Does knowledge influence visual attention? A comparative analysis between archaeologists and naïve subjects during the exploration of Lower Palaeolithic tools

María Silva-Gago1,2 · Annapaola Fedato2 · Marcos Terradillos-Bernal3 · Rodrigo Alonso-Alcalde4 · Timothy Hodgson5 · Emiliano Bruner2

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Abstract
The role of experience during the exploration of lithic artefacts can be been investigated through multiple approaches. Knowledge can influence visual perception of the environment, whilst action “affordances” can be processed at the first sight of an object. In this study, we used eye tracking to analyse whether and to what extent archaeological knowledge can influence visuospatial attention whilst interacting with stone tools. Archaeologists were found to pay more visual attention to the middle region and the knapped surface. Differences between the visual exploration of choppers and handaxes were also found. Although the general pattern of distribution of the visual attention was similar to naïve subjects, participants with archaeological experience paid more attention to functionally relevant regions. Individuals with archaeological experience directed more attention to the upper region and the knapped surface of the tools, whilst naïve participants spent more time viewing the middle region. We conclude that although both groups could direct their attention to action relevant features in stone tools, functional affordances had a greater effect in subjects with previous experience. Affordances related to manipulation triggered lower attention and showed no differences between participants.

Keywords Eye-tracking · Affordances · Cognitive archaeology · Lithic technology · Visual exploration

Introduction
Stone tools have been part of human culture for over two million years and have influenced our evolutionary history (Semaw et al. 2003). Therefore, they have been generally used to define the genus Homo (Ambrose 2001; Federico and Brandimonte 2019). Tools are objects defined by their intrinsic properties that afford manipulability and their interaction with the environment (Rüther et al. 2014). Indeed, tools have been described as problem-solving objects attached to the body, which amplify and enhance the user’s abilities (Federico and Brandimonte 2019; Federico et al. 2021a, b; Wagman and Carello 2003). Tool use requires the integration of three types of information, namely technical reasoning, semantic knowledge and sensorimotor processing (Federico et al. 2021a). In this sense, using a tool means being functionally dependent on the cognitive system, sensorimotor integration and reasoning chains (Bruner and Gleeson 2019). Neuroimaging studies also suggest that simply viewing tools activates a specific neural network, including brain areas associated with the motor system (Johnson-Frey 2004; Craighero et al. 1997; Creem-Regehr and Lee 2005; Vingerhoets et al. 2009; Makris et al. 2011). In contrast, other perspectives propose that a tool does not automatically trigger action behaviours and that explicit structural and functional knowledge-based representations of the tool must be elaborated, although evidence for activation of knowledge representations by tools is limited (Osiurak et al. 2020).

Perceiving the environment is thought to automatically provide information regarding how humans can interact with it through affordance mechanisms (Foerster and Goslin 2021).
Multiple definitions have been offered to describe this phenomenon. Initially, the term affordance referred to all action possibilities of the environment (Gibson 1979). At present, the concept refers to a characteristic of an object that informs and allows a subject to perform an action (Vingerhoets et al. 2009; Makris et al. 2011; Turvey and Carello 2011; Borghi 2007; but see also Osiurak et al. 2017). Such affordances might drive the eyes and visuospatial attention towards the regions of the tool that are most relevant to its action, such as the most comfortable grip position or the striking surface (Myachykov et al. 2013; Roberts and Humphreys 2011). From an archaeological point of view, affordances have been defined as opportunities, resources and constraints detected in the materials and the environment through active exploration (Pargeter et al. 2020; Wynn 2020). Following a neuropsychological perspective, affordance has also been described as a link between the perceived visual properties of an object and an action that may be performed with it (Humphreys and Riddoch 2001). This relationship might be based on stored information, but might also be directly guided by the visual features of an object, even if the object has never before been observed. That is, affordance perception depends on the visual processing of the structural properties of objects (Vingerhoets et al. 2009; Proverbio et al. 2011).

The perception of affordances is an involuntary daily act that can both be perceived at the early sight of an object (Makris et al. 2011; Rüther et al. 2014) or be learned from previous experience (Borghi et al. 2012; Jacquet et al. 2012). There are some aspects to be acquired such as the exact practise of using the tool or the way it is handled (Rüther et al. 2014). There is currently a theoretical debate about the use of tools. Some approaches focus on sensory processing and other perspectives emphasise conceptual reasoning. According to the first viewpoint, there exists two types of tool-related action knowledge, structural action knowledge and functional action knowledge (Binkofski and Buxbaum 2013). The former concerns the gestures on how to grasp a tool, based in motor information, and is directed to the processing of tool properties such as shape or size; the latter refers to information about how to use a tool for a purpose and commonly associated actions, including stored knowledge (Federico and Brandimonte 2019; Ni et al. 2019). Although these two mechanisms work simultaneously, functional knowledge is dominant during tool interaction (Ni et al. 2019). Nevertheless, functional knowledge of objects may not be a prerequisite for the activation of affordances (Xu and Heike 2017). Other perspectives suggest that structural features or manipulation can be related to sensorimotor processing and embodied theories of cognition, whilst functional knowledge is associated to semantic and abstract information (Osiurak and Federico 2021). Consequently, functional knowledge is a type of semantic knowledge which facilitates mechanical actions (Federico and Brandimonte 2019; Federico et al. 2021a). In a sense, mechanical knowledge (also called technical reasoning) has been proposed to connect the semantic and the sensorimotor information through physical principles (Osiurak et al., 2017; Federico et al. 2021a, b). According to this view, a reasoning process starts with semantic information, moving on to mechanical and finally sensorimotor information (Federico et al. 2021b; Osiurak et al. 2020). In other words, the activation of the sensorimotor pathways includes perceptual and semantic information (Wurm and Caramazza, 2019).

