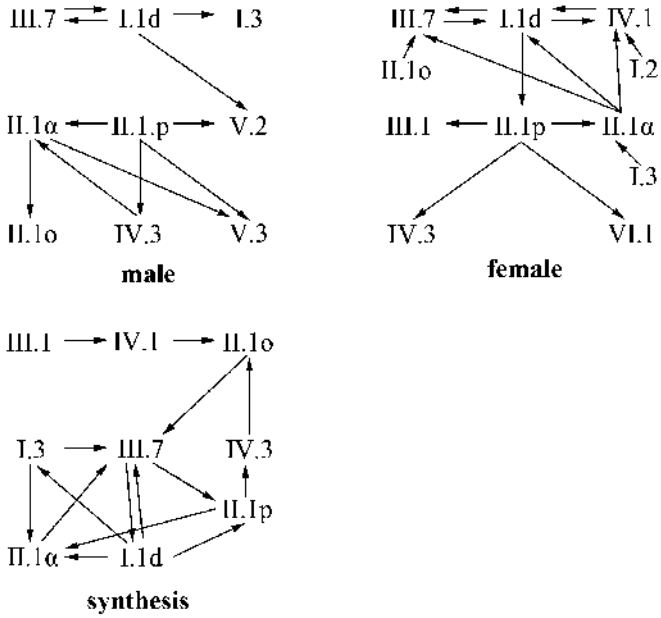


Figure 2. Communicative sequences of adult chimpanzees

I. Facial expressions
II. Postures
III. Gestures
IV. Tactile elements
V. Olfactory elements
VI. Acoustic elements. (See Table 2)

Arrows show basic transitions from one element to another. Double arrows running parallel to one another in opposite directions indicate mutual transitions.

Synthesis = male + female.

TABLE 6. Stability factors in the communicative processes of adult chimpanzees

Animal	Stability factor	Stability factor of signals	Stability factor of responses
Genghis	0.3	0.32	0.37
Lel	0.02	0.11	0.1
Otto	0.38	0.27	0.14
Gamma	0.09	0.19	0.15
Vega	0.2	0.05	0.17
Hippie	0.3	0.57	0.28
Males	0.07	0.03	0.09
Females	0.11	0.16	0.1

The stability factor in the communication processes of females is a little higher and therefore their communication pattern is more stereotypical (Table 6). However, both the maximum and minimum values for this factor are seen in males – Otto (0.39) and Lel (0.02). This suggests that the process of communication is in someway determined by the individual peculiarities of apes.

Communication pairs based on signals and responses. It was noted that after looking at a partner the females generally moved closer, whereas the males moved away. Females, while sitting side by side, offered hands or groomed themselves, whereas males tended to move away. Females were more likely than males to groom partners after having been groomed themselves. The females demonstrated higher stability factors in both signals and responses. If we look at each chimpanzee individually, then we see that males have higher stability factors in signals, but the maximum value was recorded for a female – Hippie (0.57). The females were more conservative in their responses, though the maximum value for the stability factor in responses can be seen for the male – Genghis (Table 6).

While examining the communication system of adult chimpanzees, I found that it is very variable. Individual characteristics of communication seem to have nothing to do with sex and to be only weakly connected to 'domination and submission'. Perhaps, the communication processes of chimpanzees are in some way determined by housing conditions. For example, chimpanzees from the zoo, where cages were smaller than the aviaries at Koltushi, used friendly tactile elements (grooming, touching with hands, sexual attention etc.), sniffed the anal-genital region and body more often, emitted fewer play sounds and many eating sounds. Sexual dimorphism was detected using olfactory elements, mainly used by males. The males usually initiated contacts. With other communication parameters, variability was the result of individual peculiarities in the communication process, which are probably determined by temperament, the emotional state of the individual and the general situation.

Thus, the communicative system of adult chimpanzees is quite individual. The communication process is probably affected not only by social position and sex, but also by mentality.

Young chimpanzees

Let us now move on to examine the elements, and their frequency, used by young chimpanzees of various ages (Table 7).

TABLE 7. Communication elements and the frequency of their manifestation among young chimpanzees

ELEMENTS	Alpha 3.5 yrs	Lesya 2.5 yrs	Styopa 2.5 yrs	Alpha 4.5 yrs	Lesya 3.5 yrs	Styopa 3.5 yrs
FACIAL EXPRESSIONS Neutral glance	2.39	1.90	2.59	4.36	3.50	3.73
Staring	0.50	0.62	0.41	1.00	0.40	0.09
Looking round	1.00	0.38	0.44	1.36	0.50	1.27
Open mouth	0.18	0.002	0.22	0.09	0.10	0.18
Open mouth with teeth	–	–	–	–	–	–
Half-grin	0.25	0.14	0.04	0.36	0.10	–
Half-grin with teeth	–	–	–	0.09	0.10	–
Grin	0.18	–	0.15	0.27	0.002	–
Oscitation	0.04	–	–	0.18	–	–
Bared teeth (closed grin)	0.11	0.05	–	0.18	–	–
Protruding lips	0.36	0.52	0.55	0.54	0.60	0.73
Pursed lips	0.36	0.38	0.52	–	0.10	0.09
Puckered lips	0.46	0.52	0.81	1.27	0.70	1.36
Puckered upper lip	0.07	–	0.15	0.09	–	–
Puckered lower lip	0.43	0.43	0.15	0.18	0.30	–
Turned-up lower lip	–	–	–	–	–	–
Turned-up upper lip	0.21	0.19	0.26	0.09	0.10	0.18
Both lips puckered and turned up	–	–	–	–	–	–
Saggy lower lip	–	–	–	1.09	0.70	–
Pouted lips	0.86	0.19	0.55	1.45	0.90	0.18

