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Characteristics of Growth-Inducing Exercise

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BORER, K. T. *Characteristics of growth-inducing exercise.* PHYSIOL. BEHAV. 24(4)713–720, 1980.—Characteristics of growth-inducing exercise in hamsters were studied by examining (a) dependence of this phenomenon on a specific activity device, (b) its species-specificity, and (c) features of the running pattern which produce optimal growth acceleration. Acceleration of growth by exercise occurs in hamsters running on either horizontal discs or in vertical wheels, and in gerbils running in rotating wheels, and is therefore neither device- or species-specific phenomenon. In contrast to the two rodent species demonstrating increases in the rate of weight gain at levels of voluntary activity between 10,000 and 30,000 RPD, rats running on either activity device, and gerbils and ground squirrels running on horizontal discs, generated low levels of activity and no evidence of increased somatic growth. At weight ranges associated with maximal acceleration of growth by disc exercise, hamsters ran at moderately high speeds of between 35 and 51 cm/sec for up to one hour without a pause. Their total daily activity exceeded 15,000 RPDs (5.9–8.5 km) and lasted between 5 and 10 hours. Prolonged voluntary activity at relatively low speed constitutes a sufficient condition for acceleration of somatic growth in two rodent species.

Hamsters Gerbils Rats Ground squirrels Activity patterns Activity discs Rotating wheels

THE relationship between physical activity and somatic growth is not well understood. Under some circumstances, exercise in animals and man promotes protein synthesis in skeletal [10,11] and heart muscle [21], muscle hypertrophy [9, 12, 13], and growth of skeleton [6]. In the rat, on the other hand, exercise is associated with reduced food intake, weight loss [8,22] and no change in somatic growth [24]. A clear example of exercise-induced somatic growth was recently described in golden hamsters [1]. Hamsters which have attained the relatively slower adult rates of growth, display increased somatic and skeletal growth [4] accompanied by hyperphagia [1] and increased secretion of growth hormone [3] during, and immediately following, the exposure to voluntary exercise on horizontal activity discs.

The present study examined whether (1) growth acceleration by exercise in hamsters was dependent on the specific type of activity device used, (2) increased growth was a response to exercise peculiar to golden hamsters, and (3) running activity eliciting greatest growth exhibited a characteristic pattern. The first two questions were addressed, respectively, by studying growth rates of hamsters running in two types of activity devices, a horizontal disc, and a rotating wheel, and by examining the weight changes of three other species of rodent exposed to the two exercisers. No attempt was made to equalize the moving inertia, friction and running radius in the two devices. Instead, the present study investigated behavioral and physiological differences that could be attributed to differences in mechanical properties of two exercisers or to the way the four species of closely related rodents interacted with them. Among the species used, gerbils were chosen because of their close phylogenetic relationship to hamsters (the same family Cricetidae) and similarities in body size and natural habitat [30]; rats were included because they serve as reference points in laboratory experimentation; and golden-mantled ground squirrels were selected because they are, like hamsters, hibernators and may share with them physiological responses to exercise.

Thirdly, we examined hamster running behavior in search of features that could account for acceleration of growth. We have shown previously [2] that exercise-induced growth was restricted to, and systematically related to, body weight changes within a range of about 50 to 180 g. Rapidly growing young animals of less than 50 g, and heaviest hamsters whose weight had stabilized around 180 g, were unaffected by exercise. However, within the 50 to 180 g weight range, exercise accelerated somatic growth above the spontaneous rate which generally reached zero at about 125 g (Figure 1, top, SED=0). At body weights between 50 and 180 g, ponderal growth (g/day) was inversely proportional to body weight, but the rate of its decay was attenuated by exercise up to 180 g when all somatic growth ceased (Figure 1, top, EX=0). Thus, the net exercise-induced growth, above the baseline spontaneous growth rate, exhibited an inverted U curve (Fig. 1, top).

We have, furthermore, found that within the 50–180 g weight range, total daily running activity exceeded 15,000 RPD and changed as an inverted U function similar in appearance to function describing exercise-induced net growth (Fig. 1, bottom). We have, therefore, postulated that activity levels above 15,000 RPD, exhibited by animals within the 50–180 g weight range, may be necessary for stimulation of growth (2). In the present study we analyzed the components of running behavior contributing to total daily activity levels, such as number and duration of runs, number and duration of pauses, speed of running, and total time spent running to determine which of them could be necessary and sufficient stimuli of somatic growth.

