

A Biomechanical Interpretation of the Pelvis of *Australopithecus*¹

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Abstract. DART's model of the Makapan ilium in a Bushman pelvis showed their morphological similarities in size and shape. The structural differences of the ilia have important implications for locomotion that are revealed by biomechanical reconstruction. These features relate to the ability of the anterior of the gluteus medius-minimus muscle complex to produce internal rotation. Combined with abduction, internal rotation is a fundamental motor element necessary for efficient bipedal gait; consequently, the muscle complex had important survival value. In the evolution of *Australopithecus* to *Homo*, selection was less for a particular gait than for the improvement of a joint motion element in gait as an essential part of a hunting/gathering and tool-using way of life.

Key Words
Biomechanics
Australopithecus
Bipedalism
Pelvis
Internal rotation

Introduction

Direct evidence for bipedality in *Australopithecus* appeared with the discovery of the pelvic remains from Makapan and Sterkfontein. The hominid features of the Makapan ilium indicated an upright trunk and a bipedal form of locomotion [DART, 1949a, b]. The composite model constructed by DART [1949a], which replaces a left ilium of *Australopithecus* from Makapan in a complete pelvis of *Homo sapiens*, provided a direct comparison of the ilia of *Homo* and *Australopithecus*. This fit of a fossil adolescent ilium into the configuration of an adolescent Bushman pelvis emphasized their similarities in ab-

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solute size, breadth, shortness, and orientation of the acetabulum; the expanded sacroiliac joint; the anterior position of the anterior superior iliac spine; and the developed sciatic notch. This fit is far better than could be obtained if a long narrow chimpanzee ilium were substituted for that of *Australopithecus*.

Although DART [1949a] emphasized the similarities between *Australopithecus* and *Homo*, other investigators discussed the differences [LE GROS CLARK, 1955; NAPIER, 1964; ROBINSON, 1963, 1967; WASHBURN, 1951, 1963; ZIHLMAN, 1967a; ZUCKERMAN, 1954, 1966]. The differences in the ilia, also illustrated on the DART [1949a] model, are in the curvature of the ilium and the beaking of the anterior superior iliac spine, features that seem to be group characteristics of the australopithecine pelvic fragments. Despite debate over these differences, their functional interpretation and relation to australopithecine gait have not been clarified.

At one level, a comparison of shapes is valid [BROOM and ROBINSON, 1950, 1951, 1952; DART, 1949a, b, 1957; LE GROS CLARK, 1955]. However, the structural differences represented in the bones and apparent upon visual inspection must be analyzed in biomechanical terms to reconstruct specific joint functions and thus gait pattern. Such an approach is an important basis for the excellent studies of OSBORN, [1900], GREGORY [1912], and SCHAEFFER [1947, 1948]. Biomechanical analyses in primates is admirably illustrated by KUMMER [1962, 1965] and PREUSCHOFT [1969, 1971]. In fossil forms, only bony landmarks representing muscles are available for reconstructing the magnitude, resultant, and components of force. This becomes a clear basis for discussion of the differences in the locomotor skeleton and thus, of the locomotor patterns of *Australopithecus* and *Homo* and even of the two species of *Australopithecus* [ZIHLMAN, 1970].

The DART [1949a] model provides an excellent basis for biomechanical analysis. The ilium is the point of origin for muscles crossing the hip joint. Since no adolescent femur has yet been found from Makapan, a Bushman femur was used as the point of insertion. Therefore, the only variable point in this study is the position of the Makapan anterior superior iliac spine. Although the application of such analysis to other australopithecine pelvic and femoral fossils may alter some details, it will not affect the main thesis. (The relation of australopithecine femora to this kind of model is the subject of further investigation [ZIHLMAN, in prep.].)

This paper analyzes and interprets the difference in the two anterior superior iliac spines and their differential effect on the mechanical advantage of the attached muscles that rotate the pelvis, internally or laterally, and thus on

gait differences in the two forms.² Since human bipedal locomotion combines the rotational and translatory movements of limb segments [LEVENS *et al.*, 1948; DUCROQUET *et al.*, 1968], we have focused on those aspects of hip joint morphology that indicate the effectiveness of internal rotation. We analyze the force components of internal rotation, the torque produced by these components, and the arcs of movement of the pelvis produced by these torques to demonstrate how the mechanical potentials in internal rotation differ between *Australopithecus* and *Homo*.

