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Locomotor Adaptation of the Structure of Proximal Humerus in the Primates and Other Mammals.

By

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Abstract To clarify locomotor adaptation of the human shoulder joint, structural similarity of the proximal humerus was examined between several primate species and other cursorial mammals including carnivore and ungulate. Of them the *Hylobates* humerus provides a round head, a narrow intertubecular sulcus and a low greater tubercle showing a wide range of movement for arboreal brachiation. The *Muntiacus* humerus exhibits a flat head, a wide intertubercular sulcus and a high greater tubercle indicating strong extension and active support for terrestrial running. As a whole the structure concerned gradually changes from brachiating *Hylobates* to running *Muntiacus*. In this respect human humeral structure resembles that of *Hylobates* and differs not only from those of the cursorial mammals but from those of the quadrupedal primates.

It is well known that locomotor adaptation of the primate body structure varies, not only from genera to genera but between various body parts, in a mosaic fashion (HALL-CRAGGS, 1965; STERN & OXNARD, 1973; MCHENRY, 1975; FLEAGLE, 1976). It is difficult to understand overall locomotor adaptation of the primates because of these mosaic patterns. To evaluate the primate body structure a certain standard structure which is adapted to a simple locomotion is needed (GAMBARYAN, 1974; GREGORY, 1912). With this in mind, the author had studied structural similarity and dissimilarity between the primates and the cursorial mammals such as ungulates (BABA 1985). In this report the structural similarity of the proximal part of the humerus is dealt with in reference to the function of the shoulder joint.

Materials

Humeri from eight species of Primates, Carnivora and Artiodactyla were used (Table 1). These specimens came from Dokkyo University School of Medicine. They were selected to represent various locomotor patterns following NAPIER and NAPIER (1967): *Homo*, representing bipedalism; *Hylobates*, true brachiation; *Pan*, modified brachiation; *Saimiri*, branch running and walking; *Macaca*, ground running and walking; *Felis* and *Vulpes*, ground running; and *Muntiacus*, extreme ground running.

Since there were some specimens of unknown sex and the analysis was cast at a generic, rather than a specific level, all the specimens were analysed without distinction as to sex. Adult specimens were used in all cases.

Functional Morphology

In *Muntiacus* the articular head is relatively small, round sagittally and flat transversely, which indicate that the joint movement is wide sagittally and narrow transversely (Fig. 1). The greater tubercle projects high supero-anteriorly and the supraspinatus muscle attaches on the most anterior part of the tubercle (Fig. 2). This fact

Table 1. Materials

Specimens	Numbers (♂+♀)
Primates	
Homo sapiens (Human)	4
Hylobates lar (Gibbon)	2
Pan troglodytes (Chimpanzee)	2
Saimiri sciureus (Squirrel monkey)	5
Macaca mulatta (Rhesus monkey)	3
Carnivora	
Felis domestica (Cat)	3
Vulpes vulpes japonica (Fox)	4
Artiodactyla	
Muntiacus reevesi (Barking deer)	3

