INVESTIGATIONS OF CALORIC REGULATION

NOTICE

Some portions of the data in Experiment IV are suspect as a result of possible adulteration of diets used in this experiment by a disaffected ex-member of the psychology department.

INVESTIGATIONS OF CALORIC REGULATION: INGESTION OF AN ACALORIC DIET BY DOMESTICATED RATS

BY

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SCOPE AND CONTENTS: A series of experiments investigated the ingestion of an acaloric diet (composed mainly of vaseline and methyl cellulose) by rats. While animals on an ad-lib feeding schedule seemed able to regulate caloric intake adequately in the presence of this diet, animals on a 3 hr./day schedule did not. Although ingestion of this diet resulted in retarded weight gain, they did not learn to avoid ingesting it. However, the data indicate that they did form an aversion to a nutritionally adequate diet presented in conjunction with the acaloric diet. This failure to associate the acaloric diet with the consequences of its ingestion was explained in terms of "learned safety".

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The author wishes to express his gratitude to Dr. Bennett G. Galef for his assistance and encouragement throughout the development of this thesis. Sincere thanks also go to Mertice M. Clark for her helpful suggestions in the writing of this thesis.

TABLE OF CONTENTS

LIST OF FIGURES

INTRODUCTION

The ability of rats to obtain adequate foods from the environment has been well documented. Richter's (1943) demonstration of self-selection of an adequate diet in a cafeteria-style feeding situation, studies of caloric regulation (Adolph, 1947; Smith et al., 1962), and the extensive literature on taste aversion learning (Garcia and Koelling, 1966), have all contributed to the view that rats are virtually infallible in matters of dietary selection.

However, a number of studies have demonstrated that there are limitations upon rats' regulatory abilities. Firstly, rats are able to compensate for bulk added to a diet (by eating more) only within limits: if the diet is too diluted, the animals fail to adjust (Adolph, 1947; Smith et al., 1962). Also, such caloric regulation, when it does occur, is usually seen in animals on an ad-lib feeding schedule. It seems that hungry rats are influenced more by the taste than by the caloric value of a food (Jacobs, 1969). Similarly, taste is an important factor in cafeteria-style self-selection: rats select an adequate diet only when the palatabilities of the various choices (particularly protein) are in balance (Epstein, 1967).

The present series of experiments demonstrates

another situation in which palatability interferes with the rat's regulatory abilities. In the course of an ongoing line of research it was discovered that rats would ingest a palatable but acaloric diet. It was soon realized that studies of the ingestion of this diet would provide data pertinent to the questions of food selection and caloric regulation by these animals.

EXPERIMENT I

INTRODUCTION

The first experiment was designed to determine whether rats would ingest an acaloric diet (Diet Ac) when offered it in conjunction with a nutritive diet (Diet N). If rats form learned preferences for beneficial foods, they should be expected to ingest Diet N ('positive' consequences) to the almost total exclusion of Diet Ac ('neutral' consequences). If, on the other hand, rats ingest any palatable substance having no harmful effects, they might be expected to ingest both diets.

METHOD

28 female hooded rats, approximately 30 days old and weighing 100-125 gms. at the beginning of the experiment, were obtained from the Canadian Breeding Farm. They were housed individually in standard ($9\frac{1}{2}$x7x8 in.) laboratory rack cages. Throughout the experiment, water was available ad-lib. Upon arrival in the laboratory, subjects were maintained ad-lib on Purina Rat Chow pellets for 5 days, following which formal 3 hr./day feeding sessions were begun.

During these feeding sessions, food was presented in two glass jars ($2\frac{1}{4}$ in. diam. x $2\frac{1}{4}$ in. deep) attached by means of light wire to the front of each cage (Fig. 1). Food jars were provided with metal covers in which $1\frac{1}{2}$ in. diam. holes had been drilled. Spillage was recovered and weighed at the end of each feeding session, and the 'light-on' period coincided with this period of food availability.

Subjects in the experimental group (n=20) were offered an acaloric Diet Ac, consisting of methyl cellulose (18% by weight), vaseline (28%), calcium carbonate (14%), mineral oil (11%), U.S.P. salt mix (2%), and water (27%) (Taylor and Bruning, 1968), in one food jar and a nutritionally adequate Diet N (powdered Purina Rat Chow) in the other.

