Physical Performance Capacity and Nutriture: Evaluation of Rations by Animal Experimentation

By D. R. Young, PH.D. and Harry Spector, PH.D.

Nutrition research was at first largely concerned with measurement of energy metabolism, determination of the essential nutrients, and delineation of the syndromes resulting from specific nutrient deficiencies. These studies emphasized such criteria as changes in growth, reproduction, lactation, gross and tissue pathology. It has been amply demonstrated in these investigations that nutritional deficiencies adversely affect a large number of tissues in the body—the effects varying in degree and in kind with the individual tissue[1] from simple alterations in chemical composition to profound morphologic changes. Other investigations indicated that nutritional inadequacies resulting either from dietary deficiencies or conditioned malnutrition may in many cases become more manifest as changes in physical performance or as alterations in the biochemical and physiologic responses to work stresses.[2]

That performance is the ultimate criterion of physical fitness is axiomatic. It is logical, therefore, that the attention of the nutritionist has been directed to the influence of nutrition on work capacity. Theoretical considerations led some enthusiasts to pursue the hope that a special state of robust health and "superman" performance capacity could be achieved by special diets, particularly those abundant in the vitamins and the "ergogens".[3] While research has exploded this idea it has undeniably demonstrated that deficiency of any essential nutrient results sooner or later in physical deterioration. But how low the dietary intake of specific nutrients can be without evidence of deterioration in the ability to do work is still unsettled. This situation has resulted in part from difficulties in objective measurement of performance in man: human performance is conspicuously dependent on motivation, and long training periods may be required in order to establish a reasonably stable level of skilled performance.

Nowhere is the premium on maximum performance greater than in military personnel of the modern army. In the last analysis, its efficiency is determined by the ability of individual men to perform assigned missions. In order to design and develop rations which will maintain the performance capacity of the human engine at a level essential to realization of a full military potential, it is important to utilize criteria of military significance for the evaluation of the nutritional adequacy of combat rations. Physical performance capacity has obvious appeal as such a criterion. Maximum utilization of this criterion in military ration development requires that tests be developed which take advantage of the speed, economy, and rigor of control of animal experimentation.[4]

The purpose of this paper is to review critically the methods available for the measure-

From the Quartermaster Food and Container Institute for the Armed Forces, Chicago, Illinois. This paper has been assigned number 640 in the series of papers approved for publication. The views or conclusions contained in this report are those of the authors. They are not to be construed as necessarily reflecting the views or endorsement of the Department of Defense.

Presented at a Symposium on Nutrition and Behavior held at the Laboratory of Physiological Hygiene, University of Minnesota, April 27, 1956, with the cooperation of the National Vitamin Foundation, Inc., New York and under the sponsorship of the School of Public Health, University of Minnesota.

ment of physical performance capacity in man and animals, to examine briefly the literature on the relationship of diet to performance, and finally to appraise the potential for developing suitable technics for measurement of physical performance capacity of animals as a criterion of nutritional adequacy of the diet.

PERFORMANCE TESTS IN MAN

The physical performance tests now in use fall into two major categories: (a) direct measurements of performance under standard conditions and (b) indirect tests involving the measurement of physiologic or biochemical changes at the end of, or during recovery from a work task. In the latter type of measurement the work task may be maximal or submaximal. For man the problems of performance analysis with special reference to the impact of nutrition on performance, have been discussed by a number of authors.[5–10] Tests of industrial performance have measured such human abilities as (a) general dexterity of finger, hand-wrist, and arm, (b) dual hand dexterity, (c) bilateral hand dexterity, (d) hand-foot coordination, (e) machine tending ability, and (f) inspection ability. A large number of work situations have been set forth by Brožek and Monke[11] as potential tools for investigating the numerous variables associated with occupational performance.

Much more, however, has been done in the area of strictly physical (non-productive) performance, with procedures and test methods designed to determine either strength or endurance, or both. Coordination of will power, mechanical precision, and the durability of the physiologic and biochemical processes, lend themselves to factor analysis and estimates of the variables involved in the continuous performance of a motor task. Each component of overall fitness is in itself a function of many parameters, of which nutritional effects are but one element. Constitutional type ("body build") has been related by Sheldon[12] to capacity for strenuous physical work and to nutriture by Brožek.[13] Several interrelationships between body composition and physiologic requirements for specialized activities have been set forth by Behnke.[14] Keys, *et al.*[15] found that chronic undernutrition produced marked deterioration in strength, and especially in endurance.

Government agencies have used the "physical fitness" tests with both military and civilian personnel.[16–20] Numerous athletic tests have been evaluated by Cureton, *et al.*[21] The most useful endurance tests have been found to involve rowing, pedalling, step-ups with or without added weights (pack test), weight lifting (bucket test), pulling (stoneboat test), swimming, walking or running, and treadmill running. All can be graded in terms of intensity to permit investigation of the effects of light, heavy, or moderate work. Measurements taken after the completion of light or moderate work have provided much useful information for the general study of the physiology of exercise. However, most of the quantitative relationships between physical fitness and nutritional state have been established by tests that have approached maximal physical performance.

