UNIT ACTIVITY IN THE SEPTAL NUCLEI DURING WATER DEPRIVATION, DRINKING, AND REHYDRATION

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ABSTRACT

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To investigate changes in the firing rates of septal cells during and after drinking, single and multiple unit activity in the septal nuclei of unanesthetized and unrestrained rats was monitored with multiple electrodes. In rats adapted to a 23.5 hour water deprivation schedule, cells discharged nearly twice as fast before the 0.5 hour drink period as they did afterward. Electrical activity recorded for one hour in a control group of rats on ad libitum food and water did not change significantly. Similarly, in a group adapted to a 23 hour food deprivation schedule, electrical activity recorded during 23 hour deprivation, one hour of eating, and 15 minutes of food satiation showed no significant changes. Septal unit activity changed markedly during drinking if the animal had undergone 23.5 hours of water deprivation, but not if it had drunk water on an ad lib schedule; unit activity in rats deprived of food did not change significantly during eating.

Sensory stimuli were relatively ineffective in altering firing rates of septal neurons, except in the gustatory

mode with hypertonic saline as the stimulus. Units also appeared responsive to proprioceptive feedback from swallowing.

The finding that septal cells are much more active during dehydration than rehydration supports the hypothesis generated by studies using anesthetized preparations: that one septal role in water regulation is to stimulate during dehydration supraoptic cells which then release more anti-diuretic hormone, causing the animal to conserve water. Changes in septal activity during drinking suggest that septal neurons influence lateral hypothalamic units not only as a consequence of the hydration conditions, but also during the drinking behavior per se. The nature of this influence is yet unknown, since septal units may either increase or decrease discharge rates during drinking.

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By

John G. Bridge

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INTRODUCTION

Extensive evidence implicates the septal nuclei in consummatory behavior. Lesions of the septal area cause hyperdipsia in rats (Harvey and Hunt, 1965; Lubar, Schaefer, and Wells, 1969; Blass and Hanson, 1970). Electrical stimulation of the septal area reduces the water intake both of rats with water available ad libitum and of those on 23 hour water deprivation schedules (Wishart and Mogenson, 1970). Carbachol stimulation of the septal area increases drinking (Fisher and Coury, 1962), and atropine blockage of the medial septal nucleus reduces drinking (Grossman, 1964). According to Bridge and Hatton (1973), septal unit activity in rats anesthetized with urethane is usually faster during and after stimuli which are associated with or which induce dehydration (water deprivation; subcutaneous and carotid injections of hypertonic saline) than during and after stimuli which are associated with or which induce hydration (the 0.5 hour drink period of a 23.5 hour water deprivation schedule; carotid injections of hypotonic saline; stomach loads of tap water).

The septal area also appears to be involved in eating and/or in controlling food intake, though not to the extent that it is involved in drinking. When the lateral septal area is stimulated with carbachol, rats eat more than before

stimulation. Food deprivation (or water deprivation) increases septal self-stimulation rates in cats and rats (Brady, Boren, Conrad, and Sidman, 1957). According to Johnson and Thatcher (1972), as food deprivation time increases, septal lesioned rats increase lever-pressing rates for food reward significantly faster than do unlesioned control rats. Although hyperdipsia has been reported as a consequence of septal lesions more often than has hyperphagia, one study (Stoller, 1971) found that septal lesioned Holtzman rats eat more but do not drink more than sham lesioned or unlesioned controls.

The septal nuclei also appear to influence various components of sexual behavior. MacLean and Ploog (1962) found that septal stimulation elicits penile erection; electrical self-stimulation of the human septal region produces a sensation of sexual gratification (Heath, 1963).

Though researchers have studied several ways in which septal activity is related to consummatory behaviors, however, the mass of septal stimulation or septal lesion data still does not allow us to describe the unit activity during these behaviors and, therefore, to construct and support logical hypotheses about the septal role in them. Soulairac, Tangapregassom, and Tangapregassom (1972) recorded with gross electrodes slow wave potentials in the septal area during dehydration, drinking, and rehydration, but their effort did not suggest how the septal nuclei function. Bridge and Hatton (1973) measured septal unit activity during different

hydration states in rats anesthetized with urethane. But although their technique measured the vegetative aspects of water regulation, it could not evaluate septal activity during the behavioral act of drinking. Furthermore, Calaresu and Mogenson (1972) have found that the effects of septal stimulation on cardiovascular response can depend in part on the anesthetic used (chloralose versus urethane), thus casting doubt on the extent to which a urethane preparation reflects events in a normal, awake animal. And while Ranck (1973) has reported an extensive examination of unit activity in the hippocampus and the septal region, this experiment focuses on the hippocampus and on non-consummatory behaviors. When Yamaoka and Hagino (1974) measured the diurnal rhythms of septal unit activity in awake and unrestrained animals, they found that spontaneous activity decreases shortly after lights go off and increases shortly after lights are turned on; they did not report septal activity during eating or drinking, however. None of these experiments, then, adequately describes septal unit activity before, during, and after consummatory behaviors.

There are two inconsistencies in the literature about the septal area and consummatory behavior. First, while studies showing that lesions often produce hyperdipsia (Harvey and Hunt, 1965), stimulation can reduce water or food intake (Wishart and Mogenson, 1970), and unit activity is greater during dehydration than during hydration (Bridge and Hatton, 1973) imply that the septum is hyperactive

during deprivation and relatively inactive during satiation, other studies indicate the septal area is a potent site of self-stimulation (Stein and Ray, 1959). If electrical stimulation activates septal cells and if active septal cells are associated with deprivation, why then would animals eagerly self-stimulate? Another discrepancy is that while septal lesions produce hyperdipsia and electrical septal stimulation reduces water intake, carbachol stimulation of the septal area also results in hyperdipsia (Fisher and Coury, 1962). At present it is impossible to infer how the septal nuclei function during water regulation and other consummatory behaviors. That is, are septal cells relatively active during hydration, as the self-stimulation and carbachol stimulation studies suggest; or are the septal units relatively active during dehydration, as the electrical lesion and stimulation experiments indicate? A description of septal unit activity during naturally occurring consummatory behavior may help us to understand these apparent discrepancies and related phenomena, such as the effects of stimuli and anesthetics on septal activity.

To observe septal unit activity during consummatory behaviors requires a recording system capable of sensing cellular discharges in an awake and freely moving animal. Septal cells can fire at extremely slow rates, and to avoid a sampling error of missing slow cells, a multiple electrode assembly would be superior to a single electrode. In the present experiment, such an apparatus was developed and used

to record septal unit activity before, during, and after consummatory behaviors (with particular attention to drinking).

METHOD

Thirty-two adult male Holtzman rats were each implanted with an assembly of six recording electrodes of either 62.5 μm diameter nickel-chromium conductor insulated with enamel except at the tip or 25 μm diameter platinum-iridium wire insulated, except at the tip, with teflon. One 125 μm diameter nickel-chromium ground electrode insulated with enamel except for approximately 0.5 mm at the tip was lowered to a position just above the septal area. See Appendix C for a detailed description of microelectrodes and their construction. Rats were housed singly in cylindrical plexiglas cages of approximately 35 cm diameter. The light-dark cycle in the colony room was 14 hours light: 10 hours dark, and to ensure that changes in electrical activity during a recording session could not be attributed to the rat's prior contact with a female rat, no females were housed in this colony room.

Rats scheduled to be tested in water-deprived or food-deprived conditions were adapted to a 23.5 hour water deprivation schedule or a 23.0 hour food deprivation schedule for 10 days before the implantation surgery. Maintained on water or food deprivation, rats were allowed a minimum of 10 days of post-operative recovery before the first recording day. Rats scheduled for ad lib recording

had food available ad lib for at least 10 days before surgery and were allowed 10 days of post-operative recovery with food and water available continuously.

A recording session began when the rats were two hours into the light portion of their light-dark cycle. Home cages served as recording chambers, and the procedure involved carrying the rat in his home cage to the recording room, removing the rat from his cage, plugging the leads from the recording apparatus into the implanted socket, and returning the rat to the cage. Electrical activity at each electrode tip was observed on a dual-beam oscilloscope, and the activity of electrodes with good signal-to-noise ratios were recorded on channel one and/or channel two of a stereo tape recorder. Most units were recorded bipolarly, using one of the remaining five electrodes as a reference electrode.

Impulses from the brain that were sensed by the recording electrode went to an off-lesion-record junction box via three-strand phono wire. In the lesion position, the junction box could supply current to the electrode tip for a marking lesion; in the recording position, impulses from the electrode went to channel one and channel two, respectively, of a stereo tape recorder via a low level preamplifier set to amplify times 1000. Impulses were monitored with a loudspeaker, and an on-line counter was available to record the rates of impulses whose amplitude exceeded the threshold of the oscilloscope trigger.

Recording sessions which focused on drinking and on

the consequences of water intake lasted approximately one hour: 15 minutes of 23.5 hour water-deprived base rate activity were recorded, then the 30 minute drink period, and, finally, a 15 minute rehydration period. During the half hour drink period, approximately half the rats were allowed to eat; the food was removed from the cages of the remaining rats during this period. Recording sessions under ad lib conditions lasted one hour. To observe the effects of food deprivation and eating on septal unit activity required 90 - 120 minutes of recording: 15 minutes of food-deprived base rate activity, a one hour eat period, and a 15 minute satiated period. Recording sessions began at 9:00 A.M. (two hours into the light period of the light-dark cycle).

On some days additional activity was recorded; these data included up to 0.5 hours of exposure to a female rat, up to 0.5 hours of sensory stimulation, and (on the day the animal was to be sacrificed) up to 0.5 hours of ether or urethane anesthetic. Sensory stimuli included tactile (touch, pinch, poke, or stroke), visual (house lights on or off), auditory (claps, shouts), gustatory (saline, sucrose, or quinine solutions; cold tap water), and olfactory (alcohol, ether, or litter from the tray of a female rat's cage) stimuli.

Recording sites were marked with direct current lesions ranging from 8 μA for 6 seconds to 30 μA for 15 seconds. Animals were perfused transcardially with 0.9% saline solution followed by a mixture of one part 37% formaldehyde

and nine parts saline. To confirm the location of the marking lesion, brains were frozen and sectioned at 50 μm intervals and the cells stained with cresyl violet.

The data from each recording session were considered those of a unique cell or a unique group of cells, even when an electrode in one particular rat was recorded from on two successive days and appeared to be monitoring the same cell on each day. That is, units recorded on different days from the same rat and the same electrode are considered related events, but not the same unit. Winer (1962) has suggested expressing repeated measures as a percentage of the total behavior or score. This method has an advantage that expressing activity as a percentage of a base rate does not: by assigning the value of 100% to base rates of each subject, the latter method loses the variability among them; the method Winer recommends preserves the variability among base rates. The data are described with means and standard errors and analyzed with repeated measure (treatment by subjects) design because this statistic is robust against deviations from the normal distribution by the population sampled (Welkowitz, Ewen, and Cohen, 1971, p. 141).

RESULTS

When unit activity was measured during dehydration, drinking, and rehydration, the cells characteristically fired at a faster than average rate during the dehydrated period (Figure 1). When the animals drank, the mean firing rates did not change significantly, but the variance of this mean increased markedly. That is, some cells fired much more rapidly and others slowed considerably, while the mean did not change significantly; approximately half the cells increased and half decreased firing rates during the initial drink period. The mean absolute change of discharge rates (without regard to direction) from the water-deprived base to the first prolonged drinking bout of the 0.5 hour drink period showed the largest change (45%) measured in any sequential comparison between non-consummatory and consummatory behavior (see Figure 2). When the rat terminated its initial drinking bout, discharge rates returned during the non-consummatory period that followed to near deprived levels. Discharge rates during non-consummatory behavior then decreased until they reached approximately 57% of the water-deprived base rate. When the rats were allowed to eat during the drink period, the non-consummatory discharge rates only decreased to 67% of the water-deprived base rate.

Figure 1.--Indicated are mean discharge rates per second expressed as a percentage of the mean discharge rate for all data points (within animals). On the abscissa is the recording time in minutes. Panel one (H_2O DEP) shows 15 minutes recorded when rats were water-deprived for 23.5 hours. Panel two (DRINK) shows 30 minutes recorded when rats were allowed free access to water. Panel three (REH) shows a 15 minute rehydrated period recorded after the 0.5 hour drink period. Below the abscissa are the sample sizes of each group (N).