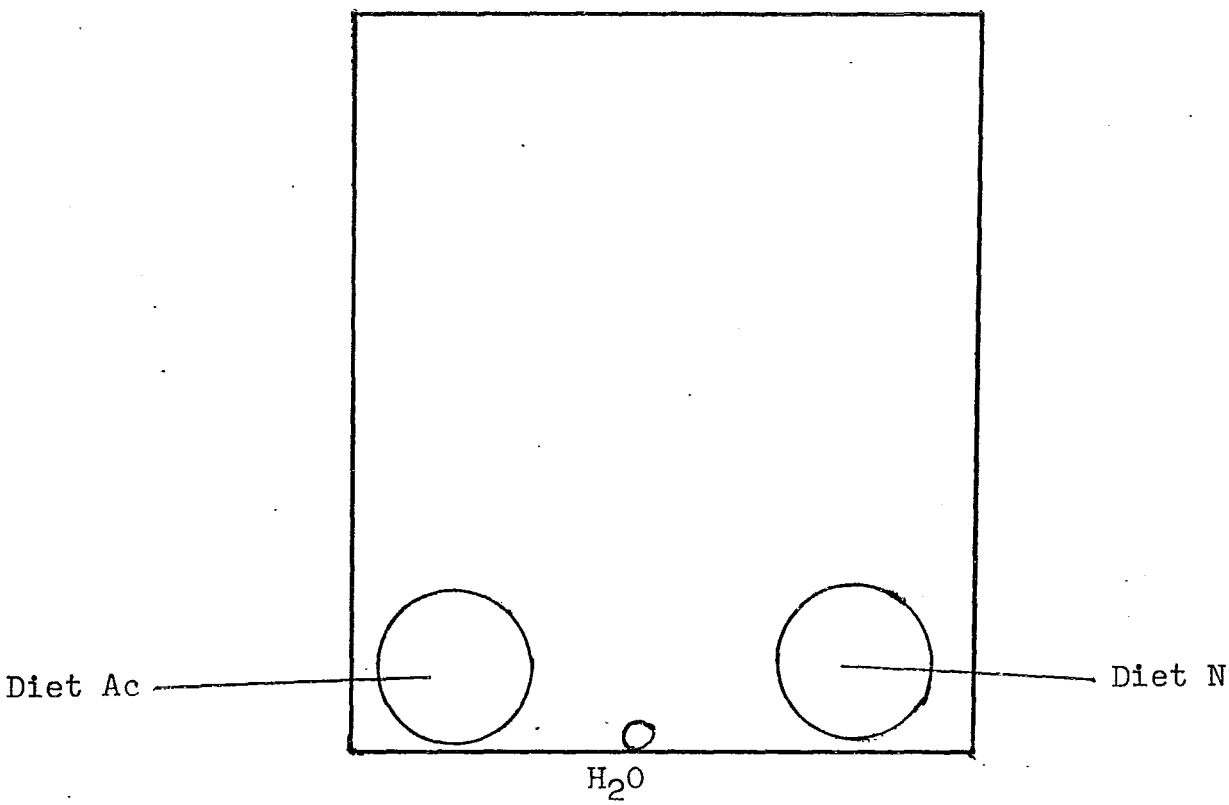

Fig. 1

Cages used in Experiments I through IV.

Control animals (n=8) were offered Diet N in both jars.

Food intakes were recorded daily, and the weight of each animal was determined every third day for the duration of the experiment.

RESULTS AND DISCUSSION

Fig. 2 indicates the amount of Diet Ac ingested by animals in the experimental group as a proportion of total intake. It can be seen that the intake of this diet remained remarkably constant at approximately 25% over the 29 days of the experiment.

Fig. 3 presents the mean weights of the two groups. The weight loss seen in both groups between DAY 1 and DAY 4 is assumed to be due to the fact that on DAY 1 the feeding period was reduced from 24 to 3 hrs., and it took the animals several days to adjust to the new schedule. Groups began differing in weight by DAY 10, and the difference became progressively larger. On DAY 13 and thereafter the difference is significant beyond the .01 level (t-test, 25 d.f.).

The most obvious explanation for the greater weight gain by the controls is that these animals simply ingested more of the nutritive Diet N than did experimental animals. Fig. 4 demonstrates that this was indeed the case. Subjects in the control group consistently ingested more Diet N than did experimental subjects. t-tests revealed that the differences in Diet N intake were significant beyond the .05 level on 20 of the 29 test days.

Subjects in the experimental group not only

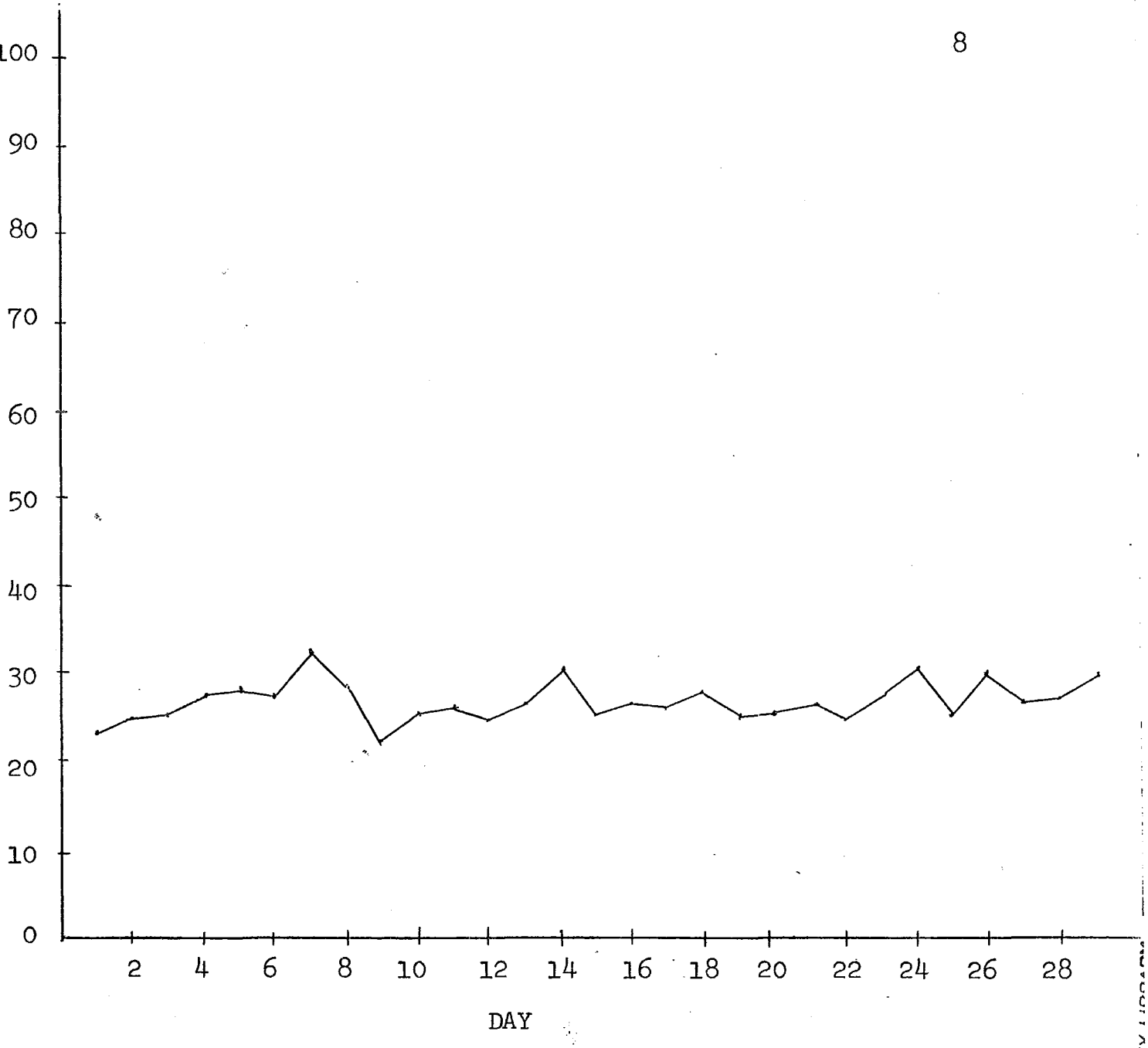

Figure 2

Mean proportion Diet Ac ingested by animals in the experimental group in Experiment I.

