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Facial expressions in a small monogamous ape: In search of the playface in gibbons

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Content

Zusammenfassung

Diese Studie gibt als eine der ersten genau definierte und objektive Einblicke in Gesichtsausdrücke, die bei Gibbons während des Spielens auftreten. 2 Arten wurden mit Fokus auf deren visuelle Signale genauer untersucht, Siamangs (*Symphalangus syndactylus*) und Schopfgibbons (*Nomascus sp.*). Das Analysieren der Ausdrücke fand mit Hilfe des GibbonFACS statt. 14 Siamangs aus sechs verschiedenen Gruppen und 13 Schopfgibbons aus 3 verschiedenen Gruppen und Unterarten (*Nomascus leucogenys, Nomascus gabriellae, Nomascus siki*) wurden beobachtet und deren Gesichter gefilmt. 8 unterschiedliche „action units“ (AUs) in 14 verschiedenen Kombinationen (AU combinations) wurden gefunden. In beiden Arten wurden 2 Gesichtsausdrücke mehr als alle anderen gezeigt, somit wurden charakteristische Spielgesichter gefunden. Zusätzlich kamen alle bis auf ein Ausdruck in beiden Arten vor, weswegen auf eine Universalität der Spielgesichter, zumindest in Gibbons, geschlossen werden kann. Es wurden allerdings Unterschiede im Vorkommen der Gesichtsausdrücke in Abhängigkeit vom direkten Augenkontakt zwischen den beiden Arten gefunden, des Weiteren zeigten sich bei den Siamangs sowohl zwischen den Geschlechtern, als auch zwischen den verschiedenen Altersgruppen ebenfalls Differenzen. Zusätzlich konnte bei den untersuchten Gibbons ein gerichteter Gebrauch von Gesichtsausdrücken während des Spiels durch direkten Augenkontakt nachgewiesen werden, ohne dass das Spiel zu einem Kampf eskalierte. Dies widerspricht zuvor aufgestellten Behauptungen. Durch diese Arbeit existieren neue Sichtweisen und neues Wissen über das Spielverhalten und in diesem Kontext vorkommende Gesichtsausdrücke von kleinen Menschenaffen.

Abstract

This study is the first that gives accurate and objective insights into facial expressions occurring in play bouts of captive gibbons. Two species were seen over, siamangs (*Symphalangus syndactlyus*) and crested gibbons (*Nomascus sp.*) with focus on visual signals of their faces. Analysing took place with the help of the GibbonFACS. 14 siamangs from six different groups and 13 crested gibbons of 3 different groups and subspecies (*Nomascus leucogenys, Nomascus gabriellae, Nomascus siki*) were observed and their facial expressions filmed. 8 various action units (AUs) were found in fourteen different combinations (AU combinations). In both of the species 2 facial expressions occurred more than the others, therefore characteristical play faces were found. Supportively all but one facial expression occurred equally in both of the species; therefore a universality of the play faces could be given. But the expressions differed in their appearance with direct eye-to-eye contact between the species. Additionally, for siamangs appeared variety in the facial expressions of the sexes as well as in the comparison of different age groups. It also revealed differences in the use of facial expressions depending on eye contact between the playing individuals. Thus this study proves the intentional use of facial signals during play in gibbons by the use of direct eye-to-eye contact in the play bouts without escalating into a fight, other than presumed before. So now there exist interesting new views and knowledge of play behaviour and facial expressions in the social context of play for small apes.

Background

Evolution of facial muscles in general and in primates

"*As a part of our efforts to understand the evolutionary factors involved in shaping human communication, societies and cognitive processes, a comparative understanding of primate facial expression, its musculature and facial processing is crucial"*(Burrows, 2008).

The first remarks and attention on facial expression and its roots and evolution were given by Charles Darwin in 1872, in *The Expression of Emotions in Man and Animals.* Facial expression is defined as production and neural processing of facial movements (Darwin, 1872; Burrows, 2008). These facial movements are shown in communicative situations to show the emotional or motivational intent of the sender, besides they have functions in mate or kin recognition (van Hooff, 1972; Burrows, 2008). They can signal conciliation (if an individual is frightened by a superior) as well as aggressive behavior or threat, but appear in social contexts, like grooming (Andrew, 1963) or playing (Chevalier-Skolnikoff, 1974b). Other functions concern eating and respiratory issues as well as the context of sound production and vocalisation (Andrew, 1963). Facial displays can also give an account of a conditional action tendency of the sender (Hinde, 1985) who tries to influence the receiver's behaviour using his expressions as an instrument of social manipulation (Dawkins and Krebs, 1978).

The primary function of facial expressions was not communication (van Hoof, 1962), but concerned functions like feeding, soliciting food, suckling, biting and chewing and only ritualized, they acquired a signalling function (van Hooff, 1962). However, it is unique for mammals that the facial musculature also adopts the role of communication (Burrows, 2008).

Facial expressions are produced by mimetic and/or facial musculature and are a kind of non-vocal communication used inter alia by primates which have some of the most complex facial musculature in all mammals. Therefore they make the most-intricate facial displays (Burrows, 2008). The mobility of facial behaviour can vary from very simple expressions, concerning the mouth area (as in reptiles) to complex multidimensional expressions of humans or chimpanzees (van Hoff, 1972).

Darwin held a view, that human facial expression musculature and facial movements that reveal “feelings” were modified and descended from primate ancestors (Darwin, 1872).

Compared to most other mammals, primates are highly social animals. They spend either all of their live or at least until they reach adulthood in a social setting. These social groups can range in size from at least two individuals to over a hundred (Goodall, 1986). So, with other words, in primates every species is highly social for at least one part of the individual’s life cycle (Sussman, 1999).

To be able to manage these complex social networks, primates rely on facial expressions as a mechanism of close-proximity communication with conspecifics (Sussman, 1999; Zeller, 1987; Schmidt, 2001). Thus, one can say, that *“in general, a working knowledge of primate (and general mammalian) facial musculature has been cited as a potentially valuable tool for increasing our understanding of phylogenetic relationships among primates as well as in general mammals”* (Burrows, 2008).

The facial expressions of primates include movements of the cartilage of the external ear and the alar cartilages of the nose, the skin of the face, the vibrissae, the lips, the eyelids and nares. All mammals possess these facial or mimetic musculatures, which produce the facial movements (Young, 1957; Gasser, 1967).

Generally it was assumed that lower primates, like lorises, galagos, lemurs and tarsiers possess only few muscles which are relatively simple and undifferentiated without much complexity. In contrast to this, monkeys, apes and humans were thought to feature “*an increasing number of small, discrete facial muscles and greater muscle complexity in a linear, step wise fashion as the primate phylogenetic scale is ascended toward humans”* (Burrows et al. 2011), for example, that chimpanzees are able to identify facial expressions in fellow animals and, in addition, identify kinship on the basis of their faces (Parr, 2003; Parr & de Waal, 1999).

But recent works have shown that these assumptions need to include more than just the phylogeny concept and that parameters like group size, mating system, dietary niche, environment, and dominance hierarchies are strongly connected with facial expressions (Burrows and Smith, 2003; Sherwood et al., 2005; Dobson, 2009).

Nowadays, facial expressions can be a decisive determining factor of what and how individuals are feeling (Ekman, 1984) and what they could do next (Hinde, 1985a).

Emotions

It is challenging to find a general admitted definition for emotion, especially in animals. Reasons for this could be that primarily social emotions are conceded to humans and there is only little focus on whether nonhuman species are able to discern feelings like embarrassment, empathy or pride (Preston & de Waal, 2003).

For a better understanding of emotions in humans, it would be expedient to take a look on several closely related species (not only one), because one can liaise between a decisive expression that is shared by all nonhuman primates and humans and the presence of this particular trait in our common ancestor (Haun et al., 2006).

Facial movements can be visual hints when the emotion in animals (in this case especially in primates) is studied and therefore "*facial expressions in primates seem to be a highly salient and empirically robust unit of measurement for understanding the evolution of emotion in primates*" (Parr & Waller, 2007).

To being able to compare nonhuman primate and human facial expressions it is needed to locate homologies in the underlying mimetical facial muscles as well as to understand their role in a social context (Liebal et al., in preparation). This is very important, because not every similar facial expression has the same meaning or the same underlying emotional state when being compared (Waller & Dunbar, 2005). Therefore, it is very important to develop a standardized and objective method to be able to quantify facial movement. Otherwise there could be biases caused by emotional impressions of faces (Waller et al., 2008).

Therefore, Ekman and Friesen developed the Facial Action Coding System, short FACS, to solve such problems and avoid such biases in humans (Ekman and Friesen, 1978; Ekman et al., 2002a).

Facial Action Coding Systems (FACS)

The basic principles of FACS are anatomical works of Hjortso (1970) and others, which are needed to get knowledge of the underlying facial muscle contractions of the observable movements. 33 facial muscle movements were found and labelled into numbered Action Units (AUs). Additionally, 25 head/eye movements were found and called Action Descriptors (ADs). A manual was made where every AU and AD is termed, for example AU1 stands for the inner brow raiser.

"FACS can compare facial movements regardless of individual differences in other aspects of facial anatomy, such as long hair covering, facial coloration, bone structure etc. This latter characteristic makes FACS ideal for modification across species" (Waller et al., in press).

Because of this reason FACS has been modified for the use with chimpanzees (*Pan troglodytes:* Vick et al., 2007), rhesus macaques (*Macaca mulatta:* Parr et al., 2010), orang-utans (*Pongo pygmaeous:* Caeiro et al., in prep.) and gibbons (*Hylobatidae:* Waller et al., 2011).

In this work, only the development of the GibbonFACS will be described, because it was the most important tool of this master thesis, all other FACS follow more or less the same procedure.

GibbonFACS

The development of GibbonFACS consists of several steps. First, anatomical dissections were conducted on 4 gibbon species, siamang (*Symphalangus syndactylus*), lar gibbon (*Hylobates lar*), mueller's gibbon (*Hylobates muelleri*) and nomascus gibbon (*Nomascus gabriellae*). They showed that the facial muscles of gibbons resemble them of chimpanzees, rhesus macaques and humans (see **Tab. 1**), but presented coincidental that some muscles were absent in gibbons (Burrows et al., 2011).

Table 1 Absence of some muscles in a direct comparison with other species

	Number of Muscles
Gibbon	22
Human	24
Chimpanzee	23
Rhesus	22

In all other species for which a FACS was so far developed, an intramuscular electrical stimulation was made, but in contrast to chimpanzees or macaques, gibbons are not found in laboratory conditions and therefore unavailable for such experiments and it would not be ethically appropriate (Waller et al., in press).

The next step was to collect video footage, which contains all in all of 72 hours of detailed observation in several zoological gardens. 57 individuals from 7 different species were filmed. Specialized coders identified the different AUs and ADs and created a manual for the facial expressions of gibbons, the GibbonFACS. This was possible, because no differences in the facial movements of the different species were found, so the GibbonFACS manual can be used for coding all gibbon species (Waller et al., 2011).

To become a certified coder a reliability test (Ekman et al., 2002b), consisting of 20 video clips, has to be completed successfully.

To better understand the relevance of gibbons, a short introduction into the world of gibbons is given below.

Gibbons-a general view

Taxonomy

Gibbons (*Hylobatidae*) belong to the superfamily of *Hominoidea*, which can be divided into two families: The small or lesser apes (*Hylobatidae)* and the great apes (*Hominidae*) with a common ancestor which branched off about 16-20 million years ago (Thinh et al., 2010).

The family of *Hylobatidae* is the most species-rich and numerous group of apes with approximately 17 species. They can be classified into four genera: *Hylobates* (lar gibbons), *Bunopithecus* (hoolock), *Symphalangus* (siamangs) and *Nomascus* (crested gibbons) (Geissmann, 2002).

Biology

Their bodyweight can range from 5-7 kg (“dwarf gibbons”) to 10-12kg (siamang). Gibbons show no gender dimorphism as to body size or canine tenurial and length. They have, compared to their body size, the longest arms of all recent primates and too, very long lower extremities (Geissmann, 2003).

Furthermore, they are the only apes that always possess Sitzschwielen.

In the wild gibbons are diurnal and exclusively arboreal. Therefore they developed specialized kinds of locomotion, the brachiation and the bipedal walk. Brachiation permits them to move very quickly and wide gaps between trees or branches can easily be transcended. The trees provide cover, serve as sleeping berth and food source.

Gibbons prosecute the so called branch feeding which means that they have specialized in the most ambient branches of the trees and nourish on the ripe fruits and leaves that grow there. An explanation for this is the evasion of food competitions with other animals. In addition they also live on insects from time to time.

Distribution and social structures

Their distribution areas are the tropical rainforests of south-east Asia. They live in monogamous nuclear families consisting of one adult pair of parents and their juvenile offspring until they reach adulthood. Usually the adult pair remains together for their whole life, extramarital copulations with other individuals only happen rarely.

The offspring leave their parents when reaching puberty, because presumably there would be great conflicts between individuals of the same gender. Puberty is reached at the age of 6-8 years, in captivity even sometimes 4 years.

One offspring to be born is normal, twins are rather rare. Gestation time is about 7 months, whereat female siamangs can be pregnant up to 8 months.

Life duration of wild gibbons is about 25-35 years, in captivity the age can be up to 50 years (Geissmann, 2003).

The families live in constant territories, whose size lies in between 20 and 40 ha and which are defended vehemently. They mark their territories with loud singing, which can last up to 10-20 minutes. This singing often consists of duet songs, at which females and males sing different strophes, which succeed in a certain order. The duets serve different functions. One is to defend the resources and the territory as well as it has a pair-bonding function for the couple. The singing takes mainly place in the wee hours of the morning and the different gibbon species can be identified very well because of their different song forms (Geissmann, 2003).

In the next chapter it is dwelled on two genera, because they are highly relevant for this thesis and were worked with.

Symphalangus syndactylus

With a body weight up to 12kg they are the largest substitutes of the family *Hylobatidae*. All animals possess a unitary black pelt, but male ones can be easily distinguished from females by their long genital hair coat (**Pict. 1 and 2**).

