

Rehabilitation of research chimpanzees: Stress and coping after long-term isolation

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Abstract

We report on the permanent retirement of chimpanzees from biomedical research and on resocialization after long-term social isolation. Our aim was to investigate to what extent behavioral and endocrine measures of stress in deprived laboratory chimpanzees can be improved by a more species-typical social life style. Personality in terms of novelty responses, social dominance after resocialization and hormonal stress susceptibility were affected by the onset of maternal separation of infant chimpanzees and duration of deprivation. Chimpanzees, who were separated from their mothers at a younger age and kept in isolation for more years appeared to be more timid personalities, less socially active, less dominant and more susceptible to stress, as compared to chimpanzees with a less severe deprivation history. However, permanent retirement from biomedical research in combination with therapeutic resocialization maximizing chimpanzees' situation control resulted in reduced fecal cortisol metabolite levels. Our results indicate that chimpanzees can recover from severe social deprivation, and may experience resocialization as less stressful than solitary housing.

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Introduction

This study reports on the rehabilitation of former biomedical research chimpanzees who were resocialized into one all-male group. Permanent retirement of research chimpanzees was recommended by the U.S. National Research Council in tribute to the profound psychological and social similarities between chimpanzees (*Pan troglodytes*) and humans (Gagneux et al., 2005; National Research Council, 1997). However, chimpanzees entering into retirement programs are often burdened with the consequences of inadequate rearing and housing conditions. Therefore, retirement of chimpanzees is to be combined with their rehabilitation including diagnosis and care of behavioral

problems to enable them to lead more species-appropriate lives (Brent, 2001; Brüne et al., 2006).

Adverse early life experiences like maternal separation can seriously compromise the behavioral and psychological adjustment of primates and lead to stress-related behavioral deficiencies (Harlow et al., 1965; Rogers and Davenport, 1970). Infantile trauma and chronic stress such as long-term isolation may result in a lasting increase in sensitivity of the HPA axis (hypothalamo-pituitary–adrenocortical axis) as expressed by heightened levels of the stress hormones ACTH (adrenocorticotrophin) and glucocorticoids (i.e., cortisol; Anisman et al., 1998; Cavigelli and McClintock, 2003; Levine et al., 1957; Lyons et al., 2000; Matthews, 2002; Weiss et al., 2004). Stress responses are mediated by a primate's ability to control a stressor through prediction and active interference with onset, duration, or intensity of the stressor (Anisman et al., 1998; Levine and Mody, 2003; Weiss et al., 2004). Repeated exposure especially to unpredictable and inescapable stress can lead to learned helplessness in humans and nonhuman species, a state

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that is characterized by anxiety, inactivity and neophobia, as well as chronically increased cortisol values (Seligman, 1974; Weiss et al., 2004). On the other hand, repeated physical restraint in rhesus macaques has led to physiological adaptation combined with a general decrease of the output of HPA hormones (Ruys et al., 2004), and adult humans with posttraumatic stress disorder show lower basal cortisol excretion compared to normal people (Yehuda et al., 2004).

The extent to which an individual can control stressors is influenced by personality factors such as boldness versus timidity, which in turn are influenced by learning and rearing history (Capitanio, 2004; Capitanio and Mason, 2000; Cavigelli and McClintock, 2003; Hall et al., 1997; Lyons et al., 2000; Weiss et al., 2004). Moreover, in gregarious species such as chimpanzees stress can be efficiently modulated by social support – affiliation and agonistic coalitions – and by dominance status (Aureli and Schino, 2004; Sapolsky, 2005). Personality has been identified in several primate and nonprimate species (Capitanio, 1999; Gosling and John, 1999; King and Figueredo, 1997; Lilienfeld et al., 1999; Stevenson-Hinde et al., 1980) and is operationalized through behavior which is related to four personality dimensions: sociability, confidence, excitability, and equability (Capitanio, 1999). One personality dimension indicates an individual's tendency to respond to strange situations with fear versus exploration (excitability). An objective method to assess this personality dimension is to confront subjects in a standard situation with a novel object or environmental challenge. An individual's reaction to those situations reflects the personality dimension “bold versus timid” (Boissy and Bouissou, 1995; Manteca and Deag, 1993).

The purpose of this study was to investigate how former laboratory chimpanzees cope with the stress of being relocated to a more species-appropriate environment and the challenges of resocialization and group living in one all-male group. We investigated personality in terms of boldness–timidity, social dominance after resocialization and how these traits were affected by the onset of maternal separation of infant chimpanzees and duration of deprivation. In addition to behavioral data, stress susceptibility was determined by measuring fecal glucocorticoid metabolites.

