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Review

'*Snakes and ladders*' in paleoanthropology: From cognitive surprise to skillfulness a million years ago

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ABSTRACT

A paradigmatic account may suffice to explain behavioral evolution in early *Homo*. We propose a parsimonious account that (1) could explain a particular, frequently-encountered, archeological outcome of behavior in early *Homo* — namely, the fashioning of a Paleolithic stone 'handaxe' — from a biological theoretic perspective informed by the free energy principle (FEP); and that (2) regards instances of the outcome as postdictive or retrodictive, circumstantial corroboration. Our proposal considers humankind evolving as a self-organizing biological ecosystem at a geological time-scale. We offer a narrative treatment of this self-organization in terms of the FEP. Specifically, we indicate how 'cognitive surprises' could underwrite an evolving propensity in early *Homo* to express sporadic unorthodox or anomalous behavior. This co-evolutionary propensity has left us a legacy of Paleolithic artifacts that is reminiscent of a '*snakes and ladders*' board game of appearances, disappearances, and reappearances of particular archeological traces of Paleolithic behavior. When detected in the Early and Middle Pleistocene record, anthropologists and archeologists often imagine evidence of unusual or novel behavior in terms of early humankind ascending the rungs of a figurative phylogenetic 'ladder' — as if these corresponded to progressive evolution of cognitive abilities that enabled incremental achievements of increasingly innovative technical prowess, culminating in the cognitive ascendancy of *Homo sapiens*. The conjecture overlooks a plausible likelihood that behavior by an individual who was atypical among her conspecifics could have been disregarded in a community of Hominina (for definition see Appendix 1) that failed to recognize, imagine, or articulate potential advantages of adopting hitherto unorthodox behavior. Such failure, as well as diverse fortuitous demographic accidents, would cause exceptional personal behavior to be ignored and hence unremembered. It could disappear by a pitfall, down a 'snake', as it were, in the figurative evolutionary board game; thereby causing a discontinuity in the evolution of human behavior that presents like an evolutionary puzzle. The puzzle discomforts some paleoanthropologists trained in the natural and life sciences. They often dismiss it, explaining it away with such self-justifying conjectures as that, maybe, separate paleospecies of *Homo* differentially possessed different cognitive abilities, which, supposedly, could account for the presence or absence in the Pleistocene archeological record of traces of this or that behavioral outcome or skill. We argue that an alternative perspective — that inherits from the FEP and an individual's 'active inference' about its surroundings and of its own responses — affords a prosaic, deflationary, and parsimonious way to account for appearances,

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disappearances, and reappearances of particular behavioral outcomes and skills of early humankind.

1. Introduction

1.1. Why 'snakes and ladders'[1]?

Wikipedia states that the ancient game "***snakes and ladders"*** *is a board game for two or more players regarded today as a worldwide classic*[1]." Fancifully speaking, it could almost be a parable for the slow, hesitant, stumbling, and sometimes backward steps taken at snail pace during two million years by our genus *Homo* in the development of technology and culture — the '*Ascent of Man*'[2] was neither smooth going nor straight forward. The argument we propose explains why that development had to be faltering and discontinuous. The argument rests on underlying theoretical considerations, derived from the physics of self-organization, about the processes that underwrite the evolution of neurobiological propensities — of our primordial human forerunners — to attend to 'cognitive surprises'. In brief, the physics of self-organization, far from equilibrium, necessarily entails a certain kind of *itinerancy*[2] that has many of the hallmarks of the board game '*snakes and ladders.*' When viewed through the lens of the free energy principle (FEP), itinerancy can be seen as an emergent property of various free-energy minimizing processes at phylogenetic and ontogenetic scales respectively [1]; specifically, the FEP gives pride of place to the mechanistic role of behavior in shaping the itinerant '*Ascent of Man*'. Our ensuing proposal opens up a hitherto unexplored way to consider the development of human behavior, in the deep past of the Pleistocene, from a *normative* standpoint that is compatible with the concept of 'evolutionary systems theory' developed by Badcock [2] for consideration in Evolutionary Psychology.

The analogy with '*snakes and ladders*' is helpful in so far as it suggests an alternative to those kinds of *ad hoc* explanations that often form the basis of *non-normative* interpretations that, supposedly, could account for the appearances, disappearances, and reappearances of particular archeological traces of Paleolithic behavior. *Unsystematic* explanations are offered frequently as being credible — despite being unfalsifiable or untestable — justifications for singular or unusual aspects of an archeological record that is testimony to erstwhile human behavior. The *'snakes and ladders*' analogy, however, directs our attention toward an alternative explanation that is economical, non-trivial, and coherent. This alternative refers evidence about the evolution of past behavior to *systematic* processes that are widely applicable in the life sciences, and they can embrace recorded observations of findings (or aspects of them, e.g., traits, attributes, measurements, data) that arouse our interest. It is aroused especially where records indicate irregular regularities or regular irregularities in space or time. We consider here a matter where the Pleistocene record of the Paleolithic outcomes of behavioral itinerancy indicates the spatial or temporal discontinuities shown by appearances, disappearances, and reappearances of those stone artifacts that were shaped by removal of flakes into forms that are found widely, and include those which archaeologists call 'handaxes', 'cleavers', and 'spheroids', and often regard as 'heavy-duty tools', in contrast to smaller, 'light-duty tools' knapped on flakes (Appendix 2 provides some explanatory information for readers unfamiliar with Paleolithic archeology). The systematic approach that we shall propose allows for the possibility of their sporadic appearance being explicable in terms *other* than accommodative explanations (e.g., that we could account satisfactorily for sporadicity by conjecturing a continuous 'social transmission' or 'cultural transmission' of making 'handaxes' that has been preserved incompletely in the archeological record) or appeals to folk wisdom (e.g., 'an exception "proves" the rule' without explaining precisely just what the 'rule' is, let alone the causative mechanism responsible for outcomes regulated by it). Whilst our normative approach may be no more open to attempts to falsify it empirically than are *ad hoc* accounts, it has the merit of providing a unifying framework underpinned by first principles (moreover, it may be able to accommodate various *ad hoc* interpretations). We will provide a narrative (non-mathematical) account of the approach that we believe could lead to a shift in thinking about how behavior underwent evolution in the genus *Homo*. The resulting account presumes a certain familiarity with technical terms in human evolution and theoretical neurobiology (e.g., 'active inference' under the FEP). To help readers who are new to either — or both — fields, we have tried to unpack the basic terms and ideas in appendices and footnotes (in this MS the three appendices are placed in Section ***7. Appendices***, after the Section ***6. Footnotes***).

1.2. 'Handaxes': an archeological case study

Stone 'handaxes' are among the evidence of Early and Middle Pleistocene behavior of the genus *Homo* during the time-span of 1.76–0.1 Ma (Ma = million years ago), but they are distributed unevenly across the Old World (other kinds of analogous evidence will be mentioned in passing). We offer some reflections on the irregular spatiotemporal presence of 'handaxes' in the Paleolithic record. Consideration of the irregular regularities and regular irregularities of the appearance of 'handaxes' in the substantive Paleolithic record, has led to various explanations, by paleoanthropologists and archeologists, which often are accommodative conjectures. One that is frequently voiced appeals to the logic that absence of evidence is not evidence of absence. Because of the power of his theory of the origin of species by natural selection of potentially adaptive variants in populations of organisms, Charles Darwin could use just such a conjecture to explain away the presence, in his day, of chronological gaps in the paleontological evolutionary record conserved in the Earth's rocks. His theory was corroborated by instances and examples drawn from biology and the fossil record. Today there are far fewer gaps in the substantive paleontological record. Furthermore, development of genetic science provides powerful tools for investigating biological mechanisms involved in natural selection. The advances led to fusion of paleontology with genetics in the 'Modern' (or 'Neo-Darwinian') Synthesis,' and particularly in its updated version that is the Extended Evolutionary Synthesis (EES)

which considers epigenetics. The current view enjoys universal approval as a normative systematic explanation of the evolution of plants and animals. The free energy principle (FEP), as we shall explain, can be viewed as providing a basis for a normative systematic explanation of the evolution of cognitive abilities in the genus *Homo* that is compatible with a Paleolithic record of regular irregularities and irregular regularities (e.g., appearances, disappearances, and reappearances in it of 'handaxes') because this itinerancy is explicable as an emergent property of various free-energy minimizing processes that have impinged, at ontogenetic and phylogenetic scales, on the evolution of our behavior.

To begin at the beginning, human behavior in the deep prehistoric past likely evolved from that of australopithecines which, in turn, evolved (probably) from that of Miocene and Pliocene hominid apes, though behavior of homininans evolved in an increasingly divergent way from that of today's great apes. In our opinion, neither the time-scale nor the evolutionary processes involved are commensurable with conjectural interpretations of the distant Paleolithic that invoke, as being allegedly analogous ethnographic observations drawn out on the Procrustean bed of a fleeting 'ethnographic present'. There are limitations to the applicability to the Pleistocene of such relativistic extrapolations ([3]; cf., [4,5]). Archeologist Lew Binford [3] took good note that 'ethnoarcheological' remains differ increasingly from recorded Paleolithic finds, as the depth of Late Pleistocene time is plumbed. He preferred the null hypothesis that excavated 'ethnoarcheological' remains left behind by modern hunter-gatherers should be mirrored by remains excavated at Paleolithic sites before inferring any analogous behavioral comparability. In like vein, it can be argued that if the alleged commensurability of an anthropocentric perspective ought to be held up against a mirror of skeptical realism, then, so too, should be any alleged commensurability of a 'simiocentric' perspective — namely, that great-ape ethology offers analogies that throw light on erstwhile behaviors with stone performed by extinct homininans. It is our opinion that neither perspective offers a systematic approach toward achieving a satisfactory understanding of behavior in the genus *Homo* during the vast time-span of 1.76–0.1 Ma.

We propose an alternative approach that is utterly different. It is founded on existential, non-trivial, scientific principles that underpin the evolution of living organisms in a systematic manner. From this perspective, simple flaked stone artifacts (see Appendix 1), such as 'choppers', or elaborate ones, such as 'handaxes' and 'cleavers', which are bifacially-flaked large cutting tools, BFLCTs (see Appndix 2) — and manually-struck stone flakes from making those artifacts — are "*the almost inevitable by-products of least-effort flake-production using hard-hammer percussion*" ([6], p. 219), echoing Ambrose [[7], p. 1749] who considered they "*reflect least-effort strategies*". These comments by Paleolithic archeologists are especially prescient with regard to interpreting the preparation of stone artifacts, found at Early and Middle Pleistocene Paleolithic sites, in terms of minimizing the effort involved[3].

1.3. 'Handaxes': handiwork of early Homo in space and time

Two questions intrigue us. First, what is it that could provoke cognitive awareness of the possibility of fashioning stone 'handaxes' in relation to the *affordances*[4] of raw materials and the ensuing potential advantages for minimizing bioenergetic effort? Secondly, how could the provocation affect the irregular appearance of this regular technique in the Paleolithic spatiotemporal record?[5] Before addressing those questions, we shall introduce some relevant aspects of human evolution and stone-tools[6] to help those readers who require background knowledge (see also Appendices 1, 2, and 3).

The oldest flaked stone artifacts come from African Late Pliocene sediments of 3.4 Ma. Australopithecine homininans may have flaked them. The oldest fossil bones assigned to *Homo* date from 2.8 Ma. Following the onset at 2.58 Ma of the Early Pleistocene, cooperative homininan behavior is implied by sporadic finds of non-local stone particularly suitable for permitting the conchoidal flaking of stone by hand (see Appendix 1). Bifacially-flaked large cutting tools, BFLCTs, appear first in East Africa ca. 1.76 Ma [8–12], a time when *Homo erectus* had supplanted several earlier taxa of homininans. 'Handaxes' seem to be present ca. 1.6 Ma in South Africa [13], and thereafter appearances of 'handaxes' pepper the Paleolithic record of Africa and Eurasia, albeit unevenly in time and space (see Appendix 3). From the later Early Pleistocene, BFLCTs occur at a few sites in western and southern Asia dating from 1.5 to 1 Ma. It should be borne in mind that nowadays most authorities regard the Early (Lower) Pleistocene as lasting from 2.58 Ma to 0.772 Ma, a time-span characterized by the inverse magnetic polarity of some minerals which is detectable in various geological beds, which then gave way to the present normal polarity that characterizes beds formed not only during the Middle Pleistocene but also, subsequently, in the Late (Upper) Pleistocene (the onset of which was ca. 0.13 Ma at the beginning of the last interglacial period). It is unclear by what mechanism transmission of any such package could have been sustained over the spatiotemporal dimensions involved. BFLCTs were made by various forms of *Homo* for more than 1500,000 years.

1.4. What might it be reasonable to infer from 'handaxes'?

Even where several assemblages containing 'handaxes' exist in geographic regions $\geq$500 km across, assignable to a broadly similar period of time, perhaps $\geq$200,000 years long, it is imprudent to infer that they necessarily instantiate an unbroken 'cultural tradition' of manual behavior, handed down from generation to generation by 'social transmission'. If a generation lasts 25 years on average, then 200,000 years imply 8000 generations, which presents a major challenge to the likelihood, let alone the plausibility, of 'social transmission', 'cumulative culture', and a trivial, 'culture-history' approach to interpretation of the Pleistocene archeological record (cf., [4,14,15]). Nevertheless, it may not be altogether unthinkable that some archeological deposits might reflect intergenerational transmission of the manual fashioning of 'handaxes', over centuries, or perhaps even a few millennia, maybe as linguistic fluency (and intercommunal contacts) increased during the Middle Pleistocene, thereby enhancing the reproduction of skills in particular ways that became engrained in some social groups, such as congruent flake-removal from the opposing surfaces of a 'handaxe' (cf., [16,17]). It could have led to an acceleration of non-Darwinian selection for social 'functionality' [18], perhaps if an intricate 'Theory of Mind' were to have been evolving neurobiologically, in response to increases in complexity of social intercourse and communicative fluency.

Statistical considerations of classical population genetics hardly encourage enthusiasm for a sanguine notion that Darwinian fitness in Pleistocene *Homo* increased imperceptibly through gradual coevolution by 'dual inheritance' (of genetically inherited biological adaptations and hereditable technological innovations, in continuous and continual reciprocity).

We are skeptical (cf., [19]) of a popular notion that 'social transmission', underpinned by notional demographic increases during the Early and early Middle Pleistocene in the sizes of human groups and their incidence in Africa, Asia, and Europe, led inexorably to widespread evolution of 'cumulative culture', exemplified by 'handaxes' quite often. A more parsimonious view is that probably no earlier than 0.3 Ma could increases in the demographic size of human groups likely have facilitated extensive 'social' transmission of behavior, intra- and intergenerationally, whether horizontally, vertically, or diagonally, and that intercommunal contacts were infrequent, unstable, and restricted in space and time, as well as by limited communicative fluency. Instead of giving pride of place to 'group size' as playing a significant part in facilitating 'social' transmission of the fashioning of 'handaxes', we prefer to focus our attention onto the plausibility of responses or lack of responses from one onlooker experiencing 'cognitive surprise' at another individual's unorthodox manual enactment on stone that produced 'handaxes', such that the responsiveness or unresponsiveness of bystanders could have sufficed for a 'handaxe' made by an individual to be registered or disregarded. In this respect, our consideration of a knapper's 'enactive embodiment' of the creative manual process of flaking a stone into a 'handaxe' is even more 'radical' than the reasonable proposal of Garofoli [20] with which we are broadly in sympathy.

In Section 3 we shall outline the concept of brains as generative models that can be construed as '*hierarchically mechanistic minds*' (HMM) that avoid surprises and resolve uncertainty through exploration. In particular, human brains are neurobiological inference machines that can make and assess predictions appropriately, whether in order to avoid unwelcome surprises, or to resolve uncertainty through 'active inference' [21]. In that regard, it is pertinent here to reflect on what many archeologists interpret as tendencies during the Pleistocene towards Paleolithic development of: (1) alternative irreversible chains of manual reduction of stone (even present together in some assemblages); (2) symmetric and asymmetric fashioning of stone (e.g., 'heavy-duty' tools, such as 'handaxes', 'cleavers', and 'picks', or as 'blanks' or 'cores' from which flakes of more-or-less regular shapes could be struck off; (3) increasing bifacial congruence of flake-scars on 'handaxes'; and (4) some recurrent forms ('types') of modified or 'retouched' stone flakes, not to mention a tendency towards an increasing range of raw materials. These tendencies seem confined to the genus *Homo*. They could offer retrodictive support for considering that any underlying exo- or non-genetic heritability of behavior could be secondary to a genetically-based neurobiological inheritance, favored by natural selection; namely, of that cerebral propensity for alertness to salience and novelty, which is a remarkable characteristic of our toddlers. Our suggestion brings to mind the way by which the 'Neo-Darwinian' synthesis, of genetics with retrodictive corroboration from the fossil record, came to support the theory of the evolution of species by natural selection. It is conceivable that selection for a cerebral neurobiological propensity could have led to significant evolutionary phylogenetic divergence of the genus *Homo*, perhaps rendering increasingly permeable what has been called a cognitive 'zone of bounded surprisal' (narrowness of which likely restricts the ability of great apes to reproduce, copy, or imitate novel behavior: [22]).

Plausibly, in Pleistocene *Homo* there was an increasing awareness by observers (and protagonists) of novelties — introduced by a protagonist (agent) while executing behavioral perception-action cycles [22] — such that variations were appreciated on which further modification could be planned and tried out, from which a cascade of diverse outcomes, predictable and unpredictable, could be envisaged. An important distinction, therefore, exists between, on the one hand, an organism's cognitive surprise encountered in its econiche, and, on the other, its awareness of novelty in '*active inference*' as planning[7]. Both are aspects of salience. However, whereas cognitive surprise is a response to an unexpected state, awareness of novelty is a response to an unforeseen impingement that does not seem to be in accordance with a remembered regularity [23] and which can intrude during the execution of otherwise predictable skillful behavior [24]. Such behavior relies on predictions derived from prior beliefs about policies which configured procedures that theretofore had been efficacious and therefore had been committed to memory. Predictability itself could be a consequence of cerebral 'mirror-neuron'[8] circuitry [25] and, possibly, of neuroepigenetic modification of the expression of those genes that in anthropoid Primate brains underpin 'mirror-neuron' circuitry, though stabilization of particular behavioral traits is likely to be a prerequisite in order for natural selection to establish inheritable circuitry that is adaptable for such traits [26].

In the face of otherwise predictable skillful behavior, awareness of unforeseen novelty may support 'active inference' prerequisites for performing appropriate behavioral correction or alternative manual responses during experiments with stones (e.g., fashioning them by knocking flakes off). Such behavior may have paved the cognitive way toward the evolution of 'selective social learning' [27], observant 'apprentice' learning [28], and 'social transmission' of behavior in the genus *Homo* during later Middle Pleistocene and thereafter. Conceivably, adaptive structural priors in the evolving cerebral neurobiology of Pleistocene *Homo* influenced the precision of expectations that then could be juxtaposed against error-prediction, perhaps leading to anticipation of unexpected outcomes that then could be available for experimental behavioral practices.

Coming back down to Earth, at the neuronal level of basic neurobiological research it has yet to be shown precisely how 'social transmission' of human behavioral activities might cause genetic or neuroepigenetic modification in the brain. How might cerebral 'adaptive structural priors' be characterized in terms of intra-and inter-neuronal biophysics? It is not known how, exactly, the evolutionary process impinges on neuronal microcircuits in the brain. How might a neurobiological mechanism evolve which could provide all who inherit it with the adaptive advantage (over whoever does not) of the endowment of a 'propensity for social transmission' when performance of particular actions is registered by their brains and stored in memory? We have grave doubts about the plausibility that such a heritable adaptive advantage could underpin phenotypical behavioral traits that developed during the ontogeny of individual members of paleospecies of *Homo* throughout the phylogenetic evolution of the genus.

2. Another approach

2.1. Spontaneous enactment by early Homo and 'snakes and ladders'

Our approach invokes a methodologically normative paradigm grounded in systematic existential principles that underpin the evolution of living organisms. The proposal is that some irregular regularities and regular irregular phenomena (e.g., 'handaxes') attributable to *Homo* in the Pleistocene record reflect the kinds of plausibly anomalous behavioral outcomes that occurred often in a '*snakes and ladders*' fashion in early members of our genus, regardless of their skeletal classification as paleospecies (e.g., *H. erectus georgicus, H. erectus ergaster, H. erectus, H. antecessor, H. heidelbergensis, H. rhodesiensis, H. sapiens 'idaltu', H. neanderthalensis, H. sapiens*).

We argue that the Paleolithic record likely reflects some anomalous or unorthodox behavioral outcomes. Just as in other creatures, behavior in early humankind no doubt was constrained by an overwhelming tendency to conserve deeply ingrained practices. Almost three million years ago, distant forebears made sharp-edged stone 'choppers' after removing flakes of stone by hammering, and the practice has continued into recent millennia. Doubtless it formed part of the normative, orthodox, Paleolithic behavior of early *Homo* 1.76 million years ago. That is when 'handaxes' began to be fashioned by elaborate bifacial removal of flakes, executed by sequential manual procedures that were different from those of the prevailing orthodoxy by which 'choppers' were made. Thus, 'handaxes' were outcomes of unorthodox procedure. However, the previous, simpler, manual techniques continued to be widespread in time and space, in marked contrast to the fashioning of 'handaxes' which are sporadic and sparse for over a million years following their first appearance. Their infrequency supports an inference that it took hundreds of thousands of years before bifacial fashioning was to play any significant part in Paleolithic behavior. Plausibly, bifacial fashioning of artifacts before half-a-million years ago was restricted to isolated instances, perhaps where a fashioner of a stone was unaware of the affordances made possible by her idiosyncratic enactment, or maybe when an onlooker was so constrained by ingrained, received orthodox practices that the anomalous behavior was ignored and went unnoticed.

Had either of them been aware of the affordances, one or other would have experienced 'cognitive surprise' which would have expanded his or her 'zone of bounded surprisal' [22]. In terms of the FEP, this can be read as failing to model or infer the counterfactual outcomes of some novel behavior, simply because there was no (evolutionarily endowed) generative model at hand (or in the head) to predict this kind of behavior. Cognitive surprise can be regarded as analogous to 'surprisal' (a.k.a., self-information) in Information Theory or, more simply, prediction error in predictive coding accounts of the Bayesian brain. The FEP posits that the minimization of surprise — as scored by variational free energy — is a hallmark of self-organizing systems; including the brain. Plausibly, the experience of cognitive surprise is an outcome of an evolved neurobiological propensity for exploring unorthodox possibilities. The propensity likely has evolved further in humans than in great apes which, unlike human toddlers, seem unable to envisage "*how things might be as well as how they actually are*" ([29], p. 86), whereas by coupling recall of past experience with prospective memory humans are capable of "*blending reality among different potential spheres*" ([30], pp. 41–53).

How was remembered awareness, retrieved from personal short- and long-term memory, transmitted as knowledge to others, in whose memories it could become embedded, with a degree of fidelity sufficient to enable 'social transmission' by intergenerational or intercommunal diffusion? How far was observational learning involved? Neither biological nor behavioral reproduction were assured in tiny bands of small-brained *Homo erectus* whose early anatomical and physiological maturity (e.g., 'Turkana Boy' of 1.53 Ma) furnished few childhood years for acquiring behavioral alternatives. Language barely existed. Intercourse between bands was rare, whether social, or sexual. The risk of extinction was ever-present, which eradicated any accumulated lore as well as further opportunities for observational learning. Unbalanced sex-ratios hampered reproduction of tiny bands. Untimely deaths were commonplace. Knowledgeable elders were scarce. Precocious consolidation of cerebral circuitry hindered development of the coactivity between prefrontal and caudal cortices that underlies the agile working memory of our teenagers (cf., [22,31,32]). Because of its inherent tendency toward conservation, natural selection underlay prepotent impediments in those mirror-neuron circuits[5] that likely play a part in imitative behavior [25,33]. Plausibly, the aforementioned possibilities could have led, in early *Homo*, to evolution of behavior in a spatiotemporal '*snakes and ladders*' fashion, involving mind-numbing technological stasis, and impinging with tedious slowness on multidimensional landscapes, wherein might take root a seed of reproductive success (a.k.a., adaptive value; Darwinian fitness).

Biological evolution by natural selection is inherently conservative, and neurobiology can have been no exception. Emergent neural representations exploited behaviorally by lone individuals need not have been shared automatically by other minds in groups of largely inarticulate homininans (i.e*., Australopithecus*, Paranthropus, *Kenyanthropus*, early *Homo*). Their adaptive priors guided their neuronal action-perception cycles toward *un*surprising adaptive states, by way of minimizing variational free energy, VFE (see below). Perhaps those priors involved neuro-epigenetically modifiable expressions of genes, favoring routine expectations (i.e., consolidating habitual behavior, cf. [34]), to the detriment of recognizing the epistemic affordances that underwrite curiosity and novelty-seeking behavior. In consequence, some technological aspects of behavior that are represented irregularly in the worldwide spatiotemporal record (e.g., manual flaking of stone to fashion a 'handaxe') could result severally from unrelated spontaneous enactments, separate in time and space, performed by individuals on occasions during the Early and Middle Pleistocene, at least until such time as 'active inference' (see below), brought about adaptive modification of 'cerebral structural priors', permitting adoption of novel behavior that hitherto had failed to afford adaptive advantage. By 'cerebral structural priors' are implied priors that determine the structure or form of hierarchical generative models in the brain; 'structure learning' (a.k.a., 'Bayesian model selection') thus can be read as the selection of new forms of generative model, e.g., retaining new connections or levels in hierarchies of neuronal circuits in the brain.