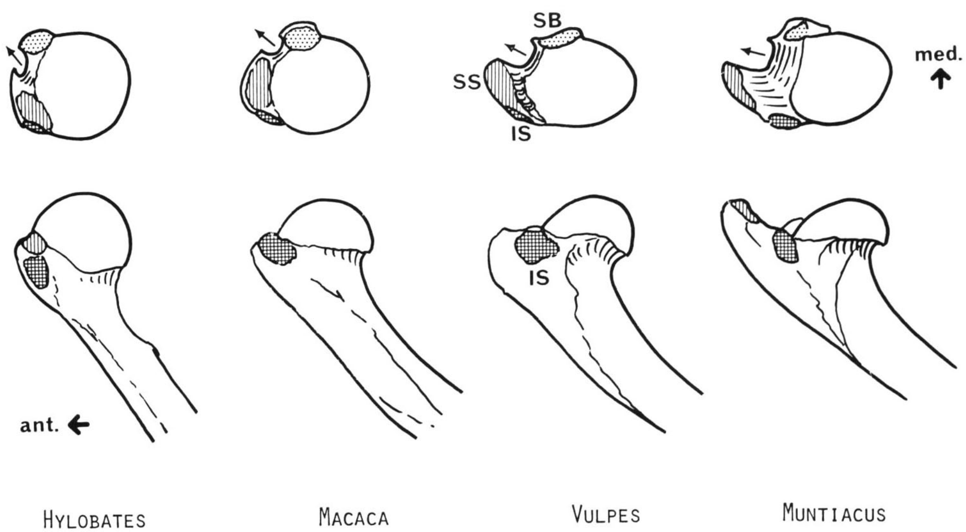

Fig. 1. Structure of proximal humerus. Superior and lateral views of left humeri. Shaded areas are attachments of the supraspinatus muscle (SS), the infraspinatus (IS) and the subscapularis (SB). Arrows indicate direction of the intertuberuclar sulcus. Note the gradual change of the general shape and functional traits from *Hylobates* to *Muntiacus*, in roundness of the head, projection of the greater tubercle, position of the muscle attachments, and width and direction of the intertubercular sulcus.

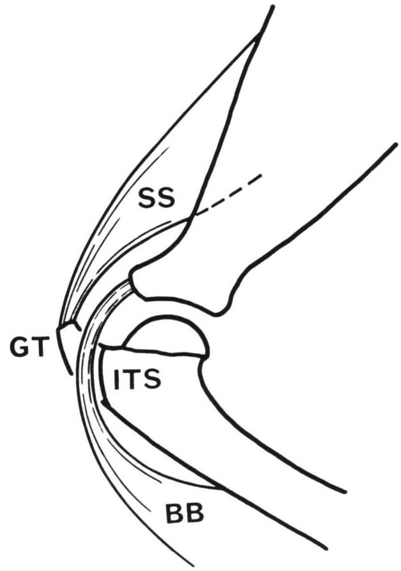

Fig. 2. Efficient extension and active support of the shoulder joint. In cursorial mammals such as *Muntiacus* the greater tubercle (GT) is so projected that the power arm of the supraspinatus (SS) is long. Therefore, the torque for extension is large. The tendon of the biceps brachii muscle (BB) fits in the intertubercular sulcus (ITS) and functions not only as an extensor but as an active supporter of the joint during movement.

means that the supraspinatus muscle which extends shoulder joint has a longer power arm than those of the other animals, i.e. the torque is larger (HILDEBRAND 1974).

The intertubercular sulcus is wide and faces anteriorly. It is situated far from the head. The biceps brachii muscle, therefore, functions not only as an extensor but as an active supporter for the shoulder joint during movement (Fig. 2). In addition, the joint provides no rotatory movement (decrease in freedom of joint). These structures are interpreted as an adaptation to strong extension in a parasagittal plane in order to attain high speed in ground running (ALEXANDER & GOLDSPINK, 1977).

In *Hylobates*, on the contrary, the head is relatively large and round indicating wide range of joint movement (Fig. 1). The greater tubercle is situated laterally to the median axis of the head and is lower than the head. The supraspinatus, infraspinatus and subscapularis muscles are set around the head making up the rotator cuff, i.e. flexible active supporter of the joint. The intertubercular sulcus is narrow facing medially. These structures are interpreted as an adaptation to produce a torque equal in every directioin during flexible movement for arboreal brachiation. Accroding to general morphological views, the features of other animals vary in a range between *Hylobates* and *Muntiacus*.

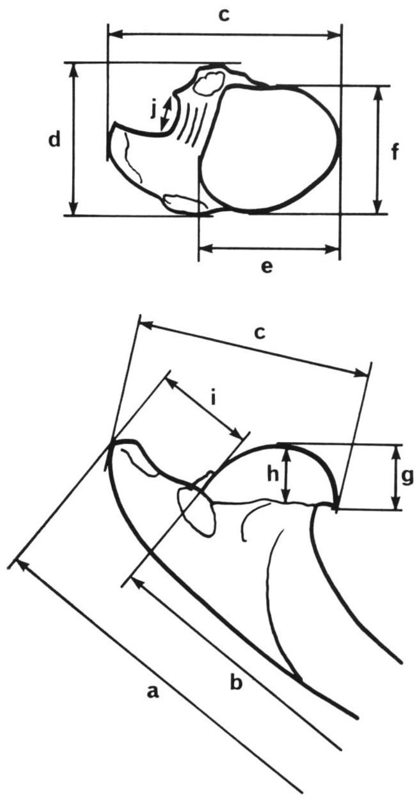

Fig. 3. Measurements of proximal part of the humerus. Superior and lateral views of *Muntiacus*. For explanation see text.

