

DISSERTATION

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Physiological and Cognitive Determinants of Behavior in
Primate Societies

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To my mother

*“The physicist's problem is the problem of ultimate origins and ultimate natural laws.
The biologist's problem is the problem of complexity.”*
Richard Dawkins, *The Blind Watchmaker* (1996), p15.

*“Just as the physiologist asks how the individual, or the organ, or the cell, manages
to maintain itself by organized co-operation of its constituents, so the sociologist has
to ask how the constituents of the group -the individuals- manage to maintain the
group.”*

Nikolaas Tinbergen, *Social Behaviour in Animals with Special Reference to
Vertebrates* (1953), p 2.

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Abstract

Primate sociality, especially living in large groups of unrelated individuals, has strongly shaped and coevolved with primate behavioral, physiological, and cognitive traits, leading to primates' ability to cope with increasingly complex (social) environments. In addition to the challenges of mating and raising young that typify all mammals, the additional challenges associated with primate group living affect not only the social realm of an individual's life, but extend to other aspects, such as long-term relationships with potential mates and cognitive mechanisms to cope with and maintain multiple relationships. The resulting adaptive strategies to sociality are as diverse as the various social systems of different primate species. Differences in social style not only impact the behavior of individuals but also their coping mechanisms with the physiological stress that can accompany group living. In the relatively relaxed society of Barbary macaques, we found rank-dependent grooming patterns connected to physiological stress alleviation, whereas in despotic species focusing grooming on few selected partners was associated with low physiological stress levels across the dominance hierarchy. Social behavior is also integrated into mating tactics: the type of copulation that occurred (either with or lacking male ejaculation) influences male and female post-copulatory grooming. These grooming patterns can be explained by sex-specific mating strategies. Despite, or rather because of, the extraordinary demands associated with sociality, novel cognitive abilities have also emerged in primates and other group-living vertebrates. For instance, with the evolution of social learning, individuals can learn from each other, reducing the need for time-consuming individual trial and error learning and allowing for transmission and conservation of acquired skills and knowledge within a population. The need to process complex social structures may also have led to enhanced cognitive capacities, which may extend to other non-social domains and allow for more flexible, abstract cognitive abilities. To address questions on how and to what extent social systems influence cognition, comparative studies integrating physiological investigations with observational and experimental data may open up new paths for research and help to broaden our understanding of the evolution of complex cognitive capacities.

1 | Introduction

Associations between the developments of more sophisticated, more compound behavioral and cognitive repertoires and increasing social complexity have often been noted (Byrne and Whiten 1988; Cheney and Seyfarth 2008; David-Barrett and Dunbar 2013; Dunbar 2012; Dunbar 1998b; Dunbar 2003; Freeberg et al. 2012; Humphrey 1976; Jolly 1966; Kudo and Dunbar 2001; Pawlowski et al. 1998; Shultz and Dunbar 2007; Whiten and Van Schaik 2007) and can be found in many different animal taxa (Emery and Clayton 2004; Marino 2002). Social bonds are formed and maintained not only with a mating partner, but also with multiple kin (e.g., offspring or siblings) and non-kin individuals, which has been hypothesized to enhance social cognition in particular (Cheney and Seyfarth 2008; Dunbar and Shultz 2007; Dunbar 2003; Humphrey 1976; Jolly 1966). Social life may bring many advantages (e.g., protection from predators, enhanced foraging, opportunities for social learning) but group living also raises new challenges and potential for conflict. Therefore behavioral, cognitive, and physiological adaptations to sociality are manifold and as diverse as the diversity of social systems we find in nature.

Coping strategies to deal with the stressful aspects of sociality have been studied extensively. Conflict resolution (Aureli and de Waal 2000), consolation (e.g., De Waal and Aureli 1996), or conflict avoidance (e.g., Judge and de Waal 1993) have received special attention in the literature. Another strand of research focused on social strategies for coping with physiological stress (for reviews see Cheney and Seyfarth 2009; Sapolsky 1992). Living in social aggregations often has a stressful component to it, which may have negative effects on an individual's long-term reproductive fitness. Therefore adapting social behavior to counterbalance such negative effects (e.g., by establishing, maintaining, and repairing social bonds; or by developing social means to reduce physiological stress loads) seems to constitute a central evolutionary challenge for group-living species (Silk 2014). Furthermore, we find that social behavior is also incorporated in reproduction. For instance, many primate species exchange social interactions for mating (e.g., Clarke et al. 2010; Gumert 2007; Massen et al. 2012; Noë and Hammerstein 1994; Norscia et al. 2009;

Schino et al. 2003). Overall, all of these behaviors and mechanisms, and many others can be understood as adaptations to sociality.

This diversity of features and adaptations can be organized within the framework of Tinbergen's "four whys" (Tinbergen 1963), which highlight the need to consider social behavior from multiple perspectives including both adaptive value and mechanistic implementation. Bateson and Laland (2013) emphasized that, as envisaged by Tinbergen (1963), some or all of the four questions about the utility, mechanism, development, and evolution of a behavior should be considered together. Increasing evidence supports the notion that social behavior, not only between related individuals or mating partners but also between non-related individuals, may have an adaptive function (e.g., decreasing glucocorticoid levels, reduction of heart rate, or increased reconciliation rates with opponents an individual has social bonds with) (for a summary see Silk 2002; Silk 2007a). Furthermore, research indicates that interacting socially and establishing and maintaining social bonds is also associated with fitness benefits in both monogamous (e.g., Black 2001; Gubernick and Teferi 2000; Matysioková and Remeš 2013; Ophir et al. 2008) and gregarious species (Packer and Pusey 1983; Schülke et al. 2010; Silk et al. 2003; Silk et al. 2006a; Silk et al. 2009; Silk et al. 2010).

Theoretical models have suggested how the major demands associated with sociality may have enhanced the evolution of multifaceted cognitive abilities (David-Barrett and Dunbar 2013). Developing and maintaining complex minds and brains comes at a high physiological and developmental cost (e.g., Leonard et al. 2003). Nevertheless heightened demands for coordination and social bonding to ensure group stability may have facilitated the co-evolution of complex, large societies and sophisticated cognitive capacities (David-Barrett and Dunbar 2013).

For instance, female baboons classify group mates according to both their kinship and individual rank (Bergman et al. 2003). This categorical flexibility allows baboon females to react to changes in quality in their social environment and thus is of paramount importance for living in philopatric, gregarious, social groups. Japanese macaques can also classify group mates according to rank and kinship when recruiting individuals for support (Schino et al. 2006).

Barrett and colleagues (Barrett et al. 2003) argue that in fission-fusion societies the computational demands for recognizing, storing, and updating social information are even further increased from those of ordinary group living. Chimpanzees for instance form social bonds mainly with, and gain support primarily from, non-kin or distantly related individuals (Langergraber et al. 2007; Mitani 2009). Division into sub-parties occurs frequently in chimpanzees and composition of such subgroups is usually very variable and changeable (Aureli et al. 2008). The potentially very fast and frequent changes in subgroups have been argued to be connected to behavioral and cognitive adaptations (Amici et al. 2008). Playback studies revealed that chimpanzees react differently to calls of members of their social group, individuals of neighboring groups, or strangers (Herbinger et al. 2009), and indicate that responses to potential intruders are dependent on numerical proportions of in-group and out-group individuals (Wilson et al. 2001). A recent study demonstrated that chimpanzees know about and keep track of affiliations between their group mates and adjust their behavior based on others' relationship qualities (Wittig et al. 2014b). These studies clearly show that non-linguistic animals possess cognitive skills for rule-governed processing of (social) information (Bergman et al. 2003; Seyfarth et al. 2005).

The collection of studies comprising this thesis aims to contribute to scientific understanding of multiple facets of how sociality in general, and different social systems in particular, coevolved with physiological, behavioral, and cognitive traits. Heeding Tinbergen's advice, the work here attempts to consider the determinants of behavior from multiple proximate and ultimate perspectives. The key questions address the following key issues in primate sociality:

- (i) How is social behavior related to physiological stress levels in socially tolerant primates?
- (ii) How do males and females use social behavior in mating contexts, and what potential mating strategies may underlie these behaviors?
- (iii) Which abstract rules can be processed by different primate species and is this related to the complexity of their social system?

To tackle these questions observational, hormonal, and experimental approaches were all employed.

How this thesis is organized

In the next (2nd) chapter (“Rank-dependent grooming patterns and cortisol alleviation in Barbary macaques”, published in *American Journal of Primatology*) I present a study investigating female Barbary macaques’ social/behavioral strategies for coping with physiological stress (Sonnweber et al. 2015b), thus focusing on two different components of proximate causation. While living socially adds a potential source of stressors to the daily ecological and environmental challenges individuals have to face, it also opens new windows of opportunity to cope with stressful situations by employing social behaviors to mitigate physiological stress levels. Previous studies on despotic, philopatric female monkeys revealed that strong social bonds within a focused social network are associated with low physiological stress measures for individuals of all ranks (Cheney and Seyfarth 2009; Crockford et al. 2008; Wittig et al. 2008); such social bonds are beneficial in terms of longevity and reproductive success (e.g., Silk 2014; Silk et al. 2003; Silk et al. 2006a; Silk et al. 2006b; Silk et al. 2009; Silk et al. 2010). In the presented field study my collaborators and I examined female grooming strategies for urinary cortisol alleviation in a comparably tolerant species, the Barbary macaques. We found that female dominance rank had an impact on how different grooming patterns were associated with reduced urinary cortisol levels. We argue that the rather relaxed social style of this species comes with increased behavioral flexibility for individuals of differing rank relationships, reflecting a more diverse palette of social strategies for stress alleviation in Barbary macaques relative to many other well-studied apes and Old World monkeys.

Chapter Three (“Post-copulatory grooming: a mating strategy?” under review in *Behavioral Ecology and Sociobiology*) concerns another important aspect of life where social behavior can be employed as a strategic tool: the various non-sex behaviors leading up to, and following, mating behavior. In this field study, male and female Barbary macaque post-copulatory grooming behavior was investigated (Sonnweber et al. under review). I differentiated in particular between behavior following copulations with and without ejaculations because, depending on the type of mating that occurred, male and female reproductive interests might differ. After

copulations with ejaculation, females might seek further mating with other males to confuse paternity, while under these circumstances males might want instead to monopolize the female to dissuade other males from mating and thus reduce sperm competition. By grooming males after matings without ejaculation, females could keep their copulation partner in proximity and receive additional (ejaculatory) copulations or form stronger social bonds with the male (for instance to reduce aggression).

I found that males and females showed differential post-mating social behavior not only depending on the type of copulation, but also on female's lactation state. This could be related to the potentially reduced fertility of lactating females and/or advantages (e.g., tolerance or reduced aggression) females gain from strong social relationships with males, which are particularly important to females with dependent offspring.

My focus turns now to more cognitive mechanisms. When individuals live closely together they have the potential to learn from each other and can circumvent, at least to a certain extent, time-consuming, individual, trial-and-error learning. But not only learning socially, but also teaching others may be advantageous for individuals (both for the recipient of information or skills, as well as the provider of information or skills, the teacher) living in social aggregations. Scientists of various disciplines have addressed research questions concerning teaching in humans, and in animal societies. As is often the case when researchers of different backgrounds concern themselves with the same questions, arguments and disagreements arise, but often boil down to differences in definitions and vocabularies used. Kline (Kline 2014) presented a novel framework, integrating different perspectives and approaches to the study of teaching. She proposes that teaching should be understood as a set of adaptive behaviors that serve a problem-solving function. Kline argues for defining teaching types (social tolerance, opportunity provisioning, stimulus/local enhancement, evaluative feedback, and direct active teaching) according to the adaptive problems they solve.

In Chapter Four ("Measuring teaching through hormones and time series analysis: Towards a comparative framework", in press in *Behavioral and Brain Sciences*) of this thesis I present a commentary to Kline's article, in which we suggested that

hormonal measurements and time-series analyses of teachers' and pupils' movements could be used as objective tools for exploring and differentiating between different teaching types (Ravignani and Sonnweber in press).

Chapters Five ("Non-adjacent visual dependency learning in chimpanzees", published in *Animal Cognition*) and Six ("Chimpanzees process structural isomorphisms across sensory modalities", submitted to *Current Biology*) present two studies on chimpanzees' ability to learn and process complex structural rules and exploring the idea that such regularities can be encoded, in this species, at a modality-general level (Ravignani, Sonnweber and Fitch submitted; Sonnweber et al. 2015a). In these papers we argue, as proposed earlier by others (Seyfarth and Cheney 2007; Seyfarth et al. 2005), that the cognitive capacity for processing hierarchical, discrete, combinatorial information may rest in how complex social systems shaped cognition in the course of evolution.

Commemorating Darwin, Steven Pinker (2010) proposed to study the human mind by employing the most parsimonious means of explanation for its characteristics: that is, that the human mind originates and was shaped by natural selection. He argues that humans' ancestors occupied a 'cognitive niche' where extraordinary abilities in causal reasoning, cooperation, and language co-evolved with life-history and sexual adaptations. These cognitive features allow dealing with components of both, the physical and the social world. But what were the pressures selecting for the evolution of these cognitive abilities?

In particular in the context of language evolution, but also in research on physical cognition (e.g., transitive inference tasks) hypotheses on a 'social origin' of the evolution of these abilities have been voiced (Cheney and Seyfarth 1997; Dunbar 1998a; Kummer 1978; MacLean et al. 2012; MacLean et al. 2008; Seyfarth et al. 2005). It is argued that heightened demands for coordination and social bonding to ensure group stability facilitated the co-evolution of complex, large societies and sophisticated cognitive capacities (David-Barrett and Dunbar 2013). If sociality shaped cognition across domains then animals in different social systems with different demands of processing and book-keeping of social information may show different abilities in abstract rule-learning and pattern processing tasks.

After presenting and discussing these aforementioned individual investigations I conclude by discussing the overall picture drawn from the studies presented and by summarizing their implications for future research of primate social systems.

2 | Social Strategies for Stress Coping

Rank-dependent grooming patterns and cortisol alleviation in Barbary macaques

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RESEARCH ARTICLE

Rank-Dependent Grooming Patterns and Cortisol Alleviation in Barbary Macaques

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Flexibly adapting social behavior to social and environmental challenges helps to alleviate glucocorticoid (GC) levels, which may have positive fitness implications for an individual. For primates, the predominant social behavior is grooming. Giving grooming to others is particularly efficient in terms of GC mitigation. However, grooming is confined by certain limitations such as time constraints or restricted access to other group members. For instance, dominance hierarchies may impact grooming partner availability in primate societies. Consequently specific grooming patterns emerge. In despotic species focusing grooming activity on preferred social partners significantly ameliorates GC levels in females of all ranks. In this study we investigated grooming patterns and GC management in Barbary macaques, a comparably relaxed species. We monitored changes in grooming behavior and cortisol (C) for females of different ranks. Our results show that the C-amelioration associated with different grooming patterns had a gradual connection with dominance hierarchy: while higher-ranking individuals showed lowest urinary C measures when they focused their grooming on selected partners within their social network, lower-ranking individuals expressed lowest C levels when dispersing their grooming activity evenly across their social partners. We argue that the relatively relaxed social style of Barbary macaque societies allows individuals to flexibly adapt grooming patterns, which is associated with rank-specific GC management. *Am. J. Primatol.*

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Key words: urinary cortisol; Barbary macaques; dominance hierarchies; glucocorticoides; relaxed social styles

INTRODUCTION

A wide body of research has demonstrated that—especially for females—social behaviors can function as tools for physiological stress mitigation as reflected by glucocorticoid (GC) measures (for a review see [Cheney and Seyfarth, 2009]). However, as Cheney and Seyfarth [2009] point out: not sociality alone, but relationship quality (e.g. stability or strength of social bonds) between social partners is essential for coping with and managing GCs. For most social primate species, grooming represents one of the most important social behaviors [Hinde and Stevenson-Hinde, 1976; Kummer, 1978; Silk et al., 2010]. Grooming increases fitness [Kummer, 1978; Berghänel et al., 2011] in that it has positive effects on reproductive success [Silk et al., 2003] and is associated with longevity [Silk et al., 2010]. The variety of different grooming patterns, that is how individuals distribute grooming between group members, depends on various parameters such as

group size [Dunbar, 1991; Henzi et al., 1997], grade of cohesion, fission–fusion dynamics, sex ratio [Henzi et al., 1997; Lehmann et al., 2007], and social organization (egalitarian–despotic, for a review see [Thierry et al., 2004]), as well as on individual factors such as number of kin and rank [Schino, 2007]. As early as the 1970s Robert Seyfarth [1977] proposed a

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model for predicting grooming patterns among non-human primate females. Determining factors for grooming distributions were predicted to be (1) attraction to kin and (2) high-ranking individuals, as well as (3) competition over access to preferred grooming partners. A meta-analysis on different primate species (not including Barbary macaques, but other macaque species) verified the predictions of the model to a great extent and found an effect of rank on grooming distribution [Schino, 2001]. Female primates across species tend to groom up the dominance hierarchy (see [Small, 1990] for an example in Barbary macaques). Thus, high-ranking individuals can be viewed as preferred grooming partners and consequently competition over access to such partners should be expected [Seyfarth, 1977]. Furthermore, Seyfarth [1980] reasoned that high-ranking females should direct their grooming in relation to the grooming partner's rank position if competition is affecting grooming distributions, as dominant females would be least constrained in choosing whom to groom. Middle-ranking females on the other hand should have less flexibility in adapting their grooming behavior. For low-ranking females, no connection between rank and grooming direction was expected. Again, this pattern was confirmed with actual data on *cercopithecoidea* and *ceboidea* species [Schino, 2001]. Thus, certain social pressures seem to act on the expression of grooming patterns that can be observed in a given society of primates.

The more relaxed a species is in its social style (*in sensu* [Thierry et al., 2004]), the less impact hierarchies should have on access to grooming partners, and fewer constraints in grooming up the hierarchy would be expected [Butovskaya, 2004]. In hierarchical societies, there is evidence for low-ranking individuals attempting to groom higher-ranking individuals [Schino, 2001] and trading grooming for rank-related commodities such as agonistic support [Hemelrijk, 1994; Seyfarth and Cheney, 1984; Schino, 2007], tolerance at feeding sites [Richter et al., 2009; Ventura et al., 2006], and reduced aggression [Gumert and Ho, 2008]. In more tolerant societies, such as in Barbary macaques, Carne et al. [2011] found for females that the rank of the recipient was not a significant predictor for grooming given. Other studies showed that individuals gave more grooming to higher-ranking females than lower ranking ones and preferentially groomed their female kin, who are usually of similar rank [Paul and Kuester, 1987; Prud'Homme and Chapais, 1993a; Prud'Homme and Chapais, 1993b]. Grooming for rank-related benefits (agonistic support and tolerance around food) was limited.

When looking at the relation of rank hierarchies and GC measures (an endocrine hallmark for stress) studies on non-human primates have found no consistent relationship between the two parameters

[Sapolsky, 2005; Creel et al., 2013]. In general, subordinate females seem to be more likely to have higher GC measures than dominant females [Cavigelli and Chaudhry, 2012]. This is particularly true for females in socially despotic organizations [Cheney and Seyfarth, 2009]. Styles of dominance seem to modify patterns in GC physiology [Ray and Sapolsky, 1992]. Correlates to rank impact the interaction between dominance and GC largely: whether or not GC levels and rank are connected for a given species depends on various factors, such as the extent of social support available to low-ranking individuals [Abbott et al., 2003; Cheney and Seyfarth, 2009], differential access to resources, the stability of social hierarchy structures, and low-ranking individuals' coping strategies [Sapolsky, 2005]. In Barbary macaques, findings concerning rank and GC are inconsistent: middle rank is connected to highest and most variable GC measures according to Edwards et al. [2013], the most dominant individuals express highest GC levels in a study by Gustison and colleagues [2012], while no connection between the two parameters was found in a study by Shutt et al. [2007]. Behavioral proxies (scratching rates) for stress suggest that subordinate rank is associated with highest stress loads [Kaburu et al., 2012].

Although group life comes with many social stressors and potential for conflict social interactions have been found to constitute an effective tool for mitigating GC levels in various species (prairie voles: [DeVries et al., 2003]; baboons: [Crockford et al., 2008; Wittig et al., 2008]; chimpanzees: [Fraser et al., 2008b]; rhesus macaques: [Brent et al., 2011]). Although both giving and receiving grooming served as a tool for promoting GC-resistance, previous studies on primates demonstrated that grooming actively was more effective in terms of GC alleviation [Dunbar, 2010]. Studies on despotic species found that these primates seem to adapt their grooming patterns to social and environmental conditions. According to Crockford et al. [2008] female baboons, who concentrated their grooming activity on a small number of partners, had lower GC levels than those females who distributed those interactions more evenly among grooming partners. As the same group went through a period of social instability, GC levels initially increased for all females, but then decreased for individuals, who reduced their grooming network the most or already had had few predictable bonding-partners to begin with [Wittig et al., 2008]. Brent et al. [2011] found similar results for high-ranking female rhesus macaques, who had lower GC levels during periods with more focused proximity networks.

So far such detailed investigations on short-term changes in GC physiology and social behavior are not available for more relaxed species. A first indication for comparable mechanisms in rather tolerant species comes from a study in Barbary macaques,

which found that active—but not received—grooming as well as a high number of grooming partners were connected to reduced GC concentrations in females [Shutt et al., 2007]. This study pooled data over a whole observation period. Thus, potential changes in behavior and physiology within short time windows were not reflected in the data. Also, rates of given and received grooming as well as clique size were analyzed without a more detailed description of grooming patterns. Two main aspects discussed earlier make Barbary macaques a particularly interesting species to look at in more detail: (i) the very inconsistent findings regarding the influence of social rank on GC levels [Edwards et al., 2013; Gustison et al., 2012; Shutt et al., 2007], and (ii) the seemingly high behavioral flexibility associated to their social style [Carne et al., 2011; Gumert and Ho, 2008; Paul and Kuester, 1987; Prud'Homme and Chapais, 1993a; Prud'Homme and Chapais, 1993b]. We hypothesized that the rather relaxed social style (when compared to despotic species like baboons, Japanese macaques, or rhesus macaques) allows females of all rank groups to flexibly change their grooming behavior and that specific grooming styles associate to reduced GC measures. As time available for grooming and access to grooming partners differs for females of different dominance [Butovskaya, 2004; Paul and Kuester, 1987] we hypothesized that rank would impact which grooming patterns were connected to C-mitigation. Thus, the main aim of this study was to determine short-term grooming patterns expressed by female Barbary macaques and connect them to urinary cortisol (C) measures, while considering rank as a potential influencing parameter. We expected specific grooming patterns (that might be different for females of different rank) to be connected to C levels: females with a focused grooming network, high ratios of active grooming, and females, who modified their grooming focus according to changing conditions, were predicted to show lowest levels of urinary C. We analyzed grooming patterns with regard to grooming partner diversity, relative grooming activity, and grooming distribution among partners (grooming skew). Instead of pooling behavioral and physiological data from entire observational periods (e.g. [Shutt et al., 2007]), we followed the recent trend to focus on processes within smaller time windows to get a detailed picture of how grooming behavior and C management are interrelated.

METHODS

Ethical Standards

As the study consisted of behavioral observations and non-invasive hormonal sample collection there were no animal welfare implications. The Gibraltar Ornithological and Natural History Society

(GOHNS) of Gibraltar authorized non-invasive collection of behavioral and hormonal data in accordance with Gibraltar's legislative requirements for both observation periods. All research was conducted in accordance with Austrian legislation. The research adhered to the American Society of Primatologists principles for ethical treatment of primates.

Subjects and Study Site

The study was conducted on Gibraltar Barbary macaques (*Macaca sylvanus*) over two consecutive mating seasons (from November through February) in 2004, 2005, and 2006, respectively. Barbary macaque females are philopatric and female bonded [Wrangham, 1980], with females forming the core of the social group. Daughters inherit their ranks from their mother, resulting in adjacent rank positions for members of a matriline. Dominance hierarchies between matriline remain stable over generations. Previous research suggests that the most valuable social partners for adult females Barbary macaques are other adult females [McFarland and Majolo, 2011]. The groups "Apes Den (AD)" and "Prince Phillips Arch (PPA)" were chosen due to their good accessibility, the good view over the respective territories, and because group composition was similar. The population in AD consisted of 13 adult females, between three and nine adult males (immigration from neighboring groups took place during the study period), three subadult females, three subadult males, eight juveniles and five infants in the first season. In the second season, the group was composed of 14 adult females, nine adult males, four subadult females, five subadult males, five juveniles and seven infants. The PPA group consisted of 12 adult females, nine adult males, six subadult females, six subadult males, eight juveniles and seven infants. Age was classified after Burton [1972]. AD was observed over two consecutive reproductive seasons; PPA was included in the second observation period only. Tourist pressure, a potential cause for elevated stress levels [Maréchal et al., 2011], was similar at both sites as both territories are part of the standard sightseeing itinerary. Consequently, animals were well habituated to humans without being overrun, as the winter months are a lot quieter than the summertime. There are indications that the mating season in itself is more stressful than the non-mating season, at least for males (male squirrel monkeys: [Coe and Levine, 1995]; male Assamese macaques: [Ostner et al., 2008]). Although this may well have been the case for the females in our study groups as well, this general period of possibly higher anxiety was not unstable, as to our knowledge no catastrophic occurrences (e.g. storms, deaths, predator interactions) occurred during the observation periods. As background

information on the individuals was sparse and no rank order was available for either group at the onset of data collection, focal females (first season $n = 7$ for AD, second season $n = 6$ for AD as one female died between observational periods, and $n = 6$ for PPA) were selected to represent all age classes within the group of mature females (after analyzing agonistic interactions we found that females of all rank classes were represented in our list of focal females, ranging from high ranking females to the lowest ranking individual). While we acknowledge that the sample size of seven (1st season), respectively 12 (2nd season) individuals is relatively small, we focused on these females to grant sufficient hormonal and behavioral sample density. Information on kinship among the focal animals was not available. Only females without hormonal treatment were chosen as focal individuals. Hormonal samples and focal behavioral protocols were collected for these females only. All females (excluding the two females on contraceptives) were recorded in focal behavioral protocols as interaction partners only. *Ad lib* behavioral data were collected for all individuals of the groups. All females were cycling during the study periods. Some were lactating, as they were nursing offspring from the previous mating season. The Gibraltar Ornithological and Natural History Society (GONHS) provisioned both groups daily with fruit and vegetables, as the vegetation at the observation sites was nutritionally not sufficient for the number of animals present.