Whereas work tests have been successfully conducted both in the field and in the laboratory, the most successful tests of mental or neuromuscular function have been conducted only in the laboratory, although some useful information pertaining to neuromuscular fitness has been brought to light by field agility testing. The laboratory tests include measures of strength, speed, and coordination and provide data on visual and auditory acuity as well as motor performance. Many of these have been listed by Keys *et al.*[15] and by Brožek and Taylor.[22] The neuromuscular and strictly mental tests will not be discussed here since it is believed that extension of these measures to laboratory animals is in most cases unrewarding due to difficulties in the standardization of such tests and interpretation of results. Moreover, intellective functions are not significantly altered by undernutrition even though the chemical alterations may be severe.[9,10]

Some of the problems of the measurement of fatigue and of exhaustion as an end point of work capacity have been discussed.[23] Fatigue is a resultant of many factors, including training and motivation. Motivation is especially difficult to assess since it is so susceptible to extrinsic and intrinsic factors, and, according to Carmichael *et al.*[24] in some cases not a continuous function of the duration of work. The effects of training on performance are well known and have been attributed by some exclusively to improved coordination.[25] However, the effects of training and motivation have been minimized in previous work tests where each subject has served as his own control in longitudinal studies, where motivation has been kept at a uniformly high level, and where body responses have been used to supplement performance time and efficiency as criteria of work capacity. Included in these are the measurement of bioelectric potentials of muscles,[24] changes in electrical impedance on the body surface,[26] alterations in the neuromuscular responses to galvanic stimulation,[27] changes in the thresholds of reflexes,[28] and the coagulation reaction of urine.[29] However, of the numerous attempts to relate work intensity to physiologic alteration, the most successful formulations have evolved from cardiovascular and respiratory responses to specific endurance tests. Effects of physical fitness on the physiologic responses to work are noted in Table I.

Extrapolation of respiratory and cardiovascular responses to work of known intensity

TABLE I[30–46]

Effect of Physical Fitness in Man on Physiologic Responses to Work

Level of activity	Index	Relative change* in unfit subjects	Reference
A. At rest	1. Pulse	+	30, 31
	2. Standing diastolic pressure	–	32, 33
	3. Standing systolic pressure	–	32, 34
	4. Pulse pressure	–	32, 34
B. Easy work that can be sustained in the steady state	1. O_2 consumption	+	35
	2. CO_2 production	+	35
	3. R.Q.	+	34
	4. Ventilation	+	36, 37
	5. Respiratory rate during work	+	36
	6. O_2 pulse	–	38
	7. Ventilatory efficiency	–	36
	8. Pulse rate during work	+	35, 39
	9. Pulse rate deceleration after work	–	35, 40
	10. Systolic pressure during work	+	39
	11. Rate of decline of systolic pressure after work	–	39
	12. Cardiac output-stroke volume	–	39, 41
	13. Mechanical efficiency	–	35, 39
	14. Blood lactate during work	+	42, 41
C. Exhausting work that cannot be sustained in the steady state	1. Duration	–	32, 33, 44
	2. Maximal O_2 consumption	–	43, 45
	3. Maximal CO_2 production	–	43
	4. R.Q.	+	35
	5. Maximal ventilation	+	36
	6. Ventilatory efficiency	–	34
	7. Oxygen pulse	–	38
	8. Maximal pulse rate during work	+	38, 45
	9. Pulse rate deceleration after work	–	38, 45
	10. Systolic pressure during work	–	32
	11. Rate of decline of blood pressure after work	–	32
	12. Blood lactate at end of work	–	43
	13. Blood sugar at end of work	–	46
	14. O_2 debt	–	30, 43

* + or – refers to relative increase or decrease as compared to a physically fit subject.

in order to predict work capacity in untried situations is usually complicated by the nonlinearity of relationships at high levels of work output. One example is the use of the maximal oxygen consumption as a measure of work capacity: at high levels of work intensity oxygen uptake is relatively constant or begins to decrease while the blood oxygen tension may not be significantly decreased. Moreover, because of the relatively fixed character of vital capacity, maximal ventilation and oxygen consumption may be only rough approximations of work capacity. Breath holding, which measures relative sensitivity to both low blood pO_2 and pCO_2, has also been proposed as a test of physical endurance. If a maximal value is desirable, recovery oxygen uptake may be a more rewarding criterion. On theoretical grounds there is also merit in using the blood lactate level in conjunction with respiratory data as a measure of performance capacity since its appearance in the blood in excessive quantities corresponds to a work output approximating two-thirds of the maximal.

Attempts to predict working capacity from cardiovascular responses to work have employed the relative changes in pulse rate and blood pressure, the recovery pulse rate, and a combination of blood lactate and blood pressure. Using these criteria, problems of fitness scoring frequently arise from the fact that for a given physical work intensity the maximal pulse will never be as high during certain types of malnutrition—due to concomitant bradycardia—as is found with normal dietary conditions.

PERFORMANCE TESTS IN ANIMALS

Three general methods of studying activity in experimental animals have been used: (a) artificial stimulation of perfused muscles, (b) measurements of voluntary activity, and (c) measurements of forced activity of the whole animal.

Artificial stimulation of muscles by the usual laboratory technics offers a method of successfully reproducing muscular activity, the advantage of careful control of extrinsic factors, and the possibility of obtaining precise measurements. However, it is difficult from the results obtained to predict causal factors which would limit muscular activity in the whole animal or to quantitatively extrapolate the measured activity to the physical capacity of the intact animal. In anesthetized animals numerous attempts have been made to evaluate the work done by artificially stimulated muscles in terms of the increased whole animal oxygen consumption invoked by the method. Despite stimulation of a diffuse area, whole animal oxygen intake has seldom been raised to a level higher than five times the basal rate. This intensity corresponds to steady state work and is unsatisfactory for evaluating nutritional effects on work performance. However, since the findings of Heron *et al.*[47] that intact muscles of anesthetized rats could contract continually for ten days, the method has been used extensively with a large variety of animals to study the biochemistry of muscular training, to assay endocrine function, and to study the metabolism of muscles and other tissues.[48–53] Recently Levine *et al.*[54] have used the method with rats and dogs to demonstrate that local vascular incompetence is of major importance in the onset of muscular fatigue.

Voluntary activity of animals has been used more extensively to provide information on physical performance, and has also provided measures of learning, drives, and aggressiveness. Three general technics have been used for quantifying voluntary activity; these employ (a) running drums (b) specially mounted cages from which diffuse activity is recorded, or (c) strictly observational measurements.