A conjecture that is by no means implausible is that adaptive structural modification could have involved a propensity toward neuroepigenetic impingements which modified the expression of genes involved in cerebral neuronal circuitry. However, such

impingements need not to have taken place hand in hand with the evolution of genes involved with shaping skeletal morphology during evolution in the genus *Homo*, even though natural selection doubtless played a significant part in all aspects of biological evolution in Pleistocene *Homo* (it should be borne in mind here that epigenetic transmission is less constrained than is the evolution by genetic inheritance– which can be frequency-dependent– of polymorphous genes in populations of sexually-reproducing organisms).

2.2. The hierarchically mechanistic mind and Tinbergen's 4 questions

Our proposal is grounded in the *free-energy principle* (FEP) which affords us a non-trivial, first principles approach, based on statistical physics to understanding how evolution can be mediated by responses in self-organizing systems, such as living organisms, and hence can involve behavioral responses of creatures that are sentient: i.e., can experience sensations as agents and thereby in particular, we consider animals that have a '*hierarchically mechanistic mind*' or HMM [35,34]. "*The HMM defines the embodied, situated brain as a complex adaptive system that actively minimizes the entropy (*i.e.*, the spread or decay) of human sensory and physical states by generating action-perception cycles that emerge from dynamic interactions between hierarchically organized neurocognitive mechanisms*" ([35], pp. 104–105). The HMM can be regarded as a neurobiological inference machine.

With regard to biological evolution, the HMM concept is compatible with 'evolutionary systems theory' (or EST, [2]) which it "*leverages… to bridge two complementary perspectives on the brain. First, it subsumes the free-energy principle (FEP) in neuroscience and biophysics to provide a biologically plausible, mathematical formulation of the evolution, development, form, and function of the brain… Second, it follows an EST of psychology by recognizing that neural structure and function arise from a hierarchy of causal mechanisms that shape the brain-body-environment system over different timescales… According to this perspective, human neural dynamics can only be understood by considering the broader context of our evolution, enculturation, development, embodiment, and behavior*" ([35], p. 105).

Nikolaas Tinbergen's Four Questions		Objects of explanation	
		Diachronic aspects (sequential/evolving)	***Synchronic*** aspects (static/result)
Kinds of Explanation	***Proximate*** explanation (mechanisms)	**ONTOGENY** Development during life-cycle	**CAUSATION (MECHANISMS)** 1. Awareness; 2. Nuts-and-bolts of what happens
	Ultimate explanation (evolutionary outcome)	**PHYLOGENY** How evolution of a trait developed in a species	**SURVIVAL VALUE** for adaptive fitness and reproductive success
1973 Nobel Laureate for Physiology or Medicine, Oxford' University zoologist and ethologist Professor Nikolaas Tinbergen reflected, in 1963, on the relationships between Causation, Ontogeny, Phylogeny, and Survival Value. Recent analyses (Bateson and Laland 2013, Nesse 2019, Lee 2021) favor a 4-way appreciation of them (above) that we suggest is relevant to understanding their relationships in eco-niche construction and neuroethology in the genus *Homo* between 2,000,000 and 100,000 years ago (below), from considerations of 'active inference' and the minimization of variational free energy, which offer a coherent, parsimonious, prosaic, deflationary explanation of some recorded aspects of the early Paleolithic behavior of the genus *Homo*.			
Nikolaas Tinbergen's Four Questions: 'Snakes and Ladders' and Active Inference		Objects of explanation	
		Diachronic aspects (sequential/evolving) Paleolithic behavior	***Synchronic*** aspects (static/result) 'handaxes' (also: flake-tools, fire, sites, caves, etc.)
Kinds of explanation	***Proximate*** explanation (mechanisms)	**ONTOGENY** Development during life-cycle: lack of adolescent growth-spurt cut short *Homo erectus*' hierarchically mechanistic mind	**CAUSATION (MECHANISMS)** 1. Awareness: AI, FEP, VFE 2. What happens: neurophysiological brain-hand versatility, and cerebral flexibility, WM, LTM, PM
	Ultimate explanation (evolutionary outcome)	**PHYLOGENY** How evolution of a trait developed in a species: 'Snakes & Ladders'	**SURVIVAL VALUE** for adaptive fitness and reproductive success *Homo erectus*→ **US**!

The HMM concept is applicable at several levels of 'evolutionary systems theory' (cf., [2]), namely, (1) in instantaneous real-time, in individual development (ontogeny) (2) in intergenerational processes of phylogenetic inheritance and heredity, and (3) in archeological and geological timescales of evolutionary adaptation and natural selection [35]. It thus offers a scientifically intelligible way of giving a coherent, non-trivial, systematic response to Nikolaas Tinbergen's well-known insightful '4 Questions' [36]. In 1973 the Nobel Prize for Physiology or Medicine was awarded jointly to Konrad Lorenz, Karl von Frisch, and Niko Tinbergen for their contributions to ethology. About Lorenz, Tinbergen [[36], p. 410] wrote, "*I consider his insistence that behavior phenomena can, and indeed must, be studied in fundamentally the same way as other biological phenomena to be his major contribution.*" We likewise insist on giving pride of place to that scientific approach. We confine our attention here to an archeological matter, on which the HMM concept may throw light, concerning the long time-scale of human evolution. Tinbergen's 4 Questions can be summarized as follows:

3. Biological evolution meets physics

3.1. The free-energy principle (FEP), 'active inference', and the evolution of human behavior

Biological theory cannot ignore basic physical principles that underpin the existence and evolution of life and the living world, but are not always easily digestible by biologists, let alone by paleoanthropologists and archeologists. We shall try to offer an intelligible account. All organisms tend to expend the least energy compatible with survival; this underlies the existential perspective on biological homeostasis. Adaptable self-organizing systems expend further energy however, by generating not only predictions, but also, responses, via active inference (AI), to changing circumstances. Minimizing their internal entropy postpones death that causes dissipation of energy (and increased entropy at large). This thermodynamic (or metabolic) account of self-organization can be formulated as a variational principle of least action, where the action (cf., effort) is the long-term time average of effective variational free-energy (VFE). VFE is a cousin of thermodynamic free-energy but affords a more abstract and general description of self-organization; in terms of the probability of any organism or phenotype finding itself in a particular state. It should be borne in mind that because VFE is an extensive quantity, the free energy of a group of conspecific creatures can be read as the sum of the free energies of each phenotype, on average, over time. The argument that follows is complex, and perhaps rather dense in places, but nevertheless necessary for understanding a non-trivial interpretation of our '*snakes and ladders*' example of Paleolithic 'handaxes'.

The concept of 'active inference' is of particular importance here, and represents an application of the FEP to sentient behavior and, implicitly, the HMM: "*active inference separates the problems of optimising action and perception by assuming that action fulfils predictions based upon perceptual inference or state-estimation. Optimal predictions are based on (sensory) evidence that is evaluated in relation to a generative model of (observed) outcomes. This allows one to frame behaviour as fulfilling optimistic predictions, where the inherent optimism is prescribed by prior preferences* [37]. *Crucially, the generative model contains beliefs about future states and policies, where the most likely policies lead to preferred outcomes. This enables action to realise preferred outcomes, based on the assumption that both action and perception are trying to maximise the evidence or marginal likelihood of the generative model, as scored by variational free energy*" ([38], p. 864). The preferred outcomes are those that agents believe to be characteristic of the kinds of agents they are and their generative models include their prior beliefs.

Technically speaking, VFE is a mathematical bound on the negative log (marginal) likelihood of outcomes experienced by an organism (or any system) when exchanging with its environment. This means that minimizing free-energy corresponds to maximizing the likelihood of sensory exchanges for any system that can be regarded as engaging in sentient behavior [39–41]. The mathematical formalism is useful because it offers a number of complementary interpretations of adaptive (sentient) behavior. At the level of the physics of self-organization, it provides a first-principles account of existence, defined as maintaining a far from equilibrium steady-state when exchanging with the environment.

With early *Homo* in our sights as a protagonist in human evolution of the adaptation represented by her manual flaking of stone 'handaxes', we must keep in mind that, in terms of evolutionary theory, /negative free-energy can be regarded as adaptive fitness: namely, by scoring the likelihood of a particular phenotype, and being understood as the adaptive 'fit' of the phenotype to its econiche [42–45]. We can relate the minimization of VFE to thermodynamic energetics by bearing in mind that VFE can be decomposed into accuracy and a complexity-cost [46]. The complexity-cost entails the expenditure of thermodynamic energy (via 'Landauer's principle' which relates any irreversibility of the manipulation of information to an increase in entropy, provided that Shannon entropy in Information Theory can be subsumed within classical thermodynamics; for further reading see, for instance, [47–49] . In short, minimizing VFE requires a thermodynamically efficient engagement with the econiche.

Specifically, VFE can be regarded as an information theoretic measure of how surprising various outcomes are, on average, for any organism. An organism that can model and predict its exchange with the econiche can therefore be said to have adapted to that environment and to avoid surprising exchanges with it (e.g., excursions from homeostatic setpoints), or else being in very unlikely states (e.g., injury, death). This is where the notion of 'cognitive surprise' comes in, where surprise can be regarded as being a kind of prediction error. In Information Theory and Bayesian conditional probabilistic analysis of predictive coding, the formal term is 'surprisal' or 'self-information' (and is given by the negative log probability of an outcome). In Bayesian statistics, the probability of an outcome under an organism's (generative) model of how its outcomes were generated is called 'Bayesian model evidence'. In this sense, an organism's very existence can be construed as the result of self-evidencing [50].

The notion of self-evidencing underwrites much of our following argument. However, there is an important nuance. Certain creatures, for instance *Homo*, have evolved deep generative models, with the ability to *predict the consequences* of their action. This kind of creature now has the capacity to entertain *counterfactual* futures under different actions: put simply, it can plan [51–55]. Because the causes perceived by the creature include its own action or situation, actions or plans can be inferred by it, leading to active (planning

as) inference. This is a key aspect of 'active inference' under the FEP: namely, actions and plans are selected on the basis of minimizing expected free energy (cf., effort) under that plan. More simply, actions are selected to minimize expected surprise by avoiding unlikely states of affairs (e.g., injury, death) and by resolving uncertainty about environmental states by generating outcomes. Reducing uncertainty is important, because it means that sentient behavior, prescribed under a deep generative model of the (future) consequences of action, has an epistemic aspect, rendering sentient behavior sensitive to salience and novelty. Only systems with this kind of deep generative model will show such exploratory behavior, because they alone can respond to epistemic affordances and the possibility of answering "*What would happen if I did that?*" [56–58]. The expected free energy that drives planning or policy selection can be decomposed into epistemic and pragmatic components that underwrite exploratory and exploitative behavior, respectively [59].

So just what is free energy in the context of biological evolution? Briefly stated, free energy can be regarded as the negative logarithm of input-samples experienced by self-organizing systems such as biological organisms. Its minimization underwrites their existence and, implicitly, their reproductive success [44,45,60,61]. Natural selection is gradual and conservative. Faced by environmental interdependencies and regularities, the integrity of generative self-organizing systems is underpinned by adaptive reciprocity involving 'active inference'[9] referable to prior expectations entailed by a generative model and endowed by evolution [21,39,62–64]. Active inference instantiates a generative model, the components of which are neuronal networks in the brain that are capable of making predictions as to *what next is most likely to be sensed*. In terms of Bayesian statistics of conditional probability, evolution and natural selection can be regarded as *natural* 'Bayesian model selection' (a.k.a., 'structure learning', cf., [65]). Evolution thus develops imperceptibly and intermittently at the biological, technological, and, indeed, psychosocial levels [35,34,66–68]. The FEP is biologically, and, in particular, *neuro*biologically relevant, both at *onto*genetic levels of cellular dynamics, neural circuitry, and behavior, and at *phylo*genetic levels of populations evolved through natural selection of biological adaptations and adaptability.

Our consideration of the FEP — in the context of sentient behavior — draws on the studies of the nineteenth-century physicist and physician Hermann von Helmholtz who determined that the work obtainable from a closed thermodynamic system at a constant temperature can be calculated as a thermodynamic potential. In such a 'Helmholtz box', the maximum amount of work performed by the thermodynamic process is given by the change in 'Helmholtz free energy', and under isothermal conditions its value is minimized when the process reaches equilibrium and hence its final entropy is highest. Helmholtz free energy is measurable as a system's thermodynamic potential calculated as the internal energy of a system. To complement this thermodynamic formulation of self-organization to thermodynamic equilibrium, Helmholtz also introduced the concept of unconscious inference based upon the notion of minimizing a 'neuronal energy' [69–71]. Variational free energy (VFE) can be read as a formalization of Helmholtz's notion, and 'neuronal energy' in terms of Information Theory (inherited formally from Richard Feynman's work in quantum physics and Jaynes' maximum entropy principle: [72–74]). From this perspective, expected free energy can be regarded as decomposable in terms of expected cost and expected information gain ([1] in press). From a statistical perspective, variational free energy can be regarded as complexity minus accuracy. This means that to minimize VFE is to maximize evidence for an observer's generative model by explaining sensory samples accurately and simply. Similarly, active sampling of the sensorium is done in a way to minimize the variational free energy expected after acting. Expected free energy (EFE) can be regarded as decomposable in terms of expected cost and expected information gain [75]; where cost just is the surprise, in relation to prior preferences.

The FEP concept can relate neurobiological evolution of the brain in *Homo* (and our capacity for memory) to the evolution of the prosociality and cooperative behavior that promote the reproductive success of humankind (a.k.a., adaptive value, Darwinian fitness). The concept accords not only with evo-devo theory, but also with the genetic and epigenetic mechanisms involved in Neo-Darwinian evolution. Furthermore, it can explain the asynchrony that is detectable before ~0.2 Ma between developments in the Paleolithic record of technology on the one hand, and the successive appearances in the paleoanthropological record of *Homo erectus, H. neanderthalensis*, and *H. sapiens*, on the other. As stated in the *Introduction*, the major spatiotemporal demarcations are not coterminous in the archeological, paleoanthropological, and geological records of the Pleistocene. Thus, whilst coevolution may have taken place between Paleolithic technological developments and phylogenetic evolution in *Homo*, it cannot be taken for granted that they always coevolved in lockstep (see also Appendix 1).

At the ontogenetic level of the individual, autopoiesis can involve action-perception cycles that, with regard to pre-existing preference, induce cognitive surprises permitting, and even mandating, novel behavioral outcomes. At the phylogenetic level, an archeological consequence could have included frequent unawareness by onlookers that an individual companion's exceptional behavior could afford them new cooperative opportunities for minimizing the group's VFE, e.g., by performing unaccustomed behavior for uncertain personal benefit. The individual's cognitive surprise that was expressed in an unorthodox behavioral outcome was not reciprocated by onlookers for whom the behavior was inconsistent with those stereotypical activities in their phenotypical repertoire which conformed their exploitative pragmatic priors. Normative confidence in exploitative pragmatic priors usually trumped explorative epistemic priors; i.e., the expected information gain afforded some behavior (cf., [34,35]). Very likely this was the norm in tiny bands of early *Homo*, particularly given our taxon's tendency to show greater prosociality and cooperative helpful behavior than does even that most prosocial of the great apes which is the bonobo (e.g., [76–79]).

Without foresight or fluent communication, innovations often must have disappeared unremarked, seen as irrelevant, or useless, and their creators' 'prowess' as misplaced energy and wasting time needed for satisfying the group's existentially implacable energetic requirements. Significantly, in maintaining basal homeostasis our *resting* brain exhausts 11.2 Watts/kg, compared with 1.25 Watts/kg for the whole body [80], consuming 50% of its glucose intake, and 20% of its oxygen intake of which 75–80% powers cerebral neurons

[81]. It goes without saying that a million years ago, *Homo erectus* activity must have met *greater* daily energy requirements, otherwise we ourselves would not exist today. Doubtless, tried-and-trusted routines predominated, and whoever performed them with daily efficiency was trusted by the group, whereas eccentric, unorthodox, or idiosyncratic conduct was treated with indifference and not retained in collective memory or lore.

Such, we suggest, was the fate of various anomalous, idiosyncratic, behavioral activities performed by members of *Homo* during Early Pleistocene and early Middle Pleistocene times. Put simply, idiosyncratic personal attainments, ostensibly reached, as it were, atop a 'ladder' of technical abilities, could well have been disregarded by friends and family alike, who failed to imagine or articulate possible advantages that might enhance their survival. Moreover, when percussive actions remove flakes from a stone core, "*certain core forms may be 'spandrels' (after [82]): patterns created inevitably without prior hominin intention*" ([83], p. 23); thus, such fortuitous enactive outcomes may not have been regarded by even their creator as 'tools', even though archeologists classify them as such from a standpoint of comparative morphology. Moreover, interpersonal communication was restricted, and language rudimentary if present. Furthermore, lifespan was short, with biological maturity attained earlier than nowadays, which limited the development of neurobiological flexibility in what in any case was a small adult brain, barely two-thirds the size of ours today. In short, prepotent, routine behavior in prosocial early *Homo* plausibly resulted in failure to become aware of the potential of idiosyncratic enactive outcomes. That failure, as well as sundry demographic accidents, would thus erase idiosyncratic behavior from collective memory more often than not. Even when collective memory may have been retained by tiny hunter-gatherer bands it would have been lost whenever they were extinguished owing to demographic vagaries, such as unequal sex-ratios of available partners, deaths during child-birth or resulting from sickness or ill-health as a consequence of congenital disability, infection, gum-boils, tooth-loss, or from such unforeseeable perils as venomous bites/stings, food-poisoning, attacks by predators, or debilitating weakness when food or water are scarce on account of pestilence, blight, drought, flood, wildfire, frost, blizzards, or other violent climatic events.

There is a crucial difference, however, between a spatiotemporal '*snakes and ladders'* picture of untoward disappearances of tiny hunter-gatherer bands and appearances of others, which is unrelated to responses of people's '*hierarchically mechanistic minds*' (HMM), and the '*snakes and ladders'* model of individual idiosyncratic or unorthodox activity and the *receptivity to it, or not, of an observing HMM*, be it that of an onlooker or the selfsame protagonist. The fundamental necessity for mental registration of the observation of an unfamiliar technique or its outcome is considered elsewhere in relation to effective variational free energy and the FEP [22]. The heterogeneous composition of the former picture renders it inappropriate for making predictions that can be compared or contrasted with archeological findings at early Paleolithic sites, whereas the latter model, by focusing on the information theoretic and energetic constraints on biological, neurobiological and psychosocial evolution, allows for the consideration of whether by doing so it may offer a reasonable interpretation of the material record and, in particular, of the uneven worldwide distribution of stone 'handaxes'.

3.2. Early paleolithic enactment and the FEP

Conceivably, some kinds of artifacts that occur sporadically, infrequently, and intermittently in the early Paleolithic record were simply outcomes of spontaneous enactment with raw material. It might have involved both exteroceptive and interoceptive neural networks in idiosyncratic behavior that might or might not reflect creative originality or innovation. This skeptical critique may offer a way to understanding what lay behind early bifacial flaking of large cutting tools, such as 'handaxes' (and maybe also the opportunistic exploitation of fire or frequenting of caves). A prosaic approach to interpreting the uneven spatiotemporal record from an FEP standpoint is not a pseudoscientific vacuous pronouncement of the blindingly obvious. Rather, it inverts that imaginative, phenomenological approach to interpreting the deep past which draws for its inspiration on humane and social studies. The inversion subordinates unsystematic approaches to critical scrutiny, particularly with regard to existential biological constraints on early Paleolithic behavior, such that those approaches may seem no longer to be the most appropriate ones, much less the most parsimonious interpretations available when compared with a systematic explanation that underpins neuroethological processes.

The FEP leads to embodied brains that learn Bayesian probabilistic statistical models of the many regularities in its surroundings. Such brains permit the emergence of generative models that can be construed as '*hierarchically mechanistic minds*' (HMM) that avoid surprises and resolve uncertainty through exploration. This uncertainty could be about the physical aspects of the natural *environment*, such as stones or wildfire or, indeed, conspecific creatures generating sensory information. The marginal relevance of stone ca.3 Ma for the existential biological imperative of maintaining homeostatic integrity, and consequent reproductive success and survival of inarticulate homininans, plausibly led stones to be regarded as quintessentially predictable and unsurprising and, crucially, lacking epistemic affordances implicit in tool use. Nonetheless, sporadically, infrequently, and intermittently, an individual could entertain more expressive (i.e., deeper) generative models and respond to exploratory (epistemic) and exploitative (pragmatic) values (cf., [75, 84]). She might discover novel ways of attaining predictable (unsurprising) outcomes, though her behavior, and its outcome, may well have been disregarded by her companions, who learnt nothing from it, much less foresaw potential uses for the novelty. All the same, such idiosyncratic behavior may trump prevailing expectations that normally are *un*surprising and therefore favor minimization of VFE, in line with FEP.

As remarked above, the minimization of VFE describes an organism's propensity to adapt by self-organization, and can be understood as upper bounding the average of 'surprise', often described in terms of *prediction errors*. In these systems, *priors conformed by prediction errors in hierarchically-organized neuronal circuits underwrite active inference*. Hierarchical self-evidencing brain architectures juxtapose 'bottom-up' prediction errors, referred from both interoception (e.g., proprioceptive inputs from joints and somatoceptive inputs such as headache, deep pain, sweating, bowel and bladder contractility, heartbeat, blood pressure, respiration, glandular

secretions, hormone levels) and exteroception (e.g., sight, touch, hearing, smell, taste), with 'top-down' predictions based upon prior expectations [85]. This way of minimizing free energy (i.e., prediction errors) engendered by interoceptive and exteroceptive sensory modalities may underpin self-awareness [53,86]. On this view, minimal selfhood emerges as part of a generative model that provides a parsimonious explanation for all the sensations; namely "*these sensations are generated by my body*", especially, interoceptive sensations that come from the embodied self. This aspect of self-evidencing is potentially important, because the ability to infer or differentiate itself from non-self is a key aspect of encultured active inference. Moreover, viewed in that light, 'enactive embodiment' is open to the evolutionary possibility that selection could winnow out maladaptive behavior (cf., [87], esp. pp. 67–68) — though also it is undeniable that flaking a stone could be maladaptive if doing so diverted time and energy away from gathering food!

4. The brain of *Homo erectus*

4.1. *'Turkana Boy'*

Undoubtedly the '*snakes and ladders*' picture owes much to unforeseeable perils and demographic imbalances in tiny hunter-gatherer bands. Life was brutish *and* short. The *Homo erectus* 'Turkana Boy' ca. 1.53 Ma died ca.9 years old, nearing adulthood [88–90] and already as tall as adults nowadays; our slow-growth childhood and adolescent growth-spurt evolved subsequently with consequences for cerebral development [91]. His brain-to-body size ratio was below ours [92]. His cognitive capacity was between australopithecines' and ours. Early consolidation of brain circuitry likely constrained his mental agility. Were he to have attained adulthood, his 880 cm^3 brain probably would not have exceeded 900 cm^3 — a mere two-thirds the size of our adult brain and *less* than even that of our one-year-old children, though twice that of great apes and australopithecines. Plausibly, the storage size of his working memory was intermediate between that of chimpanzees and ours (cf., [93]), probably somewhere between that of Late Pliocene habitual bipeds (e.g., *Australopithecus afarensis* ca. 3.5 Ma) and ours; like us, 'Turkana Boy' was an obligate biped. The parietal, temporal and frontal lobes of Early Pleistocene *H. erectus* brains were smaller than ours. The prefrontal cortex, important when making choices [94], was relatively small and narrow when compared against our modern brain. Moreover, the relatively anterior situation of the precentral sulcus in Turkana Boy ([95], esp. Fig. S2-F) implies that the expansion of the inferior prefrontal cortex, which can be inferred from endocasts of later crania, had not yet evolved in the brain of early *H. erectus*.

Nowadays, between ages 12 and 30 human intracerebral connectivity is enhanced as fatty-acid myelin sheaths envelop axons in white-matter nerve-fiber tracts between gray-matter brain areas. Even if *H. erectus* prefrontal cortices contained incipient tracts [96], precocious adulthood curtailed the cerebral development that in modern people continues [97] with neuronal myelination beyond age 20 together with the synaptic pruning of neuronal dendritic spines that seems to enhance cognitive ability [98]. Perhaps protracted corticogenesis evolved in *Homo* ca. 0.5 Ma, during the Middle Pleistocene. Moreover, learning can modify myelin development which is influenced by neuronal action-potential firing and axonal conduction-velocity ([99]; cf., [100]). Protracted maturation of prefrontal neurons may induce experience-dependent changes in prefrontal neuronal circuitry that support monitoring alternative goals and facilitate corresponding behavioral modification [94]. There are genetic influences on cortical folding and surface area in human fetuses [101], and on post-natal development of cortical thickness; plausibly, differentiation of genetic effects of '*Wnt*' signal-transduction pathways (q.v., [102]) became pronounced during cerebral neuronal evolution in *Homo* after ca. 2 Ma. There are well-studied regional differences in the development of gray matter, which may be prolonged in temporal cortex, perhaps related to its role in integrating memory, object-recognition, and audio-visual inputs [103]. From the perspective of the FEP, these differences testify to 'structural priors' that inherit from epigenetics, and contextualize experience-dependent learning (and planning as inference) at a somatic timescale.

