Hand grip diversity and frequency during the use of Lower Palaeolithic stone cutting-tools

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Abstract

The suite of anatomical features contributing to the unique gripping capabilities of the modern human hand evolved alongside the proliferation of Lower Palaeolithic flaked tool technologies across the Old World. Experimental studies investigating their potential co-evolution suggest that the use of flakes, handaxes, and other stone tools is facilitated by manipulative capabilities consistent with the evolutionary trajectory of the hominin hand during this period. Grip analyses have provided important contributions to this understanding. To date, however, there has been no large-scale investigation of grip diversity during flaked stone-tool use, empirical comparative analyses of grip use frequencies, or examination of ergonomic relationships between grip choice and stone tool type and form.

Here, we conduct four experimental studies, using replica Lower Palaeolithic stone tools in a series of actualistic and laboratory-based contexts, to record grip type and frequency of grip use during 1067 stone tool-use events by 123 individuals. Using detailed morphometric data recorded from each tool, we demonstrate how grip choice varies according to the type and form of stone tool used, and how these relationships differ between tool-use contexts. We identify 29 grip types across all tool-use events, with significant differences recorded in their frequency of use dependent on tool type, tool form, and the context of use. Despite the influence of these three factors, there is consistency in the frequent use of a limited number (≤4) of grip types within each experiment and the consistent and seemingly forceful recruitment of the thumb and index finger. Accordingly, we argue that there are deep-rooted, ergonomically-related, regularities in how stone tools are gripped during their use, that these regularities may have been present during the use of stone tools by Plio-Pleistocene hominins, and any subsequent selective pressures would likely have been focused on the first and second digit.

Keywords: Manipulation; Stone Tool Variation; Flake; Handaxe; Hominin; Hand Evolution

1. Introduction

The modern human hand is known for its high degree of dexterity. The human hand's ability to forcefully and precisely manipulate and rotate objects using pad-to-pad precision grips between the thumb and fingers is unrivalled amongst other extant primates (Marzke and Wullstein, 1996; Marzke, 1997; Pouydebat et al., 2011; Kivell, 2015; Marzke et al., 2015). The morphological features associated with these manipulative abilities are thought to have evolved in response to increasingly complex tool-related behaviours throughout hominin evolution (e.g Susman, 1998; Tocheri et al. 2008; Marzke, 1997, 2013; Kivell, 2015; but see Almecija et al. 2010; 2015). Fossil evidence indicates that although these manipulative abilities likely evolved in a complex, heterogeneous manner, hominin taxa generally display morphological features of the hand interpreted as reducing the capacity for arboreal locomotion and increasing manipulative capabilities over the past ~4 million years (Tocheri et al., 2008; Marzke, 2013; Kivell, 2015; Trinkaus, 2016; but see Kivell et al., 2015).

The first flaked stone technologies appear in the archaeological record from as early as ~3.3 million years ago (Mya) and from ~2.6 Mya there is both an increased relative abundance of stone tool artefacts, first across Africa and then the remainder of the Old World, and a series of chronologically-demarcated developments in lithic technology (Lycett and Gowlett, 2008; Rogers and Semaw, 2009; Semaw et al., 2009; Tryon and Faith, 2013; Harmand et al., 2015; Proffitt, in press). In particular, Oldowan flake and core technologies (~2.6-1.7 Mya) and Acheulean large cutting tools (LCTs), such as handaxes and cleavers (~1.75-0.3 Mya), characterise over two million years of the archaeological record. Flakes, cores, and LCTs were the principal flaked stone technologies produced by hominin populations during the Lower Palaeolithic, and were thus likely to have contributed to selective pressures acting on the hominin hand during this period. Although stone-tool related activities were not the only selective force acting on the hominin hand (e.g., bone tool use, non-modified tool-related activities, arboreal locomotion [Blackwell and d'Errico, 2008; Kivell, 2015; Williams-Hatala et al. 2018]), all three tool types have evidence supporting their use during activities that plausibly would have influenced the survival and reproductive success of Lower Palaeolithic hominins (Key and Lycett, 2017a); although the extent that cores were used is debated (Toth, 1985).

To understand how the production and use of stone tools during the Lower Palaeolithic may have influenced the evolution of the hominin hand, it is necessary to understand the relationship between anatomy and behaviour. The pursuit of an understanding of these relationships has taken many forms, including kinematic (Faisal et al., 2010; Williams et al., 2010), electromyographic (Hamrick et al., 1998; Marzke et al., 1998), pressure and/or force distribution (Rolian et al., 2011; Williams et al., 2012; Key and Dunmore, 2015) and biometric (Key and Lycett, 2011, in press) analyses. However, perhaps the most established analytical technique is the investigation of grip use during stone tool-related behaviours; that is, the analysis of the relative position of the digits and palm in relation to each other and the object (Napier, 1956; Landsmeer, 1962; Toth et al. 1992; Marzke et al. 1992; Marzke and

Shackley, 1986; Marzke and Wullstein, 1996; Pouydebat et al. 2011; Bardo et al. 2017). In the absence of being able to directly observe hominin manipulative behaviour, we suggest that if the grips associated with the use of Palaeolithic stone technologies are consistent with the unique manipulative capabilities of the human hand and the underlying anatomy, then it is reasonable to propose that stone tool-related behaviours may have provided the necessary selective pressures contributing to the evolution of these adaptations in hominins.

Napier (1955, 1956, 1962, 1980) was amongst the first to define different human grips, identifying distinctions between ‘power’ and ‘precision’ grips and the associated anatomical features. Precision grips were described as when “the object may be pinched between the flexor aspects of the fingers and the opposing thumb,” while power grips were described as when “the object may be held in a clamp formed by the partly flexed fingers and the palm, counter pressure being applied by the thumb lying more or less in the plane of the palm” (Napier, 1956: 903). These two basic manipulative patterns have permeated through anthropological studies of gripping, with Napier (1962, 1980) himself linking the evolution of these capabilities with stone-tool use and production.

Marzke and colleagues refined the definition of ‘precision grip’ and galvanised the importance of understanding how Palaeolithic tool-related behaviours, and their associated grip requirements, may inform our understanding of how the human hand evolved (Marzke 1983, 1997, 2013; Marzke and Shackley, 1986; Marzke and Wullstein, 1996). Using precision and power grip definitions provided by Long (Long et al., 1970; Long, 1981), Marzke (1983) was one of the first to suggest direct links between hand morphology and the ability of extinct hominins (*Australopithecus afarensis*, in this case) to perform pad-to-side and three-jaw chuck grips to manipulate flake stone tools and hammerstones, respectively (Table 1). Marzke and Shackley (1986: 440) went on to experimentally demonstrate there to be an “important interaction between the evolution of the hominid hand and the use of stone tools.” Furthermore, Marzke and Shackley (1986) identified problems associated with the power and precision grip distinctions described by Napier (1956), particularly when applied to stone-tool use and production; principally because the grips they observed incorporated elements of both. New grip classifications and definitions outlined by Marzke and colleagues (Marzke and Shackley, 1986; Marzke and Wullstein, 1996; Marzke, 1997; Marzke et al., 2009) have since gone on to inform the last 30 years of discussion regarding stone tool-related grips (Table 1). Further, these studies suggest that just three forceful precision grips –‘buttressed pad-to-side’, ‘extended three-jaw chuck’, and ‘cradle’ grips, which are depicted in Figure 1 – characterise the majority of grips used during stone tool production and use (Marzke, 1997, 2013; Marzke et al., 1998; Marzke and Marzke, 2000; Marzke et al., 2009).

INSERT FIGURE 1 ABOUT HERE

Comparative studies of object manipulation in humans and other primates have highlighted the challenges of accurately describing and recording differences in hand grips (Christel, 1993; Christel et al. 1998; Pouydebat et al., 2008, 2011; Bardo et al., 2016; Neufuss et al., 2016). Marzke and colleagues (2009) helped to highlight these issues and clarify precision grip terminology, while Borel and colleagues (2017) have since trialled a video-based classification technique for identifying which areas of the hand contact tools during their use. Together, we now have a better understanding of the complexities of gripping and the challenges faced when systematically quantifying stone-tool related manual activities.

To date, however, there has yet to be a large-scale analysis of the hand grips employed during stone tool-use, an empirical analysis of the frequency with which different grips are utilised, or an analysis of the ergonomic relationships between grip choice and variation in tool type and form. Previous experimental research, which has formed the critical foundation for this study, has also been limited in the number of participants investigated (often ≤5; Marzke and Shackley, 1986; Marzke, 1997; Borel et al., 2017), which may obscure the potential variation in grips used. A large-scale experimental study of grip diversity and frequency will allow adequate assessment of potential inter-individual variation and analysis of which grips (and, in turn, manipulative capabilities) are central to the effective use of stone tools. Such results can inform our understanding of the potential selective pressures acting on hominin hand anatomy, and how such selective pressures may vary depending on the type and form of stone tool being used.

We conducted a series of three laboratory-based experiments and one actualistic experiment with participants (n=123 individuals) using replica Lower Palaeolithic stone tools to cut a diverse range of materials (i.e. different tool use contexts). We recorded the hand grips used throughout each tool-use event to examine the diversity and relative frequency of grips and how this relates to the type (e.g. flake, handaxe) and form (e.g. mass, shape) of stone tool used. The laboratory-based experiments provide conditions displaying high internal validity and allow variables to be standardised across participants, while the actualistic animal butchery experiment better replicates the conditions of Palaeolithic tool use and, in turn, displays greater external validity (i.e., the extent to which the results are applicable to Palaeolithic situations) (Lycett and Eren, 2013; Eren et al., 2016). Based on previous literature (Marzke and Shackley, 1986; Marzke, 1997, 2013), we predict that forceful precision grips will represent the majority of recorded hand positions and will most commonly be categorised as 'buttressed pad-to-side', 'extended three-jaw chuck', and 'cradle' grips (Fig. 1). Moreover, we hypothesise that the most frequently observed grips will be facilitated by derived biomechanical conditions and anatomical traits observed in the modern human hand, particularly those of the thumb, index finger, and middle finger (e.g. a robust thumb, a proximodistal orientation to the radial carpometacarpal joints, third metacarpal styloid process; Marzke, 1997; Tocheri et al. 2008). Given the significant impact tool type, form and context of use can have on stone tool cutting performance and loading requirements (e.g. Jobson, 1986; Jones, 1994; Key and Lycett, 2014, 2017b, 2017c), we also predict there to be a strong correlation between the grips used by participants and these three independent variables.

2. Methods

The analyses presented here investigate grip use in four distinct experiments that were initially undertaken for archaeological purposes (either to investigate the functional consequences of stone tool form variation or the production of cut marks on bones during butchery). For each experiment, all tool-use events were recorded with a digital video camera and detailed metrics pertaining to the form of each stone tool used were recorded. Although permissions were sought to record tool-use events, all were undertaken without the participant's or investigator's prior knowledge that the videos would be used for hand grip analyses; in turn, we are confident that the participants were not intentionally or unintentionally altering their grips to bias the results. All experiments were conducted after ethical approval from the University of Kent (Experiments 1-3) and Rutgers University (Experiment 4). All participants for Experiments 1-3 were recruited from students and staff at the University of Kent, and most had limited experience using stone tools. Each participant gave informed consent prior to participating and confirmed that they had no pre-existing conditions that may impede their use of the tools.

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Experiment 1: Flakes

Experiment 1 included 33 female and 24 male (n = 57 in total) participants that each used six replica flake stone tools to cut through a segment of hessian rope secured to a wooden platform (Fig. 2). Each participant was provided with a flint flake from six size-controlled groups (Table 2), with within-group size variation never exceeding 5mm (Fig. 3). The smallest flake tools averaged 29.2mm in length and sizes increased by ~15mm until the largest flake groups averaged 103mm in length (n = 342 flakes in total). These flake categories principally address the hypothesis of how stone tool size variation influences grip choice. The six flakes were used in a randomly assigned order (determined using www.randomizer.org; this randomization method is replicated in all experiments detailed here), with 3 minute breaks being enforced between the use of each tool.

Each flake was used to cut through a 10mm thick piece of hessian rope once only and participants were instructed to use their dominant hand in all instances. All participants were seated in front of a table, on which the wooden platform, to which the taut rope was secured, was placed. Each flake was typically used for 5-15 seconds. Video records were taken from the left of participants and in-line with the hand as it used a flake (Fig. 2). Further methodological details and justification can be found in the associated published article (Key and Lycett, 2014) and the attached supplementary information (Supplementary Information 1).

Experiment 2: Handaxes

Experiment 2 included five male participants and used 500 replica flint handaxes displaying considerable variation in their shape and size. Each handaxe was used during a contextually varied (materials and cutting dynamics) but standardised cutting task (Fig. 4). The tools were purposefully produced to display considerable morphological variation, with some going beyond forms typically observed in the archaeological record (Table 2; Fig. 3; Gowlett [2015]). Mass, for example, ranged between 8-4484g. Although highly variable, the extremes of the replica assemblage conform with rare examples from the archaeological record (e.g. Barkai et al., 2013), and were utilized to push the ranges of grip variation observed. This tool-form variation allowed assessment of the influence of multiple morphological attributes on grip choice. Each participant was randomly assigned 100 handaxes, which were in turn, used in a randomly assigned order. Participants used 10-15 handaxes per experimental session (undertaking 7-10 tool-use sessions in total), with a minimum rest period of 5 minutes separating the use of each tool.

The task consisted of cutting 16 segments of material that were standardised across participants. In total, 11 lengths of double-ply cardboard, two strips of neoprene, and three lengths of 6mm thick polypropylene rope were required to be cut. All segments of material were attached to a wooden frame that supported the material, keeping it taut and allowing for varied and dynamic cutting actions (Fig. 4). The frame was positioned on the floor and participants undertook the task when kneeling. Durations of tool-use varied depending on the handaxe being used, but typically ranged between 1-3 minutes. Due to health and safety concerns, the five participants were required to wear a synthetic leather glove on their dominant tool-using hand, although the distal aspects of the glove's fingers (from the proximal interphalangeal joint) were cut off so that there was direct contact between the tool and distal ends of the digits. It is unlikely that the modified glove significantly influenced grip choice as ergonomic requirements to resist forces through specific aspects of the palm and proximal phalanxes, in response to a tool's morphology and cutting motion, would have remained constant. Video records were taken from the right of participants, at a distance of 1-3 meters, and were from a superior angle of ~35-45˚relative to the tool-using hand (Fig. 4). Further methodological details and justification have been published by Key and colleagues (Key et al. 2016; Key and Lycett 2017b) and can be found in the attached supplementary information (Supplementary Information 1).

INSERT FIGURE 4 ABOUT HERE

Experiment 3: Flakes, Handaxes, and 'Lomekwian-sized' Flakes

Experiment 3 included 38 female and 22 male (n = 60 in total) participants and used 60 'standard' flake tools, 60 handaxes, and 60 large 'Lomekwian-sized' flakes (Harmand et al., 2015) produced from British flint. The Lomekwian-sized flakes were of equal size and mass to the handaxes (Table 2; Fig. 3). Each participant was randomly assigned one tool from each tool-type category. The order in which the three tools were used was also randomized for each participant and a 10-minute rest period was enforced between each tool-use event. Experiment 3 principally tests the effect that stone tool type variation and context of use has on grip choice during cutting activities.

