

STUDIES IN THE
TOTAL SLEEP DEPRIVATION
OF RATS

By

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TABLE OF CONTENTS

ACKNOWLEDGMENTS.....	11
LIST OF TABLES.....	iv
LIST OF FIGURES.....	vi
ABSTRACT.....	vii
INTRODUCTION.....	1
METHOD.....	2
EXPERIMENT I.....	7
METHOD.....	9
RESULTS AND DISCUSSION.....	11
SUMMARY.....	22
EXPERIMENT II.....	23
METHOD.....	27
RESULTS.....	28
DISCUSSION.....	35
SUMMARY.....	41
EXPERIMENT III.....	43
METHOD.....	44
RESULTS AND DISCUSSION.....	47
SUMMARY.....	53
EXPERIMENT IV.....	56
METHOD.....	63
RESULTS AND DISCUSSION.....	64
SUMMARY.....	83
REFERENCES.....	86
BIOGRAPHICAL SKETCH.....	90

LIST OF TABLES

1.	Shocks per Hour per Individual <u>S</u> in Shock-S, Shock-W, Group A and Total per <u>S</u> after 19 Hours of Deprivation.....	13
2.	Analysis of Variance Based on First 19 Hours of Deprivation for all Three Groups for Data in Table 1.....	15
3.	Hours of Deprivation by Procedure A for Individual <u>Ss</u> till Override of Shock Whose Intensity and Duration are Specified.....	16
4.	Frequency of Occurrence of Each Permutation of Intershock Intervals for Group A.....	21
5.	Summary of the Literature on the Limit of Sleep Deprivation.....	24
6.	Baseline and Recovery Sleep after Deprivation Procedures A and P in Mean Percent per 24-Hour Day.....	48
7.	Summary of Analyses of Variance for Data for which Group-by-Day Means are in Table 6.....	49
8.	Circadian Rhythm: Daytime and Nighttime TS and Day/Night Ratio for Baseline and Days after Deprivation Procedures A and P.....	50
9.	Circadian Rhythm: Increase in Percent Sleep over Baseline after Deprivation Procedures A and P.....	51
10.	Sleep Episodes in Terms of Frequency of Occurrence of Specified Length of Episodes...	54
11.	Overall Analyses of Variance for TS, SWS and PS per 24-Hour Day for which Data are in Tables 12, 13 and 14.....	65
12.	SWS Group Means in Percent Pre and Post Deprivation (per 24-Hour Day).....	66
13.	PS Group Means in Percent Pre and Post Deprivation (per 24-Hour Day).....	67
14.	TS Group Means in Percent Pre and Post Deprivation (per 24-Hour Day).....	68
15.	Percent of Lost SWS, PS and TS Recovered During Days 1 to 9 per Individual Subject and Group.....	73

16.	Circadian Rhythm: Daytime and Nighttime TS and Day/Night Ratios for Groups A and P....	78
17.	Circadian Rhythm: Increase in Percent Sleep over Mean of Two Baseline Measures for Daytime and Nighttime Hours after Deprivation Procedures A and P.....	79
18.	Frequency of Occurrence of Minute Sleep Episodes Grouped in Three Class Intervals.....	82

LIST OF FIGURES

1.	Mean number of shocks/h of deprivation for three levels of shock intensity.....	12
2.	Intershock interval for <u>S</u> A-1.....	19
3.	Percent weight loss as a function of days of deprivation.....	30
4.	Sleep percent despite deprivation procedures as a function of days of deprivation.....	31
5.	Sleep percent despite deprivation as a function of time of day during deprivation....	32
6.	Midnight and noon sleep latencies for two <u>Ss</u> as a function of days of deprivation...	34
7.	Slow-wave sleep group means pre and post deprivation per 24-hour day.....	70
8.	Paradoxical sleep group means pre and post deprivation per 24-hour day.....	71
9.	Total sleep group means pre and post deprivation per 24-hour day.....	72

Abstract of Dissertation Presented to the Graduate Council
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STUDIES IN THE TOTAL
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Two deprivation procedures were used to keep rat Ss awake. The first, Procedure A, consisted of delivering shock to the feet contingent upon the appearance of SWS in the EEG. The effect of shock intensity on the number of shocks/h required to keep Ss awake was inconclusive. The number of shocks/h was an increasing function of the time or duration of deprivation. After about 15 to 20 h of deprivation, there was a relatively sharp increase in the number of shocks/h reflecting sleep override of the shock. That is, Ss obtained substantial amounts of sleep by falling asleep about 20 s after each shock of 10 consecutive shocks.

The other deprivation method, Procedure P, consisted of presenting a wide variety of changing stimuli, excluding shock, that were not contingent upon the appearance of EEG SWS. When the assistants delivering the stimuli and monitoring the EEG made a maximal effort, the procedure resulted in Ss being awake up to 99% of the time. As deprivation proceeded, it was found that the latency of sleep onset, when Ss were placed in a cage and briefly left undisturbed, decreased during the first three days to about 20 s. Also, Ss' muscle tonus decreased greatly with time or duration of deprivation.

With deprivation Procedure A, the limit or terminal point was sleep override of shock. Ss fell asleep about 20 s after being shocked and were obtaining substantial amounts of sleep after 15 to 20 h of deprivation. With deprivation Procedure P, the terminal point seemed determined by lowered arousal which made responses necessary for Ss' survival impossible. One S developed a pulmonary problem and one showed a disinterest in food and a sharp weight loss. The deprivation procedure was still keeping both Ss awake.

With deprivation Procedure A, it seemed possible to keep Ss awake for a maximum of about 40 h. With Procedure P, Ss could be kept awake for about 12 to 15 days.

It was tentatively concluded that Procedure A was far less effective than Procedure P for two reasons. First,

intense pain is a stimulus for sleep even when SS are not sleep-deprived. Secondly, SS may have habituated to shock in Procedure A, but could not habituate to a wide variety of stimuli which were changed when SS seemed adapted to any one, as in Procedure P.

When SS were kept awake for a 24-h period, it was found that Procedure A reduced the recovery of lost sleep from about 74% with Procedure P, to about 31%.

After the 24-h deprivation period, more SWS was recovered than PS, 84.6 to 54.0% with Procedure P and 33.0 to 21.3% with Procedure A.

Recovery of the sleep lost with 24 h of deprivation involved a shift toward more long sleep episodes and fewer short and medium-length episodes. This shift was greater with Procedure P.

Lost sleep was recovered by an increase in both the daytime and nighttime sleep percentages. Generally, the increases in daytime and nighttime sleep percent were not proportional to the respective baseline amounts which resulted in changes in the day/night ratio, which was a measure of circadian rhythm. The only consistency in the changes in the day/night ratio seemed to be that groups that were initially different in the baseline day/night ratio became more alike after deprivation.

INTRODUCTION

The purpose of this dissertation was to explore intensively four separate aspects of sleep deprivation. The selection of the variables resulted from an intensive review of the literature which revealed that these problems associated with sleep deprivation had been quite neglected. The selected variables were (a) the temporal course of sleep demand resulting from sleep deprivation, i.e., the intensity of the sleep need as a function of time of deprivation, (b) the temporal limit of total sleep deprivation beyond which wakefulness cannot be maintained, (c) the consequences of sleep deprivation on the subsequent sleep response, and (d) the effect of methods of sleep deprivation, particularly the effect of aversive stimulation, used to maintain wakefulness.

Each of these variables seemed critical in an understanding of sleep deprivation. The discussion of each experiment will attempt to explicate this reasoning. The decision was made to explore all four variables rather than to intensively concentrate on any one. As a consequence, the findings are recognizably incomplete, but do yield sufficiently provocative findings to warrant attention and further work.

Method

Subjects

Male Long-Evans hooded rats were used as Ss. Animals were used after they had fully recovered from surgery (about one month) and had regained all their lost weight or more. Each S was about 150 days old at the beginning of the experiment in which it participated.

Recording Technique

Swisher (1961) studied the EEG sleep stages of the rat. The recording technique used was adapted from his work after a number of trials. The initial trials made it clear that an EEG recording method was available in which there was high discriminability between the EEG sleep stages as commonly defined (e.g., see Swisher, 1961, or Levitt, 1965). Also, the EEG and sleep-wake behavior were well correlated, as Swisher found.

The Ss were anaesthetized with Nembutal and given antibiotics to prevent infection. Using a stereotaxic instrument, four points were marked on the skull. These were (a) over the left motor cortex (1 mm to the left of bregma), (b) over the right frontal cortex (1 mm to the right and 5 mm anterior to bregma), (c) over the left sensory cortex (4 mm to the left and 5 mm posterior to bregma), and (d) over the right sensory cortex (4 mm to the right and 5 mm posterior to bregma). A small stainless steel screw was forced into a small hole drilled at each point on the skull, so that the screw was in contact with the unpunctured

dura. One stainless steel wire, from a four-contact receptacle to be implanted, was then wrapped around each of the four screws. Dental acrylic cement was used to mold the receptacle wires and screws into one unit. The receptacle held four cylindrical female contacts in a square pattern.

A plug which held four wire-brush contacts in a square pattern was joined to the receptacle for recording. A four-wire shielded cable, easily flexed by Ss, connected the plug to a Grass Instruments Model 3D or Model 4 electroencephalograph.

The Ss were trained to avoid touching the cables so that they would not chew through them. This was done by arranging a 45 v difference between the cable's shield and the bottom grid of the cages for a 24-h training period. If an S chewed through a wire, this was repeated as necessary.

EEG records and scoring

Two EEG channels were used for each S. The upper channel was a recording of the voltage difference between the dural screws on the left side of the head, one over the motor and the other over the sensory cortex. The lower channel recorded the voltage difference between the right frontal and right sensory screws. During wakefulness (W) both channels had a high frequency pattern. The excursions of the pen, relative to the paper speed (10 cm/s), were sufficiently frequent that the written lines overlapped and the individual movements of the pen could not

be discriminated. This defines W as used herein (Swisher, 1961). At the onset of slow-wave sleep (SWS) excursions of the pen gradually became less frequent and the amplitude of the excursions increased so that individual excursions of the pen were discriminable. This is the definition of SWS as used herein. Paradoxical sleep (PS) or activated sleep onset occurred after Ss had obtained some SWS. It was marked by the reversion of the upper channel from an SWS pattern to a W pattern, in some Ss intermingled with a theta pattern. The lower channel then changed from SWS to a regular theta pattern. This is the definition of activated sleep or PS as used herein when scoring sleep in undisturbed Ss (Swisher, 1961).

The main purpose in scoring the sleep records of undisturbed Ss was to determine how much lost sleep was recovered. Thus, in scoring each minute of EEG record, it was first decided whether there were 31 or more s of W EEG, and if so, the minute was scored as W. If the episode had 29 s or less of W, the minute was scored as either PS or SWS, depending upon which of the two sleep stages predominated.

About five estimates of E's rescoring reliability were made using 100-min samples. It was found that E was highly consistent with himself, as there was between 95 to 98% agreement between the original and the rescoring.

Deprivation Procedures

Procedure A

Deprivation Procedure A consisted of delivering shock to Ss upon the appearance of slow waves in the EEG record. Shock was delivered from a square wave or constant current shock generator. Duration and intensity of the current could be varied. Because of Ss' skin resistance, the most intense constant current shock deliverable was 1.7 ma. The shock was delivered to Ss through grids placed on the floors of Ss' cages. Alternate bars of the grid were oppositely charged during delivery.

Procedure P

Subjects were kept awake by students who could discriminate between EEG SWS and EEG W. It was emphasized that one cannot know whether Ss are awake or asleep by the fact that their eyes are open. Assistants were told to keep Ss awake by (a) using enforced movement, (b) placing Ss in novel environments, and (c) anything they could invent that would not harm Ss by endangering their health. Assistants were instructed to try to keep Ss awake and prevent them from falling asleep rather than to frequently re-awaken Ss. After deprivation began, assistants learned to anticipate when Ss would fall asleep. The main cue was that Ss would slow down and stop moving first. Assistants were also instructed to keep food always in the presence of Ss and to offer them water frequently.

The final form that Procedure P took was highly

variable and depended largely upon the individual assistant. Some assistants placed the Ss in a shallow pan and tilted it frequently so that Ss were forced to move. Others placed the Ss at the bottom of a bucket and shook them frequently. Others sought incentives that Ss would work for. One incentive was to place Ss in shallow water which resulted in escape attempts. Other assistants used a soft area such as a lab coat as an incentive. The Ss attempted to sleep on the coat and returned many times when removed from it. When an S began to fall asleep, its environment was changed or a new means of maintaining wakefulness was found.

Comparison of procedures

- (a) While Procedure A used shock as its sole stimulus source, Procedure P did not use shock at all.
- (b) While Procedure A used only one stimulus, Procedure P used a wide variety of stimuli.
- (c) In Procedure A, shock delivery was contingent upon the appearance of SWS in the EEG. In Procedure P, stimuli were delivered so as to prevent Ss from falling asleep. Although at times Ss were awakened, for the most part, stimuli were not contingent upon SWS.
- (d) The two procedures were approximately equally effective for the first 24 h of deprivation in that, while Ss were being successfully kept awake, both procedures kept Ss awake about 97% of the time.

EXPERIMENT I

Webb (1957) studied the relationship between the amount of time of sleep deprivation and latency of going to sleep. Subjects were kept awake by being placed on a slowly revolving wheel that was two-thirds submerged in water. They were allowed to fall asleep in observation cages. There was a distinct relationship between sleep deprivation in hours and sleep latency. Webb found that when ss were taken off the wheel even after 30 h of deprivation, before they fell asleep they went through grooming and exploratory activity, which took an average of over 10 min.

