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# Differential Onset of Infantile Deprivation Produces Distinctive Long-Term Effects in Adult Ex-Laboratory Chimpanzees (*Pan troglodytes*)

**ABSTRACT:** Maternal or social deprivation during early infancy inevitably produces social deficiencies in juvenile chimpanzees. Hypothesizing such deficiencies to persist into adulthood (a), and, as in humans, a sensitive period in early infancy for attachment formation (b), we predicted and found behavioral differences in resocialized adult ex-laboratory chimpanzees after about 20 years of solitary confinement depending on their age at onset of deprivation: early deprived (ED; mean: 1.2 years) chimpanzees engaged significantly less in social interactions, spent less time associated, and showed more nonsocial idiosyncrasies than did late deprived (LD; mean: 3.6 years) chimpanzees. In addition to these individual attributes relational qualities, specifically the combination of ED and LD chimpanzees within social groups, have an impact on social recovery. LDs can best exploit their social potential in the company of other LDs and EDs tend to stagnate in their recovery when socialized with other EDs. © 2008 Wiley Periodicals, Inc. *Dev Psychobiol* 50: 777–788, 2008.

**Keywords:** chimpanzees; deprivation; attachment; resocialization; activity budget; relational qualities; sensitive period

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## INTRODUCTION

For humans the detrimental effects of insufficient physical, social, and emotional care during infancy are well documented (e.g., Beckett et al., 2006; Blumenthal, 2005; Rauh, 1982). In his groundbreaking review Bowlby (1951) described maternal deprivation and its harmful effects, especially “the child’s inability to make relationships as a central feature from which all other disturbances sprang.” Based on Bowlby’s (1969/1982) attachment theory, experimental evidence highlighted the importance

of well-developed secure social attachment early in life for both human and nonhuman primates as well as for other mammalian species (e.g., Ainsworth, 1962; Gilmer & McKinney, 2003; Harlow & Harlow, 1962; Rajecki, Lamb, & Obmascher, 1978). Maternal and/or peer *deprivation* prohibits such attachments from ever forming and inevitably causes behavioral deficiencies. Disruption of already developed bonds of attachment caused by social and/or maternal *separation* has both short and long-term consequences (Bowlby, 1973; Gilmer & McKinney, 2003). The absence of a primary attachment figure leads to severe debilitation of the maturing individual in terms of socio-emotive adjustment and of cognition (e.g., Bowlby, 1969/1982, 1973, 1980). Securely bonded infants are more exploratory and tolerate stronger stimuli than infants with problematic or missing attachments whose coping with stressors is less effective (Ainsworth, Blehar, Waters, & Wall, 1978). To develop normally all primates need to form relations with

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other secondary attachment figures (reviewed in Marvin & Britner, 1999) in addition. For example, rhesus monkeys raised with their mother alone turn out behaviorally maladjusted albeit to a lesser extent than when raised in total social isolation (Alexander & Harlow, 1965). Social peers, either nonconspecific or conspecific, can reduce the development of abnormal behaviors in maternally deprived primates (Pazol & Bloomsmith, 1993; Spijkerman, Dienske, van Hooff, & Jens, 1994).

Most crucial for normal development appears to be the period of infancy, between birth and weaning, and both maternal deprivation and separation at this age reliably leads to stereotypies and other abnormal behavior patterns in all primates (*humans*: Albers, Johnson, Hostetter, Iverson, & Miller, 1997; Bowlby, 1951, 1969/1982, 1973; Bromwich, 1977; Miller & Hendrie, 2000; *apes*: Codner & Nadler, 1984; *chimpanzees*: Bard & Nadler, 1983; Berkson & Mason, 1964; Berkson, Mason, & Saxon, 1963; Brent, Lee, & Eichberg, 1989; Bruene, Bruene-Cohrs, McGrew, & Preuschoft, 2006; Davenport, 1979; Davenport & Menzel, 1963; Davenport, Menzel, & Roger, 1966; Fritz & Fritz, 1985; Maki, Fritz, & England, 1993; Mason, 1968; Mason, Davenport, & Menzel, 1968; Turner, Davenport, & Rogers, 1969; *macaques*: Berkson, 1968; Harlow & Harlow, 1962; Kraemer, 1997; Suomi & Harlow, 1975; Suomi, Mineka, & DeLizio, 1983). Early experience, whether adverse or protective, has long-term effects on the hypothalamic–pituitary–adrenocortical (HPA) axis which plays a central coordinating role in the regulation of stress reactivity (Gunnar, 2000). Critical is the age, or developmental stage, at which deprivation hits (Hall, 1998). Neurobiological studies on humans indicate that the period from 7 to 18 months is critical for the maturation and wiring of limbic and cortical association areas related to the development of attachment behaviors (Schore, 2001). Social deprivation during this critical phase is especially harmful and may cause enduring neurological defects (*humans*: Fries, Ziegler, Kurian, Jacoris, & Pollak, 2005; Gottlieb & Lickliter, 2004; *rhesus monkeys*: Martin, Spicer, Lewis, Gluck, & Cork, 1991; other *mammals*: Gilmer & McKinney, 2003; Gos et al., 2006; Hall, 1998; Montagu, 1972). These are mirrored in lasting changes in stress physiology (e.g., Anisman, Zaharia, Meaney, & Merali, 1998; Levine, Alpert, & Lewis, 1957; Matthews, 2002; Reimers, Schwarzenberger, & Preuschoft, 2007; Sapolsky, 1994; Seligman, 1974). Behaviorally, the early deprivation syndrome is characterized by anxiety (e.g., avoiding proximity to conspecifics), inactivity and neophobia, and a general failure to actively cope with stressful situations, to the extent of developing a characteristic type of personality (Capitanio, 2004; Capitanio & Mason, 2000; Harlow & Suomi, 1971; Lyons, Yang, Nickerson, & Schatzberg, 2000; Weiss, Pryce, Jongen-