While standing, participants were required to use each tool to cut standardised lengths of polythene (wrapped around clay), cardboard, and hessian rope (all of which were secured on a table; Fig. 5). Each type of material had six identical sections that were undertaken in sequential order across the three tasks. For example, polythene section one was followed by cardboard section one and then rope section one, before participants moved onto polythene section two, cardboard section two and rope section two; this was repeated six times. Each tool was typically used for 4-5 minutes in total. Tool-users were instructed to grip the tools with their dominant hand. Video records were taken from in front of the participants, at a distance of ~1m and were from a superior angle relative to the tool using hand (Fig. 5). Further methodological details and justification are published in Key and Lycett (2017c) and have been provided in the attached supplementary information (Supplementary Information 1).

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Experiment 4: Flakes and Cores

Experiment 4 consisted of a series of butchery events undertaken by a single skilled Dassanech pastoralist from Ileret, Kenya. In total, the butcher used 15 flake and 13 core tools during the disarticulation and defleshing of six cow and seven goat carcasses purchased from the Dassanech (Fig. 6). Each tool was used to either disarticulate or deflesh a single fore- or hind limb from one of the carcasses, although some tools were used to deflesh or disarticulate two limbs (each limb is recorded here separately and, therefore, the total number of tool-use events in this experiment is 23 flakes and 22 cores). A single flake tool was used to deflesh a goat ribcage. In total, 45 tool-use events were recorded. Both the flake and core tools varied in size and raw material (primarily chert, phonolite, and chalcedony from modern gravel beds, but these materials are also common in Plio-Pleistocene deposits at Koobi Fora, Kenya); all were chosen by the butcher from a selection of tools provided to him (Table 2).

Each butchery (tool-use) event lasted between 5-30 minutes. Defleshing typically involved the severance of tendons and connective tissue attaching muscles to bone, and cutting through fat, muscle fibres and connective tissues. Disarticulation included the severance of ligaments, tendons, and joint capsule tissues within the tarsal and stifle joints. All cow butchery activities were undertaken on the ground, while those concerning the goat were split between being conducted on the ground or the carcass being suspended from a tree (Fig. 6). The Dassanech man undertaking the disarticulation and defleshing was experienced in livestock butchery with both metal knives and lithic tools, including unmodified flakes made from cryptocrystalline silicate materials like chalcedony and chert (principally to process animal carcasses when knives were not available). Video records were usually taken from a superior position, although there was considerable variation in the angle and positioning of the camera as butchery events proceeded. Further methodological details on the butchery activities can be found in Merritt (2012, 2016).

INSERT FIGURE 6 ABOUT HERE

2.1 Tool Use Contexts

Experiments one, two and three utilised modern, industrially-produced materials that were not cut or modified within Lower Palaeolithic tool use contexts. As previously highlighted in both engineering and archaeological research (e.g. McCarthy et al., 2007; Sisk and Shea, 2009; Schuldt et al., 2016; Key et al. 2018; Werner et al., in press), use of modern synthetic materials as an alternative to organic biomaterials (e.g., meat, wood or bone) when investigating cutting processes (including projectile tests) can have substantive methodological and ethical benefits.

Here, rope, cardboard, neoprene and polythene segments were required to be modified with stone tools using a number of different types of cutting and upper limb motions (Supplementary Information 1). A key benefit provided by these materials is the ability to easily source and standardise experimental conditions across participants, and, in turn, more precisely allow any variation in grip choice to be determined by the variables under consideration (e.g. tool form variation). As such, the interval validity of the results increases (Lycett and Eren, 2013; Eren et al., 2016). In addition, the use of these materials allows the physical properties of materials to be controlled such that those of varying resistance, depth and form were guaranteed to be cut, allowing reliable and replicable discussion on how the context of a tools use may influence grip choice. The materials used in Experiments 1-3 can, at a general level, be divided into those requiring forceful and relatively inaccurate cutting motions, where substantial lengths of material are required to be cut (i.e., the cardboard), and those requiring more precise cutting motions being applied repeatedly (localised cutting) on more limited material volumes (i.e., rope/neoprene strips). These materials do not specifically represent butchery or plant processing events, for example, but rather characterise a series of unique and replicable cutting conditions that present variable and known material contexts to a stone tool's cutting edge. Certainly, the actualistic tool use conditions presented in Experiment 4 were more varied, even within specific butchery events (e.g. defleshing of goat hind limbs). Finally, the tasks presented in these experiments do not require any prior knowledge or skill, with the cultural knowledge and manipulative abilities underpinning these cutting tasks already being present in the modern human participant sample (via the use of metal knives). Therefore, an absence of required skill, knowledge or technical ability is unlikely to influence the ergonomic relationships under investigation. It is also useful to emphasise that actualistic experiments on the scale of those presented here (e.g. n = 500) are often not practical, ethical or robust in their conclusions. For example, Machin et al. (2007) conducted some of the most substantial actualistic stone-tool use experiment to date, and yet the authors were open about the ambiguity of the results and identified a number of methodological and material limitations.

The majority of cutting behaviours in Experiments 1-3 were slicing or sawing actions, whereby a tool's edge is drawn longitudinally across a material while simultaneously providing force into the cut substrate (Key, 2016). Further, cutting actions were required in multiple angular, horizontal and vertical plains, thereby more accurately replicating varied actualistic conditions (particularly in Experiments 2 and 3). Although the majority of cutting actions undertaken during Experiment 4 (i.e. animal butchery) were similar cutting actions, it is important to note that tool use conditions in the laboratory-based experiments likely presented a more limited range of cutting motions. Moreover, our experiments do not consider other types of cutting actions, such as scraping, drilling and digging, or percussive stone tool activities, which also may have been key tool-use behaviours in the Lower Palaeolithic (Leakey, 1950; Shea, 2007; Rots et al., 2015) and may elicit alternative grips.

2.2 Grip Analyses

Table 1 provides an overview of previous methods used to describe hand grips during anthropological studies of humans manipulating objects, including stone tools. Here we follow similar procedures to those used elsewhere (e.g. Marzke and Wullstein, 1996; Neufuss et al., 2016) and define a series of grip classifications dependent on the number of digits recruited, the position of the digits relative to each other and the tool, the recruitment of the palm, and the inferred direction of load applied by the digits and palm. Where possible, we have used terminology and definitions consistent with those used by Marzke and colleagues (Marzke and Shackley, 1986; Marzke and Wullstein, 1996; Marzke, 1997; Marzke et al., 2009). In part, this will allow renewed assessment of these classic stone tool-related grip definitions, but it also works to promote consistency within the literature (*c.f.* Marzke et al., 2009).

Principally, grip types are defined relative to the positioning of the thumb, index and middle finger and the tool, with additional sub-types dependent on the total number of digits employed and whether the palm and metacarpal heads are actively recruited. Although there were a few instances in which two hands were used to manipulate the stone tools (see Discussion), all analyses presented here relate to the dominant hand. Grip classifications were defined on a cumulative video-by-video basis, where each grip was identified and recorded on the first occasion that it was observed. Subsequent to a grip being identified and defined, every time that it was used by a participant it was easily identifiable and recordable. Experiments 1 through 4 were examined in a sequential order. Each grip was assigned a two-digit numerical code reflecting the number of digits recruited and their relative positioning. For example, in the grip code 3.5 the first number (3) indicates that three digits were used and the second number (5) indicates the type of grip, in this case a buttressed pad-to-side grip (i.e., a three jaw buttressed pad to side grip). Grips recruiting all five digits and the palm were coded with a '6'.

INSERT FIGURE 7 ABOUT HERE

Once a grip was identified, the duration of its use was recorded in seconds. Time records only included periods that a tool was actively applied to cutting tasks and excluded pauses due to inactivity and tool or body readjustment. If a tool was used with a specific grip before being readjusted and used once again with the same grip, then this counted as the use of a single grip and the two time records were combined. In turn, for every tool-use event it was possible to produce a clear sequence of when different grips were used, and the length of time that each was used for. In some cases, it was difficult to see the complete grip at a given video frame but the grip could be confidently identified after watching several video frames and it was clear that the hand had not changed position. Further, any movement of digits or the tool when readjusting and applying a new grip were relatively easily identified and provided clear signals that may indicate the use of a new grip (often this included a pause in any cutting actions). If it was not clear which grip was being employed by a tool-user, then a note of 'not visible' was recorded for the relevant length of time that this occurred. All videos were analysed by AK. To test inter-observer error, a random sample of 44 videos from across all four experiments were reanalysed by TLK. Time records and grip classification records were consistent between the two analysts, although some variation was noted in the recruitment of digits 3, 4 and 5 due to visual limitations associated with only having one view of the tool-use activities. Although the recruitment of digits 3-5 were often clearly visible, or their recruitment could be inferred by their relative distance from the tool (e.g. in Fig. 2b, digits 4 and 5 are clearly separated from the tool, despite only their proximal phalanx being visible to the camera), the analysis undertaken here was limited in some instances by having only a single camera angle (also see the Discussion).

2.3 Data Analysis

Analysis of each tool-use event provided a record of the grips used to manipulate the stone tool, how long individual grips were used, and a total overall record of how long each tool-use event lasted. Given that individual tools were used for varying lengths of time due to external variables, such as biometric differences across participants or differing tool-use contexts (Key and Lycett, 2011, 2017c, in press; Merritt, 2012, 2016), it was not always possible to directly compare time records across different tool types and forms. Therefore, we calculated an additional variable, 'Percentage of Use' (PoU), which was the percentage of time that a specific hand grip was used relative to the overall time record for which that tool was used. For example, if only one grip was recorded during a tool-use event, then the respective grip would have a PoU value of 100%. However, if that grip was only used for 20 seconds of a 60-second-long cutting task, then it would have a percentage of use value of 33.33%. PoU values therefore provided a useful way to gauge the relative importance of each individual grip type without potential bias of variation in the duration of a tool-use event.

Comparisons across Tool-Use Contexts

There are clear differences between Experiments 1-3 and 4 insofar as the latter represents an actualistic butchery experiment and the former three are more controlled, laboratory-based cutting tasks. Further, there are differences in the materials cut across all of the experiments. To explore the potential for variation in experimental context to influence grip use, the PoU values for each grip within the same tool types (e.g. handaxes, flakes) across Experiments 1-4 were compared. First, records of which grip types were recruited during each experiment were detailed in order of their PoU at a whole experiment level (i.e. the percentage of time that a grip was used across all tool-use events in a particular experiment). This provided a general overview of any similarities of differences in the grips used by participants across the four different experiments.

Subsequently, Mann-Whitney U tests were used to investigate whether there were significant differences in the PoU values for specific grip types between experiments. Comparisons were independently undertaken for flake tools and handaxes/core tools using grips with PoU values greater than 10% during any of the experiments. Thus, for flake tools, grip types with a PoU value >10% were compared between Experiments 1 and 3, Experiments 1 and 4, and Experiments 3 and 4. A Bonferroni correction was applied such that $\alpha = .001$ (here and elsewhere in the text, this is achieved by dividing an assumed significant at .05 by the number of statistical tests run per null hypothesis). For handaxes and cores, hand grips with a PoU values of >10% were compared between Experiments 2 (handaxes) and 3 (handaxes), Experiments 2 (handaxes) and 4 (cores), and Experiments 3 (handaxes) and 4 (cores). A Bonferroni correction was applied such that $\alpha = .0083$.

Comparisons across Stone Tool Types

In addition to the potential influence of the different materials cut across the tool-use experiments, there is potential for differences in grip use to arise as a result of the type of stone tool being used. Experiments 3 and 4 provide useful opportunities to compare across grips dependent on the type of stone tool used while cutting identical (Experiment 3), or near-identical (Experiment 4), materials. Mann-Whitney U tests with a Bonferroni correction were undertaken to identify whether there were significant differences in the types of grips used by participants dependent on the type of stone tool. Again, only grip types with a PoU value of >10% were compared between stone tool types. In Experiment 3, comparisons of grip type were made between flakes vs. large flakes, flakes vs. handaxes, and large flakes vs. handaxes, with a Bonferroni correction of $\alpha = .0023$, while in Experiment 4, comparisons were made between flakes vs. cores, with a Bonferroni correction of $\alpha =.0125$.

Grip Recruitment Dependent on Stone Tool Form

To investigate whether grip use was dependent on the form of a specific stone tool type, multinomial logistic regression was used to analyse relationships between PoU values and tool form variables (PoU values were assigned to ten categories [e.g. 0-10%, 10.1-20%]). Due to the larger sample sizes, only the relationship between grip type and tool form variation in the flakes used in Experiment 1 (n = 342) and handaxes used in Experiment 2 (n = 500) were investigated in this analysis. In each, grip types displaying PoU values of 5% or more were analysed. Any potential influence exerted by tool size was investigated via the mass (g) and maximum length (mm) of flakes and handaxes.

In addition, it has been well-documented that, relative to flakes, handaxes display higher standardisation in form, with a series of morphological traits conforming to produce a general handaxe *bauplan* (*sensu* Lycett and Gowlett, 2008) describing their form (Gowlett, 2015). This includes their shape and the presence of a 'globular butt' (Gowlett, 2006), both of which have been previously linked to their ease of manipulation during use (Kleindienst and Keller, 1976; Jones, 1994; Grosman et al., 2011; Key et al., 2016). Here, handaxe 3D shape was recorded using a size-adjusted (scale-free) dataset of 29 morphometric variables from each of the 500 handaxes. Using Principal Component Analysis, the major patterns in shape variation were described for each tool and the first two principal components were separately regressed against the PoU data. The 'globular butt' of each handaxe was quantified by their 'refinement' index, calculated as a tool's maximum thickness divided by its maximum width, and the mean angle recorded from nine evenly distributed measurements on the proximal 50% of each tool's edge. Further methodological details on how the morphology of the tools was quantified are published by Key and colleagues (Key and Lycett, 2014, 2017b; Key et al., 2016). Spearman's rank-order correlations were also performed in support of the logistic regression analyses, and results are presented in Supplementary Information 2.

Further, the relationship between the mass (g) of the flake and core tools used in Experiment 4 and the PoU values for the grips used (with values >5%) was analysed using Spearman's rank-order correlation. This conservative correlation produces an *r* value similar to the Pearson's product-moment correlation, detailing variation between a perfect negative correlation (-1) and perfect positive correlation (1), but makes no assumptions regarding normal distribution. Two flake and two cores tools did not have their mass recorded, and thus sample sizes for each were n = 21 and n = 20, respectively.

