

CAUSES OF BODY ROCKING IN CHIMPANZEES (*PAN TROGLODYTES*)

R P Spijkerman^{†1}, H Dienske, J A R A M van Hooff² and W Jens

Primate Centre TNO, Rijswijk, The Netherlands

¹ Present address: Azoren 1, 3524 ET, Utrecht, The Netherlands

² Ethology and Socio-ecology, Rijksuniversiteit Utrecht, The Netherlands

[†] Contact for correspondence and requests for reprints

Abstract

Animal Welfare 1994, 3: 193-211

The behavioural development of 90 chimpanzees (Pan troglodytes) was followed. Of these, 65 had been separated from their mothers to prevent casualties or, at a later age, to increase breeding success. Some showed body rocking and others did not. To obtain insight into the causes of the onset and development of body rocking, chimpanzees raised with peers, with their mother, or in a semi-natural group were compared. Rocking was never observed in the semi-natural group. It was occasionally seen when with the mother. Separation from the mother soon after birth induced anxiety and rocking developed after sitting upright had developed. Rocking levels of three per cent of the time were still present at seven to nine years of age.

The most probable causes of the development of rocking are frustrating social circumstances and the inability to cope with these. Merging groups, disturbances and the introduction of a fearful object increased rocking in the individuals that had developed the habit. However, rockers reacted less to those circumstances than non-rockers, showing smaller increase in body contact and less reduction of play. This finding suggests that rocking, instead of being a bizarre reaction to unsurmountable stress, could be a behaviour that helps an individual to cope with difficulties and stress. In terms of animal welfare, rocking in chimpanzees housed in laboratory conditions is an indication of a less optimal reaction pattern to frustrating circumstances. The development of rocking may be prevented if the babies are left with the mother and in their social group. Rocking after (late) separation may be prevented when transfer takes place together with familiar peers.

Keywords: *animal welfare, behaviour development, captive management, chimpanzees, early rearing conditions, stereotyped body rocking*

Introduction

It is well-documented that animals living in an impoverished environment may develop forms of behaviour that are absent in the natural habitat. These abnormal behaviours are often distortions of normal movements with an inflexible, fixed form. Examples are stereotyped locomotion, head waving, object licking or biting and head shaking (see Wemelsfelder 1990 and Mason 1991 for recent reviews). Other abnormal behaviours, for example aberrant body postures (eg Goosen 1981) and body rocking are less clearly related to normal counterparts.

© 1994 Universities Federation for Animal Welfare
Animal Welfare 1994, 3: 193-211

193

In socially impoverished environments, chimpanzees (*Pan troglodytes*) and other apes commonly develop body rocking behaviour (Berkson *et al* 1963; Davenport & Menzel 1963; Berkson & Mason 1964; Dienske & Griffin 1978; Meder 1989).

This paper is the first report on a project that assessed the effects of being separated from the mother followed by placement in a peer group on behavioural development in chimpanzees. We studied these effects in 65 young chimpanzees at the Primate Centre TNO, a centre of the national organization for 'Toegepast Natuurwetenschappelijk Onderzoek', ie Applied Natural Sciences Research, Rijswijk. The most conspicuous abnormal behaviour observed was body rocking. Some individuals showed considerable amounts of rocking, whereas others showed none. This raises the question of which factors influenced the occurrence of rocking:

1. What are the causes of the onset and development of rocking? Several suggestions have been made concerning the causation of the development of rocking (these suggestions are not mutually exclusive):
 - a) social isolation and a lack of stimulation causing frustration (Mason 1991);
 - b) frustration, unavoidable stress and fear (Mason 1991) caused by the separation procedure itself and an inability to cope with general arousal (Berkson & Mason 1964; Berkson 1967);
 - c) a (too) early separation from the mother (Davenport & Menzel 1963) which may cause a lack of motion stimulation that is normally provided by the mother (Berkson 1968; Mason 1968; Davenport & Rogers 1970; Davenport 1979; Capitano 1986; Mason 1991). However, other reports contradict this explanation (Dienske & Griffin 1978; Spijkerman 1987; Fritz *et al* 1992). Furthermore, rocking may be prevented by the presence of (peer) companions (Goosen *et al* 1983), however others reported little or no effect of the presence of peers (Davenport & Rogers 1970; Fritz & Fritz 1985);
 - d) boredom and frustration (Baumeister & Forehand 1973; Wemelsfelder 1990);
 - e) restraint and lack of stimulation when with the mother (Mason 1991), and consequently frustration.
2. What kind of events provoke actual rocking? Once rocking has developed, it is often shown without noticeable reason. Nonetheless, stressful events might temporarily increase rocking, as was also found for stereotypies in other species (reviewed by Mason 1991). In contrast, provision of interesting objects might reduce rocking, as Berkson *et al* (1963) reported when objects were given to singly-housed chimpanzees.

It has been suggested that stereotypies relieve anxiety (decrease arousal) in that they are a coping response, eg a stereotypy's repetitiveness and rigidity may increase the average predictability of an otherwise unpredictable environment (Forrester 1980). Alternatively, results suggested that stereotypies are of no consequence at all (eg as an expression of anxiety, fear or arousal). Both functional hypotheses are extensively discussed by Mason (1991) who concluded that most data are correlational and that it remains an open question.

In the present study, the circumstances around separation from the mother and subsequent housing conditions varied. For comparison, we observed young chimpanzees in cages with several mothers at TNO and in a large group in Arnhem Zoo. Data from these various

situations made it possible to address the following more specific questions about factors concerning the onset of body rocking, later influences on this behaviour, and the possible function of the behaviour:

1. Under which circumstances does rocking develop in captive chimpanzees and is rocking also observed when infants are kept with the mother?
2. At what age does rocking first develop and does the rocking level change with age?
3. Is the amount of rocking dependent on the time spent with the mother before separation?
4. What are the circumstances that temporarily increase rocking in individuals that exhibit the behaviour?
5. Is there evidence that rocking, like some stereotypies in other species, is a way of coping with difficulties (see Mason 1991)?

