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Journal

International Journal of Comparative Psychology, 26(2)

ISSN

0889-3675

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Publication Date

2013

DOI

10.46867/ijcp.2013.26.02.03

International Journal of Comparative Psychology, 2013, 26, 135-157.

Social Competence of Adult Chimpanzees (*Pan troglodytes*) with Severe Deprivation History: A Relational Approach

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The development of social competence depends on feedback from partners. We evaluated the social competence of 18 adult re-socialized chimpanzees with respect to (1) social group membership and (2) deprivation history combination. The groups comprised either a majority of early (EDs; mean age at onset of deprivation: 1.2 years) or late deprived chimpanzees (LDs; mean age at onset of deprivation: 3.6 years). We reapplied our model of social competence with five grades of social stimulation and found a diminished toleration of social stimulation (1) in ED-majority groups compared to the group where LDs predominate and (2) in homogeneous ED-majority dyads compared to homogeneous LD-majority dyads. LDs but not EDs representing the minority within their group were able to adjust their stimulation seeking to the majority of partners. Only the LD-dominated group and the homogeneous LD-majority dyads, respectively, showed improvements of social competence from the first to the second year following re-socialization.

Chimpanzees are profoundly social beings. Their success in life essentially depends on their social intelligence, and intelligent social behavior crucially depends on a chimpanzee's ability to modify the behavior relative to social context (Byrne & Whiten, 1988; de Waal 1982/1998; Preuschoft & van Schaik, 2000; van Schaik, Preuschoft, & Watts, 2004). This ability to behave appropriately in social interactions is a common characteristic of the diverse definitions of social competence in humans (Rose-Krasnor, 1997).

A chimpanzee's earliest social experience arises exclusively from the relationship with his mother, who provides continuous care and contact during the first months of life (Goodall, 1986). On average, wild chimpanzees are nursed for five years, reach adolescence at eight years, and achieve independence from their mothers at between 14 and 16 years. Maternal loss reveals the infant's complete dependence on the mother. For unweaned infants maternal loss leads to behavioral disorders, if not the death of the infant itself (Boesch & Boesch-Achermann, 2000; Boesch, Bolé, Eckhardt, & Boesch, 2010; Davenport & Rogers, 1970; Goodall, 1986).

In his pioneering attachment theory, Bowlby (1969/1982) highlighted the significance of a secure mother-infant bond on the development of social, emotional and cognitive skills in the human infant and suggested that the infant's early experience shapes future social experiences and relationships. The formation of a secure attachment depends on a responsive and supportive primary attachment figure sensitive to the infant's needs (Ainsworth, Blehar, Waters, & Wall, 1978; Bowlby, 1969/1982). Insensitive and/or inappropriate caregiving, in contrast, compromises

This research was funded by the Karl-Franzens-University of Graz, the Gandolph-Doelter Foundation and the JungforscherInnenfonds der Steiermaerkischen Sparkasse. We are grateful to Baxter Inc. for financing the reported part of the rehabilitation project, to Gertrud Desch for statistical advice, to Doris Muszi, Sabine Macherhammer and Christine Hrubesch for help with data collection, to Caitlin Ahern for proof-reading, and to the two anonymous reviewers for their valuable comments. Correspondence concerning this article should be addressed to Elfriede Kalcher-Sommersguter, Institute of Zoology, Karl-Franzens-University of Graz, Universitaetsplatz 2, 8010 Graz, Austria. (elfriede.kalcher@uni-graz.at)

the formation of a bond with an available attachment figure and contributes to the development of an insecure attachment. More specifically, an insecure-avoidant attachment is associated with unresponsive care, an insecure-resistant attachment with inconsistent care (Ainsworth et al., 1978) and an insecure-disorganized/disoriented attachment is associated with several environmental risk factors such as maltreatment, severe neglect and institutional rearing, among others (Main & Solomon, 1990; van Ijzendoorn, Schuengel, & Bakermans-Kranenburg, 1999; Zeanah et al., 2005). Additionally, early traumatic life events are conducive to the development of psychopathologies (Breier et al., 1988; Schore, 2001) and influence relational synchrony (Feldman, 2007).

The biologically rooted and adaptive attachment system, as conceived by Bowlby (1969/1982), is also found in nonhuman primates and other mammals (e.g., *chimpanzees:* van Ijzendoorn, Bard, Bakermans-Kranenburg, & Ivan, 2009; *rhesus monkeys:* Suomi, 2008; *Japanese macaques:* Kondo-Ikemura & Waters, 1995; *capuchin monkeys:* Weaver & de Waal, 2002; *elephants:* Bradshaw & Schore, 2007; *horses:* Henry, Richard-Yris, Tordjman, & Hausberger et al., 2009; *rats:* Hofer, 1994) as well as the diverse maladaptive outcomes of detrimental experiences in early infancy (*development of psychopathologies*: Brüne, Brüne-Cohrs, McGrew, & Preuschoft, 2006; *stereotypic behaviors*: Latham & Mason, 2008; *relational synchrony*: Field, 1985).

The component of relational synchrony between two or more individuals is vital to the psychobiological attunement theory (Field, 1985), which assumes that each individual provides stimulation for the other and has a modulating influence on the other's arousal level. The first attunement of psychobiological systems occurs between a mother and her infant. The mother provides both the stimulation and the security necessary for well-adjusted exploratory behavior. She thus helps the infant to modulate its arousal and achieve a psychobiological equilibrium vis-à-vis varying situations and thus to cope with diverse challenges (Field, 1985). Loss of the mother or adverse early rearing experience interferes with arousal modulation by evoking aversively high arousal levels. This disrupts the "attachment-exploration balance" (see Ainsworth, Bell, & Stayton, 1971 for humans). The primate infant's underdeveloped arousal-modulation abilities in turn lead to impaired behavioral coping and stress regulation (Kraemer, 1992; Reite & Capitanio, 1985). Therefore, to Field (1985), an individual's optimal stimulation threshold in adulthood reflects the relational synchrony or quality of attunement as experienced early in life. This is similar to Bowlby's (1969/1982) notion of inner working models deriving from infantile attachment relationships.

Our study population comprised 18 adult ex-laboratory chimpanzees, re-socialized into one of three social groups (Table 1) in the course of a retirement project in Austria. We studied these chimpanzees during their first and second year of group living, 18-28 years after their arrival at the laboratory. All of these chimpanzees had undergone severe and prolonged social deprivation but differed in their age at onset of deprivation. For early deprived (ED) chimpanzees, attachment disruption and social deprivation started within the sensitive period for infant-mother attachment formation, which presumably lasts for the first 24 months of life as inferred from behavioral responsiveness to a novel environment (Miller, Bard, Juno, & Nadler, 1999). Late deprived (LD) subjects, by contrast, experienced the onset of social deprivation after this sensitive period. In a related paper (Kalcher-Sommersguter, Preuschoft, Crailsheim, & Franz, 2011) we established social competence as a personality feature, i.e., an individual attribute. We found social competence to be affected by deprivation history, with late deprived chimpanzees tolerating higher levels of social stimulation than early deprived ones, despite their shared experience of being singly-caged for decades (Kalcher, Franz, Crailsheim, & Preuschoft, 2008;

Kalcher-Sommersguter et al., 2011; Reimers, Schwarzenberger, & Preuschoft, 2007). Taken together, the results indicated that early deprived chimpanzees (EDs) had almost insatiably high security needs and little tolerance for stimulation. Late deprived chimpanzees (LDs), on the other hand, had higher stimulation thresholds and seemed able to experience the company of others as pleasant, or even tension-reducing. This could be confirmed at least for the LD males of our study population, as their glucocorticoid metabolite levels during the early re-socialization period were significantly below those found at the laboratory (Reimers et al., 2007). Sex, in contrast, had very little effect on social competence. However, as the causation of these individual differences by differences in rearing/deprivation history showed, regarding social competence as static is not sufficient. Rather, social competence develops through feedback from social partners, well beyond the processes taking place during primary attachment. This means social competence is more appropriately conceived as a relational quality, rather than a static individual attribute (Field, 1985; Holmes, 2000; Preuschoft & van Schaik, 2000). Therefore, in this paper, we tried to detect the effects on social competence as influenced by the available group members. We hypothesized that just as an infant's development depends on how the balance between security and stimulation needs is negotiated with the primary caregiver, so does a rehabilitant chimpanzee's developing social competence depend on his social partners' abilities and preferences in balancing security and stimulation needs. We expected this relational approach to reflect the development of social competence more accurately because it would reveal individuals' (in)abilities to respond differentially to their social partners' stimulation thresholds relative to their own. To our knowledge no such approach has been undertaken yet. We reapplied our previously developed model of social competence, using increasing levels of social stimulation and tested two interrelated hypotheses:

1) The toleration of social stimulation among dyads is affected by the stimulation preference of the group's majority. Our social groups differed in the respective proportion of LD vs. ED group members, with EDs representing the majority in two groups, and LDs representing the majority in the third group. We expected the majority to set the tone for interactions among the group members, which would thus lead to systematic differences in the toleration of social stimulation between the three social groups. We predicted a diminished toleration of social stimulation in ED-majority groups compared to the group where LDs predominate.