METHOD

Animals and Maintenance

Animals were individually housed in temperature (22°C) and light-controlled (12L:12D) rooms in suspended wire cages except during the exposure to exercise, at which time

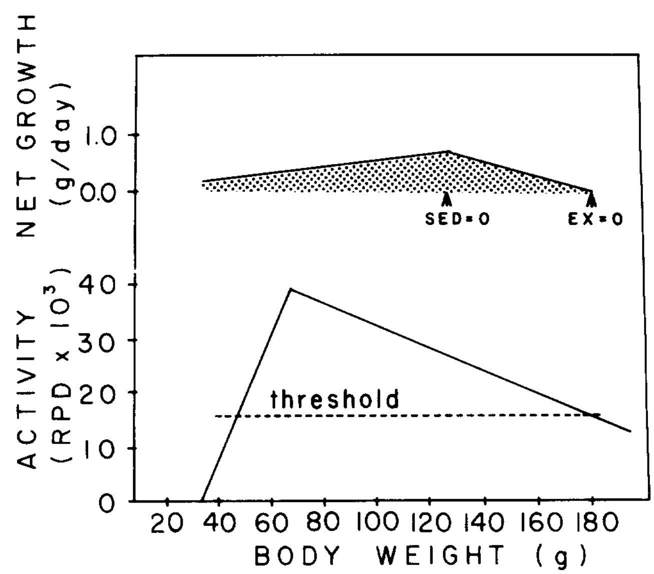

FIG. 1. Top: Net growth stimulated by exercise in excess of the spontaneous growth rate displayed by sedentary animals which is represented by the baseline (net growth 0.0 g/day). Arrows indicate starting body weights at which sedentary growth rate was 0.0 g/day, SED=0, and at which exercise failed to increase body weight, EX=0. Bottom: Levels of voluntary running activity on horizontal discs as a function of 5 g increments in body weight. Adapted, with permission, from reference [2].

they were housed in cages with activity devices. They were maintained on ad lib supplies of Purina laboratory chow, unshelled sunflower seeds, and water, supplemented by fresh vegetables and fruit. All animals were adults. Female hamsters (*Mesocricetus auratus*, family Cricetidae) were obtained from Con Olson, Madison, WI and Engle Laboratory Animals, Farmersburg, IN. Gerbils of both sexes (*Meriones unguiculatus*, family Cricetidae) were obtained from a colony maintained at The University of Michigan Anatomy Department. Female albino rats (*Rattus norvegicus*, family Muridae) of Sprague-Dawley strain were obtained from the Carworth Division of Charles River Breeding Laboratories, Wilmington, Mass. Golden-mantled ground squirrels (*Callospermophilus lateralis*, family Sciuridae), of both sexes, were trapped in Texas and were maintained in laboratory three years prior to the start of this study.

Experimental Design

In Experiments 1 and 2 animals were matched by weight and, where appropriate, by sex, and assigned to three conditions: sedentary, disc exercise, and wheel exercise. In Experiment 1, female hamsters, weighing 120.0 ± 2.8 g were assigned to three conditions in groups of 12, 17, and 18 animals, respectively. In Experiment 2, distribution of animals among sedentary, disc exercise, and wheel exercise groups was, respectively, for 12 male and 12 female gerbils 12, 6, and 6, for female rats 20, 8, and 18, and for 4 male and 8 female ground squirrels 4, per group. Three additional ground squirrels were removed from the study because of intermittent hibernation resulting in smaller final groups of uneven weight.

In Experiment 3, 22 hamsters, ranging in age between 27 and 160 days, and three litters of hamsters, 10 to 26 days old and containing between 8 and 13 pups, were exposed to exercise for 5–7 days to record the pattern of their running activity. Litters were deliberately left to vary in numbers of pups to produce greater diversity of body weights.

Activity Devices and Duration of Running

Animals were exposed to disc activity in acrylic boxes with a freely-turning horizontal activity disc. Boxes for rats and ground squirrels were 40 cm long, 35 cm wide, and 42 cm high, with activity disc 30 cm in diameter. Boxes for hamsters and gerbils were 40 cm long, 30 cm wide, and 40 cm high, with activity disc 25 cm in diameter. Animals were exposed to rotating wheels in cages containing a living compartment with a side entrance to an adjacent vertically-rotating wheel. Rats and ground squirrels were housed in Acme activity boxes (Hazelton Systems, Cincinnati, OH), which consisted of a living compartment 37 cm long, 15 cm wide and 18 cm high, and a rotating wheel 14 cm wide and with a 113 cm circumference. Hamsters and gerbils were housed in Wahmann activity boxes (Wahmann Manufacturing Co., Timonium, MD) which had a living compartment 25 cm long, 13 cm wide and 15 cm high, and a rotating wheel 11 cm wide and with a 111 cm circumference. Activity of hamsters prior to weaning on Day 26 was obtained by housing litters of hamsters with their lactating mother in specially designed acrylic boxes previously described [2]. A playground area containing three freely-moving disc exercisers (15 cm in dia.) was accessible to pups but not to the lactating female. The most frequently used disc in each box was equipped with a microswitch and was used to record running activity.

In Experiment 1, exposure to exercise lasted 35 days. Six hamsters on wheels were allowed to continue running through Day 55. Extended exposure to exercise was used to determine with greater confidence whether or not exercise-induced growth took place. In Experiment 2, gerbils were given a 30-day exposure to exercise and ground squirrels a 55 day exposure. In rats, exposure to exercise lasted 38 days for animals on discs and for 10 animals in wheels, and 55 days for 8 animals in wheels.

