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A BEHAVIORISTIC STUDY OF THE ACTIVITY OF THE RAT

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CONTENTS

INTRODUCTION

Interest in human psychology is moving rapidly toward problems of general adaptation involving responses of the whole organism in actual working life-situations. This change of interest is due probably in large part to the healthy impetus given to psychological research by recent work and discoveries in the allied field of psychiatry. But, undoubtedly, it is also due to the strong influences from biology, especially that part of biology which is spoken of as behavior.

This change of interest is probably more radical than it appears at first glance. It really represents an entirely different approach to things. The older psychology began with the study of the function of parts of the organisms, isolated responses (witness the work on sensations and memory) and then attempted to put these parts together. The error was made in neglecting the fact that the integration of parts often produces something—a novelty (Holt)—which could never be predicted from the study of the function of the parts alone. This older psychology was further characterized by a complete unwillingness to see the biological aspects of the organism's reactions, the place of the reactions in the life situations.

The trend of present day psychology stands in marked contrast to this older view. The tendency is now to begin with the study of the responses of the total organism—intact—and in the situation in which it ordinarily finds itself. Here the biological aspects of the problems stand decidedly to the fore as is evidenced by the general current usage of such terms as adaptation, responses, reactions, adjustments. It is the behavior of the organism that is of most interest, what the organism *does*, and how it *works*.

By what the organism does, is meant simply the description of all of the operations and activities involved in the adjustment of the organism to its environment. This would include the description of the objects in the environment responded to, the nature and kind of responses made to these objects, the various activities elicited by these objects. Further this would include also an account of the interrelation of these different activities, hunger, sex, social and work activities, for instance, the rôle played by each, the relative importance of each in the life adjustment of the organism.

The problem of how the organism *works* deals with the more dynamic aspects of behavior. This requires in the first place the determination of the origin of the organism's activity, what it is that *drives* it, so to speak, about in the environment. Further, a knowledge of the working of an organism requires a description of how the various specific responses are set up as the organism is driven about in the environment, how these responses are knit together. Here belongs also a knowledge of how the development and knitting together of the responses are affected by such factors as early frights, shocks, trauma, distortions and limitations of activities.

At present these problems can not easily be attacked in humans for obvious reasons, despite the fact that many abnormal patients may be considered as Adolf Meyer so interestingly suggests, as "experiments of nature." In most humans the early determining factors are rarely definitely known and controlled. Because of these difficulties recourse must be had for the present to study of the behavior of animals, where the life situations are after all very much less complicated, and where the activities and reactions may be changed and distorted at will under controlled conditions.

It is largely for the solution of problems of this nature that animal psychology must be looked to for help in the future. Work in this field is at present at a very low ebb, chiefly for the reason that investigators have limited their interests almost completely to the study of the part reactions of animals (reactions to lights, colors, sounds, learning problems) and have entirely neglected the broader biological aspects of the lives of animals.

The work presented in the following pages represents an attempt to attack these problems from the angle of the life and responses of the whole organism. The attack is made on the most easily approachable and least difficult points. It includes only a small part of the total behavior problem, the study of gross bodily activity before it has become specifically connected with any of the many complicated features of the environment. The relation of this activity to certain vital factors of the environment, food, temperature, illumination is first examined. This is followed by an examination of the origin of the activity, what it is that causes the animal's activity. Finally the relation of this diffuse undirected activity to one of the animal's most important specific responses, its food-seeking activity (hunger reaction), is examined.

In making this study of the gross bodily activity of the rat the emphasis is laid throughout on what the animals do of their own accord, free from all external stimulation. For after all, there is a marked difference however not well recognized, between what an organism can be made to do and what it does of its own account (internal stimuli). The emphasis is usually placed on the former, that is on the training element—this is true particularly in the whole field of education probably even more so than in the field of animal psychology. Interest has only recently begun to be directed toward the spontaneous activities of humans and animals.

The present work was carried on in the Psychological Laboratory of the Johns Hopkins University under the direction of Dr. John B. Watson. I am deeply indebted to Dr. Watson for his help and encouragement and for the complete freedom allowed me in carrying on my work. The inspiration to this work came to a very great extent from the numerous suggestive experiments of Cannon and Carlson on the Hunger Problem. It came also from the Behavior work of Jennings on the Lower Organisms and from the many stimulating experiments of Szymanski on Activity Problems. I am very much indebted to all of these workers. I am indebted for help and criticism to Dr. Edwin B. Holt, Dr. Knight Dunlap, Dr. H. H. Donaldson, and Dr. E. Sanford. I am also indebted to my friends Mr. Ging Wang and Mr. David Brunswick for many helpful suggestions and assistance.

I. PERIODIC NATURE OF SPONTANEOUS ACTIVITY

For carrying out the purposes of the following experiments two things were required: (1) A situation as free as possible from all active external stimulation, and (2) an arrangement for recording the activity of animals over long periods of time without in any way stimulating the animals themselves.

The conditions of the first requirement were met in the following way. Noises were eliminated by carrying on the experiments in a room fitted with large double sound-proof doors and very thick sound-proof walls. All avoidable odours were taken care of by a very good ventilation system. The air was always fresh and free from the usual odors found in animal laboratories. The room was made completely impervious to light rays from the outside by placing heavy covering of cloth and many layers of thick opaque paper over the window. Because of the double doors and thick wall the room was also almost completely impervious to temperature changes from the outside. It was possible to maintain the temperature at one constant level for weeks at a time. The conditions of the second requirement were met by means of the construction of small triangular shaped wire cages large enough to permit the animals to move about freely. A photograph of one of these cages is shown in figure 1. This cage is 10 inches high and each side is 14 inches long. It has an aluminum bottom fastened to the cage. The bottom is supported under each corner on a rubber membrane stretched tightly over a large tambour. The tambours are connected together immediately under the cage into one tube which is led to a small Marey tambour, the lever of which records on the smoked paper of a kymograph. By this means every movement of the animal, even the slightest, is recorded on the drum with a single mark. The cage and support are rigid enough to prevent any stimulation arising from shaking of the cage or from insecurity of foot-hold.

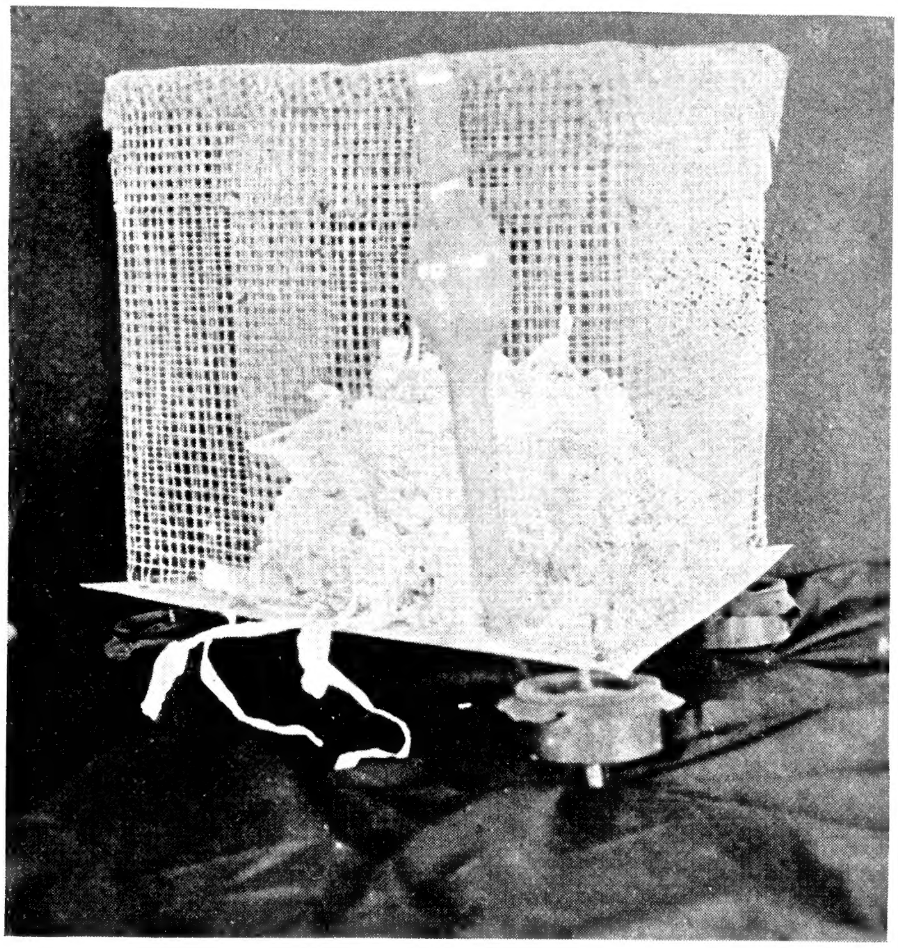

FIG. 1. ACTIVITY CAGE

The attack on this problem of the spontaneous gross bodily activity of the rat was begun with the simple experiment of observing what happens to the activity when the animals are placed in a situation described above free from all external stimulation in constant complete darkness. A typical record

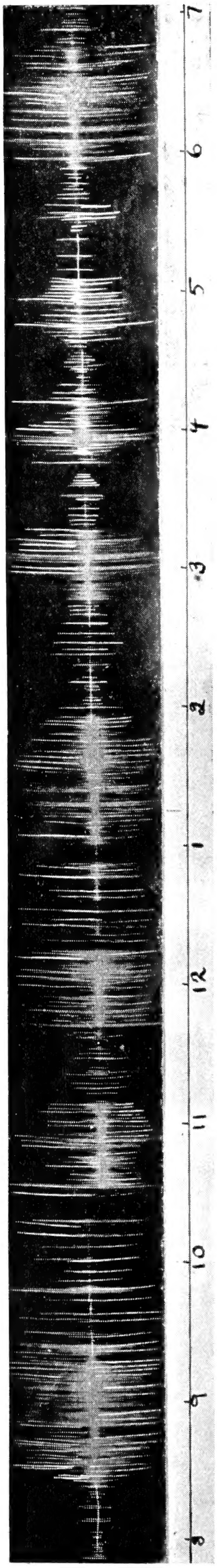

Fig. 2. Record of Spontaneous Activity Showing Regular Recurrence of Periods of Activity

obtained from an animal under these conditions is shown in figure 2. It is seen that the rat is alternately active and inactive and that the regularity of the recurrence of the periods is quite striking. This regularity is brought out even better in figure 23 on page 50. Frequently when the conditions of the experiments are particularly well controlled the differences in the intervals between the periods does not vary more than just a few minutes.

The rate of the periods was found to vary with the age of the animals. In very young animals this rate is most rapid, averaging about fifteen for the twenty-four hours. In old animals the rate averages about ten. The length of the activity periods also shows some variation with age, being longer in younger animals and becoming progressively shorter in older animals.

Szymanski (1) has recently also studied the activity of the rat along with the activity of many different animals, from the simplest insects to the human infant. He used an "Aktograph" for his work on rats—a device very similar to the activity cage described above, except that it is supported on springs and registers activity directly with a lever rather than pneumatically. Szymanski found that the activity of the rat is divided into ten periods per twenty-four hours. What was found in the experiment above seems to agree fairly well with this result, except that Szymanski makes no statement as to the age of the animals that he used for his experiments. He did not notice the great regularity of the recurrence of the periods probably for the reason that he made no attempt to keep the conditions of the experiment constant over longer periods of time. He did his work in an ordinary room subject to the daily changes of temperature and illumination due to the day and night on the outside.

For the reason that the rat shows a number of periods during the twenty-four hours Szymanski speaks of it as a polyphasic animal in contrast to the monophasic animals, like the human adult for instance, which show only one long period of activity and one period of inactivity during the twenty-four hours. That this classification is of somewhat doubtful value, and that it describes their reactions to external stimuli rather than the function of any mechanism inherent in the organism itself may be brought out by the consideration of some experiments on the human infant and adults carried out in the Phipps Clinic Psychological Laboratory during the past year by Miss Tomi Wada of Columbia University (11).

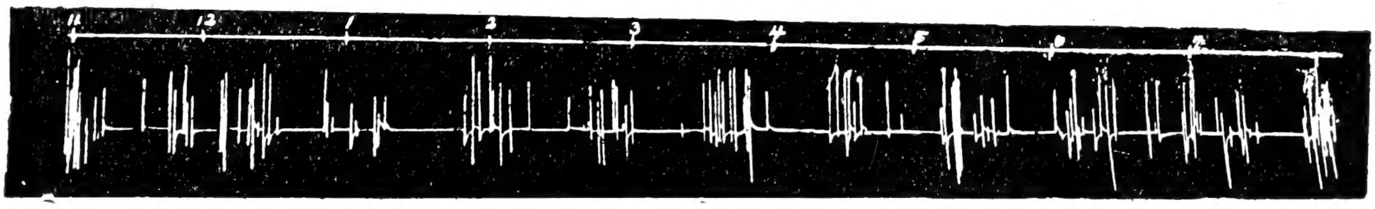

FIG. 3. RECORD OF SPONTANEOUS ACTIVITY OF TEN MONTHS HUMAN INFANT DURING UNINTERRUPTED SLEEP

Time in hours. From work of Miss Tomi Wada

Miss Wada was able to confirm on humans what was found in the experiments on rats. She used the same technique that was employed in the rat work. In the human infant she found that the same regularity of the alternation of the periods of activity and inactivity prevails. She obtained her records chiefly during the long period of sleep at night. The frequent interruptions for feeding and bathing etc. make it difficult to obtain records of activity during the day. A typical curve of the activity of a ten months infant during sleep is shown in figure 3. These periods come at the rate of one every fifty to fifty-five minutes. The regularity of these periods is very striking. Miss Wada found further that the activity of the human adult during sleep is also periodic. The interval between the periods in the adult is however considerably longer than in the infant, usually about one and one half to two hours.

Experiments are now being carried on by Mr. Ging Wang in the Hopkins Laboratory on the activity of the newly born rat before it has had any contacts with the environment, before it has ever nursed, in order to establish whether the periods are present at birth or dependent on later environmental influences. The results obtained so far seem to indicate that the activity at birth is continuous and uninterrupted by regular intervals of quiescence.

The probable relation of these activity periods to certain environmental influences (the hunger reactions) as well as to the rest of the behavior of the organism will be discussed in detail in the last two chapters.

II. RELATION OF SPONTANEOUS ACTIVITY TO FOOD

It was found at the beginning of this work that the spontaneous activity of the rat is very intimately related to the food habits of the animal. This relation will now be examined in some detail from the following points of view: (1) what happens to spontaneous activity (simply the amount of activity, disregarding for the moment the periods of activity) when the animal is deprived of all food, when it is starved; (2) how spontaneous activity is distributed over the day with relation to the last feeding periods and also with relation to the time of next feeding (anticipation of feeding).

The general conditions were maintained practically the same as above. The laboratory was kept constantly either illuminated or darkened over longer periods of time. The temperature was kept constant at 23°C. All noises and odors were eliminated.

The animals were fed punctually at a certain time each day (in most of the experiments at twelve noon). Food was placed in each cage in specially arranged receptacles and left there for twenty-five minutes. Then all of the remaining food was carefully removed. This method of feeding gave each animal plenty of time to satisfy its hunger under fairly natural conditions. It also ensured an accurate control of the amount of food eaten from day to day. Actual weighing of the food showed that the amount eaten in twenty minutes remains almost constant from day to day. The animals developed normally on this method of feeding.[1]

For the first part of the experiment eight animals were used. Normal activity records were taken for five days preceding the beginning of starvation. Four of the animals of this group were also deprived of water after the five days in order to obtain additional information on the relation of activity to water intake.

The amount of activity per day was obtained by counting the marks made on the smoked paper by each movement of the animal in the activity cage described above. The kymograph was set running just fast enough to enable the marks to be recorded individually.

Three of the animals starved but permitted to have water all the time showed a definite increase in activity for the first two to three days after the beginning of starvation and then a steady marked decrease to a point of almost complete inactivity on the eighth day. All of the animals deprived of both food and water showed a steady marked decrease in activity immediately. This group reached the point of complete inactivity already on the fifth day. The results of this experiment are shown in figure 4 where the days of the experiment are given on the abscissae and the total amount of activity per day in activity units (single

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[1] In this present work a synthetic diet was used after the formula of Dr. E. V. McCollum of the School of Hygiene, Johns Hopkins University. This is an excellent diet. For behavior work on the rat it is ideal.