Methods

Environments and subjects

The 90 chimpanzees studied lived either in Arnhem Zoo or the Primate Centre TNO Rijswijk, both in the Netherlands. During three years of data collection, individuals between 0 and 10 years of age were observed at weekly intervals when younger than two years and at least once in two weeks when older. Some older chimpanzees were followed for only one year. Except for the object reaction experiment (see below), the housing procedures described below were those of normal routine.

Zoo (n = 25)

The individuals (see Table 1) were studied for three years each. We collected more than 600 hours of focal animal data. In Arnhem Zoo, male and female chimpanzees of various ages (including mother–infant pairs) spent most of their daytime in a 0.7ha outdoor enclosure. The enclosure contained grass interspersed with patches of sand, wooden climbing structures, and trees protected by electrified barriers. The ground was covered with various natural objects, such as branches, sticks, wooden blocks, stones, acorns and leaf litter. See Adang *et al* (1987) for a further description of the zoo housing condition.

The animals were fed before leaving and after returning to their night cages. Additional titbits were provided once or twice during the day (eg fruits, carrots, lettuce or grains were thrown into the outside area).

Table 1 The sex ratios and age class distribution of chimpanzees at the zoo.

Age class	Zoo male–female ratio		Total
	m	f	
0-3	3	9	12
4-6	2	3	5
7-10	5	3	8
<i>Total</i>	10	15	25

Late-separated (TNO, n = 29)

These animals had remained with the mother for periods of 110 to 478 days. They will all be denoted as 'late-separated' in order to distinguish them from the TNO 'early-separated' animals. Of the late-separated animals, 12 were also observed while with the mother. In this situation, we collected 40 hours of focal animal data. Mothers and infants were usually with several other mother-infant pairs. The ceiling, floor and three sides of the cages were constructed of iron bars. One wall was concrete with climbing structures on it. The cage size was 4x3x3m. Infants that had remained with their mother subsequently were placed into peer groups to allow the mothers to breed again. The other animals in this class lived with the mother until separation before this study started. See Table 2 for sex ratios.

Early-separated (TNO, n = 36)

If a baby was not carried, did not receive enough milk or was ill, it was separated from its mother. For these reasons, 24 babies were separated within one week after birth. Seven others were separated at between 8 and 30 days. Five were separated later, at ages of 38, 40, 72, 73 and 82 days (see Figure 2 for separation age distribution on the *x*-axis). All these babies were kept individually in transparent incubators until an average age of two months. Interactions with humans were largely restricted to bottle feeding. After this incubator period they were housed together in small peer groups of similar age (iron bar cages, 2x1x1m). Seven were actually observed while in the incubator. We collected 20 hours of focal animal data. Of the others, the time spent in the incubator was derived from archival data. They will all be denoted as 'early-separated' (see Table 2 for sex ratios).

Table 2 The sex ratios and age class distribution of chimpanzees at TNO: L = late-separated, E = early-separated.

Age class	Separation	TNO male-female ratio		Total
		m	f	
0-3	E	9	7	16
	L	2	11	13
4-6	E	4	9	13
	L	4	4	8
7-10	E	3	4	7
	L	5	3	8
<i>Total</i>		27	38	65

Peer groups (TNO, n = 65)

All the animals of the former two categories were eventually placed in peer groups. Initially groups exclusively consisted of two to three early-separated individuals. Later (mostly between 5 and 12 months of age) a few late-separated individuals were added to these groups. It was attempted to match ages as much as possible. If available two or sometimes three late-

separated individuals from the same mother–infant group were added simultaneously; these are called ‘friends’. In several cases, however, no similar aged conspecifics were available. These grouping procedures were already a routine for years preceding this study.

The resulting peer groups were housed in cages of 2x1x1m. Cages were constructed of iron bars (also the ceiling and floor) and of one concrete wall with climbing materials on it. Cages were provided weekly with several plastic jerrycans or cardboard boxes. Later, at ages of several years, such groups were merged and placed in much larger cages (4x3x2m). Their group size then was 8-12 individuals. We collected 540 hours of focal animal data.

The animals at TNO were fed at 0800h, 1200h and 1800h. The food consisted of combinations of rice, fruits, carrots, lettuce or grains.

So, we could make the following comparisons:

1. Between the animals living in the socially and environmentally complex zoo condition with those at TNO.
2. Between the animals living at TNO in either of the three conditions, depending on the age class of the individuals: with mother, incubator and in peer groups after late or early separation. Twelve late- and seven early-separated chimpanzees are represented in ‘with mother’, respectively in ‘incubator’ and at an older age in the ‘peer group’ category.

Object reaction experiment

This was aimed at studying the influence of previous history on the reaction of chimpanzees to various objects. At TNO six temporary groups of four individuals from the same group (two early- and two late-separated; age range 2-5 years) were formed. Two days before the experiment started, the four individuals were placed together in a new cage. They remained in a test cage for two weeks. After becoming accustomed, they were provided with one of nine objects from 1230h to 1330h on nine subsequent days. One object was familiar (a plastic jerrycan); four objects were expected to be attractive (a plastic barrel, a food tin, a jute sack, a plastic bottle filled with raisins); three others were supposed to be intermediate between interesting and fear-inducing (a mirror, a chimpanzee mask, a plastic reptile), and the last object shown was expected to be fear-inducing (a moving and noisy toy robot). The behaviour of all four group members was recorded simultaneously for one hour before the object was given (control) and for the next hour while the object was present.

Behaviour categories

Behaviour category selection was based on a pilot study and on the literature (van Hooff 1973; Plooij 1979, 1984; Dienske & van Vreeswijk 1987). Many were selected because of their relevance for social development, the main objective of the entire project. Here, we will only describe the categories used in this paper.

Body rocking: a rhythmic trunk movement, either back-and-forth or sideways. Standing bipedally and swaying was only regarded to be rocking in the absence of pilo-erection and other bluff elements (described by van Hooff [1973] and Adang [1986]).

Body contact: all types of steady body contact. It usually consisted of sitting against each other; prolonged holding without touch of trunks was also included. However, brief hand touching (<5s) and pushing are excluded. Touching during conflicts, social play and sexual behaviours were recorded separately as such.