The Latin name *Symphalangus syndactylus* stands for the translation “coadunated fingers”, which can be explained by a connective-tissued anastomosis of the second and third frog of the feet.

Siamangs live in Sumatra and the southern Malayan peninsula as far as to the southernmost Thailand. It’s the sole species which lives sympatric (it means that their territory overlaps with one of another) with other gibbon species, for example *Hylobates lar*. Therefore, because of their body size, siamangs are able to switch to lower-energy leaves by reason that they have a longer gastrointestinal tract for a better digestion. For this reason siamangs have smaller home range and spend more time with feeding.

Their duet songs rank among the most complex mammal duets and serve most notably as pair bonding and territorial marking. Siamangs possess large throat pouches which are distended during the callings and duets. Their detailed function is widely still ambiguous, but it is assumed that they are used for amplifying particular frequency domains.

The songs of siamangs can be heard for kilometres and mostly occurs in the wee hours of morning. Certainly, because of their sympatric life style, they start singing later than the white handed gibbons. In the majority of cases singing takes only place at fair weather, because under this condition the best sound propagation can be found (Geissmann, 2003).

Siamangs not only differ in their body height from the other species of *Hylobatidae*, but also they differ in the caring behaviour concerning their offspring. In all other species female animals show caring behaviour until pubescence of the offspring. In siamangs the female is the attachment figure in the first year of the juvenile's life. She lactates it, plays with him, carries it and takes care in all cases. The sire defends the female and offspring against intruders or conspecifics, but takes no interest in other caring behaviour concerning the offspring, aside from gentle play. But as soon as the offspring is about two years the sire starts to carry it (Chivers, 1974). Additionally the male becomes the preferred play partner of the offspring, except there is a sibling. The sire shares his food with the offspring and takes care of it in almost every concern. From this point in time the female only serves as retreat of too rough play with the sire or the sibling and as food source if the offspring is not yet weaned (Lembeck, 2009).

Fig.1 Male siamang with good visible genital hair coat
(Pictures by: Wiebke Hoffmann)

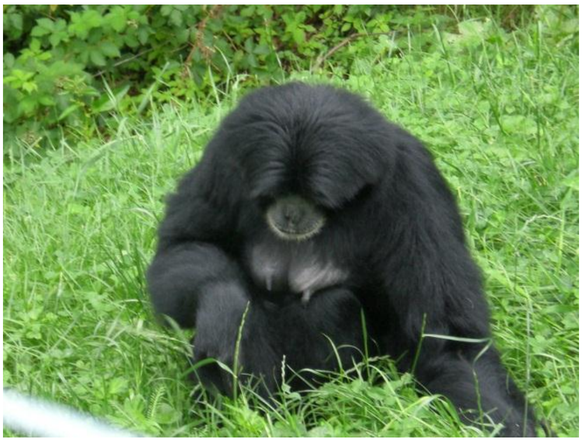

Fig.2 Female siamang

Nomascus sp.

The genus Nomascus consists of four species (*N.concolor, Nsp.cf.nasutus, N.gabriellae, N.leucogenys including N. siki*) with several subspecies. Nomascus

gibbons, also called crested gibbons can reach a weight between 7-10 kg. The genders differ strongly from each other. The pelt of the male animals is mostly black, but with bright parts on the cheek area in some species. The name crested gibbon can be explained by their elongated and vertically uprised crest hair. In contrast to this the females have a yellow to light brown coloured fur with a black spot on the crest (**Pict.3**). An interesting fact is the changing of the fur colour in juvenile and subadult animals. New-borns show a light brown to beige pelt colour without any dark spots. At the age of 8 months to 1½ years the colour changes to black, which remains in male crested gibbons, whereas the fur of the female ones changes back to yellow or light brown at the age between 5 and 8 years, when they reach adulthood (Geissmann, 2003; Geissmann et al., 2000; Groves, 1972).
Their distribution area ranges over Indochina, to the east of the Mekong. Mated animals produce duet songs, whose organisation is, compared to other duet songs, stereotype. Their functions could be of mate-guarding or ally-showing nature (Geissmann, 2003).

Fig. 3 Male (left), female (right) and juvenile (in front) animal of *Nomascus siki* (picture by Wiebke Hoffmann)

Relevance of Gibbons

It is only very little known about the communicative and social-cognitive abilities of the various species of lesser apes (Tomasello and Call, 1997). Many studies about their singing behavior have been made (e.g. Geissmann, 1993), but there was only little attention on their communicative behaviour not only concerning their singing (Orgeldinger, 1999).

Gibbons live exclusively arboreal in dense vegetation and it was assumed that there is more focus on vocal than on visual communication. Above all, species that live in stiff dominance structures with fixed kinship structures do not need many communicative signals compared to primates living in egalitarian systems with weaker kinship structures that need more of them (Maestripieri, 1999).

As smaller apes have a monogamous mating system without a dominance hierarchy, but a strong bonding between male and female, Chivers concluded in 1976 that the repertoire of his study objects, the siamangs, only contain very few and simple structured communication signals (Chivers, 1976) and additionally deduced in former studies on siamangs that they only have a limited communicative repertoire of facial expressions (Chivers, 1974). This thesis is supported by Dobson and Maestripieri, who argue, that facial mobility correlates with group size and not terrestrial or arboreal lifestyle and that a rich communicative repertoire is usually linked to a complex, egalitarian social structure (Dobson, 2009; Maestripieri, 1999).

So nowadays it is possible to objectively oppose facial expression in primates living more terrestrial and in large groups to ones living exclusively arboreal and in small family groups, due to the FACS and there emerged interesting results (see **Tab.2**). Gibbons possess fewer facial muscles as humans or chimpanzees indeed, but show the most facial expressions in all non-human primates (Waller et al., subm.).

Action Unit	Action descriptor name	Muscle[a]	HumanFACS	ChimpFACS	MaqFACS	GibbonFACS
AU1	Inner brow raiser	Medial frontalis	✓	×*	×*	×*
AU2	Outer brow raiser	Lateral frontalis	✓	×*	×*	×*
AU 1+2	Brow raiser	Frontalis	✓	✓	✓	✓
AU4	Brow lowerer	CS[b], DS[c], Proc[d]	✓	×*	×*	×*
AU41	Glabella lowerer	Procerus	✓	×*	✓	✓
AU5	Upper lid raiser	Orbicularis oculi	✓	×*	×*	✓
AU6	Cheek raiser	Orb. oculi (orbital)	✓	✓	✓	✓
AU7	Lid tightener	Orb. oculi (palpebral)	✓	×*	×*	✓
AU8	Lips toward each other	Orbicularis oris	✓	×*	✓	✓
AU9	Nose wrinkle	Llsan[e]	✓	✓	✓	✓
AU10	Upper lip raiser	Levator labii sup	✓	✓	✓	✓
AU11	Nasolabial furrow deepener	Zygomaticus minor	✓	×*	×*	×*
AU12	Lip corner puller	Zygomaticus major	✓	✓	✓	✓
AU13	Cheek puffer	Caninus[f]	✓	×*	×*	×*
AU14	Dimpler	Buccinator	✓	×*	×*	×*
AU15	Lip corner depressor	Depressor anguli oris[g]	✓	×*	×*	×*
AU16	Lower lip depressor	Depressor labii inf	✓	✓	✓	✓
AU17	Chin raiser	Mentalis	✓	✓	✓	✓
AU18	Lip pucker	Orbicularis oris	✓	×*	✓	✓
AU20	Lip stretcher	Risorius	✓	×*	×	×
AU21	Neck tightener	Platysma	✓	×*	×*	✓
AU22	Lip funneler	Orbicularis oris	✓	✓	×*	✓
AU25	Lips parted	Various	✓	✓	✓	✓
AU26	Jaw drop	Various	✓	✓	✓	✓
AU27	Mouth stretch	Various	✓	✓	✓	✓
AU28	Lip suck	Orbicularis oris	✓	✓	×*	✓

Table 2 Comparison of different muscles, facial expressions and their appearance in the 4 FACS. Check marks stand for the appearance of the described muscle movement, a cross marks the absence of those. * marks it, if the muscle was found, but has no independent movement. Taken from: Waller BM, Lembeck M, Kuchenbuch P, Burrows AM, Liebal K (subm.). *GibbonFACS: A muscle-based facial movement coding system for the monogamous small apes.p.8*

Additionally gibbons are apes that are closely related to Old World monkeys as well as to great apes, therefore they can be found taxonomically in-between them and have characteristics of both families.

Especially in the play contexts there is a rich repertoire of facial expressions.

Play

Play behaviour is present in animals, from mammals and birds (Heinrich & Smolker, 1998) up to reptiles (Burghardt, 1998) and is said to have an important role in animals´ development and life (Fagen, 1993) but "*may have a more important socialising function in some species than in others"* (Poirier and Smith, 1974).

Therefore social play is crucial especially for group living animals, because adult animals are always assigned to new tasks and social challenges (Palagi et al., 2006) and former play experience may help them to regulate their emotional responses and to perform appropriate actions in the appropriate context and this in turn may help to increase their social competence (e.g. Pellis and Pellis, 2006). Also, "*by increasing one's knowledge about the environment, also increases one`s chances of survival"* (Campbell, 1966).

Therefore, social play even occurs in adult animals both in sexual and non-sexual contexts (Pellis and Iwanuk, 2000).

Play is closely linked with learning and especially mammals benefit strongly from trial and error learning (e.g. Poirier, 1972), therefore they are capable of adapting to new situation (Porier and Smith, 1974).

Additionally play in social contexts is a good possibility for practicing intraspecific communication, strengthening social bonds and finding a position within the group for younger animals, moreover it is a basic pattern to prepare for behavioural functions in group life (Poirier et al., 1978; Bekoff & Byers, 1981), e.g. "*The basis of the adult dominance hierarchy may be formed in the play group"* (Poirier and Smith, 1974), because they have to cope with dominant as well as with subordinate situations and to learn how to adequate behave in such (Dolhinow and Bishop, 1970). Furthermore, "*…within the play group animals learn to predict one another's behaviour"* (Poirier and Smith, 1974).

Interestingly play only occurs if the individual is free from physical or social stress (Fagen, 1981) and is strongly needed for a full social and physical development (Poirier and Smith, 1974).

Relevance and Aim of the Project (master thesis)

Play bouts are usually attended by play signals, which occur "*either before or during a playful interaction"* and *"Little is known about the positioning of playing signals within a play bout…."* (Bekoff, 1975).

"*One of the most prominent features of play is the play face"* (Chevalier-Skolnikoff, 1974) which has the meaning of a metacommunicative signal (Bateson, 1955) defined as *"communication that affects the interpretation of other communication*" (Altmann, 1962). It can occur during contact play with another animal (Chevalier-Skolnikoff, 1974) as well as in solitary play bouts (Redican and Mitchell, 1974).

Little was known about the actual play faces of primates although several attempts were made to describe them (e.g. van Lawick-Goodall, 1968; van Hooff, 1972; Chevalier-Skolnikoff, 1974; Oppenheimer, 1977; Preuschott, 1992), but all of them differ in their accurate depictions and most of them were universally and simply designated as "open mouth play face" (van Hoof, 1967). The specifications of the play faces can differ distinctly, not only for different species bur also within the same species which is very confusing and makes it hard to find common definitions for play faces (Pellis & Pellis, 1996) and to describe them accurately.

In the case of gibbons, only a few descriptions of facial expression during play exist and those only for siamangs (Orgeldinger, 1999; Liebal et al., 2004).

A siamangs play face was described by Orgeldinger with slightly to fully squinting in addition to a slightly to strongly opened mouth (Orgeldinger, 1999). This is the most specified declaration of a play face in gibbons that could be found.

By using the GibbonFACS it is possible to determine more exactly facial expressions in general and to specify those occurring in a play context, because it is necessary to look closer at facial expressions in specific social contexts to get knowledge about actual functions of facial expressions and their underlying emotional state. This allows to being able to compare facial expressions in several kinds of primates and to find similarity or dissimilarity among and between non-human and human primates, great apes, lesser apes and monkeys and, maybe, to find, based on facial expressions, a common ancestor. Furthermore it is a suitable tool to investigate the flexibility and intentionality of use of facial expressions which can be reconsidered in two different ways. Firstly as a "means-end dissociation" which can be described as "*the use of a particular signal in different functional contexts and /or diverse signals for one context"* (Liebal et al., 2004). Second as "audience effect" which is defined as "*the sender's sensitivity to the presence/absence of a potential recipient as well as the choice of signals depending on the attentional state of the recipient"* (Liebal et al., 2004) and until now it was challenging to find a satisfying method to get this assurance. In addition, facial expressions are gradual signals and are often characterised as automatically, nearly reflexive concepts of emotions (Tomasello, 2008). To get better understanding and more efficient knowledge about this intentional and directed use of signals an adapted tool had to be found – in this case the GibbonFACS. Out of these points of view some interesting questions resulted.

Question 1: What is/are the most common facial expression/s in play?

It is important to answer this question to get knowledge of facial expressions in gibbons occurring during play in general. As said before, the only description was given by Orgeldinger in 1999 and a more specified characterization has been missing since then. Therefore the results would be a good foundation to solve further problems concerning "the" play face. There will be a closer look if there are differences in-between the species and what they look like in the playing context, or if one can say that the most common play face found can be used universal for all gibbons.

Question 2: Is there eye contact between the play partners within a play bout?

Pursuant to Chevalier-Skolnikoff eye contact between the play partners is avoided to prevent the danger of escalation (Chevalier-Skolnikoff, 1973, 1974a). But due to Liebal et al. for a facial expression used to change the recipient's behaviour it is essential that the other one is visually attending (Liebal et al., 2004) which allows a hypothesis that there has to be eye contact between playing individuals.

Question 3: Are there differences in facial expression use depending on the age and/or the sex?

Liebal et al. found out, that there are discrepancies in siamangs in the use of facial expressions within different age groups and even in the sexes (Liebal et al., 2004). For this reason it can be assumed that maybe there are as well differences in facial movement when specialising in the playing context.

Question 4: Are there differences depending on eye contact during play?

