Frequency, duration, and speed of wheel running of rats as a function of age and starvation*

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The purpose of this experiment was to determine whether age differences in amounts of wheel running of starved rats were due to the frequency of bursts of running, to the average duration of bursts, to speed, or to any combination of these parameters. The experiment was carried out according to a 3 by 2 by 2 mixed model design. The independent variables were age (67, 293, and 746 days old at the start of starvation), food deprivation (total starvation vs ad lib), and occasion of measurement (initial vs maximum activity). The dependent variables were number of wheel revolutions, number of bursts of activity, number of seconds of running per burst, and revolutions per second. The results indicated that acutely starved rats run more often, for longer periods, and at higher speeds than do sated rats, and that with increased age rats run less often, for a shorter time, and at slower speeds.

The purpose of this experiment was to determine whether age-dependent decrements in the amounts of daily wheel running of starved rats were due to differences in the frequency of bursts of running, to differences in the average duration of running, to differences in the speed of running, or to differences in any combination of these parameters. With increasing weight loss, the amount of wheel running of young starved rats increases to a maximum and then decreases shortly before death (Campbell, 1964). This pattern of running changes only quantitatively with increasing age. A previous experiment (Jakubczak, 1967) indicated that, independent of drive level, amounts of wheel running of starved rats decrease with increasing age. In that investigation, the cumulative total of wheel running of starved rats decrease with increasing age. In that investigation, the cumulative total of wheel revolutions during 24 h was used as the dependent variable. However, rats do not run continually during the 24-h period, but distribute their running in a number of episodes or bursts of running (Slonaker, 1912). More recently, Premack and Schaeffer (1963) found that during a 1-h sample of running, starvation increases the cumulative amount of wheel running of rats by increasing both the frequency and average duration of bursts of running, but has little effect on speed of running. Consequently, the age differences in the amounts of wheel running of starved rats (Jakubczak, 1967) may have been due either to differences in the

frequency of bursts of running, to differences in the average duration of bursts, to differences in speed of running, or to differences in any combination of these parameters. A precise location of the source or sources of age differences in the total amount of running of starved rats should result in more specific hypotheses about the mechanisms underlying these age differences than is possible with the traditional drive-habit distinction.

METHOD

Design

The experiment was carried out according to a 3 by 2 by 2 mixed model design (Winer, 1971, Case II). The independent variables were age (67, 293, and 746 days old at the start of starvation), food deprivation (total starvation vs ad lib), and occasion of measurement (initial vs maximum activity). The dependent variables were number of wheel revolutions, number of bursts of activity, number of seconds of running per burst, and revolutions per second.

Procedure

Forty-eight male Sprague-Dawley (Charles River) rats were assigned randomly to Wahmann activity cages (LC-34) and to the food-deprivation conditions within each age group (8 per subgroup). However, because of either mortalities or equipment failure, the number of rats in the respective subgroups were: 67E-7, 67C-5, 293E-6, 293C-7, 746E-5, 746C-6. The frictional torque was equalized among the wheels at approximately .003 ft lb (Lockard, 1965). The rats were adapted to the activity cages for 24 days, during which time they were fed Purina rat pellets and water ad lib. The door between the living compartment and the drum remained open daily for 22 h. During the remaining 2 h (starting at 1:00 p.m.), the rats were locked in their living compartments. These 2 h were used to determine and record body weights and wheel revolutions of the rats and to maintain the equipment. At the end of the adaptation period, food was totally withdrawn from the rats of the starvation subgroup of each age group. The starvation was continued from 5 to 18 days until the rat had lost 35% of its initial weight, at which time food again was made available. The previous study (Jakubczak, 1967) had indicated that, regardless

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Fig. 1. Geometric means of revolutions, bursts, sec/burst, and revolutions/sec as a function of food deprivation and occasion of measurement, averaged across age. Note differences in scale among measures.

of age. 35% body weight loss constitutes approximately 90% of total survival time during starvation. The laboratory lights were turned on automatically between 6:00 a.m. and 6:00 p.m. The temperature of the laboratory during the food deprivation was regulated at 72° F, and the relative humidity varied between 35% and 45%.

The distribution of activity over each 22-h period was recorded by Esterline Angus operations recorders (Model AW), using a chart speed of $\frac{3}{4}$ in./min. Records were made daily throughout the entire experiment. Each revolution of the wheel moved the arm of the Veeder counter up and down, thus opening and closing a sensitive miniature switch (Model CTMLD-0102, Robertshaw Controls Co., Columbus, Ohio) and activating a pen on the recorder. In order to analyze the initial levels of activity, the 5 days prior to food deprivation were examined and the graphic record of the day on which a particular rat's median wheel revolutions occurred was analyzed with respect to burst frequencies and durations. In order to analyze the maximum levels of activity of food-deprived rats, the graphic record of the day on which each food-deprived rat's maximum wheel revolutions occurred was similarly analyzed. Finally, in order to analyze the "maximum" activity of the control rats during the deprivation period of their experimental counterparts, the graphic record of the day within the appropriate range of days on which each control rat's median wheel revolution occurred was analyzed as above. A burst of running was defined as a collection of one or more revolutions (pen excursions) separated by less than 60 sec from any preceding response. Burst duration was defined as the sum of durations of bursts in seconds to the nearest 10 sec, divided by the number of bursts.

