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The Advantage of Throwing the First Stone: How Understanding the Evolutionary Demands of *Homo sapiens* Is Helping Us Understand Carpal Motion

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Abstract

Unlike any other diarthrodial joint in the human body, the "wrist joint" is composed of numerous articulations between eight carpal bones, the distal radius, the distal ulna, and five metacarpal bones. The carpal bones articulate with each other as well as with the distal radius, distal ulna, and the metacarpal bases. Multiple theories explaining intercarpal motion have been proposed; however, controversy exists concerning the degree and direction of motion of the individual carpal bones within the two carpal rows during different planes of motion. Recent investigations have suggested that traditional explanations of carpal bone motion may not entirely account for carpal motion in all planes. Better understanding of the complexities of carpal motion through the use of advanced imaging techniques and simultaneous appreciation of human anatomic and functional evolution have led to the hypothesis that the "dart thrower's motion" of the wrist is uniquely human. Carpal kinematic research and current developments in both orthopaedic surgery and anthropology underscore the importance of the dart thrower's motion in human functional activities and the clinical implications of these concepts for orthopaedic surgery and rehabilitation.

Reference to the wrist as a "joint" is a misnomer; the wrist is a collection of articulations with complex interosseous kinematics, which collectively provide the hand with a wide hemisphere of circumduction. Numerous ligaments extend between and across the carpal bones to maintain anatomic and functional integrity. It might be expected, therefore, that the inherent anatomic complexity suggests a similar complexity of motion. An appreciation of these movements is a requirement to understand the natural history of carpal injury and resultant dysfunction and to develop appropriate treatment strategies for these conditions. Although several concepts have emerged within the past century to explain the intricate motions of the wrist, investigators differ on specific contributions of the individual carpal rows between individuals and in different motion planes.[1–4] Recent comparative anatomic and evolutionary findings from several centers suggest that the "dart thrower's motion" of the wrist, from radial extension to ulnar flexion, may be a unifying concept of functional wrist motion.[5–7] Speculation continues regarding the interrelationship between changes in carpal morphology, human evolution into tool-using, carnivorous primates, and the development of carpal kinematic patterns that persist today.[8,9] Improved understanding of

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the motion pattern may lead to changes in functional rehabilitation following injury and in surgical management.

Historical Explanations of Wrist Motion

Throughout history, newly developed imaging technologies were applied to the wrist for study of the carpus. In 1896, 1 year after radiography was developed by Roentgen, Bryce[1] used the modality to describe carpal motion in normal subjects. Carson[10] may have been one of the first investigators to suggest that the axes of wrist motion were oblique to radiographic planes. Fick,[11] in 1901, used early three-dimensional modeling to determine that the oblique axes of the wrist intersect in the proximal capitate. Subsequent studies during the next century involved other techniques, such as anatomic dissection,[2] cineradiography,[3] stereoscopic radiography,[4] sonic digitization, [8,9] and fluoroscopy.[12] Most recently, CT and MRI techniques were developed specifically to permit highly precise and noninvasive kinematic tracking of the carpus in live subjects.[13–17]

The "column theory" of carpal motion, first described by Navarro[18] in 1921 and redefined by Taleisnik[2] in the 1970s, divides the wrist into radial, central, and ulnar columns, based largely on phylogenetic studies of birds and other species. In this theory, the scaphoid constitutes the radial column, the capito-lunate joint is the central flexion-extension column, and the triquetral-hamate joint provides a rotational axis in the ulnar column (Figure 1). A contemporary of Navarro, Destot studied radiographs of a sculptor with a scaphoid fracture and, in 1926, introduced the concept of two independent rows of the carpus.[19] Destot[20] underscored the importance of the scapholunate ligament as a critical stabilizer of the proximal row (Figure 2). This theory was elucidated by Landsmeer,[21] who noted the independence of the proximal carpal row and coined the term "intercalated segment" to emphasize the interposition of the inherently unstable proximal row between the relatively fixed distal row and the stationary articular surfaces of the radius and ulna (Figure 3). The motion of the intercalated segment was proposed to be guided mechanically by its neighboring articulating surfaces and constrained by its complex intrinsic and extrinsic ligamentous attachments. The intercalated segment concept was explained in more detail by Linscheid et al[22] with the introduction of the terms "dorsal intercalated segment instability" and "volar intercalated segment instability" to describe pathologic postures of the lunate bone resulting from disruption of the crucial scapholunate and radioscaphocapitate or lunotriquetral interosseous and dorsal intercarpal ligaments, respectively.

