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Visuospatial integration and cognitive archaeology:

The relationship between body, material culture and human brain

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PhD Thesis

Visuospatial integration and cognitive archaeology – the relationship between body, material culture and human brain

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Ad Angela
E a tutto quello
che il suo Spirito
può regalare
a questo
Mondo.

A Noè
Porqué tenemos
toda la vida
por delante...
Siempre.

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Abstract

The emergence of stone tools is a crucial moment in the human lineage (Shea, 2016). Palaeolithic stone tools not only offer an abundant record, they also provide us with information regarding technological changes and document the expression of new behavioural capabilities (Stout, 2011). With the advent of tool use, the human adaptive niche expanded and it started a trend of technological elaboration that has continued to the present day.

The parallel trends of brain expansion and increased technological levels are crucial features of human evolution, even if their co-evolutionary relationships still lack information (Gibson, & Ingold 1993; Ambrose, 2001; Wynn, 2002; Stout, 2006). However, it is irrefutable that modern humans display advanced capacities in complex technological, symbolic and social actions, which stand out among other primates and among extant species. It remains unclear whether or not these peculiarities are due to a more advanced cultural transmission, or are due to the increase in greater cognitive capacity in our ancestors (Stout, 2011). In order to shed more light on the evolution of cognition, there is a branch of archaeology (namely, cognitive archaeology) which aims to study past minds.

Although it is not possible to study the cognitive capabilities of extinct human species directly, some proxies can be used to solve this problem. For example, the morphological properties and technological characteristics of Palaeolithic stone tools are used to gain an insight into everything from the evolutionary trajectory of human cognition to changes in diet, social systems and landscape use. Yet, every stone tool ever produced was made by, and intended to be used by, the human (or early human) hand. One of the most important factors to consider when interpreting what Palaeolithic stone tool technologies can tell us about early humans is whether or not stone tools were designed following criteria determined by ergonomic principles.

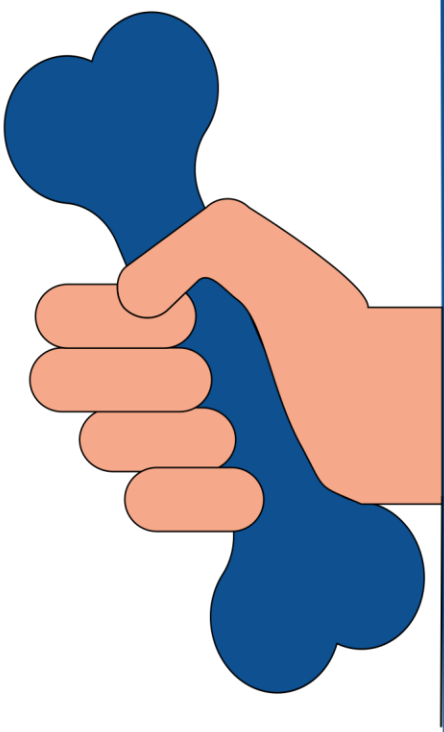
An ergonomic understanding of Palaeolithic stone tools does not mean they cannot also provide us with information about other important behavioural and evolutionary considerations. Instead, they can provide base-line information about their principal purpose – being used and applied by the hand – and this information can in turn be used to interpret the relevance and potential impact of other factors that may influence stone tool

morphologies (e.g., cognitive variation, functional context, cultural variation). Palaeolithic archaeologists have long recognised the vital importance of understanding how the human hand interacts with stone tools, and the impact this could have had on their design, and in turn, their morphological properties (Napier, 1956; Marzke and Shackley, 1986; Foley, 1987). Yet our understanding of Palaeolithic stone tool design and use from an ergonomic perspective is surprisingly sparse. It is therefore necessary to reconsider and implement knowledge on the hand-stone tool relationship, by providing experimental information on biomechanical and cognitive aspects.

In this study, two ground-breaking experimental methodologies are used to provide information on the biomechanical and psychophysiological relationship between the hand and two types of Lower Palaeolithic stone tools, the above-mentioned Oldowan choppers and Acheulean handaxes.

01

INTRODUCTION



1. Introduction

Archaeologists work with small sample sizes from non-repeatable excavations. This means it is difficult to test any reliable archaeological hypothesis. For the past few centuries, people have used replicative archaeological experiments for a variety of reasons. Often researchers come across questions that cannot otherwise be answered. Or they are fascinated by primitive or ancient crafts and are seeking to challenge common conceptions of the past. Or simply they have an interest in the role of specific artefacts or processes. Regardless of the reason, for the most part, experiments in archaeology have been justifiably ignored because of their lack of a strong theoretical basis and their lack of applicability in testing the archaeological hypothesis. Even if archaeologists employ scientific technologies, the development of hypotheses lacks the ability in many aspects to be a replicative, controlled science.

Over the past 10 years, this situation has changed. Experimental archaeology has started to follow rigorous scientific procedures in designing and executing experiments. The aim of experimental archaeology is still to understand how people created and used a variety of items in the past. However, descriptive methods have given way to more innovative techniques. The approach has become multidisciplinary, and it is now common to apply modern technologies to study prehistoric human behaviour.

The aim of this research is to explore the ergonomics and the cognitive aspects of hand–tool relationships during stone tool manipulation. The approach used here is experimental, and the thesis is based on two different experiments. The experiments were made possible thanks to the many volunteers that participated.

Each experiment has a specific aim and methodology and is designed to provide information on the research topics.

1.1 Structure of the Dissertation

The objectives of this PhD research are:

a. Biomechanical analysis of the hand during Lower Palaeolithic stone tool grasping.

b. Psychophysiological analysis during Lower Palaeolithic stone tool manipulation.

The respective experiments are:

a. Analysis of the pattern of finger flexion during the comfortable grasping of Lower Palaeolithic stone tools.

b. Analysis of the individuals' electrodermal activity (attention and emotion) during Lower Palaeolithic stone tool manipulation.

This is an article-based thesis. A total of six articles, five published and one under review, are included in the dissertation. These articles represent the core of the research and thus the following sections are structured in accordance with the different methodologies used in the surveys. The following sections will include:

i. A general overview of cognitive archaeology and the theories on visuospatial integration and extended mind. The biomechanical aspects of stone tool use and production and the general aspects of tool manipulation and haptic perception will be introduced. It will also briefly and simply include some general information on the evolution of the human hand.

ii. The **Materials and Methods** section comprises all the methodologies used to assess the ergonomics and the cognitive aspects of the hand–tool relationship. In this section, all the techniques employed in research through the years are described. The techniques applied in each study can be found in the corresponding articles, including a complete description of the technique, established protocols and achieved results. This section is divided into three subsections regarding: morphometrics, biomechanics, and psychophysiology.

iii. The **Results** section is the core of the research and includes the four published articles and the one under review.

iv. The **Discussion** section will interpret the results of the surveys and take the existing bibliography into consideration.

v. The **Conclusion** section summarizes the most relevant outputs of this PhD research.

vi. The **Bibliography** includes the reference list of the works cited through this manuscript.

1.2 Cognitive archaeology

1.2.1 Human cognitive evolution

Humans are unusual animals and our cognitive skills are probably the most prominent uniqueness of our species. Over the past 25 years, research on the evolution of human cognition has been dominated by a type of evolutionary psychology where the human mind is seen as a large collection of computationally distinct 'modules'. Each of these modules was presumed to be shaped by natural selection in order to solve a particular type of problem faced by extinct species. This hypothesis suggests that the brain is the only factor responsible for cognition, and the technological evolution is due to brain enlargement and development. On the other hand, in the 60s and 70s, archaeologists organized stone tool variability using labels, which were useful for description and communication purposes, but did not take the functional implications of the types into consideration. Most archaeologists followed a typological approach regarding material culture, in which case emphasis was placed on artifact classes rather than the human behaviours and cognition involved in their production (Putt, 2016). André Leroi-Gourhan Laid the foundations for understanding the evolution of hominin cognition and especially language from technical procedures (Leroi-Gourhan, 1964). In 1969, paleoneurologist Ralph Holloway proposed stone tools as evidence for early human linguistic ability (Holloway, 1969). Albeit with initial difficulty, archaeologists started to consider stone tools as a proxy of prehistoric cognitive levels, and not only components of thinking (Pelegrin, 2009).

Lately, theories on human cognition interpret the archaeological record as an integral part of the thinking process, and treats stone tools as active participants in mental life (Wynn et al., 2021). This second approach is at the basis of this thesis, and cognitive archaeology is the main component of the surveys presented here.

Cognitive archaeology studies human cognitive evolution by applying cognitive-science theories and concepts to archaeological remains of the prehistoric past. The material remains of past activities are used as traces to understand some feature of the prehistoric minds (Coolidge and Wynn, 2016). When studying the cognitive aspect of the technological evolution, the primary source of information is stone tools, which represent the best preserved remaining evidence of prehistoric behaviour and cognition (Stout et al., 2002). Stone tools provide evidence of individual technical skills and they indicate certain minimum required competences (Gowlett, 1996) for the production of some artifacts (Currie and

Killin, 2019). Moreover, lithic implements can be a source of information concerning prehistoric mental abilities (Toth and Schick, 1993; Schlanger, 1996; Stout et al., 2002; Nowell and Davidson, 2010; Baena and Dominguez-Rodrigo, 2012; Moore and Perston, 2016). In order produce solid inferences, cognitive archaeology needs to apply an interdisciplinary approach (Iliopoulos and Malafouris, 2014). In fact, in the last decade, anthropology, archaeology, neurobiology and cognitive science have shared information (Bruner et al., 2018) and cognitive archaeology has started to use psychological models to interpret the archaeological record (Coolidge et al. 2015).

Cognitive archaeology relies on a variety of theories, and most of them take a "Cartesian position" (see Nolan, 1997) on the ontological status of the mind itself. Namely, they consider minds to be distinct from bodies, and to consist of internal representations that structure action (Coolidge and Wynn, 2016). Cognitivist models have been used to interpret the existence of the artifacts, which were seen as a physical realization of representations existing within the mind of ancient humans. In fact, for cognitivism, the brain recreates the external world in the form of internal representations (Clark, 1997) and the separation between the mind and the body is clear (Malafouris, 2013). However, more recently, the neurocentric view of cognition has been progressively replaced with new theories where the body and the environment have a complementary role in cognition. The "*extended mind theory*" claims that the cognitive processes that make up our minds can reach beyond the boundaries of individual organisms to include aspects of the organism's physical and socio-cultural environment (Kiverstein et al., 2013). Already in 1979, Gibson shows how visual perception is the result of a dynamic coupling of perceiver and environment in which the perceiver manipulates information found in its environment (Gibson, 1979). In recent years, some anthropological studies have attempted to draft the cognitive basis of the engagement of the mind with the artefactual world. In particular, the aim was to use the contributions from various disciplines (ranging from neurobiology, psychology, to archaeology and anthropology) in order to show that our minds have co-evolved in symbiotic partnership both with brain and culture (Donald, 2000).

1.2.2 Material culture

Material culture refers to the physical objects, resources, and spaces, which could define a culture and could define aspects of the behaviours and perceptions of the members of that same culture. When studying material culture, the focus is not only on the objects and on their physical properties, but it is also on the ways in which these items are central to an understanding of a culture. In this sense, the study of material culture explores the tangled relationships between people and things.

There are two approaches to study "things". From one point of view, the study can be "*object-cantered*", where the focus is on the object itself and its specific physical attributes like the material the object is made of, its shape and weight, its design and the style or decorative status that it could have (Herman, 1992). The physical attributes of objects play a crucial role for archaeologists, which can be used to place objects into broader categories or groups such as the technological modes. From another point of view, the study can be "*object-driven*", where the emphasis is on how objects relate to the peoples and cultures that make and use them. Here, contextualization is a pivotal factor because the meaning of objects may change through time and space. From these perspective, objects are not merely passive tools; they have an active role, they transcend their material status, and create symbolic meaning rather than simply reflect it (Herman, 1992). Moreover, through niche construction, minds are "scaffolded" and cognition is intimately sculpted by the activities conducted in the cognitive niche (Sterelny 2010).

Regarding human evolution, material culture is a component of the environment, and it acts like a selection factor, favouring some individuals and disadvantaging others. The first intentionally modified stone tools date back to 2.6 Myr ago, in the form of cores and flakes, which were probably used for cutting up carcasses to access high nutrient meat from animals (Semaw et al., 1997) (Figure 1). This early technology is referred to as the Oldowan Industry (Plummer and Finestone, 2018) and it was progressively substituted by Acheulean cutting tools, which include handaxes (large flakes, and retouched flakes made through a bifacial knapping process), where percussion extends over almost all or all the stone's surface (Lycett, 2011) (Figure 2). In the archaeological record, these kind of technological changes are considered significant indicators of human cultural evolution (Schick and Toth, 1994), and have been linked to the increase of human brain size (Semaw et al., 2009).

The interpretation of stone tool use and production is an intricate topic in the archaeological field. In the 50s, the main interpretation was mainly object-cantered and lithic tools were studied through their physical properties. The most influential approach to study the lithic industries was based on a "type list", which labelled and organized Lower and Middle Palaeolithic stone tools (Bordes, 1950). Later, researchers started to give more importance to the underlying dynamic processes of lithic production and, the existence of neural similarities between toolmaking and language was proposed (Leroi-Gourhan 1964; Holloway, 1969). The switch from a typological description to the exploration of hidden properties makes it possible to interpretat the archaeological remains as evidence of human cognition. Apart from the physical aspects of material culture, there are also the ideas associated with these objects. Archaeologists started to take into consideration these non-physical aspects of objects, considering the archaeological remains as traces of past activities and as data attesting to the cognition of extinct species (Malafouris, 2016).

One theoretical attempt to bridge cognition and archaeology is the "Material Engagement Theory," where artefacts are seen not as inert and passive instruments, but rather loaded with meanings (Malafouris, 2016). Namely, there is a synergy between cognition and material culture: a interlacing of brains, bodies and things (Renfrew and Malafouris, 2009). The objects are, therefore, rich in significance, and influence the relationships between humans and their environment (Malafouris, 2016). Even if Malafouris' attempt was ground-breaking, these models remain theoretical, and his arguments are not supported by experimental studies. Clearly, testing cognitive hypotheses in extinct species is challenging, but it can be done through the integration of independent sources of information (Bruner et al., 2018).

Experiments with living humans have provided insights into the cognitive and biomechanical aspects of lithic technology. Early stone tools provide direct evidence of human cognitive and behavioural evolution that is otherwise unavailable. A proper interpretation of these data requires a robust interpretive framework linking archaeological evidence to specific behavioural and cognitive actions. In order to interpret results of archaeological experiments from the perspective of extended cognition, it should necessary to firstly evaluate whether or not tools are real parts of the body-brain-tool system and their role in the cognitive structure (Bruner, 2021).

In this sense, an innovative experimental approach in cognitive archaeology has been proposed by Dietrich Stout (2015). In the survey, the authors proved that the production of

Acheulean tools demands higher cognitive control when compared to Oldowan toolmaking (Stout et al., 2015). Oldowan flake production primarily concerns the evaluation of core morphology and object manipulation, and it that does not seem to be related with executive capacities for strategic planning (which are critical for the development of complex tool use and tool making abilities). Acheulean tool production is a complex visuospatial task, which requires higher cognitive demands and increased visuomotor coordination when compared with Oldowan production (Stout and Chaminade, 2007; Stout and Chaminade 2012). The differences in technological complexity between Oldowan and Acheulean tools could indicate a cognitive transition. Clearly, we cannot know if the cognitive processes of modern humans resemble those of early humans. However, we can assume that to complete the same task there are at least the same basic cognitive operations (Putt et al., 2017). Finally, this study is an attempt to infer the functional brain activity of earlier human species using modern humans (Putt et al., 2017).

Figure 1: Oldowan chopper.

Figure 2: Acheulean handaxe.

1.3 Visuospatial integration: The brain, the body, the tools

Current theories in extended mind suggest that cognition is the result of an integrative process involving brain, body, and environment (Bruner and Iriki, 2016). In primates (and most of all in humans), the relationships between inner and outer components strictly rely on the body (the functional interface). The outer environment is in contact with the nervous system mainly through the eyes and the hand. In this sense, the parietal areas are essential nodes of the processes of visuospatial integration, coordinating the eye-hand system and the outer and inner environments. The parietal elements primarily involved in visuospatial management are the intraparietal sulcus and precuneus, both of which lie hidden in the depths of the cerebral volume (Ebeling and Steinmetz 1995). Morphological differences in the parietal lobes are particularly interesting in human evolution, and it can be hypothesized that the visuospatial functions and the role of the body as an interface have experienced important evolutionary changes in our species. When compared with more archaic human species, both Neanderthals and modern humans display a similar cranial capacity (Bruner and Holloway, 2010), and an enlargement of the parietal cortex (albeit to a different pattern and degree) (Bruner, 2018). Neanderthals displayed a lateral bulging of the upper parietal surface, while modern humans displayed dilation of the upper parietal volume, both laterally and longitudinally (Bruner et al., 2003; Bruner, 2004) (Figure 3). Moreover, Neanderthals are the most encephalized non-modern taxon, with a relatively shorter parietal lobe.

The morphological changes can be tentatively associated with changes in brain structure, but this remains speculation. However, changes in the brain morphology is not the only way to investigate cognition in extinct species. Behavioural aspects are pivotal in the identification of cognitive skills and the capacity to integrate the environment. A really good example has come from dental anthropology, which provides information about scratches on Neanderthals teeth, which led researchers to hypothesise that they were using the mouth as a "third hand" (Bermúdez de Castro et al., 1988, Lozano et al., 2008). This same behaviour can be seen in the modern population (Clement et al., 2012). However, most modern hunter-gatherers do not use their teeth in handling and there are few scratches on the dental surface, and they are limited to a small percentage of individuals. This controversial behaviour found in Neanderthals could be due to an insufficiency in the eye-hand system in integrating the visuospatial processes required by complex culture (Bruner and Lozano, 2014). Therefore, additional body elements (the mouth) are needed to interact with the material culture.

Curiously, in the cortical somatosensory representation (the "homunculus"), the mouth is the next element in importance after the hand. This is an example of how we can evaluate possible functional changes in extinct human species by using visuospatial behaviours that are evident from human ecology and material culture (Bruner and Iriki, 2016). Finally, visuospatial integration, within the perspective of extended cognition, may have had a major influence in establishing current human intellectual abilities and social patterns (Bruner et al., 2018).

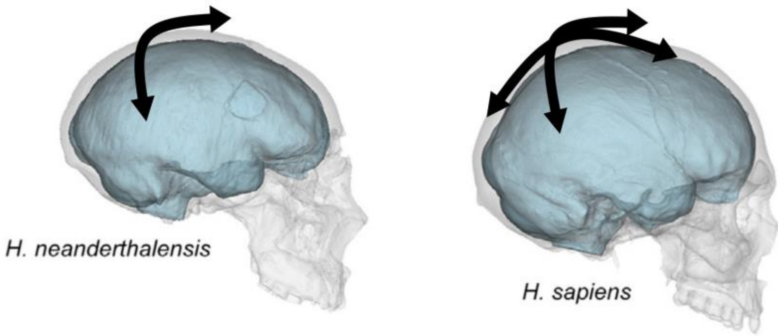


Figure 3: Neanderthals display a lateral bulging of the upper parietal surface. Modern human display a longitudinal bulging of the whole upper parietal profile. Image: Bruner and Iriki, 2016.

1.4 Handling tools

1.4.1 Haptic perception

The hands' tactile properties regard the ability to perceive touch (passive tactile perception). However, when we use our hands to examine an object, we do so through exploratory movements of the fingers. This is called *haptics* (active tactile perception) and through haptic perception, we are able to recognize objects using our sense of touch. It involves both the somatosensory perception of patterns on the skin surface (e.g., edges, curvature, and texture) and the proprioception of hand position and conformation. Humans can accurately recognize three-dimensional objects through touch (Klatzky et al., 1985). The haptic exploratory procedures (e.g. moving the fingers over a surface or holding the entire object in the hand) is what we use for object recognition (Lederman and Klatzky, 1987). The haptic system puts together sensory information obtained from the receptors of the skin (mechanoreceptors and thermoreceptors) together with the receptors of the muscles, tendons, and joints (Lederman and Klatzky, 2009). Cutaneous receptors are located on the whole surface of the body. However, the mechanoreceptors and the thermoreceptors located in the glabrous skin of the human hand have been studied deeper that other parts of the body (Jones and Lederman, 2006) (Figure 4). Mechanoreceptors perceive extracellular stimuli (touch, pressure, stretching etc.) and translate them into intracellular signals (Iheanacho and Vellipuram, 2019). Thermoreceptors perceive changes in skin temperature and mediate the human experience of warmth and cold (Stevens and Choo, 1998). The kinesthetic inputs from mechanoreceptors in muscles, tendons and joints contribute to the human perception of limb position and limb movement in space (Gandevia, 1996; Taylor, 2009). Both cutaneous and kinaesthetic contributions are necessary in the haptic process. They are combined and weighted in different ways to serve various haptic functions. Human haptic experience is influenced by a variety of factors at multiple levels of processing. Accordingly, it is neither possible nor particularly fruitful to separate human haptic function into modular compartments as was once done (e.g., sensations, percepts, and cognitions) (Lederman and Klatzky, 2009).

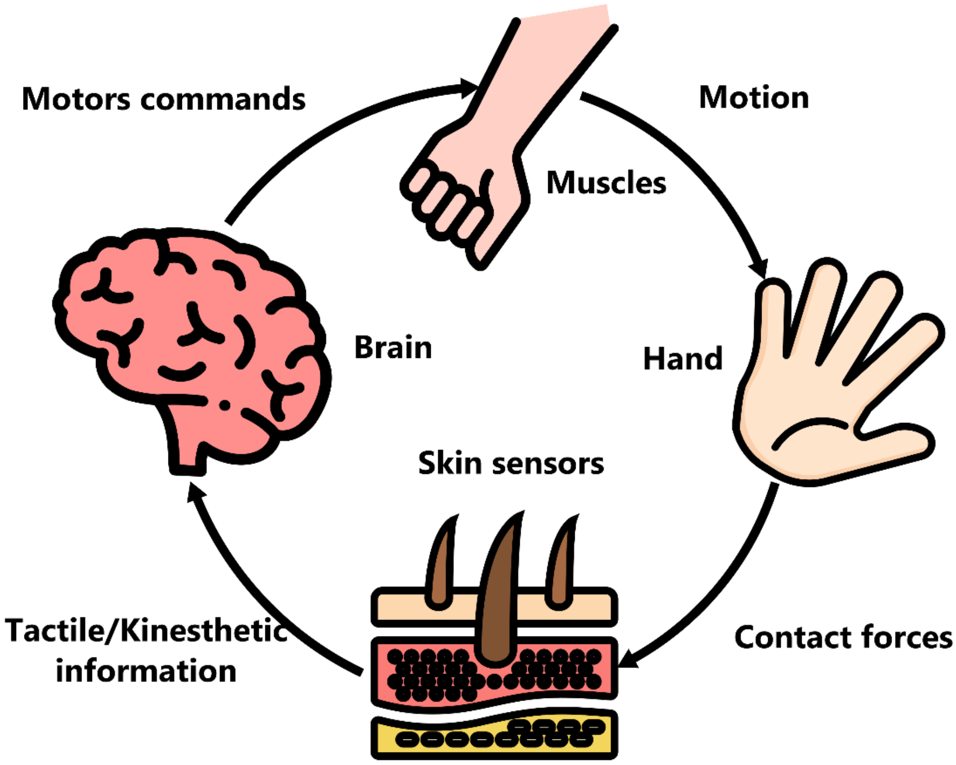


Figure 4: Human haptic system.

1.4.2 The evolution of the human hand

Although the whole body represents the functional and structural interface between brain and environment, for primates, the eye and the hand are the main "ports" through which information is directed inward and outward (Bruner and Iriki, 2016). Primates importantly rely on their handling capacity (Iriki, 2006) and brachiation and suspensory behaviour represented a relevant locomotor pattern in hominoids (Gebo, 1996). Bipedalism, in turn, generates an enhanced integration between the visual system (brain areas and sensory system) and the distal extremities (hands and fingers) (Bruner and Iriki, 2016).

In humans, the hand may be one of the most fascinating and complex structures which provide us with an interface with the world. As remarked by many authors, humans display the best manual manipulative skills among the anthropoids (Napier, 1960, Napier et al., 1993) and possess a larger repertoire of manipulations (Parrish and Brosnan, 2012). The fact that the thumb is opposable to the other four fingers has been considered the most special features of the human hand. The others primates also possess five digits. However, without the opposition of the thumb, they do not have the advance functioning capability that we humans possess as toolmakers (Marzke, 1997). It has been hypothesized that the fingers-to-thumb proportion in our genus probably evolved in relation with habitual bipedalism, before stone tools (Almécija et al., 2015; Richmond et al., 2016). Moreover, in humans, fingers do not display the elongated proportions found in living apes, and this absence can represent a plesiomorphic trait shared with quadrupedal primates, or a parallelism due to an absence of specialization for suspensory locomotion (Almécija et al., 2015) (Figure 5).

Over the course of human evolution, the hand was free from the constraint of locomotion, and evolved primarily for manipulation (Jones and Lederman, 2006; Marzke, 1971). The selective forces associated with tool making and tool use had an influence on biological factors, such as hand anatomy and the musculature associated with effective tool manipulation (Young, 2003; Marzke, 2013; Williams-Hatala et al., 2018). Namely, among the variability of tool uses, hammerstone use during marrow acquisition and flake production could have had the greater influence on the anatomical and functional evolution of the human hand (Williams-Hatala et al., 2018).

Apart from the physical changes suffered by the hand, the appearance of tools in the human behaviour could also have had an influence on the body schemes of early humans. The theories mentioned in chapter 1.1.1 and 1.1.2 suggest that the cognitive processes could be due to integration between brain, body (especially the hand and the eyes) and tools (Malafouris, 2010, Malafouris, 2013; Bruner and Iriki, 2016). In summary, the hand is not just a biomechanical structure, but it also functions as a sensory device associated with neural feedback mechanisms that enables it to perform as an active biological interface (Ingber, 2008; Turvey and Carello, 2011).

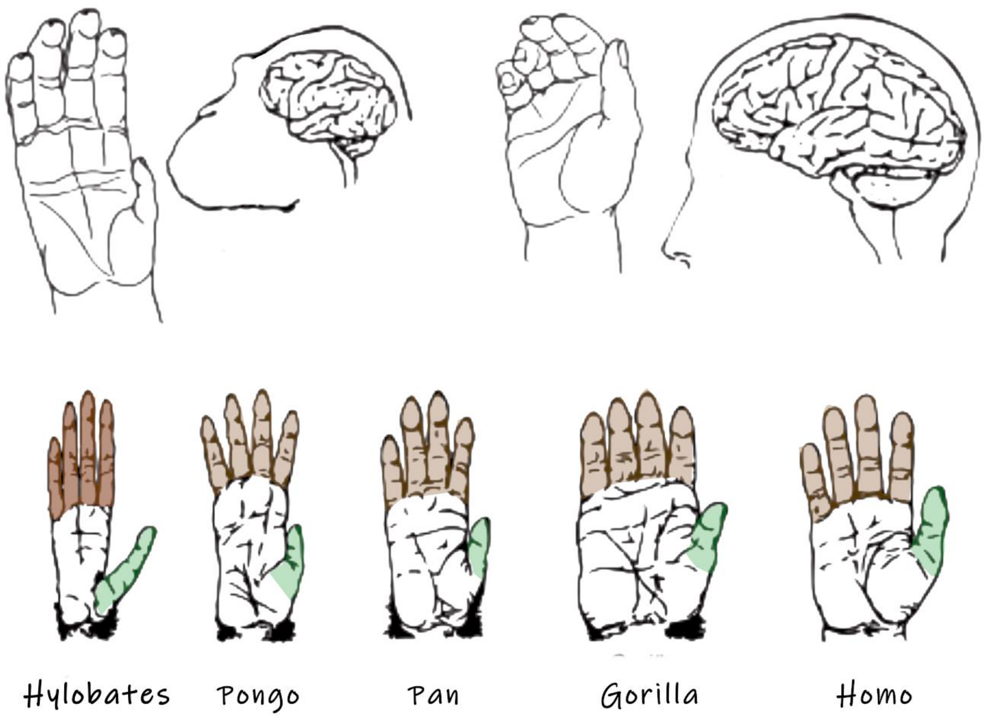


Figure 5: Chimpanzee and human hands and brains compared. The image is modified after Napier, 1993. As compared to other living hominoids, humans exhibit a long thumb relative to the digits, facilitating precision grasping. Imagine modified after Schultz, 1968.

1.5 Biomechanical aspects of stone tool use and production

Besides the studies on cognitive and neurological aspects of stone tool production (e.g., Stout and Chaminade, 2007; Stout et al., 2008; Stout et al., 2015), archaeologists are also interested in the different types of grips used in making and using tools. The knowledge regarding the use and production of stone tools is achieved through comparative studies of manipulative behaviour in humans and non-human primates (Marzke and Marzke, 2000). The opposability of thumbs and fingers in primates produce two categories of grip: *power grip* and *precision grip*. In the power grip, objects are squeezed mainly by the fingers, and are actively stabilized in the palm. In the precision grips, objects are pinched between the flexor aspects of the fingers and the opposing thumb (Napier, 1956).

More recent analyses of manipulative behaviour in primates found that when knappers replicate Oldowan tool types, they primarily use three types of precision grip based on the forceful opposition of the thumb to different aspects of the second and third fingers. These results suggest that forceful grips would have been important for early stone tool users. Probably, hand structure and function underwent relevant evolutionary specializations in the bones and muscles related with tool use and tool making (Almécija et al., 2015; Diogo et al., 2012; Tocheri et al., 2008). Derived musculoskeletal features of the human hand could be adaptations to generate the required forceful grips (Marzke, 1997).

Experimental analysis on human subjects confirm that individuals with longer digits require less muscle force to stabilize digital joints, and are exposed to relatively lower joint contact stresses during stone tool use (Rolian et al., 2011). A large-scale experimental study of grip diversity and frequency revealed that during stone tool use only four grip types are used, and that there is a forceful recruitment of the thumb and index finger. Accordingly, regularities in how stone tools are gripped during their use may have been present in early tool makers (Key et al., 2018b). Experimental analysis on human subjects also evidence that Lower Palaeolithic stone tool efficiency is related to hand strength and hand size. These results indicate that biometrics individuals' traits have to be considered when studying Lower Palaeolithic stone tool use and production.

1.6 Integrating the tools into the body-schema

Tools induce different cognitive and neural responses when positioned outside the range of the body (extra-personal space) or when positioned within the range of physical interaction (peri-personal space) (Serino, 2019) (Figure 6). More importantly, tools are incorporated into the body-schema when they are touched or handled (Maravita and Iriki, 2004). When this happens, the brain interprets the handled object as an extension of the body. The classic example of this effect is the blind man's stick, whose neural incorporation extends tactile perception to the tip (Malafouris, 2008). In this sense, objects function as "extra-neural" elements of the cognitive system, and, as mentioned in chapter 1.2, the parietal areas integrate internal neural processes with external environment features (Bruner et al., 2018).

Gibson defined the haptic system as "*the sensibility of the individual to the world adjacent to his body, by the use of his body*" (Gibson, 1966). This definition highlights the close bond between haptic perception and body movement. Neurons controlling finger movements during haptic perception react to a tool as if it was part of the hand, and the object is perceived by the brain as a prolongation of the hand (Maravita and Iriki, 2004). When we use a tool, the perceptual experience is transferred to the tool as if it were a prolongation of the body. Namely, tools extend the possibility for action and perception (Shaw et al., 1995; Smitsman, 1997) and, from an ecological point of view, tools can be both detached objects of the environment (separated from the user's body) and a functional extension of the environment (prolongation of the user's body) (Gibson, 1986).

In this latter case, we can talk about embodiment. When an object is embedded, it becomes part of the user's cognitive processes, and the tool extends the user's possibilities for action (Hirose, 2002). Tools are treated by the nervous system as sensory extensions of the body rather than as simple distal links between the hand and the environment (Miller et al., 2018). Some tools seem to be easier to "embody", due to certain properties related with affordances (Hirose, 2002). Gibson coined the term affordances to define the possibilities for action offered by objects and their environment (Gibson, 1979). Affordances are the *opportunities* to produce a certain action given by an object (Turvey, 1992) and the same functional part of a tool can elicit different behaviours (Cini et al., 2019).

Because the physical body and material environment might be part of human cognition, we can talk about extended cognition (Clark and Chalmers, 1998; Clark, 2008).

This latter definition is especially relevant to human cognitive evolution, considering the unparalleled relation between our species and material culture. It is worth noting that *tool* in this context has to be intended as a class of objects with intrinsic action and motor features, as even the passive observation of a tool engages the activation of the same brain areas that are typically involved in its use (Chao and Martin, 2000; Johnson-Frey, 2004; Króliczak and Frey, 2009).

An object, to be a tool, must fulfil at least three crucial criteria (Bruner and Gleeson, 2019). First, it must be integrated within the body schemes of the brain, as a real extension of its space and functions (Maravita and Iriki, 2004; Tunik et al., 2007; Heed et al., 2015). Second, it must be part of a productive chain, in which a propaedeutic sequence of tools is necessary to achieve a final target (Muller et al., 2017). Third, it must not simply assist the ecological and economical behavior of a species, but must be integrated-with, and necessary-to, a cultural niche (Plummer, 2004). Humans accomplish the three conditions by integrating technology into cognitive processes (Kaplan, 2012).

It is also worth noting that handling processes (e.g. grasping objects, manipulating tools, and recognizing characteristics like size, texture, and quantity) are functionally subserved by distinct neural and cognitive mechanisms (Goodale et al., 1994). Therefore, "producing a tool" may rely on different processes from "*using a tool*", which in turn may only partially correspond to "*sensing a tool*" in terms of perception.

Clearly, the study of the evolution of the human hand needs to integrate the knowledge regarding the neural components of the manipulative process, and the hand-tool relationship should be studied deeper, in order to evidence some of the underlying cognitive components of these processes. Moreover, the study of the human haptic system also requires an understanding of sensory features (motor control) even if the discussion on how the hand is controlled or coordinated by the brain is complex. In fact, to date, there is no general agreement on how motor control works.

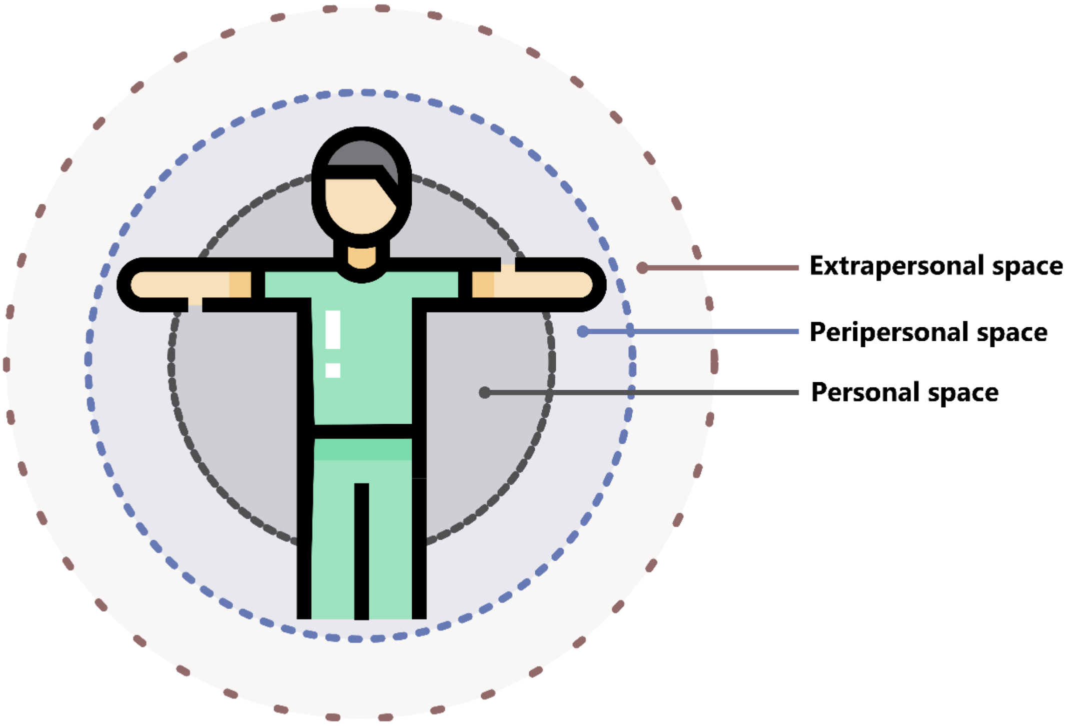
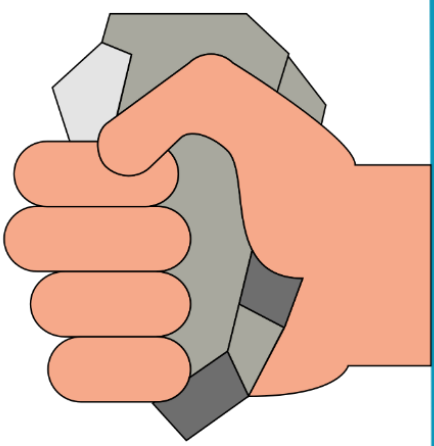


Figure 6: Spaces around the body. The peripersonal space is the space that directly surrounds us and with which we can directly interact. The extrapersonal space is the space that is far away from the subject and that cannot be directly acted upon by the body.

02

AIMS AND SCOPES



2. Aims and scopes of the experimental studies

Tool use requires integration among sensorial, biomechanical, and cognitive factors. During interaction between hand and tool, the body includes the tool in its schemes (Turvey and Carello, 2011), which becomes a body element that is integrated into the somatic schemes of the brain (Iriki and Taoka, 2012; Maravita and Iriki, 2004). Because of the importance of tool making and tool use in our species, grasping patterns and hand morphology are a major topic in evolutionary anthropology (Marzke, 1997; Marzke and Marzke, 2000; Susman, 1998). In this survey, we investigate Lower Palaeolithic stone tools ergonomic and physiological features related with their manipulation. The sample will include Oldowan choppers and Acheulean handaxes. In previous works it have already assed that there are cognitive-related differences between these two tool types (Stout et al., 2015), and that the biomechanical aspects of the hand influences the efficiency of tool use (Key and Lycett, 2011). Taking into account the hypotheses on extended cognition mentioned in the previous chapters, we hypothesized that both hand features and tool features might affect the ergonomic system and the psychophysiological system. To corroborate this hypothesis, we designed two experimental settings which employed the following methods:

i. Hand Morphometrics

Using traditional morphometrics, hand dimensions can be measured. Individuals' variability in hand dimensions and proportions will be related with the ergonomics and psychophysiological feedback.

ii. Tool morphometrics

Using traditional morphometrics, tool dimensions can be measured. Tool shape and dimensions will be related with the ergonomics and psychophysiological feedback.

iii. Finger flexion

The pattern phalanx flexion of the fingers is used here to define the ergonomic aspects of the hand-tool interaction. The ergonomic features during the manipulation of Oldowan choppers and Acheulean handaxes will be analyzed.

iv. Electrodermal activity

The individuals' electrodermal activity is used here to identify changes at psychophysiological level. The psychophysiological feedback during the manipulation of Oldowan choppers and Acheulean handaxes will be analyzed.

03

MATERIALS AND METHODS

3. Materials and Methods

Given the fragmentary nature of the material record, archaeology is expanding its methodological toolbox to include interdisciplinary methodologies. These scientific methods are reliable way of writing a narrative on the past as they provide measurable, testable, and reproducible information. The objectives of the thesis will be addressed through experimental procedures that are novel to archaeological science, and I will utilize biomechanical techniques more commonly used in robotics, ergonomics and medical sciences.