Table 3 Number of individuals showing different amounts of rocking under the different conditions.

Amount of rocking	While with mother		While with peers only; TNO separation history			
	Zoo	TNO	With friends to peer group (late)	Alone to peer group (late)	Complicated or unknown (late)	First in incubator (early)
<i>Much rocking</i> (<i>>0.1% of the observation time</i>)	0	1	2	5	4	33
<i>Occasional rocking</i> (<i><0.1% of the observation time</i>)	0	2	3	1	3	0
<i>No rocking</i>	23	9	5	0	6	3

Gymnastics: movements of the trunk. Characteristic are dangling from one hand and possibly one or two feet, swinging either sideways or forwards and backwards.

Social play consisted of three different types: *gnaw-wrestling*, where two or sometimes more animals repeatedly grasp and gnaw at various parts of each other's body; *tickling*, a variety of quick but relaxed grasping or poking movements of fingers, hands or feet directed at the partner; *chase-play*, where one animal follows the other playfully, often galloping. Play faces were separately recorded as such. In this paper, the durations of the three social play types are summed.

Behaviour recording

Behavioural data were collected by means of the focal animal method. If the infant had been taken from the mother before this study, the separation age was not made known to the observer until after data collection. The results are based on a total of 3,600 observation periods of 20 minutes. The onset and termination of each act was recorded by means of a keyboard and a floppy disk unit or a portable computer.

Statistics and treatment of data

There was large variation in the duration and frequency of behaviours both between and within individuals, as is evident from standard deviations in Table 4. Behaviours were exponentially distributed, therefore non-parametric tests are used. In most cases, individual means are computed before testing differences between groups.

The Mann-Whitney *U* test and the Kendall rank correlation test were used (Siegel 1956), with an alpha level of 0.05 to determine significance, and, if significant, an alpha level indication is given.

A 'relative rocking level' independent of age was computed in order to test an effect of the age of separation from the mother. For each individual the mean percentage of time spent in rocking (x) was expressed as the fraction of the pertinent age class mean for rockers (M), ie $(x-M)/M+1$. This index denotes how much an individual's level is larger or smaller than the mean for its age (age means are represented with value 1). A value of zero means that rocking was absent.

Results

Initial development of body rocking

Effects of the housing environment

The number of individuals that developed rocking under the various circumstances is given in Table 3. A somewhat arbitrary category of occasional rockers (less than 0.1% of the total observation time) is distinguished in the table. These individuals will not be used in analyses of the factors that influence rocking because they are less likely to be sensitive to these. In all other results they are included with non-rocking individuals.

Results for the various housing environments are the following:

1. With mother in the zoo. In the zoo rocking was never seen. Since we recorded the behaviour of 25 young individuals during a total of 600 observation hours, this is a strong result. Moreover, the zoo group has been intensively observed by others for 10 years and no one has ever seen body rocking.

2. With mother at TNO. Of the 12 infants observed while with their mother at the TNO Primate Centre, three rocked a little. Two individuals were observed to rock once for 0.02% and 0.10% of the observation time respectively and while off mother. The third individual rocked during three of the nine observation periods; the total was 1.2% of all the observation time. In these three observation periods, rocking took place when the mother shifted her infant to a different body contact position to groom another female.
3. Peer groups at TNO. If there were infants of similar age in a with-mother group these were kept together when transferred to a peer group. Only two of the 10 individuals thus separated with 'friends' developed rocking and five were never seen to rock. In contrast, of the six individuals that could not be transferred together with friends, five developed much rocking. The percentage of time spent rocking was significantly less in friend-separated infants (Mann-Whitney *U* test, $n_1 = 6$, $n_2 = 10$; means 2.8 and 0.5% of the time; SD 2.6 and 0.9 respectively; $P = 0.012$). The separation procedure of the additional 13 late-separated chimpanzees was complicated or insufficiently documented and therefore cannot be used for testing a friend effect. However, this group is presented in the table to show a diversity of rocking levels of juvenile and adolescent peer group raised individuals. Of these the rockers will be used in analyses of the factors that influence rocking.

The behaviour immediately after transfer to the peer group demonstrates the importance of the presence of friends. We observed seven chimpanzees after separation with friends and one that was transferred alone. Signs of fear disappeared among friends within half an hour. In the individual separated without familiar age-mates, signs of fear lasted much longer (up to one week); it also received more hits and bites than chimpanzees transferred with friends. In chimpanzees housed with friends, body contact was increased during the first week after separation (mean of 50% of the time as compared with 30% during stable situations for same-aged chimpanzees). The friendless chimpanzee, in contrast, had less body contact (21%) than normal and less than each of the 'with friends' transferees. Nearly all individuals that had spent some time in an incubator (ie were early-separated) showed rocking (33 of the 36).

Age when rocking was first seen and its relation to motor abilities

The behaviour of seven infants in the incubator was recorded from the day of birth onwards. Initially these babies' movement was so undeveloped that rocking was impossible. After 60 days of age incubator infants were able to lift their trunk partly from the floor. This motor ability did not enable the infants to rock. Brief sitting upright with little or no arm support was first observed at 80 days of age. The first rocking was recorded between 70 and 103 days with an average of 88, ie at about the age they were able to sit upright unsupported. So rocking develops as soon as it is physically possible. When rocking was first seen it took only a small percentage of time, probably because the babies could not sit for long.

Changes with age after initial development

The individual amount of rocking is plotted against age in Figure 1. There is considerable variation between as well as within individuals. Still, individuals appeared to be constant in their rocking levels over nine-month periods (Kendall's Rank correlation per individual not significant). However, the means per age class (solid points) slightly (but significantly)

decrease from 6% during the first two years to 3-4% later. Non- and occasional rockers are not included in these age class means since we were interested in the influence of age on rocking levels: rocking still persisted in the oldest individuals studied (see Figure 1).