2) ED and LD chimpanzees differ in how they respond to immersion in a group with a stimulation preference that differs from their own, i.e., to over- or under-stimulation. If the social competence of individual chimpanzees echoed their attunement to the stimulation tolerance of the majority of chimpanzees in their group, the observed social competence of chimpanzees immersed in a "congenial" majority (i.e., a majority with the same deprivation history), should differ from that of chimpanzees immersed in a more "alien" social environment, i.e., a majority with a deprivation history deviating from their own. We predicted that stimulation tolerance should be lowest in dyads consisting of two ED subjects living in a social group with an ED majority and highest in the dyads containing two LD individuals living in a social group with an LD majority (*cf.* Field, 1985). Socially competent chimpanzees, however, would adjust their behavior to the stimulation tolerance of their partners, whereas socially incompetent chimpanzees would behave rigidly, i.e., fail to develop over time as well as to adjust to the stimulation preference of their partners.

Method

Subjects and Biographies

This study was conducted with a total of 18 adult chimpanzees (10 males, 8 females) living in three different social groups at the primate house in Gänserndorf, Austria (Table 1). The chimpanzees were imported from Africa to Austria between 1976 and 1986. Individuals arriving between 1976 and 1982 were socially deprived as very young infants; thus we classified them as "early deprived" (EDs, *n* = 10, mean estimated age ± SD of 1.2 ± 0.4 years upon arriving at the laboratory). The chimpanzees imported 1986 reached the laboratory in their late infancy and spent the first year as a peer group before being separated; hence they were classified as "late deprived" (LDs, *n* = 8, mean estimated age ± SD of 3.6 ± 0.5 years upon arriving at the laboratory). An exception was male Blacky, who arrived in 1986 at an estimated age of one year and was kept singly caged immediately upon arrival; he is therefore categorized as an ED chimpanzee in this study.

The chimpanzees spent up to 27 years without physical contact to conspecifics prior to arrival at the primate house (see Table 1). The re-socialization project, initialized in 2003 and carried out in accordance with the recommendations of the US National Research Council (1997) and the Austrian Federal Act on the Protection of Animals, resulted in the formation of three social groups: a one-male mixed-sex group of 5 adult chimpanzees (MS1), a two-male mixed-sex group of 6 adult and 3 juvenile individuals (MS2) and an all-male group of 7 adults (AM) by October 2003 (Table 1). During daytime the three groups inhabited separate large indoor enclosures of 10 x 13 x 6 m (MS1 group) and 16 x 13 x 6 m (AM and MS2 group) furnished with tree trunks, wooden plateaus, ropes and wood chip flooring. The male chimpanzees spent the night in single cages of 2 x 3 x 3 m, equipped with hammocks and straw for bedding, females spent the night in pairs or with their offspring in two interconnected cages. Food was provided four times a day: at 8:00 a.m. in the night cages, at 11:30 a.m. and 2:15 p.m. in indoor enclosures and at 5:00 p.m. in the night cages. Additional foraging material was provided frequently. For further details on the study population see Kalcher-Sommersguter et al. (2011).

Data Base

Observations were conducted between January and July 2004 and between March and June 2005 and distributed evenly over the chimpanzees' activity period while inhabiting the indoor enclosures. Social interactions were recorded by all-occurrence sampling (Altmann, 1974), i.e., each occurrence of brief socio-positive contacts, social play, allo-grooming and non-hostile approaches within a social group was recorded. Data on spatial proximity, i.e., being within 5m as well as being within 1 m distance to a conspecific, were recorded by 5-min scan sampling (Altmann, 1974). Results are based on 463 hrs of observation in 2004 (166 hr in AM, 129 hr in MS1, 168 hr in MS2) and 101 hrs in 2005 (62 hr in AM, 19 hr in MS1, 20 hr in MS2).

Independent Variables / Predictors

We used two predictors, (1) membership in a social group (see Table 1) and (2) deprivation history combination across social groups. Note that deprivation history combination takes into account not only the interacting dyad's deprivation history, e.g., ED-ED, but also the deprivation history of the majority of the group to which this dyad belongs, e.g. ED-majority. We had two social groups with an ED majority comprising homogeneous ED majority-ED majority dyads as well as one LD minority-LD minority dyad and heterogeneous ED majority-LD minority dyads. The third group was predominated by LD chimpanzees. This group contained homogeneous LD majority-LD majority dyads and heterogeneous LD majority-ED minority dyads (see Table 1).

Table 1
Biographic information on the study population

Name	Sex	Arrival at Laboratory	Est. Age at Arrival	Social Embeddedness
ALL-MALE GROUP (AM)				
Gogo	M	1976	2	ED majority
Max	M	1979	1	ED majority
Isidor	M	1979	1	ED majority
Johannes	M	1982	1	ED majority
Michi	M	1982	1	ED majority
Blacky	M	1986	1	ED majority
Jakob	M	1986	3	LD minority
MIXED-SEX GROUP 1 (MS1)				
Clyde	M	1986	4	LD minority
Pünktchen	F	1986	3	LD minority
Martha	F	1979	1	ED majority
Ingrid	F	1980	1	ED majority
Gabi	F	1980	1	ED majority
MIXED-SEX GROUP 2 (MS2)				
Moritz	M	1986	3	LD majority
Anton	M	1986	4	LD majority
Schuscha	F	1986	4	LD majority
Helene	F	1986	4	LD majority
Bonnie	F	1986	4	LD majority
Susi	F	1976	2	ED minority
		Birth		
ALFRED[a,b]	M	1996		
DAVID[a,c]	M	1998		
XARA[a,c]	F	1999		

Abbreviations: ED/LD = early/late deprived.
[a]Immatures were excluded from analyses. [b] = mother: Helene, [c] = mother: Schuscha; father of all three immatures died in 2001.

Dependent Variables

See Kalcher-Sommersguter et al. (2011) for a more detailed explanation.

1. Tolerance of social stimulation.

We analyzed social behavior and spatial proximity as indicators of how individual chimpanzees tolerated or coped with different intensity levels of social intimacy and stimulation, from moderate to intense.

Grade 1 was assigned to the ***toleration of stationary vicinity***, i.e., being out of reach but within 5 m distance of another chimpanzee without further social interaction, due to the comparatively great distance between conspecifics and the lack of physical contact.

Grade 2 was assigned to the ***initiation of brief socio-positive contacts*** (including kiss, gentle or erotic touch, embrace, ano-genital inspection, hold out hand, holding hands, hand to/in mouth, hand kiss, mouth on partner's body, muzzling, patting, nodding) because of an increasing proximity between conspecifics compared with grade 1 and the possible occurrence of brief body contact.

Grade 3 was assigned to the ***engagement in gentle social play***, including non-contact play of low intensity as well as mild play with brief but repetitive body contact, because of the potentially higher occurrence of brief body contacts between conspecifics compared to grade 2. Play interactions were recorded as dyadic play bouts. A bout starts with any play behavior by one of the partners toward the other, and it ends when one of the partners ceases play behavior for more than 10 s. In addition, latencies for social play, i.e., the time period elapsing between an approach within an arm's reach of a potential social partner to the onset of social play were recorded. Note that physically vigorous rough-and-tumble play (defined according to Palagi, 2006), which was assigned in our model as the sixth and highest grade of social stimulation, did not occur.