The purpose of this experiment was the same as Webb's (1957) study, i.e., to investigate the temporal course of the intensity of the sleep demand as a function of the amount of time of sleep deprivation. An analog of Warden's obstruction or barrier technique was used. In the classical Columbia-obstruction-box studies, rats ran across an electrified grid to get to food or some other goal object (see Kimble, 1961, p. 454). In this experiment, rats were shocked whenever they were found to be asleep and shocks/h was used as the measure of intensity of the sleep demand

rather than sleep latency. Exploration of a novel environment was not a factor, since Ss were always kept in the same cages.

Webb (1957) visually monitored Ss and used cessation of movement and relaxation of muscle tonus as the criterion of sleep. The following evidence leads to the conclusion that such monitoring is inadequate. Boren (1960) noted that monkeys could appear to be asleep with eyes closed, hunched into typical sleep posture and still maintain a steady rate of avoidance responding. Levitt (1967) found that short bursts of sleep-like waves, which he called microsleap, were found in the EEG of rats on a slowly revolving treadmill. The Ss learned to sleep as much as 14 min/h within 32 h by moving to the front of the wheel and remaining stationary while riding to the rear. Because Ss obtained slow-wave sleep on the treadmill, both Levitt (1967) and Dement, Henry, Cohen and Ferguson (1967) used treadmills to deprive Ss selectively of paradoxical sleep.

Preliminary experiments for this research study attempted to keep Ss awake by observing them and moving them when it seemed necessary. However, it appeared that Ss may have been asleep with their eyes open, since at times they seemed unresponsive to visual stimuli such as E's finger near Ss' eyes. Recording of EEG during preliminary attempts at sleep deprivation revealed that at times, while Ss stood on all four legs and appeared to be

staring at E, EEG SWS was simultaneously present. Thus in this experiment, Ss' state of sleep and wake was monitored by means of the EEG during sleep deprivation.

Method

In order to use the classical obstruction procedure to study sleep in the rat, Ss had previously been prepared for EEG recording and shock was delivered to the feet whenever EEG signs of sleep appeared.

The data resulting from this procedure were used to answer the following questions: (a) What is the relationship of amount of sleep deprivation measured to the number of shocks per unit time presented to maintain wakefulness? (b) Does the pattern of the length of the intershock interval or interval between instances of Ss' manifesting EEG sleep signs reflect either (1) a tendency to learn to stay awake or (2) a tendency to learn to sleep despite shock or (3) a random or other pattern? (c) What is the effect of shock intensity?

Subject Groups

Five Ss participated in each of three groups which differed in shock parameters and the number of hours for which each group was successfully kept awake by means of Procedure A. Deprivation was always started at 9:00 A.M. which was hour 1.

Shock-S

1) The shock intensity was 0.6 ma, and each shock lasted 0.5 s.

2) Shock intensity was constant.

3) Deprivation proceeded until sleep "overrode" the shock. Override was defined as having occurred when 10 consecutive shocks were delivered with less than 20 s intervening between shocks, i.e., when Ss were obtaining substantial amounts of sleep.

4) All Ss were effectively deprived for 19 h.

Shock-W

1) Initial shock intensity was 1.0 ma for 0.5 s. This shock level made most Ss vocalize and jump off the grid.

2) After 15 h, one S was sleeping despite the shock and had achieved override. Since the goal was sleep deprivation for 24 h, shock intensity and duration were gradually increased to the limit of the generator which was 1.0 s and 1.7 ma.

3) After 20 h of deprivation, shock was not adequate in keeping this S awake. Thus, data for this group are presented for 20 h of deprivation.

Group A

1) Group A was used in another experiment, where sleep was recorded for two days prior to and 11 days after deprivation by Procedure A. The Ss were to be kept awake for 24 h as part of the design of that experiment.

2) The shock level for Group A was set at the reliable maximum of the shock generator (1.7 ma). The

duration of shock delivery was 1.0 s. This shock resulted in extremely vigorous escape attempts by Ss.

3) The shock level was not varied since the shock was sufficient to keep Ss awake for 24 h.

Results and Discussion

As may be seen in Figure 1, the number of shocks/h is an increasing function of the amount of time of deprivation. Table 1 presents the ungrouped data upon which Figure 1 is based. Examination of these data suggests that the form of the curve in Figure 1 is not an artifact of grouping data from individual Ss. Table 2 presents the analysis of variance based on the first 19 h of deprivation data for all three groups, as in Table 1. As may be seen in Table 2, amount of time of deprivation had a highly significant effect upon the number of shocks/h.

Table 3 presents the override data. Five Ss were kept awake for between 19 and 26 h, while two Ss were kept awake for only 13 and 15 h respectively.

According to Murray (1965, p. 210), the effect of sleep deprivation is to lower the level of arousal so that sleep-deprived Ss are in a state between sleep and wakefulness. The level of arousal was so lowered as a result of sleep deprivation that eventually either (a) shock did not result in enough arousal to awaken Ss or (b) shock resulted in enough arousal to awaken Ss for only a few seconds.

It was found in Experiment II that Ss could be kept awake for much longer periods of time with Procedure P.

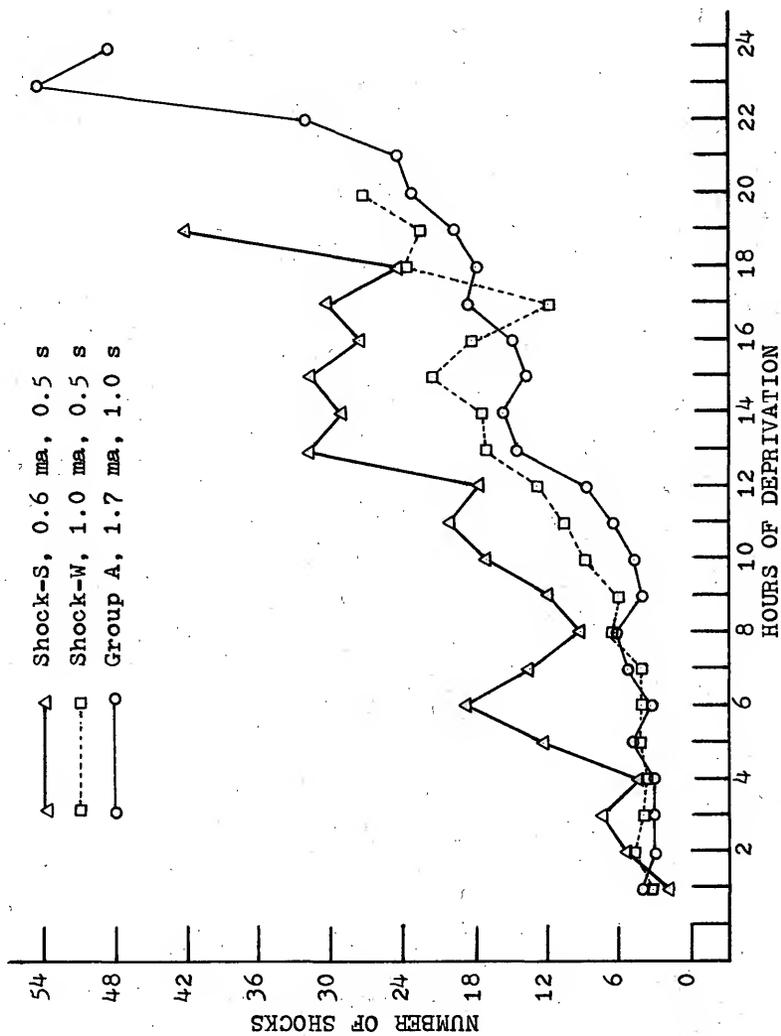


Figure 1. Mean number of shocks/h of deprivation for three levels of shock intensity.

TABLE 1
 Shocks per Hour per Individual \bar{S}
 in Shock-S, Shock-W, Group A
 and Total per \bar{S} after 19 Hours of Deprivation

Hour	Shock-S			Shock-W			Group A								
	S-1	S-2	S-3	S-9	S-10	W-2	W-7	W-9	W-11	W-12	A-1	A-4	A-5	A-8	A-9
1	0	3	3	2	2	7	3	2	3	2	3	3	6	6	3
2	3	1	4	7	13	9	3	6	3	2	5	3	4	3	1
3	3	5	5	6	19	8	1	8	3	0	5	1	5	3	1
4	4	6	3	3	7	9	0	4	5	1	2	3	4	5	2
5	6	10	10	12	24	11	1	5	3	2	2	2	10	2	2
6	8	38	18	8	22	8	2	6	3	2	5	1	5	2	2
7	5	11	17	15	23	11	2	9	2	1	7	1	5	6	4
8	5	9	9	7	15	15	2	8	4	3	5	3	8	5	5
9	7	9	16	11	17	14	2	10	3	4	4	2	5	9	1
10	5	21	23	26	11	21	3	8	6	5	6	2	5	6	1
11	7	36	14	13	41	31	1	11	5	5	4	2	8	7	1
12	4	22	8	11	44	46	2	18	6	3	15	2	9	6	1
13	4	36	11	21	88	60	3	15	3	5	20	7	13	8	3
14	5	31	13	47	50	56	3	20	4	5	38	5	17	5	5
15	5	47	13	19	75	84	2	15	4	4	46	5	16	2	2
16	6	24	37	13	59	72	2	11	4	3	36	6	15	12	4
17	12	48	22	8	62	36	4	9	4	7	31	10	16	18	5
18	5	31	22	9	55	76	7	20	5	12	27	6	18	34	5
19	16	83	58	10	44	74	10	17	4	8	34	6	22	30	8
Total	110	470	306	248	671	190	74	648	75	53	329	70	204	213	58

TABLE 1 - Continued

Hour	Shock-S			Shock-W				Group A							
	S-1	S-2	S-3	S-9	S-10	W-2	W-7	W-9	W-11	W-12	A-1	A-4	A-5	A-8	A-9
20	31					97	9	24	3	4	58	7	14	33	6
21	27										36	9	19	44	15
22	8										56	16	24	54	11
23	16										108	48	43	82	23
24	21										86	18	50	68	22
25	58														
26	90														

TABLE 2

Analysis of Variance Based on
 First 19 Hours of Deprivation for all Three Groups
 for Data in Table 1.

Source	df	F	p
Between Subjects	14		
Shock Level	2	1.21	
error (b)	12		
Within Subjects	270		
Hours of Deprivation	18	7.83	<.0001
Hours of Deprivation by Shock Level	36	0.62	
error (w)	216		
Total	284		

TABLE 3

Hours of Deprivation by Procedure A
for Individual Ss till Override of Shock
Whose Intensity and Duration are Specified

Subject	Hours till Override	Shock Intensity and Duration
S-1	26	.6 ma, 0.5 s
S-2	19	.6 ma, 0.5 s
S-3	19	.6 ma, 0.5 s
S-9		.6 ma, 0.5 s
S-10	13	.6 ma, 0.5 s
W-2	15	1.7 ma, 1.0 s
W-7		1.0 ma, 0.5 s
W-9		1.0 ma, 0.5 s
W-11		1.0 ma, 0.5 s
W-12		1.0 ma, 0.5 s
A-1	20	1.7 ma, 1.0 s
A-4		1.7 ma, 1.0 s
A-5	24	1.7 ma, 1.0 s
A-8	22	1.7 ma, 1.0 s
A-9		1.7 ma, 1.0 s

Note.--Where no number of hours is given,
the S had not overridden the shock when shock
delivery was stopped.

It was also found with one S that after 40 h of deprivation by Procedure A, shock was ineffective, while stroking its fur was very effective in maintaining wakefulness. It was concluded that Procedure P was much more effective as a means of long-term deprivation because of the use of multiple types of stimulation and because intense shock may have a de-arousal effect. Thus it is not possible to say how much the data in Figure 1 reflect the effect of accumulated hours of sleep deprivation versus the de-arousal effect of intense shock and habituation to shock.

Effect of shock intensity

As may be seen in Figure 1, the more intense the shock, the fewer were delivered to each group. As may be seen in Table 2, neither the differences in the total number of shocks for 19 h between groups, nor the hours by group interaction effect was significant.

As may be seen in Table 3, there is a great deal of variance between Ss within groups in terms of the total number of shocks required to keep an S awake. Since lack of statistical significance may be due to error variance, no conclusion can presently be reached regarding the effect of shock intensity upon the number of shocks/h required to keep Ss awake.

Pattern of intershock intervals

Figure 2 displays the intershock intervals of a single S. An important question regarding these data is the

source of the variability between intershock intervals. One possibility is that Ss may learn and relearn to stay awake a number of times as deprivation proceeds. Thus if each intershock interval is labeled '+' or '-' depending upon whether the interval is longer or shorter than the immediately preceding interval respectively, then one would expect series of intervals labeled '+' to occur more often than chance, if Ss learn and relearn to stay awake as a function of shock. If there is a repeated extinction process, i.e., if Ss extinguish the learned 'wakefulness' response, or if the sleep demand consistently increases from shock to shock, one might expect series of intershock intervals labeled '-' to occur more often than by chance. To see if such learning and/or extinction sequences occurred more often than chance, sequences of four of the signs were written out for the initial series of intershock intervals. Thus the first sequence used the 2nd, 3rd, 4th and 5th signs, the second sequence used the 3rd, 4th, 5th and 6th, etc. The initial series of intershock intervals where there was maximum variability (e.g., the first 44 shocks for S A-1, Figure 2) was used on the assumption that the effect of the sleep drive would be less and learning or extinction effects would be more dominant. (After about the first 50 shocks, the intershock intervals varied little.) Group A data were used.

