Social Competence of Adult Chimpanzees (Pan troglodytes) With Severe Deprivation History: I. An Individual Approach

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In highly social mammals, including humans, group living requires the capability to establish and maintain social relationships, to seek and tolerate the company of conspecifics, and to cope with unpredictable and possibly stressful social events. This ability is often termed social competence (reviewed in Rose-Krasnor, 1997) and is reflected in the performance of species-appropriate social behavior.

Wild chimpanzees are among the primates with the most complex social behavior, probably because of the complex fission-fusion structure of their societies. Group members of a certain community (ranging in number from 10 to 80 individuals) travel, forage, and rest in constantly changing subgroups (reviewed in Boesch & Boesch-Achermann, 2000). Whereas males usually remain in their natal community, females disperse to other groups as adolescents (Goodall, 1986). As a result, male chimpanzees are more strongly associated with one another than with females and are more strongly associated than are females with one another (Boesch & Boesch-Achermann, 2000; Goodall, 1986). A further characteristic of chimpanzees is their prolonged dependency on the mother as their primary attachment figure, evident in behavioral disturbances caused by the disruption of mother–infant bonds (Goodall, 1986).

In humans the sensitive period for attachment formation between an infant and its caregiver ranges from six to 36 months of age (Bowlby, 1969/1982). The formation of a secure socioemotional bond is reliant on the presence of a sensitive, supportive primary attachment figure meeting the infant’s needs and demands (Ainsworth, Blehar, Waters, & Wall, 1978; Bowlby, 1969/1982, 1973). A secure attachment, in turn, is crucial for a normal social development (i.e., to behave in a socially competent manner later on; Bowlby, 1969/1982, 1973). If, by contrast, the infant’s needs and the responsiveness of the primary attachment figure are mismatched, the outcome is the formation of an insecure attachment, classified as either insecure-avoidant if the caregiver is rejecting or insecure-resistant if the caregiver is inconsistent (Ainsworth et al., 1978). An infant experiencing maltreatment and neglect may develop an insecure-disorganized attachment style, identifiable by confused and stereotyped behaviors of the infant (Main & Solomon, 1990), as documented for neglected infants raised in Russian, Greek, or Romanian orphanages (Muhamedrahimov, Nikiforova, Palmov, Groark, & McCall, 2008; Vorria et al., 2003; Zeanah, Szyme, Koga, Carlson, & the BEIP Core Group, 2005). Early traumatic experience, including parental loss, is a significant factor for the development of psychopathologies apparent in particular in...
the debilitated capacities of establishing and maintaining relationships, of coping with stressful stimuli and in emotion regulation later in life (Breier et al., 1988; Schore, 2001). The different patterns of attachment are usually persistent from infancy to adulthood (Grossmann, Grossman, & Kindler, 2005; Main, Hesse, & Kaplan, 2005; Sroufe, 2005; Sroufe, Egeland, Carlson, & Collins, 2005) mirrored in distinctive social and emotional capacities indicating differences in social competence. Moreover, an extremely adverse early environment in terms of severe deprivation may cause a reactive attachment disorder (RAD), defined as exhibiting only minimal or no attachment behavior at all (World Health Organization, 2007), and characterized by emotional withdrawal and unresponsiveness (Zeanah & Smyke, 2008).

Bowlby’s (1969/1982) assumption that the attachment system represents a phylogenetic adaptation was confirmed by several empirical studies on monkeys and apes (e.g., Harlow & Harlow, 1962; Hinde & Spencer-Booth, 1967; Kondo-Ikemura & Waters, 1995; Reite & Capitiano, 1985; Schino & Troisi, 2001; van Ijzendoom, Bard, Bakermans-Kranenburg, & Ivan, 2009; Weaver & de Waal, 2002). Mother–infant attachment in chimpanzees, as indicated by an increase in exploratory behavior with the mother serving as a secure base, is established at around 4 to 6 months of age (Tomonaga, 2006). Numerous studies on primates highlight the significance of social experience during infancy and the detrimental short-term effects of social separation and deprivation on social behavior (e.g., Bastian, Sponberg, Suomi, & Higley, 2003; Harlow, Dodsworth, & Harlow, 1965; Harlow & Harlow, 1962; Harlow & Suomi, 1971; Kemptes, Gulickx, van Daalen, Louwerve, & Sterck, 2003; Mason, Davenport, & Menzel, 1968; Sackett, Holm, & Ruppenthal, 1976; Suomi & Harlow, 1975). Studies on long-term effects reaching into adulthood, however, are rare. Among wild elephants, for example, the devastating effects of attachment disruption in early infancy were found to persist into adulthood (Bradshaw & Schore, 2007). Furthermore, maternal and/or social deprivation among other factors can lead to the development of stereotyped behaviors in primates especially (e.g., Berksoc, 1968; Berksoc & Mason, 1964; Harlow & Harlow, 1962; Latham & Mason, 2008; Mason, 1968; Mason et al., 1968; Pazol & Bloomsmith, 1993; Walsh, Bramblett, & Alford, 1982). Raising infant chimpanzees under conditions of extreme deprivation results in high incidence of attachment disorganization (van Ijzendoom et al., 2009), similar to that of humans raised in orphanages (Muhamedrahimov et al., 2008; Vorria et al., 2003; Zeanah et al., 2005). Hence, the impact of early trauma on the development of psychopathologies in nonhuman primates (Briët, Briët-Cohrs, McGrew, & Preuschoft, 2006; Coplan et al., 1996; Sánchez, 2006) is comparable to that in human primates, although the crucial dimensions of early experience have not yet been precisely identified in either humans or apes.

The rehabilitation of ex-laboratory chimpanzees at Gaensern-dorf, Austria, provided us with the unique opportunity to assess long-term effects of severe and prolonged social deprivation in adult chimpanzees. We investigated this population in their first and second years following resocialization, 18–28 years after the chimpanzees’ arrival at the laboratory. The chimpanzees, deprived for more than 16 years, could be classified as either early deprived (ED) or late deprived (LD), according to their age at onset of infantile deprivation. Based on chimpanzees’ life span and physical development, it is generally assumed that their ontogenetic development proceeds 1.5 times faster than that of humans (Murai, 2006). Accordingly, the sensitive period for attachment formation in chimpanzees is expected to be terminated at around 24 months of age. Evidence for this assumption is provided by tests on stranger anxiety (Miller, Bard, Juno, & Nadler, 1990). Hence, for ED chimpanzees (M age = 1.2 ± 0.4 years at onset of deprivation), attachment disruption and social deprivation started within the sensitive period of attachment formation; for LD chimpanzees (M age = 3.6 ± 0.5 years at onset of deprivation), on the other hand, deprivation started after this sensitive period.