The main kinds of knowledge described can be related to the well-known distinction proposed in tool making between knowledge of a savoir-faire (Pelegrin 1993). The former refers to the abstract knowledge of the procedures necessary to achieve an objective, whilst the latter refers to the concrete knowledge required to implement these procedures (Pargeter et al. 2020). In this sense, the influence of knowledge and expertise has been broadly investigated from an archaeological perspective (e.g., Geribás et al. 2010; Pargeter et al. 2019; Rivero and Garate 2020; Stout et al. 2011; Williams-Hatala et al. 2020). Experimental studies focusing on knapping have revealed differences between naïve individuals and experts in terms of brain activation, gestures, kinematics, flake size and flake distribution or prediction (Bril et al. 2010; Geribás et al. 2010; Lombao et al. 2017; Nonaka et al. 2010; Pargeter et al. 2020; Stout et al. 2011; Torres and Preysler 2020; Williams-Hatala et al. 2020; Zorrilla-Revilla et al. 2021). Specifically, neuroscience studies show that naïve individuals relied more on bottom-up strategies of visual attention during tool production, whilst experts employed a top-down approach associated with parietal activation (Stout et al. 2011). Expert archaeologists can perceive more relevant functional relationships during knapping than novice individuals, who can only identify basic significant parameters (Bril et al. 2010).

Certain key regions in tools can be considered as constituting affordances and their perception is strongly related to vision, because it is the main source of sensory information in humans (Atkinson 2008; Kassuba et al. 2013; Stone and Gonzalez 2015). Indeed, humans are evolutionarily specialised experts in eye-hand coordination and have possibly experienced a specific visuospatial enhancement (Bruner et al. 2018a; Vaesen 2012). As part of the visuospatial system, affordance processing is associated with the activity of the parietal lobes (Bruner and Iriki 2016; Natraj et al. 2018; Rüther et al. 2014), which show derived evolutionary features in the human brain (Bruner 2018, a, b; Bruner et al. 2018a,b; Pereira-Pedro et al. 2020). In this sense, different visuospatial behaviours have been hypothesised for past human species (Bruner 2021; Bruner and Lozano 2014; Bruner and Iriki 2016; Burke 2012). The exploration of these indirect behavioural traces can be carried out through eye tracking technology and the analysis of the visuospatial attention allocated in different regions of a scene. For
instance, visual perception has recently been explored in archaeological artefacts, suggesting that objects influence the way people pay attention to them (Criado-Boado et al. 2019; Silva-Gago et al. 2021a; 2022b). In particular, stone tools trigger attention towards those parts that can be interpreted as affordances (Silva-Gago et al. 2022).

In previous studies, we explored visual attention during a free observation of stone tools and during tool physical manipulation, applying eye tracking technology to examine the visual exploration of experimental stone tools in naïve individuals (Silva-Gago et al. 2021a). In these studies, subjects with no archaeological knowledge were selected in order to avoid the influence of expert knowledge of tool functions, and to focus the analysis on spontaneous visual responses only. Knowledge can influence this reaction, involving reasoning on possible functions and planning or executive functioning. Hence, in the present survey, the same explorative behaviour was analysed in expert archaeologists and compared with the results of the previous study (Silva-Gago et al. 2021a). The aim of this survey was to evaluate the experience bias during the exploration of stone tools, by analysing whether the pattern of visuospatial attention was different between naïve participants and subjects with prior archaeological knowledge.

**Material and methods**

**Participants**

Thirty-one participants (16 females and 15 males) took part in the experiment. All subjects had normal or corrected-to-normal vision; they were right-handed according to Oldfield Questionnaire (Oldfield 1971) and aged between 26 and 43 years old (mean and s.d.: 34 ± 7). They were archaeologists with at least postgraduate studies in Palaeolithic archaeology or human evolution. The sample included students who had completed the master’s degree, PhD candidates and researchers with more than 5 years’ experience. All subjects signed an informed consent for their participation in the study, which was approved by the ethical committee of the University of Burgos. All trials were performed under the same environmental and experimental conditions in a laboratory, where the participants were seated 50 cm away in front of a platform where the stone tools were displayed. Subjects were allowed to place their hands on the table without touching the platform.