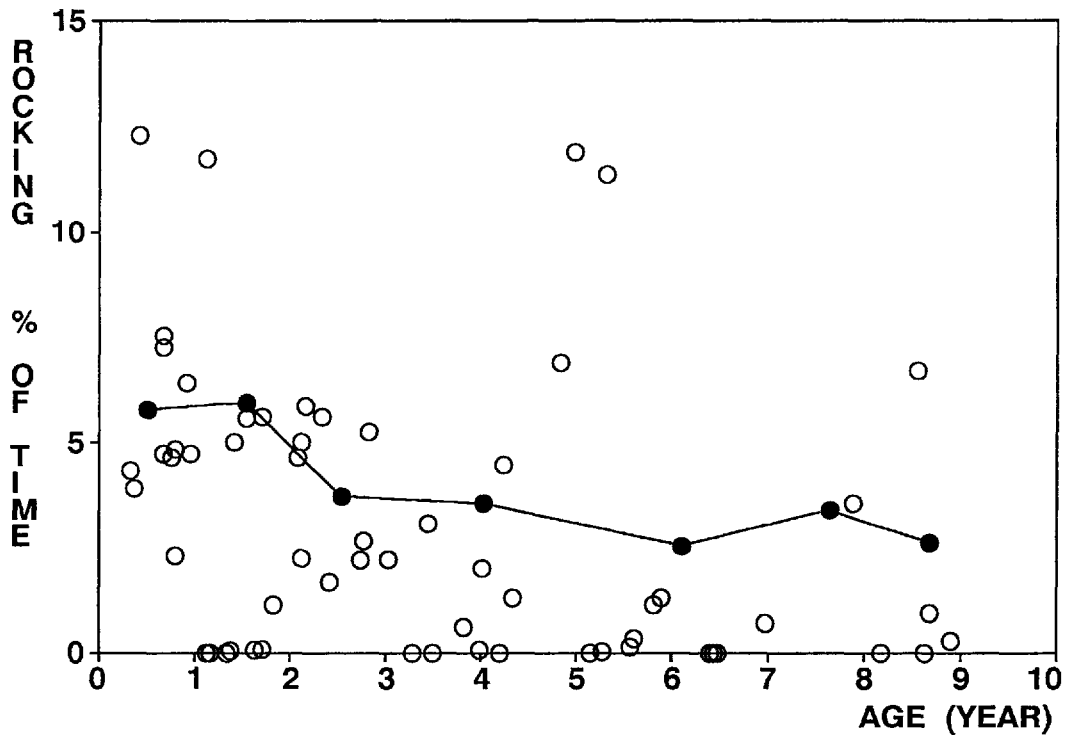


Figure 1 Mean levels of rocking per individual for various ages. Solid points are age class means for rockers only (>0.1% of the observation time; both early- and late-separated).

Influence of the time spent with the mother

One would expect that an individual separated at a very young age, thus having experienced the longest deprivation period, would rock more than one separated much later. To test this possibility, we must correct for the decrease with age. To this end a 'relative rocking level' independent of age was computed.

Relative rocking levels per individual are plotted against the time spent with the mother in Figure 2. Since it was found that separation with or without friends was important, these cases are depicted with distinct symbols. It can be seen that most of the individuals separated with friends (black points) did not rock, whereas those without friends (squares) mostly did (cf Table 3 and *Effects of the housing environment: 3*). Of the remaining individuals separated after month 3 (open circles), the history was complex or unclear and hence cannot be used to test a 'friend effect'.

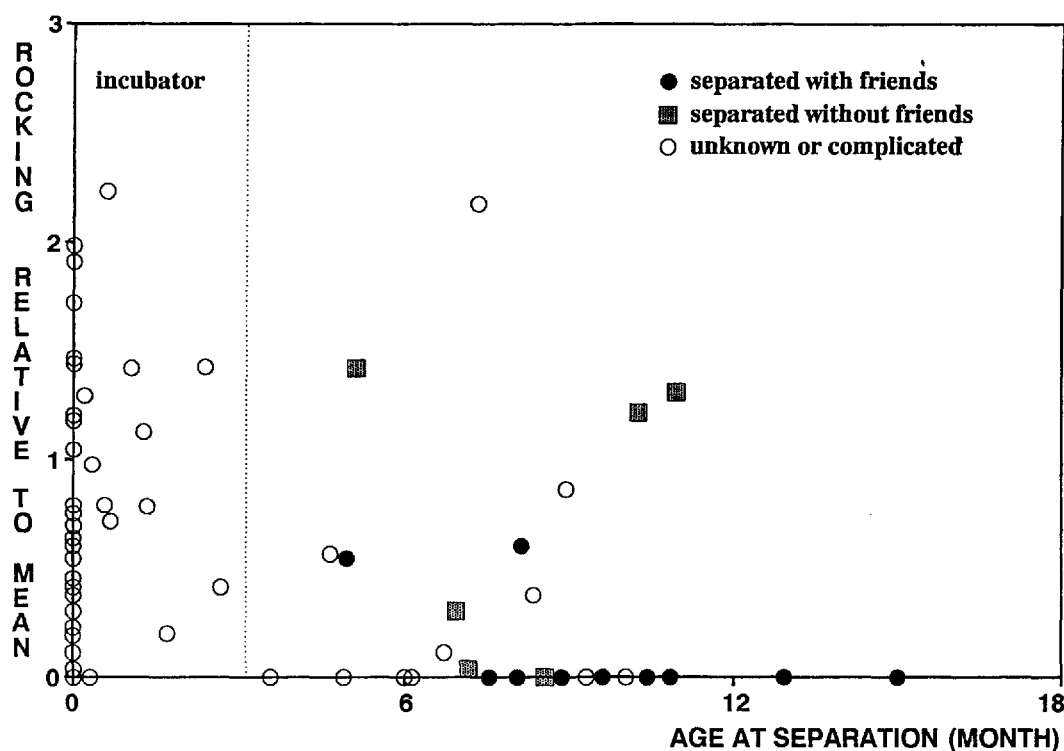


Figure 2 Age-corrected rocking levels per individual and the age at separation. The value 'one' is the mean level of an individual's age class.