This section will contain a presentation of the experimental materials, the equipment used in each experiment, the protocol, the methods used to measure the results and the methods used for data analysis. As previous stated, the objectives of this dissertation are related to the hand-tool system. The surveys presented here aim to explore the biomechanical and psychophysiological aspects of the manipulation of stone tools.

The first part of the research involves the analysis of the metric properties of both the hands and the tools involved in the experiments. In this part, there will be an explanation regarding how the tools and the hands have been measured.

The second part will present the analysis of the biomechanical and psychophysiological aspects of hand-tool interaction. The functioning of the data glove that we used to record the flexion of the fingers during the comfortable handling of stone tools will be explained. There will also be an explanation of the principles of electrodermal activity and the functioning of Sociograph© technology, the device that we used to record the emotion and attention during the comfortable handling of stone tools.

3.1 Morphometrics

3.1.1 Hand morphometrics

Morphometrics is the quantitative analysis of a form. Traditional morphometrics analyzes lengths, widths, masses, angles, ratios and areas. In general, traditional morphometric data are measurements of size. Hand outlines have been utilized in biometric studies for purposes of individuation and sex estimation in a forensic setting. In particular, shape variation in the hand has been classified using the length and width of the fingers, their curvatures, the relative location of these features, or the relative placement of the palm in relation to the digits. Most methods require the capture and analysis of a significant number of chord distances or morphological features.

Hand anthropometric parameters are categorized into anatomical measurement variables such as the length, width, and circumference and functional measurement variables such as the handgrip span and flexion of the fingers (Garrett, 1971; Greiner, 1991). Hand anthropometry can be directly measured using digital calipers, circumference tapes, and finger circumference gauges and can also be measured from photographs (Ghosh and Poirier, 1987) and scans (McQueen et al., 1998).

The human hand presents a strong sexual dimorphism. Anthropometric measurements of hand dimensions can actually estimate the sex of an individual with high accuracy. The proportion of the human hand is known to differ between males and females. For example, it is historically well known that males tend to have relatively shorter second but longer fourth digits than females (Peters et al., 2002; Robertson et al., 2008), possibly due to the prenatal hormonal environment (Putz et al., 2004; Hönekopp et al., 2007; Zheng and Cohn, 2011; Klimek et al., 2016). The length of hand bones can be used for sex determination (Case and Ross, 2007) and males have, on average, larger hands compared to females (Barut et al., 2014; Kanchan & Rastogi, 2009).

In humans and also in other animal species, precision tool use normally involves the use of the dominant hand. For humans, the right hand is the preferred one in the majority of the cases, and right handedness has been predominant even in early species of genus *Homo* (Steele and Uomini, 2005). In the studies presented here, participated only right hand individuals.

In order to acquire hand dimensions, we scanned the hand of the participants using a 2D scanner. Images were imported in ImageJ (version 1.46r, Rueden et al., 2017) in order to take the measures. Flexion creases of the hand were used as references (Hall et al., 2006; Kanchan & Krishan, 2011; Barut et al., 2014) to measure:

Thumb finger	(F1)	The straight distance between the tip of the first finger to the proximal digital creases of the first finger
Index finger	(F2)	The straight distance between the tip of the second finger to the proximal digital creases of the second finger
Middle finger	(F3)	The straight distance between the tip of the third finger to the proximal digital creases of the third finger
Ring finger	(F4)	The straight distance between the tip of the fourth finger to the proximal digital creases of the fourth finger
Little finger	(F5)	The straight distance between the tip of the fifth finger to the proximal digital creases of the fifth finger
Palm length	(PL)	The chords between the midpoint of wrist crease and the highest point on the head of the third metacarpal.
Hand breadth	(HB)	Distance between the radial side of metacarpal D2 (index finger) and ulnar side of metacarpal D5 (small finger)
Wrist width	(F1)	Distance between the ulnar side and the radial side of the wrist at the distal wrist crease
Hand length	(HL)	The distance from the base of the hand to the top of the middle finger measured along the long axis of the hand (M3+PL)

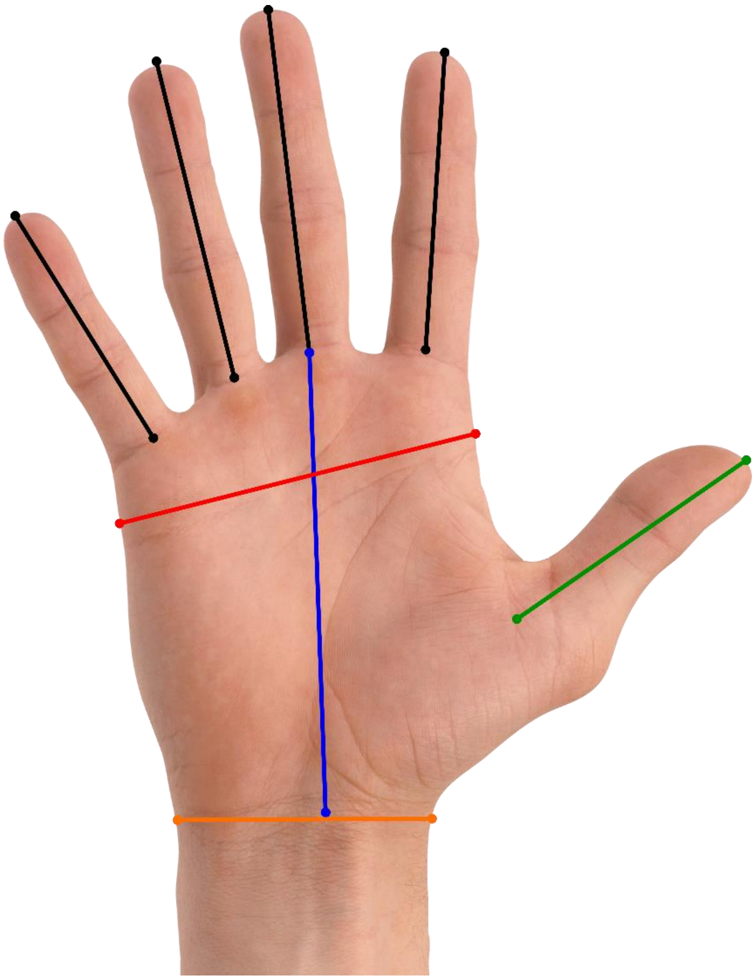


Figure 7: Hand measures.

We also calculated the following ratios:

Hand index	(HI)	Determines the basic hand proportions (Hand width × 100/Hand length)
Digit index	(PL)	Determines the fingers-to-hand proportions (third digit length × 100/ hand length)
PL/width ratio	(PW)	Determines the palmar proportions (PL/palmar width)

3.1.2 Tool morphometrics

Most metric analyses in archaeology and experimental archaeology deal with tool measures. Morphometrics applied to stone tools has been traditionally used to analyze the morphological variation of different tool types, in order to produce categories and investigate tools' morphological aspects (e.g., Serwatka and Riede, 2016; Cardillo, 2010). Particular measurements vary among different time periods and with differences in research questions. In our experiments, we use two types of Lower Palaeolithic stone tools: Oldowan choppers and Acheulean handaxes.

Although there is evidence of earlier tools (Harmand et al., 2015), the first technology for which we have a robust and consistent archaeological record is called Mode 1 or Oldowan technology (Clark, 1969) and appeared around 2.6 million years ago (Braun et al., 2019; Semaw et al., 2003; Stout et al., 2010). It includes worked or shaped pebbles, chopper-cores, polyhedrons, spheroids, etc. One of the most iconic elements of Mode 1 is the worked pebble. This tool is characterized by being knapped in one (chopper) or two faces (chopping tool) with few extractions to generate a short, convex, abrupt or semi-abrupt and usually sinuous edge. They are usually made from round and thick pebbles through direct percussion with a hard hammer (Clark, 1969). Choppers have been long debated because there is no agreement as to whether or not they can be considered tools. However, several studies have shown use-wear evidence on these worked pebbles and, at present, they can be interpreted as both cores to produce flakes or pebble tools (Shea, 2020; Venditti et al., 2021).

Handaxes were the most representative tool of Mode 2 or Acheulean technology, and their earliest record dates to around 1.7 million years ago (Beyene et al., 2013; Diez-Martín et al., 2015; Lepre et al., 2011).These stone tools are large, symmetrical, and tear-drop shaped with a more qualified selection of raw materials (Harmand, 2009; McHenry & de la Torre, 2018; Roche, 2005; Shipton et al., 2018; Wynn, 2002).

Tool geometry is relevant in terms of functions (Chacón et al., 2016) and technological procedures (Eren & Lycett, 2012; Herzlinger et al., 2017; Magnani et al., 2014). The most common measurements for this kind of tool are the object's longest dimension (length), the longest dimension perpendicular to length (width) and the longest dimension perpendicular to the plane defined by the intersection of length and width (Thickness) (Shea, 2013). More recently, metric approaches have been also used to deal with technological and functional issues (Chacón et al., 2016).

The tools that we used in our experiments were prepared according to experimental procedures. An expert on tool making prepared all the samples. To have tools with homogeneous texture, the same Paleozoic material (quartzite) was used , which were knapped from large irregular pebbles with an average length of 10 cm. The grain was thin and the structure homogeneous with no major fissures or fractures (Terradillos-Bernal & Rodríguez-Alvarez, 2014).

For each tool, we measured:

Maximum length **(ML)**

Maximum width **(MW)**

Maximum thickness **(Mth)**

Width at 25% of the max. length **(W25)**

Width at 50% of the max. length **(W50)**

Width at 75% of the max. length **(W75)**

Thickness at 25% of the max. length **(Th25)**

Thickness at 50% of the max. length **(Th50)**

Thickness at 75% of the max. length **(Th75)**

Elongation (Maximum Length/Maximum Width)

Weight

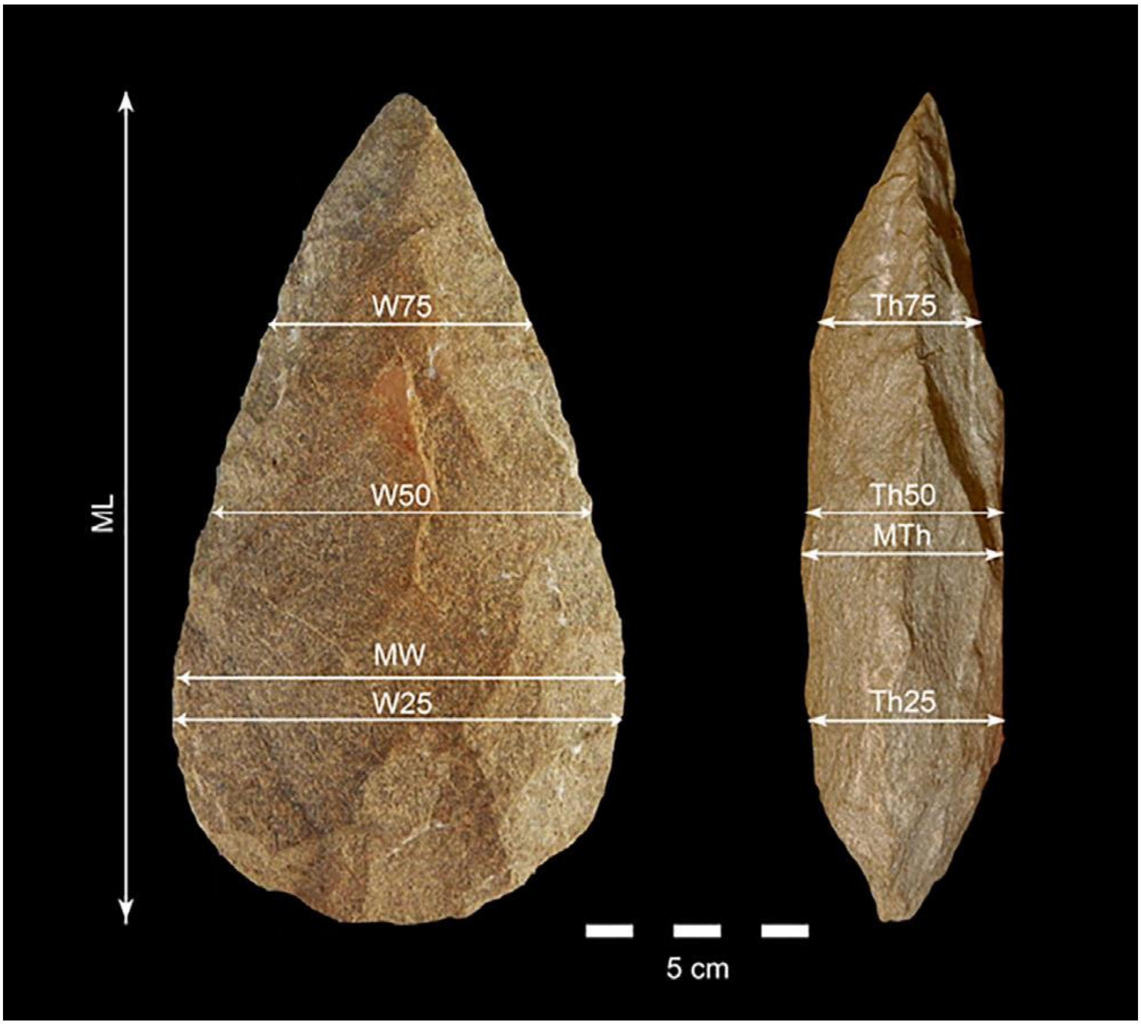


Figure 8: Tool measures (see Silva Gago et al., 2021).

3.2 Finger flexion

3.2.1 Hand biomechanics

The hand consists of the wrist, palm and fingers. Movements of the hand are controlled by muscles in the forearm (extrinsic muscles) as well as muscles within the hand itself (intrinsic muscles). The extrinsic muscles control the hand, are located near the elbow and are responsible for powerful grip ability (Brorsson, 2008). Hand function requires the interaction of muscles, tendons, bones, joints and nerves. The fingers contain 19 bones of distal phalanges, middle phalanges, proximal phalanges and metacarpal bones. Joints are formed wherever two or more of these bones meet. Each of the fingers has three joints:

- Metacarpophalangeal joint (MCP) – the joint at the base of the finger
- Proximal interphalangeal joint (PIP) – the joint in the middle of the finger
- Distal interphalangeal joint (DIP) – the joint closest to the fingertip.

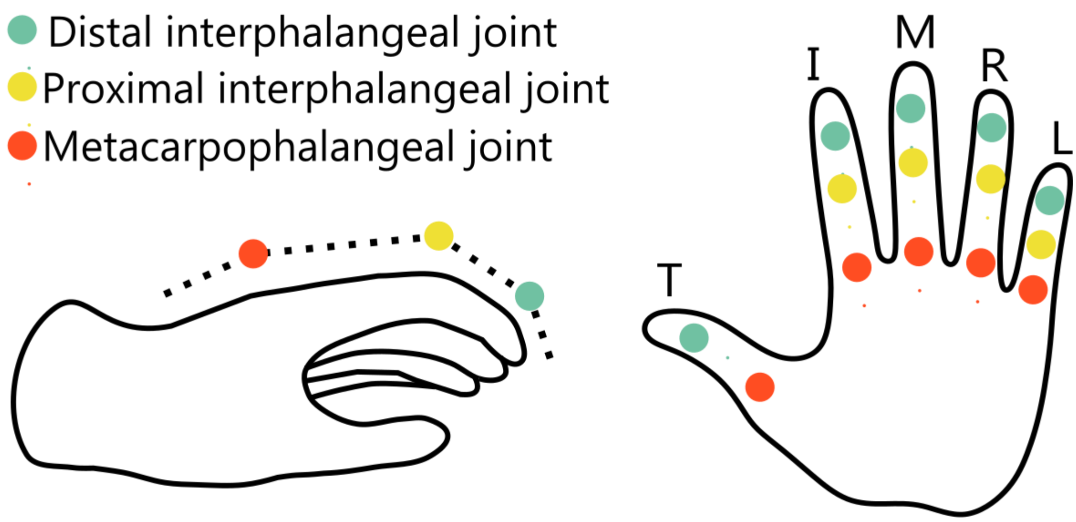


Figure 9: Hand joints.

The MCP joint permits front/back movements, circular movement, as well as side-to-side movements of the fingers. The PIP and DIP only allow front/back movements. The unique construction of the hand provides a wide range of important functions such as manipulation, sense of touch, communication and grip strength (Schieber and Santello 2004). Many researchers in the ergonomics field have been trying to understand how humans use their hands and which factors affect the hand-function capacity. In this survey, we recorded the values of phalanx flexion in order to define the grasping pattern during ergonomic stone tool manipulation. In this context, the pattern of finger flexion can be used to detect ergonomic differences between the manipulations of different tools (in this case, stone tools). To obtain this information, we chose to use a cyberglove, a technological instrument which, among other things, can be used to measure finger flexion.

3.2.2 Ergonomics and Data Glove

In the field of robotics, anthropomorphism (namely, to imitate human gestures) has always been a great challenge. The aim is to achieve high dexterity in imitating human hand's kinesthetic and sensory abilities (Powell, 2016). A data glove (or cyberglove) is an interactive device that resembles a glove worn on the hand. It facilitates tactile sensing and fine-motion control in robotics and virtual reality. Data gloves are widely used in many applications, including virtual reality applications, robotics, and biomechanics (Tarchanidis and Lygouras, 2003). Moreover, data gloves are one of several types of electromechanical devices used in haptics applications. Tactile sensing involves simulation of the sense of human touch and includes the ability to perceive pressure, linear force, torque, temperature, and surface texture. Fine-motion control involves the use of sensors to detect the movements of the user's hand and fingers, and the translation of these motions into signals that can be used by a virtual hand (for example, in gaming) or a robotic hand (for example, in remote-control surgery). A data glove allows normal interaction with objects, and the individual is able to feel the object as if it were in the hand (Tran et al., 2009).

3.2.3 VMG30 data glove

In the experiments, we use a VMG30 (Virtual Motion Labs®) (Figure 10). The VMG30 is a multi-sensor haptic glove that records hand and joint positions through its different sensors. As specified by the producers of the glove, the measuring sensor is located at the metacarpophalangeal joint, at the proximal interphalangeal joint, and at the distal interphalangeal joint. In total, the glove provides 14 joint-angle measurements. It uses resistive bend sensing technology to accurately transform finger and hand motion into real-time data. Values are expressed as degree of flexion.

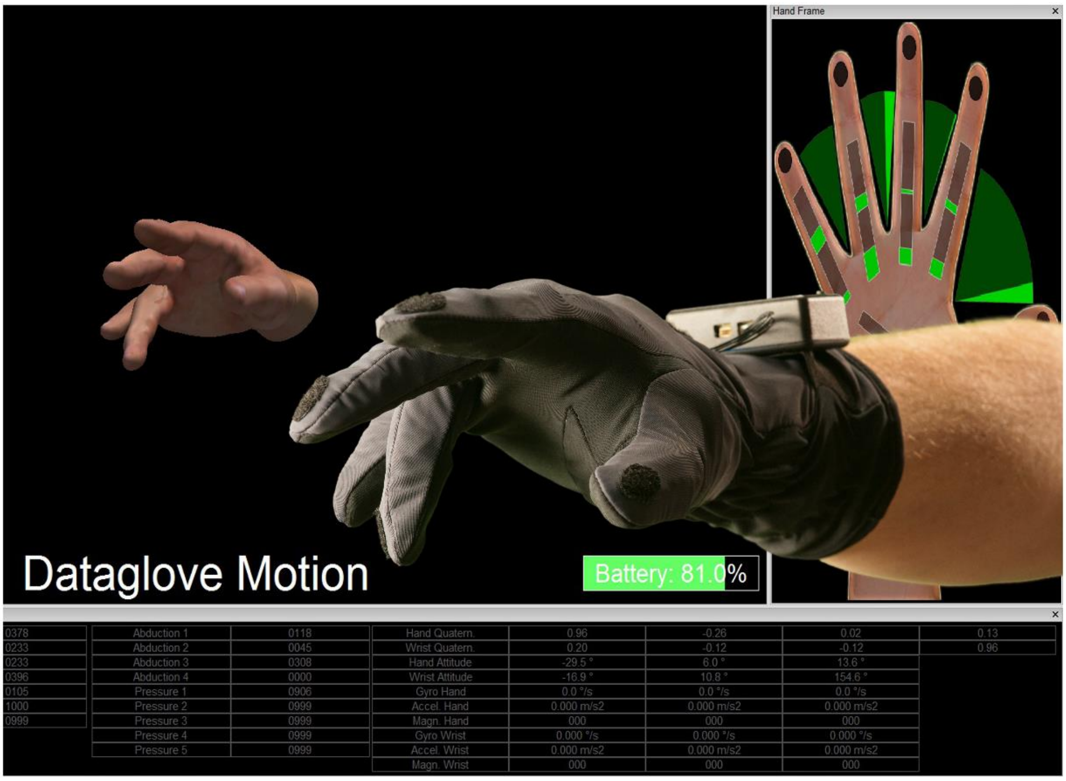


Figure 10: A VMG30 (Virtual Motion Labs®) and its software interface.

3.2.4 Samples and experimental procedure

In the experiment, a VMG30 (Virtual Motion Labs®) cyberglove is used to measure the finger flexion of the 82 participants during tool manipulation. In the experiment, there were 52 female and 30 male participants with ages ranging from 23 to 67 years of age. All of them were right-handed. They had no previous knowledge of archaeology and they did not know the purposes of the experiment. Each of them had a scheduled appointment. Before starting the session, we provided them with information regarding the experiential procedures and they signed an informed consent. They were asked to wear a glove, and to manipulate some objects in order to find the most comfortable position to handle them. We specified that they should not think about any specific action, and that they should just look for an ergonomic position to grasp the tool. Before starting each session, the glove was calibrated. Calibration processes are fundamental to obtain reliable gains for the sensors that record each flexion. The automatic calibration procedure comes with the software (the glove calibration interface). During the calibration, the subjects were asked to mimic the actions shown in short videos on the screen of the laptop with their right hand. All the subjects were asked to concentrate on mimicking the movements rather than on exerting high forces. The calibration lasts one minute.

The experimenter placed the first tool in front of the subject. The subjects could pick up and manipulate the tool with both hands, but the final (comfortable) position had to involve the right hand only. Once the position was found, the participants were asked to stay still for 5 seconds to let the device precisely record the position. After that, participants put the tool in front of them and the experimenter replaced that tool with the following one. This procedure was repeated for the 40 tools. The tool sample consisted of an experimental reproduction of 20 choppers and 20 handaxes.

We obtained the values of finger flexion of each individual during his/her session. Flexion values are recoded at the metacarpophalangeal joint, at the proximal interphalangeal joint, and at the distal interphalangeal joint of the index, the middle, the ring and the little finger, and ofr the thumb at the metacarpophalangeal and the interphalangeal joints.

3.3 Electrodermal activity

3.3.1 Physiology of the skin and principles of electrodermal activity

When we touch an object, we generate vibrations in the skin of the fingertips. In the hand, there are large numbers of sensory receptors (mechanoreceptors), which respond to pressure, vibrations or stretching. Tactile stimulation of the sensory receptors of the fingers generates electric signals in large myelinated nerve fibers of the hand, which reach the somatosensory cortex. Thus, the sensory stimuli occur in the fingertips, but the perception and sensory experiences occur in the brain (Lundborg, 2014) (Figure 11).

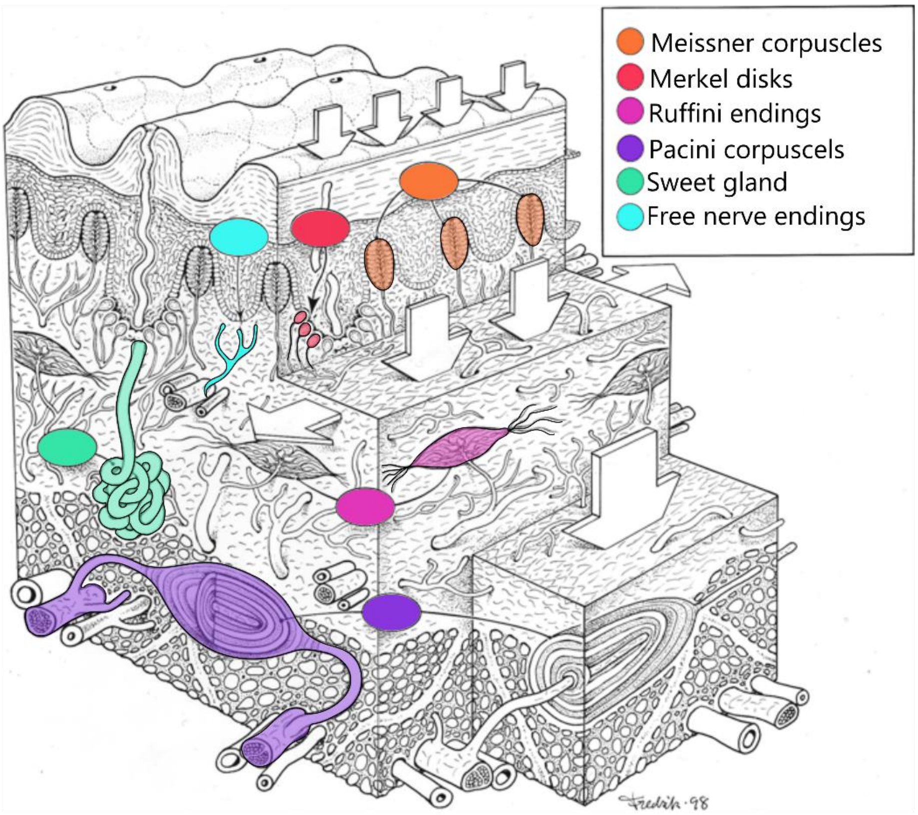


Figure 11: Superficial skin segment from the pulp of a finger with the ridges of the fingerprint visible at the top. Mechanoreceptors in the skin of the hand and fingers detect pressure (Merkel end organs), vibration (Meissner and Pacini end organs) and tension and stretching (Ruffini end organs) (Modified after Lundborg, 2014).

Apart from perception, another pivotal role of the skin is the regulation of perspiration (sweating). Namely, the production of fluids secreted by the sweat glands in the skin of mammals. The human body has about three million sweat glands, the greatest density being found on the palms, soles, and forehead (Kuno, 1956). The innervation of sweat glands at the palmar and plantar sites is peculiar and differs from the sweat gland innervation in the rest of the body because it seems to be more related with emotional rather than thermoregulatory sweat gland activity (Kerassidis, 1994).

The principles of electrodermal activity dates back to 1880, when psychological factors related to electrodermal phenomena were observed for the first time. Since that moment, those properties of the skin have become one of the most frequently used biosignals in psychophysiology. In 1966, the term electrodermal activity (EDA) was used for the first time to refer to all electrical phenomena related to the skin (both active and passive electrical properties) (Johnson and Lubin, 1966). EDA is a generic term used for defining autonomic changes in the electrical properties of the skin (Braithwaite et al., 2013). It is based on the fact that the body reacts physiologically to an external stimulus revealing affective fluctuations, cognitive changes, or other variations in mental state (Critchley et al., 2013). The physiological system responsible for EDA consists of the eccrine sweat glands, the sympathetic innervation from the autonomic nervous network, and the limbic-cortical control circuitry (Boucsein, 2012). It is one of the most sensitive indicators of responses to stimulus novelty (the orienting response) (Edelberg, 1993). When eccrine gland activity increases on the surface of the skin, the path between the energized terminal and the ground terminal of the EDA apparatus becomes more conductive (exhibits less electrical impedance to the electrical current transmitted between the energized and the ground terminals). The physiological changes in perspiration level result in fluctuations in electrical current that can be measured and quantified as EDA (Dawson et al., 2007). The eccrine gland activity, therefore, is a response to *arousal*, the generalized term describing the physiological activation of the sympathetic nervous system as well as its associated behaviours such as increased attention and readiness-to-act (Zhu & Thagard, 2002). Arousal is a process that enhances attention to potentially important environmental affordances and threats. While arousal can improve the performance of an important task, it can also represent a more general physical state of action-readiness, and both are identified through autonomic outputs such as changes in electrodermal activity (Critchley et al., 2013). Arousal can be formally separated into two components: *tonic* and *phasic arousal*. The former is a state of vigilance (attention) that is relatively constant and less responsive to a stimulus when compared with the latter. Phasic arousal occurs in short durations and is more dependent upon stimulus conditions (in the case of haptic manipulation, the perceived arousal associated with interest in the manipulated object).

Once continuities between central mechanisms and the peripheral autonomic responses were assessed, its fluctuations became markers of affect, attention, decision making, motor preparation, and other aspects of cognitive activity (Theodoros, 2014). The application of EDA measures to a wide variety of fields — including psychological assessments, police investigations, and neuromarketing — is due in large part to its relative ease of measurement and quantification, combined with its sensitivity to psychological states and individual reactions (Critchley et al., 2013). EDA has both individual and group specific signatures.

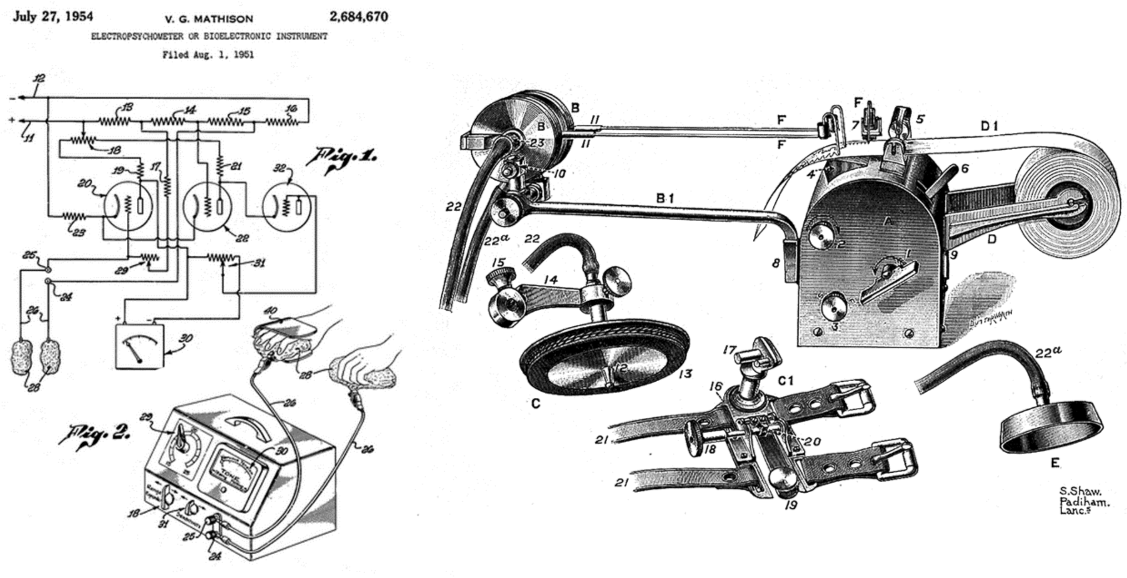


Figure 12: During the late nineteenth century, autonomic responses were measured using a "psychometer". Original scheme of the Electropsychometer, or bioelectronic instrument (US Patent 2684670 by Volney G. Mathison). The earliest polygraph machine was invented by the cardiologist James Mackenzie in 1902 (right). This machines were aimed at detecting physical fluctuations in blood pressure and jugular pulse, as to determine when a person is stressed, which is supposed to be an indication of lying. Mackenzie's polygraph also measured the galvanic responses of the skin, and was first used in a criminal investigation in 1911 by the Berkeley California police department (images available under Creative Commons Attribution).

For example, it seems to differ between infants and children compared to adults (Sohn et al., 2001). Studies have also reported a decrease in tonic level and phasic response in older participants, suggesting age-related physiological and psychological changes (Venables & Mitchell, 1996). Concerning sex differences, females in general display higher tonic levels, while males tend to show higher electrodermal response. These differences can be due to biological or cultural factors (Boucsein, 2012).

In this survey, we studied the variation of the electrodermal activity during the manipulation of stone tools. The analysis of electrodermal activity is a proxy to detect differences in the psychophysiological responses to different tool types.

3.3.2 Electrodermal device

To record the individuals electrodermal activity variation, we used Sociograph© technology. It is a technical innovation that comes from electronic engineering, and originally arises to measure collective reactions) thanks to an electronic instrument that records the electrodermal activity of an individual (Figure 13) (Martínez et al., 2016).

Figure 13: The electrodermal remote device (Sociograph® Technology) is wrapped around the left forearm, connecting two diodes at the 2nd and 3rd fingertips, and recording both tonic and phasic activity.

The device delivers a constant current and records the level of cortical activation and emotional responses while the individual performs an activity or is exposed to a stimulus (Aiger et al., 2013). The device consists of a wireless bracelet with two sensors placed on the index and middle fingers and a central unit that measures, records and processes the resistance of the skin of subjects with a frequency of 32 measurements per second. The series of resistors obtained is decomposed into two signals:

- EDL (electrodermal level), which measures the tonic activity associated with attention or arousal.
- EDR (electrodermal response), which captures rapid changes in resistivity and measures phasic activity related to emotion.

3.3.3 Sample and experimental procedure

In the first experiment, a Sociograph© device is used to record the electrodermal activity of the subjects of the study. There were 46 adult participants, with ages between 21 and 65 years (mean age: 43 ± 11 years). The sample included 22 female individuals and 24 male individuals. All of them were right handed.

Each participant had a scheduled appointment, and participants entered the room one by one. At the beginning of each session, we explained the procedure and provided an informed consent. The task consisted in an active tactile exploration in order to perceive the form of some objects, and to look for a comfortable way to grasp them. We tried not to give unnecessary information, and participant could not see the objects, which were hidden under a cloth. Because the aim of the experiment was related with haptic perception, we also decided to blindfold the participants to avoid the visual stimulus. Before starting the session, the operator placed the Sociograph© device on the index and middle fingers of each participant. The device recorded the changes in the EDA during the whole duration of the session. The sample of objects consisted of 13 replicas of stone tools (7 Oldowan choppers and 6 Acheulean handaxes). Once a comfortable position was reached with the first tool, the participant informed the operator in order to move on the next object. In order to allow participants to become accustomed to the task, we used 4 further tools (2 Oldowan choppers and 2 Acheulean handaxes) at the beginning of the session. The EDA values recorded during the manipulation of those further 4 tools were later removed from the study.

We obtained the EDA values of attention (EDL) and emotion (EDR) of the participants during the tool manipulation. The device measures the parameters with a frequency of 32 inputs per second. In order to simplify the analysis, we computed the average value per second.

It should be specified that the Sociograph© technology records the electrical resistance values, which are, in the case of EDL, inversely proportional to the values of attention. In this sense, lower levels of resistance will be associated with a higher degree of attention and therefore better predisposition to receive, analyze and respond to information. On the contrary, increases in resistance levels correspond to moments of lack of attention. In the case of EDR, the higher the mean, the greater the emotional response.

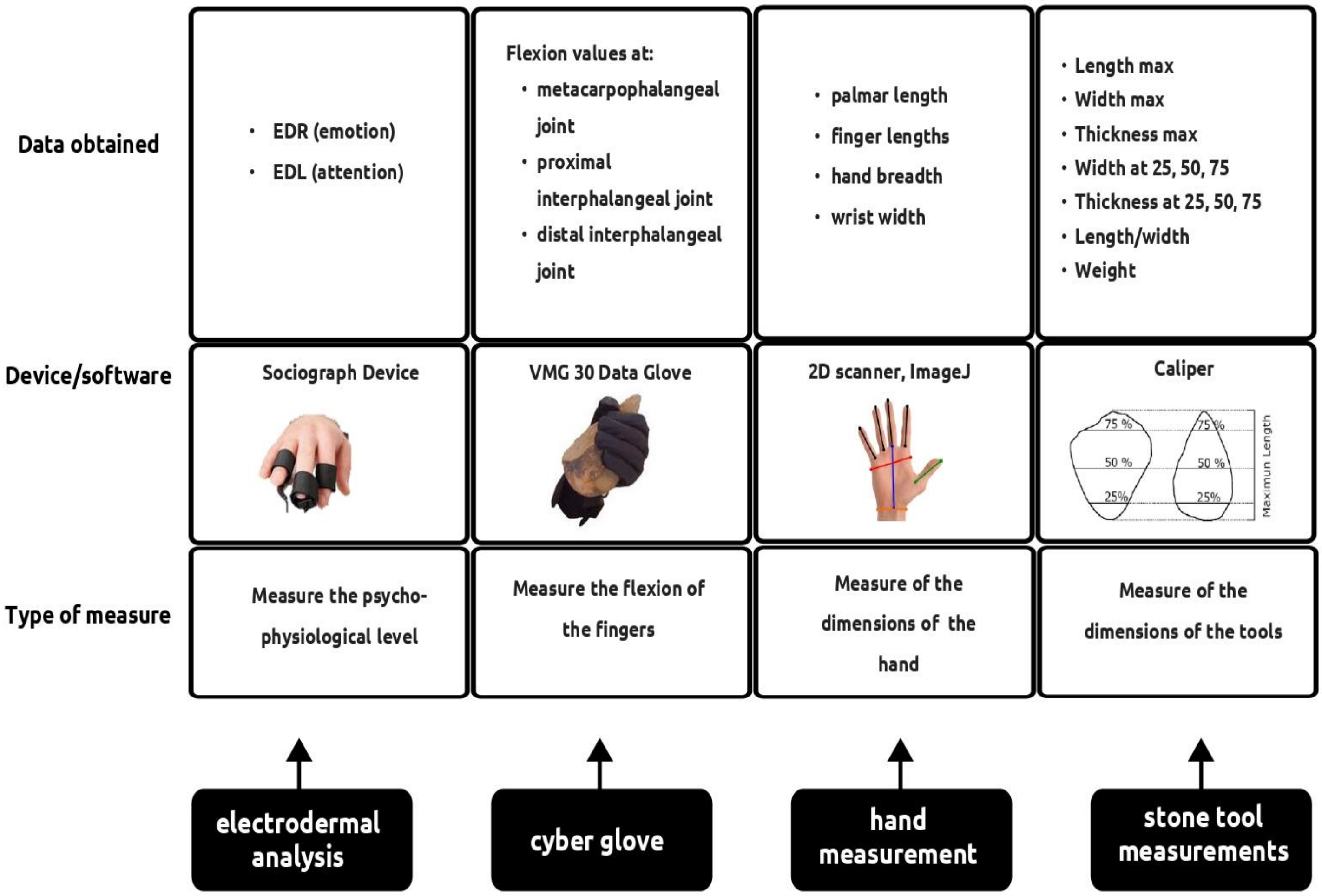
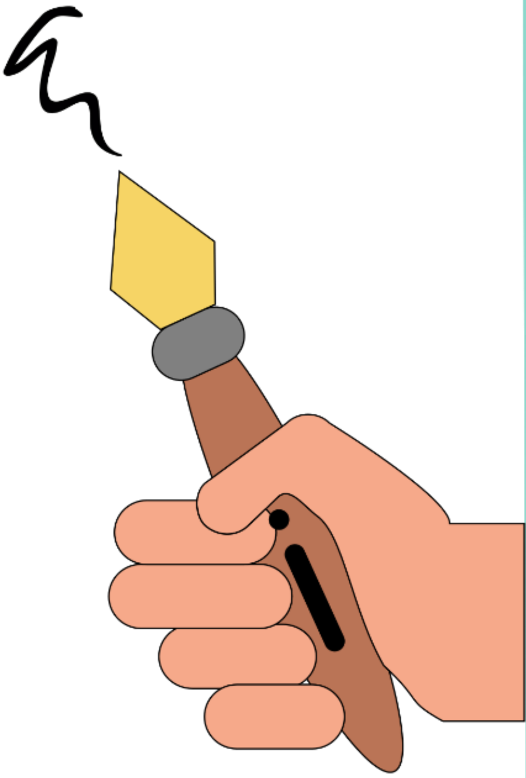


Figure 14: Summary of the methods

04

RESULTS



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Subfield: Please select 2 subfields. Select the main subject first.:	Human biology [living humans; behavior, ecology, physiology, anatomy], Theory

The influence of hand dimension in phalanx flexion during Lower Paleolithic stone tool manipulation

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Abstract.