Of these three methods the revolving drum has been the most extensively used laboratory apparatus for investigating activity.[55,56] Depending upon the experiment, the animal may live entirely within the drum, have a separate living cage, or have access to supplemental diffuse activity cages.[57–63] The usual method of recording running activity has been by means of a counter which records the number of revolutions, thus measuring total activity. Skinner,[64] however, realizing the limitation of this measurement, used a Harvard work-adder attached to a writing lever which recorded activity on a kymograph—the slope of the line providing a measure of activity as a function of time.

With respect to diffuse activity, Szymanski[65,66] has described a spring mounted cage in which any movement of the cage due to animal activity actuates a recording system. The disadvantage of lack of damping encountered in the spring mechanism has been somewhat overcome by the tambour-mounted activity cages.[67] Measurements of diffuse activity include recordings of the activity of new born children, of chicks, and of monkeys.[68–70] Numerous modifications of this technic which provide greater sensitivity and improved precision have been discussed by others.[71–77] Along these lines Richter and Hines[78] have described a kinesthesiometer for monkeys in which the animal was attached by a chain to a rod—any movement of the rod activated a counter.

Additional measures of voluntary activity include the use of a tilt box in which movement of the animal from one end to another advances a counter or activates a photoelectric relay connected to a counter;[79,80] the use of a horizontal turntable from which activity can be measured either photographically or with a suitable recording device;[81] and the use of a pedometer which has been employed to record gross activity in the sheep and pig and head shaking in chickens.[82,83]

Purely observational means of measuring voluntary activity have been used by Beach,[84] Hall,[85] and Fredericson[86] who recorded either the time required or the behavioral pattern of rats while traversing a prescribed distance. Numerous maze studies reported in the literature will not be discussed here, since the primary purpose of these tests is to investigate learning and animal drives with only secondary attention being paid to work performance.

The most successful tests of *forced activity* in animals have been swimming tests for rats and dogs, treadmill tests for dogs, and work wheel tests for rats and mice.[87–97] Unfortunately many of the voluntary and forced activity measures mentioned above have been classified under the general term "animal activity." This failure to distinguish types of activity in terms of its measure has led to false concepts. Animal activity does not constitute a single behavioral category which can be measured with any single instrument, but must be considered for the present in terms of its method of measurement.

Several biologic and physical variables are known to contribute to intra-animal and inter-group variability. One is the difficulty in estimating the overall intensity of the work test. Although swimming to exhaustion offers the advantage of obtaining a reproducible end-point, swimming time in both rats and dogs is markedly affected by water temperature. Both high- and low-water temperatures decrease swimming capacity; these effects are related to the inability of the animal to maintain body temperature under extreme conditions.[98,99] In addition, work capacity might be limited by hyperventilation (panting for evaporative cooling) and the resulting alkalosis brought about by high water temperatures. It has been reported that the rat can swim as long as 48 hours at comfortable water temperatures; this period is obviously too long for a useful measurement of specific nutritional defects.

Although running tests have been satisfactorily conducted with dogs and larger animals, the use of work wheels and treadmills for rodents is limited. While reports have indicated that rats will voluntarily run a distance of 5 to 15 miles per day, forced activity at this rate has in many cases induced mortality indicating that factors other than muscular activity are involved.

Intrinsic as well as extrinsic factors contribute to the variability in results of voluntary activity tests. These factors include heredity, age, hunger, external environment, endocrine imbalance, and activity following confinement. Although uniformly high correlation coefficients for voluntary activity under specified conditions have been reported, it is believed that this is merely a reflection of the consistency of the equipment and fortunate selection of animals. This belief is strengthened by consideration of reports that rats in larger wheels run farther than those in smaller wheels, that within litter-mates some rats run only 200 revolutions per day and others as much as

2000, and that the number of revolutions per day are reduced when the rat is presented with a choice of physical distraction.[62] In addition, special consideration must be given to the fact that factors which influence diffuse activity in one direction may affect running activity in another direction.

By selective breeding Rundquist[100] has been able to get active and inactive breeds of rats, and although the daily activity periods were determined by the internal rhythm of the animal, the genetic factors could be obscured by certain environmental influences especially light and darkness. In this respect Browman[101,103] and Johnson[104] have been able to alter the daily activity rhythm of small animals by changes in light intensity. The reported effects of environmental temperature on voluntary activity have not been consistent. In young (poikilothermic) mice Stier[105] has found that the rate of activity is a function of body temperature and of several other factors, including quiescence and frequency of activity. More recently Jones *et al.*[106] have reported that when environmental conditions of temperature, light, and sound are controlled, activity of normal male rats in wheel cages is a function of the animal's experience in the wheel and age. For animals of equal experience, activity varies inversely with age, while in animals of equal age, activity varies directly with experience. The fact that the relationships are not linear indicates a possible interaction between these two factors affecting activity.

Considered *in toto* the measurement of voluntary activity, despite careful control of environmental factors and in the selection of animals to remove endocrine and genetic effects, leaves much to be desired as a measure of work performance. While such measurements have a recognized value in the study of animal behavior, this approach does not lend itself to a careful evaluation of nutriture. The interested reader is referred to other articles for further reviews on spontaneous activity.[107–111]

DIET AND PERFORMANCE

The literature on the influence of nutrition on work performance has been reviewed by Keys[10] and by Simonson[9] who questioned the reliability of a substantial part of the data because of the failure to define precisely performance uninfluenced by extraneous factors such as environment, training and motivation, and the questionable nature of the criteria used for definition of nutritional states and working capacity. It is our purpose, then, in this section to briefly re-emphasize the need for more exacting control and standardization of type and intensity of work tests, and to extract guiding information on the effect of dietary insufficiency on performance.