Grade 4 was assigned to the ***engagement in allo-grooming***, either as groomer or groomee, as it requires sustained body contact between conspecifics compared to grade 3. Grooming interactions were recorded as dyadic grooming bouts. In addition, latencies for allo-grooming, i.e., the time period elapsing between the approach within an arm's reach of a social partner to the onset of grooming, were recorded.

Grade 5 was assigned to the ***toleration of passive close proximity***, i.e., being within an arm's reach of another chimpanzee without further interaction, because it requires the ability to perceive the social environment as predictably safe and trust-worthy.

2. Changing the level of social stimulation/Initiative to change a social situation.

We analyzed individual chimpanzees' attempts to establish socio-positive contacts as evident in non-hostile approaches.

Non-hostile approach. Approaching another chimpanzee within 5 m distance; approach initiative is followed by either play or allo-grooming attempts of the approaching or the approached individual.

3. Social network size.

The social network size was calculated for the three social groups as well as for the different deprivation history combinations separately and is reflected in the proportion of dyads where socio-positive behaviors, i.e., allo-grooming and social play, were exchanged out of the total number of dyads per respective predictor category.

4. Development of social competence.

To evaluate potential changes in the course of re-socialization we compared data on the lowest grade of social stimulation, i.e., the toleration of stationary vicinity, and on the highest grade of social stimulation, i.e., the toleration of close proximity, between 2004 (first year after resocialization) and 2005 (the second year after resocialization).

Definitions of behavior patterns follow van Lawick-Goodall (1968) and van Hooff (1973). Social interactions and spatial associations were analyzed only for adult group members, i.e., interactions and associations of adult group members of MS2 with the three immatures were excluded from analysis, to achieve comparability between ED and LD individuals.

Data Analysis

In this study all analyses were conducted on the dyadic level. Social behaviors can be either symmetrically exchanged or directional. For instance, 'Being in body contact' is symmetrical by necessity – in the dyad A-B, A will always have the same value as B. By contrast, behaviors such as 'Approach' are directional and the frequency with which individual A approaches B is likely to differ from the frequency with which B approaches A. Therefore, for the symmetrical behaviors – spatial proximity, play bout duration and percent of total observation time spent on social play – we compiled one value per dyad. In contrast, values for the directional behaviors – initiation of brief socio-positive contacts, allo-grooming bout duration, latencies to start playing and/or grooming, percentage of total observation time spent on grooming given, and non-hostile approach – were compiled separately within each dyad for A → B and for B → A.

Dyadic values were then pooled according to predictor: (1) social group membership, or (2) deprivation history combination, respectively. For instance, to evaluate potential differences in social competence with respect to group membership, medians as well as first and third quartiles of dependent variables were calculated across all dyads in the respective social group (see Table 1).

Calculations differ for symmetrical and directional interactions. For symmetrical interactions such as proximity we pooled the dyads according to the respective predictor: social group membership, homogeneous deprivation history combination and heterogeneous deprivation history combination. For directional interactions, e.g. approach, calculations are more complicated. For predictors social group membership and homogenous deprivation history combination, all dyadic interactions were pooled (individual A → individual B and individual B → individual A). Directional interactions in heterogeneous deprivation history combinations had to be assigned to different categories, e.g. within heterogeneous dyads consisting of an ED majority and a LD minority partner, the initiative of the interaction had to be taken into account. If the initiator was the ED partner, the observation fell into the ED majority-LD minority category; if the initiator was the LD partner, the observation fell into the LD minority-ED majority category. Medians of these interactions were thus calculated per combination category.

To avoid bias from different interaction frequencies of individual dyads, we calculated medians for allo-grooming bout durations and latencies to start play and/or grooming per dyadic initiator and computed the median for the deprivation class combination and social group membership from these medians. Due to small sample size of individual latencies for social play, the latencies for allo-grooming and social play were summed up.

The number of dyads in our sample per category of deprivation history combination varied substantially from 1 to 18 dyads (ED majority-ED majority: *n* = 18, LD majority-LD majority: *n* = 10, LD minority-LD minority: *n* = 1, ED majority-LD minority: *n* = 12, LD majority-ED minority: *n* = 5). Note that for calculations of grooming bout durations, play bout durations and latencies to start play and/or grooming, only interacting individuals could be taken into account.

Normality tests and multivariate analyses were not feasible due to small sample size. Therefore non-parametric Kruskal-Wallis tests and Dunn's post hoc tests were performed to evaluate potential differences with respect to *social group membership* and between *deprivation history combinations*. Pearson's Chi-square tests were performed to find potential differences with respect to social network size. Social network size was expressed as the percent of dyads in which allo-grooming and social play was exchanged in the respective predictor category. Wilcoxon Signed Rank tests were conducted comparing data from 2004 and 2005 on stationary vicinity and close proximity within the predictor classes. The alpha level was set at 0.05 for all tests. Effect size and confidence intervals could not be calculated due to small sample sizes (with respect to deprivation history combination) and heterogeneous data (with respect to social groups).

Results

Differences in Social Competence Emerging in the First Year after Resocialization (2004 data only)

Levels of social stimulation.

Effects of social group membership. On the lowest grade of social stimulation, i.e., the *toleration of stationary vicinity*, we found significant differences between the three social groups. Dyads of the mixed-sex group 2 (MS2) significantly exceeded dyads of the all-male group (AM) in the percentage of scans during which they were observed within 5m distance from each other (see Table 2).

Significant differences between the three social groups were also apparent on the second grade of social stimulation, i.e., the median rate per hour of *initiated brief socio-positive contacts* (see Table 2). MS1 dyads had a significantly higher median rate per hour of brief socio-positive contacts than had AM dyads (see Table 2).

On the third grade of social stimulation, i.e., the *engagement in gentle social play*, the three social groups did not differ significantly with respect to their median play bout duration. However, the median percentage of time spent on social play was significantly higher in MS1 dyads compared to MS2 dyads (see Table 2 and Figure 1).

On the fourth grade, the *engagement in allo-grooming*, the three social groups did not differ with respect to median grooming bout duration (see Table 2). However, with respect to median percentage of time spent on grooming given, MS2 dyads exceeded both AM and MS1 dyads (see Table 2 and Figure 2). Moreover, members of MS2 group started a play or grooming interaction without any hesitation, i.e., significantly faster than did members of AM or MS1 group (see Table 2).

The three social groups did not differ significantly on the fifth grade of social stimulation, the *toleration of passive close proximity* (see Table 2).

Table 2

Social group differences on each level of social stimulation

Levels of social stimulation	**AM [EDs in majority] Median Q1 - Q3**	**MS1 [EDs in majority] Median Q1 - Q3**	**MS2 [LDs in majority] Median Q1 - Q3**	**Kruskal-Wallis Test**	**Dunn's Post Hoc Test**
Grade 1 – Toleration of stationary vicinity					
Stationary vicinity (Percentage of scans)	$N = 21$ 1.0% 0.2 - 3.2	$N = 10$ 2.9% 1.6 - 7.2	$N = 15$ 7.4% 2.8 - 9.3	H = 10.133 $p = 0.006$	AM vs. MS2: $p < 0.01$
Grade 2 – Initiation of brief socio-positive contacts					
Brief socio-positive contacts (Rate/hr)	*N = 42* *0.02/hr* *0.01 - 0.03*	*N = 20* *0.05/hr* *0.02 - 0.09*	*N = 30* *0.02/hr* *0.01 - 0.06*	*H = 8.491* *p = 0.014*	*AM vs. MS1:* *p < 0.05*
Grade 3 – Engagement in gentle social play					
Percentage of social play (Percent of total observation time)	$N = 21$ 0.00% 0.00 - 0.29	$N = 10$ 0.21% 0.07 - 0.42	$N = 15$ 0.00% 0.00 - 0.01	H = 10.376 $p = 0.006$	MS1 vs. MS2: $p < 0.01$
Play bout duration (Minutes)	$N = 11$ 1.7 min 0.9 - 2.0	$N = 10$ 0.6 min 0.4 - 0.8	$N = 6$ 0.6 min 0.4 - 1.2	H = 5.916 $p = 0.051$	n.s.
Grade 4 – Engagement in allo-grooming					
Percentage of grooming given (Percent of total observation time)	*N = 42* *0.00%* *0.00 - 0.02*	*N = 20* *0.00%* *0.00 - 0.04*	*N = 30* *0.16%* *0.00 - 1.42*	*H = 14.564* *p < 0.001*	*AM vs. MS2:* *p < 0.001* *MS1 vs. MS2:* *p < 0.05*
Grooming bout duration (Minutes)	*N = 17* *0.9 min* *0.3 - 1.7*	*N = 8* *1.9 min* *0.7 - 2.9*	*N = 23* *1.7 min* *0.8 - 2.7*	*H = 5.134* *n.s.*	
Latencies (Minutes)	*N = 23* *0.4 min* *0.2 - 0.5*	*N = 14* *0.2 min* *0.1 - 0.4*	*N = 21* *0.0 min* *0.0 - 0.0*	*H = 21.077* *p < 0.001*	*AM vs. MS2:* *p < 0.001* *MS1 vs. MS2:* *p < 0.01*
Grade 5 – Toleration of passive close proximity					
Close proximity (Percentage of scans)	$N = 21$ 0.1% 0.0 - 0.5	$N = 10$ 0.4% 0.1 - 0.9	$N = 15$ 1.0% 0.0 - 2.0	H = 3.992 n.s.	
Changing a social situation					
Non-hostile approach (Rate/hr)	*N = 42* *0.00/hr* *0.00 - 0.02*	*N = 20* *0.09/hr* *0.04 - 0.22*	*N =30* *0.05/hr* *0.01 - 0.16*	*H = 27.528* *p < 0.001*	*AM vs. MS1:* *p < 0.001* *AM vs. MS2:* *p < 0.001*