In previous studies on this population of former biomedical research chimpanzees, we found that the age at onset of deprivation, but not years spent in deprivation or individual’s current age, predicted differential responses to novelty, stress coping, and social adjustment (Kalcher, Franz, Crailshiem, & Preuschoft, 2008; Reimers, Schwanzenberger, & Preuschoft, 2007). More specifically, ED chimpanzees responded timidly to nonsocial novelty comparable to the behavior of socially restricted nursery reared infant chimpanzees (Mason et al., 1968; Menzel, Davenport, & Rogers, 1963). Furthermore, EDs experienced more stress in a novel environment, showed more nonsocial idiosyncrasies, and were less engaged in social interactions in the first months following resocialization. By comparison, LD chimpanzees were bolder, recovered from nonsocial stress more rapidly, experienced the resocialization as eustress, and exhibited an eagerness to engage in social interactions subsequent to resocialization (Kalcher et al., 2008; Reimers et al., 2007).

On the basis of these studies, we tested the prediction that the social competence of individuals of the same population differs according to differences in sex and deprivation history in their first and second year of group living. As there is no overall definition for social competence, we chose an ethological approach and operationalized social competence in terms of the ability to tolerate and to search actively for social stimuli. To this end, we developed a stepwise model of social competence with increasing levels of social stimulation from moderate to intense in terms of increasing proximity and/or duration of body contact. According to our model, we expected LD chimpanzees (a) to have a greater tolerance of social stimulation; (b) to show greater social initiative; (c) to be less selective concerning the partners they seek out for sociopositive interactions and, accordingly, to have more expanded social networks compared to ED individuals. Differences caused by deprivation history may be confounded by sex differences, especially because males are expected be more severely affected by impoverished early rearing histories (Fritz & Fritz, 1979). Therefore, differences between males and females were also investigated. To evaluate effects of rehabilitation considering the two deprivation groups, we investigated their tolerance of social stimulation comparing the first (2004) and second (2005) year following resocialization.

Method

Subjects and Biographies

The present study was conducted with a total of 18 adult chimpanzees (10 males, eight females) living in three different social groups at the hopE (Home of primates Europe) primate house in Gaensern-dorf, Austria (see Table 1). The chimpanzees...
were wild caught and subsequently imported from Africa to Austria between 1976 and 1986. Until 1990, the chimpanzees were housed in small single cages of 2.25 m² at a laboratory in Vienna (Goodall, 1990). The chimpanzees imported in 1986 spent the first year in the laboratory as a peer group and were split into pairs of individuals in 1987 (according to documents viewed by Signe Preuschoft). After 1987, all chimpanzees were singly caged and became part of research protocols, mainly on Hepatitis and HIV. From these experiments, our subjects emerged uninfected and without major physical debilitations.

The chimpanzees imported in 1986 reached the laboratory in their late infancy, whereas those arriving between 1976 and 1982 were maternally and peer deprived as very young infants (see Table 1). We classified the former as LD (n = 8, M age = 3.6 ± 0.5 years at onset of deprivation), and the latter as ED (n = 10, M age = 1.2 ± 0.4 years at onset of deprivation). Note that the mean ages of chimpanzees are estimates. An exception was the male chimpanzee Blacky, who arrived in 1986 at an estimated age of 1 year and was kept singly caged immediately upon arrival; he is therefore categorized as an ED chimpanzee in this study.

In 1990 the chimpanzees were moved to a new laboratory facility (Hans Popper Primate Center, Orth, Austria) with modern squeeze cages of approximately 3 × 3 × 3 m. The front and top were made of steel mesh, the floor was formed with steel grille, and three walls were opaque. The chimpanzees were still singly housed, but bullet-proof windows of ca. 0.5 m² were set into the interconnecting cage walls. Each room contained four or eight such cages, so chimpanzees had both auditory and some limited visual contact with others. Accordingly, the chimpanzees have spent up to 27 years without physical contact to conspecifics (see Table 1), and for most of them social experience is limited to (early) infancy, visual and acoustic interactions with conspecifics, and what limited contact was possible with human caretakers operating on Biosafety Level 3 or 4 (cf. United States Department of Health and Human Services, 1999). In the late 1990s, some chimpanzees participated in a breeding program from which three infants resulted, born to two female subjects (see Table 1). As a result of incompetent mothering, the infants were human and peer reared until 2001. At the end of 2002, the chimpanzees were moved to their new “retirement home” designed for group housing, and in 2003, the resocialization project was initialized, which yielded a one-male mixed-sex group of five adult chimpanzees (MS1), a two-male mixed-sex group of six adult and three juvenile individuals (MS2) and an all-male group of seven adults (AM) by October 2003 (see Table 1). The three social groups differed in terms of adult sex ratio and relative numbers of ED versus LD individuals (see Table 1). All adult females were treated with a hormonal contraceptive (Implanon) that suppressed the ano-genital swellings typical of cycling female chimpanzees. During daytime, all three groups inhabited separate large indoor enclosures of 10 ×
13 × 6 m (MS1 group) and 16 × 13 × 6 m (AM and MS2 groups) furnished with tree trunks, wooden plateaus, ropes, and wood chip flooring. No outdoor enclosures were available during this study. Males spent the night singly in cages of 2 × 3 × 3 m. Females spent the night in pairs, or with their offspring in two interconnected night 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 at irregular times.

Data Base

Observations on social behavior and spatial proximity among group members were conducted in each of the three social groups between January and July 2004 and March and June 2005. Observations were distributed evenly over the chimpanzees’ activity period while they were in the indoor enclosures. Elfriede Kalcher-Sommersguter collected all data presented here, except for parts of data on MS1 and MS2 group, which were collected by Christine Hrubesch, Sabine Macherhammer, and Doris Muszi. All observers were trained by Elfriede Kalcher-Sommersguter, and high inter-observer reliability (r ≥ .95) was obtained (Martin & Bateson, 1993). Social interactions such as the occurrence of brief socio-positive contacts, gentle social play, allogrooming, nonhostile approaches, appeasement, and assertive behavior were recorded by all-occurrence sampling (i.e., each occurrence of these behaviors of each individual within a social group was recorded; Altmann, 1974). Being out of an arm’s reach but within 5 m distance and being within an arm’s reach to a conspecific were recorded by 5-min scan sampling (i.e., the current proximities among group members were recorded at preselected moments in time; Altmann, 1974). All data were recorded with paper and pencil on specifically designed check sheets. Onset and end of social play, allogrooming, and latencies were recorded to calculate durations later on. Results are based on 463 observation hours in 2004 (166 hr in AM, 129 hr in MS1, 168 hr in MS2) and 101 observation hours in 2005 (62 hr in AM, 19 hr in MS1, 20 hr in MS2).

Independent Variables/Predictors

We pooled behavioral data on chimpanzees across social groups according to sex and age at onset of deprivation (i.e., age at arrival at the laboratory), respectively (see Table 1).

Dependent Variables

Dependent variables reflect coping behavior of individual chimpanzees in terms of tolerance of social stimulation, and taking the initiative to shape the social situation.

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 tolerance of stationary vicinity (i.e., being out of reach but within 5 m distance of another chimpanzee without further social interaction) because of the comparatively great distance between conspecifics and the lack of physical contact. We chose 5 m as the cutoff point because this corresponds to the length of the wooden plateaus furnishing the enclosures. Accordingly, we assumed that two chimpanzees are tolerating the vicinity of a conspecific if they chose to share a wooden plateau or were vertically within 5 m distance via two connected plateaus.

