Stone toolmaking and the evolution of human culture and cognition

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Although many species display behavioural traditions, human culture is unique in the complexity of its technological, symbolic and social contents. Is this extraordinary complexity a product of cognitive evolution, cultural evolution or some interaction of the two? Answering this question will require a much better understanding of patterns of increasing cultural diversity, complexity and rates of change in human evolution. Palaeolithic stone tools provide a relatively abundant and continuous record of such change, but a systematic method for describing the complexity and diversity of these early technologies has yet to be developed. Here, an initial attempt at such a system is presented. Results suggest that rates of Palaeolithic culture change may have been underestimated and that there is a direct relationship between increasing technological complexity and diversity. Cognitive evolution and the greater latitude for cultural variation afforded by increasingly complex technologies may play complementary roles in explaining this pattern.

Keywords: Palaeolithic; technology; hierarchical behaviour; cumulative culture; Oldowan; Acheulean

1. INTRODUCTION

Humans display evolved capacities for complex technological, symbolic and social action that are unique among extant species. But what exactly has evolved to produce these capacities? A prime candidate is the human brain, long viewed as the source of our distinctive ‘mental powers’ and the *sine qua non* of human uniqueness [1]. However, early evolutionary theorists also recognized the importance of culture [2,3] in accounting for the complexity of modern human behaviour. More recently, it has been suggested that the full range of modern human behaviour may be explicable as a product of cumulative cultural evolution [4], and that key behavioural transitions in human prehistory reflect the dynamics of cultural, rather than biological, evolution [5]. To further dissect the complex interaction of human cognitive and cultural evolution, it will be necessary to better understand these patterns of prehistoric culture change.

There is general agreement that human and animal ‘cultures’ are distinguished by the much greater diversity and complexity of the former. What remains unclear is whether this difference arises from the increased fidelity of human cultural transmission [4,6], from the greater cognitive capacity of individual humans [7] or from some complex interaction of the two [8]. This is a difficult question to address because modern humans differ from even our closest living relatives on a wide array of interdependent somatic, cognitive and cultural dimensions. The question of which trait(s) may have had evolutionary/causal priority in human evolution is a historical one regarding developments that appear simultaneous from a comparative perspective.

Archaeological evidence provides a complementary data source that is better positioned to answer questions about developments since the last common ancestor with *Pan*. Palaeolithic stone tools offer a relatively abundant and continuous record of technological change over the past 2.5 Myr, documenting the gradual expression of new behavioural capabilities. Exploitation of this evidence will depend on the development of increasingly robust inferential links between archaeological remains, past behaviours, and the necessary cognitive and cultural mechanisms supporting these behaviours. High on the list of tools needing to be developed is a systematic method for describing the complexity and diversity of Palaeolithic technologies.

It might be supposed that 150 years of Palaeolithic archaeology had already solved this problem, and that the wealth of named cultures, ‘industries’ and ‘modes’ in the literature would be sufficient for comparison. Indeed, it has been argued that the longevity of the Oldowan and Acheulean Industries reflects an absence of cumulative cultural evolution in the Lower Palaeolithic [7,9]. However, the nature of cultural variation in the Oldowan is a matter of ongoing debate [10,11] and many researchers do see evidence of progressive technological change within the Acheulean (e.g. [12–14]). One difficulty with classical archaeological approaches to technological variation has been a tendency to focus on the form of artefacts rather than on the processes that produced them. This is problematic because it conflates many potential sources of...
variation [15] and because it is biological capacities and cultural ‘recipes’ [16] that evolve, not artefact morphologies. Analysis of the hierarchical organization of toolmaking action sequences may provide a better foundation for inferences about culture and cognition.