3. Results

Grip Diversity

Table 3 details the 29 grips identified across the four experiments and 1067 stone tool-use events analysed here. While the terminology and definitions typically follow those reported by Marzke and colleagues (Marzke and Wullstein, 1996; Marzke, 1997), we identified four grips that had not been previously described in the literature (Table 3; Fig. 7). These include a pad-to-pad grip where the first and second digits secure the tool in opposition while the lateral side of the third supports the cutting edge (grip 3.8), pad-to-side grips where the tool is secured by the pad of the first digit and medial side of the second digit in opposition to the lateral side of the third or third and fourth digits (grips 3.7 and 4.7, respectively), and a squeeze power grip where the index finger is adducted towards the distal tip of a tool to support its cutting edge and aid cutting precision (grip 6.9). Of the remaining 25 grips two were power grips and 23 were precision grips, all of which have been previously described or defined (Marzke and Shackley, 1986; Marzke and Wullstein, 1996; Marzke, 1997). Power grips were rarely used and accounted for only 0.8% of tool-use durations across all experiments. In a number of instances grips displayed identical positioning of digits 1-3 but are distinguished only by the recruitment of digits 4 and/or 5, the 2nd metacarpal head or the palm. The thumb was always actively employed during grips and only one grip type did not recruit digits 1-5 in a sequential order (grip 2.3c, where digits 1 and 3 were recruited, but the 2nd was not).

All experiments displayed the use of ≥12 grips, however, within individual tool-use events the greatest levels of diversity occurred during longer duration tasks. Figure 8 provides several examples of grip-use-sequences demonstrating this trend. Further, Figure 8 highlights that the index finger displayed varied roles during the use of all tools, often switching between being recruited seemingly forcefully in opposition to the cutting edge or principally being recruited to secure the tool in the hand. Figure 9 provides an overview of the number of instances and durations that individual grips were recruited within each experiment. This highlights the diversity of grips identified across each experiment and the high frequency of specific grip types relative to others. The grips most heavily recruited across all experiments were: two-jaw chuck pad-to-side between the thumb and side of index finger (grips 2.3a, 2.3b), three-jaw chuck pad-to-side with the index finger opposing the tool's cutting edge (grips 3.4a, 3.4b), three, four or five-jaw buttressed pad-to-side (grips 3.5, 4.5, 5.5), buttressed three or five-jaw chuck full finger pad-to-side (grips 3.6, 5.6), and the cradle grip (grip 6.1).

Comparisons across Tool-Use Contexts

Table 4 details the percentage of use (PoU) values for each grip within each of the four experiments, dependent on the type of tool being used. Comparisons between the butchery experiment (Exp. 4) and the laboratory-based experiments (Exp. 1-3) highlight both similarities and differences in grip use. In all flake experiments (Exp. 1, 3, and 4), a robust three-jaw chuck pad-to-side grip (grip 3.4b; Table 3) was frequently used; PoU values ranged from 17.1% (Exp. 1) to 33.2% (Exp. 4) (Table 4; Figs. 2, 9 and 10). It is only the three-jaw buttressed pad-to-side grip (grip 3.5) in Experiment 3 that shows a higher PoU value (45.4%) across any of the flake use experiments. Grip 3.5 is also regularly used in the other two flake use experiments (13.5% in Exp. 1 and 15.3% in Exp. 4). A robust two-jaw chuck pad-to-side grip (Grip 2.3b) was commonly used in Experiments 1 (30.8%) and 3 (20.3%), but not in the butchery Experiment 4 (2.3%). Conversely, a three-jaw chuck pad-to-side, with the distal side of the third digit recruited (grip 3.4a) was more commonly used (21%) in Experiment 4 but more rarely in Experiments 1 (5.5%) and 3 (0.1%). In Experiment 1, the index finger or the proximal phalanx of the index finger were less often recruited in opposition to a flake's cutting edge than during the other two flake-use experiments, especially in comparison to Experiment 4.

Handaxes, large 'Lomekwian-sized' flakes and core tools also displayed similarities and differences in grip recruitment frequencies across Experiments 2-4. During the use of these tools in all three Experiments, the grips displaying PoU values greater than 10% were 6.2, 6.1, 6.6, 3.5 and 4.5. These grips can be broadly describe as grips that involved all five digits (e.g. cradle and five-jaw chuck grips) or three- or four-jaw chuck grips (Table 3). Both handaxes and large flakes in Experiment 3 displayed a ~20% increased reliance on a cradle grip (grip 6.1) compared with the handaxes used in Experiment 2. Further, three-jaw (grip 3.5) and four-jaw (grip 4.5) buttressed pad-to-side grips appeared to be only heavily (PoU = ~20%) recruited during Experiment 2. A buttressed-five jaw chuck pad-to-side grip with full finger and active palm recruitment (grip 6.6) was commonly used during handaxe use in Experiment 3 (28.6%) and core use in Experiment 4 (29.5%), but not Experiment 2 (4.8%). Further, grip 3.4b was recruited for 41.7% of the time during Experiment 4, but only 1.1% of the time during Experiment 2 and not at all during large flake or handaxe use in Experiment 3. This represents a reduced reliance on the active recruitment of the palm or metacarpal head during the use of core tools in Experiment 4. The low frequency of grip 6.2 during core tool-use in Experiment 4 was also notable, as was the butcher's heavy reliance on two grips, 3.4b and 6.6.

Mann-Whitney U tests identified several significant differences in PoU of grips across the different experiments (Tables 5 and 6). When using flakes in Experiments 1 and 3, grips 2.3b, 3.4b, and 3.5 were most commonly used, however, there were significant differences in relative frequency of each grip in each experiment (Table 5). Experiment 4 showed significantly higher use of grip 3.4a compared with Experiments 1 and 3, and significantly higher use of grip 3.4b than Experiment 1. Conversely, Experiment 4 showed significantly lower frequency of grip 3.5 compared with flake use in Experiment 3 (Table 5).

When using handaxes, Mann-Whitney U tests also revealed significant differences between Experiments 2 and 3 in the use of grips 3.5, 4.5, 6.1 and 6.6 (Table 3). Regarding grips 3.5 and 4.5, Experiment 2 recruited these grips significantly more frequently during handaxe use than in Experiment 3. Conversely, grips 6.1 and 6.6 were recruited significantly more frequently during Experiment 3. These differences reflect both a varied positioning of the index finger and the recruitment levels of the palm. Handaxe use during Experiments 2 and 3 recruited grip 6.2 to a similar extent and significantly more often than the core tools used in Experiment 4. The use of handaxes during Experiment 3 also recruited grip 6.1 significantly more frequently than the use of core tools in Experiment 4. Conversely, core tools in Experiment 4 displayed significantly greater PoU values for grip 3.4b than handaxes in Experiments 2 and 3, but similar levels of recruitment for grips 3.5 and 4.5.

INSERT FIGURE 8 ABOUT HERE

Comparison of Grip Use across Stone Tool Types

There was a clear preference across all flake-use experiments (Exp. 1, 3 and 4) for grips recruiting two or three digits. Indeed, three-jaw pad-to-side grips (grips 3.4b, 3.4a, 3.5) or the two-jaw chuck pad-to-side grip (grip 2.3b) were the most frequently used grips in all three flake use experiments (Table 4; Fig. 9). Similarly, when using handaxes, large flakes or core tools, grips that have active recruitment of the palm and all five digits (grips 6.1, 6.2, 6.6) were most commonly used (with the notable exception of grip 3.4b being frequently used during Experiment 4) (Table 4; Fig. 9). There was variability in the positioning of the index finger (or 2nd proximal phalanx) across all tool types and experiments. In other words, all experiments displayed variability in how force was applied in opposition to a stone tool's cutting edge (Fig. 8).

In Experiment 3 – the only experiment to include large 'Lomekwian-sized' flakes— grips 3.5, 2.3b, 3.4b and 3.6 were significantly more common when using flakes, while grips 6.1, 6.2, and 6.6 were significantly more commonly used when using large flakes and handaxes (Table 7). Between the use of large flakes and handaxes, only grip 6.2 displayed a significant PoU difference, being more frequently used with handaxes. In Experiment 4, grips 3.5 and 3.4a were significantly more frequent during the use of flake tools, while grip 6.6 was significantly more common during the use of cores (Table 7). Interestingly, in Experiment 4 grip 3.4b was recruited to a similar extent (i.e., not significantly different) during the use of both flake and core tools.

INSERT FIGURE 9 ABOUT HERE

Comparison of Grip Use across Stone Tool Forms

Multinomial logistic regression was used to investigate relationships between grip PoU values and tool form attributes in flakes (Experiment 1) and handaxes (Experiment 2). Table 8 displays regression results between flake mass and maximum length and the frequencies with which grips 2.3b, 3.4b, 3.5, 3.6, 3.1 and 3.4a were recruited (all grips with PoU values >5%). The relationships between grip PoU values and both flake mass and flake length were similar as both variables describe tool size. Indeed, grips 2.3b, 3.4b, 3.1 and 3.4a all displayed a significant (but occasionally weak) negative relationship with both flake mass and length , showing that as the size of the flakes increase, these grips (two- or three-jaw chuck pad-to-pad or pad-to-side grips) were significantly less likely to be recruited by tool users (Fig. 10). Conversely, grips 3.5 and 3.6 only displayed near-significant (due to the Bonferroni correction) positive relationships with the flake length (and not flake mass), showing that these grips (buttressed three-jaw pad-to-side grips) were more likely to be recruited by participants as the size (but not mass) of flake tools increased (Fig. 10). This result suggests that it is specifically the form of tools, rather than the weight, that elicits the more frequent recruitment of grips 3.5 and 3.6.

Table 9 presents multinomial logistic regressions between the PoU values of grips 6.2, 6.1, 4.5 and 3.5 (all grips with PoU values >5%) and handaxe size (mass and maximum length), shape (PCA components 1 and 2), 'refinement', and proximal edge angles. The first and second PCs accounted for

57% and 17% of the total shape variation in the handaxes, respectively. Regarding handaxe size, there were significant relationships between the increasing size (mass and length) of handaxes and the increased use of grips 6.2 and 6.1. Similarly, as the size of handaxes increase, grips 4.5 and 3.5 were less likely to be recruited (Table 9). These size-related differences were primarily characterised by digits 4 and 5 and the palm being recruited more frequently as handaxes increased in size. The first PC, which was most heavily weighted by the length and proximal (base) width of handaxes, and PC2, which was most heavily weighted by the distal width of handaxes, did not display any significant relationships with grip PoU values Edge angle returned one significant relationship, identifying grip 6.2 to be used more frequently as edges become more obtuse, although the low R^2 value indicates that this relationship is weak.

INSERT FIGURE 10 ABOUT HERE

Finally, there were weak but significant negative relationships between grip 3.5 and the refinement index and the mean edge angle observed in their proximal aspect of the handaxes. Thus, the relative thickness of handaxes or the angles observed on their proximal aspect may influence the grips used by participants, but, given the strength of these relationships further investigations are required. The Spearman's rank-order correlations performed on these data broadly supported the multinomial logistic regression analyses (Supplementary Information 2).

Spearman's rank-order correlations between grip PoU values and the mass of flake and core tools used in Experiment 4 identified two significant relationships for each tool type (Table 10). For flakes, the recruitment of grips 3.4a and 3.1 were significantly negatively correlated with flake mass. For cores, the use of grip 3.4b was significantly negatively correlated with core mass, while grip 6.6 was significantly positively correlated.

4. Discussion

Presented here is empirical evidence detailing the diversity and frequencies of grips employed during Lower Palaeolithic stone tool cutting activities. We provide data derived from multiple large-scale experiments on novice stone tool users that undertook 1067 replica tool-use events allowing, for the first time, assessment of how variation in stone tool type, morphology, and context of use influences grip.

Results indicate that the diversity of grips used during flake and LCT tool use has the potential to be considerable, with 29 grip types being recorded across the four experiments, including 26 precision grips and three power grips. When the results of individual experiments and tool types are considered, the number of grips recruited by participants was still substantial, ranging between 12 and 24 (Table 4). We identified four new grips that had not been previously described in the literature, including a pad-to-pad grip (grip 3.8), two pad-to-side grips (grips 3.7 and 4.7), and a squeeze power grip (grip 6.9;

Table 3; Fig. 7). Grip 3.8 was unique in its recruitment of the lateral side of the 3rd digit to support a tool's cutting edge, while grips 3.7 and 4.7 were unique in their placement of digit 2 alongside the thumb when opposing digits 3-5. Grip 6.9 was distinct in its adduction of digit 2 in support of a tool's distal cutting edge. While digit 2 was applied seemingly forcefully and with precision in the squeeze grip, it did not oppose any other aspects of the hand (only the tool and worked material) while digit 1 and digits 3-5 maintained a typical squeeze power grip position. For these reasons, we argue that this grip is distinct to the precision grips described here and elsewhere (e.g., Marzke and Shackley, 1986) and can be considered a true power grip. However, none of these new grips were frequently used in any of the experiments (PoU values ranged from 0.01 to 1.5%).

The high diversity of grips recorded here appears in contrast to previous reports by Marzke and colleagues (Marzke and Shackley, 1986; Marzke, 1997, 2013), whom emphasised that just three types of grips (pad-to-side between the thumb and side of the index finger, the three-jaw chuck grip, and cradle grip [Table 3; Fig. 1]) facilitate the majority of stone tool related behaviours. We would argue, however, that our results are in fact consistent with, and supportive of, this previous research. Marzke and colleagues (Marzke and Shackley, 1986; Marzke, 1997) did not distinguish between grips dependent on the number of digits recruited, but rather their grips were defined primarily on the positioning of digits 1-3 and any buttressing provided by the palm (see Table 2 in Markze [1997] for example). When the 29 grips recorded here are considered in a similar way (i.e. based on the positioning of digits 1-3 rather than the number of digits recruited), participants in our experiments used 14 different grips, three of which were power grips. In line with previous findings by Marzke and Shackley (1986) who did not identify the use of power grips during stone tool use, we also found power grips to be rarely used (0.8% of tool-use durations across all experiments).

When further considered in terms of the frequency with which different grips were recruited, the picture becomes even clearer. For each type of stone tool used, no more than four grips displayed percentage of use (PoU) values greater than 10% in any one experiment. In each case, these grips accounted for between 70-97% of total tool-use durations. In other words, a limited number of grips characterised the majority of stone tool-use behaviours in all experimental contexts. Further, across all experiments only nine types of grips displayed PoU values above 10% (2.3b, 3.4a, 3.4b, 3.5, 3.6, 4.5, 6.2, 6.6, and 6.1), of which, 3.4a and 3.4b are variants of the same grip. Moreover, differences between 6.1, 6.2, and 6.6 are dependent on the relative positioning of the index finger alone, differences between 6.2, 3.5 and 4.5 depend on the recruitment of digits 4 and 5 or the palm, while differences between 3.5 and 3.6 are dependent on the distal 2nd phalanx being recruited in opposition to the tool's cutting edge. In sum, when considered at a broad level, 70-97% of the 1067 tool-use events analysed here were characterised by five fundamental grip types. These are: two-jaw chuck pad-to-side between the thumb and lateral side of index finger, three-jaw chuck pad-to-side grip with the index finger opposing the tool's cutting edge, three, four or five-jaw buttressed pad-to-side, buttressed three or five-jaw chuck full finger pad-to-side, and the cradle grip. Taken together, presented here are robust empirical data in support of Marzke and colleagues' (Marzke and Shackley, 1986; Marzke, 1997) previous statements regarding the limited number of grips frequently utilised during stone tool-use.