There are existing different positions due to that question. Chevalier-Skolnikoff described in macaques, that eye-to-eye contact is avoided during play (Chevalier-

Skolnikoff, 1973, 1974a). She argues in 1974 that “*the eye-contact avoidance aspect of the expression is probably what most clearly differentiates it from the threat face,.....”* (Chevalier-Skolnikoff, 1974b). Therefore in this thesis is given attention to the question if and how the facial expression change if there is or isn`t eye contact during play. Moreover it is analysed if there are differences in the facial expressions in the different age groups or sexes in play reliant on the eye contact, to control Chevalier-Skolkinoffs proposition for gibbons.

Methods

Subjects

Subjects were 12 siamangs of six captive groups at the Twycross Zoo, The World Primate Center (United Kingdom) and at Zoo Zurich (Switzerland); and 12 crested gibbons, consisting of 3 captive groups at the Mulhouse Zoo (France). The age groups in **Table 2** are defined after Geissmann (1991):

0-2 years = infant; 2-4 years = juvenile; 4-6 years = subadult; > 6 years = adult.

Table 3 Composition of the different family groups in the two zoos

Zoo	Species	Group	Individual	Age group	Sex	Date of birth
Twycross	Symphalan-gus syndactylus	1	Basil	adult	male	13.12.1994
		2	Betony	adult	female	27.03.1980
			Daclen	subadult	male	03.05.2004
			Dylan	subadult	male	14.02.2003
		3	Spike	adult	male	25.11.2000
			Tarragona	adult	female	18.11.2000
			Stig	infant	male	15.07.2009
		4	Daniel	adult	male	26.05.1996
			Tango	adult	female	27.03.1994
			(Baby)	(infant)	unknow n	ca. 10.02.2010
		5	Kane	adult	male	02.11.1990
			Sheena	adult	female	30.01.1991
Zurich	Symphalan-gus syndactylus	6	Daw	adult	female	04.08.2003
			Gembira	subadult	male	14.01.2006

Mul-house	Nomascus leucogenys	1	Chukao	juvenile	unknown	15.08.2007
			Conny	adult	female	01.04.1990
			Old hope	adult	male	ca.01.12.1968
	Nomascus gabriellae	2	Banguin	subadult	unknown	13.10.2006
			Bebe	infant	unknown	19.09.2010
			Chloe	adult	female	06.01.1990
			Dan	adult	male	10.1991
			Petit	infant	unknown	12.11.2008
	Nomascus siki	3	Anoie	subadult	female	25.10.2005
			Chanchi	juvenile	unknown	13.11.2007
			Dorian	adult	male	23.12.1989
			Fanny	adult	female	13.06.1993
			Tiny	infant	unknown	20.03.2010

Basil was kept alone and therefore showed no play behaviour during the recordings, even no solitary play. Old Hope never intended to play and was therefore excluded from the analysis.

All the siamangs at the Twycross zoo had an inner and outer compound of the same size for all animals with climbing opportunities like ropes and branches and wooden boards to sit on. Only the inner enclosure was visible for the observer.

The animals at Zurich had a bigger inner and a not visible outer compound. The inner enclosure was equipped with ropes ad branches as well; additionally they had some kind of toys inside for enrichment.

The crested gibbons had a big outer compound where they were visible and an indoor enclosure not visible for the observer. The outer compound consisted of tree trunks, ropes, branches, wooden boards and toys; additionally the ground was covered with grass.

Wood wool was placed in all cages of all animals for enrichment.

Most of the groups consisted of 1-3 adult and several young animals. Siamangs were kept in smaller families consisting of 1-3 animals: Only one infant, all other animals were subadult or adult.

In contrast to this crested gibbons lived in bigger family groups of 3-5 animals, consisting of more infants, juveniles and subadults and 2-3 adult ones. In two of the 3 groups more than one young animal could be found.

Procedure

Video footage was collected with a digital video camera. In total, 35 hours of social play interactions; more precisely 20h 45min for the siamangs and 14h 15min for the crested gibbons were collected. Observation time for each animal was 1 hour of play in steps of 4x15 minute video footage from different days and daytimes to prevent biases,

A total of 24 hrs of play sequences of crested gibbons and siamangs. Focal animals were randomly selected, at random days and daytime. First, a GibbonsFACS test had to be passed to ensure that the coding of the material was conducted in a consistent and reliable way. If an animal disappeared out of the focus frame and did not return within 5 minutes the analysing was stopped and another video was taken instead.

Analysis of the video footage was conducted with the Adobe Premiere Pro CS3. This is a programme enabling a frame-by-frame analysis, which was very important, because facial expressions can change very fast and many can appear within a small time slot.

Coding started with the beginning of a play bout. In this thesis the beginning of a play bout is defined after Fox (1977), namely that a play is initiated through catching, shaking or tossing a play partner or trough hitting, accessing and climbing or rolling on the other individual.

A play sequence ended, if one of the play partners stopped answering the play invitations by turning away, threatening, stop chasing the partner or pushing the other animal away.

The coding principle conformed to the guidelines of the GibbonFACS manual (Waller et al., 2011) and every viewable muscle contractions occurring in play bouts were coded into AUs.

More precisely, if a muscle contraction occurred it could be identified and translated into an AU with help of the descriptions given in the manual consisting of 4 points:

"*A. Proposed muscular basis*: *describing underlying facial musculature*

B. Appearance changes: *multiply cues supporting AU identification*

C. Subtle differences: Notes differences and similarities to other AUs

D. Comparison: describing use, context, difficulties and also species comparison among gibbons but also according to other existing FACS' (Human FACS, ChimpFACS and MaqFACS)" (Waller et al., 2011).

All AUs is assigned a particular number for easier coding. If more than one AU is occurring in a facial expression they are combined as "AU combinations" starting with the lowest number. Eye contact for sender and receiver of the play bouts was coded individually, because in many cases it occurred that only the sender looked at the receiver or the other way round. Thus, when the sender was looking at the receiver it was coded as eye contact from the sender and depending on if the receiver was looking as well or not, eye contact or no eye contact was coded for the receiver. The same coding took place in switched places for sender and receiver.

Statistics

Because of the small sample sizes of 12 animals for each of the 2 species, non-parametric tests were applied. All of them were two-tailed and rejected a null-hypothesis at an alpha-level of 0.05.

Half of the data were coded by a second certified coder to assure reliability. A Friedman's test was used to test for differences between the frequencies of the AUs and their combinations. Wilcoxon test was used for pairwise comparison. To compare the frequencies of the AU combinations in the two different species or sex a Mann-Whitney-U-test was applied.

A Kruskal-Wallis-test test was also accomplished to test significant differences within species, e.g. when comparing differences in age classes.

Results

8 different AUs were found in fourteen different combinations in the context of play. That's a total of 1373 facial expressions, with 535 which were unseizable. All but 3 AU combinations were used by both siamangs and crested gibbons: unlike siamangs, only crested gibbons used the combination N whereas combination K and M were exclusively shown by siamangs (**Table 1**).

Table 4 AUs and their combinations (except J which only consists of one AU) and number of appearance in siamangs and crested gibbons with direct eye-to-eye contact (dec), eye contact (ec) and no eye contact (nec) as possible play faces

	AU combination	**Siamangs**	**Crested gibbons**
		dec/ec/nec	dec/ec/nec
a	12+25+26	45/64/110	8/29/36
b	12+25+27	41/61/50	11/24/12
c	25+26	29/17/39	11/19/9
d	25+27	19/17/16	3/5/2
e	10+12+25+27	0/5/18	0/5/7
f	10+12+25+26	0/0/1	6/2/1
g	12+16+25+26	1/4/9	0/1/2
h	12+16+25+27	1/5/4	0/1/1
i	12+25	2/6/6	1/2/2
j	25	4/7/14	1/2/1
k	19+25+26	0/2/6	0/0/0
l	10+25+27	3/6/4	1/2/0
m	16+25+26	3/2/8	0/0/0
n	6+12+25+27	0/0/0	0/0/1

In the following section the descried AU combinations will be specified for a better understanding of the results. All pictures shown are taken from the GibbonFACS manual (Waller et al., 2011)

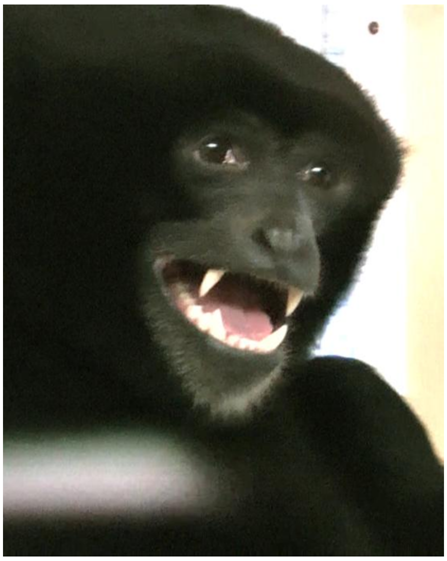

Fig.4 AU combination A

- AU combination A: consists of AU12 (defined as lip corner puller), AU25 (defined as lips part) and AU 26 (defined as jaw drop). Thus, the facial expression looks like a "grin" with parted lips and a slightly opened mouth (see **Figure 4**)

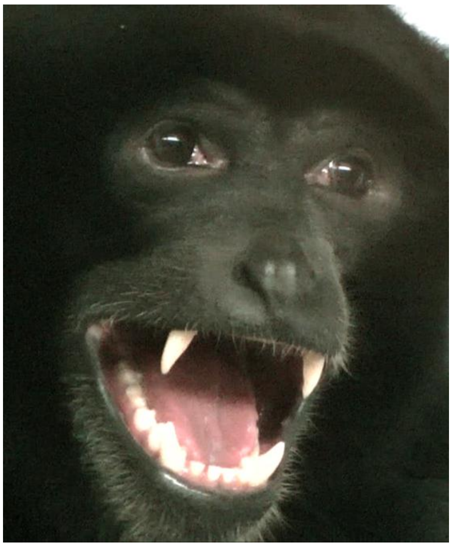

Fig.5 AU combination B

- AU combination B: consists of AU12, AU25 and AU27 (mouth stretch); the facial expression is similar to Au combination A with distinction in the opening grade of the mouth (**Figure 5**)

Fig.6 AU combination C

- AU combination C: consists of AU25 and AU26; basically like AU combination A, but without the “grin” (**Figure 6**)

Fig.7 AU combination D

- AU combination D: consists of AU25 and AU27; almost like AU combination B but without the “grin” (**Figure 7**)

Fig.8 AU combination E (only lower face)

- AU combination E: consists of AU10 (upper lip raiser), AU12, AU25 and AU27; like AU combination B, with the discrepancy that the upper teeth row is revealed (**Figure 8**)

Fig.9 AU combination F (only lower face)

- AU combination F: consists of AU10, AU12, AU25 and AU26; basically like AU combination A, but with revealed upper teeth rows (**Figure 9**)

Fig.10 AU combination G

- AU combination G: consists of AU12, AU16 (lower lip depressor), AU25 and AU26; looks like AU combination A, but the lower lip is pulled downwards and the lower teeth and gums get exposed (**Figure 10**)

Fig.11 AU combination H

- AU combination H: consists of AU12, AU16, AU25 and AU27; like AU combination G, but with fully opened mouth (**Figure 11**)

Fig.12 AU combination I (without AU 26)

- AU combination I: consists of AU12 and AU25; means there is a “grin” with parted lips (**Figure 12**)

Fig.13 AU combination J (in a silver gibbon)

- AU combination J: consists of AU25; only the lips are parted, nothing else (**Figure 13**)

Fig.14 AU combination K (other AUs present)

- AU combination K: consists of AU19 (tongue show), AU25 and AU26; looks like AU combination C with the difference of a protruded tongue (**Figure 14**)

Fig.15 AU combination L (only lower face)

- AU combination L: consists of AU10, AU25 and AU27; basically like AU combination D but with revealed upper teeth row (**Figure 15**)

Fig.16 AU combination M

- AU combination M: consists of AU16, AU25 and AU26; like AU combination C but with a pulled down lower lip and visible gums (**Figure 16**)

Fig.17 AU combination N (without AU 10)

- AU combination N: consists of AU6 (cheek raiser), AU12, AU25 and AU27; only observed in crested gibbons; like AU combination B, but with visible wrinkles beneath the eye due to the closing of these (**Figure 17**)

Siamangs

AU combinations A and B were the most frequently used facial expressions during play in general, the so called play faces. The main difference between these two facial expressions lies in the opening of the mouth. In AU combination A it is slightly and relaxed opened, whereas in AU combination B a muscle contraction is necessary, because the mouth is opened fairly to fully. Siamangs use AU combinations A and B significantly more often than all other AU combinations, as can be seen in **Figure 18** where only the four most common expressions are shown (for the Friedman test x^2 = 106.311, *df*= 13, *P* <0.001; for the Wilcoxon test for A versus C *Z*= -2.943, *P*= 0.003, *n*=12; for A versus D *Z*= -2.746, *P*= 0.006, *n*=12; for B versus C *Z*= -2.312, *P*= 0.021, *n*=12; for B versus D *Z*= -2.934, *P*= 0.003, *n*=12). Further no significant difference between the appearance of the AU combinations A and B was found (for the Wilcoxon test for A versus B *Z*= -0.235, *P*= 0.814, *n*= 12). No other significances were discovered, for detailed information see appendix 1.

