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DID THE BIOMECHANICS OF MAKING AND USING STONE TOOLS INFLUENCE THE ORIGIN OF HUMAN HAND AND WRIST ANATOMY?

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INTRODUCTION

Modern humans' hand and wrist anatomy is highly derived with respect to extant great apes and our fossil human ancestors such that we now possess an extremely dexterous hand capable of enhanced object manipulation and the application of forceful precision grips (*1*). The manufacture and use of early Paleolithic stone tools is commonly cited as a principal selective pressure that acted on the evolution of aspects of our hand and wrist anatomy (*2, 3*) due to the significant advantages stone tool behaviors offered early hominins (human ancestors and their extinct relatives) including increased access to high-quality foods and defensive implements (*4, 5*). These advantages, in turn, are hypothesized to have accelerated a series of further adaptations that culminated in the emergence of our own genus, *Homo* (*6*). The nature of the anatomy and behaviors in question has historically made it difficult to evaluate the functional significance of many of our derived hand and wrist features for stone tool behaviors. However, recent advances in technology are enabling researchers to test many of the hypotheses linking our derived upper limb condition to the manufacture and use of stone tools. Here we present our results from a series of biomechanical experiments testing the primary hypothesis that aspects of the modern human upper limb condition significantly contribute to the performance of Paleolithic stone tool behaviors, followed by a discussion of the selective implications of these results.

METHODS

Two series of tool behavior experiments were conducted: the first analyzed upper limb kinematics, and the second examined the distribution of manual pressure. Upper limb kinematics were captured from experienced stone tool makers (i.e., knappers, n = 8) during the production of Paleolithic stone tools using a Vicon Nexus motion capture system (200 Hz). Data were captured under two conditions: while subjects were able to use their full muscular-induced wrist extension ranges and while subjects wore a brace which limited extension to ~35°, the extension limit typical of extant chimpanzees and the hypothetical limit of some of our hominin ancestors (*7*). Each subject made eight bifacial tools known as Oldowan choppers (figure 1, C&D). During tool manufacture, a small rounded stone (i.e., hammerstone) held in the dominant hand is forcefully struck against a stone nodule in order to remove sharp-edged flakes from the nodule. 435 swings were analyzed (237 unbraced, 198 braced). Reflective markers were placed as following: 1) acromion process 2) olecranon process, 3 & 4) radial and ulnar styloid processes (RSP and USP, respectively), 5-7) metacarpal heads I, II, and V. Subjects' muscular-induced wrist excursion ranges and knapping kinematics were recorded in the unbraced and braced conditions. Each trial consisted of a single knapping swing, from initiation (the frame prior to the start of the ascent of the RSP) to termination (the frame immediately following the lowest vertical position of the RSP post strike) and all analyses were conducted on the down-swing portion of the swing. Prior to each swing, subjects drew an "X" on the nodule at their intended point of percussion. Accuracy was measured as the distance from the intended to the actual point of percussion (which remains visible on the nodule).

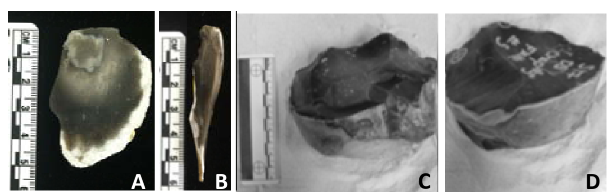

Figure 1: (A&B) front and profile of a standard flake. (C&D) front and back of a standard Oldowan chopper.

Joint angles and upper limb segment excursions were calculated relative to subjects' neutral position. Joint linear and angular velocity and acceleration and segment excursions were calculated through each swing using R statistical programming language. Intra-subject averages are reported for all variables. Kinematic data were analyzed using a Kruskal-Wallis test. All *P*-values were determined using a post-hoc pairwise Mann-Whitney U test and treated with a Bonferroni correction to determine significance.

Manual force (N, captured normal to the palmar sensor element) and pressure (kPa) were captured from amateur (n = 9) and experienced (n = 17) knappers during tool manufacture and use (200Hz). Amateur and experienced knappers made flakes and choppers, respectively (figure 1, A&B, C&D) using flint and performed the following tool use behaviors: cracking open four types of nuts with a hammerstone (n = 562), slicing animal tissue with a flake and an Acheulean handaxe (n = 148, 146, respectively), and accessing the marrow cavity of a long bone with a hammerstone and a chopper (n = 98, 96, respectively). Three sensor strips (100 x 10 mm^2) were attached to the palmar surfaces of subjects' 1^{st} – 3^{rd} digits. Each trial consisted of a single swing. Peak force and pressure were extracted from each trial, as well as strike force and pressure. Force and pressure data were standardized relative to the sum of peak force or peak pressure, respectively. Wilcoxon Signed Rank tests, run in JMP 10.0.0, were used to test for differences among the digits.