Growth Measurements

The influence of exercise on somatic growth was evaluated by daily measurements of weight change in all species. Ponderal growth rates (g/day) were determined from the slopes of least squares linear regressions of body weight as a function of time during periods when the rates of weight gain were linear.

Ponderal growth rates were determined for Days 7–35 for hamsters in Experiment 1, for Days 7–30 of exercise and 31–38 of retirement for gerbils in Experiment 2, for Days 7–38 of exercise for rats, and Days 7–55 for ground squirrels. In addition, measurements of linear growth in hamsters were taken on the first and last day of wheel exercise based upon a standardized method [4]. Length measurements were taken between the tip of the nose and the tip of the tail by extending the hamster to its maximal extent with its ventral surface down over a cm scale. This type of measurement correlates well ($r=0.98$) with the composite of length measurements of skull, body, and tail determined radiographically [4].

Activity Measurements

Daily activity measurements were recorded in revolutions

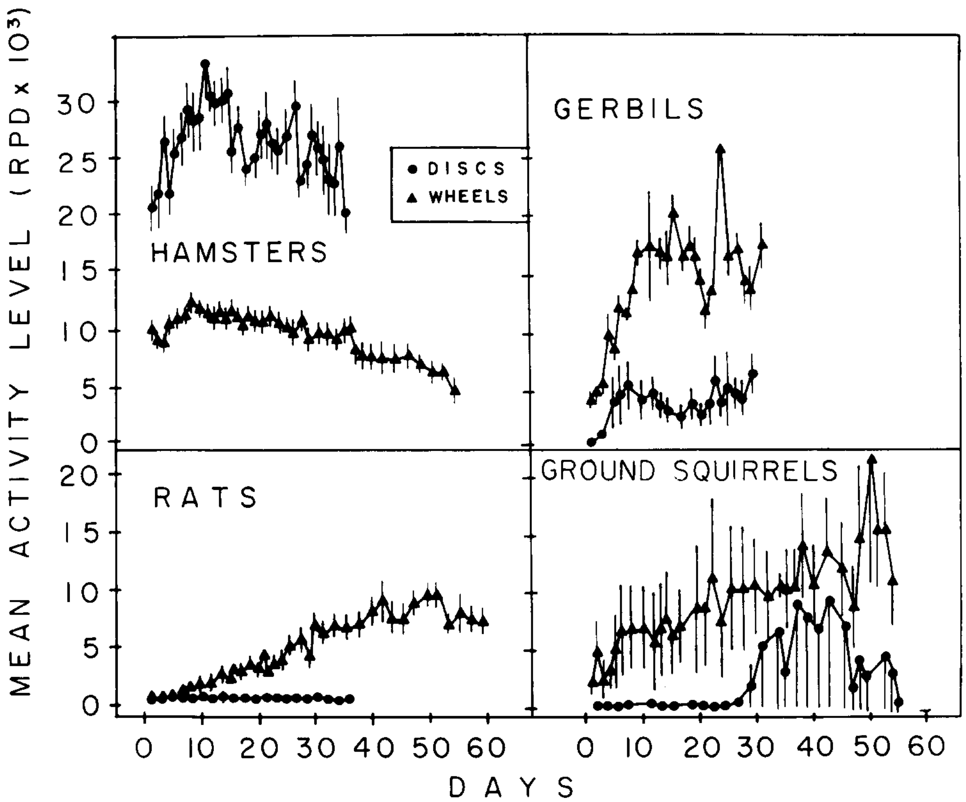

FIG. 2. Mean daily revolutions generated by hamsters, Mongolian gerbils, rats, and golden-mantled ground squirrels exposed to horizontal discs (solid circles) or vertical rotating wheels (solid triangles).

per day (RPD) on mechanical (rotating wheels) or electromechanical (horizontal discs) counters every 24 hr. Running pattern was determined from pen markings of disc turns on Harvard cumulative event recorders. Paper speed was 5 mm/min. Disc turns induced an 0.25 mm sideway pen excursion. From these paper records the following aspects of activity patterns were determined by measurements of time spent running or resting: duration and number of runs, duration of pauses, and speed of running during runs. Runs were defined as episodes of activity consisting of 20 disc revolutions or more which were flanked by inactive periods of 150 sec or longer. Pauses were periods of inactivity lasting 150 sec or longer. Speed of running was number of revolutions per minute (RPM) measured from the rate of sideway pen excursion within individual runs.

To make activity measurements from the two activity devices amenable to statistical analysis revolutions were also converted to linear velocities (km/day) using wheel circumferences and the running radii for the two sizes of horizontal discs. The 25 cm disc had a running radius of between 6.25 and 9 cm and the 30 cm disc, a radius of between 7.5 and 11 cm, as determined from animal footprints on soiled discs.

To facilitate inter-species comparisons of various features of running activity, linear running speeds and total daily activity levels have also been expressed in body length units (UBL) by using the mean length values characteristic for a given species [30].