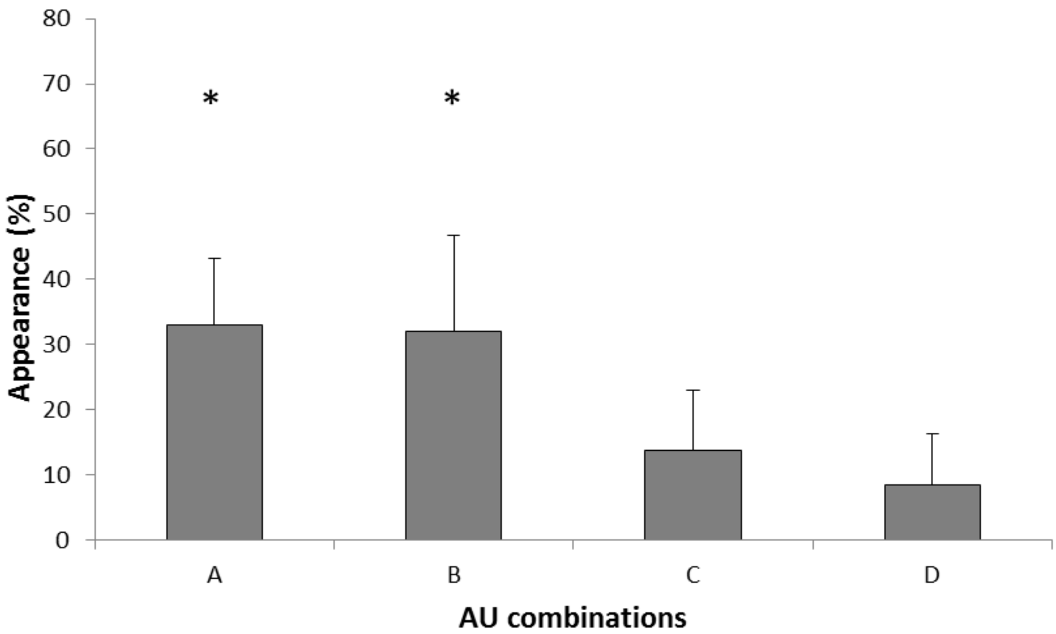

Fig.18 The 4 most common AU combinations in siamangs in general (* means $P< 0.05$)

Taking a closer look at play with direct eye-to-eye contact revealed a highly significant major appearance of combinations a and b, but not until combination e (for the Friedman-test x^2= 93.970, *df*= 9, *P* <0.001; for the Wilcoxon test for a versus b *Z*= -0.275, *P*= 0.783, *n*= 12; for a versus c *Z*= -1.683, *P*= 0.092, *n*= 11; for a versus e *Z*= -2.936, *P*= 0.003, *n*= 12; for b versus c *Z*= -1.244, *P*= 0.214, *n*= 11; for b versus e *Z*= -2.666, *P*= 0.008, *n*= 12). In contrast to this, these 2 combinations are only significantly higher than AU combination d (for the Wilcoxon test for a versus d *Z*= -2.549, *P*= 0.011, *n*= 12; for b versus d *Z*= -2.395, *P*= 0.017, *n*= 12), whereas combination c is only significant from e (for the Wilcoxon test for c versus d *Z*= 1.859, *P*= 0.064, *n*= 12; for c versus e *Z*= -2.524, *P*= 0.012, *n*= 12) (**Figure 19**).

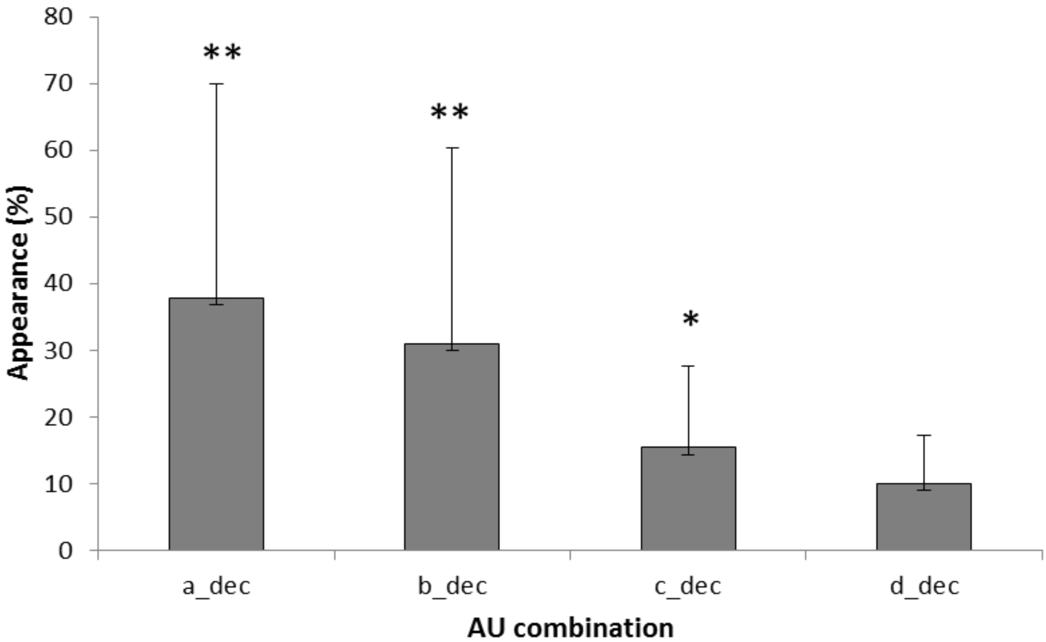

Fig.19 Mean appearances of the 4 most common shown facial expressions in siamangs with direct eye-to-eye contact (* has a P<0.05; ** has a P< 0.01)

The comparison of all AU combinations concerning play with eye contact found that AU combinations a (12+25+26) and b (12+25+27) are shown significantly more than all the other AU combinations. However, there was no difference between a and b (for the Friedman test x^2 = 69,217, *df*= 13, *P* <0.001; for the Wilcoxon test for a versus b *Z*= -0.507, *P*= 0.612, *n*= 10). In **Figure 20** only the four most common AU combinations are shown.

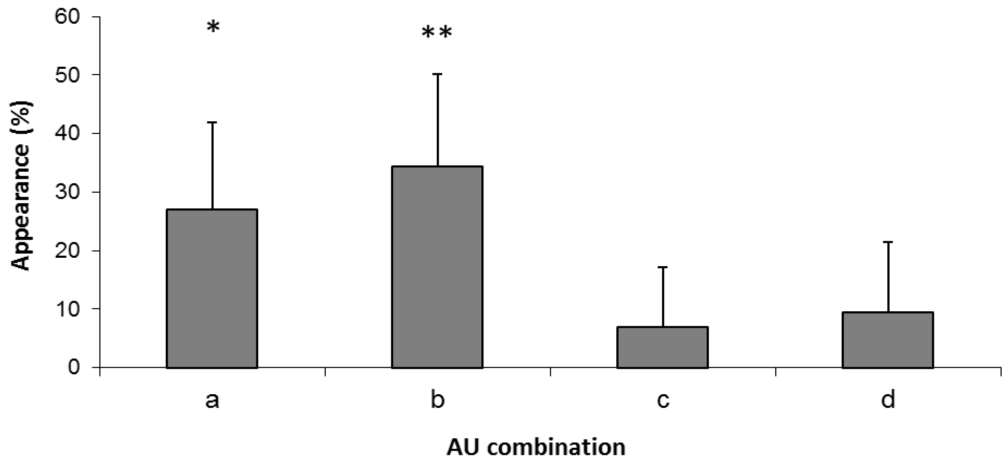

Fig.20 The mean appearance of the action unit combinations with eye contact in siamangs (* means P<0.05; ** means P<0.01)

When playing without eye contact siamangs use significantly more often AU combination a (12+25+26) than all the others (**Figure 21)** (Friedman test x^2 = 81,691, *df*= 13, *P* <0.001; Wilcoxon test for a versus b *Z*= -2.599, *P*= 0.009, *n*= 12; for a versus c *Z*= -2.551, *P*= 0.011, *n*= 12; for a versus f *Z*= -2.191, *P*= 0.028, *n*= 12). No significant differences were found for all other combinations (for the Wilcoxon test for b versus c *Z*= -0.714, *P*= 0.475, *n*= 12; for b versus f *Z*= -0.561, *P*= 0.575, *n*= 12; for c versus f *Z*= -0.051, *P*= 0.959, *n*= 12).

Thus, when they have no eye contact during play, they use action unit combination a more than all the other combinations.

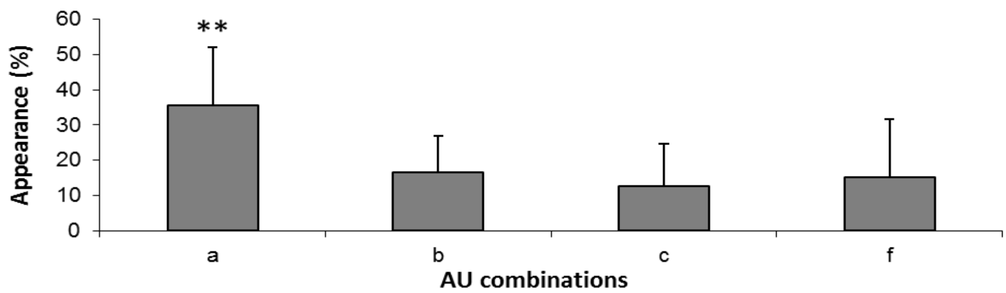

Fig.21 The mean appearance of action unit combinations in siamangs without eye contact (** means P<0.01)

Interesting results emerged when comparing facial expressions during direct eye-to-eye contact versus no eye contact at all while playing.

AU combination b appears significantly more in play bouts with direct eye-to-eye contact than in ones without (for the Friedman test x^2= 175.072, *df*= 27, *P*< 0.001; for the Wilcoxon test for b_nec versus b_dec *Z*= -1.956, *P*= 0.05, *n*= 12). Therefore combination b is used significantly more in the context of direct eye-to-eye contact (**Figure 22**).

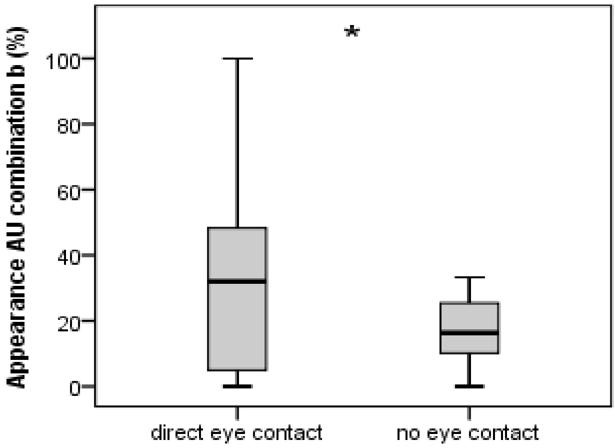

Fig.22 Appearance of a specific combination when comparing eye contact statuses (* means $P \leq 0.05$)

It also appeared that combination d is shown more in the context of direct eye-to-eye contact than of no eye contact during play bouts (for the Wilcoxon test for d_nec versus d_dec *Z*= -2.192, *P*= 0.028, *n*= 12; **Figure 23**).

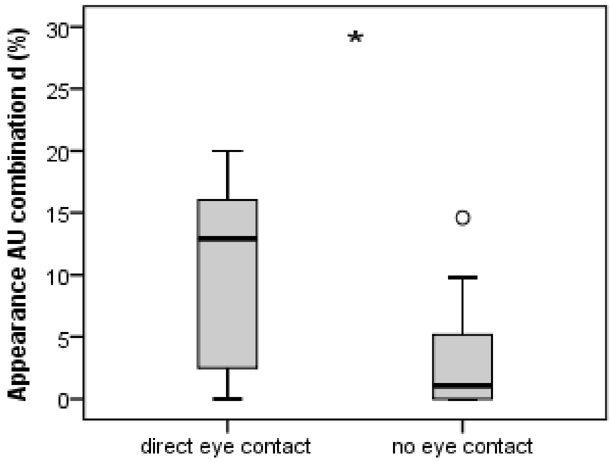

Fig.23 Appearance of a specifc AU combination in connection with eye contact (* means $P < 0.05$)

Furthermore siamangs present AU combination f exclusively when there is no eye contact during play, so there is a highly significant discrepancy concerning the appearance (for the Wilcoxon test Z= -2.666, P= 0.008, n= 12).

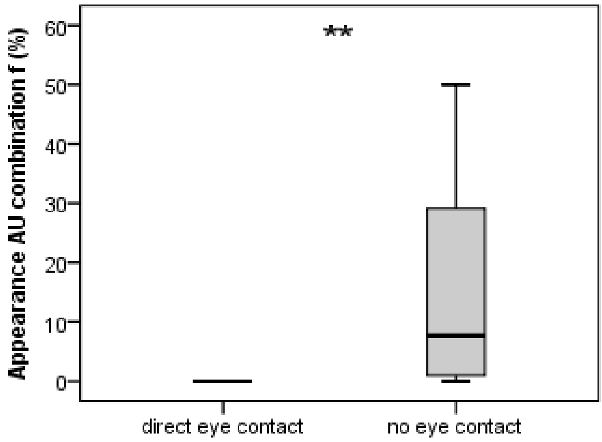

Fig.24 Appearance of a specific AU combination regarding eye contact (** means P< 0.01)

The comparison of every AU combination with and without eye contact revealed significance in the occurring of combination f (**Figure 25**).

Siamangs use this combination (12+25+27) significantly more often when they have no eye contact during play (Wilcoxon test for f vs. f_nec Z= -2,666, P= 0.008, n= 12).

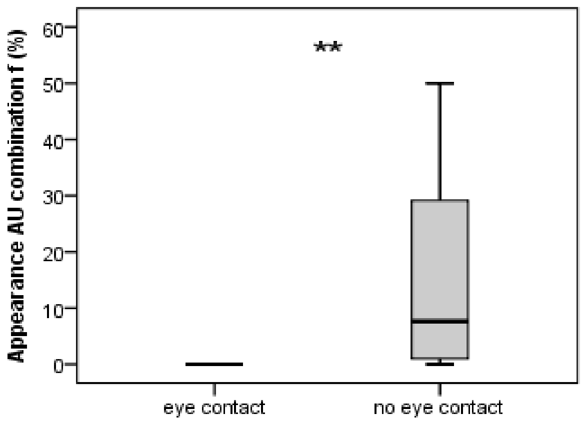

Fig.25 Differences in a specific combination with (ec) or without (nec) eye contact (** means a P< 0.01)

Age class comparison

Subadult siamangs show AU combination L significantly more often than adult individuals (Mann-Whitney U-test Z= -2.696, P= 0.007, n= 10).

However, because there were only one infant and one juvenile siamang that furthermore did not use AU combination L, the sample size was too small to be included into the statistical analysis (**Figure 26**).

Thus, the subadult animals show significantly more often their upper teeth row during play than adult ones.