Lack of adequate controls and standardization has led frequently to conflicting reports on the effects of either dietary restriction or supplementation on work performance.

TABLE II

Rate of Onset of Deficiency Syndromes in Working Men Exposed to Complete Deficiency of One or More of the Important Nutrients*

Nutrient	Time before earliest deleterious effects appear in complete deficiency	Earliest deficiency syndromes and end results
Water	A few hours	Easy fatigue, poor performance. Eventual exhaustion of dehydration.
Calories	Two or three days	Easy fatigue, poor performance.
Sodium chloride	Several days	Easy fatigue, poor performance. Eventually, heat cramps.
Carbohydrate	Several days	Easy fatigue, poor performance. Eventually, nutritional acidosis.
Vitamin B complex	One or two weeks	Easy fatigue, poor performance. Eventually, one of the B-deficiencies, usually beri-beri.
Vitamin C	Several weeks	Easy fatigue, poor performance. Eventually, scurvy.
Protein	Probably several weeks	Earliest effects not known; late result, nutritional edema.
Vitamin A	Several months	Earliest effects not known.
Fats	Many months	Earliest effects not known.

* From Johnson, R. E.; Nutritional standards for men in tropical climates, *Gastroenterology,* 1: 838, 1943.

TABLE III[87,95,96,115–136]

Some Effects of Diet on Performance in Animals

Nutrient	Dietary treatment	Animal	Type of activity	Effect on activity*	Reference
A. Water	1. Deprivation	Rat	Running†	+	115
B. Minerals	1. Total deprivation	Rat	Running	+	116
	2. Mg deprivation	Rat	Running	−	115
	3. P or Fe deprivation	Rat	Learning	−	117
C. Calories	1. Total deprivation (fasting)‡	Rat	Enforced running	−	96
D. Fat	1. 1–10% fat	Rat, mouse	Swimming at 37° C	0	118
	2. 10% fat	Rat, mouse	Swimming at 20° C	−	118
	3. 40% fat	Rat	Swimming at 32° C	+	119
E. Protein	1. Protein restriction	Rat	Running	−	120
	2. Protein deprivation	Rat	Learning	−	121
	3. Lysine deprivation	Rat	Running	+	122
	4. Supplementation with cystine or glutamic acid	Rat	Learning	0	123
F. Vitamins	Deprivation				
	1. Vitamin A	Rat	Learning	0	124
	2. Thiamine				
	a. Acute	Rat	Running	+	95
	b. Chronic	Rat	Running	−	95
	c. Chronic	Mouse	Aggressiveness	0	125
	3. Thiamine and riboflavin	Rat	Learning	−	126, 127
	4. Thiamine, riboflavin, and nicotinic acid	Rat	Running	0	128
	5. B-complex				
	a. Acute	Rat	Learning	−	129
	b. Chronic	Rat	Running	−	130
	Excess supplementation				
	1. Thiamine	Pigeon	Flying	+	131
	2. B-complex (in perfusion medium)	Frog	Muscle contraction	+	132
G. Miscellaneous "Factors"	Addition of:				
	1. Propylene glycol	Rat	Running	+	133
	2. Diethylene or dipropylene glycol	Rat	Running	−	133
	3. Thyroxine, diiodothyronine, or methylene blue	Dog	Running (treadmill)	0	134, 135
	4. Desiccated liver	Rat	Swimming at 20° C	+	87
	5. Wheat germ oil	Guinea pig	Swimming at 37° C	+	136

* + = increase in activity; − = decrease in activity; 0 = no change in activity.

† Spontaneous running unless otherwise indicated.

‡ Decrease in running was influenced by the previous diet in the following order: Fat < Carbohydrate <Protein.

Thus, effects of a given dietary treatment as measured by moderate (steady-state) work may be unlike those obtained by measures of heavy work of relatively short duration. Bicycle ergometer tests and treadmill tests may elicit significantly different responses.[112,113] In past considerations of these methods, it has been argued that one measures endurance and coordination while the other measures endurance and strength. It is entirely possible that the requirements for one do not necessarily reflect the immediate needs of the other.

Bearing in mind the various factors involved in nutritional deficiencies, what sort of picture may be drawn of the course of events which may be expected to occur as the deficient state develops? Current knowledge is inadequate to establish precisely the pattern of deterioration in fitness. For general guidance a chart was developed by Johnson[114] and is reproduced here as Table II. It can be seen that easy fatigue and poor performance are generally amongst the earliest deleterious effects to appear in working men exposed to complete deficiency of an essential nutrient.

Some relationships between diet and animal performance are set forth in Table III.

EVALUATION OF POTENTIAL OF MEASURING NUTRITIONAL ADEQUACY OF RATIONS BY PERFORMANCE IN ANIMALS

What loss in operational efficiency may result from drastic dietary changes? It is particularly germane to ask if populations adapted to a normally *luxus* consumption of nutrients would suffer a significant loss in performance capacity if the diet were abruptly altered and limited.

When is the deterioration of performance likely to reach serious proportions if the dietary deficiency continues unabated? Why does the ability to do physical work fall off at different rates with different nutrient deficiencies? And conversely, why does rate of recovery of ability to perform vary with the nutrient which has been depleted?

It is believed that animal studies offer many advantages for the development of basic data which will provide the answers to these important questions. Desired test methods are those which impose a measurable and recognized strain on the animal. Severity should be sufficiently flexible to permit investigation not only of acute "all-out" effort, but submaximal work sustained for prolonged periods. Equipment and procedures should be versatile enough to permit investigations of the effects of environment superimposed on dietary and work stress. A review of the literature reveals two promising methods: (a) swimming and (b) running.