Methods

Study animals

The study was conducted with 13 male adult chimpanzees who previously served in pharmaceutical research. All chimpanzees had been imported as infants from Africa between 1976 and 1986. Upon arrival at the laboratories they were kept in individual indoor cages preventing tactile social contact, and used mainly in hepatitis and HIV research. Although during the 1990s efforts were made to provide environmental and social enrichment the biographies of these chimpanzees remain marked by early maternal separation, extreme spatial restriction, and virtually complete lack of control over managemental and keeping procedures.

Biographically, the study population was divided into two groups (Table 1). The older individuals of the study population (ED) were apparently separated from their mothers and conspecifics earlier and have spent a longer period in social isolation than the younger ones (LD). Of the 13 males studied, six had

Table 1
Biographical differences of deprivation groups

	Early deprived	Late deprived
<i>N</i> males	6	7
Age at study begin	Ø 22.5 years	Ø 19.3 years
Estimated age at arrival	1–2 years	3–4 years
Time isolated	Ø 21.3 years	Ø 17 years
Peer group	No	1 year

reached the laboratory as orphans aged between 1 and 2 years, and there was no documentation that they were ever peer-housed or human-reared; these were labeled early deprived (ED). Seven males were labeled late deprived (LD), because they arrived as orphans of 3–4 years of age and they spent 1 more year in a peer group before being separated. At study begin the ED males had a mean age of 22.5 years (range 17–28) and had spent a mean of 21.3 years in deprivation, while the LD males were on average 19.3 years old (range 19–20) and had spent a mean of 17 years in deprivation.

The study was divided into the 4 project phases Laboratory (3 months), Transport (7 days), Habituation (6 weeks) and Resocialization (1 year). We monitored fecal cortisol metabolites and behavior across all four phases. At the laboratory we conducted a novel object test with each male individually. Within 3 months after these tests all chimpanzees were translocated to new facilities at 20 km distance of the laboratory. It took several days to transport the whole chimpanzee population (44 chimpanzees) although the transport for any single chimpanzee took less than 3 h. Chimpanzees were transported without sedation, because all of them were trained to enter into small wheeled transport cages that had previously been used to transfer them within the laboratory facilities. Transports were made in groups of three chimpanzees, caged individually, who had been cage neighbors at the laboratory. We considered the transport and the following adjustment to the new facility as a possible challenging period and therefore included 7 days post transport into our definition of the Transport phase. After this phase the chimpanzees had 6 weeks to habituate to the new environment. During Habituation males were individually and repeatedly admitted to the new spacious indoor enclosure (176 m², 6 m high) furnished with natural tree stems, wooden plateaus and wood chip flooring. The first time a male entered the new enclosure was used as a novel environment test. After arrival and during Habituation chimpanzees were kept in individual cages; they were cared for by the identical staff as in the laboratory, and daily routines remained unchanged.

After Habituation, Resocialization started by introducing pairs of chimpanzees to each other while gradually increasing opportunities for social interaction. Compatible dyads and polyads were managed in a fission–fusion fashion, allowing the chimpanzees to gather social experience in small groups of varying compositions. Socialization sessions were conducted every day with different chimpanzees so that social times were interspersed with resting periods in individual cages. The length of these sessions lasted on average between 1 and 5 h and depended on the perceived wellbeing and the progress the individuals made. This grouping method was designed to maximize chimpanzees' individual situation control in that the chimpanzees themselves decided whether or not to intensify social contacts. Escalated fighting and serious injuries were virtually absent because unrestricted physical access was granted only once affiliative and calm behavior predominated in the restricted-contact situation (Preuschoft and van Schaik, 2000).

Behavioral tests

To test for boldness versus timidity (Boissy and Bouissou, 1995; Manteca and Deag, 1993), we conducted two standardized novelty tests, a novel object test and a novel environment test. The novel object test was conducted at the pharmaceutical laboratory while apes were still housed in individual cages. The novel object consisted in a fantasy plush toy that offered different sensory experiences when touched. This novel object was placed in the food drawer of the chimpanzees' cages and observations were conducted for 20 min after the drawer was opened for the chimpanzees. The novel environment test was conducted during the Habituation phase at the new primate house, when

chimpanzees had access to the new spacious indoor enclosure for the first time. Again, observations were conducted for 20 min, starting when a male entered the enclosure.