**Experimental design**

We employed the same sample and methodology used in a previous study (Silva-Gago et al. 2021a), in order to compare the results. We tested the visual exploration behaviour for the same 40 experimental stone tools (20 choppers and 20 handaxes) used in the preceding analysis (Silva-Gago et al. 2021a). These tools were chosen because they show clear technological differences, can be grasped with the whole hand and are representative of the most iconic elements of earliest technologies, despite the still present debate about whether they were tools or cores (Baena Preysler et al. 2018; Peretto et al. 1998; Shea 2020; Venditti et al. 2021). Stone tool diameters can be found at Silva-Gago et al. (2021a).

The experimental procedure consisted of tracking eye movements whilst participants were visually exploring and manipulating the stone tools. First, each tool was placed on a platform in front of the participants and positioned along its technological axis, showing the more knapped side, for approximately 5 s. Then, participants had to manipulate the stone tool until they reached an ergonomic grip in their right hand. Eye movements were recorded with a portable eye tracker (Pupil Core, Pupil Labs, Berlin, Germany) sampling participants’ pupil position at 500 Hz. Eye position was calibrated through the fixation of five predefined dots that were sequentially presented on a screen. Two additional tools were also added before each recording session as a familiarisation procedure and were not included in the analysis.

**Data analysis**

Video recordings were analysed using Pupil Player software (version 2.0.182). We consider the fixation record for each stone tool and measured the dwell time (DT, in milliseconds) per area of interest (AOI). The same AOI described in the previous study (Silva-Gago et al. 2021a) was defined, namely the upper, the middle region or tool body and the base, as well as cortex and knapped surface. In the manipulation task, we added a new area, called edges, which consist of the sharp border when the tool is oriented in side view (Fig. 1). Then, each fixation was associated with a tool region and surface. We summed the dwell time in each tool region and computed the median duration of the fixation for the different areas as an indirect measure of the amount of visuospatial attention allocated by participants to different parts of the visual scenario (Federico and Brandimonte 2019).

Results included the tool visual-only exploration and the visual perception whilst the tool is physically manipulated. Then, we compared the current results of archaeologists with the data from the previous study carried out with naïve subjects (Silva-Gago et al. 2021a). A Mann–Whitney test and Kruskal–Wallis test were run between tool regions and between groups in order to test differences. Differences were also tested between males and females. All data were analysed using PAST 3.20 (Hammer et al. 2001).
Results

When comparing the different tool regions of the complete tool sample (choppers and handaxes) during the archaeologists visual-only exploration (Fig. 2), the middle region triggered more attention than the upper region and the tool base ($H = 49, p < 0.0001$). During manipulation, the middle region also attracted more attention than the upper region, followed by the tool base ($H = 61.3, p < 0.0001$). Comparing knapped and cortex surfaces of the overall sample, knapped areas elicited more attention than the cortex during visual exploration ($U = 6, p < 0.0001$) and also during the manipulation task ($U = 84, p < 0.0001$). If we separate choppers and handaxes, all regions showed significant differences between the two stone tools. Handaxes were more observed in the middle region ($U = 374, p = 0.01$), tool base ($U = 317, p = 0.001$) and knapped surface ($U = 209, p < 0.001$), whilst choppers were more explored at the upper region ($U = 299, p < 0.001$) and cortex ($U = 390, p = 0.02$). Sex differences were not found for any area of interest, neither during visual exploration nor during manipulation ($p > 0.05$).

Figure 3 shows the distribution of the dwell time during visual exploration in archaeologists and naïve subjects. Archaeologists directed their attention more to the upper region and knapped surface, whilst naïve individuals directed more attention to the tool body. Tool base and cortex showed no differences. During the manipulation task, archaeologists also paid more attention to the top and the edges of the tool (Table 1). Other areas showed no statistical differences. If we consider the tool groups separately, we also found differences between archaeologists and naïve subjects (Table 2). Figure 4 shows the percentages of dwell time dedicated to each area of interest. When comparing archaeologists and naïve people together, there were differences in terms of the amount of time allocated to each tool area ($p < 0.05$). During visual exploration, archaeologists spent more time observing the upper and middle region of the tool, as well as the knapped surface in both choppers and handaxes. Naïve individuals directed their attention more to the body of the tool. Base and cortex did not show any statistical differences. During the manipulation task, archaeologists paid more attention to the upper region in both tool types. Moreover, they also spent more time observing the knapped surface in handaxes and the edges in choppers. Other areas did not show any statistical differences.