Flour (graham)	72.5
Casein	10.0
Milk powder (skimmed)	10.0
Calcium carbonate	1.5
Salt	1.0
Butter fat	5.0

The importance of using a good diet for all animal behavior work was convincingly demonstrated by the findings of Dr. E. V. McCollum in connection with work on feeding problems. He found that the maternal reactions, nest-building, caring for young, nursing, are absent in animals fed on poorly balanced diets especially diets low in proteins. These animals often eat their young.

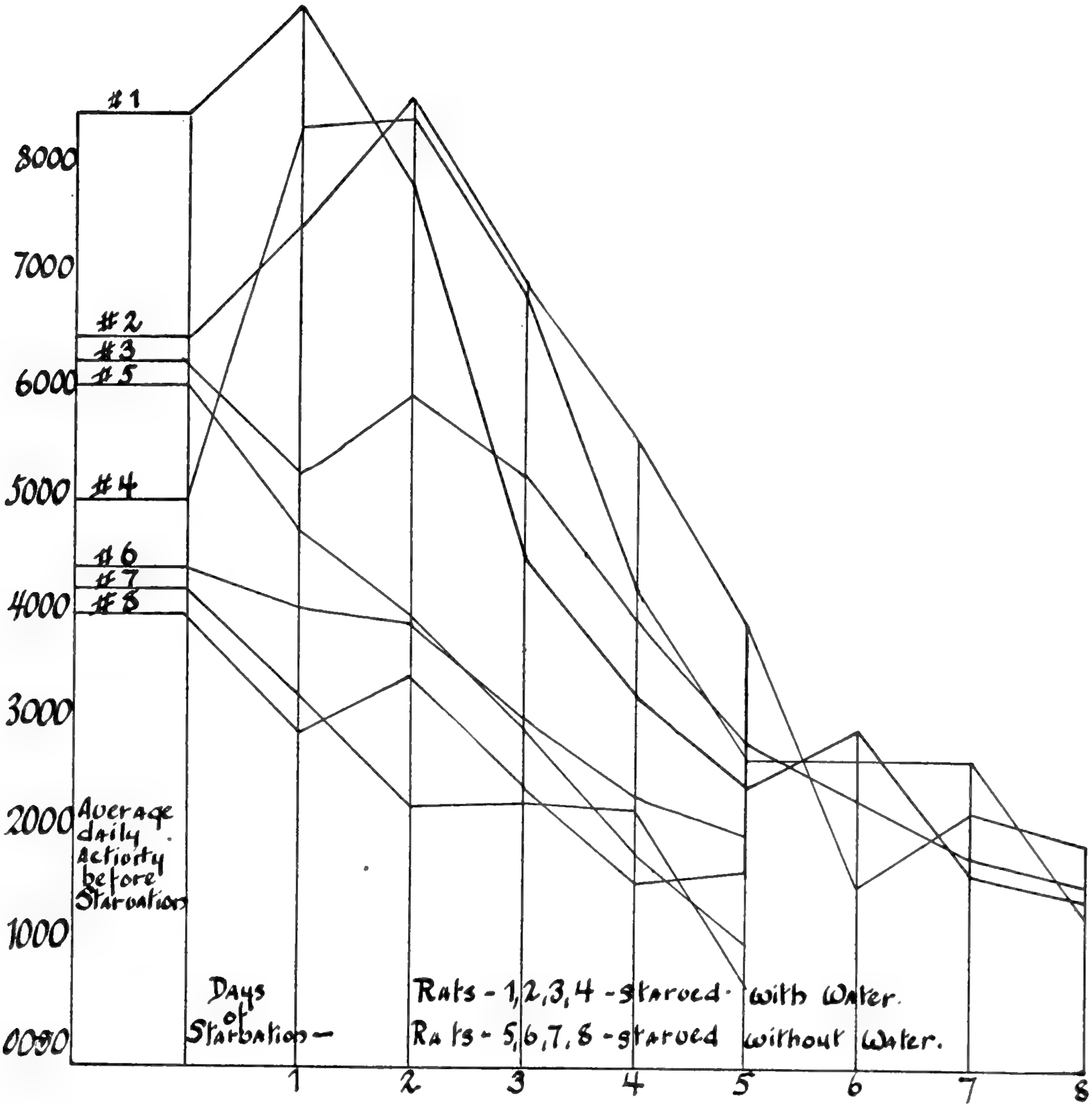

FIG. 4. STARVATION EXPERIMENT

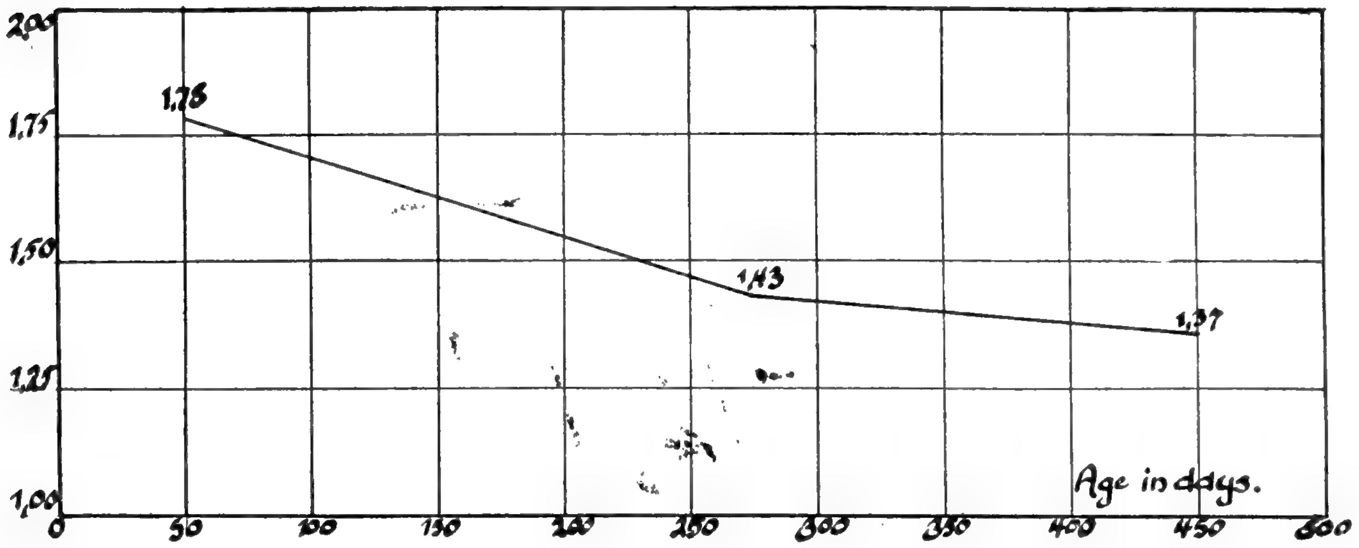

FIG. 5. RATIOS OF TOTAL AMOUNT OF ACTIVITY DURING FIRST AND SECOND TWELVE HOUR PERIODS FOLLOWING SINGLE DAILY MEAL

marks on the kymograph paper) on the ordinates. The average daily activity for the five days preceding the experiment is given on the first ordinate.

In the next experiment on the distribution of activity with relation to the time of feeding it was first undertaken to determine simply how the amount of activity of the first half of the day (the first twelve hours after the feeding period) compares with the activity during the second half. It was found that the activity during the first twelve hours is very much greater than during the second twelve. But the ratio of the amount of activity during the first twelve hours to the activity during the second was found to depend on the age of the animal. This is shown in figure 5 where the age in days is given on the abscissae and the ratio of the amount of activity during the first and second halves of the day are given on the ordinates. It is seen that the very young animals are almost twice as active during the twelve hours immediately following the daily meal than during the next twelve. In the very old animals the amount of activity during these two periods is almost evened out. This curve is based on records from thirty-five animals of three different ages.

When instead of dividing the twenty-four hours following the time of feeding into two twelve-hour periods they are divided into one hour periods, the curve of the distribution of activity has a very characteristic form. Such a curve is shown in figure 6. This curve is based on the records obtained from forty animals 250 days old. In this figure the time of the day is indicated on the abscissae in hours, while the amount of activity per hour is indicated on the ordinates. The animals were fed at 12 o'clock noon. The room was kept in constant illumination. It is seen that immediately following the daily feeding period there is a period of relative inactivity lasting from four to five hours. Then there follows a period of very intense activity for eight to ten hours. This is followed in turn by a period, lasting from five to seven hours, of almost complete inactivity. During the last two to three hours of the twenty-four the activity increases very rapidly again right up to the time of the next feeding period.

In order to avoid misunderstanding it may be well to emphasize here that this curve is a composite curve made up of the individual curves of forty animals. The individual curves of course look rather different. A typical individual curve is shown in figures 17 and 18 on pages 33 and 34. In these curves the alternation of periods of activity and inactivity stands out very clearly. These periods give the curves a very ragged and irregular outline. The general form of these curves corresponds however to that of the composite curve shown in figure 6. During the inactive parts of the curve the amount of activity in each activity period is relatively very small but the periods are present nevertheless. The discrepancy between Szymanski's results and the results presented in the previous chapter on the number of activity periods per day may be due to the fact that Szymanski failed to take these small periods into account. The importance of these small periods will be brought out in another place.

The activity distribution curve shown in figure 6 was for animals 250 days old. The form of this curve becomes very much modified in very young animals and as well in very old animals. In the former the "hump" of activity begins almost immediately after the daily feeding period, figure 7, while in the latter its onset is very much delayed. The "hump" of activity is most striking in animals about 200 days old. After that age it becomes less and less marked until in old age, over two years, the curve becomes smoothed out and the hump is obliterated. This is shown schematically in figure 8.

In order to make certain that the shape of the activity distribution curve shown in figure 6 did not depend on any external factors, for instance very slight changes of illumination imperceptible to the human eye due to the daily change of light and darkness on the outside of the laboratory, or else that the curve did not depend on the general city noises and sounds of the day, the time of feeding was changed from 12 o'clock noon to 12 o'clock midnight, also to 8 o'clock in the evening. In all cases the shape of the curve remained practically the same. This was true also when records were taken during constant illumination which seems rather conclusive evidence against changes in illumination having anything to do with results obtained.

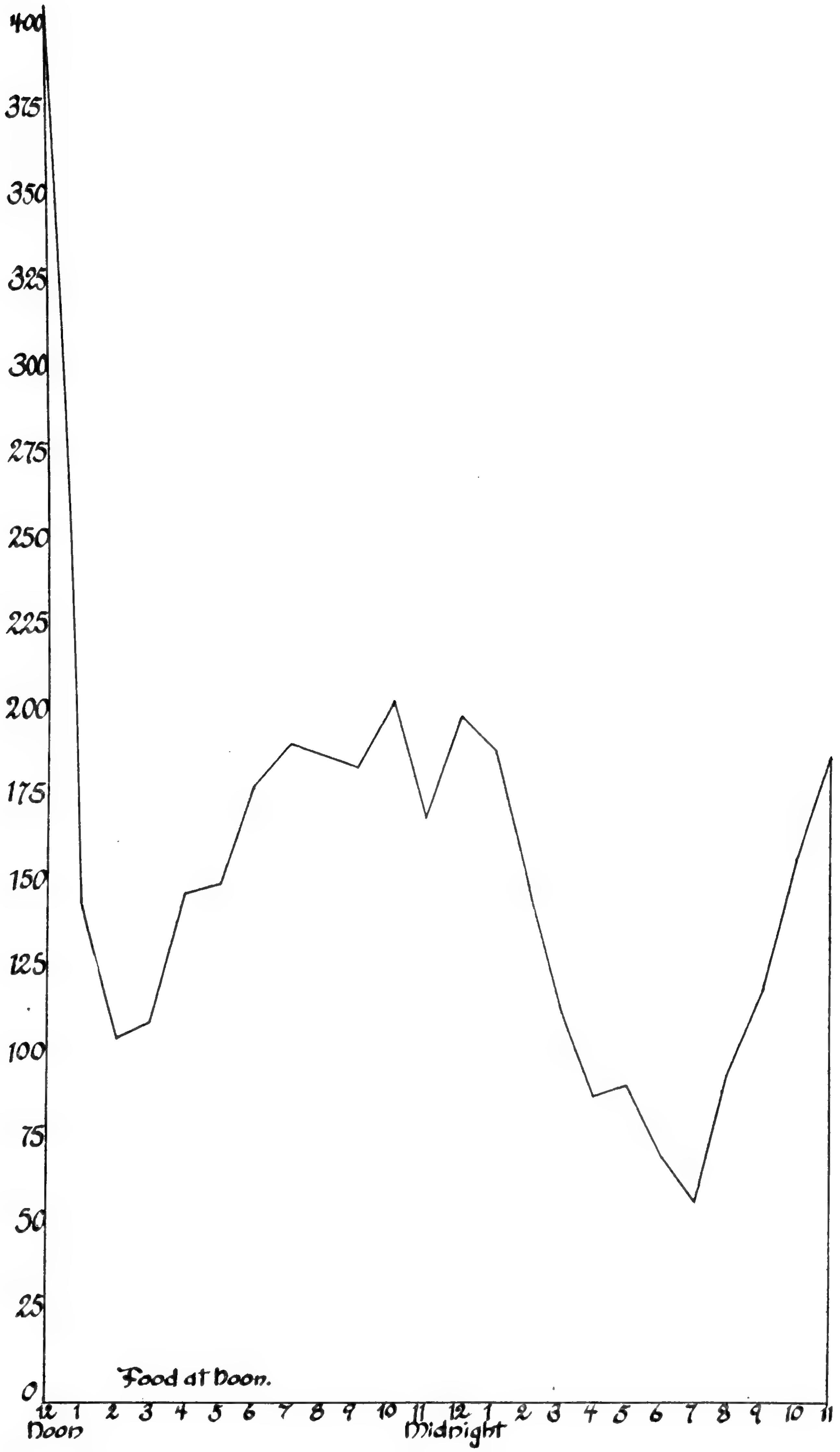

FIG. 6. CURVE SHOWING DISTRIBUTION OF SPONTANEOUS ACTIVITY DURING TWENTY-FOUR HOURS WITH RELATION TO TIME OF FEEDING

Time is given on the abscissae in hours. The amount of activity during each hour is given on the ordinates. For animal 250 days old.