In both tests procedures were consistent for all chimpanzees but data collection was restricted to first, i.e., novel, confrontation with the situation. In both test situations the latencies to first action as well as the mode of the chimpanzees' explorative behavior were investigated. Behavioral measures and categorizations were adapted from Boissy and Bouissou (1995) and Manteca and Deag (1993). Latencies to take the toy out of the food drawer in the novel object test and the latency to enter the hall in the novel environment test were measured. Additionally, the apes were categorized into their predominant mode of exploration. Exploration categories were defined as cautious and explorative:

Novel object test

cautious: chimpanzee did not take the toy out of food drawer, short and gentle touches, exploration without using teeth or destructive work of the hands, grooming;

explorative: analytic exploration of the toy, bite, tear, jerk, destruction of the toy;

Novel environment test

cautious: moving gently, using only familiar substrates (e.g., mesh), preferring sheltered places near walls;

explorative: moving abundantly, using the full 6 m height of the enclosure, climbing, manipulating objects, using also unfamiliar substrates (e.g., wood).

Social behavior

In the course of group formation, three LD males became members of mixed-sex groups, while the remaining 10 males (6 ED and 4 LD) were gradually introduced into one all-male group. Here we are presenting social interaction data of the individuals in the all-male group. A total of 349.3 observation hours were recorded on different male subgroups during the first year of group living. Interactions were recorded by all occurrence sampling (Martin and Bateson, 2002), and were broken down into dyadic interactions, noting the identities of actor and receiver to assess overall initiative versus passivity per individual. We transformed absolute frequencies of affiliative, aggressive, submissive and play behavior into rates per individual per hour of observation. Definitions and recording methods were followed from the studies of Baker and Aureli (2000); de Waal (1986); de Waal and van Hooff (1981); Preuschoft and van Schaik (2000); and van Hooff (1973).

Affiliative behavior included approach to within 3 m, gentle touching, inspection, body contact, embracing, muzzling and grooming.

Aggressive behavior included quasi-aggression, undirected or directed partial or full bluff and contact aggression (hit, punch, bite, and tug).

Submissive behavior included avoidance in clear response to aggression or approach, unidirectional panting in response to intimidation, bow, receive hunch-over, pant-grunts, pant-screeches.

Social play included play-invitation, play-face, knocking, play-chase, gnaw-wrestle, tickling.

Dominance index

Dominance–subordination relationships in chimpanzees are expressed by pant-grunting of the subordinate individual in any given dyad (Muller and Wrangham, 2004; Noe et al., 1980). Sender–receiver matrices of pant-grunting can be statistically tested for unidirectionality and linearity (de Vries et al., 1993; Muehlenbein et al., 2004). However, since our chimpanzees did not form a coherent group during Resocialization but were managed in a fission–fusion fashion a sender–receiver matrix for all males would have included structural zeros. Furthermore, in the course of the study period the most reliable indicators of dominance–subordination, pant-grunting, pant-screeching, bowing and hunch-over were rare. For these reasons we calculated an individual dominance index on the basis of received submissive behaviors including also less reliable indicators. To balance for this reduction in reliability we grouped the behaviors into four reliability classes (A1–A4), and weighted these differentially. For each individual male subject we thus summed his received weighted submissive behaviors, divided this number by the total time he was observed, and multiplied

this by the percentage of group members submissive to him by the below formula:

$$X = ((A1 + 2 \times A2 + 3 \times A3 + 4 \times A4)/D) \times (C/B)$$

A1 degree 1 (avoid, flee in clear response to aggression or approach)

A2 degree 2 (unidirectional panting in response to intimidation)

A3 degree 3 (bow, receive hunch-over)

A4 degree 4 (pant-grunts, pant-screeches)

B number of possible social partners

C number of B, who showed submissive behavior

D observation hours for a given individual.

Glucocorticoid hormone assays

Glucocorticoid metabolite (GCM) levels were analyzed from fecal samples. A total of 1414 fecal samples from 13 male chimpanzees were collected in the course of the project. Collection of fecal samples commenced at the laboratory, 2 months prior to moving (Laboratory=baseline levels), continued through Transport (daily from the day of transport until day 7 after transport) and the subsequent project phases of Habituation and Resocialization albeit no longer on a daily basis. We took morning feces from the floor of the night cages, and stored them frozen at -20°C until analysis.

Extraction of fecal samples was done using methanol and diethyl ether as described and used for several other mammalian species (Berger et al., 2006). In brief, 0.5 g feces were mixed with water (0.5 ml) and methanol (4.0 ml). After vortexing and centrifugation, 1.0 ml of the methanol solution was mixed with 0.5 ml of a 5% NaHCO₃ solution and re-extracted with 5.0 ml of diethyl ether. The ether was transferred into a new vial, evaporated and the residue was redissolved with assay buffer and aliquots were analyzed by enzyme immunoassays (EIA).