Whether the scaphoid should be considered part of the proximal row or as an independent link between the proximal and distal carpal rows[23] has been the subject of considerable controversy.[11,23,24] Several investigators have challenged the widely accepted row theory of carpal motion by demonstrating different degrees and patterns of scaphoid motion depending on the direction of wrist motion studied. Craigen and Stanley[25] studied static radiographs of 52 volunteers in different positions of radial and ulnar deviation; they proposed that human wrists vary widely in their kinematic behavior, across a spectrum that combines row and column theories of motion. These authors proposed sex-specific kinematic patterns, stating that women were more likely to exhibit column-type motion. In a similar study of radioulnar deviation in 60 volunteers, Garcia-Elias et al[26] proposed that the degree of joint laxity was directly correlated with scaphoid "out of plane" motion, adding to the argument that human wrists display a spectrum of carpal motion. Wolfe et al[12] and Moojen et al[27] demonstrated considerable independence of the scaphoid from the bones of the proximal carpal row during uniplanar motion of wrist flexion-extension.

Different acquisition modalities and investigative approaches, as well as limitations associated with cadaver studies and technical aspects of imaging studies, may explain some

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of the discrepancies among wrist kinematic theories and descriptions. No unifying theory that accommodates these approaches and the apparent discrepancies exists. We propose, by examining studies in comparative anatomy as supportive evidence in wrist evolution, a potential unifying theory based on functional activity and the uniqueness of the human wrist.

Clues From Physical Anthropology and Evolutionary Theories

Although historically it might have been convenient and practical to think of wrist motion in the traditional orthogonal PA and lateral radiographic planes, it became apparent that few, if any, functional activities are performed using pure planar wrist motions. Indeed, several authors had noted that most functional and occupational tasks require simultaneous flexion-extension and radioulnar motions of the wrist.[28,29] Fisk[29] noted that many diverse activities, such as "casting a fly, throwing a dart, or conducting an orchestra," could be performed only with motion of the wrist from a position of radial extension to ulnar flexion. Palmer et al[30] coined the term "dart thrower's motion" to describe the arc of motion from radial deviation and wrist extension to ulnar deviation and wrist flexion and detailed the degree of combined motion in a study of several functional and occupational tasks. It became apparent that uniplanar analysis of wrist motion could not be used to accurately describe the complex movement patterns of the carpal bones in functional activities. Indeed, it appears likely that most, if not all, functional activities occur in one or several oblique or "coupled" planes of motion, defined as some proportion of combined flexion-extension and radioulnar deviation.[31]

Structurally, the configuration of the scaphocapitate articulation and the distal ridge of the scaphoid articular surface maintains congruity during oblique planar motion.[32–35] The scaphotrapezial-trapezoidal (STT) ligament, which inserts on the anterolateral aspect of the scaphoid tuberosity, and the scaphocapitate ligament, which inserts on its medial aspect, can be considered collateral ligaments of the STT joint. Recent studies demonstrate that these ligaments have very few proprioceptive functions—implying that their principal function is mechanical—in contrast to the dorsal intercarpal ligaments and triquetral-hamate-capitate ligaments, which are thought to constrain the end points of the dart thrower's motion (ie, "stops") via their substantial proprioceptive properties.[36] Functionally, we recognize that the dart thrower's plane of motion is accomplished by firing of the dual extensor carpi radialis muscles and the opposing flexor carpi ulnaris; in fact, the insertions of the flexor carpi radialis and extensor carpi ulnaris are uniquely positioned to oppose and modulate midcarpal motion in this oblique plane.[37]

Several biomechanical studies offer supporting evidence of this perspective on carpal kinematics. Investigations of uniplanar and multiplanar wrist motion using an electromagnetic motion-measuring system demonstrated that whereas the capitate moves with the third metacarpal because of its stout ligamentous attachments, the proximal carpal row tends to move predominantly in flexion and extension.[5] Shortly after these studies were undertaken, Ishikawa et al[38] noted that the radiolunate contribution to coupled wrist motion in the dart thrower's plane is less than that of radiolunate motion during uniplanar flexion-extension of the wrist. Li et al[31] demonstrated that the area of maximum wrist circumduction produces an ovoid pattern with its longest axis in the dart thrower's plane, again suggesting a potential obliquity of functional wrist motion.

