“Visual and tactile communication of a captive hamadryas baboon group (*Papio hamadryas hamadryas*) with special regard to their intentionality”

D i s s e r t a t i o n

zur Erlangung des akademischen Grades

Dr. rer. nat.

vorgelegt der

Naturwissenschaftlichen Fakultät I
Biowissenschaften

der Martin-Luther-Universität Halle-Wittenberg

von

Frau Anja Dube

geb. am: 25.07.1969 in: Köthen

Gutachter/in

1. Prof. Dr. Michael Tomasello

2. PD Dr. Dietmar Weinert

3. Prof. Dr. Katja Liebal

Halle (Saale), 18.01.2013

Lovingly dedicated to my late parents

1. INTRODUCTION

1.1 Communication

Communication is a crucial element of the social life of many species. Animals are interested in influencing the living world around them. They are able to change the behaviour of other animals not only by actions like biting, hitting or pushing but also by using communication.

Several authors emphasize the difference between “communication” and “action”. “Communication is often seen as a way of changing another’s behavior without physical force or any large expenditure of energy” (Rogers & Kaplan, 2000, p. 3). An animal “… does not act physically to alter things to suit his needs, pushing or dragging other individuals about, beating them into submission, or the like. Instead, the actor's behavior provides other individuals with information, and the actions that they take on the basis of this information lead to any functions that are obtained” (Smith, 1977, p. 389).

Communication is a change in the behaviour of a recipient caused by a signal (Gattermann, 2006). In a communicative interaction the sender codes information into signals, which are transmitted through specific channels to a recipient who decodes them. These signals are relayed through chemical, acoustic, visual, tactile and electromagnetic channels (Gattermann, 1993) and often along more than one simultaneously.

Sender and recipient have adapted to each other under selection pressure and at least the sender should have an advantage by the communicative process (von Helversen & Scherer, 1988). Signals have evolved as an adaptation to the physical and the social environment (Rogers & Kaplan, 2000). These signals are phylogenetically ritualized. Other signals emerge during ontogeny. An individual learns or develops them during its lifetime – these signals are ontogenetically ritualized (Tomasello & Call, 2007).

Signals can be honest or deceptive. Very costly signals, e.g. for sexual selection such as a peacock’s tail, should be reliable (Zahavi, 1997). Relatively inexpensive signals, such as imitated warning colours, often cheat the receiver about the real state of the sender.

Signals have been classified into vocal and nonvocal signals. Tomasello and Call (2007) described bodily nonvocal communicative acts as gestural signals. “Gestures can use as a perceptual channel either the visual (e.g. arm raise), the tactile (e.g. poke at), or the auditory (e.g. ground slap) modality – or some combination of these” (p. 8).

Some authors exclude “facial expressions” from “gestures” (e.g. Tomasello et al., 1997; Liebal et al., 2004b, 2006; Pika et al., 2005; Pollick & de Waal, 2007;), while others regard both features as “gestural communication” (e.g. Maestripieri, 1997; Hesler & Fischer, 2007).

1.2 Intentional signals

Communication can be automatically without any intention of the sender. Many signals are involuntary (e.g. piloerection in mammals, colour change, sexual swellings in some primate species or the output of particular pheromones) and are controlled by physiological processes. Such signals are elicited by internal or external stimuli and are inflexible. Often the sender does not know that he is displaying these signals but they reach the recipient and can influence his behaviour.

On the other side of the continuum are voluntary signals where the sender has the intention to communicate. "The question of intentional versus unintentional signalling in animals is a hotly debated topic and one of major significance for the way in which we view and treat animals, but it is very difficult to study" (Rogers & Kaplan, 2000, p. 2).

Tomasello et al. (1997) characterised intentional signals by two criteria. First, there is a flexible relation between signal and goal (means-end dissociation). A single signal can be used for different goals and different signals can be used for the same goal. Secondly, the sender shows a special sensitivity to the social context such as gaze alternation between goal and recipient, waiting for a response from the recipient or regarding the attentional state of the recipient. Having an audience and regarding its behaviour (audience effects) is an important factor of intentional communication. Rogers and Kaplan (2000, p. 49) wrote: "If an animal communicates … unintentionally, it might be expected to signal in exactly the same way whether it is alone or in the company of other animals; if it communicates intentionally, we might expect it to confine its signalling to occasions when it has an audience."

The best approach to study intentional communication in higher animals is to focus on visual and tactile signals. Chemical signals are conveyed involuntarily and electrical signals do not occur. Some acoustic signals could be regarded as intentional (e.g. hitting at an object making a loud noise like chimpanzee males often do) but most of them, especially vocal signals such as screaming or barking, are linked to emotional states and are emitted in the case of arousal. Call and Tomasello (2007) pointed out that "… nonhuman primates seem to have only limited control over their vocalizations – very little in terms of call morphology and a bit more in the case of call usage, including some adjustments for audience presence or absence" (p. 5).

However, Cheney and Seyfarth (2007) wrote that while "giving particular calls in particular contexts" is probably genetically predisposed, it does not mean that a monkey's vocalization is totally involuntary. The repertoire of the calls may be relatively fixed but the usage and "their choice of whether to call or remain silent is more flexible" (p. 225). As an example they stated that predator alarm calls that were surely sometimes given in a threatening situation without an intention were also often given with

regard to the caller's audience. They concluded that "it seems likely … that the spontaneous vocalizations of monkeys are also under some voluntary control" (p. 227).

1.3 Primate social cognition

Primates are good candidates to investigate social cognition because many of them live in complex groups and establish long-term relationships. They also have a relatively large relative brain size and an extended developmental and learning period before reaching adulthood. They have a large repertoire "of means for expressing themselves socially in terms of species-typical displays that make manifest their emotional states and behavioral intentions" (Tomasello & Call, 1997, p. 342). In addition to communication, primate social cognition also includes social strategies, social knowledge and interaction as well as social learning and culture (Tomasello & Call, 1997).

In describing the baboons they observed, Cheney and Seyfarth (2007) wrote that "each animal maintains a complex network of social relationships with relatives and non-relatives … Navigating through this network would seem to require sophisticated social knowledge and skills" (p. 10) and "each individual must predict the behavior of the others and form those relationships that return the greatest benefit" (p. 12). Additionally baboons have to deal with a great variety of ecological challenges, such as finding food and avoiding predators.

Tomasello and colleagues conducted a long-term and trans-generational study about the ontogeny, learning, development and use of gestures in chimpanzees (Tomasello et al., 1985, 1989, 1994, 1997). They found that the chimpanzees used their gestures very flexibly and that their signal choice was often based on the attentional state of the recipient. Furthermore, they observed much individual variability within and between groups. It was concluded that youngsters learned their gestures not by imitation but through individual ritualization in social interactions with other chimpanzees, a process called ontogenetic ritualization (Tomasello et al., 1997).

Between 1999 and 2002 several comparative studies were begun to enlarge the knowledge about intentional communication in higher nonhuman primates, including the gestural communication in bonobos and gorillas (Pika et al., 2003; Pika, 2003; Pika et al., 2005) as well as orangutans and siamangs (Liebal, 2001; Liebal et al., 2004b; Liebal, 2005); see Call and Tomasello (2007). Besides these studies on apes and because "there are almost no systematic studies of intentional gestural communication of monkeys" (Tomasello & Call, 1997, p. 243) for the present study a monkey species was chosen – the hamadryas baboon (*Papio hamadryas hamadryas*).

1.4 Baboon ecology and behaviour

Baboons are Old World monkeys (Catarrhini/Cercopitheciodea) and belong together with mangabeys, guenons and macaques to the family Cercopithecidae/subfamily Cercopithecinae (e.g. Dunbar & Rowell, 2001; Rowe, 1996).
Old World monkeys are diurnal animals (Rowe, 1996) and have a well developed and sharp vision (Gautier & Gautier, 1999; Barrett, 2000) which is their primary sense (Barrett, 2000).
All monkeys of the genera *Papio*, *Mandrillus* (drill and mandrill) and *Theropithecus* (gelada) are called baboons.

There are two classification systems of *Papio* depending on author – either the species of *Papio* or the subspecies of *Papio hamadryas* were distinguished. In this study, the system by Rowe (1996) is used in which he described five subspecies: olive or anubis baboon (*Papio hamadryas anubis*), yellow baboon (*P. h. cynocephalus*), hamadryas or sacred baboon (*P. h. hamadryas*), guinea baboon (*P. h. papio*) and chacma baboon (*P. h. ursinus*). *Papio h. hamadryas* is often called the "desert baboon" and so is ecologically distinguished from the other *Papio hamadryas* subspecies of the grasslands called "savanna baboons".

Today hamadryas baboons are found in Somalia, Ethiopia, Sudan, Eritrea, Djibouti, Yemen and Saudi Arabia (van Hooff; 1988; Rowe, 1996; Swedell, 2006). Rowe (1996) estimated their conservation status as "rare". Along the Awash River in Ethiopia they hybridise with olive baboons *P. h. anubis* (Rowe 1996). In the mixed colony of the Madrid zoo *P. h. hamadryas* and *P. h. cynocephalus* as well as *P. h. hamadryas* and *P. h. anubis* mate and have fertile offspring (personal communication, Zaragoza, 1999).

Baboons are quadrupedal and terrestrial, spending most of the day on the ground and covering distances of about 10 km per day (Stammbach, 1987). During the night they use rock ledges and steep cliffs as sleeping sites (Stammbach, 1987). Their diet consists of grass, seeds, roots, tubers, leaves, flowers, fruits, nuts and animal prey including small vertebrates (Stammbach, 1987; van Hooff, 1988; Rowe, 1996).

Kummer and colleagues conducted a long-term study on the social behaviour of hamadryas baboons in the Southern Danakil subdesert in Ethiopia (Kummer, 1984) and found a uniquely complex four-level social structure: troops, bands, clans and one-male-units.
The largest unit is the troop, a variable association of several hundred baboons using the same sleeping cliff (Kummer, 1984).
The troop splits into stable and closed units – the bands. Bands number roughly 60 baboons that travel together and even sometimes fight as a unit (Kummer, 1984).

There are almost no social interactions between members of different bands (Stammbach, 1987).

A band consists of several clans – stable subunits, which separate during foraging. Usually a clan contains a couple of harem leader males with their families (one-male-units), one or two old males who have lost their females and a few subadults or young adults, the so-called followers. Stammbach (1987) noted that there are more social interactions within a clan than between clans. While females are transferred across clans and bands, hamadryas males remain in their natal clan. Therefore, the males of a clan should be relatives (Kummer, 1984).

The smallest unit is the one-male-unit (OMU) consisting of one adult male, some females and their offspring. They never divide. Hamadryas baboons have a harem system in which one male monopolises all sexually mature females of the unit. He herds them and threatens them when they separate from him (Kummer, 1984). Followers are not allowed to copulate with harem females and only rarely gain access to groom them. Harem leaders prevent every attempt by followers to get in contact with their adult females. But followers are able to establish their own OMU by "adopting" a juvenile pre-reproductive female and form the so-called initial unit (Kummer, 1982). In a study by Sigg et al. (1982) males were between 9 and 11 years old when they acquired their first female. All females left their natal unit before reaching the age of 3.5 years. The alternative way to form an OMU is through direct conflict with an established harem leader. Most harem leaders are able to retain their females for three years or more (Sigg et al., 1982). Females change OMUs two to three times throughout their life. They prefer transferring to harems that include females with whom they have previously lived (Stammbach, 1987).

Grooming is usually restricted to members of the same OMU. The harem leader is the focus of grooming by his females. Single males of one clan groom one another (Stammbach, 1987).

Kummer and Kurt (1965) compared the social behaviour of captive and wild hamadryas baboons and found only few differences. The captive animals spent more time with social activities. Also, zoo-born juveniles continued to play fight until subadulthood and thus longer than wild-born juveniles did. Out of 61 behavioural elements recorded in the wild only two did not occur in the zoo, and nine elements observed in the zoo colony were not found in the wild.

Baboons have developed a high mobility of facial structures (especially lips and brows) and numerous visible expressions combined with contrasting colours on the eyelids. They are able to send and receive graded and distinct signals to express subtle shadings of emotions and intentions (Estes, 1991).

1.5 Baboon cognition and communication

Hamadryas baboons are social animals living in a complex society with many conspecifics. It is necessary for them to effectively communicate with many different individuals. Therefore, they should have a large communicative repertoire.

Systematic studies about baboon cognition are scarce. In a study by Wolfle and Wolfle (1939) hamadryas baboons cooperated to obtain food. Beck observed hamadryas baboons who had learnt to use a stick to rake out of reach food and one hamadryas female who brought a tool to a male in an adjoining cage who needed to retrieve some food (1972, 1973). Baboons also use tools in the wild: leaves for cleaning, sticks and stones for throwing during aggressive encounters with conspecifics and also to extract food (Tomasello & Call, 1997).

Hamadryas baboons seem to have cognitive maps of their home area, e.g. they use shortcuts to their daily destinations or speed up their travel approaching water before they can actually perceive it (Sigg & Stolba, 1981).

Kummer (1982) made several observations about wild hamadryas baboons' social cognition. He described their use of social tools such as the "protected threat" (in which a female presents her rear to the harem leader while simultaneously threatening another female in the opposite direction). He also found that females in oestrus sometimes hid behind a rock and groomed or mated with a subadult male – an encounter the harem leader would not have tolerated in his presence. During these hidden encounters females occasionally looked to check the location of the leader. Kummer assumed that these females knew that an attack would be unlikely if the leader was unable to see them. Moreover, he observed while transporting two trapped adult males in one cage that the males sat at opposite ends of the cage oriented back to back to avoid looking at the other, seemingly to prevent confrontation. He also witnessed hamadryas baboon clans communicating in the morning about the direction of the waterhole where they would meet in the afternoon by walking together for a small part of the way exactly in the direction of the "daily meeting drinking place".

As experiments by Kummer et al. (1974) had shown, a male respects the pair bond between another male and a female if he was able to observe the interactions of this pair before he was admitted to them. Kummer also wrote that hamadryas baboons often use a kind of proactive recruiting: they show various sociosexual behaviours (like presenting or mounting) with a recruitee before a conflict with another animal (1967).

Kummer also developed a general ethogram for hamadryas baboons (1968). Various elements of this ethogram are signals: seven of them could be classified as vocal and nearly 15 as nonvocal.

Hall and DeVore (1965) described 28 visual (facial expressions included) and 15 tactile communicative elements as well as 14 vocalizations for baboons. Jolly (1975) compared 12 facial expressions of eight primate species and found 11 of them in baboons. A comparative study of communicative elements of some African monkeys was made by Bolwig (1978). He reported for anubis baboons eight assertive and aggressive signals. Pellat (1980) analyzed 13 facial expressions of *Papio ursinus*. Ransom (1981) found for the baboons in Gombe 14 vocal signals. Furthermore, he reported 38 visual (facial expressions included) and 17 tactile signals. Strum (1987) investigated anubis baboons and focused on presenting variations, elements of play, aggression and uncertainty. Coelho and Bramblett (1989) gave a detailed ethogram of the genus *Papio*. Colmenares (1990, 1991a and b) investigated the greeting behaviour of baboon males, Easley and Coelho (1991) the signal lipsmacking, and Mehlmann (1996) analysed branch shaking displays. A detailed report about play signals was given by Pellis and Pellis (1997). Cheney et al. (1995, 1996) and Cheney and Seyfarth (1997) analysed baboon grunts and barks, Cowlishaw (1997) baboon alarm calls and Rendall et al. (1999) grunts in different contexts in chacma baboons. Barrett (2002, personal communication) reported 12 vocal, 11 visual (facial expressions included) and three tactile signals.

1.6 The study

This work should add much needed comparative research to the field of nonhuman primate communication. The aim of this study was to investigate the intentional usage of visual and tactile communication of hamadryas baboons.

Communication is here defined as the “indirect” achievement of a goal via information conveyed by means of signals from the sender to the recipient (without physical force). The term “signal” as it is used here includes facial expressions (“expressive movements of different parts of the face, like mouth, lips and eyes”, Liebal, 2005, p. 22) as well as gestures (“expressive movements of limbs or head and body postures”, Liebal, 2005, p. 22) because both elements are important for monkey communication and for the purpose of the study being presented here.

Only nonvocal signals were investigated (some of them occurred also together with audible components): postures, movements and also facial expressions respectively components of them.

Some parts of this study were purely descriptive.

First, it was analysed how many different and what kind of visual and tactile signals were produced, how and by whom the signals were used as well as which signals were used most frequently. Moreover, differences with regard to sex, age class and

individual were investigated. In addition to single signals, simultaneously combinations of two or three signals were analysed. Furthermore, spatial and visual relations between sender and recipient (distance and gaze contact), attentional state and response of the recipient as well as context of the single signals were investigated.
The main question being addressed here is whether the monkey species hamadryas baboon shows intentional communication.

2. MATERIAL AND METHODS

2.1 Observation times and methods

This study was conducted with captive hamadryas baboons (*Papio hamadryas hamadryas*) in Leipzig Zoo, Germany. The group was composed of more than 30 baboons and was housed in an indoor-outdoor facility.

At the beginning of 1999, pre-observations were made to practise the recognition of the individuals and to study the group structure and the behaviour of the baboons.
There were two observation periods – the first (OP1) from March to September 1999 and the second (OP2) from May to October 2000. These observations were made in the outdoor enclosure from the visitor area in front of the baboon enclosure. Data were collected between 9:00 a.m. and 7:00 p.m.
There were almost no interactions between the observer and the baboons. Those signals that did occur between observer and baboons were not counted whereas signals directed towards visitors or keepers were regarded as regular signals.

During OP1 the whole group was observed using ad libitum sampling (Martin & Bateson, 1993). Data were recorded by dictaphone (Professional Pocket Memo 598, Philips) and videotapes (NV-SX50EG, S-VHS, Panasonic). The audiotapes were scanned with a transcription device (Transcription System 720, Philips).

For OP2 14 focal animals (FAs) from all age classes were chosen (Martin & Bateson, 1993), data were collected by videotaping (Hi8 66E/77E, Sony).
A focal animal was tracked for five minutes (bout). The order of the animals depended on the availability and visibility of the focal animals. If it was impossible to follow or if the animal disappeared then recording was interrupted.

2.2 Subjects

Hamadryas baboons have pronounced sexual dimorphism (see figure 2.2 a). Full-grown males are grey, have a large shoulder cape and are almost twice as large as adult females, whereas females are olive-brown and have no shoulder cape (Stammbach, 1987).

There are several age classifications and some authors also distinguish between sexes.
For example, Kummer (1968) defined the following age groups: adult males > 7 years, adult females > 5 years; subadult males 3.5 to 7 years, subadult females 3.5 to 5 years; three-year-old males and females 2.5 to 3.5 years; two-year-old males and females 1.5 to 2.5 years; one-year-old males and females 0.5 to 1.5 years; black males and females: < 0.5 years. Females are sexually mature at the age of about 4 or 5 and males at the age of 5 to 7 years (Stammbach, 1987).
Females give birth first around the age of 6 years. After a gestation of about 170 days females give birth usually to a single infant (Rowe, 1996) which is first black in colour and changes to brown after approximately six months. The interbirth interval is about 2 years (Stammbach, 1987). In captivity there is an acceleration of growth and maturity and female baboons are able to have an infant every year. Some of the females of this study first conceived and the harem leaders first sired offspring at approximately 4 years of age. Sigg et al. (1982) found that feral males were between 9.5 and 13 years old when their first infant was born.

Figure 2.2 a
One of the harem leaders with two adult females (the female on the right is fully swollen)

Rowe (1996) wrote that hamadryas baboon females have an oestrus cycle of 30 days. Zinner (personal communication, 2000) reported a cycle length of about 40 days for captive animals (n=18). He found that the anogenital swelling lasts 18 days (maximal tumescence: 4-5 days).

For the present study the following age classes were created (in years):

		male	**female**
black infant	**INF1**	< 0.5	< 0.5
brown infant	**INF2**	0.5 - 1.5	0.5 - 1.5
juvenile	**JUV**	1.5 - 4	1.5 - 3.5
subadult	**SAD**	4 - 8	3.5 - 6
adult	**AD**	8 - 18	6 - 20
senescent	**SEN**	> 18	> 20

In the following, INF1 and INF2 as well as AD and SEN are sometimes combined (because of the small number of subjects). Occasionally only two age classes were created: older baboons (SEN+AD+SAD) versus younger baboons (JUV+INF2+INF1).

At the beginning of the first observation period (OP1) the baboon group consisted of 34 animals. During this period, one female infant (*Cora*) died (and as this occurred only shortly after the beginning of observation this animal was excluded from in the analysis) and one female infant (*Bea*) was born (and as this happened at the end of the observation period this animal was also not included in the analysis).
Between the two observation periods a juvenile male (*Steven*) was given to another zoo and three female infants (*Ayleen, Gela, Irina*) were born.
So the group consisted of 36 members at the beginning of the second observation period (OP2). The oldest female (*Eva*) as well as an infant female (*Gela*) died during this period.

Table 2.2 a
Age distribution of the baboons during observation periods 1 and 2

OP1	March to September 1999		**OP2**	May to October 2000	
	MALE	FEMALE		MALE	FEMALE
senescent	0	2	senescent	0	3
adult	0	10	adult	0	9
leader, SAD	2		leader, AD	2	
subadult	2	1	subadult	5	3
juvenile	3	5	juvenile	3	6
brown infant	4	3	brown infant	0	3
black infant	0	1	black infant	0	2
total	**11**	**22**	**total**	**10**	**26**

The recognition of individual animals was possible due to individual features and face tattoos. All individuals except the smallest infants were marked with various dots at particular locations on their faces coding a number.

The group was partitioned into two one-male units lead by the oldest males *Gunter* and *Kuno*. *Gunter* had eight *(Karin, Ina, Claudia, Edith, Anna, Gerda, Iris, Elke*) and *Kuno* had three sexually mature females (*Gesine, Brigitte, Steffi*) in his unit. The majority of females were sterilised in order to reduce the number of offspring. There were many subadult and juvenile males as followers (*Karlson, Bernd, Kevin, Erwin, Gerd*).
All animals are listed in appendix 1.

Paula was delayed in her physical and perhaps also mental development and started cycling later than normally developed females. Throughout the first observation period she appeared uncommitted to any particular OMU, and in the second observation period she was observed founding an initial group with one of the subadult males, *Bernd*. *Caroline* and *Grit* started cycling in the second period and copulated usually with followers during this time.
Until the end of 1998 all baboons composed one large harem. The leader was Karel, a very old male. After his death the group split into the two OMUs. Because of their mutual history the females of these different units were relatively familiar with one another. Furthermore the kin degree was generally very high in the group. These conditions together with the limited space of the enclosure and a lack of emigration and immigration caused special social relations and situations in the baboon group, e.g. friendly interactions between females of different OMUs and copulations between females and followers.

Scheumann (2001) investigated rank order and social behaviour of the same group and found the following results for the adult and subadult age classes:
Gunter group: INA = CLAUDIA > KARIN > Elke > Iris > Anna > *Gerda* > *Caroline* > *Edith*
Kuno group: GESINE > Steffi > Brigitte > *Selma*
Males: GUNTER > KUNO > Karlson > Bernd > *Kevin* = *Gerd* > *Erwin*
(Caps mark high-ranking, italics mark low-ranking, the others middle-ranking animals.)

2.3 Keeping conditions

The biggest part of the outdoor enclosure was composed of an artificial rock. It was surrounded by concrete surfaces of different levels and a part with soft ground for digging (wood chips). Logs and stumps and a hanging car tire provided environmental enrichment. The outdoor facility was bordered on three sides by a low clinker edge and

a ditch and on the backside by a high clinker wall. The enclosure measured about 10 m x 20 m (Scheumann, 2001). It is shown in figures 2.3 a and 2.3 b.
The indoor facility consisted of one large and two smaller cages and where not open to the zoo visitors.

The baboons were usually able to move freely between facilities. In winter they could choose between indoor and outdoor enclosure until the water in the ditch was frozen. During this time the animals were restricted to the indoor enclosure but were allowed access to a greater number of cages in order to avoid conflicts and stress within the group. In summer the monkeys spent most of their time outside during the day. The doors were closed until afternoon feeding given inside. After this feeding the baboons could move freely between the indoor and outdoor enclosures.

In the morning (at approximately 8:00 a.m.) the baboons were fed grains and later (at approximately 9:30 a.m.) were given porridge indoors. Between 11:00 and 12:00 a.m. they were fed vegetables and fruit and were again fed in the afternoon in the indoor enclosure. Additionally they received monkey pellets, bread and foliage.
The cages were cleaned every morning after the porridge feeding. During the cleaning the baboons were kept outdoors or in another cage. The outdoor area was swept clean while the group was present. Once a month (and more frequently in summer) the outdoor facility was cleaned and the water in the ditch was changed. During these days the monkeys had to stay in the inner cages.

Figure 2.3 a
The baboon facility seen from the right side

Figure 2.3 b
The baboon facility seen from the left side

2.4 Coding procedure and analysis

OP1:

The observation sessions of the first period resulted in approximately 85 hours of audio and 13 hours of video recording. The signals of 33 baboons were analysed.

These data were descriptive and were analysed for single signals and for every individual. An ethogram of communicative elements was made.

The ad libitum sampling method used in this part of the study had two notable limitations. One is that the more active individuals might attract more of the researcher's attention thereby biasing the data. The other is the possibility that the observer would miss the beginning or end of a particular communicative interaction.

OP 2:

The observation sessions of the second period resulted in 71 hours of video recording.

The tapes were carefully looked over and all signals produced by or directed to the focal animals (as sender or as recipient) were entered into a special coding scheme.

The analysis of the data of OP 2 was descriptive as well as quantitative.

Because of the difficulty to decide what element is “communication” and what is an “action”, signals displayed during play bouts were not counted except for those very well defined. In contrast, all signals displayed before play activities or in pauses were included.
Some new signals appeared in this observation period and others from OP1 were refined.

There were three data sources according to the origin of the signals:
S1: all observed signals of all animals of the group (as an overview)
S2: all signals displayed by the 14 focal animals (as main part of the analyses)
S3: only the signals produced by the current focal animal (sender = focal animal, in order to investigate frequencies)
These sources will be indicated for every analysis.

In total 4284 minutes of observation time were analysed:

	number of bouts	observation time
Ina	62	310.0 min
Gesine	62	310.0 min
Claudia	60	299.0 min
Kuno	62	310.0 min
Iris	61	304.5 min
Elke	62	307.0 min
Bernd	63	313.5 min
Erwin	63	310.5 min
Grit	62	307.5 min
Claire	63	315.0 min
Gundel	56	278.5 min
Igor	63	306.5 min
Gabi	63	311.5 min
Irina	61	300.0 min

2.5 Statistical methods

SPSS 8.0 was used for statistical analyses and only nonparametric tests were applied. The level of significance was $\alpha = 0.05$.
Data concerning age and sex classes were independent data and were analysed with a KRUSKAL-WALLIS test (four and six age classes) and a MANN-WHITNEY-U test, two sided (two age classes and the sex classes).
Data concerning the signals and combinations were regarded as connected samples and analysed with FRIEDMAN (four categories) and WILCOXON (two categories).

3. RESULTS

3.1 List of communication elements

31 different visual and tactile signals were found across both observation periods. These were classified into four categories according to sensory modality.
The category “visual signal” contains signals that the recipient received only by visual sense. In category “visual signal possibly making some noise” (“visual/noise”) the signal perhaps was accompanied by a sound that was secondary. “Visual signal often combined with touching” (“visual/touch”) means that a sender often touched the recipient while sending a visual signal. In the case of “tactile signal” there was always body contact between sender and recipient.

I. Visual signals

Eyebrow raising (Observation period 1+2) *eyebrow rais., ER*
The sender lifts its eyebrows, white areas beneath become visible.
See figures 3.1 b and c.

Enlisting (Observation period 1+2) *enlisting, EN*
The sender looks for support from a second animal (helper) by glancing back and forth between the helper and a third animal (victim).

Lowering the (upper part) of the body (Observation period 1+2) *low. body, LBo*
The sender bends arms (and sometimes stretches forward); sometimes also bending all limbs and lowering its whole body to the ground
See figures 3.1 d and e.

Lowering back (Observation period 1+2) *low. back, LBa*
The sender lowers its rear by bending its legs.
In the case that the sender is already in a sitting position, it turns its back into the direction of the recipient (often with its posterior slightly above the ground) and waits until the recipient climbs up onto its back before leaving place.
This signal was also recorded when it occurred during play. See figures 3.1 f and g.

Relaxed open mouth (Observation period 1+2) *relaxed o. m., RM*
The sender shows an open mouth display in a relaxed way (“play face”').

Head shaking (Observation period 2) *head shaking, HS*
Shaking the head rapidly from side to side.

Rolling on ground (Observation period 1+2) *rolling on gr., RG*
Sender lies down on the ground and rolls over on its side.

Hand-/Headstand (Observation period 1+2) *h./headstand, HH*

Unfinished or incomplete hand- or headstands were also counted.

See figure 3.1 h.

Threat mouth (Observation period 2) *threat mouth, TM*

The sender displays an open mouth (relatively wide, teeth mostly not visible).

See figure 3.1 l.

Head bobbing (Observation period 2) *head bobbing, HB*

Moving the head up and down similar to nodding.

Head movement (Observation period 2) *head mov., HM*

A slight movement of the head (and the eyes) in a specific direction looking like a request for a particular action.

Yawning (Observation period 2) *yawning, YW*

The sender opens its mouth very widely retracting its lips and showing its canines.

See figures 3.1 j and k.

Waving (Observation period 2) *waving, WV*

Sender makes a waving movement with one hand.

Head tapping (Observation period 2) *head tapping, HT*

Sender taps with its finger at its head.

Spinning (Observation period 2) *spinning, SP*

Sender whirls around its centre, also performed while walking or running.

II. Visual signals possibly making some noise

Chasing (Observation period 1+2) *chasing, CH*

The sender chases the recipient a short distance without reaching it.

This action may be very minor (sometimes only a skip or a step towards the recipient), but is distinguishable from a stiff threat.

Jumping in the air (Observation period 1+2) *jump. in air, JA*

Sender jumps using both its arms and legs.

This signal was also recorded when it occurred during play. See figure 3.1 i.

Pumping (Observation period 1+2) *pumping, PU*

Sender rapidly opens and closes the mouth (often with inflated jowls).

Senders occasionally appear to be chewing.

Stiff threat (Observation period 1+2) *stiff threat, ST*

The animal (sitting or standing) slaps more or less the ground with stiff arms using

either one or both hands (sometimes also thrusts out and lowers the body). They also occasionally hopped slightly forward while performing the stiff threat.

Displaying (Observation period 1+2) *displaying, DP*

The sender stands on a branch and swings up and down.

See figures 3.1 m and n.

Lipsmacking (Observation period 1+2) *lipsmacking, LS*

Rapid smacking of the lips, also with tongue protrusion and jaw-clapping.

It was not counted when it occurred during grooming.

Tapping ground (Observation period 1+2) *tapping gr., TG*

Sender taps or knocks the ground with its hands or other objects.

Object movement (Observation period 1+2) *object mov., OM*

Sender has an object in its hand and slightly moves it up and down.

Diving (Observation period 1+2) *diving, DG*

Sender stands with its limbs in the water and puts its head under water.

III. Visual signals often combined with touching

Presenting (Observation period 1+2) *presenting, PR*

The sender turns so that the posterior faces the recipient (only back present was counted). Often the sender looks back, slightly lowering its back, and raising its tail. The recipient often reacts by touching and sniffing the sender's back (not counted separately).

This signal was also recorded when it occurred during play.

See figures 3.1 q, r and s.

Greeting (Observation period 1+2) *greeting, GR*

A kind of saluting, both animals are positioned inverse parallel to each other. There are several versions, the majority occurred with presentation of the posteriors and mutual touching. It can be either unilateral or reciprocal.

See figures 3.1 o and p.

IV. Tactile signals

Poking (Observation period 1+2) *poking, PK*

A very short poke or grip or slightly touch of the recipient (without "physical power").

It was not considered when it occurred during presenting or greeting. See figure 3.1 t.

Mounting (Observation period 1+2) *mounting, MG*

The sender mounts the recipient by putting its upper extremities on the back of the recipient. Often the recipient looks back at the sender.

Subadult and adult females were counted only as recipient if they were not in oestrus to avoid recording copulations. Nevertheless, it is not possible to exclude any sexual context. It was also counted during play. See figures 3.1 u, v and w.

Pulling on (Observation period 1+2) *pulling on, PO*

The sender very briefly pulls the recipient's tail or foot.

Penis grab (Observation period 1+2) *penis grab, PG*

The sender briefly pulls the recipient's penis, usually while passing one another.

Jumping on back (Observation period 2) *jump. on back, JB*

The sender jumps over another animal briefly touching the recipient's back.

Figure 3.1 a: Relaxed baboon

Figure 3.1 b: Eyebrow raising

Figure 3.1 c: Several baboons show eyebrow raising *towards another animal (in front)*

Figures 3.1 d and e: Lowering upper part of the body

Figure 3.1 f: Lowering back *(by a female to a black infant)*

Figure 3.1 g: Lowering back *(by a young male to a black infant)*

Figure 3.1 h: Handstand

Figure 3.1 i: Jumping in the air

Figures 3. j and k: Yawning *(by males)*

Figure 3.1 l: Threat mouth *(by a young male)*

Figures 3.1 m and n: Displaying *(by males)*

Figure 3.1 o: Greeting *(adult females)*

Figure 3.1 p: Greeting *(harem leaders)*

Figures 3.1 q and r: Presenting

Figure 3.1 s: Presenting

Figure 3.1 t: Poking

Figure 3.1 u: Mounting *(harem leaders)*

Figure 3.1 v: Mounting *(youngsters)*

Figure 3.1 w: Mounting *(female to another baboon)*

3.2 Results of the first observation period

3.2.1 General occurrence of the signals

19 tactile and visual signals were found in a group of 33 baboons. Seven signals were categorised as “visual signal”, six as “visual signal possibly making some noise”, two as “visual signal often combined with touching” and four as “tactile signal”.

None of the 19 signals was used by all 33 animals. *Relaxed open mouth*, *presenting* and *poking* were the most common signals (used by 29 out of 33 individuals), followed by *eyebrow raising* (27 individuals), *mounting* (23), *stiff threat* (20) and *lipsmacking* (20). *Lowering body* (15), *greeting* (15), e*nlisting* (14), *chasing* (13), *rolling on ground* (11) and *pulling on* (11) were used by between one third and one half of the group. In contrast, very few baboons showed *pumping* (6), *lowering back* (5), *displaying* (4), *jumping in the air* (3), *hand/headstand* (3) and *penis grab* (2). The median for a signal was 14 individuals.

On average, more baboons (about two thirds of the whole group) used signals from the category “visual often combined with touching” than from the categories “visual” and “tactile” (roughly half of the group in both categories) and “visual signal possibly making some noise” (around one third of the group), but the differences were not significant. See also figure 3.2.1 a.

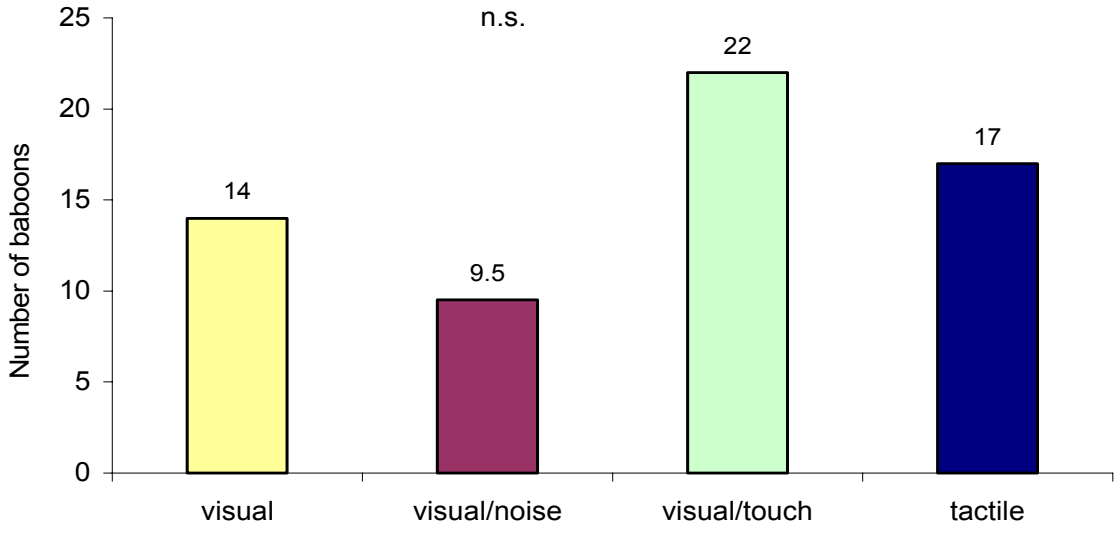


Figure 3.2.1 a
Median of the baboons using the signals in the four categories: “visual” (n=7 signals), “visual possibly making some noise” (n=6), “visual often combined with touching” (n=2) and “tactile” (n=4)

3.2.2 Number of different signals

Individuals

No baboon used all 19 different signals. Overall, the oldest and the younger baboons showed a smaller range of signals than the others.

13 baboons performed more than half of the signals (among these animals was no senescent and only one infantile baboon). An adult female (Claudia) and a juvenile female (Grit) displayed the highest number with 13 signals (68.4% of all signals) followed by one of the harem leaders (Kuno), a subadult female (Elke) and a juvenile male (Erwin), each with 12 different signals (63.2%).

The oldest female (Eva) and the youngest infant (Gabi) used the least number of signals (two and three; 10.5% and 15.8%). The retarded subadult female Paula and an infantile male (Elias) both used four signals (21.1%) and the second eldest female used five signals (26.3%). The median number of signals for all 33 baboons was 9 different signals (47.4%). The values for all animals can be seen in table 3.2.2 b.

Table 3.2.2 b
Number of different signals shown by the baboons (maximum: 19)

senescent		**adult**		**subadult**		**juvenile**		**brown infant**		**black infant**	
Eva	2	Ina	10	Kuno	12	Kevin	10	Steven	9	Gabi	3
Karin	5	Gesine	9	Gunther	9	Gerd	9	Gina	7		
		Claudia	13	Karlson	7	Erwin	12	Bert	7		
		Brigitte	10	Elke	12	Caroline	11	Gundel	8		
		Gerda	10	Bernd	11	Selma	8	Elias	4		
		Anna	11			Grit	13	Igor	6		
		Steffi	7			Gretel	8	Antje	6		
		Edith	11			Claire	6				
		Iris	9								
		Paula	4								

Age/sex classes (median)

The one black infant displayed 3.0 out of the 19 investigated different signals. The other infantile baboons used 6.7 different signals. The senescent baboons performed 3.5 different signals and adult, subadult and juvenile baboons showed nearly the same. Subadult baboons exhibited the widest range of signal usage with 10.2 different signals. The adults used 9.4 and the juveniles used 9.6 different signals.

The difference between the six age classes was significant (p=0.013). If four age classes were regarded (adult including senescent, subadult, juvenile and infantile) the difference remained below significance level (p=0.036). There was no difference between the sexes (females: 8.3 signals; males: 8.7 signals).

3.2.3 Range in usage of the different signals

No age class used all 19 different signals. The group of the senescent baboons (two females) showed five (26.3%) different signals (*eyebrow raising*, *lowering body*, *stiff threat*, *lipsmacking* and *presenting*). The class of the adults (ten females) used 14 signals (73.7%). They did not perform *rolling on ground*, *jumping in the air*, *hand/head-stand*, *pumping* and *penis grab*. In the category of the subadults (one female, four males) 16 signals (84.2%) were observed. Signals not found here were *jumping in the air*, *hand/headstand* and *pulling on*. The group of the juvenile baboons (five females, three males) displayed the widest range of signals with 18 (94.7%). Absent was only the *penis grab*. The class of brown infants (three females, four males) used 13 signals (68.4%) and did not show *enlisting*, *lowering back*, *displaying*, *lipsmacking*, *greeting* and *penis grab*. The one black infant (female) displayed the least range of signals (three), which were *relaxed open mouth*, *poking* and *pulling on*.

The class of females did not show *pumping* and *penis grab*. They used 17 different signals (89.5%) whereas the class of male baboons displayed all 19.

Nine out of ten age/sex classes showed *eyebrow raising, stiff threat* and *presenting* (except for the black infant female) as well as *relaxed open mouth* and *poking* (except for the senescent females).

Mounting was observed in all age classes with the exception of the black infant and the senescent baboons. *Lipsmacking* was not performed by infants (black and brown of both sexes) and *greeting* was absent in the senescent females and infants (black and brown of both sexes). *Enlisting* was used by adult and subadult females and by juveniles of both sexes. *Chasing* occurred in adult and juvenile females, in subadult and brown infant males. While females of all age classes (except for the black infant) showed the *lowering body*, only the juvenile males also performed this signal. *Lowering back* was displayed by adult and subadult females as well as subadult (but not in the harem leaders) and juvenile males. *Jumping in the air* and *hand/headstand* were only seen in juvenile females and brown infant males. Subadult females, juveniles and brown infants of both sexes showed *rolling on ground*. *Pumping* was found in all age classes of males. *Displaying* appeared in adult females, harem leaders and juvenile males. Adult females, juveniles and infants of both sexes used *pulling on*. *Penis grab* was seen only in subadult males.

An overview of the usage of all signals in age classes and sexes is given in the following table.

Table 3.2.2 c
Signal occurrence by age and sex classes

	eyebrow raising	*enlisting*	*chasing*	*lowering body*	*lowering back*	*relaxed o. m.*	*rolling on gr.*	*jumping in the air*	*hand/headstand*	*pumping*	*stiff threat*	*displaying*	*lipsmacking*	*presenting*	*greeting*	*poking*	*mounting*	*pulling on*	*penis grab*
FEMALES	**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**		**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**	
senescent (2)	x			x							x		x	x					
adult (10)	x	x	x	x	x	x					x	x	x	x	x	x	x	x	
subadult (1)	x	x		x	x	x	x				x		x	x	x	x	x		
juvenile (5)	x	x	x	x		x	x	x	x		x		x	x	x	x	x	x	
brown infant (3)	x			x		x	x				x			x		x	x	x	
black infant (1)						x										x		x	
MALES	**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**
subadult leader (2)	x		x			x				x	x	x	x	x	x	x	x		x
subadult (2)	x		x		x	x				x	x		x	x	x	x	x		x
juvenile (3)	x	x		x	x	x	x			x	x	x	x	x	x	x	x	x	
brown infant (4)	x		x			x	x	x	x	x	x			x		x	x	x	

A complete table of the individuals' signal usage can be found in appendix 2.

3.2.4 Summary of the first observation period

Eyebrow raising was seen in most of the individuals (81.8% of all baboons; 86.4% of the females, 72.7% of the males), except the oldest (senescent) female, a subadult male, one juvenile female, two brown infant males and the black infant female. *Eyebrow raising* was sometimes combined with *stiff threat*, *chasing* or *enlisting*.

Enlisting was observed in seven adult, one subadult and four juvenile females as well as in two juvenile males (42.4% of all baboons; 54.5% of the females, 18.2% of the males). Often the helper was a harem leader. *Enlisting* could be combined with *presenting* (in the direction to the helper).

Chasing was found in seven adult and two juvenile females, three subadult males (including the two harem leaders) and one brown infant male (39.4% of all baboons; 40.9% of the females, 36.4% of the males).

Lowering (upper part of the) body was performed by one senescent, eight adult, one subadult, three juvenile and one brown infant females and one subadult male (45.5% of all baboons; 63.6% of the females, 9.1% of the males). *Lowering body* was found in combination with *lipsmacking*, *poking* or *pulling on*.

The two adult females with young infants used ***lowering back***, but it was also seen in one subadult female and one subadult and one juvenile male (15.2% of all baboons; 13.6% of the females, 18.2% of the males). *Lowering back* was often combined with *poking* or *lipsmacking*.

Relaxed open mouth was seen in almost all individuals (87.9% of all baboons; 81.8% of the females, 100% of the males). It was not observed in the two senescent and in two adult baboons (all females). It appeared in some combinations such as with *poking* or *lowering body*.

Only younger animals – one subadult, four juvenile and three brown infant females as well as two juvenile and one brown infant males – showed ***rolling on ground*** (33.3% of all baboons; 36.4% of the females, 27.3% of the males). ***Jumping in the air*** appeared in two juvenile females and one brown infant male (9.1% of all baboons; 9.1% of both sexes) and ***hand/headstand*** in one juvenile female and two brown infant males (9.1% of all baboons; 4.5% of the females, 18.2% of the males).

Pumping was a male-typical signal shown by the two harem leaders and another subadult male as well as by a juvenile and two brown infant males (18.2% of all ba-

boons; no females, 54.5% of the males). On some occasions the recipient was out of sight of the human observer.

Stiff threat occurred in many individuals – one senescent, seven adult, one subadult, four juvenile and one brown infant females as well as two subadult (inclusive one of the harem leaders, Kuno), three juvenile and one brown infant males (60.6% of all baboons; 63.6% of the females, 54.5% of the males). It was found in combination e.g. with *eyebrow raising* or *chasing*.

