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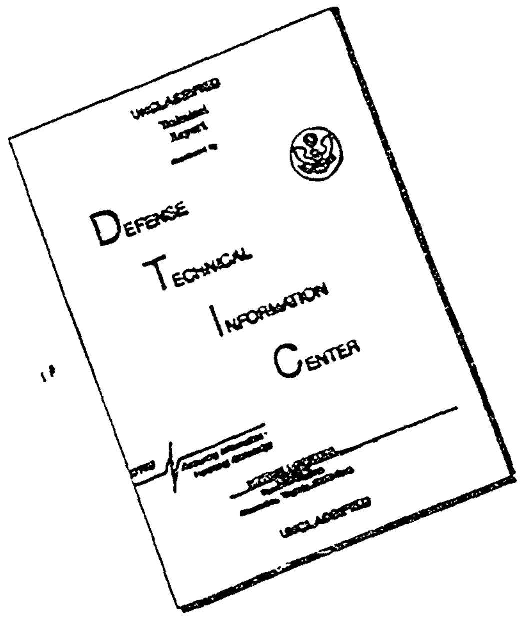

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STUDY OF MONKEY, APE AND HUMAN MORPHOLOGY AND PHYSIOLOGY RELATING TO STRENGTH AND ENDURANCE

PHASE II

FACTORS IN THE POSTURE AND GRASPING STRENGTH OF MONKEYS, APES, AND MAN

TECHNICAL DOCUMENTARY REPORT NO. ARL-TDR-63-21

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6571st Aeromedical Research Laboratory
Aerospace Medical Division
Air Force Systems Command
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(Prepared under Contract No. AF 29(600)-3466 by William E. Edwards, Contractor and Author, Columbia, S.C., and Chicago, Ill.)

FOREWORD

Initiated by the contractor some years ago as portions of research on the determinants of many aspects of form and function in man and other primates, the studies described herein have never previously been more than very briefly and incompletely presented in papers read at professional meetings.

In the preparation of this more formal and complete report, the very helpful cooperation and encouragement of Lt. Col. Hamilton H. Blackshear, USAF, MC, Maj. James Cook, USAF, VC, and Maj. Robert H. Edwards, USAF, MC, of the Aeromedical Research Laboratory of Holloman Air Force Base, New Mexico, is gratefully acknowledged.

ABSTRACT

Maximum suspension time from a parallel rod for infant primates, including humans (155 seconds, two-handed), chimpanzees (5 minutes, one-handed), and rhesus monkeys (33 minutes, one-handed) approximately equals or exceeds that of adults of the same species, remarkably. Interspecific and interage differences are ascribable to geometrical similitude, because, with morphological proportionality and physiological equivalence, larger animals are relatively weaker.

Equally perplexing, the legs and feet of gibbons are proportionately less massive and architecturally more poorly constructed for supporting strength than those of great apes, yet gibbons walk erect with great frequency and duration; the same surprising contrast exists between immature and adult pongids. In both instances geometrical similitude is operative, with optimum form only partially compensating for the handicap of larger body-size.

Since man's bipedalism-adopting ancestor was probably very small upon descent from arborealism, the time of descent and initiation of the hominid radiation was probably very early geologically, likely Late Eocene or Early Oligocene.

These analyses also provide the key to the interpretation of many other phenomena of primate form and function.

PUBLICATION REVIEW

This technical documentary report has been reviewed and is approved.

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FACTORS IN THE POSTURE AND GRASPING STRENGTH OF MONKEYS, APES, AND MAN

1. INTRODUCTION

The remarkable ability of human infants to support themselves with almost superhuman (or at least super-infant) strength while hanging from a horizontal rod, as well as the almost equally peculiar ability of the gibbon to walk erect more frequently and for longer distances than any other ape -- despite the fact that the gibbon is more specialized for brachiation and has less well-developed supporting legs and feet than any of his simian relatives -- constitute two of the most perplexing phenomena in primatology. As will be exemplified in this paper, the explanations for these phenomena are not only of interest *per se* but have applications, through comparisons of morphological, physiological, and behavioral characteristics, to seemingly unrelated phenomena and even to the phylogenetic history of the higher primates.

2. GEOMETRICAL SIMILITUDE

The principles of geometrical similitude pertain to the fact that geometrically similar organisms of different size do not maintain geometrically similar component structures when maintaining equivalent functions. Despite their recognition by Galileo centuries ago (Thompson, 1942, p. 27), these principles have been employed only rarely in the biological sciences, and virtually not at all in primatology.

