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# How similar are nut-cracking and stone-flaking? A functional approach to percussive technology

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Various authors have suggested similarities between tool use in early hominins and chimpanzees. This has been particularly evident in studies of nut-cracking which is considered to be the most complex skill exhibited by wild apes, and has also been interpreted as a precursor of more complex stone-flaking abilities. It has been argued that there is no major qualitative difference between what the chimpanzee does when he cracks a nut and what early hominins did when they detached a flake from a core. In this paper, similarities and differences between skills involved in stone-flaking and nut-cracking are explored through an experimental protocol with human subjects performing both tasks. We suggest that a 'functional' approach to percussive action, based on the distinction between functional parameters that characterize each task and parameters that characterize the agent's actions and movements, is a fruitful method for understanding those constraints which need to be mastered to perform each task successfully, and subsequently, the nature of skill involved in both tasks.

## 1. Introduction

Percussive actions are perhaps the most quintessential form of tool use. They are exhibited in a range of functional and recreational tasks—from hammering a nail, to playing a drum or hitting a tennis ball with a racquet. From an evolutionary perspective, archaeological evidence indicates the use of tools has been fundamental to human life for more than 3 Myr [1–4]. Indeed, it is generally accepted that cultural and technological innovation, manifested through tool use and tool production, emerged in a process of coevolution with musculoskeletal adaption of the upper limb, proliferation of the primate brain and the acquisition of higher level cognitive skills and language [5–8].

Tool-use abilities, however, are not exclusive to humans. A range of tool-use behaviours can be observed in various species and, in particular, non-human primates [9]. Man, however, has traditionally been distinguished from other species—firstly for his dexterous tool-use abilities, and secondly for his almost unique and elaborate ability for the production of tools [10]. Stone-knapping, a percussive technique involving the removal of sharp-edged stone flakes by striking a core with another stone, has long been considered as providing the first known evidence of organized tool production. Recent archaeological discoveries have confirmed that bipolar stone-flaking techniques, where Lomekwian knappers placed the target core upon an anvil prior to pounding it with another object, predate the genus *Homo* [4]. Freehand stone-knapping techniques, where the actor holds the core as the strike is delivered are believed to have become increasingly widespread during the subsequent Plio-Pleistocene period. This transition in functional capacities witnessed by early hominins has been considered as a form of 'threshold' in the evolution of man and technological adaptation.

Above all else, freehand stone-knapping signals an important step in terms of dexterity, motor control and understanding of one's own effects upon one's environment. This increased sophistication of tool-use behaviours has been credited with laying the foundation for subsequent capacities for planning, hierarchical thinking and discipline required in the production of tools produced in the subsequent Acheulean and Mousterian periods [11]. In such a way, stone tool production has even been interpreted as being diagnostic of the cognitive and motor skills of extinct hominins [12–14]. Numerous recent studies have sought to improve understanding of the origins of Plio-Pleistocene percussive technology [12–17]. These publications all stress the relevance of comparative cross-species approaches to tool use for the assessment of early hominin cognition, as well as the necessity of actualistic studies with interdisciplinary expertise [12,15,16,18,19].

## (a) Nut-cracking and stone-flaking

This search for the evolutionary origin of manual dexterity and technological skills in early hominins has given rise to studies of the parallels between the motor and cognitive capacities of great apes when engaged in tool-use tasks and those hypothesized to be necessary to early stone-knapping techniques. Primates, including chimpanzees, capuchins and macaques, have all been observed to use hammer and anvil techniques in order to break hard food casings in their natural environments [9,20]. The use of such a technique for nut-cracking is generally considered as the most complex technical skill mastered by non-human primates [21–23].

Various authors have suggested behavioural similarities between the nut-cracking activity of primates and tool use in early hominins, the inference being that nut-cracking abilities might be interpreted as a precursor to those employed in stone-knapping [24–27]. This has led to considerable speculation with respect to similarities and differences in the cognitive and manual abilities implied in the two different tasks. Several controversial claims have emerged. Wynn & McGrew [28] for example, wrote ‘all the behaviour that can be inferred from Oldowan tools falls within the range of the ape adaptive grade. There is nothing exclusively human-like about this oldest known archaeological evidence’ (p. 383). Quite similar statements can be found in the studies of Davidson & McGrew [25], Joulian [29], Marchant & McGrew [26] and Wynn [30]. However, other work, relying on the fact that no great apes appear to have knapped stone as early hominins did, question such similarities [31–36].

The question is then: does the production of cutting tools require different skills, and different levels of functional understanding than the use of stone hammers to fracture casings of hard food objects? To the best of our knowledge, no systematic comparisons of stone-knapping and nut-cracking have been undertaken. Such a comparison is the purpose of this paper.

Whereas much prior interest has been placed on the mental operations necessary in these tasks (coordination, symbolic representation, planning and comprehension of cause–effect relationships), such comparisons are limited by the fact that each activity is technically distinct, defined by a different *chaîne opératoire* [36]. Here, focus will be placed on the elementary actions themselves—the use of a stone hammer to crack a nutshell and retrieve the nut inside, and the use of the (same) stone hammer to remove a sharp-edged flake from a flint core.

It is necessary at this point to describe the two tasks under study. In both stone-knapping and nut-cracking, the blow delivered to the stone or to the nut must be an elastic blow, the total impulse being constant before and after the blow so that, in theory, all energies are used to generate the fracture to either the stone or the nut. In both cases, to achieve the goal the right amount of kinetic energy must be generated and transferred to the object to be worked on, be it the nut or the stone.

In the case of nut-cracking, the blow must be delivered in such a way that the shell cracks leaving the kernel intact. The kinetic energy produced must result in an adequate deformation of the shell so that it breaks. In addition, the direction of the blow must be more or less perpendicular to the surface on which the nut rests. This means that the reference frame is typically defined by the ground and the vertical direction is defined by gravitational forces. This reference frame is therefore allocentric: it is determined exclusively by external, or environmental properties. Moreover, this is the simplest possible reference frame as the vertical direction provides the axis for the intended vectors in production of potential and kinetic energies necessary for cracking the nut. In other words, in this situation the striking movement benefits maximally from the gravitational vertical acceleration and this minimizes required control of the velocity vector.

The fracture mechanics of stone-flaking are very different. In order to intentionally control the removal of stone flakes, it is necessary to initiate a conchoidal fracture [32]. It requires the identification of an appropriate point of percussion and the delivery of a precise blow to this point. However, the constraints of the task are more numerous than in nut-cracking. The shape and size of the flake depend on several parameters: the exterior platform angle, the point of percussion, the angle of blow relative to the platform and the kinetic energy. A peculiarity of the kinetic energy necessary to produce a conchoidal fracture is the existence of a threshold value [37]. Once a minimum effective quantity of kinetic energy is produced, an increase in this value has limited impact on the flake produced—a value far too large, however, may cause the flake to fragment into many pieces. As such, the characteristics of the flakes depend on the convergence on multiple interrelated variables [38–40].

Also, it must be recognized that stone-knapping is distinct from nut-cracking in that it requires assessment and adaptation of the stone core features following each strike. In order to succeed, the actor must (i) orientate the platform that defines the reference frame for the striking movement and (ii) stabilize the flint core with the postural hand. Here, the reference frame is egocentric. The movement of the striking hand must be accomplished with respect to the position of the desired contact point, and indeed, the orientation of the platform surface—the stability or variation of which is modulated (continually) by the activity of the postural hand.

From a prehensile perspective, the handling of the core typically involves a precision cradle grip where the stone is supported by the pads of the fingers and secured by the opposing pressure of the thumb pad [41]. The stone-knapping task is also observed to elicit the use of precision grips to control the hammer stone in modern-day knappers [41]. This, however, is not a prerequisite for success as experimental studies have demonstrated that stone tool production is possible when modern-day knappers use spherical power grips resembling those used in percussive tool use by non-human primates, where the whole palm is used to support the hammer tool with the fingers wrapping around [42].

Put simply, the nut-cracking and stone-flaking tasks share several key elements, most notably with respect to the production of an adequate level of kinetic energy and the ability to transfer this to a specific point of impact. Nonetheless, certain specific conditions required for the production of a conchoidal fracture with the freehand technique do introduce additional parameters which must be accounted for in carrying out the stone-flaking action.

Results from our previous work on percussive technology demonstrated that chimpanzees, human children and human adult subjects generally produced relatively comparable amounts of kinetic energy when required to crack nuts with hammer stones of varying mass (see [7] for a review). This observation suggests a sound appreciation of this key parameter in the context of the nut-cracking task, even across species. By contrast, such consistency was not observed when modern-day stone knappers (adult humans) were faced with the equivalent condition, that of producing stone flakes with hammer stones of varying mass. Only expert knappers effectively adapted their action to ensure a consistent level of kinetic energy as the mass of the hammerstones was varied [37]. It then holds that non-expert knappers are by comparison less sensitive to this key parameter in the context of stone-knapping and its relation to the other parameters involved in accomplishing the conchoidal fracture.