2. STONE TOOLMAKING ACTION HIERARCHIES

Analysis of toolmaking action sequences is not new in archaeology. For over 30 years, the chaîne opératoire approach has focused on describing the processes of Palaeolithic tool production, based on insights gained from the experimental replication and the ‘reading’ of production scars left on tools (e.g. [12,17]). However, this approach has yet to be fully integrated with theoretical and methodological insights from other disciplines. As the name implies, the chaîne opératoire approach involves the reconstruction of action ‘chains’ or sequences, commonly represented as flow charts. This sequential approach has been useful in reconstructing the details of particular past technologies, but is less suitable for generalizing comparisons or cognitive analyses. The presence of hierarchical as well as sequential structure in human action has been a cornerstone of cognitive science since the demise of behaviourism [18–20], and is especially relevant to understanding the goal-oriented flexibility [18] of behaviours like stone toolmaking, in which consistent products are generated from inherently variable raw materials and action outcomes [17]. Elements of hierarchical analysis are implicit in many technological descriptions produced by the chaîne opératoire approach, but the formal description of Palaeolithic technologies in these terms should help provide a more uniform framework for comparison and promote better integration with research on the hierarchical structure in motor control [21], functional neuroanatomy [22,23] and social transmission [16,24–26].

In a hierarchy, individual elements are grouped into increasingly inclusive nested categories. This is commonly depicted using tree diagrams, with multiple nodes at lower (subordinate) levels being linked to single nodes at the next higher (superordinate) level, culminating in a single node at the top of the diagram. In action hierarchies, superordinate levels correspond to more abstract goals and/or temporally extended processes, from the overall objective (e.g. ‘make coffee’) down through more particular sub-goals and operations (‘add sugar’) to highly specific motor acts (‘grasp spoon’). This multi-level organization provides flexibility by allowing context-specific adaptive variation at subordinate levels to be combined with more global stability at superordinate levels. For example, ‘turn on light’ is a coherent goal that might be accomplished by flipping a switch, twisting a knob or pulling a cord [23]. Critically, information can flow both up and down within hierarchies so that superordinate goals determine subordinate action selection (‘top-down’ influence) but are themselves driven by subordinate action outcomes (‘bottom-up’ influence). This bi-directional interaction is an important mechanism supporting the learning and adaptability of complex behaviours [21] like stone toolmaking.

Hierarchical structure is interesting from a cognitive perspective because it implies the existence of superordinate representations abstracted from, and maintained over, the course of multiple subordinate events [23]. As such, it implicates processes of stimulus generalization, relational integration, temporal abstraction and goal abstraction associated with the distinctive response properties and anatomical connections of prefrontal cortex [22]. Hierarchical structure is also interesting with respect to cultural evolution because it relates to questions about the ‘level’ of copying [6] and potential biases in transmission [25].

Early hierarchical analyses of stone toolmaking action sequences were developed by Holloway [27] and Gowlett [28]. More recently, the hierarchical structure of toolmaking has been described in relation to models from cognitive neuroscience and developmental psychology [29–31]. Moore [30] presented a tree structure notation, adapted from Greenfield [32], which is further modified here to describe the organization of major Lower Palaeolithic toolmaking methods as inferred from modern experiments and the analysis of archaeological materials.

(a) Oldowan (ca 2.6–1.4 Ma; figure 1a)

The earliest known stone tools [33] are assigned to the Oldowan Industry and consist of sharp stone flakes struck from cobbles ‘cores’ by direct percussion with another stone (the ‘hammerstone’). Experimentally, Oldowan flake production minimally involves: (i) procurement of raw materials (both core and hammerstone) of appropriate size, shape and composition and (ii) actual flaking, including core examination, target selection, core positioning/support, hammerstone grip selection and accurate percussion. This may be represented by a tree diagram (figure 1a) with six nested levels, ranging from the overall goal of flake production to specific manipulations of the core and hammerstone. Within this structure, certain discrete action ‘chunks’ can be repeated an indefinite number of times, as indicated by numbers 1, 2,..., n (dashed lines indicate optional elements, boxes enclose ‘collapsed’ action chunks where subordinate elements have been omitted to avoid crowding). For example, previous authors have identified a ‘basic flake unit’ [30] or ‘flake loop’ [28] (here termed ‘flake detachment’), which is duplicated until some superordinate goal (e.g. desired numbers of flakes of appropriate size and sharpness) is achieved. Similarly, a basic ‘raw material procurement’ chunk may be repeated until quality and quantity criteria are met. Such modular structure is an efficient and productive characteristic of hierarchical organization that has received much attention in the study of language under the heading of ‘discrete infinity’ [34]. It is made possible by the combination at a superordinate level of units that remain distinct at the subordinate level, a possibility that would be absent in a ‘flat’ behavioural chain.