TABLE 7. continued

Pouted upper lip	0.54	0.14	0.30	0.64	0.10	0.09
Pouted lower lip	0.11	0.05	–	–	–	–
Compressed lips	0.21	0.05	–	–	–	–
Pursed lips	–	–	–	–	–	0.18
Bitten lower lip	0.07	–	0.04	–	–	–
Bitten upper lip	–	–	–	–	–	–
Chewing with lips	0.29	0.05	0.30	–	0.20	–
Protruding tongue	–	–	–	–	0.10	–
Licking lips	0.04	–	–	–	–	–
Smacking lips	0.07	–	0.04	0.18	–	–
Chattering teeth	0.04	–	–	0.09	0.10	–
Flush	–	–	–	–	–	–
Eyebrow movements	–	–	–	–	–	–
Ear movements	0.04	–	–	–	–	–
Wrinkled forehead (with horizontal folds)	–	–	–	–	–	–
Play face (smile, half-open and upward-sloping mouth)	2.36	1.71	2.26	2.09	2.30	3.54
MOVING AND POSTURES Coming closer	1.07	1.57	2.81	1.36	4.00	7.82
Moving away	1.54	1.10	2.11	2.91	2.90	5.18
Sitting alone	0.75	0.52	0.52	1.73	0.70	0.82
Sitting side by side	1.61	1.62	1.48	4.82	3.60	6.54
Walking after someone	0.71	1.14	1.19	0.36	0.20	1.18
Walking side by side	–	–	–	0.90	0.20	0.82

TABLE 7. continued

Hanging and swinging	0.11	1.10	0.44	0.09	0.90	1.27
Swaying when seated	–	–	–	–	–	–
Swaying when standing	–	–	–	0.27	0.60	0.64
Walking and swaying	–	–	–	–	–	–
Thrust (body throw)	0.50	–	0.78	1.00	0.20	0.64
Bouncing	0.18	–	0.19	0.09	–	–
Turning	–	–	–	–	0.20	–
Turning away	–	–	0.07	0.54	–	0.27
Exposing	0.36	0.05	0.26	–	0.10	–
Lifting up head	–	–	–	–	–	–
Waggling head	–	–	–	–	–	–
Nodding	–	–	–	–	–	–
Head thrust	0.11	–	0.04	0.18	–	–
Lying	0.25	0.57	0.07	0.82	0.10	0.27
Standing	0.43	0.24	0.26	0.09	0.20	0.07
Hanging	0.54	0.62	0.63	0.27	1.70	2.00
Climbing	0.25	0.14	0.55	0.45	0.20	1.64
Walking	0.04	0.24	0.30	0.18	0.50	0.27
Running	–	–	–	–	–	–
Jumping	0.25	–	0.26	–	–	–
Standing on hind limbs	–	–	–	0.27	0.20	0.18
Demonstration of genitals	0.04	–	–	0.09	0.02	–
Penis erection	–	–	0.04	–	–	–
Raised hackles	0.07	–	0.022	–	–	–
GESTURES Autogrooming	0.74	0.33	0.55	1.54	0.20	1.00
Slapping hands	0.04	0.29	0.04	–	–	–

TABLE 7. continued

Knocking surface with hands	0.61	0.24	0.29	0.18	0.20	0.09
Knocking surface with objects	–	–	0.04	–	–	–
Shaking bars	0.04	–	0.07	–	–	–
Targeted throwing	0.74	–	0.07	0.18	–	0.45
Offering supine hand	0.43	0.62	0.48	0.45	0.40	0.64
Offering prone hand	0.25	0.04	0.11	0.09	0.10	0.18
Waving hand	0.25	0.48	0.30	–	–	–
Chopping with hand	0.57	0.04	0.52	0.27	0.20	0.36
Waving hand with object	0.04	0.10	0.07	0.09	0.10	–
Offering hand with object	0.04	0.05	0.19	–	–	–
Shaking hands bent at elbows	–	–	–	–	–	–
Shaking palm in front of face	0.07	0.19	0.15	–	–	–
Raising hand	0.07	–	0.07	–	–	–
Covering face with palm	–	–	–	–	–	–
Waving aside	0.11	–	0.04	–	0.20	0.09
Pointing hand	–	–	0.04	–	–	–
Hand thrust	0.07	–	0.04	0.64	0.30	0.18
TACTILE ELEMENTS Touching with hand	0.54	0.43	0.48	0.54	0.80	1.36
Pushing with hand	0.57	0.05	0.30	0.45	–	0.18
Grasping with hand	1.96	0.86	1.30	1.73	1.70	2.36
Dash with hand	0.64	0.48	0.96	1.36	1.20	1.27