Rejo, Nanz-Bahr, & Feldon, 2004). Moreover, these changes are not readily reversible. In rhesus monkeys cessation of deprivation later on in life cannot extinguish effects of infantile deprivation (Bastian, Sponberg, Suomi, & Higley, 2003; Harlow & Harlow, 1972). Similarly, in humans the effects of early deprivation may persist, even if the social situation is dramatically improved, for example, through adoption (Barry & Lindemann, 1960; Bowlby, 1980; Goldfarb's follow-up studies reviewed in Bowlby, 1951; *for adoptees*: Beckett et al., 2006; Fries et al., 2005; Hoksbergen, ter Laak, Rijk, van Dijkum, & Stoutjesdijk, 2005; Rutter et al., 1999).

Similar effects as in humans are to be expected for chimpanzees, because both species have very similar developmental trajectories (Goodall, 1986). Short-term effects of sustained maternal deprivation have so convincingly been demonstrated that fundamental changes in captive chimpanzee management were made in response (Berkson et al., 1963; Davenport, 1979; Davenport & Menzel, 1963; Mason et al., 1968). These classical studies, however, were conducted before there was firm evidence of a sensitive period in humans, and consequently fell short of investigating potentially differential effects related to the age at onset of deprivation. At this point, therefore, we are lacking evidence of a sensitive period for attachment formation in chimpanzees. We are also missing detailed information on how long the debilitating effects found in young chimpanzees are persisting further on in life.

The rehabilitation of former biomedical research chimpanzees at Gänserndorf, Austria, provided us with the unique opportunity to assess the behavioral repercussions of severe and prolonged social deprivation in adult chimpanzees. For early deprived (ED) chimpanzees deprivation started at a mean age of 1.2 ( $\pm .4$ ) years from which point on they were kept in solitary confinement; for late deprived (LD) chimpanzees, on the other hand, deprivation started at a mean age of 3.6 ( $\pm .5$ ) years. We investigated this population in their first year after resocialization, 16–27 years after the chimpanzees' arrival at the laboratory.

We hypothesized that (a) compared to other captive and free chimpanzees unusual general activity budgets with behavioral aberrancies and idiosyncrasies would be characteristic for all of these adult chimpanzees with a history of deprivation, and (b) that a sensitive period in early infancy would have led to more severe social debilitations in ED than in LD chimpanzees. Specifically, we predicted LD chimpanzees to engage more in social interactions and be spatially associated more often than ED individuals. We also expected EDs to deviate more from the "normal" activity budgets, in terms of higher standard deviations, and to display higher rates of aberrant behaviors than LDs.

## METHODS

### Subjects and Biographies

This study focuses on a total of 18 adult chimpanzees (10 males, 8 females) living in three different social groups at the Home of primates Europe (hopE) primate house in Gänserndorf, Austria (Tabs. 1 and 2). The chimpanzees were wild caught and subsequently imported from Africa to Austria between 1976 and 1986. Until 1990, the chimpanzees were housed in individual small cages of 1.5 m<sup>2</sup> at a laboratory in Vienna (Goodall, 1990). The group of chimpanzees imported in 1986 spent the first year in the laboratory as a peer group, and was in 1987 split into pairs of individuals (according to documents viewed by S.P.). After 1987 all chimpanzees were isolated and became part of research protocols, mainly on Hepatitis and HIV. From these experiments our subjects emerged as uninfected, and without major physical debilitations.

The chimpanzees imported 1986 reached the laboratory in their late infancy, whereas those arriving between 1976 and 1982 were maternally and peer deprived as very young infants (Tab. 1). We classified the former as "late deprived" (LD,  $n = 8$ ), and the latter as "early deprived" (ED,  $n = 10$ ). An exception

was male Blacky who arrived in 1986 at an estimated age of 1 year and was kept singly caged immediately upon arrival and is therefore addressed as ED chimpanzee in this study.

In 1990 the chimpanzees were moved to a new laboratory facility (Hans Popper Primate Center, Orth) with modern squeeze cages of approximately 3 m × 3 m × 3 m. The front and top was made of steel mesh, steel grille formed the floor, and three walls were opaque. The chimpanzees were still kept in solitary confinement, but bullet proof windows of ca. .5 m<sup>2</sup> were set into the interconnecting cage walls. Four and eight such cages respectively were in one room, 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 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. U.S. Department of Health and Human Services, 1999). In the later 1990s some chimpanzees participated in a breeding program from which three infants resulted, born to two female subjects (Tab. 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