In this way, basic core manipulations (grasp, rotate) are combined in a superordinate process of core positioning, which is combined with an appropriate hammerstone grip and striking movement in the

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larger process of percussion, which is combined with the selection of an appropriate target in the process of flake detachment. At this level, it is possible that individual flake detachments might form a simple linear chain, with the location of each detachment being selected purely on the basis of current core affordances (produced in part by the immediately preceding detachments [30]). However, it is now clear from the archaeological record that some early Oldowan assemblages exhibit systematically biased patterns of flake detachment that are undetermined by the morphological variability of Oldowan cores. Examples [10,11] include removal of flakes predominantly from a single core surface ("unifacially") or alternately from two intersecting surfaces ("bifacially"). This patterning implies some superordinate relationship between individual flake detachments, perhaps in the form of relatively complex 'technological rules' and conscious planning [11], but minimally involving a learned tendency to select targets in relation to the position of previous detachments (e.g. laterally adjacent, alternate face, same plane, etc.). This superordinate relationship between flake detachments is represented in figure 1b by the node labelled ‘flaking’. This added level of hierarchical organization allows for some diversity in Oldowan flake production patterns, however, the relation of such variation to ecological, functional and/or cultural factors remains to be further explored [10].

(b) Early Acheulean (ca 1.6–0.9 Ma)
Around 1.6 Ma, a number of technological innovations begin to appear in the archaeological record. These include more elaborate methods of flake production, such as 'hierarchical centripetal' [35] flaking and single-platform ‘Karari scraper’ cores [36], as well as the production of intentionally shaped Acheulean tools including ‘handaxes’ and ‘picks’. The new flake production methods are not technically considered part of the Acheulean, however, they are contemporaneous with the Early Acheulean [37] and are
considered here as part of the same general phenomenon of Lower Pleistocene technological change.

(i) Elaborate flake production (figure 1b)
Karari scrapers are a distinctive artefact type known from the basal Okote Member (1.6–1.5 Ma) at Koobi Fora, Kenya, and are produced by removing flakes from around the circumference of large flake or fractured cobble. This is thought to be a particularly efficient way to generate useful flakes and to require a ‘higher degree of planning’ insofar as a morphologically suitable large flake or cobble fragment must first be produced with the intent for subsequent use as a core [38]. The hierarchical centripetal method reported from the ST Site Complex (1.2–1.1 Ma) at Peninj, Tanzania, also appears to be aimed at the efficient production of useful flakes and similarly involves preparatory operations [35]. In this case, one or more subordinate ‘preparatory’ flakes are removed from a lateral ‘preparation surface’ in order to establish an advantageous morphology for the removal of desired ‘primary’ flake from the ‘main surface’.

These different forms of elaborate flake production reflect a similar underlying innovation in action organization: modification of the core specifically in order to enable subsequent flake detachments. This differs from bifacial and unifacial flaking patterns seen in the Oldowan in that modification, as an explicitly preparatory action, is actually embedded within the process of primary flake detachment. As depicted in figure 1b, this involves inserting at least one subordinate instance of preparatory flake detachment within the primary flake detachment tree, much as in the ‘complex flake unit’ of Moore [30]. This results in an increase from six to seven nested levels. In the case of Karari scraper cores, a single subordinate detachment is involved in the production of the initial large flake or split cobble, which is then iteratively flaked according to a particular (circumferential) pattern. In hierarchical centripetal flaking, one or more subordinate flakes are removed in order to alter the configuration of the core prior to primary flake detachment.