Comprehensive test systems should include measurements of performance of the body as a whole as well as the function of component parts; and data should discriminate between the variables under consideration, predict deterioration, and establish the time-factor relationships in recovery or return to physiologic "normalcy." The promising tests which reflect the physical strain and the biochemical distortions include measurements of: (a) endocrine function (thyroid, adrenal), (b) liver function (serum cholinesterase), (c) kidney function (clearance, pre-formed elements), (d) nutrient balance, (e) cardiovascular responses (cardiac output, pulse rate, blood pressure), (f) respiratory changes (maximal oxygen consumption, O_2 debt, blood buffers), and (g) blood chemistry (blood sugar, lactate, pyruvate). These measurements have been found to reflect the insults of water and caloric deficits. Little information however, is available regarding the immediate and long range effects of protein, fat, vitamin, and mineral insufficiency which can be interpreted by current clinical thought. For this purpose long observational periods of severe physical exertion are needed; carcass and organ analyses provide important data for explaining the observed functional changes. It is in this area that animal tests are particularly useful.

REFERENCES

1. FOLLIS, R. H.: *The Pathology of Nutritional Disease.* Charles C Thomas, Springfield, Ill., 1948.
2. *Modern Nutrition in Health and Disease.* Edited by M. G. Wohl and R. S. Goodhart, Lea and Febiger, Philadelphia, 1955, Chapter 36.
3. PHIPSON, E. S.: Doping in athletic contests. *Indian Med. Gaz.* 75: 484, 1940.
4. BROŽEK, J.: Nutrition and performance in animals in *Method for Evaluation of Nutritional Adequacy and Status.* National Research Council, Washington, D. C., December 1954, p. 155.
5. BROŽEK, J.: Psychological factors in relation to performance and fatigue. *Fed. Proc.* 2: 134, 1943.
6. MORELL, T.: Combat of fatigue by active substances. *Bull. War Med.* 2: 420, 1941–42.
7. HERLITZKA, A.: Physiology of human work. *Science* 107: 282, 1948.
8. DILL, D. B., BOCK, A. V., EDWARDS, H. T., and KENNEDY, P. H.: Industrial fatigue. *J. Indust. Hygiene* 18: 417, 1936.

9. SIMONSON, E.: Influence of nutrition on work performance. *Nutrition Fronts in Public Health* No. 3, p. 72, 1951.
10. KEYS, A.: Physical performance in relation to diet. *Fed. Proc.* 2: 164, 1943.
11. BROŽEK, J., and MONKE, J. V.: Miniature work situations as a research tool. *Indust. Hyg. and Occ. Med.* 2: 63, 1950.
12. SHELDON, W. H., STEVENS, S. S., and TUCKER, W. B.: *The Varieties of Human Physique.* Harper and Bros., New York, 1940.
13. BROŽEK, J.: Measuring nutriture. *Am. J. Phys. Anthrop.* 11: 147, 1953.
14. BEHNKE, A. R.: Physiologic studies pertaining to deep sea diving and aviation especially in relation to fat content and composition of the human body. *Harvey Lectures* 37: 198, 1942.
15. KEYS, A., BROŽEK, J., HENSCHEL, A., MICKELSON, O., and TAYLOR, H. L.: *The Biology of Human Starvation.* Vol. 2. The University of Minnesota Press, Minneapolis, 1950.
16. Bureau of Naval Personnel. *Physical fitness manual for the U. S. Navy,* p. 17. Training Division, Physical Fitness Section, Washington, D. C., 1943.
17. Federal Security Agency. *Physical fitness through physical education for the victory corps,* p. 80. U. S. Office of Education, Washington, D. C., 1942.
18. Federal Security Agency. *Physical fitness of students in colleges and universities,* No. 3, p. 58. U.S. Office of Education, Washington, D. C., 1943.
19. STANSBURY, E. B.: The physical fitness program of the Army Air Force. *J. Health and Phys. Educ.* 14: 463, 1943.
20. BANK, T. P.: The Army physical conditioning program. *J. Health and Phys. Educ.* 14: 195, 1943.
21. CURETON, T. K., HUFFMAN, W. J., WELSER, L., KIREILIS, R. W., and LATHAM, D. E.: Endurance of young men. *Monog. Soc. Res. Child Develop.* Vol. 10, 1945.
22. BROŽEK, J., and TAYLOR, H. L.: Tests of motor functions in investigations of fitness. *Am. J. Psychol.* 67: 590, 1954.
23. FORBES, W. H.: Problems arising in the study of fatigue. *Psychosomatic Med.* 5: 155, 1943.
24. CARMICHAEL, L., KENNEDY, J. L., and MEAD, L. C.: Some recent approaches to the experimental study of human fatigue. *Science* 110: 445, 1949.
25. STEINHAUS, A. H.: Physiology of movement and measures of coordination. *J. Health Phys. Educ.* 3: 44, 1932.
26. ELBEL, E. R., and RANKIN, R. R.: Palmer skin resistance as a measure of physical fitness. *Am. J. Physiol.* 147: 1, 1946.
27. BEEBE, G. W.: Medical evaluation of nutritional status. *Milbank Mem. Fund Quart.* 21:311, 1943.
28. QUO, SUNG-KER.: A new method of measuring fatigue by the threshold stimulus of the Achilles Tendon reflex. *J. Appl. Physiol.* 2: 148, 1949.
29. TAKANO, S.: The nature of the coagulation reaction of copper ferrocyanide colloid solution. *Science* 21: 297, 1951.
30. KNEHR, C. A., DILL, D. B., and NEUFELD, W.: Training and its effects on man at rest and at work. *Am. J. Physiol.* 136: 148, 1942.
31. PROSCH, F.: The effect of exercise on heart rate. *Research Quart.* 4: 75, 1932.
32. DAWSON, P.: *The Physiology of Physical Education,* Baltimore Press, Baltimore, 1935.
33. SCHNEIDER, E. C.: *Physiology of Muscular Activity.* W. B. Saunders, Philadelphia, 1939.
34. STEINHAUS, A. H.: Chronic effects of exercise *Physiol. Rev.* 13: 103, 1933.
35. DILL, D. B., TALBOTT, J. H., and EDWARDS, H. T.: Studies in muscular activity. *J. Physiol.* 69: 267, 1930.
36. BRIGGS, H.: Physical exertion, fitness, and breathing. *J. Physiol.* 54: 292, 1920.
37. TAYLOR, C.: Studies in exercise physiology. *Am. J. Physiol.* 135: 27, 1941.
38. SCHNEIDER, E. C., and CRAMPTON, C. B.: Comparison of some respiratory and circulatory reactions of athletes and non-athletes. *Am. J. Physiol.* 129: 165, 1940.
39. BOCK, A. V., VAN CAULAERT, C., DILL, D. B., FOLLING, A., and HURXTHAL, L. M.: Studies in muscular activity. III. Dynamical changes occurring in man at work. *J. Physiol.* 66: 136, 1928.
40. DILL, D. B., and BROUHA, L.: Studies on heart rhythm during exercise. *Travail Humain* 5: 1, 1937.
41. DILL, D. B.: The economy of muscular exercise. *Physiol. Rev.* 16: 263, 1936.
42. EDWARDS, H. T., BROUHA, L., and JOHNSON, R. E.: Effects of training on blood lactic acid during muscular work. *Travail Humain* 8: 1, 1940.
43. ROBINSON, S., and HARMON, P. M.: The lactic mechanism and certain properties of the blood in relation to training. *Am. J. Physiol.* 132: 757, 1941.
44. BAINBRIDGE, F. A.: *The Physiology of Muscular Exercise.* Longmans Green, New York, 1931.
45. ROBINSON, S., EDWARDS, H. T., and DILL, D. B.: New records in human power. *Science* 85: 409, 1937.
46. ROBINSON, S.: Experimental studies of physical fitness in relation to age. *Arbeitsphysiologie* 10: 251, 1938.
47. HERON, W. T., INGLE, D. J., and HALES, W. M. Work output of rats subjected to continuous faradic stimulation. *Science* 76: 550, 1932.
48. FLOCK, E. V., INGLE, D. J., and BOLLMAN, J. L.: Formation of lactic acid, and initial process in working muscle. *J. Biol. Chem.* 129: 99, 1939.
49. GOLDSTEIN, M. D., MULLICK, V., HUDDLESTON, B., and LEVINE, R.: Action of muscular work on transfer of sugars across cell barriers:

