



Fig. 1. Course of the elaboration of the conditioned reflex (solid line) and of the re-elaboration of the conditioned reflex (broken line) in rats weaned on the 15th, 16th, 17th, 25th, and 30th day after birth. Abscissa: number of sessions; ordinate: average of positive responses during one session.

with the slowest and the intermediate rates of elaboration (Table 1).

In testing for stability of the memory trace we found that the percentage of positive responses during the first session after an interval of 4 months is highest in rats weaned on days 30, 17, and 16. Compared with the memory trace in rats weaned at 30 days of age (Table 2), statistically fewer positive responses were found in rats weaned on day 25 ( $P \leq .05$ ), and least evidence of the memory trace was found in rats weaned on day 15 ( $P \leq .003$ ).

For the reelaboration of the old conditioned reflex, rats weaned at the age of 30, 25, 17, and 16 days need fewer connections of conditioned and unconditioned stimuli than they did during the first elaboration. Rats weaned at the age of 15 days need practically the same number of connections of the conditioned and unconditioned stimuli for the reelaboration as they did for the first elaboration (Table 3 and Fig. 1).

Sudden change from a diet of breast milk to one of high carbohydrates on day 15 led to essential changes in reactions of the nervous system—the conditioned reflexes were elaborated more slowly and the memory trace was very weak (6, 7). Therefore we consider weaning on the 15th day of life to be premature. By this criterion weaning performed on day 15 is most unfavorable and weaning on day 30 is opti-

mum. The removal of the mother from the young on days 16, 17, and 25 is also premature.

According to Scott's theory (8), the development of the individual, as well as the postnatal ontogenesis, goes on in so-called critical periods; Denenberg (9) demonstrates that we can presume the existence of critical periods in development by the fact that the same impulse applied at different ages evokes a different response. According to this criterion, weaning of rats in various stages of the suckling period can aid in determining both the optimal time of weaning for development of the highest functions of the brain and the decisive periods for this development—before the 30th day of life and at or after the 30th day.

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## Free-Ranging Rhesus Monkeys: Age and Sex Differences in Individual Activity Patterns

**Abstract.** Two hundred thirty of the feral rhesus monkeys on Cayo Santiago were observed individually for postural adjustments, locomotor behavior, manipulation, and other nonsocial activities. Both form and frequency of activity were influenced strongly by age; sex differences were minimal. Most activities decreased with age, but head movements, presumably reflecting visual scanning, were more frequent in adults.

Free-ranging rhesus monkeys have been studied rather extensively with regard to patterns of social and sexual behavior (1, 2). Although many investigators have made reference to the general activity of monkeys, no formal data have been available on the frequency with which individuals, not actively involved in social acts, assume different postures and engage in various behaviors such as locomotion, climbing, manipulation of inanimate objects, and self-grooming. Data of this type on individuals are useful for comparison with studies of the motor behavior of monkeys maintained in more restricted settings, that is, in laboratory cages or compounds; it can also serve as a base line for estimating the effect of ecological and social factors on activity in the field. This is a report of a survey of approximately two-thirds of the monkeys on Cayo Santiago, Puerto Rico. Special attention was paid to the influence of age and sex on selected postures and activity patterns.

The study was made during February and March 1964. At that time the colony on Cayo Santiago consisted of approximately 368 rhesus monkeys (*Macaca mulatta*) grouped in six distinct bands ranging in size from over 100 members to less than 20 (2). Over the 2-month period, 230 individually identified monkeys were observed on one or more occasions for 2-minute periods (eight consecutive 15-second intervals), and the incidence of various postures and activities was recorded on a checklist. Since only the occurrence or nonoccurrence of a given posture or activity was scored for each 15-second interval, the maximum possible score per observation period was 8 for any one behavior category. The categories of the checklist were (i) postures: quadrupedal, bipedal, seated, lying (on chest, back, or side) and (ii) ac-

tivities: horizontal locomotion (walking or running), vertical locomotion (climbing or jumping), self-manipulation, object manipulation, and head movements which were distinct from other ongoing locomotor or manipulatory activities. High reliability among observers (less than 5 percent disagreement) had been found previously when this checklist was used to record activity of caged monkeys. Records were also made of the monkey's approximate distance from the observer and his vertical position (high, more than 4 m off the ground; medium, 0 to 4 m; or on the ground).