To test for a separation age effect we omitted the individuals that were separated with friends, since in the case of with-friend separation there is already a different explanation. As can be judged from Figure 2, inclusion of this particular group of non-rockers would have biased the results because it includes the majority of chimpanzees that had been separated relatively late. Given this exclusion, there was no significant relationship between rocking and separation age (Kendall's Tau = -0.047 , $P = 0.663$, one-tailed). We conclude that separation age did not influence the amount of rocking.

There was also no sex difference in the relative rocking level (Mann-Whitney U test).

Events that evoke or suppress habitual rocking

Rocking and changes in group composition

Merging of two unfamiliar groups might be stressful for group members. Five times groups were merged when the individuals were 1-2 years old. Vocalizations (whimpering) were heard more often during 30 days after merging than in other periods (Mann-Whitney U test, $n_1 = 148$, $n_2 = 275$; $P < 0.001$), which indicates distress. Individual rocking levels during these 30-day post-merge periods were on average twice as high (6%) than before or afterwards (3%; see Table 4; non-rockers excluded).

In the object reaction experiment, habitual rockers rocked significantly more on the day of translocation (8%) than during control observations (2%; see Table 4; control is after having become accustomed for two days, see Methods, and without an object). However, when – in five other cases – an entire group was translocated to a different cage, the rocking level did not change (3.2% and 3.8%; Mann-Whitney U test not significant).

Rocking and disturbing events

Potentially disturbing events were noted in observation periods of the three groups with the youngest individuals (6 months to 2 years old). The events were screams in other cages ($n = 17$) and the passing of strangers ($n = 3$). Although probably not fear-inducing, entering of caregivers ($n = 9$) into a room with young early-separated infants (6-12 months) was also included, since we noticed that this could elicit rocking.

Rocking was more frequent during observation periods with these types of events than during other observations with rocking (an increase from 16 to 53 times per hour; Mann-Whitney U test, $n_1 = 29$, $n_2 = 128$; $P = 0.004$). Correspondingly, they also rocked for longer (from 7% to 14% of the observation time).

Rocking and conflicts

Conflicts among peers comprised hits, bites and screams. Conflicts were recorded in 32 of the 1,800 observation periods. Rocking did not increase after these conflicts as judged from cumulative plots of rocking time. Moreover, there were no higher frequencies of conflicts during the month after merging in which the rocking levels were doubled (Table 4). In conclusion, and contrary to our expectations, there is no evidence for an influence of conflicts on rocking.

Rocking and objects

The effects of introducing interesting objects to the chimpanzees could be explained by competition in the time budget between 'rocking' and 'object holding and manipulation'. In the object reaction experiment, behaviour was measured before and during the presence of various objects. Rocking levels did not change while interesting objects were present (2% and 2%). Various explanations for absence of an expected reduction are possible. In our situation, rocking was scarce (2%), possibly because the subjects were in groups and not solitary. In addition, usually only one of the chimpanzees could handle the object which left the others time to rock. The time spent in handling objects differed much for the group members. This might have influenced rocking. However, those who handled more did not rock less ($n = 80$; Kendall's Tau = -0.179 ; $P = 0.300$; rockers only tested for the five interesting objects).

In contrast, a fear-inducing object (a noisy robot) caused a huge increase in rocking in all rockers (from 2% to 27%; see Table 4).

Is rocking a way to cope with anxiety?

The results given above indicate that rocking increased during anxiety. We therefore hypothesize that rocking was used to reduce anxiety and that this constitutes a form of coping with stress, as was suggested for the function of stereotypies in other species (see Mason 1991). The hypothesis is supported if rockers react with less fright to disturbing events, which is expected if rocking has a soothing effect.

Table 4 Levels of various behaviours after a change in group composition or during particular circumstances. The table gives the mean percentages of time over all observation of individuals in the classes 'rockers' and 'non-rockers', \pm standard deviation.

Behaviour category	Home cage (age 1-3yr)		Object reaction experiment (age 2-5yr)			
	Control %	First month after merging %	Control %	Day of translocation %	Objects	
					Interesting	Fear-inducing
<i>Rocking:</i> <i>rockers</i>	3 \pm 4.4	6 \pm 9.3***	2 \pm 2.7	8 \pm 9.3*	2 \pm 3.3	27 \pm 23.8***
<i>Body contact:</i> <i>rockers</i>	25 \pm 24.7	37 \pm 30.2**	7 \pm 6.2	13 \pm 13.0*	8 \pm 6.7*	60 \pm 29.0***
<i>non-rockers</i>	29 \pm 29.7	59 \pm 33.5***	6 \pm 9.3	9 \pm 9.5	13 \pm 14.2***	87 \pm 10.8***
<i>Social play:</i> <i>rockers</i>	6 \pm 11.1	2 \pm 5.7**	21 \pm 20.5	3 \pm 6.9***	9 \pm 9.7***	0***
<i>non-rockers</i>	7 \pm 12.2	1 \pm 2.5**	22 \pm 22.1	8 \pm 15.0***	11 \pm 11.3**	0***
<i>Gymnastics:</i> <i>rockers</i>	12 \pm 13.9	9 \pm 10.8*	No data	No data	No data	No data
<i>non-rockers</i>	9 \pm 11.5	1 \pm 1.8***				

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$ (Mann-Whitney U test; comparison with control)

Home cage (age 1-3yr) number of observations per class: control $n(\text{rockers}) = 193$, $n(\text{non-rockers}) = 94$; after merging groups $n(\text{rockers}) = 81$, $n(\text{non-rockers}) = 29$

Object reaction experiment (age 2-5yr) number of observations per class: control $n(\text{rockers}) = 147$, $n(\text{non-rockers}) = 57$, translocation $n(\text{rockers}) = 48$, $n(\text{non-rockers}) = 21$, interesting object $n(\text{rockers}) = 106$, $n(\text{non-rockers}) = 42$; fear-inducing object $n(\text{rockers}) = 42$, $n(\text{non-rockers}) = 14$

Table 4 shows that stressful situations such as merging groups, translocation at the start of the object reaction experiment and provision of objects generally resulted in more body contact, and a decrease in social play and gymnastics (the last recorded for merging groups only). These reactions to stress are well known for young primates.