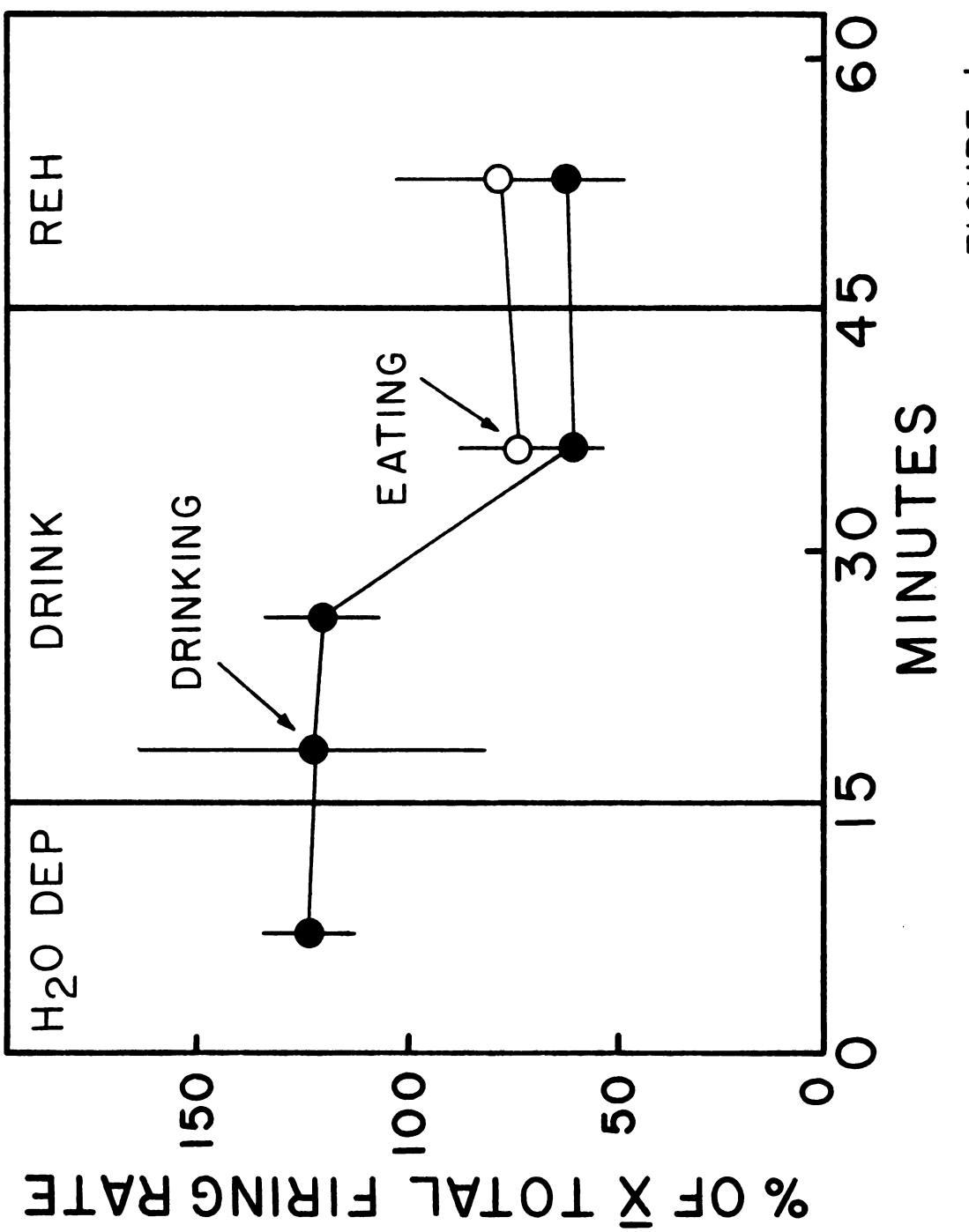

% OF $\bar{X}$ TOTAL FIRING RATE
150
100
50
0
H_2O DEP
DRINK
REH
DRINKING
EATING
15
30
45
60
MINUTES

FIGURE 1

Figure 2.--Panel A indicates the distribution of changes at the onset of drinking in firing rates of cells in rats deprived of water for 23.5 hours. Panel B shows the distribution of changes in firing rates at the onset of drinking in rats with food and water available *ad lib*.

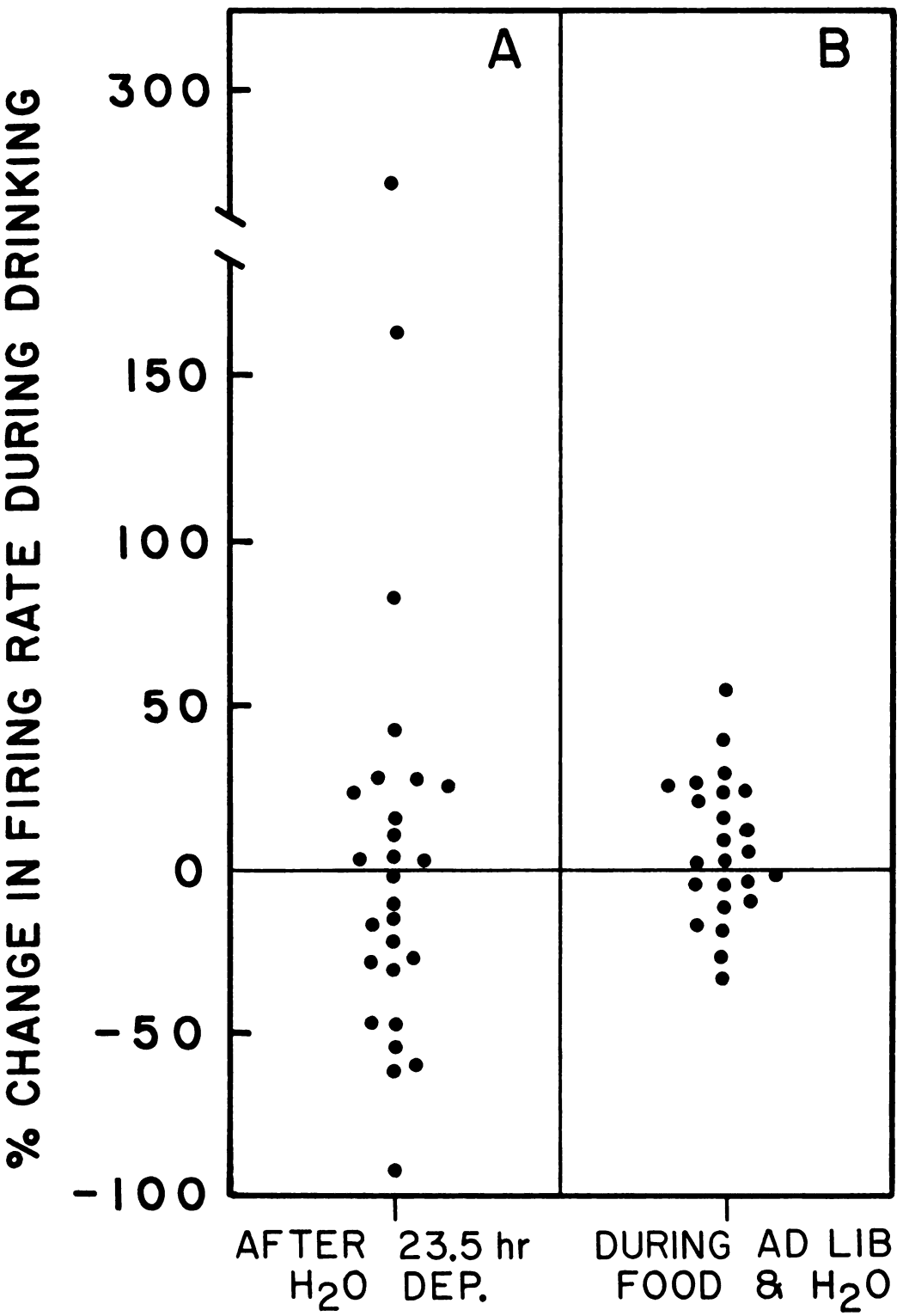

A
B
300
150
100
50
0
-50
-100
% CHANGE IN FIRING RATE DURING DRINKING
AFTER 23.5 hr H_2O DEP.
DURING AD LIB FOOD & H_2O

FIGURE 2

Under all conditions, the mean changes in firing rates while rats were eating were much smaller than those during drinking, even when animals had been deprived of food. During the eating period, it was possible to measure the discharge rates of components of the eating behavior: rooting about in the food pile, picking up and carrying food, chewing, and swallowing. Cells often fired faster during a specific component of this behavioral sequence, usually swallowing (see Figure 3). Cells also fired faster during swallowing in the ad lib periods and after 23.0 hours of food deprivation. The lick-swallow sequence of drinking was too rapid to measure each component separately.

For food-deprived rats, the apparent trend of septal unit activity during eating and during the post-eat period was not statistically significant (Figure 4). On some occasions rats were still eating at the end of the one hour eat period and appeared to be not yet satiated. Discharge rates of cells in these rats did not differ from the rates of those that had finished eating. And discharge rates during eating did not consistently differ from those during non-consummatory behavior. Food-deprived rats drank in short bouts which occurred at such different times throughout the recording session that representing them on single data points was impossible. Generally, the firing rates of these food-deprived animals changed slightly to moderately; the direction of the change was consistent within but not among animals.

Figure 3.--Indicated are mean discharge rates of the chewing and swallowing components of eating by one rat. One swallow lasts approximately 700 ms.

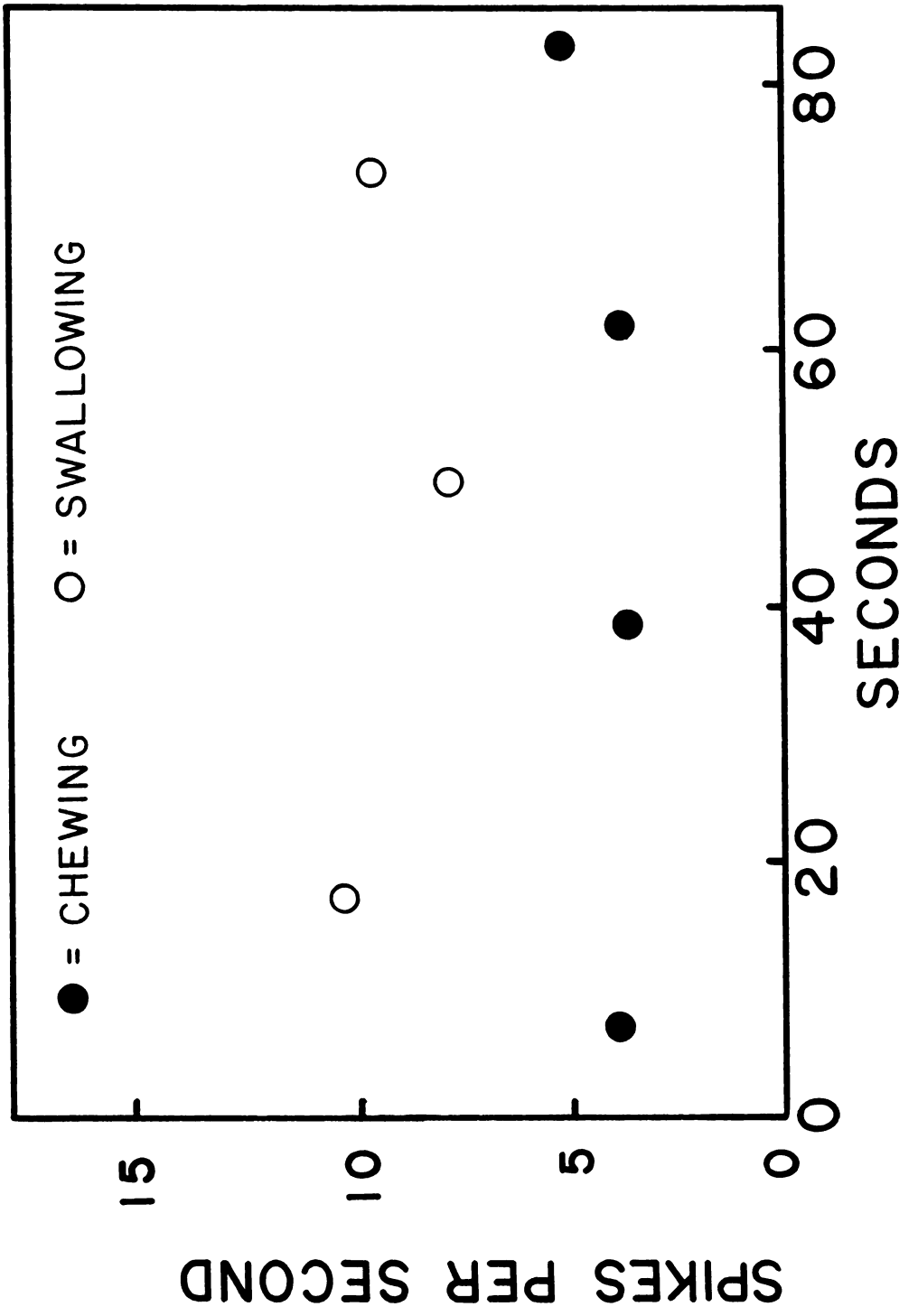

SPIKES PER SECOND
15
10
5
0
0
20
40
60
80
SECONDS
● = CHEWING
O = SWALLOWING

FIGURE 3

Figure 4.--Indicated are mean discharge rates per second expressed as a percentage of the mean discharge rate for all data points (within animals). On the abscissa is the recording time in minutes. Panel one (FOOD DEP) shows a 15 minute period recorded when animals had been deprived of food for 23.0 hours. Panel two (EAT) shows a one hour period recorded when food was available *ad lib*. Panel three (SAT) shows a 15 minute post-eat period. N = 11 during non-consummatory behavior; during eating, N = 6.