One adult female, the two harem leaders and one juvenile male (12.1% of all baboons; 4.5% of the females, 27.3% of the males) used ***displaying***.

Lipsmacking was used by all senescent, all adult and all subadult baboons as well as by one juvenile female and two juvenile males (60.6% of all baboons; 63.6% of the females, 54.5% of the males). It was found in several combinations: with *presenting*, *poking*, *lowering body, lowering back*, *greeting* and others.

Presenting was found in all senescent, all adult, all subadult baboons except one of the harem leaders (Gunter; he was the most frequent recipient of *presenting*), in all juveniles and all brown infants, except for two males (87.9% of all baboons; 95.5% of the females, 72.7% of the males). Presenting was occasionally combined with *lipsmacking*, *relaxed open mouth*, *poking* or *enlisting*.

Greeting was used by seven adult and one subadult females, all four subadult males (including leaders), one juvenile female and two juvenile males (45.5% of all baboons; 40.9% of the females, 54.5% of the males).

Poking was a common signal performed by almost all individuals (87.9% of all baboons; 81.8% of the females, 100% of the males) except for the two oldest (senescent) females, the retarded adult and a juvenile female. *Poking* appeared sometimes in combination with *pulling on*, *relaxed open mouth*, *lowering back* or *presenting*.

Seven adult, one subadult, three juvenile and one brown infant females and all males showed ***mounting*** (69.7% of all baboons; 54.5% of the females, 100% of the males).

Pulling on was performed by one adult, three juvenile, three brown and one black infant females and one juvenile and two brown infant males (33.3% of all baboons; 36.4% of the females, 27.3% of the males).

Penis grab was only used by two subadult (including one harem leader) males (6.1% of all baboons; no females, 18.2% of the males). *Penis grab* could be combined with *presenting* or *lipsmacking*.

3.3 Results of the second observation period

3.3.1 Single Signals

3.3.1.1 General occurrence of the signals (Source 1)

In the second observation period 12 new signals were found: *head shaking*, *threat mouth*, *head bobbing*, *head movement*, *yawning*, *waving*, *head tapping*, *spinning* ("visual"); *tapping ground*, *object movement*, *diving* ("visual possibly making some noise"); and *jumping on back* ("tactile").

Altogether 31 different signals were recorded. 15 signals were categorised as "visual signal", nine as "visual signal possibly making some noise", two as "visual signal often combined with touching" and five as "tactile signal" (see also at 3.1).

Five signals were performed exclusively by one animal (*head movement, waving* and *diving* once; *tapping ground* and *object movement* twice) and therefore only described under 3.3.1.8 as idiosyncratic signals and were excluded from the analyses.

Therefore, 26 visual and tactile gestures of the baboons were analysed: 13 "visual", six "visual/noise", two "visual/touch" and five "tactile".

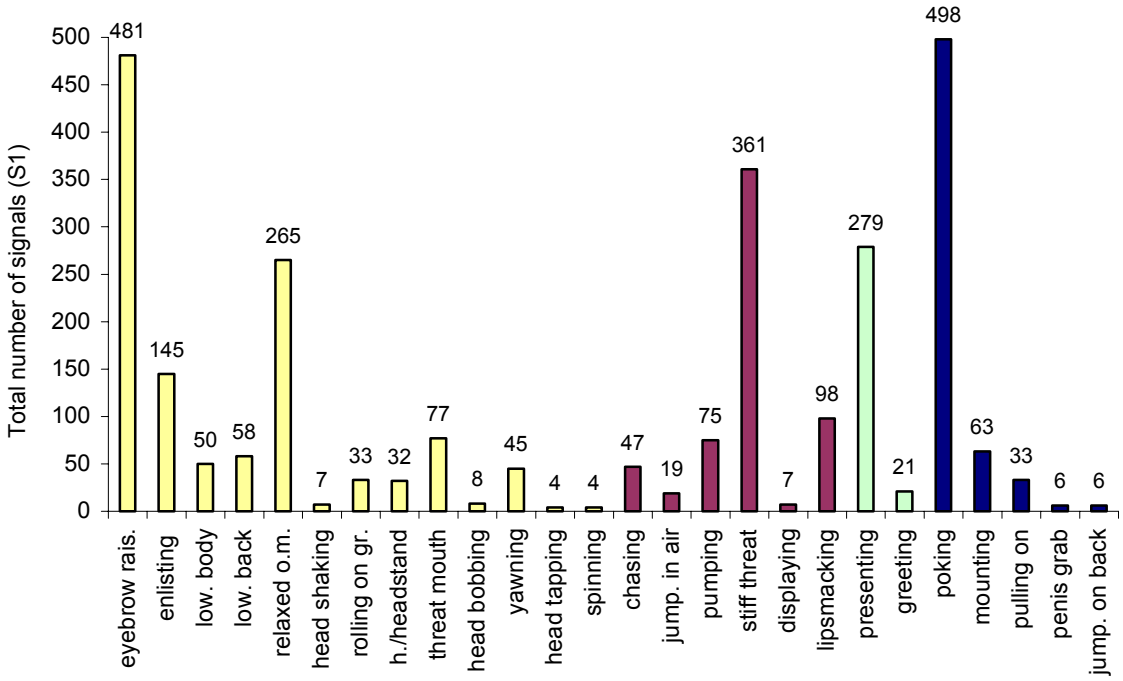


Figure 3.3.1.1 a
Total number of all signals seen during observation period 2 (4284 min)
light yellow: visual claret-red: visual/noise light green: visual/touch dark blue: tactile

2722 signals were analysed. The most common signals were *poking* and *eyebrow raising*, followed by *stiff threat*, *presenting* and *relaxed open mouth*. *Head shaking*, *head bobbing*, *head tapping*, *spinning*, *displaying*, *penis grab* and *jumping on back* were observed less than ten times each.

Almost half (44.4%) of all signals were “visual” and about a fifth of all signals were “tactile” (22.3%). From the mixed categories “visual/noise” accounted for 22.3% and “visual/touch” for 11.0% of the total.

3.3.1.2 Signal usage by focal animals (Source 2)

Two signals, *eyebrow raising* and *poking*, were seen in all 14 focal animals (FAs). Also common were *enlisting* (13 FAs), *relaxed open mouth* (13 FAs), *stiff threat* (13 FAs), *lipsmacking* (13 FAs), *presenting* (13 FAs), *lowering body* (12 FAs), *mounting* (12 FAs), *threat mouth* (11 FAs) and *chasing* (11 FAs), used by more than three quarter of all focal animals.

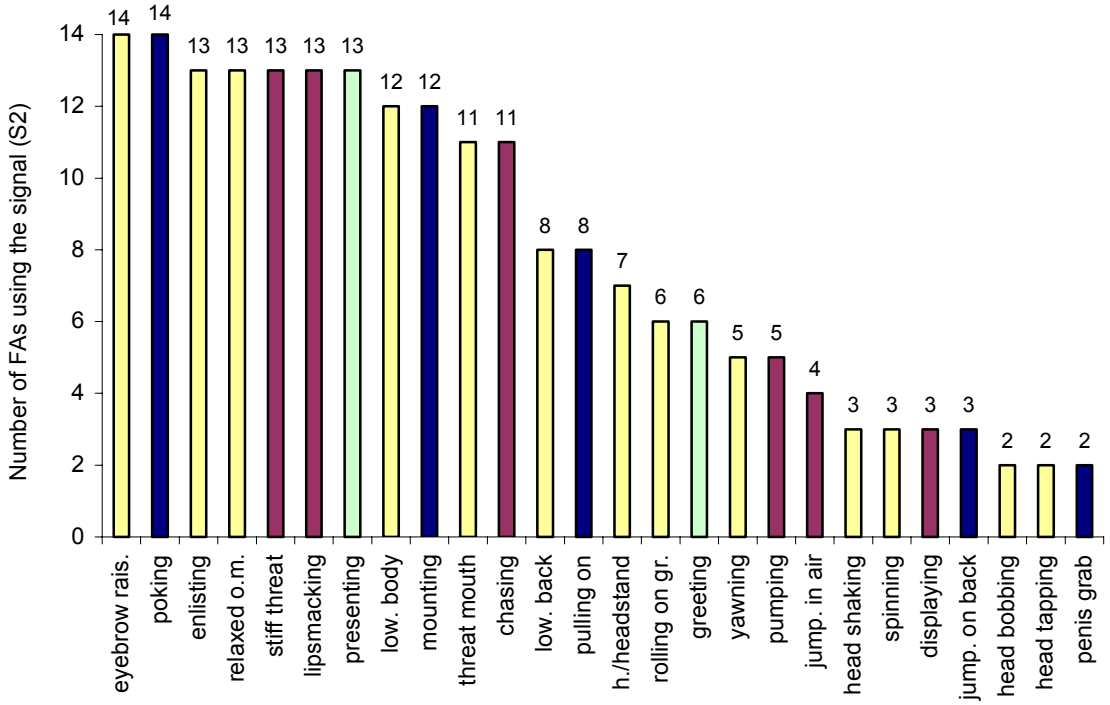


Figure 3.3.1.2 a
Signal usage by the focal animals (FAs)
light yellow: visual claret-red: visual/noise light green: visual/touch dark blue: tactile

About half of the focus group showed *lowering back* (8 FAs), *pulling on* (8 FAs), *hand/headstand* (7 FAs), *rolling on ground* (6 FAs) and *greeting* (6 FAs). *Yawning* and *pumping* were performed by five baboons each. *Jumping in the air* (4 FAs), *head shaking* (3 FAs), *spinning* (3 FAs), *displaying* (3 FAs), *jumping on back* (3 FAs), *head bobbing* (2 FAs), *head tapping* (2 FAs) and *penis grab* (2 FAs) were found only in few FAs (see figure 3.3.1.2 a).

There were almost no differences in the number of focal animals between the four categories. A “visual signal” was used on average (median) by 6.0 and a “tactile signal”

by 12.0 FAs. A “visual/noise” signal was on average (median) shown by 8.0 and a “visual/touch” signal by 9.5 FAs (see figure 3.3.1.2 b).

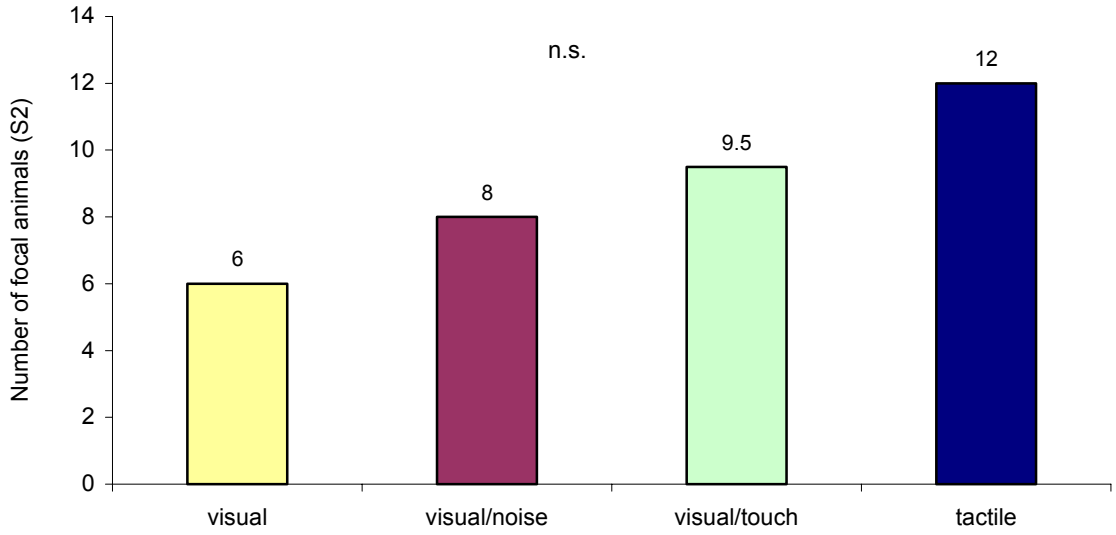


Figure 3.3.1.2 b
Median of FAs using the signals in the four categories: “visual” (n=13), “visual possibly making some noise” (n=6), “visual often combined with touching” (n=2) and “tactile” (n=5)

3.3.1.3 Number of different signals (Source 2)

Individuals

All focal animals used more than 10 different signals but none displayed the maximum range of 26 signals. Nine individuals showed more than half of the signals.

The highest number of different signals, 23 (88.5% of all signals), was performed by the subadult male Erwin, followed by the subadult male Bernd with 18 different signals (69.2% of all signals). The senescent female Ina showed the smallest range with 11 different signals (42.3%), followed by the adult female Iris and the subadult female Elke, each with 12 different signals (46.2%).

On average, a focal animal used with 14 out of 26 signals nearly half of all different signals (53.8%).

The values for the other individuals can be found in figure 3.3.1.3 a.

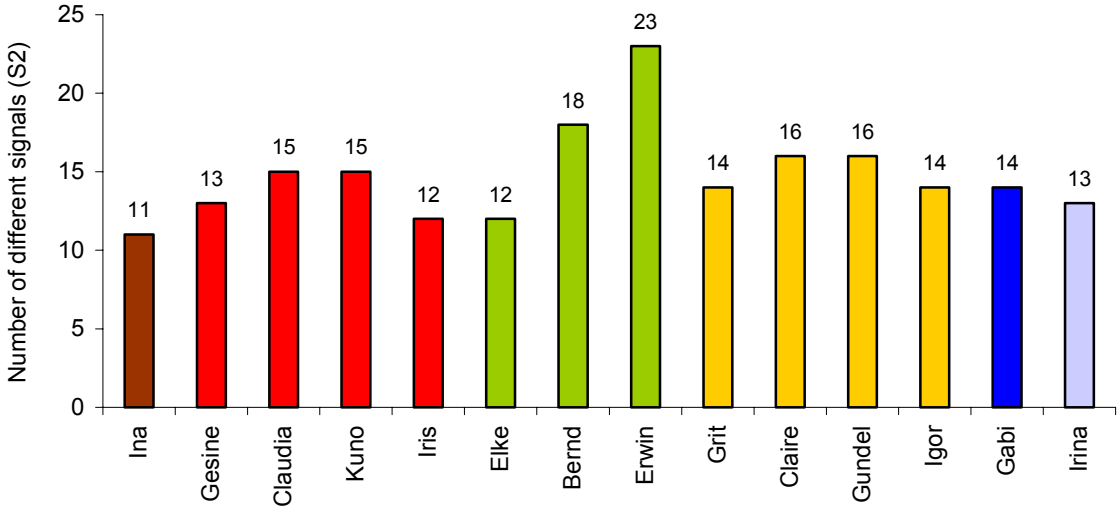


Figure 3.3.1.3 a
Number of different signals shown by the focal animals (maximum: 26)
brown: senescent adults *yellow: juveniles*
red: adults *blue: brown infants*
green: subadults *light blue: black infants*

Age/sex classes (median)

The subadult baboons used the greatest variety of signals with 18 out of 26 signals (69.2% of all different signals). The juveniles performed 15 (57.7%), the adults and the brown infant 14 (53.8%) and the black infant 13 (50.0%) out of 26 signals. The senescent female showed with 11 (42.3%) the lowest number of different signals. The differences between the age classes were not significant.

The female focal animals (n=10) tended to use with 13.5 out of 26 (51.9%) less different signals than the male focal animals (n=4) with 16.5 (63.5%) out of 26 (p=0.054).

3.3.1.4 Range in usage of the different signals (Source 2)

Table 3.3.1.4 a shows which focal animal displayed which signal.

The group of the subadult baboons displayed the widest range of all different signals with 92.3% (24). They do not show *jumping in the air* and *jumping on back.* The group of juveniles performed 80.8% of all different signals (21). Signals not represented here were *head shaking*, *displaying*, *penis grab*, *head bobbing* and *tapping head*. The group of adults used 76.9% (20) of all different signals. *Rolling on ground*, *jumping in the air*, *penis grab*, *jumping on back*, *tapping head* and *spinning* were not found in this group.

Table 3.3.1.4 a
Signal usage by the FAs

	eyebrow rais.	enlisting	chasing	low. body	low. back	relaxed o. m.	head shaking	rolling on gr.	jump. in air	h./headstand	pumping	stiff threat	displaying	lipsmacking	poking	mounting	pulling on	penis grab	jump. on back	presenting	greeting	threat mouth	head bobbing	yawning	head tapping	spinning
Ina	x	x	x	x			x					x		x	x					x	x	x				
Gesine	x	x	x	x	x	x						x		x	x					x	x	x	x			
Claudia	x	x	x	x	x	x				x		x		x	x	x				x	x	x		x		
Kuno	x	x	x	x		x	x				x	x	x	x	x	x					x	x		x		
Iris	x	x	x		x	x						x		x	x	x	x			x		x				
S/AD	**x**	**x**	**x**	**x**	**x**	**x**	**x**			**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**			**x**	**x**	**x**	**x**	**x**		
Elke	x	x	x	x		x						x		x	x	x				x		x				x
Bernd	x	x	x	x	x	x					x	x	x	x	x	x	x	x		x		x		x	x	
Erwin	x	x	x	x	x	x	x	x		x	x	x	x	x	x	x	x	x		x	x	x	x	x	x	
SAD	**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**		**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**	**x**		**x**	**x**	**x**	**x**	**x**	**x**	**x**
Grit	x	x	x	x	x	x						x		x	x	x	x			x	x	x				
Claire	x	x		x		x		x	x	x	x	x		x	x	x				x		x		x		x
Gundel	x	x	x	x	x	x		x	x	x		x		x	x	x	x		x	x						
Igor	x	x	x			x		x	x	x	x			x	x	x	x			x		x				
JUV	**x**	**x**	**x**	**x**	**x**	**x**		**x**	**x**	**x**	**x**	**x**		**x**	**x**	**x**	**x**		**x**	**x**	**x**	**x**		**x**		**x**
Gabi	x	x		x	x	x		x		x		x			x	x	x		x	x						x
Irina	x			x		x		x	x	x		x		x	x	x	x		x	x						
INF	**x**	**x**		**x**	**x**	**x**		**x**	**x**	**x**		**x**		**x**	**x**	**x**	**x**		**x**	**x**						

Because the groups of senescents, brown infants and black infants are composed of only one individual each, the results are the same like for the individuals Ina (42.3% respectively 11 signals), Gabi (53.8% respectively 14 signals) and Irina (50.0% respectively 13 signals). If the black and the brown infant baboons are pooled together, they show 57.7% of all different signals (15). The senescent animal did not use other signals then the adults hence there is no change of the result if both age classes are summarised. See also figure 3.3.1.4 b.
The class of female focal animals used 88.5% (23) of all different signals. They did not perform *displaying*, *penis grab* and *tapping head*. The class of male focal animals showed 92.3% (24) of all different signals. They did not use *jumping on bac*k and *spinning*.

A comparison of the two observation periods revealed similar results. Subadults and juveniles showed the greatest variety of different signals (more than 80%), followed by the adults (approximately 75%). The older infants in observation period 1 used nearly four times more different signals than the black infant; in observation period 2 the brown and the black infant had almost the same values. In both periods, the senescent animals had a relatively small range of signals. Overall, differences between age

classes were smaller in observation period 2. Males tended to show more different signals than females across both periods.

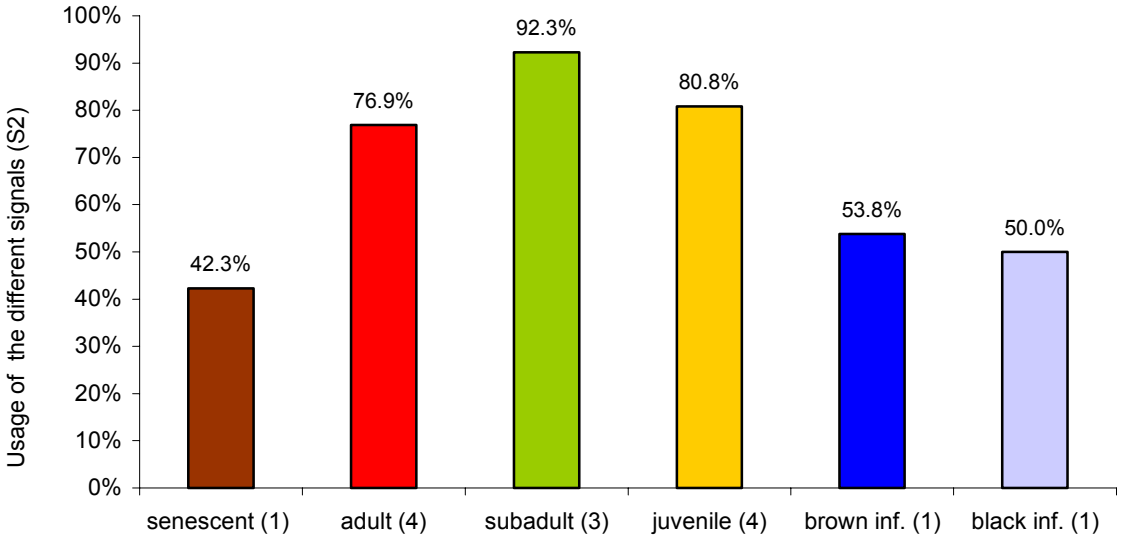


Figure 3.3.1.4 b
Range of signal usage by age class

3.3.1.5 Total number and frequency of signals shown by the focal animals (Source 3)

Individuals

The total number of signals shown by the focal animals during their focal time ranged from 70 to 274 signals (the values for the FAs can be seen in appendix 3).

Because the observational times for the FAs were not exactly the same for each baboon here the frequency (total number of signals/observational time) was used.

The adult male and harem leader Kuno showed the highest frequency of signals. He performed 0.88 signals per minute (sig/min). The adult female Claudia (0.67 sig/min) and the subadult males Bernd (0.57 sig/min) and Erwin (0.54 sig/min) were also highly active signal users. The senescent female Ina (0.23 sig/min), the adult female Iris (0.24 sig/min) and the subadult female Elke (0.25 sig/min) showed the lowest frequencies. The other FAs had frequencies between 0.32 and 0.40 signals per minute (see also figure 3.3.1.5 a).

A focal animal performed 0.36 signals per minute (median).

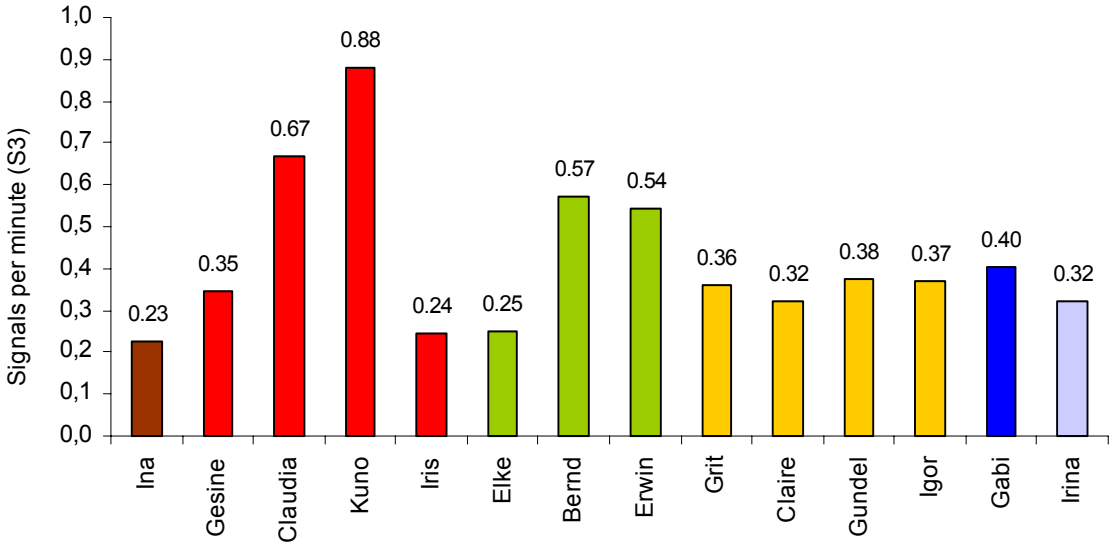


Figure 3.3.1.5 a
Frequency of signal usage in the FAs (signals per minute)
brown: senescent adults
red: adults
green: subadults
yellow: juveniles
dark blue: brown infants
light blue: black infants

Age/sex classes (median)

The subadult baboons performed the highest number of signals per minute (0.54 sig/min), followed by the adults (0.51 sig/min). The senescent female used the lowest number. The infants and the juveniles showed frequencies between 0.32 and 0.40 signals per minute. The differences between the age classes were not significant. The females used 0.33 and the males 0.56 signals per minute (p=0.036).

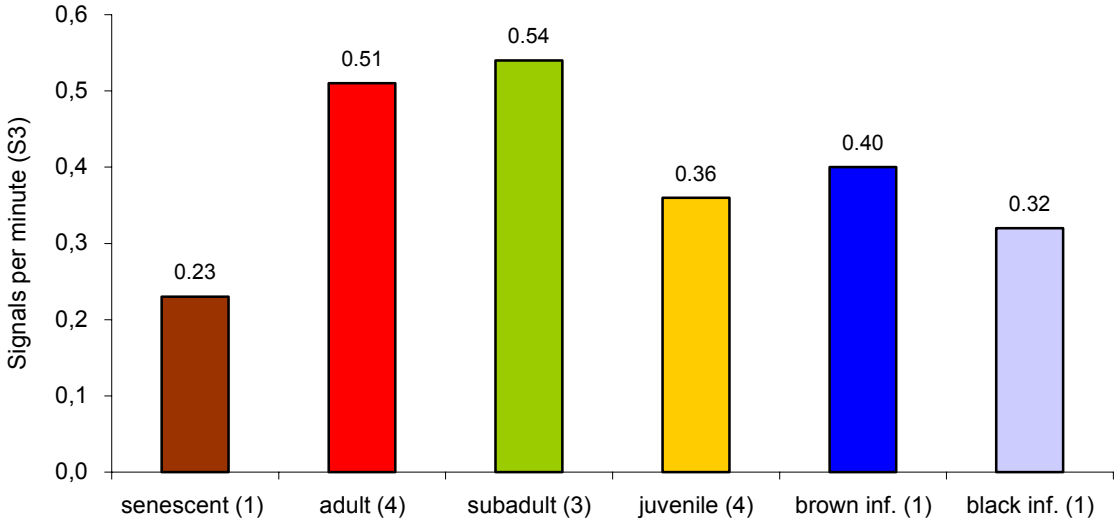


Figure 3.3.1.5 b: Median of signal usage frequency by age class

3.3.1.6 Signal occurrence in the focal animals (Source 3)

For comparison of the occurrence of the 26 signals in the FAs the value “times per hour” (ts/h) was used.
The detailed data for all individuals can be found in appendix 4.

Eyebrow raising

The harem leader Kuno displayed the highest number of *eyebrow raising* events. He showed this signal 15.3 ts/h and was followed by the adult females Claudia (12.2 ts/h) and Gesine (10.8 ts/h). The senescent female Ina performed it 6.2 ts/h, the subadult males Bernd and Erwin 4.7 ts/h, the juvenile female Claire 4.0 ts/h and the adult female Iris 3.9 ts/h. The females Gundel (juvenile), Gabi (brown infant), Grit (juvenile) and Elke (subadult) as well as juvenile male Igor had values between approximately two and three times per hour. Only the black infant Irina displayed almost no *eyebrow raising* (0.4 ts/h).
The median of all 14 baboons was 3.9 ts/h.
In age and sex classes the following values were found (median): senescent 6.2 ts/h, adult 11.5 ts/h, subadult 4.7 ts/h, juvenile 3.0 ts/h, brown infant 2.9 ts/h and black infant 0.4 ts/h as well as females 3.5 ts/h and males 4.7 ts/h (differences not significant).

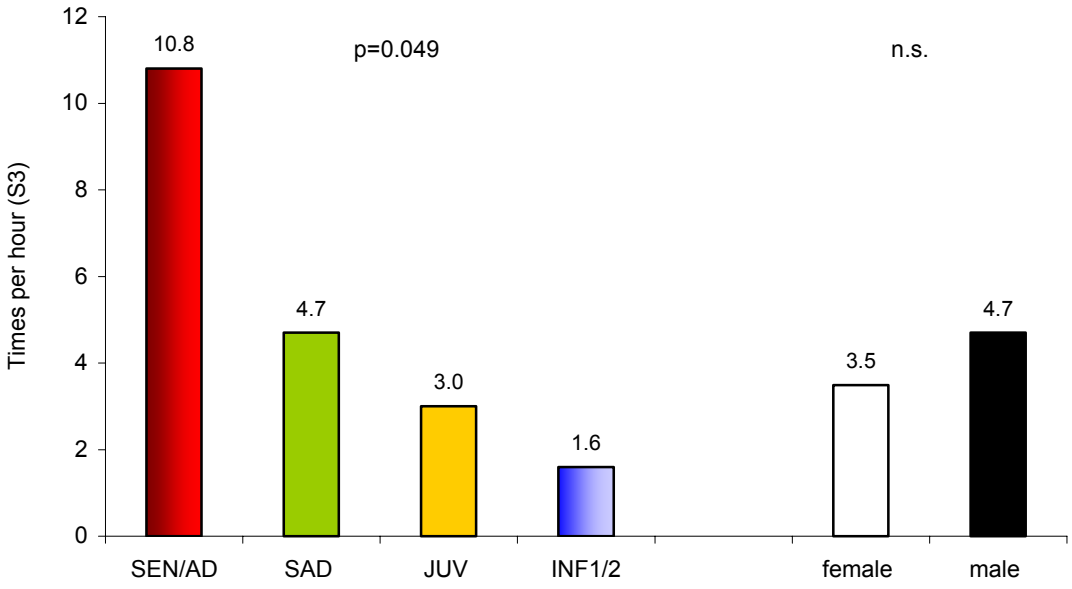


Figure 3.3.1.6 a
Frequency of eyebrow raising *per hour grouped by age (four classes) and gender*

When pooling together the senescent and adult animals as well as both infants (four age classes) the differences between the age classes were significant (p=0.049) and when comparing the older animals (senescent, adult and subadult) to the younger ones (juveniles, brown and black infants), the difference was highly significant (p=0.02).

Thus, younger baboons used *eyebrow raising* less frequently than older baboons.
See also figure 3.3.1.6 a.

Enlisting

The highest number of *enlisting* events was observed in the adult female Claudia with three times per hour. Six focal animals used *enlisting* between one and two times per hour: the subadult male Erwin, the harem leader Kuno, the juvenile female Gundel as well as the juvenile male, the brown infant and the juvenile female Claire. All other focal animals showed this signal less than once per hour, and the black infant never used it.
The median of all 14 baboons was 0.9 ts/h.
In age and sex classes the following values were recorded (median): senescent 0.2 ts/h, adult 1.2 ts/h, subadult 0.6 ts/h, juvenile 1.2 ts/h, brown infant 1.2 ts/h and black infant not once as well as females 0.6 ts/h and males 1.5 ts/h (no significant differences). Even by summarising some age classes the level of difference was not reached.
See also figure 3.3.1.6 b.

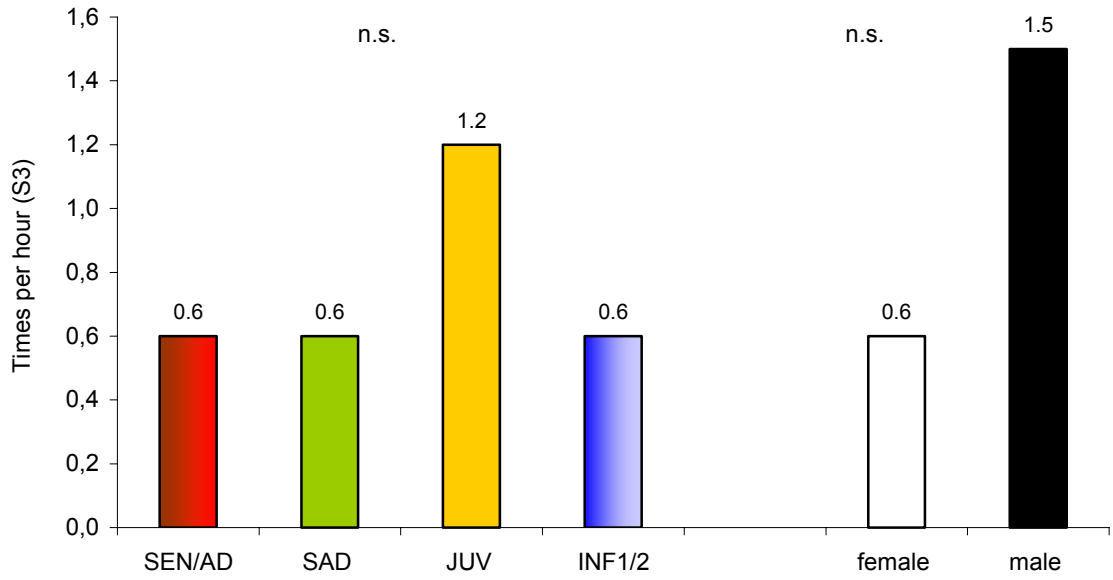


Figure 3.3.1.6 b
Frequency of enlisting *per hour grouped by age (for classes) and gender*

Lowering body and lowering back

Overall, the values for *lowering body* were low. The juvenile female Grit showed this signal frequently with 1.2 ts/h, followed by the adult female Claudia (1.0 ts/h). The juvenile female Gundel showed *lowering body* 0.9 ts/h, the senescent female 0.6 ts/h, the black infant, the subadult female Elke, the subadult male Erwin and the juvenile female Claire 0.4 ts/h and the brown infant 0.2 ts/h.

While the adults Gesine and Kuno as well as the subadult Bernd also performed *lowering body*, they did not do so as focal animals. Therefore, frequency could not be determined.
The median of all 14 baboons was 0.4 ts/h.

Iris and Gesine, both adult females who had black infants during this observation period, were nearly the sole users of *lowering back*. They displayed it 3.0 and 2.9 ts/h respectively. The juvenile female Gundel, the adult female Claudia, the subadult males and the brown infant used this signal only 0.2 ts/h.
The juvenile female Grit also performed it but not as a focal animal, and therefore no frequency could be determined.
For both signals there were no significant differences between age or sex classes.

Relaxed open mouth

Younger individuals used this signal most often. The highest value was found for the brown infant with 5.6 ts/h, followed by the juveniles Grit with 3.9 ts/h and Igor with 3.3 ts/h. The adult with the highest number of *relaxed open mouth* was Claudia with 3.0 ts/h. Seven animals showed the signal between once and 2.6 times per hour: the juvenile female Gundel, the black infant, the juvenile female Claire, the subadult males Erwin and Bernd and the adult females Iris and Gesine. The subadult female Elke and the harem leader had values below 1.0 ts/h. The senescent female never used this signal.
The median of all 14 baboons was 1.8 ts/h.
In age and sex classes the following values were found (median): senescent not once, adult 1.2 ts/h, subadult 1.0 ts/h, juvenile 3.0 ts/h, brown infant 5.6 ts/h and black infant 2.4 ts/h as well as females 2.2 ts/h and males 1.3 ts/h. The differences between the age classes and the sexes were not significant. But if the senescent, adult and subadult as well as the juvenile and infantile animals were pooled together (two age classes) the younger baboons showed significantly more *relaxed open mouth* than the older ones ($p=0.005$).
See also figure 3.3.1.6 c.

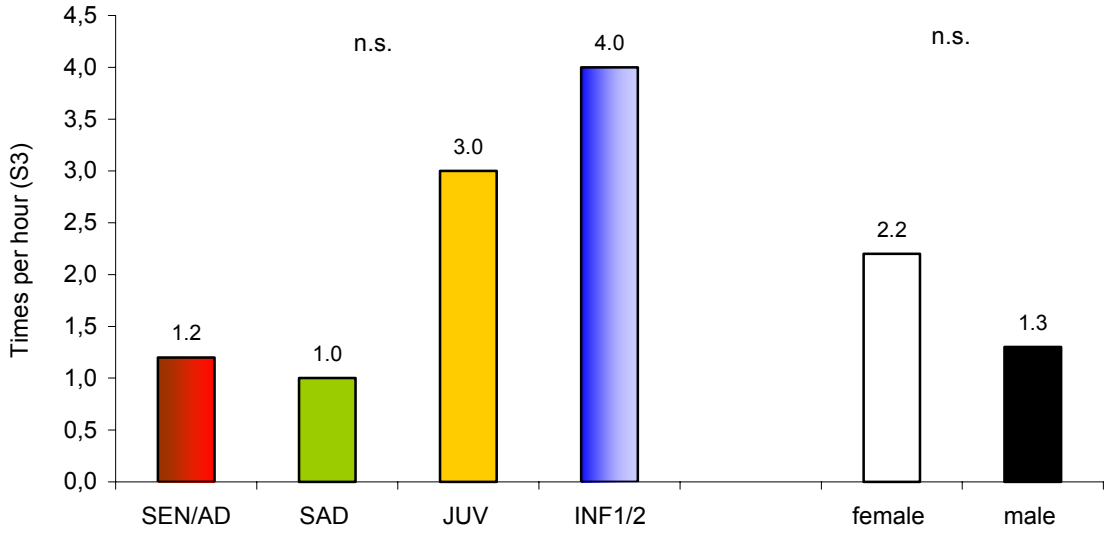


Figure 3.3.1.6 c
Frequency of relaxed open mouth *per hour grouped by age (four classes) and gender*

Head shaking, rolling on ground and hand/headstand

Only three baboons showed *head shaking*. The senescent female used it 1.0 ts/h. The harem leader and the subadult male Erwin performed it 0.2 ts/h.

Rolling on ground and *hand/headstand* were mainly displayed by younger animals. Both signals were used by the same individuals.

Rolling on ground was seen in the juvenile male 2.0 ts/h, in the juvenile females Gundel and Claire 0.8 and 0.6 ts/h respectively, in the subadult male Erwin 0.6 ts/h, in the brown infant 0.4 ts/h and in the black infant 0.2 ts/h.

Hand/headstand was used by the juvenile female Claire 1.5 ts/h, the black infant 1.4 ts/h, the brown infant 0.8 ts/h, the juvenile male 0.6 ts/h, the subadult male Erwin and the juvenile female Gundel 0.2 ts/h.

The adult female Claudia was also observed using this signal but not as a focal animal, and therefore no frequency could be determined.

Threat mouth

Three males used *threat mouth* most often: the subadult male Bernd performed it approximately three times per hour, and the harem leader as well as the subadult male Erwin showed it approximately two times per hour. Seven other animals displayed this signal between 0.2 and 0.8 ts/h: the adult female Claudia, the juvenile female Grit, the juvenile male, the senescent female, the juvenile female Claire, the subadult female Elke and the adult female Iris. The adult female Gesine also performed this signal but not as a focal animal, and therefore no frequency could be determined. *Threat mouth*

was not used by the youngest females Gundel (juvenile), Gabi (brown infant) and Irina (black infant).

The median value of all 14 baboons is 0.6 ts/h.

In age and sex classes the following values were recorded (median): senescent 0.6 ts/h, adult 0.5 ts/h, subadult 1.7 ts/h, juvenile 0.6 ts/h, no occurrences in the brown and the black infant; females 0.3 ts/h and males 1.8 ts/h. While differences between the age classes (including pooled age classes) were not significant difference between the sex classes reached level of significance (p=0.014).

See also figure 3.3.1.6 d.

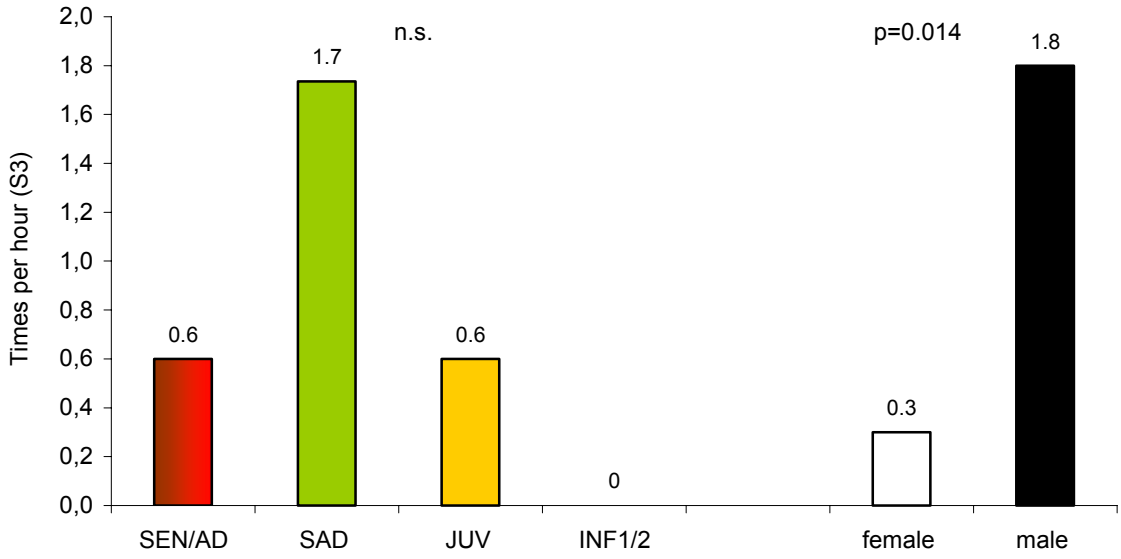


Figure 3.3.1.6 d
Frequency of threat mouth *per hour grouped by age (four classes) and gender*

Head bobbing, yawning, head tapping and spinning

Very few baboons used these signals.

The adult female Gesine was the only individual using *head bobbing*, which she did at a rate of 0.6 ts/h.

The subadult male Erwin also performed this signal but not as a focal animal, and therefore no frequency could be determined.

Five baboons showed *yawning*. The subadult male Bernd had the highest value and used *yawning* 2.7 ts/h, followed by the harem leader with 1.7 ts/h and the subadult male Erwin with 1.4 ts/h. The adult female Claudia performed it only 0.2 ts/h.

The juvenile female Claire did not perform it as a focal animal, and therefore no frequency could be determined.

Only the subadult males displayed *head tapping*, which they did at a rate of 0.4 ts/h.

The juvenile female Claire and the brown infant used *spinning* 0.4 ts/h and 0.2 ts/h respectively.

The subadult female Elke also performed this signal but not as a focal animal, and therefore no frequency could be determined.

Chasing

The harem leader showed the most *chasing* events with 1.4 ts/h, followed by the adult female Claudia with 1.0 ts/h. Nine baboons had values lower than once per hour: the juvenile male, both subadult males, the senescent female, the subadult female Elke, the juvenile female Gundel, the adult females Iris and Gesine and the juvenile female Grit. The juvenile female Claire and the two infants did not perform this signal.

The median of all 14 baboons is 0.4 ts/h.

The following median values for age and sex classes were found: senescent 0.8 ts/h, adult 0.6 ts/h, subadult 0.8 ts/h, juvenile 0.3ts/h, brown and black infant not at all as well as females 0.2 ts/h and males 0.8 ts/h. The differences between six and four age classes were not significant but overall the younger (juvenile, brown and black infants) baboons used *chasing* somewhat less frequently than the older (senescent, adult and subadult) animals (p=0.043). The difference between females and males was significant (p=0.024).

See also figure 3.3.1.6 e.

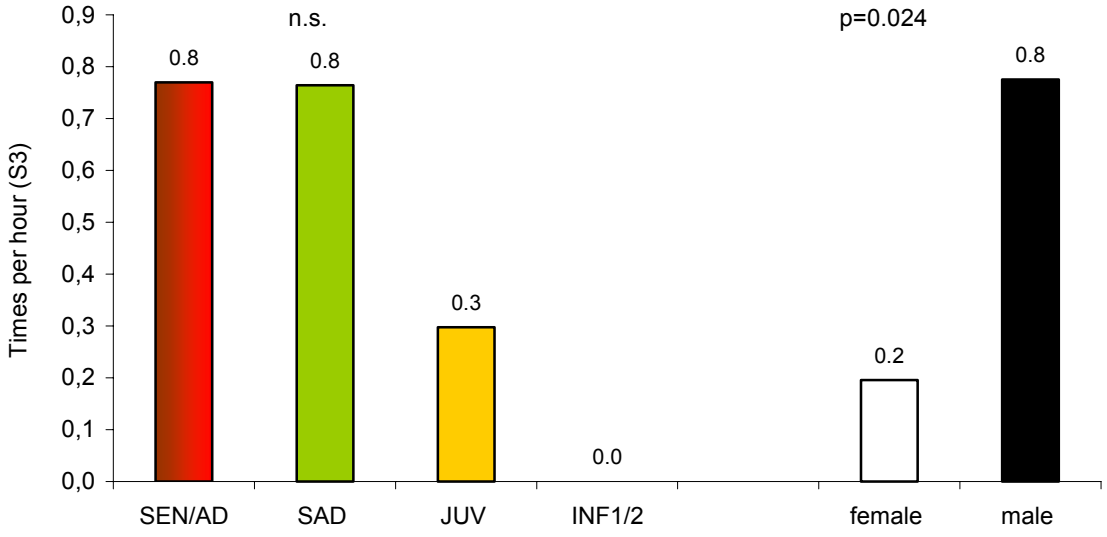


Figure 3.3.1.6 e
Frequency of chasing *per hour grouped by age (four classes) and gender*

Jumping in the air

Four juvenile and infantile baboons displayed this signal. The juvenile male used it 1.2 ts/h, the juvenile females Claire and Gundel 1.0 and 0.4 ts/h respectively and the black infant 0.4 ts/h.