Before 1 Ma, *H. erectus'* working memory (WM) capacity would have been less than ours. Modern human WM is positively correlated with the developmental extent, between ages 6 and 25, of white-matter frontostriatal tracts, especially left-sided fronto-parietal tracts [104–106]. Left-sided frontal, parietal and temporal cortices are important in memory, language, and tool-use [107–110]. The complex relationships between short-term WM, long-term memory (LTM), and prospective memory (PM), are the object of considerable ongoing neuroscientific research. Interaction between modern human WM and long-term memory (LTM) is a complex matter. Whilst increased maintenance in WM of a stimulus enhances its later recognition in LTM [111], if WM capacity is overstretched LTM can be involved in task-performance [112], and, after age ten, LTM can be involved in inhibitory control when updating encoded information [113]. It is imprudent, therefore, to make simplistic inferences about the relationship between WM and LTM in *H. erectus*.

It is well-known that neuronal myelination in young adults is complete at different ages in different parts of the human brain [114]. It develops differentially from before birth [115] and continues beyond late adolescence [97,116,117]. By contrast, myelination is already complete in pubertal macaques, and, although perhaps incomplete in pubertal chimpanzees [118–121], it is complete in these at sexual maturity, whereas in modern humans it continues for some years afterwards. The extent to which this could have happened in 'Turkana Boy' cannot be known, but had he survived to age fifteen it could have been complete by then. If so, then the range of behavioral options open to him is likely to have been narrow. The foregoing thumbnail sketch suggests that *onto*genetic limitations of early *H. erectus* could well have had *phylo*genetic consequences owing to a constrained ability, at most, to communicate idiosyncratic 'cognitive surprises' and consequently predictable outcomes of possible alternative behavioral responses at either individual or

communal levels.

4.2. Keeping in mind the work in hand

Practicing haptic manual activities is known to enhance neuronal myelination in the brain. Stone-knapping is haptic behavior. It involves grasping solid objects. When grasping things is investigated in people and chimpanzees, cerebral neuroimaging registers more activity in human parietal and occipitotemporal regions than in those of chimpanzees [122]. Whereas in that respect chimpanzees resemble macaques, they differ from those in sharing with humans coincident prefrontal somatotopic responses to transitive behavior and intransitive observation of actions. Humans differ from both species in our arcuate fasciculus white matter which underwent evolutionary modification affecting temporal lobe connectivity and perhaps linguistic ability [123] of which a rudimentary form may have been present in *H. erectus (*cf., [124–132]; but see [133,134]).

Stone-knapping is haptic behavior. Haptic working-memory (WM) tasks (Fuster 1999, [135]) enhance cerebral white-matter plasticity, and white-matter microstructural changes show positive correlation with cognitive enhancement and refinement of motor behavior ([136,137]; R.E. [138–142]). Paleolithic stone-knapping very likely had similar effects. Cerebral neuroimaging of undergraduates learning to knap 'handaxes' shows changes in superior longitudinal fasciculus white matter between frontal, parietal, temporal, and occipital cortices [122,143,144,145], with impingements, that plausibly facilitate rapid attentional switching, on ventrolateral prefrontal cortices, the right inferior frontal gyrus pars triangularis involved with determining practical outcomes, and the inferior parietal lobule in which the anterior supramarginal gyrus (that appears to contain proportionally more gray matter in humans than in apes) is a cortical area well-known to be associated with tool-use [107–110]. Meta-analysis indicates that coactivation of tool-use and linguistic syntax engages the pars opercularis of the human left inferior frontal gyrus, where it may have been co-opted for linguistic purposes during human evolution [146].

The circumstantial evidence seems to imply the adaptive evolution of human neurobiological propensities that support prospective memory in tool-making, together with short-term WM (including haptic WM), long-term WM, and long-term procedural memory and episodic memory of past matters and things. Those propensities were, and are, phylogenetic outcomes of existential ontogenetic programs adapted through natural selection for satisfying the bioenergetic requirements of organisms. However, teaching and learning stone-knapping skills are very different from a communicatively-challenged *H. erectus* individual's idiosyncratic spontaneous enactment resulting in a disregarded 'handaxe' outcome of iterative, enactive haptic lithic manipulations, regardless of any neurobiologically-evolved cognitive/neuronal propensity for such enactment.

Despite an incipient propensity of cerebral neurons favoring the evolutionary enhancement of both memory and alertness to alternative perspectives, Turkana Boy likely was mnesically challenged, regarding the requisite prospective memory for the consequences of actions. In late *H. erectus* foresight is implied when by 1.1–0.77 Ma 'handaxes' were present at sites where fire was tended, namely, in the South African Wonderwerk Cave [147], in the Spanish Cueva Negra del Estrecho del Río Quípar [148,149], and in Israel at the open-air site of Gesher Benot Ya'aqov [150–152]. Tinder and kindling, stored with foresight could be set *alight* by embers, brought from dying wildfires, and fire in caves was protected from extinction by bad weather. Only in Africa are earlier signs of combustion recorded in Paleolithic contexts, e.g., at the open-air site at Chesowanja in Kenya ca. 1.42 Ma [153,154] albeit lacking 'handaxes'. Tending fire can provide warmth, light, deterrence of predators, smoking/drying of wood, skins, and foodstuffs, maybe including roasting/baking thereby gelatinizing starch and enhancing energy-intake by facilitating digestion and absorption of metabolites while eliminating pathogens [155–160], and genomics hints that cooking began ca. 0.8 Ma [161]. A study of aspects of the oral microbiome preserved in dental plaque of *H. sapiens* and *H. neanderthalensis* [162] indicates a common tendency to ingest starchy foodstuffs that does not characterize apes and monkeys, implying an evolutionary trajectory of consumption of energy-rich roots, tubers, and seeds by Pleistocene *Homo*.

Nevertheless, before 0.4 Ma convincing evidence is conspicuous by its absence from Old World Paleolithic sites of those fire-pits or hearthstones that could imply mastery of the requisite heat-control needed for efficient cooking. Sporadic heat treatment of foodstuffs before then was probably inefficient. It may have appeared, disappeared, and reappeared in '*snakes and ladders*' fashion. Nonetheless, from a neurophysiological standpoint it is plausible that energy-rich foodstuffs, especially fatty acids, by enhancing myelination and neuronal development [163] in *H. erectus* brains, underpinned cerebral enlargement (e.g., in later Middle Pleistocene *H. neanderthalensis* and *H. sapiens*), with evolutionary development of intracerebral connectivity, mnesic (memory) capacities, communicative abilities, and cognitive awareness. These reduced uncertainty around explorative epistemic affordances, and inspired greater confidence in possible outcomes of hitherto disregarded activities, thereby favoring pragmatic cooperative behavioral responses.

Memory informs our responses. Incipient evolution of human memory is suggested by Early Pleistocene Paleolithic finds and fossil homininan skulls. Neurobiological differences separate paninan from human brains [164–166]. The differences arose via evolutionary divergence in cerebral corticogenesis, doubtless involving genetic and epigenetic transcription factors (cf., [167–173]). Whereas ca. 4–2 Ma australopithecine brains resembled paninans' in size and shape, *Homo erectus* skulls ca. 2 Ma enclosed bigger brains, approaching later human sizes and shapes ca. 0.5 Ma. Big brains have high bioenergetic requirements: chewing foodstuffs facilitates their release, hence, unsurprisingly, brain-size in Pleistocene *Homo* increased faster than tooth-size decreased [174].

There were consequences for behavior. African homininans ca. 2 Ma seem to have become aware sometimes that the physical affordances of some kinds of stone indicated that these were suitable for fashioning large cutting tools (see Appendix 2). Some, including 'handaxes', have been found among Proboscidean skeletal remains (M.D. [175], pp. 64–66), implying cooperative activities. Getting and fashioning stone for subsequent use suggest awareness of potential, albeit delayed, advantages for lessening the efforts needed to acquire bioenergetic resources. Such behavior draws on short-term and long-term WM, episodic and procedural memory, and prospective memory or forethought, to a degree well beyond the capacity of living anthropoid apes. Short-term energetic costs when weighed against unpredictable medium-term gains could have led to such activities being at first infrequent or sporadic rather than widespread or commonplace, and accrual of reproductive advantage probably developed slowly over several hundred generations. Nevertheless, 'social transmission' of infrequent human behavior need not have been responsible for reproduction of that behavior which sometimes and in some places could have been generated independently by '*hierarchically mechanistic minds*' widely separated in space or time, giving rise to reappearances in a worldwide '*snakes and ladders*' archeological record

The generative process can be referred to the formal terminology of the free energy principle (FEP) applied to ecological niche construction [66,68] by saying that selection of adaptive actions by organisms involves their assessment of the alternatives in terms of the expected free energy expressed as the combination of epistemic and pragmatic affordances. Of particular relevance to the '*snakes and ladders*' interpretation of the Pleistocene record is that a mathematical consequence of the Markov Blanket formalism[10] underpinning the variational ecology model implies vastly slower rates of selective adaptation at the phylogenetic timescales than the ontogenetic timescales at which individual phenotypes, including behavioral dynamics, develop within its lifespan, or the timescales of cellular or intracellular responses, measurable in days, hours, minutes, seconds or even milliseconds. In other words, individuals faced with a surprisal, for which VFE can be regarded as a proxy, were unlikely to introduce novel behaviors that could gain a ready foothold within Early Pleistocene communities before communicative skills developed in some of them, which widened the social scope for active inference and perhaps had evolved by natural selection within a shared framework of adaptive prior beliefs, favoring alignment of common expectations and joint activities that affected their ecological niche [176]. Development of communicative skills may well have been uneven in communities that, in any case, were very widely dispersed in time and space, and it would be unwise to presume that all of those were equally eloquent who were responsible throughout the Old World for archeological assemblages of the Early and early Middle Pleistocene.

5. Concluding remarks

Innovative behavior (e.g., fashioning 'handaxes') enacted during the Pleistocene by individuals who were unable to keep their 'cognitive surprise' bounded were ignored by onlookers (and perhaps by protagonists themselves) who failed to register it or lacked the cerebral architecture that could have enabled them to envisage contexts where it might have been advantageous. Neurobiological evolution in the brain of early *Homo* must have been influenced by genes and by neuroepigenetic modification of genetic expression, about the evolution of which we know next to nothing, but which need not have taken place necessarily hand in hand with the evolution of genes involved with shaping skeletal morphology during evolution in the genus *Homo*. We consider it plausible, and in accord with epistemologically sound, scientific principles, that neuroepigenetic and genetic processes led to an evolved neurobiological propensity toward cerebral neuronal circuitry that involved structural priors that impinged on individual (ontogenetic) and collective (phylogenetic) variational free energy in line with the free energy principle, and that were selected in favor of modulating biological and technological behavioral responses sporadically to salient and novel circumstances confronted by early *Homo*. The implicit nesting of free energy minimizing processes at phylogenetic (evolutionary), and ontogenetic (somatic) timescales provides, on the one hand, a mechanistic link between sentient behavior — and its 'social transmission' — and the natural (Bayesian) selection of the most likely phenotypes in a co-constructed niche. On the other hand, the implicit separation of timescales and circular causality renders self-organization inherently *itinerant*; necessarily revisiting (free-energy minimizing) regimes of some vast state space — in exactly the same way evinced by a game of '*snakes and ladders*.' This *itinerant* evolution may be reflected in the Pleistocene record of irregular regularities or regular irregularities — in time and space — of artifacts such as stone 'handaxes' which appear, disappear, and reappear, more resembling, as it were, a '*snakes and ladders game of life*', rather than a monotonic, uninterrupted '*Ascent of Man*'.

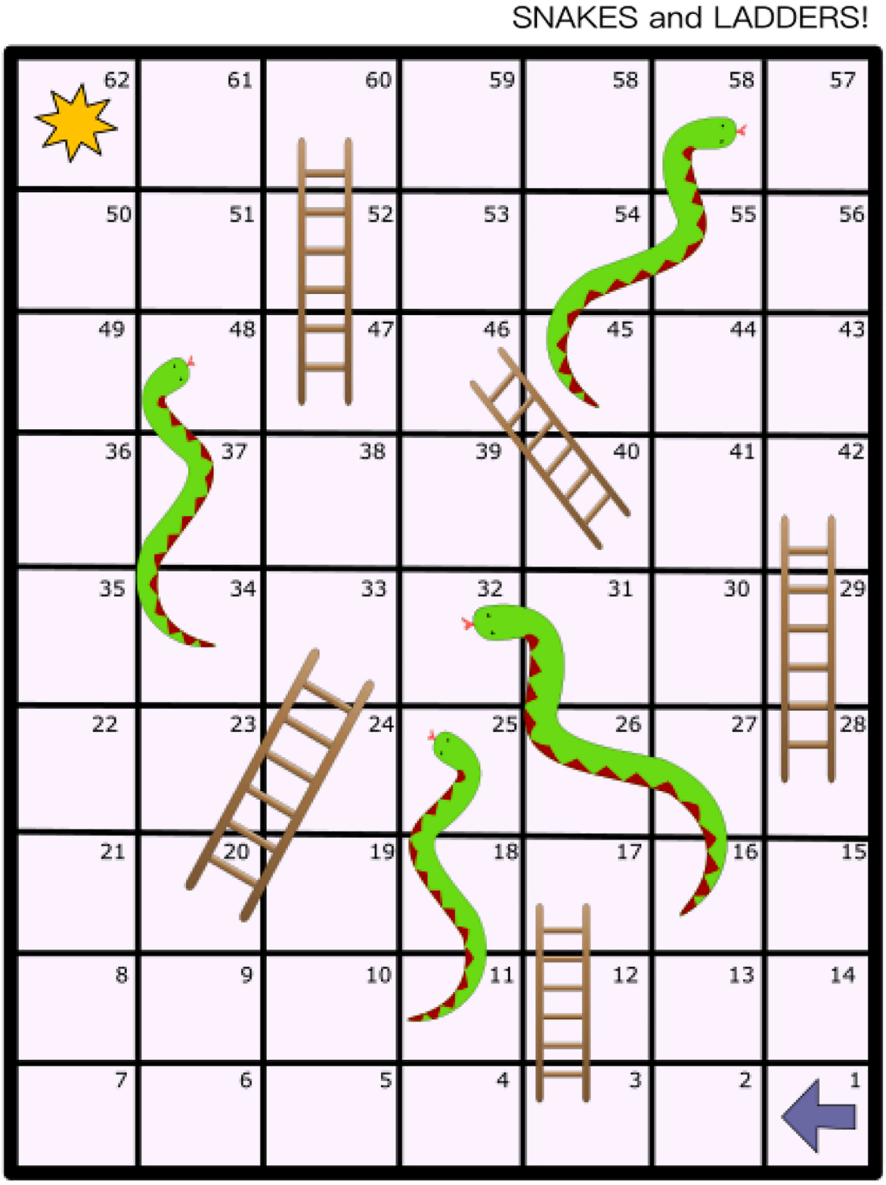
6. Footnotes

[1]Wikipedia explains that: "***snakes and ladders***" *is a board game for two or more players regarded today as a worldwide classic… It is played on a game board with numbered, gridded squares. A number of "ladders" and "snakes" are pictured on the board, each connecting two specific board squares. The object of the game is to navigate one's game piece, according to die rolls, from the start (bottom square) to the finish (top square), helped by climbing ladders but hindered by falling down snakes. The game is a simple race based on sheer luck, and it is popular with young children… The size of the grid varies, but is most commonly 8 × 8, 10 × 10 or 12 × 12 squares. Boards have snakes and ladders starting and ending on different squares; both factors affect the duration of play. Each player is represented by a distinct game piece token. A single die is rolled to determine random movement of a player's token in the traditional form of play; two dice may be used for a shorter game. Each player starts with a token on the starting square (usually the "1" grid square in the bottom left corner, or simply, at the edge of the board next to the "1" grid square). Players take turns rolling a single die to move their token by the number of squares indicated by the die rolled. Tokens follow a fixed route marked on the gameboard which usually follows a boustrophedon (ox-plow) track from the bottom to the top of the playing area, passing once through every square. If, on completion of a move, a player's token lands on the lower-numbered end of a "ladder", the player*

moves the token up to the ladder's higher-numbered square. If the player lands on the higher-numbered square of a "snake" (or chute), the player moves the token down to the snake's lower-numbered square. If a 6 is rolled, the player, after moving, immediately rolls again for another turn; otherwise play passes to the next player in turn. The player who is first to bring their token to the last square of the track is the winner."

https://en.wikipedia.org/wiki/Snakes_and_ladders

Wikicommons:



"*…if you land on the bottom of a ladder you climb up to that square, if you land on the head of a snake you slide down*"

Original URL https://openclipart.org/detail/292313/snakes-and-ladders-board-game

[2]*Itinerancy*: for an instance of its specialized usage in mathematical considerations in neuroscience, see [177].

[3]*The Ascent of Man* is the title of a television documentary and the book [178] based on it by the mathematician Dr. J. Bronowski (1908–1974) published in 1973 in London by the British Broadcasting Corporation and at Boston, MA, by Little, Brown & Co., with a Foreword by Richard Dawkins. The title alludes to Darwin's *The Descent of Man* (1871). Plate 11 on p. 39 of an "Acheulian hand axe" seems to be a photograph of a 'cleaver'. Bronowski had been a brilliant mathematics student ('senior wrangler') at Cambridge University where he was awarded his doctorate. He was a mathematician with an interest in physics. He taught at the University of Hull, though during World War 2 he became involved exclusively in military research, until the atomic bombing of Hiroshima led him to turn his attention to peaceful matters. Among them was a statistical analysis that he undertook in 1950 of an *Australopithecus africanus* child's skull (from Taung, South Africa). He shared the worldwide interest of scientists in the growing impact of genetic research on Darwin's theory of evolution by natural selection. When in 1960 Jonas Salk founded the Salk Institute for Biological Studies, at San Diego CA, Francis Crick and Jacob Bronowski were prominent consultants, and in 1964 Bronowski became a Resident Fellow and

Assistant Director of the Institute, and was its Deputy Director at the time of his death in 1974. He was a tireless communicator of science to a wide public audience, and wrote several books, among which is his widely-read *The Origins of Knowledge and Imagination* based on lectures he had given at Yale and published posthumously in 1978 by Yale University Press. The evolution of technology and knowledge during the biological evolution of humankind was the theme of *The Ascent of Man*.

[3]Simple stone artifacts occur in later contexts, e.g., quarries where Neolithic axeheads were prepared, sites where gun-flints were knapped, or where, in twentieth-century Spain, pickaxes and sledgehammers were wielded at rock outcrops to strike off flakes for insertion into wooden threshing sleds or to break up nodules coated with calcium carbonate into pieces that then were burnt for lime at on-site kilns.

[4]We use the word *affordance* in the sense of [179,180] (see also [181], passim). Plausibly, the affordance of acutely-angled edges of a stone for flaking by homininans could indicate the "attunement of cognitive constraints" (cf., [182]).

[5]The approach adopted here can be broadened to embrace the manipulation or modification of materials obtained from animals (e.g., bones, horns, sinews, skins, fleeces, hair, bladders, fats, tusks, milk, honey, feathers, shells), plants (e.g., wood, fibers, gourds, oils, resins, pitch, seeds, nuts, spices), minerals (e.g., powders, tar, clays, fluxes, metals), and the manipulation, ignition, and heat-control of fire (hearths, ovens, kilns, furnaces). Increasingly complex extractive and concomitant or consequent procedures appear in several parts of the world at various times towards the end of the Late Pleistocene, including increased killing, taming, culling, reaping, and controlled breeding of domesticated animals and plants, with the development of technologies such as cordage, matting, basketry, weaponry, spear-throwers, wood-working, carving, archery, harpoons, traps, nets, hooks, needles, drilling, digging, reaping-knives and sickles, grinding, polishing, engraving, sculpting, painting, pottery, plastering, milling, mining, metallurgy, tree-felling, carpentry, building, water-craft, machinery, signing-writing, vehicles, cookery, brewing, etc. Once again, some seem to have arisen separately and independently, and with different outcomes at different places and times: a well-known instance is that of wheels, which, in pre-Columbian Mexico ([183] and references therein), were attached to 4-wheeled effigies or toys, but neither handcarts nor wheelbarrows were made that could have been used easily in low-lying Vera Cruz where wheeled effigies are found.

[6]Tooling stone and stone tools (see also Appendices 1, 2, and 3):

A group of manually-flaked artifacts that are *not* 'large cutting tools' (LCTs) consists of small 'muffin'-shape cores (often but not always discoidal) where a notional secant plane separates two unequal volumes, of which at least one and sometimes both surfaces were flaked, but from one surface only of which one or more usable flakes were removed, sometimes by repetitive striking. The flakes can be more or less regular in shape depending on the extent to which the core had been modified or prepared beforehand, sometimes by peripheral knapping of small facets that could favor removal, variously, of triangular, oval, or oblong flakes, by subsequent centripetal or orthogonal flake-removal. Cores were abandoned often, usually when they had become too small for further removals. Early examples of the centripetal technique are attributable to *Homo erectus* because they have been excavated ca. 1.6–1.2 Ma at African locations that have 'handaxes' [184,185]. It has been detected in Italy ca. 1.3 Ma [186–188] and ([189], p. 7 Fig. 3a,b) at a Spanish site with a 'handaxe' (Appendix 2, Fig. 1) that dates from 0.99 to 0.77 Ma ([148,149,189,190], 2022).

A Pleistocene spatiotemporal '*snakes and ladders*' scenario for obtaining flakes in such a manner is not implausible, though, to judge from some outcomes, the manual sequences of this flake-removal technique need not always have been predetermined or envisaged beforehand [191,192]. Just as with a tendency towards increasing congruence of 'handaxe' symmetry after ca. 0.5 Ma, so, also, there developed thereafter an increasing regularization of the outcomes of alternative techniques of flake-removal, particularly from prepared cores in some parts of the world and likely fostered by inter-group contacts.

Strengthening the edges of flakes by secondary knapping ('retouch') could enhance and prolong their utility. Such secondary modification is found only sporadically before the Middle Pleistocene but thenceforth became more frequent; it is seen also on many flakes that had been struck from simpler cores that had not undergone preparation beforehand. Secondary modification of flakes may have facilitated the fashioning of wooden spears that appeared in the mid-Middle Pleistocene. It also may have facilitated hafting of stone flakes. By ca. 0.2 Ma stone flakes bearing traces of an adhesive substance (e.g., tar, pitch) suggest the hafting of tools. Somewhat later on, a few more examples come from the early Late Pleistocene. They imply an ability to combine three different materials, namely, a stone flake, tar/pitch, and a haft of wood or bone. Moreover, the elaboration of pitch for adhesive use implies an ability to control heat. The sporadic, intermittent, spatiotemporal discoveries are compatible with a '*snakes and ladders*' interpretation.

The alternative ways of modifying stones that appeared after 2 Ma, namely, on the one hand, to make 'large cutting tools' (LCTs), including 'bifacially-flaked large cutting tools' (BFLCTs) such as 'handaxes', and, on the other, to remove usable flakes from cores that also may have undergone modification sometimes in order to facilitate their removal, implies not only that *Homo erectus* could carry out two different irreversible chains of the manipulative reduction of stone, but also possessed cerebral capacities for haptic and short-term working memory, long-term memory, and prospective memory, that were greater than those of earlier homininans or the extant paninans. Artifact diversity implies that, at times, *Homo erectus* could recognize not only the *irreversibility* of their respective chains of sequential manual reduction of stone, but also their correspondence to *distinct* morphological sets, which at least is comparable to the kind of 'second-order' cognition that is understood implicitly by preverbal toddlers nowadays who sometimes achieve subsequent 'third-order' hierarchical arrangements ([193–195],; cf., [196–203]; cf., 'second-order representations' [203]; cf. 'secondary representations' [204]). Conceivably, heterochronous evolution enhanced such cognitive capacities, though they may have been less 'representational' and more emergent neurobiological phenomena [205]; nevertheless, representation is not incompatible with the concept of a 'hierarchically mechanistic mind'. Immediate cost-benefit considerations, from the standpoint of the FEP, probably laid a heavy brake on the adoption of technological innovation.

[7]Parr et al. [21], pp. 192–193] consider that "*the brain is a prediction machine, endowed with a generative model: a probabilistic representation of how hidden causes in the world generate sensations (*e.g.*, how light reflected off an apple stimulates the retina). By inverting this model, it infers the causes of its sensations (*e.g.*, whether I am seeing an apple, given that my retina is stimulated in a certain way). This view*

*of perception (aka perception-as-inference) has its historical roots in the Helmholtzian notion of unconscious inference and, more recently, in the Bayesian brain hypothesis. Active Inference extends this view by bringing action control and planning within the compass of inference (aka control-as-inference, planning-as-inference). Most importantly, it shows that perception and action are not quintessentially separable processes but fulfill the same objective. We first described this objective more informally, as the minimization of a discrepancy between a model and the world in two ways: by changing one's mind to fit the world (perception) or by changing the world to fit the model (action). These can be described in terms of Bayesian inference. However, exact inference is often intractable, so Active Inference uses a (variational) approximation (noticing that exact inference may be seen as a special case of approximate inference). This leads to the second, more formal description of the common objective of perception and action, as variational free energy minimization. This is the core quantity used in Active Inference and may be unpacked in terms of its constituent parts (*e.g.*, energy and entropy, complexity and accuracy, or surprise and divergence). Finally, we introduced a second kind of free energy: expected free energy. This is particularly important during planning, as it affords a way to score alternative policies by considering the future outcome that they are expected to generate. This too may be unpacked in terms of its constituent parts (*e.g.*, information gain and pragmatic value, expected ambiguity and risk).*" In other words, expected information gain and expected cost can be rearranged into terms corresponding to ambiguity and risk.