TABLE 7. continued

Active grooming	0.18	0.14	0.07	0.54	–	0.27
Pulling with hand	–	–	–	0.18	–	0.18
Touching with face	0.18	0.19	0.30	0.27	0.20	0.45
Licking body	–	–	–	–	–	–
Kissing	–	0.10	0.07	0.82	–	1.18
Hugging	1.36	0.43	1.22	2.09	0.80	2.91
Touching partner's body with own body	–	0.14	–	0.09	0.10	–
Cuddling	0.14	0.05	0.19	0.27	0.50	0.27
Resting hand on anal-genital region	–	–	–	–	–	–
Mass fight	–	–	–	–	–	–
Touching with object	–	–	–	–	–	0.09
Hit with body, foot, head	0.32	0.62	0.92	0.18	0.60	1.18
Hit with object	0.04	–	0.07	0.09	–	–
Covering with hand	–	–	–	–	–	–
Clambering and hanging	–	0.52	0.19	–	0.40	–
Biting	0.39	0.14	0.59	1.09	0.20	1.18
Wrestling	2.54	1.71	3.14	1.36	2.80	2.73
Tickling	–	0.14	–	0.18	–	0.18
Holding with hand	0.04	–	0.04	0.54	0.20	0.45
OLFACTORY COMMUNICATION Naso-nasal	0.04	0.14	0.15	0.09	0.50	0.64
Naso-anal	0.07	0.10	–	–	–	0.18
Naso-corporal	–	–	0.04	–	–	–

Facial expressions. For young chimpanzees, 29 elements of facial expressions were distinguished (Table 6). During the first year of observations, the young chimpanzees used glances, open mouths, pursed lips, puckered upper lips, chewing and compressed lips more often. One year later the same individuals started to use more elements like protruding lips, pouted lips, puckered lips, thrusting-out the lower lip, jaw popping, and play face. Thus, during their first year the young apes had extended their range of facial expressions connected with lip movements.

A comparison of frequencies in the use of various miming elements showed that the most similar behaviour was seen in two females of the same age: Alpha, during the first year of observation, when she was 3.5 years, and Lesya, during the second year of observation, when she was also 3.5 years. The behaviour of Styopa (male, 3.5 yrs.) and Alpha (female, 4.5. yrs.) was different. Miming of 2.5-3.5-year-old females and 2.5-year-old males turned out to be similar. Alpha (female) showed a dramatic improvement in the use of facial expressions by the age of 3.5 to 4.5 years. Almost the same level of improvement was observed in a young male by the age 2.5 to 3.5 years. Unfortunately, I can not draw any specific conclusions here since the number of animals studied was very small – even though this information is valuable, nevertheless, particularly since there are no other chimpanzees in Russia, and it could be useful for formulating future hypotheses for studies conducted elsewhere. A few years later, after the collapse of the Soviet Union, all of these young chimpanzees, and some adults too, were sold to various zoos and soon afterwards died, but thankfully the figures and tables have helped me to preserve my observations of their development and specific features.

Posture. I have described 24 elements of posture, movement and types of locomotion with implications for communication (Table 7). During the first year of observation, the young chimpanzees moved and climbed in aviaries less actively than when they walked after one another and exposed their anal-genital regions. A year later, Alpha moved closer to other young chimpanzees less frequently than before and moved away from them more often, she also began to sit alone quite regularly. Styopa, on the other hand, started to approach other young chimpanzees more often and to sit by their side. Lesya also started to sit near other chimpanzees, but moved closer less frequently than the year before (Table 7).

During the second year of observation, I first noted elements such as ‘standing on hind limbs’ or ‘sitting and swaying from side to side,’ i.e., elements found in aggressive contexts (Borutskaya & Vasilyev, 1996). Moreover, these elements were observed in all three young chimpanzees. With age, Alpha and Lesya started to display their genitals more often. The general frequency with which they adopted postures, movements and conducted physical activity also increased with age. With regard to postures in communication, the behaviour of Alpha and Lesya showed more similarities, which is probably attributable to elements associated with sex and role.

Gestures. 17 elements related to gesture communication were recorded (Table 7). It is interesting, though, that during the second year of observation the young chimpanzees demonstrated less gesture elements - only 11. With age they became occupied by autogrooming and demonstrated hand thrusts more often. They also started to hit surfaces with the fore limbs and made chopping gestures less frequently. Handclapping, shaking palms in front of the face, hitting surfaces with objects, offering the hand with an object - were elements observed only in the young, aged 2.5-3. For example, when he was 2.5, Styopa used to point his hand when he saw a stranger near to his aviary. At the same time, he would get on his hind limbs and look back at Alpha, who was older than him. In general, it appeared that the older the animal, the less frequently it used gestures during the course of communication.

Tactile elements. 19 elements were noted to be associated with tactile or contact communication. As younger chimpanzees grew older, they used friendly and aggressive tactile elements more often. With age, they wrestled less frequently. Styopa (2.5 yrs.) and Lesya (3.5 yrs.) had the most similar tactile communication indices. When Lesya grew older, she became as active in contact communication as Styopa had been when he was 2.5 years. The behaviour of adult Alpha (4.5 yrs.) and Styopa (3.5 yrs.) was different, although they employed tactile communication more frequently than the other animals (Table 7).

Olfactory elements. Table 7 shows that Lesya and Styopa used naso-nasal sniffing increasingly with age. Styopa started to sniff the anal-genital regions of females when he was 3.5 years. In general, elements of olfactory communication were used rarely by young chimpanzees, with the exception of naso-nasal (friendly) sniffing, which was demonstrated by Styopa and Lesya when they were 3.5 years.