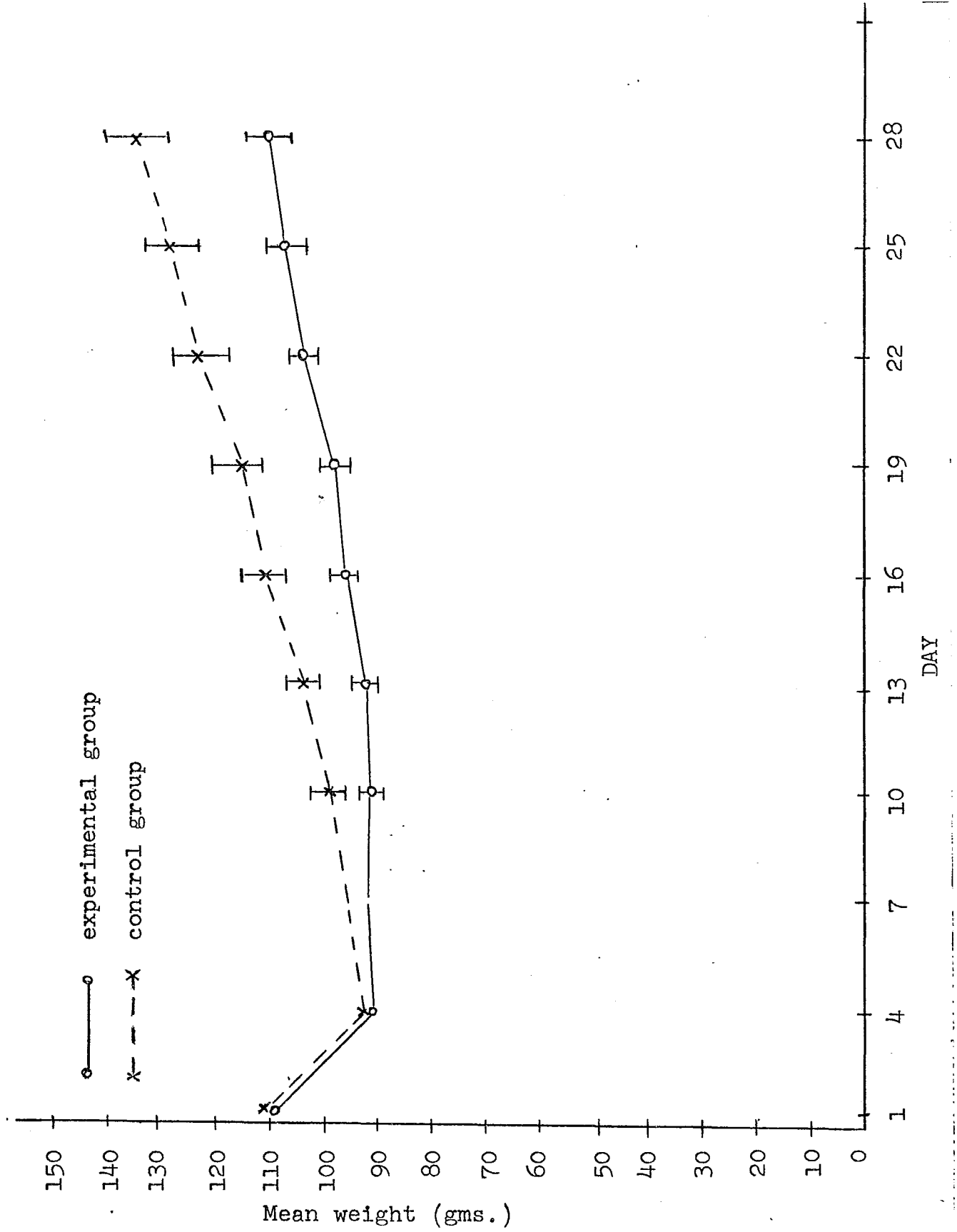

Figure 3

Mean weights of animals in both groups in Experiment I.