Objectives. The comfortable grasping of a tool is pivotal for both ergonomic handling and efficient tool use. Hand dimensions do have an influence on the ergonomics of grasping, not only at biomechanical level but also because they influence the sensing components of touch. In humans, men have, on average, larger and stronger hands than women. Here, we study the ergonomic pattern of phalanx flexion during the manipulation of Lower Paleolithic stone tools. The aim is to evaluate the influence of hand dimension on grasping patterns.

Materials and Methods. The static hand posture during the comfortable grasping of each tool is measured using a VMG 30™ motion capture hand glove (Virtual Motion Labs®). The flexions are measured at the metacarpophalangeal joint, the proximal interphalangeal joint and the distal interphalangeal joint of each finger.

Results. Males display more finger flexion than females when handling these lithic tools and, when males and females are considered together, hand dimensions correlate with the pattern of phalanx flexion. However, the correlation is no longer significant when sexes are analyzed separately.

Discussion. At present, there is no patent evidence suggesting that allometric effects and hand size can determine tool grasping in the two sexes. Differences in the degree of finger flexion between males and females are therefore also due to biological or cultural factors other than hand size.

Keywords: Oldowan; Acheulean; haptics; ergonomics; hand size; sexual dimorphism;

Short title: Hand dimension and stone tool manipulation

Introduction

Fossil hominin hand morphology suggests that their hands were increasingly exposed to prolonged stresses associated with tool making and tool use (Marzke, 2013). Some of the characteristics that have been related with the tool use (such as the human-specific thumb/index length proportion) are thought to provide greater control during precision handling (Trinkaus and Villemeur, 1991; Feix et al., 2015; Key and Dunmore, 2015; Key et al, 2019; Karakostis et al., 2021). Most f Paleolithic stone tools require only two general categories of grips to be handled, one involving exclusively the thumb and the fingertips, while the other requires locking the tool into the palm of the hand (Marzke and Shackley, 1986). A recent study confirms previous results of Marzke and Shackley, who demonstrated that there is a limited number of grips adopted during the use of lower Paleolithic stone cutting-tools (Key et al., 2018). The consistency of grasping types, therefore, suggests similarities between stone tool manipulation in living and extinct humans (Key et al., 2018). Experimental archaeology shows that specific biomechanical responses could be exerted by differences in the morphology of the stone tools (Patiño et al 2017), and the ergonomic study of Lower Paleolithic technology, based on the comfortable grasping of tools, showed that there is an influence of tool type and tool metrics on the pattern of phalanx flexion (Williams-Hatala et al., 2018; Fedato et al., 2020). Apart from functional and biomechanical issues, it must be also considered that effective tool manipulation depends on the individual's ability to perceive object affordances (Sartori et al., 2011), which therefore introduces a cognitive component into the manipulative process. This cognitive component depends on sensing capacity

(Miller et al., 2018), and triggers physiological responses associated with attention and arousal (Fedato et al., 2019 ab; Silva-Gago et al., under review). The parietal cortex of the brain is essential in the process of visuospatial integration, and the cognitive aspects associated with stone tool use is largely associated with the evolution of our visuospatial capacities (Bruner and Iriki, 2016; Bruner et al., 2018a).

When studying Lower Paleolithic ergonomic patterns, hand size is a major factor to be taken into consideration, because the applied forces and the contact area are related with grip diameter and hand size (Seo and Armstrong, 2008). On average, males are able to produce greater grip force than females (Petersen et al., 1989; Nevill and Holder, 2000; Peolsson et al., 2001; Ruiz-Ruiz et al., 2002; Imrhan, 2003; Peebles and Norris, 2003; Nicolay and Walker, 2005) and hand dimensions are very good predictors of grip strength (Nicolay and Walker, 2005). In particular, palm width seems to be the best single linear measurement to predict grip force (Nicolay and Walker, 2005). In our latest work (Fedato et al., 2020), we measured the phalanx flexion of 82 subjects during comfortable stone tool handling for both Oldowan pebble tools and Acheulean handaxes. We found differences in the pattern of phalanx flexion among the two tool types and in relation with tool dimensions.

Here, we present a further experimental study on the ergonomic hand pattern of phalanx flexion associated with the grasping of Lower Paleolithic stone tools in order to evaluate whether hand dimensions and allometric factors can be responsible for differences in the manipulation patterns.

Material and methods

In this survey, we focused on two representative Lower Paleolithic stone tool types (namely 20 choppers and 20 handaxes), under the null hypothesis of no effect of hand size on their ergonomic pattern of grasping, according to the degree of finger flexion. One experienced tool maker (MTB) reproduced forty stone tools with common standard dimensions and form (see Fedato et al., 2020), so they could be manipulated and grasped with one hand. Smaller lithic types require controlled pad-to-pad pinch to be handled (Marzke, 1997), and are not considered in this current analysis.

Hand dimensions

Participants were adult right-handed individuals (52 females and 30 males) with ages ranging from 23 to 67 years of age. The subjects had no previous experience in archaeology in order to limit the study to the ergonomic relationship between hand and tool, namely focusing on the hand-tool haptic feedback. Other components such as the knowledge of tool functions or tasks were thus excluded. Hand images were acquired with a 2D scanner, and used to measure hand length (HL), palmar length (PL) and palmar width (PW) with ImageJ 1.46r (Schneider et al., 2012). HL is the distance between the distal flexion crease at the wrist and the tip of the third digit. PL is calculated from the mid-point of the distal transverse crease of the wrist flexures to the most proximal flexion crease of the third finger. PW is measured between metacarpal radial and metacarpal ulnar (Fig. 1a, Table 1; see Kanchan & Krishan, 2011).

Data acquisition

Finger flexion towards the palm of the hand relies on the metacarpophalangeal joint, the proximal interphalangeal joint and the distal inter phalangeal joint (Fig. 1bc). In this survey, the static hand posture during the comfortable grasping of each tool was measured by recording the angular position of the 14 joint angles of the fingers and of the thumb. We used a VMG 30™ motion capture hand glove (Virtual Motion Labs®) to measure the finger flexion (see Fedato et al., 2020 for further details). The degree of flexion is measured as the external angle of the phalanx. In the figures, the degree of flexion is represented in the form of a chromatic scale. Flexion values at the metacarpophalangeal joint are labelled as T1, I1, M1, R1 and L1 respectively for the thumb, the index, the middle, the ring and the little finger. Values at the proximal interphalangeal joint are labelled as T2, I2, M2, R2, and L2. Values at the distal interphalangeal joint are labelled as I3, M3, R3, and L3 (Fig 1bc). In each trial, a subject manipulated 20 choppers and 20 handaxes. Subjects were asked to explore the tool haptically in order to achieve a comfortable grip that had to involve the right hand only. They were asked to inform the experimenter when they reached a final comfortable position with the tool, and the flexion values were recorded at this final position. All subjects signed an informed consent regarding the experimental procedure and privacy policy.

For each participant, we calculated the median value of phalange flexion for the forty Lower Paleolithic stone tools. We compared the 14 phalanx flexion values between males and females through a Mann-Whitney test (U), and computed a Principal Component Analysis (PCA) on the median values of the phalanx flexions for each participant. Finally, we studied the correlation between the first principal components of the phalanx flexion and the dimensions of the hand. All data analyses were performed with PAST (Paleontological Statistics v. 3.18, Hammer et al. 2001).

Results

Males and females show several significant differences in their degree of finger flexion (Tab 2, Fig 2). Differences are larger in T1, followed by the little (L2, L3, and L1) and index (I2 and I3) finger. Only T2, R1 and I1 show no significant differences between males and females. Furthermore, we calculated the coefficient of variation of each variable (14 angles of phalange flexion) for males and for females, and we computed the mean for each group (female average coefficient of variation=41; male average coefficient of variation=25).

Analyzing together the values of the 14 joint angles, the first Principal Component (PC1) explains 64% of the variance, while the second Principal Component (PC2) explains 13%. The eigenvalue of the PC2 is slightly below the threshold of random variation and, therefore, this vector must be interpreted with caution.

Figure 3a shows the loadings of the variance-covariance matrix of all the flexion variables for PC1, and the violin plot of PC1 shows the scores for males and females. For this component, the flexion of the first phalanx of all the fingers (apart from the thumb) shows negative loadings (increasing flexion), while the second and the third phalanx display positive loadings (decreasing flexion).

Pc2 is mainly influenced by M1 flexion, followed by index finger flexion. All the other variables show increasing flexion along PC2, except the second and third phalanx flexion of the little finger and the second phalanx flexion of the thumb. Figure 3b shows the loadings of all the flexion variables for PC2 and the violin plot displays the PC2 scores for males and females.

Taking into account the distribution along the PC1, males are spread toward positive scores and display higher values of phalanx flexion when compared with females (Mann Whitney Test: $U = 373$, $p = <0.001$), although female variance is larger (Levene´s test from medians: $p = 0.002$). This is true also for the second component, and males display larger values of phalanx flexion when compared with females (Mann Whitney Test: $U = 428$, $p = <0.004$).

We correlated PC1 and PC2 of phalanx flexion with hand dimensions (Fig. 4). Considering the number of variables we tested, a Bonferroni adjustment was applied to control type I errors. Correlations are therefore considered significant for $p < 0.017$. The hand dimensions significantly correlate with PC1 when the sample is pooled (for HL: $R2=0.16$, $p<0.001$; for PL: $R2=0.16$, $p<0.001$; for PW: $R2=0.13$, $p=0.001$). The same is true for PC2, which significantly correlates with hand metrics (for HL: $R2=0.17$, $p<0.001$; for PL: $R2=0.15$, $p<0.001$; for PW: $R2=0.16$, $p<0.001$).

However, when males and females are analyzed separately, correlations are no longer significant (Table 3). We also correlated each variable of the phalanx flexion (the 14 original joint angles) with hand dimensions (Table 4). Considering the number of variables, correlations are considered significant for $p < 0.003$. None of them correlates with hand dimensions.

Discussion

In this study, we analyze comfortable grasping patterns for choppers and handaxes as quantified by the degree of phalanx flexion, taking into account the possible effect of hand dimensions. Hand length, palmar length and palmar width are correlated with finger length (Fedato et al., 2019b), display sexual dimorphism (Barut et al., 2014; Kanchan & Rastogi, 2009), and can be used to study the effect of hand dimension on grasping behaviour. The first grasping pattern, according to a principal component analysis, is associated with the degree of flexion of the distal phalanges, in particular of the little and ring finger. The second pattern is also associated with the degree of flexion of the distal phalanges, but principally of the index and middle finger. The flexion of the first (proximal) joint is negatively correlated with the flexion of the distal ones, which means that the more the finger is flexed at its base, the less is flexed in the other two segments.

This can be the result of a biomechanical or spatial constraint between the finger joints, which should be considered when analyzing tool grasping patterns and ergonomics. These patterns are similar to those already described in our previous study on the comfortable manipulation of choppers and handaxes (Fedato et al., 2020). These two grasping patterns are both modestly correlated with the hand dimensions (R^2~0.15), which appears to confirm previous experiments that indicated that specific biometric traits of the hand can have an influence on the use of Lower Paleolithic stone tools, and that the variation in the size, strength and digit ratios can have an effect on the efficiency of tool use (Key and Lycett, 2018). Handle diameter is an important parameter for grip force and contact area, and grip strength increases with increasing hand size (Seo and Armstrong, 2008). It has also been found that the maximum grip strength for the dominant side is higher for males when compared to females (Edgren et al., 2004). According to our results, males and females show a different distribution for both grasping patterns, with males displaying, on average, more flexion. However, when males and females are analyzed separately, the two grasping patterns are no longer correlated with hand size. Therefore, we must assume that the allometric influence on these grasping patterns is absent or, at least, negligible. Males and females have different hand size (smaller in females) and different grasping behaviours (more flexed for males), but these two differences are not correlated. Pooling the two sexes, there is a spurious correlation between hand size and grasping patterns due to the fact that males and females have differences in both dimensions and behaviour, but their reciprocal influence, when the two groups are separated, cannot be confirmed, which means that it is absent or extremely feeble. Therefore, the different grasping behaviour must be intended as a sex-specific feature, and not due to consequences in size differences and shared allometric factors. When dealing with sexual differences, studies on biomechanics and haptics mainly focus on grip strength and handle size, rather than on hand size. To date, sexual differences related with the behavioral aspects of grasping have not been taken into consideration. Excluding hand size as a factor that influences the grasping pattern, other aspects of hand-tool interaction have to be considered. Cultural or biological factors might be responsible for these sex-related differences, and should be integrated when studying the process of tool manipulation and hand-tool ergonomic relationships. Individual grasping behavior could be related, for example, to cognitive abilities and future studies should take into account individual differences at visuospatial level, since visuospatial skills influence interaction with the objects (Bruner et al., 2018).

It must be also taken into consideration, nonetheless, that this analysis considers specific grasping parameters and behaviour, that is the degree of finger flexion during ergonomic and comfortable grasping. Grasping behavior does include mechanical and haptic components that go beyond finger flexion (e.g., Seegelke et al., 2013; Bozzacchi et al., 2014) and therefore are not considered here. We also considered tools that must be manipulated with the whole hand. Smaller tools, that can be manipulated with only the fingers or fingertips, do involve distinct haptic and cognitive mechanisms. Finally, in this study, we investigated the haptic exploration and ergonomic relationships between hand and tool, without any reference to functions or aims associated with tool manipulation. These additional behavioral components should be investigated within a more complex scenario, including both visuospatial and executive functions.

Conclusion

During Lower Paleolithic comfortable stone tool manipulation, males and females show different patterns of phalanx flexion. Hand dimension is related to the patterns of phalanx flexion only when the sample is pooled. However, when males and females are considered separately, the correlation no longer stands. Although the sample size is not particularly large, the lack of a relevant association between hand size and grasping behavior is patent. We therefore conclude that, if hand size does influence the grasping scheme during ergonomic grasping of choppers and handaxes, this effect is very small, negligible, or even absent. If not due to hand size, sexual differences in grasping behaviour could be due to cultural or biological aspects. These results should be interpreted in two different contexts. Firstly, they add to the general study of haptic exploration behavior, bridging perception and cognition associated with hand-tool interaction (Tunik et al., 2007; Turvey and Carello, 2011; Ackerley and Kavounoudias, 2015; Bruner et al., 2018). Secondly, taking into consideration that these large-sized tools represent the earliest record of a consistent human technology that has flourished through millions of years, we should consider whether or not these behaviors can also provide information regarding the evolution of the hand-tool interaction system. We humans are obligatory tool users (Shea, 2017), have a tool-dependent culture (Plummer, 2004), and a technology-based cognition (Malafouris, 2010; Bruner et al., 2018), and we should hence consider that our haptic capacities are deeply rooted in our personal phylogenetic history.

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Captions

Fig. 1

a) The hand dimensions measured in this study are: hand Length (HL), palmar length (PL) and palmar width (PW). b) Phalanx joints are situated at the metacarpo-phalangeal joint (MCP – red dots), proximal-interphalangeal joint (PIP – yellow dots) and distal inter-phalangeal joint (DIP – green dots). (c) Static hand posture was measured by recording the angular position of the 14 joint angles (b) of the fingers and of the thumb, during the comfortable grasping of each tool.

Fig. 2

Distribution of the values of phalanx flexion in males and females (median, interquartile and range). Significant differences between males and females are marked with an asterisk.

Fig. 3ab

a) PC1 of phalanx flexions: the loading values of the 14 joint angles are shown as a color gradient. PC1 scores of males and females are plotted in a violin plot. b) PC2 of phalanx flexions: the loading values of the 14 joint angles are shown as a color gradient. PC2 scores of males and females are plotted in a violin plot.

Fig. 4

Correlation between hand measures and principal components of phalanx flexion.

Tables

Table 1: Summary statistics of hand dimensions (cm) for females (F) and males (M).

	F **PL**	M **PL**	F **PW**	M **PW**	F **HL**	M **HL**
N	50	28	50	28	50	28
Median	9.9	11.2	8	8.9	17.8	19.7
25 prcntil	9.7	10.8	7.8	8.8	17.2	19
75 prcntil	10.3	11.6	8.2	9.2	18	20.3
Coeff. var	4.6	5.4	4.5	5.1	4.3	4.8

Table 2: Mann-Whitney U test with male/female used as grouping variable.

	T1	T2	I1	I2	I3	M1	M2	M3	R1	R2	R3	L1	L2	L3
U	265	527	553	372	372	438	418	418	545	416	441	357	331	333
Z	-4.5	-1.8	-1.5	-3.4	-3.4	-2.7	-2.9	-2.9	-1.6	-3.0	-2.7	-3.6	-3.8	-3.8
Sig.	**<0.001**	0.072	0.126	**0.001**	**0.001**	**0.006**	**0.003**	**0.003**	0.106	**0.003**	**0.007**	**<0.001**	**<0.001**	**<0.001**

Table 3: Correlation between the first components of phalanx flexion and the hand dimensions, for males and females.

	Females		Males	
PC 1 Flexion	R	*p*	R	*p*
HL	0.27	0.06	-0.04	0.82
PL	0.28	0.05	-0.07	0.72
PW	0.09	0.51	0.11	0.58

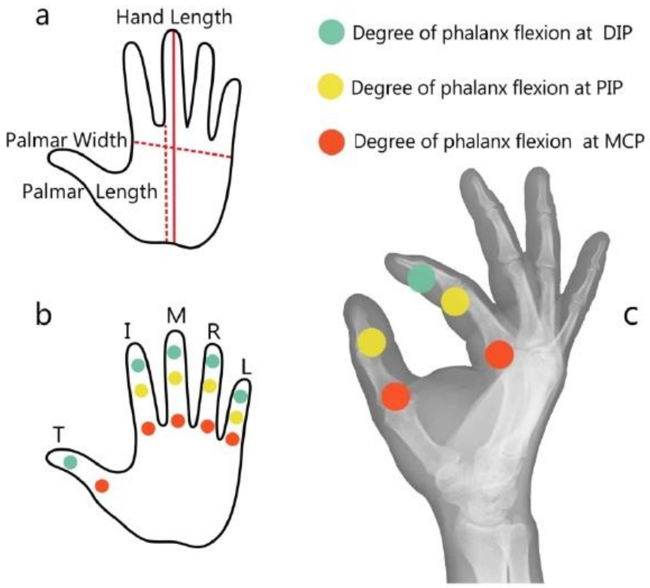
	Female		Male	
PC 2 Flexion	R	*p*	R	*p*
HL	0.25	0.08	0.15	0.28
PL	0.16	0.26	0.08	0.34
PW	0.32	0.02	0.50	0.13

Table 4: Correlation between the 14 variables of phalanx flexion and hand dimensions, for males and females.

	HL		PL		PW	
Females	R	*p*	R	*p*	R	*p*
T1	0.16	0.26	0.16	0.27	0.09	0.55
T2	0.23	0.11	0.31	0.03	-0.01	0.93
I1	0.09	0.52	-0.01	0.94	0.18	0.22
I2	0.37	0.01	0.35	0.01	0.23	0.11
I3	0.38	0.01	0.35	0.01	0.23	0.10
M1	0.22	0.12	0.13	0.36	0.24	0.10
M2	0.11	0.47	0.16	0.26	0.10	0.50
M3	0.10	0.47	0.16	0.26	0.10	0.50
R1	0.02	0.91	-0.02	0.88	0.23	0.11
R2	0.21	0.14	0.23	0.11	0.10	0.51
R3	0.21	0.14	0.21	0.15	0.11	0.43
L1	-0.32	0.03	-0.28	0.05	0.00	0.99
L2	0.30	0.03	0.27	0.05	0.05	0.75
L3	0.31	0.03	0.27	0.06	0.06	0.70

	HL		PL		PW	
Males	R	*p*	R	*p*	R	*p*
T1	-0.12	0.53	-0.17	0.37	-0.19	0.34
T2	0.00	0.99	-0.04	0.83	0.28	0.16

I1	0.19	0.33	0.19	0.33	0.07	0.73
I2	0.02	0.92	0.10	0.60	0.11	0.57
I3	0.02	0.92	0.10	0.60	0.11	0.57
M1	0.35	0.07	0.35	0.06	0.17	0.38
M2	-0.08	0.67	-0.10	0.60	0.09	0.65
M3	-0.08	0.68	-0.10	0.60	0.09	0.64
R1	0.32	0.10	0.36	0.06	0.11	0.59
R2	0.04	0.83	0.02	0.93	0.03	0.90
R3	0.03	0.90	-0.02	0.91	0.09	0.65
L1	0.08	0.69	0.18	0.37	0.07	0.73
L2	-0.04	0.85	-0.11	0.58	0.06	0.75
L3	-0.04	0.85	-0.11	0.58	0.06	0.74



a) The hand dimensions measured in this study are: hand Length (HL), palmar length (PL) and palmar width (PW). b) Phalanx joints are situated at the metacarpo-phalangeal joint (MCP – red dots), proxi-mal-interphalangeal joint (PIP – yellow dots) and distal inter-phalangeal joint (DIP – green dots). (c) Static hand posture was measured by recording the angular position of the 14 joint angles (b) of the fingers and of the thumb, during the comfortable grasping of each tool.

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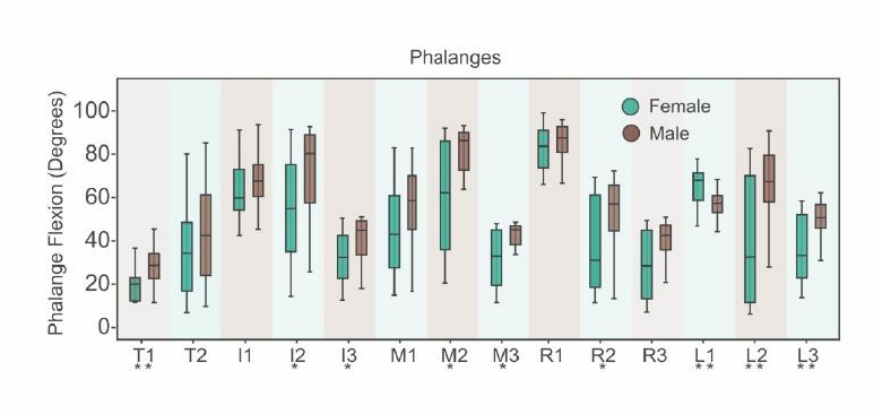

Distribution of the values of phalanx flexion in males and females (median, interquartile and range). Significant differences between males and females are marked with an asterisk.

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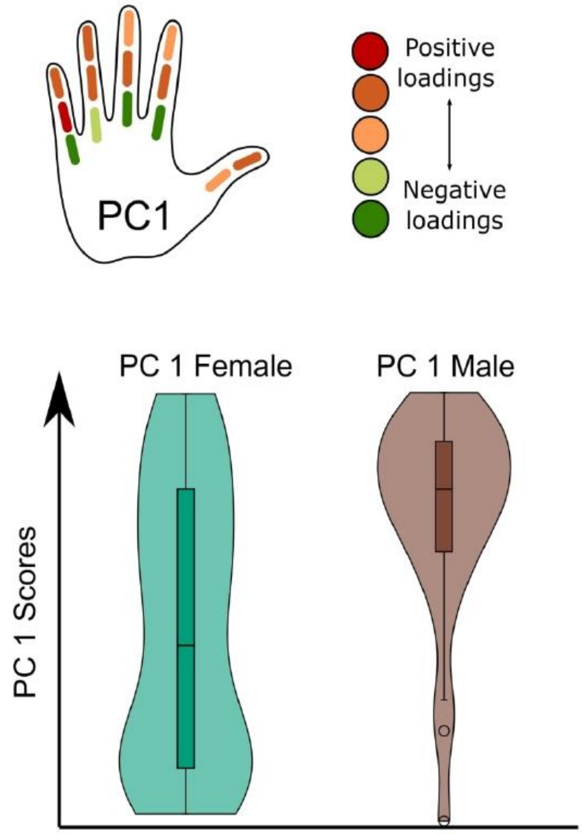

PC1 of phalanx flexions: the loading values of the 14 joint angles are shown as a color gradient. PC1 scores of males and females are plotted in a violin plot.

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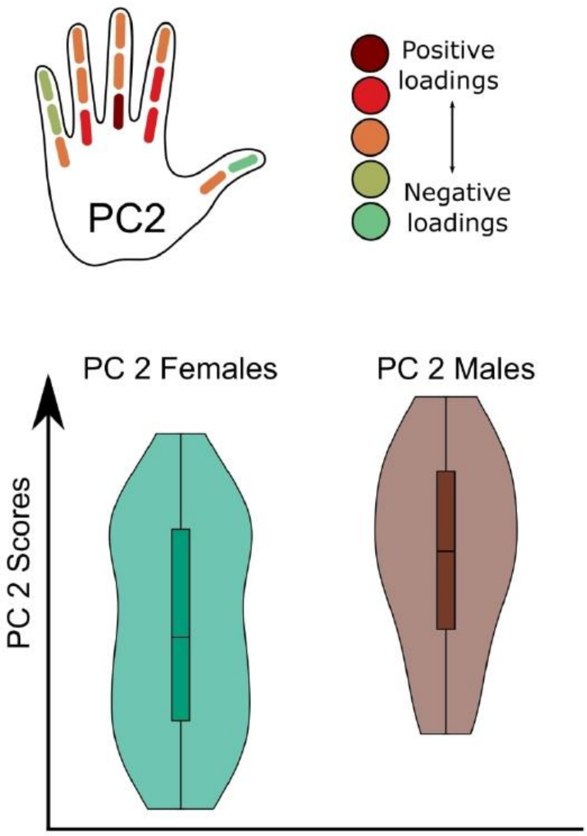

PC2 of phalanx flexions: the loading values of the 14 joint angles are shown as a color gradient. PC2 scores of males and females are plotted in a violin plot.

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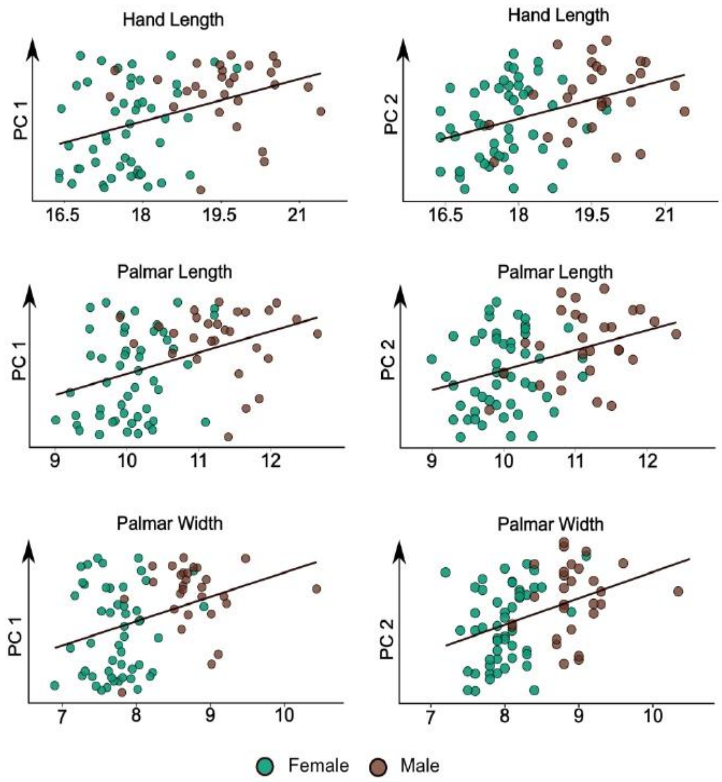

Correlation between hand measures and principal components of phalanx flexion.

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ORIGINAL PAPER

Hand grasping and finger flexion during Lower Paleolithic stone tool ergonomic exploration

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Abstract

Lower Paleolithic stone tool features and shape have been studied in detail; traceology and experimental archaeology have provided us with a lot of information about possible tool use and functionality. The way modern humans use these tools has been used as a proxy for the study of early stone tool-makers' behavior, taking into account that our ancestors could have had similar manipulative capabilities to us. Less importance has been given to stone tool ergonomics, even if comfortable and ergonomic grasping prevent hand damage and improve tool use. Here, we measured the phalanx flexion of 82 subjects during comfortable stone tool handling for both Oldowan pebble tools and Acheulean handaxes. We expected differences in the pattern of phalanx flexion in the two tool types and in relation with tool dimensions. In fact, Oldowan pebble tools and handaxes show differences in finger flexion and in the single finger contribution to comfortable grasping.

Keywords Oldowan · Acheulean · Haptics · Ergonomics · Tool manipulation

Introduction

Systematic stone tool use is an essential component of human behavior, and it is generally used to define the genus *Homo* (Ambrose 2001). Selective forces associated with this capacity could influence biological factors and parameters, such as hand anatomy and the musculature associated with effective tool manipulation (Young 2003; Marzke 2013; Williams-Hatala et al. 2018). Functional skills are related to hand morphology (Hu et al. 2018), and handedness requires specific anatomical structures as well as a proper neural control system (Wing et al. 1996). The study of the human hand hence requires an understanding of both sensory and mechanical features (Taylor and Schwarz 1955). From a morphological point of view, when compared with other apes, humans have shorter fingers relative to the thumb, shorter and less curved phalanges, and a specialized wrist allowing first tool users to develop precision grips (Napier 1956; Marzke 1997; Kivell 2015). In particular, the human-specific thumb/index length proportion is a characteristic that is thought to provide greater control during precision handling (Feix et al. 2015).

The first evidence of tool use in hominins dates back to 3.3 Ma (Harmand et al. 2015). However, only after 2.6 Ma, with the Oldowan technology, early humans were able to produce sequential flakes and perform systematic flake removal (Braun et al. 2019). Subsequently, human evolution has been characterized by increasing technological complexity, brain enlargement, and worldwide population dispersal (Ambrose 2001; Schick and Toth 2006). Stone tool technology expanded the ecological niche of early tool users, who gained access to high-quality food resources and benefitted from reproductive advantages (Biro et al. 2013). Among early tool behaviors, the use of hammerstones during flake production and the use of cutting tools crucially influenced the anatomical and functional evolution of the human hand (Key et al. 2018; Williams-Hatala et al. 2018). Stone tool size and shape have an impact on the ergonomics of the tool (Seo and Armstrong 2008; Key et al. 2018). Despite the many grasping possibilities of the human hand, stone tools are grasped similarly by different individuals, suggesting spatial constraints and, probably, even similarities between stone tool manipulation in living and extinct humans (Key et al. 2018). In this sense, the role of the thumb is crucial, although cause for debate (Young

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2003; Domalain et al. 2017). Compared to extant apes, the modern human thumb relies on an enhanced pollical musculature, probably as part of an evolutionary response to stone tool production (Marzke 1997). The longer and more robust thumb could have helped the first tool-makers to produce more force and to reduce hand stress during tool use (Rolian et al. 2011). Nevertheless, experimental studies have shown that, during Oldowan stone tool production, the maximal force is exerted by the second and the third digit, and it is significantly lower in the thumb (Williams et al. 2012). The little finger also plays a crucial role during hammer stone percussion (Key et al. 2019). In fact, the little finger exerts an opposition to the thumb allowing a better grip force (Marzke et al. 1992; Marzke 1997; Marzke et al. 1998) and it is particularly important during the propulsion phase for a precise strike (Patiño et al. 2017). The dimension and the biomechanical constraints of the hand are both involved in the manipulation and production of stone tools (Patiño et al. 2017; Key and Lycett 2018). Hand size was found to be the better predictor of handaxe cutting efficiency (Key and Lycett 2018) and there is a significant relationship between hand size and a comfortable tool grasp. We must assume that stone tool-makers were able to design ergonomic features aimed at improving body-tool interaction (Walker and Lee 2016).

Apart from biomechanical issues, handling also has a cognitive component. Haptics concerns the response of the body to hand exploration and hand-tool integration, through touch, proprioceptive and kinesthetic information, and imagery (Arditi et al. 1988; Marchand 2012; Vaesen 2012). Furthermore, tool use modifies the body/space relationship, expanding the boundaries of the peripersonal space (Maravita and Iriki 2004), and extending perception-action capabilities (Hirose 2002). All these mechanisms bridge body, technology and cognition, extending information processing beyond the brain's boundaries (Clark 2007, 2008; Malafouris 2008; Malafouris 2010; Kaplan 2012; Bruner and Iriki 2016). Within this perspective, tool use can be investigated in terms of hand-tool morphometrics, treating the hand-tool system as the proper functional units for metric analyses (Silva-Gago et al. 2019). In this study, we focus on the hand ergonomic responses to Lower Paleolithic tool manipulation in order to quantify different grasping patterns during exploratory behavior of different tool types. In this sense, grasping patterns can supply information on both biomechanical (Marzke and Marzke 2000; Niewoehner et al. 2003; Maki and Trinkaus 2011; Patiño et al. 2017) and cognitive aspects of hand-tool interaction (Tunik et al. 2007; Turvey and Carello 2011). We consider the contribution of each finger and evaluate the correlation between hand position and tool physical variables in terms of degree of phalanx flexion, under the null hypothesis of no differences between tool types and no influences of tool morphology.

Materials and methods

Sample and tools

We quantified tool grasping in 82 subjects for 40 tools. Participants were adult right-handed individuals (52 females and 30 males) with ages ranging from 23 to 67 years of age. The subjects had no previous experience in archaeology and had no information about lithic technology. We performed the experiment with novel subjects to limit the study to the ergonomic relationship between hand and tool, excluding other components such as the knowledge of tool functions and tasks. The tool sample included 40 experimental lithic tools, namely 20 choppers and 20 handaxes. The stones were knapped by the same expert (MTB) and from the same quartzite material, to achieve a homogeneous texture.

The earliest consistent evidence of early human technology is the Oldowan Industrial Complex (Semaw et al. 2003). The most common items of these assemblages are small cores and flakes, although they also comprise large "heavy-duty tools." The term (*chopper*) has a long history of use in the context of the Oldowan culture (Leakey 1971, 1976). Despite this long tradition, the distinction between core and tool is still under discussion (Leakey 1971, 1976; Toth 1985, 1987; Lemorini et al. 2014). In this study, experimentally knapped choppers have been designed as tools. Their distal edge is convex and not sinuous. We will refer to these tools as choppers (CHO) for this tool type. The second type consists of handaxes (HAN), namely pebbles knapped on both sides. The handaxes are large, flat, roughly symmetrical tools, with retouched lateral edges that converge to a sharp distal point (Shea 2020). Handaxes are typical of the Acheulean tradition and present evidence of a targeted shape (Shipton and Nielsen 2018), and need more complex cognitive networks to be knapped (Stout et al. 2015; Toth and Schick 2015).

Table 1 Median and standard deviation of stone tool measurements (values expressed in mm)

	Handaxes		Choppers		*t* test
	Median	St Dev	Median	St Dev	*p*
Length max	172.7	20.5	109.2	15.1	< 0.001
Width max	88.9	14.1	113.0	16.1	< 0.001
Thickness max	35.2	5.9	53.9	6.4	< 0.001
Width at 25	88.1	14.2	102.1	20.4	0.066
Width at 50	78.5	11.9	107.9	15.7	< 0.001
Width at 75	49.9	7.2	95.1	18.8	< 0.001
Thickness at 25	34.9	6.3	43.8	5.3	< 0.001
Thickness at 50	31.6	6.0	51.6	5.1	< 0.001
Thickness at 75	25.3	5.8	36.5	8.0	< 0.001
Length/width	1.8	0.3	0.9	0.1	< 0.001

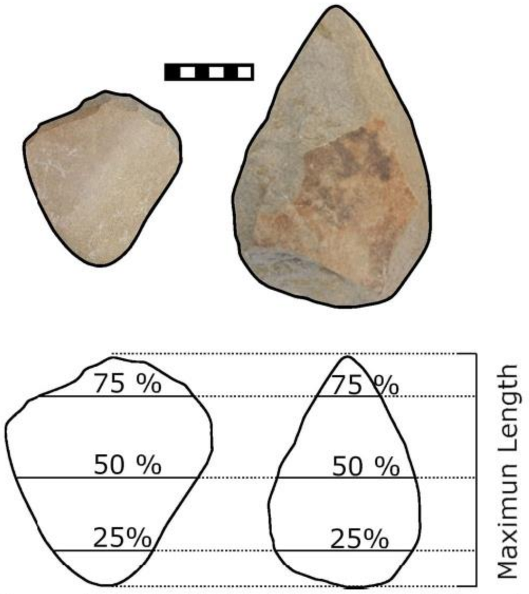

Fig. 1 A chopper and a handaxe from the experimental lithic tools sample. Tool measurements were taken at 25% of the maximum length, at 50% of the maximum length, and at 75% of the maximum length

Each tool type generally displays a pronounced variability through time and geography, triggering several open debates on their functions and anthropological background (Shea 2013). In this survey, we have reproduced and employed stone tools (Oldowan and Acheulean, Fig. 1) with common standard dimensions and form, as to be manipulated and grasped with one hand. For each tool, we measured the maximum length, width, and thickness. We also measured the length, width, and thickness at the base of the tool (at 25% of the maximum length), at the middle (at 50% of the maximum length), and at the tip (at 75% of the maximum length) (Table 1).

Data acquisition

We used a VMG 30™ motion capture hand glove (Virtual Motion Labs®) to measure the pattern of finger flexion during the comfortable grasping of the tools (Fig. 2 a). The flexion of each finger digit was recorded at each finger joint through the data glove. Flexion values at the metacarpophalangeal joint are labeled as T1, I1, M1, R1, and L1 respectively for the thumb, the index, the middle, the ring, and the little finger. Values at proximal interphalangeal joint are labeled as T2, I2, M2, R2, and L2. Values at distal interphalangeal joint are labeled as I3, M3, R3, and L3 (Fig. 2 b shows thumb and index joint angles as examples). After calibration, the system transforms finger motion into real time sensory data through joint angle measurements (see Cobos et al. 2010; Fig. 2 b, c). Each individual session included 40 trials (manipulation of 20 choppers and 20 handaxes), in which the subject was asked to manipulate the tool to achieve a comfortable position. The subjects were instructed to explore the tool haptically to achieve a natural grip. They were allowed to use both hands to manipulate the tool until they found the most comfortable way to grasp it. The final position had to involve the right hand only. We recorded the angles of flexion of the joints for each finger, taken in the final resting position. All subjects signed an informed consent regarding the procedure and privacy policy.

We compared the flexion values between handaxes and choppers through a paired sample *t* test, cluster analysis (unweighted pair group method with arithmetic mean—UPGMA), and principal component analysis (PCA) on the median values of each tool. We also computed a correlation analysis between the principal axes of the finger flexion patterns and tool metrics, and a multiple regression analysis.