Several kinematic studies examining the dart thrower's arc of motion have been performed. Werner et al[5] recorded scaphoid and lunate motion in vitro in nine different dartthrower's planes of motion in seven cadavers. Their work confirmed previous investigations demonstrating that the scaphoid and lunate moved primarily in the plane of flexion-extension when the wrist was moving in either pure flexion-extension or radioulnar

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deviation. However, the authors were able to identify a unique dart thrower's plane, composed of nearly equal contributions of flexion-extension and radioulnar deviation, in which minimal motion of the scaphoid and lunate was observed. [39]

Coincident advancement of imaging technology with a better understanding of coupled wrist motion has allowed accurate in vivo measurements of carpal motion over the past decade. Crisco and colleagues[12–14,40] developed a "markerless bone registration" technique to enable precise kinematic calculations using sequential computed tomographic volume images of bony surfaces. This technique permits highly accurate three-dimensional motion studies of live subjects. The method takes advantage of the unique shapes of the carpal bones to track features of bone surfaces at each position and subsequently describe detailed motion.[13] Accuracy of this technique has been found to be within 0.5° of rotation and 0.5 mm of translation along a helical axis of motion for the capitate and scaphoid motion and 1.5° and 0.5 mm for the lunate.[14] Most recently, volume-based bone registration using MRI has been introduced.[6]

Use of these advanced modalities has enabled investigators to add new perspectives to more than a century of carpal motion analysis.[13,15,24,27,41] Technological limitations confined the scope of previous investigations, either because studies were limited to uniplanar motions of flexion-extension or radioulnar deviation (ie, radiography) or because available three-dimensional motion techniques could be applied only to cadaver wrists because of the need for implanted marker systems. The emergence of in vivo three-dimensional motion analysis techniques enabled precise analysis of these complex motions of the individual carpal bones in live subjects for the first time. Limitations of the current three-dimensional motion analysis techniques include their "quasistatic" analysis of multiple fixed positions and the inability to study dynamic functional tasks.

In a recent study, markerless bone registration with CT was used to study 28 healthy subjects in a total of 504 wrist positions.[42] Scaphoid and lunate motion was noted to be significantly less along the path of the dart thrower's motion than in any other direction of wrist motion ($P < 0.01$ for both carpal bones) (Figure 4). Minimal elongation of the scapholunate interosseous ligament also has been observed during wrist motion in the dart thrower's arc.[43] These and other investigations have produced more consistent results than have those performed with the wrist moving in traditional planes of motion; for the first time, there appears to be consensus among investigators in different parts of the world that there is minimal scaphoid and lunate motion throughout the dart thrower's arc.[38,39,42,44,45] These collaborative efforts and new analytical techniques have built on the kinematic foundations of the past 100 years and confirm earlier observations of a functional oblique motion plane. This recent kinematic theory complements current concepts in functional adaptation as they relate to evolution of the wrist.[37]

The Dart Thrower's Motion: Tools and Evolutionary Adaptation

There is evidence to support the concept that certain adaptations of the hand and wrist were critical to enable use and manufacturing of tools, which, like upright stance and increased cranial capacity, defined the evolutionary line from which *Homo sapiens* arose.[46,47] It is entirely plausible that morphologic adaptations in the carpal bones enabled the development of a dart thrower's arc of wrist motion. This in turn lent an evolutionary advantage to early hominids. Chance of survival for the early primate might have been improved by having mechanisms that increased the ability to hunt and gather food as well as defend oneself; such skills included rock throwing and club wielding, activities that require the full ulnar deviation and wrist flexion follow-through of the dart thrower's motion.[48] It is by studying the evolution of the hand and wrist along with the development of tools that we come to

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understand the intriguing influence that survival had on current anatomy and function of the wrist.

Observed contrasts in nonhuman primate osteology can be explained by differences in functional requirements. For example, like spider monkeys, Asian apes (ie, gibbons and orangutans) perform many activities while suspended from tree limbs, which is consistent with the ball-and-socket configuration of the capitate and the hamate with the proximal row. It is thought that this ball-socket configuration allows suspensory locomotion and feeding on tree fruit, and, in turn, rotation around a fixed hold on the limb.[49] In contrast, the terrestrial African apes (the closest living relative of humans) ambulate by knuckle walking on the dorsum of their middle phalanges. Wrist mobility is dramatically restricted in this lineage by morphologic adaptations within the proximal carpal row that likely allow better load transmission and increased wrist stability during knuckle walking.[50] The same wrist structure, however, is not permissive of a wide range of radioulnar deviation, thus limiting coupled wrist motion.