Pumping and displaying

All four males and the juvenile female Claire displayed *pumping*. The subadult male Bernd performed it 8.4 ts/h and the harem leader 2.3 ts/h. The other subadult male Erwin and the juvenile male showed it 0.6 ts/h, and the juvenile female Claire 0.4 ts/h.

Only three males used *displaying*: the subadult male Erwin performed it 0.4 ts/h and the harem leader as well as the other subadult male Bernd showed it 0.2 ts/h.

Stiff threat

The harem leader used *stiff threat* 24.4 ts/h. The adult female Claudia performed the signal 11.2 ts/h and the subadult males Bernd and Erwin showed it 7.8 and 6.2 ts/h respectively. The subadult female, the juvenile female Grit and the adult female Iris displayed approximately two *stiff threats* per hour. The signal was found 1.4 ts/h in the adult female Gesine. The senescent female, the juveniles Gundel and Claire and both infants had values between 0.2 and 0.8 ts/h. The juvenile male never used s*tiff threat*. The median of all 14 baboons is 1.6 ts/h.

The following median values for age and sex classes were found: senescent 0.8 ts/h, adult 6.5 ts/h, subadult 6.2 ts/h, juvenile 0.4 ts/h, brown and black infant 0.2 ts/h each as well as females 1.1 ts/h and males 7.0 ts/h (these differences were not significant). If the senescent and adult animals as well as the both infants were pooled together (four age classes), the differences between the age classes were slightly significant (p=0.046) and if the older animals (senescent, adult and subadult) were compared to the younger ones (juvenile, brown and black infants), the difference was highly significant (p=0.005). Thus, younger baboons used less *stiff threat* than older baboons.

See also figure 3.3.1.6 f.

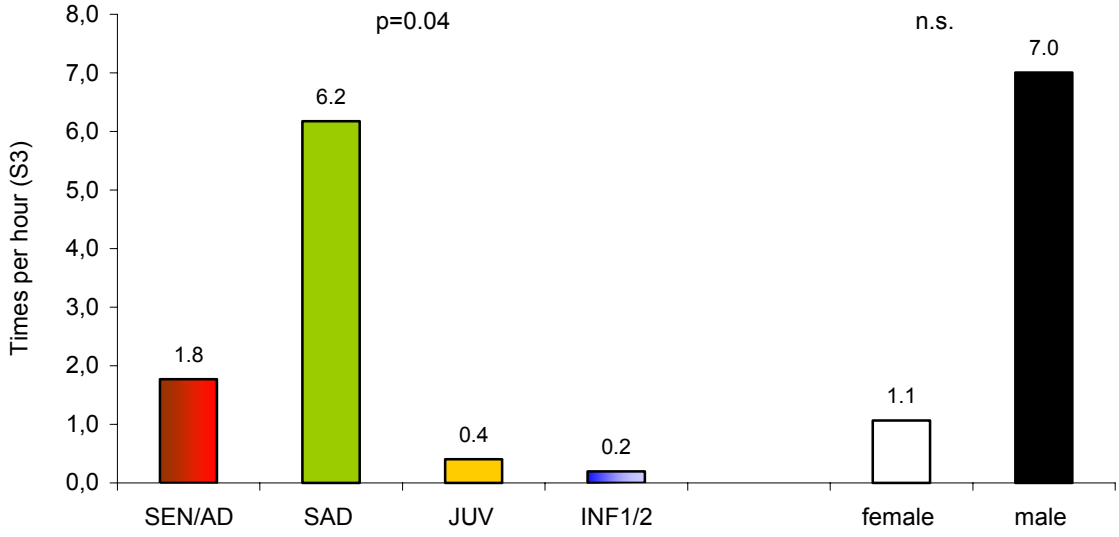


Figure 3.3.1.6 f
Frequency of stiff threat *per hour grouped by age (four classes) and gender*

Lipsmacking

The subadult male Erwin used the most *lipsmacking* signals per hour (2.3 ts/h), followed by the harem leader with 1.7 ts/h. The subadult male Bernd, the adult female Claudia, the senescent female and the subadult female Elke had values between 1.0 and 1.3 ts/h. The adult female Iris and the juvenile male performed the signal 0.6 ts/h. The black infant, the juvenile female Grit and the adult female Gesine displayed *lipsmacking* 0.4 ts/h, and the juvenile female Gundel 0.2 ts/h. The brown infant never used this signal.

The juvenile female Claire also performed this signal but not as a focal animal, and therefore no frequency could be determined.

The median of all 14 baboons is 0.6 ts/h.

The following median values for age and sex classes were found: senescent 1.2 ts/h, adult 0.9 ts/h, subadult 1.3 ts/h, juvenile 0.3 ts/h, brown infant not at all and black infant 0.4 ts/h as well as females 0.4 ts/h and males 1.5 ts/h. The differences between the six age classes were not significant but females and males differed significantly (p=0.014). When pooling together the senescent and adult individuals as well as the two infants (four age classes), the differences between the age classes were slightly significant (p=0.037). When comparing the older animals (senescent, adult and subadult) to the younger animals (juveniles, brown and black infants), the difference was highly significant (p=0.003). Thus, younger baboons used less *lipsmacking* than older baboons.

See also figure 3.3.1.6 g.

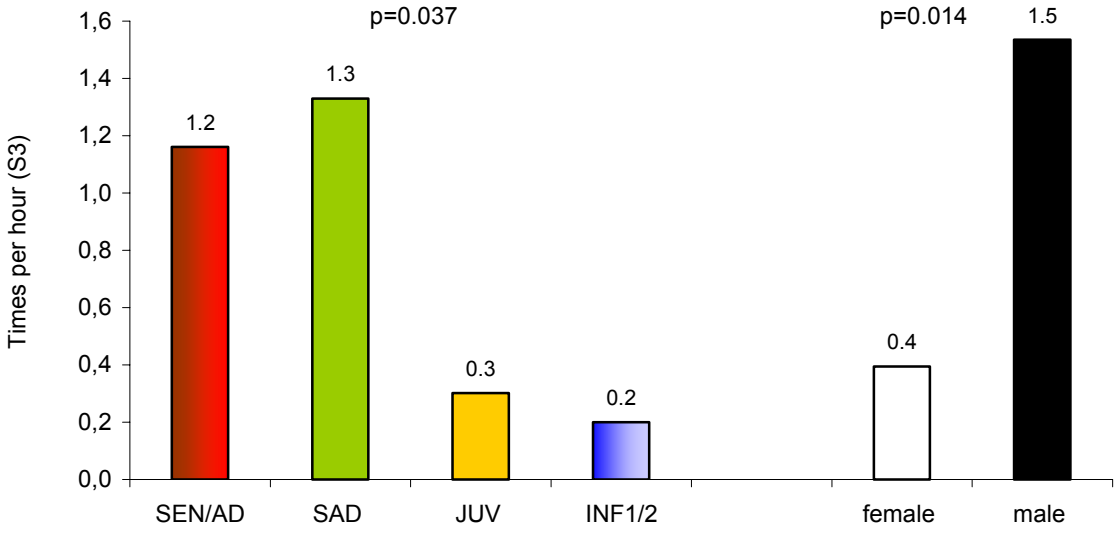


Figure 3.3.1.6 g
Frequency of lipsmacking *per hour grouped by age (four classes) and gender*

Presenting

The juvenile female Grit showed the highest frequency of *presenting* (5.8 ts/h). The signal occurred 4.1 ts/h in the subadult female, 3.0 ts/h in the adult female Claudia as well as in the juvenile female Gundel and 2.5 ts/h in the subadult male Erwin. The other individuals performed *presenting* between 2.0 and 0.6 ts/h. The harem leader generally did not use this signal.

The median of all 14 baboons is 1.6 ts/h.

The following median values for age and sex classes were found: senescent 1.0 ts/h, adult 1.2 ts/h, subadult 2.5 ts/h, juvenile 2.4 ts/h, brown infant 1.9 ts/h and black infant 1.0 ts/h as well as females 1.7 ts/h and males 1.5 ts/h. There were no significant differences between age or sex classes. See also figure 3.3.1.6 h.

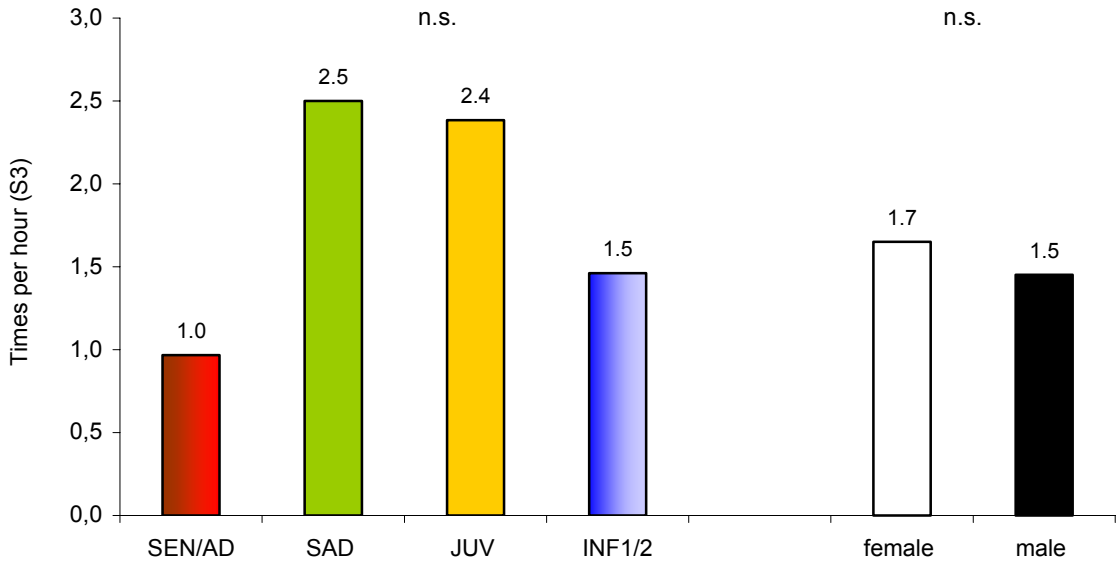


Figure 3.3.1.6 h
Frequency of presenting *per hour grouped by age (four classes) and gender*

Greeting

Greeting was not frequently exhibited and was used by only six animals with values below once per hour. The subadult male Erwin performed it 0.8 ts/h and the harem leader 0.6 ts/h. It was observed 0.2 ts/h in the adult females Claudia and Gesine, the senescent female and the juvenile female Grit.

Poking

The youngest baboon, the black infant, showed *poking* most frequently with nearly 12 ts/h, followed by the second youngest animal, the brown infant, with 9.4 ts/h. The juveniles Gundel, Igor and Claire used *poking* about six times per hour. It was seen in the subadult male Erwin 4.8 ts/h and in the juvenile female Grit 3.3 ts/h. The subadult female Elke, the adult female Gesine and the subadult male Bernd had values of about

two times per hour. *Poking* appeared 1.6 ts/h in the adult female Iris, 1.4 ts/h in the adult female Claudia and 1.2 time/h in the senescent female. The harem leader displayed it only 0.6 ts/h.

The median of all 14 baboons is 2.7 ts/h.

In age and sex classes the following values were recorded (median): senescent 1.2 ts/h, adult 1.5 ts/h, subadult 2.1 ts/h, juvenile 6.0 ts/h, brown infant 9.4 ts/h and black infant 11.8 ts/h as well as females 2.7 ts/h and males 3.4 ts/h. The difference between the sex classes was not significant. The differences between the six age classes (p=0.049), the four age classes (p=0.012) as well as the two age classes (p=0.001) showed that the younger baboons used *poking* more often than the older baboons.

See also figure 3.3.1.6 i.

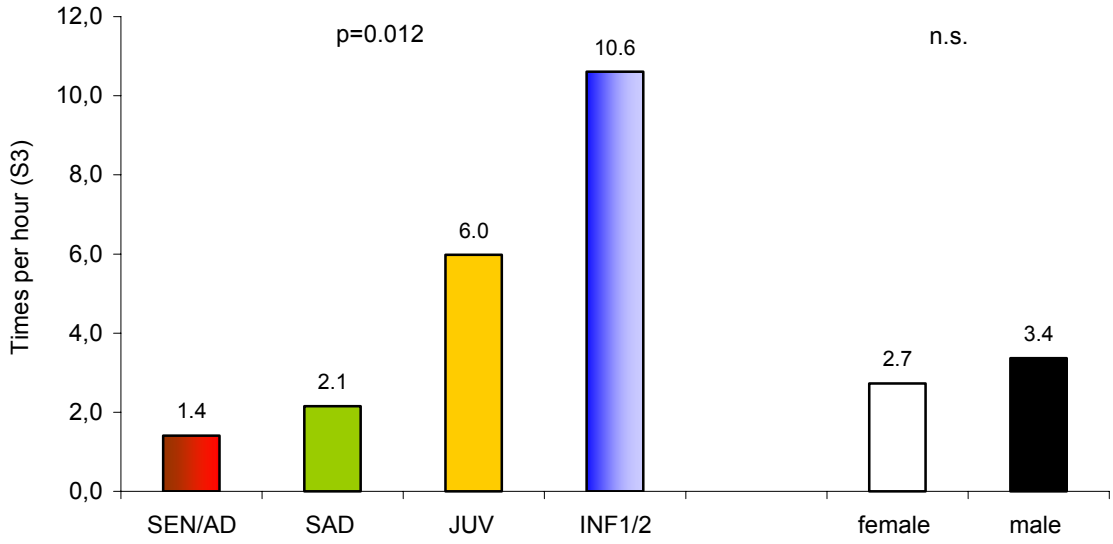


Figure 3.3.1.6 i
Frequency of poking *per hour grouped by age (four classes) and gender*

Mounting

Overall, *mounting* occurred with low frequencies. The adult female Claudia and the subadult female Elke used it once per hour. The juvenile female Gundel performed *mounting* 0.9 ts/h, the juvenile male 0.8 ts/h and the harem leader as well as the juvenile female Claire 0.6 ts/h. The other baboons used it less than 0.5 ts/h. The senescent female and the adult female Gesine never showed *mounting*.

The median of all 14 baboons is 0.4 ts/h.

In age and sex classes the following values were found (median): senescent not once, adult 0.4 ts/h, subadult 0.4 ts/h, juvenile 0.7 ts/h, brown infant 0.4 ts/h and black infant

0.2 ts/h as well as females 0.4 ts/h and males 0.5 ts/h. There were no significant differences between age or sex classes. See also figure 3.3.1.6 j.

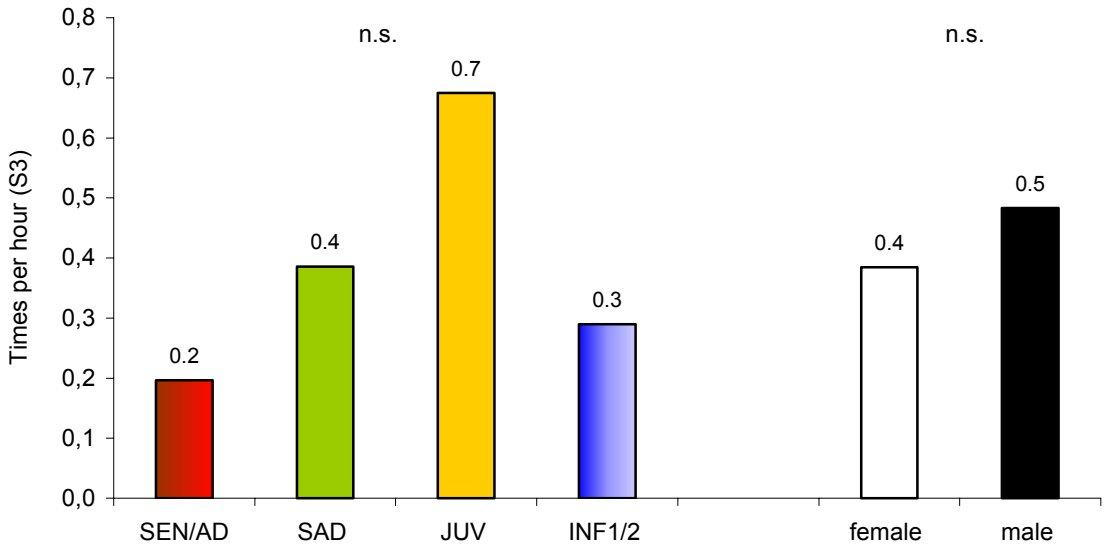


Figure 3.3.1.6 j
Frequency of mounting *per hour grouped by age (four classes) and gender*

Pulling on, penis grab and jumping on back

Pulling on was observed in eight animals: in the juvenile female Grit and in the brown infant 0.8 ts/h, in the juvenile female Gundel 0.6 ts/h, in the black infant and in the subadult male Erwin 0.4 ts/h and in the juvenile male and in the adult female Iris 0.2 ts/h. The subadult male Bernd also performed this signal but not as a focal animal, and therefore no frequency could be determined.
The median of all 14 baboons is 0.1 ts/h.

The subadult male Erwin exhibited *penis grab* 0.2 ts/h. The subadult male Bernd also displayed this signal but not as a focal animal and therefore no frequency could be determined.

Jumping on back was shown by the juvenile female Gundel 0.4 ts/h and by the brown infant 0.2 ts/h. The black infant Irina also performed this signal but not as a focal animal, and therefore no frequency could be determined.

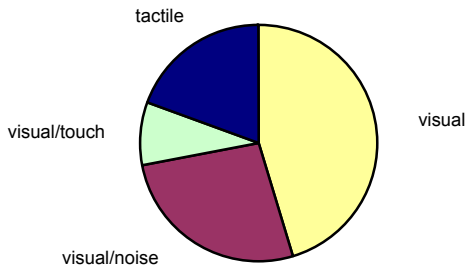
3.3.1.7 Quantitative communication ethogram (Source 3)

The detailed data for the focal animals can be found in appendix 5.

Summarised values for all 14 focal animals

When summarising the data of all focal animals the following values were found: 21.4% *eyebrow raising* (median: 14.7%), 16.8% *stiff threat* (median: 7.7%), 16.5%

poking (median: 14.6%), 8.2% *relaxed open mouth* (median: 7.8%), 7.9% *presenting* (median: 7.6%), 4.1% *enlisting* (median: 3.6%), 3.6% *pumping* (median: 0.0%), 3.2% *lipsmacking* (median: 2.8%), 3.1% *threat mouth* (median: 2.6%), 2.0% *chasing* (median: 2.1%), 1.9% *lowering back* (median: 0.2%), 1.8% *mounting* (median: 1.5%), 1.7% *yawning* (median: 0.0%), 1.5% *lowering body* (median: 1.6%), 1.3% *hand/headstand* (median: 0.0%), 1.3% *rolling on ground* (median: 0.0%), 0.9% *pulling on* (median: 0.4%), 0.8% *jumping in the air* (median: 0.0%), 0.6% *greeting* (median: 0.0%), 0.4% *head shaking* (median: 0.0%), 0.2% *head tapping, head bobbing, displaying, spinning* and *jumping on back* (median 0.0% at each case) as well as 0.1% *penis grab* (median: 0.0%).



For the signal categories the following values resulted: 45.4% “visual”, 26.5% “‘visual possibly making some noise”’, 8.6% “visual often combined with touching” and 19.5% “tactile”.

Age and sex classes (median; source 3)

A senescent/adult animal showed 59.9% “visual signals”, 20.0% “visual signals possibly making some noise”, 8.0% “visual signals often combined with touching” and 8.6% “tactile signals”. A subadult animal performed 36.3% “visual signals”, 31.4% “visual signals possibly making some noise”, 10.1% “visual signals often combined with touching” and 17.2% “tactile signals”. A juvenile baboon displayed 44.9% “visual signals”, 10.3% “visual signals possibly making some noise”, 10.7% “visual signals often combined with touching” and 32.8% “tactile signals”. An infant baboon used 35.9% “visual signals”, 3.0% “visual signals possibly making some noise”, 6.6% “visual signals often combined with touching” and 54.5% “tactile signals”.

A female showed 49.5% “visual signals”, 10.5% “visual signals possibly making some noise”, 8.3% “visual signals often combined with touching” and 20.9% “tactile signals”. A male performed 40.5% “visual signals”, 42.8% “visual signals possibly making some noise”, 5.7% “visual signals often combined with touching” and 11.7% “tactile signals”.

The senescent/adult and juvenile baboons showed “visual signals” and the subadult and juvenile baboons used “visual signals often combined with touching” slightly more than other age classes. The differences were not significant. In contrast, the categories “visual signal possibly making some noise” and “tactile signals” showed slightly significant differences (see figure 3.3.1.7 a).

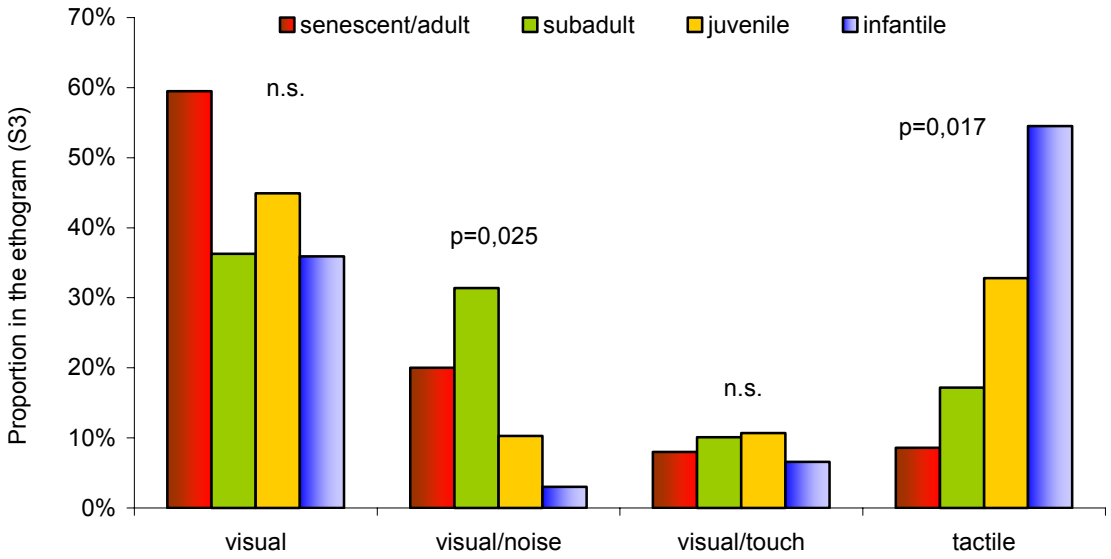


Figure 3.3.1.7 a
Proportion of the four signal categories in the ethogram grouped by four age classes (median)

Male baboons performed significantly more “visual signals possibly making some noise” than female baboons. Females tended to use more “visual signals” and “tactile signals” as well as slightly more “visual signals often combined with touching”, but these differences were not significant (see figure 3.3.1.7 b).

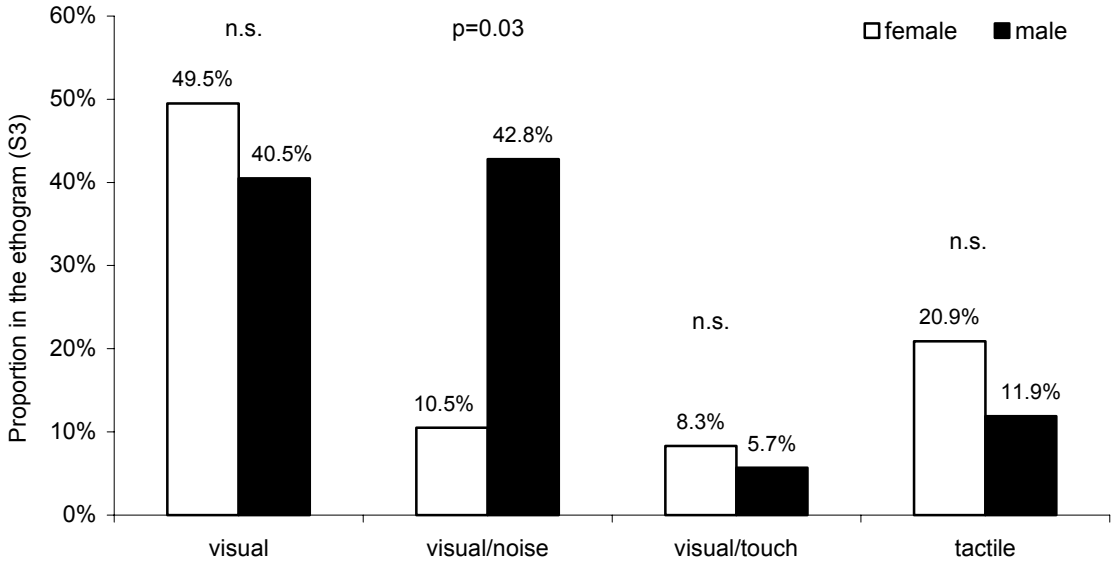


Figure 3.3.1.7 b
Proportion of the four signal categories in the ethogram grouped by sex classes (median)

3.3.1.8 Idiosyncratic signals

There were five signals exclusively found in one animal each. They were categorised as idiosyncratic signals and were excluded from the analyses.
Head movement was shown by the subadult female Elke, *waving* by the subadult male Bernd and *diving* by the juvenile female Claire. Each of these three signals was observed only once.
Tapping ground was seen in the harem leader Kuno and *object movement* in the juvenile female Claire. Each of the two signals was observed twice.

3.3.2 Combined Signals

In addition to single signals, individuals also sent two or three signals simultaneously. In the following, these events are called combinations. Double and triple combinations are distinguished depending on how many parallel signals were involved.

3.3.2.1 Frequency of the single signals in the different combinations (Source 2)

19 different signals occurred in combinations: eight “visual signals” (out of 13), five “visual signals possibly making some noise” (out of six), both “visual signals often combined with touching” and four “tactile signals” (out of five).
The most frequently combined signal was *eyebrow raising* occurring in 15 different combinations (three of them being triple combinations), followed by *poking* used in eight different combinations (one triple). *Threat mouth* (three triple*)* and *relaxed open mouth* (one triple) were each shown in seven different combinations. *Presenting, lowering body* and *stiff threat* (two triple) were each found in six different combinations, *enlisting* in five, *lipsmacking* and *chasing* (two triple) each in four, and *pumping* in two combinations. *Lowering back*, *jumping in the air*, *mounting*, *pulling on*, *penis grab*, *greeting*, *head bobbing* and *yawning* were each seen in only one combination.

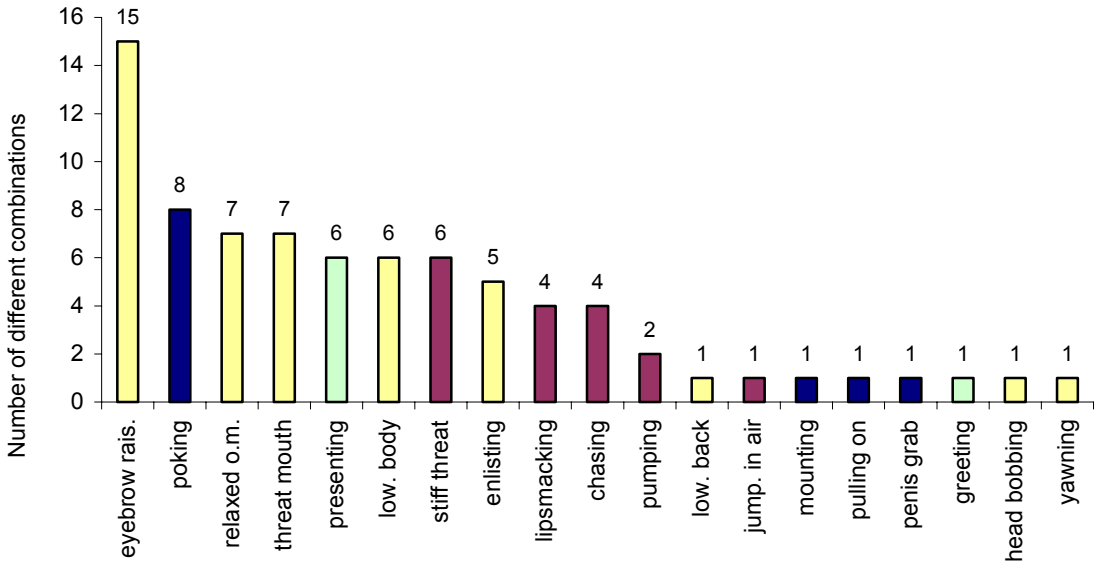


Figure 3.3.2.1 a
Frequency of the single signals in different combinations
light yellow: visual claret-red: visual/noise light green: visual/touch dark blue: tactile

3.3.2.2 Use of the single signals in combination (Source 2)

Eyebrow raising was found in combination with *enlisting*, *lowering body*, *relaxed open mouth*, *threat mouth*, *head bobbing*, *yawning*, *chasing*, *pumping*, *stiff threat*, *lipsmacking*, *presenting* and *poking*. ***Relaxed open mouth*** was observed in combination with *eyebrow raising*, *lowering body*, *presenting*, *poking*, *mounting* and *pulling on.* ***Stiff threat*** was found in combination with *eyebrow raising*, *enlisting*, *threat mouth*, *chasing* and *pumping*. ***Lipsmacking*** was observed used together with *eyebrow raising*, *lowering body*, *presenting* and *greeting*. ***Presenting*** was shown combined with *eyebrow raising*, *enlisting*, *lowering body*, *relaxed open mouth*, *lipsmacking* and *penis grab*. ***Greeting*** was only seen together with *lipsmacking*. ***Poking*** was observed in combination with *eyebrow raising*, *enlisting*, *lowering body*, *lowering back*, *relaxed open mouth*, *threat mouth* and *jumping in the air*.
All combinations of the signals are shown in the following figure.

Table 3.3.2.2 a
Observed signal combinations

signal 2 / signal 1	eyebrow raising	enlisting	lowering body	lowering back	relaxed open mouth	threat mouth	head bobbing	yawning	chasing	jumping in air	pumping	stiff threat	lipsmacking	presenting	greeting	poking	mounting	pulling on	penis grab
eyebrow raising		x	x		x	x	x	x	x		x	x	x	x		x			
enlisting	x		x									x		x		x			
lowering body	x	x			x								x	x		x			
lowering back																x			
relaxed o. m.	x		x											x		x	x	x	
threat mouth	x								x			x				x			
head bobbing	x																		
yawning	x																		
chasing	x					x						x							
jumping in air																x			
pumping	x											x							
stiff threat	x	x				x			x		x								
lipsmacking	x		x											x	x				
presenting	x	x	x		x								x						x
greeting													x						
poking	x	x	x	x	x	x				x									
mounting					x														
pulling on					x														
penis grab														x					

3.3.2.3 Overall occurrence of the combinations (Source 2)

37 different combinations were found: 33 double (two simultaneously produced signals) and four triple (three simultaneously produced signals) combinations. Eight double and two triple combinations occurred each only one time in one animal. They were discussed under 3.3.2.10 and not used for the following analyses. Here 27 different combinations, 25 double and two triple, were analysed.

The most commonly occurring combination was *eyebrow raising + stiff threat* (48 times respectively 23.5% of all shown combinations). The FAs also frequently used *relaxed open mouth + poking* (22 times respectively 10.8%) and *eyebrow raising + threat mouth* (16 times respectively 7.8%). *Eyebrow raising + stiff threat + threat mouth* was the most frequently observed triple combination (13 times respectively 6.4% of all shown combinations). All other combinations had an incidence of less then 5% of all combinations. The rarest combinations (two times respectively 1.0% of all combi-

nations) were *eyebrow raising + poking*, *eyebrow raising + presenting, jumping in the air + poking*, *poking + threat mouth*, *lowering body + lipsmacking*, *relaxed open mouth + pulling on* (see also figure 3.3.2.3 a).

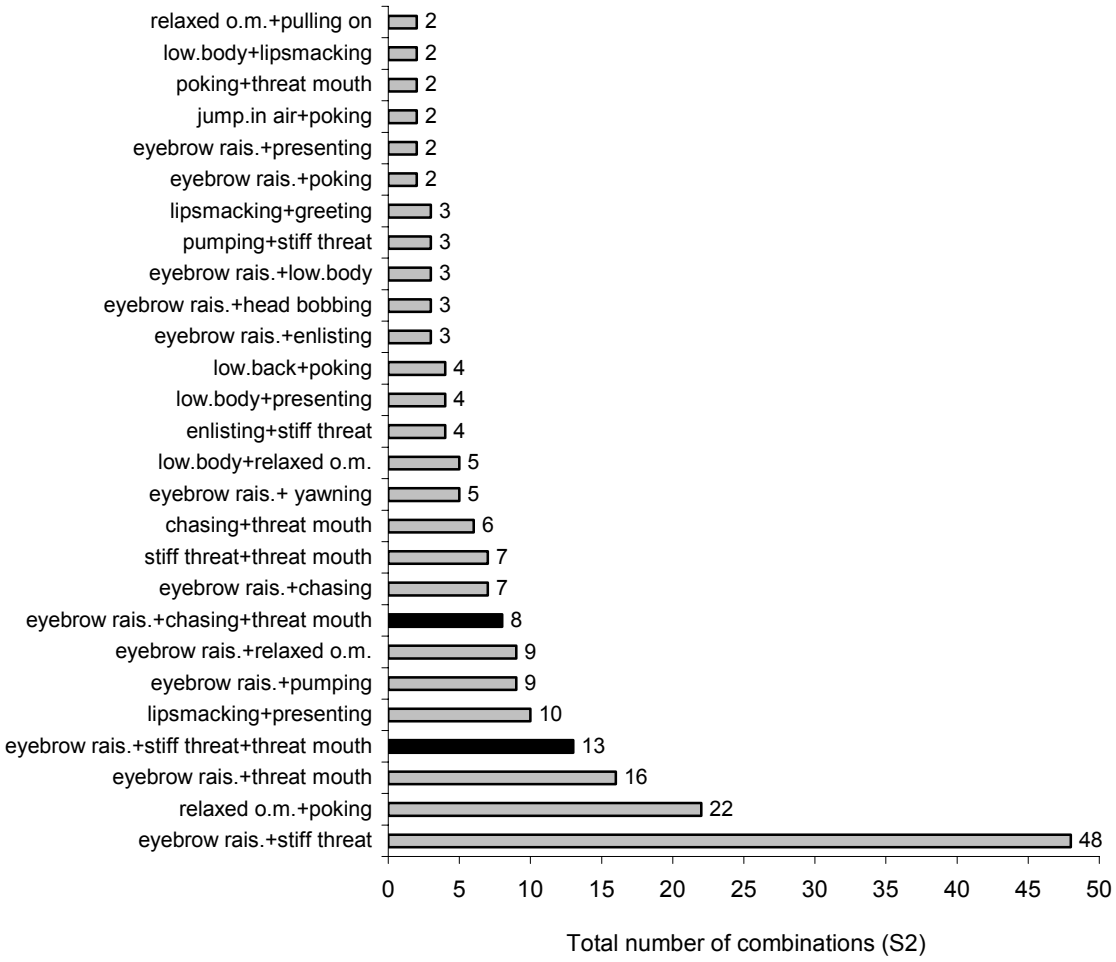


Figure 3.3.2.3 a
Total number of combinations (black: triple combinations)

3.3.2.4 Combinations grouped by signal categories (Source 2)

The combination “visual + visual/noise” was the most frequent one, found in nine different combinations. “Visual + visual” and “visual + tactile” were also common with seven and five different combinations respectively. “Visual + visual/touch”, “visual/ noise + visual/noise”, “visual/noise + visual/touch” and “visual/noise + tactile” occurred rarely. “Visual/touch + visual/touch”, “visual/touch + tactile” as well as “tactile + tactile” were not observed.

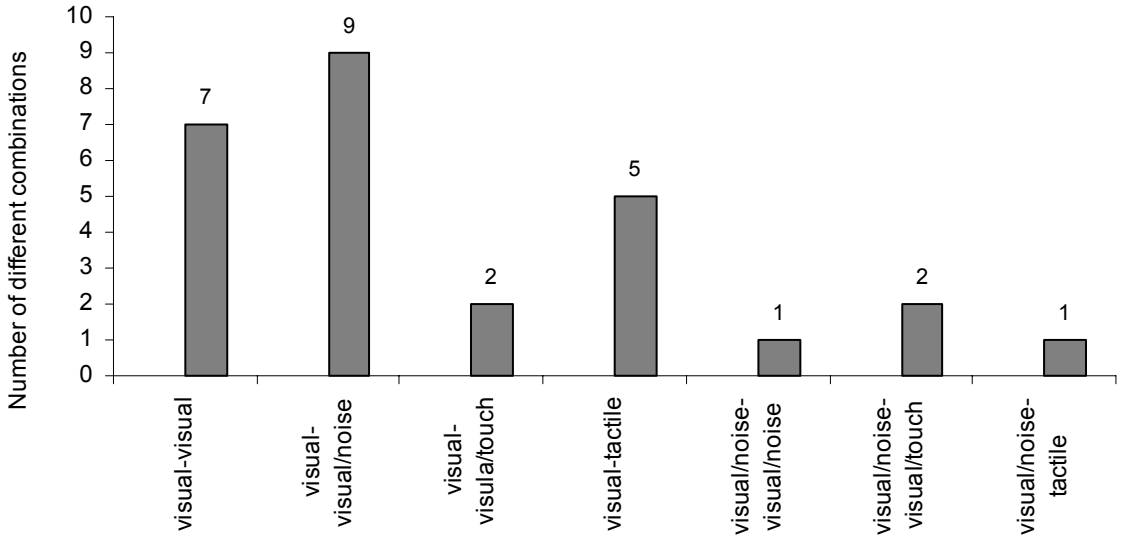


Figure 3.3.2.4 a
Combinations grouped by signal categories

3.3.2.5 Usage of combinations by the focal animals (Source 2)

24 of the 27 different combinations were observed in less than half of the focal animals. *Relaxed open mouth + pulling on, jumping in the air + poking, pumping + stiff threat, eyebrow raising + head bobbing, eyebrow raising + enlisting*, *lowering back + poking* and *enlisting + stiff threat* were each shown by only one focal animal (7.1% of all FAs). These combinations can be called idiosyncratic combinations. *Lowering body + lipsmacking, poking + threat mouth, eyebrow raising + presenting, eyebrow raising + poking* and *lowering body + presenting* were also rare and each was seen in use by only two focal animals (14.3%). *Stiff threat + threat mouth*, *lipsmacking + greeting, eyebrow raising + lowering body, eyebrow raising + yawning*, *eyebrow raising + chasing* and *eyebrow raising + pumping* (three baboons respectively 21.4% of all FAs) as well as *lowering body + relaxed open mouth, chasing + threat mouth* and *eyebrow raising + relaxed open mouth* (four baboons respectively 8.6%) were each observed in approximately a quarter of the focal animals. *Eyebrow raising + threat mouth* as well as the triple combinations *eyebrow raising + stiff threat + threat mouth* and *eyebrow raising + chasing + threat mouth* were each found in six focal animals (42.6%). Seven focal animals (50%) showed the combination *lipsmacking + presenting*. *Eyebrow raising + stiff threat* and *relaxed open mouth + poking* had the widest range of occurrence and were each used by 11 of the 14 focal animals (78.6%).

3.3.2.6 Number of different combinations (Source 2)

Individuals

All focal animals showed combinations, but none of the focal animals used all 27 different combinations. The harem leader Kuno performed the highest number with 12 different combinations (44.4% of all combinations). The subadult males Bernd and Erwin had ten (37.5%) and the adult females Gesine and Claudia had nine (33.3%) different combinations in their repertoire. The juvenile female Grit performed eight (29.7%), the senescent female Ina as well as the juvenile female Claire seven (25.9%) different combinations. The juvenile male Igor displayed five (18.5%) and the females Elke (subadult) and Gundel (juvenile) four (14.8%) different combinations. The lowest numbers with three (11.1%) different combinations were shown by the females Iris (adult), Gabi (brown infant) and Irina (black infant).

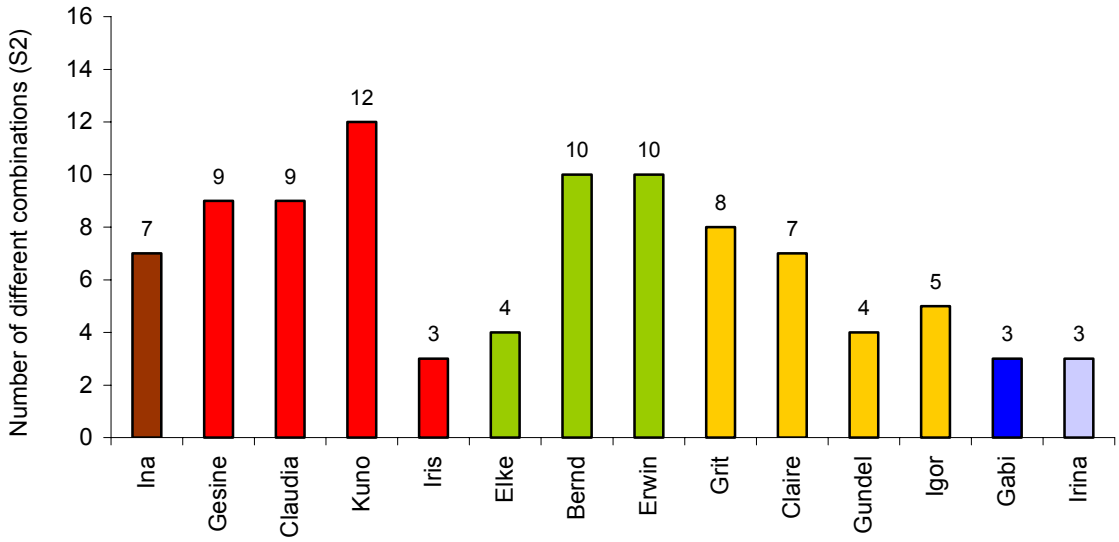


Figure 3.3.2.6 a
Number of different combinations shown by the focal animals (maximum: 27)
brown: senescent adults *yellow: juveniles*
red: adults *dark blue: brown infants*
green: subadults *light blue: black infants*

One adult female (Gesine), the subadult female Elke and the five youngest baboons showed only double combinations.

There were 25 different double combinations but no more than ten of these were observed in a focal animal.

The harem leader Kuno used the largest variety of double combinations (ten versions respectively 40% of all different double combinations), followed by the adult female Gesine (nine versions respectively 36%). The subadult males Bernd and Erwin displayed eight (32%), the females Claudia (adult) and Claire (juvenile) seven (28%), and Ina (senescent) as well as Grit (juvenile) six (24%). The remaining focal animals

showed less than a quarter of all double combination types (Igor five/20%, Elke and Gundel four/16%, Gabi and Irina three/12%). The smallest number was seen in the adult female Iris with two different double combinations (8%).

Seven of the focal animals – the senescent female Ina, the adult females Claudia and Iris, the adult harem leader Kuno, the subadult males Bernd and Erwin as well as the juvenile female Grit – performed triple combinations, too. Claudia, Kuno, Bernd, Erwin and Grit used two different triple combinations, Ina and Iris only one. See also figure 3.3.2.6 b.

A focal animal performed with seven (out of 27) about a quarter of all different combinations (median).

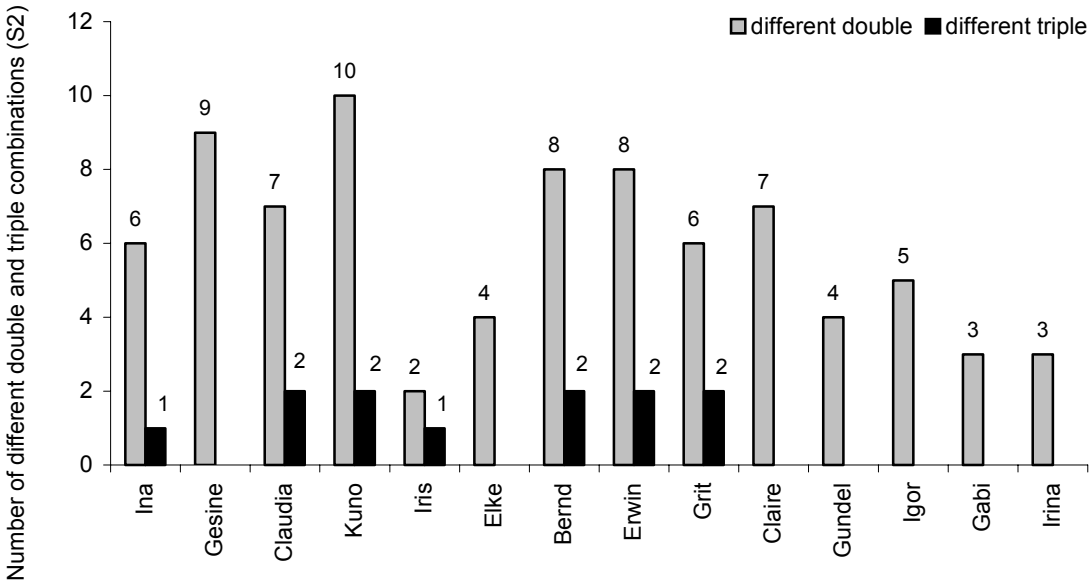


Figure 3.3.2.6 b
Number of different double (max.25) and triple combinations (max.2) shown by the FAs

Age/sex classes (median)

The highest numbers with 10.0 and 9.0 out of 27 different combinations (37.0% and 33.3% of all different combinations) were found in the subadult and adult baboons. The senescent female used 7.0 different combinations (25.9%) and the juveniles 6.0 (22.2%). The brown and the black infant showed the lowest number of different combinations (3.0/11.1%).