Sample size (N) represents number of dyadic combinations and *directions*, respectively. Abbreviations: Q1 = first quartile; Q3 = third quartile; AM = all-male; MS = mixed-sex.

Standard font = symmetrical behaviors; *italics = directional behaviors.*

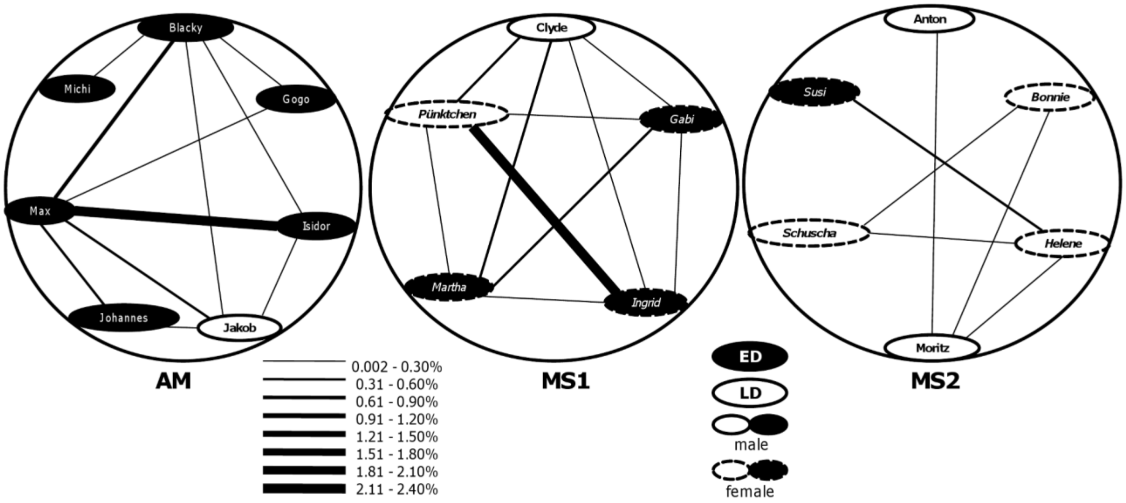

Figure 1. Dyadic social play within the three social groups. Lines represent percentage of total observation time spent on dyadic social play. Kruskal-Wallis Test: H = 10.376, *p* = 0.006; Dunn's Post Test: MS1 vs. MS2: $p < 0.01$. Abbreviations: ED/LD = early/ late deprived, AM = all-male; MS = mixed-sex.

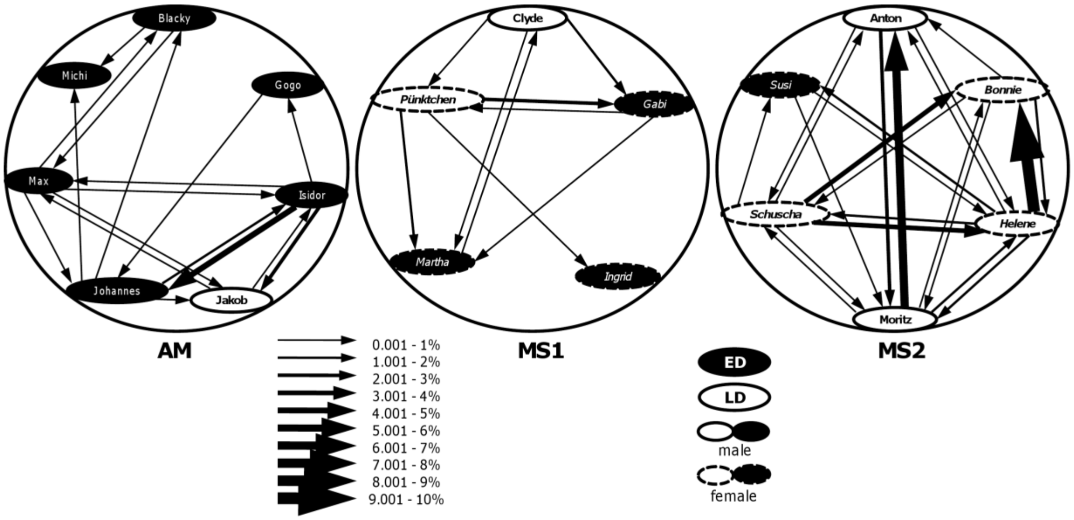

Figure 2. Grooming networks within the three social groups. Lines represent percentage of total observation time spent on grooming given. Kruskal-Wallis Test: H = 14.564, $p < 0.001$; Dunn's Post Test: AM vs. MS2: $p < 0.001$, MS1 vs. MS2: $p < 0.05$. Abbreviations: ED/LD = early/ late deprived, AM = all-male; MS = mixed-sex.

Effects of deprivation history combination. The *toleration of stationary vicinity* differed significantly between the deprivation history combinations. Dyads consisting of two EDs out of an ED majority were significantly less often within 5 m distance than were dyads consisting of two LDs out of an LD majority (see Table 3).

Deprivation history combination had no significant effect on the second grade of social stimulation, the *initiation of brief socio-positive contacts* (see Table 3).

Likewise, on the third grade of social stimulation, *engagement in gentle social play*, deprivation history combinations differed neither in play bout duration nor in their percentage of time spent on gentle play, even though gentle play was most common in dyads containing one or two LD(s) out of an LD minority (see Table 3).

With respect to the *engagement in allo-grooming,* the predictor deprivation history combination revealed no differences in overall grooming bout duration (see Table 3), but LD maj-LD maj dyads significantly exceeded ED maj-ED maj, ED maj-LD min, and ED min-LD maj dyads in their median percentage of time spent on grooming given (see Table 3). Moreover, ED maj-ED maj and LD min-ED maj dyads hesitated significantly longer before they started gentle play and/or allo-grooming than did LD maj-LD maj dyads (see Table 3). Deprivation history combination significantly affected the fifth grade of social stimulation, *toleration of passive close proximity*: LD maj-LD maj dyads were significantly more often in close proximity than were either ED maj-ED maj or ED min-LD maj dyads (see Table 3).

In sum, on the first grade of social stimulation, toleration of stationary vicinity, the three social groups differed, with the ED-dominated AM group being least and the LD dominated MS2 group being most tolerant of a group member's presence within 5m distance (Figure 3, top row). These group differences were reflected by a significant difference between deprivation history combinations in that homogeneous LD-majority dyads were most tolerant and homogeneous ED majority dyads were least tolerant. On grade 2, brief socio-positive contacts were observed most frequently in the MS1 group. Contrary to expectation the LD-dominated MS2 group did not differ from the ED-dominated AM or MS1 group.

Gentle social play, grade 3, was observed most often in the MS1 group (Figure 1). These findings are reflected in extraordinary amounts of play among LD and ED chimpanzees in the groups with an ED majority.