Results

Comparing choppers and handaxes, all flexion variables show significant differences at $p < 0.05$, except the first phalanx of

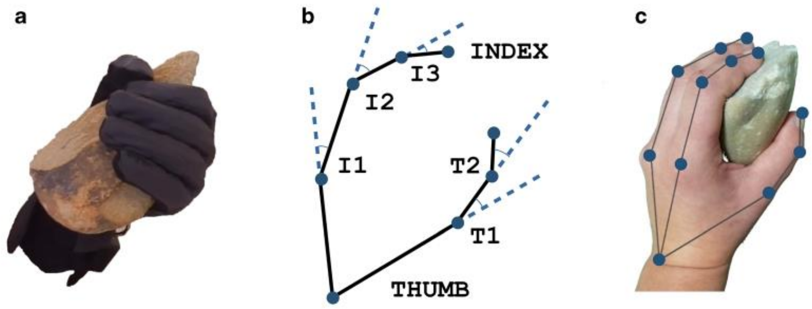

Fig. 2 **a** VMG 30™ motion capture hand glove (Virtual Motion Labs®). **b**, **c** For each tool, measurements were taken of the phalanges flexion at the metacarpophalangeal joint (1), proximal interphalangeal joint (2), and distal interphalangeal joint (3)

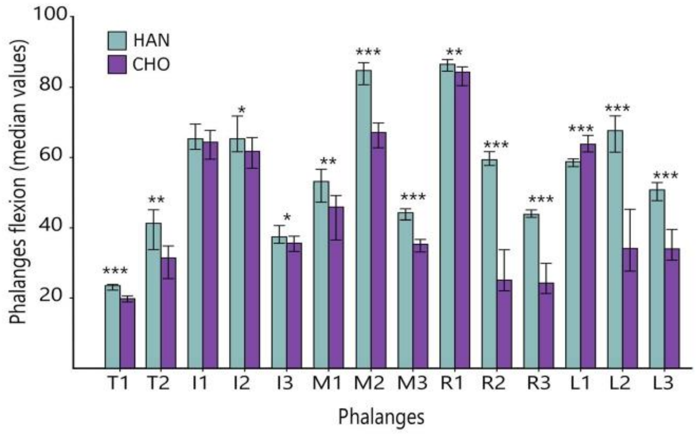

Fig. 3 Boxplot representing the median finger flexion values for each phalange, calculated for the 82 individuals, for both choppers and handaxes. Differences were evaluated through a paired sample *t* test (significance $*p < 0.05$, $**p < 0.005$, $***p < 0.0005$)

the index finger (Fig. 3). Considering all flexion variables together, choppers and handaxes are grouped in distinct clusters, with only one handaxe and two pebbles misgrouped (Fig. 4). Computing the median values of finger flexion of the two main groups, the grasping of choppers is characterized by a major extension of the fingers (less flexion) while the grasping of handaxes is characterized by a higher finger flexion. This difference is stressed in the middle, ring, and little fingers. Figure 5 shows the principal component analysis computed on the variance-covariance matrix of all the flexion variables associated with each stone tool. PC1 explains 78%. This axis separates choppers and handaxes, and it is associated with (in the latter) flexion of the little, ring, and middle second phalanx, and of the little and ring third phalanx. Therefore, in this case, the grasping pattern is progressively more associated with the third, fourth, and fifth fingers. Apart from separating choppers and handaxes, this pattern is also associated with a pronounced variation within the choppers. PC2 explains 9%, but it is below a threshold of random variation, and should be therefore interpreted carefully. It does not separate choppers and handaxes, and it is associated with flexion of the middle first phalanx and of the index first phalanx, and extension of the index second phalanx, index third phalanx, and middle second phalanx. Thus, in this case, the grasping pattern is associated with the second and third fingers. Subsequent components explain less than 5% and will not be discussed here.

Independent PCAs for choppers and handaxes were also computed, showing one PC above the random threshold level for the former group, and four for the latter (Fig. 6). In this case, each sample includes only 20 items, and therefore, the following analyses will consider only the first principal component. In general, the manipulation of choppers is more sensitive to the flexion of the middle finger, when compared with handaxes where the variation is mainly due to the little and ring fingers.

The two PC1s from choppers and handaxe manipulation were also correlated with the metrics of the respective stone tool groups in order to analyse if and how much these patterns are related with the tool dimensions (Fig. 7). For choppers, the main finger flexion pattern is only correlated with maximum tool length. For handaxes, the main flexion pattern is influenced by maximum width, length/width ratio, and by the width of the tool (at 25%, 50%, and 75% of the maximum length) (Table 2).

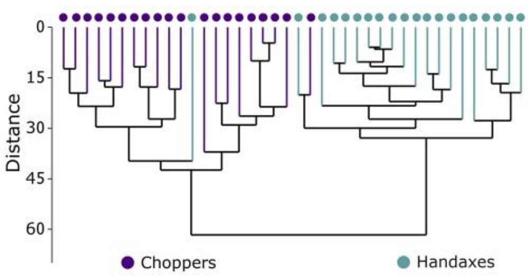

Fig. 4 Results of cluster analysis (unweighted pair group method with arithmetic mean—UPGMA) from the median values of phalange flexion of the 82 individuals calculated for each tool (20 choppers, 20 handaxes)

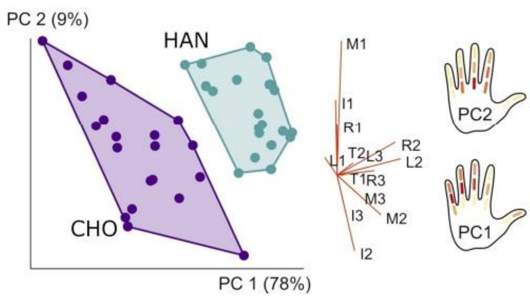

Fig. 5 Principal component analysis (PCA) computed on the median values of each tool (40), calculated for the 82 individuals. For each phalange, darker colors represent higher loading, while lighter colors represent lower loadings

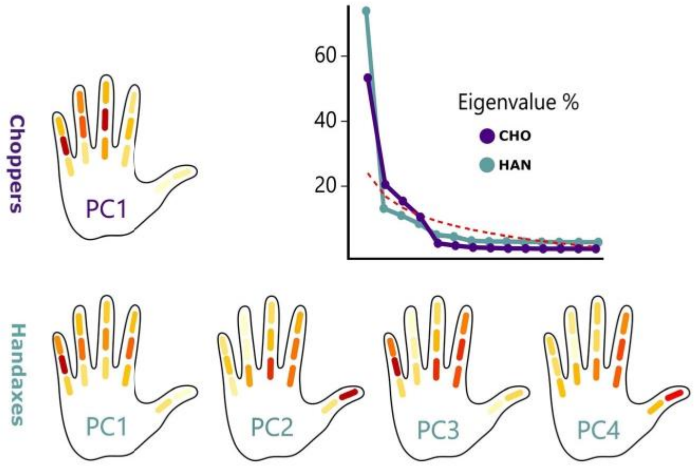

Fig. 6 Principal component analysis (PCA) of the choppers and of the handaxes computed separately. The median values of the 82 individuals were calculated for each tool. For each phalange, darker colors represent higher loading, while lighter colors represent lower loadings

In order to explain the relationship between the phalanx flexion and the tool dimension, we also computed a multiple regression analysis. As predictors, we chose to use the three principal measures of the tools (maximum length, maximum thickness, and maximum width). We did not use all the metrics variables in order to avoid collinearity. When the PC1 of phalanx flexion during choppers handling was predicted, it was found that only maximum length was a significant predictor (Beta = − 0.583, $p < 0.05$). The overall model fit was $R^2_{adj.} = 0.388$, $F = 5.012$, $p = 0.012$. For handaxes, maximum length (beta = − 0.320, $p < 0.05$), maximum thickness (beta = − 0.344, $p < 0.005$), and maximum width (beta = − 0.868, $p < 0.001$) were significant predictors. The overall model fit was $R^2_{adj.} = 0.688$, $F = 14.975$, $p < 0.001$.

Discussion

Tool grasping is thought to be influenced by co-evolutionary factors associated with biomechanical and cognitive relationships between hand and technology (Vaesen 2012). In this survey, we evaluated differences in handling for two representative stone tool technologies (choppers and handaxes) that have been used for over two million years. Previous studies on hand biomechanics during Lower Paleolithic stone tool use focused on the level of pressure experienced by the hand, the type of grips used during tool use, or the importance of the wrist (Key and Dunmore 2015; Key et al. 2017; Key and Lycett 2018; Key and Dunmore 2018; Williams-Hatala et al. 2018; Key et al. 2019). Here, we analysed Lower Paleolithic stone tool handling in terms of comfortable finger flexion, namely focusing on the haptic feedback between body and tool, without considering functional responses associated with tool making or operational tasks. Tool comfortability and hand posture are pivotal factors to avoid muscular stress (Jaffar et al. 2011; Lee and Jung 2015), and we must assume that stone tool morphology was somehow designed to deal with ergonomic sensing.

For handaxes, tool length influences the grasping pattern because of the different involvement of ring finger, little finger, and palm (Key et al. 2018). Compared to choppers, handaxes are generally thinner, more elongated, and with a longer cutting edge, and they have a rounded base which is thicker than the tip (Gowlett 2006). Accordingly, although in both cases the main grasping pattern involves a power grip with all fingers and palm (Bruner et al. 2019), finger flexion is expected to be distinct in these two lithic typologies. Our survey suggests that, comparing choppers and handaxe ergonomic grasping, there are significant differences in the degree

Table 2 Correlation between the PC1s of handaxes and choppers and the metric variables of each tool. Results are considered significant for $p < 0.005$

HAN	PC 1		CHO	PC 1	
	R	*p*		*R*	*p*
Max length	− 0.15	0.529	Max length	− 0.63	*0.003*
Max width	− 0.77	< 0.001	Max width	− 0.40	0.081
Max thickness	− 0.33	0.152	Max thickness	− 0.03	0.895
Width at 25	− 0.77	< 0.001	Width at 25	− 0.27	0.259
Width at 50	− 0.78	< 0.001	Width at 50	− 0.29	0.207
Width at 75	− 0.69	*0.001*	Width at 75	− 0.11	0.640
Thickness at 25	− 0.45	0.049	Thickness at 25	0.00	0.995
Thickness at 50	− 0.34	0.146	Thickness at 50	0.14	0.564
Thickness at 75	− 0.38	0.101	Thickness at 75	0.20	0.388
Length/width	0.62	*0.004*	Length/width	− 0.12	0.626

of flexion in all phalanges, except the first phalanx of the index finger. In general, handaxes require more finger flexion to be comfortably grasped. This difference is particularly evident in the distal parts of middle, ring, and little fingers. The thumb and the index phalanx flexion do not substantially change between handaxes and choppers. In general, there is a great variability in the employment of the index finger when stone tools are used to perform a task that requires a functional force to be applied on a surface (Key et al. 2018). However, in a natural grip posture, finger forces vary in relation to the type of grip (Kinoshita et al. 1996). In the circular grip (used for discoidal and spherical shapes), the thumb, ring, and little fingers play a major role in force generation, whereas in a prismatic grip (flat shapes, thumb and fingers in opposition), the thumb, index, and middle fingers share about the same or even a larger proportion of the total grip force (Kinoshita et al. 1996). A power prismatic grip is better suited for handaxes, which are more commonly grasped with the palmar side of index, and middle fingers placed in opposition to thumb (Key et al. 2018). On the other hand, the unflaked base of choppers suggests a circular power grip.

Apart from differences between choppers and handaxes, we also analysed the finger flexion variability within these two tool types. In choppers, grasp variation largely depends on the flexion of the second phalanx of middle finger, and then by the flexion of the little and ring fingers. In this case, tool length is apparently the only variable that influences phalanx flexion. Longer choppers are grasped with a minor finger flexion, while shorter choppers require more flexion of the last three fingers. In handaxes, instead, the main grasping variation is due to the flexion of the medial and distal phalanges of the little finger, which is influenced by the width of the tool and its elongation (length/width ratio). During a power grip, a relevant factor is the stability that makes it possible to resist external forces and prevent slipping (most of all through involvement of the distal phalanges; Hamill and Knutzen 2006), and grasp force decreases as tool size increases (Amis 1987). The grip strength is particularly associated with the contribution of the middle finger (Amis 1987; Ejeskär and Örtengren 1981; Hazelton et al. 1975; Lee and Rim 1991; Radhakrishna and Nagaravindra 1993; Talsania and Kozin 1998) which is, in our survey, a main factor of variation for choppers but not for handaxes. Hence, we must assume that choppers, in this sense, trigger more diverse responses in terms of strength requirements. In our study, the longer the choppers, the lesser is the flexion of the distal phalanges of the middle, ring, and little finger, suggesting less force applied (Hamill and Knutzen 2006).

In general, when handle diameter increases, the fingers become less flexed. The shorter fingers (little, ring, and index) lose more of their mechanical advantages compared with the middle finger, which is the longest and can exert more force (Chen 1991). Beyond rough dimensions, object shape may also have a crucial role in grasp and force distribution; a given

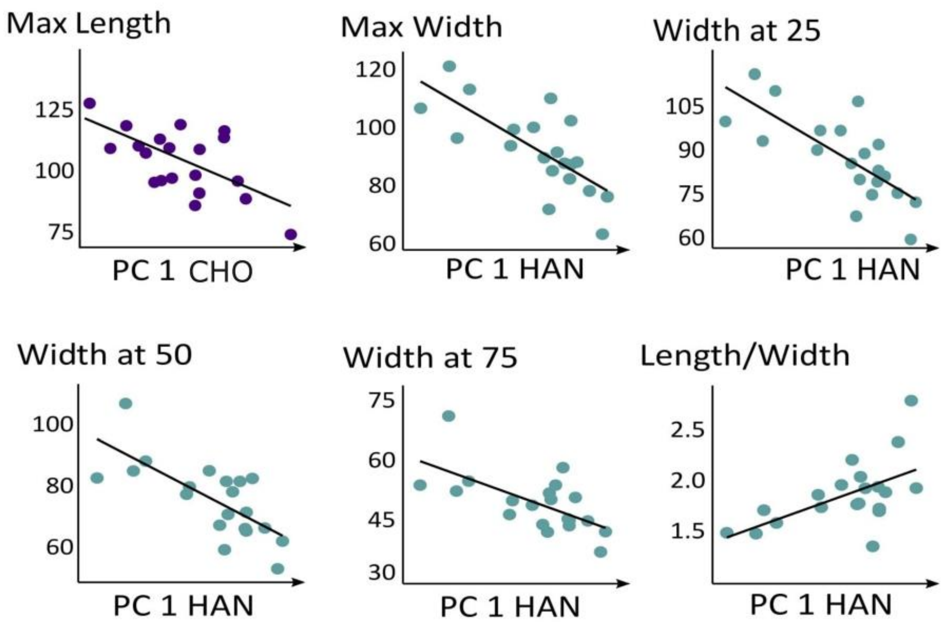

Fig. 7 Correlation between the PC1s of the choppers and of the handaxes computed separately and the metric values of each tool. In this image, only the correlation significance $p < 0.005$ is shown

handle shape can be more adapted to maximize grip force or to homogenize the distribution of grip force (Cochran and Riley 1986; Rossi et al. 2014). Experimental studies have shown that the total grip force is influenced by the object's weight, the object's diameter, and the grip mode. The thumb is the highest contributor to the total grip force, followed by the ring and the little finger, while index finger contribution is the smallest (Kinoshita et al. 1996).

Moreover, some "non-ergonomic" features can be considered indicative of a different task. For handaxes, leaving the basal portion unflaked would increase the ergonomics of the tool. However, a handaxe base is frequently flaked probably to obtain an effective working edge (Key et al. 2016).

The results of the present study must be interpreted in terms of ergonomic evolutionary advances in body-tool integration. In general, in archaeology, tool shape is largely investigated according to functional tasks. Nonetheless, tool morphology and other physical features of the tool may also play a major role in the cognitive perception of the tool and in the integration of the tool into the body schemes (Miller et al. 2014; Bruner et al. 2018a). Future studies on hand-tool relationships should consider that the shape of the object modulates the contact position of the digits and that the effective manipulation of objects depends on the individual's ability to perceive object affordances (Sartori et al. 2011). In this sense, ergonomics can be more influential than, for example, task-dependent or even esthetic aims.

Conclusions

Experimental archaeology relies on modern human behaviors to investigate the archeological record in order to provide inference on cultural or even cognitive aspects of extinct human species or historical populations. With this limitation in mind, stone tool grasping and hand-tool integration have been investigated through many distinct biomechanical and functional aspects (Key and Lycett 2018; Key and Dunmore 2018; Key et al. 2019). In this study, finger flexion was quantified to analyse the ergonomic response to tools associated with Lower Paleolithic technology. When considering a comfortable grasping pattern for handaxes and choppers, the hypothesis of no influence of tool type or tool metrics on finger flexion is rejected. Therefore, we must consider that the differences of tool morphology in Lower Paleolithic technology can exert and reveal both biomechanical (Patiño et al. 2017; Key and Dunmore 2018; Key and Lycett 2011, 2018) and cognitive (Iriki 2006; Heed et al. 2015; Miller et al. 2018) responses. Hand size is also a factor to be taken into consideration, because the gripping force depends on the manipulative proportions of the individual using the tool (Hall 1997; Seo and Armstrong 2008). Moreover, the grasping morphometrics should take into account the whole hand-tool system (Silva-Gago et al. 2019).

Although there is uncertainty on whether or not Lower Paleolithic stone tools were used with hafting, experimental evidence suggests that they can be efficiently employed by direct hand grip (Claud 2015). Future analyses should be anyway designed to include hafting in these kinds of haptic studies. Apart from grasping, haptic exploration is also associated with cognitive (Miller et al. 2014) and physiological responses (Fedato et al. 2019a, 2019b), which suggests a complex behavioral scenario that bridges archaeology with the evolution of our visuospatial capacities (Bruner and Iriki 2016; Bruner et al. 2018b). Ongoing surveys are also considering the association of tools and functions, as well as real case studies associated with specific archaeological sites.

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ORIGINAL RESEARCH ARTICLE

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Hand morphometrics, electrodermal activity, and stone tools haptic perception

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Abstract

Objectives: Tool use requires integration among sensorial, biomechanical, and cognitive factors. Taking into account the importance of tool use in human evolution, changes associated with the genus *Homo* are to be expected in all these three aspects. Haptics is based on both tactile and proprioceptive feedbacks, and it is associated with emotional reactions. Previous analyses have suggested a difference between males and females, and during haptic exploration of different typologies of stone tools. Here, we analyze the correlation between electrodermal reactions during stone tool handling and hand morphology to provide evidence of possible allometric factors shared by males and females.

Methods: Electrodermal analysis was used to investigate some specific parameters involved in these reactions, such as changes in the level of attention and arousal. We analyzed the responses of 46 right-handed adults to 20 distinct stone tools while blindfolded.

Results: Females have smaller hands and a wider range of electrodermal reactions. Within males and females, hand diameters and general hand size do not correlate with the degree of electrodermal level and response.

Conclusions: Sex differences in electrodemal reaction during stone tool handling are apparently not due to the effect of hand size or proportions. Differences between males and females are better interpreted as real sex differences, either due to a biological or cultural influences. Hand size does not influence the degree of arousal or attention during tool exploration, suggesting that other factors trigger individual reactions. These results add to a general cognitive approach on hand-tool evolution and tool sensing.

1 | INTRODUCTION

In the human genus, tool use and tool making represented a crucial shift toward a new ecological and dietary niche (Key & Lycett, 2016; Williams-Hatala et al., 2018). Accordingly, hand structure and function underwent relevant evolutionary specializations in the bones and muscles (Almécija, Smaers, & Jungers, 2015; Diogo, Richmond, & Wood, 2012; Tocheri, Orr, Jacofsky, & Marzke, 2008). This was possible through the coevolution with those parietal cortical regions involved in reaching, grasping, and object exploration (Goldring & Krubitzer, 2017). Body-tool relationship is based on both tactile and proprioceptive information (Tunik, Rice, Hamilton, & Grafton, 2007; Turvey & Carello, 2011), and this haptic experience finally leads to an integration of the tool within the body scheme of the brain (Iriki, 2006), through a remapping process bridging biomechanics with cognition (Heed, Buchholz, Engel, &

Röder, 2015). This means, in terms of body perception and nervous responses, sensed tools actually represent a neural and physical prolongation of the body itself (Miller et al., 2018).

In humans, fingers do not display the elongated proportions found in living apes, and this absence can represent a plesiomorphic trait shared with quadrupedal primates, or a parallelism due to absence of specialization for suspensory locomotion (Almécija et al., 2015). It has been hypothesized that the fingers-to-thumb proportion in our genus probably evolved in relation with habitual bipedalism, before stone tools appearance (Almécija et al., 2015; Richmond, Roach, & Ostrofsky, 2016). The ratio between the thumb and the other fingers is actually one of the traditional indices used to define manual dexterity (Feix, Kivell, Pouydebat, & Dollar, 2015). When compared with living apes, humans evolved specific grasping capacities such as enhanced dexterity and precision grip (Hu, Xiong, & Liu, 2018; Napier, 1956). Tool handling requires specific hand and upper limb features, to perform an efficient manipulation (Williams-Hatala, 2016), and tool form and use may have generated pivotal selective feedback between biology and culture (Williams-Hatala et al., 2018). Within adult modern humans, the largest morphological differences are due to general hand size, which is highly variable, and noticeably larger in males than females (Buffa, Marini, Cabras, Scalas, & Floris, 2007; Jee & Yun, 2016; Varu, Gajera, Mangal, & Modi, 2016; Bruner et al., 2018a; Vergara, Agost, & Gracia-Ibáñez, 2018).

Touch is intimately related to vision, and both capacities do represent the main primate specialization to interact with the outer environment (Goodale, 1990). Some of their sensorial and cognitive components, which are particularly developed in humans, can be investigated in evolutionary anthropology (Bruner, Spinapolice, Burke, & Overmann, 2018). Touch also plays a crucial role in communication and it is involved in socio-emotional development (Nardelli, Greco, Bianchi, Scilingo, & Valenza, 2018). Together with vision, we perceive the spatial context through manipulation (Gazzaniga & LeDoux, 2013), with haptic experiences that activate areas of the inferior and superior parietal lobules, the premotor cortex and the prefrontal cortex (Binkofski et al., 1999). These cortical regions are crucial to process and categorize information of the personal and peri-personal spaces (Cléry, Guipponi, Wardak, & Hamed, 2015). These visuospatial functions are therefore implicated in the general relationships between brain, body, and environment, and in particular deal with the relationships between eye and hand, and between body and tools (Bruner & Iriki, 2016). Interestingly, these regions are larger and more complex in humans than in apes, and are enlarged in *Homo sapiens* when compared with extinct human species, including Neanderthals (Bruner, 2018). Some of these functions may be associated with specific biomechanical capacities (like precision), while others are thought to be related to the capacity of sensing the tool and integrating the tool within the cognitive schemes. Among the latter mechanisms, the "prosthetic capacity" (Bruner & Gleeson, 2019; Overmann, 2015) can be defined as the capacity to integrate an object within the cognitive system through the interface of the body, outsourcing and offloading information processing to external elements (Malafouris, 2010; Japyassú & Laland, 2017). It is something that is not necessarily related with specific mechanical abilities (like precision), but instead something that deals with body cognition and sensing. In cognitive archeology, we must consider the possibility that changes in this cognitive relationship between brain, body, and tools, can influence the evolutionary fitness of a species, promoting or demoting tool use capacity.

The haptic experience and object sensing involve somatosensory perception (through the skin surface) and proprioception of hand position and conformation (Yau, Kim, Thakur, & Bensmaia, 2015), and the spatial properties of handled tools are perceived through dynamic touch and gravitational effects on the body (Turvey & Carello, 2011). This means that the physical interaction with the tool and the integration of the tool within the body scheme can influence and alter the cognitive and emotional condition of a subject during tool use and exploration. In this sense, it can be interesting to consider the system formed by the hand and the tool as a single structural unit, also in an archeological context (Silva-Gago, Fedato, Rios-Garaizar, & Bruner, 2019).

Recently, we proposed electrodermal analysis (EDA) as a fast and easy method to detect cognitive changes during stone tool manipulation, integrating electrophysiology with stone tool handling (Bruner et al., 2018a, 2018b). EDA fluctuations are used as proxy for emotional and attentional engagement (Boucsein, 2012; Dawson, Schell, & Filion, 2000), and can be used to measure psychophysiological variation during haptic stimulation (Greco et al., 2015). Different stone tools exert different electrophysiological reactions, with modest but significant differences between tool types (handaxes and choppers) and between males and females (Fedato et al., 2019). Choppers trigger, on average, more arousal and more attentional reaction than handaxes, although they require a shorter manipulation time to reach a stable and comfortable position (choppers: 13.0 seconds; handaxes: 17.5 seconds). This could be probably due to the choppers dimension and smoother edges. Women are able to perceive finer surface details when compared with men (Peters, Hackeman, & Goldreich, 2009), probably by virtue of smaller finger size and higher density of sweat pores (Sanders & Walsh, 2007; Peters et al., 2009; Morimoto, 1978). Males and females display a noticeable difference in hand size, larger in the former group, although it is not known whether hand dimensions can influence the electrodermal activity (Bruner, et al., 2018a). In this study, we evaluate the influence of hand morphology on electrodermal reaction during stone tool tactile exploration, under the null hypothesis of no effect. The first aim is to investigate possible allometric effects due to hand size. The second aim is to consider whether sex differences in electodermal activity may be related to hand size differences.

2 | MATERIAL AND METHODS

2.1 | Sample

This study was performed on a sample of 46 right-handed adult individuals (22 females and 24 males) with ages ranging from 21 to 65 years old. The previous general analysis on the same sample suggests that electrodermal activity is not influenced by age (Fedato et al., 2019). This survey aims to evaluate the electrodermal reaction during haptic exploration of distinct lithic tools, without any specific functional task. Accordingly, the subjects had no previous experience in archeology, and were naive to stone tool handling. Subjects were also blindfolded in order to limit the sensorial experience to the haptic inputs. All subjects signed an informed consent about the procedure and privacy policy. Subjects were asked to manipulate and explore each tool haptically with the right hand, until a comfortable position was reached.

Stone tools are often the only type of cultural remains at Paleolithic sites and, accordingly, they are one of the most important sources of information about early humans' behavior (Nowell & Davidson, 2010).

TABLE 1 Metrics (means and SDs) of the stone tools used in this survey

		Weight (kg)	Length (mm)	Width (mm)	Thickness (mm)
Choppers (n = 7)	Mean	0.50	98.05	92.49	43.83
	SD	0.27	26.35	36.28	12.06
Bifaces (n = 6)	Mean	0.50	160.36	84.94	34.68
	SD	0.25	26.27	20.30	10.06
Flakes (n = 5)	Mean	0.14	63.62	81.58	20.60
	SD	0.10	17.16	24.62	4.57
Stones (n = 2)	Mean	1.08	143.70	84.85	42.95
	SD	0.08	11.30	1.15	19.55

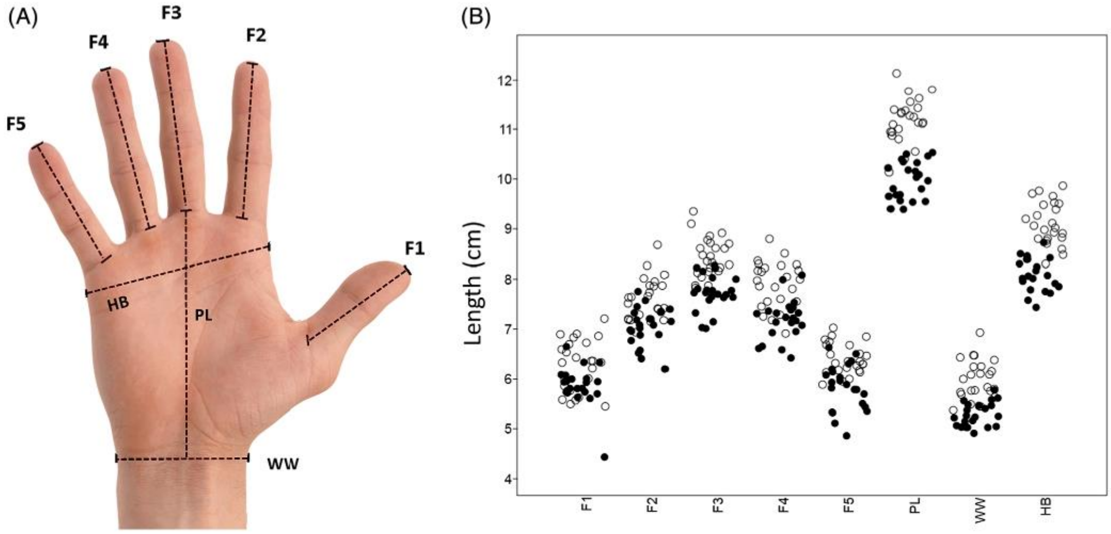

FIGURE 1 Hand metrics (A) and jitterplot (B) showing the value distributions for males (white dots) and females (black dots). See text for labels

Early Paleolithic includes lithic technologies known as Oldowan and Acheulean. Oldowan (with an early occurrence around 2.6 Ma) includes irregularly knapped tools like the choppers, namely pebbles with an asymmetric cutting edge formed by the removal of flakes. Acheulean is instead largely characterized by roughly symmetric handaxes (1.76 Ma), produced by the removal of large flakes from both sides of a cobble. However, they can also be made on a large flake (Debénath & Dibble, 1994; Diez-Martín et al., 2015; Lepre et al., 2011). In its early phase (associated with *Homo ergaster/erectus*), handaxes are made on large cobbles using a hard hammer percussion. Late Acheulean bifaces show pronounced geometrical properties probably produced by the soft hammer technique, like a progressive decrease of the tool thickness (Stout, Apel, Commander, & Roberts, 2014). The ability to impose bilateral symmetry underlies an increase in hierarchical complexity and higher cognitive abilities (Stout, 2011; Toth & Schick, 2006). Following technological types (like Middle Paleolithic tools, described in the archeological record after 385 ka; Scott & Ashton, 2011; Akhilesh et al., 2018) are generally made from retouched flakes or through prepared core technology (Levallois tools), and are particularly related with late *Homo heidelibergensis*, early Neanderthal, and archaic forms of *H. sapiens* (Toth & Schick, 2006). In this study, tool sample included 20 experimental lithic tools, belonging to different Lower Paleolithic morphotypes (choppers, handaxes, and flakes; see Table 1 for length, width, thickness, and weight descriptive statistics). We also included two natural (not knapped) stones. Accordingly, each subject underwent a recording session with 20 trials. The tool sequence was randomized for every subject. The stones were knapped by the same expert (Marcos Terradillos-Bernal) from the same quartzite to obtain a homogeneous texture. Four additional tools were used in each session for a preliminary familiarization procedure, and not included in the statistical analysis.

TABLE 2 Descriptive statistics of hand measures (cm) in males and females, a Mann–Whitney (MW) test, and discrimination analysis (percentage of correct assignments)

	Sex	Mean	SD	CV	Q25	Q50	Q75	MW	DA (%)
F1	F	5.87	0.41	0.07	5.74	5.87	6.00	$P < .015$	69.57
	M	6.28	0.52	0.08	5.84	6.35	6.70		
F2	F	7.04	0.38	0.05	6.88	7.08	7.30	$P < .01$	71.74
	M	7.60	0.42	0.05	7.27	7.57	7.87		
F3	F	7.72	0.36	0.05	7.64	7.73	7.95	$P < .01$	82.61
	M	8.44	0.40	0.05	8.16	8.40	8.71		
F4	F	7.20	0.41	0.06	6.98	7.23	7.38	$P < .01$	82.61
	M	7.90	0.47	0.06	7.55	7.99	8.23		
F5	F	5.82	0.46	0.08	5.46	5.86	6.13	$P < .01$	80.43
	M	6.40	0.31	0.05	6.18	6.34	6.68		
PL	F	9.97	0.37	0.04	9.66	10.00	10.30	$P < .01$	93.48
	M	11.18	0.45	0.04	10.95	11.19	11.40		
WW	F	5.28	0.24	0.05	5.05	5.24	5.47	$P < .01$	86.96
	M	5.98	0.39	0.07	5.72	5.92	6.25		
HB	F	8.10	0.33	0.04	7.87	8.07	8.39	$P < .01$	93.48
	M	9.11	0.43	0.05	8.81	9.04	9.49		
HL	F	17.69	0.64	0.04	17.25	17.74	18.20	$P < .01$	91.30
	M	19.63	0.74	0.04	19.18	19.54	20.00		
HI	F	45.81	1.48	0.03	45.00	45.87	46.69	$P = .25$	60.87
	M	46.44	1.78	0.04	45.63	46.33	47.76		
DI	F	43.65	1.01	0.02	43.1	43.64	44.43	$P = .03$	63.04
	M	43.02	1.02	0.02	42.5	43.04	43.70		
PI	F	1.23	0.04	0.03	1.20	1.23	1.26	$P = .82$	45.65
	M	1.23	0.05	0.04	1.19	1.23	1.26		
2D:4D	F	0.98	0.04	0.04	0.96	0.98	1.00	$P = .22$	60.87
	M	0.96	0.04	0.04	0.96	0.97	0.98		

2.2 | Hand morphometrics

Hand images were acquired with a 2D scanner, and used to measure palmar length (PL), finger lengths, hand breadth (HB), and wrist width (WW) with ImageJ 1.46r (Rueden et al., 2017), by using flexion creases as references (Barut, Dogan, & Buyukuysal, 2014; Hall, Allanson, Gripp, & Slavotinek, 2006; Kanchan & Krishan, 2011) (Figure 1A). PL is calculated from the mid-point of the distal transverse crease of the wrist flexures to the most proximal flexion crease of the third finger. HB is the distance between metacarpal radial and metacarpal ulnar. Finger lengths (F1-F5) are measured, for each finger, as the distance between the proximal flexion crease of the finger, to the tip of that finger. Hand length (HL) is the distance between the distal flexion crease at the wrist and the tip of the third digit. A previous Principal Component Analysis with the same sample and variables showed a first component (75%) associated with general hand size increase, and a second component (9%) associated with thumb/palmar ratio (Bruner, Fedato, et al., 2018a). Three ratios were also measured as described by Barut, Sevinc, & Sumbuloglu (2011) and Barut et al. (2014). The hand index (HI) determines the basic hand proportions (hand width × 100/HL); the digit index (DI) determines the fingers-to-hand proportions (third digit length × 100/HL); and the PL/width ratio (PI) determines the palmar proportions (PL/palmar width). Finally, we calculated the ratio of the lengths of the second and fourth digits (2D:4D) (Manning, Bundred, Newton, & Flanagan, 2003; Manning, Trivers, Thornhill, & Singh, 2000; Trivers, Manning, & Jacobson, 2006).

2.3 | Electrodermal analysis

EDA was recorded with a Sociograph Portable Device wrapped on the left forearm, with electrodes at the second and third fingertips. EDA is a measure of skin conductance, which is influenced by eccrine activity due to stress, arousal, or emotional excitement. It is used as proxy for changes in emotional processing and sympathetic activity in visual and auditory modalities (Khalfa, Isabelle, Jean-Pierre, & Manon, 2002; Baumgartner, Willi, & Jäncke, 2007), as an autonomic psychophysiological variable that is not influenced by

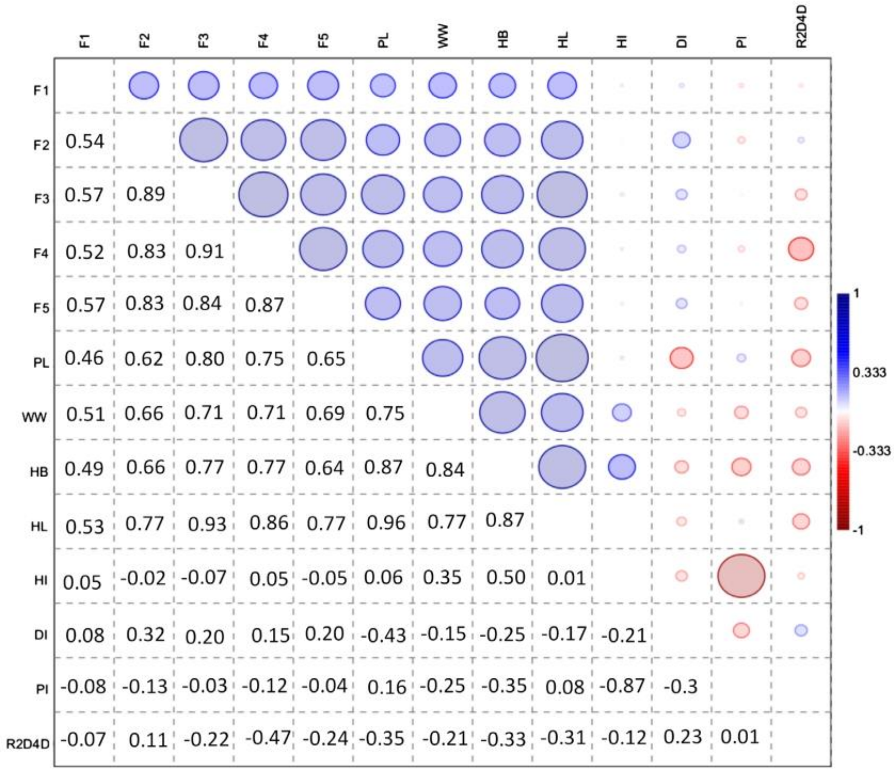

FIGURE 2 Correlation matrix. Lower triangle shows the correlation coefficient, upper triangle graphically displays the magnitude (size) and sign (color) of the correlation coefficients

parasympathetic condition (Greco, Valenza, & Scilingo, 2016). We measured the tonic level of electrical conductivity (electrodermal Level [EDL]) and the phasic change (EDR). The former is influenced by changes in attention, and the latter by the arousal level. Both values are measured in kilohms (KΩ), with a frequency of 32 Hz. During the experiment, the room temperature was set constant at 23°C. EDR value is directly proportional to the arousal level, while for EDL the decrease of the resistance value is associated with an increase in attention. EDR and EDL were recorded for each trial (one tool) from the beginning of the exploration until the achievement of a stable and comfortable position. For EDR, we computed the average value for each trial in order to quantify the mean arousal of the subject associated with each tool. For EDL, we computed the standardized average rate of change, namely, for each trial, the ratio between the peak of maximum attention and its average value. Values exceeding 1.5 times the interquartile range were considered as outliers and were not included in the pooled statistical analysis. Statistics were computed with SPSS.

3 | RESULTS

3.1 | Hand morphometrics

Figure 1B shows the jitterplot for the male and female distributions of the hand variables. Table 2 shows the descriptive statistics for the hand variables measured in this study, a Mann-Whitney comparison between males and females, and the percentage of correctly classified subjects after discriminant analysis. Males display larger values and larger variation for all the diameters, but there are no significant differences for the ratios apart from the DI. PL is the variable that better discriminates the two sexes, followed by HL and HB. WW is a good estimator for sex and, among finger lengths, F3 is the most accurate to predict sex, while the thumb is the less reliable. Ratios are not accurate in discriminating males and females.

Figure 2 displays the correlation plots and coefficients between the hand measures. Hand measures are strongly correlated, in particular the second, third, and fourth fingers. Thumb length is the variable that shows the lowest correlation with the rest of the variables. Ratios (HI, DI, PI, and 2D:4D) do not correlate with finger length, except DI with the second finger and the 2D:4D with the fourth finger. HB correlates with HI, palm index, and 2D:4D. PL correlates with DI and 2D:4D while WW only correlates with hand proportions (HI). HL correlates with all hand measures and 2D:4D, but displays no correlation with the other ratios. PI correlates with HI and slightly with DI. 2D:4D does not correlate with any of the other ratios.

3.2 | Electrodermal analysis

As reported in a previous survey (Fedato et al., 2019), females show a higher mean and larger variation than males for both EDL and EDR ($P = 0.02$ and $P = 0.01$ respectively). EDL and EDR show a moderate correlation ($r = -.63$, $P < .001$), which is stronger in females than in males ($r_{\text{females}} = -.67$, $r_{\text{males}} = -.41$).