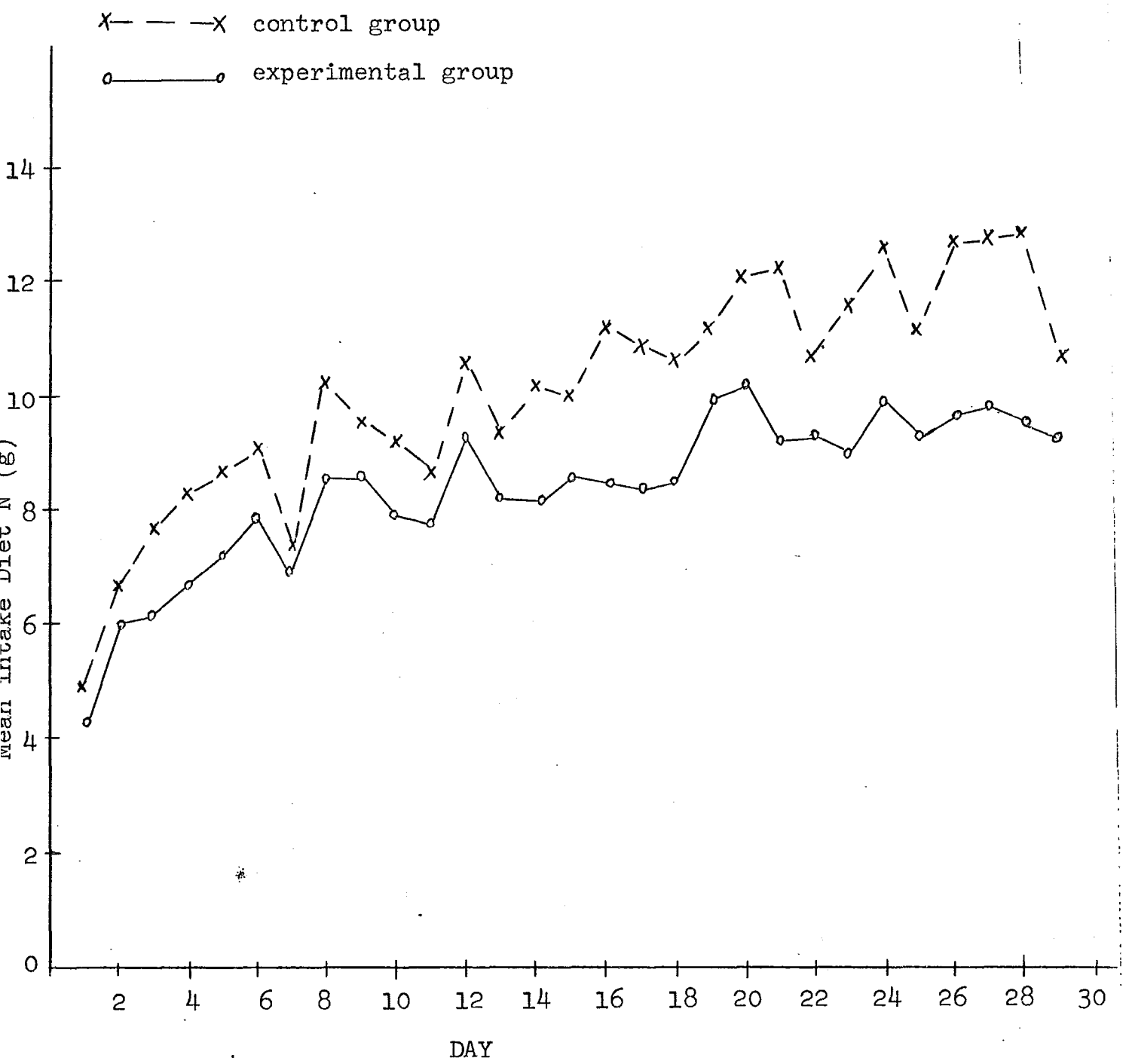

Figure 4

Mean food intakes of the two groups in Experiment I.

gained an average of 30 gms. less weight than did control animals, 2 of the 20 animals in the former group died during the course of the experiment (their data were included in Figures 2-4 until they died). In Experiment II (below), under identical conditions, 3 of 16 experimental animals died. Meanwhile, no control animal expired in either experiment. Thus, of 36 rats offered both Diet Ac and Diet N, 5 died, whereas none of the 24 offered Diet N only did. This difference is significant beyond the .05 level (X^2=3.63, 1 d.f.).

A similar pattern was observed in the feeding behavior of all 5 rats which succumbed during the experimental period. The proportion of Diet Ac ingested progressively increased, while the amount of Diet N ingested decreased, until death ensued, presumably due to malnutrition.

The results of this experiment demonstrate quite clearly that the rats' response to Diet Ac was maladaptive. This diet was definitely harmful, in that animals ingesting it either became emaciated and sluggish or died. Nevertheless, as Fig. 2 made clear, they did not learn to avoid Diet Ac; rather, they continued to ingest it at a steady rate for over four weeks.

EXPERIMENT II

INTRODUCTION

That animals in Experiment I continued to ingest Diet Ac is somewhat surprising in view of the considerable literature on taste aversions suggesting that rats learn to avoid a diet associated with feelings of sickness (Rozin and Kalat, 1971; Garcia and Koelling, 1966). The obvious failure of experimental subjects to avoid ingestion of Diet Ac in Experiment I suggests that animals may not be able to associate Diet Ac with the consequences of its ingestion. It is possible, however, that they learned an aversion to both Diet Ac and Diet N; but, as no other choice was available to them, they continued to ingest both diets in their usual proportions. If this was the case, the aversions should become apparent when a novel third diet is introduced.

METHOD

Subjects in this experiment were 32 female hooded rats, approximately 30 days of age (100-125 gms.) at the beginning of the experiment. They were assigned to one of two groups, and these groups were treated identically to those of Experiment I for the first 28 days of the experiment. During daily 3 hr. feeding sessions subjects in the experimental group (Group E) were offered both Diets Ac and N, while subjects in the control group (Group C) were offered only Diet N. The purpose of this 28 day pretraining period was to retard the weight gain of subjects in Group E and to allow these animals to experience the adverse consequences of ingestion of Diet Ac. During this period, 3 of the 16 animals in Group E died.

Following the pretraining period, subjects in both groups were offered a novel Diet X, consisting of Turtox "Fat Sufficient Diet" adulterated with 0.04% quinine hydrochloride so as to avoid a ceiling effect. Diet X was offered to all subjects in conjunction with one or the other of the two original diets (Ac and N) during seven 3 hr./day feeding sessions, and the proportional intake of Diet X was recorded daily.

Prior to the seven test days, Group E was divided into two subgroups: Group E-Ac (n=6) was offered

Diet X and the acaloric Diet Ac, and Group E-N (n=7) was offered Diet X with the nutritive Diet N.

Group C was similarly divided: Group C-Ac was offered Diet Ac and Diet X (both of which were novel to these animals), while Group C-N was offered the choice of Diets N and X. Subjects in these control groups, then, were identical to the corresponding experimental groups (i.e. Groups E-Ac and C-Ac; Groups E-N and C-N) in all respects save one: they had had no previous experience with Diet Ac, and therefore should be expected to have formed an aversion to neither Diet Ac nor Diet N. These control groups provided a baseline for the intake of Diet X in the presence of either of the other diets.

RESULTS AND DISCUSSION

During the 28 day pretraining period, animals in the experimental group ingested Diet Ac at a mean rate of 20.1% of their daily intake. This figure is similar to that obtained in Experiment I, and was sufficient to retard weight gain in these subjects: animals in Group E gained an average of 13.1 gms. less than those in Group C. Thus, when the testing days began, animals in Groups E-Ac and E-N had had ample opportunity to learn to avoid Diet Ac (and/or Diet N).