   Grade 2 was assigned to the initiation of brief sociopositive contacts (including kiss, gentle or erotic touch, embrace, anogenital 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 single-body contact. For analyses of brief sociopositive initiatives, we distinguished between tense and relaxed social situations, because brief sociopositive contacts usually serve as active interpersonal conflict management and thus should occur more often in tense versus in relaxed situations. Tense situations were characterized by the occurrence of swaggering, swaying, hooting, and/or bluffing of group members or an agonistic interaction between group members within 5 min prior to the actual observation. Relaxed situations were marked by the absence of these events within 5 min prior to the actual observation.

   Grade 3 was assigned to the engagement in gentle social play (i.e., noncontact play of low intensity and mild play with brief but repetitive body contact) because of the 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. Play invitations were thus excluded. The threshold of 10 s was chosen because play in some dyads lasted only for a few seconds, the median play bout length over all subjects was 0.92 min (range = 2 s – 26.10 min). 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 conventional rough-and-tumble play, which would have been assigned as the highest level of social stimulation, did not occur.

   Grade 4 was assigned to the engagement in allogrooming, 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. One bout started with one (or both) partner(s) beginning to groom the other. The individual initiating is called “groomer.” A bout stops when grooming is interrupted for more than 10 s (according to Nishida, 1988). This threshold was chosen because some individuals groomed only for short periods of time (a few seconds); the median grooming bout length over all subjects was 2.23 min, (range = 2 s – 33.72 min). In addition, latencies for allogrooming (i.e., the time period elapsing between the approach within an arm’s reach of a potential 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 of the mandatory basic trust in the friendly intention of the conspecific nearby.

   2. Changing the level of social stimulation/initiative to change a social situation. The bipolar social life demands—the need for security and the desire for stimulation—are oppositional and intertwined. Thus, if the need for security is fulfilled, an individual is expected to search for social stimulation, for instance by approaching another individual to start a social interaction. If,
by contrast, an individual is overstrained by social stimulation, it is expected to behave accordingly to decrease social tension, for instance by displaying appeasement behavior. Therefore, we analyzed individual chimpanzees’ attempts to establish sociopositive contacts and to dampen tension, as evident in nonhostile approaches, appeasement, and assertive behavior.

Nonhostile approach. Approaching another chimpanzee within 5 m distance; approach initiative is followed by either play or allogrooming attempts of the approaching or the approached individual.

Appeasement. Panting, ano-genital presentation, pant-grunting, bowing (cf. van Hooff, 1973, equivalent to Goodall’s bobbing; van Lawick-Goodall, 1968). Each of the specified behaviors was recorded separately and subsequently assigned to the generic category.

Assertive behavior. Directed bluff, swaggering, swaying and stamping within 5 m of group members, hunching over, teasing, charging, chasing, hitting. Each of the specified behaviors was recorded separately and subsequently assigned to the generic category.

3. Social network size. The individual network size is reflected in the number of group members with whom a chimpanzee exchanged sociopositive behaviors.

4. Development of social competence. To evaluate potential changes in the course of resocialization we compared data on stationary vicinity, social grooming and close proximity between 2004 (first year after resocialization) and 2005 (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 juveniles were excluded from analysis).

Data Analysis

In this study, individual attributes were taken into consideration. Individual values were normalized across all possible interaction partners (i.e., \(N - 1\) per social group) and not solely across partners with whom social interaction actually took place, as we found the approach to include all possible interaction partners more conservative. Individual spatial proximity values as well as data on individual rates per hour of initiated brief sociopositive contacts, grooming bouts given, nonhostile approaches, and assertive and appeasement behavior were normally distributed. The individual durations of grooming bouts, play bouts, and latencies to start play and/or grooming were not normally distributed. The individual medians of these values, however, were normally distributed. To ascertain the individual rate per hour of initiated brief sociopositive contacts, grooming bouts given, nonhostile approaches, and assertive appeasement behavior, the mean initiation rate per individual over all possible interaction partners was calculated. To calculate the mean duration of a grooming bout per deprivation group and sex class, respectively, the median of all grooming bouts an individual directed to other group members within the social group was selected. The same holds true for play bouts and latencies to start gentle social play or grooming. Because of the small sample size of latencies for social play, all latencies for allogrooming and social play per individual were summated.

We could rule out group size effects, as the mean group size for EDs (\(M \pm SD = 6.3 \pm 0.9\)) and LDs (\(M \pm SD = 5.9 \pm 0.6\)) did not differ significantly (\(X^2 = 0.000, \text{ns}\)). The individual’s social network size was quantified as the proportion of group members in percent (i.e., percentage of \(N - 1\) per group) with whom sociopositive behaviors (i.e., allogrooming and social play) took place.

Mann-Whitney \(U\) tests were conducted to compare the two deprivation groups (ED vs. LD) as well as males and females. To find potential differences between deprivation-by-sex classes (i.e., ED and LD males and females separately) Kruskal-Wallis tests and Dunn’s post hoc tests were performed. To compare brief sociopositive contacts in tense versus relaxed situations and to compare spatial proximity, grooming given and received in 2004 versus 2005, Wilcoxon signed ranks tests were conducted. The alpha level was set at 0.05 for all tests, one-tailed for comparing deprivation groups according to the above-mentioned hypotheses. In addition, effect size (classified as low, moderate or large effect according to Cohen, 1977) and confidence intervals were calculated, even though effect statistics may be partially biased because of heterogeneous data (Nakagawa & Cuthill, 2007).

**Results**

Differences in Social Competence Emerging in the First Year After Resocialization (2004 Data Only)

Levels of social stimulation tolerance. On the two lowest grades of social stimulation, ED and LD chimpanzees did not differ significantly in their toleration of stationary vicinity or in their mean overall rate per hour of initiated brief sociopositive contacts. However, a moderate effect of deprivation group was found (see Table 2). This is also evident when brief sociopositive contacts are divided in contacts with and without body contact (see Table 2). Since brief sociopositive contacts may serve as active conflict management, we compared their frequency of occurrence in tense versus relaxed social situations. Individual chimpanzees over both deprivation categories (\(n = 18\)) initiated significantly more brief sociopositive contacts in tense situations than in relaxed situations (tense: \(M \pm SEM = 0.05 \pm 0.02/h\) vs. relaxed: \(M \pm SEM = 0.01 \pm 0.00/h\); \(Z = -3.574, p < .001\); see Figure 1). Although ED and LD subjects did not differ in tense situations (see Table 2), LDs initiated brief sociopositive contacts significantly more often in relaxed situations than did EDs (see Table 2).

On the third grade of social stimulation, engagement in gentle social play, EDs and LDs differed neither in the proportion of time spent in gentle social play nor with respect to their mean play bout duration (see Table 2 and Figure 2). In contrast to the first three grades of social stimulation, where no substantial differences between early and LD chimpanzees were found, LDs differed significantly from EDs in their engagement in allogrooming, representing the fourth grade. LDs spent significantly more time as groomers as a proportion of the total observation time than did EDs (see Table 2).