Data Analysis

All data are presented as means and standard errors. Comparisons involving two, three, or four experimental groups were made, respectively, with Student's *t* test, one-way and two-way analyses of variance and Scheffe's simultaneous inference procedures [27]. Durations and numbers of runs, duration of pauses, and running speed were determined on a daily basis. The 175 data points obtained in this way for each variable were then analyzed for their relationship to body weight of the individual hamsters on a given day. Relationships of various parameters of running activity to body weight were evaluated by means of least squares linear regression (and an F test for slope) as a function of 5 g increments in body weight. To determine the accuracy of measurements of disc revolutions from cumulative paper records, total computed number of daily events was compared to RPDs registered on counters and the error obtained was less than 1%.

RESULTS

EXPERIMENT 1: IS EXERCISE ON HORIZONTAL DISCS NECESSARY FOR ACCELERATION OF GROWTH IN HAMSTERS?

Although hamsters readily run in rotating wheels [7,31] as well as on horizontal discs [1,2] acceleration of somatic growth was noted so far only in the latter activity device [4]. Experiment 1 examined whether running activity on horizontal discs and in vertical wheels induced comparable acceleration of somatic growth in adult hamsters.

On discs, hamsters generated 27,468 ± 1646 RPD's and on wheels they registered 10,601 ± 686 RPD's (Fig. 2). Activity levels in both activity devices rose to highest values within the first 10 days of running and showed a gradual decline throughout the remaining 3–4 weeks. Hamsters ran 11.8 ± 0.8 km/day in wheels and between 10.8 ± 0.6 km/day

TABLE 1

ACTIVITY LEVELS, IN KILOMETERS PER DAY, FOR THE FOUR SPECIES OF RODENTS EXPOSED TO HORIZONTAL DISC AND VERTICAL WHEEL. TWO FUNCTIONAL RADII FOR DISCS WERE USED, 9 cm (A) AND 6.25 cm (B) FOR THE 25 cm DISC AND 11 cm (A) AND 7.5 cm (B) FOR THE 30 cm DISC TO ESTIMATE LINEAR VELOCITY ON DISCS

Hamsters	A	15.5 ± 0.9	11.8 ± 0.8
	B	10.8 ± 0.7	
		(n=18)	(n=17)
Gerbils	A	1.9 ± 0.6	18.3 ± 1.6
	B	1.7 ± 0.4	
		(n=6)	(n=6)
Rats	A	0.2 ± 0.03	4.6 ± 0.6
	B	0.2 ± 0.02	
		(n=8)	(n=18)
Ground squirrels	A	1.7 ± 1.6	11.4 ± 3.6
	B	1.2 ± 1.1	
		(n=4)	(n=4)

(NS) and 15.5 ± 0.9 km/day ($p<0.01$) on discs depending on which running radius, 6.25 cm or 9 cm, is assumed as best representation of their disc activity (Table 1, A and B, respectively).

Exercise-induced changes in somatic growth are shown in Fig. 3 and Table 2. Both types of exercise led to significant increases in ponderal growth rate in hamsters relative to sedentary controls (0.1 ± 0.1 g/day), although the growth rate induced by disc exercise was significantly greater (0.7 ± 0.1 g/day $p<0.001$) than that associated with wheel exercise (0.5 ± 0.1 g/day, Table 2). Exercise in wheels induced significant linear growth (0.81 ± 0.15 cm, $p<0.02$) relative to sedentary hamsters (0.30 ± 0.09 cm) over the corresponding 35-day period of time. On the final, 55th day of the experiment, body weights of both exercised groups were significantly greater (disc hamsters: 144.8 ± 4.6 g, wheel hamsters: 142.0 ± 4.8 g, $p<0.05$) than in sedentary hamsters (120.8 ± 3.8 g).

Thus, acceleration of growth by exercise is not restricted to hamsters exercising on horizontal discs [1] but takes place also in hamsters running in vertical wheels.

Since the activity levels, expressed as distance traveled daily, are not convincingly greater for hamsters running on discs than for hamsters activating wheels (Table 1) different mechanical properties of the two activity devices may be responsible for greater acceleration of growth by disc exercise (Table 2).

EXPERIMENT 2: IS ACCELERATION OF GROWTH A RESPONSE PECULIAR TO HAMSTERS?

Although voluntary running in activity wheels has been noted in invertebrates [28], birds [19], marsupials [23], primates [18], carnivores [18,20] and rodents [7, 15, 16, 17] little information is available on somatic and physiological consequences of such activity. In one study [15] three months of voluntary wheel activity did not affect body weights of two specimens of white-footed mice. Experiment 2 was done to determine whether voluntary exercise in activity wheel or on horizontal discs influences somatic growth in three species of rodents other than hamster.