It is important to note that our descriptions reflect the digits that made contact with the tool. However, in several instances, particularly when using pad-to-side grips, additional fingers were buttressed against the recruited fingers but without making contact with the tool. Thus, these digits (most often digits 4 and 5) likely play an important role in maintaining tool stability and experience some degree of loading that is not acknowledged in our hand grip terminology. Moreover, and as discussed above, there was some difficulty in accurately identifying whether digits 4 and 5 made contact with the tool due to the single camera view, which may have influenced the results. It is also important to note that within any group of finitely defined 'grip types' there is fluidity between grips and the relative positioning of digits and the palm. This is to be expected when segmenting ranges of movement into distinct individual positions.

Stone Tool Types

We found clear differences in the frequency that specific grips were employed when different stone tools (i.e. flakes, large flakes, handaxes and cores) were used (Fig. 9). When using 'simple' flake cutting tools, grips 2.3b, 3.4b and 3.5 were most common. These pad-to-side grips recruit two or three digits with the latter two grips forcefully recruiting the index finger in opposition to the tool's cutting edge. When using handaxes, cores, and large flakes, grips 6.1, 6.6 and 6.2 were most common. All of these grips recruit five digits and the palm and are principally differentiated mainly by the positioning of the index finger relative to the tool's cutting edge. Differences in grip recruitment frequencies between stone tool types were, in many instances, significant. Thus, more precise precision grips between the pad of the thumb and specific aspects of individual fingers were used for flakes, while more expansive grips recruiting more fingers and the palm were used for handaxes and large 'Lomekwian-sized' flakes. This result is not necessarily surprising; these grip differences largely reflect the gross size of tool being used, and, in turn, the extent to which the fingers and palm have space to be in physical contact with the tool. The fact that there was only one significant difference in hand grip frequency identified between handaxes and the 'Lomekwian' flakes of equal size and mass, supports this conjecture. Grip 6.2, which recruited the proximal aspects of the index finger in opposition the tool's cutting edge, was recruited significantly more frequently during handaxe use relative to large flake tools. This difference may reflect a greater requirement to control against torque (i.e. the tool turning in the hand) when using handaxes by extending the reach of the hand towards the tip of these relatively elongated tools (Gowlett, 2013).

A similar pattern between hand grip and tool type was found during the actualistic butchery experiment (Exp. 4). As in Experiment 3, grips 3.5 and 3.4a, which are versions of three-jaw pad-to-side grips, were significantly more common when cutting with flakes, while grip 6.6, involving all five digits and the palm, was significantly more frequent when cutting with core tools. In other words, there appears to be a similar disparity in the type of grip and the size of tool being used. However, in Experiment 4 there was much greater overlap in the size of the flake and core tools compared to those used in Experiment 3. Thus, in Experiment 4, grip 3.4b – a three-jaw chuck pad-to-side grip with the index finger recruited in opposition to the tools cutting edge – was commonly used for both tool types. Here again, grip choice appears to be less dependent on the type of tool being used, but rather the size of the tool. We therefore contend that when used during slicing and sawing cutting motions, stone tool type *per se* has a limited influence on the grips recruited by tool users. Moreover, it is clear that the flaked (knapped) edge often present on handaxes does not prevent the seemingly forceful application of the palm or index finger to any greater extent than other types of stone cutting tools. Further investigation is needed to see how grip use may vary during the use of stone tool types during other cutting actions (e.g. scraping).

Stone Tool Form Variation

The importance of a tool's size in determining the type of grip applied by tool-users is supported by the regression analyses undertaken between grip PoU values and different aspects of tool form variation in Experiments 1 and 2. Although a few of the significant relationships between grip and tool size variables were weak and thus should be interpreted with caution, other tool size variables accounted for up to 40% of the grip PoU values. Most notably, the recruitment of grips 2.3b and 3.4b – two- and three-jaw chuck pad-to-side grips, respectively – in Experiment 1 were strongly and negatively related to the mass and maximum length of the flakes used, meaning that as tools increased in size, these grips were significantly less likely to be used (although there is variation in the strength of the individual regressions). Hence, these grips may not be able to secure large flakes in the hand effectively or facilitate their efficient use. Overall, grips that recruited the most digits and/or buttressed the tool by the 2nd metacarpal were associated with the use of larger flake tools (Figs. 9 and 10).

During the use of handaxes there was a similarly significant negative relationship between the use of grips 3.5 and, less so, 4.5 – three- and four-jaw pad-to-side grips with the tool buttressed against the second metacarpal, respectively – and handaxe mass and maximum length, indicating that as handaxes got larger, these grips were used less frequently. When combined with the significant and positive relationship between grip 6.2 – five-jaw buttressed pad-to-pad grip – and handaxe size, it suggests that during the use of handaxes of any size there are similar requirements for positioning digits 1-3. For example, the proximal aspect of the index finger was positioned on the top of the tool, opposing the cutting edge in 69% of the total time of handaxe use in Experiment 2. However, as handaxes get larger, digits 4 and 5 and the palm were more frequently recruited. Grip 6.1—cradle grip using all 5 digits and the palm— showed the strongest relationship with handaxe size. Given the highly variable handaxe sizes used in this study, it is perhaps not surprising that the cradle grip was so frequently used with larger handaxes, as it provides an expansive grip suited to securing large and heavy objects (Marzke, 1997; Key and Dunmore, 2015). These results are broadly in line with the object volumetric studies of gripping undertaken by Pouydebat et al. (2009), including the near absence of power grips. Pouydebat et al. (2009: 270) also reported that adult humans never used the palm of their hand when grasping large objects, whereas we found that the palm was recruited in 44% of the total tool-use time across all experiments (not including metacarpal head recruitment). However, this variation can be explained by methodological differences; participants in Pouydebat et al. (2009) had to grasp and handle apples and tomatoes, while in this study participants needed to grip comparatively large handaxes and flakes and forcefully manoeuvre them to cut different materials.

The strong relationship between tool-size and grip use found in this study is consistent with industrial and occupational ergonomic studies of hand use (e.g. Lewis and Narayan, 1993; Edgren et al., 2004; Kong and Lowe, 2005; Rossi et al., 2015). Kong and Lowe (2005), for example, found handle diameters ranging between 30-40mm to be ergonomically preferential when performing maximum voluntary gripping actions, a range that it surprisingly close to mean thickness values in Lower Palaeolithic handaxe assemblages (Petraglia and Shipton, 2008; Key and Lycett, 2017b). Thus, it is possible that Palaeolithic stone tools would have been subject to the same biomechanically-related functional selective pressure on their form as any modern hand-held tool (Gowlett, 2011; Lycett et al., 2016). While it was not possible here to look at relationships between biometric variation in tool users and grip choice, past research indicates that such factors are relevant in determining stone tool-use proficiency (Key and Lycett, 2011, in press; Rolian et al., 2011). Thus, it is reasonable to suggest that the grips used by different individuals were likely 'fine-tuned' to account for variations in hand size or digit length (e.g., individuals with smaller hands would have found it more challenging to grip larger tools). More in-depth ergonomic relationships between tool size and grip choice require further investigation to shed light on if and how this potentially influenced the design and production of Palaeolithic stone tools. Moreover, across all of our experiments, tools were occasionally (e.g. 4.4% of the handaxes in Experiment 2) gripped by two hands during cutting tasks. Thus, a tool may potentially be functionally effective even if it is unable to be manipulated by a single hand.

We also found a weak but significant positive relationship between the use of grip 6.2 and edge angle. Although this relationship should be interpreted with caution, it suggests that more obtuse edges may facilitate this large expansive grip, which makes direct contact with the tool's edge from the intermediate phalanx down to proximal aspects of the palm. This appears logical as more obtuse edges will decrease the stress created by the tool's edge on the skin, in turn reducing chances of injury or pain during use (Key et al., 2016). Thus, this relationship between grip use and variation in handaxe form may reflect ergonomic choices (i.e. greater comfort, ease of use) by the tool-user. No significant relationships were found between either PC1 or PC2 and any of the four grips analysed. This suggests that the shape of a handaxe does not have a significant influence over the types of grips used by participants. This does not mean that handaxe shape does not influence grip choice during some specific cutting activities, but rather, across a series of generalised cutting actions there does not appear to be a strong relationship. In sum, while there are clear relationships between the size of stone tools and the grips used by tool-users, there is still a lack of clarity regarding how the shape of stone tools influences grip choice.

Variation in Tool-Use Context

The large diversity of grip types (n = 29) found in this study could arguably reflect the large number of participants (n = 123) studied. However, in Experiment 4 there was only one participant and they used 17 and 19 different grips during flake and core tool-use, respectively. Similarly, Experiment 2 had five participants and they used 24 different grips while cutting with handaxes. However, as discussed above, there were a limited number of grips (n = 9) that were frequently used by all participants across all tools, and an overall total of 29 types of grips could be considered a relatively low number given the scale of the experiments (1067 tool-use events). Hence, the number of grips able to be used by tool-users appears to be both relatively finite and a consequence of the contexts in which the tools are being used (rather than being the result of the individual tool users). Further, given the heavy reliance on ≤4 grips types during individual experiments (i.e. grips displaying PoU values >10%), and the low PoU values reported for other grips, it appears that much of the variation identified here may have been a result of 'trial and error'. As highlighted in Figure 8, the quick transition between multiple types of grips was repeatedly observed throughout many longer-duration tool-use events (Experiments 2-4). It is tempting to link rapid grip transitioning to the inexperience of some tool-users. However, examination of the final 20 handaxes used by participants in Experiment 2, after they had already used 80 of these tools and were comfortable with their use, continued to reveal this trend. Instead, we would suggest there to be a substantial part played by the context of a tool's use on the choice and duration of grips used by participants. For example, extended periods of tool use increase the chances of fatigue and differing grips being recruited to relieve muscle groups. Similarly, the cutting of particularly tough or resistant materials, which in turn creates an extended period of cutting with relatively little observable progress, also likely adds to individuals switching between different grips in the hope of speeding up progress.

When the same types of tools that were used across different experiments were compared, we found significant differences in the frequency of grips used. There are two potential reasons for this variation. First, it is possible that these differences were caused by different individuals using the tools. Any potential influence of individual tool-user grip preferences is limited in Experiments 1-3 due to the large number of participants, however, it is possible that the heavy reliance on grip 3.4b in Experiment 4 is the result of the butcher's preference for that grip type. Alternatively, it is possible that the different material contexts in which tools were used across experiments influenced grip choice. The majority of differences between tool-use contexts were found in grips that recruited the same number of digits but positioned the digits on the tool in slightly different ways (Tables 5 and 6). In particular, most of the variation in hand grips used across different cutting contexts can be explained by the relative positioning of digits 2 and 3 with respect to the tool and the thumb. For example, when using a flake to cut through tough double-layered cardboard in Experiment 3, it was advantageous to position the proximal aspect of the index finger in opposition to the working edge of the tool. However, when cutting through rope in Experiment 1, which seemingly required less force, the index finger was more frequently used in opposition to the thumb (two-jaw chuck pad-to-side). Moreover, differences in the relative precision required for specific cutting tasks likely also influences the grips used. Indeed, as suggested by Marzke and Shackley (1986), the distal aspect of the index finger is likely more often recruited in opposition to a cutting edge during precision cutting tasks, a trend we noticed here and which led to the use of grip 6.9, the newly identified squeeze grip with the index finger adducted in support of a tool's cutting edge. The potential influence that tool-use context may have on grip choice therefore provides an additional layer of complexity when trying to reconstruct Palaeolithic manual behaviours from stone tool artefacts. Certainly, there is potential for the ergonomic relationships relating to tool size and type to vary based on the tool-use context.

Implications for Fossil Hominin Tool-Use and Hand Morphology

Given the consistent use of particular grips across the four experiments, as well as the repeated observation of these grip types in previous works (Marzke and Shackley, 1986; Marke, 1997), we might expect that the grips habitually used by hominins during the Palaeolithic – particularly hominins with similar hand proportions and/or morphology to that of recent humans (i.e., early *H. sapiens*, Neanderthals, and potentially *H. erectus s.l.*) – may have been similarly consistent across different tool types and cutting behaviours. When securing a stone cutting tool against the forces associated with its use (e.g. torque, cutting edge loading), Lower Palaeolithic hominins would have experienced similar requirements to position the digits and palm against specific aspects of a tool in opposition to these forces. Thus, these basic functional requirements may have canalised the hand grips across different individuals, species and tool behaviours. Essentially, the relationships prompting the use of a limited number of grips in modern humans in these experiments would likely have similarly been present during the Lower Palaeolithic.

The present results provide insight into our understanding of the context of hominin hand evolution and adaptation in response to stone cutting tool-use (Marzke, 2013; Kivell, 2015). There are only a few fossil hominin taxa – *Au. afarensis*, *Australopithecus prometheus* (i.e. StW 573), *Australopithecus sediba*, *Homo naledi*, and *Homo neanderthalensis* – that have sufficient preservation of hand bones to assess intrinsic hand proportions and morphology (Bush et al. 1982; Marzke, 1983; Trinkaus 1983;

Clark, 1999, 2013; Alba et al. 2003; Kivell et al. 2011, 2015). These taxa show subtle and not-so-subtle differences amongst them that likely had implications for hand function (Bush et al. 1982; Marzke, 1983; Trinkaus 1983; Alba et al. 2003; Kivell et al. 2011, 2015). However, in all of these taxa the hand proportions and morphology can generally be described as more human-like than ape-like (but see Rolian and Gordon, 2013 for *Au. afarensis*), suggesting that the repertoire of potential hand grips may not have been drastically different from that of recent humans. This inference is supported by living great apes who, although displaying much longer fingers, a shorter thumb and different joint morphology, are able to capably perform some of the same precision grips as humans (Pouydebat et al., 2011; Marzke et al., 2015; Neufuss et al., 2016). The greater adaptive significance of tool use to the hominin lineage does, however, explain our derived hand anatomy relative to other extant apes.