**Table 1. Biographic Information on the Subjects**

Name	Sex	Acquisition Date	Est. Age at Arrival	Age in 2003	Years in Deprivation	Deprivation Group
(a) All-male group (AM)						
Gogo	M	June 24, 1976	2	29	27	ED
Max	M	May 16, 1979	1	25	24	ED
Isidor	M	July 18, 1979	1	25	24	ED
Johannes	M	March 11, 1982	1	22	21	ED
Michi	M	March 11, 1982	1	22	21	ED
Blacky	M	July 30, 1986	1	18	17	ED
<b>Jakob</b>	M	July 30, 1986	3	20	17	LD
(b) Mixed-sex group 1 (MS1)						
<b>Clyde</b>	M	July 30, 1986	4	21	17	LD
<b>Pünktchen</b>	F	July 30, 1986	3	20	17	LD
<i>Martha</i>	F	May 16, 1979	1	25	24	ED
<i>Ingrid</i>	F	April 14, 1980	1	24	23	ED
<i>Gabi</i>	F	April 14, 1980	1	24	23	ED
(c) Mixed-sex group 2 (MS2)						
<b>Moritz</b>	M	July 30, 1986	3	20	17	LD
<b>Anton</b>	M	July 30, 1986	4	21	17	LD
<b>Schuscha</b>	F	July 30, 1986	4	21	16	LD
<b>Helene</b>	F	July 30, 1986	4	21	16	LD
<b>Bonnie</b>	F	July 30, 1986	4	21	16	LD
<i>Susi</i>	F	June 24, 1976	2	29	27	ED
		Birth				
ALFRED <sup>a,b</sup>	M	November 11, 1996		7		
DAVID <sup>a,c</sup>	M	April 04, 1998		5		
XARA <sup>a,c</sup>	F	February 26, 1999		4		

ED/LD, early/late deprived; MS, mixed-sex; AM, all-male.

Names: standard font = early deprived, bold = late deprived, italics = females.

<sup>a</sup>Immatures were excluded from analyses.

<sup>b</sup>Mother: Helene.

<sup>c</sup>Mother: Schuscha; father of all three immatures died in 2001.

**Table 2. Characteristics of the Two Deprivation Groups**

Deprivation Group	Sex Ratio, m/f	Age at Onset of Deprivation Mean ( $\pm$ SD)	Age in 2003 Mean ( $\pm$ SD)	Years in Deprivation Mean ( $\pm$ SD)
ED	6:4	1.2 ( $\pm$ .4)	24.3 ( $\pm$ 3.3)	23.1 ( $\pm$ 3.0)
LD	4:4	3.6 ( $\pm$ .5)	20.6 ( $\pm$ .5)	16.6 ( $\pm$ .5)

Age in years.

home" designed for group housing, and in 2003 the resocialization project was initialized, which had yielded an one-male bisexual group of five adult chimpanzees (MS1), a two-male bisexual group of six adult and three juvenile individuals (MS2) and an all-male group of seven adults (AM) by October 2003, when this study began (Tab. 1). The three social groups differ in terms of adult sex ratio and relative numbers of ED versus LD individuals (Tab. 2). All adult females were treated with a hormonal contraceptive (Implanon) that suppressed the ano-genital swellings typical of cycling chimpanzees.

During daytime all three groups inhabited separate large indoor enclosures of 10 m  $\times$  13 m  $\times$  6 m (MS1 group) and 16 m  $\times$  13 m  $\times$  6 m (AM and MS2 group) furnished richly 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 m  $\times$  3 m  $\times$  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 a.m. in the night cages, at 11.30 a.m. and 2.15 p.m. in indoor enclosures and at 5.30 p.m. in the night cages. Additional foraging material was provided at irregular times.

#### Data Collection

Between October 2003 and January 2004 the first author collected all data presented here. Sampling was distributed

evenly between 9 a.m., when the subjects were released into the enclosures, and 5 p.m., when they returned to their night cages. Results are based on 72 hr of 5-min scan sampling (Altmann, 1974), which corresponds to 24 hr per group and 291 scans per individual. Behaviors were categorized as shown in Table 3.

For each scan each individual's momentary behavior and distance to other group members was recorded with paper and pencil. Spatial associations with other group members were recorded in four categories: (i) body contact (ii) no body contact but within an arm's reach (iii) beyond one arm's reach up to 5 m distance and (iv) beyond 5 m distance. We chose 5 m as the cutting point as this corresponds to the length of the wooden plateaus furnishing the enclosures. Social interactions and spatial associations were analyzed only for adult group members, that is, interactions and associations of adult group members of MS2 with the three immatures were excluded from analysis.

#### Data Analysis

Activity budget was analyzed on the individual level, that is, per subject. For each behavioral category we calculated the percentage of scans during which each individual was engaged in a given behavior, for example, resting. To identify potential differences between deprivation groups in the extent of

**Table 3. Definitions of Behavior Patterns (Adapted According to van Lawick-Goodall, 1968; van Hooft, 1973; Aberrant Behavior Adapted and Adjusted According to Walsh, Bramblett, & Alford, 1982)**