Fig. 5 presents the results on the seven test days of this experiment. Considering first the lower portion of this graph, it can be seen that Group E-N ingested a considerably greater proportion of Diet X than did Group C-N. The differences are statistically significant (t-test, 12 d.f., $p < .05$) for the first five days of the experiment. That Diet X was relatively unpalatable is shown by the small proportions of that diet ingested by the controls (Group C-N). The greater proportion of Diet X (and consequently the smaller proportion of Diet N) ingested by the experimental group (Group E-N) therefore suggests that these animals had formed an aversion to Diet N as a consequence of their previous experience

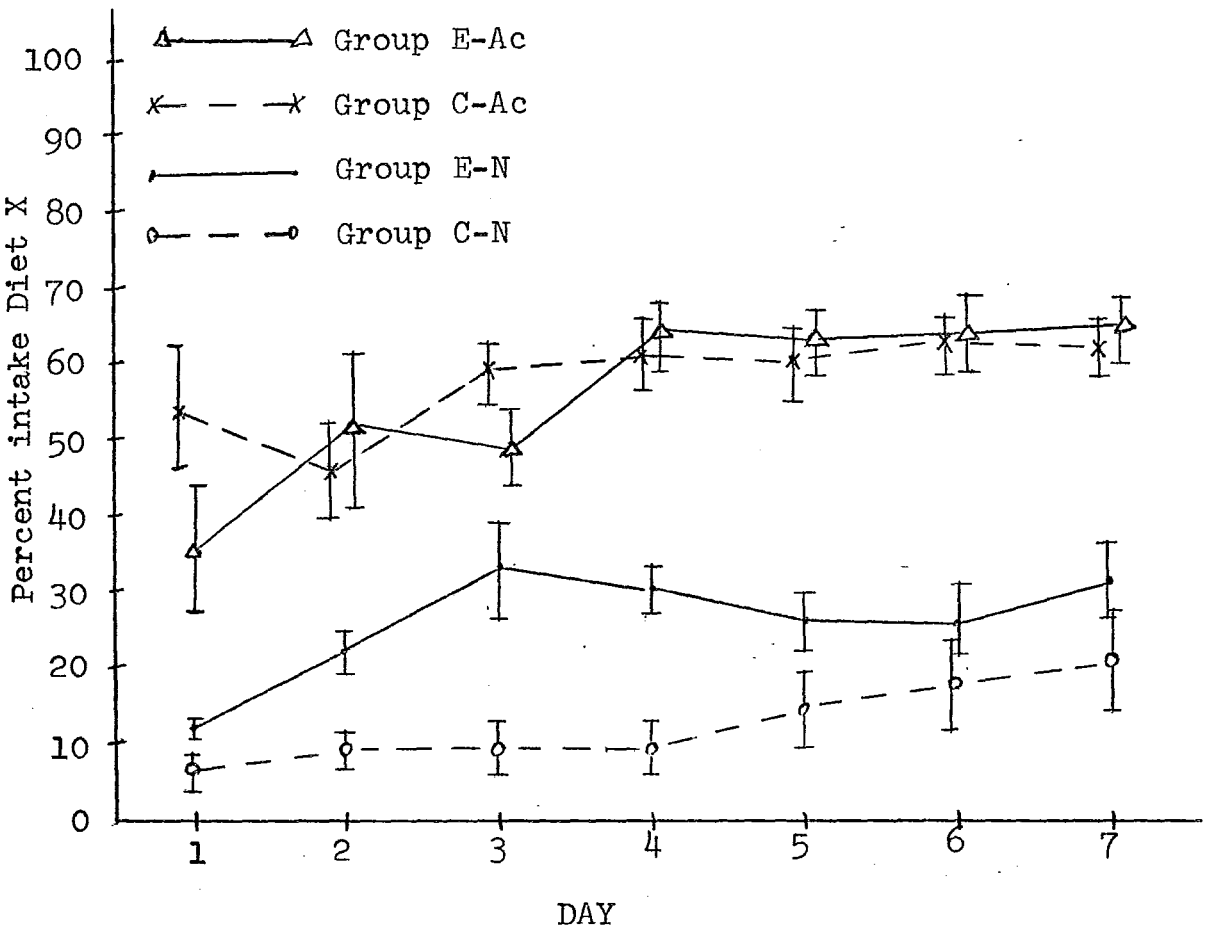

Figure 5

Mean proportion Diet X ingested by the four groups in Experiment II.

with Diet Ac.

On the other hand, no such aversion seems to have been formed to Diet Ac. The upper portion of Fig. 5 reveals that there were no great differences between Groups E-Ac and C-Ac. Although the intakes of Diet X did not stabilize until the fourth day, the differences between these groups were not statistically reliable on any of the seven test days. A further line of evidence suggesting that animals did not form an aversion to Diet Ac is that 2 of the 6 animals in Group E-Ac died during the test period as a result of having ingested too much of the nonnutritive Diet Ac and too little of the nutritive but unpalatable Diet X. Had these animals learned an aversion to Diet Ac it is somewhat unlikely that they would have ingested it to the almost total exclusion of Diet X, which, although unpalatable, was ingested by other animals.

The present experiment therefore demonstrates that rats learned an aversion to the nutritive Diet N as a consequence of having ingested it in conjunction with the acaloric Diet Ac; surprisingly, the animals did not form an aversion to Diet Ac itself.

EXPERIMENT III

INTRODUCTION

The failure to learn an aversion to the acaloric diet in Experiment II suggests that rats may be incapable of learning to avoid this diet. Diet Ac tasted remarkably "bland" to human observers, and it is possible that a lack of salient taste cues prevented the animals from associating Diet Ac with the consequences of its ingestion. Kalat and Rozin (1970) have reported that "salience" is an important factor in determining whether a learned taste aversion will be formed to a solution. These authors discovered that the more salient of two solutions would be the one associated with poison.

In the present experiments, it is possible that Diet Ac was much less salient than Diet N, explaining why the aversion was learned to Diet N rather than Diet Ac in Experiment II. However, in pilot experiments it was found that manipulating the salience of Diet Ac (by introducing various amounts of sodium saccharin or vanilla extract to that diet) did not allow animals to learn to drop it from their diets; the baseline intake merely varied according to the relative palatabilities of the various forms of Diet Ac.

Fortunately, a more direct method of testing whether rats are capable of learning to avoid Diet Ac

exists: associating ingestion of this diet with poison. In the usual paradigm for studying taste aversions, toxicosis is produced in animals shortly after they ingest a novel diet or solution. If utilization of this method were to produce an aversion to Diet Ac, it would of course demonstrate that the diet is indeed sufficiently salient; on the other hand, failure to produce an aversion under these conditions would suggest that rats are completely unable to associate ingestion of this diet with feelings of sickness.