Given these observations, we would propose that despite commonalities between the nut-cracking and stone-knapping tasks, the perceptual-motor skills or technical abilities in play are not the same—that those in play during the stone-flaking action are more demanding than those at play during nut-cracking. Any verification of this claim, however, necessitates experimentation of nut-cracking and stone-knapping performed by the same subjects and inclusion of subjects with varying levels of stone-knapping expertise. Before describing the experiment presented in this paper, it may be useful to succinctly present the theoretical framework to which we refer (a more detailed presentation may be found in [16]).

### (b) Tool use: a functional approach

A considerable amount of research regarding the question of tool-use abilities has focused upon cognitive and neural correlates. Hence tool use is often regarded primarily as a product of intrinsic capacities, developed through the evolutionary process and manifested by anatomical structures and neurological mechanisms [43–45]. Adaptive behaviour such as tool use, however, implies somewhat more than this. It entails continuous interaction between the nervous system, the body and the environment [46]. The ecological psychology movement [47] and dynamical systems approach to the study of human behaviour [48,49] emphasize this point. From this perspective, understanding behaviour cannot be reduced to either cognitive or biomechanical capacities of the organism alone. It is the system itself comprising both organism and environment that becomes the unit of interest. Adaptive behaviour is thus an expression of the functional coupling between these two elements. Successful accomplishment of a desired action by the organism then requires the organism to mobilize the degrees of freedom across this system in order to satisfy the constraints of the task at hand [50–53]. Given the dynamic nature of the system, successful performance is dependent upon active exploration of the said system on the part of the organism and identification of opportunities for action afforded by the environment.

Following this principle, we propose that consideration of how an individual responds to task constraints is fundamental to the study of tool-use behaviours. Based upon our prior study on the subject, we propose a framework for understanding the various parameters involved in percussive tool-use actions [7,37]. Using this model, we define firstly the task constraints, i.e. those conditions which must be satisfied in order to accomplish the intended action. The task constraints may be defined in terms of a handful of parameters with immediate consequence upon the outcome; we refer to these as functional parameters. For percussive actions like nut-cracking and stone-flaking, these include kinetic energy, angle of the blow and point of percussion. Following this, we may define those elements of the task over which the actor may exert direct control. More specifically, in managing the blow the actor can adapt the level of kinetic energy both through the mass of the hammer chosen and the velocity at the time of impact—we refer to these as functional parameters. Further, an actor may employ different combinations of regulatory parameters, such as muscular effort or potential energy, in managing the velocity parameter. The motor performance of the actor himself (and the subsequent hammer trajectory) may then be described in terms of movement parameters such as kinematics or kinetics. Importantly, these latter may be recorded using biomechanical modelling and thereby allow for the computation of regulatory and functional parameters.

### (c) General hypothesis

The general aim of this paper is to directly compare nut-cracking and stone-knapping when performed by the same adult humans in order to better understand the relative complexity of each task. Based upon the existing body of work regarding percussive technologies, we suggest that the motor and cognitive-perceptual demands involved in cracking a nut using the hammer and anvil technique would be less complex than those required for removal of a sharp-edged stone flake from a flint core using a freehand stone-knapping technique. We propose to evaluate this relative complexity by comparing measures of task performance, grip configurations, motor behaviours and the regulation of functional parameters by adult human subjects when performing each task.

Assuming that both tasks implied equivalent skills, several results would be expected. (i) The rate of success in both tasks would be comparable. (ii) If subjects performed both tasks using the same tool, they would appropriate that tool in the same manner, a fact which would be reflected by a similar grasp of that tool. (iii) Comparable combinations of motor behaviours (i.e. the form and succession of actions) could be observed across tasks. Finally, if both tasks implied the same skills, it would be expected that (iv) the ability to regulate the functional parameters in one task would indicate the ability to regulate the same parameters in the other. In other words, the relative level of skill in one task would be evidenced in the other.

## 2. Method

### (a) Participants

A total of 19 human subjects (eight males and 11 females) participated in this study. The mean age of the sample was 35.3 years (median 28 years, s.d. 14.5 years; range 23–71 years). The absence of pathology impacting upon upper limb function was a condition for participation in this experiment. Only one subject, a flint worker by profession, was remunerated for his participation. All other subjects were unpaid volunteers. Individuals with prior training in lithic tool production were recruited through academic institutions in the Paris region. The flint-working professional and one experienced hobbyist were recruited separately through existing professional relationships. Subjects having no training in stone-flaking were recruited from visitors and staff at the Paris-Descartes University STAPS campus. In total, four expert subjects, nine trained subjects and six untrained subjects were included for the purposes of this study. Allocation to the expert group was based upon peer recognition and validated by subject performance in a series of flaking tasks using various tools (refer to [54] for further details on this method). Prior experience in nut-cracking was not considered in the context of this experiment.

## (b) Apparatus

Quartzite hammerstones of 600 g were used in both the nut-cracking and stone-knapping tasks. Each tool was ovoid in shape and was specifically selected as having the properties required for hard-hammer percussion in Oldowan lithic tool production. The hard-hammer stone permits a stone knapper to produce stone flakes with little or no platform preparation [11].

Macadamia nuts were used exclusively in the nut-cracking tasks. The macadamia nut has been used previously in similar studies [37,55–57] as it provides a suitably consistent shape and elastic modulus (a measure of the resistance to permanent deformation under compressive loading). All nuts were examined and sorted in advance to minimize variability in size and to exclude those with irregular shells.

Flint stone cores were used for the purposes of stone-flaking. Each was preformed into a frustrum (a truncated pyramid) by a flint working professional (www.flintknapping.co.uk: Kings Lynn, Norfolk, UK) in order to facilitate the immediate production of conchoidal flakes by all participants.

Movement parameters were recorded using a spatial tracking system (Polhemus Liberty, Polhemus Corporation; Colchester, VT, USA). This system uses an electromagnetic field to determine the positions and orientation of the sensors relative to a stationary system. The Polhemus permits the recording of movements in six degrees of liberty ($x$, $y$, $z$ and rotation along the axes $x$, $y$, $z$). Data were sampled at a frequency of 240 Hz and recorded online using MotionTracker v. 1.43 (Biometrics France; Gometz-le-Châtel, France). Each task series was equally recorded using a camcorder to support behavioural analyses.

## (c) Protocol

Polhemus sensors were placed upon the dorsal surface of the striking hand, the base of the frustrum and the anvil. The platform surface of the frustrum in relation to the sensor placed upon the frustrum was recorded using the Polhemus stylus with 10–16 points taken on the outer surface. For the first 11 subjects, the anvil used in the nut-cracking task was fixed to the ground; hence its striking surface was defined in relation to the Polhemus stationary system. For subjects 12–19, a further sensor was placed on the anvil so that the striking surface could be calculated with respect to this sensor.

Subjects were given the choice of several tools and stone frustrums prior to commencement. Each participant completed the stone-flaking and nut-cracking tasks successively. All participants received the same instructions. They were directed to use their chosen tool to: (i) crack the nutshell and retrieve the nut, without crushing it, and to (ii) produce a stone flake corresponding to the requested size (small or large). The nut-cracking task involved trials on five macadamia nuts. The stone-flaking task involved six attempts as subjects were asked to produce three small and three large flakes. Three strikes were permitted in the production of a stone flake; no limit of strikes was imposed on the nut-cracking task. The order of each task and that of the required stone flake size required were determined prior to each experiment with use of a random number generator.

A small and a large stone flake (14 g and 110 g, respectively) used in previous experiments [37] were provided to subjects as a model of the product required. Each attempt was classified as a success or failure. Success in the nut-cracking task was defined as the retrieval of a nut in three or fewer morsels. The removal of a stone flake was rated as a success, regardless of size and mass. Stone flakes were collected, weighed and labelled for each subject to provide an indicator of the control of stone-flaking.

Following each percussive task (being the five to six attempts with one tool), photos were taken of the grip used. Maintaining this grip, the subject was then asked to indicate the intended point of impact on the tool's surface. Using the stylus, this point was then recorded as the working point of the tool in relation to the striking hand.

All movement analysis and modelling was performed using MotionInspector v. 1.43 (Biometrics France; Gometz-le-Châtel, France).

## (d) Analysis of task performance

Only one stroke from each attempt at the stone-flaking and nut-cracking task was used for the purposes of analysis. In the case of stone-flaking, the operative blow extracted was that which had removed a stone flake. In the event that no flake was removed, the third and final blow was selected as being representative of what the subject conceived to be the movement most adapted to that specific situation. Similarly, the blow selected for analysis in the nut-cracking task was also taken from one of the first three strikes. The processes of selecting this operative blow in nut-cracking was based upon examination of the audio recording (a loud audible crack was frequently evident when the shell had been broken cleanly), vertical velocity of the hand and general behaviour (for example, if a shell was already deformed, a subject may have paused to reassess prior to the following strike or even adjusted the orientation of the nut on the anvil). For those cases where the shell was not evidently deformed on the first two blows, the third blow was selected by default.

Qualitative classification of grip configuration was carried out with reference to the conventions presented by Marzke [42]. Observations pertaining to motor behaviour were noted during the analysis of task performance to characterize general strategies employed across both tasks.