Glucocorticoid metabolites (GCM) were analyzed with group-specific enzyme immunoassays (11-oxoetiocholanolone and 11 β -hydroxyetiocholanolone). These specifically developed assays were validated and have been proven to be suitable for the measurement of fecal GCM in a wide range of animal species (for a review see Touma and Palme, 2005), including chimpanzees (Bahr et al., 2000; Heistermann et al., 2006). Here, we are presenting the results of the 11-oxoetiocholanolone assay, because these were superior to the 11 β -hydroxyetiocholanolone EIA in our biological validation study.

The 11-oxoetiocholanolone enzyme immunoassay (EIA) was validated in a radio metabolism study (Bahr et al., 2000). In this study [³H] cortisol metabolites were injected into one chimpanzee and fecal and urine samples were collected over an extended period after injection. [³H] cortisol metabolites were extracted, separated by HPLC and the levels of immunoreactivity assessed with established cortisol, corticosterone, and 11-oxoetiocholanolone enzyme immunoassays were compared to radioactivity. Results found that 20% of excreted [³H] cortisol metabolites were excreted in feces. The peak of excretion in feces occurred within 26 h post-injection and [³H] cortisol metabolites compared well to the immunoreactivity measured in the 11-oxoetiocholanolone EIA (Bahr et al., 2000).

Results of a recent study based on fecal samples collected from one chimpanzee described a clearer excretion profile with an 11 β -hydroxyetiocholanolone enzyme immunoassay than with the previously described 11-oxoetiocholanolone assay (Heistermann et al., 2006). We performed a biological validation for both enzyme immunoassays. We determined which of the two assays showed a higher increase in GCM relative to a baseline subsequent to a known stressor. Each chimpanzee's GCM metabolite levels at the laboratory served as baseline; transport to the new holding facility represented the known stressor. Individuals of both deprivation groups showed a higher increase of GCM measured with the 11-oxoetiocholanolone EIA (Table 2). Additionally, we found a more pronounced stress reaction in response to renewed separation in a chimpanzee when his GCM was assessed through the 11-oxoetiocholanolone EIA as opposed to the 11 β -hydroxyetiocholanolone EIA.

All procedures were non-invasive, and in accordance with the Austrian laws and regulations on Animal Welfare and experiments with animals.

Statistical procedures

Normality of the data was tested with Kolmogorov–Smirnov test. Since parts of the data were not normally distributed, non-parametric tests were used

Table 2
Increase (in %) of GCM measured with the 11 β -hydroxyetiocholanolone and 11-oxoetiocholanolone enzyme immuno assay after a transport of the ED and LD chimpanzees and after separation of one chimpanzee from his group

	Increase of fecal GCM	
	11 β -Hydroxyetiocholanolone (%)	11-Oxoetiocholanolone (%)
6 ♂ ED	44	79
7 ♂ LD	83	132
Separation	24	72

for all analyzes. Group differences of novelty test ($n=13$) and social behavior data ($n=10$) were compared with Mann–Whitney U test. Spearman-Rho was used to test correlations between the dominance index and behavior or hormone levels. Fisher’s Exact Test was used to evaluate values in the Chi-square test with a small falling number and zero values. The level of statistical significance for these variables was set at $p<0.05$.

Hormonal data ($n=13$) were log transformed in order to normalize their distribution and permit inclusion of outliers. Statistical differences were tested by analyzes of variance (ANOVA) and Scheffé’s post hoc tests and the level of significance for these variables was set at $p<0.01$.

Results

Novelty tests

The latencies to first action as well as the mode of exploration served as indicators of boldness–timidity; results are presented as mean latencies \pm SEM in Fig. 1A. In both tests ED chimpanzees