Activity levels of gerbils, rats, and ground squirrels in two types of activity devices are presented as revolutions per day in Fig. 2 and as linear velocities (km/day) in Table 1. All three ran more vigorously in rotating wheels (gerbils:

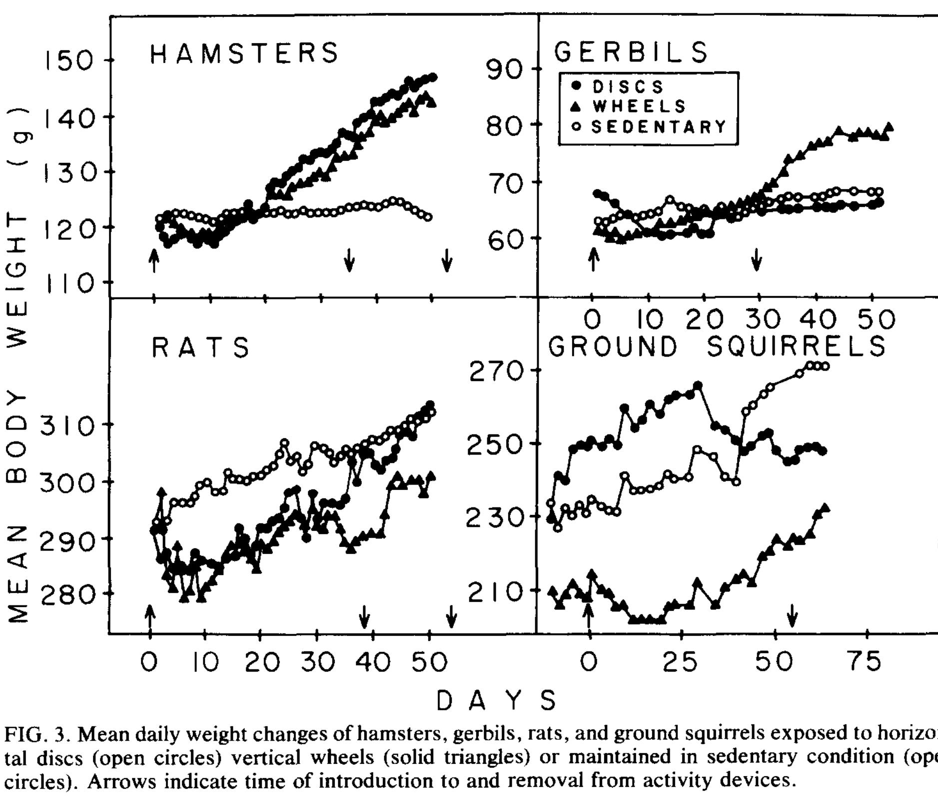

FIG. 3. Mean daily weight changes of hamsters, gerbils, rats, and ground squirrels exposed to horizontal discs (open circles) vertical wheels (solid triangles) or maintained in sedentary condition (open circles). Arrows indicate time of introduction to and removal from activity devices.

TABLE 2

PONDERAL GROWTH RATES (g/day) AS A FUNCTION OF EXERCISE ON HORIZONTAL DISCS, IN VERTICAL WHEELS, OR OF SEDENTARY CONDITION

	Exercising		Sedentary			
	Discs	Wheels		F	(*df*)	$p<$
Hamsters (Day 7–35)	0.73 ± 0.05 (n=16)	0.52 ± 0.07 (n=17)	0.11 ± 0.08 (n=12)	20.84	(2,42)	0.001
Gerbils (Day 7–30)	0.05 ± 0.08 (n=6)	0.29 ± 0.03 (n=6)	0.07 ± 0.05 (n=12)	5.058	(2,21)	0.025
Rats (Day 7–38)	0.56 ± 0.11 (n=8)	0.39 ± 0.11 (n=18)	0.23 ± 0.08 (n=20)	2.026	(2,43)	N.S.
Ground squirrels (Day 7–55)	−0.29 ± 0.53 (n=4)	0.43 ± 0.08 (n=4)	0.79 ± 0.33 (n=5)	1.280	(2,10)	N.S.

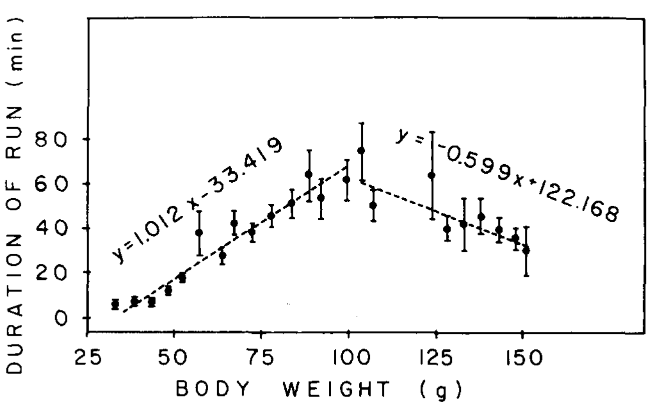

FIG. 4. Mean duration of runs as a function of 5 g increments in body weight for hamsters running on horizontal discs.