As one example of their application, the eyes of the whale need be no larger than those of a mouse, though the additional "price" paid for larger eyes is so small in the larger animal that natural selection has determined larger resultant absolute size, albeit much smaller relative size; therefore, although eyes do not "need" to change in magnitude with change in a given linear (parallel to the body's main axis) bodily dimension, l (therefore tending to vary with essentially l^0), altered selective pressures yield change in eye volume roughly proportionate to a given dimension (l^1). But as an example of different effects, the quantity of insulating hair in mammals needs to increase approximately with the square of a dimension (l^2), although the larger animal may have proportionately more hair because it can with less detrimental effects sustain more hair (for example, shrew versus musk-ox) or may have less because its larger bulk provides in essence its own improved insulation (shrew versus elephant). Other portions of the organism, such as the volume of the circulatory system, need to vary in mass approximately with l^3.

The strength of muscles is proportionate to their cross-sectional area, so for equivalent strength in body movements -- since length for most muscles must remain proportionate to a given linear dimension -- the muscles might be expected to vary in cross-sectional area with l^3, so muscle mass would vary with l^4, or, if the expanding muscles constitute a significant portion of body-weight and body-weight is the force resisting the muscle action, muscle volume or mass would theoretically tend to increase by as much as l^7 (Edwards, 1960a). But the feasible proportionate lateral expansion of all major muscles is obviously limited; furthermore, as a muscle expands laterally it becomes progressively weaker in proportion to cross-sectional muscle area because of limitations concerned with fiber alignment. Thus only muscles especially crucial to survival and relatively thin in smaller variants of a general animal type find relatively much thicker analogues (generally homologues, if the organisms are fairly closely related) in larger forms. So musculature volume and mass, generally the largest system of the body in all but the smallest animals, in most cases increases by less than l^4, and between individuals of a species by little more than l^3.

As the first of only two among many recognizable illustrations of the application of principles of similitude to human muscular phenomena, one investigator (DeWitt, 1944, p. 63) concluded: "Heavier and taller men appear to be handicapped in performing tests of the sit-up type." This observation is readily explicable if it is recognized that when the primary or total resistance to muscle action is the body itself, strength varies with l^2 but body-weight with l^3, and that when all factors except body-size are equal the proportion of muscular tissue is fairly constant. Larger humans are thus appreciably weaker in moving body portions. Likewise, it is understandable that gymnasts are much smaller, relatively stronger, and absolutely weaker than most other athletes (DiGiovanna, 1943).

Another system which, like the muscular, "should" increase with more than the fourth power of a given dimension is the skeletal, for the supporting strength of a bone is proportionate to cross-sectional area, support needs vary with weight (l^{3+}), and bone length must remain approximately proportionate to a given linear dimension ($l^{3+} \cdot l = l^{4+}$). For two reasons, there is for larger vertebrates much less compromise toward the more feasible geometrically similar increase (l^3) from the needed increase (l^{4+}) for the skeletal than for the muscular system. First, a muscularly weaker animal may, depending upon the medium in which it lives, survive despite relative lack of speed and bodily dexterity; for example, increased bulk provides compensatory defense against predators. But one with very frequent skeletal fractures because of compression stresses cannot survive. There is thus less tolerance in the demands for skeletal strength. Second, approximately proportionate strength in larger bones can be achieved by the deposition of more mineral salts within the bone, with little if any change in proportionate external dimensions; that is, more spongy substance can be replaced by compact substance in larger animals, and the central cavity of bones possessing this feature can be proportionately reduced. Thus, although muscle weight may for a given order of mammalian quadrupeds be on the average approximately proportionate to $l^{3.3}$, the exponent of a given linear dimension may for skeletal weight approximate 3.6. The rate of increase is most rapid with larger body-size, when least "afforded," for by the human level of size the minimal skeletal proportions are approached, so beyond human size there is a progressively smaller range of tolerance within which natural selection can operate in seeking the optimum compromise proportion (Edwards, 1960*b*).

The maximum size of the largest terrestrial animals, if not determined by available food resources and the other species competing for that food, is most frequently limited by the proportionately decreasing muscular strength and especially skeletal strength, in accord with the principles of geometrical similitude indicated. But aquatic forms, such as whales, supported in a liquid medium, have very different limitations.