Comparison with action of insulin. *Am. J. Physiol.* 173: 212, 1953.
50. INGLE, D. J., TORRALBA, G., and FLORES, V.: Comparative effects of muscle work and insulin upon plasma amino acids in eviscerated rats. *Proc. Soc. Exp. Biol. & Med.* 89: 625, 1955.
51. FORSGREN, E.: The relation between liver glycogen and muscular work. *Nord. med.* 3: 2859, 1939.
52. PALLADIN, A. V.: The biochemistry of muscle training. *Science* 102: 576, 1945.
53. EMBDEN, G., and HABS, H.: Chemical and biological changes in muscles after repeated faradic stimulation. *Ztschr. Physiol. Chem.* 171: 16, 1927.
54. LEVINE, R., GOLDSTEIN, M. S., and RAMEY, E. R.: Studies on the mode of action of cortisone in stress situations. *Bull. New England Med. Center* 13: 114, 1951.
55. STEWART, C. C.: Variations in daily activity produced by alcohol and by changes in barometric pressure and diet with a description of recording methods. *Am. J. Physiol.* 1: 40, 1898.
56. SLONAKER, J. R.: Description of apparatus for recording the activities of small animals. *Anat. Rec.* 2: 116, 1908.
57. SHIRLEY, M.: Studies in activity. I. The consistency of the revolving drum method of measuring the activity of the rat. *J. Comp. Psychol.* 8: 23, 1928.
58. SHIRLEY, M.: Studies in activity. II. Activity rhythms, age and activity, activity after rest. *J. Comp. Psychol.* 8: 159, 1928.
59. SLONAKER, J. R.: The normal activity of the white rat of different ages. *J. Comp. Neurol. Psychol.* 17: 342, 1907.
60. PARK, O., and WOODS, L. P.: A modified Hemmingsen-Krarup mammalian activity recorder. *Proc. Soc. Exp. Biol. & Med.* 43: 366, 1940.
61. RICHTER, C. P.: A behavioristic study of the activity of the rat. *Comp. Psychol. Monogr.* 1: 1, 1922.
62. RICHTER, C. P.: Animal behavior and internal drives. *Quart. Rev. Biol.* 2: 307, 1927.
63. RICHTER, C. P.: Contributions of psychology to the understanding of problems of personality and behavior. IV. Biological foundations of personality differences. *Am. J. Orthopsychiat.* 2: 345, 1932.
64 SKINNER, B. F.: The measurement of spontaneous activity. *J. Gen. Psychol.* 9: 3, 1933.
65. SZYMANSKI, J. S.: A method for the investigation of rest and activity periods in animals. *Arch. ges. Physiol.* 158: 343, 1914.
66. SZYMANSKI, J. S.: Activity and rest in animals and humans. *Zeitschr. allg. Physiol.* 18: 105, 1920.
67. SMITH, K. U.: An accurate method of recording activity in animals. *J. Gen. Psychol.* 27: 355, 1942.
68. IRWIN, O. C.: Effect of strong light on the body activity of newborns. *J. Comp. Psychol.* 32: 233, 1941.
69. WILBUR, K. M.: A method for the measurement of activity of small animals. *Science* 84: 274, 1936.
70. KENNARD, M. A., SPENSER, S., and FOUNTAIN, G.: Hyperactivity in monkeys following lesions of the frontal lobes. *J. Neurophysiol.* 4: 512, 1941.
71. SCOTT, C. C., and WORTH, H. M.: An improved device for recording activity of rats. *Proc. Soc. Exp. Biol. & Med.* 66: 285, 1947.
72. SCHULTE, J. W., TAINTER, M. L., and DILLE, J. M.: Comparison of different types of central stimulation from analeptics. *Proc. Soc. Exp. Biol. & Med.* 42: 242, 1939.
73. HARNED, B. K., CUNNINGHAM, R. W., and GILL, E. R.: An activity analyzer for small animals. *Science* 116: 369, 1952.
74. RICHARDS, T. W.: An inexpensive apparatus for the measurement of bodily activity. *Science* 81: 568, 1935.
75. WATERMAN, F. A.: A kinesimeter for studying the spontaneous activity of small animals. *Science* 106: 499, 1947.
76. CAMPBELL, C. J., and MCLEAN, R. A.: An electronic integrating circuit for recording the spontaneous activity of animals. *Rev. Scient. Instruments* 19: 808, 1948.
77. CASTANERA, T. J., KIMELDORF, D. J., and JONES, D. C.: An apparatus for measurement of activity in small animals. *J. Lab. & Clin. Med.* 45: 825, 1955.
78. RICHTER, C. P., and HINES, M.: Increased spontaneous activity produced in monkeys by brain lesions. *Brain* 61: 1, 1938.
79. BOUSFIELD, W. A., and MOTE, F. A.: The construction of a tilting activity cage. *J. Exp. Psychol.* 32: 450, 1943.
80. SIEGEL, P. S.: A simple electronic device for the measurement of the gross bodily activity of small animals. *J. Psychol.* 21: 227, 1946.
81. FARRIS, E. J., and ENGVALL, G.: Turntable for exercising rats. *Science* 90: 144, 1939.
82. CURTIS, Q. F.: Diurnal variations in the free activity of sheep and pig. *Proc. Soc. Exp. Biol. & Med.* 35: 566, 1937.
83. LEVY, D. M.: On the problems of movement restraint, tics, stereotyped movements, hyperactivity. *Am. J. Orthopsychiat.* 14: 644, 1944.
84. BEACH, F. A.: Effects of lesions to corpus striatum upon spontaneous activity of the male rat. *J. Neurophysiol.* 4: 191, 1941.
85. HALL, C. S.: Emotional behavior in the rat. III. The relationship between emotionality and ambulatory activity. *J. Comp. Psychol.* 22: 345, 1936.
86. FREDERICSON, E.: The theory of psychomotion as applied to a study of temperament. *J. Comp. Psychol.* 39: 77, 1946.