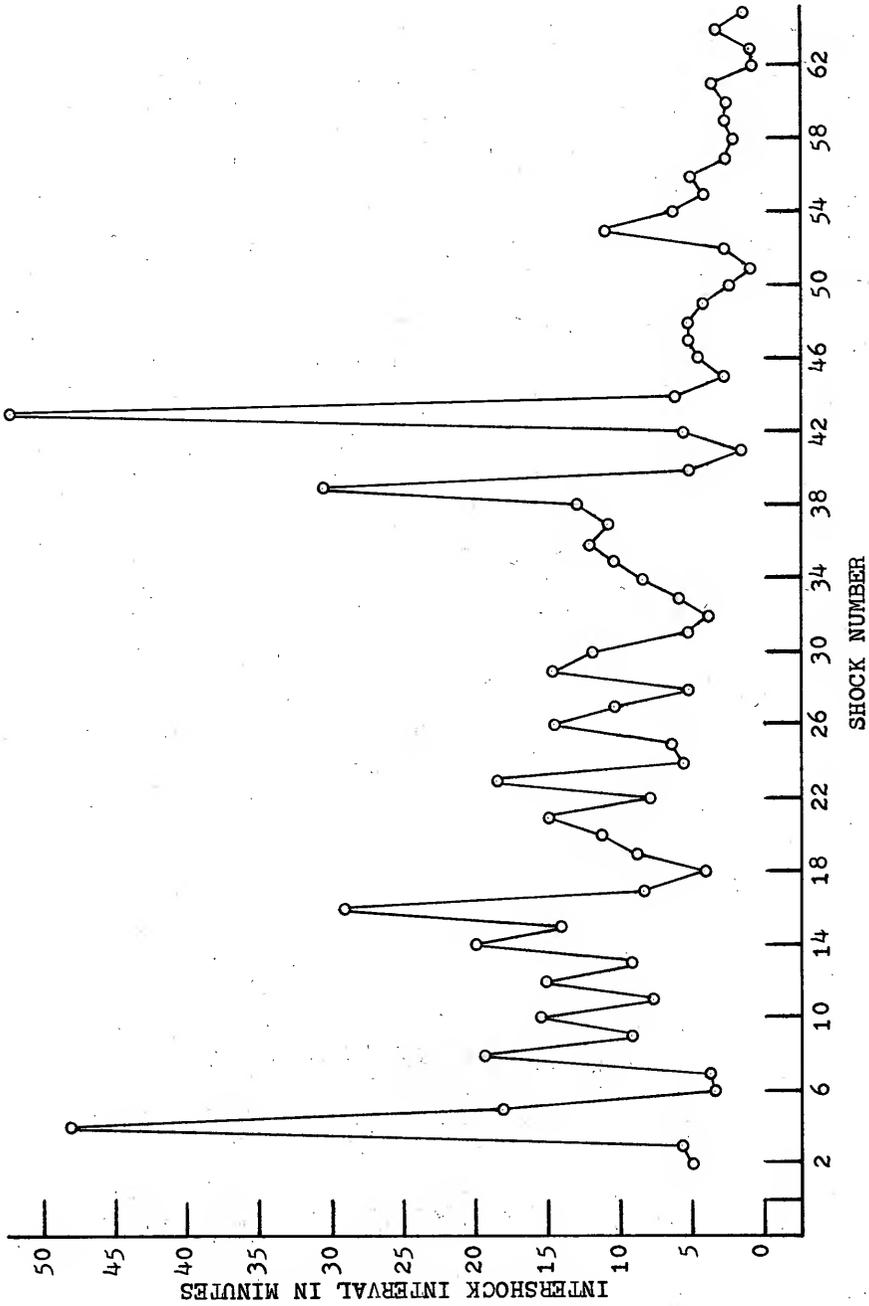


Figure 2. Intershock interval for SA-1.

In Table 4, all possible sequences of pluses and minuses were written out. Any sequence of three or four consecutive plus signs (++++, +++-, -++) is considered to be evidence of learning of shock avoidance. Any sequence of three or four minus signs (----, ----, +---) is considered to be evidence of extinction of learned shock avoidance or of the effect of the increasing sleep need. The sequences +-+ and -+- are considered to reflect an oscillating tendency, i.e., for a longer inter-shock interval to be followed by a shorter interval. Other combinations of plus and minus signs are considered to represent chance and uninterpretable events.

In Table 4, there are 16 permutations of plus and minus signs and 261 events. Thus one would expect that on the basis of chance only, each permutation should have had 16.3 ($261 \div 16$) as the expected frequency. The data in Table 4 suggest that an oscillation between shorter and longer shocks was the predominant tendency and these (+---, -+-) occurred about twice as frequently as would have been expected by chance. On the other hand, probability of intervals becoming continuously longer (++++) or continuously shorter (----, ----, +---) for the part of the data showing maximum variation, occurred about one fourth as often as one would have expected on a chance basis. Thus, no evidence of a tendency for Ss to learn, extinguish and re-learn to stay awake was found.

TABLE 4
 Frequency of Occurrence
 of Each Permutation
 of Intershock Intervals for Group A

Sequence of Intershock Intervals	Frequency
++++	4
+++-	15
++-+	20
+-+-	15
+--+	21
-+-+	32
-+--	28
+---	4
-+++	14
--+-	19
-+-+	31
-+--	19
---+	12
----	20
-----	4
	3
Total	261

Summary

The intensity of the sleep demand was studied as a function of time of deprivation using a procedure analogous to Warden's obstruction or barrier technique. The Ss were shocked whenever they fell asleep. Sleep was operationally defined as occurring when SWS appeared on the EEG, as a review of the literature indicated that other methods such as visual monitoring of Ss were unreliable.

Using three groups of five Ss each, it was found that the number of shocks/h required to maintain wakefulness was an increasing function of the time of deprivation. After 13 to 26 h, the tendency to fall asleep became sufficiently strong that Ss overrode the shock, i.e., fell asleep within 20 s after being shocked 10 times consecutively, and obtained substantial amounts of sleep despite the deprivation procedure.

Since the differences between the three shock level groups were not statistically significant, no conclusions about shock intensity could be reached.

The pattern of intershock intervals was analyzed for one group of Ss. No evidence of a tendency for Ss to learn, extinguish and relearn to stay awake was found.

EXPERIMENT II

Many investigators have tried to keep organisms awake to the point where it became impossible to keep them awake any longer. Table 5 summarizes those studies in which Ss were deprived of sleep to their limit. As may be seen in Table 5, various animals, with the use of various techniques of sleep deprivation, have been kept awake from one up to 77 days. Some of the variability in the limit of deprivation is probably the result of the inadequate means of monitoring Ss to determine sleep or wakefulness, as was discussed in Experiment I (see pp. 8-9 above). Presumably, Ss were only partially sleep-deprived when the EEG was not monitored. It is assumed that the more complete the deprivation, the shorter the deprivation limit found.

Another factor which may have contributed to the variability in the limit of deprivation concerns the sleep deprivation procedures. As may be seen in Table 5, most procedures are much like Procedure A in this study. Typically, some presumably arousing stimulus situation is presented or results when Ss fall asleep. In the revolving treadmill studies, for example, Ss fall into water (Webb and Agnew, 1962). Pegram (1968) kept his monkey Ss awake by adminis-

TABLE 5

Summary of the Literature on the
Limit of Sleep Deprivation

Experimenter	Organism	Method	Reason for Termination	Limit
Manacéine (1894)	Puppies	-	Death	4-5 days
Tarozzi (1899)	Three adult dogs	Walking when necessary	Death	9, 13 and 17 days
Legendre and Piéron (1912)	Dogs	Stimulation	Extreme sleepiness	1-21 days
Crile (1921)	Rabbits	Medical students	Death	4-5 days
Okazaki (1925)	Dogs	Nails protruding from all sides of special cage	Death	14-77 days
Bast <i>et al.</i> (1927)	Rabbits	Revolving cage	Death or complete collapse	6-31 days
Leake, Grabb and Senn (1927)	Rabbits	Revolving cage	Death or complete collapse	6-31 days
Kleitman (1928)	Puppies	Walking and stimulation	Extreme sleepiness	2-7 days
Licklider and Bunch (1946)	Rats	Treadmill	Death due to fighting	3-14 days

TABLE 5 - Continued

Experimenter	Organism	Method	Reason for Termination	Limit
Webb and Agnew (1962)	Rats	Treadmill	Exhaustion or termination of experiment	1-27+ days
Anderson and Gorfein (1964)	Humans	-	Set new record	10½ days
Gulevich et al. (1966)	Humans	-	Set new record	11 days

tering sharp puffs of cool, compressed air to the back of the neck and the side of the head when there were behavioral or EEG signs of sleep. On the other hand, when the procedures used to keep human Ss awake are specified, these appear to be much like Procedure P in which a variety of non-contingent stimuli are presented to maintain wakefulness. Thus Berger and Oswald (1962, p. 458) stimulated their Ss to keep awake by playing a variety of games. They considered the repeated introduction of variety into the activity essential for the maintenance of wakefulness.

The original goal of this experiment was to determine how long rat Ss could be kept awake before it became impossible to keep them awake any longer, using deprivation Procedure A to maintain wakefulness and the EEG to monitor it. One S was kept awake until it fell asleep a few seconds after being shocked. It was then found that although the S could no longer be kept awake by shock, it was easily kept awake by gently stroking its fur. It was apparent that Procedure A was not the method of choice, and it was discontinued as a long-term method of deprivation. The data from this one S and relevant data from Experiment I will be used to compare the effectiveness of the two deprivation procedures. It is believed that this is worthwhile because experimenters tend to use procedures much like Procedure A with animal Ss when there is some evidence that a method like Procedure P is more effective.

Method

One male Long-Evans hooded rat, prepared for EEG recording, was kept awake by Procedure A. Initial shock amplitude was 0.5 ma of 0.5 s duration. Amplitude and duration were gradually increased as necessary. In the last hours of the deprivation period, a very intense shock, which made S jump and squeal vigorously, was used.

Three male Long-Evans hooded rats were kept awake by Procedure P. Continuous EEG recordings were taken for all Ss. The last two Ss deprived by Procedure P were weighed every 12 h. Immediately after each weighing, Ss were placed in cages, and left undisturbed till asleep, allowing a measure of sleep latency.

The EEG recordings of the last two Ss deprived by Procedure P were used to determine how effective the deprivation procedure had been. (The EEG data for the first S could not be reliably scored and are not presented.) During deprivation, sleep tended to appear in short episodes of about 10 s every few minutes. The procedure for scoring records of undisturbed Ss does not consider sleep to have occurred unless 31 or more s of a minute was SWS, and was therefore inappropriate here. Instead, a 10-min sample was taken from every hour of deprivation and the number of seconds of sleep was counted and recorded. These data were used to extrapolate an estimate of the total amount of sleep obtained during deprivation. These data were examined also to see if Ss were more likely to fall asleep as a function

of days of deprivation and of the time of day.

Results

Long-Term Deprivation by Procedure A

For the one S deprived to the limit by deprivation Procedure A, it was found that after about 40 h, S's feet were extremely reddened and bleeding, both from the shock and because S attacked and chewed its own feet. Also, at that time, even though the shock made S jump and squeal vigorously, SWS was manifest on the EEG within about 10 to 15 s after shock delivery and S was receiving a substantial amount of SWS. It was then found that stroking S's fur gently was adequate to maintain wakefulness, while shock was ineffective.

Long-Term Deprivation by Procedure P

The attempt to keep the first S awake by Procedure P succeeded in keeping S awake for six days. The experiment was terminated because a loose stylus holder on the EEG machine had given the appearance of persistent slow waves in one channel.

The deprivation procedure for the last two Ss was started at 8:40 A.M. The first S was terminated when death due to pneumonia seemed imminent, since S was struggling to breathe. Unfortunately, assistants had kept this S wet as a method of maintaining wakefulness. This S seemed no harder to keep awake in the last hours than a few days before. This S was kept awake 97.3% of the time for 296 h or 12 days and 8 h. It obtained 7.8 h of sleep during the

period of enforced wakefulness. Rats in this S's population sleep 51.6% when undisturbed. Thus, S would have obtained 152.7 h of sleep in 296 h (the duration of the period of enforced wakefulness) if it had been left undisturbed. Since S slept only 7.8 h in that period, it had been deprived of, or had a sleep debt of, 144.9 h. This debt is equivalent to the amount of sleep S would have obtained if it had been undisturbed for 11 days and 17 h.

The second S was terminated when, refusing to eat and drink, it suffered a sudden weight loss (see Figure 3). This S was kept awake 94.6% of the time for 365 h or 15 days and 5 h. It slept 5.4% or 19.9 h during the period of enforced wakefulness. It is assumed that this S would have obtained 188.5 h of sleep (51.6%) in that time if left undisturbed. Since S slept 19.9 h, it had a sleep debt of 168.6 h at the end of the deprivation period. This is the amount of sleep that a rat S would obtain in 13 days and 14.4 h if undisturbed.