Acoustic signals. I distinguished 7 classes of sound. The findings are shown in Table 8.

TABLE 8. The Acoustic signals of young chimpanzees

Signal	Frequency of use		Bioacoustic characteristics	Situation
	Year 1	Year 2		
1. Sharp and short ‘ooh’	0.21	0.25	Mixed sound, Basic formant – 100-500 Hz. Maximum frequency – 2-3 kHz. Sound duration – 200-300 ms.	Used by Styopa and Alpha when threatened.
2. Series of ‘ah’ sounds	0.10	0.13	Mixed sound. Basic formant – 600-1100 Hz, maximum frequency – 4-4.5 kHz. Sound duration – 350-450 ms. Series with interval of about 300 ms.	Contact sound emitted by Alpha.
3. Series of longer ‘ooh’ sounds	0.17	0.24	Mixed sound. Basic formant – 100-450 Hz. Maximum frequency – 2-3.5 kHz. Sound duration – 150-200 ms. Series with interval of about 200-700 ms.	Emitted by Lesya when pursuing Styopa with outstretched hand, while Styopa was manipulating an object. An asking sound.
4. Series of breathy ‘ah’ sounds	0.42	0.43	Mixed sound. I distinguished 2 formants: 1) 80-300 Hz; 2) 500-750 Hz. Maximum frequency – 4-4.5 kHz. Sound duration – 220-400 ms. Series with interval of 300-600 ms.	Play sounds
5. Series of short and sharp guttural ‘oh’	0.08	0.06	Noisy sound. The interval of 600-1500 Hz is more intense. Maximum frequency – 8 kHz. Sound duration – about 200 ms. Series with interval of about 500 ms.	Eating sound.
6. Cries			Harmonic sound, 6-9 harmonics. I distinguished 2 formants: 1) 1.5-2 kHz, 2) 2.5-3 kHz. Frequency-modulated with waves. Maximum frequency – 6-7 kHz. Sound duration – 170-200 ms. Series with intervals of 180-260 ms.	Sound response to external aggression. The signal was emitted by Alpha.
7.Groaning			Mixed sound. Basic formant 5.2-5.7 kHz. Maximum frequency – 8 kHz. Sound duration – 120 ms. Series with intervals of 50-150 ms.	Emitted by Lesya when upset because she had been left alone.

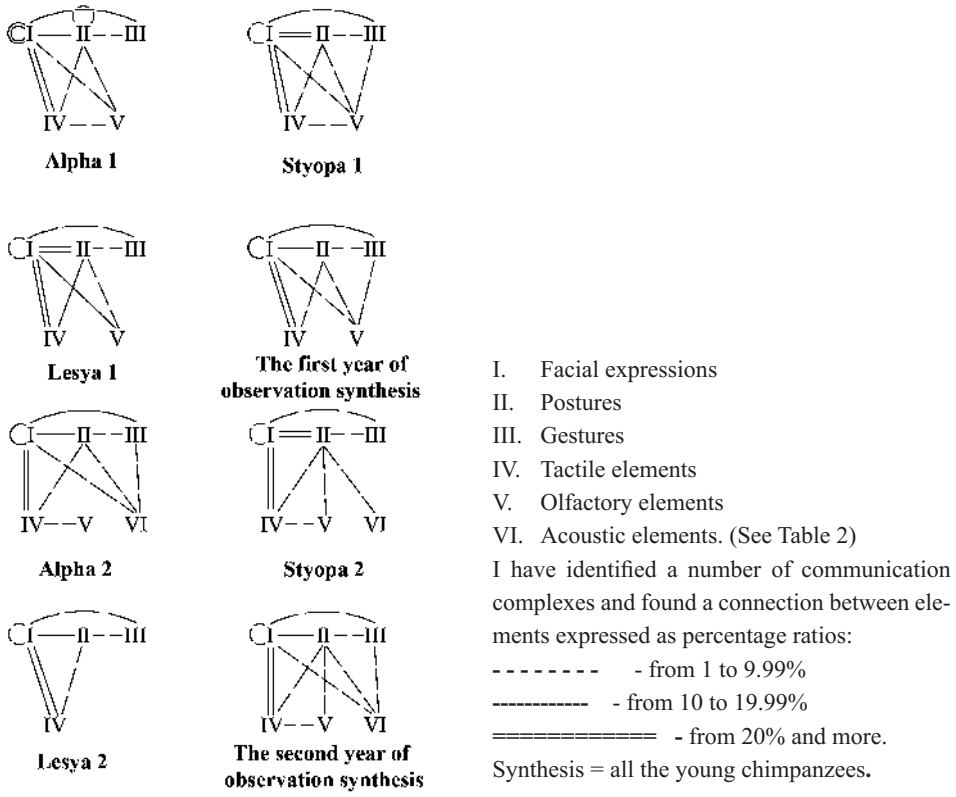
Communication complexes

An analysis of the connection between elements in the communication complexes of young chimpanzees, observed during the first year of observation, showed that when Styopa and Lesya were 2.5 years, there were close connections between facial expressions, postures and tactile elements. A year later, only Styopa retained such connections. Alpha, when she was 3.5 years, often demonstrated mime complexes and rarely complexes related to posture. She and Styopa demonstrated a more pronounced connection between facial expressions and gestures than Lesya. When Lesya was 2.5 years, she displayed close connections between facial expressions and acoustic signals and between tactile elements and posture. During the first year of observation, connections between gestures and sound were detected only for Styopa, but a year later they were no longer perceivable. On the other hand, Alpha started to demonstrate this connection when she was 4.5 years. Lesya showed no acoustic signals during the second year of observation. Therefore, the progressive connection between gestures and sound was demonstrated earlier in males and in older females. However, the cessation of acoustic signals in Lesya's communication complexes when she was 3.5 years, suggests that these connections develop individually. A year later, Styopa and Alpha started to use olfactory elements that are generally connected with tactile elements or postures (Figure 3). When Alpha was 4.5 years, he started to demonstrate mime complexes more infrequently.