Allo-grooming, grade 4, was most problematic for members of the AM group. They almost never groomed, and had the shortest grooming bout lengths and the longest hesitation to start grooming. The MS1 group was overall intermediate in allo-grooming between the AM and MS2 groups. From the perspective of deprivation history combination, it became evident that ED chimpanzees essentially did not groom, irrespective of the deprivation history of their available partners or their group's majority. Grooming was the domain of the LD chimpanzees. This is most evident in the group with LD majority; but even in minority, LDs directed grooming at unreciprocating ED group members (Figure 2) and even adjusted to the EDs' hesitation to start engaging in socio-positive interactions by exhibiting the long latencies preferred by the ED chimpanzees.

The highest grade of social competence reached by any chimpanzees in this population was grade 5, toleration of passive close proximity. The non-significant tendency of the MS2 group to be most tolerant of a group member within an arm's reach (Figure 4, top row) became explicable from the perspective of deprivation history combination. LD chimpanzees in majority were clearly most often in proximity of each other, and LDs in minority were unable to achieve similar rates with their avoidant ED majority partners.

Changing the level of social stimulation/initiative to change a social situation.

Effects of social group membership. Non-hostile approaches occurred significantly less often in AM dyads compared to MS1 and MS2 dyads (see Table 2).

Effects of deprivation history combination. With respect to the median rate per hour of *non-hostile approaches*, LD maj-LD maj dyads and LD min-ED maj dyads significantly exceeded ED maj-ED maj dyads and ED min-LD maj dyads (see Table 3).

Thus, non-hostile approaches clearly were employed only by LD chimpanzees and EDs almost never approached group members, irrespective of the available partners' deprivation history.

Social network size.

Effects of social group membership. Differences in the social network size, i.e., the percentage of dyads in which social play and allo-grooming occurred, respectively, became apparent between the three social groups. Play behavior occurred in all 10 dyads of the MS1 group (100%); it was performed in only 53% of the dyads (11 out of 21) of the AM group and in only 40% (6 out of 15) of the dyads of the MS2 group ($\chi^2 = 87.500$, $df = 2$, $p < 0.001$). Allo-grooming, on the other hand, occurred most frequently in the MS2 group dyads (77%, i.e., 23 out of 30), and only in 40% of the AM group dyads (17 out of 42) and the MS1 group dyads (8 out of 20; $\chi^2 = 36.586$, $df = 2$, $p < 0.001$).

Effects of deprivation history combination. Network size for gentle play differed significantly between deprivation history combinations ($\chi^2 = 162.185$, $df = 4$, $p < 0.001$). The largest play networks were found among LD min-ED maj dyads (83%, 10 of 12), and the only LD min-LD min dyad also played frequently. This was followed by ED maj-ED maj dyads (56%, i.e., 10 of 18) and LD maj-LD maj dyads (50%, i.e., 5 of 10). LD maj-ED min dyads had the smallest "network" with 1 of 5 dyads (i.e., 20%).

Likewise, grooming network size differed significantly between deprivation history combinations ($\chi^2 = 105.369$, $df = 6$, $p < 0.001$). The most expanded grooming network was found between LD maj-LD maj dyads (95%, i.e., 19 out of 20). ED maj-ED maj dyads, by contrast, maintained the smallest grooming networks (33%, i.e., 12 out of 36). All other combinations were intermediate (LD min-LD min: 50%; ED maj-LD min: 42%, LD min-ED maj: 58%, LD maj-ED min: 40%, ED min-LD maj: 40%).

In sum, the differences in network size between social groups are based on the differences between deprivation history combinations. Homogeneous LD-majority dyads had the largest grooming networks and homogeneous ED-majority dyads had the smallest. Heterogeneous combinations, i.e., the LD-minority combinations, had intermediate grooming network sizes. However, LD chimpanzees in minority had by far the largest gentle play networks of all, and thus differed from the homogeneous LD maj-LD maj and ED maj-ED maj combinations.

Development of Social Competence (2004 and 2005 data)

To examine possible improvements in social competence we compared the toleration of stationary vicinity and that of passive close proximity, i.e., the lowest and the highest grades of social stimulation, between the first and second year of group living.

Stationary vicinity.

Effects of social group membership. From 2004 to 2005, dyads of the MS2 group significantly increased their percent of scans spent within 5m distance (*n* = 15; 2004: median ± Q1, Q3 = 7.4% ± 2.0, 10.0; 2005: median ± Q1, Q3 = 25.0% ± 3.8, 32.6; Z = -2.897, *p* = 0.002; see Figure 3). The same was true for dyads of the MS1 group (*n* = 10; 2004: median ± Q1, Q3 = 2.9% ± 1.4, 8.7; 2005: median ± Q1, Q3 = 13.2% ± 8.2, 21.1; Z = -2.803, *p* = 0.002), but not for dyads of the AM group (*n* = 21; 2004: median ± Q1, Q3 = 1.0% ± 0.2, 3.2; 2005: median ± Q1, Q3 = 2.0% ± 0.4, 4.4; Z = -1.199, n.s.; see Figure 3).

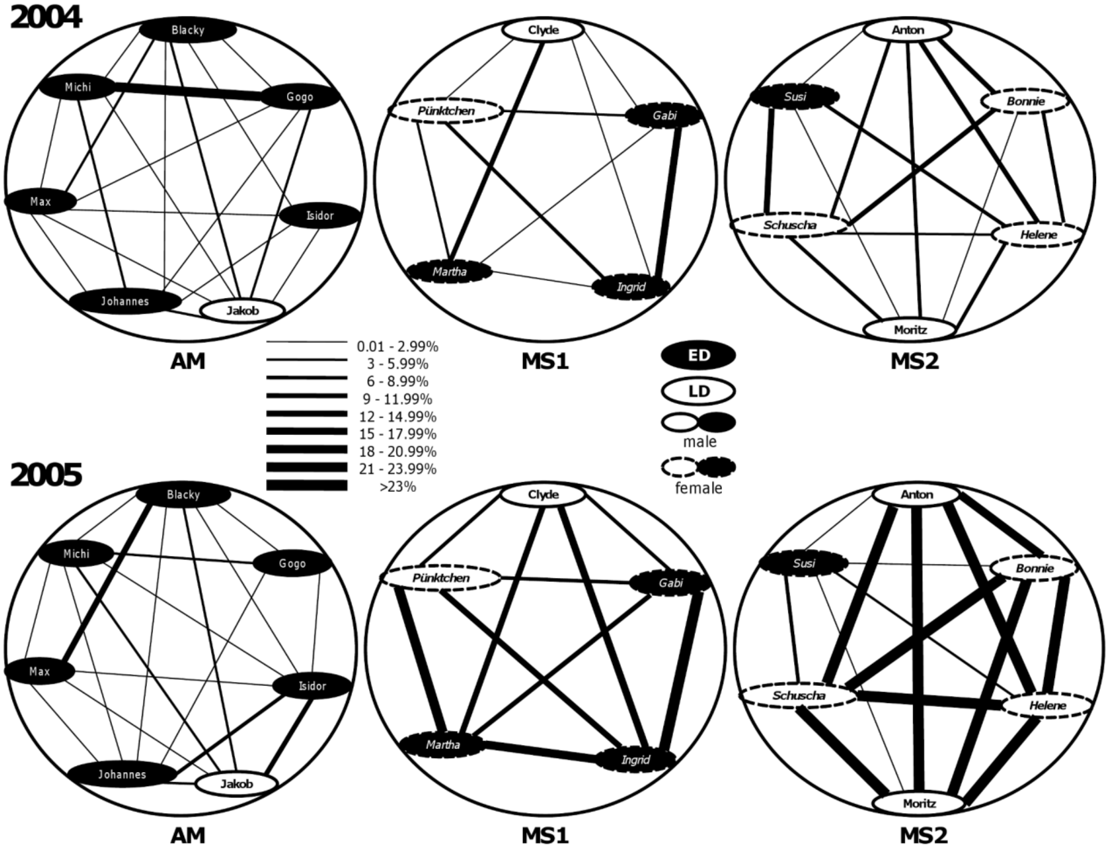

Figure 3. Development of stationary vicinity within the three social groups. Lines represent percent of scans spent within 5m distance to group members. Wilcoxon Signed Rank Test: AM 2004 vs. 2005: Z = 1.199, n.s.; MS1 2004 vs. 2005: Z = -2.803, *p* = 0.002; MS2 2004 vs. 2005: Z = -2.897, *p* = 0.002. Abbreviations: ED/LD = early/ late deprived, AM = all-male; MS = mixed-sex.