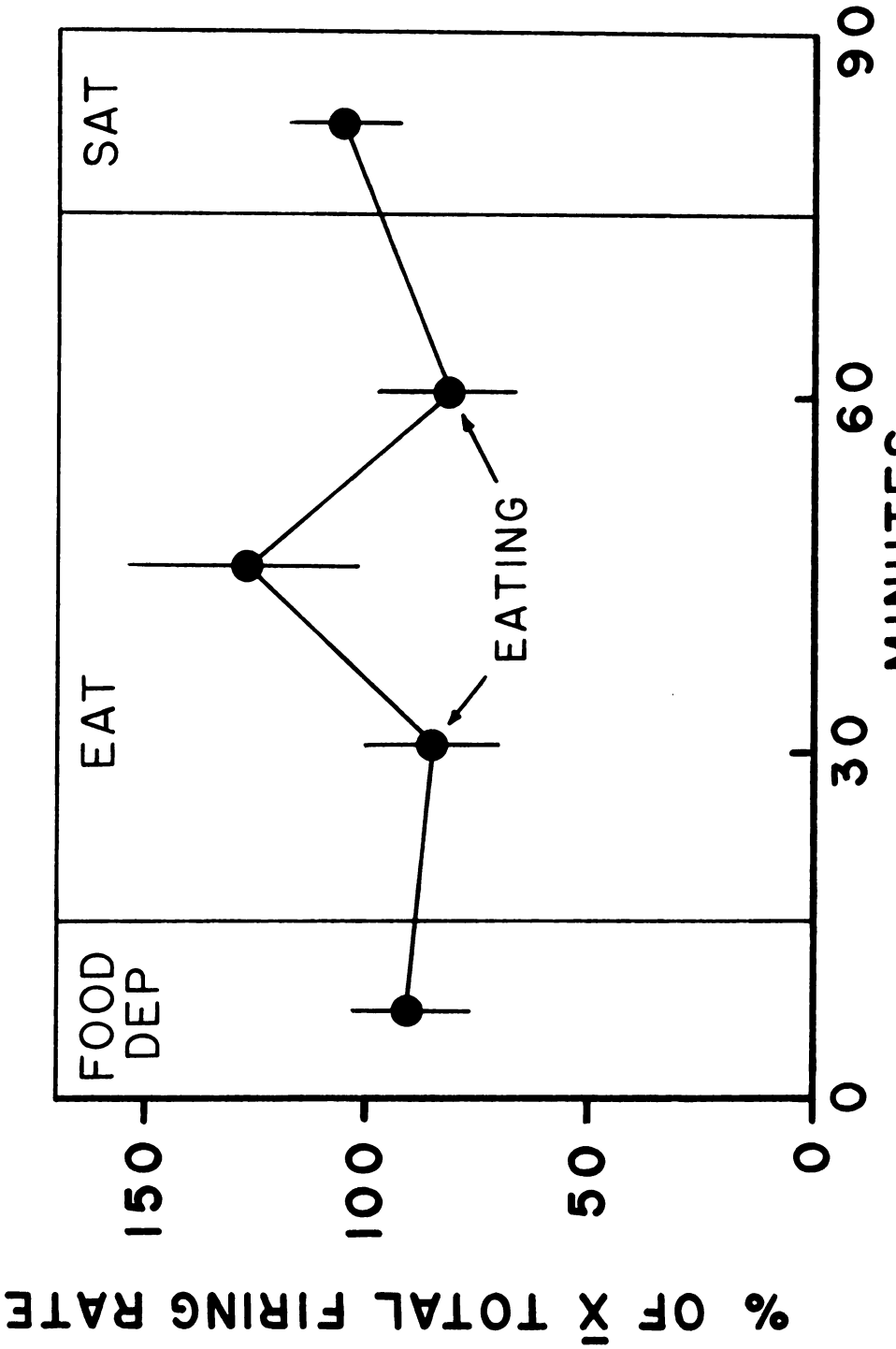

% OF $\bar{X}$ TOTAL FIRING RATE
150
100
50
0
FOOD DEP
EAT
SAT
EATING
0
30
60
90
MINUTES

FIGURE 4

During grooming, the discharge rates of cells usually increased or did not change; rarely did they decrease. Firing rates changed when the rat was licking its pelt or rubbing its head with its forepaws (see Figure 5). In a sample of the first two grooming behaviors in 10 recording sessions, 20% of the cells discharged faster than during non-consummatory behavior, 5% of the cells slowed, and 75% did not change.

Firing rates of septal cells in rats with food and water available ad lib did not change significantly over the course of the one hour recording session. Nor was there a trend within recording sessions: no mean discharge rate of the final 15 minutes had changed more than 12% from its firing rate during the first 15 minutes. With the onset of drinking, the firing rates of water-deprived animals changed more than those of water-replete animals. The mean absolute change (without regard for direction) was less under ad lib conditions than when rats were adapted to a 23.5 hour water deprivation schedule: mean absolute change for water-replete animals = 17%; mean absolute change for water-deprived animals = 45%, $p < .001$.

To avoid overlooking cells which were not discharging during the condition at the start of the recording (such as water deprivation) but which might fire when the condition changed (to drinking, for example), background activity (multiple units with small signal-to-noise ratios) was recorded for one hour sessions in one of two ways: 1) when

Figure 5.--Indicated are firing rates of one septal unit during different components of grooming.

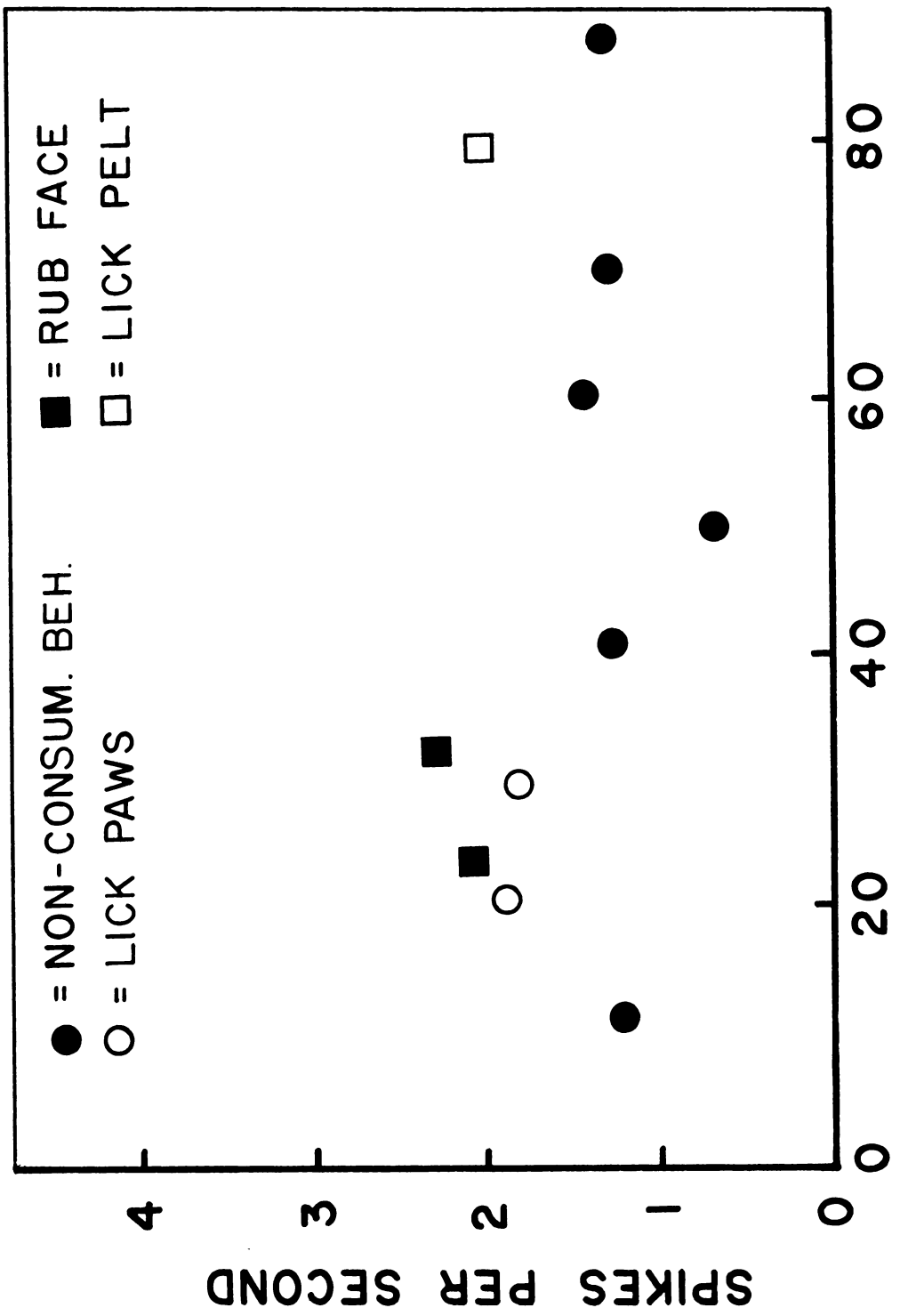

SPIKES PER SECOND
4
3
2
1
0
0
20
40
60
80
SECONDS
● = NON-CONSUM. BEH.
○ = LICK PAWS
■ = RUB FACE
□ = LICK PELT

FIGURE 5

only one electrode was yielding good signal-to-noise ratios, two electrodes that received good background noise but no large units were recorded on the second channel and, 2) when no electrodes yielded good signal-to-noise ratios, data from two electrodes were recorded on both channels. Twenty-six hours of this sort of activity was recorded. One recording showed two cells that never discharged during consummatory behavior and rarely discharged during non-consummatory behavior. When they did discharge, it was usually during rapid neck movements. No activity was observed during the other 25 one-hour recordings.

After six recording sessions (of three rats in two sessions each), a female Holtzman rat was placed in the cage of the male, and additional units were recorded from the male's septum. None of these encounters resulted in successful copulation or even in mounting or lordosis, nor did the animals mate on numerous other occasions, even without the recording leads attached. Because Holtzman rats are notoriously hyposexual, this line of investigation was discontinued after recording sessions in which four of the units increased in firing rates, one did not change, and one decreased while the female was in the cage. During the session in which the discharge rates decreased, the male rat sat immobile, without attempting to mount the female. In the other five sessions, the male repeatedly attempted to mount the female.

After many of the drinking, eating, or ad lib recording

sessions, additional recordings were made during non-consummatory behavior to observe septal unit activity in response to sensory stimuli. Because previous sensory stimulation of rats anesthetized with urethane (Bridge and Hatton, 1973) indicated that septal cells habituate rapidly, the modes, intensities, and types of the stimuli in the present experiment were varied rather than repeated. Yet, in general, septal units did not respond to sensory stimuli (Table 1).

Table 1.--Effects of Sensory Stimulation on Firing Rates of Septal Cells

Panel A

Stimulus Mode	Effect		
	INC	NC	DEC
Auditory	1	11	3
Olfactory	2	10	1
Gustatory	10	21	4
Visual	1	14	1
Tactile	3	10	0
Total	17	66	9
Control	8	27	5

Panel B

	Inc	NC	Dec
20%sucrose	2	6	0
1.2-15% NaCl	3	4	0
quinine	0	4	1
cold tap	1	2	2
5% NaCl	4	5	1

Responses to sensory stimuli were measured for 10 seconds and compared to activity during the one minute unstimulated period of non-consummatory behavior preceding the stimulus. A change was defined as an increase or decrease of 50% or more. To establish a control, 10 second

unstimulated periods were compared to the one minute of unstimulated unit activity that preceded them. Control data came from five measures of eight rats; stimuli data came from a varying number of measures of 14 rats. (Figure 6 shows the response of an individual septal unit to sensory stimulation.)

Panel A of Table 1 lists the effects of all the sensory modes. Auditory stimuli consisted of claps or shouts; olfactory stimuli included 95% ethanol, ether, and litter from the cage of a female rat; house lights, on or off, were the visual stimuli; a tactile stimulus was a stroke or a poke with a pencil or finger. Panel B lists the gustatory stimuli in detail. Because the rats would lick aversive fluids for no more than a second voluntarily, their tongues were bathed with quinine and 5.0% NaCl while the animals were anesthetized with urethane (immediately before sacrificing). As the table indicates, the gustatory mode was the most effective stimulus in producing change; within the gustatory mode, sodium chloride appeared most effective.