These experiments show that the rat is naturally inactive for a time after eating, and that it does not become active again of its own accord for several hours afterwards. These results bear out essentially the observations man has made on his own behavior, for there is a general saying that it is not a good thing to

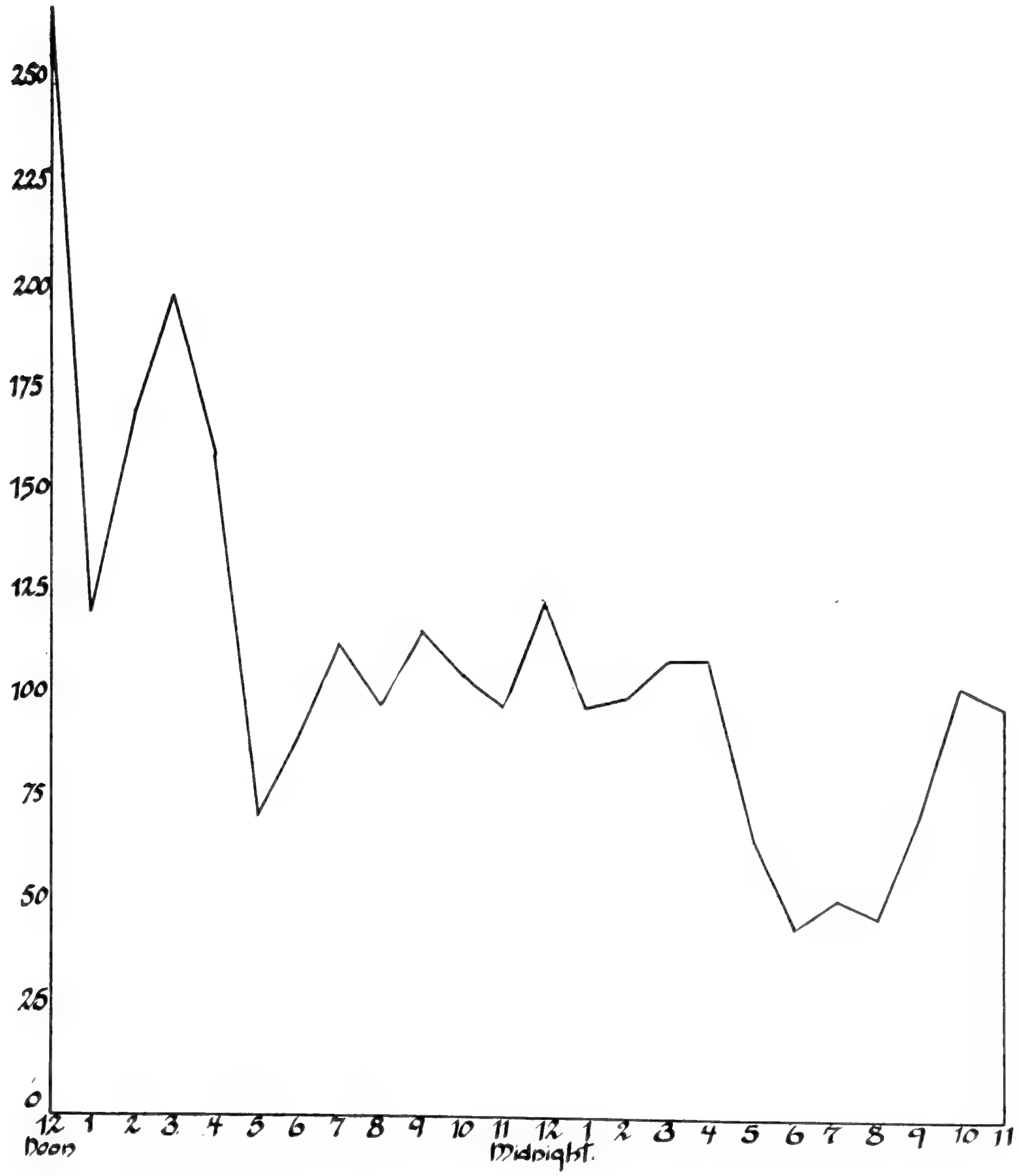

FIG. 7. CURVE SHOWING DISTRIBUTION OF SPONTANEOUS ACTIVITY WITH RELATION TO TIME OF FEEDING

For animals about forty days old

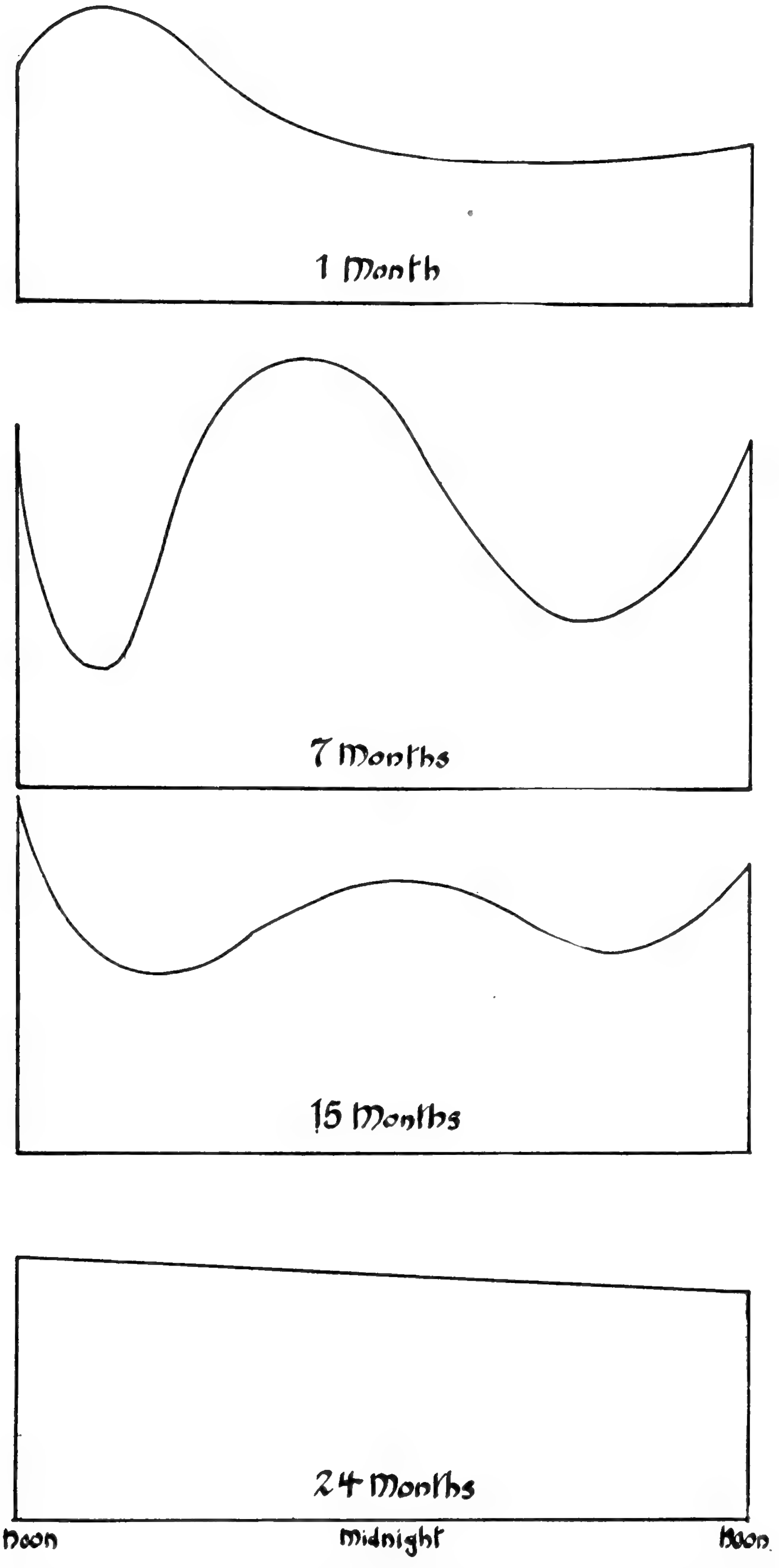

FIG. 8. SCHEMATIC CURVES FOR DIFFERENT AGED ANIMALS SHOWING HOW SPONTANEOUS ACTIVITY IS DISTRIBUTED OVER THE TWENTY-FOUR HOURS WITH RELATION TO THE TIME OF THE SINGLE DAILY FEEDING

work directly after eating. Sayings of this nature are frequently apt to be colored by fictions and superstitions, but this one seems to be based on fact. If the same curve holds for man that holds for the rat it would then seem advisable for man when he has work to do, to do it during the period of maximum spontaneous activity, that is when the body coöperates, rather than during the period of natural inactivity when the body does not coöperate.

III. RELATION OF SPONTANEOUS ACTIVITY TO EXTERNAL TEMPERATURE

Temperature and illumination are factors which are present in the environment of all organisms at all times and which can never be eliminated. They are vital factors. They are present in all situations from the simplest to the most complex, so that a thorough knowledge of their relation to activity is of prime importance for the solution of any kind of behavior problems.

The difficulties of studying the relation of behavior to external temperature in animals are many. A rather highly specialized equipment and technique for obtaining and controlling temperatures at all levels are absolutely essential. Without them conclusive results are obtained only with the greatest difficulty. In the present work many different temperature experiments were tried, but with the exception of one or two all of them failed to give satisfactory results.

The following experiments deal only with the modifications of the normal activity distribution curve, described in the previous chapter, with relation to external temperatures. The conditions of these experiments were essentially the same as for the others. The experiments were carried out over long periods of constant illumination and constant complete darkness. Higher temperatures than the normal 23°C. were obtained by means of two electric heaters, while temperatures lower than normal were obtained from natural sources during the cold months of winter.

The results of these experiments showed that the characteristic shape of the activity distribution curve is very definitely affected by changes in external temperature. These modifications affect chiefly the position of the period of maximum activity—the "hump" in the curve. In a comparatively low temperature 10° to 15°C. this period of maximum activity begins almost immediately after the daily feeding period. The usual interval of relative quiescence following the taking of food is absent. This may be seen in figure 9. This curve is based on the records of four animals of from 200 to 300 days old, taken in an external temperature of 12° to 13°C. In a temperature considerably higher than the normal 29° to 30°C. on the other hand, the onset of the period of activity is very much delayed. The interval of quiescence following the taking of food is greatly lengthened and the "hump" of activity is not as conspicuous as before. This may be seen in figure 10 based on activity records from animals of middle age about 300 days in an external temperature of 29° to 30°C.

It will be noticed that the form of the activity curve for middle aged animals taken in a cold external temperature is very similar to the activity curve for very young animals taken at a normal temperature. In both cases the period of maximum activity begins immediately after the taking of food. Compare figure 8 and figure 7. Conversely in higher temperature it will be noticed that the form of the activity curve of the young animals becomes very much like the normal curve for middle aged animals. In both cases the period of maximum activity falls near the middle of the twenty-four hours.

The attempt was made to throw some light on quite another phase of the relation of activity to external temperature by the determination of the external temperature in which an organism is most active. In the previous experiments 23°C. was chosen quite arbitrarily as the normal temperature. It was found that both below (13°C.) and above (30°C.) this temperature the amount of activity per day was diminished. Somewhere between these two extremes there must be a point at which the animals are most active, a "critical" point of activity. It was not possible to make the determination of this point for the rat for the reason that the means at hand of regulating the temperature of the laboratory were not sufficient to obtain anything more than the very crudest gradations in temperature.[2]

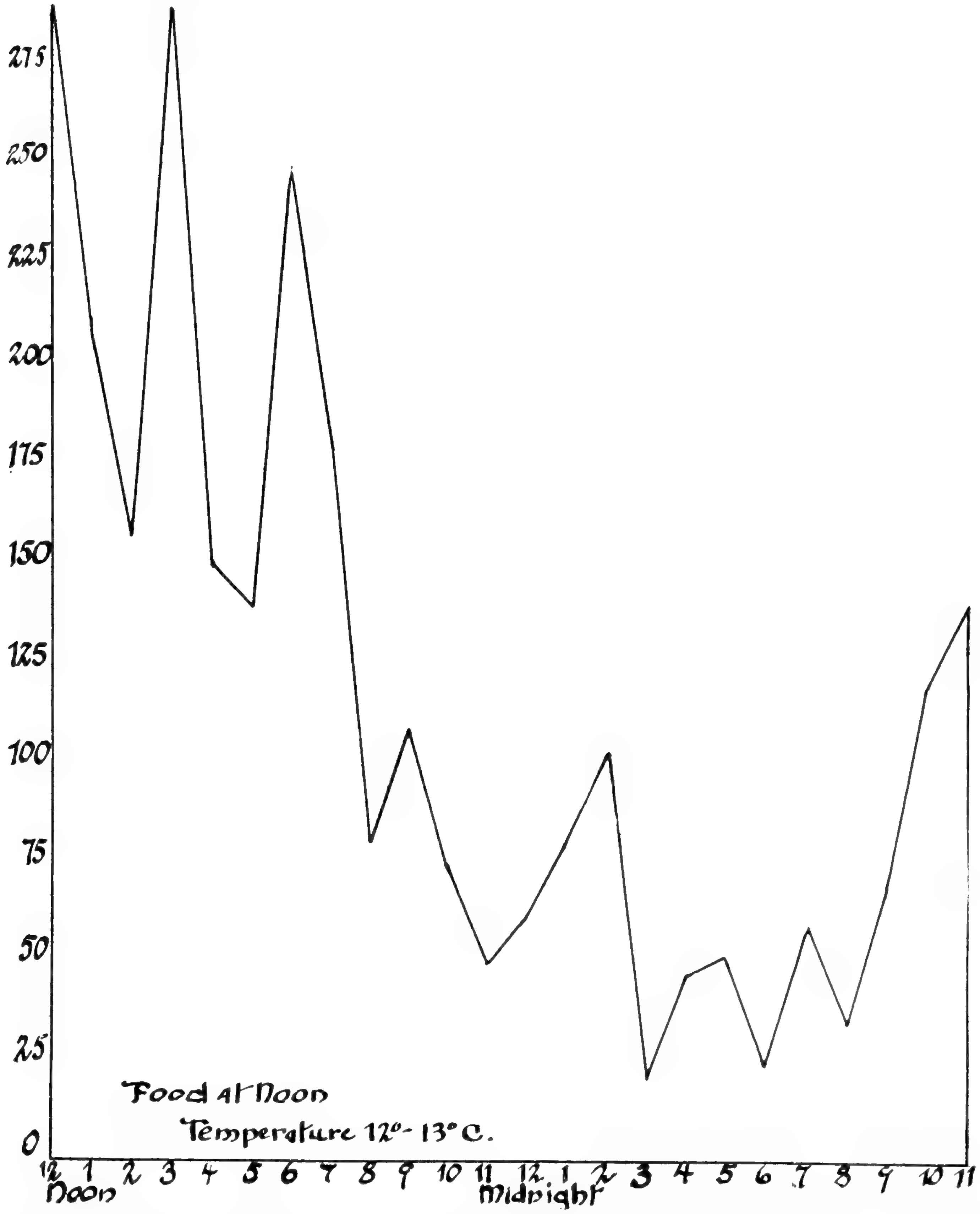

FIG. 9. DISTRUBUTION OF SPONTANEOUS ACTIVITY WITH RELATION TO TIME OF DAILY FEEDING IN A LOW EXTERNAL TEMPERATURE

Age of animals 200 to 300 days

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[2] The attempts that were made to correlate activity with barometric pressure and humidity were not successful. It is very difficult to control these factors without an equipment especially adapted to this purpose.

The determination of this critical point of activity might be of help to the physiologist in solving several of the problems of animal heat. Work in this field does not seem to have progressed very much since the nineties chiefly for the reason that the

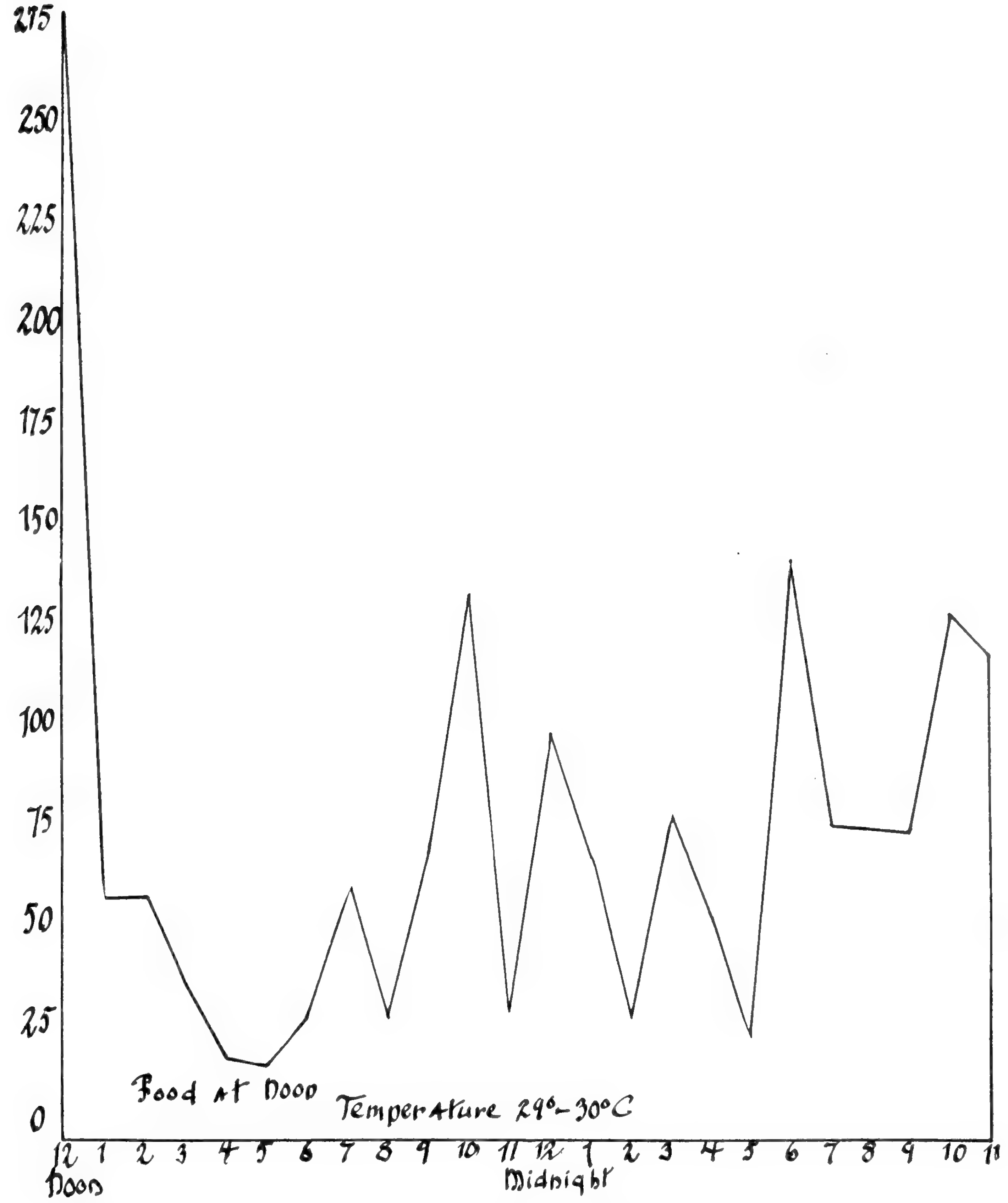

Fig. 10. Distribution of Spontaneous Activity in a High External Temperature

Age of animals about 300 days

behavior side of the problem—the total reactions of the organisms to different temperatures—has been neglected. This may be brought out by a consideration of the problem of the relation of metabolic processes of the body to external temperature. Physiologists speak of a critical point of the temperature of the air surrounding an organism at which the metabolism of the organism is at a minimum. The increase in metabolism below this point is brought about by chemical processes, while the increase above this point is brought about either by vaso-motor or by respiratory changes, or by muscular or glandular changes. Nothing is said however regarding the organism's activity, its total reactions to the changes in temperature. Indeed in most of the experiments on this problem the animals are confined and tied in very small chambers where not even the slightest movement is possible. Without this information of the behavior of total activity the physiologist's study of the problem must remain on a purely static level.