On the fourth grade of social stimulation, engagement in assertive behavior, EDs and LDs differed neither in the proportion of time spent in assertive behavior nor with respect to their mean assertion bout duration (see Table 2 and Figure 2). In contrast to the first four grades of social stimulation, where no substantial differences between EDs and LDs were found, LDs differed significantly from EDs in their engagement in assertive behavior, representing the fifth grade. LDs spent significantly more time as assertive than did EDs (see Table 2). On the fifth grade of social stimulation, engagement in appeasement behavior, EDs and LDs differed neither in the proportion of time spent in appeasement behavior nor with respect to their mean appeasement bout duration (see Table 2 and Figure 2). In contrast to the first five grades of social stimulation, where no substantial differences between EDs and LDs were found, LDs differed significantly from EDs in their engagement in appeasement behavior, representing the sixth grade. LDs spent significantly more time as appeasers than did EDs (see Table 2). On the sixth grade of social stimulation, engagement in assertive and appeasement behavior, EDs and LDs differed neither in the proportion of time spent in assertive and appeasement behavior nor with respect to their mean assertive and appeasement bout duration (see Table 2 and Figure 2). In contrast to the first six grades of social stimulation, where no substantial differences between EDs and LDs were found, LDs differed significantly from EDs in their engagement in assertive and appeasement behavior, representing the seventh grade. LDs spent significantly more time as assertive and appeasers than did EDs (see Table 2).
Furthermore, LD chimpanzees had significantly shorter latencies from an approach to the onset of grooming and/or gentle social play (see Table 2). The combined percentages of time spent on gentle social play and allogrooming (given and received) was significantly higher in LDs (10.7 ± 2.2%) than in EDs (3.4 ± 1.0%; U = 10,000; one-tailed p = .003; d = 1.59; 95% confidence interval [CI] = −2.74, 3.72). In addition, the total time spent in sociospositive interaction, LDs spent a higher percentage of time grooming actively (LD: M ± SEM = 47.6 ± 9.6%; ED: M ± SEM = 12.3 ± 6.7%; U = 11,000; p = .004; d = 1.48; 95% CI = −17.29, 14.62), whereas EDs spent more time in gentle social play (ED: M ± SEM = 42.3 ± 11.4%; LD: M ± SEM = 14.1 ± 6.8%; U = 18,000; p = .027; d = 0.98; 95% CI = −21.35, 14.25). EDs and LDs did not differ significantly in their percentage of time of grooming received (LD: M ± SEM = 38.4 ± 11.5%; ED: M ± SEM = 45.4 ± 11.0%; U = 32,000; ns; d = 0.21; 95% CI = −21.40, 22.74). The clear-cut differences between early and LD individuals in the fourth grade became even more significant on Grade 5, the highest level of social stimulation defined as the tolerance of passive close proximity. LDs were significantly more often in close proximity of other group members than were EDs (see Table 2).

Sex class comparison revealed significant differences between males and females with respect to the tolerance of stationary vicinity; females were significantly more frequently within 5 m distance to a group member compared to males (see Table 3). Males and females differed neither in the mean overall rate per hour of initiated brief sociopositive contacts nor when comparing type (with or without body contact) and context (tense versus relaxed) of initiated brief sociopositive contacts (see Table 3). Sex classes did not differ either, with respect to their engagement in

### Table 2

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<tr>
<th>Differences in Social Competence Between ED and LD Chimpanzees</th>
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<td>Level of social stimulation</td>
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<td>Grade 1—Toleration of stationary vicinity</td>
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<td>Stationary vicinity (Percentage of scans)</td>
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<td>Grade 2—Initiation of brief sociopositive contacts</td>
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<td>Brief sociopositive contacts—overall (rate/h)</td>
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<td>Brief sociopositive contacts—with body contact</td>
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<td>Brief sociopositive contacts—without body contact</td>
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<td>Brief sociopositive contacts—tense</td>
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<td>Grade 3—Engagement in gentle social play</td>
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<td>% of social play (% of total observation time)</td>
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<td>Play bout duration (min.)</td>
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<td>Grade 4—Engagement in allogrooming</td>
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<td>% of grooming given (% of total observation time)</td>
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<td>Initiation of grooming bouts (rate/h)</td>
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<td>Grooming bout duration (min.)</td>
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<td>Latencies for allogrooming and/or gentle social play (min.)</td>
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<td>Close proximity (Percentage of scans)</td>
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<td>Changing a social situation</td>
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<td>Nonhostile approach (rate/h)</td>
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<td>Appeasement behavior (rate/h)</td>
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Note. ED = early deprived; LD = late deprived; CI = confidence interval.

a Cohen’s d and 95% CIs were calculated since data were normally distributed.
gentle social play or their engagement in allo-grooming, although moderate effects of sex on the duration of play bouts were found (see Table 3). Further, males (5.3 ± 1.6%) and females (8.3 ± 2.5%) did not differ in their social interaction time (U = 30,000; ns; d = 0.50; 95% CI = −4.42, 3.54) or in their percentage of time of grooming given, of grooming received and of gentle social play (grooming given: \( M_{\text{males}} \pm \text{SEM} = 27.4 \pm 8.5\%; M_{\text{females}} \pm \text{SEM} = 28.7 \pm 12.3\%; U = 34,500; ns; d = 0.04; 95\% \text{ CI} = −24.10, 16.30; \) grooming received: \( M_{\text{males}} \pm \text{SEM} = 40.0 \pm 11.0\%; M_{\text{females}} \pm \text{SEM} = 45.2 \pm 11.6\%; U = 36,000; ns; d = 0.15; 95\% \text{ CI} = −22.63, 21.69; \) social play: \( M_{\text{males}} \pm \text{SEM} = 32.6 \pm 11.5\%; M_{\text{females}} \pm \text{SEM} = 26.1 \pm 10.1\%; U = 36,000; ns; d = 0.20; 95\% \text{ CI} = −22.35, 19.97\). However, sex differences were found on the highest level of social stimulation, the toleration of passive close proximity, as values for females were significantly higher than those for males (see Table 3).

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

Nonhostile approaches were significantly more frequent in LD than in ED chimpanzees (see Table 2). LDs also directed significantly more appeasement behavior to other group members than did EDs (see Table 2). With respect to assertive behavior, we found no significant difference between LD and ED chimpanzees, although a Cohen’s d of 1.19 revealed a large deprivation group effect (see Table 2).