A female baboon performed with 5.5 versions (20.4%) significantly less different combinations ($p=0.024$) than a male baboon with 10.0 (37.0%).

3.3.2.7 Range in usage of the different combinations (Source 2)

Individuals

Table 3.3.2.7 a shows which focal animal displayed which combination.

Table 3.3.2.7 a
Combination usage by the FAs

	Ina	Gesine	Claudia	Kuno	Iris	Elke	Bernd	Erwin	Grit	Claire	Gundel	Igor	Gabi	Irina
eyebrow rais. + enlisting		x												
eyebrow rais. + chasing	x		x	x										
eyebrow rais. + low. body	x		x							x				
eyebrow rais. + relaxed o. m.										x	x		x	x
eyebrow rais. + pumping				x			x					x		
eyebrow rais. + stiff threat	x	x	x	x	x	x	x	x	x	x			x	
eyebrow rais. + poking								x			x			
eyebrow rais. + presenting									x	x				
eyebrow rais. + threat mouth	x			x			x	x		x		x		
eyebrow rais. + head bobbing		x												
eyebrow rais. + yawning			x	x			x							
enlisting + stiff threat				x										
chasing + threat mouth				x		x		x				x		
low. body + relaxed o. m.		x	x					x	x					
low. body + lipsmacking		x				x								
low. body + presenting			x											x
low. back + poking		x												
relaxed o. m. + poking		x	x	x			x	x	x	x	x	x	x	x
relaxed o. m. + pulling on									x					
jump. in the air + poking											x			
pumping + stiff threat							x							
stiff threat + threat mouth		x		x			x							
lipsmacking + presenting	x	x			x	x		x	x			x		
lipsmacking + greeting	x			x				x						
poking + threat mouth							x			x				
eyebrow rais. + chasing + threat m.			x	x	x		x	x	x					
eyebrow rais. + stiff threat + threat m.	x		x	x			x	x	x					

Sex/age classes

With 74.1% (20 out of 27) the group of the adult baboons displayed the widest range of different combinations. The groups of subadult and juvenile baboons each performed 59.3% (16) of all different combinations. Because the classes of senescent, brown infant and black infant contain only one animal, these data are the same like for the

individuals Ina (25.9% respectively seven different combinations), Gabi and Irina (each 11.1% respectively three different combinations).

The female baboons used a greater variety of different combinations (88.9% respectively 24 combinations) than the male baboons (63.0% respectively 17 combinations).

See also table 3.3.2.7 b and figure 3.3.2.7 c.

Table 3.3.2.7 b
Combination usage by age and sex classes

	senescent	**adult**	**subadult**	**juvenile**	**brown infant**	**black infant**	**female**	**male**
eyebrow rais. + enlisting		x					x	
eyebrow rais. + chasing	x	x					x	x
eyebrow rais. + low. body	x	x		x			x	
eyebrow rais. + relaxed o. m.				x	x	x	x	
eyebrow rais. + pumping		x	x	x				x
eyebrow rais. + stiff threat	x	x	x	x	x		x	x
eyebrow rais. + poking			x	x			x	x
eyebrow rais. + presenting				x			x	
eyebrow rais. + threat mouth	x	x	x	x			x	x
eyebrow rais. + head bobbing		x					x	
eyebrow rais. + yawning		x	x				x	x
enlisting + stiff threat		x						x
chasing + threat mouth		x	x	x			x	x
low. body + relaxed o. m.		x	x	x			x	x
low. body + lipsmacking		x	x				x	
low. body + presenting		x				x	x	
low. back + poking		x					x	
relaxed o. m. + poking		x	x	x	x	x	x	x
relaxed o. m. + pulling on				x			x	
jump. in the air + poking				x			x	
pumping + stiff threat			x					x
stiff threat + threat mouth		x	x				x	x
lipsmacking + presenting	x	x	x	x			x	x
lipsmacking + greeting	x	x	x				x	x
poking + threat mouth			x	x			x	x
eyebrow rais. + chasing + threat mouth		x	x	x			x	x
eyebrow rais. + stiff threat + threat m.	x	x	x	x			x	x

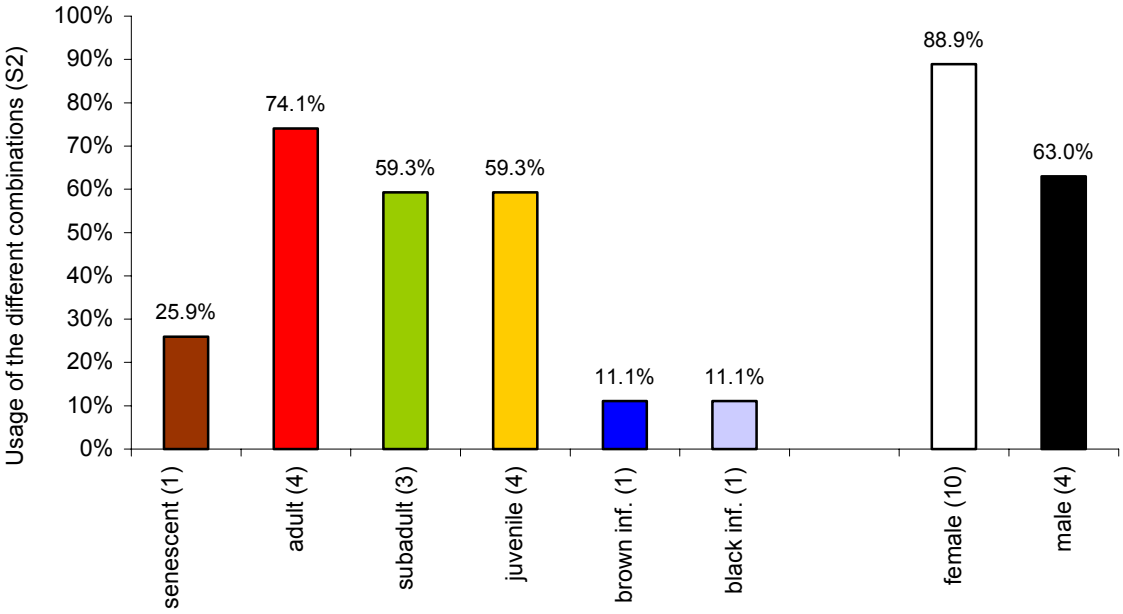


Figure 3.3.2.7 c
Range of the different combinations grouped by age and sex classes

3.3.2.8 Total number and frequency of combinations (Source 3)

Individuals

The total number of combinations shown by the focal animals during their focal time ranged from three to 34 combinations. They mostly consisted of double combinations. The highest numbers of triple combinations were found in Claudia, Kuno, Erwin and Grit (four each). Bernd performed three, Ina and Iris each used one triple combinations. See figure 3.3.2.8 a.

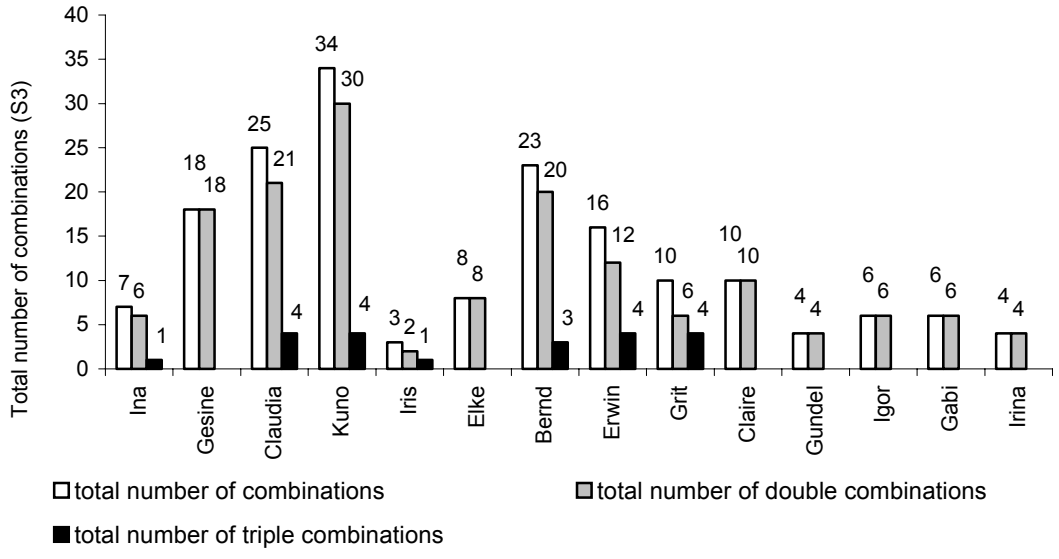


Figure 3.3.2.8 a
Total number of combinations shown by FAs

Because the observational times are not exactly the same for each focal animal, the frequency (total number of all combinations/observational time – comb/hour) was used.

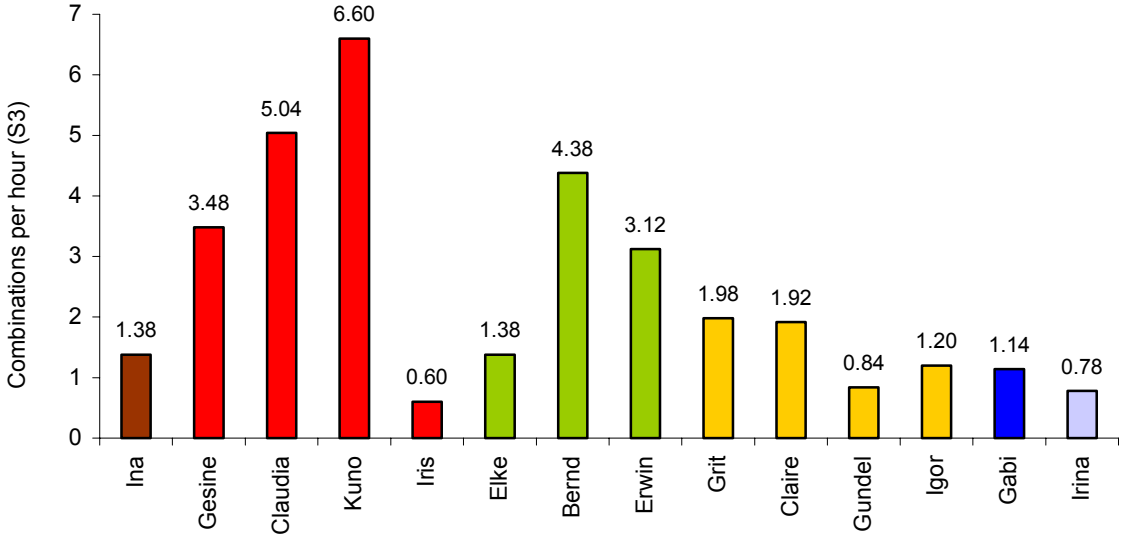


Figure 3.3.2.8 b
Frequency of combination usage in the FAs (per hour)
brown: senescent adults *yellow: juveniles*
red: adults *dark blue: brown infants*
green: subadults *light blue: black infants*

The highest frequency of combinations was found in the harem leader Kuno. He displayed 6.6 combinations per hour. The adult females Claudia (5.04 comb/hour) and Gesine (3.48 comb/hour) as well as the subadult males Bernd (4.38 comb/hour) and Erwin (3.12 comb/hour) also used combinations frequently. Six baboons performed between one and two combinations per hour (Ina, Elke, Grit, Claire, Igor and Gabi). The females Iris (adult), Gundel (juvenile) and Irina (black infant) used less than one combination per hour (see also figure 3.3.2.8 b).

A focal animal performed 1.65 combinations per hour (median).

Age/sex classes (median)

The adult baboons performed the highest number of combinations per hour (4.26 comb/hour), followed by the subadults (3.12 comb/hour). The juveniles used 1.56 comb/hour. The senescent baboon and the brown infant showed frequencies under 1.5 comb/hour, the black infant under one combination per hour.

A female baboon used 1.38 combinations per hour whereas a male baboon displayed 3.75 combinations per hour. The differences between the age or sex classes were not significant.

See also figures 3.3.2.8 b and c.

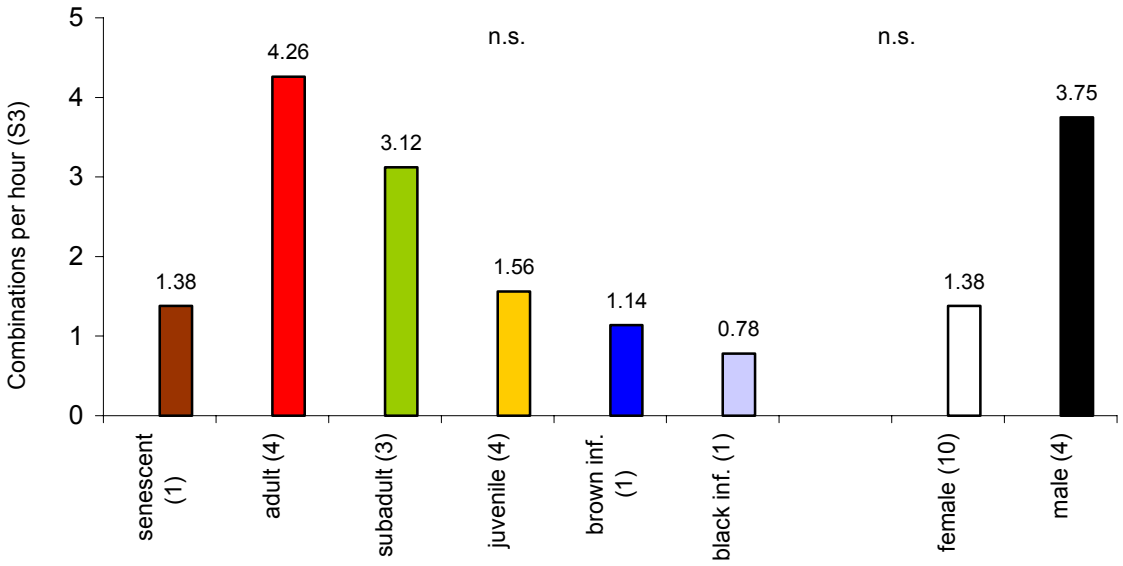


Figure 3.3.2.8 c
Median frequency (per hour) of combination usage in age and sex classes

3.3.2.9 Comparisons

Number of different single signals and different signal combinations (Source 2)

A focal animal (median) used twice as many different single signals (14.0) as different combinations (7.0). That amounted to a ratio of 2.0.

A low value of the ratio of number of different signals to number of different combinations meant that a baboon performed more different combinations in relation to different single signals than a baboon with a high value, and that it used many signals of its repertoire for combinations (see figure 3.3.2.9 a).

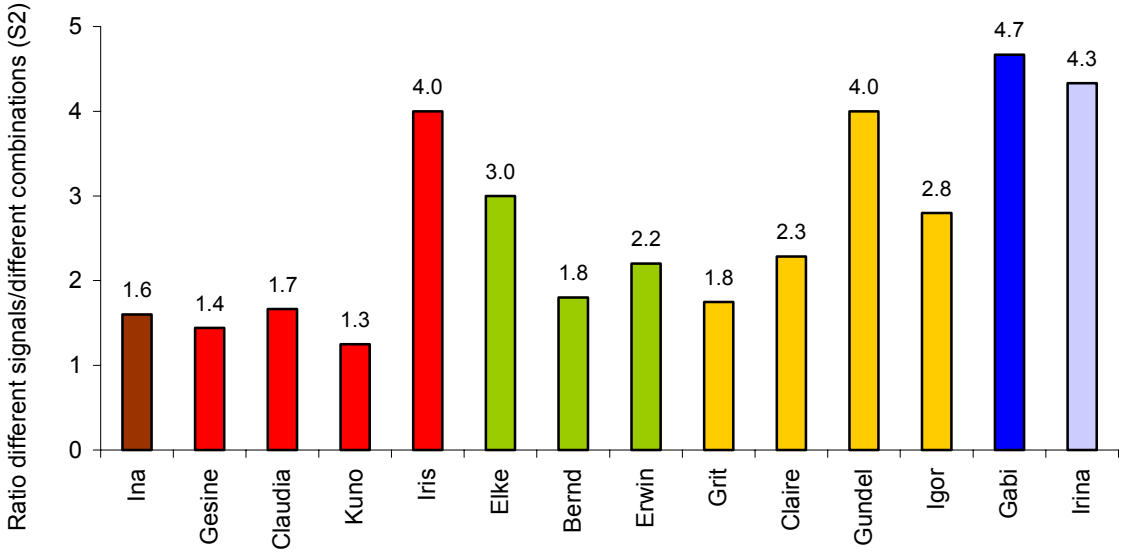


Figure 3.3.2.9 a
Ratio of number of different signals to number of different combinations used by the FAs (S2)

Gabi (14 signals versus three combinations), Irina (13 sig. vs. 3 comb.), Iris (12 sig. vs. 3 comb.) and Gundel (16 sig. vs. 4 comb.) showed ratios of 4.0 and more and used relatively less different combinations in relation to their different single signals. In contrast, Kuno (15 sig. vs. 12 comb.), Gesine (13 sig. vs. 9 comb.), Ina (11 sig. vs. 7 comb.) and Claudia (15 sig. vs. 9 comb.) had low ratios and showed more than half as many different combinations than different single signals.

The other focal animals had the following values: Grit 1.8 (14 sig. vs. 8 comb.), Bernd 1.8 (18 sig. vs. 10 comb.), Erwin 2.2 (22 sig. vs. 10 comb.), Claire 2.3 (16 sig. vs. 7 comb.), Igor 2.8 (14 sig. vs. 5 comb.) and Elke 3.0 (12 sig. vs. 4 comb.).

Age/sex classes (median)

The senescent and adult animals showed more different combinations in relation to different signals than the infants and hence had a lower ratio of different signals to different combinations.

There was a tendency of older baboons using more different combinations in relation to different signals than younger baboons. When comparing the pooled age class senescent/adult/subadult to the pooled age class juvenile/brown infant/black infant, the difference is slightly significant (p=0.043).

A female baboon tended to perform fewer different combinations compared to different signals than a male baboon. See also figure 3.3.2.9 b.

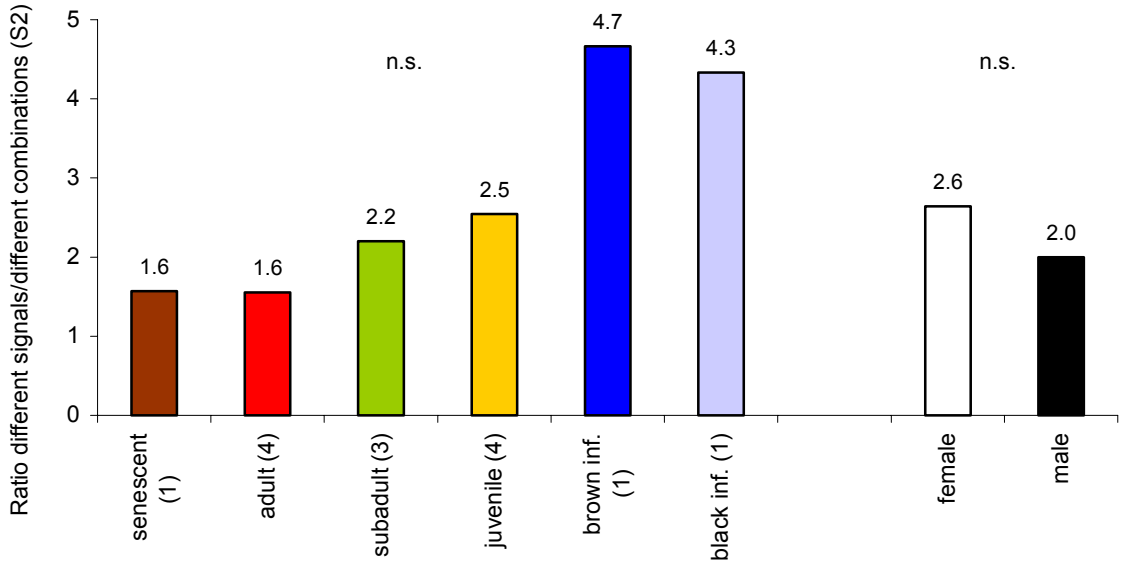


Figure 3.3.2.9 b
Ratio of number of different signals to number of different combinations shown by age and sex classes (S2)

Frequency of single signals and signal combinations (Source 3)

Individuals

A focal animal (median) used about ten times more single signals per hour (21.6 sig/hour) than combinations per hour (1.65 comb/hour).

Five baboons – the adult female Iris (14.4 sig/h vs. 0.6 comb/h), the juveniles Gundel (22.8 sig/h vs. 0.84 comb/h) and Igor (22.2 sig/h vs. 1.2 comb/h) as well as the infants Gabi (24.0 sig/h vs. 1.14 comb/h) and Irina (19.2 sig/h vs. 0.78 comb/h) – had a high ratio. Thus, they used far fewer combinations in relation to signals per hour than did the other baboons. In contrast, the adults Gesine (21.0 sig/h vs. 3.48 comb/h), Claudia (40.2 sig/h vs. 5.04 com/h) and Kuno (52.8 sig/h vs. 6.6 comb/h) and the subadult male Bernd (34.2 sig/h vs. 4.38 comb/h) showed more combinations in relation to signals per hour. Ina (13.8 sig/h vs. 1.38 comb/h), Elke (15.0 sig/h vs. 1.38 comb/h), Erwin (32.4 sig/h vs. 3.12 comb/h), Grit (21.6 sig/h vs. 1.98 comb/h) and Claire (19.2 sig/h vs. 1.92 comb/h) ranged around the average. See also figure 3.3.2.9 c.

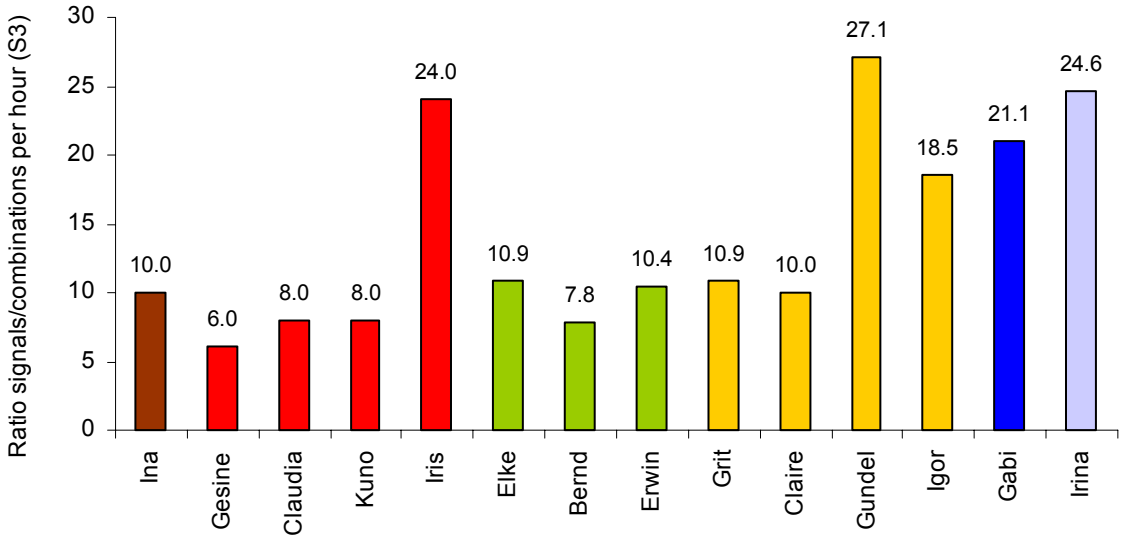


Figure 3.3.2.9 c
Ratio of signal frequency to combination frequency by the FAs (S3)

Age/sex classes (median)

As shown in figure 3.3.2.9 d below, the older baboons tended to perform more combinations in relation to signals per hour than the younger individuals. There was no significant difference for the six age classes, but when pooling the senescent/ adult/subadult together and testing against pooled juvenile/brown infant/black infant, the difference is significant (p=0.029).

A female baboon displayed slightly less combinations in relation to signals per hour than a male baboon, but the difference was not significant.

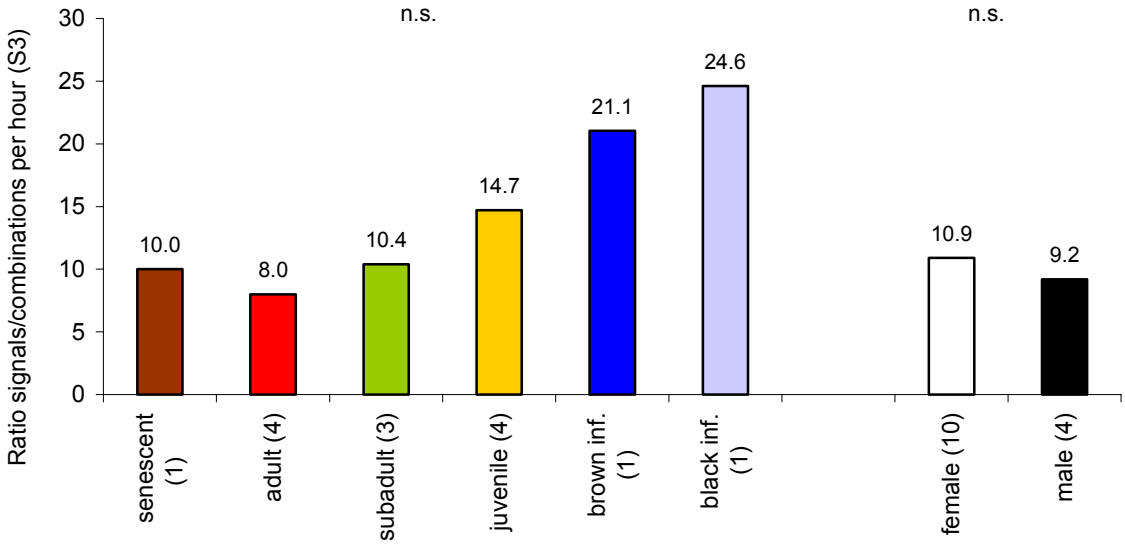


Figure 3.3.2.9 d
Ratio of signal frequency to combination frequency shown by age and sex classes (S3)

3.3.2.10 Idiosyncratic combinations (excluded from the analyses)

Idiosyncratic combinations

Ten combinations (eight double and two triple) were observed only once. Because they each occurred in only one baboon they can be considered idiosyncratic combinations. Neither the black infant, nor the adult or senescent baboons did use any of these idiosyncratic combinations.

The subadult males showed the double combinations *enlisting* + *presenting* (Bernd) and *penis grab* + *presenting* (Erwin) as well as the triple combination *chasing* + *stiff threat* + *threat mouth* (Bernd). The juvenile females performed *eyebrow raising* + *lipsmacking* (Claire), *enlisting* + *lowering body* (Gundel), *lowering body* + *poking* (Grit), *relaxed open mouth* + *mounting* (Grit) as well as *eyebrow raising* + *relaxed open mouth* + *poking* (Claire). *Enlisting* + *poking* was recorded in the juvenile male Igor and *relaxed open mouth* + *presenting* in the brown infant Gabi.

Combinations with idiosyncratic signals

There were three combinations involving one idiosyncratic signal, each combination being used once by only one individual. The subadult male Bernd used *threat mouth* + *waving*, the harem leader Kuno *eyebrow raising* + *tapping ground* and the subadult female Elke a triple combination *lipsmacking* + *presenting* + *head movement*. These combinations were not considered in the analyses.

3.3.3 Attentional state

To investigate the intentionality of sender's signal use, the attentional state of the recipient was evaluated. The recipient was considered attentive if he was able to see the signal (if the sender was in the visual field of the recipient).

The source for this analysis was S1 (all recorded signals of all animals from 4284 minutes of observation). Almost only single signals could be regarded because the most combinations were mixed combinations between different categories. Therefore, the quantity of signals is lower than the number reported in section 3.3.1.

All single events in which the recipient was clearly attentive and all single events in which the recipient was clearly not attentive were considered and summarised.

Some signals did not yield enough data for the analysis.

Results

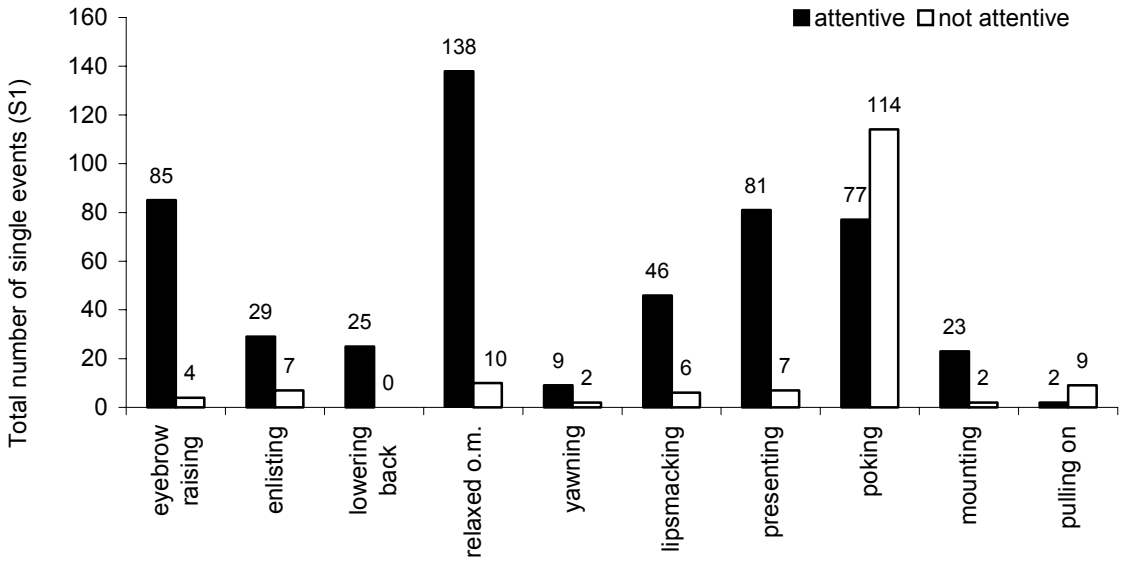


Figure 3.3.3 a
Attentive state of the recipient for some signals

Visual signals

The recipient was in an attentive state in 95.5% of all *eyebrow raising* and 93.2% of all *relaxed open mouth* events. When a sender gave the *enlisting* signal, the recipient was also usually attentive (80.6%). The *lowering back* signal was only given when the recipient was attentive. In 81.1% of all *yawning* events the recipient was attentive. See also figure 3.3.3 a.

For *lowering body* only six cases could be analysed from which half were directed to an attentive recipient. In all six events of *hand/headstand* the recipient was in an attentive state. For the other visual signals only very few or even no cases could be analysed (see also table 3.3.3 b).

In sum, the sender gave the signal when the recipient was in an attentive state in 91.5% of all single events of the category “visual signals”. The difference between “attentive” and “not attentive” was significant (p=0.015).

If visual-visual combinations (e.g. *eyebrow raising* + *relaxed open mouth* and *eyebrow raising* + *threat mouth*) were considered as well, the recipient was attentive in 83.3% of all cases (30 out of 36 cases).

Therefore, “visual signals” seemed to demand the attention of the recipient and the sender took this attentive state into account when communicating. See also figure 3.3.3 e.

Table 3.3.3 b
Overview of the attentive state of the recipient when a “visual signal” was given

signal	analysed	number of cases where the recipient was			
VISUAL	cases	**attentive**		**not attentive**	
eyebrow raising	89	85	95.5%	4	4.5%
enlisting	36	29	86.0%	7	19.4%
lowering body	6	3	50.0%	3	50.0%
lowering back	25	25	100.0%	0	0.0%
relaxed o. m.	148	138	93.2%	10	6.8%
head shaking	0	0	0.0%	0	0.0%
rolling on gr.	4	2	50.0%	2	50.0%
h./headstand	6	6	100.0%	0	0.0%
threat mouth	4	4	100.0%	0	0.0%
head bobbing	1	1	100.0%	0	0.0%
yawning	11	9	81.8%	2	18.2%
head tapping	0	0	0.0%	0	0.0%
spinning	0	0	0.0%	0	0.0%
SUM	330	302	**91.5%**	28	**8.5%**

Visual signals possibly making some noise

During most *lipsmacking* events (46 out of 52) the recipient was able to see the signal (see also figure 3.3.3 a). In all cases of *pumping* the recipient was attentive (eight cases). For *stiff threat* there was almost no difference in attentiveness (see also table 3.3.3 c).

In sum, the sender gave the signal when the recipient was in an attentive state during 85.7% of all single events of the category “visual signals possibly making some noise”.

This shows that the category “visual signal possibly making some noise” also seemed to demand the attention of the recipient and the sender took into account the recipient’s attentional state when communicating within this signal category. See also figure 3.3.3 e.

Table 3.3.3 c
Overview of the attentive state of the recipient when a "visual signal possibly making some noise" was given

signal	analysed	number of cases where the recipient was			
VISUAL/NOISE	cases	**attentive**		**not attentive**	
chasing	0	0	0.0%	0	0.0%
jump. in the air	1	1	100.0%	0	0.0%
pumping	8	8	100.0%	0	0.0%
stiff threat	9	5	55.6%	4	44.4%
displaying	0	0	0.0%	0	0.0%
lipsmacking	52	46	88.5%	6	11.5%
SUM	70	60	**85.7%**	10	**14.3%**

Visual signal often combined with touching

When the signal *presenting* was shown, recipients were attentive in 92.0% of all events (81 out of 88 cases). Only three *greeting* events could be analysed here and all were directed to an attentive recipient.

In sum, in 92.3% of all single events from the category "visual signals often combined with touching" were directed towards an attentive recipient.

So it can be assumed that signals from the category "signals often combined with touching" also demand an attentive recipient and that therefore the attentional state of the recipient was important for senders using this signal category. See also figure 3.3.3 e.

Tactile signals

In 59.7% of all *poking* (114 out of 191 cases) and 81.8% of all *pulling on* events (nine out of 11 cases) the recipient was not attentive. Within this category only for *mounting* there were more attentive than inattentive cases (23 out of 25) registered. See also figure 3.3.3 a and table 3.3.3 d.

Table 3.3.3 d
Overview of the attentive state of the recipient when a "tactile signal" was given

signal	analysed	number of cases where the recipient was			
TACTILE	cases	**attentive**		**not attentive**	
poking	191	77	40.3%	114	59.7%
mounting	25	23	92.0%	2	8.0%
pulling on	11	2	18.2%	9	81.8%
penis grab	0	0	0.0%	0	0.0%
jump. on back	3	1	33.3%	2	66.6%
SUM	230	103	**44.8%**	127	**55.2%**

In sum, in 55.2% of all single tactile events the recipient was not in an attentive state. The difference between "attentive" and "not attentive" was not significant (p=0.465). It seems that the attention of the recipient is not essential for using tactile signals. There-

fore, it is not important for a sender to regard the attentional state of a recipient if the communication takes place by using tactile signals. See also figure 3.3.3 e.

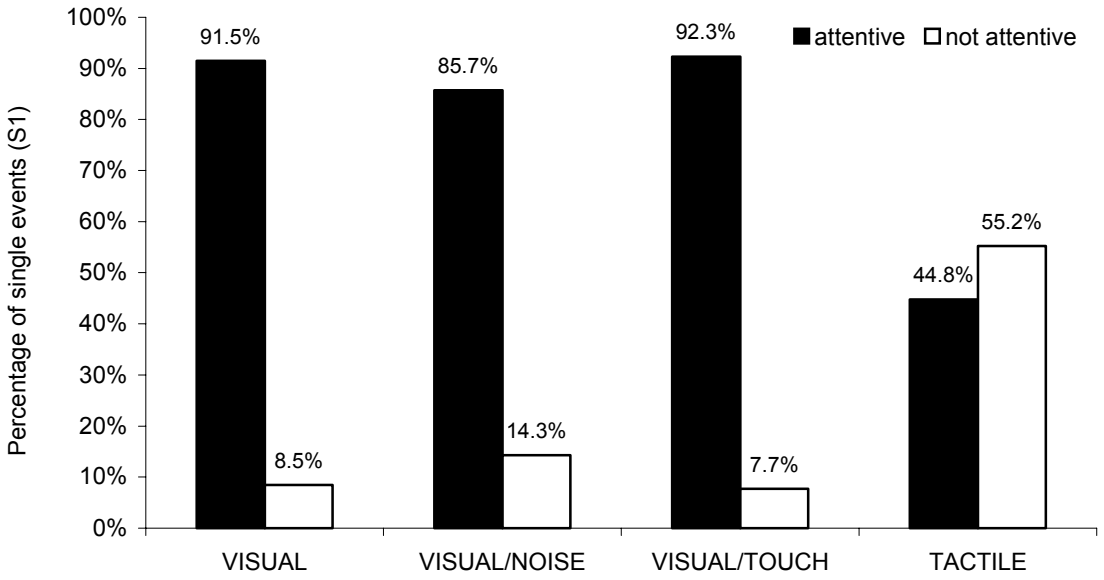


Figure 3.3.3 e
Attentional state regarding the four categories

There was a strong tendency for senders to prefer an attentive recipient when using categories including visual signals. For the tactile category there was no difference regarding the attentional state of the recipient.

If all signals were summarised 76.2% of the signals were directed towards an attentive recipient and 23.8% to an inattentive recipient.

3.3.4 Gaze

Gaze contact between sender and recipient was noted before, during and after the sender gave the signal (before/during/after signalling).
The source of these analyses was S1 (all recorded signals of all animals from 4284 minutes of observation). Only single signals could be regarded because most combinations were mixed combinations between different signal categories. Therefore, the quantity of signals is lower than the number reported in section 3.3.1.
All single events with and without clear gaze contact were considered and summarised.

Results

Overview

For all three time points (before, during, after signal) there were more than twice as many events without gaze contact between sender and recipient than events with gaze contact (see figure 3.3.4 a). This difference was especially high for the time point after signals were given. This suggests that after signalling very often no further gaze contact was necessary.

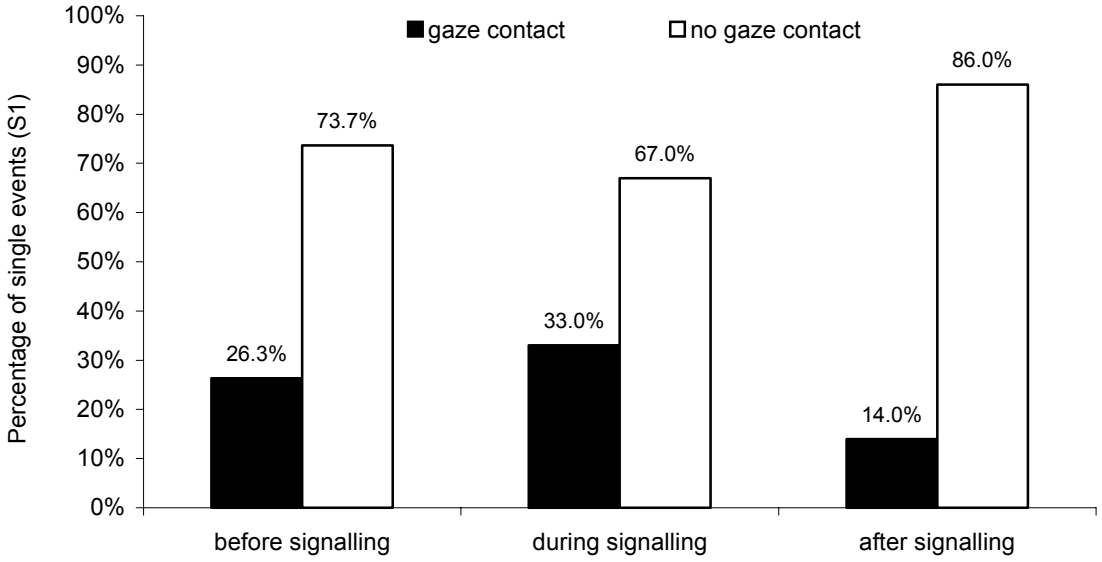


Figure 3.3.4 a
Overview of the percentage of single events where gaze contact took place or not

Gaze contact before signalling

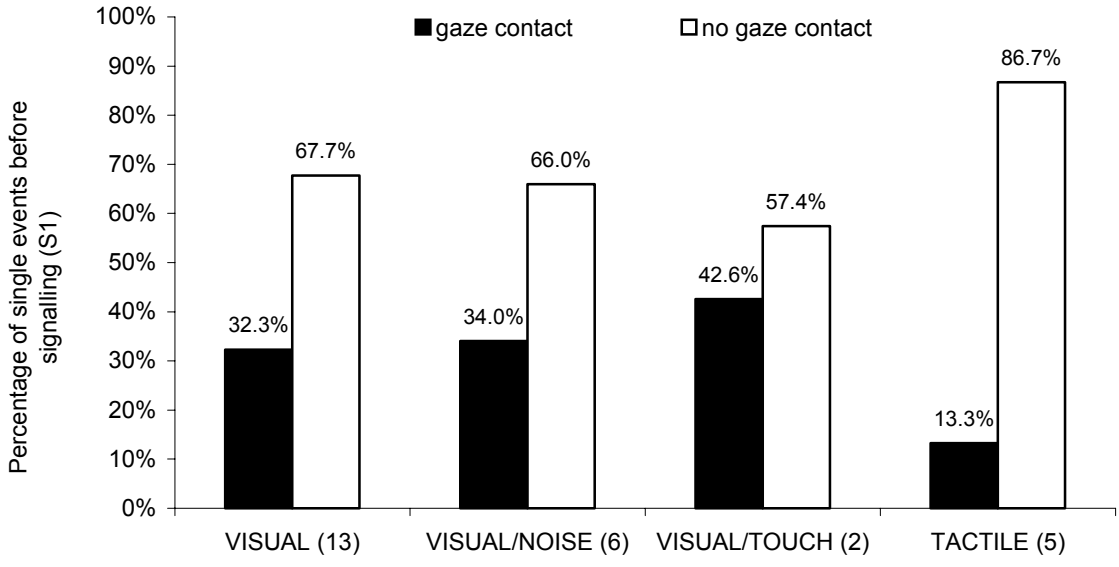


Figure 3.3.4 b
Percentage of single events with and without gaze contact before signalling shown for the four signal categories

There were more events without than with gaze contact in all four categories. This difference was small for “visual signals often combined with touching”. There was approximately twice the number of events without gaze contact than with gaze contact for the categories “visual signals” and “visual signals possibly making some noise”. Before sending a “tactile signal” gaze contact occurred in only in 13.3% of all events. Most tactile events (86.7%) took place without gaze contact. See also figure 3.3.4 b.

Gaze contact during signalling

During “visual signals” sender and recipient had more gaze contact (59.3%) than no gaze contact (40.7%). In contrast, during “tactile signals” sender and recipient used gaze contact only in 6.8% of all events. Also for the other two categories more cases without gaze contact than with gaze contact were registered. See also figure 3.3.4 c.