IV. THE RELATION OF SPONTANEOUS ACTIVITY TO ILLUMINATION

In the environment of all animals and at all times there is some degree of illumination or else no illumination at all, that is complete darkness. It is of greatest importance in studying behavior problems to know just how these ever present factors affect the activity of organisms. On the basis of the present knowledge on this subject animals are classed as being either nocturnal or diurnal, according to whether they are more active at night or during the day. This classification as it stands at present is based not only on the reactions of the animals to the light and darkness of the day and night, but also on the reactions of the animals to other factors of their environment, such for instance as possibilities of getting food, attacks from other animals, etc. This is a decided limitation. There is still a further limitation of this classification, in that it places animals in either one group or the other and does not tell just to what extent the animals are more active in the dark than in the light, or the converse.

In the present experiments the attempt is made to determine whether the rat is nocturnal, and also just to what extent it is nocturnal; that is just how much more active it is in the dark than in the light.

This experiment was carried on in the following way. The laboratory in which the records were taken was alternately illuminated and completely darkened every twelve hours. The amount of activity (in activity units) in these two periods was measured. Then the ratio of the amount of activity in the dark period to the amount in the light period was taken as a numerical indication of the active extent to which the animal may be said to be nocturnal.

All conditions were kept the same in both periods, except the conditions of giving food. The animals were fed just once per day just as was done in all of the previous experiments. Records were taken in two series. In one series the animals were fed at the beginning of the dark period. In the other they were fed at the beginning of the light period. It proved necessary to take two series of records in this way because of the fact demonstrated in figure 5 above that spontaneous activity is not equally distributed over the twenty-four hours with relation to the time of feeding. There it was shown that the amount of activity in the first twelve hours following the daily meal is very much greater than during the second twelve hours. Thus in the first series of records the effect of the food is added to the effect of the darkness, while in the second it is subtracted. Records obtained in this way are shown in figure 11. Curve A gives the results in the first series in which the animals were fed at the beginning of the dark period. The ratios of the amount of activity in the dark period to the amount in the light period are given on the ordinates and the ages of the animals are given on the abscissae. The ratios for animals fed at the beginning of the light period are given in Curve B. The great discrepancy between these two curves is quite obvious.

The method by which the effect of food was eliminated may be brought out most simply by the following example. It will be noticed in the curves *A* and *B* in figure 11 that the animals

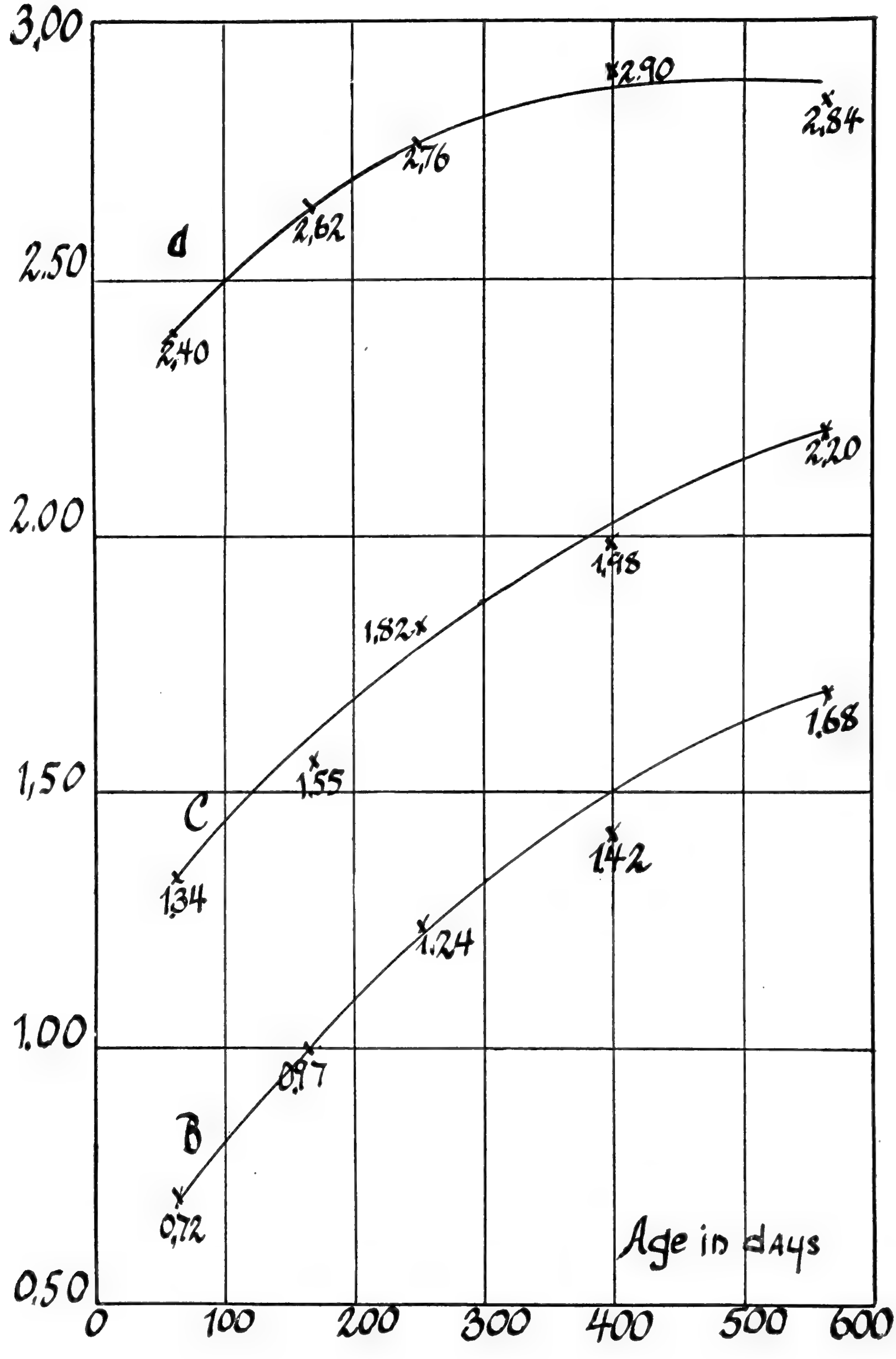

FIG. 11. CURVES SHOWING RATIOS OF NOCTURNAL TO DIURNAL ACTIVITY AT DIFFERENT AGES.

Figure shows that these animals become more nocturnal with age become progressively more active in the dark than in the light as they grow older. At 400 days when the animals are fed at the beginning of the dark period they are 2.90 times more active in the dark than in the light. When fed at the beginning of the light period they are only 1.42 times as active in the dark. This is shown in a diagram in figure 12. In the first series the ratio of the activity in the dark to activity in the light, 2610/900 is 2.90. In the second series this ratio, 2090/1460, is 1.42. The effect of the food was eliminated then by taking the total amount of activity in the dark periods in the two series to the total amount in the light periods (2610+2090) 4700/(900+1460) 2360 or 1.99. Ratios obtained in this way are shown in curve *C* in figure 11.

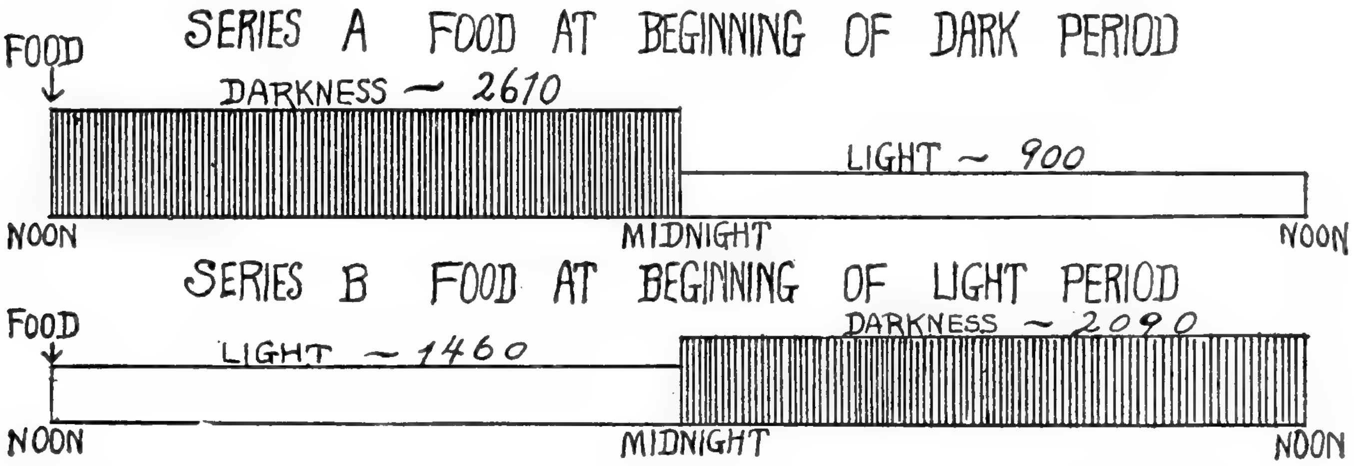

FIG. 12. DIAGRAM SHOWING HOW CURVES IN FIGURE 11 WERE OBTAINED

This curve shows conclusively that the rat is more active in the dark than in the light, in other words that the rat is a nocturnal animal. This curve shows further that the rat becomes progressively more nocturnal as it grows older. At 60 days it is 1.34 times more active in the dark than in the light. From this age on this ratio increases rapildy until at 600 days the animal is more than twice as active in the dark as in the light.

Whether or not nocturnal and diurnal tendencies change with age in other animals and in man is not definitely known. It is generally said that man also becomes more nocturnal in his habits with age. There seems to be some truth in this statement for it is well known that at birth and for a considerable time afterwards the human infant is almost totally inactive in the dark.

Only as he grows older does he begin to stay awake in the dark. Gradually he becomes more and more a night animal until in ripe old age much of his activity is manifested during the hours of twilight or the night. The progressive tendency toward nocturnal habits with age in the rat may be explained in a number of ways, all of them, however, quite unsatisfactory. First, as the animals grow older they find that they can forage and climb about more freely, with less molestation at night than during the day. This would certainly be true in part anyway for animals living in the open, but for animals living in the laboratory all the time from birth on, it seems quite questionable. Then from the point of view of the recapitulation theory, it might be said that these results would show that the Albino belongs to a species which is in the progress of changing its habitat from places on the surface of the earth, trees and bushes, to burrows and holes in the dark under the ground. According to this theory as it is generally understood the diurnal activity would represent a former stage in the life of the rat, just as it is said that the grasping reflex of the human infant belongs to an earlier stage in the development of man. Such theories do not seem to be very well-founded. A further possible explanation of the progressive change toward nocturnal activity may be sought in the changes of the structure of the eye with age, but about this very little is known.

V. RELATION OF ACTIVITY TO AGE

It was shown in the previous chapters how spontaneous activity of the rat is modified by the intake of food, by temperature and by illumination. It was brought out incidentally in a number of places in these chapters that the expression of activity is also dependent on age. This relation between activity and age will now be examined in more detail. In the first place a determination was made of the actual amount of activity at the different stages of the animal's life. This necessarily included also a determination of the age at which the animal is at its maximum of spontaneous activity.

These determinations were made in three different ways: (1) On the basis of the spontaneous activity in the simple stationary cages, described above. (2) On the basis of the amount of work done in the revolving drums, the total number of revolutions made at different ages. (3) On the basis of the readiness and completeness with which nests are built under normal conditions.

The technique employed in the first method was essentially the same as that described in the experiments above. For the reason that it was not possible to obtain continuous uninterrupted records on a group of rats throughout the entire period of their lives records were taken instead at frequent intervals for fifteen months on a very large group (40) of animals of all different ages (26 to 700 days). Records were taken for five to eight days at frequent intervals. In this way a sufficiently large number of records were obtained for all stages in the development of the rat. Before each series of experiments the animals were given two to three days time or longer in which to accustom themselves to the cages. Twelve of the animals of the group were left in stationary cages all the time in order to eliminate the effects on the activity which might be caused by frequent changes back and forth from the activity cages to the ordinary cages. The effects of these changes on the rest of the group did not prove to be very great. Records were taken always under the same conditions of temperature and illumination.

The relation of activity to age determined by this first method is shown in figure 14, in the curve marked "Stationary Activity Cages." In this curve the age of the animals is shown on the abscissae in days, while the average amount of activity per day in activity units is given on the ordinates in the second column labelled "Activity Units." In this curve it may be seen that at 25 days the rat is quite inactive. From this age to the age of its maximum activity, 175 days, its activity increases very rapidly. After 175 days its activity begins to fall off, slightly at first, then fairly rapidly until at 600 days it reaches the original level of inactivity from which it started.

In the second method ordinary revolving drums were used. They were 12 inches in diameter and 10 inches wide, and revolved very easily as was demonstrated by the fact that 30-gram rats were able to turn them as many as 12,000 times in twelve hours. A photograph of the drums is shown in figure 13. Six such drums were used in this experiment.

By placing the animals in the drums alternately every six hours it was possible to take records on twelve animals at one time. Six animals were always running in the cages while the other six rested in small separate stationary cages. In this way each animal spent twelve out of every twenty-four hours in the drums.