Males and females did not differ significantly in their mean rates per hour of approach initiatives (see Table 3). Appraesement behavior, however, differed significantly between the sexes insofar as females performed appeasement behavior significantly more often than did males (see Table 3). Comparing deprivation-by-sex classes (i.e., ED vs. LD males and females separately) shows the same pattern for LD and ED chimpanzees: Females of both deprivation groups performed appeasement behavior more often than did corresponding males, but rates of ED individuals fell below those of LDs. LD females (n = 4) performed appeasement behavior most often (rate/h: \( M \pm \text{SEM} = 0.17 \pm 0.03\); ED females (n = 4) and ED females (n = 4) showed similar but lower rates of appeasement behavior (rate/h: LD males: \( M \pm \text{SEM} = 0.04 \pm 0.02\); ED females: \( M \pm \text{SEM} = 0.04 \pm 0.01\) and ED males (n = 6) performed appeasement behavior least often (\( M \pm \text{SEM} = 0.02 \pm 0.01; H = 11,055, p = .011\), Dunn’s post test: ED males vs. LD females: \( M \) rank difference = −1.147, \( p < .01\). Assertive behavior was significantly more frequent in males than in females (see Table 3). Comparison of deprivation-by-sex classes revealed that deprivation history did influence the frequency of assertive behavior within sex classes. Assertive behavior was more frequent in LD males than in ED males (rate/h: LD males: \( M \pm \text{SEM} = 0.15 \pm 0.04\); ED males: \( M \pm \text{SEM} = 0.03 \pm 0.01\). LD females and ED females both exhibited assertive behavior less frequently than males did but at similar rates (LD females: \( M \pm \text{SEM} = 0.01 \pm 0.01\); ED females: \( M \pm \text{SEM} = 0.01 \pm 0.00\). A significant difference was found between LD males and ED females (\( H = 11,785, p = .008\), Dunn’s post test: LD males vs. ED females: \( M \) rank difference = 12.000, \( p < .01\); see Figure 3).

### Social network size.

LDs had significantly more grooming partners, both as groomers (\( M \pm \text{SEM} = 75.4 \pm 0.1\% \) of available group members) and as groomees (\( M \pm \text{SEM} = 31.6 \pm 0.1\% \) of available group members) than had EDs (groomer: \( M \pm \text{SEM} = 31.6 \pm 0.1\% \) of available group members; \( U = 6,500; \) one-tailed \( p = .002; d = 1.86; 95\% \text{ CI} = 1.71, 2.01\); groomee: \( M \pm \text{SEM} = 44.8 \pm 0.0\% \) of available group members; \( U = 17,000; \) one-tailed \( p = .022; d = 1.16; 95\% \text{ CI} = 0.98, 1.25\); see Figure 4). The mean number of play partners, however, did not differ between LD and ED chimpanzees (LD: \( M \pm \text{SEM} = 60.9 \pm 0.1\% \) of available group members; ED: \( M \pm \text{SEM} = 61.9 \pm 0.1\% \) of available group members; \( U = 38,500; \) ns; \( d = 0.03; 95\% \text{ CI} = −0.19, 0.23\).

No sex differences were found either with respect to the mean number of grooming partners (donor: males: \( M \pm \text{SEM} = 44.9 \pm 0.1\% \); females: \( M \pm \text{SEM} = 58.8 \pm 0.1\% \); \( U = 28,500; \) ns; \( d = 0.44; 95\% \text{ CI} = 0.19, 0.62\); recipient: males: \( M \pm \text{SEM} = 48.8 \pm 0.1\% \); females: \( M \pm \text{SEM} = 63.1 \pm 0.1\% \); \( U = 24,000; \) ns; \( d = 0.61; 95\% \text{ CI} = 0.48, 0.77\) or with respect to play partners (males: \( M \pm \text{SEM} = 54.6 \pm 0.1\% \); females: \( M \pm SD = 70.0 \pm 0.1\% \); \( U = 27,000; \) ns; \( d = 0.48; 95\% \text{ CI} = 0.25, 0.66\).

---

**Figure 1.** Initiation of brief sociopositive contacts. Columns represent mean rate per hour (±SEM) of initiated brief sociopositive contacts across all individuals (n = 18) in tense versus relaxed situations (Wilcoxon signed ranks test; \( Z = 3.574, p < .001\)). ***p < .001.

**Figure 2.** Mean length of play and active allogrooming bouts. Columns represent mean (±SEM) length of bouts of play and active grooming of early deprived (ED) versus late deprived (LD) individuals (play: Mann-Whitney \( U = 28,000; \) ns; grooming: \( U = 6,000, \) one-tailed \( p = .002\). **p < .01.**
Table 3

Differences in Social Competence Between Male and Female Chimpanzees

<table>
<thead>
<tr>
<th>Level of social stimulation</th>
<th>Males $M \pm SEM$</th>
<th>Females $M \pm SEM$</th>
<th>Mann-Whitney U</th>
<th>Effect size/CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grade 1—Toleration of stationary vicinity</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stationary vicinity (Percentage of scans)</td>
<td>$N = 10, 3.3 \pm 0.7%$</td>
<td>$N = 8, 5.8 \pm 0.6%$</td>
<td>$U = 14,500, p = .026$</td>
<td>$d = 1.33$, CI = 0.22, 2.63</td>
</tr>
<tr>
<td>Grade 2—Initiation of brief socio—positive contacts</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Brief socio—positive contacts—overall (rate/h)</td>
<td>$N = 10, 0.06 \pm 0.02/h$</td>
<td>$N = 8, 0.04 \pm 0.01/h$</td>
<td>$U = 29,000, ns$</td>
<td>$d = 0.48$, CI = 0.45, 0.51</td>
</tr>
<tr>
<td>Brief sociopositive contacts—with body contact</td>
<td>$0.04 \pm 0.02/h$</td>
<td>$0.03 \pm 0.01/h$</td>
<td>$U = 38,000, ns$</td>
<td>$d = 0.24$, CI = 0.21, 0.26</td>
</tr>
<tr>
<td>Brief sociopositive contacts—without body contact</td>
<td>$0.01 \pm 0.00/h$</td>
<td>$0.01 \pm 0.00/h$</td>
<td>$U = 37,000, ns$</td>
<td>$d = 0.00$, CI = 0.01, 0.02</td>
</tr>
<tr>
<td>Brief sociopositive contacts—tense</td>
<td>$0.06 \pm 0.03/h$</td>
<td>$0.03 \pm 0.01/h$</td>
<td>$U = 36,000, ns$</td>
<td>$d = 0.40$, CI = 0.33, 0.42</td>
</tr>
<tr>
<td>Brief sociopositive contacts—relaxed</td>
<td>$0.02 \pm 0.01/h$</td>
<td>$0.01 \pm 0.00/h$</td>
<td>$U = 33,500, ns$</td>
<td>$d = 0.64$, CI = 0.63, 0.65</td>
</tr>
<tr>
<td>Grade 3—Engagement in gentle social play</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>% of social play (% of total observation time)</td>
<td>$N = 10, 0.82 \pm 0.28%$</td>
<td>$N = 8, 1.02 \pm 0.39%$</td>
<td>$U = 35,000, ns$</td>
<td>$d = 0.20$, CI = -0.55, 0.76</td>
</tr>
<tr>
<td>Play bout duration (min.)</td>
<td>$N = 10, 1.58 \pm 0.44$ min.</td>
<td>$N = 8, 0.88 \pm 0.11$ min.</td>
<td>$U = 25,000, ns$</td>
<td>$d = 0.76$, CI = 0.11, 0.97</td>
</tr>
<tr>
<td>Grade 4—Engagement in allogrooming</td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>% of grooming given (% of total observation time)</td>
<td>$N = 10, 2.23 \pm 0.97%$</td>
<td>$N = 8, 3.62 \pm 1.82%$</td>
<td>$U = 35,500, ns$</td>
<td>$d = 0.55$, CI = -3.18, 2.27</td>
</tr>
<tr>
<td>Initiation of grooming bouts (rate/h)</td>
<td>$N = 10, 0.07 \pm 0.03/h$</td>
<td>$N = 8, 0.10 \pm 0.04/h$</td>
<td>$U = 34,500, ns$</td>
<td>$d = 0.34$, CI = 0.27, 0.39</td>
</tr>
<tr>
<td>Grooming bout duration (min.)</td>
<td>$N = 9, 1.89 \pm 0.36$ min.</td>
<td>$N = 7, 1.79 \pm 0.40$ min.</td>
<td>$U = 30,000, ns$</td>
<td>$d = 0.09$, CI = -0.63, 0.91</td>
</tr>
<tr>
<td>Latencies for allogrooming and/or gentle social play (min.)</td>
<td>$N = 10, 0.25 \pm 0.07$ min.</td>
<td>$N = 8, 0.29 \pm 0.12$ min.</td>
<td>$U = 40,000, ns$</td>
<td>$d = 0.00$, CI = -0.12, 0.21</td>
</tr>
<tr>
<td>Grade 5—Toleration of passive close proximity</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Close proximity (% of scans)</td>
<td>$N = 10, 0.5 \pm 0.1%$</td>
<td>$N = 8, 1.2 \pm 0.3%$</td>
<td>$U = 16,000, p = .034$</td>
<td>$d = 0.47$, CI = -0.01, 1.77</td>
</tr>
<tr>
<td>Changing a social situation</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Nonhostile approach (rate/h)</td>
<td>$N = 10, 0.07 \pm 0.02/h$</td>
<td>$N = 8, 0.12 \pm 0.03/h$</td>
<td>$U = 25,000, ns$</td>
<td>$d = 0.60$, CI = 0.53, 0.64</td>
</tr>
<tr>
<td>Appeasement behavior (rate/h)</td>
<td>$N = 10, 0.03 \pm 0.01/h$</td>
<td>$N = 8, 0.11 \pm 0.03/h$</td>
<td>$U = 11,500, p = .013$</td>
<td>$d = 1.39$, CI = 1.34, 1.42</td>
</tr>
<tr>
<td>Assertive behavior (rate/h)</td>
<td>$N = 10, 0.08 \pm 0.02/h$</td>
<td>$N = 8, 0.01 \pm 0.00/h$</td>
<td>$U = 7,000, p = .001$</td>
<td>$d = 1.42$, CI = 1.37, 1.42</td>
</tr>
</tbody>
</table>