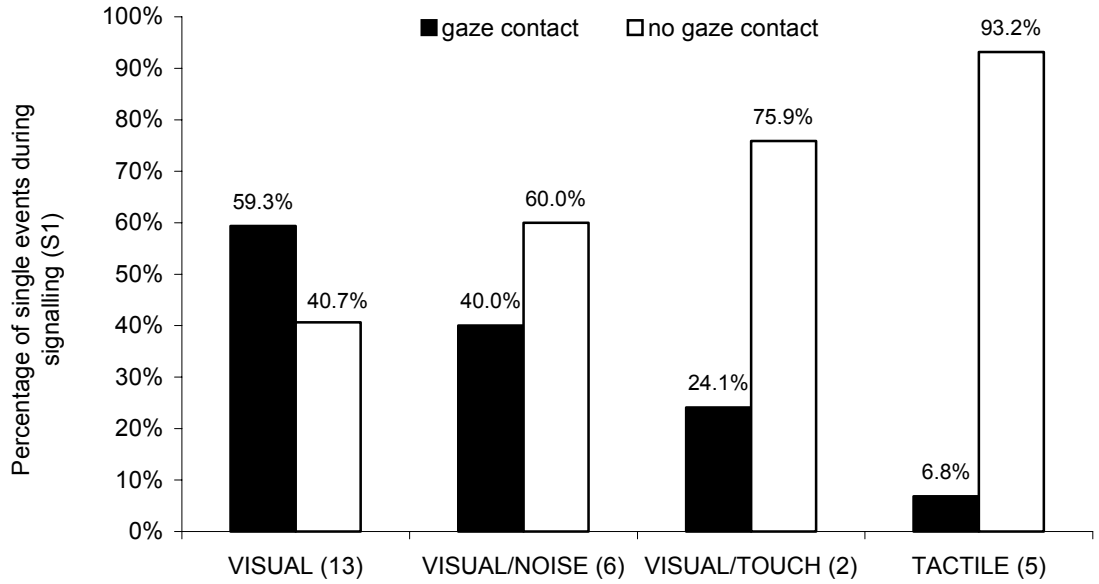


Figure 3.3.4 c
Percentage of single events with and without gaze contact during signalling shown for the four signal categories

Gaze contact after signalling

More events without gaze contact than with gaze contact occurred for all four signal categories. After “visual signals” were sent gaze contact was observed in 19.5% and after “tactile signals” in 9.3% of all events. See also figure 3.3.4 d.

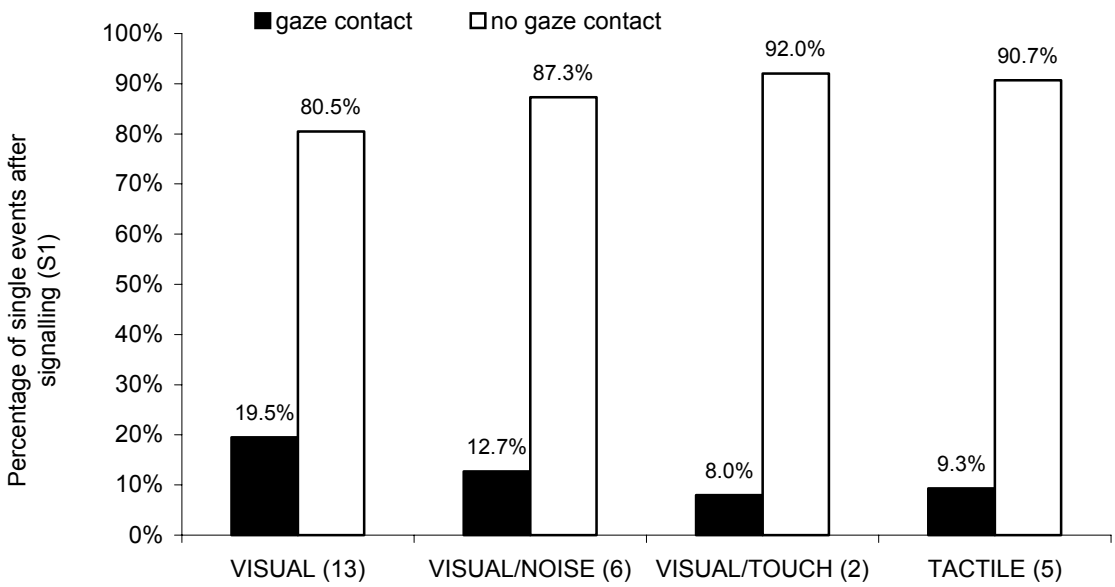


Figure 3.3.4 d
Percentage of single events with and without gaze contact after signalling shown for the four signal categories

Analysis of some signals regarding gaze contact during signalling

Here only signals which occurred more than ten times in total for the two situations "gaze contact" and "no gaze contact" were analysed: those were four "visual signals", one "visual signal possibly making some noise", one "visual signal often combined with touching" and three "tactile signals". See also figure 3.3.4 e.

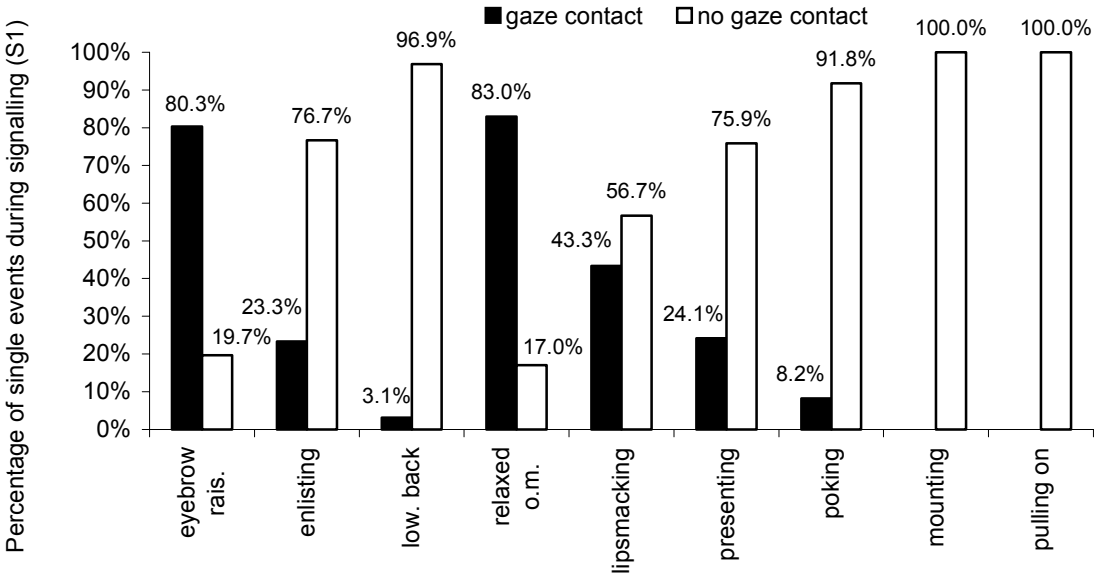


Figure 3.3.4 e
Percentage of gaze contact and no gaze contact during signalling

There was no clear tendency for the "visual signals". 80.3% of all *eyebrow raising* events and 83.0% of all *relaxed open mouth* events were accompanied by gaze contact between sender and recipient. In contrast, in 76.7% of all *enlisting* and even 96.9% of all *lowering back* events the baboons did not show gaze contact.
During the mixed signal *lipsmacking* ("visual signal possibly making some noise") there was almost no difference for "gaze contact" (43.3%) and "no gaze contact" (56.7%).
In 75.9% of all *presenting* events ("visual signal often combined with touching") the involved baboons had no gaze contact during signalling.
The difference between "gaze contact" and "no gaze contact" was very high for the "tactile signals". *Poking* was accompanied by gaze contact in 8.2% of all cases, during *mounting* and *pulling on* gaze contact was not observed at all.

3.3.5 Distance

The distance between sender and recipient was estimated. The following distance classes were generated: body contact/< 0.5 m (about one's arm length, any distance between body contact and 0.5 m), 0.5 m - 1 m, 1 m - 5 m and > 5 m.
The source of these analyses was S1 (all recorded signals of all animals from 4284 minutes of observation). Only single signals could be taken into account because the most combinations were mixed combinations between different categories of signals. Therefore, the quantity of signals is lower than the number reported in section 3.3.1.

Results

Overview

The majority of all communicative events (81.0%) took place while sender and recipient were within 0.5 m of each other. In 13.5% of all events individuals were within 0.5 m and 1 m of each other. Only about 5% of events occurred at a "1 m - 5 m" distance. Distances over five meters were rare. See also figure 3.3.5 a.

"Visual signals"

Approximately two thirds (70.8%) of all visual signals took place while sender and recipient were within body contact and 0.5 m of each other. In 19.4% of all visual events, the communicating individuals were within 0.5 m and 1 m of each other. Only 8.7% occurred at a "1 m - 5 m" distance, and 1.1% at "> 5 m". See also figure 3.3.5 b.

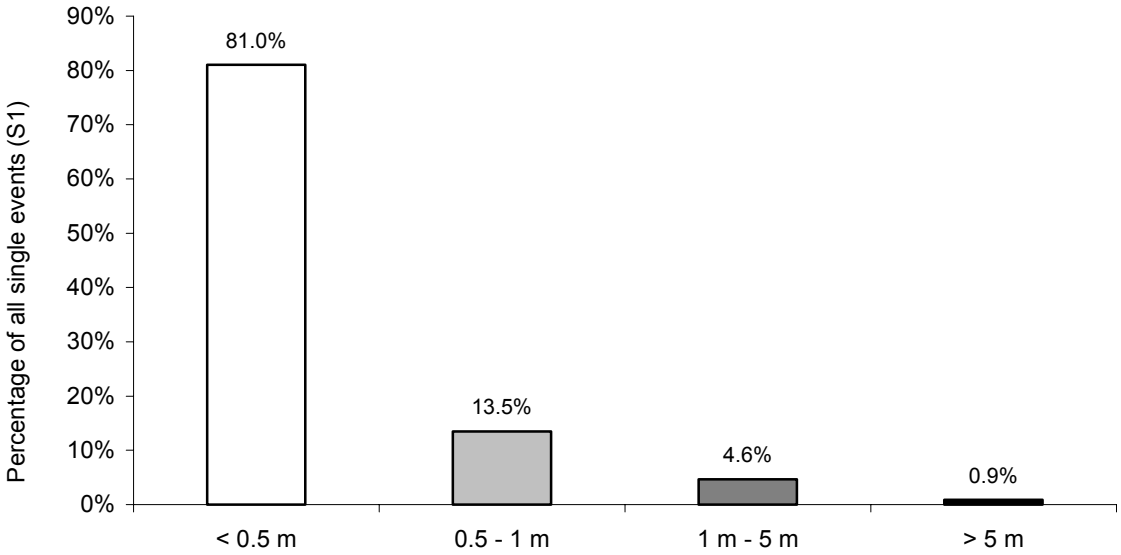


Figure 3.3.5 a
Overview of the percentage of single events grouped by distance classes

"Visual signals possibly making some noise"

68.5% of the events in this category took place while sender and recipient were positioned at distances lower than 0.5 m. About a quarter (22.5%) occurred while the communicating partners were within 0.5 m and 1 m of each other. Distances "1 m - 5 m" were used in 5.6% and "> 5 m" in 3.4% of all events. See also figure 3.3.5 b.

"Visual signals often combined with touching"

The distance "< 0.5 m" was very frequent (88.7% of all events in this category). The remaining "visual signals often combined with touching" were shown when sender and recipient were within 0.5 m and 1 m of each other (11.3%). The other distance classes were not observed in this category. See also figure 3.3.5 b.

"Tactile signals"

Nearly all tactile signals were given while sender and recipient were within body contact and 0.5 m of each other (97.3%). The remaining 2.7% occurred within 0.5 m and 1 m. The distance classes "1 m - 5 m" and "> 5 m" were not observed for this category. See also figure 3.3.5 b.

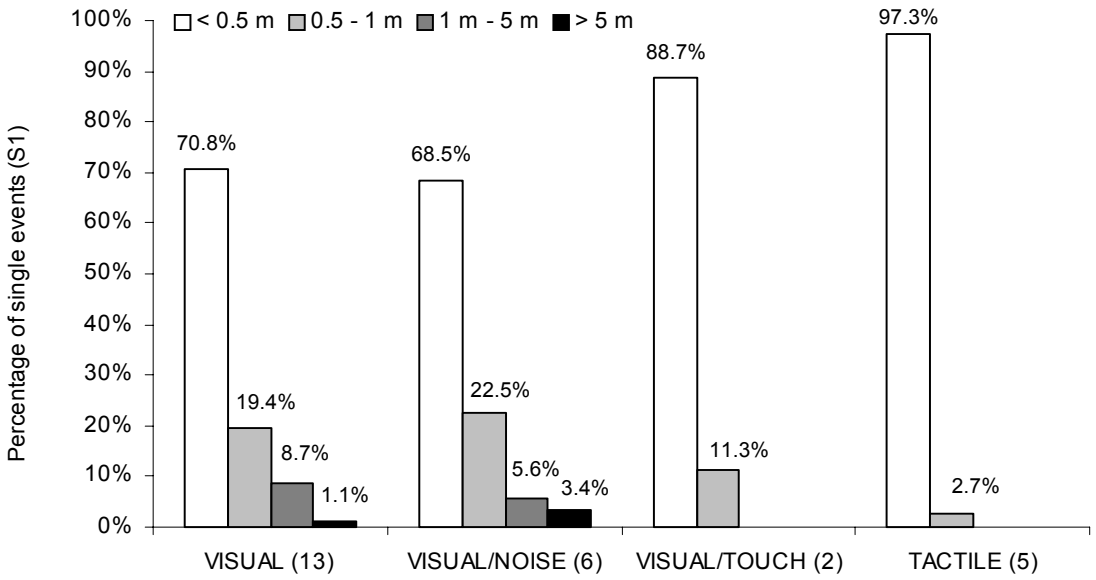
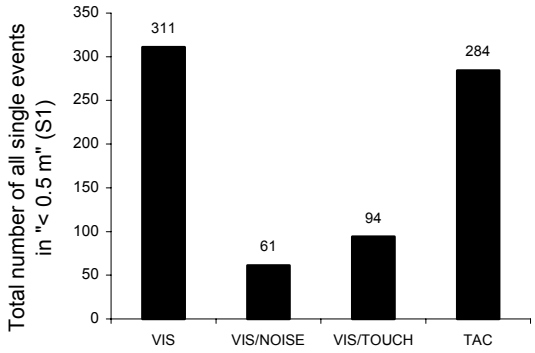


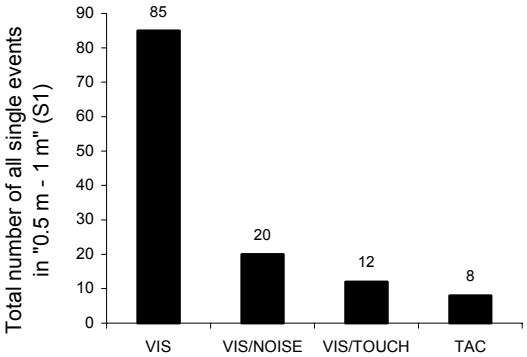
Figure 3.3.5 b
Overview of the percentage of single events in the four signal categories regarding the distance between sender and recipient

Distance < 0.5 m



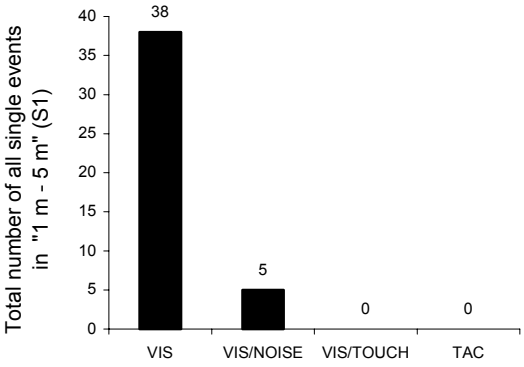
The distance class "< 0.5 m" was most frequently observed. It was used in 311 cases of visual signals and 284 cases of tactile signals. For the mixed categories there were fewer cases, 61 for "visual signals possibly making some noise" and 94 for "visual signals often combined with touching".

Distance 0.5 m - 1 m



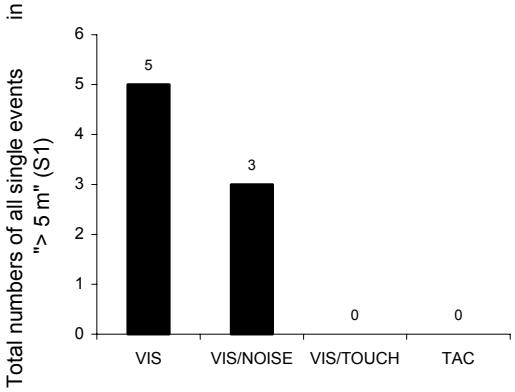
The majority of events in this distance class were "visual signals" (85 cases). The other categories occurred less frequently: 20 "visual signals possibly making some noise", 12 "visual signals often combined with touching" and eight "tactile signals".

Distance 1 m - 5 m



No "visual signals often combined with touching" and "tactile signals" occurred within this distance class. "Visual signals possibly making some noise" were rare (five cases). The most frequent category was pure "visual signals" with 38 cases.

Distance > 5 m



This distance class was the rarest one. Only five "visual signals" and three "visual signals possibly making some noise" were found. No "tactile signal" or "visual signals often combined with touching" were observed.

Analysis of some selected signals

Eyebrow raising and *yawning* were used in all four distance classes.

Half of all events (51.9%) of *eyebrow raising* occurred at a distance of "< 0.5 m" and approximately one third occurred at "0.5 m - 1 m". The third most frequent distance was "1 m - 5 m" (15.1%), followed by "> 5 m" (3.8%).

Similar results were found for *yawning*. Exactly half of all *yawning* events occurred at a distance of "< 0.5 m" and one quarter between "0.5 m - 1 m". The third most frequent distance was "1 m - 5 m" (16.7%). *Yawning* was the most frequently occurring visual signal at a distance "> 5 m" (8.3%).

Enlisting and *lowering body* were also most often used at a distance of "< 0.5 m" (62.2% and 81.8%). They were found at the same proportions for distances of "0.5 m - 1 m" (19.5% and 9.1%) and "1 m - 5 m" (18.3% and 9.1%). Both signals never occurred at distances over 5 m.

All *lowering back* events were observed at distances of "< 0.5 m".

Relaxed open mouth appeared in 82.8% of events at a distance of "< 0.5 m" and in 17.2% at distances between 0.5 m - 1 m. Distances over 1 m were never observed. *Lowering body*, *lowering back* and *relaxed open mouth* can be regarded as "short distance visual signals".

For visual signals see also figure 3.3.5 c.

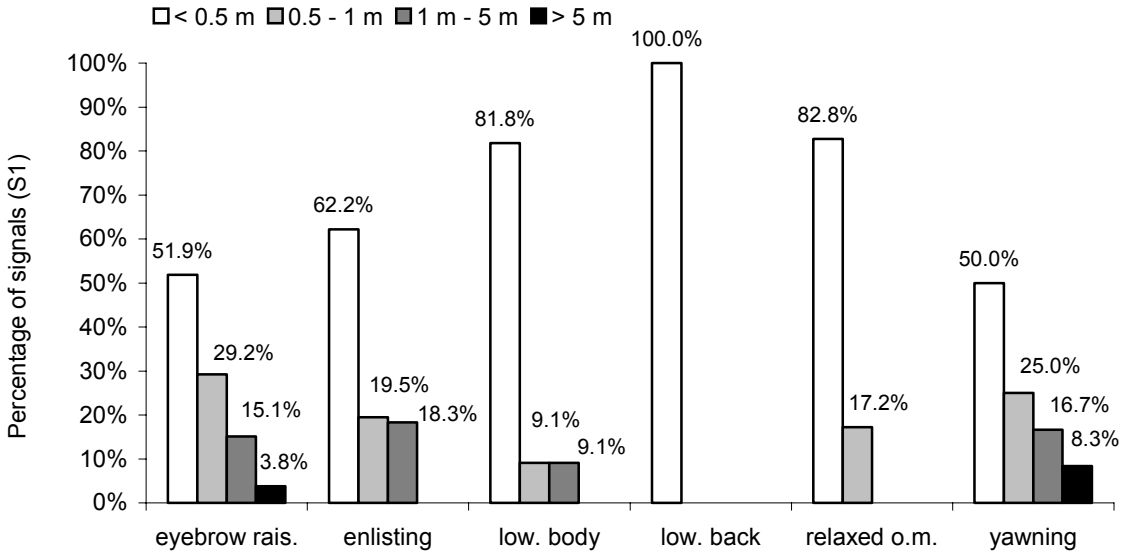


Figure 3.3.5 c
Overview of the distance range for particular visual signals

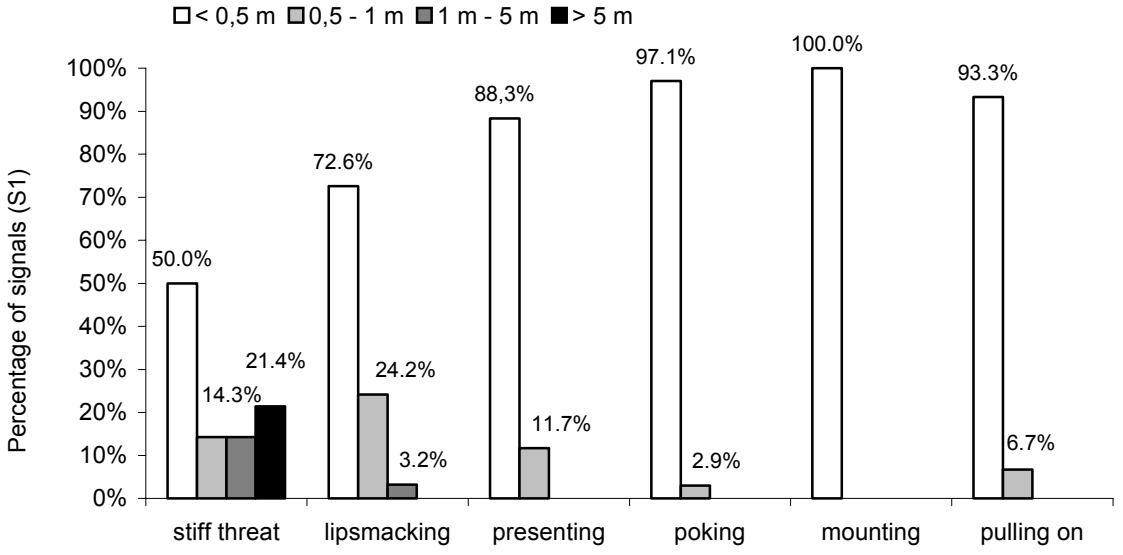


Figure 3.3.5 d
Overview of the distance range for particular visual/mixed and tactile signals

The two analysed "visual signals possibly making some noise" (*stiff threat*, *lipsmacking*) occurred at a wider range of distances than the analysed "visual signal

often combined with touching" (*presenting*) and the analysed "tactile signals" (*poking*, *mounting*, *pulling on*).

Stiff threat was used in half of the events at distances less than 0.5 m and in 14.3% for both distance classes "0.5 m - 1 m" and "1 m - 5 m". It was the signal with the highest usage of distances more than five meters (almost one quarter). *Lipsmacking* was observed in 72.6% of all events at a distance of "< 0.5 m" and in 24.2% between "0.5 m - 1 m" and in 3.2% between "1 m - 5 m". It was never found at distances of over five meters.

Presenting was most frequently used at a distance of "< 0.5 m" (88.3%) and in the remaining cases between "0.5 m - 1 m" (11.7%).

Tactile signals were restricted to close distances in which animals could touch each other. *Poking* took place almost exclusively at a distance of "< 0.5 m" (97.1%). Only 2.9% were shown at distances between 0.5 m - 1 m. *Mounting* was only seen when the communicating partners were located at a distance of < 0.5 m. For *pulling on* a very high proportion (93.3%) of events were recorded at "0.5 m - 1 m". Here also some events were found at distances between 1 m - 5 m.

For visual/mixed and tactile signals see also figure 3.3.5 d.

Age and sex classes

All age classes preferred closer distances for communication.

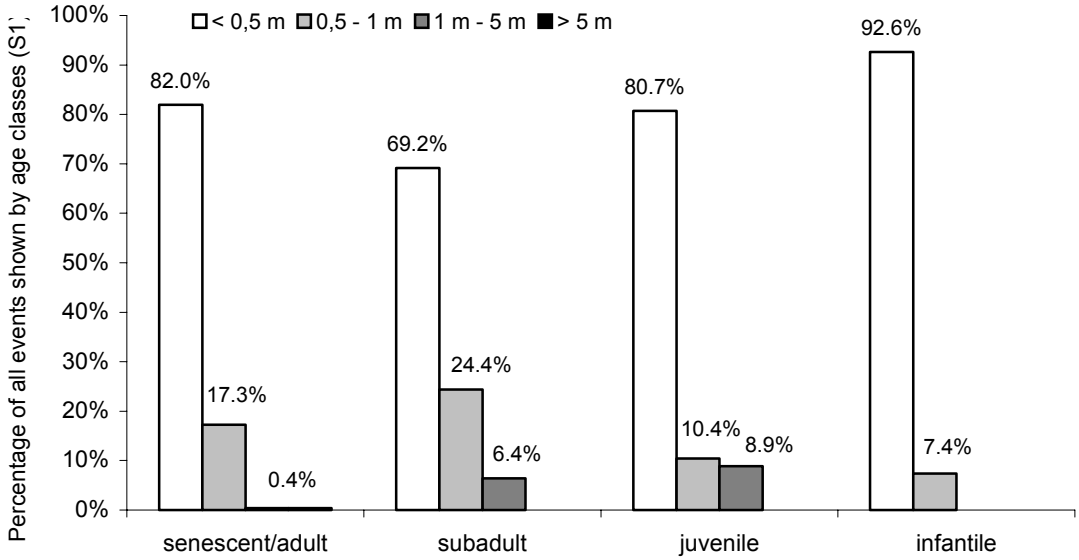


Figure 3.3.5 e
Overview of the distance range for the four age classes

Infants showed the highest usage of the distance class "< 0.5 m" (92.6%), followed by the senescent/adult (82.0%) and juvenile (80.7%) baboons. The lowest percentage of this distance was found in the subadults (69.2%).

Subadult baboons showed the highest rate for the distance class “0.5 m - 1 m” (24.4%), followed by the senescent/adult (17.3%) animals. The juveniles used this distance for signalling in 10.4% of all events and the infants in 7.4%.

The distance class “1 m - 5 m” was registered in the groups of subadult (6.4%) and juvenile (8.9%) baboons. The senescent/adult animals communicated only in 0.4% of all events over this distance and in the infants it did not occurred.

Only the group of senescent/adult baboons communicated over distances of more than five meters, but the percentage of these events was very low (0.4%). See also figure 3.3.5 e.

Females communicated at the shortest distance “< 0.5 m” in 82.5% of all events, males only in 75.2%. Males showed slightly more usage of the distances “0.5 m - 1 m” (19.6%) and “1 m - 5 m” (5.3%) than females (13.8% and 3.6% respectively). Males never showed signals over distances of more than five meters, females very rarely (0.2%). See also figure 3.3.5 f.

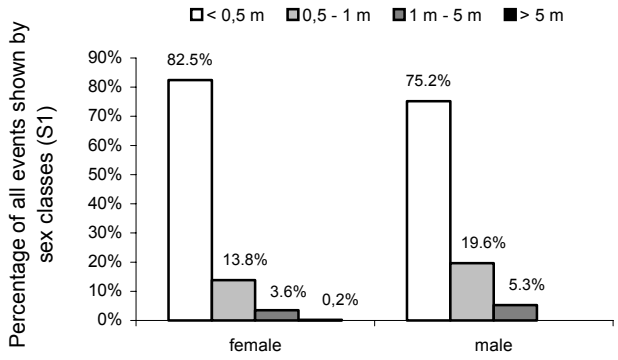


Figure 3.3.5 f
Overview of the distance range for the sex classes

3.3.6 Response

The response elicited by particular signals was analysed in order to investigate the effect of the signal and the reaction of the recipient.

The following possibilities were registered: no reaction of the recipient, the recipient changed its behaviour after receiving the signal of the sender (counted as reaction), a signal was displayed by the recipient after receiving the sender’s signal (counted as reaction).

The source of these analyses was S1 (all recorded signals of all animals from 4284 minutes of observation). Only single signals could be taken into account because the most combinations were mixed combinations between different categories of signals. Therefore, the quantity of signals found was lower than the number reported in section 3.3.1.

All single events with or without a clear response were considered and summarised. Also the conditions “the recipient changed its behaviour” and “a signal was shown by

the recipient" were summarised under "reaction" and compared to the condition "no reaction".

If the recipient reacted with a signal, the signal was analysed with regard to its frequency and its signal category type.

During data collection, a fourth possibility appeared: the recipient simultaneously showed the same signal as the sender. These "parallel signals" were: *relaxed open mouth* seen 35 times, *greeting* seen three times and *poking* seen two times during the whole observation period. These cases were dropped from the analyses as they were in fact signals sent simultaneously rather than elicited responses or signals.

Results

Overview

In 13.5% of all single signals the sender elicited a signal as response from the recipient. In 58.1% of all cases the recipient changed its behaviour after the sender showed a signal. In 28.4% of all signal events the recipient did not react to the signal of the sender.

Overall, there were more events where the recipient showed a reaction than without a reaction. Visual and visual mixed signals elicited more reactions (over three quarters of all events) than tactile signals (59.8% of all events). See also figure 3.3.6 a.

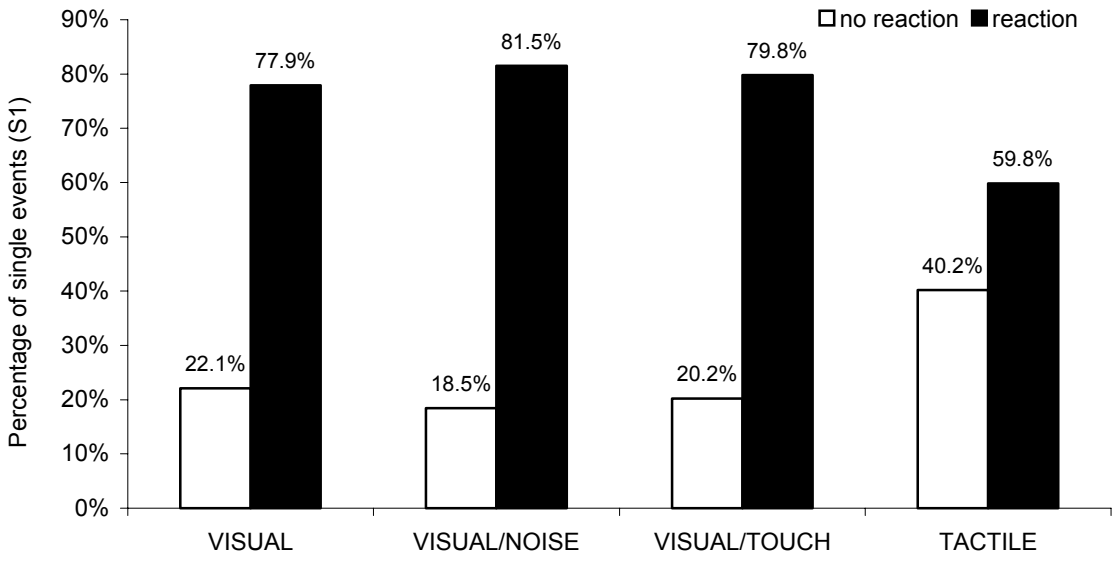


Figure 3.3.6 a
Overview of the percentage of single signals eliciting reactions or not

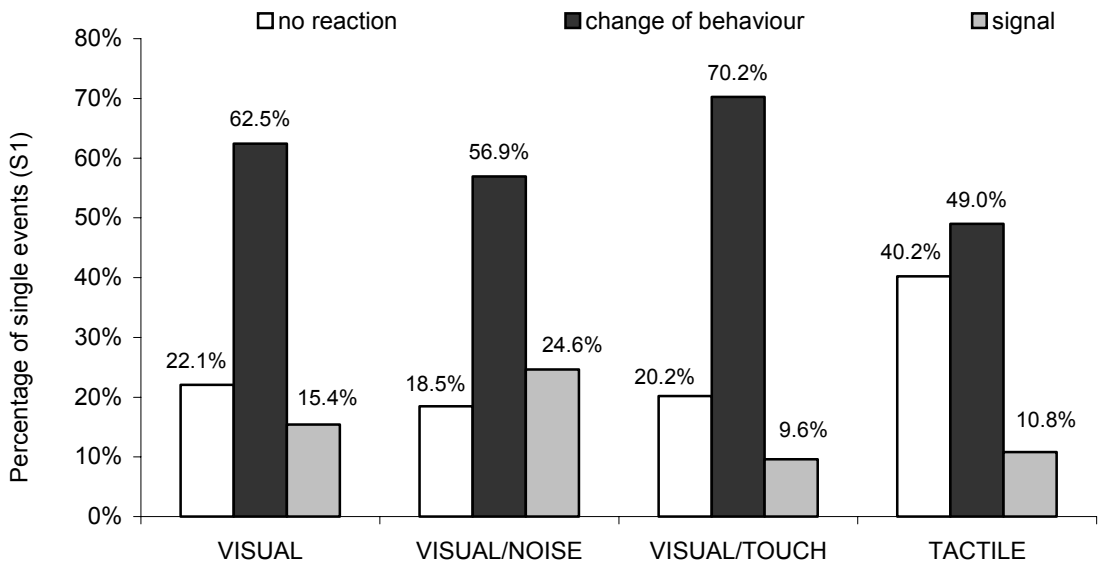


Figure 3.3.6 b
Percentage of "no reaction", "change of behaviour" and "signal" by the recipient

When the sender used a "visual signal possibly making some noise", the recipient more often responded by emitting a signal (24.6% of all events) than when the sender used a signal from the other categories. "Visual signals" elicited a signal in 15.4%, "tactile signals" in 10.8% and "visual signals often combined with touching" in 9.6% of all events.

"Visual signals often combined with touching" caused the most changes of behaviour in the recipient (70.2% of all events). "Visual signals" elicited a change of behaviour in the recipient in 62.5%, "visual signals possibly making some noise" in 56.9% and "tactile signals" only in 49.0% of all events.

"Tactile signals" failed to elicit any reaction in 40.2% of all events, approximately twice as often as the other categories. The recipient did not react to a "visual signal" in 22.1% of all events, to a "visual signal often combined with touching" in 20.2% and to a "visual signal possibly making some noise" in 18.5% of all events.

See also figure 3.3.6 b.

<u>Selected signals</u>

Here also the attentional state of the recipient (for events with clearly attentive and inattentive state) was investigated. Nine signals occurred more than ten times each and the recipient's response to these signals was analysed.

"Visual signals"

Eyebrow raising was most frequently directed towards attentive recipients (94.8% of investigated cases). In 84.5% of the events attentive recipients showed a reaction

(42 cases or 72.4% consisting of change of behaviour and seven cases or 12.1% of another signal). In 10.3% of the events the attentive recipient ignored *eyebrow raising*. The inattentive recipient showed a reaction in 1.7% of the events and did not react in 3.4%.

When *enlisting* was displayed towards an attentive recipient (76.0% of the events), a response was observed in 48.0% of the events (11 cases or 44.0% elicited a change of behaviour and one case or 4.0% elicited another signal), no reaction was registered in 28.0% of the events. *Enlisting* was directed towards an inattentive animal in 24.0% of the events and no responses were found there.

Lowering back was exclusively used to communicate with an attentive recipient and in all cases there was a reaction (change of behaviour – the recipient climbed onto the signaller's back).

Relaxed open mouth was also frequently used when the recipient was attentive (94.4% of the investigated cases). In 89.8% of the events the attentive recipient reacted to the given signal (in 63 cases or 58.3% by changing behaviour and in 34 cases or 31.5% by showing another signal). Attentive recipients showed no response in 4.6% of the events. In 5.6% of the events the sender signalled to an inattentive recipient and half of these signals were answered.

"Visual signal possibly making some noise"

Only one signal from this category was analysed: *lipsmacking*.

When this signals was directed towards an attentive recipient (86.8% of the events) there was a reaction in 84.2% (20 cases or 52.6% of the events elicited a change of behaviour and 12 cases or 31.6% elicited another signal). An attentive recipient showed no reaction in 2.6% of the events. A inattentive recipient responded to lipsmacking in 7.9% of the events and did not react in 5.3%.

"Visual signal often combined with touching"

Only one signal from this category was analysed: *presenting.*

This signal was directed towards an attentive recipient in 92.8% of the events. The attentive recipient showed a reaction in 79.5% (57 cases or 68.7% resulted in a change of behaviour and nine cases or 10.8% resulted in another signal) and ignored it in 13.3% of the events. An inattentive recipient responded to *presenting* in 2.4% of the events and did not react in 4.8%.

"Tactile signals"

Poking was directed towards an attentive recipient in 42.7% of the events. The attentive recipients responded in 32.0% of the events (in 38 cases or 22.5% by changing behaviour and in 16 cases or 9.5% by showing another signal) and ignored the signal in 10.7% of the events. *Poking* was also often used when the recipient was not attentive (57.4%). The inattentive recipients reacted in 25.4% of the events (in 36 cases or 21.3% of the events by changing behaviour and in seven cases or 4.1% by giving another signal). In 32.0% of the events the sender gave the signal to an inattentive recipient and elicited no response.

Mounting was addressed to an attentive recipient in 90% of the events. There was a response by attentive recipients in 70.0% of the events (13 cases or 65% elicited a change of behaviour and one case or 5.0% elicited another signal). 20.0% of the events were ignored by an attentive recipient. An inattentive recipient responded in 5.0% and did not react in 5.0% of the events.

Pulling on was used for communication with an attentive recipient only in 20.0% of the events. Half of these signals were ignored by the attentive recipient. 80.0% of *pulling on* were sent when the recipient was not attentive. The inattentive recipient also reacted to half of the signals.

Analysis of response-eliciting signals and the signals shown as response

Sender's side

Senders used signals from all four categories to elicit a signal response in recipients. When analysing all 188 registered response-eliciting single events the following picture emerged: 71 were "visual signals" and 62 "tactile signals"; fewer signals were used from the mixed categories: 26 "visual signals possibly making some noise" and 29 "visual signals often combined with touching".

Signals which most frequently elicited signals from the recipient were *poking* (55 events), *relaxed open mouth* (48 events), *presenting* (27 events), *lipsmacking* (14 events) and *eyebrow raising* (nine events). *Stiff threat* elicited signals seven times, *lowering body*, *mounting* and *yawning* four times each, *enlisting* and *chasing* three times each, and *pumping*, *pulling on* and *greeting* two times each. The other single signals acted only one time (*rolling on ground*, *head/handstand*, *jumping on back, threat mouth*) or never as response-eliciting signal. See also figure 3.3.6 c.

Recipient's side

The response signals of recipients could be single and also combined signals. 172 of the 188 signals the recipients emitted were single and 16 were combined signals. The

single signal answers were distributed as follows: The majority (68) were “visual signals”, 42 were “visual signals often combined with touching” and 47 were “tactile signals”. The least common category with 15 signals was “visual signals possibly making some noise”.

The most common response signals (single) were *relaxed open mouth* (51 times), *poking* (40 times) and *presenting* (38 times). In comparison, the remaining response signals were relatively rare: *eyebrow raising* occurred seven times, *stiff threat*, *lipsmacking* and *mounting* six times each, *greeting* and *yawning* four times each, *enlisting*, *chasing*, *lowering body* and *hand/headstand* two times each. All other signals were observed as a response only once (*pumping*, *penis grab)* or not at all. See also figure 3.3.6 c.

The most frequent combination was *relaxed open mouth + poking* (seven times). *Eyebrow raising + relaxed open mouth* was observed twice.

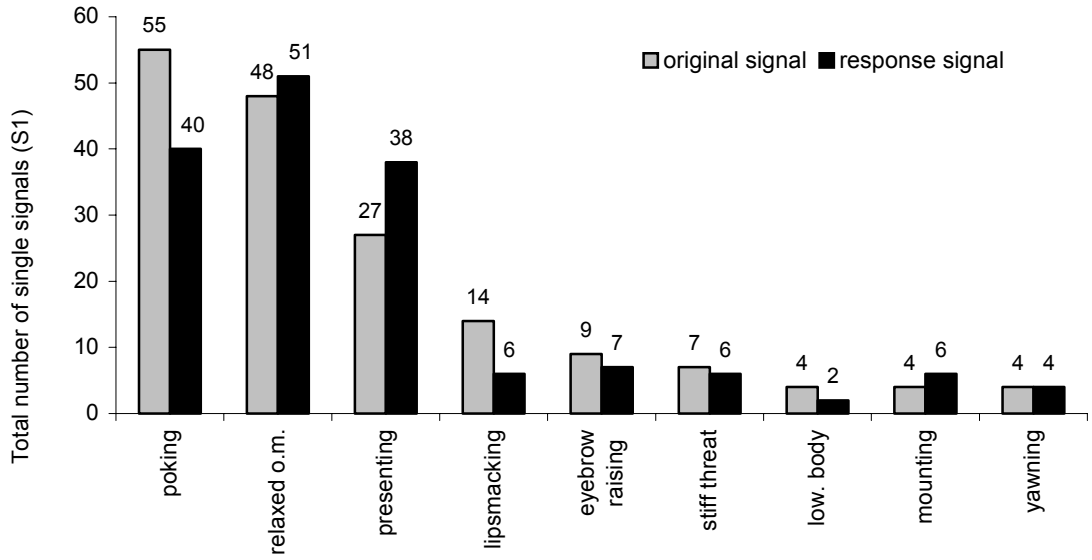


Figure 3.3.6 c
Selection of response-eliciting signals (sender’s side) and response signals (recipient’s side)

Which single signal caused which single signal response?

The two most effective signals for eliciting either the same or another signal were *relaxed open mouth* and *poking*. ***Poking*** elicited 15 cases of *relaxed open mouth*, 18 cases of *poking* and 19 cases of *presenting*. ***Relaxed open mouth*** elicited 26 cases of *relaxed open mouth,* 10 cases of *poking* and three cases of *presenting*.

Presenting elicited *poking* nine times, *mounting* six times, *lipsmacking* and *eyebrow raising* four times each and *relaxed open mouth* twice.

Lipsmacking caused nine cases of *presenting*.

Eyebrow raising elicited *eyebrow raising, yawning* and *lowering body* one time each, *relaxed open mouth* three times and *presenting* two times.
Stiff threat caused *stiff threat* and *poking* one time each and *presenting* four times.

3.3.7 Context

The behavioural situation in which the signal appeared was estimated and the following contexts were distinguished: friendly, play, nursing, appeasement/submission and aggressive.
Because the situation was often difficult to determine and because behavioural elements sometimes overlapped, the context classes in particular analyses were merged: “friendly”, “play” and “nursing” into “affiliative”, “appeasement/submission” and “aggressive” into “agonistic”.
The source of these analyses was S1 (all recorded signals of all animals from 4284 minutes of observation). Only single signals could be taken into account because the most combinations were mixed combinations between different categories of signals. Therefore, the quantity of signals found was lower than the number reported in section 3.3.1.

Results

Overview

1156 cases of single signals were analysed. 552 events (47.8% of all cases) took place in a clearly affiliative and 604 events (52.2% of all cases) in a clearly agonistic context. For details see figure 3.3.7 a.
Signals used in an agonistic context were predominantly “visual signals” (389 events) and “visual signals possibly making some noise” (141 events). Only 36 cases of visual signals with a tactile component and 38 cases of purely tactile signals were performed for agonistic purposes.
Signals shown during affiliative encounters were mostly purely visual (245 events) or purely tactile (203 events) signals. Signals from both mixed categories were observed about four times less often (55 times for “visual/noise” and 49 times for “visual/touch”).

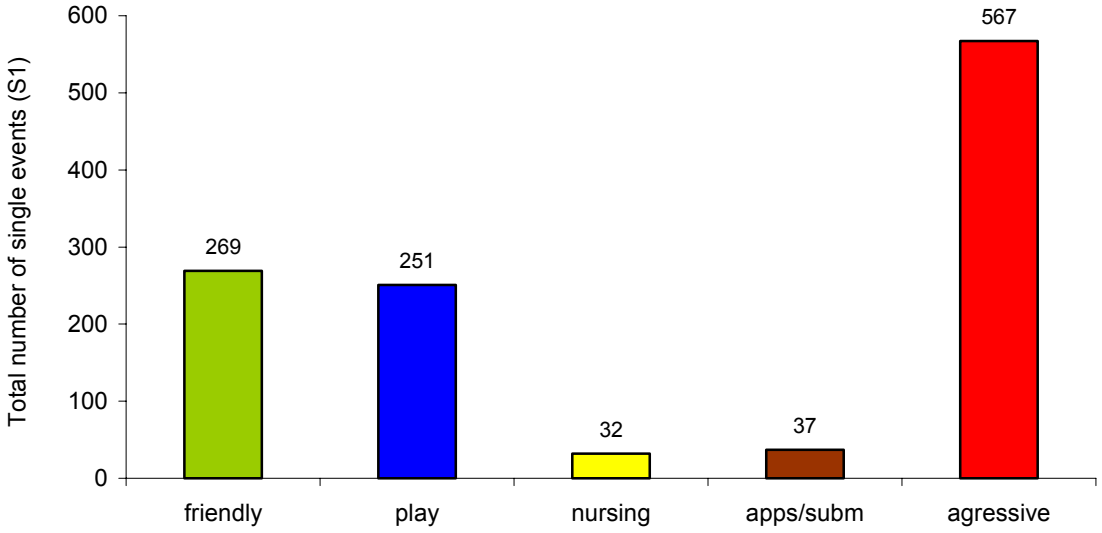


Figure 3.3.7 a
Overview of the distribution of all analysed single events according to context

While visual signals with or without some noise seemed to be slightly preferred in agonistic encounters, tactile signals were more often used for affiliative purposes. See also figure 3.3.7 b.