[8]Mirror-neuron circuits in monkey prefrontal and parieto-temporal cortices of the brain track observed manual actions, be these performed by the monkey itself or by its handler [33,206–217]. Cerebral neuroimaging shows analogous responses in humans (e.g., [218]), in prefrontal, motor, and parietal cortices, as well as [219] medial temporal cortex. Whilst neither is involved directly with memory, nor with 'embodiment' of motor cognition (cf., [220]), mirror neurons nevertheless support cognition [221] by registering sensitivity to perceived actions of self or others. They subserve working memory via perceptual-mnemonic components for computing outcomes ('goals'; cf., [222]) and plausibly are important for procedural memory [24]. Monkey mirror-neuron circuits respond to transitive actions that are observed, though, in contrast to human infants, intransitive actions, mimed silently, elicit no response, from which it may be wondered whether monkey neuronal circuitry is biased by an inherent pre-potent impediment against responding to silent mime, and whether a similar pre-potent impediment existed in human precursors, which could have diminished the contribution of mirror-neuron circuits to the evolution of human working memory. Our working memory affords us the cognitive flexibility for weighing 'top-down' predictions against 'bottom up' prediction errors, thereby enabling our '*hierarchically mechanistic mind*' to register unexpected sights, and because of its depth of planning it allows us to recognize a series of movements, whether enacted by us or by others, as being interconnected while being at the same time related to a final goal, thereby enabling us to recognize a sequence of actions as connected in the service of a particular goal (as opposed to seeing an unintelligible series of disconnected actions).

[9]Lehmann et al. [223] consider that "*Active inference models formalize the dynamics of the brain, claiming that it instantiates a generative model: the networks of the brain, on this view, produce predictions of what should be sensed next. These predictions are compared against sensory input and (subpersonal Bayesian) beliefs — on which predictions are based — are updated when error or discrepancy is detected. This results in Bayes optimal inference about the most likely cause of the sensory input… Crucially, the causes of sensory input can include the agents own action, which means actions or plans are also inferred; leading to active (planning as) inference…. In the past decades, there has been a shift away from conceptions of the brain as a passive organ that merely awaits and reactively processes bottom-up sensory input, to conceptions that emphasize the fact that cognition and perception find themselves in a mutual embrace with action. These are enactive, ecological, pragmatist, and embodied approaches to the study of the brain…. One version of this view casts the brain as a phantastic organ that actively generates predictions of its environment…. In this model, the dynamics of the brain are said to embody or instantiate a generative model that generates predictions that are compared against sensory input, resulting in a Bayes optimal inference about the most likely cause of the sensory input… According to the active inference framework, these predictions are compared to sensory input continuously throughout the hierarchical networks of the brain… To model the extrapersonal and internal* (i.e.*, bodily) world in an optimal way, the brain is thought to minimize prediction error throughout the hierarchical generative model. Heuristically, on this view, when predictions and sensory data clash, conflict is resolved in one of two ways: either by updating one's beliefs in a Bayes-optimal manner (perception and learning;* i.e.*, changing the internal model to make it more predictive of current sensory input), or changing the world to make future data consistent with one's expectations* (i.e.*, action)…"* (… = bibliographical references that are omitted here for ease of reading).

[10]*A Markov Blanket is the set of states that statistically isolates (insulates) internal (systemic) from external (non-systemic) states, such that changes in internal states are mediated by the states of the MB. The MB itself can be partitioned into active and sensory states, which are defined by the following relations: internal states do not influence sensory states, and external states do not influence active states. Now, we should note that the terms 'active' and 'sensory' are potentially misleading. They are only meant to capture relations of statistical dependence between random variables. This will be crucial to our argument…, as things that we would not readily describe as literally acting or sensing in any meaningful sense can still be captured with this formalism, since it entails only a statistical enshrouding of systemic states from external ones, and the systematic statistical partition of the whole organism–niche system.*" ([68], p. 190).

Authors' declaration

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix 1

Clarification of some classificatory terms used in the text

We think it helpful to introduce readers unacquainted with human evolution to some widely-used terms — and spatiotemporal demarcations — relevant to humankind's deep past. Biologists assign humans and great apes to the hominid *family* of Hominidae, which is divided into the well-defined *subfamilies* of Ponginae (orangutans) and Gorillinae (gorillas), and the less homogeneous hominin *subfamily* of Homininae (homin*ins*: chimpanzees, bonobos, humans). Zoologists separate the Homininae subfamily into the *tribes* Panini (chimpanzees, bonobos) and Hominini (homin*ines*). We follow the practice of those paleobiologists who separate the tribes into *subtribes* of Paninina (paninans: chimpanzees, bonobos) and Hominina (homin*inans: Homo sapiens* plus extinct taxa, e.g., *H. neanderthalensis, H. erectus, Australopithecus, Paranthropus*, and *Kenyanthropus*); thus, homin*inan* is a collective noun for humans and phylogenetically-related, extinct bipedal hominids. The practice is regarded as pedantic by many anthropologists and archeologists who shudder at the cacophonous sound of 'homininan', but we regard its exclusivity as having the advantage of classificatory precision, unlike 'hominid', 'hominin', and 'hominine' which have the classificatory drawback in common that they include not only bipedal Homininae but also species that are not *habitually bipedal* as well as fossil taxa that have not been shown to have been habitual bipeds. Evolutionary separation between paninans and homininans may have begun ca. 6 Ma. Our genus *Homo* evolved from bipedal australopithecine homininans, and appears in the African geological record just before the Pliocene epoch gave way ca. 2.58 Ma to the Pleistocene epoch. The Pleistocene has three main phases, based on geophysical, palaeoclimatological and paleontological criteria, namely: ca. 2.58 – ca. 0.77 Ma, Early (or Lower) Pleistocene; ca. 0.77 – ca. 0.13 Ma, Middle Pleistocene; ca. 0.13 – ca. 0.012 Ma, Late (or Upper) Pleistocene. The geological Tertiary period ends with the Pliocene epoch; the Quaternary period consists of the Pleistocene epoch plus the Holocene or Recent epoch (ca. 0.012 Ma – present).

For readers unacquainted with the Paleolithic or Old Stone Age archeological record, here is a bird's-eye view. During the early (or 'Lower') Paleolithic (ca. 3.4 – ca. 0.4 Ma), assemblages have been excavated of stones bearing concave scars where flakes had been detached (they typify a 'mode 1′, or 'Oldowan', Paleolithic 'industry', named after assemblages from the Olduvai Gorge in East Africa). Reminiscent of impressions in fossilized beach sand left by clam shells, concave scars are attributed to the manual technique of 'conchoidal' flaking, whereby flakes can be struck off by a strong blow aimed at where the surface of a stone of suitable siliceous petrology affords the striker an angle of no more than 90°. Conchoidal detachment of flakes by natural processes usually can be excluded, e.g., the churning of river pebbles under a waterfall, or the rolling of beach pebbles by waves and tides. Those processes cannot account for those cases where overlapping conchoidal scars retain stigmata that reflect impacts of successive blows aimed along the same part of the surface of a stone, which were caused by percussive striking with a hammer-stone (e.g., a hard pebble). Because contiguous scars can extend and increase an acutely-angled area, further ('bidirectional') percussive striking by counter-blows on it can produce sharp, narrow edges, notably where scars on each side intersect at edges. Sharp edges typify artifacts designated 'choppers' or 'chopping tools' that could have been held in the hand.

Growing cognitive appreciation by homininans that acutely-angled edges provided an *affordance*[4] for further technical exploitation is presumed to have led to developments in the fashioning of hand-held stone tools (cf., [224]). From ca. 1.76 Ma there are found stone artifacts known as 'handaxes' and 'cleavers'. They are regarded widely as typifying 'Acheulian', 'Acheulean', or 'mode 2′, Paleolithic 'traditions' (see Appendix 2). 'Handaxes' were fashioned by blows struck by hammer-stones that detached flakes from two opposed surfaces of stones that thus became 'bifacial' artifacts ('bifaces'). At Olduvai, stratigraphic considerations suggest that bifacial fashioning of stone developed from making 'choppers' that coexisted there with the earliest 'handaxes'.

'Handaxes' often have an amygdaloid (i.e., 'almond'-like) or 'tear-drop' shape, with sharp edges and two more-or-less symmetric opposing surfaces (hence 'bifacial'), though with a blunt 'butt' that is thicker and broader (and often easily held in an adult's hand) than the opposite end (i.e., distal to the butt), where the sharp edges converge and form usually a narrow thin 'tip' (or less often a short, sharp, bifacially-flaked convex or straight edge); many if not most 'handaxes' are at least 6 cm long. 'Cleavers' are artifacts with flaked sides that, instead of converging at a tip, end at a broad, transverse, sharp edge. 'Cleavers' were made either by extraction of a large flake by striking a single blow from a suitably-fashioned stone, or by detachment from a large rock of a big flake the sides of which were modified later together with the 'butt' in order to form a handy cutting tool.

Small, chipped, stone artifacts of irregular shape, sometimes with knapped edges indicative of small-tool 'light-duty' use, are present in several early Paleolithic assemblages, well before 1 Ma. After 0.5 Ma a predominant feature of many assemblages was the preparatory fashioning of stone cores into various shapes that were suitable for repeated removal of flakes for use as small tools ('mode 3′, or Middle Paleolithic 'industries' in western Eurasia [including 'Levalloisian' and 'Mousterian' forms], or African Middle Stone Age 'industries'; see Appendix 2), though chipped stone artifacts of irregular shape and BFLCTs continued to appear (often found together, e.g., [225], p. 22 Fig. 10). After ca. 0.1 Ma, elongated stone flakes and linear 'blades', often showing finely-knapped edges or points, as well as bone and shell artifacts, come from several sites in Africa and also, after ca. 0.05 Ma, in central and western Eurasia ('mode 4′, or Late [or Upper] Paleolithic industries).

Paleolithic terminology can be confusing. It was ever thus (cf., [226], esp. pp. 128–168). We accept as being reasonable those definitions of 'Culture', 'Culture Group', 'Industry', 'Technocomplex', 'Tradition', and 'Type Complex', which were proposed by D.L. Clarke ([227], pp. 664–670). They offer a possible basis for a systematic classificatory hierarchy. In such a taxonomic hierarchy, the term 'Acheulean Culture' seems out of place, and therefore its use can induce confusion ([227], p. 31). Nevertheless, some Paleolithic archeologists defend it (e.g., [228]), though others criticize it (e.g., [229]). In the spirit of Shea [14,230], we have misgivings about, and therefore will be sparing in our use of, fundamentally locational descriptors (e.g., 'Oldowan', 'Acheulean', 'Levalloisian', 'Mousterian', etc.) when referring to Paleolithic artifacts and assemblages that are separated widely in time and space. We also share the misgivings of Bar-Yosef [[231], p. 483] about the 'modes 1, 2, 3, 4, etc.' that had been proposed by J.G.D. Clark [[232], p. 31;

[233], pp. 74–79] as a way of indicating supposedly cumulative evolutionary (albeit homotaxial) development of Paleolithic technology. We shall use them sparingly, because, notwithstanding Clark's injunction that none of his 'modes' should be regarded as the prerogative handiwork of any homininan species in particular, often they have been elided into insubstantial conjectures by other writers about 'cultural' behaviors or 'mental templates' that could have evolved differentially in different species of *Homo* represented in the Pleistocene fossil record.

Here, paleoanthropology adds a further layer to the Paleolithic complexity by assigning various skeletal remains that date from ca. 2 Ma onward to the fossil species *Homo erectus*, widespread remains of whose successors belong to *Homo sapiens* in Africa after ca. 0.3 Ma, and after ca. 0.45 Ma in western Eurasia to *Homo neanderthalensis* before being replaced by *Homo sapiens* ca. 0.05–0.04 Ma. (We are not concerned with paleoanthropological debates about whether remains assigned to *Homo heidelbergensis* represent the first successors throughout the Old World of *H. erectus*, or whether *H. heidelbergensis* should be used only when referring to Eurasian precursors of *H. neanderthalensis*, with *H. rhodesiensis* being applied to African intermediaries between *H. erectus* and *H. sapiens*). The foregoing thumbnail sketch indicates not only the different conceptual priorities of geology, archeology, paleoanthropology, and homininan paleontology, but also, especially, that their **spatiotemporal demarcations are *not* coterminous**. We share the outlook of the late Berkeley Professor F. Clark Howell (1925–2007) that "*paleoanthropology should be a science that integrated archaeology, geology, biological anthropology, ecology, evolutionary biology, primatology, and ethnography… he helped transform paleoanthropology from a discipline focused on discovering hominid fossils to one that investigates the paleontology, geology, geochronology, archaeology, and paleoenvironment…*" ([234], p.109).

Appendix 2

What's in a name?

'Handaxes' do not look much like the axes with which we chop firewood or fell trees. Names given by archeologists to Paleolithic artifacts "***have no functional significance***" ([235], p.84; her emphasis), which our use of inverted single commas keeps in mind. Microscopic detection of polish ('micropolish') on the edges of some Middle Pleistocene 'handaxes' from England indicates that some were applied to animal tissues [236–242] and a residue of adipocere adhering to a 'handaxe' from Israel and microscopy indicate use on animal tissue [243]. At Olduvai Gorge, 'handaxes' lay among Proboscidean skeletal remains excavated in Early Pleistocene sediment (M.D. [175], pp. 64–66). When used to butcher mammals that weigh >100 kg 'handaxes' and 'cleavers', especially those BFLCTs with a cutting edge of about 8 cm, were found to be more efficient than 'choppers' and stone flakes ([244,245], cf., L.S.B. [246] [and 1960], p. 58; cf., [247]; cf., [240]; cf., [248]). 'Cleaver' invokes an analogy with a butcher's meat-cleaver; Parfitt and Roberts [249], Roberts [250], and Roberts et al. [251] suggested 'cleavers' were used for cutting (more than for cleaving) during the butchery of horses at the Middle Pleistocene site of Boxgrove. In the East African Early Pleistocene, application to plants is evident from phytoliths adhering to some 'handaxes' [252] and flakes [253], but whilst micropolishes on some flakes from ca1.5 Ma imply application to plants, on others it points to use on animal tissues [254], though micropolish on two 'handaxes' of ca. 1 Ma from the South African Wonderwerk Cave indicates their use on plants [255], and a similar use is indicated by micropolish detected on some Middle Paleolithic bifaces [256]. Early Paleolithic stone artifacts probably were used in expedient fashion on a variety of different materials, whether for extracting bioenergetic resources or for modifying the properties of other materials, such as wood or bone (e.g., the 1.4 Ma 'handaxe' from Konso, in Ethiopia, that was fashioned on part of a hippopotamus femur: [257]); despite their durability, 'handaxes' made of bone are uncommon (two Early Pleistocene examples come from Olduvai, and there are a few from Middle Pleistocene sites in the Levant and Europe).

Longitudinal and transverse symmetry are widespread features of 'handaxes'. 'Handaxe' symmetry is seen as early as ca. 1.7–1.6 Ma [258]. It is interpreted often as reflecting a deliberate intention to create a preconceived artifact [259], implying a neurobiological propensity for cognitive awareness, from time to time, that an imagined three-dimensional shape or form, such as that of a 'handaxe', could be fashioned from a lump of stone ([260], pp. 64–74, [17]; cf.,[30,261–263], pp. 61–101). Nevertheless, before 'handaxes' appeared in the Early Pleistocene archeological record, the presence of flaked 'spheroids' could reflect an imagined three-dimensional shape [264] and has led to a proposal that 'spheroids' are indicative of late 'Oldowan' assemblages [265].

It is widely accepted by Paleolithic archeologists that morpho-technological regularity, perceivable in their forms, marks 'handaxes' out from manually-flaked stones lacking it, regardless of whether these come from sites where 'handaxes' are present or absent. Albeit often imprecise and rough, the double symmetry characteristic of 'handaxes' can be considered in terms of one notional secant plane at a right-angle to another. How could appreciation of this have arisen in members of early *Homo*? How did it arise? How often could it have arisen? Did it appear and disappear at several times and places? This possibility has been mentioned tentatively from time to time (e.g., [231], p. 486; [266], p.131; [229,267–269], pp. 39, 262–263).

Or did it arise once only, and, thereafter, not only was handed down skillfully from one generation to the next, but also transmitted as a skill from one community to another, with far-reaching incidence in space and time? This possibility is held to be plausible by several Paleolithic archeologists and paleoanthropologists. It seems to rest on a 'progressivist' supposition that BFLCTs afforded early *Homo* functional advantages that were of adaptive value, for survival and burgeoning reproductive success, by enabling the exploitation of life-sustaining resources over a wide range of ecozones and biotopes, with consequent demographic and geographic expansion. This sanguine notion was viewed with skepticism by Isaac [[270], p. 193] who remarked that: "*the assumption of regularity in functional determinism is just as dangerous as the assumption of regularity in culture history*".

Instead, Isaac suggested ([270], p. 185) that "*stochastic change*" might account for "*drifts*" in "*standardized forms such as handaxes and with regard to assemblage composition,*" and that ([270], p. 186) "*the persistence of the basic features of Acheulean stone tool assemblages over large parts of three continents during approximately a million years may be connected with features of the cultural transmission system as*

well as with neurophysiological limitations on the craftsmen's 'inventiveness'" in spatiotemporal contexts characterized by "*a low density network of population (bands) with considerable variability in the permutations of a very restricted number of artefact traits.*" Ergodic models specifically were referred to by the Cambridge University archeologist David Clarke ([271], p. 28) for the useful part they had begun to play in geographic spatial analysis, and he wrote that their adoption in archaeology could help toward throwing light on the processes that likely were involved in generating the spatiotemporal distributions of the material remains of former human behavior. This is because ergodic models can relate to those dynamic systems or stochastic processes which, given enough time, will include or impinge on all points throughout the space wherein the system or process moves in a uniform and random manner. Clarke had a deep interest in dynamic systems and stochastic processes that likely brought about the transformative evolution of "*different states of shared groups of multistate artefact types*" in dispersed "*homeomorphic assemblages*" ([227], p. 262).

With regard to the presence in Africa, Asia, and Europe of 'handaxes', Isaac rejected the possibility of their technological evolution in parallel from choppers but separately and independently in different continents ([270], p. 187) because it is uneconomical from the standpoint of Occam's Razor. However, if Isaac's rejection stemmed from his assuming that always a 'mental template' had to have been transmitted more or less (quite often *less*) then an alternative can be considered. It is that the extent of the "*neurophysiological limitations*" depends on a person's neurobiological propensity to his or her enactment in modifying stone. The alternative can be contemplated in terms of the advice given to archeologists by Clarke [[227], p. 79] not to dismiss out of hand a 'Converse-Occam' approach to a problem, but, instead, to leave open a way for considering alternative interpretations.

This seems especially appropriate to those problems for which there can be developed a plausible, coherent, scientific explanation based on first principles. Such is our recourse to the FEP and active inference with regard to the matter of appearances, disappearances and reappearances of 'handaxes' in the intercontinental '*snakes and ladders*' archeological record. We wish to make clear that our standpoint is unrelated to (though not necessarily incompatible with) the proposal of a null hypothesis of phylogenetically innate 'latent' spontaneity, which was put forward by Tennie et al. [272].

What's in a name?

What does 'Acheulian' mean? What does it stand for? Named after the French site at Saint-Acheul by Gabriel de Mortillet [273], the concept of 'Acheulian' was criticized for its vagueness by Ernest d'Acy though de Mortillet [274] replied that its broad scope was an advantage in the same way that our concept of 'knife' embraces a wide range of different tools today. A century-and-a-half later, the dispute rumbles on. It can be unpacked into two intertwined matters, namely, (a) whether an Acheulian 'culture' or 'tradition' ever existed or not (and if so, where and when?), and (b) whether or not 'handaxes' and 'cleavers' are always evidence of it (or even a *sine qua non* for its identification). A third strand (c) has been introduced in recent decades, which refers to human cognitive neuroscience and its homininan neurobiological evolution in relation to the appearance of 'handaxes' and 'cleavers' soon after 2,000,000 years ago.

Returning briefly to (a) and (b), most archeologists discount a proposal derived from some African studies that "*there should be no less than 40–60 per cent of bifaces if an industry is to be classed as Acheulean*" (M.D. [175], p. 270; cf., [235]) because in several European 'Acheulian' assemblages 'handaxes' and 'cleavers' form a minuscule percentage of flaked or chipped stone artifacts present (often barely 2%: [229], p. 25). The 'handaxe' shown here in Fig. 1 is the only BFLCT among the numerous Paleolithic artifacts excavated in a

Fig. 1. An early 'handaxe' and a 'chopper' from Western Europe (scales in centimeters). Fashioned on a limestone cobble, the only 'handaxe' (left) found at Cueva Negra del Estrecho del Río Quípar (southeastern Spain) was excavated in a layer bedded between over- and underlying levels that yielded an abundant of various small artifacts (all less than 6 cm long) of chipped chert, limestone, and quartzite (34 are illustrated in [189], pp. 6–16, Figs. 2a–c, 4a–m,5a–s) comparable to those surrounding the 'handaxe' and a flaked limestone cobble 'chopper' (right) excavated close to it in the same layer, where they all could suggest an 'activity area' of ca. 2 m^2s 5 cm thick ([225], p.22, Fig. 10), about 1.5 m in sediments that had accumulated to a depth of over 5 m on the underlying bed-rock of the cave between 0.99 and 0.772 Ma [149], probably during the marine isotope stage of MIS-21, between 0.867 and 0.812 Ma, when temperate conditions prevailed and sporadic overflow from an erstwhile swampy lake washed sediment into the cave. The 'handaxe' could have lost during use because the break was not recent. The 'handaxe' and 'chopper' are the only 'heavy-duty' fashioned artifacts to have been found at the site where excavation campaigns have been carried out regularly since 1990. Both artifacts are of the micritic limestone that characterizes the Jurassic Lower Middle Lias in mountains near the cave; X-ray diffraction of powder scraped from the artifacts and x80 optical microscopic petrography found them to consist of 94% calcite and 6% quartz that contributes to their hardness. (Photographs by courtesy of M. López Martínez and ©MUPANTQUAT).

layer at the Spanish site of Cueva Negra del Estrecho del Río Quípar (see lists in Appendix 3), which has similar artifacts in layers above and below it. Furthermore, there are excavated assemblages that have no BFLCTs whatsoever, but where flakes have been interpreted as plausibly removed by 'Acheulian' reduction techniques (e.g., [275]; see also [276]). Our '*snakes and ladders*' proposal can take account of those *variations*. It also can account for appearances, disappearances, and reappearances of BFLCTs during at least 1500,000 years, in Africa, Europe, and Asia.

Strand (c) is a matter of the greatest importance. Once more, variation concerns us. Underlying morpho-technological aptitudes and skills seem to have been responsible for a range of various forms of bifacially-flaked artifacts, from 'handaxes' to 'cleavers' that is reported in several early Paleolithic assemblages [277]. A convincing explanation was offered by Gowlett [278], whose 'imperatives approach' embraces the wide variety observed in BFLCTs, not only on a local scale — even, indeed, in assemblages from a single site —, but also on the vast spatiotemporal scale of the Early and Middle Pleistocene in three continents. Gowlett's 'imperatives approach' could lessen "*the heavy cognitive load, perhaps especially on short-term working memory*" ([278], p 215) that might be imposed by otherwise having to intuit or conceive "*a multivariate object*" — such as a biface — and coordinate two-handed actions appropriately when fashioning it. Put simply, its maker has "*imperatives or pressing needs that must be balanced or traded off to get a solution. This behavior, responding to need, is likely to demand the handling of geometric concepts in the realization (packaging) of a solution… it is this very pressure for simple solutions that encourages certain decouplings of 'concepts', which we can begin to see as elements of design form*" ([278], p. 216). Although Gowlett [[278], p. 216] considered the 'imperatives approach' likely to have become "*imprinted*" in a "*cultural tradition*" (e.g., transmitted by social learning) he added that he would "*hesitate to say 'also in the human brain'*." We hesitate less, because we think his 'imperatives approach' is compatible with 'active inference' and enactive embodiment which are underpinned by the free energy principle. (His use of "*imprinted*" recalls the celebrated ethological research of the 1953 Nobel laureate Konrad Lorenz.)

There is something counterintuitive about the manual procedures involved in the initial preparation of a stone from which a 'handaxe' will be fashioned. It has to do with appreciating just which ones, among a variety of acutely-angled aspects on a stone, will be the ones, or the one, most likely to present those affordances that are the best for beginning an efficient sequence of flake-removals that will reduce the stone to an envisaged 'handaxe' outcome (cf., [228]). The difficulty of appreciating the best aspect to select initially, highlights the significance of watching and learning from an experienced practitioner [279].

Although transmission of the appropriate appreciation can take place by watching and learning from someone at work, social transmission of 'handaxe' preparation is far from being satisfactory as an explanatory panacea. It does not account for how the appreciation arose in the first fashioner ever, whose unprecedented actions produced a 'handaxe', nor how, or why, it was then transmitted to individuals who adopted it.