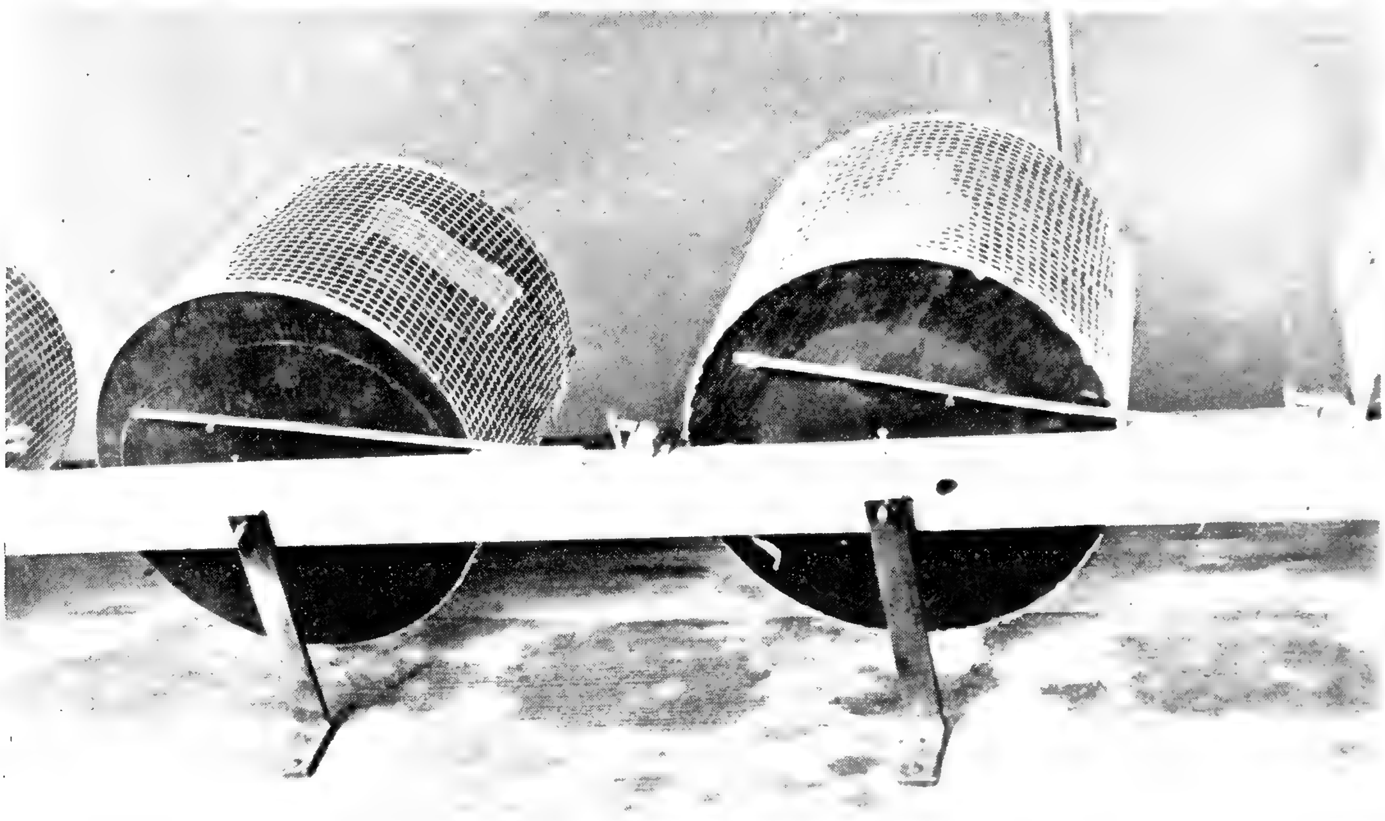

FIG. 13. PHOTOGRAPH OF REVOLVING DRUM

The animals used in this experiment were of six different ages, 30, 100, 210, 250, 450 and 600 days. Records were taken continuously for one month with the exception of an occasional day of rest. Only the scores made during the last twelve days of the experiment are included in the final record for the reason that all of the animals showed very great irregularities during the first part of the month while they were adapting themselves to the drums. A curve based on data obtained in this way is shown in figure 14 in which the age of the animals in days is given on the abscissae, and the number of complete revolutions per day are given on the ordinates.

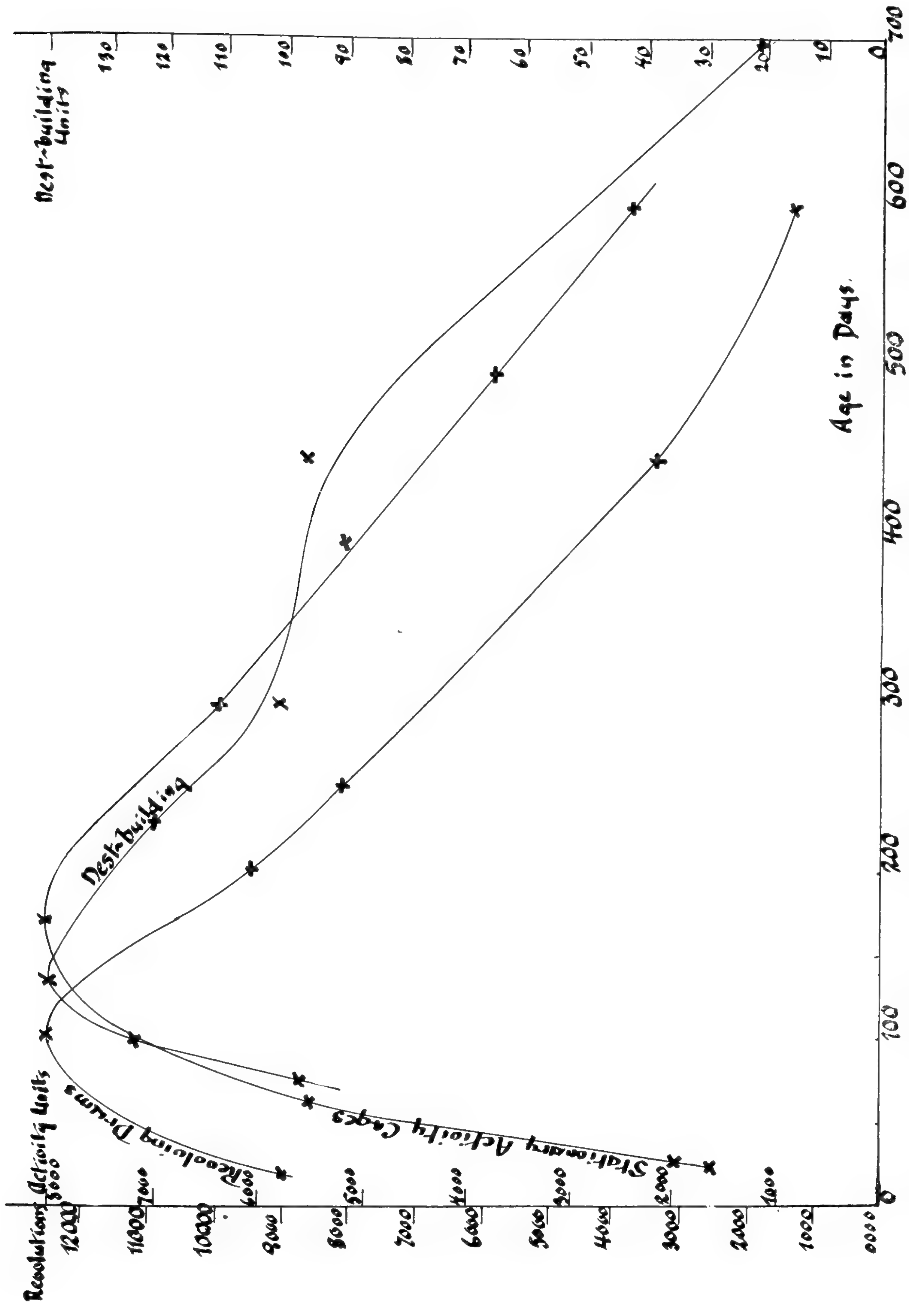

FIG. 14. CURVES SHOWING RELATION OF ACTIVITY TO AGE ACCORDING TO THREE DIFFERENT METHODS

The data from this second method gave the following results. In the revolving drums at thirty days the rat is quite active, as is demonstrated by the high average at that age of 9000 complete revolutions per day. Its activity increases however from this age until at 100 days it reaches its maximum. This confirms the work of Slonaker (2), who found period of maximum activity lies between 81 to 120 days. After 100 days the rat's activity falls off very rapidly so that at 240 days it is already less active than it was at thirty days, and at 600 days it is almost completely inactive, averaging at this age about 1000 revolutions per day.

In the third method the relation of activity to age was determined on the basis of the completeness with which the rat builds a nest for itself at different ages under ordinary conditions. For this purpose a standard situation was arranged in which the rat normally builds itself a nest. A square cardboard frame 3 feet wide and 1 foot high was placed on the floor and covered with wire cloth. A definite number of small strips of crepe paper (200) all of the same size and shape were evenly distributed over the floor on the inside of the frame. Four such frames were used. A single rat was placed in each frame for a given length of time, usually about twelve hours. At the end of this time the number of strips of paper gathered into a nest was counted. The ratio of this number to the total number available (200) was taken as measure of the animal's activity. The nests included all strips within a radius of four inches of the densest spot. During this experiment all external conditions were kept constant. It is particularly important to keep the temperature constant for it is well known how easily the nest-building activity is changed and influenced by changes of temperature.

In this way the curve marked "Nest-building" in figure 14 was obtained. The number of strips formed into a nest is given in the column headed "Nest-building Units" at the right side of the curve. This curve is based on the records for three continuous days of twelve animals of six different ages. The irregularity of this curve is very largely due to the very small number of records taken.

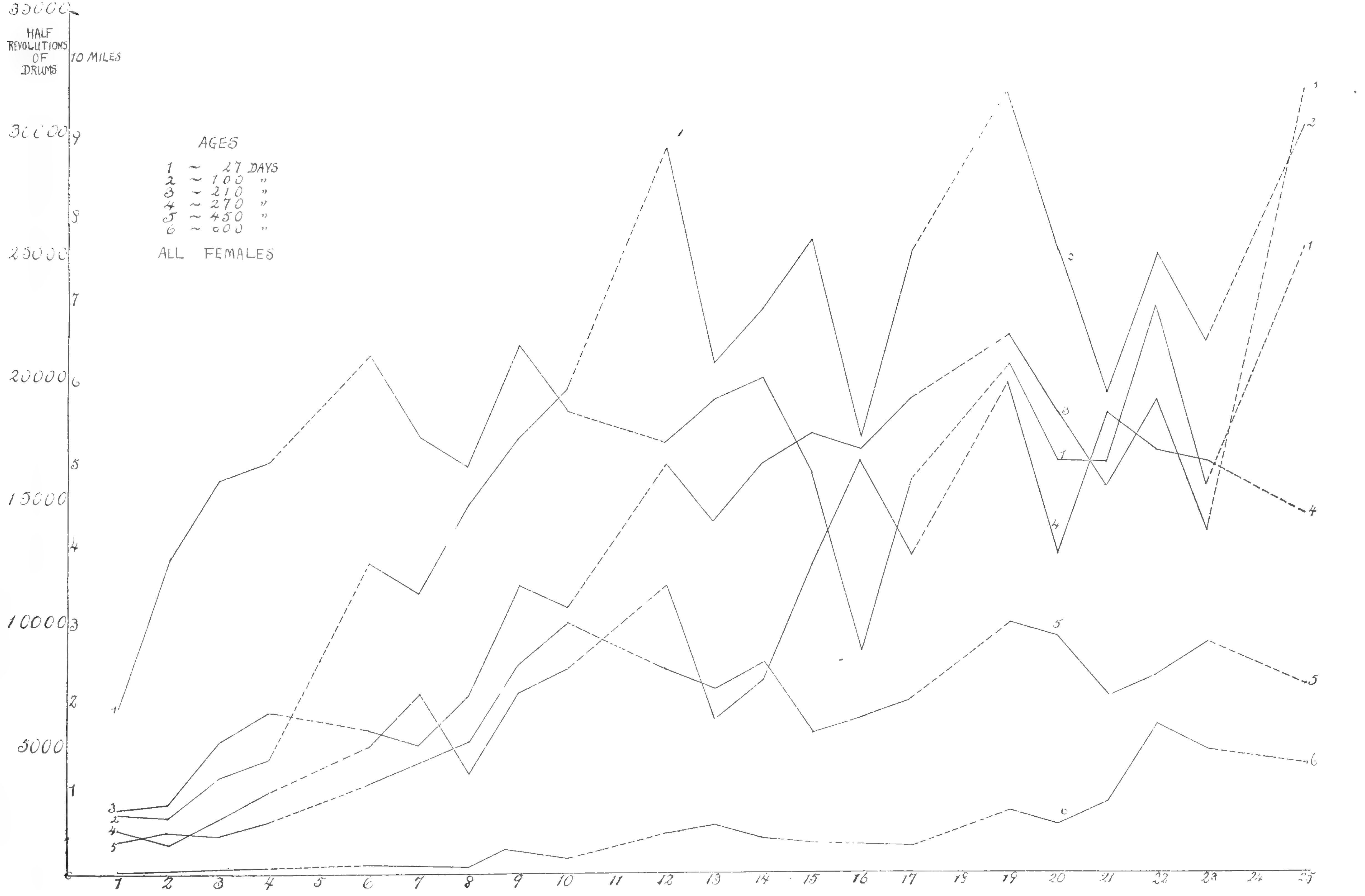

Fig. 15. Revolving Drum Experiment

This curve despite its irregularities has in general the same shape as the curves obtained by the other two methods. The age of maximum activity determined in this manner lies near 135 days, which is about half way between 100 and 160 days, the ages of maximum activity determined by the other methods.

Another aspect of this problem of the relation of activity to age was brought out incidentally in connection with the experiments on the revolving drums described above.

It may be well to emphasize at this point that there is a tendency among workers interested in the activity of animals to confuse the activity of an animal due to external stimulation with the activity which manifests itself more or less spontaneously when the animal is free from all active external stimulation. Due to this confusion a number of workers say that the rat is most active at the age of thirty to forty days. They base this opinion very largely on the fact that every time they enter their laboratories they find animals of this age active, while older animals remain inactive. They fail to take into consideration that the greater activity of the younger animals at these times may be due simply to the fact that these animals may be more sensitive to any external stimulation, noise made in entering the laboratory, and that during the rest of the time when they are not stimulated they may remain quite inactive. That is to say that younger animals are spontaneously less active than older animals, but that they are more sensitive to external stimulation.

The differences between these two kinds of activity are brought out by the records of the activity of six animals of six different ages in the revolving drums. These drums both serve to stimulate the animals and at the same time to record the activity in reaction to the stimulation. The stimulating effect of the drums is well known and can easily be demonstrated for every movement even the slightest destroys the equilibrium and causes counter compensatory movements to be elicited. How are animals of different ages affected by this stimulation?

The records of this experiment are shown in figure 15 where the abscissae give the days of the experiment, while the ordinates give the total number of half revolutions made each day and their equivalents in miles. The dotted ordinates indicate that no records were taken on the day preceding.

It is seen that for the first day in the drums—none of these rats of course had ever been in the drums before,—the youngest rat 1 begins with by far the highest number of revolutions (7000) while the second and third youngest come next with 2500 revolutions, the fourth next with 1700, the fifth next with 1200, then the last with 30. This same relation holds for the rate of increase in the daily record for the first part of the experiment.

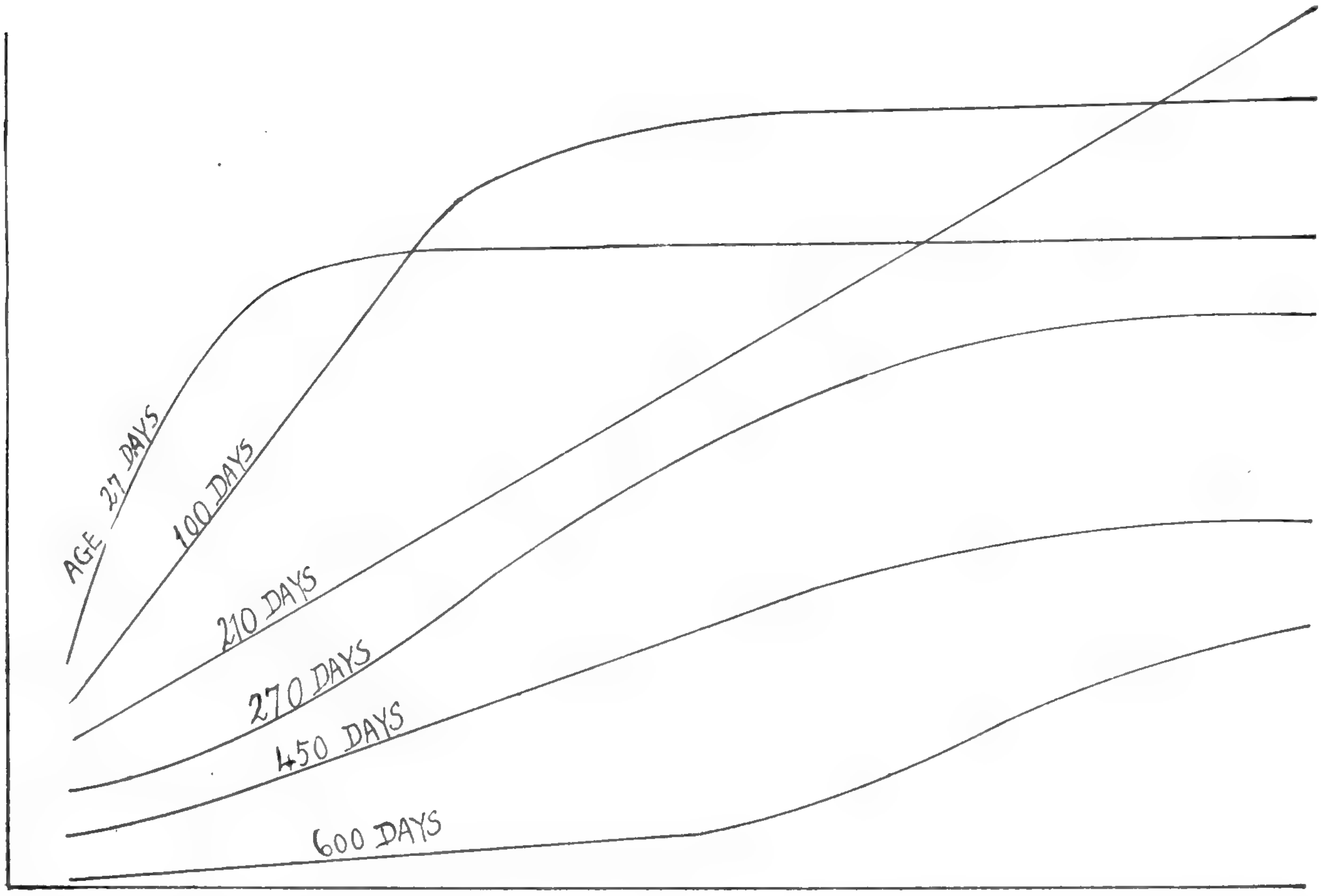

FIG. 16. CURVES SHOWING SCHEMATICALLY THE RESULTS OF THE REVOLVING DRUM EXPERIMENT

This daily increase as well as the general relation of the records of these animals is shown schematically in figure 16.