When rats were anesthetized just before they were to be sacrificed, the effects of ether or intraperitoneal urethane on septal unit discharge rates were observed. Unit activity was measured when the animal appeared anesthetized to a level appropriate for surgery (e.g., the animal did not respond to pinches or pokes). During ether anesthesia unit activity decreased to 58% of the non-consummatory activity rate prior to the anesthetic ($p < .02$, $N = 6$, two-tailed

Figure 6.--Indicated are responses of septal units to a gustatory stimulus of hypertonic saline, administered by substituting the saline bottle for the regular water bottle. Each data point shows the mean of 10 seconds. Open circles represent unstimulated non-consummatory behavior. Closed circles show the rat's drinking of 1.2% saline solution. (Rat 20, tape 45)

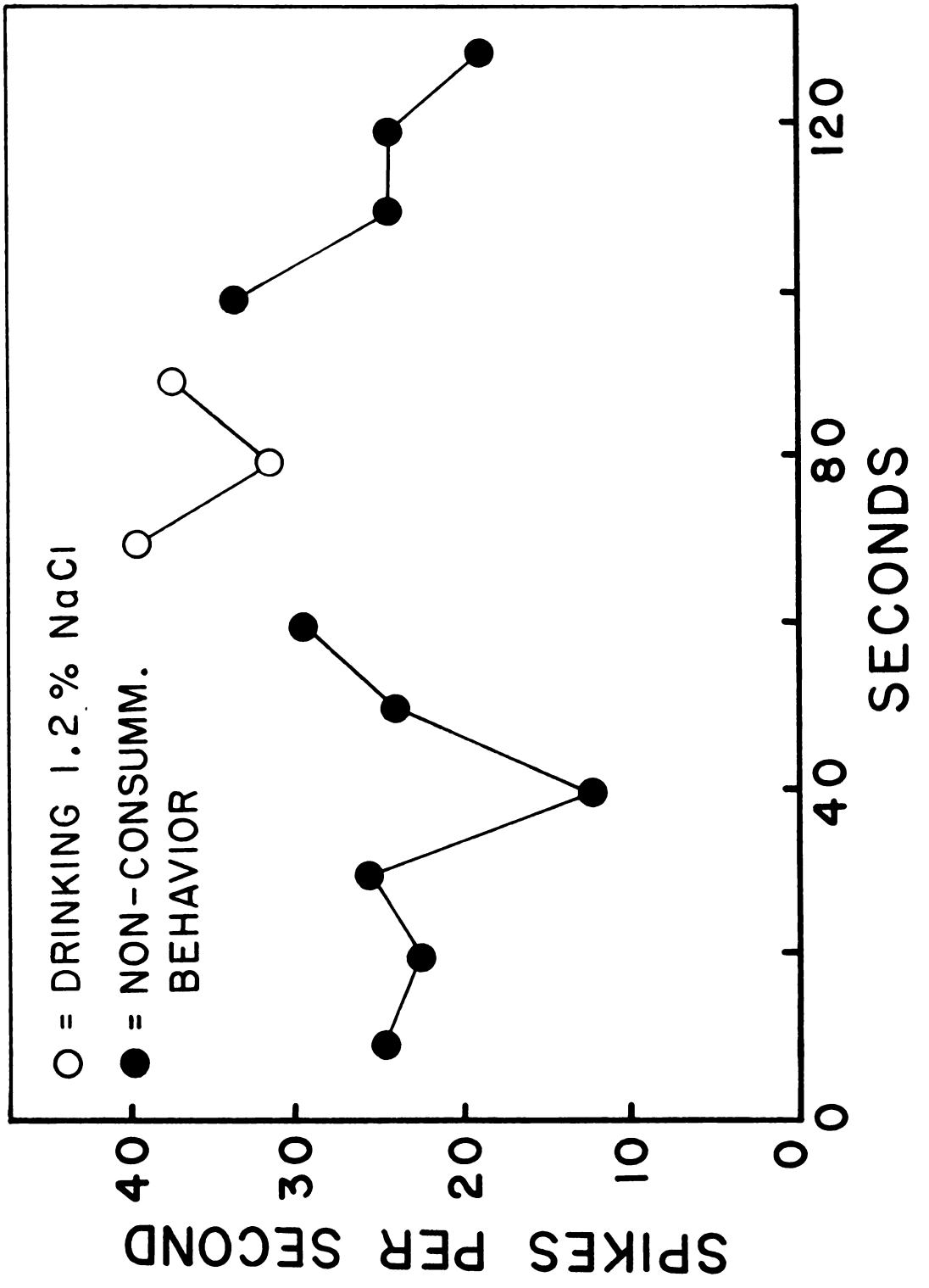

SPIKES PER SECOND
40
30
20
10
0
0
40
80
120
SECONDS
O = DRINKING 1.2 % NaCl
● = NON-CONSUMM. BEHAVIOR

FIGURE 6

t-test). During urethane anesthesia discharge rates dropped to 61% of pre-anesthetic levels ($p < .02$, $N = 6$, two-tailed t-test). The effects of both drugs appeared related to the dosage.

On three occasions unit activity was recorded for 90 minutes after the rat had been deprived of both food and water. In general, the effects of total deprivation were intermediate to those observed in rats adapted either to water or to food deprivation. For example, if cells at the electrode tip had increased firing rates during eating (after food deprivation) and decreased firing rates during drinking (after water deprivation), even after a totally deprived animal had eaten and drunk, the cells continued to fire at approximately the same rate as when the rat was totally deprived. In totally deprived animals, discharge rates during drinking did not change as greatly (from non-consummatory discharge rates that preceded the drinking) as when the animals were deprived only of water.

Electrode size (62.5 μm or 25 μm) did not produce observable differences. When more than one unit was recorded on a particular electrode, two characteristics were observed: 1) Drinking occasionally affected the units differently (one might increase and the other decrease its discharge rate), but rehydration usually affected cells at a given electrode site in the same manner. 2) Units with larger action potentials discharge more slowly than those with smaller action potentials. This was true in over 90%

of the multiple unit recordings, and in each exception the electrical activity was judged to be recorded from fibers rather than cell bodies. Rise time and spike duration were used as criteria to determine whether an electrode was recording from an axon or from a cell body. (When recording from a cell body, the rise time is slower and the spike duration longer than when recording from an axon: Chow and Lindsley, 1964). Only one type of response depended on locus within the septal area: some units that decreased discharge rates during rehydration would occasionally fire rapidly in "rushes" of 1 - 5 seconds at rates not reached even during dehydration. This type of response was observed only in the medial septal area.

DISCUSSION

The two strongest findings in this experiment were the changes in septal unit activity in water regulation and in drinking behavior. As water-deprived rats became rehydrated during the 0.5 hour drink period, septal unit activity decreased significantly. And during the initial drinking bout by water-deprived rats, individual septal units changed markedly: many increased and many decreased firing rates, although the mean remained relatively stable.

The 23.5 hour water deprivation schedule was chosen for this experiment because it is a natural sequence of dehydration and rehydration, because many other researchers use this schedule, and because other studies have reported the details of its osmotic and volemic correlates. Hatton and Bennett (1970) have shown that as rats adapt to a 23.5 hour water deprivation schedule over a 10 day period: 1) the animals drink their fill progressively earlier in the half hour session until, by the 10th day, they drink in the first 15 minutes nearly all the water they will drink, and 2) the difference between pre-drink and post-drink osmotic pressure increases as a function of days of deprivation. The difference between pre-drink and post-drink plasma protein did not change over days of adaptation. Hatton and Bennett also reported that by the time rats stopped drinking, their

osmotic pressure had dropped to ad lib levels or below. After 6 minutes of access to water, rats are still hyperosmotic; from 8 - 10 minutes, osmotic pressure is near ad lib levels, and by 13 minutes the osmotic pressure has dropped below ad lib levels.

Rats in the present experiment that were adapted to 23.5 hour water deprivation and received no food during the drink period were under conditions similar to those analyzed by Hatton and Bennett. By the end of the drink period, discharge rates in this group had decreased significantly, though they dropped more slowly than osmotic pressure decreased or volume increased in the Hatton and Bennett study. Unit activity in the group for which food was available during the drink period decreased less markedly (Figure 1), and firing rates of cells in the ad lib group did not change. These results indicate that, in general, septal cells are hyperactive during hyperosmotic (dehydrated) conditions and hypoactive during hypo-osmotic (rehydrated) stimuli; they corroborate an earlier report (Bridge and Hatton, 1973) of this effect in urethane-anesthetized rats.

Firing rates changed considerably during the first drinking bout by rats adapted to 23.5 hours of water deprivation. These changes were smaller later on in the 0.5 hour drink period and when rats were on an ad lib, rather than a water-deprivation schedule. Furthermore, when rats are deprived of water for only 2 - 3 hours, and not adapted to this schedule, the changes observed during drinking are

also small (Ranck, J. B., personal communication). Therefore, these results strongly suggest an interaction between drive state (water deprivation) and the effect drinking has on septal unit activity.

That the septal units were relatively unresponsive to sensory stimuli except when the mode was gustatory and the particular stimulus hypertonic saline suggests that when their discharge rates change during drinking, units are responding to proprioceptive feedback of the behavior per se. It was not possible to detect whether firing increased during licking or swallowing, since both occurred very rapidly. During eating, septal cells responded most frequently during the swallowing component. If it is true that swallowing water also alters septal activity, then the greater frequency of swallowing during drinking than during eating may account for the greater changes in firing rates during drinking. The greater frequency of swallowing during drinking may also contribute to the consensus among researchers that the septal area is more involved in water regulation than in food ingestion.

But while other sensory modes were relatively ineffective in the present study, other literature shows that sensory stimulation can change septal activity, although it also suggests that septal cells habituate frequently to this sort of stimulation. Cross and Green (1959) have reported that many septal units respond for 2 - 5 seconds to tactile, visual, and auditory stimuli and frequently habituate to

them. Bridge and Hatton (1973) found that 10 second carotid infusions of hypertonic saline often activated septal units; these units frequently habituated after only one or two infusions. Brown and Remley (1971) found septal lesioned rats hyperreactive to thermal, sound, shock stimuli, but not to taste and light. According to Hayat and Feldman (1974), photic, contralateral sciatic, and acoustic stimuli alter discharge rates of most medial septal and diagonal band of Broca cells. Although their results report only responses up to 256 ms, they reported studying responses up to 5 seconds.

In the present study all stimuli except auditory were presented for the duration of the 10 second response measurement. The changes in firing rates after saline stimulation of the tongue generally lasted longer than those Bridge and Hatton reported (1973), perhaps because rats in this study, which presented most sensory stimuli after rehydration, were hypo-osmotic when stimulated with saline. Since a rat's daily colony room life presents many visual, tactile, and auditory stimuli similar to those presented in this study, septal units may have habituated to these stimuli before the experiment. Often firing rates would increase initially after sensory stimulation, drop below base rate for 2 - 3 seconds, and then return to pre-stimulus rates, as Figure 6 shows. This evidence, in effect, corroborates both the report of Hayat and Feldman (1974) that septal cells respond for very short durations to sensory stimulation and the

strong habituation effect first reported by Cross and Green (1959).

Why do septal cells respond to hypertonic solutions in contact with the tongue, and how does this mechanism serve the rat in normal daily existence? As a recipient of information from exteroceptors, the septal area apparently inhibits responses to environmental stimuli, as numerous reports of the septal startle response or hyperreactivity phenomenon suggest (see Lubar and Numan, 1973). Septal lesioned rats drink more of palatable solutions than do control rats (isotonic saline: Donovick, Burright, and Lustbader, 1969; saccharine: Beatty and Schwartzbaum, 1967). They also drink less of aversive solutions (hypertonic saline solutions: Donovick, Burright, and Lustbader, 1969; quinine: Beatty and Schwartzbaum, 1967). Thus one septal function may be to moderate or inhibit responses to aversive or rewarding gustatory stimuli.

On the other hand, taste buds also respond to chemicals in the blood (Bradley, 1973). By recording from the chorda tympani nerve, Bradley showed that when solutions were perfused into the tongue, units responded to sodium, but not to other solutions, such as sucrose and glucose. Furthermore, cells habituate to sodium stimulation when the solution is perfused into the tongue, but not when it is delivered to the surface of the tongue. Responses of septal cells often habituated to carotid infusions of hypertonic saline (Bridge and Hatton, 1973), yet in the present study,

cells habituated less frequently to hypertonic saline applied to the exterior of the tongue.

When considered together, the experiments on the responses of septal cells to gustatory stimulation suggest that information about the salinity of the external and internal environments may reach the septal area via the chorda tympani nerve. Stimulation of the chorda tympani could activate the septal area, which would modify or inhibit behavior by decreasing or increasing the intake of substances containing sodium. The response is mediated via the lateral hypothalamus (Miller and Mogenson, 1971; see below).

Changes in the animal's behavior or responses could also elicit the charateristic response of unit activity to sensory stimuli: to increase immediately after stimulation and then decrease for 2 - 3 seconds before returning to base rate. Often when a rat changed behaviors, by beginning to groom, for instance, cells fired faster immediately after the change, decreased in rate below the previous mean, then returned to levels near the mean. Thus septal cells appear to fire in response to a novel situation, whether it is a change in stimuli or a change in behavior. Septal lesioned rats are severely impaired in their ability to habituate to novel stimuli (Feighley and Hamilton, 1971). One role of the septum may be to transmit to the hippocampus information that a stimulus or a response has just been initiated. Hippocampal cells are able to respond to specific novel

stimuli, for instance to novel water-related stimuli, but not to novel photic stimuli (Ranck, 1973).

Ranck (1973) has also estimated that 75% of the lateral septal units are "neck movement cells" which fire when the rat changes the position of his head. These cells did not fire when Ranck moved the head and neck of the rat, and the neurons did not react to specific objects as did hippocampal cells. In the present experiment, responses similar to those of the neck movement cells were observed in units which were primarily in the lateral septum.

Hayward and Smith (1963) found that septal stimulation decreases urine flow by, they suggested, activating supraoptic neurons and increasing the release of antidiuretic hormone. The rapid discharge rates of septal cells during dehydration and their slower discharge rates during rehydration found in the present study strongly support this hypothesis. The septal area may also influence water regulation by two other routes. Septal stimulation can decrease blood pressure (Covian and Timo-Iaria, 1966; Calaresu and Mogenson, 1972). If the activity of the septal area generated by water deprivation causes hypotension of the renal artery, both sodium and water will be retained. Septal stimulation reduces corticosteroid levels in adrenal venous blood (Endroczi and Lissak, 1963), and septal lesions increase ACTH secretion (Bohus, 1961). In this system septal stimulation by dehydration would reduce ACTH, which would in turn lower aldosterone, thereby reducing the

retention of sodium and water.

But the septal area is not involved only in water-saving; it is also involved in the behavior of drinking. Wishart and Mogenson (1970) found that septal stimulation can inhibit ongoing drinking; Miller and Mogenson (1971) reported that septal stimulation can alter discharge rates of lateral hypothalamic neurons, but the effect depends on the rate of the lateral hypothalamic unit. If the unit is in a fast phase, septal stimulation usually decreases its discharge rate and septal stimulation activates the firing of a lateral hypothalamic cell in a slow phase. That is, septal stimulation moderates the discharge rates of lateral hypothalamic neurons. This dual effect makes the septal function in drinking behavior difficult to understand. It is interesting that the septal area also moderates the intake of aversive solutions (see above, p. 34; Donovick, Burright, and Lustbader, 1969 ; Beatty and Schwartzbaum, 1967). Unfortunately, the bi-directional change of septal discharge rates during drinking complicates matters more, and no simple explanation is available.