Differences between the ilia of the ancestral ape and of *Australopithecus* illustrate the evolutionary origin of the basic bipedal pattern. The evolutionary change in the ability to abduct and rotate the pelvis internally is directly correlated with advances in the efficiency of bipedal locomotion from *Australopithecus* to *Homo*.

Method

A copy of the original DART [1949a] model was generously provided by Prof. P. TOBIAS, University of Witwatersrand, and duplicated by A. HUGHES and B. HUME. In addition, plaster copies of the femora of the same Bushman individual were made. The casts of the Makapan ilium and of the Bushman pelvis and femora were checked with measurements against the originals in the Anatomy Department, University of Witwatersrand. The fossil ilium in cast and original was studied in conjunction with the other South African fossils and a sample of human and ape pelvis and femora.

The assigned points of attachment for analyzing the anterior gluteus medius-minimus complex are the anterior part of the greater trochanter and the anterior superior iliac spine. Although this muscle complex attaches over the anterior part of the gluteal iliac surface, for purposes of analysis, the anterior superior iliac spine was used to represent the 'idealized' situation [FRANKEL and BURSTEIN, 1970]. At this point, the lowest extent of muscle attachment of the horizontally oriented muscle fibers have the greatest potential to rotate. This well-defined point is homologous in the specimens and can be accurately measured. Among human populations, the degree of development of a lumbar lordosis, which determines anterior pelvic tilt, varies considerably. Analysis without tilt illustrates the *minimum* amount of internal rotation; the diagrams present the ilia from the same side for clarity of comparison.

² It should be noted here that lateral pelvic rotation (the pelvis moving about the stable femur) and internal rotation (the femur moving about the stable pelvis) are the same motion with different fixed points that result from the action of the anterior gluteus medius-minimus muscle complex. During gait these muscles act when the femur is the fixed point and the pelvis rotates about it. Often these two terms are used interchangeably; in this paper we used 'internal rotation' because it is more common. (This variation illustrates the semantic problem of designating muscle functions.)

The action of the anterior gluteus medius-minimus complex is determined by analyzing the components of muscle force that lie in the three axes intersecting at the insertion of these muscles on the anterior superior iliac spine. As figure 1 shows, each plane of movement in this system is perpendicular to the other planes when the center of the hip joint is taken as the axis of movement [STEINDLER, 1955]. The resultant action line as representative of this muscle complex, vector D in figure 2, forms an angle with each of the three axes. The force in each axis as well as its proportional contribution to the total force represented by the resultant can be calculated. Within the transverse or horizontal plane represented by vectors a and b (fig. 2), the anterior gluteus medius-minimus complex develops rotatory components. Vector c produces vertical stabilization and no rotation.

From the DART [1949a] model, the absolute lengths of vectors a , b , c and D were measured for the Makapan ilium (fig. 2B) and the Bushman ilium (fig. 2C). The angle of application in each plane for each hip joint was computed with trigonometric functions [WILLIAMS and LISSNER, 1962; STEINDLER, 1955]. As a check, the angles in each plane for each hip joint were measured directly on the model; these measurements agreed with those angles computed trigonometrically.

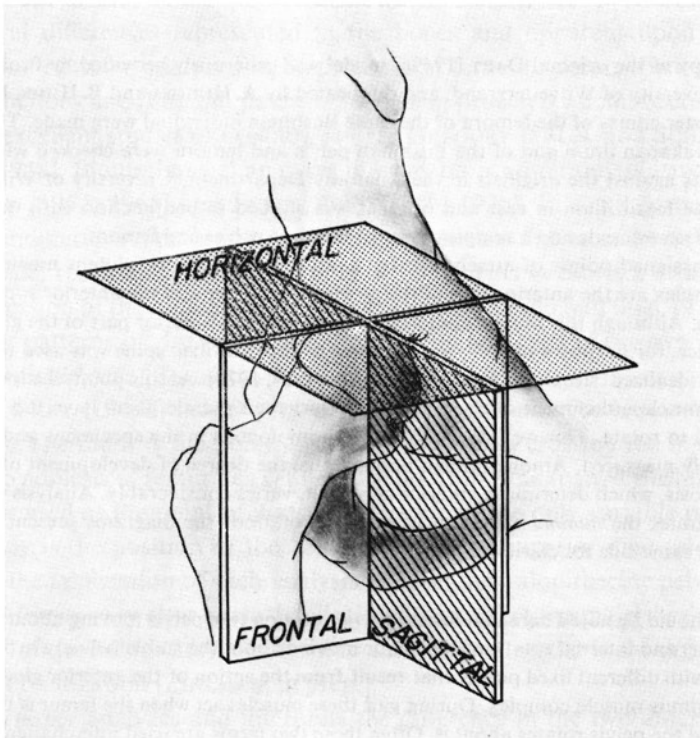


Fig. 1. The orientation planes of the hip joint.