Note. CI = confidence interval.

* Cohen’s $d$ and 95% CIs were calculated since data were normally distributed.


**Stationary vicinity.** EDs did not differ significantly in their toleration of stationary vicinity of group members between 2004 and 2005 (see Table 4). In contrast, LDs showed a threefold increase from the first to the second year following resocialization (see Table 4).

Males did not differ significantly in the percentage of scans during which they were within 5 m distance of another group member between the first and second year following resocialization (see Table 5). Females, however, showed a significant threefold increase from the first to the second year following resocialization (see Table 5).

Grooming given and received. Grooming values of ED and LD chimpanzees either as groomer or as donee remained almost constant from the first to the second year following resocialization (see Table 4).

Likewise, no significant changes are obvious in the proportion of grooming given and received for male or for female chimpanzees (see Table 5).

**Close proximity.** With respect to the toleration of passive close proximity no significant changes, either among deprivation categories (see Table 4) or among sex classes (see Table 5), were found.

Discussion

Social competence is not strict but, rather, a fluid concept referring to the skills and behaviors needed for succeeding in...
social life (Welsh & Bierman, 2001). However, these behavioral skills vary depending on factors such as age or sex or in particular social situations. Therefore, we developed a model of social competence based on graded levels of social stimulation which helps to identify an individual’s abilities in and limits of social competence by means of an ethological operationalization. Assuming a sensitive period for attachment formation in early infancy in chimpanzees similar to humans, we expected ED individuals who experienced attachment disruption within this sensitive period to be more impaired in their social competence than LD individuals who experienced social deprivation after this sensitive period of attachment formation. On the basis of our hypothesis, we found that chimpanzees socially deprived in their late infancy (a) tolerate higher levels of social stimulation, (b) show greater social initiative in changing a social situation, and (c) have more expanded social networks than those deprived in early infancy. On the lower grades of social stimulation (i.e., the toleration of stationary vicinity, initiation of brief sociopositive contacts, and time spent with gentle social play), ED chimpanzees behaved similarly to LDs. As expected, LD individuals sought higher levels of social stimulation, as they spent more time grooming than in gentle social play, initiated grooming bouts more frequently, and were more frequently in close proximity to conspecifics than were ED individuals. They also showed greater social initiative, as they approached group members more often to initiate sociopositive interactions and performed appeasement behavior more frequently than did ED chimpanzees. In addition, LDs had larger social grooming networks compared with EDs, suggesting that LDs, contrary to EDs, have the ability to maintain multiple social relationships. We interpret these findings as evidence for the greater social competence of LD, as opposed to ED, chimpanzees. When we looked at the development of social competence after these chimpanzees started living socially, we found that LDs and ED females increased their toleration of stationary vicinity from the first to the second year after resocialization, whereas ED males tended to stagnate even on that lowest level of social stimulation.

Levels of Social Competence

The results of our study suggest that the a priori defined levels of social stimulation were chosen appropriately, reflecting increasing social stimulation. On the first three grades of social stimulation (i.e., toleration of stationary vicinity, initiation of brief sociopositive contacts, and time spent with gentle social play), both deprivation groups behaved similarly indicating the toleration of low levels of social stimulation. Among chimpanzees, brief sociopositive contacts serve different functions such as to establish relationships among unfamiliar individuals (Baker & Aureli, 2000), to cease interpersonal conflicts among familiar chimpanzees (de Waal & van Roosmalen, 1979; Preuschoft, Wang, Aureli, & de Waal, 2002), and to reduce stress (Fraser, Stahl, & Aureli, 2008). Accordingly, these contacts should occur more often in tense compared to relaxed situations, and this is confirmed by the results of our study. This shows that early as well as LD individuals exhibited some degree of social competence to cope actively with social tension.