METHOD

Subjects were 55 female hooded rats, approximately 30 days of age (100-125 gms.) at the beginning of the experiment. They were individually housed in the cages described in Experiment I, and water was available ad-lib. Following an adaption period of four days (during which they were maintained on ad-lib Diet N in pellet form), they were put on a 3 hr./day feeding schedule with both Diets Ac and N available for a further five days. The proportion of Diet Ac ingested was recorded on each of these five test days.

Subjects in Group I (n=15) were injected with 0.12M lithium chloride (2% by body weight) immediately following the feeding period on DAY 1; they thus had had only 3 hrs. experience with Diet Ac prior to poisoning. Subjects in Group II (n=8) and Group III (n=8) were injected with the same dosage of LiCl immediately following the feeding period on DAYS 2 and 3 respectively. They therefore had had 27 or 51 hrs. in which to evaluate the consequences of ingestion of Diet Ac. Group C (n=24) consisted of 8 saline injected, and 16 uninjected, control animals. As there was no difference between these animals, their results were pooled.

While this design was similar to that used in most taste aversion experiments, there was one major difference: in the present study animals were poisoned after ingestion of two diets, whereas usually only one diet is offered. However, this was not expected to prevent animals in the present experiment from learning to avoid Diet Ac. Poisoning is usually associated with the more novel of two tastes (Revusky and Bedarf, 1967; Maier et al., 1971), and subjects in the present experiment had had four days experience with Diet N (albeit in pellet form) during the adaption period. They were therefore expected to associate the poisoning experience with Diet Ac, if they were at all able to do so.

RESULTS AND DISCUSSION

Fig. 6 indicates the amount of Diet Ac ingested by animals in the three experimental groups on the day following their respective LiCl injections, and the mean amount of Diet Ac ingested by control animals over the five days of the experiment, as a proportion of total intake.

The results of this experiment clearly demonstrate that rats are indeed capable of learning to avoid Diet Ac. Fig. 6 reveals that following injection of LiCl, animals in Group I ingested considerably less of the acaloric diet than did the control animals. The difference between Group I and Group C in Diet Ac intake was significant beyond the .01 level (t-test, 37 d.f.).

Fig. 6 also reveals that Groups II and III did not seem to form an aversion to Diet Ac. Although the proportion of Diet Ac ingested by Group II did decrease slightly after injection of LiCl, that of Group III did not.

That animals were able to learn to avoid Diet Ac if poisoned after a single presentation of that diet, but not after two or more presentations, can be explained nicely in terms of the "learned safety" mechanism recently postulated by Kalat and Rozin (in

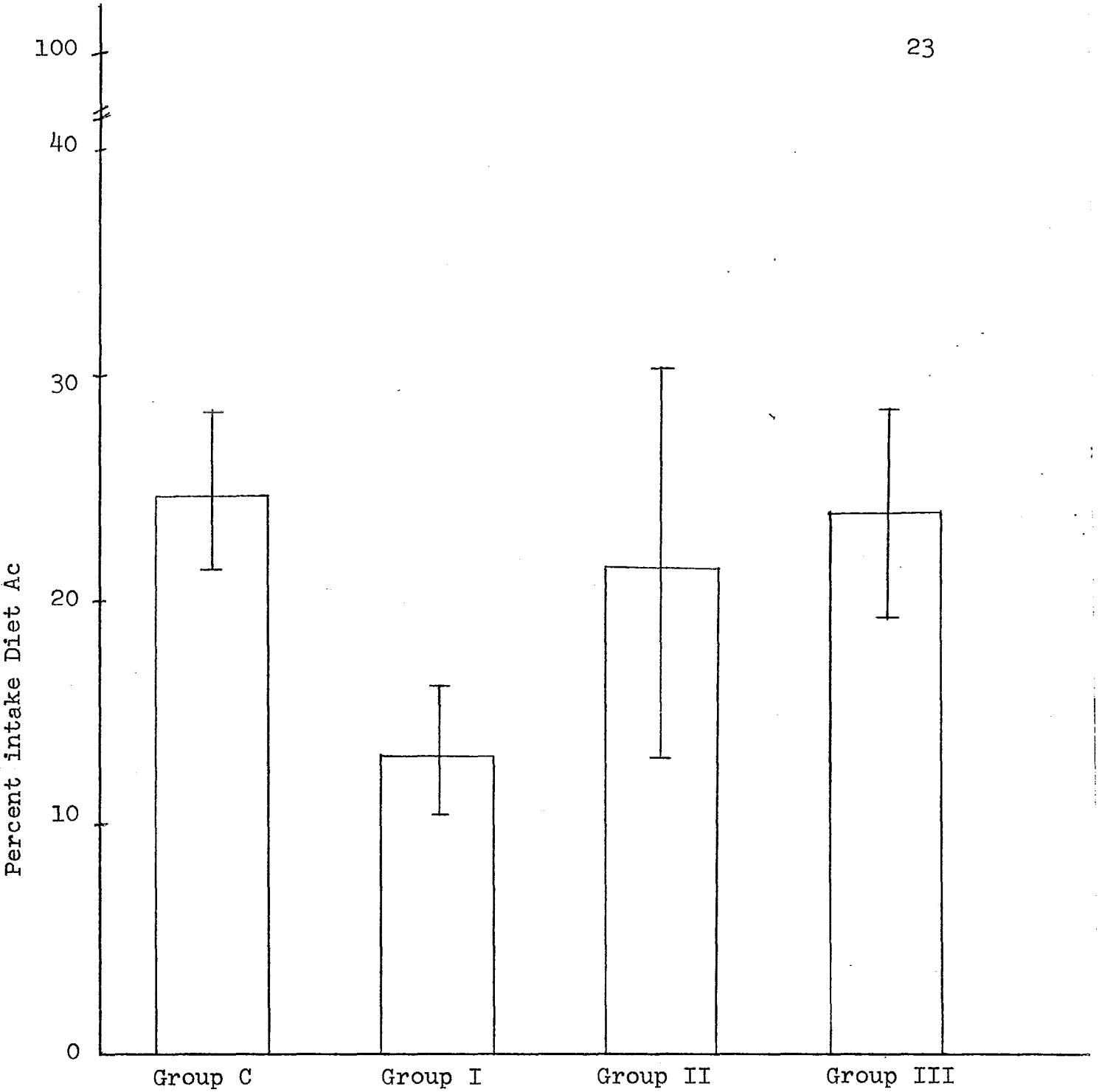

Figure 6

Mean proportion Diet Ac ingested in Experiment III.

preparation). These authors suggest that a rat, faced with a novel taste, treats the food as "'possibly dangerous, associable with poison'". If, however, as time passes after ingestion of the novel food no adverse effects occur, the novel taste is gradually reclassified as "'probably safe, relatively unassociable with poison'". If the animals is then poisoned after ingestion of the (now familiar) food, Kalat and Rozin state that the previous learning (of safety) will interfere with learning that the food is toxic. (However, they point out that "...rats can learn some aversion to a familiar solution." Experiment II demonstrated that this was true of foods as well).