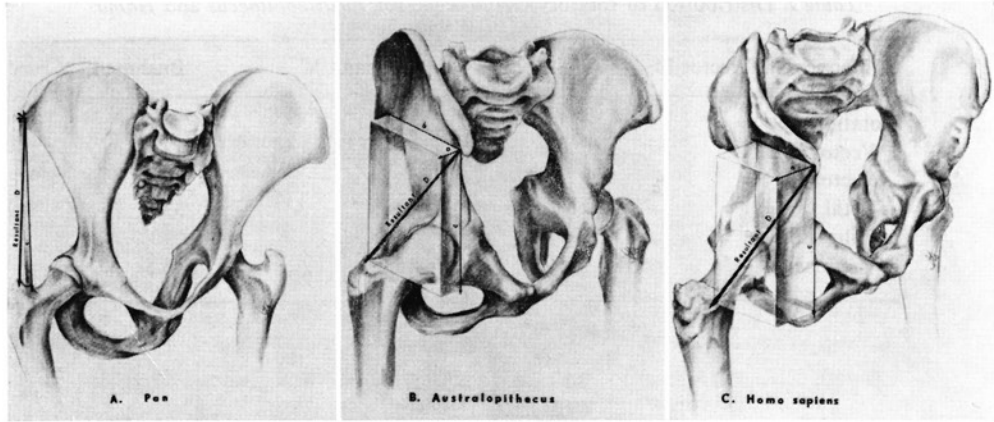


Fig. 2. Resultant D and its components a , b , and c as shown in (A) *Pan* (upright), (B) *Australopithecus* and (C) *Homo sapiens*: rotatory force components a and b and stabilization component c .

From these measurements we calculated for each hip joint: (1) components a and b (fig. 2B and 2C) and (2) the torque (rotatory force) that each component contributes. Differences in the speed and range of movement and the relationship of these factors to torque are discussed.

These measurements are only an approximation of muscle action. The action and strength of a muscle are the result not only of mechanical position, but also of the structure of the muscle (e.g. fiber length, mass, color, and tendon and fiber arrangement) which influences its power and speed of action [LOCKHART, 1960].

The emphasis on internal rotation suggests a certain bias. However, the importance of abduction – the function of the middle and posterior fibers of the gluteus medius-minimus complex – is not meant to be thereby minimized [INMAN, 1947]. On the contrary, as MERCHANT [1965] has shown, increased abductor muscle force is necessary to maintain a level pelvis when the femur is rotated. During the supporting phase of gait, it is the interaction of these two motions that is important. The abductor or stabilizing aspect has been emphasized most often; our emphasis shows the importance of internal rotation in the total complex. Since normal human locomotion would be impossible without rotational forces, an understanding of these motions is essential to the analysis of human gait [EBERHART *et al.*, 1954; ELFTMAN, 1954; SAUNDERS *et al.*, 1953]. The anterior gluteus medius-minimus muscles are the primary muscles that produce internal rotation during the support phase [BASMAJIAN, 1967; DUCHENNE, 1949]. Because there is so much disagreement over the function of tensor fasciae latae, it has not been included here as an internal rotator. MERCHANT [1965] reviews the argument over its abductor function; BASMAJIAN [1967] reviews the argument over its internal rotator function, a motion which he says tensor fasciae latae does not perform during the supporting phase of gait.

Table I. Distribution of rotatory components for *Australopithecus* and *Homo*

Components of vector D	Makapan, %	Bushman, %
Rotation:		
Vector <i>a</i>	5.8	14.6
Vector <i>b</i>	42.7	38.9
Total	48.5	53.5
Stabilization:		
Vector <i>c</i>	51.5	46.5