The differences between rockers and non-rockers for group merging support the hypothesis of a stress-reduction effect of rocking. Rockers increased contact less (from 25% to 37%, or a change of +12%) than non-rockers (+30%; Mann-Whitney *U* test; $P = 0.002$). They had a smaller reduction of play (−4% versus −6%; $P < 0.001$) and gymnastics (−3% versus −8%; $P < 0.001$).

For the object reaction experiment no significant differences were found between rockers and non-rockers for the day of translocation (change in body contact: +6% in rockers and +3% in non-rockers; social play: −18% versus −14%). Interesting objects are not expected to elicit much stress. Nonetheless, there was somewhat more body contact (+1% and +7%) and notably less play (−12% and −11%) but without a significant difference between rockers and non-rockers. A strong effect was expected for the noisy robot; in accordance with the hypothesis the increase in contact of +53% in rockers was clearly less than in non-rockers (+81%; Mann-Whitney *U* test; $P = 0.039$). Rockers may have increased contact less than non-rockers because rocking reduced the capacity to perform other activities within the time available. A complication was that about half of the rocking bouts were when in contact with another individual. So we computed the contact time as a percentage of the observation time minus (0.5 x rocking time). The mean contact time in rockers was thus raised to 66.5 per cent of the remaining time, which is clearly still less than that of non-rockers (Table 4: 87%).

The effect of the introduction of a fear-inducing object on play was a total abolishment in both rockers and non-rockers; this precludes testing a difference between them.

Discussion

Causes of the onset and development of rocking

Rocking developed in nearly all chimpanzees that had been separated from the mother in the absence of a familiar agemate. This happened in two different situations:

1. Nearly all individuals that had spent some time in an incubator showed rocking. These chimpanzees were separated when very young; they remained alone in an incubator until at least two months of age and they were understimulated, receiving stimulation from humans nearly solely during bottle feeding.

The age at which we observed that baby chimpanzees were able to sit upright (80 days) corresponds with the literature: Riesen and Kinder (1952) gave a mean age of 112 days; Kellogg and Kellogg (1933) 84 days; Plooi (1984) reported ages of 56 and 80 days, and Pazol and Bloomsmith (1993) 70 days. The condition of understimulation existed already before rocking could be shown; rocking appeared as soon as the ability to sit upright, a prerequisite of rocking, had developed. This suggests that the cause of rocking was present at an early age. In human infants, a modal age for the onset of rocking of six months was reported (Brody 1960; Kravitz *et al* 1960; Sallustro & Atwell 1978; Field *et al* 1979). So, as in chimpanzees, human rocking appears when sitting upright has developed. After that, rocking levels, though extremely variable, mainly remained constant for at least a year.

Pazol and Bloomsmith (1993) observed a similar change with age: 6.5 per cent of time during the first six months of age followed by a decline to about 2 per cent when older than two years.

2. When placed in a peer-only group at a more mature age, after an early period with the mother, rocking still developed in most cases. However, animals transferred in the company of a familiar peer (a 'friend') were less likely to develop rocking than those transferred without a friend. The unfamiliarity with the new peers, which could be hostile and provided little body contact comfort, was apparently a causal factor. A 'friend' mainly provided comfort through body contact. It is remarkable that this often prevented the development of rocking and thus may be assumed to alleviate much of the tension of being away from the mother and being placed in a strange situation.

Some of the early-separated animals were housed with peers after two months of age. The only interactions that were seen at this age were body contact and firm clasping. This suggests that deprivation of certain types of stimulation (by mother,agemates or humans) is a possible cause of their development of rocking, as has been reported for stereotypies in other species (Mason 1991).

Clearly the lack of motion stimulation cannot be the full causal explanation, since even when with the mother, rocking is not entirely lacking. This is found both in captivity and in the wild (Goodall 1971; Dienske & Griffin 1978; Plooij 1984). In this light it is remarkable that the behaviour was never seen in Arnhem Zoo in spite of extensive observation. A possible explanation is that mother-infant body contact in the zoo group declined much slower than under other circumstances (Spijkerman *et al* in prep). The often close presence of group members, especially mature males, may have been the reason (Spijkerman *et al* 1990). The resulting maternal restriction in the zoo group might have prevented the occasional poor attention that would have led to some rocking. In nature, mother and infant are more often alone; frustration can then arise from being off mother, and little attention. Not being picked up, little attention and fear of conspecifics were obviously factors that promoted rocking. The environmentally complex zoo condition as compared with the barren environment at TNO cannot explain this non-rockers effect, since in the even more complex natural habitat rocking does occasionally occur.

Dienske and Griffin (1978) observed an increase in body rocking upon the sight of a familiar caregiver, as was found in this study. They hypothesized, following Brody (1960), that rocking replaced impossible (frustrated) locomotion towards the caregiver in anticipation of being picked up. Thus, perhaps the expected stimulation caused frustration, and rocking may occur to obtain at least some compensation. Kravitz *et al* (1960) reported that, in human children, rocking especially was shown before falling asleep alone. In this case, frustration is again the likely cause, since young human children prefer body contact at that time.

An alternative causal explanation is possible. Rocking might simply be due to the same reasons for which the young babies had been taken from the mother at TNO, such as undernutrition and maternal neglect. We considered this a less likely explanation, since adverse conditions did not last more than a few days (often less) and several late-separated animals also showed rocking.

In conclusion, lack of comforting stimulation, anxiety, stress, the inability to change the situation and consequently frustration, are the most likely causes of body rocking. The development of rocking in both early- and late-separated individuals as well as in infants living with their mother is thus explained by one causal factor: frustration.

Influences on rocking

It seems reasonable to think that an infant which has been separated at a later age, which has benefited longer from maternal influences and is anyway older, is better buffered against separation than a young helpless baby. However, rocking levels in chimpanzees (transferred without friends) did not depend on the age at separation, which ranged from the day of birth to one year. This may be explained by the strong, long-lasting dependence on the mother in chimpanzees; later separation (after two or three years of age) may prevent the rocking habit.