Fig.26 Combination L in the different age classes in siamangs (* means P< 0.05)

No other differences were found when age classes were compared. None of the action unit combinations are used more frequent in one of the different age classes. Therefore, all animals use the same facial expression independently of their age class except combination L.

AU combination k typifies a special case which cannot be introduced in this chapter despise the significance because of the too small sample size (1 infant animal).

Sex differences

A significant difference was found when comparing the frequencies of the action unit combinations between males and females with no eye contact (**Figure 27**).

Not only all animals, especially females show significantly more often action unit combination f when there is no eye contact than males (for the Mann-Whitney U-test, Z= -2.208, P= 0.027, n= 12). So they reveal more often their upper teeth row during play when they have no eye contact with their play partner than the male animals.

There was no difference in the comparison of the frequency of the combinations with eye contact between the genders. All of them used the same facial expressions during play with eye contact and also the same frequencies irrespective of their gender.

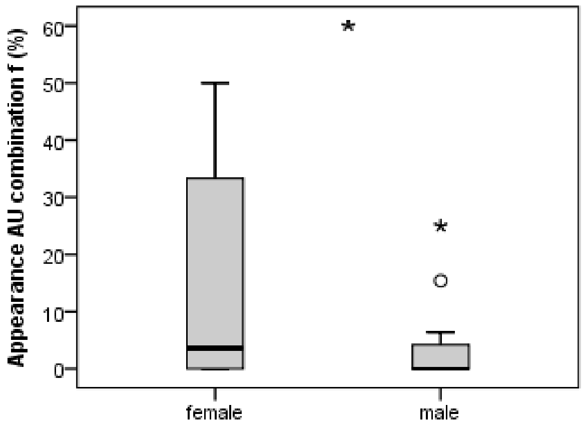

Fig.27 Appearance of a specific AU combination in the different sexes without eye contact (* means P< 0.05)

Crested gibbons

In crested gibbons, AU combination A was used significantly more often compared to all other combinations, except B. (for the Friedman test x^2 = 72.915, *df*= 13, *P* < 0.001; for the Wilcoxon test for A versus B *Z*= -1.125, *P*= 0.260, *n*= 9; for A versus C *Z*= -2.380, *P*= 0.017, *n*=9; for A versus D *Z*= -2.666, *P*= 0.008, *n*=9). No significant differences were found for the comparisons of the combinations E-N, but combination B appears significant more as from E (for the Wilcoxon test for B versus C *Z*= -0.560, *P*= 0.575, *n*= 9; for B versus D *Z*= -1.859, *P*= 0.063, *n*= 9; for B versus E *Z*= -2.366, *P*= 0.018, *n*= 9). **Figure 28** only shows the four most common facial expressions). Combination C shows significance from F (for the Wilcoxon test for C versus D *Z*= -1.521, *P*= 0.128, *n*= 9; for C versus E *Z*= -1.859, *P*= 0.063, *n*= 9; for C versus F *Z*= -2.201, *P*= 0.028, *n*= 9). In contrast to this, combination D is not significantly more shown than all other combinations.

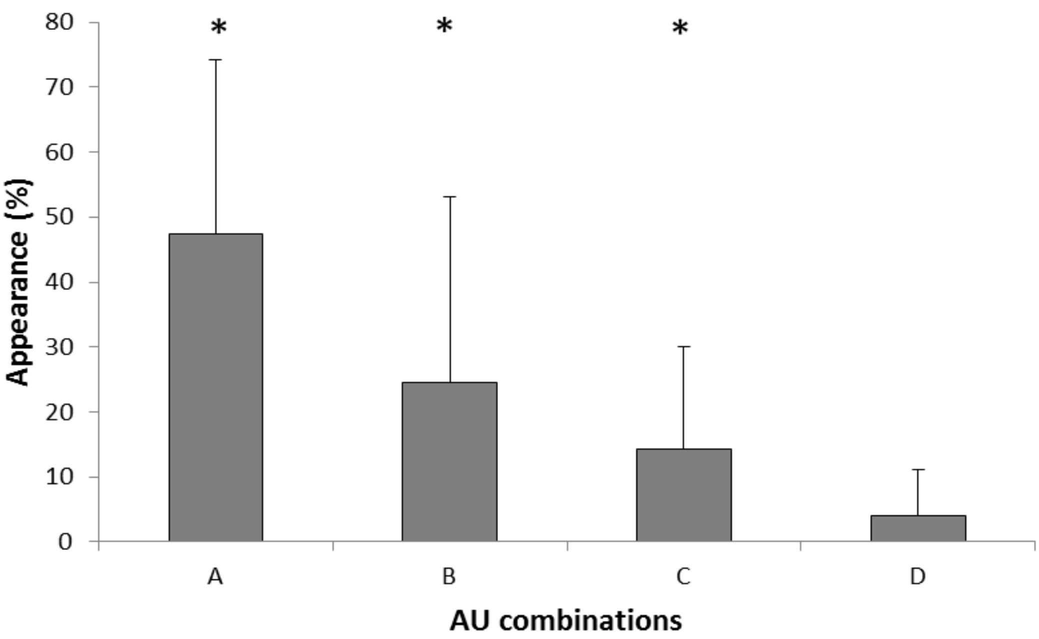

Fig.28 Appearance of the 4 most common AU combinations in crested gibbons in general (* means $P <$ 0.05)

Dealing with direct eye-to-eye contact reveals three more shown combinations, namely a, b and c. Whereas b and c are both significant in their appearance from combination g on (for the Friedman-test x^2= 47.815, *df*= 13, *P*< 0.001; for the Wilcoxon test for b versus g *Z*= -2.201, *P*= 0.028, *n*= 8; for c versus g *Z*= -2.201, *P*= 0.028, *n*= 8) and as well over e (for the Wilcoxon test for b versus e *Z*= -2.201, *P*= 0.028, *n*= 8; for c versus e *Z*= -2.201, *P*= 0.028), AU combination appears only significantly more than combinations e, g, h, k, m and n (for the Wilcoxon test for a versus e *Z*= -2.023, *P*= 0.043, *n*= 8; for a versus g *Z*= -2.023, *P*= 0.043, *n*= 8; for a versus h *Z*= -2.023, *P*= 0.043, *n*= 8; for a versus k *Z*= -2.023, *P*= 0.043, *n*= 8; for a versus m *Z*= -2.023, *P*= 0.043, *n*= 8; for a versus n *Z*= -2.023, *P*= 0.043, *n*= 8).

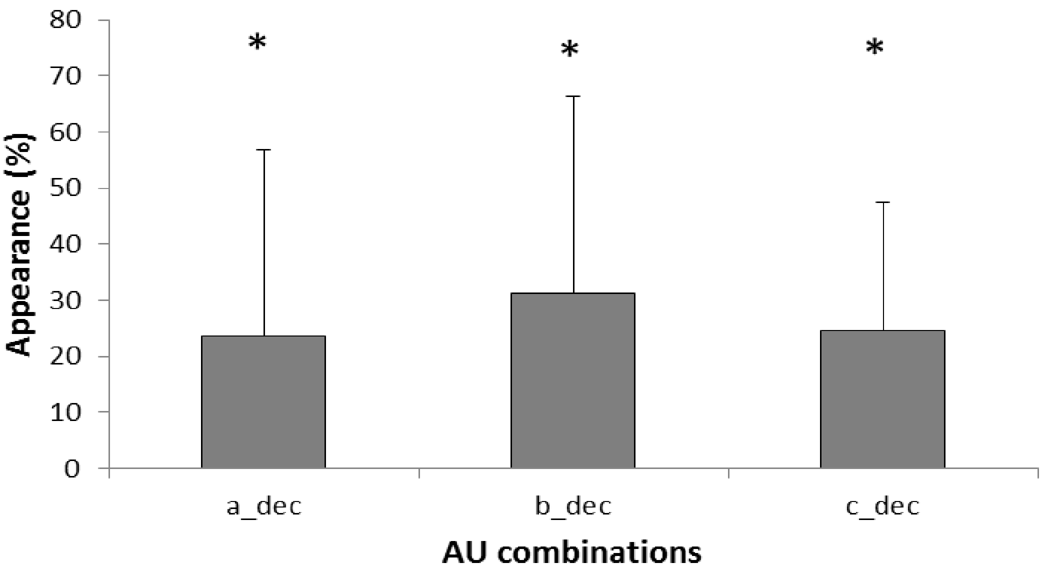

Fig.29 Appearance of the 3 most common AU combinations with direct eye-to-eye contact in crested gibbons (* means *P*< 0.05)

In **Figure 30** the 4 most common facial expressions in crested gibbons during play with eye contact are presented. In crested gibbons AU combination a (12+25+26) is only significantly more shown than AU combination d and f, but not more than b or c (for the Friedman test, x^2 = 56.087, *df*= 13, *P* <0.001; for the Wilcoxon test for a versus b, *Z*= -1.101, *P*= 0.271, *n*= 9; for a versus c, *Z*= -1.363, *P*= 0.173, *n*= 9; for a versus d, *Z*= -2.197, *P*= 0.028, *n*= 9; for a versus f, *Z*= -2.366, *P*= 0.018, *n*= 9).

Action unit combination b is not shown significantly more until f (for the Wilcoxon test for b versus c, *Z*= -0.507, *P*= 0.612, *n*= 9; for b versus d, *Z*= -1.521, *P*= 0.128, *n*= 9; for b versus f, *Z*= -2.023, *P*= 0.043, *n*= 9) and combination c is significant more shown than combination e (for the Wilcoxon test for c versus e *Z*= -2.201, *P*= 0.028, *n*= 9) and then again from combination g on (for the Wilcoxon test for c versus g *Z*= -2.201, *P*= 0.028, *n*= 9).

Between other AU combinations no significant differences were found.

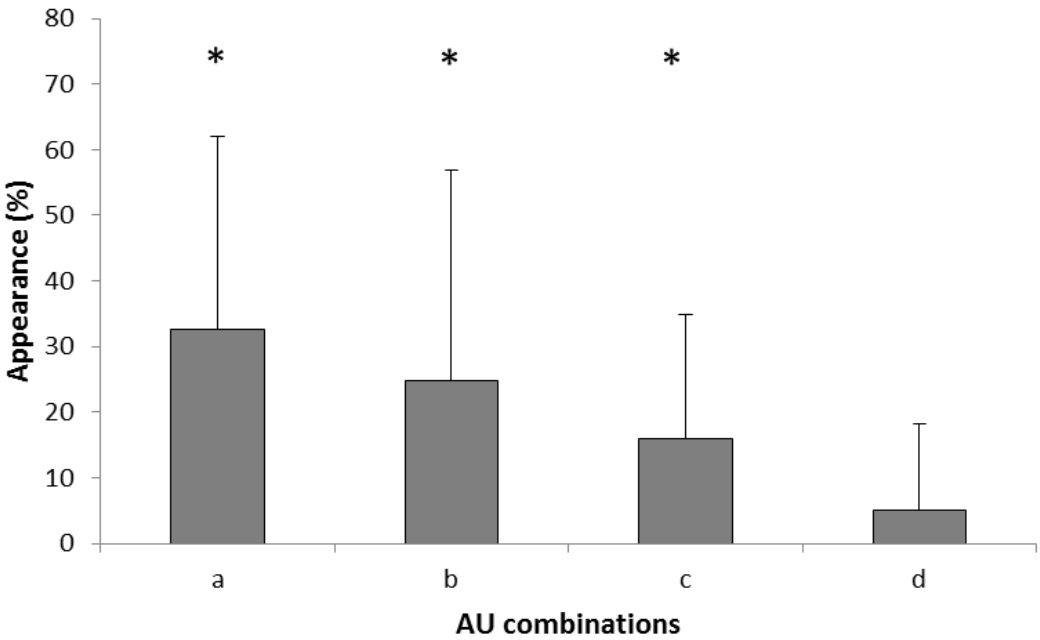

Fig.30 The appearance of the action unit combinations in crested gibbons when they have eye contact

During play with no eye contact AU combinations a, b and c are the three most used by crested gibbons, whereby action unit a is significantly more shown from c on (for the Friedman test, x^2 = 53.202, *df*= 13, *P* <0.001; for the Wilcoxon test for a versus b, *Z*= -1.541, *P*= 0.123, *n*= 9; for a versus c, *Z*= -2.201, *P*= 0.028, *n*= 9), although there is a trend that they tend to use b more than c (see **Figure 31**). Combination b occurred significantly more often than d and e, but not than c and f. As recently as combination g significance can be found compared to all remaining combinations (for the Wilcoxon test for b versus c *Z*= -0.507, *P*= 0.612, *n*= 9; for b versus d *Z*= -2.023, *P*= 0.043, *n*= 9; for b versus e *Z*= -2.201,

P= 0.028, n= 9; for b versus f Z= -1.826, P= 0.068; for b versus g Z= -2.197, P= 0.028, n= 9).

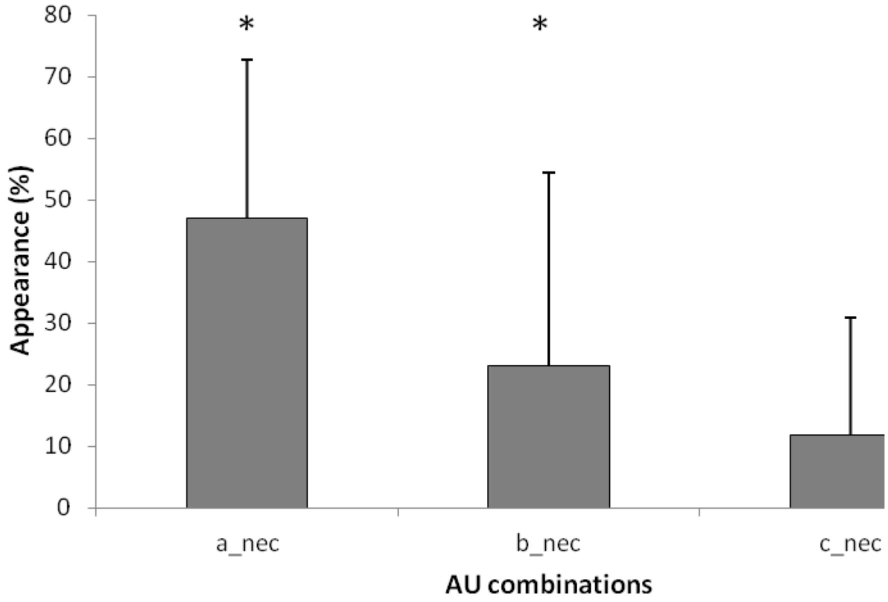

Fig.31 The appearance of the action unit combinations in crested gibbons when they have no eye contact

No other differences were discovered (for further information see the appendix).

