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STUDY OF MONKEY, APE, AND HUMAN MORPHOLOGY AND PHYSIOLOGY RELATING TO STRENGTH AND ENDURANCE

PHASE IX

THE STRENGTH TESTING OF FIVE CHIMPANZEE AND SEVEN HUMAN SUBJECTS

William E. Edwards Thomas Erskine Clarke

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6571st Aeromedical Research Laboratory Aerospace Medical Division Air Force Systems Command Holloman Air Force Base, New Mexico The animals used in this study were handled in accordance with the "Principles of Laboratory Animal Care" established by the National Society for Medical Research.

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FOREWORD

This is the last in a series of nine papers concerned with the Study of Monkey, Ape, and Human Morphology and Physiology Relating to Strength and Endurance. This study was conducted in part under Contract AF 29(600)-3466, Project 6892, Task 689201, monitored by Major James E. Cook, Veterinary Services Division, ARV.

In 1958 the writer initiated a study on the strength of humans and other primates. This study was conducted from 1959 to 1961 at the University of Chicago as a National Science Foundation Science Faculty fellow. In 1961 the author was employed as a consultant by the 6571st Aeromedical Research Laboratory and the co-author of this paper was employed as his assistant to conduct a program of training and testing chimpanzees for flexion strength of the arms. The data acquired was analyzed in 1963 and compiled for this report.

The author wishes to acknowledge the cooperation of Lt Col Frederick H. Rohles, Lt Col Hamilton H. Blackshear, Major Clyde H. Kratochvil, Major James E. Cook, Major Marvin E. Grunzke and Major Robert H. Edwards, all of the 6571st Aeromedical Research Laboratory for their help in the preparation of this paper.

Publication of this report does not constitute Air Force approval of the report's findings or conclusions. It is published only for the exchange and stimulation of ideas.

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ABSTRACT

Five chimpanzees (two immature of each sex and one adult male) were trained for testing of elbow flexion strength. Resulting scores were compared with those of seven young (20 to 37 years) adult human males. The apes manifested a 2-1/2 fold superiority by body-weight and, sex and age equivalent, an appreciable superiority by brachial cross-sectional area.

AD-469585

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1. INTRODUCTION

Various types of anecdotal and other general observational evidence have indicated that chimpanzees are very much stronger than humans. Some tests (Bauman, 1923 and 1926) have corroborated such indications of strength superiority, while others (Finch, 1943) have indicated no appreciable difference.

Knowledge of whether marked differences in strength exist in chimpanzees and humans is highly significant to relevant aspects of pure science and of applied science, such as to the development of the manin-space program (Edwards, 1965b, pp. 1-2) -- for example, marked differences in muscular strength are associated with appreciable differences in tissue damage under high acceleration forces.

The training and testing program herein reported was effected to determine valid strength comparisons between the two primates.

2. RESEARCH HISTORY

In 1959, the writer conducted fairly extensive library research on the problem of relating the strength of man and other primates to size, at which time it was recognized that the most ideal non-human subjects were chimpanzees -- because the only significant prior studies of non-human strength had utilized the chimpanzee, because of their better responsiveness to training in some respects, and especially because their comparisons with humans would be facilitated by their approximately equivalent body-size. Derived data on the chimpanzee would also be more directly applicable to certain practical problems -- including some of those involved in space flight, as already noted.

The senior author was employed by the 6571st Aeromedical Research Laboratory as a consultant in 1961 and the results of this investigation were subsequently prepared for this report under Air Force Contract 29(600)-3466.

The author and the co-author collaborated in the training and testing program for this study.

3. RESEARCH METHODOLOGY

On a steel platform 128.6 by 71 cm. was mounted a steel chair with adjustable seat and back as well as adjustable neck, chest, thigh, and ankle braces to restrain the simian subjects of the experimentation (Figs. 1-3). An adjustable 53.6 by 45.6 cm. steel table was affixed immediately in front of the subject. Upon this table was mounted a handle of 3.7 cm. (almost 1.5 inches) diameter, readily shifted to either right or left side, attached perpendicularly to a rod which slides within a cylinder, the angle of which to the table was adjustable. Attached in turn to the handle-rod was a 0.39-cm.-diameter, seven-strand twisted steel cable, which connected via a system of pulleys to a rectanguloid steel bucket with a capacity of more than 400 pounds of measured weights. Alternatively, the cable was attached to a dynamometer, but testing revealed proportionately large inaccuracies and caused it to be abandoned; all of the scores here reported are the actual weights of bucket plus weights. The handle-rod in its cylinder, the cable, and the pulleys were all well-fitted and well-lubricated, so the Holloman Air Force Base machinists who meticulously fashioned the apparatus were confident that friction was reduced to less than 1 per cent, in contrast to the enormous friction of the apparatus of others, such as that of Finch (1943).

The bucket was kept either suspended entirely so that the slightest lift would be evident or was in contact with the floor only along one edge. The latter arrangement had the psychological advantage of encouraging the subject by permitting slight movement of the handle before the maximum force required was applied, while simultaneously insuring that no lift would be incorrectly recorded as successful since complete lifting of the bucket along the contacting edge was quite evident when it occurred.