Returning to the present experiment, it seems that animals in Group I did not learn that Diet Ac was safe. Rather, they associated this diet with the effects of the LiCl and therefore learned to avoid it. On the other hand, animals in Groups II and III, having had at least 24 hrs. in which to learn that Diet Ac was 'safe', failed to associate it with poisoning.

Two important conclusions can be drawn from the results of Experiment III. Firstly, rats are not incapable of learning to avoid the acaloric Diet Ac. However, they learn that it is 'safe', probably within 24, and definitely within 48, hours of its initial

presentation. Thus, by the time adverse effects became apparent in Experiments I and II, animals had already learned that the diet was 'safe', and therefore failed to drop it from their diets.

EXPERIMENT IV

INTRODUCTION

To investigate the generality of the phenomenon, it was decided to offer Diet Ac to animals feeding on an ad-lib schedule. It may be that in Experiments I and II animals were unable to sort out the effects of the two diets during the 3 hr. feeding period, and wrongly attributed some of the nutritive value of Diet N to Diet Ac. Rozin (1969) reported that thiamine deficient rats, offered four different foods, tended to sample only one or two per 'meal', leaving a gap of several hours between 'meals'. He suggested that this sampling pattern allowed his rats to evaluate the consequences of ingestion of the various foods offered and thereby learn to choose that diet to which a vitamin supplement had been added.

Rozin's animals were feeding on an 8 hr. schedule, which allowed them ample time to ingest discrete 'meals'. In Experiment I and II, however, the feeding period of 3 hrs. was probably not long enough for animals to utilize the above method of sampling. Therefore, in the present experiment, a group was run on a 24 hr. feeding schedule.

METHOD

24 female hooded rats, approximately 30 days of age (100-125 gms.) at the start of the experiment, served as subjects. These were divided into two groups of 12, each of which was offered both Diets Ac and N. One group (Group 3-24) was on a 3 hr./day feeding schedule, while the other (Group 24-3) had both diets available ad-lib. After ten days the feeding schedules of the two groups were reversed, and after a further 12 days the experiment was terminated. The proportional intake of Diet Ac by both groups was recorded daily.

(The results of a third group, Group 24-3-Rep (n=8), are presented below. The data from this group, treated identically to Group 24-3, are included due to the great disparity in the results).

RESULTS AND DISCUSSION

The results are presented in Fig. 7. It can be seen that during the first part of the experiment, before reversal, Group 3-24 ingested a considerably greater proportion of Diet Ac (25%) than did either of the two 24 hr. groups (10-15%). The differences between Group 3-24 and Group 24-3 are significant (t-test, $p < .01$) on all ten days, while the differences between Group 3-24 and Group 24-3-Rep are significant ($p < .05$) on all but three of the days. After reversal, Group 3-24 lowered its intake of Diet Ac to roughly the level observed in the 24-3 groups before reversal. Meanwhile, Group 24-3-Rep increased its intake of Diet Ac to the level seen in Group 3-24 prior to reversal. Statistical analysis revealed that Group 24-3-Rep ingested significantly ($p < .05$) greater proportions of Diet Ac than Group 3-24 on DAYS 16-20. Thus the results of these two groups suggests that the proportion of Diet Ac ingested by rats is dependent upon the feeding schedule. However, Fig. 7 also reveals that, following reversal, Group 24-3 differed markedly from Group 24-3-Rep. Animals in this group did not increase their intake of Diet Ac, but continued to ingest the same small proportion of Diet Ac on the