In view of recent interest in the evolution of recursive cognition (e.g. [39]), it is interesting to note that this embedding of flake detachments within flake detachments is formally recursive, with the theoretical potential to embed an infinite number of subordinate detachments (i.e. detach a flake to prepare to detach a flake to prepare to detach a flake . . .). This is depicted in figure 1b as optional nodes corresponding to second through nth-order embedded detachments. As in recursive linguistic syntax, however, there are pragmatic limits to the actual number of embedded nodes in recursive flaking, including both physical and cognitive constraints. Karari and hierarchical centripetal methods, at least as described here, need not involve more than one level of recursive embedding.

(ii) Large cutting tools (figure 1c)
The production of Early Acheulean ‘large cutting tools’ (LCTs) involves both structured flaking and intentional shaping. Two LCT forms typical of the earliest Acheulean sites are pointed handaxes produced on large (greater than 10 cm) flakes and relatively thick, pointed picks typically produced from cobbles [37]. The production of large flakes (called ‘blanks’) suitable for shaping into a handaxe was a key innovation [15] of the Early Acheulean, and involves an elaboration of raw material procurement into a multi-component quarrying process, depicted to the left of figure 1c. Raw material selection criteria must now privilege size over composition, allowing for the production of large flakes. Even given an adequately sized core, however, the consistent production of suitable blanks is quite challenging [40]. Blank production requires a heavier hammerstone and much greater force than Oldowan flake production, and the largest cores would have necessarily been supported on the ground instead of in the hand. This requires the use of additional small boulders or cobbles to brace the core in an appropriate position [41]. Manipulation and rotation of both core and hammerstone may have required two hands and a variety of new body postures. These fundamental differences in perceptual-motor organization, not depicted in figure 1c, make Acheulean blank production qualitatively different from Oldowan flaking [37].

At a higher level of organization, however, there are important structural similarities. The earliest blank production strategy may have been a simple iteration of flake detachments, leaving behind a ‘casual core’ resembling a large Oldowan core [41]. Adoption of a bifacial flaking pattern, which helps to maintain adequate edge angles during sequential blank removals, was also common [41]. This may have been an explicit strategy but, as in the Oldowan, can be minimally modelled as a simple target selection bias. Even in these simple strategies, however, recursive flaking would sometimes have been necessary to ‘open’ the boulder core by removing a subordinate flake, itself too small to serve as a blank, intended to establish the first viable striking surface. By 1.2–1.1 Ma, de la Torre et al. [42] report evidence of more extensive recursive flaking to establish core edge angles and surface morphology during blank production at the sites of RHS-Mugulud and MHS-Bayasi from Peninj. These blank production strategies can be compared with the elaborate flake production methods described above, and are diagrammed as repeated instances (1, 2, . . . , n) of recursive flaking in figure 1c.

The production of an LCT directly from a cobble involves different raw material criteria (smaller size, oblong shape), omission of the entire blank production sequence, and more extensive shaping [40]. This coordination of production elements requires that the top node of the model contains some stable representation of intended tool form (e.g. handaxe or pick; importantly, these forms co-occur at single sites) and associated lower level actions. As has long been recognized, the production of standard forms from variable materials requires some such higher order representation [15,27]. This need not be a fully specified geometric archetype and, especially in the early record, seems more likely to comprise certain learned characteristics of effective tools.
Desired tool characteristics were achieved through ‘shaping’: a sequence of flake detachments that result in a particular core form. In the case of a pick, for example, removal of one or more rows of flakes from two parallel sides of an oblong cobble would result in a thick pointed form with a triangular cross section. This might be modelled as a massively recursive sequence with each flake detachment enabling subsequent detachments culminating in the final removal required to achieve a pre-specified form. However, this depth of structure and planning is unnecessary and unlikely. Modern toolmakers (e.g. [17]) describe shaping in terms of the pursuit of local sub-goals resulting in the successive approximation of an overall target form. For example, a short series of flakes might be aimed at creating an edge, followed by a reappraisal of the overall form, selection of the next appropriate sub-goal and so on. This is depicted to the right of figure 1c, with multiple duplications of (potentially) recursive flaking action chunks being combined to achieve local sub-goals which are themselves combined to achieve overall shaping goals. The result is a further increase in the hierarchical complexity of the associated tree, which now includes nine nested levels.