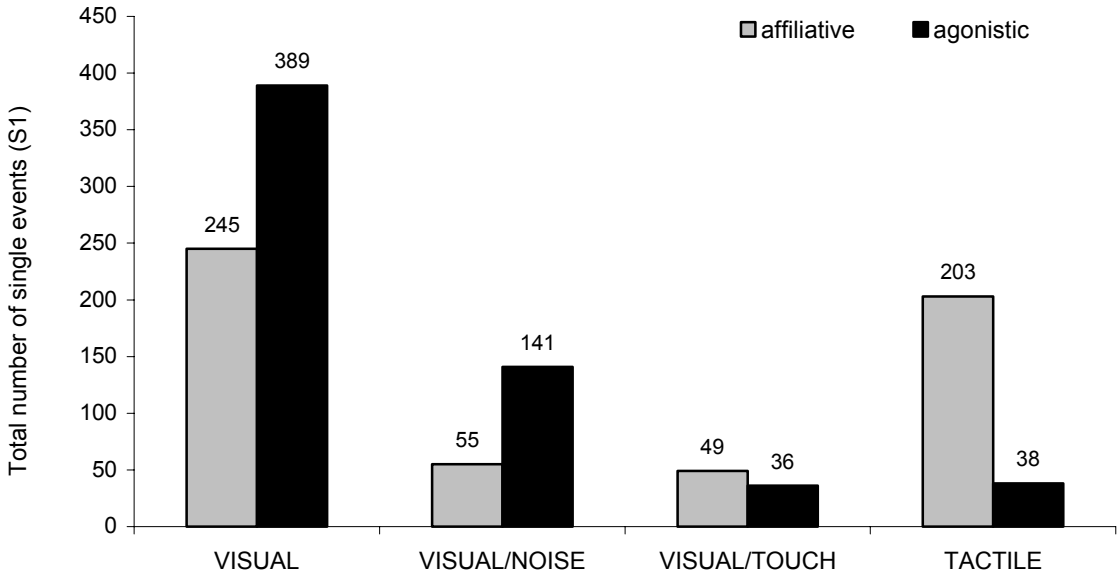


Figure 3.3.7 b
Overview of the total number of affiliative and agonistic single events grouped by signal category

Contexts

The signal most frequently used in the friendly context was *poking* (42%), followed by *relaxed open mouth* (13.8%), *lipsmacking* (15.9%) and *presenting* (16%). *Eyebrow raising*, *lowering body* and *mounting* occurred less frequently (between 2.6% and 3.3%).

Relaxed open mouth (54.2%) and *poking* (23.5%) were very common in the play context. *Eyebrow raising*, *hand/headstand*, *lipsmacking*, *presenting*, *mounting* and *pulling on* were observed least (between 3.6% and 2.4%) in this context.

The signal performed most often in the submission/appeasement context was *presenting* with 81.1% of all cases. Also in the nursing context only one signal was important: *lowering back* (93.8%).

In the aggressive context the baboons predominantly used *eyebrow raising* (42%) followed by *enlisting* (20.6%) and *stiff threat* (12.9%). *Pumping* (6.9%), *poking* (6.0%), *chasing* (4.6%) and *yawning* (3.7%) were also shown in this context.

The most common signals for the five contexts are shown in figure 3.3.7 c.

For an overview of single signal occurrence in the different contexts see also appendix 6.

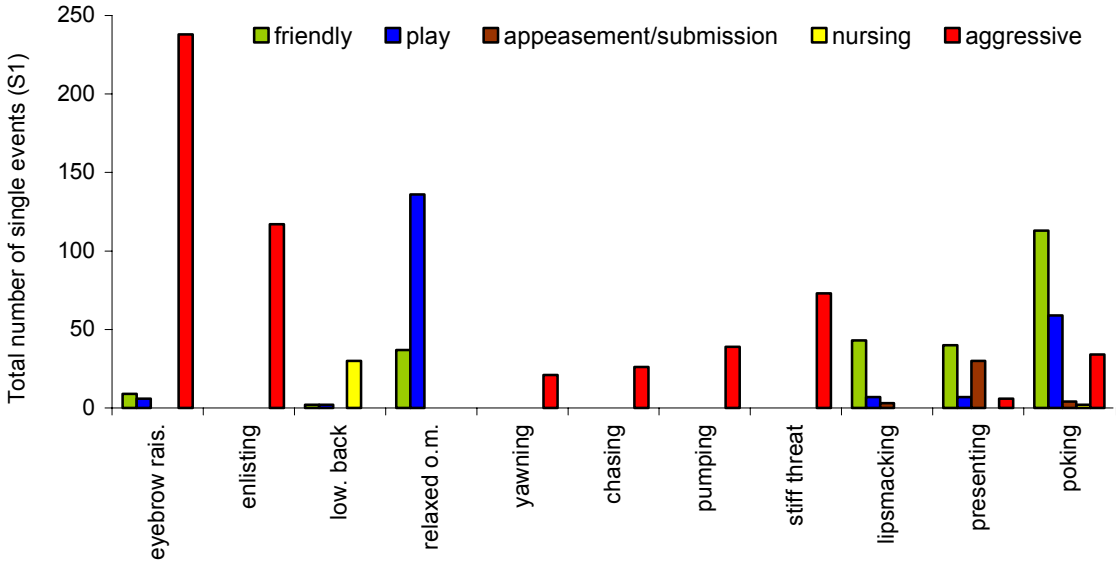


Figure 3.3.7 c
The most common signals grouped by the five contexts

Signals

Here only signals occurring more than one time in the respective context were analysed.

Ten signals were used in more than one context and in all five contexts more than one signal was found (means-end-dissociation). Friendly, play and aggressive contexts contained more than ten signals each. See also figure 3.3.7 d.

Table 3.3.7 d
Signal usage across contexts

	friendly	play	appeasement/submission	nursing	aggressive	**total (contexts per signal)**
poking	x	x	x	x	x	5
presenting	x	x	x		x	4
eyebrow raising	x	x			x	3
lowering back	x	x		x		3
lipsmacking	x	x	x			3
lowering body	x	x				2
relaxed open mouth	x	x				2
hand/headstand	x	x				2
mounting	x	x				2
pulling on	x	x				2
enlisting					x	1
rolling on ground		x				1
threat mouth					x	1
head bobbing					x	1
yawning					x	1
head tapping					x	1
chasing					x	1
jumping in the air		x				1
pumping					x	1
stiff threat					x	1
greeting	x					1
jumping on back		x				1
total (signals per context)	11	13	3	2	11	

"Visual"

Eyebrow raising was most frequently used for agonistic purposes (94.1%). It was rarely observed in affiliative encounters (5.9%). Overall, it was found in three contexts (friendly with 3.5%, play with 2.4% and aggressive with 94.1%).

Enlisting and *yawning* were exclusively observed during agonistic interactions (aggressive context). This was also the case for the rare signals *threat mouth*, *head bobbing* and *head tapping*.

Relaxed open mouth was observed in two affiliative contexts – friendly (78.6%) and play (21.4%). *Lowering back* was mainly used for nursing (88.2%) but also appeared in the two other affiliative contexts (friendly and play, each 5.9%). The less frequent signals *lowering body* (friendly and play), *hand/headstand* (friendly and play) and the very rare *rolling on ground* (only play) were exclusively shown in affiliative situations.

"Visual/noise" and "visual/touch"

Chasing, pumping and *stiff threat* were only seen in the aggressive context. The baboons used *lipsmacking* most frequently in the friendly context (81.1%), occasionally in the play context (13.2%) and rarely for appeasement/submission (5.7%). *Jumping in the air* was exclusively observed in the play context.

Presenting was observed in all contexts except nursing. 56.6% of the events were affiliative (friendly: 48.2%; play: 8.4%) and 43.4% of the events were agonistic (appeasement/submission: 36.1%; aggression: 7.3%). *Greeting* was rare and only observed in the friendly context.

"Tactile"

Poking was the only signal used in all five contexts. 82.1% occurred in affiliative contexts (friendly: 53.3%; play: 27.8%; nursing: 1%) and 17.9% occurred in agonistic contexts (appeasement/submission: 1.9%; aggressive: 16%).

Mounting and *pulling on* were exclusively seen during affiliative contexts (friendly and play). *Jumping on back* was rare and exclusively observed in the play context.

For more details see also appendix 6.

Individual differences

The focal animals showed many differences in regards to the percentage of affiliatively and agonistically used signals.

The senescent female performed 65.4%, the adults 68.7% and the subadults 71.0% agonistic signals whereas the juveniles showed 34.3%, the brown infant only 18.4% and the black infant even only 4.7% agonistic signals. See also figure 3.3.7 e.

When regarding all six age classes, the difference was not significant ($p=0.081$). But when pooling together the senescent female with the adults as well as the two infants (four age classes), the differences became significant ($p=0.022$). And when the older individuals (classes 1-3) were tested against the younger individuals (classes 4-6) the difference is even highly significant ($p=0.003$). This means that the older baboons used more agonistic signals than the younger ones who more frequently showed affiliative signals.

The females used more friendly signals (56.1%) than the males (31.3%), but the difference was not significant ($p=0.24$).

Interestingly, the median for all 14 animals was nearly fifty percent for each (49% affiliative and 51% agonistic signals) which means that on average a focal animal used the same number of agonistic as affiliative signals.

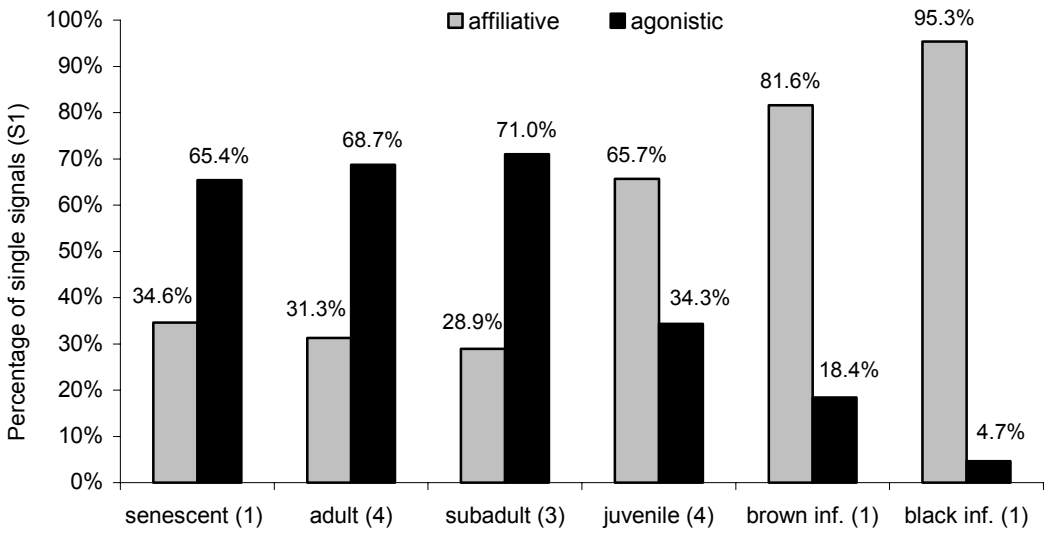


Figure 3.3.7 e
Total number of single signals used by the age classes in affiliative and agonistic interactions

4. DISCUSSION

The aim of this study was to investigate intentional signal use in a group of captive hamadryas baboons. A signal was considered intentional when it had a flexible means-end dissociation and was used with special regard to the social context of the recipient. Therefore, signals were not recorded which seemed to be involuntary and tied to emotional states, such as some signals of fear. Because of the difficulty to recognize the sender and especially the recipient of acoustic signals, and because of the likely unintentional nature of many vocal signals, calls and sounds were not considered in the present study.

Some observations (see Pollick & de Waal, 2007) about the deception of some facial expressions and the more likely cultural transmission of gestures than of facial expressions let assume that facial expressions are possibly more tied to emotions than gestures.

In the result section of the present study, no difference was made between gestures and facial expressions. They were summarized and regarded as signals and specified according to the involved sensory channel of the recipient. In this section however, in order to better compare the results of this study with others, sometimes gestures were separated from facial expressions.

4.1 Number of different signals and relations between categories

The hamadryas baboons in the present study showed 26 different visual and tactile signals (plus five idiosyncratic signals). 20 of these can be regarded as gestures and six as facial expressions (*eyebrow raising, relaxed open mouth, threat mouth, pumping, yawning* and *lipsmacking*). A focal animal on average used 14 different signals respectively 10 different gestures – that means a baboon showed approximately half of all recorded different signals respectively gestures.

Several comparative studies of gestural communication in apes were carried out by Tomasello's research group throughout the 2000's. Liebal found 20 gestures and four facial expressions (Liebal et al., 2004b) used by siamangs (*Symphalangus syndactylus*) and 29 gestures and five facial expressions (Liebal, 2005) used by Sumatran orangutans (*Pongo pygmaeus abelii*) as well as 27 gestures (Liebal et al., 2004a) used by chimpanzees (*Pan troglodytes*). Pika (2003) investigated 33 gestures used by subadult gorillas *(Gorilla gorilla*) and 20 used by subadult bonobos (*Pan paniscus*). Smith (2007) found 27 gestures in gorillas.

Hamadryas baboons live terrestrially and are therefore able to transmit non-acoustic signals across larger distances (good visibility of the signals) than siamangs or orangutans who live aboreally and with a limited visual signal range due to the dense vegetation of their habitat (short visibility of signals). Also, in contrast to siamangs and orangutans living in small family groups, in pairs or solitary, baboons live in complex four-level social structures. Given these factors, hamadryas baboons might be expected to use more gestural communication than siamangs or orangutans.

The data from the above literature do not support this. Presumably, a reason for this deviation could be that the group of Tomasello (included the author of the present study) had concentrated on intentional signals, but the overall non-acoustic communication repertoire of the species will be larger and perhaps in monkeys the proportion of non-intentional signals in the repertoire could be higher than in apes.

More comparative studies of primate gesture use are needed in order to determine whether the relatively low number of gestures of baboons compared with gorillas and chimpanzees or even orangutans is due to ecological, social or cognitive factors or whether the differences are referred to age (the bonobos and gorillas in Pika's studies were subadults) or individual features. And it is also not unlikely that different observers' judgments about what is or is not a signal and what is or is not intentional could lead to the differences in the number of signals recorded in the ape and monkey species .

Overall, it can be stated that the hamadryas baboons in the present study exhibited nearly the same number of different gestures as siamangs and bonobos. It seems that

a monkey species, the hamadryas baboon, does not deviate very much from some ape species regarding the number of different gestures.

With the exception of gorillas, all investigated species used nearly the same mean number of different gestures per animal: chimpanzees 9.5, baboons 10, siamangs 10.5, bonobos 11, orangutans 12. The baboons showed similarity to the siamangs – lesser apes with another ecology and social structures than baboons – in this respect, too. Gorillas outperformed all the others – they showed a repertoire of 20 gestures per individual.

Hesler and Fischer (2007) found 24 gestures and 13 facial expressions in Barbary macaques (*Macaca sylvanus*). Compared to the baboons, and also the siamangs and orangutans, the macaques showed a much greater variety of facial expressions.
Maestripieri (1996a, b) investigated 15 of the most common visual and tactile signals (10 gestures and 5 facial expressions) of stump-tailed macaques (*Macaca arctoides*) and found 13 of these (9 gestures and 4 facial expressions) used as well by pigtail macaques (*Macaca nemestrina*). He further analysed the communicative repertoire of three species of *Macaca* (*nemestrina, arctoides, mulatta*) belonging to the same sub-family as *Papio*, and proposed that primates living in despotic-nepotistic societies such as rhesus macaques should use fewer signals than primates living in egalitarian-individualistic societies such as stump-tailed macaques. He could confirm this theory for gestures within the contexts of dominance and submission.
Hamadryas baboons can be regarded as living in a more despotic system whereas savannah baboons as having a more egalitarian system. But the theory could not be tested in the present study because of the lack of comparable data for other baboon species.

Gautier and Gautier (1999) described for Old World monkeys that the signal structure is influenced by mode of action and habitat. At shorter distances, the signals are multi-modal and variable, while at larger distances (and more dense habitat) the signals tend to be unimodal and stereotyped. For hamadryas baboons living in a relatively open habitat, the authors stated a predominance of visual signals. In the hamadryas baboon group of the present study, the category “visual signals” was the largest one with approximately 45% of all observed signals. Together with the other two mixed visual categories the proportion of visual signals increased to approximately 78% compared to approximately 22% for “tactile signals”. As acoustic signals were not investigated in this study, the relation between visual and vocal signals can not be explored.

4.2 Repertoire

4.2.1 Eyebrow raising (ER)

Eyebrow raising was among the most frequently observed communicative elements used by the hamadryas baboons of the present study. In observation period 2, it was the signal with the highest frequency and was found in all age and sex classes. Younger animals used it less often than older baboons. *ER* was the most often combined signal.

Some authors (e.g. Hesler & Fischer, 2007) regarded it not as an independent signal but as a component of a facial expression.

ER is a purely visual signal and requires – for being effective – the attention of the recipient as well as an unobstructed line of sight between the sender and recipient. This was confirmed in the results. Approximately 95% of single *ER* events were given when the recipient was attentive, and in approximately 80% gaze contact between sender and recipient was recorded. *ER* elicited a response of the recipient in more than 80% of the observed cases. The signal was found in three contexts and therefore could be regarded as a flexible signal.

ER is often described in the literature and can be considered typical for the Cercopithecinae.

Maestripieri investigated communication of several species of *Macaca*. He observed that *ER* was a relatively common signal in *M. nemestrina* (1996b) (as it was also true for the hamadryas baboons of the present study). It was performed as an affiliative signal, and was displayed by males more often than by females. Further the author stated that *ER* was frequently used between males assuming that it could serve as a bonding pattern between males. Both findings were not confirmed for the hamadryas baboons in the present study. Here, no differences regarding the sexes were found and *ER* was mostly observed in the agonistic context. The harem leader and the high-ranking adult females who are naturally the senders of many aggressions in a baboon group showed the highest *ER* frequency. In the most cases the signal was used as a threat. Typical reactions of the recipient were for instance screaming and/or *presenting*. Harem leaders used *ER* to request their females to follow and younger males were observed directing it to subadult and adult females in order to request copulations. *ER* was rarely used for friendly encounters and play, although baboons occasionally appeared to raise their eyebrows as a greeting and as an invitation for play.

M. arctoides (Maestripieri, 1996a) and *M. mulatta* (Maestripieri & Wallen, 1997) rarely showed *ER.* Zeller (1996) found *ER* in *M. sylvanus*, *M. fuscata* and *M. fascicularis* as component of threat signals.

Hesler and Fischer (2007) considered *ER* in Barbary macaques as a component part of three facial expressions: “stare” was found in subadult males and adults of both sexes and in the context “dominant”; “rounded mouth threat face” was seen in all age and sex classes except infants and in the context “dominant”; and “staring open mouth pant face” occurred in subadults and adults of both sexes and in the context “undecided”. In contrast, *ER* use was observed in hamadryas baboons in all focal animals. The contexts for *ER* use in Barbary macaques could be summarized as “agonistic”, as for the hamadryas baboons.

ER has been described as an agonistic signal by many baboon researchers: Barrett (2002, personal communication) for chacma baboons, Strum (1987) for olive baboons, Hall and DeVore (1965) for olive and chacma baboons, Ransom (1981) and Smuts (1985) for olive baboons, Kummer and Kurt (1965), Kummer (1968), Abegglen (1976), Gockel (1993) and Swedell (2006) for hamadryas baboons. Pellat (1980) analysed the facial expressions of chacma baboons regarding the involved muscles and registered *ER* in several agonistically used facial expressions such as “attack face” and “aggressive threat face”. Coelho and Bramblett (1989) analysed “brow raise” for the genus *Papio* and defined it as threat behaviour. It was shown by all age and sex classes and also with similar frequencies of use (mean values between 0.19 and 0.39 acts/hour). The median values of frequency for the hamadryas baboons in the present study were much higher (with the exception of the black female infant).

ER was not investigated in the comparative studies by Call and Tomasello, Liebal and Pika (see Call & Tomasello, 2007).

4.2.2 Enlisting (EG)

Enlisting was observed in less than half of the baboons in observation period 1 and in nearly every focal animal in period 2. There were no significant differences in age or sex classes. *EG* was found in five different combinations. It was a purely visual signal and therefore required the attention of the recipient. The results show that in approximately 80% of all *EG* events the recipient was attentive.

In contrast, gaze contact during signalling was rare. Probably, for the sender it was not necessary to have direct gaze contact to the recipient. On the other hand, direct gaze contact would maybe improve the effectiveness of *ER* because only approximately half of all attentive recipients reacted to the signal. But the reason for this result could be that the wanted response to *EG* was probably social support for the signaller, and this could be costly for the recipient. Besides, not every addressed recipient would be a good ally.

EG was described by several authors but sometimes called differently. Hesler and Fischer (2007) called *EG* “show-look” and found it used by subadult and adult Barbary macaques in the context “undecided”. The hamadryas baboons in the present study used *EG* at an earlier age. Both species showed the signal exclusively in agonistic contexts. Smuts (1985) described *EG* as a submissive behaviour in olive baboons. Coelho and Bramblett (1989) reported it as a threat behaviour and observed it in all age and sex classes (genus *Papio*).

4.2.3 Lowering (upper part of the) body (LBo) and back (LBa)

In observation period 1, *lowering upper part of the body* was observed in approximately half of all animals and in period 2 in nearly every focal animal. It was found in six different combinations and was exclusively shown in affiliative situations. *LBo* seemed to be predominantly used for greeting and as a request for play and more rarely as a signal to climb onto the back of the signaller. Recipients of *LBo* often reacted by approaching to the sender. In some cases males lowered their body to request copulations. *LBo* may have also been used as an attempt by larger baboons to make contact with or come into the visual field of a smaller baboon (infant).

Lowering back was observed in only five individuals in observation period 1 but in more than half of the focal animals in period 2. It was used in the three affiliative contexts (predominantly for nursing) and was not exclusively performed by mothers but also by other females and males. They showed it when they wanted to carry an infant. *LBa* was only given when the recipient was attentive but mostly used without gaze contact. In all cases the recipient reacted and climbed onto the signaller’s back.

For both signals there were no significant differences in usage, neither for age nor for sex classes.

LBa could be regarded as iconic signal and is likely to be understood by many species, humans included. The signal and its usage seem to be universal in Cercopithecine monkeys and also Old World apes. Maestripieri and Call reported for chimpanzees and gorillas: “mothers also signalled their infants to climb on by bending their knees, presenting the hindquarters, ...” (1996, p. 630). Hesler and Fischer (2007) analysed “invitation to ride” in Barbary macaques and observed this signal in subadults and adults of both sexes. It occurred only in affiliative contexts. Abegglen (1976) described *LBa* as “invitation to carry” in the category “maternal behaviour”, and Kummer reported “invitation to back carry” (1968) for hamadryas baboons. Other authors described *LBa* as a variation of *presenting* (e.g. as “present with lowered hindquarters”, Coelho & Bramblett, 1989).

4.2.4 Relaxed open mouth (RM)

In both observation periods *relaxed open mouth* was among of the most frequently used signals shown by nearly every baboon. It was found in seven different combinations.

In approximately 95% of all *RM* events the recipient was in an attentive state and in 83% of all events there was gaze contact between sender and recipient. It elicited a response in approximately 93% of all single events. *RM* was used in two affiliative contexts. In general it appeared to convey a friendly mood and particularly was used to initiate play or while senders were approaching recipients.

RM often is called “play face” and was described with slight variations (regarding the upper lip) by many primate researchers (e.g. Redican, 1975, and Estes, 1991, for Cercopithecidae; Goodall, 1991, for chimpanzees; Meder, 1993, for gorillas). All consider it exclusively a friendly signal. Pellis and Pellis (1997) regarded “open mouth face” as the most reported play signal in primates. Van Hooff (1967) described this signal for playing individuals among many representatives of catarrhine monkeys as well as for chimpanzees and gorillas. He supposed that it is in some parts similar to “staring open mouth” (used for aggression). Some elements of “play face” “are seen in the agonistic ‘aggressive threat face’, but in the ‘play face’ the lips are relatively relaxed and the fear elements… (retraction of eyebrows,…) are absent” (Pellat, 1980, p. 416), and “… there is an obvious difference in the eyes, which are often ‘slitted’ or partially closed” (Gautier & Gautier, 1999, p. 934).

De Marco and Visalberghi (2007) investigated facial displays in young tufted capuchin monkeys. They also described *RM* for this New World primate species and observed this signal emerging in monkeys as young as 1.5 months. Owens (1975) found *RM* used for the first time by a 17 days old *Papio anubis* infant. In the hamadryas baboons of the present study *RM* was also found already in the black infants. Redican (1975) pointed out that the signal can be shown by adults as well as younger primates. Hesler and Fisher (2007) found that the “relaxed open mouth face” was frequently used by infant, juvenile and subadult Barbary macaques but rarely by adults. Coelho and Bramblett (1989) also listed *RM* as “play face” for the genus *Papio*. It was more often used by younger individuals (especially juveniles and subadult males) than by adults. In the present study, *RM* was a typical signal of infantile and juvenile baboons, too. Only one adult female showed it relatively often, the harem leader performed it least frequently and the oldest female never used it. The difference between the younger and the older baboons was significant.

De Marco and Visalberghi (1997) also reported that *RM* was frequently associated with playful or other affiliative behaviours and that it was reciprocated. Hesler and Fischer

(2007) as well as Coelho and Bramblett (1989) observed it exclusively in the context of play. Symons (1974) examined aggressive play in rhesus macaques and wrote that *RM* or "play face" is a gesture exclusively occurring in the play context. The hamadryas baboons in the present study also used this signal preferably in the play context but as well in the friendly context. Of course, these findings also depend upon the observers' rating of the context. "There is general agreement that this gesture communicates (or metacommunicates) a playful mood, the intention to play-fight but not to fight" (Symons, 1974, p. 321). *RM* gives information to the recipient about how to interpret the subsequent signals – saying "don't worry, I'm just playing" – so that signals from other contexts, such as aggressive, can be used for play without conveying their usual meaning. Van Hooff (1967) regarded *RM* as intention movement of gentle biting during play.

Symons (1974) described the recipients' reaction to a "play face" as follows: "play face", approach and play-fight (whereas *open mouth threat* – being somewhat resembling to "play face" – caused usually flee or submissive gestures). The hamadryas baboons in the present study also mostly responded to *RM* with *RM*, *poking* or by changing their behaviour.

"Play face" "appears either as an invitation from a distance or during the acting out of the behavior" (Gautier & Gautier, 1999, p. 934). In the present study *RM* was not recorded when it occurred during play because of the difficulty of distinguishing between its use as a signal or simply as an action of biting.

4.2.5 Head shaking (HS)

Three focal animals (the harem leader, the senescent female and one subadult male) used *head shaking* in the observation period 2, and overall its use was infrequent. The contexts in which this signal was performed could not be determined due to the rarity of its occurrence.

Ransom (1981) observed *HS* in olive baboons. He wrote that it was a friendly signal (a type of greeting) shown by adults, subadults and large juveniles. Estes (1991) described *HS* as a facial expression for some members of Cercopithecidae, performed in conflict situations. Call and Tomasello (2007) observed *HS* in their long-time study of gestural signals in young chimpanzees. They found it exclusively in six-year-old chimpanzees in the play context (Tomasello et al., 1997). Liebal et al. (2004a) registered *HS* in chimpanzee gestural sequences during agonistic and play situations. Coelho and Bramblett (1989) listed *HS* as an affinitive behaviour in their ethogram for the genus *Papio*. It was shown more often by adults and infants (mainly by adult males) and more rarely by juveniles and subadults.

4.2.6 Rolling on ground (RG) and hand-/headstand (HH)

Rolling on ground and *hand-/headstand* were infrequently used. They were performed almost exclusively by juvenile and infantile baboons and were found only in affiliative contexts. These signals appeared to be used for the purpose of initiating play. Occasionally, they were also performed when no recipient was visible for the observer. In all *HH* events the recipient was attentive, whereas both attentional states were registered for *RG*.

RG and *HH* are rarely found in the literature. Hesler and Fischer (2007) described "headstand" occurring during play for older juvenile and subadult female Barbary macaques. The authors found this signal in three contexts: play, affiliative and submissive. In the present study, the baboons used *HH* in play and in friendly contexts. Coelho and Bramblett (1989) observed "roll or tumble" in the genus *Papio* (mostly among juvenile males) and rated it as play behaviour. Pika (2007a & b) mentioned "somersault" (making a flip) – which could be comparable to *RG* and *HH* – for subadult bonobos in play and affiliative contexts, and for gorillas, too. Estes (1991) also named "somersaulting" as a play signal for *Cercopithecidae*. Liebal (2005) recorded "head-stand" as a rare visual gesture in orangutans.

4.2.7 Threat mouth (TM)

Threat mouth was first observed in observation period 2 and was used relatively frequently both as single signal as well as combined signal. It was performed by all adults and subadults and three (of four) juveniles. *TM* was combined with *eyebrow raising, chasing, stiff threat* and *poking.* The recipients were attentive and gaze contact between the communicators could be often observed. *TM* was seen exclusively during agonistic interactions (aggressive context). For differences between *threat mouth* and *relaxed open mouth* see also 4.2.4.

Hesler and Fischer (2007) described "rounded mouth threat face" for Barbary macaques. The teeth were not shown. The signal always occurred together with *eyebrow raising* and occasionally with a "ground slap" (comparable to *stiff threat*) or a quick approach toward the recipient (comparable to *chasing*). With the exception of infants it was observed in all age classes and exclusively seen in the context of dominance.

Van Hooff (1967) gave a detailed description of several variations of "staring open-mouth face" in catarrhine monkeys. The eyebrows were often lifted, the teeth mostly not visible. In *Papio* it was often combined with hitting movements of the ground (comparable to *stiff threat* or "ground slap"). The behaviour was observed in agonistic contexts.

Also Gautier and Gautier (1999) reported that in Old World monkeys "the open mouth threat face appears in most species as an expression of threat …" (p. 937). Estes (1991) described that in Cercopithecidae "staring with open mouth" with covered teeth was used as a facial expression of threat. Pellat (1980) listed for *Papio ursinus* "aggressive threat face" with a round mouth and non-visible teeth. Zeller (1996) found "mouth open threat" to be the most common facial expression of threat in *Macaca fascicularis* and also to be used frequently by *M. sylvanus* and *M. fuscata*. Chevalier-Skolnikoff (1974) mentioned "rounded-mouth stare" in stump-tailed macaques.

De Marco and Visalberghi (2007) investigated the appearance of facial displays in capuchin monkeys and found that the "open-mouth threat face" was associated with agonistic behaviours and emerged as the latest facial display, performed between 4.5 and 10 months of age. In the baboons of the present study *TM* even was not observed in animals younger than 18 months. Other researchers described this signal as being used in combination with "staring".

4.2.8 Head bobbing (HB)

Head bobbing was only found in observation period 2. It occurred less than ten times, only in two animals and with very low frequencies.

HB was reported for many monkey species by several authors. All described concurrently that the context was aggressive/agonistic. The same was found for the hamadryas baboons of the present study where the context of *HB* was aggression.

Estes (1991) listed *HB* as a threat display for the entire family Cercopithecidae. Coelho and Bramblett (1989) classified "head bob" as a threat in the genus *Papio*.

Hesler and Fischer (2007) observed it in Barbary macaques of all age classes except infants and only in the context of dominance. Hall and DeVore (1965) reported "jerking of head down and forward" as an attack-threat signal used exclusively by adult and young baboon males. Ransom (1981) found "bobbing" in olive baboons. It was shown by all sex and age classes and used for agonistic purposes. Smuts (1985) described "bobbing the head" as an aggressive behaviour of adult baboon females. In the present study, *HB* was observed in one adult female and in one subadult male.

Chevalier-Skolnikoff (1974) described "bob head" being used during dominance respectively aggressive interactions. Also Bolwig (1978) pointed out that an anubis baboon male in a zoo used "jerking" (with head) to control the movements of his females. He also found that "bobbing heads" were typical threats used by arboreal guenons. Kummer and Kurt (1965) and Swedell (2006) listed *HB* as an agonistic behaviour in hamadryas baboons.

While Gautier and Gautier (1999) reported hamadryas baboons as using *HB* in combination with "open-mouth threat face", the present study found *HB* in combination with *eyebrow raising* only.

Apes seem to use *HB* more flexibly. Tomasello et al. (1997) observed "head-bob" in young chimpanzees across several ages and different contexts. The individuals used it mainly in the play context. Liebal et al. (2004a) also registered *HB* in chimpanzees as part of gestural sequences in the play context.

4.2.9 Yawning (YW)

Abegglen (1976) listed *yawning* in his ethogram for the hamadryas baboons but he did not mentioned any specific meaning or context. Stein (1984) described *YW* as a threat in yellow baboons and Bolwig (1978) considered it an aggressive behaviour in anubis baboons.

Mostly *YW* was regarded as an ambiguous behaviour. Hall and DeVore (1965) listed *YW* as "attack-threat" communication shown by adult males (combined e.g. with *eyebrow raising,* and directed towards another baboon) and as a signal of "escape-fear-uncertainty" (undirected and shown mainly by adult males).

Also in the hamadryas baboon group of the present study (OP 2) males (harem leader and two subadult males) were the most frequent users of *YW*, further it was rarely observed in one adult and one juvenile female. *YW* was combined with *eyebrow raising* and exclusively used in the agonistic context (aggression).

Ransom (1981) found that in olive baboons *YW* was used as an agonistic signal in all age and sex classes and as a signal of "escape-fear-uncertainty" in adults and young adults. Some authors regarded *YW* as tension behaviour respectively as a sign of uncertainty in baboons (Kummer, 1975; Coelho & Bramblett, 1989; Barrett, 2002). Hinde and Rowell (1962) wrote that "yawning often occurs in situations of mild stress, and especially in aggressive contexts" (p. 20). Gautier and Gautier (1999) pointed out that "in *Papio anubis* and *ursinus* … yawning is considered a threat display. Most authors, however, observing that yawning is often undirected and can even be done with closed eyes, think that it has no more than very low communicative value and constitutes rather an individual expression of an animal, hence its name: 'tension yawning.'" (p. 938). Further they assumed that males use *YW* to display their social status. Hesler and Fischer (2007) analysed *yawning* in Barbary macaques as a correlate of internal tension and as an agonistic signal. They found the signal in all age and sex classes except infants and younger juveniles and did not classify its use within specific contexts. Estes (1991) pointed out that *yawning* is used in a directed threat and as expression of tension, and that the main function may be advertising of status. Redican

(1975) wrote “yawning often occurs in monkeys and apes experiencing some degree of conflict or stress. When oriented directly at another animal it is a form of threat … it is displayed more frequently by males than females” (p. 153).
Gautier and Gautier (1999) also mentioned that *YW* often was observed without any answer by other baboons. In the present study, *YW* was used infrequently, and few of these events elicited a response from the recipient (*stiff threat*). But there is too little data for a proper evaluation of this signal. Probably *YW* sometimes was used intentionally (in 81.1% of all *YW* cases the recipient was attentive) as a threat signal respectively to display social status, and sometimes it was performed relatively involuntarily as displacement behaviour. And of course there is the possibility that the yawning animal is simply tired or needs more oxygen. Redican (1975) wrote that “the external features of a fatigue yawn and a display yawn are quite similar” (p. 147). But it can be supposed that an animal being in an agonistic situation will not be in a “fatigue mood” and therefore *YW* used in agonistic contexts can be considered a signal.

4.2.10 Head tapping (HT) and Spinning (SP)

Both signals were only seen in observation period 2 and were the most rarely used signals.
Head tapping was displayed by both subadult males and *spinning* by one subadult, one juvenile and one infantile (brown) female, and always with very low frequencies. *HT* was observed in the aggressive context, no context for *SP* could be determined.
The only signal looking similar to *SP* was found by Pika (2003, 2007a, b). She described “ice skate” – in which the animals pirouette with their hands on the ground or in air – performed by subadult gorillas (as a play signal) and subadult bonobos.

4.2.11 Chasing (CH)

Chasing was shown by approximately 40% of all baboons in OP 1 and approximately 80% of the focal animals in OP2. Mainly older baboons as well as male baboons performed this signal. The harem leader used it most frequently (OP 2). Combinations occurred with *eyebrow raising*, *stiff threat* and *threat mouth*.
Gautier and Gautier (1999) wrote that Old World monkeys “during a threat … strike in the direction of a partner … make sudden forward movements …”, p. 937. *CH* in the observed hamadryas baboons could also be very brief sometimes it was only a skip or a step in the direction of the recipient.
Many baboon researchers described *CH.* The term is often used for an incomplete hunt without reaching and attacking the recipient. But sometimes it is not clear if the authors

understand *CH* as a signal or as an action. *CH* seems to be a borderline case between communication and action.

Coelho and Bramblett (1989) investigated the signal in the genus *Papio*. The authors classified the signal as an attack behaviour. It was shown especially by infant and juvenile males but was found across all sex and age classes. Stein (1984) listed "chase" as an aggressive behaviour in male yellow baboons.

For hamadryas baboons, several researchers described signals which can be compared with *CH*. Kummer (1957) mentioned "Scheinangriff" (mock attack), used especially by alpha-males toward subadults, and "Drohlauf" (threatening run) where the sender approached close to the recipient and then quickly withdrew both as elements of threat and fear. Kummer and Kurt (1965) mentioned "chasing" and "short running attacks" as elements of aggression. Swedell (2006) listed "short running attack" ("A … runs toward B …, as if intending to attack, then stops before reaching B", p. 217) as an agonistic behaviour. Also in the present study, *CH* was only reported in the aggressive context.

Other papers investigated *CH* as a play behaviour. Chevalier-Skolnikoff (1974) found "chase" in aggressive and play sequences in stump-tailed macaques. Pika (2007a, b) observed subadult gorillas and bonobos performing "gallop-run" (in an exaggerated and dashing manner) in the direction of other individuals. The bonobos used it for play but also in aggressive contexts. It was shown by 4 of 7 bonobos and 3 of 13 gorillas.

4.2.12 Jumping in the air (JA)

Jumping in the air occurred in both observation periods. It was observed only in juvenile and infantile baboons of both sexes and was registered exclusively in the play context. This signal appeared to be used for the purpose of initiating play but occasionally it was also performed when no recipient was visible for the observer. *JA* was used in combination with *poking*.

Call and Tomasello (2007) mentioned "bipedal jump" in young chimpanzees. Liebal et al. (2004a) found it in gestural sequences used in play context in a chimpanzee group. Also in the baboons of the present study, *JA* was often observed as a form of bipedal jumping (see figure 3.1i) in cases in which the animal jumped higher with its forelegs than with its hindlegs. Estes (1991) listed "jumping" as signal for play invitation in Cercopithecidae.

For rhesus macaques Hinde and Rowell (1962) described "bouncing" as repeated jumping on the same spot. It was used in communication during attack and threat. Gautier and Gautier (1999) listed "jump in place" as a threat signal in baboons. In the present study, *JA* was never observed in an agonistic context.

4.2.13 Pumping (PU)

In both observation periods, *pumping* was (with one exception) exclusively observed in males. It was a typical signal of harem leaders but was also used by some subadult males. *PU* was found in combinations with *eyebrow raising* and *stiff threat*. In all analysed cases the recipient was attentive and it was only seen in aggressive context.

Kummer (1968) listed "pumping cheeks with chewing movements" and Abegglen (1976) "pumping cheeks" in their ethograms for hamadryas baboons as aggressive behaviour. Gautier and Gautier (1999) mentioned openings and closings of the mouth for geladas.

Coelho and Bramblett (1989) listed for the genus baboon "chew" as "rotational motion of the jaw accompanied by an opening and closing of mouth" (p. 135). It could be either directed and undirected. Both variants were used more or less by all age and sex classes. The authors did not classify the context of the signal. In the present study, *PU* also sometimes looked like chewing. Furthermore, the recipient sometimes could not be identified so that *PU* might be also undirected.

4.2.14 Stiff threat (ST)

Stiff threat was frequently observed in both observation periods in all sex and age classes. In the second period, 13 focal animals showed this signal, and the harem leader had the highest frequency. It was found in some combinations such as with *eyebrow raising, threat mouth* or *chasing*. There was no clear difference between attentive and inattentive state of the recipient. *ST* was only recorded in the aggressive context. Often individuals used *ST* to request something. Recipients frequently reacted by *presenting* or going away.

While "ground slap" can often be found in the primate literature, the authors did not mention stiff arms. In the present study, *ST* consisted of slapping the ground with hands while keeping the arms stiff.

Pika (2003) listed "slap ground" as an auditory gesture in the ethogram of communication for subadult gorillas and bonobos. All gorillas showed it, and one gorilla used it in more than one functional category. In bonobos it was described as a play signal. Tomasello et al. (1997) observed "ground-slap" in different chimpanzee age classes in all of the investigated contexts (affiliation, agonistic, access, food, ride/walk, nurse, play, sexual). It was a very frequently used signal and was seen in all individuals. Liebal et al. (2004a) found it in gestural sequences in a chimpanzee group during agonistic, play and sexual behaviour.

Hesler and Fischer (2007) found "slap ground " in all sex and age classes except in infants and young juveniles. The macaques used it during play as well as during

dominance interactions. Symons (1974) mentioned “slapping the ground toward another monkey” as part of rhesus macaques’ agonistic communication.
Estes (1991), referring to the group of Old World monkeys, described “slapping and scrubbing the ground” as “strong threats made by most monkeys during aggressive encounters at close range” (p. 482) and Gautier and Gautier (1999) listed “slap the ground” as a signal associated with agonistic interactions.
Male yellow baboons (Stein, 1984) and hamadryas baboons (Kummer & Kurt, 1965; Kummer, 1968; Abegglen, 1976; Gockel, 1993; Swedell 2006) showed “ground-slap/ slapping ground” as a threat signal during aggressions respectively as agonistic behaviour. Coelho and Bramblett (1989) investigated “slap ground” in the genus *Papio* and found it to be used as a threat in all age and sex classes (mainly in adults). Hall and DeVore (1965) listed “slapping ground with hand” as a signal of attack/threat used by adult and young adult baboons. Smuts (1985) described “threaten by slapping the ground” as an aggressive behaviour in baboons. Owens (1975) named “slapping ground or vegetation” as a gesture of aggression in baboons. Ransom (1981) observed “stiff-arm threat” (with jumping) in all baboons except young infants. He noted that it was a “mild threat at a distance” and an “intense threat and prelude to attack when close” (p. 96-97). Rowell (1966) described “hit ground threat” and regarded it as a warning to young importunate baboons.
Whereas *ST* in baboons in the literature and the present study were only seen in agonistic contexts, apes and some groups of rhesus macaques use it also as a play signal and in other contexts (e.g. Tomasello et al., 1997; Pika, 2003; Liebal et al., 2004a).

4.2.15 Displaying (DP)

Displaying was recorded in the first observation period in the two harem leaders, one juvenile male and one of the highest-ranking females, and in the second observation period in the harem leader and the two subadult males. It seems to be an agonistic signal respectively a signal of dominance. Unfortunately, no context data for *DP* was available due to the rarity of the signal. Harem leaders occasionally used it to call the females to follow them.
DP can also be desribed as “branch shaking”. It is supposed to have a communicative function as “inter- and intra-group aggressive threat, attraction of females in oestrus, and non-specific contexts of ‘excitement’” (Mehlmann, 1996, p. 503). In his study on Barbary macaques he found that the signal was primarily performed by adult males. It rarely occurred in inter-group encounters and predominantly in intra-group contexts

(sexual, agonistic and neutral). Hesler and Fischer (2007) also described “shake branch” use in Barbary macaques in a variety of situations, but no specific context was reported. Chevalier-Skolnikoff (1974) noted that in captive stump-tailed macaques “shake branch” was almost exclusively directed toward human observers and concluded that in the wild it is probably used as an inter-group threat. Hinde and Rowell (1962) investigated “branch-shaking” in rhesus macaques. They observed it as jumping up and down on a branch, mostly performed by males but occasionally also by females, and frequently associated with threat. They found a “strong aggressive element in branch-shaking” (p. 8) and discovered that different males used different techniques. Estes (1991) mentioned “branch-shaking” in Cercopithecidae as “aggressive display addressed to predators (including human observers) and distant rivals …“ (p. 481).

Hall and DeVore (1965) listed “shaking of rocks, branches” as an attack-threat communication and observed it in adults and young adults. Coelho and Bramblett (1989) mentioned “branch shake” for the genus *Papio* and defined it as a threat. It was seen in all age and sex classes, with highest values in adult and juvenile males. The frequencies found for the hamadryas baboons of the present study were much lower.

4.2.16 Lipsmacking (LS)

Lipsmacking was frequently used in both observation periods (it was not counted when it occurred during grooming). *LS* was seen in several combinations e.g. with *eyebrow raising, greeting*, *presenting* and *lowering body*. It was observed e.g. in individuals approaching one another, as a greeting, before grooming and as a lure. The recipient could respond e.g. by *presenting*, grooming or playing.