The similarities across Palaeolithic hominin hand morphology relative to living apes and *Ardipithecus* (Lovejoy et al. 2009), suggests that the general trends in grips used in our experimental studies may shed light on the grips used, and thus loads incurred, by hominin hands in the past. Of course, all *in vivo* experiments are biased by the fact they can only include modern humans with modern human hand anatomy, and manipulative and cognitive abilities. Furthermore, we again acknowledge that these experiments only test cutting behaviours, and there may have been other manipulative, and in some taxa locomotor, selective pressures acting on hominin hand morphology throughout hominin evolution (e.g. Marzke, 1983; Tocheri et al. 2008; Kivell 2015; Kivell et al., 2011, 2015). Certainly, hypotheses addressing the co-evolution of the hominin hand and stone tool technologies is complicated by the selective influence that other manipulative or locomotor behaviours may have had on the hominin hand (e.g. Rolian et al. 2010), and that manipulative behaviours and tool forms evolve faster than morphology. Whether hominin manipulative capabilities and the associated morphology evolved in response to stone tool use, or aspects of hominin hand morphology were exapted for tool-related behaviours (Alba et al. 2003; Almécija et al. 2015) remains unclear. Attempts to understand the relationship between hand morphology, grip use and tool design will also vary depending on the time period in human evolution and how much of a fitness advantage tool behaviours provided to an individual. However, irrespective of this ‘chicken and egg’ scenario, archaeological evidence makes clear that cutting activities have likely been a part of the hominin behavioural repertoire for more than >3 million years (McPherron et al., 2010; Harmand et al., 2015), and were likely important to our survival from ~2.6 Mya (Isaac, 1971; Toth, 1985; Semaw et al., 2003; Braun et al., 2010; Key and Lycett, 2017a; Wynn and Gowlett, 2018). Our results demonstrate the recurrent and seemingly forceful roles played by the thumb and index finger during the use of flakes and LCTs in all four experiments. Indeed, previous research has highlighted the significant impact that the thumb and index finger play during the efficient, effective and forceful use of stone cutting tools (Marzke and Shackley, 1986; Marzke, 1997; Rolian et al., 2011; Key and Lycett, 2011, in press; Borel et al., 2017; Williams-Hatala et al. 2018). Our study builds upon this work to show the relative frequency of their recruitment during multiple cutting behaviours using Lower Palaeolithic stone tools. In every one of the 1067 stone tool-use events observed here, the thumb was recruited to secure tools in the hand. Further, when data from all experiments are combined, the index finger (either its full length or just the proximal phalanx) was recruited (seemingly forcefully) in opposition to the tool's cutting edge in 77.3% of total tool-use time. In all other instances (excluding the 0.007% of time when the index finger was not recruited at all), the lateral or palmar side of the index finger was recruited in opposition to the thumb. The role and relative recruitment of digits 3 and 4 and the palm were, as discussed above, more varied. Therefore, as previous research has suggested, it is likely the thumb and index finger that were under the strongest selective pressure in response to flaked stone tool-use. At the very least, the absence of an ability to forcefully and precisely use the index finger and thumb would have made it challenging for Lower Palaeolithic hominins to efficiently or effectively utilise stone tools across a broad range of tool-type and tool-use contexts. Anatomical features, such as a robust bony morphology and musculature of the thumb and proximodistally-oriented radial carpometacarpal joints (e.g. Marzke, 1997, 2013; Tocheri 2007; Tocheri et al. 2008), that aide forceful precision manipulation and the transfer of load from the thumb across the wrist and palm in modern humans, were are likely the focus of any selective pressures.

Conclusion

Presented here is evidence that variation in the type and form of Lower Palaeolithic stone tools influences the grips recruited during their use, and that these relationships can be altered by the context of their use. Despite the influence of these three factors on grip use there is, however, consistency in the heavy recruitment of a limited number (≤4) of grips types within each experimental context and five general grip types used across all experiments. These results are consistent with previous research (Marzke and Shackley, 1986; Marzke, 1997) and suggest that there are deep-rooted regularities in the grips used by modern humans when manipulating and using Lower Palaeolithic stone cutting tools. It is therefore possible that Plio-Pleistocene stone tool-using hominins, and particularly species with similar hand proportions and morphology to that of modern humans, used similar types of grips and were subject to similar ergonomic relationships with tool types and forms. The consistent and seemingly forceful use of the thumb and index finger when securing tools in the hand or opposing a tool's cutting edge (respectively) would, then, have similarly been represented by Lower Palaeolithic hominins and these digits are most likely to show morphological adaptations to flaked stone tool use.

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Figures

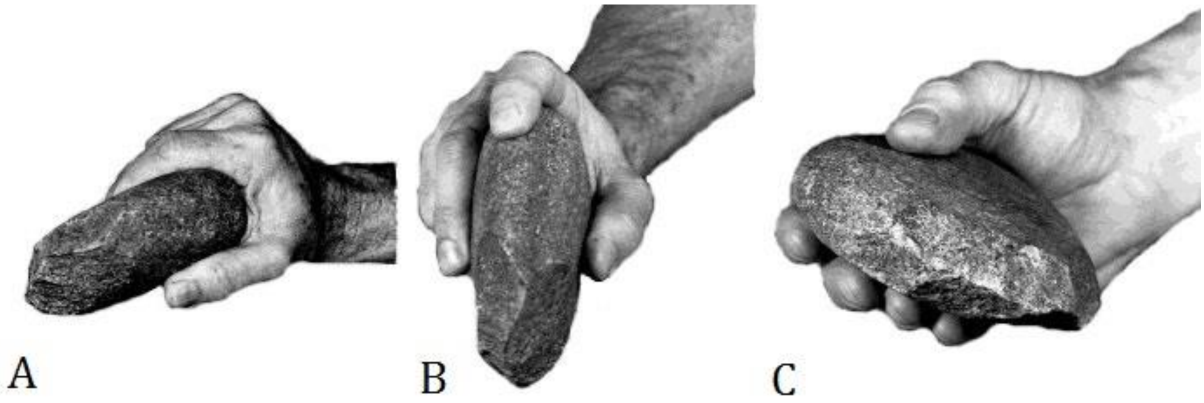

Figure 1: Examples of a ‘buttressed pad-to-side’ (A), ‘extended three-jaw chuck’ (B) and ‘cradle’ grip (C) when holding a bifacially flaked core. Modified from Marzke (1997).

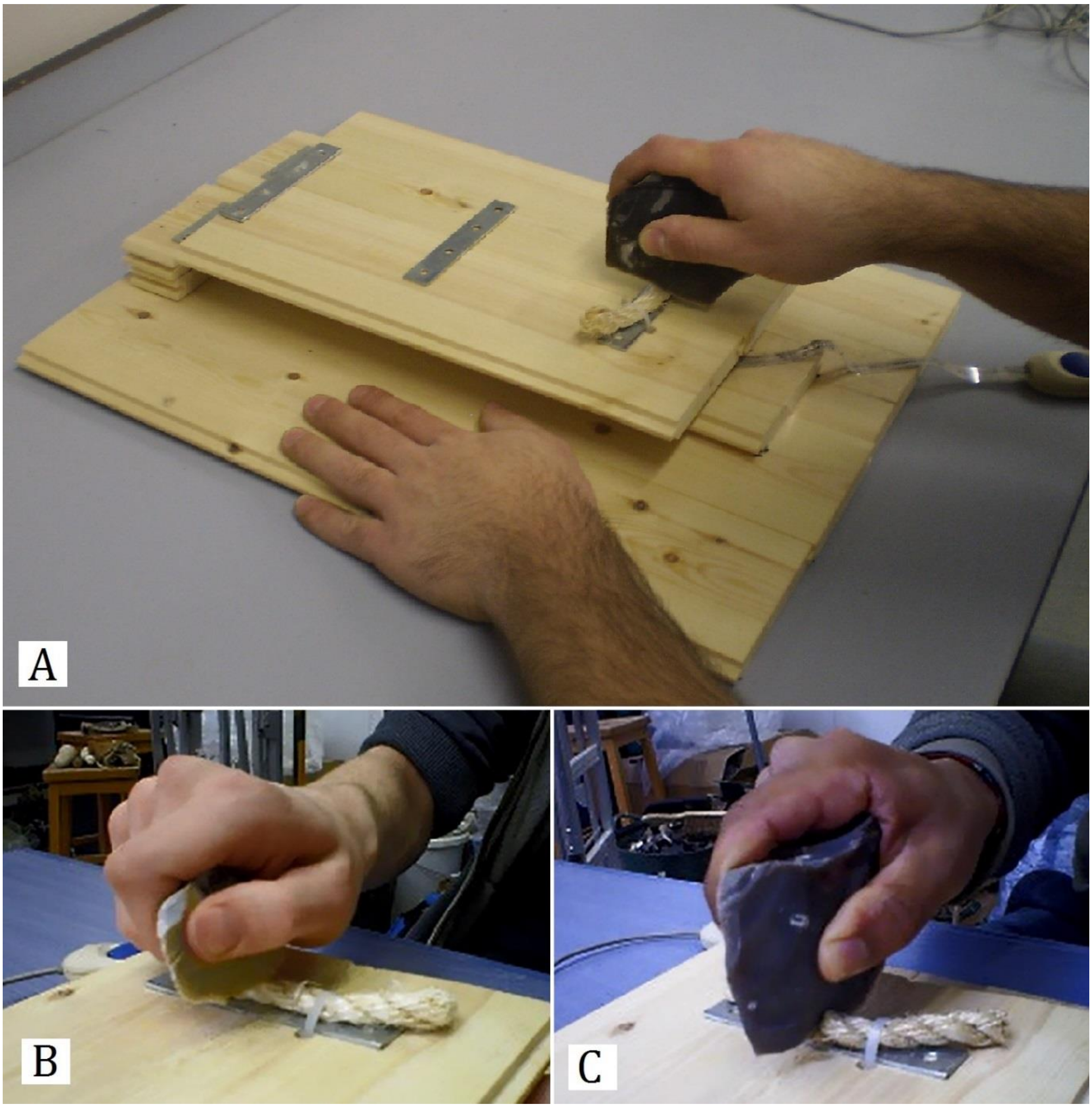

Figure 2: The tool-use conditions presented to participants in Experiment 1 (A), where lengths of hessian rope to be cut through while attached to a wooden platform. Images B and C highlight the ease with which grips could be identified during this experiment.

Figure 3: The replica Lower Palaeolithic stone tools used in Experiments 1(A), 2 (B), and 3 (C). The tools used in Experiment 4 were not photographed as a complete assemblage. Note that the scale bar is 10cm in each instance and that the perspective in image C is biased towards the handaxes in the foreground appearing relatively larger. Figures reproduced from Key and Lycett (2014, 2017b, 2017c) with publisher's permission.

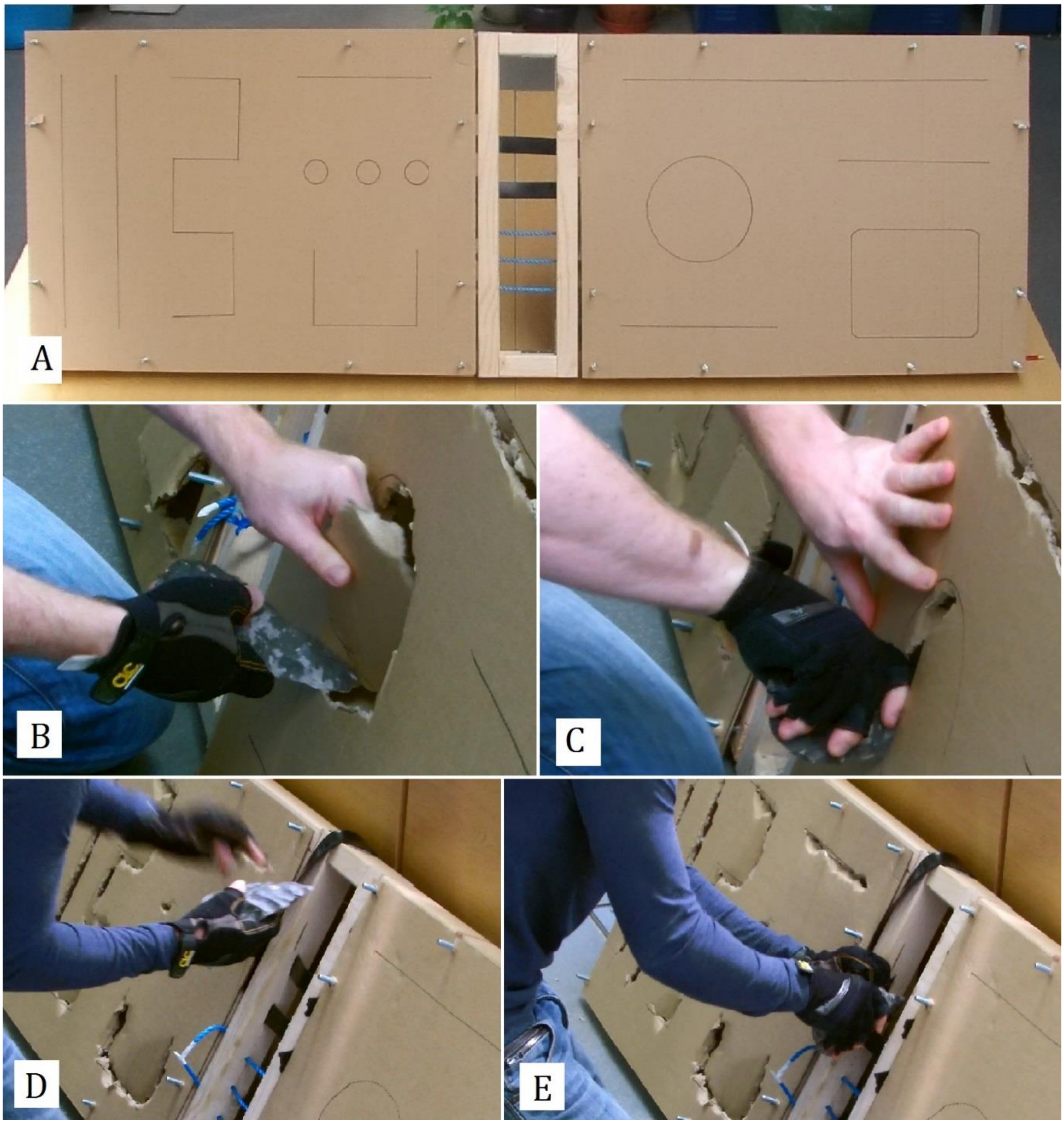

Figure 4: The tool-use conditions presented to participants in Experiment 2, where 16 segments of cardboard, rope, and neoprene strips to be cut in a standardised order (A). Images B and C, and D and E, highlight that on occasions it was necessary to watch a tool being used over several frames of a specific cutting action (i.e. not a video still) to accurately identify the positioning of the thumb and fingers.