It was possible to satisfy virtually all of the thirty-seven criteria previously formulated by the writer as essential to proper comparisons of ape and human strength (Edwards, 1963a). Among these criteria, the number of muscles involved in the given performance is especially crucial; the relatively large forces which can be developed but minimal number of muscles which contribute to the force make elbow flexion perhaps as near-ideal for this purpose as is possible (Wilkie, 1950, pp. 250-251 and 266-269).

4. DESCRIPTION OF HUMAN SUBJECTS

The seven human subjects were all adult males in good health and with perhaps one exception at least somewhat active in physical sports. The three heaviest subjects had the highest proportion of adipose tissue, with the third lightest intermediate in this respect between the three heaviest and the remainder. Although he manifested some excess adipose tissue, the heaviest subject was quite muscular despite his weight, largely through having just participated for one year (June, 1960, to



Figure 1 Assistant Author, Fourth Chimpanzee, and Testing Apparatus



Figure 2

Fourth Chimpanzee at Start of Pull, Left Hand and Overhanded (When turned on, the light indicates a lift should be attempted for positive and negative incentives.)



Figure 3

Fourth Chimpanzee Momentarily after Near-Maximal Weight Has Cleared Floor in Early Stage of Successful Lift



May, 1961) in a standard weight-lifting program to which he devoted one hour per day. The third and sixth subjects had years earlier scored in approximately the top two percentiles in "physical fitness index" tests -- primarily of strength and secondarily of endurance (Cureton, 1947). In summary, however weaker than their physically much more active distant and even very near ancestors, the majority of the human subjects employed in this study were quite certainly at least moderately stronger than average Americans, sex, size, and age considered.

All subjects but the lightest -- who was tested a day later -- were tested 4 September, 1961.

Data on the subjects, all of whom except the fifth are right-handed, are provided in Table 1.

5. EXPERIMENTAL RESULTS OF HUMAN STRENGTH TESTING

The training of human subjects consisted of verbal instruction and of brief trials to provide sufficient familiarity with the apparatus for near-optimum functioning during the tests; since the performance required only very simple patterns of muscular contraction (a major consideration in the design of the apparatus), procedural familiarity quite surely did not decrease maximal scores at all appreciably (Cureton, 1947), and any slight decrease due to this factor was at least fairly equivalent for all the human subjects.

Motivation consisted of a combination of interest in and desire to aid the research project, curiosity regarding the subject's own strength, and the competitive desire to score favorably in comparison with others. A given performance was generally observed by several of those selected for testing, and all to some degree sought and, in an attempt by the writer to maximize all of the human scores, were informed of the scores of the others.

To minimize the influence of the fatigue factor, the subjects were given rest-intervals between individual pulls until they reported feeling rested. At near-maximal pulls, these rest-intervals averaged slightly more than two minutes. Between series (A, B, C, and D), the rest-intervals approximated five minutes while adjustments were made. To provide indications of the fatigue factor, the sequences of right versus left and underhanded versus overhanded series were varied and recorded; comparisons reveal clearly that the subjective appraisals of essentially complete recovery from fatigue were probably erroneous in every case.

Rough approximations of the optimum angles were determined by brief experimentation prior to the series here recorded. For the testing of all overhanded pulls, the handle-rod was set at horizontality. In preparation for overhanded pulls, the table was adjusted to the height and distance from the subject which, at the moment the raising of the

Table 1

(in centimeters or square centimeters where not otherwise indicated) Anthropometric Data on the Human Subjects

Characteristic				Subject	6		
	1	2	м	4	Ŋ	9	7
Age (in years) Weight (in pounds) Stature (in inches)	30 125.5 68.0	20 144.5 71.5	33 167.0 69.0	36 169.0 68.7	37 186.5 71.4	35 221.0 74.7	28 248 5 73 0
Mid-brachial girth* Right Left	24.0 23.2	27 .6 26 .5	30 ° 0 29 • 4	28.4 27.2	30.8 32 . 6	34.6 32.2	35.8 35.3
Distance of maximum forearm girth from proximal tip of ulna (olecranon) Right Left	44	00	N N	0 V	ω ω	4 4	8 8
Maximum forearm girth* Right Left	25.4 25.0	26.2 26.1	27.5 27.2	27.3 26.5	27 .3 27 .8	30.1 29.3	35 °1 34 °9
Distance of minimum forearm girth above distal tip of ulna (styloid process) Right Left	2.5	мм	2.5	мм	мм	MM	, n , n
Minimum forearm girth* Right Left	15.9 15.6	16.2 15.7	17.2 16.4	15.9	17.2	19.1 18.6	28 8 28 8
Distance from acromion to tip of ulna (styloid process), measured palm down Right Left	56.6 56.4	57.1	53.6 52.6	55.4 54.9	57.0 56.8	60 . 4 60 . 0	58 ° 2 59 ° 0
Ulna length (olecranon to styloid process) Right Left Brachial cross-sectional area**	27.8 27.4 44.39	29.1 28.5 58.21	26.4 26.0 70.17	27.4 26.6 61.48	30.3 30.0 79 .9 4	29.2 28.4 88.75	29.5 29.7 100.54
and and the the limb extended and	elaxed.						