Hormonal and Behavioral Data Sampling

The collection of behavioral and physiological data took place during two seasons of roughly equal length (109 and 115 days, respectively). In the first season, data collection at AD took place on a daily basis from 08:00 to 17:00. Daily observations (also from 08:00 to 17:00) in the second season alternated between the two study groups (an observation day at AD was followed by data collection at PPA the following day).

In most mammals and all primates the main GC that is released in response to stressors is cortisol (C) [Bercovitch and Ziegler, 2002; Heistermann, 2010]. The analysis of free urinary C has proven to be a reliable method for stress monitoring (e.g. [Bahr et al., 2000; Crockett et al., 1993; Dittami et al., 2008]). Although potential confounding factors (circadian rhythms, female cycle, lactation or pregnancy) have to be considered in the analyses of urinary C excretion rates, urine samples offer one big advantage compared to fecal samples: while GC levels in feces represent an aggregate of several days (although see [Edwards et al., 2013]), urinary concentrations indicate physiological measures of shorter time periods.

Urinary C is subject to diurnal variation. Heistermann [2010] suggests collecting the first morning urine for optimal results. However, this was not feasible in our free-ranging study species, as roosting places were either unknown or inaccessible. Instead, we controlled for time of collection in our statistical models. An impact of the female ovarian cycle on C concentrations has been demonstrated. GC-increase is connected with an elevation of sex steroids [Bercovitch and Ziegler, 2002]. Also, pregnancy is associated with heightened C levels [Keller-Wood and Wood, 2001]. This may be due to the increased levels of estrogens, as they enhance sensitivity to adenocorticotrophic hormones (ACTH) and thus affect the release of GC [Brunton et al., 2008]. Many studies [Brauch et al., 2007; Brauch et al., 2008; Grant et al., 2011] use the average gestation length of their study species to count back from the date of birth of the offspring to consider pregnancy stages in their data. Since we were looking at one-week time windows in our data, we considered individual variation in gestation length to be too high to apply this method. Instead, we analyzed urinary estrogen (E) levels that undergo fluctuations during pregnancy and ovarian cycles in order to control for effects of reproductive physiology on C measurements. We did not consider progesterone concentrations in our data, since progesterone is a precursor to C and discriminating between ovarian and adrenal progesterone would not have been possible [Wirth et al., 2007]. Lactation also affects GC levels, as has been demonstrated in various primate species (e.g. long-tailed macaques: [van Schaik et al., 1991]; rhesus macaques: [Hoffman et al., 2010]) and decreases the responsiveness to stressors, which may be due to low estrogen levels during lactation [Brunton et al., 2008]. Therefore we differentiated between nursing and non-nursing females and accounted for this information in our statistical models.

Urine Sample Collection

Urine samples were collected whenever possible on a daily basis between 08:00 and 17:00. Samples were only collected when a cross-contamination with urine of other individuals or fecal matter could be excluded, and the urinating female was reliably identified. Urine was soaked up on the excretion site using a cotton roll and stored at -20°C in salivettes (Sarstedt, Germany) until analysis. As the Gibraltar Barbary macaques were very habituated to humans, urine collection could take place immediately after excretion in proximity to the female (especially on slopes) or urine was soaked up as soon as the female moved. Samples were collected from rocks, soaked up from leaves, or from concrete around the feeding sites. The total number of samples in the first season was 165, giving an average of 2.06 samples a day. An

average of 24.1 samples per focal female were collected. In the second season, 226 samples were collected in total, averaging 1.96 samples per day. That is an average of 18.8 samples per focal female.

Cortisol and Estrogen Analysis

Before analysis, steroids were deconjugated with a glucuronidase/sulphatase after Palme and Möstl [1993]. All hormone concentrations were adjusted to urine dilution by analyzing creatinine concentration according to the standard Jaffe method [Slot, 1965]. Native C was measured (after [Dittami et al., 2008]) with an enzyme immunoassay (EIA) applying DADOO-biotinylated cortisol-3-CMO labels (1:250) and bovine serum albumin-coupled antibodies (1:20; raised in rabbits) against cortisol-3-CMO. Relevant cross-reactions with other steroids are described in [Palme and Möstl, 1997]. Main cross reactions were found with 4-pregnene-11 β ,17 α ,21-triol-3, 20-dione; 100%; 5 α -pregnane-11 β ,17 α ,21-triol-3,20dione 4.6%; 5 α -pregnane-3 α ,11 β ,17 α ,21-tetrol-20-one 0.8%; 5 β -pregnane-3 α ,11 β ,17 α ,21-tetrol-20-one 0.1%; all other steroids cross-reacted < 0.01%. The assay was previously used in several primate species, including macaques [Bahr et al., 2000]. Urinary concentrations were shown to correlate significantly with plasma levels of cortisol in baboons [French et al., 2004] and macaques [Crockett et al., 1993]. Intra-assay coefficient of variation (CV) was 9.86%, inter-assay CV was 14.65%.

Previous studies reported estrone, estriol, and estradiol to be dominantly excreted in the urine of macaques [Monfort et al., 1984; Shideler et al., 1993,2001] and baboons [Wasser et al., 1994]. Hence hydrolyzed urine samples were analyzed for estrogen concentrations with an antibody against total estrogens [Palme and Möstl, 1993]. Total estrogens were demonstrated an accurate measure for female macaque reproductive functions [Heistermann et al., 2001; Ostner and Heistermann, 2003]. Cross-reactions with relevant steroids were estrone 100%, estriol 129%, 1,3,5(10), 7-estratene-3-ol-17-one 87%, estradiol-17 β 70%, 1,3,5(10), 7-estratetraene-3,17 β -diol 20%, estradiol-17 α 19%, 1,3,5(10), 7-estrapentane-3-ol-17-one 1%. All other tested steroids had reactions below 1%. Intra-assay CV was 7.96% and inter-assay CV was 14.84%.

Behavioral Data Collection

In line with other studies [Brent et al., 2011; Crockford et al., 2008; Shutt et al., 2007; Wittig et al., 2008] we excluded males, juveniles, and subadult individuals from analyses and concentrated on female-female grooming interactions only.

Behavioral data were collected using continuous focal animal sampling according to Altmann [1974]. In addition dyadic agonistic interactions were noted

ad libitum, to gain a sufficiently large data set for establishing an unambiguous rank order. Individual protocols lasted 20 min in the first season and 15 min in the second. Both, affiliative and agonistic behavior was noted. Specifically, all grooming interactions (given and received), the identity of the grooming partners as well as the duration of the grooming bout was recorded. Agonistic interactions included threats, displacements, chases, attacks, and submissive behaviors. Females were observed in pseudo-random order, and no female was ever observed more than once on the same day. Morning, midday, and afternoon observations were balanced across focal females. Bad weather conditions or inaccessibility of specific areas on certain days limited behavioral observations. Individuals' behavioral data were corrected for total observation time.

A rank order was established by analyzing intra-sexual dyadic agonistic interactions [Deag, 1974] between all adult females of the group. Dominance rank was calculated using Mat Man 1.0 (Noldus, Wageningen, The Netherlands). The rank order was calculated separately for the two seasons. In order to be able to include rank information in our analyses, relative rank positions, controlled for the absolute amount of total rank places available, were established.

Data Analysis

Silk et al., [2013] published a summary on methods to study and describe social relationships. Hinde indices measure the symmetry or directionality of dyadic grooming interactions, while the Shannon Wiener Diversity index (SWDI) informs about the distribution of grooming across partners [Silk et al., 2013]. As these methods were previously used in studies comparable to ours [Brent et al., 2011; Crockford et al., 2008; Engh et al., 2006; Wittig et al., 2008], we applied these indices to describe grooming behavior of our subjects.

We calculated grooming indices to account for diversity and directionality in grooming behavior (see [Crockford and Boesch, 2005; Crockford et al., 2008; Hinde and Atkinson, 1970; Silk et al., 2013; Wilson and Bossert, 1971]). In all cases, only grooming interactions between adult females were included. The SWDI accounts for the spread and heterogeneity in grooming partners. This measure was then normalized (see [Silk et al., 1999]) by the number of total grooming partners, and standardized. Thus, this index does not reflect network size, but describes how an individual allocates grooming within its network. We termed this index "grooming distribution" (GD). The smaller the index, the more focused was the grooming behavior of an individual, and the higher the index the more dispersed an individual distributed grooming across all its interaction partners. Hinde indices account for activity in

relation to passivity in grooming behavior when looking at number of partners, grooming time, or grooming initiations (see supplementary material, Annex 1). The Hinde indices were found to have a high mutual correlation. Principle Component Analysis (PCA) can be used to reduce a set of correlated parameters and/or achieve non-collinear data [Fraser et al., 2008a; Osborne and Costello, 2004; Silk et al., 2013]. Therefore we extracted three orthogonal variables from the Hinde indices (through PCA, see supplementary material, Annex 1). These were (our interpretation in brackets):

(i) GGA (General Grooming Activity, Comp1, 93% of the variance explained): As this component increases as the Hinde indices increase, and these indices rise as the balance active versus received grooming (time, frequency, or number of partners) increases, GGA can be a good proxy for the amount of general active grooming the subject performs. As this component explained 93% of the variance in our data, we included GGA in further analyses.

(ii) GTA (Grooming Time Allocation, Comp2, 5%): This component increases as the active grooming time increases but drops whenever the number of active partners or active grooming frequency rises. Therefore, keeping in mind a naïve tradeoff between quantity and quality, this component can be interpreted as measuring how persistent subjects are in grooming. At one extreme, we have individuals with high GTA who groom rarely and have few active partners, but groom these partners for long periods. At the other extreme, we find subjects with low GTA, frequently grooming their many partners but only over short periods of time, while also having long periods of received grooming. However, as only a small percentage of variance was explained by this component, we did not include GTA measures in further analyses.

(iii) GBS (Grooming Bond Strength, Comp3, 2%): The last component is solely influenced by frequency and number of partners, with similar strength but opposite direction. A high GBS is achieved with many partners who are groomed infrequently. A low GBS characterizes a subject with few, frequent active grooming partners. Therefore this component can be seen as a proxy for network size and strength of social bonds. As only 3.2% of variance in the data is due to this component, we excluded it from further analyses.

Pooling all behavioral and hormonal data together and applying a test over an entire season may result in relevant information being overlooked [Brent et al., 2011]. In order to investigate the connection between variations in behavioral patterns and the corresponding fluctuations in C levels over time an analysis of changes in both parameters over short time windows is required. A day-by-day analysis would have required daily focal and hormonal sampling of each individual. As a compro-

mise, we calculated grooming measures (GD, GGA, grooming duration) and averaged our samples over a weekly moving time window. The dataset can thus be regarded as a multidimensional, cross-sectional time series. Ultimately our sample data consisted of the calculation of grooming indices (as described above) based on the behavioral records (frequency and duration of grooming interactions described above) of one week, and the averaged hormonal samples of the same time period. The dataset used for statistical analyses therefore featured one entry for each week and individual. As contraceptives were found to be connected to anxiety and aggressive behavior [Pazol et al., 2004] we performed our analyses with subsets of our data: excluding and including grooming partners on contraceptives (results did not differ; statistics for the data set including females on contraceptives are presented in the supplementary material only).

Finding relationships between physiological measures and either rank or grooming in primate societies is not straightforward [Brent et al., 2011]. Since both inter-individual differences and time-dependent intra-individual variation may play an important role in social dynamics, our statistical analysis consisted in mixed effects models on panel data (both longitudinal and cross-sectional). The latter can statistically explain variance due to individual heterogeneity, while the former deals with intra-individual variance over time (e.g. an individual's different C levels). Therefore, our method utilizes and combines in one model both, the explanatory power of individual differences and of time variation in behavior relative to C changes.

In order to take account for multicollinearity we either dropped or transformed some of the variables so regressors would not be correlated. Due to non-normality and non-linearity of the data, transformations (like those operated on C) were undertaken to achieve normally distributed data (standard scores). Independence and homoskedasticity were taken into account by the random effects approach and by modeling the residuals as an autoregressive process of order 2.

Our dependent variable was the natural logarithm of averaged (by week) cortisol (C). After log-transforming C, skewness and kurtosis tests for normality showed that our new variable did not significantly differ from a normal distribution (skewness: 0.51; kurtosis: 0.06; adjusted $\chi^2 = 4$, $P = 0.135$).

Additional parameters were considered as independent variables in our models. Fixed effect variables were (i) grooming distribution (GD), (ii) general grooming activity (GGA, as this first principal component explained 93% of the variance in the data, we excluded the other two principal components from our models), (iii) standardized rank, (iv) time of collection of hormonal samples, and (v) log-

transformed estrogen (E) values. As we hypothesized that rank might modulate the connection between grooming behavior and C, we also included the interactions of standardized rank and grooming measures in our models. Furthermore we included random effects: individual (with random slopes for E and lactation), group, season, and the number of samples collected.

The analysis included fitting several regressions using mixed (fixed, random and between) effects models. Fixed effects were included in the models as: (i) E and time of sample collection (null model), (ii) the null model and standardized rank, (iii) the null model and measures of grooming behavior, (iv) the null model and interactions between standardized rank and grooming measures, and (v) the null model and measures of grooming measures and their interaction with standardized rank. Independent variables were hierarchically nested in the models in that individuals were nested in group, nested in seasons. We estimated the fit of our model using Maximum Likelihood (ML) analysis. Model selection was based on Akaike Information Criterion (AIC), and weighted AIC (wAIC), respectively Bayesian Information Criterion (BIC) and weighted BIC (wBIC) scores [Burnham and Anderson, 2002]. Weighted scores indicate probabilities of how likely a given model is the best model of the set of available models.

RESULTS

First we fitted several regressions and compared these models against each other to find the model that explained C best (Table I). All models included the time of sample collection and standardized E, as well as individual (with random slopes for lactation and E) nested in group nested in season, and the number of C samples as random effects. In addition we included rank, measures of grooming behavior (grooming distribution (GD), the first principal component GGA, and grooming duration) as well as their interactions with rank into the diverse models.

The models (Table I) with the lowest AIC scores (grey background in the AIC column in Table I: models 1, 5, 6, 8, 9, and 12; scores between 165.27 and 173.09) all included the GD index. Models (model 2, 7, 10, 13, and 15) including the principal component 1 (GGA), but not the GD index clustered together with higher AIC scores (205.53 to 211.33). The highest scores (AIC from 429.25 to 436.07) were found for models (0, 3, 4, 11, and 14) containing rank only or grooming duration, but no grooming indices (the duration of grooming given ($z = -2.53$, $P = 0.011$, $n = 19$) and the interaction of grooming time given with rank ($z = 2.98$, $P = 0.003$, $n = 19$) were significant predictors of C(model 11)).

When models differ only marginally in their AIC and BIC scores (<10) they are to be treated as equivalent [Burnham and Anderson, 2002]. Consequently, models with fewer variables have to be preferred over models with many variables. Model 1 and 9 both contained the same (lowest) number of variables (that were E, time of sample collection, GD, and random effects in model 1; and E, time of sample collection, r^*GD , and random effects in model 9) and did not differ substantially in their AIC or BIC scores. When looking at wAIC scores the model with the rank-GD interaction (wAIC = 0.14) is much more probable than the model containing solely GD (wAIC = 0.01). Calculating wAIC for these two models only showed that the rank-GD interaction model was more likely (wAIC = 0.94) to predict C levels accurately. The r^*GD model (model 9) also had lower BIC (188.32) and better wBIC (0.39) scores. This and the above make the model including the rank-GD interaction (model 9) our final model as it fits the data best.

In our final model (Table II) the interaction between rank and GD ($z = 2.70$, $P = 0.007$, $n = 17$) as well as E ($z = 6.65$, $P < 0.001$, $n = 17$) were significant predictors of C levels. Lowest levels of C were detected when higher-ranking individuals focused their grooming and when lower ranking females dispersed their grooming evenly among partners. High levels of C were associated with higher-ranking individuals grooming indiscriminately or lower ranking ones focusing grooming on few grooming partners (for the same results including female grooming partners, who were on contraceptives see supplementary material, Annex 2). In other words, once we controlled for rank in our model, GD had an effect on C. Analogously, after grooming behavior was accounted for, rank could statistically explain urinary C levels. Thus our results show that in female Barbary macaques GD and dominance as well as their reciprocal influence are associated with differences in C levels. (See Fig. 1 for a time series visualization and discussion of the relationship between C and grooming behavior over time in a high and a low ranking individual.)

DISCUSSION

In line with other studies, our results demonstrate that grooming behavior is associated with C alleviation. Looking at social patterns, we observed a gradual rank-dependence in the connection with specific grooming distributions and C measures. That is not to say that individual females did show specific grooming patterns that were stable over time. Individuals varied grooming behavior, but depending on their rank, certain grooming patterns were associated with alleviated C measures. Higher-ranking females, who focused grooming on a preferred partners within their grooming network

TABLE I. Model comparison and selection

model	measure	interactions	likelihood	AIC	BIC	wAIC	wBIC
0			-207.19	432.38	462.33	0.00	0.00
1	GD		-76.54	173.09	196.26	0.01	0.01
2	GGA		-92.94	205.87	231.2	0.00	0.00
3	rank		-207.03	436.07	472.67	0.00	0.00
4	duration active		-206.31	432.62	465.9	0.00	0.00
5	GD, GGA		-72.63	165.27	188.17	0.43	0.43
6	GD, rank		-75.77	171.54	194.71	0.02	0.02
7	GGA, rank		-92.36	206.72	234.58	0.00	0.00
8	GD, GGA, rank		-71.84	165.68	190.87	0.35	0.11
9		rank $\times$ GD	-74.73	167.46	188.32	0.14	0.39
10		rank $\times$ GGA	-96.67	211.33	234.13	0.00	0.00
11		rank $\times$ duration	-205.43	432.86	469.47	0.00	0.00
12	GD	rank $\times$ GD	-74.73	169.46	192.63	0.05	0.05
13	GGA	rank $\times$ GGA	-92.77	205.53	230.86	0.00	0.00
14	duration	rank $\times$ duration	-202.63	429.25	469.19	0.00	0.00
15	GGA, rank	rank $\times$ GGA	-92.16	208.33	238.72	0.00	0.00

All models included E and time of sample collection as fixed effects, and individual (with random slopes for E and lactation) nested in group, nested in season, and the number of samples collected as random effects. In addition, rank, grooming measures as well as interactions between grooming measures and rank were included in the various models. Grooming measures were grooming distribution (GD), general grooming activity (GGA, the first principal component), and grooming duration. Model selection was based on AIC and BIC scores, as well as on wAIC and wBIC values. The models with the lowest AIC and BIC scores that differed less than 10 units from each other are highlighted with gray background. Two models (model 1 and 9) in the set of models with lowest AIC scores contained fewest variables. wAIC and wBIC scores indicate that model 9 including the rank-GD interaction is the more probable of the two models. This model also has lower BIC scores.

(independent of network size) showed lower C levels. This association was less pronounced for females with intermediate dominance status. For lower-ranking females, C measures were predicted to be lower when they distributed their grooming evenly among their female grooming partners. Hence, whether focusing or dispersing grooming across social partners within a social network was associated with C mitigation depended on female dominance rank. This stands in partial contrast to other research demonstrating a general connection of focused social activity and low concentrations of GC hormones (baboons: [Crockford et al., 2008]), or showing GC-alleviating effects of focused social activity for high-ranking individuals only (rhesus macaques: [Brent et al., 2011]). These studies on despotic primate species [Brent et al., 2011; Crockford et al., 2008; Wittig et al., 2008] indicate that

focused social networks are beneficial in terms of GC mitigation, which begs the question, why do not all individuals in a rather tolerant society (such as Barbary macaques) have focused networks?

Barbary macaques are socially more relaxed than rhesus macaques and baboons (see [Thierry et al., 2004]). Therefore, we argue that low-ranking female Barbary macaques may have more behavioral flexibility and more social options to adapt their grooming to certain circumstances. In contrast to despotic species, low-ranking females of our study species are eventually able to gain access to more valuable higher-ranking females [McFarland and Majolo, 2011; Seyfarth, 1980] and gain advantages from grooming them. At the same time it is important to strengthen social bonds with more stable social partners [Henzi et al., 1997]. Thus subordinates profit from dispersing their grooming among all their

TABLE II. The Final Model

log-likelihood = -74.73				Wald χ^2 (3) = 51.96 $P < 0.001$			
	coefficient	St.Error	z	P	95% confidence interval		
rank $\times$ grooming distribution (GD)	0.205	0.758	2.7	0.007	0.056		0.353
log E	0.686	0.103	6.65	<0.001	0.483		0.888
time of sample collection	-1.261	0.849	-1.49	0.137	-2.924		0.402
constant	4.01	0.399	10.05	<0.001	3.228		4.792

The model that explained C best contained E, time of sample collection, rank, and the rank-grooming distribution (r $\times$ GD) interaction as fixed effects. Individual (with random slopes for E and lactation) nested in group, nested in season and number of samples were included as random effects. The r $\times$ GD interaction ($z = 2.7$, $P = 0.007$) and E ($z = 6.65$, $P < 0.001$) were significant predictors of C.

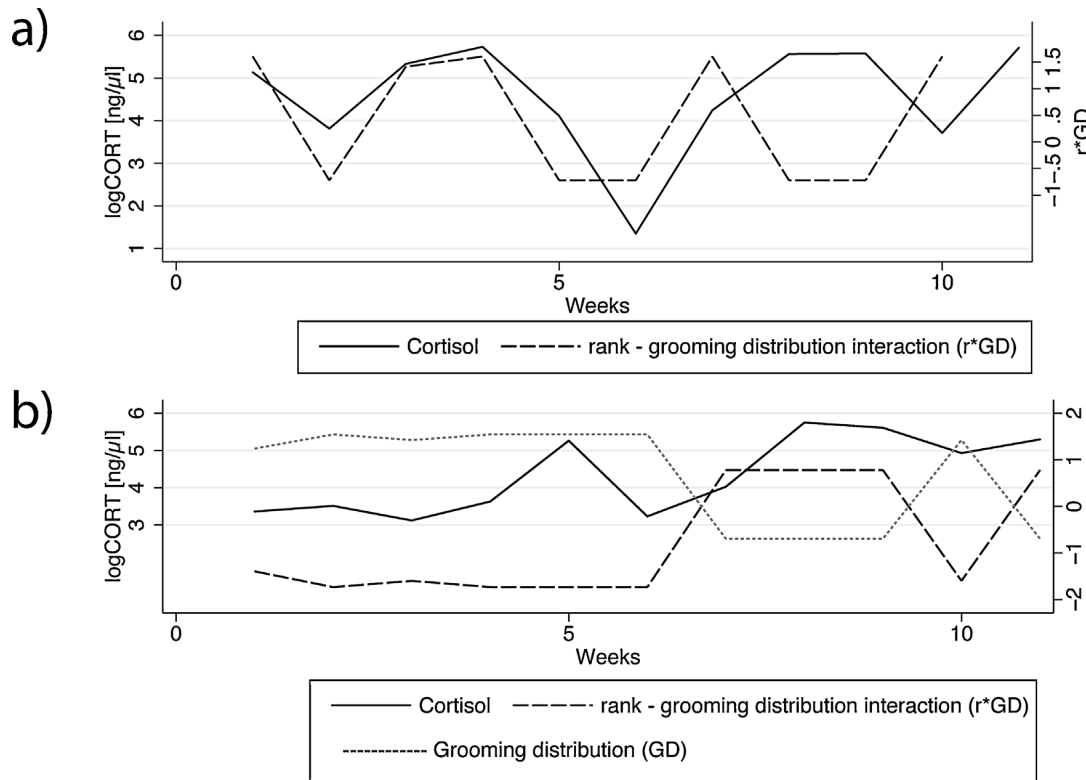


Fig. 1. (a) Time series of C and the rank - grooming distribution interaction ($r \times GD$) for a high-ranking individual over the first season. (b) Time series of C and grooming distribution (GD, dotted line) respectively $r \times GD$ (dashed line) for a low-ranking individual. For the dominant female, as her relative rank equals 1, GD and $r \times GD$ (equal in this case to $GD \times 1$) coincide, and both show an association with C. For the low-ranking female on the other hand there is no connection between C and GD. Only when the interaction between GD and rank is considered, does the association with C become apparent. (1a) shows the C and the rank-grooming distribution ($rank \times GD$) interaction for a high-ranking female over the first season. One might suspect that the GD, coinciding in this case with the time series of the interaction, would be a good candidate for mutual prediction with the C time series. However, the time series of a low-ranking female (1b) makes this hypothesis less likely. While the distribution of grooming activity (GD, dotted line) cannot predict C levels, its interaction with rank (dashed line) predicts C (unbroken line) more reliably. This is confirmed by the cross-correlation function (calculated up to a lag of 2), reaching maxima of +0.28 (high-ranking individual, Figure 1a) and +0.62 (low-ranking individual including the interaction, Figure 1b).

available partners evenly. In contrast, high-ranking females can benefit from focusing their grooming efforts on a selected partners. This reduces social bonding time and leaves more time for foraging and other important activities. McFarland and Majolo, [2011] predicted relationship asymmetry for Barbary macaques due to the importance of *resource holding potential*, which in turn implies that lower ranking females would need to groom more as a trade-off for social commodities. Another key aspect may be consistency [Silk et al., 2010] and security [McFarland and Majolo, 2011] of social partners. Even in a relatively tolerant society, dominant females represent long-term attractive partners, as they remain dominant for life. They most likely have the luxury of not only choosing but also keeping their friends a lot easier than subordinate animals.