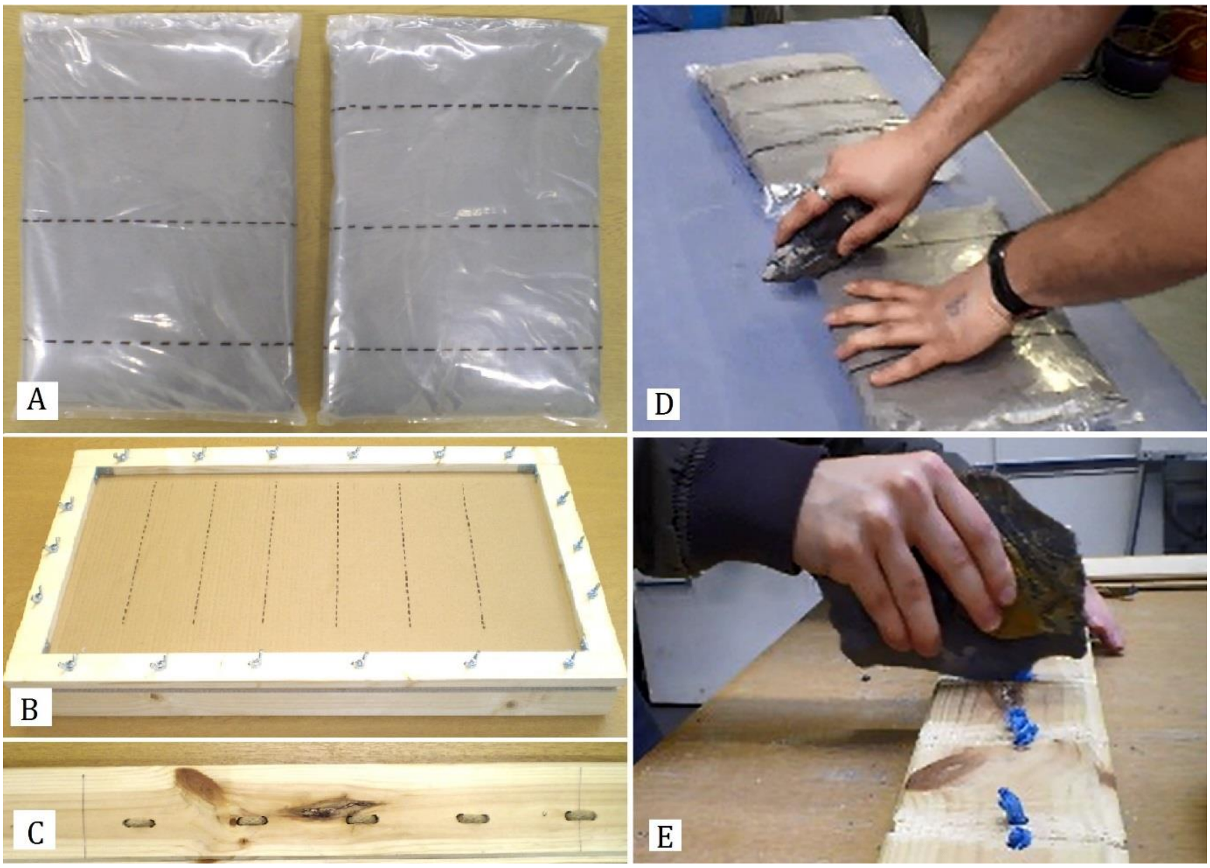

Figure 5: The tool-use conditions presented to participants in Experiment 3, where six lengths of polythene (A), cardboard (B) and rope (C) were required to be cut in sequential order. Images D and E depict typical tool use events, from which grips were identified.

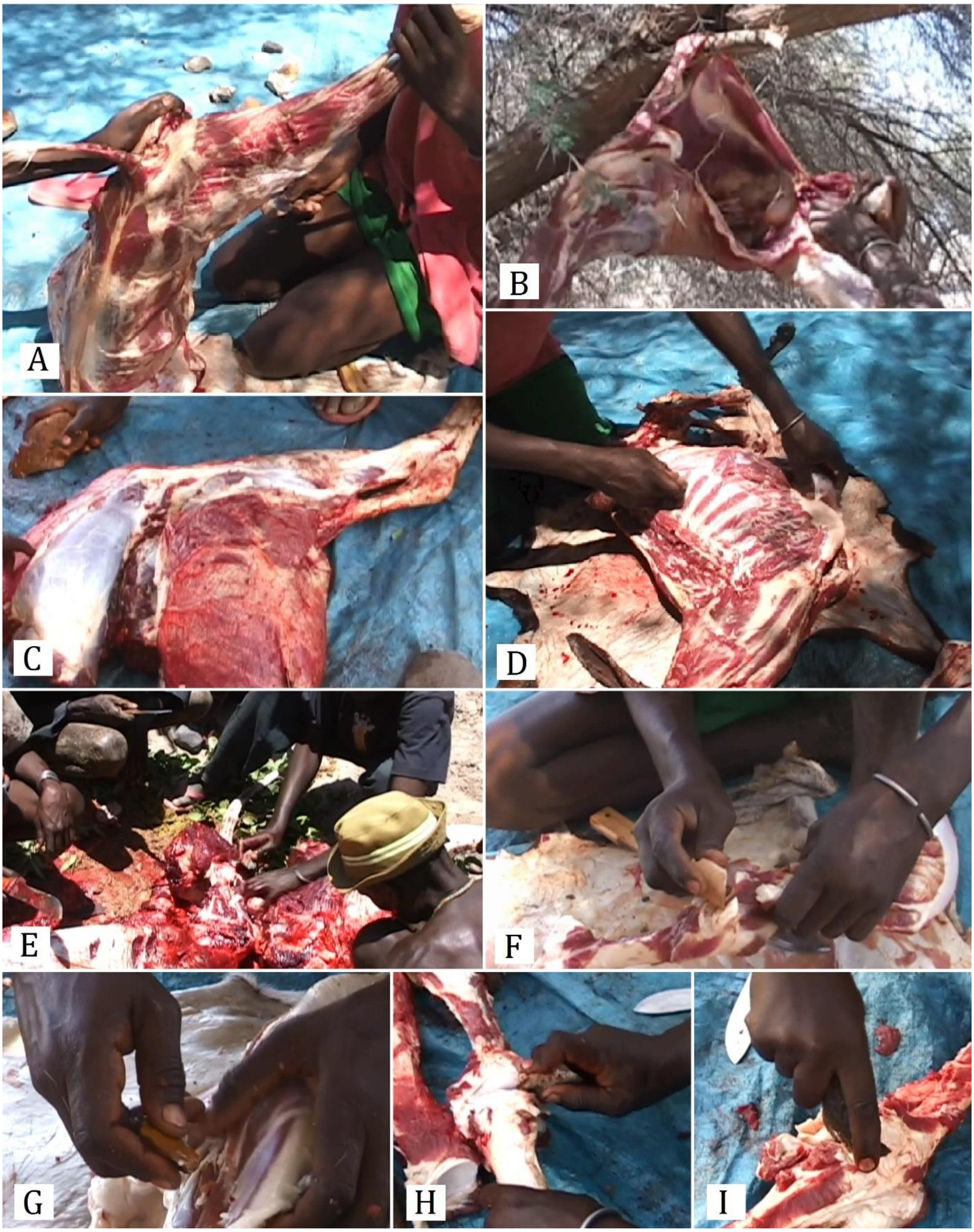

Figure 6: The tool-use conditions presented to participants in Experiment 4, required goat (A, B, D) and cow (C, E) carcasses to be defleshed and disarticulated. Principally Experiment 4 was undertaken on the ground, but on a few occasions the goat carcasses were suspended from a tree (B). Images F-I are video stills identifying the ease with which grips could often be identified.

Figure 7: The 29 grips identified during the 1067 stone tool-use events. Please refer to Table 3 for details relating to each grip. Note that all aspects defining each grip cannot always be observed in these images.

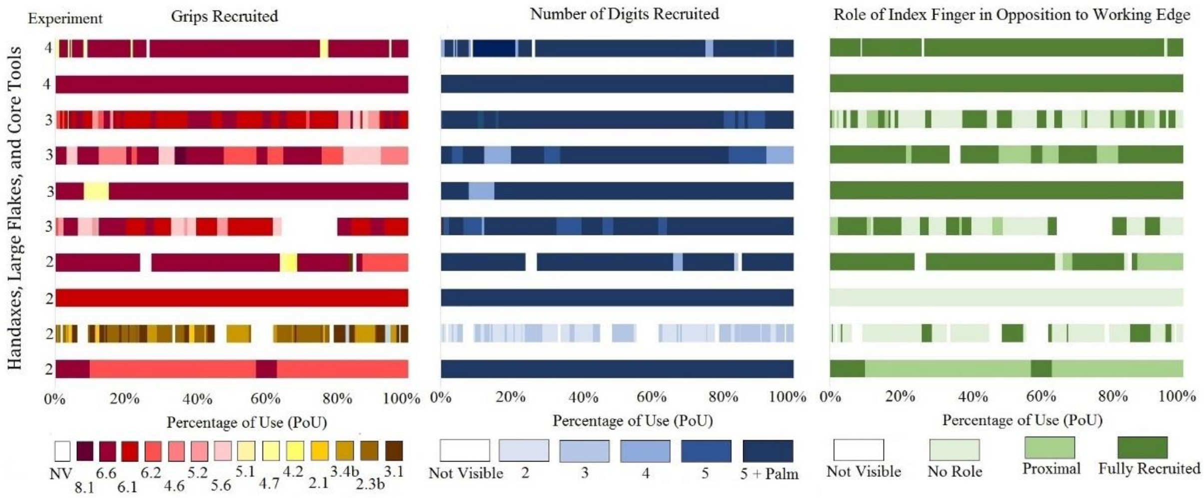

Figure 8: Demonstrative examples of grip-use sequences from experiments two, three and four. Each coloured bar equates to the total time (100%) that the tool was used during the cutting tasks. Grip sequences have been replicated three times each for handaxes, large flakes and core tools, differentiating between the use of a different type of grip (A), the number of digits recruited (B), or the loading-related role of the index finger (C) for a percentage of the total time. “NV”, not visible.

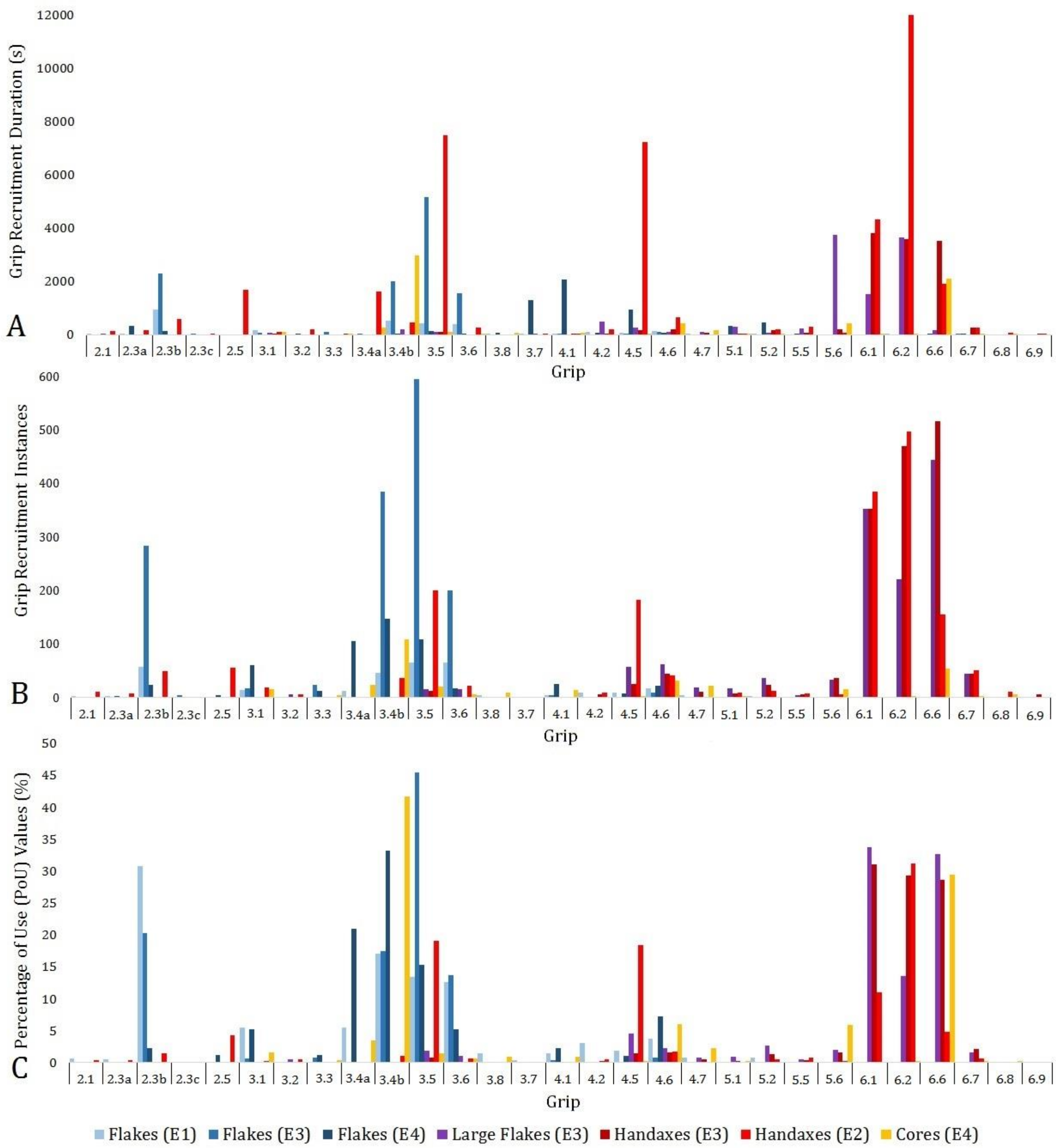

Figure 9: Durations of use for individual grips (A), the number of individual instances that grips were recruited (B), and the percentage of use (PoU) values (C) for each grip type across all experiments (E#) and tool types. Grips are arranged from left to right in order of the number of digits and aspects of the hand actively recruited.