The amount of sleep per day per S was examined to see if Ss slept more as a function of days of deprivation. Figure 4 presents these data. One possibility suggested by the data is that after about eight or nine days of deprivation, Ss obtained much more sleep. However, these data are confounded by an experimenter variable. As may be seen in Figure 5, Ss obtained more sleep during the night hours (which is opposite to the normal pattern for rats). Correspondingly, E tended to supervise least from midnight

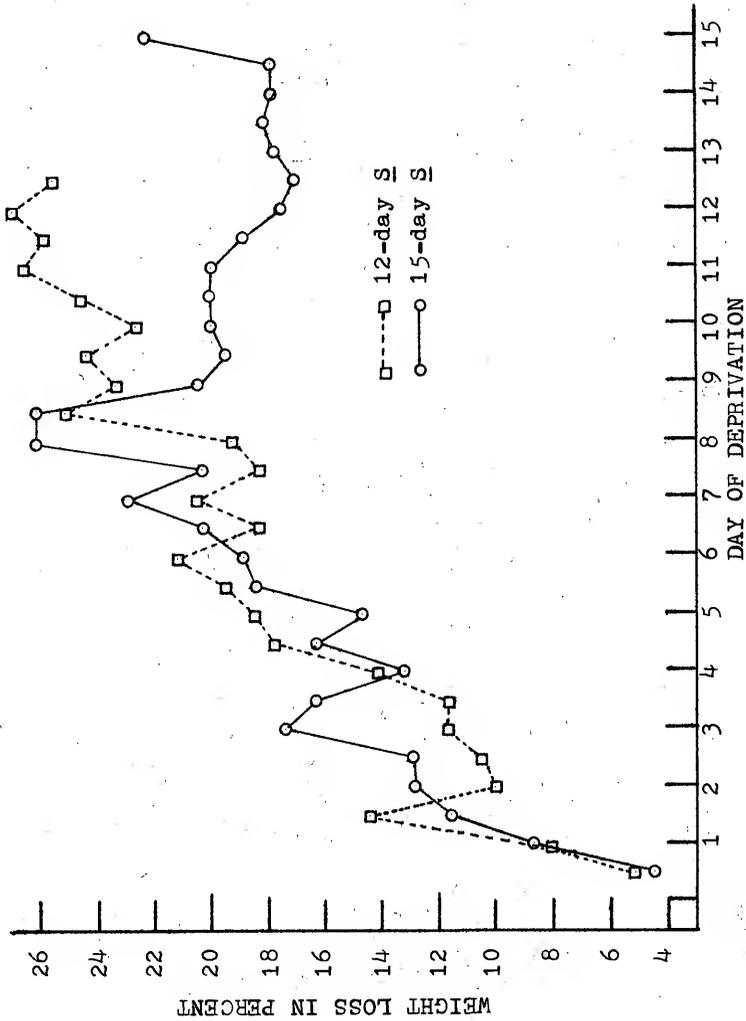


Figure 3. Percent weight loss as a function of days of deprivation. (Midnight weighings have day numbers under them.)

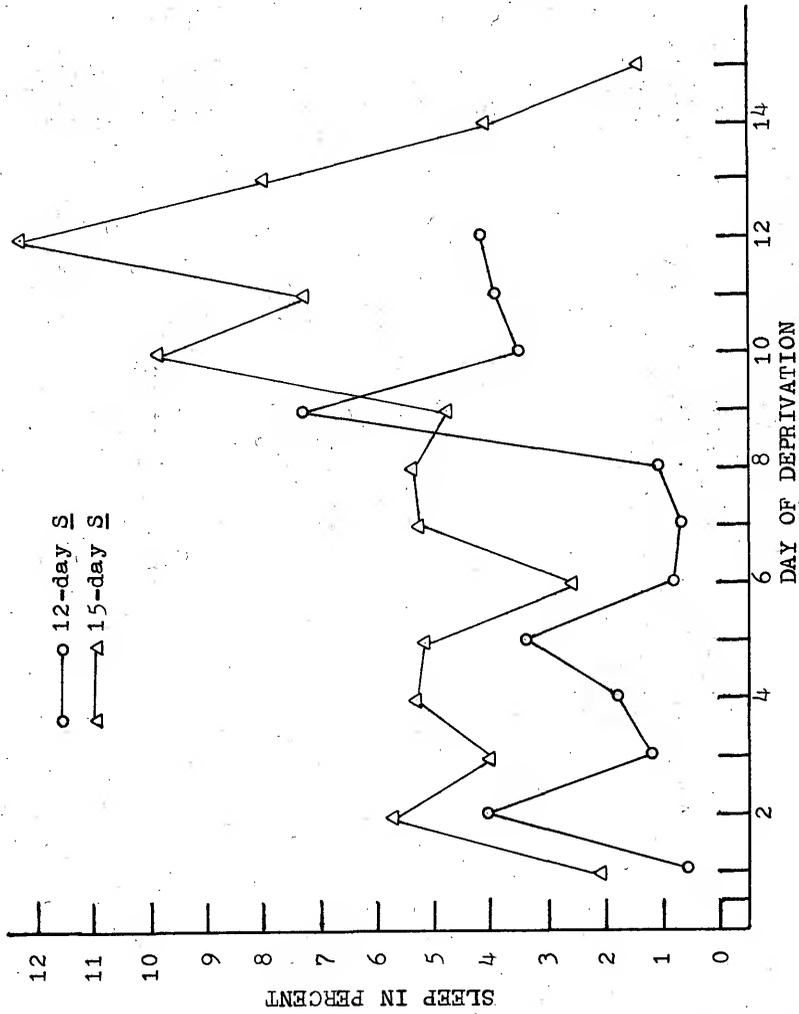


Figure 4. Sleep percent despite deprivation procedures as a function of days of deprivation.

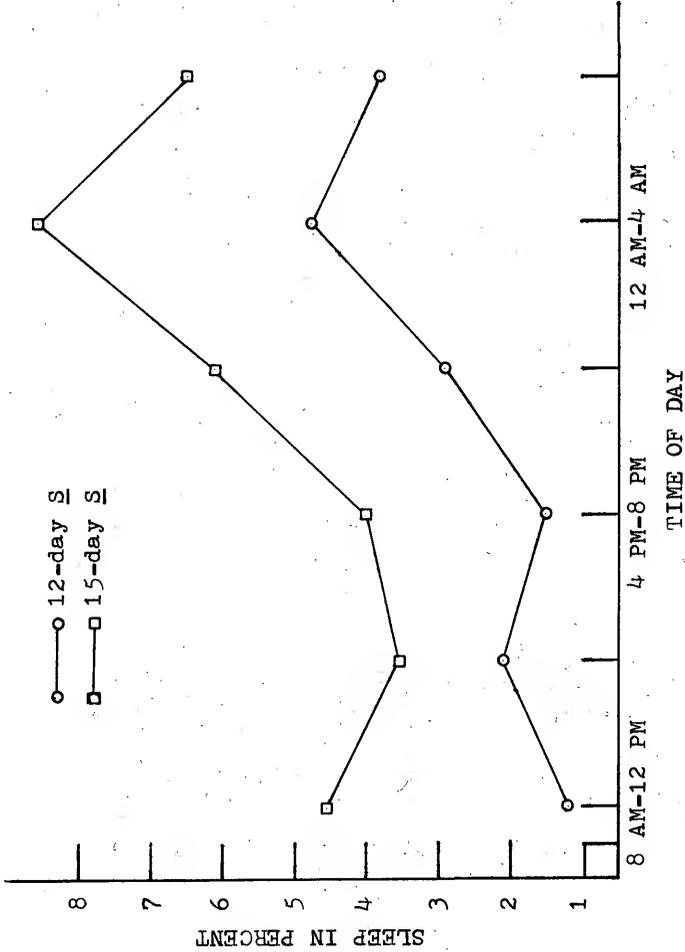


Figure 5. Sleep percent despite deprivation as a function of time of day during deprivation.

to 8:00 A.M. Also, for the last three days of deprivation when only one S was yet to be terminated, E, who was aware of the amount of sleep Ss were obtaining during deprivation, increased supervision of assistants and exhorted them to monitor the EEG and provide continuous stimulation to Ss. Thus, that S which had 14% sleep on deprivation day 12 had only 2% sleep on day 15 (see Figure 4).

Figure 6 summarizes the latency data, i.e., the number of seconds between Ss being placed in cages and the first SWS episode. There was no systematic difference between the midnight and noon latencies.

Two factors appear to account for the latency measure changes as seen in Figure 6. The first factor appears to be a systematic tendency for the latencies to decrease over the first three days to a minimum range which is between 5 to 20 s. In addition, there seems to be a random tendency to have sleep latencies much longer than about 20 s. One contributor to this random factor was the fact that Ss were often wet when put into the cages and Ss would groom, or partially dry themselves, or eat and drink food and water that was in their cages before falling asleep.

The following effects of the long-term deprivation by Procedure P were apparent with non-quantifiable observations. As deprivation proceeded, Ss' muscular tonus decreased greatly so that when an S was lifted by the shoulders, it tended to hang limply as if anaesthetized. The Ss tended to move more slowly and by the end of deprivation

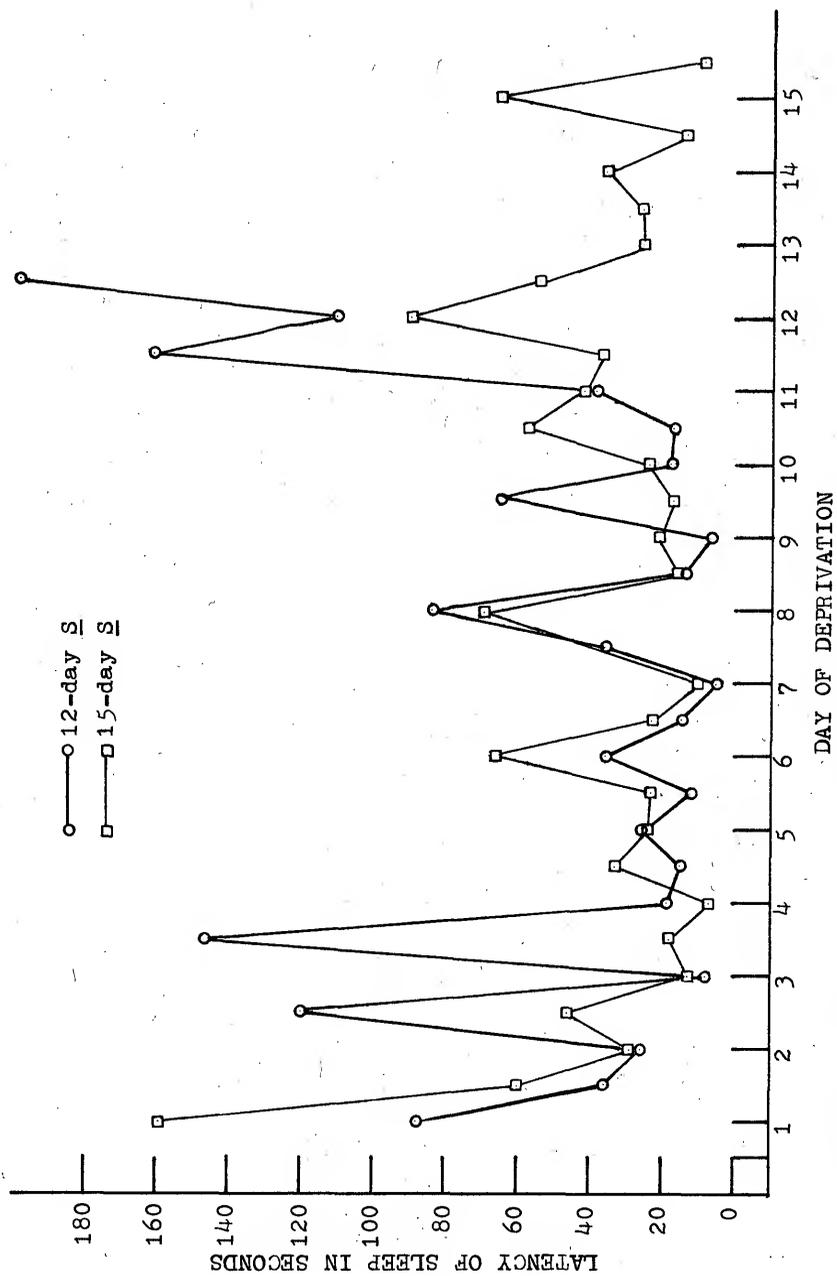


Figure 6. Midnight and noon sleep latencies for two Ss as a function of days of deprivation. (Midnight latencies have day numbers underneath.)

tended not to walk at all. They jumped off table tops, did not right themselves and hit the ground snout first, cutting their lips. (Since Ss were kept walking far more than usual, the bottoms of their feet began to bleed; Band-aids were put on their feet, making small boots.) Also, Ss showed no apparent signs of increased aggressiveness.

The EEG had not been calibrated for testing the amplitude and form of SWS during deprivation. However, inspection of a number of samples of SWS episodes that occurred during deprivation revealed no EEG differences as a function of time of deprivation.

Discussion

The Limit of Deprivation

A deprivation procedure, Procedure P, was found which kept two Ss awake about 95 to 97% of the time during deprivation for about 12 to 15 days. A sleep debt was calculated, taking into account both the amount of sleep that rats obtain when undisturbed and the amount of sleep that Ss obtained despite deprivation. It was found that rat Ss can be kept awake till they accumulated sleep debts, one of 144.9 h, the other 168.6 h. These debts are equivalent to the amount of sleep that rat Ss would obtain in about 12 to 14 days of undisturbed sleep. Comparable data with a statement of sleep debt are not available elsewhere for comparison. Human Ss, however, have been kept awake for up to 11 days and presumably incurred a sleep debt of about 88 h.