That EDs did not differ from LDs with respect to gentle social play may be due to the fact that social play in mammals, in general, primarily takes place during a short period of time in early infancy referred to as a “socialization period,” when social skills are learned most rapidly (Bekoff, 2001). The fact that our adult ED chimpanzees also played with conspecifics indicates that they acquired these basic social skills during their first or second years of life. In addition, in gentle social play, individuals have the opportunity to cease the interaction by being passive a strategy apparently favored by the socially withdrawn ED individuals. In fact, social play was ceased immediately by EDs as soon as LDs began to play more roughly (personal observation, Elfriede Kalcher-Sommerguter), indicating that rough play may represent too much stimulation for the socially impaired ED individuals. Overall, gentle social play accounted for about 1% of total observation time in both deprivation groups. Comparable data are available from a mixed-sex group with a deprivation history similar to...
that of our LD chimpanzees. These chimpanzees spent on average twice as much time engaging in social play compared with our LDs, probably because play with a 3-year-old infant was included; play among adults occurred only rarely, however (Noon, 1991). Primates, in general, form and maintain affiliative bonds by allogrooming (Dunbar, 1991). Accordingly, allogrooming represents one of the most important parameters for evaluating social competence. The fact that LD chimpanzees exceeded EDs in all investigated parameters concerning grooming behavior may be caused by two factors. First, allogrooming, contrary to social play, is rarely performed by infants under 2 years of age, and it does not become frequent until the 4th year of life (Nishida, 1988). Hence, only LD chimpanzees were able to acquire at least some allogrooming skills during infancy, whereas social experience of EDs

### Table 4

**Development of Social Competence of ED and LD Chimpanzees**

<table>
<thead>
<tr>
<th>Variable</th>
<th>2004 M ± SEM</th>
<th>2005 M ± SEM</th>
<th>Wilcoxon signed ranks test</th>
<th>Effect size/CI</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Stationary vicinity (% of scans)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ED</td>
<td>3.7 ± 0.6%</td>
<td>8.9 ± 3.1%</td>
<td>Z = -1.478, ns</td>
<td>d = 0.87 CI = -5.21, 2.13</td>
</tr>
<tr>
<td>LD</td>
<td>5.3 ± 0.8%</td>
<td>19.1 ± 3.2%</td>
<td>Z = -2.521, ns</td>
<td>d = 2.45 CI = -3.79, 4.02</td>
</tr>
<tr>
<td><strong>Grooming given (% of total observation time)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ED</td>
<td>0.9 ± 0.7%</td>
<td>0.9 ± 0.7%</td>
<td>Z = -0.140, ns</td>
<td>d = 0.02 CI = -1.26, 1.37</td>
</tr>
<tr>
<td>LD</td>
<td>5.3 ± 0.6%</td>
<td>5.1 ± 1.2%</td>
<td>Z = -0.140, ns</td>
<td>d = 0.04 CI = -3.17, 2.43</td>
</tr>
<tr>
<td><strong>Grooming received (% of total observation time)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ED</td>
<td>1.4 ± 0.5%</td>
<td>1.5 ± 0.6%</td>
<td>Z = -0.866, ns</td>
<td>d = 0.07 CI = -1.13, 1.04</td>
</tr>
<tr>
<td>LD</td>
<td>4.7 ± 1.6%</td>
<td>4.4 ± 1.0</td>
<td>Z = -0.140, ns</td>
<td>d = 0.07 CI = -3.12, 2.05</td>
</tr>
<tr>
<td><strong>Close proximity (% of scans)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ED</td>
<td>0.4 ± 0.1%</td>
<td>0.3 ± 0.1%</td>
<td>Z = -1.274, ns</td>
<td>d = 0.51 CI = 0.36, 0.65</td>
</tr>
<tr>
<td>LD</td>
<td>1.2 ± 0.3%</td>
<td>3.1 ± 0.8%</td>
<td>Z = -1.820, ns</td>
<td>d = 1.24 CI = -0.41, 1.74</td>
</tr>
</tbody>
</table>

*Note. CI = confidence interval.

a Cohen’s d and 95% CIs were calculated since data were normally distributed.

### Table 5

**Development of Social Competence of Male and Female Chimpanzees**

<table>
<thead>
<tr>
<th>Variable</th>
<th>2004 M ± SEM</th>
<th>2005 M ± SEM</th>
<th>Wilcoxon signed ranks test</th>
<th>Effect size/CI</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Stationary vicinity (% of scans)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Males</td>
<td>3.3 ± 0.7%</td>
<td>7.7 ± 2.6%</td>
<td>Z = -1.580, ns</td>
<td>d = 0.86 CI = -4.24, 2.15</td>
</tr>
<tr>
<td>Females</td>
<td>5.8 ± 0.6%</td>
<td>20.5 ± 3.2%</td>
<td>Z = -2.380, p = .016</td>
<td>d = 2.78 CI = -3.45, 3.91</td>
</tr>
<tr>
<td><strong>Grooming given (% of total observation time)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Males</td>
<td>2.2 ± 1.0%</td>
<td>2.6 ± 0.9%</td>
<td>Z = -0.652, ns</td>
<td>d = 0.11 CI = -1.72, 2.02</td>
</tr>
<tr>
<td>Females</td>
<td>3.6 ± 1.8%</td>
<td>3.1 ± 1.5%</td>
<td>Z = -1.521, ns</td>
<td>d = 0.11 CI = -3.45, 2.98</td>
</tr>
<tr>
<td><strong>Grooming received (% of total observation time)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Males</td>
<td>2.3 ± 0.9%</td>
<td>2.7 ± 0.9%</td>
<td>Z = -0.153, ns</td>
<td>d = 0.14 CI = -1.71, 1.92</td>
</tr>
<tr>
<td>Females</td>
<td>3.6 ± 1.6%</td>
<td>3.0 ± 0.9%</td>
<td>Z = -0.700, ns</td>
<td>d = 0.18 CI = -2.88, 1.98</td>
</tr>
<tr>
<td><strong>Close proximity (% of scans)</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Males</td>
<td>0.5 ± 0.1%</td>
<td>1.1 ± 0.5%</td>
<td>Z = -0.357, ns</td>
<td>d = 0.58 CI = -0.49, 0.81</td>
</tr>
<tr>
<td>Females</td>
<td>1.2 ± 0.3%</td>
<td>2.2 ± 0.9%</td>
<td>Z = -0.980, ns</td>
<td>d = 0.62 CI = -1.11, 1.13</td>
</tr>
</tbody>
</table>

*Note. CI = confidence interval.

a Cohen’s d and 95% CIs were calculated since data were normally distributed.
was restricted to early infancy. Second, in contrast to social play, allogrooming requires sustained physical contact which cannot be terminated by remaining passive, because the partner may simply take over the active role. Socioemotional and behavioral problems, such as avoiding physical contact or social interaction, were also found in human toddlers exposed to traumatic life events within the sensitive period of attachment formation (Mongillo, Briggs-Gowan, Ford, & Carter, 2009). Thus, it can be assumed that for EDs who underwent social deprivation within their sensitive period of attachment formation, allogrooming may not be experienced as tension-reducing and relaxing (Schino, Scucchi, Mestrup, & Turillazzi, 1988) but, rather, as stressful arousal instead. With 5% the amount of time LDs spent grooming actively is equal to that of a comparable group of chimpanzees with a similar deprivation history (Noon, 1991).

The proportion of time EDs spent on social grooming either as groomer or groomee is two percent and thus equals that of wild-born chimpanzees, orphaned and socially deprived within the first 2 years of life, recorded 5 to 8 years after they were released back into the wild (Farmer, Buchanan-Smith, & Jamart, 2006). Hence, EDs fell below in all the abovementioned comparative values and can therefore be regarded as less competent or less motivated than LDs in establishing and maintaining grooming relationships. It seems that grooming represents high-level social stimulation, which is perceived as pleasant and tension reducing by LDs but as overstimulation by EDs.