Table 3

Deprivation history combination differences on each level of social stimulation

	ED maj-ED maj	**ED maj-LD min**		**LD maj-ED min**		**LD maj-LD maj**	**LD min-LD min**		
Levels of social stimulation	***EDmaj◄►EDmaj*** **Median Q1 - Q3**	***EDmaj►LDmin*** **Median Q1 - Q3**	***LDmin►EDmaj*** **Median Q1 - Q3**	***LDmaj◄►LDmaj*** **Median Q1 - Q3**	***LDmin◄►LDmin*** **Median Q1 - Q3**	***LDmaj◄►LDmaj*** **Median Q1 - Q3**	***LDmin◄►LDmin*** **Median Q1 - Q3**	**Kruskal-Wallis Test**	**Dunn's Post Hoc Test**
Grade 1 – Toleration of stationary vicinity									
Stationary vicinity (Percentage of scans)	$N = 18$ 1.5% 0.2 - 2.5	$N = 12$ 3.2% 0.9 - 3.8		$N = 5$ 2.0% 0.4 - 7.8		$N = 10$ 7.4% 6.2 - 9.6	$N = 1$ 0.5%	H = 11.052 $p = 0.026$	EDmaj-EDmaj vs. LDmaj-LDmaj: $p < 0.05$
Grade 2 – Initiation of brief socio-positive contacts									
Brief socio-positive contacts (Rate/hr)	$N = 36$ *0.01/hr* *0.01 - 0.04*	$N = 12$ *0.02/hr* *0.01 - 0.05*	$N = 12$ *0.03/hr* *0.02 - 0.09*	$N = 5$ *0.02/hr* *0.01 - 0.02*	$N = 5$ *0.03/hr* *0.01 - 0.05*	$N = 20$ *0.03/hr* *0.02 - 0.07*	$N = 2$ *0.09/hr* *0.09 - 0.09*	*H = 8.656* *n.s.*	
Grade 3 – Engagement in gentle social play									
Percentage of social play (Percent of total observation time)	$N = 18$ 0.00% 0.00 - 0.03	$N = 12$ 0.21% 0.08 - 0.37		$N = 5$ 0.00% 0.00 - 0.00		$N = 10$ 0.00% 0.00 - 0.01	$N = 1$ 0.43%	H = 10.270 $p = 0.036$	n.s
Play bout duration (Minutes)	$N = 10$ 0.7 min 0.6 - 1.8	$N = 10$ 1.0 min 0.5 - 1.6		$N = 1$ 1.6 min		$N = 5$ 0.4 min 0.4 - 0.8	$N = 1$ 0.5 min	H = 2.623 n.s.	
Grade 4 – Engagement in allo-grooming									
Percentage of grooming given (Percent of total observation time)	$N = 36$ *0.00%* *0.00 - 0.01*	$N = 12$ *0.00%* *0.00 - 0.04*	$N = 12$ *0.01%* *0.00 - 0.81*	$N = 5$ *0.00%* *0.00 - 0.12*	$N = 5$ *0.00%* *0.00 - 0.00*	$N = 20$ *0.74%* *0.12 - 1.92*	$N = 2$ *0.02%* *0.01 - 0.03*	*H = 30.582* $p < 0.001$	*EDmaj-EDmaj vs. LDmaj-LDmaj:* $p < 0.001$ *EDmaj-LDmin vs. LDmaj-LDmaj:* $p < 0.05$ *EDmin-LDmaj vs. LDmaj-LDmaj:* $p < 0.05$

Grooming bout duration (Minutes)	*$N = 12$ 0.9 min 0.4 - 1.4*	*$N = 5$ 1.3 min 0.9 - 1.9*	*$N = 7$ 1.7 min 0.8 - 2.7*	*$N = 2$ 1.4 min 1.2 - 1.5*	*$N = 2$ 0.5 min 0.3 - 0.7*	*$N = 19$ 1.8 min 0.8 - 3.1*	*$N = 1$ 3.1 min*	*$H = 9.661$ n.s.*	
Latencies (Minutes)	*$N = 19$ 0.4 min 0.1 - 0.6*	*$N = 8$ 0.2 min 0.1 - 0.3*	*$N = 8$ 0.3 min 0.1 - 0.5*	*$N = 2$ 0.0 min 0.0 - 0.0*	*$N = 1$ 0.5 min*	*$N = 18$ 0.0 min 0.0 - 0.0*	*$N = 2$ 0.1 min 0.0 - 0.1*	*$H = 26.109$ $p < 0.001$*	*EDmaj-EDmaj vs. LDmaj-LDmaj: $p < 0.001$ LDmin-EDmaj vs. LDmaj-LDmaj: $p < 0.05$*
Grade 5 - Toleration of passive close proximity									
Close proximity (Percentage of scans)	$N = 18$ 0.1% 0.0 - 0.4	$N = 12$ 0.5% 0.1 - 1.0		$N = 5$ 0.0% 0.0 - 0.0		$N = 10$ 1.6% 0.8 - 2.4	$N = 1$ 0.2%	$H = 14.139$ $p = 0.007$	EDmaj-EDmaj vs. LDmaj-LDmaj: $p < 0.05$ EDmin-LDmaj vs. LDmaj-LDmaj: $p < 0.05$
Changing a social situation									
Non-hostile approach (Rate/hr)	*$N = 36$ 0.00/hr 0.00 - 0.02*	*$N = 12$ 0.03/hr 0.02 - 0.07*	*$N = 12$ 0.15/hr 0.01 - 0.25*	*$N = 5$ 0.01/hr 0.00 - 0.05*	*$N = 5$ 0.00/hr 0.00 - 0.00*	*$N = 20$ 0.10/hr 0.05 - 0.20*	*$N = 2$ 0.19/hr 0.13 - 0.25*	*$H = 38.630$ $p < 0.001$*	*EDmaj-EDmaj vs. LDmin-EDmaj: $p < 0.05$ EDmaj-EDmaj vs. LDmaj-LDmaj: $p < 0.001$ EDmin-LDmaj vs. LDmaj-LDmaj: $p < 0.05$*

Sample size (N) represents number of dyadic combinations and *directions*, respectively. Abbreviations: Q1 = first quartile; Q3 = third quartile; ED/LD = early/late deprived; maj = majority; min = minority.
Standard font = symmetrical behaviors; *italics = directional behaviors*.

Effects of deprivation history combination. LD maj-LD maj dyads significantly increased their time spent in the vicinity of conspecifics (*n* = 10; 2004: median ± Q1, Q3 = 7.4% ± 5.6, 10.1; 2005: median ± Q1, Q3 = 29.5% ± 24.7, 34.6; Z = -2.805, *p* = 0.002). This was paralleled by a dramatic increase in the one LD min-LD min dyad (2004: 0.5%; 2005: 6.9%). By contrast, values of ED chimpanzees remained about the same (in ED maj-ED maj combinations: *n* = 18, 2004: median ± Q1, Q3 = 1.5% ± 0.2, 2.8, 2005: median ± Q1, Q3 = 2.1% ± 0.5, 7.4; Z = -1.502, n.s.; and in ED min-LD maj dyads: *n* = 5; 2004: median ± Q1, Q3 = 2.0% ± 0.2, 10.9; 2005: median ± Q1, Q3 = 2.6% ± 2.1, 6.1; Z = -0.405, n.s.), except when their partners were LDs in minority, in which case their time in vicinity significantly increased (ED maj-LD min: *n* = 12; 2004: median ± Q1, Q3 = 3.2% ± 0.9, 4.6; 2005: median ± Q1, Q3 = 7.3% ± 4.0, 13.7; Z = -2.589, *p* = 0.007).

Close proximity.