We computed a correlation analysis between electrodermal variables and each hand measure. Considering the number of variables we tested, a Bonferroni adjustment

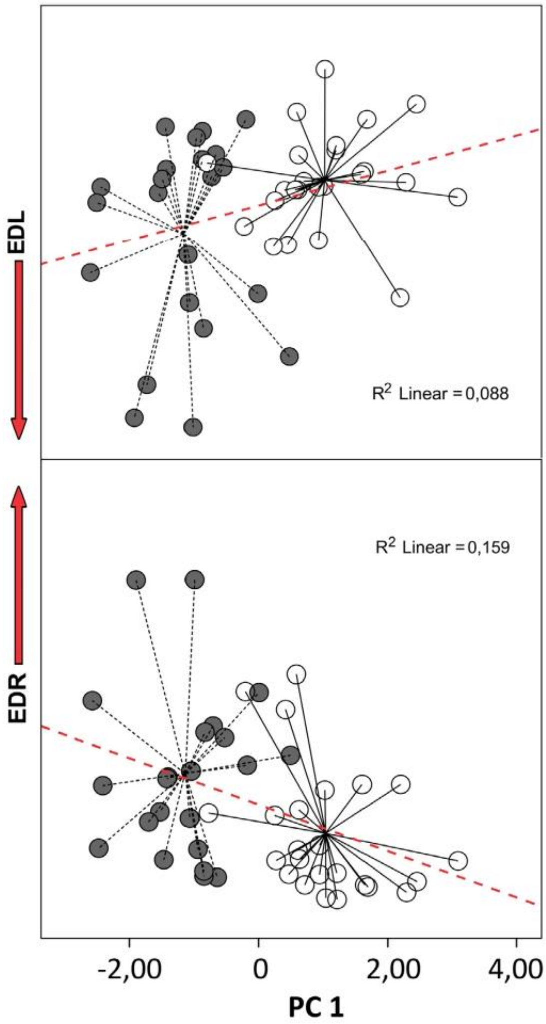

FIGURE 3 PC1 (hand size) plotted on EDL and EDR values (males: white dots; females: gray dots). Spikes show individual distance from group centroid. Determination coefficient and least square regression lines are computed on the pooled sample. EDL, electrodermal Level; EDR, electrodermal response

was applied to control type I errors. Correlations are therefore considered significant for $P < .004$. As a result, the third and the fourth fingers display a significant correlation with EDR when the pooled (males and females) sample is taken into account ($R = -.41$ and $-.43$, respectively). However, these correlations are not significant when males and females are analyzed separately, suggesting that there is no allometric effect of hand diameters on electrodermal reaction within the two groups. Similarly to the results obtained with the individual hand diameters, also the PC1 of the all variables—dealing with general hand size—is correlated with both electrodermal variables (pEDL = 0.045, pEDR = 0.006) only when the pooled sample is analyzed, but not when males and females are analyzed separately (Figure 3). It is worth noting that males and females display overlapping ranges, but females have a larger variation toward higher electrodermal reactions. Correlation is not significant between EDA variables and PC2. Interestingly, PC2 correlates with both HI and DI (particularly with this latter one). PC2 is associated with a decrease in palmar size and, accordingly, DI has a negative correlation with PL. HI also correlates with the second principal component. Nonetheless, this component only explains a minor percentage of variation, and must be considered with caution.

4 | DISCUSSION

Tool haptic exploration triggers an electrodermal reaction that is interpreted as a proxy for arousal and attentional changes (Bruner, et al., 2018a). During stone tool handling, females display larger variation toward higher reactions than males (Fedato et al., 2019). Such differences can be associated with sexual differences in perception or engagement, or else to allometric factors, due to hand size differences. In this study, we analyzed the metric variation of the adult human hand and, subsequently, we evaluated whether hand diameters can be correlated to specific electrodermal reactions during lithic tool haptic exploration. Accordingly, the main aim of this survey is to test whether hand morphology can be associated with specific autonomic responses during stone tool exploration.

The human hand shows a pronounced sexual dimorphism, with males having, on average, bigger hands when compared to females (Bruner, Fedato, et al., 2018a). Anthropometric measurements of hand dimensions can actually estimate the sex of an individual with high accuracy (Barut et al., 2014; Kanchan & Rastogi, 2009). As reported in many studies, the male hand is significantly larger and wider (Buffa et al., 2007; Kanchan & Krishan, 2011; Kanchan & Rastogi, 2009), and sex differences have been also found in specific hand and finger proportions (Kanchan, Krishan, Sharma, & Menezes, 2010; Kulaksiz & Gözil, 2002; Barut et al., 2014; Kanchan & Rastogi, 2009; Sharifi-Mollayousefi et al., 2008; Ibeachu, Abu, & Didia, 2011). In particular, males have relatively wider hands (higher HI) while females have relatively longer fingers (higher digital index). In our survey, the PL is the most reliable sex discriminator, followed by HL and HB. These measures are strongly related with the overall size of the hand and, accordingly, they represent main factors of variation among adult individuals. The hand dimensions and ratios presented in this study are coherent with previous works (Barut et al., 2014). However, differently from previous analyses, in our case we are not able to confirm a significant sex difference for HI and palmar index. Therefore, in our sample, females have relatively longer fingers (digital index) but the general proportions of the hand and of the palm are similar in the two sexes.

Most somatic sexually dimorphic traits are influenced by prenatal exposure to testosterone (Gobrogge, Breedlove, & Klump, 2008), which may have also contributed to the sexual dimorphism in hand morphology (Buffa et al., 2007; Dogan, Barut, Konuk, & Bilge, 2008). The ratio between the length of the second and fourth digits (2D:4D) has been particularly investigated in this sense, and hypothesized to be associated with physiological, pathological, and behavioral aspects (Beaton, Rudling, Kissling, Taurines, & Thome, 2011; Coolican & Peters, 2003; Jackson, 2008; Williams et al., 2000). This ratio, although very variable, is frequently higher in females than in males (Galis, Ten Broek, Van Dongen, & Wijnaendts, 2010; Manning, Kilduff, Cook, Crewther, & Fink, 2014). In our study this difference does not reach significance.

Bearing these patterns of hand morphological variation among adult humans in mind, we tested the correlation between hand metrics and electrodermal reactions during haptic exploration of stone tools. Previous analyses showed that there are subtle but consistent electrodermal differences when exploring different kinds of stone tools, and between males and females (Fedato et al., 2019). Correlations between hand diameters (F3 and F4) and hand size (PC1) with the two electrodermal variables are significant only when sexes are pooled together, but there is no correlation when males and females are analyzed separately. Accordingly, pooled correlations must be interpreted as a bias due to the fact that females display different hand morphology (smaller hands) and at the same time larger electrodermal variability (toward higher electrodermal reactions). Within males and females, electrodermal activity does not depend on hand size or morphology, so their differences are not due to a shared allometric pattern associated with hand dimensions. We can therefore reject the hypothesis of influence of hand size on the electrodermal reaction. Accordingly, differences between males and females must be interpreted as proper sex differences, and not as secondary and allometric consequences of hand size. Few studies have analyzed the effects of sex on the physiological components of emotional and attentional responses and, in general, there is no agreement about specific sex-related effects (Boucsein, 2012; Venables & Christie, 1980). Sex differences in EDA response seem to be related with endocrine system (Boucsein, 2012). Some experiments have showed sex differences in both tonic level and phasic response (Kimmel & Kimmel, 1965; Kopacz & Smith, 1971; Purohit, 1966). In particular, a study about effects of sex on emotional responses showed that females displayed a greater increase in skin conductance than males (Chentsova-Dutton & Tsai, 2007). Sex-related differences have been also found in tactile perception, with women being able to perceive finer surface details compared to men. This phenomena seems to be related with sweat pores, which are packed more densely in smaller fingers. Tactile perception increases with decreasing finger size and women have, on average, smaller hands compare to men (Peters et al., 2009; Morimoto, 1978).

According to our data, arousal and attentional responses, as measured by skin impedance fluctuations, do not depend on hand size and, therefore, other physiological or behavioral parameters are probably involved. However, it is worth noting that males and females show overlapping values for both EDL and EDR, and the differences are in part due to larger variation of the female range toward higher engagement. Namely, among females, there are more individuals peaking to stronger arousal/attention. It has been suggested that negative stimuli elicit higher corticospinal excitability when compared with pleasant and neutral ones, probably because anxiety-related events require motor actions to be more urgently mobilized (Borgomaneri, Gazzola, & Avenanti, 2014; Hajcak et al., 2007; Van Loon, van den Wildenberg, van Stegeren, Ridderinkhof, & Hajcak, 2010). It may hence be evaluated whether the stronger reaction in women may be due to a higher sensitivity to some kinds of negative perceptions during the haptic experience. However, in other cases, the separation between positive and negative reactions is less clear (Khalfa et al., 2002). In any case, the absence of any clear correlation between hand size and electrodermal reaction does not support the interpretation of the differences in attention or engagement in terms of higher or lower comfort during handling due to the limitations of hand size.

5 | LIMITATION AND FUTURE PERSPECTIVES

EDA represents a quick and easy tool to investigate behavioral and cognitive reaction during specific tasks, and it can therefore be a useful tool in cognitive archeology. Nonetheless, the electrophysiological reaction associated with fluctuations of skin impedance is but a proxy of the underlying mental mechanisms. It is therefore useful to evidence gross differences between groups or individuals, but it is not able to reveal subtle changes or to explain the process behind those variations. Namely, the electrodermal reaction of a subject is due to multiple biological and cultural factors, and the overall value is then influenced by distinct independent aspects. Also, EDR is interpreted as general arousal, with no information on the values and polarity of such emotional changes. In this case, although the sample size is not particularly large, the absence of correlation between hand and electrodermal variables within the two groups is rather patent, suggesting that this result, although very general, is nonetheless consistent. If hand morphology is not crucial to elicit different electrodermal reactions, then tool properties may have a more relevant role, in this sense. In fact, tool length and weight can partially influence the electrodermal reaction (Fedato et al., 2019). An ongoing study is analyzing whether and to what extent stone tool shape and physical properties can have an influence on the electrophysiological reactions. Concerning hand variation, it must be stressed that there are differences in hand morphology in distinct geographic groups (Barut et al., 2014; Davies, Abada, Benson, Courtney, & Minto, 1980; Gnaneswaran & Bishu, 2011; Okunribido, 2000) or distinct social/occupational classes (Imrhan, Sarder, & Mandahawi, 2009; Mandahawi, Imrhan, Al-Shobaki, & Sarder, 2008; Stanford, Allen, & Antón, 2011). It could be interesting, therefore, to evaluate distinct behavioral reactions in samples with particular finger, hand, or arm proportions, most of all taking into account extreme or special cases.

In the future we are planning to test the same electrophysiological reaction in individuals with previous archeological knowledge. This study was aimed at investigating the electrodermal effect due to the hand-tool contact and exploration, independently on the tool functions or tasks. It is expected that a subject with specific archeological background would manipulate the tool with functional information in mind, adding further factors to the modulation of the arousal/attentional signal.

As further cautionary note, it must be considered that an implicit limitation in cognitive archeology is the employment on modern humans to investigate behaviors associated with prehistoric contexts. The results presented in these kinds of surveys (and the conclusion therein) strictly refer to the behavioral responses of *Homo sapiens* during the experimental performances. Extrapolations to extinct human species, although reasonable because of the taxonomic affinity, would require additional and complementary information from multiple source of information.

6 | CONCLUSION

Most studies in hand evolution and human tool grasping have focused on biomechanical aspects (eg, Almécija et al., 2015; Diogo et al., 2012). Indeed, biomechanical capacities (like precision or dexterity) are crucial to a proper hand-tool interaction. Nonetheless, according to theories in cognitive extension, grasping has also a cognitive counterpart, that is not directly associated with biomechanics, but instead depends on sensing capacity (Miller et al., 2018). Such capacity is part of a comprehensive cognitive toolkit that also include emotional processes (Miller & Clark, 2018). The analysis of these electrophysiological reactions when handling stone tools can supply information on possible changes in the level of engagement associated with hand-tool interaction in human evolution.

This survey suggests that hand size and proportions are not influential in eliciting distinct electrodermal reaction during stone tool haptic exploration. Mean differences between males and females, therefore, are probably due to real sex differences, and not to secondary consequences of having different hand dimensions. Individuals display different levels of perceptual learning capacity (Withagen & Van Wermeskerken, 2009), and tactile acuity is subject to considerable improvement with practice (Goldreich & Kanics, 2003; Grant, Thiagarajah, & Sathian, 2000). At present, it is not known whether these sex differences are due to biological or cultural factors. Tool-making was probably an activity shared by males and females (Kohn & Mithen, 1999; Weedman Arthur, 2010), although with distinct biomechanical constraints (smaller hand in females) and, according to the current results, some minor differences in emotional feedback during haptic exploration. Considering the noticeable morphological hand changes associated with hominid evolution, we can also wonder whether some specific features could have promoted a more comprehensive cognitive engagement between body and tool, increasing the human prosthetic capacity not only in biomechanical and ergonomic aspects, but also at perceptual level (Bruner & Gleeson, 2019). Taking into account the ability to integrate technology within our cognitive system, any adaptation in this sense would have been crucial.

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AUTHOR CONTRIBUTIONS

E.B. designed the study. A.F., M.S.-G., and E.M.-G collected the data. A.F. analyzed the data. R.A.-A. and M.T.-B. prepared the stone tools. E.B., A.F., and M.S.-G. wrote the article.

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Electrodermal activity during Lower Paleolithic stone tool handling

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Abstract

Objectives: Hand coordination is a key feature in primate evolution at both behavioral and cognitive levels. Humans further improved their manual abilities, and their cognitive niche is deeply associated with hand-tool relationships and technological capacity. A main cognitive change is thought to be related to the transition from Oldowan to Acheulean stone tool technology around 1.7 million years ago. In this survey, we test whether distinct Lower Paleolithic tools induce different electrophysiological reactions during haptic exploration.

Methods: Electrodermal activity is a relatively quick way to measure emotional and attentional changes during specific tasks. We analyzed changes of the electrodermal response and electrodermal level during Oldowan and Acheulean stone tool handling in a sample of 46 right-handed adult subjects with no previous archeological knowledge.

Results: Electrodermal proxies for attention and emotion display a skewed distribution. Females present more variable reactions than males and more emotional engagement. Acheulean tools require longer manipulation time and exert less emotional response than Oldowan tools. Attention is influenced by tool length and weight, emotion is sensitive to tool thickness and weight, and manipulation time depends on tool length and width.

Conclusions: This study suggests subtle but detectable perceptual differences when handling Oldowan and Acheulean stone tools. Such variations associated with hand-tool interaction can provide information on haptic and prosthetic capacities associated with our specialized technological resources. Perceptual changes in the archeological record can reveal evolutionary changes in the corresponding body-tool cognitive mechanisms.

1 | INTRODUCTION

In archeology, cultural traces are generally used to make inferences about the behavior and cognition of past or extinct human populations. In cognitive archeology, this information is integrated with current theory in cognitive sciences (Coolidge, Wynn, Overmann, & Hicks, 2015; Wynn & Coolidge, 2016), while in neuroarcheology, those behaviors are investigated with functional imaging or other neurofunctional correlates (Stout & Chaminade, 2007; Stout & Hecht, 2015). Stone tools have a key role in this sense, because the complexity behind their production is used as proxy of behavioral and cognitive complexity of the tool-makers (Muller, Clarkson, & Shipton, 2017; Stout, Semaw, Rogers, & Cauche, 2010).

A relevant change in the archeological record can be traced back 1.7 million years, when simpler shaped pebbles (choppers) were progressively replaced by complex, symmetrical, and multifunctional tools (Wynn, 2002). This change marked the transition from mode 1 to mode 2 (or Oldowan to Acheulean culture), which was hypothesized to be associated with relevant cognitive variations (Clark, 1969; Hodgson, 2005; Moore & Perston, 2016; Wynn, 2010). In particular, functional imaging suggests that Oldowan production largely relies on visuospatial functions, while Acheulean tool-making involves a larger frontoparietal system, integrating spatial and executive cortical centers (Stout, Hecht, Khreisheh, Bradley, & Chaminade, 2015).

Acheulean tools include handaxes, large flakes, and retouched flakes made through a bifacial knapping process, where percussion extends over almost all or all the stone's surface (Lycett, 2011). Handaxes are symmetric, flat, and elongated, suggesting more sophisticated geometrical properties (Gowlett, 2013) and the usage of wider hammerstone typologies (Stout, 2011).

Recent theories propose material culture as a functional element of the cognitive system (Malafouris, 2010, 2013). Whether or not such a continuity between the neural and technological components can be tested (Kaplan, 2012), there is plenty of evidence suggesting that the haptic experience has a key role in channeling and organizing the cognitive process (Ackerley & Kavounoudias, 2015; Tunik, Rice, Hamilton, & Grafton, 2007; Turvey & Carello, 2011). Furthermore, the evolution of language may also have a connection with tool use, as both processes rely on similar brain networks as well as on social learning (Buccino, Binkofski, & Riggio, 2004; Stout & Chaminade, 2012).

Primates have evolutionarily derived cortical areas, which deal with body control and hand manipulation through specializations of the posterior parietal cortex, which are even more patent in humans, because of tool use and body-tool coordination (Goldring & Krubitzer, 2017; Krubitzer & Stolzenberg, 2014; Nowell & Davidson, 2010). Interestingly, the dorsal parietal cortex also displays a noticeable morphological change in Neanderthals and, in particular, in modern humans, in regions corresponding to the superior parietal lobule, precuneus, and intraparietal sulcus (Bruner, 2018). The precuneus is particularly involved in body-vision integration (including visual imaging, simulation, and body-centered spatial and chronological management; Bruner et al., 2014; Cavanna & Trimble, 2006; Margulies et al., 2009), while the intraparietal sulcus is involved in eye-hand coordination (Grefkes & Fink, 2005). Visuospatial functions and tool use are intimately related (Gibson, Gibson, & Ingold, 1994) and, accordingly, the parietal cortex, visuospatial functions, and technological development represent an integrated functional system targeted by selection during human evolution (Bruner & Iriki, 2016).

Recently, we proposed electrodermal activity (EDA) as a tool to investigate emotional and attentional effects during tool manipulation (Bruner et al., 2018a, 2018b). EDA has been used for a long time in psychology and medicine, and more recently in neuroscience and neuromarketing (Ariely & Berns, 2010; Lee, Broderick, & Chamberlain, 2007). Variations in skin impedance are used in cognitive analyses as a proxy for the degree of emotional and attentional engagement (Boucsein, Schaefer, Kefel, Busch, & Eisfeld, 2002; Martin & Venables, 1966). EDA deals with changes in the electrical properties of the skin (conductivity) due to the increase of secretion by the eccrine sweat glands (Zangróniz, Martínez-Rodrigo, Pastor, López, & Fernández-Caballero, 2017). These glands are found mainly in the dermis of the palmar and plantar areas and are under the control of the autonomic nervous system (Sequeira, Hot, Silvert, & Delplanque, 2009).

In a first article, we introduced the methods and, using three different tools, we showed that stone tool manipulation does influence EDA in a tool-specific way (Bruner et al., 2018a). In a second article, we used a larger set of stone tools, showing that individual responses are very variable, but distinct tools can display different mean figures (Bruner et al., 2018b). Therefore, the hand-tool haptic interaction influences the attentional and emotional condition of the subject, channeling and orienting the following behaviors. If the manipulation of the tools modifies the emotional condition of the subject, we can assign to the hand-tool system some emergent properties absent in the two elements before interaction. If the pattern or degree of these modifications changes according to different tool type, sex, or distinct tool dimensions, we can identify specific factors underlying this interaction. Here, we present the first comprehensive statistical analysis of the electrodermal changes during Oldowan and Acheulean tool manipulation. We analyzed the distribution of the individual trials for all the tools, testing differences between the two typologies and between sexes. We also considered the manipulation time, and the influence of the dimensions of the tools on the electrophysiological parameters. In particular, we tested the null hypothesis of no electrodermal difference during haptic exploration with Oldowan and Acheulean tools, no correlation of EDA with the physical dimensions of the tool, and no electrodermal differences between sexes. The comparison with Oldowan and Acheulean technology was aimed at analyzing whether they exert similar perceptive responses during hand-tool integration or, conversely, if the differences in their respective designs are associated with a change in the effect they induce during explorative handling. The analysis of the tool dimensions was aimed at considering if specific physical variables can influence the electrophysiological response. Differences between males and females were of interest to evaluate sex-specific responses and sample effects.

2 | MATERIAL AND METHODS

The sample used in this study included 46 subjects and 13 stone tools. Subjects (22 females, 24 males) were right-handed adults, aged between 21 and 65 years (mean age: 43 ± 11 years). All participants signed an informed consent. Participants had no previous experience with lithic tool use or archeology. Tools were prepared according to experimental procedures to reproduce seven Oldowan choppers and six Acheulean handaxes. These two typologies were chosen because they correspond to the most abundant and representative Lower Paleolithic material tradition (Clark, 1969; De la Torre, 2016; Stout, 2011; Stout & Chaminade, 2012; Toth & Schick, 2018; Wynn & Gowlett, 2018; Figure 1A,B). To have tools with homogeneous texture, they were knapped from the same Paleozoic material (quartzite), from large irregular pebbles with an average length of 10 cm. The grain was thin and the structure homogeneous with no major fissures or fractures (Terradillos-Bernal & Rodríguez-Alvarez, 2014).

Table 1 shows a list of the tools and their dimensions. There is no weight difference between the two samples ($P = .28$). Subjects were asked to handle each tool until a comfortable position was reached. The task consisted in an active tactile exploration, to perceive the form of the object. Namely, the aim was to record the haptic interaction between hand and tool without any specific functional purpose, to investigate the emotional and attentional reaction during hand-tool exploration. This experimental setting is, at present, independent of any explicit theory of cognition, and only aimed to evaluate if and to what extent different tool types exert different electrodermal reactions associated with the haptic stimulation. To limit the experience to the tactile processes, subjects were blindfolded. For each subject, tool order was randomized to control for the effect of different levels of attention and tiredness during the session. Four additional tools were added before each individual's recording session and not included in the analysis as a familiarization procedure to limit peaks due to the novel experience. Sessions were conducted in a silent room with stable temperature. There was no interaction between the subject and the operator during handling.

TABLE 1 Tool metrics

	Length (mm)	Width (mm)	Thickness (mm)	Weight (kg)
Old 1	91.4	67.5	25.8	0.24
Old 2	89.1	75.6	38.6	0.34
Old 3	134.3	95.0	66.0	0.16
Old 4	178.0	64.2	35.5	0.58
Old 5	65.0	83.5	42.0	0.30
Old 6	133.2	74.8	54.3	0.84
Old 7	107.1	72.1	44.1	0.42
Ach 1	173.4	92.0	37.0	0.66
Ach 2	142.6	114.7	53.1	1.0
Ach 3	173.4	61.6	31.5	0.35
Ach 4	165.0	86.4	35.0	0.48
Ach 5	112.8	56.5	19.0	0.13
Ach 6	195.0	98.4	32.5	0.68

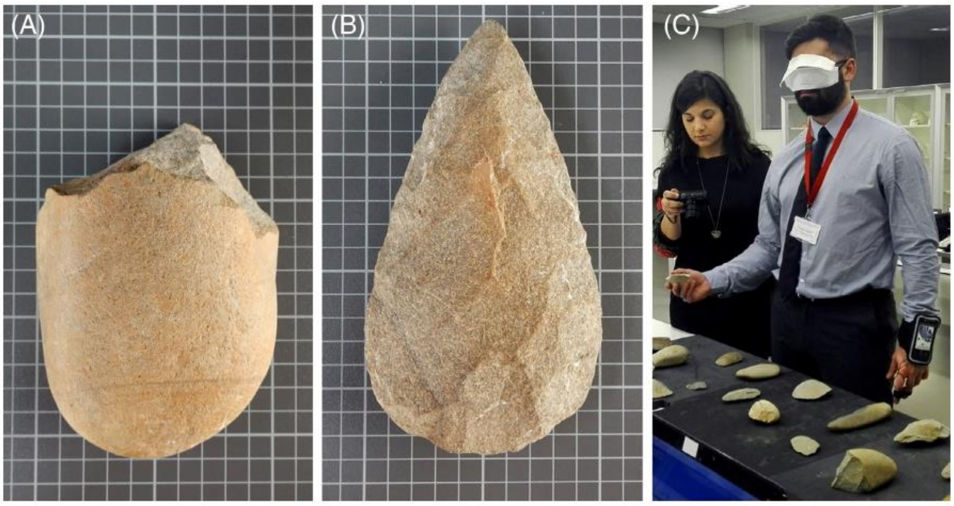

FIGURE 1 In this study, we compared the electrodermal reaction to manipulation of Oldowan (A) with Acheulean (B) tools. Subjects were asked to manipulate tools until they reached a comfortable hand-tool position, while electrodermal response was recorded with a portable device wrapped around the left forearm (C)

EDA was recorded during each trial. We used a remote device (Sociograph Technology, Palencia - Spain) wrapped round the left forearm, connecting two diodes at the 2nd and 3rd fingertips, and recording both tonic and phasic activity (Figure 1C). The tonic activity is associated with electrodermal level (EDL), namely attention, while the phasic activity is associated with electrodermal response (EDR), namely emotional engagement (Boucsein, 2012). In the case of EDL, the lower the resistance whereas the higher the level of attention. Therefore, higher attention is associated with lower EDL values. In the case of EDR, the higher values are associated with higher emotional response. Importantly, the term *emotion* here is intended as general arousal, with no information on the valence (positive or negative; see Harmon-Jones, Gable, & Price, 2013) or implication. Emotion is in fact a broad concept and, in psychology, it includes goal-based components and past experiences (Barrett, 2017). In this case, we use the term only to refer to the emotional engagement as recorded by the electrodermal changes.

For each electrodermal variable, we used one single value per second after averaging 32 recordings per second. EDL and EDR are measured in kilohms (kΩ). In this analysis, we used the average value of each trial to quantify the mean emotional/attentional level for each subject when manipulating each tool. We also measured the time elapsed from the beginning of the manipulation to the reaching of a stable position (total manipulation time [TMT]) because it supplies a proxy to evaluate the difficulties to engage a proper haptic balance. Outliers, defined as values exceeding 1.5 times the interquartile range, were not included in the final statistics. Groups were compared with Kruskal-Wallis and Wilcoxon tests. Statistics were computed with PAST 3.0, Statistica 13, SPSS Statistics 24, and R 3.5.0.

3 | RESULTS

Despite the lack of any previous archeological knowledge, most subjects reached a comfortable and ergonomic hand-tool match in a position roughly close to a standard functional grasp, using the whole hand and fingers to hold the tool from the posterior and heavier region. Only few subjects (<10%) handled the tools from the opposite side (cutting edge), namely, grasping the top instead of the butt end.

Figure 2 displays the distributions of EDL, EDR, and TMT for all the trials and sessions. All distributions are skewed toward lower attentional, lower emotional, and shorter manipulation time values. There is no correlation among these three variables.

Figure 3 displays overall differences between males and females. Both EDL and EDR are different for males and females ($P = .043$ and $P = .001$, respectively), with the latter group showing larger variability toward higher levels of attention and emotion. TMT shows no significant sex differences, although females display larger variation toward higher values.

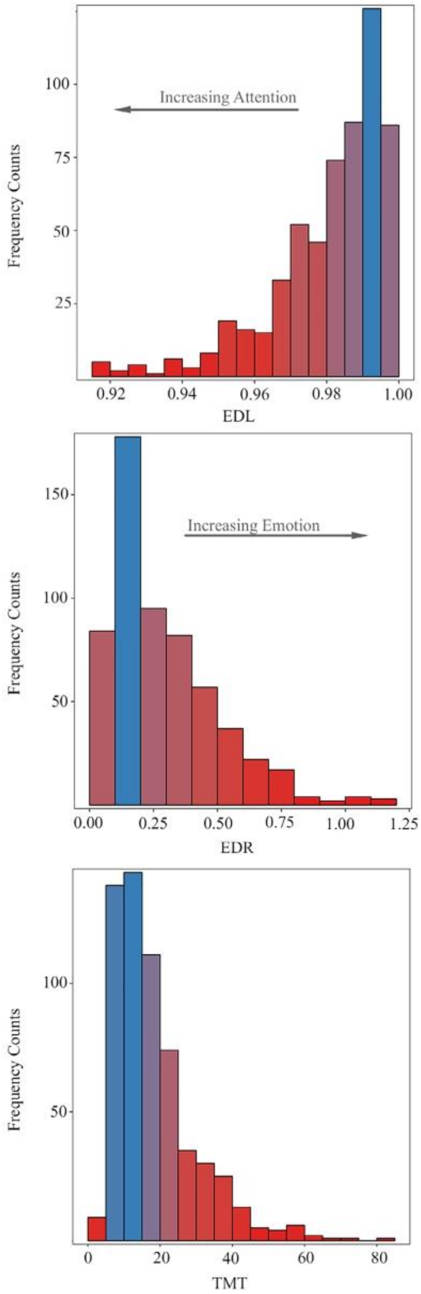

FIGURE 2 Distribution of electrodermal level (EDL; kΩ), electrodermal response (EDR; kΩ), and total manipulation time (TMT; s) for all sessions and trials

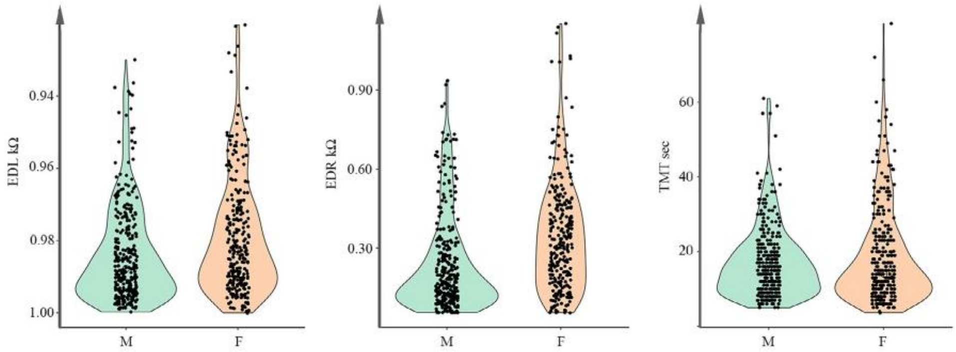

FIGURE 3 EDL, EDR, and TMT for males (M) and females (F). Violin plots show all the data with a Kernel density function plot at each side. EDL, electrodermal level; EDR, electrodermal response; TMT, total manipulation time. Please note the EDL axis is inverted, with lower values (higher attention) on the top

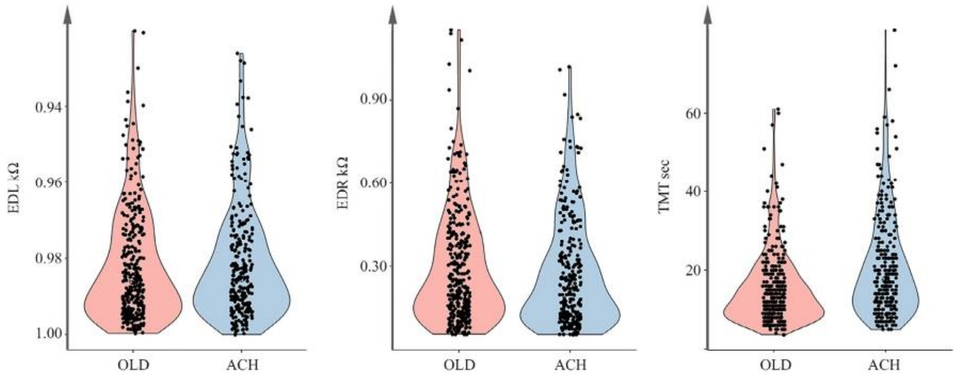

FIGURE 4 EDL, EDR, and TMT for Oldowan (OLD) and Acheulean (ACH) tools. EDL, electrodermal level; EDR, electrodermal response; TMT, total manipulation time

TABLE 2 Correlations between manipulation variables and tool metrics

	EDR	TMT	Length	Width	Thickness	Elongation	Weight
EDL	−0.57	−0.55	**−0.61***	−0.55	−0.55	0.40	**−0.56***
EDR		0.08	0.26	0.34	**0.54***	−0.28	**0.69***
TMT			**0.63***	**0.74****	0.13	−0.10	0.42

Abbreviations: EDL, electrodermal level; EDR, electrodermal response; TMT, total manipulation time.
*$P < .05$; **$P < .005$.

Figure 4 shows the distribution for EDL, EDR, and TMT for the two tool groups. Differences in EDL do not reach significance between tool types ($P = .072$), while differences are significant for EDR ($P = .005$) and TMT ($P < .0001$). Acheulean tools, on average, involve less emotional engagement when compared with Oldowan and are handled for a longer time (17.5 s vs 13.0 s).

Table 2 shows the correlation analysis between manipulation variables and tool metrics. EDL shows a correlation only with tool length ($R = -0.61$; $P = .03$) and tool weight ($R = -0.56$; $P = .04$), namely, heavier or longer tools do exert more attentional reaction. EDR displays a tendency to be correlated with thickness ($R = 0.54$; $P = .06$) and is correlated with weight ($R = 0.70$; $P = .008$). TMT is correlated with stone length ($R = 0.63$; $P = .02$) and width ($R = 0.74$; $P = .004$). There is no correlation between EDL, EDR, TMT, and the age of the subjects.

4 | DISCUSSION

Fluctuations in dermal impedance were used to detect variations in attentional and emotional levels (Boucsein, 2012).

Preliminary surveys have shown that such EDA changes during stone tool manipulation, and that these changes are influenced by individual factors and tool properties (Bruner et al., 2018a, 2018b). In this study, we analyzed the electrodermal reaction in a sample of adult humans during manipulation of Oldowan and Acheulean tools, considering attention, emotional engagement, the time needed to achieve a stable position between hand and tool, and the dimensions of the tools.

All three manipulation variables display a skewed distribution toward lower values. The standard responses are therefore characterized by short manipulation time (approximately 10 s), and low attentional and emotional engagement, when averaged through all the manipulation trials. Proportionally, few individuals display larger manipulation time, attention, and emotion. There is no evidence for any correlation between EDL and EDR, as already evidenced in other case studies (Boucsein, 2012). In this survey, neither of the two electrodermal variables is correlated with manipulation time, and therefore each subject displays a distinctive and idiosyncratic combination of the three parameters.

When considering all the sessions, there are differences between males and females. Such differences are of interest for evaluating the influence of sex in the haptic experience, but also to assess the effect of sex distribution in these kinds of electrophysiological analyses. The ranges of the electrodermal values are largely overlapping, but females display, on average, more attentional and emotional engagement. Females also show a larger degree of variation in their responses. Males and females are known to score differently for some visuospatial tasks (Dolins & Mitchell, 2010; Falk, 1993), and these differences can be associated with different spatial abilities (Coren & Porac, 1987), as well as with sex-related differences in the neural basis of visuospatial processes (Clements-Stephens, Rimrodt, & Cutting, 2009). At present, we ignore whether these sexual differences are associated with a possible evolutionary and genetic background or else with sociocultural influences and environmental conditioning (eg, Burke, Kandler, & Good, 2012; Koscik, O'Leary, Moser, Andreasen, & Nopoulos, 2009; Silverman, Choi, & Peters, 2007). However, it is worth noting that females have smaller hands when compared with males, and this can have a major effect on haptic and sensorial perception (Peters, Hackeman, & Goldreich, 2009; Bruner et al., 2018a). It remains, hence, to be evaluated as to whether these different electrodermal reactions are due to actual sexual differences or else to shared allometric factors associated with hand size.

The second target of this survey was to compare electrodermal reaction while manipulating Oldowan and Acheulean tools. In general, tool complexity is used as proxy for cognitive complexity because of the underlying planning capacity, something largely rooted in executive functions. In some other cases, tool complexity is associated with biomechanical capacity, like precision or dexterity. Instead, in this case, complexity refers to the cognitive mechanisms behind body-tool sensorial integration, something more grounded in body cognition and spatial integration. If technological integration is sensitive to the influence of the tool on body perception and reaction, therefore, tool evolution can supply indirect evidence of these underlying cognitive changes. The transition to Acheulean technology is generally interpreted as an increase in cognitive and behavioral complexity. Considering our capacity to integrate tools into the body schemes and cognitive machinery (Iriki & Sakura, 2008; Malafouris, 2010; Maravita & Iriki, 2004) in this study, we tested whether handaxes and choppers exert a different reaction when explored haptically. The value distributions of their respective EDR are largely overlapping, but with some differences. In particular, Acheulean tools trigger less emotional engagement, and require more manipulation time to reach a comfortable and stable hand-tool position. Surveys in neuroarcheology suggest that, at least during tool-making, Oldowan largely relies on visuospatial inputs, while Acheulean also involve executive functions (Stout et al., 2015). Visual and haptic processes are based on distinct pathways when dealing with perception and prehension (Goodale et al., 1994) and, accordingly, tool-making and tool-use probably involve distinct cognitive resources. Nonetheless, also according to this evidence, we can tentatively interpret the differences in EDA in terms of an increasing reasoning process, at least with two alternative possibilities. A first hypothesis involves geometrical complexity, suggesting that Acheulean tools require a finer degree of body-tool interaction, which decreases the emotional reaction and increase the manipulation time and attention. Namely, we can speculate that the increased morphological complexity of handaxes, requiring more cognitive buffer, can constrain the emotional response. According to this perspective, the irregular form of the choppers triggers more emotional arousal because of the more problematic and less predictable morphology, which hinders a convenient hand-tool spatial coordination. The increase in the EDR in this case would be associated with a lack of comfort, and a less satisfying prosthetic condition. A second hypothesis involves the cortical surface, suggesting that Oldowan tools exert more emotion and less attention because of their smaller knapped area. The natural surface of the tool base induces more comfort and involves less haptic exploration. In this case, the increase in the EDR would be associated with an increase in comfort, and a more satisfying perceptive condition. These two hypotheses, based on geometrical complexity and surface complexity, are not necessarily exclusive, and can be tested with future targeted experiments. Namely, following the principles of theories in body-tool integration and cognitive extension, we should evaluate whether geometrical complexity and surface irregularity can enhance our prosthetic capacity in terms of sensing and embodiment. Tool integration requires feedback between external references, skin interface, body response, and neural remapping (Heed, Buchholz, Engel, & Röder, 2015). Regular geometric tools (like handaxes, when compared with choppers) can facilitate such a cognitive sequence because of more standard haptic signals (proportions) reducing emotional reactions, and/or complex interface (the grasping region) triggering attention. However, the differences we found between choppers and handaxes are consistent but subtle, and these speculations will require a proper development based on different and multiple sources of evidence. For example, future analyses can consider the type of grip used to hold the tool, as to evaluate whether variations of the EDA may be influenced by the grasping pattern. In general, choppers and handaxes are all held with similar grips (often power grips) which involved the whole hand and fingers, but with some differences in the position of the thumb (Key, Merritt, & Kivell, 2018). Minor changes in the grasping pattern can actually influence the stability of the hand-tool spatial arrangement, influencing the emotional reaction.

Preliminary information on the relationships between stone tool physical properties and EDA come from the analysis of their general dimensions. Both attention and emotional engagement are particularly correlated with the weight of the tool ($R = -0.56$ and 0.69, respectively). Therefore, it is likely that the electrophysiological reaction largely depends on gravitational contrast during handling and the force required manipulating the object. Nonetheless, in this survey, there were no weight differences between the Oldowan and Acheulean samples and, hence, the two factors (typology and weight) do not interact. In contrast, handling time is mostly influenced by the width of the tool ($R = 0.74$), which implies that width is a major factor in manipulability, at least when using only one hand to explore the tool. In our sample, there were no width differences between the two typologies ($P = .52$), and therefore, also in this case, typology and width do not interact in the final response distribution. Interestingly, elongation, which is a major factor characterizing the evolution of the Acheulean tools (Gowlett, 2013) shows no apparent correlation with emotion, attention, or manipulation time. Certainly, subtle differences in these aspects can be masked because of limitations of the tool sample size.