This multi-level goal structure adds flexibility, reduces the requirement for extended contingency planning, and takes advantage of the core itself as a continuously available external resource structuring behaviour. It also provides latitude for substantial technological variation in that similar forms may be achieved from different raw materials using different subordinate goal structures. For example, at the Olдуvai site of TK (1.33 Ma) LCTs were produced using a consistent ‘rhomboidal’ strategy of unifacial removals from opposite sides of tabular quartz blocks [43], while at sites OGS-12 and BSN-17 from Gona, Ethiopia (approx. 1.6 Ma) [37] and Kokisele 4, from West Turkana, Kenya (approx. 1.7 Ma) [12], variable combinations of unifacial and bifacial removals from two or three worked edges were used to fashion trihedral picks from lava cobbles.

(c) Late Acheulean (ca 0.7–0.25 Ma; figure 1d)

Although the Acheulean has been characterized as a monolithic, unchanging industry (e.g. [9]), this may in part reflect the fact that the earliest well-known European Acheulean sites date to only about 0.5 Ma (e.g. [44]) (although sites dating to 0.6–0.8 Ma have been reported in southern Europe [45,46]). African archaeologists have long recognized an important technological transition between the Early and Late Acheulean, occurring sometime before 0.5 Ma [13]. Classically, this transition involves the appearance of smaller, thinner, more regular and symmetrical LCTs thought to require the use of a ‘soft hammer’ technique during production. Less-refined forms persist after this time, and may dominate some assemblages or even entire regions [47,48], however, it is clear that the global range of Acheulean variation expanded to include new forms. The 0.7 Ma of Isenya in Kenya [12] is currently one of the earliest reported examples of such tools. The site also provides examples of ‘cleavers’, a typical Late Acheulean LCT form involving the production of morphologically predetermined blanks.

(i) Predetermined blank production

In a typological sense, cleavers have been defined as LCTs with a transverse, blade-like ‘bit’ more than half the width of the tool [49], however, this is recognized as an arbitrary division of a morphological continuum. In the technological sense [12] followed here, cleavers are the product of a predetermined blank production process designed to yield a long, sharp cleaver bit on the blank prior to any shaping. Strategies documented at Isenya include a ‘unipolar’ method in which a subordinate, preparatory flake parallel to the objective flake shapes the cleaver bit, and the surprising ‘Kombewa’ method in which a primary blank is produced and a secondary blank then removed from it, yielding a biconvex shape with a sharp edge around almost the entire perimeter. These predetermination strategies represent an elaboration of Early Acheulean recursive blank production, involving an increase in the number of subordinate detachments required, and are included within the superordinate node ‘quarrying’ to the left of figure 1d. Fully predetermined blank production is clearly documented at Isenya 0.7 Ma and may even date to greater than 1.0 Ma in South Africa [50]. Certainly, by ca 0.4–0.3 Ma, it is widespread and includes a range of variants like the ‘Victoria West’ and ‘Tabel-bala-Tachengit’ methods [13,51].

Late Acheulean ‘proto-Levallois’ methods are widely seen as transitional to subsequent Middle Stone Age (MSA) ‘Levallois’ prepared core flake production strategies [51], with the main shifts being a reduction in size (probably related to the introduction of hafting in the MSA) and a further diversification of methods (e.g. preferential, centripetal, convergent, etc.). In fact, production of diverse small tools in ‘Late Acheulean’ times may have been underestimated (cf [50]), and standardized blade production (long considered a hallmark of modern humans) has been reported from two 0.5 Ma sites in the Kapthurin Formation, Kenya [52].