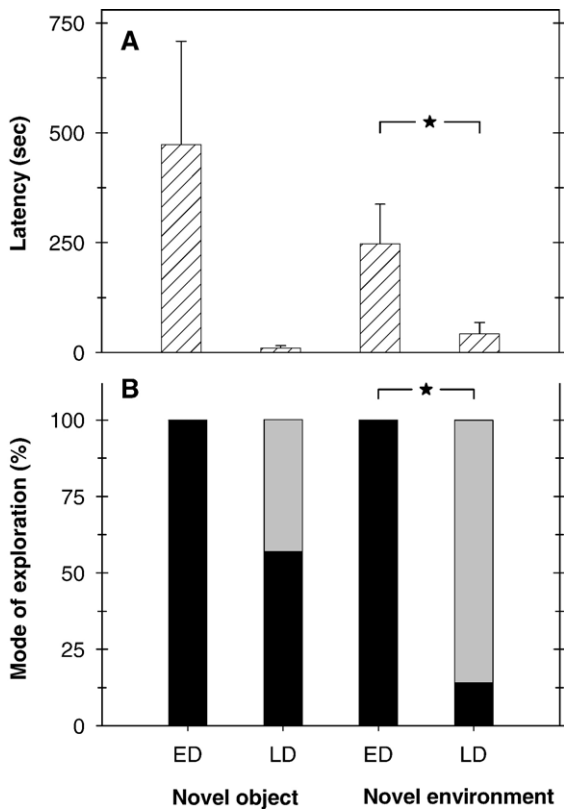


Fig. 1. Novelty Responses of early (ED) and late (LD) deprived chimpanzees. (A) Mean latency to exploration (seconds \pm SEM) during the novel object and the novel environment test situation. (B) Percent of ED and LD chimpanzees using a cautious (black bars) or bold (grey bars) manner of exploration.

took longer than LD ones until performing the first action. The difference between the groups was more obvious during the challenging novel environment test (mean ED=247 \pm 91, mean LD=42 \pm 26, $U=5$, $n=13$, $p=0.022$) than in the toy test (mean ED=473 \pm 236, mean LD=10 \pm 5, $U=7.5$, $n=13$, $p=0.053$).

ED chimpanzees’ mode of exploration was always cautious (Fig. 1B); the novel object was touched only briefly and gently, in the novel environment they moved carefully, using only familiar substrates such as wire mesh and preferring sheltered places near the walls. In contrast, LD chimpanzees used bolder ways of exploration in addition to the cautious style. 42.9% of LD chimpanzees bit, tore, jerked or even destroyed the novel object, and 85.7% of them moved about in the novel enclosure at leisure using its full height, climbing wooden structures and unfamiliar substrates. The difference between the groups was significant for the exploration of the novel environment (Fisher Exact Test, $N=13$, $p=0.004$). Thus, the younger LD chimpanzee males exhibited bolder responses to novelty than did the older ED males, who reacted primarily in a timid fashion.

Initiation of social behavior and dominance

We are presenting social interaction data (mean rates per hour \pm SEM, Fig. 2) of the individuals in the all-male group ($N=10$, 6 ED and 4 LD). LD males initiated (ED mean rate per hour=2.0 \pm 0.2 SEM, LD=4.9 \pm 0.9 SEM, $U=2$, $p=0.038$) and

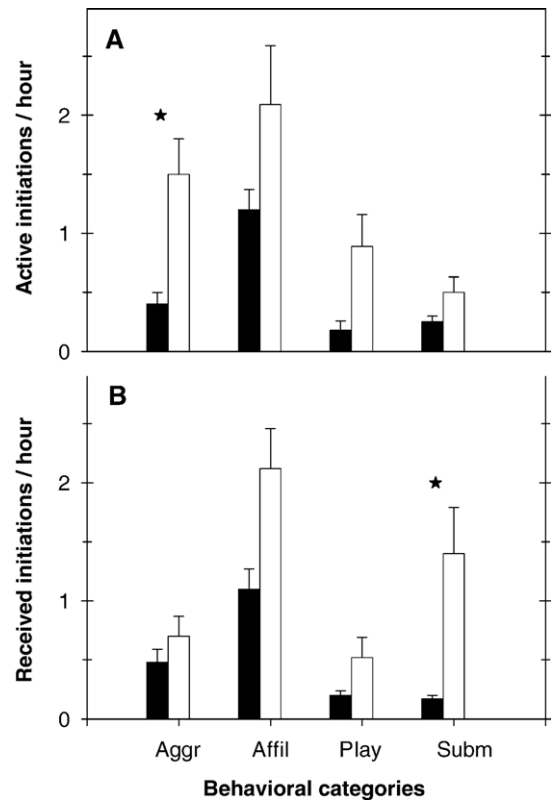


Fig. 2. Behavioral interactions of chimpanzees (ED: black bars and LD: white bars) during the first year of Resocialization. Shown is Aggression (Aggr), Affiliation (Affil), Social play (Play) and Submission (Subm) as mean rate per hour \pm SEM directed at (A) and received from (B) group mates.

received ($ED=1.9\pm 0.2$ SEM, $LD=4.7\pm 0.9$ SEM, $U=1$, $p=0.019$) more social interactions than did ED males, irrespective of the quality of social behavior. This difference was significant for initiated aggression ($U=0$, $p=0.01$, Fig. 2A) and received submission ($U=0$, $p=0.01$, Fig. 2B).