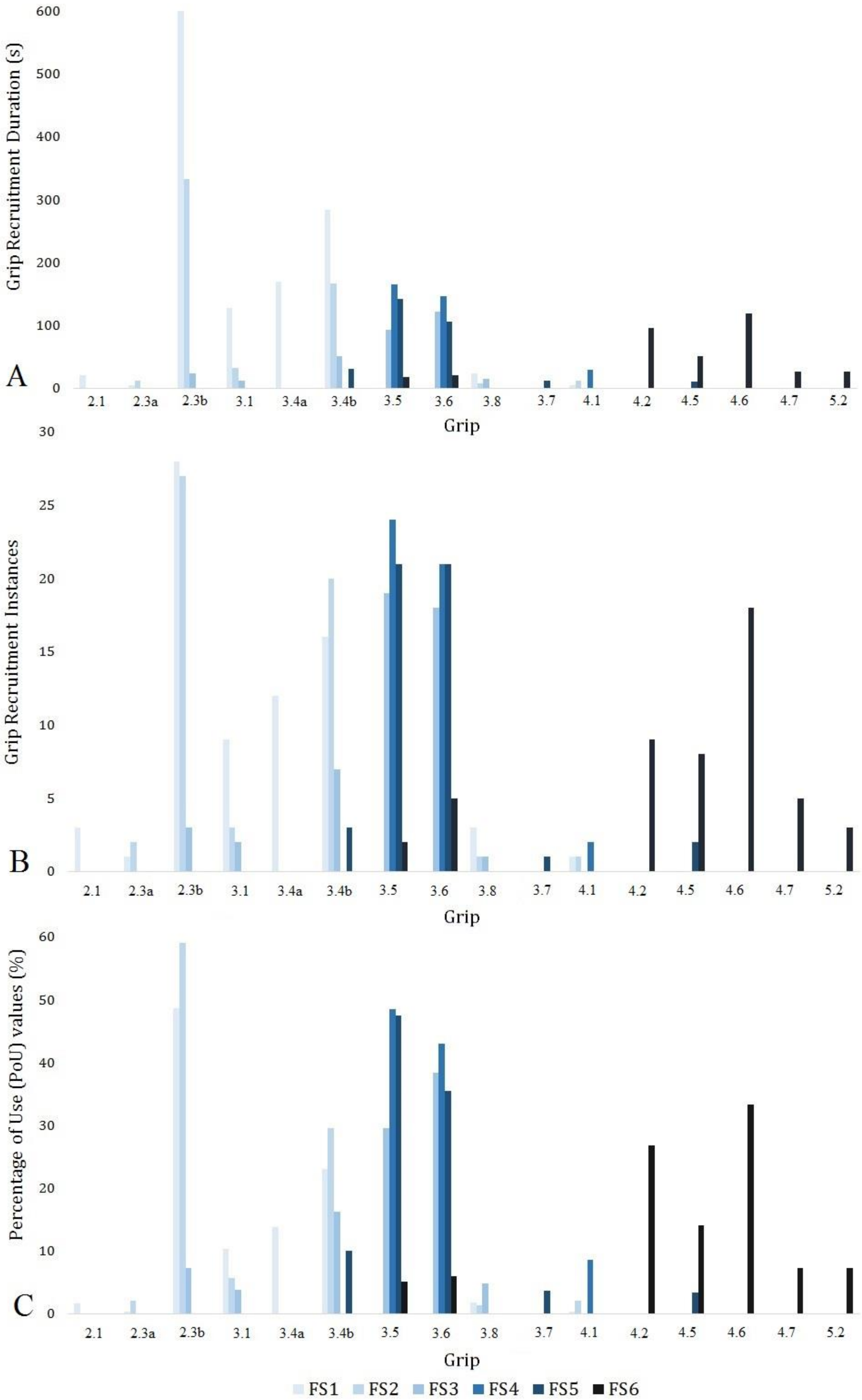

Figure 10: Durations of use for individual grips (A), the number of individual instances that grips were recruited (B), and the percentage of use (PoU) values (C) for each grip type across the six flake sizes (FS1-6) used in Experiment 1. Grips are arranged from left to right in order of the number of digits and aspects of the hand actively recruited.

Tables

Table 1: Previous terminology and definitions used within anthropological literature describing the grips used by humans when manipulating objects. In many instances these definitions and distinctions may be describing the same types of 'precision', 'power' or forceful precision grips, although it should be stressed that there is fluidity between finitely defined 'grip types' (as would be expected when attempting to segment ranges of movement into distinct individual positions).

Napier (1956)	
Precision Grip	Power Grip
"The object may be pinched between the flexor aspects of the fingers and the opposing thumb."	"The object may be held in a clamp formed by the partly flexed fingers and the palm, counter pressure being applied by the thumb lying more or less in the plane of the palm."

Shrewsbury and Sonek (1986)			
Type I	Type II	Type III	Type IV
"The apposition of the distal or proximal ungal pulp of a digit (pollex included) to a non-pulp aspect of another."	"The apposition of the distal ungal pulp of the pollex to that of one or more of the other digits."	"The apposition of the distal ungal pulp or the proximal ungal pulp of the pollex to another digit or, conversely, a digit to the pollex."	"The apposition of the proximal ungal pulp of the pollex to the proximal pulp of another digit."

Marzke and Shackley (1986)
Distinctions dependent on the number of fingers recruited in the grip (1), the positioning of the thumb and fingers (2), the role and position of the palm and its relation to the finger and thumb (3). (1) 2, 3, 4, and 5-jaw chuck, 4 fingers. (2) Tip-to-tip, pad-to-pad, pad-to-side, thumb-to-fingers, hook. (3) Buttressed pad-to-side, extended 3-jaw chuck, cradle, digitopalmer, squeeze.
Christel (1993)
Eight contact areas used in human precision grasping are distinguished between. 13 different combinations of these contact areas were identified as different grips during experiments.

Marzke and Wullstein (1996) See also: Marzke, (1997)	
Distinctions dependent upon the number of digits in a grip (1), the relative position of the thumb, fingers (2) and palm (3), and the movements performed by the thumb and fingers (4). (1) 2, 3, 4, and 5-jaw chuck, 2-finger scissor. (2) Tip-to-tip, pad-to-pad, pad-to-tip, pad-to-side, side-to-side, distal finger pad-to-pad, full finger pad-to-pad. (3) Buttressed pad-to-side, extended 3-jaw chuck, cradle. (4) Tip/pad translation and rotation, pad/pad rotation and translation.	
Transverse hook grip (power finger grip) Fingers 2-5 flexed around object, thumb adducted or opposes fingers. May included passive palm.	Squeeze (Power finger/active palm grip) Object held diagonally across palm by convergence of metacarpals 1 and 5 and by flexed fingers. Thumb adducted or opposed.

Pouydebat et al. (2008) See also: Marzke et al. (2009)				
Precision Contact between the distal phalanx of the thumb, the distal part of the index finger and the object.	Thumb-Distals Contact between the distal phalanx of at least three fingers and the object.	Thumb-Lateral Contact between the distal part of the thumb, the lateral side of the middle and proximal phalanges of the	Without Thumb Contact between one or several fingers, except the thumb, and the object.	Power Contact between the palm, one or several fingers and the object.

		index finger and the object.		
Pouydebat et al. (2011)				
Category 1 Contact between the distal phalanges of the thumb and the index finger and the object, involving the pincer grip between the tips of the first and second finger in more than 80% of the cases.	Category 2 Contact between the distal phalanx of the thumb and at least one distal part of another finger than the index.	Category 3 Contact between the distal phalanx of the thumb, the lateral side of the middle proximal phalanges of the index finger and the object.	Category 4 Contact between one or several fingers, except the thumb, and the object.	Category 5 Contact involving the palm, the thumb and one or several ventral part of other fingers and the object
Borel et al. (in press)				
61 contact areas were identified on the hand (A-I on the thumb, A-L on each finger, and A-D on the palm). The combinations of these contact areas used during object manipulation represented variation in the grips used during the manipulation of objects. 59 and 54 contact area combinations were observed for the left and right hands (respectively) in this study, although this does not preclude the possibility of combinations not recorded being used by humans.				

Table 2: Descriptive morphological data for the replica stone tools utilised in the four experiments. Presented here are those attributes most likely to be of concern during their manipulations. For more detailed morphometric data from these assemblages pleases see their respective original publications (see methods).

<table>
<tr><td colspan="13">Experiment One: Flakes</td></tr>
<tr><td></td><td colspan="2">Flake Size 1
(n = 57)</td><td colspan="2">Flake Size 2
(n = 57)</td><td colspan="2">Flake Size 3
(n = 57)</td><td colspan="2">Flake Size 4
(n = 57)</td><td colspan="2">Flake Size 5
(n = 57)</td><td colspan="2">Flake Size 6
(n = 57)</td></tr>
<tr><td></td><td>Mass (g)</td><td>Length (mm)</td><td>Mass (g)</td><td>Length (mm)</td><td>Mass (g)</td><td>Length (mm)</td><td>Mass (g)</td><td>Length (mm)</td><td>Mass (g)</td><td>Length (mm)</td><td>Mass (g)</td><td>Length (mm)</td></tr>
<tr><td>Mean</td><td>5.3</td><td>29</td><td>14.9</td><td>43</td><td>36.2</td><td>58</td><td>66.7</td><td>73</td><td>115.4</td><td>88</td><td>239.5</td><td>103</td></tr>
<tr><td>S.D.</td><td>1.419</td><td>0.615</td><td>4.4</td><td>1.261</td><td>10.8</td><td>1.308</td><td>20.4</td><td>1.437</td><td>32.6</td><td>1.635</td><td>66.9</td><td>1.568</td></tr>
<tr><td colspan="13">Experiment Two: Handaxes (n = 500)</td></tr>
<tr><td></td><td colspan="2">Mass
(g)</td><td colspan="2">Length
(mm)</td><td colspan="2">Width
(mm)</td><td colspan="2">Thickness
(mm)</td><td colspan="2">Elongation
(width/length)</td><td colspan="2">Refinement
(thickness/width)</td></tr>
<tr><td>Min-Max</td><td colspan="2">8-4484</td><td colspan="2">39-296</td><td colspan="2">25-200</td><td colspan="2">7-106</td><td colspan="2">0.31-1.1</td><td colspan="2">0.19-1.1</td></tr>
<tr><td>Mean</td><td colspan="2">577</td><td colspan="2">136</td><td colspan="2">92</td><td colspan="2">41</td><td colspan="2">0.688</td><td colspan="2">0.428</td></tr>
<tr><td>S.D.</td><td colspan="2">559</td><td colspan="2">38</td><td colspan="2">26</td><td colspan="2">17</td><td colspan="2">0.12</td><td colspan="2">0.131</td></tr>
<tr><td colspan="13">Experiment Three: Flakes, Handaxes, and ‘Lomekwian-sized’ Flakes</td></tr>
<tr><td></td><td colspan="4">Flakes (n = 60)</td><td colspan="4">‘Lomekwian’ Flakes (n = 60)</td><td colspan="4">Handaxes (n = 60)</td></tr>
<tr><td></td><td>Mass (g)</td><td>Length (mm)</td><td>Width (mm)</td><td>Thickness (mm)</td><td>Mass (g)</td><td>Length (mm)</td><td>Width (mm)</td><td>Thickness (mm)</td><td>Mass (g)</td><td>Length (mm)</td><td>Width (mm)</td><td>Thickness (mm)</td></tr>
<tr><td>Min-Max</td><td>11-85</td><td>46-75</td><td>30-69</td><td>4-36</td><td>224-1821</td><td>103-203</td><td>72-190</td><td>23-72</td><td>257-1953</td><td>112-206</td><td>76-141</td><td>25-67</td></tr>
<tr><td>Mean</td><td>34</td><td>60</td><td>46</td><td>14</td><td>677</td><td>145</td><td>119</td><td>44</td><td>598</td><td>148</td><td>101</td><td>41</td></tr>
<tr><td>S.D.</td><td>16</td><td>8</td><td>7</td><td>5</td><td>312</td><td>23</td><td>28</td><td>12</td><td>295</td><td>20</td><td>14</td><td>10</td></tr>
<tr><td colspan="13">Experiment Four: Flakes and Cores</td></tr>
<tr><td></td><td colspan="6">Flakes (n = 21)</td><td colspan="6">Cores (n = 20)</td></tr>
<tr><td></td><td colspan="6">Mass (g)</td><td colspan="6">Mass (g)</td></tr>
<tr><td>Min-Max</td><td colspan="6">5 - 194</td><td colspan="6">25 - 731</td></tr>
<tr><td>Mean</td><td colspan="6">54</td><td colspan="6">221</td></tr>
<tr><td>S.D.</td><td colspan="6">58</td><td colspan="6">245</td></tr>
</table>

Table 3: A description of the 29 grips identified during the 1067 stone tool-use events. Terminology and definitions follow those reported by Marzke and colleagues (Marzke and Wullstein, 1996; Marzke, 1997), although this was not possible in all instances due to the identification of previously unrecorded grips (highlighted in grey). Recruitment of the 'palm' refers to large areas of the metacarpals and/or thenar muscles, while 'MCP' refers to distal aspect of the metacarpal(s), the metacarpophalangeal joint. Only digits that make contact with the stone tool are described as being 'recruited'. In many instances, but particularly during pad-to-side grips, additional fingers were buttressed against 'recruited' fingers, and likely experienced some loading, but if they did not make contact with the tool, they were not included in this hand grip description.

Grip		**Number of Digits Recruited**	**Aspects of Rays 2-5 Recruited**	**Description**
Code	**Type** (Following Marzke, 1997)			
2.1	Two-Jaw Pad-to-Pad	2	2nd palmar distal phalanx	Pads of thumb and index finger recruited in opposition to secure tool.
3.1	Three-Jaw Pad-to-Pad	3	2nd and 3rd palmar distal phalanx	Pads of index and middle finger recruited in opposition to thumb to secure tool.
4.1	Four-Jaw Pad-to-Pad	4	2nd, 3rd and 4th palmar distal phalanx	Pads of index, middle and fourth finger recruited in opposition to thumb to secure tool.
5.1	Five-Jaw Pad-to-Pad	5	2nd to 5th palmar distal phalanx	Pads of index, middle, fourth and fifth fingers recruited in opposition to thumb to secure tool.
6.1	Cradle	5 + Palm	2nd to 5th palmar phalanges and metacarpals	Pads of index, middle, fourth and fifth fingers recruited in opposition to thumb to secure tool. Palm actively recruited to stabilise tool or oppose the cutting edge.
3.2	Three-Jaw Buttressed Pad-to-Pad	3 + MCP	2nd and 3rd palmar phalanges, proximal 2nd phalanx in opposition to cutting edge. 2nd MCP head may be used in buttressing role.	Palmar side of index and middle fingers recruited in opposition to thumb. Proximal aspect of index finger, and on occasion 2nd metacarpal head, rests on top of tool opposing cutting edge.
4.2	Four-Jaw Buttressed Pad-to-Pad	4 + MCP	2nd, 3rd and 4th palmar phalanges, proximal 2nd phalanx in opposition to cutting edge. 2nd MCP head may be used in buttressing role.	Palmar side of index, middle and fourth fingers recruited in opposition to thumb. Proximal aspect of index finger, and on occasion 2nd metacarpal head, rests on top of tool opposing cutting edge.

5.2	Five-Jaw Buttressed Pad-to-Pad	5 + MCP	2nd to 5th palmar phalanges, proximal 2nd phalanx in opposition to cutting edge. 2nd MCP head may be used in buttressing role.	Palmar side of index to fifth fingers recruited in opposition to thumb. Proximal aspect of index finger, and on occasion 2nd metacarpal head, rests on top of tool opposing cutting edge.
6.2	Five-Jaw Buttressed Pad-to-Pad	5 + MCP + Palm	2nd to 5th palmar phalanges and metacarpals, proximal 2nd phalanx in opposition to cutting edge. 2nd MCP head may be used in buttressing role.	Palmar side of index and middle fingers recruited in opposition to thumb. Proximal aspect of index finger, and on occasion 2nd metacarpal head, rests on top of tool opposing cutting edge.
2.3a	Two-Jaw Chuck Pad-to-Side	2	Lateral side of 2nd distal phalanx	Object secured between thumb and lateral side of the index finger. Less robust version of 2.3b, usually only the distal phalanx of index finger recruited.
2.3b	Two-Jaw Chuck Pad-to-Side	2	Lateral side of 2nd phalanges	Object secured between thumb and lateral side of index finger. More robust version of 2.3a, usually two or three phalanges on index finger recruited.
2.3c	Two-Jaw Chuck Pad-to-Side	2	Lateral side of 3nd phalanges	Object secured between thumb and lateral side of middle finger. Index finger not recruited.
3.3	Three-Jaw Chuck Pad-to-Side	3	Lateral side of 2nd and 3rd phalanges	Object secured between thumb and lateral side of index and middle fingers.
3.4a	Three-Jaw Chuck Pad-to-Side	3	Palmar 2nd phalanges and lateral side of 3rd distal phalanx.	Object secured between thumb and lateral side of middle finger. Index finger used in forceful opposition to cutting edge. Less robust version of 3.4b, often only distal phalanx of middle finger recruited.