Even in a tolerant society, a different time allocation may represent a good balance for animals of different ranks. Subordinate animals may need

more time to forage, as they do not have unrestricted access to prime food. They may also be considered less “valuable” as social partners and therefore need to compensate by offering more social investment time. In addition, they may need to use grooming as a social currency to barter for rank-related benefits (such as tolerance around food and agonistic support). Although these are surely key aspects in social patterns of macaque societies, factors such as frequency and duration of grooming, or the social network size did not show significant association with C levels in our study. This finding agrees with results by Edwards et al. [2013], whose data did not find a connection between daily rates of social behavior and associated fecal GC levels in Barbary macaques (grooming patterns were not analyzed in more detail). In contrast, Shutt et al. [2007] demonstrated that measures of ‘grooming per female’ and clique size was associated with GC levels in Barbary macaques: the more a female groomed, and the bigger her clique

size was, the lower her GC levels were. This difference to our study might be due to differences in study design: Shutt et al. [2007] pooled behavioral and hormonal data over a whole study period, while Edwards et al. [2013] and our data were analyzed for smaller time windows. Thus, our data allowed a more fine-grained analysis of short-term changes in behavioral and stress measures.

Tourism can impact behavior (scratching rates) and GC-physiology [Maréchal et al., 2011] in that it increases anxiety levels. As both our study groups were visited by tourists this might have had an influence on our results. However, exposure to tourists was comparable for all individuals and both groups. Consequently macaque-human interactions might be random noise in our data, but its impact should be similar for all our study subjects. Furthermore, tourist pressure was comparably low during the study periods (autumn and winter) as compared to summer months when tourists mainly visit the macaques. Aggressive interactions between macaques and humans were found to affect GC levels (in male macaques), but no other form of interaction was reflected in hormonal measurements Maréchal et al. [2011]. We did not observe such aggressive interactions within our observation periods, thus it is unlikely that we measured human disturbance in our hormonal samples. In the future data on tourist pressure and macaque-human interactions should be collected and accounted for in statistical analyses.

In a matrilineal society, it is challenging to distinguish between the influence of kinship and rank. Seyfarth [1977] proposed an effect of kin and high rank on grooming patterns and thus hypothesized that dominant matrilineal females would be more cohesive than lower-ranking ones. As we had no information on kinship for our study population, we were not able to include kinship in our analyses. However, Schino [2001] did not confirm the prediction of Seyfarth's model and argued that high-ranking females did not show a kin preference since they could demand grooming from kin and non-kin. Also for baboons, no relationship between the number of close kin and GC levels was found [Crockford et al., 2008]. Although female baboons focus their grooming on kin [Silk, 2009; Silk et al., 1999, 2006, 2009] they compensate with non-kin social partners if related individuals are not available [Cheney and Seyfarth, 2009]. Furthermore, the identities and attributes of the grooming recipients were not a focus of this study, as we were mainly interested in finding a general overlaying grooming pattern expressed by our focal individuals. So far, key aspects of complex social behavior such as "reconciliation" in Barbary macaques showed high rates of affiliative behavior with non-kin [Thierry et al., 2008]. By definition, kin bias is less pronounced in relaxed species [Thierry et al., 2004]. This cannot exclude the possibility that matriline size influenced social network size and thus

played into our results. Nevertheless, it is unlikely that kinship was a decisive factor. Grooming focus within a network was independent of network size and number of relatives. Further studies on social networks in relaxed macaque societies with known kinship would be needed to resolve this issue.

Also, and not very surprisingly, our model revealed significant effects of E levels on C concentrations. Various other studies already demonstrated that the reproductive state of females has an impact on GC levels (e.g. [Brent et al., 2011; Cheney and Seyfarth, 2009; Pepe et al., 1982; Smith and Norman, 1987; Stavisky et al., 2003; Weingrill et al., 2004]). Our prediction of finding an effect of E concentrations on physiological stress measures in our study population was confirmed.

Past research demonstrated conclusively that close social bonds with other females are beneficial for female primates in matrilineal societies. Cheney and Seyfarth [2009] argue that focusing grooming on selected individuals has GC mitigating effects because these social bonds tend to be stable and predictable. Females with strong and consistent ties have lower GC levels [Seyfarth et al., 2012] and their longevity is enhanced [Silk et al., 2010], offspring survival and thus fitness is improved [Silk, 2009]. There appears to be an ideal size and strength for a social network, which varies with the circumstances and social standing of an individual. For instance, baboons extend their grooming network to as many individuals as time constraints allow [Henzi et al., 1997]. Within this network however they form particularly strong social bonds with a subset of these individuals (as reflected by their grooming distribution). When group size exceeds a level that allows individuals to have some social interaction with the majority of the group members, groups will split [Dunbar, 1992; Henzi et al., 1997]. In Barbary macaques dominant females express similar patterns: they concentrate their grooming activity on selected individuals within their network. Lower ranking females on the other hand might profit from dispersing their grooming activity across all their social partners.

According to Cheney and Seyfarth [2009], the degree to which rank plays a role in GC measures depends on the availability of support and the possibility of avoiding aggression. Our data suggest that female Barbary macaques, who live in relatively relaxed societies, are able to adapt their grooming patterns flexibly and have the behavioral options to potentially express rank-dependent grooming patterns that may be associated with efficient GC mitigation across all dominance ranks.

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Annex 1: Principal Component Analysis (PCA) of Hinde Indices

A Hinde index equal to one means that the subject only actively grooms other individuals without being reciprocated, while an index equal to zero means the reverse. An index close to 0.5 stands for an individual whose grooming behavior is equally distributed between active and received grooming when it comes to number of partners, grooming time or grooming initiations, respectively.

HIGP (Hinde Index for Grooming Partners) equals the ratio of active grooming partners over total grooming partners.

HIGT (Hinde Index for Grooming Time) stands for the total time an individual spends actively grooming others, divided by the sum of active plus received grooming duration.

HIGF (Hinde Index for Grooming Frequency) equals the ratio of active grooming initiations over the total grooming initiations in which an individual was involved.

Three components we found (see Table A1): GGA (General Grooming Activity, PComp1 - 93% of the variance explained), which increases as the Hinde indices increase. GTA (Grooming Time Allocation, PComp2 - 5%), which increases as the active grooming time increases but drops whenever the number of active partners or active grooming frequency rises. GBS (Grooming Bond Strength, PComp3 - 2%) solely influenced by frequency and number of partners, with similar strength but opposite direction (a proxy for how dispersed among individuals grooming behavior is).

Table A1: Principal Component Analysis of grooming indices. The first component entails a general increase of all grooming Hinde indices. The second component increases with grooming time, but decreases with the number of active grooming partners and grooming frequency. Grooming frequency and the number of partners influences the third component.

Component	Eigenvalue	Difference	Proportion	Cumulative
1	2.80156	2.64722	0.9339	0.9339
2	.154344	.110248	0.0514	0.9853
3	.0440061		0.0147	1.0000
Principal Components				
Variable	component 1	component 2	component 3	unexplained
HIGT	0.5653	0.8241	0.0368	0
HIGF	0.5825	-0.4303	0.6896	0
HIGP	0.5842	-0.3683	-0.7232	0

Note that the correlation between the 3 components with the SWDI is weak (see Table A2).

Table A2: Correlation matrix of the three PCAs, the SWDI and the rank-grooming skew interaction.

	nSWDI	rank*SWDI	PC1	PC2	PC3
nSWDI	1				
rank*SWDI	0.1041	1			
	0.3403				
PC1	-0.0102	-0.1207	1		
	0.9267	0.2740			
PC2	0.1732	-0.0870	-0.0000	1	
	0.1151	0.4657	1.0000		
PC3	0.0292	0.0625	0.0000	-0.0000	1
	0.7919	0.5721	1.0000	1.0000	

Annex 2: The final model (including the rank-grooming distribution interaction model) including females on contraceptives as interaction partners.

Previous research suggests that contraceptives can have an impact on anxiety and aggressive behavior (Pazol et al., 2004). Therefore we run our models excluding female social partners (two females from the PPA group), who were on contraceptives. Here we present our final model including females on contraceptives (see Table A4), which did not affect the results of the model.

Table A4: The final model including females on contraceptives. The rank-grooming focus interaction and estrogen levels were significant predictors of urinary C concentrations. Including the two females, who had contraceptive implants, did not alter the results obtained by the model.

log-likelihood = -76.909				Wald chi2 (3) = 55.47 p>chi2 <0.001		
	coefficient	St.Error	z	p	95% confidence interval	
r*sw	0.209	0.077	2.73	0.006	0.059	0.36
logE	0.69	0.101	6.87	<0.001	0.493	0.887
timeCort	-1.415	0.874	-1.67	0.106	-3.129	0.299
cons	4.076	0.411	9.92	<0.001	3.271	4.882

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3 | Social Behavior and Mating

Post-copulatory grooming: a mating strategy?

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Post-copulatory grooming: a mating strategy?

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Abstract

In behavioural ecology the connection between sexual and social behaviours is mainly analysed and interpreted in light of mate-guarding behaviour or in the context of biological mating markets, and usually these studies do not differentiate between types of copulation (ejaculatory and non-ejaculatory). However, not all mating results in ejaculation, which may have different implications for the two sexes and consequently may elicit sex-specific behavioural responses. Here we study such behavioural adaptations by looking at male and female Barbary macaque post-copulatory grooming patterns in connection with copulation type. Furthermore, we investigate the role of female lactation state on the expression of grooming behaviour. Our results show that males and females express different grooming behaviour after ejaculatory and non-ejaculatory copulations, with males being more likely to groom after copulations with ejaculation and females being more likely to groom after non-ejaculatory mating. Moreover, lactating females were more likely to groom the males they had mated with than being groomed by that male, whereas we did not find such a difference for grooming behaviour after copulations with non-lactating females. These behavioural patterns may reflect sex-specific mating strategies: females can gain repeated (potentially ejaculatory) copulations by grooming male partners after non-ejaculatory mating, while males may profit from grooming females after ejaculatory copulation by keeping them from mating with another male thus decreasing sperm competition. Finally, females that are lactating potentially gain support and protection for their already born offspring from increased grooming of their mating partners.

Keywords: Barbary macaques, mating tactics, ejaculatory copulations, non-ejaculatory copulations, single mount ejaculations

Introduction

Pre- and post-copulatory mating strategies of males and females of various species are well-studied phenomena in the sexual selection literature (Cunningham and Birkhead 1998; Pizzari 2001; Snook 2001). Typically, when looking at post-copulatory mating strategies, evolutionary biologists focus on sperm competition, cryptic female choice, or sexual antagonism. All these mechanisms concern male and female strategies after insemination to optimize reproductive success. On a behavioural level mating is often associated with social behaviours, such as grooming, both before and after copulation. This has mainly been investigated in connection with mate guarding (Berenstain and Wade 1983; Grafen and Ridley 1983; Poole 1989; Alcock 1994; Manson 1997; Watts 1998; Kokko and Morrell 2005; Schülke et al. 2013; Elias et al. 2014; Girard-Buttoz et al. 2014) or mating markets (Noë and Hammerstein 1994; Gumert 2007; Norscia et al. 2009; Barelli et al. 2011). While mate guarding research usually tests predictions on the adaptive value of social associations in mating contexts (such as partner protection, avoidance of sperm competition, or gain of repeated mating (Alcock 1994)), mating market theory investigates how different commodities (such as grooming and mating access) are traded between individuals (Noë et al. 2001).

Both theoretical and empirical research have demonstrated that the value of commodities like mating may differ between the sexes, and thus that males and females may have different sexual interests, leading to sex-specific mating strategies (Johnstone et al. 1996). This could also apply to the expression of post-copulatory social behaviour. However, only a few studies have investigated copulation-associated behaviour of mating partners immediately after copulation. A survey on university and college students found differences in male and female post-coital behaviour (Hughes and Kruger 2011). While females initiated and engaged in bonding behaviour after copulation, males preferentially showed behaviours that were extrinsically rewarding (e.g., smoking) or increased the likelihood of repeated copulation (e.g., through continued sexual activity). Similarly, male and female snub-nosed monkey mating partners huddle together or allogroom after copulations, though females show more of such post-mating grooming than males (Li and Zhao 2007). Among chimpanzees, in contrast,

males groom females after inspecting their hindquarters and initiate post-copulatory grooming (Nishida 1997). These studies suggest that socio-positive behaviours immediately after copulation might serve sex-specific mating strategies that in turn may be species specific.

Interestingly, among various animal species some copulations do not lead to ejaculation (e.g., voles: (Dewsbury 1973); opossum: (McManus 1967); mice: (McGill 1962); in primates muriquis: (Possamaia et al. 2005); golden monkeys: (Ren et al. 1995); chimpanzees: (Goodall 1986); for a review see (Dewsbury 1972)), but only when ejaculation has occurred can an egg be fertilized. Consequently, non-ejaculatory copulations have been largely neglected in the literature and have often been excluded from analyses in studies on reproduction and mating strategies (Furtbauer et al. 2011; Dixson 2012; Young et al. 2013), or evaluated solely outside reproductive periods in seasonally breeding species (Li et al. 2007). But non-ejaculatory mating is widespread in the animal kingdom (Dewsbury 1972). Diamond (1970) proposed that species-specific copulation patterns promote neuronal and endocrine reactions necessary for successful fertilization. Macaques, baboons, and voles evolved mating patterns that include non-ejaculatory copulation and multiple ejaculations (in some species of these genera multiple intromissions are necessary to achieve ejaculation) (Dewsbury 1972). However, the exact function of non-ejaculatory mating remains unresolved, although it is likely that they have some adaptive advantages for males and/or females. These advantages could lie within animals' reproductive biology (e.g., sperm retention: (Small et al. 1988), or vaginal stimulation: (Dewsbury 1972)) and/or could be connected to social bonding if mating without ejaculation serves sort of a "social copulation" function.

Mating strategies may also vary between and across the sexes according to differing reproductive status of the female. In mammals, several studies indicate that females nursing offspring may show lactation-associated reduced fertility (Wilson et al. 1983; Maeda et al. 1991; Mitsunaga et al. 1994; Kondo et al. 2003; Wallner et al. 2011). While non-lactating females show typical changes in oestrogen and progesterone throughout the ovarian cycle, females nursing offspring often lack pronounced changes in progesterone and oestrogen concentrations, which leads to irregular menstrual cycles (Maeda et al. 1991; Mitsunaga et al. 1994). This may be due to the increased energetic costs of lactation (Prentice and Prentice 1988). In turn, decreased fertility associated with lactation may be a relevant factor in understanding differences in post-copulatory social behaviour expressed by and directed

towards lactating and non-lactating females, respectively. Furthermore, previous research suggests that females with infants may be inclined to bond with male (mating) partners as they can offer protection and support for the females as well as for their offspring (Palombit et al. 1997; Palombit et al. 2001; Lemasson et al. 2008). Grooming, and in particular post-copulatory grooming, may be employed for establishing and maintaining social bonds with males.

Barbary macaques have received special attention regarding male and female mating strategies because they seem to have particularly high mating-partner turnover rates (Taub 1980; Small 1990b; Kuester and Paul 1992). Moreover, their mating system seems to be primarily shaped by female choice (Taub 1980; Small 1990b; Brauch et al. 2008), although data restricted to fertile periods challenge this claim (Kuester and Paul 1992). The majority of females tend to mate no more than twice in succession with a male before copulating with another partner, but repeated copulations in succession have also been observed (Kuester and Paul 1992). Barbary macaques breed seasonally and have single-mount-to-ejaculation patterns (Taub 1982), thus ejaculation can occur at the first instance of a male mounting a female (in contrast to the multiple-mount-to-ejaculation patterns seen in Japanese macaques for instance). While frequencies of ejaculatory copulations increase around female fertile periods, non-ejaculatory mating occurs throughout the mating period (Heistermann et al. 2008; Pfefferle et al. 2008). Finally, two thirds of all mating contacts in this species are associated with post-mating close body contact or grooming, with males being the more active groomers (Kuester and Paul 1992). These patterns make Barbary macaques an interesting species to investigate post-copulatory mating strategies in the two sexes.

Here we analyzed post-copulatory grooming behaviour in two wild groups of Barbary macaques to investigate sex-specific post-mating grooming patterns after ejaculatory and non-ejaculatory copulations. We predicted that male and female post-copulatory grooming behaviour depends on the type of copulation. We predicted males to be more inclined to groom a female after ejaculatory copulations to keep her from mating with competitors. Females on the other hand should groom the male more after non-ejaculatory mating to solicit additional (ejaculatory) copulations. Finally, we expected nursing females to groom male mating partners more than non-lactating females to potentially gain protection for themselves and their offspring, and counterweigh lactation-associated fertility reduction.

Material and Methods

Subjects and Study Site

Adult male and female Barbary macaques (*Macaca sylvanus*) inhabiting the Rock of Gibraltar, Gibraltar, UK, were observed over two consecutive mating seasons (October 2004–February 2005 and October 2005 – March 2006). All females were cycling and some were nursing offspring from the previous season (three in the first, nine in the second season). In the first season we collected data on the “Apes Den” group (AD), which encompassed 13 adult females and nine adult males (six of whom immigrated from neighbouring groups). In addition AD had six subadult individuals, eight juveniles, and five infants (age was classified after (Burton 1972)). In the second season AD consisted of 14 adult females and nine adult males (two of which emigrated at the beginning of the season), as well as nine subadults, five juveniles and seven infants. Additionally, in the second season we observed the “Prince Phillips Arche” group (PPA), consisting of 12 adult females and six adult males (and twelve subadult individuals, eight juveniles and seven infants). Two females in the PPA group had contraceptive implants. Contraceptive implants can affect social and sexual behaviour in macaques (Pazol et al. 2004), and therefore the two females on hormonal contraceptives were excluded from data analysis. Thus, in total we observed 31 adult individuals (18 females and 13 males) of which 17 (11 females and 6 males) were observed in two consecutive seasons. The home ranges of the two study groups had good accessibility and allowed for a good view over the territory. The Gibraltar Ornithological and Natural History Society (GONHS) provisioned the animals with fruits and vegetables on a daily basis.

Behavioural Data Collection and Sampling

Behavioural data collection spanned 109 days in the first and 115 days in the second season. Observations started at 08:00 and ended at 17:00. In the first season AD was observed daily. In the second season data collection alternated between groups: after a day of observations at AD, data were collected at PPA the following day. We collected behavioural data *ad libitum* (Altmann 1974). To establish rank hierarchies we collected data on intra-sex agonistic interactions. Furthermore, we recorded copulations and consecutive grooming between adult male and female individuals. When copulation occurred we noted identities of the copulation partners and the type of copulation (ejaculatory or non-ejaculatory). Ejaculatory copulations were identifiable by an ejaculation pause in pelvic thrusting and visible sperm threads either on the male or female genitalia right after copulation (as described earlier in (Kuster and Paul

1984; Brauch et al. 2007)). The sex initiating grooming and grooming polarity (female grooming the male or vice versa) that occurred within 30 seconds after the male dismounted the female was recorded.

Data Analysis

We used intra-sexual dyadic agonistic interactions (Deag 1974) between adult individuals to establish male and female rank hierarchies (per group and season). Mat Man 1.0 (De Vries et al. 1993) was used to calculate linear dominance ranks. As the number of males and females differed across seasons and groups, we calculated relative rank positions by dividing the absolute rank by the number of rank places in the groups. Due to insufficient data three young males in the PPA group (second season) and males immigrating into the AD group during the first season were not assigned a dominance rank.

We entered all observed copulations twice in our data set, once for the male and once for the female mating partner and added information on whether the individual groomed after the mating (binary data: either the individual groomed or the individual did not groom). These data were entered into binomial Generalized Linear Mixed Models with a logit link function (GLMM, using the lme4 package in R, (Bates et al. 2014)) to assess the relationship between male and female post-copulatory grooming after ejaculatory and non-ejaculatory copulations and in relation to female lactation state. Since individuals were sampled repeatedly and over consecutive seasons, we applied a repeated measures design. Our response variable was the binary grooming variable. Intercepts for male and female identity nested in group and season were entered as random factors into our models. As all copulations were entered twice in the data set, the copulation identification number was also included as a random effect. We fitted a full model, containing the following predictor variables: (i) type of copulation (ejaculatory or non-ejaculatory), (ii) the sex of the individual (male or female), (iii) female lactation state (lactating or not lactating), (iv) female and male relative rank, (v) the interaction between the copulation type and individual's sex, (vi) the interaction between lactation state and sex, (vii) the interaction between the ranks of the mating partners, (viii) the interaction between copulation type and lactation state, (ix) the three-way interaction between copulation type, sex, and lactation state, (x) the three-way interaction between the copulation type, female rank, and sex, as well as (xi) the three way interaction between the copulation type, male rank, and sex. By reducing the set of predictor variables (stepwise reduction procedure: we

eliminated the parameter that explained the least variance in the data and build a new model) we evaluated the model that fit the data best. We calculated Akaike Information Criterion (AIC) scores controlled for small sample sizes (AICc) and Akaike weights (wAICc) to compare competing models and to select the model predicting the probability of grooming to occur most efficiently (Burnham and Anderson 2002; Aho et al. 2014). The variable elimination procedure was repeated until variable reduction no longer decreased AIC scores and thus did not increase the explanatory power of the model.

With regard to our repeated measures design, for post-hoc testing of interaction effects we split the data frames (according to significant predictors in the final model) and re-ran models. All statistics were computed with R (version 3.1.1 (2014-07-10), (Team 2014)), all tests were two-tailed and alpha was set to 0.05.

Results

A total of 490 copulations between 18 adult females and 13 males were observed throughout the observation period. The number of copulations varied across individuals: between three and 58 copulations per female and between two and 83 copulations per male were recorded in the first season. In the second season between two and 41 copulations per female and between two and 40 copulations per male were observed. 224 of the 490 copulations were ejaculatory, and 266 occurred without ejaculation. No grooming was initiated within 30 seconds after dismounting after 242 copulations, whereas 248 copulations were followed by either the female grooming the male (in 146 instances), or by the male grooming the female (in 102 instances) (for a detailed overview of grooming frequencies see Table 1).

Table 1: Overview of grooming distribution. The numbers indicate grooming frequencies (i.e. males groomed their female partners in 102 instances: 81 times after ejaculatory copulations and 21 times after non-ejaculatory mating; males groomed lactating females 39 times and non-lactating females 63 times across copulation types).

grooming by	general	ejaculatory	non-ejaculatory	lactating females	non-lactating females
	out of 490	out of 224	out of 266	out of 235	out of 255
male	102	81	21	39	63
female	146	50	96	81	65
no grooming	242	93	149	115	127

To analyze factors influencing the probability of whether an individual would groom its mating partner subsequent to copulation we ran a GLMM including several predictor variables (as described in the methods above). The best fitting model (Table 2; the full model is provided in the Online Resources 1) included the type of copulation, the sex of the individual, female lactation state, the two-way interaction terms of copulation type and sex, copulation type and lactation state, sex and lactation state, male and female relative rank, as well as the three-way interaction of copulation type, sex, and lactation state. In this model, significant predictors of grooming probability were the type of copulation, the sex of the individual, and the interaction of copulation type and sex. Additionally, the interaction of sex and lactation state was close to significant.

Table 2: The final model on the probability of an individual to groom its mating partner after copulation. Female and male identity nested in group and season, as well as the copulation identification number were included as random factors. *P*-values of significant predictors are displayed in bold typeface.