(ii) Late Acheulean shaping (figure 1d)

Production of the thinner, more regular LCTs characteristic of the Late Acheulean requires a more elaborate shaping process. Cross-sectional thinning is one of the most distinctive and technically demanding characteristics of the process [14,53,54], requiring the reliable production of flakes that travel more than half-way across the surface of the piece without removing large portions of the edge. Examples of well-thinned Late Acheulean LCTs have been described from Europe (e.g. [53]), Western Asia (e.g. [56]) and Africa (e.g. [54]) in a variety of raw materials.

Experimentally, thinning flakes are often achieved using a soft hammer of bone or antler that can initiate fracture without gouging the edge, and such hammers have been found in Late Acheulean contexts [44]. However, it is possible to achieve similar results with
a hammerstone if the surface to be struck (the ‘striking platform’) is properly prepared [57]. Indeed, some such ‘platform preparation’ is also required for the effective use of a soft hammer. This preparation involves the small-scale chipping and/or abrasion of edges to alter their sharpness, bevel and placement relative to the midline [53] and can take place on both striking and release surfaces [54]. Small-scale chipping is usually accomplished with light, glancing blows of a smaller, specifically selected hammerstone held in a more flexible grip. Whether or not a soft hammer is used, various different sized hammerstones may be required for different sub-goals within the shaping process.

Following Moore [30], platform preparation is modelled as a subordinate process within percussion. This adds a further level of hierarchical structure, as well as qualitatively different perceptual-motor elements. Together with selection of a hammer appropriate to the intended percussion, platform preparation becomes part of a new structural unit, ‘complex flake detachment’, which is depicted in the inset box to the left of figure 1(d). Complex flake detachment constitutes an action ‘chunk’ may be substituted for simple flake detachment and combined iteratively and/or recursively to achieve sub-goals during shaping and especially thinning (marked by asterisk in figure 1d).

Archaeologists generally recognize at least two major stages of Late Acheulean LCT shaping: ‘roughing-out’ and ‘finishing’, depicted to the right of figure 1d. Roughing-out is somewhat comparable with Early Acheulean shaping, but involves the specific aim of establishing a centred, bifacial edge with adequate geometry to support subsequent thinning operations. This superordinate goal is implemented through various sub-goals addressing particular portions of the core through structured complex flaking. Roughing-out generally involves hard hammer percussion, large flake production and little or no platform preparation. Finishing involves the detachment of thinning flakes and small marginal flakes in order to achieve sub-goals of thinning and regularizing the core, through localized episodes of recursive (often complex) flaking. Smaller and soft hammers may be used, and platform preparation can be extensive. The result is a relatively thin, lightweight tool with sharp, regular bifacial edges, associated with the most complex action tree considered so far, comprising 10 nested levels.

3. LOWER PALAEOLITHIC CULTURE CHANGE

This paper examines one of the best known, widely accepted and well-documented characteristics of the Lower Palaeolithic record: the increase over time in the upper limits of variation in technological complexity on a global scale. Fine-grained patterns of change are of course more complicated, yet there can be little doubt that the most complex technologies known from 0.25 Ma far exceed those of 2.5 Ma. What remains controversial is the tempo, mode and magnitude of this change, and whether it is more consistent with biological or cultural explanation. One prevalent view emphasizes the ‘remarkable conservatism’ of Acheulean technology [58], which is thought to reflect punctuated rather than gradual change and to exemplify a dearth of cumulative cultural evolution in the Lower (and even Middle) Palaeolithic [7,9]. It has been argued that this slow, punctuated pattern of Palaeolithic technological change is best explained in terms of underlying cognitive constraints (i.e. biological evolution) [9,59]. Analysis of the hierarchical structure of toolmaking action sequences provides a standard format for technological comparison, which may be useful in assessing these arguments.