Discussion

Experience plays an important role during interaction with the environment. Previous studies have shown that activation of action affordances is dependent on the prior visual
processing of an object’s properties (Xu and Heinke 2017; Makris et al. 2011; Rüther et al. 2014; Vingerhoets et al. 2009; Proverbio et al. 2011), although knowledge can also influence the way subjects perceive objects (Noorman et al. 2018). In fact, theories of tool use involve two distinct approaches: “manipulation-based” models, which emphasise the role of sensorimotor processing, and “reasoning-based” perspectives, which refer to semantic knowledge and technical reasoning (Federico et al. 2021a). According to the former approach, knowledge can be divided into structural action knowledge, associated to how to use a tool, and functional action knowledge, related to the purpose (Binkofski and Buxbaum 2013; Ni et al. 2019). Both functional and manipulation information is part of the artefact concept (Cosentino 2021). In this sense, two main kinds of affordances have been suggested, related to function or manipulation reasoning (Cosentino 2021). Stable or standard affordances, associated to the activation of the parietal and frontal cortex, deal with functions; whilst variable or ad-hoc affordances, whose network is localised in the dorsal stream, deal with manipulation knowledge (Cosentino 2021; Sakreida et al. 2016). On the other hand, technical reasoning focuses on the rationale about the physical properties of tools to solve common tasks, rather than passively perceiving information about how to interact with them (Federico et al. 2021b). According to this point of view, the functional information of the tool involves the conceptual level, whilst the manipulative region is related to the sensorimotor information (Osiurak et al. 2020). Therefore, the activation of action affordances needs the visual processing of both kinds of information.

Our first studies on the visual perception of stone tools suggested that individuals naïve to archaeology identified affordances at first sight and during physical interaction (Silva-Gago et al. 2021a). However, previous experience influenced the way people perform an action, as revealed from different archaeological perspectives (Geribás et al. 2010; Pargeter et al. 2019; Rivero and Garate 2020; Stout et al. 2011; Williams-Hatala et al. 2020). Hence, the aim of this second study was to analyse whether the pattern of visual attention in stone tools was different between naïve participants and participants with archaeological knowledge.

In the analysis of experienced participants, the central area was the most observed region, followed by the upper regions (tip or cutting edge) and tool base. In addition, the knapped surface also triggered more attention than the cortex. This pattern of visual exploration can be explained by the attention directed to functional regions (Ambrosini and Costantini 2016; Federico and Brandimonte 2019; Land 2006; Natraj et al. 2015), despite the tendency to look at the centre of objects (Ioannidou et al. 2016; Tatler 2007; Tseng et al. 2009). In general, the information needed to process the mechanical action provided by the functional part of the tool is accessed first, and then the information needed to execute the motor action involving the manipulative part can be focused on (Osiurak et al. 2020). Other
reasons may be related to the experts’ training of studying knapped areas because they show technological information on tool-related behaviour. Furthermore, differences between choppers and handaxes were also observed. Archaeologists directed more attention to the upper region and cortex in handaxes, and to the middle region, base and knapped surfaces in handaxes. Choppers showed a simpler morphology and they may require less attention related with the grasping strategy. In contrast, handaxes had more complex shape and more grasping and use possibilities. Hence, they may need a higher exploration of its base, where they would be grasped (García-Medrano et al. 2014; Gowlett 2006; Key et al. 2016). Additionally, there were no differences in the visual exploration patterns whether or not the tools are physically manipulated, and there were no significant differences between males and females.

Overall, the general pattern of visual attention in individuals with archaeological knowledge is similar to the naïve participants (Silva-Gago et al. 2021a), but with minor local differences. The most observed regions were the same in both groups. Despite the centre bias, functional and action-relevant areas triggered more visual attention instead of handling regions (Ambrosini and Costantini 2016; Federico and Brandimonte 2019; Foerster and Goslin 2021; Xu and Heinke 2017). However, when analysed together, the results from naïve individuals and archaeologists show significant differences in some areas of interest. It is worth noting that, for the manipulation task, we have included an area consisting of dwell time directed to the tools’ edges for both participant groups. In general, individuals with archaeological experience directed more attention to the upper region and the knapped surface of the tools during