Similarly, distinct differences have been noted between human hands and those of the most closely related nonhuman primates. Human hand differences include shorter fingers relative to thumb length, broader distal phalangeal tufts (for grasp), a hypothenar pad that absorbs impact during forceful grip,[46,47] and carpometacarpal and metacarpophalangeal joint alterations that allow rotation of the second, fourth, and fifth rays. Such adaptations enabled development of the three-jaw chuck, or baseball, grip, which employs the pads of the thumb and the index and long fingers[49,50] (Figure 5). This has been referred to as a “forceful precision grip,” which allows firm grasp of an object while allowing modification of the tool without injuring the fingers.[50] The precision grip capability of humans differs from that of other primates by allowing not only grip but also a firm precision pinch and a handling ability that facilitates effective tool use without squeezing the object into the palm.[43] Shortening of the fourth and fifth metacarpals and changes of the hamatometacarpal articulation enabled another grip, the “modified power grip,” by which an object is held obliquely across the palm in an axis collinear with the forearm[42,47] (Figure 6). The “squeeze” modification of the power grip was enabled by morphologic adaptations of the hand over the past 2.5 million years, including radial rotation of the fourth-fifth carpometacarpal articulations and a stronger, shorter, and more mobile fifth metacarpal. The modified grip allowed tools and clubs to be held in line with the forearm axis, effectively lengthening the swing length and power of impact when accelerated through the dart thrower’s plane of motion.

Employing the precision three-jaw chuck grip (eg, holding a stone) or power squeeze grip (eg, grasping hammers, spears, or clubs) effectively necessitates use of a power swing, which is generated by using the dart thrower’s motion of the wrist, in concert with coordinated motions of the shoulder, elbow, and forearm.[51] The power swing enables a biomechanical advantage of the longer lever and recruits the powerful forearm musculature to increase the impact of the club or tool. An additional adaptation of humans in this area is the relative increase in the ratio of forearm extensor muscle mass to flexor muscle mass compared with the chimpanzee;[11] greater extensor strength and extensor-flexor balance in humans allows positioning during the cocking phase and therefore more effective use of the power swing.

The emergence of coupled wrist motion combined with an upright stance, which increased pelvic rotation and full shoulder circumduction, enabled throwing and hammering by early hominids. Similarly, coupled wrist motion provided for manual tool use in these species and translates directly to activities performed in modern daily life. Movements ranging from

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using a hammer or club to pouring from a pitcher or throwing a ball employ coupled arcs of wrist radial-extension and wrist ulnar deviation-flexion.

Clinical Implications

The implications of minimal radio-scaphoid and radiolunate motion throughout the dart thrower's arc of wrist motion are intriguing. Traditionally, lengthy immobilization has been recommended for injuries or surgical reconstruction involving the radiocarpal joint (ie, scapholunate ligament repair, treatment of scaphoid fractures and nonunions, distal radius articular fracture repair). It is reasonable that early motion along the dart thrower's plane of motion can be allowed following certain types of radiocarpal and proximal row surgery without concern for disruption or attenuation of the surgical reconstruction, because the proximal row remains relatively still during midcarpal motion.[37–39,42]

As a result of better understanding of carpal motion, the position for partial wrist arthrodesis procedures might be redefined. For example, limited fusions that preserve the midcarpal joint (eg, radioscapholunate fusion) have been demonstrated clinically to permit motion almost exclusively in an oblique plane of radial extension to ulnar flexion.[50] Although early clinical studies demonstrated some functional limitations with an exclusive midcarpal motion plane, a recent technical modification that removes the distal scaphoid has led to improved functional outcomes by permitting increased radio-ulnar deviation.[52] Cadaver-based evidence suggests that resection of the triquetrum results in an additional increase in motion following radio-scapholunate arthrodesis without compromising carpal stability.[7] Similarly, although scapholunocapitate arthrodesis was demonstrated in the laboratory to result in improved radiocarpal load transmission compared with STT fusion,[12] the procedure likely sacrifices too much midcarpal motion to be widely used clinically.

Novel kinematic studies using gait laboratory motion-tracking technology to quantitatively measure hand, wrist, forearm, and upper extremity motion in live subjects during a variety of occupational, recreational, and daily living activities are under way to identify the degree and duration of coupled wrist motion necessary for functional tasks (Figure 7). This information, along with future studies of surgical interventions, such as partial and complete wrist arthrodesis, proximal row carpectomy, scapholunate ligament reconstruction, and wrist arthroplasty, will enable surgeons and patients to make more informed choices when deciding on elective surgery.