The present experiment indicates there are two distinct responses of septal units in water regulation. First, septal units fire significantly faster during water deprivation than during rehydration. Second, at the onset of drinking the absolute change in septal firing rates is greater when rats are water-deprived than when rats are on ad lib food and water or are food-deprived. Because the

septum has two distinct roles in water regulation, the apparently contradictory results of electrical stimulation and lesion experiments versus chemical stimulation and blockage studies are not necessarily incompatible. The septum's excitation of the supraoptic nucleus most parsimoniously explains why electrical septal stimulation reduces water intake while electrical septal lesions increase drinking. When activated, the supraoptic nucleus releases antidiuretic hormone, which causes the kidney to reabsorb water. In one role, then, the septum governs water retention. But changes of septal firing rates during drinking may also influence lateral hypothalamic cells and may be mediated by cholinergic synapses. In this role, the septum influences water ingestion.

While this experiment has shown that urethane and ether reduce firing rates of septal cells, there is evidence that unit activity recorded in unanesthetized and unrestrained animals may be slower than in animals with no electrodes implanted. This evidence comes from the curious phenomenon that when two cells are recorded on the same electrode, the larger one (the unit with the largest voltage) almost always discharges more slowly than the smaller one. This phenomenon has also been observed in septal (Bridge and Hatton, 1973) or hypothalamic (Bennett, C. T., personal communication; Walters, J., personal communication) units under urethane anesthetic. Apparently, the electrode is a heat sink, and cells in its vicinity

are subjected to mild hypothermal anesthesia. The cell with the larger action potential is usually closer to the electrode and will be cooled more, causing it to discharge more slowly.

APPENDICES

APPENDIX A

Histology

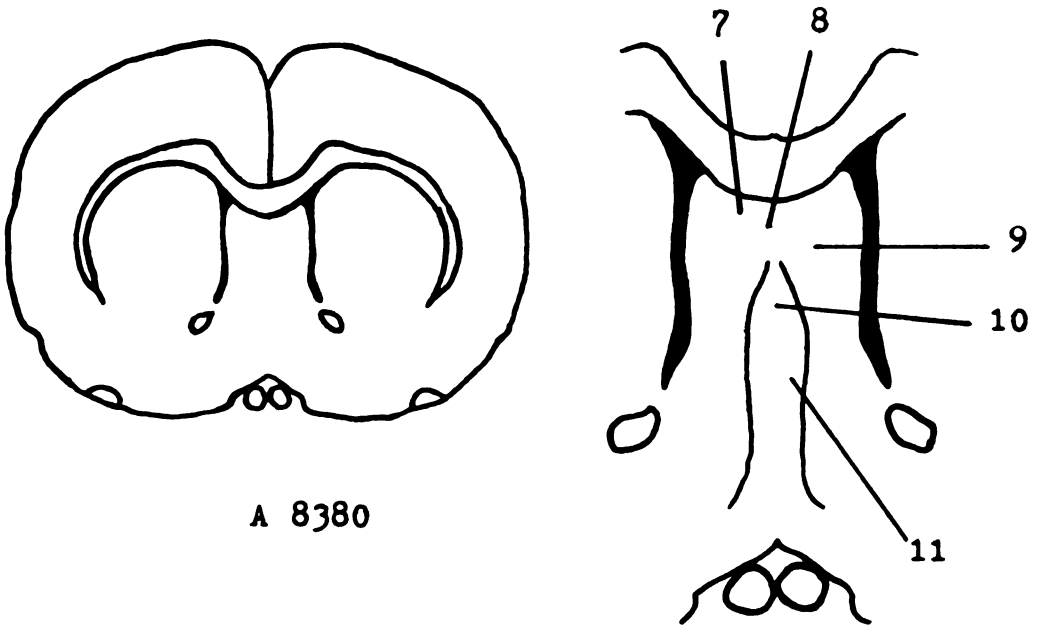
Table 2 lists confirmed recording sites (1 - 22). Columns two and three identify the 28 electrodes listed at these 22 sites by rat number and electrode number. The location of each site is shown on one of the six atlas sections on the three following pages (Figures 7, 8, and 9). The sections are redrawn from Konig and Klippel (1970), and the numbers next to each refer to the distance in microns anterior to ear bar zero these sections appear in the Konig and Klippel atlas.

Table 2.--Confirmed Recording Sites 1 - 22.

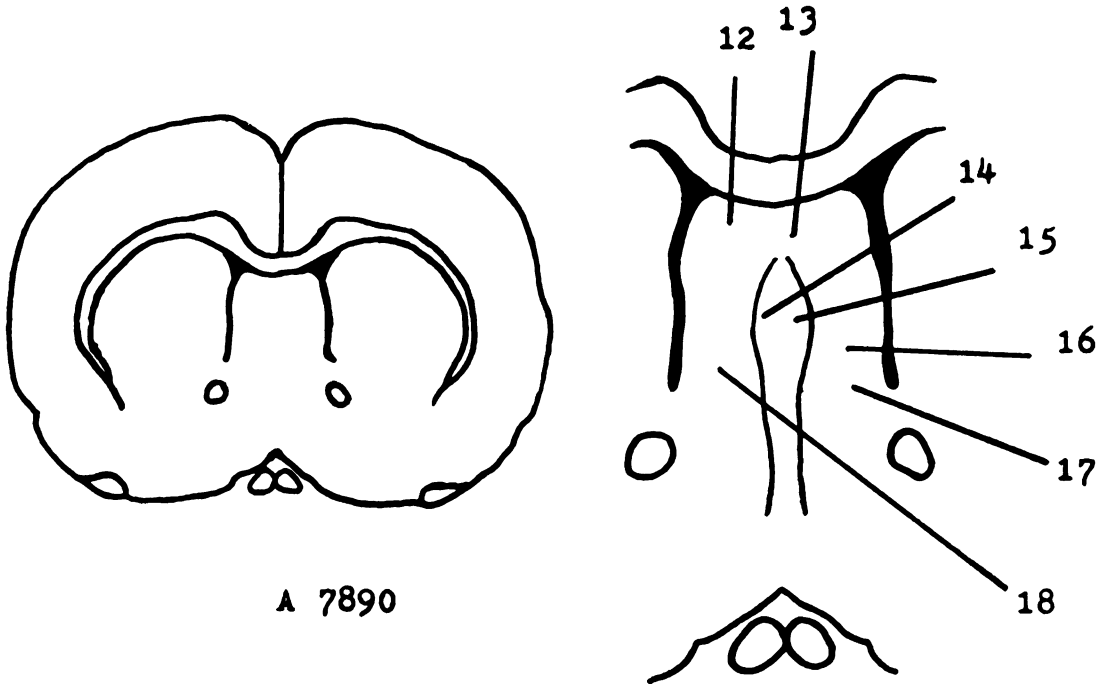
Electrode Site	Rat	Electrode
1	25	b
2	5	b,d,f
3	30	e
4	32	a
5	6	a
6	28	a
7	22	a,d
8	22	e
9	21	c
10	32	d
11	6	f
12	17	c
13	21	a,f
14	3	f
15	3	e
16	2	a
17	23	e
18	28	e,f
19	24	e
20	20	a,b
21	18	f
22	26	b

Figure 7.--Indicated are confirmed recording sites 1 - 6.

Figure 8.--Indicated are confirmed recording sites 7 - 18.



A 8380



A 7890

Figure 8

Figure 9.--Indicated are confirmed recording sites 19 - 22.

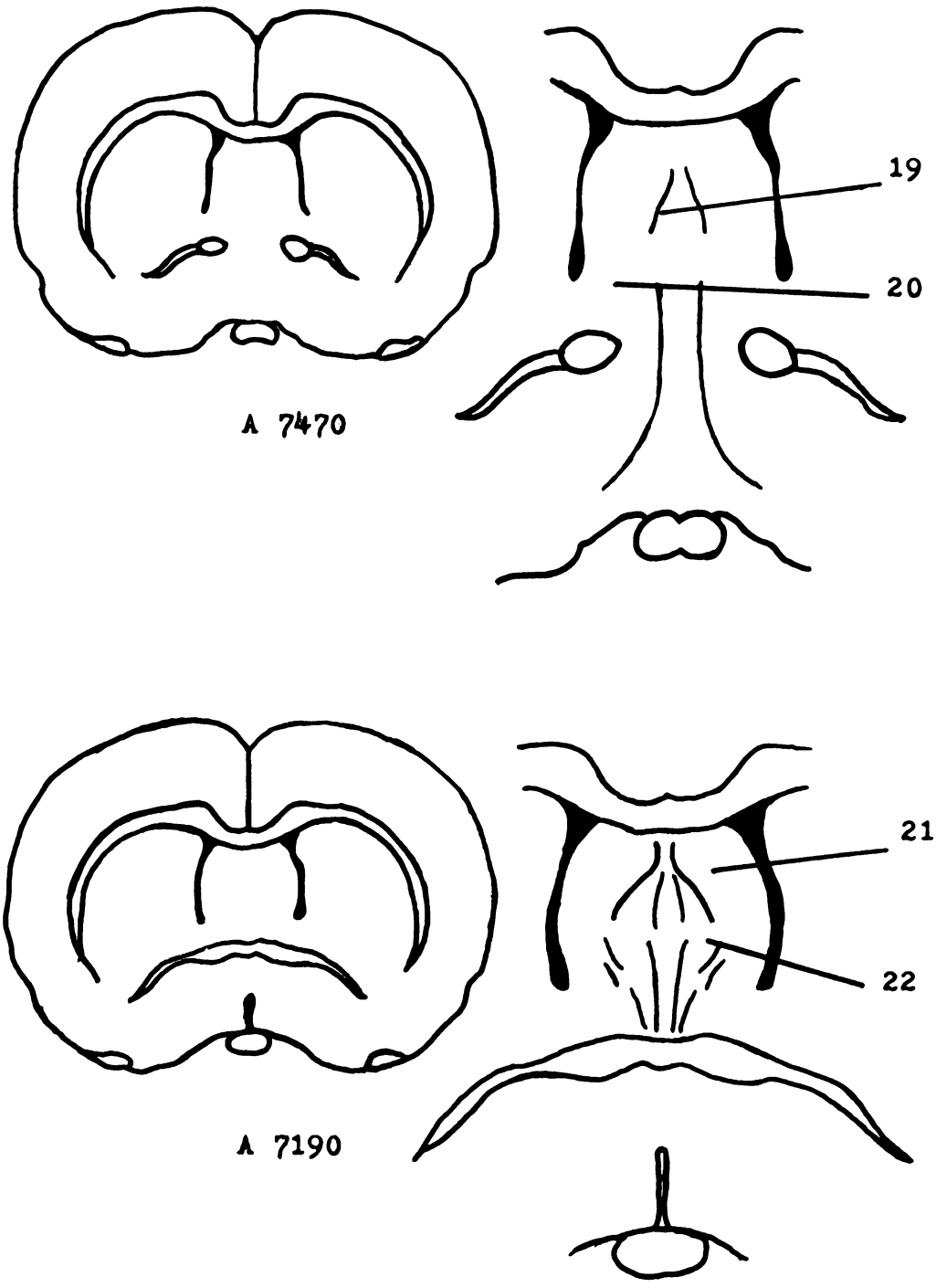


Figure 9

APPENDIX B

Equipment and Suppliers

Equipment and suppliers for microelectrode construction:

1. Female Amphenol hexagonal 7-pin socket, $.86, and male Amphenol hexagonal 7-pin plug, $.97, Amphenol Corp., Endicott, N.Y.

2. Nickel-chromium enamel-insulated wire, 62.5 μm and 125 μm dia., "Nichrome" brand, Driver-Harris Corp., Harrison, N.J.

3. Platinum-iridium teflon-insulated wire, 25 μm dia., 10 ft. for $41.00, Medwire Corp., Mt. Vernon, N.Y.

4. Three-strand phono wire, 30% shielding, 10 ft. for $1.69, Belding Corp., Chicago, Ill.

5. Liquid Tape, $1.09, CG Electronics, Rockford, Ill.

Equipment and suppliers for bioelectric data recording and analysis:

1. Stereotaxic instrument, $750, Stoelting Co., 424 N. Homan Ave., Chicago, Ill.

2. Preamplifier (122), $165; power supply (125), $335; dual beam oscilloscope (502A), $1395; Tektronix, Inc., P.O. Box 500, Beavertown, Oregon.

3. Tape recorder (1028, $1196, Magnacord, Main Electronics, 5558 S. Pennsylvania Ave., Lansing, Mich.

4. Electronic counter (5512A), $1050, Hewlett Packard, E. Hartford, Conn.

5. Audiomonitor with speaker (AM8), $157, Grass Electronics, Quincey, Mass.

APPENDIX C

Construction of a Multiple Electrode for Unit Recording from Unanesthetized and Unrestrained Animals

Abstract

This appendix describes in detail the construction of a single and multiple unit recording system using either 62.5 μm or 25 μm diameter wires as recording electrodes and a 125 μm diameter wire as an in-brain ground electrode. The wires are soldered to the pins of an Amphenol 7-pin or 9-pin socket, then insulated with Epoxylite or Insul-X, and the assembly affixed to the skull with dental acrylic and anchor screws; a 7 or 9-pin plug is inserted into the socket during recording sessions, and impulses reach the recording equipment via 3-cable phono wire. Comparison of recordings from the septal area using the two electrode sizes showed that electrodes of 62.5 μm diameter yielded a higher proportion of records with acceptable signal-to-noise ratios than did the 25 μm diameter electrodes, while the 25 μm electrodes generally maintained acceptable records for a longer time.