| Task        | Tool   | Area of interest | Arch | Naive | $U$ test | $p$ value |
|-------------|--------|-----------------|------|-------|---------|-----------|
| Vision-only | Handaxes | Upper           | 1247 | 556   | 284     | < 0.001   |
|             |        | Middle          | 2168 | 2757  | 418     | 0.014     |
|             |        | Base            | 813  | 518   | 515     | 0.171     |
|             |        | Knapped         | 4095 | 3686  | 348     | < 0.001   |
|             |        | Cortex          | 561  | 698   | 492     | 0.104     |
|             | Choppers| Upper           | 2173 | 996   | 342     | < 0.001   |
|             |        | Middle          | 1806 | 2603  | 441.5   | 0.028     |
|             |        | Base            | 261  | 210   | 575.5   | 0.490     |
|             |        | Knapped         | 3390 | 2565  | 378     | 0.003     |
|             |        | Cortex          | 1094 | 1232  | 496     | 0.114     |
| Manipulation| Handaxes | Upper           | 649  | 231   | 195.5   | < 0.001   |
|             |        | Middle          | 2881 | 2563  | 541     | 0.285     |
|             |        | Base            | 459  | 486   | 629     | 0.945     |
|             |        | Knapped         | 3574 | 2662  | 422     | 0.015     |
|             |        | Cortex          | 605  | 701   | 620     | 0.865     |
|             |        | Edges           | 396  | 201   | 478.5   | 0.074     |
|             | Choppers| Upper           | 1533 | 1082  | 409     | 0.010     |
|             |        | Middle          | 1722 | 1850  | 606     | 0.742     |
|             |        | Base            | 133  | 224   | 535     | 0.247     |
|             |        | Knapped         | 2228 | 1908  | 477     | 0.072     |
|             |        | Cortex          | 1057 | 1373  | 590     | 0.609     |
|             |        | Edges           | 56   | 0     | 427     | 0.010     |

![Fig. 4](image_url) Comparison between archaeologist and naïve individuals in terms of percentages of dwell time (DT) according to each tool area of interest during visual exploration. Knapped and cortex surfaces are shown on the left of the tool, whilst upper, middle and base regions are shown on the right.
its visual exploration, whilst naïve participants spent more time on the middle region. In the manipulation task, the upper region and the tool’s edges attracted more attention for archaeologists. The pattern of visual exploration for choppers and handaxes also showed differences for individuals naïve to archaeology and experts. In the visual-only task, there were significant differences for both tool technologies in the upper, middle region and the knapped surface. In both cases, experienced individuals directed more attention to the upper region and knapped surfaces in handaxes and choppers, whilst naïve individuals spent more time observing the middle region of both tools. In this sense, during passive viewing, participants naïve to archaeology are more affected by the centre bias (Ioannidou et al. 2016; Tatler 2007; Tseng et al. 2009). During the physical manipulation of the tool, archaeologists directed more attention to the upper region and the knapped surface in handaxes, and to the upper region and edges in choppers. Hence, participants with archaeological knowledge paid more attention to the functional regions of stone tools, following a top-down perceptual mechanism (Stout et al. 2011), and were able to identify the most complex significant features (Bril et al. 2010; Nonaka et al. 2010).

Whether we consider that previous experience is related to conceptual or functional information, expert archaeologists have more semantic knowledge about Lower Palaeolithic tools compared to naïve participants (Federico et al. 2021a, b). Additionally, sensorimotor information is associated to manipulation knowledge, which is not affected by experience (Federico and Brandimonte 2019). In this sense, experienced participants have knowledge of stone tools, so they can process the tool faster. They need less effort to solve the motor control question (manipulation), directing a lower number of fixations to the centre and manipulative areas. Therefore, gaze remains more fixed on the functional regions of the stone tools. According to the technical reasoning theories of tool use, the perception of the environment is based on the interaction of sensorimotor, technical and semantic knowledge (Federico et al. 2021a). Subsequently, an action reappraisal mechanism has been proposed, which refers to a “semantic-mechanical-motor cascade system” that first generates the mechanical actions and then imposes constraints on the motor actions selected to perform a task (Federico et al. 2021b). However, familiarity with an object or tool causes functional areas to attract less attention whilst fixations on manipulative areas remain constant (Federico and Brandimonte 2019; Federico et al. 2022). Accordingly, previous experience only affects the amount of visuospatial attention on the functional areas (Federico et al. 2022). Despite the expertise on stone tools, archaeologists directed more visuospatial attention to functional areas although the semantic processing decreased. These evidences can refer to different levels of information or knowledge (i.e. affordances, semantics) which affects the tool visual exploration in an integrative way (Bar et al. 2006; Lambon-Ralph et al. 2017; Wurm and Caramazza 2019).

To summarise, although visual behaviour was similar in expert and naïve subjects, there were differences concerning the proportion of attention directed to specific areas. Therefore, knowledge or experience influences the visual behaviour of stone tools. Archaeologists directed more visuospatial attention to the functional aspects of stone tools (tip, knapped surface or edges). Haptic or sensorimotor interaction (Fedato et al. 2019, 2020; Silva-Gago et al. 2021b) is not affected by experience, and hence is apparently considered less central to the experts’ visual exploration. In other words, knowledge causes the visual exploration and processing of the tool to focus on the possible functions to be performed with it. The affordances related to manipulation, and, hence, manual processing can be considered more inherent to the Lower Palaeolithic stone tools.