During the second year of observation, the young chimpanzees adopted the use of double complexes more and more increasingly and triple ones less so. At the same time, the frequency of quadruple complexes increased (Table 9).

If one were to regard the general view of connections between elements in the communication complexes of young chimpanzees, one would note that mime complexes occur less and less frequently. The connection between facial expressions and gestures becomes weaker, elements of olfactory communication emerge, and the connection between tactile and acoustic elements disappear with age (Figure 3).

Figure 3. Connections between elements in the communication complexes of young chimpanzees



Communication chains. The study of communication chains is represented in Table 9. Older chimpanzees engaged in shorter contacts more often, and longer-lasting ones rarely. Contacts were increasingly initiated by Styopa. During the second year of observation, his contact initiation index increased. Lesya's contact initiation index also became slightly higher. Alpha initiated contacts less frequently than the others, and when she was 4.5 years the percentage of these contacts became even lower. Possibly caused by an age-related decrease in play activities.

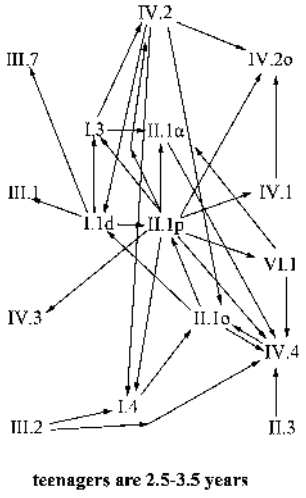
Table 9. Percentage ratios of the various communication complexes and types of communication chains among young chimpanzees

Usage	Alpha 3.5 yrs.	Styopa 2.5 yrs.	Lesya 2.5 yrs.	Alpha 4.5 yrs.	Styopa 3.5 yrs.	Lesya 3.5 yrs.
Double complexes	85.7	78.0	73.0	83.7	85.5	94.7
Triple complexes	14.3	18.7	25.0	10.2	11.6	2.7
Quadruple complexes	–	3.3	2.0	4.1	2.9	2.6
Quintuple complexes and more	–	–	–	2.0	–	–
CHAINS Type A	39.3	52.5	44.9	63.9	67.5	87.5
Type B	39.3	28.8	40.8	29.7	20.5	10.0
Type C	21.4	18.7	10.3	8.2	12.0	2.5
Contact initiation	75.0	85.0	83.7	65.6	97.6	87.5

TABLE 10. Stability factors in the communication processes of young chimpanzees

	Alpha 3.5 yrs.	Styopa 2.5 yrs.	Lesya 2.5 yrs.	Alpha 4.5 yrs.	Styopa 3.5 yrs.	Lesya 3.5 yrs.
Communication sequences						
Basic transitions	5.0	11.0	12.0	1.0	17.0	–
All transitions	87.0	113.0	54.0	32.0	6.5	–
Stability factor	0.06	0.1	0.22	0.03	0.26	1.0
System of signals						
Basic transitions	9.0	8.0	13.0	20.0	15.0	–
All transitions	60.0	59.0	48.0	48.0	43.0	–
Signal stability factor	0.15	0.14	0.27	0.42	0.35	1.0
System of responses						
Basic transitions	4.0	15.0	9.0	21.0	7.0	–
All transitions	60.0	56.0	33.0	47.0	33.0	–
Response stability factor	0.07	0.27	0.27	0.45	0.21	1.0

Communicative sequences. Alpha's communication process when she was 4.5 years, became more labile. The stability factor of her behaviour decreased (Table 10). The communication processes characteristic of Styopa and Lesya, when they were 3.5 years, became stereotyped. The signal and response stability factors of all chimpanzees increased with age. If one examines the general stability factors for the first and second years of observation, one can see a doubling of all three factors. This is probably associated with active socialization processes characteristic of chimpanzees from 2.5 to 4.5 years. Diagrams of the communicative sequences of young chimpanzees in two age categories are shown in Figure 4.



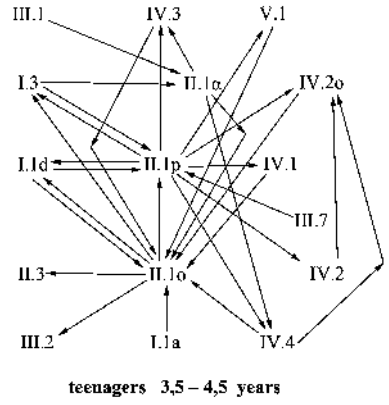


Figure 4. Communication sequences of young chimpanzees

I. Facial expressions
II. Postures
III. Gestures
IV. Tactile elements
V. Olfactory elements
VI. Acoustic elements. (See Table 2)

Arrows show basic transitions from one element to another. Double arrows running parallel to one another in opposite directions indicate mutual transition.