Summary

Our understanding of carpal motion has changed considerably during the past century. We have moved from "three column" and "two row" concepts of wrist motion, developed using the relatively limited investigational capabilities of their historical times and defined by the constraints of orthogonal planes of motion, toward suggesting a potential unifying concept of carpal motion that recognizes what researchers have been observing with modern techniques: that most upper extremity activities make use of "coupled" wrist motions. The combination of radial deviation and extension (radial extension) with ulnar deviation and flexion (ulnar flexion)— the dart thrower's motion— and has been described recently as the predominant functional arc for many occupational and recreational activities. Innovations in imaging have revealed that the scaphoid and lunate motion remain minimal throughout this arc of motion. Further studies of carpal motion in the face of injury and disease are warranted, because this new information has the potential to change the way we conceptualize and treat carpal pathology.

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Figure 1.
Illustration of the "column theory" of wrist kinematics, initially described by Navarro.[18] The carpal bones are clustered in radial (red), central (blue), and ulnar (orange) columns.

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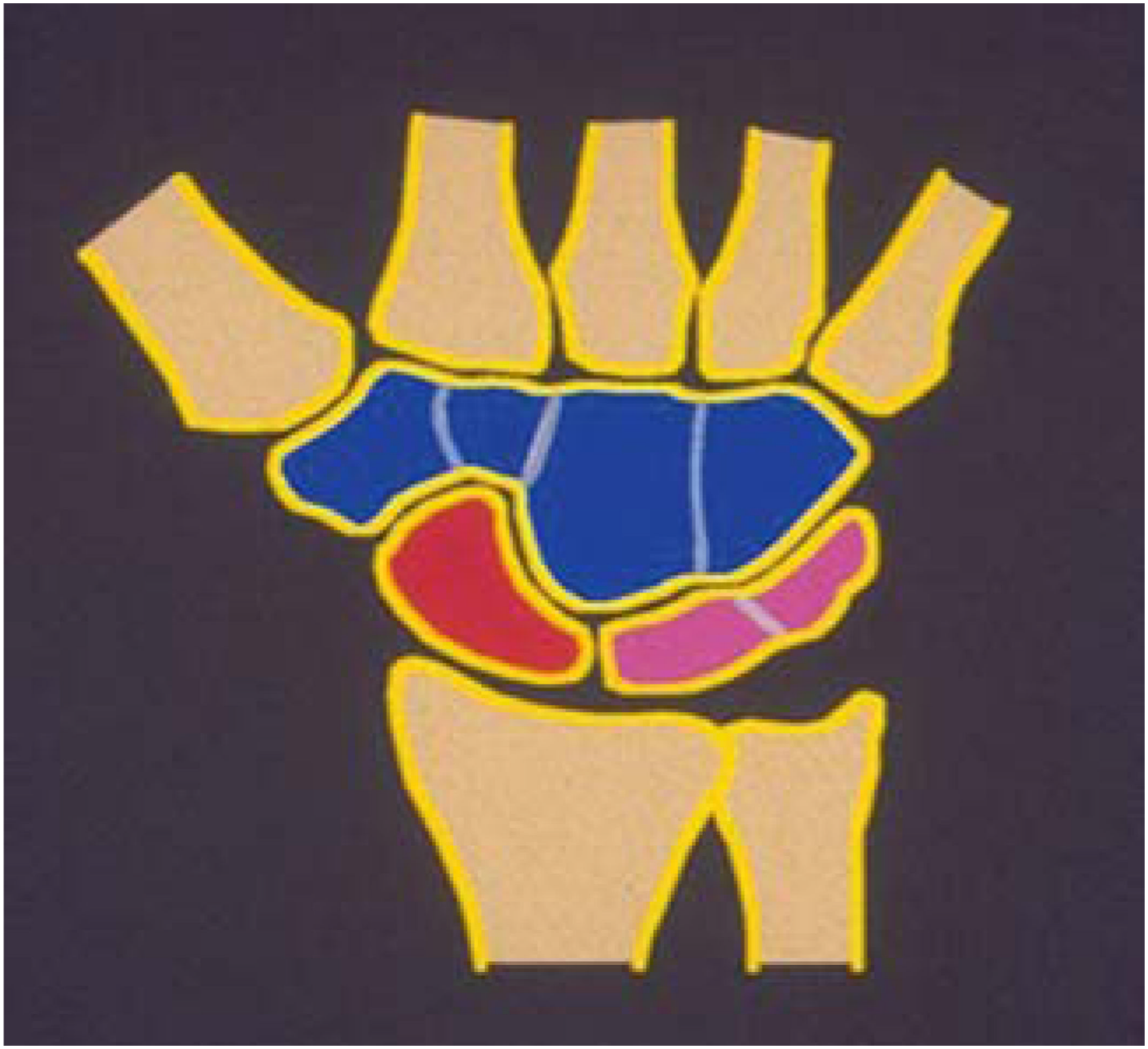