Effect of Long-Term Deprivation

The attempt to keep an S awake indefinitely by deprivation Procedure A resulted in the S sleeping despite being shocked. In contrast, the results from the two Ss subjected to deprivation Procedure P suggested that the terminal point is likely to be determined by physiological variables other than sleep. One S developed a pulmonary condition; the other showed a sharp weight loss. The weight loss is interpreted as having been due to the lowering of arousal, which was a consequence of sleep deprivation. For any motor performance to occur, a certain level of arousal is essential. Murray (1965, p. 210) has concluded that sleep deprivation leads to a lowered state of arousal. This was observed by E in this experiment. Ss' muscular tonus dropped greatly and Ss became quite inactive. Eventually, the arousal level was so low that eating and drinking were not possible.

One seems forced to conclude, based on the above data, that while powerful mechanisms exist to lower Ss' level of arousal with time of deprivation, sleep deprivation per se did not result in death. Rather, death would have resulted secondarily from the lowered level of arousal and resulting starvation or other physiological concomitants.

Effectiveness of Procedure A versus Procedure P

In Experiment I, it was found that deprivation Procedure A succeeded in preventing override (falling asleep 20 s after being shocked for 10 consecutive shocks) up to

26 h. The most intense shock used was 1.7 ma for 1.0 s. In this experiment, with only one S, shock intensity was minimal at first and increased only as needed. Also, S was kept awake beyond the override criterion. (The Ss frequently achieved override and afterward began responding to the shock by staying awake for periods longer than 20 s.) This S was shocked when SWS appeared, until S was asleep within about 7 to 10 s after being shocked most of the time. Since it took E a few seconds to determine EEG SWS, S was obtaining about 10 or more s/min of sleep. (The EEG was obliterated for about 5 s after a shock was delivered. With this S, SWS appeared as the EEG record returned to normal at the time of termination.) This S initially achieved override at about 30 h. At this point, it may be tentatively concluded that increasing shock intensity to a level where S attacks its own feet merely forestalls, not only override as defined herein, but also S's falling asleep within about 5 s after being shocked. In sharp contrast to this is the fact that one S was kept awake for six days and another two Ss were kept awake for about 12 and 15 days using deprivation Procedure P.

The most important finding of this study was the wide difference between the two limits of deprivation found using the two different procedures. Interpretation of this difference, however, must be tentative because the two procedures differed in a number of ways as was outlined above (see the comparison of procedures on p. 6).

Pavlov (1927) believed that "the fundamental condition of the appearance and development of internal inhibition and sleep is exactly the same" (p. 251).

Furthermore:

One means by which the state of inhibition could be produced was by exposing the dog to certain stimuli which would have evoked a response had they not been excessively intense-- "such conditioned stimuli too strong to give the maximal conditioned reflex, Pavlov termed transmarginal or supramaximal." (W. H. Gantt in his introduction to his translation of Pavlov, 1941, p. 14.) Oswald, 1960, p. 1450.

In the sense that shock (used in this experiment, however, as a UCS) is a very intense stimulus, it may be considered to be transmarginal or supramaximal, and thus a producer of inhibition or sleep.

Oswald (1962) has concluded that sleep or some state having many characteristics of sleep appears in response to five situations, only two of which are relevant here and are presented below.

First, Oswald has concluded:

Monotonous repetition of stimulation brings about decreased responsiveness or habituation.... We can think merely in terms of stimuli entering the reticular formation via collateral afferents over and over again, with consequent habituation of the usual response of arousal. As reticular formation responsiveness declined, sleep would tend to appear. P. 160.

In this experiment, animals kept awake by Procedure A could be described as receiving monotonous stimulation. However, deprivation Procedure P was deliberately designed

to avoid monotony. Sources of stimulation included (a) cooling, (b) vestibular stimulation, (c) all forms of tactile stimulation (excluding pain), (d) various new odors from different foods, assistants and rooms, (e) a wide variety of sounds, and (f) a wide variety of visual stimulation. Thus, the mechanism of habituation to any one source of stimulation was circumvented, since the sources of stimulus input were modified as frequently as was found to be necessary.

Secondly, Oswald has concluded that sleep appears in response to "a continued situation which may be interpreted as overwhelmingly terrifying" (p. 160). The following data, which Oswald apparently used to infer his conclusions, will make it clear that deprivation Procedure A is very similar to situations which Oswald considered to be overwhelmingly terrifying, particularly since many involved shock.

An inert, stuporose state is found in some infants immediately following, for instance, the sudden pain of the dislocation of a joint. Burton and Derbyshire (1958) reported also the case of a one-year-old boy with acute secondary glaucoma.

After an hour of frenzied screaming at the onset, he stopped abruptly and fell asleep and on examination was found to be unrousable. He remained so until, after seven days, the eye was enucleated, whereupon he became alert and responsive within a few hours. P. 154.

Oswald also cites Jouvett and Hernandez-Peon's (1957) finding, with one cat, that

if stimulus combinations of a tone and an electric shock were given "at a high rate" (three or four per minute), and if the shock was made

strong, EEG signs of sleep were produced. Pavlov (1955) described the appearance of sleep in dogs subjected to regular electric shocks.

...

Liddell (1956) has described experiments in which most profound states of inert unresponsiveness occurred in lambs and kids subjected to repeated mild electric shocks (provided they were deprived of their mothers' company), and these had full freedom of movement within a room. P. 149.

In experiments with six human volunteers (Oswald, 1959c) who were not sleep-deprived and who received electric shocks, sleep appeared in four subjects. Powerful shocks were given by the regular discharge, half a dozen times a minute, of a 0.1 microfarad capacitor charged to 320 volts, and discharged through the wrist or ankle of the subject. Sleep tended to appear between each shock. In one case it became continuous and deepened to the C stage (Fig. 30) and ended following a dishabituating stimulus, viz. a clap. P. 151.

The above data indicate that sleep may occur in response to intense shock. Thus, deprivation Procedure A may have self-defeating features, which Procedure P does not have. This and the counter-habituation measure may have made Procedure P more effective.

Sleep Latency

As may be seen in Figure 6, sleep latencies decreased as a function of time of deprivation. Webb (1957) had a similar result. However, his shortest latencies were in the range of 11 to 12 min, even after 30 h of deprivation. In this experiment, the latencies were much shorter, ranging from 5 s to about 3 min despite the fact that in both experiments, latency measures were taken by placing Ss in an environment different from the one in which they were

being kept awake. Dement et al. (1967) deprived cats of REM (PS) sleep and reported that Ss did not show evidence of excessive sleepiness. They stated that the animals were restless, prowled a great deal and in general were quite active. Levitt (1967) reported that the revolving-water-wheel method of deprivation differentially deprived his rat Ss of PS. The Ss were able to learn to obtain as much as 14 min/h of SWS within 32 h of deprivation by walking to the front of the wheel and remaining stationary for 3 to 4 s while riding to the rear. It is thus possible that Webb deprived Ss mostly of PS, and that his Ss were more active and took longer to fall asleep than the PS- and SWS-deprived Ss in this experiment.

Summary

Rat Ss were kept awake by means of two deprivation procedures. One, Procedure A, used shock contingent upon the appearance of EEG SWS. The other, Procedure P, used a wide variety of changing stimuli that were not contingent upon the appearance of EEG SWS.

Using two Ss, the EEG was monitored in order to evaluate the effectiveness of deprivation Procedure P, which was measured as about 94% for one S, and about 97% for the other. However, when the individuals keeping the Ss awake made a maximal effort, the procedure resulted in Ss being awake up to about 99% of the time.

Using Procedure P, three Ss were kept awake, one for 6, one for 12 and one for 15 days.

During the first three days of deprivation by Procedure P, the latency of sleep onset when Ss were undisturbed decreased to about 20 s.

Subjects' muscle tonus decreased greatly with deprivation. The terminal point seemed determined by variables other than sleep. One S developed a pulmonary condition and one showed disinterest in food with a resulting sharp weight loss. It was concluded that Ss' level of arousal fell to a point where essential responses necessary for Ss' survival became impossible.

It was concluded that Procedure A was ineffective in keeping Ss from obtaining substantial amounts of sleep after about 15 to 20 h because sleep occurs as a response to intense shock. Also, Procedure A relied on only one stimulus (shock) which resulted in habituation of the arousal response to shock. With Procedure P, habituation was circumvented by changing the stimulus when Ss fell asleep.

EXPERIMENT III

In order to deprive an organism of sleep, active intervention is required to maintain wakefulness. In much of the animal research, this intervention was much like Procedure A. Pegram (1968), for example, kept his monkey Ss awake by administering sharp puffs of cool, compressed air to the back of the neck and the side of the head when there were behavioral or EEG signs of sleep. The air puffs' being made contingent upon sleep may well have been an unintentional contaminating variable. Only one reviewer has considered the difference in the effects of different methods of deprivation. Murray (1965) reviewed the deprivation literature relative to the degree of frustration/aggression in sleep deprivation studies with human Ss. He concluded that a major factor contributing to the degree of aggression observed in subjects was whether gentle or coercive and frustrating techniques were used.

The primary goal of this experiment was to see if making shock contingent upon the sleep response, i.e., Procedure A, versus non-contingent, multiple stimulation, Procedure P, changes the sleep response after deprivation. This was done in order to investigate the possibility that

sleep might decrease after deprivation, since Procedure A resembled a learning paradigm in which a negatively reinforcing event follows a response whose frequency is to be decreased.

In addition to the amount of post-deprivation sleep, a number of relevant subsidiary questions or dependent variables were studied in this experiment: Is the circadian rhythm affected by the deprivation techniques? Does recovery of lost sleep occur during daytime hours, nighttime hours or both? Is the length of sleep episodes affected by the deprivation procedures?

Method

Six male Long-Evans hooded, 264-day-old rats were deprived of sleep for 24 h by deprivation Procedure P. One day of baseline was recorded before deprivation and sleep records were obtained for the two days immediately after deprivation and for the eighth day after deprivation. Thirty-three days later, the same Ss were deprived of sleep using deprivation Procedure A. A shock of 1.0 ma of 0.5 s duration was adequate to keep Ss awake for 24 h.

Analysis of Data

TS^{*}, SWS and PS.--The data for each S, for each day, were divided into four components, and converted to percent as follows: (a) The number of minutes of SWS per daytime

* TS is total sleep, which is SWS and PS.

hour (9:00 A.M. to 9:00 P.M.) was divided by the number of minutes of record with lights on, and then multiplied by 100. (b) The number of minutes of PS per daytime hour (9:00 A.M. to 9:00 P.M.) was divided by the number of minutes of record with lights on, and multiplied by 100. (c) The same as (a) but for nighttime hours or lights-off. (d) The same as (b) but for nighttime hours or lights-off. TS percent per day was obtained by adding all four components and dividing by 2. Slow-wave sleep percent per 24-h day was obtained by adding components (a) and (c) and dividing the sum by 2. Paradoxical sleep percent per 24-h day was obtained by adding components (b) and (d) and dividing the sum by 2. In the various tables in the results section below, TS percents per day as derived above were summed across Ss for individual days separately, divided by the number of Ss and presented as group means for days as specified within the various tables. Paradoxical sleep and SWS were treated and presented in the same way as TS. Where the overall main days or treatment effects were significant according to analysis of variance, paired comparisons of days post deprivation with baseline were done with Dunnett's test (Kirk, 1968) using the same error mean square as for the F test. To contrast the effects of Procedure P and Procedure A, paired comparisons were made between corresponding days after deprivation by Procedure P and Procedure A using t tests with the same error term as for Dunnett's test. All probabilities presented are based upon two-tailed tests.

Circadian rhythm.--The day/night ratio was obtained for individual SS for individual days by dividing TS day by TS night. A decrease in this ratio would reflect a decrease in circadian rhythm.

Length of sleep episodes.--To best explicate the analysis of the data for length of sleep episodes, a sample of raw data is given as illustration. Numbers refer to the number of consecutive minute episodes scored as SWS, PS and W.

W2 [SWS5, W1, SWS3, PS2, W1, SWS11] .

W3 [SWS4, PS1, SWS1] W5.

The square brackets isolate episodes of sleep. Paradoxical sleep and SWS were not differentiated. Single minute episodes of W which were both preceded by and succeeded by minutes of SWS or PS were counted as sleep. Wake episodes of 2 or more min divide the record into sleep episodes. Accordingly, the illustration above shows two sleep episodes of 23 and 6 min. Chi square was used as a descriptive statistic since the data did not meet the requirements of independence (since data from SS were pooled).

Results and Discussion

TS, SWS and PS

As may be seen in Tables 6 and 7, sleep amounts increased after deprivation. For day 1 post deprivation for both deprivation Procedures P and A, TS, SWS and PS were all statistically significantly increased relative to the baseline day.

Significantly more PS was obtained on day 1 after Procedure P when compared to day 1 after Procedure A. There is also a trend in the data ($p < .1$) suggesting that less TS was recovered on day 1 after Procedure A (see Table 6).

Circadian rhythm

Table 8 presents the data reflecting the changes in daytime and nighttime sleep and in the day/night ratio after 24 h of both deprivation procedures. The same data are presented again in Table 9 where the increase over baseline percent sleep post deprivation is presented rather than the actual percentage of sleep as in Table 8.

As may be seen in Tables 8 and 9, both daytime and nighttime sleep increased on days 1 and 2 after both deprivation procedures. Thus, sleep lost during 24 h of deprivation is recovered during both daytime and nighttime hours.