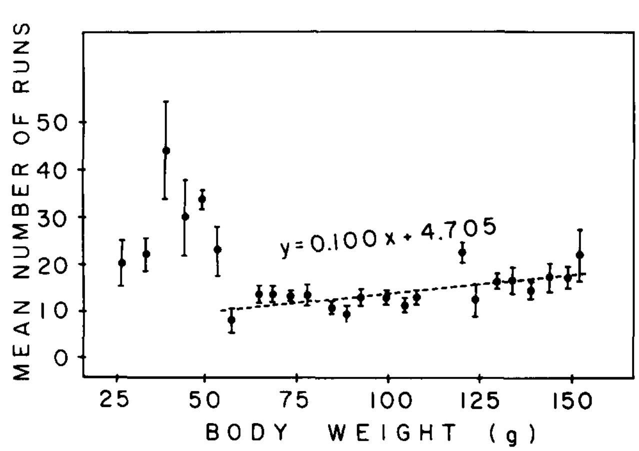

FIG. 5. Mean number of runs as a function of 5 g increments in body weight for hamsters running on horizontal discs.

16,481 ± 1400 RPDs; ground squirrels: 10,065 ± 3205 RPDs; rats: 4112 ± 599 RPDs) than on discs (gerbils: 4208 ± 946 RPDs; ground squirrels: 2442 ± 2357 RPDs; rats 322 ± 39 RPDs). Rats and ground squirrels showed sustained and gradual increases in activity levels in rotating drums, while gerbils, like hamsters, reached maximal levels of running activity within one week of exposure to both activity devices (Fig. 2).

When rodent running rates are expressed as linear velocities (km/day) to allow comparisons between the two activity devices, consistently high values are shown by three species running in wheels, gerbil, hamster, and ground squirrel, and by hamsters running on discs ($p<0.001$), and consistently low rates are displayed by rats running in either device and by gerbils and ground squirrels running on discs (Table 1). The same conclusion is reached regardless of which running radius, a 9 cm one, Table 1, A, $F(7.80)=37.794, p<0.001$, or a 6.25 cm one, Table 1, B, $F(7.80)=35.43, p<0.001$, is used to compare linear velocities on discs. The use of the more conservative value of 6.25 cm abolishes the significant difference ($p<0.001$) between the running rates of hamsters on discs and in wheels which is apparent when the 9 cm radius is used.

Changes in the rate of weight gain as a function of exercise on the two types of activity devices in the three species of rodents are shown in Fig. 3 and Table 2. Only gerbils running in wheels displayed a significant 4 to 6-fold increase in ponderal growth rates relative to sedentary and disc-running animals. In addition, ponderal growth rate of these animals remained significantly greater (0.96 ± 0.16 g/day, $p<0.01$) than in sedentary gerbils (0.27 ± 0.5 g/day) during the first week of retirement from exercise. Weight levels of gerbils exercising in wheels did not differ on the last day of exercise but diverged significantly by Day 42 of the experiment (wheel gerbils: 77.1 ± 1.2 g, disc gerbils: 66.0 ± 3.2 g, sedentary animals: 67.9 ± 2.4 g, $p<0.05$). There was no sex difference in activity levels or in ponderal growth rates.

Body weights of exercising rats were significantly lower than the weights of sedentary controls on Day 38 of exercise (wheel rats 290.0 ± 3.6 g, disc rats 303.7 ± 6.5 g, sedentary rats 307.8 ± 3.9 g, $p<0.05$), but did not differ on Day 55 of the experiment showing clearly that rats respond to voluntary exercise with a temporary weight loss [8, 17, 18] rather than with increased ponderal growth rate, regardless of the type of activity device employed. Exercise did not affect the rate of weight change in the ground squirrels (Table 2) suggesting a pattern of weight changes during exercise comparable to that of rats.

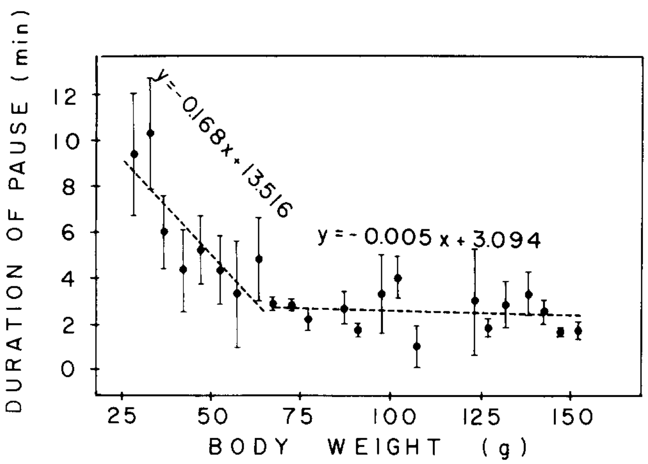

FIG. 6. Mean duration of pauses as a function of 5 g increments in body weight for hamsters running on horizontal discs.