Were the higher number of revolutions made by the younger rat due to greater activity then it should continue to make higher scores throughout the experiment. But it failed to do this. It was overtaken first by the 100 day rat and then by the 210 day rat. This same thing happened in turn to the 100 day rat. It is also finally overtaken by the 210-day animal. The higher number of revolutions at the beginnning of the experiment and the more rapid increase and arrival at the maximum must have been due to the greater sensitivity of the younger animals to external stimulation. The very old animals were apparently not stimulated in the least by the drums. Their increase in activity from day to day was very gradual and seemed to depend almost entirely on the slow progressive adaptation and adjustment of the whole bodies to the drums.

VI. PERSISTENCE OF RHYTHMS OF ACTIVITY AFTER WITHDRAWAL OF RHYTHMIC STIMULUS

It may be well to add here a preliminary account of two experiments which help to throw further light on the general nature of spontaneous activity but from rather a different angle than in the previous experiments. Only a preliminary account is offered at this time because the experiments were carried out on just a few individuals and no opportuniy has presented itself for confirming the results on larger groups.

The first experiment was carried out in connection with the work described in Chapter II on the relation of spontaneous activity to starvation. In that work the interest was limited only to the changes in amount of activity during starvation. In the present experiment the interest was focused on the changes in the manner of expression of activity changes in the form of the activity distribution curve during starvation. It will be recalled that when the rat is kept in an environment of constant temperature and illumination and fed just once per day at a definite time, the spontaneous activity is distributed in a regular way with relation to the time of the single daily meal. What happens to the shape of this curve when the factor upon which it depends is removed, that is when the animal is starved?

Two animals were used for this experiment. They were kept in the laboratory under conditions of constant darkness and constant temperature for four months preceding the beginning of the experiment. During this time they were fed very regularly and punctually at a certain time just once per day. Care was taken to keep all of the conditions just as constant as possible throughout this entire period.

The records for the two animals are shown in figures 17 and 18. In these figures the time of the day is indicated on the abscissae, the amount of activity during each hour on the ordinates. A record of normal activity was taken on the day preceding the experiment, that is on the day before the animals were deprived of food. The record of the distribution of activity on this day is shown in the top curves marked 'normal'. The shape of these curves corresponds in general outline to the composite distribution curve in figure 6. The records for the following days of starvation show that the general shape of this distribution curve is maintained for three to four days after the removal of food. The curve becomes more and more flattened out with each day of starvation until on the fifth day it is practically a straight line.

In the second experiment similar evidence was obtained. It was shown earlier that the rat is more active in the dark than in the light—and that progressively with age it becomes more and more active in the dark. The spontaneous activity then of animals that live in the open places where they are subjected to the daily changes of light and darkness of the day and night will not be evenly distributed over the twenty-four hours, but will be confined for the greater part to the night hours. This will depend partly of course on the time the animals are fed. When however the food factor is eliminated by leaving the food in the cage all the time, then the activity should be limited even to a greater extent to the night hours. An animal in the open then is alternately active approximately for a period of twelve hours and then inactive for a period of twelve hours throughout its entire life. What happens to these alternating periods of activity and inactivity when the animals are placed in an environment of constant darkness?

This was tried out in the following way. An animal was chosen for the experiment that was fairly old, 650 days, and which was still quite active, and which also had been subjected to the daily change of light and darkness throughout its entire life. This animal was placed in the laboratory in complete darkness. There it was confined in a cage which was somewhat larger than the ordinary triangular cages. This cage had two small exits, one

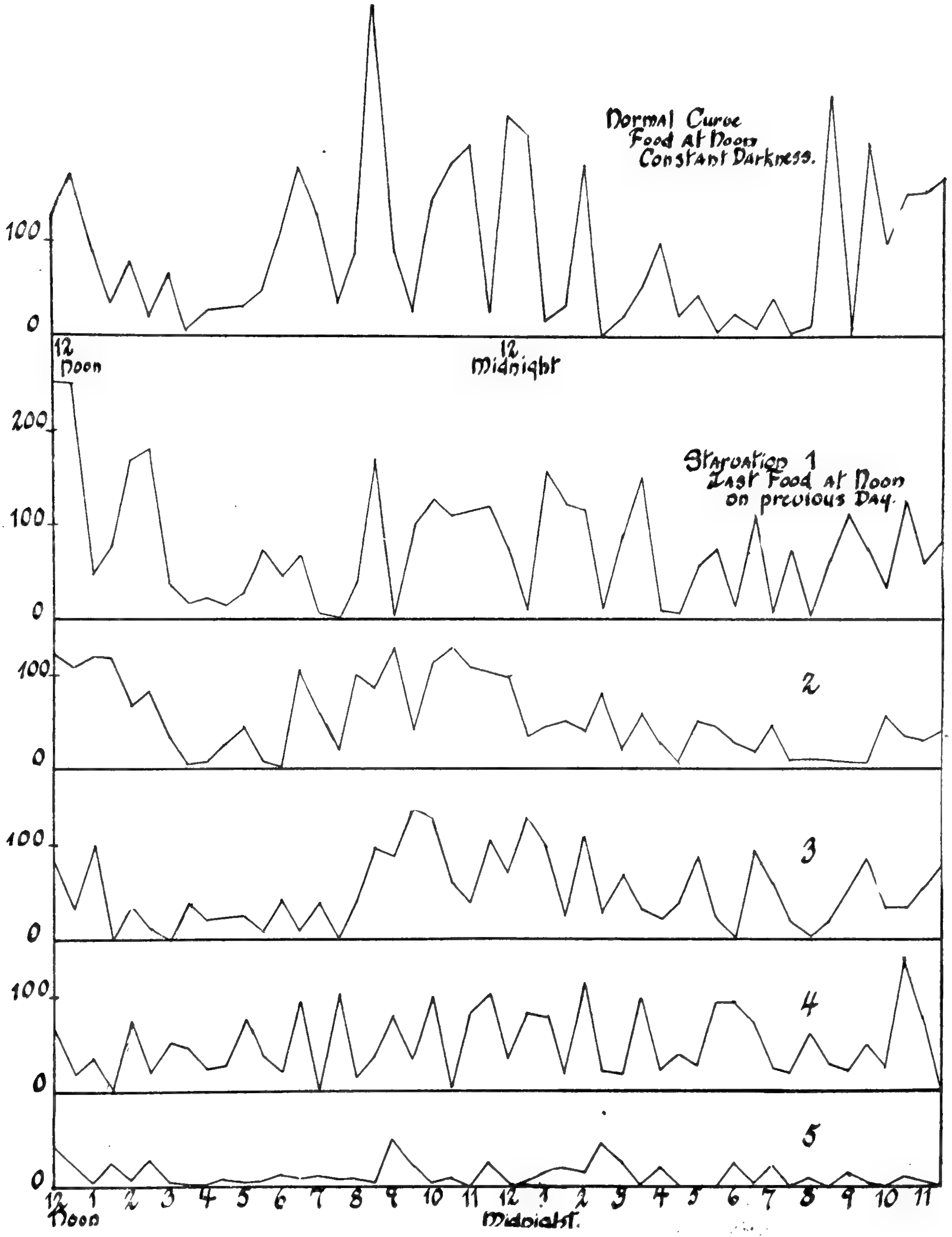

FIG. 17. DISTRIBUTION OF ACTIVITY DURING STARVATION

Figure shows the persistence of the typical distribution curve for several days after the removal of food

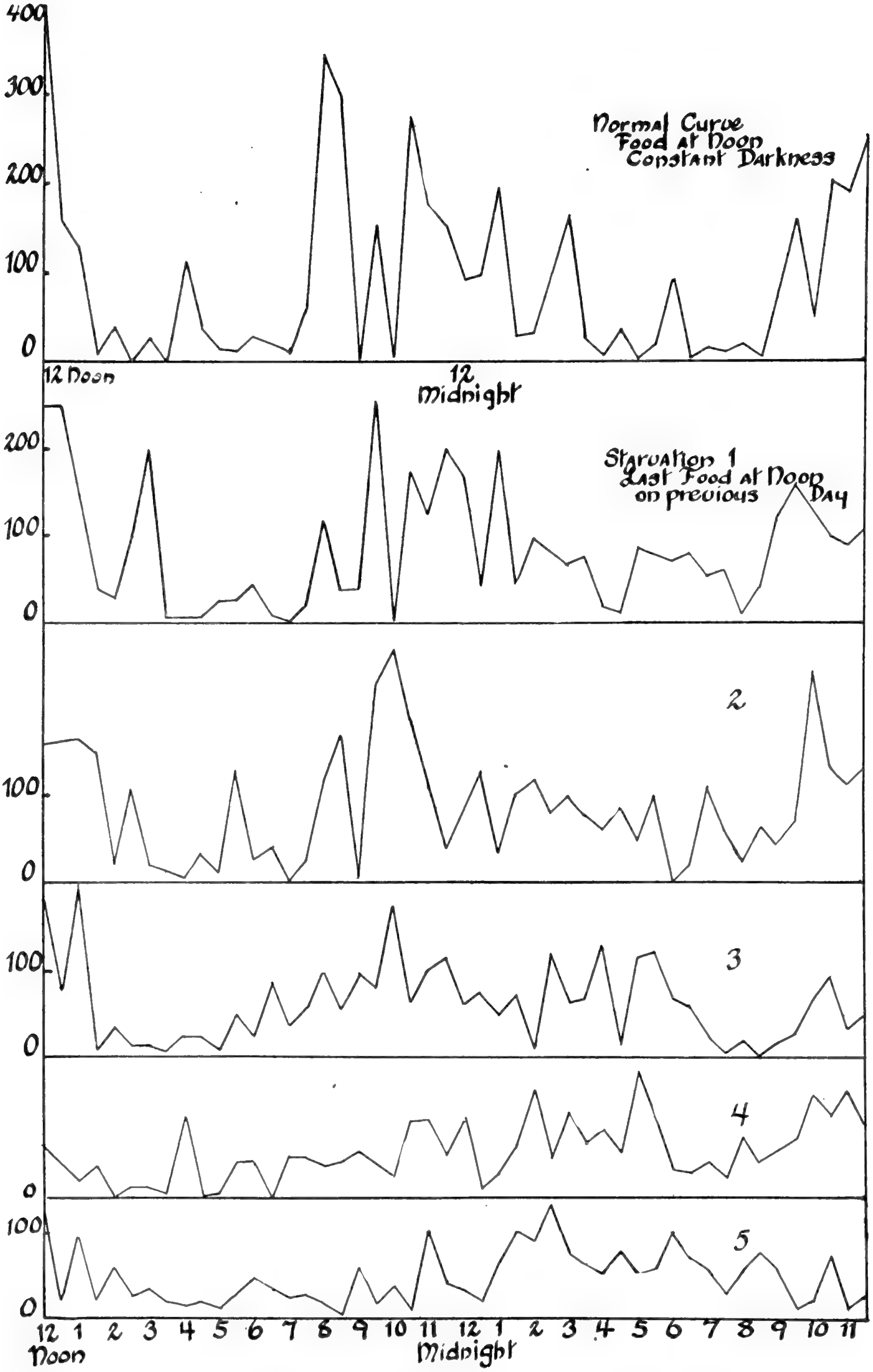

FIG. 18. SAME AS FIGURE 17, BUT FOR ANOTHER ANIMAL

leading into a revolving drum, the other into a food box in which food was left all the time. The animal could move freely from one cage to another as it chose.

What then under these conditions happens to the periods of activity and inactivity set up throughout the 650 days of the animal's life on the outside? The results of this experiment are shown schematically in figure 19. In this figure only the activity in the drums is recorded. The first line gives the alternating periods of light and darkness in twelve hour periods 8:00 p.m. to 8:00 a.m. and 8:00 a.m. to 8:00 p.m. for the 650 days of the animal's life preceding the experiment. Also it shows the period of constant darkness during the experiment. The second line gives the probable relation of activity of the animal to the changes of light and darkness for the period of life before the experiment. It also gives schematically for twelve days the time relations of the revolutions of the drum made by the animal when placed in the environment of constant darkness. At the end of the twelve days the experiment had to be discontinued for unavoidable reasons. It may be seen that during these twelve days the regular daily alternation of activity and inactivity is fairly definitely maintained despite the constant darkness. How much longer this regular alternation of periods would have continued is difficult to conjecture.

The fact of the persistence of rhythms of activity after the withdrawal of the rhythmic stimulus has been observed in a number of different animals in the past. Bohn and Keeble have interested themselves very much with this phenomenon especially with relation to the life and habits of a small animal *Convoluta roscoffensis* which has its habitat

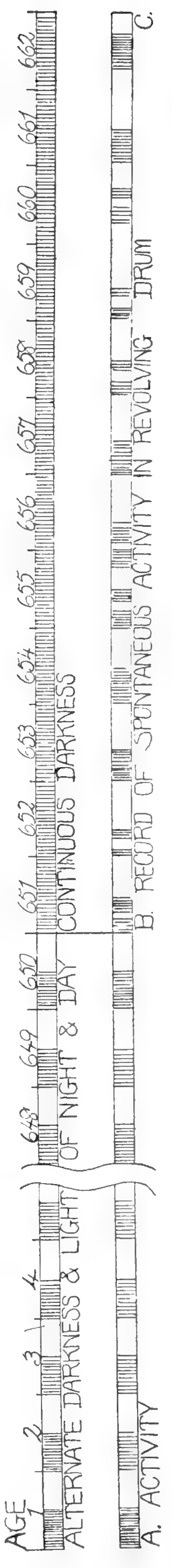

Fig. 19. Schematic Record Showing Persistence of Activity Rhythm after Withdrawal of Original Stimulus

on the foreshore of the sandy beaches of Normandy and Brittany. These workers found that the habits of this animal are to a very considerable extent dependent on the movements of the tide. Just before the tide reaches them at each flow they disappear into the sand, and just as soon as they are uncovered during the ebb they come up on the surface again. In this a very regular alternation of downward and upward movement is set up. Bohn (3) and Keeble (4) found further that when these animals are scooped up in a cup with some sand and placed in the laboratory where they are no longer subjected to the periodic coming and going of the tides they still continue for several days to make the upward and downward movements just the same. Benjamin Moore (5) has also described the persistence of a rhythm in absence of the wonted stimulus in the case of phosphorescent organisms in the sea. The organisms give off their light only at night. When they are placed in a dark room this daily alternation of phosphorescence and inactivity persists over a period of fourteen days after which time the animals usually die.

VII. ON THE ORIGIN OF SPONTANEOUS ACTIVITY

Throughout all of the experiments described thus far in this present study it was seen that a large part of the activity of the rat cannot be accounted for in terms of stimulation from outside sources. It was shown how some of the ever present factors, such as illumination and temperature may modify the expression of activity, but it was also shown that these factors could not be called upon to account for the activity. For this reason all that part of the activity of the rat that occurs in situations free from all external stimuli was spoken of as "spontaneous" activity. The source of this activity must lie somewhere within the organism. What organ or mechanism is there within the body of the rat which might serve to bring about this gross bodily activity?

In looking for this source of stimulation the chief characteristics of the manifestation of spontaneous activity studied above must be kept in mind; this is the very regular alternation of periods of activity and inactivity at the rate of ten to fourteen per twenty-four hours. What mechanism is there within the body which functions in this way and at this rate?