## (e) Calculation of functional parameters

Figure 1 illustrates the two reference frames considered for computing the kinematic and kinetic variables. Stone and hand sensor position and orientation were initially calculated in the global reference frame system (Rg) of the Polhemus (O, X, Y, Z) and used to reconstruct the three-dimensional trajectory of the working point (Wp). In addition to this, the striking surface of the stone reference frame system (Rs) was calculated using the calibration points of the striking surface and then used to compute the different functional parameters. From the calibration points, a corresponding plane was computed using a least-square algorithm. The normal vector (N) and the centre of the plane (C) were computed. The point of impact (Pi) was evaluated as the minimal distance between the Wp and the computed surface during the striking movement. The stone reference frame system was then defined by C, Pi, $y$ and N, where $y$ is the vector perpendicular to C, Pi and N. Stone orientation was calculated as the rotation matrix between this stone reference frame system and the global reference frame.

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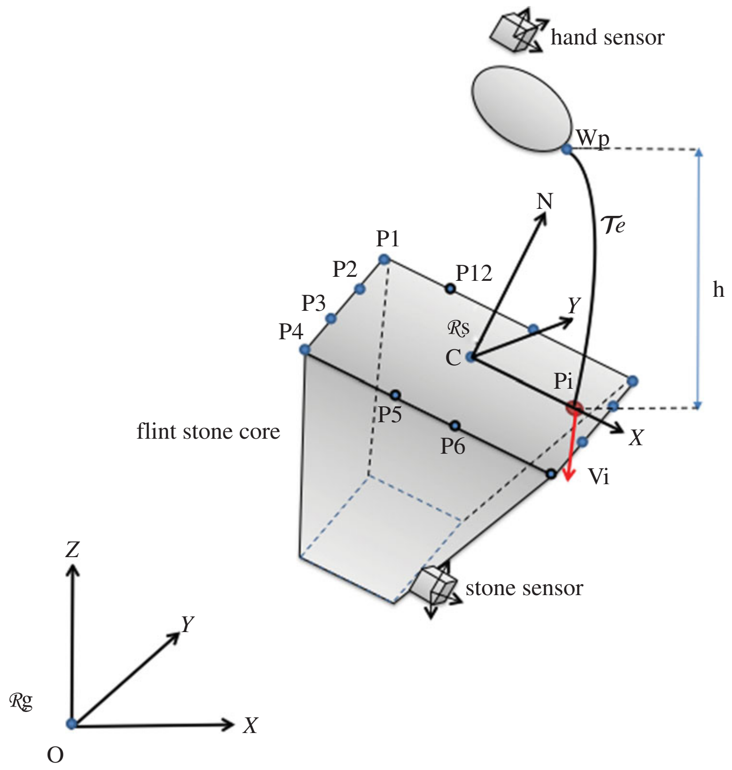


**Figure 1.** Experimental set-up illustrating the two reference frames.

All kinematic and kinetic variables were calculated in the global reference frame for the nut-cracking strikes and in the stone reference frame system for the flaking strikes. The trajectory of the tool's working point was defined as the path of this marker in three-dimensional space during the striking action. The instantaneous velocity of the hammer was defined as the derivative of the tool's position. Kinetic energy ($1/2\,mv^2$) and potential energy ($mgh$) were calculated for the working point of each actor's tool during the whole striking movement and at specific events (e.g. impact, maximum value, instantaneous value).

Several ratios of kinetic energy to potential energy ($E_k/E_p$) were also computed to observe the relative differences in the movement strategies employed. These measures provide a crude manner of determining whether a person uses relatively greater muscular force (reflected by a higher ratio when additional velocity is generated through the strike) or relies more exclusively upon the passive gravitational force accelerating the hand-hammer system as the strike is delivered.

### (f) Statistical analysis

Two-way $t$-tests were employed for statistical comparison of task performance variables (rate of success, number of strikes, flake mass), while a two-way ANOVA was used for the analysis of functional parameters. In all cases, $p$-values were set at 0.05 and adjusted for multiple comparisons using a Bonferroni correction. A Pearson correlation coefficient was used to compare success rate across tasks; the threshold for significance was considered as 0.7.

## 3. Results

### (a) Task performance

In total, 209 trials were recorded for analysis: 95 for the nut-cracking task and 114 for the stone-flaking task. Nuts were successfully retried in 89 trials and stone flakes were removed in 96 trials. This accounted for success rates of 95% and 84%, respectively, in the two tasks.

On a group by group basis, success rates for the stone-knapping task was 73% for the untrained group, 89% for the trained group, and 100% for the expert group. Their success rates in the nut-cracking task were 97%, 89% and 100%, respectively. Overall, production rate for small stone flakes (91%) was observed to be higher than the production rate of large flakes (77%). The correlation coefficient of production rate in nut-cracking and stone-knapping tasks (less than 0.02) indicated that performance was not related across tasks.

The average number of strikes to fracture the macadamia nut shell was 2.7 while the average total number of strikes to remove the kernel was 4.3. The number of strikes used to fracture the macadamia nut shell was similar across groups (2.6, 2.3 and 3.8 for untrained, trained and expert participants, respectively). The average total strikes used to remove the kernel were also comparable (4.4, 3.8 and 5.4).

For the stone-flaking task, the number of strikes employed per trial was observed to decrease according to expertise, with the untrained group using 1.97 strikes, the trained group 1.63 and the expert group 1.41 strikes on average. Differences in the number of strikes between groups were not statistically significant in either nut-cracking or stone-knapping tasks. It is, however, interesting to note that the difference in number of blows for stone-knapping between untrained and expert subjects yielded a $p$-value of 0.049, the significance of which was negated upon application of the Bonferroni correction.

Generally speaking, expert stone knappers tended to produce more ample flakes than counterparts, their mean flake masses being 22.00 g (s.d. 10.99 g) for small flakes and 87.17 g (s.d. 52.13 g) for large flakes. The mean flake sizes for members of the trained group were 21.70 g (s.d. 21.53 g) for small flakes and 64.63 g (s.d. 34.48 g) for large flakes. Untrained subjects produced small flakes with an average mass of 19.08 g (s.d. 17.22 g) and 14.96 g (s.d. 10.48 g) for large flakes.

Experts exhibited greater stability of performance with an average coefficient of variability of 0.64 in small flake production

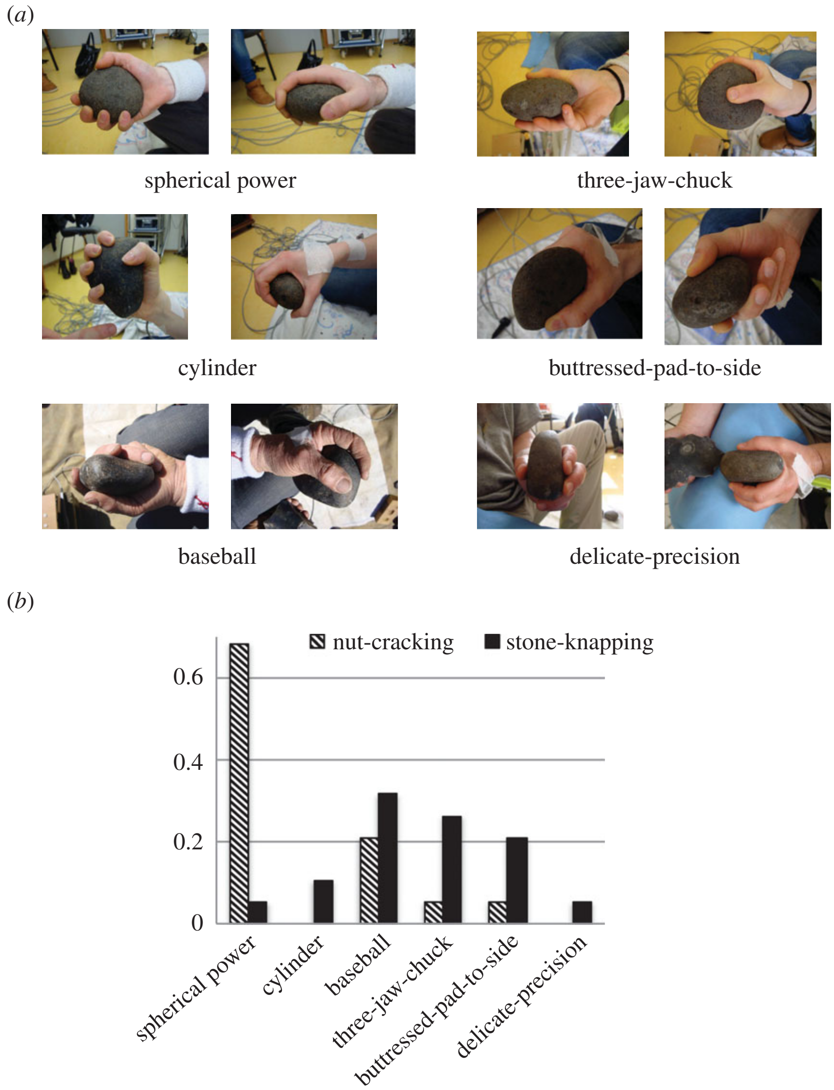


**Figure 2.** Types of grip observed in the two conditions, nut-cracking and stone-flaking. (*a*) Examples of grip types observed. (*b*) Frequency of type of grip for both nut-cracking and stone-knapping conditions (all participants pooled).

and 0.64 in large flake production. Trained subjects produced flakes with an average coefficient of variability of 0.92 for small flakes and 0.68 for large flakes. The untrained subjects produced small flakes with an average coefficient of variation of 1.00 for small flakes and 1.15 with large flakes. Of these parameters only the mean of large flake mass between untrained and expert groups was statistically significant ($p < 0.01$) with two-way $t$-test after Bonferonni correction.