Conclusion

To conclude, let us now analyze the postnatal ontogenesis of the communication system of chimpanzees. I will start by examining the changes that occur in young chimpanzees' communication over time, and then compare young chimpanzees' communication systems with those of adults.

Facial expressions

The study of mime communication indices revealed, first, a difference between those of young chimpanzees and adult chimpanzees, and second, a difference between those of chimpanzees at the zoo and those at the laboratory in the village of Koltushi. The zoo chimpanzees showed a tendency to use glances, open mouth, and eyebrow movements.

Postnatal ontogenesis was characterized by an increase in the frequency of friendly glances, half-grins, oscitation, protruding lips, and lip smacking, and a decrease in staring, some elements of lip expressions (pouted, turned-up and puckered lips), and play face. Yet with regard to some elements, young chimpanzees during the first year of observation (2.5-3.5 yrs.), were closer to adults than to the young chimpanzees monitored during the second year of observation (3.5-4.5 yrs.). The elements I am referring to were: puckered lower lip, saggy lower lip, compressed lips, chewing with lips, and jaw popping. As a rule, young chimpanzees, aged 3.5-4.5 years, used them more often.

All of these changes are apparently related to socialization (the establishment of clear relations) within the chimpanzees' community. The chimpanzees start to employ more elements for maintaining a state of peace within the group. Both 'play face' and staring are used less frequently with age, since adults play less and the establishment of stable roles within the community results in the disappearance of frequent threats. However, the middle of ontogenesis was marked by a surge in the frequency of friendly elements of facial expressions, which probably indicates that chimpanzees establish social relations when they are 3.5-4.5 years old and that this process commences with the use of friendly facial expressions. Subsequently, the frequency of these expressions decreases. Thus, the postnatal ontogenesis of chimpanzees is above all characterized by friendly mime elements connected with lip movements.

Postures

The study of posture components in the visual communication of chimpanzees showed that the zoo chimpanzees were less active in their movements than the chimpanzees from the laboratory.

I discovered that posture communication in ontogenesis is characterized by an increase in the use of the following elements: sitting alone, lying alone, walking alone, and a decrease in the use of elements such as walking behind someone and walking side by side. However, I also noted a rise in the use of posture elements in 3.5-4.5-year-

old chimpanzees. These elements were: moving closer, moving away, sitting side by side, swaying from side to side, thrusts, the display of genitals, standing on hind limbs, hanging and climbing. Thus, there was a tendency to reduce activity with age and the frequency of elements associated with childhood (i.e., those demonstrating a need to be beside someone) decreased. However, as in the case of miming, the middle phase of postnatal ontogenesis was marked by an increase in activity. Thus, the development of chimpanzees' posture in communication is characterized by an increase in the frequency of elements associated with the establishment of certain connections in the community and the development of sexual and social roles.

Gestures

An analysis of gesture communication indices showed that Alpha (a female of 4.5 yrs) had similar values to adults, while and the other young chimpanzees had values that were similar to one another. I also noted some similarities in the behaviour of the oldest animals – Otto and Gamma. Gestures were most frequently used by the young, between the ages of 2.5-3.5 years. The use of gestures decreased with age. The only element employed by Otto and Gamma with maximum frequency was autogrooming. 3.5-4.5-year-old chimpanzees were characterized by a considerable increase in the use of hand thrusts, which was probably associated with the establishment of hierarchical relations at that age. Styopa first pointed his hand at the age of 2.5 years.

Tactile elements

I discovered strong similarities in the tactile communications of Genghis and Gamma, who carried out active grooming more often than the others. The behaviour of the other adult chimpanzees was distinguished by an increase in the importance of friendly contact elements. The young chimpanzees exhibited a greater diversity of tactile elements compared to adults. Elements such as hitting with the body, hind limbs and objects, placing hands on the anal-genital region, biting, tickling and wrestling were only seen in the young and were not found in the behaviour of adult chimpanzees. The use of active grooming increased with ontogenesis and pushing with hands decreased. The frequencies of other elements demonstrate an extraordinary surge in contact communication in 3.5-4.5-year-old chimpanzees. Sometimes, the frequencies of these elements were higher in this age group, by one or two orders of magnitude, than in those of adult chimpanzees. Consequently, I can affirm that the establishment of hierarchical relations in groups of 3.5-4.5-year-old chimpanzees is mainly based on an increase in contact or tactile communication – both friendly and aggressive.

Olfactory elements

Olfactory elements in communication were more often used by zoo chimpanzees. Frequencies for sniffing body and anal-genital regions increased with ontogenesis, while naso-nasal sniffing became more frequent in 3.5-4.5-year-old chimpanzees, i.e. this element was used during a specific period of development.

Acoustic elements

The acoustic signals of adults and 2.5-4.5-year-old chimpanzees were quite different. Let us examine several classes of sounds.