Many species of monkeys use *LS* frequently in a variety of social circumstances. Hesler and Fischer (2007) found the signal in all age classes of Barbary macaques except infants. They observed it in two contexts – affiliative and submission. Maestripieri (1997) described *LS* as a submissive and affiliative signal for macaques, too. Also in the present study, the signal was predominantly used in the affiliative context (friendly and play) and rarely for appeasement/submission. It was seen in all senescents, adults and subadults as well as in many of the juveniles but very rarely in brown infants. It was never observed in black infants. Younger baboons used significantly less *LS* than older baboons.

Estes (1991) wrote that *LS* “has evolved into a social display that generally signifies peaceable intentions. As such it facilitates approach to or by individuals that may otherwise feel insecure, and is the common prelude to social grooming, infant-handling, and copulation … This positive social rule is particular clear in baboons and manga-

beys." (p. 483). Estes determined *LS* to be a submissive, appeasing and friendly expression. Coelho and Bramblett (1989) listed *LS* as an affiliative behaviour found in all age classes of the genus *Papio*. Hall and DeVore (1965) desribed the signal as a friendly behaviour directed towards another baboon used by adults and young adults. Ransom (1981) observed *LS* in all age classes of olive baboons as a general greeting. Chevalier-Skolnikoff (1974) pointed out that *LS* in stump-tailed macaques "occurred during dominance interactions in which the subordinate was submitting to the dominant, and during positive or cohesive interactions as, for example, when an adult approached an infant ..." (p. 131).

Gautier and Gautier (1999) described many uses of *LS* for Old World monkeys: combined with *eyebrow raising* as threat, as a prelude to (or during) grooming and especially preceding various types of approach (e.g. for the purpose of infant handling or copulation). Pellat (1980) pointed out that the occurrence of *LS* could also be the expression of an interior conflict between "fear" and "social attraction". Redican (1975) mentioned that in some species, *LS* was also observed during agonistic encounters. Hinde and Rowell (1962) wrote that *LS* occurred in rhesus monkeys in diverse situations "but always involve positive social advances to another individual; this is often combined with slight fear" (p. 15). They stated that *LS* was occasionally associated with threat postures and "it may also involve an element of slight aggression". For other situations they assumed *LS* being used to reduce fear and aggression.

Easley and Coelho (1991) found for anubis baboons a positive correlation between *LS* and several affiliative behaviours and a negative correlation with most agonistic behaviours. Furthermore, *LS* was not associated with social status.

Rowell (1966) observed that male baboons lipsmacked more frequently to females than vice versa. In the present study, males generally showed more *LS* than females.

While some authors such as Hesler and Fischer (2007) did not see the signal in infants De Marco and Visalberghi (2007) found it to be the first signal in one-month old infants. Redican (1975) pointed out that *LS* could have its origin in neonatal nursing or non-nutritive sucking movements. In both observation periods of the present study, no black infant ever used this signal. Very young primate infants have a special position in their group. They are situated outside the social rules, and maybe they do not need signals for appeasement or for reduction of distance such as *LS.* Nearly every member of a primate group attempts to come into close contact with the infants. But for older youngsters looking for their role in the group, and of course for subadults and adults, a signal like *LS* is necessary to show friendly intention or submissive behaviour.

It is very important that the recipient is able to see the signal (in spite of the smacking sound sometimes audible). In the present study, the signal was directed to an attentive recipient in 88.5% of the cases.

4.2.17 Presenting (PR)

Nearly all individuals frequently used *presenting* in both observation periods. It was never observed in the highest-ranking males. It could be combined with *eyebrow raising*, *enlisting*, *lowering body*, *lipsmacking*, *relaxed open mouth, poking* and *penis grab.*
PR was predominantly used when the recipient was attentive (92.0% of all events) and in all contexts except nurse (friendly: 48.2%, appeasement/submission: 36.1%, play: 8.4%, aggression: 7.3%). Some responses were: *mounting*, grooming, *lipsmacking*, *jumping on back*, play and copulation.
Pika (2007a and b) observed *PR* in two of seven bonobos (function: sex). Hesler and Fischer (2007) found *PR* in Barbary macaques of all ages except infants and young juveniles as submissive gesture. “Hindquarter presentation” was a frequently used signal in pigtail and rhesus macaques and the most frequently used signal in stump-tailed macaques (Maestripieri, 1996a and b; Maestripieri & Wallen, 1997). The macaques displayed it as a submission/appeasement gesture and especially in cases when the distance to a higher-ranking individual was reduced. Higher-ranking individuals used it significantly less than lower-ranking individuals. In the present study, the highest-ranking hamadryas baboon males never showed *PR* (contrary to *GR*, see also 4.2.18). Maestripieri (1997) assumed that “hindquarter presentation” is the second most frequently used submissive signal in macaques and that it is derived from the sexual repertoire. He also found some *PR* events during play in pigtail macaques.
Chevalier-Skolnikoff (1974) mentioned that in stump-tailed macaques *PR* is often a sexual/precopulatory behaviour of oestrous females. In addition she described *PR* as a signal used by subordinate individuals during dominance interactions, by dominant individuals toward subordinates and by both as appeasement gesture.
Ransom (1981) observed “rear present” as a general greeting in all age classes (used rudimentarily in infants) and as a friendly behaviour, and Hall and DeVore (1965) described *PR* as a friendly signal (both studies were made on savannah baboons).
According to Rowell (1966), captive subordinate anubis baboons present more to dominants than vice versa. Females mostly present to males whereas males present equally often to females and other males. In the present study, no significant difference for the sexes was found.
Hinde and Rowell (1962) pointed out that *PR* was seen in diverse social situations in which dominance relationships played an important role.

Also Kummer (1968) listed “presenting rear” as a submissive behaviour. Additionally, he mentioned “presenting anogenital region” in females as a sexual behaviour. He also described a special behaviour of leader males that he called “notifying” in which mostly one male “… slowly approaches a seated neighbour, while both look at each others’ face … As soon as the approaching male has come very close … to the other, he turns abruptly and presents, … his anal field … then he immediately begins his peculiarly hasty retreat.” (p. 128). In the present study, this behaviour was not distinguished from *PR*. Kummer wrote also that “presentation of the anal field” in adult hamadryas males was not a signal of submission. Abegglen (1976) mentioned *PR* only as a sexual behaviour in hamadryas baboons. Barrett (2002, personal communication) reported “social presenting” by females and juvenile males directed towards higher-ranking males as a submissive display. Swedell (2006) considered “present” as a sexual behaviour in hamadryas baboons.

Estes (1991) gave a good overview for *PR*: “Sexual and social presenting look so similar that telling one from the other may hinge on the identity and condition of the presenter and the response of the receiver. When a male or a female whose sexual skin indicates nonestrus presents and the receiver fails to copulate …, it is clearly ‘social presenting’. In its commonest form, presenting is a brief greeting given by one monkey as it passes before another, usually higher-ranking one, … Social presenting is the most obvious and important display of peaceable intentions among primates and probably the most effective in appeasing aggression, …” (p. 481).

Gautier and Gautier (1999) mentioned “genital presentation” in Old World monkeys occurring in sexual and various other forms of social interactions during friendly and agonistic encounters. Subordinates demonstrate the recognition of rank and dominants show their friendly intentions.

4.2.18 Greeting (GR)

Greeting was used by approximately half of all baboons but with low frequencies. It was observed in adults and subadults, rarely in juveniles and never in infants. *GR* mostly occurred when two individuals (female-female, male-male, female-male) met, and it was often accompanied by vocalisation. Usually *GR* was shown nearly simultaneously by two animals. The sender started signalling and the recipient immediately responded with the same signal while the initial sender continued displaying *GR*. Occasionally, the greeting baboons touched each other. *GR* was found in combination with *lipsmacking* and was observed exclusively in friendly context.

Gautier and Gautier (1999) described “mutual social presenting*”* in Old World monkeys but they found it mainly in males. Hesler and Fischer (2007) pointed out that female

Barbary macaques frequently “present each other in the antiparallel position” combined with *lipsmacking* and inspecting each others’ behinds. In the present study, adult and subadult males as well as females performed *greeting* simultaneously and this signal appeared as a real greeting rather than an inspection of genitals.

Other authors have investigated *GR* exclusively among males (Peláez, 1982; Colmenares, 1990, 1991a, 1991b). Peláez (1982) observed hamadryas, yellow and hybrid baboon males. He found that the hamadryas males used a greater number and had a wider repertoire of greetings than the yellow baboon males and explained the differences in terms of the social systems of the two subspecies. Peláez also described different types of “greeting” in adult baboon males, such as “circular” and “semi-circular” greeting. In the present study, no differentiation was made.

Colmenares (1990) pointed out that “baboon watchers agree that social tension seems to be the general context eliciting greeting interactions between males” (p. 103). He wrote that hamadryas baboon males used “greeting tactics” during agonistic encounters whereas females used “grooming tactics”. In the present study, both sexes showed *greeting* and all encounters were in friendly context. Maybe there is some excitement in the animals, too.

4.2.19 Poking (PK)

Poking was among the most frequently used signals shown by approximately 90% of all baboons in OP 1 and the most frequently used signal by all focal animals in OP 2. It was a typical signal of the younger baboons. *PK* appeared often in combination with other signals (mostly visual) such as *eyebrow raising, enlisting*, *lowering body, lowering back*, *relaxed open mouth* and *threat mouth.*

Poking was shown to inattentive recipients in more than half of the cases and was accompanied by gaze contact in only 8.2% of all cases. *PR* was the only signal observed in all five contexts. It usually occurred in friendly and play contexts but was also used for agonistic purposes. Possible responses were *presenting*, grooming, going away, approaching, climbing on back, following, playing, *lipsmacking* and copulating.

“Poke at” and “touch” are often mentioned in the literature (e.g. Rowell, 1966; Liebal et al. 2004a and b; Swedell 2006; Hesler & Fischer, 2007; Pika, 2007a and b). The context of “touch” was friendly. It was not totally clear how much physical power accompanied these signals and how long they continued. In the present study, *PK* meant just a very short poke or slight touch.

Estes (1991) mentioned “touch” in baboons as a “gesture of reassurance or appeasement” (p. 488).

Weber (1973) described langurs' "touching" signal in a similar way to how "poking" was defined in the present study: "An animal very lightly touches the shoulder or back of another … When touching occurs it is always at the beginning of a communication sequence; it represents the first call for relations" (p. 483).
Tanner and Byrne (1996) investigated "tap other" in gorillas which would correspond to *PK*. It was a quick contact and withdrawal of the knuckles or open hand and appeared to be performed without use of force. Sometimes the gesture may have served to gain the other's attention for visual signals, and it was often accompanied by a play face.
Liebal (2007a) described "nudge" in captive orangutans: a touching of the recipient with fingers or knuckles. It was shown by almost all animals in her observation groups and used in several contexts (access, affiliation, agonistic, ingestion, nursing, play).
Tomasello et al. (1997) analysed "poke at" in young chimpanzees – it occurred as a very flexible signal and was found in play context in all investigated age classes (from one to eight years). It was also used by some age classes/individuals in the contexts "agonistic", "ride/walk", "nurse" and "sexual". In the hamadryas baboons of the present study, *PK* was the most flexibly used signal being shown in all analysed contexts (with the emphasis on play).

4.2.20 Mounting (MG)

Mounting was observed in both observation periods in female-female, male-male or male-female combinations. It was occasionally found in combination with *relaxed open mouth.* All encounters in OP 2 appeared to be affiliative (friendly and play contexts) whereas in OP 1 it was also seen in agonistic encounters (no quantitative analysis). Sometimes the recipient turned its head to the sender during the signal. After the signal, the recipient often started to groom the sender.
Hesler and Fischer (2007) found *MG* in female Barbary macaques in "undecided context". Only males performed it (to other males or to females). Maestripieri (1996b) observed *MG* in several macaque species and found it mostly displayed by dominants to subordinates of the opposite or same sex. He regarded *MG* as a display of power and compared it e.g. with branch shaking. Hinde and Rowell (1962) wrote that "the occurrence of mounting is also related to the dominance relations of the individuals involved …" (p. 19). In the observed rhesus macaques, *MG* between females was not an uncommon behaviour and usually the dominant mounted the subordinate one. They also recorded some cases in which females mounted males as well. Chevalier-Skolnikoff (1974) mentioned events of *MG* in stump-tailed macaques in several contexts (e.g. play and aggression).

Gautier and Gautier (1999) wrote that *MG* in males often occurred when there was tension between them. *MG* use between females was characterized as rare. The behaviour was shown “before and after grooming, in play, and during agonistic exchanges“ (p. 946).

Estes (1991) wrote that *MG* “generally considered an expression of dominance, is often seen before and after grooming, in play and during aggressive interactions” (p. 488). Langurs showed *MG* towards the same as well as the opposite sex and in all ages with the exception of adult-subadult females (Weber, 1973). “In general, mounting seems to indicate the dominance of a partner, …” (p. 484). In the present study, no analysis of dominance was made but there appeared to be no connection between frequency of mounting and social rank. The qualitative data showed that the older baboon typically mounted the younger one but sometimes *MG* also occurred vice versa. While all variations were observed, female-female mounting seemed to be most common. Male-male, female-male and male-female mounting were less frequent (mounting of females in oestrus by males were not counted).

For the whole genus *Papio*, the signal was also observed in juveniles and between adult baboons of the same sex (Coelho & Bramblett, 1989). It was often shown by adult males and classified as tension behaviour. Hall and DeVore (1965) listed *MG* as a friendly behaviour of dominant baboons. Ransom (1981) recorded *MG* as friendly communication in free-living olive baboons. It was shown by all individuals and in all combinations (except *mounting* of adult males by adult or young adult females).

Kummer (1968) found *MG* occurring between aggressive acts in hamadryas baboons (outside of sexual behaviour). Barrett (2002, personal communication) described “social mounting” as a response to presenting and as a friendly signal but also occurring during aggressive encounters.

4.2.21 Pulling on (PO), penis grab (PG) and jumping on back (JB)

Pulling on, *penis grab* and *jumping on back* were shown by few of the individuals and in general were used infrequently.

Pulling on was performed predominantly by younger baboons. It was occasionally combined with *relaxed open mouth. PO* seemed to be a request to play and to approach and was exclusively observed during friendly and play contexts. In approximately 80% of all cases the recipient was not attentive.

Penis grab was found exclusively in two males (one harem leader and his half brother) in both observation periods. It was sometimes combined with *presenting* or *lipsmacking* and seemed to be a form of greeting as well as an elicitor of play. *PG* can be regarded as special case of *PO*.

Jumping on back was recorded in three focal animals (juveniles and infants) and was used exclusively in play context.

Maestripieri (1997, 1999) investigated “touch-genitals” in macaques, but it is not clear whether this behaviour corresponds to *PG* in the present study which was characterized as a very short event. He found that it mostly occurred between two males and assumed that it served an appeasement function. In the present study, the signal was also observed between two males.

Barbary macaques of both sexes and all age classes used “touch genitalia” in different variations, e.g. one male touched the penis of another male. All individuals with the exception of infants showed “grab” with a short pull. Both gestures were performed during play, affiliative and dominant contexts (Hesler & Fischer, 2007).

Chevalier-Skolnikoff (1974) found “grab, pull” occurring during aggression and play and often as initiation of play for stump-tailed macaques. Like in many other studies no statement was made about the force of these movements.

Kummer (1968) mentioned “touching genitals” as a notifying behaviour between adult hamadryas males and “touching anogenital region” in males as sexual behaviour. Abegglen (1976) listed “penis-grip” (touching of an erected penis or scrotum) as sexual behaviour in hamadryas baboons. For both behaviours it is not clear whether it was a short grip or a long touch respectively a signal or an action.

Also for hamadryas baboons Swedell (2006) described “grab” which looked very similar to *PO* in the present study: “A uses hand to grasp a piece of skin or body part of B, often pulling B’s skin or hair slightly away from B’s body.” (p. 218).

Ransom (1981) found (gentle) “hair-pulling” in juvenile free-ranging olive baboons during harassment sequences (agonistic context). In the present study, *PO* was only observed in friendly context. The olive baboons also showed “diddling” - reaching for and/or handling of genitals – during friendly encounters (Ransom, 1981).

Liebal et al. (2004a) investigated the use of “pull” (on body parts such as legs or arms) in gesture sequences in chimpanzees but it was not obvious how strong the movement was. She found it in all analysed contexts (friendly and agonistic).

Gautier and Gautier (1999) mentioned “grasping hair” and “pulling the tail” as signals used in the context of play.

Call and Tomasello (2007) described a rapid “pull” on a body part in chimpanzees but they did not mentioned how forcefully this gesture was performed. Pika (2007a and b) and Liebal (2007a and b) also used the term “pull” for orangutans, bonobos, gorillas and siamangs, and they wrote that it was a forceful movement. Therefore, this gesture was more an “action” than a “signal”, following the definition of signal by the author of this study.

Tanner and Byrne (1996) investigated “tactile close-range” gestures in gorillas, e.g. “pulling gently on a body part”, and regarded them as iconic gestures. They found that recipients were often not visually attentive when these gestures were given.
JB was not found in the literature. Some authors (Chevalier-Skolnikoff, 1974; Coelho & Bramblett, 1989) mentioned “jump on” in which one animal jumped on a recipient. But this does not correspond to the “jumping on back” signal observed in the present study because the latter (*JB*) described a sender jumping over the recipient while only briefly touching the recipient’s back.

4.3 Combinations

Combinations were recorded when a sender showed two or three signals simultaneously. Because in the present study single elements of facial expressions were counted separately, some combinations could correspond to facial expressions described by other authors.
19 out of 26 different signals occurred in combinations. The signal most often used in combinations was *eyebrow raising*, which appeared in 15 different combinations.
27 different combinations were investigated: 25 double and 2 triple.
All focal animals used combinations. Subadult and adult baboons showed the highest average number. Females performed significantly less different combinations than males. Because of the limited number of focal animals and observation hours and the disproportionate distribution of individuals in the age and sex classes it is possible that differences were more specific to individuals than to age or sex.
There were several combinations of the four categories. The most common was “visual signal” combined with “visual signal possibly making some noise” followed by “visual signal/visual signal” and “visual signal/tactile signal”. By using different combinations of single signals, the baboons showed flexibility in communication and knowledge of the attentional state of the recipient. The combination of two visual signals can reinforce the effect of one signal alone. The combination of a visual signal with a signal which has an auditory or tactile component helps to ensure that the recipient will be attentive and therefore receptive for the signal.
The composite meaning of the combined signals was either the same as the meaning of the single signals they were made of (affiliative or agonistic) or a signal with both meanings (contexts) was combined with an affiliative or agonistic one. Additionally, two or three different signals were used for one context. Therefore, combinations could be regarded as sign of intentionality.
In general, the investigation of signal combinations was not often found in the literature. Tomasello et al. (2004) described combinations as two or three signals used

one after the other and not at the same time. Also Liebal et al. (2004a) investigated gesture sequences in a chimpanzee group and Genty and Byrne (2010) in gorillas. Liebal (2007a and b) described combinations for orangutans and siamangs as sequences respectively successive combinations, as well. These do not correspond with the definition in the present study in which combination means that two or three signals were shown simultaneously.

Tomasello et al. (2004) found that the function of a gesture combination was the same as the function of a single signal used in this combination.

Hesler and Fischer (2007) observed that Barbary macaques used the majority of their gestures in simultaneous combinations. Usually facial expressions were combined with other signals, including postures. The same was found in the present study.

Pollick and de Waal (2007) investigated ape gestures and also combinations of these gestures with facial and vocal signals. They called these events "multimodal communication" and defined them "as the occurrence of two signals within 10 s of each other, and in the majority of such combinations, the two signals overlapped in time" (p. 8187). In their study, the bonobos showed 7.8% of their signals as combinations of gestures and facial/vocal signals, whereas the chimpanzees even used 21.6% of such combinations. The authors found that in bonobos "multimodal communication elicited more responses than did gestures alone, …, whereas no such difference was found in chimpanzees".

Bolwig (1978) wrote that "lifting or lowering of eyebrows … movement of lips … lifting or lowering of head and tail … are visible signals which may combined with one another ..." and "… exposure of the pale skin above the eyelids nearly always accompanied bobbing, … and hitting the ground …" (p. 69).

4.4 Gaze contact and distance

Gaze contact during signalling between communicative partners seemed to be especially important for "visual signals". By establishing gaze contact the sender ensured that the signal was seen and understood by the recipient. Moreover, the signal became more intense. After the signal was given, gaze contact in general decreased – apparently not being necessary any longer.

For "tactile signals" gaze contact did not play an important role, neither before, during or after the signal was given. The contact between the partners was established by touching. Visual factors were minor.

The preferred distance for communication, independent of signal category, was within body contact distance and 0.5 m. "Visual signals" with or without auditory information were also used when partners were located at distances of up to 5 m. Senders had no

possibility of sending “tactile signals” when recipients were farther away than 1 m and this was confirmed by the results. Analysis of age showed that infants and adults nearly exclusively used distances of up to 1 m, whereas juveniles and subadults communicated also at distances of more than 1 m.

4.5 Variability

The highest number of different signals as well as the highest number of signals per minute were performed by the subadults, but the differences between the age classes were not significant. Female baboons tended to use a smaller variety of signals and showed significantly less signals per minute as well as less different combinations than males.

Five signals were exclusively found in one animal each and therefore considered to be idiosyncratic.

Older baboons used significantly more agonistic signals than younger baboons that preferred affiliative signals for communication. Females tended to perform more friendly signals than males.

Liebal et al. (2004a) found that in a group of chimpanzees juveniles performed the largest number of gestures. Tomasello et al. (1997) reported an increase in the number of gestures used by young chimpanzees until the age of six and a decrease after that. 14% of the gestures were idiosyncratic (Tomasello et al., 1994) – almost the same result was found for the hamadryas baboons in the present study: approximately 16% idiosyncratic signals. But contrary to the chimpanzees, in the baboons these particular signals were seen only once or twice and therefore excluded from the analysis (considered anecdotal events).

In a chimpanzee group of 22 individuals, 50% of the investigated signals were shown by four animals or less (Tomasello & Call, 2007). In the present study, 13 out of 33 baboons in observation period 1 and 11 out of 14 focal animals in observation period 2 used 50% of the signal repertoire. Only six gestures out of 29 were registered in 50% or more of the chimpanzees while 14 signals out of 31 signals (including idiosyncratic signals) were found in 50% or more of the baboons. It has to be taken into consideration that all chimpanzees in the above study were no older than eight years (infants to subadults) whereas the focal baboons in the present study were recruited from all age classes. Compared to the chimpanzees in Tomasello’s study, the hamadryas baboons seemed to have less individual differences and to use a larger portion of the signal repertoire of the species.

The most frequently used gesture in the chimpanzees was “ground slap” observed in all individuals (Tomasello & Call, 2007). The corresponding signal s*tiff threat* occurred in approximately 92% of the hamadryas baboons.

In subadult bonobos Pika (2007a) found three gestures performed by all focal animals. One of these gestures was “touch”. All focal animals of the present baboon study used the similar signal *poking*.

Subadult gorillas (Pika, 2007b) showed eight gestures which were used by all individuals in the group.

Liebal (2007a) stated that the orangutans she observed had a median number of 14 gestures and that only two gestures of the repertoire were used by all individuals. Both results were true for the baboons of the present study. Moreover, like in the baboons, in the orangutans there was a increase in the number of gestures used from infants to juveniles/subadults and a decrease in adults. But male orangutans performed 10 different signals and females 13.5 – an opposite trend to that observed in the baboons.

In siamangs, Liebal (2007b) found four gestures used by all individuals but also four idiosyncratic signals. The median number of different gestures increased from infants to subadults and decreased slightly in the adults. Some gestures were only seen in adults. The baboons communicated with age specific signals as well.

Subadult and adult Barbary macaques used the highest number of different signals compared to the other age classes, with nearly 30 different signals (Hesler & Fischer, 2007).

Young primates need more signals for play and other affiliative contexts like nursing whereas adults perform more signals in agonistic contexts. Subadult animals lie somewhere in between – they still use play signals and already apply signals from agonistic contexts. This could explain why in some of the investigated species subadults have the widest variety of signals.

Old baboons may display fewer different signals because they have attained a certain place and status in the group as experienced and “retired” group members and in general may have less need for using signals than younger and more active group members.

4.6 Flexibility

4.6.1 Attentional state and response

The sender’s consideration of the recipient’s attentional state is a crucial element of the investigation of intentionality in primates.

In the hamadryas baboons of the present study there were differences between visual and tactile signals with regard to attentional state. Approximately 90% of all single

visual signals and approximately 80% of visual-visual combinations were performed when recipients were attentive. In addition, signals from other categories with a main visual component ("visual signal possibly making some noise" and "visual signal often combined with touching") showed a strong tendency for being used for attentive recipients only. On the other hand, visual attention is not necessary for receiving tactile signals. Here the sender did not distinguish between attentive and inattentive recipients.

It could be assumed that a sender "knows" that a visual signal demands the attention of the recipient, otherwise the signal could not be perceived. Possibly a sender first assesses the attentional state of the recipient and then decides between the use of a visual or a tactile signal but this aspect was not investigated in the present study.

The results of this study were similar to those found for other primate species. Call and Tomasello (2007) reported that 85% of visual gestures in chimpanzees were sent to attentive recipients. However, there was almost no difference regarding the recipient's attentional state when tactile signals were used. The authors did not find evidence that chimpanzees perform auditory gestures before using visual gestures in order to get the attention of inattentive recipients. Also Liebal et al. (2004a) found that for chimpanzees "visual gestures were used significantly more often if the recipient was attending compared to when it was not attending" (p. 391). The chimpanzees did not manipulate the attentional state of the recipient.

In a long term study of Tomasello et al. (1994, 1997), chimpanzees used visual signals to solicit play only when the recipient was able to perceive the signals. If the recipient was interacting with other chimpanzees the sender often used "poke at" as an attention getter. In the present study, the baboons also preferred *poking* when recipients were not attentive.

Also for bonobos and gorillas, Pika (2007a and b) found significant differences in visual and tactile gesture use. They performed visual signals when the recipient was attentive in approximately 70% (bonobos) and 89% (gorillas) of all cases.

Orangutans even performed visual gestures exclusively to attentive recipients (Liebal, 2007a). However, they also directed approximately 77% of their tactile gestures to an attentive recipient. Also siamangs (Liebal, 2007b) gave visual signals nearly exclusively to attentive recipients. Maybe arboreal and less gregarious species – living in a dense forest canopy and having larger distances between individuals – are more sensitive to the attentive state of other individuals.

Cartmill and Byrne (2007a) showed that orangutans, signalling a human companion to get food, paid attention to the comprehension of their desires. The apes adapted the use of their gestures to the reaction of the recipient. When the experimenter had given

them all of the desirable food, they stopped signalling. When they had received only part of the desired food, they continued with the same signals. When they received the wrong (undesirable) food, they changed their strategy and performed different gestures from what they had previously used. This showed a great flexibility in signal usage and suggested that the apes indeed pursued a specific goal with specific intention. The same authors also investigated the orangutans' gesture usage towards conspecifics (2007b). When a recipient did not react to the gestures, the signaller occasionally touched the partner and/or moved closer to them or also into its visual field. By doing this, the sender provided information about his intended goal and showed his awareness of the recipient's attentional state.

Tanner and Byrne (1996) described a significant variation in the visual attention of a gorilla: a highly visual attention group with silent limb and head gestures, a medium attention group with audible gestures and a low attention group with tactile-close gestures.

Tomasello and Zuberbühler (2002) wrote that "audience effects are very clear in the case of ape gestures, and there may be such effects for monkey gestures as well" (p. 296). They explained that "primate gestural communication shows more flexibility than primate vocal communication, perhaps because it concerns less evolutionary urgent activities than those indicated most often with vocalizations" (p. 296). The authors also stated that ape's gestural communication showed audience effects and flexibility in usage and that more research is needed in monkeys. Monkey cognition was investigated in the present study and the results suggest that also the observed hamadryas baboons showed audience effects and flexibility in signal usage.

In 13.5% of all single events the recipient replied with a signal and in 58.1% the recipient altered its behaviour. That means that about 72% of the signals caused a response. Liebal et al. (2006) reported that the median of response in orangutans was approximately 60%.

4.6.2 Context

Context was analysed for 22 of the 26 signals that the hamadryas baboons of the present study used. Ten of these were observed in more than one context. Five signals were used very flexibly: *poking* (five contexts), *presenting* (four contexts), *eyebrow raising*, *lowering back* and *lipsmacking* (three contexts each). It could be demonstrated that the baboons employed one single signal for multiple contexts. Furthermore, they communicated with different signals within the same context (e.g. 13 signals were performed for play).

Almost all young chimpanzees in a study by Tomasello et al. (1994) used some gestures for more than one context and for some contexts they used more than one signal. Pika (2007a) found that 50% of the bonobos' gestures were performed in more than one context and that in every context different gestures were used. Pika (2007b) also described that more than 72% of all gestures in subadult gorillas were observed in more than one context and that in every context many different gestures were used. Orangutans used 80% and siamangs used approximately 70% of their gestures in more than one context, and in approximately 78% (for orangutans) and 75% (for siamangs) of the contexts more than one signal was recorded (Liebal, 2007a and b).
Barbary macaques showed almost half of their signals in at least two contexts and in all contexts several signals were found (Hesler & Fischer, 2007). Macaques also "have several gestures that serve a similar function and … each gesture can be used in different contexts with different meanings" (Maestripieri, 1997, p. 213).

4.7 Conclusion

The observed elements of communication in a captive hamadryas baboon group met the criteria for intentional signals. The baboons showed a flexible relation between signal and goal as well as special sensitivity to the social context.
The present study supports the theory that not only apes but also some monkey species use their signals intentionally. As is the case for other cognitive skills, the differences between apes and monkeys are more quantitative than qualitative. This corresponds with the conclusion of Tomasello and Call (1997, p. 399): "Apes and monkeys do not differ significantly in how they recognize their physical and social worlds."

Further detailed studies of baboon intentional communication are needed, with comparisons of several groups to get data about inter-group variations, too.

5. SUMMARY

The goal of this dissertation was to investigate the visual and tactile communication of a group of captive hamadryas baboons (*Papio hamadryas hamadryas)* and the intentionality of the signals expressed by flexibility of signal use and audience effects.

26 different visual and tactile signals (and five idiosyncratic signals) were analysed. Some of them such as *eyebrow raising* and *relaxed open mouth* are very frequently observed in the Cercopithecinae.

Two signals, *poking* and *eyebrow raising*, were observed in all focal animals. Furthermore, many signals were used by a broad range of baboons across all age and sex classes (e.g. *lipsmacking* or *stiff threat*). Other signals seemed to be restricted to specific groups (e.g. *rolling on ground*, *jumping in the air* as well as *jumping on back* to animals up to subadults, and *displaying* to males).
Nearly half (44.4%) of all observed signals were purely visual signals.

No baboon showed all of the 26 different signals. On average, a focal animal with 14 used approximately half of the different signals (53.8%). The highest number (18 signals/69.2%) was registered in the subadult baboons. Males tended to perform more different signals than females.

On average, a focal animal showed 0.36 signals per minute. The age class of subadults performed the highest number of signals per minute. Males used more signals per minute than females. The highest individual signal frequency was found in the harem leader.

The frequencies (median for 14 focal animals, in times per hour) for particular signals were as follows: *eyebrow raising* 3.9, *poking* 2.7, *relaxed open mouth* 1.8, *presenting* 1.6, *stiff threat* 1.6, *enlisting* 0.9, *lipsmacking* 0.6, *threat mouth* 0.6, *chasing* 0.4, *lowering body* 0.4, *mounting* 0.4, *head shaking* 0.2 and *pulling on* 0.1.

19 signals were used in simultaneous combinations. The most frequently combined signal was *eyebrow raising.* 27 different combinations (and ten idiosyncratic combinations) were recorded (25 double and two triple), the most common was *eyebrow raising + stiff threat.* The most frequently combined signal types were “visual signal” and “visual signal possibly making some noise”. On average, a focal animal performed 1.65 combinations per hour. Females tended to use fewer combinations per hour than males.

There were more communicative events without gaze contact between sender and recipient than events with gaze contact.

The analysis of the distance between sender and recipient showed that over 80% of all observed communicative events took place when sender and recipient were positioned within less than half a meter from each other. Roughly 13% of events occurred when the individuals were positioned between 0.5 to 1 meter from each other.

“Visual signals” were given significantly more frequently when the recipient was in an attentive state than when in an inattentive state. This suggests that a “visual signal” demanded the attention of the recipient and that the sender when communicating took into account the recipient’s attentional state. The data further suggest that “visual signal possibly making some noise” and “visual signal often combined with touching” demanded the recipient’s attention as well, since were used more often towards an attentive recipient. There was, however, no preference for an attentive recipient when “tactile signals” were used. Therefore, it can be assumed that the attention of the recipient is not essential for perceiving tactile signals.

In general, in the majority of events, the recipients showed a reaction to the given signal. About three quarters of all analysed single signals elicited a response.

Ten signals were observed in more than one context, five signals in more than two contexts. *Poking* and *presenting* were used especially flexibly (five and four contexts). Moreover, the baboons used different signals for one context (e.g. for play).

It is important to note that the number of focal animals in each age and sex group was limited in the present study. The influence of individual differences hence cannot be ruled out. Moreover, some results reported throughout this study were merely tendencies. Nevertheless, the following conclusions can be drawn.

The captive hamadryas baboons in this study showed flexibility in signal usage as well as sensitivity to the attentional state of the recipient. Some signals were age- and/or sex-specific. Several signals were used in more than one context, and for every context there were several signals.

It can be stated that hamadryas baboons have many visual and tactile signals being used voluntarily and intentionally. They need these signals to manipulate group members and to achieve or maintain their place in the hierarchy.

Finally, these data suggest that not only apes but also monkeys are able to communicate intentionally.

ZUSAMMENFASSUNG

Diese Arbeit hatte zum Ziel, die visuelle und taktile Kommunikation einer zoolebenden Mantelpaviangruppe (*Papio hamadryas hamadryas*) zu untersuchen. Der Schwerpunkt lag dabei auf dem Grad der Intentionalität der Signale, welcher sich durch Flexibilität im Gebrauch der Signale und der Beachtung des Zustandes des Empfängers auszeichnet.

26 verschiedene visuelle und taktile Signale (und fünf idiosynkratische Signale) wurden analysiert. Einige von ihnen wie *eyebrow raising/Augenbrauen hochziehen* und *relaxed open mouth/entspannter offener Mund* sind generell sehr häufig in der Gruppe der Cercopithecinae.

Zwei Signale, *poking/leichtes Anstupsen* and *eyebrow raising/Augenbrauen hochziehen*, wurden bei allen Fokustieren gesehen. Es gab eine große Anzahl von Signalen mit einem breiten Spektrum an Nutzern durch alle Alters- und Geschlechtsklassen hindurch (z. B. *lipsmacking/Lippenschmatzen* und *stiff threat/Bodenschlag*). Andere schienen auf spezielle Gruppen beschränkt zu sein (z. B. *rolling on ground/Rollen auf dem Boden*, *jumping in the air/in die Luft springen* oder *jumping on back/über ein Tier springen* auf Tiere bis zum subadulten Alter; *displaying/imponieren* auf männliche Paviane).
Fast die Hälfte (44,4 %) aller beobachteten Signale waren reine visuelle Signale.

Kein Pavian zeigte alle der 26 unterschiedlichen Signale. Im Mittel benutzte ein Fokustier mit 14 davon etwa die Hälfte aller unterschiedlichen Signale (53,8 %). Die höchste Anzahl (18 Signale bzw. 69,2 %) wurde in den subadulten Pavianen registriert. Tendenziell setzten Männchen mehr unterschiedliche Signale ein als Weibchen.

Im Mittel zeigte ein Fokustier 0,36 Signale in der Minute. Die Altersgruppe der Subadulten wies die höchste Anzahl von Signalen pro Minute auf. Männchen verwendeten mehr Signale pro Minute als Weibchen. Die höchste individuelle Signalfrequenz wurde beim dominanten Männchen (Haremsführer) festgestellt.

Die Frequenzen für einige der Signale (Anzahl pro Stunde, Median über die 14 Fokustiere) lauteten wie folgt: *eyebrow raising/Augenbrauen hochziehen* 3,9; *enlisting/Hilfe suchen* 0,9; *lowering body/Körper absenken* 0,4; *relaxed open mouth/entspannter offener Mund* 1,8; *head shaking/Kopf schütteln* 0,2; *threat mouth/Drohmund* 0,6; *chasing/verfolgen* 0,4; *stiff threat/Bodenschlag* 1,6; *lipsmacking/Lippenschmatzen* 0,6; *presenting/Präsentieren* 1,6; *poking/leichtes Anstupsen* 2,7; *mounting/aufreiten* 0,4; und *pulling on/ziehen an* 0,1.

19 Signale wurden in gleichzeitigen Kombinationen verwendet, das am häufigsten kombinierte Signal war *eyebrow raising/Augenbrauen hochziehen.* 27 verschiedene Kombinationen (sowie zehn idiosynkratische Kombinationen) wurden registriert (25 doppelte und zwei dreifache), am häufigsten kam *eyebrow raising + stiff threat/Augenbrauen hochziehen + Bodenschlag* vor. Sehr gebräuchlich war es, ein „visuelles Signal" mit einem „visuellen Signal, welches möglicherweise ein Geräusch erzeugt" zu kombinieren. Ein Fokustier verwendete im Durchschnitt 1,65 Kombinationen in der Stunde. Es war der Trend erkennbar, dass Weibchen weniger Kombinationen pro Stunde aufwiesen als Männchen.

Es gab mehr kommunikative Ereignisse ohne Blickkontakt zwischen Sender und Empfänger als mit.

Die Analyse des Abstandes zwischen den Partnern ergab, dass über 80 % der registrierten Kommunikation stattfand, wenn Sender und Empfänger weniger als einen halben Meter voneinander entfernt waren. Rund 13 % ereigneten sich in einem Abstand von einem halben und einem Meter.

„Visuelle Signale" wurden signifikant häufiger gegeben, wenn sich der Empfänger in einem aufmerksamen Zustand befand als in einem unaufmerksamen. Das bedeutet, dass ein „visuelles Signal" anscheinend die Aufmerksamkeit des Empfängers erfordert und dass der Sender den Aufmerksamkeitsstatus des Empfängers berücksichtigt, wenn er kommunizieren will. Die Daten zeigen weiterhin, dass ein „visuelles Signal, welches möglicherweise ein Geräusch erzeugt" und ein „visuelles Signal, welches oft mit Berührung verbunden ist" ebenfalls die Aufmerksamkeit des Empfängers erfordern und häufiger verwendet werden, wenn der Empfänger aufmerksam ist. Dagegen zeigte sich kein Unterschied für „taktile Signale", so dass vermutet wird, dass die Aufmerksamkeit des Empfängers für taktile Signale nicht notwendig ist.

Generell gab es mehr Ereignisse, in denen der Empfänger eine Reaktion auf ein gegebenes Signal zeigte, als ohne jegliche Reaktion. Über drei Viertel aller analysierten Einzelsignale lösten eine Antwort aus.

Zehn Signale wurden in mehr als einem Kontext registriert, fünf Signale wurden in mehr als zwei Kontexten verwendet. Als besonders flexibel erwiesen sich *poking/leichtes Anstupsen* und *presenting/präsentieren.* Die Paviane nutzen auch verschiedene Signale für einen Kontext (z. B. für Spiel).

Es sollte berücksichtigt werden, dass in der vorliegenden Studie nur eine kleine Anzahl von Fokustieren pro Altersgruppe beobachtet wurde und daher ein Einfluss durch individuelle Unterschiede nicht ausgeschlossen werden kann. Zudem stellen einige Ergebnisse nur Trends dar. Dennoch können die folgenden Aussagen getroffen werden.

Die beobachtete Mantelpaviangruppe zeigte sowohl Flexibilität im Signalgebrauch als auch hinsichtlich der Beachtung des Aufmerksamkeitsstatus' des Empfängers. Einige Signale wurden nur bei jungen Pavianen registriert und andere nur bei älteren, und einige waren typisch für ein Geschlecht. Eine Anzahl von Signalen wurden für mehr als einen Kontext verwendet und für jeden Kontext wurden mehrere verschiedene Signale eingesetzt (die Kontextanalyse war in dieser Studie allerdings sehr grob).

Es kann festgestellt werden, dass Mantelpaviane eine große Anzahl visueller und taktiler Signale freiwillig und absichtlich verwenden. Sie benötigen diese, um Gruppenmitglieder zu manipulieren und ihren Platz in der Hierarchie zu erobern bzw. zu festigen. Die Daten deuten darauf hin, dass nicht nur Menschenaffen sondern auch Tieraffen zur intentionalen Kommunikation fähig sind.

REFERENCES:

Abegglen, J. J. (1976). *On socialization in hamadryas baboons*. Dissertation, Universität Zürich.

Barrett, L. (2000). *Baboons: Survivors of the African continent*. DK, London.

Beck, B. B. (1972). Tool use in captive hamadryas baboons. *Primates*, *13*, 276-296.

Beck, B. B. (1973). Cooperative tool use by captive Hamadryas baboons. *Science*, *182*, 594-597.

Bolwig, N. (1978). Communicative signals and social behaviour of some African monkeys: a comparative study. *Primates*, *19(1)*, 61-99.

Call, J. & Tomasello, M. (2007). The gestural repertoire of chimpanzees (*Pan troglodytes*). In J. Call & M. Tomasello (Eds.), *The gestural communication of apes and monkeys*. Lawrence Erlbaum Associates, Inc., New Yersey, 17-39.

Cartmill, E. A. & Byrne, R. W. (2007a). Orangutans modify their gestural signaling according to their audience's comprehension. *Current Biology*, *17 (15)*, 1345-1348.

Cartmill, E. A. & Byrne, R. W. (2007b). What failed communication attempts tell us about the mind of the signaler; gestural communication in captive Bornean orangutans (*Pongo pygmaeus*). *American Journal of Physical Anthropology*, *Suppl. 42*, 73-74.

Cheney, D. L., Seyfarth, R. M. & Silk, J. B. (1995). The role of grunts in reconciling opponents and faciliating interactions among adult female baboons. *Animal Behaviour*, *50*, 249-257.

Cheney, D. L., Seyfarth, R. M. & Palombit, R. A. (1996). The function and mechanisms underlying baboon contact barks. *Animal Behaviour*, *52*, 507-518.

Cheney, D. L. & Seyfarth, R. M. (1997). Reconciliatory grunts by dominant female baboons influence victims' behaviour. *Animal Behaviour*, *54*, 409-418.

Cheney, D. L. & Seyfarth, R.M. (2007). *Baboon metaphysics: the evolution of a social mind.* The University of Chicago Press, Chicago.

Chevalier-Skolnikoff, S. (1974). *The ontogeny of communication in the stumptail macaque* (*Macaca arctoides*). Contributions to Primatology Vol. 2. Karger.

Coelho, A. M. & Bramblett, C. A. (1989). Behaviour of the genus Papio: ethogram, taxonomy, methods, and comparative measures. *Perspectives in Primate Biology*, *3*, 117-140.

Colmenares, F. (1990). Greeting behaviour in male baboons. I. Communication, reciprocity and symmetry. *Behaviour*, *113(1-2)*, 81-116.

Colmenares, F. (1991a). Greeting, aggression and coalitions between male baboons: Demographic corelates. *Primates*, *32(4)*, 453-463.

Colmenares, F. (1991b). Greeting behavior between male baboons: Estrous females, rivalry and negotiation. *Animal Behaviour*, *41(1)*, 49-60.

Cowlishaw, G. (1997). Alarm calling and implications for risk perception in a desert baboon population. *Ethology*, *103*, 384-394.

De Marco, A. & Visalberghi, E. (2007). Facial displays in young tufted capuchin monkeys (*Cebus apella*): Appearance, meaning, context and target. *Folia Primatologica*, *78*, 118-137.

Dunbar, R. & Rowell, T.E. (2001). Guenons, macaques, and baboons. In D. MacDonald (Ed.), *The encyclopedia of mammals. Volume II. Primates and large herbivores.* Facts On File, Inc., New York, 356-375.

Easley, S. P. & Coelho, A. M. J. (1991). Is lipsmacking an indicator of social status in baboons? *Folia Primatologica*, *56(4)*, 190-201.

Estes, R. D. (1991). Old World Monkeys – Communication in the family Cercopithecidae. In R. D. Estes, *The behavior guide to African mammals.* The University of California Press. Berkely, Los Angeles, London.

Gattermann, R. (1993). *Wörterbücher der Biologie*. *Verhaltensbiologie*. Gustav Fischer Verlag Jena.

Gattermann, R. (2006). *Wörterbuch zur Verhaltensbiologie der Tiere und des Menschen*. Elsevier Spektrum Akademischer Verlag München.

Gautier, J.-P. & Gautier, A. (1999), Communication in old world monkeys. In T. A. Sebeok, *How animals communicate, Part II*. Indiana University Press, Bloomington & London, 890-964.