5 | FUTURE PERSPECTIVES

Our current data falsify the null hypotheses of no differences in EDA during manipulation of Lower Paleolithic stone tools between different tool types and sexes, according to the tool dimensions. Namely, tool manipulation exerts an electrodermal reaction which shows some differences between Oldowan and Acheulean tools, some differences between males and females, and it is associated with with some physical features. This analysis of the EDA during haptic experience with prehistoric tools represents a first survey on the topic, aimed at investigating the general trends and behavior of the variables involved. Electrodermal results per se cannot provide information on specific archeological issues concerning the functions of the tools, but on possible variations in the effects of the hand-tool interactions. Such interaction is particularly relevant during the Lower Paleolithic, which is associated with the earliest lithic cultures and with large tools requiring the involvement of the whole hand to be manipulated. Both Oldowan and Acheulean tools can display remarkable variability in time and space, and future surveys can be targeted to specific chronological, geographical, or typological groups. An inclusive analysis of tool morphology will also require many more variables and parameters, because haptic interaction is a multifactorial process based on many geometrical and structural properties of the stone tools. A more detailed analysis of a larger array of tool features is currently in process.

Ongoing analyses are also considering further factors potentially involved in hand-tool interaction, like hand size and proportions. The current study is mainly centered on emotional and attentional reactions during tool manipulation, which is something dealing more with sensing than biomechanics. Actually, there is no reason to think that biomechanical capacities (like precision) are necessarily correlated with sensing. In fact, a robotic arm can be incredibly precise, but it lacks the possibility of sensing and integrating the tool into its own body schemes. However, interactions and shared factors between biomechanics and sensing are expected. The analysis of hand morphology and tool shape can supply a structural bridge between these two aspects. In this case, metrics from fossils can be tentatively employed to evaluate whether some results can be used to make inference and extrapolations to extinct human species. Unfortunately, the hand fossil record is still scanty, and barely allows statistical or phylogenetic validations (Bruner, Lozano, & Lorenzo, 2016). Different cognitive resources are involved during manipulation with one or two hands (Wenderoth, Debaere, Sunaert, & Swinnen, 2005), and this difference should be also taken into account during more specific surveys.

Finally, it is also worth noting that in electrodermal analyses emotional engagement is intended as "general arousal" (Boucsein, 2012), and future surveys can add further information in this sense through subjective reports, facial expression analysis, and electroencephalography. This study is focused on the average electrodermal reaction, and following surveys will also consider individual fluctuations during handling.

6 | CONCLUSION

Many current tools in cognitive science rely on biomedical imaging and computer graphics (Hecht, Gutman, Bradley, Preuss, & Stout, 2015; Rilling, 2008). These methods guarantee a comprehensive approach to quantify psychological and behavioral functional responses but, at the same time, they involve general logistic limitations (eg, costs and portability). In this study, we explore the application of EDA to cognitive archeology, a method that is characterized by limited costs, fast processing, and manageability in the experimental setting. We found differences associated with haptic cognition when handling Lower Paleolithic stone tools. In general, there is noticeable individual variability, which suggests important idiosyncratic factors which must be considered in future analyses. Differences between males and females can be interesting in behavioral perspectives, although in this case the influence of hand size is probably relevant. EDA is also influenced by some dimensions of the tool, as well as by typological features. All these parameters should be considered when taking into account the technological evolution in our genus. During tool use, brain and body are structurally and functionally integrated with external technological elements (Iriki & Taoka, 2012), and this has represented a key feature in human cortical evolution (Goldring & Krubitzer, 2017). Such capacity of extending cognitive and functional properties of the body to external tools is thought to be a feature targeted by selective processes and, accordingly, cognitive archeology can investigate cultural remnants of this relationship. This analysis aimed to investigate whether different tool types exert distinct emotional responses during handling, and it is not intended to test or support any specific theory of cognition. Results can be interpreted according to distinct cognitive perspectives, like Material Engagement Theory (Malafouris, 2013), in which embodiment and integration between body and tools are hypothesized to be a structural component of mind. In this sense, structural changes or discontinuities in the archeological record can reveal underlying evolutionary changes or discontinuities in the cognitive relationships between humans and material culture. Such evidence, integrated with anatomical and behavioral data (Bruner, Spinapolice, Burke, & Overmann, 2018), can represent a major contribution to the study of the evolution of human cognition.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

E.B. designed the study. A.F., M.S.-G., and E.M.-G. collected the data. A.F. analyzed the data. R.A.-A. and M.T.-B. prepared the stone tools. E.B., A.F., and M.S.-G. wrote the article.

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CHAPTER

Cognitive archeology, body cognition, and hand–tool interaction

12

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Abstract

Body cognition and lateralization can be investigated in fossils by integrating anatomical and functional aspects. Paleoneurology cannot provide strong evidence in this sense, because hemispheric asymmetries are shared in all extinct human species, and motor cortical areas are difficult to delineate in endocranial casts. However, paleoneurological analyses also suggest that modern humans and Neanderthals underwent an expansion of parietal regions crucial for visuospatial integration and eye–hand–tool management. Because of our technological specialization, haptic cognition can be particularly targeted by evolutionary processes. Hand–tool relationships can be investigated through physical and physiological correlates. In terms of metrics, size is the main factor of hand morphological variation among adult humans, followed by the ratio between thumb length and palmar size. In modern humans, emotional changes during hand–tool contact can be measured by electrodermal activity. During tool manipulation, electrodermal response, which is a physiological correlate of emotional engagement, shows differences between males and females, and it is different for distinct Paleolithic technologies. Emotional engagement, hand management, and haptic cognition are part of a specialized prosthetic technological capacity of modern humans and can provide indirect evidence of cognitive discontinuities in the archeological record.

Keywords

Endocranial asymmetry, Paleoneurology, Parietal cortex, Visuospatial integration, Hand morphology, Haptic cognition, Electrodermal activity

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1 PALEONEUROLOGY AND ENDOCRANIAL ASYMMETRIES

Brain and behavioral asymmetries are hallmarks of our species and, accordingly, they have received considerable attention in cognitive science. There have been plenty of reviews investigating this topic in living humans, nonhuman primates, and even fossil human species (e.g., Cashmore et al., 2008; Lozano et al., 2017; Uomini, 2009). Of course, behavioral asymmetries are thought to be a consequence of brain asymmetries, and this is why this issue is of interest in evolutionary neuroscience, particularly when dealing with language (Rilling, 2013, 2014). Taking into consideration that fossils provide the only direct anatomical evidence of species evolution, paleoneurologists have always been interested in hemispheric asymmetries (e.g., Balzeau et al., 2012; Holloway, 1980, 1981). In paleoneurology, brain morphology is inferred by the anatomy of the endocranial cavity, which supplies information on brain size, brain proportions, some sulcal patterns, vascular traits, and cerebral spatial relationships (Bruner, 2017; Holloway et al., 2004). In terms of gross morphology, in modern humans, the frontal cortex is larger on the right side, while the occipital cortex is larger on the left side (Li et al., 2018). Such a pattern generates a "torque" of the brain axis, which is generally called right-frontal left-occipital petalia. This same pattern can also be found in apes, although it is less frequent and less pronounced (Holloway and De La Costelareymondie, 1982). However, brain size is much larger in humans, and there are no extant primates with an intermediate brain volume. Therefore, at present we cannot exclude that the torque and asymmetry displayed by our brain is a scaled version of the same pattern expressed, to a lesser extent, by other primates (Gómez-Robles et al., 2013; Kyriacou and Bruner, 2011). Extinct human species apparently show our same asymmetry pattern (Balzeau et al., 2012), and hence paleoneurology cannot provide any clear information on this topic, at least when investigating evolutionary changes within the human lineage.

Apart from this general background, there are several problems that hamper a reliable approach on hemispheric asymmetries when dealing with fossils. First, asymmetric cortical traits can present large individual (intraspecific) variation and subtle evolutionary (interspecific) differences. Therefore, among the species of the genus *Homo*, any possible mean difference in endocranial asymmetry is easily obscured by the large individual variability. Accordingly, gross volumetric asymmetries could only be investigated through very large samples, in order to guarantee proper statistical power. Of course, this limitation is hardly constrained to paleoanthropology. A second limit concerns the biological meaning of these morphological traits. We estimate asymmetries through volumetric figures and sulcal schemes, but to date the relationships between these macroscopic features and functional or histological factors are scarcely known. Furthermore, for many aspects, we still ignore the degree and patterns of cortical variability in our own species. Any inference on extinct taxa will be seriously affected by such a vast lack of information. A third limit regards the functional matrix associated with the brain and skull growth and development. Brain and braincase are reciprocally integrated in terms of ontogeny and phylogeny, through complex functional and structural relationships between soft and hard tissues (Bruner, 2015; Moss and Young, 1960). Such integration is generally local and driven by physical and spatial interaction between anatomical elements. A complex system of pressures and tensions is generated during morphogenesis, and the final phenotypic and evolutionary output is a balanced result between distinct anatomical influences. Apart from the histological components behind volumetric asymmetries, we currently ignore their general biomechanical and morphogenetic background. In fact, differences in the general volume of two counterlateral regions can be due to a difference in the brain growth force, or to a difference in cranial resistance. Paradoxically, the increase in the surface of a specific lobe can result from a major pressure exerted by its counterlateral hemisphere. Often the falx cerebri, which separates the two hemispheres and attaches the brain to the vault, displays a curved trajectory, evidencing a spatial conflict between the two sides. This differential distribution of the brain mass can also influence sulcal patterns and their degree of expression (Tallinen et al., 2016; Toro, 2012). For example, the frontal and parietal volumes are often larger on the right side, while their gyri (forming the Broca's and Wernicke's area) are most clearly shaped on the left side (see Holloway et al., 2004). Any inference on gross brain asymmetries will be partial and incomplete (and possibly biased) with no information regarding the processes behind this biomechanical redistribution of cortical tissues.

This situation is even more complicated if we deal strictly with the motor cortex. Sulcal morphology and cortical regions in paleoneurology are generally identified by localizing possible traces of the folding elements (bosses and grooves) and by positioning different elements so as to constrain the position of the others (Bruner, 2018a). At present, no reliable methods have been proposed to identify the boundaries of the sensory-motor cortex in fossils. Central, postcentral, and precentral sulci can be tentatively identified on endocranial casts, but the uncertainty is noticeable, and differences among distinct human species were probably subtle, if any. In contrast, there is paleoneurological evidence suggesting specific and localized differences for areas of the posterior parietal cortex involved in the cognitive integration of the body elements, crucial for visuospatial associative functions (Bruner, 2018b).

2 PARIETAL LOBES AND VISUOSPATIAL EVOLUTION

Modern humans have long been said to have "rounded heads" when compared with extinct human species. It turns out that such globularity of the braincase is mainly due to the size and curvature of the parietal bones (Bruner et al., 2004, 2011a). Although the correspondence between brain and cranial elements is not firm and constant, expanded parietal bones in our species are apparently due to an actual expansion of the parietal lobes, probably of their dorsal regions (Bruner, 2010;

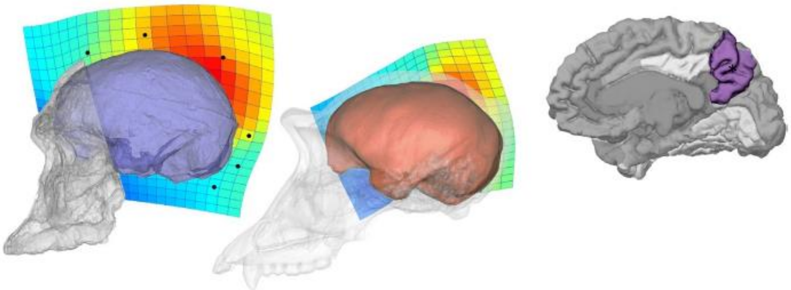

FIG. 1

Compared with extinct hominids (on the *left*, a digital reconstruction of skull and endocast of an *Australopithecus*), modern humans display larger and bulging parietal bones and lobes. Compared with chimpanzees (*middle*), we have a larger parietal cortex because of a larger precuneus (*right*). The same area is also extremely variable among adult individuals.

Bruner et al., 2003, 2018a). Also Neanderthals display wider superior parietal lobules when compared with more archaic hominids, but only modern humans show a general enlargement of the whole dorsal cortex, with an increase in the longitudinal extension of the upper parietal areas (Fig. 1). In this region, morphogenesis is rather linear, with the bone shaped by cortical pressure (Moss and Young, 1960). Therefore, an association between bone and lobe form and size is to be expected. In terms of spatial correspondence, the sagittal region involved in these changes roughly matches the precuneus and the superior parietal lobule, and the lateral region matches the position of the intraparietal sulcus (Pereira-Pedro and Bruner, 2016). The intraparietal sulcus is more complex (and possibly even expanded externally) in humans than in other primates, and it is particularly involved in eye–hand integration, handedness, and tool manipulation (Grefkes and Fink, 2005; Martin et al., 2011; Stout et al., 2015; Tunik et al., 2007; Verhagen et al., 2012). It is hence not by chance that the endocranial surface corresponding to this region underwent a visible enlargement in the two human species (*Homo sapiens* and *Homo neanderthalensis*) that have evolved complex tools and technology. Precuneus is involved in body–vision integration, egocentric spatial coordinates, visual imaging and simulation, and memory retrieval (Cavanna and Trimble, 2006; Freton et al., 2014; Margulies et al., 2009; Zhang and Li, 2012). All these functions are central also for visual representations and imagination, and for integration between physical, chronological, and social spaces (Hills et al., 2015; Land, 2014; Maister et al., 2015; Peer et al., 2015). It is therefore interesting that this cortical element could have undergone a marked expansion in the only species (*H. sapiens*) associated with a remarkable visual and symbolic culture, and with a unique social and technological development. The precuneus is extremely variable among adult humans (Bruner et al., 2014, 2015) and much larger in humans than in chimpanzees (Bruner et al., 2017). Because of its role in visual imaging and simulation, the phylogenetic differences, and spatial correspondence, a specialization of its morphology and role in modern humans is likely (Bruner, 2018b). Interestingly, early modern humans (about 150–300,000 years ago) apparently did not display such morphological changes in the parietal region, suggesting that the origin of modern humans did not match the origin of a modern brain form (Bruner and Pearson, 2013). It is likely that parietal morphology underwent a following and gradual change in later *H. sapiens*, achieving a modern appearance 50–100,000 years ago, roughly at the same time we can find a relevant visual culture in the archeological record (Bruner et al., 2018a; Neubauer et al., 2018).

Parietal cortex is largely involved in body perception and representation (Daprati et al., 2010), namely, processes that intimately combine the sense of the body with self-awareness and action (Borghi and Cimatti, 2010; Gallese and Sinigaglia, 2010). These cognitive mechanisms bridge body perception (an admixture of egocentric, exteroceptive, and interoceptive feedbacks) with psychological and emotional responses (Longo et al., 2010). Accordingly, we can broadly define *body cognition* as those cognitive processes that rely and depend upon the experience, sensing, feedback, and recognition of the own body. Body cognition and visual imaging are essential for a technological species like *H. sapiens*, taking into account that they are crucially involved in tool making, hand–tool management, and symbolic communication. Most of the functions involved in body–environment management are generally labeled as *visuospatial integration* and deal with the capacity of coordinating a *personal space* (the body) with a *peripersonal space* (external reachable elements close to the body) within an *extrapersonal space* (the surrounding environment, out of the body range) (Cléry et al., 2015; Farnè et al., 2005; Maravita and Iriki, 2004; Maravita et al., 2003). Tools are a particular case of environmental elements and can modify the perception of the body and of the peripersonal space through alteration of the visuotactile perception (Brozzoli et al., 2010; Macaluso and Maravita, 2010). In fact, distinct cortical areas and neural networks of the frontoparietal system are involved in processing objects depending upon their distance from the egocentric references of the body (hand, arm, head), with mechanisms that undergo both dynamic and plastic changes after tool use (Cléry et al., 2015).

Body cognition may also have a direct relevance on language. Language and dexterity have long been supposed to be evolutionarily related, sharing functions and cortical resources (Binkofski and Buccino, 2004). Additionally, functional evidence also suggests that motor simulation is associated and integrated with speech comprehension (Buccino et al., 2005; Jirak et al., 2010; Marino et al., 2012). Language and handedness can be hence associated in terms of neural mechanisms and lateralization, but also in terms of body experience.

Such a perceptual system bridging body and cognition is extremely stimulating for current cognitive sciences and can be tentatively investigated in an evolutionary context, within the perspective of the field called *cognitive archeology*.

3 HAPTIC COGNITION AND COGNITIVE EXTENSION

Recent theories in cognitive science suggest that “mind” might not be a *product* of the brain, but instead a *process* generated by the interaction between brain, body, and environment (Malafouris, 2010, 2013). These hypotheses are generally named “extended cognition” and are aimed at evaluating if and to what extent the body and the environment are integrated and necessary parts of our cognitive mechanisms. Our culture is not simply *tool-assisted*, but is actually *tool-dependent* (Plummer, 2004). Like a spiderweb, it should be intended as an essential part of the organism’s cognitive system in both functional and evolutionary terms, even though it is external to the body. For humans, environment also means culture, and in particular material culture, namely, technology. If such a “prosthetic capacity” (Overmann, 2015) has a major role in human evolution, then visuospatial functions may be central to its proper development (Bruner and Iriki, 2016).

Visuospatial integration can be partially tested in extinct human groups by integrating information from their anatomy, archeology, ecology, and social organization (Bruner et al., 2016, 2018b). Of course, there are many difficulties when analyzing behavior and cognition in extinct species, but nonetheless we can collect multiple and independent evidence in order to support or reject a specific hypothesis. Visuospatial integration in Neanderthals is an interesting case study and example. They had similar brain size and ecological niche than modern humans, but apparently distinct behaviors. In fact, as far as we know, Neanderthals did not display modern parietal bulging, they heavily relied on their mouth to handle tools, they did not apparently have any projectile technology or a noticeable visual culture, and they had smaller social groups and smaller territories (Bruner and Lozano, 2014, 2015). All these independent sources of information converge in supporting a lack of visuospatial specialization, at least to a degree comparable with our species. Namely, we can hypothesize that those extinct humans lacked our visuospatial specialization (including aspects of body cognition and body–tool integration), and all the evidence we have on Neanderthals (brain anatomy, archeology, ecology, skeletal morphology, etc.) is not able to reject this possibility, so making the hypothesis more probable.

During the interaction between hand and tool, the body undergoes a structural adjustment to include the information of the tool in the physical management (dynamic touch; Turvey and Carello, 2011), and the tool can be represented as an actual body element in the body schemes of the brain (Iriki and Taoka, 2012; Maravita and Iriki, 2004). The functional unit is hence the hybrid body–tool system, which has new emerging properties, new qualities, and capacities that are generated thanks to the combination of the two elements. Hand–tool integration is therefore directly intermingled with cognitive extension (Iriki, 2006), in which some cognitive functions are exported and delegated to extraneural elements. Apparently, motor behavior and sensorial experience, despite generally associated with distinct cortical territories, are strongly integrated at both neural and behavioral levels

(Ackerley and Kavounoudias, 2015; Tunik et al., 2007). Because of the importance of tool making and tool use in our species, grasping patterns and hand morphology are a major topic in evolutionary anthropology (Marzke, 1997; Marzke and Marzke, 2000; Susman, 1998). These same topics also represent a fruitful research area in ergonomics, orthopedics, robotics, and cognitive science (Feix et al., 2016; Landsmeer, 1962; Napier, 1956; Serino and Haggard, 2010), as well as in experimental archeology (Key and Dunmore, 2015; Marzke et al., 2015; Rolian et al., 2011). It is therefore mandatory, when dealing with cognitive archeology and visuospatial capacity, to investigate the behavioral basis of hand–tool interaction. In Section 4, we present two complementary aspects that can provide quantitative approaches to the study of the hand–tool system: hand morphometrics and electrodermal activity.

4 TOUCHING STONES: HANDS AND EMOTION

4.1 HAND MORPHOLOGY

Hand anatomy has undergone several changes during human evolution (Kivell, 2015; Tocheri et al., 2008), and hand morphological changes are supposed to be directly involved in tool management (Rolian et al., 2011; Williams et al., 2012). Human hand morphology might have evolved from ape-like proportions with longer digits adapted for suspensory behavior and brachiation, or else be based on a primitive and generalized short-fingered primate scheme (Almécija et al., 2015). In this latter case, the human hand retains the primitive nonspecialized features (short fingers and manual dexterity), observed in many quadrupedal monkeys like baboons or macaques, while apes underwent finger elongation because of a suspensory adaptation. The hand fossil record associated with early and archaic humans is scant (see Bruner et al., 2016). However, despite their similar brain size, modern humans and Neanderthals apparently displayed different hand proportions since the evolution of their respective early forms (Niewoehner, 2001). Therefore, it turns out that we modern humans have a distinct morphology of the parietal regions associated with visuospatial integration (the paleoneurological evidence), distinct body and hand proportions (the skeletal evidence), and a distinct cultural capacity (the archeological evidence). Although these evolutionary changes are still not completely clear, they should be considered as associated with our special technological niche.

Of course, before we can design research for and interpret research from fossils, we should investigate general patterns and variations in our own species. In Fig. 2 eight basic hand diameters in a sample of adult modern humans (46 normal right-handed adults; 22 females, 24 males) were analyzed through principal component analysis based on a correlation matrix, showing that the first vector of variation (explaining 75% of differences) is basically associated with an increase in all the diameters. Namely, the main factor channeling hand morphological variability is general hand size, and it is not associated with specific hand proportions. This size component strongly separates males and females (Mann–Whitney $P < 0.001$). In this

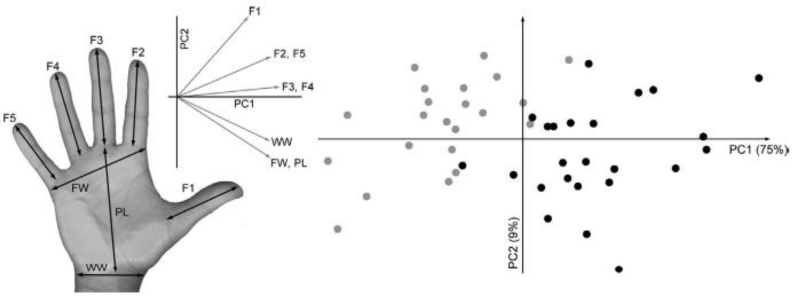

FIG. 2

Principal component analysis computed on eight hand diameters (*F1–F5*: finger 1–5 length; *FW*: fingers width; *PL*: palmar length; *WW*: wrist width). PC1 is associated with size, i.e., increase of all the variables. This vector explains 75% of the variance and separated females (*gray dots*) from males (*black dots*). The second component is associated with longer fingers (mostly the thumb) and smaller palm.

case, the following components are not statistically significant, although the second component is above the Jolliffe cutoff value (a threshold commonly used to evaluate stability of these multivariate vectors) and explains 9% of the variance. It is associated with an increase in finger length (particularly the thumb) and decrease in palmar size. In this case, values are slightly larger, on average, in females ($P = 0.02$). A discriminant function using the same hand variables is able to classify sex in 96% of the individuals, and it is correlated to both PC1 ($R = -0.89$) and PC2 ($R = 0.37$). This means that 75% of the hand variation is due to size, and 79% of the sex variation is due to size, too. Interestingly, PC2 is moderately correlated to age ($R = -0.45$; $P = 0.002$), and aging is therefore associated with relatively shorter fingers and wider palms. In this example, sexes have slightly different ages (males 46 ± 10 years; females 40 ± 11 years; $P = 0.04$), and analysis of covariance suggests that PC2 sex differences are no more significant when corrected for age ($P = 0.14$).

This simple exploratory survey suggests that morphometric differences between male and female hands concern only size, being larger in males. It also means that hand variation, in terms of general patterns, is not channeled according to some specific finger proportion. The only widely discussed sexual difference in finger length is the ratio between the second and fourth finger (2D:4D), which is larger in females because of a shorter proximal and middle phalanx of the fourth finger, a morphogenetic effect that might be due to early (prenatal) hormonal effects (Zheng and Cohn, 2011). As far as we know, it remains to be evaluated how much these factors are also related to hand size, and the extent of such male–female differences. In our sample, although males have a slightly lower mean value for this ratio, the difference between sexes is not significant ($P = 0.21$).

In sum, size is the most common factor involved in our adult hand variability, including sexual differences. Accordingly, hand size should be regarded as a key issue in hand–tool interactions. Hand size is known to influence biomechanical grasping mechanisms, but also sensory features. Smaller hands (more frequent in women) have thinner skin and higher concentration of receptors, and both factors increase tactile sensitivity (Peters et al., 2009). Of course, although size is apparently the principal factor of hand group variation, individual aspects other than size can promote or demote grasping capacity or sensory responses. In this example, the second component deals with the ratio between palm dimension and the length of the fingers, mostly of the thumb, a pattern that accounts for almost 10% of the variance and apparently changing with age. In this case this component does not reach a statistical significance but, if confirmed, such an inverse relationship between palmar size and thumb length could represent a second integrated pattern of hand variation. This can be relevant when considering the role of the thumb in tool use, especially during the transition from Oldowan to Acheulean (Rolian et al., 2011; Williams et al., 2012—see later). The rest of the variation (including specific finger proportions) is probably due to idiosyncratic characters, based on individual features that should be evaluated independently.

4.2 ELECTRODERMAL ACTIVITY

A crucial issue in cognitive archeology concerns whether or not interactions with tools influence brain functions. Obviously, specific tool uses are associated with specific cortical activation, as evidenced though experiments in neuroarcheology (Stout and Chaminade, 2007). Brain imaging largely relies on hemodynamic responses, metabolic processes, expensive technical resources, and complex experimental paradigms. Costs and logistics apart, these methods may involve operational difficulties, mostly when dealing with the observation of complex behaviors in real time (Hecht and Stout, 2015). Additional methodologies come from psychometrics that can be useful to test correlation between cognitive performance and anatomical characters (Bruner et al., 2011b, 2015).

Some generalized cognitive aspects can be also investigated with simpler approaches, like devices for the detection of Electrodermal Activity (EDA; Critchley, 2002; Vecchiato et al., 2014). Electrodermal response is typically quantified in terms of skin conductance levels, mainly in the hands and feet (De Houwer and Hermans, 2010). These systems are based on electric impedance (reduction of electrical resistance and increase in conductance) and are designed to capture and measure emotional reactions in individuals or groups. Following empirical evidence, sensors are employed to detect skin electric signals associated with emotional changes (Boucsein, 2012; Martin and Venables, 1966). *Electrodermal level* (EDL) measures the tonic activity of the skin and is associated with basal level of activation, and its value is interpreted as proportional to attention, namely, the predisposition to receive, analyze, and react to, new incoming information. *Electrodermal response* (EDR) deals with a psychophysiological reaction due to fast conductivity changes and is interpreted as a generalized emotional reaction. These methods were originally applied at the beginning of the past century in psychological

FIG. 3

The three stone tools used in this survey: a chopper (*left*), a handaxe (*middle*), and a scraper (*right*).

experiments regarding arousal and emotion (Boucsein, 1992; Kreibig, 2010; Stemmler, 2002). Since then, their use has increased, applying EDA quantification methodologies in legal contexts, and they are currently employed in neuromarketing, to investigate customer reactions to given commercial strategies and choices (Ariely and Berns, 2010; Boucsein, 2012; Lee et al., 2007; Morin, 2011). These kinds of physiological recordings have been employed often in cosmetics, to test the emotional reaction to haptic (Boucsein et al., 1999) as well as visual and olfactory (Eisfeld et al., 2005) stimulation.

In cognitive archeology, these methods can be used to evaluate different behavioral and emotional responses during interaction with Paleolithic tools, under the null hypothesis of no differences in electrodermal activity between individuals or groups during tool manipulation, or between different tool typologies. We recorded the EDR in the same sample used to analyze hand morphology (see earlier), while handling three representative stone tools belonging to different lithic typology (Fig. 3). The chopper is a classic Oldowan element, associated with the earliest human technology with a robust archeological record, largely used between 1.5 and 2.5 million years ago. It is but a flaked core with a cutting edge, probably handled with a force grip and used to beat and crash, taking advantage of the weight of the stone tool. The toolmaker was historically thought to be *Homo habilis*, although at present this species is not commonly recognized as a real evolutionary unit, probably representing a “basket taxon” in which we have grouped fossils from distinct (and largely undetermined) species. The handaxe is the typical Acheulean element, a technology that was dominant between 1.5 and 0.5 million years ago. The core is refined through a long

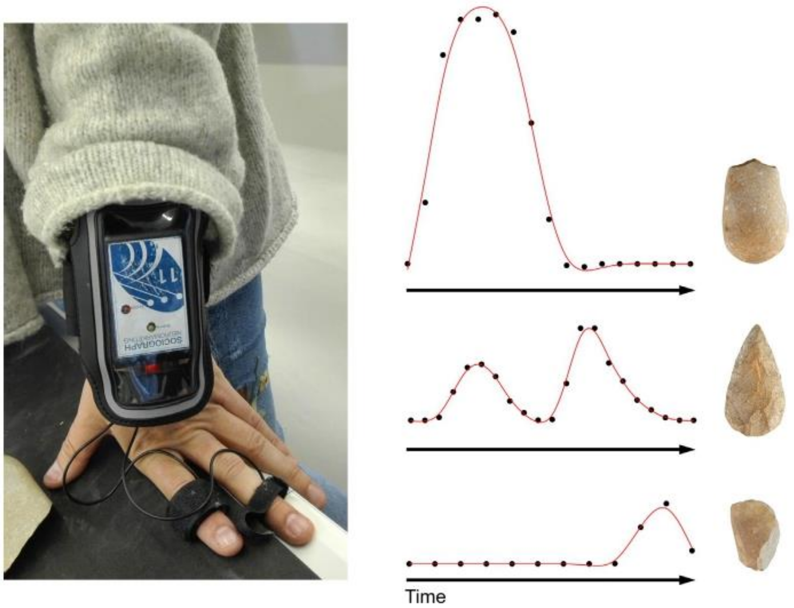

FIG. 4

Electrodermal activity was detected and recorded with a portable remote device wrapped around the forearm (*left*). Electrodermal response (EDR) for each individual was recorded during the handling of the three tools. The same individual (*right*) can show different patterns of emotional engagement for the three tools. Trials were randomized and preceded by a familiarization procedure with a set of lithic tools.

portion of the outline, and the tool is generally elongated, roughly symmetrical, and probably employed in multiple tasks. Handaxes are generally flatter than choppers and can be handled from the base but also grasping the lateral edge. They are generally associated with *H. ergaster*, *Homo erectus* and *Homo heidelbergensis*. The scraper is a much smaller tool also used by *H. heidelbergensis* but typical of large-brained hominids like Neanderthals or early modern humans, and frequently used between 500 and 50 thousand years ago.

We used a remote device that is wrapped on the forearm and senses the bioelectrical responses through electrical resistance at the second and third finger (Sociograph Technology; Martínez Herrador and Garrido Martín, 2003), measuring electrodermal parameters on the left hand, while the participant manipulates the tool with the right hand (Fig. 4). Participants were asked to manipulate the tool until a stable sensation and a comfortable position are reached. We recorded the electrodermal values through the whole trial, from the beginning of the manipulation to the achievement of a stable position. We have therefore quantified the variations in

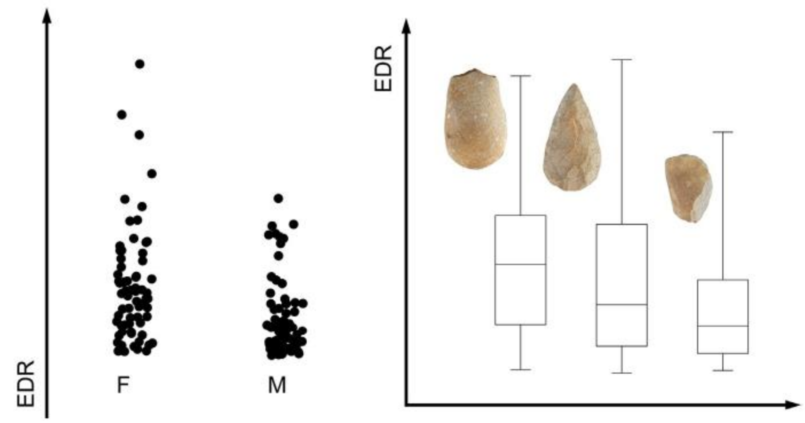

FIG. 5

Mean EDR for males and females (F, M; jitterplot) and for the three tools (nonparametric boxplots) computed from all the sessions.

emotional responses during the haptic experience, according to the hand–tool interaction. Visual inputs play a crucial role in object affordance, grasping mechanisms, and spatial perception (Lacey et al., 2014), although there are distinct and independent neural pathways involved (Goodale et al., 1994). Accordingly, individuals were blindfolded so as to limit the interaction between hand and tool to the haptic experience. Signals were captured with a frequency of 32 recordings per second. For this demonstration survey, we reduced the data to one recording per second after arithmetic mean, and only the mean values for each trial (a single session of one person with one object) were used to compute comparisons.

Fig. 5 shows the distribution of EDR values in males and females, and the differences for the three tools. Females display a stronger emotional involvement when handling the tools ($P < 0.0001$), with a higher average and larger variation. Also the EDR values for the three tools are distinct ($P = 0.005$), particularly because of the difference between chopper and scraper ($P = 0.001$). The handaxe shows an intermediate value, but differences do not reach significance with either the chopper ($P = 0.12$) or with the scraper ($P = 0.10$). According to these results, emotional engagement is lower for the scraper and larger for the chopper, with the handaxe in an intermediate position.

This exploratory survey is aimed at showing how electrodermal activity can be applied in an archeological context. It suggests that even a simple contact can exert an emotional alteration when handling an object, and that this emotional change can be different in distinct lithic tools. This approach can be employed to test responses to different tools or even to different behaviors associated with Paleolithic ecological, economical, or social aspects. Dealing with visuospatial integration, it can be employed to evaluate the response during physical contact or during specific visuospatial tasks (e.g., throwing).

5 PERSPECTIVES IN HAPTIC COGNITION AND COGNITIVE ARCHEOLOGY

Primates "think" with their hands more than any other mammals, by exploring and interacting with the surrounding elements largely through their specialized eyes and hands, imagining and simulating hand-centered actions, and planning according to their body perceptions and body-based expectations (Ackerley and Kavounoudias, 2015; Byrge et al., 2014; Haggard, 2005; Tunik et al., 2007). This specialization is the result of an integrated functional package made of body and brain elements. Humans are particularly specialized in this sense, and it is no coincidence that we display complex cortical areas dedicated to eye–hand and body–environment coordination (Goldring and Krubitzer, 2017). In humans, the intraparietal sulcus is particularly complex, probably because of a specialization in hand–tool interaction (Choi et al., 2006; Grefkes and Fink, 2005; Kastner et al., 2017; Zlatkina and Petrides, 2014). Also the precuneus is larger, and it is a central node for visual imaging, body cognition, and self-consciousness based on body-centered egocentric imagination and memory (Bruner et al., 2017; Cavanna and Trimble, 2006; Freton et al., 2014; Margulies et al., 2009; Zhang and Li, 2012). The body, and particularly the eye–hand ports, is therefore an active interface between brain and environment, and in humans especially between brain and technology. Perception and action are, in fact, intimately associated (Ackerley and Kavounoudias, 2015), and the same cortical regions dedicated to body integration are also involved in attentional, intentional, and executive management (Andersen and Buneo, 2002; Andersen et al., 1997; Bisley and Goldberg, 2003; Freedman and Assad, 2006; Rushworth et al., 2001; Tunik et al., 2007). Technology itself is a crucial part of this cognitive system, although we still do not know to what extent and with what specific roles (Iriki and Taoka, 2012; Malafouris, 2010). In the last 2 million years, humans have evolved a culture that is dependent on technology, and accordingly we have evolved a cognitive system that is dependent on technology too. The "prosthetic capacity" itself can be an evolutionary characteristic, and a behavioral ability targeted by natural selection.

The human brain is more plastic than a chimpanzee brain, which in turn is more anchored to genetic inheritance (Gómez-Robles et al., 2015). This sensitivity to environmental influences is probably necessary to delegate cognitive functions to extraneural elements, a process based on loops and feedbacks between biology and culture. Such a cognitive shift, extending the body functional interface through technological components, is likely to have occurred with the evolution of the genus *Homo*, and especially with the evolution of our species, *H. sapiens*. These topics should be investigated within a comprehensive framework, including neurobiology, neuropsychiatry, cognitive science, psychology, robotics, and medicine.

In cognitive archeology, we should evaluate what kind of cognitive alterations can be associated with the contact between body and tools. Body experience can represent a crucial part of the cognitive process, mostly when dealing with the interaction between hand and technology. In fossils, brain anatomy and paleoneurology can only provide minor clues on this topic. Endocasts revealed that modern humans—and partially Neanderthals—underwent an expansion of parietal cortical areas which are relevant nodes for visuospatial integration, and also hand morphology displays interesting changes in our species (Bruner et al., 2016; Patiño et al., 2017). In modern human adults, size is apparently the only main factor involved in overall hand variation. The relationship between thumb length and palmar size also may be based on shared patterns of variability. It is likely that, apart from these two factors, the rest of morphological variation is due to individual and independent features, which should be considered separately.

Further inferences can be supported by evidence in ecology and behavior (Bruner et al., 2018b). For example, the development and use of projectile technology can be an interesting proxy to evaluate visuospatial projecting capacity (Williams et al., 2014). In this sense, discontinuity in the archeological and paleontological record can reveal underlying changes in body cognition and visuospatial capacity in different human lineages.

In terms of emotional engagement, electodermal activity suggests that there are differences between males and females, and also differences associated with different stone tool types. Such differences in cognitive engagement can reveal different haptic responses which, ultimately, are supposed to be associated with part of the processes involved in body technological extension (Bonifazi et al., 2007; Iriki and Sakura, 2008; Malafouris, 2013).

Women apparently display a higher and more diverse emotional reaction. Females have, on average, a smaller parietal cortex and less visuospatial capacity than males, although we still ignore whether this is a genetic or cultural effect (Koscik et al., 2009). Visuospatial cognitive differences between males and females can be in fact the result of specific evolutionary adaptations associated with the distinct social roles (Silverman et al., 2007), or else consequences of different behavioral training due to cultural influences (Burke et al., 2012). It should be considered whether or not such stronger emotional responses in females may be associated with those spatial and visual capacities that are influenced by sex. If this is the case, then increased in visuospatial capacity should be associated with decrease of emotional engagement.

Taking into account that hand size is a major factor channeling hand diversity, and that females have smaller hands than males, it should be also considered to what extent size can influence emotional feedback. Tactile receptors and sweat pores are more densely packed in smaller hand, and generally women are able to perceive finer surface details when compared to men (Edelberg, 1971; Morimoto, 1978; Peters et al., 2009). We ignore if this increased tactile sensitivity in females is a real sexual character or in contrast if it is a secondary (allometric) consequence of having smaller hands. Interestingly, the contact with the large and rough tool (the chopper) induces more emotional reaction than the small and fine one (the scraper). It remains to be tested whether this is mainly due to dimension or to other ergonomic factors like shape, weight, roughness, or other specific properties of the object. A study on a larger and more diverse lithic sample, and a statistical analysis of the whole electrodermal patterns, is in preparation.