The majority of observations took place in fair weather between 7 a.m. and 2 p.m. The following procedure was used. When a group of monkeys was located, the observer stationed himself quietly in or near the group and then identified and observed as many animals as possible, one at a time. Repeated observations of the same monkey were not made in the same area; however, if a previously observed animal was seen in a different place after at least a 1-hour interval, its behavior might again be sampled. Duplicate observations rarely occurred on the same day. Care was taken to select monkeys at varying distances for observation and, in each case, the approximate distance was recorded for future analysis. A 2-minute observa-

tion period was found to be optimal and enabled the observer to keep the monkey in full view without shifting position.

Several restrictions were placed on the sampling procedure. Because of the frequent intense social interaction at the feeding stations, the monkeys were not observed there. In order to obtain indices that were relatively independent of immediate social influence, monkeys were not sampled if they were grooming, fighting (including play-fighting and chasing), or threatening the observer. The terrain had to include trees so that the animals could be observed in varying vertical positions. A monkey was observed only if he was in the area at the time of the observer's arrival or if at least 5 minutes had elapsed after the animal's entry. Finally, if generalized fighting broke out or the whole group began to move off, observations were discontinued. Thus, observations were made of monkeys in a group occupying a limited area and with minimum interference from each other and from other bands. Social behavior is an important part of the feral monkey's total activity, and individual differences influence the nature and frequency of direct social interactions. The above selective procedure was designed to supplement and extend previous studies of age and sex differences in (social)

activity, rather than to give a fully representative account of the level of activity.

In all, 515 2-minute observations were made. Where repeated samples were obtained on the same individual, mean values were computed for each checklist category. These scores were then broken down according to sex and four age groups, and an analysis of variance was performed separately for each behavior category. Table 1 summarizes the mean category scores and the *F* ratios resulting from the analyses of variance. Younger monkeys, yearlings and 2- to 3-year-olds especially, had higher scores than older ones in nearly every category. Younger animals assumed quadrupedal and bipedal postures more frequently and also walked, ran, climbed, jumped, and changed from one posture to another more. They manipulated objects in the environment more frequently and were more arboreal than the older ones. In contrast, older monkeys showed much less locomotor activity but increased movements of the head, which presumably represent visual scanning of the environment. Sitting behavior showed no changes with age. However, younger monkeys tended to shift postures within a 15-second period and sitting, although frequent, occurred for briefer spans of time.

Table 1. Mean behavior scores for free-ranging rhesus monkeys (Cayo Santiago colony) according to age and sex. Maximum value, 8.00; M, male; F, female.

Behavior categories	Age in years								<i>F</i> ratios	
	Yearling		2 to 3		4 to 5		6 and over		Age	Sex
	M(n=9)	F(n=21)	M(n=35)	F(n=41)	M(n=19)	F(n=27)	M(n=34)	F(n=44)	(df 3/222)	(df 1/222)
<b>Postures</b>										
Quadrupedal	2.86	3.73	2.48	2.70	0.68	1.21	0.56	0.61	45.81*	4.01†
Bipedal	0.23	0.18	0.29	0.13	0.00	0.05	0.01	0.07	2.74†	.22
Seated	7.31	6.70	7.36	7.10	7.61	7.47	7.27	7.20	1.43	1.62
Lying down										
Chest	0.00	0.13	0.21	0.20	0.05	0.30	0.21	0.15	.67	.03
Side	0.04	0.10	0.15	0.21	0.24	0.15	0.59	0.37	2.16	.45
<b>Activities</b>										
Walking	2.65	3.56	2.45	2.56	0.61	1.13	0.36	0.48	46.49*	3.67
Running	0.11	0.19	0.17	0.17	0.05	0.05	0.00	0.00	4.70‡	.01
Climbing	1.43	2.37	1.22	1.34	0.15	0.10	0.08	0.00	54.91*	2.44
Jumping	0.58	0.65	0.70	0.70	0.09	0.05	0.00	0.00	13.54*	.02
Head movement	6.23	6.54	7.22	7.18	7.34	7.35	7.50	7.25	3.55†	.36
Self-manipulation	3.00	1.84	2.44	2.19	2.65	2.24	2.26	2.09	.02	1.77
Object manipulation	3.26	3.67	3.29	2.27	1.83	1.58	0.69	0.54	20.93*	1.25
<b>Position</b>										
High (over 4 m)	2.92	3.77	1.74	1.44	0.81	0.68	0.66	0.06	11.20*	2.49
Medium (0 to 4 m)	3.86	4.67	4.96	4.67	3.85	3.40	3.44	3.02	3.92‡	.33
On ground	1.22	1.39	1.30	1.88	3.34	3.92	3.90	4.91	18.11*	2.77

\*  $p < .001$ . †  $p < .05$ . ‡  $p < .01$ .