**Conclusion**

The differences between expert and novice individuals have been broadly explored during stone tool-making and tool use (e.g. Geribás et al. 2010; Pargeter et al. 2019; Stout et al. 2011; Williams-Hatala et al. 2020). However, the role of the visual system in stone tool handling has been rarely explored, even though identifying relevant features is a key requirement for making and using a stone tool (Geribás et al. 2010; Nonaka et al. 2010). Perception is a cognitive activity that is mainly carried out through vision, in order to associate action and body-environment relationships (Atkinson 2008; Kassuba et al. 2013; Stone and Gonzalez 2015). In fact, the main way to identify action affordances in objects is through vision (Makris et al. 2011; Turvey and Carello 2011). This study explored visual behaviour whilst interacting with stone tools. The results suggest the processing of different kinds of affordances according to whether the user did or did not have any archaeological experience. Whilst naïve individuals directed more attention to the tool body due to a centre or centre of gravity bias, archaeologists focused more on functional areas such as edges and upper regions. Grasping affordances triggered lower attention and showed no differences amongst participants. In this sense, functional parameters of tools are more significant for experienced people, whilst the affordances related to manipulation are considered more elementary and therefore easier to identify. Hence, we can speculate that grasping information is more deeply rooted in our relation with stone tools (Key et al. 2018) since it does not depend on previous experience. However, the relatively small differences in the distribution of visual attention might suggest a stronger role for action
affordances, rather than experience and knowledge in controlling visual attention.

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Declarations

Ethics approval All procedures performed were in accordance with the ethical standards of the institutional and/or national research committee and with the 1964 Helsinki Declaration and its later amendments or comparable ethical standards.

Consent to participate Informed consent was obtained from all the individual participants included in the study.

Consent for publication Publication consent was obtained from all individual participants included in the study.

Conflict of interest The authors declare no competing interests.

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References

Ambrose SH (2001) Paleolithic technology and human evolution. Science 291:1748–1753
Ambrosini E, Costantini M (2016) Body posture differentially impacts on visual attention towards tool, graspable, and non-graspable objects. J Exp Psychol Hum Percept Perform 42:360–370. https://doi.org/10.1037/xhp0000330
Atkinson J (2008) The developing visual brain. Oxford University Press
Baena Preysler J, Torres Navas C, Sharon G (2018) Life history of a large flake biface. Quatren Sci Rev 190:123–136. https://doi.org/10.1016/j.quascirev.2018.04.015
Bar M, Kassam KS, Ghuman AS et al (2006) Top-down facilitation of visual recognition. PNAS 103(2):449–454. https://doi.org/10.1073/pnas.0507062103
Binkofski F, Buxbaum LJ (2013) Two action systems in the human brain. Brain Lang 127:222–229. https://doi.org/10.1016/J.BANDL.2012.07.007
Borghi AM (2007) Object concepts and embodiment: why sensorimotor and cognitive process cannot be separated. J Exp Psychol Gen 135:1–11
Borghi AM, Flumini A, Natraj N, Wheaton LA (2012) One hand, two objects: emergence of affordance in contexts. Brain and cognition. https://doi.org/10.1016/j.bandc.2012.04.007
Bril B, Rein R, Nonaka T et al (2010) The role of expertise in tool use: skill differences in functional action adaptations to task constraints. J Exp Psychol Hum Percept Perform 36:825–839. https://doi.org/10.1037/A0018171
Bruner E (2018) Human paleoneurology and the evolution of the parietal cortex. Brain, Behaviour and Evolution 91:136–147
Bruner E, Iriki A (2016) Extending mind, visuospatial integration, and the evolution of the parietal lobes in the human genus. Quaernt Int 405:98–110. https://doi.org/10.1016/j.quaint.2015.05.019
Bruner E, Lozano M (2014) Extended mind and visuo-spatial integration: three hands for the Neanderthal lineage. J Anthropol Sci 92:273–280
Bruner E (2021) Evolving human brains: paleoneurology and the fate of Middle Pleistocene. J Archaeol Method Theory. https://doi.org/10.1007/s10816-020-095008
Bruner E, Gleeson BT (2019) Body cognition and self-domestication in human evolution. Front Psychol 10. https://doi.org/10.3389/fpsyg.2019.01111
Bruner E, Fedato A, Silva-Gago M et al (2018a) Visuospatial integration and hand-tool interaction in cognitive archaeology. In: Hodgson T (ed) Processes of Visuospatial Attention and Working Memory. Curr Top Behav Neurosci 41:13–36
Bruner E, SpinaPoliCE, Burke A, Overmann KA (2018b) Visuospatial integration: paleoanthropological and archaeological perspectives. In Di paolo LD, DI Vincenzo F, De Petrillo F (eds) Evolution of Primates Social Cognition. Springer, pp 299–326.
Burke A (2012) Spatial abilities, cognition and the pattern of Neanderthal and modern human dispersals. Quatern Int 247:230–235
Cosentino E (2021) Artifacts and affordances. Synthese 198:4007–4026. https://doi.org/10.1007/s11229-019-02297-4
Craigierho L, Fadiga L, Umittà CA, Rizzolatti G (1997) Evidence for visuomotor priming effect. NeuroReport 8:347–349. https://doi.org/10.1097/00001756-199612200-00068
Creem-Regehr SH, Lee JN (2005) Neural representations of graspable objects: are tools special? Cogn Brain Res 22:457–469. https://doi.org/10.1016/j.cogbrainres.2004.10.006
Criado-Boado F, Alonso-Pablos D, Blanco MJ, et al (2019) Coevolution of visual behaviour, the material world and social complexity, depicted by the eye-tracking of archaeological objects in humans. Sci Rep 9. https://doi.org/10.1038/s41598-019-39661-w
Fedato A, Silva-Gago M, Terradillos-Bernal M et al (2020) Hand morphometrics, electrodermal activity, and stone tools haptic perception. Am J Hum Biol 32:e23370. https://doi.org/101002/ajhb.23370
Fedato A, Silva-Gago M, Terradillos-Bernal M et al (2019) Hand morphology, electrodermal activity, and stone tools haptic perception. Am J Hum Biol 32:e23370. https://doi.org/101002/ajhb.23379
Federico G, Osirak F, Brandimonte MA (2021) Hazardous tools: the emergence of reasoning in human tool use. Psychol Res 85(8):3108–3118. https://doi.org/10.1007/s00426-020-01466-2
Federico G, Osirak F, Reynaud E, Brandimonte MA (2021) Semantic congruency effects of prime words on tool visual exploration. Brain Cogn 152:105758. https://doi.org/10.1016/j.bandc.2021.105758
Federico G, Brandimonte MA (2019) Tool and object affordances: an ecological eye-tracking study. Brain and Cognition.https://doi.org/10.1016/j.bandc.2019.103582
Federico G, Osirak F, Brandimonte MA, Salvatore M, Cavaliere C (2022) The visual encoding of graspable unfamiliar objects. Psychol Res. https://doi.org/10.21033/rs.3.rs-766686/v1