Effects of social group membership. From 2004 to 2005, dyads of the MS2 group significantly increased their time spent within an arm's reach of a group member (*n* = 15; 2004: median ± Q1, Q3 = 1.0% ± 0.0, 2.1; 2005: median ± Q1, Q3 = 3.4% ± 0.4, 5.8; Z = -2.062, *p* = 0.038). By contrast, values of neither the dyads of the MS1 group (*n* = 10; 2004: median ± Q1, Q3 = 0.4% ± 0.1, 1.0; 2005: median ± Q1, Q3 = 0.4% ± 0.0, 0.5; Z = -0.459, n.s.) nor those of the AM group changed significantly (*n* = 21; 2004: median ± Q1, Q3 = 0.1% ± 0.0, 0.5; 2005: median ± Q1, Q3 = 0.0% ± 0.0, 0.1; Z = -1.790, n.s.; see Figure 4).

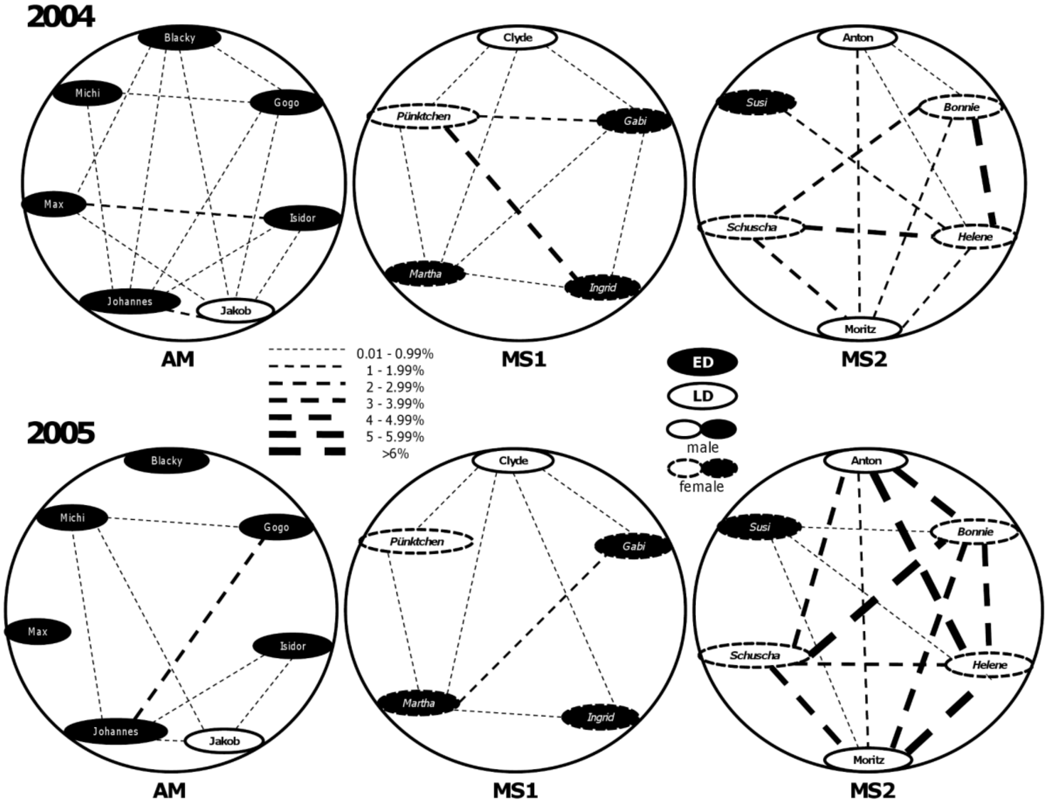

Figure 4. Development of close proximity within the three social groups. Lines represent percent of scans spent within an arm's reach of group members. Wilcoxon Signed Rank Test: AM 2004 vs. 2005: Z = -1.790, n.s.; MS1 2004 vs. 2005: Z = -0.459, n.s.; MS2 2004 vs. 2005: Z = -2.062, *p* = 0.038. Abbreviations: ED/LD = early/ late deprived, AM = all-male; MS = mixed-sex.

Effects of deprivation history combination. LD maj-LD maj dyads significantly increased their time spent in close proximity (*n* = 10; 2004: median ± Q1, Q3 = 1.6% ± 0.6, 2.7; 2005: median ± Q1, Q3 = 4.6% ± 3.2, 10.3; Z = -2.191, *p* = 0.027), and the one LD min-LD min dyad also improved (2004: 0.2%; 2005: 0.9%). No other deprivation history combination showed a significant improvement over the first two years of group living (ED min-LD maj dyads: *n* = 5; 2004: median ± Q1, Q3 = 0.0% ± 0.0, 0.5; 2005: median ± Q1, Q3 = 0.4% ± 0.0, 0.6; Z = -1.089, n.s.). In fact, the rest slightly declined (ED maj-ED maj dyads: *n* = 18, 2004: median ± Q1, Q3 = 0.1% ± 0.0, 0.4, 2005: median ± Q1, Q3 = 0.0% ± 0.0, 0.2; Z = -0.978, n.s.; ED maj-LD min dyads: *n* = 12, 2004: median ± Q1, Q3 = 0.5% ± 0.1, 1.1, 2005: median ± Q1, Q3 = 0.3% ± 0.0, 0.4; Z = -1.648, n.s.) and the variances between dyads stabilized on the low level of proximity tolerance.

Discussion

Group Differences

The two groups dominated by early deprived (ED) chimpanzees – the all-male group (AM) and the one-male mixed-sex group (MS1) – were characterized by a lower stimulation tolerance than the two-male mixed-sex group (MS2) which is dominated by late deprived (LD) individuals. Thus, our findings supported our hypothesis that the security-to-stimulation balance preferred by the group majority would set the tone for interactions within the group. From the first grade of social stimulation onward, we found significant differences between the social groups. This shows that the relational definition of social competence is more sensitive to systematic differences than is the individual attribute definition. In terms of toleration of stationary vicinity (grade 1), latency to start a socio-positive interaction (grades 3/4), time spent allo-grooming (grade 4), and toleration of passive close proximity (grade 5), the LD-dominated MS2 group exhibited the highest social competence. The MS2 group also formed the most tightly knit grooming network. Over the course of the first two years after re-socialization, the MS2 group dramatically increased in cohesiveness, showing a significant increase of time spent in 5m-vicinity and in close proximity of each other. For most of these indicators, the ED-dominated AM group differed most profoundly from the LD-dominated MS2 group. Yet, there were also differences between groups, notably between the ED-dominated groups, AM and MS1, which indicated additional complexities.

Immersion Effects: Deprivation History Combination

In line with our expectations, we found the homogeneous ED-majority dyads (ED maj-ED maj) to exhibit the least social competence: In comparison with homogeneous LD-majority dyads (LD maj-LD maj) they were significantly less tolerant of stationary vicinity (grade 1), more hesitant to start socio-positive interactions (grades 3/4), spent less time engaged in allo-grooming (grade 4), and were less tolerant of each other within an arm's reach (grade 5). They developed no grooming networks, initiated non-hostile contacts significantly less often, and remained intolerant of each other in either an arm's reach or 5m distance during the first two years of group life.

These results indicate that, relative to their own preferences the chimpanzees immersed in an "alien" majority were confronted with either an over-stimulating (EDs in minority) or under-stimulating (LDs in minority) social environment, respectively.

LDs in minority: Coping with social under-stimulation. Three LD chimpanzees were immersed in an ED-majority: male Jakob in the AM group, and male Clyde and female Puenktchen in MS1 group. LD minority-ED majority dyads were intermediate between homogeneous ED-majority dyads and homogeneous LD-majority dyads, with respect to the toleration of 5m-vicinity (grade 1), latency to start socio-positive interaction (grades 3/4), toleration of close proximity (grade 5), non-hostile approaches, grooming network size, and improvement of their toleration of 5m-vicinity over the first two years of group living. This suggests that with respect to these forms of interaction, LD-minority chimpanzees found a compromise between what we might expect to be their genuine stimulation preference as represented by the behavior of the homogeneous LD-majority dyads and the limitations of their ED-majority group mates. That the only LD-minority dyad exhibited remarkably low values with respect to the toleration of stationary vicinity, percentage of grooming given and the toleration of passive close proximity may be due to the fact that this dyad contained a male and a female chimpanzee. We found similarly low values in the LD-dominated MS2 group between the two LD males and some, but not all, LD females. However, the LD-minority dyad exhibited its potential to behave socially competent by increasing the toleration of stationary vicinity and that of passive close proximity from the first to the second year of group living.