3. RELEVANT GENERAL DATA ON SELECTED ANTHROPOIDEA

An aberrant representative of the platyrrhine monkeys, the spider monkey (*Ateles*) is relatively abundant throughout most of the tropical forest areas of South and Central America, and has the northernmost extent of all subhuman New World primates, at least to central Tamaulipas, Mexico. The spider monkey is primarily frugivorous, but it also occasionally eats bird eggs and insects. Adult trunk height (superior border of pubic symphysis to suprasternal notch) averages perhaps 24 to 30 cm., tail length is usually 60 to 80 cm., and adult body-weight generally varies from 5 to 7 kg. (Hill, 1962). The tail, likely the largest among the primates both absolutely and, at least in mass, relatively (Edwards, 1961), is a grasping structure employed from birth as the most highly developed caudal "fifth hand" in the animal kingdom (Romer, 1959, p. 312); among primates, prehensile tails are limited to some American genera. As the mother progresses through the forest, the infant's tail is coiled about the base of her tail, while "the infant's feet grasp the mother's flanks and the hands grip the hair on her sides" (Hill, 1962, p. 456). Older spider monkeys locomote primarily by walking quadrupedally along the tops of branches, but, especially between branches, they frequently brachiate -- swinging rather like a pendulum with the body alternately suspended from one hand and arm and then the other, as successive branches are grasped. As adaptations for brachiation, a mode of locomotion unique among New World monkeys, limbs are extremely long and thumbs are almost absent. Even when not brachiating, spider monkeys tend to keep the trunk of the body in a more nearly orthograde (vertical) position than other platyrrhines. In fact, "they often assume an erect attitude [;] the tail is raised high, parallel with the spinal column, and used as a balancing organ" (*ibid*., p. 451).

The spectacled langur (*Trachypithecus obscurus*), a leaf-eating native of southeast Asia approximating the spider monkey in size, is the only non-hominoid brachiator discovered by Avis in her recent (1959) survey of the Old World primates. Although even in cages such arm-swinging is rare and only incipient in development, an orthograde posture of the trunk is frequent while climbing through the trees. But typical quadrupedalism is the customary locomotion.

Most baboon (*Papio*) species, of many areas of Africa and Arabia, are omnivorous and appreciably heavier than the monkeys just mentioned but have shorter limbs of equal length -- although relatively longer than those of most catarrhines (Morton, 1927, p. 181). The little-specialized, equal limbs reflect typical terrestrial quadrupedalism, a primarily non-arboreal adaptation -- along with a reversion to an elongated, dog-like muzzle -- to grassland areas, with only sparse if any trees. Defensive compensations for non-arborealism include huge canine teeth, likely the highest animal intelligence with the exception of that of the great apes and man, and fairly complex and effective social organization.

The omnivorous rhesus monkey of India is a member of the genus Macaca, abundantly represented from Gibraltar to Japan and the East Indies. With a trunk height of roughly 35 cm. (Hooton, 1942, p. 201), a newborn weight of .45 kg., and adult body-weights of 11.0 kg. for males and 8.0 kg. for females (Spector, 1956, pp. 128 and 158-159), the rhesus is moderately larger than the spider monkey, langur, or gibbon. Their present primary terrestrialism, the writer would suggest, is mainly the result of human deforestation; in the trees and on the ground, locomotion is generally quadrupedal.

A single polytypic species of gibbon comprises the genus Hylobates of southeast Asia and the East Indies (Montagu, 1951, p. 72); the writer would suggest that eventually this genus will be combined with that of the closely related siamang (Symphalangus) of Sumatra, with a single monotypic species. About 80 per cent of the food consumed by the gibbon is fruit, while leaves, buds, and flowers make up most of the remainder, supplemented by various insects, bird eggs, and young birds (Carpenter, 1940, pp. 81-89). At birth, the infant gibbon weighs less than 0.4 kg. (Schultz, 1936, p. 268). With extremely little sexual dimorphism, most races of adult gibbons average some 28 cm. in trunk height, less than 90 cm. in total stature, and approximately 6.0 kg. in weight, about half the body-weight of the siamang. The very long and thin limbs, with hands of similar proportions (but retaining a thin thumb of moderate length), represent adaptations to brachiation. Despite very "long, thin spindly legs and arms," the infant gibbon manifests surprising grasp-supporting strength, grasping around the mother's body or its hair alone, and from birth it is apparently never carried on its mother's back (Carpenter, 1940, pp. 141-144). Unequalled even by the spider monkey, this smallest hominoid is the most proficient arborealist among the primates, with speed of brachiation -- approximately 90 per cent of locomotion -- often as great as that of a very fast human runner on the ground (Carpenter, 1940, p. 78). "They are so. . .strong that they can jump with ease from one branch to another 15 or 20 feet away" (Felce, 1948, p. 11), and may even cross spaces of 35 to 40 feet (Hooton, 1946, p. 27). Some 10 per cent of locomotion is by walking along branches, with the arms generally extended laterally for balance or to grasp branches to the side or above for additional security. Walking on the ground (very rare in nature) is alternatively by clumsy quadrupedalism, another special kind of quadrupedalism involving swinging the trunk and legs between the enormously long arms used as crutches, and bipedalism, with the arms used as balancing devices, except in captive individuals after much practice (Carpenter, 1940, pp. 66-79).