*Girths were measured with the limb extend

**Calculated from average mid-brachial girth on assumption of round section, which slightly overstates actual cross-sectional area

weight commenced, provided an angle of the forearm's main axis sloping down toward the subject of 5 degrees from the horizontal and of the upperarm's main axis sloping up toward the subject at 6 degrees. For underhanded pulls, the handle-rod sloped up toward the subject at 10.5 degrees, while the forearm and upper arm angles were increased to 18 and 23 degrees respectively. These angles were approximated as closely as was feasible for all subjects, except for underhanded series D2 (immediately following D1) for the second subject, for which the slightly lower maximum score was obtained with the handle-rod horizontal.

To insure insofar as was feasible that the muscles tested were those providing flexion of the forearm at the elbow-joint, in all but one brief series the shoulder of the subject was braced by the arms of assistants and by boards held by them to minimize shoulder movement, and the changing angle of flexion at the elbow was observed while the handle was drawn back (on all but a few of the successful lifts to its maximum range of motion of approximately 3.5 cm.). It should be emphasized that in the one series designed to indicate the approximate degree of superiority of scapular muscles -- D2 for the third subject, immediately following D1 -- the upper extremity was held rigidly straight at the elbow, so no effort was required of the flexors at the elbow to maintain flexion at that joint.

The results of the tests are recorded in Table 2.

6. METHODOLOGY OF TRAINING AND TESTING CHIMPANZEES

The high interindividual and even intraindividual variability in chimpanzee characteristics such as temperament, cooperativeness, and response to electric shock can hardly be overemphasized. For this reason, a wide variety of both positive and negative motivations, which need not be discussed here since they have already been considered in another recent paper (Edwards, 1963a), were employed. By the somewhat unorthodox adjusting of motivation to fit the individual subject, it was possible thoroughly to train the chimpanzees -- none of which had experience with trained performance requiring maximum muscular effort -- with great rapidity.

The primary test of adequate training for strength testing is whether maximum scores in different series closely approximate one another, for such correlations should occur if consistent and adequate motivations are operative and if the limiting asymptote of muscular strength is fairly closely approached (Edwards, 1963a). The data presented subsequently in this paper demonstrate the adequacy of this training.

7. DESCRIPTION OF CHIMPANZEE SUBJECTS

Large quantities of panometric and other types of data on the chimpanzee subjects of the experimental program were recorded. Only the data

Table 2

Weightlifting Performances of Human Subjects

Subject and Series Seque	ence	Lifts Attempted	Neximum Lift	Average Naximum Lift	Body-Weight (in pounds)	Average Max- inum Lift in Pounds per Pound of Body- Weight	Average Brachisl Cross-Sec- tional Area	Aversge N ax- inum Lift in Pounds per Squsre Centimeter
1(C,D,B,A)*	A B C D	80,100,120,140,(160)**(150) 80,100,120,(140),(130),(130 80,100,120,140,(145),(145) 80,(100),(90),90,(95)) 140)) 120 140 90	122.5	125.5	.976	44.39	2.76
2(C,D,A,8)	A B C D1 D2	100,120,140,150,160,180,200 190,200,(205) 80,100,120,(130),125,(130) 80,100,100,120,140,160,180, 200,(210) 100,120,(140),(130),(120),((120),100,(100),110	200 125 200 120) 120	161.3	134.4	1.108	58,21	2.77
3(A,B,C,D)	A B C D1 D2	80,100,120,140,160,180,(185 185,(190),(190) 80,100,120,(140),135 80,100,120,140,(160),(160), 150,160,(170),165,(170) 80,100,120,130,140,(150), (145) 155,165,(170)	185 135 165 140	156.3	167.0	.936	70.17	2.23
4(B,A,C,D)	A B C D	130,150,(180),(160),150, 155,(160) 100,120,130,140,(150),(140) 130,135,140,145,(150),(150) 100,150,120,170,(180),(175) 175,180,(190),(190),(185) 80,100,(120),120,(125),(125)	155) 145) 180 5) 120	150.0	169.0	.888	61.48	2.44
5(D,C,A,B)	A B C D	80,100,120,140,150,160, (170),(170),(165) 80,100,(120),(110) 80,100,120,140,(150),150, 155,(160) 80,100,120,130,(140)	160 100 155 1 3 0	136.3	186.5	.731	79.94	1.70
6(A,8,D,C)	A B C D	80,100,120,140,160,180,200, 220,225,(230),230,(235) 80,100,120,140,150,155,160, (165) 80,100,120,140,160,180,200, 210,220,(230),(225) 80,100,120,140,(150),(145)	230 160 220 140	187.5	221.0	.848	88 .7 5	2.11
7(A,B,D,C)	A B C D	110,130,150,170,190,190, 210,230,250,(260),(255) 80,100,120,140,150,160,(180 170,(175),(175) 110,130,150,170,190,210,230 240,(250),(250) 80,100,120,140,(160),(150), 140,(145)	250 0), 170 0, 240 140	200.0	248,5	.805	100,54	1.99

A = Right, overhanded B = Right, underhanded C = Left, overhanded D = Left, underhanded

*Sequence of the four tested

**Psrentheses enclosing a score denote strenuous attempt but failure to lift that weight

most relevant to comparisons of chimpanzee and human size and strength are given in Table 3.