The data in Tables 8 and 9 suggest that the increases in daytime and nighttime percent sleep are not proportional to the respective baseline amounts. For example, on the

TABLE 6

Baseline and Recovery Sleep after Deprivation
Procedures A and P in Mean Percent per 24-Hour Day

	Day after Procedure P			Day after Procedure A		
	1	2	8	1	2	8
TS						
Baseline	46.3	64.5	51.4	45.4	60.3	51.4
Recovery vs. Baseline ^a		p<.01			p<.01	
Procedure A vs. Procedure P ^b		p<.1				
SWS						
Baseline	36.8	49.1	41.9	36.0	47.1	42.1
Recovery vs. Baseline ^a		p<.01			p<.05	
Procedure A vs. Procedure P ^b						
PS						
Baseline	9.5	15.4	9.5	9.4	13.2	9.3
Recovery vs. Baseline ^a		p<.01			p<.01	
Procedure A vs. Procedure P ^b						
Baseline						
Recovery vs. Baseline ^a						
Procedure A vs. Procedure P ^b						

^aDunnett's test.

^bContrasting corresponding days after deprivation, using t test.

TABLE 7

Summary of Analyses of Variance for Data
for which Group-by-Day Means are in Table 6

Source	df	TS		SWS		PS	
		F	p	F	p	F	p
Days	6	31.1	<.001	16.2	<.001	27.1	<.001
<u>SS</u>	5	6.2	<.001	8.1	<.001	7.3	<.001
Days x <u>SS</u>	30						
Total	41						

TABLE 8

Circadian Rhythm: Daytime and Nighttime TS
and Day/Night Ratio for Baseline and Days after
Deprivation Procedures A and P

	Day after Procedure P			Day after Procedure A		
	1	2	8	1	2	8
Baseline						
Daytime TS	61.5	77.0	63.9	56.2	75.2	65.7
Nighttime TS	31.1	52.0	38.8	34.5	45.4	37.1
Day/Night Ratio	2.11	1.50	1.67	1.68	1.70	1.93

TABLE 9

Circadian Rhythm: Increase in Percent
Sleep over Baseline after Deprivation
Procedures A and P

	Day after Procedure P			Day after Procedure A			
	1	2	8	1	2	8	
Daytime TS	61.5	15.5	2.4	-5.3	13.7	4.3	-0.7
Nighttime TS	31.1	20.9	7.8	3.5	14.3	6.0	6.8

first night after deprivation Procedure P, sleep percent was about one and two-thirds of the baseline level, whereas the daytime sleep on the same day was only about one and one-quarter of the baseline level. Rather the increase in percent sleep seems to be additive in that during the first 12 daytime and the first 12 nighttime h, sleep percent increased by an absolute amount of about 14 to 21%. Because the recovery increase was approximately additive, the circadian rhythm, as measured by the day/night ratio in Table 8, decreased on day 1 after deprivation from 2.11 to between 1.68 and 1.93.

Levitt reported a decrease in circadian rhythm post deprivation by dextroamphetamine, and that sleep recovery occurred during nighttime only (1965, p. 37). However, after deprivation by treadmill, recovery occurred during both daytime and nighttime, with the circadian rhythm being significantly increased for days 3 to 5 post deprivation (Levitt, 1965, pp. 65-66). The results of this experiment support the findings that when behavioral or non-chemical deprivation techniques are used, sleep is recovered during both daytime and nighttime hours. It is possible that a side-effect of deprivation by dextroamphetamine was to somehow modify the post-deprivation circadian rhythm.

Sleep episode length

Examination of the sleep episode data suggested that the episodes be grouped into three intervals: up to 15 min (short episodes), 16-40 min (medium episodes) and 41 min or

more (long episodes). The number of episodes between 16 and 40 min changed little from baseline as a function of deprivation. Chi square was calculated* in fourfold tables contrasting (a) the proportion of long (41+) and short episodes (up to 15 min) for the individual days post deprivation with baseline, and (b) corresponding days after the two deprivation methods. The frequency data and Chi square analyses are presented in Table 10. After deprivation, the proportion of sleep episodes shifted so that the proportion of short episodes decreased and the proportion of long episodes increased. This change was observed on day 1 after both deprivation Procedures P and A. This shift was greater after Procedure P than after Procedure A. Thus, (a) when Ss were recovering lost sleep, sleep episodes tended to lengthen and (b) deprivation Procedure A tended to reduce this effect.

Summary

One group of six rat Ss was kept awake for two 24-h periods, 33 days apart, and after a baseline day had been recorded. Two techniques of deprivation were used, both of which used the EEG to monitor the sleep-wake state. The first, Procedure P, involved many stimuli, not contingent upon the sleep response, while the second, Procedure A,

* Since the data did not meet the requirements of independence (since data from Ss were pooled), Chi square was used only as a descriptive statistic.

TABLE 10

Sleep Episodes in Terms of Frequency of Occurrence
of Specified Length of Episodes

Length	Baseline	Day after Procedure P		Day after Procedure A	
		1	2	1	2
1-15 min	224	92	180	153	170
16-40 min	74	62	86	74	72
41+ min	18	49	25	35	29
			8	8	8

 χ^2

Day after Deprivation vs. Baseline Day	46.05	1.596	3.6798	12.24	5.838	.8698
Procedure A vs. Procedure P Corresponding Days	11.03	.493	.0574			

involved shock to the feet contingent upon EEG SWS.

Total sleep, SWS and PS were all significantly increased for the first 24 h after both methods of deprivation. Significantly more PS was obtained on day 1 after Procedure P and there was a trend in the data suggesting that more TS was obtained after this procedure.

Sleep (TS) was recovered after both methods of deprivation during both daytime and nighttime hours. The sleep increase was approximately additive and not proportional to the baseline daytime and nighttime sleep. This resulted in a decrease in the circadian rhythm as measured by the day/night sleep ratio.

Examination of the sleep episode data indicated that after deprivation there were fewer short sleep episodes (15 min or less) and more long episodes (41 min or more). This change was greater after Procedure P than after Procedure A.

EXPERIMENT IV

A major question in the area of sleep remains essentially unanswered: When an organism loses sleep, what proportion of the lost sleep is later recovered? In the literature on human sleep post deprivation, the question which has received most attention has been the percent sleep time of various sleep stages post deprivation.

Berger and Oswald (1962) recorded ss' baseline sleep for four nights, deprived ss of sleep for four nights and then recorded the recovery of sleep for four nights. Subjects were allowed 12 h of sleep on the first recovery night. On the baseline and other recovery nights ss were allowed 7 to 8 h of sleep. This procedure prevented answers to the question of amount of recovery of lost sleep. Detailed comparisons of sleep stages were made between the recovery nights and the baseline nights. Percent of time taken by Stages 1-REM and 2 were significantly decreased when the first $7\frac{1}{2}$ h of the first recovery night was compared to the baseline nights which were $7\frac{1}{2}$ h. Based on the first $7\frac{1}{2}$ h of sleep on the first recovery night, percent Stage 1-REM time was 7.4 as compared to 22.5% on baseline. For the full 12 h, Stage 1-REM time was 18.2%. On the second

recovery night, Stage 1-REM time was 27.5%, 26.9% on the third and 23.8% on the fourth. No other details were given by the authors. Berger and Oswald's basic finding of increased Stage 4 and decreased Stage 1-REM on the first night after deprivation and then increased Stage 1-REM on the second recovery night has been supported by Naitoh, Kales, Kollar and Jacobson (1968), after 204 h of wakefulness, by Kollar, Slater, Palmer, Docter and Mandell (1966), after 120 h, by Williams, Hammack, Daly, Dement and Lubin (1964), after 64 h, and by Williams and Williams (1966), after 64 h of wakefulness. Gulevich, Dement and Johnson (1966) studied one S that had stayed awake for 264 h. This S, unlike all of those in the studies above, was allowed to sleep until he awoke spontaneously. For this S, both Stages 1-REM and 4 were increased for the first as well as the second and third recovery nights. This suggested that the reports of decreased Stage 1-REM on the first night after deprivation were a result of terminating the first night's sleep arbitrarily, after some predetermined number of hours. The Berger and Oswald study above, with Stage 1-REM sleep percentages of 7.4 and 18.2 for the first 7½ and 12 h respectively, would support this notion. The data of Gulevich et al. (1966) also suggested that recovery was not complete after three days. One week after deprivation, S slept 424 min as compared to 388 and 391 min, 6 and 10 weeks later respectively.

A number of additional phenomena in the recovery sleep of humans after deprivation have been described. Gulevich et al. mentioned that Stage 1-REM periods were unstable and were often interrupted by bursts of Stage 2 activity, i.e., spindles. Naitoh et al. (1968) noted a similar phenomenon. In both studies, Ss were deprived for over 200 h. A decrease in body movements in the sleep after deprivation was reported by Williams and Williams (1966) after 64 h of wakefulness, by Cooperman, Mullin and Kleitman (1934) after 60 h of wakefulness, and by Marbach and Schaff (1960) with one night's sleep loss. Williams et al. (1964) reported a decrease in Ss' responsiveness to stimuli as measured by changes in EEG, vasoconstriction and the response of pressing a microswitch after deprivation.

The data on the amount of total sleep humans make up after sleep deprivation are very sparse, inadequate and variable. Edwards (1941) reported that Ss required between 86 and 29% of lost sleep time for recovery. Apparently, Edwards meant that Ss recovered between 86 and 29% of the sleep lost during deprivation in the weeks after deprivation. Katz and Landis (1935) summarized the studies done prior to this report, and concluded that a very small percentage of the lost sleep was made up. Except for Edwards, authors since Katz and Landis have not attempted to estimate the proportion of lost sleep made up by human Ss.

A number of authors have studied various indices which may have reflected the effects of sleep deprivation, after some recovery sleep. Essentially, one can conclude that one night of sleep after deprivation is not adequate to restore Ss to the pre-deprivation state. Ax and Luby (1961) reported that autonomic measures were not at baseline after three days. Nine h of sleep, taken on the day after 98 h of sleep deprivation, were not enough to restore EEG alpha to normal. An additional night's sleep was required for EEG alpha to be essentially normal (Armington and Mitnick, 1959). Based on subjective reports, the Ss studied by Edwards (1941) had not returned to normal until they had lived and slept normally for a week or even more. Wilkinson (1963) studied the after-effect of one night's sleep loss on performance after one recovery night of sleep. His Ss had about an extra 2 h of sleep beyond the night's sleep by napping in the evening before going to bed for the night. Performance on a vigilance and on serial reaction tasks were below the control levels. Williams, Granda, Jones, Lubin and Armington (1962) found a similar result with a vigilance task, when Ss slept for 9 h following 64 h of deprivation.

Based on the review above, one could conclude that after sleep deprivation, human Ss manifested their increased need for sleep by sleeping more than before deprivation. However, the question of the absolute amount of

sleep recovered relative to that lost is not answerable. The data on sleep stage recovery are not easily interpretable. Studies need to be done in which Ss are allowed to sleep as much as they like both before and after deprivation.

Since laboratory animals can be allowed to sleep without the interference of social conditioning of sleep, they offer a much better opportunity to study the question of recovery of lost sleep. In this area, Levitt (1965, 1966 and 1967) performed the most extensive experiments available on sleep after deprivation. These experiments were done in the same laboratory and using the same strain of Ss used by this E. In one experiment (Levitt, 1965), three groups of rat Ss were kept awake by injections of dextro-amphetamine sulphate for 24, 72 and 120 h respectively. The dependent variable measure of sleep was activity, recorded by an ultrasonic device. Levitt found that following sleep deprivation, there was a decrease in circadian rhythm. He found no difference in total amount of compensatory sleep due to amount of deprivation. He estimated the average amount of compensatory sleep. Compensation was arbitrarily considered to have ended on the first day that the mean sleep time for a deprivation group was equal to the baseline mean. The 24-h-deprivation group recovered 829 min of sleep whereas it lost only 784 min of sleep. The 72-h-deprivation group and the 120-h-deprivation

group lost 2,517 and 3,970 min of sleep respectively; they regained 450 and 568 min or 18 and 14% of the lost sleep respectively. Unfortunately, the multiple effects of the drug and sleep loss are confounded in this study.

Pegram (1968) has provided data which allow an important contrast to Levitt's findings. Unfortunately, his deprivation procedure was similar to Procedure A. Pegram kept rhesus monkeys awake for eight days and recorded their EEG for five baseline and eight recovery days. He found that PS percent returned to its baseline level after about two days. Stage 4 recovery was similar in showing a rapid recovery occurring mostly in the first 4 h of recovery sleep. However, Stage 2 was elevated for all eight recovery days and together with total sleep time was still substantially above baseline on the eighth recovery day. Although Pegram did not analyze his data in terms of the amount of sleep recovered, calculations based on his raw data suggested that Ss slept enough over baseline in the eight recovery days to make up for the sleep lost in about two to three days of normal sleep. (Pegram presented raw data for only five of the eight recovery days. The data for the three days not presented were interpolated by averaging the day before and the day after the omitted days.) These data were in sharp contrast to Levitt's data where the rats deprived for three and five days recovered less than one day's lost sleep. Also, Pegram's data were in sharp

contrast to the human Stage 1-REM recovery data. Pegram's Ss did not recover the Stage 1-REM sleep lost and in fact recovered more Stage 2 than Stage 1-REM.