Hooting in adult chimpanzees is used as a threat or as a contact sound. In the case of excitement before an aggression, hooting is produced with a frequency of 150-600 Hz, with increased loudness and frequency of emissions in a series. As a contact sound, hooting is generated with a frequency of 200-1200 Hz with weak intensity. In the case of a threat, the young animals reproduce individual sharp and short 'ooh' sounds with a frequency of 100-500 Hz. Hooting to convey asking was noted while observing Styopa and Lesya – with a frequency of 100-450 Hz and was characterized by a weak intensity. Thus, chimpanzee hooting is a polyfunctional sound. It is generally reproduced with a frequency interval of 100 to 1000 Hz. Depending on the situation and the emotional state of the chimpanzee, the frequency of sound generation in a series and the intensity varies. J. Goodall (1992) is of the opinion that hooting is among the distant signals, which she defined as interrogative, salutatory, growling or roaring and spontaneous hooting.

Acoustic signals related to eating made by young and adult chimpanzees are similar and represent a series of short, snappy guttural 'oh' sounds. This is a noisy sound with more intense intervals of 600-1500 Hz. This sound is usually described as grunting (Marler & Tenaza, 1977; Goodall, 1992). As V.Y. Plotnikov (1989) noted, the eating sounds of chimpanzees younger than 3 years of age are directed towards inedible objects.

The play sounds of adult and young chimpanzees are similar. These are a series of 'ah' sounds with breathing. Wrestling is sometimes accompanied by various sounds expressing pleasure and comfort. Such sounds are squeaking, whining, creaking, laughing. One of the most interesting buffering sounds recorded for adult and young chimpanzees was a female's cry. By comparing cries emitted by Vega and Alpha when they were attacked, I came to the conclusion that they were virtually uniform. It was a harmonic sound with two pronounced formants: 1-2 kHz and 2.25-3 kHz, frequency-modulated. Alpha's cry was almost two rimes longer. The cries and barking recorded for adult males during threats or aggressions were not heard in 2.5-4.5-year-old animals. J. Goodall (1992) considers all cries and barking to be among distant signals. Marler and Tenaza (1977) wrote that males can use cries as threats. The cry I observed had one formant of 1-1.75 kHz and a duration of 900-1100 ms.

Young chimpanzees emitted a high-frequency sound of discomfort – groaning. Adult chimpanzees did not make this sound.

The frequency of acoustic signals increases slightly with age. Play sounds prevail among young chimpanzees, together with play.

Communication complexes

There were similarities between adult and 2.5-3.5-year-old chimpanzees in the use of double and triple complexes. The 3.5-4.5-year-old animals had a greater share of double complexes and a smaller share of triple ones. Percentage of quadruple complexes

increased with age. Quintuple and higher complexes were recorded only for adult chimpanzees.

The connection between elements in communication complexes was very different in young and adult chimpanzees, i.e. it was highly individual. However, based on my findings, I was able to compare young and adult chimpanzees, and therefore, to examine changes in characteristic connections between elements in postnatal ontogenesis. With age, young animals' complexes start to include some of the elements of olfactory communication connected with posture and tactile elements. Adult chimpanzees retain the connection between olfactory elements and posture. Young chimpanzees are characterized in communication complexes by a close connection between facial expression and tactile elements, caused by their frequent wrestling. Adult chimpanzees play less frequently and therefore such a connection in their communication complexes is absent. However, they demonstrate a connection between facial expression and posture, much more so than in young animals. Adult chimpanzees have more rigid connections between facial expressions and gestures, and facial expressions and acoustic signals. They also demonstrate more mime complexes and complexes of posture elements.

Communication chains

Adult chimpanzees – like the young chimpanzees during the first year of observation – engaged in medium and long-term contacts more often. Most of the contacts witnessed among 3.5-4.5-year-old chimpanzees were short. Table 11 shows how the communication processes of 3.5-4.5-year-old chimpanzees were more stereotypical. This feature was manifested by a sharp decrease of transitions between communication elements, i.e., an increase in the share of basic transitions in the communication process. Adult chimpanzees show an increase in all transitions and a decrease in basic ones, and therefore, the variability of their communication increases when compared to that of young chimpanzees.

Table 11. Stability factors in the communication of chimpanzees

	Young animals 2.5-3.5 yrs.	Young animals 3.5-4.5 yrs.	Adults
Communication sequences			
All transitions	171	100	238
Basic transitions	31	32	15
Stability factor	0.18	0.32	0.06
System of signals			
All transitions	102	72	107
Basic transitions	24	31	3
Signal stability factor	0.24	0.43	0.03
System of responses			
All transitions	103	75	83
Basic transitions	22	35	5
Response stability factor	0.21	0.47	0.06

Let us compare the communication sequences shown in Figures 2 and 4. If one were to select one of the key elements in communication, e.g. moving closer, among young chimpanzees, this may be followed by such elements as: grooming, lip expressions, sitting side by side, hugging, touching with the hand, play face, contact sound signals, aggressive tactile elements, and naso-nasal sniffing. Whereas in adults, after moving closer to a partner, they usually start to groom or just sit nearby. However, the total number of transitions in adult chimpanzees is higher than that of young chimpanzees. It is also interesting to note that the system of basic transitions characteristic of young chimpanzees also includes some aggressive tactile elements. While adults do not have such elements among their own. As for 2.5-3.5-year-old chimpanzees, such contacts were generally caused by 6 aggressive tactile elements. A year later, young chimpanzees only had 2 contact elements of this kind.