Linear mixed-effects model fit by maximum likelihood					
	AIC	BIC	logLik	deviance	df residuals
	852	926.9	-410	820	782
Scaled residuals:					
	Min	1Q	Median	3Q	Max
	-0.915	-0.649	-0.369	-0.237	3.949
Fixed effects					
	estimate	Std. Error	z value	<i>P</i> -value	
Intercept	-3.316	0.651	-5.090	<0.001	
copulation type	4.800	0.847	5.667	<0.001	
sex	1.250	0.370	3.384	0.001	
lactation state	-1.774	1.080	-1.642	0.101	
copulation type*sex	-2.904	0.538	-5.398	<0.001	
copulation type*lactation state	-0.790	1.307	-0.604	0.546	
sex*lactation state	1.138	0.596	1.910	0.056	
female relative rank*male relative rank	-0.025	0.049	-0.509	0.611	
copulation type*sex*lactation state	0.658	0.776	0.848	0.396	

Copulation type and sex of the individual significantly predicted post-copulatory grooming. In general females were more likely to groom after mating than males (Figure 1a) irrespective of the type of copulation that occurred. The likelihood for grooming to occur was significantly higher after mating with ejaculation than after non-ejaculatory copulations (Figure 1b).

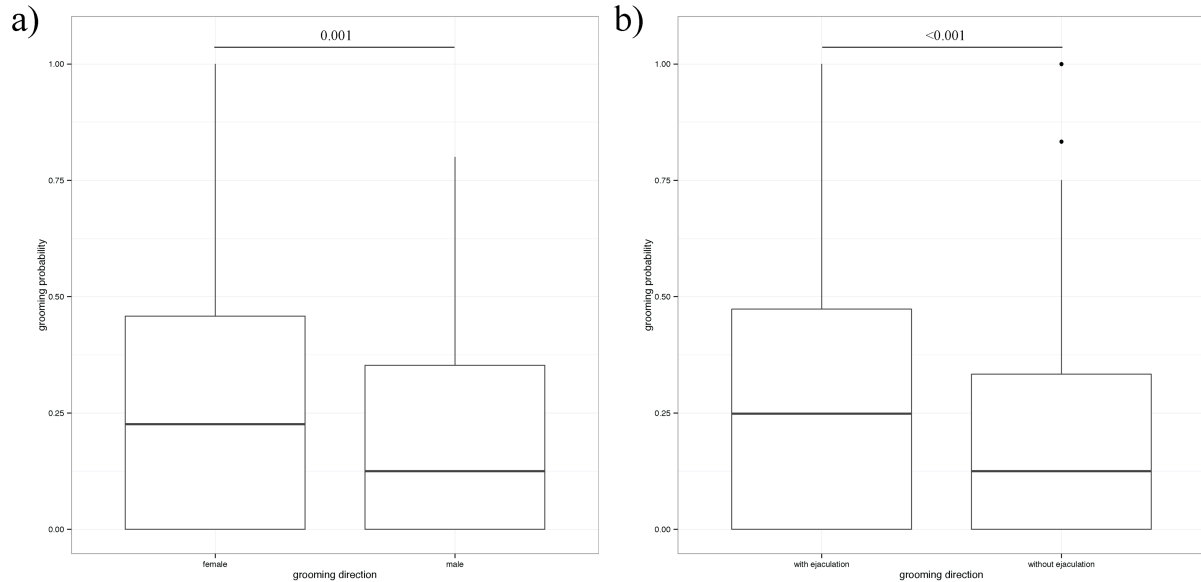


Figure 1: Median grooming probabilities (i.e. the number of instances when grooming occurred divided by the total number of copulations) for (a) females and males and (b) after mating with ejaculation and without ejaculation.

Because the interaction of copulation type and sex of the individual had a significant effect on grooming probability the dataset was split into subsets (by copulation type, sex). Post-hoc models revealed several differences in post-copulatory grooming behaviour. Males were more likely to groom after ejaculatory mating than after copulations without ejaculation ($z=6.654$, $SE=0.303$, $P<0.001$; Figure 2). When compared to female grooming behaviour, males were less likely to groom after copulations without ejaculation ($z=7.268$, $SE=0.268$, $P<0.001$), but more likely after mating with ejaculation ($z=-2.961$, $SE=0.217$, $P=0.003$; Figure 2). Because the interaction between lactation state and individual sex was very close to being significant, we also performed post-hoc tests on these data, again by running simple models on split data sets. This revealed that lactating females were significantly more likely to groom than the males they had mated with ($z=4.350$, $SE=0.223$, $P<0.001$), whereas non-lactating females and their mating partners were equally likely to groom after mating ($z=0.528$, $SE=0.211$, $P=0.598$).

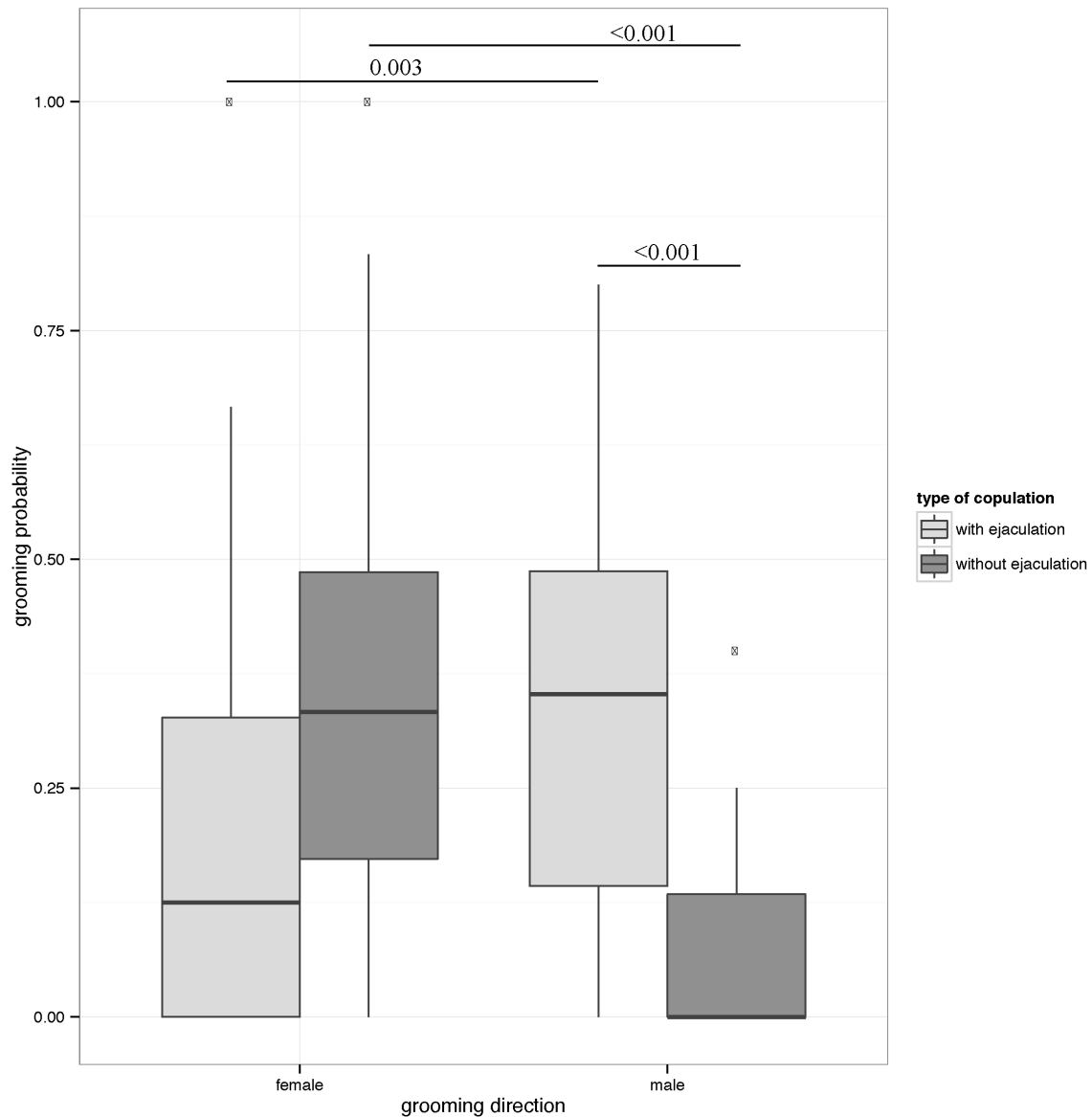


Figure 2: Median grooming probabilities (i.e. the number of instances when grooming occurred divided by the total number of copulations) for females and males after copulations with ejaculation (light grey boxes) and after copulations without ejaculation (dark grey boxes).

Discussion

In this study we found that sex-specific post-copulatory grooming patterns depend on copulation type and female lactation state. Overall, copulations with ejaculation are more likely to be followed by grooming than non-ejaculatory ones, and the probability of the female grooming the male mating partner after copulation is higher than of the male grooming the female. The likelihood of a male grooming a female is higher after copulations with ejaculation than after non-ejaculatory ones. Females in contrast are as likely to groom after

mating with and without ejaculation. When comparing the two sexes our results show that males are more likely to groom after ejaculatory mating than their female partners. The probability that the female grooms after non-ejaculatory copulations is higher than the likelihood of male grooming after non-ejaculatory mating. Finally, among females, lactating individuals are more likely to groom than their non-lactating peers.

Overall, grooming followed about half of all observed copulations, which is consistent with earlier findings in non-human primates (Taub 1980; Small 1990b; Kuester and Paul 1992). An absence of grooming after mating may be due to audience effects (Overduin-de Vries et al. 2012): refraining from social interactions potentially reduces the risk of interference or attacks through higher-ranking females (Kuester and Paul 1996) or males, although high-ranking male Barbary macaques are relatively tolerant towards subordinate males, (Kuester and Paul 1992). For copulations followed by grooming we found interesting patterns of grooming distribution. More generally, we found that males and females appear to show discriminative grooming behaviour.

Males were more likely to groom after copulations with ejaculation than after non-ejaculatory mating. Grooming the female after ejaculatory mating may keep her from copulating with other males, in turn reducing sperm competition. This is in accordance with previous findings where both ejaculation rates (Heistermann et al. 2008) and male grooming (e.g., (Soltis 1999; Koyama et al. 2012)) increase around the time of ovulation, and thus should often, in principle, coincide. Along those lines we expected an increase in male grooming after ejaculatory copulations. While previous research described an increase of male social activity during the mating season in general (Kaufmann 1965; D'Amato et al. 1982; Mehlman et al. 1997; Soltis 1999) or around the time of female ovulation (Wallis 1992; Nishida 1997; Van Belle et al. 2009) and at peak of female sexual characteristics conspicuousness (Rowell 1963; Higham et al. 2009), ours is the first study to report similar results on male grooming activity directly after mating. However, it is difficult to disentangle how different aspects (such as female cycle stage, female signalling through secondary sex characteristics, or copulation type) that impact male social activity towards females influence each other and to infer causal relations between them. So far the results suggest that evolution shaped multiple adaptations on various levels to cope with the special challenges coming with sexual reproduction in complex, stable social groups.

While males were more likely to groom after ejaculatory mating than females, females groomed more than their male partners after non-ejaculatory copulations. A possible explanation for these sex-specific grooming pattern could lie in the copulation pattern of this species, which follows a polyandrous single-mount-to-ejaculation pattern (Taub 1982): females might be interested in mating with another partner after having received an ejaculate from the current partner (Small 1990b; Kuester and Paul 1992; Brauch et al. 2008), and thus refrain from grooming the male. By grooming the male after non-ejaculatory mating the female may keep the male close by and in an aroused state (Slob et al. 1986; Rao 1995; Bancroft 2005; Lee et al. 2009) and increase the likelihood of re-mating. Ultimately, non-reproductive mating can increase female reproductive success as non-ejaculatory copulations are often followed by further (potentially ejaculatory) copulations (Small et al. 1988).

The increase in female grooming probability may simply be a response to a decrease in male grooming likelihood: if the male does not start grooming after a mating, the likelihood of the female grooming increases. This might imply that the female is not aware of the type of copulation that occurs, as she may simply react to the absence of male social activity (our results show that males show reduced grooming probability after non-ejaculatory mating). Alternatively, females may be more likely to groom as a response to the type of copulation they received. Crucially, this would imply that females are aware of the type of mating they receive, namely if an ejaculation occurred or not. Looking at the data of lactating and non-lactating females makes the latter interpretation more likely. Males and non-lactating females groom at similar rates after copulations. Nursing females however express higher grooming probability than their male partners. This finding suggests that the post-copulatory grooming pattern between males and lactating females is female-driven. Nursing females increase post-copulatory grooming after copulations, while males groom lactating and non-lactating equally often. Male lemurs have been shown to keep female mating partners interested (and thus gain additional copulations) by post-copulatory mountings, a behaviour solicited by females (Parga 2010). A similar mechanism might underlie lactating female post-copulatory grooming in Barbary macaques: increasing grooming rates might at the same time increase repeated copulation likelihood. A detailed examination of nursing and non-lactating female grooming probabilities after ejaculatory and non-ejaculatory copulations shows that non-lactating females are less likely to groom after copulations with ejaculation than after non-ejaculatory ones ($z=-2.792$, $SE=0.598$, $p=0.005$). In contrast, females nursing offspring from the previous

season are not more likely to groom after copulations with ejaculation than after non-ejaculatory ones ($z=-0.364$, $SE=1.301$, $p=0.716$). This pattern further supports the notion that females are aware of the type of mating they receive, and show differential behavioural responses.

Generally, females were more probable to groom their male partner after mating than vice versa. This seems to stand in contrast with earlier findings on Barbary macaques, which reported males to be the more active groomers in mating contexts (Kuester and Paul 1992). However, these different results can likely be explained by differences in methodologies: while Kuester and Paul (1992) recorded grooming interactions between males and females in contact bouts that lasted between few seconds and two hours, we report results on grooming behaviour solely immediately after copulations. Otherwise, differences in the number of lactating females between the two study populations could be responsible for the different results: our study revealed that particularly females nursing offspring from the previous season are likely to groom their male partners after copulation. Thus our study population might simply have had a much higher number of lactating females than the study group of Kuester and Paul (1992). We found that copulations with ejaculation were more likely to be followed by grooming than non-ejaculatory mating, again an effect probably driven by lactating females: while males and non-lactating females were equally likely to groom after mating (with females grooming after non-ejaculatory mating and males after ejaculatory copulations), females nursing offspring from the previous season were likely to initiate grooming irrespective of the copulation type.

But why do lactating females in particular show these increased grooming probabilities? On the one hand side, as suggested earlier, increasing grooming may increase the likelihood of repeated copulation (e.g., (Matsumoto-Oda 1999)). This may be particularly relevant to lactating females, as the energetic demands associated with lactation potentially reduce female fecundity (Maeda et al. 1991; Mitsunaga et al. 1994; Kondo et al. 2003; Wallner et al. 2011) and through repeated copulations they might still be successful in conceiving new offspring. On the other hand females nursing offspring from the previous season may gain protection and support (Palombit et al. 1997; Palombit et al. 2001; Lemasson et al. 2008) from their male copulation partners, and thus benefit from establishing stable, long term social relations (usually established, maintained, and repaired by social grooming), or "friendships",

with them. Barbary macaque males show care for infants, both to later gain mating access to the mother, and to use infants as social tools for “agonistic buffering” in conflicts with other males (Deag and Crook 1971; Small 1990a; Paul et al. 1996; Ménard et al. 2001). Thus, good social relations with males may also be important to a female when trying to retrieve her offspring from a male handling it.

Friendship between males and females may be of paramount importance also to mating behaviour. Massen and colleagues (2012) did not find a direct exchange of grooming for mating in rhesus macaques, but friendship between male and female rhesus macaques predicted male mating success. Male and female Barbary macaques may potentially have already established social bonds with their female mating partners before the mating season, and non-ejaculatory copulations may function as social copulations. Analyses of social network data between males and females, using longer-term data than available here, could help to shed light on this issue.

A connection between grooming and mating behaviour, with females grooming males more at the onset and end of the menstrual cycle and males grooming females preferentially at mid-cycle, has been known since the early 1960s in rhesus macaques (Michael and Herbert 1963; Kaufmann 1965). Similarly, a recent study showed that females are more socially active prior and during the mating season, and males more during and after the mating season (Massen et al. 2012). In this study we find distinct sex-specific grooming behaviour that is connected to both copulation type and female lactation state. Grooming in the context of mating behaviour presumably serves some function with potential adaptive value; some clues to this may be obtained by considering the mechanisms underlying these behaviours. A proximate cause for the co-occurrence of social and reproductive behaviour may be that grooming is associated with oxytocin release (Amico et al. 2004; Crockford et al. 2013). Changes in peripheral oxytocin are known to be associated to consorting behaviour in baboons: (Moscovice and Ziegler 2012) and oxytocin is involved in social as well as in mating behaviours (Lee et al. 2009). Moreover, it is involved in sexual arousal, penile erections, and muscle contractions and hence improves fertilization chances (Arletti et al. 1985; Caldwell et al. 1986; Slob et al. 1986; Arletti et al. 1990; Arletti et al. 1992; Carter 1992; Rao 1995; Bancroft 2005; Lee et al. 2009). Thus, investigating post-copulatory social behaviour in connection with oxytocin (or related hormones in non-mammalian species) may provide insights into the function of post-

copulatory grooming. Future studies that include information on female and male hormonal states and differentiate between ejaculatory and non-ejaculatory grooming patterns of males, and between lactating and non-lactating females may provide deeper insight into the mechanisms and functions underlying social post-copulatory mating strategies.

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Ethical Standards

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. The nature of the study was purely observational: No invasive methodologies were applied at any point of the study. The Gibraltar Ornithological and Natural History Society (GONHS) approved data collection for the study. All procedures were in accordance with British, Austrian, and European Union law.

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Online Resources

Online Resource 1: The full GLMM model. Copulation type, sex, female lactation state, male and female relative rank as well as interactions of these parameters were entered as predictor variables for grooming probability.

Linear mixed-effects model fit by maximum likelihood				
AIC	BIC	logLik	deviance	df residuals
852	926.9	-410	820	782
	estimate	Std.Error	z value	P-value
Intercept	-3.408	0.767	-4.441	<0.001
copulation type	4.812	0.849	5.669	<0.001
sex	1.250	0.370	3.384	0.001
lactating	-1.777	1.081	-1.644	0.100
female relative rank	0.025	0.107	0.234	0.815
male relative rank	0.183	0.668	0.274	0.784
copulation type*sex	-2.986	0.631	-4.734	<0.001
copulation type*lactation	-0.793	1.307	-0.607	0.544
sex*lactation	1.138	0.596	1.910	0.056
female relative rank* male relative rank	-0.074	0.156	-0.477	0.633
copulation type* sex*lactation	0.666	0.777	0.857	0.392
copulation type*sex* female relative rank	-0.002	0.051	-0.030	0.976
copulation type*sex* male relative rank	0.134	0.420	0.319	0.750

4 | Social Learning and Teaching in Societies

Measuring teaching through hormones and time series analysis: Towards a comparative framework.

Ravignani A*, Sonnweber R* (in press) Measuring teaching through hormones and time series analysis: towards a comparative framework.

Behavioral and Brain Sciences

* equal contributions

Measuring teaching through hormones and time series analysis: Towards a comparative framework

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ABSTRACT

Arguments about the nature of teaching have depended principally on naturalistic observation and some experimental work. Additional measurement tools, and physiological variations and manipulations can provide insights on the intrinsic structure and state of the participants better than verbal descriptions alone: namely time-series analysis, and examination of the role of hormones and neuromodulators on the behaviors of teacher and pupil.

MAIN TEXT

We welcome Kline's emphasis on comparing behavioral measurements between learning episodes, and suggest including novel measures applicable to taught/learned behaviors across species and tasks.

Hormonal or neuromodulatory states are well known to affect learning, for example in bird-song acquisition (Ball et al., 2002). So far, little research was undertaken on the role of hormonal states of teachers and learners in teaching episodes, although such examinations offer promise for intraspecies and interspecies comparisons. The few animal studies linking endocrine parameters with social learning showed that oxytocin and arginine-vasopressin mediate the social transmission of food preferences and that oxytocin plays an important role in mate-choice copying (Dore et al., 2013). Until more direct evidence is available, predictions on the endocrinology of teaching can be established by linking hormonal measures to behaviors that are essential to teaching. For instance oxytocin and vasopressin mediate social approach and aversion (Porges, 2001). Arguably, increased approach motivation, respectively decreased social aversion is essential in teaching contexts. Other relevant behaviors, such as social motivation, affiliation, individual recognition, aggression, anxiety, and stress are associated with and

regulated by oxytocin, vasopressin, testosterone, estrogens and progesterone (McCall & Singer, 2012; Mehta & Josephs, 2012). These hormones also regulate and are influenced by trust, prosociality, empathy (empathic concern, perspective taking), reward sensitivity, and status seeking (Bos et al., 2012; Crockford et al., 2014; Heinrichs et al., 2009; Insel, 2010; Mehta & Josephs, 2012; van Anders et al., 2011). To what extent these behaviors play a role in teachers or pupils may depend on the teaching type. Thus, we propose that Kline’s teaching types can be mapped to hormonal variations in teachers and learners via social and cognitive building blocks (Figure 1). This approach parallels existing frameworks for the study of cooperation (Soares et al., 2010), and according to Kline, teaching is a cooperative behavior.

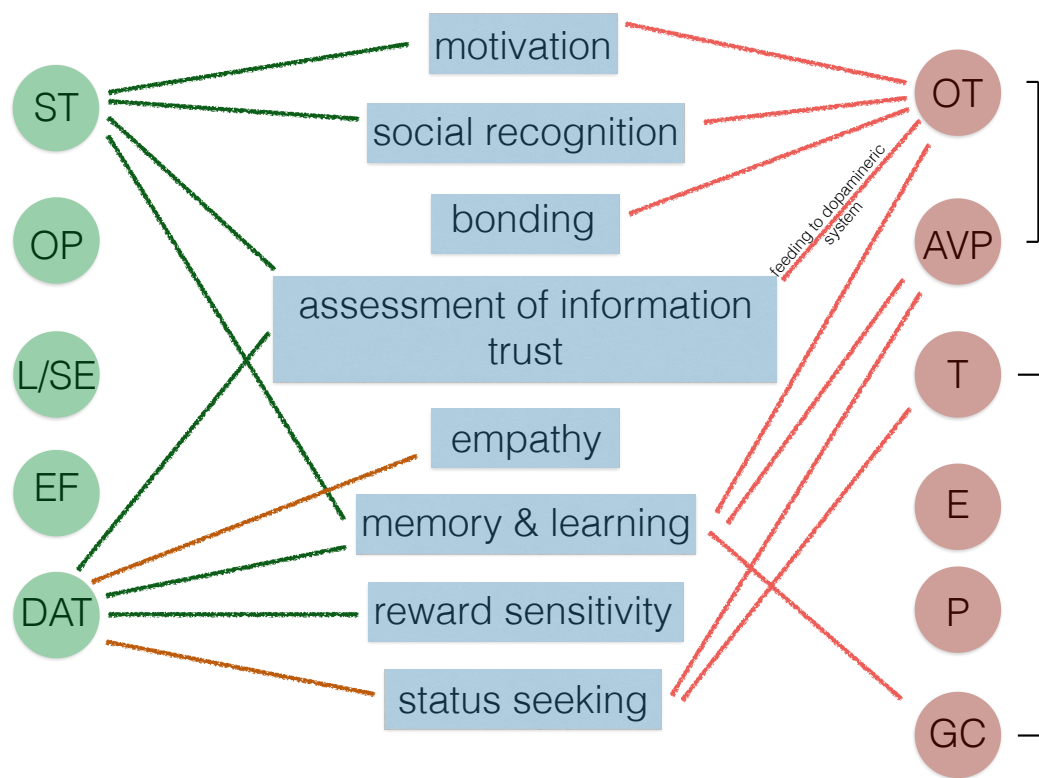


Figure 1: Exemplary mapping of teaching types to hormonal measures via behaviors. The “building blocks” of teaching (in the middle with blue background) are mediated by and fed-back to different hormones (right with red background), such as oxytocin (OT), vasopressin (AVP), testosterone (T), estrogens (E), progesterone (P) or glucocorticoides (GC) (actual although incomplete results on behavior-hormones interactions are indicated with red lines). Hormonal measures allow investigating motivational and emotional changes in teaching contexts and can be linked to cognitive processes and behavioral modifications associated with teaching. Kline distinguishes five teaching types based on the adaptive problem they solve: teaching by social tolerance (ST), opportunity provisioning (OP), stimulus or local enhancement (SLE), evaluative feedback (EF) and direct active teaching (DAT). A precise mapping between building blocks and different teaching types needs to be investigated: Predictions on possible connections

are indicated on the left (brown lines for teachers and green lines for pupils). Mapping teaching types to hormones and behaviors may help understand basic processes and mechanisms of teaching across and within species.