Behavior patterns	
Resting	Sit, lie, sleep
Monitoring	Visual monitoring of group members without social interaction
Self-directed behavior (SDB)	Auto-grooming, solitary play, rough scratching
Aberrant behavior <sup>a</sup>	Regurgitation, lip spluttering, coprophagy, stereotyped solitary play, hair pulling, self-patting, sucking at one's own upper arm, nipple stimulation, mutilative self-grooming, nail chewing, finger nibbling, masturbation directed at humans, self grasping, self slapping, slapping with palm at one's own face or open mouth, crouching and repeated moving of the head sideways, repetitive pushing and pulling of finger into mouth rapidly
Locomotion	Walk, run, climb
Feeding	Ingestion, chewing, foraging, handling of food items
Vigilance	Attention directed at events outside the social group while individual is otherwise inactive
Other	Chewing cardboard and paper; manual or oral exploration of plastic and cardboard; hooting; drumming; directed bluffs targeted to visitors; undirected bluffs, swaggering and sway walk in >5 m distance to conspecifics; brief scratching; building a nest; peering; food grunts; masturbating; inspection of one's own penis
Affiliation	Allo-grooming, social play, play invitation, kiss, gentle touch, embrace, ano-genital inspection
Agonistic	Aggression (directed bluffs and swaggering and stamping within 5 m of group members, tease, charge, chase, hit, cough grunt) and Submission (avoidance, flight, crouch, scream, pant-grunt)

<sup>a</sup>A separate publication on this issue is in preparation.

idiosyncrasies we compared standard deviations of EDs and LDs from the mean of their respective deprivation group.

Since values were normally distributed, a multiple regression was conducted to determine which of the following factors accounts for inter-individual differences in activity budgets: (a) age at onset of deprivation, (b) age in 2003, and (c) years in deprivation.

In order to compare spatial association between individuals we developed an "Association Score" which permitted comparisons between groups with different numbers of conspecifics. To this end we assigned ranks to the distance categories: 3 = body contact, 2 = within an arm's reach, 1 = up to 5 m distance, and 0 = beyond 5 m distance. For each single scan we now transformed the observed distances between each subject and each of its group members into the respective distance rank. For each subject the distance ranks were then summed up across all scans and all group members providing an association score per subject. Theoretically, a chimpanzee could have spent a maximum of body contact association (i.e., distance rank of 3) with all group members in all scans. This Theoretical Maximum Association Score (TMAS) is thus

$$N(\text{scans}) \times N(\text{group members} - 1) \times 3$$

To derive a Standardized Individual Association Score (SIAS) for each chimpanzee we expressed each subject's association score as percentage of the theoretical maximum, TMAS.

Note, that while the SIAS values permit direct comparisons between subjects they do not differentiate between selective but strong associations and unselective but weaker associations.

Differences between the two deprivation groups (early vs. late deprived) were analyzed by unpaired *t*-tests with Welch correction. To test whether EDs exhibited more idiosyncrasies than LDs in any of the behavior categories we compared the standard deviations per deprivation group by paired *t*-tests. We used one-way ANOVAs in combination with Dunnett's T3 post tests to compare deprivation-by-gender groups (i.e., early vs. late deprived males and females separately), the three social groups (AM, MS1, MS2) as well as group differences in the relative proportions of ED to LD individuals, and to identify which group was responsible for a significant difference. All tests were carried out using SPSS 11.5. The alpha level was set at .05 for all tests, one-tailed for unpaired *t*-tests according to above-mentioned hypotheses.

## RESULTS

### Activity Budget

Overall, the resocialized chimpanzees spent most of their time with nonsocial behavior (68.3%, Tab. 4). Social behaviors directed at group mates were shown in 9.0% of the scans. Among these, affiliation, including the temporally more extended grooming, was particularly frequent (mean  $\pm$  SD:  $7.5 \pm 8.4\%$ ), while the temporally short events of agonistic interactions were less prominent ( $1.5 \pm 2.0\%$ ). Chimpanzees also evinced social interest by

spending  $21.6 \pm 8.9\%$  of scans monitoring group members without engaging in interactions. Within each of the ten behavioral categories high standard deviations indicate major differences between subjects (Tab. 4).

A stepwise multiple regression yielded a significant correlation between affiliative ( $r = .479, p = .022$ ) as well as agonistic ( $r = .487, p = .020$ ) behavior and age at onset of deprivation. None of the other behavioral categories was significantly correlated with any of the predictor variables. Age at onset of deprivation is the predictor variable accounting for individual differences in affiliative ( $t = 2.18, p = .044$ ; Tab. 5) and agonistic behavior ( $t = 2.23, p = .040$ ; Tab. 5).

Differences in affiliative interactions between EDs and LDs were attributable to LD females (ANOVA:  $F = 3.213, p = .056$ ), who showed the highest percentage of affiliative behavior ( $n = 4$ , mean  $\pm$  SD:  $17.2 \pm 12.1\%$ ; Fig. 1), but the difference between deprivation-by-gender groups was not significant (Dunnett's T3 test, n.s.). LD males, on the other hand, engaged in agonistic interactions most often ( $n = 4$ , mean  $\pm$  SD:  $3.7 \pm 3.6\%$ ), but again the difference is not significant (ANOVA:  $F = 2.995, p = .067$ ).