Males who had taken more time before entering the novel enclosure initiated fewer social interactions (Spearman-Rho, $r=-0.718$, $p=0.013$). Males with short latencies to enter the novel enclosure exhibited more initiative in affiliative ($r=-0.627$, $p=0.039$) and submissive ($r=-0.845$, $p=0.001$) interactions. LD males had higher dominance indices than ED chimpanzees, who exhibited little within-group variance ($ED=5.5\pm 1.3$ SEM, $LD=72.9\pm 33.1$, $U=0$, $p=0.01$).

Cortisol metabolites

Glucocorticoid metabolite (GCM) levels were analyzed from fecal samples of the 13 male subjects. Results ($n=1414$ fecal samples, $ED=766$, $LD=650$) are presented as log-transformed mean \pm SEM in Fig. 3. Project phases (Laboratory, Transport, Habituation, Resocialization) were reflected in GCM levels ($F_{(3,1408)}=40.6$, $p>0.001$). Regarding the combined results of all chimpanzees Transport caused a marked increase in GCM concentrations (mean difference to Laboratory= 0.27 ± 0.03 , $p<0.001$). GCM levels declined significantly during Habituation (mean difference to Transport= 0.22 ± 0.03 , $p<0.001$), and Resocialization (mean difference to Habituation= 0.08 ± 0.02 , $p<0.001$). Overall, the ED group had significantly higher GCM levels than the LD group ($F_{(1,1408)}=31.07$, $p<0.001$). There was a significant interaction between deprivation group and project phase ($F_{(3,1408)}=7.6$, $p<0.001$). ED males continued to have elevated levels during Habituation and returned to significantly below Habituation values during Resocialization (mean difference between Habituation and Resocialization= 0.13 ± 0.03 , $p<0.001$; mean difference between Resocialization and Laboratory= 0.03 ± 0.03 , n.s.). In contrast, GCM levels in LD males were already lower during Habituation, and during Resocialization their levels fell well below those at the Laboratory (mean difference to Laboratory= 0.11 ± 0.03 , $p=0.002$).

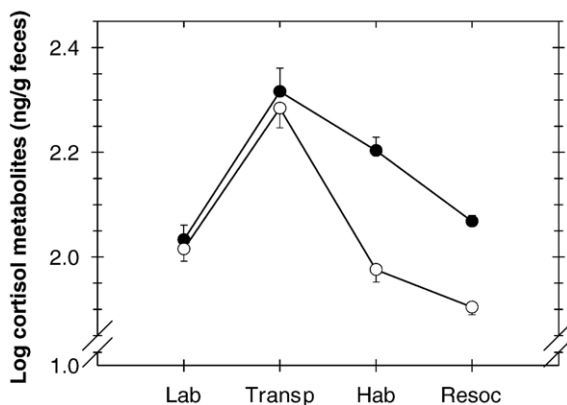


Fig. 3. Mean log-transformed fecal (ng/g \pm SEM) GCM profiles for ED (black dots) and LD males (white dots) across the project phases Laboratory (Lab), Transport (Transp), Habituation (Hab) and Resocialization (Resoc).

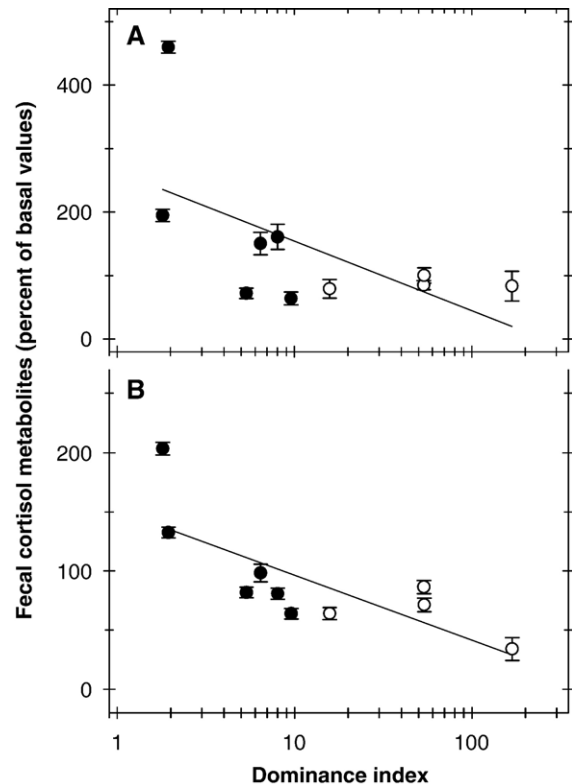


Fig. 4. Log-transformed dominance index of ED (black dots) and LD male (white dots) chimpanzees during Habituation (A) and Resocialization (B). Cortisol excretion was expressed in percent (\pm SEM) as compared to baseline values collected at the Laboratory (100%).