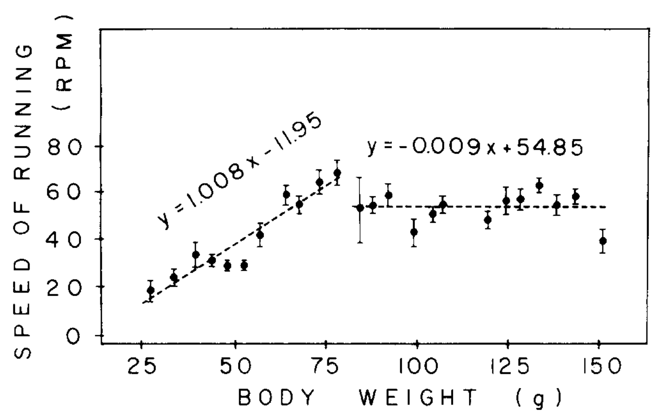

FIG. 7. Mean speed of running as a function of 5 g increments in body weight for hamsters running on horizontal discs.

Thus, exercise-induced growth appears to take place in at least one additional rodent species, gerbil, which shares close phylogenetic relationship, similar body size, and adaptation to existence in similar habitats, with hamsters.

EXPERIMENT 3: WHAT TYPE OF RUNNING PATTERN ACCOMPANIES MAXIMAL ACCELERATION OF GROWTH IN HAMSTERS?

Experiment 3 examined the pattern of changes in number and duration of runs, duration of pauses and in speed of running as a function of increasing body weight.

Mean duration of runs as a function of 5 g increments in body weight is shown in Fig. 4. Runs grew longer by 1 min for each 1 g increase in body weight at body weights between 35 and 100 g as described by a linear regression $y=1.012 \times -33419$ ($r=0.964$). At body weights above 100 g, runs became shorter by about 36 seconds for each 1 g increase in body weight as descibed by a linear regression $y=-0.599 \times +122.168$ ($r=0.674$).

Mean number of runs is shown in Fig. 5. At body weights below 55 g, numbers of runs fluctuated widely. Since these values were obtained from litters varying in numbers of pups and from one out of three available activity discs, they do not reflect accurately numbers of runs for individual animals. At body weights above 55 g, there was an orderly and gradual increase in number of daily runs from 10 runs in hamsters weighing 52 g to 20 runs in hamsters weighing 153 g, as described by a linear regression $y=0.100\times +4.705$ ($r=0.734$).

Duration of total daily running time as a function of body weight can be derived from recorded activity levels and regressions for the speed of running as a function of body weight (50 and 100 g hamsters) and can be predicted (180 g hamsters) from regressions for total number (Fig. 5) and duration of individual runs (Fig. 4). At 100 g, when exercise leads to near-maximal acceleration of growth (Fig. 1), hamsters spend 10 hours per day in active running. At body weights of 50 and 180 g which mark the limits of exercise-induced growth (2, Fig. 1), hamsters engage in between 4.3 and 5.4 hours of running, respectively.

Mean duration of pauses is presented in Fig. 6. At body weights below 65 g, duration of pauses sharply declines by about 10 sec for each 1 g increase in body weight as described by a linear regression $y=-0.168\times +13.516$ ($r=0.800$). At body weights above 65 g, pauses remain relatively stable at between 150 and 170 sec. Mean number of pauses corresponds to mean number of runs which were shown in Fig. 5.

Mean running speed is shown in Fig. 7. At body weights below 80 g hamsters accelerate their running levels by 1 RPM for each g of weight increase as described by a linear regression $y=1.008\times -11.952$ ($r=0.945$). At body weights above 80 g, running speed remains relatively constant at about 55 RPM as described by a linear regression $y=0.009 \times +54.85$ ($r=0.009$).

This experiment thus shows that within the weight range permitting exercise-induced growth, hamster running activity has the following characteristics: (1) Hamsters run at, or slightly below, their highest disc speeds of 55 RPM (Fig. 7) or 35–51 cm/sec., (2) They generate between 10,000 and 32,500 revolutions per day, an equivalent of between 3.9 and 18.4 km or of between 23,000 and 108,000 UBLs, (3) They spend between 4.3 and 10 hours in active running, (4) distributed in between 10 and 23 runs (Fig. 5), (5) each lasting between 17 and 62 min (Fig. 4), (6) They break their runs for brief pauses of between 150 and 170 sec (Fig. 6).

DISCUSSION

Unambiguous exercise-induced growth has so far been described only in one experimental situation, in adult golden hamster freely running on a horizontal disc [1, 2, 4]. It was of interest to determine whether this phenomenon was peculiar to this species and activity device or had a wider significance. We found that hamsters respond with increased growth to voluntary activity in either of the two activity devices (Table 2, Fig. 3). The phenomenon is therefore not device-specific. Hamsters maintained similar levels of activity in both devices, but disc exercise was more effective in stimulating growth than wheel exercise (Table 1). It is probable that physical differences in the two activity devices, such as momentum, friction at the axis, and running distance from the axis of rotation, influence some aspect of running behavior and the resulting somatic growth. In addition, the two exercisers may provide different opportunities to engage in a variety of locomotor behaviors as well as in taking of free rides.