Introduction

This electrode assembly has evolved from a number of previously described chronic unit recording systems, particularly that of Johnson, Clemens, Terkel, Whitmoyer, and Sawyer (1972), who developed an in-brain ground wire preparation and have compared the performances of floating and rigid electrodes, and that of Chorover and Deluca (1972), who developed a technique for implanting wire so flexible that it essentially floats with the brain. Constructing the present multiple electrode is so simple that, after practice, fabricating a 7-electrode system requires only an average of 46 minutes; there is virtually no waste; and a novice can manufacture perfect electrodes from the start. The accompanying equipment (leads, etc.) is also inexpensive, reliable, and simple both to fabricate and to use. The animal, merely plugged into the recording apparatus and unplugged at the end of the recording session, experiences very little stress. Because the system uses either the 62.5 μm diameter nickel-chromium or the 25 μm diameter platinum-iridium wire with equal facility, their recording properties can be compared. Although either the 7 or 9-pin Amphenol sockets may be used, the 7-pin apparatus, along with the 62.5 μm wire, is described here as an example.

Construction

A female Amphenol socket (Figure 10) is chosen into which the male Amphenol plug (Amphenol Corp., Endicott, N.Y.) to be used on the lead will easily fit. Usually the individual sockets are out of round when purchased, so that the fit is too tight for recording purposes. In this case, a metal probe is inserted into the individual sockets, and, by moving the probe back and forth, the sockets are rounded out until the plug fits easily into the socket. Then six 2 - 4 cm lengths of 62.5 μm diameter, enamel-coated, nickel-chromium wire and one length of 125 μm diameter wire (Driver-Harris Corp., Harrison, N.J.) are cut. Using a scalpel, 1 - 2 mm of the enamel insulation are scraped off one end of each wire, and the scraped ends of these wires are soldered to the beveled ends of the pins on the Amphenol socket (Figure 11, A): the 125 μm ground is soldered to the center pin.

The integrity of the assembly depends in part on three alterations of the Amphenol socket: (1) to form a single, rugged unit, the beveled pins, which are loosely held by the hexagonal plastic case, must be made rigid; (2) the pins and solder must be electrically insulated; and, (3) so that subdermal fluids will not flow into the plug-socket contact area and short the circuit, the junction of the individual sockets with the plastic which houses them must be made watertight. These transformations are all accomplished by

Figure 10.--Basic female Amphenol socket.

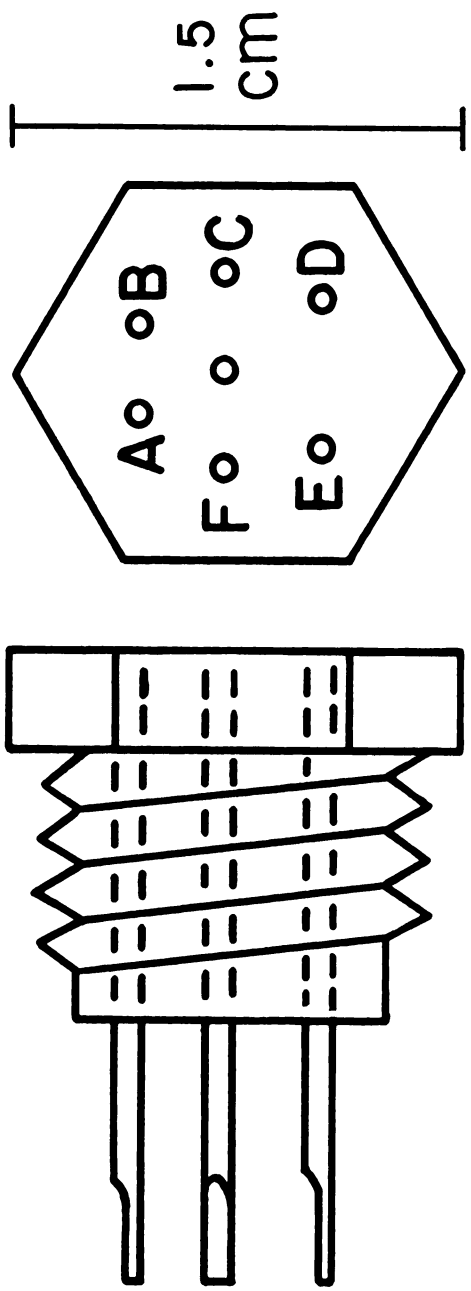


Figure 10

Figure 11.--A: Recording electrodes and ground electrode have been soldered to the beveled pins of the female socket. B: Wires have been drawn together through a PE-50 tube, straightened, and clipped to an appropriate length for recording.

the following steps: a small portion of modeling clay is spread thinly about the base of each pin, and both the end surface of the plastic casing and the pins are covered with Epoxylite or Insul-X. Insul-X usually performs satisfactorily, requires only a few layers, and needs no baking, but it sometimes bubbles and does not form as hard an insulating cover; although Epoxylite requires numerous layers (often 10 - 15) which must be baked individually, it forms a superior surface.

To draw them together (Figure 11, B), the wires are inserted into a 1 mm length of PE-50 plastic tubing, which is drawn down to the base of the 125 μm wire at the center pin. At this point the ground wire is cut to a length which will allow the tip, when implanted, to reach a point just above the target nucleus. (The end of the PE-50 tube that is distal to the pin is flush with the interior surface of the skull after implantation.) Approximately 1 mm of enamel is scraped from the distal end of the 125 μm ground electrode. By holding the PE-50 tube near the base of the ground wire, it is possible to straighten the recording wires to a nearly parallel position. A small drop of Elmer's Glue-All is placed at the edge of the PE-50 tube distal to the pins (Figure 11, B: point c): the drop will be drawn into the tube and, after the glue is hard, further straightening of the wires is possible. With a pair of very sharp scissors, the recording wires are cut to

an appropriate length, depending on the depth of the target area. If 25 μm wires (Medwire Corp., Mt. Vernon, N.Y.) are used, they must be fused to the beveled pins with electro-conductive cement. Using a ring lamp with a 2X magnifying lens, it is a simple matter after 10 minutes practice to scrape with a scalpel approximately 1 mm of the teflon insulation from the end of each 25 μm wire to increase the conductive area which will contact the electroconductive cement. Before implantation, the electrodes are collectively coated with melted dextrose; the dextrose hardens when cooled and allows the electrodes to be implanted as a rigid unit, yet after implantation the dextrose dissolves and disperses. See Chorover and Deluca (1972) for a complete description.

The leads are made from four 30 - 35 cm lengths of 3-strand phono wire with 30% shielding (Beldon Corp., Chicago, Ill.), two Amphenol plugs, and one Amphenol socket combined as Figure 12 shows. The six conductive strands found in the pair of phono wires are soldered to the beveled prongs of plug pins A - F, the shields are soldered to the center prong, and the prong and solder are covered with Liquid Tape (CG Electronics, Rockford, Ill.). The shield wire goes to ground, and the six phono wires go to the recording equipment. To reduce noise that the two strands would create if they rubbed together, they are held apart with lengths of masking tape spaced 3 - 5 cm apart. If the

Figure 12.-- Leads in recording position.

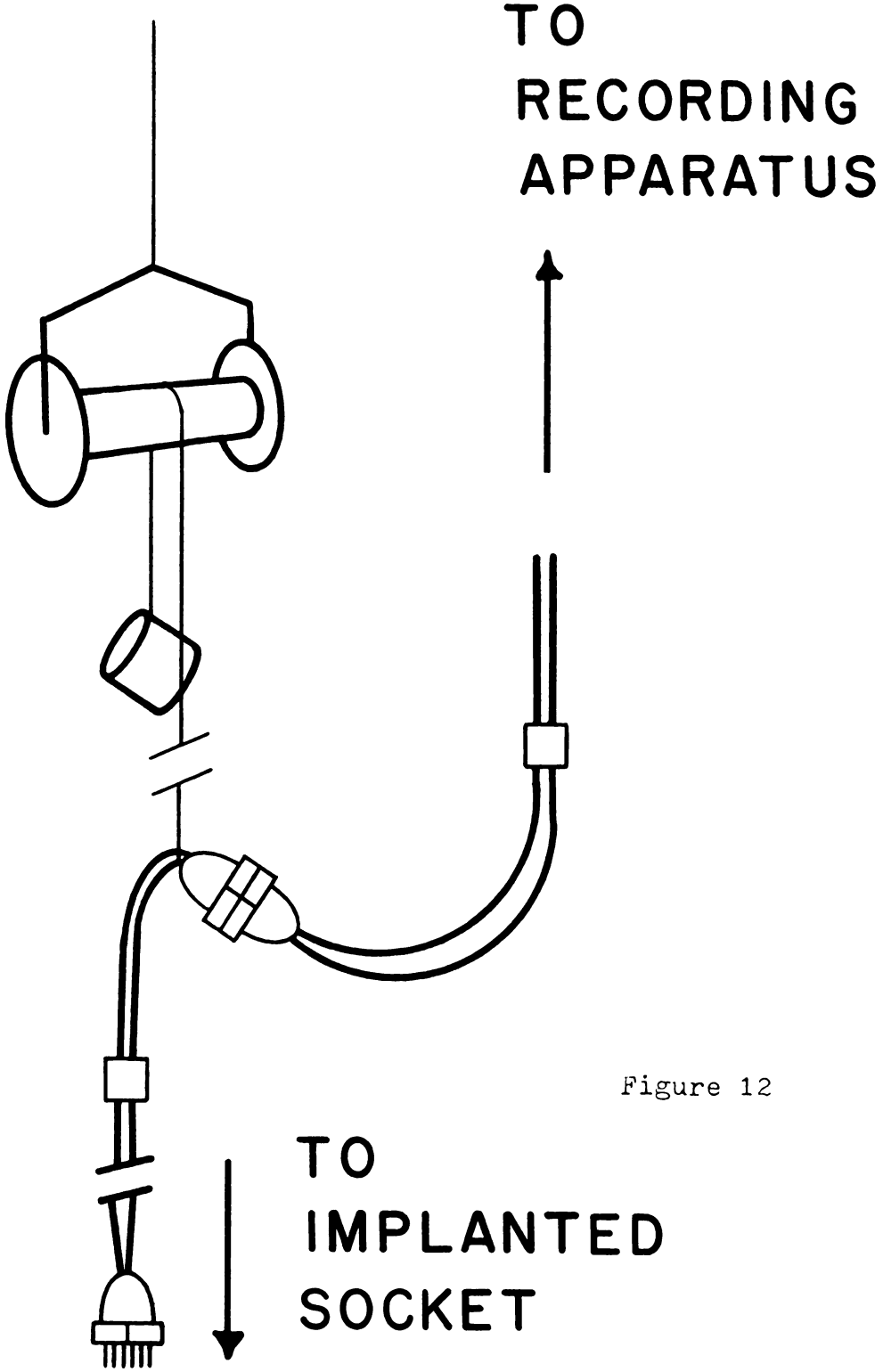


Figure 12

counterweight is set slightly heavier than the combined weights of the plug and the wires, the animal draws the wires out of the way when he stands on his hind feet, and the only weight the rat supports is the 5.5 g implanted portion.

Discussion

The complete sysem is designed for simplicity and minimal expense. For example, this lead apparatus replaces the more expensive and cumbersome mercury commutator swivel. If a continuous record is required, then the leads used here should go to a mercury commutator, for if the rat turns in one direction five or six times more than in the opposite direction, the leads will have to be unwound by separating them at the plug-socket junction near the counterweight string and untwisting the wires. The wires usually tangle about twice an hour and require approximately 10 seconds to unravel. If a completely continuous record is not necessary, the present lead system is quite sufficient.

Prefabricating the 62.5 μm electrodes requires less time and cost than constructing the 25 μm electrodes. But since the latter is a floating system, it retains good single and/or multiple unit activity for a more extended period of time than does the more rigid 62.5 μm wire. Thus the 62.5 μm wires are advantageous for the sort of experiment in which a large number of electrodes are implanted for a relatively short period of time (such as that required

to map unit activity in an area of the brain during a specific behavior); 25 μm electrodes are superior if fewer electrodes are to be implanted for a longer period of time (such as that required to examine unit activity during a complex learning sequence). To construct a 7-pin Amphenol unit with six 62.5 μm recording electrodes costs approximately $1.50, or $.25 per electrode; the 25 μm system is $2.50, or about $.42 per electrode.

As well as the purpose of recording, the cytoarchitecture and discharge rates of the cells in the target nucleus may also influence the choice of an electrode. Chorover and Deluca (1972) have reported that all 51 of their 25 μm electrodes implanted in the olfactory bulbs yielded acceptable unit data, and Norgren (1970) found that 70% of the 62.5 μm electrodes implanted in the hypothalamus gave good data. In the present experiment, electrodes were evaluated three to five times each, and approximately one of four 25 μm electrodes and one of three 62.5 μm electrodes yielded good signal-to-noise ratios. Part of this discrepancy between these and other reported results may be caused by the extremely slow spontaneous base rates of septal cells: there are even "silent pockets" in the septal area, where there is little or no activity at all (DeFrance, J. F., personal communication). In such areas it seems reasonable that the larger electrode would yield more data.