## (b) Type of grip

For both tasks, the type of grip used by each participant was recorded and categorized as power grip (spherical power grip and cylinder grip) and precision grip (three-jaw-chuck grip, baseball grip, buttressed-pad grip and delicate-precision grip; figure 2*a*). Sixty-eight per cent of participants used a spherical power grip in the nut-cracking task while another large portion of subjects used a baseball grip (21%). In the flaking task, however, most participants demonstrated a strong preference for precision grips, with the three-jaw-chuck, baseball, buttressed-pad-to-side and delicate-precision grip accounting for 84% of the observed grasp configurations (figure 2*b*).

Among the six participants who did not use the spherical-power grip for nut-cracking, three held the nut with the postural hand while striking. Two of these subjects were observed to use a baseball grip, the other using a three-jaw-chuck grasp to deliver the blow.

## (c) Motor behaviour

Multiple different motor behaviours were observed through the course of these two percussive activities. The nut-cracking task in particular was carried out with a range of percussive behaviours (electronic supplementary material, figure S1 provides a selection of contrasting motor behaviours). Subjects were observed using a single blow to break the nutshell and retrieve the kernel (e.g. electronic supplementary material, figure S1a) or otherwise using combinations of blows to complete the task (e.g. electronic supplementary material, figure S1b–S1e). The use of multiple blows was observed to involve movements of regular amplitude on the vertical axis with reasonably consistent vertical velocity (e.g. electronic supplementary material, figure S1b) or, in other cases, movements of increasing amplitude and vertical velocity until the desired fracture was obtained (e.g. electronic supplementary material, figure S1c). A number of percussive motor behaviours involved the use of blows adapted to the progressive fracturing of the shell. For example, in certain instances, subjects were observed to use a primary blow to fracture the shell followed by a series of

**Table 1.** Mean values and standard deviation of the different parameters of the striking action according to condition (stone-flaking versus nut-cracking) and level of expertise (untrained, trained and expert).

| | | untrained | | trained | | expert | |
|---|---|---|---|---|---|---|---|
| | condition | mean | s.d. | mean | s.d. | mean | s.d. |
| $V_i$ (m s$^{-1}$) | stone | 4.022 | 0.834 | 2.752 | 1.078 | 2.427 | 0.802 |
| | nut | 2.042 | 0.438 | 1.80 | 0.637 | 1.698 | 0.408 |
| $V_{max}$ (m s$^{-1}$) | stone | 5.188 | 0.975 | 3.861 | 1.063 | 3.457 | 1.085 |
| | nut | 2.431 | 0.501 | 2.278 | 0.544 | 2.267 | 0.683 |
| $E_{k_{ip}}$ (J) | stone | 3.614 | 1.513 | 1.769 | 1.420 | 1.036 | 0.939 |
| | nut | 0.725 | 0.328 | 0.541 | 0.298 | 0.505 | 0.270 |
| $E_{k_{max}}$ (J) | stone | 6.932 | 2.907 | 3.442 | 2.273 | 2.527 | 1.573 |
| | nut | 1.756 | 0.749 | 1.369 | 0.635 | 1.225 | 0.706 |
| $E_{p_{max}}$ (J) | stone | 2.245 | 0.861 | 1.304 | 0.696 | 1.042 | 0.350 |
| | nut | 1.120 | 0.287 | 0.823 | 0.336 | 1.066 | 0.350 |
| $E_{k_{max}}/E_{p_{max}}$ | stone | 3.112 | 0.847 | 2.708 | 0.946 | 2.744 | 2.064 |
| | nut | 1.531 | 0.465 | 1.659 | 0.528 | 1.088 | 0.387 |
| $E_{k_{ip}}/E_{p_{max}}$ | stone | 1.632 | 0.486 | 1.323 | 0.592 | 1.171 | 1.135 |
| | nut | 0.641 | 0.226 | 0.634 | 0.231 | 0.460 | 0.153 |
| length (m) | stone | 0.525 | 0.141 | 0.322 | 0.134 | 0.234 | 0.075 |
| | nut | 0.202 | 0.055 | 0.157 | 0.042 | 0.128 | 0.034 |
| orientation | stone | 17.138 | 6.562 | 28.640 | 14.615 | 33.763 | 10.553 |
| (degrees) | nut | 0.000 | | 0.000 | | 0.000 | |

smaller blows to loosen and remove the shell from the kernel (e.g. electronic supplementary material, figure S1d). In other cases, certain individuals were observed to use their postural hand to change the orientation of the nutshell between several different blows (e.g. electronic supplementary material, figure S1e). Owing to the often progressive nature of the fracture of the nutshell, individuals were also frequently observed to change or adapt percussive motor behaviours during the removal of a nut.

For the stone-flaking task, both unique blows and successive blows were also observed (examples are provided in the electronic supplementary material, figure S2). Unique blows of optimal energy resulted in a flake being detached on the first attempt (e.g. electronic supplementary material, figure S2a). For successive strikes, different behaviours were observed. After having not succeeded with the first attempt, some subjects paused momentarily to revaluate and change the properties of their blow (e.g. electronic supplementary material, figure S2b) while other subjects carried out further strikes with in a more rhythmic fashion, making only slight adjustments to the amplitude and velocity (e.g. electronic supplementary material, figure S2c). Unlike the nut-cracking task, adaptation observed in successive strikes was not due to a progressive nature of fracture but rather an adaptation to achieve an optimal blow.

## (d) Values of the functional parameters

The mean values and standard deviation of the functional parameters taken into account, i.e. maximum velocity ($V_{max}$), velocity at impact ($V_i$), maximum kinetic energy ($E_{k_{max}}$), kinetic energy at impact ($E_{k_{ip}}$), maximum potential energy ($E_{p_{max}}$), ratios of kinetic energy with respect to potential energy ($E_{k_{ip}}/E_{p_{max}}$ and $E_{k_{max}}/E_{p_{max}}$), length of the hammer trajectory and platform orientation are provided in table 1 (see also figure 3). Statistical results of a two-way ANOVA comparing values of these functional parameters with respect to task (stone-flaking versus nut-cracking) and with respect to expertise (untrained versus trained, untrained versus expert, trained versus expert) are provided in table 2.

### (i) Nut-cracking/stone-flaking comparison by levels of expertise

The task condition (nut-cracking versus stone-flaking) shows significant differences for multiple parameters in all groups (table 2 and figure 3). Both the untrained and trained group showed significant differences between conditions for all parameters. In the expert group, no statistically significant difference was observed between the two activities with respect to $E_{p_{max}}$ and $E_{k_{max}}$.

### (ii) Comparison of levels of expertise for nut-cracking

Post-hoc pairwise comparisons using Bonferroni test indicate that level of expertise in stone-knapping had no significant impact upon regulation of functional parameters in the nut-cracking task. The only exception to this was the ratio of $E_{k_{max}}/E_{p_{max}}$ of the untrained group with respect to the trained and expert groups (figure 3).

### (iii) Comparison of levels of expertise for the stone-flaking task

As can be observed in table 1, untrained subjects had the highest values for $V_i$, $V_{max}$, $E_{k_{ip}}$, $E_{k_{max}}$, $E_{p_{max}}$, $E_{k_{ip}}/E_{p_{max}}$,