Kline proposes to conduct comparative research with emphasis on socio-environmental niches in which teaching and specific teaching types evolve. In cooperatively breeding New World monkeys, after the birth of an infant, fathers experience changes in vasopressin, oxytocin, and testosterone (Kozorovitskiy et al., 2006) and siblings show increases in oxytocin (Ragen & Bales, 2012), suggesting physiological adaptations to infants and juveniles (the individuals who are usually taught). Rearing conditions influence later oxytocin balance and social behavior (Fries et al., 2005; Winslow et al., 2003), and altruistic behaviors, sibling relationships, or decision making are genetically associated with different vasopressin-receptor types (Israel et al., 2008; Knafo et al., 2008). Parental investment and siblings' infant care predict changes in vasopressin and oxytocin in cooperatively breeding monkeys (Ragen & Bales, 2012). Hence developmental and epigenetic forces might contribute to the evolution of teaching behavior (Bjorklund, 2006; Soares et al., 2010). Future comparative data will elucidate the epigenetics of teaching.

While hormones elucidate internal states, Kline's focus is on external, observable behaviors. She claims that the only example of direct active teaching in non-human animals comes from anecdotes of chimpanzees learning to crack nuts (Boesch, 1991). Building on recent work on synchrony and motor mimicking in chimpanzee dyads (Fuhrmann et al., 2014), we propose additional tools to measure teaching and learning over time *across species* and *behaviors*.

A chimpanzee performing quasi-periodic movements to crack nuts can be tracked over time, for example via video coding (Fuhrmann et al., 2014) or movement sensors (Nagasaka et al., 2013; Ravignani et al., 2013). This produces, for each individual, evenly spaced samples (time series) of rhythmic, learnable behaviors. Behaviors can be movements, fundamental frequency of vocalizations or any other possible recordable semi-repetitive behavior within short time scales (few seconds). Kline stresses the importance of comparing behaviors in teaching and non-teaching contexts and argues that finding differences in rates of behaviors between baseline and teaching contexts suffices to conclusively demonstrate teaching. Time series of teachers and pupils can be plotted together and statistically related to test hypotheses on teaching types.

Autocorrelation (correlation of a series with itself at different time lags) can be employed to investigate practice and self-consistency in learning movement patterns. Increased learning can be shown via an increase in between-trial autocorrelation (i.e. increased predictability of the pupil's next step once the action is almost completely learnt).

Faithfulness of action copying and individual learning performance can be investigated using cross-correlations: the higher the correlation between teacher and pupil, the more accurate the learning. A cross-correlogram provides a measure in the delay of copying: a high cross-correlation (near zero lag) provides evidence for simultaneity of actions (high cross-correlation at short lag is predicted in stimulus/local enhancement). Alternative methods, originally developed to infer similarity between geometrical curves, can measure resemblance between taught/learnt behaviors, such as Fréchet distance (Alt & Godau, 1995), procrustes analysis (Gower, 1975) and dynamic time warping (Verhoef et al., 2014).

Granger-causality (Granger, 1969; Seth, 2010) enables to investigate directionality of information transmission in the teaching process; a teacher's time series Granger-causes a pupil's if past teacher's data significantly improve the prediction of future pupil's actions (when compared to forecasts based on past pupil's actions alone). Granger-causality can be used to show that teacher-pupil synchrony is unilaterally driven by one of the two (Fuhrmann et al., 2014). Alternatively, two time series Granger-causing one another constitute evidence for bilateral information transmission: not only the pupil's series depend on the teacher's series, but also the teacher's behavior will be triggered by a pupil's (imperfect) behavior (as needed in evaluative feedback). An alternative to measure the amount and directionality of information transmission is partial directed coherence (Baccalá & Sameshima, 2001; Ghazanfar et al., 2012).

The proposed quantitative tools can serve to analyze behaviors in teaching contexts. Hormonal measures allow for conclusions about motivational and emotional states or reward mechanisms. Controlled correlation studies measuring relevant hormones (i.e. via saliva, urine, or feces) or experimental administration studies can help shed light on basal processes involved in teaching and social learning. The tools we suggest here will hopefully contribute to a more empirical and quantitative approach to teaching, transcending verbal descriptions alone.

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5 | A Social Basis for Abstract Concepts?

Non-adjacent visual dependency learning in chimpanzees.

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Non-adjacent visual dependency learning in chimpanzees

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Abstract Humans have a strong proclivity for structuring and patterning stimuli: Whether in space or time, we tend to mentally order stimuli in our environment and organize them into units with specific types of relationships. A crucial prerequisite for such organization is the cognitive ability to discern and process regularities among multiple stimuli. To investigate the evolutionary roots of this cognitive capacity, we tested chimpanzees—which, along with bonobos, are our closest living relatives—for simple, variable distance dependency processing in visual patterns. We trained chimpanzees to identify pairs of shapes either linked by an arbitrary learned association (*arbitrary associative dependency*) or a shared feature (same shape, *feature-based dependency*), and to recognize strings where items related to either of these ways occupied the first (leftmost) and the last (rightmost) item of the stimulus. We then probed the degree to which subjects generalized this pattern to new colors, shapes, and numbers of interspersed items. We found that chimpanzees can learn and generalize both types of dependency rules, indicating that the ability to encode both feature-based and arbitrary associative regularities over variable distances in the visual domain is not a human prerogative. Our results strongly suggest that

these core components of human structural processing were already present in our last common ancestor with chimpanzees.

Keywords Feature based · Arbitrary associative · Operant task · Touch screen · Non-human primates

Introduction

Humans have a strong tendency to mentally arrange their perceptual worlds into structured elements and sequences and to organize their surroundings into patterns. This is particularly evident when looking at natural languages, music, or visual patterns humans produce (e.g., Fitch 2006; Westphal-Fitch et al. 2012). Statistical or rule-based strategies are applied to learn and detect such regular structures (Pena et al. 2002; Perruchet et al. 2004), and the ability to extract rules from perceptual stimuli is present early in human infants (Aslin et al. 1998; Kirkham et al. 2002; Marcus et al. 1999; Saffran et al. 1996).

Structural regularities are also present in many animal species' own communication systems, and a recent review by ten Cate and Okanoya summarizing the main findings from non-human animal patterning experiments concluded that several non-human species possess basic rule learning abilities (ten Cate and Okanoya 2012). However, such abilities remain unexplored in many species.

A crucial requirement for processing regularities (e.g., in speech streams) is the ability to perceive and represent relationships between elements separated in space and time (Gebhart et al. 2009; Newport and Aslin 2004; van Heugten and Shi 2010). A multitude of such non-adjacent dependency structures is found in natural languages, at both word and morphemic levels (van Heugten and Shi

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2010). A standard morphosyntactic example for non-adjacent regularities is “agreement”, for example, the matching of auxiliary verb (e.g., *is*) and main verb endings (e.g., *-ing*) in English (Santelmann and Jusczyk 1998). Humans can also track relationships between non-adjacent, perceptually similar elements in artificial languages (Newport and Aslin 2004).

Relationships, or dependencies, may be either *feature-based* or based on *arbitrary associations* (for examples see Fig. 1). Recognizing that two adjacent or non-adjacent elements belong to the same perceptual or logical category, based on one or more shared features, is necessary for feature-based dependency encoding (Newport and Aslin 2004). Dependent elements are not identical, but share traits that belong to the same class (e.g., same shapes or same colors, cf. Fig. 1a). Such representations are abstract

in that they allow generalization to unfamiliar, novel perceptual items. On the other hand, establishing associative relationships between a priori unrelated elements is crucial to detecting arbitrary associative regularities (Toro and Trobalon 2005). Some combination of specific elements must be learned, and a certain relationship between them represented (e.g., A always precedes B, Fig. 1a). Because this type of dependency is encoded on a less abstract level, less flexible computations are possible (i.e., no inferences about C and D can be made from the learned association between A and B). However, if the position of first items (A and C) and last items (B and D) of several learned associative pairs, as well as the relation between them, are represented on a more abstract level, computations recombining elements will be possible (i.e., A precedes D and C precedes B).

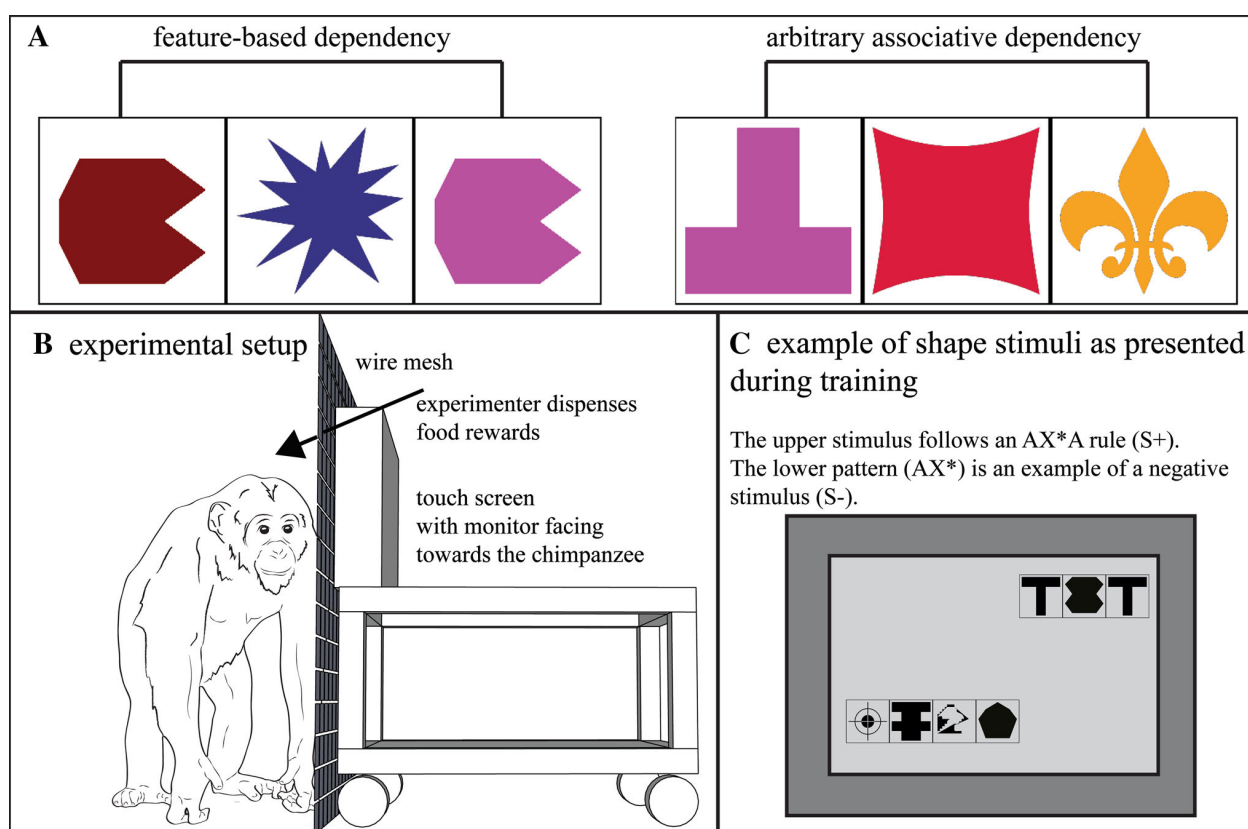


Fig. 1 **a** Examples of feature based and arbitrary associative dependencies in artificial visual patterns. In feature-based dependencies (*left*), two adjacent or non-adjacent elements share a common feature (here shape). Dependent elements are not identical (here they may differ in *color*), but belong to identical classes (any shape, but the same shapes for both dependent elements). Arbitrary associative regularities (*right*) have dependencies between a priori unrelated elements. **b** Touch screen setup. The setup was mounted on a table with wheels to allow for flexibility in the testing location. The setup consisted of a touch-sensitive monitor (facing toward the

experimental subject), an experimenter monitor (facing toward the experimenter), a Mini Mac, a keyboard, and an optical mouse. Chimpanzees could reach through a wire mesh with their fingers to touch stimuli on the screen. The experimenter dispensed pieces of high quality food rewards with a tong for correct choices in training trials. **c** Examples of training stimuli. Training stimuli consisted of a series of abstract black-and-white geometrical shapes (2–4, each with a square black frame) arrayed in a horizontal row. Two stimuli were presented simultaneously (a positive, S+ stimulus and a negative, S– stimulus)

In addition, matched elements can exhibit positional regularities. Not only do dependent items and their relation to each other have to be represented mentally in such a case, but information about their (absolute and/or relative) position in relation to other elements in a sequence must be encoded as well. For example, two items may be adjacent or only present at the edges, that is, items that are linked by a dependency occurring at the beginning and end of the string (Endress et al. 2010).

Previous studies demonstrate dependency sensitivity in various animal species in the acoustic domain: van Heijningen and colleagues (van Heijningen et al. 2009, 2013) demonstrated for zebra finches that simple adjacent dependency rules (same or different elements) can explain results from complex pattern processing experiments. Cotton-top tamarins (Newport et al. 2004) and rats (Murphy et al. 2008) can successfully learn abstract dependencies between elements at fixed distances, while chimpanzees can process dependencies between specific items at variable distances in the acoustic domain (Endress et al. 2010). In an auditory task similar to the one used here, squirrel monkeys proved capable of spontaneously detecting (without training) abstract, non-adjacent dependencies between elements in acoustic strings and generalizing to novel classes and to new stimulus lengths (Ravignani et al. 2013b).

Abstraction, rule formation, and rule application across different tasks have been argued to contribute to the high flexibility underlying human intelligence (Emery and Clayton 2004). Because chimpanzees (along with bonobos) are our closest living relatives, they are a key species for understanding the roots of human cognitive abilities such as the ability to detect particular types of dependencies. Many previous studies employed habituation–discrimination paradigms (Endress et al. 2010; Newport et al. 2004; Ravignani et al. 2013b), which provide insights into *spontaneous* detection of sensory dependencies. However, spontaneous capabilities do not necessarily indicate the cognitive limitations present in a particular species: Animals may notice changes in presented stimuli but fail to respond with an observable behavioral change, leading to “false negative” results. A clear demonstration of strong limitations typically requires considerable training, for example, using operant techniques (ten Cate and Okanoya 2012). The reward system applied in operant tasks keeps the animals motivated to respond to all perceived changes in presented stimuli. Furthermore, operant tasks allow for a more fine-grained battery of test stimuli than is possible with habituation/discrimination methods.

In this study, we tested chimpanzees’ ability to learn variable distance dependency rules in visual patterns in an operant task and then explored their ability to generalize such rules to previously unseen stimuli. Chimpanzees were trained to detect dependencies between elements at the

edges of visual stimuli of different lengths. These dependencies could either be feature based (henceforth: AA group) or based on arbitrarily associated item pairs (AB group). The purpose of testing feature-based dependencies (patterns following an AX^*A rule, where A’s are items sharing a particular feature, X indicates a nontarget object, and * a variable number of items) was to establish whether chimpanzees can represent relational categories between elements located at a distance and process the dependency relationship between them (Abe and Watanabe 2011; Ravignani et al. 2013b). The purpose of testing arbitrary associative dependencies (with patterns following an AX^*B rule, where As and Bs were previously trained associative pairs) was to ascertain whether chimpanzees can, once exposed to specific pairs of items (which are linked by an arbitrary learned association, rather than physical features of the stimulus), generalize this relation across variable numbers of intervening items, and to previously unseen combinations of elements (Rey et al. 2012). Furthermore, we wanted to understand to what extent chimpanzees encode positional relations between dependent elements in visual patterns (e.g., recognizing that dependent elements are always located at the edges of visual patterns).

In principle, the necessary mental representations underlying feature-based and arbitrary associative dependencies should differ in the degree of abstraction and consequently in the flexibility of generalizations they allow. We therefore hypothesized that mental representations of dependencies between elements that share a common feature, assigning them to the same category (feature-based), would allow flexible generalizations. Since chimpanzees are relatively proficient in categorization tasks (Spinozzi 1993, 1996; Tanaka 1995), while some monkeys have been shown to be sensitive to abstract dependencies (Ravignani et al. 2013b), we predicted that chimpanzees could learn a feature-based dependency rule and would be capable of generalizing this rule to novel stimuli.

Establishing arbitrary associative relationships between specific pairs of items, in contrast to feature-based dependencies, demands little abstraction. Previous studies with chimpanzees demonstrated that, at least in the auditory domain, regularities with target elements at the edges of strings are particularly easy to detect (Endress et al. 2010). This suggested that our study subjects would also be able to successfully encode positional relation between dependent items and their relation to each other in abstract visual stimuli. We thus predicted that chimpanzees would be capable of detecting arbitrary associative dependencies involving trained pairs of elements, independently of stimulus length and amount of distracting information.

Finally, more flexible computations with arbitrary associative dependencies would be possible if relations between classes of items (e.g., “beginning” and “ending”

items, assuming reading from left to right) were encoded at a more abstract level than necessary for simply representing specific single item pair associations. Thus, we also tested if our chimpanzee subjects could flexibly recombine beginning and ending elements across associative pairs. We hypothesized that if representations of this spatial dependency rule were encoded on an abstract level, chimpanzees should be able to perform more flexible computations and thus generalize arbitrary associative regularities across trained item pairs (e.g., when trained on AXB and CXD, they should accept AXD but reject DXA stimuli).

Methods

Animal welfare and ethics

The study was approved by the scientific board of the Living Links and Budongo Research Consortium (Royal Zoological Society Scotland). All experimental procedures were in accordance with British, Austrian, and European Union law. No invasive methodologies were applied at any point of the study: There was no food or water deprivation, and only positive reinforcement techniques were used for chimpanzee training. Individuals who participated in this study did so on a strictly voluntary basis, in return for food reward, and could leave the experiment at any time.

Study site and study subjects

Research was conducted at the *Budongo Trail* facility at Edinburgh Zoo, Scotland, UK. At the beginning of this study, this socially housed group of chimpanzees encompassed 19 individuals: 11 females and 8 males between 14 and 49 years of age. The chimpanzees were housed in three interconnected indoor enclosures (pods of $12 \times 12 \times 14$ m each) and an outdoor enclosure (1,832 m²), which was accessible to the chimpanzees during the day (Ravignani et al. 2013a). The design of the facility allowed the group to split into subgroups or join into one group, exhibiting the natural fission–fusion behavior of this species. Water was available ad libitum, and food was provided four to five times a day.

Fourteen of the 19 resident chimpanzees had previously been trained to use a touch screen (Herrelko 2011) and perform a simple two-alternative forced-choice (2AFC) task (choosing a red over a green circle of equal size). Eleven of these 14 touch screen-skilled individuals participated on a regular basis and received training for the experiments reported here (detailed description below).

Experimental setup and procedure

Chimpanzees gave responses using a touch-sensitive screen (15 in. Elo Touch Systems, Carroll Touch Technology), connected to an Apple Mini Mac computer (Fig. 1b). An additional computer monitor (for the experimenter), a keyboard, an optical mouse, and a set of loudspeakers providing acoustic feedback for correct and incorrect choices (one sound assigned to correct answers and another to incorrect answers), were also connected to this computer. The setup was mounted on a rolling table, allowing testing in all compartments of the chimpanzee testing area (for a detailed description see supplementary material Annex A). Custom-written Python code (www.python.org) was used to generate stimuli, control experiments and log the data.

The chimpanzees were trained and tested using a 2AFC task (Fig. 1c). Each training and testing session consisted of 12 trials, and within one research session, a maximum of four sessions per individual was possible (48 trials). In order to move to the next training stage, or proceed to testing, a chimpanzee had to make 33 first correct choices within a total of 48 trials (power analysis performed using a binomial distribution, $P < 0.001$). Positive reinforcement was used for training: Correct choices elicited an acoustic secondary reinforcement signal (a clicker sound familiar to all chimpanzees from previous husbandry training), and the experimenter dispensed a highly preferred food reward with tongs (depending on individual and day: grapes, blueberries, peanuts, date pieces, or raisins). After wrong answers in training trials, an unappealing acoustic signal (short irregular series of non-pulsatile sounds) was played, and a red penalty screen displayed for 3 s; failed training trials were repeated immediately until the individual chose the correct stimulus.

Because previous work in visual artificial grammar learning (AGL) experiments suggests that staged input training can promote learning performance (Conway et al. 2003), our study subjects were trained in stages of gradually increasing difficulty (for a detailed description of training stages see supplementary material Annex B). Six individuals were trained for *feature-based dependencies* (“AA group”), while five chimpanzees received training for *arbitrary associative dependencies* (“AB group”) in a series of training steps. Stimuli were randomly presented at four possible positions of the monitor (upper and lower right and left corners) to discourage side or location biases. By touching anywhere within either of these stimuli, the individual registered its choice and (in training trials only) received feedback.

During subsequent test sessions, six rewarded trials familiar from training (“repetition trials”) with contingent rewards were interspersed with six novels “test trials”

lacking any explicit differential feedback (Fig. 2). Rewarded repetition trials were presented during test sessions to prevent decreased motivation and consequent non-participation (since 50 % of all trials were still potentially rewarded). These trials also provided a measure of our subjects' attentiveness during any particular test session. Only when most of the previously trained trials were correctly answered ($P < 0.05$) were responses to test trials considered representative of the chimpanzee's potential performance (see Results). This criterion was specified before any analysis commenced and applied to all test trials. To investigate whether this method of session validation was justified, we tested whether performance in familiar repetition trials predicted performance in test trials, based on percentages of correct choices per session. Percentages of correct choices in familiar repetition trials were positively correlated with performance in test trials ($r = 0.208$, $df = 291$, $P < 0.001$).

Stimuli

Visual stimuli consisted of a series of square, framed individual elements arrayed in a horizontal row. Single elements incorporated many different abstract geometrical shapes, surrounded by a square black frame (outer dimensions 225×225 pixels). Black shapes were used as elements for training stimuli, while during testing, shapes were differently colored (testing shapes were never black, and all shapes could, but did not necessarily, differ in color). To construct positive (S+) and negative (S-) stimuli (Figs. 3, 4), between two and seven elements were linearly concatenated. In the following description of the visual patterns, we use capital letters A and B to denote target elements within strings. Recurrences of those (e.g., AA) indicate two elements with identical shapes (but different colors during testing). When two different elements, say A and B, become associated by training, we use a lower common index to refer to this arbitrary learned association (e.g., $A_1 B_1$ denotes two associated but different shapes). Xs stand for nontarget distractor elements, which are not members of the categories above. Unlike As and Bs,

recurrence of distractors (e.g., XX) stands for two elements of different shape. Finally, the exponent is used to indicate recurrences, e.g., $X^2 = XX$ and $AX^3A = AXXXXA$, while a star AX^*A indicates a variable number of X elements. Stimuli used in training varied only in shape (black shapes in frames of identical outer dimensions).

Feature-based dependency (AA) group

In the AA group, the positive stimuli followed an AX^*A pattern, where the dependencies between elements involved the abstract feature of shape: A elements could be any possible shape, as long as it was the same for both A elements (regardless of color). Hence, the shape of the first and last element of the positive stimulus was identical, defining a "same shape" relation independent of any particular shape (see Fig. 3). The pool of shapes from which elements were sampled encompassed 70 different shapes, which were used for stimulus creation for all training phases. By sampling from this relatively large pool of elements, we tried to encourage individuals to learn the abstract relationship, rather than to memorize specific shape configurations. A and X shapes for the AX^*A pattern were sampled from the same pool of shapes. Any shape could occur as either an A or X element in different stimuli. However, within a stimulus, if a shape was used as an A element, it was never used as an X element (and vice versa). Training stimuli were maximally four elements long (AXA , AX^2A as S+ and AX^2 , AX^3 as S-). The same pool of shapes was used during testing, where all 70 shapes were presented, but now in one of 21 different non-black colors. Here, dependent elements still shared the same feature "shape", but could differ in color. Thirty additional shapes in 15 different colors (not black) were introduced in Test 3 (for a description of test stimuli and test types see Fig. 3).