Significant sex differences were found in one category only—quadrupedal posture. This finding is important since the observations were made during the birth season and it might be expected that older pregnant females or females with newborns would be less active than males. In contrast, however, there was a general decrease in activity with age regardless of sex. A significant interaction between age and sex was found only in the high-position category ( $F$ , 11.90;  $df$ , 3/222;  $p < .001$ ); female yearlings tended to be found in high positions more frequently than did males, whereas the opposite was true for older monkeys. Mean distance of the observed monkeys was 7.04 m, and there were no significant differences beyond the .05 level of confidence due to age or sex (age  $F$ , 2.18;  $df$  3/222; sex  $F$ , .71;  $df$  1/222). However, this refers to sampled monkeys only and no data were obtained on age or sex differences in all monkeys surrounding the observer.

Age differences in overall frequency of overt activity are not very surprising, but considerable research remains to be done before we know all of the specific forms of activity that change, or the relationships between various changes, or the physiological and behavioral mechanisms that produce such changes. This study was of course concerned with the first two, logically prior, problems. There are many possible reasons for the observed general reduction of overt responsiveness with age. The activities of young monkeys have not been fully channeled into social behavior patterns (such as grooming); they are more varied and remain somewhat diffuse with respect to objects. The characteristic arousal levels of young and old probably differ, and minimum environmental stimuli certainly produce more immediate changes in the overt activity of the young. Also, in a highly dominance-oriented social order, monkeys learn to communicate through subtle cues which need not involve gross motor activity. Indeed, learning to live in the group may depend upon the ability of young monkeys to learn to inhibit locomotor activity in favor of alert watchfulness

in a relatively still posture. The more frequent head movements in the older monkeys would certainly support such a notion. Finally, since the study was conducted during the birth season, yearlings and 2- and 3-year-olds had been rejected or forced away from the mother to some extent in favor of the newborn, and this may have led to a concomitant increase in exploration and locomotion.

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#### Galactose Metabolism

In H. M. Kalckar's otherwise satisfying exposition of the present state of knowledge of the galactose pathways [*Science* **150**, 305 (1965)], the statement is made that reaction 4 ( $\text{UDPG} + \text{PP} \rightleftharpoons \text{G-1-P} + \text{UTP}$ ) is "required in order to label the carbon of the glucose metabolic pool" and is important in assessing the block site in routine screening of galactosemics. That is clearly not true, as inspection of reactions 1–3 will show, since labelled G-1-P arises through displacement from UDPG by Gal-1-P. Assessments of block sites for UDPG pyrophosphorylase are important in so far as they reveal lesions in the route of synthesis of galactosides from other hexose precursors.

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Razzell's point is correct. The formulation depends somewhat on the kind of system one is dealing with. In the *Science* article, I had so much territory to cover that I did not take space to elaborate on the function of these enzymes.

In a model system the first three steps (catalyzed by galactokinase, Gal-P/G-1-P uridyl transferase, and UDP-Gal-4-epimerase, respectively) suffice to introduce the carbon-14 of galactose into the glucose metabolic pool, as Razzell points out. However, in intact cells, the UDP-glucose levels are usually whittled down constantly by anabolic reactions (for instance, Le-loir's type of enzymes, which catalyze glycosyl transfer in the service of oligo- or polysaccharide synthesis). In incubation experiments over more extended periods (that is, over more than a small fraction of the generation time of the cells used), step No. 4 becomes therefore also important for the rate of incorporation of carbon-14 from galactose into the glucose metabolic pool. For earlier discussions of some of these problems see *Advan. Enzymol.* **20**, 111 (1960). An article dealing with the kinetics of incorporation is in press (Robinson, Kalckar, Troedsson, Sanford, *J. Biol. Chem.*)

I use this opportunity to recommend a slight but important change in terminology when equations dealing with uridyl transferases are concerned. Instead of writing:  $\text{Gal-1-P} + \text{UDPG} \rightleftharpoons \text{G-1-P} + \text{UDPGal}$  for reaction 2, write:  $\text{Gal-1-P} + \text{URPPG} \rightleftharpoons \text{G-1-P} + \text{URPPGal}$ . "URPPG" still reads uridine diphosphoglucose, of course. The formulation may provide better orientation for teaching. I have even tried more detailed equations indicating the fate of the carbon and phosphorus as well as of the oxygen (of the phosphate) in the uridyl transferase reactions [see H. M. Kalckar and H. Klenow, *Ann. Rev. Biochem.* **23**, 527 (1954)]. However, I believe that the suggested formulation usually suffices.

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