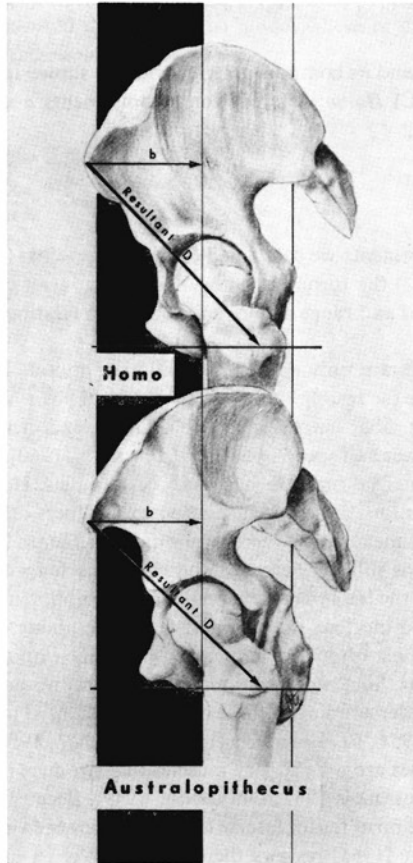


Fig. 3. Sagittal view of component *b* and resultant *D* in *Australopithecus* and *Homo*.

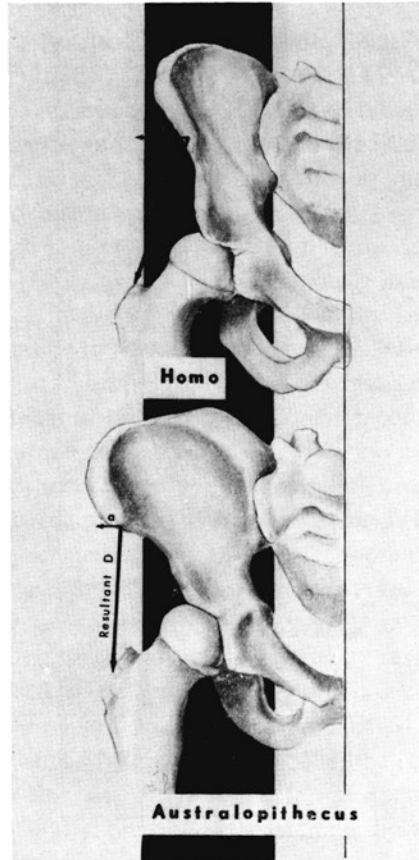


Fig. 4. Frontal view of component *a* and resultant *D* in *Australopithecus* and *Homo*.

Results and Discussion

Components of Force

The relative amount of force divided along each of the three axes of each hip joint (Makapan and Bushman) is shown in table I. The different views (fig. 1-5) clarify the three-dimensional nature of this force-vector problem.

Table I summarizes the percentage contribution of each component of the total force in the three axes. Component *a* of the total force of resultant *D* in Makapan contributes only 5.8%; component *a* in Bushman contributes

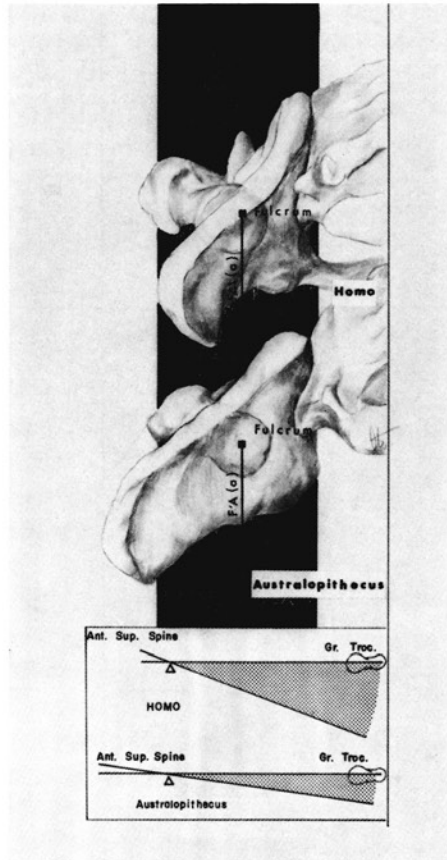


Fig. 5. Horizontal view from above to show the relative length of force arms (F'A) through which components a and b act in *Australopithecus* and *Homo*. Difference in linear displacement is a result of the length of F'A (b) in *Australopithecus* and *Homo*.

14.6%. The percentage of rotatory force of resultant D is similar in the two forms, though in Bushman it is 5% greater. Component c contributes no rotation.

If we consider the rotatory components (a and b) as 100%, then in Makapan component a is only 12% of the total rotatory force, whereas in Bushman, it is 25.5% (fig. 6). The beaking of the anterior superior iliac spine of Makapan places it lateral to the hip joint; thus component a is very small (fig. 2B and 4).