Metrics

Measurements were taken on the humerus as follows (Fig. 3): a, maximum length; b, interarticular length; c, sagittal diameter of the proximal epiphysis; d, transverse diameter of the proximal epiphysis; e, sagittal diameter or the head; f, transverse diameter of the head; g, height of sagittal curvature of the head from the line of "e"; h, height of transverse curvature of the head from the line of "f"; i, height of the greater tubercle; j, width of intertubercular sulcus. Eight indices were chosen to express functional triats of locomotor adaptation, which will be explained later.

Results

Metric data and indices are listed in Table 2. Functional meaning and variation of the indices are as follows;

Table 2. Measurements and indices (mm, %).

	Homo	*Hylobates*	*Pan*	*Saimiri*	*Macaca*	*Felis*	*Vulpes*	*Muntiacus*
a	297	222	283	67.7	140	97.9	129.5	96.7
b	297	222	283	67.7	139	96.1	126.7	88.1
c	48.4	19.7	42.2	9.2	20.2	20.7	24.5	28.3
d	42.8	17.6	39.1	9.1	18.7	16.8	20.0	21.0
e	43.0	17.8	35.7	8.3	16.6	14.7	18.6	16.3
f	40.5	17.1	36.4	7.3	16.0	13.5	16.3	17.5
g	16.3	7.3	13.4	3.6	7.6	7.2	8.4	6.5
h	15.3	9.3	15.9	2.3	5.6	5.4	4.5	3.3
i	−6.8	−3.6	−0.6	−0.9	0	1.9	2.8	8.6
j	6.2	2.7	5.6	1.5	3.0	3.5	4.6	5.3
d/c	89.9	89.6	92.6	99.0	92.3	81.2	81.9	75.7
f/e	94.2	98.5	102.1	88.3	95.8	91.8	87.7	107.9
e/c	88.9	89.6	84.6	90.2	82.2	70.9	75.9	57.5
g/e	37.2	41.6	37.5	43.1	45.7	48.7	45.1	39.9
h/f	37.8	54.0	43.6	31.5	35.8	39.8	27.6	18.6
i/b	−2.2	−1.6	−0.2	−1.4	0	2.0	2.2	9.8
j/f	15.0	15.8	15.4	20.3	18.8	26.2	27.9	30.2

a-j, items of measurements, see Fig. 3.

d/c (transverse diameter/sagittal diameter of the proximal epiphysis) expresses general shape or relative roundness of the epiphysis seen from above. It is rather high in the primates. On the contrary, it is low in the cursorial mammals.

f/e (transverse diameter/sagittal diameter of the head) expresses general shape of the head seen from above. It varies to some extent but indicates no clear tendency with locomotor modality.

e/c (sagittal diameter of the head/sagittal diameter of the proximal epiphysis) expresses relative size of the head. It is low in the cursors, which reflects development of the area for attachment of the extension muscles as the supraspinatus. In addition, this area limits the movement range in extreme extension. Therefore this index also shows the range of movement in sagittal direction.

g/e (height of sagittal curvature/sagittal diameter of the head) expresses sagittal roundness of the head. It varies in a narrow range and has no tendency with locomotor modality. This fact indicates that as far as the shape of the articular surface concerns the joint movement in a parasagittal plane does not much differ among all animals.

h/f (height of transverse curvature/trasnsverse diameter of the head) expresses transverse roundness of the head. In the primates it is almost equal to the value of g/e, that is, the head is round in every direction. The cursors have low values, which means that their shoulder movement is narrow in transverse direction. Especially in *Muntiacus* the head is not hemispheroid but rather hemicylindroid. In addition this index of the Felis lies in a range of the primates indicatinig considerable flexibility of