On the highest level of social stimulation, operationalized by the toleration of passive close proximity of conspecifics, the difference between early and LD individuals became most obvious. ED chimpanzees appear to generally lack basic trust in the friendly intentions of other conspecifics because of their lack of secure attachment experience during the sensitive period; therefore, they feel more secure within a certain distance to other group members. Approach within an arm’s reach of a conspecific may cause arousal in ED chimpanzees comparable to the response of young restrictively reared chimpanzees upon approach of objects (Mason et al., 1968; Menzel, 1962).

Rough-and-tumble play, which we originally assigned as the sixth and highest grade of social stimulation, did not occur at all during the observation time. It was observed on a few occasions outside the observation period, but only between LD chimpanzees (personal observation, Elfriede Kalcher-Sommersguter and Signe Preuschoft). These findings are in line with data on wild chimpanzees, where rough-and-tumble play among adults is virtually absent (Goodall, 1986). Play-fighting experience during the juvenile period, however, seems to be important for the development of social competence as demonstrated in rats (Pellis & Pellis, 2007). In human children, rough-and-tumble play is positively correlated with social competence among popular elementary school children (Pellegrini, 1988).

Over all grades of social stimulation, sex differences became solely evident with respect to association patterns as female–female dyads tolerated stationary vicinity and close proximity more frequently than did male–male dyads, a pattern typical for captive settings (Baker, 1996; Baker & Smuts, 1994; de Waal, 1994).

Besides differences in toleration of social stimulation, LDs showed greater social initiative: They approached group members in order to initiate play or grooming more often than did EDs. The impaired social engagement of ED chimpanzees resembles that reported from young children who developed a reactive attachment disorder (World Health Organization, 2007) in response to adverse rearing conditions in early infancy (Zeahah & Smyke, 2008). Appeasement behavior serves to reduce aggression and is usually performed in response to aggressive acts (Bygott, 1979) or in tense situations (de Waal, 1989). LDs exceeded EDs in the rate of appeasement behavior, but LD females exceeded all other deprivation-by-sex classes. Thus, LD females were primarily responsible for mitigating tension among the social groups. Assertive behavior did not differ significantly between deprivation groups, but it did between sexes. The male-biased differences in aggression are consistent with observations in captive (Dutton, 2008) and free chimpanzees (Bygott, 1979; Goodall, 1986).

Concerning the social network, LDs exhibited a broader grooming network compared with EDs and thus could be categorized as more competent networkers, because social grooming is an essential trading good for other commodities, such as alliance formation and food sharing, in chimpanzees’ societies (e.g., de Waal, 1997). The scarce grooming relationships of ED chimpanzees were characterized by exclusivity and avoidance of contact with others, corresponding to the relationship pattern of insecure-avoidant children (Sroufe, 2005).

Although social deprivation did not seem to affect social competence of LD chimpanzees severely in terms of their desire for stimulation, it must be mentioned that significant impairment is apparent in partially high levels of aberrant behaviors (Kalcher-Sommersguter, Franz-Schaidere, Preuschoft, & Crailsheim, 2010) and in the absence of competent sexual behavior similar to that of ED chimpanzees.

**Development of Association and Grooming Patterns**

From the first to the second year of social life, no substantial change was observable in ED chimpanzees, neither in the toleration of stationary vicinity, nor in their grooming pattern, nor in the toleration of passive close proximity. In contrast, LDs did show a significant increase in stationary vicinity and a slight but nonsignificant increase in close proximity. The proportion of time spent grooming given and received remained high but unchanged. Thus, in LDs the desire for social stimulation prevails over social fear, whereas in EDs, social fear seems to impede social exploration. Comparing the sex classes, however, revealed that only ED males tended to stagnate in their toleration of stationary vicinity. On the other hand, females, irrespective of deprivation history, showed a significant increase in stationary vicinity. This stagnation among males could be attributed to the fact that male chimpanzees seem to be more strongly affected by an adverse early environment than females (Fritz & Fritz, 1979). That ED males seemed to stagnate in their development even on the lowest level of social stimulation may be because their social group comprised only one (male) LD chimpanzee. The impact of group composition will be discussed in detail in a separate study taking the relational perspective into account (Kalcher-Sommersguter, Franz-Schaidere, Crailsheim, 2010). Overall, our data do not suggest that males are more impaired than females. It seems that the severe early rearing history of our EDs in terms of maternal and/or social deprivation did override possible sex differences. To estimate the entire po-
tential of recovery, especially of ED chimpanzees, further long-term investigations are required.

Comprehensive studies on chimpanzees and rhesus monkeys in the 1960s highlighted the effects of early social restriction on social response patterns in juveniles, in particular the correlation between responsiveness and social and nonsocial stimuli characteristics, such as novelty, size, and movement of objects or subjects (Mason, 1965; Mason et al., 1968; Menzel, 1962; Menzel et al., 1963). Turner, Davenport, and Rogers (1969) documented the detrimental and lasting effects of early extensive deprivation on the social behavior of adolescent chimpanzees. Scientific investigations on the long-term consequences of early and enduring social restrictions of adult apes, however, are lacking so far. In humans, inadequate institutional care in early infancy may cause social difficulties in adult life (Quinton, Rutter, & Liddle, 1984; Zoccolillo, Pickles, Quinton, & Rutter, 1992). More specifically, Henry and Wang (1998) found that the exposure of infants to chronic states of arousal, especially during attachment formation, may influence hormone systems with enduring consequences for affiliative behavior persistent into adulthood. Inversely, studies on institutionalized human infants demonstrate the positive effects of adequate perceptual and social stimulation in early infancy on psychosocial development (Brossard & Decarie, 1971; Taneja et al., 2002).

In conclusion, based on similar developmental trajectories in humans and chimpanzees (Goodall, 1986), we predicted and found adult chimpanzees socially deprived and traumatized within the sensitive period of attachment formation to be more affected in their social competence and less effective in coping with social situations than chimpanzees for whom social deprivation commenced after this period, despite their shared experience of single housing for decades.

References


Grossmann, K., Grossmann, K. E., & Kindler, H. (2005). Early care and development of institutionalized children. In K. E. Grossmann, K. Grossmann, & E. Waters (Eds.), Attachment from infancy to adulthood: The...
major longitudinal studies (pp. 98–136). New York, NY: Guilford Press.


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Correction to Kalcher-Sommersguter et al. (2011)

In the article “Social Competence of Adult Chimpanzees (Pan troglodytes) With Severe Deprivation History: I. An Individual Approach,” by Elfriede Kalcher-Sommersguter, Signe Preuschoft, Karl Crailsheim, and Cornelia Franz (Developmental Psychology, 2011, Vol. 47, No. 1, pp. 77–90), Table 4 (p. 86) contained an error. The development of stationary vicinity for LD (late deprived) chimpanzees is misstated as ns. However, the difference is highly significant as $p = .008$.

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