8. EXPERIMENTAL RESULTS OF CHIMPANZEE STRENGTH TESTING

The authors wrote as many as 34 pages of condensed notes on cards per day of the testing program; at night such data were even more extensively recorded on "dictaphone" belts, which in toto constitute the equivalent of several hundred typed pages. It is therefore evident that high selectivity must be utilized in the succinct presentation of experimental results.

Such data are presented in highly condensed form in the following pages. All successful scores and all unsuccessful attempts (in parentheses) involving near-maximal effort are listed in sequence for every day each of the five subjects was tested; attempts for which a marked effort was not required or at least was not given are not here recorded. A semicolon represents a major temporal hiatus in the testing, generally with appreciable resting by the subject. In the data listed below for each of the five subjects successfully trained, each lift recorded in a series was attempted with the arm, right or left, indicated at the start of the series. Occasionally the subject changed from an overhanded to an underhanded grip or vice versa during a series; the grip for each attempt was that indicated at the start of the series except where individually indicated to the contrary in the list.

Prior to 25 August, 1961, tests were conducted in a slightly simpler steel restraining chair than that subsequently employed; the weight was attached to a rope which, after passing around a pulley, was in turn attached to a simple rod handle of wood. All tests on and after 25 August were conducted with the more elaborate steel apparatus previously described.

To the data which follow may be added the fact that only the largest chimpanzee (which, despite his apparent viciousness, proved to be the most cooperative of all) was anaesthetized (by sodium pentathol, followed by the counteracting drug mikedimide) before being moved from his cage to the restraining chair -- and even he returned from the testing building without restraint. But the smaller subjects were unwilling participants in the program, and as many as six skilled handlers required as much as 45 minutes to subdue and force one of them into the restraining chair.

It should also be observed that fairly extensive attempts were made on the two most tractable subjects, the third and the fifth, to test differences in muscular force at varying angles of elbow flexion. But in the time available, the two subjects could not learn to pull at markedly different (and apparently somewhat less "natural") angles; the fundamental change required was apparently never comprehended by the apes. Table 3

(in centimeters or square centimeters where not otherwise indicated) Panometric Data on the Chimpanzee Subjects

Characteristic		100	ubject		
	-	2	м	4	ي ا
Sex	Male	Female	Fenale	Male	Male
Age (in months)	65	56(est.)	54(est.)	68(est.)	144(est.)
Weight (in pounds)	45.5	48.0	56.0	60.0	98.0
Maximum forearm girth* Right Left	22.5 22.7	23.0 22.0	22 .6 22 . 9	23.2 24.3	30,5 29 .8
Mid-brachial girth* Right Left	21.8 21.9	22.0	20.6 21.5	21.5 22.5	30.5 30.1
Brachial cross-sectional area**	37,99	38.51	35.27	38,51	73,06

*Girths were measured with the limb extended and relaxed

**Calculated from average mid-brachial girth on assumption of round section, which slightly overstates actual cross-sectional area

Subject 1 (ARL #80)

8/25 (right, overhanded): 80, 90, (100), (100), 80, 90, 100, 105; (105); (105), 80, 90, 100, (103), 110; (112), (112), (112), 112, (112), (112), (100), 80, 90, 100, 110, 112, 112, 116, (118), (118), (118); (118), (117), 80, 100, 110, (115), 115, (116), (116), 116, 117, (120), (120), (120), (120), (120), (120).

8/29 (left, overhanded; while recuperating from illness): (70), (70), 70, 70, (70), (70), 75, 60, 70.

9/6 (left, overhanded): 80, 100, 110, 120, 130, 140, (145), (145), (145).

Subject 2 (ARL #46)

8/7 (right, overhanded): 74, 79, 84, 89, 94, 100, (105).

8/8 (right, overhanded): 74, 101, (109), (109), (109), (109), (109; weight almost completely lifted for total of 5 seconds of 7-second interval encompassing last two attempts).

8/21 (right, overhanded): 90, 90, 100, 105, 110, (115), (115).

8/22 (right, overhanded): 70, 80.

8/24 (right, overhanded): 80, 80, 90, 100, (105), (105); 80, 90; 80; 80, (90), (90); 80, 90, 100, 103, 110 (both hands), (110), (110), 110, (112), (112; under), 100, (110); 80, 80, 80, 90, (100), 100, 103, 110, (112), (112), (112); 100, 100.