The use of this multiple electrode system can

circumvent a bias toward selecting relatively fast-firing cells, a sampling error which can occur when an experimenter lowers a single electrode and monitors feedback simultaneously to select a cell for recording. The electrode may bypass a cell that discharges only once per minute, for example, while the cell is inactive. This problem may be avoided by recording on one channel of a two-channel tape recorder from electrodes with good unit activity, while recording on the other channel from electrodes with neural background activity free from extraneous noise, but with no units. Re-playing channel two of the whole experiment can reveal extremely slow-firing cells or cells that fire under one experimental condition but not another. Septal cells firing as slowly as three times an hour (under urethane anesthetic) and 15 times per hour (in an unanesthetized rat) have been recorded in our laboratory.

Because Norgren (1970) reported that unit activity during implantation did not correlate with that during subsequent recording sessions, units in this investigation were not monitored during implantation. However, a number of implants showed activity which was acceptable during the first recording session (on the 10th post-operative day), but which diminished in quality until, by about the fifth recording session, the data were unacceptable; this suggests that monitoring electrical activity during implantation may be worthwhile, at least if the target nucleus is the septal area and the electrodes are 62.5 μm. This problem of

diminishing quality of unit activity may be attenuated by housing the rats in cylindrical Plexiglas cages, eliminating dark corners into which rats can poke their heads (thus bumping the electrode socket). Plexiglas can be shaped easily by heating it to approximately 117° C and cooling it around a cylindrical object. Rounding out the individual sockets with a metal probe before constructing th electrode and implanting 25 μm rather than 62.5 μm wires also prolonged collection of acceptable data by reducing the loss of good signal-to-noise ratios caused by repeated insertion and removal of the plug. Since most artifact noise in this system is considerably lower in frequency than is the signal, it can be reduced significantly more than the signal by filtering the current through a 22 picofarad high pass capacitor (see Figure 13).

If the target area is relatively large, such as the rat septum or hypothalamus, or if the target is small and the experiment requires numerous control cells in the vicinity of the target nucleus, then this multiple electrode system is very satisfactory. But, especially when using the flexible 25 μm wires, this system is difficult to implant accurately. If a small area such as the supraoptic nucleus is the target, then a movable microelectrode such as that described by Teyler, Bland, and Schulte (1974) may be superior.

Figure 13.--Top trace: unit activity recorded with 62.5 μm electrode. Bottom trace: the same activity as the top trace filtered through a 22 picofarad capacitor. Both sweep durations are 10 seconds.

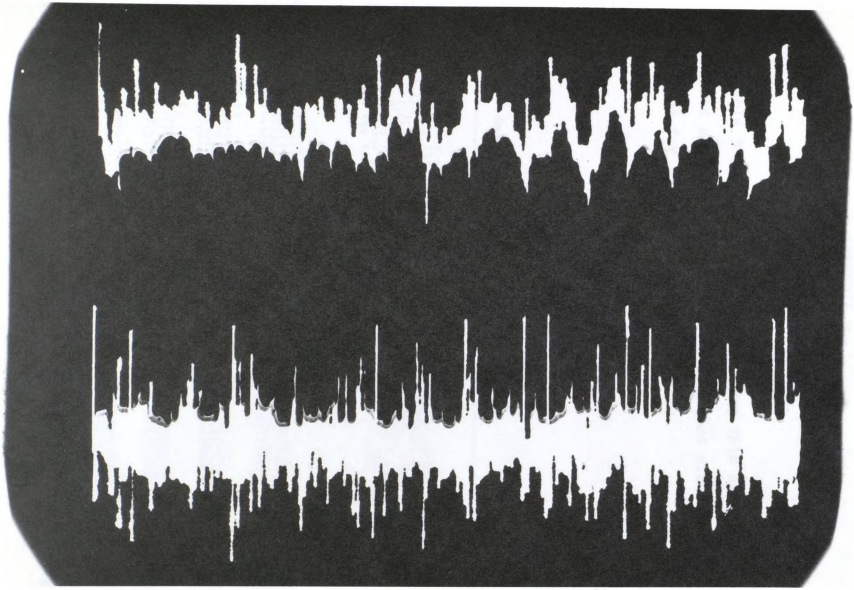


Figure 13

APPENDIX D

Raw Data

Table 3 (below) lists raw data from this experiment as entered on computer cards; the first card gives instructions for interpreting data.

Table 3.--Raw Data

```
1       THERE ARE 6 DATA ENTRIES PER CARD.  EACH ENTRY IS 13 COLUMNS =
2       1-13, 14-26, 27-39, 40-52, 53-65, 66-78.  COL 79-80 ARE TAPE NOS.
3       COL 1 IS ACTIVITY ID.  B = BASE NON-CONSUM., D = DRINK, E = EAT,
4       G = GROOM, N = NON-CONSUM.  COL 2-5 ARE TAPE FOOTAGE.  COL 6-9 ARE
5       MEAN SPIKES PER SECOND.  COL 10-12 ARE STANDARD ERRORS.  COL 13
6       IS NO. OF 10 SEC BINS WHICH COMPOSE THE MEAN.  DECIMALS HAVE BEEN
7       DROPPED FROM THE MEAN AND S.E.  COLS 47 AND 52 OF THE TAPE ID
8       CARDS SHOW HOW MANY DECIMAL PLACES HAVE BEEN DROPPED FROM
9       THE MEAN AND S.E. RESPECTIVELY.
```

RAW DATA

```
TAPE 05   RAT 02   H20 DEP   SINGLE   EL = A  3    3
B005016332406B0090166720168012015173416B014517502796B017022003916B019524333026O5
B022025671436D025018502236D028010672116D030510333416N045040673776N046025334336O5
N050522500002N052220332736N056522173166N059524003256N067030004156N069025333005
N082531171856N084522672946N087033003206N094033334366N095831333786N105543834836O5
N116019502466                                                                  05

TAPE 07   RAT 03   H20 DEP   MULTI    EL = F  2    2
B011506580756B016812671176B024969081016B030410271056B034710130516B041712431186O7
D049502720416D051803750316D053504050416D055605780606D057705950446D059505870466O7
F071715600002D081906230463N102610001645N105009420886N107309750676N111209980686O7
N114509530816N117006830626N120086531906N122507830756                          07

TAPE 09   RAT 03   H20 DEP   MULTI    EL = F  2    2
B002014781966B009961770093580141166B093686020315130986B023816501076B026915020436O9
B029215680526B031217100002D032018020886D035015370776D037515320426D039515150476O9
D041717070496D043616980196D047514820676N048524801043D049520850002N050225300001O9
N052024700001N057523301363D059622150002D061618150002                          09

TAPE 10   RAT 03   H20 DEP   SINGLE   EL = F  3    2
B003004500106B009504670126B015907000096B020006670156B022612000276B025106170186I0
B028011500346D032541500726D035064830526D037364670566D039142830446D042039670416I0
D044427330476N046490800600308483550000004005005560059560531258305960054582000001I0
N056005830216N065490300000300557700000001N059017800475E064030330323D065255500002I0
N066424000002E067503500128D069464440665N071025670003607295740127500755422504541O
N078218250218D084389751544608529488048N091529830356N093725750624E095810930156I0
E096717670183N097553671523N098625330853N099826671146N101014170446N102526830446I0
N107020500536N108513000225N112025330676                                        10
```