Sex comparison

No differences were found between the genders, all facial expressions were used equally, not matter if male or female.

Age class comparison

Taking a closer look on comparing facial expressions in age classes revealed no differences in the use of such. All of them were used equally through all age classes.

Siamangs versus crested gibbons

The comparison of the frequencies of the different combinations of AUs between the two species revealed a significant difference for AU combination N (**Figure 32)**.

Thus, as opposed to siamangs, crested gibbons use this facial expression during play (Mann-Whitney U-test, $Z= -2.101$, $P = 0.036$, $n = 21$). No other significances were found between the two species.

In summary, those results show that there are no differences in the variety and frequency of facial expressions used during play between siamangs and crested gibbons and further, that they use the same repertoire of AU combinations for their play faces.

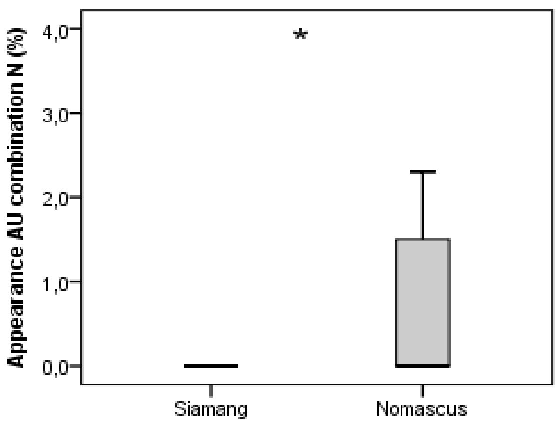

Fig.32 Comparison of the appearance of the AU combination N between crested gibbons and siamangs in general (* means $P< 0.05$)

Significance occurred when comparing facial expression in the context of direct eye-to-eye contact among the two species (for the Mann-Whitney U-test $Z= -2.488$, $P= 0.013$, $n= 21$). Thus, crested gibbons use combination f significantly more in direct eye-to-eye issues than siamangs do.

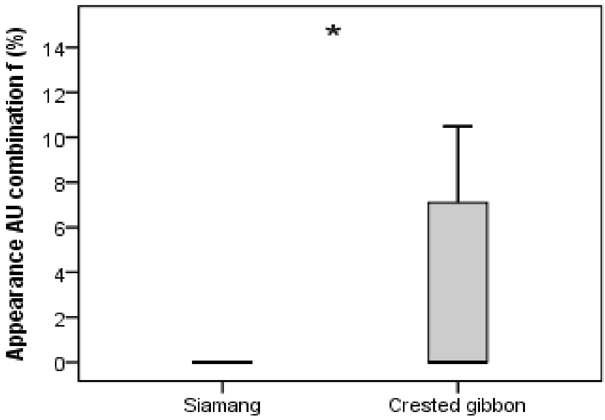

Fig.33 Appearance of a specific combination when comparing the different species concerning direct eye-to-eye contact (* means $P < 0.05$)

Discussion

This thesis gives one of the first accurate insights into facial expressions during social interactions, in this case play, in gibbons. This was possible because of the GibbonFACS, which enables detailed and especially non-biased, objective descriptions.

General discussion

In this project, a total of 8 different AUs and fourteen of their combinations were found in siamangs and crested gibbons. Because all combinations except three occur in both species, it can be assumed that these expressions are used universal in all other gibbon species as well. This can be confirmed by the findings of Burrows et al. in 2011, where it was descried that individuals of *Hylobates lar, Hylobates muelleri*, *Symphalangus syndactylus* and *Nomascus gabriellae* possess identical muscles and are therefore able to show the same facial expressions (Waller et al., 2011) and those of Liebal et al. in 2004 that "*both siamangs and white handed gibbons seem to use very similar…..facial expressions".*

The two most common combinations differed only in regard to the extent of mouth opening. A possibility for the differences between them could be that the AUs for "Jaw drop" and "Mouth stretch", 26 and 27, only differ in the degree of the opening of the mouth. Whereas AU26 is described as "*…the jaw is dropped loosely by relaxation of non-mimetical (masticatory) muscles"* (Waller et al., 2011), AU27 is defined as "*…the jaw is pulled downwards by several non-mimetical muscle actions"* (Waller et al., 2011). So it resulted, that sometimes the two of them were hard to distinguish.

Aside from the opening of the mouth most facial expressions tagged themselves by the subducting of the mouth corners into a smile, the parting of the lips and the openness of the eyes. These most common play faces were seen in average in siamangs in over 30%, in crested gibbons AU combination A even in over 40% of all possible alternatives.

The occurrence of the AU combination N in crested gibbons could be explained with the intensity of play in the 2 species. In the crested gibbons more juvenile, infant and subadult individuals were kept together, whereas in the siamangs only 2 subadult siblings who played a lot with each other could be observed. The play between young siblings was always a bit more intensive than the one between one adult with his offspring. Therefore it can be assumed that in more intensive play bouts, AU combination N occurs more often than in gentler ones.

Siamangs

Age class comparison

The significant occurrence of combination L in subadult siamangs includes the showing of the teeth, in addition to a wide-ripped mouth without the subducted mouth corners which can be interpreted as a threatening sign. In subadult animals play fighting can easily become serious and escalate to serious aggression (Fagen, 1981; Biben, 1986). Because gibbons have no forms of dominance hierarchies (Chivers, 1976) it would bring no benefits but great disadvantages for the whole family if the play would escalate and one of the play partners would be hurt. It can be suspected that, under these circumstances, they firstly show this threat face in order to prevent the play from escalating because especially subadult animals are already strong enough to be able to seriously hurt each other when play would escalate.

Sex differences

In the study of Liebal et al. in 2004 it was discovered that only male siamangs performs the so called “grin”, which is defined in this thesis as AU combination A, in general. In contrast to this finding, here it was descried that males as well as females show this facial expression at least in the playing context with no differences in the number of occurrence.

Additionally, no other differences were found between the sexes according to their facial movements in playing bouts, neither in siamangs nor in crested gibbons. This allows the conclusion that in general, males and females both use the same repertoire of facial expressions in play, so there is no dimorphism, supporting the findings of Chau et al. in 2008 that "*monogamous mammals show little sexual dimorphism in contact play behaviour" (*Chau et al., 2008).

When comparing the play faces of siamangs and crested gibbons with focus on eye contact in 288 cases occurred eye contact between the sender and the receiver of the play bout and the other way round, and in 359 cases play took place without any eye contact. Even direct eye-to-eye contact appeared in a total of 190 cases without the play escalating into a fight. That confutes the declaration of Chevalier-Skolnikoff that eye-to-eye contact is avoided in play bouts (Chevalier-Skolnikoff, 1973, 1974a, 1974b) and supports the proposition of Liebal et al. in 2004.

When taking a closer look at play of siamangs with direct eye-to-eye contact taking place it attracts attention that combinations a and b (and in some cases even c) appear more than others. Therefore the most common play faces take place most of the time when there is direct eye-to-eye contact between the two playing partners. Thus, it can be supposed that at least combination a and b are "the" playing faces which have been searched for. Even when there is only eye contact from one of the playing individuals AU combination a or b is shown more than all others which also confirms the former declaration.

However, in the context of no eye contact siamangs also show AU combination a more than all others which indicates the universal use of this typical play face.

In the single comparison of the unique AU combinations with direct eye-to-eye and no eye contact emerged a difference in the use of combination b, d and f.

AU combination b was in conjunction with direct eye-to-eye contact more important than without. It has already been shown that AU combination b is one of the most important play faces in gibbons in general, so apparently the subducted mouth corners in addition to an opened mouth is a very important visual signal sign which is used intentionally during a play bout. Thus, this typical play face is a clear visual signal ensuring that this is only play without aggressive intentions in siamangs.

In contrast to this finding combination d also has a higher incidence when there is direct eye-to-eye contact compared to no eye contact. This could be some kind of alleviated threat face due to the absence of the uncovered upper teeth row. Another alleviated threat face, in this thesis AU combination f, is exclusively shown in context of no eye contact, probably to prevent the play from escalating into a serious fight. These expressions are classified as alleviated threat faces because either the revealing of the upper teeth row is missing (as in combination d) or the mouth corners are still subducted (like in combination f) which is categorised as a clear sign for play.

The finding of females using more often combination f than males in play without eye contact is difficult to discuss, because there are no acceptably explanations for this behaviour. Maybe a more precisely study on the differences in facial expressions between males and females has to be made.

Crested gibbons

Taking a closer look at crested gibbons, interestingly they show combination a, b and c the most but with insufficient significance. Nevertheless a clear trend is visible for them to be the facial expressions that are used to a greater extent than other ones with direct eye-to-eye contact.

Very similar results were found for the context of eye contact, but with more statistical significance. Even in the context of eye contact the combinations a, b and c dominate significantly the appearance of facial expressions.

Even in the context of no eye contact at all, AU combinations a and b are shown more often than the others. These findings confirm the findings of the most common play faces in general. Further, they use the same facial expressions, no matter if there is direct eye-to-eye contact, eye contact from one individual to the other or no eye contact at all.

Sex differences

No differences could be found when comparing sex differences. A possible explanation for these results could be the small sample size (for sex differences n= 4) of crested gibbons, because a reliable differentiation between the sexes is feasible at the earliest of 5-8 years, the time of sexual maturity (Geissmann, 2003). Thus, only 3 females and 1 male could be identified without doubt.

Age group comparison

In crested gibbons the so called “chasing play” (where one individual is chasing the other; Chivers, 1974) has been observed most of the time. Chasing bouts are accompanied by very fast movements of the playing individuals therefore it was not always possible to get analysable data because often the whole face was not visible or no facial expression noticeable. Maybe this could also be a reason for the lack of significance when comparing age groups.

Because chase is more intensive than other forms of play, it is consequential that crested gibbons use combination f in direct eye-to-eye situation more than siamangs. In addition, every of the 3 crested gibbon groups consisted of at least one youngster and because play occurs most of the time between the younger animals (Beach, 1945), it can be assumed that they need this alleviated threatening sign to be able to show constraints before play would escalate.

Conclusion and Outlook

So this leads to the conclusion that expressions a, b and c are the most important ones concerning direct eye-to-eye contact, eye contact as well as no eye contact in order to signal “it’s just play” by the use of subducted mouth corners or the revealing of the upper teeth row, or to give an alleviated warning sign by the absence of these subducted mouth corners or the revealing of the upper teeth to prevent the play from escalating into a real fight. These findings show that at least in play an intentional use of facial expressions is absolutely common in gibbons. Play bouts hardly ever escalate into serious fights because of the directional use of facial expressions as warning signals.

These findings differ from the description of a play face already given by Orgeldinger in 1999. In contrast to his description of the play face in this work neither a squinting of the eyes nor fully bared teeth were shown, in addition to this it occurred intentional with direct eye-to-eye contact every now and then unlike it was supposed from Chevalier-Skolnikoff (1974b).

Another description of facial expressions occurring in play contexts was made by Liebal et al. who used terms like "mouth-open-half” and “grin” (Liebal et al., 2004). These observations accord with those made in the context of this thesis, because “grin” can be equalized with AU 12 and “mouth-open-half” with AU 25+26. This confirms the declaration about the play face made in this work.

Interestingly no great differences were found between the sexes, but this could be explained by the monogamous lifestyle of gibbons, because the same facial demands are made on male, female and their offspring concerning play. Play faces should be universal at least within a family group to avoid misunderstandings and to prevent escalation of play into fights.

With these findings it is shown that the play faces are universal for at least siamangs and crested gibbons. To get a studier corroboration of the universality of these play faces further studies with other gibbon species as well as monkeys, great apes and also humans would be very interesting. At least in their basic descriptions they seem to be related, for example gorillas are “*placing open mouths on each other*” (Brown, 1988) and in chimpanzees the play face is described as opened mouth with lips partially covering the teeth and raised lip corners (van Hooff, 1972). Maybe there is universal play face, but to be able to compare this more data are highly necessary. Furthermore gibbons possess a lot more facial expressions than it was assumed when comparing their number of muscles with great apes (Waller et al., subm.), therefore it would be very interesting to take a closer look on facial expressions in further social interactions as well to get better knowledge and be able to compare them with monkeys, great apes and humans for a better understanding of our common evolution and our close affinity.