Arbitrary associative dependency (AB) group

In the AB group, five chimpanzees had to learn to associate five specific pairs of different shapes with each other (A_1B_1 , A_2B_2 , A_3B_3 , A_4B_4 , A_5B_5). Unlike AA stimuli, these

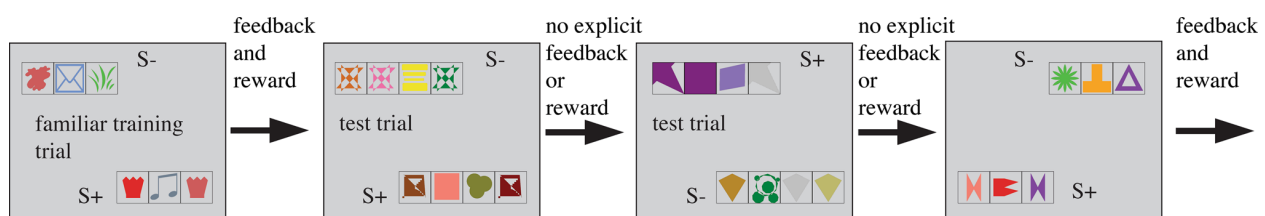


Fig. 2 Example sequence of trials as presented during test sessions. A familiar repetition trial (showing one S+ and one S- stimulus) was presented. A sound signal provided feedback after a choice, and a penalty screen was shown after wrong choices. After correct choices a food reward was provided. Then, a test trial with one S+ and one S-

stimulus was presented. Choices in test trials did not trigger feedback and were not rewarded. Then, another test trial (never more than two in a row) or a familiar repetition trial was shown randomly. A total of six test trials were interspersed with familiar repetition trials

Feature-Based Dependencies		
	S+	S-
training:		
testing:		
1. color:		
2. extension:		
3. novel shapes:		
4. duplication:		
5. dependency position:		
6. center near edges foils:		
7. category transfer:		

Fig. 3 Training and test stimuli for the AA group (feature based). Training stimuli always consisted of a series of black shapes, where elements in S+ were arrayed following an AX^nA pattern ($n = 1$ or 2) and S- strings followed an AX^{n+1} ($n = 1$ or 2) rule. This was maintained for Test 1 (*color test*), but the shapes composing the strings were colored. The dependency distance was varied by increasing the number of Xs in Test 2 (extension test) (S+: AX^nA and S-: AX^{n+1} , where $n = 3, 4$, or 5). For Test 3 (novel shapes test), stimulus length was reduced (S+: AX^nA and S-: AX^{n+1} , where $n = 1$ or 2), but entirely unfamiliar shapes and colors were used for stimulus design. Test 4 (duplication foils) tested AX^nA (S+) against

$AAX^{n-1}A$, where $n = 2$ or 4 . To test absolute and relative dependency position (Test 5), chimpanzees were presented with S+ following AX^nA and S- following $AX^{n-1}AX^{n-1}$, or $X^{n-1}AX^{n-1}A$, where $n = 2$ or 4 . Foils with additional recurrences of dependent elements in the center or near the edges of visual strings were presented in Test 6 (center foils: S+: AX^nA , where $n = 3$ or 5 and S-: AX^nAX^nA , where $n = 1$ or 2 ; near edges foils: S+: AX^nA , where $n = 4$ or 5 and S-: AX^mAX^nA or AX^nAX^mA , where $n = 3$ and $m = 1$). Test 7 followed the same patterns as Test 1, but colors (not shapes) had to be matched

pairs of shapes had neither any obvious a priori connections nor non-random shared features with each other (see Fig. 4). Instead, we trained the chimpanzees on specific associations between arbitrary pairs (denoted here with the same numeric index), involving arbitrary associative dependencies. Elements used to define A and B dependency could *not* occur as distractor X shapes (and vice versa). Hence, clear categories for distractor shapes (a pool of 60 different shapes and 30 additional shapes from Test 3 onwards) and associative pairs of target shapes (10 different shapes) were created. The same pool of stimuli was used for all subjects. Again, no color was used in training stimuli—all shapes were black, and training stimuli did not exceed a length of four elements (AXB , AX^2B as S+ and X^3 , X^4 as S-). Specific A elements were always displayed with corresponding B elements (A_1 with B_1 , A_2 with B_2 , etc.). No scrambles, such as A_1 with B_2 , occurred during training. Again, during testing the dependent and the distractor elements were colored (21 colors for the first shape pool and 15 colors for shapes in the second shape pool, all

non-black; colors were assigned randomly to individual shapes), and colors of the two dependent elements could differ from each other (for further details see Fig. 4).

Test types

Both groups (AA and AB group) were tested with a series of “generalization” tests (see Figs. 3, 4 for visual representations and stimulus descriptions: Test 1–3 for both groups, Test 7 for the AA group, and Test 9 and 10 for the AB group). The aim was to present our study subjects with stimuli containing the dependencies from training, but also possessing some novel features (such as color, distance between dependent elements, etc.) over which the subjects had to generalize the learned rule. Both positive and negative stimuli were coupled in a way that depended on the generalization type (i.e., when stimulus length was increased to test for generalization over dependency distance, the number of elements in the stimuli was increased by the same number in positive and negative stimuli).

Arbitrary Associative Dependencies		
5 trained associative pairs          		
	S+	S-
training:	   	   
testing:	  	  
1. color:	     	     
2. extension:	     	     
3. novel shapes:	  	  
4. duplication:	   	   
5. dependency position:	   	   
6. center/ near edges:	    	    
8. edge foil:	  	  
9. inversion:	   	   
10. crossing:	   	  
	A1 B5	

Fig. 4 Training and test stimuli for the AB group (arbitrary association). Training stimuli consisted of a series of black shapes, where A_i and B_i were associated by learning and separated by one or two X elements [S+ followed an AX^nB pattern ($n = 1$ or 2) and S— strings an X^{n+2} ($n = 1$ or 2) rule]. The same configurations were used in Test 1 (color test), but the individual shapes were colored. To test for increased dependency distances, more Xs were introduced in between associated AB pairs (S+: AX^nB and S—: X^{n+2} , where $n = 3, 4$, or 5) in Test 2 (extension test). For Test 3 (novel shapes test), S+ followed AX^nB and S— X^{n+2} , where $n = 1$ or 2 and stimuli consisted of novel shapes and colors. In Test 4, AX^nB (S+) and four variants of S— ($AAX^{n-1}B$, $AX^{n-1}BB$, $ABX^{n-1}B$ or $AX^{n-1}AB$, where $n = 2$ or 4) were used. Absolute and relative dependency position were tested

with S+ following AX^nB and S— following either $AX^{n-1}BX^{n-1}$ or $X^{n-1}AX^{n-1}B$, where $n = 2$ or 4 . Foils with recurrences of dependent elements in the center or near the edges of the visual patterns were presented in Test 6 (center foils: S+: AX^nB , where $n = 3$ or 5 and S—: AX^nBX^nB or AX^nAX^nB , where $n = 1$ or 2 ; near edges foils: S+: AX^nB , where $n = 4$ or 5 and S—: AX^mAX^nB , AX^nBX^mB , AX^nAX^mB or AX^mBX^nB where $n = 3$ and $m = 1$). Test 8 (Test 7 only for the AA group) presented S+ (AX^nB , where $n = 1$ or 3) with foils missing the first or the last dependency element ($X^{n+1}B$, AX^{n+1} , where $n = 1$ or 3). In the inversion test (Test 9), positions of As and Bs were swapped (S+: AX^nB and S—: BX^nA , where $n = 1$ or 2). Finally, in Test 10, As and Bs of different associative pairs were scrambled (S+ $A_iX^nB_j$ and S— $A_iX^nA_i$ or $B_jX^nB_j$, where $n = 1, 2$ or 3)

In another set of tests (“foil tests, see Fig. 4 for visual representations and stimulus descriptions: Test 4, 5, and 6 for both groups as well as Test 8 for the AB group) a stimulus containing the dependency was presented with a foil pattern altering or lacking the dependency in a specific way. These tests allowed us to test for specific strategies individuals used to solve the task and to draw conclusions concerning what rule (if any) they had learned.

In Test 1, we presented subjects with colored stimuli (familiar rewarded repetition trials showed black stimuli). As in either group’s last training step, visual patterns consisted of three or four elements, but unlike in the training, test stimuli were colored. Colors were assigned randomly to individual elements such that all shapes could

have the same or different colors. This first test probed chimpanzees’ ability to ignore irrelevant, distracting color information. After Test 1, colored stimuli (instead of black stimuli) were used for subsequent familiar repetition trials so that chimpanzees could not easily distinguish between novel, unrewarded, and not fed-back test trials (colored elements) and rewarded, fed-back repetition trials. In Test 2, we increased the length of the visual patterns by introducing more distractor elements. Strings now contained five, six, or seven elements (including the dependent elements). This probed chimpanzees’ ability to generalize across variable dependency distances. In Test 3, visual patterns were constructed with novel, unfamiliar shapes (30 different shapes in 15 different colors) for the AA group.

These novel unfamiliar shapes were also used for distractor elements in the AB group patterns, while elements of the associative pairs remained the same. Hence, this test is particularly relevant for the AA group. While the AB group had to generalize over different distractor shapes, individuals of the AA group had to additionally generalize to dependency elements with novel shapes, thus broadening their “same” relation to include previously unseen shapes.

After these three generalization tests, we confronted the study subjects with a set of three different foil tests. None of the foils presented during these tests violated the dependency rule, but altered it in some way. S– stimuli in Test 4 showed additional recurrences of a dependency element either at the beginning or at the end of the string (thus S– exhibited an AAX*A, AX*AA, or AAX*B and AX*BB pattern, respectively). These additional recurrences were consistently located at the edges of the stimuli. In Test 5, we tested for the processing of the position of the target items: We presented stimuli containing the relative, but not the absolute positional relation between dependent elements. Foil strings following X*AX*A, AX*AX* or X*AX*B and AX*BX* patterns were presented with S+ stimuli displaying the usual dependency elements at the edges. Finally, in Test 6, strings with additional recurrence of a dependent element near the edges (AXⁿAX^mA, AX^mAXⁿA, and AXⁿAX^mB, AX^mBXⁿB, respectively) or in the center of the patterns (AXⁿAXⁿA, AXⁿAXⁿA, and AXⁿAXⁿB, AXⁿBXⁿB, respectively) were displayed. Thus, Test 4 and Test 6 examined whether chimpanzees differentiated patterns containing the (binary) trained dependency relation only from foils with additional recurrence of the dependent elements at different positions: at the edges, near the edges, and at the center of a string. Earlier experiments demonstrated that edges of acoustic strings can function as anchor points when processing positional regularities in acoustic sequences (Endress et al. 2010) suggesting that chimpanzees may be more likely to reject foils with recurrences at the edges of visual patterns.

The final test for the AA group (Test 7) examined whether chimpanzees would spontaneously over-generalize the dependency rule from shapes to colors as category classes. While all training and testing steps showed shape class-dependent elements, and color represented an irrelevant variation within this category, Test 7 reversed this relationship: Individuals had to spontaneously match color and ignore variation in shape. This was a very ambitious test, as success would require a particularly high level of flexible abstraction of “same feature”, going beyond the previous test stimuli. Furthermore, it demanded an inversion between the formerly irrelevant distractor feature and the shape feature previously relevant for categorization.

The AB group was presented with three further tests. Test 8 was another foil test. Either the A at the beginning or

the B at the end was missing in foil stimuli (S–). This test was designed to allow inferences concerning the amount of attention individuals paid to the matched pair when at the edges of the stimuli. The two final tests were particularly relevant for language-relevant interpretations. In the probe stimuli in Test 9, the positions of As and Bs were inverted (assuming a left to right parsing direction: A’s now at the end, and B’s at the beginning of strings). Discriminating these patterns from strings in the trained configuration (normal: A’s at the beginning and B’s at the end) would imply that individuals had constructed a positional, sequential relationship between the two categories, namely A’s must occur to the left of any B. Finally, in Test 10, the chimpanzees’ ability to process novel combinations of dependent item pairs (that is A_iX*B_j, where $i \neq j$) was probed (cf. Rey et al. 2012). Corresponding S– stimuli followed an A_iX*A_i or B_iX*B_i pattern (with shapes in different colors, see Fig. 3). Accepting shuffled A–B combinations would imply that chimpanzees had formed categories of A elements (“starting” or “left”) and B elements (“ending” or “right”) and could flexibly combine members of these categories to accept novel AB configurations.

Statistical analysis

Choices were analyzed for each individual, considering each test separately. One-tailed binomial tests were computed using custom Python code. Furthermore, we analyzed success on the previously trained repetition trials to check for distraction or an overall lack of attentiveness to the testing situation in these test sessions.

Results

Because the chimpanzees participated voluntarily, and the tasks became more difficult with time, our sample sizes declined progressively by attrition of participation during testing. Crucially, however, because the current study is focused on species capabilities, success by even a single individual suffices to demonstrate that some members of the species in question can perform the task. Two of the six chimpanzees trained in the feature-based dependency group successfully finished all training stages and continued with testing. Four chimpanzees of the arbitrary associative dependency group passed criterion in all training stages and were tested. Test results for all individuals are shown in Table 1. Performance in familiar repetition trials (that were differentially fed back and rewarded, and shown in between test trials) was used as a proxy for individuals’ attentiveness during test sessions: across a total of 34 test sessions (including all individuals and tests), repetition

Table 1 Binomial test results for individual chimpanzees and tests

	1. Color	2. Extension	3. Novel shapes	4. Duplication	5. Position	6. CNE	7. CT	8. Edges	9. Inversion	10. Crossing
<i>Feature-based dependencies group</i>										
FK	48/60 <0.001	22/30 0.01	24/30 0.00	32/40 <0.001	27/40 0.02	36/60 0.08	36/60 0.08			
KL	50/60 < 0.001	21/30 0.02	20/30 0.05	25/40 0.08	26/40 0.04	33/60 0.26	36/60 0.08			
<i>Arbitrary association dependencies group</i>										
CI	44/71 0.03	20/30 0.049	20/30 0.049	23/40 0.21	27/40 0.02	24/47 0.50				
EV	40/60 0.01	16/30 0.43	19/30 0.10	18/36 0.57						
PA	37/60 0.05									
PE	37/60 0.05	21/30 0.02	19/30 0.10	16/40 0.92	26/40 0.04	31/60 0.45	29/40 <0.001	18/30 0.18	37/60 0.05	

Numbers of correct or non-foil choices out of total number of trials above, with *P* values of binomial tests below. Significant test results are highlighted with italic in the respective cells. Bold cells indicate that the individual failed the familiar repetition trials presented during the test

trials were mastered successfully in 30 sessions and failed in four instances. Below, if not indicated otherwise, familiar repetition trials were passed.

Generally (a detailed presentation of the results is given below), all individuals tested (including both feature-based and arbitrary associative dependency groups) successfully generalized to colored stimuli (Test 1) after being trained with black shape stimuli only. All but one chimpanzee generalized the dependency rule over variable distances (Test 2), and three out of five individuals generalized to novel shape stimuli (Test 3). Both individuals trained for feature-based dependencies rejected stimuli lacking the dependency relation between the first and the last element. Unlike chimpanzees of the feature-based dependency group, individuals of the arbitrary dependency group did not have to generalize to novel-dependent elements, but had to ignore novel distractor elements. Only one chimpanzee of the arbitrary associative dependency group differentiated successfully between stimuli containing and lacking the dependency.

Further tests (Test 4–6) probed stimuli altering the dependencies in a specific way. Individuals across groups accepted stimuli with dependent elements at the edges of the visual patterns, while rejecting shifted dependency relations (Test 5). Most individuals accepted probes containing additional recurrences of dependent elements (Test 4 and 6).

Feature-based dependency

Both individuals (FK and KL) in the feature-based dependency group successfully passed all generalization

tests: they (i) generalized from black training stimuli to colored test stimuli, (ii) successfully completed the extension test (increasing stimulus length), and (iii) generalized the dependency rule to relationships between novel shapes (Tests 1, 2 and 3, see Table 1).

When tested with foils altering the AX*A rule in some way, both individuals rejected foils shifting the dependency position (Test 5), but accepted foils containing recurrences of dependent “A” elements in the center or near the edges of a visual pattern (Test 6). Individuals differed in how they treated recurrences of dependent elements at the edges of strings (Test 4).

Test 4 (Duplication Test) featured foils following an AAX*A or AX*AA pattern. While one individual (FK) rejected foil stimuli containing an additional recurrence of dependent elements at the edges of strings (32 first correct choices out of 40 test trials, $P = 0.02$), the other individual (KL) did not discriminate between stimuli with and without element duplication (25 correct out of 40, $P = 0.08$). Both individuals were above chance with familiar repetition trials presented during the duplication test (FK: 32 out of 42, $P < 0.001$; KL: 30 out of 42, $P = 0.004$), indicating good attentiveness during these sessions.

When tested for dependency position (Test 5), both individuals chose strings with dependent elements at the edges significantly more often than patterns with shifted dependency positions (FK: 27 out of 40, $P = 0.02$; KL: 26 out of 40, $P = 0.04$).

Finally, neither of the chimpanzees rejected foil strings in the last two tests. When tested with foil patterns containing recurrences of dependent elements in the center or near the edges of the string, both individuals treated foils

and non-foils indiscriminately (FK: 36 out of 60, $P = 0.08$, KL: 33 out of 60, $P = 0.26$). Both were presented with 28 foils containing the recurrence in the center of the patterns (AX*AX*A) and 32 foils with recurrence of the first element near the edges of the stimulus (AXAX²A or AX²-AXA). FK chose 18 ($P = 0.09$) and KL chose 16 ($P = 0.29$) non-foil strings out of a total of 28 trials presenting recurrences of dependent element in the center of the visual pattern. For foils with additional recurrences of dependent element near the edges, FK picked non-foil stimuli 18 times ($P = 0.3$), and KL did so 17 times ($P = 0.43$) out of 32 test trials. In both cases, the animals had statistically significant results for the familiar repetition trials shown in the same session (FK: 57/72, $P < 0.01$; KL: 59/66, $P < 0.01$).

Finally, neither of the two chimpanzees spontaneously transferred to a novel feature (color instead of shape) (FK: 36/60, $P = 0.08$; KL: 36/60, $P = 0.08$), but, once again, both were successful in the familiar repetition trials (FK: 53/60, $P < 0.01$; KL: 60/66, $P < 0.01$).

Associative dependencies

Individuals in the associative dependencies group differed in their performance in the generalization tests: while all four subjects generalized to colored stimuli, and two out of three tested individuals generalized the AX*B rule over varying dependency distances, only one out of three tested chimpanzees rejected violations when novel distractor shapes were introduced (however, one of the two individuals who failed to generalize had below chance performance in familiar repetition trials).

Four chimpanzees successfully trained for arbitrary associative dependencies proceeded to Test 1 and generalized to colored stimuli (Table 1). Subject PA did not continue with further testing, thus three chimpanzees participated in the following probes: two generalization tests (“extension” and “novel shapes” test) and the first foil test (“duplication” test).

For the generalization tests, we found that individuals CI (20/30, $P < 0.05$) and PE (21/30, $P = 0.02$) applied the dependency rule to a varying dependency distance (Test 2). Although CI successfully generalized over dependency distance, she failed in familiar repetition trials (17/28, $P = 0.173$). Individual EV did not differentiate between patterns that did and did not contain the dependent items when stimulus length was increased (16/30 test trials, $P = 0.43$; training trials: 26/36, $P = 0.01$). When novel distractor shapes (Test 3) were introduced between dependent items, only CI (20/30, $P < 0.05$) preferentially chose patterns containing the trained associative pairs. Neither EV (19/30, $P = 0.10$) nor PE (19/30, $P = 0.10$; repetition trials 22/30, $P = 0.01$) rejected strings lacking

the dependency when patterns included novel distractor shape elements. However, EV’s unsuccessful choices in familiar repetition trials suggested a general lack of attentiveness (17/29, $P = 0.23$).

In the course of the foil tests, sample size decreased successively. None of the three chimpanzees rejected foils with recurrences of dependent elements at the edges of strings (Test 4). Two subjects tested with dependent element recurrences in the center or near the edges of visual patterns (Test 6) correctly differentiated between foils and non-foils. All individuals tested with shifted dependency positions (Test 5, two individuals tested) correctly rejected foil stimuli. One individual was presented with stimuli missing elements at the edges of strings (Test 8), inverted (B before A, Test 9), and scrambled (AiX*Bj, Test 10) dependency stimuli. She rejected foils in all tests except in Test 9 (where she also failed familiar repetition trials).

In Test 4, none of the three individuals rejected duplication foils (CI: 23/40, $P = 0.21$; EV: 18/36, $P = 0.57$; PE: 16/40, $P = 0.92$). CI (32/42, $P < 0.01$) and PE (31/42, $P < 0.01$) succeeded at familiar repetition trials in that test.

Two individuals were tested further (CI and PE). Both chimpanzees were significantly more likely to choose strings with dependent elements at the edges over foils with shifted dependency positions (Test 5) (CI: 27/40, $P = 0.02$; PE: 26/40, $P = 0.04$).

In Test 6, foils containing recurrences of either As or Bs in the center or near the edges of the visual patterns were accepted by both subjects (but CI did not complete all trials of the test: 24/47, $P = 0.5$; PE: 31/60, $P = 0.45$). CI chose the non-foil stimulus 13 out of 19 times when presented with recurrences in the center ($P = 0.08$), but only 11 out of 28 times when presented with recurrences near the edges of the patterns ($P = 0.91$). PE had similar results for both center and near-edge foil patterns (center: 13/25, $P = 0.5$; near edges: 18/35, $P = 0.5$). Choices in familiar repetition trials indicated good attentiveness during the test for both individuals (CI: 31/48, $P = 0.03$; PE: 48/60, $P < 0.01$).

Only one female (PE) underwent and completed the last three tests. Strings missing either an A or a B at the edges of patterns (Test 8) were rejected (29/40, $P < 0.001$). However, a closer examination showed that PE rejected foil stimuli with the first element missing (18/21, $P < 0.01$) but treated foils lacking the last dependency element as acceptable (11/19, $P = 0.32$), suggesting an “initial” or left-edge bias. When A’s were placed at the end of the stimulus and B’s at the beginning (Test 9), this subject chose randomly between foil and non-foil patterns (18/30, $P = 0.18$), but also failed in the familiar repetition trials (19/30, $P = 0.1$) suggesting distraction or a lack of attentiveness during this test. In the final test (Test 10) where the associative pairs were scrambled (A_i was presented with B_j at the edges of the stimuli), PE differentiated between foils

and scrambled associative pairs (37/60, $P < 0.05$), potentially indicating some generalization over the arbitrary associative item categories.

Discussion

Overall, our results demonstrate success and considerable flexibility in extracting and generalizing dependency regularities in artificial, abstract, visual patterns by chimpanzees. Our study subjects successfully formed identity relations between elements based on the common shared feature “shape”, and also based on learned associative pairings of specific items. Generalization tests demonstrated that chimpanzees matched elements independently of additional distracting information (color) across varying distances and to novel items or item combinations. Similarly monkeys are able to ignore distracting information (such as color, shape, or surface area) in number matching experiments (Cantlon and Brannon 2007; Jordan et al. 2008), and can even match number information across sensory modalities (Jordan et al. 2008).

When computing *feature-based dependencies*, two different items have to be identified as sharing some feature. Spatial or temporal relationships between linked individual elements could then be further processed and computed (Marcus et al. 1999). Our chimpanzees proved capable of generalizing to novel shapes: both individuals of the AA group applied this dependency rule to novel arbitrary shapes, and did so regardless of dependency distance. Stimuli could not be discriminated on the basis of color information or length alone. Moreover, as any arbitrary shape could become a dependency element, individuals could not decide on the correctness of a pattern by looking merely at either the first or the last element. That is, individuals could not have differentiated between AX*A and AX* strings without matching the dependent elements. This finding supports and expands previous results in squirrel monkeys, who matched same class acoustic elements located at the beginnings and ends of strings (Ravignani et al. 2013b). While the elements for the squirrel monkeys were drawn from two perceptually distinct categories (high- or low-pitched sounds), chimpanzees in our study were able to process a more abstract and multi-dimensional relational dependency (same or different shape). Crucially, both AA-subjects generalized to stimuli containing entirely unfamiliar elements (novel shapes and novel colors). This stands in contrast to results in various bird species that have shown comparatively limited generalization capabilities (van Heijningen et al. 2009, 2013; Stobbe et al. 2012; ten Cate and Okanoya 2012). Our results show that chimpanzees are capable of representing a

same feature dependency rule and also to perform some location-based computations with them.

Both individuals of the AA group were tested for their ability to spontaneously transfer the dependency regularity to a novel feature (Test 7), while training stimuli contained dependencies between shapes, and this test probed whether chimpanzees would spontaneously extend the “same edges” rule to dependencies between items with the same color but different shapes. While neither generalized to this novel category, the results can presumably be simply attributed to training circumstances, because both individuals learned to ignore color as distracting information in the previous six test stages. In the future, further tests presenting entirely novel categories (e.g., based on size, orientation, etc.) could shed more light on chimpanzees’ transfer capabilities and consequently on the level of encoding.

Recognizing the presence of specific items is not sufficient to process arbitrary associative dependencies. Instead, relations between two elements have to be established by repeatedly experiencing their co-occurrence and thereby learning their association (i.e., A always appears with B). In our experiment, because elements defining arbitrary associative dependencies did not share any non-arbitrary feature, generalization to novel, unfamiliar items could not be tested in the AB group. However, when multiple pairs with the same item relations were learned, individual elements of associative pairs could be rearranged. The only individual who successfully completed all tests (PE) did accept novel combinations of prefix (any A) and suffix (any B) items (Test 10), suggesting that this subject formed a category-wide precedence rule. Arguably, the individual could have based her choices on the presence or the absence of the first or the last element only, which would have allowed for significant results in the “crossing” test (Test 10) without noticing the recombination of trained item pairs. Looking at side biases in the “position” and the “edges” test renders this unlikely however; PE did show a left-edge bias (first element missing: 18/21, $P < 0.01$; last element missing: 11/19, $P = 0.32$) in the “edges test” (Test 8; lacking one dependent element either at the beginning or at the end of the visual pattern), but a right-edge bias (first element shifted inwards: 11/20, $P = 0.42$; last element shifted inwards: 15/20, $P = 0.02$) in the “position test” (Test 5; one of the dependent elements shifted inwards). Thus, the individual seems to be sensitive to both stimulus edges. But positive results in the crossing test (Test 10) have to be contrasted with results in the inversion test (BXA, Test 9) to show category-wide generalization. Due to a lack of task attentiveness during the inversion task (based on failed familiar trials), we do not attempt to draw conclusive inferences from this test.