Communication pairs based on signals and responses

In 3.5-4.5-year-old chimpanzees, basic transitions in communication pairs based on signals and responses, account for almost half of all transitions. Consequently, their signal and response stability factors were the highest. Examining the dialogues illustrated in Figure 5, if one were to take an element that usually indicates the end of a contact, e.g. moving away, 3.5-4.5-year-old chimpanzees moved away in response to 11 elements displayed by the individual with whom they were engaged in the contact. Adults moved away more often when another chimpanzee approached. Young chimpanzees had 7-8 mutual transitions, i.e. transitions between pairs of elements representing responses to each other. 3.5-4.5-year-old chimpanzees used 5 elements representing responses to elements of the same group. Adult chimpanzees only had one such element – grooming.

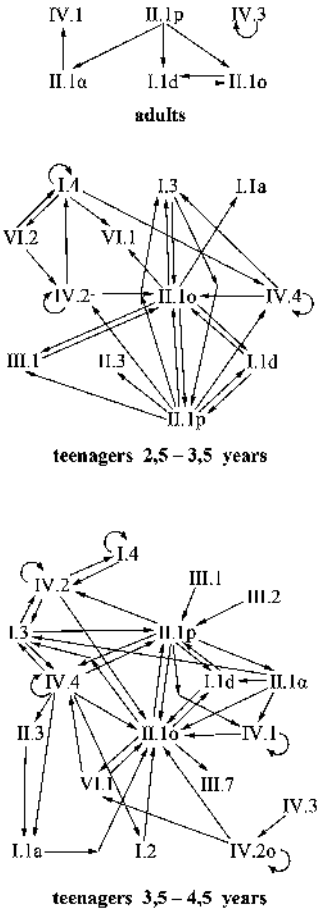


Figure 5. Communication pairs based on signals and responses in young and adult chimpanzees.

I. Facial expressions
II. Postures
III. Gestures
IV. Tactile elements
V. Olfactory elements
VI. Acoustic elements. (See Table 2)

The arrows show basic transitions from one animal's signal to the other animal's response.

To conclude, the findings of my research on the development of the communication system of chimpanzees during ontogenesis revealed that 3.5-4.5-year-old chimpanzees were characterized by a more frequent use of communication elements associated with the establishment of the 'domination/submission' system of the group and with their own inclusion in its social structure. The frequent use of certain posture elements suggested the importance of the functions of sex and role when communicating at this age. This hypothesis was also confirmed by the emergence of olfactory elements in communication complexes also at the age of 3.5-4.5 years. However, the communication processes of young chimpanzees at this age were quite stereotyped. This uniformity was determined by a decrease in the number of overall transitions, an increase in a number of basic transitions, and a great deal of elements resulting in the same elements in response. Young chimpanzees were further characterized by the frequent use of aggressive contact elements which were uppermost in their communications. Communication between adult

chimpanzees was friendlier and very variable. This may be accounted for by the fact that 4-5-year-old chimpanzees generally undergo a process of socialization.

The 2-3.5-year-old chimpanzees were much involved in games, which helped with the development of motor functions and their applications (Ladygina-Kots, 1935). When certain situations for using particular communication elements arose, the young chimpanzees started to search for new, less likely applications/responses.

At the age of 4-5 years, the young chimpanzees started to establish primary hierarchical relations within the group on the basis of established connections between signals and situations. Aggressive tactile contacts were very important for the latter. I surmise that it was this process that caused the stereotyped nature of young chimpanzees' communication.

As younger male chimpanzees generally become more mature, sexual relations are included in their primary social relations, i.e., hierarchical relations are now supplemented by the need to possess a female, to protect a group and territory. Therefore, relations between chimpanzees become more complex with age, which results in a sharp increase in the number of situations in which chimpanzees are likely to participate. The established connections observed between signals and situations disappeared at the age of 4-5 years. The number of signals became less than the number of potential situations for using them. That is why the signals of adult chimpanzees are polyfunctional. Now the main information load (or content) depends on the situation, and not the signal. J. Goodall (1992) also described some acoustic signals containing different information depending on the situation. Consequently, variability in the communication process characteristic of adult chimpanzees may also have been determined by the polyfunctionality of signals. It is also interesting to note that adult chimpanzees rarely engage in aggressive contacts.

Communication between anthropoid apes serves to increase the sociability of intergroup members. The most significant elements were those that were friendly, especially with regard to acoustic and visual communication channels. Friendly gestures were accompanied by friendly sounds, the connection between friendly visual and acoustic communication became stronger. In aggressive contexts, I noted harmonic sounds and in the friendly ones – mixed articulatory sounds like 'ah', 'oh', 'ooh'. The elements in communication complexes were not very variable and were used as established communication units. The communication process was quite labile and the communication systems were characterized by high individual variability.

One can assume that communication among their pongid ancestors occurred mainly via visual cues. Gestures developed into a friendly context of behaviour and their connection with similar acoustic signals became stronger. The phylogenesis of primates saw the disappearance of noisy sounds in aggressive acoustic signaling and their replacement by harmonic ones, as well as the emergence of various mixed articulatory sounds in friendly contexts. The communication complexes became more and more established communication units, and the communication process probably became increasingly variable as a result of the polyfunctionality of signals. More complex and diverse in-

formation transmitted due to signal polyfunctionality resulted in the development of creative thinking. Codes for this type of thinking were probably represented by sensory images connected to various situations. In the stage of primate and hominid phylogenesis corresponding with modern pongids, there occurred the emergence of primary conceptual signs – gestures that could convey meanings and reflect the emotional states of the interacting individuals, together with elements from other communication channels.

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