The orangutan (Pongo) of Borneo and Sumatra (and formerly extending at least to southern China) is almost exclusively frugivorous. With marked sexual dimorphism, adult male trunk height is some 55.5 cm. (writer's estimate from miscellaneous data) and body-weight averages about 75 kg., with females only half that weight. In its natural habitat, it prefers to test the strength of stouter branches before entrusting its appreciable weight to them (Hooton, 1946, p. 29), but it frequently progresses fairly rapidly by brachiation, which does not permit such testing (Kroeber, 1948, p. 47). Except under duress, it apparently never descends to the ground, where it can walk, without training, only in very slow and clumsy quadrupedal fashion (Felce, 1948, p. 9).

The chimpanzee (Pan), broadly distributed in the tropical forests of Africa, is represented by at least three "species" (or likely only races) and is primarily frugivorous (Nissen, 1931). The most nearly human in many respects, it is the best-known non-human primate. After a 237-day (216-261) gestation (Spector, 1956, p. 128), the trunk height is about 13 cm. (Riesen and Kinder, 1952, p. 12), and the average weight of seventeen chimpanzees measured within 36 hours after birth (Yerkes, 1943, p. 54) was 1.89 (1.61 to 2.26) kg., although the writer would suggest that captivity may tend to reduce the gestation if not the birth-weight. In infancy, the arms of the chimpanzee are very thin, while its legs are much more muscular; however, during ontogeny there occurs a trend culminating in near-reversal of relative muscularity, with the arms, over a third longer than the legs, increasing to almost equal massiveness. Excluding the rare pygmy chimpanzee, adult male trunk height is some 44.6 cm., while body-weight is about 46.5 kg. in males and almost 40 kg. in females (these figures represent a synthesis by the writer from various sources). Since each adult female has one young approximately every two to three years (Nissen, 1942), brachiation is apparently learned to a fair degree of proficiency by the age of two. As adults, despite the fact that only a third of the time is spent in the trees and only a minority of that at brachiation (Nissen, 1931, p. 35), they are almost as adept at climbing and brachiating as their exclusively arboreal and far more specialized cousins, the orangutans (Kroeber, 1948, p. 48). Locomotion during the two-thirds majority of time is virtually exclusively quadrupedal -- plantigrade on the hand-like feet but on the knuckles of the hands; the longer arms and knuckle-walking cause the trunk to slope somewhat upward to the shoulders. Erect sitting and occasional standing are also characteristic, while at least captive chimpanzees walk erect at times, mostly while immature.

Probably because of relatively recent human incursions, the lowland and mountain species, or more likely races, of gorillas of central Africa are separated by some 650 miles of Upper Congo forest (Hooton, 1942, p. 63). Like the other great apes, they are primarily frugivorous, with bamboo shoots providing another major item of the diet. They weigh only about 2.0 kg. at birth (ibid., pp. 85-86), but are the largest of the primates, present and likely past, as adults, with total stature for both lowland and mountain male gorillas to 196 cm. and averaging approximately 168 cm. (5 ft. 6 in.), trunk height 56.2 cm. (lowland) and 60.3 cm. (mountain), and body-weight 193 kg. (lowland) and 210 kg. (mountain); females are roughly two-thirds as heavy. Although primarily terrestrial, with the largest adults almost never climbing trees, "youngsters of intermediate size seemed to frequent the trees more than the smallest or largest representatives of a group. /They/ were observed playfully climbing trees in the cold forest with skill not greatly inferior to that of captive chimpanzees" (Bingham, 1932, pp. 32, 37, and 60). "When young. . .climbing antics and acrobatics, which include frequent brachiations or climbing or swinging by the arms, are endless and are executed with vigor and agility" (Polyak, 1957, p. 1015). On the ground, gorillas employ the same knuckle-walking quadrupedalism as chimpanzees, but the trunk is more nearly horizontal. But unlike adults, which occasionally stand or wrestle in erect posture, young gorillas apparently walk erect with moderate frequency, with human-like stride and with hands at their sides or clasped behind their backs (Hooton, 1942, p. 77).