Once developed, rocking was regularly seen in the absence of apparent stress or other potentially frustrating events. As in stereotypies by other species, rocking had possibly 'become independent of the stimulus that originally elicited its performance' (Mason 1991, p 1015). Some of this independence may be responsible for a lack of decline in rocking between two and nine years of age. Rocking occurred more during the first two years of life. This may be due to a greater vulnerability to such fearful stimuli in younger individuals. After a few years, peer group chimpanzees were well accustomed to each other, which predicts stable mean rocking levels that are found.

Independence from specific stimuli was not complete. Rocking by habitual rockers was roughly doubled by fearful situations such as merging or splitting groups, screams by other infants, people entering and the provision of a frightful object. Translocation of whole groups did not increase rocking levels (as was also found by Pazol & Bloomsmit 1993), so the increase in rocking before the object reaction experiment appears to be due to a change in group composition (possibly missing favoured peers) which is the only additional factor.

In the object reaction experiment, potentially interesting objects might have been expected to reduce rocking in peer groups, but a reduction was not found. This result indicates that in these socially-housed chimpanzees at TNO, boredom is not a factor that promotes rocking. Pazol and Bloomsmit (1993) additionally found that almost continuous presence of a dog in the cage of young chimpanzees made them rock less (1.3%) than when a dog was absent (4.7%).

We did not find an influence of sex on rocking nor did Pazol and Bloomsmit (1993).

The function of rocking

There is evidence for various species that stereotypies are accompanied by lowered arousal and less responsiveness to stimuli (Cooper & Nicol 1991; reviewed by Mason 1991). Reduced arousal and responsiveness might enable an individual to cope better with stress. We found that rockers maintained less body contact and played more under stress than non-rockers did. So, most of the relevant data on social behaviour indicate that the fear reactions of rockers were partly replaced by rocking. The hypothesis that rocking is a way of coping with stress is supported. This suggests that having learned that rocking both reduces arousal under very stressful circumstances and reduces frustration in situations that cannot be changed, enabled

rockers to use the behaviour for coping. However, in conflicts among peers (comprising screams) an increase of rocking would be expected but this was not found. Perhaps conflicts are relatively controllable through body contact, flight and fending for oneself. An alternative explanation, that rocking is simply an expression of stress, is not likely since rocking is regularly seen in the absence of apparent stress or other potentially frustrating events and is not found in or after conflicts.

Sallustro and Atwell (1978) found a prevalence of 19 per cent in normal human children from California. So in humans, rocking may be a normal reaction to stressful or frustrating circumstances. One of these might be a lack of parental attention (Brody 1960).

In conclusion, rocking can be seen as a reaction to unpleasant, frustrating or fearful circumstances and is possibly used for coping with these.

Why rocking and not a different stereotypy?

In rhesus macaques, stereotyped locomotion was common after separation from the mother and placement in peer groups in the TNO Primate Centre (Paulk & Dienske 1977). Rocking was rarely seen. Rarity of rocking in rhesus peer groups was also noted in the review by Capitanio (1986). However, in rhesus macaques isolated with a stationary surrogate mother, rocking developed after 50 days of age. Rocking in rhesus macaques perhaps develops mainly in total social isolation.

We have not seen stereotyped locomotion in chimpanzees, nor are we aware of reports. Rocking is also the prominent whole-body stereotypy in human children. A reason for the absence of stereotyped locomotion in chimpanzees and humans could be that both species can develop rocking before the age that locomotion is developed (see *Causes of the onset and development of rocking*: 1 above).

However, chimpanzees separated without friends, and able to walk, also rocked and did not show stereotypic walking. Moreover, rhesus monkeys socially isolated at an age when locomotion is possible in this species did develop rocking (Mason & Berkson 1975). So an inability to walk cannot be the full answer. Possibly, a longer dependence on the motor activity and physical support from the mother causes this species difference.

Animal welfare implications

The most probable causes of the development of rocking are frustrating social circumstances and the inability to cope with these. The frequent development of rocking under different circumstances in young chimpanzees and humans demonstrates that the behaviour is not a bizarre reaction to unsurmountable stress, but a behaviour which may help an individual to cope with difficulties.

In terms of animal welfare, rocking in chimpanzees housed in laboratory conditions is an indication of a less optimal reaction pattern to frustrating circumstances. The development of rocking may be prevented if the babies are left with their mother and in their social group. Rocking after (late) separation may be prevented when transfer takes place together with familiar peers.

Acknowledgements

We are grateful to the directorate and animal caretakers of Burger's Zoo Arnhem and the TNO Primate Center, Rijswijk, for continuously providing the facilities and the opportunities to study the chimpanzees. Furthermore, we would like to thank G van Dinteren, J van 't Land, E van Rhijn, G Schoonman and W van Willigen, students at Utrecht University who participated in 9 or 12 month observation and analysis projects. This work was supported by grant 811.430.282 from the Netherlands Organization for Scientific Research (NWO), the Netherlands.