Figure 2.
Illustration of the carpus as described by Destot.[20] Two distinct rows of carpal bones are evident: the proximal carpal row (fuschia), comprising the triquetrum and the lunate, and the distal carpal row (blue), comprising the trapezium, trapezoid, capitate, and hamate. The scaphoid (red) was initially described as a critical and independent link between the proximal and distal rows.

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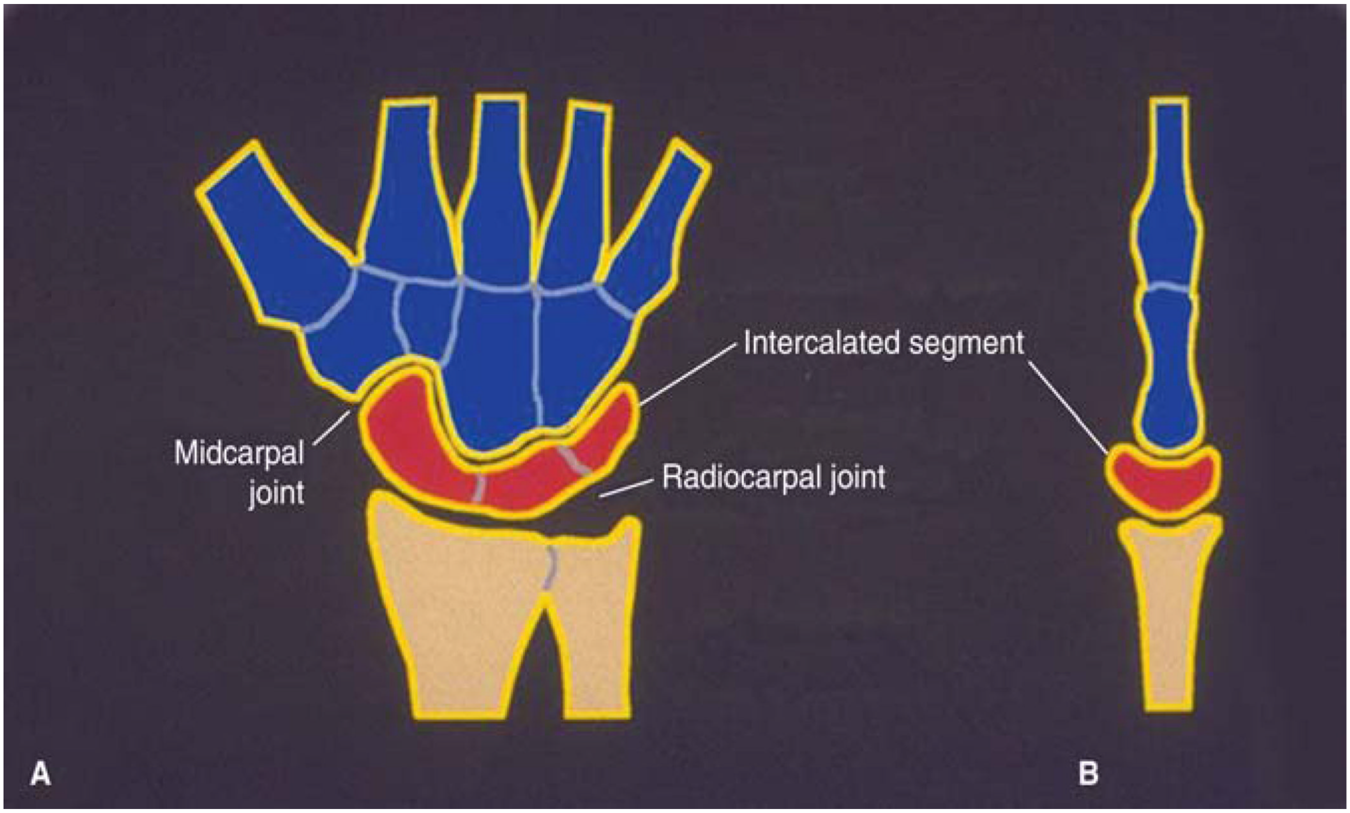