All further tests presented foils altering, but not violating, the dependency rule of the trained visual patterns. One male (FK) of the abstract dependency group rejected patterns where the first or the last dependency element was duplicated (duplication test, AAX*A, AX*AA). Three other individuals (one from the AA group and two of the AB group) did not differentiate between foils and S+ strings. This result strongly suggests that FK (AA group) not only matched the first and the last elements of a string, but also paid attention to the second and next to last elements. He seemed to be unique in that respect, as the test results of the other three individuals suggest that they ignored internal elements. FK's differentiation is particularly noteworthy, as he developed it spontaneously: no previous training step or test required attention to other elements besides the first and the last. This was different in Test 5, where the relative position of the dependency was tested. The dependent elements were contained in the strings, but their positions were shifted. The foil strings followed an XAX*A or AX*AX and an XAX*B or AX*BX pattern, respectively. As in the training trials, the stimulus feature that was being tested was located at the edges of the stimulus, and all four individuals rejected these foils. Looking at performance for center or near-edge foils (Test 6), we found further support for a bias to focus on stimulus edges. None of the four chimpanzees rejected foils containing a center or near-edge additional recurrence of a dependency element.

In sum, our results show that one crucial requirement for processing regularities, namely the ability to understand and represent relationships between elements separated in space and time (Gebhart et al. 2009; Newport and Aslin 2004; van Heugten and Shi 2010), is also present in one of humans' closest living relative, the chimpanzee. The ability to form abstractions and rules, and flexibly apply these rules to novel stimuli, is essential for such regularity computations.

Given that humans are not the only species capable of such computations, we may ask what selective value they possess in the absence of language or music. Similar instances of flexible dependency processing have been demonstrated for computing and representing social information, or when planning or observing motor actions (Bergman et al. 2003; Emery and Clayton 2004; Maclean et al. 2008; Wittig et al. 2014; Wolpert et al. 2001, 2003), and analogies between the computational processes underlying motor actions, action observation, and social cognition have been suggested (Wolpert et al. 2001, 2003). Understanding relationships between phenomena that are separated in space and time is a fundamental cognitive ability that is valuable when processing social relationships between group members or understanding connections between distant elements in an action chain (e.g., during tool use; McGrew 2004; Sanz et al. 2004).

Alternatively, recent results using relatively arbitrary auditory and visual stimuli might suggest that encoding regularities allowing an organism to process relevant structures might take place at an abstract level that applies across multiple cognitive domains. Such multi-domain capabilities may have been employed by the chimpanzees in our study when learning feature based and arbitrary associative dependency regularities in visual patterns. We hope that future research testing and connecting regularity processing abilities in the general sensory, social, and technological domains will help shed further light on this topic.

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Conflict of interest There are no conflicts of interest to report.

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Supplementary Material

Annex A: Experimental Area in Budongo Trail

Budongo Trail allows for strictly non-invasive research. Individuals were participating on an entirely voluntary basis, and could leave the experiments at any time. The experiments described below were conducted in an off-show area of the chimpanzee enclosure, located in between two indoor pods. Individuals could access the experimental area from two sides on two levels (tunnel system above the experimental area and entrance from the pods). The experimental area was divided into 5 chimpanzee compartments adjacent to each other and a “researcher aisle”, which was separated from the chimpanzee area by a wire mesh (Figure A1). Chimpanzees could participate to trainings and experiments in any of the 5 compartments. All compartments were open and accessible at all times.

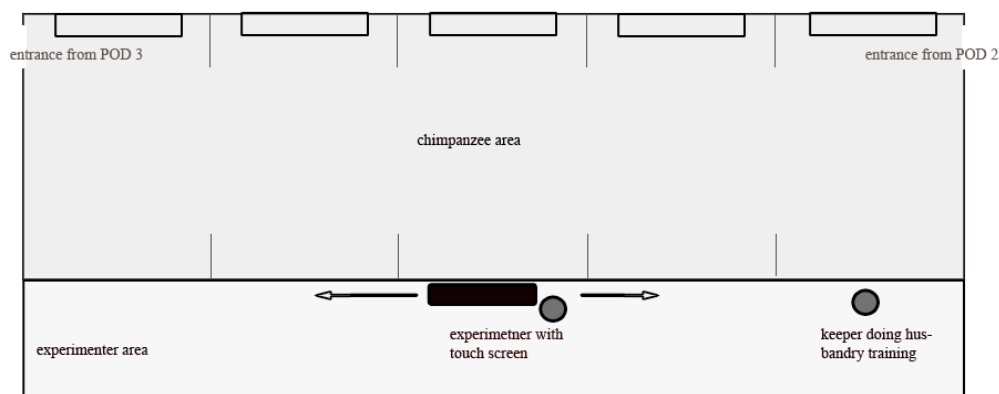


Fig A1: The testing area. The chimpanzees were tested in an off-show area located in the middle of two indoor pods (2 and 3). Individuals could access this area on the lower level from two sides (Pod 2 and Pod 3) as well as from two sides on an upper level (tunnel system linking Pod 1 and Pod 2). The

chimpanzee testing area was divided in five individual compartments, which were never shut during the experiments (individuals were not separated from the group). A wire mesh divided the chimpanzee area from the experimenter area. The touch screen setup (touch screen, computer, loud speakers) was mounted on a movable table. Thus the experimenter could position the setup flexibly in front of individual chimpanzees in any of the five chimpanzee compartments. A keeper was present at all times during the experiments performing husbandry training. This guaranteed that an individual taking part in the experiment would not be disturbed by others interfering.

Annex B: Description of training units per group

1. Training for the AAgroup:

Individuals had to pass (criterion was set to 33 first correct choices within a total of 48 trials; power analysis using a binomial distribution, $P < 0.001$) two training units before they were tested:

- (i) Two-element stimuli (geometrical shapes in black on transparent background with black frames, Figure A2) were presented. Individuals were rewarded for choosing stimuli with homogenous elements (AA) over heterogeneous ones (AX) in a 2AFC-task.

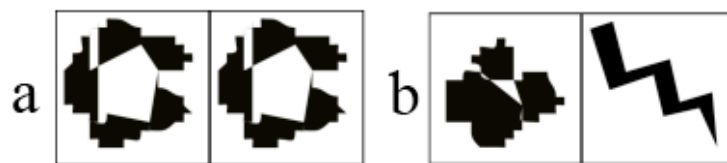


Fig A2: Example of a training stimulus. The chimpanzees were trained to choose the stimulus containing identical elements (a) over the stimulus with heterogeneous elements (b).

- (ii) Individuals who successfully finished the first training unit continued with the second training stage where one or two “distractor” elements were introduced in between dependency elements (AXA and AXXA) (Figure A3).



Fig A3: Example of stimuli in training unit 2. The sequence of pictures follows an AX^nA pattern, where $n=1$, or 2.

Two individuals successfully completed these training units and were tested consequently.

2. Training for the ABgroup:

- (i) In a first training step individuals were trained to choose any two-element heterogeneous (AB) stimuli over homogenous (AA) ones (see Figure A4.1).
- (ii) Subsequently individuals were presented with a set of five specific associative pairs of heterogeneous elements (A_1B_1 , A_2B_2 , A_3B_3 , A_4B_4 , and A_5B_5). These had to be chosen over any other heterogeneous element pair (XY, sampled from another pool of 45 different shapes). Those were perceptually different (numbers and letters drawn in fine line) from the AB-associative pair elements (Figure A4.3).

- (iii) For the next training step AB-pairs were presented with heterogeneous element stimuli that were perceptually similar (distractor shapes) to the ones of the AB-pairs (see Figure A4.4).
- (iv) In the final training unit (Figure A4.4), one or two “distractor” elements (X’s) were inserted between associative pairs, producing stimuli such as A_iXB_i and $A_iXX'B_i$ (where $X \neq X'$). These positive stimuli were presented together with negative ones composed of three or four heterogeneous elements (XXX, XXXX).

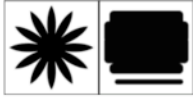
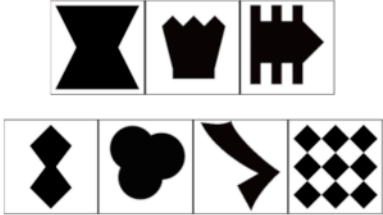
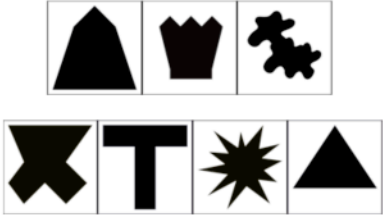
	S+	S-
a.		
b.		
c.		
d.		

Fig A4: Training stages for the AB group. The right column shows examples of rewarded stimuli (S+), the left column depicts examples of negative stimuli (S-). In a first training stage (1) any pair of heterogeneous elements had to be chosen over homogenous ones. In a second training stage (2), S+ and S- stimuli consisted of heterogeneous elements, where S+ was any of the associative pairs (A_iB_i) and S- consisted of two different elements sampled from a pool of numbers and letters (perceptually markedly

different to S+ stimuli). In the third training step (3) 2-element S+ and S- stimuli that were perceptually similar were presented. Any of the five associative pairs (S+) was presented with two heterogeneous shapes (S-). In the final training stage (4) one or two distractor elements were inserted in between associative pair elements ($A_i X A_j$ and $A_i X X A_j$) and presented simultaneously with stimuli consisting of three or four heterogeneous elements.

6 | Abstract Concepts across Modalities and Domains?

Chimpanzees process structural isomorphisms across sensory modalities.

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Chimpanzees process structural isomorphisms across sensory modalities

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Evolution has shaped animal brains to detect and take advantage of sensory regularities in environmental stimuli (e.g. social information, such as rank hierarchies and kin relations, or ecological information, such as fruiting patterns of trees)[1, 2]. In addition, many species relate and integrate one-dimensional quantities across sensory modalities, such as relating conspecific faces to voices, or high-pitched sounds to bright light [1, 3]. If basic patterns like repetitions and identities are perceived in different sensory modalities, it could also be advantageous to detect cross-modal isomorphisms, i.e. develop modality-independent representations of structural features, which could be used in visual, tactile, and auditory processing. Indeed, humans exposed to a visual sequence (e.g. nonsense strings of letters where H always occurs between two Ls) can tell whether unfamiliar sound sequences contain similar structural regularities (high-pitched sounds always occur between two low-pitched sounds) [4]. To date, this ability to map similar structures across domains has not been demonstrated in other animals. We show that two chimpanzees trained to choose symmetric sequences of geometric shapes spontaneously detected a visual-auditory isomorphism. Although chimpanzees were never trained to associate sounds to images, their response latency in choosing symmetric sequences was shorter when presented with (structurally isomorphic) symmetric, rather than scrambled, sound triplets. Our result provides the first evidence of structure learning across modalities in a non-human animal. It suggests that cross-modal abstraction capacities transcend linguistic abilities, and might involve evolutionary ancient neural mechanisms.

Different forms of cross-modal processing exist in nature. A *discrete mapping* is a pairwise association between discrete units in different domains, for instance mapping faces to voices (Figure 1A). Some species have a modality-independent representation of conspecifics, showing surprise when they see one individual appear immediately

after hearing a vocalization from another [1]. Discrete mapping builds upon basic neural mechanisms seemingly available to a range of organisms. For instance, flies exposed to combinations of visual and olfactory stimuli develop a cross-modal memory, which can be retrieved by light or odour alone [5]. A *continuous mapping* relates graded percepts across modalities, e.g. when deeper voices are associated to larger body sizes (Figure 1B). Chimpanzees show this sort of graded mapping spontaneously: If trained to discriminate light from dark squares, they perform better when white is suddenly paired with a high-pitched sound and black with a low-pitched sound than vice versa [3]. Recognizing cross-modal *structural isomorphisms* requires recognition that two percepts in different modalities share a common structural property. The 3-note sequence in Figure 1C is isomorphic to both visual sequences; in particular, all sequences are structurally symmetric, i.e. they begin and end with the same (note or shape) element, with a different element between. This similarity transcends the particular physical characteristics of the stimuli and cannot be obtained by simply combining discrete mappings: it instead maps similar structures across modalities.

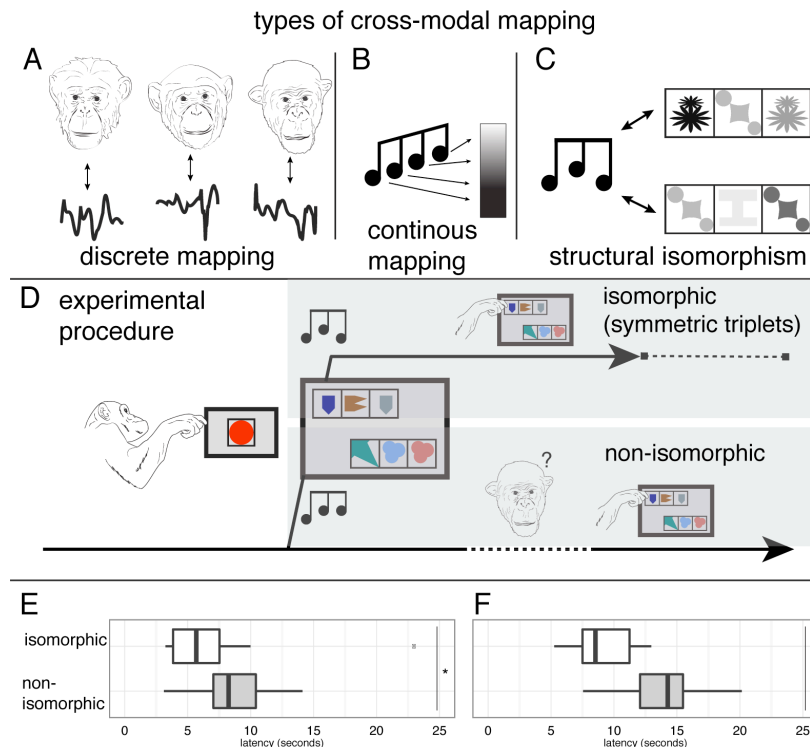


Figure 1. Types of cross-modal correspondences, experimental procedures and results. Cross-modal mappings can be discrete (A), continuous (B), or involve whole structures mapped across domains with

no need to establish specific associations between constituent elements (C). (D) Schematic representation of a single trial (which started with the presentation of a red circle: once the chimpanzee touched it, the visual and auditory sequences were shown simultaneously and chimpanzees' latency to respond recorded) and predictions (the dashed line denotes an expected difference in response latencies between conditions). (E-F) Boxplot of FK's and KL's latency in providing the correct response. Median latencies across trials were shorter in the isomorphic than in the non-isomorphic condition, namely 5.68 vs. 8.25 seconds (ape FK) and 8.52 vs. 14.27 seconds (KL).

Here we investigated whether non-human animals can map structures across modalities. (See Supplemental Information and [6] for details.) Chimpanzees were presented with pairs of visual patterns on a touch-sensitive screen and could respond by touching one of them. The two patterns were (Figure 1D, large screen): (i) a symmetric triplet, consisting of two identical geometrical shapes separated by a different shape, which was positively reinforced only in previous experiments [2], and (ii) a scrambled asymmetric triplet. Presentation of the visual sequences was preceded by one of two sound sequences: (i) a symmetric triplet, where the first and last note were identical pure tones, isomorphic to the symmetric structure of reinforced images, and (ii) a scrambled triplet, which violated this symmetry.

We hypothesized that if chimpanzees perceived the symmetric triplets as isomorphic, presentation of symmetric or scrambled auditory triplets would differentially affect processing of the symmetric visual triplet. If so, an inconsistent audio-visual pairing should increase the time needed to respond (Figure 1D, bottom timeline) relative to an isomorphic audio-visual pairing (top). Indeed, both chimpanzees were significantly slower in choosing the correct symmetric visual triplet after hearing a scrambled sound triplet rather than an isomorphic symmetric triplet (Mann-Whitney U test; chimpanzee FK: $U(33)=80$, $Z=-2.384$, $p=0.017$, see Figure 1E; chimpanzee KL: $U(15)=10$, $Z=-2.440$, $p=0.014$, see Figure 1F). As these acoustic sequences were completely novel to the animals before the experiment, their structural properties must have interfered with processing of the learnt symmetry rule.

Chimpanzees were never trained to associate specific sounds with images: hence simple associative learning cannot explain our results. Scrambled stimuli have the same proportion of element types as symmetric stimuli: simple comparison of the number of element types or entropy across modalities are insufficient alternative

explanations. Crucially, isomorphisms are of a higher order than both analogical reasoning and cross-modal mappings [7]. Analogies often consist in isomorphisms within the same modality, while training specific sound-shapes associations via discrete mapping would only enable mapping low-high-low sound triplets to either star-cross-star or cross-star-cross patterns, but not both simultaneously.

Our results provide the first evidence we know of sensory binding capacities beyond discrete/continuous mappings, suggesting that this crucial human ability was present in our last common ancestor with chimpanzees (at latest). These findings indicate that human language is not a prerequisite to map abstract structures between modalities, and that cross-modal ability might instead have constituted a precursor to human linguistic abilities [8-10]. Our chimpanzee data dovetails with recent neural evidence that humans constantly integrate information across modalities via synchronized activity in visual and auditory areas of the cortex [10]: Further research is needed to determine the neural mechanisms underpinning isomorphism identification. Our findings suggest that cross-modal encoding might be more common across animals than previously surmised, and introduce a new experimental paradigm to test this suggestion.

Acknowledgements

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Supplemental Experimental Procedures

Animal Welfare and Ethics

The board of the Living Links - Budongo Research Consortium and the Royal Zoological Society of Scotland (UK) approved the conduction of the study. The ethics board of the University of Vienna confirmed that the project raised no ethical concerns (approval number: 2014-010). No invasive methods were used at any time and the chimpanzees participated in all experiments voluntarily. All procedures were in accordance with the Austrian, British, and European Union legislation.

Subjects and Study Site

At the beginning of the study 18 adult chimpanzees (10 females and 8 males), between 49 and 14 years of age, lived socially in an 1832m² outdoor enclosure and three interconnected 12x12x14m indoor enclosures in Budongo Trail at Edinburgh Zoo [1]. Food was provided between four to five times per day while water was available *ad libitum*. During training and experiments individuals were not separated from their social group and could leave the sessions at any time. While one individual participated in a training or experiment, a keeper distracted other individuals with husbandry training. Only positive reinforcement techniques were used in animal training.

Two individuals, one male (FK) and one female (KL), both 20 years of age, took part in this study. Both were previously trained to use a touch sensitive screen [2] and participated in a visual pattern learning experiment testing their ability for non-adjacent dependency processing in visual patterns [3].

Learning Dependencies in the Visual Domain

Two chimpanzees (FK and KL) were trained to differentiate between visual stimuli, which contained non-adjacent dependencies between the first and the last elements of a string of variable length and those lacking such a dependency (Figure S1). Stings consisted of a series of horizontally concatenated geometrical shapes (individual shapes were surrounded by a black square frame, outer dimensions: 225x225 pixels) in different colors (Figure S1). These strings were up to seven elements long, but consisted of a minimum of three individual elements. Dependencies were feature-

based in the sense that categories of elements (geometrical shapes) were matched at the dependent string positions (first and last element of a sequence had the same shape). Variation within element classes (color of the geometrical shapes) was introduced as irrelevant, distracting information. Thus, consistently all correct stimuli had shape-dependencies between the first and the last elements, whereby the color of the shapes of these elements could but did not necessarily need to be the same.

Chimpanzees were trained and tested using a two-alternative-forced-choice (2-AFC) task on a touch-sensitive screen (15 in. Elo Touch Systems, Carroll Touch Technology) connected to an Apple Mini Mac computer. Stimuli design, control of experiments, and data logging was managed by custom written Python code (www.python.com). For a more detailed description of the setup, visual stimuli, and training/testing regime see [3]. The two individuals, who participated in this study, successfully learned the feature-based dependency rule and generalized it over novel patterns. Thus, both chimpanzees were shown to be capable of processing non-adjacent, feature-based dependencies in strings of visual shapes [3].

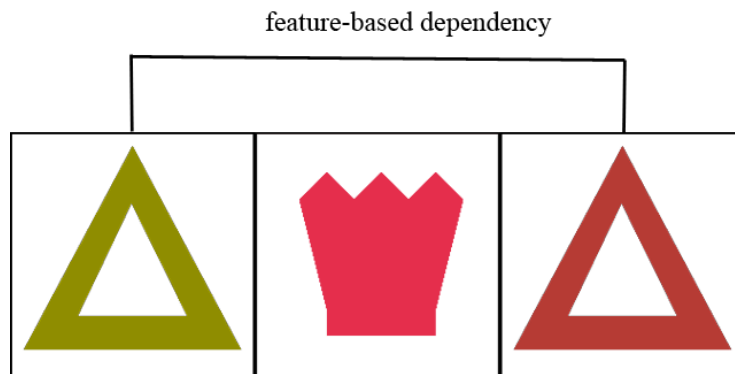


Figure S1: Example of a visual stimulus containing a feature-based dependency. The first and the last element (dependent elements) of the string are matched in shapes (dependency feature; both elements belong to the same category, in this case triangles) but not in color (variation within the category). The middle element differs in shape from the dependency elements.

Testing Cross-Modal Processing

To test if a structural rule (such as the dependency rule) learned in the visual domain was encoded at a domain general level we applied a *cross-modal interference paradigm*. The assumption here was that if a structural regularity is encoded on a modality-general level, isomorphic (the structure of a stimulus in one modality is

equivalent to the stimulus structure in another modality) or non-isomorphic (structures inconsistent across modalities) input in one modality (e.g., auditory) should influence responses to stimuli in another modality (e.g., visual).

We used the simplest form of patterns that contained or violated the feature-based dependency rule the chimpanzees had been trained for in the visual domain. Those were triplets of visual elements that had a symmetric (first and last element are the same, interspersed with a different element in the middle) or a scrambled (first and last element differ from each other, but the first and second, or the second and third elements match) pattern respectively.

Before presentation of a set of visual stimuli an acoustic sound sequence was played (for a more detailed description of acoustic and visual stimuli see below). The acoustic pattern played was either isomorphic (symmetric; first and last tone are the same) or non-isomorphic (scrambled; first and last tone differ) with the symmetry rule reinforced and learned in the visual domain. As the two chimpanzees had been trained extensively for symmetric strings and successfully tested for generalizations of the rule to novel visual patterns they should choose symmetric stimuli over patterns consisting of scrambled elements, irrespective of the structure of the sound sequence played previously. However, if the structural regularity learned in the visual domain is encoded on a cross modal cognitive level an effect of the acoustic stimulus type will be expected: acoustic strings isomorphic/consistent with the symmetric structure of the correct visual stimulus should not alter the chimpanzees' behavior. When an acoustic stimulus with a scrambled structure interferes (as it is non-isomorphic/inconsistent with the visual rule learned) with processing the symmetry rule in the visual domain, a delay in choosing the symmetric visual stimulus should occur. Such a delay would be expected only if the structural regularity was encoded on a modality-general level.

To avoid a drop of motivation during the experiment each test trial was preceded by presentation of a set of familiar stimuli (chimpanzees had been trained previously to choose a red over a green circle, Figure S2, panel 1). In this pre-trial, responses were fed-back with two different types of sounds for correct (clicker sound familiar to the chimpanzees as a positive reinforcement sound) and incorrect (unappealing signal

consisting of short, irregular sounds) answers. Additionally, a red penalty screen was displayed (for 3 seconds) after incorrect responses, or a highly preferred food reward (e.g., grapes, blueberries, peanuts, raisins, or pieces of dates) was given for correct choices. (This procedure was analogous to the testing regime used in the previous visual pattern learning experiment [3]).

Consequently a test trial started (these trials were not fed-back or rewarded) with a screen displaying a red circle (Figure S2, panel 2). When the individual touched the circle an acoustic pattern was played. Right after the acoustic sequence ended a set of visual stimuli – one symmetrical, one scrambled - was displayed until the individual touched either of them (Figure S2, panel 3). In 50% of the trials (isomorphic trials) the audio equivalent of the symmetric visual sequence was played before the visual patterns appeared, and in 50% of trials (non-isomorphic trials) the audio equivalent of the scrambled visual pattern was played. Afterwards, a new pre-trial screen was displayed. Latencies to respond (from the onset of a trial, that is the presentation of the red circle (Figure S2, panel 2), until touching either visual stimulus) were measured. The chimpanzees did not receive any training, other than the training for the visual symmetrical patterns, for this experiment on structural isomorphisms across sensory modalities.

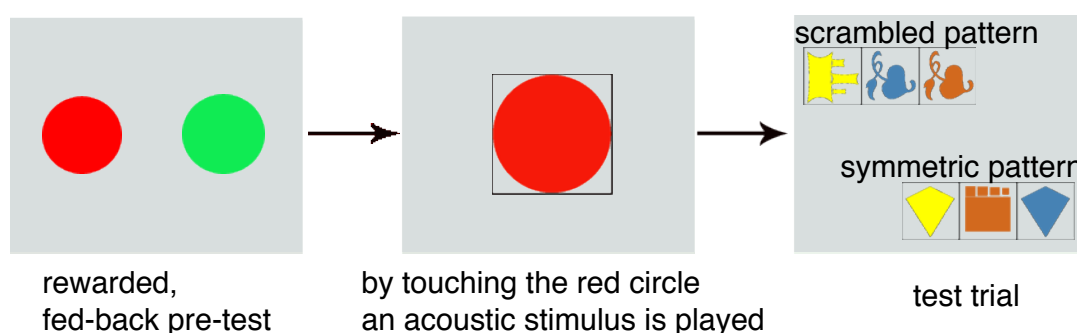


Figure S2: Schematic of the experimental procedure. The chimpanzees were presented with a screen depicting a red and a green circle (pre-trial, panel 1). Previously they had been trained to choose the red over the green stimulus. When an individual touched the red circle a clicker sound was played and a food reward given. If the individual touched the green circle an unappealing, irregular sound signal was played, a red penalty screen was displayed (for 3s), and no food reward was given. After the pre-trial, a screen with a red circle was shown (panel 2). The moment the animal touched the circle a symmetric (isomorphic with the visual rule) or scrambled (non-isomorphic with the visual rule) acoustic stimulus was played. Consequently two visual stimuli (one symmetric and one scrambled, panel 3) were

displayed and the chimpanzee could make its choice by touching either of them. Next another pre-test screen was shown.