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Appendix

Table 5 Wilcoxon test for the general appearance of the AU combinations in both species

	Art			
	Siamang		Nomascus	
	Z	Asymptotische Signifikanz (2-seitig)	Z	Asymptotische Signifikanz (2-seitig)
B - A	-,235	,814	-1,125	,260
C - A	-2,934	,003	-2,380	,017
D - A	-2,746	,006	-2,666	,008
E - A	-3,059	,002	-2,666	,008
F - A	-3,059	,002	-2,521	,012
G - A	-3,061	,002	-2,666	,008
H - A	-3,059	,002	-2,666	,008
I - A	-3,059	,002	-2,666	,008
J - A	-2,934	,003	-2,666	,008
K - A	-3,059	,002	-2,666	,008
L - A	-3,059	,002	-2,666	,008
M - A	-2,934	,003	-2,666	,008
N - A	-3,059	,002	-2,666	,008
C - B	-2,312	,021	-,560	,575
D - B	-2,934	,003	-1,859	,063
E - B	-3,059	,002	-2,366	,018
F - B	-3,059	,002	-2,366	,018
G - B	-3,061	,002	-2,366	,018
H - B	-3,059	,002	-2,366	,018
I - B	-3,059	,002	-2,028	,043
J - B	-3,061	,002	-2,366	,018
K - B	-3,059	,002	-2,366	,018
L - B	-3,059	,002	-2,366	,018
M - B	-3,059	,002	-2,366	,018
N - B	-3,059	,002	-2,366	,018
D - C	-1,334	,182	-1,521	,128
E - C	-2,805	,005	-1,859	,063
F - C	-2,701	,007	-2,201	,028
G - C	-2,803	,005	-2,366	,018
H - C	-2,193	,028	-2,366	,018
I - C	-2,803	,005	-2,366	,018

J - C	-2,668	,008	-2,197	,028
K - C	-2,803	,005	-2,366	,018
L - C	-2,803	,005	-2,366	,018
M - C	-2,599	,009	-2,366	,018
N - C	-2,803	,005	-2,366	,018
E - D	-2,521	,012	-,405	,686
F - D	-2,312	,021	-,674	,500
G - D	-2,701	,007	-1,826	,068
H - D	-2,045	,041	-1,826	,068
I - D	-2,803	,005	-1,826	,068
J - D	-2,803	,005	-1,095	,273
K - D	-2,803	,005	-1,826	,068
L - D	-2,599	,009	-1,826	,068
M - D	-2,401	,016	-1,826	,068
N - D	-2,803	,005	-1,826	,068
F - E	-,524	,600	-,405	,686
G - E	-,674	,500	-1,841	,066
H - E	-,943	,345	-1,841	,066
I - E	-2,023	,043	-1,214	,225
J - E	-,135	,893	-1,604	,109
K - E	-,943	,345	-1,841	,066
L - E	-,105	,917	-1,604	,109
M - E	-,169	,866	-1,841	,066
N - E	-2,023	,043	-1,826	,068
G - F	-,105	,917	-1,342	,180
H - F	-,365	,715	-1,342	,180
I - F	-,405	,686	-,535	,593
J - F	-,314	,753	-,365	,715
K - F	-,730	,465	-1,342	,180
L - F	-,365	,715	-,365	,715
M - F	-,135	,893	-1,342	,180
N - F	-1,604	,109	-,730	,465
H - G	-,365	,715	,000	1,000
I - G	-1,219	,223	-1,342	,180
J - G	-,535	,593	-1,342	,180
K - G	-,535	,593	,000	1,000
L - G	-,676	,499	-1,604	,109
M - G	-,405	,686	,000	1,000
N - G	-1,604	,109	-1,604	,109
I - H	-,135	,892	-1,342	,180
J - H	-,674	,500	-1,342	,180
K - H	-,535	,593	,000	1,000
L - H	-,524	,600	-1,604	,109
M - H	,000	1,000	,000	1,000

N - H	-1,342	,180	-1,604	,109
J - I	-,943	,345	,000	1,000
K - I	-,368	,713	-1,342	,180
L - I	-1,483	,138	-,365	,715
M - I	-,406	,684	-1,342	,180
N - I	-1,633	,102	,000	1,000
K - J	-,730	,465	-1,342	,180
L - J	-,169	,866	-,552	,581
M - J	-,365	,715	-1,342	,180
N - J	-1,826	,068	-,730	,465
L - K	-,674	,500	-1,604	,109
M - K	-,535	,593	,000	1,000
N - K	-1,000	,317	-1,604	,109
M - L	,000	1,000	-1,604	,109
N - L	-1,826	,068	-1,000	,317
N - M	-1,342	,180	-1,604	,109

Table 6 Wilcoxon test for comparing the different AU combinations with eye contact in siamangs

	Z	Asymptotische Signifikanz (2-seitig)
b - a	-,507	,612
c - a	-2,547	,011
d - a	-2,073	,038
e - a	-2,601	,009
f - a	-2,668	,008
g - a	-2,668	,008
h - a	-2,668	,008
i - a	-2,666	,008
j - a	-2,521	,012
k - a	-2,668	,008
l - a	-2,666	,008
m - a	-2,701	,007
n - a	-2,668	,008
c - b	-2,550	,011
d - b	-2,310	,021
e - b	-2,803	,005
f - b	-2,805	,005
g - b	-2,803	,005
h - b	-2,803	,005

Table 7 Wilcoxon test for comparing the different AU combinations without eye contact in siamangs

	Z	Asymptotische Signifikanz (2-seitig)
b - a	-2,599	,009
c - a	-2,551	,011
d - a	-2,934	,003
e - a	-2,934	,003
f - a	-2,191	,028
g - a	-2,936	,003
h - a	-2,936	,003
i - a	-2,936	,003
j - a	-2,803	,005
k - a	-2,936	,003
l - a	-2,629	,009
m - a	-2,805	,005
n - a	-2,936	,003
c - b	-,714	,475
d - b	-2,666	,008
e - b	-2,803	,005
f - b	-,561	,575
g - b	-2,803	,005
h - b	-2,666	,008

i - b	-2,805	,005
j - b	-2,666	,008
k - b	-2,803	,005
l - b	-2,803	,005
m - b	-2,805	,005
n - b	-2,805	,005
d - c	-,507	,612
e - c	-,679	,497
f - c	-2,023	,043
g - c	-2,023	,043
h - c	-,845	,398
i - c	-1,084	,279
j - c	-,507	,612
k - c	-2,023	,043
l - c	-1,014	,310
m - c	-1,153	,249
n - c	-2,023	,043
e - d	-1,352	,176
f - d	-2,366	,018
g - d	-2,197	,028
h - d	-1,352	,176
i - d	-1,260	,208
j - d	-1,262	,207
k - d	-2,366	,018
l - d	-1,823	,068
m - d	-1,540	,123
n - d	-2,366	,018
f - e	-1,604	,109
g - e	-,944	,345
h - e	-,365	,715
i - e	,000	1,000
j - e	-,474	,635
k - e	-1,461	,144
l - e	-,314	,753
m - e	-1,069	,285
n - e	-1,604	,109
g - f	-1,604	,109
h - f	-1,826	,068
i - f	-1,826	,068
j - f	-2,201	,028
k - f	-1,000	,317
l - f	-2,023	,043
m - f	-1,342	,180
n - f	,000	1,000

i - b	-2,803	,005
j - b	-2,666	,008
k - b	-2,803	,005
l - b	-1,836	,066
m - b	-2,293	,022
n - b	-2,803	,005
d - c	-2,380	,017
e - c	-2,521	,012
f - c	-,051	,959
g - c	-2,521	,012
h - c	-2,073	,038
i - c	-2,521	,012
j - c	-1,836	,066
k - c	-2,380	,017
l - c	-2,366	,018
m - c	-1,660	,097
n - c	-2,521	,012
e - d	-2,201	,028
f - d	-1,511	,131
g - d	-1,992	,046
h - d	-1,183	,237
i - d	-1,992	,046
j - d	-,339	,735
k - d	-1,992	,046
l - d	-,700	,484
m - d	-1,014	,310
n - d	-2,201	,028
f - e	-2,599	,009
g - e	-,365	,715
h - e	-,535	,593
i - e	,000	1,000
j - e	-1,826	,068
k - e	-,447	,655
l - e	-1,604	,109
m - e	-,730	,465
n - e	-1,000	,317
g - f	-2,429	,015
h - f	-2,090	,037
i - f	-2,521	,012
j - f	-1,859	,063
k - f	-2,192	,028
l - f	-2,395	,017
m - f	-2,040	,041
n - f	-2,666	,008

h - g	-,406	,684
i - g	-,944	,345
j - g	-1,355	,176
k - g	-,535	,593
l - g	-1,352	,176
m - g	-,135	,893
n - g	-1,604	,109
i - h	-,105	,917
j - h	-,840	,401
k - h	-1,095	,273
l - h	-,135	,893
m - h	-,314	,753
n - h	-1,826	,068
j - i	-1,219	,223
k - i	-1,483	,138
l - i	-,405	,686
m - i	-,631	,528
n - i	-1,826	,068
k - j	-1,992	,046
l - j	-,420	,674
m - j	-1,270	,204
n - j	-2,201	,028
l - k	-1,782	,075
m - k	-,535	,593
n - k	-1,000	,317
m - l	-,943	,345
n - l	-2,023	,043
n - m	-1,342	,180

h - g	,000	1,000
i - g	-1,342	,180
j - g	-1,753	,080
k - g	,000	1,000
l - g	-,943	,345
m - g	-,365	,715
n - g	-1,604	,109
i - h	-,535	,593
j - h	-,943	,345
k - h	-,447	,655
l - h	-,734	,463
m - h	-,730	,465
n - h	-1,342	,180
j - i	-2,023	,043
k - i	-,447	,655
l - i	-1,214	,225
m - i	-,730	,465
n - i	-1,342	,180
k - j	-1,753	,080
l - j	-,105	,917
m - j	-,943	,345
n - j	-2,023	,043
l - k	-,944	,345
m - k	-,730	,465
n - k	-1,000	,317
m - l	-,420	,674
n - l	-1,826	,068
n - m	-1,604	,109

Table 8 Wilcoxon test for comparing the appearance of each AU combination with direct (dec) and no eye contact (nec) in siamangs

	Z	Asymptotische Signifikanz (2-seitig)
a_nec - a_dec	-,445	,657
b_nec - b_dec	-1,956	,050
c_nec - c_dec	-,533	,594
d_nec - d_dec	-2,192	,028
e_nec - e_dec	-1,000	,317
f_nec - f_dec	-2,666	,008
g_nec - g_dec	-1,069	,285
h_nec - h_dec	-,535	,593

Table 9 Wilcoxon test for comparing the appearance of each AU combination with eye and without eye contact (nec) in siamangs

	Z	Asymptotische Signifikanz (2-seitig)
a_nec - a	-1,423	,155
b_nec - b	-1,867	,062
c_nec - c	-1,540	,123
d_nec - d	-,980	,327
e_nec - e	-1,461	,144
f_nec - f	-2,666	,008
g_nec - g	-1,089	,276
h_nec - h	-,365	,715

i_nec - i_dec	,000	1,000
j_nec - j_dec	-,338	,735
k_nec - k_dec	-1,000	,317
l_nec - l_dec	-,405	,686
m_nec - m_dec	-1,604	,109
n_nec - n_dec	,000	1,000

i_nec - i	-1,214	,225
j_nec - j	,000	1,000
k_nec - k	-1,000	,317
l_nec - l	-,420	,674
m_nec - m	-,674	,500
n_nec - n	,000	1,000

Table 10 Kruskal Wallis test to compare the AU combinations for differences in the various age groups in siamangs and crested gibbons

	Art					
	Siamang			Crested gibbon		
	Chi-Quadrat	df	Asymptotische Signifikanz	Chi-Quadrat	df	Asymptotische Signifikanz
A	2,099	3	,552	1,500	2	,472
B	2,626	3	,453	,894	2	,640
C	4,525	3	,210	4,440	2	,109
D	3,562	3	,313	2,880	2	,237
E	1,617	3	,656	3,337	2	,189
F	,738	3	,864	,833	2	,659
G	2,935	3	,402	,000	2	1,000
H	1,558	3	,669	,000	2	1,000
I	2,711	3	,438	1,875	2	,392
J	1,851	3	,604	,646	2	,724
K	11,000	3	,012	,000	2	1,000
L	8,892	3	,031	4,765	2	,092
M	1,558	3	,669	,000	2	1,000
N	,000	3	1,000	4,765	2	,092

Table 11 Mann-Whitney-U test to compare the AU combinations for differences in the sexes in siamangs

	Mann-Whitney-U	Wilcoxon-W	Z	Asymptotische Signifikanz (2-seitig)	Exakte Signifikanz [2*(1-seitig Sig.)]
a	16,000	44,000	-,244	,807	,876
b	11,000	26,000	-1,057	,290	,343
c	15,000	43,000	-,413	,679	,755
d	16,500	31,500	-,173	,862	,876
e	15,000	30,000	-,845	,398	,755
f	4,000	32,000	-2,208	,027	,030

g	15,000	30,000	-,533	,594	,755
h	12,500	27,500	-1,248	,212	,432
i	12,500	27,500	-1,248	,212	,432
j	12,000	27,000	-,996	,319	,432
k	15,000	30,000	-,845	,398	,755
l	15,000	30,000	-,483	,629	,755
m	16,000	31,000	-,320	,749	,876
n	17,500	45,500	,000	1,000	1,000

Table 12 Wilcoxon test for comparing the different AU combinations with direct eye-to-eye contact (dec) in crested gibbons