Torque and Linear Displacement

Internal rotation, a function of torque or rotational force, is the product of the components multiplied by the true force arm ($F'A$), i.e. the perpendicular distance of the action line from the center of the hip joint or the lever arm through which the components act [WELLS, 1966]. F is arbitrarily set at 100 force units since the absolute force is unknown, and the magnitude of each component is calculated as a percentage of F .

The torque for each component and the total torque in each specimen are summarized in table II and figure 6. The differences in the total amount of torque and its percentage distribution in the two are significant. The total torque of internal rotation in Makapan is almost twice that in Bushman: the difference is in the contribution of component b , which generates most of the total torque in Makapan. In Bushman, component a contributes 69 % of the torque; however, in Makapan, only 11 %.

Considered alone, the torque might be misleading because of the complementary relations between torque and arc of movement. In such movements, speed and linear displacement are interdependent: both depend upon the relative length of the resistance and force arms [WELLS, 1966]. A relatively short force arm favors speed and linear displacement but lacks force. Reciprocally, if the $F'A$ is increased, torque is increased, but speed and linear displacement are decreased; inversely, if the force arm is decreased, torque is decreased, but speed and linear displacement are increased.

In this analysis in both Makapan and Bushman the resistance arm is 6'' – the distance from the fulcrum (hip joint of the stable femur) to the opposite (moving) greater trochanter. Since in Makapan and Bushman the force arms through which components a act are similar (table II and fig. 6), the speed and linear displacement do not differ significantly. However, the difference in length of the force arms through which components b act illustrates the dif-

Table II. Amount of torque for internal rotation in *Australopithecus* and *Homo*

Component	Makapan			Bushman		
	(F) vector size	F'A,"	units of torque	(F) vector size	F'A,"	units of torque
Vector a	8.7	1.125	9.8	22.5	1.5	33.8
Vector b	64.3	1.25	80.3	60.2	0.25	15.1
Total			90.1			48.9

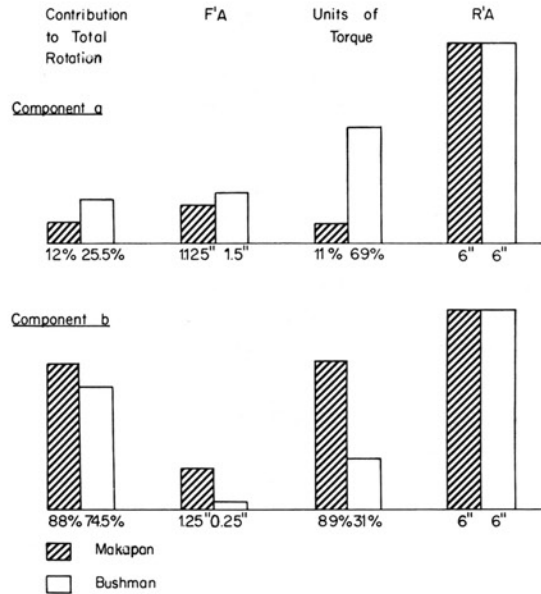


Fig. 6. Summary of relative torque relationships in *Australopithecus* and *Homo*.

ference in linear displacement. As figure 5 shows, given the same distance of linear muscle contraction and, therefore, the same arc, the linear displacement (and the speed of movement) in *Homo* is greater. Therefore, considering this interrelationship, greater torque in Makapan is achieved at the expense of speed and linear displacement.

Functional Interpretation of Differences

These differences of contraction of the muscle complex alter the torque, speed of movement, and magnification of arc. The beaking of the anterior superior iliac spine in Makapan increases the F'A through which component *b* acts to rotate (fig. 5).

If the muscle mass in the two forms is similar, ³then *Australopithecus* had developed internal rotation generating twice the torque of modern man. The difference in torque, however, indicates that *Australopithecus* exerted more

³ With closely related species like *Australopithecus* and *Homo*, similarities in internal muscle structure is assumed.

force and more muscular energy to rotate the trunk less distance at less speed. Arc of movement (not power) is important for internal rotation because it increases step length in normal walking, and only air and inertia resist internal rotation. From *Australopithecus* to *Homo*, torque decreases and the power arm shortens for component *b* as the anterior superior iliac spine becomes medially oriented and, therefore, places the fibers more in a horizontal axis. This provides more direct pull in the plane of internal rotation and increases the arc of movement by shortening the power arm.