8/24 (right, underhanded): 80, 80, 90, 90, (100), (100), 100, 100, 100.

Subject 3 (ARL #35)

8/19 (left, overhanded): 90, 100, 110, (110), 110, (120); 90, 110.

8/29 (left, overhanded): 80, 80, 90; 80, 90, 100; 80, 80, 90, 100, 105; 90, 100, 105, 108, 110, 112, 100, 110, 115.

8/30 (left, overhanded): 80, 90, 100, 105, 110, 113, 115, 118, (120), (120), (120), (120), (122), (122), (122); 100, 110, 115, 120, 122, 125, 127, (127), (127), (127); 80, 80, 90, 100, 110, 115, (120), 120, 125, 127, 130, (132), (132), (132), (132).

8/30 (right, overhanded): 80, (90), (90), 80, 90; 80, (90), 80, (90), 80, 80, 80, 80, 80, 90, (100).

8/31 (left, overhanded): 80, 90, 100, 110, 120, 125, 130, (132), (132), (130).

8/31 (right, overhanded): 80, 100, 105; 80, 90; 80, 90; 80, 80.

9/2 (right, overhanded): 80, 90, 100, 110; 80; 80, 85, 90, 100; 80, 90, (110), (110), 100; 80, 90; 80, 90, (95), (95), (95).

9/6 (right, overhanded): 2 hours of attempted training and testing at several handle-shaft, brachial, and antebrachial angles; maximum lift only 60.

Subject 4 (ARL #32)

8/21 (right, overhanded): 80; 50.

8/22 (right, overhanded): 80, 90, (100), 90, 100, 105, (110); 80, 90, 100, 105, 110, 110, (115), (115); 80, 80, 90, 90, 100, 100, 110, (115), (115), (115).

8/23 (right, overhanded): 80, 100, 100, (115), (115), (115), (113), 110, (111); 80, 90, 100, (110); 80, 90; 80, 80, 100, 110, (115), (115), (115), (115).

8/23 (left, overhanded): 70, 70, 90, 90, 100, 105, 110, (115), 115, (120), (120), (117), (117), (117), (117), (120).

8/26 (right, overhanded): 80, 90, 100, 105, 110, 112, 115, 118, (120), (120), (120), (120), (120), (120), (120), (120); 80, 100, 110, (115), (115), (115), (115), (115), 110, 113, 115, 118, (120), (120), (120), (120).

8/26 (right, underhanded): 70, (90), 80, (90), (90), (90), (80).

8/26 (left, overhanded): 80, 90, 105, 115, 120, 125, 127, 125, 127, 130, 135, (140); 130, (140), (140), (140; under); 100, 110; 100, 100, 110, 120, (130), 120, 130, (135), (130), (130); 80, 80, 80, 100, 115, 125, (130), (130).

8/26 (left, underhanded): 30.

8/30 (right, overhanded): 80, 100; 80.

8/31 (right, overhanded): 80, 80, 90, 90; 80, 80, 90; 80, 90, 90, 95, 100, 105; 90; 80, 90, 100; 80, 80, 80, 90, 100, 105, 105, 110; 90; 80, 80, 90, 100, 105 (under), 105; 80, 80, 90, 100, 105, 107, 110, 112, (115); 80, 80, 90, 100, 110, 115, 120, 122, 127, 130, 135 (barely lifted).

9/2 (right, overhanded): 80, 90, 100, 110, 115, 117, 120, 125, (127), 127, 130, (132), (132); 80, 80, 80, 80, 80, 100, 110; 80.

9/2 (right, underhanded): 80, 90, (100), 95, 100, (105), (105), 90 (over), 90, (100), 100, (105), 105, 110, (115), 115, (120), (120), (120), (120).

9/2 (left, overhanded): 80, (90; under), 90, 100; 90, 100, 110, (120), 120, 125, (130), 130, 135, (138), (138).

9/2 (left, underhanded): 80, 100, 110 (over).

Subject 5 (ARL #134)

8/28 (right, overhanded): 180, 230, 200, 200, (250), 250, (280), (280), 180, 230, (250), (250), 250, (260), (260), (260), (260), (260), (260), (260), 260; 230, 250, (260), 260 (under), (270; under), 270, (280), (280; under), (280), (280), (280; under), (280; under), (280), (280), (280); 230, 230, 230, 230; 180, 230, 250 (under), (250), (250; under), (250), (250; under), (250), 250 (under), (230), 230 (under).

8/28 (left, overhanded): 180, (210), (210), 210, 210, 230, 240, 240, 250, 260.

8/28 (both, overhanded): 270, (270; left under), 270, 270 (writer slapped subject's hand and verbally indicated disapproval), 270 (subject raised digit III of right hand and showed to writer, apparently for approval of alternative plan to lift weight, unsuccessfully attempted by left arm only and underhanded 4 minutes earlier; not understanding, writer replied "fine"; subject immediately placed this digit overhanded on handle beside overhanded left hand and readily lifted weight), 270, 270, 270, 250, 250, 250, 250, 250, 250, 250, 250, 250, 230 (left, over), 250 (left, under), 260 (left, over, plus digit III of right hand), 300 (left, over, plus digits II and III of right hand), 330 (left, over, plus digits II-IV of right hand), (380; steel platform of apparatus bent, so unable to raise weight), 380 (left, over, plus digits II and III of right, under; back of platform weighted, so bent less), (410; platform bent barely too much for weight to rise).