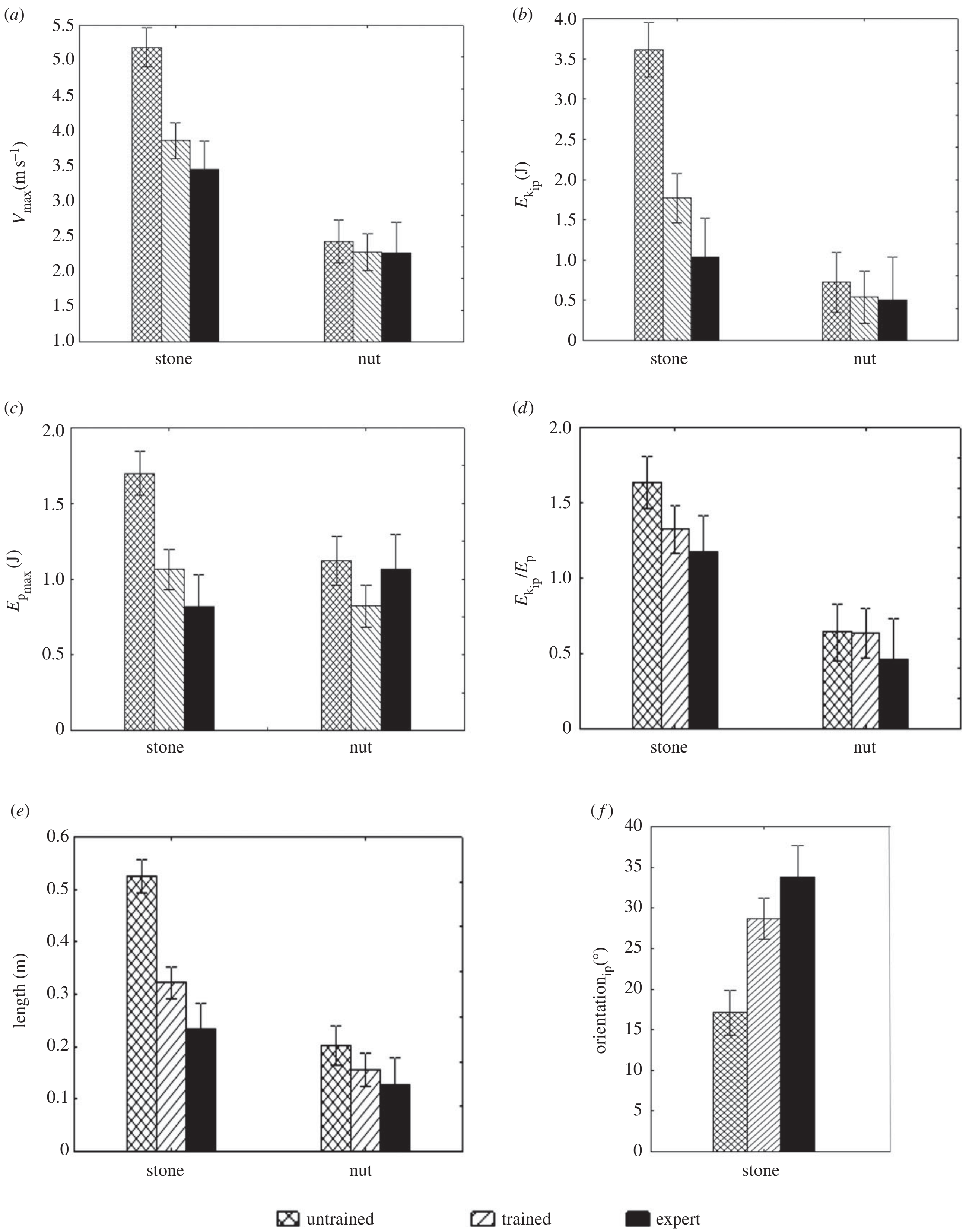


**Figure 3.** Mean values of the strike parameters for the two conditions (stone-flaking and nut-cracking) by level of expertise (untrained, trained and expert). Vertical bars denote 0.95 CIs. (*a*) Maximum velocity of the hammer during the strike; (*b*) kinetic energy of the hammer at contact; (*c*) maximum potential energy; (*d*) kinetic energy on potential energy ratio; (*e*) length of the hammer trajectory; (*f*) orientation of the striking surface for the flaking condition only (the striking surface being horizontal for the nut-cracking condition).

$E_{k_{max}}/E_{p_{max}}$, length of trajectory in the stone-flaking task with the smallest degree of platform surface orientation. The expert group, on the other hand, exhibit the smallest values for all those parameters, with the highest degree of platform surface orientation. The functional parameters observed in the stone-flaking task by the trained group were typically between those exhibited by the two other groups, although for most parameters differences with the expert group were not significant except for $E_{k_{max}}$, and length of trajectory (table 2). Post-hoc pairwise comparisons indicate that for

**Table 2.** Main effect on the different parameters according to condition (stone-flaking versus nut-cracking) and level of expertise (untrained (Untr.), trained (Tr.) and expert (Exp.)).

| | stone-flaking vs nut-cracking | | | stone-flaking | | | nut-cracking | | |
|---|---|---|---|---|---|---|---|---|---|
| | **Untr.** | **Tr.** | **Exp.** | **Untr./Tr.** | **Untr./Exp.** | **Tr./Exp.** | **Untr./Tr.** | **Untr./Exp.** | **Tr./Exp.** |
| $E_{k_{max}}$ | 0.000 | 0.000 | 0.052 | 0.000 | 0.000 | 0.000 | n.s. | n.s. | n.s. |
| $E_{k_{ip}}$ | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | 0.182 | n.s. | n.s. | n.s. |
| $E_{p_{max}}$ | 0.000 | 0.000 | n.s. | 0.000 | 0.000 | n.s. | n.s. | n.s. | n.s. |
| $E_{k_{ip}}/E_{p_{max}}$ | 0.000 | 0.000 | 0.002 | n.s. | 0.042 | n.s. | n.s. | n.s. | n.s. |
| $E_{k_{max}}/E_{p_{max}}$ | 0.000 | 0.000 | 0.000 | n.s. | n.s. | n.s. | 0.000 | 0.000 | n.s. |
| length | 0.000 | 0.000 | 0.045 | 0.000 | 0.000 | 0.036 | n.s. | n.s. | n.s. |
| platform orientation | 0.000 | 0.000 | 0.000 | 0.000 | 0.000 | n.s. | | | |

the untrained group the values of all parameters in the stone-knapping task are significantly different from all other groups except for the ratio $E_{k_{ip}}/E_{p_{max}}$ when compared to the trained group, and for the ratio $E_{k_{max}}/E_{p_{max}}$ when compared to both trained and expert groups (table 2).

## 4. Discussion

This study compared two percussive tasks: nut-cracking and stone-flaking. This was done in order to determine the extent to which these primordial tool-use activities engage similar or different kinds of abilities. From the outset, we proposed that the motor and cognitive demands necessary for nut-cracking were less complex than those required for freehand stone-knapping [7,34]. This study used an experimental protocol involving adult human subjects, each of them performing the two tasks with the same percussive tool to verify this claim.

Beginning with the null hypothesis that both tasks implied the same skills, four specific postulates were considered. The first of these was based upon relative success across tasks. Assuming that each activity required comparable abilities, rates of success in one task would have been expected to be predictive of the rate of success in the other. This, however, was not the case: no linear correlation existed between subject success rates across the two tasks in question.

The second postulate addressed the manner in which individuals appropriated the same tool for the two different tasks, a comparison based upon qualitative classification of the grip used for the striking action. Again, this measure provided a strong contrast between tasks with the nut-cracking task strongly associated with the use of power grips and stone-flaking strongly associated with precision grips.

Patterns of motor behaviour during task performance constituted the third aspect of comparison. In the nut-cracking task, multiple combinations of striking behaviours (unique blow, successive blows of increasing kinetic energy, etc.) were observed to be equally valid for obtaining the desired effect, while only unique blow effects were functionally valid for the stone-flaking task. In other words, the way in which the elementary actions were combined to fulfil task objectives was not comparable across tasks.

Our fourth and last postulate examined relative ability across nut-cracking and stone-flaking activities with regard to expertise. Assuming that both tasks involved comparable skills, the ability to regulate functional parameters in one task would be associated with the ability to manage those parameters in the other. Again, this was not the case. While regulation of functional parameters was shown to be highly correlated with the subject's level of expertise in stone-knapping, this background did not distinguish these subjects (trained and expert groups) from those with no training (untrained group) on the nut-cracking task where overall rate of success in task performance was greater for all subjects.

Several points may thus be directly inferred from these results. (i) The relative difficulty of the nut-cracking task is inferior to that of stone-flaking. (ii) Individuals adjust their grip in order to reflect the specificity of the different task demands in the nut-cracking and stone-flaking tasks. (iii) Success in the nut-cracking task may be achieved by a more varied range of motor behaviours, whereas stone-flaking is dependent upon the punctual effects of a singular percussive action. (iv) Stone-flaking expertise is distinct from that involved in nut-cracking. Using a behavioural science perspective, we propose a synthesis of these findings which we hope may contribute to ongoing debate regarding percussive technology and the evolution of human tool-use abilities.

### (a) Grasp configuration in the man–tool–environment system

One of the key functions of a chosen grasp configuration when holding a tool is to assure the relative stability of that tool regardless of the relative force direction between the hand and the object [58]. As such, it is generally considered that the hand is adapted to the tool. In the results of this study, however, human subjects were observed to adapt their grip when changing from nut-cracking to stone-flaking (or vice versa), despite using the very same hammerstone. That is to say, grasp configuration was dictated not by the tool, but by the task with which the actor was confronted.

For the purposes of the nut-cracking task, participants showed a strong preference for power grips (notably the spherical power grip), while firm precision grips were employed in stone-flaking with more or less equal preference for three-jaw-chuck, baseball and buttressed-pad-to-side grips (cf. [6]). Interestingly, strong preference for firm precision grips in stone-knapping was observed to be the case even for subjects of the untrained group who possessed no prior knowledge regarding the technique.