The heart and lungs although very regular and periodic in their functioning must be excluded for reason of their rate which is a matter of seconds and minutes rather than hours. The liver, rectum and bladder and intestines must be excluded for reason of their irregularity of periodicity. The sex glands, although periodic in their function, must be excluded because of their rate which is a matter of days, weeks or even longer intervals.

There still remains the stomach. This organ has been the subject of very thorough investigation by a number of physiologists, chiefly Cannon (6) and Carlson (7), so that its action is rather clearly understood. It has been established in the first place that the stomach when empty is not subject to continuous contractions as might be supposed, but rather that its activity is broken up into more or less clear-cut periods. During the intervals between the periods of activity this organ quite relaxed and almost completely inactive. During the activity periods it undergoes a series of contractions which may involve usually the greater part of the musculature of this organ. The rate of the recurrences of these periods differs in different species of animals, but also in members of the same species but of different ages. The average rate for most mammals when the stomach is empty is ten to fifteen per day. Under carefully controlled and regulated conditions these periods of activity may come with an astonishing regularity.

These contractions of the stomach when this organ is empty must not be confused with the contractions that occur during the process of digestion when the stomach is full. These latter contractions are known as digestion contractions, while the former are known as hunger contractions. They differ in a number of ways, first as to parts of the stomach involved, and secondly their relation in time to the last meal. The digestion contractions begin almost immediately after an ordinary meal and continue until the stomach is empty. Just as soon as any of the food is prepared for the assimilative processes in the alimentary canal below the stomach it is slowly expelled through the pylorus. The process of expulsion involves the musculature from the sphyncter at the antrum to the sphyncter at the pylorus. Contractions begin at the antrum and work downward, one following another peristaltically. During the time the process of expulsion is going on the part of the stomach above the antrum is engaged in macerating and churning the food in acids preparatory to its descent below. These processes go on until the stomach is completely emptied of food. As this process nears completion a new group of contractions begin, at first almost imperceptibly, gradually increasing until finally the musculature of the entire stomach is involved. These are the so-called hunger contractions (see fig. 20). They occur only when the stomach is empty or nearly empty of food. These contractions begin at first at the lower end of the pylorus and work downward, each time however they begin farther and farther up on the wall of the stomach until they involve the entire fundus, and finally the entire stomach right up to the cardia. During these contractions marked changes take place in the entire organism, changes in blood pressure, intra-cranial pressure, reflex excitability, and in the heart-rate, while during the digestion contractions no such changes have been found to occur. The former contractions give rise to the sensations of hunger while the latter are not known to give rise to any kind of sensations.

It is with these hunger contractions that this work will concern itself at this point. It was stated above that in the empty stomach they come in regular periods at the rate of ten to fourteen per twenty-four hours. This rate corresponds very closely with the rate of the spontaneous activity periods. The fact of this close correspondence in rate may be taken then to indicate that these two phenomena occur simultaneously or nearly simultaneously.

Unfortunately it was not possible in the rat to get conclusive evidence of the simultaneity of the action of the stomach and the spontaneous gross bodily movments. Many attempts were made with the balloon method, but the difficulties of the technique due to the small size of the animals were too great. A number of animals were trained to take a very small stomach tube with a balloon attached to the end, but in every case, some time before a record was taken, either the rat destroyed the tube by biting a hole through it, or else was destroyed itself by asphyxiation. The possibility of gastrostomy was considered—that is making a small hole through the wall of the abdomen and introducing the balloon into the stomach that way, but it was feared that the effects of the operation which are necessarily quite severe in such a small animal, because of the difficulty of handling such small parts, would too greatly modify the behavior to make the experiment practicable.

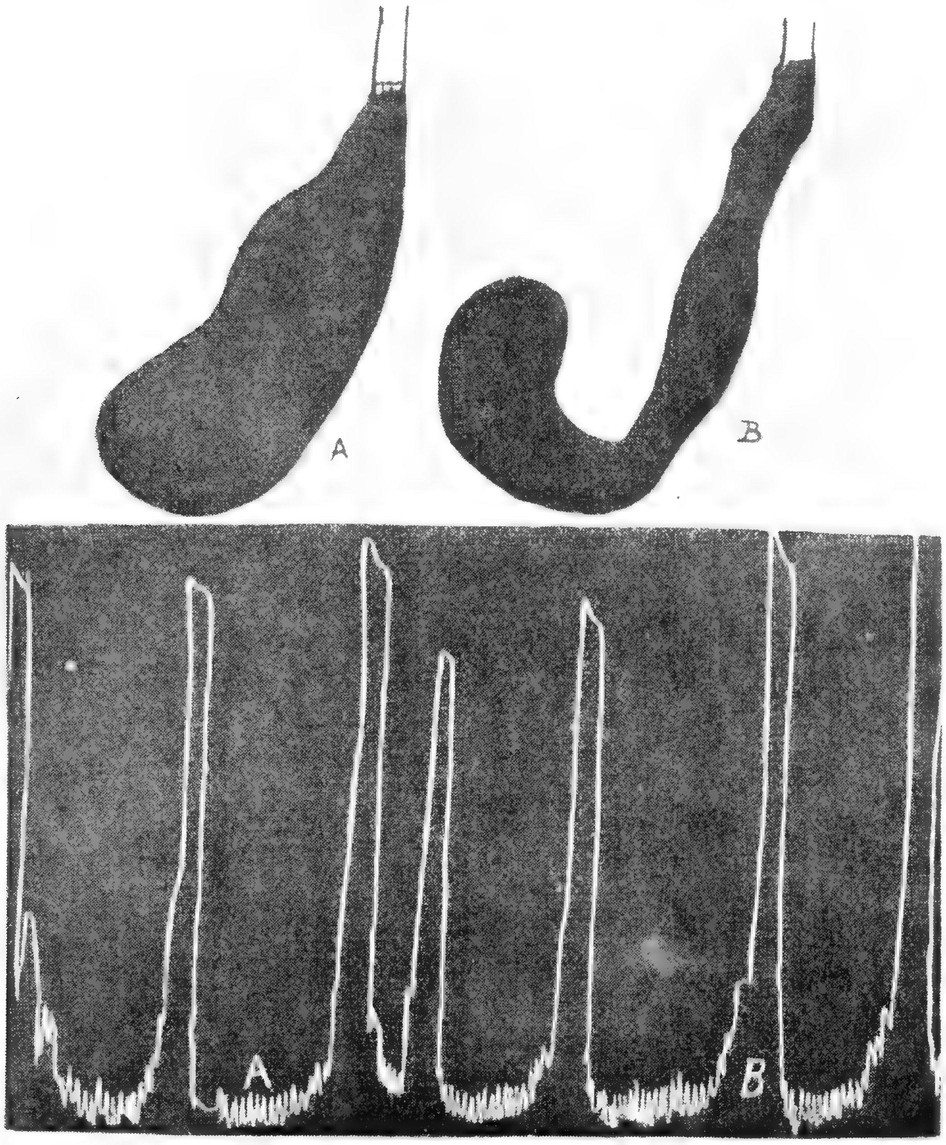

Fig. 20. Hunger Contractions of the Dog's Stomach Hours After a Meal

A, Outline of bismuth coated balloon in stomach between the gastric contractions; *B*, outline of balloon at the height of a hunger contraction (Rogers and Hardt)

In humans however it has been possible to demonstrate this simultaneity of the contractions of the stomach and gross bodily movements. Miss Tomi Wada took simultaneous records on medical students of gross bodily movements and stomach contractions during sleep. The stomach contraction records were obtained by the usual method employed by Cannon and Carlson. The subjects swallowed the balloon and tube just before going to bed. The record of the gross bodily movements was obtained by means of a simple system of tambours placed under the bed. Records were taken during sleep because during the waking periods the subjects are exposed to many external stimuli, and it is not possible to differentiate the part of the activity which is due to these external stimuli from the part that is spontaneous. Miss Wada found that the spontaneous movements during sleep, what few there are, rolling over in bed, etc. come periodically in regular groups. Miss Wada found further that in every case these periods of gross bodily activity coincided with the activity periods of the stomach. During the intervals between, when the stomach is quiescent, the body is also completely quiet. These results leave little doubt about the simultaneity of gross bodily movements and the activity of the stomach.

Up to this point it has been shown that the stomach contractions and the periods of spontaneous bodily activity in all probability occur simultaneously. In any case of this kind where two phenomena occur simultaneously in this way the following possible explanations of the causal sequence may be made. (1) either both are due to some other common agent, (2) or else the bodily activity is the cause of the stomach activity (3) or finally that the stomach activity is the cause of the gross bodily activity.

One of these explanations is easily eliminated; that the stomach activity is due to gross bodily activity. It is an experimental fact easily verified that contractions of the stomach cannot be elicited in anyway by activity of the whole body, rather on the contrary bodily activity tends to inhibit the contractions (Carlson and others).

The second possibility that the stomach contractions and the activity have a common origin, a common stimulus may be eliminated by the following evidence. (1) It is a well-known fact that the stomach when completely excised from the body still continues to contract very much as before. This excised organ will continue to function for a considerable period of time if it is kept warm and moist and given the proper nourishment of oxygen. (2) Carlson and others have shown that the stomach functions quite normally in the body after complete nervous isolation from the rest of the body, after section of both vagi and both splancnics. Carlson sums up the evidence on this point in this way: ". . . . The essential point is that since the empty stomach, completely isolated from the central nervous system, does exhibit the typical hunger contractions, the primary role of the gastric nerves is that of modifying or regulating essentially automatic mechanisms in the stomach wall." (3) The autonomous function of the stomach was further demonstrated by Carlson by means of a very ingenious experiment in which he used a Pavlov accessory pouch. In this experiment he found that "when the muscularis and myenteric isthmus joining the main and accessory stomachs is relatively narrow, the two stomachs exhibit complete independence of the hunger contractions, even to the point of vigorous activity of the one during quiescence of the other. . . . ."[3]

There remains then the last of the three possibilities; that the spontaneous gross bodily activity is due to the activity of the stomach. This explanation seems to square best with the facts at hand at present on the activity of the stomach and the activity of the total organism. There are still so many gaps in our information regarding both of the subjects that it is not possible

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[3] Carlson regards the results of this experiment as very good evidence for the independence of the stomach from the stimulation of agents in the blood-stream. Carlson argues that the blood can have nothing to do with the stimulation since the stomach and the accessory pouch function independently though they are both supplied by the same blood. In interpreting these results in this way he does not give consideration to the fact of the local rhythms of the different parts of the stomach. It is well-known that strips of muscle taken from different parts of the walls of the stomach and placed in Ringer solution contract at quite different rates. Every part has its own rhythm. In Carlson's experiment then the possibility still remains that the main stomach and accessory pouch were stimulated by agents in the blood stream, but that because of their different inherent rhythms they responded independently.

at this time to be quite certain of any explanations of how the organism works. The investigations in recent years of Cannon and Carlson on the sensation of hunger and its relation to the stomach contractions have rather definitely established the fact that these contractions precede the hunger sensations in time, that they are the origin of these sensations. The results obtained in the present work seem to show that the stomach contractions do not alone bring about sensations of hunger, but they also bring about movements of the entire organism by means of which, as it will be shown in the following chapter, the organism is brought into contact with the materials necessary for stopping the contractions.

A very important gap in our knowledge regarding the relation of the action of the viscera to the reactions of the whole organism was recently filled in by the work of Carlson and Luckhardt (8) on the visceral nervous system of frogs and turtles. In this work it was definitely established that stimulation of the visceral organs brings about reactions of the skeletal muscles, reactions of the whole organism. 1. "Mechanical or electrical stimulation of the lungs, the gall bladder, the heart, the urinary bladder and the entire intestinal tract induces skeletal reflexes both in decerebrated and purely spinal preparations. 2. These visceral skeletal reflexes, at least as regards the extremities, are essentially of the defensive or escape type."[4]

The facts obtained in the present work on spontaneous activity and the facts known from physiological work on the stomach may tentatively be formulated in the following way: There is a tendency in all living organisms to maintain a metabolic balance or equilibrium. The various substances of the body are present in a fairly definite quantitative relationship. Whenever the balance is destroyed there is an immediate reaction to reestablish it. During fasting or during any time when the stomach is empty and the body is in need of nourishment this balance is temporarily destroyed. There is a minus of some substances and

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[4] We found recently in a series of experiments on the behavior of foetuses (cats) still attached to the cord that stimulation of the stomach or intestine (slight pinching) elicits very vigorous movements of the entire body.

a plus of others. The products of this deficiency—whatever they are—may be looked upon as the agents which set up the process of reestablishing the equilibrium. (This process has for its final step the movements of the entire organism about in the environment until contact with food is made and the food is ingested.) As far as is known there is no way for these deficiency products, which are probably carried in the blood stream, to stimulate the skeletal muscles directly—the muscles which bring about the movements of the entire organism. How then is the equilibrium reestablished? It is known from direct work on the stomach and from analogous work on the heart that the stomach responds to chemical stimulation, that its activity may be influenced and changed by chemical stimulation. It is safe to assume that these deficiency products stimulate the stomach, bring about in it an increase in size and rate of the contractions. These contractions in turn when they become large enough send impulses to the skeletal muscles through the vagi and central nervous system, efferent nerves, and release there the stored energy which starts the organism in operation of getting food for filling the stomach. The fact then that the energy in the muscles is only released periodically as was demonstrated above must be accounted for by the periodicity of the action of the stomach. This organ is subjected during times when the body is in need of nourishment to a continuous stimulation from the deficiency stimuli. Progressively as the strength of the stimuli increases more and more of the stomach wall responds until the entire organ from the cardia to the pylorus becomes involved. After a long series of contractions of this kind the musculature finally reaches a condition in which suddenly the deficiency stimuli are no longer able to elicit a reaction, the contractions cease and the stomach becomes quiescent. This quiescent phase which follows may be thought of as a period of fatigue in which for the time being the muscles are temporarily no longer responsive to stimulation. As the muscles recuperate the contractions begin again, and progressively as the recuperation process goes on they become larger and larger until finally the height of another period is reached and the entire reaction is repeated. This accounts for the periodicity of the action of the stomach and at the same time for the periodicity of the spontaneous gross bodily activity of the whole organism.

Schematically this tentative formulation may be expressed in the following manner. Before presenting this schema, however, it is necessary to recall in this place several points brought out above in Chapter I in the experiments which deal with the periodic nature of spontaneous activity, when the animals were kept in a small cage and fed just once per day. In these experiments it was found that the spontaneous activity comes in regular periods which are separated by intervals of almost complete quiescence and that the activity is not evenly distributed throughout each period. There is only very slight activity at first. Progressively as the period goes on the activity increases until a maximum is reached either in the middle or toward the end of the period. It must also be recalled here that the stomach contractions are not all of the same size. Each of the contraction periods begins with very small contractions which involve only a limited part of the stomach. The contractions become larger and larger until the entire stomach is involved from the cardia to the pylorus. This maximum of activity is usually maintained right up to the end of each period. Following the cessation of the contractions the stomach becomes completely quiescent. The relation of spontaneous activity to the function of the stomach is shown schematically in figure 21. In this figure spontaneous activity is given on the top line while the probable relation of the stomach contractions to this activity is given on the second line. In this schema it is intended to show that the gross bodily activity of the organism increases progressively as the activity of the stomach increases. The maximum of spontaneous activity is reached when the whole stomach becomes involved in the contractions. With the cessation of the contractions of the stomach at the end of each period the animal becomes inactive. This process repeats itself with each new period of stomach contractions. This relation will be discussed in more detail in the following chapter.