Besides any future interpretation, the take-home message concerns the fact that there is an emotional response that alters the cognitive state during the handling of a stone tool, and that this response may be different for males and females, and different for different tools. Trends and discontinuities in the emotional response associated with the archeological record may be able to identify trends and discontinuity in the evolution of the human cognition and prosthetic technological capacity, following genetic, epigenetic, or environmental influences.

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Visuospatial Integration and Hand-Tool Interaction in Cognitive Archaeology

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Contents

Abstract Testing cognitive hypotheses in extinct species can be challenging, but it can be done through the integration of independent sources of information (e.g., anatomy, archaeology, neurobiology, psychology), and validated with quantitative and experimental approaches. The parietal cortex has undergone changes and specializations in humans, probably in regions involved in visuospatial integration. Visual imagery and hand-eye coordination are crucial for a species with a remarkable technological and symbolic capacity. Hand-tool relationships are not only a

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matter of spatial planning but involve deeper cognitive levels that concern body cognition, self-awareness, and the ability to integrate tools into body schemes, extending the body's functional and structural range. Therefore, a co-evolution between body and technology is to be expected not only in terms of anatomical correspondence but also in terms of cognitive integration. In prehistory, lithic tools are crucial in the interpretation of the cognitive abilities of extinct human species. The shape of tools and the grasping patterns associated with the corresponding haptic experience can supply some basic quantitative approaches to evaluate changes in the archaeological record. At the physiological level, electrodermal activity can be used as proxy to investigate the cognitive response during haptic experiences, revealing differences between tools and between subjects. These approaches can be also useful to evaluate whether and to what extent our complex cognitive resources are based on the capacity to export and delegate functions to external technological components.

Keywords Electrodermal activity · Grasping pattern · Human evolution · Neuroarchaeology · Parietal lobes · Tool shape · Visuospatial integration

1 Prehistory and Neuroscience

Cognitive inferences in prehistoric archaeology have often been provided on the grounds of general terms and processes, rather than specific cognitive theories. The main framework has been a gross and generalized assumption that relies on anatomical and cultural complexity as a proxy for behavioral and cognitive complexity. That is, complex brains are supposed to generate complex behaviors, and complex behaviors are supposed to be necessary to produce complex tools. In the last decade, however, there has been an increasing exchange between anthropologists, archaeologists, neurobiologists, and cognitive scientists, and these research areas have undergone a stimulating multidisciplinary development. Thanks to technical improvements (from digital anatomy to numerical modeling) and the increase in the archaeological record, prehistoric and cognitive sciences have stepped into a more intense and reciprocal process of integration. Some fields have been enhanced, and some others have been introduced as brand-new methodological perspectives. *Paleoneurology* deals with the anatomical study of the endocranial cavity in fossil species and has been improved by the introduction and development of biomedical imaging (Bruner 2017). *Neuroarchaeology* concerns the study of prehistory-related behaviors through physiological and neurobiological approaches, such as functional imaging (Stout and Hecht 2015). *Cognitive archaeology* integrates the archaeological evidence with theories in cognitive science, through neuropsychological perspectives (Coolidge et al. 2015).

Despite the noticeable advantage of mixing archaeological and cognitive knowledge, the limitations are also clear: prehistoric studies are based on indirect traces of structures or processes, and not on the actual targets of interest. In terms of fossil anatomy, paleoanthropology generally works with the fragmented bones of few individuals. Instead of a brain, there is a mold of the endocranial cavity or *endocast*. An endocranial cast can provide information on brain size, some gross cortical proportions, brain geometry and spatial organization, sulcal patterns, and meningeal vascular morphology. All this information is extremely valuable, because it is the only direct evidence we have on the brain anatomy of extinct species. Nonetheless, an endocast is not a brain and should be interpreted with this limitation in mind.

In the case of neuroarchaeology and cognitive archaeology, a main drawback is due to the fact that cognitive processes are investigated and simulated according to the information we have on modern humans (*Homo sapiens*), and not on extinct species. This is of course an intrinsic limitation of these fields. Nonetheless, we often use other species as models when investigating our own biology and evolution (mice, macaques, or chimpanzees), and the differences among species of the same genus (*Homo*) are supposed to be plausibly smaller. The fact that we use cognitive information on modern humans to make cognitive inference on extinct humans must be taken into account, but it should not be taken as a reason to reject the field as a whole. The aim of disciplines that integrate prehistory and neuroscience is to provide consistent hypotheses according to the available information, which can be tested against parallel and independent evidence. Testing hypotheses may be more difficult in extinct species than in living organisms, but the methods and rules are, after all, exactly the same as in any other scientific context.

2 Working Memory and Visuospatial Integration

Early steps in cognitive archaeology were particularly focused on working memory, following the model proposed by Baddeley (see Baddeley 2000, 2001), attempting to trace its components back to archaeological evidence (Coolidge and Wynn 2005; Wynn and Coolidge 2016). Frederick Coolidge and Thomas Wynn, integrating archaeology and neuropsychology, investigated the appearance of behaviors associated with a central executive system, a visuospatial sketchpad, and a phonological loop, in order to evaluate whether our species, *Homo sapiens*, could have enhanced its working memory capacity through a process of selection and adaptation. They suggested, for example, that, according to the technological evidence, Neanderthals' long-term working memory was similar to modern humans, while their working memory capacity was less developed, possibly because of a smaller phonological store or reduced attention levels (Wynn and Coolidge 2004). This conclusion, based on archaeological information, can be used for making behavioral predictions than can be contrasted against the ecological, cultural, and social evidence we have on Neanderthals. Following a similar principle, they also investigated specific behaviors like those associated with managed foraging, as a proxy for cognitive capacities linked to working memory, response inhibition, or space-time integration (Wynn and Coolidge 2003).

The Baddeley model (Baddeley and Hitch 1974) is assumed to rely mainly on a frontoparietal cortical network, and, according to the principles of cognitive archaeology, its functional units can be tentatively tracked back in the cultural remnants of human behaviors, looking for specific aspects associated, for example, with tool use and production, food storage, navigation, art, or social and economic dynamics. The executive system works through inhibition of emotional and spontaneous behaviors, which is probably a crucial hallmark of modernity. The phonological store influences speech and cognitive capacity associated with recursion and hierarchical cognitive organization. The visuospatial sketchpad deals with an egocentric perspective based on imagery (visual) and relational (spatial) capacity.

This last component was relatively neglected in many working memory analyses, but nonetheless it could have been crucial in human evolution. In fact, if we consider the paleoneurological evidence, a major morphological change along the human lineage has been precisely described for the dorsal parietal cortex (Fig. 1), a brain region which is crucial to visuospatial functions (Bruner 2018). Neanderthals display wider superior parietal lobules when compared with more archaic human species, and modern humans show an even larger parietal lobe expansion, which causes a bulging of the parietal profile and their classic "rounded head" (Bruner et al. 2003, 2011; Bruner 2004). Ontogenetic changes suggest that only modern humans have a specific morphogenetic stage of "brain globularization," expressed very early during ontogeny, which is lacking in Neanderthals or chimpanzees (Gunz et al. 2010).

It is interesting, therefore, that the two human species with more complex technological levels display a cortical expansion of areas dedicated to brain-body-environment management and integration, especially when considering that for the human genus "environment" also means "tools." Spatially, the lateral dorsal enlargement of Neanderthals can be tentatively associated with the intraparietal sulcus and superior parietal lobules, while the longitudinal enlargement in modern humans matches the position of superior parietal lobules and precuneus (Bruner 2010; Bruner et al. 2014a; Pereira-Pedro and Bruner 2016). The intraparietal sulcus is more complex in humans than in other primates, and it is largely involved in eye-hand coordination and tool use (Grefkes and Fink 2005; Choi et al. 2006; Tunik et al. 2007; Martin et al. 2011; Verhagen et al. 2012; Zlatkina and Petrides 2014; Kastner et al. 2017). Human specializations of this region are supposed to be directly associated with the evolution of our unique technological skills (Peeters et al. 2009; Goldring and Krubitzer 2017). The precuneus is extremely variable among adult humans, and it is much larger in humans than in chimpanzees (Bruner et al. 2014b, 2017a). It is considered crucial for processes based on integration between somatic (body) and visual cognition, like spatial coordination, visual imagery, mental simulation, autonoesis, and egocentric memory (Fletcher et al. 1995; Cavanna and Trimble 2006; Margulies et al. 2009; Zhang and Li 2012; Freton et al. 2014; Land 2014). The precuneus can be seen as a bridge between the external environment (vision), body cognition, and self-perception, with imagery and inner levels of consciousness. The correspondences

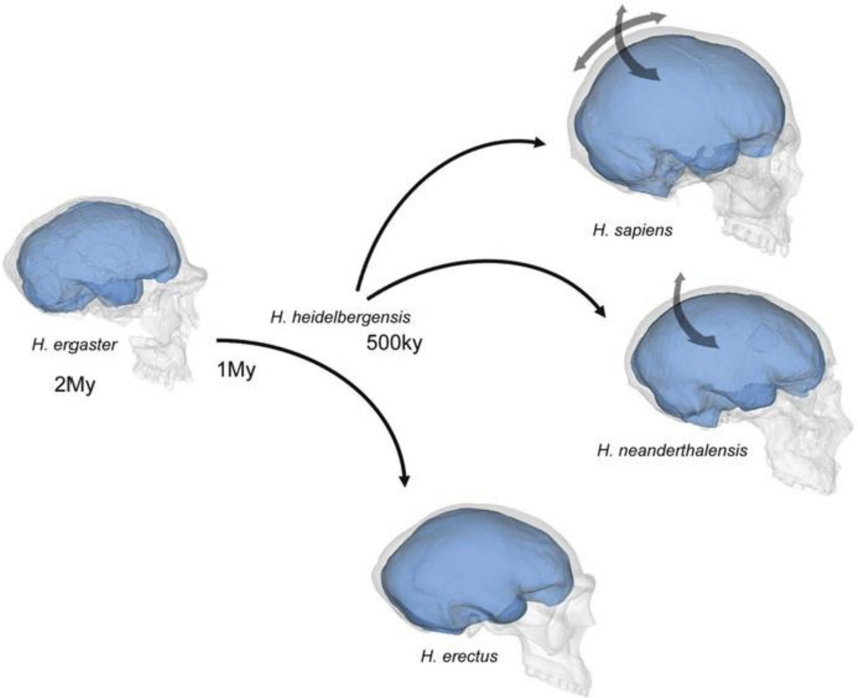

Fig. 1 The earliest fossils of the human genus (*Homo*) are dated to around 2 million years (My). In terms of endocranial morphology, the difference between these early African representatives and later *H. erectus* is apparently a matter of brain size, larger in the latter species. *H. sapiens* and *H. neanderthalensis* also evolved a larger brain size, but in these two cases, there was also evidence for changes in cortical proportions. Some of these changes are related to parietal cortex. Neanderthals display wider parietal lobes, and modern humans have wider and longer parietal lobes. Both lineages probably diverged after 500,000 years (ky) and derived from *H. heidelbergensis* which, as with *H. erectus*, had larger brain size then *H. ergaster* but no noticeable changes of the brain form

between humans and nonhuman areas are not completely clear, although some areas on the primate intraparietal sulcus may have outfolded in humans and the superior parietal lobule might be largely an outer extension of the precuneus (Scheperjans et al. 2008). These cortical areas are also very sensitive to environmental influences, including training and sensorial/somatic stimulation (Quallo et al. 2009; Iriki and Taoka 2012). Furthermore, they are all naturally crucial to specific conceptual and technical skills which range from imagination to tool use. Together, they have all the features of a very powerful visuospatial sketchpad.

3 Visuospatial Integration and Human Evolution

3.1 Body and Space

Most mammals possess homologous areas to the posterior parietal cortex, associated with functions that involve aspects of the body management, but this region is particularly developed in primates, and in particular in humans, due to manipulation skills and technological capacity (Goldring and Krubitzer 2017). The posterior parietal cortex is also crucial to processes aimed at filtering the sensorial information to coordinate attentional and intentional mechanisms (e.g., Posner et al. 1984; Mountcastle 1995; Rushworth et al. 2001; Yantis et al. 2002; Andersen and Buneo 2002; Bisley and Goldberg 2003; Corbetta et al. 2005; Wardak et al. 2004; Freedman and Assad 2006). Such filters are based on experience, as well as on somatic and visual feedbacks. Vision is used to coordinate body and environment, and the body is used as a metric unit of such an environment, in terms of space, time, and even social perspective (Land 2014; Hills et al. 2015; Maister et al. 2015; Peer et al. 2015). Our body perception is largely based on the hands, and the same areas involved in eye-hand coordination are also recruited in decision-making (Tunik et al. 2007). Namely, we can probably say that we often "think with our body," particularly with our hands, planning and simulating actions by using our own body as reference and taking decisions according to simulated or expected body experiences, feedbacks, and capacities. In a behavioral and even neurobiological perspective, the somatosensorial experience is therefore intermingled with the motor experience, generating a blurred separation between "feeling" and "acting" (Ackerley and Kavounoudias 2015).

This framework between body and action becomes further entangled when the body interfaces with technological extensions, namely, during tool use (Bruner and Iriki 2016). Tools are intended as extension of the body schemes, through a functional distinction between *personal space* (the body), *peri-personal space* (within the range of the body), and *extra-personal space* (out of the range of the body) (Maravita et al. 2003; Maravita and Iriki 2004; Farnè et al. 2005; Cléry et al. 2015). The relationship between personal, peri-personal, and extra-personal spaces is particularly relevant when dealing with our evolutionary capacity to extend our body and cognitive functions into technology. The frontoparietal system, in fact, reacts differently to objects positioned in the three spaces, which map to different cortical areas as a function of distance from the body (see Cléry et al. 2015 for a detailed review). A crucial cognitive change takes place when an object is included into the peri-personal space, becoming a potential tool, reachable in terms of body contact and extension. The own body is the metric unit that defines the peri-personal range, and vision supplies the feedback to establish its frontiers, mainly centered on the position of the whole body, of the head, and of the hands. This peri-personal space is updated according to both dynamic changes (momentary and punctual variations) and plastic changes (neural changes after training), and tools have a special role in this sense, artificially altering the extension and capacity of the arms.

Even in simple physical terms, the contact between the body and the tool influences the muscular and sensorial perception of the body itself and, accordingly, all the cognitive mechanisms that use the body as a functional and structural reference (Turvey and Carello 2011). Therefore, visuospatial integration not only concerns gross spatial and mechanical adjustments, but it is also central to fine cognitive functions that deal with self-properties.

In sum, the posterior parietal cortex is involved in cognitive integration between the brain, body, and environment, between body and tools, and between vision and body, using the same resources to coordinate space and time, egocentric perspectives, imagery, and personal memories. This is particularly interesting in the light of the so-called *extended cognition theory*, which interprets cognition as a process generated by the interaction between the nervous system, body experience, and material culture (e.g., Malafouris 2010, 2013; Bruner et al. 2018a).

3.2 A Case Study in Cognitive Archaeology

Neanderthals represent an interesting case study in body cognition because, although they had a brain size comparable with modern humans, the archaeological and paleontological evidence point to distinct visuospatial behavior (see Bruner and Lozano 2014, 2015; Bruner et al. 2016). In particular, the cut marks on their incisors suggest that Neanderthals – and probably their ancestors – used their teeth and mouth to manipulate their technology much more than any extant or extinct modern human population. The mouth is second to the hands in terms of cortical representation of the somatic territories (the "cortical homunculus"), so it is expected that it can be used to provide an additional manipulative body element when hands do not suffice. However, its involvement in manipulation is indeed a risky choice and should be intended as a suboptimal alternative. The significant involvement of the mouth as a "third hand" in Neanderthals may hence suggest a lack of manipulative specialization, when technology reaches a given degree of complexity. These dental marks would not be sufficient to support such cognitive hypothesis, unless associated with many other independent sources of evidence. In Neanderthals the parietal cortex, crucial for visuospatial integration, was probably not enlarged as in modern humans (Bruner 2018). For this species there is no evidence of projectile tools, a technology which is specific of modern humans and associated with throwing ability and visuospatial capacity (Williams et al. 2014; Gärdenfors and Lombard 2018), and Neanderthal hunting techniques were probably based on physical confrontation with the prey (another risky choice, if you are able to catch a prey by shooting from a distance). Also, for Neanderthals there is no evidence of a noticeable iconographic or visual culture. Their few minor suspected graphic manifestations are extremely simple (Hoffmann et al. 2018) and definitely incomparable with both the early and late artistic expressions of *Homo sapiens*. Paradoxically, many people are surprised to see that Neanderthals could have been the authors of very naïve sketches, but in reality we should ask the opposite question: taking into account their large brain size and high encephalization index, why did they not display more complex behaviors? If brain size really matters, with such a large brain (the same size as *Homo sapiens*), they would be expected to go well beyond a scratch or a colored shell. Although the Neanderthal archaeological record may be incomplete, the discrepancy with modern humans is, even only by grade, enormous, suggesting noticeable cognitive differences between the two groups (Wynn et al. 2016). Taken together, all this information (smaller parietal cortex, manipulation by teeth, no projectile technology, absent or negligible graphic culture) supports the hypothesis of a lack of visuospatial specialization and body cognition in Neanderthals when compared with modern humans. Of course, a less specialized cognitive ability is not necessarily a sentence to extinction, and we should not even discard the possibility that Neanderthals may have had other cognitive skills that we did not evolve.

Despite subtle uncertainties in chronology and definitions, it is worth noting that the morphological expansion of the parietal cortex in our species is probably a late acquisition of our lineage, and it matches the appearance of a definite behavioral modernity, including a noticeable visual and iconographic culture and complex technology. In fact, early modern humans shared similar lithic industries with Neanderthals and display only a partial development of the parietal surface (Bruner and Pearson 2013; Bruner et al. 2018b; Neubauer et al. 2018). However, they already had different hand proportions when compared with coeval Neanderthals, and a distinct use of the mouth when supporting manipulative procedures, more associated with the strength of the grip than with its precision (Niewoehner 2001; Fiorenza and Kullmer 2013).

It remains to be considered whether the neuroanatomical changes of the posterior parietal cortex are due to genetic evolution and selection or else to feedback between biology and culture, including training or epigenetic effects (Bruner and Iriki 2016; Krubitzer and Stolzenberg 2014). According to the traditional parcellation approach after Brodmann (see Zilles and Amunts 2010), it can be hypothesized that specific areas evolved, enlarged, or were reused for new emerging functions. By contrast, if brain organization is the result of gradients between sensorimotor regions (Huntenburg et al. 2017), the specialized posterior parietal cortex in primates – and in particular in humans – must be interpreted as an increase of connections and integration between the sensorimotor elements it bridges: body and vision.

4 Haptics and Body Cognition

Human evolution has been characterized by bio-cultural adaptive feedbacks between hand and tool morphology (Susman 1998; Marzke 1997; Almécija et al. 2015). Force distribution during tool use largely depends on the action performed, and it is likely that some behaviors may have had a major influence on hand shape, mostly when dealing with the thumb and the distal phalanxes (Rolian et al. 2011; Williams-Hatala et al. 2018). Hand size is also relevant for tool use, and it is a major factor of variation also among modern adult humans (Key and Lycett 2011; Bruner et al. 2018c).

We can expect that this coevolution between the brain, body, and technology was not only a matter of biomechanics but involved specific cognitive functions associated with hand-tool integration. In general, most studies in this sense are interested in those cognitive abilities that concern planning, decision-making, and the executive functions of the brains. Nonetheless, additionally, we should also consider whether the hand-tool relationship may also require some cognitive process that enhances the integration of the tools into the body schemes.

Visuospatial functions are indeed necessary when planning tools or tool use (the visual imagery functions associated with the precuneus and the intraparietal sulcus). However, beyond these aspects, taking into consideration the importance of the neural management of the personal, peri-personal, and extra-personal spaces, it should be expected that the capacity to integrate tools as body extensions (e.g., in terms of neural plasticity) could be a crucial target of adaptive processes. Although modern humans (*Homo sapiens*) evolved a very specialized tool-based functional extension, the whole human genus (*Homo*) is characterized by a culture and behavior which make us *dependent* on technology (Plummer 2004). In the last 2.5 million years, our ecological, economic, and cultural niches have depended on tools, as essential elements of our behavioral abilities (Key et al. 2016). Such "prosthetic capacity" (Overmann 2015) can therefore not only be an important part of our cognitive system but also a specific ability influenced by natural selection. Interestingly, functional specialization within human brain areas has been shown to be less constrained by genetic factors compared with other living apes and so may be more plastic and sensitive to external influence (Gómez Robles et al. 2015). Such capacity to export cognitive functions to technological (extra-neural) extensions would depend on neural mechanisms, on body experience, and also on the properties of the tools themselves. It is hence mandatory, in cognitive archaeology, to investigate all these three elements, as well as their interactions.

This target is not easy, because of the many factors involved (individual cognitive and sensorial differences, multiple cognitive tasks involved, physical and functional tool parameters and variables, etc.). At experimental levels, simplistic paradigms can be easier to analyze, but scarcely informative. Moreover, many processes involved in behavior and cognition follow complex networks in which the final mechanism is not the simple sum of its parts, and there are emergent properties that can be observed only when analyzing the system as a whole. Actually, the network underlying cognitive extension is supposed to be complex itself, in the sense that, according to the extended cognition hypothesis, there are processes that are activated specifically by the interaction between the brain, body, and culture. Finally, there are major difficulties when trying to quantify specific behavioral resources emerging from body-tool integration because, at present, we still do not know what kind of ability is directly involved in such prosthetic capacity and how to measure it. All these limitations mean that this research area is still in a preliminary methodological stage, in which distinct targets and techniques are investigated so as to evaluate their applications and potentialities. Quantitative methods are, of course, necessary, to step into a full experimental perspective. Three basic components behind body-tool interactions are tool shape, grasping patterns, and cognitive response to hand-tool integration. In the next sections, we show some applications in this sense.

5 Tools, Hands, and Attention: A Synthetic Analysis

5.1 Shape and Technology

Tool physical and geometrical properties influence the interaction with our body by virtue of both visual and haptic information. Beyond affordances associated with possible functional employment of the tool (purpose), the haptic experience is essential to generate an ergonomic spatial and physical integration between body and tool (Turvey and Carello 2011), which is ultimately projected into the newly emerging body schemes. The term "cyborg" has been popularized in a context of science fiction, but technically it refers to any functional integration between a body and a technological element, and humans are a special evolutionary case study of prosthetic extension (Clark 2004). Such "hybrid bodies," in which external components come in contact with the body generating new emerging functions, can be traced back at least 2.5 million years to Africa, when we found the most ancient human technology, the Oldowan. Actually, there is preliminary evidence of older tools (see, e.g., Harmand et al. 2015), but Oldowan is the first technology for which we have a robust and consistent archaeological record (Semaw et al. 1997; Braun et al. 2008; Stout et al. 2010). It was essentially composed by flaked stones with a cutting edge, like the typical "choppers." The raw materials were collected, prepared, and used locally, probably for a quick and momentary utilization. This technology was initially associated with *Homo habilis*, although at present this species is not regarded as a real and homogeneous taxonomic unit, and the hominid (or hominids) associated with this industry remains yet to be determined.

The earliest species undoubtedly assigned to the human genus (*H. ergaster* and *H. erectus*) are associated with stone tools which are much more elaborate and generally labeled as Acheulean technology (Lycett and von Cramon-Taubadel 2008; Hodgson 2015). Acheulean archaeological record begins after 1.7 million years, and the most typical tool in this case is the handaxe, a stone flaked for a larger part of its border, elongated and roughly symmetrical, probably used for multiple tasks. Some features of this industry can be due to stone geometrical constraints (Moore and Perston 2016), but nonetheless it is generally assumed that the complexity of handaxes, when compared with choppers, reveals a cognitive change, because of their design, preparation, and geometry (Wynn 2010; Gowlett 2013). Although Oldowan is more archaic and simpler, it was not substituted by Acheulean, and the two different technologies coexisted independently for at least 600,000 years (Clark and Schick 2000).

Because of the differences between their design and structure, Oldowan and Acheulean technological modes could be particularly interesting when evaluating changes of the human prosthetic capacity to integrate tools as body extensions. It is also worth noting that the same visuospatial processes involved in body cognition and visual imagery are involved as well in integrating self-perception and social context (Coward and Gamble 2008; Hills et al. 2015; Maister et al. 2015; Peer et al. 2015) and that the volume of the cortex in primates is correlated to social group size (Dunbar 1998; Dunbar and Shultz 2007). Tool making and tool use necessarily rely on social learning and imitation (Mesoudi and O'Brien 2008; Schillinger et al. 2015; Gärdenfors and Högberg 2017; Lombao et al. 2017), and technological complexity represents therefore an additional bridge between visuospatial processes and social behavior.

Shape analysis based on coordinates is nowadays a standard in morphometrics, and it can provide a quantitative background to investigate geometric variation and its underlying schemes (e.g., Mitteroecker and Gunz 2009; Adams et al. 2013). In Fig. 2, we have analyzed the shape of some representative lithic tools (seven Oldowan choppers and six Acheulean handaxes obtained through experimental knapping) through landmark analysis of their outline. Outlines were sampled with 30 equally spaced landmarks in two dimensions, after photographs. We also included two natural (not knapped) stones of similar size and of similar composition. Coordinates were superimposed by Procrustes registration to minimize shape differences and then analyzed through Principal Component Analysis (see Zelditch et al. 2004). In this sample there is only one consistent component of shape variation (explaining 76% of the variance) that separates narrower tools (mostly Acheulean) from wider tools (mostly Oldowan). Narrowing/widening appears to be specially

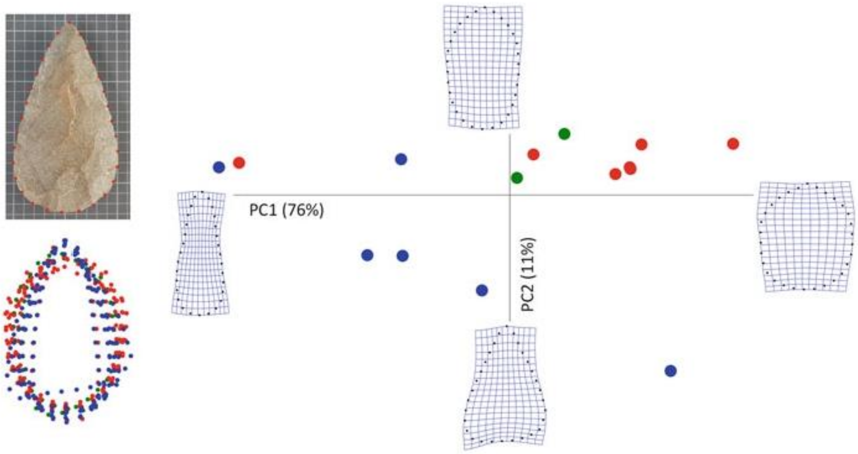

Fig. 2 Shape analysis of the outline of natural stones (green), Oldowan choppers (red), and Acheulean handaxes (blue) after Procrustes superimposition and Principal Component Analysis

pronounced at 2/3 of the tool length, that is, before the tip. Although this shape component largely distinguishes Oldowan and Acheulean tools, there are some exceptions. Natural stones are largely similar to choppers. A second component (11%) separates tools with wide bases and narrow tips (mostly Acheulean) from tools with narrow bases and wider tips (Oldowan, natural stones, and some handaxes). Following principal components explain less that 5%. Tool shape (PC1, PC2, or the overall shape coordinates) is not correlated to tool size (computed as centroid size, namely, the sum of squared distances of all the points from the centroid). Therefore, according to this descriptive tool sample, the main and dominant tool variation deals with elongation (narrow vs wide), while a second minor pattern concerns the inverse proportions between base and tip. When compared with choppers, handaxes are characterized by elongation, wider base and sharper tip. There is only a very minor overlap between these two technological typologies, and apparently their geometric variation does not depend on size. Elongation is a main feature of Acheulean tools, and it is generally interpreted as a proxy of cognitive complexity because it denotes technical skills in knapping procedures (Gowlett 2013). Nonetheless, elongation also influences affordance, extension of the peripersonal space, and dynamic body responses, triggering crucial haptic processes (Turvey and Carello 2011). Accordingly, elongation is expected to have a specific role in inducing alterations of body schema, sensu Maravita and Iriki (2004). This specific pattern of narrowing is really determinant in the variation of these two archaic stone tool typologies, and therefore we should evaluate whether and to what extent it is associated with specific haptic changes, and eventually with relevant body-tool cognitive feedbacks. The same can be proposed for the second shape component (tip-base inverse proportions), although in this case the pattern explains only 10% of the difference and a larger sample is probably necessary to investigate further its reliability.

5.2 *Grasp and Tools*

We asked 46 adults (24 males and 22 females), blindfolded, to handle the same sample of tools until they found a comfortable hand-tool position. Participants were right-handed and not trained in archaeology. They were not allowed to see the tools before the survey. For each tool, when participants reached a stable hand-tool position, the final grasping modality was classified according to Feix et al. (2009). Grasping categories include two power grips (types A and B, with the thumb opposed or else aligned to the other finger) and three precision grips (types C, D, and E, with the index finger on the edge, pinching, or surrounding the tool, respectively). Type C is labeled as precision grip because the thumb approaches the fingertips, but actually it is a sort of intermediate position between power an precision grip. Figure 3 shows the different grasping types and the frequency of each category (A–E) for each tool type (natural stones, Oldowan, Acheulean). All tools were spontaneously grasped primarily with a power grip. Natural stones are predominantly grasped through opponent thumb. Oldowan and Acheulean tools

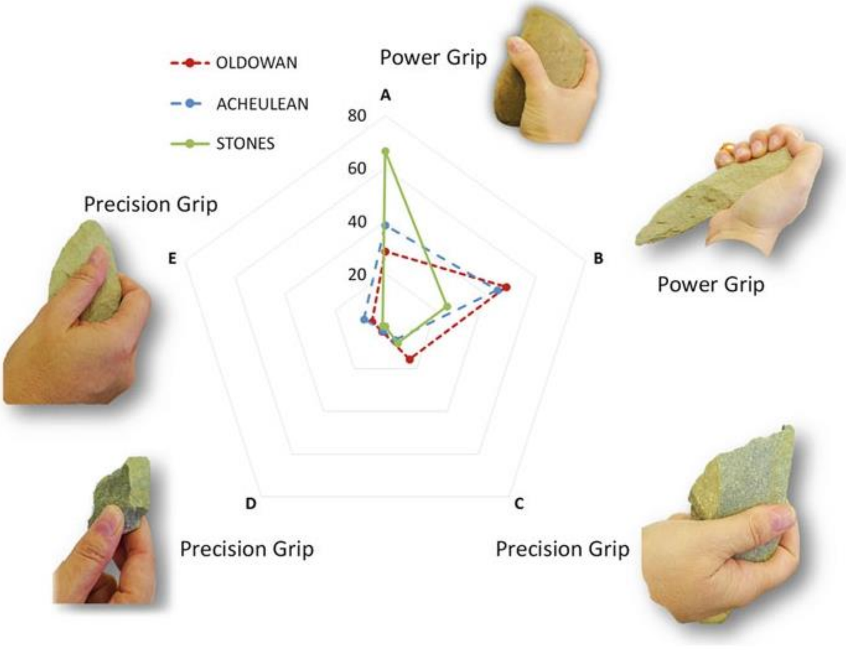

Fig. 3 Percentage of the five grasp types in natural stones, Oldowan choppers, and Acheulean handaxes. Subjects were blindfolded and, without previous archaeological knowledge, were asked to grasp each tools in a way that felt comfortable

display a similar grasping pattern, different from that of natural stones, although the thumb is slightly more lateral (type C) for the choppers and opponent (type A) for the handaxes. In type C grip, the thumb is closer to the fingertips if compared with classic power grips but is also less involved in holding the tool. In this aspect, it is more similar to a power grip that to a real precision grip. Actually, the involvement of the thumb is less relevant in Oldowan than in later technology (Williams et al. 2012), and this can explain the minor difference we detect in this survey between the two tool typologies.

Figure 4 shows a cluster analysis displaying the similarity between tools according to grasp frequencies, basic tool size (maximum length, width, and thickness), and shape (Procrustes coordinates). Similarity is based on Euclidean distances (raw metric differences), and clustering is computed according to an UPGMA (Unweighted Pair Group Method with Arithmetic Mean) criterion, which pairs the most similar figures and then clusters the value most similar to their average. This quantitative comparison suggests that geometry is more efficient in separating choppers from handaxes than their general dimensions or than the grasping modality with which they are handled. Tool affinity based on grasping frequencies looks less determined by tool typology, suggesting that there are factors other than the gross

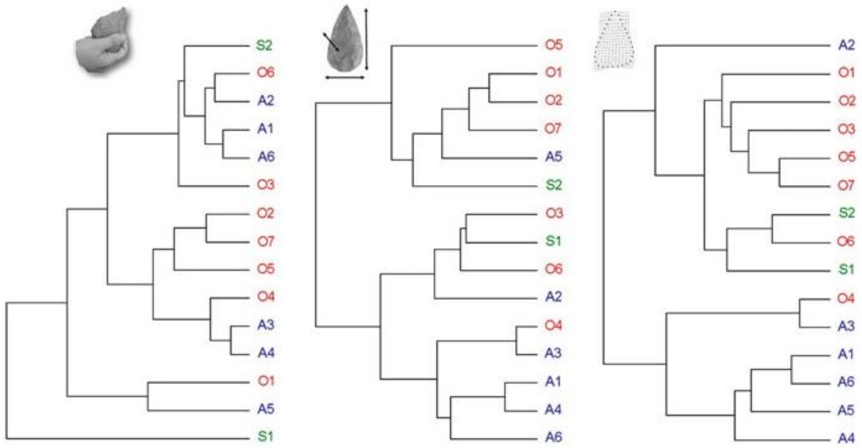

Fig. 4 Cluster analysis based on grasp frequency (left), tool main diameters (center), and tool shape (right), for natural stones (S, green), Oldowan choppers (O, red), and Acheulean handaxes (A, blue)

outline of the object influencing the choice of the hand position. For example, choppers are more similar to natural stones in shape, but the latter involve apparently much more opponent thumb. Acheulean tools are more different from Oldowan tools in shape, but showing a more similar grasping pattern, although with larger frequency of opponent thumb as well. Thus, spontaneous grasping of a tool seems only partially determined by the different degree of technological complexity of these two kinds of industry. This result is partially expected, because shape is actually a major factor when classifying tool typology, and we use to classify stone tools by their shape more than by their haptic properties. But this result also suggests that tool shape and grasping, although sharing reciprocal influences, involve independent additional aspects. Tools are generally categorized according to their form, to the underlying knapping procedure, and to their supposed functions (e.g., Akoshima and Kanomata 2015; Key and Lycett 2017; Ollé et al. 2017). We may wonder whether features associated with grasping and handling should also be taken into account in typological classifications of tools, because of the functional relevance (ergonomics) but also because of possible cognitive involvement (dynamic touch, affordance, prosthetic capacity, etc.).

5.3 Haptic Stimulation and Attention

Neural activity during stone-tool manipulation can be visualized through neuroimaging, namely, investigating structural and functional cortical changes associated with archaeologically relevant behaviors (Stout and Chaminade 2007). From earlier to later lithic technologies, we can observe an increase of the hierarchical complexity of the knapping procedures, which is interpreted as a proxy for cognitive complexity (Muller et al. 2017). Functional imaging revealed that Oldowan toolmaking largely relies on parietal cortex activation, while Acheulean toolmaking also implies prefrontal activation (Stout et al. 2015). This suggests a larger cognitive demand for the latter industry, which likely involves a central executive system aimed at evaluating strategies and alternatives to deal with bifacial shaping. Therefore, it looks like Acheulean toolmaking required/induced a relevant response of the frontoparietal network and of the associated working memory processes. At the same time, Acheulean tools also suggest enhanced communication capacity (Gärdenfors and Högberg 2017).

It is important however to note that toolmaking and tool handling do not necessarily rely on the same cognitive capacities and perceptual resources (Goodale et al. 1994). Toolmaking has an important problem-solving component, while haptic feedback and functional extension are more centered in sensorial mechanisms. Similarly, specific abilities associated with dexterity (e.g., the precision of the grip) are not inevitably associated with the capacity of brain-artefact functional integration. Dexterity is largely a mechanical issue, while prosthetic competence involves more crucial cognitive aspects. We can assume that these two characteristics have important reciprocal influences, but not necessarily a stringent correspondence. Namely, body extension, embodiment, and technological integration should not be confounded with specific spatial skills of the osteo-muscular mechanical system.

A quick and practical method to analyze a basic cognitive response to hand-tool interaction is electrodermal activity (Critchley 2002; de Houwer and Hermans 2010). Changes of impedance/conductivity, as recorded at the fingertips, are associated with *attention* (electrodermal level, EDL) and *emotional engagement* (electrodermal response, EDR) (Martin and Venables 1966; Boucsein 2012). Electrodermal variations can be detected during stone tool manipulation (Bruner et al. 2018c). We analyzed EDL and EDR in all the 46 participants handling the tools described previously, with a portable remote electrodermal device Sociograph (Fig. 5). The absolute EDR value was used in this comparison. EDL, in contrast, is a variable that depends on individual characteristics. Therefore, we compute EDL %, as the ratio between the peak of maximum attention (corresponding to minimum EDL value) and the average individual value, in order to quantify the maximum shift of attention according to the performance-specific mean figure. Both EDR and EDL show differences for different tools, in terms of mean values and degree of variation (Fig. 5). Therefore, different tools may exert different demands on emotion and attention, during a novel tactile experience. We must assume these different emotional responses depend on the physical features of the tool, mostly size, shape, weight, and texture. In this case, the tools were experimentally prepared, and texture is reasonably homogeneous. Individual variation is large, and this means that, beyond different tool-specific mean values, a tool can exert distinct emotional responses in different persons. The fact that also the degree of variation is not the same for all the tools suggests that some tools can exert more diverse personal responses than others. Both mean value and degree of variation are parameters that

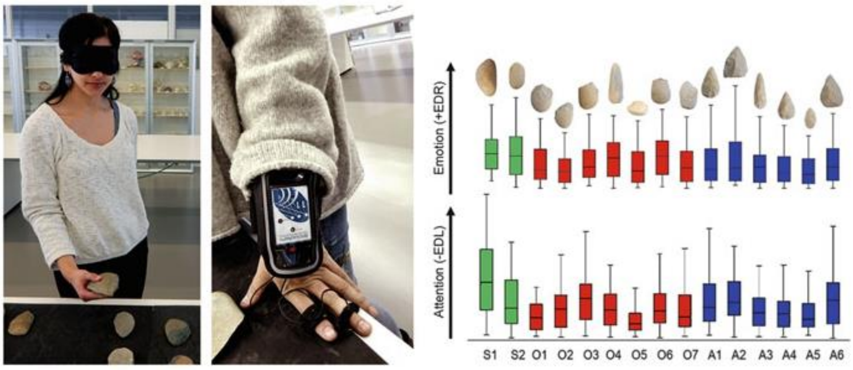

Fig. 5 Subjects were asked to handle the tools (left) while a remote recorder (center) was detecting the variation of electrodermal response and electrodermal level (right: mean, interquartile and range for each tool)

can be investigated through the archeological record to evaluate changes or discontinuity in the patterns of cultural evolution. In this specific case, on average, Oldowan tools induce more emotional response and less attention response than the Acheulean tools, and females display higher attention levels than males (Fig. 6). Both EDL and EDR can be analyzed using also other parameters, like the individual range (difference between minimum and maximum) for each tool, the value at rest (when reaching the comfort position), the value during some specific action, or the whole curve during the entire haptic experience. What is important is that these kinds of interactions can be quantified and used to investigate changes in the cultural record or else specific cognitive hypotheses.