Visual and Acoustic Patterns

Visual and acoustic strings consisting of three individual elements served as stimuli for the experiment. As in [3], visual stimuli were composed of a series of horizontally arrayed, black-framed geometrical shapes (outer dimensions: 225x225 pixels) in different colors. Visual stimuli were generated by sampling elements from a pool of 30 different geometrical shapes in seven colors each (a total of 210 elements). Positive stimuli followed a symmetric pattern. That is to say that two identical shapes were separated by a different shape appearing between them. The corresponding negative stimuli followed a scrambled pattern: the first shape was repeated twice and then followed by another shape, or twice the same shape was concatenated to the first. All elements of the visual patterns could have any of the seven colors.

Acoustic stimuli consisted of pure sine wave tones. All stimuli lasted one second and contained three tones of 300 msec each, separated by 50 msec silence. The sounds were randomly sampled from low (196, 200 and 204 Hz) and high (384, 400 and 416 Hz) tone categories (see [4] for details concerning the auditory stimuli). To compose acoustic stimuli analogous to symmetric visual stimuli either two high tones were at the edges of a sound sequence and a low tone in between them, or vice versa. For acoustic equivalents to scrambled visual stimuli two high (or low) tones were concatenated to each other, and preceded or followed by a low (or high tone). For half of the stimuli “same” elements were sampled from the low category and “different” elements from the high category, for the other half of the stimuli the mapping was inverted. Thus, “same” geometrical shapes (e.g., two triangles) corresponded to tones sampled from the same tone category (e.g., two high tones). “Different” geometrical shapes (e.g., a triangle and a square) were mapped to tones sampled from different tone categories (e.g., a high and a low tone). Any two same shapes could correspond to any two tones sampled from the same tone category and any two different shapes could be mapped to any two tones sampled from different tone categories.

Test stimuli were sampled from 80 acoustic-visual stimuli combinations, namely 40 isomorphic (symmetric acoustic pattern matching the visual rule) and 40 non-

isomorphic (scrambled acoustic pattern violating the visual rule) acoustic-visual pairings (Table S1).

Table S1: Overview of acoustic-visual stimuli combinations. Half of the acoustic patterns (low-high-low or high-low-high sounds) matched the (previously learned) symmetric visual pattern, while the other half (low-low-high, high-high-low, low-high-high, high-low-low) followed the scrambled pattern of the negative visual stimuli.

isomorphic / non-isomorphic	number of stimuli	acoustic patterns	visual patterns	
			scrambled	symmetric
non-isomorphic	10	LLH	AAX	AXA
non-isomorphic	10	HHL	AAX	AXA
isomorphic	10	LHL	AAX	AXA
isomorphic	10	HLH	AAX	AXA
non-isomorphic	10	LHH	XAA	AXA
non-isomorphic	10	HLL	XAA	AXA
isomorphic	10	LHL	XAA	AXA
isomorphic	10	HLH	XAA	AXA

Statistical analyses were performed using SPSS 19. Unless stated otherwise, all p-values are exact and two-tailed.

Supplemental Results

Both subjects (FK and KL) showed no significant effect of the auditory stimulus on providing a correct response, i.e. no significant association between auditory stimulus heard and visual stimulus chosen (Fisher's exact test=.646 (ape FK) and =.515 (ape KL)).

Significant differences in response latencies were found between isomorphic and non-isomorphic conditions. Chimpanzee FK's latency in choosing the symmetric visual stimulus was significantly longer when an non-isomorphic auditory stimulus was played than when the auditory stimulus had a symmetric (isomorphic) pattern (Mann-Whitney U test N=35, U(33)=80, W=270, Z=-2.384, p=0.017; mean ranks:

(isomorphic) 14.21; (non-isomorphic) 22.50). When choosing the scrambled visual stimulus however, ape FK did not show any difference between patterns of auditory stimuli (Mann-Whitney U test $N=41$, $U(39)=199$, $W=452$, $Z=-.261$, $p=0.806$; mean ranks: (isomorphic) 21.53; (non-isomorphic) 20.55).

Chimpanzee KL presented a response pattern analogous to FK. Playing an non-isomorphic, scrambled auditory pattern increased KL's latencies to choose the symmetric visual pattern (Mann-Whitney U test $N=17$, $U(15)=10$, $W=65$, $Z=-2.440$, $p=0.014$; mean ranks: (isomorphic) 6.50; (non-isomorphic) 12.57), while latencies did not differ between auditory conditions when the scrambled visual stimulus was chosen (Mann-Whitney U test $N=21$, $U(19)=48$, $W=126$, $Z=-.426$, $p=0.702$; mean ranks: (isomorphic) 11.67; (non-isomorphic) 10.50).

As chimpanzees were tested on a strict voluntary basis neither of our study subjects completed the full set of test trials. Chimpanzee FK was tested with 38 isomorphic test trials and 39 non-isomorphic trials. Chimpanzee KL underwent 20 isomorphic trials and 19 non-isomorphic trials. To obtain a balanced sample, FK's last non-isomorphic trial and KL's last isomorphic trial are not considered in the analyses above; their inclusion however leaves all statistical tests and our conclusions unchanged (see below).

Analyses without exclusions

Both subjects showed no significant effect of the auditory interference stimulus on providing a correct response, i.e. no significant association between auditory stimulus heard and visual stimulus chosen (Fisher's exact test=.650 (ape FK) and =.523 (ape KL)).

Chimpanzee FK was significantly slower in answering when an non-isomorphic auditory stimulus interfered (median latency=8.24 s) than when an isomorphic acoustic stimulus was played (median latency=5.68 s). Similarly, ape KL showed longer latencies in the non-isomorphic condition (median latency=14.27 s) than in the isomorphic condition (median latency=8.52 s) (Table S2).

Table S2: Results when last trial is included (results, conclusions, and interpretation remain unaltered from results with balanced trial data set)

Ape	Response	N	df	U	W	Z	p	Mean rank symmetric	Mean rank scrambled
F	Correct	36	34	90	280	-2.266	.023	14.74	22.71
F*	Incorrect	41	39	199	452	-0.261	.806	21.53	20.55
K*	Correct	17	15	10	65	-2.440	.014	6.50	12.57
K	Incorrect	22	20	55	133	-0.330	.771	12.00	11.08

Latencies to respond to visual stimuli without acoustic interference

A possible explanation for differences in latencies to respond between isomorphic and non-isomorphic conditions could be that the individuals simply reacted differently to the two types of auditory stimuli without being sensitive to the isomorphism with the visual patterns (e.g., hesitating to react after scrambled sound sequences as opposed to symmetric sound sequences). If this was the case we would have expected different latencies between conditions also in trials where the individuals chose the scrambled visual stimulus – this however was not the case (see above).

To assure that this result was not due to differences in response latencies to symmetric and scrambled visual stimuli, we compared latencies between correct and incorrect choices when presented with visual stimuli only (no acoustic stimuli played before presentation of a set of visual stimuli). All responses to three-element long (comparable to visual stimuli used in this experiment), reinforced stimuli presented during tests in [3] were used for this analysis. We found no differences in latencies between correct (symmetric stimulus was chosen) and incorrect (scrambled stimulus was chosen) answers (Mann-Whitney U test; FK: N=108, U=891, W=4719, Z=-.175, p=0.861; mean ranks: (correct responses) 54.24; (incorrect responses) 55.57; KL: N=106, U=868, W=1193, Z=-1.075, p=0.282; mean ranks: (correct responses) 55.28; (incorrect responses) 47.72). Therefore we conclude that differences in latencies to respond in isomorphic and non-isomorphic audio-visual trials are due to a cross-modal interference of the acoustic sequence with the structure of the visual stimulus.

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7 | General Discussion and Conclusions

The studies presented in this thesis investigated social complexity and social organization from different proximate and ultimate perspectives: they addressed Tinbergen's questions (Tinbergen 1963) about both the adaptive value and underlying mechanisms of a character or trait – in this case social behavior. Living socially may affect behavioral, cognitive, and physiological components of animals' biology, and societies differing in social organization and social complexity may shape these aspects differently. For instance, this seems to be the case when looking at the link between physiological stress measures and grooming behavior in despotic and more relaxed species. In line with other studies (Galef and Giraldeau 2001; Palombit et al. 1997; Silk 2007a; Silk 2007b; Silk 2014; Silk et al. 2003) results on grooming patterns in Barbary macaques (Chapter Two: Social Strategies for Stress Coping; Sonnweber et al. 2015b) showed a connection between glucocorticoid measures and different grooming patterns. Although from these observations we cannot infer causal relations between the two parameters (that is, whether grooming others lowers glucocorticoid concentrations or lower concentrations lead to increased allogrooming), but only demonstrate correlational associations, the results further support the notion that social behavior serves an adaptive function in that both low glucocorticoid levels and strong, stable social bonds, have positive fitness consequences for an individual (Silk 2002; Silk 2007a). While this seems to be true for both despotic and more tolerant species, the relationship between the distribution of grooming amongst social partners and physiological stress measures differs between societies with these different social styles. This may be due to higher behavioral flexibility in relaxed species compared to more despotic ones (De Waal and Luttrell 1989; Jaeggi et al. 2010; Øverli et al. 2007) and/or to the strong role of kinship in despots (Aureli et al. 1997).

Independent of social style, what makes primate sociality so special is that it is built on social relationships that can go beyond bonds between pairs, extending to whole social networks (Dunbar 2009; Dunbar and Shultz 2007) (although this is also found

in other species, e.g., whales and dolphins: (Cantor and Whitehead 2013; Fraser and Bugnyar 2012; Lusseau 2007; Williams and Lusseau 2006); corvids: (Braun and Bugnyar 2012; Fraser and Bugnyar 2010; Fraser and Bugnyar 2012)). Although not all social behavior we observe is adaptive (e.g., Silk 1999), social relationships may mirror which behavioral strategies have been selected for due to inclusive fitness maximization (Schülke et al. 2010; Silk 2007a; Silk 2007b; van Schaik 1989).

Social factors may also impact mating patterns, reproductive strategies, and reproductive success to a considerable extent (Kappeler and van Schaik 2002; Silk 2007b; Silk et al. 2003; Silk et al. 2009; Silk et al. 2010). While the research discussed above focused primarily on female-female interactions, social behavior between the sexes may also have important implications for reproduction-related factors. Post-copulatory grooming between male and female mating partners (Chapter Three: Social Behavior and Mating, (Sonnweber et al. under review)) seems to follow sex-specific mating strategies. Grooming after copulations potentially has an adaptive component to it: males who preferentially groom after ejaculatory mating, might keep females from copulating with other males and thus decrease sperm competition by grooming the female after copulation. Females on the other hand potentially gain additional (ejaculatory) matings when grooming the male after *non*-ejaculatory copulations. Furthermore hormones released during grooming (such as oxytocin) might increase the chances of successful fertilization (e.g., Arletti et al. 1985; Arletti et al. 1990; Arletti et al. 1992; Bancroft 2005; Lee et al. 2009). In the future more research is required to discriminate between these possible explanations.

Individuals living socially seem to have adapted behavioral and physiological patterns to cope with the special demands inherent to the nature of their social surrounding (Bercovitch and Ziegler 2002). Ultimately, all these behaviors may be regarded as strategies to increase an individual's fitness and reproductive success. At the same time these adaptations may have opened a way for a more effective way of transmitting knowledge and skills within a population, namely social learning and teaching. An advantage accompanying sociality is that within stable social groups individuals are aggregated in space and time and face the same challenges. This offers the potential to learn about the environment or acquire new skills from other knowledgeable group mates. Learning and teaching usually takes place within a

structured social context and is influenced by learning pathways (Coussi-Korbel and Frigaszy 1995). Social learning or teaching often require close physical proximity between a knowledgeable and a naïve individual, and therefore may be constrained by the social relationships between the two individuals (Laland 2004). Furthermore the spread of information within a population depends on characteristics of the social network. A recent study comparing multiple primate species showed that tolerant (and cognitively sophisticated) species tend to have more effective social networks (in terms of information transmission) (Pasquaretta et al. 2014). The authors argue that these more-effective nets result from fitness maximization of individuals, who, in order to increase their information access, affiliate with many social partners.

As discussed earlier, social interactions reduce stress-related hormones, anxiety, and aggression. Thus hormonal adaptations to social relationships can be expected to play a central mechanistic role in the emergence of social learning and teaching. For instance, the presence of, and interaction with a closely affiliated partner is associated with an increase in oxytocin in chimpanzees (OT) (Crockford et al. 2014; Crockford et al. 2013; Wittig et al. 2014a). Therefore, integrating physiological measures and social network analysis into the study of social learning and teaching may break new ground and broaden our understanding of the underlying mechanisms (Chapter Four: Social Learning and Teaching in Societies; Ravignani and Sonnweber in press). The ability to learn from others has often been argued to be a crucial factor underlying the evolution of complex cognitive abilities, which ultimately can lead to the emergence of traditions and culture (Heyes et al. 1996; Whiten 2000; Whiten and Van Schaik 2007). Studies comparing the spread of information, networks, and physiological correlates in different species (and not solely primates, but also corvids, cetaceans, or felids for instance) will help to gain a better understanding of the proximate mechanisms underlying social learning and teaching.

Intensive study of primate intelligence and sociality has led to the suggestion that social complexity shaped and enhanced primate cognition in a domain-specific manner, but that the resulting skills can be applied for general purposes (Byrne and Bates 2007; Cheney and Seyfarth 2008; Deaner et al. 2006). One crucial requirement for flexible processing of social information is the ability to process discrete units of social organization and relate these to each other (e.g., matriline, alliance groups,

groupmates vs. strangers) (Bergman et al. 2003; Seyfarth and Cheney 2003; Seyfarth et al. 2005). Category formation capacity is equally useful for planning and performing motor actions (Tikhanoff and Fontanari 2006) in general, and action sequences connected to tool use specifically (for instance the category or set of “hard and heavy tools” might be useful to crack nuts open, while another category of “long tools” are effective for termite fishing). Furthermore, understanding temporal and spatial relationships between elements in a sequence (i.e. action chains, linear dominance hierarchies), especially non-adjacent relationships, may be particularly useful for animals living in dynamic fission fusion societies, with strong social bonds and alliances between non-kin (Aureli et al. 2008; Lehmann and Boesch 2008; Wittig et al. 2014b). A great deal of flexibility may be gained if regularities are encoded at a modality- or even domain-general level (e.g., social domain and sequences of motor actions), as this may allow solving novel problems and integrating new information without re-learning a rule for every experience or situation (Emery and Clayton 2004).

Intensive research investigating acoustic and visual pattern learning and spontaneous regularity processing capabilities in various species, has been conducted since the publication of an influential study on cotton-top tamarins by Fitch and Hauser in 2004 (Fitch and Hauser 2004). Most of these studies examined these abilities in light of questions concerning the evolution of language and music (Abe and Watanabe 2011; Arbib 2005; Chen et al. 2015; de la Mora and Toro 2013; Fitch et al. 2012; Fitch et al. 2010; Petkov and Wilson 2012; Ravignani et al. 2013a; Ravignani et al. 2013b; ten Cate and Okanoya 2012; van Heijningen et al. 2013; van Heijningen et al. 2009). Revisiting these studies and attempting to connect species’ abilities for abstract rule encoding with their species’ social complexity may help to clarify if and to what extent these aspects are interrelated. For instance, a study on the cooperatively breeding cotton-top tamarins investigated their ability to learn abstract and (so-called) item-based regularities in visual stimuli (Versace, 2008 unpublished PhD thesis). While the monkeys successfully learned associations between specific A and B tokens and understood their relative positional relation, they failed to acquire an abstract regularity rule. In contrast, squirrel monkeys, who aggregate in larger groups that often encompass several families, were shown to be sensitive (without training) to

abstract, non-adjacent dependencies amongst elements in acoustic stimuli and to generalize to novel classes and stimulus length (Ravignani et al. 2013b).

My colleagues and I were able to show not only high flexibility in processing feature-based and arbitrary-associative dependencies in visual stimuli (Chapter Five: A Social Basis for Abstract Concepts?; Sonnweber et al. 2015a), but also found that abstract structural regularities are encoded on a modality-general level in chimpanzees, well known for their fission fusion system (Chapter Six: Abstract Concepts across Modalities and Domains?; Ravignani, Sonnweber and Fitch submitted). These results could provide some first indication for a species-wide correlation between the complexity of social systems and competences in the processing of abstract regularities and structures (e.g., the cooperatively breeding marmosets live in less complex social groups than we see in the fission fusion organization of chimpanzees). This notion is supported for instance by studies on transitive inference tasks (Boysen et al. 1993; Gillan 1981; Treichler and Van Tilburg 1996). Animals living in highly social groups outperform less social species in transitive reasoning tasks, even when presented with non-social stimuli (Bond et al. 2003; MacLean et al. 2012; MacLean et al. 2008). Cognitively, the crucial factor for good performance in transitive tasks is an ability for abstraction and rule formation which goes beyond a single, isolated learning experience (Emery and Clayton 2004).

In their book on baboon social cognition Dorothy Cheney and Robert Seyfarth wrote “... *the most human features of monkeys and apes lie not in their physical appearance but in their social relationships*” (Cheney and Seyfarth 2008). In contrast, after reviewing and comparing studies on intelligence across animal species Byrne and Bates (2010) concluded that “*primate cognition is not uniquely social*”.

My PhD thesis attempted to address these contrasting opinions by bringing together three strands of research, namely (i) experiments on abstract, non-social information and structure processing in multiple modalities, (ii) analysis of complexity of social systems, and (iii) studies of social information processing. While the studies collected here address only small parts of this important issue, I think that the overall approach may allow scientists to further enhance our understanding of the interplay between the evolution of social systems and cognitive abilities. Furthermore, understanding non-human primate social behavior, how primate physiology is adapted to social life, and

how social complexity shapes cognition might ultimately also help us better understand human society and its biological basis, in all of its complexity.

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Appendix

Overview of contribution to publications in the thesis

Sonnweber RS, Ravignani A, Stobbe N, Schiestl G, Wallner B & Fitch WT (2015) Rank-dependent grooming patterns and cortisol alleviation in Barbary macaques. *Am J Primatol* 1-13. DOI: 10.1002/ajp.22391.

RS designed the study, collected the data in the field, was involved in data analysis, and wrote the manuscript

Sonnweber R & Fitch WT (under review) Post-copulatory grooming: a female mating strategy? *Behav Ecol Sociobiol*

RS designed the study, collected data in the field, analyzed the data, and wrote the manuscript

Ravignani A* & **Sonnweber R*** (in press) Measuring teaching through hormones and time series analysis: towards a comparative framework. *Behav Brain Sci*

[* equal contributions]

RS was responsible for the hormone-related part of this commentary. AR and RS contributed equally to the writing of this manuscript.

Sonnweber R, Ravignani A & Fitch WT (2015) Non-adjacent visual dependency learning in chimpanzees. *Anim Cog* 18(3) 733-745. DOI 10.1007/s10071-015-0840-x.

RS designed the study, collected the data, analyzed the data, and wrote the manuscript.

Ravignani A*, **Sonnweber R*** & Fitch WT (submitted) Chimpanzees process structural isomorphisms across sensory modalities. *Curr Biol*

[* equal contributions]

RS was involved in the study design, collected the data, and was involved in statistical analyses. AR and RS contributed equally to manuscript writing.

Zusammenfassung

Eine Vielzahl der bekannten Primatenarten leben in sozialen Verbänden. Gruppenleben bringt Vorteile mit sich, stellt Individuen aber auch vor neue Herausforderungen. Daher entwickelten sich Anpassungen an die besonderen Umstände gemeinsam mit verschiedenen sozialen Systemen, die wir in den heutigen Primatenarten finden. Diese Anpassungen betreffen nicht lediglich das Sozialverhalten sondern spiegeln sich auch in physiologischen und kognitiven Bereichen wider. So finden wir in despotischen Arten andere Zusammenhänge zwischen sozialen Verhaltensmustern und physiologischen Stressparametern als beispielsweise in eher relaxten verwandten Arten. Männchen und Weibchen setzen soziales Verhalten in geschlechtsspezifischer Weise als reproduktive Strategien ein. Aber auch kognitive Fähigkeiten wurden durch das Gruppenleben verändert. Einerseits eröffnete es die Möglichkeit, dass Individuen voneinander lernen, was dazu führt, dass erworbene Fähigkeiten und Wissen innerhalb einer Population erhalten bleiben können. Andererseits müssen sozial lebende Tiere komplexe Strukturen über lange Zeiträume erkennen und sich merken um erfolgreich im Gruppenleben sein zu können. Dieser evolutionäre Druck könnte dazu geführt haben, dass flexible kognitive Fähigkeiten entstanden, die nicht nur im sozial-kognitiven Bereich eingesetzt werden sondern auch abstraktere kognitive Bereiche beeinflussen.

Curriculum vitae

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Work Experience

Project Employee (Learning from a Friend: The Role of Social Bonds and Oxytocin in Social Learning, Anniversary Fund of the Austrian Academy of Sciences), Department of Cognitive Biology, *University of Vienna* (2014-ongoing)

PhD position, Department of Cognitive Biology, *University of Vienna* (2011-2014)

Employee at the Department of Cognitive Biology, *University of Vienna* (2010-2012)

Assistant to behavioural and endocrinological research projects at the Department of Behavioural Biology, *University of Vienna* (2009-2011), Advisor: Prof. Bernard Wallner

Study assistant, *University of Vienna* (2007)

Census work on the Barbary macaque (*Macaca sylvanus*) population of Gibraltar and development of population record strategies, Prof. John Dittami (Biology, Vienna) and Prof. Bernard Wallner

Education

PhD candidate, Department of Cognitive Biology, *University of Vienna* (2011-2015)

Dissertation: “Physiological and Cognitive Determinants of Behavior in Primate Societies”, Advisor: Prof. W. Tecumseh Fitch (Biology, Vienna)

MSc *Zoology*, Behavioural endocrinology and cognitive biology, Department of Behavioural Biology *University of Vienna* (1999-2009)

Thesis: “Effects of tourist pressure on the follicular cycles and reproductive behavior in female Barbary macaques (*Macaca sylvanus*)”, Advisor: Prof. John Dittami (Biology, Vienna)

Akademisches Gymnasium Innsbruck (1991-1999)

Exchanges and Research Visits

Research visit, *Living Links to Human Evolution Research Center, RZSS Edinburgh Zoo, University of St Andrews*, UK

Research visit, *Budongo Trail, RZSS Edinburgh Zoo, University of St Andrews*, UK

Research visit, *Gibraltar Ornithological and Natural History Society*, UK

Publications & Ongoing Work

Journals

Ravignani A.* & **Sonnweber R-S.*** (in press) Measuring teaching through hormones and time series analysis: Toward a comparative framework *Behavioral Brain Sciences*. [*Equal contributions]

Sonnweber R., Ravignani A., Stobbe N., Schiestl G., Wallner B. & Fitch WT. (2015) Rank-dependent grooming patterns and cortisol alleviation in Barbary macaques. *American Journal of Primatology*, 1-13. DOI: 10.1002/ajp.22391

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Dittami J., **Sonnweber R-S.**, Schiestl G., Shaw E., Wallner B., Machatschke I. (2008) Tourism on the rock. The apes demise in Gibraltar *Ethologische Gesellschaft Regensburg*.

Dittami J., Prossinger H., Wallner B., Schiestl G., **Sonnweber R-S.**, Shaw E., Fieder M. (2006) Estrogen-Progestin ratios may affect both the size and form of female anogenital swellings in Barbary macaques. Poster at the 10th Annual Meeting of the Society for Behavioral Neuroendocrinology. Pittsburgh, Pennsylvania, USA.

Under Review/Submitted/In Preparation

Ravignani, A.*, **Sonnweber, R.*** & Fitch, T. (submitted) Cross-modal sequence encoding in chimpanzees. [*Equal contributions]

Sonnweber, R., Massen J.J.M., & Fitch, T. (under review) Post-copulatory grooming: a female mating strategy?. *Behav Ecol Sociobiol*

Sonnweber, R., Claidiere N., Guevara Rivera, L.M., & Fitch, T. (in preparation) Cuddle and Huddle: The social modulation of the stress response in a New World Primate.

Sonnweber, R., Claidiere N., Guevara Rivera, L.M., & Fitch, T. (in preparation) The role of salivary cortisol in operant task solving. Cognitive tasks as enrichment tools for zoo animals.