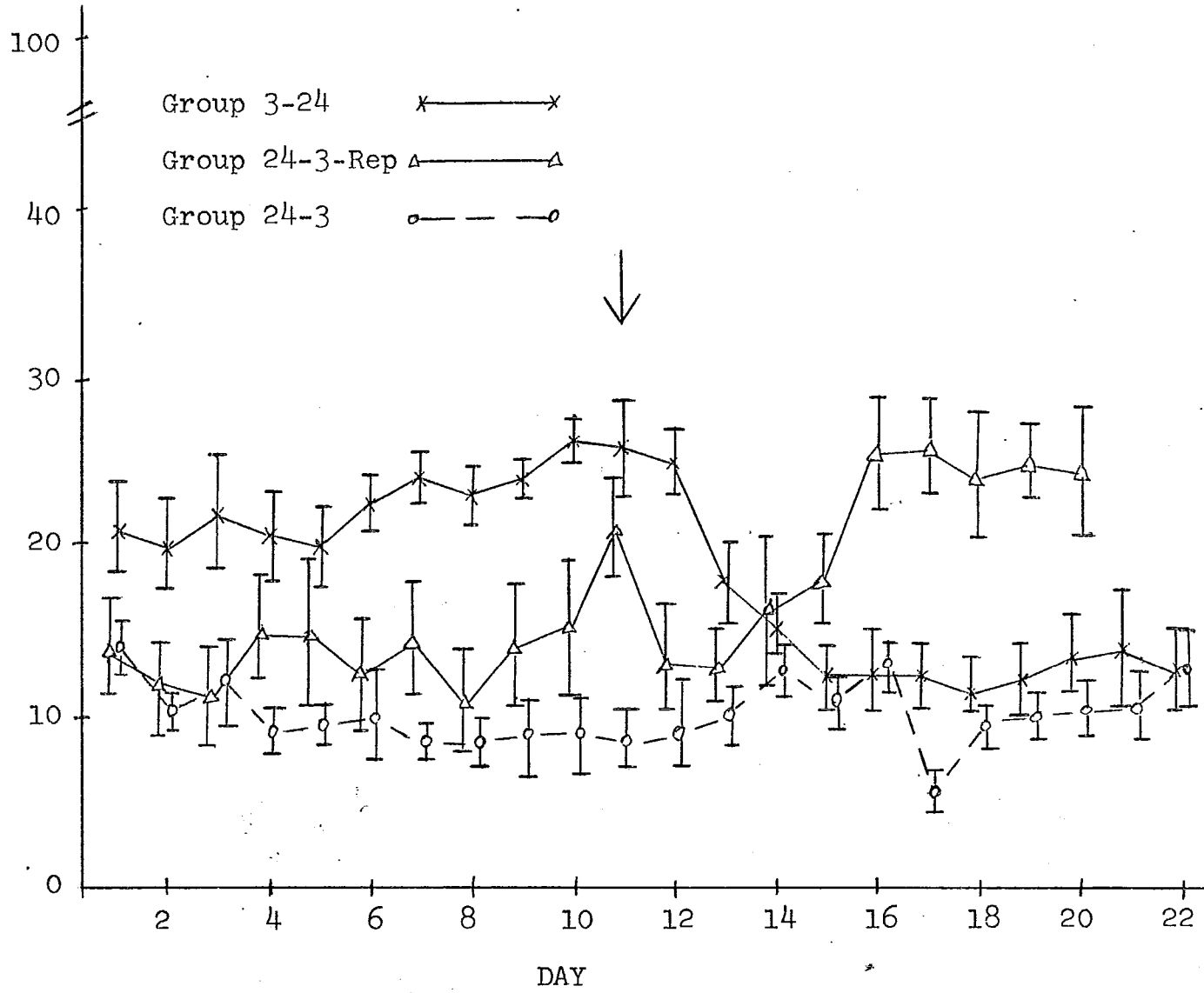

Figure 7

Mean proportion Diet Ac ingested by animals in the three groups of Experiment IV. The arrow indicates the point at which the feeding schedules were reversed.

3 hr. schedule that they had previously ingested when feeding ad-lib. The reason for the difference between the two 24-3 groups is not clear.

The lower proportion of Diet Ac ingested by animals on the 24 hr. schedule suggests that these animals may not have become ill as a consequence of ingestion of the acaloric diet. Unfortunately, weight data were not recorded in this experiment. However, inspection of individual intakes reveals that, on the average, animals on the ad-lib schedule ingested 14-17 gms. of the nutritive Diet N daily. This is considerably more than the 9-12 gm. intake of control animals in Experiment I; therefore, under conditions of ad-lib feeding, there are probably no (or very little) adverse consequences of ingestion of the acaloric diet.

The smaller proportion of Diet Ac ingested by animals feeding ad-lib does not appear to be due to a learned aversion to this diet. Firstly, in Groups 24-3 and 24-3-Rep, the intake of Diet Ac was low from the outset: it did not decline after animals had experienced the diet. Secondly, as mentioned above, these animals were ingesting a large amount of the nutritive diet and therefore most likely experienced no ill effects. They therefore would have had no cause to form an aversion. Finally, animals in

Group 24-3-Rep increased their proportional intake of Diet Ac when switched to the 3 hr. feeding schedule. This strongly implies that these animals had no aversion to the diet.

An alternate explanation for the finding that animals ingest less Diet Ac and therefore better regulate caloric intake when feeding ad-lib can be made in terms of a "working hypothesis and model" recently proposed by Jacobs (1969; Jacobs and Sharma, 1969). He suggests that a dual system is involved in control of food intake. In essence, Jacobs feels that in matters of dietary selection food-deprived animals are more influenced by the taste, while sated animals (i.e. those feeding ad-lib) are more influenced by the caloric value of a food. Thus this hypothesis provides a likely explanation for the finding that food deprived rats ingest a greater proportion of the palatable but calorically valueless Diet Ac.

GENERAL DISCUSSION

The continued ingestion of an acaloric diet demonstrated in the present series of experiments provides further evidence for the role of affect in the control of feeding behavior. One line of support for the hedonic theory of P.T. Young (1966) has come from demonstrations that rats prefer saccharin solution to plain water (Beebe-Center et al., 1948; Carper and Polliard, 1953), and the present experiments support Young's theory in much the same way.

There is a possible alternate explanation for the rats' ingestion of Diet Ac, namely that the animals ate it for the small amount of salt which the diet contained. However, a control experiment demonstrated that this was not the case (author's observations). Rather, it seems that Diet Ac was ingested in large part because of the greasiness provided by its vaseline ingredient, for it is known that rats like greasy foods (Hamilton, 1964). Similarly, rats have been reported to eat wax crayons (Walker and King, 1962), probably for the same reason.

It was suggested above that the failure to associate Diet Ac with the consequences of its ingestion in Experiments I and II was most likely due to "learned safety". Although acaloric substances

are usually thought of as being neutral, Diet Ac might more properly be regarded as a 'slow-acting' poison: it took several days of ingestion for adverse effects to become apparent. By this time animals had had ample opportunity to learn that Diet Ac was 'safe'. It seems that the rat, remarkably well equipped to deal with 'fast-acting' poisons (Rozin and Kalat, 1971), may, due to this mechanism of "learned safety", be particularly vulnerable to slow-acting ones.

It remains unclear why animals did form an aversion to the nutritive Diet N. They had the same— indeed, more— opportunity to learn that it was safe.

In the typical experiment on learned aversions, illness is produced in the presence of a single, novel taste. Little is known about the factors which influence taste aversion learning in the presence of two familiar diets. However, two possible factors which suggest themselves are salience and palatability. As mentioned above, Diet Ac was probably less salient than Diet N; alternately, Diet N was relatively unpalatable to rats (see for example, Galef and Clark, 1971). Either of these factors might have been responsible for the animals learning an aversion to Diet N rather than Diet Ac. However,

this is mere speculation; further research in this area is obviously needed.

There is presently some controversy in the literature as to whether rats learn to prefer beneficial foods or merely to avoid harmful ones (Rozin and Kalat, 1971). The present series of experiments supports the latter view. That the animals did not learn to prefer Diet N is clear; that they continued to ingest the acaloric diet suggests that rats eat any palatable substance having no initial ill effects rather than learn to prefer substances having good effects.

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