The most obvious result of the preceding analysis is that Lower Palaeolithic technological change is indeed cumulative. Elaborate flake production and shaping methods build on previously established technologies by adding levels of hierarchical structure and/or modifying the content of existing sub-processes. However, it might still be argued that the rate of change is slow enough to imply cognitive differences from modern humans. This leads to questions of how to quantify culture change, and what exactly a ‘modern’ rate would be. Neolithic rates of change would surely dwarf those of the Lower Palaeolithic, but pale in comparison to the twentieth century. Simply assigning a value of ‘1’ to each of the technological innovations discussed above produces a similar pattern of increasing rate of change over time (figure 2), suggesting that the entire history of human technological evolution might follow a single exponential curve. This heuristic exercise remains far too crude, and the evidence too sporadic, to rule out major discontinuities and inferences owing to biological change and/or other extrinsic factors. For example, the absence of incremental change 1.6–2.6 Ma constitutes an Oldowan ‘stasis’ [10,33], however, it is not inherently obvious whether this represents a discontinuity or merely the long tail of an exponential curve. In any case, the apparent pattern does provide a case for more seriously considering intrinsic factors that might tend to produce a uniform curve at this coarse level of analysis. One such factor is the intrinsic relationship between technological complexity and diversity.

The action hierarchy analysis suggests that complexity constrains diversity. Simply put, there just is not that much potential for variation in Oldowan flake production. It is only with more complicated technologies that multiple variants become possible, because more choices are possible. Technical innovations like recursive flaking and platform preparation alleviate raw material constraints, allowing for the emergence of more hierarchically complex strategies with multiple, differentiated end-products. Increasing hierarchical complexity in turn favours the emergence of technical innovations by providing greater latitude for the recombination of action elements and sub-assemblies. Across such diverse disciplines as physics, chemistry, genetics and linguistics, hierarchical recombination has been recognized as a fundamental process driving ‘self-diversification’ [34]. For example, there is an analogy [16] to be made with the way in which genetically regulated developmental hierarchies enable evolutionarily productive processes of segmental duplication and...
differentiation. In much the same way, increasing technological complexity might become autocatalytic, contributing to the apparently exponential pattern of human technological evolution seen at the largest scale of analysis.

All of this implies that Lower Palaeolithic hominins possessed adequate cognitive substrates for some degree of cumulative cultural evolution, an unsurprising result considering the transmission capacities of modern chimpanzees [60]. Nevertheless, significant evolutionary elaborations of these shared capacities might have occurred during the Lower Palaeolithic, relaxing constraints on the complexity of transmitted techniques and allowing for increasing rates of change. One candidate for such cognitive evolution is the modern human propensity for detailed copying of behavioural means (imitation) as opposed to ends (emulation) [6,60]. However, consideration of the action hierarchies presented above immediately raises a question as to what exactly counts as a means and what as an end. How far down the hierarchy must one go to be engaged in imitation, and how far up for emulation?

Studies of imitation in children suggest that copying is better understood in terms of goal hierarchies rather than a strict means/ends dichotomy [26]. Thus, a specific arm movement trajectory would be a subordinate goal to the superordinate goal of displacing an external object rather than a qualitatively different ‘behavioural means’. When cognitive resources are limited and multiple goals compete for attention, children tend to reproduce superordinate goals at the expense of subordinate goals [26], paralleling a similar hierarchical bias in adults’ selective perception, memory and transmission of narrative event information [25]. When competing superordinate goals are removed, children are more successful at copying ‘low-level’ goals, including movement trajectories [26]. In apes, similar capacities for low-level copying are illustrated by the ‘Do-as-I-do’ imitation of specific bodily actions [60], whereas in more complex, instrumental tasks the subordinate ‘means’ are often omitted [6]. For both apes and children, it would seem that the fidelity of imitation is constrained more by the complexity (especially, the number of hierarchical levels) of behaviour to be copied rather than by the level of copying per se.

At a given processing capacity, we should thus expect copying fidelity to be negatively correlated with hierarchical complexity. Insofar as copying errors introduce variation, this would again contribute to the intrinsic relationship between complexity and diversification in cultural evolution. At relatively high levels of behavioural complexity, however, copying fidelity would decrease to the point that transmission might fail entirely. For example, Late Acheulean shaping is the most complex Lower Palaeolithic technology analysed here and a failure in its transmission (cf [61]) might help to explain the greater thickness of LCT’s in eastern Asia [47,48].