The correlation of the dominance index with the increase/decrease of GCM levels relative to their baseline levels at the Laboratory is shown in Fig. 4. During Habituation (Fig. 4A) the correlation between the relative increase of the GCM levels and the future dominance index was not significant (Spearman-Rho, $r=-0.47$, $p=0.17$, Fig. 4A). In contrast, the decrease of GCM levels during Resocialization (relative to their baseline levels at the Laboratory), correlated significantly with the dominance index (Spearman-Rho, $r=-0.77$, $p=0.01$; Fig. 4B). In an analysis of covariance, the dominance index was predicted by the onset of deprivation (factor ED/LD: $F=17.4$, $p=0.004$), but not by the relative increase of GCM levels during Transport and Habituation. During Resocialization only the two lowest ranking ED males showed elevated GCM levels relative to their baseline levels whereas in the other chimpanzees a reduction in GCM correlated with higher dominance.

Discussion

We examined behavioral and endocrine measures of stress across the early phases of rehabilitation and resocialization of chimpanzees after decades of deprivation. In this study, early deprived chimpanzees were timid, less explorative, less social and less dominant and they showed a higher stress response during rehabilitation. This general “helplessness” may be attributable to the age at which they experienced the presumably traumatic separation from their mothers and natal groups,

combined with a resulting drastic change in living conditions (Anisman et al., 1998; Gagneux et al., 2005; Kormos et al., 2003; Matthews, 2002), to the length of deprivation (Seligman, 1974), and their rearing without conspecifics (Dettling et al., 2002; Harlow et al., 1965).

In the behavioral tests used to judge fear-related reactions ED chimpanzees had long latencies and used a cautious mode of exploration while a bolder fashion of tackling novelty characterized the LD chimpanzees, who reacted with short latencies and investigated with an active/destructive mode of exploration. These results are in line with previous studies indicating that traumatic early life experiences (e.g., isolation) result in an impaired response to novelty and anxiety even in adulthood (Capitano and Mason, 2000; Cavigelli and McClintock, 2003; Hall et al., 1997; Weiss et al., 2004).

During the Resocialization period chimpanzees of the two rearing groups behaved differently, which we attribute to rearing history as the main cause, but we cannot exclude that the confounded factors (absolute age at resocialization and number of years spent in isolation) are also important. Superior social skills, i.e., more initiative, of the LD chimpanzees have probably contributed to their ability to acquire higher dominance ranks. In contrast, the diminished ability to initiate social behavior, especially socio-positive interactions in the ED chimpanzees correlated with an impaired response to novelty. This corroborates findings on rhesus monkeys in which rearing conditions predicted dominance ranks (Bastian et al., 2003). Surrogate mother reared monkeys were low ranking as adults and showed inadequate development of aggressive, affiliative, play and sexual behavior. Adult mother-reared monkeys outranked peer-

reared adults and both these groups dominated their surrogate-reared conspecifics.

The response to social and non-social challenges, as well as the attained dominance rank of our chimpanzees was also reflected in their fecal glucocorticoid metabolite (GCM) levels. Overall, LD chimpanzees had lower GCM levels than ED chimpanzees. We expected Resocialization to be most stressful, because the chimpanzees were evidently socially inexperienced, and essentially unfamiliar to one another. However, after onset of Resocialization, ED chimpanzees showed significantly lower GCM levels than during Habituation and LD chimpanzees even significantly lower levels than at the Laboratory. This decrease in GCM levels suggests that early and late deprived chimpanzees alike profited from Resocialization. It further implies that even profoundly socially deprived chimpanzees (ED) were better able to cope with social stressors (Resocialization) than solitarily with environmental stressors (Habituation). A reversion of negative effects of maternal separation on GCM levels is described in rats with the onset of environmental enrichment (Francis et al., 2002). However, no comparable study in chimpanzees is available, although altered cortisol levels during challenging situations in adult primates were already described by Levine et al., in 1957 (cf. Matthews, 2002).