The behavior of the LD chimpanzees immersed in an ED majority explained many of the peculiarities found for MS1 group. Surprisingly, MS1 group had the highest values for brief socio-positive contacts (grade 2), time spent with gentle play (grade 3) and for non-hostile approaches. Members of this group also dramatically improved their toleration of others in 5m-vicinity over the first two years, but did not improve their tolerance for passive close proximity. LD-minority chimpanzees briefly contacted each other as well as ED-majority group members as often as did LDs in majority contact each other, and ED-majority group members briefly contacted LD-minority chimpanzees almost as frequently. For brief, friendly interactions the limited stimulation tolerance of ED-majority chimpanzees therefore does not seem to be an obstacle, but amongst each other they seem unable to overcome their inhibition.

The MS1 group spent more time in gentle play than any other group. When comparing the medians of the percentage of time spent on gentle social play between deprivation history combinations, the homogeneous LD-minority dyad (Puenktchen and Clyde) was leading, and the LD min-ED maj dyads rated second. The highest values, however, were reached by an LD minority-ED majority dyad in the MS1 group and a homogeneous ED-majority dyad in the AM group who spent 2.31 and 2.20 percent of time in social play, respectively. LD-minority chimpanzees also had the most extensive play networks. However, time spent allo-grooming was minimal for LD minority-ED majority dyads, indicating that the inability of ED group members to sustain grooming interactions hindered the LD-minority chimpanzees from engaging in a species-typical and even order-typical (Goosen, 1987) interaction that was well within the competence of their LD-majority peers. Taken together with gentle play, it appears as if the LD-minority chimpanzees were able to compensate for the lack of grooming interactions by increasing the time they spent with gentle play, both among each other, but especially with their ED-majority group mates, as well. The compensatory relationship between grooming and gentle play also explains why the pattern of association between grades 3 and 4 and deprivation history is somewhat unclear.

With respect to resting in an arm's reach of group members, LD-minority chimpanzees were again handicapped by the avoidant behavior of their ED-majority group mates. And, in contrast to the toleration of 5m-vicinity, this did not improve over the second year of group life. That LD-minority chimpanzees worked hard to initiate contacts is evident from their non-hostile approaches. LD-minority chimpanzees approached each other and their ED-majority group mates more than 50% more frequently than did LD-majority chimpanzees.

EDs in minority: Coping with social over-stimulation. The only ED chimpanzee who represented a minority in her own group, Susi, appeared rigidly intolerant of social stimulation. On all 5 grades of social stimulation she had a similar range as the homogeneous ED-majority dyads. Like the ED-majority chimpanzees, Susi hardly ever changed a social situation by approaching. She rarely engaged in play or grooming interactions, and thus did not compensate her limited grooming network with a playing network. In addition, her toleration of group members in 5m or within an arm's distance did not increase over the two years of group living.

Comparisons with Socially Raised Chimpanzees

Although relational data on other chimpanzees are rare and comparisons are affected by differences in group composition, methodology etc. (and for free-living chimpanzees by ecological constraints), it seems important to contrast the behavior of our chimpanzees with that of subjects without the experience of long-term deprivation. Social play is rare among adult chimpanzees in captivity (Palagi, 2006) and in the wild (Goodall, 1986). Similarly, gentle social play was performed infrequently by most of our chimpanzees, although all subjects entertained play relationships with at least one other group member. However, while in adult chimpanzees social play usually is replaced by social grooming (Goodall, 1986), this is only true for our LD-majority chimpanzees, not for ED chimpanzees, irrespective of their partner's social competence. And LDs in minority seem to adapt to this deficit of ED chimpanzees by increasing the amount of social play with their ED group mates.

The median grooming bout duration of the different deprivation history combinations of our study population ranged from 0.5 to 1.8 minutes. By comparison, grooming bouts of free chimpanzees lasted on average 3.1 minutes (Lehmann & Boesch, 2008). But while the homogeneous LD-minority dyad as well as the homogeneous LD-majority dyads were able to achieve similar durations (as indicated by the third quartiles for LD-majority dyads), values of EDs irrespective of the groomee's deprivation history resembled those of juvenile chimpanzees (Nishida, 1988).

The mean dyadic association indices of free chimpanzees vary between 12% (Gombe and Kibale) and 19% (Tai; reviewed in Boesch & Boesch-Achermann, 2000). We calculated a comparable association index by incorporating median values for stationary vicinity, percent of time spent on social play, percent of time spent on grooming given and received, and passive close proximity per deprivation history combination. Values ranged from only 1.6% for ED-majority dyads to 10.5% for LD-majority dyads. Heterogeneous EDmaj-LDmin dyads remained in between by spending 3.9% of observation time associated; hence, all our chimpanzees spent less time associated compared to free chimpanzees. Unfortunately, comparable data on captive chimpanzees are not available. However, LD-majority dyads improved their social competence by significantly increasing their toleration of stationary vicinity and that of passive close proximity in the second year of group living. This suggests that at least LDs in majority seem to be able to partially overcome the detrimental effects of long-lasting social deprivation.

Conclusion

In summary, the relational approach revealed systematic differences in the toleration of social stimulation between ED and LD chimpanzees, most obviously an inability of ED chimpanzees to adjust their stimulation toleration to the preference of their social partners. LDs, in contrast to EDs, were able to attune their stimulation toleration to that of the majority of group members, apparent in the different stimulation thresholds of LD-minority and LD-majority chimpanzees. Therefore social recovery was most successful in LD-LD combinations out of a LD majority.

The rigidity of ED chimpanzees in terms of toleration of social stimulation is likely caused by insufficient experience of psychobiological attunement; this is a result of their social and notably maternal deprivation in early infancy, as the experience of psychobiological attunement is generally provided by a supportive primary attachment figure. In mammals, an insecure or inhibited attachment is assumed to affect neuroception, reflected in the inability to perceive an environment as safe and interactions as thrust-worthy (Porges, 2003). Moreover, complex childhood trauma has similar long-lasting outcomes in terms of interpersonal difficulties and impaired social adjustment in chimpanzees (Bradshaw, Capaldo, Lindner, & Grow, 2008) and humans (Cloitre, Miranda, Stovall-McClough, & Han, 2005). Thus, the varying stimulation thresholds of ED and LD chimpanzees confirmed Field's (1985) assumption that an individual's optimal stimulation threshold in adulthood depends on the amounts of stimulation and arousal modulation received during early infancy and that the loss of an arousal-reducing primary attachment figure results in poor social adjustment. Comparable studies on adult humans are lacking so far; however, adolescent Romanian adoptees who had been institution-reared during the sensitive period of attachment formation had substantial social impairments by ages 6 and 11, respectively (Kreppner et al., 2007). An individual's stimulation threshold in turn will affect his or her compatibility with social partners because physical contact is such an important communication channel among apes (Hertenstein, Verkamp, Kerestes, & Holmes, 2006). This is evident in our LD chimpanzees who represented the minority within their social groups and were under-stimulated by their ED companions, as well as in the only ED subject who was immersed in an LD majority and appeared to be overtaxed by the social stimulation of LD individuals. For this reason, we strongly suggest considering the individuals' rearing histories in selecting social partners for chimpanzees in human care, as social compatibility plays a key role for wellbeing in chimpanzees (Cords & Aureli, 2000; Fraser, Schino, & Aureli, 2008). Our results indicate that degrees and timing of species-inappropriate management conditions have a lasting effect on social competence. Moreover, the formation of new social groups out of (formerly) deprived chimpanzees and normally socialized conspecifics must be understood as potentially risky and may seriously compromise the wellbeing of the deprived chimpanzees, especially if the "normal" ones are in the majority. Based on our findings we predict that the introduction of deprived chimpanzees into existing groups of normally socialized conspecifics will succeed only under specific circumstances, e.g., reliable protection of the deprived chimpanzee by a dominant group member.

In conclusion, our findings suggest that the relational approach leads to a more dynamic understanding of social competence than does an individual-attributes approach and thus offers new possibilities for therapeutic application. Instead of only looking backwards at the etiology of bonding disorders, an understanding of social competence as the capacity to attune one's behavior to that of another, which depends on the bonding experiences of each partner, allows us to deduce social scenarios in which a problematic individual can learn to cope better and to predict social combinations in which behavioral deficiencies will be exacerbated.

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