Levitt (1965) also deprived two groups of rat Ss of sleep by means of a treadmill for 24 and 72 h respectively. Again, sleep was measured by activity recordings. In this experiment, (a) there was no circadian rhythm reduction, (b) deprivation level did not have a significant effect, and (c) the 24-h group lost 810 min of sleep and recovered 168 min or 21%, while the 72-h group lost 2,430 min and made up 313 min or 13% of the lost sleep. However, in another experiment, Levitt (1967) noticed that bursts of slow-wave sleep, which he referred to as microsleap, appeared in the EEG of Ss on the treadmill. In the same study, sleep was recorded using an EEG, before and after total sleep deprivation by means of dexedrine for three Ss and by means of the treadmill for three other Ss. Slow-wave sleep increased following deprivation by dexedrine only, whereas PS increased after both deprivation procedures. The finding of an increase in PS only, following deprivation, was reported by Kiyono, Kawamoto, Sakakura and Iwama (1965) using cats. They used visual monitoring to determine whether Ss were awake or asleep, and their results, like Levitt's, were not surprising considering the fact that their deprivation procedures deprived animals almost completely of PS and only partially of SWS.

In this experiment, two groups of Ss (Group A and Group P*) were deprived of sleep for 24 h by Procedures A and P respectively. This eliminated any interaction effects between the two methods since each group was deprived once and by one method only. Subjects were selected so that their baseline sleep levels were equivalent, and a very intense shock was used to keep Group A awake.

Method

Five male Long-Evans hooded rats were selected at random from a pool of 11 rats, all of which had been prepared for EEG recording. They were kept awake by deprivation Procedure P, and are thus referred to as Group P. These Ss were about 160 days old on the first baseline recording day.

A second group of eight Ss was prepared for EEG recording and five were selected to form a group whose baseline sleep percents matched those of Group P as closely as possible. This second group was deprived of sleep by means of Procedure A and is therefore called Group A.

Two baseline days were recorded a few days prior to deprivation. Recordings were begun immediately after deprivation and continued until the end of the ninth day after deprivation.

*These groups are defined in greater detail below.

Analysis of Data

The data were converted to sleep percentages and analyzed as described in Experiment III. The statistical design for the analysis of variance used is described by Lindquist (1953, pp. 266-273). The difference between the mean percent of sleep for any one group for any one day and the mean amount of sleep for that day for any other group was tested by a t test as recommended by Lindquist.* The difference between the baseline mean and the means of days post deprivation for any one group were tested by Dunnett's test for multiple comparisons using a control mean.

Results and Discussion

The data were analyzed in a manner which allowed measuring the effect of the deprivation procedures on SWS and PS as well as on TS, as in Experiment III. Table 11 presents the overall analyses of variance for SWS, PS and TS. Tables 12, 13 and 14 present group means in percent per 24-h day before and after deprivation for SWS, PS and TS respectively. Tables 12, 13 and 14 also present probabilities for Dunnett's test, which contrast each day after deprivation with the mean of the two baseline days, and the probabilities for the t tests as suggested by

*The t test used the square root of twice the mean square for error within cells divided by the N for either group since N s were always the same. A cell in this analysis included the individual scores of S s in a particular treatment group (aversive or positive deprivation) for any one particular day.

TABLE 11
 Overall Analyses of Variance for TS, SWS and PS
 per 24-Hour Day for which Data are in
 Tables 12, 13 and 14

Source	df	TS		SWS		PS	
		F	p	F	p	F	p
Between <u>Ss</u>	9						
Deprivation Groups	1	1.02		1.03		.25	
error (b)	8						
Within <u>Ss</u>	100						
Days	10	27.63	<.001	13.35	<.001	23.89	<.001
Days x Deprivation Groups	10	1.45		1.80	<.10	1.97	=.05
error (w)	80						

TABLE 13

PS Group Means in Percent
Pre and Post Deprivation
(per 24-Hour Day)

Group	Baseline Mean	Day Post Deprivation								
		1	2	3	4	5	6	7	8	9
Group P	9.15	12.80	9.18	9.62	9.72	8.66	8.62	9.70	9.08	9.26
		< .01								
Group A	9.17	13.92	8.18	9.40	8.90	8.34	8.54	9.24	10.04	7.76
		< .01								
Group P vs. Group A										< .05

^aDunnett's test.
^bt test.

TABLE 14

TS Group Means in Percent
Pre and Post Deprivation
(per 24-Hour Day)

Group	Baseline Mean	Day Post Deprivation								
		1	2	3	4	5	6	7	8	9
Group P	51.3	67.1	57.2	57.6	54.4	52.2	52.5	54.3	52.9	51.3
^a p		< .01	< .01	< .01	< .05					
Group A	51.5	63.3	52.3	53.4	52.6	50.4	51.3	52.4	53.5	50.1
^a p		< .01								
Group P vs. Group A			< .1	< .1						

^aDunnett's test.

^bt test.

Lindquist (1953, p. 272), which contrast the effect of the two deprivation techniques on corresponding days after deprivation. Figures 7, 8 and 9 are graphic plots of the data presented in Tables 12, 13 and 14 respectively.

Table 15 presents the percentage (or proportion) of lost SWS, PS and TS respectively, recovered during days 1 to 9 after deprivation per individual subject and per group.

Increase in SWS, PS and TS post deprivation

As may be seen in Table 11, the treatment days effect was statistically significant for SWS, PS and TS. Only for PS was the interaction of days by treatment groups statistically significant. As may be seen in Tables 12, 13 and 14, there is a significant increase in SWS, PS and TS relative to the baseline after both techniques of deprivation, for at least the first day after deprivation. This is the same as was found in Experiment III, Table 6.

In the literature review, it was suggested that the reports, in the human sleep literature, of decreased Stage 1-REM percent on the first night after deprivation, were a result of terminating the first night's sleep arbitrarily after some predetermined number of hours. Although this suggestion ultimately can only be validated or rejected by research with human Ss, the results of this experiment offer some limited support to the notion. The Ss in this experiment and in Experiment III showed a significant increase for the first 24-h recovery day, after both techniques of deprivation, in the percentage of the

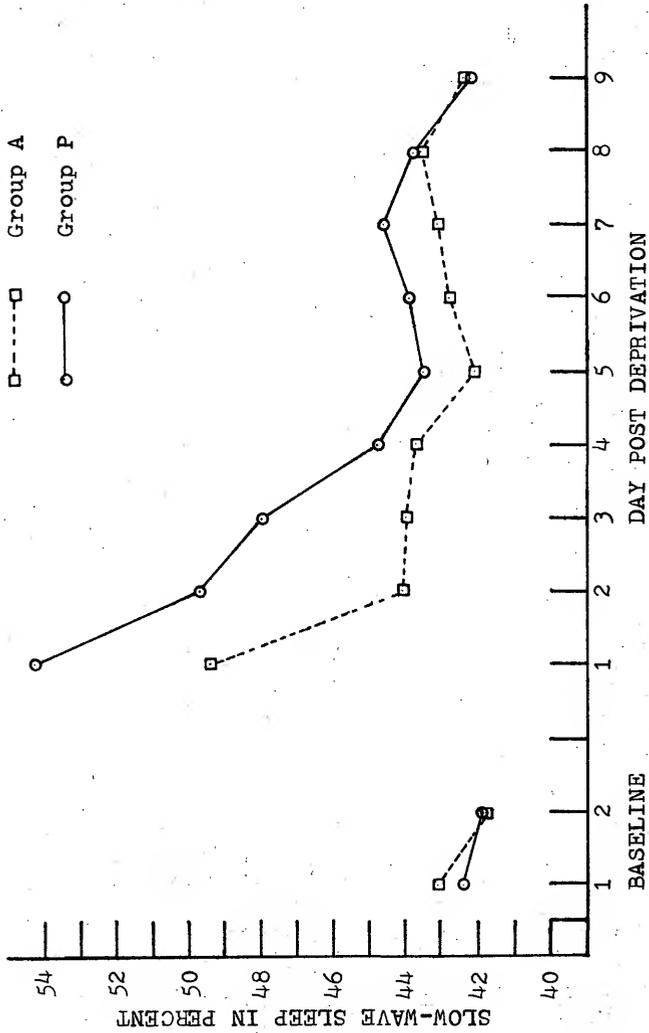


Figure 7. Slow-wave sleep group means pre and post deprivation per 24-hour day.

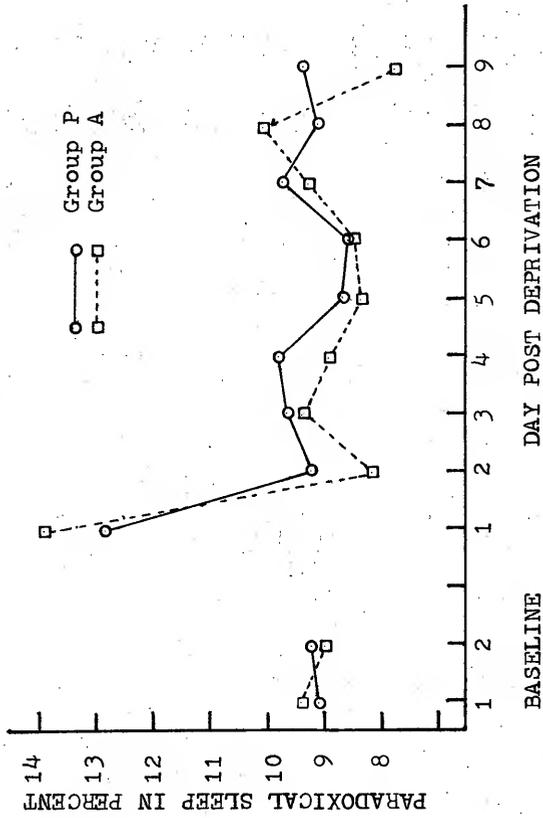


Figure 8. Paradoxical sleep group means pre and post deprivation per 24-hour day.

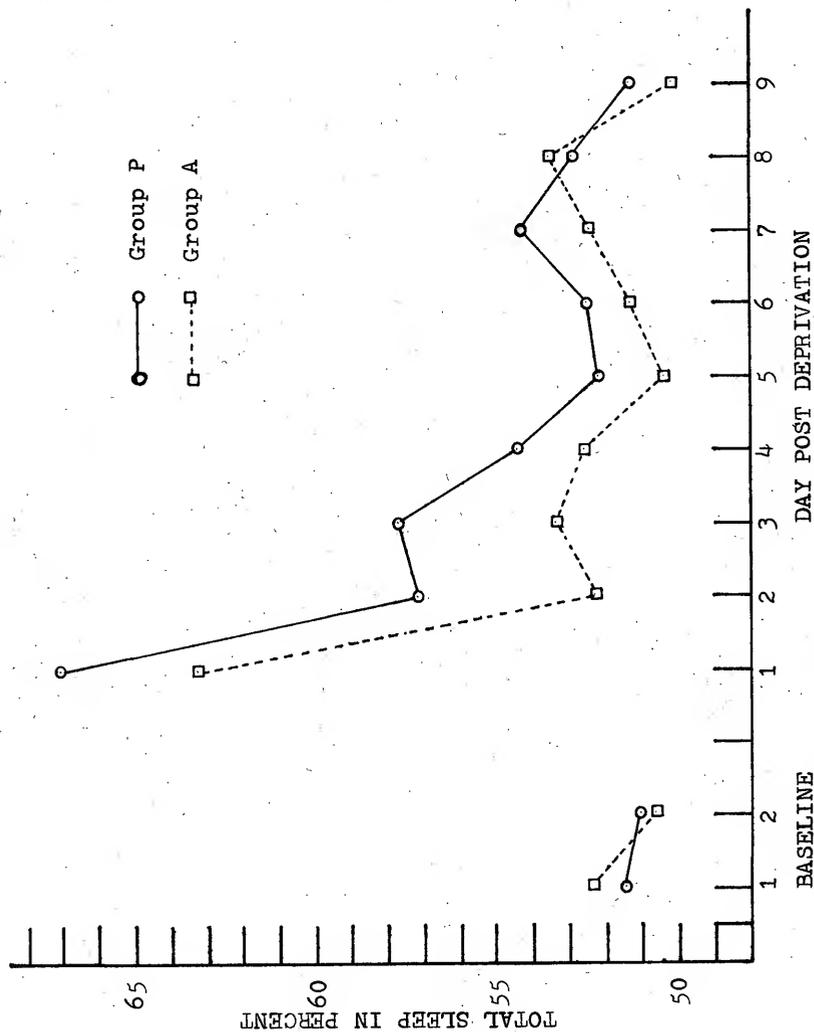


Figure 9. Total sleep group means pre and post deprivation per 24-hour day.

TABLE 15

Percent of Lost SWS, PS and TS Recovered^a
During Days 1 to 9 per Individual Subject and Group^b

Subject	Percent of Lost Sleep Recovered for		
	SWS	PS	TS
Group P 1	47.2	244.66	76.1
3	63.4	76.14	70.6
5	100.0	8.79	67.1
8	61.7	-122.0	19.5
10	150.9	60.42	134.8
Mean	<u>84.6</u>	<u>54.0</u>	<u>73.6</u>
Group A 1	9.3	-53.19	-4.7
4	67.0	11.70	56.5
5	2.1	75.48	11.4
8	-8.9	19.59	-2.3
9	95.3	53.13	93.6
Mean	<u>33.0</u>	<u>21.34</u>	<u>30.9</u>

^aEach 1% of sleep may be thought of as a unit of sleep; thus Ss obtained about 50 units of sleep per day. Recovery sleep percent is the number of units of extra sleep over baseline divided by the number of units of sleep on baseline.

^bMinus signs indicate a net loss of sleep relative to baseline during recovery days 1 to 9.

24-h day devoted to PS, which is the rat's equivalent to Stage 1-REM (see Table 6, Table 13 and Figure 8).