Figure 3.
AP (**A**) and lateral (**B**) illustration of the "intercalated segment," the term coined by Landsmeer[21] to describe the proximal row with respect to the forearm and the distal row. The intercalated segment (red) describes the proximal carpal bones (ie, scaphoid, lunate, and triquetrum) that have no tendon insertions and are balanced between the articular surface of the distal forearm (beige) and the bones of the distal row (blue). Their motion is guided by mechanical signals from the distal row and is constrained by a complex system of intrinsic and extrinsic ligaments.

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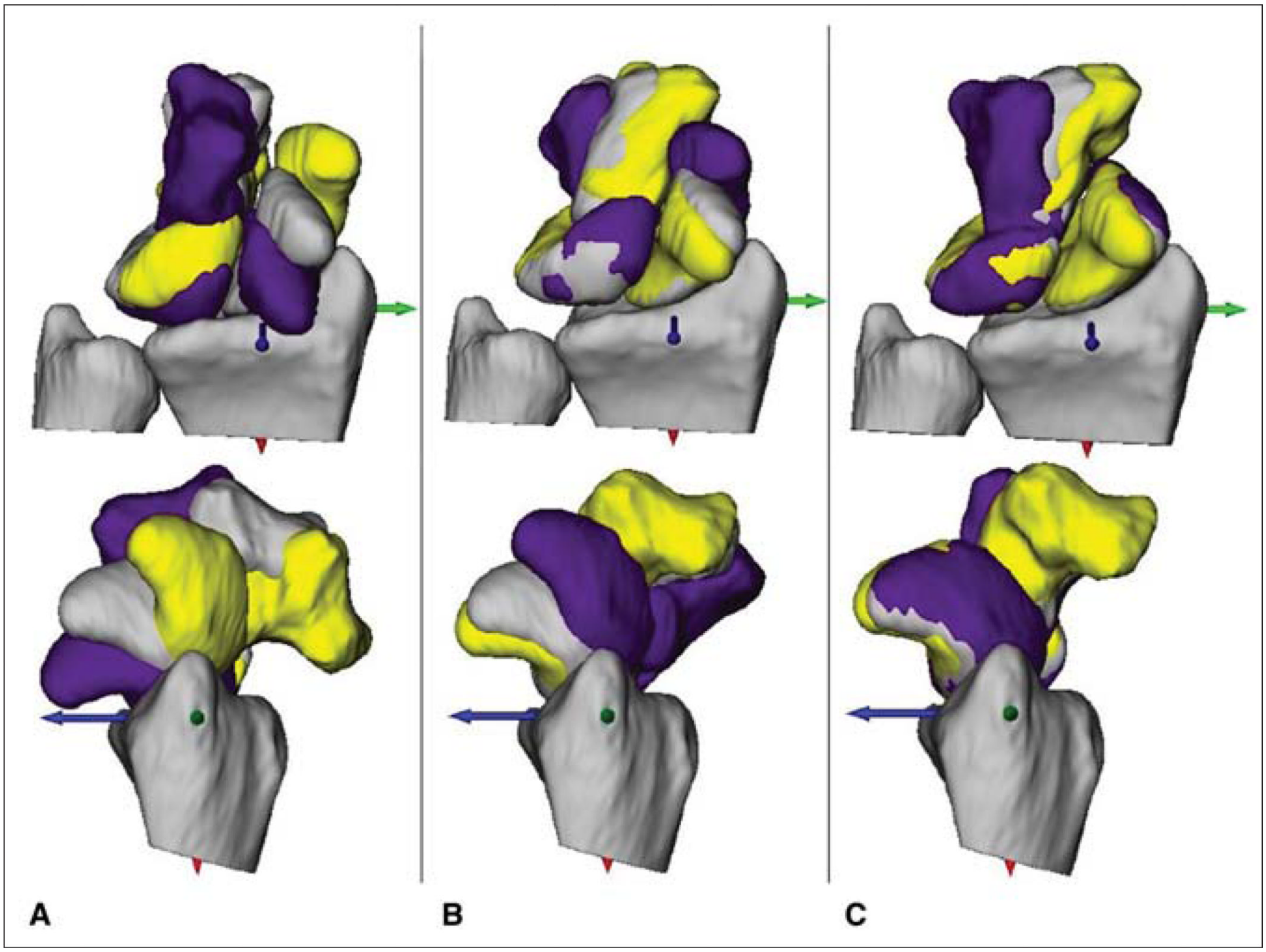