From this perspective, successful transmission of complex technological behaviours would depend on two factors: individual capacities for hierarchical information processing (cf [7]) and social mechanisms of skill acquisition [62]. Neither of these need remain constant, and both are likely to have been influenced by the biological evolution of hominin brains [63], which nearly tripled in size during the Lower Palaeolithic. Hierarchical cognition is supported by lateral frontal cortex [22], the more anterior portions of
which are disproportionately expanded in humans [64]. Increasing levels of abstraction in action organization place demands on increasingly anterior portions of frontal cortex [22] and precisely this pattern of increased anterior activation has been observed in a brain imaging study comparing Late Acheulean versus Oldowan toolmaking [29]. This is consistent with the possibility that evolving neural substrates for complex action organization could have interacted with autocatalytic increases in technological complexity to produce a ‘runaway’ process of biocultural evolution [8,65].

Complex hierarchical cognition is not, however, sufficient for the reproduction of Palaeolithic technological behaviours. Stone toolmaking, from the Oldowan on, requires bodily skills [29,66] that cannot be acquired directly through observation. These pragmatic skills can only be developed through deliberate practice and experimentation leading to the discovery of low-level dynamics that would remain ‘opaque’ (cf [67]) to observation alone. Available evidence indicates that it takes more than a few hours of practice for modern humans to master even simple Oldowan flake production [68], and personal experience suggests that Late Acheulean skill may demand hundreds of hours.

In the modern community of Langda in Papua Provence, Indonesia, traditional stone toolmaking skills are transmitted through semi-formal apprenticeships that can last 10 years or more [62]. Motivation and commitment through this extended period are promoted by the social context of toolmaking, which occurs in a supportive group setting and is a source of pride, pleasure and personal identity for practitioners. Central to the learning process is a heavy investment in the individual practice needed to consolidate basic perceptual-motor skills. This is encouraged by the positive social value placed on practice and is supported by instruction, demonstration, intervention and assistance from more experienced toolmakers, all of which acts as a social ‘scaffold’ promoting individual skill acquisition. Experimental studies similarly show that, while novice toolmakers rapidly learn to identify and select appropriate targets [68], it takes much longer to develop the perceptual-motor skill needed to predict and control flake detachments [29,69,70]. Such skill development requires the discovery of appropriate techniques through behavioural experimentation [71] with various different grips, postures and angles of percussion, as well as with hammerstones of varying size, shape and density. Discovery of optimal techniques might be facilitated by social scaffolding [62], explicit instruction or high-fidelity imitation of an expert model, but minimally requires focused attention, self-monitoring and the inhibition of automatic reactions during repetitious practice [71,72]. Social motivation and support for such protracted practice are important contributing factors that appear to be uniquely developed in humans [6,73] and may reflect further interactions between biologically evolving neural and endocrine substrates of prosocial behaviour [63,65,74] and culturally evolving hominin technologies.

5. CONCLUSIONS
Stone toolmaking action analyses presented here demonstrate the presence of cumulative cultural evolution in the Lower Palaeolithic and suggest that this accumulation displays an accelerating rate of change continuous with that seen in later human history. This should encourage interest in intrinsic processes of cultural evolution that might tend to produce such a uniform curve, including the potentially autocatalytic effects of increasing technological complexity. As illustrated here, Lower Palaeolithic technologies clearly do increase in hierarchical complexity through time, raising the possibility of important interactions with the evolution of human cognitive control [63] and socially supported skill acquisition [6,62]. Analyses developed here have attempted to build on previous contributions [12,17,27,28,30,32] but remain quite limited in scope. For example, they are semi-arbitrarily bounded at the lower end by relatively large-scale and under-specified reaching, grasping and manipulating actions and at the upper end by the articulation with other major domains of hominin behaviour, especially including tool use. Continued efforts in these directions will be needed to adequately characterize the pattern, mechanisms and rate of Lower Palaeolithic technological change.

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