These tendencies of LD males and females to engage in social interactions more than any other deprivation-by-gender group are also reflected in the differences between the three social groups. The group with the highest proportion of LD individuals, MS2, was the only one that significantly exceeded the mean of one of the other two groups for affiliation but not for agonism (Tab. 4, Affiliation: means  $\pm$  SD of AM =  $4.8 \pm 5.7\%$ , MS1 =  $2.1 \pm 1.2\%$ , MS2 =  $15.2 \pm 9.6\%$ , ANOVA:  $F = 6.308, p = .010$ ; Dunnett's T3: AM vs. MS2: mean diff.:  $-10.312$ , n.s., MS1 vs. MS2: mean diff.:  $-13.103, p = .052$ , AM vs. MS1: mean diff.:  $2.791$ , n.s.; Agonism: means  $\pm$  SD of AM =  $.5 \pm .4\%$ , MS1 =  $.4 \pm .2\%$ , MS2 =  $3.6 \pm 2.5\%$ , ANOVA:  $F = 8.962, p = .003$ , Dunnett's T3: n.s.).

In sum, the members of MS2 group who were primarily LD individuals interacted more frequently with each other than those of AM or MS1 group who were primarily ED chimpanzees (Tab. 4). No significant differences between social groups were found with respect to other behavioral categories.

To investigate whether ED individuals exhibited more idiosyncrasies than LDs we compared the standard deviations per deprivation group for social and nonsocial behaviors separately. LD subjects were more variable in the categories affiliation and agonism (paired *t*-test,  $t = -2.178$ , n.s.), but for all other categories, that is, rest, monitor, feed, locomotion, vigilance, SDB, aberrant and other behavior, ED individuals deviated significantly more from the mean than did LD individuals (paired *t*-test,  $t = 3.555, p = .005$ ).

**Table 4. Individual Activity Budgets**

Name	Rest	Monitor	SDB	Aberrant	Locomotion	Feed	Vigilance	Other	Affiliative	Agonistic
Blacky	9.7	21.9	4.2	22.6	11.8	23.3	1.4	.7	3.8	.7
Gogo	33.2	25.2	1.7	4.5	16.4	4.5	12.9	1.0	0	.3
Isidor	18.8	18.1	16.7	19.8	7.3	7.3	1.7	1.4	8.7	.3
Johannes	55.1	21.6	5.6	4.9	1.0	5.2	1.4	1.7	2.4	1.0
Max	5.6	24.6	4.9	28.4	8.1	7.0	4.6	1.1	15.8	0
Michi	24.3	39.6	23.6	1.7	5.9	2.4	0	1.7	.3	.3
<b>Jakob</b>	18.8	29.5	19.4	18.4	5.9	3.1	0	.7	3.1	1.0
Mean ± SD AM	23.6 ± 16.6	25.8 ± 7.0	10.9 ± 8.8	14.3 ± 10.5	8.1 ± 4.9	7.5 ± 7.2	3.1 ± 4.6	1.2 ± .4	4.9 ± 5.6	.5 ± .4
<b>Clyde</b>	29.6	18.8	24.4	4.2	3.8	3.5	11.1	2.8	1.4	.3
<i>Gabi</i>	30.4	15.2	28.6	9.2	4.6	3.2	6.0	1.1	1.4	.4
<i>Ingrid</i>	28.9	8.2	33.3	10.3	7.2	3.8	1.7	4.1	2.1	.3
<i>Martha</i>	5.8	23.7	18.3	14.0	10.1	8.6	1.8	15.8	1.4	.4
<b>Pünktchen</b>	47.8	18.6	5.5	9.3	4.8	2.1	2.4	4.8	4.1	.7
Mean ± SD MS1	28.5 ± 14.9	16.9 ± 5.7	22.0 ± 10.8	9.4 ± 3.5	6.1 ± 2.6	4.2 ± 2.5	4.6 ± 4.0	5.7 ± 5.8	2.1 ± 1.2	.4 ± .2
<b>Anton</b>	18.1	38.2	12.8	1.7	6.9	3.1	1.7	2.4	7.6	6.3
<b>Moritz</b>	26.3	29.3	9.7	.7	6.1	2.2	2.5	4.3	9.1	7.2
<b>Bonnie</b>	31.6	11.6	11.6	11.2	4.9	2.1	1.4	.8	18.2	2.5
<b>Helene</b>	20.3	22.1	9.0	1.0	3.4	3.4	2.1	1.4	33.1	1.7
<b>Schuscha</b>	17.4	16.0	9.3	18.5	6.8	5.3	1.1	.7	18.5	1.4
<i>Susi</i>	58.4	7.2	3.8	12.0	3.4	1.4	1.0	.7	9.6	2.4
Mean ± SD MS2	28.7 ± 15.5	20.7 ± 11.5	9.4 ± 3.1	7.5 ± 7.4	5.3 ± 1.6	2.9 ± 1.4	1.6 ± .6	1.7 ± 1.4	15.2 ± 9.6	3.6 ± 2.5
Grand Mean ± SD	26.7 ± 15.1	21.6 ± 8.9	13.4 ± 9.4	10.7 ± 8.2	6.6 ± 3.5	5.1 ± 5.0	3.0 ± 3.6	2.8 ± 4.0	7.5 ± 8.4	1.5 ± 2.0
Range	5.6–58.4	7.2–39.6	1.7–33.3	.7–28.4	1.0–16.4	1.4–23.3	0–12.9	.7–15.8	0–33.1	0–7.2

Values are percent of scans, mean and standard deviation (SD) per group, grand mean (±SD), and range over all subjects for each behavioral category. AM, all-male; MS, mixed-sex. Names: standard font = early deprived, bold = late deprived, italics = females.