Are we to conjecture a unique neurobiological response, perhaps made possible by a fortuitous genomic configuration? This is improbable. Are we then to suppose that her cognitive attunement to the appropriate affordances on a stone in her hand led to an incorporated or embodied outcome of an unforeseeable spontaneous enactment? Was it from such extraordinary circumstances that there evolved a stone tool, the 'handaxe', the usefulness of which led to social transmission about how to reproduce one?

Was that responsible for the widespread presence of 'handaxes' in Africa and beyond during the middle of the Early Pleistocene, including in regions where already the flaking of stone was practiced? How far do conjectural inferences like those lie behind the conceit that an ascendancy of 'handaxes' reflects ascent of, as it were, an evolutionary 'ladder', by particular forms of early *Homo* endowed with cognitive and behavioral aptitudes?

A matter of practical concern, is that, if some Early Pleistocene stone-flakers were to have lacked appropriate fore-knowledge, were inexperienced (e.g., playful young children), clumsy, or unskillful, or had no experienced practitioner from whom to learn, or had abandoned uncompleted artifacts ('roughouts', 'preforms', and technically-unfinishable 'rejects'), then their erratic handiwork could have given rise to that variety of shapes of heavily-flaked chunky stones, including 'choppers', 'picks', or merely cobbles bearing traces of conchoidal flaking, which is found — often together with small chipped stones, flakes, and 'débitage' fragments or 'knapping waste' — in many excavated assemblages, including several that have 'handaxes.'

Where 'handaxes' are sparse in an archeological assemblage, or are found in only a few of the layers that form a stratified sequence at a site, they could have been fashioned by any individual who, albeit lacking in fore-knowledge, was endowed, nevertheless, with appropriate cognitive aptitude for their spontaneous manual creation in the *absence* of any social transmission by example. Learning from watching experienced practitioners need not have been the *only* way by which constraints on cognition could have evolved to become relaxed enough to enable appreciation of those affordances of a stone which in some of our distant ancestors had elicited the fashioning of a 'handaxe'.

Do some artifacts warrant the designation 'handaxe' more than others that at first glance seem quite similar in appearance? Do some merit the designation 'Acheulian' more than others? The questions have given rise to a voluminous literature that is beyond the scope of our review. In particular, several finds of BFLCTs in China have long preoccupied Paleolithic archeologists. Recently, Gao and Guan [[280], p. 137] considered that "…*handaxes in China are not a simple, single typological or functional entity. Variability and diversity can been* (sicut) *found in different assemblages and developmental stages and their origin may also have different sources and mechanisms. It is reasonable to suggest that the pick-like handaxe, as a variant of typological picks within Pick-Chopper Industries, evolved locally as part of large pebble tool assemblages… If handaxes are the result of hominid inmigration* (sicut) *or cultural influences from the West, such must have happened very early, probably when the initial Acheulian was developing in Africa and when pick-like handaxes prevailed... We believe that Acheulian or Acheulian-like assemblages with standardized handaxes and cleavers are more likely the result of outside cultural influence… especially in the Bose Basin that is close to the Indian subcontinent… In the Luonan Basin, we need to look for possible routes and directions for such in-migrations and interactions. On the other hand, cultural or technological convergence cannot be ruled out; that is, these standardized Acheulian-like implements could have originated locally and independently.*"

We think that our 'active inference' approach that draws on the free energy principle is compatible with interpretations of the

Chinese 'handaxes' as outcomes whether of "*drift*" caused by "*stochastic change* ([270], 185–186), or "*iterative founder effect (repeated bottlenecking)*" [281], or even, as Bar-Yosef [[231], p. 486] reminded us, of the possibility "*that different human groups in the Old World reinvented the bifacial knapping techniques*."

It is remarkable that there is widespread comparability of the principal morphological features of 'handaxes', given their presence in widely-differing biotopes that no doubt led to differential behavioral evolution of subsistence strategies and diets appropriate for human survival. 'Handaxes' are found at sites with contrasting paleoenvironments and different spatiotemporal contexts or paleoanthropological taxa [15]. This renders unlikely any notion (*pace* [282]) of a straightforward Mendelian genetic basis favoring natural selection for specific behavioral adaptations and thereby giving rise to a convergent outcome of making 'handaxes'. Other accommodative conjectures include interpreting fundamental similarity as indicative of activities not requiring direct application of the artifact in the extraction of bioenergetic resources. Those activities could include demonstrating skillful manual ('manly'?) prowess ([283]; but see [284,285]), or maybe the removal of sharp stone flakes to use as tools, in which case some 'bifacial pieces' or 'handaxes' could be left-over cores ([286,229], pp. 54–55; Noble and Davidson [287], p. 198).

Notwithstanding plausible flexibility of purposes and manual techniques underpinning 'handaxe' outcomes, the late Derek Roe, a renowned authority on African and European Paleolithic handaxes, remarked that we are "*confronted with the phenomenon that some prehistoric artifact assemblages seem to display a strong tradition of bifacial tool manufacture, whereas in others, bifaces are virtually absent… Explanation is certainly required, even if it may vary from case to case. If it can ever be satisfactorily shown that such differences relate to chronology, or to a genuine process of technological evolution, or to the traditional behaviors of different human groups, that would clearly be of the greatest importance. In the past, assumptions of precisely that kind were frequently made, although not often carefully argued*" ([288], p. 276).

Some scholars subscribe to a long-held conjecture that 'handaxes' formed part of a 'life support' package or tool-kit that early paleospecies of *Homo* bore, as a hall-mark from Africa, perhaps to Spain (cf., [289–292]). Absence of such a quasi-cultural package at early sites with *Homo erectus* beyond Africa (e.g., Dmanisi in Georgia ca. 1.8 Ma, and East Asian sites with *H. erectus*) is then explained *away* with self-serving conjectures such as that some *H. erectus* individuals likely left Africa *before* the package had been developed. Furthermore, there are European Middle Pleistocene Paleolithic assemblages with thousands of chipped-stone artifacts that lack handaxes, (e.g., Vértesszőlős, Hungary; Bilzingsleben, Germany; Isernia La Pineta, Italy), or have only small numbers irregularly distributed in different levels or deposits (e.g., Caune de l'Arago, Terra Amata, and Orgnac, France; Notarchirico, Italy; Swanscombe, England; Aroeira, Portugal; the Atapuerca sites of Sima de los Huesos and Gran Dolina, Spain), whereas at other sites 'handaxes' show significant presence (e.g., Boxgrove, United Kingdom), though notwithstanding the different representation of 'handaxes', all of those sites have provided skeletal remains (bones or teeth) of individuals, ultimate descendants of *Homo erectus*, commonly assigned to *Homo heidelbergensis*, which often include specimens with anatomical features that presage or belong to *Homo neanderthalensis*. In the late Middle Pleistocene, 'handaxes' were made by precursors of *Homo sapiens* in Africa (e.g., *H. sapiens 'idaltu'* from Herto in Ethiopia) and by Neanderthals and their ancestors in Europe. Nevertheless, the uneven spatiotemporal distribution of 'handaxes' is undeniable.

Plausibly, some early 'handaxes' in western Europe, particularly those made on smallish cobbles of locally-available stone suitable for conchoidal flaking, such as flint, chert, quartzite, limestone, etc., may owe very little indeed ([290], p. 14; [229], pp. 260–263; [189], pp. 52–56) to East African techniques of fashioning of 'handaxes' from big cobbles or large flakes of igneous rocks, but, instead, could represent local behavioral responses involving idiosyncratic personal enactment with stones. The technical skillfulness of those responses reflects both cognitive versatility and manual dexterity.

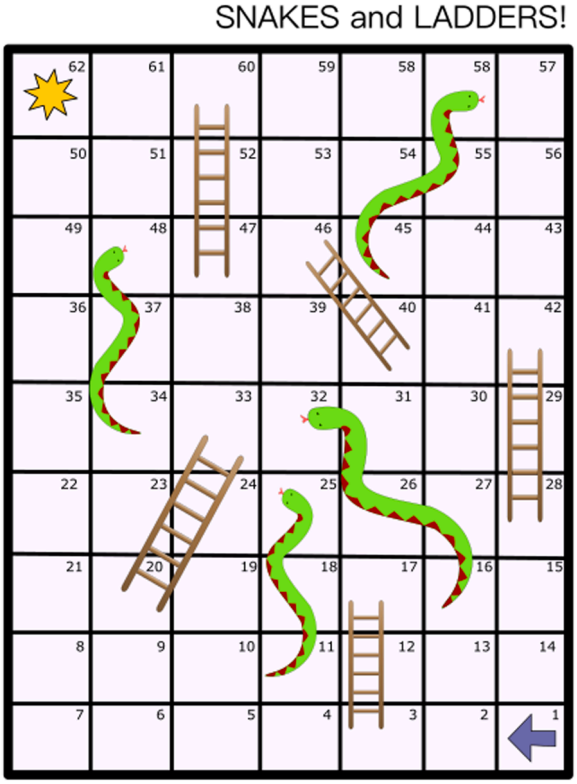
'Handaxes' undoubtedly appeared at different times during the Pleistocene (and perhaps in the Holocene) in widely-separated parts of the world [37,267,293] including Australia where a few have been published ([294,295], p. 21 and p. 24 Fig. 8; [296]) — though probably *not* Cuba (*pace* [297]). Intriguingly, a 'handaxe' was reproduced by an Australian Aboriginal stone-knapper who was shown one but never had made one before [298]. In Australia, as well as 'handaxes', there are sporadic instances of flakes struck from prepared cores, comparable in morphology to European Lower and Middle Paleolithic 'Levallois' flakes, and stone blades struck from prismatic cores, comparable with European Upper Paleolithic blades [299,300]. The infrequency of those sporadic cases, over the space of the Australian continent and the duration of $\geq$60,000 years of human presence on it, suggests that it is just as plausible that they were the handiwork of isolated local enactment by individuals, as that they reflect failures of long-term and long-distance spatiotemporal 'social transmission'.

The implausibility of such transmission in Eurasia in general, and Europe in particular, during the far longer time-span of the Middle Pleistocene, was argued cogently by Nicoud [[229], pp. 37–39]. We think that sporadic local enactment by *Homo heidelbergensis* could well have been responsible for puzzling exceptional finds in Europe of what, at first sight, look like extraordinarily early instances of stone-working techniques that flowered only much later on. Among such 'precocious' finds that have been likened to Mousterian ('Charentian') convex scrapers of the early Late [Upper] Pleistocene are finds from the early-to-mid Middle Pleistocene at High Lodge in England ([301], pp. 238–240) and from Caune de l'Arago in France ([302], p. 776; [303], p. 854; [304], p. 298). At Arago, a well-fashioned, thin, quartzite handaxe with signs of soft-hammer treatment of its edges ([305], p. 310, Fig. 3 bottom), excavated in a layer immediately above a level dated to ca. 0.565–0.525 Ma, shows that 'handaxes' could be knapped with exquisite care and attention in Europe before the middle of the Middle Pleistocene, and not only in the late Middle Pleistocene as often is asserted.

By no means all 'handaxes' had to have been made for obtaining bioenergetic resources for human subsistence, though, regardless of their purposes, the underlying cognitive and manual strategies were responses in common to neurobiological propensities shared by their Early and Middle Pleistocene creators. Early human strategies for obtaining suitable stone were somewhat eclectic. Artifacts at many sites were made more often on stone from nearby outcrops of rock that was less than ideal for flaking, than from outlying ones of more suitable rock. This could reflect a strategy of least effort, given that stone is heavy [306], and, furthermore, once made, stone

artifacts still have to be carried to wherever they are to be used (carrying stone can be hard work). Most Paleolithic archeologists consider that only well into the Late (Upper) Pleistocene did long-distance transport of stone for subsequent flaking become widespread, and many consider long-distance movement of stone for knapping as having developed specifically in *H. sapiens*, though late Middle Pleistocene *H. sapiens* skeletal remains are associated with 'handaxes' (e.g., *H. sapiens 'idaltu'* at Herto in Ethiopia), and even with 'Mousterian' tools made on small stone flakes (e.g., at Irhoud in Morocco and Qafzeh in Israel) that are comparable to those that are characteristic of Neanderthal sites.

Fig. 1 An early 'handaxe' and a 'chopper' from Western Europe (scales in centimeters). Fashioned on a limestone cobble, the only 'handaxe' (left) found at Cueva Negra del Estrecho del Río Quípar (southeastern Spain) was excavated in a layer bedded between over- and underlying levels that yielded an abundant of various small artifacts (all less than 6 cm long) of chipped chert, limestone, and quartzite (34 are illustrated in [189], pp. 6–16, Figs. 2a–c, 4a–m,5a–s) comparable to those surrounding the 'handaxe' and a flaked limestone cobble 'chopper' (right) excavated close to it in the same layer, where they all could suggest an 'activity area' of ca. 2 m^2s 5 cm thick ([225], p.22, Fig. 10), about 1.5 m in sediments that had accumulated to a depth of over 5 m on the underlying bed-rock of the cave between 0.99 and 0.772 Ma [149], probably during the marine isotope stage of MIS-21, between 0.867 and 0.812 Ma, when temperate conditions prevailed and sporadic overflow from an erstwhile swampy lake washed sediment into the cave. The 'handaxe' could have lost during use because the break was not recent. The 'handaxe' and 'chopper' are the only 'heavy-duty' fashioned artifacts to have been found at the site where excavation campaigns have been carried out regularly since 1990. Both artifacts are of the micritic limestone that characterizes the Jurassic Lower Middle Lias in mountains near the cave; X-ray diffraction of powder scraped from the artifacts and x80 optical microscopic petrography found them to consist of 94% calcite and 6% quartz that contributes to their hardness. (Photographs by courtesy of M. López Martínez and ©MUPANTQUAT)



Appendix 3

'Handaxes' in time and space

Below is a selection of the several places around the world from which 'handaxes' found in acceptably-dated contexts have been published. Some places are single sites, including ones where levels with and without 'handaxes' are recorded in publications; some sites are or were caves or rock-shelters (indicated by *), in which sedimentary sequences were less often subject to disturbance, regardless of whether those were deposited horizontally or accumulated by vertical in-filling. Other places are locations where investigative fieldwork or excavation of individual sites or trenches (that may lie horizontally or vertically apart from one another) can lead to 'handaxes' from them being considered by researchers as representing a spatiotemporally continuous behavioral persistence of fashioning them at the location: particularly, in places where 'handaxes' have been found in abundance at exposures of gravel beds or in deserts (though because a 'handaxe' can be fashioned in less than an hour, collections of several thousand could represent workmanship of a mere few centuries). Sites from which only one 'handaxe', or only two, are recorded are indicated respectively by † and ††,

or by ?†? where only one was alleged to have been found albeit unconfirmed. Approximate ages or age-ranges, taken from publications, are given in Ma ('million years ago'; > 'older than'; ≥ 'older than or equal to'; < 'no older than'; ≤ 'no older than or perhaps equal to'; ~ 'approximately'; ? 'doubtful'. (Key et al. [307] state that some 'handaxes' were fashioned in parts of Africa and South-West Asia until as late as 0.174 – 0.166 Ma, in parts of Europe until 0.141 – 0.131 Ma, and in parts of China and Korea until 0.057 - 0.053 Ma.)

Places with published dates for first appearances at them of 'handaxes'.

East Africa:
1.76 Ma Kokiselei, Kenya
1.7 Ma Olduvai, Tanzania
≥1.4 Ma Konso Gardula, Ethiopia
1.2 Ma Peninj, Tanzania
1 Ma Kilombe, Kenya
1–0.8 Ma Melka Kunture, Ethiopia
0.9 Ma Olorgesailie, Kenya
0.5 Ma Kalambo Falls, Tanzania
*0.21 Ma Mieso, Ethiopia
Southern Africa:
≥1.4 Ma Rietputs, South Africa
≥1.4 Ma Sterkfontein*, South Africa
1.1 Ma Wonderwerk*, South Africa
0.8 Ma Gladysvale*†, SouthAfrica
≥0.6 Ma Swartkrans*, South Africa
North Africa:
1.4. Ma Thomas Quarry I (OHI Bed 2), Morocco
0.7 Ma Tighenif, Algeria
0.5 Ma Sidi Abderhamane Quarry, Morocco
South Asia:
1.51 Ma Attirampakkam, India
≥1.2 Isampur, India
>0.77 Ma Chirki-Nevasa, India
>0.77 Ma Morgaon, India
>0.77 Ma Anagwadi, India
0.7–0.4 Ma Dina, Pakistan
0.7–0.4 Ma Jalalpur, Pakistan
>0.67 Ma Bori, India
>0.6 Ma Satpati, Nepal
>0.35 Ma Yedurwadi, India
0.29 Ma Sadab, India
0.29 Ma Tegginhalli, India
0.25–0.18 Ma Singi Talav. India
0.14–0.12 Ma Son valley sites at Nakhjar Khurd, Sihawak, Patpara and Bamburi, India
0.1–0.09 Ma Bhimbetka*, India
East Asia:
0.8 Ma Bose basin sites of Nanbanshan and Fengshudao, China
?0.8 Ma Danjiankou Reservoir Regio, China
0.336–0.128 Ma Dingcun, China
0.12–0.05 Ma Chongokni, Korea
Australia:
<0.05 Ma Barkly Tableland, Australia
<0.05 Ma Coorong, Australia
Western Eurasia:
<1.6 - >1.2 Ma 'Ubeidiya, Israel
>1 Ma Evron Quarry, Israel
<0.99 - >0.772 Ma Cueva Negra del Estrecho del Río Quípar, Spain*†
≤0.77 Ma Gesher Benot Ya'aqov, Israel
0.7 Ma La Noira, France
<0.69 Ma Caune de l'Arago level P, France*
0.62–0.56 Ma Brandon Fields, United Kingdom
0.56 Ma Fordwich, United Kingdom
0.55 Ma Amiens Rue du Manège, France
0.55–05 Ma Abbeville Carrière Carpentier, France
0.525–0.475 Ma Boxgrove, United Kingdom

<0.5 Ma Colombiers La Grande Vallée, France
0.5 Ma Notarchirico unit 2.6, Italy
0.5 Ma Atapuerca Gran Dolina TD10, Spain*
≤0.5 Ma Atapuerca Galería, Spain*
0.484–0.374 Ma Cagny La Garenne, France
0.48–0.4 Ma Marathousa, Greece ?†?
0.46 Ma Fontana Ranuccio, Italy
0.45 Ma Aroeira, Portugal*
0.43 Ma Atapuerca Sima de los Huesos, Spain*†
0.43–0.3 Ma Ambrona, Spain
0.4 Ma Swanscombe Barnfield Pit, United Kingdom
0.4 Ma Barnham, United Kingdom
0.42 – 0.22 Ma Qesem*, Israel
0.4–0.38 Ma Terra Amata, France
0.4–0.033 Ma Nor Geghi 1, Armenia
≤0.04 Ma Karain*, Turkey
? ≤0.4 – ≥0.22? Ma Tabun*, Israel
0.374–0.3 Ma Cagny L'Épinette, France
≤0.35 - ≥28 Ma Orgnac, France*††
0.31 Ma Gürgürbaba, Turkey
0.26–0.16 Ma Rodafnidia, Greece
0.24–0.19 Torralba, Spain
0.19 Ma Saffaqah, Saudi Arabia
0.16 Ma Arbo, Spain

Some sites with levels containing 'handaxes' intercalated between other levels containing only other types of Paleolithic artifacts (age-range of all early Paleolithic evidence is shown).

1.7 Ma Olduvai FLKWest
<0.99 - >0.772 Ma Cueva Negra del Estrecho del Río Quípar, Spain*†
0.69 - 0.2 Ma Caune de l'Arago, France*
0.65 – 0.25 Ma Notarchirico, Italy

0.424–0.374 Ma Swanscombe Boyn Hill Thames terrace, United Kingdom (at the Barnfield Pit site, the Swanscombe 'middle gravels' containing 'handaxes' lie above the 'lower gravels and loam' containing 'Clactonian' artifacts that date from 0.42 Ma, while at the Rickson's Pit site a deposit containing only flake tools seems to be later than the Barnfield Pit gravels of MIS-11 and could belong to the MIS-10 cold stage that began around 0.374 Ma).

0.43–0.3 Ma Ambrona, Spain, and ≤0.35 - ≥28 Ma Orgnac, France: bifacial artifacts are present only in the deeper sedimentary deposits whereas flakes abound throughout the sequences.

0.37–0.12 Ma Cueva del Ángel, Spain*

A few European sites with published dates of Lower Paleolithic assemblages that lack 'handaxes':

1.8 Ma Dmanisi, Georgia
1.3 Ma Orce Barranco León 5, Spain
1.3 Ma Orce Fuente Nueva 3, Spain
1.3 Ma Pirro Nord P13*, Italy
<1.37- >0.91 Ma Vallonnet, Frace*
1.1 Ma Atapuerca Sima del Elefante, Spain
<1.3 - >1.1 Ma Bois de Riquet, France
<1.07 - >0.87 Ma Barranc de la Boella, Spain
1.06 Ma Monte Poggiolo Cà Belvedere, Italy
0.97–0.81 Happisburgh 3, United Kingdom (the 'handaxe' from Happisburgh is regarded as later, perhaps 0.5 Ma)
0.9–0.8 Ma Atapuerca Gran Dolina TD6, Spain
0.85 Ma Vallparadís-Cal Guardiola, Spain
0.7 Ma Pakefield, United Kingdom
0.6 Ma Isernia La Pineta, Italy
0.6–0.5 Ma Soleilhac, France
0.4 Ma Yarımburgaz*, European Turkey
0.37 Ma, Bilzingsleben, Germany
0.35–0.12 Ma Bolomor*, Spain
0.337–0.3 Ma Schöningen, Germany
0.3–0.25 Ma Vértesszőlős, Hungary

References

[1] Friston K, Da Costa L, Sakthivadivel DAR, Heins C, Pavliotis GA, Ramstead M, Parr T. Path integrals, particular kinds, and strange things. Phys Life Rev 2023. https://doi.org/10.1016/j-plrev.2023.08.016. PLREV 1451 (pre-proof).

[2] Badcock PB. Evolutionary systems theory: a unifying meta-theory of psychological science. Rev Gen Psychol 2012;16(1):10–23. https://doi.org/10.1037/a0026381.

[3] Binford LR. Isolating the transition to cultural adaptations: an organizational approach. In E. Trinkaus (editor). The emergence of modern humans: biocultural adaptations in the later Pleistocene. Santa Fe, School for Advanced Research, SARS Press, "School for Advanced Research Advanced Seminar Series", and Cambridge, Cambridge University Press; 1990. p. 18–41.

[4] Bailey GN. Concepts of time in Quaternary prehistory. Annu Rev Anthropol 1983;12:165–92. https://doi.org/10.1146/annurev.an.12.100183.001121.

[5] Murray T, Walker MJ. Like WHAT? A practical question of analogical inference and archaeological meaningfulness. J Anthropol Archaeol 1988;7:248–87. https://doi.org/10.1016/0278-4165(88)90010-4. Please note: The published version contains numerous errors, of which the most egregious– with the very opposite result to our intended meaning!– is on p. 263 where "$x=p=a=m$ *and that* $y=q=b=n$" appears in place of the submitted manuscript's "$x\neq p\neq a\neq m$ *and that* $y\neq q\neq b\neq n$" and among other errors and typos are "*worked*" for "*word*"(p. 262) and "*con-linear*" for "*non-linear*" (p. 264): all the mistakes owe to the editor informing the authors that, on account of an editorial logistical inconvenience, proofs would be corrected by the editor himself and not sent to the authors who therefore never saw them; his input was slipshod, and the unfortunate result has disconcerted readers.

[6] Shea JJ. Lithic archaeology, or, what stone tools can (and can't) tell us about early hominin diets. In P. Ungar (editor). Evolution of the human diet: the known, the unknown and the unknowable. Oxford: Oxford University Press; 2007. p. 212–29.

[7] Ambrose SH. Paleolithic technology and human evolution. Science 2001;219(5509):1748–53. https://doi.org/10.1126/science.1059487.

[8] Asfaw B, Beyene Y, Suwa G, Walter RC, White TD, WoldeGabriel G, et al. The earliest Acheulean from Konso-Gardula. Nature 1992;360(6406):732–5. https://doi.org/10.1038/360732a0.

[9] Beyene Y, Katoh S, WoldeGabriel G, Hart WK, Uto K, Sudo M, Kondo M, Hyodo M, Renne PR, Suwa G, Asfaw B. The characteristics and chronology of the earliest Acheulean at Konso, Ethiopia. Proc Natl Acad Sci USA 2013;110(5):1584–91. https://doi.org/10.1073/pnas.1221285110.

[10] Duke H, Feibel C, Harmand S. Before the Acheulean: the emergence of bifacial shaping at Kokiselei 6 (1.8 Ma), West Turkana, Kenya. J Hum Evol 2021;159:103061. https://doi.org/10.1016/j.jhevol.2021.103061.

[11] Lepre CJ, Roche H, Kent DV, Harmand S, Quinn RL, Brugal JP, Texier PJ, Lenoble A, Feibel CS. An earlier origin for the Acheulian. Nature 2011;477(7362):82–5. https://doi.org/10.1038/nature10372.

[12] Roche H, Brugal JP, Delagnes A, Feibel C, Harmand S, Kibunjia M, Prat P, Texier PJ. Les sites archéologiques plio-pléistocènes de la formation de Nachukui, Ouest-Turkana, Kenya: bilan synthétique 1997–2001. C R Palevol 2003;2(8):663–73. https://doi.org/10.1016/j.crpv.2003.06.001.