From *Australopithecus* to *Homo*, the anterior superior iliac spine migrates medially and inferiorly and facilitates internal rotation. This change was

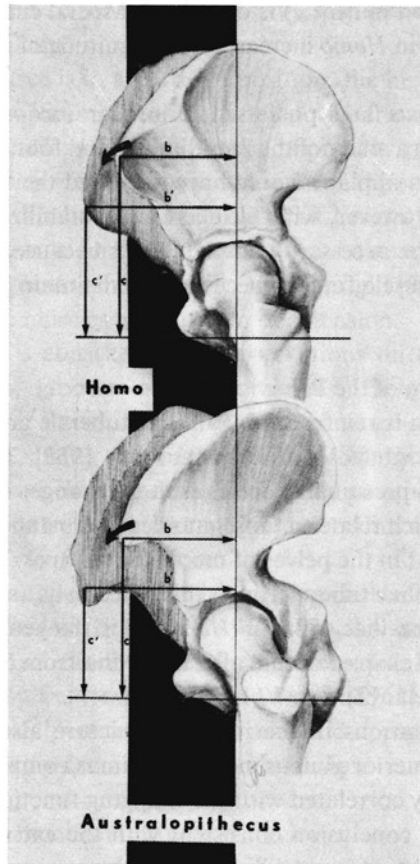


Fig. 7. Sagittal view of components *b* and *c* altered by 25° of anterior pelvic tilt (shaded) in *Australopithecus* and *Homo*.

achieved not only by altering the shape of the ilium – greater iliac crest curvature and less beaking of the anterior superior iliac spine – but also by increasing anterior pelvic tilt. Since internal rotation takes place only in the horizontal plane, these changes influence the amount of internal rotatory efficiency by bringing more muscle fibers into the horizontal plane.

Internal rotation was calculated without anterior pelvic tilt; however, if the model is tilted 25° (although the degree of lumbar lordosis varies in modern man, 25° is considered optimum) [PHELPS *et al.*, 1956], resultant *D* and component *a* remain the same magnitude as before the tilt in both individuals, but component *c* is decreased in magnitude in both. Therefore, as figure 7 shows, the component of rotation represented by vector *b* is increased and stabilization (component *c*) is decreased. Medial curving of the anterior superior iliac spines in *Homo* increases the magnitude of the rotatory component *a*.

If *Australopithecus* had possessed a lumbar lordosis, as PREUSCHOFT [1971] suggests from a study of the femur, tibia, and foot, then more fibers directed in the horizontal plane would have increased their mechanical advantage for rotation. However, with tilt decrease in stabilization which follows (vector *c*) may not be necessarily advantageous because during rotation, increased abductor muscle force is necessary to maintain a level pelvis [MERCHANT, 1965].

Internal Structure of the Pelvis

The human ilium is reinforced by an iliac tubercle and iliac pillar on the anterior part of the gluteal surface [MEDNICK, 1955]. These structures are correlated with, and presumably are a result of, changes in the internal structure of the ilium which relate to those muscles that balance and rotate during gait. They are absent in the pelvis of monkeys and apes. The Makapan ilium has no pronounced iliac tubercle, but is thickened in its anterior part, probably homologous to the iliac pillar in *Homo*. This thickening, noted by DART [1949b, 1957] for Makapan occurs also in the ilia from Sterkfontein, Swartkrans, and Kromdraai [ZIHLMAN, 1970].

Therefore, adaptations in the internal structure also indicate the reinforcement for the anterior gluteus medius-minimus complex. The incipient iliac pillar is probably correlated with the changing function of abduction and internal rotation, a conclusion consistent with the external morphology of the ilium. Internal changes in the ilium reflect the mechanical stress produced by gluteus medius and minimus, and the change in position of the anterior superior iliac spine mirrors an increase in mechanical advantage for rotation.

Origin of Internal Rotation

Australopithecus possessed an increased, but not necessarily efficient, system of stabilization and internal rotation. This ability was acquired during the transition from its quadrupedal ancestor, that is, during the change from quadrupedal to bipedal locomotion. The curved ilium of *Australopithecus* orients the muscles of internal rotation across all three planes of the hip joint whereas the ilium of quadrupedal apes in bipedal posture orients these muscles only in the frontal plane (fig. 1 and 2). During the origin and very earliest stages of bipedal locomotion, the relationship of the vertebral column and the pelvis to the base of support was probably similar to that of a bipedal chimpanzee. If another ape or an Old World monkey were used as a model, the conclusions would be the same because they all possess long and narrow ilia oriented in one plane.