**Table 5. Age at Onset of Deprivation, Age in 2003, and Years in Deprivation as Predictors of Affiliative and Agonistic Behavior**

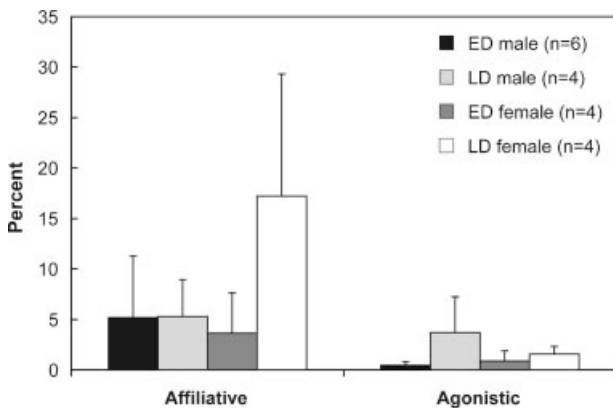
	Age at Onset of Deprivation				Age in 2003 <sup>a</sup>			Years in Deprivation <sup>a</sup>		
	<i>b</i>	$\beta$	SE	<i>t</i>	$\beta$	<i>t</i>	VIF	$\beta$	<i>t</i>	VIF
Affiliative behavior	3.05	.48	1.39	2.18*	.07	.29	1.21	.00	-.00	2.01
Agonistic behavior	.76	.49	.34	2.23*	-.08	-.33	1.21	-.06	-.20	2.01

*b* is the unstandardized regression coefficient and  $\beta$  the standardized coefficient, VIF is a measure of collinearity, a large value is indicating a strong relationship between predictor variables; *n* = 18.

<sup>a</sup>Excluded variables in stepwise multiple regression.

\**p* < .05.

When we compared the activity budgets of ED individuals representing the majority within their groups (*n* = 9) with those of LD individuals in groups with a LD majority (*n* = 5) and those of LD individuals in groups with a LD minority (*n* = 3) significant differences were apparent for the social behavior categories affiliation and agonism (Affiliation: means  $\pm$  SD for ED majority = 3.9  $\pm$  5.1%, LD majority = 16.3  $\pm$  10.3%, LD minority = 2.9  $\pm$  1.4%, ANOVA: *F* = 6.193, *p* = .012, Dunnett's T3: n.s.; Agonism: means  $\pm$  SD for ED majority = .4  $\pm$  .3%, LD majority = 3.8  $\pm$  2.7%, LD minority = .7  $\pm$  .4%, ANOVA: *F* = 9.078, *p* = .003, Dunnett's T3: n.s.). In other words, LD chimpanzees were significantly more affiliative and agonistic when being in the majority as opposed to being the minority in their social group. LD chimpanzees in LD majority were also more affiliative and agonistic than ED in an ED majority. No comparison could be conducted with EDs representing the minority within their group since only one individual met this criterion.

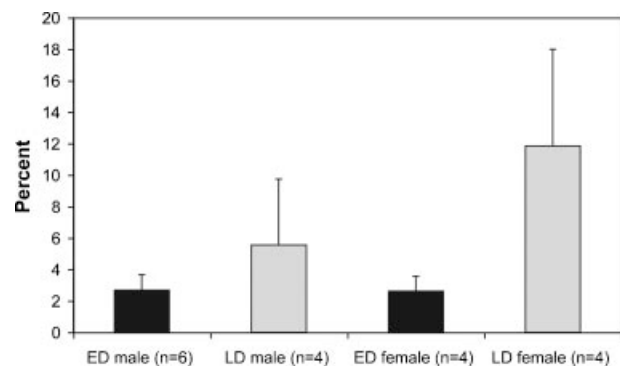


**FIGURE 1** Social behavior of early (ED) versus late deprived (LD) males and females separately. Columns represent mean ( $\pm$ SD) for affiliation and agonism across ED versus LD males and females separately. ANOVA for affiliative behavior: *F* = 3.213, *p* = .056, for agonistic behavior: *F* = 2.995, *p* = .067.

**Association Pattern**

ED chimpanzees exhibited significantly lower association scores (SIAS mean  $\pm$  SD: 2.7  $\pm$  .9%) than LD chimpanzees (mean  $\pm$  SD: 8.7  $\pm$  5.9%; unpaired *t*-test with Welch correction: *t* = 2.859, one-tailed *p* = .012) indicating that ED chimpanzees spent significantly less time in proximity of other group members than LD subjects. Separate analysis of males and females in the two deprivation groups revealed significant differences (ANOVA: *F* = 6.492, *p* = .006; Dunnett's T3: n.s.): LD females spent most time in spatial association with others (mean  $\pm$  SD: 11.9  $\pm$  6.1%, Fig. 2), LD males ranged second, but spent much less time in spatial association with others than LD females (mean  $\pm$  SD: 5.6  $\pm$  4.2%). In contrast, ED males as well as ED females reached considerably lower scores (means  $\pm$  SDs for ED males: 2.7  $\pm$  1.0%, ED females: 2.6  $\pm$  .9%).

Embeddedness in an ED or LD majority resulted in significantly different Standardized Individual Association Scores for ED and LD chimpanzees (SIAS mean  $\pm$  SD for ED majority = 2.6  $\pm$  1.0%, LD majority = 12.4  $\pm$  3.9%, LD minority = 2.5  $\pm$  1.2%,



**FIGURE 2** Association pattern of early (ED) versus late deprived (LD) males and females separately. Columns represent mean ( $\pm$ SD) of Standardized Individual Association Scores per deprivation-by-gender group. ANOVA: *F* = 6.492, *p* = .006, Dunnett's T3: n.s.