Humans in the United States have at birth a trunk height of approximately 17 cm. (Riesen and Kinder, 1952, p. 12) and weight of 3.49 kg. (Spector, 1956, p. 162). Adult American Caucasoid males and females have total statures averaging 177 and 163 cm. and body-weights of 70 and 56 kg. (ibid., p. 176); adult male trunk height is roughly 74 cm. (estimated by the writer from data in Bayer and Bayley, 1959). All humans go through a quadrupedal stage of locomotion, in very rare individuals to the age of five years, but, like the gibbon, fingers as well as toes are extended, although rare knuckle-walking of the hands has been reported.

4. GRASP REFLEX AND GRASP-SUPPORTING STRENGTH

Although not too frequently observed, or at least noted in published reports, the grasp reflex is fairly surely common to all middle and higher primates, and likely at least most prosimians as well. This reflex is operative from the moment of birth, with the hands and feet closing tightly about any object touching the palms, soles, or ventral surfaces of the digits. Sufficiently great strength is manifested to support the body of the infant, generally from a single limb and for a considerable duration. Adults usually exhibit roughly equivalent grasp-supporting strength, but of a voluntary nature, except when influenced by certain drugs or some forms of brain damage, including certain experimental lesions, when the reflex returns (Richter, 1934, p. 328) -- or its cortical learned inhibition is removed, the writer would suggest.

Richter (1931) reported experimentation on five newborn rhesus monkeys (subsequently extended to nine), which supported themselves on a horizontal rod by only one hand for as long as 33 minutes, with maximum duration at 15 to 38 days after birth. Two of the five monkeys manifested two peaks of supporting strength, at 16 and 21 and at 6 and 26 days; a third apparently experienced three peaks, at 15, 21, and 63 days. One monkey still showed the reflex when experimentation was discontinued at 63 days. The maximum duration of suspension for drugged or operated-upon adult monkeys was only two minutes (ibid., p. 328).

The newborn gibbon's great grasp-supporting strength and endurance, despite very thin limbs, has already been noted. Despite arms proportionately almost as thin as the newborn's, the adult gibbon also manifests an extreme amount of grasp-supporting strength, as indicated by brachiation itself -- especially the remarkable case of a one-armed gibbon which had presumably continued to locomote fairly satisfactorily for some time (Carpenter, 1940, p. 75) -- and, more directly, by the habit of hanging for lengthy intervals by one arm or even one leg while using the other three limbs in feeding (ibid., pp. 84-85), a performance exceeded only by the spider monkey, which often employs all four extremities in manipulation while suspended by its prehensile tail (Hill, 1962).

Despite the relative thinness of the arms of young chimpanzees, the average one-day-old infant is able to hang by one hand for some 60 seconds, and several times longer at two weeks, with a five-minute maximum at that age (Riesen and Kinder, 1952, p. 141). Riesen and Kinder (1952, pp. 141-143) have analyzed the grasp reflex into several components; the first failure of closere to stretch occurs at approximately 12 weeks, and the first withdrawal from palmar contact at 16 weeks. Although Jacobsen, Jacobsen, and Yoshioka (1932, p. 54) state that "Alpha" showed no decline in the ability to hang by one hand throughout infancy, Riesen and Kinder (1952, p. 140), noting the likely significant role of variable exercise (Nissen, 1931, pp. 83-85), indicate a marked diminution in such relative strength after a two-week maximum, as likely exemplified by the 2½-month chimpanzee able to support itself with both hands for only one minute (Schultz, 1936, pp. 263-264). Despite the fact that, because of much-reduced exercise, young caged chimpanzees are not nearly so strong as those in the wild, the writer has observed, at the Aeromedical Field Laboratory of Holloman Air Force Base, one two-year-old chimpanzee of twenty pounds climbing with facility up the side of a wire-net cage with another of equal weight clinging to it, by grasping its pelage only.

Gorillas manifest the grasp reflex at birth, but their suspensory ability has apparently never been tested. In young individuals, it must be considerable, however, as manifested by their excellent climbing and brachiating ability, previously noted. But adults become very slow climbers (Hooton, 1942, p. 78).