Foerster FR, Goslin J (2021) Tool use and function knowledge shape visual object processing. Biol Psychol 164:108143. https://doi.org/10.1016/j.biopsycho.2021.108143

García-Medrano P, Ollé A, Mosquera M et al (2014) The earliest Acheulean technology at Atapuerca (Burgos, Spain): oldest levels of the Galería site (GH Unit), Quatern Int 353:170–194. https://doi.org/10.1016/j.quaint.2014.03.053

Geribàs N, Mosquera M, Vergès JM (2010) What novice knappers have to learn to become expert stone toolmakers. J Archaeol Sci 37:2857–2870. https://doi.org/10.1016/j.jas.2010.06.026

Gibson JJ (1979) The ecological approach to visual perception. Psychology Press

Gowlett JAJ (2006) The elements of design form in Acheulian bifaces: modes, modalities, rules and language. In: Goren-Inbar N, Sharon G (eds) Axe Age: Acheulian Tool-making from Quarry to Discard. Equinox, London, pp 203–221

Hammer DAT, Ryan PD, Hammer Ø, Harper DAT (2001) Past: paleontological statistics software package for education and data analysis

Humphreys GW, Jane Riddoch M (2001) Detection by action: neuropsychological evidence for action-defined templates in search. Nature Neuroscience 2001 4:1 4:84–88. https://doi.org/10.1038/82940

Ioannidou F, Hermens F, Hodgson TL (2016) The central bias in day to day viewing. J Eye Mov Res 9:5–6. https://doi.org/10.16910/jemr.9.6.6

Jacquet PO, Chambron V, Borghi AM, Tessari A (2012) Object affordances tune observers’ prior expectations about tool-use behaviors. PLoS ONE 7:e39629. https://doi.org/10.1371/journal.pone.0039629

Johnson-Frey SH (2004) The neural bases of complex tool use in humans. Trends Cogn Sci 8:71–78. https://doi.org/10.1016/j.tics.2003.12.002

Kassuba T, Klinge C, Hölic C et al (2013) Vision holds a greater share in visuo-haptic object recognition than touch. Neuroimage 65:59–68. https://doi.org/10.1016/j.neuroimage.2012.09.054

Key A, Profitti T, Stefanì E, Lycett SJ (2016) Looking at handaxes from another angle: assessing the ergonomic and functional importance of edge form in Acheulian bifaces. J Anthropol Archaeol 44:43–55. https://doi.org/10.1016/j.jaah.2016.08.002

Key A, Merritt SR, Kitwell TL (2018) Hand grip diversity and frequency during the use of Lower Palaeolithic stone cutting-tools. J Hum Evol 125:137–158. https://doi.org/10.1016/j.jhevol.2018.08.006

Land MF (2006) Eye movements and the control of actions in everyday life. Progress in Retinal and Eye Research

Lombao D, Guardiola M, Mosquera M (2017) Teaching to make stone tools: new experimental evidence supporting a technological hypothesis for the origins of language. Scientific Reports 2017 7:1:7.1–14. https://doi.org/10.1038/s41598-017-14322-y