When a chimpanzee is in an upright position, the hip joints are extended and the long, narrow ilium is in a line parallel with the supporting femur. In such a position, there are essentially no components of force for rotation from gluteus medius or gluteus minimus nor from any other muscle, because in a bipedal stance the ilium is not curved and lies only in the frontal axis (fig. 2A). The anterior superior iliac spine forms almost a 90° angle in the frontal and sagittal planes; theoretically, in an upright position the only possible action for these muscles is abduction or extension.

This conclusion is consistent with observations on the bipedal gaits of Japanese macaques, gibbons and chimpanzees [GRAND and SHININGER, 1968; ELFTMAN, 1944; PROST, 1967; ZIHLMAN, personal observations], whose bipedal patterns are similar: during support on one limb, the animals lean the trunk laterally over the supporting foot while pivoting forward. This decreased stability is due to the position of gluteus medius and gluteus minimus oriented predominantly for extension.

Occasionally these species, as well as other primates, do move bipedally under natural conditions [ELLEFSO, 1967; VAN LAWICK-GOODALL, 1968; KORTLANDT, 1967], but it is not normally their most frequent pattern of locomotion. As studies by ELFTMAN [1944] and PROST [1967] have shown, the bipedal pattern of apes differs from that of man and apparently is less efficient in terms of energy expended in forward progression.

Internal Rotation and Total Motor Behavior

When a chimpanzee becomes bipedal, reduction of step, balance, and timing are combined with loss of internal rotation: with each step he must displace his center of gravity with extraneous lateral movements. Man walks

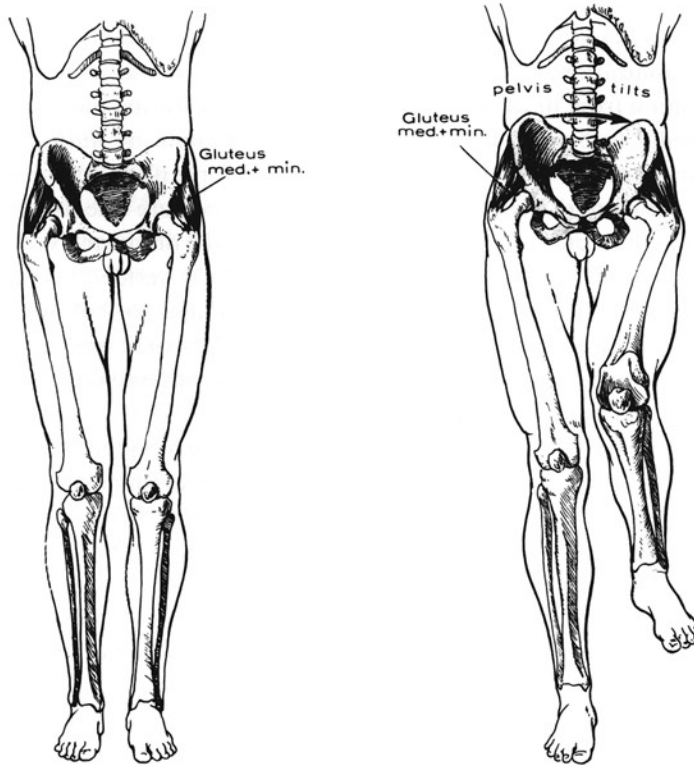


Fig. 8. Frontal view in *Homo* of pelvis and lower limbs to illustrate stabilization in walking. From ZIHLMAN [1967a]; modified after GARDNER *et al.* [1963].

around his center of gravity and progresses almost in a straight line; the chimpanzee uses more energy.

Internal rotation, averaging about 4° [LEVENS *et al.*, 1948] and lateral pelvic tilt (abduction) are illustrated in figure 8 and 9. The gluteus medius and gluteus minimus reduce both vertical and lateral displacement of the trunk [SAUNDERS *et al.*, 1953] and, therefore, reduce energy expenditure in normal walking [HALL, 1965]. This assists in the even transfer of weight onto the forward-swinging limb by maintaining the center of gravity over the supporting limb. Gluteus medius and gluteus minimus contract for two thirds of the stance phase, 40% of a one-step cycle.