The grasp reflex, present initially in humans, constitutes one of the very few items of innate behavior found in all human infants at birth (La Barre, 1954, p. 105), or indeed in primate infants in general. "The very real power of an infant's hand-grasp [is] extraordinary [,] one of the most astonishing features of a newborn baby" (Jones, 1926, pp. 205-206). "Early grasping is reflexive. It is a two-component activity consisting of finger closure and gripping. Closure occurs in response to light pressure stimulation on the palm, whereas gripping is a static proprioceptive reaction to a pull against the finger tendons. Finger closure first appears at about 11 weeks in fetal life and is quite complete at 14 weeks. The gripping reflex appears during the 18th (prenatal) week" (Gesell et al., 1940, p. 80). As highly variable in strength as that of the rhesus, the maximum suspension time for 60 infants grasping a horizontal rod by both hands recorded by Robinson (1891), who was apparently the first to report the reflex and associated suspensory ability in any primate, was 155 seconds. Richter (1934) conducted comparable two-hand tests on two parallel horizontal rods, with a maximum duration of 128 seconds at 18 days of age and a maximum average duration of 66 seconds in six tests in a premature infant between 1 and 8 days of age. "Infants with long fingers are in general superior to those with short fingers in strength of reflex gripping. . . . The closure reflex apparently disappears at *16 to 24 weeks* after birth and is eventually succeeded by facile digital prehension. Its proprioceptive component attains its greatest strength at or soon after birth and shows no appreciable weakening until after about 12 weeks. It disappears after 24 weeks but vestiges of this 'stretch' reflex are evidenced in the 'phasic' reactions of the fingers of adults" (Gesell *et al.*, 1940, p. 80). It might be noted that voluntary release, the counterpart of grasp, is "one of the most difficult prehensile activities to master in early life," beginning about 44 weeks, but difficulties persist throughout the first four years (*ibid.*, p. 82).

Moderately correlated with grasp-supporting strength, although involving extensor instead of flexor muscles, the number of push-ups generally attainable increases throughout preadolescence and until early adulthood, except for a plateau which is attained and maintained in the typical human male from 8 through 12 years of age (Buxton, 1957, p. 214). Yet even at adulthood, the grasp-supporting strength, or at least endurance, is in many and likely most cases even less than at two or three weeks, as indicated by the maximum suspensory time of 150 seconds among adults tested by Richter (1934, p. 331).

5. INTERPRETATIONS OF THE GRASP REFLEX AND GRASP-SUPPORTING STRENGTH

There seems little doubt that the grasp reflex of man represents a vestigial survival of a trait still essential among his primate cousins for the continued existence of the infant by clinging to the parent in an environment in which active locomotion of very young individuals is not feasible. Contrary to the interpretation of apparently all other students of the problem, the writer does not recognize clear evidence for any weakening of the reflex, for it has likely retained, during many millions of years of terrestrialism, essentially its level in arboreal ancestors of man, not only because of the likely low mutation pressure for alteration of the reflex and the lack of anti-adaptive selection for its removal but also because of probably slight selective pressure for its retention among primitive migratory populations, which characterized all hominids until the last small fraction of one per cent of their evolution. But associated muscular strength and endurance has declined since man's ancestors descended to the ground through lack of equivalent selective pressure for grasp-supporting strength, and relative strength has greatly declined because of the many-fold increase in neonatal body-size.

The interpretation of the fluctuating grasp-supporting performances by the same infant and the great differences in performances between different infants of the same species may be considered next. The writer would suggest that, although due at least in part to factors the relative intensity of which at different times is subject to chance variations, the multiple peaks evident for the majority of rhesus and at least some human subjects may to a large degree reflect simple maturation of the muscle tissue, muscular hypertrophy due to the experimental exercise, or perhaps learning at least semi-voluntary control. It should also be emphasized that slight changes in relative strength can effect great changes in endurance when the load (in this case, body-weight) approaches the maximum sustainable, and this phenomenon also largely explains the great differences in duration of suspension between individuals.

Human infants with longer than average fingers (assuming equal finger and object diameters and proportionate points of muscle attachment) experience the same advantage in strength of grip as the chimpanzee relative to man -- a simple mechanical advantage of leverage.

Since strength is proportionate to cross-sectional muscle area, which varies directly with the square of a given dimension in geometrically similar (equally proportioned) animals, while body-weight is proportionate to the cube of a given dimension, suspensory strength is inversely proportionate to the height, or the cube root of the weight. Thus assuming for the sake of analysis that all the primates here considered were proportionately identical, the relative strength would be inversely proportionate to the cube root of body-weight. Employing the body-weights previously cited, infants of the species indicated would have the following grasp-supporting strength relative to that of the human infant: rhesus, 198 per cent; gibbon, 209; chimpanzee, 123; and gorilla, 120. Comparable percentages for adult males are quite different, however: rhesus, 185; gibbon, 227; chimpanzee, 113; and gorilla, 69. Similar calculations indicate how the infants can have grasp-supporting strength superior to that of their parents: rhesus, 290; gibbon, 251; chimpanzee, 291; gorilla, 472; and man, 272 per cent. Thus the fundamental reason, geometrical similitude operating on differential body-size, is apparent for the superiority in relative strength of smaller species and, generally, younger individuals, as well as the likely superiority of smaller newborn human infants, despite some correlated prematurity.