The speed of revolution (revolutions/sec) could not be determined from the Esterline-Angus records because of the slow paper speed that was required to record for 22 h. However, the average speed of revolutions was derived by dividing total revolutions by total seconds of running.

The values of each variable were transformed into $\log(1 + X)$ equivalents in order to meet the assumption of homogeneity of variance. Each set of data was analyzed by a modified unweighted means analysis of variance (Winer, 1971, Case II; Huitson, 1966). The magnitude of experimental effects was estimated by computation of ω^2 (Vaughan & Corballis, 1969).

RESULTS

The Age by Deprivation by Occasion interaction was

not significant for any of the four variables. Thus disregarding age, there was, as Fig. 1 indicates, a significant increase in revolutions between the two occasions of measurement under food deprivation, while ad lib feeding produced no change ($F = 29.77$, $df = 1/28$, $p < .01$). This increase was associated with significant increases in bursts, sec/burst, and revolutions/sec under food deprivation ($F = 33.57$, 6.84 , and 13.55 , $p < .01$, $.05$, and $.01$, respectively, $df = 1/28$). In the analyses of variance, the proportion of the within-Ss variance due to the Deprivation by Occasion interaction was 21%, 15%, 6%, and 13% for revolutions, bursts, sec/burst, and revolutions/sec, respectively.

Disregarding deprivation and occasion, there was a significant decrease in revolutions with increasing age ($F = 32.40$, $df = 2/28$, $p < .01$). This decrease in revolutions was associated with significant decreases of bursts, sec/burst, and revolutions/sec as a function of age ($F = 22.47$, 18.75 , and 11.60 , respectively, $df = 2/28$, $p < .01$). On all measures, the youngest group was significantly higher than the other age groups that did not differ between themselves (Fig. 2). The effects of age grouping on revolutions, bursts, sec/burst, and revolutions/sec in each of the four analyses of variance accounted for 44%, 35%, 33%, and 22% of the between-Ss variances, respectively.

Finally, there were no significant differences among the age groups with respect to the relative weight at which maximum activity occurred: 26%, 28%, 26% (in order of age).

DISCUSSION

The results indicated that the increase in the total amount of running of starved rats in activity wheels is associated with increases in the frequency and the average duration of bursts of running, as well as the speed. The results are, in part, consistent with those of

Fig. 2. Geometric means of revolutions, bursts, sec/burst, and revolutions/sec as a function of age, averaged across food deprivation and occasion of measurement. Note differences in scales among measures.

Premack and Schaeffer (1963), who found that 23 h of starvation increased the total amount of activity wheel running of rats during a 1-h sample by increasing both the frequency and average duration of bursts of running, but had little effect on speed of running. The discrepancy with respect to speed may be due to procedural differences between the two studies, such as degree of food deprivation, duration of observation, measurement of speed, etc. Nevertheless, the two studies taken together indicate that acutely starved rats run more often, for longer times, and perhaps at higher speeds than do sated rats. In contrast, Campbell and Lynch (1967) found that 4-6 days of starvation increased the number of revolutions per burst, but not the frequency or the duration of bursts. This discrepancy probably is due to differences in the definition of a burst between the two sets of studies. Several bursts, as defined in the study by Premack and Schaeffer (1963) and in the present study, could have been included in one burst as defined by Campbell and Lynch (1967).¹ Thus, the definition of burst is critical in studies of activity.

The results also indicate that the decrease in wheel running with increasing age is associated with decreases in the frequency and average duration of bursts of running as well as speed. These results are consistent with those of the previous study (Jakubczak, 1967), in which equal increments in weight loss produced increments in running that were proportional to the age differences in initial levels, and they extend the previous findings to other parameters of running. The age-related decrements in the frequency and average duration of bursts of running and speed were probably due to differences in nondrive mechanisms that underlie running, since the three age groups lost the same percentage of weight between the initial and maximum levels of running and since the degree of drive that results from starvation is proportional to relative weight

loss regardless of age (Campbell, Teghtsoonian, & Williams, 1961; Williams & Campbell, 1961; Jakubczak, 1967; Collier, 1969). The decrease in the frequency of bursts with increasing age represents an increase in the duration of pauses between bursts of running, since the frequency of bursts and the duration between bursts of running are inversely related (Premack & Schaeffer, 1963). Thus, with increasing age, the rat runs at slower speeds, for a shorter time, and pauses longer. This pattern of differences may be due to age-related decrements in speed of responding, resistance to fatigue, and recovery from it. Such age-related decrements were observed in swimming rats (Birren & Kay, 1958). Alternatively, since a running burst may terminate whenever levels of free fatty acids exceed a certain value (Collier & Hirsch, 1971), the age-related decrease in burst frequency and duration may be due to age-related increases in levels of free fatty acids and decreases in the rate of their metabolism. Further research is needed to specify the mechanisms of these age differences in running.

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NOTE

1. Revolutions/burst were derived from the data of the present experiment and analyzed. Age decreased and starvation increased revolutions/burst.