Makris S, Hadar AA, Yarrow K (2011) Viewing objects and planning actions: on the potentiation of grasping behaviours by visual objects. Brain Cogn 77:257–264. https://doi.org/10.1016/j.bandc.2011.08.002

Myachykov A, Ellis R, Cangelosi A, Fischer MH (2013) Visual and linguistic cues to graspable objects. Exp Brain Res 229:545–559. https://doi.org/10.1007/s00221-013-3616-z

Natraj N, Pella YM, Borghi AM, Wheaton LA (2015) The visual encoding of tool–object affordances. Neuroscience 310:512–527. https://doi.org/10.1016/j.neuroscience.2015.09.060

Natraj N, Alterman B, Basunia S, Wheaton LA (2018) The role of attention and saccades on parietofrontal encoding of contextual and grasp-specific affordances of tools: an ERP study. Neuroscience 394:243–266. https://doi.org/10.1016/j.neuroscience.2018.10.019

Ni L, Liu Y, Yu W (2019) The dominant role of functional action representation in object recognition. Experimental Brain Research 2018 237:2 237:363–375. https://doi.org/10.1007/s00221-018-5426-9

Nonaka T, Bril B, Rein R (2010) How do stone knappers predict and control the outcome of flaking? Implications for understanding early stone tool technology. J Hum Evol 59:155–167. https://doi.org/10.1016/j.jhevol.2010.04.006

Noorman S, Neville DA, Simanova I (2018) Words affect visual perception by activating object shape representations. Scientific Reports 2018 8:1 8:1–10. https://doi.org/10.1038/s41598-018-32483-2

Oldfield RC (1971) The assessment and analysis of handedness: the Edinburgh inventory. Neuropsychologia 9(1):97–113. https://doi.org/10.1016/0006-352-90640-7

Osirak F, Federico G (2021) Four ways of (mis-)conceiving embodiment in tool use. Synthese 199:3853–3879. https://doi.org/10.1007/s11229-020-02960-1

Osirak F, Rossetti Y, Badets A (2017) What is an affordance? 40 years later. Neurosci Biobehav Rev 77:403–417

Osirak F, Federico G, Brandimonte MA, Reynaud E, Leosoud M (2020) On the temporal dynamics of tool use. Front Hum Neurosci 14:579378. https://doi.org/10.3389/fnhum.2020.579378

Pargeter J, Kreisheh N, Stout D (2019) Understanding stone tool-making skill acquisition: experimental methods and evolutionary implications. J Hum Evol 133:146–166. https://doi.org/10.1016/j.jhevol.2019.05.010

Pargeter J, Kreisheh N, Shea JJ, Stout D (2020) Knowledge vs. know-how? Dissecting the foundations of stone knapping skill. J Human Evol 145:102807. https://doi.org/10.1016/j.jhevol.2020.102807

Pelegrin J (1993) A framework for analysing prehistoric stone tool manufacture and a tentative application to some early stone industries. In: Berthelet A, Chavaillon J (eds) The use of tools and technology in tool use. Clarendon Press, Oxford, pp 302–314

Pereira-Pedro AS, Bruner E, Gunz P, Neubauer S (2020) A morphometric comparison of the parietal lobe in modern humans and Neanderthals. J Hum Evol 142:102770. https://doi.org/10.1016/j.jhevol.2020.102770

Peretto C, Amore FO, Antoniazzi A, et al (1998) L’industrie lithique de Ca’Belvedere di Monte Poggiolo : Stratigraphie, matière première, typologie, remontages et traces d’utilisation

Prouvost AM, Adorai R, D’Aniello GE (2011) 250 ms to code for action affordance during observation of manipulable objects. Neuropsychologia 49:2711–2717. https://doi.org/10.1016/j.neuropsychologia.2011.05.019

Ralph MA, Jeffries E, Patterson K, Rogers TT (2017) The neural and computational bases of semantic cognition. Nat Rev Neurosci 18(1):42–55. https://doi.org/10.1038/nrn.2016.150

Rivero O, Garate D (2020) Motion and gesture: analysing artistic skills in Palaeolithic art. Journal of Archaeological Method and Theory 2020 27:3 27:561–584. https://doi.org/10.1007/S10816-020-09476-5

Roberts KL, Humphreys GW (2011) Action relations facilitate the identification of briefly-presented objects. Atten Percept Psychophys 73:597–612. https://doi.org/10.3758/s13414-010-0043-0

Rüther NN, Tettamanti M, Cappa SF, Bellebaum C (2014) Observed manipulation enhances left fronto-parietal activations in the processing of unfamiliar tools. PLoS ONE 9:e94901. https://doi.org/10.1371/journal.pone.0094901

Sakreida K, Effertt I, Thill S et al (2016) Affordance processing in segregated parieto-frontal dorsal stream sub-pathways. Neurosci Biobehav Rev 69:89–112. https://doi.org/10.1016/j.neubiorev.2016.07.032