Of course, through natural selection somatic proportions are adjusted to compensate to the extent optimally feasible for differences in body-size, both ontogenetically and interspecifically. A very thin muscle paralleling the humerus, for example, would need to increase its cross-sectional area with the cube of increased height, and thus increase its volume to the fourth power of a representative linear dimension, as discussed earlier. But if the entire musculature of the body needed to increase in order to maintain constant relative strength -- more nearly the case for arboreal primates -- because the mass of the skeleton is large and has the same theoretical needs as the musculature and because the musculoskeletal system constitutes more than a third to well over a half of the total body-weight in primates, the muscles would tend to increase in volume by almost the seventh power and in diameter by almost the third power of their length. Since such enormous increases in bulk are clearly impossible with great changes in length or stature, increased massiveness, especially of the arms, is combined with reduction of proportionate arm length and especially leg length, as well as all dimensions of the lower trunk, in the largest primates. For the same reason, older primates develop proportionately heavier arms. Nevertheless, the optimum compromise toward which selection aims involves relatively less grasp-supporting strength for larger species and generally for older individuals.

The great suspension time superiority of the rhesus monkey over the chimpanzee is obviously due to the fact that there is not only a marked difference in relative strength (61 per cent), but also endurance increases disproportionately with relatively slight reductions in sub-maximal loading. The chimpanzee and human data reveal that the ape understandably is clearly stronger both relatively and absolutely.

The rareness of adult gorilla arboreality and the gorilla's slow and clumsy climbing when arboreality occurs has apparently always been ascribed primarily to the danger of branches breaking. The foregoing analysis reveals that the major determinant is that, despite its great massiveness of musculature, the gorilla is relatively weak.

Finally, the decline (deemed probable from push-up studies) in infancy followed by gradual rise to maturity in grasp-supporting strength and endurance in humans is due to the interrelationship between the disadvantages of larger body-size and the advantages of proportionately larger and -- associated in part, almost surely, with maturation as well as exercise -- more "efficient" muscles.

6. POSTURE OF ANTHROPOIDEA

The posture of monkeys and apes has already been described in almost sufficient detail for the purposes of this paper. In very brief summary, with some additional data, it may be noted that various primates occasionally stand and even walk erect, including the indri lemur (Hooton, 194?, p. 310), many platyrrhines, and the Japanese macaque. A greater number of primates, such as langurs, frequently climb about trees with the trunk in an orthograde position. Some lemurs and most monkeys spend a large portion of their time sitting, with the trunk erect (thereby freeing the hands for other purposes). But the most frequantly orthograde primates, other than man, are the true brachiators. The spider monkey and the gibbon both walk bipedally a large portion of the time in the trees and customarily on the ground as well, when encouraged by fruit to descend briefly (Carpenter, 1940, p. 84). Although gibbon muscle proportions are fairly similar to those of man (Tappen, 1955, pp. 417-419), adult great apes have, at least in most respects, much better developed lower extremities for support than the smaller brachiators, both in relative leg thickness and in proportionate massiveness and "architectural" design for support (McMurrich, 1927; Morton, 1927). The sequence of progressive morphological specialization of the legs for the function of supporting the body is orangutan to chimpanzee to gorilla, which is the same sequence as that of relative terrestrialism and almost that of relative size. So it might be expected that the great apes exhibit the greatest amount of bipedalism. Yet the frequency of bipedalism in the apes is almost precisely the reverse sequence of those adaptations which might seem to have developed to make it possible. All three great apes are bipedal much of the time in the trees, but not often truly so, for branches are held by the arms not only for more secure balance, as frequently with the gibbon, but generally for additional support of the body-weight as well. On the ground, adult great apes (the orangutan, of course, is terrestrial only momentarily unless forced to be) often sit with the trunk orthograde but only rarely stand and virtually never walk bipedally. But, like rhesus monkeys (Hines, 1960, p. 470), orangutans (Yerkes and Yerkes, 1929, pp. 113-116; Hooton, 1942, p. 124), chimpanzees (observations of the writer at Holloman Air Force Base), and gorillas (Hooton, 1942, p. 77) do very frequently walk erect in captivity when young, despite the rarity of such bipedalism as adults. Whether the much greater incidence of bipedalism in captivity is due to imitation of humans and greater frequency of (playful) carrying of objects, as the writer would suggest, or to some other factors (Riesen and Kinder, 1952, p. 170), the fundamental fact is that young great apes readily adopt terrestrial bipedalism, but instead of improving in this ability apparently must largely abandon it as adults.