Pegram (1968) found that after eight days of deprivation with rhesus monkeys, PS returned to its baseline level after about two recovery days while Stage 2 was elevated for all eight recovery days. In the rat, SWS is probably equivalent to primate Stages 2 and 4 combined, since the rat has only PS and SWS. In this experiment, as may be seen in Table 12, it was found that SWS (or non-PS) was noticeably elevated (more than 1%) for eight of the eight days after deprivation Procedure P and for five of the eight days after deprivation Procedure A. On the ninth day, both groups had returned to the baseline level. As may be seen in Tables 6 and 13, PS was elevated for only day 1 post deprivation, after both techniques of deprivation, in this experiment and in Experiment III. This suggests that whatever PS is recovered after deprivation by subhumans, or possibly by all Ss allowed to sleep ad lib after deprivation, is recovered in less time than it takes for recovery of non-PS or SWS. Pegram's data strongly suggest that his Ss recovered proportionately more non-PS than PS. Similarly, in this study, it was found that proportionately more SWS was recovered than PS.

Proportion of lost sleep recovered

Levitt (1965) kept a group of rat Ss awake for 24 h by using dextroamphetamine sulphate. This group recovered more sleep than it lost. As may be seen in Table 15, only

one of six Ss kept awake by Procedure P recovered more sleep than it lost and no Ss kept awake by Procedure A recovered as much as was lost. This suggests that Levitt's chemical means of deprivation may have had some unusual effects on recovery sleep, not found when behavioral means are used to keep Ss awake. (This is also suggested by the fact that Pegram's Ss recovered about two to three days' worth of the eight days' sleep lost while Levitt's five-day-deprived groups recovered less than one day's worth of sleep.)

As may be seen in Table 15, the group deprived of sleep by Procedure A recovered less than one-half as much PS, SWS and TS as the group deprived by Procedure P. Definitive evidence that these differences are not a function of chance is not available. This is because, as may be seen in Table 11, the overall differences between the total amounts of SWS, PS and TS obtained by the two deprivation groups for the sum of the two baseline days plus the nine recovery days are not statistically significant despite the fact that the baseline sleep levels were almost identical. However, there is some evidence which suggests that the differences, particularly for SWS, are not a function of chance. This evidence comes from the t tests which reflect the significance of the differences between the mean percent of sleep for any one group for any one day and the mean amount of sleep for that day for any other group. As may be seen in Table 12, Ss in Group P obtained significantly more SWS

on days 1 and 2 post deprivation than did Group A. The Ss in Experiment III obtained more (but not significantly more) SWS on day 1 after deprivation by Procedure P than on day 1 after Procedure A. However, this difference was non-existent on day 2 post deprivation and was reversed on day 8 post deprivation.

As may be seen in Table 13, there were non-significant differences for PS between the two groups, except for recovery day 9, when Group P obtained significantly more PS than Group A. In Experiment III however, as may be seen in Table 6, Ss obtained significantly more PS on day 1 post deprivation by Procedure P.

As may be seen in Table 14, there were trends in the data ($p < .1$) suggesting that more TS was obtained on days 2 and 3 after Procedure P than after Procedure A for the same day. (The critical t at the .1 level was 1.68 and the t for day 1 was 1.63 which was thus just short of significance at the .1 level. Also, the critical t at the .05 level was 2.18 and the t for day 2 was 2.11.) There was also a similar trend in Experiment III as more TS was obtained on day 1 after Procedure P, the difference being significant at about the .1 level. In the light of all this evidence, it may be tentatively concluded that making delivery of shock contingent upon the sleep response, as a means of deprivation for 24 h, results in a large decrease in the amount of sleep recovered after deprivation. Ss may have learned to sleep less.

Recovery pattern

As may be seen in Figure 7, after Procedure P, SWS is recovered in a pattern describable as a decelerating curve of the percent of sleep as a function of time so that the bulk of the recovery is complete after three days and the level declines slowly back to the baseline level for another five days. The pattern for recovery after Procedure A is similar, the only apparent difference being that there is a consistently smaller increase after deprivation. As may be seen in Figure 8, the recovery pattern of PS is irregular except for the large increase in PS on day 1 after deprivation. As may be seen in Figure 9, the pattern for TS does not differ notably from the pattern for SWS.

Circadian rhythm

Table 16 presents the data reflecting the changes in daytime and nighttime sleep, and in the day/night ratio for Groups A and P. The same data are presented again in Table 17, where the increase over baseline percent sleep after deprivation is presented rather than actual percent sleep as in Table 16.

As may be seen in Tables 16 and 17, both daytime and nighttime sleep increased substantially on day 1 after deprivation for both groups. The conclusion in Experiment III that sleep lost in 24 h of deprivation is recovered during both daytime and nighttime hours is thus supported. This conclusion is very different from Levitt's (1965, pp. 41-42). After deprivation by dextroamphetamine,

TABLE 16

Circadian Rhythm: Daytime and Nighttime TS
and Day/Night Ratios for Groups A and P

Group	Baseline Mean	Day Post Deprivation								
		1	2	3	4	5	6	7	8	9
Group P										
Daytime TS	58.7	76.5	68.2	71.5	69.1	67.9	66.9	66.6	68.5	65.1
Nighttime TS	43.9	57.7	46.3	43.7	39.8	36.5	38.1	42.1	37.3	37.3
Day/Night Ratio	1.36	1.31	1.48	1.64	1.77	1.88	1.78	1.60	1.86	1.85
Group A										
Daytime TS	67.4	77.7	63.8	67.1	64.6	63.3	64.9	66.4	65.7	64.0
Nighttime TS	35.7	48.9	40.7	39.6	40.6	37.6	37.8	38.3	41.3	36.3
Day/Night Ratio	1.92	1.61	1.58	1.74	1.61	1.70	1.73	1.76	1.62	1.81

TABLE 17

Circadian Rhythm: Increase in Percent Sleep over
 Mean of Two Baseline Measures for Daytime and Nighttime
 Hours after Deprivation Procedures A and P

Group	Baseline Mean	Increase over Baseline Day after Deprivation								
		1	2	3	4	5	6	7	8	9
Group P										
Daytime	58.7	17.8	9.5	12.8	10.4	9.2	8.2	7.9	9.8	6.4
Nighttime	43.9	13.8	2.4	-2	-4.1	-7.4	-5.8	-1.8	-6.6	-6.6
Group A										
Daytime	67.4	10.3	-3.6	-3	-2.8	-4.1	-2.5	-1.0	-1.7	-3.4
Nighttime	35.7	13.2	5.0	3.9	4.9	1.9	2.1	2.6	5.6	.6

Levitt found

a slight decrease in sleeping time during the day. The entire compensation is accounted for by an increased sleep time during the dark or night phase of the light cycle. An explanation of this phenomenon may be that the rat, being a nocturnal creature, sleeps maximally during the day, awakening only to satisfy other need states which require attention. The rat, according to this hypothesis, cannot constantly remain asleep for 8-12 hours because of other need requirements. Thus, only at night is there time available to compensate for the heightened sleep need.

In this experiment, ss on day 1 after deprivation slept more than 75% of the time, which is equivalent to 8 h of sleep in the 12 daytime h.

The data in Tables 16 and 17 suggest that the increases in daytime and nighttime sleep percent for day 1 after deprivation are not proportional to the respective baseline amounts. For example, for Group A, on the first night after deprivation, sleep percent was about one and one-third of the baseline level, whereas the daytime sleep was about one and one-seventh the baseline level. Because of the disproportionality, the day/night ratio for Group A decreased from the baseline level of 1.92 to 1.61 on day 1 after deprivation.

As may be seen in Table 16, for Group P on day 1 post deprivation, more sleep was recovered during nighttime hours. For the other eight days after deprivation by Procedure A, there was a shift toward more nighttime TS than on baseline, and a decrease in TS relative to baseline during

daytime hours. This resulted in an increase in circadian rhythm. For Group A, as may be seen in Table 16, this shift was reversed with a resulting decrease in circadian rhythm. These changes seem to represent a tendency for the two groups to become more alike in terms of circadian rhythm. Group P during baseline had a smaller day/night ratio than Group A, and after deprivation Group P increased in circadian rhythm while Group A decreased. After the second recovery day, the ratio was between 1.6 and 1.9 for both groups. This range also includes the post-deprivation data in Experiment III.

Sleep episode length

The data were analyzed to reflect length of sleep episodes as described in Experiment III. In Experiment III, the frequency of episodes between 16 and 40 min did not change after deprivation. In this experiment, the frequency of episodes between 16 and 40 min increased by a factor of almost one-third and Chi squares* were calculated using the three class intervals as presented in Table 18. For Group P, the baseline days differed from each other very little ($\chi^2 = .67$) and the mean of the two baseline days was used in the baseline and the post-deprivation contrasts. For Group P, for days 1 to 9 post deprivation, sleep episodes between 1 and 15 min (short

* Since these data did not meet the exact criteria of independence (because of pooling of data from Ss) Chi square was used only as a descriptive statistic.

TABLE 18

Frequency of Occurrence of Minute Sleep
Episodes Grouped in Three Class Intervals

Group	Lengths (min)	Baseline		Day Post Deprivation								
		1	2	1	2	3	4	5	6	7	8	9
Group P	1-15	187	199	121	157	141	172	159	157	163	177	146
	16-40	65	64	86	91	94	76	67	85	55	66	71
	41+	24	31	45	30	32	33	32	27	35	32	33
	χ^2		.7 ^a	21.9	8.2	13.9	2.7	2.3	6.2	2.3	.9	5.1
Group A	1-15	199	149	114	198	160	194	174	206	151	134	156
	16-40	54	68	67	69	67	72	61	51	55	55	51
	41+	20	20	34	17	22	16	20	20	24	27	24
	χ^2	6.4 ^a	13.1	.7	.8	1.1	0	2.6	1.0	3.4	1.1	
Group P versus Group A	χ^2	1.7	3.6	1.2	30.7	7.0	7.3	3.9	16.0	1.4	3.0	4.3

^a Contrast of baseline days 1 and 2.

episodes) decreased in frequency while episodes of 16 to 40 min (medium episodes) increased notably for days 1 to 4. Episodes of 41 min or more (long episodes) increased notably for only day 1 post deprivation. For Group A, short episodes decreased and long episodes increased notably in frequency for only day 1 post deprivation.

Thus the conclusions in Experiment III are supported:

(a) During recovery of lost sleep, length of minute episodes increases so that there are fewer short episodes and more medium and long episodes. (b) Procedure A reduces this effect.

Summary

Two groups of five rat Ss were kept awake, each for one 24-h period, after two baseline days of sleep had been recorded. A different deprivation technique was used with each group, but with both groups, the EEG was used to monitor the sleep-wake state. Group P was kept awake by means of Procedure P, which involved a variety of stimuli, not contingent upon the sleep-wake state. Group A was kept awake by means of the deprivation Procedure A, which involved shock to the feet contingent upon EEG SWS.

As in Experiment III, TS, SWS and PS were all significantly increased for at least day 1 post deprivation for both groups. As in Experiment III, PS was increased for day 1 post deprivation only and SWS was increased for more than day 1. Thus the data for both experiments suggest that a larger proportion of the lost SWS is re-

covered than PS. In Experiment IV, the group deprived by Procedure P recovered 84.6 and 54.0% of the SWS and PS respectively, lost during deprivation, while the group deprived by Procedure A recovered correspondingly 33.0 and 21.3%.

The data from both experiments suggest that Procedure A results in decreased recovery of both PS and SWS relative to the amount recovered after Procedure P. Possibly, Procedure A resulted in ss' learning to sleep less.

Sleep was recovered, in both experiments and after both deprivation techniques, during both daytime and nighttime hours. These sleep increases were generally not proportional to the baseline daytime and nighttime sleep. This resulted in changes in the circadian rhythm, as measured by the day/night sleep ratios. These changes seemed to be in the direction of making all groups alike after the second day post deprivation.

SWS was recovered in a pattern describable as a decelerating curve of the percentage of sleep as a function of time so that the bulk of the recovery is complete after three days and the percent sleep level declines slowly back to the baseline level for another five days. All the lost PS that was recovered was obtained on day 1 post deprivation only.

The data reflecting the length of sleep episodes indicated that there was a shift in both experiments toward

longer sleep intervals after deprivation. Procedure A appeared to have decreased this shift in both experiments.

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BIOGRAPHICAL SKETCH

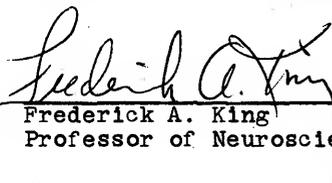
Hyman Solomon Sternthal was born in Montreal, Canada on September 19, 1939. He attended Strathcona Academy and graduated from high school in June, 1956. In 1960, he received the B.Sc. degree from McGill University in Montreal. In 1963, he moved to Gainesville to attend the University of Florida and there received the M.A. degree in 1965. From 1965 to the present time, he pursued his work toward the degree of Doctor of Philosophy in Experimental Psychology. He also completed an internship in Clinical Psychology at the University of Kansas Medical Center in 1971. Presently, he is employed at Florida State Prison. He has established permanent resident status in the United States and, with his wife and daughter, now makes his home in Florida.

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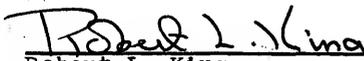
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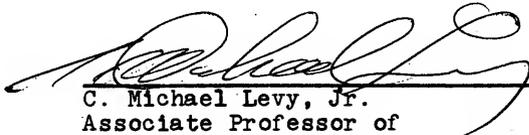
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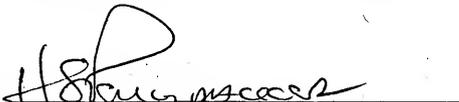


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This dissertation was submitted to the Department of Psychology in the College of Arts and Sciences and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

March, 1973


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