Our results suggest that social situations are easier to influence by captive primates than environmental or managemental conditions, at least when the resocialization method maximizes the chimpanzees' situational control. We are proposing that not only the nature of the stressor (social or environmental) but perhaps more importantly the perceived locus of control enabled chimpanzees to cope more successfully

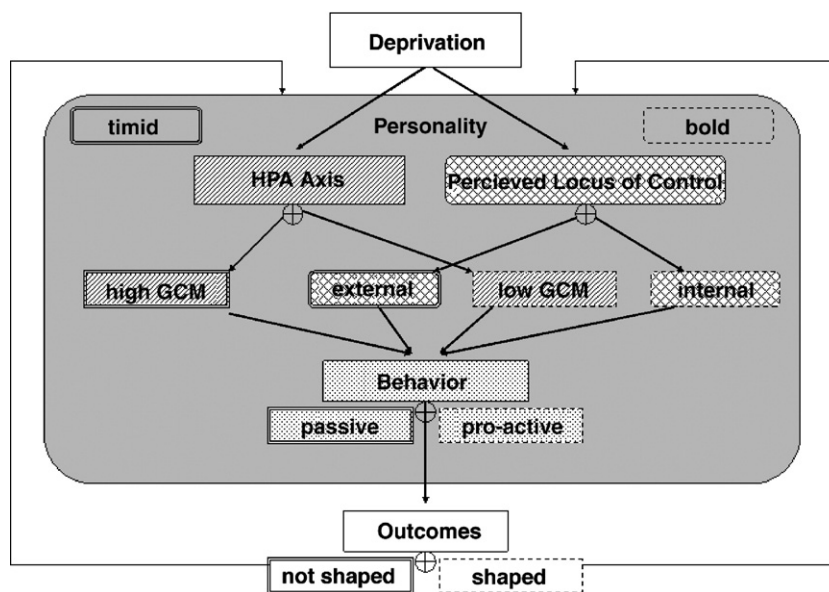


Fig. 5. Relationships between internal (physiological and psychological) and external variables (biography, behavior, outcomes) as suggested by the data. Deprivation moulds both HPA axis, and Perceived Locus of Control. Together, the latter two cause Behavior. Behavior produces Outcomes which are, or are not shaped by the subject. These Outcomes feed back on Personality. What we call Personality (grey) is a syndrome of physiological response dispositions (hatched), Perceived Locus of Control (cross hatched) and Behavior (dotted). The feedback from Outcomes probably acts directly on HPA dispositions and Locus of Control, and influences Behavior only through these intermediaries. Ovals: non-observable constructs; rectangles: directly observable; double frames: Timid Personality syndrome (high GCM, external Locus of Control, and passive Behavior); hatched frames: Bold Personality syndrome (lower GCM, internal Locus of Control, and active Behavior).

with the resocialization than with the translocation experience. This is also in line with the found differences in GCM levels between ED and LD males during Resocialization: control over the social situation was exerted by the more socially initiative, high ranking LD males, whereas by their disinclination to tackle social situations pro-actively ED males probably failed to exert situational control, which is reflected in their higher GCM levels and lower dominance ranks.

Sapolsky (2005) reviewed a number of conditions that affect the correlation of dominance rank and endocrinology. In chimpanzees status fluctuates due to shifting alliances and chimpanzee “politics” (de Waal, 2000; Goodall, 1968). As a consequence, what is experienced as a stressful period of hierarchical instability in baboons may be the norm in chimpanzees. In general, primates with superior social skills, especially the ability to predict and control behavior of other group members, show an overall lower stress burden, independent of their social rank (Abott et al., 2003; Sapolsky, 2005; Virgin and Sapolsky, 1997). Here, we found that the incipient high rankers exhibited lower GCM increases in response to social stress than incipient low rankers (during Resocialization, Fig. 4B). This covariation is mediated by deprivation history. Rearing history affected ED and LD males differentially already prior to the establishment of dominance relationships (i.e., during Habituation, Figs. 3 and 4A). We therefore attribute the relatively higher GCM levels of early deprived males to fundamental differences in the organization of the HPA axis as caused by deprivation history. Deprivation history also made ED males timid in novel and in social situations, which led to low situational control and low dominance (Fig. 5).

In conclusion, this study indicates that the onset and duration of deprivation shape chimpanzee personalities with respect to boldness–timidity and this in turn influences coping strategies and thus stress profiles during rehabilitation. While such therapeutic rehabilitation is costly in terms of time and money, results of this study show that these investments pay off in terms of increased wellbeing of our closest relatives.

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