In sum, we have shown some basic methods than can be useful to consider the cognitive interaction between haptic experience and lithic technology. These examples indicate that, when compared with choppers, Acheulean tools are characterized by elongation and further involvement of the thumb, two features that can enhance the cognitive and behavioral extension of the personal and peripersonal space. Taking into account the reciprocal influence between brain and culture, and the possible role of technology as extension of our cognitive system, polarities and causal networks in terms of evolutionary changes are of course difficult to sort out. Generally, it has been assumed that the evolution of a complex brain induces the evolution of a complex culture, but probably this view is too simplistic. Cultural changes can influence behavioral changes, and even channel successive selective pressures (e.g., Crispo 2007; Krubitzer and Stolzenberg 2014). Whatever the causal mechanism behind the transition from Oldowan to Acheulean, we can hypothesize that features like elongation and the involvement of the thumb reveal an increase of the brain-body-tool functional extension and spatial integration. If this is the case, the properties of the Acheulean tools disclose an enhancement of the prosthetic capacity and technical embodiment of the human genus.

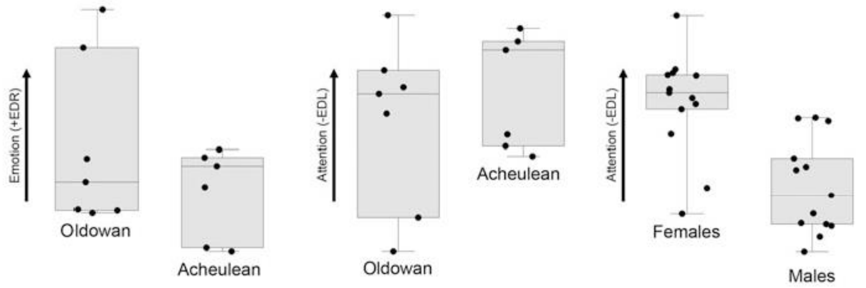

Fig. 6 There are differences in the distribution of mean EDR and EDL for Oldowan and Acheulean tools and for males and females

Although it may be difficult to disentangle causes and effects in such composite system, we can nonetheless use the archaeological record to recognize specific cognitive trends or shifts, according to specific biological signals. We have also seen that different tools can exert different emotional and attention responses, and our Acheulean tools evoked, on average, less emotion but more attention. However, object affordances (both visual and haptic) are based on many distinct factors, and variability (among objects as among subjects) is extremely large. Therefore, these relationships must be investigated through more targeted and specialized samples and, when possible, corroborated by robust statistical validations. Electrodermal activity may represent a useful technique to analyze psychological responses associated with behaviors specifically relevant in the archaeological context and to detect discontinuities in our cultural evolution that may indicate changes in the brain-body-environment relationships. A detailed analysis of these variables and samples is currently in progress.

6 Exploring Body Cognition and Human Evolution

Attention is most often considered in the context of visual selection, but we can also consider attentional processes associated with bodily experience. In terms of technological extension and hand-tool relationships, we can talk of *haptic attention*, when dealing with mechanisms that channel and orient behavioral responses during manipulative experiences. Visual and haptic responses are both crucial to shaping body cognition and visuospatial capacity, and a key question concerns their reciprocal influences. These topics are investigated in psychology, neurobiology, medicine, or even robotics, but they can also be examined by anthropology to provide a comprehensive interpretation of behavior in extinct species (prehistory), in past populations (history) or even between distinct cultures (ethnology).

Although recognizing the importance of environmental influences, a neurocentric paradigm has generally been accepted within which the brain is a computer-like self-sufficient machine. Recent hypotheses on extended cognition suggest an alternative scenario, in which what we call "mind" is not a *product* of the brain but instead a *process* generated by the integration between the brain, body, and environment. This can be particularly relevant in primates, a taxon with a specialized eye-hand system, and most of all in humans, which are characterized by unique technological adaptations. Of course, such a perspective is still in its preliminary stages, in which many terms and definitions are still not clear, interpretations are provisional, and methods are still under construction.

The first step is to evaluate whether technology is a product of our cognitive process, implementing our capacities, or else a constitutive element of the cognitive system. This aim can be hard to achieve, although different scholars are trying to define proper criteria than can be used to validate the hypotheses through quantitative and experimental designs (see Kaplan 2012). For example, the *mutual manipulability criterion* suggests that two entities that alter their reciprocal states pertain to the same system, and the *bandwidth criterion* uses the amount of connectivity to localize relational boundaries between different functional units. All these approaches, bridging biology, philosophy, system theory, and computational neuroscience, although difficult to apply in specific empirical conditions, may supply new perspectives on cognition and behavior and, ultimately, in the interpretation of the archaeological and paleontological records. Of course, we still have some major methodological limitations, because most of our conceptual and experimental tools are based on reductionist perspectives that isolate single elements or single functions, interpreting results through linear causal associations. These cognitive paradigms are relatively recent in our culture, and we probably have to deal with many conceptual and empirical issues before we can adapt our experimental toolkits to different points of view.

An excellent analogy in this sense is the spider's web, in which the threads are an outer extension of the spider's nervous system, produced and shaped by the spider itself (Japyassú and Laland 2017). The web outsources information processing beyond the body of the spider, being a crucial part of the spider's sensorial and cognitive toolkit, essential to its ecological survival. The web, as a peripheral processing element, is involved in spider's memory and attention cognitive machinery and coevolves with the spider's body. Our technology represents an analogous situation, extending our cognitive capacities through external elements which have become necessary to sustain our behavioral abilities as well as our ecological niche. In this sense, the capacity of generate such connection between internal (brain) and external (tools) components is a key feature for selection and adaptation. If the brain, body, and tools are actually part of a single cognitive system, then we have to investigate their respective roles and importance, at both the individual and evolutionary levels.

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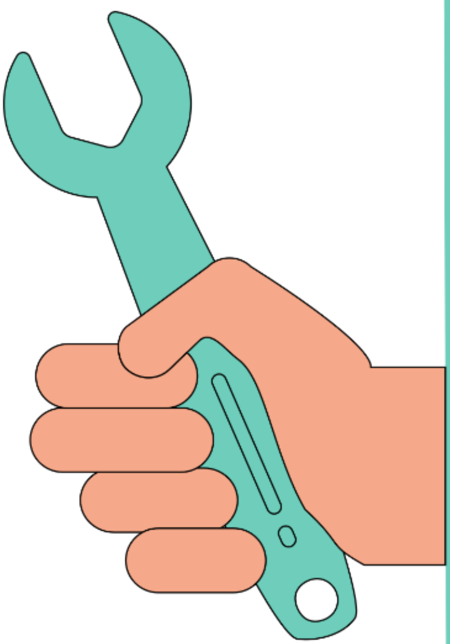
05

DISCUSSION



5.1 Structure of the discussion

In this section, the results of the surveys are discussed in the light of current bibliography. Firstly, the results will be quickly summarised (Figure 15). Then, the contribution of these results to the existing knowledge of the evolution of the human hand will be taken into consideration. Similarly, the results regarding choppers and handaxes will be discussed. Our studies will be compared with the other research and there will be analysis of the contribution of these results to the knowledge about stone tools. Then, human cognitive evolution will be considered.

There are two principal approaches in the archaeological field that aim to shed light on the hand-stone tool relationship. The first relies on reconstructing the biomechanical capabilities and comparative tool-use abilities of fossil humans. The second examines the morphology of stone tools recovered from the archaeological record and interprets how efficiently or effectively they could have been used during cutting tasks. Both approaches rely on experimental analysis, using modern human subjects. The first approach relies on rich literature, and our results will be contextualized in section 5.3. Regarding the second approach, to date, studies have focused on stone tool use and production, without taking into account the hand tool relationship in a comfortable still position. Moreover, experiments aimed at recording finger flexion during lower Palaeolithic stone tool use are almost inexistent. It is therefore difficult to directly compare our results with previous ones. However, some experimental studies can give some cues to discuss our results and they will be presented in section 5.4.

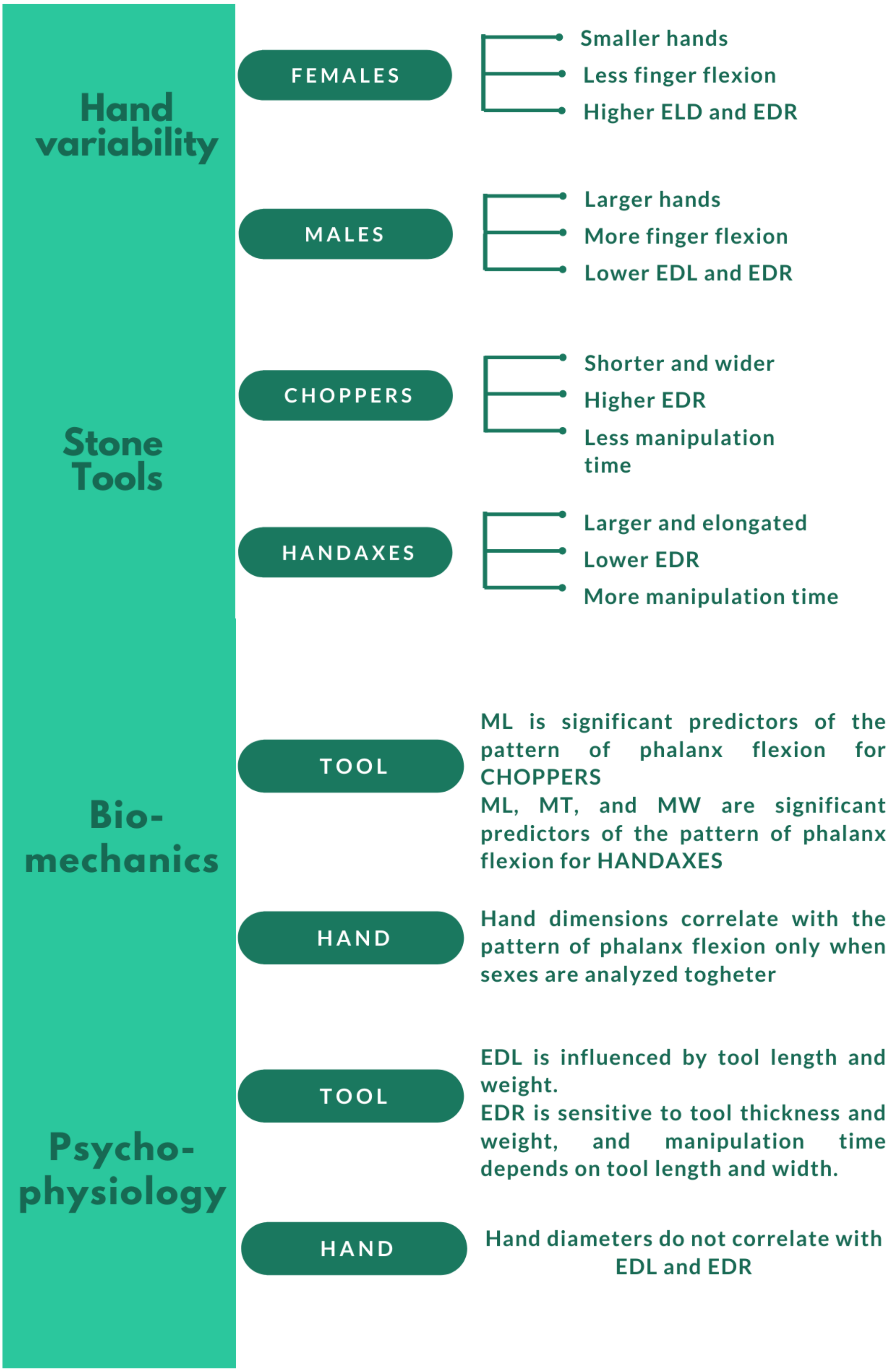


Figure 15: Summaty of the results

5.2 The hand

Since Darwin, it has been accepted that the hand has played a key role in primate and human evolution. Compared to most other mammals, primates' hands present greater prehension, dexterity, and control and, among primates, humans have particularly pronounced manipulative capabilities (McGinn, 2015). Despite the remarkable capacity of the human hand, our extraordinary dexterity is not a structurally unique. In fact, years of research have proved that primates have relatively "simple" hands with roughly equal finger lengths and fewer hand muscles compared to many non-primate mammals. Already Napier (1956) pointed out that, in many ways, the modern human resembles primitive forms, and that its uniqueness is linked to evolving functions that the hand is capable of performing. Even if it is true that the modern human hand retains an overall primitive form in many respects, it has also undergone functionally significant changes that, in combination with associated neural and cognitive developments, enable us to perform a myriad of tasks that would be far beyond our ancestors and closest living relatives. Moreover, some important hand features have evolved in response to the habitual stresses of the hand related to Palaeolithic stone tool manufacture and use throughout our evolutionary history (Marzke, 1997; Marzke and Marzke, 2000). Thanks to the new methodologies used in experimental archaeology, in the last ten years, researchers have been able to quantify the biomechanics of stone tool behaviours, and test hypotheses about modern human hand anatomy and stone tool behaviours. Experimental data have demonstrated that an individual's biomechanical capabilities and biometric traits can impact the efficiency and effectiveness of stone tool use. Key and Lycett (2018) have demonstrated how the strength and dimensions of a tool user's hands are correlated with the cutting performance of flake tools and handaxes, with different biometric traits contributing to tool efficiency in variable ways depending on the type of tool used. Williams-Hatala et al. (2018) further emphasizes the high muscular recruitment and loading required by the thumb and index finger during effective flake and handaxe use.

Different modern methodologies have been used to study the biomechanics aspect of tool use and production. Technologies such as high-speed motion capture devices, in vivo computer-based imaging and modelling, and real time pressure sensing systems generate high-resolution biomechanical and functional data that document the rapid motions associated with stone tool behaviours. The approach we used to assess the comfortable grasping of Lower Palaeolithic stone tools (Cyberglove) was similar to those methods, and thanks to that we have been able to compare our results with previous similar studies. When comparing other studies to ours, the first interesting similarity that was found is that, despite the complexity of the motions involved in stone tool behaviours (and the technology used to record them), it appears that the majority of grips are variants of the power and the precision grips (Napier 1956). Power grips include those in which an object is secured between the flexed fingers and the palm of the hand. Here the thumb acts as a buttress, further securing the object in the hand, though it is not necessarily the primary stabilizing component of the grip (Napier 1962, 1993). Other precision grips include those in which an object is pinched between the palmar aspects of the fingers and the pollical distal phalanx. In this grip the thumb plays the main supportive role (Napier 1956, 1993). These two typologies have been widely used to identify the majority of grips. Some years later, Marzke (1997) arranged the range of precision behaviours used when interacting with stone tools to better describe their use and production (Marzke and Shackley, 1986). According to her description, the palm in a precision grip is not a requirement. She also subdivided the grips into *precision finger pinch grips* in which objects are manipulated within a single hand, and *palm pinch grips* (which involve greater contact between the object and the hand) (Marzke, 1997).

Interestingly, humans are the only species able to apply large forces with just one hand during precision grips (Marzke 1997, 2009; Marzke et al. 1992). This skill is related to our thumb anatomy, which is responsible for a thumb-to-finger length ratio that facilitates full palmar contact between the digits, well-developed intrinsic and extrinsic pollical muscles that provide grip strength, and a large range of motion at the first carpometacarpal and metacarpophalangeal joints (Kuczynski, 1974; Napier, 1962; Marzke, 1992, 1997; Marzke et al., 1998; Tocheri et al., 2008). Because of all these factor, humans are able to guarantee a forceful application of precision grips (Tocheri et al. 2008). In fact, studies on experienced stone tool knappers showed that they tend to use the precision pinch grip during tool making processes (Marzke and Shackley 1986; Williams et al. 2012) and during Lower Palaeolithic stone tool use individuals used only the same limited number (≤4) of grips. 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 extinct human species with similar hand morphology to that of modern humans used similar types of grips of the one found in experimental studies with modern humans (Key et al., 2018b).

The main difference between our studies and previous similar studies is that we do not study tool use or tool making. Instead, we recorded only the comfortable grasping. In simple terms, a comfortable grip implies a secure handling, preventing the object from slipping. Before going any further, it is important to indicate that different tasks may require completely different grasps for the same object (Murali et al., 2020), and the majority of stable grasps assume an end goal. When we grasp an object, we do so with a particular purpose in mind. For example, when we grasp a cup, we use the handle to drink from it though several other stable grasps exist. In our study, we asked people to grasp the stone tool in the most comfortable way, without thinking about its purpose. The final grasping would be therefore the result of the simple interaction between the individual's hand morphology and the structural properties of the tool.

Although humans perform grasping tasks naturally, studies on biomechanical functioning suggest that there is a limited number of joint postures for the successful grasping of an object. Moreover, humans spontaneously adopt the posture that guarantees the highest grip force compared with other possible positions (Caumes et al., 2019). During the comfortable handling of a stone tool, we would expect participants to adopt the grasping that allows the highest grip force. Grip force is higher in males than females and it is strongly associated with gender, age, height, and habits (Beasley, 1973).

In our study, during the comfortable manipulation of Lower Palaeolithic stone tools, males and females show different patterns of phalanx flexion. In fact, males are able to obtain higher phalanx flexion compared to females. Intuitively, the tool-hand proportion could be responsible for this matter. However, hand dimension is related to the patterns of phalanx flexion only when the sample is pooled but when males and females are considered separately, the correlation no longer stands. We suppose that cultural or biological factors could be therefore responsible for these results. For example, the differences in grip force (a biological factor) between males and females could be responsible for different grasping strategies. As already mentioned, males have greater handgrip strength compared to females (Asadi, 2018). Handgrip strength is positively related with bone mineral density (Kritz-Silverstein and Barrett-Connor, 1994; Sinaki et al., 1989; Schwarz et al., 2014), and muscle mass (Kallman, et al., 1990). Handgrip strength also varies as a function of developmental factors including nutrition, exercise, and health (Geliebter et al., 1997; Hunt et al., 1985) and it is strongly influenced by genetic factors (Arden and Spector, 1997; Fredericksen et al., 2002; Reed et al., 1991). A number of studies have shown that handgrip strength is a highly sexually dimorphic trait (Kamarul et al., 2006) and it is likely due to higher levels of androgenic hormones in males (Page et al., 2005). Therefore, we are inclined to suggest that handgrip strength, instead of hand dimensions, could be responsible for the different pattern in males and females. Key and Lycett (2011) studied the influence of biometric variation in the efficiency of simple cutting tools. They found that grip strength and hand size have a statistically significant influence on efficiency variation. In our experimental setting, the subjects did not perform any task, and this could be the reason why we are not able to find a clear influence of the hand dimensions in the grasping pattern. Despite the many degrees of freedom present in whole-hand grasping, in a still position, the subjects simplify the control of the grasping by creating fixed relationships between the forces distributed at each digit (Reilmann et al., 2001). Therefore, we would expect that the hand during still grasping undergoes a stress related with the tool weight, and that the fingers are positioned to maximize their contribution during the static phase.

Regarding the individuals' psychophysiological response during stone tool manipulation, females show a higher level of attention and emotion compared to males. Concerning the other study, male and female hand diameters do not correlate with the degree of electrodermal level and response and therefore sex differences in electrodermal reaction during stone tool handling are apparently not due to the effect of hand size or proportions. Previous studies have already found similar sex differences in electrodermal responses (Kopacz and Smith, 1971) but, at present, there is no study that could be directly compared with ours. The interpretation of these results is therefore difficult. Interestingly, in both experiments, we found sex differences, but the different hand dimensions in males and females are not responsible for them.

It is possible that the same factors that are responsible for the differences in grasping strategies could also play a role in the electrodermal responses. For example, if the handgrip strength were responsible for the grasping pattern, individuals with stronger hands would experience less stress while individuals with weaker hand would experience a negative sensation related with a non-ergonomic grasping. Thus, individuals with weaker hands could feel uncomfortable related to tool weight ("too heavy") and dimensions ("too big for a comfortable grasping"). In fact, previous studies have demonstrated that unpleasant emotions are associated with an increase in EDL (Frade et al., 2017). It is possible that the wider range of EDL responses in females (and their higher attention levels) are related to uncomfortable grasping. In the next section, we will focus on the tool properties and we will discuss this possibility in more detail.

5.3 The tools

5.3.1 Research on grasping

Tools should be designed to minimize muscular effort and maximize grip effectiveness in order to increase efficiency (Pheasant and O'Neill, 1975), reduce fatigue (Rohmert, 1973) and prevent mechanical trauma injuries (Tichauer and Gage, 1977; Silverstein et al., 1986). Static hand posture has already been used as a proxy to assess comfort during gripping (Kong et al., 2007; Kuijt-Evers et al., 2007; Vigouroux et al., 2011; De Monsabert et al., 2012; Rossi et al., 2015). Among the factors that could influence the grasping effectiveness include handgrip strength, the contact area between the object and the hand and the object properties (shape size and weight).

From an ergonomic point of view, the correct distribution of grip forces during tool use is a pivotal factor in order to prevent hand injuries. The strength of the hand is greatly influenced by the size of the object grasped (Hertzberg, 1955; Ayoub and LoPresti, 1971). The relationship between the handle size and the hand dimensions has a great effect on hand posture and grip strength, so the larger the hand length, hand width, and palm length, the stronger total grip strength (Kong and Lowe, 2005).

The contact pressure between the hand and the object can be used as a predictor of gripping comfort (Fransson-Hall and Kilbom, 1993; Johansson et al., 1999; Kuijt-Evers et al., 2007). The contact area between the object and the hand influences the muscular stress of the hand. A grasping where the contact area is maximized provokes less stress than a grasping where the contact is minor (Pheasant and O'Neill, 1975).

Very different contact forces may be exerted with the hand in the same posture, depending on the object that is being grasped. In fact, the dimensions of the object grasped are predominant factors that influence grasping. A small, lightweight object is typically grasped only with the index finger and thumb. An increase in object size and weight demands the use of more digits and a greater palmar surface area (Castiello et al., 1993). The necessary force to pick up an object increases linearly with object weight (Kinoshita et al., 1996).

Regarding the dimensional properties, the object width seems to have a strong influence on joint postures (Chao et al., 1989; Cooney & Chao, 1977; Harding et al., 1993). The grip force varies according to object width and many ergonomic studies have focused on the determination of the optimal object width that maximizes the grip force (Blackwell et al., 1999; Dempsey & Ayoub, 1996; Fathallah et al., 1991; Fransson & Winkel, 1991). The optimal grip width has been found to vary around 4-5 cm, depending on the posture adopted, the number of fingers involved, and the shape of the object (Blackwell et al., 1999; Dempsey & Ayoub, 1996; Fathallah et al., 1991; Fransson & Winkel, 1991). Concerning shape, elliptical objects require a relatively equal contact-pressure distribution on all fingers, whereas rectangular objects have demonstrated a contact-pressure concentration in the proximal region of the thumb, the tip of the index finger, and the proximal region on the palm. With elliptical objects, the hand can uniformly grip the object and evenly contact its entire surface (Rossi et al., 2015). In contrast, rectangular objects cause partial contact between the hand and the corners of the object and generate gaps in several places. This condition was considered to cause a pressure concentration on the three areas, which affects gripping comfort.

5.3.2 Grasping stone tools

Archaeologists often aim to assess how efficiently lithic artefacts could have been used by the different human species (Key and Lycett, 2017a; Marzke, 2013; Shea, 2007). Experimental research over the past 40 years has, for example, demonstrated that the characteristics and functionality of stone tools are influenced by their size, edge morphology and sharpness (Key and Lycett, 2014, 2015; Key et al., 2018a; Prasciunas, 2007; Walker, 1978). It has been shown that edge curvature and regularity influence the performance of scraping tools (Clarkson et al., 2015; Collins, 2008), while size, edge angle and symmetry can influence the functional capabilities of Acheulean bifaces (Key et al., 2016; Key and Lycett, 2017b; Machin et al., 2007). Moreover, the cutting edges of stone tools have an impact on how forces are distributed along this edge (Ackerly, 1978; Atkins, 2009; Key, 2016). Overall tool-size and shape attributes affect the ergonomic nature of the tool, how precisely it may be applied during cutting and how much force is required to stabilize the tool in the hand, as well as the length of utilizable cutting edge (Rossi et al., 2014; Seo and Armstrong, 2008; Toth and Schick, 2009; Wynn and Gowlett, 2018). In other words, it has been clearly demonstrated that some tool-form attributes can have a strong and statistically significant impact on a stone tool's performance during its use and this could have had a direct impact on the tool users' survival (Key and Lycett, 2017a; Shea, 2007).

It is important to note that in our studies, we have not investigated all Lower Palaeolithic stone tool variability. We have only focused on typical Oldowan choppers and Acheulean handaxes with standardized measurements. The tools we chose to use would normally be handled with the whole hand (due to their dimensions and weight). This arrangement was chosen to minimize the variability of the grips. Basically, we wanted to exclude two or three-fingers grips and only focus on whole-hand grasping. By doing this, we could better analyse the subtle differences between more similar grasping types.

We chose to focus on choppers and handaxes because particular interest has been addressed to the reason why one type or form of stone was replaced with another (Ashton and McNabb, 1994; Bar-Yosef, 1998; Ambrose, 2001; Foley and Lahr, 2003; Gowlett, 2009; Ollé et al., 2013; Shea, 2017). Some attempts to answer this question investigated hominin cognitive and anatomical capabilities (Wynn and Coolidge, 2004; Stout et al., 2008; Faisal et al., 2010; Pargeter et al.; 2019), the effect of ecological context for tool-use characteristics (Shea, 2007; Key and Lycett, 2017a), raw material economic strategies (Muller and Clarkson, 2016), and cultural transmission mechanisms (Clark, 1987; Lycett, 2010). Moreover, it has been proposed that Lower Palaeolithic technological transitions are related to improvements in the ergonomic design of stone tools (Wynn and Gowlett, 2018). The hypotheses concerning ergonomics has not been directly tested yet, but the main idea is that new stone technologies may have come to dominate over previous alternatives because of their increased ease of use when held by the hand (Key et al., 2020). Even if this concept is intuitive and reasonable, for what regards their use, the large, bifacially flaked core tools were found to be a more complex and demanding technology compared with simple Oldowan flakes (Stout et al., 2015; Key et al., 2020). In fact, Key et al. (2021) evidenced that handaxe use is more muscularly demanding compared to smaller flake tools so relatively small 'Oldowan-like' flake tools would have been easier to use during cutting tasks. Therefore, the occurrence and prolonged production of handaxes requires an alternative explanation. Functional advantages are still likely a primary cause underpinning the production of handaxes. In fact, handaxes are known to be more effective and rapid compared with flakes during heavy-duty cutting tasks (Toth and Schick, 2009, Galán and Domínguez-Rodrigo, 2014, Key and Lycett, 2017b). Finally, we should also consider the potential influence of other factors (among them cognitive factors) in promoting handaxe production (Diez-Martin et al., 2015, de la Torre, 2016, Key and Lycett, 2017b, Semaw et al., 2018, Wynn and Gowlett, 2018, García-Medrano et al., 2019, Herzlinger and Goren-Inbar, 2020).

In our survey, we found that choppers and handaxes have different patterns of phalanx flexion, with the former requiring less flexion than the latter. In the middle, ring, and little fingers, this difference is more evident than in the index finger. Among choppers, the variability of the pattern of phalanx flexion is mainly related with the flexion of the middle finger. Among handaxes, the variability of the pattern of phalanx flexion is mainly related with the little and ring fingers. The maximum dimensions of the tools are responsible for the grasping patterns. For choppers, only maximum length is a suitable predictor, while for handaxes also the maximum thickness and width can predict the pattern of flexion. In the sample that we used, handaxes are longer and thinner compared to choppers. Clearly, handaxes require more phalanx flexion because they are normally thinner than the choppers and with a more elongated shape and an approximate bilateral symmetry around the long axis (Gowlett, 2013). From a technological point of view, cutting objects such as handaxes benefit from their elongated shape because this means a longer working edge and application of work at a greater distance from the body (Gowlett, 2013). But this explanation alone is insufficient.

In an experiment with cylindrical objects with diameters varying from 3 to 6 centimetres, it was found that finger flexion at the metacarpophalangeal and proximal interphalangeal joints gradually increase as cylinder diameter decreases. Moreover, total finger force increases as cylinder size decreases (Lee and Rim, 1991). It is plausible, therefore, that the thinner shape of handaxes guarantees stronger handgrip compared to the thicker shape of the choppers. Moreover, in our sample, the difference in the thickness at the base (where tools are normally grasped) between choppers and handaxes is evident (chopper average thickness at the base= 4.33 cm; handaxe average thickness at the base=3.43 cm) and becomes even more evident in the upper parts.

Interestingly, as already mentioned, the optimal grip width which maximizes the handgrip strength has been found to vary around 4-5 cm in diameter (Blackwell et al., 1999; Dempsey & Ayoub, 1996; Fathallah et al., 1991; Fransson & Winkel, 1991). Even if the variability of lower Palaeolithic stone tool size and shape is huge, in this survey, we used artifacts with "standardized dimensions" (Emery, 2010). Therefore, at least in our sample, the stone tools have dimensions that should allow optimal grip strength and a comfortable grip. Obviously, handaxes and choppers are not cylinders and the previous sentence has to be taken with caution. We can presume that choppers or handaxes with the same average maximum length and width as ours, but with a thickness that is greater than 6-7 centimetres and less than 3-4 centimetres should be less comfortable than tools belonging to the optimal range. However, this consideration is mere supposition which would a need specific experiment to be proved.

Kong and Lowe (2005) studied the grip force on cylinders with a diameter between 2.5 and 5.0 centimetres and the relationship between perceived comfort, finger and phalange force distribution, and electromyography efficiency of finger flexor and extensor muscle activity. The total finger force, which is defined as the sum of all phalangeal segments, showed a significant inverse relationship with handle diameter as the fingers were more extended to grasp larger handles. The forces imposed by the middle finger and distal phalanges were always significantly higher than those imposed by the other fingers and phalanges, respectively. In addition, the contributions of the middle finger and distal phalange to the total finger force were increased as the handle diameter increased. Curiously, we found that the variability between choppers and handaxes is particularly influenced by the flexion of the middle fingers and that, among choppers, the proximal phalange is responsible for almost the whole variation of the grasping pattern. Nevertheless, we did not find any direct correlation between the way choppers are grasped and any measure besides chopper length. It is possible that the importance of the middle finger during chopper manipulation is related to the required force to produce optimal grasping. However, different studies (e.g. electromyography) would be necessary to prove this hypotheses.

Regarding handaxes, in our study, the variability of the grasping pattern is mainly due to the amount of flexion of the last three fingers, and it is related with object width. When handling wider handaxes, finger flexion is minor compared to the narrower. This pattern is pretty intuitive but curiously it is not present in choppers.

While, we found, handaxe morphological changes are related to an adjustment of finger flexion in order to maximize the contact between the object and the hand, regarding choppers, there are morphological constraints that do not permit this adjustment. Clearly, this preliminary observation requires more future research to establish the specific restrains that do not allow this adjustment.

The above-mentioned results could also shed light on the psychophysiological responses experienced by the subjects. When compared with choppers, handaxe tools require longer manipulation time. Handaxe morphology (in particular their width) allow a finger adjustment to obtain optimal grasping. This is not also the case for choppers. Therefore, it is possible that the tools that allow an adjustment could require more time to find a comfortable position compared to tools that do not permit morphologically-related adjustments. Handaxes need more time to be comfortably grasped because of their morphology which requires longer haptic exploration.

Concerning emotion and attention, compared to neutral or positive stimuli, a negative stimulus or unpleasant sensation exerts significantly higher averages of both responses. Among the tool variables that we correlated with the psychophysiological responses, weight is the only one that strongly influences both attention and emotion. In other words, the heavier the object the higher the attention and the emotion. The two technological groups that we used in our experiment do not differ in average weight (both handaxes and choppers have an average weight of 0.5 kg). Therefore the correlation is not biased by tool type. Therefore, there is a real correlation between tool weight and psychophysiological responses.

Also tool length, width and thickness correlate with one or the other responses. However, due to the collinearity between these factors with tool weight, we are inclined to think that weight is the main factor responsible for the changes in electrodermal activity. If this were correct, we could suppose that heavier tools are less comfortable during stone tool handling and therefore less ergonomic. Jones (1980) carried out a series of butchery experiments using various stone tools. He assessed that handaxes are more efficient than small plain flakes for most butchery tasks due to their weight, their long cutting edges, and the ease with which such tools can be held in the hand. Merrit and Peters (2018) also confirmed that bigger and heavier flakes were better for processing meat. Terradillos-Bernal and Rodríguez (2012) highlighted the importance of weight and cutting edge in cutting tasks, and proposed a model to determine the relationship between these factors and tool efficiency.

5.4 Final considerations and limitation of the study

The surveys presented here are attempts to shed light on the hand-stone tool relationship. Many studies have already investigated the biomechanical aspects of tool making and tool use. However, to date, the ergonomic aspects have not been considered. We used an experimental approach, to study finger flexion and the psychophysiological responses during stone tool comfortable handling. We found interesting differences between both, males and females and choppers and handaxes.

Regarding sexual differences, we expected that hand metrics would be responsible for the variability of grasping. In other words, we expected that regardless of the individuals' sex, individuals with similar hand dimensions would display similar flexion patterns. Our results reject this hypothesis and future studies should focus on the reason behind these differences. In fact, it would be interesting to prove if hand strength is responsible for the pattern of finger flexion.

The data glove has been shown to be a useful instrument to study the biomechanics of the hand during stone tool manipulation. The difference between the grasping of choppers and handaxes were expected. The two tool types differ in many dimensional factors that have an impact on finger flexion during comfortable handling. Future studies will consider other Lower Palaeolithic tool types with more diverse shape and dimensions. Tool use and tool production are different tasks compared to the simple handling of a tool. The grasping pattern during these activities should be evaluated.

Mental activity is structured by dynamic interactions between the brain, body, and environment (in both a physical and social sense). Humans find support in the external world through tools that become part of our cognitive and bodily capacities. There are several ways in which we can determine whether an artefact can form part of an extended mind process (Newen et al., 2018).

The electrodermal survey confirmed that the metric aspects of a stone tool influence the psychophysiological response. According to Material Engagement Theory (Malafouris, 2013 – section 1.1.2), structural changes or discontinuities in the archaeological record can reveal underlying evolutionary changes or discontinuities in the cognitive relationships between humans and material culture. Following the material engagement approach, stone tools are not a mere output of cognitive processes but they constitute (or participate in) at least some of the cognitive processes involved in the process of tool use. The changes in emotion and attention related with stone tool metrics show how humans perceive object properties, and we could infer that Lower Palaeolithic stone tool users underwent similar alterations related to tool shape, weight and metrics.

The main limitation of this study regards the use of modern humans to make inferences on Lower Palaeolithic stone tool users. At biomechanical level, the main problem is related to hand musculature. The muscle structure of the hand is a pivotal factor for tool grasping and use, and we lack information for fossil species. At psychophysiological level, the main problem is due to the fact that modern humans live in a hyper technological environment that profoundly changed our cognition and the way we interact with an object. This is the main reason why we chose not to study stone tool use or production, but we just limited the surveys to the ergonomic aspect of handling.

5.5 Future studies

Despite the increasing interest in ergonomic topics, it is clear that basic biomechanical information about the ergonomics of stone tools is still lacking. Before going any further with the application of new technology to the study of stone tools, a better understanding is needed regarding the ergonomics and functional relationship between the hand and stone tools. Therefore, in the future, it is important to assess which grasping strategies are most effective during stone tool use and production. Grasping strategies are related to the stress suffered by the hand, and the most effective, stress-reducing manual behaviours need to be highlighted because of their impact on the tool users' survival. It is important to evaluate the contribution of hand strength and experience to stone tool use and production. The influence of individuals' variability on the success of a task has pivotal evolutionary significance and needs to be evaluated. Differences between novice and expert toolmakers have already been assessed (Geribàs et al., 2010; Baena et al., 2019), demonstrating that we can deduce the presence of particular models of social production and learning processes during the Lower and Middle Palaeolithic (Torres and Baena, 2020).

It is also important to look into which grasping types are the most used during stone tool use and production. Besides the lack of information on the grasping strategies during stone tool use, there is also a general confusion concerning how this information is presented. In fact, a reorganization of the variability of stone tool grasping behaviour would be very useful.

Finally, individuals' psychophysiological aspects should be considered. An ongoing work is measuring three psychometrics traits: haptic abilities, spatial ability to mentally rotate solid figures and spatial visualization. The individuals' abilities will be related to grasping patterns in order to highlight a correlation between cognitive aspects and manipulative aspects.

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CONCLUSIONS

6. Conclusion

There is no patent evidence which suggests that hand size can determine tool grasping in the two sexes. Differences in the degree of finger flexion between males and females are therefore also due to aspects other than hand size. We suggest that handgrip strength could be responsible for the differences given that it is strongly related to sex and grasping strategies.

Choppers and handaxes show differences in finger flexion and in the single finger contribution to comfortable grasping. Handaxes allow flexion adjustment according to their shape, while choppers do not. Therefore, we suggest that choppers are less ergonomic tools than handaxes. We also propose that (due to their general dimensions) Mode 1 large unretouched flakes are more comfortable than choppers.

Handaxe morphology allows the adjustment of finger flexion and therefore it is maximizes the contact between the object and the hand. In choppers, there are morphological constraints that do not permit maximization. Therefore, we suggest that the use of choppers is less ergonomic and could produce more hand stress when compared to handaxes.

Emotional engagement and haptic cognition are part of a specialized prosthetic technological capacity of modern humans and can provide indirect evidence of cognitive discontinuities in the archaeological record. There are subtle but detectable perceptual differences when handling Oldowan and Acheulean stone tools. Tools are intimately tied to human cognitive processes. The properties of stone tools (like weight and dimensions) might have had an impact on initial development of the cognitive machinery of the prehistoric stone tool makers.

Differences in electrodermal reaction during stone tool handling between males and females are probably due to biological or cultural influences. Hand size does not influence the degree of arousal or attention during tool exploration, suggesting that other factors trigger individual reactions. These results add to a general cognitive approach on hand-tool evolution and tool sensing.

Variations associated with hand-tool interaction provide information on haptic and prosthetic capacities associated with our specialized technological resources. Perceptual changes in the archaeological record can reveal evolutionary changes in the corresponding body-tool cognitive mechanisms. The features that trigger an electrodermal reaction are the general tool size (a spatial issue), the tool weight (a gravitational issue), and the morphology of the tool base (a grasping issue). Such electrophysiological responses are supposed to be associated with cognitive brain-body feedback, and possibly with those sensing capacities that support a good prosthetic ability.

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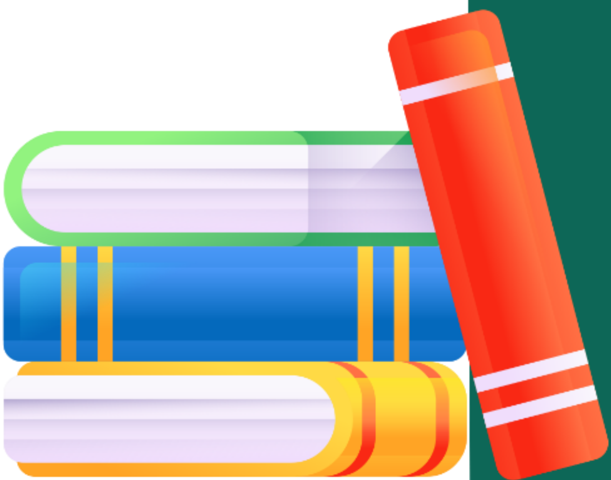

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