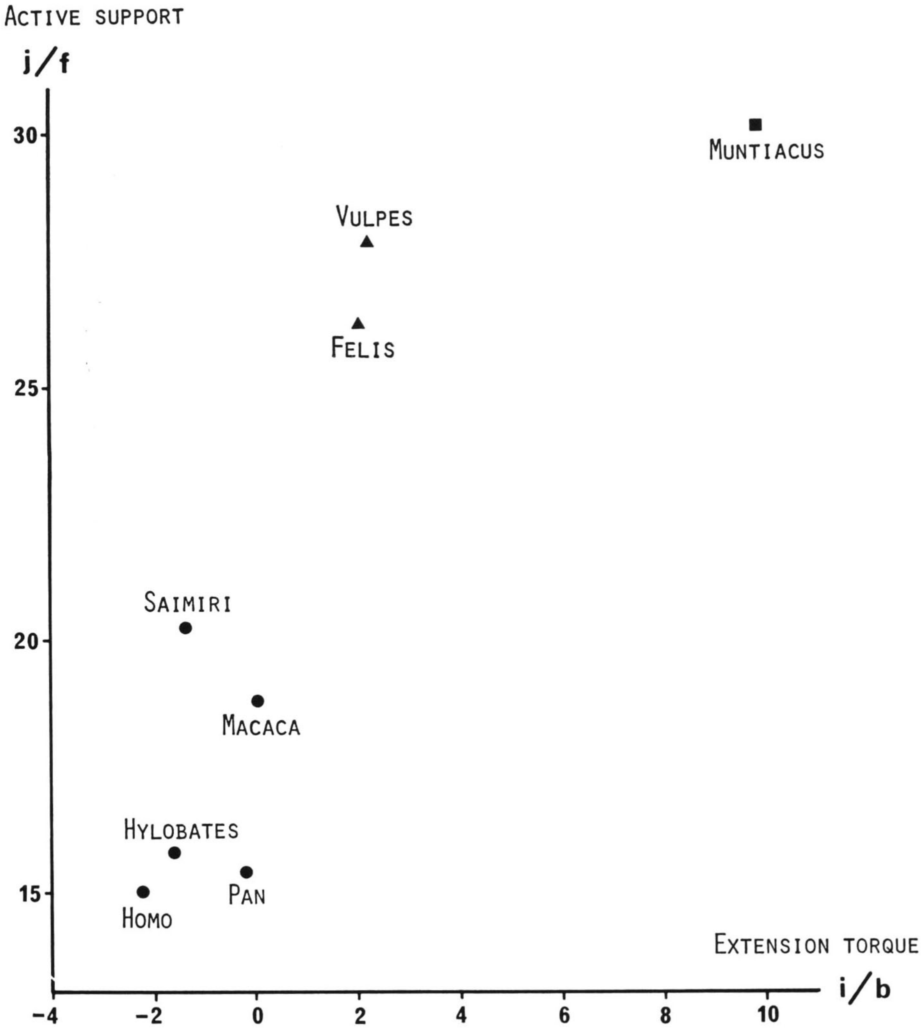

Fig. 4. Adaptation for shoulder extension.

the shoulder joint.

i/b (height of the greater tubercle/interarticular length) expresses relative projection of the greater tubercle from the head, reflecting the length of power arm (torque) in shoulder extension. When the value is minus, the greater tubercle is lower than the head. It is clear that the primates have lower values and the cursors have higher values adapting high speed running.

j/f (width of the intertuberclar sulcus/transverse diameter of the head) expresses relative width of the sulcus reflecting development of active support of shoulder joint