7. INTERPRETATIONS OF THE POSTURE OF ANTHROPOIDEA

The explanation, based largely on principles of geometrical similitude, of the differences in the postural phenomena is so similar to that previously considered for arm-supporting strength that no extensive discussion is needed. Adults are larger and therefore cannot, because of relatively weaker legs and feet, walk erect as readily as immature individuals of the same species. Species of larger body-size have, as an attempt to comply with the demands of similitude, legs and feet better adapted to support body-weight, bipedally or otherwise, but as with grasp-supporting strength, the optimal compromise of adjustment does not fully compensate for the handicap of larger body-size. Thus is accounted the empirically observed "correlation of a high arm-body ratio with arboreal habits and with terrestrial bipedalism" (Morton, 1927, p. 184), and the quadrupedalism of the pongids is seen to bear no relationship to "their prolonged arboreal existence," as has been suggested (ibid., p. 186).

Finally, the implications of the determinants of posture to human evolution may be considered. Many students of human evolution have agreed that man's ancestor was forced to descend from the trees because of the retreat of the forest boundary (Howells, 1945, p. 105), or because of the development of excessive body-size (Linton, 1936, p. 11; Hooton, 1946, p. 106; Kroeber, 1948, p. 21). Both explanations are based upon fallacies;

the primary cause of descent was probably population pressure (at least seasonally) in the forests and the need for additional food. But such innovators almost surely had to walk erect "immediately" (actually a transitional interval of at least hundreds of millenia, undoubtedly) or else employ terrestrial quadrupedalism, for adaptation to either mode of locomotion is cumulatively self-reinforcing. As soon as the arboreal ancestor of baboons became terrestrial, it adopted a quadrupedal posture, and selection for greater specialization for terrestrial quadrupedalism was initiated quite irrevocably as the present dog-like form developed. Although it is barely possible that a generally but not exclusively quadrupedal ground ape might shift gradually to erect posture, especially if aided by body-size reduction, as seems indicated if the conclusion of Le Gros Clark (1955) and others that the australopithicines had developed only very imperfectly erect posture is correct (which the writer very much doubts), man's ancestor probably had to make an immediate "choice," as Howells (1945, p. 103) has commented. Man's ancestor had developed some proclivity to an orthograde posture arboreally, but not necessarily through true brachiation, and he had quite surely practiced at least occasional arboreal bipedalism, or he could hardly have chosen such a mode of progression upon his descent. But his lower extremities were quite surely at the start no better developed for terrestrialism than in the modern gibbon. Since the gibbon is apparently just slightly on the bipedal side of the fence of choice for terrestrial locomotion, it seems probable that man's ancestor was at most not much larger than the gibbon.

The descent to the ground probably occurred before the grassland environment, developing at the end of the Oligocene, had been exploited, that is, before its major ecologic niches had been filled with forms becoming progressively "improved" and specialized to maintain their positions. But the consideration of small body-size implies even earlier descent. The gibbon descends only rarely and briefly because it is relatively defenseless against modern terrestrial carnivores, so man's ancestor, since his social organization was probably little better than that of the modern gibbon, if as good, must have descended before the carnivores had developed greater speed, intelligence more nearly matching that of man's ancestor, and body-size markedly superior to the individual or group inaugurating terrestrialism. The last consideration seems to indicate the surprisingly early date of the Late Eocene or Early Oligocene for man's descent from the trees and the establishing of the hominid family of bipedal primates.

8. CONCLUSIONS

The long-perplexing phenomena of grasp-supporting strength -- as great in human infants as in adults and much greater in infant rhesus monkeys than in infant chimpanzees, despite the equivalent arboreality and the chimpanzees' specialization for brachiation -- are properly ascribable to the operation of principles of geometrical similitude, which determine that, all else being equivalent, larger animals are relatively weaker animals.

Similarly puzzling has been the fact that the adult gibbon walks erect much more frequently than any of the great apes, despite the better-developed-for-support legs and feet of the latter, and the fact that bipedalism is more readily achieved by young great apes than by adults. The operation of geometrical similitude on species or individuals of larger body-size, for which optimal form only partially compensates for greater size, again explains the phenomena. Since bipedalism becomes increasingly difficult with increasing body-size, it seems highly probable that man's ancestor, at the time of descent from the trees, was quite small, and therefore the descent was probably accomplished at a very early time, before terrestrial carnivores became too formidable to cope with.

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