TAPE 12 RAT 03 FD DEP SINGLE EL = F 3 2

TAPE 13 RAT 03 FD DEP SINGLE EL = F 2 2

TAPE 16 RAT 05 H20 DEP MULTI EL = F 2 2

TAPE 17 RAT 05 H20 DEP MULTI EL = F 1 2

TAPE 18 RAT 05 H20 DEP MULTI EL = F 2 2

TAPE 19 RAT 05 H20 DEP MULTI EL = F 2 2

TAPE 20 RAT 05 H20 DEP MULTI EL = F 2 2

TAPE 21 RAT 05 F000 DEP MULTI EL = F 2 2

```
TAPE 22    RAT 05    FOOD DEP   MULTI       EL = F   1     1
N0015373642759003545553352N0955234989 5E0986498710 76E0117486311 36E01483848130622
F01794052122 6F0210365311965024135780556E0272355824 06F0303338211 06E033433971406 22
F0360295716 96F0380272715 06E0342276917 56D04093860130 2N0430224020 45E0455308220 6622
F047534800 645D0490326339 93N0505298330 93F0525479530 86F057559300616E06156082082622
E06505825 0386F06855750074 6F07205745071 6E07555817060 6F0825586307 46F08655648088622
E09055725066 6F09455285053 6E09855560062 6N10054287119 3N10204200161 4E10455005066622
F1085524002 66E11055270046 6E11355062052 6E11654920066 6                                22

TAPE 24    RAT 06    H20 DEP    MULTI       EL = A   3     3
B00285967444 6B0071620072168 0093571759 66B01195367856 6B01454200530 6D03111067123624
D0342086706 26D0365090012 46D0508256 30003                                             24

TAPE 251   RAT 06    H20 DEP    SINGLE      EL = A   3     3        CH 1
B0040523335 86B01125116773 6B015232002216 B01702900632 5B0242470047 06B027549008 46425
D0320275031 26D0343178309 56D0366158318 56D04141850250 4D0435202532 84N0451410000 0325
D0458295000 02N0515428081 16N0542304043 35D0635235000 2N0698247556 84D0730183300 0325
N0725226737 76N0747155040 18D0839011590 0002F09920983147 6F10101200221 6F10321312317625
N1080283329 46N1093200047 06E11022133000 3E11241217135 6F11361283117 6E11571583241625

TAPE 255   RAT 06    SINGLE     H20 DEP     EL = A   3     3        CH 1
B0030271773 406B00683983500 6B01642767343 6B01513316300 6B01872750200 6B0249218324 5625
D0316278327 06D0339250150 6D03582350118 6D03902450200 6D0430280822 06D044425055103 25
N0524183619 06D0532235001 02D0707182526 16D0733355000 02N0803275028 56N0827095010 5625
N0849078315 76N0857240000 2F09211492160 4E09951634197 6F10140283040 6E10280754085625
E1041050805 05N1051266769 63N1079095007 06E11260283566 6F11371983331 6E11583255204 25

TAPE 26    RAT 06    FOOD DEP   SINGLE      EL = A   2     2
B0050013802 86D0075010000 01B0100292037 6D01130120000 1B01390350039 6B01820387027626
B0215023902 36B0248022703 86E03250295053 6E03502270376 N03660200000 2E03790319036426
D0390025000 02N0400042000 02F04250248020 6E04500177923 6F04750180018 7D04980500000126
G0504052000 01N0507036000 01F05130320000 2N05500448052 6N05750307026 6D05950300000126
F0620016201 56F0645912501 26E06500130015 6E06750108013 4D06870510000 1N07180323051626
N0737024001 86N0755022504 06F07700870156 5E07910112014 6F08090115020 6E08260095017626
F0843012001 76D0855030704 13N0859628500 2608700103011 6N08960435044 6N09270387047626
D0967024500 02N1000035007 66N1025033503 86D10420470075 3N10550333055 4G10680130000226
N1093017202 56N1109020001 56N1124015002 66N11400160011 6N10500255000 2G11620180018526
D123702730273                                                                           26

TAPE 32    RAT 17    H20 DEP    MULTI       EL = C   3     2
B0016415001 96B0444500027 6B0080485004 36B01084450032 6B01434000040 6B017557330 51632
B0200493305 76B0239463302 76B02634483033 6B0298455004 46B03193367047 6B0341281702 3632
D0385316794 06D0407323304 16D04273267014 6D04503267017 6D04703033013 6D048837630 36832
D0515306702 36D0530406703 83D05704633103 6N05904100051 6N06103550031 5N06503000095332
N0675341705 26N0700383301 46N07253459022 6F07753033047 6F07952933038 6E08152983037632
E0835320002 36E0855220001 96E08752867072 6N09152517038 6N09303850057 6N09453150055632
N0960305005 46N0975253301 06D09903000025 6N10092900022 6G10183167020 3N10402650032632
N1060280003 36N1117325004 76N11403283031 6N11802100025 6N12002183012 6N12152183056632

TAPE 38    PAT 18    AD LTB     SINGLE      EL = F   3     3
B0050025011 56B0100033311 46B01500383119 6B02000567131 6B02500383114 6B03000417133638
N0350030012 16N0400033306 76N04500333123 6N05000483140 6N05500317128 6D05750433102638
D0590025000 02N0600025006 76N06500550099 6N07000233049 6N07500317108 6N08000367084638
N0850041708 76N0900360021 06N09500400009 76N10000400129 6N10500233123 6N11000417087638
N1150036705 66N1200020004 56                                                           38

TAPE 39A   RAT 20    H20 DEP    SINGLE      EL = B   3     3
B0045030009 76B0090040012 96B01400400103 6B01900333109 6B02500367102 6B02850500086639
B0335033312 06D0380095023 56D04051133150 6D04300783130 6D04550967123 6D04881100000239
N0495055000 02D0519100000 2N05500317167 6N05750367030 6N06000250089 6D06810950000239
N0700028313 56N0730030008 66N10000483236 6N10200250145 6N11370217087 6N12050350089639

TAPE 39B   RAT 20    H20 DEP    MULTI       EL = A   3     3        CH 2
B0040153320 66B0095121716 86B01501283234 6B02001433242 6B02501583291 6B03001633204639
B0350088314 56D0380136712 66D04151383199 6D04551383108 6D05201200108 4N08751467196639
N0915116718 46N1100196712 66N1205115023 26                                             39

TAPE 43    RAT 20    H20 DEP    MULTI       EL = B   3     3
B0040078314 06B0080073310 56B01200433138 6B01600650112 6B02000700118 6B02400493140643
B0280083313 96B0320045605 6B03600583114 6D03901300106 6D04151117098 6D04401017083643
D0470113315 26D0500118313 06G05221967088 3N05550550141 6N05850433141 6G06501500000143
N0662050015 33N0705033309 26N07420350075 6N07950200063 6N08550317111 6N10550450118643
N1145053311 76N1170040014 46N11950533067 3                                            43

TAPE 44    RAT 20    H20 DEP    MULTI       EL = A   3     3
B0050138327 36B0105120015 56B01601233348 6B02051317305 6B02651450182 6B03301667293644
D0375196718 96D0425201723 66D04751200181 6D05101833067 3605662800000 1D05941925214444
N0612130020 44G0643212020 01E06650833117 6E06951433176 3N08051200291 6N08501167426344
D0898210000 02N0932105024 96N09760950214 6N10350767143 6N1078100019 64                 44

TAPE 45    RAT 20    H20 DEP    MULTI       EL = B   3     3
B0028300039 56B0069260029 66B01352117241 6B01682833302 6B02302083256 6B02652633383645
B0290243316 73D0315391719 06D03667211 6D03903267220 6D04153517247 6N04322100000245
D0465325023 56N0495228312 56D05163350000 2N05402050119 4N05802250337 6N06052100300345
N0660198327 56N0700193325 86N07352000451 3N07851617296 6F08352250198 6E09152600173345
N097023172636                                                                          45
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TAPE 50    RAT 21    H2O DEP    MULTI      EL = C  3    2
R0021610006962004964830706R007759330586R0105435007768013251330396801585317056650
R01905383023680210545094268023349500556802684450095168029248500326603183667033650
D038540330556004113767045500435466703260046049000416004874050023605154933101650
N05285783079600563490000406N06904350078400617546711173N069552670766N07154250037650
N07285483095 6N0741458304 76N07545467073 6N07676483051 6N0830590007 76N08565163028850
N09205233073 6N0975448304 46N10096833042 6N102842670566N106052670396N10905900027650
N112264000606N113862170356N112059170496                                         50

TAPE 51    RAT 22    FOOD DEP   SINGLE     EL = D  3    3
R0035026708868007502330996801150250076680145021709868019004001106802300450099651
R0260031707068028503671096N043206332193N046004170956N049004000866N05750700173351
D0665060000030069005330676N073002000001N076505000001D091005670673N09250350088651
N098503830986N103504171306N106504331026D118507000001                           51

TAPE 52    RAT 22    FOOD DEP   SINGLE     EL = D  3    3
N009004001416D01100650002N014003171146N030804001136N032504001066                 52

TAPE 53    RAT 22    FOOD DEP   MULTI      EL = A  3    3
R00304233474680065042004876800905433292680120498319468015539335706R02054367343653
G0215490000018025545002146802955033263580320530035168037052173466E04555700407653
F061053833346D069049172226007004667241300725476727566074060000001E08254683328653
D098641502726N100841002944N102759000001D105646500002N106546002003N12244767485353

TAPE 54    RAT 22    FOOD DEP   MULTI      EL = A  3    3
N010045173166N017548333966N022539331986N026041401695N030042503184N03304467203354

TAPE 55    RAT 21    FOOD DEP   MULTI      EL = A  3    3
R0030241736368007521671696801152350274680165240026368020018332236R02401867209655
R0280191721268030518671676D09424167171600980492511140101043672636N10292800178455

TAPE 56    RAT 21    FOOD DEP   MULTI      EL = A  3    3
N016237006025D020731832636D021225500002N023031832826D037523333206D04002417166656
N047530003525D052526000002N054027332236N055025173076D056220000001N05852650305656

TAPE 61    RAT 21    FOOD DEP   MULTI      EL = F  3    3
R0035205015768007025502946801051900341680140230019168017519831856D01802100000161
R0210136723368024522501456802802350211600849243309530099027331156D09102500124661
N101725000001N102825000001N104526332146D102023831746D103429674103N11503550000261

TAPE 62    RAT 21    FOOD DEP   MULTI      EL = F  3    3
N0010303332830004031832366D036031503176N010028000002N012528203485D05283067121362
D056129252504N057234500002N069031332536N064228001216N068328831966                62

TAPE 64    RAT 23    H2O DEP    MULTI      EL = F  2    2
R0022401839468010742153695801354055169680160439527568018534831936802094252150664
R025334302526803153505256803353938176600360501053060037839100546D04003780123664
D042335460535D0437396305830044837801363N049541582104N052939301876N05463137176364
G055736600026056734000002N0575407000029058243201553N060737022346N06253548149564
N064734131036N067535702176N069534772176N071330470736N073531271126D07553353150364
N076242100002D076547500001N077432261575G078834801844N080032122376N08193303163664
N083528501306N085741634006N087843282896E091046132496E093042621616E09424308196664
E095439951256N096840780994N100034800648G102233731594N106234881055E10854000305664
E110040933026F111541553166N1113034501396N114538731268G116932802587N11833588293664
N120034451416N121034422096                                                       64

TAPE 66    RAT 23    AD LIB     MULTI      EL = E  2    2
R0015172000768004219721076800702007123680102192312068013018750986R01542122139666
R0182203521868020921402626802441933123680280166712468032017231516D03372195000266
N035318280766N0388175510466042019281244N044718931226N048517820426N05141943196666
N054816561105D056516050002N057022650001E058218981456E060017251286E06171875000266
N063516220626N066416902425D068119781754N070115801566N073416371906N07581607140666
N079018852096N082215820436D084717280926N087016231834G088517488515N09021816121566
D092723700001N093618651436N096718402026G099016450002N100418651156N10391568152666
N106718701513G107123750002N108717131606N110021050002D111218300002N11231933095666
N115018252156D117513500002N119019500001D1118421800001G119021200001N12051763087666
N123019671976                                                                    66

TAPE 67    RAT 25    H2O DEP    SINGLE     EL = B  3    3
R0039632067968009449002486801264633971680156468358068018532834226802113800399667
R0235395051468026049033546802955083476680317616726568034066175246803555033285367
D037807672016D094009567136600425040005860044501330566D046702500975604750250000267
D048206000002N0488950000010095050750000260520085000027055006331863F06000133042667
F065002290757N07099250006209718027511140072902000002N075506672816N07800317007667
N081001330496N082591170466N084553000635D08670600200300890004002714N08900125048467
N092000759484F093590060096N096200500346N104502671386N105502250634N11250333158667
N115303001246N118594671763N120306502254N121102000002N123802000586                 67

TAPE 69    RAT 26    H2O DEP    SINGLE     EL = B  3    3
R00404717455680080369031758012051674826801603683269680200466742668024046617339669
R0295340035568033033001756803553317243600380160018460039617672126D04272500216669
D045126333383004652000002N0347120500002N050728173496D052923000002N05652433226669
N058638332046N062829572336N0665039001736N072721502836N082036333986N08553333487669
F096007831836F098003751304E101011002204N105522172946N107322500002N10982200267669
N112118502326N114015833306N116328503604N118931333286                             69
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TAPE 74   RAT 25   AD LIB   MULTI   EL = B  3   3
B00550817128600095093314038011508001136801700867120600200120000010021712000001 74
D00235085000028028010171598680315086717568036006831706704001033133300575100000174
D0071308000000 2M073209251804N091509171016N098006831426N100007331126N105008171146 74
D10771050000 2                                                              74

TAPE 76   RAT 28   H2O DEP   SINGLE   EL = A  3   3
B002823672296800522683259680072281723268012524501846801503033184680190271727367 6
B022126932144802452567275680273270014168030029002006803273067287680357326026857 6
D038013500856004002133213600424218312560044322330766N048032830546D05712400187576
N067234000002606922725103480725333319 86N07753367 2706N080033433087E083026500002 76
N087530177206N091534603615N0955312922 37N094783267 2206N099532002415610053400000276
N103034331966N105033001446N107026833646N109630673206N114131671876              76

TAPE 77   RAT 28   H2O DEP   SINGLE   EL = A  3   3
B00271517160680070123316168012013331716801471683152680257161707568030216501416 77
D039009333016D04200467042600445026726730046502751444D0525090025 23N054503000001 77
D055504500002 N06160583191 6N06450583135 6N06700583040 6N069506330726N07200640144577
D0738030000001N07505801 85N07730683108 6N079505670676N081605000775N106407001326 77
N114605670883611620600010111700683151 6N119509171306N122007500996              77

TAPE 78   RAT 28   H2O DEP   MULTI   EL = A  3   3
B002536672326800874733643680125393379568016551174106802133883401680240280030467 8
B027539672366803033883279680328535061560037058000002D0412260000002N052839000001 78
D0534370000001N069535003886N0335300045 06N086034333496N090030501486E106025333416 78
F109031003406N115027502586N117532838846                                        78

TAPE 79   RAT 28   AD LIB   SINGLE   EL = D  3   3
D008210000002600921250002800980800100200166115000028019507001516802151133251679
B023506331696802600850154680235080010668030505667194680330066715068035509172366 79
D0375110000015041906330506N048008672126N052006830706G05701400000010058313000001 79
D0592123309660625165900240730115020 86E08201033067 3F086507500676N09150633080679
N095010002136N097506501486N103508001156N110508330806N113005331026D115009000002 79
N12001000144 6                                                                 79

TAPE 83   RAT 30   FOOD DEP   SINGLE   EL = E  3   3
B002565333136800756467492680125638388568017554674786802154067642680240353339668 3
B027541674286803904267709583325473309 93E03754583192600460190018 86E05104367812683
D06322133623300688282590140070820002684007261400000200774180000020079232000002 83
D081615500002D09712333449301060311726 86                                      83

TAPE 84   RAT 30   FOOD DEP   SINGLE   EL = F  3   3
D01502800289300232213320330025516000002D038622003513N040542507896N045537678976 84

TAPE 85   RAT 32   FOOD DEP   MULTI   EL = D  2   2
B003513501686800701267133680399112513268012515980686801651552090680260154307058 5
B0283131809365039405630734066215750020075714420856607701690000200842123305648 5
D098513920376D09951487144 3N100021200383N101516522016012121563106 6N12201250337385
G12300935000 2                                                                 85

TAPE 86   RAT 32   FOOD DEP   MULTI   EL = D  2   2
N0025192225 36N0050201315946006724200002D0182234514 26N020519100002G022421400001 86
N025021931366N027519231396N030021981166N032529061725N035022352446N038529833646 86
N041236382656N041730503173D041822200002N043532983126N046524883176N04903172155686
N051025171636                                                                  86

TAPE 87   RAT 32   AD LIB   MULTI   EL = D  2   2
B002711032366D02301011092760266073516 04E040007271593004451425161400575091739638 7
N078008811526N082506532816N086008851886N089010202526                           87

TAPE 88   RAT 32   H2O DEP   MULTI   EL = A  2   2
B002420800846F00481943193 6E00881915196 6E011516531606F015716651386E020620122235 88
B025021721016802802087124680302193314368034523332024D03752248271 6D04001698103 688
D042017521336D0438195813066045013100002D047421721115N053019371076N055519361615 88
G058723951316N062219907 36N065720021726N067220281426N068719780796N071020271306 88
N073018151336N075019681396N077019570896N079017100946N081015521136N082817371796 88
N083816220776N0835017220415009551563039 4N088616172216N091516701086N093517120886 88
N096215821246N098716521036N101514570526N104211170436N106711820796N109219631946 88
N111215601276N112516551796E114115931266E117014621286                          88

TAPE 89   RAT 32   H2O DEP   MULTI   EL = A  3   3
B004012172126800801417233680120130023868016009331456802001167242680240080011 3689
B028013672876803101000058 3E035008601215003835283380600415585058 16D042226334063 89
D044612333713D0430140000016050114000001D05231317149600543060000001F0572130000028 9
E064508502206F068008503666007103317422600797130000016083023000002D0087803000002 89
N091531178176N092731500002600402450002N099541338776N102541171946N105530176946 89
N108529755254N111218674796N113006172566N114817834186N116227174426N118024331866 89
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TAPE 90   RAT 32   TOT DEP   MULTI    EL = A  2    2
R0035116513068300701500063680105148514368014011870806801751087172680210089208669O
R0245090709163022951267104466E03951653807666E0405202215566E0465170718966E05031540175690
F0532147321266E05711385132665061015231076E0628160715366E0650161008460068113130896 90
D0697148303966E07301128037666E0750146024066E0785109507366E0300116308360086015672986 90
G0875184012436E0400108804166E0045146532360098023441865E1010254510766E1030256809969O
E1060255015860104227482135E1125173707366E1155226220460119027403585                90

TAPE 91   RAT 32   TOT DEP   MULTI    EL = A  2    2
F0050166024566E0075155811956E0130173804866E0128191813166E0157182810866E0177182004869 1
F0203208310666E0230219207466E0255321550956E0275236711356D0308201508046031828000002 91
E0350161011366E0375199810166E0420190000466E0442191313666E0462277334740D0472233508269 1
G0488253021536E0526214503266E0556210011336E0624192807466E0686213212966E0760205713469 1
F0802191715866D8272322423500911197811205N0922201000026E1006151714066E1050175126079 1
D1082205009854N1125163708866N1140171307866N1156187214166N1170184018866N1185150710869 1
N1202182011340120819201603                                                        91

TAPE 92   RAT 32   ADJ LIM   MULTI    EL = F  2    2
R0025180300840005517329669D0070215000016000902200000280250159716364028519101336920
R0260183804466B029018300806D0043622501156N0495208005630650163509660066522500001920
G0677216000002N0750139709965N0800134105174045013050806N0900127707566N0950133807269 2
N1055181806266N1090269009566N1115208712266N1155227511166N1206175819755                92
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