Propensity for paradoxical sleep following deprivation in rats of different age groups*

T. L. HOLDSTOCK and G. J. VERSCHOOR University of the Witwatersrand, Jan Smuts Avenue Johannesburg, South Africa

The propensity for paradoxical sleep (PS) during different maturational stages was investigated by depriving adolescent and adult rats of PS for 72 h. Despite more PS under baseline conditions, adolescent rats did not have significantly more PS than did older animals on two postdeprivation sessions. However, before any meaningful conclusion can be drawn about the differential need for PS following deprivation by different age groups, such variables as period of deprivation and stage of maturation must be considered with great care.

It has repeatedly been demonstrated in a number of species that amount of paradoxical sleep (PS) is inversely related to age. For instance, not only the human infant (see Hartmann, 1966), but kittens (Hartmann, 1966), infant monkeys (Berger & Meier, 1966; Meier & Berger, 1965), chicks (Corner & Bakhuis, 1969; Greenberg, Kelty, & Dewan, 1966), and lambs (Hartmann, 1966) exhibit more PS than do older members of the species. It can, therefore, be assumed that deprivation of PS (PSD) would be more disruptive to the young of a species and that the propensity for compensatory amounts of PS would be more in evidence in them than in older animals. Preliminary results from our laboratory (Holdstock & Franks, 1971) were in support of this notion. In our work, adolescent and young adult rats exhibited enhanced PS compensation following deprivation, although they did not differ from older animals in terms of amounts of baseline PS. However, Berger & Meier (1966) reported that infant, in contrast to juvenile, monkeys failed to show any real compensatory effects following PSD. Although this interesting finding is contrary to what might be expected, it nevertheless suggests a functional inequality of PS between the two age groups (Berger & Meier, 1966). Comparison of the results of the two studies is premature, however, since they differed in too many aspects. Besides the fact that different age groups were compared in the two studies, the species used also differed, and it has been suggested by Berger & Meier (1966) that postdeprivation effects might be species specific. Since our previous report on postdeprivational age differences was only of a preliminary nature, the purpose of the present experiment was to determine the propensity for PS following

deprivation in rats with age differences roughly equivalent to that of our previous report.

PROCEDURE

Sixteen male hooded rats of the Long-Evans strain were used. Eight animals were 29-30 weeks old and weighed 400-440 g. The other eight rats were 11-15 weeks old and weighed 230-270 g. They were housed under conditions of constant illumination.

All animals were chronically implanted under sodium pentothal anaesthesia for electroencephalographic (EEG) and electromyographic (EMG) recordings. The electrodes were similar to those previously used (Holdstock & Franks, 1971) and consisted of unipolar amphenol Type 27-9 connectors that were modified to serve a bipolar function. EEG electrodes were placed on the cortex, 2 mm lateral to the midline, at points 3 mm anterior and 4 mm posterior to the bregma; EMG electrodes were inserted into the dorsal neck muscles of the rat, while both electrode assemblies were fixed on the skull following standard procedures.

Five days after surgery, the animals were adapted to the experimental environment for the first of two daily sessions. On each session, they were allowed to sleep for 6 h with the recording leads attached. Baseline sleeping behavior was next recorded during a 6-h session (Session 1) on the day following the second adaptation session. The animals were tested four 23 cm) with aluminum sides and perspex fronts. The cages were housed in a semisoundproof room, maintained at 74° F and 50% humidity. A one-way mirror allowed observation of the animals. The EEG and EMG of each animal were recorded on a Beckman Type R polygraph. All recordings were continuously monitored, and notations made on the EEG record of the behavioral state of the animal.

Deprivation of PS was initiated immediately at the end of the baseline

session. Since the size of the younger animals was the same from front to hind shoulder as that of the older group, each rat was placed on an inverted flower pot with a 6.5-cm base (Morden, Mitchell, & Dement, 1967). The flower pots were kept in plastic buckets filled with approximately 4.0 cm of water. This arrangement caused the animals to slide down the pot when they experienced muscle relaxation during PS without getting wet unnecessarily, as is the case with a water level coming up to the base of the pot. Food and water were in easy reach of the animals. After the rats had been subjected to these deprivation conditions for 3 days, two postdeprivation recordings were made on consecutive days (Sessions 2 and 3). Session 3 started 18 h after termination of Session 2. The animals were maintained on the flower pots during the 18 h. All sessions started at 9:00 a.m. and lasted 6 h.

The records were scored for wakefulness, slow-wave sleep (SS), and PS (see Holdstock & Franks, 1971). Awake was defined by the presence of theta and low-voltage mixed-frequency EEG in conjunction with the tonic EMG activity; SS by the presence of irregular slow waves of large amplitude and spindles in the EEG; PS by synchronous theta lasting at least 20 sec in the presence of EMG suppression. A distinguishing feature of the EEG rhythms during PS was the regularity of amplitude. At times, the EEG activity during PS was interrupted by short periods of attenuated and irregular amplitude characteristic of the waking EEG. Although this activity was sometimes accompanied by a shifting of position or circling movement by the animal, it did not appear as if waking occurred, for the EEG record regained the appearance of PS after only a few seconds. Such periods, classified as Stage III by Roldan, Weiss, & Fifkova (1963), were scored as PS in this study.

RESULTS

Mixed design analysis of variance (Myers, 1966) was carried out on the baseline and postdeprivation data for three sets of data: percent sleep of total recording time; percent PS of total sleep time; and percent SS of total sleep time. In addition, Mann-Whitney U-tests were used to compare the age groups with respect to baseline, first postdeprivation and second postdeprivation sessions, on each measure of sleeping activity.

The PS of young and adult rats on postdeprivation sessions did not differ with respect to amount (F = 3.66, df = 1/14, p > .05) or pattern (Group by Session: F = 0.97, df = 2/28, p > .05), while younger rats had somewhat

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Fig. 1. Mean percent time adolescent and mature adult rats spent asleep and in the various stages of sleep.

more PS than adult rats on the baseline session (U = 8, p = .005) (see Fig. 1). The only other aspect of sleep on which the groups differed was the amount of baseline SS (U = 8, p =.005). Since this measure was the complement of PS, younger animals experienced relatively less SS than adult rats (Fig. 1).

Concomitant with an increase in all animals in the duration of the total sleep time following deprivation (F =17.67, df = 2/28, p < .001), Fig. 1 shows that the proportionate amount of time spent in PS increased as well (F = 83.27, df = 2/28, p < .001).

DISCUSSION

The fact that PSD decreased, rather than enhanced, differences between the two age groups with respect to amount of PS does not support the idea that young animals have a greater

need to compensate for loss of PS. Thus, the observation (Holdstock & Franks, 1971) that young rats were more prone to PSD could not be replicated with a larger number of animals. If anything, younger animals seemed to have less propensity to make up lost PS.

However, a number of factors must be considered in interpreting the present results. In the first place, it is possible that the difference in age was not sufficiently great or did not span sufficiently distinctive maturational periods in the life of the rat to maximize any possible postdeprivational differences. In the second place, the number of days the animals were deprived of PS could be an all important variable. Compared to the 6-7 days animals were maintained on small flower pots in our earlier

work (Holdstock & Franks, 1971). they stayed on the flower pots for only 3-4 days in the present study. Evidence arguing in favor of the importance of the period of deprivation relates to the tendency of young animals to exhibit enhanced PS on the second postdeprivation session compared to adult rats. Consideration will have to be given to these and other experimental variables, such as species differences, in order to evaluate satisfactorily the maturational importance of PS by means of deprivation techniques.

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