9/1 (right, overhanded): 180, 230 (under), 230; 230; 130, 130, 180, 230 (under), 250 (under), (260; under), (260), 250 (under), (260; under), (260), (260; under), (260), (255), (255; under), (255; under), (230; under), 230, 230 (under), 230, (250), (255), (255), (255), (255), (255; under), (255), (255), (255; under), (255), (250), (250), (250; under), (250; under), (250); 180, 230, 250, (260), (260), (260), 260, (260), 265.

9/5 (right, overhanded and underhanded): 7 hours of attempted training and testing at varying handle-shaft heights and angles and at varying brachial and antebrachial angles; apparently no pulls in alignment with the handle-shaft; despite repeated effort by subject, maximum lift only 160. The results of all of the strength testing of chimpanzees are summarized in Table 4.

Scores lacking clear indication of being normal maximal scores were omitted or set in parentheses, and were in either case excluded from subsequent calculations. The final scores of the first subject were the only scores excluded as excessive. This subject had on 6 September almost escaped after being placed in the restraining chair, and resubduing required half an hour of great effort, so it is felt that these scores were probably raised "abnormally" by epinephrine release and associated phenomena. Simillar phenomena -- in addition to a moderate degree of muscular hypertrophy resulting from the training and testing program -- likely affected the scores of the fourth subject on 2 September, for the tests on that date were associated with frequent screaming and struggling, but the presumed increase by epinephrine release was apparently counter-balanced by fatigue. For reasons obvious upon inspection of the data previously presented, other scores were not included in calculations because they were quite surely markedly less than potential maxima. The percentages by which the underhanded lifts were less than the over-handed lifts for the three subjects for which such scores were available were calculated -- second, 9.1; fourth, 14.8; and fifth, 3.7 and 3.8. With scores for both arms, the fifth subject determined half the average difference of 7.85 per cent, but this subject's scores were also the most reliable, for all this subject's trials were performed cooperatively, calmly, and methodically. This average percentage of difference was employed in computing the underhanded scores for the first and third subjects and for the left arm of the fourth; from the derived estimates, the adjusted average maximum values were calculated.

9. CONCLUSIONS

Bracing to avoid movement of the shoulder and observations of the changing angle of flexion at the elbow were employed in an attempt to minimize the chance of a decisive contribution from the scapular muscles, the significance of which is indicated by the 17.9 per cent increase (140 versus 165) in the maximum lift of the third subject in series D2 when the upper limb was fully extended. But the greater difficulty of making other requisite observations during the testing of the chimpanzee subjects and the greater difficulty of bracing the shoulders of the apes cause the writers to lack complete confidence that many of the chimpanzee scores are not somewhat higher due to the action of muscles of scapular origin; for example, among these muscles, the long head of triceps is relatively much heavier and has a longer scapular attachment than that of man (Edwards, 1965c). Also, the postulated frequent reliance upon elevation and retraction of the shoulderjoint (Hollinshead, 1951, pp. 91-97) would in part explain the difficulty experienced in attempting to teach the third and fifth subjects to pull at varied angles. On the other hand, flexion at the elbow was observed

	Maximum Lift bject (in pour	A 117 B C (140) D	A 110 B 100 C	A (110) B C 130 D	A 135 B 115 C 135 D (100)	A 270 B 260 C 260
Methicittering reitor	Adjusted Average Maximum Lift ds) (in pounds)	112.4	105	124.9	127.4	260.0
mances of on the	Body-Weight (in pounds)	43.0	44.5	54.25	60.0	98.0
	Average Max- imum Lift in Pounds per Pound of Body-Weight	2.614	2.360	2.302	2,123	2.653
	Average Bra- chial Cross- Sectional Area	37.99	38.51	35.27	38.51	73.06
	Average Max- iuum Lift in Pounds per Square Centi- meter	2.99	2.73	3.54	3,31	3.56

Table 4

Weightlifting Performances of Chimpanzee Subjects

A = Right, overhanded
B = Right, underhanded
C = Left, overhanded
D = Left, underhanded