ANOVA:  $F = 34.179$ ,  $p < .001$ , Dunnett's T3: ED majority vs. LD majority: mean diff.:  $-9.794$ ,  $p = .011$ , ED majority vs. LD minority: mean diff.:  $.086$ , n.s., LD majority vs. LD minority: mean diff.:  $9.880$ ,  $p = .008$ ). This means that LDs immersed in an LD majority spent significantly more time in proximity of others than either EDs in an ED majority or LDs in an LD minority.

This result is also reflected in significant differences between the three social groups (ANOVA:  $F = 14.431$ ,  $p < .001$ ): Members of LD-dominated MS2 group spent most time in proximity (SIAS mean  $\pm$  SD:  $10.9 \pm 5.1\%$ ), whereas members of the two other groups—which were both ED-dominated—were close to conspecifics in only  $2.5 \pm 1.1\%$  (MS1) and  $2.7 \pm .9\%$  (AM) of their scans, respectively. These differences are significant (Dunnett's T3: AM vs. MS2: mean diff.:  $-8.192$ ,  $p = .029$ , MS1 vs. MS2: mean diff.:  $-8.361$ ,  $p = .025$ ).

These differences were apparent at the dyadic level as well. While ED–ED dyads spent between 0% and 15.8% and ED–LD dyads between .3% and 18.7% of their scans within 5 m distance, the LD–LD dyads in MS2 group were outstanding by spending between 16.8% and 50.0% of their scans in association. (ED–ED: mean  $\pm$  SD:  $5.5 \pm 5.2\%$ ,  $n = 18$ ; ED–LD: mean  $\pm$  SD:  $5.4 \pm 6.2\%$ ,  $n = 17$ ; LD–LD: mean  $\pm$  SD:  $31.7 \pm 9.4\%$ ,  $n = 10$ .) Thus, the LD–LD dyads of MS2 group were forming a proximity network, whereas the other groups composed of ED–LD and ED–ED combinations did not.

## DISCUSSION

We observed 18 adult chimpanzees retired from biomedical research during their first year of rehabilitation and immediately after their resocialization into three different social groups. Our hypothesis was that those for which social and environmental deprivation started in early infancy would exhibit stronger debilitations than those deprived during late infancy. We found that ED chimpanzees engaged less in social interactions, both affiliative and agonistic, spent less time in proximity of group members, and showed more nonsocial idiosyncrasies. We conclude that the LD chimpanzees were indeed more socially competent than the ED chimpanzees who came earlier to the laboratory and had not been peer housed during early infancy.

Significant differences between the three social groups draw attention to an additional aspect, that of group composition, in particular the number of available partners of the same deprivation category. The group with the highest proportion of LD–LD dyads (MS2) had values in all above variables comparable to other captive settings, whereas the LD individuals in the other two groups, who lived with a majority of ED group members, were less

socially active and spent less time in proximity of others than the LD chimpanzees of MS2 group. In terms of nonsocial idiosyncrasies, however, they resembled the other LD individuals. The one ED female living immersed among LD group members behaved like the ED subjects socialized with an ED majority. This indicates that the handicaps of ED chimpanzees represented a limiting factor for the development of intense social networking by the LD chimpanzees living as a minority among them.

## Differences between Early and Late Deprived Chimpanzees

Prior to our study it was known (1) that maternal deprivation during infancy causes social deficiencies in juvenile chimpanzees, and (2) that social deprivation later in life compromises social competence of adult chimpanzees (e.g., Fritz & Fritz, 1985). Our study adds to this knowledge by showing that (1) infantile deprivation has long-term effects that can be diagnosed over two decades later in adult chimpanzees and (2) that chimpanzees deprived early in infancy were more debilitated than those deprived later in infancy.

The differences between ED and LD chimpanzees are explicable by neurobiological studies on humans showing that the first 18 months of life are critical for the myelination and therefore the maturation of particular rapidly developing limbic and cortical association areas (Schore, 2001). Being the phylogenetically ancient substrate of emotions, the limbic system nonetheless exhibits plasticity with respect to learning effects. Immature limbic nuclei are “experience-expectant,” and seem to be differentially injured depending on the age at which they suffer deprivation (Joseph, 1999). Thus, in humans there is behavioral and neurobiological evidence for a sensitive phase in the first 18 months of life. In this phase experiences with primary attachment figures are necessary for the development of normal social behavior.

Thus, when the attachment is disrupted by maternal and peer deprivation during this sensitive phase we can expect low tolerance levels for social contact and social interaction of any kind to arise along with a strong tendency to behave passively and helplessly. This is exactly the pattern that characterizes our ED chimpanzees: they chose not to spend much time in proximity to group members or even avoided social association and interacted less than did LD chimpanzees. For the same population Reimers et al. (2007) found that ED chimpanzees responded timidly to novel nonsocial situations, experienced more stress during rehabilitation, and showed less social initiative than did LD chimpanzees. That the LD chimpanzees tolerated and sought higher stimulation levels is understandable in view of the fact that they

experienced social bonding with and stimulation by peers until the age of 4–5 years.