3.4b	Three-Jaw Chuck Pad-to-Side	3	Palmar 2nd phalanges and lateral side of 3rd phalanges.	Object secured between thumb and lateral side of middle finger. Index finger used in forceful opposition to cutting edge. More robust version of 3.4a, two or three phalanges of middle finger normally recruited.
2.5	Two-Jaw Buttressed Pad-to-Side	2 + MCP	Lateral side of 2nd phalanges, palmar side of 2nd metacarpal.	Object secured between thumb and side of index finger. 1st and 2nd metacarpals recruited in opposition to cutting edge and to aid tool securing.
3.5	Three-Jaw Buttressed Pad-to-Side	3 + MCP	Proximal 2nd phalanx, palmar side of 2nd metacarpal, lateral side of distal 2nd phalanx and 3rd phalanges.	Tool secured between thumb and side of middle finger. Index finger has dual role; proximal aspect has forceful role in opposition to cutting edge, distal aspect opposes thumb.
4.5	Four-Jaw Buttressed Pad-to-Side	4 +MCP	Proximal 2nd phalanx, palmar side of 2nd metacarpal, lateral side of distal 2nd phalanx and 3rd and 4th phalanges.	Tool secured between thumb and side of middle and fourth fingers. Index finger has dual role; proximal aspect has forceful role in opposition to cutting edge, distal aspect opposes thumb.
5.5	Five-Jaw Buttressed Pad-to-Side	5 + MCP	Proximal 2nd phalanx, palmar side of 2nd metacarpal, lateral side of distal 2nd phalanx and 3rd to 5th phalanges.	Tool secured between thumb and side of middle, fourth and fifth fingers. Index finger has dual role; proximal aspect has forceful role in opposition to cutting edge, distal aspect opposes thumb.
3.6	Buttressed Three-Jaw-Chuck Full Finger Pad-to-Side	3 + MCP	2nd phalanges (palmar), 2nd metacarpal, lateral side of 3rd phalanges.	Tool secured between the thumb and side of middle finger, with the palmar side of the index finger and 2nd metacarpal used in forceful opposition to the cutting edge.
4.6	Buttressed Four-Jaw-Chuck Full Finger Pad-to-Side	4 + MCP	2nd phalanges (palmar), 2nd metacarpal, lateral side of 3rd and 4th phalanges.	Tool secured between the thumb and side of middle and fourth fingers, with the palmar side of the index finger and 2nd metacarpal used in forceful opposition to the cutting edge.

5.6	Buttressed Five-Jaw-Chuck Full Finger Pad-to-Side	5 + MCP	2nd phalanges (palmar), 2nd metacarpal, lateral side of 3rd to 5th phalanges.	Tool secured between the thumb and side of middle, fourth and fifth fingers, with the palmar side of the index finger and 2nd metacarpal used in forceful opposition to the cutting edge.
6.6	Buttressed Five-Jaw-Chuck Full Finger Pad-to-Side w/ Active Palm	5 + Palm	2nd phalanges (palmar), 2nd metacarpal, lateral side of 3rd to 5th phalanges.	Tool secured between the thumb and side of middle, fourth and fifth fingers, with the palmar side of the index finger and 2nd metacarpal used in forceful opposition to the cutting edge. Palm actively recruited in opposition to cutting edge and to secure tool.
3.8	Not Previously Described	3	Distal 2nd phalanx, lateral side of distal and/or medial 3rd phalanx.	Tool forcefully secured between pads of thumb and index finger. Lateral side of middle finger recruited in supportive role across lateral side of tool.
3.7	Not Previously Described	3	Medial side of 2nd digit and lateral side of 3rd digit.	Tool secured by the thumb and medial side of index finger against the lateral side of the middle finger. May or may not be buttressed against the 2nd metacarpal.
4.7	Not Previously Described	4	Medial side of 2nd digit and lateral side of 3rd and 4th digits.	Tool secured by the thumb and medial side of index finger against the lateral side of the middle and fourth fingers. May or may not be buttressed against the 2nd metacarpal.
6.7	Transverse Hook	2-5 + Palm	Palmar aspects of digits 2-5 and metacarpals 2-5.	Fingers 2-5 flexed around object, thumb adducted or opposes fingers, palm may or may not be recruited.
6.8	Squeeze	2-5 + Palm	Palmar aspects of digits 2-5 and metacarpals 2-5.	Fingers 2-5 flexed around object held diagonally across metacarpals 1-5. Thumb may be adducted of opposing fingers.

6.9	Not Previously Described	2-5 + Palm	Palmar aspects of digits 2-5 and metacarpals 2-5.	Fingers 3-5 flexed around object, thumb in opposition to fingers 3-5. Palm passively recruited. Index finger adducted towards distal tip of tool in opposition to direction of cutting.

Table 4: Records of the grips used during each of the four experiments in descending order relative to their PoU. Highlighted in bold are those with PoU values ≥10. If one of the 29 grips detailed in Table 3 are not listed for an experiment then it displayed a PoU value of 0 and was not recruited. 'NV' refers to the time (PoU) that a grip could not be determined during an experiment.

	Experiment 1		Experiment 2		Experiment 3						Experiment 4			
	Flakes (n = 342)		Handaxes (n = 500)		Flakes (n = 60)		Large Flakes (n = 60)		Handaxes (n = 60)		Flakes (n = 23)		Cores (n = 22)	
Relative Importance	Grip	PoU (%)	Grip	PoU (%)	Grip	PoU (%)	Grip	PoU (%)	Grip	PoU (%)	Grip	PoU (%)	Grip	PoU (%)
1	**2.3b**	30.8	**6.2**	31.2	**3.5**	45.4	**6.1**	33.7	**6.1**	31	**3.4b**	33.2	**3.4b**	41.7
2	**3.4b**	17.1	**3.5**	19.1	**2.3b**	20.3	**6.6**	32.7	**6.2**	29.3	**3.4a**	21	**6.6**	29.5
3	**3.5**	13.5	**4.5**	18.4	**3.4b**	17.5	**6.2**	13.6	**6.6**	28.6	**3.5**	15.3	4.6	6
4	**3.6**	12.7	**6.1**	11.0	**3.6**	13.7	4.5	4.5	6.7	2.2	4.6	7.2	5.6	5.9
5	3.1	5.5	6.6	4.8	3.3	0.8	5.2	2.6	4.6	1.6	3.1	5.3	N V	3.5
6	3.4a	5.5	2.5	4.2	4.6	0.8	4.6	2.2	5.6	1.6	3.6	5.3	3.4a	3.5
7	4.6	3.7	4.6	1.7	3.1	0.7	5.6	2	4.5	1.5	N V	4.2	4.7	2.3
8	4.2	3.1	N V	1.6	4.1	0.4	3.5	1.9	5.2	1.4	2.3b	2.3	3.1	1.6
9	4.5	1.9	2.3b	1.5	6.7	0.1	6.7	1.6	3.5	0.8	4.1	2.2	3.5	1.5
10	3.8	1.5	3.4b	1.1	2.3c	0.1	N V	1.3	4.7	0.5	3.3	1.2	3.8	1
11	4.1	1.5	5.5	0.7	3.4a	0.1	3.6	1	5.5	0.5	2.5	1.2	4.1	0.9
12	5.2	1.0	3.6	0.7	4.5	0.1	5.1	1	5.1	0.3	4.5	1.1	3.6	0.7
13	4.7	0.8	6.7	0.7	N V	0.04	4.7	0.8	N V	0.3	2.3a	0.1	3.3	0.3
14	2.1	0.7	4.2	0.5	-	-	3.2	0.5	4.2	0.2	5.6	0.1	6.2	0.3
15	2.3a	0.5	5.2	0.5	-	-	5.5	0.5	6.9	0.2	4.2	0.1	6.8	0.3
16	3.7	0.4	3.2	0.5	-	-	4.1	0.1	3.1	0.07	2.3c	0.03	6.7	0.3
17	-	-	2.3a	0.4	-	-	2.3a	0.01	4.1	0.02	4.7	0.03	5.1	0.3
18	-	-	2.1	0.4	-	-	-	-	-	-	6.7	0.03	4.5	0.3
19	-	-	3.1	0.3	-	-	-	-	-	-	-	-	6.1	0.1
20	-	-	5.6	0.2	-	-	-	-	-	-	-	-	5.2	0.4
21	-	-	6.8	0.2	-	-	-	-	-	-	-	-	-	-
22	-	-	5.1	0.1	-	-	-	-	-	-	-	-	-	-
23	-	-	3.7	0.02	-	-	-	-	-	-	-	-	-	-
24	-	-	6.9	0.01	-	-	-	-	-	-	-	-	-	-
25	-	-	4.1	0.01	-	-	-	-	-	-	-	-	-	-

Table 5: Mann-Whitney U tests comparing the PoU values for grips 2.3b, 3.4b, 3.5, 3.4a and 3.6 while using flake tools between Experiment 1 and Experiment 3, Experiment 1 and Experiment 4, and Experiment 3 and Experiment 4. Subsequent to the Bonferroni Correction being applied (α = .001) significant differences are highlighted in bold. Italicized significant differences indicate that the higher numbered experiment has the greater PoU values, as indicated in Table 4.

Experiment Comparison	Grip Type				
	2.3b	3.4b	3.5	3.4a	3.6
1 ↔ 3	**.0001**	***.0001***	***.0001***	.4317	.4734
1 ↔ 4	.2050	***.0001***	.0113	***.0001***	.0618
3 ↔ 4	.0036	.0732	**.0002**	***.0001***	.0193

Table 6: Mann-Whitney U tests comparing the PoU values for grips 6.2, 6.6, 6.1, 3.5, 4.5 and 3.4b during the use of handaxes and core tools in Experiment 2 and Experiment 3, Experiment 2 and Experiment 4, and Experiment 3 and Experiment 4. Subsequent to the Bonferroni Correction being applied (α = .0083˙) significant differences are identified in bold. Italicized significant differences indicate that the higher numbered experiment has the greater PoU values, as indicated in Table 4.

Experiment Comparison	Grip Type					
	6.2	6.6	6.1	3.5	4.5	3.4b
2 ↔ 3	.5511	***.0001***	***.0001***	**.0058**	**.0016**	.2341
2 ↔ 4	**.0002**	.0124	.0299	.7802	.0379	**.0001**
3 ↔ 4	**.0001**	***.0058***	**.0001**	.0384	.8135	***.0001***

Table 7: Mann-Whitney U tests comparing the grip PoU values between different tool types within Experiments 3 and 4. Subsequent to the Bonferroni Correction being applied (α = .0023 and .0125 for Experiments 3 and 4, respectively) significant differences are highlighted in bold.

<table>
<tr><th rowspan="2">Experiment</th><th rowspan="2">Tool Type Comparison</th><th colspan="7">Grip Type</th></tr>
<tr><th>3.5</th><th>2.3b</th><th>3.4b</th><th>6.1</th><th>6.6</th><th>6.2</th><th>3.6</th></tr>
<tr><td rowspan="3">3</td><td>Flakes ↔ Large Flakes</td><td>.0001</td><td>.0001</td><td>.0001</td><td>.0001</td><td>.0001</td><td>.0001</td><td>.0001</td></tr>
<tr><td>Flakes ↔ Handaxes</td><td>.0001</td><td>.0001</td><td>.0001</td><td>.0001</td><td>.0001</td><td>.0001</td><td>.0001</td></tr>
<tr><td>Large Flakes ↔ Handaxes</td><td>.4445</td><td>1</td><td>1</td><td>.882</td><td>.5236</td><td>.0003</td><td>1</td></tr>
<tr><td rowspan="2">4</td><td></td><td>3.5</td><td colspan="2">3.4b</td><td colspan="2">6.6</td><td colspan="2">3.4a</td></tr>
<tr><td>Flakes ↔ Cores</td><td>.0078</td><td colspan="2">.229</td><td colspan="2">.0078</td><td colspan="2">.0063</td></tr>
</table>

Table 8: Multinomial logistic regression between PoU values for grips and tool form attributes in Experiment 1. Only grips with PoU values above 5 are investigated. Reported here are the Cox and Snell measure of R^2 and the likelihood ratio test of significance, which reports whether variables significantly predict the outcome category (in this case grip type). Significance is assumed in line with the Bonferroni correction ($\alpha = .0042$) and is highlighted in bold.

	2.3b		3.4b		3.5		3.6		3.1		3.4a	
	p	R^2	*p*	R^2	*p*	R^2	*p*	R^2	*p*	R^2	*p*	R^2
Mass (g)	**.0001**	.404	**.0001**	.170	.875	.004	.751	.007	**.0001**	.107	**.0001**	.122
Max. Length (mm)	**.0001**	.369	**.0001**	.161	.025	.039	.007	.049	**.0001**	.083	**.0001**	.133

Table 9: Multinomial logistic regression between PoU values for grips and tool form attributes in Experiment 2. Only grips with PoU values above 5 are investigated. Reported here are the Cox and Snell measure of R^2 and the likelihood ratio test of significance, which reports whether variables significantly predict the outcome category (in this case grip type). Significance is assumed in line with the Bonferroni correction (α = .0014) and is highlighted in bold.

	Experiment 2							
	6.2		6.1		4.5		3.5	
	p	R^2	*p*	R^2	*p*	R^2	*p*	R^2
Mass (g)	**.0001**	.129	**.0001**	.333	**.0001**	.087	**.0001**	.343
Max. Length (mm)	**.0001**	.287	**.0001**	.239	.006	.045	**.0001**	.327
PC1	.685	.013	.057	.033	.140	.027	.179	.025
PC2	.072	.0001	.082	.0001	.358	.020	.174	.025
Refinement Index	.032	.036	.126	.027	.191	.025	**.001**	.054
Edge Angle	**.0001**	.059	.221	.023	.457	.017	**.0001**	.093

Table 10: Spearman's rank-order correlation between the mass of the flake and core tools used in Experiment 4 and the PoU values for their respective grips (Dytham, 2011). Only grips with PoU values above 5 within each experiment are investigated. Significance is assumed in line with the Bonferroni corrections (α = .0083 and .0125 for flake and core tools, respectively).

		Grip					
		3.4b	3.4a	3.5	4.6	3.1	3.6
Flake Mass	*p*	.019	**.0001**	.037	.105	**.008**	.562
	r	.507	-.816	.457	.363	-.560	.134
		Grip					
		3.4b	6.6	4.6	5.6		
Core Mass	*p*	**.005**	**.0001**	.370	.210		
	r	-.559	.804	.212	.289		