It must be emphasized that with this tentative formulation it is not intended to imply that the stomach is the only organ in the body upon which spontaneous activity may depend. But it is true however that a larger part of the activity of the rat does fall into these regular clear-cut periods, which have been associated with the action of the stomach. Besides this activity which falls into the regular periods there still remains some activity which the limited scope of the present work did not permit to be studied in detail. Most important here is a rather considerable amount of irregular activity of females. Whether this irregular activity is related to the action of any part of the sexual apparatus was not determined. The role that the stomach mechanism plays with relation to spontaneous activity probably varies very greatly in the different species of animals. In the lower organisms it must undoubtedly account for a very much larger part if not all of the spontaneous activity. In man, on the other hand, it probably accounts for only a limited part of the activity. Still the work described above on the relation of spontaneous activity to the stomach contractions in humans during sleep would indicate that the stomach still plays a very important role in bringing about activity even in humans, however greatly covered over this activity seems to be by the flood of reactions elicited by the many different external stimuli during waking periods. In this connection it would be of importance to determine the relation of spontaneous activity to the kind and structure of the

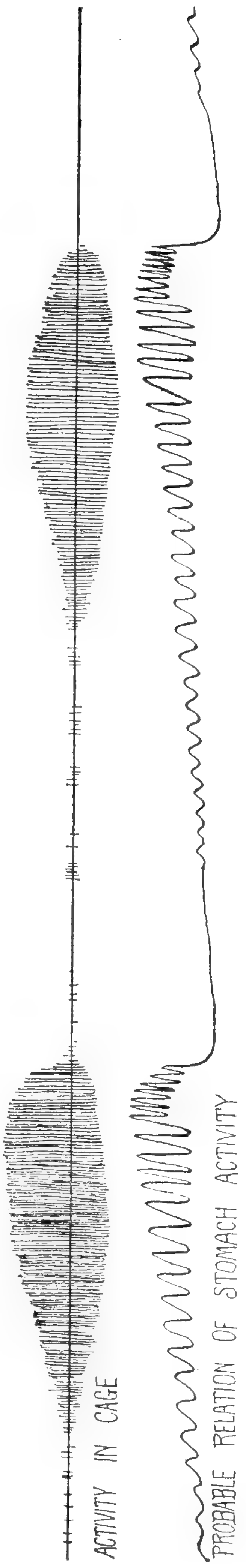

FIG. 21. RELATION OF STOMACH CONTRACTIONS TO ACTIVITY

stomach. In frogs for instance the stomach happens to be so constructed that it is able to adapt itself to very large quantities of food. This animal gets its food only at rather great intervals—weeks or months—but then usually in a single large quantity, other smaller frogs or the like, which take many days to be digested. What is the relation between this kind of a stomach and the spontaneous activity of the animals? The human stomach on the other hand is so constructed that it is able to take only relatively small quantities of food at one time, but this food is digested almost immediately. A study also of the relation of activity to the action of the stomach should be very interesting in ruminants where the stomach is made up of several separate parts. What does the animal do spontaneously during the function of each of these parts?

There is still another point which argues very strongly for the prime importance of the stomach with relation to the other internal organs especially the bladder and rectum, in bringing about about activity. This is the fact that in all animals, and in man living in the wilds, distention of the bladder and the rectum is relieved wherever the individual happens to be while the contractions of the stomach can only be relieved by movements of the organism about in the environment until contact with food is actually made and the food is ingested.

In light of this explanation some of the results obtained in earlier chapters especially from the work on the distribution curve of activity may now be discussed again. It will be recalled that in these experiments it was shown that when the animal is fed just once per day and under conditions of constant illumination and temperature the spontaneous activity is distributed over the twenty-four hours in a very definite way (see figure 6). The form of the activity distribution curve was shown to depend on the time of the last feeding. The two phases of inactivity and the single period of intense activity shown in this curve may be explained on the basis of the formulation given above in the following way. The first period of inactivity immediately after the daily meal occurs at a time when the processes of digestion are going on in the stomach and when the hunger contractions are absent. After the stomach empties the hunger contractions begin again and become more and more vigorous with each succeeding period. The animal is stimulated in this way only slightly at first but increasingly more intensely until it reaches its maximum of activity some twelve hours after the daily meal. At this time the nervous system and the large muscles of the body employed in making the spontaneous movements become fatigued so that although the stimulation from the stomach still continues in its periodic fashion these muscles respond only with a very small amount of activity. During this period of fatigue the attempts of the stomach to gain control of the organism, to start it to activity are clearly manifested by the small but regular periods of activity shown at this time. This may be looked upon as the period of sleep. Actual observation showed that during this period the animals are very difficult to arouse they are curled up in balls and are as far as can be made out "sleeping." It has already been pointed out in Miss Wada's work on the activity of humans that during sleep the period of activity and inactivity come and go with great regularity synchronous with the stomach contraction periods. The stomach continues to function during this period of sleep just as vigorously as before. The amount of activity becomes larger and larger with each successive period until finally, after a condition of sufficient recuperation of the nervous system and skeletal muscles is reached, the stomach contractions again gain possession of the reactions of the whole organism and the individual awakes. The regular anticipation of the feeding periods may also be explained on the basis of the clock-like functioning of this internal organ. When all external conditions are kept fairly constant and when a regular routine of activity is gone through each day the accuracy of this time piece is quite astonishing. This is seen very well in the activity record of individual rats, but it is much better known from numerous observations from the great regularity and punctuality of the reactions of many farm animals, especially of the braying of the mule at a very definite time near noon at which it is accustomed to be fed. The ability to carry on other rhythms may be explained on this basis (9 and 10).[5]

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[5] A good example of the persistence of a rhythm of activity of an internal organ after the removal of the original exciting stimulus is found in the case of the

VIII. RELATION OF SPONTANEOUS ACTIVITY TO HUNGER

The intimate relation of gross bodily activity and the action of the stomach was pointed out in the previous chapter. There still remains the question as to the relation of this gross bodily activity to the hunger reactions of the animal. Does it follow that because this diffuse form of activity is due to the stimulation from the stomach that it must all necessarily be translated into hunger reactions, searching for food, eating, etc.? It was shown that each of the regularly recurring periods of gross bodily activity is connected with simultaneous periods of activity of the stomach. Is all of the activity in each of these periods hunger activity?

In order to answer these questions and a number of allied questions a simple construction was used, the 'double cage.' This arrangement consists of an ordinary triangular activity cage with a hole cut in one side large enough to permit of the easy introduction, without contact, of the snout of an inverted pipe-shaped smaller tube containing food. Both cages were supported on a separate set of tambours and the activity in each cage was registered separately. A photograph of the double cage is shown in figure 22. The small round cage contains a metal food receptacle which is so constructed that the food may be easily gotten at through the hole at the top large enough to accommodate the head of the rat, but too small to permit the rat to pick up food in its paws and to scatter it about or possibly even to take some of it back into the other cage. In this experiment food was left in the food receptacle all the time, and water was left in the waterglass attached to the outside of the triangular cage. Of course, there is an obvious possibility of the animal's entering the food box for other purposes than replenishing itself with food. In order to eliminate this possibility the food cage was made just

human uterus. This organ, especially in multiparous women, continues to contract for a number of days after the birth of the child. The contractions are originally set up by the presence of the foetus. All during pregnancy these contractions go on. But interestingly in this connection they are not felt until labor begins, when they serve to expel the foetus. After labor they still continue to be felt for a number of days (that is they are still strong enough to dominate the organism).

large enough to permit the rat to enter and to get at the food, but too small to permit of very much sniffing or moving about. This arrangement was quite successful. It was possible to verify this by actual observation over rather long periods of time,

FIG. 22. PHOTOGRAPH OF DOUBLE CAGE

after the animals had had a good chance to accommodate themselves to the particular form of cage. After the first day in the double cage, they rarely, if ever, entered the food box when just generally active and sniffing about. When they did enter they seemed to do so solely for the purpose of getting food.

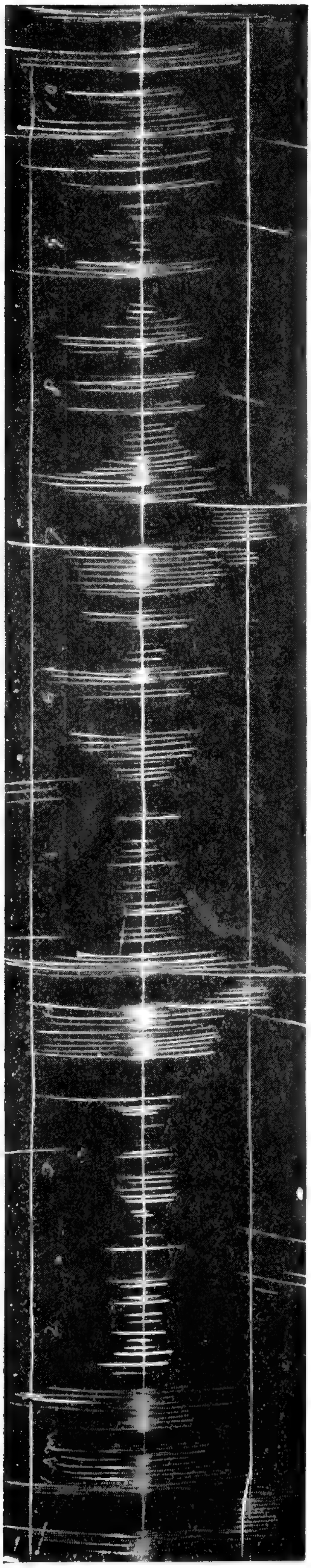

Fig. 23. Record from Double Cage

The results obtained from this experiment (see figure 23) showed: (1) In this situation where the animals had free access to food all the time the periods of activity and inactivity come and go with the same regularity as before only at a slower rate from six to ten per twenty-four hours. (2) The animals enter the food box at least once during each activity period, occasionally twice. (3) The time spent in the food box compared with the length of the entire period is very short. (4) The entrance into the food box does not take place at the beginning of the activity period but usually toward the end. Only in a few cases did any of the animals enter the food box at the beginning of a period. No instance of an entrance between periods was recorded. (5) The amount of activity increases progressively from the beginning of each period to the point when the animal enters the food box. (6) There is always some activity after the animal returns from the food box. This activity consists chiefly in all kinds of cleansing manoeuvers very much like those of an ordinary house cat. (7) The activity which precedes the entrance into the food box is diffuse and undirected. It consists usually of such movements as jumping, climbing, playing with paper, sniffing and gnawing at the sides of the cage, etc. The element of search for food plays no rôle in this activity. The animals are so thoroughly adjusted to every part of the cage that the necessity of search drops out entirely.

In order to bring these results into relation with the activity of the stomach it is necessary to bring out some additional facts regarding the function of the stomach. (1) Each period of activity of the stomach begins with small contractions. These contractions come with a very regular rate, one every eighteen to twenty seconds. For the reason of this rate Carlson speaks of these contractions as the "twenty-second rhythm." These contractions become larger and larger as the period advances without changing their rate. (2) After these contractions have reached a certain size, quite abruptly a new series of very much larger contractions beings. These larger contractions come at a different and irregular rate, and also have a different form. These are the so-called "main hunger contractions." Whether or not there is any real difference between the small and the large contractions besides what can be explained in terms of the different extent to which the musculature of the stomach is involved in the two cases is not definitely known. (3) Cannon was the first to show that these large contractions give rise to the sensation of hunger and (4) Carlson has shown that the intensity of the hunger sensation is roughly proportional to the size of the contraction.

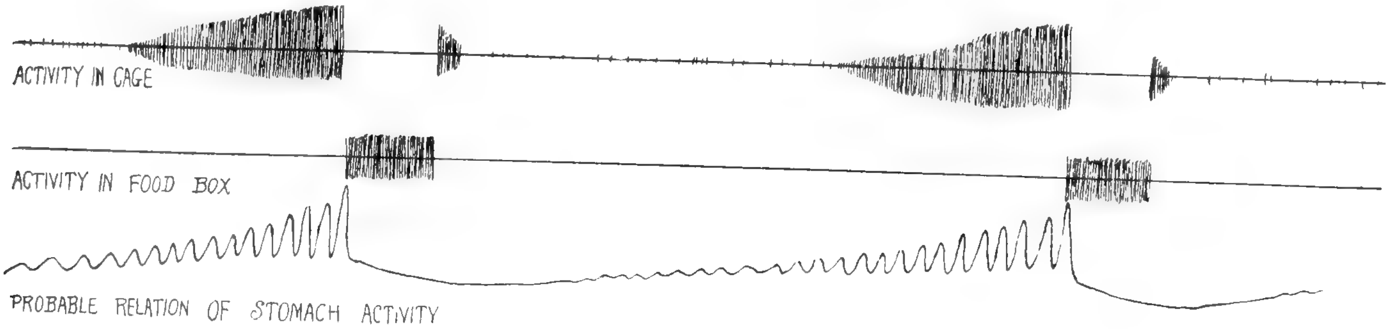

FIG. 24. RELATION OF STOMACH CONTRACTIONS TO ACTIVITY IN DOUBLE CAGE

The relation of the results obtained in the 'double cage' to these facts is brought out in figure 24. In this figure the diffuse spontaneous activity in the double cage is shown on the top line. The entrances into the food box are shown on the second line. The probable relation of the stomach contractions to the diffuse activity and to the entrances into the food box is shown on the bottom line. The small contractions serve only to stimulate the animal to diffuse activity, restlessness. It is not until the onset of the large contractions, the main hunger contractions, that the animal enters the food box. With the introduction of food into the stomach the contractions cease. Once started at eating, however, the animal continues until the stomach is filled. The activity in the cage following the return from the food box is made up entirely of cleansing manoeuvres elicited by the various kinds of external stimulation connected with eating.

The fact that the animal does not enter the food box until the onset of the large contractions may be explained in the following way: At birth the members of all mammalian species are known to have contractions of the stomach almost continuously (Carlson). Driven then by these contractions the animals are active diffusely and remain active until either stomach contractions are in some way stopped, or else due to gross exhaustion the animals are no longer able to move. They move and toss their heads about here and there, suck at everything that happens to stimulate their lips, bits of straw, hair of the mother's body, feet and ears of sisters and brothers, and finally the teats of the mother. It is only the last of these activities that brings about a change within the organism. When the teats touch the lips sucking movements are elicited; a warm stream of milk flows down the animal's throat; the stomach contractions are stopped; hunger pangs are relieved; the animal lies down and goes to sleep. Each time the contraction periods begin again the animal becomes active; begins moving about and sucking at everything and the whole process is repeated. As this trial and error process goes on, the onset of the stomach contractions gradually becomes more and more definitely associated with the sucking of the teats, becomes the main motor outlet, while the others fall into disuse. This process goes on for a time; in the rat it is a matter of days (as near as I could determine by observation, eight or ten days); in the human infant it is a matter of months until the stomach contractions elicit the one reaction of crying and actually seeking food. This process is somewhat complicated by the fact that the stimulus to activity is not at all times the same, for, as was shown above, the stomach contractions vary considerably in amplitude, also possibly even in their nature during different parts of the contraction period. If the animal happens to find the teats during the part of its activity which is caused by the milder contractions it will nurse just as at any other time; but the changes that take place within the organism when milk or food is taken during this part of the contraction period are so slight that no definite associations can be built up between them and the sucking at the teats and the taking of food. When however, the animal happens to find the teats during the period of main stomach contractions things are quite different. Now the changes resulting from the taking of the milk are strong enough to become associated with the stomach activity, and form the basis of the cycle: stomach contractions—going out to teats—nursing—inhibition of contractions—relief. There are further reasons why these reactions become associated more readily during the period of strong contraction: first the fact that during the period of strong contractions the animals are more active and vigorous than during the period of milder contractions; secondly chances and the frequency on a simple trial and error basis of finding the teats during the former period will be much greater. Then also for the reason that milder contractions are more easily stopped the animal will nurse for a shorter time during this part of the period. Besides these simple factors of frequency, duration, recency of stimulation, there will be other rather more situational factors which will help to build up the association; such things as odor of the teats, the warmth of the mother's body, etc., and, of course, the encouraging reaction of the mother herself.

Gradually the main stomach contractions and the sucking of the teats become permanently associated and there is less tendency for the animal to suck at the teats during the period of weaker contractions. The onset of the main stomach contractions comes to serve as a signal for the taking of food and the animal no longer hesitates but goes directly to the teats. Later on, after the animals are weaned, as was the case in the double cage, the onset of the main contractions served as a signal for the animal to go to the food box.

It is hoped that further light may be thrown on the origin of these specific food reactions by work that is now being carried on by Mr. Ging Wang on the activity of the newly born of rats and cats before they have ever been fed. Mr. Wang is attempting to find out when the periodicity begins, whether or not it is present at birth, and what relation it has to the times of feeding, and the time required for the complete emptying of the stomach. He also hopes to get some information on these reactions during the period of the animal's life before it is born. It is astonishing how little definite information is available at present regarding the activities during this very important time of development.

The facts on hand from work on the activity of the human infant present certain difficulties which are not easily explained. Miss Wada found in her work that the gross bodily movements of the infant during sleep come in periods at the rate of one every fifty-five minutes. It is difficult to see how this rhythm could have been set up by any external stimuli in as much as the infant on which these records were taken was fed once every four hours from birth on. In adults the periods of activity come at the rate of one every two hours. But in adults we have shown definitely that these periods occur simultaneously with the periods of activity of the stomach. Here again, however, the relation of the food habits to the periods of activity is difficult to explain. The solution of these problems must wait for further evidence.

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