87. Ershoff, B. H.: Beneficial effect of liver feeding on swimming capacity of rats in cold water. *Proc. Soc. Exp. Biol. & Med.* 77: 488, 1951.
88. Kimeldorf, D. J., and Jones, D. C.: The relationship of radiation dose to lethality among exercised animals exposed to roentgen rays. *Am. J. Physiol.* 167: 626, 1951.
89. Harris, R. E., and Ingle, D. J.: The capacity of vigorous muscular activity of normal rats and of rats after removal of the adrenal medulla. *Am. J. Physiol.* 130: 151, 1940.
90. Rice, H. A., and Steinhaus, A. H.: Studies in the physiology of exercise. V. Acid-base changes in the serum of exercised dogs. *Am. J. Physiol.* 96: 529, 1931.
91. Schultz, F. W., and Morse, M.: Factors influencing the serum bicarbonate concentration of the dog during treadmill exercise. *Am. J. Physiol.* 122: 105, 1938.
92. Schultz, F. W., and Morse, M.: Factors influencing the concentration of the serum protein, chloride, and total fixed base of dog. *Am. J. Physiol.* 121: 293, 1938.
93. Hastings, A. B.: An investigation of changes in the blood and urine resulting from fatigue. *Public Health Rep.* 34: 1682, 1919.
94. Campos, F. A., Connor, W. B., Lundin, H., and Walker, T. T.: Some conditions affecting the capacity for prolonged muscular work. *Am. J. Physiol.* 87: 680, 1929.
95. Guerrant, N. B., and Dutcher, R. A.: The influence of exercise on the growing rat in the presence and absence of vitamin B_1. *J. Nutrition* 20: 589, 1940.
96. Samuels, L. T., Gilmore, R. C., and Reinecke, R. M.: The effect of previous diet on the ability of animals to do work during subsequent fasting. *J. Nutrition* 36: 639, 1948.
97. Hart, J. S.: Use of daily metabolic periodicities as a measure of the energy expended by voluntary activity of mice. *Canad. J. Zool.* 30: 83, 1952.
98. Tan, E. M., Hanson, M. E., and Richter, C. P.: Swimming time of rats with relation to water temperature. *Fed. Proc.* 13: 150, 1954.
99. Dureuil, M., and Ratsimanga, A. R.: Effect of sudden variations in temperature on the capacity for forced work of the normal rat. *Compt. rend. Soc. de Biol.* 142: 70, 1948.
100. Rundquist, E. A.: Inheritance of spontaneous activity in rats. *J. Comp. Psychol.* 16: 415, 1933.
101. Browman, L. G.: Light in its relation to activity and estrous rhythms in the albino rat. *J. Exp. Zool.* 75: 375, 1937.
102. Browman, L. G.: The effect of controlled temperatures upon the spontaneous activity rhythms of the albino rat. *J. Exp. Zool.* 94: 477, 1943.
103. Browman, L. G.: Modified spontaneous activity rhythms in rats. *Am. J. Physiol.* 142: 633, 1944.
104. Johnson, M. S.: Effect of continuous light on periodic spontaneous activity of white-footed mice. *J. Exp. Zool.* 82: 315, 1939.
105. Stier, T. J. B.: Spontaneous activity of mice. *J. Gen. Psychol.* 4: 67, 1930.
106. Jones, D. C., Kimeldorf, D. J., Rubadeau, D. O., and Castanera, T. J.: Relationships between volitional activity and age in the male rat. *Am. J. Physiol.* 172: 109, 1953.
107. Shirley, M.: Spontaneous activity. *Psychol. Bull.* 26: 341, 1929.
108. Munn, N. L.: *An Introduction to Animal Psychology.* Houghton Mifflin Co., New York, 1933.
109. Morgan, C. T.: *Physiological Psychology.* McGraw-Hill Co., New York, 1943.
110. Hall, C. S.: Emotional behavior in the rat. III. The relationship between emotionality and ambulatory activity. *J. Comp. Psychol.* 22: 345, 1936.
111. Hoskins, R. G.: Studies on vigor. XVI. Endocrine factors in vigor. *Endocrinology* 11: 97, 1927.
112. Henschel, A., Taylor, H. L., Brožek, J., Mickelsen, O., and Keys, A.: Vitamin C and ability to work in hot environments. *Am. J. Trop. Med.* 24: 259, 1944.
113. Hoitink, A. W. J. H.: Inquiries into the influence of work and of the administration of Vitamin C on the human organism. *Biol. Abstracts* 23: 14461, 1949.
114. Johnson, R. E.: Nutritional standards for men in tropical climates. *Gastroenterology* 1: 838, 1943.
115. Wald, G., and Jackson, B.: Activity and nutritional deprivation. *Proc. Nat. Acad. Science* 30: 255, 1944.
116. Smith, P. K., and Smith, A. H.: The effect of a diet low in inorganic constituents on the voluntary activity of the albino rat. *Abstr. Proc. Am. Physiol. Soc.* 1934.
117. Bernhardt, K. S.: Phosphorus and iron deficiencies and learning in the rat. *J. Comp. Psychol.* 22: 273, 1936.
118. Ershoff, B. H.: Beneficial effect of low fat diets on the swimming performance of rats and mice in cold water. *J. Nutrition* 53: 439, 1954.
119. Scheer, B. T., Dorst, S., Codie, J. F., and Soule, D. F.: Physical capacity of rats in relation to energy and fat content of the diet. *Am. J. Physiol.* 149: 194, 1947.
120. Slonaker, J. R.: Effects of different per cent of protein in the diet. II. Spontaneous activity. *Am. J. Physiol.* 96: 557, 1931.
121. Bernhardt, K. S.: Protein deficiency and learning in rats. *J. Comp. Psychol.* 22: 269, 1936.