[13] Kuman K. 21. Development of the archaeological record in southern Africa during the earlier stone age. In J. Kingh, & S.W. Grab (editors). Quaternary environmental change in southern Africa: physical and human dimensions. Cambridge: Cambridge University Press; 2016. p. 349–70. https://doi.org/10.1017/CBO9781107295483.021.

[14] Shea JJ. Sink the Mousterian? Named Stone Tool Industries (NASTIES) as obstacles to investigating hominin evolutionary relationships in the later Middle Paleolithic Levant. Quat Int 2014;350:169–79. https://doi.org/10.1016/j.quaint.2014.01.024.

[15] Shea JJ. Stone tools in human evolution: behavioral differences among technological primates. Cambridge and New York: Cambridge University Press; 2017. https://doi.org/10.1017/9781316389355.

[16] Moore MW. Flake making the 'cognitive Rubicon': insights from stone-knapping experiments. In K.A. Overmann, & F.L. Coolidge (editors). Squeezing minds from stones. cognitive archaeology and the evolution of the human mind. Oxford: Oxford University Press; 2016. p. 179–99.

[17] Wynn T. Archaeology and cognitive evolution. Behav Brain Sci 2002;25(3):389–438. https://doi.org/10.1017/s0140525x020000794.

[18] Read DW, Lane D, Van der Leeuw S. The innovation innovation. In D. Lane, D. Pumain, S.E. Van der Leeuw, & G. West (editors). Complexity perspectives in innovation and social change. Dordrecht: Springer Science + Business Media; 2009. p. 45–84. https://doi.org/10.1007/978-1-4020-9663-1. "Methodos Series 7".

[19] Read DW. Population size does not predict artifact complexity: analysis of data from Tasmania, Arctic hunter-gatherers, and Oceania fishing groups. eScholarship University of California; 2012. http://www.escholarship.org/uc/item/61n4303q.

[20] Garofoli D. Chapter 19 Embodied cognition and the archaeology of mind: a radical reassessment. In A.M. Prentiss (editor). Handbook of evolutionary research in archaeology. Cham, Switzerland: Springer Nature Switzerland AG; 2019. p. 379–405. https://doi.org/10.1007/978-3-030-11117-5_19379380.

[21] Parr T, Pezzulo G, Friston K. Active inference: the free energy principle in mind, brain, and behavior. Cambridge MA and London: The MIT Press; 2022.

[22] Manrique HM, Walker MJ. To copy or not to copy? That is the question! From chimpanzees to the foundation of human technological culture. Phys Life Rev 2023;45:6–24. https://doi.org/10.1016/j.plrev.2023.02.005.

[23] Barto A, Mirolli M, Baldassarre G. Novelty or surprise? Front Psychol 2013;4:907. https://doi.org/10.3389/fpsyg.2013.00907.

[24] Proietti R, Pezzulo G, Tessari A. An active inference model of hierarchical action understanding, learning and imitation. Phys Life Rev 2023;46(September 2023):92–118. https://doi.org/10.1016/j.plrev.2023.05.012.

[25] Kilner JM, Friston KJ, Frith CD. Predictive coding: an account of the mirror neuron system. Cogn Process 2007;8(3):159–66. https://doi.org/10.1007/s10339-007-0170-2.

[26] Tramacere A, Ferrari PF, Iriki A. Epigenetic regulation of mirror neuron development, and related evolutionary hypotheses. In P.F. Ferrari & G. Rizzolatti (editors). New frontiers in mirror neurons research. Oxford: Oxford University Press; 2015. p. 222–44.

[27] Heyes C. Cognitive gadgets. Cambridge MA and London: The Belknap Press of Harvard University; 2018.

[28] Sterelny K. The evolved apprentice. How evolution made humans unique. Cambridge, MA: The MIT Press; 2012. 'A Bradford Book'.

[29] Great ape cognitive systems. In A.E. Russon, & D.R. Begun (editors). In: Russon AE, editor. The evolution of thought: evolutionary origins of great ape intelligence. Cambridge and New York: Cambridge University Press; 2004. p. 76–100.

[30] Manrique HM, Walker MJ. Early evolution of human memory: great apes, tool-making, and cognition. Cham (Switzerland): Springer-Nature; 2017. 'Palgrave-Macmillan, Palgrave Pivot'.

[31] Finn AS, Sheridan MA, Kam CLH, Hinshaw S, d'Esposito M. Longitudinal evidence for functional specialization of the neural circuit supporting working memory in the human brain. J Neurosci 2010;30(33):11062–7. https://doi.org/10.1523/JNEUROSCI.6266-09.2010.

[32] Manrique HM, Read DW, Walker MJ. On some statistical and cerebral aspects of the limits of working memory capacity in anthropoid Primates, with particular reference to *Pan* and *Homo*, and their significance for Human Evolution. Neurosci Biobehav Rev 2024;158:105543.

[33] Rizzolatti G, Craighero L. The mirror-neuron system. Annu Rev Neurosci 2004;27:169–92. https://doi.org/10.1146/annurev.neuro.27.070203.144230.

[34] Badcock PB, Friston KJ, Ramstead MJD, Ploeger A, Hohwy J. The hierarchically mechanistic mind: an evolutionary systems theory of the human brain, cognition, and behavior. Cogn Affect Behav Neurosci 2019;19:1319–51. https://doi.org/10.3758/s13415-019-00721-3.

[35] Badcock PB, Friston KJ, Ramstead MJD. The hierarchically mechanistic mind: a free-energy formulation of the human psyche. Phys Life Rev 2019;31(10):104–21. j.plrev.2018.10.002.

[36] Tinbergen N. On aims and methods of ethology. Z Tierpsychol 1963;20(1):410–37.

[37] Friston K, Schwartenbeck P, FitzGerald T, Moutoussis M, Behrens T, Dolan RJ. The anatomy of choice: dopamine and decision-making. Philos Trans R Soc Lond Ser B 2014;369:20130481. https://doi.org/10.1098/rstb.2013.0481.

[38] Friston K, FitzGerald T, Rigoli F, Schwartenbeck P, O'Doherty J, Pezzulo G. Active inference and learning. Neurosci Biobehav Rev 2016;68(6):862–9. https://doi.org/10.1016/j.neubiorev.2016.06.022.

[39] Friston K. Life as we know it. J R Soc Interface 2013;10:20130475. https://doi.org/10.1098/rsf2013.04700005.

[40] Friston K, Ao P. Free energy, value, and attractors. Comput Math Methods Med 2012;2012:937860. https://doi.org/10.1155/2012/937860.

[41] Friston K, Kilner J, Harrison L. A free energy principle for the brain. J Physiol Paris 2006;100:70–87. https://doi.org/10.1016/j.jphysparis.2006.10.001.

[42] Campbell JO. Universal Darwinism as a process of Bayesian inference. Front Syst Neurosci 2016;10:49. https://doi.org/10.3389/fnsys.2016.00049.
[43] Constant A, Ramstead MJD, Veissière SPL, Campbell JO, Friston KJ. A variational approach to niche construction. J R Soc Interface 2018;15:141. https://doi.org/10.1098/rsif.2017.0685. 20170685.
[44] Frank SA. Natural selection. V. How to read the fundamental equations of evolutionary change in terms of information theory. J Evol Biol 2012;25(12):2377–96. https://doi.org/10.1111/jeb.12010.
[45] Friston K, Friedman DA, Constant A, Knight VB, Fields C, Parr T, Campbell JO. A variational synthesis of evolutionary and developmental dynamics. Entropy 2023;25:964. https://doi.org/10.39390/e25070964.
[46] Friston, K. (2019). A free energy principle for a particular physics. Preprint in arXiv:1906.10184. 10.48550/arXiv.1906.10184.
[47] Bennett CH. Notes on Landauer's principle, reversible computation, and Maxwell's Demon. Stud Hist Philos Sci Part B Stud Hist Philos Mod Phys 2003;34(3):501–10. https://doi.org/10.1016/S1355-2198(03)00039-X.
[48] Jarzynski C. Nonequilibrium equality for free energy differences. Phys Rev Lett 1997;78(14):2690–3. https://doi.org/10.1103/PhysRevLett.78.2690.
[49] Landauer R. Irreversibility and heat generation in the computing process. IBM J Res Dev 1961;5(3):183–91. https://doi.org/10.1147/rd.53.0183.
[50] Hohwy J. The self-evidencing brain. Noûs 2016;50(2):259–85. https://doi.org/10.1111/nous.12062.
[51] Attias H. Planning by probabilistic inference. In: Proceedings of the Ninth International Workshop on Artificial Intelligence and Statistics; 2003. p. 9–16. PMLR R4.
[52] Botvinick M, Toussaint M. Planning as inference. Trends Cogn Sci 2012;16(10):485–8. https://doi.org/10.1016/j.tics.2012.08.006.
[53] Friston K, FitzGerald T, Rigoli F, Schwartenbeck P, Pezzulo G. Active inference: a process theory. Neural Comput 2017;29(1):1–49. https://doi.org/10.1162/NECO_a_00912.
[54] Friston KJ, Lin M, Frith CD, Pezzulo G, Hobson JA, Ondobaka S. Active inference, curiosity and insight. Neural Comput 2017;29(10):2633–83. https://doi.org/10.1162/neco_a_00999.
[55] Millidge, B., (2019). Deep active inference as variational policy gradients. Preprint in arXiv:1907.03876.
[56] Schmidhuber J. Developmental robotics, optimal artificial curiosity, creativity, music, and the fine arts. Connect Sci 2006;18(2):173–87. https://doi.org/10.1080/09540090600768658.
[57] Schwartenbeck P, Passecker J, Hauser TU, FitzGerald THB, Kronbichler M, Friston KJ. Computational mechanisms of curiosity and goal-directed exploration. eLife 2019;8:41703. https://doi.org/10.7554/eLife.41703.
[58] Still S, Precup D. An information-theoretic approach to curiosity-driven reinforcement learning. Theory Biosci 2012;131(3):139–48. https://doi.org/10.1007/s12064-011-0142-z.
[59] Constant A, Ramstead MJD, Veissière SPL, Friston K. Regimes of expectations: an active inference model of social conformity and human decision making. Front Psychol 2019;10:679. https://doi.org/10.3389/fpsyg.2019.00679.
[60] Vanchurin V, Wolf YI, Katsnelson MI, Koonin EV. Toward a theory of evolution as multilevel learning. Proc Natl Acad Sci USA 2022;119(6):2120037119. https://doi.org/10.1073/pnas.2120037119.
[61] Vanchurin V, Wolf YI, Koonin EV, Katsnelson MI. Thermodynamics of evolution and the origin of life. Proc Natl Acad Sci USA 2022;119(6):2120042119. https://doi.org/10.1073/pnas.2120042119.
[62] Friston K. The free-energy principle: a unified brain theory? Nat Rev Neurosci 2010;11:127–38. https://doi.org/10.1038/nrn2787.
[63] Friston KJ, Rosch R, Parr T, Price C, Bowman H. Deep temporal models and active inference. Neurosci Biobehav Rev 2018;90:486–501. https://doi.org/10.1016/j.neubiorev.2018.04.004.
[64] Parr T, Friston KJ. Generalised free energy and active inference. Biol Cybern 2019;113(5–6):495–513. https://doi.org/10.1007/s00442-019-00805w.
[65] Smith, R., Schwartenbeck, P., Parr, T., & Friston, K.J. (2019). An active inference approach to modeling structure learning: concept learning as an example case. Preprint in *bioRxiv*: 633677. 10.1101/633677.
[66] Ramstead MJD, Badcock PB, Friston KJ. Answering Schrödinger's question: a free-energy formulation. Phys Life Rev 2017;24:1–16. https://doi.org/10.1016/j.plrev.2017.09.001.
[67] Ramstead MJD, Badcock PB, Friston KJ. Variational neuroethology: answering further questions: reply to comments on 'Answering Schrödinger's question: a free-energy formulation. Phys Life Rev 2018;24:59–66. https://doi.org/10.1016/j.plrev.2018.01.003.
[68] Ramstead MJD, Constant A, Badcock PB, Friston KJ. Variational ecology and the physics of sentient systems. Phys Life Rev 2019;31:188–205. https://doi.org/10.1016/j.plrev.2018.12.002.
[69] Dayan P, Hinton GE, Neal RM, Zemel RS. The Helmholtz machine. Neural Comput 1995;7:889–904. https://doi.org/10.1162/neco.1995.7.5.889.
[70] Helmholtz H. Concerning the perceptions in general, treatise on physiological optics, vol. III. /1962. New York: Dover; 1866.
[71] Von Helmholtz H. The facts of perception (1878). In R. Karl (editor). The selected writings of Hermann von Helmholtz. Middletown CT: Wesleyan University Press; 1971.
[72] Feynman RP. Statistical mechanics: a set of lectures. Reading MA, W.A. Benjamin, 'Frontiers in Physics'; 1972. https://doi.org/10.1201/9780429493034.
[73] Jaynes ET. Information theory and statistical mechanics. Phys Rev 1957;106(4):620–30. https://doi.org/10.1103/PhysRev.106.620.
[74] Sakthivadivel, D.A.R. (2022). A constraint geometry for inference and integration. Preprint in arXiv:2203.08119.
[75] Friston K, Rigoli F, Ognibene D, Mathys C, Fitzgerald T, Pezzulo G. Active inference and epistemic value. Cogn Neurosci 2015;6(4):187–224. https://doi.org/10.1080/17588928.2015.1020053.
[76] Hamlin JK, Wynn K. Young infants prefer prosocial to antisocial others. Cogn Dev 2011;26(1):30–9. https://doi.org/10.1016/j.cogdev.2010.09-001.
[77] Hamlin JK, Wynn K, Bloom P. Social evaluation by preverbal infants. Nature 2007;450:557–9. https://doi.org/10.1038/nature06288.
[78] Hamlin JK, Wynn K, Bloom P. 3-month-olds show a negativity bias in their social evaluations. Dev Sci 2010;13(6):923–9. https://doi.org/10.1111/j.1467-7687.2020.00951x.
[79] Krupenye C, Hare B. Bonobos prefer individuals that hinder others over those that help. Curr Biol 2018;28(2):280–6. https://doi.org/10.1016/j.cub.2017.11.061.
[80] Aiello LC, Wheeler P. The expensive tissue hypothesis: the brain and digestive system in human and Primate evolution. Curr Anthropol 1995;36(2):199–221. https://doi.org/10.1086/204350.
[81] Hyder F, Rothman DL, Bennett MR. Cortical energy demands of signaling and nonsignaling components in brain are conserved across mammalian species and activity levels. Proc Natl Acad Sci USA 2013;110(9):3549–54. 10.1073 pnas.1214912110.
[82] Gould SJ, Lewontin RC. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist program. Proc R Soc Lond Ser B 1979;205(1161):581–98. https://doi.org/10.1002/rspb.1979.0086.
[83] Moore MW. 'Grammars of action' and stone flaking design space. In A. Nowell, & I. Davidson, (editors). Stone tools and the evolution of human cognition. Boulder: University Press of Colorado; 2010. p. 13–43.
[84] Friston K, Adams R, Montague R. What is value - accumulated reward or evidence? Front Neurorobot 2012;6:11. https://doi.org/10.3389/fnbot.2012.00011999.
[85] Pezzulo G, Rigoli F, Friston K. Active inference, homeostatic regulation and adaptive behavioural control. Prog Neurobiol 2015;134:17–36. https://doi.org/10.1016/j.neurobio.2015.09.001.
[86] Allen M, Friston KJ. From cognitivism to autopoiesis: towards a computational framework for the embodied mind. Synthèse 2018;195(6):2459–82. https://doi.org/10.1007/s11229-016-1288-5.
[87] Gärtner K, Clowes RW. Enactivism, radical enactivism and predictive processing: what is radical in cognitive science? Kairos J Philos Sci 2017;18:70–83. https://doi.org/10.1515/kjps-2017-0003.
[88] Dean MC. Measures of maturation in early fossil hominins: events at the first transition from australopiths to early *Homo*. Philos Trans R Soc Lond Ser B 2016;371(1698):20150234. https://doi.org/10.1098/rstb.2015.0234.

[89] Dean MC, Smith BH. Growth and development of the Nariokotome youth, KNM-WT 15000. In F.E. Grine, J.G. Fleagle, & R.E. Leakey (editors). The first humans: origin and early evolution of the genus *Homo*. Dordrecht, Heidelberg, New York and London: Springer Science+Business Media; 2009. p. 101–17. https://doi.org/10.1007/978-1-4020-9980-9. Vertebrate Paleobiology and Paleoanthropology Series.

[90] Smith BH. The physiological age of KNM-WT 15000. In A. Walker, & R. Leakey (editors). The Nariokotome *Homo erectus* skeleton. Berlin, Springer; and Cambridge, MA: Harvard University Press; 1993. p. 195–220.

[91] Semendeferi K, Hanson KL. Plastic and heterogeneous: postnatal developmental changes in the human brain. In W.R. Trevathan, & K. Rosenberg (editors). Costly and cute: helpless infants and human evolution. Santa Fe: School for Advanced Research Press, SARS Press; 2016. p. 133–47. 'Advanced Seminar Series'; and Albuquerque, University of New Mexico Press.

[92] Ruff CB, Walker A. Body size and body shape. In A. Walker, & R. Leakey (editors). The Nariokotome Homo erectus skeleton. Berlin, Springer; and Cambridge, MA: Harvard University Press; 1993. p. 234–65.

[93] Read DW, Manrique HM, Walker MJ. On the working memory of humans and great apes: strikingly similar or remarkably different? Neurosci Biobehav Rev 2022;134:104496. https://doi.org/10.1016/j.neubiorev.2021.12.019.

[94] Mansouri FA, Koechlin E, Rosa MGP, Buckley MJ. Managing competing goals - a key role for the frontopolar cortex. Nat Rev Neurosci 2017;18(11):645–57. https://doi.org/10.1038/nrn.2017.111.

[95] Ponce de León MS, Bienvenu T, Marom A, Engel S, Tafforeau P, Alatorre Warren JL, Lordkipanidze D, Kurniawan I, Murti DB, Suriyanto RA, Koesbardiati T, Zollikofer CPE. The primitive brain of early *Homo*. Science 2021;372(6538):165–71. https://doi.org/10.1126/science.aaz0032.

[96] Sherwood CC, Holloway RL, Semendeferi K, Hof PR. Is prefrontal white matter enlargement a human evolutionary specialization? Nat Neurosci 2005;8(5): 537–8. https://doi.org/10.1038/nn0505-537.

[97] Sherwood CC, Gómez-Robles A. Brain plasticity and human evolution. Annu Rev Anthropol 2017;46:399–419. https://doi.org/10.1146/annurev-anthr-102215-100009.

[98] Petanjek Z, Judaš M, Šimić G, Rašin MR, Uylings HBM, Rakic P, Kostović I. Extraordinary neoteny of synaptic spines in the human prefrontal cortex. Proc Natl Acad Sci USA 2011;108(32):13281–6. https://doi.org/10.1073/pnas.1105108108.

[99] Fields RD. A new mechanism of nervous system plasticity: activity-dependent myelination. Nat Rev Neurosci 2015;16(12):756–67. https://doi.org/10.1038/nrn4023.

[100] Pope SM, Taglialatela JP, Skiba SA, Hopkins WD. Changes in frontoparietotemporal connectivity following Do-As-I-Do imitation training in chimpanzees (*Pan troglodytes*). J Cogn Neurosci 2018;30(3):421–31. https://doi.org/10.1162/jocn_a_01217.

[101] Grasby KL, 360 coauthors of the ENIGMA CONSORTIUM. The genetic architecture of the human cerebral cortex. Science 2020;367(6484):eaay6690. https://doi.org/10.1126/science.aay6690.

[102] Komiya Y, Habas R. Wnt signal transduction pathways. Organogenesis 2008;42(2):68–75. https://doi.org/10.4161/org.4.2.5851.

[103] Gogtay N, Giedd JN, Lusk L, Hayashi KM, Greenstein D, Vaituzis AC, Nugent IIIrd TF, Herman DH, Clasen LS, Toga AW, Rapoport JL, Thompson PM. Dynamic mapping of human cortical development during childhood through early adulthood. Proc Natl Acad Sci USA 2004;101(21):8174–9. https://doi.org/10.1073/pnas.0402680101.

[104] Darki F, Klingberg T. The role of fronto-parietal and fronto-striatal networks in the development of working memory: a longitudinal study. Cereb Cortex 2015; 25(6):1587–95. https://doi.org/10.1093/cercor/bht352.

[105] Giedd JN, Blumenthal J, Jeffries NO, Castellanos FX, Liu H, Zijdenbos A, Paus T, Evans AC, Rapoport JL. Brain development during childhood and adolescence: a longitudinal MRI study. Nat Neurosci 1999;2:861–3. https://doi.org/10.1038/13158.

[106] Paus T, Zijdenbos A, Worsley K, Collins DL, Blumenthal J, Giedd JN, Rapoport JL, Evans AC. Structural maturation of neural pathways in children and adolescents: *in vivo* study. Science 1999;283(5409). https://doi.org/10.1126/science.283.5409.1908. 1108-1011.

[107] Mars RB, Passingham RE, Neubert FX, Verhagen L, Sallet J. 4.12 Evolutionary specializations of human association cortex. In: Preuss TM, editor. The evolution of the human brain: apes and other ancestors. Elsevier; 2017. p. 185–205. https://doi.org/10.1016/8978-0-12-804042-3.00114-7. Volume 4 of J.H. Kaas (General Editor) Evolution of nervous systems (2nd edition) Amsterdam, Boston, Heidelberg, London, New York, Oxford, Paris, San Diego, San Francisco, Singapore, Sydney and Toronto, 'Academic Press'.

[108] Orban GA, Rizzolatti G. An area specifically devoted to tool use in human left inferior parietal lobule. Behav Brain Sci 2012;35(4):234. https://doi.org/10.1017/S0140525X11001944.

[109] Peeters R, Simone L, Nelissen K, Fabbri-Destro M, Vanduffel W, Rizzolatti G, Orban GA. The representation of tool use in humans and monkeys: common and uniquely human features. J Neurosci 2009;29(37):11523–39. https://doi.org/10.1523/JNEUROSCI.2040-09.2009.

[110] Ramayya AG, Glasser MF, Rilling JK. A DTI investigation of neural substrates supporting tool use. Cereb Cortex 2010;20(3):507–16. https://doi.org/10.1093/cercor/bhp141.

[111] Hartshorne JK, Makovski T. The effect of working memory maintenance on long-term memory. Mem Cogn 2019;47(4):749–63. https://doi.org/10.3758/s13421-019-00908-6.

[112] Jenesen A, Squire LR. Working memory, long-term memory, and medial temporal lobe function. Learn Mem 2012;19(1):15–25. lm.0240.18.111.

[113] Artuso C, Palladino P. Long-term memory effects on working memory updating development. Public Libr Sci One PLoS ONE 2019;14(5):0217697. https://doi.org/10.1371/journal.pone.0217697.

[114] Flechsig PE. Anatomie des menschlichen Gehirns und Rückenmarks auf myelogenetischer Grundlage. Leipzig, G.Thieme; 1920.

[115] Lebenberg J, Mangin JF, Thirion B, Poupon C, Hertz-Pannier L, Leroy F, Adibpour P, Dehaene-Lambertz G, Dubois J. Mapping the asynchrony of cortical maturation in the infant brain: a MRI multi-parametric clustering approach. Neuroimage 2019;185:641–53. https://doi.org/10.1016/j.neuroimage.2018.07.022.

[116] Miller DJ, Duka T, Stimpson CD, Schapiro SJ, Baze WB, McArthur MJ, Fobbs AJ, Sousa AMM, Šestan N, Wildman DE, Lipovich L, Kuzawa CW, Hof PR, Sherwood CC. Prolonged myelination in human neocortical evolution. Proc Natl Acad Sci USA 2012;109(41):16480–5. https://doi.org/10.1073/pnas.1117943109.

[117] Sowell ER, Thompson PM, Holmes CJ, Jernigan TL, Toga AW. *In vivo* evidence for post-adolescent brain maturation in frontal and striatal regions. Nat Neurosci 1999;2(10):859–61. https://doi.org/10.1038/13154.

[118] Sakai, T., Hirai, D., Mikami, A., Suzuki, J., Hamada, Y., Tomonaga, M., Tanaka, M., Miyabe-Nishiwaki, T., Makishima, H., Nakatsukasa, M., & Matsuzawa, T. (2010). Nature precedings, pre-publication research and preliminary findings: prolonged maturation of prefrontal white matter in chimpanzees. hdl:10101/npre.2010.4411.1.

[119] Sakai T, Mikami A, Tomonaga M, Matsui M, Suzuki J, Hamada Y, Tanaka M, Miyabe-Nishiwaki T, Makishima H, Nakatsukasa M, Matsuzawa T. Differential prefrontal white matter development in chimpanzees and humans. Curr Biol 2011;21(16):1397–402. https://doi.org/10.1016/j.cub.2011.07.019.

[120] Sakai T, Hirata S, Fuwa K, Sugama K, Kusunoki K, Makishima H, Eguchi T, Yamada S, Ogihara N, Takeshita H. Fetal brain development in chimpanzees versus humans. Curr Biol 2012;22(18):R791–2. https://doi.org/10.1016/j.cub.2012.06.062.