References

- Adang O M J 1986 *Teasing, Harassment, Provocation: The Development of Quasi-aggressive Behaviour in Chimpanzees*. PhD Thesis, Utrecht University
- Adang O M J, Wensing J A B and Hooff J A R A M van 1987 The Arnhem Zoo colony of chimpanzees *Pan troglodytes*: development and management techniques. *International Zoo Yearbook* 26: 236-248
- Baumeister A A and Forehand R 1973 Stereotyped acts. *International Review of Research in Mental Retardation* 6: 55-96
- Berkson G 1967 Abnormal stereotyped motor acts. In Zubin J and Hunt H F (eds) *Comparative Psychobiology: Animal and Human* pp 76-94. Grune & Stratton: New York
- Berkson G 1968 Development of abnormal stereotyped behaviors. *Developmental Psychobiology* 1: 118-132
- Berkson G and Mason W A 1964 Stereotyped behaviors of chimpanzees: relation to general arousal activities. *Perceptual and Motor Skills* 19: 635-652
- Berkson G, Mason W A and Saxon S V 1963 Situation and stimulus effects on stereotyped behaviors of chimpanzees. *Journal of Comparative Physiological Psychology* 56: 789-792
- Brody S 1960 Self-rocking in infancy. *Journal of the American Psychoanalytic Association* 8: 464-491
- Capitanio J P 1986 Behavioral pathology. In Michell G and Erwin J (eds) *Comparative Primate Biology: 2A Behavior, Conservation and Ecology* pp 411-454. Alan R Liss: New York
- Cooper J J and Nicol C J 1991 Stereotypic behaviour affects environmental preference in bank voles, *Clethrionomys glareolus*. *Animal Behaviour* 41: 971-977
- Davenport R K 1979 Some behavioral disturbances of great apes in captivity. In Hamburg D A and McCown E R (eds) *The Great Apes: Perspectives on Human Evolution, Volume V* pp 341-357. The Benjamin/Cummings Publishing Company: Menlo Park, California
- Davenport R K and Menzel E W 1963 Stereotyped behavior of the infant chimpanzee. *Archives of General Psychiatry* 8: 99-104
- Davenport R K and Rogers C M 1970 Differential rearing of the chimpanzee, a project survey. In Bourne G H (ed) *The Chimpanzee* 3 pp 337-360. S Karger: Basel

- Dienske H and Griffin R 1978 Abnormal behaviour patterns developing in chimpanzee infants during nursery care – a note. *Journal Child Psychology and Psychiatry* 19: 387-391
- Dienske H and Vreeswijk W van 1987 Regulation of nursing in chimpanzees. *Developmental Psychobiology* 20: 71-83
- Field T, Ting G and Shuman H H 1979 The onset of rhythmic activities in normal and high risk infants. *Developmental Psychobiology* 12: 97-100
- Forrester R 1980 Stereotypies and the behavioural regulation of motivational state. *Applied Animal Ethology* 6: 386-387 (Abstract)
- Fritz J and Fritz P 1985 The hand-rearing unit: management decisions that may affect chimpanzee development. In Graham C E and Bowen J A (eds) *Monographs in Primatology, Volume 5: Clinical Management of Infant Great Apes* pp 1-34. Alan R Liss Inc: New York
- Fritz J, Fritz P, Alford P L and Bowan J A 1992 Abnormal behaviors, with a special focus on rocking and reproduction competence in a large sample of captive chimpanzees (*Pan troglodytes*). *American Journal of Primatology* 27: 161-176
- Goodall J 1971 Some aspects of mother–infant relationships in a group of wild chimpanzees. In H R Schaffer (ed) *The Origins of Human Social Relations* pp 115-128. Academic Press: London
- Goosen C 1981 Abnormal behavior patterns in rhesus monkeys: symptoms of mental disease? *Biological Psychiatry* 16: 697-716
- Goosen C, Schrama A, Brinkhof H, Schonk J and Hoek L A van 1983 Housing conditions and breeding success of chimpanzees at the Primate Center TNO. *Zoo Biology* 2: 295-302
- Hooff J A R A M van 1973 A structural analysis of the social behaviour of a semi captive group of chimpanzees. In Cranach M and Vine I (eds) *Social Communication and Movement* pp 75-162. Academic Press: London
- Kellogg W N and Kellogg L A 1933 *The Ape and the Child: A Study of Environmental Influences upon Early Behaviour*. McGraw-Hill: New York
- Kravitz H, Rozenthal V, Teplitz Z, Murphy J B and Lesser R E (1960) Head-banging in infants and children. *Diseases of the Nervous Systems* 21: 203-208
- Mason G J 1991 Stereotypies: a critical review. *Animal Behaviour* 41: 1015-1037
- Mason W A 1968 Early social deprivation in the nonhuman primates: implications for human behavior. In Glass D C (ed) *Environmental Influences* pp 70-101. The Rockefeller University Press: New York
- Mason W A and Berkson G 1975 Effects of maternal mobility on the development of rocking and other behaviors in rhesus monkeys: a study with artificial mothers. *Developmental Psychobiology* 8: 197-211
- Meder A 1989 Effects of hand-rearing on the behavioral development of infant and juvenile gorillas (*Gorilla gorilla*). *Developmental Psychobiology* 22: 357-376

- Paulk H H and Dienske H** 1977 Abnormal behavior in relation to cage size in rhesus monkeys. *Journal of Abnormal Psychology* 81: 87-92
- Pazol K A and Bloomsmith M A** 1993 The development of stereotyped body rocking in chimpanzees (*Pan troglodytes*) reared in a variety of nursery settings. *Animal Welfare* 2: 113-129
- Plooij F X** 1979 How wild chimpanzee babies trigger the onset of mother-infant play and what the mother makes of it. In Bullow M (ed) *Before Speech: The Beginnings of Human Communication*. Cambridge University Press: London
- Plooij F X** 1984 *The Behavioral Development of Free-living Chimpanzee Babies and Infants*. Ablex Publishing Company: Norwood, New Jersey
- Riesen A H and Kinder E F** 1952 *Postural Development of Infant Chimpanzees*. Yale University Press: New Haven
- Sallustro F and Atwell C W** 1978 Body rocking, head banging, and head rolling in normal children. *The Journal of Pediatrics* 93: 704-708
- Siegel S** 1956 *Nonparametric Statistics for the Behavioral Sciences*. McGraw-Hill Inc: New York
- Spijkerman R P** 1987 Behaviour development of infant chimpanzees with the mother and in peer groups. *Annual Report, Division of Health Research TNO Primate Center*: 309-312
- Spijkerman R P, Dienske H, Hooff J A R A M van and Jens W** (in prep) Differences in behaviour development between young chimpanzees living with peer-only and those living in a semi-natural group.
- Spijkerman R P, Hooff J A R A M van and Jens W** 1990 A case of lethal infant abuse in an established group of chimpanzees. *Folia Primatologica* 55: 41-44
- Wemelsfelder F** 1990 Boredom and laboratory animal welfare. In Rollin B E (ed) *The Experimental Animal in Biomedical Research* pp 243-272. CRC Press: Boca Raton, USA