on many lifts and was in some cases described in the writer's notes immediately upon the tests' completion. Thus it is recorded that on 24 August the second subject "flexed arm but shoulder immobile" as for 3 seconds a 100-pound weight was lifted overhanded the entire range of handle-shaft motion; this lift was only 9.1 per cent less than the maximum. Likewise, all of the 1 September testing of the fifth subject was performed with meticulous bracing of the right shoulder with wooden blocks and with the left arm strapped to the left wall of the apparatus; yet overhanded and underhanded lifts were 265 and 250 pounds, only 1,9 and 3.8 per cent, respectively, less than previous maxima of 270 and 260 pounds. Furthermore, unlike the third human subject during series D2. the upper limbs of all the simian subjects were slightly flexed. and the muscular force required to maintain the slight flexion at the elbow during the pull is almost as demanding on the flexors of the elbow as their further contraction to produce additional flexion would be (Martin, 1921). Although any comparable testing program should seek to nullify shoulder movement more completely, perhaps by contoured braces of the shoulder and by training the chimpanzee subjects to pull at higher (though less optimal) angles of elbow flexion, the foregoing considerations indicate that any increase in these scores due to retraction at the shoulder is probably very moderate. It may therefore be concluded that with the satisfying of the recently analyzed thirty-seven criteria (incompletely satisfied in a few cases because of the limitations of available time) for adequate strength testing (Edwards, 1963a), both simian and human scores are quite accurately representative of the strength of the subjects tested, and interspecific comparisons are thus also valid.

The remarkable reliability of the chimpanzee scores accords with their validity. As indicated earlier in the paper, equivalent motivation was achieved through a widely varying assortment of positive and negative incentives, adjusted to the individual simian subject. It is of some interest to observe that only for the adult male was the primary motivation that of pleasing his human friends.

Intraspecific comparisons reveal the anticipated tendency for larger humans and chimpanzees to be stronger than smaller humans and chimpanzees (Edwards, 1965b). As would have been anticipated from studies of humans and from theoretical considerations, the maximal scores of chimpanzee females (second and third subjects) averaged less than those of males both in lift per unit of body-weight and in lift per unit of brachial crosssectional area; but the number of subjects was too small and these ratios -- especially that of the force per unit of area, for which the third subject almost tied for highest score -- too inconsistent to be considered more than suggestive. The extent to which the scores of these second and third subjects averaged lower than those of the others might also be ascribed to the fact that they were the two youngest subjects. In any event, the fact that the highest scores both relative to brachial crosssectional area and, despite the operation of geometrical similitude, relative to body-weight were those of the adult male chimpanzee may tend to some degree to confirm an anticipated correlation between strength and

both masculinity and maturity for these apes, as for humans; but firm conclusions are again precluded by the limited sample size.

Inspection of the data presented evinces the finding that, despite the fact that all of the human subjects were adult males but 40 per cent of the chimpanzees were females and 80 per cent were pre-adolescent or earliest-adolescent, chimpanzees are much stronger than humans per unit of bodyweight. The outpulling by the largest chimpanzee of a human weight-lifter fully $2\frac{1}{2}$ times as large in body-weight seems especially noteworthy. The striking average ratio of superiority of chimpanzees to humans is 2.681: 1 (2.410 to 0.899), approximating the ratio reported by Bauman (1923 and 1926). Much of this superiority is ascribable to geometrical similitude operating on the individuals of different body-size and to the proportionately heavier arms of the apes. For example, if a 64-pound chimpanzee, identical physiologically and in proportions to a 216-pound human, lifted 64 pounds, the human would lift 144 pounds, 33.3 per cent less than the 216 pounds which would have been lifted if strength were proportionate to the cube of a given dimension (or body-weight) instead of to the square of a given dimension (Edwards, 1963d). But general geometrical similitude provides only a very small factor in accounting for the 2.951; 1 superiority of the adult male fifth subject.

As noted in a companion paper (Edwards, 1965b), unfortunately completed before the data here presented had been quantitatively analyzed, it is concluded that four to six other factors contribute significantly to the chimpanzee's marked superiority in strength. The most important of these other factors is the proportionately much greater massiveness of the chimpanzee upper limbs. Thus, per unit of brachial cross-sectional area, the chimpanzees manifest only a 41.1 percentage of average superiority over the humans (3.226 to 2.286). In fact, the ranges actually meet, but the immaturity and sexual heterogeneity of the chimpanzee subjects should again be emphasized, and it should be observed that only the proportionately weakest of the apes, a $4\frac{1}{2}$ -year-old female, demonstated a ratio as low as the highest among the humans here tested.

Further comparisons between the two species reveal marked contrasts in the degree of overhanded superiority. The average amount by which the fatigue-adjusted (by 15 pounds for the second series maximum, as analyzed presently) underhanded scores were less than the overhanded scores for humans was 51.8 pounds (35, 62.5, 22.5, 35, 42.5, 75, 90 for the seven subjects, respectively). This average difference is equivalent to 27.7 per cent of the overhanded lifts, averaging 187.1 pounds, as compared with only some 7.85 per cent difference for chimpanzees, as discussed above. The writer has not yet had time to attempt a complete analysis of the presumed anatomical factors determining most of this contrast; but at least a small part of the contrast is surely due to the equivalent effort on all maximum lifts by the chimpanzees, while the human subjects were, in the opinion of the writer, more concerned about the maximum score for each arm than the overhanded-plus-underhanded average maximum.