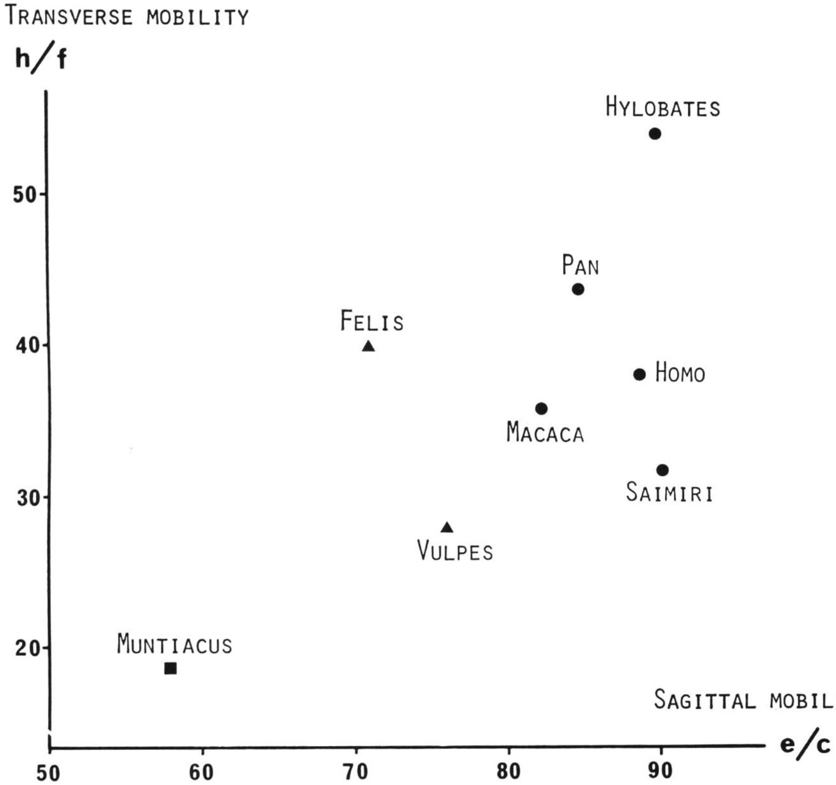

Fig. 5. Adaptation for shoulder mobility.

during movement. It is low in *Homo* and brachiating primates as *Hylobates* and *Pan*, moderate in quadrupedal primates as *Saimiri* and *Macaca*, and high in the cursors.

Discussion

In quadrupedal cursors the forelimb is kept more or less in a flexed position and not only supports the body weight but accelerates and decelerates the body movement. Therefore the shoulder joint mainly acts for extension to support the weight and to decelerate the movement. This shoulder extension is considered to characterize the terrestrial running.

It is well known that the full arm-raising movement in humans is carried out by the movement of the shoulder joint and the rotation of the scapula itself (WARWICK & WILLIAMS, 1973). It is also true in the brachiators. Moreover, the scapulae of the brachiators are longer cranio-caudally than those of the human showing efficient muscular mechanism for rotation (OXNARD, 1963). This scapular rotation is considered to characterize the brachiation (OXANRD, 1973; TUTTLE, 1974). However, for arm-raising movement the mobility of the shoulder joint, which depends chiefly on the structure of the proximal humerus, is also needed.

Therefore, to distinguish arboreal arm-raising locomotion from terrestrial cursorial locomotion, two antagonistic structural traits should be important; efficiency of joint extension and mobility of the joint. For the efficiency of joint extension the author selected two indices: j/f representing active support and i/b representing torque for extension, both of which were plotted in Figure 4. The animals vary in position along the diagonal of the graph and are divided into four clusters. Near the origin are situated the hominoids including *Homo*, *Pan* and *Hylobates*, which indicate less adaptation for the extension of the shoulder. At the extreme lies *Muntiacus*, which indicates complete adaptation for the extension. Quadrupedal primates such as *Macaca* and *Saimiri* are situated close to the hominoids. *Felis and Vulpes* are intermediate between the quadrupedal primates and extreme cursorial *Muntiacus*.

For the mobility of the joint the author selected two indices: h/f representing transverse mobility and e/c representing sagittal mobility, both of which were plotted in Figure 5. the Animals are scattered along the diagonal. *Muntiacus* lies near the origin showing poor mobility. *Hylobates* lies at the extreme showing ample mobility. Other animals are lumped together between the two. Though the difference is not clear, *Pan* and *Homo* lie close to *Hylobates*, and *Vulpes* lies close to *Muntiacus*. *Macaca*, *Saimiri* and *Felis* are in the middle.

As a whole, *Muntiacus* provides extreme daptation for ground running and does not show any adaptation for arm-raising or arm-using except walking and running on the ground. *Vulpes* and *Felis* provide considerable degree of adaptation for ground running and slight degree of adaptation for arm-raising. In *Vulpes* the structure for arm-raising might be necessary for catching their games. In *Felis* this structure should be necessary for not only catching the games but climbing trees. *Saimiri* and *Macaca* provide the reverse condition of *Vulpes* and *Felis*, that is moderate degree for ground running and considerable degree for arm-raising.

Hominoids including *Hylobates*, *Pan* and *Homo* provide high degree of adaptation for arm-raising locomotion such as arm-swinging or brachiation and do not show adaptation for ground running. This shoulder morphology suggests close hominid-pongid correspondence (CORRUCCINI & CIOCHON). It can be said that so-called knuckle-walking of *Pan* and bipedalism of *Homo* are secondary adaptation, and that they still preserve ancestral adaptation for arm-swinging or brachiation in this feature.

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