Comparative anatomy of the rotator cuff

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While the evolution of the bony skeleton of the shoulder girdle is well described, there is little information regarding the soft tissues, in particular of the rotator cuff. We dissected the shoulders of 23 different species and compared the anatomical features of the tendons of the rotator cuff. The alignment and orientation of the collagen fibres of some of the tendons were also examined histologically. The behaviour of the relevant species was studied, with particular reference to the extent and frequency of forward-reaching and overhead activity of the forelimb.

In quadrupedal species, the tendons of supraspinatus, infraspinatus and teres minor were seen to insert into the greater tuberosity of the humerus separately. They therefore did not form a true rotator cuff with blending of the tendons. This was only found in advanced primates and in one unusual species, the tree kangaroo. These findings support the suggestion that the appearance of the rotator cuff in the evolutionary process parallels anatomical adaptation to regular overhead activity and the increased use of the arm away from the sagittal plane.

In evolution, environmental changes result in altered requirements for posture and locomotion, which in turn predispose to anatomical adaptations, presumably by a process of natural selection. Studies on evolution and comparative anatomy are therefore intimately related. Appreciation of the comparative anatomy of the rotator cuff is important in terms of its evolutionary significance. It adds considerably to our understanding of the function of the cuff and the relevance of various animal models used for research on the shoulder. Codman,1 a self-professed student of contemporary anatomy, stated in his book that “possibly I was the first to draw attention to a fundamental difference between the human and the quadruped mechanism in the use of the forelimb. The quadruped uses his supraspinatus to accelerate a pendulum, while in man, in raising the arm, this muscle acts at a disadvantage against gravity and under great strain”. While movement of quadrupedal shoulders is largely restricted to the sagittal plane, those of bipedal primates can additionally rotate and move in the coronal plane, thereby allowing much more mobility. This necessitates adaptations in the architecture of the bone and soft tissue.

In their classic article in 1944, Inman, Saunders and Abbott2 made a number of observations on the comparative skeletal anatomy of primates. They noted the tendency for a relative increase in the size of the infraspinous fossa with progression from quadrupedal primates, through arboreal (tree-living) to bipedal species. They observed the progressive distal migration of the point of insertion of the deltoid, together with the increasing size of the acromion, and noted that these changes increased the functional advantage of the deltoid. They also described the development of torsion in the shaft of the humerus, which allowed an increased range of movement. Other morphological changes described during the evolution of the shoulder have included a more distal location of the greater and lesser tuberosities, an increasingly oblique orientation of the scapula with a more laterally directed glenoid, a longer clavicle and a relatively small, round glenoid fossa articulating with a considerably larger surface area on the head of the humerus.3-7 While the evolution of the bony skeleton of the shoulder girdle is well described, there is relatively little information available regarding the associated soft-tissue structures and, in particular, the rotator cuff.2,4,5,8 Evolutionary changes in the relative size and site of attachment of the muscles about the shoulder have previously been described2 and electromyography has been used to study the relative activity of these muscles in various species of primates.
muscles in different species. However, we are not aware of any studies which have examined the comparative anatomy of the rotator cuff, or have described or discussed the inter-relationship of the tendons in forming, or not forming, a true rotator cuff.

Animal models help us to understand the natural history of various diseases and conditions, and provide a means by which the effectiveness of different therapeutic interventions can be assessed. Various models have been used to study the pathology and repair of the tendon of the rotator cuff in the goat, rat, rabbit and sheep. While each of these animal species may possess bony and soft-tissue anatomy with varying similarities to the human shoulder, none is the same. These animals are all quadrupeds, using the forelimbs for weight-bearing during locomotion, with no or minimal overhead activity.

In our study, we have sought to determine the anatomy of the rotator cuff in a number of different species. We also hoped to provide evidence to support the hypothesis that the appearance of the rotator cuff in the evolutionary process parallels anatomical adaptation to regular overhead activity and increased use of the arm away from the sagittal plane.

Materials and Methods

Anatomical dissections. In addition to human specimens, we examined 22 animal species including marsupials (koala, wombat, wallaby, red kangaroo, quokka and tree kangaroo), eutheria (grey-headed flying fox or ‘fruit bat’), langomorpha (rabbit), rodents (rat and mouse), carnivores (dog and cat), ungulates (sheep, cow, pig and horse) and other primates (macaque monkey, squirrel monkey, spider monkey, baboon, orangutan and chimpanzee). Most of the animals dissected had died from natural causes in the Taronga Park Zoo, Sydney, Australia. The shoulders of rats, rabbits, sheep, dogs, macaque monkeys and baboons were obtained from experimental animals studied by other investigators at the Universities of New South Wales and Sydney, Australia. The shoulders of a tree kangaroo were obtained after a road accident, courtesy of the Australian Museum. All the specimens were dissected fresh or after thawing, except the tree kangaroo which had been preserved in solution of formaldehyde.