### Comparisons with Captive and Free Chimpanzees

Although comparisons with other chimpanzees are hindered by differences in group composition, housing, and methodology it seems important to understand if there are major deviations between our study population and captive or free chimpanzees.

**Social Behavior.** Affiliative and agonistic behaviors appear to be within a similar range in captive settings and in the wild (Tab. 6), and differences are mostly due to sex–age composition of the groups. Our study population fell within this range (Tab. 6), but while rates of MS2 group reached the upper limit, rates of AM and MS1 group hit the lower limit or fell even below (Tab. 4).

**Behavioral Aberrance.** We expected ED chimpanzees to exhibit aberrant behaviors more often than LD, but the data indicate otherwise. Some of the highest values were reached by the socially well adjusted LD members of MS2 group. One reason for this might be that we classified behaviors as aberrant by virtue of their quality, ignoring quantitative abnormalities (Bruene et al., 2006; Erwin &

Deni, 1979). While this is methodologically sound it may not reflect what is truly abnormal in the behavior of these chimpanzees. Another possibility is that the extent of deprivation obliterated differences between both deprivation groups in terms of time spent acting abnormal, but the ED chimpanzees' repertoires of abnormal behaviors could still exceed those of the LD ones. These questions will be tackled in an independent study (Kalcher et al., in preparation).

**Association Pattern.** In free chimpanzees association patterns vary between populations and sexes. Males usually are more strongly associated with one another than female–female dyads in all populations (c.f. Boesch & Boesch-Achermann, 2000; Goodall, 1986; Nishida, 1968). We found differences in association rates between our three social groups that corresponded to these of social interaction frequencies. But in contrast to free chimpanzees inter-female association was more frequent than inter-male association in LD individuals of MS2 group. However, this is also typical for females in other captive settings (Baker, 1996; Baker & Smuts, 1994; de Waal, 1994).

Even though association values at dyadic level suggest normal association patterns for our ex-laboratory chimpanzees it is important to remember that the associations among free chimpanzees are largely dictated by ecology whereas those among our subjects were limited by the social evasiveness of the ED individuals.

**Table 6. Affiliative and Agonistic Behavior of Free, Captive, and Ex-Laboratory Chimpanzees in Comparison**

	Affiliative Behavior (%)	Agonistic Behavior
Free		
East African (P.t.s.) <sup>a</sup>	6–14 <sup>i</sup>	.1–.69/hr <sup>j</sup>
West African (P.t.v.) <sup>a</sup>	9 <sup>i</sup>	Frequent <sup>j</sup>
Captive		
LCS, California <sup>b</sup>	4–17	—
Washington P. Zoo <sup>c</sup>	9	1%
LCS, California <sup>d</sup>	13	.4%
Zool. Gardens, Chester <sup>e</sup>	13	.18/hr <sup>j</sup>
YRPRC, Atlanta <sup>f</sup>	3–13 <sup>i</sup>	.27/hr <sup>j</sup>
Ex-laboratory		
LCS, Florida <sup>g</sup>	12	2%
hopE, Austria <sup>h</sup>	8	1.5% (= .13/hr <sup>j</sup> )

<sup>a</sup>Reviewed in Pruett and McGrew (2001).

<sup>b</sup>Merrick (1977).

<sup>c</sup>King et al. (1980).

<sup>d</sup>Leger (1977).

<sup>e</sup>Caws and Aureli (2003).

<sup>f</sup>Aureli and de Waal (1997).

<sup>g</sup>Noon (1991).

<sup>h</sup>Data from this study.

<sup>i</sup>Social grooming only.

<sup>j</sup>Aggression only.

### CONCLUSION

In conclusion, we found clear-cut differences between chimpanzees exposed to severe deprivation depending on their age at onset of deprivation. Later deprived individuals were more socially active. Yet, although we correctly expected personality differences caused by the onset of deprivation the found differences between social groups indicate a modifying effect of the social market (Noë & Hammerstein, 1995) on social adjustment, and the potential of relational qualities to override individual attributes (Preuschoft & van Schaik, 2000). LD chimpanzees can better exploit their social potentials when grouped with other LD chimpanzees, whereas LD chimpanzees who form a minority among ED group members become more socially inactive and distant.

It thus seems as if social company dominated by ED chimpanzees tended to under-tax both ED and LD individuals, whereas ED individuals risked to be over-taxed by an LD majority. The fact that during the study period two additional LD males could not yet be integrated into the ED-dominated all-male group (and therefore failed to become subjects of the present study)

suggests that profound differences in response dispositions and stimulus thresholds between the deprivation groups can seriously impede their compatibility (Preuschoft & Schüttler, in preparation). By contrast, LD chimpanzees could provide each other with more congenial stimulation levels conducive to the development of social bonds and social skills. On this molar level of frequencies of social behaviors these LD chimpanzees, but not those in groups with many ED chimpanzees, were similar to captive chimpanzees without a history of severe deprivation. On the other hand, even several of the LD chimpanzees in the socially rich group exhibited similarly high frequencies of aberrant behaviors as ED ones.

Our study shows that although long-term deprivation does not necessarily make chimpanzees abnormal in terms of their overall activity profile the onset of deprivation during a critical developmental stage in early life does effect pronounced and characteristic long-term debilitations that can be diagnosed over two decades later in adult chimpanzees.

## NOTES

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