Marzke [42] refers to the hominid ability for precision grips as a 'significant element of the hand/brain/tool complex' (p. 91). Indeed, it is difficult to deny that the specific morphology of the human hand permits a unique capacity for dexterous interaction with the environment. Regarding stone-knapping capacities, Marzke contends that even though stone-knapping tasks may be possible using power grips, the use of firm precision grips facilitates stone flake production to such an extent that it is difficult to conceive this activity becoming habitual without this prehensile ability [42]. Following a similar logic, we would suggest that the spontaneous (and rapid) selection of firm precision grips in the stone-flaking task, even on the part of the untrained subjects represents two complementary abilities. The first of these is an elementary perception of inherent complexity of the task itself. The second is the mobilization of additional degrees of freedom in the hand–tool–environment system with the supple responsiveness offered by the distal phalanges and their inherent fine motor control.

## (b) Fracture mechanics and motor behaviour

One of the more simple yet consequent aspects of the nut-cracking/stone-flaking comparison was the description of different blow combinations across the tasks. As stated above, numerous different blow combinations were effectively mobilized for nut-cracking, whereas stone flake production was dependent upon the effect of unique blow actions. The nut-cracking task, as opposed to stone-flaking, may be accomplished by the progressive fracturing of the shell. Multiple different behavioural combinations are therefore possible to achieve the overall aim. Accordingly, we propose that the relative simplicity of the nut-cracking is related to the simple fact that the mechanics of the task imply a greater number of opportunities/possibilities of valid actions. Even where a blow has a suboptimal effect, this may be compensated with an additional blow. In stone-knapping, the properties of the stone core may afford several viable surfaces for the removal of a stone flake. Despite this, once the striking point for removal of the desired flake is identified, the selected action must be optimal in terms of precision, kinetic energy and angle of the blow with respect to the exterior angle in order to have the desired effect.

## (c) Stone-flaking and the simultaneous regulation of multiple parameters

Several observations can be made with respect to the values of functional parameters measured (i.e. velocity, kinetic energy, potential energy, trajectory length, platform orientation), both across tasks and with respect to expertise. As presented in figure 3, regulation of functional parameters varies according to expertise in the stone-flaking task. No such effect is observed in nut-cracking where most subjects experience high success rates regardless of experience in stone-knapping. Based upon these results, it may be said that despite the fact that cracking a macadamia nut using a hammer and anvil technique may be a novel activity, adult human subjects are able to rapidly master the required parameters and accomplish the task at hand. Conversely, the ability to remove stone flakes is more complex and regulation of these parameters is dependent upon training and experience.

The fact that no prior experience is required for success in the nut-cracking task provides a clear indication that adult human subjects are generally capable of managing the hammer stone velocity to generate a desired amount of kinetic energy at the moment of impact. It also indicates that delivery of a strike to a reasonably precise location and along a desired trajectory poses no significant challenge for this population. What (or which) aspect(s) of the stone-flaking task then account for the strong effect of experience upon task performance? Logically, the relative difficulty must be due to the additional parameter which must be satisfied (i.e. the direction of the strike with respect to the external angle), and by extension its relationship to the other parameters in question.

We therefore propose that the inherent difficulty of stone-flaking with respect to nut-cracking is a direct consequence of being able to simultaneously satisfy multiple parameters. In order to be successful, any knapper must first understand the relationships between such parameters and secondly execute an action satisfying the identified task constraints. The present data regarding platform orientation at the moment of impact may provide further insight into this ability. As shown in figure 3, platform orientation at the moment of impact increased as a function of expertise. Statistically significant differences were observed when the untrained group was compared to their trained and expert counterparts. This result corroborates the findings of an earlier comparative study between novice knappers (meeting the same criteria as the untrained participants of the present experiment) and experts, where the latter preferred a tilted position of the striking surface while the former preferred horizontal positions of the striking surface significantly more often [18]. We would thus infer that competent knappers exploit this opportunity to modulate the platform surface orientation in order improve the way they manage the angle of their strike [38].

## (d) Bimanuality in the nut-cracking and stone-flaking tasks

The coordination of the striking action while orientating the platform surface away from the horizontal also highlights the egocentric and bimanual aspects of the stone-flaking task. As this deviation increases, the external gravitational reference, fundamental to movement strategies highly dependent on potential energy, becomes increasingly abstract with respect to the movement trajectory. The evidence that trained and expert knappers have a preference for increased platform orientation suggests that they capably operate in an egocentric reference frame where the coordination of the strike is made with reference to the position/movement of their postural hand. As such, we emphasize the bimanual nature of the striking action in the stone-flaking task.

Clearly, the broader activities of nut-cracking and stone-flaking typically engage the use of both hands in qualitatively differentiated roles [59,60]. In the case of nut-cracking, however, once the nut is placed upon a support surface, the postural hand will have limited contribution to the functional aspects of the blow itself. Indeed, some actors may choose to hold the nut with the postural hand as the blow is delivered—as was the case for three subjects of the present experiment. But even in this case, the postural hand remains fixed for the purposes of the strike itself, having no dynamic impact upon the man–tool–environment reference frame.

This assertion regarding the relative complexity of bimanual coordination in stone-knapping is supported by the results of several prior studies. Using a data glove to measure hand kinematics, Faisal *et al*. [61] found that the postural hand which supports the striking surface in Oldowan and Acheulean technologies exhibits increased manipulative complexity than a control task analogous to that of holding and positioning a nut on a striking surface. Nonaka & Bril [62] in a study of expertise in knapping techniques by counter-blow focused specifically upon the question of movement dynamics between the postural and percussive hand actions. It was found that level of expertise was correlated with more deterministic coupling of the hands and suggested that skilled bimanual actions such as stone-knapping are characterized by the flexible nesting of differentiated functions across hands in order to manage task parameters.

## 5. Conclusion: from hammer and anvil nut-cracking to freehand stone-knapping techniques

The results of this study support the assertion that motor and cognitive-perceptual demands necessary for nut-cracking are inferior to those of stone-flaking. The successful removal of a desired stone flake from a flint core is defined by a rather specific set of mechanical constraints—more complex than those involved in nut-cracking. Freehand stone-knapping techniques thus require the ability to understand relationships between the functional parameters which define the conchoidal fracture. The elaboration of an action corresponding to the desired effect necessitates complex bimanual skills and benefits significantly from the use of the fine motor properties of firm precision grips. We argue, therefore, that this transition from anvil and hammer percussive techniques (such as nut-cracking) to freehand knapping techniques in early hominins necessitated improved perceptual abilities, learning capacities and bimanual dexterity superior to that of non-human primates.

Although no clear archaeological evidence remains, percussive behaviours such as the pounding of organic substances such as seeds or nuts are believed to predate stone-knapping techniques [63]. Indeed, it is argued that these basic pounding and nut-cracking abilities, associated with both apes and early hominins, constitute the origin of subsequent stone-knapping industries (refer to [63] for an extended discussion). How then might this progression have occurred, and what functional milestones may this have implied?

The progression from opportunistic pounding to the integration of an anvil itself represents one important component. Common in bipolar knapping during the Oldowan period and more recently in the processing of quartz cobbles [64,65], the systematic use of a hard surface in order to apply a strong bipolar force would indicate the understanding of the dynamic relationship between the three objects [66,67]. Insight into how to exploit mechanical properties between these three elements is not as trivial as it may first appear. Children may require many years to acquire an understanding that, without the benefits of the elastic blow afforded with the introduction of the anvil, huge amounts of energy would be dispersed if using a comparably softer substrate as a working surface [68,69].

Based upon the description of bipolar knapping techniques presented by other research teams [65,70,71] and the results of this study, we would suggest that this ability may be seen as both a chronological and functional intermediary between basic hammer and anvil techniques such as nut-cracking and the more sophisticated freehand knapping techniques. This perspective reflects the argument presented by Hayden [72] based upon ethnographic observations of contemporary hunter-gatherer populations. Prior studies confronting bipolar reduction methods have described the technique as ‘requiring little to no skill’ [65, p. 241] and easily learned [71]. When compared to freehand techniques, the form and quality of flakes produced in bipolar knapping is more irregular, the transmission of energy being less precisely controlled [66]. These reports certainly suggest, however, that once the principle of conchoidal fracture is understood, coordination of a functional blow may be relatively straightforward.

Certainly, to the naked eye, those three subjects of the present experiment that were observed to use their postural hand to maintain the nut combined with a precision grasp of the hammer stone appear to exhibit a behaviour similar to those records of experimentalist knappers performing bipolar knapping. We would venture that the purely motor components of both tasks are highly comparable. But while the additional understanding of the principle of conchoidal fracture may be sufficient to allow for the rapid acquisition of basic competences in bipolar knapping, the same does not apply for freehand techniques. Further to this, it is interesting to note that those subjects of the trained group in this study were predominantly archaeologists, for the most part possessing extensive academic understanding of conchoidal fracture and knapping techniques. Their ability to manage the functional parameters was nonetheless inferior to the expert group, particularly for the production of large stone flakes. This suggests that their formal knowledge may not be embodied to the extent where it can be translated into an optimal motor solution [34]. The milestone of freehand knapping may hence be best surmised as the capacity to manage, perceive and generate a flexible, bimanual action responding to multiple nested task parameters [38]. It is an ability that would necessitate a certain level of experience in order to generate effective synergies across multiple segments in the bimanual system, thereby stabilizing the salient functional parameters [50].