The human maximum strength scores per square centimeter of brachial cross-sectional area manifest decidedly more interindividual variability than the chimpanzee scores, as shown by the contrasting ranges -- 1.70-2.77 versus 2.73-3.56 -- and by the contrasting average percentages by which the individual values differ from the mean values (2.286 and 3.226) in each group -- 13.9 versus 9.08. Thus, by the index here employed, human variability is some 53 per cent larger. Much of the lesser variability of the apes reflects more uniformity of exercise, but much of it is probably due to less genetic variability, as theorized in a previous paper (Edwards, 1965b) should be the case. Furthermore, chimpanzee intraindividual variability for maximum scores on different days also seems to be less than that indicated by the typical retest coefficient of correlation of .90 to .92 reported for humans (Hunsicker, 1955; Clarke, 1960), as was also theorized earlier on the basis of the chimpanzee's apparently greater ease of approaching strength maxima, presumably asymptotically (Edwards, 1963a, p. 14).

There is moderate indication of handedness in the humans tested, with higher scores for the preferred limb in all underhanded-plus-overhanded maximum scores except for the identical totals of the fourth subject, and with a 10.4-pound average superiority of the preferred arm in scores fatigue-adjusted for the first five subjects, as calculated below. Also, all seven humans exhibit slightly to moderately larger brachial girths for the preferred extremity. Insufficient time was available in the present study for observations on chimpanzee handedness per se. Since these apes are adapted to arboreal locomotion by varied climbing and brachiation, less handedness than in man would be anticipated theoretically (Edwards, 1963a and 1965b), and observational data procured by others confirm this expectation (Yerkes and Yerkes, 1929, p. 217). Some further confirmation of handedness to a lesser degree than in man is provided by the present study. as indicated by the generally greater similarity in chimpanzees of both contralateral strength scores and girths of the upper extremities. In the simian subjects -- two of whom manifested slightly larger right arm girths, two larger left arm girths, and one almost identical girths -- no clear correlation between the few contralateral strength scores and brachial girths is evident, but this is at least consistent with a more limited degree of handedness, although likely primarily reflecting the inadequate sample size. It may be somewhat significant to observe that in the subject most adequately tested, the largest, the right brachial cross-sectional area, roughly (as accurately as could be measured) 2.7 per cent larger, is associated with an average 3.9 per cent greater lift. In neither species does greater size and strength of one limb show direct genetic origin, however, since greater use of one arm results in its relative hypertrophy.

The two largest human subjects did not manifest any clear evidence of fatigue in the alteration of overhanded to underhanded sequences, for the overhanded superiority increased by 10 and by 20 pounds when preceded by the underhanded test. The lack of clearly manifested fatigue in these two humans may reflect better muscular endurance than that of the others, for one had for a year practiced weightlifting, while the other had during the previous two months exercised his arms to an unusual extent; these two subjects were also likely the best motivated among the seven.

The five remaining humans apparently exhibited rather marked effects of fatigue by the lessening of the anticipated maximum score for the latter of the two series (overhanded and underhanded) for a given limb. The seven pairs with overhanded priority averaged a 57.1-pound overhanded superiority, but three pairs with underhanded priority averaged only an 18.3-pound overhanded superiority. It is estimated by approximate consensus of available data -- including some consideration of the inconsistent scores for the two largest subjects -- that the fatigue resulting from the first series for a given limb reduces the second series for that limb roughly 15 pounds.

In comparing the chimpanzee with the human performances, it seems evident that the proportionate superiority of chimpanzee endurance is much greater than that of strength, for many of the near-maximal pulls of the chimpanzees were made in much more rapid succession than those of the humans without apparent reductions in the scores achieved. Nevertheless, the fatigue factor was perhaps of slightly greater consequence in proportionate reductions of maximum scores achieved by the chimpanzees, for in addition to the briefer rest-intervals permitted between near-maximal pulls (in most cases a maximum of one minute for the apes compared to an average of more than two for the humans), much longer series of preliminary trials, primarily composed of lifts of less than 80 pounds not shown in the data previously presented, were mandatory for all but the largest chimpanzee subject. Furthermore, many successive series were generally employed for the apes, in many cases during four to six hours without a single very lengthy rest-interval.

There might also have been anticipated some evidence of a general fatigue factor in the human tests. Comparison of intralimb fatigue-adjusted (15 pounds for the first five men) and interlimb handedness-adjusted (10 pounds for all humans) scores reveals that the first limb to be tested scored higher than was anticipated by an average superiority of only 1.79 pounds over the contralateral limb for the fourteen pairs compared. It should be considered, however, that even should a larger series also fail to yield statistically significant results, a general fatigue factor would not necessarily be invalidated, for there may also be psychological, epinephrine-associated, and/or other compensating factors. The chimpanzee test results failed to manifest any such correlation, as would have been anticipated in view of the smaller sample of comparative scores and the better endurance of the apes.

Through the study here presented, it is now possible to state the approximate strength of chimpanzees relative to humans. Chimpanzees are two to three times as strong as humans per unit of body-weight and, at least for the brachial flexors, roughly 50 per cent stronger than humans per unit of cross-sectional muscle area, sex and age being equivalent.

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