Figure 4.
Three-dimensional images demonstrating the unique pattern of proximal row kinematics during the dart thrower's motion, as revealed by in vivo studies of carpal kinematics. The top row is a volar view and the bottom row a radial view of the capitate, scaphoid, and lunate in the neutral position (gray bones) during wrist flexion (purple)-extension (yellow) (**A**), wrist ulnar deviation (purple)-radial deviation (yellow) (**B**), and dart thrower's motion of wrist radial extension (yellow)-ulnar flexion (purple) (**C**). The total range of wrist motion, as illustrated by the positions of the capitate, is approximately the same for each direction of wrist motion in each panel. Despite the nearly identical amount of wrist motion, the motion of the proximal row is substantially and significantly reduced as the wrist moves along the dart thrower's path, as seen in panel C. This difference is most readily appreciated by focusing on the distance the scaphoid tubercle has traveled in each panel of the figure. The motion of the capitate, scaphoid, and lunate are visualized relative to the radius that was mathematically fixed by its coordinate system (red, blue, and green vectors).

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Figure 5.
Photograph of the three-jaw grip, which was refined during primate evolution by morphologic adaptations in carpometacarpal mobility, finger-to-thumb-length ratio, and hypothenar pad development, allowing for precision handling of tools and weapons. (Reproduced with permission from Wolfe SW, Crisco JJ, Orr CM, Marzke MW: The dart-throwing motion of the wrist: Is it unique to humans? *J Hand Surg Am* 2006;31 : 1429–1437.)

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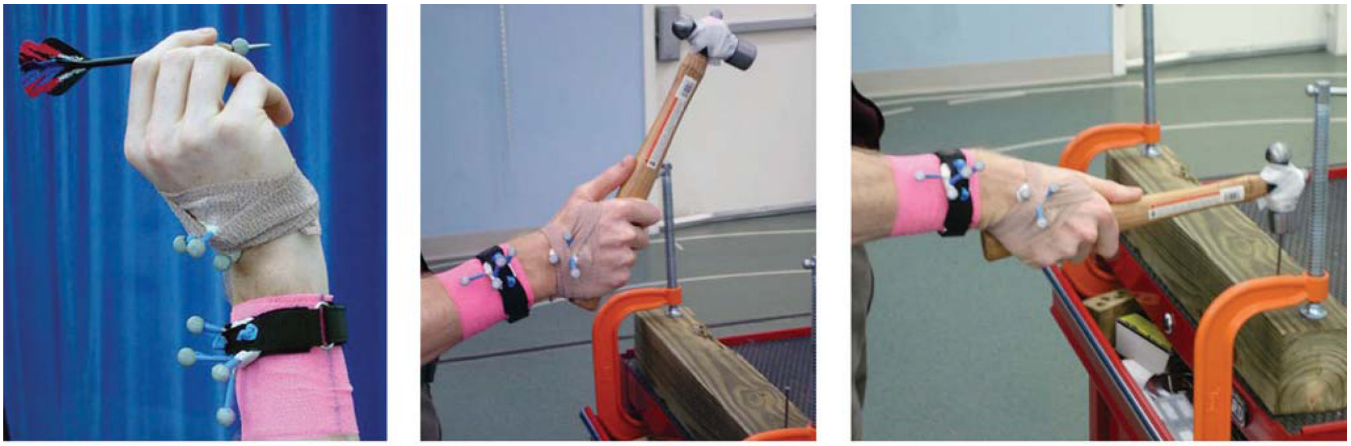
Figure 6.
Photograph demonstrating the relatively recent “squeeze” modification of the power grip. (Reproduced with permission from Wolfe SW, Crisco JJ, Orr CM, Marzke MW: The dart-throwing motion of the wrist: Is it unique to humans? *J Hand Surg Am* 2006;31 : 1429–1437.)



A B C

Figure 7.

Photographs of kinematic studies of the dart thrower's plane of motion using clusters of reflective skin markers and motion-analysis technology. Dart throwing (**A**) and hammering (**B** and **C**) involve a similar coupling of wrist flexion-extension and ulnar-radial deviation. This is exemplified by the wrist extension posture of the cocking phase of hammering and the follow-through of ulnar flexion.

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