[121] Sakai T, Matsui M, Mikami A, Malkova L, Hamada Y, Tomonaga M, Suzuki J, Tanaka M, Miyabe-Nishiwaki T, Makishima H, Nakatsukasa M, Matsuzawa T. Developmental patterns of chimpanzee cerebral tissues provide important clues for understanding the remarkable enlargement of the human brain. Proc R Soc Lond Ser B 2013;280(1753):20122398. https://doi.org/10.1098/rspb.2012.2398.

[122] Hecht EE, Murphy LE, Gutman DA, Votaw JR, Schuster DM, Preuss TM, Orban GA, Stout D, Parr LA. Differences in neural activation for object-directed grasping in chimpanzees and humans. J Neurosci 2013;33(35):14117–34. https://doi.org/10.1523/JNEUROSCI.2172.13.2013.

[123] Eichert N, Robinson EC, Bryant KL, Jbabdi S, Jenkinson M, Li L, Krug K, Watkins KE, Mars RB. Cross-species cortical alignment identifies different types of anatomical reorganization in the primate temporal lobe. eLife 2020;9:53232. https://doi.org/10.7554/elife-53232-v1.

[124] Aboitiz F, Aboitiz S, García RR. The phonological loop. A key innovation in human evolution. Curr Anthropol 2010;51(Supplement 1):S55–65. https://doi.org/10.1086/650525.

[125] Arbib MA. From mirror neurons to complex imitation in the evolution of language and tool use. Annu Rev Anthropol 2011;40:57–73. https://doi.org/10.1146/annurev-anthro-081309-145722.
[126] Arbib MA. How the brain got language: the mirror system hypothesis. Oxford and New York: Oxford University Press; 2012. https://doi.org/10.1093/acprof:osobl/9780199896684.001.0001.
[127] Arbib MA, Rizzolatti G. Neural expectations: a possible evolutionary path from manual skills to language. Commun Cogn 1996;29(3–4):393–424. https://doi.org/10.4324/9780203266069. Reprinted 1998 in P.R. van Loocke (Ed.), The nature of concepts: evolution, structure and representation, (pp. 128-154). London, Taylor and Francis, Routledge, Frontiers in Cognitive Science.
[128] Barnard PJ. From executive mechanisms underlying perception and action to the parallel processing of meaning. Curr Anthropol 2010;51(Supplement 1): S39–54. https://doi.org/10.1086/650695.
[129] Boë LJ, Sawallis TR, Fagot J, Badin P, Barbier G, Captier G, Ménard L, Heim JL, Schwartz JL. Which way to the dawn of speech? Reanalyzing half a century of debates and data in light of speech science. Sci Adv 2019;5(12):eaaw3916. https://doi.org/10.1126/sciadv.aaw3916.
[130] Petrides M, Pandya DN. Distinct parietal and temporal pathways to the homologues of Broca's area in the monkey. Public Libr Sci Biol PLoS Biol 2009;7(8): 1000170. https://doi.org/10.1371/journal.pbio.1000170.
[131] Stout D, Chaminade T. The evolutionary neuroscience of tool making. Neuropsychologia 2007;45(5):1091–100. https://doi.org/10.1016/j.neuropsychologia.2006.09.014.
[132] Stout D, Chaminade T. Making tools and making sense: complex, intentional behaviour in human evolution. Camb Archaeol J 2009;19(1):85–96. https://doi.org/10.1017/S0959774309000055.
[133] Berwick RC, Chomsky N. Why only us: language and evolution. Cambridge MA: MIT Press; 2016.
[134] Putt SS, Wijeakumar S, Franciscus RG, Spencer JP. The functional brain networks that underlie Early Stone Age tool manufacture. Nat Hum Behav 2017;1:102. https://doi.org/10.1038/s41562.017.0102.
[135] Fuster JM. The prefrontal cortex (5th edition). Elsevier-Academic Press; 2015. Amsterdam, Boston, Heidelberg, London, New York, Oxford, Paris, San Diego, San Francisco, Sydney and Tokyo.
[136] Bengtsson SL, Nagy Z, Skare S, Forsman L, Forssberg H, Ullen F. Extensive piano practicing has regionally specific effects on white matter development. Nat Neurosci 2005;8(9):1148–50. https://doi.org/10.1038/nn1516.
[137] Mandl RCW, Schack HG, Zwiers MP, Van der Schaaf A, Kahn RS, Hulshoff Pol HE. Functional diffusion tensor René imaging: measuring task-related fractional anisotropy changes in the human brain along white matter tracts. Public Libr Sci One PLoS ONE 2008;3(11):3631. https://doi.org/10.1371/journal.pone.0003631.
[138] Roberts RE, Anderson EJ, Husain M. Expert cognitive control and individual differences associated with frontal and parietal white matter microstructure. J Neurosci 2010;30(50):17063–7. https://doi.org/10.1523/JNEUROSCI.4879-10.2010.
[139] Roberts RE, Anderson EJ, Husain M. White matter microstructure and cognitive function. Neuroscientist 2013;19(1):8–15. https://doi.org/10.1177/1073858411421218.
[140] Roberts RE, Bain PG, Day BL, Husain M. Individual differences in expert motor coordination associated with white matter microstructure in the cerebellum. Cereb Cortex 2013;23(10):2282–92. https://doi.org/10.1093/cercor/bhs219.
[141] Scholz J, Klein MC, Behrens TEJ, Johansen-Berg H. Training induces changes in white-matter architecture. Nat Rev Neurosci 2009;12(11):1370–1. https://doi.org/10.1038/nn.2412.
[142] Van den Heuvel MP, Mandl RCW, Luigjes J, Hulshoff Pol HE. Microstructural organization of the cingulum tract and the level of default mode functional connectivity. J Neurosci 2008;28(43):10844–51. https://doi.org/10.1523/JNEUROSCI.2964-08.2008.
[143] Hecht EE, Gutman DA, Bradley BA, Preuss TM, Stout D. Virtual dissection and comparative connectivity of the superior longitudinal fasciculus in chimpanzees and humans. Neuroimage 2015;108:124–37. https://doi.org/10.1016/j.neuroimage.2014.12.039.
[144] Hecht EE, Gutman DA, Khreisheh N, Taylor SV, Kilner J, Faisal AA, Bradley BA, Chaminade T, Stout D. Acquisition of Paleolithic toolmaking abilities involves structural remodeling to inferior frontoparietal regions. Brain Struct Funct 2015;220(4):2315–31. https://doi.org/10.1007/s00429.014.0789.6.
[145] Stout D, Passingham R, Frith C, Apel A, Chaminade T. Technology, expertise and social cognition in human evolution. Eur J Neurosci 2011;33(7):1328–38. https://doi.org/10.1111/j.1460-9568.2011.07619.x.
[146] Kulik V, Reyes LD, Sherwood CC. Coevolution of language and tools in the human brain: an ALE meta-analysis of neural activation during syntactic processing and tool use. Prog Brain Res 2023;275:93–115. https://doi.org/10.1016/bs.pbr.2022.10.003.
[147] Berna F, Goldberg P, Horwitz LK, Brink J, Holt S, Bamford M, Chazan M. Microstratigraphic evidence of *in situ* fire in the Acheulean strata of Wonderwerk Cave, Northern Cape province, South Africa. Proc Natl Acad Sci USA 2012;109(20):7593–4. https://doi.org/10.1073/pnas.117620109.
[148] Walker MJ, Anesin D, Angelucci DE, Avilés-Fernández A, Berna F, Buitrago-López ÁT, Fernández-Jalvo Y, Haber-Uriarte M, López-Jiménez A, López-Martínez M, Martín-Lerma I, Ortega-Rodrigáñez J, Polo-Camacho JL, Rhodes SE, Richter D, Rodríguez-Estrella T, Schwenninger JL, Skinner AR. Combustion at the late Early Pleistocene Palaeolithic site of Cueva Negra del Estrecho del Río Quípar (Caravaca de la Cruz, Murcia, Spain). Antiquity 2016;90(351):571–89. https://doi.org/10.15184/aqy.2016.91.
[149] Walker MJ, Haber Uriarte M, López Jiménez A, López Martínez M, Martín Lerma I, Van der Made J, Duval M, Grün R. Cueva Negra del Estrecho del Río Quípar: a dated late Early Pleistocene Palaeolithic site in southeastern Spain. J Paleolit Archaeol 2020;3(4):816–55. https://doi.org/10.1007/s41982-020-00062-5.
[150] Alperson-Afil N. Archaeology of fire: methodological aspects of reconstructing fire history of prehistoric archaeological sites. Earth Sci Rev 2012;113(3–4): 111–9. https://doi.org/10.1016/j.earscirev.2012.03.012.
[151] Alperson-Afil N, Goren-Inbar N. The Acheulian site of Gesher Benot Ya'aqov, volume II: ancient flames and controlled use of fire. London: Springer; 2010. https://doi.org/10.1007/978-90-481-3765-7.
[152] Goren-Inbar N, Alperson N, Kislev ME, Simchoni O, Melamed Y, Ben-Nun A, Werker E. Evidence of hominin control of fire at Gesher Benot Ya'aqov, Israel. Science 2004;304(5671):725–7. https://doi.org/10.1126/science.1095443.
[153] Gowlett JAJ, Harris JWK, Walton D, Wood BA. Early archaeological sites, hominid remains and traces of fire from Chesowanja, Kenya. Nature 1981;294 (5837):125–9. https://doi.org/10.1038/294125a0.
[154] Gowlett JAJ, Wrangham RW. Earliest fire in Africa: towards the convergence of archaeological evidence and the cooking hypothesis. Azania Archaeol Res Afr 2013;48(1):5–30. https://doi.org/10.1080/0067250X.2012.756754.
[155] Carmody RN, Weintraub GS, Wrangham RW. Energetic consequences of thermal and nonthermal food processing. Proc Natl Acad Sci USA 2011;108(48): 19199–203. https://doi.org/10.1073/pnas.1112128108.
[156] Carmody RN, Wrangham RW. The energetic significance of cooking. J Hum Evol 2009;57(4):379–91. https://doi.org/10.1016/j.jhevol.2009.02.011.
[157] Ragir S. Diet and food preparation: rethinking early hominid behavior. Evol Anthropol 2000;9:153–5. https://doi.org/10.1002/1520-6505(2000)9:4<153::AID-EVAN>3.0.CO;2-D.
[158] Smith AR, Carmody RN, Dutton RJ, Wrangham RW. The significance of cooking for early hominin scavenging. J Hum Evol 2015;84:62–70. https://doi.org/10.1016/j.jhevol.2015.03.013.
[159] Wrangham, R. (2009). Catching fire. How cooking made us human. New York, Profile Books; and London, Basic Books.
[160] Wrangham R, Carmody R. Human adaptation to the control of fire. Evol Anthropol 2010;19(5):187–99. https://doi.org/10.1002/evan.20275.
[161] Carmody RN, Dannemann M, Briggs AW, Nickel B, Groopman EE, Wrangham RW, Kelso J. Genetic evidence of human adaptation to a cooked diet. Genome Biol Evol 2016;8:1091–103. https://doi.org/10.1093/gbe/evw059.
[162] Fellows Yates JA, Velsko IM, Aron F, Posth C, Hofman CA, Austin RM, Parker CE, Mann AE, Nägele K, Arthur KW, Arthur JW, Bauer CC, Crèvecoeur I, Cupillard C, Curtis MC, Dalén L, Díaz-Zorita Bonilla M, Díez Fernández-Lomana JC, Drucker DG, Escribano Escrivá E, Francken M, Gibbon VE, González Morales M, Grande Mateu A, Harvati K, Henry AG, Humphrey L, Menéndez M, Mihailović D, Peresani M, Rodríguez Moroder S, Roksandic M, Rougier H, Sázelová S, Stock JT, Straus LG, Svoboda J, Teßmann B, Walker MJ, Power RC, Lewis CM, Sankaranarayanan K, Guschanski K, Wrangham R, Dewhirst FE,

Salazar-García DC, Krause J, Herbig H, Warinner C. The evolution and changing ecology of the anthropoid primate oral microbiome. Proc Natl Acad Sci USA 2021;118(20):2021655118. https://doi.org/10.1073/pnas.2021655118.
[163] Fonseca-Azevedo K, Herculano-Houzel S. Metabolic constraint imposes tradeoff between body size and number of brain neurons in human evolution. Proc Natl Acad Sci USA 2012;109(45):18571–6. https://doi.org/10.1073/pnas.1206390109.
[164] Ardesch DJ, Scholtens LH, Li L, Preuss TM, Rilling JK, Van den Heuvel MP. Evolutionary expansion of connectivity between multimodal association areas in the human brain compared with chimpanzees. Proc Natl Acad Sci USA 2019;116(14):7101–6. https://doi.org/10.1073/pnas.1818512116.
[165] Passingham RE, Smaers JB. Is the prefrontal cortex especially enlarged in the human brain? Allometric relations and remapping factors. Brain Behav Evol 2014;84(2):156–66. https://doi.org/10.1159/000365183.
[166] Semendeferi K, Teffer K, Buxhoeveden DP, Park MS, Bludau S, Amunts K, Travis K, Buckwalter J. Spatial organization of neurons in the frontal pole sets humans apart from great apes. CerebCortex 2011;21(7):1485–97. https://doi.org/10.1093/cercor/bhq191.
[167] Benito-Kwiecisnki S, Giandomenico SL, Sutcliffe M, Riis ES, Freire-Pritchett P, Kelava I, Wunderlich S, Martin U, Wray GA, McDole K, Lancaster MA. An early cell shape transition drives evolutionary expansion of the human forebrain. Cell 2021;184:1–19. https://doi.org/10.1016/j.cell.2021.02.050.
[168] Boyd JL, Skove SL, Rouanet JP, Pilaz LJ, Bepler T, Gordân R, et al. Human-chimpanzee differences in a FZD8 enhancer alter cell-cycle dynamics in the developing neocortex. Curr Biol 2015;25(6):772–9. https://doi.org/10.1016/j.cub.2015.01.041.
[169] Fiddes IT, Lodewijk GA, Mooring M, Bosworth CM, Ewing AD, Mantalas GL, Novak AM, Van den Bout A, Bishara A, Rosenkrantz JL, Lorig-Roach R, Field AR, Haeussler M, Russo L, Bhaduri A, Nowakowski TJ, Pollen AA, Dougherty ML, Nuttle X, Addor MC, Zwolinski S, Katzman S, Kriegstein A, Eichler EE, Salama SR, Jacobs FM, Haussler D. Human-specific *NOTCH2NL* genes affect notch signaling and cortical neurogenesis. Cell 2018;173(6):1356–69. https://doi.org/10.1016/j.cell.2018.03.051.
[170] Kosik KS, Nowakowski T. Evolution of new miRNAs and cerebro-cortical development. Annu Rev Neurosci 2018;41:19–137. https://doi.org/10.1146/annurev-neuro-080317-061822.
[171] Lein ES, Belgard TG, Hawrylycz M, Molnár Z. Transcriptomic perspectives on neocortical structure, development, evolution, and disease. Annu Rev Neurosci 2017;40:629–52. https://doi.org/10.1146/annurev-neuro-070815-013858.
[172] Suzuki IK, Gacquer D, Van Heurck R, Kumar D, Wojno M, Bilheu A, Herpoel A, Lambert N, Cheron J, Polleux F, Detours V, Vanderhaeghen P. Human-specific *NOTCH2NL* genes expand cortical neurogenesis through Delta/Notch regulation. Cell 2018;173(6):1370–84. https://doi.org/10.1016/j.cell.2018.03.067.
[173] Wilsch-Bräuninger M, Florio M, Huttner WB. Neocortex expansion in development and evolution–from cell biology to single genes. Curr Opin Neurobiol 2016;39:122–32. https://doi.org/10.1016/j.conb.2016.05.004.
[174] Gómez-Robles A, Smaers JB, Holloway RL, Polly PD, Wood BA. Brain enlargement and dental reduction were not linked in hominin evolution. Proc Natl Acad Sci USA 2017;114(3):468–73. https://doi.org/10.1073/pnas1608798114.
[175] Leakey MD. Olduvai Gorge. Volume 3. Excavations in Beds I and II, 1960-1963. Cambridge: Cambridge University Press; 1971.
[176] Vasil J, Badcock PB, Constant A, Friston K, Ramstead MJD. A world unto itself: communication as active inference. Front Psychol 2020;11:417. 10.3389/fpsyg.2020.00417.
[177] Liberalquino RB, Monge M, Galatolo S, Marangio L. Chaotic itinerancy in random dynamical system related to associative memory models. Mathematics 2018;6(3):39. https://doi.org/10.3390/math6030039.
[178] Bronowski J. The ascent of man. London, British Broadcasting Corporation: Boston, MA, Little, Brown & Co.; and Australia, Angus & Robertson; 1973.
[179] Gibson JJ. The theory of affordances. In R. Shaw, & J. Bransford (editors). Perceiving, acting, and knowing: toward an ecological psychology. Hillsdale: Lawrence Erlbaum Associates; 1977. p. 67–82.
[180] Gibson, J.J. (1979). The ecological approach to visual perception, (esp. pp. 127-143, Chapter 8. The theory of affordances). Boston MA, Houghton, Mifflin & Co. Reprinted in 1986 by the Taylor & Francis Group in its Psychology Press at both Hove, UK, and New York, and again in 2014 at Hove, Psychology Press, and at New York under the Routledge series of "Routledge Classic Editions". 10.10.4324/9781315740218.
[181] Bruce V, Georgeson MA, Green PR. Visual perception: physiology, psychology and ecology. 4th ed. Hove: Psychology Press; 2003.
[182] Greeno JG. Gibson's affordances. Psychol Rev 1994;101(2):336–42. https://doi.org/10.1037/0033-295X.101.2.336.
[183] Urcid Serrano J. El concepto de la rueda en Mesoamérica. Arqueol Mex 2017;25(147):74–8.
[184] de la Torre I, Mora R, Domínguez-Rodrigo M, de Luque L, Alcalá L. The Oldowan industry of Peninj and its bearing on the reconstruction of the technological skills of Lower Pleistocene hominids. J Hum Evol 2003;44(2):203–24. https://doi.org/10.1016/s0047-2484(02)00206-3.
[185] de la Torre I, Mora R. The early Acheulean in Peninj (Lake Natron, Tanzania). J Anthropol Archaeol 2008;27(2):244–68. https://doi.org/10.1016/j.jaa.2007.12.001.
[186] Arzarello M, Peretto C. Out of Africa: the first evidence of Italian peninsula occupation. Quat Int 2010;223:65–70. 10.016/j.quaint.2010.01.006.
[187] Arzarello M, Peretto C, Moncel MH. The Pirro Nord site (Apricena, Fg, Southern Italy) in the context of the first European peopling: convergences and divergences. Quat Int 2015;389:255–63. 10.016/j.quaint.2014.08.051G.
[188] Arzarello M, Pavia G, Peretto C, Petronio C, Sardella R. Evidence of an Early Pleistocene hominin presence at Pirro Nord (Apricena, Foggia, southern Italy): P13 site. Quat Int 2012;267:56–61. 10.016/j.quaint.2011.01.042.
[189] Walker MJ, Anesin D, Angelucci DE, Avilés-Fernández A, Berna F, Buitrago-López ÁT, et al. A view from a cave: Cueva Negra del Estrecho del Río Quípar (Caravaca de la Cruz, Murcia, southeastern Spain). Reflections on fire, technological diversity, environmental exploitation, and palaeoanthropological approaches. Hum Evol 2016;31(1–2):1–67. https://doi.org/10.14673/HE2016121014.
[190] Walker MJ, López-Martínez MV, Carrión-García JS, Rodríguez-Estrella T, San-Nicolás-del-Toro M, Schwenninger JL, López-Jiménez A, Ortega-Rodrigáñez J, Haber-Uriarte M, Polo-Camacho JL, García-Torres J, Campillo Boj M, Avilés-Fernández A, Zack W. Cueva Negra del Estrecho del Río Quípar (Murcia, Spain): a late Early Pleistocene site with an 'Acheulo-Levalloiso-Mousteroid' Palaeolithic assemblage. Quat Int 2013;294:135–59. j.quaint.2012.04.038.
[191] Diez-Martín F, Cuartero F, Sánchez-Yustos P, Baena J, Rubio D, Domínguez-Rodrigo M. Testing cognitive skills in Early Pleistocene hominins: an analysis of the concepts of hierarchization and predetermination in the lithic assemblages of Type Section (Peninj, Tanzania) (editor). In: Domínguez-Rodrigo M, editor. Stone tools and fossil bones. Debates in the archaeology of human origins. Cambridge and New York: Cambridge University Press; 2012. p. 245–309. 10.1017CBO9781139149327.012.
[192] Diez-Martín, F. Sánchez-Yustos, P., Gómez González, J.A., de Luque, L., Fraile Martínez, C., Duque Martínez, J., & de Francisco Rodríguez, S. (2015). El yacimiento achelense antiguo EN1-Noolchalai (Peninj, lago Natrón, Tanzania): una visión geoarqueológica y tecnológica. Informes y Trabajos Excavaciones en el Exterior (2013),12, 345–58. Madrid, Ministerio de Educación, Cultura y Deporte, Secretaría General Técnica, Subdirección General de Documentación y Publicaciones.
[193] Phylogenetic and ontogenetic origins of cognition: classification. In J. Langer, & M. Killen (editors). In: Langer J, editor. Piaget, evolution, and development. Mahwah, NJ: Lawrence Erlbaum Associates; 1998. p. 33–54. 'Jean Piaget Symposia Series'.
[194] Langer J. The heterochronic evolution of Primate cognitive development. In S.T. Parker, J. Langer, & M.L. McKinney (editors). Biology, brains and behaviour: the evolution of human development. Santa Fe: School for Advanced Research, SARS Press; 2000. p. 215–35. https://doi.org/10.1162/biot.2006.1.1.41. 'School for Advanced Research Advanced Seminar Series', and Oxford, James Currey.
[195] Langer J. The heterochronic evolution of primate cognitive development. Biol Theory 2006;1(1):41–3. https://doi.org/10.1162/biot.2006.1.1.41.
[196] Langer J. The origins of logic, six to twelve months. New York: Academic Press; 1980.
[197] Langer J. Logic in infancy. Cognition 1980;10(1–3):181–6. https://doi.org/10.1016/0010-0277(81)90043-3.
[198] Langer J. The origins of logic, one to two years. New York: Academic Press; 1986.
[199] Langer J. Heterochrony and the evolution of primate cognitive development. In A.E. Russon, K.A. Bard, & S.T. Parker (editors). Reaching into thought: the minds of the great apes. Cambridge and New York: Cambridge University Press; 1996. p. 257–77.
[200] Langer J. The descent of cognitive development. Dev Sci 2001;3(4):361–78. https://doi.org/10.1111/1467-7687.00130.
[201] Langer J. The mosaic evolution of cognitive and linguistic ontogeny. In M. Bowerman, & S.C. Levinson (editors). Language acquisition and conceptual development. cambridge. Cambridge University Press; 2001. p. 19–43. https://doi.org/10.1017/CBO9780511620669. 'LCC3'.

[202] Langer J, Rivera S, Schlesinger M, Wakeley A. Chapter 7 Early cognitive development: ontogeny and phylogeny. In J. Valsiner, & K.J. Connolly (editors). Handbook of developmental psychology. London, Thousand Oaks CA, and New Delhi: SAGE Publications; 2003. p. 141–71. https://doi.org/10.4135/9781848608306.n7.

[203] Leslie AM. Pretense and representations in infancy: the origins of 'Theory of Mind'. Psychol Rev. 1987;94(4):412–26. https://doi.org/10.1037/0033-295X.94.4.412.

[204] Perner J. Understanding the representational mind. Cambridge, MA: The MIT Press; 1991. 'A Bradford Book'.

[205] Van Rooij I, Bongers RM, Haselgerd WFG. A non-representational approach to imagined action. Cogn Sci 2002;26(3):345–75. https://doi.org/10.1207/s15516709cog2603_7.

[206] di Pellegrino G, Fadiga L, Fogassi L, Gallese V, Rizzolatti G. Understanding motor events: a neurophysiological study. Exp Brain Res 1992;91(1):176–80. https://doi.org/10.1007/BF00230027.

[207] Gallese V, Fadiga L, Fogassi L, Rizzolatti G. Action recognition in the premotor cortex. Brain 1996;119(Part 2):593–609. https://doi.org/10.1093/brain/119.2.593.

[208] Iacoboni M. Understanding others: imitation, language, empathy. In S. Hurley, & N. Chater (editors). Perspectives on imitation: from cognitive neuroscience to social science. volume 1. Mechanisms of imitation and imitation in animals. Cambridge, MA: The MIT Press; 2005. p. 77–99. 'A Bradford Book'.

[209] Iacoboni M. Neurobiology of imitation. Curr Opin Neurobiol 2009;19(6):661–5. https://doi.org/10.1016/j.conb.2009.09.008.

[210] Iacoboni M, Woods RP, Brass M, Bekkering H, Mazziotta JC, Rizzolatti G. Cortical mechanisms of human imitation. Science 1999;286(5449):2526–8.

[211] Keysers C, Fadiga L. The mirror neuron system. London: Psychology Press; 2008. https://doi.org/10.1080/17470910802408513. 'A special issue of *Social Neuroscience*'.

[212] Nelissen K, Borra E, Gerbella M, Rozzi S, Luppino G, Vanduffel W, Rizzolatti G, Orban GA. Action observation circuits in the macaque monkey cortex. J Neurosci 2011;31(10):3743–56. https://doi.org/10.1523/JNEUROSCI.4803-10.2011.