122. Bevan, W., Lewis, G. T., Bloom, W. T., and Abess, A. T.: Spontaneous activity in rats fed an amino acid deficient diet. *Am. J. Physiol.* 163: 104, 1950.

123. Pilgrim, F. J., Zabarenko, L. M., and Patton, R. A.: The role of amino acid supplementation and dietary protein level in serial learning performance of rats. *J. Comp. and Physiol. Psychol.* 44: 26, 1951.

124. Bernhardt, K. S.: Vitamin A deficiency and learning in the rat. *J. Comp. Psychol.* 22: 269, 1936.

125. Beeman, E. A., and Allee, W. C.: Some effects of thiamine on the winning of social contacts in mice. *Physiol. Zool.* 18: 195, 1945.

126. Maurer, S.: The effect of early depletion of vitamin B_2 upon performance in rats. *J. Comp. Psychol.* 20: 385, 1935.

127. Maurer, S.: The effects of partial depletion of vitamin B (B_1) upon performance in rats. *J. Comp. Psychol.* 20: 309, 1935.

128. Richter, C. P., and Barelare, B.: Further observations on the carbohydrate, fat, and protein appetite of vitamin B deficient rats. *Am. J. Physiol.* 127: 199, 1939.

129. Bernhardt, K. S., and Herbert, R.: A further study of vitamin B deficiency and learning with rats. *J. Comp. Psychol.* 24: 263, 1937.

130. Jakway, I.: Voluntary activity in the rat as related to intake of whole yeast. *J. Comp. Psychol.* 26: 157, 1938.

131. Mouriquand, G., and Coisnard, J.: Muscular activity and vestibular chronaxie in normal pigeons. *Compt. rend. Soc. de Biol.* 136: 812, 1942.

132. Shock, N. W., and Sebrell, W. H.: Effect of riboflavin and other B complex vitamins on work of perfused frog muscles. *Proc. Soc. Exp. Biol. & Med.* 63: 290, 1946.

133. Van Winkle, W., and Kennedy, N. K.: Voluntary running activity of rats fed propylene glycol and other glycols. *J. Pharmacol. Exp. Therap.* 69: 140, 1940.

134. Guild, R., and Rapport, D.: Calorigenic action of methylene blue during muscular exercise. *Proc. Soc. Exp. Biol. & Med.* 34: 459, 1936.

135. Canzanelli, A., Segal, M., and Rapport, D.: The utilization of the calorigenic action of diiodothyronine and thyroxine in muscular exercise. *Am. J. Physiol.* 110: 410, 1934.

136. Ershoff, H., and Levin, E.: Beneficial effect of an unidentified factor in wheat germ oil on the swimming performance of guinea pigs. *Fed. Proc.* 14: 431, 1955.

Reprinted from THE AMERICAN JOURNAL OF CLINICAL NUTRITION
Jan.-Feb. issue, Vol. 5, No. 1, pp. 129–140, copyright 1957 and printed in U.S.A.
Published by The American Journal of Clinical Nutrition, Inc., 49 W. 45 St., N. Y. 36