We next found that exercise-induced growth is also not species specific. In rotating wheels gerbils displayed high levels of voluntary activity (Table 1, Fig. 2) and an increase in the rate of growth, which, as in hamsters [1], persisted for several days after the termination of exercise (Fig. 3, Table 2). Thus, although direct measurements of somatic growth such as radiographic measurements of bone lengths [4], determination of lean body mass [5], and standardized measurements of body length [4] have not been carried out in exercising species other than hamster, the similarities in the pattern of weight change in hamsters and gerbils and the temporal relationship of such change to exercise, strongly suggest that exercise stimulates somatic growth in both species.

We next tried to determine the distinguishing features of growth-inducing exercise. We were prompted to do so by the earlier observation that the total daily running activity in hamsters changes in a similar way the exercise-induced growth changes when body weight increases between 50 and 180 g and when hamsters generate over 15,000 RPD (Fig. 1). This prompted us to hypothesize that some aspects of running levels above 15,000 RPD may be necessary for acceleration of growth by exercise [2]. Since animals can generate the same daily activity levels by varying numbers of runs, durations of uninterrupted runs, durations of pauses and speed of running, we measured these various components of total daily activity in hamsters running on discs (Experiment 3) and compared our findings to observations made by others on running behavior in wheels by other animal species.

We first considered the possibility that exercise is most effective in accelerating growth when hamsters attain some threshold running speed. This hypothesis was not confirmed. At body weights below 80 g, running speed was inversely proportional to body size, while at body weights above 80 g, running speed was relatively constant at about 55 RPM or 35–51 cm/sec (Fig. 7). While it is possible that a running speed of 55 RPM may be necessary for acceleration of growth because it is present within the 50–180 g weight range, it is also clear that this running speed is not a sufficient stimulus for exercise-induced growth. Increased growth is possible at body weights of 50–80 g when running speed is lower, and growth acceleration is absent at high body weights when hamsters maintain the speed of 55 RPM. Furthermore, hamsters are relatively slow runners compared to other animal species. Gerbils [26] and hamsters run at similar speed (30–51 cm/sec, 2–3 UBL/sec) while rats [14,25], weasels [20], and white-footed mice [16,17] run between two and four times faster.

We next considered the duration of uninterrupted runs and found that it varies a great deal within the effective weight range for growth (Fig. 7). Furthermore, the pattern of change in duration of runs is remarkably similar (Fig. 4) to changes in exercise-induced net growth as a function of weight increase between 50 and 180 g (Fig. 1). Thus at body weight lower than 50 g and higher than 180 g hamsters run without a pause for about 10 min or less. At body weight between 90 and 110 g, hamsters run for up to one hour without a break. Such close relationship between duration of uninterrupted runs and magnitude of exercise-induced growth suggests that these two variables are functionally related. Furthermore, duration of runs at weights supporting exercise-induced growth are strikingly longer in the hamster than durations of runs reported for other animal species. Running episodes in other species are usually ten times (genets, 20), a hundred times (rat, 14,25; foxes, 18,20; weasels, 18,20) or a thousand times shorter (macaque, grison, cats, 18) than the longest runs in hamsters.

Although hamsters run exceptionally long without taking a break, they generate average levels of total daily activity in comparison to other species. Daily linear velocity (km/day) of hamsters and white-footed mice [15, 16, 17] is between 12 and 14. Gerbils (Table 1), foxes [18,20] and weasels [18,20] run twice as much, while rat [14,25] covers only 2–5 km/day.

We also examined the pattern of changes in number and duration of pauses as a function of hamster weight. We have found that throughout the effective weight range hamsters break their running activity between 10 and 20 times (Fig. 5), and that they pause for about 2–3 min at a time (Fig. 6).

This analysis depicts hamster as an average runner in terms of distances covered per day, a below average runner in terms of speed, and above average runner in terms of length of time actually spent running. Since hamsters engage in between 10 to 20 running episodes each night (Fig. 5), which at the optimal body weight of about 100 g, may last as long as one hr each, it follows that hamsters spend in excess of 10 hr per night in actual physical activity, and pause infrequently for a very brief time. Although equivalent measurements have not been carried out in gerbils, one study, uncorrected for pauses [28] indicates that gerbils spend 10–12 hr per day in vigorous running activity. In contrast, species which showed no exercise-induced growth in Experiment 2 and other studies either ran equally fast but for a shorter distance daily (foxes, macaque), ran faster but for a shorter distance daily (rats), or ran faster for the same distance as hamsters daily (mice). Only hamsters and probably also gerbils, the two species exhibiting exercise-induced growth, carried out substantial levels of voluntary running activity at moderate speeds for prolonged periods of time, and interrupted by very few brief pauses.

We conclude, therefore, that under the circumstances of slow growth such as is seen in adult hamsters and gerbils as well as in preadolescent children, some neuroendocrine mechanism suppresses somatic growth. Under such circumstances, prolonged running activity at low speed provides necessary and sufficient stimuli for acceleration of growth in the two species of rodent. A recent study [29] suggests that this hypothesis could be worth testing in stunted or undernourished children as well.

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