Ethics. Prior to commencement, the experimental procedure and required tasks were explained to each participant. The experiment followed ethical guidelines of the American Psychological Association (APA) and provision of a duly signed informed consent form was a requirement of participation.

Competing interests. We declare we have no competing interests.

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## References






1. Roche H, Delagnes A, Brugal JP, Feibel C, Kibunjia M, Mourre V, Texier PJ. 1999 Early hominid stone tool production and technical skill 2.34 Myr ago in West Turkana, Kenya. *Nature* **399**, 57–60. (doi:10.1038/19959)
2. Semaw S. 2000 The world's oldest stone artefacts from Gona, Ethiopia: their implications for understanding stone technology and patterns of human evolution between 2·6–1·5 million years ago. *J. Archaeol. Sci*. **27**, 1197–1214. (doi:10.1006/jasc.1999.0592)
3. McPherron SP, Alemseged Z, Marean CW, Wynn JG, Reed D, Geraads D, Bobe R, Béarat HA. 2010 Evidence for stone-tool-assisted consumption of animal tissues before 3.39 million years ago at Dikika, Ethiopia. *Nature* **466**, 857–860. (doi:10.1038/nature09248)
4. Harmand S *et al.* 2015 3.3-million-year-old stone tools from Lomekwi 3, West Turkana, Kenya. *Nature* **521**, 310–315. (doi:10.1038/nature14464)
5. Ambrose SH. 2001 Paleolithic technology and human evolution. *Science* **291**, 1748–1753. (doi:10.1126/science.1059487)
6. Marzke MW, Marzke RF. 2000 Evolution of the human hand: approaches to acquiring, analysing and interpreting the anatomical evidence. *J. Anat*. **197**, 121–140. (doi:10.1046/j.1469-7580.2000.19710121.x)
7. Bril B, Smaers J, Steele J, Rein R, Nonaka T, Dietrich G, Biryukova E, Hirata S, Roux V. 2012 Functional mastery of percussive technology in nut-cracking and stone-flaking actions: experimental comparison and implications for the evolution of the human brain. *Phil. Trans. R. Soc. B* **367**, 59–74. (doi:10.1098/rstb.2011.0147)
8. Stout D, Toth N, Schick K, Chaminade T. 2008 Neural correlates of Early Stone Age toolmaking: technology, language and cognition in human evolution. *Phil. Trans. R. Soc. B* **363**, 1939–1949. (doi:10.1098/rstb.2008.0001)
9. Visalberghi E, Sirianni G, Fragaszy D, Boesch C. 2015 Percussive tool use by Taï Western chimpanzees and Fazenda Boa Vista bearded capuchin monkeys: a comparison. *Phil. Trans. R. Soc. B* **370**, 20140351. (doi:10.1098/rstb.2014.0351)
10. Oakley KP. 1972 *Man the toolmaker*, 6th edn. London, UK: Natural History Museum.
11. Stout D. 2011 Stone toolmaking and the evolution of human culture and cognition. *Phil. Trans. R. Soc. B* **366**, 1050–1059. (doi:10.1098/rstb.2010.0369)
12. Haslam M *et al.* 2009 Primate archaeology. *Nature* **460**, 339–344. (doi:10.1038/nature08188)
13. Ling V, Hernandez-Aguilar A, Haslam M, Carvalho S. 2009 The origins of percussive technology: a smashing time in Cambridge. *Evol. Anthropol. Issues News Rev*. **18**, 48–49. (doi:10.1002/evan.20197)
14. McGrew WC, Foley RA. 2009 Palaeoanthropology meets primatology. *J. Hum. Evol*. **57**, 335–336. (doi:10.1016/j.jhevol.2009.07.002)
15. Gowlett JAJ. 2009 Artefacts of apes, humans, and others: towards comparative assessment and analysis. *J. Hum. Evol*. **57**, 401–410. (doi:10.1016/j.jhevol.2009.04.011)
16. Roux V, Bril B. 2005 General introduction: a dynamic system framework for studying a uniquely hominin innovation. In *Stone knapping: the necessary conditions for a uniquely hominin behavior* (eds V Roux, B Bril), pp. 1–18. Cambridge, UK: McDonald Institute for Archaeological Research.
17. Whiten A, Schick K, Toth N. 2009 The evolution and cultural transmission of percussive technology: integrating evidence from palaeoanthropology and primatology. *J. Hum. Evol*. **57**, 420–435. (doi:10.1016/j.jhevol.2008.12.010)
18. Geribàs N, Mosquera M, Vergès JM. 2010 What novice knappers have to learn to become expert stone toolmakers. *J. Archaeol. Sci*. **37**, 2857–2870. (doi:10.1016/j.jas.2010.06.026)
19. Roux V. 2007 Ethnoarchaeology: a non historical science of reference necessary for interpreting the past. *J. Archaeol. Method Theory* **14**, 153–178. (doi:10.1007/s10816-007-9030-8)
20. Wynn T, Hernandez-Aguilar RA, Marchant LF, McGrew WC. 2011 'An ape's view of the Oldowan' revisited. *Evol. Anthropol. Issues News Rev*. **20**, 181–197. (doi:10.1002/evan.20323)
21. Boesch C. 1991 Handedness in wild chimpanzees. *Int. J. Primatol*. **12**, 541–558. (doi:10.1007/BF02547669)
22. Inoue-Nakamura N, Matsuzawa T. 1997 Development of stone tool use by wild chimpanzees (*Pan troglodytes*). *J. Comp. Psychol*. **111**, 159. (doi:10.1037/0735-7036.111.2.159)
23. Sugiyama Y. 1993 Local variation of tools and tool use among wild chimpanzee populations. In *The use of tools by human and non-human primates* (eds A Berthelet, J Chavaillon), pp. 175–187. Oxford, UK: Clarendon Press.
24. Boesch C, Boesch H. 1993 Diversity of tool use and tool-making in wild chimpanzees. In *The use of tools by human and non-human primates* (eds A Berthelet, J Chavaillon), pp. 158–174. Oxford, UK: Clarendon Press.
25. Davidson I, McGrew WC. 2005 Stone tools and the uniqueness of human culture. *J. R. Anthropol. Inst*. **11**, 793–817. (doi:10.1111/j.1467-9655.2005.00262.x)
26. Marchant LF, McGrew WC. 2005 Percussive technology: chimpanzee baobab smashing and the evolutionary modelling of hominin knapping. In *Stone knapping: the necessary conditions for a uniquely hominin behavior* (eds V Roux, B Bril), pp. 341–350. Cambridge, UK: McDonald Institute for Archaeological Research.
27. Sugiyama Y, Koman J. 1979 Tool-using and -making behavior in wild chimpanzees at Bossou, Guinea. *Primates* **20**, 513–524.
28. Wynn T, McGrew WC. 1989 An ape's view of the Oldowan. *Man* **24**, 383–398. (doi:10.2307/2802697)
29. Joulian F. 1996 Comparing chimpanzee and early hominid techniques: some contributions to cultural and cognitive questions. In *Modeling the early human mind* (eds PA Mellars, K Gibson), pp. 173–189. Cambridge, UK: McDonald Institute for Archaeological Research.
30. Wynn T. 2002 Archaeology and cognitive evolution. *Behav. Brain Sci*. **25**, 389–402; discussion 403–438. (doi:10.1017/S0140525X02000079)
31. Byrne DS. 2004 The manual skills and cognition that lie behind hominid tool use. In *Evolution of thought—evolutionary origins of great ape intelligence* (eds AE Russon, DR Begun), pp. 31–44. Cambridge, UK: Cambridge University Press.
32. Pelegrin J. 2005 Remarks about archaeological techniques and methods of knapping: elements of a cognitive approach to stone knapping. In *Stone knapping, the necessary conditions for a uniquely hominid behaviour* (eds V Roux, B Bril), pp. 23–34. Cambridge, UK: McDonald Institute for Archaeological Research.
33. Roche H. 2005 From simple flaking to shaping: stone-knapping evolution among early hominins. In *Stone knapping: the necessary conditions for a uniquely hominin behaviour* (eds V Roux, B Bril), pp. 35–48. Cambridge, UK: McDonald Institute for Archaeological Research.
34. Bril B, Roux V (eds). 2005 *Stone knapping: the necessary conditions for a uniquely hominin behaviour*. Cambridge, UK: McDonald Institute for Archaeological Research.
35. Toth N, Schick K, Semaw S. 2006 A comparative study of the stone tool-making skills *Pan*, *Australopithecus*, and *Homo sapiens*. In *The Oldowan: case studies into the earliest Stone Age* (eds N Toth, KD Schick), pp. 155–222. Gosport, IN: Stone Age Institute Press.
36. De la Torre I. 2011 The origins of stone tool technology in Africa: a historical perspective. *Phil. Trans. R. Soc. B* **366**, 1028–1037. (doi:10.1098/rstb.2010.0350)
37. Bril B, Rein R, Nonaka T, Wenban-Smith F, Dietrich G. 2010 The role of expertise in tool use: skill differences in functional action adaptations to task constraints. *J. Exp. Psychol. Hum. Percept. Perform*. **36**, 825–839. (doi:10.1037/a0018171)
38. Nonaka T, Bril B, Rein R. 2010 How do stone knappers predict and control the outcome of flaking? Implications for understanding early stone tool technology. *J. Hum. Evol*. **59**, 155–167. (doi:10.1016/j.jhevol.2010.04.006)
39. Dibble HL, Rezek Z. 2009 Introducing a new experimental design for controlled studies of flake formation: results for exterior platform angle, platform depth, angle of blow, velocity, and force. *J. Archaeol. Sci*. **36**, 1945–1954. (doi:10.1016/j.jas.2009.05.004)
40. Rein R, Nonaka T, Bril B, Steele J. In preparation. It takes two hands to knap a stone: manual specialisation, bimanual coordination, handedness and hominin evolution.