	Z	Asymptotische Signifikanz (2-seitig)
b_dec - a_dec	-,493	,622
c_dec - a_dec	-,135	,893
d_dec - a_dec	-1,214	,225
e_dec - a_dec	-2,023	,043
f_dec - a_dec	-1,483	,138
g_dec - a_dec	-2,023	,043
h_dec - a_dec	-2,023	,043
i_dec - a_dec	-1,826	,068
j_dec - a_dec	-1,682	,093
k_dec - a_dec	-2,023	,043
l_dec - a_dec	-1,826	,068
m_dec - a_dec	-2,023	,043
n_dec - a_dec	-2,023	,043
c_dec - b_dec	-,405	,686
d_dec - b_dec	-1,572	,116
e_dec - b_dec	-2,201	,028
f_dec - b_dec	-1,363	,173
g_dec - b_dec	-2,201	,028
h_dec - b_dec	-2,201	,028
i_dec - b_dec	-1,778	,075
j_dec - b_dec	-2,023	,043
k_dec - b_dec	-2,201	,028
l_dec - b_dec	-2,201	,028
m_dec - b_dec	-2,201	,028
n_dec - b_dec	-2,201	,028
d_dec - c_dec	-1,483	,138
e_dec - c_dec	-2,201	,028
f_dec - c_dec	-1,367	,172
g_dec - c_dec	-2,201	,028

h_dec - c_dec	-2,201	,028
i_dec - c_dec	-2,023	,043
j_dec - c_dec	-2,207	,027
k_dec - c_dec	-2,201	,028
l_dec - c_dec	-2,023	,043
m_dec - c_dec	-2,201	,028
n_dec - c_dec	-2,201	,028
e_dec - d_dec	-1,342	,180
f_dec - d_dec	,000	1,000
g_dec - d_dec	-1,342	,180
h_dec - d_dec	-1,342	,180
i_dec - d_dec	-1,342	,180
j_dec - d_dec	-,535	,593
k_dec - d_dec	-1,342	,180
l_dec - d_dec	-,535	,593
m_dec - d_dec	-1,342	,180
n_dec - d_dec	-1,342	,180
f_dec - e_dec	-1,342	,180
g_dec - e_dec	,000	1,000
h_dec - e_dec	,000	1,000
i_dec - e_dec	-1,000	,317
j_dec - e_dec	-1,000	,317
k_dec - e_dec	,000	1,000
l_dec - e_dec	-1,000	,317
m_dec - e_dec	,000	1,000
n_dec - e_dec	,000	1,000
g_dec - f_dec	-1,342	,180
h_dec - f_dec	-1,342	,180
i_dec - f_dec	-,816	,414
j_dec - f_dec	-,816	,414
k_dec - f_dec	-1,342	,180
l_dec - f_dec	-1,069	,285
m_dec - f_dec	-1,342	,180
n_dec - f_dec	-1,342	,180
h_dec - g_dec	,000	1,000
i_dec - g_dec	-1,000	,317
j_dec - g_dec	-1,000	,317
k_dec - g_dec	,000	1,000
l_dec - g_dec	-1,000	,317
m_dec - g_dec	,000	1,000
n_dec - g_dec	,000	1,000
i_dec - h_dec	-1,000	,317
j_dec - h_dec	-1,000	,317
k_dec - h_dec	,000	1,000

l_dec - h_dec	-1,000	,317
m_dec - h_dec	,000	1,000
n_dec - h_dec	,000	1,000
j_dec - i_dec	,000	1,000
k_dec - i_dec	-1,000	,317
l_dec - i_dec	-,447	,655
m_dec - i_dec	-1,000	,317
n_dec - i_dec	-1,000	,317
k_dec - j_dec	-1,000	,317
l_dec - j_dec	-,447	,655
m_dec - j_dec	-1,000	,317
n_dec - j_dec	-1,000	,317
l_dec - k_dec	-1,000	,317
m_dec - k_dec	,000	1,000
n_dec - k_dec	,000	1,000
m_dec - l_dec	-1,000	,317
n_dec - l_dec	-1,000	,317
n_dec - m_dec	,000	1,000

Table 13 Wilcoxon test for comparing the different AU combinations with eye contact in crested gibbons

	Z	Asymptotische Signifikanz (2-seitig)
b - a	-1,101	,271
c - a	-1,363	,173
d - a	-2,197	,028
e - a	-2,371	,018
f - a	-2,366	,018
g - a	-2,366	,018
h - a	-2,366	,018
i - a	-2,366	,018
j - a	-2,366	,018
k - a	-2,366	,018
l - a	-2,366	,018
m - a	-2,366	,018
n - a	-2,366	,018
c - b	-,507	,612
d - b	-1,521	,128
e - b	-2,201	,028
f - b	-2,023	,043
g - b	-2,201	,028
h - b	-2,201	,028

Table 14 Wilcoxon test for comparing the different AU combinations without eye contact in crested gibbons

	Z	Asymptotische Signifikanz (2-seitig)
b - a	-1,541[a]	,123
c - a	-2,201[a]	,028
d - a	-2,527[a]	,012
e - a	-2,384[a]	,017
f - a	-2,524[a]	,012
g - a	-2,533[a]	,011
h - a	-2,533[a]	,011
i - a	-2,524[a]	,012
j - a	-2,533[a]	,011
k - a	-2,533[a]	,011
l - a	-2,533[a]	,011
m - a	-2,533[a]	,011
n - a	-2,524[a]	,012
c - b	-,507[a]	,612
d - b	-2,023[a]	,043
e - b	-2,201[a]	,028
f - b	-1,826[a]	,068
g - b	-2,197[a]	,028
h - b	-2,197[a]	,028

i - b	-2,028	,043
j - b	-2,023	,043
k - b	-2,201	,028
l - b	-2,201	,028
m - b	-2,201	,028
n - b	-2,201	,028
d - c	-1,483	,138
e - c	-2,201	,028
f - c	-1,753	,080
g - c	-2,201	,028
h - c	-2,023	,043
i - c	-2,201	,028
j - c	-2,023	,043
k - c	-2,201	,028
l - c	-2,023	,043
m - c	-2,201	,028
n - c	-2,201	,028
e - d	-,535	,593
f - d	-,674	,500
g - d	-1,342	,180
h - d	-1,000	,317
i - d	-1,342	,180
j - d	,000	1,000
k - d	-1,342	,180
l - d	-,365	,715
m - d	-1,342	,180
n - d	-1,342	,180
f - e	-1,461	,144
g - e	-,447	,655
h - e	-,447	,655
i - e	-,535	,593
j - e	,000	1,000
k - e	-1,000	,317
l - e	-,447	,655
m - e	-1,000	,317
n - e	-1,000	,317
g - f	-1,826	,068
h - f	-1,826	,068
i - f	-,674	,500
j - f	-1,342	,180
k - f	-1,826	,068
l - f	-1,342	,180
m - f	-1,826	,068
n - f	-1,826	,068

i - b	-2,023[a]	,043
j - b	-2,197[a]	,028
k - b	-2,201[a]	,028
l - b	-2,201[a]	,028
m - b	-2,201[a]	,028
n - b	-2,023[a]	,043
d - c	-1,461[a]	,144
e - c	-1,214[a]	,225
f - c	-,730[a]	,465
g - c	-1,826[a]	,068
h - c	-1,826[a]	,068
i - c	-1,214[a]	,225
j - c	-1,826[a]	,068
k - c	-1,826[a]	,068
l - c	-1,826[a]	,068
m - c	-1,826[a]	,068
n - c	-1,461[a]	,144
e - d	,000[b]	1,000
f - d	-1,342[c]	,180
g - d	-,535[a]	,593
h - d	-,365[a]	,715
i - d	,000[b]	1,000
j - d	-,535[a]	,593
k - d	-1,342[a]	,180
l - d	-1,342[a]	,180
m - d	-1,342[a]	,180
n - d	-1,000[a]	,317
f - e	-,365[c]	,715
g - e	-,447[a]	,655
h - e	,000[b]	1,000
i - e	,000[b]	1,000
j - e	-,447[a]	,655
k - e	-1,000[a]	,317
l - e	-1,000[a]	,317
m - e	-1,000[a]	,317
n - e	,000[b]	1,000
g - f	-1,461[a]	,144
h - f	-1,095[a]	,273
i - f	-,365[a]	,715
j - f	-1,461[a]	,144
k - f	-1,604[a]	,109
l - f	-1,604[a]	,109
m - f	-1,604[a]	,109
n - f	-1,342[a]	,180

h - g	-1,000	,317
i - g	-1,000	,317
j - g	-1,069	,285
k - g	-1,000	,317
l - g	-,535	,593
m - g	-1,000	,317
n - g	-1,000	,317
i - h	-,447	,655
j - h	-1,069	,285
k - h	-1,000	,317
l - h	-,535	,593
m - h	-1,000	,317
n - h	-1,000	,317
j - i	,000	1,000
k - i	-1,342	,180
l - i	-,365	,715
m - i	-1,342	,180
n - i	-1,342	,180
k - j	-1,342	,180
l - j	-,447	,655
m - j	-1,342	,180
n - j	-1,342	,180
l - k	-1,342	,180
m - k	,000	1,000
n - k	,000	1,000
m - l	-1,342	,180
n - l	-1,342	,180
n - m	,000	1,000

h - g	-1,000[c]	,317
i - g	-,535[c]	,593
j - g	-1,000[a]	,317
k - g	-1,000[a]	,317
l - g	-1,000[a]	,317
m - g	-1,000[a]	,317
n - g	-,535[c]	,593
i - h	-,447[c]	,655
j - h	-1,342[a]	,180
k - h	-1,342[a]	,180
l - h	-1,342[a]	,180
m - h	-1,342[a]	,180
n - h	-,365[c]	,715
j - i	-,535[a]	,593
k - i	-1,342[a]	,180
l - i	-1,342[a]	,180
m - i	-1,342[a]	,180
n - i	,000[b]	1,000
k - j	-1,000[a]	,317
l - j	-1,000[a]	,317
m - j	-1,000[a]	,317
n - j	-,535[c]	,593
l - k	,000[b]	1,000
m - k	,000[b]	1,000
n - k	-1,342[c]	,180
m - l	,000[b]	1,000
n - l	-1,342[c]	,180
n - m	-1,342[c]	,180

Table 15 Kruskal Wallis test to compare the AU combinations between the different age groups with and without eye contact in crested gibbons

	eye contact			no eye contact		
	Chi-Quadrat	df	Asymptotische Signifikanz	Chi-Quadrat	df	Asymptotische Signifikanz
a	1,078	2	,583	3,115	2	,211
b	,115	2	,944	2,218	2	,330
c	1,149	2	,563	2,653	2	,265

d	1,875	2	,392	2,813	2	,245
e	1,250	2	,535	3,500	2	,174
f	2,933	2	,231	4,765	2	,092
g	1,250	2	,535	2,000	2	,368
h	1,250	2	,535	,833	2	,659
i	1,875	2	,392	1,875	2	,392
j	,646	2	,724	2,000	2	,368
k	,000	2	1,000	,000	2	1,000
l	2,813	2	,245	,000	2	1,000
m	,000	2	1,000	,000	2	1,000
n	,000	2	1,000	2,813	2	,245

Table 16 Mann-Whitney U test to compare differences in the general appearance of the several AU combinations between siamangs and crested gibbons

	Mann-Whitney-U	Wilcoxon-W	Z	Asymptotische Signifikanz (2-seitig)	Exakte Signifikanz [2*(1-seitig Sig.)]
A	30,000	108,000	-1,706	,088	,095
B	36,000	81,000	-1,280	,201	,219
C	46,500	91,500	-,535	,593	,602
D	27,000	72,000	-1,955	,051	,058
E	48,500	126,500	-,433	,665	,702
F	53,500	131,500	-,048	,962	,972
G	40,500	85,500	-1,576	,115	,345
H	45,000	90,000	-1,255	,209	,554
I	53,500	131,500	-,048	,962	,972
J	49,000	94,000	-,445	,656	,754
K	49,500	94,500	-,866	,386	,754
L	51,000	96,000	-,254	,799	,862
M	45,000	90,000	-1,255	,209	,554
N	36,000	114,000	-2,101	,036	,219

Table 17 Mann-Whitney U test to compare differences in the appearance of the several AU combinations between siamangs and crested gibbons with direct eye-to-eye contact

	Mann-Whitney-U	Wilcoxon-W	Z	Asymptotische Signifikanz (2-seitig)	Exakte Signifikanz [2*(1-seitig Sig.)]
a	42,000	120,000	-,859	,391	,422
b	42,000	87,000	-,859	,391	,422
c	35,500	113,500	-1,391	,164	,193
d	35,000	80,000	-1,497	,134	,193
e	47,000	92,000	-,726	,468	,651
f	30,000	108,000	-2,488	,013	,095
g	48,000	93,000	-,622	,534	,702
h	42,000	87,000	-1,141	,254	,422
i	48,000	93,000	-,535	,593	,702
j	41,000	86,000	-1,057	,290	,382
k	49,500	94,500	-,866	,386	,754
l	43,000	88,000	-,932	,351	,464
m	45,000	90,000	-1,255	,209	,554
n	54,000	99,000	,000	1,000	1,000

Lebenslauf

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Ausbildung

April 2011 – August 2011	Ausbildung zur zertifizierten ChimpFACS, OrangFACS und GibbonFACS Coderin
Seit 2009	Masterstudium Verhaltens-, Neuro- und Kognitionsbiologie an der Universität Wien (voraussichtlicher Abschluss Juni 2012)
2004-2009	Studium der Biologie (Bakkalaureat Verhalten) an der Karl Franzens Universität Graz: ○ Tiermorphologie bzw. Tierphysiologie ○ Spezialisierung auf Verhalten von Tieren (Primaten) und Neurobiologie ○ Beobachtung sozialer Interaktionen bei Primaten ○ Pflanzenphysiologie, Anatomie und Zellbiologie ○ Kenntnisse im Bereich der Botanik, Ökologie, Mikrobiologie und Physik
1998-2004	Akademisches Gymnasium Linz
1996-1998	Akademisches Gymnasium Graz
1992-1996	Volksschule Puntigam, Graz

Bakkalaureatsarbeiten

Mai 2008 – Februar 2009	Altersspezifische Rollenverteilung der Eltern im Rahmen der Jungenaufzucht bei Siamangs (*Symphalangus syndactylus*) (Empirische Arbeit in Zusammenarbeit mit Zoo Herberstein)
Januar 2007	Unterschiede zwischen männlichem und weiblichem Gehirn (Literaturarbeit)

Studienbezogene Auslandsaufenthalte

März 2011 – September 2011	Aufenthalt in Berlin zur Erfassung der Daten der Masterarbeit auf der Freien Universität Berlin
Februar 2011	Studienaufenthalt in der Tropenstation La Gamba, Costa Rica

Praktika und berufliche Tätigkeiten	
Seit März 2012	Teilzeitanstellung zoopädagogische Abteilung im Tiergarten Schönbrunn
November 2009 – März 2012	Mitarbeiterin der zoopädagogischen Abteilung im Tiergarten Schönbrunn
August 2009	Praktikum als Hilfstierpflegerin im Tiergarten Schönbrunn, Wien (Revier Primaten)
August 2007	Praktikum bei der Landesregierung Steiermark in der Fachabteilung für Naturschutz (FA 13C)
August 2006	Praktikum als Hilfstierpflegerin im Tiergarten Schönbrunn, Wien (Revier Singvögel)
August 2005 *August 2004* *August 2003*	Praktikum im Marketingbereich der Brau Union Österreich

Kenntnisse	
Computer:	Microsoft Office Sehr gute Internetkenntnisse SPSS
Fremdsprachen:	Deutsch: Muttersprache Englisch: sehr gute Kenntnisse (Sprachaufenthalt in Eastbourne, UK) Französisch: gute Kenntnisse (Sprachaufenthalt in Nizza, FRA) Schwedisch: Grundkenntnisse Spanisch: Grundkenntnisse Latein