If the size of the home range is large, internal rotation contributes to the efficiency of bipedalism as a major method of locomotion. The efficiency re-

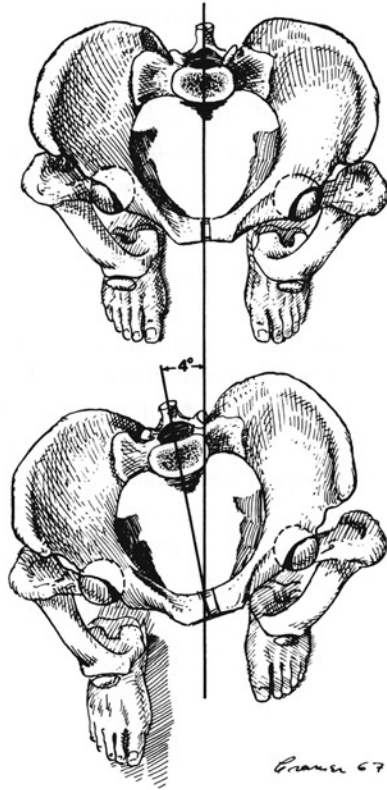


Fig. 9. Horizontal view from above to illustrate internal rotation in walking. From ZIHLMAN [1967a]; modified after DUCROQUET *et al.* [1968].

quirements of man as hunter-gatherer can best be appreciated by considering long-distance walking. In a 10-mi walk at 3 mph, for example, there are 8,800 steps with each leg and, therefore, 8,800 rotations of each hip. On one side gluteus medius and gluteus minimus contract for about 2 h. With increased speed or with adjustment to uneven terrain, pelvic rotation is significantly increased [EBERHART *et al.*, 1954; MURRAY *et al.*, 1966] so that their energy expenditure may exceed this 2-hour work estimate.

If compared to modern man, *Australopithecus* had longer or more massive upper limbs [GENET-VARCIN, 1966; ZIHLMAN, 1967b], he may have used them like the bipedal chimpanzee to assist in balance during locomotion. With acceleration and deceleration of the trunk and upper limbs, more energy would be required. Perhaps the greater relative resistance produced by heavier up-

per limbs would have required more torque of internal rotation and, therefore, would account for the differences in *Australopithecus* and *Homo*.

Movements of the trunk and upper limbs coordinated with the pelvis and lower limbs appear in a variety of other activities. Aiming, precise throwing and long-term standing (as when stalking prey) all require rotation and adequate stabilization as prerequisites.

Conclusions

The dynamics of bipedalism involve not only an upright trunk; structures emerged to increase efficiency in long-distance walking. Changes in the anterior part of the ilium and the development of an anterior pelvic tilt are the results of selection for refined hip joint motion rather than for alteration in locomotor type. Structural changes reflect functional changes, so that the evolution of the pelvis from *Australopithecus* to *Homo* can partly be explained as selection for a more efficient, though already effective, bipedal pattern. The difference in configuration had important survival value even though the difference in mechanical advantage may be slight in terms of measurements.

A species evolving a hunting-gathering way of life in an open habitat on uneven terrain presumably had a large range and traveled long distances to pursue game animals, to obtain widely dispersed food, and to explore the environment. The success of this way of life depended in part on changes in the rotatory hip mechanism that supply not only an efficient locomotor system to enable individuals to travel many miles without tiring but also to promote the coordination of the pelvis and lower limb with the trunk and upper limbs required for throwing and using tools and weapons. Selection, therefore, was not just for a particular kind of gait but for an interrelated set of behaviors involving new ways of obtaining food, using tools and weapons, and carrying objects and infants over substantial distances.

Summary

The DART model of an adolescent fossil ilium from Makapan in the adolescent pelvis of a Bushman made it possible to compare the ilia of *Australopithecus* and *Homo* and to establish mechanical advantages in the muscles of *Homo* that are responsible for internal rotation of the hip. Both the position of the anterior superior iliac spine and the amount of anterior pelvic tilt affect the mechanical advantage of the muscles of internal rotation.

From *Australopithecus* to *Homo* the increased curvature of the iliac crest and the decreased beaking of the anterior superior iliac spine brought the two anterior superior il-

iac spines into a more medial and inferior position. This change enhanced the mechanical advantage of the muscles, refined rotation of the hip joint, and so increased the efficiency of gait.

In the earliest stages, from the ancestral form to *Australopithecus*, the acquisition of internal rotation was important; but from *Australopithecus* to *Homo*, rotation was refined and improved for long-distance walking and for coordinating with the trunk and upper limbs in carrying and in using tools.

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