41. Marzke MW, Shackley MS. 1986 Hominid hand use in the Pliocene and Pleistocene: evidence from experimental archaeology and comparative morphology. *J. Hum. Evol*. **15**, 439–460. (doi:10.1016/S0047-2484(86)80027-6)
42. Marzke MW. 1997 Precision grips, hand morphology, and tools. *Am. J. Phys. Anthropol*. **102**, 91–110. (doi:10.1002/(SICI)1096-8644(199701)102:1<91::AID-AJPA8>3.0.CO;2-G)
43. Johnson-Frey SH. 2004 The neural bases of complex tool use in humans. *Trends Cogn. Sci*. **8**, 71–78. (doi:10.1016/j.tics.2003.12.002)
44. Osiurak F, Jarry C, Allain P, Aubin G, Etcharry-Bouyx F, Richard I, Bernard I, Le Gall D. 2009 Unusual use of objects after unilateral brain damage: the technical reasoning model. *Cortex J. Devoted Study Nerv. Syst. Behav*. **45**, 769–783. (doi:10.1016/j.cortex.2008.06.013)
45. Goldenberg G, Spatt J. 2009 The neural basis of tool use. *Brain* **132**, 1645–1655. (doi:10.1093/brain/awp080)
46. Chiel HJ, Beer RD. 1997 The brain has a body: adaptive behavior emerges from interactions of nervous system, body and environment. *Trends Neurosci*. **20**, 553–557. (doi:10.1016/S0166-2236(97)01149-1)
47. Gibson JJ. 1986 *The ecological approach to visual perception*. New York, NY: Psychology Press.
48. Kelso S. 1997 *Dynamic patterns—the self-organisation of brain & behaviour*. Cambridge, MA: MIT Press.
49. Thelen E, Smith LB. 1996 *A dynamic systems approach to the development of cognition and action*. Cambridge, MA: MIT Press.
50. Bernstein NA. 1967 *The co-ordination and regulation of movements*. Oxford, UK: Pergamon Press.
51. Newell KM. 1986 Constraints on the development of coordination. In *Motor development in children: aspects of coordination and control* (eds MG Wade, HTA Whiting), pp. 341–361. Amsterdam, The Netherlands: Martinus Nijhoff.
52. Newell KM. 1996 Change in movement and skill: learning, retention, and transfer. In *Dexterity and its development* (eds M Latash, M Turvey), pp. 393–429. Marwah, NJ: Lawrence Erlbaum Associates.
53. Davids K, Araújo D, Hristovski R, Passos P, Chow J. 2012 Ecological dynamics and motor learning design in sport. In *Skill acquisition in sport: research, theory and practice* (eds NJ Hodges, MA Williams), pp. 112–130. London, UK: Routledge.
54. Parry R, Dietrich G, Bril B. 2014 Tool use ability depends on understanding of functional dynamics and not specific joint contribution profiles. *Front. Psychol*. **5**, 306. (doi:10.3389/fpsyg.2014.00306)
55. Bril B, Dietrich G, Foucart J, Fuwa K, Hirata S. 2009 Tool use as a way to assess cognition: how do captive chimpanzees handle the weight of the hammer when cracking a nut? *Anim. Cogn*. **12**, 217–235. (doi:10.1007/s10071-008-0184-x)
56. Hirata S, Morimura N, Houki C. 2009 How to crack nuts: acquisition process in captive chimpanzees (*Pan troglodytes*) observing a model. *Anim. Cogn*. **12**, 87–101. (doi:10.1007/s10071-009-0275-3)
57. Hirata S, Hayashi M. 2011 The emergence of stone-tool use in captive chimpanzees. In *The chimpanzees of Bossou and Nimba* (eds T Matsuzawa, T Humle, Y Sugiyama), pp. 183–190. Tokyo, Japan: Springer.
58. Feix T, Pawlik R, Schiedmayer H, Romero J, Kragić D. 2009 A comprehensive grasp taxonomy. In *Robotics, Science and Systems: Workshop on Understanding the Human Hand for Advancing Robotic Manipulation*, pp. 2–3.
59. Sainburg R. 2002 Evidence for a dynamic-dominance hypothesis of handedness. *Exp. Brain Res*. **142**, 241–258. (doi:10.1007/s00221-001-0913-8)
60. Uomini NT. 2009 The prehistory of handedness: archaeological data and comparative ethology. *J. Hum. Evol*. **57**, 411–419. (doi:10.1016/j.jhevol.2009.02.012)
61. Faisal A, Stout D, Apel J, Bradley B. 2010 The manipulative complexity of Lower Paleolithic stone toolmaking. *PLoS ONE* **5**, e13718. (doi:10.1371/journal.pone.0013718)
62. Nonaka T, Bril B. 2012 Nesting of asymmetric functions in skilled bimanual action: dynamics of hammering behavior of bead craftsmen. *Hum. Mov. Sci*. **31**, 55–77. (doi:10.1016/j.humov.2010.08.013)
63. Goren-Inbar N, Sharon G, Melamed Y, Kislev M. 2002 Nuts, nut-cracking, and pitted stones at Gesher Benot Ya'aqov, Israel. *Proc. Natl Acad. Sci. USA* **99**, 2455–2460. (doi:10.1073/pnas.032570499)
64. Yustos PS, Diez-Martín F, Díaz IM, Duque J, Fraile C, Domínguez M. 2015 Production and use of percussive stone tools in the Early Stone Age: experimental approach to the lithic record of Olduvai Gorge, Tanzania. *J. Archaeol. Sci. Rep*. **2**, 367–383. (doi:10.1016/j.jasrep.2015.03.005)
65. Gurtov AN, Eren MI. 2014 Lower Paleolithic bipolar reduction and hominin selection of quartz at Olduvai Gorge, Tanzania: what's the connection? *Quat. Int*. **322–323**, 285–291. (doi:10.1016/j.quaint.2013.08.010)
66. Diez-Martín F, Sánchez P, Domínguez-Rodrigo M, Mabulla A, Barba R. 2009 Were Olduvai hominins making butchering tools or battering tools? Analysis of a recently excavated lithic assemblage from BK (Bed II, Olduvai Gorge, Tanzania). *J. Anthropol. Archaeol*. **28**, 274–289. (doi:10.1016/j.jaa.2009.03.001)
67. Diez-Martín F, Yustos P, Domínguez-Rodrigo M, Prendergast M. 2011 An experimental study of bipolar and freehand knapping of Naibor Soit quartz from Olduvai Gorge (Tanzania). *Am. Antiq*. **76**, 690–708. (doi:10.7183/0002-7316.76.4.690)
68. Foucart J. 2006 Etude comparée des habiletés opératoires et motrices de l'homme et du chimpanzé pour une utilisation d'outils transprimatique: le cassage de noix. PhD thesis, Ecole des Hautes Etudes en Sciences Sociales, Paris.
69. Bril B, Foucart J. 2005 Enacting the perception of the affordances of potential tools. I: the case of children hammering. In *Studies in perception and action* (eds H Heft, KL Marsh), pp. 1–4. Marwah, NJ: Lawrence Erlbaum Associates.
70. De La Pena Alonso P, Gerardo Vega Toscano L. 2013 Bipolar knapping in Gravettian occupations at el Palomar rockshelter (Yeste, Southeastern Spain). *J. Anthropol. Res*. **69**, 33–64. (doi:10.3998/jar.0521004.0069.103)
71. Eren MI, Diez-Martin F, Dominguez-Rodrigo M. 2013 An empirical test of the relative frequency of bipolar reduction in Beds VI V, and III at Mumba Rockshelter, Tanzania: implications for the East African Middle to Late Stone Age transition. *J. Archaeol. Sci*. **40**, 248–256. (doi:10.1016/j.jas.2012.08.012)
72. Hayden B. 2015 Insights into early lithic technologies from ethnography. *Phil. Trans. R. Soc. B* **370**, 20140356. (doi:10.1098/rstb.2014.0356)