[213] Papadourakis V, Raos V. Neurons in the macaque dorsal premotor cortex respond to execution and observation of actions. Cereb Cortex 2018;29(1):4223–7. https://doi.org/10.1093/cercor/bhy304.

[214] Rizzolatti G. The mirror neuron system and imitation. In S. Hurley, & N. Chater, (editors). Perspectives on imitation: from cognitive neuroscience to social science. volume 1. mechanisms of imitation and imitation in animals. Cambridge, MA: The MIT Press; 2005. p. 55–76. 'A Bradford Book'.

[215] Rizzolatti G, Fogassi L, Gallese V. Cortical mechanisms subserving object grasping, action understanding, and imitation. In M.S. Gazzaniga, (editor). The cognitive neurosciences III. Cambridge, MA: The MIT Press; 2004. p. 427–40. "A Bradford Book".

[216] Rizzolatti G, Sinigaglia C. So quel che fai: il cervello che agisce e i neuroni specchio. Milan: Raffaello Cortina Editore; 2006. 'Scienze e Idee 143'.

[217] Rizzolatti G, Sinigaglia C. Mirrors in the brain: how our minds share actions and emotions. Oxford: Oxford University Press; 2008.

[218] Shmuelof L, Zohary E. Mirror-image representation of action in the anterior parietal cortex. Nat Neurosci 2008;11(11):1267–9. https://doi.org/10.1038/nn.2196.

[219] Mukamel R, Ekstrom AD, Kaplan J, Iacoboni M, Fried I. Single-neuron responses in humans during execution and observation of actions. Curr Biol 2010;20(8):750–6. https://doi.org/10.1016/j.cub.2010.02.045.

[220] Caramazza A, Anzellotti S, Strnad L, Lingnau A. Embodied cognition and mirror neurons: a critical assessment. Annu Rev Neurosci 2014;37:1–15. https://doi.org/10.1146/annurev-neuro-071013-013950.

[221] Kemmerer D. Does the motor system contribute to the perception and understanding of actions? Reflections on Gregory Hickok's The myth of mirror neurons: the real neuroscience of communication and cognition. Lang Cogn 2014;7(3):450–75. https://doi.org/10.1017/langcog.2014.36.

[222] Umiltà MA, Escola L, Intskirveli I, Grammont F, Rochat M, Caruana F, Jezzini A, Gallese V, Rizzolatti G. When pliers become fingers in the monkey motor system. Proc Natl Acad Sci USA 2008;105(6):2209–13. https://doi.org/10.1073/pnas.0705985105.

[223] Lehmann, K., Bolis, D., Ramstead, M.J.D., Friston, K.J., & Kanske, P., (2022). An active inference approach to second-person neuroscience. Preprint in *PsyArXiv* (September 2022), 10.31234/osf.io/6y5ve.

[224] McHenry LJ, de la Torre I. Hominin raw material procurement in the Oldowan-Acheulean transition at Olduvai Gorge. J Hum Evol 2018;120:3378–401. https://doi.org/10.1016/j.jhevol.2017.11.010.

[225] Walker MJ, Rodríguez Estrella T, Carrión García JS, Mancheño Jiménez MA, Schwenninger JL, López Martínez M, López Jiménez A, San Nicolás del Toro M, Hills MD, Walkling T. Cueva Negra del Estrecho del Río Quípar (Murcia, Southeast Spain): an Acheulian and Levalloiso-Mousteroid assemblage of Palaeolithic artifacts excavated in a Middle Pleistocene faunal context with hominin skeletal remains. Eurasian Prehist 2006;4(1–2):3–42.

[226] Dunnell RC. Systematics in prehistory. London, Collier Macmillan Publishers, and New York: Macmillan Publishing Co., 'The Free Press'; 1971.

[227] Clarke DL. Analytical archaeology. 1968. London, Methuen.

[228] Shipton C. The unity of Acheulean culture. In H. Groucutt (editor). Culture history and convergent evolution. Cham (Switzerland): Springer Nature Switzerland AG; 2020. p. 13–27. https://doi.org/10.1007/978-3-030-46126-3_2. "Vertebrate Paleobiology and Paleoanthropology Series".

[229] Nicoud, E. (2013). Le paradoxe acheuléen. Paris, Éditions du Comité des Travaux Historiques et Scientifiques CTHS, 'Documents préhistoriques tome 32, Bibliothèque des Écoles Françaises d'Athènes et de Rome fascicule trois cent cinquante-sixième'.

[230] Shea JJ. Lithic modes A–I: a new framework for describing global-scale variation in stone tool technology illustrated with evidence from the East Mediterranean Levant. J Archaeol Method Theory 2013;20(1):151–86. https://doi.org/10.1007/s108016-012-9128-5.

[231] Bar-Yosef O. The known and the unknown about the Acheulian. In N. Goren-Inbar, & G. Sharon (editors). Axe age: Acheulian tool-making from quarry to discard. London and Oakville CT: Equinox Publishing Ltd; 2006. p. 479–94. "Approaches to Anthropological Archaeology".

[232] Clark JGD. World prehistory. A new outline. Cambridge: Cambridge University Press; 1969.

[233] Clark JGD. Aspects of prehistory. Berkeley, Los Angeles; and London: University of California Press; 1970.

[234] Goodrum MR. Biographical dictionary of the history of paleoanthropology. Blacksburg VA: University Library at Virginia Tech with Virginia Techn Publishing; 2022. pressbooks.lib.vy.edu/paleoanthropology/chapter/francisclarkhowell.

[235] Kleindienst MR. Components of the East African Acheulian assemblage: an analytical approach. In: Mortelmans G, Nenquin J, editors. Actes du IV^{e} Congrès panafricain de Préhistoire et de l'Étude du Quaternaire. Partie administrative. Section I. Géologie, Paléontologie générale et Climatologie. Section II. Paléontologie humaine. Section III. Pré- et Protohistoire. Tervuren: Musée Royal de l'Afrique Centrale; 1962. p. 81–111. 'Anales série in-8, Sciences Humaines 40'.

[236] Keeley LH. The functions of Paleolithic flint tools. Sci Am 1977;237(5):108–26. https://doi.org/10.10138/scientificamerican1177-108.

[237] Keeley LH. The functions of Paleolithic flint tools. In G.L. Isaac, & R.E.F. Leakey (editors). Human ancestors. San Francisco: W.H. Freeman; 1979. p. 102–9.

[238] Keeley LH. Experimental determination of stone tool uses: a microwear analysis. Chicago: University of Chicago Press; 1980. 'Prehistoric Archeology and Ecology series'.

[239] Keeley LH, Newcomer MH. Microwear analysis of experimental flint tools: a test case. J Archaeol Sci 1977;4(1):29–62. https://doi.org/10.1016/0305-4403(77)90111-X.

[240] Mitchell JC. Studying biface utilisation at Boxgrove: roe deer butchery with replica handaxes. Lithics Newsl Lithic Stud Soc 1995;15:64–9.

[241] Mitchell, J.C. (1997). Quantitative image analysis of lithic microwear on flint handaxes. *Microscopy and Analysis* (U.K.), issue 61, 15-17; *European Microscopy and Analysis* (September 1997), 53,13-15; *Microscopy and Analysis*, 26, 15-17 (U.S. edition).

[242] Mitchell JC. A use-wear analysis of selected British Lower Palaeolithic handaxes with special reference to the site of Boxgrove (West Sussex): a study incorporating optical microscopy, computer aided image analysis and experimental archaeology. Oxford: Oxford University; 1998. D.Phil. thesis.

[243] Solodenko N, Zupancich A, Cesaro SN, Marder O, Lemorini C, Barkai R. Fat residue and use-wear found on Acheulian biface and scraper associated with butchered elephant remains at the site of Revadim, Israel. PLoS ONE (Public Libr Sci One) 2015;10(3):0118572. https://doi.org/10.1371/journal.pone.0118572.

[244] Jones PR. Experimental butchery with modern stone tools and its relevance for Palaeolithc archaeology. World Archaeol 1980;12(2):153–65. https://doi.org/10.1080/00438243.1980.9979789.

[245] Jones PR. Experimental implement manufacture and use; a case study from Olduvai Gorge, Tanzania. Philos Trans R Soc Lond Ser B Biol Sci 1981;292(1057): 189–95. https://doi.org/10.1098/rstb.1981.0027.
[246] Leakey LSB. Adam's ancestors: the evolution of man and his culture. 4th ed. London, Methuen; and (1960) New York: Harper & Row; 1953. 'Harper Torchbooks'.
[247] Callahan E. The basics of biface knapping in the eastern fluted point tradition. A manual for flintknappers and lithic analysts. Archaeol East N Am 1979;7(1): 1–180. https://www.jstor.org/stable/40914177.
[248] Schick KD, Toth N. Making silent stones speak: human evolution and the dawn of technology. London: Simon and Shuster; 1993.
[249] Parfitt SA, Roberts MB. 6.5 Human modification of faunal remains. In M.B. Roberts, & S.A. Parfitt, (editors). Boxgrove. a Middle Pleistocene hominid site at Eartham Quarry, Boxgrove, West Sussex. London: English Heritage; 1999. p. 395–415. "Archaeological Report 17".
[250] Roberts MB. 6.3 Flintwork from other contexts. In M.B. Roberts, & S.A. Parfitt, (editors). Boxgrove. a Middle Pleistocene Hominid site at Eartham Quarry, Boxgrove, West Sussex. London: English Heritage; 1999. p. 378–84. "Archaeological Report 17".
[251] Roberts MB, Parfitt SA, Pope MI, Wenban-Smith FF. Sussex: rescue excavations of a Lower Palaeolithic landsurface (Boxgrove Project B, 1989-91). Proc Prehist Soc 1997;63:303–58. https://doi.org/10.1017/S0079497X00002474.
[252] Domínguez-Rodrigo M, Serralonga J, Juan-Tresserras J, Alcalá L, de Luque L. Woodworking activities by early humans: a plant residue analysis on Acheulian stone tools from Peninj (Tanzania). J Hum Evol 2001;40(4):289–99. https://doi.org/10.1006/jhev.2000.0466.
[253] Herrygers C. A comparative analysis of wood residue on experimental stone tools and early stone age artifacts: a Koobi Fora case study. McNair Sch J 2002;6 (1):65–75. http://scholarworks.gvsu.edu/mcnair/vol6/iss1/10.
[254] Keeley LH, Toth NP. Microwear polishes on early stone tools from Koobi Fora, Kenya. Nature 1981;293(5832):464–5. https://doi.org/10.1038/293464a0.
[255] Binnemann J, Beaumont P. Use-wear analysis of two Acheulian handaxes from Wonderwerk Cave, Northern Cape. S Afr Field Archaeol 1992;1(2):92–7. https://hdl.handle.net/10520/AJA10195785_20.
[256] Claud, E. (2008). *Le statut fonctionnel des bifaces au Paléolithique moyen récent dans le Sud-Ouest de la France, étude tracéologique intégrée des outillages des sites de La Graulet, La Conne de Bergerac, Combe Brune 2, Fonseigner et Chez-Pinaud/Jonzac.* Bordeaux, Université Bordeaux 1, Thèse de doctorat.
[257] Sano K, Beyene Y, Katoh S, Koyabu D, Endo H, Sasaki T, Asfaw B, Suwa G. A 1.4-million-year-old bone handaxe from Konso, Ethiopia, shows advanced tool technology in the early Acheulean. Proc Natl Acad Sci USA 2020;117(31):18393–400. https://doi.org/10.1073/pnas.2006370117.
[258] Diez-Martín F, Wynn T, Sánchez-Yustos P, Duque J, Fraile C, de Francisco Rodríguez S, Uribelarrea D, Mabulla A, Baquedano E, Domínguez-Rodrigo M. A faltering origin for the Acheulean? Technological and cognitive implications from FLK West (Olduvai Gorge, Tanzania). Quat Int 2019;526:49–66. https://doi.org/10.1016/jquaint.2019.09.023.
[259] Shipton C, Clarkson C, Cobden R. Were Acheulean bifaces deliberately made symmetrical? Archaeological and experimental evidence. Camb Archaeol J 2018; 29(1):65–79. https://doi.org/10.1017/S095977431800032X.
[260] Wynn T. The evolution of spatial competence. Urbana and Chicago: University of Illinois Press; 1989. 'Illinois Studies in Communication' and 'Illinois Studies in Anthropology No. 17.'.
[261] Hodgson D. Evolution of the visual cortex and the emergence of symmetry in the Acheulean techno-complex. C R Palevol 2009;8:93–7. https://doi.org/10.1016/j.crpv.2008.10.009.
[262] Hodgson D. The symmetry of Acheulean handaxes and cognitive evolution. J Archaeol Sci Rep 2015;2:204–8. https://doi.org/10.1017/j.jasr2015.02.002.
[263] Hodgson D. Stone tools and spatial cognition. In K.A. Overmann, & F.L. Coolidge (editors). Squeezing minds from stones. Cognitive archaeology and the evolution of the human mind. Oxford: Oxford University Press; 2019. p. 200–24.
[264] Muller A, Barsky D, Sala-Ramos R, Sharon G, Titton S, Verès JM, Grosman L. The limestone spheroids of 'Ubeidiya: intentional imposition of symmetric geometry by early hominins? R Soc Open Sci 2023;10:230671. https://doi.org/10.1098/rsos.230671.
[265] de Lumley H, Nioradzé M, Barsky D, Cauche D, Celiberti V, Nioradzé G, Notter O, Zvania D, Lordkipanidze D. Les industries lithiques préoldowayennes du début du Pléistocène inférieur du site de Dmanissi en Géorgie. L'anthropologie 2005;109(1):1–182. j.anthro.2005.02.005.
[266] Boëda E. Technogenèse des systèmes de production lithique au Paléolithique inférieur et moyen en Europe occidentale et au Proche-Orient. Paris: Université Paris-X-Nanterre, Thèse de doctorat; 1997.
[267] Moncel MH, Arzarello M, Boëda E, Bonilauri S, Chevrier B, Gaillard C, Forestier H, Yinghua L, Sémah F, Zeitoun V. The assemblages with bifacial tools in Eurasia (first part). What is going on in the West? Data on western and southern Europe and the Levant. C R Palevol 2018;17(1–2):45–60. https://doi.org/10.1016/j.crpv.2015.09.009.
[268] Moncel MH, Arzarello M, Boëda E, Bonilauri S, Chevrier B, Gaillard C, Forestier H, Yinghua L, Sémah F, Zeitoun V. The assemblages with bifacial tools in Eurasia (second part). What is going on in the East? Data from India, Asia and Southeast Asia. C R Palevol 2018;17(1–2):61–76. https://doi.org/10.1016/j.crpv.2015.09.010.
[269] Moncel MH, Arzarello M, Boëda E, Bonilauri S, Chevrier B, Gaillard C, Forestier H, Yinghua L, Sémah F, Zeitoun V. Assemblages with bifacial tools in Eurasia (third part). Considerations on the bifacial phenomenon throughout Eurasia. C R Palevol 2018;17(1–2):77–97. https://doi.org/10.1016/j.crpv.2015.11.007.
[270] Isaac GL. 4. Early phases of human behaviour: models in Lower Palaeolithic archaeology. In D.L. Clarke (editor). Models in archaeology. London: Methuen; 1972. p. 167–99.
[271] Clarke DL. 1. Models and paradigms in contemporary archaeology (editor). In: Clarke DL, editor. Models in archaeology. London, Methuen: Routledge; 1972. p. 1–60.
[272] Tennie C, Premo LS, Braun DR, MacPherron SP. Early stone tools and cultural transmission. Resetting the null hypothesis. Curr Anthropol 2017;58(5):652–72. https://doi.org/10.1086/693846.
[273] de Mortillet G. Classification des diverses périodes de l'âge de la pierre. Compte rendu du Congrès International d'Anthropologie et d'Archéologie préhistoriques 6^{e} Session, 1872; 1872. p. 432–59. Bruxelles.
[274] de Mortillet G. L'Acheuléen et le Moustérien, réponse à M. E. d'Acy. Matériaux pour l'histoire primitive et naturelle de l'homme, Revue mensuelle illustrée, XI^{e} année, 2^{e} série, VI (juillet). Toulouse: Muséum d'Histoire Naturelle; 1875. p. 342–4.
[275] Crovetto C., Ferrari M., Peretto C., Vianello F. Le industrie litiche. La scheggiatura, descrizione degli insiemi, i rimontaggi (editor). In: Peretto C., editor. Le industrie litiche del giacimento paleolitico di Isernia La Pineta, la tipologia, le tracce di utilizzazione, la sperimentazione. Isernia: Istituto Regionale per gli Studi Storici del Molise "V. Cuoco," Cosmo Iannone; 1994. p. 87–118.
[276] Goren-Inbar N, Sharon G. Invisible handaxes and visible Acheulian biface technology at Gesher Benot Ya'aqov, Israel. In N. Goren-Inbar, & G. Sharon (editors). Axe age: Acheulian tool-making from quarry to discard. London and Oakville CT: Equinox Publishing Ltd; 2006. p. 111–35. "Approaches to Anthropological Archaeology".
[277] Roe DA. Some thoughts about Acheulian cleavers. In N. Goren-Inbar, & G. Sharon (editors). Axe age: acheulian tool-making from quarry to discard. London and Oakville CT: Equinox Publishing Ltd; 2006. p. 313–33. 'Approaches to Anthropological Archaeology'.
[278] Gowlett JAJ. The elements of design form in Acheulian bifaces: modes, modalities, rules and language. In N. Goren-Inbar, & G. Sharon (editors). Axe age: Acheulian tool-making from quarry to discard. London and Oakville CT: Equinox Publishing Ltd; 2006. p. 203–21. "Approaches to Anthropological Archaeology".
[279] Geribàs N, Mosquera M, Vergès JM. What novice knappers have to learn to become expert stone toolmakers. J Archaeol Sci 2010;37(11):2857–70. https://doi.org/10.1016/j.jas.2010.06.026.
[280] Gao X, Guan Y. Handaxes and the pick-chopper industry of Pleistocene China. Quat Int 2018;480:132–40. https://doi.org/10.1016/j.quaint.2017.03.051.
[281] Lycett SJ, Von Cramon-Taubadel N. Acheulean variability and hominin dispersals: a model-bound approach. J Archaeol Sci 2008;35(3):553–62. https://doi.org/10.1016/j.jas.2007.05.003.
[282] Corbey R, Jagich A, Vaesen K, Collard M. The Acheulean handaxe: more like a bird's song than a Beatles' tune? Evol Anthropol 2016;25:6–19. https://doi.org/10.1002/evan.21467.
[283] Kohn M, Mithen S. Handaxes: products of sexual selection? Antiquity 1999;73(281):518–26. https://doi.org/10.1017/S0003598X0006507.

[284] Hodgson D. Symmetry and humans: reply to Mithen's 'Sexy Handaxe Theory. Antiquity 2009;83(319):195–8. https://doi.org/10.1017/S0003598X00098197.
[285] Nowell A, Chang ML. The case against sexual selection as an explanation of handaxe morphology. PaleoAnthropology 2009;2009:77–88.
[286] Boëda E, Courty MA, Fedoroff N, Griggo C, Hedley JG, Muhesen S. Le site acheuléen d'El Meirah, Syrie. In: Aurenche O, Mière MLe, Sanlaville P, editors. From the river to the sea: the Paleolithic and the Neolithic on the Euphrates and in the northern Levant. Studies in honour of Lorrane Copeland. Maison de l'Orient et de la Méditerranée Jean Pouilloux. Oxford: Archaeopress; 2004. p. 165–201. "British Archaeological Reports International Series 1263".
[287] Noble W, Davidson I. Human evolution, language and mind. A psychological and archaeological inquiry. Cambridge: Cambridge University Press; 1996.
[288] Roe DA. 14. An overview, with some thoughts on the study of bifaces. In M. Soressi, & H.L. Dibble (editors). Multiple approaches to the study of bifacial technologies. Philadelphia: University of Pennsylvania of Archaeology and Anthropology; 2003. p. 273–85. 'University Museum Monograph 115'.
[289] Gibert L, Scott GR, Scholz D, Budsky A, Ferràndez C, Ribot F, Martin RA, Lería M. Chronology for the Cueva Victoria fossil site (SE Spain): evidence for Early Pleistocene Afro-Iberian dispersals. J Hum Evol 2016;90:183–97. https://doi.org/10.1016/j.hevol.2015.08.002.
[290] Mosquera M, Ollé A, Saladié P, Cáceres I, Huguet R, Villalaín JJ, Carrancho Á, Bourlès D, Braucher R, Pineda A, Vallverdú J. The Early Acheulean technology of Barranc de la Boella (Catalonia, Spain). Quat Int 2016;393:95–111. https://doi.org/10.1016/j.quaint.2015.05.005.
[291] Santonja M, Villa P. The Acheulian of Western Europe. In N. Goren-Inbar, & G. Sharon (editors). Axe age: Acheulian tool-making from quarry to discard. London and Oakville CT: Equinox Publishing Ltd; 2006. p. 429–78. "Approaches to Anthropological Archaeology".
[292] Vallverdú J, Saladié P, Rosas A, Huguet R, Cáceres I, Mosquera M, García-Tabernero A, Estalrrich A, Lozano-Fernández I, Pineda-Alcalá A, Carrancho Á, Villalaín JJ, Bourlès D, Braucher R, Lebatard A, Vilalta J, Esteban-Nadal M, Bennàsar ML, Bastir M, López-Polín L, Ollé A, Vergé JM, Ros-Montoya S, Martínez-Navarro B, García A, Martinell J, Expósito I, Burjachs F, Agustí J, Carbonell E. Age and date for early arrival of the Acheulian in Europe (Barranc de la Boella, La Canonja, Spain). Public Libr Sci One PLoS ONE 2014;9(7):103634. https://doi.org/10.1371/journal.pone.0103634.
[293] Fuster JM. Memory in the cerebral cortex. an empirical approach to neural networks in the human and nonhuman primate. /1999. Cambridge, MA, and London: The MIT Press, 'A Bradford Book'; 1995.
[294] Brumm A, Rainey A. The Acheulean downunder: modern human 'handaxes' from the Barkly tableland of northern Australia. Lithics, J Lithic Stud Soc 2011;32:49–61.
[295] McCarthy FD. Australian Aboriginal stone implements: including bone, shell and tooth implements (Second revised edition). Sydney: The Australian Museum Trust; 1976. p. 21. p. 24 figure 8.
[296] Rainey AC. Some Australian bifaces. Lithics Newsl Lithic Stud Soc 1991;12:33–6.
[297] Villavicencio Finalé, R. (2004). Hachas de mano en Cuba? Santa Clara, Capiro.
[298] Rainey AC. An artist at work. Lithics Newsl Lithic Stud Soc 1997;17-18:15. -8.
[299] Dortch CE, Bordes F. Blades and Levallois technology in Western Australia. Quartär 1977;27-28:1–19.
[300] Moore MW. Australian Aboriginal blade production methods on the Georgina River, Camooweal, Queensland. Lithic Technol 2003;28(1):35–63. 10.2307 23273439.
[301] Roe DA. The Lower and Middle Palaeolithic periods in Britain. London: Boston and Henley, Routledge and Kegan Paul; 1981. "Archaeology of Britain".
[302] de Lumley H. Cultural evolution in France in its paleoecological setting during the Middle Pleistocene. In K.E. Butzer, & G.L. Isaac (editors). After the Australopithecines: stratigraphy, ecology and culture change in the Middle Pleistocene. Paris and The Hague, Mouton: World Archaeology: an Interdisciplinary Series; 1975. p. 745–88.
[303] de Lumley H. Les civilisatons du Paléolithique inférieur en Languedoc méditerranéen et en Roussillon. In: de Lumley H, editor. La Préhistoire française. Tome I,2. Les civilisations paléolithiques et mesolithiques de la France, troisième partie, La culture matérielle, II Les civilisations du Paléolithique inférieur. Publié à l'occasion du IX^{e} Congrès de l'U.I.S.P.P. , Nice. Paris: Editions du Centre National de la Recherche Scientifique; 1976. p. 852–74.
[304] de Lumley-Woodyear H. Le Paléolithique inférieur et moyen du Midi mediterranéen dans son cadre géologique. Tome II. Bas-Languedoc–Roussillon–Catalogne. Paris: Editions du Centre National de la Recherche Scientifique, Gallia Préhistoire, "V^{e} Supplément"; 1971.
[305] Barsky D. The Caune de l'Arago stone industries in their stratigraphical context. C R Palevol 2013;12(5):305–25. https://doi.org/10.1016/j.crpv.2013.05.007.
[306] Isaac GL, Harris JWK, Marshall F. Small is informative: the application of the study of mini-sites and least effort criteria in the interpretation of the Early Pleistocene archaeological record at Koobi Fora, Kenya. In: Clark D, Isaac GL, editors. Comisión VII Las industrias más antiguas pre-acheulense y acheulense, Unión Internacional de Ciencias Prehistóricas y Protohistóricas, X Congreso, México D.F., octubre 19-24. México D.F.: Union International des Sciences Préhistoriques et Protohistoriques; 1981. p. 101–19.
[307] Key AJM, Jarić I, Roberts DL. Modelling the end of the Acheulean at global and continental levels suggests widespread persistence into the Middle Palaeolithic. Humanit Soc Sci Commun 2021;8:55. https://doi.org/10.1057/s41599-021-00735-8.