Genty, E. & Byrne, R. W. (2010): Why do gorillas make sequences of gestures? *Animal Cognition*, *13(2)*, 287-301.

Gockel, J. (1993). *Soziale Beziehungen und Strategien juveniler Mantelpavianmännchen* (*Papio hamadryas hamadryas*) *in Gefangenschaftshaltung.* Zoologisches Institut, Erlangen, Friedrich-Alexander-Universität.

Goodall, J. (1991). *Wilde Schimpansen – Verhaltensforschung am Gombe-Strom*. Rowohlt Taschenbuch Verlag.

Hall, K. R. L. & DeVore, I. (1965). Baboon social behavior. In I. DeVore, *Primate Behavior. Field Studies of Monkeys and Apes.* Holt, Rinehart and Winston.

Hesler, N. & Fischer, J. (2007). Gestural communication in Barbary macaques (*Macaca sylvanus*): An overview. In J. Call & M. Tomasello (Eds.), *The gestural communication of apes and monkeys*. Lawrence Erlbaum Associates, Inc., New Yersey, 159-195.

Hinde, R. A. & Rowell, T. E. (1962). Communication by postures and facial expressions in the rhesus monkey (*Macaca mulatta*). *Proc. Zool. Soc. Lond.*, *138*, 1-21.

Jolly, A. (1975). *Kommunikation*. *Die Entwicklung des Primatenverhaltens*. Stuttgart, Gustav Fischer Verlag.

Kummer, H. (1957). *Soziales Verhalten einer Mantelpaviangruppe*. Bern.

Kummer, H. & Kurt, F. (1965). A comparison of social behavior in captive and wild hamadryas baboons. In H. Vagtborg, *The baboon in medical research*. Austin, University of Texas, 64-80.

Kummer, H. (1967). Tripartite relations in hamadryas baboons. In S. A. Altmann, *Social communication among primates.* Chicago, The University of Chicago Press, 63-71.

Kummer, H. (1968). *Social organization of Hamadryas Baboons*. Karger, Basel.

Kummer, H., Götz, W. & Angst, W. (1974). Triadic differentiation: An inhibitory process protecting pair bonds in baboons. *Behaviour*, *49*, 62-87.

Kummer, H. (1975). Eine Einführung in Primatengesellschaften. Eine Mantelpavian-Gesellschaft. In H. Kummer, *Sozialverhalten der Primaten*. Springer, Berlin, 11-33.

Kummer, H. (1982). Social knowledge in free-ranging primates. In D. R. Griffin, *Animal mind – human mind*. Berlin, Springer, 113-130.

Kummer, H. (1984). From laboratory to desert and back: A social system of hamadryas baboons. *Animal Behaviour*, *32*, 65-971.

Liebal, K. (2001). *Soziale Kommunikation in Siamang - Familien in Zoologischen Gärten*. Fakultät für Biowissenschaften, Pharmazie und Psychologie. Leipzig.

Liebal, K., Call, J. & Tomasello, M. (2004a). Use of gesture sequences in chimpanzees. *American Journal of Primatology*, *64*, 377-396.

Liebal, K., Pika, S. & Tomasello, M. (2004b). Social communication in siamangs (*Symphalangus syndactylus*): use of gestures and facial expressions. *Primates*, *45*, 41-57.

Liebal, K. (2005). *Social communication in great apes.* Dissertation, Fakultät für Biowissenschaften, Pharmazie und Psychologie, Universität Leipzig.

Liebal, K., Pika, S. & Tomasello, M. (2006). Gestural communication of orangutans (*Pongo pygmaeus*). *Gesture*, *6 (1)*, 1-38.

Liebal, K. (2007a). Gestures in Orangutans (*Pongo pygmaeus*). In J. Call & M. Tomasello (Eds.), *The gestural communication of apes and monkeys*. Lawrence Erlbaum Associates, Inc., New Yersey. 69-98.

Liebal, K. (2007b). Gestures in Siamangs (*Symphalangus syndactylus*). In J. Call & M. Tomasello (Eds.), *The gestural communication of apes and monkeys*. Lawrence Erlbaum Associates, Inc., New Yersey. 131-158.

Maestripieri, D. (1996a). Social communication among captive stump-tailed macaques (*Macaca arctoides*). *International Journal of Primatology*, *17(5)*, 785-802.

Maestripieri, D. (1996b). Gestural communication and its cognitive implications in pigtail macaques (*Macaca nemestrina*). *Behaviour*, *133*, 997-1022.

Maestripieri, D. & Call, J. (1996). Mother-infant communication in Primates. *Advances in the Study of Behaviour*, *25*, 613-642.

Maestripieri, D. & Wallen, K. (1997). Affiliative and submissive communication in rhesus macaques. *Primates*, *38(2)*, 127-138.

Maestripieri, D. (1997). Gestural Communication in macaques: usage and meaning of nonvocal signals. *Evolution of Communication*,*1(2)*, 193-222.

Maestripieri, D. (1999). Primate social organization, gestural repertoire size, and communication dynamics: a comparative study of macaques. In B. J. King. (Ed.), *The origin of language: What nonhuman primates can tell us*. Santa Fe, School of American Research, 55-77.

Martin, P. & Bateson, P. (1993). *Measuring Behaviour*. Cambridge University Press.

Meder, A. (1993). *Gorillas. Ökologie und Verhalten*. Springer-Verlag Berlin Heidelberg.

Mehlmann, P. T. (1996). Branch shaking and related displays in wild Barbary macaques. In J. E. Fa and D. G. Lindburg, *Evolution and ecology of macaque societies*. Cambridge University Press, 503- 526.

Owens, N. W. (1975). Social play behaviour in free-living baboons, *Papio anubis*. *Animal Behaviour*, *23*, 387-408.

Peláez, F. (1982). Greeting movements among adult males in colony of baboons, *Papio hamadryas*, *P. cynocephalus* and their hybrids. *Primates*, *22*, 233-244.

Pellat, A. (1980). Facial expressions of *Papio ursinus* and some other higher primates. *South African Journal of Science*, *76*, 413-418.

Pellis, S. M. & Pellis, V. C. (1997). Targets, tactics, and the open mouth face during play fighting in three species of primates. *Aggressive Behavior*, *23*, 41-57.

Pika, S., Liebal, K. & Tomasello, M. (2003). Gestural communication in young gorillas (*Gorilla gorilla*): gestural repertoire, learning, and use. *American Journal of Primatology*, *60*, 95-111.

Pika, S. (2003). *The gestural communication of subadult gorillas (Gorilla gorilla) and subadult bonobos (Pan paniscus) in captivity.* Dissertation, Fachbereich Biologie, Universität Münster.

Pika, S., Liebal K. & Tomasello, M. (2005). Gestural Communication in Subadult Bonobos (*Pan paniscus*): Repertoire and Use. *American Journal of Primatology*, *65*, 39-61.

Pika, S. (2007a). Gestures in subadult bonobos (*Pan paniscus*). In J. Call & M. Tomasello (Eds.), *The gestural communication of apes and monkeys*. Lawrence Erlbaum Associates, Inc., New Yersey, 41-67.

Pika, S. (2007b). Gestures in subadult gorillas (*Gorilla gorilla*). In J. Call & M. Tomasello (Eds.), *The gestural communication of apes and monkeys*. Lawrence Erlbaum Associates, Inc., New Yersey, 99-130.

Pollick, A. S. & de Waal, F. B. M. (2007). Ape gestures and language evolution. *Proceedings of the National Academy of Science of the United States of America*, *104(19)*, 8184-8189.

Ransom, T. W. (1981). *Beach troop of the Gombe*. East Brunswick, London, Toronto, Associated University Presses, Inc.

Redican, W. K. (1975). Facial expressions in nonhuman primates. In L. A. Rosenblum, *Primate behavior: development in field and laboratory research*. New York, Academic Press,103-194.

Rendall, D., Seyfarth, R. M., Cheney, D. L. & Owren, M. J. (1999). The meaning and function of grunt variants in baboons. *Animal Behaviour*, *57*, 583-592.

Rogers, L. J. & Kaplan, G. (2000). *Songs, roars, and rituals: communication in birds, mammals, and other animals.* Harvard University Press, Cambridge, Mass.

Rowe, N. (1996). *The pictorial guide to the living primates.* Pogonias Press, New York.

Rowell, T. E. (1966). Hierarchy in the organization of a captive baboon group. *Animal Behaviour*, *14*, 430-443.

Scheumann, M. (2001). *Grooming and conflict behaviour of a group of hamadryas baboon*. Zoologie, Uni Leipzig.

Sigg, H. & Stolba, A. (1981). Home range and daily march in a hamadryas baboon troop. *Folia Primatologica*, *36*, 40-75.

Sigg, H., Stolba, E., Abegglen, J. J. & Dasser, V. (1982). Life history of hamadryas baboons: physical development, infant mortality, reproductive parameters, and family relationships. *Primates*, *23*, 473-487.

Smith, W. J., (1977). *The behavior of communicating: an ethological approach*. Cambridge, MA, Harvard University Press.

Smith, L. W. (2007). Gestural communication in captive gorillas (*Gorilla gorilla*) at the Bronx zoo, New York. *American Journal of Physical Anthropology*, *Suppl. 44*, 221.

Smuts, B. B. (1985). *Sex and Friendship in Baboons*. New York, Aldine.

Stammbach, E. (1987). Desert, forest and montane baboons: multilevel-societies. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham & T. T. Struhsaker (Eds.), *Primates societies*. Chicago Press, 112-120.

Stein, D. M. (1984). *The sociobiology of infant and adult male baboons*. Norwood, Ablex Publishing Corporation.

Strum, S. C. (1987). *Almost human*. New York, Random House.

Swedell, L. (2006). *Strategies of Sex and Survival in Hamadryas Baboons. Through a Female Lens.* Pearson Education, Inc., New Jersey.

Symons, D. (1974). Aggressive play and communication in rhesus monkeys (*Macaca mulatta*). *American Zoology*, *14*, 317-322.

Tanner, J. E. & Byrne, R. W. (1996). Representation of action through iconic gesture in a captive lowland gorilla. *Current Anthropology*, *37(1)*, 162-173.

Tomasello, M., George, B. L., Kruger, A. C., Farrar, M. J. & Evans, A (1985). The development of gestural communication in young chimpanzees. *Journal of Human Evolution*, *14*, 175-186.

Tomasello, M., Gust, D. & Frost, G. T. (1989). A longitudinal investigation of gestural communication in young chimpanzees. *Primates*, *30(1)*, 35-50.

Tomasello, M., Call, J., Nagell, K., Olguin, R. & Carpenter, M. (1994). The learning and use of gestural signals by young chimpanzees: a trans-generational study. *Primates*, *35(2)*, 137-154.

Tomasello, M., Call, J., Warren, J., Frost, G. T., Carpenter, M. & Nagell, K. (1997). The ontogeny of chimpanzee gestural signals: a comparison across groups and generations. *Evolution of Communication*, *1(2)*, 223-253.

Tomasello, M. & Call, J. (1997). *Primate cognition*. New York, Oxford, Oxford University Press.

Tomasello, M. & Zuberbühler, K. (2002). Primate vocal and gestural communication. In M. Bekoff, C. Allen & G. M. Burghardt, *The cognitive animal: empirical and theoretical perspectives on animal cognition*. Cambridge, MA, MIT Press, 293-299.

Tomasello, M. & Call, J. (2007). Introduction: Intentional communication in nonhuman primates. In J. Call & M. Tomasello (Eds.), *The gestural communication of apes and monkeys*. Lawrence Erlbaum Associates, Inc., New Yersey, 1-15.

Van Hooff, J. A. R. A. M. (1967). The facial displays of the Catarrhine monkeys and apes. In D. Morris, *Primate Ethology*. London, Weidenfield, 7-68.

Van Hooff, J.A.R.A.M. (1988). Meerkatzenartige. In B. Grzimek (Ed.), *Grzimeks Enzyklopädie Säugetiere. Band 2*. Kindler Verlag GmbH, München, 208-259.

Von Helversen, O. & Scherer, K. R. (1988): Nonverbale Kommunikation. In K. Immelmann et al. (Eds.), *Psychobiologie. Grundlagen des Verhaltens*. Gustav Fischer Verlag/Psychologie Verlags Union. 609-646.

Weber, I. (1973). Tactile communication among free-ranging langurs. *American Journal of Physical Anthropology*, *38*, 481-486.

Wolfle, D.L. & Wolfle, H.M. (1939). The development of cooperative behavior in monkeys and young children. *Journal of Genetic Psychology*, *55*, 137-175.

Zahavi, A. (1997): *The handicap principle: A missing piece of Darwin's puzzle*. New York, Oxford University Press.

Zeller, A. (1996). The inter-play of kinship organisation and facial communication in the macaques. In J. E. Fa & D. G. Lindburg, *Evolution and ecology of macaque societies.* Cambridge University Press, 527-550.

Personal communication by:

Barrett, L. (2002)

Zaragoza, F. (1999)

Zinner, D. (2000)

Appendix 1

Table A1
Members of the baboon group from March 1999 until October 2000
OP1 means the first observation period from March to September 1999, OP2 the second period from May to October 2000. Focus animals of the second observation period are written in red.
OMU means one-male-unit, the capitals code for the leaders Gunter (G) and Kuno (K).

NAME	SEX	BORN	PARENTS	LOSS	TAT-TOO	AGE CLASS		FEC.	OMU
						OP1	OP2		
Eva	f	23.07.74	Alfons/260	08.06.00 †	11	SEN	SEN		G
Karin	f	09.11.75	Alfons/261		03	SEN	SEN		G
Ina	f	25.10.79	Karel/Karin		19	AD	SEN		**G**
Gesine	f	25.01.86	Karel/Eva		13	AD	AD	fertile	**K**
Claudia	f	01.01.89	Karel/Karin		12	AD	AD		**G**
Brigitte	f	09.07.90	Karel/262		17	AD	AD		K
Gerda	f	10.09.90	Karel/Gesine		25	AD	AD	fertile	G
Anna	f	12.11.90	Karel/266		24	AD	AD	fertile	G
Steffi	f	26.02.91	Karel/Karin		23	AD	AD	fertile	K
Kuno	m	17.02.92	Karel/Karin		01	SAD	AD		
Gunther	m	06.03.92	Karel/Gesine		07	SAD	AD		
Edith	f	09.09.92	Karel/Eva		10	AD	AD		G
Iris	f	06.01.93	Karel/262		06	AD	AD	fertile	**G**
Paula	f	14.05.93	Karel/Gesine		09	AD	AD		?
Karlson	m	23.02.94	Karel/Karin		15	SAD	SAD		
Elke	f	19.12.94	Karel/Eva		20	SAD	SAD		**G**
Bernd	m	15.01.95	Karel/Brigitte		16	SAD	SAD		
Kevin	m	13.08.95	Karel/Karin		04	JUV	SAD		
Gerd	m	05.11.95	Karel/Gerda		30	JUV	SAD		
Erwin	m	15.05.96	Karel/Eva		28	JUV	SAD		
Caroline	f	28.08.96	Gunter/Claudia		32	JUV	SAD	fertile	
Selma	f	06.09.96	Kuno/Steffi		29	JUV	SAD		
Grit	f	05.12.96	Kuno/Gesine		33	JUV	JUV	fertile	
Gretel	f	08.04.97	Gunter/Gerda		27	JUV	JUV		
Claire	f	23.11.97	Gunter/Claudia		26	JUV	JUV		
Steven	m	20.12.97	Kuno/Steffi	18.01.00	31	INF2			
Gina	f	01.02.98	Kuno/Gesine		34	INF2	JUV		
Bert	m	14.04.98	Kuno/Brigitte		35	INF2	JUV		
Gundel	f	16.08.98	Gunter/Gerda		2	INF2	JUV		
Elias	m	24.09.98	Gunter/Eva		5	INF2	JUV		
Igor	m	10.10.98	Gunter/Iris		8	INF2	JUV		
Antje	f	26.10.98	Gunter/Anna		14	INF2	JUV		
Cora	f	08.12.98	Gunter/Claudia	23.04.99 †		INF1			
Gabi	f	09.03.99	Kuno/Gesine		36	INF1	INF2		
Bea	f	30.08.99	Kuno/Brigitte		22	INF1	INF2		
Ayleen	f	24.12.99	Gunter/Anna				INF2		
Gela	f	05.02.00	Kuno/Gesine	25.06.00 †			INF1		
Irina	f	21.03.00	Gunter/Iris				INF1		

Appendix 2

Table A2
Usage of all investigated signals by every baboon

ANIMAL	*eyebrow raising*	*enlisting*	*chasing*	*lowering body*	*lowering back*	*relaxed o. m.*	*rolling on gr.*	*jumping in the air*	*hand/headstand*	*pumping*	*stiff threat*	*displaying*	*lipsmacking*	*presenting*	*greeting*	*poking*	*mounting*	*puling on*	*penis grab*	*AGE CLASS*
Eva													x	x						SEN
Karin	x			x							x		x	x						SEN
Ina	x	x	x	x							x		x	x	x	x	x			AD
Gesine	x		x	x	x	x							x	x	x	x				AD
Claudia	x	x	x	x		x					x	x	x	x	x	x	x	x		AD
Brigitte	x	x	x		x	x					x		x	x		x	x			AD
Gerda	x	x	x	x		x					x		x	x	x	x				AD
Anna	x	x	x	x		x					x		x	x	x	x	x			AD
Steffi	x	x		x									x	x		x	x			AD
Edith	x	x	x	x		x					x		x	x	x	x	x			AD
Iris	x			x		x					x		x	x	x	x	x			AD
Paula	x					x							x	x						AD
Kuno	x		x			x				x	x	x	x	x	x	x	x		x	SAD
Gunther	x		x			x				x		x	x		x	x	x			SAD
Karlson						x				x			x	x	x	x	x			SAD
Elke	x	x		x	x	x	x				x		x	x	x	x	x			SAD
Bernd	x		x		x	x					x		x	x	x	x	x		x	SAD
Kevin	x			x		x				x	x			x	x	x	x	x		JUV
Gerd	x	x				x	x				x		x	x		x	x			JUV
Erwin	x	x			x	x	x				x	x	x	x	x	x	x			JUV
Caroline	x	x	x	x		x	x				x			x		x	x	x		JUV
Selma	x	x		x		x		x			x		x	x						JUV
Grit	x	x	x	x		x	x	x			x			x	x	x	x	x		JUV
Gretel	x					x	x				x			x		x	x	x		JUV
Claire		x				x	x		x					x		x				JUV
Steven	x					x	x		x	x				x		x	x	x		INF2
Gina	x					x	x				x			x		x		x		INF2
Bert	x		x			x		x						x		x	x			INF2
Gundel	x			x		x	x							x		x	x	x		INF2
Elias						x					x					x	x			INF2
Igor						x			x	x						x	x	x		INF2
Antje	x					x	x							x		x		x		INF2
Gabi						x										x		x		INF1

Appendix 3

Table A3
Total numbers of all signals shown by the focal animals during their observational times (S3)
The numbers for enlisting *were cut in half because the focal animal did this signal to two recipients.*

signals	**Ina**	**Gesine**	**Claudia**	**Kuno**	**Iris**	**Elke**	**Bernd**	**Erwin**	**Grit**	**Claire**	**Gundel**	**Igor**	**Gabi**	**Irina**	
ER	32	54	63	79	20	10	24	24	13	21	16	13	15	2	386
EN	1	3	15	9	2	3	3	10	1	6	8	6	6	0	73
LBo	3	0	5	0	0	2	0	2	6	2	4	0	1	2	27
LBa	0	15	1	0	15	0	1	1	0	0	1	0	1	0	35
RM	0	6	15	2	6	4	5	9	20	10	12	17	29	12	147
HS	5	0	0	1	0	0	0	1	0	0	0	0	0	0	7
RG	0	0	0	0	0	0	0	3	0	3	4	10	2	1	23
HH	0	0	0	0	0	0	0	1	0	8	1	3	4	7	24
TM	3	0	4	10	1	2	16	9	4	3	0	3	0	0	55
HB	0	3	0	0	0	0	0	0	0	0	0	0	0	0	3
YW	0	0	1	9	0	0	14	7	0	0	0	0	0	0	31
HT	0	0	0	0	0	0	2	2	0	0	0	0	0	0	4
SP	0	0	0	0	0	0	0	0	0	2	0	0	1	0	3
CH	4	1	5	7	1	2	4	4	1	0	2	4	0	0	35
JA	0	0	0	0	0	0	0	0	0	5	2	6	0	2	15
PU	0	0	0	12	0	0	44	3	0	2	0	3	0	0	64
ST	4	7	56	126	9	11	41	32	10	2	2	0	1	1	302
DP	0	0	0	1	0	0	1	2	0	0	0	0	0	0	4
LS	6	2	6	9	3	5	7	12	2	0	1	3	0	2	58
PR	5	5	15	0	7	21	6	13	30	3	14	9	10	5	143
GR	1	1	1	3	0	0	0	4	1	0	0	0	0	0	11
PK	6	11	7	3	8	11	10	25	17	31	29	31	49	59	297
MG	0	0	5	3	1	5	1	2	2	3	4	4	2	1	33
PO	0	0	0	0	1	0	0	2	4	0	3	1	4	2	17
PG	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
JB	0	0	0	0	0	0	0	0	0	0	2	0	1	0	3
sum	70	108	199	274	74	76	179	169	111	101	105	113	126	96	1801
per minute	**0.23**	**0.35**	**0.67**	**0.88**	**0.24**	**0.25**	**0.57**	**0.54**	**0.36**	**0.32**	**0.38**	**0.37**	**0.4**	**0.32**	**0.36**

Appendix 4

Table A4
Times per hour for all signals shown by the focal animals during their observational times (S3)

signals	Ina	Gesine	Claudia	Kuno	Iris	Elke	Bernd	Erwin	Grit	Claire	Gundel	Igor	Gabi	Irina
ER	6.2	10.8	12.2	15.3	3.9	1.9	4.7	4.7	2.8	4.0	3.1	2.5	2.9	0.4
EN	0.2	0.6	3.0	1.7	0.4	0.6	0.6	1.9	0.2	1.1	1.7	1.2	1.2	0.0
LBo	0.6	0.0	1.0	0.0	0.0	0.4	0.0	0.4	1.2	0.4	0.9	0.0	0.2	0.4
LBa	0.0	2.9	0.2	0.0	3.0	0.0	0.2	0.2	0.0	0.0	0.2	0.0	0.2	0.0
RM	0.0	1.2	3.0	0.4	1.2	0.8	1.0	1.7	3.9	1.9	2.6	3.3	5.6	2.4
HS	1.0	0.0	0.0	0.2	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0
RG	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.6	0.0	0.6	0.8	2.0	0.4	0.2
HH	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	1.5	0.2	0.6	0.8	1.4
TM	0.6	0.0	0.8	1.9	0.2	0.4	3.1	1.7	0.8	0.6	0.0	0.6	0.0	0.0
HB	0.0	0.6	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
YW	0.0	0.0	0.2	1.7	0.0	0.0	2.7	1.4	0.0	0.0	0.0	0.0	0.0	0.0
HT	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.4	0.0	0.0	0.0	0.0	0.0	0.0
SP	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.2	0.0
CH	0.8	0.2	1.0	1.4	0.2	0.4	0.8	0.8	0.2	0.0	0.4	0.8	0.0	0.0
JA	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.0	0.4	1.2	0.0	0.4
PU	0.0	0.0	0.0	2.3	0.0	0.0	0.0	0.6	0.0	0.4	0.0	0.6	0.0	0.0
ST	0.8	1.4	11.2	24.4	1.8	2.1	7.8	6.2	1.9	0.4	0.4	0.0	0.2	0.2
DP	0.0	0.0	0.0	0.2	0.0	0.0	0.2	0.4	0.0	0.0	0.0	0.0	0.0	0.0
LS	1.2	0.4	1.2	1.7	0.6	1.0	1.3	2.3	0.4	0.0	0.2	0.6	0.0	0.4
PR	1.0	1.0	3.0	0.0	1.4	4.1	1.1	2.5	5.8	0.6	3.0	1.8	1.9	1.0
GR	0.2	0.2	0.2	0.6	0.0	0.0	0.0	0.8	0.2	0.0	0.0	0.0	0.0	0.0
PK	1.2	2.1	1.4	0.6	1.6	2.1	1.9	4.8	3.3	5.9	6.2	6.1	9.4	11.8
MG	0.0	0.0	1.0	0.6	1.0	0.2	0.2	0.4	0.4	0.6	0.9	0.8	0.4	0.2
PO	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.4	0.8	0.6	0.2	0.8	0.4
PG	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0	0.0

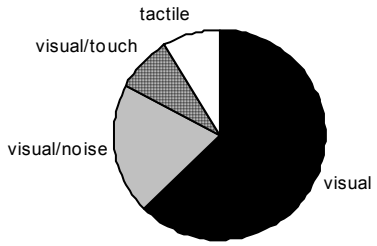
Appendix 5

Quantitative communication ethogram of the focal animals (Source 3)

Here the total numbers of all signals are summarised an animal had shown during its observational time, and displayed as percentages of the communication ethogram.

Senescent animal (Ina)

The oldest focal animal used 45.7% *eyebrow raising*, at each case 8.6% *lipsmacking* and *poking*, at each case 7.1% *headshaking* and *presenting*, at each case 5.7% *chasing* and *stiff threat*, 4.4% *threat mouth*, 4.3% *lowering body* as well as at each case 1.4% *enlisting* and *greeting.*

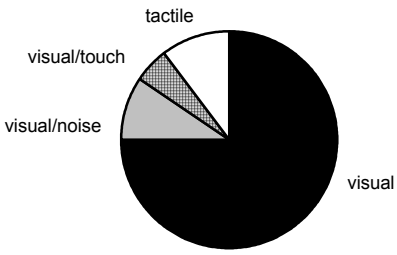


For the signal categories the following values arisen: 62.9% “visual”, 20.0% “visual possibly making some noise”, 8.6% “visual often combined with touching” and 8.6% “tactile”.

Adult animals

Gesine:

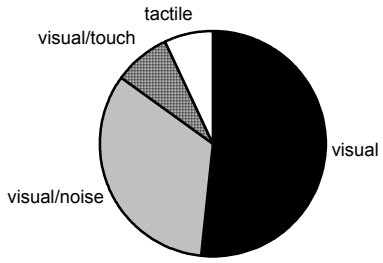
She showed 50.0% *eyebrow raising*, 13.9% *lowering back*, 10.2% *poking*, 6.5% *stiff threat*, 5.6% *relaxed open mouth*, 4.6% *presenting*, at each case 2.8% *enlisting* and *head bobbing*, 1.9% *lipsmacking* and at each case 0.9% *chasing* and *greeting*.



For the signal categories the following values resulted: 75.1% “visual”, 9.3% “visual possibly making some noise”, 5.5% “visual often combined with touching” and 10.2% “tactile”.

Claudia:

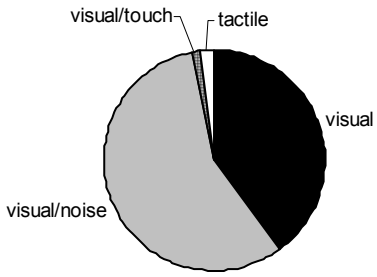
This female performed 31.7% *eyebrow raising,* 28.1% *stiff threat*, at each case 7.5% *relaxed open mouth*, *presenting* and *enlisting*, 3.5% *poking*, 3.0% *lipsmacking*, at each case 2.5% *lowering body*, *chasing* and *mounting*, 2.0% *threat mouth* as well at each case 0.5% *lowering back*, *yawning* and *greeting*.



For the signal categories the following values arisen: 52.2% “visual”, 33.7% “visual possibly making some noise”, 8.0% “visual often combined with touching” and 7.0% “tactile”.

Kuno:

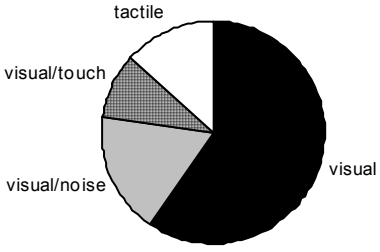
The harem leader displayed 46.0% *stiff threat*, 28.8% *eyebrow raising*, 4.4% *pumping*, 3.6 *threat mouth*, at each case 3.3% *enlisting*, *yawning* and *lipsmacking*, 2.6% *chasing*, at each case 1.1% *greeting*, *poking* and *mounting*, 0.7% *relaxed open mouth* as well as at each case 0.4% *head shaking* and *displaying*.



For the signal categories the following values resulted: 40.1% “visual”, 56.6% “visual possibly making some noise”, 1.1% “visual often combined with touching” and 2.2% “tactile”.

Iris:

The youngest animal of the adults showed 27.0% *eyebrow raising*, 20.3% *lowering back*, 12.2% *stiff threat*, 10.8% *poking*, 9.5% *presenting*, 8.1% *relaxed open mouth*, 4.1% *lipsmacking*, 2.7% *enlisting* as well as at each case 1.4% *threat mouth*, *chasing*, *mounting* and *pulling on*.

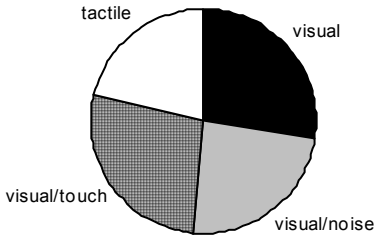


For the signal categories the following values arisen: 59.9% “visual”, 17.6% “visual possibly making some noise”, 9.5% “visual often combined with touching” and 13.5% “tactile”.

Subadult animals

Elke:

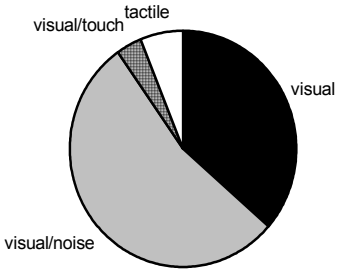
This female had 27.6% *presenting*, at each case 14.5% *stiff threat* and *poking*, 13.2% *eyebrow raising*, at each case 6.6% *lipsmacking* and *mounting*, 5.3% *relaxed open mouth*, 3.9% *enlisting* as well as at each case 2.6% *lowering body*, *threat mouth* and *chasing* in her repertoire.



For the signal categories the following values resulted: 27.6% “visual”, 23.7% “visual possibly making some noise”, 27.6% “visual often combined with touching” and 21.0% “tactile”.

Bernd:

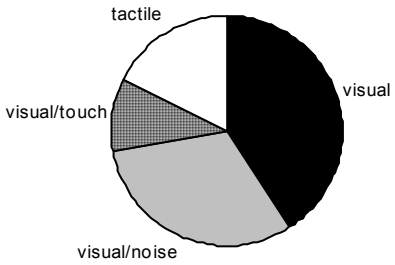
He used 24.6% *pumping*, 22.9% *stiff threat*, 13.4% *eyebrow raising*, 8.9% *threat mouth*, 7.8% *yawning*, 5.6% *poking*, 3.9% *lipsmacking*, 3.4% *presenting*, 2.8% *relaxed open mouth*, 2.2% *chasing*, 1.7% *enlisting*, 1.1% *head tapping* as well as at each case 0.6% *lowering back*, *displaying* and *mounting*.



For the signal categories the following values arisen: 36.3% “visual”, 54.2% “visual possibly making some noise”, 3.4% “visual often combined with touching” and 6.2% “tactile”.

Erwin:

He performed 18.9% *stiff threat*, 14.8% *poking*, 14.2% *eyebrow raising*, 7.7% *presenting*, 7.1% *lipsmacking*, 5.9% *enlisting*, at each case 5.3% *relaxed open mouth* and *threat mouth*, 4.1% *yawning*, at each case 2.4% *chasing* and *greeting*, at each case 1.8% *rolling on ground* and *pumping*, at each case 1.2% *lowering body*, *head tapping*, *displaying*, *mounting* and *pulling on* as well as at each case 0.6% *lowering back*, *head shaking*, *head/handstand* and *penis grab*.

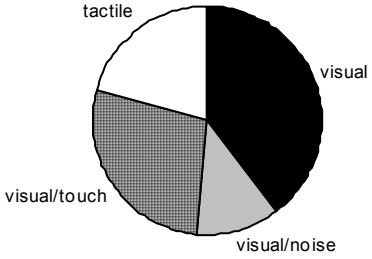


For the signal categories the following values resulted: 40.8% “visual”, 31.4% “visual possibly making some noise”, 10.1% “visual often combined with touching” and 17.2% “tactile”.

Juvenile animals

Grit:

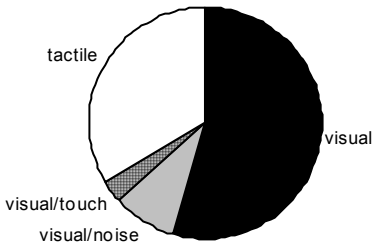
She displayed 27.0% *presenting*, 18.0% *relaxed open mouth*, 15.3% *poking*, 11.7% *eyebrow raising*, 9.0% *stiff threat*, 5.4% *lowering body*, at each case 3.6% *threat mouth* and *pulling on*, at each case 1.8% *lipsmacking* and *mounting* as well as at each case 0.9% *enlisting*, *chasing* and *greeting*.



For the signal categories the following values arisen: 39.6% “visual”, 11.7% “visual possibly making some noise”, 27.9% “visual often combined with touching” and 20.7% “tactile”.

Claire:

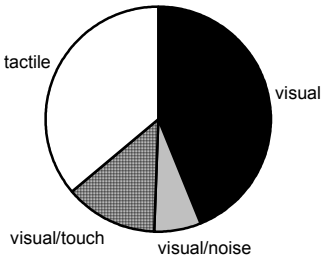
She showed 30.7% *poking*, 20.8% *eyebrow raising*, 9.9% *relaxed open mouth*, 7.9% *hand/headstand*, 5.9% *enlisting*, 5.0% *jumping in the air*, at each case 3.0% *rolling on ground, threat mouth*, *presenting* and *mounting* as well as at each case 2.0% *lowering body*, *spinning*, *pumping* and *stiff threat*.



For the signal categories the following values resulted: 54.5% “visual”, 8.9% “visual possibly making some noise”, 3.0% “visual often combined with touching” and 33.7% “tactile”.

Gundel:

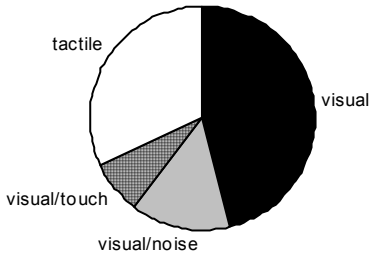
This baboon had 27.6% *poking*, 15.2% *eyebrow raising*, 13.3% *presenting*, 11.4% *relaxed open mouth*, 7.6% *enlisting*, at each case 3.8% *lowering back*, *rolling on ground* and *mounting*, 2.9% *pulling on*, at each case 1.9% *chasing*, *jumping in air*, *stiff threat* and *jumping on back* as well as at each case 1.0% *lowering back*, *hand/headstand* and *lipsmacking* in her repertoire.



For the signal categories the following values arisen: 43.8% “visual”, 6.7% “visual possibly making some noise”, 13.3% “visual often combined with touching” and 36.2% “tactile”.

Igor:

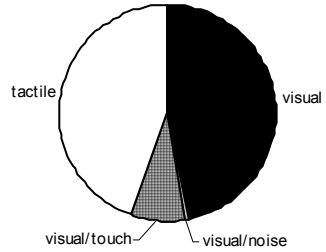
The juvenile male used 27.4% *poking*, 15.0% *relaxed open mouth*, 11.5% *eyebrow raising*, 8.8% *rolling on ground*, 8.0% *poking*, at each case 5.3% *enlisting* and *jumping in the air*, at each case 3.5% *chasing* and *mounting*, at each case 2.7% *hand/headstand*, *threat mouth*, *pumping* and *lipsmacking* as well as 0.9% *pulling on*.



For the signal categories the following values resulted: 46.0% “visual”, 14.2% “visual possibly making some noise”, 8.0% “visual often combined with touching” and 31.8% “tactile”.

<u>Brown infant (Gabi)</u>

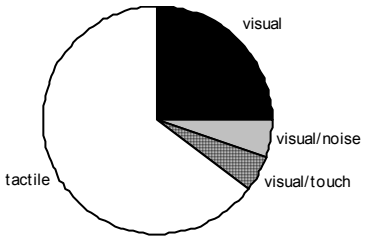
She performed 38.9% *poking*, 23.0% *relaxed open mouth*, 11.9% *eyebrow raising*, 7.9% *presenting*, 4.8% *enlisting*, at each case 3.2% *hand/headstand* and *pulling on*, at each case 1.6% *rolling on ground* and *mounting* as well as at each case 0.8% *lowering body*, *lowering back*, *spinning*, *stiff threat* and *jumping on back*.



For the signal categories the following values arisen: 46.8% “visual”, 0.8% “visual possibly making some noise”, 7.9% “visual often combined with touching” and 44.4% “tactile”.

Black infant (Irina)

The youngest baboon showed 61.5% *poking*, 12.5% *relaxed open mouth*, 7.3% *hand/headstand*, 5.2% *presenting*, at each case 2.1% *eyebrow raising*, *lowering body*, *jumping in air*, *lipsmacking* and *pulling on* as well as at each case 1.0% *rolling on ground*, *stiff threat* and *mounting*.



For the signal categories the following values resulted: 25.0% “visual”, 5.2% “visual possibly making some noise”, 5.2% “visual often combined with touching” and 64.6% “tactile”.

Appendix 6

Table A5
Occurrence of the different signals in determined contexts (total number of single events, S1)

signals	friendly	play	appeasement/submission	nursing	aggressive
eyebrow raising	9	6			238
enlisting					117
lowering body	7	4			
lowering back	2	2		30	
relaxed open mouth	37	136			
rolling on ground		2			
hand/headstand	4	6			
threat mouth					7
head bobbing					4
yawning					21
head tapping					2
chasing					26
jumping in the air		5			
pumping					39
stiff threat					73
lipsmacking	43	7	3		
presenting	40	7	30		6
greeting	2				
poking	113	59	4	2	34
mounting	9	9			
pulling on	3	6			
jumping on back		2			

ACKNOWLEDGEMENTS

During all the years of working on my dissertation there were so many people who supported and encouraged me that it turns out to be impossible to name all of them. On their behalf I would like to thank:

● Professor Mike Tomasello at the Max Planck Institute for Evolutionary Anthropology (MPI-EVA) in Leipzig who gave me the chance to study primate cognition and communication. He developed the idea of the study and provided considerable input for the dissertation. I am extremely grateful for his support and patience.

● The Max Planck Society for financial and material support.

● The State of Saxony for a half-year PhD grant.

● Dr. Rene Weinandy, Prof. Dr. Dietmar Weinert and Dr. Katja Liebal for their support and willingness to do the examinations.

● My former colleagues at MPI-EVA for their professional and moral support and the wonderful times we had.

● Leipzig Zoological Garden for the opportunity to observe their baboon group. The keepers who explained who is who and supplied me with all baboon history and news. The baboons for ignoring the observer and allowing me a glance into their fascinating life.

● My former student assistants (and now successful scientists) Katja Liebal and Marina Scheumann who helped me with the videotapes of the “kleinen Stinker”.

● Leipzig University and Martin Luther University Halle-Wittenberg.

● Julia Cissewski and Kevin Kennedy for proof-reading.

● My family and friends who supported me with everything that makes life valuable – love, friendship, encouragement, trust, joy, music, good food, and red wine. They never gave up believing that I would finish my dissertation. Thank you so much to my brothers Hartmut and Burkhard and their families, my friends from childhood Heidi and Katrin, my “Bio-Clique” Silke, Dörte, Haike and Jana, the “Kitchensingers” and friends from “Vivat academia” times Benita, Katharina, Beate, Ulrich, Jana, Malte, Silke and Ralf, my fellows from the “agricultural years” Elfi, Uta, Ingolf and Ulrike, the “Lipsians” Sylke, Sabine, Julia, Claudia, Sylvia and Katja, the “Chemnitz community” Ulrike, Maria, Rita, Anke, Elisabeth, Andreas, Holger and Günter, and last but not least “Sandra, the Gundi”, Klaus, Jens, Jutta, Frank, “Eule”, Sandra, Ilona and all the other friends from the zoo family.

● My parents who so much yearned for my finishing this dissertation but did not live to see it. I am so sorry, Mum and Dad.

CURRICULUM VITAE

Name:	Anja Dube
Address:	Rosenhof 7
	09111 Chemnitz
Date of birth:	25.07.1969
Place of birth:	Köthen
E-mail address:	papio@gmx.net

EDUCATION

1976-1988	Grammar school in Wittgensdorf and High School in Limbach/ Oberfrohna, Germany
June 1988	Abitur (final grade: 1.1)
09/1988-08/1989	Professional training at the Agricultural Production Co-operative Zettlitz, Germany
09/1989-09/1991	Agriculture at the Martin Luther University in Halle/Saale
July 1991	Pre-degree (“Vordiplom”) in Agriculture
10/1991-10/1997	Biology at the Martin Luther University in Halle/Saale, Germany Major subject: Zoology with specialisation in Behavioural Biology Subsidiary subjects: Psychology, Microbiology, Genetics Diploma thesis: *Comparing behavioural observations of chimpanzees (Pan troglodytes) kept in pairs and in a group with special consideration of behavioural deviations* Supervisor: Prof. Dr. R. Gattermann, MLU Halle
October 1997	Diploma in Biology “Diplom-Biologe“ (final grade: 1.5)
11/1998-03/2001	PhD position at the Max Planck Institute for Evolutionary Anthropology, Leipzig Topic: *Visual and tactile communication of a hamadryas baboon group* Supervisor: Prof. Dr. M. Tomasello, MPI Leipzig
4/2001-03/2003	Continuation of work on PhD thesis at the Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany

SCIENCE

1997/1998	Dube, A.: **Behavioural deviations in chimpanzees**. • 16th Meeting of the German Ethological Society in Halle (poster) • 5th Workshop of Zoo Biology in Erlangen (talk) • 2nd Meeting for Graduates of the German Ethological Society in Münster (talk) • 5th International Congress of the Society for Primatology in Berlin (poster) • Seminar about environmental/behavioural enrichment for zoo animals in Salzburg (talk)
1998	Dube, A.: **Comparative behaviour observations on chimpanzees kept in pairs (*Pan troglodytes*) and of a chimpanzee group with special regard to behaviour deviations**. Der Zoologische Garten, N.F. 68 (1998) 4, pp. 231-258, (in German)
2000/2001	Dube, A., and Tomasello, T.: **Aspects of gestural communication of a hamadryas baboon group**. Posters on the first results of the PhD thesis at the XVIIIth Congress of the International Primatological Society in Adelaide and the 17th Meeting of the German Ethological Society in Utrecht
2001	Dube, A., and Tomasello, M.: **Visual and tactile communication of a captive hamadryas baboon group**. Talk at the XXVIIth International Ethological Conference, Tübingen; Advances in Ethology 36, Supplements to Ethology, p. 145
2003	Dube, A., and Tomasello, M.: **Signal combinations in hamadryas baboons (*Papio hamadryas hamadryas*).** Poster at the 8. Kongress der Gesellschaft für Primatologie, Leipzig; Folia Primatologica 74, No. 4, p. 190
2004	Dube, A., and Tomasello, M.: Gestural communication in nonhuman primates: a comparison across different species of monkeys and apes. **The monkey part: Visual and tactile communication of hamadryas baboons.**

	Talk at the workshop “Gestural communication in human and nonhuman primates”, Leipzig
2010	Dube, A.: **Intentional nonvocal communication in hamadryas baboons (*Papio hamadryas hamadryas*).** Poster at the 5. Thementagung der Ethologischen Gesellschaft, Berlin

PROFESSIONAL EXPERIENCE

1994	Student assistant at the Institute of Zoology of the Martin Luther University Halle/Saale (analysis of behavioural experiments)
11/1997-04/1998	Practical training as a volunteer assistant at Scientific Department of Leipzig Zoological Garden
1998-2003	Special guided tours for students of Biology, Psychology, and Veterinary Science at Leipzig Zoological Garden
1999	Exhibition about the research of the Max Planck Institute for Evolutionary Anthropology at the new Wolfgang Köhler Primate Research Centre at Leipzig Zoological Garden
2001-2003	Visitor’s guide at Leipzig Zoological Garden
04/2003-06/2011	Full time position in Chemnitz zoo (curator and public relations)
2004	Seminar “Behavioral ecology and cognition of primates” for students of Psychology, Technical University Chemnitz
07/2010-06/2011	Zoo director ad interim in Chemnitz zoo
since 06/2011	Zoo director in Chemnitz zoo

Chemnitz, July 2012

DECLARATION OF ORIGINALITY

Herewith I confirm that I conducted my scientific work independently and without the help of others. I did not use other sources and devices than mentioned. Citations, literally or analogously, are marked as such directly in the text and listed as references.

Hiermit erkläre ich, daß ich meine Arbeit selbständig und ohne fremde Hilfe verfasst, andere als die von mir angegebenen Quellen und Hilfsmittel nicht benutzt und die den benutzten Werken wörtlich oder inhaltlich entnommenen Stellen als solche kenntlich gemacht habe.

Chemnitz, Juli 2012