RESULTS AND DISCUSSION

During unbraced tool manufacture subjects used a modified proximal-to-distal joint sequence (PDJS). Joints transitioned to their primary down-swing motion direction in a complete PDJS: (across all subjects) the shoulder transitioned from flexion to extension ≥ 0.022 seconds before the transition to down-swing, followed by the elbow's transition from flexion to extension 0.15-0.08 seconds prior to strike, ending with the wrist's transition from extension to flexion 0.08-0.05 prior to strike. Peak joint velocity also occurred in a PDJS, with successive joints reaching a significantly greater velocity than the previous joint. The onset of peak velocity occurred in a partial PDJS: velocity peaked at the wrist significantly prior to the velocity peak at the elbow. However, a distinct secondary peak in velocity was evident at the elbow prior to peak wrist velocity. This, in combination with early shoulder motion, appears to be sufficient to produce the sequence of greater joint velocities that is one of the benefits of the PDJS. When wrist extension was limited to ~35° (the hypothetical primitive limit of wrist extension), subjects reached significantly lower wrist flexion velocities and consequently lower strike forces. Knappers' ability to attain greater velocities when their full extension range is available is likely due to the mechanical advantage that the wrist's flexors experience as extension increases (*8*), in combination with the PDJS's whip-like motion pattern. Lower extension ranges, as some of our fossil ancestors may have possessed [*Australopithecus afarensis* and *A. anamensis* (*9*)], would limit peak wrist velocities.

When unbraced, subjects used >70% of their normal (muscular-induced) extension range. Seven of eight used >90%, however no one flexed past their neutral position. Radial deviation was emphasized over ulnar deviation due to the natural coupling between extension/radial deviation and flexion/ulnar deviation known as the "dart-thrower's arc" (*10*) (average intra-subject Spearman's *R* between extension/flexion and radial/ulnar deviation: ≥ 0.888). The "dart-throwers arc" provides a degree of radiocarpal stability that pure anatomical directions do not (*11*) and disruptions to this coupling destabilize the wrist, thereby decreasing control (*10*). This destabilization is evident in the significantly lower accuracy that all but one knapper experienced in the braced condition ($p < 0.012$). Post strike, the reaction force propelled the wrist out of flexion into high degrees of extension (~29° - 56°). With the hypothetical primitive wrist condition, this degree of extension may result in hyperextension and damage to the radiocarpal region (*12*). Modern humans' ability to achieve high degrees of wrist extension thereby contributes to target accuracy and may reduce the risk of hyperextension-related injuries.

During stone tool manufacture peak forces and pressures throughout the swing and at strike were concentrated on the 2^{nd} and/or 3^{rd} digits rather than on the 1^{st} digit ($p \leq 0.009$ and ≤ 0.01, respectively). In contrast, when subjects used tools in all behaviors save one (marrow extraction with a chopper), the thumb was subjected to significantly greater forces and pressures compared with the other tested regions of the hand ($p \leq 0.001$ and ≤ 0.047, respectively and figure 2). Further, the pollical distal phalanx experienced significantly greater forces during tool use compared with during tool production. Joint reaction forces and internal joint stress result from the combination of muscular and external forces. Due to the uniquely large size of the flexor pollicis longus muscle, activities which involve high external forces on the pollical distal phalanx will result in higher pollical joint stresses compared with activities generating lower distal phalanx forces. Together, these results suggest that the evolution of humans' unique robust thumbs was a selective response to the use rather than the production of stone tools.

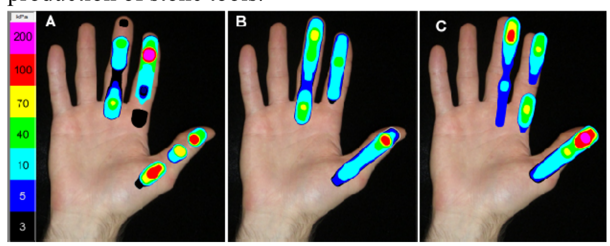

Figure 2: pressure distributions during (A) tool production, (B) nut-cracking, and (C) slicing tissue with a flake.

CONCLUSIONS

Our results demonstrate that aspects of the modern human hand and wrist anatomy (i.e., features enabling greater wrist extension and thumb robusticity) significantly contribute to the performance of stone tool behaviors and/or reduce the risk of injury during said behaviors. Overall, our studies support the hypothesis that modern humans' derived hand and wrist anatomy were selected at least in part for the performance of stone tool behaviors. However, long-standing hypotheses citing the selective predominance of stone tool *production* on hand and wrist anatomy [thumb robusticity in particular (*13*)], should be amended to highlight the role of tool *use* behaviors.

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