At least two shoulders, the right and left of the index specimen, were dissected from each species. Particular attention was directed towards the size and configuration of the muscle bellies and tendons of supraspinatus, infraspinatus and teres minor. In each dissection, it was noted whether the tendons of the spinati and teres blended to form a rotator cuff, or were inserted independently into the head of the humerus. When some blending occurred, note was made of how extensive this was. In each specimen, the capsule of the glenohumeral joint was carefully dissected from the undersurface of the tendons to ensure that capsular continuity was not mistaken for the blending of the tendons. Photographic records were made of each dissection.

Histological examination. Routine histological examination was carried out on the tendons of supraspinatus of all the primates and many of the non-primates studied. The specimens were fixed in two changes of freshly prepared 4% neutral paraformaldehyde for 24 hours and decalcified in three changes of 0.5 molar ethylenediaminetetra-acetic acid for three weeks. They were then processed through graded alcohols for 5.5 hours, cleared in two changes of chloroform overnight and embedded in paraffin. Paraffin sections, cut at 4 μm on a rotary microtome, were mounted on glass slides and dried overnight at 45°C. The sections were stained with haematoxylin and eosin and a modified version of the Picro-Sirius Red method of Junqueira, Bignolas and Brentani. In studying the sections of the tendons of supraspinatus, particular attention was directed to the orientation of the collagen fibres and the presence or otherwise of fibres running transverse to or at an angle to those mainly orientated longitudinally. The presence or absence of distinct tendon layers as described in the human supraspinatus was noted.

Behavioural observations. The behaviour of living specimens of all the species studied was also observed. Particular attention was paid to the plane and range of movement of the forelimbs of the animals. Special note was made of whether or not the animals used their forelimbs in other than the sagittal plane, whether they were capable of standing on their hind legs and raising their forelimbs above the horizontal or to an overhead position, and whether they were able to abduct their shoulders.

Results

Anatomical dissections. In most of the species studied, the tendons of supraspinatus, infraspinatus and teres minor were inserted independently into the greater tuberosities of the humerus with no intertendinous connection. Thus, these animals did not possess a true rotator cuff. This group included household and farmyard quadrupeds, such as the dog (Fig. 1a), cat, pig, sheep (Fig. 1b) and cow, the flying fox, and common laboratory animals such as the rat (Fig. 1c), mouse and rabbit. A range of Australian native marsupials, including the quadrupedal wombat, the rat-like quokka, the koala bear, the rock wallaby and the kangaroo, all similarly lacked a rotator cuff with the tendons of their spinati and teres minor attached to bone independently. One marsupial species, the tree kangaroo, had a fully-formed rotator cuff with the relevant tendons fusing well before their attachment to the greater tuberosity (Fig. 2). Of the primates, the quadrupedal macaque monkey had no evidence of the formation of a cuff. The squirrel monkey, a relatively primitive New World species, showed some minimal and fairly tenuous connection between the tendons of supraspinatus and infraspinatus. In another New World monkey, the spider monkey, a more definite, but still very limited, interconnection was found between the tendons of the spinati, but the tendon of teres minor did not appear to take part in this ‘cuff’ (Fig. 3). The baboon, which is considered
to be more advanced in the evolutionary ladder of primates, was found to have a true rotator cuff with considerable blending between the tendons of the spinati (Fig. 4). As in man, the tendon of teres minor in the baboon was much shorter than those of the spinati, but it did blend with the posterior margin of the tendon of infraspinatus, completing the rotator cuff. The three hominoids studied, namely man, chimpanzee and the orangutan (Fig. 5), all had a well-formed rotator cuff with definite connections between the tendons involved.

Histological examination. The histological appearance of the tendon of supraspinatus varied considerably between each species. The rotator cuff of the hominoid species was histologically very similar. It featured multiple layers, predominantly longitudinal, but with considerable transverse fibres, particularly in the deeper portion of the tendon, closer to the articular surface. This arrangement has been well described. In the more primitive primates, the layering of the tendon of supraspinatus was less distinct, and the percentage of transverse fibres considerably reduced. In those animals without a rotator cuff, most collagen fibres were longitudinal, with occasional transverse fibres present, but with no distinct layering. Unfortunately, no histological review of the tree kangaroo was performed.

Behavioural observations. Observations of the movements of the shoulder confirmed that the hominoid species all

Photographs showing individual tendons of supraspinatus (SSP), infraspinatus (ISP) and teres minor (TM), i.e. not forming a true rotator cuff in a) the dog, b) the sheep and c) the rat.

Photographs showing the true rotator cuff of the tree kangaroo with blending of the tendons of supraspinatus (SSP), infraspinatus (ISP) and teres minor (TM) on a) the dorsal and b) articular surface.
functioned regularly with their upper limbs overhead. The baboon was able to function with its upper limb in that position, but did so less often than the hominoids. The squirrel monkey was seen to raise its upper limb above 110° of forward flexion. The spider monkey was able to raise its upper limb beyond 150° of forward flexion but did not quite reach the vertical position. Of the animals observed, only the tree kangaroo was seen to be able to reach overhead. Among the primates, man, the chimpanzee, the orangutan and the baboon, all scratched the back of their heads with their upper limbs, while the other primates, including the squirrel monkey and the macaque, did so with their hind limbs. The tree kangaroo scratched the back of its head with its upper limbs.

Discussion
In our study, a true rotator cuff was found only in advanced primates and in one unusual species, the tree kangaroo. The presence of a true rotator cuff appeared to be associated with the ability to carry out regular overhead activity and to use the upper limb away from the sagittal plane. Orangutans and chimpanzees, considered to be advanced primates, are members of the hominoid family which also includes man. Regular overhead activity is a feature of the hominoid shoulder. We found that the rotator cuff of the orangutan and chimpanzee was almost indistinguishable from that of man. The baboon, which was less willing, although certainly able, to function overhead had a true rotator cuff which was somewhat less developed. The spider monkey and squirrel monkey both used spinal extension to assist in raising their arms above horizontal. While they appeared to be capable of flexing their glenohumeral joints, they rarely did so. The squirrel monkey had only a tenuous connection between the tendons of supraspinatus and infraspinatus. The spider monkey had a rudimentary rotator cuff, with some relatively limited distal blending of the tendons of the spinati. The lower primates which we studied, and all the non-primate species except the tree

**Fig. 3a** Photographs of the rudimentary rotator cuff of the spider monkey showing limited blending between the tendons of supraspinatus (SSP) and infraspinatus (ISP) on a) the dorsal (TM, teres minor) and b) the articular surface (the drill bit points to the fusion between SSP and ISP).

**Fig. 3b**

**Fig. 4a** Photographs of the true rotator cuff of the baboon showing blending of the tendons of supraspinatus (SSP), infraspinatus (ISP) and teres minor (TM) on a) the dorsal and b) the articular surface.
kangaroo, were neither functional overhead nor had a true rotator cuff. The tree kangaroo which, unlike its fellow marsupials, can reach overhead and to the side, did have a true rotator cuff. This suggests that two separate evolutionary pathways, one involving primates and the other marsupials, have arrived independently at the rotator cuff solution by the accumulation of parallel adaptations to overhead and side-reaching of activity of the upper limb. This example of evolutionary convergence is further evidence of the relationship of the development of the rotator cuff to overhead function.

Exactly when the modern configuration of the human shoulder with a true rotator cuff first appeared is unknown. Various theories have attempted to explain its evolution. It has been proposed that primate shoulders became differentiated from those of other mammals when they entered an arboreal environment and reduced the weight-bearing requirements of the forelimb. In keeping with the role of adaptation in evolutionary theory whereby an organism becomes better able to live in its habitat, the ability to reach overhead probably conferred an advantage in survival. Further evolution of the forelimb in early primates allowed more specialised forms of locomotion including brachiating with a pendulum-like suspensory arm-swinging locomotion and vertical climbing. According to the brachiation theory, many features of the modern human shoulder can be interpreted as adaptations to brachiation, particularly the increased glenohumeral mobility. The achievement of this increase in mobility, while preserving sufficient joint stability, required specific alterations in the anatomy of the shoulder. Observations made in our study have shown an association between increased glenohumeral movement and the presence of a true rotator cuff, suggesting a significant role for the rotator cuff in the evolution of the human shoulder.

A true rotator cuff is distinguished by the blending of individual flat tendons to form a common insertion. While most collagen fibres still run longitudinally in this setting, orthogonally aligned transverse fibres serve to hold the tendons together. Contraction of individual muscles can then exert a pull through their own and also through neighbouring tendons. This arrangement facilitates force transmission across the rotator cuff, allowing more effective and efficient function of the shoulder. The rotator cuff contributes to both the mobility and the dynamic stability of the shoulder. Non-specific recruitment of the muscles of the rotator cuff precedes activity of the deltoid and acts to stabilise the glenohumeral joint by compressing the head on the centre of the glenoid. It has been suggested that the rotator cuff acts as a depressor of the humeral head in addition to actively controlling the fulcrum of humeral rotation. Once movement of the shoulder is in progress, however, the activity of the individual muscles of the cuff becomes more movement-specific. Although the deltoid and supraspinatus muscles are considered to be the prime movers during abduction, the entire rotator cuff has been shown to act synergistically in this action. The complex biomechanics of the rotator cuff have yet to be completely elucidated. However, it seems reasonable to assume that blending of the individual tendons facilitates this synergy. A blended rotator cuff provides for more precise control of shoulder movement by forming a functional unit, thereby promoting more rhythmical glenohumeral movement and allowing subtle control of more complex patterns such as circumduction. As with evolutionary change in skeletal anatomy, the morphological changes in the soft tissues have increased the functional advantage of the shoulder. It would have been useful to have quantified the shoulder kinematics.
in each of the species using movement analysis, but financial and logistical barriers precluded this in our study.

Animal models are important in the investigation of the natural history of various conditions and for the evaluation of the effectiveness of different treatments. The rabbit, rat, dog and sheep are commonly used for assessing the pathology and repair of the rotator cuff. Our observational study has found that each of these species lacks a true rotator cuff, having individual tendons which did not blend before insertion into the humerus. This has obvious research implications. Our findings suggest that animal models utilising more advanced primates, or perhaps even the tree kangaroo, would be the most relevant to man as they possess a true rotator cuff. However, ethical concerns and costs generally preclude the use of these animals for such research.

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References